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Stepwise building of plankton functional type (PFT) models: A feasible route to complex models?

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Abstract:

We discuss the strategy of building models of the lower part of the planktonic food web in a stepwise manner: starting with few plankton functional types (PFTs) and adding resolution and complexity while carrying along the insight and results gained from simpler models. A central requirement for PFT models is that they allow sustained coexistence of the PFTs. Here we discuss how this identifies a need to consider predation, parasitism and defence mechanisms together with nutrient acquisition and competition. Although the stepwise addition of complexity is assumed to be useful and feasible, a rapid increase in complexity strongly calls for alternative approaches able to model emergent system-level features without a need for detailed representation of all the underlying biological detail.

1. Introduction

Large-scale biogeochemical processes in the ocean are, to a large extent, the result of nano-scale processes in the microbial part of the pelagic food web. With an urgent need to understand the earth system's responses to global change, there is hence an urgent need to understand how the community of pelagic microbes functions, not only at a detailed level, but even more critically at the community and system level where features emerge from organism properties and life strategies. Biologists interested in the ecology of marine microbes, and biogeochemists interested in global scale element cycles thus share a common interest in the system behaviour of the microbial food web.

This need for analysis of the microbial food web system is not restricted to a qualitative level, also quantitative and predictive power is needed. Mathematical models may thus seem an obvious tool, and the construction of a model that incorporate "all" biogeochemically important types of plankton may appear tempting. Anyone that has worked with box models knows the many degrees of freedom involved in the process of defining model structure, fixing parameter values, and choosing initial values, also has experienced the rapidly developing feeling of building castles on sand. The contemporary debate concerning the feasibility of multi-PFT approaches (Anderson 2005; Flynn, 2005; Le Quéré et al., 2005) is therefore no surprise. Skepticism to the value of ecological models is, however, far from new as illustrated by the following citation from Hedgepeth (1977) : "... but complex models require simplification and selection of data unrepresentative of nature. A model which is simply an elaborate mathematical summary of a textbook does not tell us much more than we already know, and its formulation involves a questionable diversion of funds."

Faced with what at present may appear as a void between what is possible and what is needed, we here try to explore the problem in some more detail by asking the question: Is it a viable and fruitful approach to start with simple models, amenable to analysis and experimental verification, and then add new details in bits and pieces? The answer to whether such a stepwise approach to complexity is possible is not *a priori* obvious. The process of piecewise assembly of a clock that functions only when all pieces have been correctly assembled, may not necessarily provide much insight until completed.

The usual story told in the scientific folklore is that the prevailing concept 30 years ago was one of an essentially linear structure in the lower pelagic food chain, transporting nutrients and energy via phytoplankton to mesozooplankton. This is a simplification that disregards researchers such as e.g. Krogh (1934), Sorokin (1971) and Pomeroy (1974); all with an early vision of a more complex microbial food web. Today's paradigm can be summarized as having exchanged the "phytoplankton" link in this linear food chain with a "microbes" link; where the internal structure of the "microbes" link is a complex microbial food web comprising not only a range of size-classes of phytoplankton, but also a high genetic diversity in the prokaryotic (Venter et al., 2004) and protist (Lopez-Garcia et al., 2001) communities. Many of these organisms have mixed modes of energy and materials acquisition, combining autotrophy and heterotrophy (e.g. Sieracki et al., 2006), osmotrophy and phagotrophy (e.g. Riemann et al., 1995), and with all (or at least most) of the organisms being susceptible not only to predatory processes moving energy and material "up" to higher trophic levels, but also to parasitism, in particular viral attack (e.g. Suttle, 2005), shunting material back towards smaller particles and the dissolved pools.

Presumably, each co-existing species in this community of microbes is present because it has found its own unique life strategy. If the consequence is that all the complex biological detail resulting from such a multitude of life strategies needs to be incorporated into our models, these being conceptual or mathematical, the most reliable prediction we can make is perhaps that global change will develop faster than our models. On the other hand, one may also argue that the pelagic microbial food web perhaps is (one of?) the simplest ecosystems in the world, heavily constrained by well-known physical laws such as those for molecular diffusion, sinking of particles, light penetration etc., and considerably less complicated by small-scale heterogeneities than e.g. terrestrial ecosystems. If we are not able to describe the functioning of the microbial part of the pelagic, it may seem an overwhelming challenge to understand the many complex and sometimes weakly constrained ecological, sociological and economic systems on which modern society depends.

The intuitive, and also the most common, strategy for building microbial food-web models is that of linking pre-conceived plankton functional types (PFTs) via trophic interactions; i.e. box models where each PFT is represented by one or more boxes (state variables). Each PFT thus representing a larger set of organisms sharing some property believed by the modeller to be essential (size, trophic mode, substrate utilization, common predator, essential role in biogeochemical transformation, etc., etc.). Going from the “classical” linear food chain to a more complex food web, a minimum requirement to such models seems to be that they must contain mechanisms that allow sustained coexistence of the different PFTs constructed.

A simple and highly relevant example is a two-PFT phytoplankton model containing “large” and “small” phytoplankton, linked by competition for one common limiting nutrient such as dissolved phosphate. The problem of coexistence of such competitors has haunted theoretical phytoplankton ecology since Hutchinson (1961) proposed his now classical paradox, asking why so many phytoplankton species can coexist on one limiting resource in such an apparently homogenous environment. One potential solution (Fig. 1A) to this paradox is obviously that the assumption is wrong, and the PFTs have specialized for different limiting resources. Another simple and robust solution is the inclusion in the model of a loss mechanism selective for the best competitor (Fig. 1B), sometimes referred to as the principle of “killing the winner” (Thingstad and Lignell, 1997). In the two-phytoplankton example above, this selective loss would typically be micro-zooplankton grazing selectively on the “small” phytoplankton, often believed to be the superior nutrient competitors. Without a need to resort to mathematics, the mechanism can be intuitively understood as the introduction in the model of a mechanism that selectively prevents the best competitor from consuming all the limiting resource, leaving parts of the resource for the inferior competitor. For short, we will refer to the generic 3-PFT “killing the winner” structure in Fig.1B as the “KtW”-unit.

Note how the definition of a PFT within the framework of Fig.1B is closely linked to the selectivity properties of different loss factors, while in Fig. 1A it was linked to the biogeochemical function of the PFT in terms of specialized use of nutrients. The mechanism in 1A thus gives one pathway through the food web for each class of substrate, the mechanism in 1B allows for different pathways for the *same* substrate and thus increase resilience in the system.

2. The KtW-unit links organism life strategies, food web structure, biodiversity and biogeochemistry

In a well-developed scientific discipline one expect a set of experimentally verified generic principles that link the different objects studied, allowing non-trivial predictions to be made concerning their relationships. Ecology as a discipline does not necessarily get top scores in this respect. The generic KtW-unit in Fig. 1B has, however, a taste of the desired flavours.

