Using dynamic energy budgets to understand benthic*carbon cycling

Henrik Andersson

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1 Carbon cycling in benthic ecosystems

Biogeochemists are interested in the transfer of elements between operationally defined pools such as for carbon, particulate organic carbon (POC), dissolved organic carbon (DOC),particulate inorganic carbon (PIC), dissolved inorganic carbon (DIC) and similar for nitrogen and other elements. The interest of transfer within pools (i.e. transfer from prey to predator is only taking place within POC) only becomes interesting if it affects the transfer between pools.

A long standing question is 'what is the ultimate fate of organic carbon that is deposited on the seafloor?' The fate can either be release back to the overlying water in organic form as DOC, mineralized into DIC or it can be buried in the sediment as POC for very long time (think geological timescale). If it is released, how fast is the release, this determines how the feedback behaves. If it buried it has longterm consequences for the concentration of CO_2 and O_2 in atmosphere. I hope this clarifies the interest of the biogeochemists.

The current belief is that organisms affect the fate, but detailed quantitative knowledge is lacking.

1.1 Long term burial of organic carbon

Burial of organic carbon in sediments affects the atmospheric contents of O_2 on a multi million year timescale by hiding degradable organic carbon away from exposure to oxygen. One controlling factor of organic carbon preservation is oxygen exposure time defined as, the oxygen penetration depth divided by the linear sediment accumulatin rate. The reason that oxygen exposure time (Hartnett et al.,

**benthic* means at the seafloor, as opposed to pelagic, which means in the water column

1998) controls partly the burial of organic carbon is not fully understood but believed to be connected to the production of H_2O_2 of *aerobic bacteria* which can oxidize organic matter sorbed onto inorganic minerals (Hulthe et al., 1998).

So understanding burial, means understanding the activities and presence of different bacterial groups and most certainly also the interactions with macrofauna, which is discussed more below.

1.2 Release of carbon back to the overlying water

If organic carbon is not buried, it is released back to the overlying water in one form or another. This is either as incompletely degraded dissolved organic substances, e.g amino acids or other not even identifiable substances. Most part of the organic carbon is remineralized to DIC. Depending on how deep your benthic system is situated this affects the pCO_2 of the ocean and indirectly the $[CO_2]$ of the atmosphere on different timescales (from days to the timescale of ocean circulation which is on the order of thousands of years).

It is obvious that living organisms are having a very active part in this play, although they are not explicit in any biogeochemical model covering this topic e.g. Soetaert et al. (1996); Boudreau (1996). A straightforward role bacteria, meiofauna and macrofauna play is in the process of respiration where organic carbon is converted to inorganic carbon. To understand this process we need some knowledge on how biological systems are functioning. Respiration is not equally straight forward if you have a biological view (and hence are not primarily interested in chemical fluxes, but the functioning of your pet organisms) of the benthic community because respiration have several contributions such as maintenance and overhead costs of growth. Respiration can also be measured in different ways (O_2 or CO_2 fluxes) that are not always arbitrary.

Transfer of organic carbon in a benthic system often means transfer between organisms of different size classes which have different but predictable behavior (see Section 2).

A more indirect way that benthic organisms can influence the biogeochemical transfers is by mixing their environment. This is done by just moving around or by feeding at one place and defecating some place a few centimeters below or above or by pumping fresh oxic water to sustain themselves. The mixing displaces fresh organic matter from the sediment surface and transports it down to deeper layer where it may end up being degraded by other organisms than if it would stay at the surface and released slower. Animals pumping water to sustain themselves also pump out metabolic products such as nitrogenous waste and this creates a faster feedback than by molecular diffusion only.

1.3 Particulate inorganic carbon

The above mentioned fates (i.e. burial or release) of POC also applies for PIC (e.g. calcium carbonate). Dissolution of PIC is dependent on the saturation state of the overlying water but is affected by the mineralization of organic carbon trough the production of a local slightly acid environment (CO_2 is a weak acid). This means that dissolution of inorganic carbon which is believed to be a nonbiological process is still intimately linked to the life that occur in the sediment.

2 The role of dynamic energy budget theory

Dynamic energy budget (DEB) theory (Kooijman, 2000) provides a consistent framework based on explicit assumptions applicable and tested on a great variety of living organisms. This is obviously a good start for somebody interested in improving benthic models by including living organisms explicitly.

DEB provides mechanistic explanations and mathematical expressions for feeding, assimilation, production of faeces and production of inorganic minerals. A systematic approach like this where chemical fluxes is a natural part is essential if your organisms is part of an ecoystem approach.

Other models where growth is an intrinsic property of your organisms does not always obey mass conservation and are therefore quite useless for biogeochemists (interested in mass transfers). Models where the primary interest lies in population dynamics , expressed as numbers of individuals, are also note very useful.

A benthic community consists of organisms ranging from bacteria (μm) to epibenthic fishes (dm – m). DEB has emergent properties such as the body size scaling relationships that provide us with some insight to different behavior of these size classes of organisms and therefore the relative role they can play on the benthic ecosystem scene.

3 Conclusions

Carbon cycling in benthic communities is the result of a strong interaction between chemistry and biology, you can't understand one aspect fully without considering the other. My hope (being a biogeochemist, and believing that I have some grip on the chemical stuff) is that, through using a consistent framework based on explicit assumptions applicable to organisms of all sizes i.e DEB, we can achieve a better understanding of the energetics of the benthic organisms and using this knowledge to further advance the understanding of the chemical transformations taking place in the benthic ecosystem.

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