Centre National de la Recherche Scientifique

Laboratoire d'Océanographie et du Climat : Expérimentaions et Approches Numériques

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Object : Report on PhD thesis of Francesco Santamaria

The PhD project of Francesco Santamaria studies two key characteristics of phytoplankton dynamics: the interaction between their motility and the turbulent environment they live in; and the relation between individual and macroscopic (multi-species population level) growth rates. These two themes indeed correspond to two main aspects of planktonic temporal evolution, i.e., their spatial motion, and their population dynamics.

I enjoyed very much reading this manuscript, which I find clear, interesting, and polished. The main results of the two themes (a mechanistic understanding of one aspect of planktonic layering, and a quantitative model of multi-population growth) are important, both in terms of mathematical modelling and in terms of their biological value.
I also found the two case studies well chosen, because they are examples of important biological problems that require advanced knowledge of turbulence and population dynamics theory, and therefore that are impervious to the large majority of biologists. Indeed, this thesis work is developed with a remarkable interdisciplinary consciousness, always keeping the biological problem in focus, while using at the same time advanced numerical and analytical tools from turbulence and dynamical system theory. The equations are discussed in terms of their biological meaning and the values or distributions of the parameters is always biologically meaningful, and connected to previous disciplinary studies. This interdisciplinarity is reflected in the structure of the thesis, which contains two introductory chapters, where the basics of the biology behind the problems, and the main theoretical concepts of turbulence (i.e., the two disciplinary ingredients), are described in a very clear and pedagogical way. These chapters serve as an excellent link for connecting this thesis work to a public of both theoretical physicists and biologists respectively. They also show the maturity of F. Santamaria in dealing with the complex and multifaceted subject of his thesis.

Chapter 1 introduces the concepts related to planktonic organisms, reviewing their definition and properties. I appreciate the fact that it is written with a style adapted to a public of theoretical physicists. Finding a balance between clarity and simplification is quite a challenge in every interdisciplinary introduction. Chapter 1 is remarkably successful in this regard, although as a minor remark I notice that it tends sometimes to oversimplify some definitions, for instance for the term "protist" (see below). In some cases, more details could have been added (see below, for the absence of mixotrophs). General information, like the role of phytoplankton on the biogeochemical cycles, are always correct, but adding a few more references would have been useful.

I personally see Chapter 2 as possibly addressing on the other hand a reader with a background in biology. It starts by introducing all the main concepts from turbulence theory that will be used in the result chapters, as well as the mathematical description of swimming cells and population growth. As

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Chapter 1, this chapter is also very clear and pedagogical. What I miss, either here or in Chapter 1, is maybe a more detailed description of a model organism for swimming plankton (e.g. Chlamydomonas). Some biological details could have strengthen even further the link between the theoretical results and the real system (for instance for a possible experimental application), and could have served to elucidate the physiological origin of some mathematical terms, like for instance rotational diffusion or gyrotaxis itself.

Chapter 3 is the first result chapter, and discusses an important phenomenon of phytoplankton patchiness: the formation of thin layers. One of the mechanisms leading to layering is the interaction of plankton motility with water turbulence. This subject is particularly difficult to address, because it requires advanced knowledge of both plankton dynamics and water turbulence. The skill of F. Santamaria in dealing with the literature first, and then with the equations (from both an analytical and a numerical viewpoint), is high. The reader is guided through the problem under subsequent level of complexity. The results allow to mechanistically understand how ephemeral layers are generated by coupling different aspects of cellular motility and fluid dynamics. The only criticism that I have on this chapter is that more figures could have helped a reader which is not familiar with Kolmogorov flow to better follow the derivations, and better appreciate the results.

Chapter 4 is the second result chapter and deals with the other aspect of planktonic temporal evolution: their population dynamics. This chapter focuses on an approximation that is usually assumed, that is, to model the growth of an heterogeneous population as the growth of a single species (single sized) one. It is found however that indeed important differences arise. Remarkably, a novel model of multi-population growth is obtained, and linked to mono-specific populations by allometric relations. I found this result far reaching, because it suggests an equation which could improve the representation of plankton in biophysical circulation models, without the need of including a continuous spectrum of species, but parameterizing them in terms of Santamaria's equation.

In conclusion, I am quite impressed by the variety of concepts and themes addressed by this thesis, by the quality of its presentation, and by the excellent interdisciplinary maturity that F. Santamaria has acquired during his PhD. I find this type of quantitative interdisciplinary work on plankton dynamics extremely useful, because it considers aspects important in plankton biology, but that biologists alone could not solve without the help of theoretical physicists. I also remark the need in oceanography and climate science of young scientists with this type of background.

Minor comments:

p 2: check the spelling for the Greek word "planktos". Sigma is not the form should be as last letter; the accent is missing
p 5: I think there is no a unique definition for "protist". Still protists are not only single-celled and not only algae. Please reformulate.
P 6: References are missing on the role of phytoplankton.
P 8: "sink to the ocean [..] floor". Better: "sink to the ocean interior" (oxygen is not only depleted at the bottom of the ocean).
p. 8-9: "The reduction of vertical mixing.." please add a reference.
p. 9: at the smallest scale: there is no a "smallest" scale. I would replace with "At the cellular scale".
p. 10: "Thin layers can often contain.." please add a reference.
p. 23 choiche -> choice
p. 26 which dissipate into -> which cascade into (for consistency with the definition of intertial range given above)
p. 33: "There are many.. quite appropriate." Please reformulate. To me is not clear why it is quite appropriate a simplification of studying one type of cells (hence choosing one specific feature) if there are others cells without that feature but same behavior. One could argue that the origin of such behavior is not in the feature rapresented by the chosen type of cells, if organisms without that feature have the same behavior.
p. 34 swimmin -> swimming

Eq. 2.23: why gravity has been neglected?

p. 39: What do you mean by "field population"? What about other forms of mortality besides grazing? (like viral infection)

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