As shown in Frame 1, a simple mathematical model can be used to show that the steady-state structure of the KtW-unit depends on two types of external factors: 1) How much total limiting resource (N_t) that is available for sharing (i.e. the system's position along an oligotrophy vs. eutrophy axis), and 2) the external loss rates for the individual PFTs (δ - parameters) draining limiting resources out of the community. An important insight from such an analysis is that abundance of competition specialists is independent of the total amount of resource (as long as all three PFTs are present and values of δ -parameters are independent of N_t), while abundance of defence specialists increases linearly with total resources N_t . In another terminology, competition specialists are predation controlled, while defence specialists are resource controlled. If there is a trade-off between the two strategies, organisms in such an idealized world seem to have to choose: either to go for an optimization of their competitive abilities, allowing them to dominate in oligotrophic environments, or optimize their defence mechanisms, allowing them to dominate under eutrophic conditions. Our three-member food web even seems able to allow us to hypothesize on trends in the relationship between biodiversity and trophic state of the environment: In extreme oligotrophic environments, one would seem to be left only with extreme competition specialists, in eutrophic environments, the defence specialists would become dominating.

An important feature of the KtW-unit is thus that it links so many different aspects, often studied by different disciplines: the organism life-strategies usually studied by biologists interested in physiology or evolution, food-web structure and function usually of interest to microbial ecologists, and cycling of matter of primary interest to biogeochemists. One can also see the present food web as the result of an evolutionary arms race where the typical time scale for major new technology inventions is in the order of 0.2-0.5 Gyears (Fig. 2), adding new defence and new competition strategies.

The KtW-unit has been used in some form, although usually not as explicitly as stated here, by many experimentalists, both in gnotobiotic (known species composition) laboratory systems, with mixed cultures, and in larger semi-natural and natural systems, ranging from chemostats with virus in combination with susceptible and resistant bacterial strains, to meta-analysis of open-ocean data sets (Table 1).

There is thus a huge range in scale and scope of systems where our simple KtW-unit seems to provide at least a conceptual understanding of important system properties. What this suggests is that one can explain system properties both at the "micro"-level (e.g. idealized laboratory systems of viruses and bacteria) and at the "macro"-level (i.e. using data on diversity from natural open ocean systems). This has some resemblance to the concept of self-similarity as used in fractal theory. Fractal theory also contains the concept of a fractal dimension, often illustrated by the example where length of coastline is plotted in a log-log plot against the length of the measuring stick used. The negative slope of this linear relationship is the fractal dimension. The analogy to this in the pelagic system is the size-abundance spectra (Martin et al., 2006). The contours are thus visible of a fractal theory that links principles of self-similarity to fractal dimension, perhaps opening for a theory for emergent properties less dependent upon exact formulations of biological detail.

3. Combining the two principles of coexistence

Phytoplankton growth in upper mixed layer of stratified water columns is usually thought to become limited by either N, P or Fe, although the situation may be more complex (e.g. Müller et al., 2005). Diatoms, with their extra requirement for silicon are an interesting example. Different system states exist where diatoms and other phytoplankton are limited by separate nutrients. Regarding heterotrophic bacteria as an analogous case to this is perhaps not immediately obvious. The traditional view (e.g. Jannasch, 1955) was that free-living marine heterotrophic bacteria were ‘resting cells’ exposed to such a dilute environment that they were strongly limited by the supply of labile organic material. This view has been challenged, not only by data indicating an actively growing bacterial community (Azam et al., 1983), but also by a series of observations suggesting that the marine photic zone system may be in (at least) two states, characterized by either C-limited or by mineral nutrient-limited bacterial growth (Rivkin and Anderson, 1997; Thingstad et al., 1998; Van Wambeke et al., 2002; Zohary and Robarts, 1998).

As yet, there is no solid experimental verification of the mechanisms underlying such shifts in state of the microbial food web, but we can make a qualified guess: In a system dominated by osmotroph microorganisms (phytoplankton and bacteria) there will be high competition for the mineral nutrients and little recycling, and the probability for mineral nutrient-limited bacteria would be high. If strongly nutrient stressed phytoplankton also have a tendency to excrete carbohydrates (Obernosterer and Herndl, 1995), this would enhance the tendency for mineral nutrient limitation of the heterotrophic bacteria. When, or if, succession at a later stage moves biomass up the food web to phagotrophs (predators), the expected result would be less competition and more recycling. The resulting increase in mineral nutrient supply to bacteria, possibly combined with reduced release of C-rich organic material, should theoretically increase the probability that bacteria get sufficient mineral nutrients to deplete the pool of labile DOC, and thereby shift the system to one of C-limited bacterial growth.

Using our KtW-unit as a building block, we can construct a PFT-based model incorporating these features (Fig. 3). Despite the (from a biologist's point of view) crude simplicity of this representation, it allows us to make another interesting prediction: Since we expect the diatom-copepod succession to be much slower than the flagellate-ciliate succession, the presence of silicate should allow the build-up of a large and prolonged (diatom dominated) phytoplankton bloom, immobilizing nutrients in diatom biomass. According to the argument above, the prediction would be that a stimulation of diatom growth by silicate addition should shift bacterial growth conditions towards mineral nutrient limitation and reduced ability of the bacterial community to consume labile DOC. These theoretical predictions have been tested by manipulating mesocosms with mineral nutrients, glucose and silicate, confirming the qualitative predictions (Havskum et al., 2003).

The structure in Fig.3 can relatively easily be translated into a dynamic simulation model (Thingstad et al., 2007), able to reproduce, not only the qualitative predictions made above, but for many features, also the response patterns and levels of the observed responses. For bacterial production, however, the authors were not able to find a set of parameters that simultaneously could reproduce both patterns and levels for all different manipulations. The reason suggested was that the dominating bacteria profoundly changed morphology and stoichiometric composition in treatments where an easily accessible organic carbon substrate (in this case glucose) was added in excess. Hence the assumption that heterotrophic bacteria can be represented by one single PFT with fixed parameters may thus give models too simple to reproduce this type of experiments.

4. “Winnie-the-Pooh” strategists: is it possible to simultaneously increase competitive and defence abilities?

