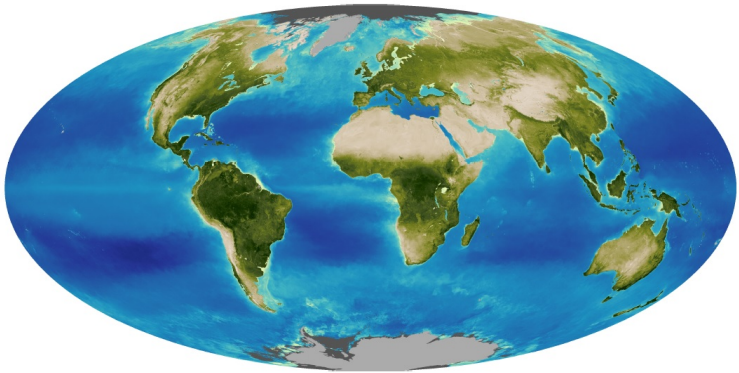
Simons Collaboration on Computational Biogeochemical Modeling of Marine Ecosystems
Annual Meeting, New York, 25TH - 27RD June 2024

Spectral wars, competition, chaos... but in the end a conservation law?!

Žarko Kovač zkovac@pmfst.hr
Department of Physics, Faculty of Science, University of Split

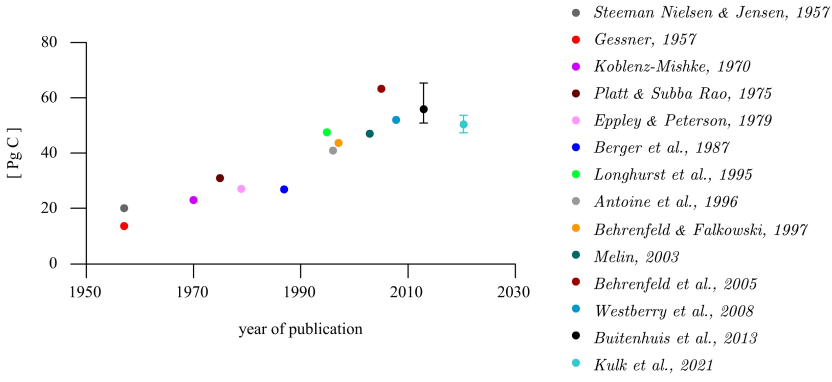
Where we are now



Anthropogenic carbon emissions per year 10 Gt C
Carbon assimilated by the biosphere per year 100 Gt C
Carbon assimilated by phytoplankton 50% of total
Phytoplankton biomass 1% of total land biomass

How we got here

Global annual marine primary production from the literature



Adopted from Buitenhuis et al. (2013)

Approaches to studying primary production

In situ

Incubation at sea under natural light conditions.
(Steemann Nielsen, 1952)

In vitro

Incubation under controlled light conditions.
(Platt i Jassby, 1976)

In silico

Computer implementation of primary production models.
(Gentleman, 2002)

Time evolution of phytoplankton biomass B in the ocean is modelled as:

$$\frac{\partial B}{\partial t} = production - losses + advection + mixing$$

Change in biomass is a result of production, losses and transport.

Mathematical description of the problem

$$\frac{\partial B}{\partial t} + w\frac{\partial B}{\partial z} = \Big(P^B(I) - L^B\Big)B + M\frac{\partial^2 B}{\partial z^2}$$

$$I(z,t) = I_0(t)\exp\left(-\int_0^z \Big(K_w + k_B B(z',t)\Big)\,\mathrm{d}z'\right)$$

With respect to light I the problem has all the qualities one seeks in physics:

nonlinear + **nonlocal** + **nonautonomous**

Many competitors

$$\frac{\partial B_i}{\partial t} + w_i \frac{\partial B_i}{\partial z} = \left(P_i^B(I) - L_i^B \right) B_i + M \frac{\partial^2 B_i}{\partial z^2}$$

$$I(z,t) = I_0(t) \exp\left(- \int_0^z \left(K_w + \sum_i k_{B,i} B_i(z',t) \right) \mathrm{d}z' \right)$$

With respect to light I the problem has all the qualities one seeks in physics:

nonlinear + **nonlocal** + **nonautonomous**

What effect does turbulence have on photosynthesis?

