965SV_L01c

0. Ethics in science, plagiarism and AI

1. Microbes in the Marine Environment

2. Metabolic Diversity and Ecophysiology of Marine Microbes

3. Diversity of Marine Bacteria, Archaea, Viruses and unicellular Eukaryotes

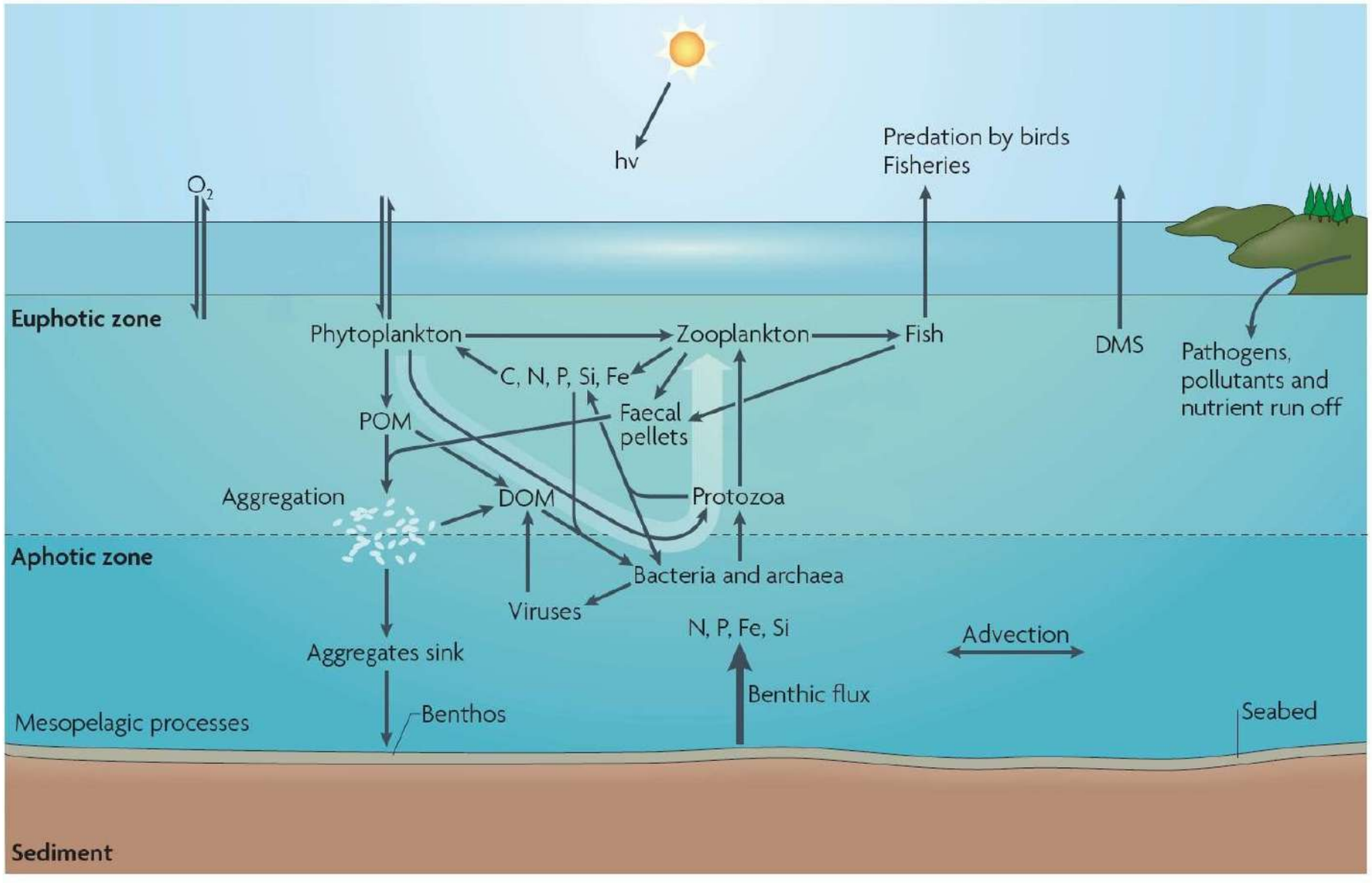
4. Microbes in Ocean Processes: Carbon and other nutrients

5. Marine Microbial Symbioses and Diseases

6. Marine Microbes, Climate and Society

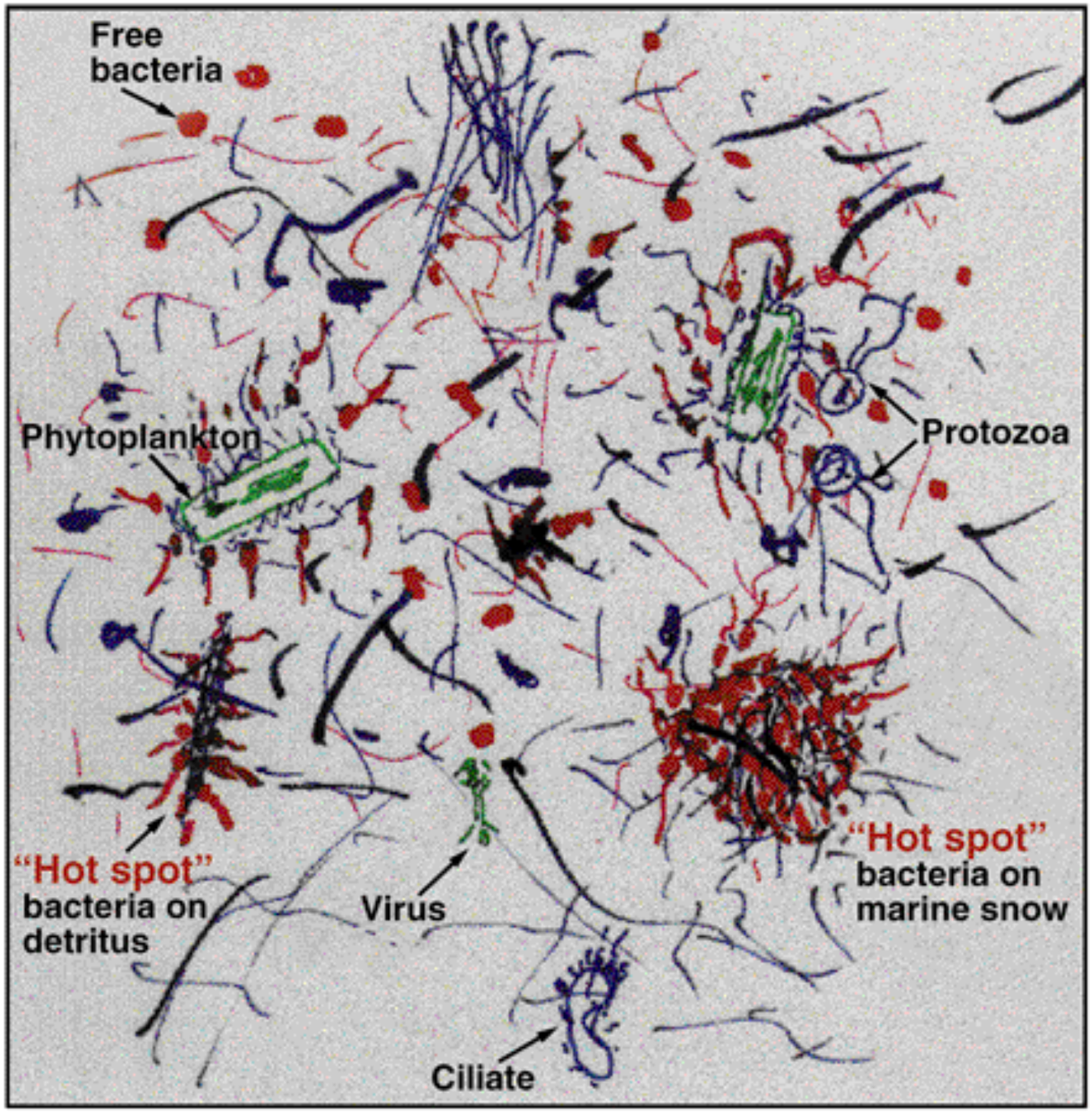
Organic matter

- Source of organic matter is biology
- C-H bond, living or once living organisms
- Production and decomposition/degradation of organic matter
- Atmospheric CO_2 is fixed by photosynthesis or chemosynthesis —> Carbon Cycle



Azam & Malfatti, 2007

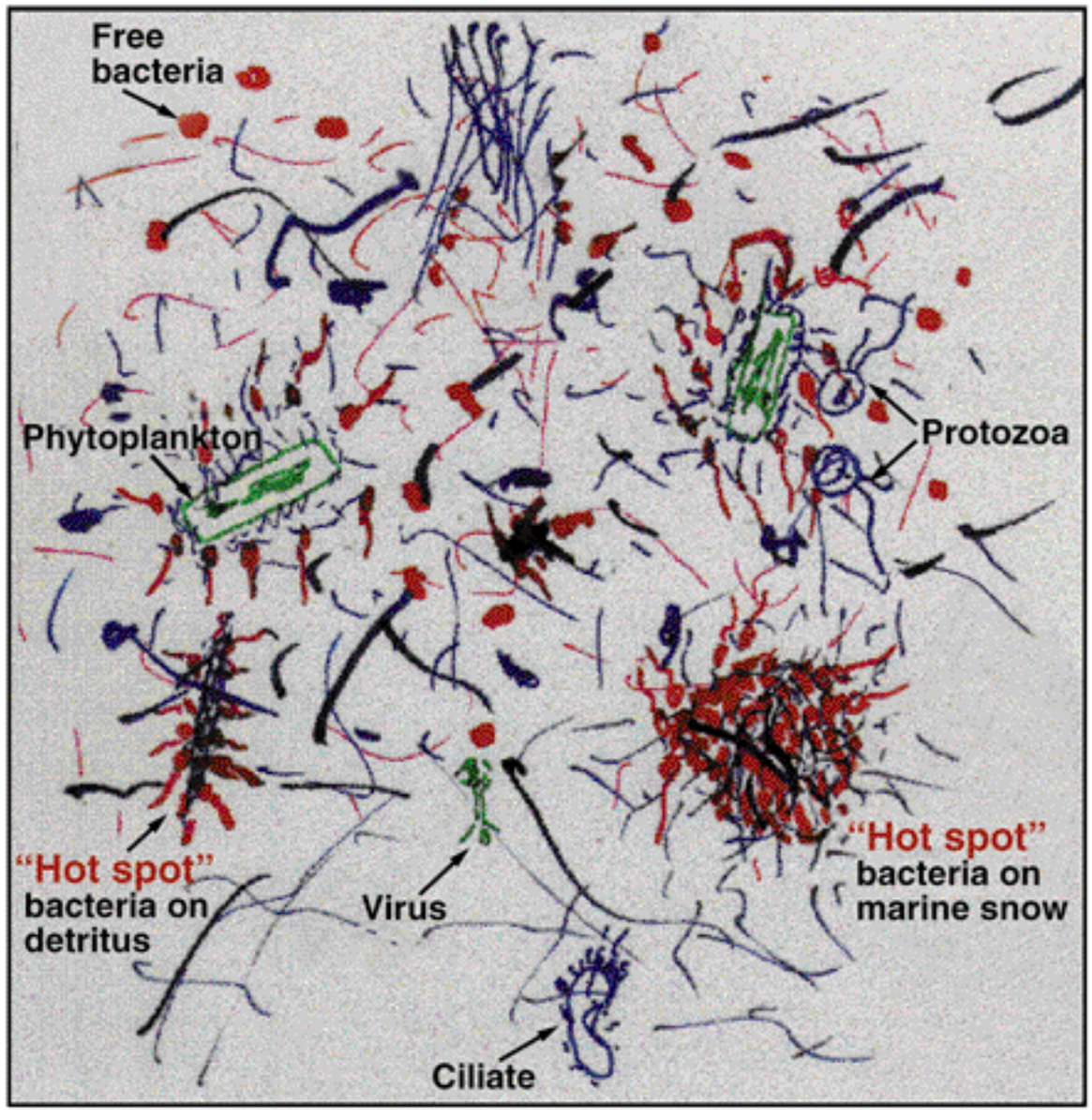
Organic matter



by Farooq Azam

Azam, F. 1998 Science 280:694-696

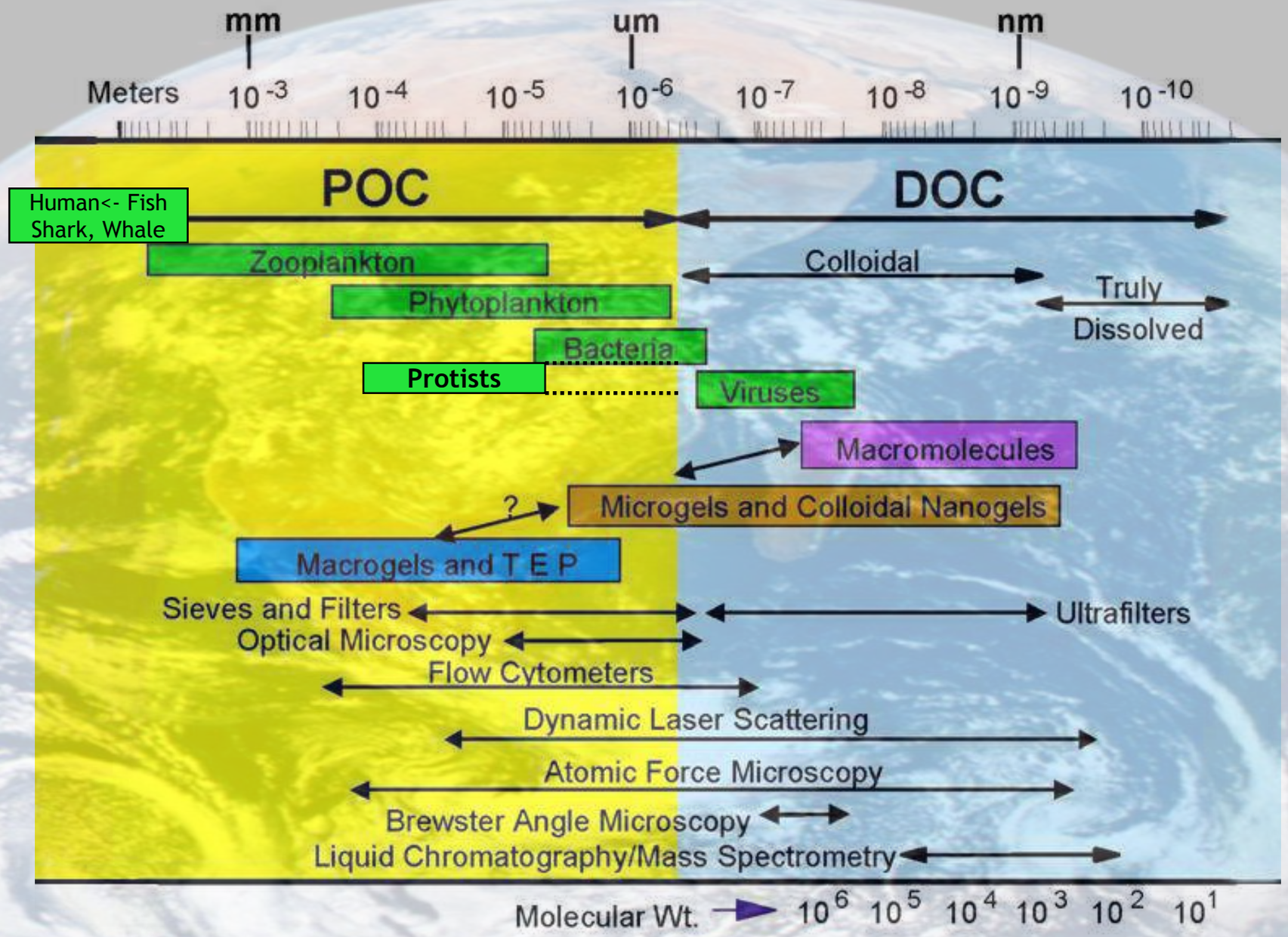
Organic matter



- Highly diverse supra-molecular shapes
- Size continuum
- Providing structure at the microscale for microbes
- Nutrient source
- Dynamic continuum in space and time
- Natural and anthropogenic compounds
- Light-active compounds

