Bacterial degradation of dissolved organic carbon (DOC): How much can we learn from simple steady-state descriptions?

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ABSTRACT

Based on practical experience gained from mesocosm experiments, it is argued that in many instances a useful description of the microbial component of photic zone pelagic ecosystems can be obtained by assuming the microbial component remains close to internal equilibrium. The dynamics observed over time scales of days in experiments, such as addition of mineral nutrients and glucose, is then described as a shift in this internal equilibrium resulting from changes in predation pressure as the nutrients are transferred up the food chain to higher predators. This approach allows derivation of simple analytical expressions to describe the state of the microbial part of the food web, a tool claimed here to be better suited for conceptual understanding of system behaviour than the more traditional approach of solving simultaneous differential equations for the whole system. Such a description also allows extremely efficient numerical calculation schemes, a feature valuable for simple implementations in spreadsheets and, potentially, for inclusion of descriptions of the microbial community in large scale circulation models.

The concepts of succession and climax in food webs are well established in traditional ecological theory (e.g., [5]). Intuitively obvious, but less applied, is the fact that different trophic levels have different characteristic time scales and, therefore, parts of a food web may be closer to a climax state than others. In the pelagic food chain, all primary producers, and a large fraction of the heterotrophs, are prokaryotic and eukaryotic micro-organisms with potential growth rates of days. This allows for rapidly developing transient states, and functional groups within this community often seem to reach states where growth more or less balances loss so that net population changes become small (e.g., [9]). Although this close balance between production and consumption for separate functional groups of the food web may be well recognised, few attempts seem to have been made to explore the consequences of this in analyses of experimental results dealing with microbial food webs. This could lead to a more general understanding of how the microbial part of the food web is controlled, as well as facilitating the more technical aspect of constructing more efficient computer models in which fast microbial processes are embedded in the often slower processes associated with biomass changes of multicellular organisms.

Perhaps the simplest mathematical description of trophic links in a microbial food chain from a food source (X_1) to its consumer (X_2), is that based on the traditional Lotka-Volterra type equations. In this case, consumption rate of food is determined by $\alpha_2 X_1 X_2$ where α_2 represents the clearance rate or affinity of organism X_2 for food X_1. When

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multiplied by a yield coefficient Y_2, this gives the growth of X_2. With a specific loss rate δ_2, the differential equation for X_2 becomes:

$$dX_2/dt = Y_2\alpha_2X_1X_2 - \delta_2X_2.$$

If growth balances loss for population X_2 (i.e. $dX_2/dt = 0$) this will lead to the following constraint on the relationship between the food concentration X_1 and the specific loss rate δ_2:

$$X_1^* = \delta_2/Y_2\alpha_2,$$

where the superscript (*) is used to denote the steady state solution. A change in δ_2 thus leads to a new steady state with a different X_1^*. With continuous, but sufficiently slow changes in δ_2, X_1 may move through a corresponding set of states close to those described by the expression for X_1^*. If changes in δ_2 are caused by relatively slow population changes in biomass of the next predator, the lower part of the food web may move through states close to the steady states corresponding to the value of δ_2 at a given time. The steady state of the simple food web of Fig.1a has been analysed using this type of description [6, but see also Thingstad and Rassoulzadegan in this Proceedings]. With ciliates (C) as the top predator (Fig. 1a), steady state concentrations of bacteria (B^*), heterotrophic flagellates (H^*) and free mineral nutrient (N^*) all become proportional to C, while phytoplankton concentration (A^*) decreases with C:

$$A^* = N_T - k_1C,$$

where N_T is the total nutrient concentration available for sharing among the different pools, and k_1 is a proportionality constant. Only as C increases will there be a response in the state variables B^*, H^*, and N^* (all proportional to C).

With differential equations describing the changes in N_T and C, the changes in state of the rest of the microbial food web can then be computed from algebraic solutions of the steady state equations.

In micro- or mesocosm experiments where nutrients are fed slowly (i.e. where N_T increases slowly), this model predicts a succession from phytoplankton to ciliates where the initial response is in A^* only. An increase in A^* means more food for ciliates, which will then grow. Furthermore, since bacterial carbon demand (BCD) is given by:

$$BCD = \mu_BB/Y_{BC},$$

where Y_{BC} is the bacterial yield on the carbon source consumed, and $\mu_B= \alpha_BN$ is the specific bacterial growth rate, insertion will show that BCD changes as the second power of C:

$$BCD = k_2C^2,$$

where k_2 is a new proportionality constant.

