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FRAGILITY OF PRIMARY PRODUCTION

Žarko Kovač¹, Shubha Sathyendranath²

¹FACULTY OF SCIENCE, UNIVERSITY OF SPLIT, CROATIA
²PLYMOUTH MARINE LABORATORY, PLYMOUTH, UNITED KINGDOM

Motivation



Adopted from Limits to growth (1972)

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Motivation



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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

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Global annual primary production from Kulk et al. (2021)



48.7 to 52.5 Gt C per year between 1998 and 2018

How we got here

Global annual marine primary production from the literature



- Steeman Nielsen & Jensen, 1957
- Gessner, 1957
- Koblenz-Mishke, 1970
- Platt & Subba Rao, 1975
- Eppley & Peterson, 1979
- Berger et al., 1987
- Longhurst et al., 1995
- Antoine et al., 1996
- Behrenfeld & Falkowski, 1997
- Melin, 2003
- Behrenfeld et al., 2005
- Westberry et al., 2008
- Buitenhuis et al., 2013
- Kulk et al., 2021

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Adopted from Buitenhuis et al. (2013)

Approaches to studying primary production

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$In \ situ$

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)

A long standing question: What limits primary production?

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 phytoglankton, 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)

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Steemann Nielsen (1952) ICES Journal of Marine Science



As the constantly increasing number of human beings on our globe requires greater and greater quantities of food, and as the food production on land can be but little increased, we must consider the sea as an important reserve.

Sverdrup et al. (1953) ICES Journal of Marine Science



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.

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Idea (Gran & Braarud, 1935)

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Measurement (Steemann Nielsen, 1952)

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Mathematics (Sverdrup, 1953)

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Still a current topic of new research



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

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

Revisiting Sverdrup's critical depth hypothesis

Shubha Sathyendranath1*, Rubao Ji2, and Howard I. Browman3

¹Phymouth Marine Laboratory, Prospect Place, Plymouth PL1 3DH, UK Department of Biology, Woods Hole Oceanographic Institution, Woods Hole, MA 02543, USA ³Institute of Marine Research, Austevoll Research Station, Marine Ecosystem Acoustics Research Group, 5392 Storebø, Norway

*Corresponding author: tel: +46 1752 633 166: fax: +66 1752 633 101: e-mail: shubboll:dates

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Published more than 60 years ago in this Journal, the article in which Sverdrup proposed the concept of critical depth to explain the initiation of the spring bloom in the North Atlantic has accrued an exceptionally large number of citations and continues to be cited more than 50 times per year. The framework provided by Sverdrup has now been applied, adapted, and tested across many aquatic systems worldwide. Datasets have been collected; models have been built on the framework: these studies have generated new insights into phytoplankton dynamics and interesting debates on the relative importance of the various factors responsible for phytoplankton blooms. This article theme set presents some of the most recent efforts to discuss and test Sverdrup's critical depth hypothesis using a diverse set of approaches, ranging from controlled experiments to field observations as well as numerical and analytical models. The set of papers celebrates an elegant and powerful hypothesis that has had long-lasting influence. It is to be expected that it will also stimulate future research, adding even more to our understanding of one of the most fundamental processes in biological oceanography.

Keywords: bloom onset, light attenuation, mixed layer, mixing depth, phytoplankton, primary production, stratification, turbulence.

Background

More than 60 years area, Swerdrup (1953) published an article in this Journal laying down the theoretical framework for analysing spring phytoplankton bloom initiation in the North Atlantic. It inspired a generation of occanographers, and continues to do so to this day. In a world where it has become fashionable to cite the most recent author to advance an idea, rather than the first, Sverdrup's article analytic result that provided insights into the processes that determine remains one of the most cited publications in the field (see below). This is a testament to its importance.

What is the secret of its longevity? Probably, the answers to this question would be as varied as the backgrounds and interests of the scientists to whom it might be posed, but we will try to list a few aspects that we find important. First of all, Sverdrup provided a rigorous, mathematical formalism to concepts and observations that had been aired before (e.g. Gran and Braarud, 1935), thereby be recognized as a theory that cannot be violated: it provides the making it possible to test hypotheses regarding phytoplankton framework for constructing details of a model. The second part, blooms in a quantitative way. Although he addressed the specific case of sprine blooms, the model presented by Svendrup was built on the broad and strong general principle of mass balance for tested. And, the model has been tested, again and again

phytoplankton in a laver of the water column, such that the model was readily applicable to the study of any type of phytoplankton dynamics just about anywhere. The model, which is deceptively simple, is rich in potential applications, providing a master class on how to construct a general model and how to simplify it for a specific case: that of the spring bloom initiation in the North Atlantic. The simplifications led to an spring blooms. Even in the current oceanographic era when numerical modelling is the norm and the aspiration, analytic solutions remain the method of choice for interpretation of model solutions.

It is useful to recognize the two distinct parts of the critical depth concept that Sverdrup introduced: the first part, that uses the principle of conservation of mass in a layer of the water column to study net change in phytoplankton concentration, is axiomatic, and may which identifies the major factors responsible for the formation of blooms, belongs more in the realm of hypotheses that can be

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Where are we going?

