Complex Phytoplankton Dynamics

The Mathematical Perspective

Arjen Doelman & Antonios Zagaris

This annotated bibliography is split into four parts. The first one maps out briefly some key work on the dynamics of NPZ systems. These are spatially non-extended models of food webs, the constituents of which belong to one of three trophic levels: nutrients (N), phytoplankton (P) or zooplankton (Z). Here, Z consumes P which, in turn, consumes N; concurrently, P and Z release N back to the environment through their death and subsequent decay. Part II focuses on spatially extended models describing phytoplankton and a single nutrient: light. Phytoplankton uses light to grow through photosynthesis, whereas the light intensity is attenuated due to absorption by planktonic and non-planktonic components (i.e., by turbid water). This description results in scalar, nonlinear, nonlocal, non-autonomous PDE models for the phytoplankton concentration. These two themes are partially combined in Part III, where the spatial dynamics of light–nutrient–phytoplankton interactions are considered. Here, the two complementary (non-substitutable) nutrients are light—which was regarded as the sole nutrient in Part II—and an additional, chemical nutrient (typically nitrogen or phosphorus). This leads to systems of PDEs for the phytoplankton and chemical nutrient concentrations of the same type as in Part II: nonlinear, nonlocal, and non-autonomous. (The combination of the two themes is only partial because although the trophic level below phytoplankton—namely chemical nutrient—is modeled explicitly, the level above it—zooplankton—is not.) The setting for all of the work covered here is either zero-dimensional (for Part I)—space is absent—or one-dimensional (for Parts II–III)—with that dimension corresponding to depth. Mathematically oriented studies of oceanic phytoplankton growth which incorporate horizontal spatial effects simply do not exist. To compensate for this lack of two-dimensional models, we briefly discuss phytoplankton blooms in estuaries, where horizontal directions are explicitly accounted for; these are considered in Part IV.

Part I — Spatially non-extended NPZ models

NPZ models have become a staple of computational oceanography, as they provide a concise way to study theoretically how nutrient levels and zooplankton grazing affect phytoplankton growth. As briefly mentioned above, NPZ models are variations of the theme 'zooplankton grazes phytoplankton which, in turn, grows on nutrient.' The simplest such models only have three compartments, each of which models an entire trophic level (N, P or Z). More elaborate models subdivide one or both of the planktonic compartments into parts, to account for physiological variations within that group, or limit phytoplankton growth by two or more nutrients. Seeing as the relevant bibliography is rather extensive and our main interest is in spatially extended models, we only summarize

below a small number of key publications with an emphasis on articles pointing to the existence of complex dynamic phenomena in models of this type.

- **A Hastings & T Powell (1991),** Chaos in a three-species food chain, *Ecology* **72**(3) 896–903.

This is the first paper that identified the presence of chaotic dynamics in three-tier predator–prey systems such as (but not limited to) NPZ models. The authors formulate the model and proceed to identify a parameter controlling the efficiency with which the middle trophic level assimilates nutrients from the lowest level. As they mention, this parameter was shown in the past to strongly influence the stability of predator–prey systems. Choosing, also, parameter values for which the two predator–prey subsystems—lower and middle levels plus middle and upper levels—exhibit oscillatory behavior, they show numerically that the full system can proceed from a stable steady state to oscillations and, eventually, to chaos. The authors conclude by noting the existence of a period doubling sequence in the associated bifurcation diagram—which they compute—and by a measured discussion of the ecological implications of their findings.

- **J Huisman & FJ Weissing (1999),** Biodiversity of plankton by species oscillations and chaos, *Nature* **402** 407–410.

This paper focuses on the 'paradox of the plankton': the principle of competitive exclusion predicts that the number of coexisting species cannot exceed the number of limiting resources. This is clearly not the case for phytoplankton: dozens of phytoplankton species persist on but a small number of resources (light, nitrogen, phosphorus, silicon, iron, inorganic carbon). From the mathematical point of view, this 'paradox' is not all that intriguing, since the principle of competitive exclusion assumes that a system is 'in equilibrium' (i.e., the system is either at/near a critical point or tracking such a point). If this equilibrium hypothesis is violated—e.g., if the system evolves in a periodic manner or behaves chaotically/erratically—there's no reason to expect this principle to hold, mathematically speaking. The present paper essentially confirms this intuition. The authors formulate a relatively straightforward—but of course nonlinear—model for the interactions between n species living on k resources. (In essence, this is a NP model, since zooplankton Z is not modeled explicitly.) Simulations reveal the dynamics of this type of model to typically exhibit 'non-equilibrium behavior' for $n, k > 2$. More specifically, an example of 6 species living on 3 resources and exhibiting 'stable (periodic) dynamics' is presented—a clear violation of the exclusion principle. Two additional systems—one with $(n, k) = (5, 5)$ and another one with $(n, k) = (12, 6)$—exhibiting chaotic dynamics are studied in some detail.