Azam, F. 1998 Science 280:694-696

Organic matter continuum: a unifying concept to understand how bacteria perceive and interact with organic matter



F. Azam

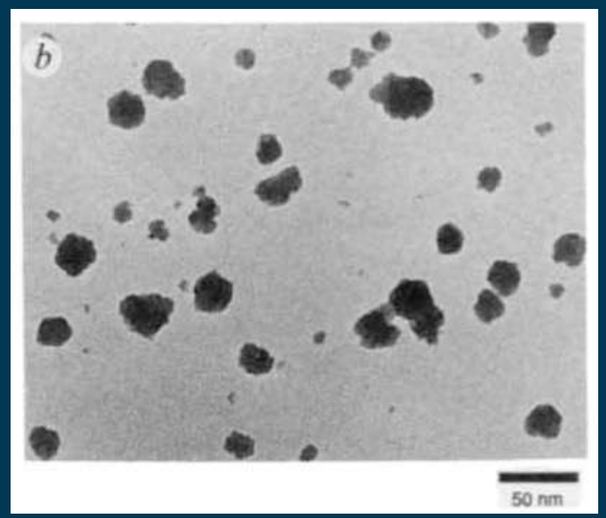
Verdugo et al. 2004

Ocean is replete with transparent gel particles (~ million/liter) creating a gel-like milieu

Bacterium-eye view of organic matter

Bacteria experience organic matter as a patchy size continuum

Colloids (10^8 mL^1)



Koike et al., 1990

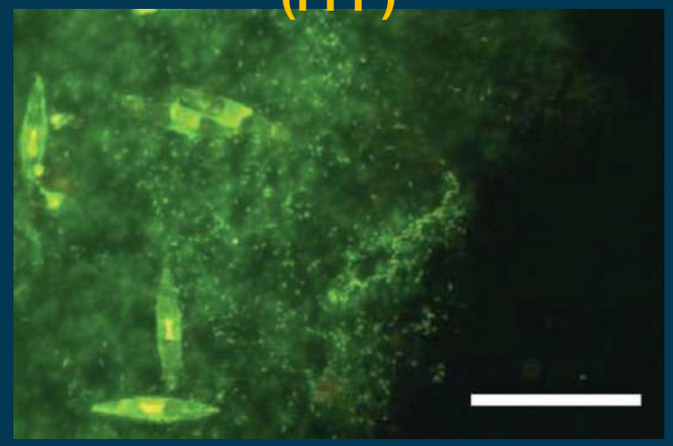
Wells & Goldberg, 1991

Coomassie Stained Particles (CSP)



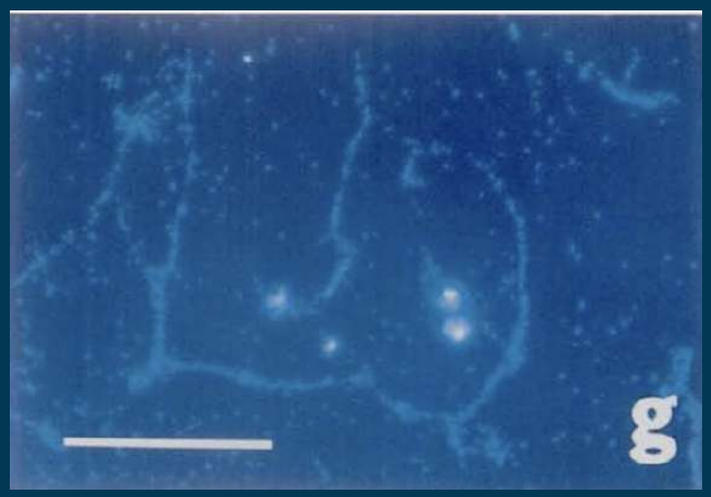
Long & Azam, 1996

Filter Fluorescing Particles (FFP)



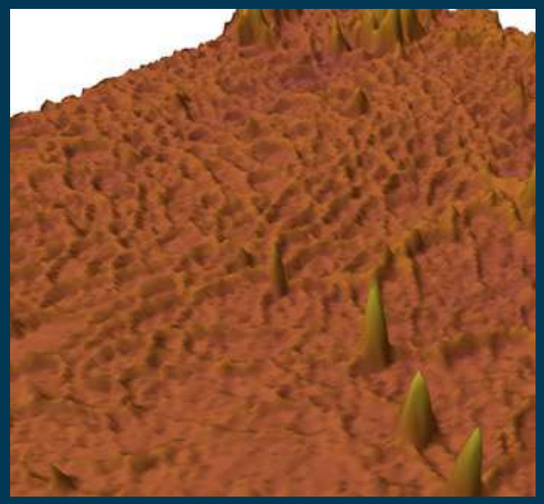
Samo, Malfatti & Azam 2008

Transparent Exopolymeric Particles (TEP)



Alledrege et al., 1993

Gel network from Adriatic Sea



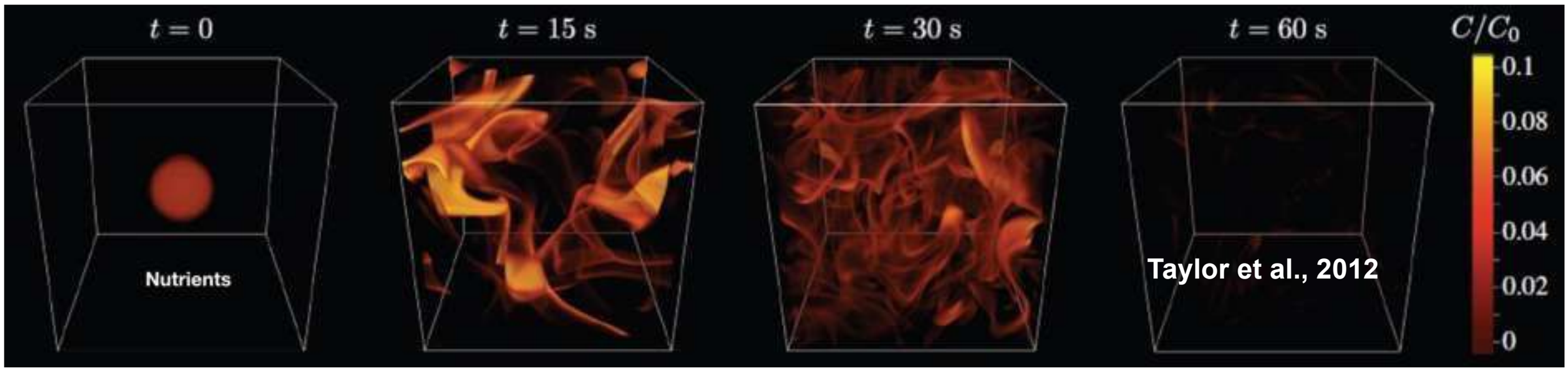
Malfatti unpub.



Nino Caressa

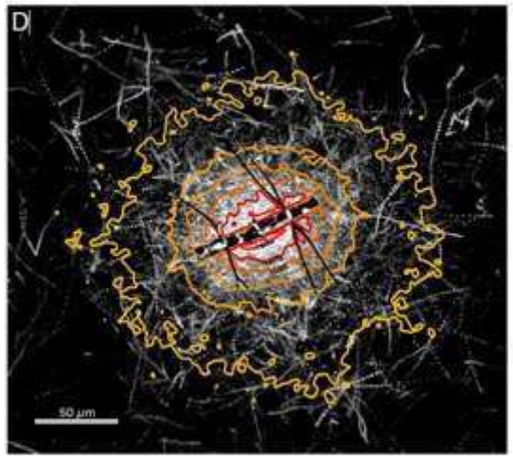
by Farooq Azam

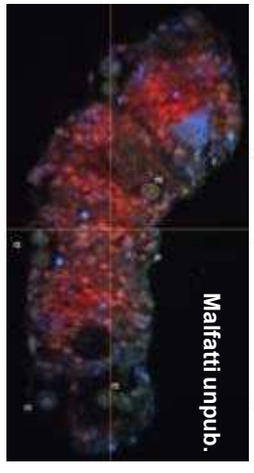
3D organic matter structure in space and time

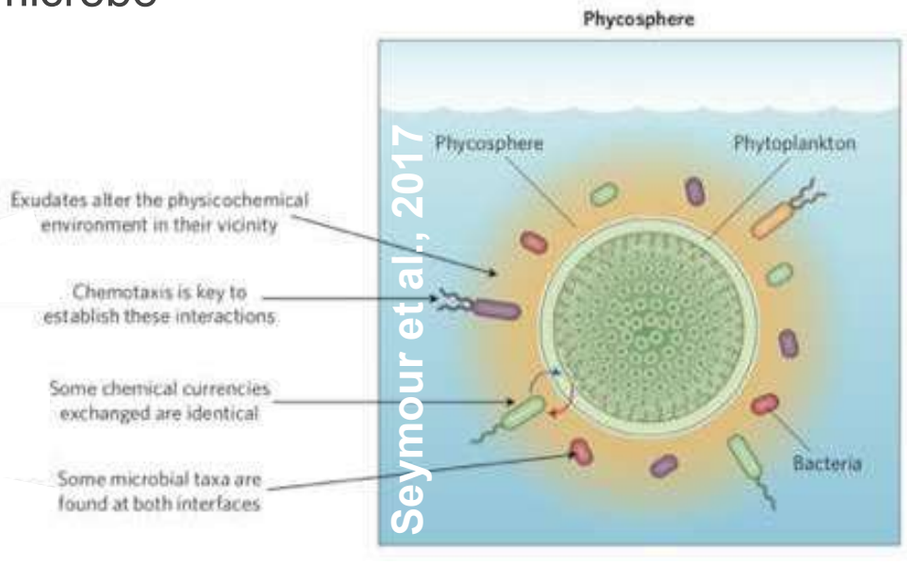


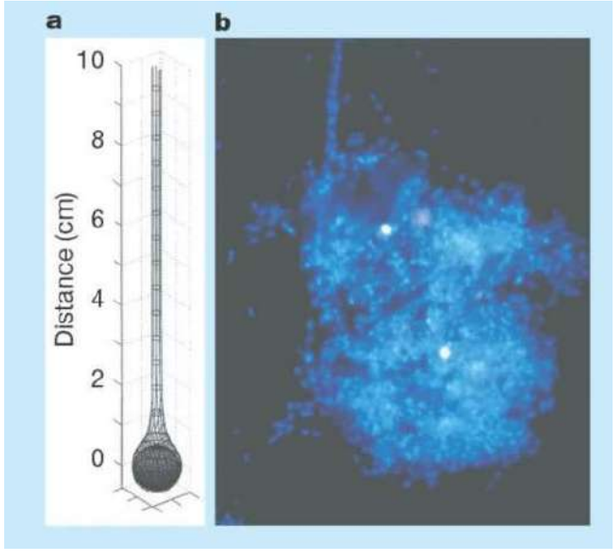
- Nutrient patch evolution and sources
- Low Reynolds number —> high viscosity
- Modelling in time and space in a turbulent flow (L= 5.65 cm)
- Nutrient sources: living phytoplankton, dying phytoplankton, dying copepods, marine snow plume, fecal pellets, dying bacteria and other microbe