Going back to 1935!

...vertical movements of the water must favour new growth of phytoplankton through the mixing which carries nutritive substances to the illuminated zone from deep waters.

On the other hand a series of facts observed in recent years indicates that vertical mixing, besides having a favourable effect, may have an unfavourable influence on the growth of the phytoqlankton, because it ***prevents the living cells from accumulating in the illuminated zone*** *where they may utilize the light for photosynthesis, and the nitrates and phosphates for growth and propagation.*

(Gran & Braarud, 1935)

Sverdrup, Johnson & Fleming (1942)

It is obvious that the compensation point is determined by physiological characteristics of the plants and may, therefore, be somewhat different for different species, just as the optimum light intensity is not the same for all species. The compensation point is independent of the time during which photosynthesis and respiration have been measured if the oxygen production per unit time remains proportional to the light intensity and the oxygen consumption per unit time remains constant. On these assumptions, the oxygen production dP in the short time interval dt equals $aIdt$, where a is a constant and I is the light intensity, and the oxygen consumption dR equals bdt where b is another constant. The compensation point, I_c, is defined by

$$dP = dR, \qquad \text{giving} \qquad I_c = \frac{b}{a}.$$

The values of oxygen production P and consumption R in the time T are

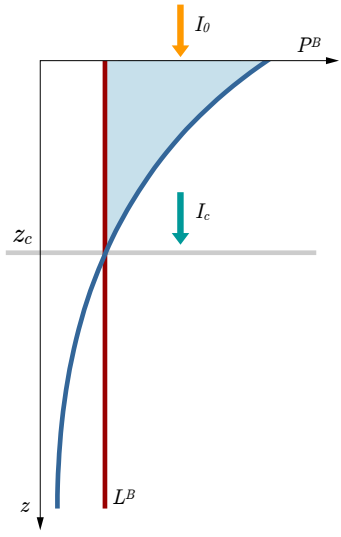
$$P = a\int_0^T Idt, \qquad R = bT.$$

The average light intensity in the time T is

$$\bar{I} = \frac{1}{T}\int_0^T Idt.$$

Therefore, if $P = R$, it follows that

$$\bar{I}_c = \frac{b}{a} = I_c;$$


I_0
P^B
I_c
z_c
z
L^B

Riley, Stommel & Bumpus (1949)

In considering the remainder of the problem, it is apparent that equation (1) does not represent the rate of change of the plankton at any particular depth in the presence of such phenomena as vertical turbulence and sinking. Methods of handling such problems were discussed by Sverdrup, Johnson, and Fleming (1942: 159–160), and an equation was proposed in which the "local time change of concentration equals effects of diffusion minus advection plus biological processes." In the present case their equation is presented in the form

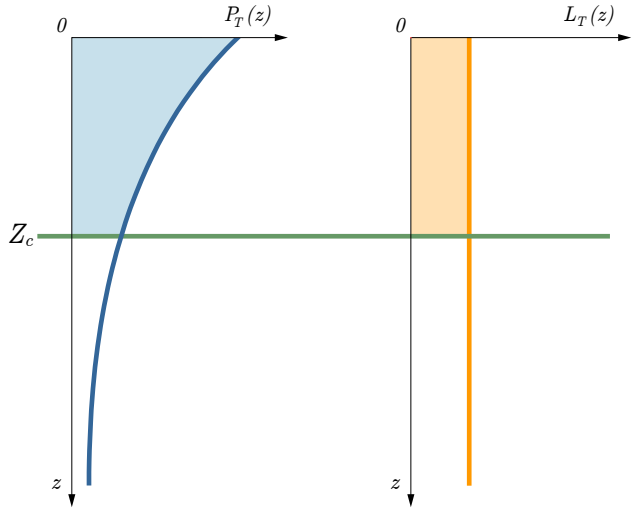
$$\frac{\partial p}{\partial t} = p\,(p_h - r - wh) + \frac{\partial}{\partial z} \cdot \frac{A}{\rho} \cdot \frac{\partial p}{\partial z} - \frac{V\mu_0}{\mu_T} \cdot \frac{\partial p}{\partial z}. \qquad (9)$$