- **PJS Franks (2002),** NPZ Models of plankton dynamics: Their construction, coupling to physics, and application, *J. Oceanogr.* **58** 379–387.

A short and concise overview of three-compartment NPZ models. Starting form this most basic NPZ model type, the author first reviews some of the most common functional responses to light, nutrient and zooplankton grazing present in the literature review. The emphasis here is on how dynamics are affected by saturated vs. unsaturated responses. He then presents a similar summary of results pertaining to different ways of encapsulating zooplankton losses—especially due to predation from higher trophic levels (closure terms)—and how this affects the presence of oscillatory and chaotic dynamics. Franks subsequently reviews the manners in which NPZ dynamics

have been coupled to circulation phenomena. He elaborates, in particular, on spatially extended NPZ models incorporating shoaling/deepening of the mixed layer in an ad-hoc, intuitive manner but also adds a (now somewhat dated) list of significantly more involved geophysical modules fed forward to NPZ models. Finally, the author discusses in detail how NPZ models have been employed by computational oceanographers, as well as how they should be employed. In doing so, he touches very briefly on questions of epistemological origin, the answers to which, nevertheless, have a resonant intrinsic value for scientific practitioners ('what is a model?' / 'how is a model tested?' / 'when should a model be rejected?' et cetera).

● **E Benincà, J Huisman, R Heerkloss, KD Jöhnk, P Branco, EH van Nes, M Scheffer, SP Ellner (2008)**, Chaos in a long-term experiment with a plankton community, *Nature* **451** 822–825.

In a sense, this paper can be seen as a companion paper to Huisman & Weissing (1999). Mathematical models generate periodic and chaotic behavior, and thus can go beyond the principle of competitive exclusion thereby 'solving' the 'paradox of the plankton'. In this very nice paper, the authors demonstrate chaos experimentally through a long-term ecological experiment involving a complex food web. The food web in question consists of bacteria, several phytoplankton species, herbivorous and predatory zooplankton species, and detritivores; it is cultured in a laboratory, kept under constant external conditions, and has been sampled twice a week for over 6 years. The quantities measured have been found to fluctuate over several orders of magnitude, despite the constancy of the envirnoment. Based on these observations, the authors compute the associated Lyapunov exponents and indeed find that these can be positive—in which case the system is chaotic. Thus, this paper presents convincing evidence that species interactions in food webs are inherently complex. Based on the estimated Lyapunov exponents, in fact, the authors conclude a predictive time horizon for this plankton community of $15 - 30$ days—only slightly longer than that for the weather forecast.

● **PJS Franks (2009)**, Planktonic ecosystem models: perplexing parameterizations and a failure to fail, *J. Plankton Res.* **31**(11) 1299–1306.

An enjoyable and enlightening discussion of certain key issues pertaining to the formulation and use of NPZ models. Franks focuses on two such issues—model parameterization and model testing—and discusses them in a manner that strongly echoes JR Platt's (now classic) 'strong inference' idea (and indeed, Platt's work is cited in the paper). As such, this paper acts as an in-depth continuation of the epistemological—yet highly practical—issues first raised in Franks (2002). Regarding model parameterization, Franks raises two sub-issues. The first one concerns erroneous parameterizing practices such as using out-of-date experimental data, copying uncritically parameter values from prior work, and even choosing parameter values to render the results more realistic. The second one concerns modeling nutrient uptake of planktonic communities made up of diverse species through Michaelis–Menten kinetics. As Franks explains, although this type of kinetics often (but not always) models nutrient uptake by a single individual adequately well, there is evidence that aggregation over species with allometric functional responses may lead to an entirely different overall functional response. (The reader can also look up PJS Franks, JS Wroblewski & GR Flierl (1986), Behavior of a simple plankton model with food-level acclimation by herbivores, *Marine Biol.* **91** 121–129 to see how non-saturated functional responses can lead to

the suppression of sustained oscillations.) The second large issue Franks takes on is the way in which plankton models are used. He discerns, in particular, a tendency to use plankton models as 'toasters': if results don't match expectations/data, one adjusts the parameter values until the two match. He then proceeds to advocate setting up comparative studies designed to test plankton models on their ability to answer a specific question, with the explicit aim of rejecting most of them, and outlines how model predictions can interact with field data to positively increase our body of knowledge.

Part II — Modeling light-limitation

Models in this category incorporate (vertical) spatial effects in the form of advection and diffusion. As mentioned earlier, phytoplankton growth is assumed to be solely limited by the light available for photosynthesis. Since light pours into the water column from above and is absorbed and scattered with depth, phytoplankton growth is maximum at the surface, so that one of the observed patterns is surface layers (SLs). Nevertheless, most phytoplankton species are denser than water, so that they tend to sink to where light is scarce. This leads to another type of planktonic pattern called a deep chlorophyll maximum (DCM): a localized phytoplankton concentration interior to the oceanic column and extending over a region much smaller than the depth of that column. The width of a DCM is strongly controlled by diffusion, which tends to disperse localized phytoplankton concentrations. If the sinking velocity is high enough and light conditions are favorable, these DCMs can be driven all the way to the bottom and become benthic layers (BLs). (This is only possible in shallow waters, naturally.) From a modeling perspective, systems of this type correspond to nonlinear, nonlocal PDEs of reaction–advection–diffusion type.

