

965SV_L01b

TABLE 1>> EXAMPLES OF HOW THE MARINE ENVIRONMENT MAY BE DIVIDED INTO DIFFERENT MICROBIAL HABITATS

Criterion	Habitats
Presence of other organisms	Symbiotic Free-living Biofilm
Proximity to the ocean surface or sediments	Euphotic (0-150 m) Mesopelagic (150-1000 m) Bathopelagic (>1000 m) Benthos (sediments)
Concentration of nutrients and required growth substrates	Oligotrophic Mesotrophic Eutrophic

The ocean is in between the cells

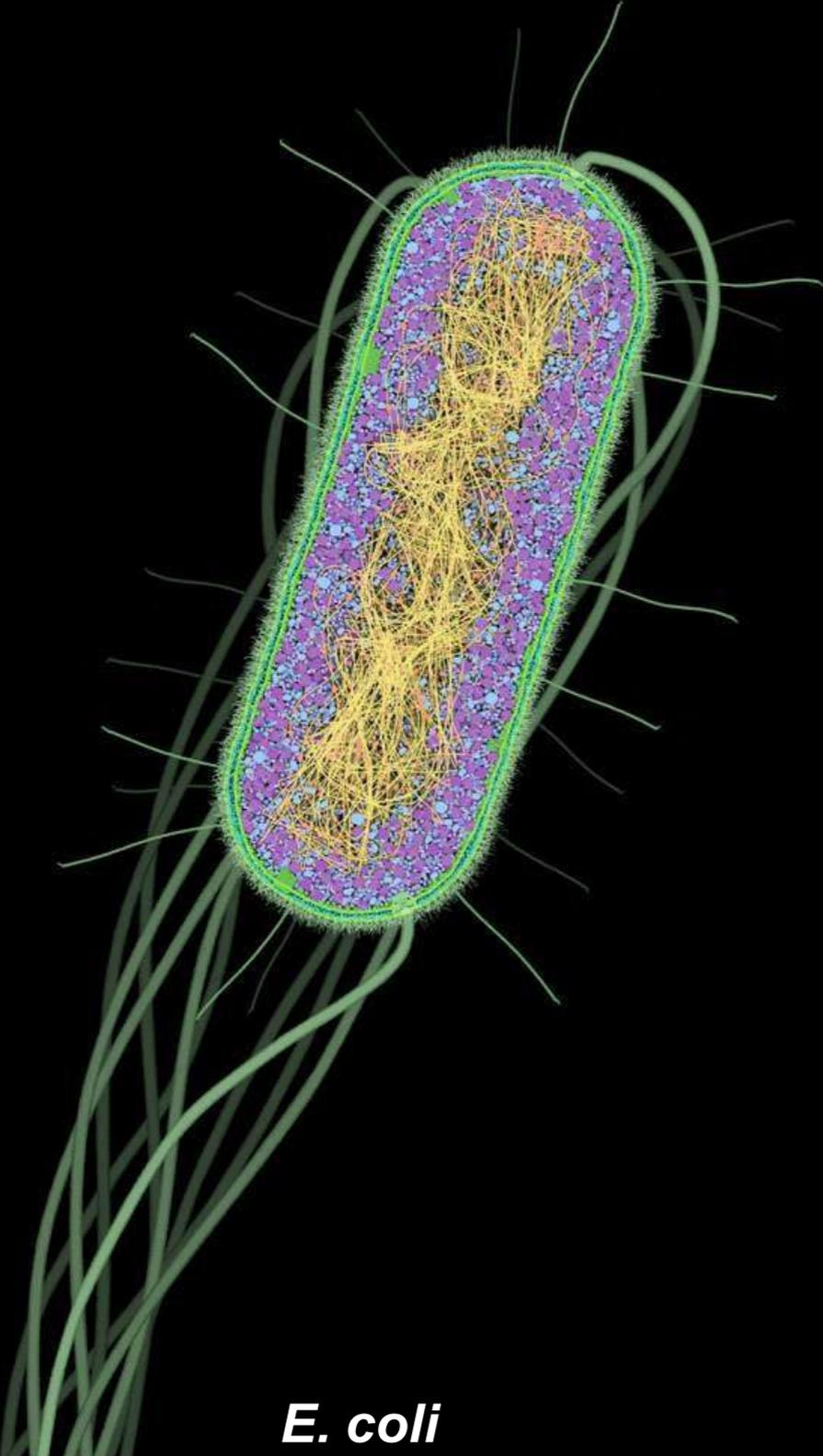


88 μm

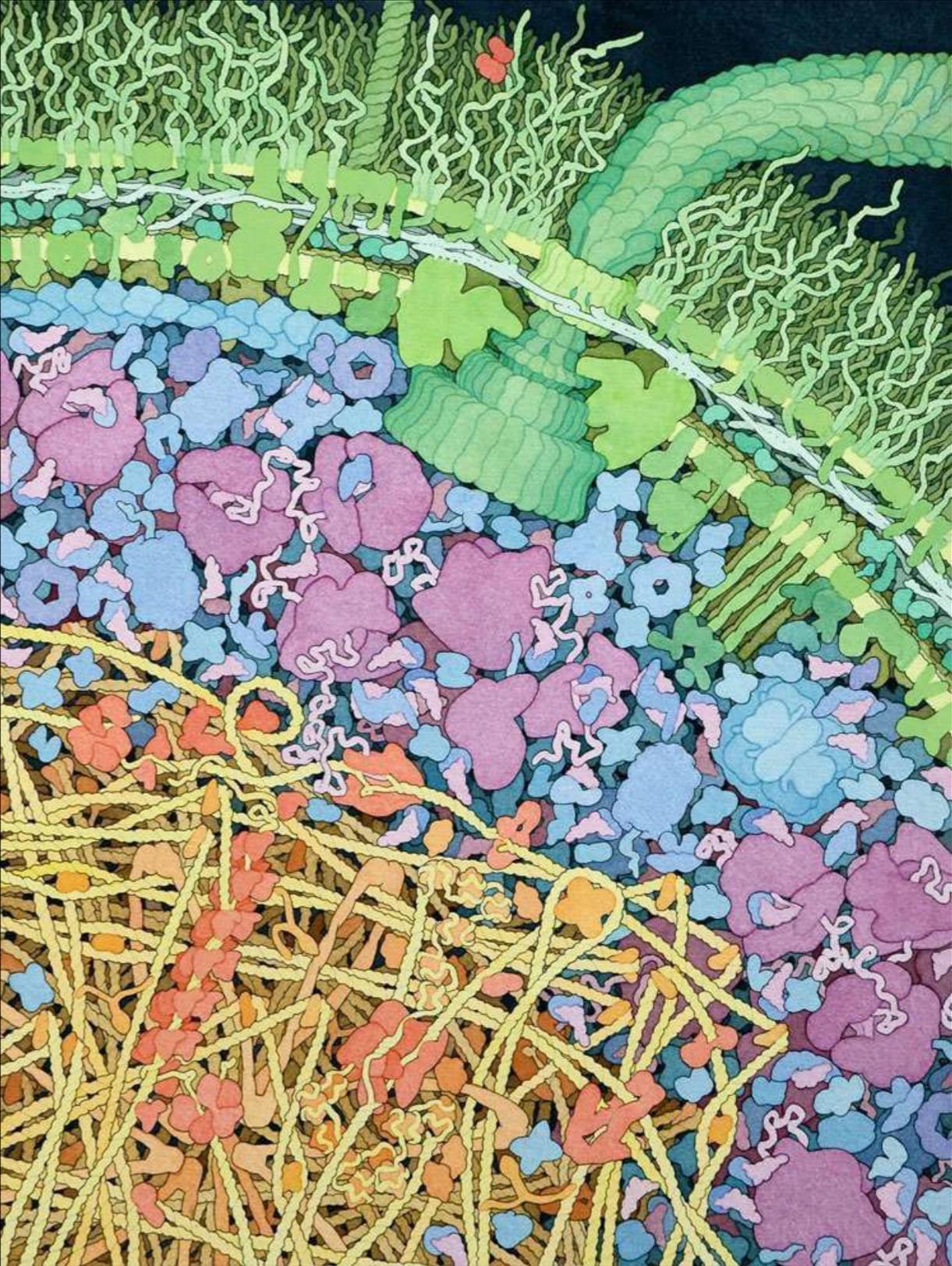
118 μm

From micro to nanoscale...at their scale

David S. Goodsell



E. coli



Microscale

- Microbes live in a microbial world
- Microbes interact intimately with molecules
- Gradients are ephemeral in space and time
- Unknown is behind the corner...dark corner!
- On a face value, at the microscale all living things/organisms are the same —> sugars, proteins and lipids —> hot spot of organic matter
- All the surfaces are the same, due to the molecular coating

Seawater = SW

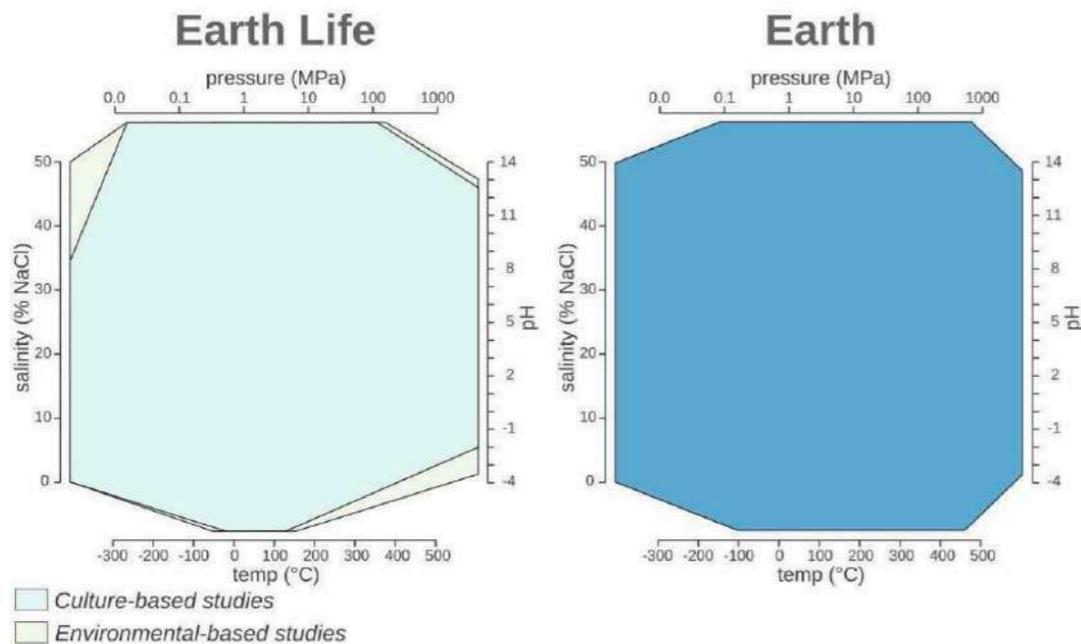
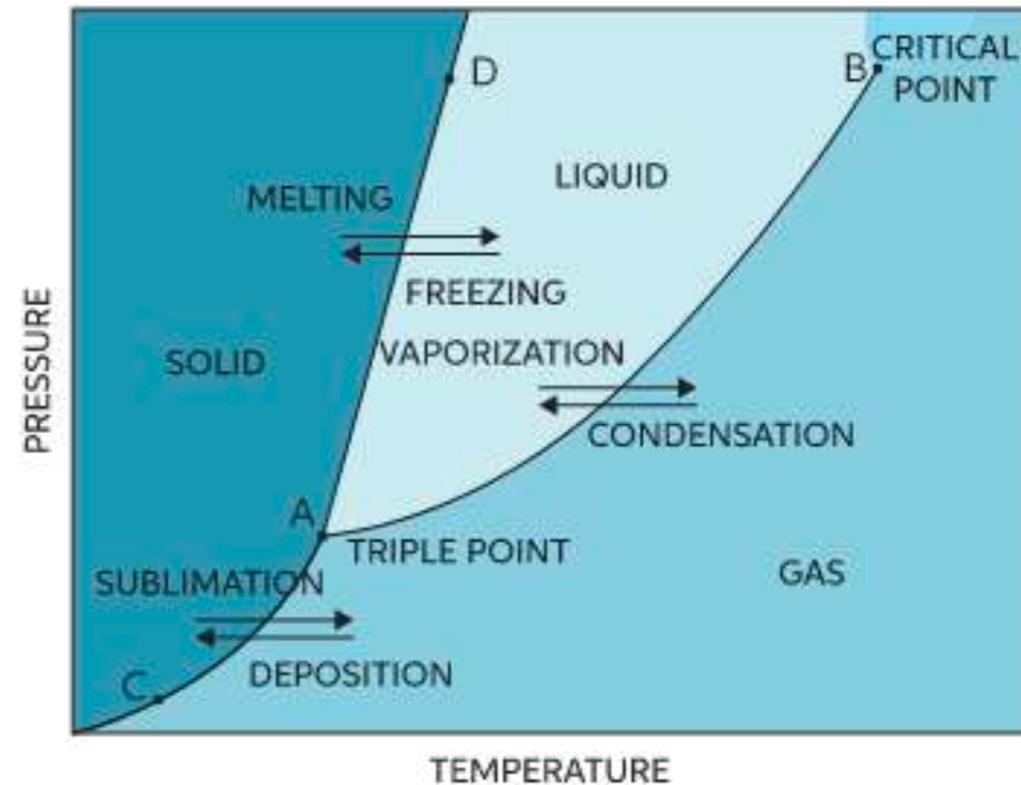
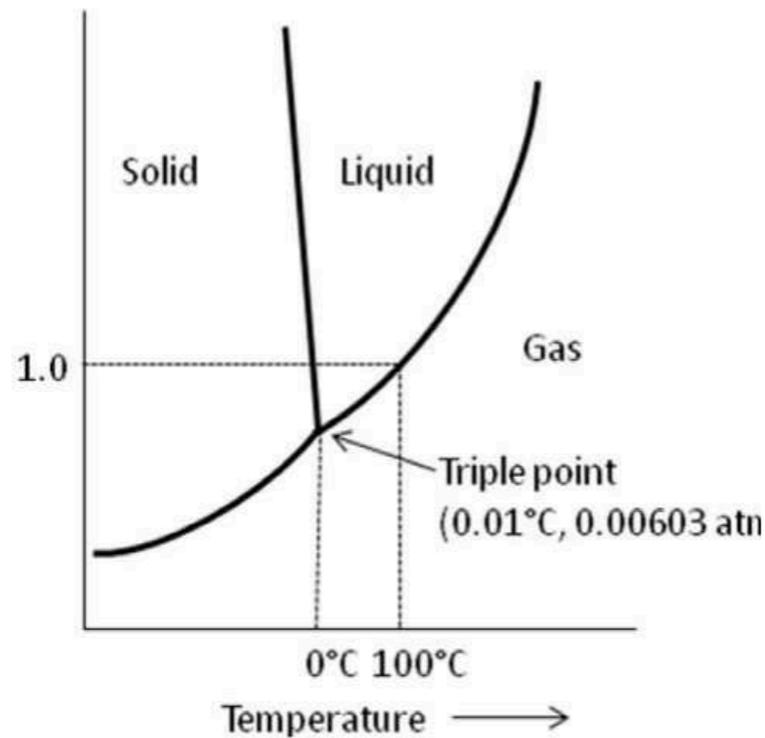
TABLE 2>> FACTORS THAT IMPACT MARINE MICROBIAL DIVERSITY

Factors

- > Turbulence
- > Light
- > Temperature
- > Nutrients
- > Surfaces and interfaces
- > Redox potential
- > Metals
- > Salinity
- > pH
- > UV and Solar flux
- > Presence of macro-organisms, such as invertebrates and macroalgae

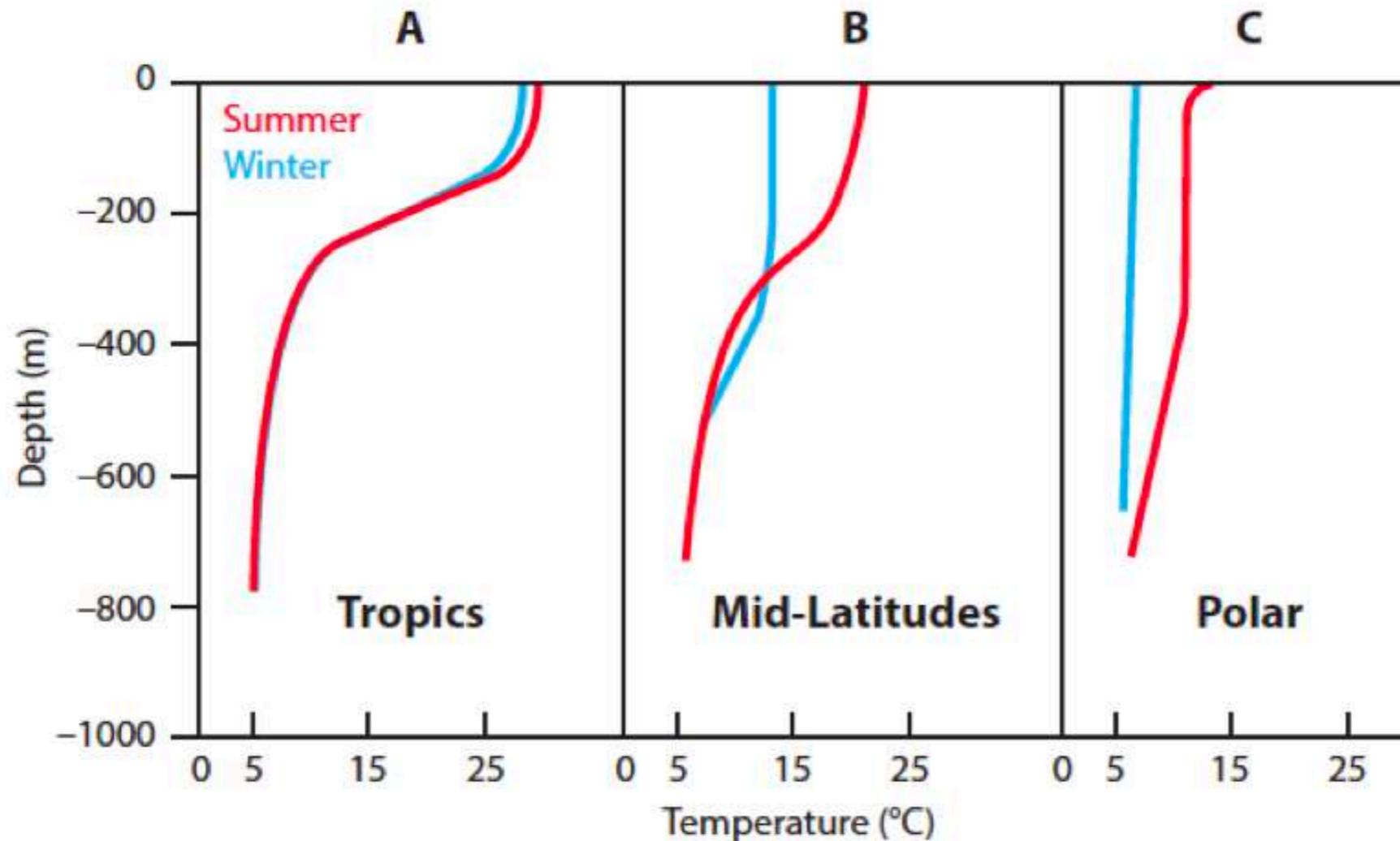
State of water

Merino et al. 2019



- Earth is a unique environment
- Microbial adaptations for the 3 state of water
- Microbes are alive in/on ice and in clouds, sea spray aerosol particles

Temperature



The **thermocline** is the zone where there is a rapid temperature change
The thermocline is also called a **transition zone** because it has characteristics of both the surface- and deep-water layers

Idealized vertical temperature ocean profiles in July and January (A) near the equator, (B) at approximately 45° N or S latitude, and (C) near the poles.