Smriga et al., 2016



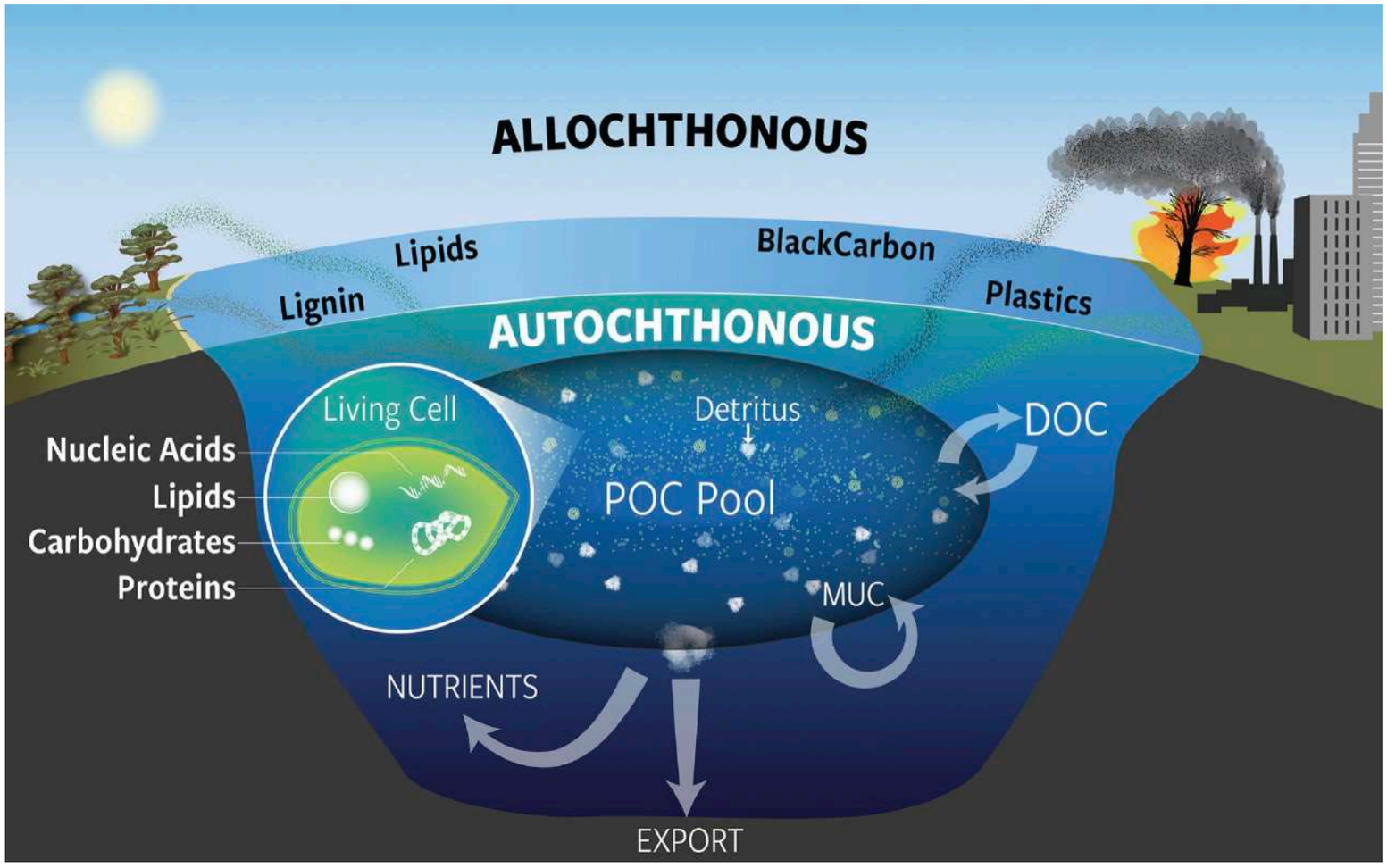






Kiørboe & Jackson, 2001 Azam, & Long, 2001

Organic matter (OM/OC): particulate pool



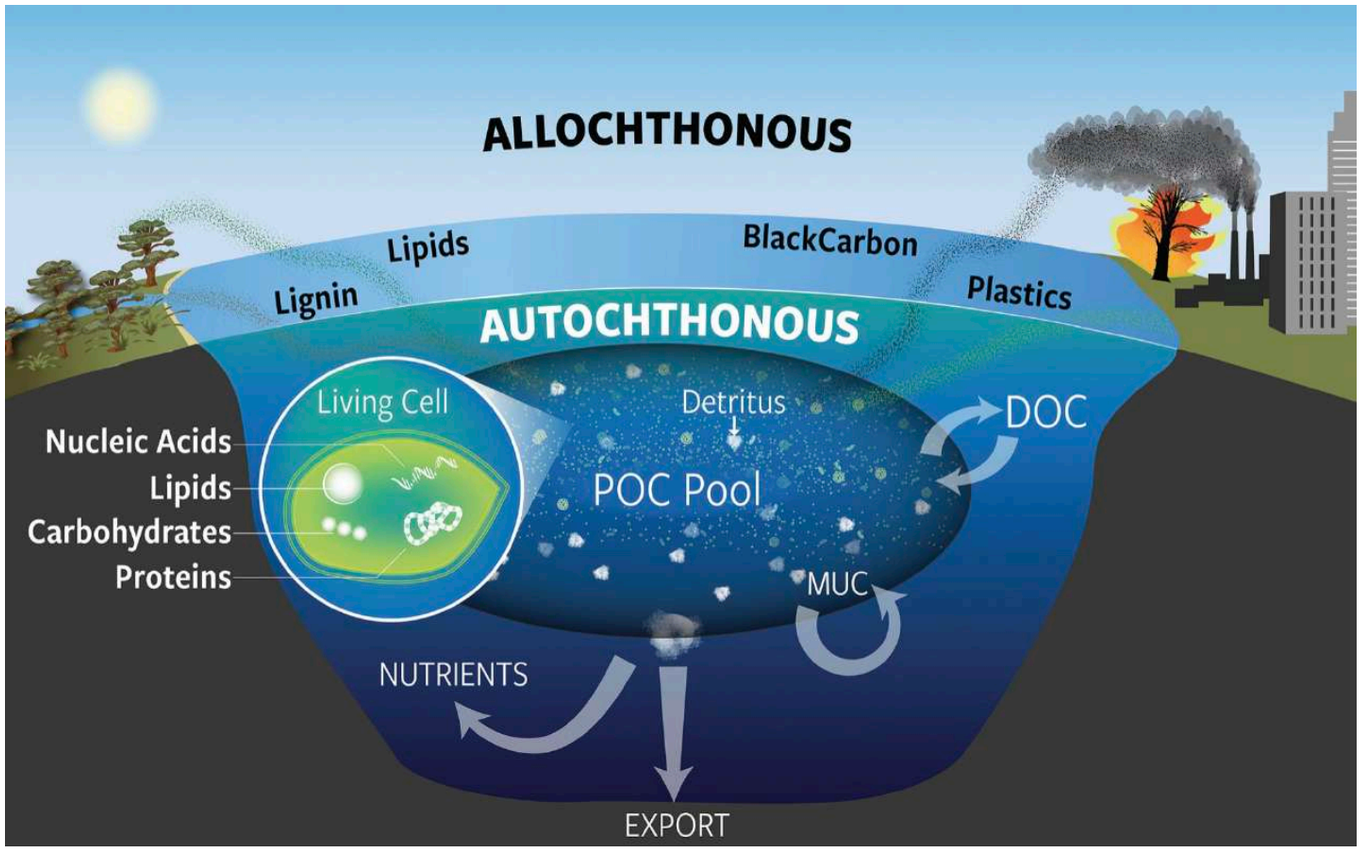
Kharbush et al., 2020

POC includes components of **living** cells as well as **dead material (detritus)**, and originates from both allochthonous and autochthonous sources

The POC pool can also **exchange** material with the dissolved OC (**DOC**) pool through **aggregation and disaggregation of particles**

This process and others may be involved in the formation of the **molecularly uncharacterized component (MUC)**, which may **incorporate both autochthonous and allochthonous OC**

Organic matter (OM/OC): dissolved pool



Kharbush et al., 2020

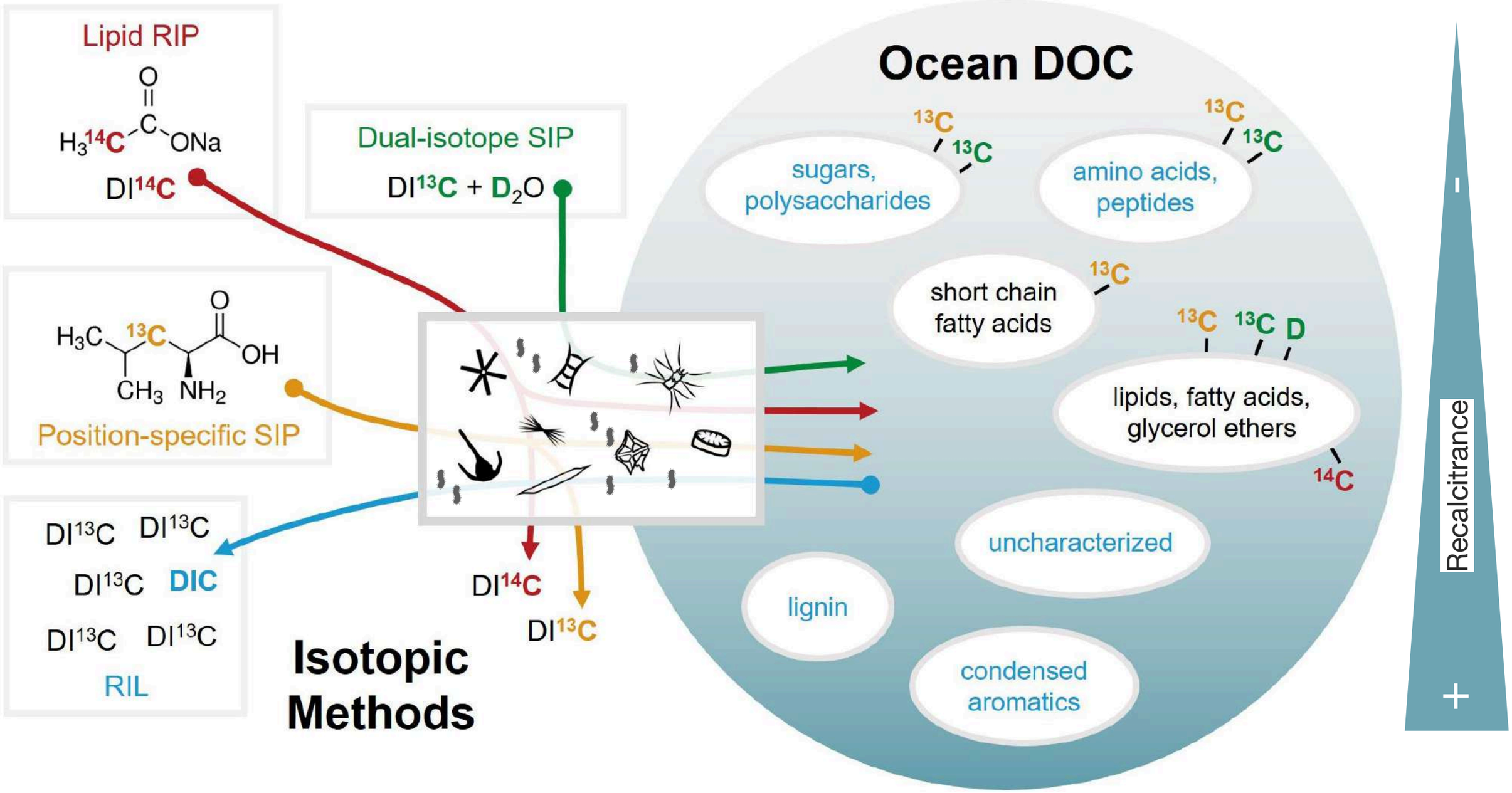
Internal, or autochthonous, DOC sources include **planktonic organisms (life and death, primary production)**, benthic microalgae, macrophytes, and sediment porewater

DOC from **external, or allochthonous, sources**, has mainly terrestrial origins, including wetlands, river and surface runoff, groundwater discharges, and atmospheric deposition

The main **sinks** for **DOC** from the water column in coastal waters are the following: (1) bubble coagulation and abiotic flocculation or sorption to particles, (2) sunlight-mediated photodegradation, and (3) **microbial degradation by mainly heterotrophic prokaryotes**

Organic matter

Wagner et al., 2020



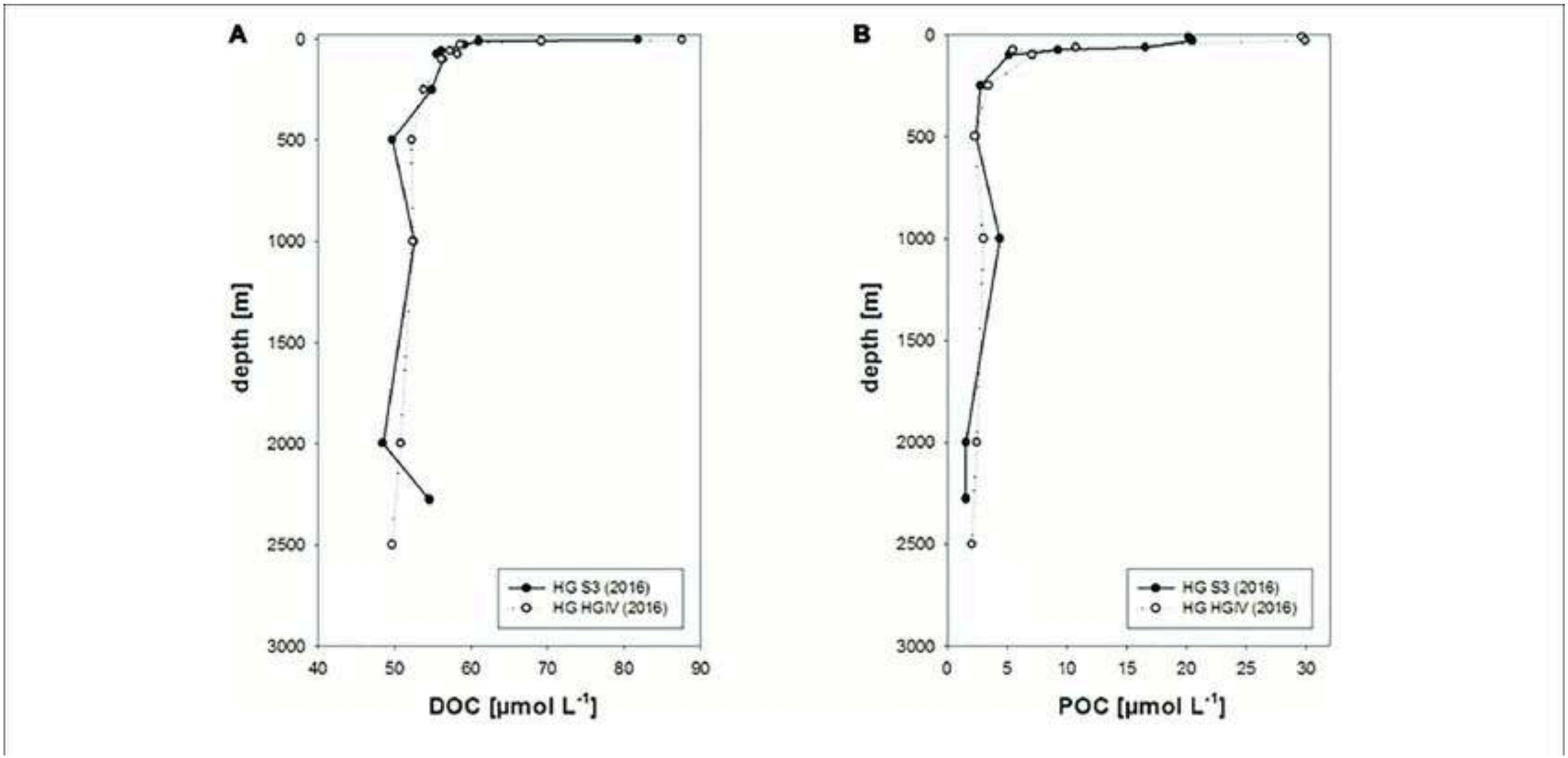
Stable (13C) and radiocarbon (14C) isotopic techniques used to probe metabolic pathways for the biosynthesis and microbial turnover of DOC by planktonic communities in the ocean

Used techniques are: position-specific and dual-isotope stable isotope probing (SIP), lipid radioisotope probing (RIP), and reversed isotope labeling (RIL)

Isotopic methods in a glance

Technique	Main question	What it tells you
^13C SIP	Where does this carbon go?	Substrate assimilation and carbon flow
^14C	How old/persistent is this carbon? How rapidly is it consumed?	DOC age and turnover
Position-specific SIP	Which carbon position is transformed?	Detailed metabolic pathway
Dual-isotope SIP	Are C and N assimilated together?	Coupled C–N metabolism
Lipid RIP	Which organisms convert this carbon into cellular lipids?	Metabolism + microbial identity
RIL	How rapidly are existing molecules replaced?	Biosynthetic/turnover rates

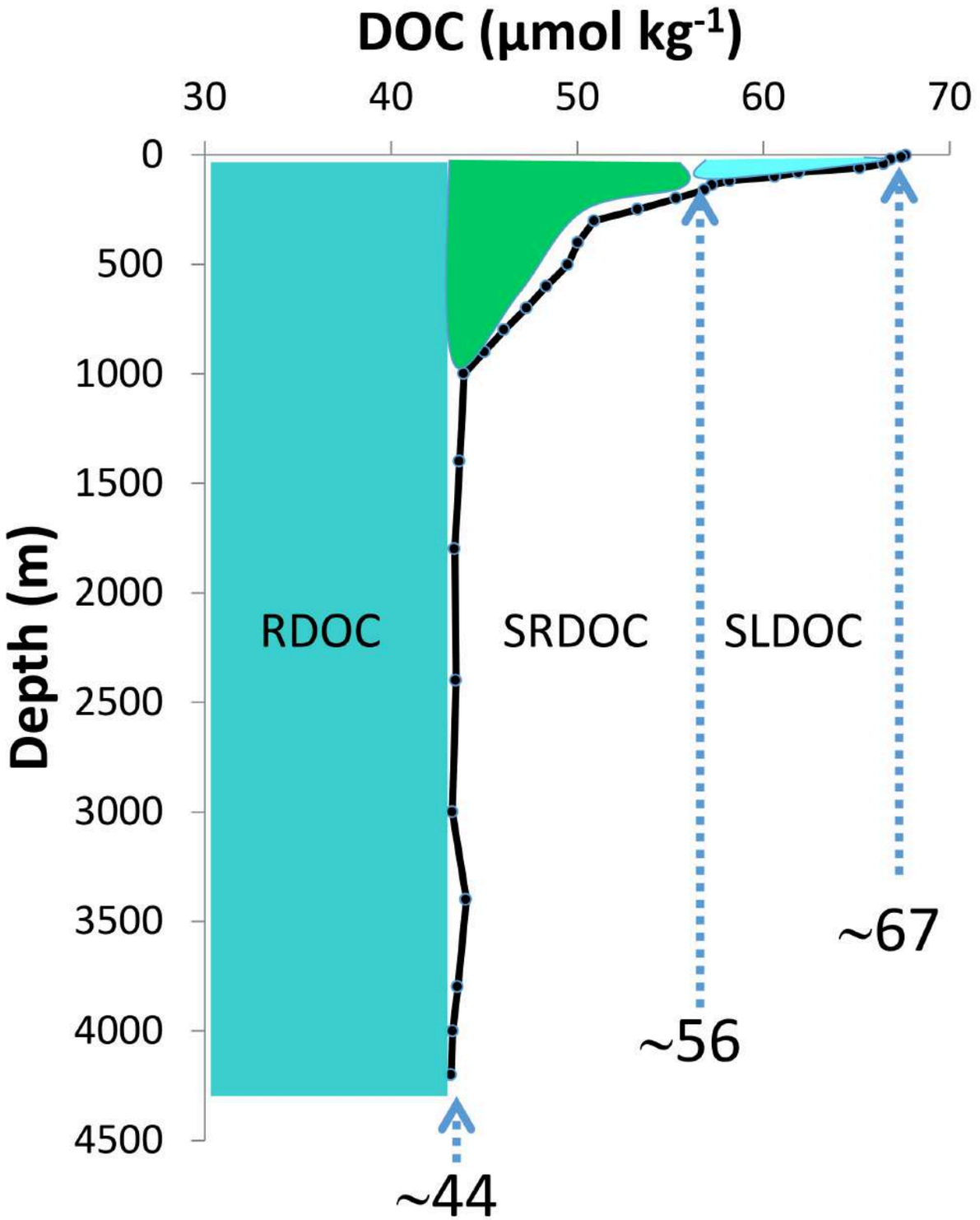
POC and DOC profile



Engel, 2019

- High concentration in surface ocean of DOC and POC
- Rapid turnover in surface ocean
- POC <—> DOC
- POC needs to be solubilized for being used by microbes

