# POPULATION DYNAMICS OF PHYTOPLANKTON

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## Contents

## Summary

The growth and decline of phytoplankton populations are the result of simultaneous reproduction and losses, which can both be described by rates according to the exponential growth equation. The reproductive rate can be limited by light and nutrients. The loss rate depends on grazing, sinking, losses by pathogens and physiological mortality. The balance between reproduction and losses can lead to blooms (reproduction strongly exceeding losses), crashes (losses strongly exceeding reproduction) and steady state (reproduction and losses almost in balance). Recurrent seasonal cycles of phytoplankton abundance are primarily caused by the seasonal pattern of stratification and mixing and the resultant temporal and spatial segregation between light and nutrients.

## 1. Introduction

Phytoplankton population densities undergo rapid changes at short time scales. Increases and declines by more than one order of magnitude per week can be observed at times. Some of these changes are regular, recurrent seasonal patterns while others appear quite irregular. The growth and decline of a population is a result of simultaneous reproduction and losses. It is generally perceived, that reproduction is controlled by physiological growth conditions (temperature, availability of light and nutrients) while losses might result from diverse sources (natural enemies, pathogens, sinking, etc.). Thus, the wax and wane of a phytoplankton population is the composite result of species specific sensitivities to the factors which limit reproduction and which induce loss. In this article, first the mathematical treatment and the factors governing reproduction and losses will be discussed. Then, the resultant patterns of population increase and decline and the consequences for phytoplankton seasonality will be discussed

## 2. Reproduction

### 2.1. The reproductive rate

In most cases, phytoplankton reproduce by binary cell division, leading to two daughter cells per mother cells, but there are some species where 4, 8 or more (usually 2n) daughter cells are produced per reproductive event. In the case of binary division, the generation time equals the doubling time of cell numbers, if there are no simultaneous losses. Typical generation times of viable phytoplankton range from several hours to a few days. The potential growth of a population unrestrained by losses can be described by the instantaneous rate of reproduction (or gross-growth rate; **μ**):

$$\ln N_2 = \ln N_1 . e^{\mu(t2-t1)} \text{ or } \mu = (\ln N_2-\ln N_1)/(t_2-t_1) \quad [d^{-1}] \qquad (1)$$

where $N_1$ is the population density (abundance) at the beginning of a time interval $t_1$-$t_2$ and $N_2$ the population density at the end of that interval. The doubling time ($t_d$) can be calculated as

$$t_d = \ln_2/\mu \ [d] \qquad (2)$$

The reproductive rate of a population with a doubling time of 1 day has a growth rate of

$$\mu = \ln 2 \ d^{-1} = \text{ca. } 0.69 \ d^{-1} \qquad (3)$$

Unrestrained growth at a constant rate according to (1) would lead to infinite growth with an ever increasing slope of the curve abundance vs. time (exponential growth). It is only possible for a few generation times in the absence of natural enemies. Sooner or later, either reproductive rates will decline because of a shortage of resources (mineral nutrients, light) or cells will be eliminated by loss factors or both will occur at the same time.

### 2.2. The maximal growth rate

The reproductive rate unrestrained by shortage of resources is called maximal growth rate (**$\mu_{max}$**). It is a species specific parameter, which depends on temperature. At suboptimal temperatures, $\mu_{max}$ increases by a factor of ca. 2. Above the optimum, there is a sharp drop of $\mu_{max}$ with increasing temperatures. Temperature optima vary from ca. $5^oC$ for extremely cold-adapted Antarctic phytoplankton to ca. $35^oC$.

As a rule, $\mu_{max}$ decreases with the cell size of phytoplankton species, but the equations available in the literature do not include autotrophic picoplankton (< 2 µm). Maximal growth rate of picoplankton published since then seem to indicate that the smallest size fraction of phytoplankton does not appear to reproduce faster than diatoms and flagellates in the 5-10 µm size range.

### 2.3. Limitation of reproductive rates.

Shortage of essential resources (mineral nutrients, light) can lead to reproductive rates well below $\mu_{max}$. Such a shortage can have occurred already prior to the onset of phytoplankton growth (in nutrient poor waters, at low surface irradiance or big mixing depth) or as a consequence of phytoplankton growth, if phytoplankton have exhausted one or several essential nutrients or reduced light penetration through the water columns ("self shading"). The limitation of reproductive rates by a limiting resource is described by saturation curves, which show an increase of reproductive rates at limiting resources and an approach to a maximum at high ("saturating") resource levels. For nutrient limitation, two models are in general use:

The Monod-model predicts reproductive rates from the concentration of the dissolved nutrient in the water (S):

$$\mu = (\mu_{max}.S)/(S+k_s) \qquad (4)$$

where $k_s$ is the nutrient concentration at which half of the maximal growth rate is attained. If more than one nutrients are present in low concentrations, reproduction is limited by the one which leads to lowest value of µ.