Image by Byron Inouye

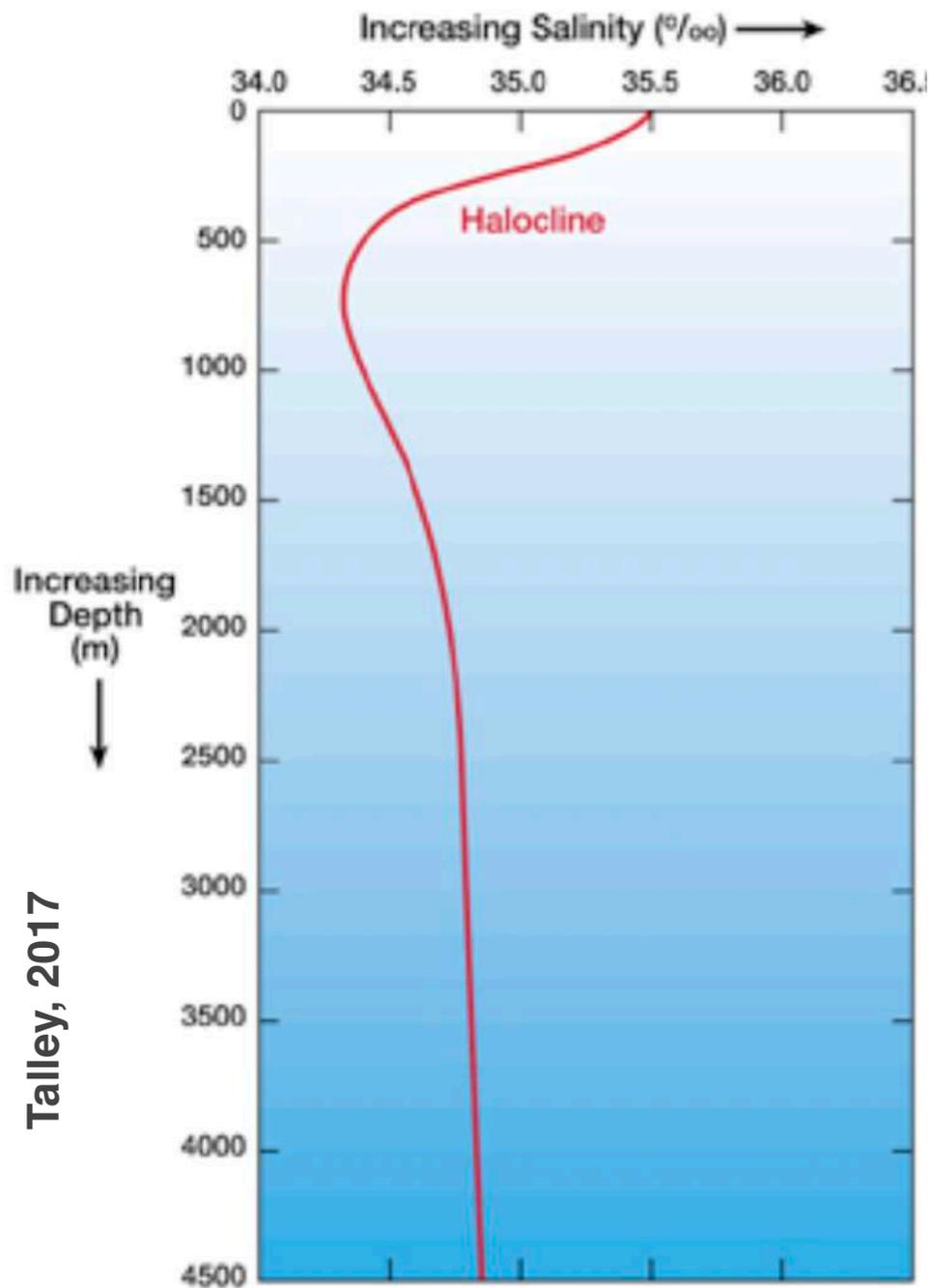
- Sunlight → longer wavelengths
- Optimal range for life
- Temperature dictates chemical reaction rates → growth
- Microbial adaptations at high and low temperature (e.g. cold or heat-shock proteins, membrane fluidity)

Salinity

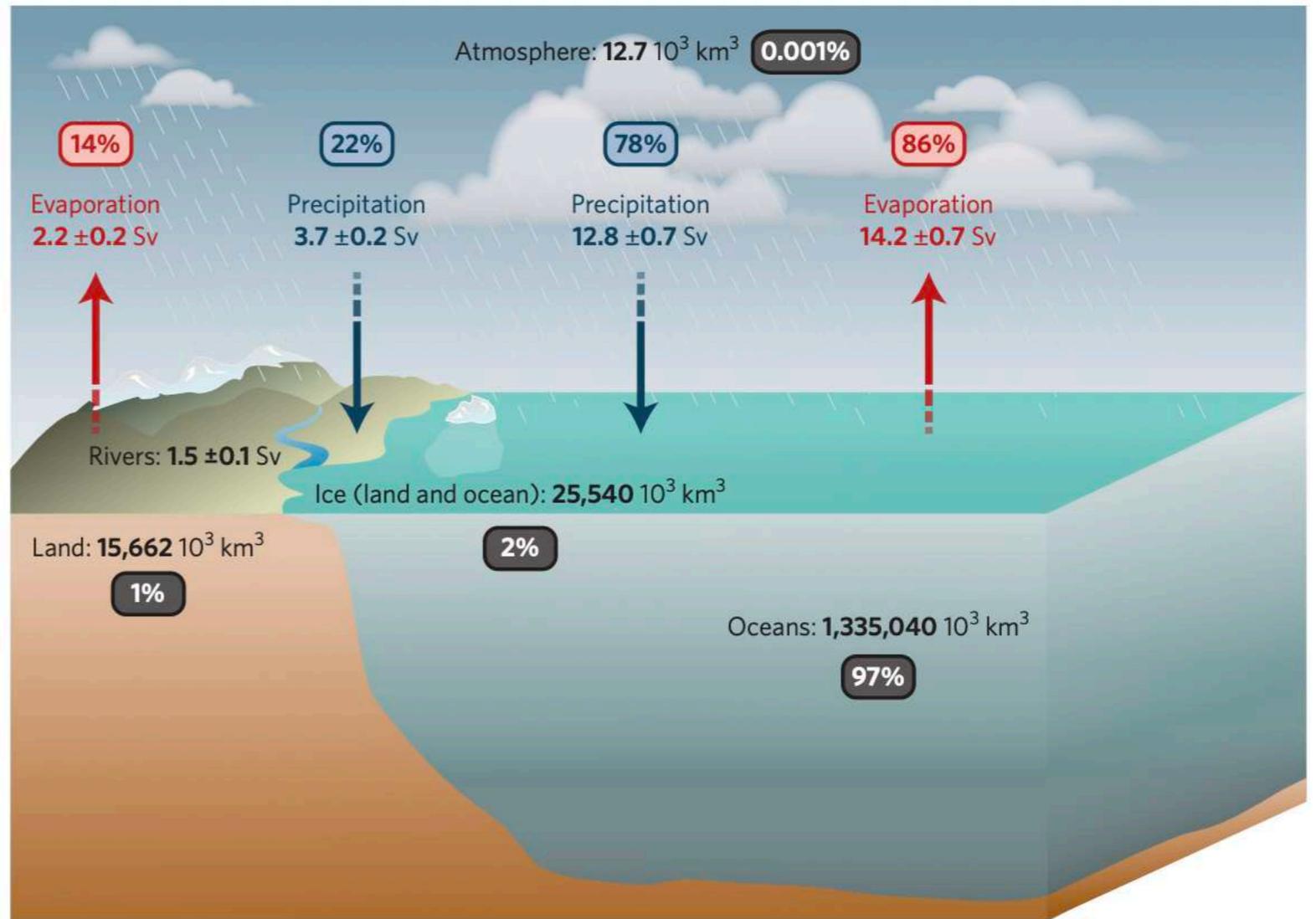
- Number of grams of salts per kilogram of seawater, in parts per thousand or without units
- **Parts per thousand:** how many parts, or grams, of salt there are per thousand parts, or kilogram (1,000 g), of seawater, ‰, ppt

$$\text{Salinity in ppt} = \frac{\text{grams of dissolved salts}}{1,000 \text{ grams of seawater}}$$

- Average SW salinity is ~ 35 grams per kilogram (g/kg), or 35 ppt
- Seawater ranges: 33 - 38 ppt
- Freshwater lakes, rivers, and streams contain some dissolved matter — 1 ppt or less
- Hydrogen and oxygen atoms in water molecules make up about 96.5 % SW mass
- In SW solution, ~ 3.5 % of the mass is made up of dissolved solutes like Na⁺ and Cl⁻
- **The constant addition of dissolved substances into the ocean over billions of years has made the ocean salty**



Talley, 2017



Durack et al., 2016

Figure 1 | The global water cycle — the oceanic perspective. Reservoirs are represented by grey boxes with units 10^3 km^3 . Fluxes are represented by arrows and the red and blue boxes with units of Sv (Sverdrups; $10^6 \text{ m}^3 \text{ s}^{-1}$). Data from refs 2, 31-35.

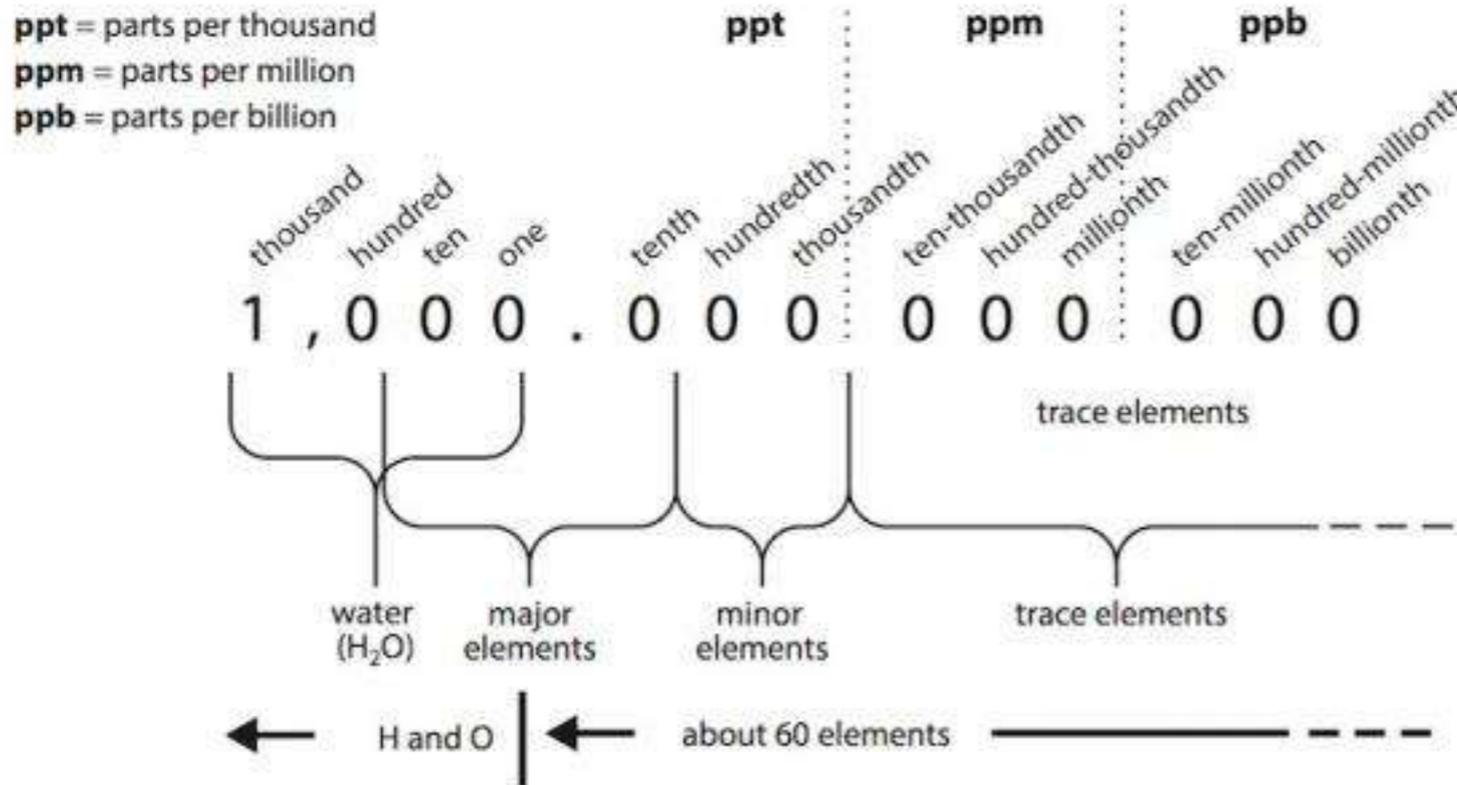
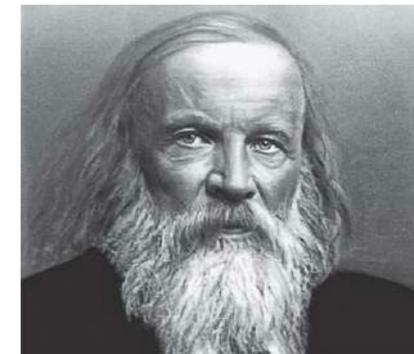
- Optimal range for life
- Brackish water to brine lakes in ocean
- Na^+ pump for movement and membrane transport of microbes vs. H^+
- Microbial adaptations at high and low salt \rightarrow osmotic pressure \rightarrow pumping out or making cytoplasm more saline
- Human pathogens (0.9%) can't survive at 3.5% salinity

Elements

Other common units of concentration in aquatic science are parts per million (ppm), the number of grams of an element dissolved in 1,000,000 g of seawater and parts per billion (ppb), the number of grams of an element dissolved in 1,000,000,000 g of seawater

Elements with concentrations measured in ppm or ppb are called trace elements. For example, if 40 g of a trace element were found in 1,000,000 g of water, the trace element's concentration would be 40 ppm

$$\frac{\text{Mass pollutant in lake sample}}{\text{Total mass of lake mixture sample}} = \frac{40 \text{ g}}{1000000 \text{ g}} = 0.000040 = 40 \text{ ppm}$$



ОПЫТЪ СИСТЕМЫ ЭЛЕМЕНТОВЪ.

ОСНОВАННОЙ НА ИХЪ АТОМНОМЪ ВѢСѢ И ХИМИЧЕСКОМЪ СХОДСТВѢ.

	Ti = 50	Zr = 90	? = 180.
	V = 51	Nb = 94	Ta = 182.
	Cr = 52	Mo = 96	W = 186.
	Mn = 55	Rh = 104,4	Pt = 197,1.
	Fe = 56	Ru = 104,4	Ir = 198.
	Ni = 59	Pd = 106,8	Os = 199.
	Cu = 63,4	Ag = 108	Hg = 200.
H = 1	Be = 9,4	Mg = 24	Zn = 65,2
	B = 11	Al = 27,1	? = 68
	C = 12	Si = 28	? = 70
	N = 14	P = 31	As = 75
	O = 16	S = 32	Se = 79,4
	F = 19	Cl = 35,5	Br = 80
	Li = 7	Na = 23	K = 39
			Rb = 85,4
			Cs = 133
			Ba = 137
			Pb = 207.
			? = 45
			Ce = 92
			?Er = 56
			La = 94
			?Yt = 60
			Di = 95
			?In = 75,8
			Th = 118?

Д. Менделѣевъ

Periodic table created by Mendeleev in 1869 with the title in the original Russian

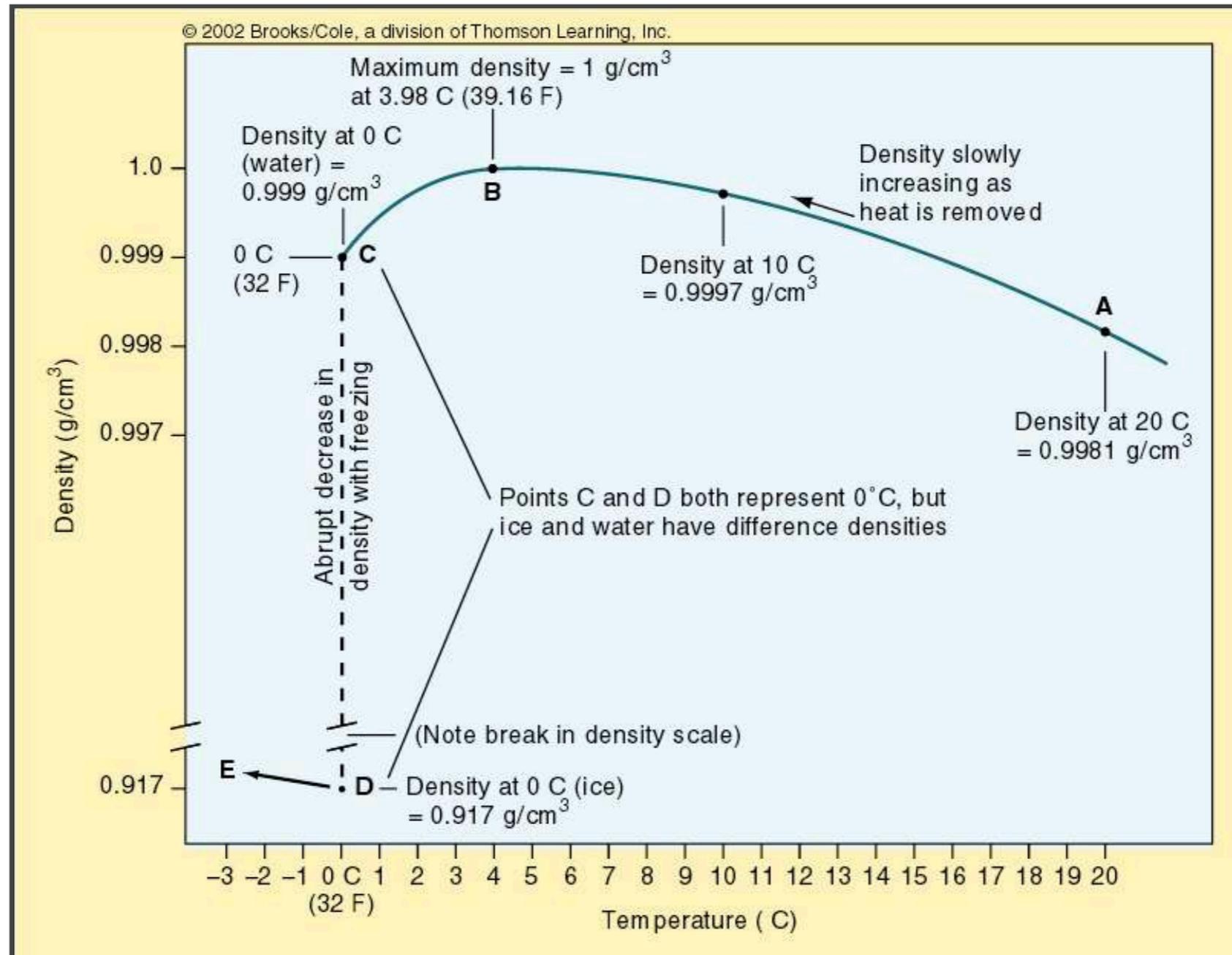
Periodic Table of Elements in the Ocean

Group	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	
Period																			
1	1 <u>H</u>																	2 <u>He</u>	
2	3 <u>Li</u>	4 <u>Be</u>											5 <u>B</u>	6 <u>C</u>	7 <u>N</u>	8 <u>O</u>	9 <u>F</u>	10 <u>Ne</u>	
3	11 <u>Na</u>	12 <u>Mg</u>											13 <u>Al</u>	14 <u>Si</u>	15 <u>P</u>	16 <u>S</u>	17 <u>Cl</u>	18 <u>Ar</u>	
4	19 <u>K</u>	20 <u>Ca</u>		21 <u>Sc</u>	22 <u>Ti</u>	23 <u>V</u>	24 <u>Cr</u>	25 <u>Mn</u>	26 <u>Fe</u>	27 <u>Co</u>	28 <u>Ni</u>	29 <u>Cu</u>	30 <u>Zn</u>	31 <u>Ga</u>	32 <u>Ge</u>	33 <u>As</u>	34 <u>Se</u>	35 <u>Br</u>	36 <u>Kr</u>
5	37 <u>Rb</u>	38 <u>Sr</u>		39 <u>Y</u>	40 <u>Zr</u>	41 <u>Nb</u>	42 <u>Mo</u>	43 <u>Tc</u>	44 <u>Ru</u>	45 <u>Rh</u>	46 <u>Pd</u>	47 <u>Ag</u>	48 <u>Cd</u>	49 <u>In</u>	50 <u>Sn</u>	51 <u>Sb</u>	52 <u>Te</u>	53 <u>I</u>	54 <u>Xe</u>
6	55 <u>Cs</u>	56 <u>Ba</u>	*	71 <u>Lu</u>	72 <u>Hf</u>	73 <u>Ta</u>	74 <u>W</u>	75 <u>Re</u>	76 <u>Os</u>	77 <u>Ir</u>	78 <u>Pt</u>	79 <u>Au</u>	80 <u>Hg</u>	81 <u>Tl</u>	82 <u>Pb</u>	83 <u>Bi</u>	84 <u>Po</u>	85 <u>At</u>	86 <u>Rn</u>
7	87 <u>Fr</u>	88 <u>Ra</u>	**																