• **GA Riley, H Stommel & DF Bumpus (1949)**, Quantitative ecology of the plankton of the western North Atlantic, *Bull. Bingham Oceanogr. Coll.* **XII**(3) 1–169.

The first article to deal with light-limitation. The authors find it sufficient to focus on the stationary spatial profiles admitted by the model for their work, which was limited to a time of the year where both environmental conditions and plankton blooms appear to be stationary. Generally speaking, nevertheless, not even these profiles can be derived analytically, because the associated steady state problem is a second order, nonlinear and non-autonomous ODE. To overcome this obstacle, Riley et al. simplified the original model they developed by modeling the zeroth order (growth) term as a simple step function of depth. (In its most general formulation, this term contains a component decreasing exponentially with depth—and modeling light attenuation by non-planktonic components—as well as a planktonic component—modeling self-shading.) The jump discontinuity for the growth term occurs at a certain depth which is assumed known; local growth conditions are favorable above it (positive growth term) and prohibitive below it (negative growth term). In this simplified form, the problem is linear and can be solved analytically; this enables the authors to derive a necessary and sufficient condition for the existence of nonzero (nontrivial), positive solutions. In particular, for this to happen, the diffusivity needs to be above a critical value scaling with the square of the sinking velocity and the inverse of the maximum growth rate. These theoretical results are then combined with field data to identify the predominant (controlling) processes in a variety of ecological settings. The main limitation of this

otherwise pioneering and ingenuous—in its simplicity—approach is that modeling growth conditions in an on/off manner is performed at the cost of abolishing control over the total biomass that can be supported by the water column. Indeed, the only term limiting the total biomass is the self-shading component (i.e., the nonlinearity), which has been discarded in this simplified formulation.

• **JH Steele & CS Yentsch (1960)**, The vertical distribution of chlorophyll, *J. Mar. Biol. Ass. U.K.* **39** 217–226.

Steele & Yentsch start from the observation that the model of Riley et al. (1949) only allows phytoplankton blooms above or at the compensation depth (i.e., the depth where the photosynthetic growth term balances (equals) the loss rate). As they remark, although this conclusion is supported by field data in a multitude of cases, there are equally many data indicating that this is not a universal truth. To explain the existence of maxima below that depth, they modify the model in question by allowing for a settling velocity which decreases with depth; this, as they show, is sufficient to generate chlorophyll maxima of that sort. They then proceed to test their hypothesis—namely, that changes in the water density with increasing depth account for maxima of that sort—by comparing their theoretical results to actual field data. (What is commendable here is that their work is driven by this discrepancy between prior theoretical results and field data: the field data comes first and the theory follows. In other words, they formulate the hypothesis to interpret existing field data rather than selectively look for field data that supports their hypothesis.) Although one set of data yields realistic values for the rate of change of the settling velocity with depth, another one shows that this hypothesis has to be abandoned as a universal explanation for the type of phenomena they are interested in. Accordingly, the authors postulate another hypothesis: that the change in sinking velocity needed to interpret the field data is not solely due to changes in water density but also to a tendency of plankton cells to increase their buoyancy as they sink to deeper, darker, nutrient-richer waters. (Note that, broadly speaking, this hypothesis might reflect the idea of actively swimming cells, cf. the work of Klausmeier & Litchman (2001).) This hypothesis is partially justified by additional experiments suggested by the hypothesis and conducted by the authors.

• **N Shigesada & A Okubo (1981)**, Analysis of the self-shading effect on algal vertical distribution in natural waters, *J. Math. Biol.* **12** 311–326.

Shigesada & Okubo's paper is the first systematic, analytical study of the effect that self-shading has on phytoplankton growth in a water column of infinite depth; as such, it applies to perfectly clear (transparent) water columns. Equally importantly, it is one of the first studies showcasing the extent to which dynamical systems considerations can reinforce and extend ecological intuition. Exploiting strongly the absence of light intensity attenuation by turbid water, the authors transform the reaction–advection–diffusion model for the local, instantaneous phytoplankton concentration into a model of the same type for the local (i.e., down to an arbitrary depth), instantaneous biomass. Through a transparent phase plane analysis, they identify a unique, positive steady state solution in a parameter range matching that derived by Riley et al. (1949); they exclude the existence of such states for parameter values falling outside that range. Additionally, they prove that these states are globally stable (each in its parameter range), in the sense that any positive initial condition converges to them in forward time, and examine the associated profiles of phytoplankton concentration—in the absence of nutrient limitation, as is the situation here,

the depth at which these profiles peak is essentially controlled by the settling velocity of phytoplankton. (In light of this, the parameter range where blooms cannot occur may be understood as corresponding to phytoplankton with a large settling velocity.) As expected, the most severe limitation of this otherwise paradigmatically clear work is that it does not generalize to turbid waters.

