Chapter 1

Existing work

1.1 Biological traits of phytoplankton

1.1.1 A difficult definition

Despite being the definition of the subject the first thing to be done in a thesis work, talking about plankton can be somehow vague. Take as an example the definition given in [4, chapter 1.1, pag. 2][1]:

> living seston [i.e. not-soluted matter], adapted for a life spent wholly or partly in quasi-suspension in open water, and whose powers of motility do not exceed turbulent entrainment

which necessarily includes a variety of organisms, ranging from unicellular ones to small multicellular animals (e.g. members from the phylum Cnidaria, like ctenophores) and not taking into account their biological and trophic role. The paraphyletic character of this definition is useful [2]: a passively moving being experiences a different environment from what an active swimmer does, and considering all this passive organisms together is in some ways natural. However, there is not such a sharp distinction, as one can see considering the example of a jellyfish, which is with no doubt an active swimmer, but is clearly carried from currents; a way to give sense to this definition is then to refer it to *small scale* motion, which plankton cannot oppose, whereas "actively swimming" creatures are transported by currents whose scale is bigger. A simpler way to state this is to say that plankton is passively transported by a current **??**

Moreover, such a classification lacks any information about the ecological role of plankton: indeed, *phytoplankton* ("plant-plankton" from the Greek φυτόν, "phytòn") and *zooplankton* ("animal-plankton" from ζώον, "zòon") are two categories which discriminate, respectively, from autotrophic and eterotrophic

---

[1]The etymology of the name comes from the Greek πλαγκτός, "planktòs", describing a wandering object.

[2]A grouping of species is said to be paraphiletic if it excludes at least one descendant of an ancestor [5, pag. 4]

organisms. Zooplanktonic species are capable of swimming, and are usually bigger than phytoplanktonic ones: unicellular organisms (flagellates, Foraminifera, Radiolaria, ciliates), jellyfishes, ctenophores, small crustaceans (copepods), fish larvae ("ichthyoplankton", "fish-plankton", from ἰχθύς, "ikhths") are included in this category.

1.1.2   Blooms

1.1.3   Limiting factors

The present thesis focuses on the dynamics of a population of plankton, ultimately considering the factors which influence the "birth" of a new cell or the "death" of an existing one. These are well-known from the biological research, and consist in a mix of trophic, physical and ecological aspects. However, during a bloom a rapid growth occurs, allowing to considerably simplify the process down to two factors, one taking into account the light availability

1.2 Unidimensional stochastic model

The first goal of this work has been to implement a cellular-based numerical model which could reproduce the results obtained by Huisman. In order to do that, a 1-dimensional Langevin equation has been considered to model the motion of the cells, while the mean rates of birth and death have been represented as probabilities and the production is modeled as a stochastic process.

1.2.1 Equation of motion

The following equation models the motion of the particles:

$$\partial_t x_i(t) = v_i + \eta(\zeta) \tag{1.1}$$

where x_I is the position of a given particle, v is the sinking velocity of that article and η takes into account the diffusive transport resulting from turbulence; ζ is a "rapidly varying, highly irregular function" so to match the requirements for ?? to be a Langevin equation[3]. To achieve the required conditions of ζ, the following properties should be verified:

$$\langle \zeta(t) \rangle = 0 \quad \langle \zeta(t)\zeta(t') \rangle = \delta(t - t')$$

A random number generator is used to simulate ζ, the details of which can be read in ??. This equation is integrated with a finite-differences Eulerian method:

$$x_i^{n+1} = x_i^n + v\mathrm{d}t + \sqrt{2D \cdot \mathrm{d}t}\zeta \; . \tag{1.2}$$

1.2.2 Production

To model the mean production rate of the population, they are converted in the probability for a single cell to die or reproduce. With the same meaning as in ??,

$$P_{birth} = \lambda \frac{I(z,t)}{h + I(z,t)}\mathrm{d}t \quad ; \quad P_{death} = \mu\mathrm{d}t \tag{1.3}$$

At each step, using the same random number generator as above, the probability for a cell to die is evaluated, then it can reproduce.