POC and DOC profile



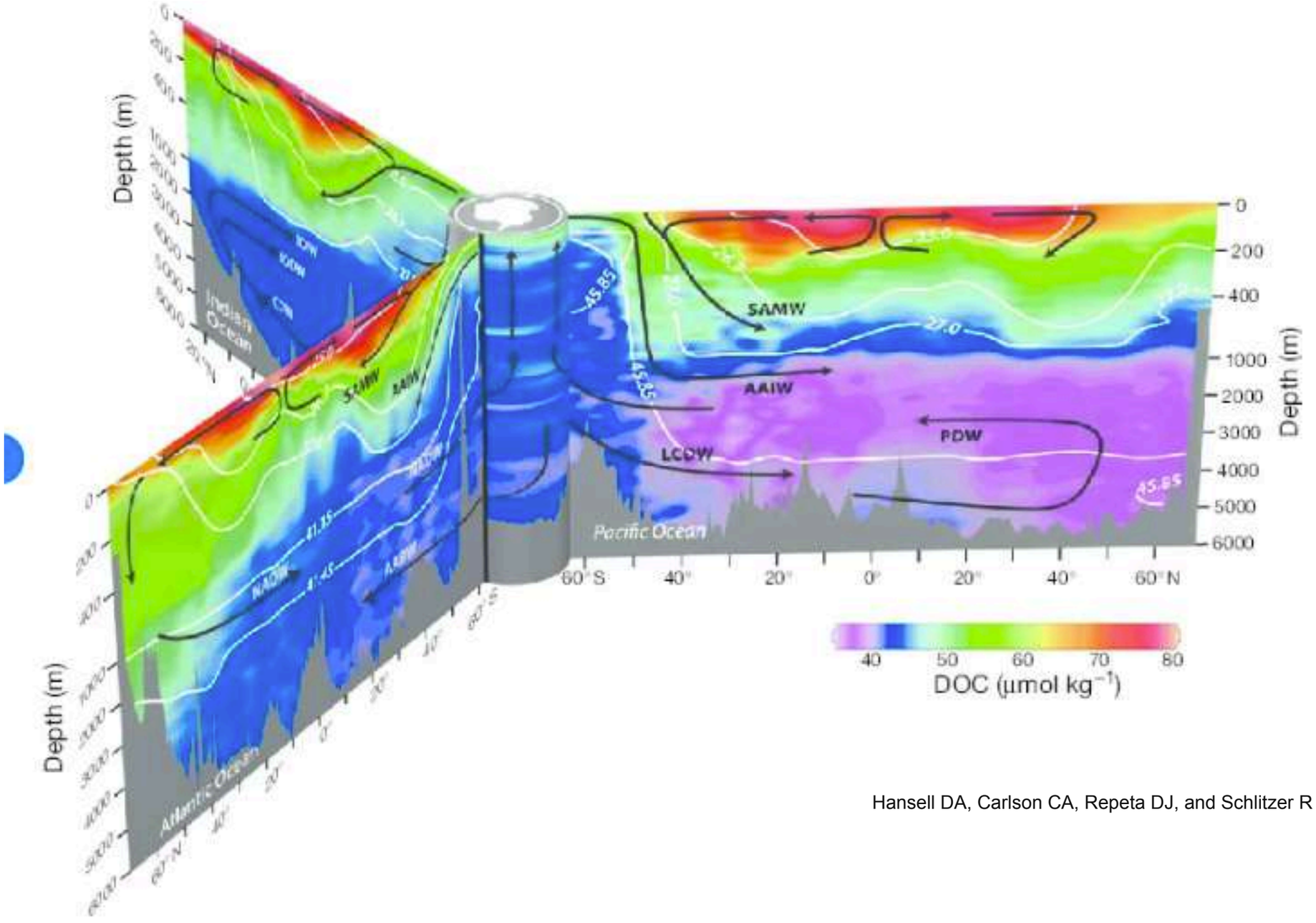
Utilization continuum R> SR>SL

Dissolved organic carbon (DOC) profile (solid line, with sampling depths from August 2008 indicated) and fractions (shaded regions) assigned in the western Sargasso Sea, in micromoles per kilogram.

Concentration boundaries of the fractions shown are approximate. RDOC, refractory DOC; SRDOC, semirefractory DOC; SLDOC, semilabile DOC

Hansel, 2013

Dissolved organic carbon (DOC) concentrations in the world ocean



Hansell DA, Carlson CA, Repeta DJ, and Schlitzer R (2009)

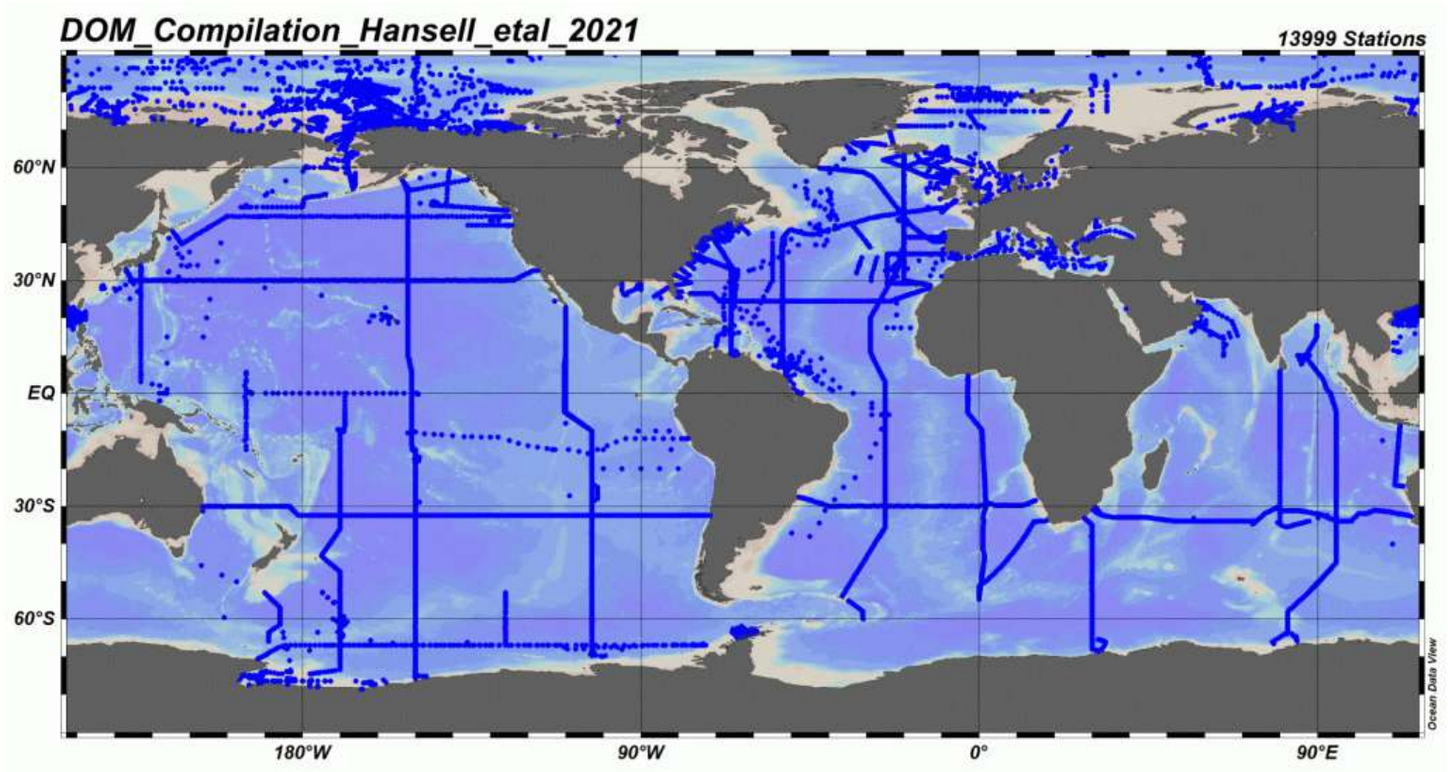
Black arrows depict main water currents. White lines indicate isopycnal surfaces (surfaces with the same density).

NADW, North Atlantic Deep Water; SAMW, Subantarctic Mode Water; LCDW, Lower Circumpolar Deep Water; PDW, Pacific Deep Water; CDW, Circumpolar Deep Water; IODW, Indian Ocean Deep Water; IOIW, Indian Ocean Intermediate Water; AAIW, Antarctic Intermediate Water

GEOTRACES

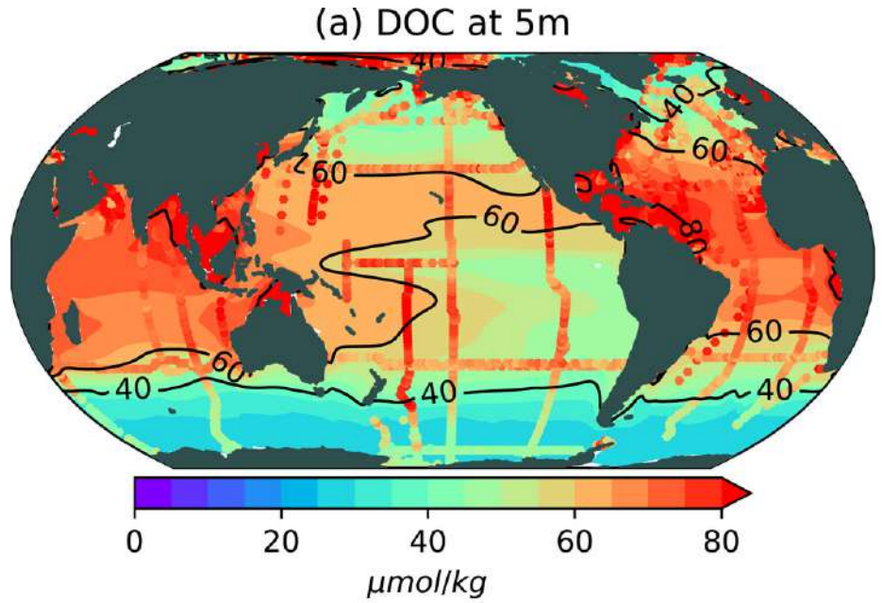
An International Study of the Marine Biogeochemical Cycles of Trace Elements and their Isotopes

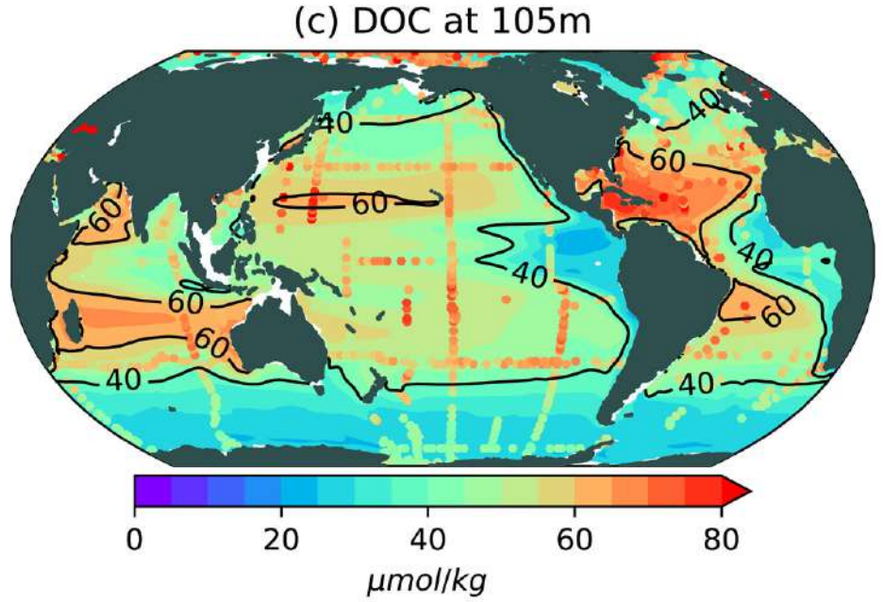
International Science Council — SCOR — Scientific Committee on Oceanic Research

