Microbes and Ocean Biogeochemical Processes

Richard B. Rivkin[1] and M. Robin Anderson[2]
1- Memorial University of Newfoundland, Canada
2- Fisheries and Oceans, Canada

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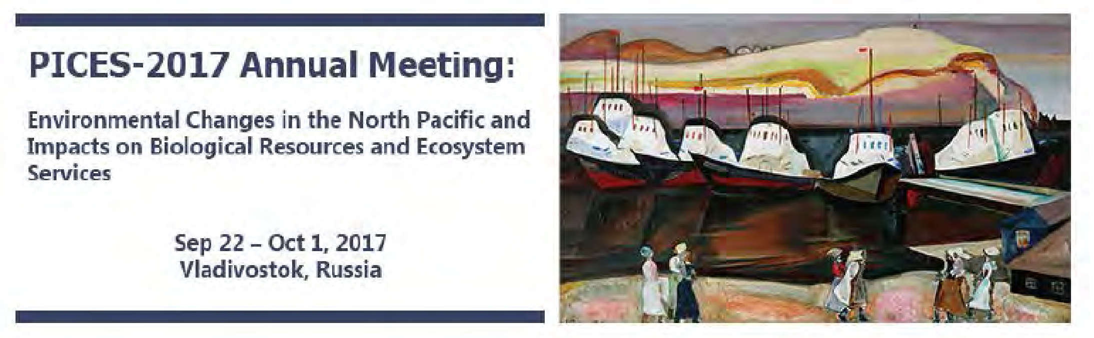

PICES-2017 Annual Meeting:

Environmental Changes in the North Pacific and Impacts on Biological Resources and Ecosystem Services

Sep 22 – Oct 1, 2017
Vladivostok, Russia

Fisheries and Oceans Canada   Pêches et Océans Canada

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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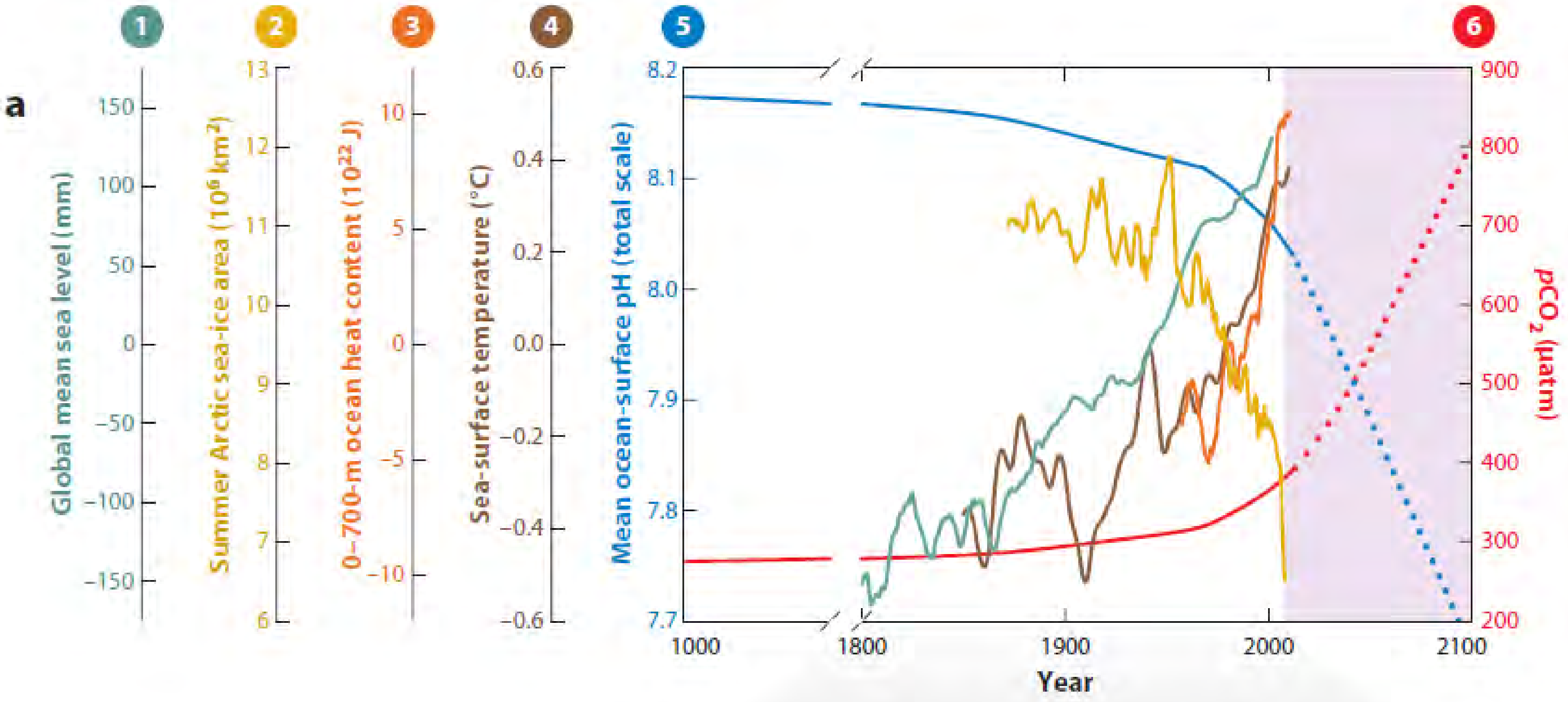
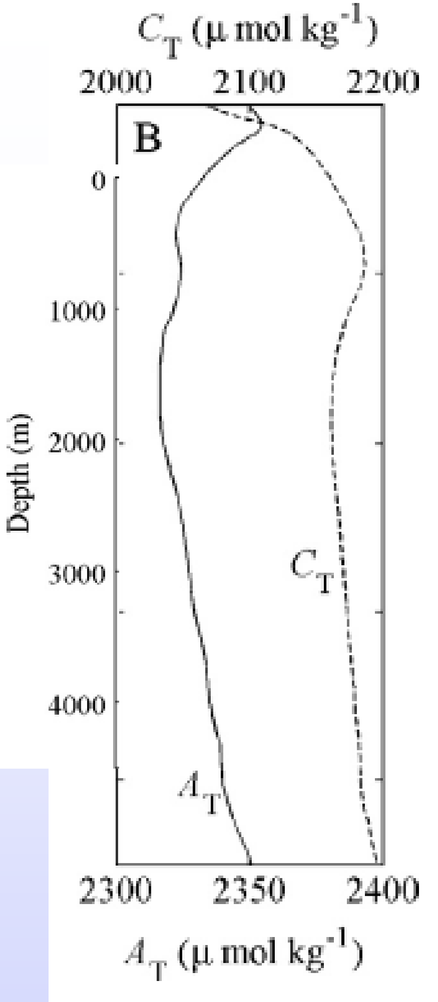
The earth climate system is changing due to anthropogenic activities!

Doney et al 2012



The ocean absorbs approximately 30% of anthropogenic CO2, thereby mitigating global warming.

What controls this and how will it change in the future?



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

Chemical and 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.