Size in microbial organisms is related to both competitive and defence abilities. Phagotrophic organisms that ingest whole prey obviously will run into problems ingesting prey larger than themselves. A 10:1 ratio as a generalized optimum predator/prey size ratio has been suggested for ciliates (Fenchel, 1980), but may differ from this in both directions (Hansen et al., 1994). In some cases this is related to the use of specialized capture techniques such as pallium and peduncle feeding in heterotrophic dinoflagellates (Hansen and Calado, 1999). In the literature, there is often a vague and non-specific allusion to “small organisms being better competitors for dissolved nutrients than large”. The theoretical foundation for this argument is based on the concept of diffusion limitation, where the assumption is that, at sufficiently low external concentrations, transport of substrate molecules to the cell surface becomes the rate-limiting process (Jumars et al., 1993). Solving Fick’s law for a spherical cell then gives a flux $J = 4\pi DrS_\infty$ where D is the molecular diffusion coefficient for the substrate in water, r is the cell radius, and S_∞ substrate concentration at infinite distance from the cell. Dividing this by the minimum amount m of limiting substrate required to build a new cell gives the growth rate $\mu = (4\pi Dr/m)S_\infty$, from which one can define a maximum affinity:

$$\alpha^{\max} = 4\pi Dr/m \text{ or, equivalently,} \quad \text{Eqn. 1a}$$

$$\alpha^{\max} = 3D/\sigma^2, \quad \text{Eqn. 1b}$$

where σ is the average cell concentration of the limiting element within the cell.

As the proportionality constant between growth and substrate concentration, α^{\max} expresses the cell’s ability for nutrient acquisition at low substrate concentration, and thus is a central parameter determining competitive ability. Obviously, if σ is independent of r , any increase in cell size has a huge cost (scaling as r^2) in competitive ability.

Interestingly, affinity estimates from strongly P-deficient environments approach the theoretical values that can be calculated from 1b, suggesting that microbial osmotrophs experience an environment where the growth limiting process is that of molecular diffusion (Moutin et al., 2002; Tanaka et al., 2006). This suggests that one can estimate some of the most central parameters in models such as the one in Fig.3 from fundamental and precise physical principles, rather than from biological experiments.

However, in the mesocosm experiments of Havskum et al.(2003), this theory does not at first sight seem to fit. Firstly, with the large size of some diatoms, an r^2 scaling of affinity would seem to make diatoms so competitively inferior hence their success becomes difficult to explain. Secondly, and more disturbing, one would expect that addition of glucose in excess would force all (or at least most) bacteria to severe mineral nutrient limitation. With an r^2 -scaling of affinity, the apparent prediction would be that glucose addition should select for a community of small bacteria. This was, however, not what was observed. In glucose-amended mesocosms the bacterial community became dominated by large-sized *Vibrio splendidus* cells, filled with electron-thin inclusions, presumably consisting of C-storage material (Øvreås et al., 2003). The

accumulation of C-rich storage material under N-limitation is of course a well-known mechanism from classical microbial physiology (e.g. Dawes and Senior, 1973), but the classical interpretation has been that this is a strategy “for a rainy day”, i.e. something of potential future value should conditions change to C-limitation. Using Eqn.1a, however, one can interpret the C-storage as a mechanism to increase size (r), without an accompanying increase in the requirement (m) for mineral nutrients. C-storage should thus increase the competitive ability for mineral nutrients. If increasing size at the same time should shift the cell into another size-class (or shape) with less loss to predators, the assumed trade-off between competition and predation would disappear, and the same strategy would serve to simultaneously enhance both. Diatoms can be considered in a similar perspective: by using an otherwise non-limiting substrate, in this case silicate, diatoms build frustules that allows them to form a large internal vacuole, potentially allowing them to increase size and change shape without increasing the need for mineral nutrients in proportion to volume. If the strength of the frustule and/or the size and shape also serves a role in defence, also diatoms avoid the trade-off between competition and defence. As a generic mechanism, the term “Winnie-the-Pooh strategists” has been suggested (Thingstad et al., 2005). In another recent terminology, the experimental addition of glucose allowed some of the bacteria (the Winnie-the-Pooh strategists) not only to improve their competitive ability, but also to create a “loophole” (Irigoien et al., 2005) in microzooplankton grazing impact. If such mechanisms are common, the construction of PFTs in models aspiring to link biogeochemistry, organism life strategies, and food web structure, may be even more complicated than usually anticipated.

5. PFTs within PFTs; combining loss mechanisms of different selectivity

A basic feature of our KtW-unit is the selectivity of the loss mechanisms. While prey selection is strongly linked to size, there are also many studies demonstrating selection based on other mechanisms in predators of both bacterial (Pernthaler, 2005) and phytoplankton (Teegarden, 1999) predators. A loss mechanism often believed, however, often to be more selective than predation, in many cases probably almost at the species level is viral lysis (Suttle, 2005). To illustrate the principles, one can make an idealized model assuming heterotrophic flagellates to be a non-selective bacterial predator, while viruses are species-specific. The consequence is a model where, at steady state, flagellate predation determines the abundance of bacteria in the total bacterial community (B_T), while lytic viruses determine the abundance within each bacterial host population (B_i). Consequently the number of host groups whose simultaneous coexistence is allowed by this mechanism is $n = \frac{B_T}{\overline{B_i}}$ where $\overline{B_i}$ is the average

abundance in the n host-groups (Thingstad, 2000). This theory thus can provide a hypothesis for the mechanism controlling diversity *within* a PFT and thus gives what might be termed a hierarchical nesting of the KtW-units.

For most biogeochemical purposes, it may seem unnecessary to include many PFTs inside the community of heterotrophic bacteria. The theory does, however, have a somewhat unexpected biogeochemical consequence: In the idealized case with non-selective protozoan predation, each bacterial host group will have the same specific loss rate to predators. If they then have different growth rates, this difference must (at steady state) be compensated by a higher loss to viral lysis from fast growing than from slow growing hosts. The consequence is non-trivial: The higher diversity in growth rates between the coexisting hosts in the same community, the higher loss to viruses, and less to predation. With a high diversity in host growth rates, more material

will thus be shunted away from transport “up” the predatory food chain, instead being returned “down” via parasites towards small particles and dissolved nutrients (Thingstad, 2000).

It is not immediately obvious how the biogeochemical effect of multiple host-PFTs within a community-PFT could be parameterized in a simpler model containing only the community level PFT.

6. Resolving the internal dynamics of phytoplankton size-classes

In typical mesocosm experiments, some kind of experimental perturbation is applied to the system and the transient responses of the plankton system is followed, typically for a period of days to weeks. A simple division of phytoplankton in two size-defined PFTs (“small” and “large”) can in some cases (Thingstad et al., 2007) give a fairly good representation of the responses in chlorophyll. Presumably this mainly requires that the characteristic time constants, not only for growth, but even more for loss of the two phytoplankton PFTs, are adequately described.