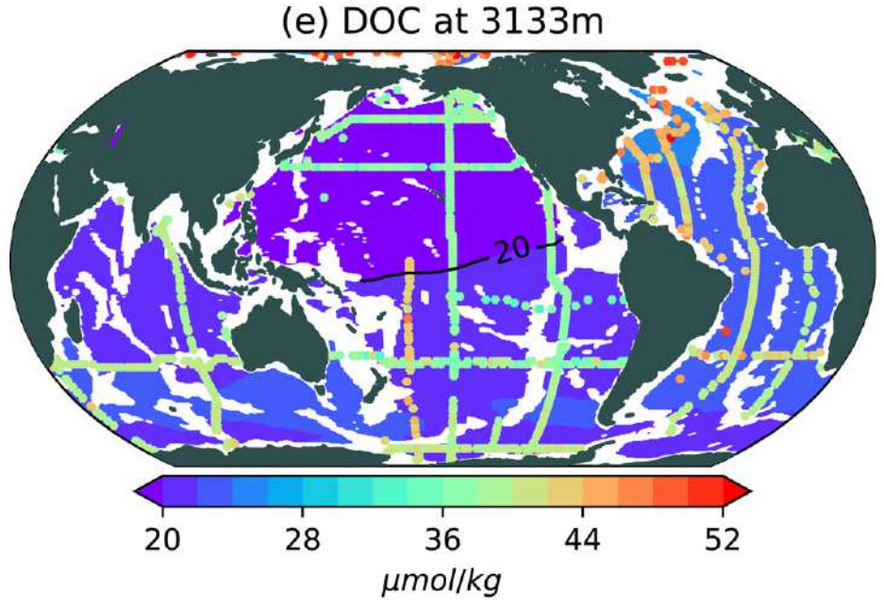


- Microbial processes regulate DOC concentrations
- Water movement causes mixing
- Fast turnover of labile DOC in the upper layers

https://www.geotraces.org/

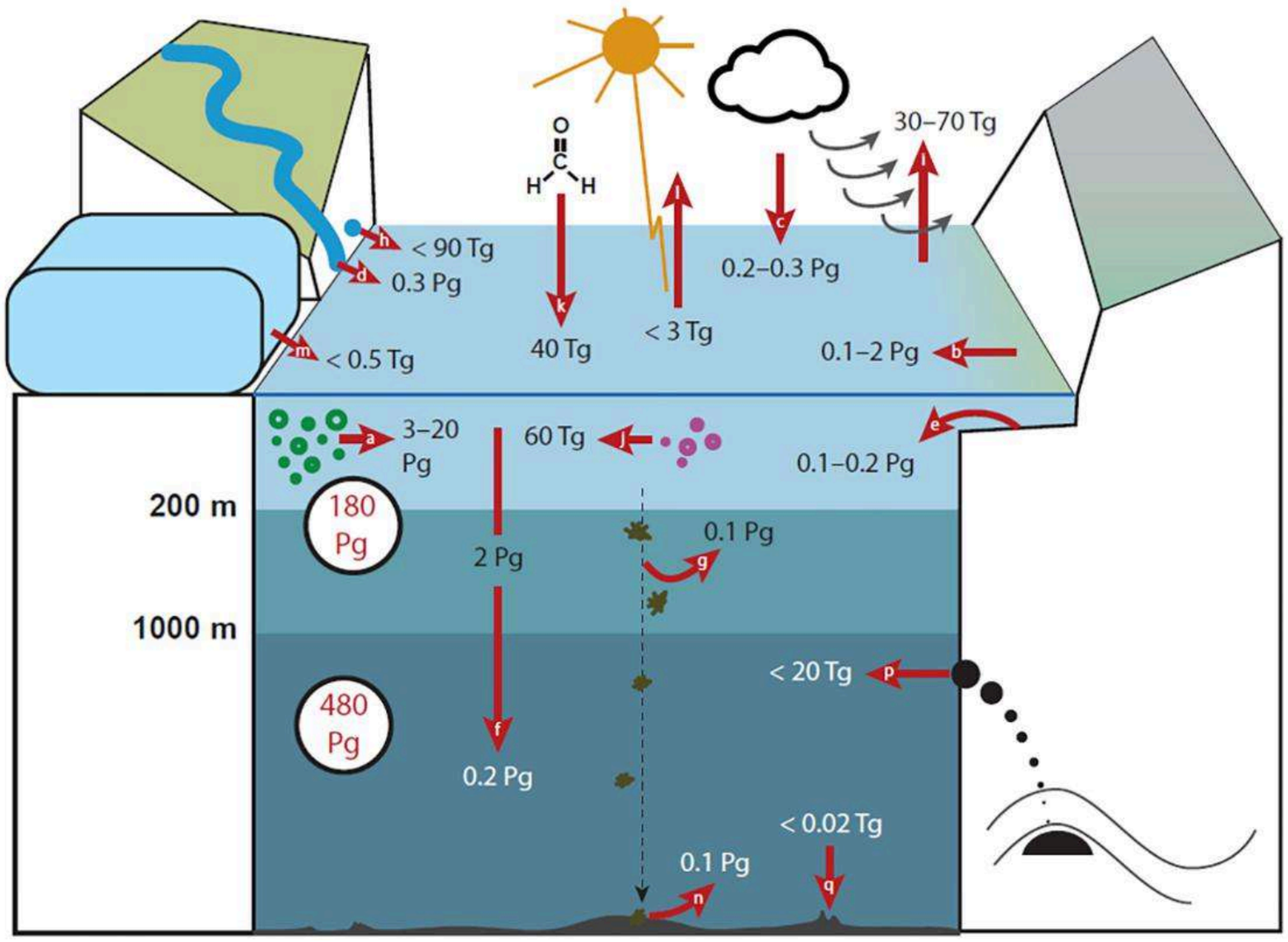


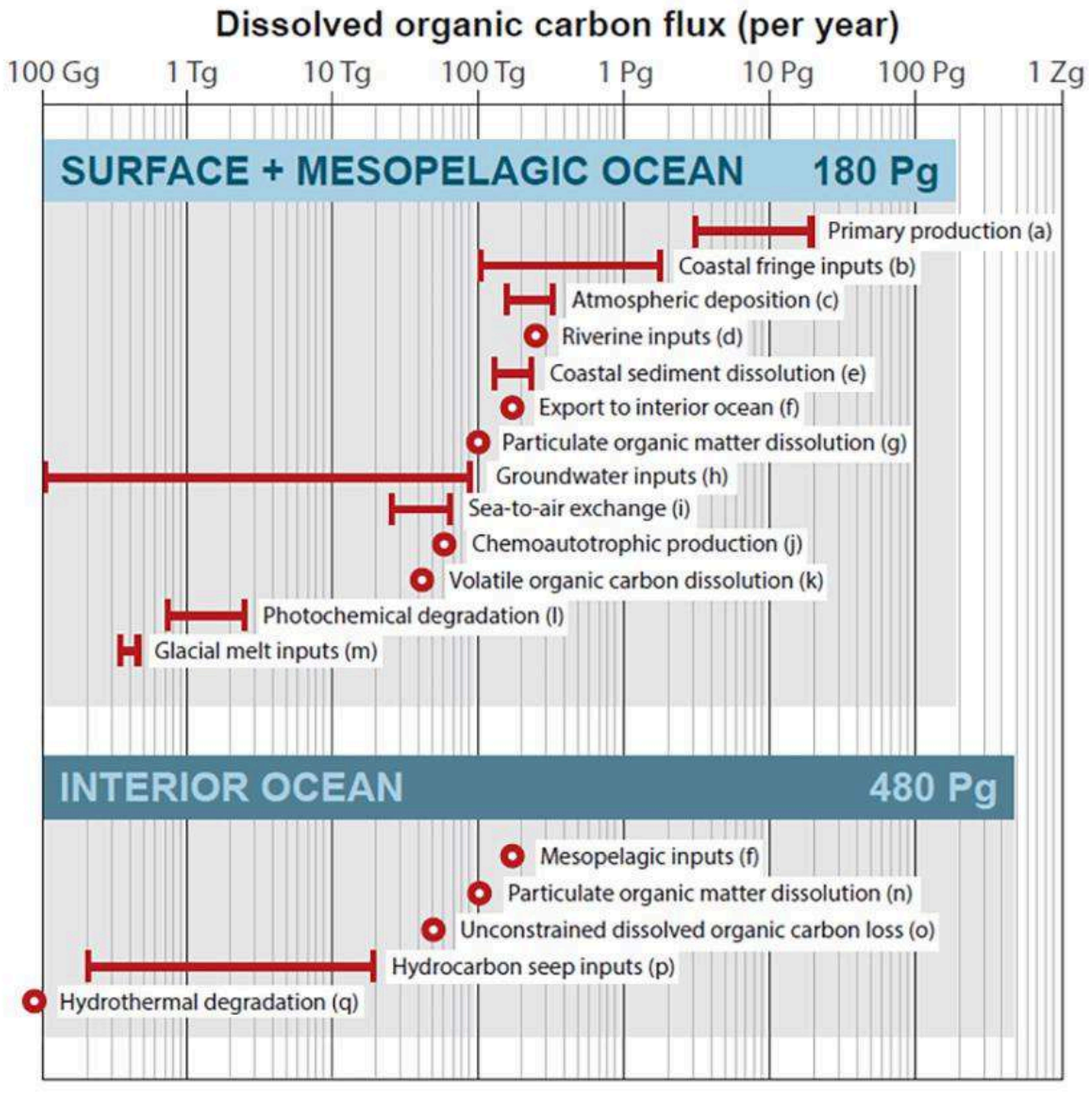




Sreeush et al., 2024

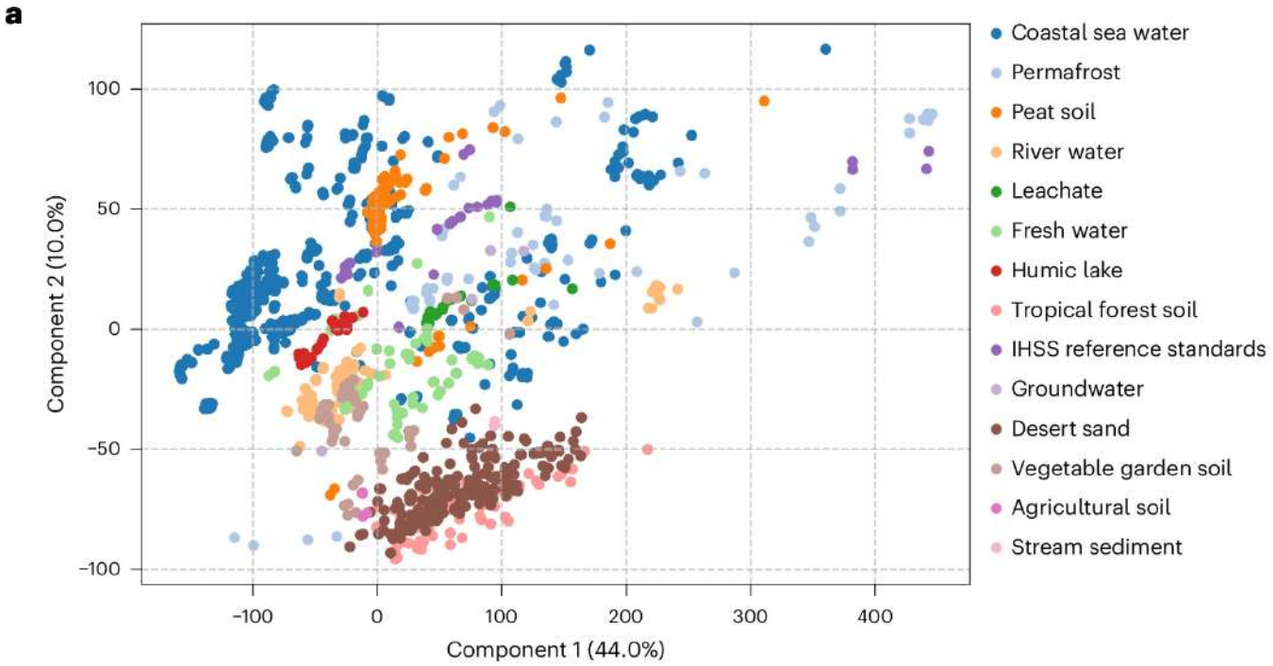
DOC fluxes

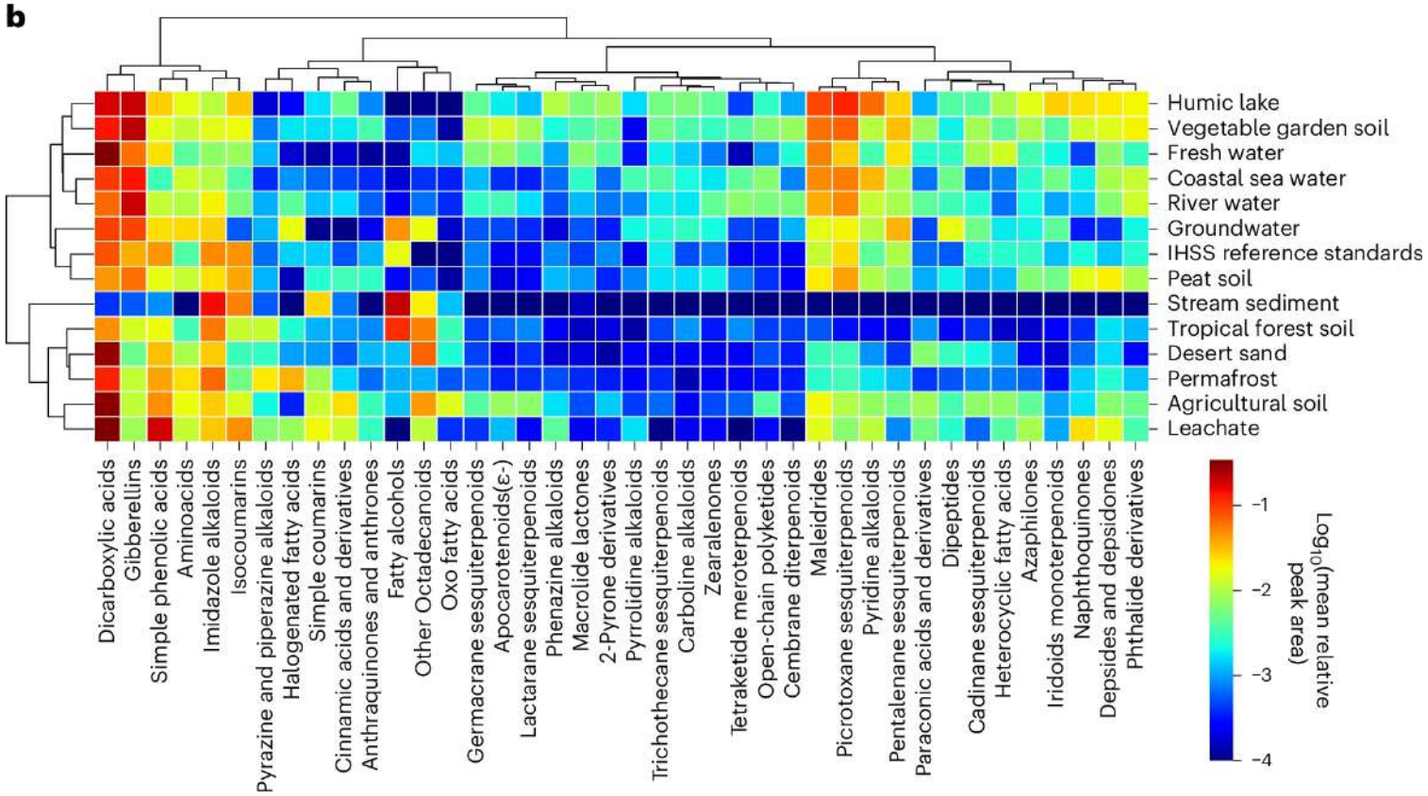




- Oceanic **DOC stocks** are shown in **black circles with red font** (Pg-C)
- **DOC fluxes** are shown in **black and white font** (Tg-C yr–1 or Pg-C yr–1)