Birth rate

In order to evaluate the birth rate at a given depth, the following countinuum equation holds:

$$B(z,t) = \lambda \frac{I(z,t)}{h + I(z,t)} \tag{1.4}$$

where

$$I(z,t) = e^{-k_{bg}z - k_{as} \int_0^z n(z,t)}$$

---

[3]1, chapter 4.1.

Converting this equation to a discrete context, for a given particle i

$$I(i,t) = e^{-k_{bg}z_i - k_{as}\sum_{\{\hat{j}\}} 1}$$

where $\hat{j}$ represents the indexes of particles which are at a shallower depth than the one labelled with i. However, this exact method of summing the particles is computationally expensive, since one has to nest two loops over the particles: the inner one increments the value of the sum with the condition above, while the outer one assigns this value to the ith cell, resulting in a $\mathcal{O}(N^2)$ operation. A much faster way to approach this is to fill an histogram with the cells, then sum incrementally over the bins in order to get the value of the sum on a discrete set of points; now it is possible to assign the birth rates either choosing the upper (or lower) value on the grid, or interpolating with the following linear espression:

$$f(x) \simeq (x_2 - x)f(x_1) + (x - x1)f(x_2)$$

Some comparisons are shown in **??**: interpolating introduces an error well below 1 in the estimate of the birth rate, so it is reasonable to use it instead of the exact method in order to make the code faster.

1.2.3 Boundary conditions

Two kinds of boundary conditions have been considered: TODO discussione generale bound.

- *no-flux* (i.e. closed boundaries)

- *absorbing*

There are two boundaries: the "top" (0 in the simulations) of the water column and its "bottom" (z_{max} in the simulations). The top has always been considered a closed boundary, while both no-flux and absorbing boundary conditions has been used for the bottom.

No-flux conditions

In order to validate the model with respects to Huisman's results, obtained in no-flux conditions, the one-dimensional diffusion-advection equation

$$\partial_t n(x,t) = -v\partial_x n(x,t) + D\partial_x^2 n(x,t) \tag{1.5}$$

is considered, with the same notation as Huisman's model: n represents a density of particles, diffused with a coefficient D and advected towards biggest values of x (for positive values of v). An analytical solution can be derived for closed boundaries: defining the current $J := vn - D\partial_x n$, **??** becomes

$$\partial_t n + \partial_x J = 0$$

for which holds the stationary condition
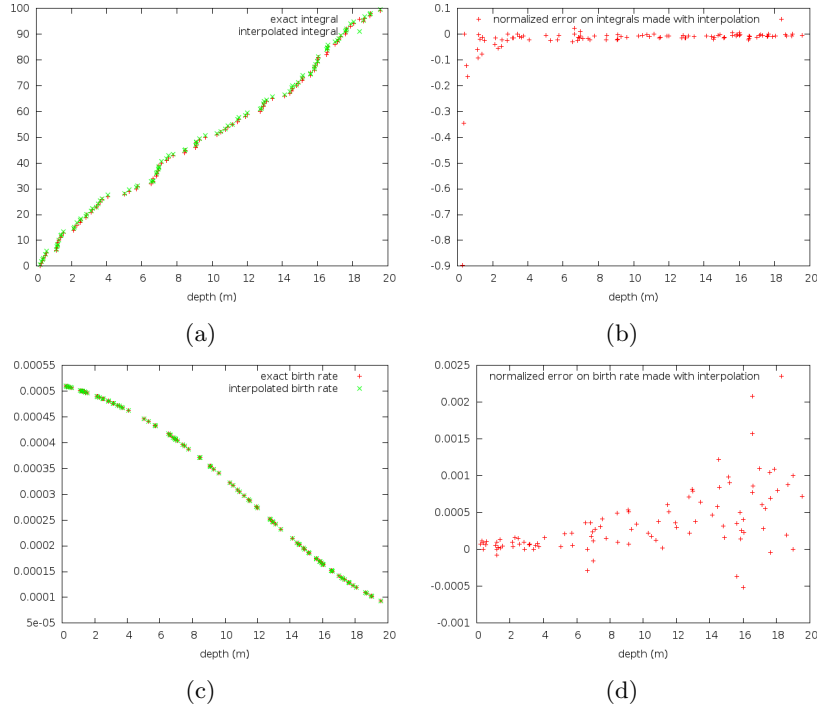
$$\partial_x J = 0$$