Sverdrup (1953) argument

In order that the vernal blooming of phytoplankton shall begin it is necessary that in the surface layer the production of organic matter by photosynthesis exceeds the destruction by respiration. On certain assumptions a "critical depth" is defined. ***The depth of a mixed surface layer must be less than this critical depth if the phytoplankton population of the mixed layer shall increase.***

$$\frac{\alpha^B I_T}{K}(1 - e^{-KZ_c}) = L_T^B Z_c$$

The classical Critical Depth Criterion (Sverdrup, 1953)



ICES Journal of Marine Science

ICES International Council for the Exploration of the Sea
CIEM Conseil International pour l'Exploration de la Mer

ICES Journal of Marine Science (2015), 72(6), 1892–1896. doi:10.1093/icesjms/fsv110

Introduction to the Themed Section: '*Revisiting Sverdrup's Critical Depth Hypothesis*'

Introduction

Revisiting Sverdrup's critical depth hypothesis

Shubha Sathyendranath[1]*, Rubao Ji[2], and Howard I. Browman[3]

Kierstead & Slobodkin (1953)

THE SIZE OF WATER MASSES CONTAINING PLANKTON BLOOMS[1]

BY

HENRY KIERSTEAD[2]

Brown University
Providence, Rhode Island

AND

L. BASIL SLOBODKIN

Bingham Oceanographic Laboratory
Yale University
New Haven, Connecticut

ABSTRACT

If a phytoplankton population is assumed to be increasing logarithmically in a mass of water surrounded by water which is unsuitable for the survival of the population, it can be shown that there is a minimum critical size for the water mass below which no increase in concentration of phytoplankton can occur. In a one-dimensional water mass with leakage at both ends, this size, after a time of the order of $L^2/8\pi^2D$, is given by

$$L_c = \pi\sqrt{\frac{D}{K}},$$

where L_c is the length of the water mass, D the diffusion, and K the rate of increase of the population. The corresponding size in a cylindrical water mass is given by

What effect does sinking have on photosynthesis?

Steele & Yentsch (1960)

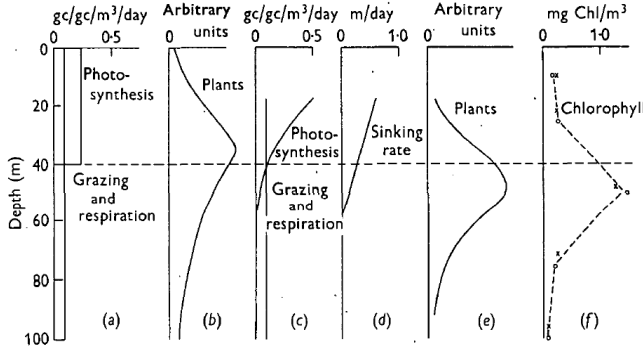
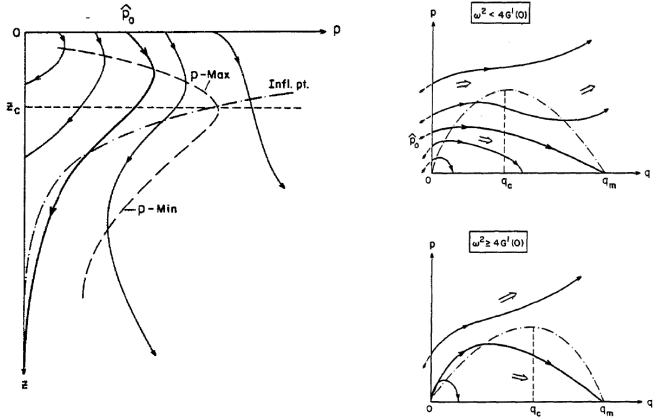


Fig. 2. (*a* and *b*) Conditions from the theory of Riley *et al.* (1949), using a constant sinking rate. (*c*, *d*, *e*) Conditions with a variable sinking rate. (*f*) Data from Station 194.