Global DOM pools





Bowen et al., 2026

High degree of DOM conservation across environments

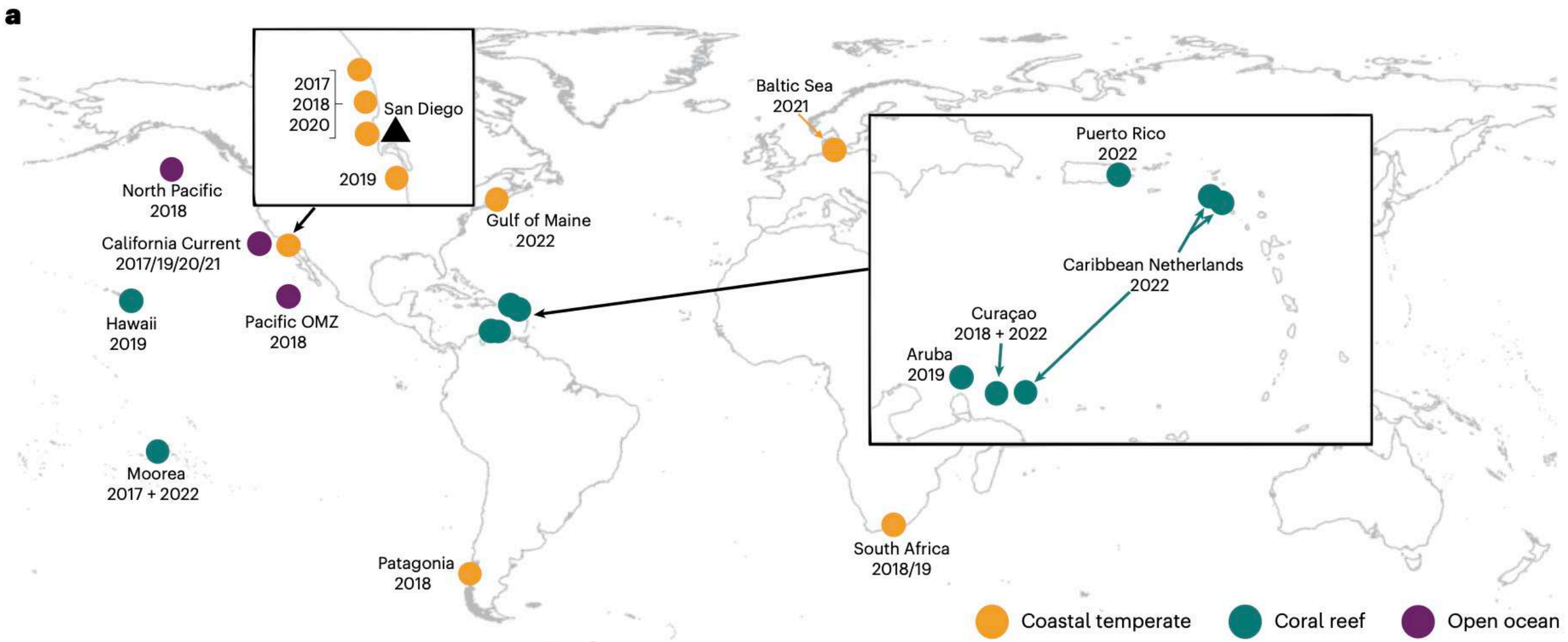
Global comparison of DOM composition reveals conserved and environment-specific molecular signatures

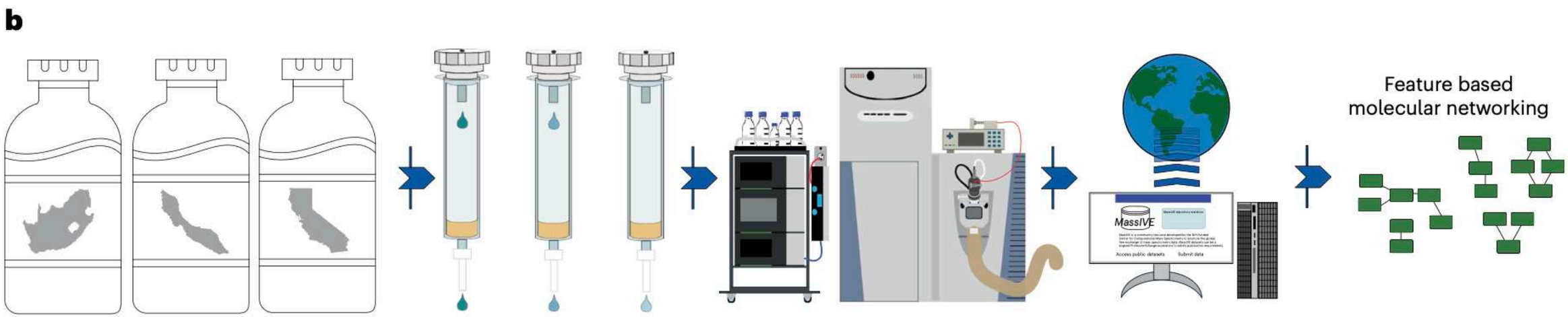
Dicarboxylic acids and simple phenolic acids common compounds

Anthropogenic related compounds are part of the DOM pools

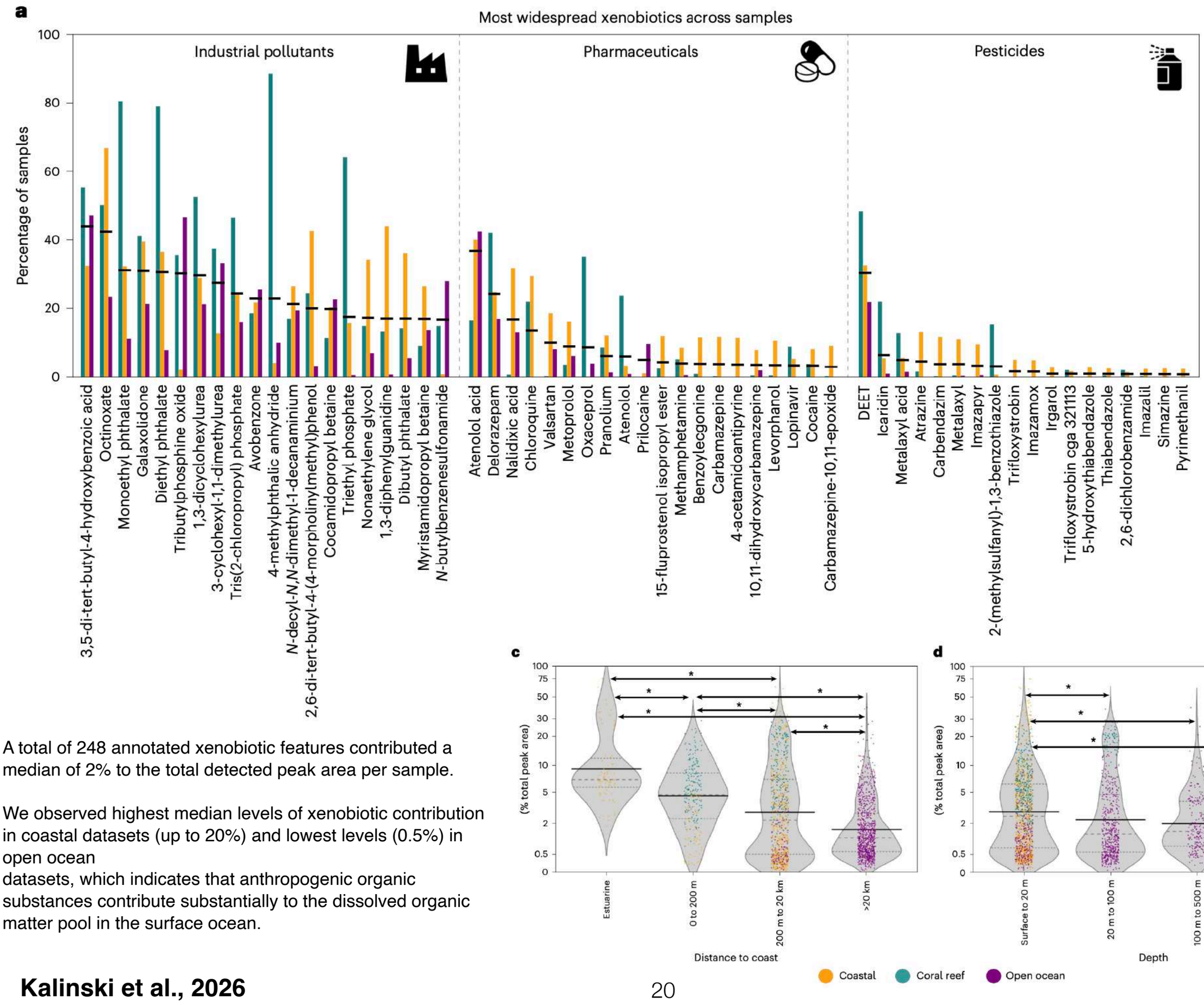
Unknown microbial control on their fate

Widespread presence of anthropogenic compounds in marine DOM





Kalinski et al., 2026



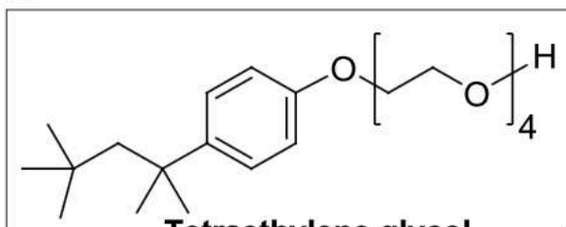
A total of 248 annotated xenobiotic features contributed a median of 2% to the total detected peak area per sample.

We observed highest median levels of xenobiotic contribution in coastal datasets (up to 20%) and lowest levels (0.5%) in open ocean
datasets, which indicates that anthropogenic organic substances contribute substantially to the dissolved organic matter pool in the surface ocean.

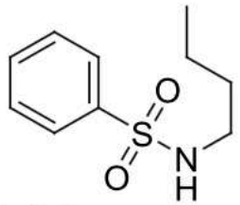
Kalinski et al., 2026

Broad anthropogenic DOM classes

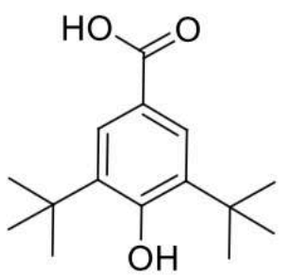
c



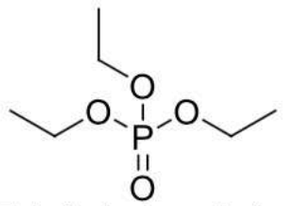
Tetraethylene glycol p-tert-octylphenyl ether (D,F-I,K,M,P-U)



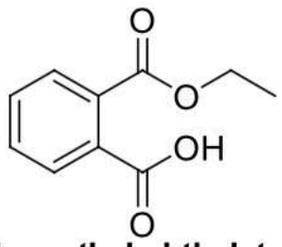
N-butylbenzene-sulfonamide (A,B,D,E,H,I,K,M-O,R,S,U)



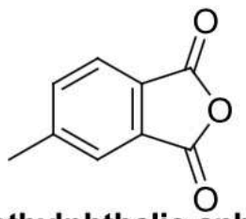
3,5-di-tert-butyl-4-hydroxybenzoic acid (all but A,F,L,J,U)



Triethyl phosphate (D,F-H,K-U)

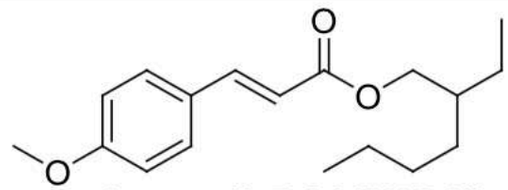


Monoethyl phthalate (B-E,H,J-L,N,P,R,S,U)

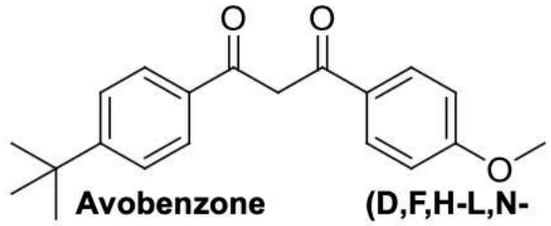


4-methylphthalic anhydride (all but A,E,F,O,T)

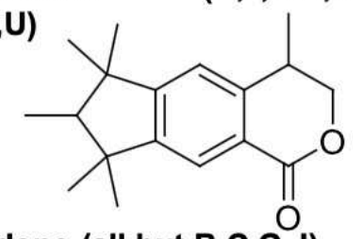
Plastics-related chemicals



Octinoxate (C-E,G,I-K,N,P-U)

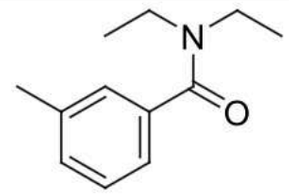


Avobenzone (D,F,H-L,N-P,R,T,U)

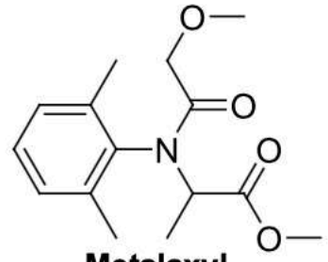


Galaxolidone (all but B,C,G,J)

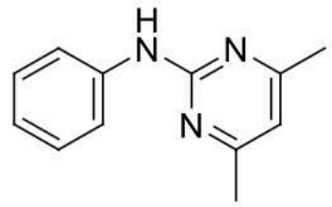
PCP-related chemicals



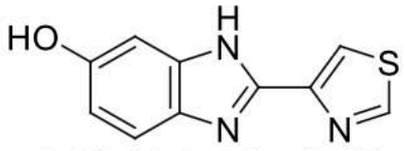
DEET (C,E,F,I,M,N,R-U)



Metalaxyl (A,F,I,J,N-Q,T,U)

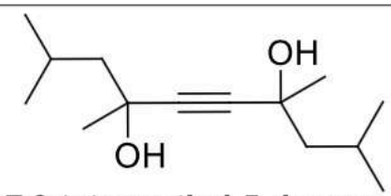


Pyrimethanil (T)

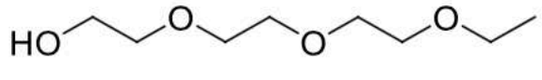


5-OH-thiabendazole (T)

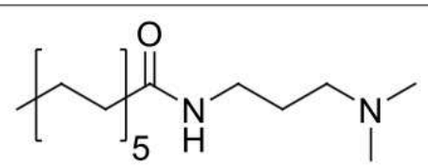
Pesticides



2,4,7,9-tetramethyl-5-decyne-4,7-diol (C-G,K,M,N,P-U)

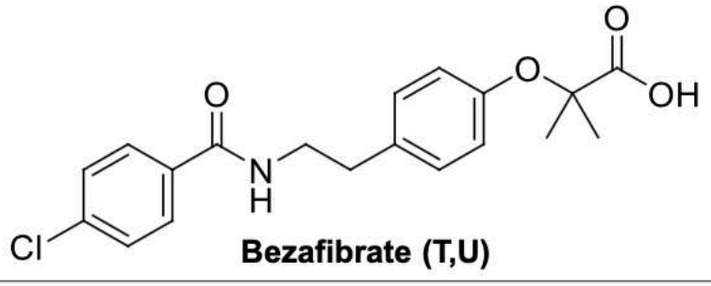


Ethyltriglycol (D-G,I-L,N,P,Q,S-U)

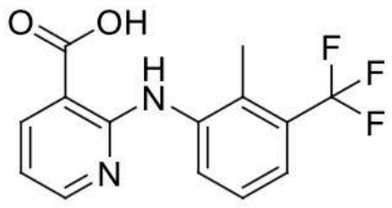


Lauramidopropyl dimethylamine (A,B,E,G,I,J,L,M,P,Q,S,T)

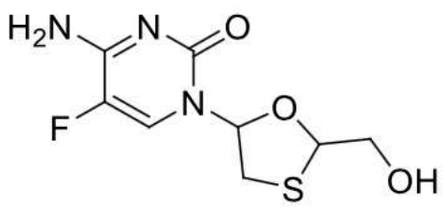
Surfactants



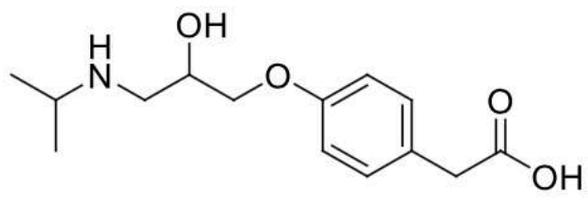
Bezafibrate (T,U)



Flunixin (U)



Emtricitabine (T)