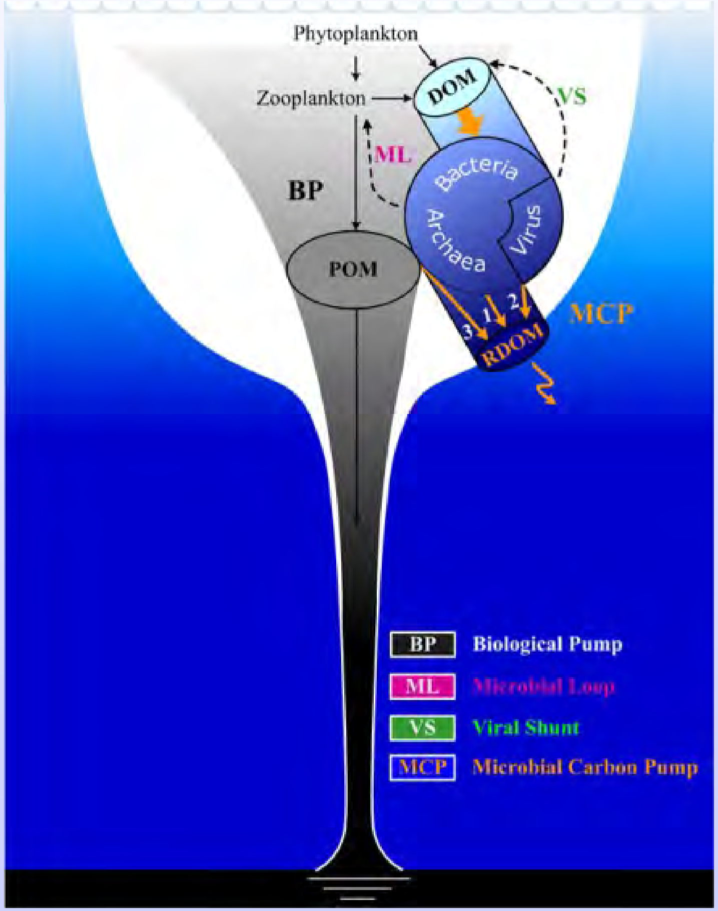
Three vertical ocean carbon pumps were defined over three decades ago! Solubility pump for C_T, the carbonate pump for particulate inorganic carbon, and the soft-tissue pump for POC and some DOC.

The expression "Biological Carbon Pump" usually refers to the organic component of the ocean carbon pump only, 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.

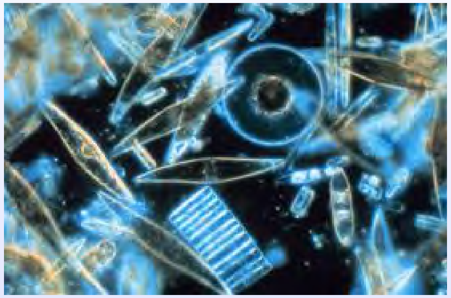
Almost a decade ago, the "Microbial Carbon Pump", was proposed by Jiao and collaborators.

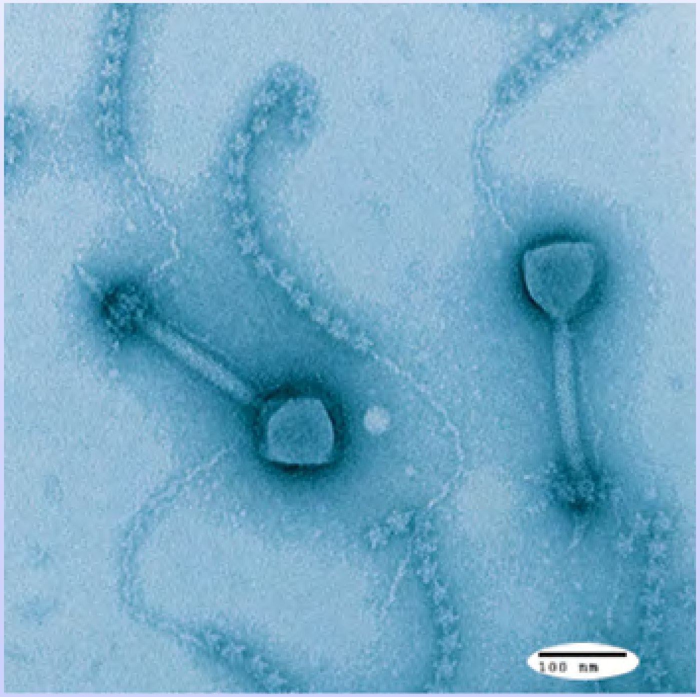
The MCP concept was developed within the context of marine microbiology with links to marine biogeochemistry.

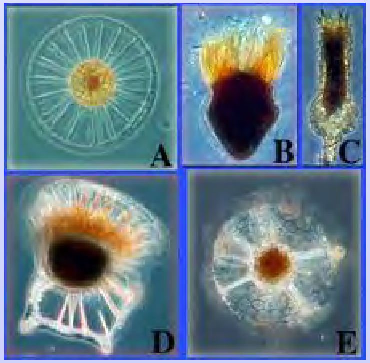
A key assumption of the MCP is that the production mechanisms of long-lived DOC (i.e. RDOC) is mediate by microbes and the food web and the process is depth independent

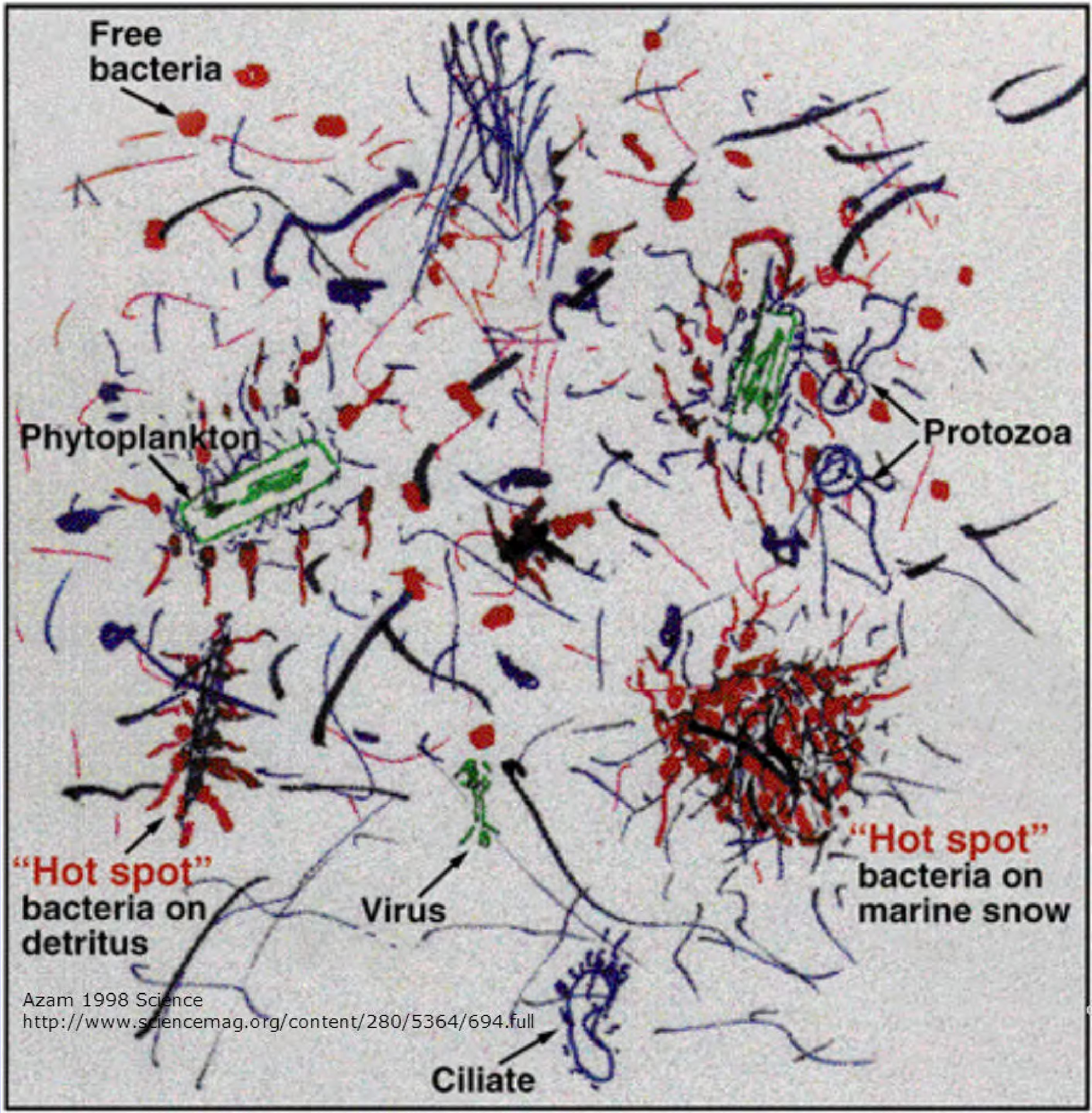


About 50% of particulate primary production is transformed via a range of mechanisms into DOC. Most of these mechanisms are microbial-mediated.