If there is a strong predator control on abundance, similar for organisms within a size class, but different between size classes, one would expect predation to promote *similarities* in the dynamic behaviour of PFTs belonging to the same size class, different from that of PFTs belonging to other size classes. Loss mechanisms with higher specificity such as the viral lysis discussed above would, however, be expected to produce within size-group *differences* in dynamic behaviour. Adding also the possibility of a specialization in nutrient requirement among PFTs within the same size-group (Fig.4) one would expect this to produce within size-group *differences* in cases where the relative rates of supply of the different nutrients change.

The introduction of flow-cytometers has allowed the collection of data on phytoplankton and bacterial abundance in mesocosm experiments at a frequency and a precision far beyond that obtainable by traditional microscopy (Fig. 5). The oscillations seen in some of these data, such as e.g. the damped oscillations in abundance of heterotrophic bacteria in Fig. 5A could be interpreted as the damped oscillations of a predator-prey pair, as one would expect it from the models discussed so far. If one assumes heterotrophic bacteria, picocyanobacteria, and picoautotrophs to share a common, size-selective, predator, one would expect similarities in the oscillations of these PFTs. In the experiment in Fig. 5A, there are some indications of this with maxima and minima coinciding relatively well. Such co-variation can, however, not be seen in the two other experiments (Fig. 5B-C). Joining these organisms in one, size-determined, prey class would therefore seem to require within-group mechanisms separating their dynamic behaviour in some cases. Since viruses would not be expected to work at the community level of heterotrophic bacteria, picocyanobacteria or picoautotrophs, it seems more logical to think in terms of substrate specialization as the mechanism separating the behaviour of these within-size class groups. One hypothetical possibility, suggested in Fig.6, is to add differences in the ability to use organic nitrogen sources between the three groups.

Another interesting case is the coccolithophorid *Emiliana huxleyi* blooming in both experiment A and B of Fig.5. In terms of size, one would tend to include *E. huxleyi* with the two groups of nanoeukaryotes detected. This also seems reasonable when comparing dynamics for these three groups in the initial phase of the bloom. However, in both experiments, however, the *E. huxleyi* bloom is terminated more abruptly than for the other two groups. *E. huxleyi* is a species, and in this case *E. huxleyi* viruses are known to play a role in termination of the blooms (Bratbak et al., 1993). Viruses can thus, with some credibility, be suggested as an important within-size group regulating factor, separating the dynamics of *E. huxleyi* from that of the other nanoeukaryotes.

7. Mixotrophs

Mixotrophy as the combination of osmotrophy and phagotrophy is a well-documented strategy in protists (Riemann et al., 1995) and they can be important, at least numerically in various environments (Christaki et al., 1999; Havskum and Riemann, 1996; Zubkov and Tarran, 2008). Mixotrophs can well be included in the framework discussed above, leading to theoretically interesting situations such as that of “eating your competitor” (Thingstad et al., 1996). The conceptually simple division in osmotrophs and phagotrophs is however no longer valid and the models will obviously be further complicated. There does not seem to be one fixed optimum strategy for the balance between osmo- and phagotrophy in mixotrophs. Filling the 2D-plane of strategies defined by organism size along one axis and a continuous range from pure osmo- to pure phago-trophy along the other with predefined PFTs, is not a particularly tempting idea.

A more fascinating approach would be to step back and look at the basic mechanisms shaping the food web. As discussed for our KtW-unit, the structure of the food web is shaped from the trade-offs organisms have to face in their evolution of life strategies. Such models can be built with genetic algorithms included (E. Strand, unpublished). If we knew the trade-offs, one could thus in principle discard models with pre-defined PFTs, instead letting the food web evolve with organism size and trophic mode as continuous variables. The task of parameterizing the trade-offs between life strategies is, however, not necessarily an easier task than defining PFTs.

8. Conclusion

We would argue from the examples above that it seems both feasible and useful to start with the understanding gained from simple models of the microbial food web, and add complexity in small steps. Insight gained by the simpler models carried over to more complex networks may thus help in building stepwise a unified and consistent model for this important part of the pelagic ecosystem.

In particular the generic “Killing-the-winner” food-web unit proposed in Fig. 1B seems a useful “LEGO-brick”, allowing analysis at many levels of resolution. One aspect stressed with this approach is the importance of loss mechanisms and defence strategies for defining useful PFTs. The central role of defence in the microbial food web system has been clearly recognized by some workers in the field (e.g. Verity and Smetacek, 1996), but is also often overlooked. If we lack some of the detailed biological knowledge required to model the growth and nutrient acquisition aspects, our lack of detailed understanding of loss and defence mechanisms is probably much more severe. The challenge met by osmotrophs in optimizing nutrient acquisition obviously has more dimensions than discussed here. At permanently low external substrate concentration, molecular diffusion does however become a common constraint all osmotrophs have to relate to, presumably limiting the diversity in possible strategies of optimization. The evolutionary arms race between predator and parasite invasion strategies on one side, and the defence strategies of their prey/hosts on the other, is part of a war much older in the microbial world web than its younger parallels in macro-biology. With a long evolutionary history and less (known) physical constraints on the possible solutions, the microbial mechanisms developed for invasion and defence are therefore likely to be diverse.

It is, unfortunately, only too easy to make a list of important aspects of microbial food web dynamics not discussed above. The roles of light, sedimentation, nitrogen fixation, flexible

stoichiometry, and metazoan grazers other than copepods, are only some of these. Rather than adding all this into PFT based structures, it is tempting to search for principles that allow the capture of higher level community features such as e.g. total production-respiration balance as derived from metabolic theory (Lopez-Urrutia et al., 2006) or organism size-spectra (Cermeno et al., 2006; Martin et al., 2006), preferably without the need to describe all underlying biology in detail. The fundamental question is perhaps what a model is built for? If the purpose is understanding generic and fundamental relationships within the system, it is usually a more challenging and rewarding exercise to ask the question of how much detail that can be removed from a model without losing the explanatory power of the model, than to add as much as possible of the myriad of biological detail we all know is there. When, however, we need predictive power of biogeochemical aspects, and these are linked to organisms with special life strategies, it is more difficult to see how some kind of PFT approach can be avoided. Export of carbon as discarded appendicularians houses, of opal by diatoms, or of calcite produced by coccolithophorides, are examples of important biogeochemical processes not easily modelled in a quantitative and predictive manner without having to resort to some kind of PFT approach. Whether current biological knowledge is sufficient to do so is, however, questionable.

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9. APPENDIX

Methodology used for data in Fig. 5:

All three mesocosm studies shown in Fig. 5 were conducted in Raunefjorden, at the Marine Biological Field Station, University of Bergen, Norway. Polyethylene enclosures were moored to a raft and the enclosures were filled with nutrient-poor, post-bloom fjord water, adjacent to the raft.

