

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.]*

Parsons, T. R., M. Takahashi, and B. Hargrave. 1984. Biological Oceanographic Processes. 3rd Edition. Pergamon Press, Oxford & New York. Pages 87-100.

Townsend, D. W. and R. W. Spinrad. 1986. Early phytoplankton blooms in the Gulf of Maine. Cont. Shelf Res. 6: 515-529. *[T & S's model can predict the timing of the spring bloom as the period when critical depth exceeds bottom depth.]*

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 major new theory and model]*

Mann, K. H. and J. R. N. Lazier. 1991. Dynamics of marine ecosystems: Biological-physical interactions in the oceans. Blackwell Scientific, Boston. 466 pp. *[Pp. 84-90 contains a concise description of **Sverdrup's (1953) critical depth concept**]*

Miller, C. B. 2004. Biological Oceanography. Blackwell Science, Malden MA. 402 pp. Chapter 1.

Mills, E. L. 1989. Biological Oceanography: An Early History, 1870-1960. Cornell University Press, Ithaca and London. *[For the historical background of the critical depth concept, read pp. 120-171: "The Water Blooms" and "Hydrography and the Control of Plankton Abundance"]*

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.

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]*

Smetacek, V. and U. Passow. 1990. Spring bloom initiation and Sverdrup's critical depth model. Limnol. Oceanogr. 35: 228-233.

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

Endocrine matter

Hourly & diel compensation depth

Mixed layer depth

optical depth

Comments on the readings

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 \approx 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_{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 $k \cdot z$, 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 $\frac{\bar{I}_z}{I_c}$ can be plotted. This type of plot should be generated for every date on which I_0 changes. The critical depth is the depth at which $\frac{\bar{I}_z}{I_c} = 1$ 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_0). Changes in I_c and I_0 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_0/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.

Smayda (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-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 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:

$$P_h = \frac{p I_0}{k z_1} (1 - e^{-k z_1}) (1 - N) (1 - V).$$

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

p = proportionality constant between photosynthesis and light intensity, I .

I_0 = surface light intensity.

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

z_1 = depth of the euphotic zone.

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

$\approx 1\%$ 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.

$\equiv \frac{z_1}{z_2}$.

z_2 = the depth of the mixed layer.

(1)

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:

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

where, P = phytoplankton biomass [$gC m^{-2}$].
 t = time [d].
 e = base of Naparien logarithms.
 R_o = phytoplankton respiration at $0^\circ C$ ($\approx 0.0175 d^{-1}$).
 $r = \frac{\ln(2)}{10}$, scales R to have a Q_{10} of 2.
 T = temperature in $^\circ C$.
 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

Fundamental quantity	Quantity Symbol	Dimension Symbol	Base Unit	Unit symbol
mass of carbon	C	[M _C]	gram carbon	g C
mass of chlorophyll a	Chl <i>a</i>	[M _{Chl}]	gram chl <i>a</i>	g Chl <i>a</i>
photons of light	photons	[hν]	mol photon	E (Einstein)
light energy	watts		watts	W
Variable	Variable Symbol	Dimension Symbol	Base unit	Unit symbol
Water depth	<i>z</i>	[L]	centimeter	cm
Specific growth rate	μ	[T ⁻¹]	$\frac{\text{grams carbon}}{\text{second}}$ <i>grams carbon</i>	s ⁻¹
Specific grazing loss	G	[T ⁻¹]	“	“
Other specific losses	l	[T ⁻¹]	“	“
Gross Photosynthesis at depth <i>z</i>	P _{g_z}	[M _C L ⁻³ T ⁻¹]	$\frac{\text{grams carbon}}{\text{centimeter}^3}$ <i>second</i>	g Ccm ⁻³ s ⁻¹
Net photosynthesis at depth <i>z</i>	P _{n_z}	“	“	“
Max. gross photosynthesis	P _{max}	“	“	“
Depth-average gross photosynthesis from the surface to depth <i>z</i>	\bar{P}_z	“	“	“
Phytoplankton respiration	R	“	“	“
light attenuation coefficient for PAR	<i>k</i>	[L ⁻¹]	$\frac{1}{\text{centimeters}}$	cm ⁻¹
Photosynthetically Available Radiation (PAR)	I	[hνL ⁻² T ⁻¹]	$\frac{\text{Einsteins}}{\text{centimeter}^2}$ <i>second</i> or $\frac{\text{Watts}}{\text{centimeter}^2}$	E cm ⁻² s ⁻¹ or W cm ⁻²

