OCEANOGRAPHY

# Escape by dilution

## Dissolved organic matter in much of the deep ocean is too dilute to be consumed by microbes

By **Jack J. Middelburg**

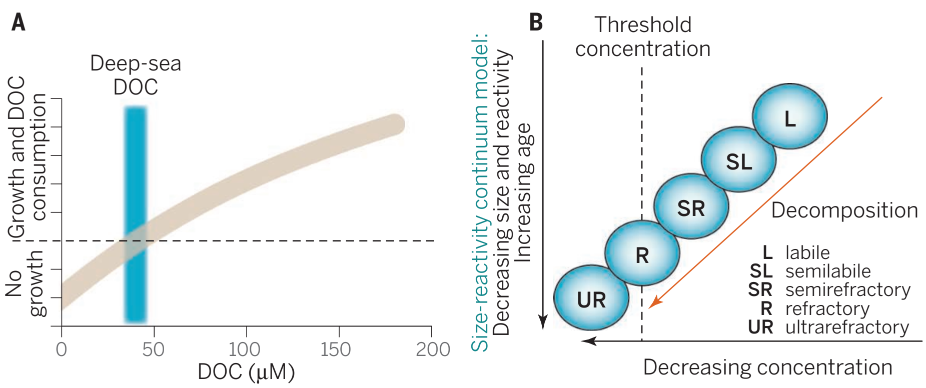
Earth's oceans contain as much carbon in the form of dissolved organic matter (DOM) as does the biosphere, and more than 200 times that of living marine biomass. Most of the DOM is in the deep sea below 1000 m. Radiocarbon data show that the bulk of the DOM is thousands of years old (*1*). This long residence of DOM in the deep ocean is intriguing: Prokaryotes (bacteria and archaea) are abundant and active in the deep ocean, and many of them require DOM for energy and carbon. Moreover, molecular biology data show high metabolic diversity in the deep ocean (*2*). Why does some DOM escape degradation in the deep sea? Nutrient limitation of consumer biomass may explain underutilization of resources in nutrient-low surface waters (*3*), but this does not apply to the nutrient-rich deep sea. On page 331 of this issue, Arrieta *et al.* (*4*) show that DOM is too dilute to be consumed.

The ruling paradigm is that deep-sea DOM accumulates because it is difficult for microbes to break down (it is recalcitrant) (*1*, *5*). This low reactivity of DOM is thought to relate to its chemical composition and degradation history. However, DOM in the deep sea is largely unidentified, and chemical structure information thus provides little guidance as to whether DOM compounds are inherently recalcitrant.

Arrieta *et al.* challenge the commonly accepted paradigm. Instead, they revisit Jannasch's dilution hypothesis (*6*), which states that the growth of microbes (and hence DOM consumption) ceases when concentrations fall below a threshold value (see the figure). They provide direct experimental proof that an increase in DOM concentration results in microbial growth under conditions similar to those in the deep sea in terms of substrate and temperature (although not pressure). No response would be expected if deep-sea DOM were intrinsically resistant to consumption. Moreover, using Fourier-transform ion cyclotron resonance mass spectrometry, the authors show that marine DOM contains thousands of different molecules, many of which were consumed during incubation.

If dilution rather than the intrinsically recalcitrant nature of compounds limits DOM utilization, one would expect DOM to never be depleted completely and deep-sea DOM concentrations to be near the threshold for consumption. This is indeed what is observed (see the figure, panel A) (*5*). Moreover, addition of dissolved organics to the DOM pool should stimulate consumption.

### Carbon consumption in the deep ocean




**Too dilute to be consumed.** (**A**) DOM concentrations in the deep sea are near the threshold below which no microbial growth occurs. Arrieta *et al*. report active DOM degradation by microbes at concentrations above the threshold. (**B**) Degradation of DOM results both in a decrease in size and reactivity and a decrease in concentration down to the threshold level identified by Arrieta *et al.* (*4*). Below the threshold, degradation of DOM is limited, but aging may continue.

Thus, addition of newly produced DOM in the sunlit layer may elevate compound concentration levels above the threshold, causing degradation of "aged" organic matter brought to the surface by upwelling. This priming may, combined with ultraviolet-induced photolysis, cause eventual removal of DOM from the ocean.

Arrieta *et al.*'s results also put an upper limit on the efficiency of the microbial carbon pump—that is, the microbial conversion of labile into more refractory DOM that remains in the ocean for long periods of time (*7*). Large increases and decreases of the deep-sea DOM reservoir have been proposed for the Precambrian and Eocene (*8*). This will not be a feasible mechanism if the dilution hypothesis is correct.

The well-established and widely accepted reactivity-size continuum model (*5*) links degradation of DOM to decreases in molecular size and reactivity and increases in radiocarbon age and chemical complexity. In contrast, the dilution hypothesis is neutral with regard to the quality of organic matter. How can we reconcile these two apparently conflicting views of DOM dynamics?

Organic matter degradation involves not only a decline in concentration but also a decrease in reactivity (*9*) because of the preferential consumption of labile organic matter (see the figure, panel B). During the initial stages of degradation, DOM concentrations are far above the threshold, and changes in reactivity, size, and composition of organic matter upon degradation are clear. Steady degradation of DOM eventually results in concentrations near the threshold level in the deep sea, and DOM consumption rates decrease. Arrieta *et al.* show that deep-sea DOM is consumed when concentrated, which suggests that the reactivity of DOM compounds is concentration-dependent. This complicates attribution of DOM survival to either quantity or quality of DOM. It also adds to the emerging picture that organic matter degradation kinetics are not merely an inherent property of the compounds, but rather depend on the context (such as oxygen availability, time frame, and concentration). ■

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