

Anthropogenic Effects on Biogeochemical Processes, Carbon Export and Sequestration: Influence of Bacteria-Particle Interactions on Oceanic Carbon Cycling

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Thanks to many colleagues and students for stimulating, exciting and critical discussions and arguments... *that which does not kill us makes us stronger!*

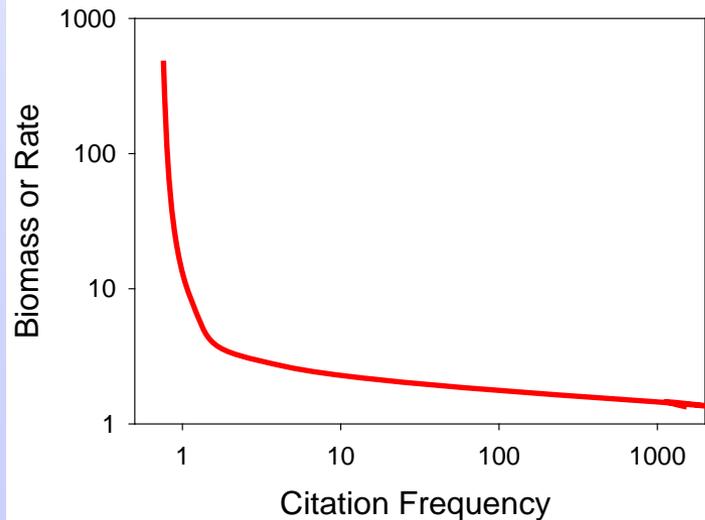
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Marine microbes influence global ecosystem dynamics by controlling the biogeochemistry and productivity of the oceans and ocean-climate interactions...

So, how many times are their “biogeochemical-related” words cited in the abstract book?

<i>Organic Carbon...</i>	11	700 Pg C
<i>Bacteria...</i>	11	2.2 Pg C
<i>Export...</i>	10	<u>10 Pg C y⁻¹</u>
<i>Phytoplankton...</i>	91	1.8 Pg C
<i>Zooplankton...</i>	98	0.5 Pg C
<i>Fish....</i>	1865	0.02 Pg C



Inverse relationship between the word use frequency and biogeochemical relevance...

Oceans are critically important in supporting food webs and controlling global climate, and provides essential **Ecosystem Services**.

Autotrophs in marine ecosystems take up CO₂ and synthesize organic carbon:

-is be transferred to pelagic and benthic food webs (*i.e. regional ecosystem service*),

-is respired to CO₂ or

-is exported from the surface and sequestered as particles in the nearshore or in the deep ocean, or transformed into long-lived dissolved organic compounds (*i.e. global ecosystem service*).

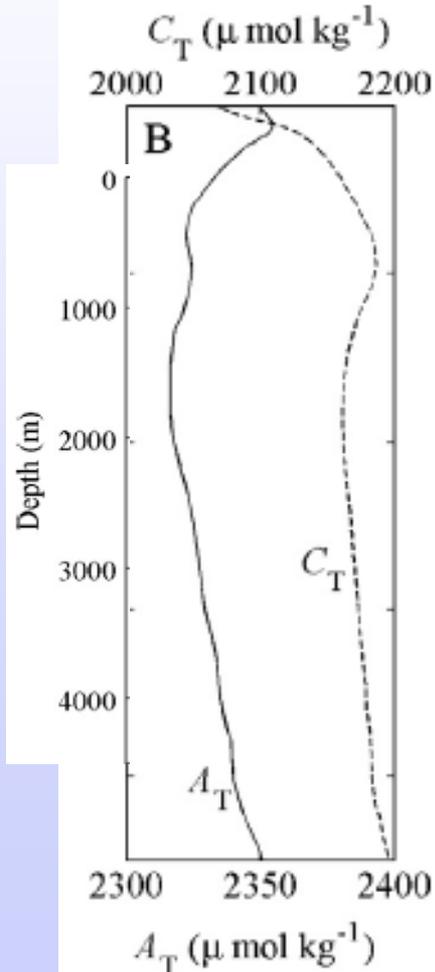
Organic carbon that is produced and transformed in the ocean that is **prevented from returning the atmosphere for >100 years is considered sequestered and is relevant for climate processes.**

The global ocean has a large reservoir of dissolved inorganic carbon, it absorbs approximately 30% of anthropogenic CO_2 , and can buffer changes in the atmospheric CO_2 concentration, thereby mitigating global warming.

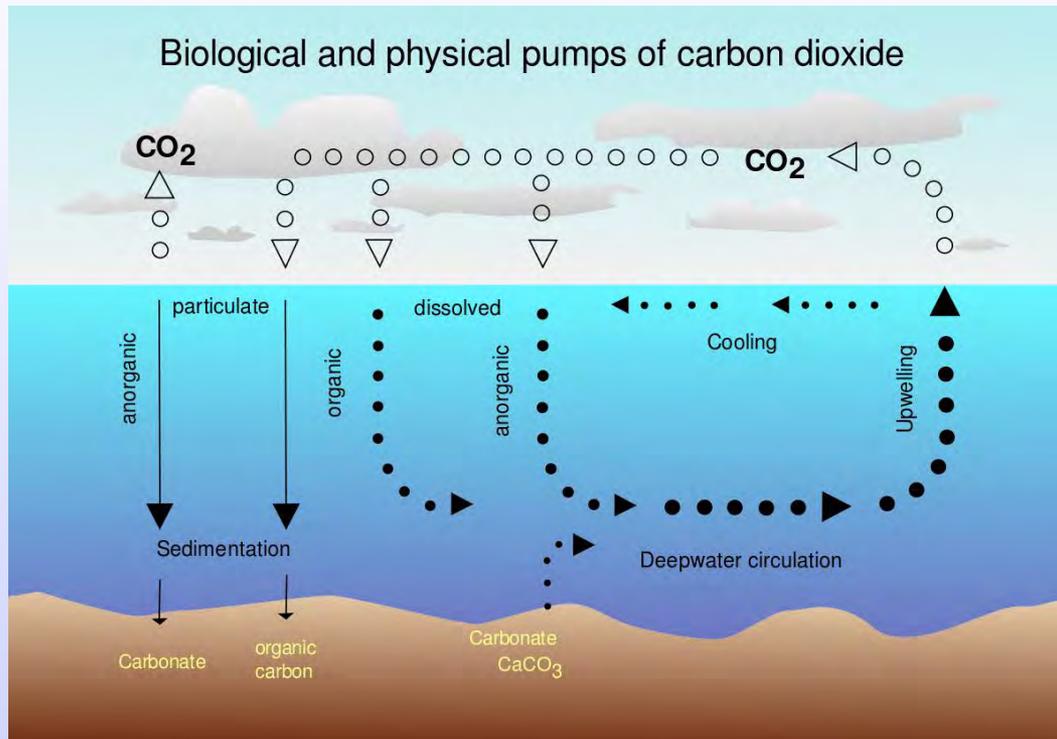
The global mean C_T in deep waters below 1200 m is higher than in the surface mixed layer.

Biological processes counteract the erosion of the vertical differences in the concentration caused by diffusive ocean mixing... **if there was no biology the gradients would be very small.**

The processes that maintain the C_T gradient in the World Oceans are called the “ocean carbon pumps”, and these pumps have an important effect on the air–sea CO_2 fluxes on century timescales.