Variable	Variable Symbol	Dimension Symbol	Base unit	Unit symbol
Net downwelling irradiance just below the water surface	I_0	“	“	“
Net downwelling irradiance at depth z	I_z	“	“	“
Average light intensity from surface to depth z	\bar{I}_z	“	“	“
Compensation light intensity	I_c	“	“	“

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 $\left(\frac{dC}{dt} \approx 0\right)$. **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**):

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

1
2
3
4
5

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 $\left(\frac{dC}{dt}\right)$ 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 from 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 (\bar{I}_z) 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:

$$\frac{D_{cr}}{1 - e^{-k_e D_{cr}}} = \frac{I_e}{I_c k_e}$$

where, D_{cr} = critical depth in meters. (4)
 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, 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 that 0.02 of a σ_t 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
- $1 \text{ langley} = \frac{1 \text{ g cal}}{\text{cm}^2} = \frac{4.185 \times 10^7 \text{ ergs}}{\text{cm}^2} = \frac{4.185 \text{ Watt sec}}{\text{cm}^2}$
- $1 \text{ Ein} = 6.02 \times 10^{23} \text{ quanta} = \frac{2.86 \times 10^8 \text{ g cal}}{\text{Angstroms}}$
 - 1 Angstrom = 10^{-10} m
 - If average wavelength of PAR = 550 nm:
 - $1 \text{ Ein} = (2.86 \times 10^8 \text{ g cal} / 5500) = 52 \times 10^3 \text{ g cal}$
- 1 Joule = mks unit of work = $10^3 \text{ g } 10^4 \text{ cm s}^2$
- 1 electron volt = 1.6×10^{-19} joules (**Falkowski & Raven 1997, p. 34**)

I_c	Original Units	$\frac{\mu E}{m^2 s}$	$\frac{E}{m^2 d}$	$\frac{ly}{d}$	Original citation	Used by
$\frac{2.48 \mu E}{m^2 s}$		2	0.2	1		Smetacek & Passow (1990)
$\frac{0.0015 \text{ g cal}}{\text{cm}^2 \text{ min}}$	$\frac{\text{g cal}}{\text{cm}^2 \text{ min}}$	5	0.4	1	—	Riley (1946)
0.17 ly/h	langley	9	0.6-0.8	2	Jenkins (1937)	Sverdrup (1953)
0.17 ly/h	langley	9	0.8	2	Jenkins (1937)	Parsons et al. (1966)
0.96-1.97	Einstein (mol photon)	12-17	1-1.5	5-8	Siegel et al. (2002)	Siegel et al. 2002
1.5-1.7 W m ⁻²	Watt	31	2.7	7	—	Mann & Lazier (1991, p. 86)
35 $\mu E \text{ m}^{-2} \text{ s}^{-1}$.	Einstein	35	3.0	8	-	Nelson & Smith (1991)
40 ly/d (Total light, not PAR)	langley	ER R	??	40	Riley (1957)	Townsend & Spinrad (1986)
9.375 J m ⁻² s ⁻¹ PAR	Joule					Gieskes & Kraay (1975)

In order to understand, the role of respiration and grazing losses, I'll start with the definition of specific growth rate (μ). We'll assume that there is one type of phytoplankton cell with growth characteristics defined by μ :

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

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

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

where, C = *Phytoplankton concentration.*
 G = *Specific grazing rate.*
 L = *Other phytoplankton losses.*
 P_g = *Gross photosynthesis.*
 R = *Phytoplankton respiration.*