*Lanthanides Rare Earth Elements	*	57 <u>La</u>	58 <u>Ce</u>	59 <u>Pr</u>	60 <u>Nd</u>	61 <u>Pm</u>	62 <u>Sm</u>	63 <u>Eu</u>	64 <u>Gd</u>	65 <u>Tb</u>	66 <u>Dy</u>	67 <u>Ho</u>	68 <u>Er</u>	69 <u>Tm</u>	70 <u>Yb</u>
**Actinides	**	89 <u>Ac</u>	90 <u>Th</u>	91 <u>Pa</u>	92 <u>U</u>	93 <u>Np</u>	94 <u>Pu</u>								

<https://www.mbari.org/science/upper-ocean-systems/chemical-sensor-group/periodic-table-of-elements-in-the-ocean/>

- Freezing point of seawater is $\sim -1.8^{\circ}\text{C}$
- Density continually increases to freezing point



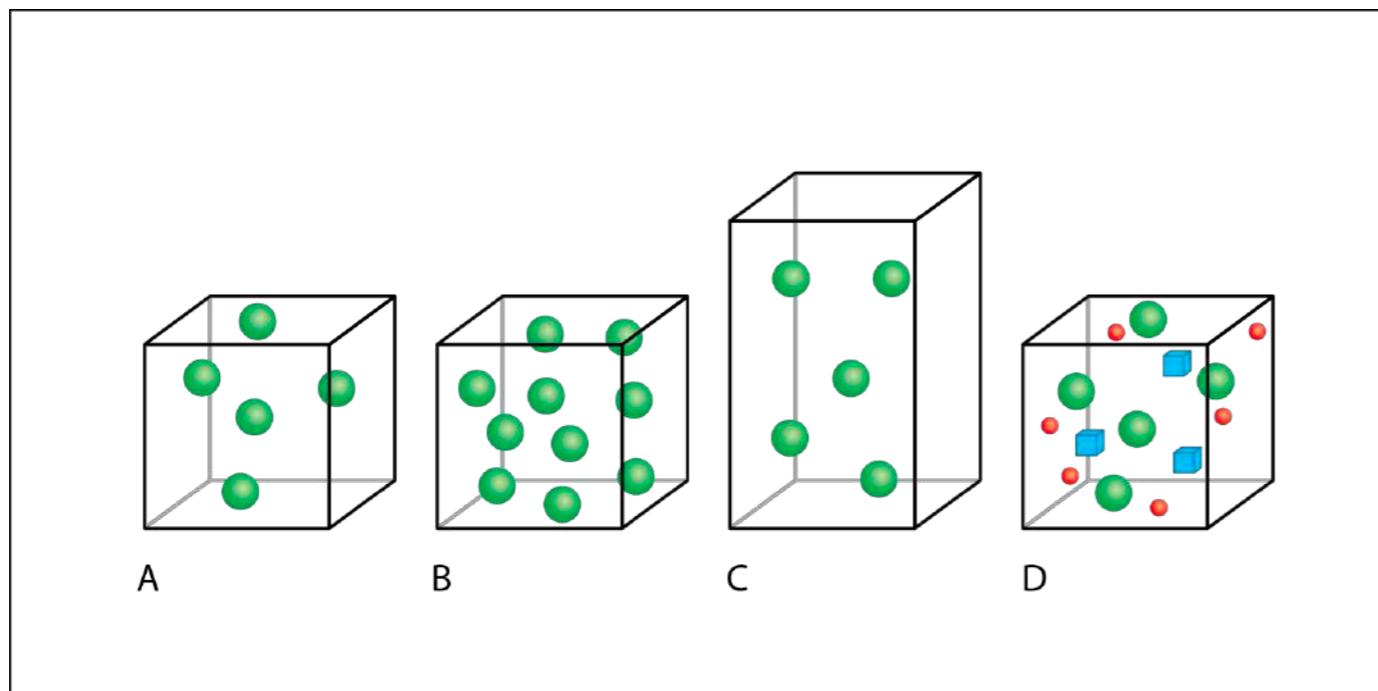
- SW freezing point $<$ pure water freezing point
- Ice floats on water !



Density

Density is a measure of how much mass there is in a given **volume** or amount of space
The density of any substance is calculated by dividing the mass of the matter by the volume of the matter

$$\text{density} = \frac{\text{mass}}{\text{volume}}$$



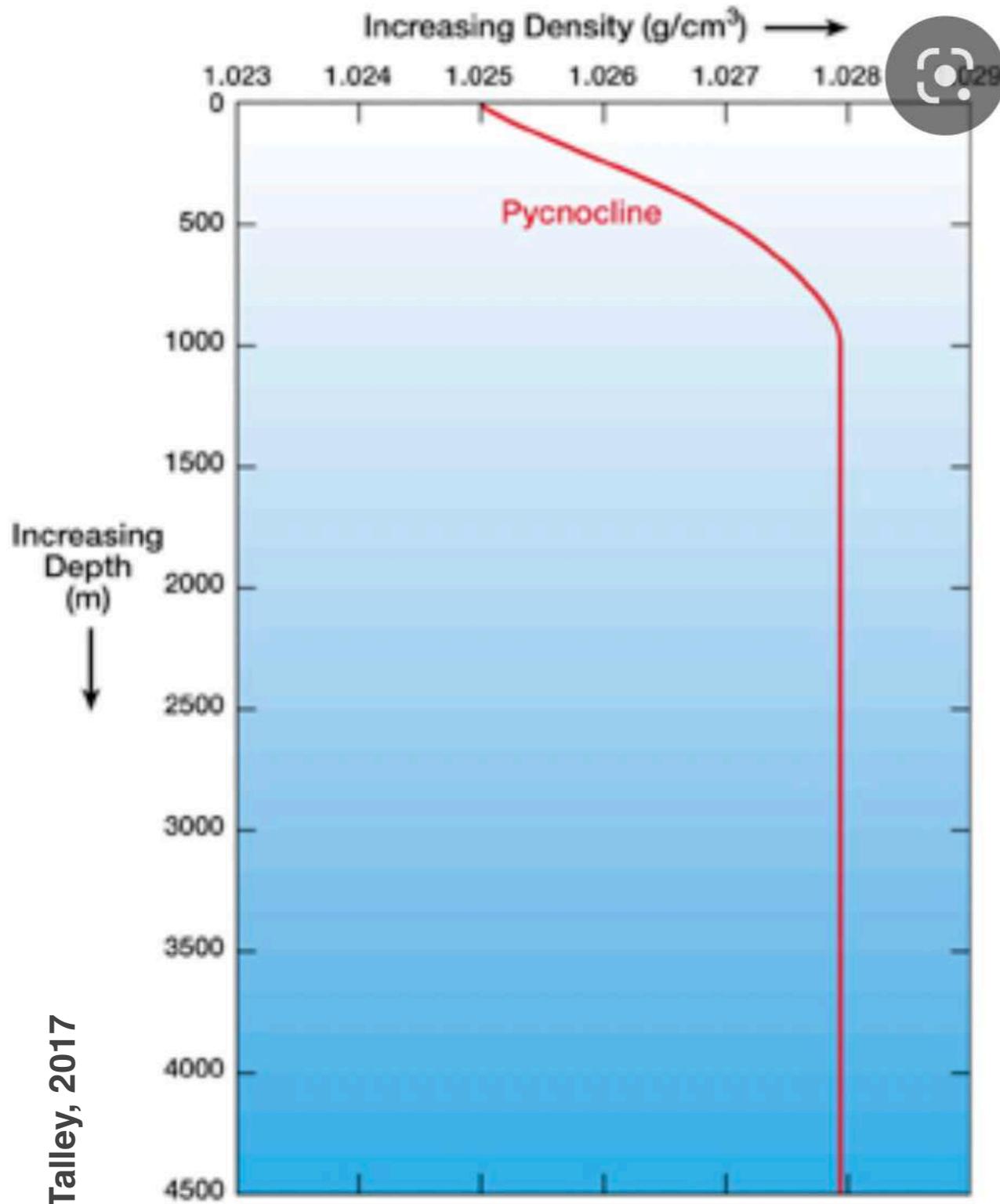
If the amount of matter is increased without changing the volume, \rightarrow density increases

If volume increases without an increase in mass, \rightarrow density decreases

Adding additional matter to the same volume also increases density, even if the matter added is a different type of matter

When salt is dissolved in fresh water, the density of the water increases because the mass of the water increases

When the water is heated, it expands, increasing in volume \rightarrow density decreases

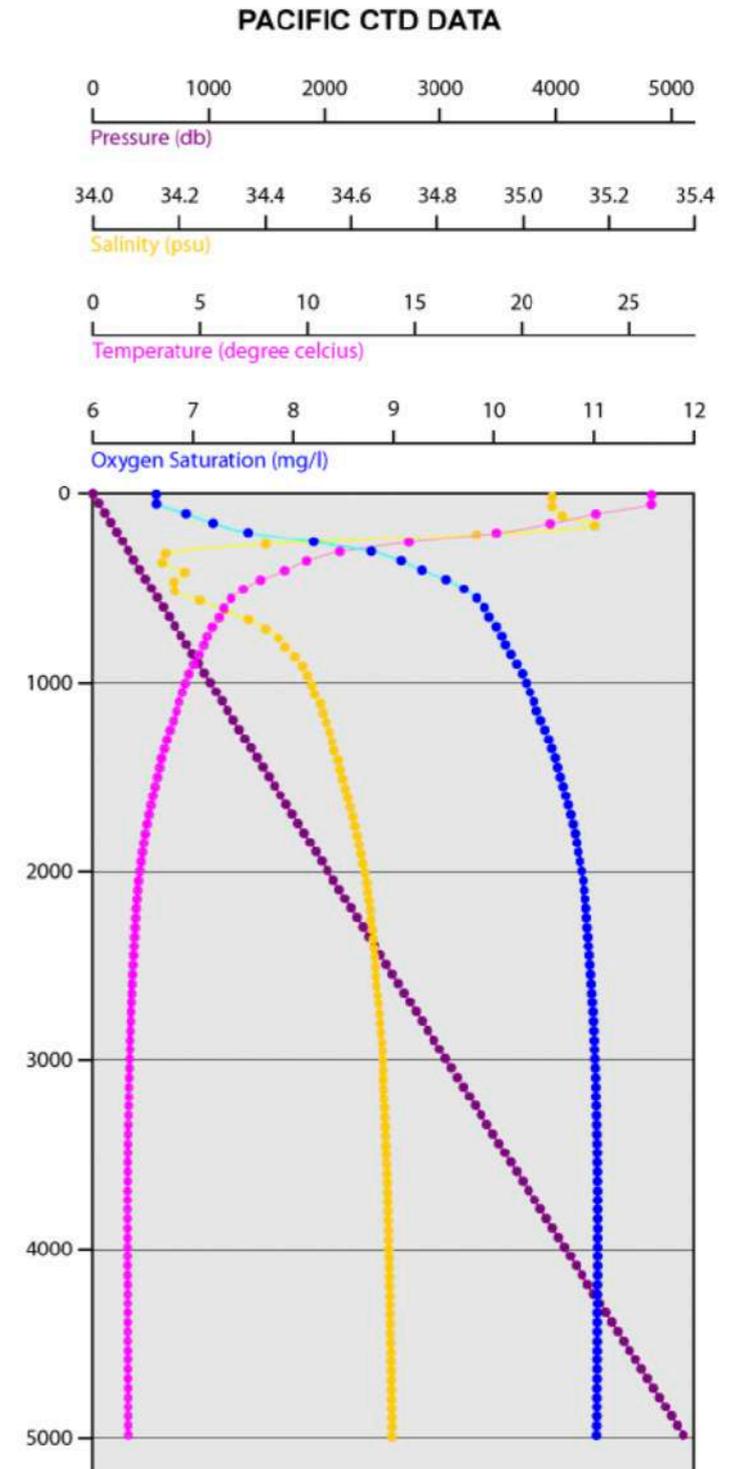


- Fresh water density is 1 g/cm^3 at 4°C but the addition of salts and other dissolved substances increases surface SW density between $1.02 - 1.03 \text{ g/cm}^3$
- SW density can be increased by reducing its temperature, increasing its salinity, or increasing the pressure
- Density of pure bacterial cultures ranged from 1.035 to 1.093 g/cm^3 → *ergo* bacteria will sink
- Strategy to change buoyancy due to gas vacuoles → not to sink out
- Cell buoyant density is controlled by the osmoregulatory system not by growth rate

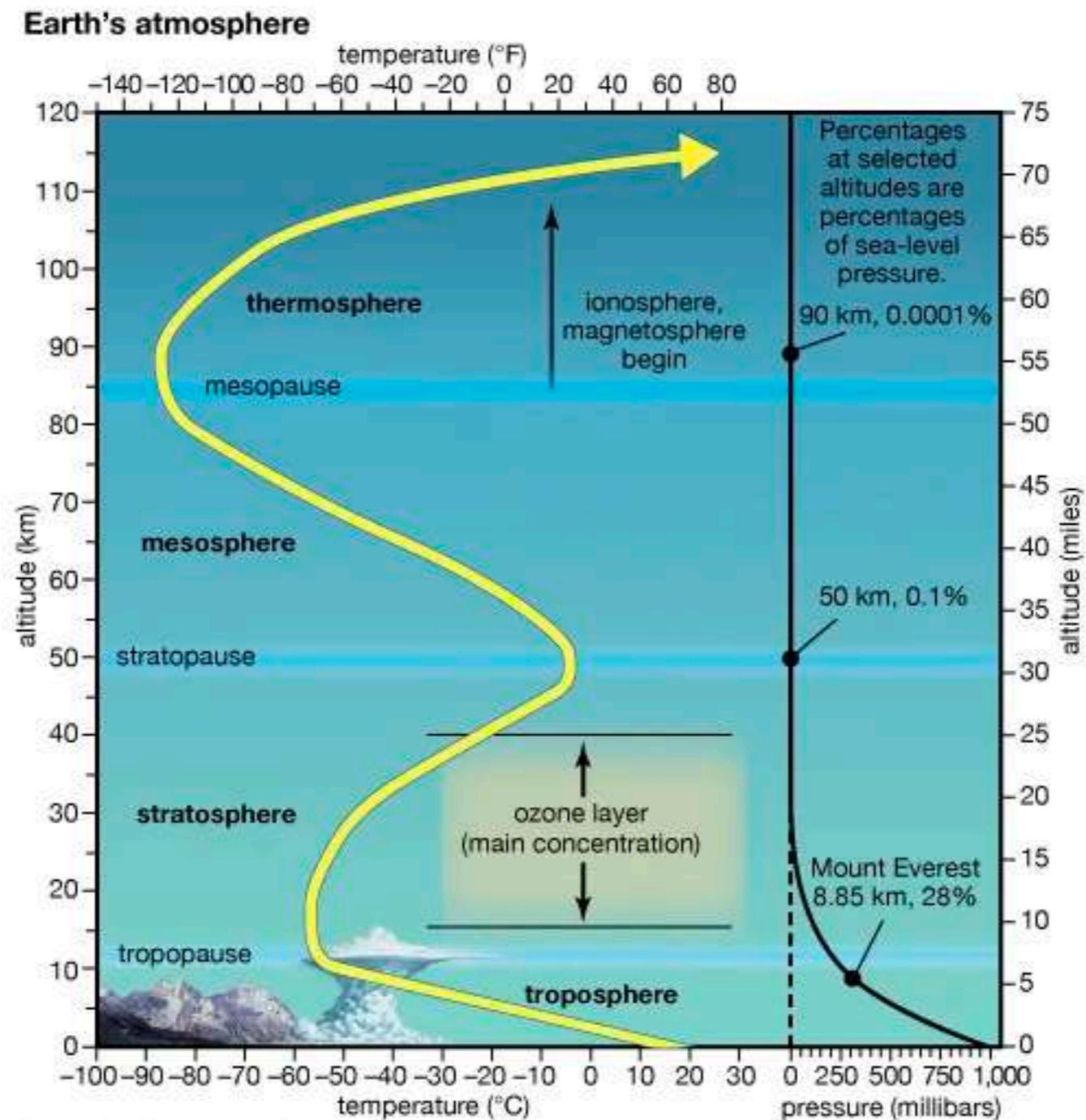
Pressure

Pressure (P) is the force applied perpendicular to the surface of an object per unit area over which that force is distributed

- Ocean covers approximately 70% of world's surface and its average pressure is 38 MPa (1 MPa = 10 bar)
- Hydrostatic pressure originates from the weight of the water column and corresponds to 10 MPa/km
- In ocean, water presses against all sides of an object or organism → feel equal pressure from all directions
- Atmospheric pressure is usually measured in bars. 1 bar = 10^6 dynes/cm² = 10^5 Pascal
- Ocean pressure is usually measured in decibars. 1 dbar = 10^{-1} bar = 10^5 dyne/cm² = 10^4 Pascal.

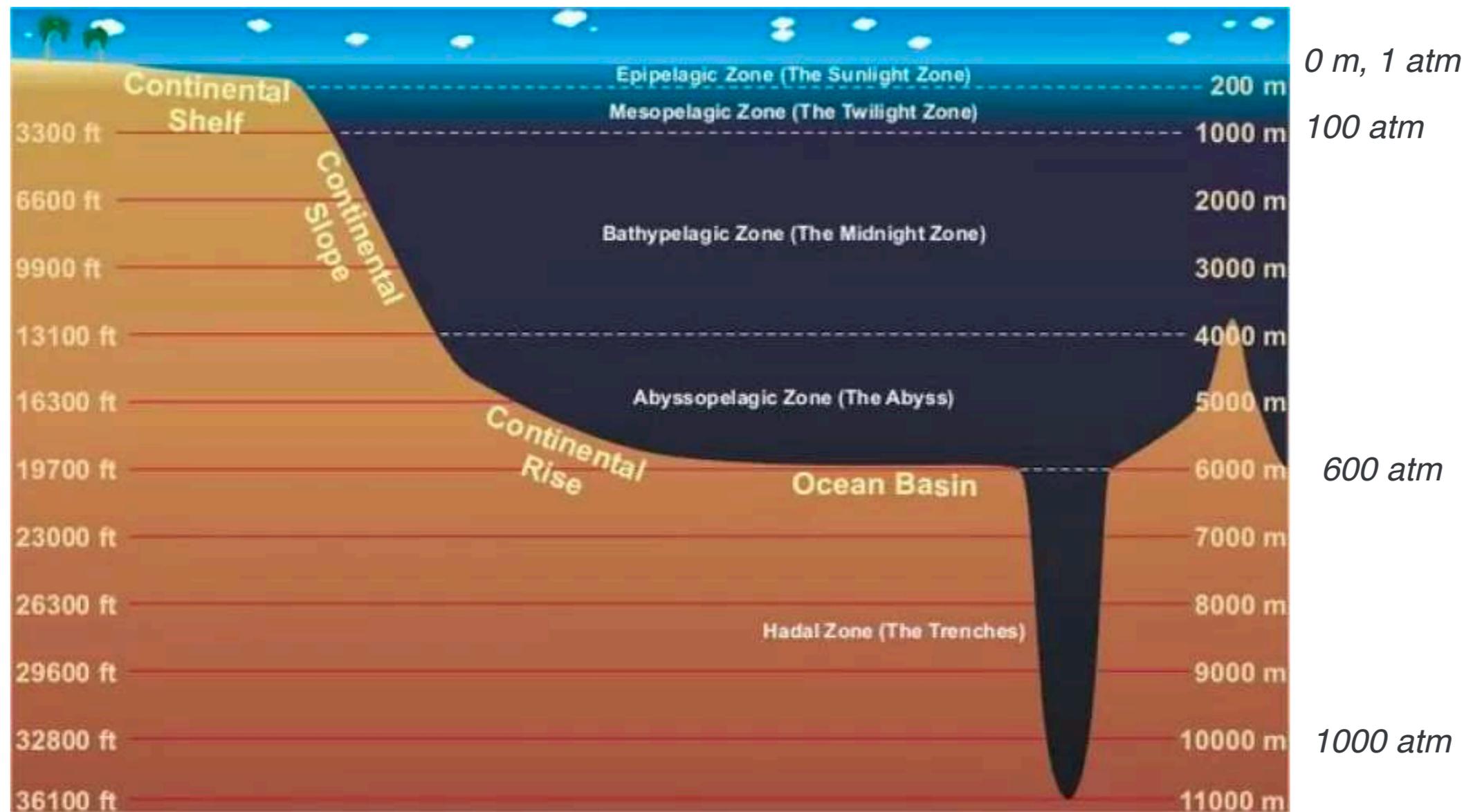


- Near the ocean's surface, that pressure is the same as on land
- This amount of pressure is called an atmosphere
- When the diver reaches 10 meters (33 feet), the pressure is double what it was at the surface



© Encyclopædia Britannica, Inc.