Three vertical ocean carbon pumps were defined over three decades ago! The solubility pump for C_T , the carbonate pump for particulate inorganic carbon ($CaCO_3$), and the soft-tissue pump (*biological carbon pump*) for POC (and now also DOC)

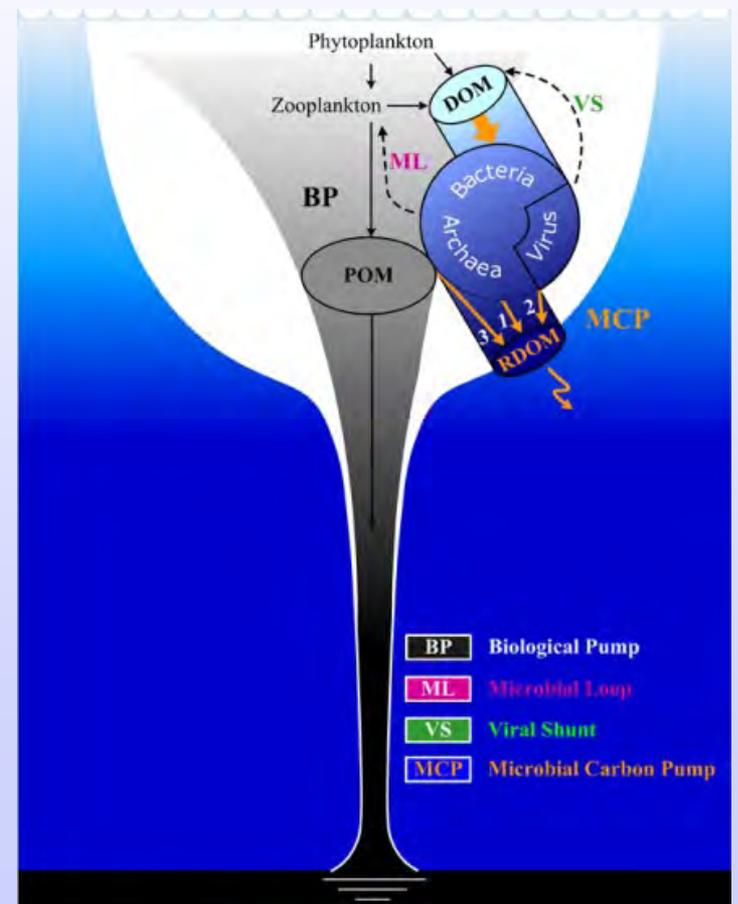


The expression “**Biological Carbon Pump**” usually refers to only the organic component of the ocean carbon pump, or sometimes both the organic and CaCO_3 components. The **BCP** concept was developed, studied and modelled within the context of marine food webs and ocean biogeochemistry and its function is depth dependent.

Almost a decade ago, the “**Microbial Carbon Pump**”, was proposed by Jiao and collaborators.

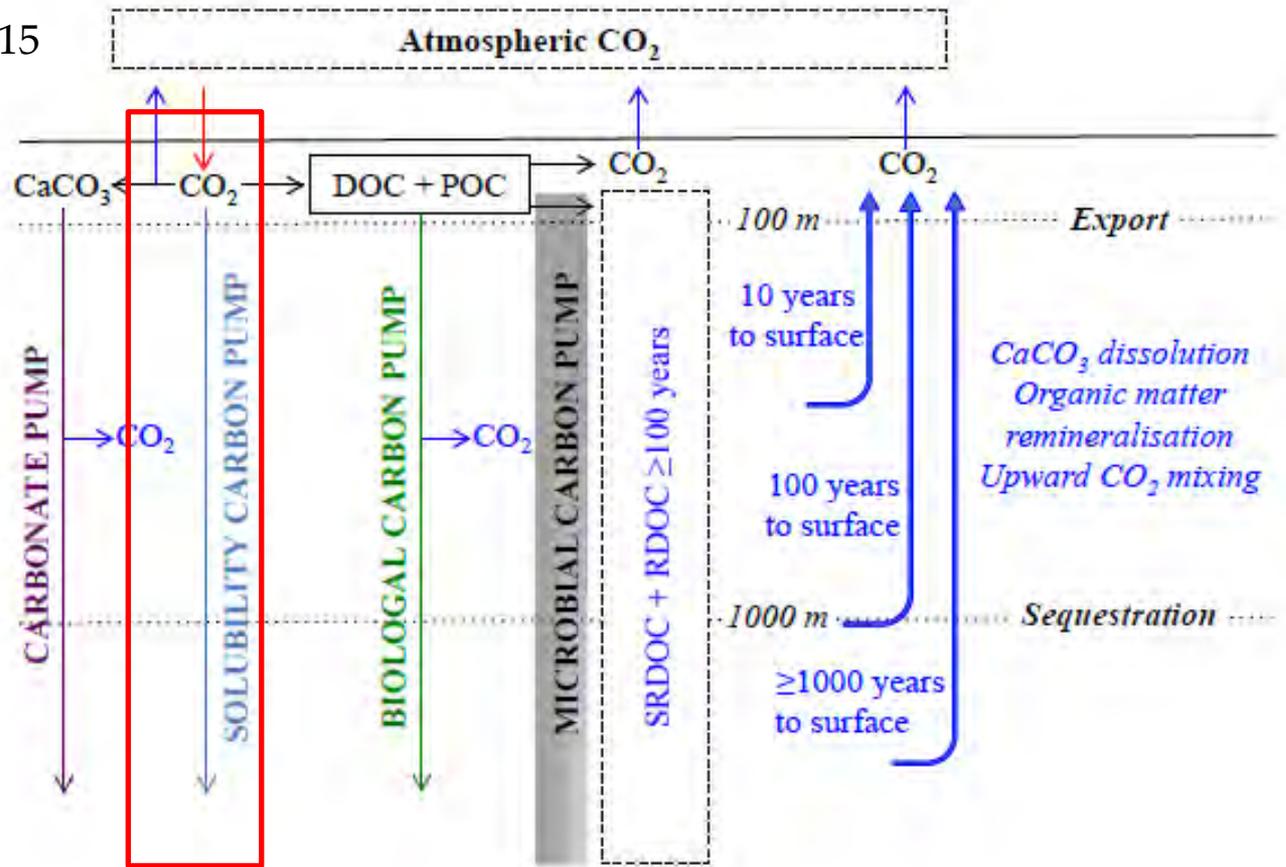
The **MCP** concept was developed within the context of marine microbiology with links to marine biogeochemistry.

A key assumption of the **MCP** is that the production mechanisms of long-lived and refractory DOC (i.e. RDOC) is mediate by microbes and the food web and the process is depth independent

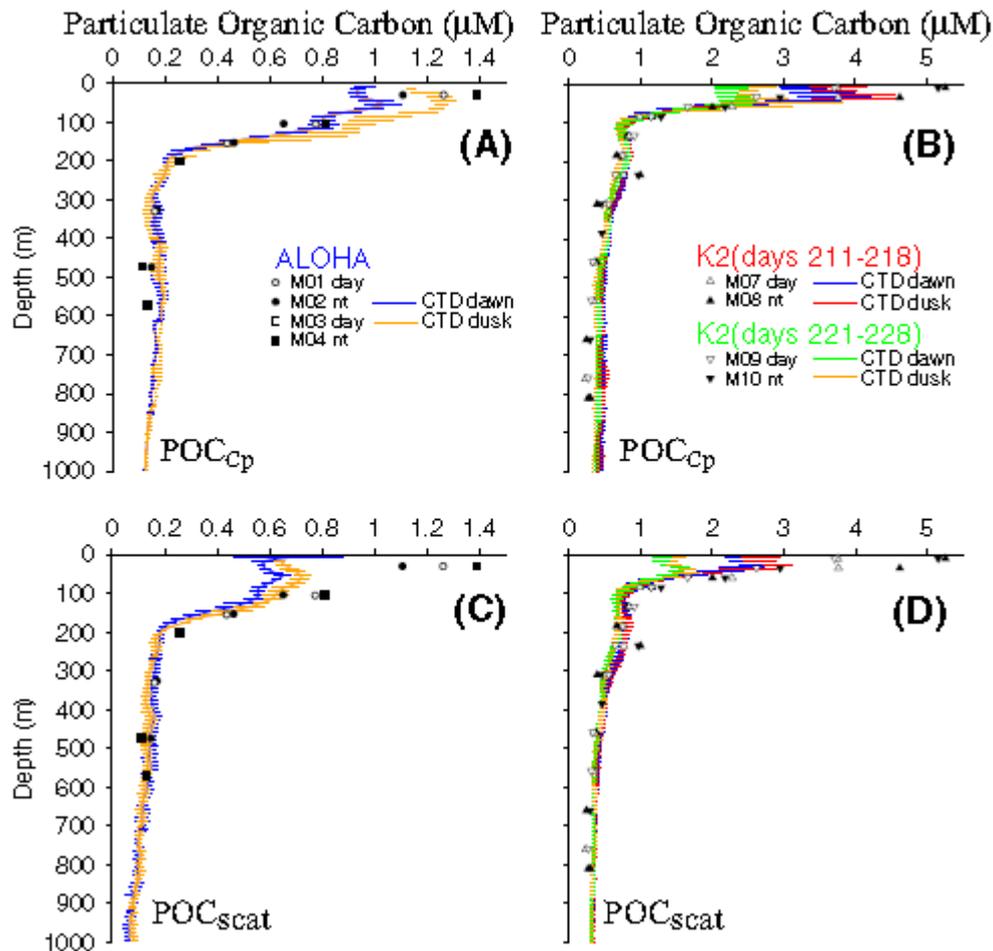


Coincident occurrence of the four ocean carbon pumps. Three “vertical” carbon pumps and the microbial carbon pump.