(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, $P_g - R$. **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:

$$\begin{aligned}
 kz &= \text{dimensionless depth} = \text{optical depth.} \\
 \frac{I_z}{I_o} &= \text{dimensionless light intensity at depth } z. \\
 \frac{\bar{I}_z}{I_o} &= \text{dimensionless average light intensity.} \\
 \frac{I_c}{I_o} &= \text{dimensionless compensation light intensity.} \\
 \frac{P_z}{P_{\max}} &= \text{dimensionless gross photosynthesis at depth } z. \\
 \frac{\bar{P}_g}{P_{\max}} &= \text{dimensionless average gross photosynthesis.} \\
 \frac{R}{P_{\max}} &= \text{dimensionless respiration.}
 \end{aligned}$$

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:

$$I_z = I_o e^{-kz} \quad (8)$$

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:

$$\frac{\bar{I}_z}{I_o} = \frac{1}{z} \int_0^z e^{-kz} dz = \frac{1}{kz} (1 - e^{-kz}). \quad (9)$$

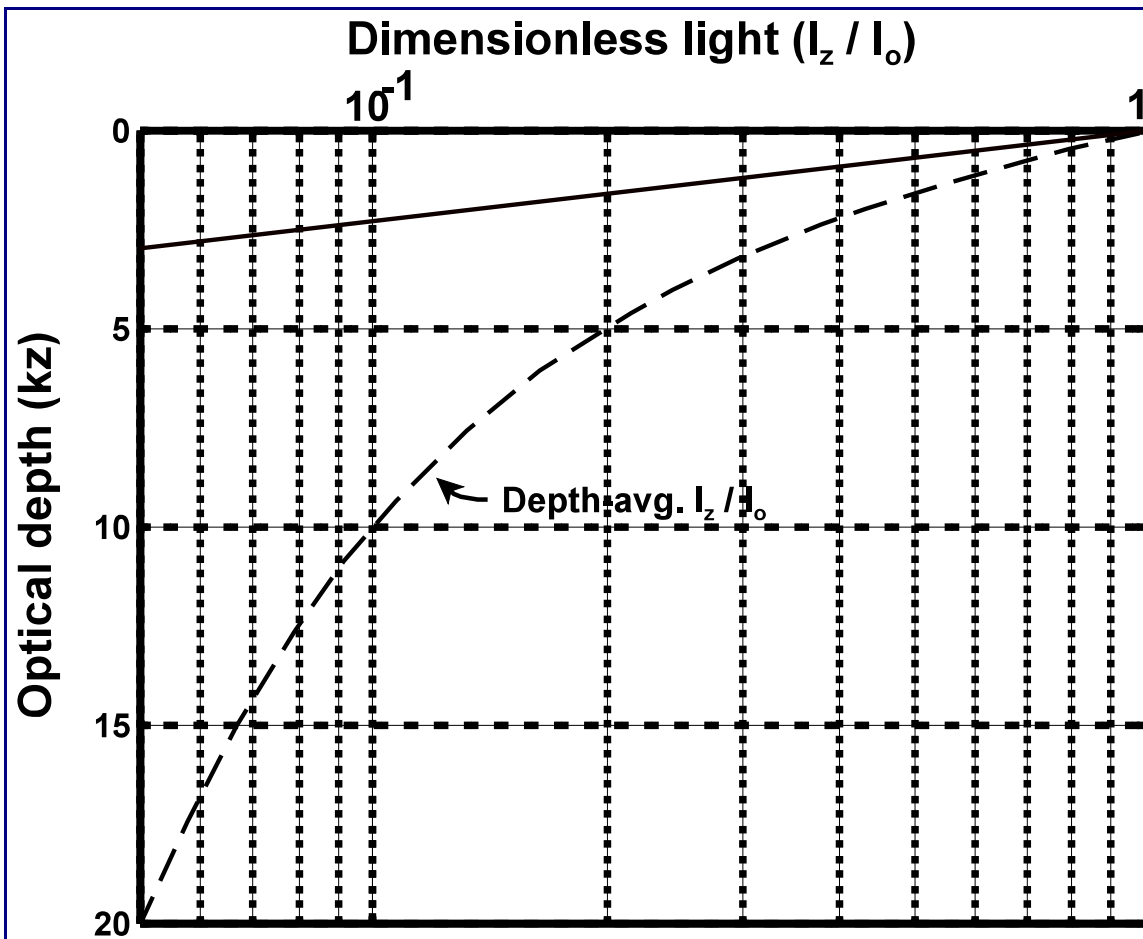