- For every 10 meters of water, hydrostatic pressure increases by one atmosphere
- At the average ocean depth (3,800 meters), pressure on the sea floor is 380 times > than at the surface
- In the deepest trenches, it's 1,100 times greater!
- Seawater is about 800 times more dense than air



Megapascal (MPa) = 10 bar \cong 9.9 atmospheres

NOAA

Living under Pressure

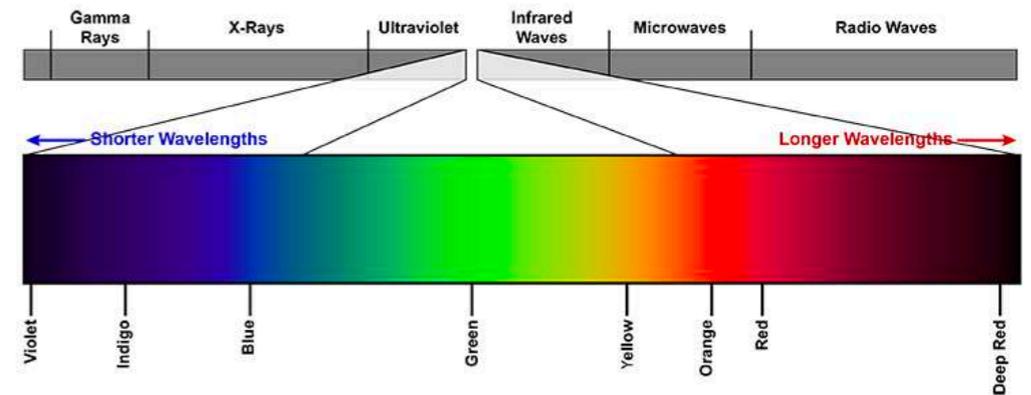
- Pressures affect the interatomic molecular bindings (such as Van der Waals, hydrogen bonding and hydrophobic interactions) altering conformations and structures of biomolecules and therefore, their physical properties (solubility, melting point, density), equilibrium states and processes' rate
- Electrostatic and hydrophobic interactions are specifically affected by pressure
- Pressures > 2 GPa impact non-covalent interactions
- Due to pressure, the biological system is favouring the acquisition of more compact structural forms
- Besides the structural alterations in biomolecules, pressure also disturbs the equilibrium of (bio)chemical reactions—> changing 3D
- With increasing pressure, lipid bilayers lose fluidity and became rapidly impermeable to water and other molecules, while protein–lipid interactions essential to the optimal function of the membrane are weakened
- Adaptive strategies to survive at high pressure and low temperature

Table 1. Pressure sensitive processes detected in *E. coli* (Oger and Jebbar, 2010).

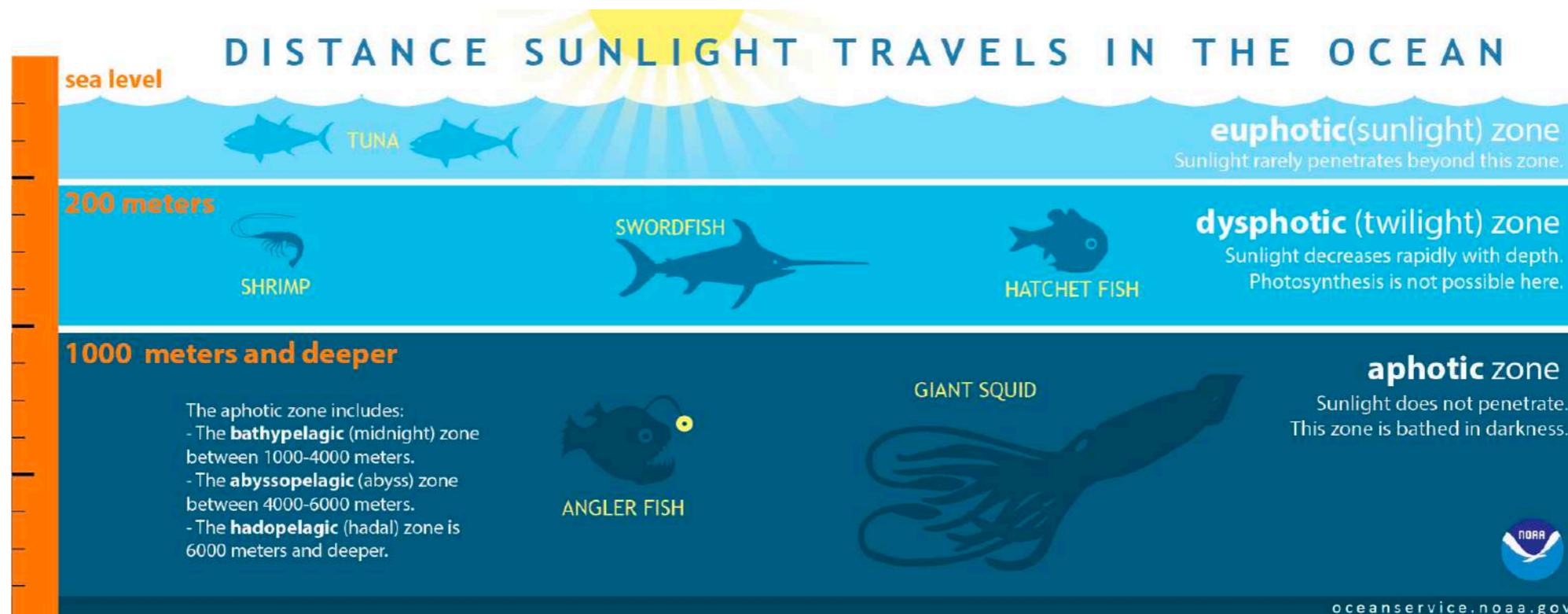
Process	Pressure abolishing process (MPa)	References
Motility	10	Meganathan and Marquis (1973)
Substrate transport	26	Landau (1967)
Cell division	20–50	ZoBell (1970) , Zobell and Cobet, 1962 , Zobell and Cobet, 1964
Growth	50	Yayanos and Pollard (1969)
DNA replication	50	Yayanos and Pollard (1969)
Translation	60	Gross et al., 2005 , Yayanos and Pollard, 1969
Transcription	77	Yayanos and Pollard (1969)
Viability	200	Pagán and Mackey (2000)

Solar radiations

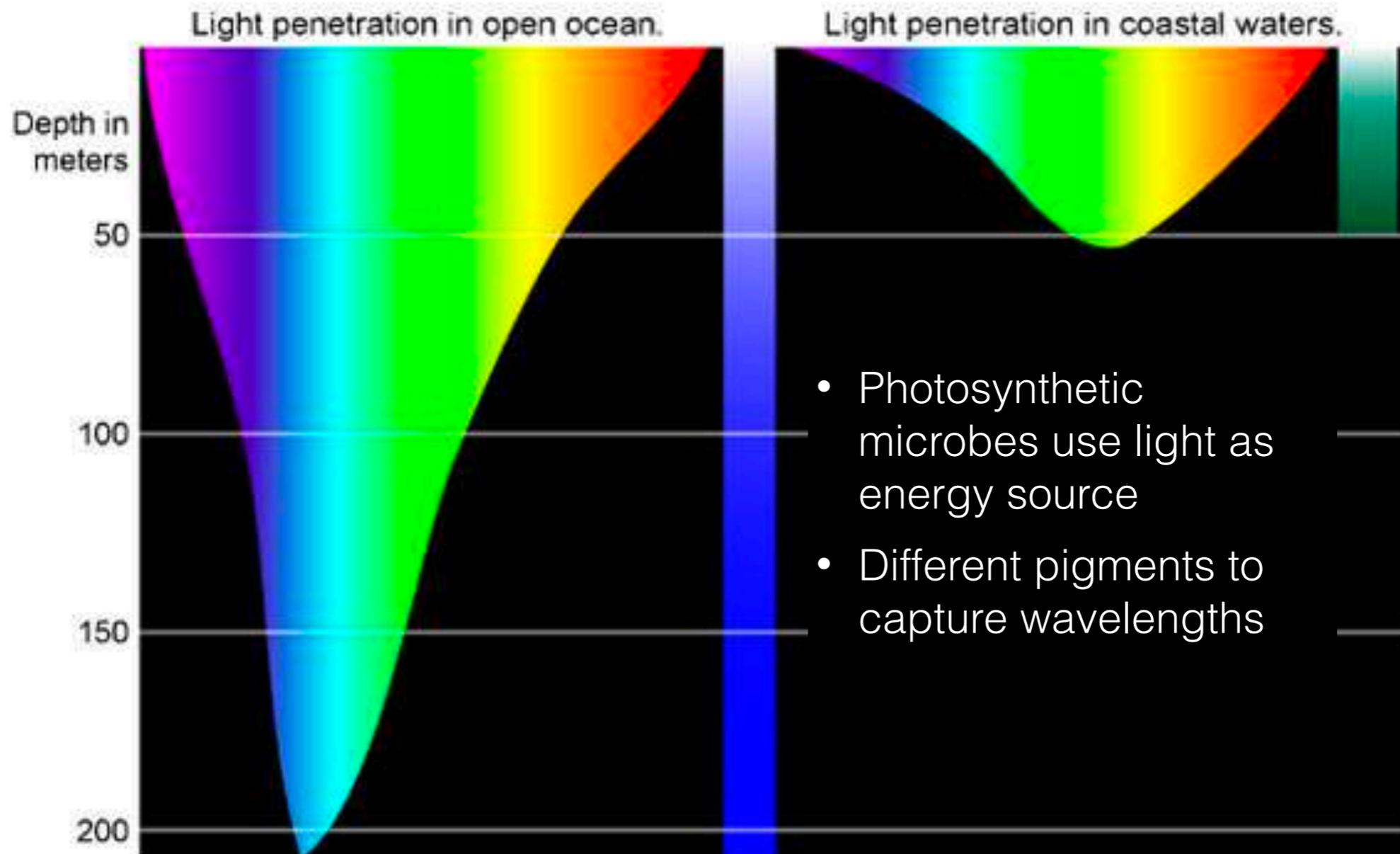
Light/Dark



- Electromagnetic radiation
- Present since the beginning of Earth
- Changes in diel cycle length caused by rotation Earth over millennia
- Changes in light period in Antarctica and Arctic



- Visible sunlight makes up about 40 % of the total energy Earth receives from the sun
- The rest of the energy Earth receives from the sun is not visible
- About 50 % is infrared (IR) energy, 9% is ultraviolet (UV) energy, and 1% is X-rays or microwaves

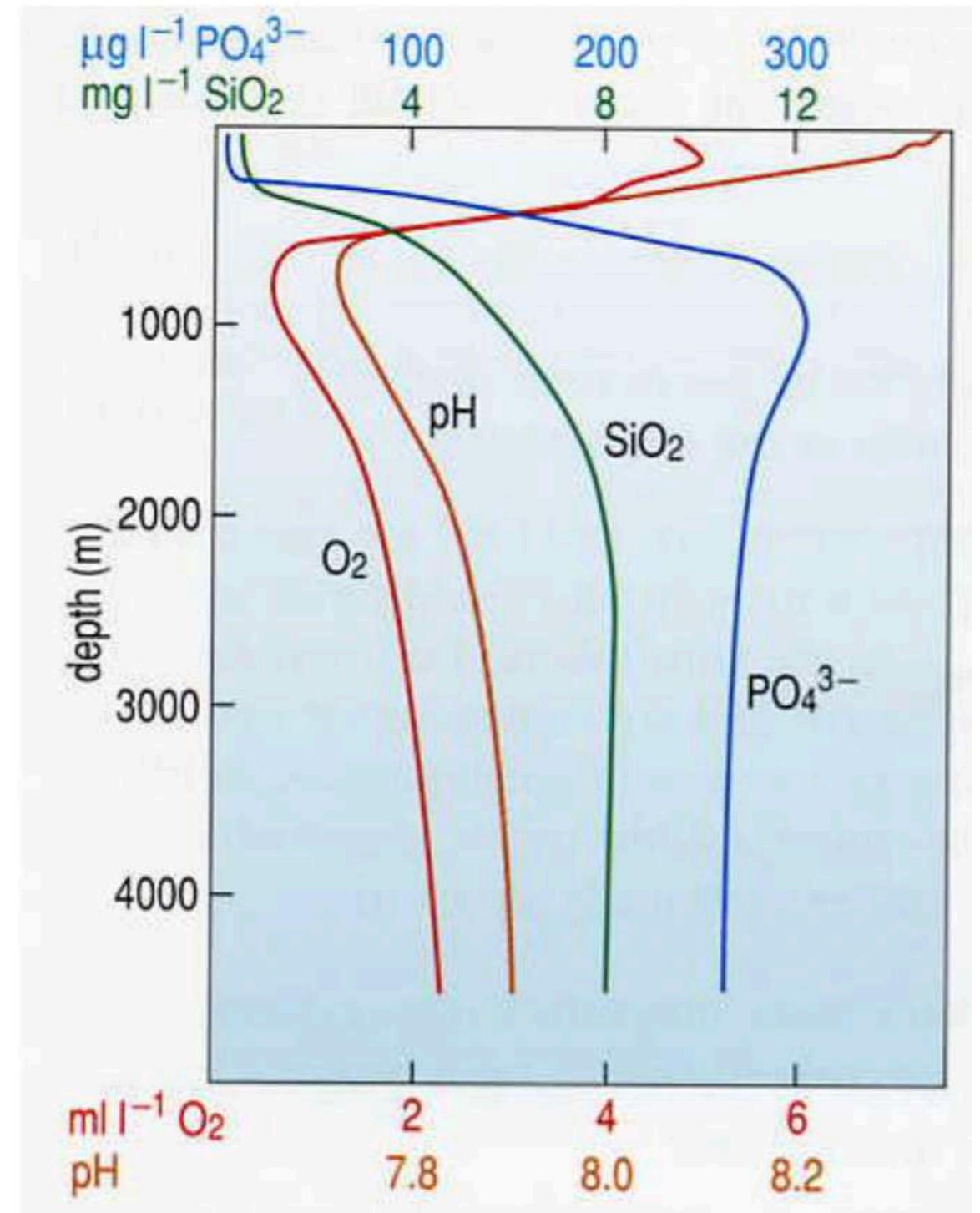


- Photosynthetic microbes use light as energy source
- Different pigments to capture wavelengths

- Depth at which different colors of light penetrate SW
- Water absorbs warm colors like reds and oranges (known as long wavelength light) and scatters the cooler colors (known as short wavelength light)

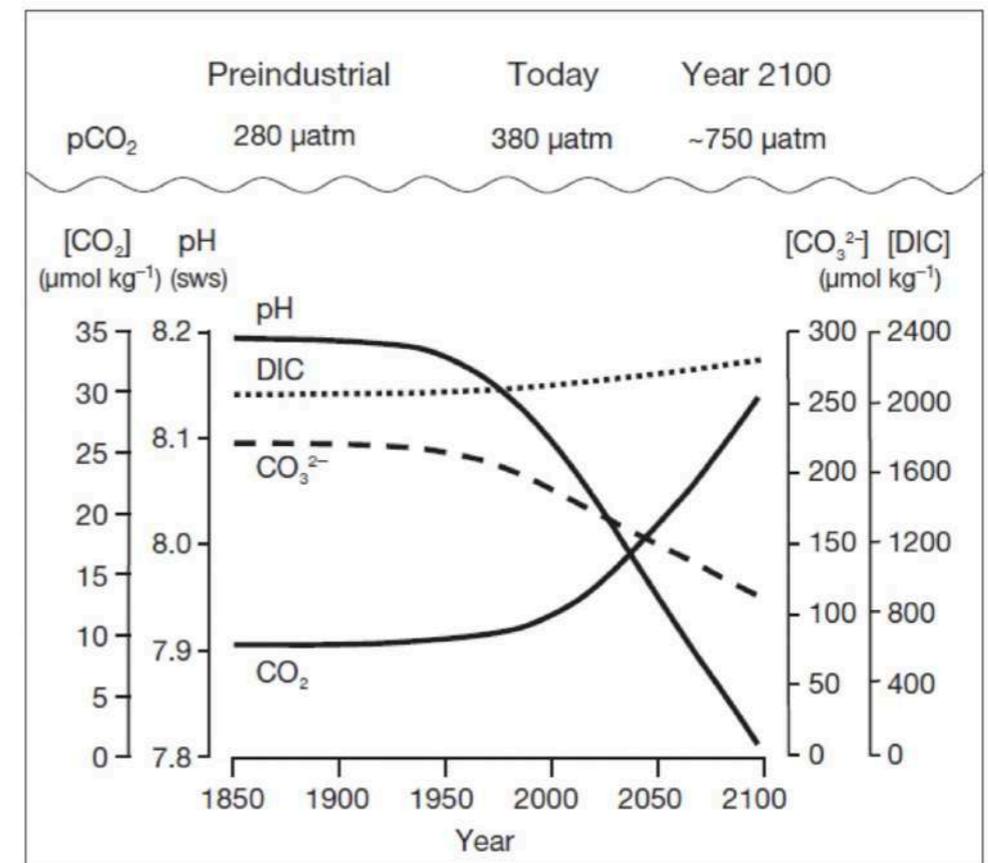
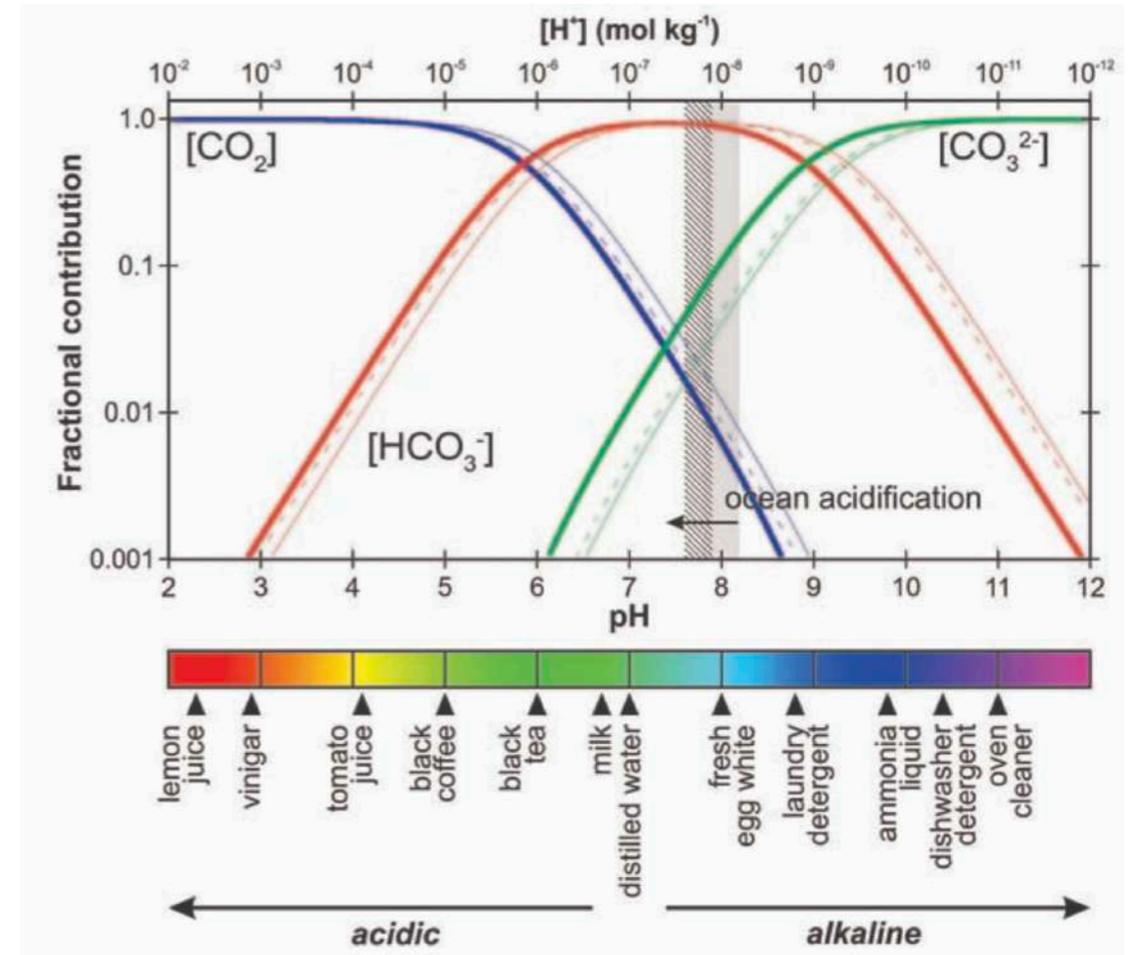
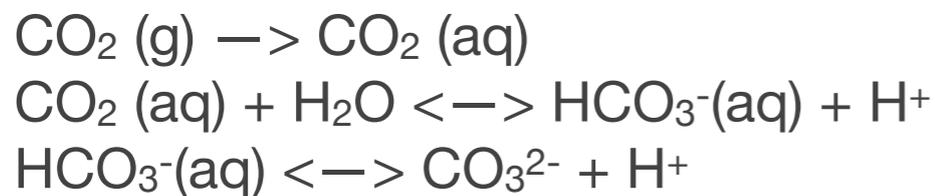
Oxygen