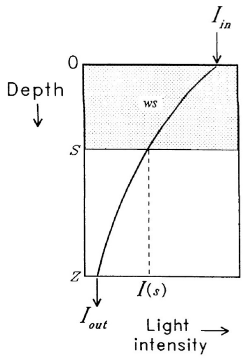
Such features are normally explained by the sinking of plants and a sinking rate constant with depth is used in the mathematical models of Riley, Stommel & Bumpus (1949) to explain some observed patterns of vertical distribution. However, ***on the basis of their model, the chlorophyll maximum must occur above the compensation depth****.*

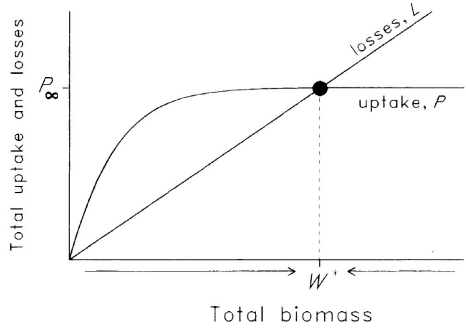
Shigesada & Okubo (1981)



Self-shading of light by algae growing in a column of water plays an important role in the dynamics of algal blooms. Thus without self-shading the algal concentration would increase more rapidly, making the nutrient limitation too strong. Apart from the practical importance of self-shading, its ***inherent nonlinearity in the growth dynamics leads to an interesting mathematical problem****...*

Huisman & Weissing (1994) and Weissing & Huisman (1994)





We argue that the crucial measure for phytoplankton growth ***is not a critical depth but a critical light intensity*** I^*_{out}. *For each species* I^*_{out} *corresponds to the equilibrium light intensity at the bottom of a water column when the species is grown in monoculture.*

Competition

Imagine N phytoplankton species competing for light in the mixed layer.

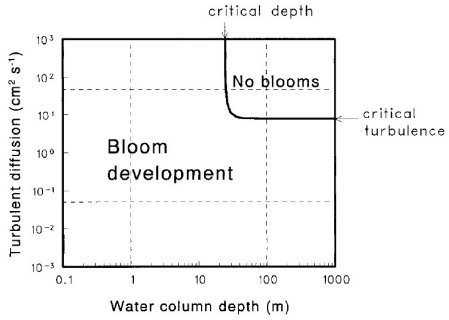
For each species, I^*_{out} is the critical light intensity, which corresponds to the light intensity at the mixed layer base at steady state in monoculture.

$$B(t) \rightarrow B_i^* \Big|_{\min I^*_{out}}$$

Following Huisman & Weissing (1994) and Weissing & Huisman (1994) the species with the lowest critical light intensity wins.

The competitive exclusion principle holds for light as a resource.

Husiman et al. (1999) Limnology and Oceanography



A turbulent diffusion model shows that ***there are two different mechanisms for the development of phytoplankton blooms****. One of these mechanisms works in well-mixed environments and corresponds to the classical critical depth theory. The other mechanism is based on the rate of turbulent mixing. If turbulent mixing is less than a critical turbulence, phytoplankton growth rates exceed the vertical mixing rates, and a bloom develops irrespective of the depth of the upper water layer.*

Some interesting exchanges

Behrenfeld (2010)
Abandoning Sverdrup's Critical Depth Hypothesis on phytoplankton blooms

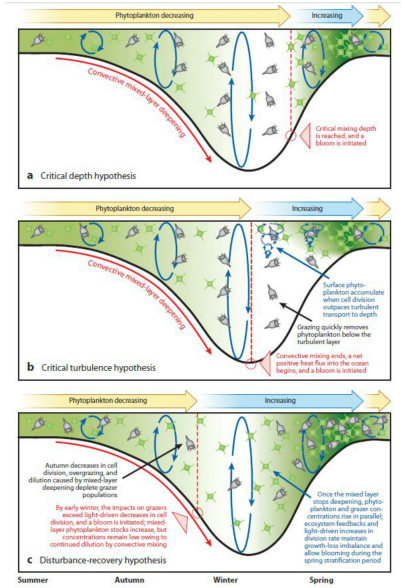
Chiswell (2011)
Annual cycles and spring blooms in phytoplankton: don't abandon Sverdrup completely