Figure 1.1: Comparison between the exact and interpolated methods described in **??**. (a) shows the value of integral increasing depth; (b) shows the normalized error on integrals made interpolating; (c) and (d) are the same, but considering the birth-rate.

D	v	z_0	z_{max}
$0.01 m^2 h^{-1}$	$0.01 m h^{-1}$	$0m$	$1m$

Table 1.1: Parameters used for the simulation of **??**.

Defining the auxiliary variable $\xi = \xi \partial_x n$ a solution is

$$\xi(x) = \xi_0 e^{\frac{v(x-x_0)}{D}}$$

which gives

$$n(x) = \xi_0 \frac{D}{v} e^{\frac{v(x-x_0)}{D}} + n_0 \ .$$

Imposing no-flux conditions means

$$J = v n_0 = 0 \quad \Rightarrow \quad n_0 = 0$$

so the general solution with no-flux boundaries is

$$\rho(x) = \alpha \frac{D}{v} e^{\frac{v(x-x_0)}{D}} \ . \tag{1.6}$$

where α is a constant depending on the initial conditions. A formula for this constant can be obtained using the fact that the number of particles

$$N(x) = \int_{x_0}^{x} \rho(x) \mathrm{d}x = \alpha \frac{D}{v} \left(e^{\frac{v(x-x_0)}{D}} - 1 \right)$$

which gives

$$\alpha = \frac{N(x)v}{D \left(e^{\frac{v(x-x_0)}{D}} - 1 \right)} \tag{1.7}$$

**??** with these parameters becomes

$$\alpha = \frac{1}{(e-1)n_{bin}}$$

where n_{bin} is the number of bins of the histogram, introduced because of the normalization. As can be seen in **??**, the fit is good. (how good?)

1.2.4   Reflective bottom

Imposing the boundary conditions of reflectivity on both the top and the bottom of the interval corresponds to a mixed layer as tall as the column of water, and matches the hypotheses made in [2]. Although not realistic, these conditions allow in this way the comparison with previous models, which can validate the results obtained if equivalent.

Figure 1.2: Fit of the distribution of particles averaged near equilibrium, according to **??**, with parameters in **??**. Simulation run with 10^5 particles.
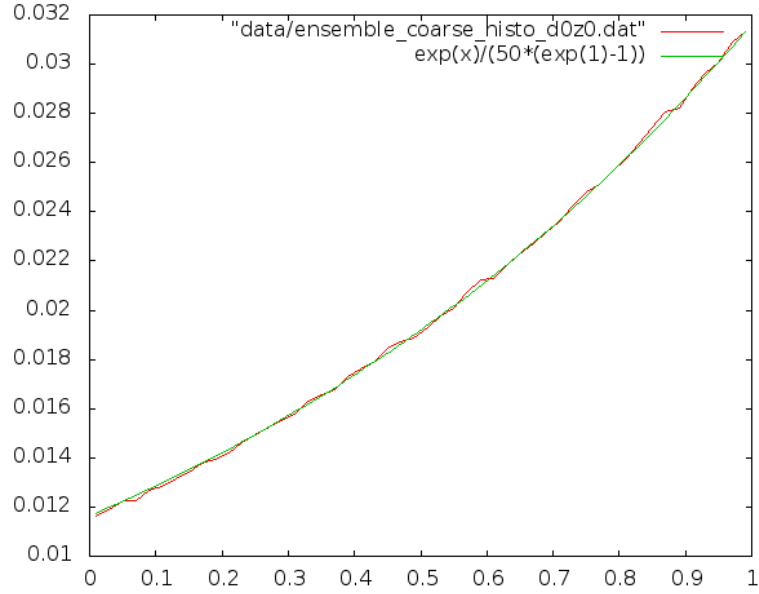
## Depth profiles