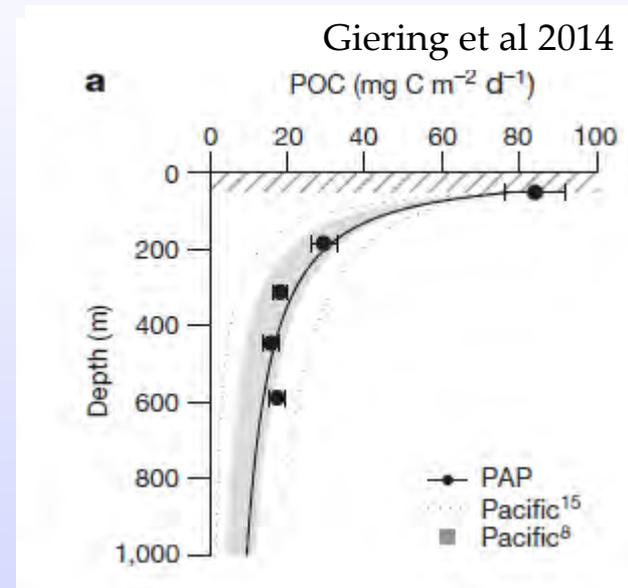
Legendre et al. 2015



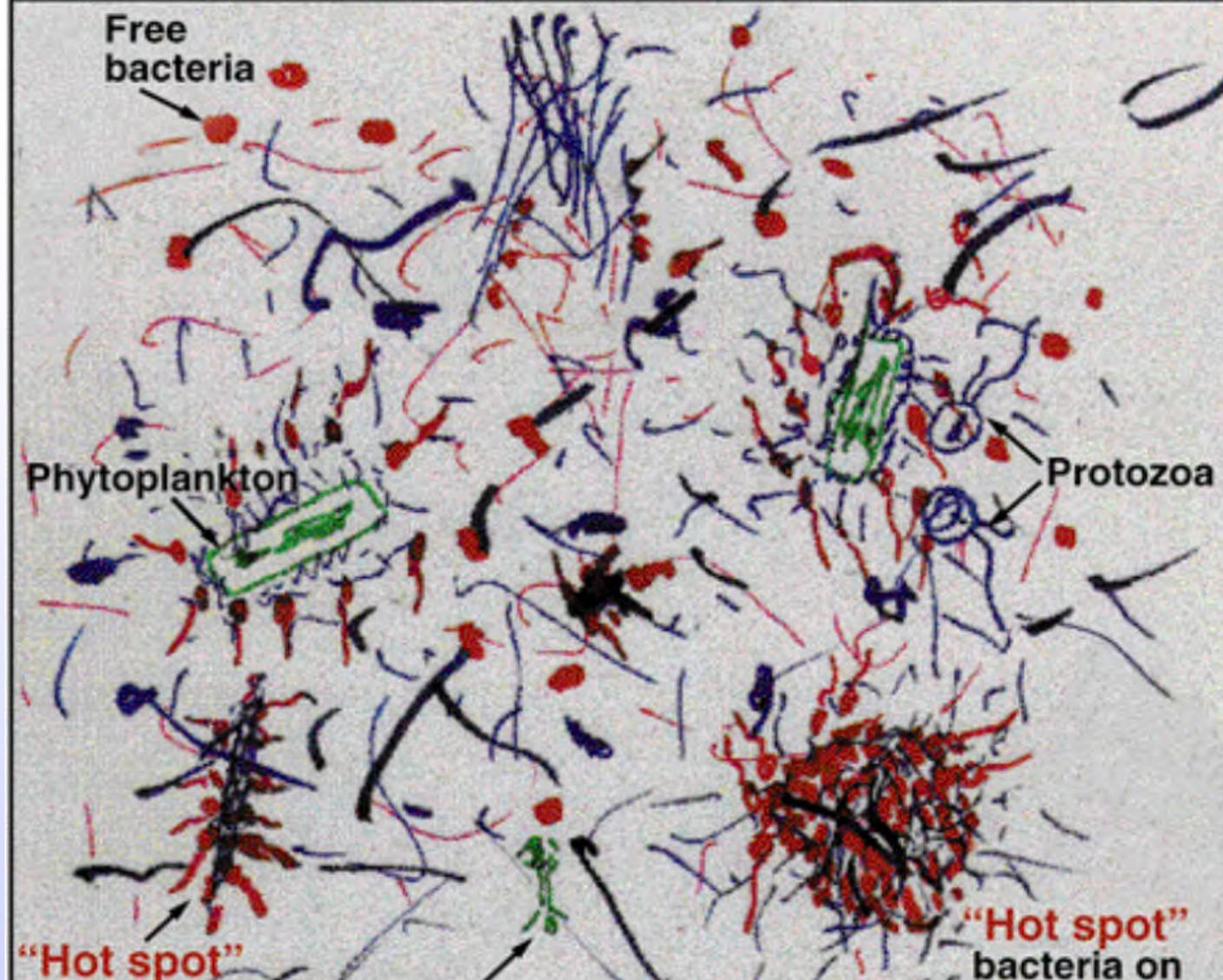
Except for the solubility pump, most of the **critical transformations are mediated by microbes!**



The vertical distributions of both concentration and flux declines with depth.



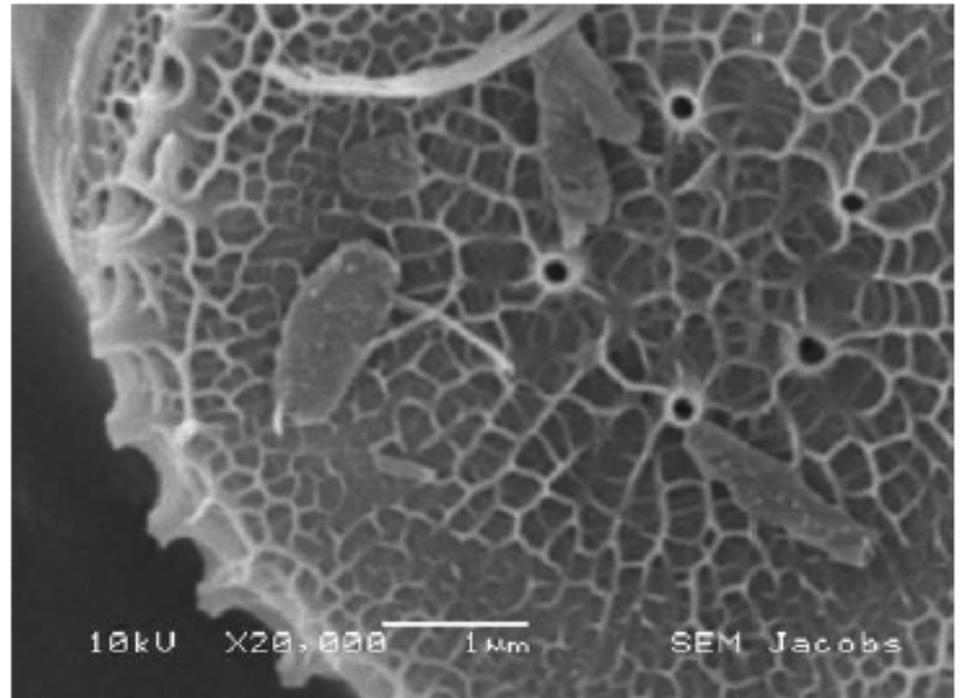
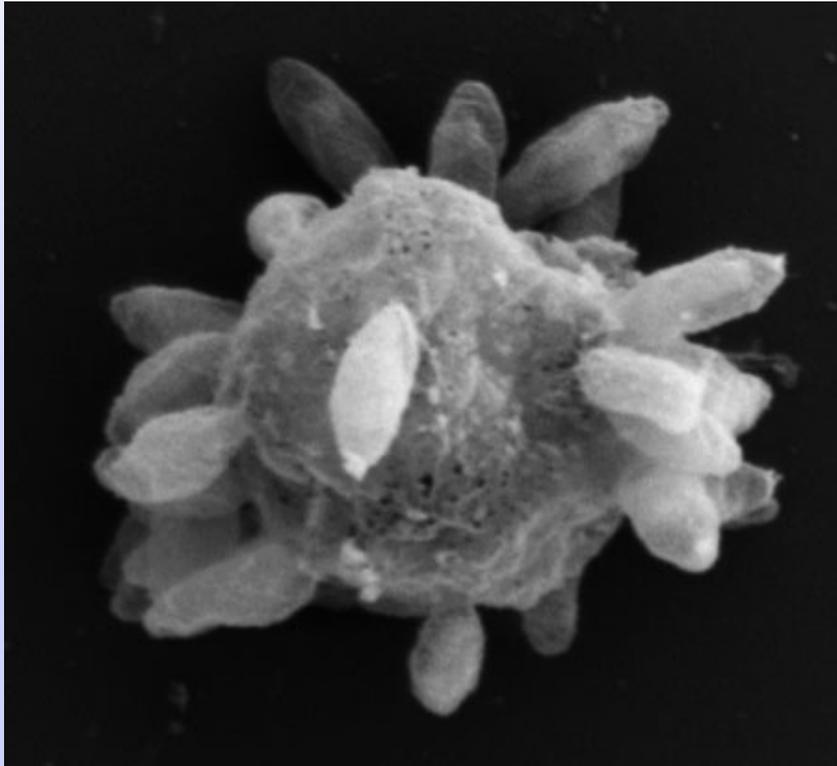
Due to disruption, dissolution and remineralization of particles by physical and biological activities, especially the colonization and metabolism of particle-attached microbes, there is decrease in both flux and concentration with depth.