Figure 1. A plot of dimensionless light intensity vs. dimensionless depth (optical depth). The upper line shows Beer's law, $I_z = I_0 e^{-kz}$. The curve is described by Equ. 9 (see text).

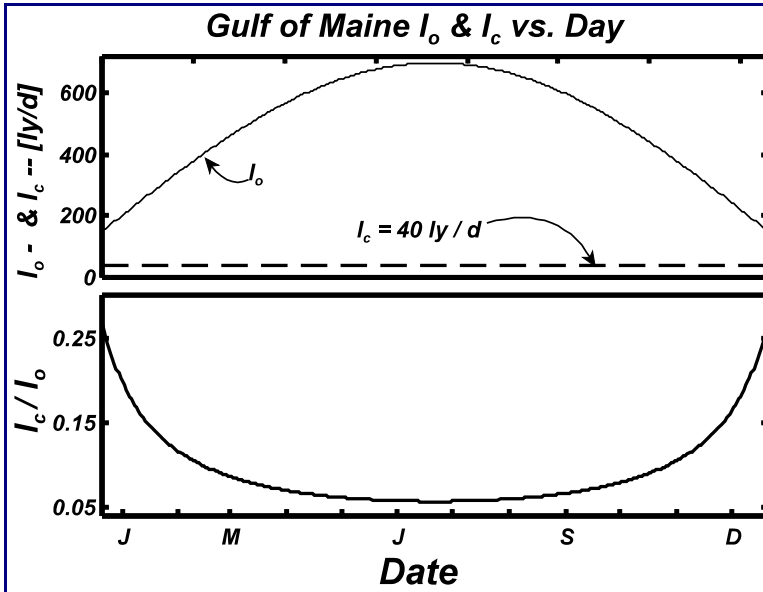


Figure 1. A plot of daily incident solar radiation, compensation light intensity and the ratio of the two. Data based on **Townsend & Spinrad 1986**.

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:

$$E_o = \alpha + \beta \sin \omega t.$$

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

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

$E_o = \text{Light at surface (PAR)}$. (10)

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

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

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.

The compensation light intensity, $I_c = 40$ ly/d, was taken from **Riley (1957)**. Riley's relatively high I_c value is based on