A: The study was carried out between 15 May and 9 June 2005. The nine enclosures (~25 m³) were manipulated by CO₂ aeration to obtain triplicates of three different concentrations, 350 µatm (1×CO₂), 700 µatm (2×CO₂) and 1050 µatm (3×CO₂). Nitrate and phosphate were added to yield initial concentrations of 14 µmol L⁻¹ NO₃ and 0.7 µmol L⁻¹ PO₄ (Riebesell et al. unpublished).

B: The study took place between 2 and 15 June 2003. The nine enclosures were divided in 3 groups and nutrients were added daily in a N: P ratio of 15:1 (1.5 µM NaNO₃ and 0.1µM KH₂PO₄) starting nutrient addition with one day delay between the groups (for detail see Martinez-Martinez et al., 2006)

C: The experiment was conducted between July 10 and July 25 2001. Five land based glass fibre tanks (2.6 m³) with different turbulence levels received an initial addition of silicate (Na₂SiO₃), nitrogen (NaNO₃) and phosphate (KH₂PO₄) in a ratio of 32:16:1 (Si:N:P) (for details see Beauvais et al., 2006).

Diatoms (Fig 5C) were counted by light microscopy, the other groups of osmotrophs by flow cytometry (FCM) performed with a FACS Calibur flow cytometer (Becton Dickinson, Franklin Lakes, NJ) equipped with an air-cooled laser providing 15 mW at 488 nm and with standard filter set-up. The algal counts were obtained from fresh samples with the trigger set on red

fluorescence. Samples for enumeration of bacteria were fixed with glutaraldehyde (0.5% final concentration), stained with SYBR Green I (Molecular Probes Inc., Eugene, OR) and analysed according to Marie et al. (1999) with the trigger on green fluorescence. Discrimination of phytoplankton and bacteria was based on dot plots of side-scatter signal (SSC) versus pigment autofluorescence (chlorophyll and phycoerythrin), and of SSC signal versus green DNA-dye fluorescence, respectively.

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Table 1. Experimental work where food web the KtW-unit in Fig.1B can be used to interpret the results.

Competition/nutrient-uptake specialist	Predator-parasite-defence specialist	or	Predator parasite	or	Shared limiting resource	System tested	Reference
Bacterial host (E. coli)	Resistant strain of host		Virus (T4; T2)		Glucose	Laboratory	(Bohannan and Lenski, 1999; Bohannan and Lenski, 2000)
Rod shaped bacterium Pedobacter	Coccus-formed bacterium Brevundimonas		Ciliate (Tetrahymena pyriformis)		?	Laboratory. Demonstrated the possibility of chaotic behaviour	(Becks et al., 2005)
Heterotrophic bacterial species	Diatom (Skeletonema costatum)		Heterotrophic flagellate		Phosphate	Laboratory chemostats	(Pengerud et al., 1987)
Edible bacteria (< 1 µm)	Inedible bacteria (filaments aggregates)	or	Protozoa		Glucose or phosphate	Laboratory, mixed bacterial communities	(Madz and Jürgens, 2003)
Edible bacteria	Inedible bacteria		Naturally occurring protozoa and viruses	and	phosphate	Natural freshwater community.	(Sime-Ngando and Pradeep Ram, 2005)
Edible phytoplankton species	Inedible phytoplankton species		Meso-zooplankton		Mineral nutrients (?)	Mesocosms manipulated with reduction in zooplankton	(McCauley and Briand 1979)
Edible algae (<35 µm)	Inedible algae (>35 µm)		Cladoceran		Nitrate and phosphate	Laboratory, mixed algal community	(Steiner, 2003)
Small phytoplankton	Large Phytoplankton		Natural zooplankton communities		?	Meta-analysis of oceanic data	(Irigoien et al., 2004)

Text Box 1. Idealized mathematical model illustrating the resource-dependent co-existence of a competition-specialist and a defence-specialist.

Assuming the total amount N_t of limiting element to be distributed between biomass of competition specialists (C), defence specialists (D), and predators (P), or as free mineral nutrient N , mass balance gives:

$$N_T = N + C + D + P,$$

Assuming all food uptake to be proportional to food availability, and fixed specific loss rates for defence specialists (δ_D) and predators (δ_P), we get three steady state conditions:

Growth = predation for competition specialists: $\alpha_C NC = \alpha_P CP,$

Growth = loss for defence specialists: $\alpha_D ND = \delta_D D,$ and

Growth = loss for predators: $Y_P \alpha_P CP = \delta_P P,$

where Y_P is the fraction of limiting element in prey incorporated into predator biomass, and α_C , α_D , and α_P are the affinity constants and the clearance rate for the osmotrophs (C , D), and the phagotroph (P).

Solving for the steady state of the two competitors gives:

$$C = \frac{\delta_P}{Y_P \alpha_P}, \text{ and } D = N_T - \left(\frac{\delta_D}{\alpha_D} + \frac{\delta_P}{Y_P \alpha_P} + \frac{\alpha_C}{\alpha_P} \frac{\delta_D}{\alpha_D} \right)$$

From which we see that:

- C is independent of the nutrient level N_T (as long as this is high enough to support all three populations, i.e. $N_T > \left(\frac{\delta_D}{\alpha_D} + \frac{\delta_P}{Y_P \alpha_P} + \frac{\alpha_C}{\alpha_P} \frac{\delta_D}{\alpha_D} \right)$, while
- D increases linearly with N_T .

Competition specialists will thus dominate at low N_T , while defence specialists will dominate at high N_T . Diversity will be low at $N_T > \left(\frac{\delta_D}{\alpha_D} + \frac{\delta_P}{Y_P \alpha_P} + \frac{\alpha_C}{\alpha_P} \frac{\delta_D}{\alpha_D} \right)$ with only the competition specialists present (low richness), and low at high N_T because of the dominance of the defence specialist (low evenness).

Notes:

- When higher level predators are included, the δ -parameters of this model become functions of the biomass of the higher predators and thus functions of N_T
- the assumption of a linear relationship between food concentration and food consumption is unrealistic at high concentrations. For a discussion of this see Thingstad and Sakshaug (1990).
- the basic requirements for coexistence is that one has as many equations as unknowns, and that the solutions for all variables are positive. Redefining the extra mechanisms (such as the competition specialist being a resource for the predator), the “killing the winner” solution to coexistence can be seen as a special case of the “as many resources as populations” principle.

Figures (all figures are original and to be reproduced in black/white only):

Fig.1. Two generic and robust principles linking organism strategies to coexistence and thus to biodiversity in food web models, here illustrated by the case where A)two PFTs can co-exist because they have specialized for different substrates and 2) two PFTs share the same limiting resource, but a selective loss mechanism prevents the competition specialist from sequestering all of the limiting resource, leaving a niche for the defence specialist.