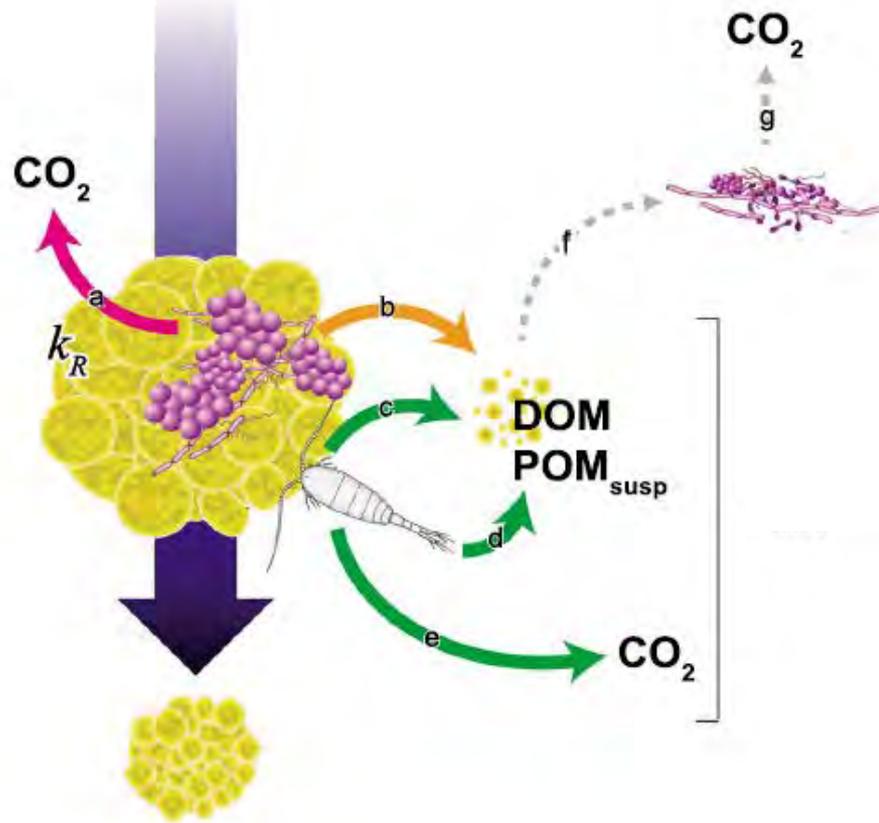


Particle-associated microbes experience an environment with intense chemical and physical gradients where their physiological characteristics and biogeochemical consequences will vary over small scales within the particle and these will differ that in the bulk solution.

Particles in the ocean are not always complex communities in marine snow or aggregates. They are often living microbes such as phytoplankton!

In 1972, Bell and Mitchell introduced the term “phycosphere”, a region that extends outward from an algal cell to a distance “in which bacterial growth is stimulated by extracellular products of the alga”.



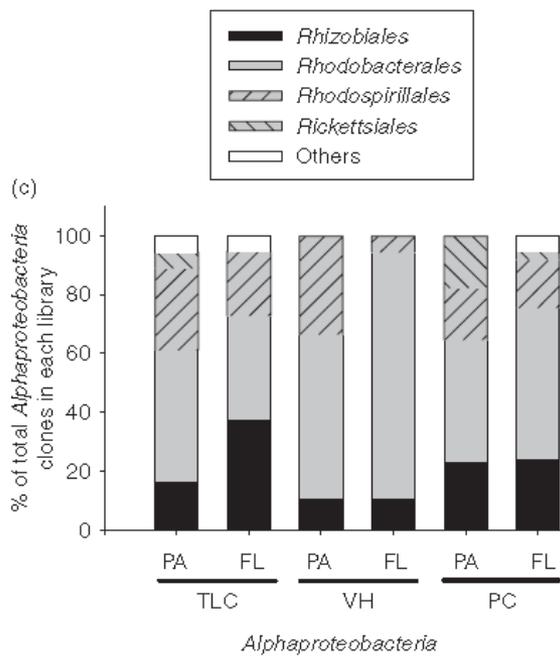
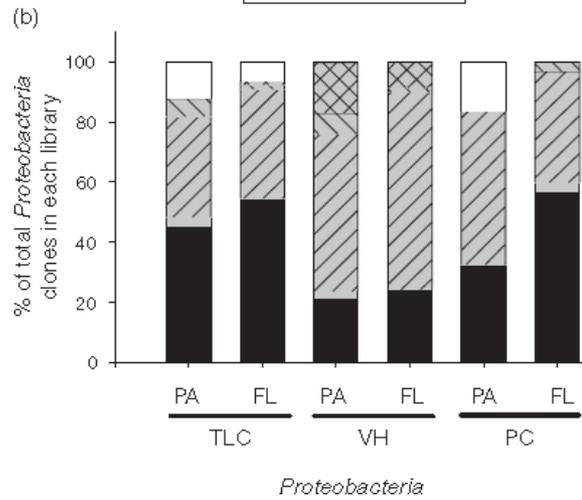
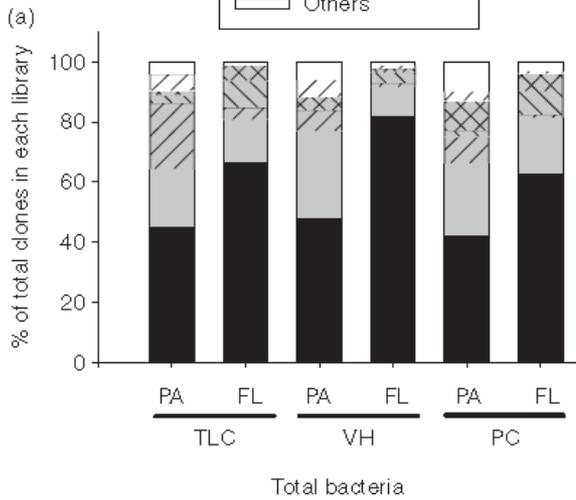


Remineralization of POM material by particle-attached bacteria degrades particles.