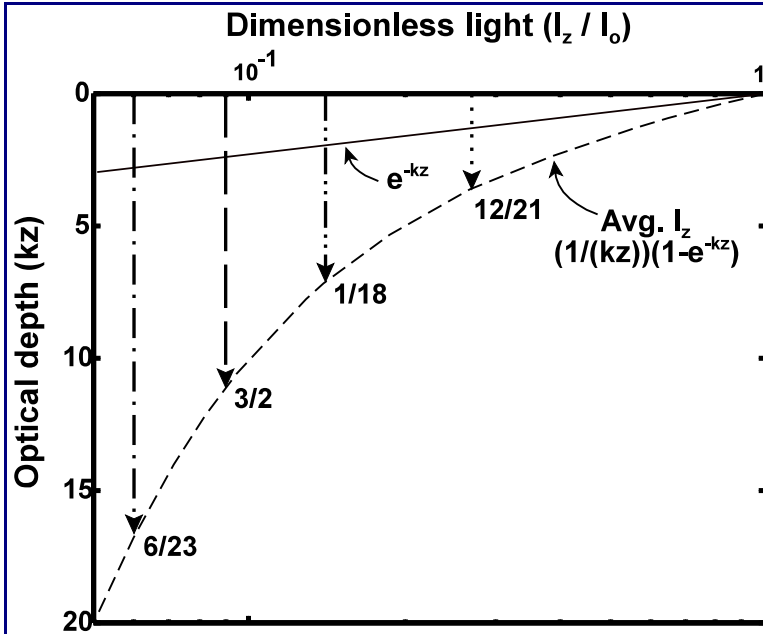


Figure 2. The I_c/I_o values for the Gulf of Maine (Fig. 1) are plotted on the critical depth plot. The intersection with the two curves provides the compensation and critical depths.

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_o as a vertical line on this graph. The I_c/I_o 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_o 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_z/I_o and \bar{I}_z/I_o 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.

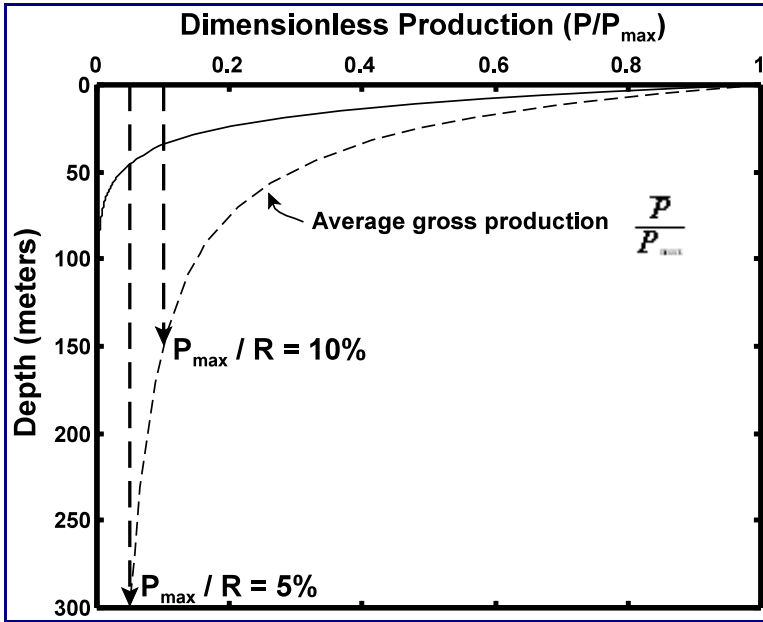


Figure 2. A ‘standard’ critical depth plot, in which respiration rate is plotted as a vertical line. The solid curve is the gross production at depth z , and the dotted curve is the average production from the surface to depth z .

changing the respiration rate from 10% of P_{max} to 5% of P_{max} changes the compensation depth by only a few meters, but doubles the critical depth (from 150 m to 200 m in Fig. 2).