A first comparison which can be performed is qualitative and concerns the depth profile of the phytoplankton population. In **??**
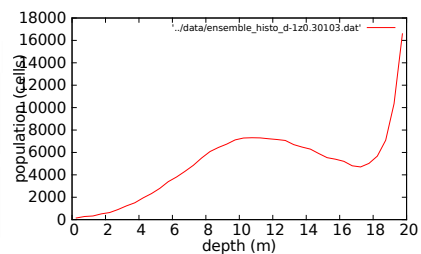
Blooming conditions

A more complete comparison between the results of the present work and those of Huisman et al. [2] can be performed evaluating the occurrence or absence of a bloom depending on the set of parameters chosen. The resulting graph by Huisman was reproduced above in **??**.
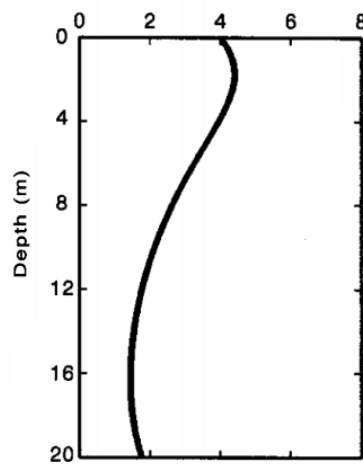A first approach to the problem is to

(a)

(b)

(c)

(d)
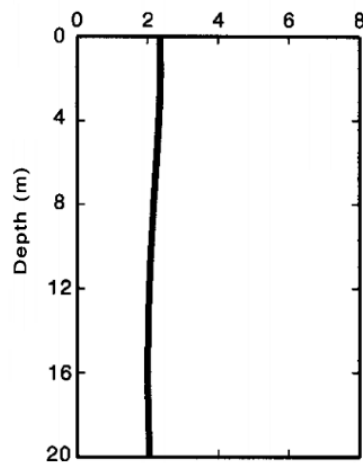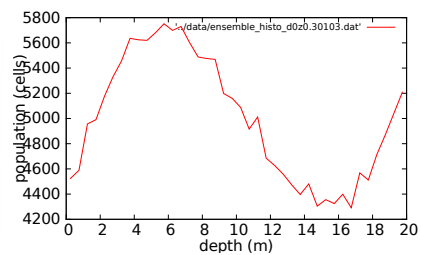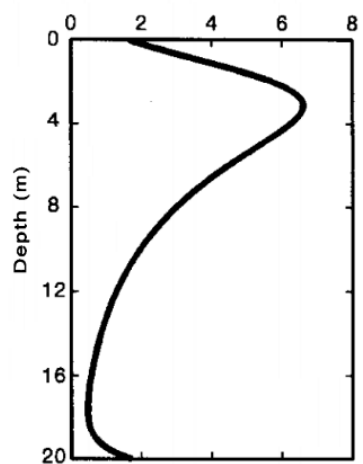
(e)

(f)

1.3 The pseudo-spectral method

1.3.1 Introduction

The Navier-Stokes equations are

$$\partial_t \vec{u} + u \cdot \vec{\nabla} \vec{u} = -\vec{\nabla} p + \nu \Delta \vec{u} + \vec{f} \tag{1.8}$$

where Δ is the Laplacian operator and the density ρ is absorbed redefining p as p/ρ and ν, the kinematic viscosity, as μ/ρ (here μ is the dynamic viscosity). f_i is a forcing term, necessary to keep the fluid moving, balancing the dissipative term.