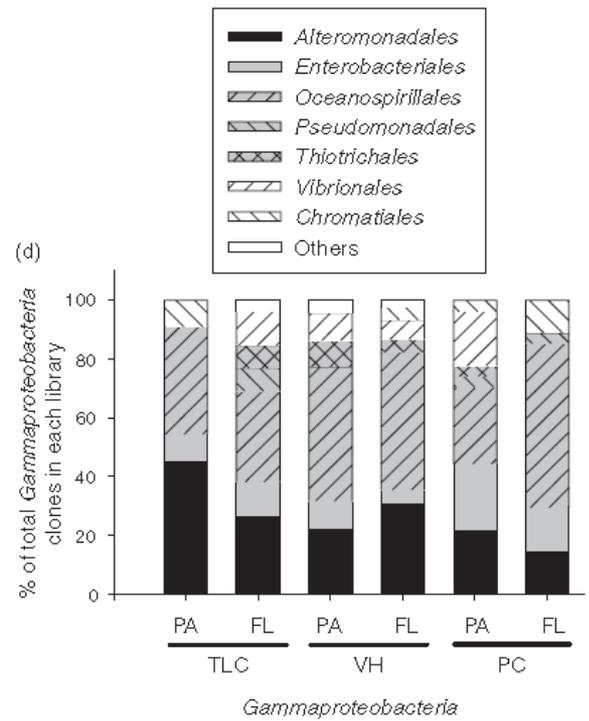
Enzymatic solubilization and mechanical disaggregation of the particle by attached bacteria transfers dissolved and particulate organic matter to the water column, where it can then be metabolized by free-living bacteria.

Mechanical disaggregation, sloppy feeding, egestion and excretion or remineralization of particles by zooplankton can transfer particle material to the dissolved or suspended organic matter pools.

Zhang et al 2007



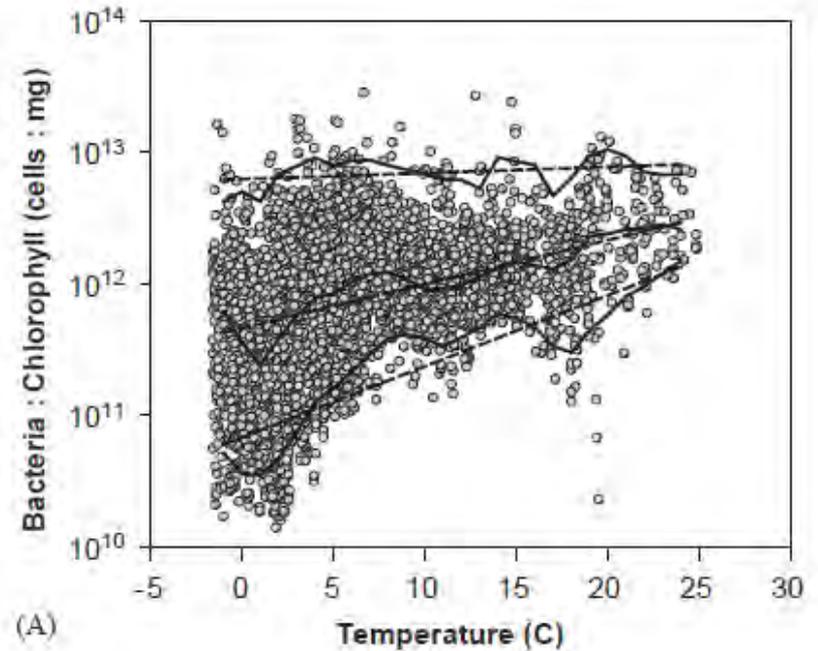
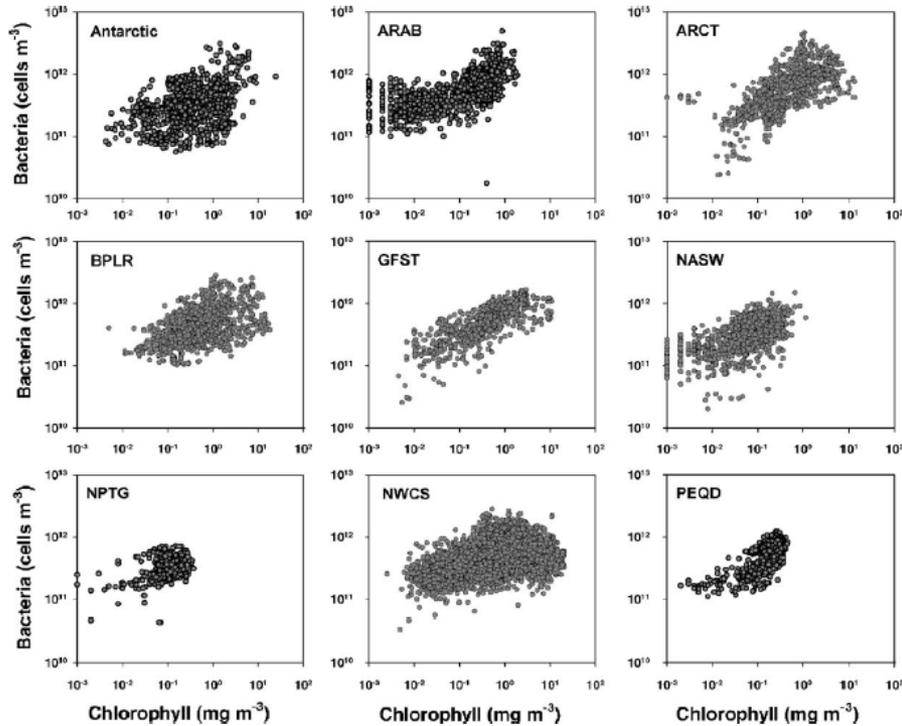
Particle attached bacteria are phylogenetically and physiologically distinct from FL bacteria. This lead to fundamental differences in the their biogeochemical impacts.



The PA community is generally represented by more anaerobic bacterial taxa which develop in the low oxygen conditions of the particle microzones.

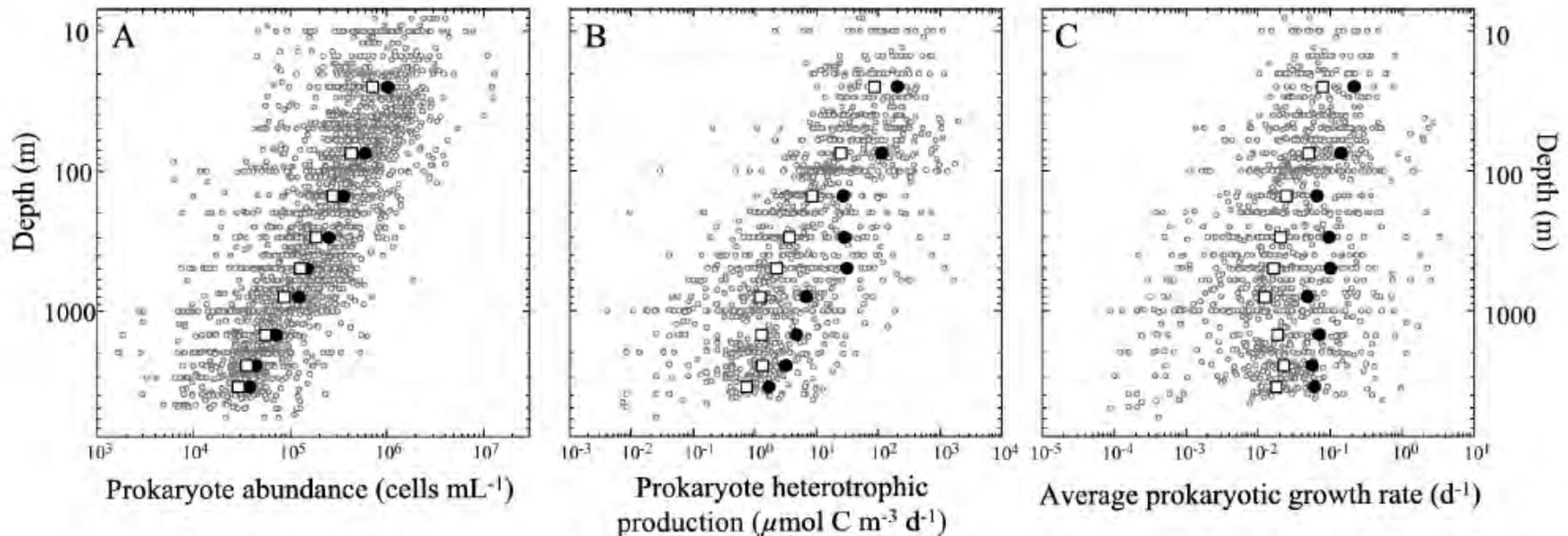
Many previous studies of the distribution of bacteria in the World

•Li et al. 2004



Important insights into large scale factors controlling food web interactions and elemental fluxes in the ocean.