• **H Ishii & I Takagi (1982)**, Global stability of stationary solutions to a nonlinear diffusion equation in phytoplankton dynamics, *J. Math. Biol.* **16** 1–24.

A landmark article for this type of problem, as the first to generalize Shigesada & Okubo's work to turbid water columns of infinite depth. The main result proven here is that the attractor for a generic, single-species model of light-limited growth is stationary: dynamic phenomena are absent in the long term. As such, any phenomena of this type present in field data can only be explained as induced by additional factors not represented in this type of models. In particular, Ishii & Takagi derive a criterion which distinguishes between the following two scenarios, which are the only possible: (a) all initial phytoplankton concentrations die out (i.e., the trivial steady state is globally stable); and (b) initial phytoplankton concentrations limit to the same stationary and positive steady state (which is a fortiori globally stable). It is additionally shown that this nontrivial solution is globally stable over the entire parameter range it exists. In other words, the trivial steady state is globally stable only when it is the only ecologically relevant (here: non-negative) steady state; as soon as a (unique) positive, nontrivial solution is created, it replaces the zero steady state as the global attractor. Finally, the authors relate their more general results to those derived by Shigesada & Okubo.

• **U Ebert, M Arrayás, N Temme, B Sommeijer & J Huisman (2001)**, Critical conditions for phytoplankton blooms, *Bull. Math. Biol.* **63** 1095–1124.
• **J Huisman, M Arrayas, U Ebert & B Sommeijer (2002)**, How Do Sinking Phytoplankton Species Manage to Persist?, *The American Naturalist* **159**(3) 245–254.

These papers can be seen as companion papers, written for somewhat different communities. The first one has a more mathematical/technical nature, while the second paper interprets the behavior of the model studied in the first one so as to make it accessible to an ecological audience. Ebert et al. (2001) is devoted to an examination of the conditions under which there exists a maximal depth, within a water column, that can support a phytoplankton bloom. By characterizing this maximal depth as the depth which can support an infinitesimal plankton population, the authors succeed in mapping the original problem to a linear problem for perfectly transparent plankton: the nonlocal term is absent. (Compare that to Shigesada & Okubo, who worked with perfectly clear water instead.) Additionally, certain asymptotic regimes—most notably, those of vanishing and of unbounded diffusivity—are examined. A downside of this paper is that the authors have chosen to model response to light intensity by a power law (and hence the response does not saturate). Although power laws often appear in empirical models, this modeling choice in this particular case only serves the role of allowing an analytical treatment of the problem. Note, also, that no mention is made of whether the nontrivial steady state is stable, when it exists. The second paper concentrates on a very natural issue. Since most phytoplankton species are heavier than water, one expects plankton individuals to sink. However, they require light to photosynthesize, which is not available at large depths. The authors simulate numerically a model of the type studied in the first paper and for intermediate levels of turbulent diffusion. They show that a

phytoplankton population can outgrow both mixing and sinking rates and form a stable attractor of DCM-type. At the depth where the DCM occurs, the (reproducing) population can maintain its position as a whole, even though its individuals tend to sink.

• **S Ghosal & S Mandre (2003)**, A simple model illustrating the role of turbulence on phytoplankton blooms, *J. Math. Biol.* **46** 333–346.

This is a variant of the on/off model introduced by Riley et al. (1949). Instead of modeling growth conditions as a step function of depth, the authors model them as a step function of the light intensity: the growth rate is constant and exceeds the loss rate for light intensity values above a certain critical value (assumed known) and identically zero for light intensity values below it. The light intensity itself, on the other hand, is attenuated because of absorption by both planktonic and non-planctonic components—i.e., as in the most general case. Naturally, this model reduces to that of Riley et al. (1949), but with a crucial difference: whereas the critical, cut-off depth had to be filled in by hand in Riley et al. (1949)—a process eradicating all nonlinear information and, together with it, any constraints on the total amount of biomass in a bloom—it is one of the unknowns in this work. This allows Ghosal & Mandre to retain nonlinear information—self-shading, in particular—and thus build constructively on the work of Riley et al. (1949): after recovering the same criterion for the existence of nontrivial steady states found in that older work, they derive an algebraic condition yielding the total amount of biomass.

• **T Kolokolnikov, C Ou & Y Yuan (2009)**, Profiles of self-shading, sinking phytoplankton with finite depth, *J. Math. Biol.* **59** 105–122.

This paper deals with the precise same problem described in Shigesada & Okubo (1981), albeit in a finite-depth setting. The authors show the analysis of Shigesada & Okubo (1981) to extend, mutatis mutandis, to this case as well. The major modification concerns settling planktonic velocities above the critical value derived by Shigesada & Okubo (1981). Whereas no blooms could occur for such velocities in an infinite water column, the authors show that this is possible in a water column of finite depth: the associated profile is that of a BL. Finally, the authors obtain partial results on the existence of profiles of mixed (DCM–BL) type: the phytoplankton concentration peaks both in the interior of the water column and at its bottom.