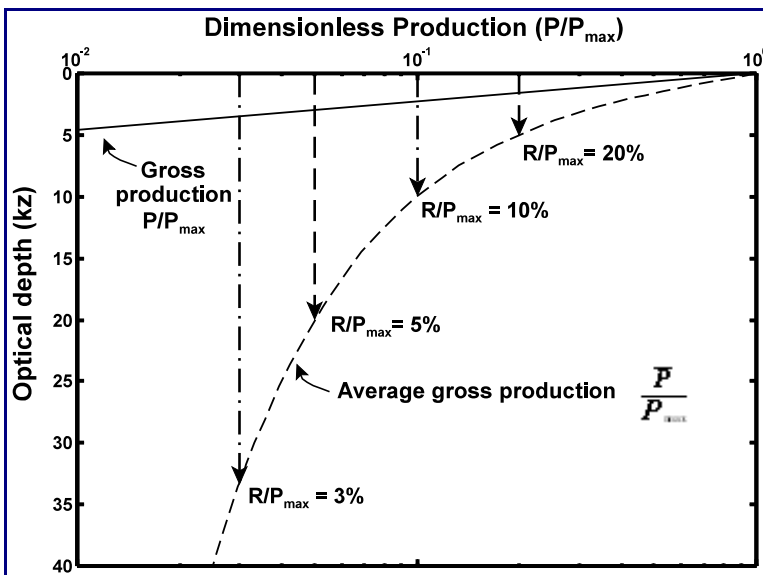
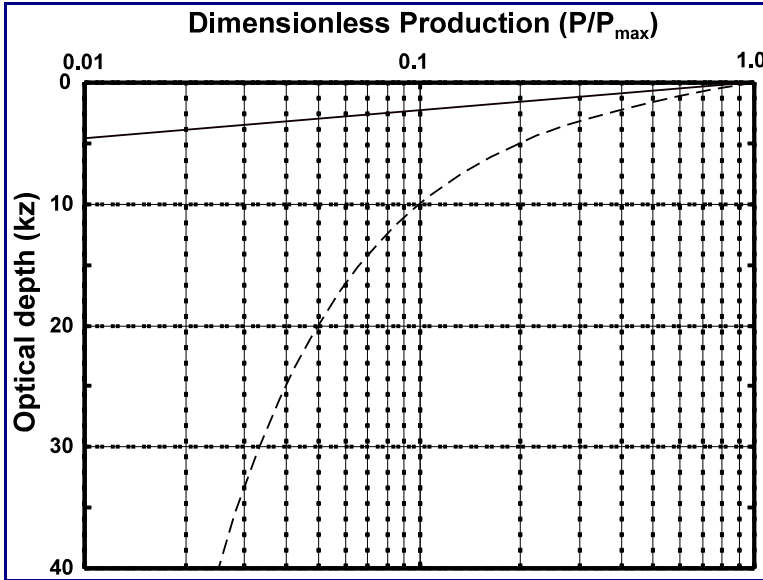


Figure 3. Dimensionless critical depth showing dimensionless gross production vs. optical depth, with R a fixed %-age of P_{max} . The solid line is gross and dashed line is net production at optical depth kz . If R is 10% of P_{max} , the critical depth is 10 optical depths. If R is 5% of P_{max} , the critical depth is 20 optical depths.

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_{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_{max} to 5% of P_{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 P_z/P_{max} and \bar{P}_z/P_{max} vs. optical depth 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_{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_{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 $\text{Resp}/P_{\max}=0.1$ 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_{\max} , the critical depth is 20 optical depths.



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

Thus, it is particularly uninformative to define critical depths using respiration as a fixed percentage of P_{\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 $\frac{P_{\max}}{R}$. If respiration is 10% P_{\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

Parsons, T. R., M. Takahashi, and B. Hargrave. 1984. *Biological Oceanographic Processes*. 3rd Edition. Pergamon Press, Oxford & New York. (p. 87-100) [24]

- I. Photosynthesis and growth of phytoplankton in the sea.
 - A. Methods of Estimating Primary Production
 1. Steemann-Nielsen's C-14 method discussed
 2. $k_c \approx 1.7/T$, 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 O₂ method
 - b. Simulated in-situ method discussed.
 - B. P vs. I curves
 1. Steele's equation [*note Jassby-Platt more commonly used*]

$$P_g = P_{\max} \frac{I}{I_{opt}} \exp\left(1 - \frac{I}{I_{opt}}\right). \quad (37, p. 89)$$

- a. I_k : intersection of initial slope and P
- b. P_{\max} varies as a function of environmental variables and the physiological state of the algae
2. **diel net photosynthesis** (p. 91 right.)

$$P_{nd} = P_{gd} - 24R \quad (50)$$
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 μ 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:

$$I_c = 0.5 I_0 e^{-kD_c} \quad (56)$$

$$@\text{avg}(I_c) = 0.5 I_0 \int_0^{D_{cr}} e^{-kD} \delta D / D_{cr}$$

$$D_{cr} = 0.5 I_0 / [kD_{cr}] * (1 - e^{-kD_{cr}}) \quad (57)$$

where, D_{cr} is large, (57) reduces to:

$$D_{cr} = 0.5 I_0 / [k \cdot \text{avg}(I_c)] \quad (58)$$

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)
 $k' = 0.04 + 0.0088 C + 0.054 C^{2/3}$, 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 $\approx 1\%$ of I_0 , compensation depth \approx depth at which light is 1% of surface light, or 4.6 light attenuation depths.