Azam 1998 Science
http://www.sciencemag.org/content/280/5364/694.full

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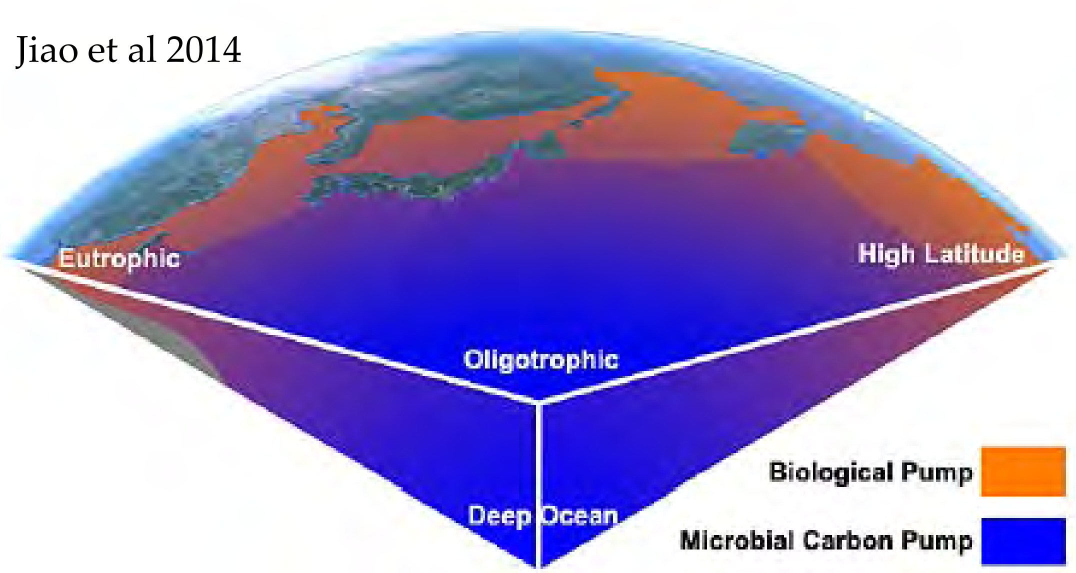
Jiao et al 2014



Along a nutrient gradient from high to low nutrient, there is a transition in the structure of the microbial food web from large phytopl → microzoopl predators to that of small auto- and hetertrophs → protistan predators.

This may lead to a shift in the relative importance in POC export via the BCP to production RDOC via MCP.

The ratio of DOC production to total PP increases with increasing oligotrophy. Some of this DOC is converted to RDOC. Thus, the contribution of the MCP to carbon storage could be higher when ambient nutrients are low.

A similar transition from dominance of the BP to MCP might be expected along a latitudinal gradient from polar regions to the tropics and from surface waters to the mesopelagic.

So a critical question is…

“what mechanisms may be regulating the relationship between BP and MCP with the food web components that are responsible for the production of exportable POC and RDOC”?

1- Food web structure and trophic flows

2- Nutrient-dependent interaction between autotrophic and heterotrophic microbes.

Cycling of biogenic carbon can be described as

Prod = Respiration + Food web + Export

Over the long term steady state,

F = R + E

Thus, P = R + E

E = P - R

This approach is overly simplistic, because a fraction of the POC channelled into **F** is released as DOC.

Food web progressively transforms the DOC into chemical forms that are used with a low efficiency (i.e. recalcitrant) and is respired very slowly. This leads to an accumulation of RDOC (lifetime of ≥ 5,000 y).

F = R + E + **RDOC**

1- Food web structure and trophic flows

There are two main fates of microbial biomass in the ocean….

Food web transfer to protistian grazers: Microbial biomass is repackaged and transferred to metazoan grazer→ a portion of the biomass will be released as DOC as a result of protistian and metazoan metabolism. The efficiency of trophic transfer varies, however DOC release is likely relatively a small fraction of the ingested ration.

Viral lysis: Releases all the microbial/bacterial cytosol into seawater.

In both cases, there can be a progressive transformation, via sequential uptake and re-release which modifies the composition and biological availability of the DOC.

Few studies separate viral- from microzooplankton- mediated mortality of bacteria and phytoplankton.

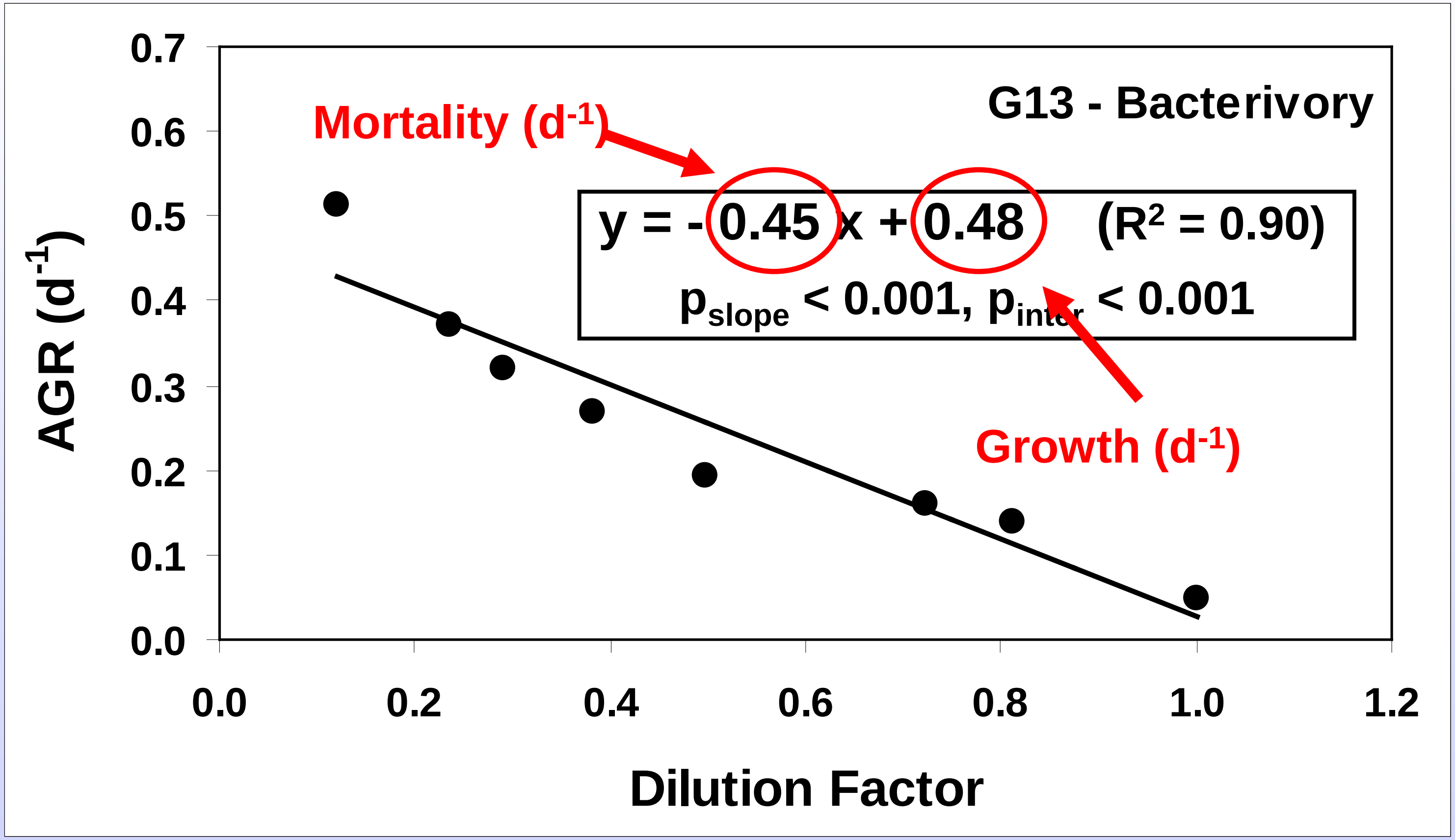
In addition, viral caused mortality of bacteria is typically greater than for phytoplankton.