- Oxygen derives from biological activity → by product of photosynthesis
- Every organism uses O_2 for aerobic respiration
- Primary producers (autotrophs) during the night behave like heterotrophs
- Gases follows the Boyle laws for solubility: lower temperature more soluble
- Oxygen is used up by microbes to “respire”/ degrade organic matter → remineralization of nutrients
- Surface water are rich in O_2 due to equilibrium with atmosphere and photosynthesis
- Below the O_2 minimum, O_2 content begins to increase again with depth → related to water circulation in the ocean



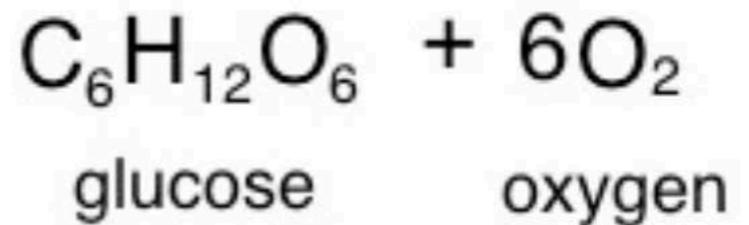
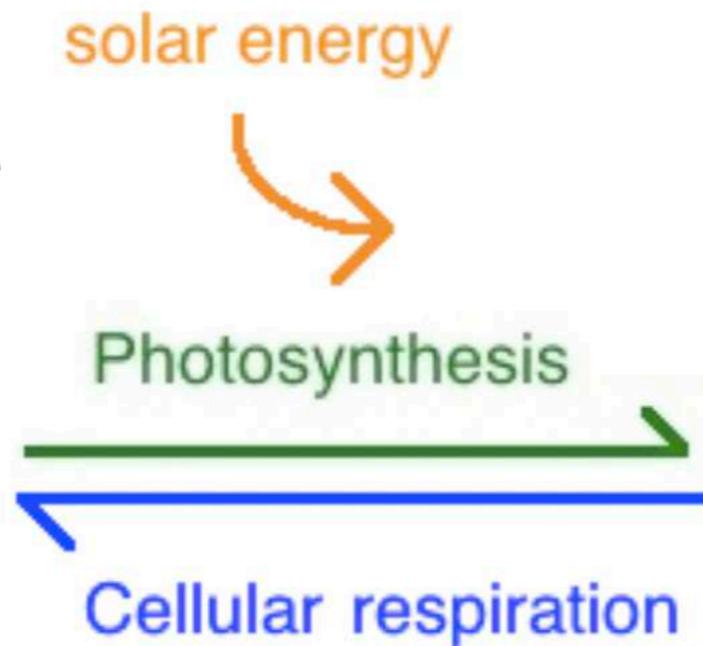
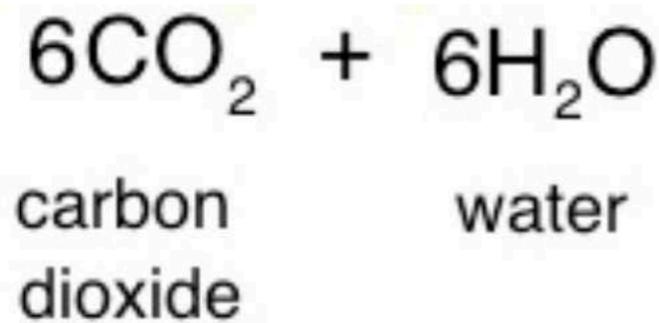
pH

- pH is defined as the negative log of the hydrogen ion concentration
- pH range extends from zero to 14; 7 is neutral
- Oceans take up CO_2 from the atmosphere and are responsible for absorbing around a third of the CO_2 emitted by fossil fuel burning, deforestation, and cement production since the industrial revolution (Sabine et al. 2004)
- Ocean acidification describes the lowering of seawater pH and carbonate saturation that result from increasing atmospheric CO_2 concentrations



O₂-LIFE-CO₂

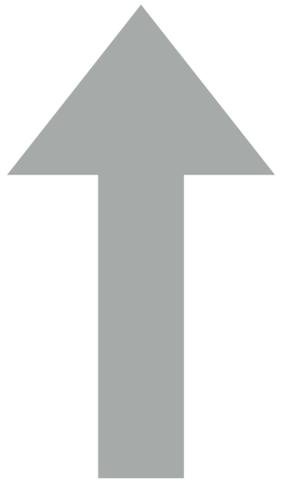
Cyanobacteria
Plants-Algae-Microalgae
Organisms with
cyanobacteria/Microalgae



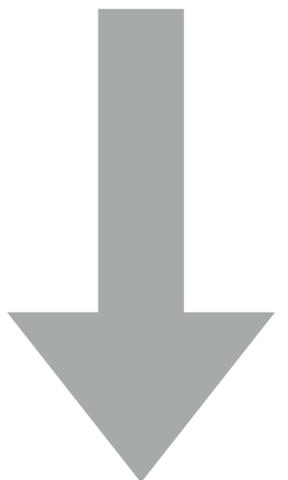
chemical energy
(ATP) + heat

All

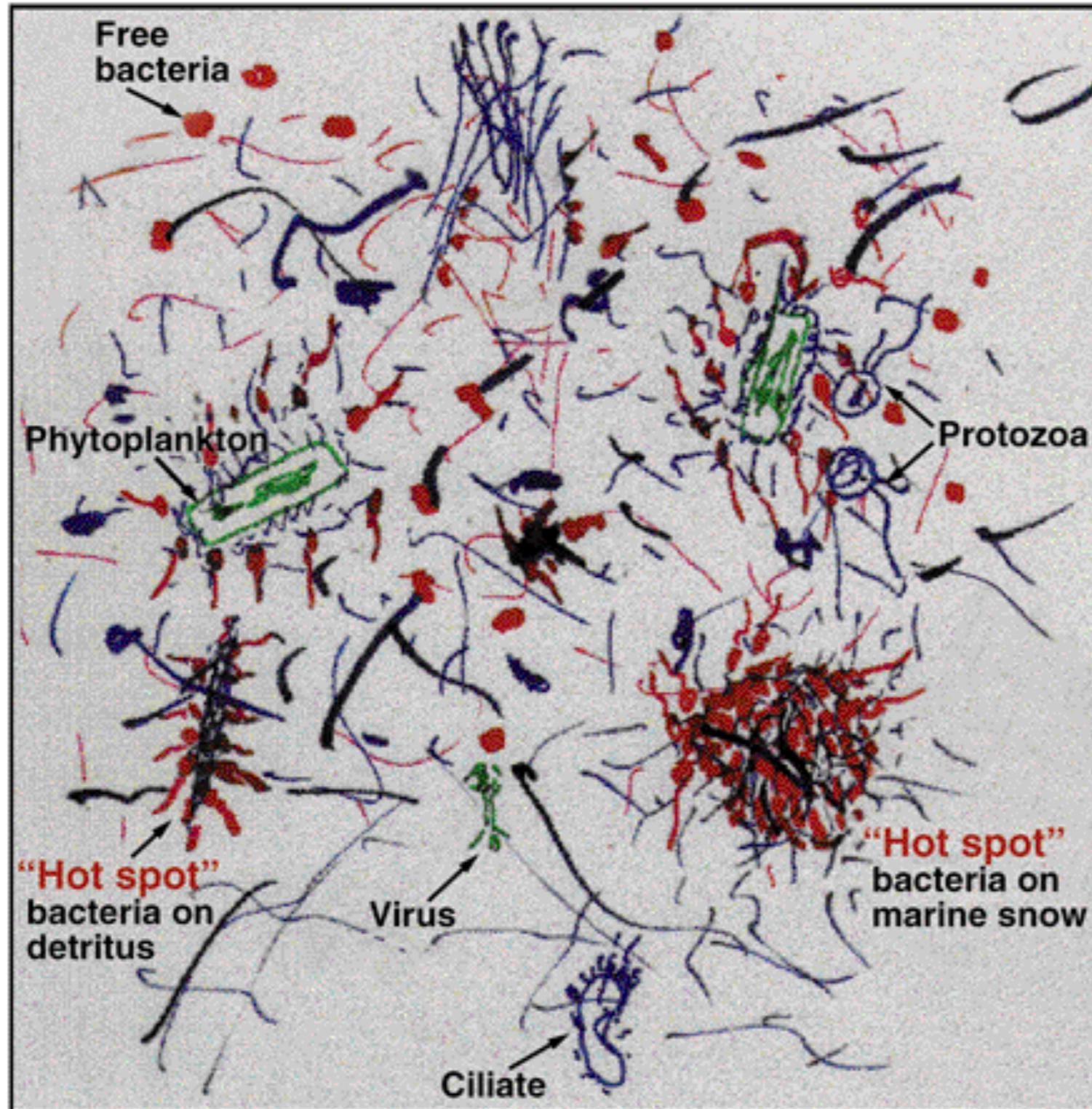
pH



pH



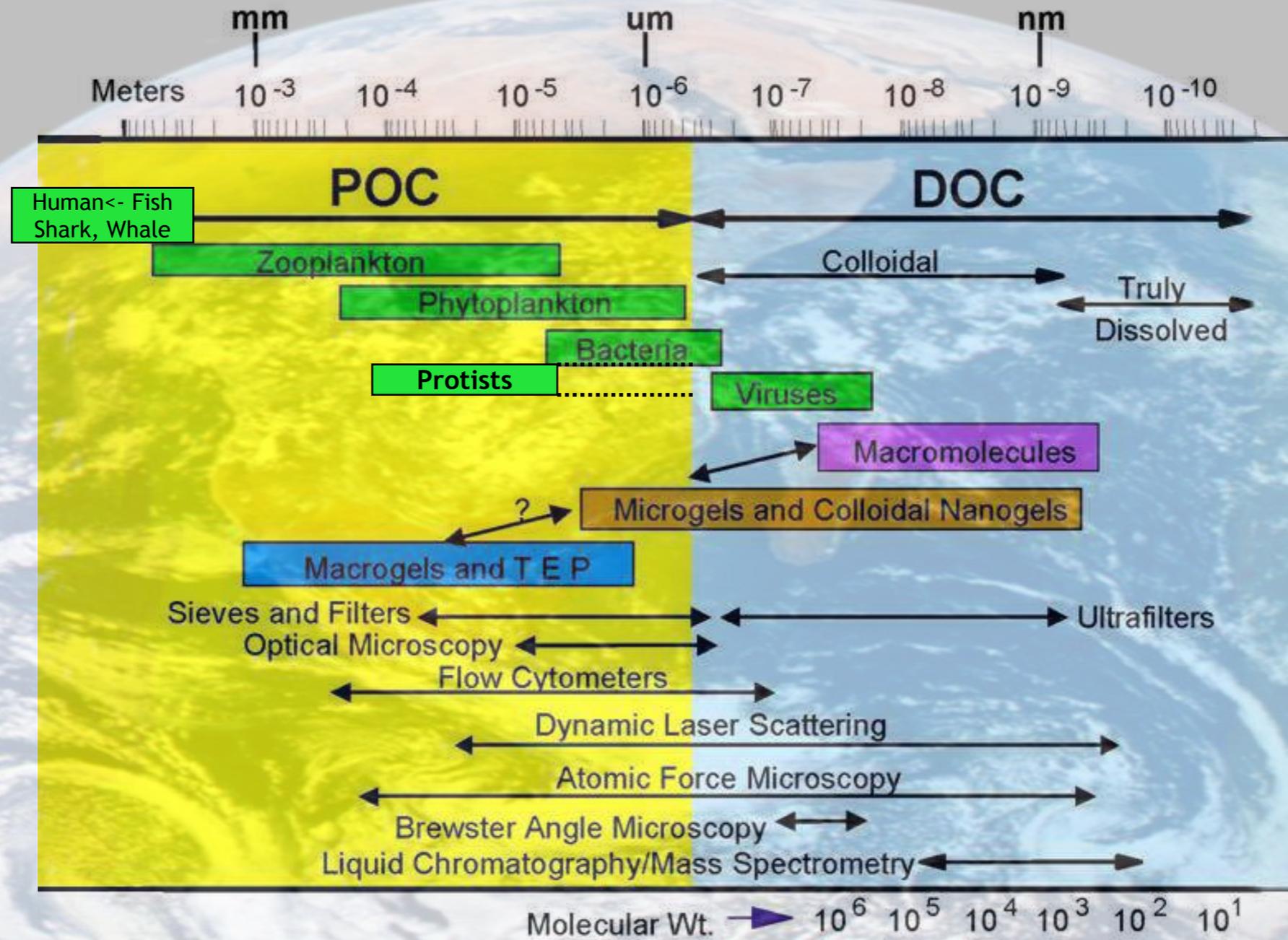
Organic matter



by Farooq Azam

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

F. Azam



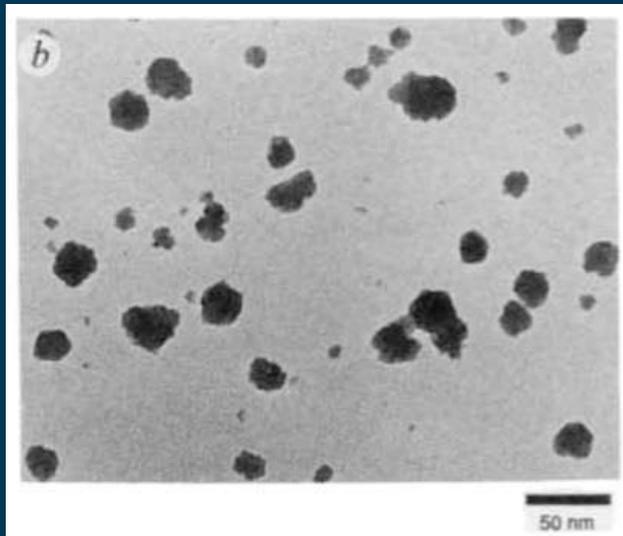
Verdugo et al. 2004

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

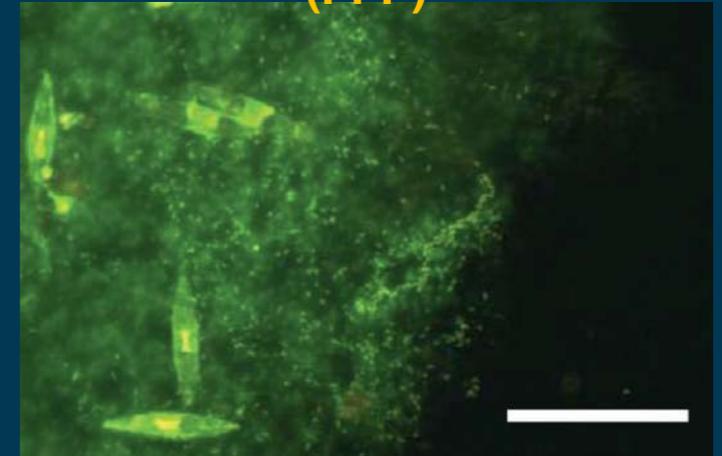
Wells & Goldberg, 1991

Coomassie Stained Particles (CSP)



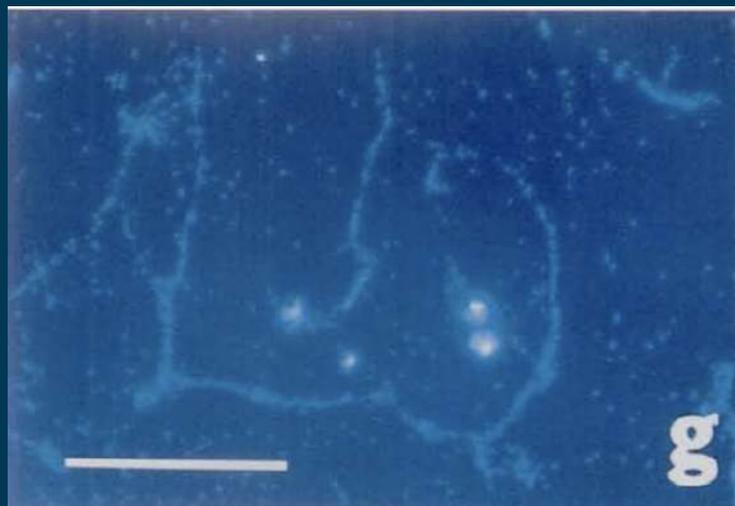
Long & Azam, 1996

Filter Fluorescing Particles (FFP)



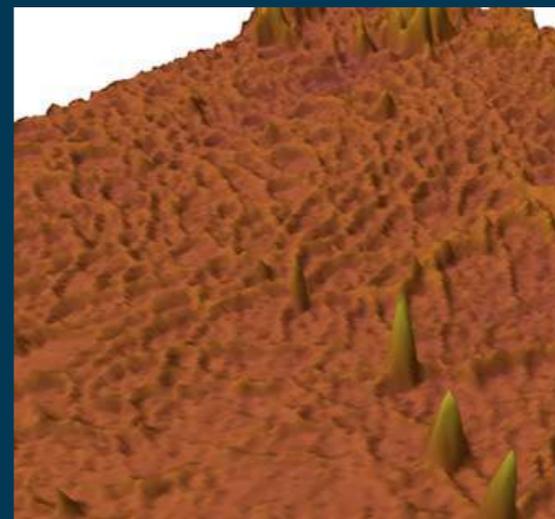
Samo, Malfatti & Azam 2008

Transparent Exopolymeric Particles (TEP)