Most studies were in the euphotic zone...



Log-log slopes and fits between depth (in km) and the prokaryote variables.

Variable	<i>n</i>	<i>r</i> ²	Log-log slope ± SE	<i>p</i> (slope = 0)	Exponential slope (km ⁻¹)	<i>p</i>
All data						
Prokaryotic abundance	3249	0.50	-0.553(±0.009)	<0.0001	-0.901	<0.0001
Prokaryotic biomass	3244	0.51	-0.551(±0.009)	<0.0001	-0.903	<0.0001
Heterotrophic production	1930	0.48	-0.968(±0.023)	<0.0001	-1.381	<0.0001
Prokaryotic growth rate	1546	0.11	-0.354(±0.026)	<0.0001	-0.502	<0.0001

Distinct depth-dependent difference among parameters. The rate of depth dependent decrease of production is ~2-fold greater than biomass and almost 3-fold greater than growth rate!

Fewer studies that distinguished free-living and particle-attached bacteria.

To examine the relationship between PA and FL bacteria over the meso- to global- scales, we reviewed >25 years of literature on particle-attached bacterial abundance and activity and associated variables and compared these with concurrent measurements of free-living bacteria.

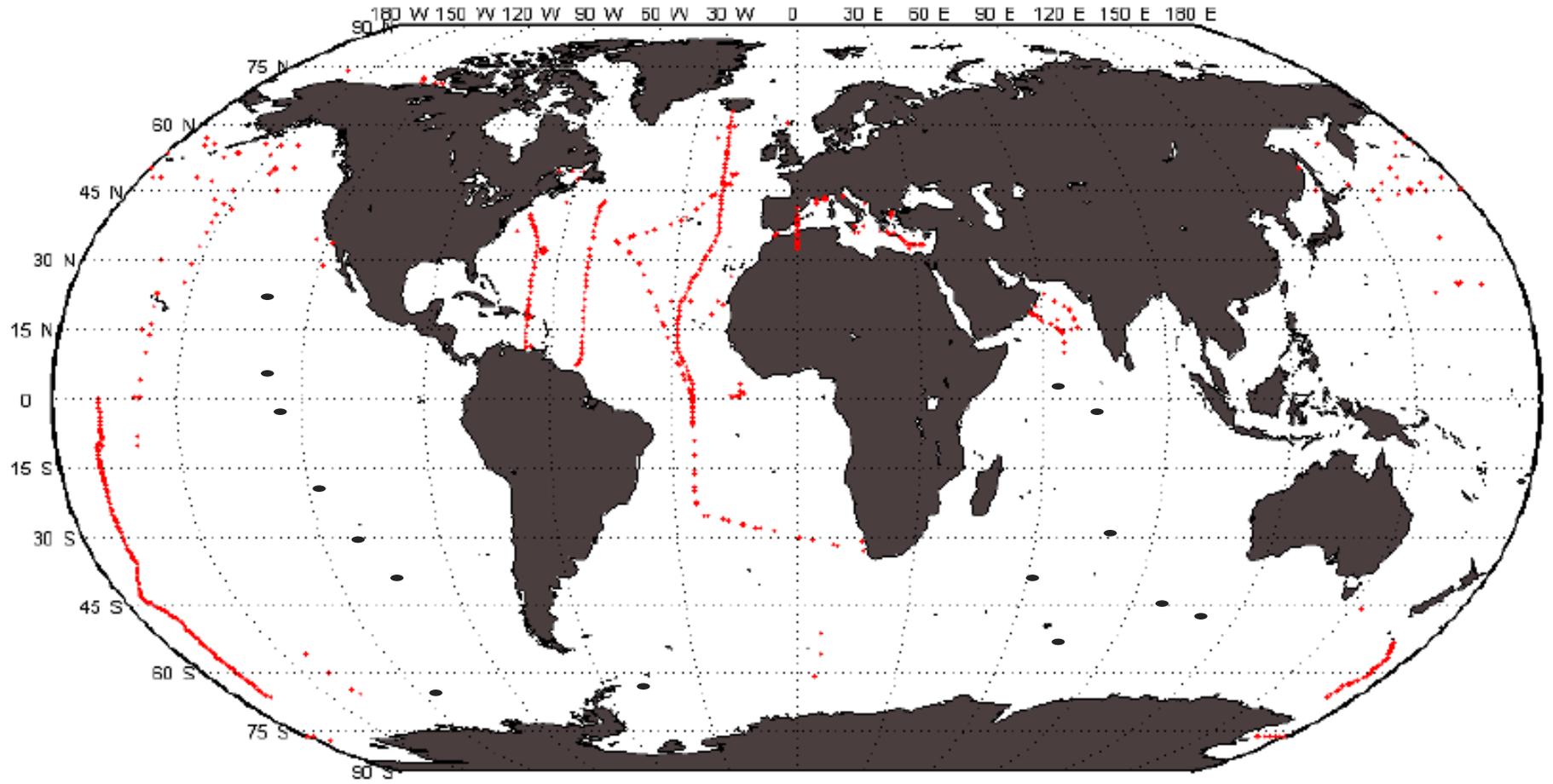
Primary and technical publications, web sites (e.g. JGOFS, BOFS, DYFAMED, etc), unpublished data from the authors or investigators directly.

For regions where temperature data could not be found, we used climatologies from NODC-NOAA data bases.

-Biological variables (bacterial abundance, production, TdR & Leu uptake, respiration).

-Physical/Chemical variables (temperature, O₂, DOC, POC, TOC).

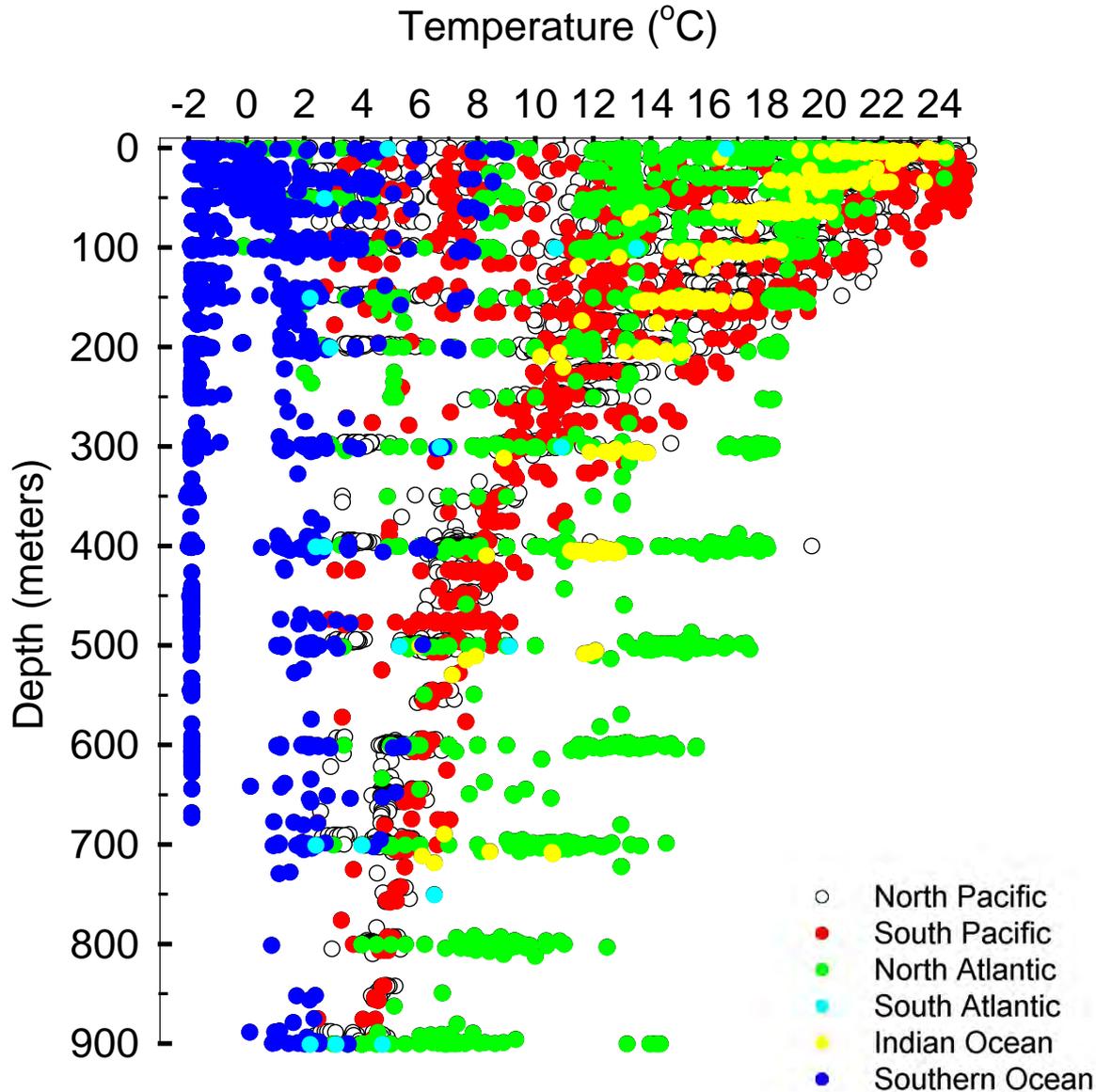
-Data compiled by depth, from surface to the maximum depth reported.