When microzooplankon are consuming mainly phytoplankton, more bacterial production may be available for viral lysis.

Here we are use the relative preference of microzooplankton for autotrophic vs. bacterial prey and the global relationship of rates of growth to grazer mediated-mortality as proxies for the channeling of bacteria towards the food web or viral lysis.

Impact of microzooplankton on microbial prey is typically estimated using dilution assays.

AGR is determined as a function of DF and DF is a proxy for relative grazer density.



Microzooplankton processes are described with respect to prey growth (μ) and prey mortality (m). Mortality is <u>not</u> a grazing or ingestion rate!

<u>I</u> = <u>m</u> x B or I = B (μ) – B (μ-m)

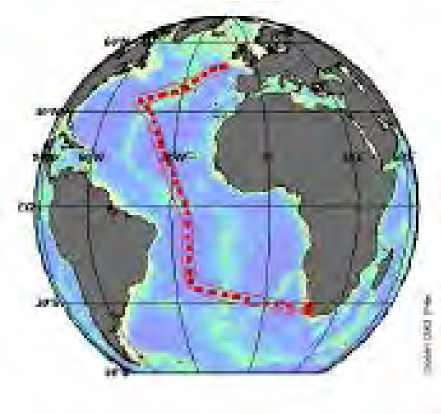
Prey may be ingested in proportion to their abundance, or they can be actively selected for or against!

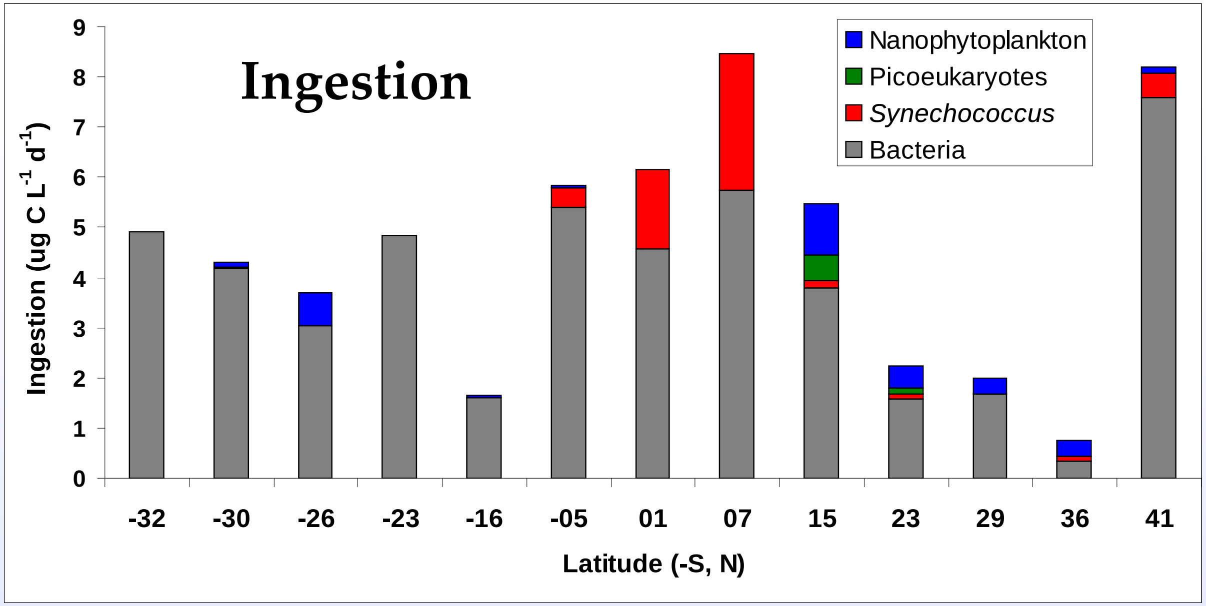
This selective ingestion can be quantified by computing the Relative Preference Index (RPI)