Alledrege et al., 1993

Gel network from Adriatic Sea



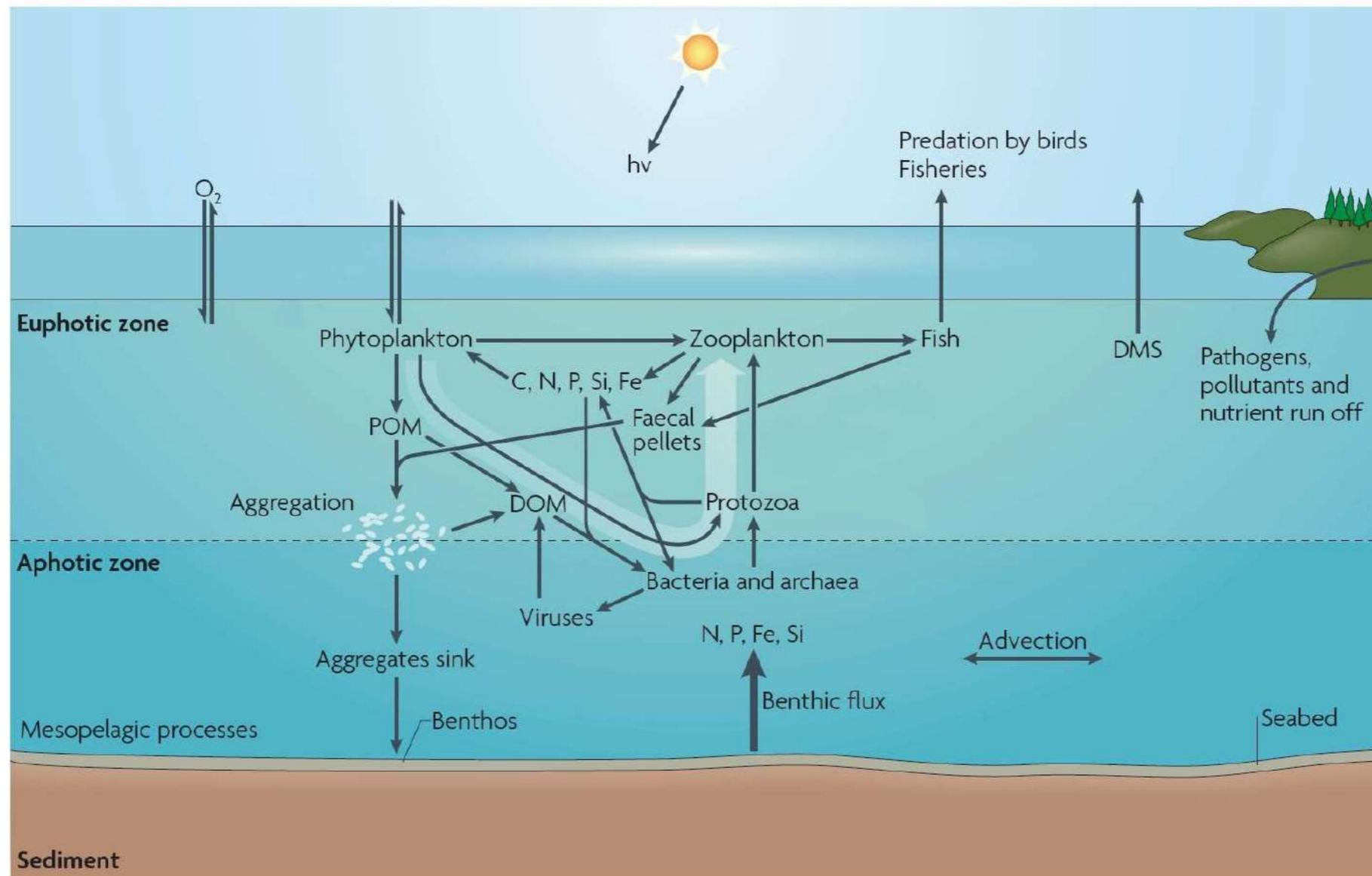
Malfatti unpub.



Nino Caressa

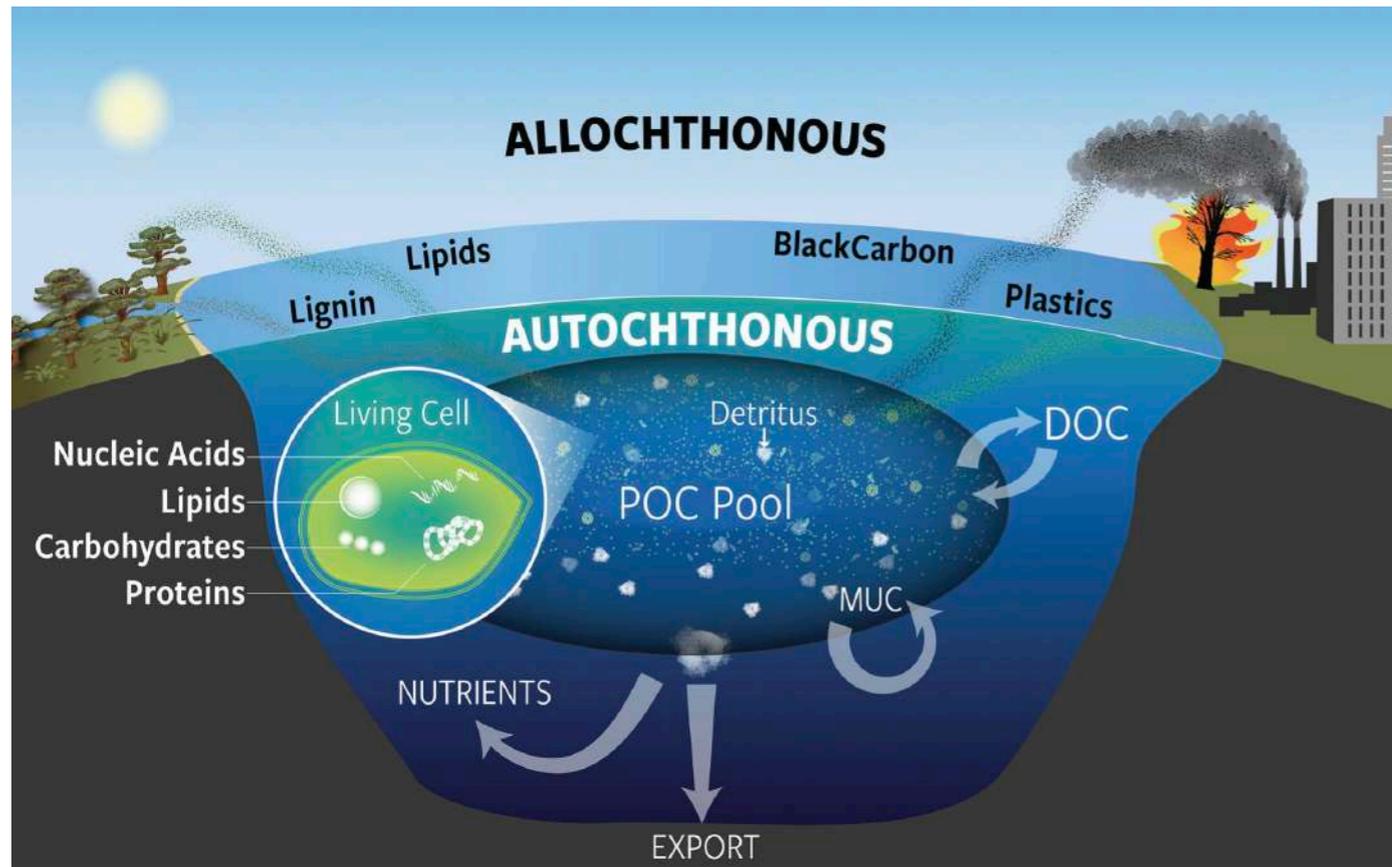
Organic matter

- Source of organic matter is biology
- Production and decomposition/degradation of organic matter
- Atmospheric CO₂ is fixed by photosynthesis —> Carbon Cycle



Azam & Malfatti, 2007

Organic matter



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

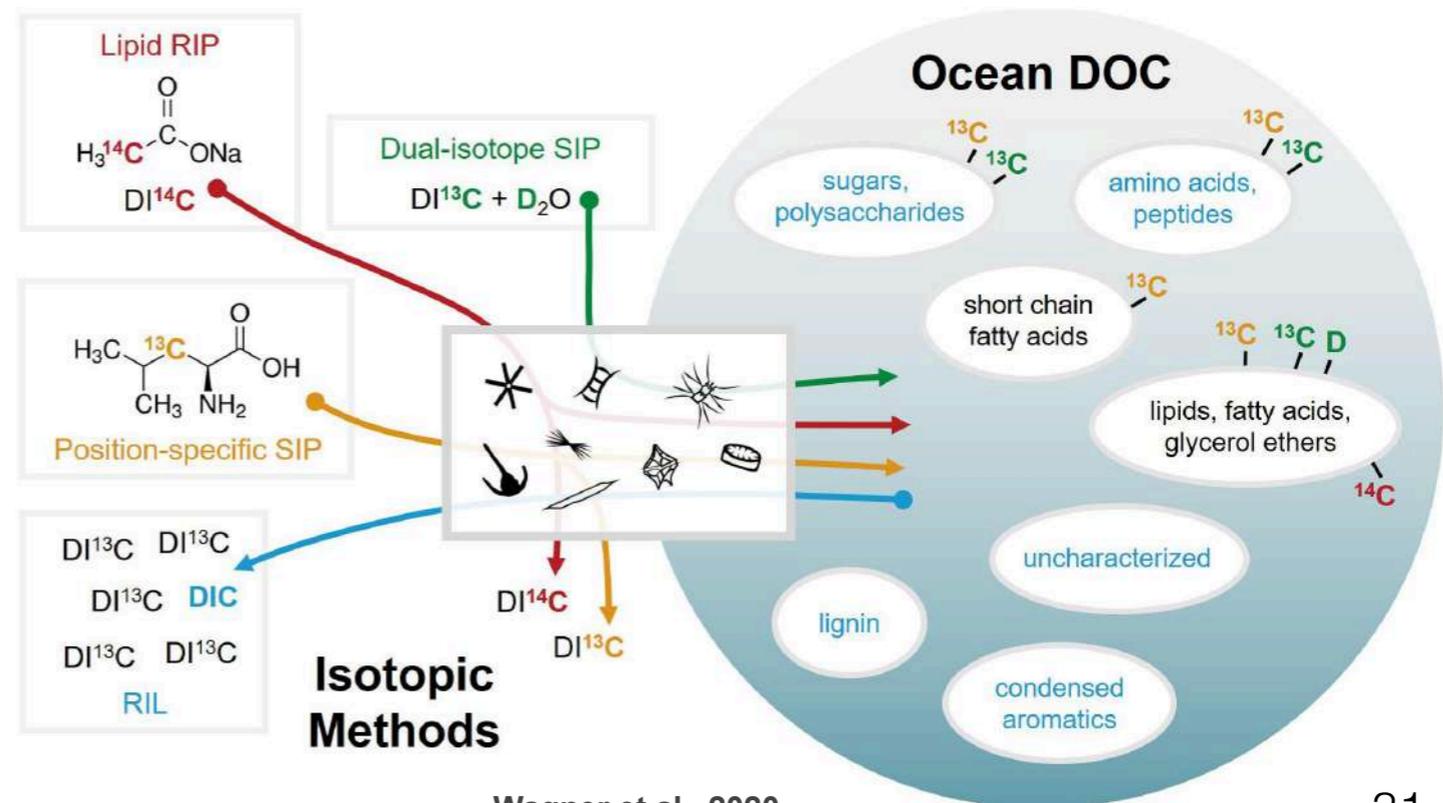
The POC pool can also exchange material with the dissolved OC (DOC) pool through aggregation and disaggregation of particles

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

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

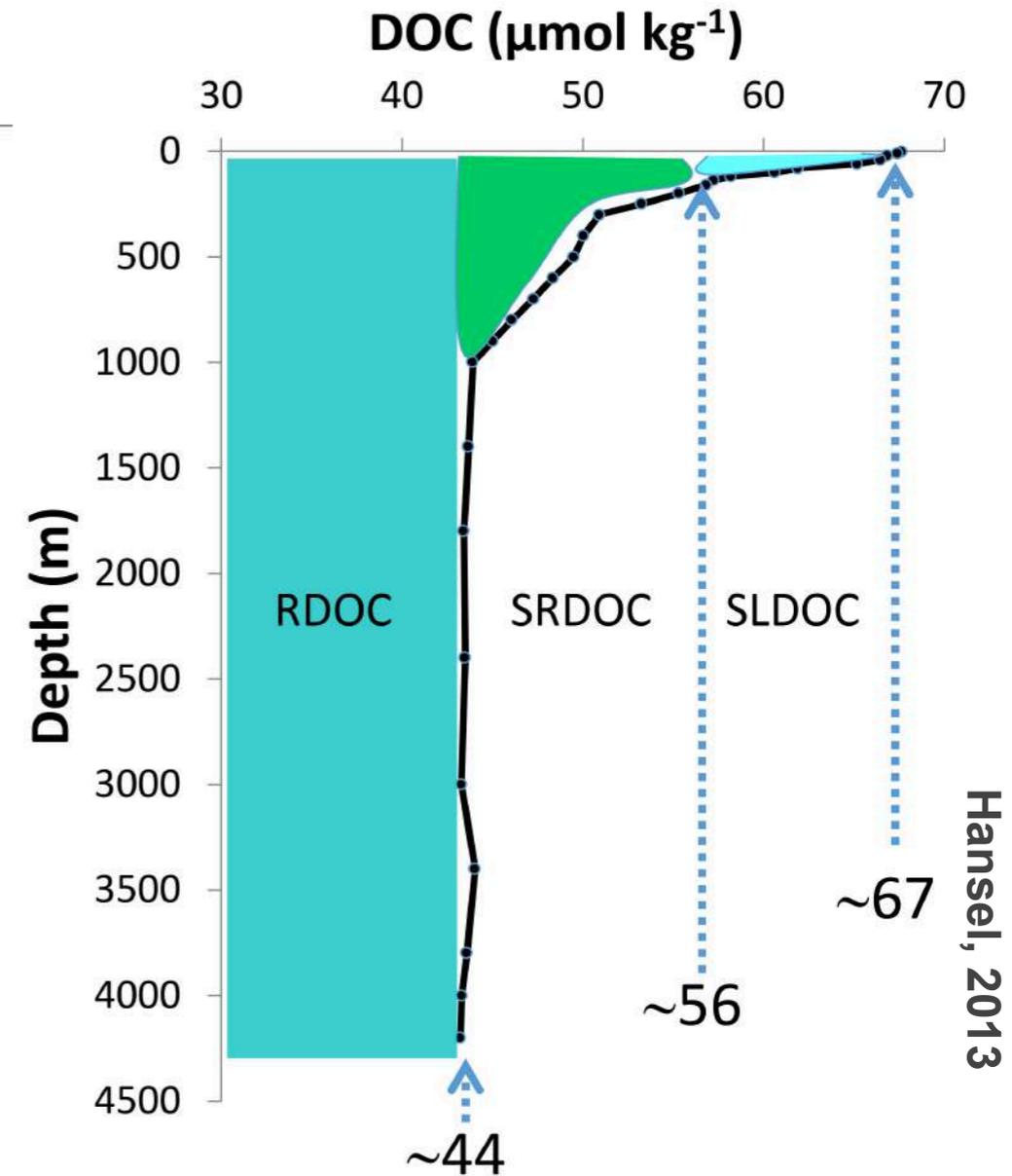
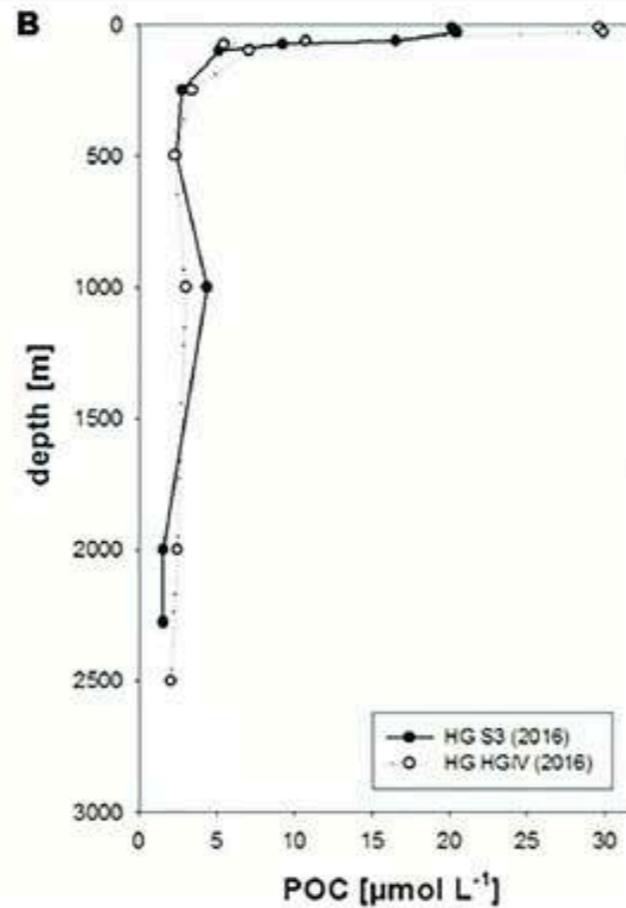
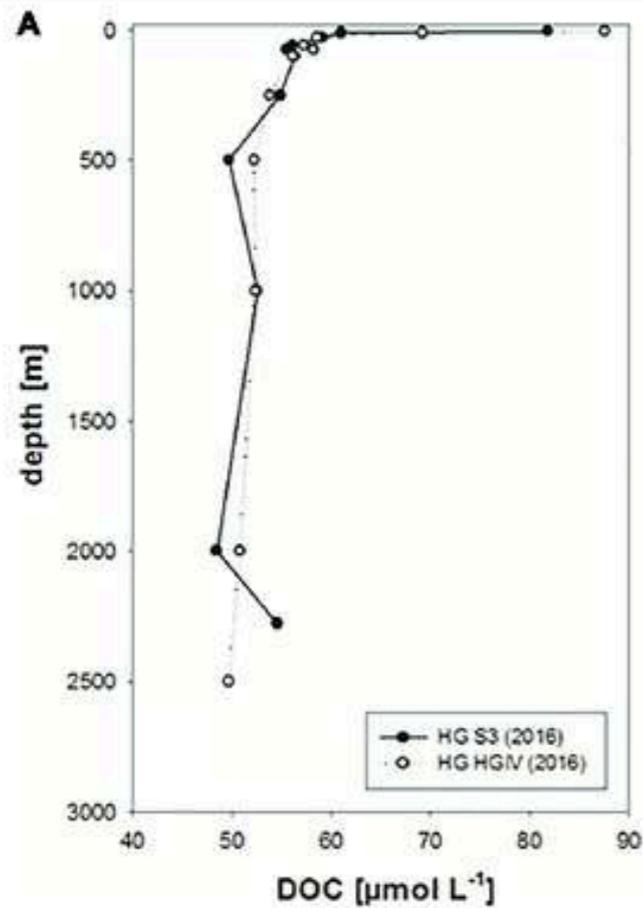
Position-specific and dual-isotope stable isotope probing (SIP), lipid radioisotope probing (RIP), and reversed isotope labeling (RIL)

The sphere is shaded according to the apparent recalcitrance of DOC compound classes