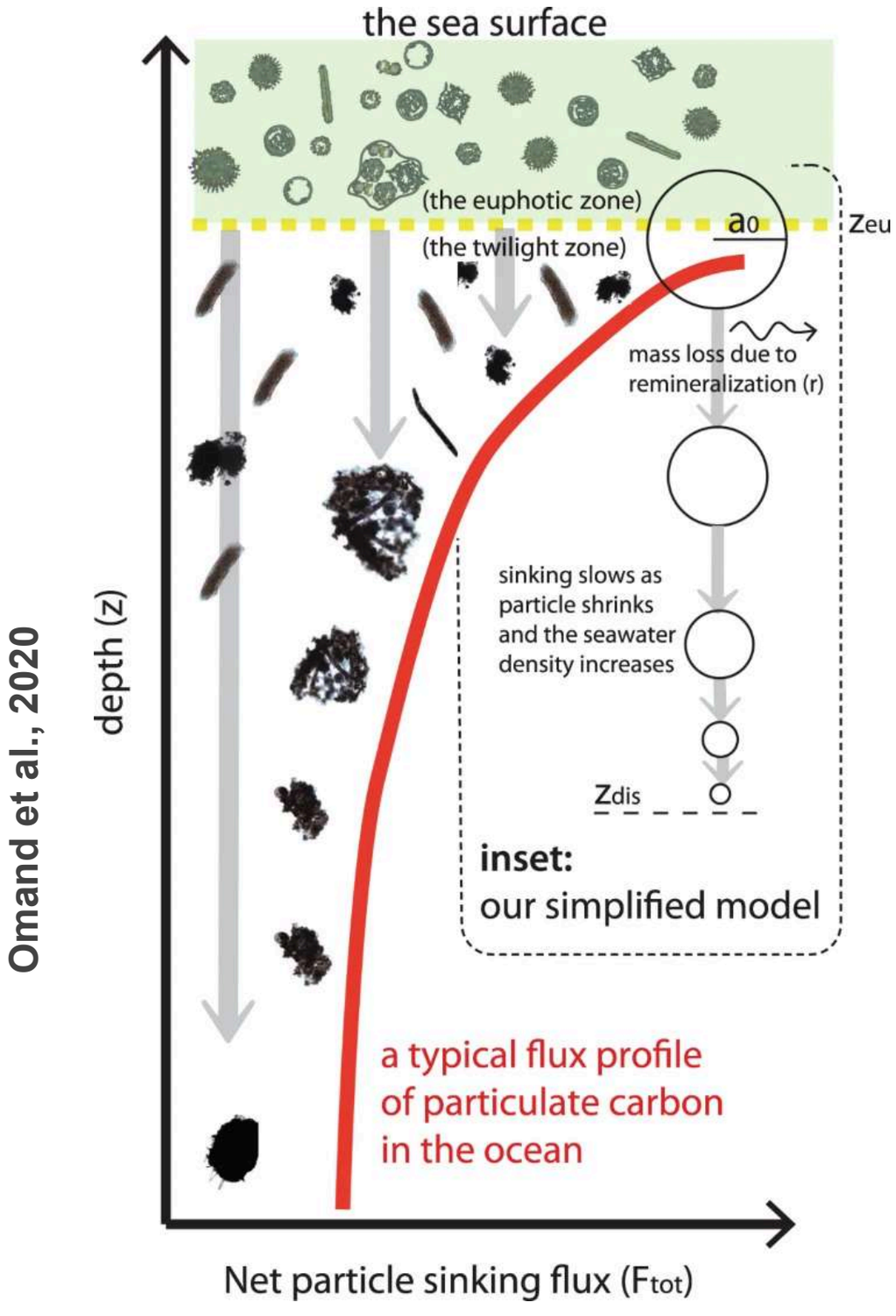


Atenolol acid (all but A,B,M)

Pharmaceuticals

Kalinski et al., 2026

POC fluxes



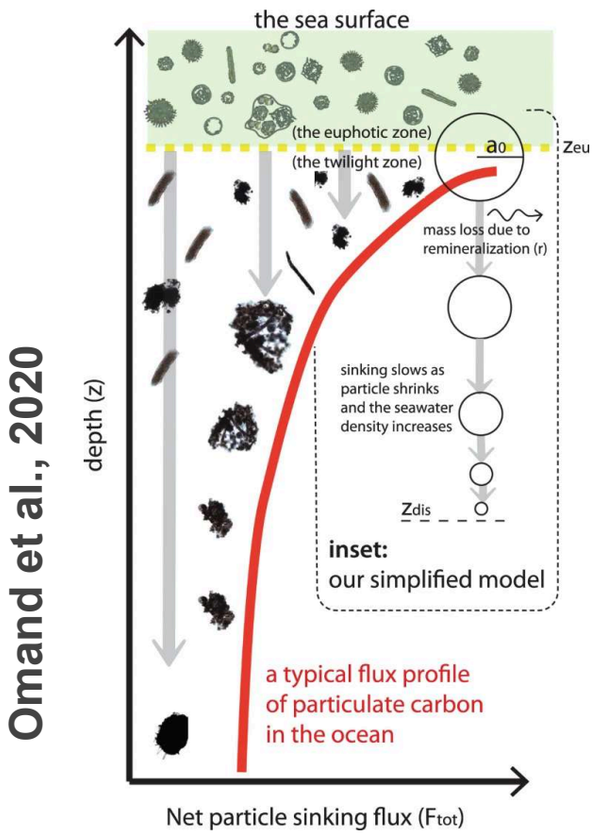
- **The biological carbon pump: processes setting carbon supply, consumption, and storage in the oceans' interior**

- Small changes in the efficiency of the biological carbon pump alter ocean carbon sequestration, atmospheric CO_2, climate and functioning of midwater ecosystems

- Transfer of C out of the sunlit euphotic zone (Ez) and through the upper twilight zone (TZ = depths below Ez down to 500 m) where the **attenuation** (**microbes**) POC flux is largest

- POC flux **differs** the most between **oceanic** provinces

POC fluxes



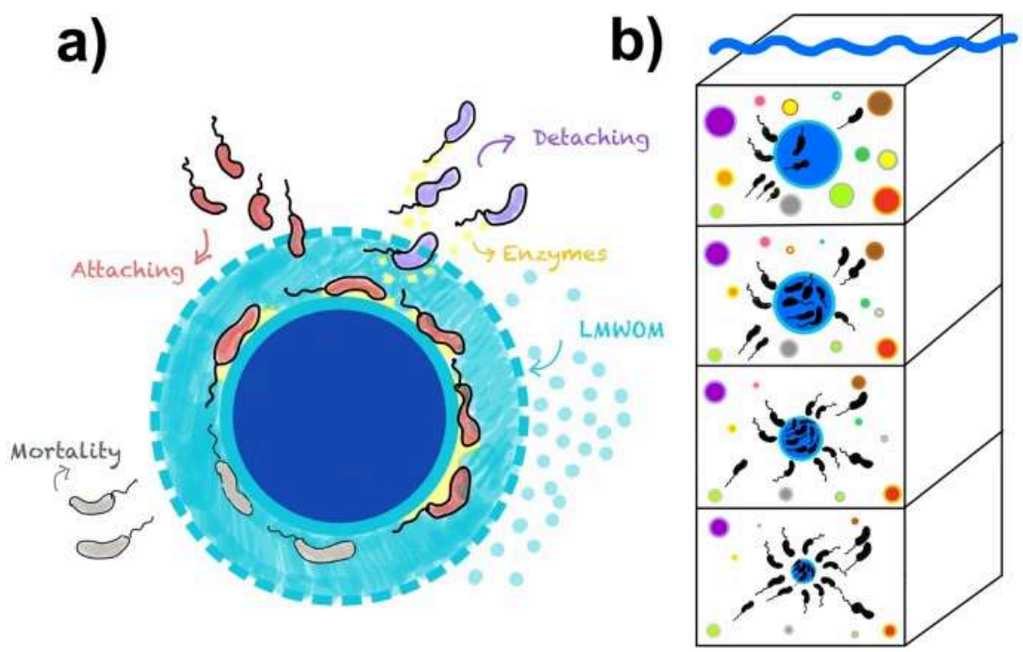
Omand et al., 2020

- The flux of **sinking particles** out of the surface ocean and its **attenuation** with depth is most often quantified in field observations by a fit to POC sinking flux data (Martin et al. 1987)
- POC export is usually measured at an upper reference depth and then followed downward: Surface production → export → sinking POC → microbial/zooplankton degradation → progressively smaller POC flux

$$F_z = F_{100}\left(\frac{z}{100}\right)^{-b}$$

- $F(z)$ = POC flux at depth z
- $F(z_0)$ = flux at a reference depth, often ~100 m
- b = **attenuation or Martin exponent**
- larger b = **more rapid attenuation**
- smaller b = **more efficient transfer of POC to depth**

- Attenuation is microbial mediated
- Microscale action
- Enzymatic cleavage of POC for microbial growth
- Leftover DOM is released as a plum for deep ocean microbes



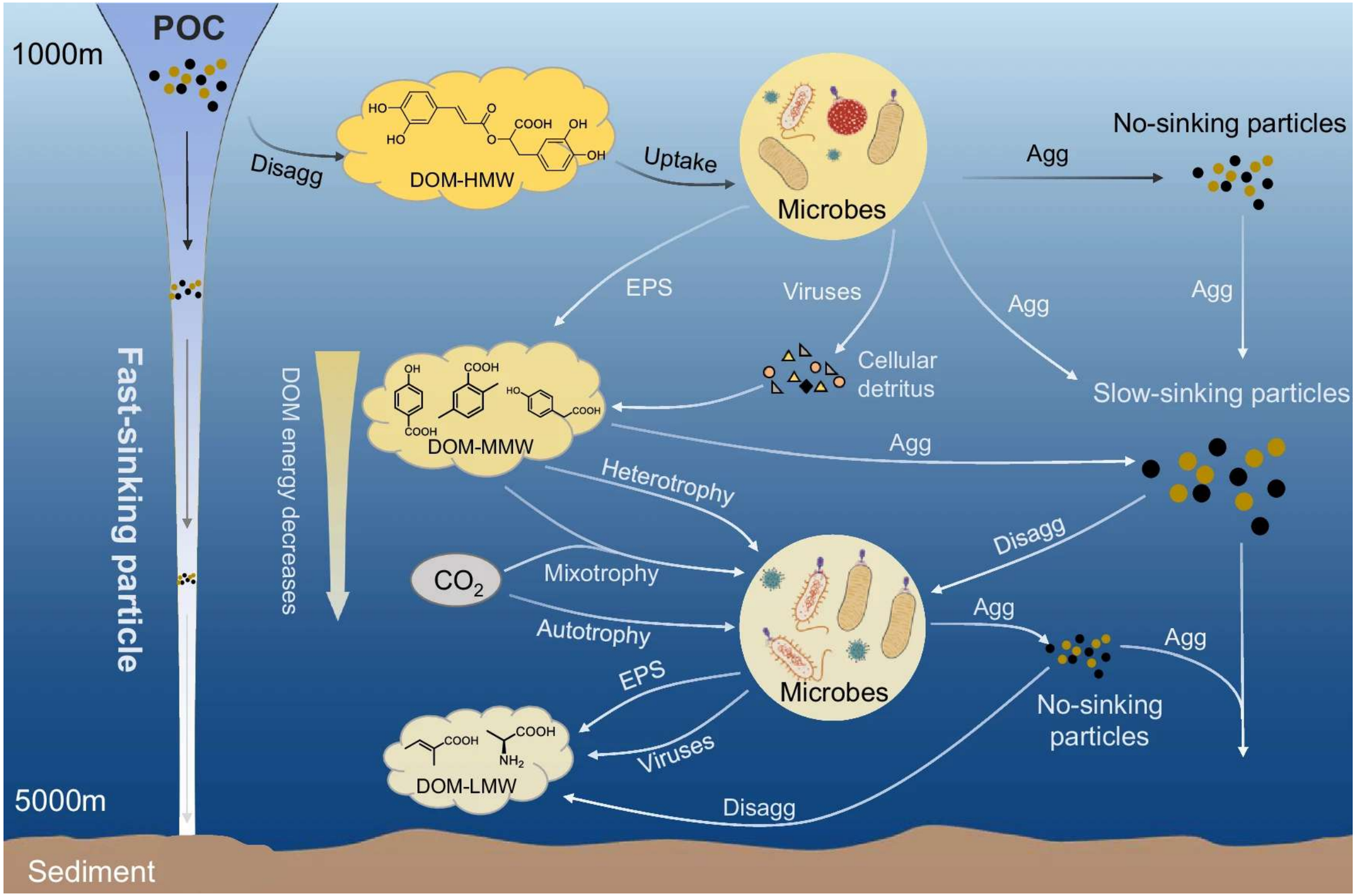
Nguyen et al., 2020

DOM fluxes in global coastal ocean

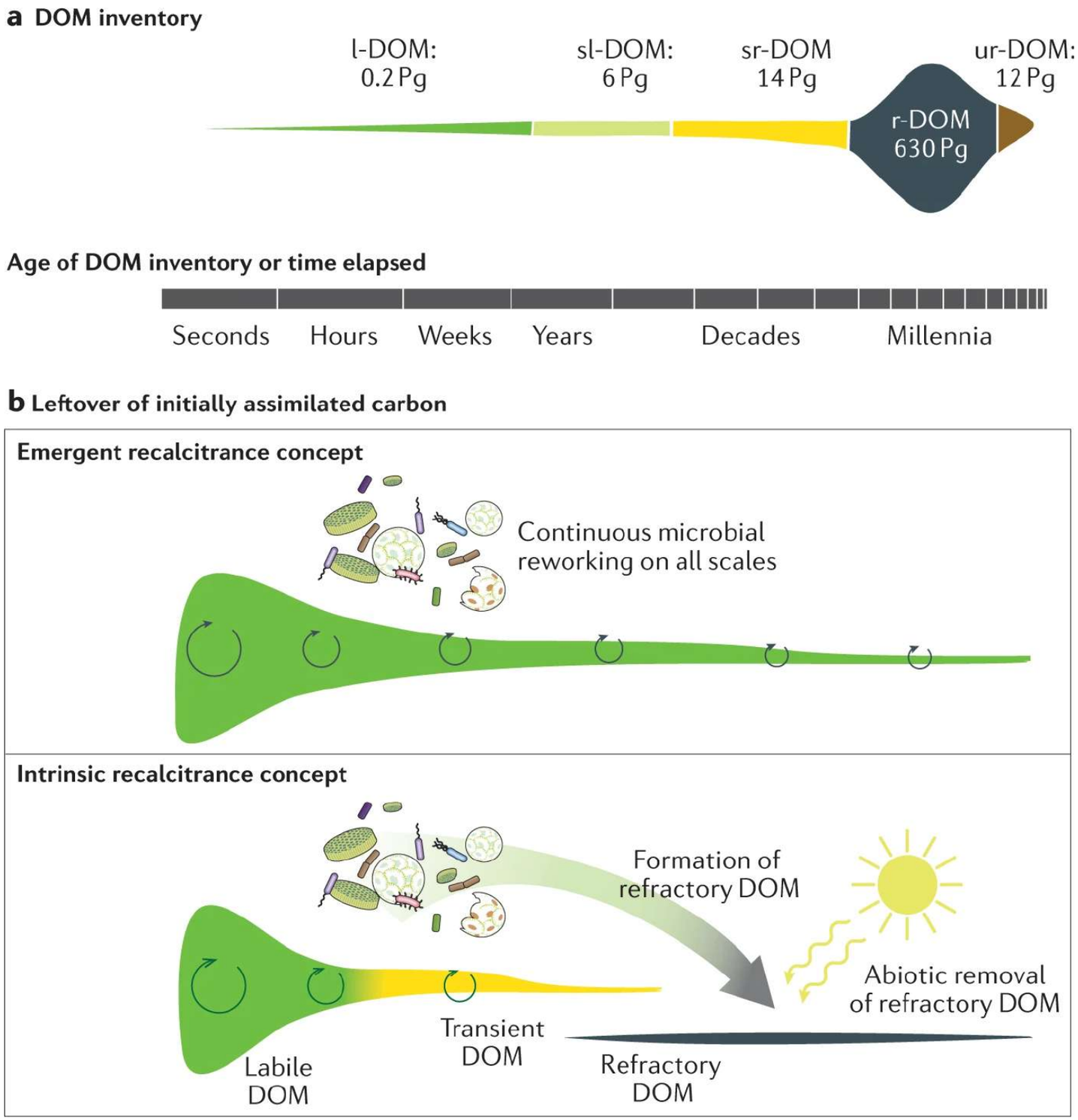
	DOC $\mu mol\,L^{-1}$	DON $\mu mol\,L^{-1}$	DOP $\mu mol\,L^{-1}$	DOC : DON	DOC : DOP	DON : DOP
Min	17	< 0.1	< 0.01	1	18	0.14
Max	30 327	2095.3	84.27	3046	248 024	8894
Avg. $\pm$ SD	182 ± 314	13.6 ± 30.4	0.34 ± 1.11	18 ± 43	1171 ± 4248	100 ± 580
Median	103	8.0	0.18	14	583	47
CV	173	224	324	244	363	578
25th percentile	77	5.5	0.11	11	401	30
75th percentile	228	15.8	0.30	18	1034	78
N	62 338	20 356	13 533	12 632	7415	12 954