The second power dependence on C results from the fact that in this simple network, by preying on the bacterial competitor, ciliates have both a top-down effect on bacteria via predation on bacterial predators, and a bottom-up effect via mineral nutrient competition. If the steady state assumption is reasonably valid, the dynamic changes in bacterial carbon demand will follow the changes in the ciliate population, enhanced by the second power relationship. An interesting aspect of this is if the system's production mechanisms for organic bacterial substrates do not increase as fast as C^2, the effect would sooner or later be a depletion of the pool of degradable organic-C resulting in a shift into a new type of steady state with C-limited bacterial growth [8]. This approach thus provides a framework within which one can describe how shifts occur between mineral nutrient and energy/carbon-limited bacterial growth.

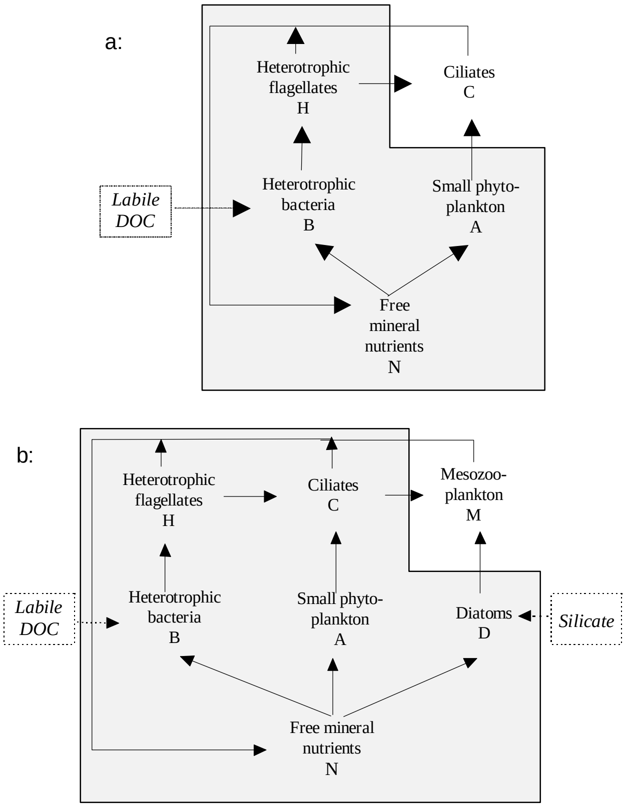

Fig. 1. Idealised food webs. The part of the system that is assumed to be in internal steady state is indicated by the shaded areas. a: System where phytoplankton is restricted to size-classes serving as prey for ciliates. b: System with large phytoplankton represented by diatoms.

One of the problems encountered when trying to compare theory with experiment is the occurrence of diatoms presumably avoiding ciliate predation [7]. The presence of an active diatom population will lead to algal-bacterial competition for free mineral nutrients, even if the biomass of smaller phytoplankton is kept low by ciliate predation. Using an identical approach to that above, the network shown in Fig.1b with the entire microbial part of the food web, i.e. all pools except mesozooplankton (M), assumed to be in steady state, one obtains:

$$BCD = k_3 M^2$$

where k_3 is a new proportionality constant. If this separation between the steady state and the full dynamic part of the food web is realistic, the response in bacterial carbon demand will now be linked to the much slower dynamics of mesozooplankton biomass change. Combining this with the observation that some diatoms excrete carbohydrates [4], the presence of diatoms may thus both reduce consumption and increase production of bacterial carbon substrates. One could then speculate that, under circumstances where silicate addition induces a diatom bloom [2], the probability of mineral nutrient limitation of bacterial growth rate would increase reducing the ability of the system to degrade added glucose.

From the above analysis it should be clear that splitting the food web into parts with different characteristic time scales facilitates analysis of the dynamics of the microbial part of the food web, and makes it possible to derive non-trivial hypotheses of control mechanisms in the food web in a manner difficult to obtain from an analysis based solely on a full dynamic description with differential equations. One conceptually important aspect is the suggested close link between bacterial activity and biomass at the level of higher predators, a result not often recognised in experimental microbial ecology. We have found this hybrid approach to be particularly useful as an aid to understanding microbial trophodynamics in mesocosms [7] and microcosms [8, Thingstad and Rassoulzadegan, this Proceedings] fed mineral and organic substrates.

The approach of treating parts of the system as being in steady state may appear less controversial if one recognises that such a separation is done either explicitly, or more often implicitly, in all dynamic models. In microbial population models, the boundary of the steady state description with Monod-type descriptions [3] usually occurs at a cellular or subcellular level assuming growth rate to be in steady state with nutrient concentration in the environment, and Droop-type descriptions [1] that assume steady state only at the lower level between growth rate and internal substrate concentration. The new approach suggested here is thus not to introduce a separation between dynamic and steady state parts of the pelagic food web but that, for many purposes, it may prove useful to move this boundary upwards to include parts of the microbial food web in the steady state part of the description.

Since this approach allows the integration time step to be adjusted to suit the time scale of processes of higher organisms, it may also have substantial practical advantages when microbial processes are included in larger 1, 2 or 3D models where computer time is a limiting resource.

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