POC and DOC profile

Engel, 2019

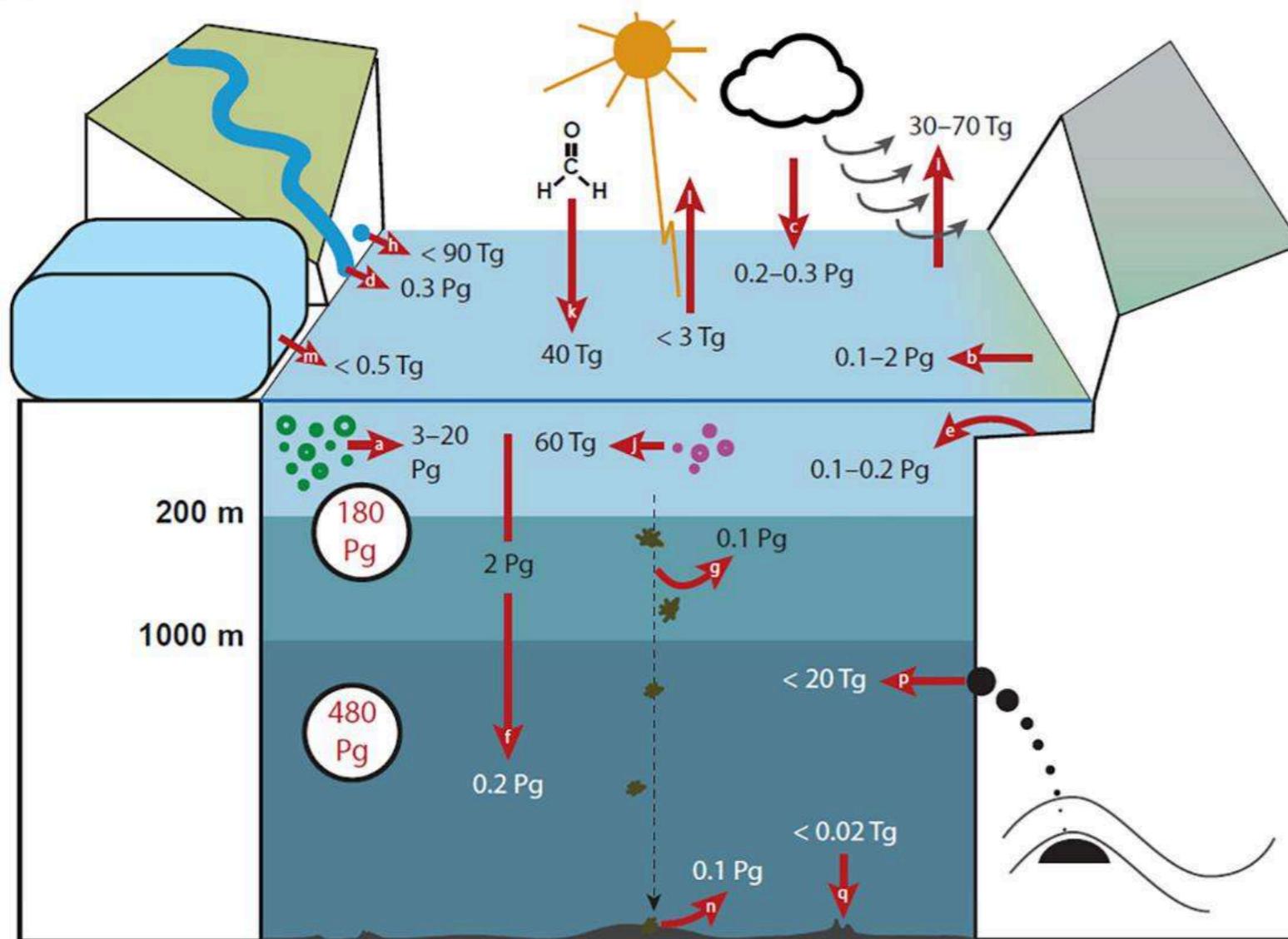


Hansel, 2013

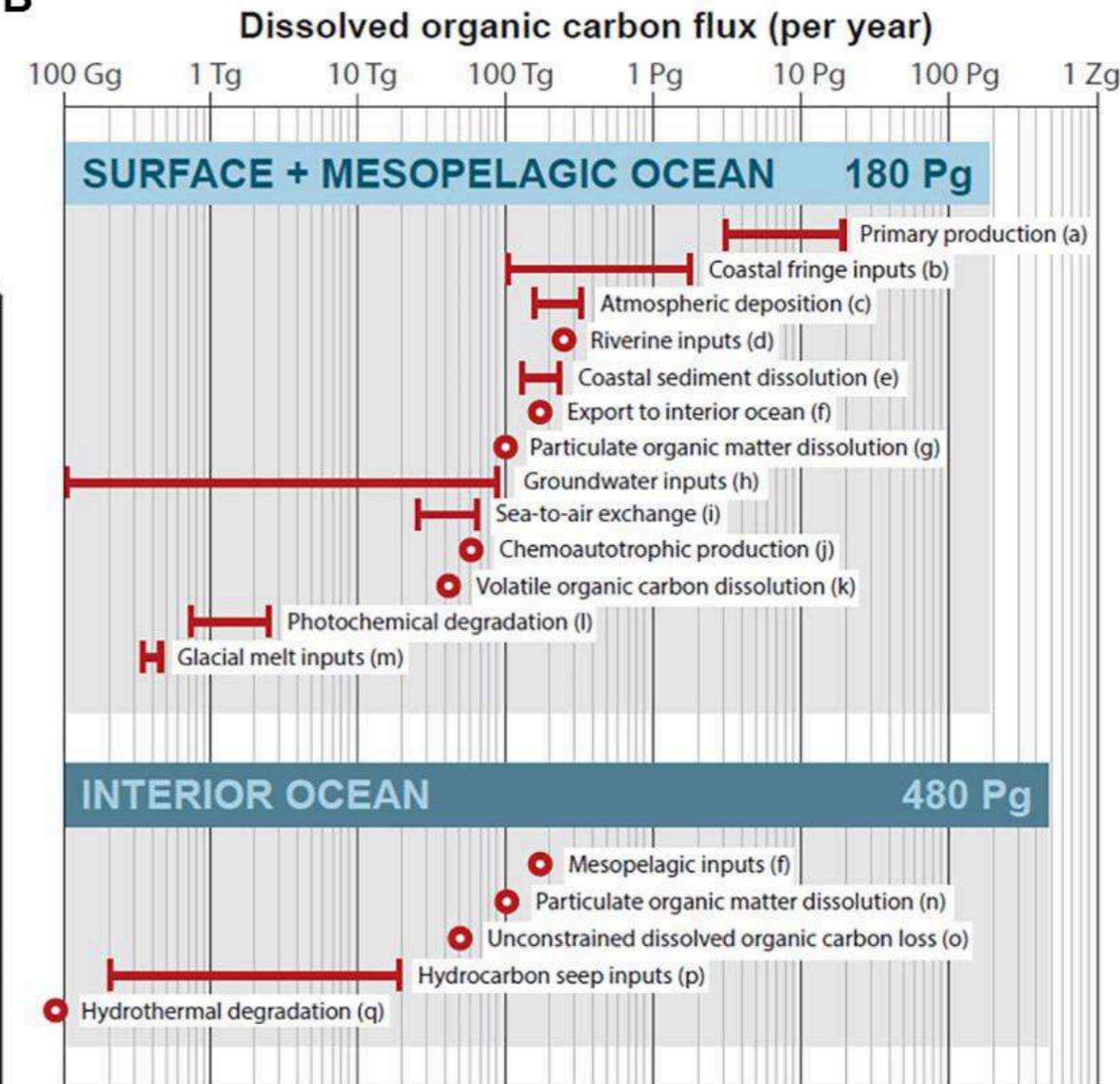
Dissolved organic carbon (DOC) profile (solid line, with sampling depths from August 2008 indicated) and fractions (shaded regions) assigned in the western Sargasso Sea, in micromoles per kilogram. Concentration boundaries of the fractions shown are approximate. RDOC, refractory DOC; SRDOC, semirefractory DOC; SLDOC, semilabile DOC

DOC fluxes

A



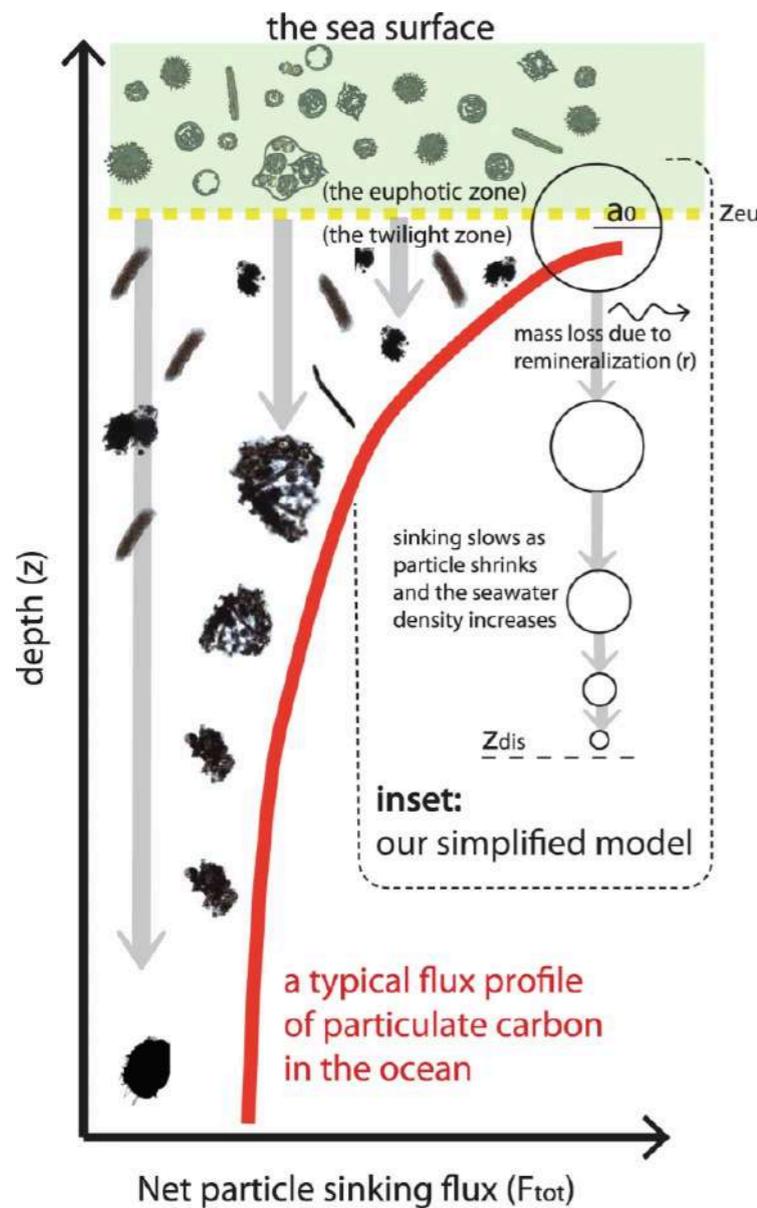
B



- In panel **(A)** oceanic DOC stocks are shown in black circles with red font and units are Pg-C. DOC fluxes are shown in black and white font and units are either Tg-C yr⁻¹ or Pg-C yr⁻¹
- Letters in arrows and associated flux values correspond to descriptions displayed in **(B)**, which lists sources and sinks of oceanic DOC described in the text (see section “Current Understanding of Marine DOM”)

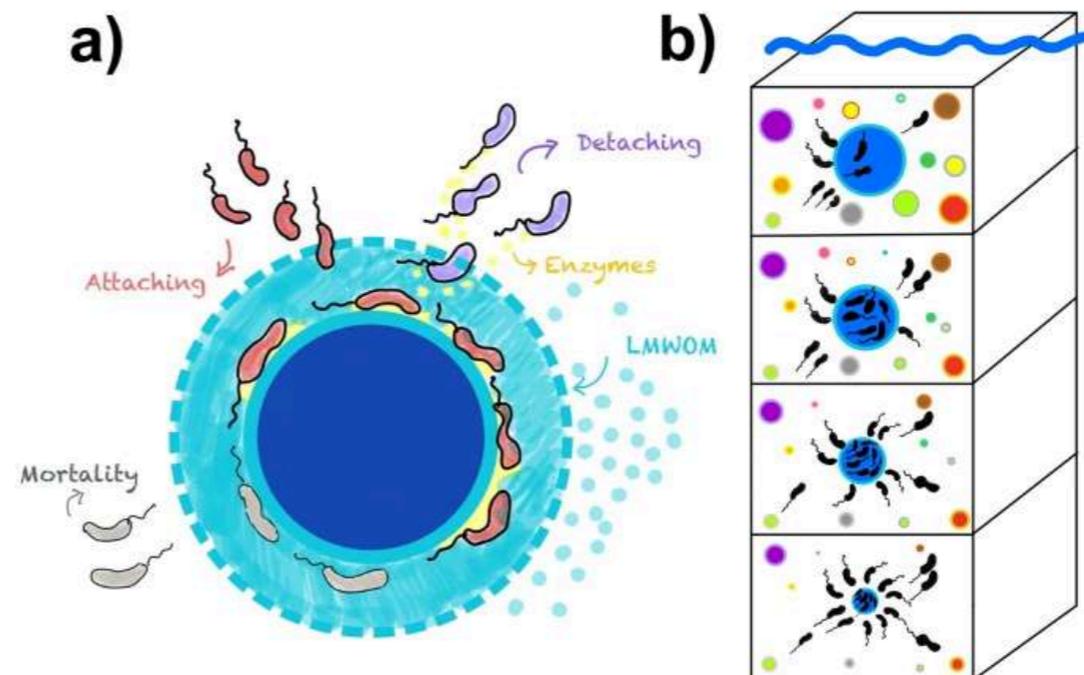
POC fluxes

Omand et al., 2020



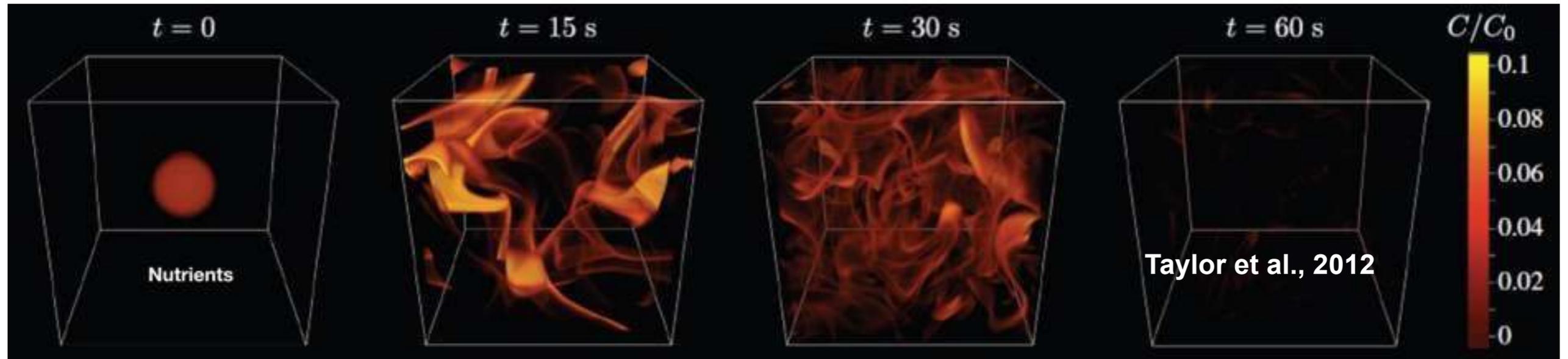
$$F_z = F_{100} \left(\frac{z}{100} \right)^{-b}$$

- 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 CO₂, 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)** of particulate organic carbon (POC) flux is largest and differs the most between oceanic provinces
- 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 as introduced by Martin et al. 1987



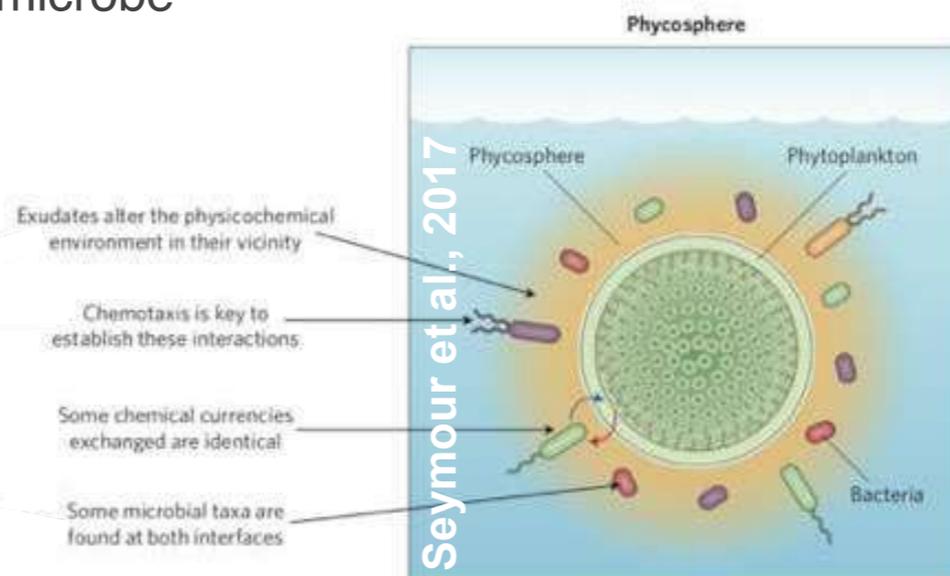
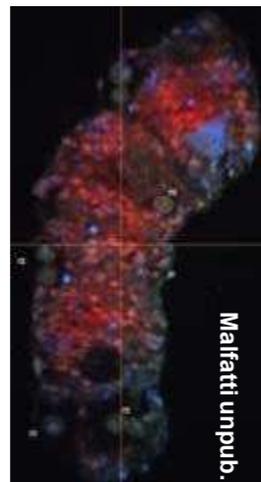
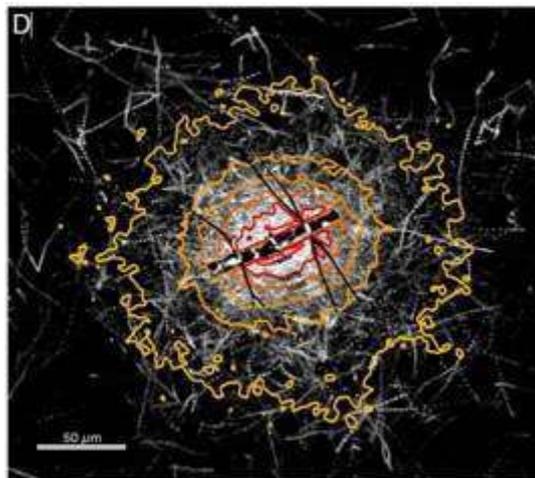
Nguyen et al., 2020

3D organic matter structure in space and time

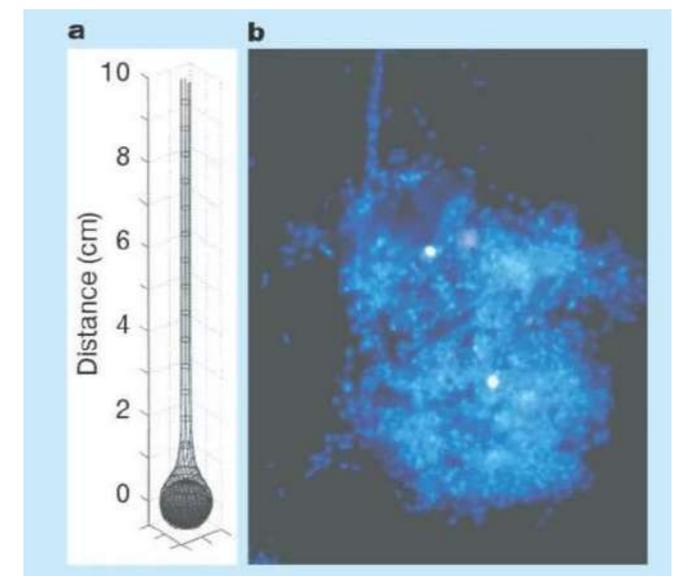


- Nutrient patch evolution and sources
- Low Reynolds number \rightarrow high viscosity
- Modelling in time and space in a turbulent flow ($L = 5.65$ cm)
- Nutrient sources: living phytoplankton, dying phytoplankton, dying copepods, marine snow plume, fecal pellets, dying bacteria and other microbe