Lønborg et al., 2024

DOM and Chromophoric dissolved organic matter (CDOM) dynamics is driven by stepped microbe-DOM loop



Mo et al., 2025

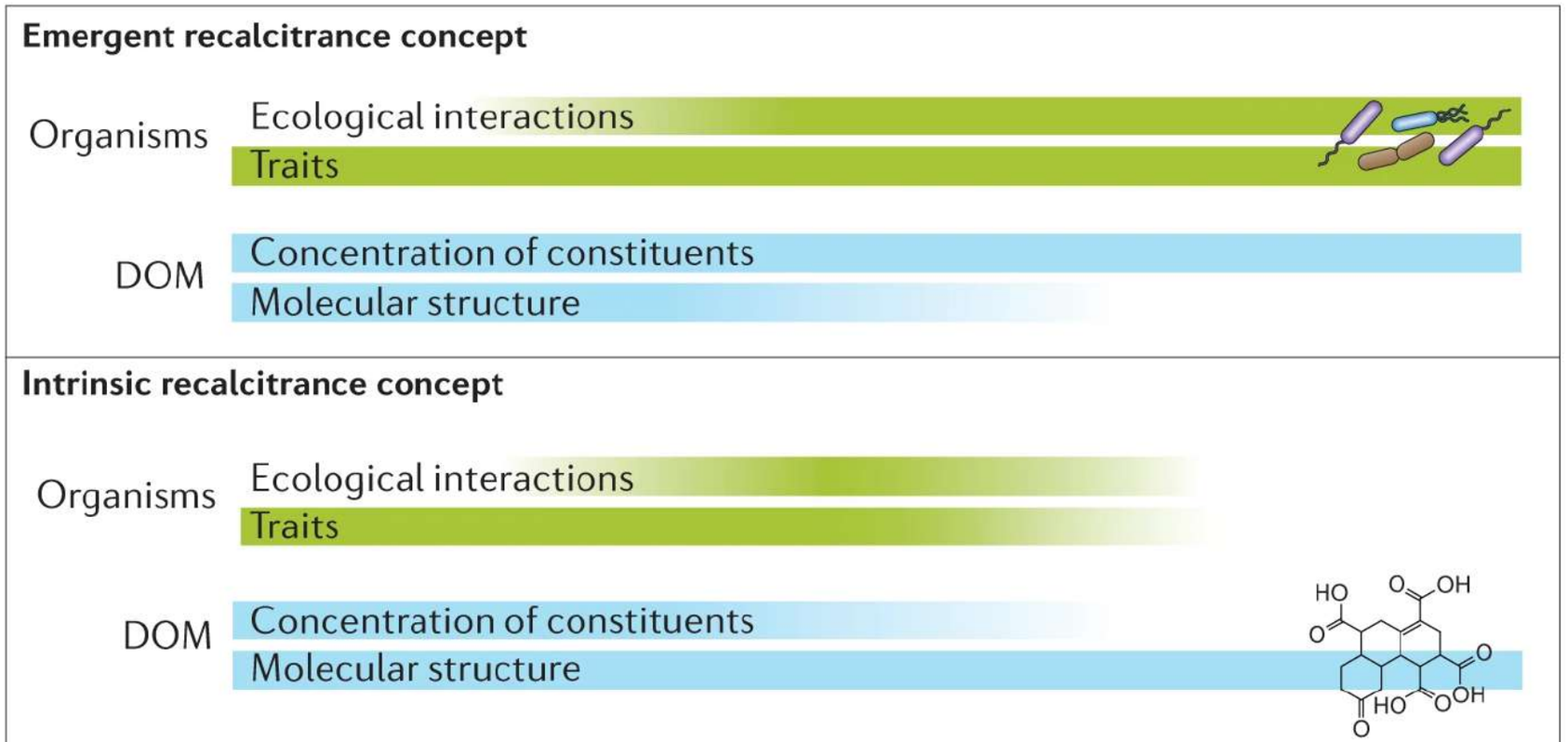


Dittmar at al., 2021

- The time and age of dissolved organic matter (DOM) advances on a logarithmical scale, from seconds to millennia
- The majority of observable DOM in the ocean has an estimated lifetime of 16,000 years and is refractory by definition
- In the emergent recalcitrance concept, microheterotrophs continuously transform all forms of DOM
- Recalcitrance emerges on an ecosystems level from ecological interactions and degradation slows as molecular diversity increases and concentrations decline
- The intrinsic recalcitrance paradigm states that lability and recalcitrance are intrinsic, molecular properties of DOM
- Microorganisms synthesize biologically recalcitrant molecules while they consume labile ones, constituting a microbial carbon pump through which carbon is sequestered from active cycles
- Refractory DOM is returned to active cycles largely via abiotic processes, such as photochemical reactions at the sea surface, although abiotic removal can occur in both concepts
- Transient DOM refers to the semi-labile and semi-refractory fractions together

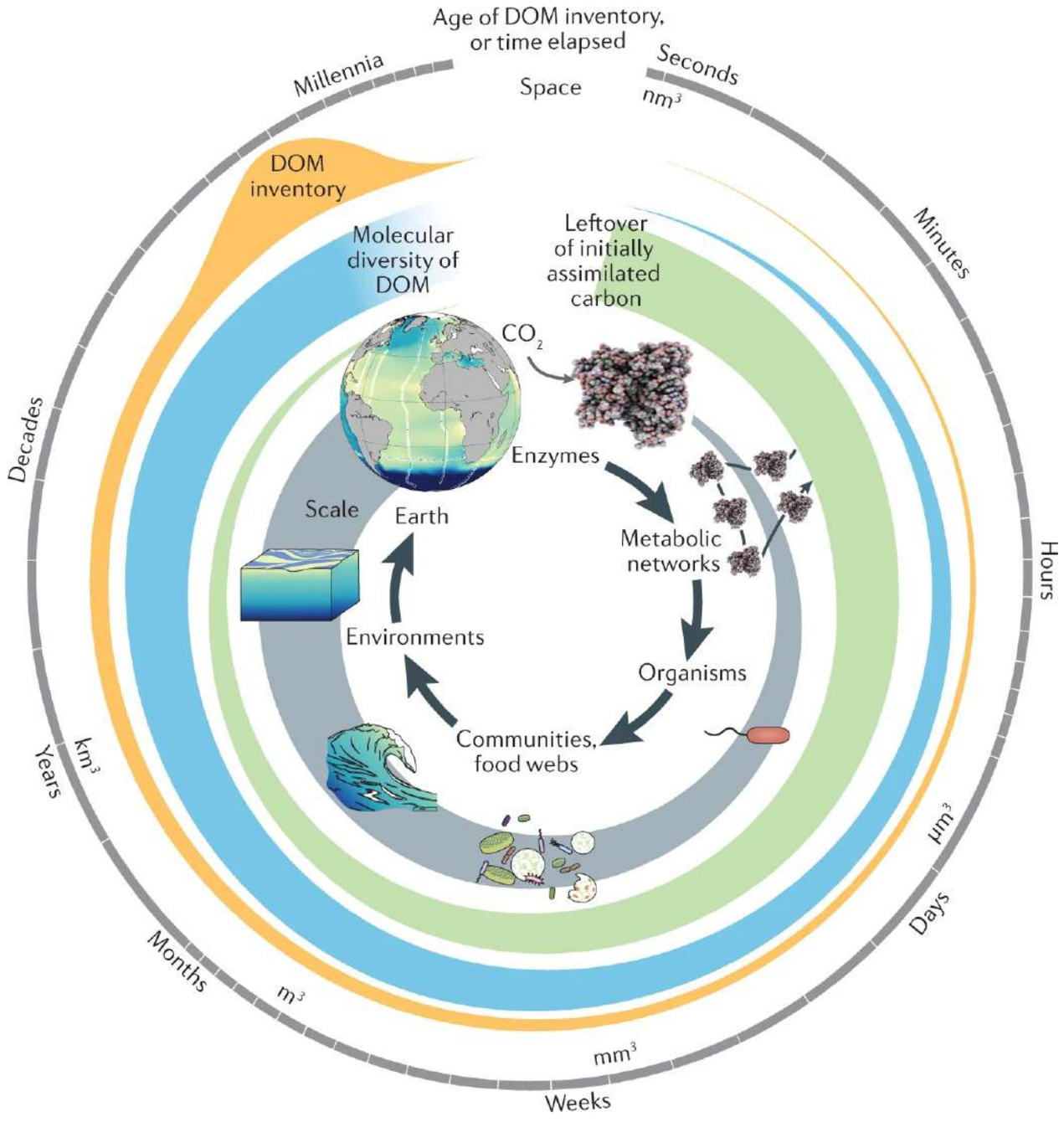
l, labile; r, refractory; sl, semi-labile; sr, semi-refractory; ur, ultra-refractory

Dittmar at al., 2021



- Rate-limiting factors for DOM degradation on the different timescales
- On timescales of phytoplankton and bacterioplankton blooms, ecological interactions, traits of organisms, substrate composition and substrate concentration are all crucial for DOM turnover
- According to the emergent recalcitrance concept, long-term turnover is largely controlled by properties of organisms and ecosystems; the molecular structure of DOM is a secondary control
- According to the intrinsic recalcitrance paradigm, the long-term fate of DOM is largely determined by molecular properties of DOM

Formation and degradation of dissolved organic matter across spatial and temporal scales



Dittmar at al., 2021

- **As organisms release DOM during growth and upon death, about half of the net primary production is quickly turned over by microorganisms within hours to days (green band)**

- Freshly produced, phytoplankton-derived DOM is largely composed of biomolecules of known building blocks, such as polysaccharides including nucleic acids, lipids and proteins

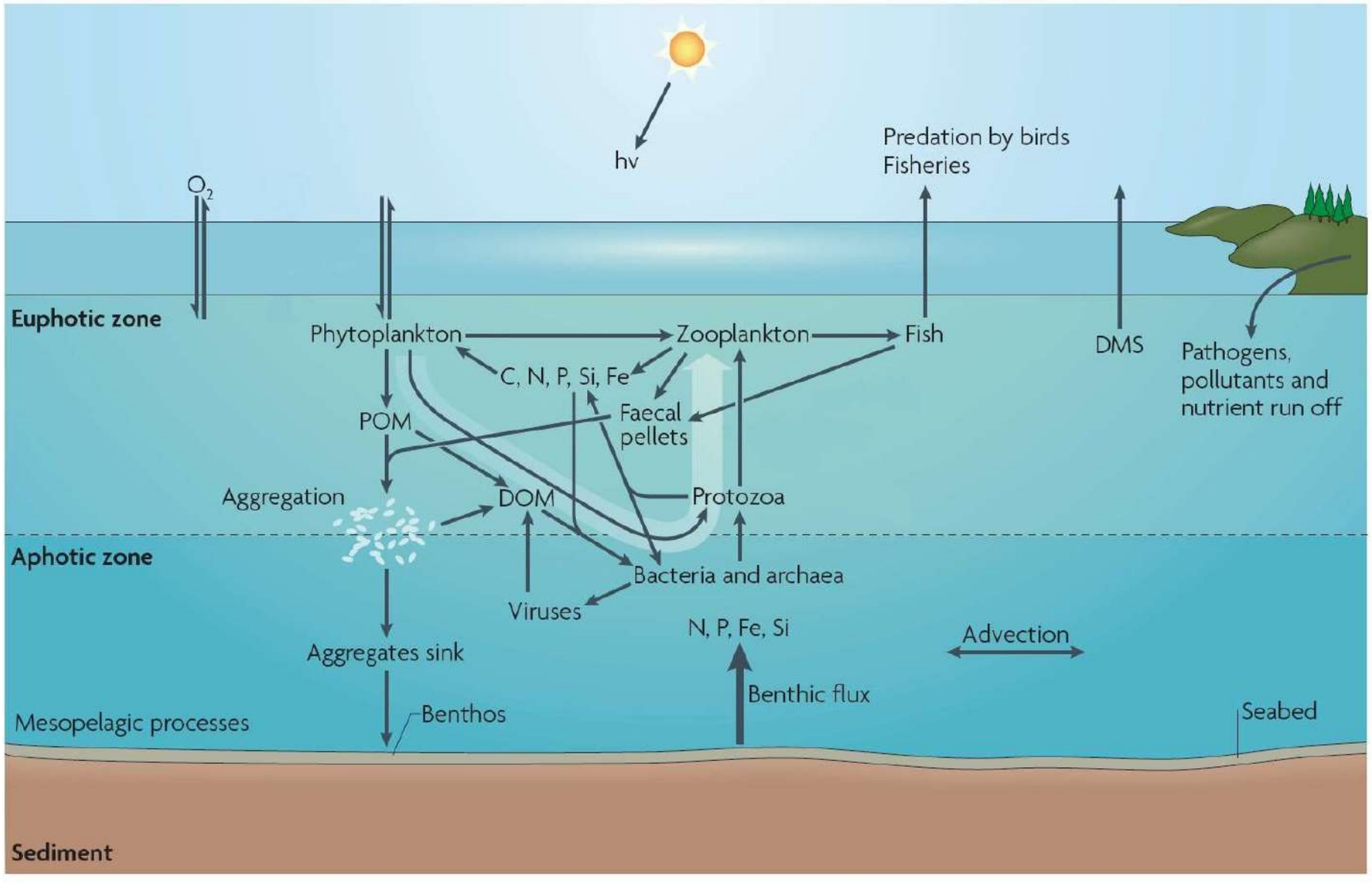
- **During microbial decomposition, DOM is molecularly diversified (blue band)**

- All relevant facets of molecular diversity cannot yet be analysed, especially that of the most persistent fraction of DOM

- **A minor fraction of the released DOM escapes the microbial loop, decomposing slowly enough to persist in the ocean for millennia, making most of the DOM pool old (orange band)**

Carbon biogeochemical cycle

- Source of organic matter is biology
- Production and decomposition/degradation of organic matter
- Atmospheric CO_2 is fixed by photosynthesis/chemosynthesis —> Carbon Cycle



Azam & Malfatti, 2007