A method to solve these equations is said to be *spectral* when working in Fourier space, so that the non-locality that would be induced by the derivatives is avoided. The present method is called *pseudo-spectral* to point out the approach used to computed the product of two Fourier-transformed elements, which would normally require a convolution: a sequence of FT (Fourier-transform) and anti-FT is used instead to compute the product in the physical space.

1.3.2 The equations

Considering **??**, some conditions are necessary to come to a solution.

Incompressibility

First of all, the fluid is assumed to be *incompressible*, a condition reflected in the flow being solenoidal ($\mathrm{div}\vec{u} = 0$), as can be seen from continuity equation: $\partial_t \rho + \vec{\nabla} \cdot (u\rho) = 0$. The velocity flow can be thus expressed with a vector potential: $\vec{u} = \mathrm{rot}\vec{b}$. The gauge $\mathrm{div}\vec{b} = 0$ is imposed. **??** becomes

$$\partial_t \vec{b} + \mathrm{rot}^{-1}(\vec{u} \cdot \vec{\nabla}\vec{u}) = \mathrm{rot}^{-1}(\vec{\nabla}p) + \nu\,\mathrm{rot}^{-1}\Delta\vec{u} + \mathrm{rot}^{-1}\vec{f} \tag{1.9}$$

Some simplifications are possible:

- The vorticity can be defined as $\vec{\omega} := \mathrm{rot}\vec{u}$. In the chosen gauge, $\omega_i = -\partial^2 b_i$ and inverting the definition of b it follows the following symbolic equivalence between operators

$$\mathrm{rot}^{-1} \doteq \Delta^{-1}\mathrm{rot}$$

  A consequence is that the term containing pressure vanishes, since the rotor of a gradient is always zero.

- Since the locality is guaranteed by the use of FT, the Laplacian operator and the rotor commute

The equations become

$$\partial_t \vec{b} + \mathrm{rot}^{-1}(\vec{u} \cdot \vec{\nabla}\vec{u}) = \nu\,\Delta\vec{b} + \vec{f_b} \tag{1.10}$$

Boundary conditions

Periodic boundary conditions allow a simple inversion of Laplacian operator. ...

1.3.3   Discretization

A second-order Runge-Kutta scheme is used, resulting in

$$\begin{cases} \dots & \dots \\ \dots & \dots \end{cases} \tag{1.11}$$

Evaluation of NLT

The non-linear term (NLT) contains a product, which in Fourier space would convert in a convolution, implying a high computational cost (N^2); instead an anti-FFT can be performed to bring the product back to physical space, where just N steps are required, so that the whole operation involves $N + N \log N$ steps.

FFT and aliasing

The reference used to discuss this is [3, chapter 12]:

1.4   Diffusivity

While in the Huisman's model, as well as in the Langevin-like model, D is a given parameter, the Navier-Stokes equations do not contain such a well-defined parameter: ν, the kinematic viscosity, is a somehow similar concept, but acts on a different scale and has a different meaning. The definition of diffusivity can be taken as following, considering an ensemble of particles diffusing in a time t:

$$< \delta r^2 >= 2Dt \tag{1.12}$$

where δr is the distance from the starting point of each particle and $< ... >$ means averaging over an ensemble. Considering this, is simple to print the values of $< \delta r^2 >$ and t during a run of the program which solves the Navier-Stokes equations. This allows one to fit the points and find the effective D. However, the resulting curve is not a perfect line, as the definition would require: initially, the path travelled by a particle is balistic, following the underlying flow; after a while, the autocorrelation fades and the diffusive behaviour is asymptotically met.

1.5   Testing

In order to check the consistence of the numerical model with expected results, some tests are performed.