Smriga et al., 2016



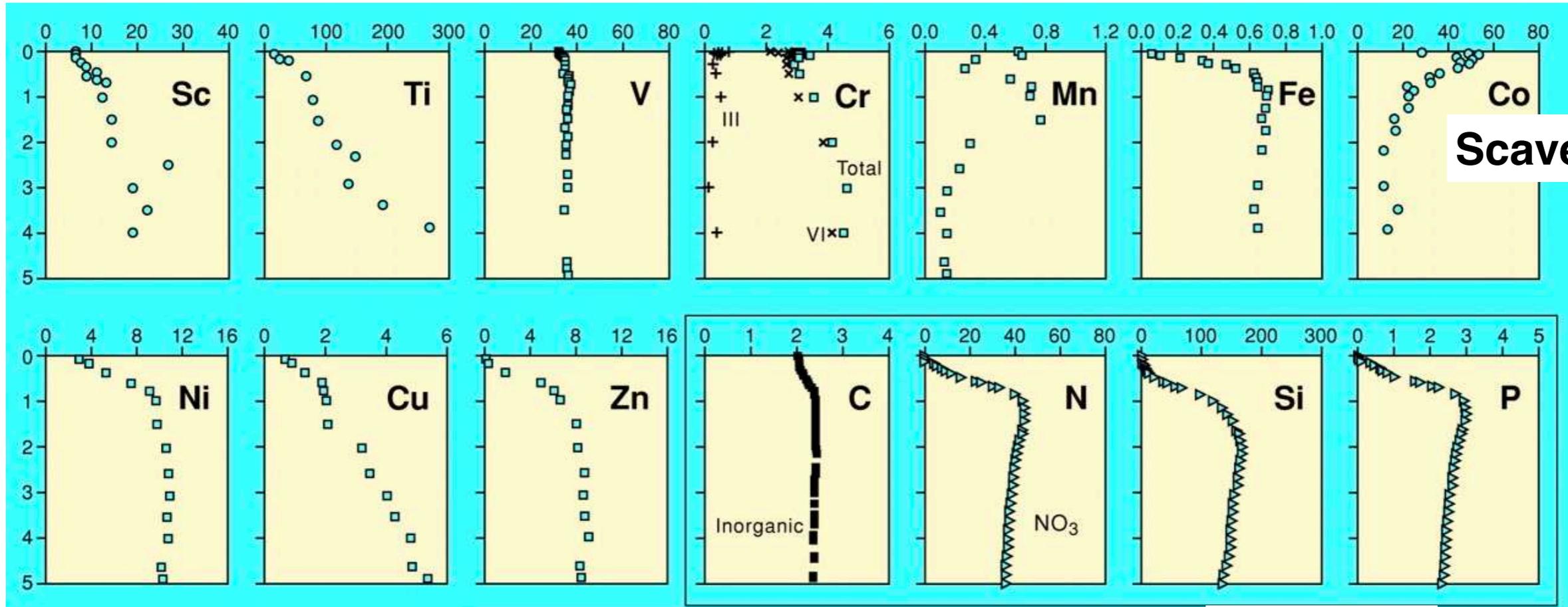
35



Kiørboe & Jackson, 2001 Azam, & Long, 2001

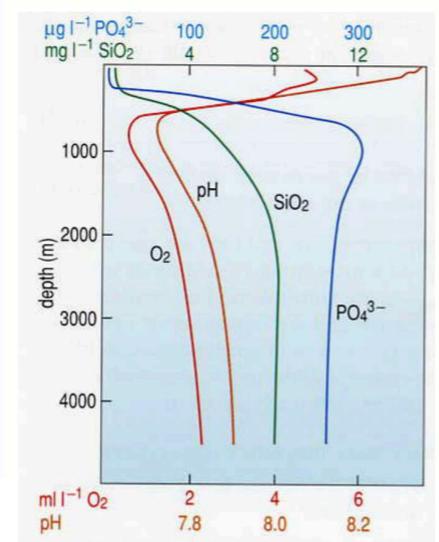
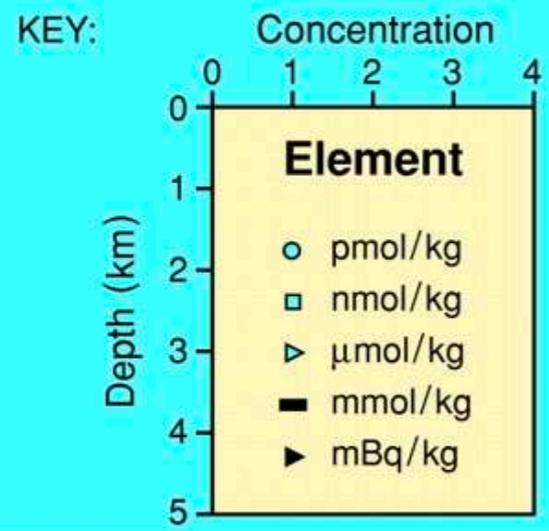
Nutrients

Conservative



Scavenged

Biolimited



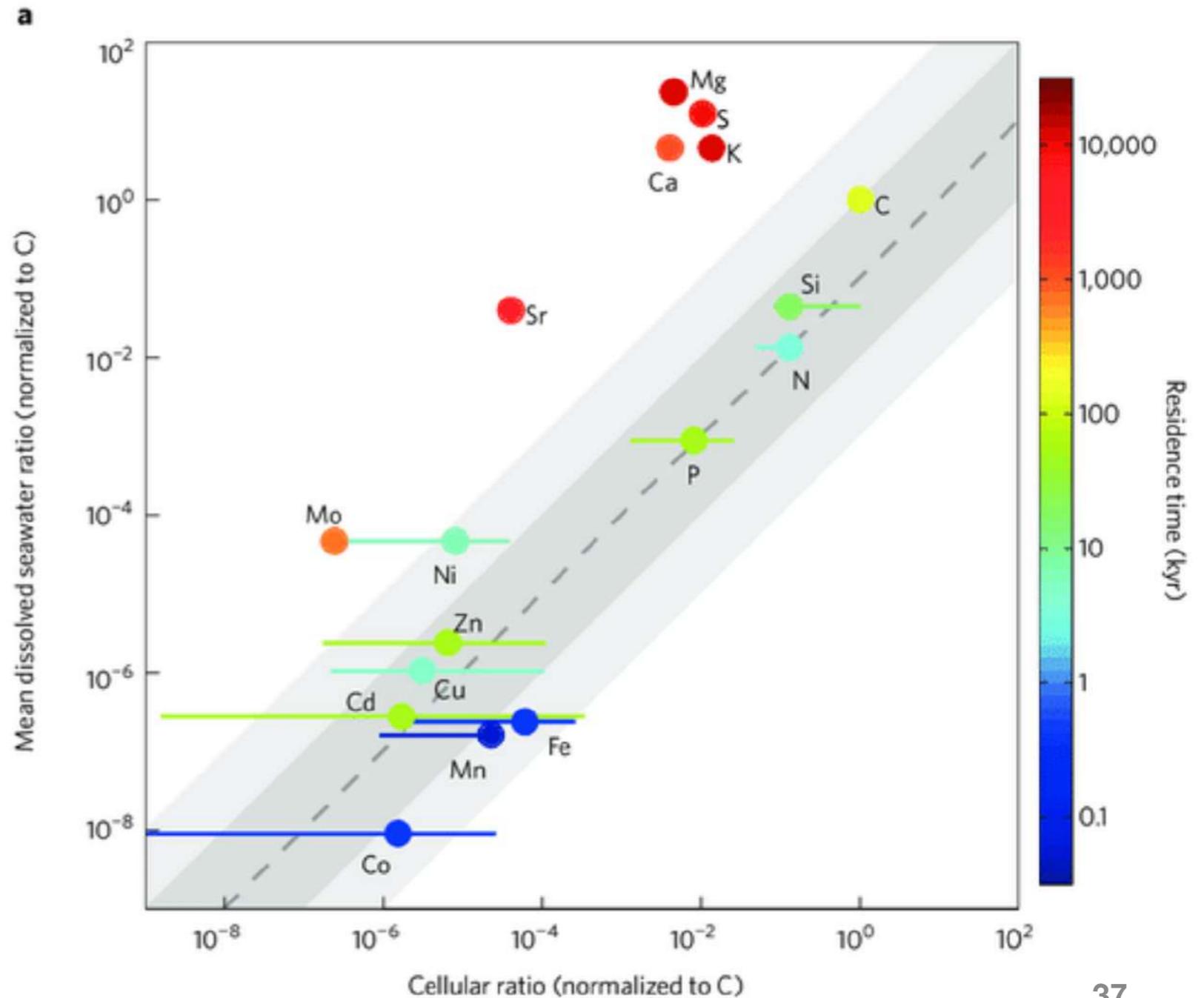
- Elements in the ocean derive from rocks
- Elements have different concentrations
- Elements have different profiles
- **Conservative Elements** are well mixed in SW since their residence times are \gg the oceanic mixing time scale
- **Non-conservative elements** - Biological and other processes produce elemental concentrations that deviate from salinity-normalized concentrations in SW
- Profiles are related to biological activities

Nozaki, 2001

Comparisons between intracellular and dissolved SW elemental stoichiometry

Marine bacteria are enriched in Fe, P, N

Elements to the top left of the shaded area are thus in great excess in sea water, and biological processing has little influence on their distribution, whereas some of those in the shaded regions have the potential to become limiting



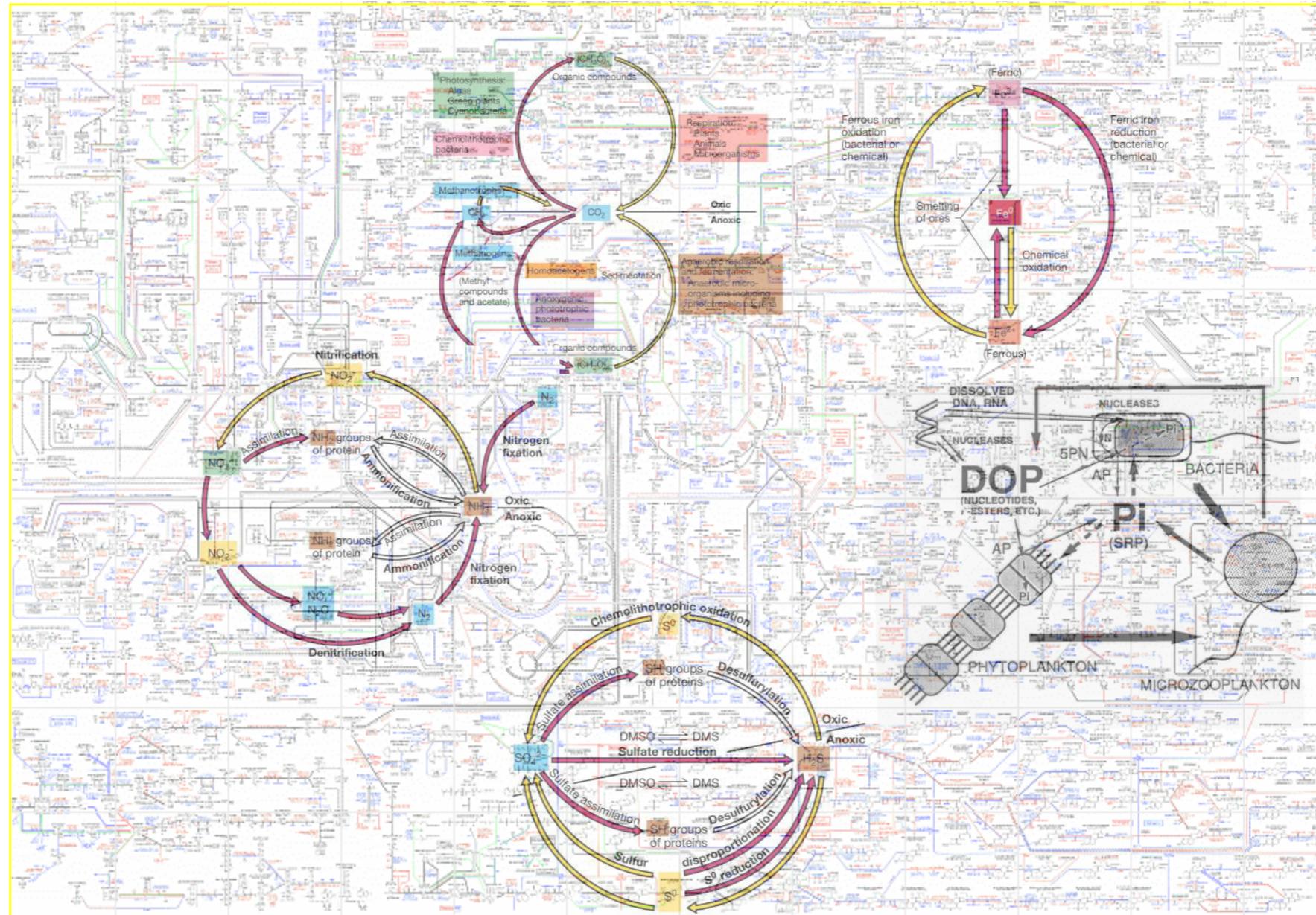
Bacteria are master recyclers

Bacteria respire/utilise organic matter and give off nutrients to other organisms

Bacteria are the main forces in the biogeochemical cycles of the elements

ALL CYCLES are connected:

Carbon
Nitrogen
Iron
Sulfur
Phosphate
Pollutants

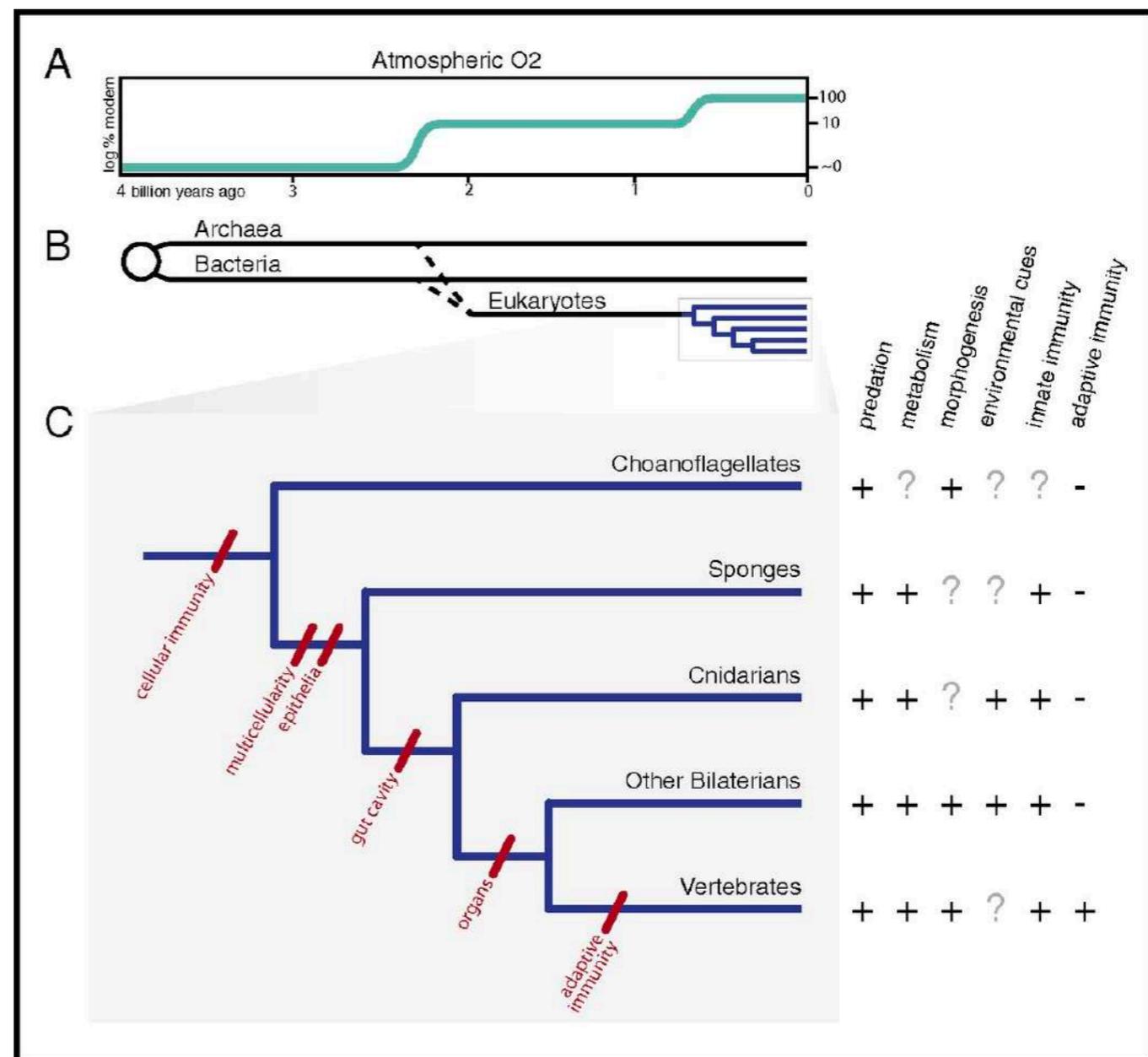


Madigan 10th edition

Redfield ratio or Redfield stoichiometry is the atomic ratio of carbon, nitrogen and phosphorus found in phytoplankton and throughout the deep oceans C:N:P = 106:16:1 (Redfield A.C. 1934)

Other micro/macro organisms

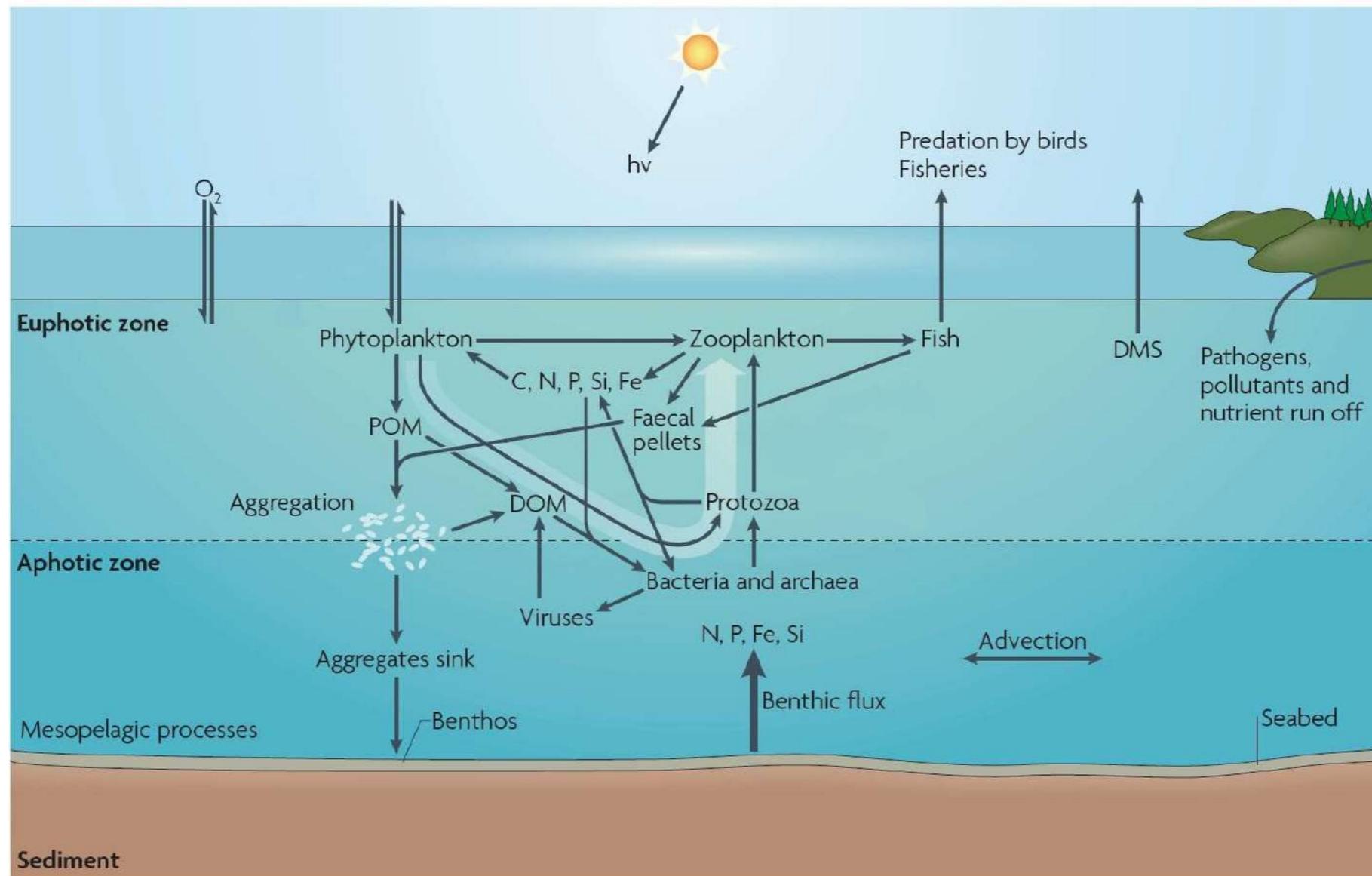
Microorganisms form symbiotic partnerships with the vast majority of *animals and plant* living on earth and are increasingly recognised as being essential for overall ecosystem functioning



McFall-Ngai et al., 2013

Carbon biogeochemical cycle

- Source of organic matter is biology
- Production and decomposition/degradation of organic matter
- Atmospheric CO₂ is fixed by photosynthesis —> Carbon Cycle



Azam & Malfatti, 2007