Fig. 2 The evolutionary arms-race perspective of the pelagic food web. Following exhaustion of organic-C in the primordial soup and the introduction of oxygenic photosynthesis, the addition of larger eukaryotic phytoplankton, ciliates, diatoms, and copepods can in this perspective be seen as major technology inventions repeating the “killing-the winner” principle for increasingly more complex organisms. Years of introduction (Gy = 10^9 years before present) only tentative. For more detailed discussions see e.g- (Anon, 2005; Bradford-Grieve, 2002; Falkowski et al., 2004; Medlin and Kaczmarek, 2004)

Fig. 3. “Minimum” model food web combining the two principles of coexistence from Fig.1 as used by Thingstad et al.(2007). Three PFTs of osmotrophs compete for the common mineral nutrients, three phagotroph PFTs prey selectively on these competitors . Growth rates of heterotrophic bacteria and diatoms can also be limit by biodegradable DOC (BDOC) and by silicate (Si), respectively.

Fig. 4. *Among* and *within* group control of PFT dynamics: While size-selective predator control would be expected to produce differences in dynamic behaviour *between* PFT size-groups, but similarities *within* the size class, loss factors with higher selectivity such as lytic viruses would be expected to create differences among PFTs *within* the size-class. If (some of) the PFTs within the size class depend on more than one potentially limiting substrate, changes in the relative supply of S_1 would be expected to produce differences in dynamics *within* the size-class.

Fig. 5. Population dynamics in three different mesocosms. Abundance data collected by flow cytometry or microscopy (for diatoms). For details of the experiments see appendix.

Fig. 6. Outline of a possible refinement of the minimum model in Fig.2 with a potential to reproduce some of the flow-cytometer data in Fig.5. For osmotrophs, the size groups are still controlled by the same size-selective predators, while within-group coexistence is ensured either by host-specific viruses as suggested for *E. huxleyi* , or by differences in substrate specialization and requirement for community-type PFTs where, in this particular scheme, heterotrophic bacteria, picocyanobacteria and picoeukaryotes, may coexist if limited by biodegradable DOC (BDOC), dissolved organic nitrogen (DON) and dissolved inorganic nitrogen (DIN) or phosphorus (DOP), respectively. Further resolution of the community type PFTs is in principle possible by including host specific viruses according to the scheme in Fig.4.

Coexistence by

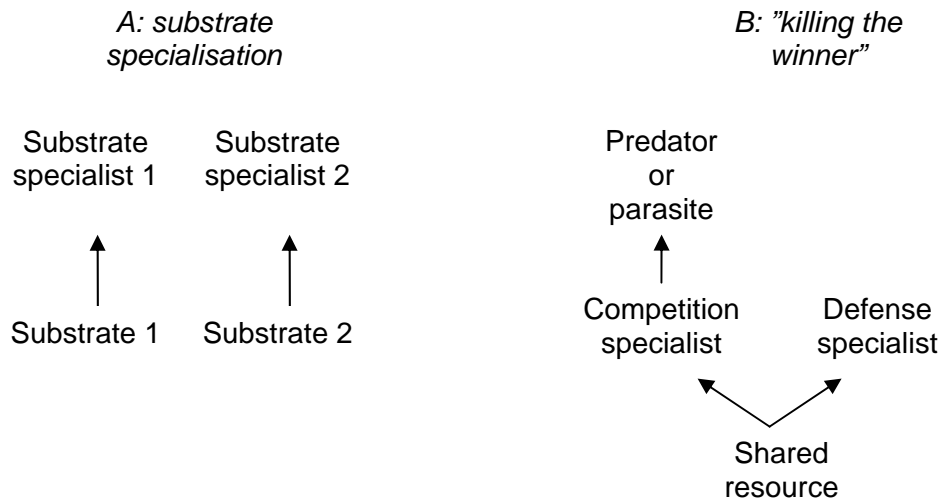


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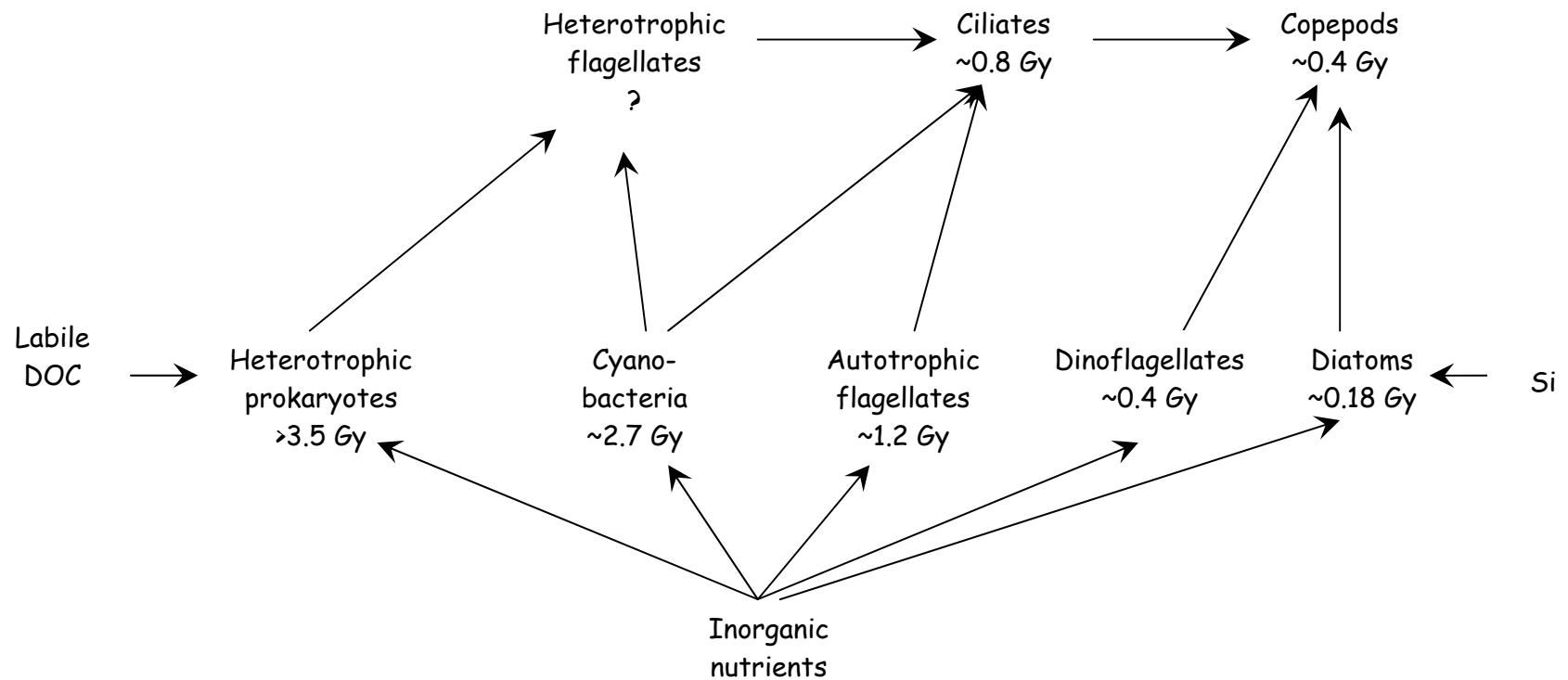