$$RPI = [Ipa/(Ipa + Ipb + Ipc\ldots)]/ [Bpa/(Bpa + Bpb + Bpc\ldots)]$$

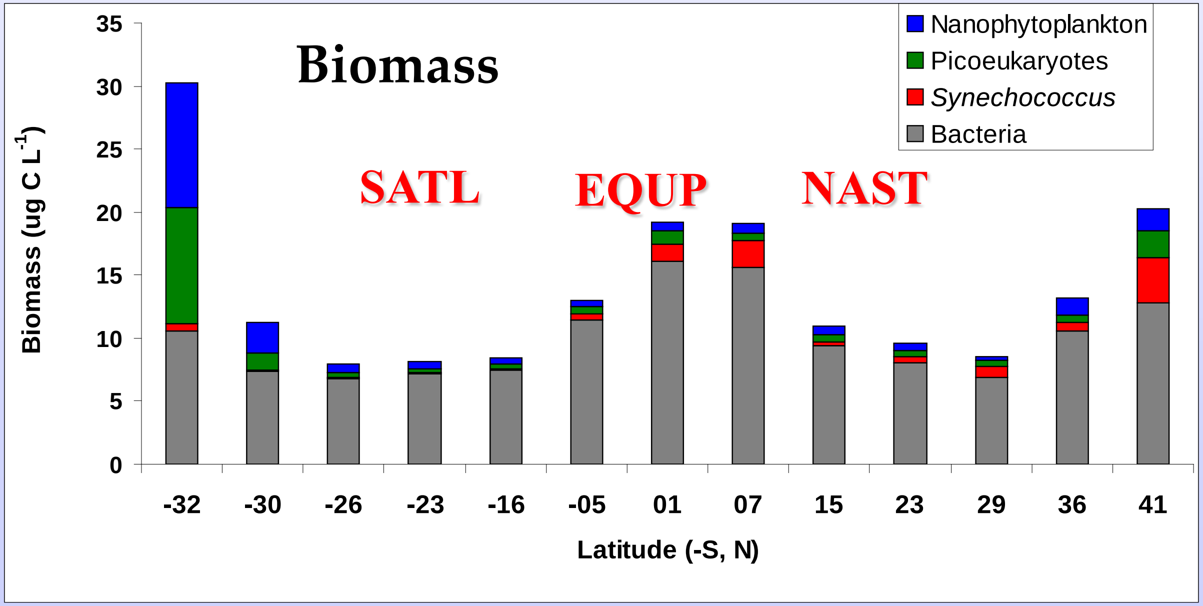
$RPR > 1$; prey selectively ingested

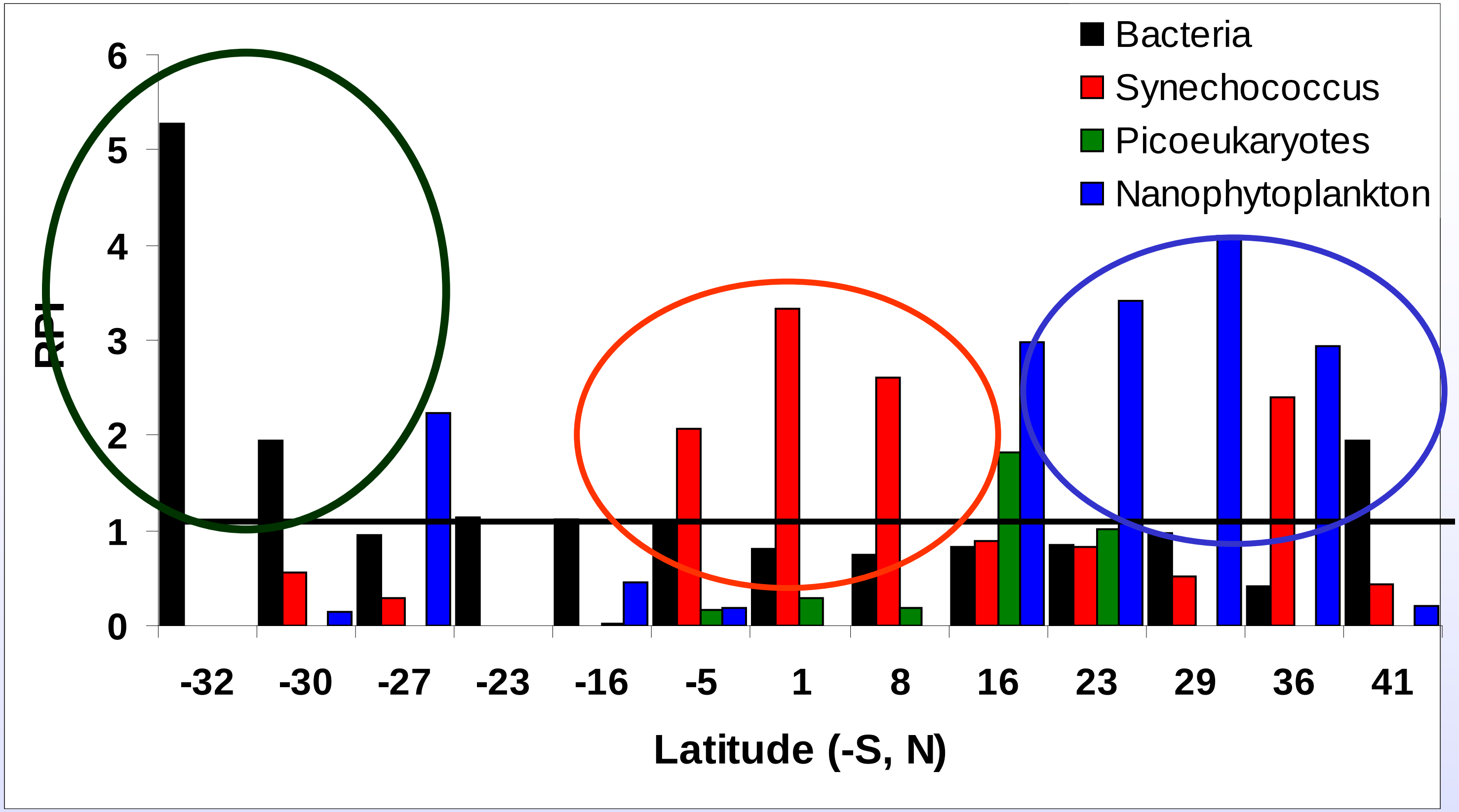
$RPI < 1$; prey selectively excluded





Biomass and ingestion higher in EQUP than gyres.





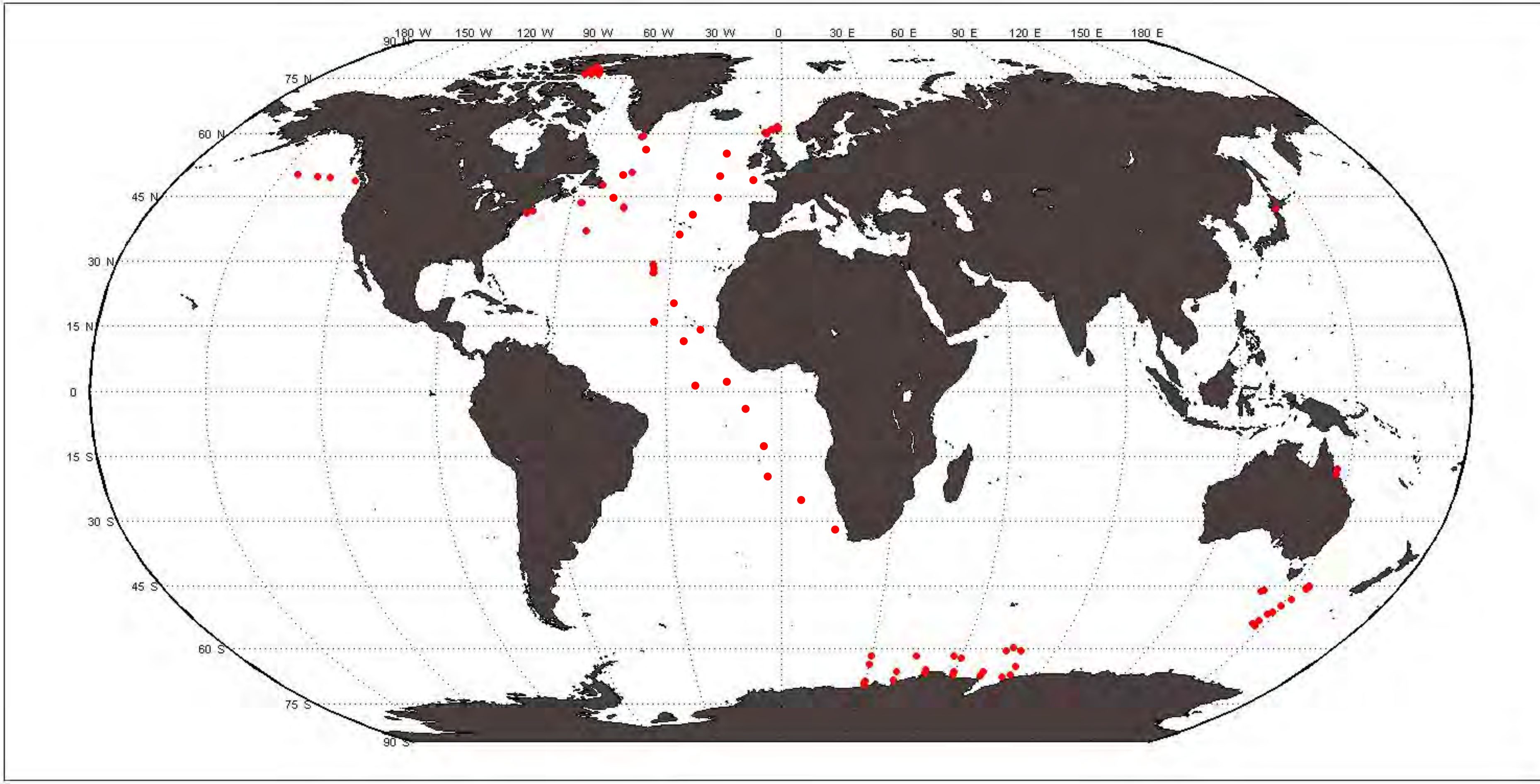
Large latitudinal gradient in feeding preferences

South → **North**

Bacteria → *Synechococcus* → Nanophytoplankton

Reviewed >25 years of literature on growth and grazing mediated-mortality of phytoplankton and bacteria.