The Droop-model predicts reproductive rates from intracellular concentrations ("cell quota", Q= of the limiting nutrient:

$$\mu = \mu_{max}(1-Q_0/Q) \qquad (5)$$

where $Q_o$ is the minimal cell quota. The Monod-model applies only under constant nutrient supply while such restrictions do not apply to the Droop-model.

## 3. Losses

### 3.1. The loss rate

Under natural conditions realized growth of phytoplankton is almost always less than predicted from reproductive rates, because phytoplankton cells are continuously lost from the population by grazing, sinking, parasitism, viral lysis and physiological mortality. Thus, the net growth rate (**r**) is almost always smaller than μ and it can be negative a times (declining abundance). It is calculated similar to μ in equ. 1 in the presence of losses. Then

$$r = (\ln N_2 - \ln N_1)/(t_2 - t_1) \quad [d^{-1}] \tag{6}$$

and

$$r = \mu - \lambda \tag{7}$$

where λ is the loss rate. All components of the loss rate (γ for grazing, σ for sinking, δ for physiological death, ....) are additive:

$$\lambda = \gamma + \sigma + \delta ... \tag{8}$$

When calculating r from field data, care must be taken to sample the same water body. Otherwise, growth or decrease might be simulated by advection of water masses with different initial phytoplankton densities. When spatial heterogeneity of phytoplankton distribution can be treated as noise, net growth rates can be calculated by a linear regression of ln N from temporally sequential samples on time. Then, r would be equivalent to the slope of the regression.

## 3.2. Grazing

All phytoplankton species are fed upon by different zooplankton species. Grazing losses to zooplankton may at time exceed reproductive rates and even maximal growth rates, thus leading to abundance declines even in periods of favorable growth conditions. If such declines affect all important populations at the same time mid seasonal biomass minima ("**clear water phases**") can be observed. Their induction by grazing has first been described from freshwater ecosystems, but now there is also increasing evidence from marine ecosystems.

Most zooplankton species are generalists feeding on a wide range of phytoplankton taxa. However, most of them feed only on a part of the phytoplankton size spectrum. Hetrotrophic flagellates feed primarily on picoplankton (<2 µm). Ciliates might be very specific in their feeding preferences, but in general they feed on pico- and nanoplankton (2-20 µm). Calanoid copepods and euphausids (krill) require minimal food sizes of 5-10 µm and have no well defined upper size limit, because they can bite off pieces from large food particles, especially if they are long and thin.

However, three-dimensionally large colonies with a gelatinous cover (e.g. *Phaeocystis*) are relatively well protected from grazing. Pelagic tunicates can filter even very fine particles (<1 µm), the upper size limit depends on the mouth size. Appendicularians feed primarily on pico- and nanoplankton, while the large salps can ingest the entire size range of phytoplankton. In addition to size, chemical properties (toxicity, bad taste) can be an important protection from grazing against those herbivores which capture food particles individually, e.g. copepods.

A key component of calculating grazing losses is the clearance rate (**C**; $ml.ind^{-1}.time-1$), which gives the volume of water which is “cleared” of phytoplankton cells of a given kind by one individual zooplankton per unit time, i.e. the volume of water in which the particles ingested per unit time have been suspended.

$$C = I/S \tag{9}$$

Where I is the ingestion rate (phytoplankton eaten per unit time) and S the concentration of phytoplankton. A simple selectivity index for zooplankton a given type (species and age class; j) on phytoplankton species i can be calculated by dividing the clearance rate on species i (Ci) by the clearance rate optimal food:

$$w_{ij} = C_{ij}/C_{maxj} \tag{10}$$

Calculating the total grazing losses of a phytoplankton species ($\gamma_i$) is a tremendous task: it is the grand sum of all $C_{ij}$-values multiplied by the abundance of each zooplankton category (species X age/size classes):

$$\gamma_i = \sum N_j.C_{ij} \tag{11}$$

Alternatively, an impression of zooplankton impact on phytoplankton population dynamics might be gained by manipulating zooplankton densities in appropriate containers and comparing net growth rates at different zooplankton densities or before and after zooplankton removal. However, it has to be considered that zooplankton is not only a loss factor. Zooplankton excrete nutrients and might therefore influence the reproductive rate µ as well.

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