Behrenfeld et al. (2013)
Annual cycles of ecological disturbance and recovery underlying the subarctic Atlantic spring plankton bloom

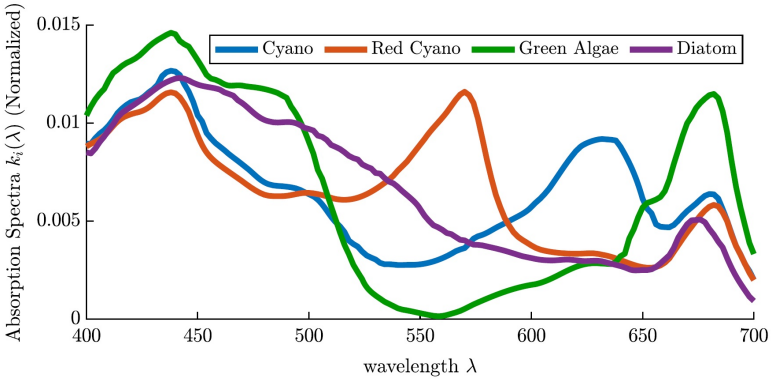
Chiswell (2013)
Comment on "Annual cycles of ecological disturbance and recovery underlying the subarctic Atlantic spring plankton bloom"

Behrenfeld et al. (2013)
Reply to a comment by Stephen M. Chiswell on: "Annual cycles of ecological disturbance and recovery underlying the subarctic Atlantic spring plankton bloom" by M. J. Behrenfeld et al. (2013)

Behrenfeld & Boss (2014) Annual Reviews of Marine Science

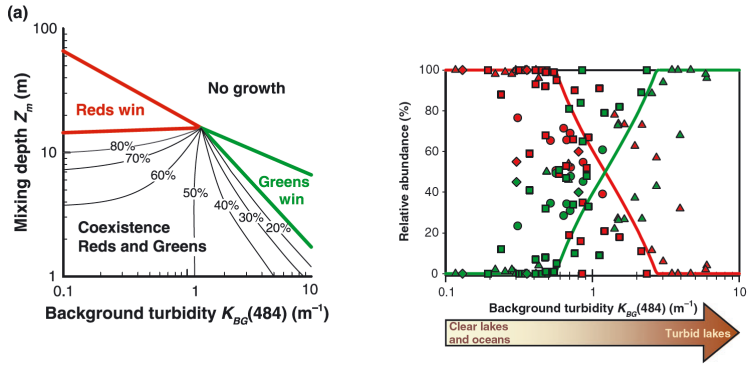


Hang on: what about light and coexistence?



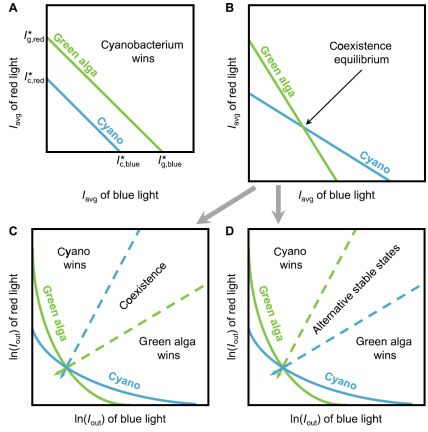
(Heggerud et al., 2023)

Stomp et al. (2007) Ecology Letters



Hutchinson's paradox of the plankton inspired many studies on the mechanisms of species coexistence. Recent laboratory experiments showed that ***partitioning of white light allows stable coexistence*** *of red and green picocyanobacteria. Here, we investigate to what extent these laboratory findings can be extrapolated to natural waters. We predict from a parameterized competition model that the underwater light colour of lakes and seas provides ample opportunities for coexistence of red and green phytoplankton species.*

Luimstra et al. (2020) Ecology



Can we advance ecological theory to predict how these differences in light-harvesting strategy affect competition between phytoplankton species? Here, we develop a new resource competition model in which the absorption and utilization efficiency of different colors of light are varied independently.

But all this time nobody actually solved Sverdrup's equation...