30 published papers with ~240 concurrent observations for bacteria and phytoplankton that used the same techniques



Summary of means and 95% CI for parameters within the dataset

	Bacteria	Phytoplankton
Biomass	47.2 ± 13.6	213.2 ± 56.2 μg C l-1
Growth Rate	0.44 ± 0.092	0.48 ± 0.096 d^{-1}
Mortality Rate	0.38 ± 0.096	0.47 ± 0.076 d^{-1}
Ingestion Rate	29.6 ± 10.4	96.6 ± 41.3 μg C l^{-1} d^{-1}
RPI	1.51 ± 0.2	0.89 ±0.04

There is a close (but not absolute) coupling between rates of growth and "grazing-mediated" mortality for both bacteria and phytoplankton.

Bacteria

$r^2 = 0.741$; $p = 0.001$; Slope = 1.19**

Phytoplankton

$r^2 = 0.305$; $p = 0.001$; Slope = 0.95

Slope >1 → higher mortality than growth.

Slope $\simeq$ 1 → balance between mortality and growth.

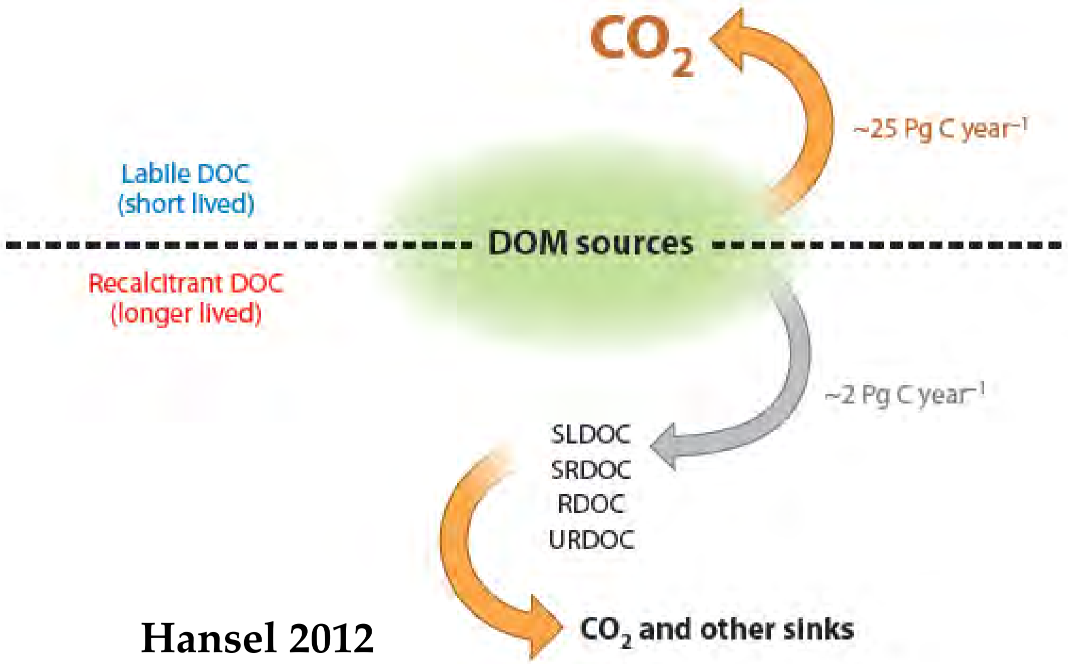
Phytoplankton- growth and mortality are in balance.

Bacteria- growth exceeds mortality by ~20%.

Bacteria production in the upper 100m of the World Ocean is estimate at 20-25 Gt C y^{-1}.

If there is a ~20% excess of bacterial growth over mortality, then a minimum of 4 to 5 Gt C y^{-1} of bacterial production could be channeled to DOC via the viral lysis.

What fraction of total DOC production is transformed to RDOC?



Hansel 2012

Labile DOC ~25 Gt C y^{-1}

RDOC ~0.043 Gt C y^{-1}

RDOC ~0.2% of LDOC production.

Bacteria could directly account for 20-25% of the LDOC uptake that would eventually be transformed into 0.05 Gt RDOC y^{-1}.

This is likely an underestimate since it assumes that the measured bacterial mortality is mainly grazer-mediated and the contribution of viral lysis to the estimated mortality is relatively small.

2- Nutrient-dependent interaction between autotrophic and heterotrophic microbes.

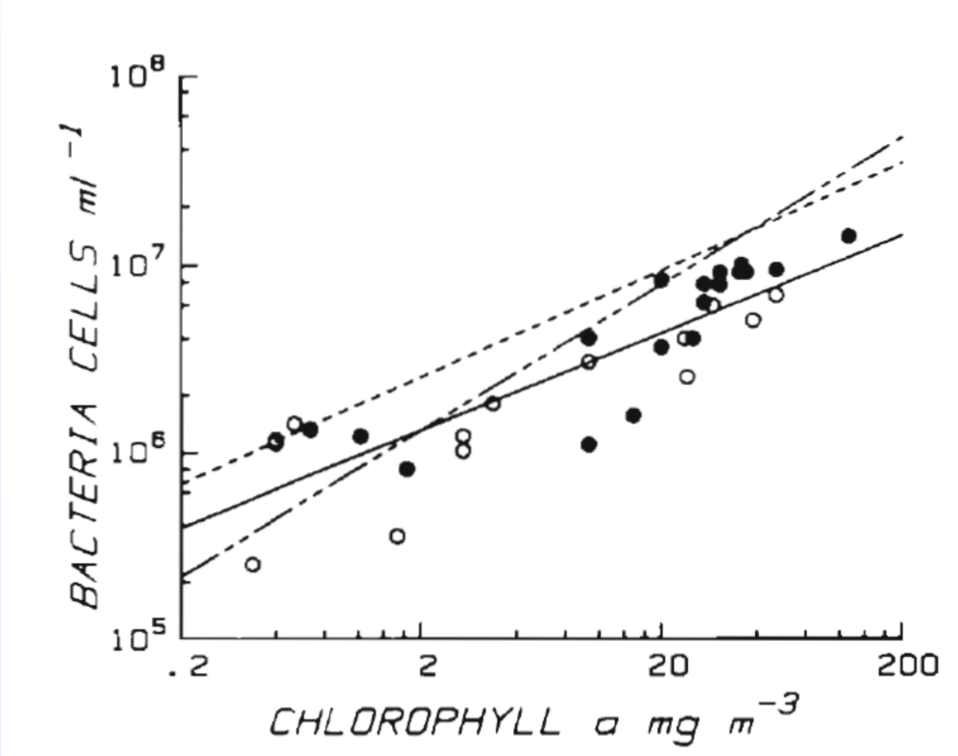
Traditionally, heterotrophic bacterioplankton were regarded as ‘mineralisers’ of nutrients from detrital organic matter → regenerated nutrients supporting algal production.

However bacteria and phytoplankton acquire inorganic nutrients from the same dissolved pool and can be concurrently limited by the same inorganic nutrients.

The influence and consequences of competition for inorganic nutrients on plankton and ecosystem dynamics and ocean biogeochemical processes is essentially unknown.

Two general views of microplankton nutrient dynamics.

In one, phytoplankton are largely regulated by nutrient availability → They in turn supply organic carbon, directly or via food webs, to bacteria. This view emerges from correlations between algal biomass and bacterial abundance and that bacterial production is 10-30% of net primary production.



Underlying this view is the implication that bacterioplankton are not limited by mineral nutrients.

Another view, bacteria and phytoplankton are competitors for inorganic nutrients.

Supported by several field and laboratory studies demonstrating limitation of bacterial growth by mineral nutrients… Which is a requisite condition for competition.

During seminal chemostat experiments by Bratbak & Thingstad, where extracellular organic carbon release by algae was the only carbon source for the bacteria… a paradoxical situation developed.

Bacteria were more competitive in sequestering P → nutrient limitation of the algae → increase DOC release.

The algae supported the growth of their own competitors → increased algal P limitation.