Data on bacterial properties from >150 oceanic sites world-wide and all major ocean basins.

Not all included data on particle attached bacteria over full depth range.

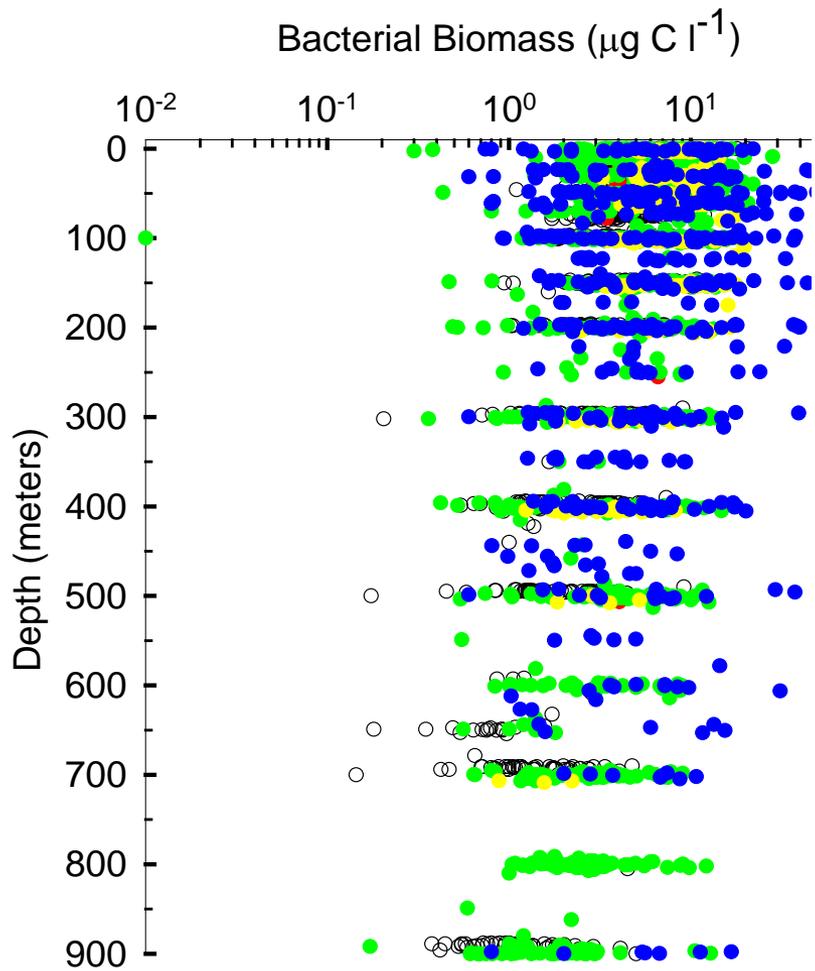
World Ocean was divided into seven regions; Arctic Ocean, North Pacific, South Pacific, North Atlantic, South Atlantic, Indian Ocean, Southern Ocean.



-2 to 28°C ,

Mean = 11°C ;