$$I_z/I_0 = e^{-kz}$$

$$\ln(0.01) = -kz_c$$

$$-4.6 = -kz_c$$

$$4.6 = kz_c, \text{ where } kz \text{ is the dimensionless light attenuation depth.}$$

$$\text{Compensation depth} = z_c = 4.6/k$$

[n.b., The compensation light intensity is not really 1% of I_0 . 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.**

$$\text{derivation: } k = 1.7/T,$$

$$\text{Compensation depth} = z_c = 4.6/k$$

$$= 4.6/(1.7/T)$$

$$= 2.7 \cdot T,$$

where, T is the Secchi 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/ hour

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%.

Sverdrup, H. U. 1953. On conditions for the vernal blooming of phytoplankton. J. Conseil perm. int. Explor. Mer. 18: 287-295. [3, 13, 14, 16, 19, 21, 22, 23, 24, 25, 26, 29, 30, 33, 35, 37]

- 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_c 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_0 , but PTH and most authors use 50% as the conversion to PAR from I_0 determined from the solar radiation-latitude equation.
- C. Double integral (depth and time) of gross production (2)
 $D_{cr}/[1-e^{-kD_{cr}}]=1/k*(@avg(I_c)/I_c)$ (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 $> z_{cr}$
 2. after middle May, $z_{cr} >$ mixed-layer depth
- B. Gran and Braarud's (1935) generalization confirmed.

Townsend, D. W. and R. W. Spinrad. 1986. Early phytoplankton blooms in the Gulf of Maine. Cont. Shelf Res. 6: 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 μM DIN

$$E_o = \alpha + \beta \sin \omega t.$$

where, $\alpha = 150$ langleys per day.
 $\beta = \text{beta} = 550$ langleys per day.

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

$t = \text{day of year (0 corresponds to 12/21)}.$ (4)

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

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

SUPPLEMENTAL

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.]

- 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 cause 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)

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.

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

$$\frac{D_{cr}}{1 - e^{-k_e D_{cr}}} = \frac{I_e}{I_c k_e}$$

D_{cr} = critical depth [meters].

k_e = 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:

$$D_{cr} \approx \frac{I_e}{I_c k_e}.$$

D_{cr} = critical depth [meters].

k_e = extinction coefficient.

I_e = Avg. energy passing sea surface.

I_c = energy at compensation depth.

(2, p. 540)

- II. Station P data described
- III. Methods used.
 - A. extinction coefficient measured by Secchi disk $k_e=1.7/D$
 - 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

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 SeaWiifs data to estimate the community compensation light intensity, see **Table of compensation light intensities above] [24]**

- 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. $1.3 \text{ mol photons m}^{-2} \text{ d}^{-1}$
 - 1. $2x$ light intensity for phytoplankton alone

Smetacek, V. and U. Passow. 1990. Spring bloom initiation and Sverdrup's critical depth model. Limnol. Oceanogr. 35: 228-233.

- 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 $2.48 \mu\text{mol quanta m}^{-2}\text{s}^{-1}$
- 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_{cr} of 2 to 10

Fig. 1. Sverdrup's model in its modern rendition.

- C. z_{cr} 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 α rather than the position of I_c (on the P vs I diagram where I_c 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 μ 's = 1, .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 $\mu\text{gC m}^{-2}\text{y}^{-1}$."

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."

Evans, G. T. and J. S. Parslow. 1985. A model of annual plankton cycles. *Biol. Oceanogr.* 3: 327-347.

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.

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- 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

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HARMFUL ALGAL BLOOMS

Comment

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

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DIMENSIONAL ANALYSIS

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