• **S-B Hsu & Y Lou (2010)**, Single phytoplankton species growth with light and advection in a water column, *SIAM J. Appl. Math.* **70**(8) 2942–2974.

The paper offers a comprehensive treatment of the full light-limited problem—i.e., with self-shading and attenuation due to non-planktonic components included—in a water column of finite depth and for a rather generic growth term expressed as a function of the light intensity. First, the authors obtain a sharp bound on the maximum loss rate that can accommodate a nontrivial (positive) steady state; in essence, this loss rate is shown to yield an infinitesimal biomass, reflecting similar considerations in Ebert et al. (2001). Second, they show that this loss rate decreases with sinking velocity. An outcome of this result concerns the asymptotic regimes of large floating and sinking velocities: in the former case, a bloom occurs if growth exceeds losses at the top of the column; in the latter case, the same conditions is derived but it concerns the bottom of the column. The authors obtain additional information for intermediate velocity values—in

particular, they characterize the maximum loss rate able to support a positive steady state as a function of that velocity—and for the existence of a critical depth below which a bloom cannot occur (cf. Ebert et al. (2001) again). The authors offer no discussion of the stability type of the nontrivial steady state, when that exists, since global stability of that state was established in Ishii & Takagi (1982). As with most other articles by this team, the main issue here is the article's limited readability by non-experts in PDE theory in general and, in particular, by ecologists.

• **Y Du & S-B Hsu (2010)**, On a nonlocal reaction–diffusion problem arising from the modeling of phytoplankton growth, *SIAM J. Math. Anal.* **42**(3) 1305–1333.
• **Y Du & S-B Mei (2011)**, On a nonlocal reaction–diffusion–advection equation modelling phytoplankton dynamics, *Nonlinearity* **24** 319–349.

These papers are, essentially, a complete reworking of the results in Ishii & Takagi (1982) in a finite-depth setting. As such, they unsurprisingly arrive at similar results. The most interesting part of the first paper concerns a model with two species competing for light. Apart from the trivial (zero) steady state and the two semi-trivial steady states (where one species vanishes), there exists the possibility of stationary coexistence (both species assume nonzero, steady state values). The authors focus on this last type of solutions and establish the existence of a branch of such nontrivial equilibria. This branch bifurcates from one of the semi-trivial steady states and proceeds to collide with the other, at which point it is annihilated. Additionally, although it is not shown that this nontrivial steady state corresponding to coexistence attracts (nearby) initial conditions, Du & Hsu establish that none of the two planktonic concentrations vanishes in the parameter range where this state exists. The second paper extends these results in the case where the diffusion and advection coefficients are depth-dependent. Additionally, the authors analyze the asymptotic regimes of small and large diffusion; they find that the total biomass is larger in the latter case, if the water is turbid (and the remaining environmental conditions are identical). No difference in the biomass is found for clear waters. These results apparently validate our ecological intuition: for large diffusion, phytoplankton is spread rather uniformly throughout the water column; for small diffusion, instead, it is concentrated at the bottom of that column. When the water is turbid, then, plankton is exposed to more light overall in the former (rather than in the latter) case. Hence, more of it is needed to arrest further growth through self-shading and achieve a stationary profile. When the waters are clear, on the other hand, phytoplankton is exposed to the same overall amount of light, irrespectively of where it is located in the water column; hence, no difference may be expected in the biomass.

Part III — Modeling co-limitation by light and nutrient

Models in this category also incorporate advection and diffusion, just like the models considered in Part II. They differ from those simpler models in that they explicitly account for one or more nutrient concentrations which, together with light, limit phytoplankton growth. As such, they are represented by coupled, nonlinear, nonlocal, PDEs of reaction–advection–diffusion type. The main planktonic patterns here are also DCMs. Whereas, in Part II, DCMs represented a balance between light (pouring in from above) and the tendency of phytoplankton to sink, here they are evocative of a balance between light and nutrient, which enter the water column from opposite ends.

• **C Klausmeier & E Litchman (2001)**, Algal games: The vertical distribution of phytoplankton in poorly mixed water columns, *Limnol. Oceanogr.* **46**(8) 1998–2007.

An ingenuous and ambitious piece of work aiming at deriving conditions which fully predict the location of a (stationary) DCM in a water column, as well as the amount of biomass it contains. The authors formulate a model of the sort described above, with no nutrient recycling and with the plankton assumed to have the ability to actively swim in the vertical direction where growth conditions are better. Their basic observation is that, in such a model, a DCM forms at a depth where it is simultaneously co-limited by light and nutrient: at that depth, growth conditions are optimal and motile phytoplankton would move neither up nor down. To exploit this principle, they subsequently make the simplifying assumption that a DCM is a $\delta-$distribution based at a well-defined depth and holding an (unknown) biomass. Under this assumption, the depth profiles of the light intensity and of the nutrient concentration are explicitly computable and the derivations become a matter of calculus. The authors also provide a somewhat cursory argument to show that these stationary DCMs are stable.