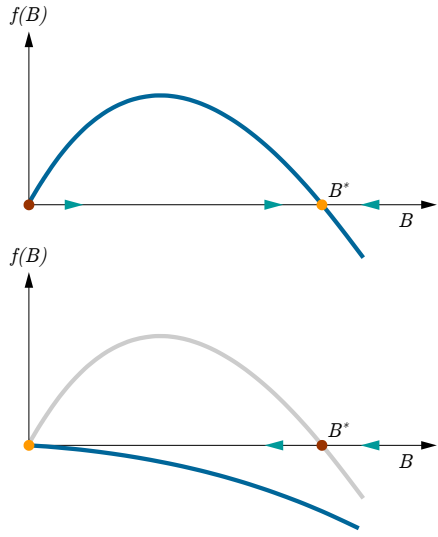
That is until Kovač et al. (2021) found the exact solution

$$C = \frac{1}{K}\left(W_0\Big(-Ae^{-A}\Big) + A\right)$$

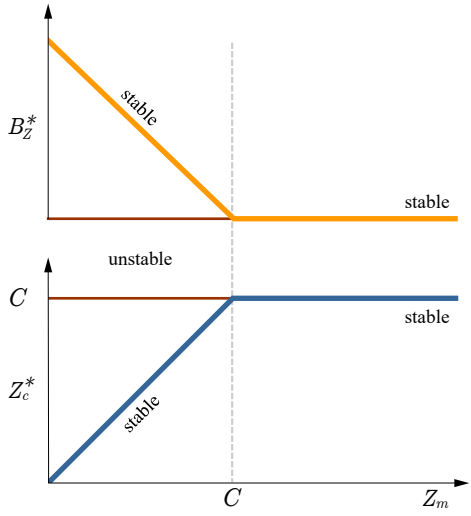
$$B^* = \frac{K_w}{k_B}\left(\frac{C}{Z_m} - 1\right)$$

These simple looking solutions opened up new unexpected avenues!

Bio-optical bifurcation



Bio-optical bifurcation



Competition

Imagine N phytoplankton species competing for light in the mixed layer.

The species with the deepest optically uncoupled critical depth wins!

$$B(t) \rightarrow B_i^* \Big|_{\max C_i} \qquad I(Z_m) \rightarrow I(C_i) \Big|_{\max C_i}$$

Following Huisman & Weissing (1994) and Weissing & Huisman (1994) the species with the lowest critical light intensity wins. This species also has the deepest optically uncoupled critical depth. Therefore the critical light argument is translated back to a critical depth argument.

Critical light and critical depth: Two sides, same coin.

Critical Depth Conservation Principle (Kovač et al., 2021)

$$\frac{\mathrm{d}(KZ_c)}{\mathrm{d}t} = 0$$

The product KZ_c is a constant of motion!

$$\frac{\mathrm{d}\zeta_c}{\mathrm{d}t} = 0$$

When expressed as an optical depth the critical depth does not change over time.

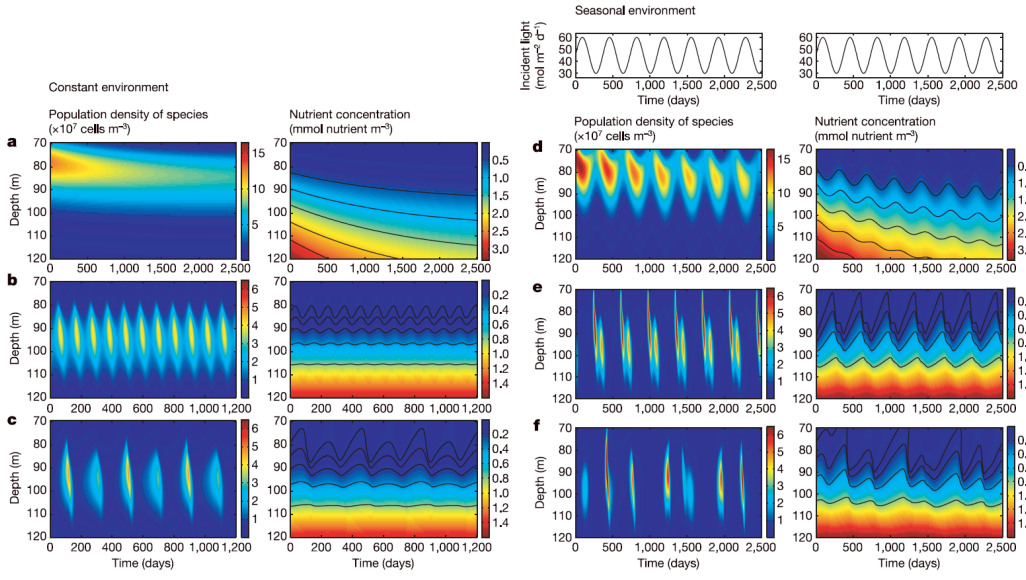
Does this hold when mixing is not strong?