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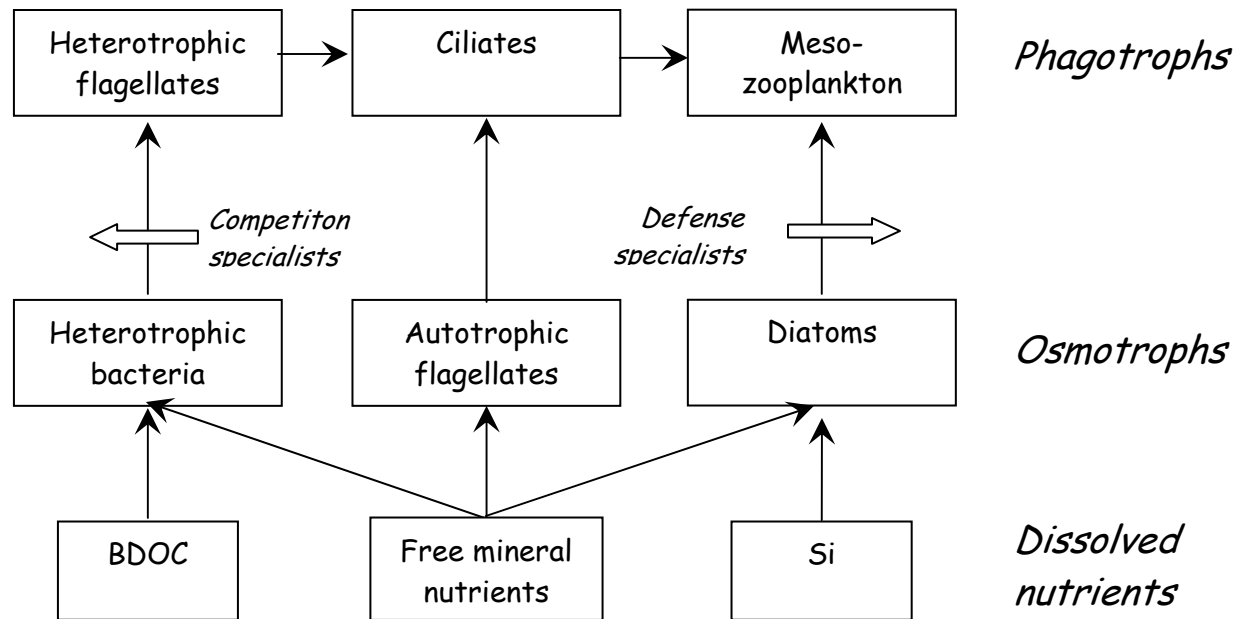


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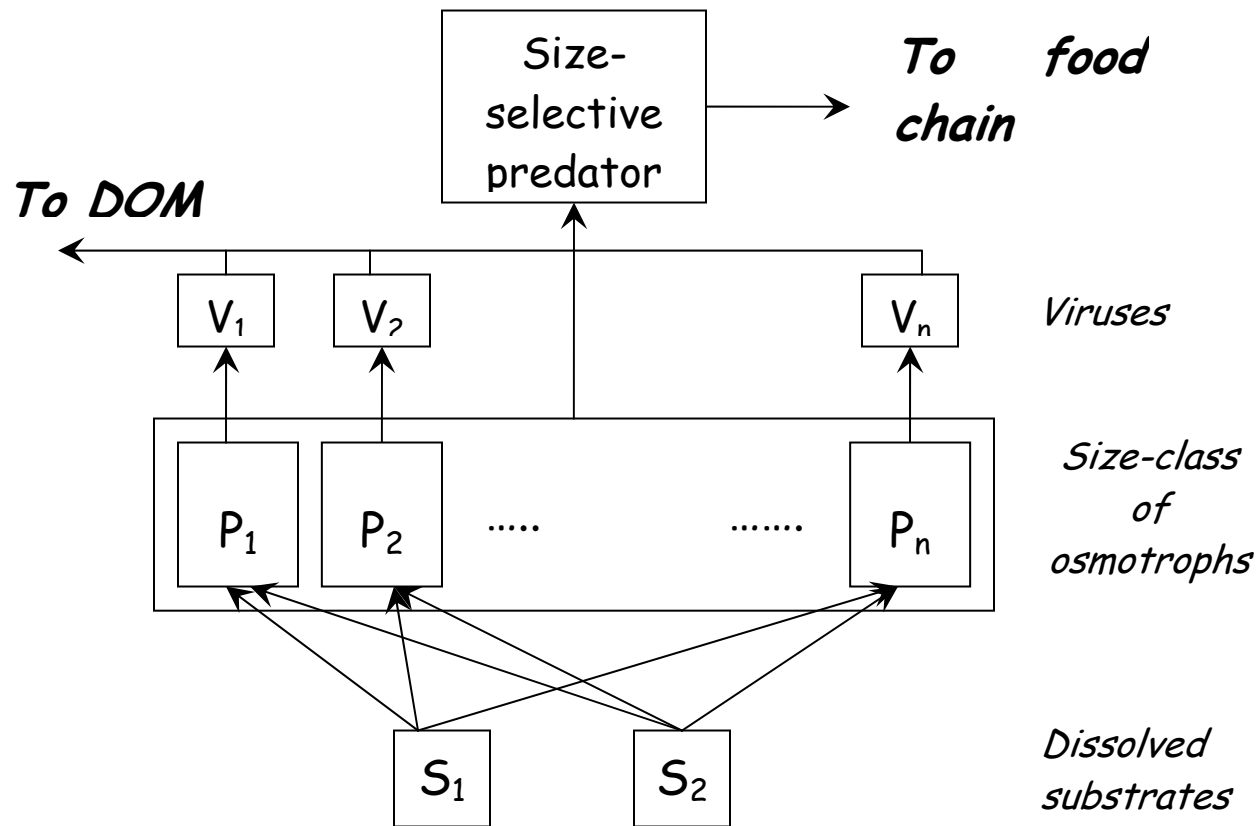