• **Y Du & S-B Hsu (2008)**, Concentration phenomena in a nonlocal quasi-linear problem modelling phytoplankton I: Existence, *SIAM J. Math. Anal.* **40**(4) 1419–1440.
• **Y Du & S-B Hsu (2008)**, Concentration phenomena in a nonlocal quasi-linear problem modelling phytoplankton I: Limiting profile, *SIAM J. Math. Anal.* **40**(4) 1441–1470.

This series of papers identifies rigorously the steady states of the model used by Klausmeier & Litchman to predict DCM location and associated biomass (or, rather, of a slightly modified version of that model). As such, it concerns itself with the stationary parts of the attractor. In the first paper, the authors establish that only the trivial steady state exists for phytoplankton loss rates higher than a maximum value; they also prove the existence of at least one nontrivial steady state for loss rates lower than a minimum value. No information is available for loss rates in between these critical values, but the gap between these is shown to vanish as the planktonic swimming velocity approaches infinity. Additionally, the authors validate and somewhat extend the game-theoretical model developed by Klausmeier & Litchman, characterizing the position and biomass of the stationary DCM in terms of the nutrient concentration at the sediment. The second paper mostly concerns the limiting DCM profile in the aforementioned limit of the swimming velocity becoming unboundedly large. The authors show that this corresponds either (i) to a thin DCM with an associated quasi-linear (in the limit) nutrient profile, or (ii) a surface layer with a linear nutrient profile or (iii) a bottom (benthic) layer with a constant nutrient profile. The two particular disadvantages of this work are, first, that the stability of these stationary solutions is not investigated, so that the long-term dynamics remain known; and second, that the limiting phytoplankton profile corresponds to an unbounded swimming velocity, despite the fact that this velocity is strongly constrained by physiology and, presumably, constant for each species.

• **J Huisman, NN Pham Thi, DM Karl & B Sommeijer (2006)**, Reduced mixing generates oscillations and chaos in the oceanic deep chlorophyll maximum, *Nature* **439** 322–325.

A paper devoted to the effects that reduced vertical mixing (due to global warming) can be expected to have on oceanic DCMs. The model used here is of the type described in this section

(with nutrient recycling). The authors of this study find that reduced mixing in a constant environment leads to oscillatory DCMs and, through a cascade of period doublings, to chaos. A plausible ecological mechanism underpinning the appearance of oscillations is presented, which is based on the timescale disparity between the sinking flux of phytoplankton (fast) and the diffusive flux of nutrients (slow). Similar results for a periodically varying environment are also outlined, together with coexistence results in a model with multiple phytoplankton species competing for light and a single nutrient.

• **A Zagaris, A Doelman, NN Pham Thi & BP Sommeijer (2009)**, Blooming in a nonlocal, coupled phytoplankton–nutrient model, *SIAM J. Appl. Math.* **69**(4) 1174–1204.
• **A Zagaris & A Doelman (2011)**, Emergence of steady and oscillatory localized structures in a phytoplankton–nutrient model, *Nonlinearity* (to appear).

These two theoretical papers focus on the destabilization mechanism of the trivial steady state (no phytoplankton, undepleted nutrient) in the model of Huisman et al. (2006), culminating in the identification of phytoplankton oscillations. As such, this theoretical result is the first proof of existence of a non-stationary attractor for this type of models. The first paper endows the model with a natural singularly perturbed structure (expressing the length scale disparity between DCM width and ocean depth) and proceeds to sketch the results of a linear bifurcation analysis. Concrete formulas predicting the parameter values for which a DCM is created are derived. Additionally, it is found that reduced diffusivity drives the DCM deeper, where bigger nutrient concentrations at the sediment are needed to support it. For unrealistic (in an oceanic setting) parameter values, the DCMs are replaced by BLs; it is hinted that these BLs might contribute to the complex dynamics found numerically in Huisman et al. (2006), although they are seemingly irrelevant from an ecological point of view. Some numerics that complement and support the theoretical findings are also presented. The second paper takes this bifurcation analysis to the weakly nonlinear level. First, it is shown that the bifurcating DCMs identified in the paper above are locally stable: they attract nearby initial profiles as soon as the trivial steady state is destabilized. Employing the classic method of weakly nonlinear analysis and exploiting the model's singular perturbed structure, these DCMs are tracked until they are destabilized through a Hopf bifurcation very shortly after they come into existence; at that point, stationary DCMs give their place to oscillatory ones. A downside of this bifurcational approach is that it can only capture parts of the attractor and only for parameter values close to the first bifurcation (through which the stationary DCM is generated). On the other hand, there is candid hope that this limited information suffices to unravel the appearance of complex dynamics in the system.