The authors termed their observations the 'phytoplankton–bacteria paradox'.

Bacteria, like all microbes, require carbon, nitrogen, and phosphorus for biosynthesis in a stoichiometric balance set by the physiological state of the cells.

Because of their relatively high nucleic acid content, bacteria generally have a lower C:N:P ratio than in phytoplankton.

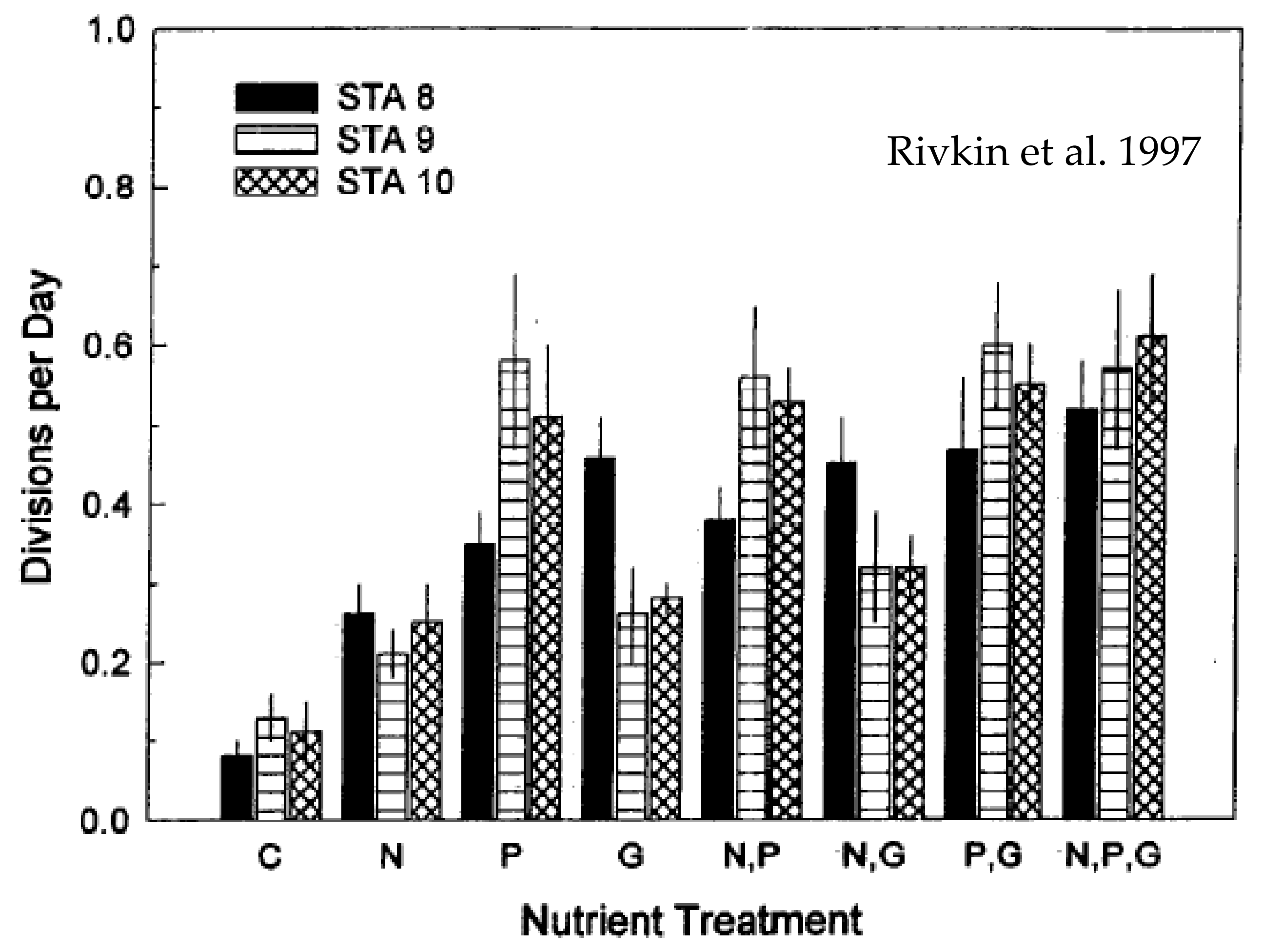
Stoichiometric ratios of bacteria

	C:N:P	C:N
Exponential	35:6.7:1	5.2
C-limited	42:12:1	3.8
N-limited	49:7.5:1	7.2
P-limited	150:18:1	8.3

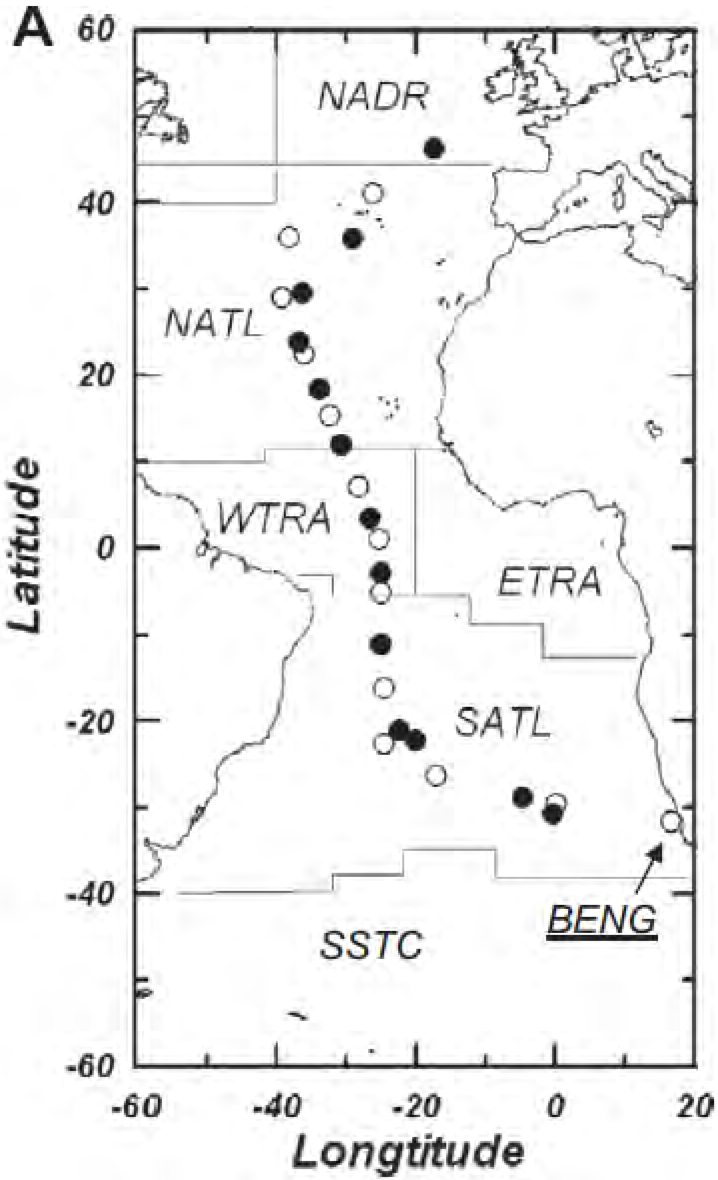
(summary from Vrede et al 2002).

Phytoplankton	106:16:1	6.6:1

So… what 'field' evidence is there for mineral limitation of bacteria?



Inorganic P limitation of bacterial growth in the Caribbean (#8) and Sargasso (#9) Seas and Gulf Stream (#10).



May to June- O

October to November - ●

Hale et al 2016

Organic carbon limitation-	5 of 26 stations.
Inorganic nutrient limitation-	15 of 26 stations
Inorganic + organic co-limitation-	26 of 26 stations

Of the 20 published studies, *8 showed inorganic nutrient limitation* of bacterial growth, and 6 showed no limitation!