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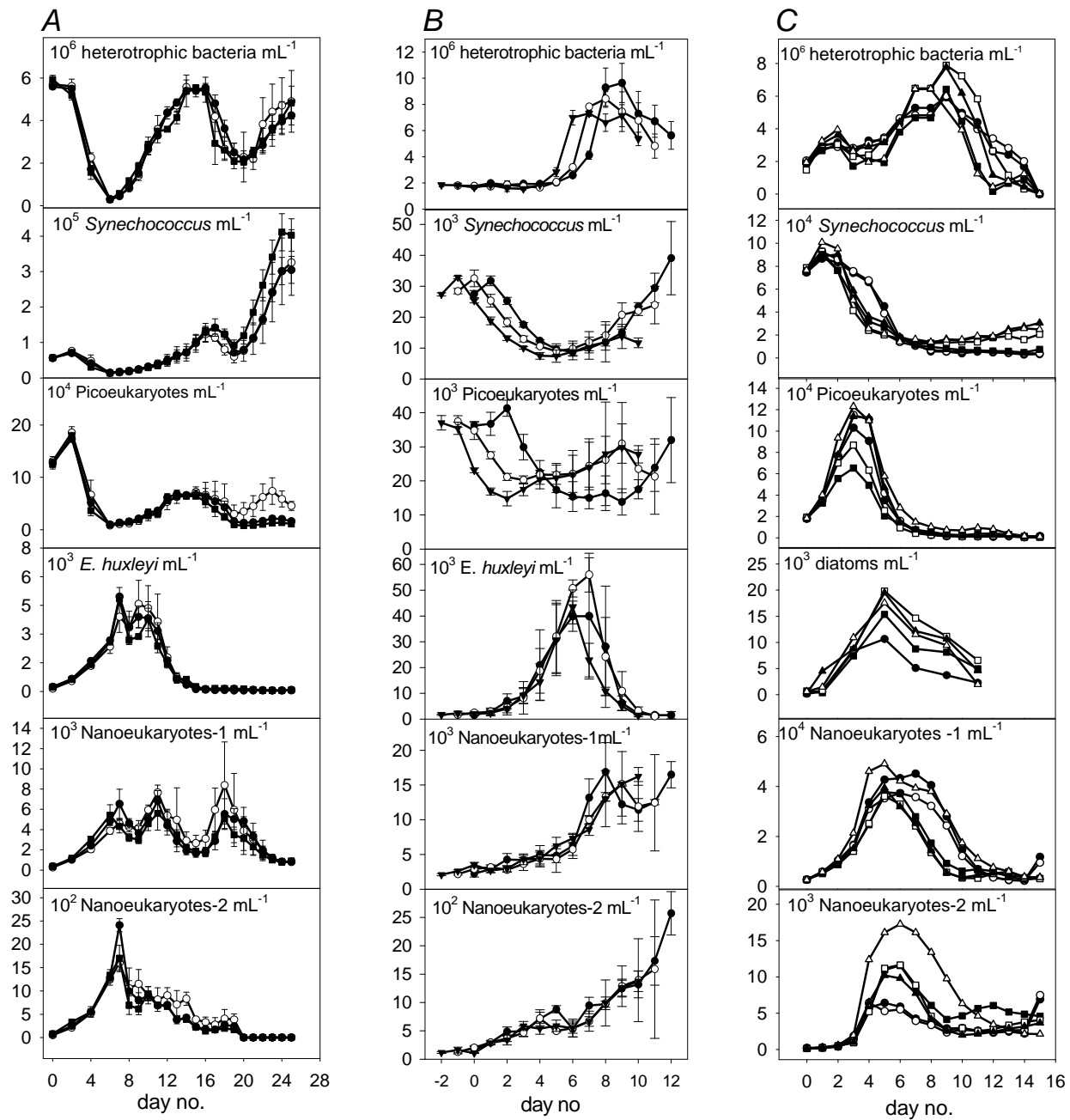


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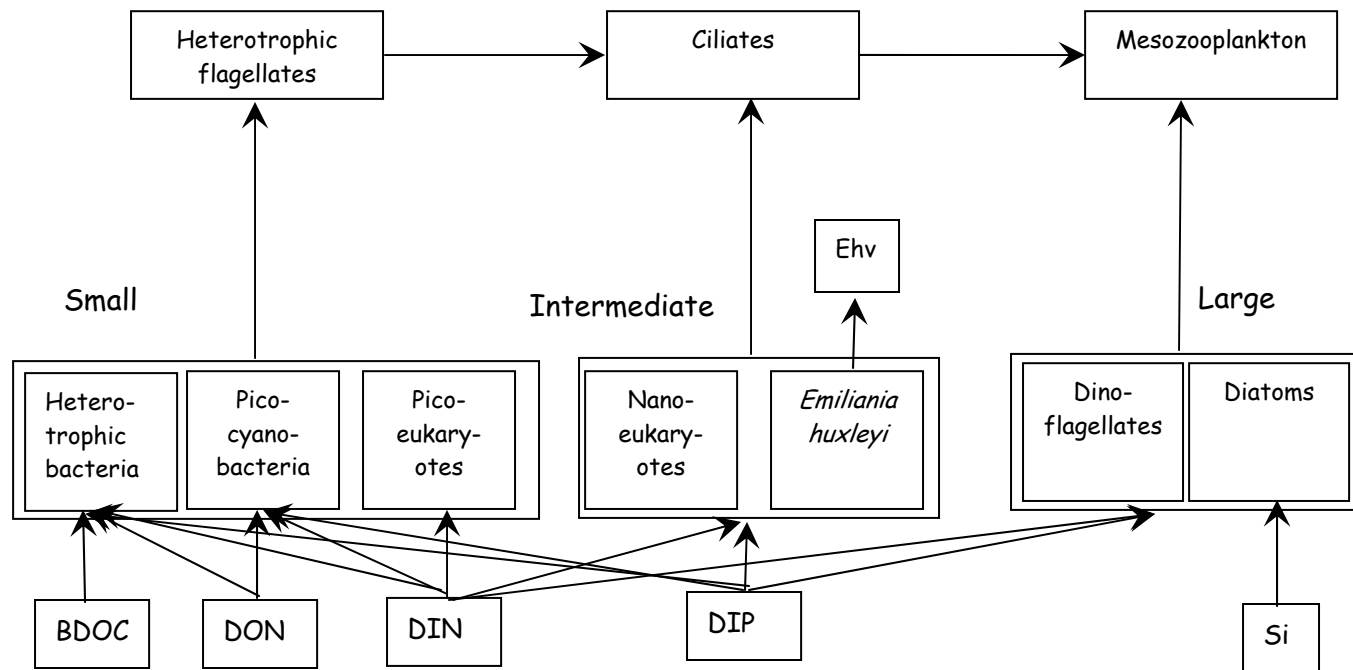


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