• **AB Ryabov, L Rudolf & B Blasius (2010)**, Vertical distribution and composition of phytoplankton under the influence of an upper mixed layer, *J. Theor. Biol.* **263** 120–133.

This paper also deals with nutrient–phytoplankton interactions in a spatially extended setting. The model used for this study matches that of Huisman et al. (2006); the sole difference is the inclusion of a nutrient recycling term. The first part of the paper is devoted to a single species model, which is simulated numerically in a setting of constant diffusivity, as well as in the presence of an upper mixed layer (UML) (i.e., in a stratified water column). The authors establish the formation of DCMs in the former case, as well as the existence of sustained oscillations for small values of the diffusivity (cf. Huisman et al. (2006)). In the latter case, DCMs can also form if co-limitation

occurs below the UML; if, instead, it occurs within the UML, the bloom is spread throughout it and we speak of an upper chlorophyll maximum (UCM). In this case, the authors also identify a parameter regime where bistability is present: both aforementioned profiles are stable. Broadly speaking, the DCM occurs because the UML has no effect on it; the UCM, on the other hand, can only occur if the associated biomass is high enough to arrest growth below the UML. Next to bistability, the authors observe oscillations in the presence of a UML; interestingly, these can and do persist for diffusivity values below the critical value allowing phytoplankton growth (cf. Riley et al. (1949)). The second part of the paper deals with a two species model. Here, the authors have chosen to consider a strongly light-limited species and a strongly nutrient-limited species in the presence of a UML. Their simulations reveal a host of dynamic scenarios, including exclusion and niche differentiation in the form of coexistence of stationary UCMs, of a stationary UCM (for the light-limited species) and a stationary DCM (for the nutrient-limited one), and of a stationary UCM coupled to an oscillatory DCM.

Part IV — Phytoplankton blooms in estuaries

The models presented so far had zero or one spatial dimensions—the depth of the water column. This does not mean that horizontal flows in the ocean are inconsequential. To the contrary, horizontal diffusion, for example, is several orders of magnitude stronger than the vertical. Instead, this modeling choice reflects modelers' interest in depth-dependent structures (such as DCMs, BLs and SLs) over patchiness (horizontal patterns). Nevertheless, the assumption that horizontal directions can be modeled separately (if at all) must be relaxed in the context of estuaries and rivers, as horizontal flow effects are crucial to system behavior. In such horizontally extended systems, phytoplankton also localizes (blooms) in a natural manner at a preferred (horizontal and vertical) position.

• **JE Cloern (1996)**, Phytoplankton bloom dynamics in coastal ecosystems: a review with some general lessons from sustained investigation of San Francisco Bay, California, *Rev. Geophys.* **34**(2) 127-168.
• **CL May, JR Koseff, LV Lucas, JE Cloern & DH Schoellhamer (2003)**, Effects of spatial and temporal variability of turbidity on phytoplankton blooms, *Marine Ecol. Progr. Ser.* **254** 111-128.

The first paper gives an extensive review of the mechanisms playing a role in the formation of blooms and describes the type of models needed to understand the underlying dynamics. The author puts a strong emphasis on data, which are harvested from the core measurement program running in San Fransisco Bay, and does an excellent job of using the extensive bibliography on the subject to offer interpretations of blooming events evident in that data. The second paper focuses especially on the effects of turbidity. In the models considered in Parts II−III, turbidity only enters through the explicit—typically exponential—decay of the light intensity in a system without phytoplankton. In estuaries, and more generally in (shallow) coastal ecosystems, the turbidity is a dynamic component controlled by the sediment concentration. Thus, one needs to couple the model to an additional module modeling sediment, which is transported by water and can either erode from or deposit on the bottom of the basin. Although the planktonic aspects of the models discussed in these two papers share essential features with those discussed in the previous parts of this literature review, the models here are of a separate conceptual type and thus not necessarily

directly amenable to mathematical analysis.

• **HE de Swart, HM Schuttelaars & SA Talke (2009)**, Initial growth of phytoplankton in turbid estuaries: A simple model, *Cont. Shelf Res.* **29** 136-147.

This paper bridges the gap between the complex models for bloom dynamics in estuaries of Cloern (1996) and May et al. (2003), on one hand, and the conceptual models of Parts II and III on the other. The model proposed here consists of a hydrodynamical/suspended sediment concentration (SSC) module coupled to a biological one. The latter is very similar to the model proposed in Huisman et al. (2006). Since the hydrodynamical/SSC module has been reduced to its bare essentials, a linear stability analysis of the trivial, no-phytoplankton steady state proves possible. In a sense, the approach here is very similar to that of Zagaris et al. (2009). It is refreshing, nevertheless, to see that the parameter ε (which is asymptotically small in the oceanic setting of that latter study) cannot be and is not assumed to be small in this estuarine setting. Therefore, the singular perturbation approach of Zagaris et al. (2009) breaks down here. As a result, and since one must take the non-biological effects into account, the linearized stability problem cannot by studied by a fully analytical approach; one has to investigate the spectral problem (of Sturm-Liouville type) numerically. The analysis validates the observations that phytoplankton blooms occurr seaward of estuarine turbidity maxima.