Hale et al 2016

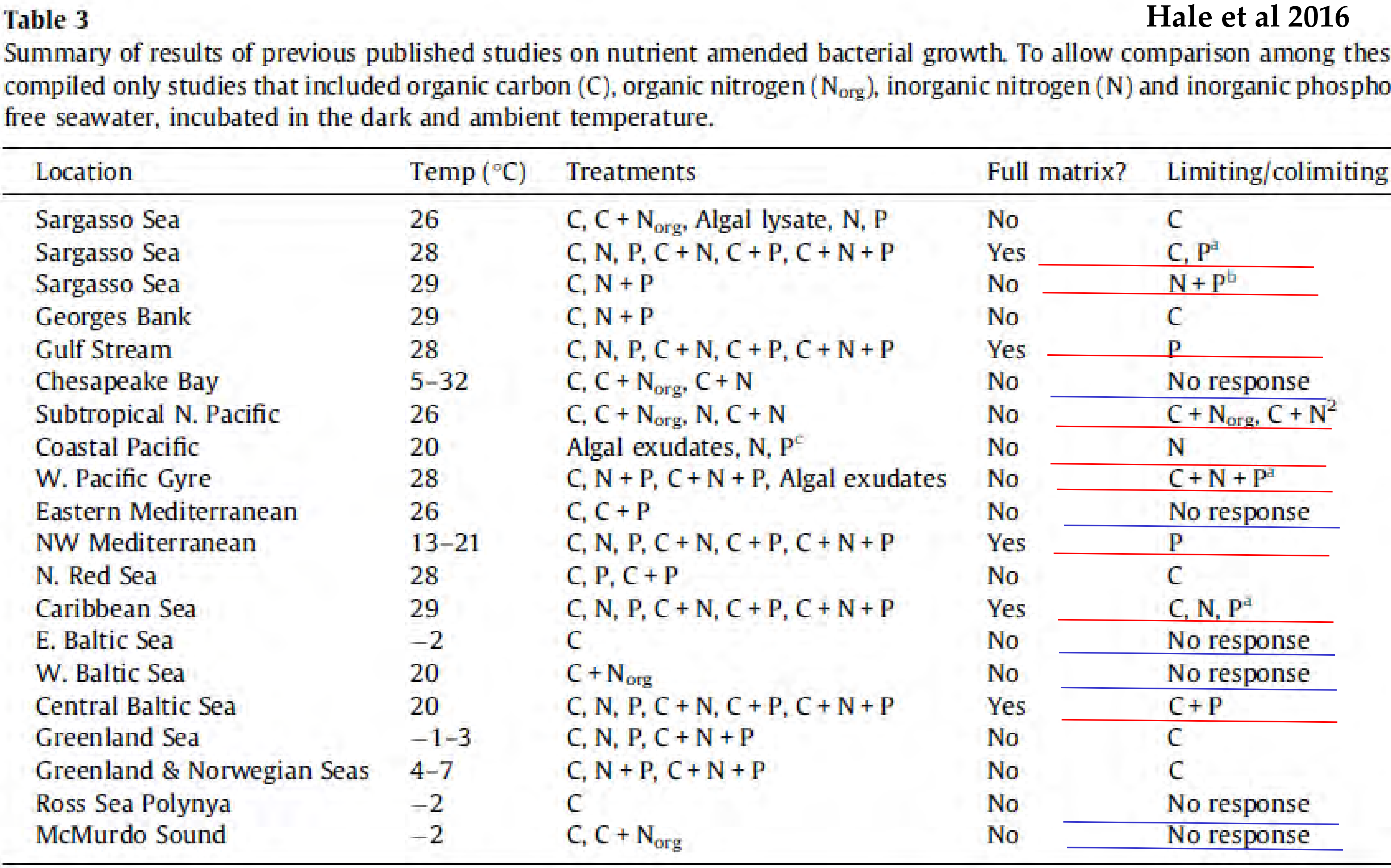


Table 3

Summary of results of previous published studies on nutrient amended bacterial growth. To allow comparison among thes compiled only studies that included organic carbon (C), organic nitrogen (N_{org}), inorganic nitrogen (N) and inorganic phospho free seawater, incubated in the dark and ambient temperature.

Location	Temp (°C)	Treatments	Full matrix?	Limiting/colimiting
Sargasso Sea	26	C, C + N_{org}, Algal lysate, N, P	No	C
Sargasso Sea	28	C, N, P, C + N, C + P, C + N + P	Yes	C, P^a
Sargasso Sea	29	C, N + P	No	N + P^b
Georges Bank	29	C, N + P	No	C
Gulf Stream	28	C, N, P, C + N, C + P, C + N + P	Yes	P
Chesapeake Bay	5–32	C, C + N_{org}, C + N	No	No response
Subtropical N. Pacific	26	C, C + N_{org}, N, C + N	No	C + N_{org}, C + N^2
Coastal Pacific	20	Algal exudates, N, P^c	No	N
W. Pacific Gyre	28	C, N + P, C + N + P, Algal exudates	No	C + N + P^a
Eastern Mediterranean	26	C, C + P	No	No response
NW Mediterranean	13–21	C, N, P, C + N, C + P, C + N + P	Yes	P
N. Red Sea	28	C, P, C + P	No	C
Caribbean Sea	29	C, N, P, C + N, C + P, C + N + P	Yes	C, N, P^a
E. Baltic Sea	−2	C	No	No response
W. Baltic Sea	20	C + N_{org}	No	No response
Central Baltic Sea	20	C, N, P, C + N, C + P, C + N + P	Yes	C + P
Greenland Sea	−1–3	C, N, P, C + N + P	No	C
Greenland & Norwegian Seas	4–7	C, N + P, C + N + P	No	C
Ross Sea Polynya	−2	C	No	No response
McMurdo Sound	−2	C, C + N_{org}	No	No response

As part of a long term study of microbial dynamics in high latitude cold oceans, we examined the growth of bacteria and phytoplankton with different nutrient amendments using dilution cultures.

Newfoundland coastal waters, Labrador Sea, Resolute Bay , & North Water Polynya, Arctic, McMurdo Sound, Antarctic, *Line P, OS Papa, mid-Atlantic Shelf, Sargasso Sea, Caribbean Sea*

Temperature	-1.7 to 29 ^{o}C
Chlorophyll a	< 0.01 to ~ 25 μg/l
Bacterial abundance	~5 x 10^{7} to ~5 x 10^{9} cells/l

Effect of nutrient additions on bacterial and phytoplankton growth rates (expressed as a percent of the un-amended control).

	Bacteria	Phytoplankton
+ Inorganic	114% ± 13%	162% ± 49%
+ Organic	191% ± 31%	58% ± 31%
+ Inorganic & Organic	229% ± 61%	68% ± 37%

Addition of inorganic nutrients enhanced phytoplankton growth and had a small and variable effect on bacterial growth. Enhancement of growth generally at higher temperatures.

Addition of organic nutrients enhanced bacterial and reduced phytoplankton growth.

Addition of inorganic + organic nutrients generally enhanced bacterial and reduced phytoplankton growth.

When bacteria are supplied with organic nutrients, they out-competed phytoplankton for inorganic nutrients.

Heterotrophic microbes dominate trophic interactions and biogeochemical processes and control ocean ecosystem services.

Although there responses to environmental forcings have important implications for understanding ocean-climate interactions and biogeochemical cycles, there are still a large number of uncertainties about fundamental aspects of trophic interactions.

Estimating the strength of the BCP and MCP and their responses to changing climate depends on understanding the processes contributing to the production of DOC and its transformations. These processes are poorly constrained, in part, because some have yet to be identified, and where processes are known, the experimental approaches have yet to be developed or applied.

Thank you for your attention!