1.5.1   Sinking velocity

The Lagrangian code is modified in order to nullify the effects of advective flow and reactions of the cells. Since $dt = 5 \cdot 10^{-3}$ and $v = 1$, after 1000 iterations the particles are expected to have travelled 5.

1.5.2   Growth reaction

Modifying the code to eliminate transport both by advective flow and sinking velocity, an exponential growth should be seen if $k_a s$ (the auto-shading parameter) is set to zero. The modeling equation is (see **??**)

$$\partial_t n(t, z) = \left(\frac{\lambda}{1 + \frac{h}{I_0} e^{k_{bg} z}} - \mu \right) n(t, z) = f(z) n(t, z)$$

so the resulting numerical density at a depth z is

$$n(t, z) = n(0, z) e^{f(z) t}.$$

1.6   Numerical methods

1.6.1   Random number generator

By G. Boffetta. rann, gaus

1.7   Notes

1.7.1   Articles

Huisman 2002 1D differential equation includes light attenuation, constant loss, sinking velocity and diffusion; no-flux conditions at boundaries. Phase transition: "water-column depth determines the population size of phytoplankton in shallow systems, whereas turbulence determines the population size of phytoplankton in deep systems" (figure 3). Highest sinking volocities recorded are similar to the limit predicted.

Taylor 2011 Sverdrup: critical depth hypothesis assumes strong enough turbulence. Hypothesis: "a bloom can de velop when the atmospheric cooling shuts off". 1D equation provides two timescales: mixing (τ_M) and growth-loss (τ_P). When τ_M is much smaller, Sverdrup's theory is matched. When τ_M is much smaller in the upper layer, but not in the lower one (weakly mixed), "there is a critical turbulence level [...] below which growth [...] can occur regardless of the mixing-layer depth", that is phytoplankton is fluxed out of the euphotic layer at a faster pace than growth can occur. The maximum achieved growth rate is independent of the initial conditions, i.e. "depends exclusively on measurable physical and biological parameters". The authors describe their simulation, providing useful suggestions on this topic. Surface heat flux is a good predictor of blooms, as shown in graphs comparing flux and chlorophyll during time. But this is valid only when "when the surface heat flux varies more slowly than the biological response".

Visser2015 Review of artificial mixing results in lakes: it is remarked that there is some consistency with results, namely diatoms' growth is promoted to the detriment of cyanobacteria's, since the latter possess buoyancy regulation mechanisms.

Lindemann2017 A theoretical model similar to Huisman's one is used to make basic predictions, further explored with a simulation, which is carried on in conditions similar to the ones found in oceans: a 2D vortex cell (descending in its center) is resolved looking for bloom conditions.

Shigesada1981 A mathematical study of self-shading in the dynamics of algal blooms is performed. $I(z,t) = I_0(t)\exp\left[-\int_0^z (k_0 + mp)\mathrm{d}z\right]$. Profiles of concentration are reproduced in graphs and resemble the ones observed in sea.

Bibliography

[1] Crispin W. Gardiner. *Handbook of Stochastic Methods*. 2nd ed. Springer, 1985.

[2] Jef Huisman et al. "How do sinking phytoplankton species manage to persist?" In: *The American Naturalist* 159.3 (2002), pp. 245–254.

[3] William H. Press et al. *Numerical recipes in Fortran 77: The Art of Scientific Computing*. 2nd ed. Cambridge University Press, 1992.

[4] C.S. Reynolds. *The Ecology of Phytoplankton*. Ecology, Biodiversity and Conservation. Cambridge University Press, 2006. ISBN: 9781139454896. URL: https://books.google.it/books?id=gDz5jGsPWZYC.

[5] E.O. Wiley and D. Siegel-Causey. *The Compleat Cladist: A Primer of Phylogenetic Procedures*. 1991. URL: http://www.amnh.org/learn/pd/fish_2/pdf/compleat_cladist.pdf.