Other Articles

• **JK Hale & A Somolinos (1983)**, Competition for fluctuating nutrient, *J. Math. Biol.* **18** 255–280.

One of the very few studies with rigorous mathematical content that focuses on a parametrically forced system. The model in question describes the competition of n species for a single nutrient, which is assumed to be in periodic supply from the environment. As such, this model does not fit in any of the categories above: zooplankton is absent, but so is a spatial dimension; a wash-out (dilution) term, on the other hand, is included. From one point of view, then, this is a NP model with P partitioned into n compartments. From another point of view, this is a type-II model describing blooms that occur at the same depth (e.g., surface layers), without self-shading, and with 'poor man's diffusion' (i.e., dilution). First, the authors show that a species which has negative growth, on (temporal) average, necessarily dies out. For growth functions of Michaelis–Menten type, this condition reduces to the break-even concentration (where growth is zero) being less than the nutrient concentration available on average. More generally, all species die out for an average nutrient concentration below a certain threshold. Subsequently, they prove the existence of another threshold, so that only one species survives between these two thresholds (competitive exclusion)—this is the species having the lowest break-even nutrient concentration, and its concentration remains well away from zero. Finally, they derive an explicit lower bound for the nutrient concentration, above which all species coexist. They then turn their attention to the regime where the wash-out rate is much larger than the planktonic decay rates and find that the system approaches a periodic solution having the period of the nutrient input. Systems of this sort having two species ($n = 2$) are particularly amenable to analysis, and the authors study in detail the number and properties of the periodic solutions the full system may approach as time increases.

• **AD Barton, S Dutkiewicz, G Flierl, J Bragg & MJ Follows (2010)**, Patterns of diversity in marine phytoplankton, *Science* **327** 1509–1511.
• **J Huisman (2010)**, Comment on "Patterns of diversity in marine phytoplankton", *Science* **329** 512.
• **AD Barton, S Dutkiewicz, G Flierl, J Bragg & MJ Follows (2010)**, Response to comment on "Patterns of diversity in marine phytoplankton", *Science* **329** 512.

A thoroughly enjoyable debate on the extent of planktonic diversity under constant and variable environmental conditions instigated by results produced by a computational model considered in the first publication. The discussion in this series of articles is quite strongly connected to the Hale & Somilinos (1983) article, although, of course, of much larger scope.

• **PG Falkowski (2002)**, The ocean's invisible forest, *Scientific American* **287**(2) 54–61.

This text is, of course, aimed at quite a general audience. Its first part gives a nice—actually inspiring—general introduction to phytoplankton and especially to its role in regulating the climate. Phytoplankton accounts for less than 1% of the 600 billion metric tons of carbon contained in the earth's photosynthetic biomass. Nevertheless, it (nearly) draws as much CO_2 out of the atmosphere through photosynthesis as trees, grasses and all other terrestrial plants combined. Although this is a well-known fact nowadays, Falkowski explains that it took decades of measuring to eventually reach that conclusion; he also presents an outline of the research that led to it and explains why it has proved such a hard problem. The second—less convincing—part of the paper is devoted to research directed towards mitigating global warming through a stimulation of phytoplankton growth effectuated by fertilization—adding iron to the oceans as per the idea of J Martin. Falkowski briefly reviews the idea, preliminary data that lent it some credibility, the most recent experiment (SOFeX, 2002) to that date, and lays out some related concerns. (For an assorted, rather detailed discussion, the interested reader can consult *Oceanus* **46**(1)—a 2008 issue devoted entirely to the topic of iron fertilization.)

• **W Gentleman (2002)**, A chronology of plankton dynamics in silico: how computer models have been used to study marine ecosystems, *Hydrobiologia* **480** 69–85.

A beautifully written and well thought out paper detailing the advent of phytoplankton modeling from the very first plankton model (Fleming 1939) to the much more recent large-scale models. Roughly, the chronology is divided in the following periods: (i) 1930's–1940's, during which time plankton modeling was pioneered by R Fleming and G Riley; the models developed in this period introduced many fundamental processes—nutrient uptake, zooplankton grazing, light limitation, diffusive–advective effects—found in models developed in subsequent decades. (ii) 1950's–1970's, a period dominated by J Steele and collaborators; among other achievements, Steele essentially introduced the first NPZ model in a two-layer water column and the first structured model. He also recognized the significant role played by zooplankton. (iii) (roughly) 1980's, at which time the advent of the personal computer added significant versatility to plankton modeling. This period saw the appearance of a new generation of computational oceanographers, as well as a further shift towards structured plankton models and the development of the first 2-D models. (iv) 1990's, when the development and use of models reflected the newly awakened interest in the effects of climate variability on oceanic production. (v) Future directions.