Tragedy of the commons

If decisions about the use of renewable natural resources are based exclusively on profits, even long-term profits, **renewable natural resources will be used on a sustainable basis only if their biological growth rate is greater than the expected growth rate of alternative investments.** Because the growth rate of the world economy today is greater than the biological growth rate of most renewable resources, there are powerful economic incentives not to use renewable natural resources on a sustainable basis. If people accept the rules of the game in a free market economy, it is rational to use renewable resources unsustainably whenever biological production fails to compete with alternative forms of investment.

(Marnet, 2001)

Considerations of sustainable growth are particulary problematic in the context of climate change. The stress on marine primary production comes from exploitation as well as from environmental changes.

Where do we use production estimates?

To estimate the time evolution of biomass and carbon fluxes in the ocean:

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

Where do our formidable computational capabilities fit in the larger social picture?

A quick look at what physical economics says

A model of a closed natural production circuit



Labourers from N households work in the fields (their capital, K). In return for their work, W, consumer goods, G, are brought back from the fields to the households.

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Critique: A far too simple description for modern day economy!

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Is it really?!

A model of a closed natural production circuit



Ships from N harbours go to sea (their capital, K). In return for their effort, W, fish, G, are brought back from the sea to the harbour.

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Consequence? Are we fishing down marine food webs?



(Branch et al., 2010)

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The issue of sustainability at once presents itself.

A plausible way to think about marine primary production?



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Stability and resilience of primary production

It is straightforward to show that mathematical definitions of both these terms can be defined for phytoplankton models (Kovač et al., 2020).

Both are difficult to quantify for in situ populations due to the vast number of parameters in ecosystems models.

Operational measures of such terms that are straightforward to quantify would be of high value.

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Do we currently have measurements at relevant time and spatial scales?

An example of a dynamic environment



(Orlić et al., 2011)

Does biology dampen or amplify these oscillations?

Internal waves around islands



A peculiar case of coastal trapped internal waves which occurs around closed shorelines. Wave energy is confined on a closed path, with waves having an integral number of wavelengths reinforcing themselves, with the potential of creating a resonant system. If the island geometry and stratification coincide with external forcing, pronounced internal island trapped waves can be excited.

What is the effect on primary production?

What happens when we add noise to surface irradiance?

$$I_0^m(t) = \langle I_0^m \rangle + \delta I_0^m$$

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Biomass is suppressed despite having received same total energy.

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What happens when we add noise to mixed-layer depth?

$$Z_m(t) = \langle Z_m \rangle + \delta Z_m$$

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In this case the opposite holds: biomass is increased on average.

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An analogy to illustrate the concept



FRAGILE

suffers from disorder

ROBUST ANTIFRAGILE

stays the same

gains from disorder

A candidate definition of anti/fragility for primary production

Marginal production

$$M_x = \frac{\partial P}{\partial x}$$

Fragility

$$F_x = \frac{\partial M_x}{\partial x}$$

x is the controlling variable, such as irradiance, nutrients, mixed layer depth, ...

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Fragility with respect to irradiance



The idea of fragility comes from economics and was introduced by Nassim Taleb.

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Antifragility of primary production



Antifragility is the opposite of fragility. Antifragile systems gain from variability.

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Quantification from in situ data



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Looking at the seasonal cycle



An extract of a typical year from a longer model run.

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Interpreting the model behaviour



Even though the critical depth criterion is met, biomass can be suppressed due to high frequency variability. Is there an optimal zone for the phytoplankton to thrive and production to be sustained in the long run? Can we speak of tipping points in primary production?

What the theory is telling us

Primary production displays both fragility and antifragility.

For primary production to be affected we don't need to change the mean values in the forcing variables, fluctuations can have an effect.

The problem has to be address at the right scale to incorporate the effect of fluctuations.

We have all we need from remote sensing data to estimate fragility at large scales.

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Looking at longer time scales



55 year long in situ time series from the Adriatic (Kovač et al., 2018)

Do we properly value primary production at these time scales?

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Valuation: a hard problem

What would you rather: a tree today or two trees tomorrow?



Valuation: a hard problem

What would you rather: a tree today or two trees tomorrow?



Depends on how fast the trees grow!

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Discounting



$$P = P_0 e^{\gamma t} \qquad \rightarrow \qquad P_0 = P e^{-\gamma t}$$

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The process of converting value received in the future to value received now.

Do we properly value primary production?

Present value of future primary production:

$$J = \int_{0}^{\infty} e^{-\gamma t} \left(P - L \right) B \, \mathrm{d}t$$

where (P - L)B equals the carbon stored by primary producers at time t.

Back to the start



Adopted from Limits to growth (1972)

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Knowledge gaps

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Does anti/fragility extend up the food web?

The effect of photoadaptation on anti/fragility.

Spectral effects and anti/frafility.

Valuation of primary production: how to even start?

What is the discount rate for the ocean?

What are the limits to growth for the ocean?

Opportunities

We have the computational capacities to implement these calculations at large scales using remote sensing data.

We have a lot of in situ data that can be used to quantify stability, resilience, fragility, antifragility, \ldots

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To objectively quantify marine ecosystem services.

To explore high frequency data and look for signs of anti/fragility.

Exploration of tipping points in primary production.

Thank you!

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