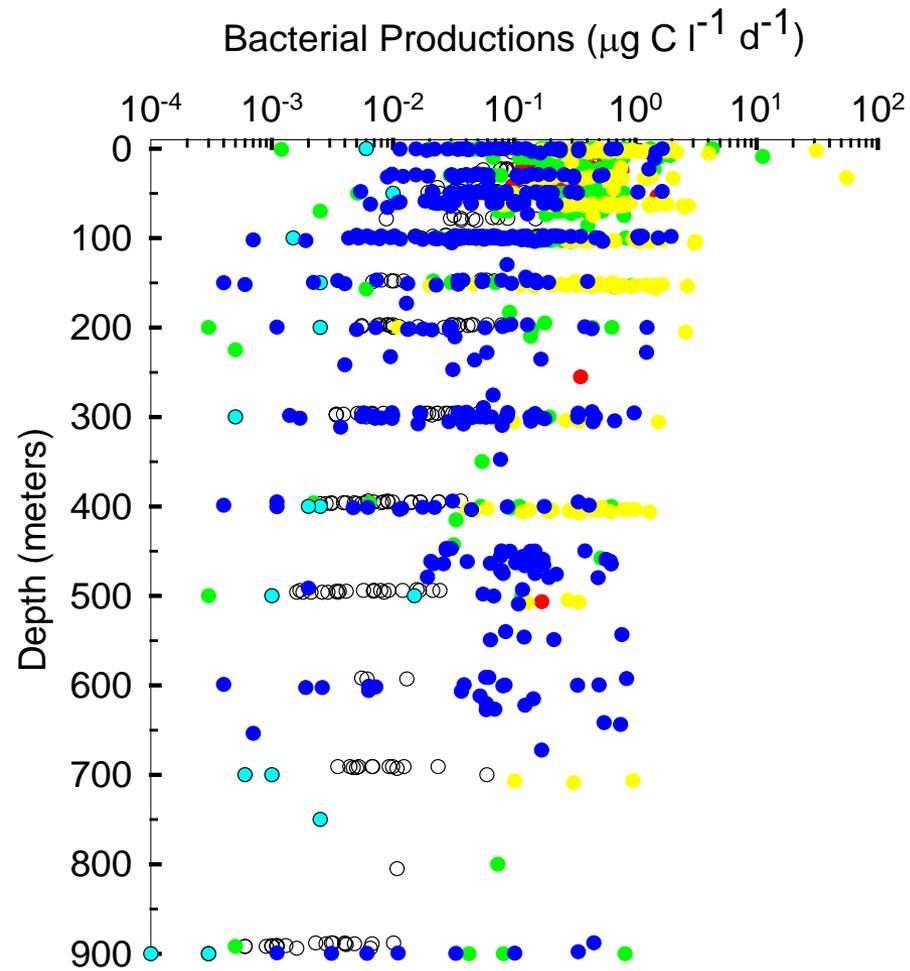
Median = 12.2°C



0.01 to 58 $\mu\text{g C l}^{-1}$

Mean = 6 $\mu\text{g C l}^{-1}$

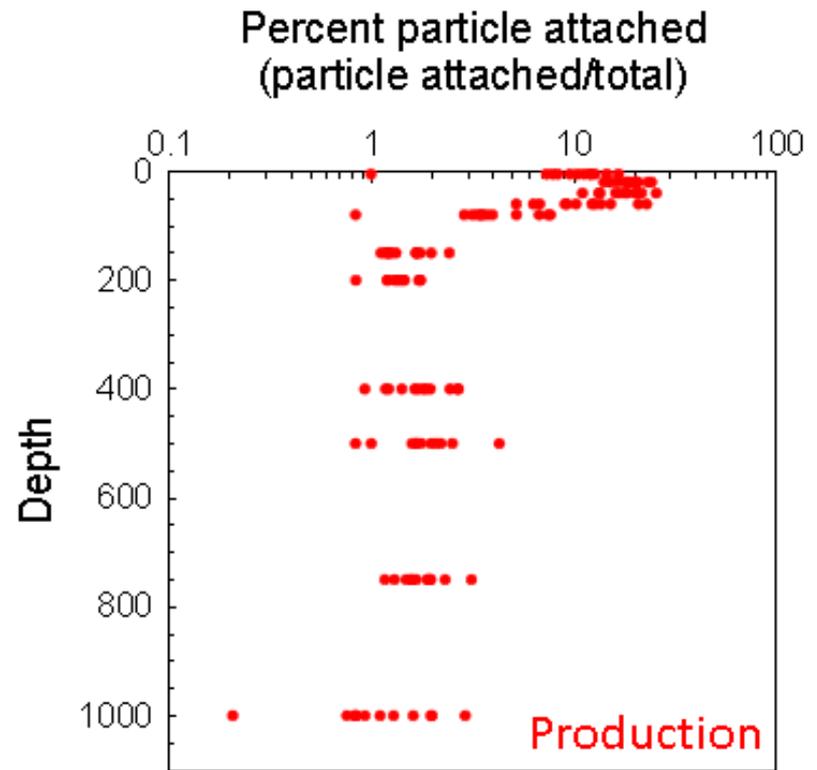
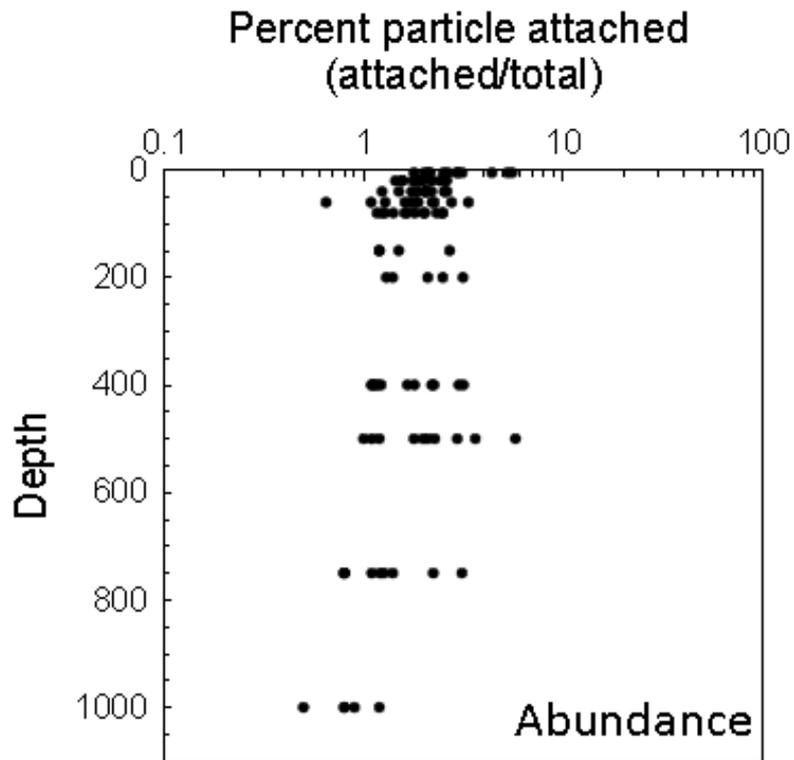
Median = 5 $\mu\text{g C l}^{-1}$



0.005 to 55 $\mu\text{g C l}^{-1} \text{ d}^{-1}$

Mean = 0.4 $\mu\text{g C l}^{-1} \text{ d}^{-1}$

Median = 0.1 $\mu\text{g C l}^{-1} \text{ d}^{-1}$



A representative data set of concurrently measured PA and FL bacteria:
 Significant depth-dependent declines in the percent PA bacterial
 abundance ($p = 0.01$) and a production ($p = 0.05$)

At the meso- to global-scale, PA bacteria are:

Abundance- **0.2 to 25%**; **mean = ~5.5%**.

Production- **1.1 to 38%**; **mean = ~26%**.

Spearman rank correlations among bacterial and related properties

	% Attached production per cell	Total abundance	Total production	Temp	Chl a	Depth
% Attached abundance	0.88**	0.75**	0.72**	0.56**	0.11	-0.71**
% Attached production per cell		0.45*	0.55**	0.42*	0.35*	0.15
Total abundance			0.62**	0.34*	0.29*	-0.56**
Total Production				0.78**	0.31*	-0.49**
Temperature					0.21	-0.35*
Chlorophyll a						-0.34*

*Correlation is significant at the 0.05 level (2-tailed).

**Correlation is significant at the 0.01 level (2-tailed).

Data set n > 1000

The relationships among variables were complex.

-Positive correlations among biotic variables and temperature.

-Negative correlations with depth.

Bacterial cell-specific production rate (fg Carbon cell⁻¹ d⁻¹).

	Total	FL	PA
Mean	0.345	0.355	0.969

Cell-specific production rate of particle attached-bacteria was significantly greater (ANOVA; $p = 0.001$) than free-living bacteria.

The rates of cell-specific production of free-living and total bacterial production were not significantly different.

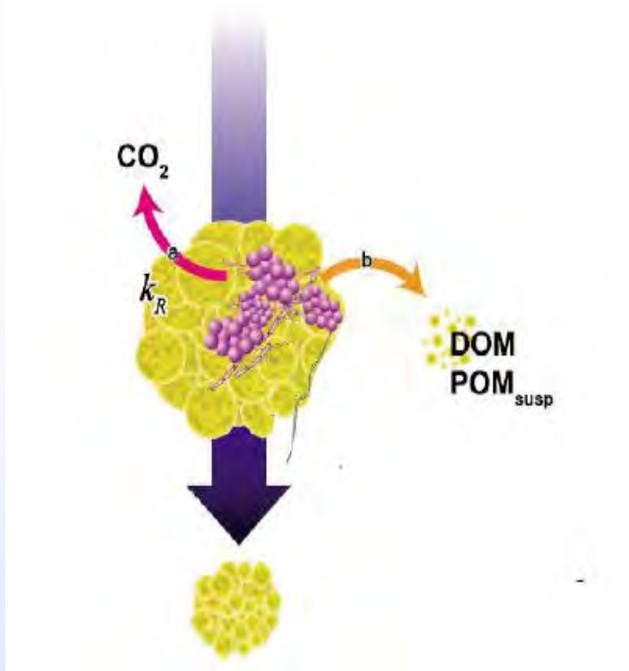
Suggests that although the physiological characteristics of PA and FL differ, the contribution of PA bacteria to total bacterial community production was small.

Similar patterns are observed for cell-specific exoenzyme activity...

Compared to free-living bacteria, particle attached cells are phylogenetically distinct with higher diversity and volume specific abundances, cell specific rates of production, growth exoenzymatic activities.

While cell specific activity of PA activity is significantly greater than FL bacteria, their overall contribution to “*total water column*” bacterial activity and production appears to be relatively small and likely does not require unique parameterization in models of bacterial process.

However PA bacteria may have significant roles in the hydrolyzing sinking organic matter and the cycling of organic carbon.



Relative to FL bacteria, PA bacteria inhabit a microenvironment enriched with organic nutrients and have higher rates of production, respiration and substrate hydrolysis, and will have a disproportionately large role in the transformations of POC to DOC.

$$POC_{(200m)} \sim 0.2 \text{ Pg C}; POC_{(global)} \sim 20-30 \text{ Pg C}$$

$$DOC_{(global)} \sim 670 \text{ Pg C}$$

The degradation of particles by bacteria transfers carbon from the POC to DOC pool. This reduces the efficiency of the BCP, and the production and repeated re-processed of DOC, will increase the strength of the MCP.

Climate-driven increases in ocean processes that differentially influence PA and FL will need to be included in prognostic models of carbon sequestration and ocean-climate interactions.

Has not yet been done!



Thank you for your attention!