nature Vol 439|19 January 2006|doi:10.1038/nature04245

LETTERS

Reduced mixing generates oscillations and chaos in the oceanic deep chlorophyll maximum

Jef Huisman[1]*, Nga N. Pham Thi[2]*, David M. Karl[3] & Ben Sommeijer[2]


Constant environment
Seasonal environment
Incident light (mol m-2 d-1)
Time (days)
Population density of species (×10^7 cells m-3)
Nutrient concentration (mmol nutrient m-3)
Depth (m)
a
b
c
d
e
f

New results seem to indicate a positive answer!

As we have recently shown the compensation depth is governed by:

$$\frac{\partial z_c}{\partial t} = -\frac{k_B}{K_w + k_B B(z_c)} \int_0^{z_c} \frac{\partial B(z')}{\partial t} \, \mathrm{d}z'$$

And has the following constant of motion:

$$\frac{\mathrm{d}}{\mathrm{d}t} I(z_c(t)) = 0$$

Riley (1948)

FACTORS CONTROLLING PHYTOPLANKTON POPULATIONS ON GEORGES BANK[1]

By

GORDON A. RILEY

Woods Hole Oceanographic Institution

and

Bingham Oceanographic Laboratory

A complex field such as oceanography tends to be subject to two opposite approaches. The first is the descriptive, in which several quantities are measured simultaneously and their inter-relationships derived by some sort of statistical method. The other approach is the synthetic one, in which a few reasonable although perhaps over-simplified assumptions are laid down, these serving as a basis for mathematical derivation of relationships.

Each approach has obvious virtues and faults. Neither is very profitable by itself; each requires the assistance of the other. Statistical analyses check the accuracy of the assumptions of the theorists, and the latter lend meaning to the empirical method. Unfortunately, however, in many cases there is no chance for mutual profit because the two approaches have no common ground. Until such contact has been established no branch of oceanography can quite be said to have come of age. In this respect physical oceanography, one of the youngest branches in actual years, is more mature than the much older study of marine biology. This is perhaps partly due to the complexities of the material. More important, however, is the fact that physical oceanography has aroused the interest of a number of men of considerable mathematical ability, while on the other hand marine biologists have been largely unaware of the growing field of bio-mathematics, or at least they have felt that the synthetic approach will be unprofitable until it is more firmly backed by experimental data.

However valid the latter objection may be, the present paper will attempt, in the limited field of plankton biology, to establish continuity between some purely descriptive studies that have been made and mathematical concepts based on what seem to be logical assumptions about plankton physiology. The need for such an attempt has

[1] Contribution No. 353 from the Woods Hole Oceanographic Institution.

Riley's words still resonate today

A complex field such as oceanography tends to be subject to two opposite appraches. *The first is the* ***descriptive****, in which several quantities are measured simultaneously and their inter-relationships derived by some sort of statistical method. The other approach is the* ***synthetic*** *one, in which a few reasonable although perhaps oversimplified assumptions are laid down, these serving as a basis for mathematical derivation of relationships.*

Each approach has obvious virtues and faults. *Neither is very profitable by itself; each requires the assistance of the other. Statistical analyses check the accuracy of the assumptioms of the theorists, and the latter lend meaning to the empirical method. Unfortunately, however, in many cases there is no chance for mutual profit because the two approaches have no common ground.* ***Until such contact has been established no branch of oceanography can quite be said to have come of age.***

(Riley, 1948)

Thank you!