Bacterial remineralization and respiration

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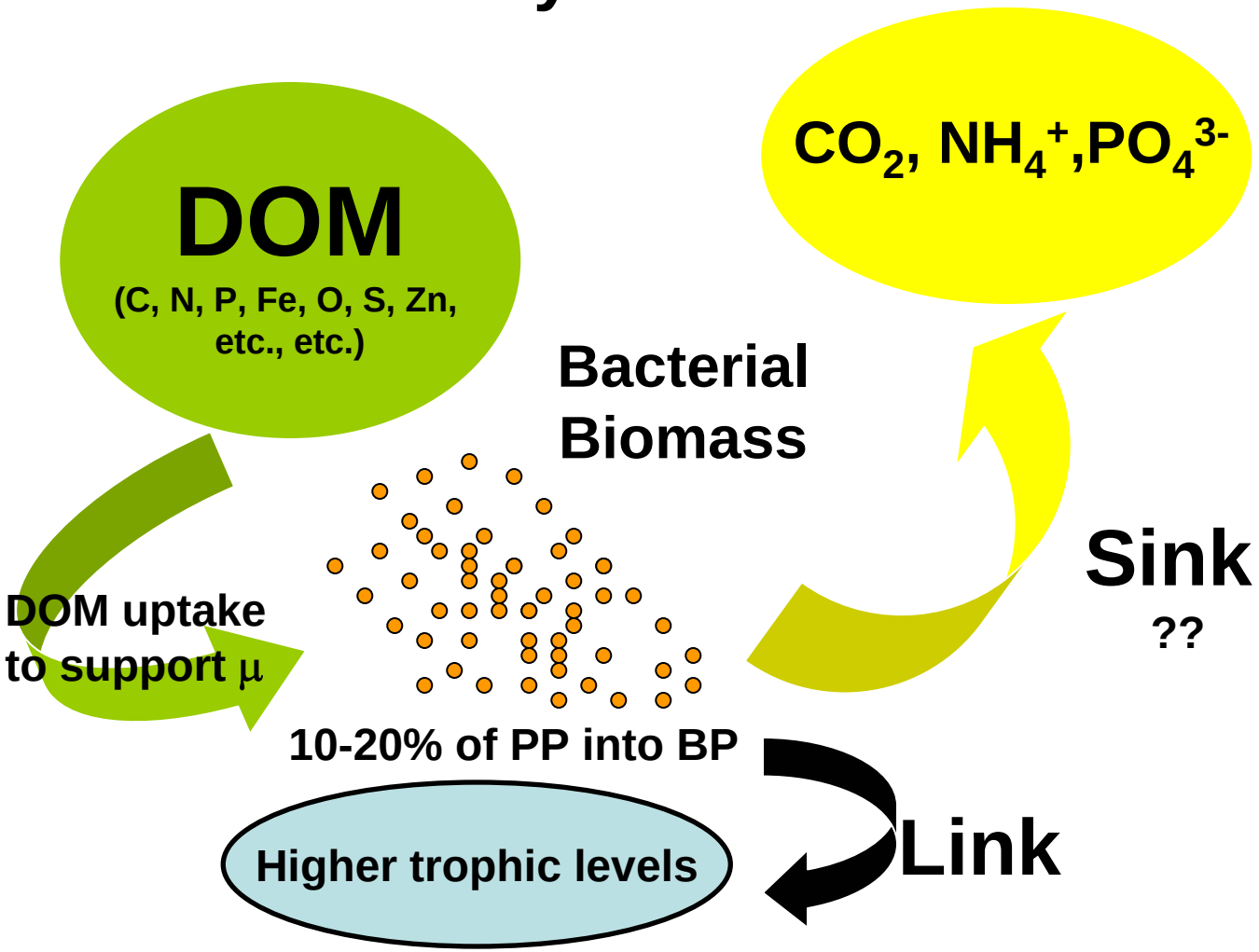
Marine Microplankton Ecology
OCN 626

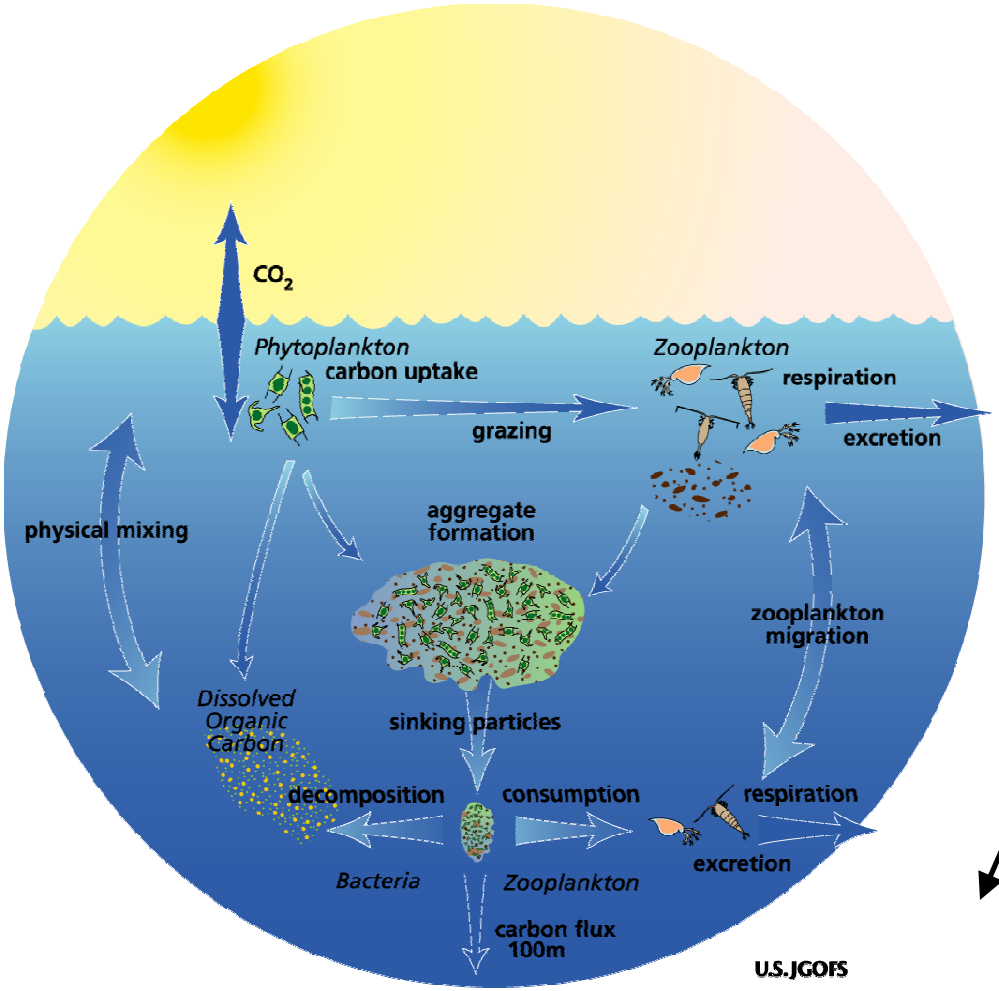
Motivation

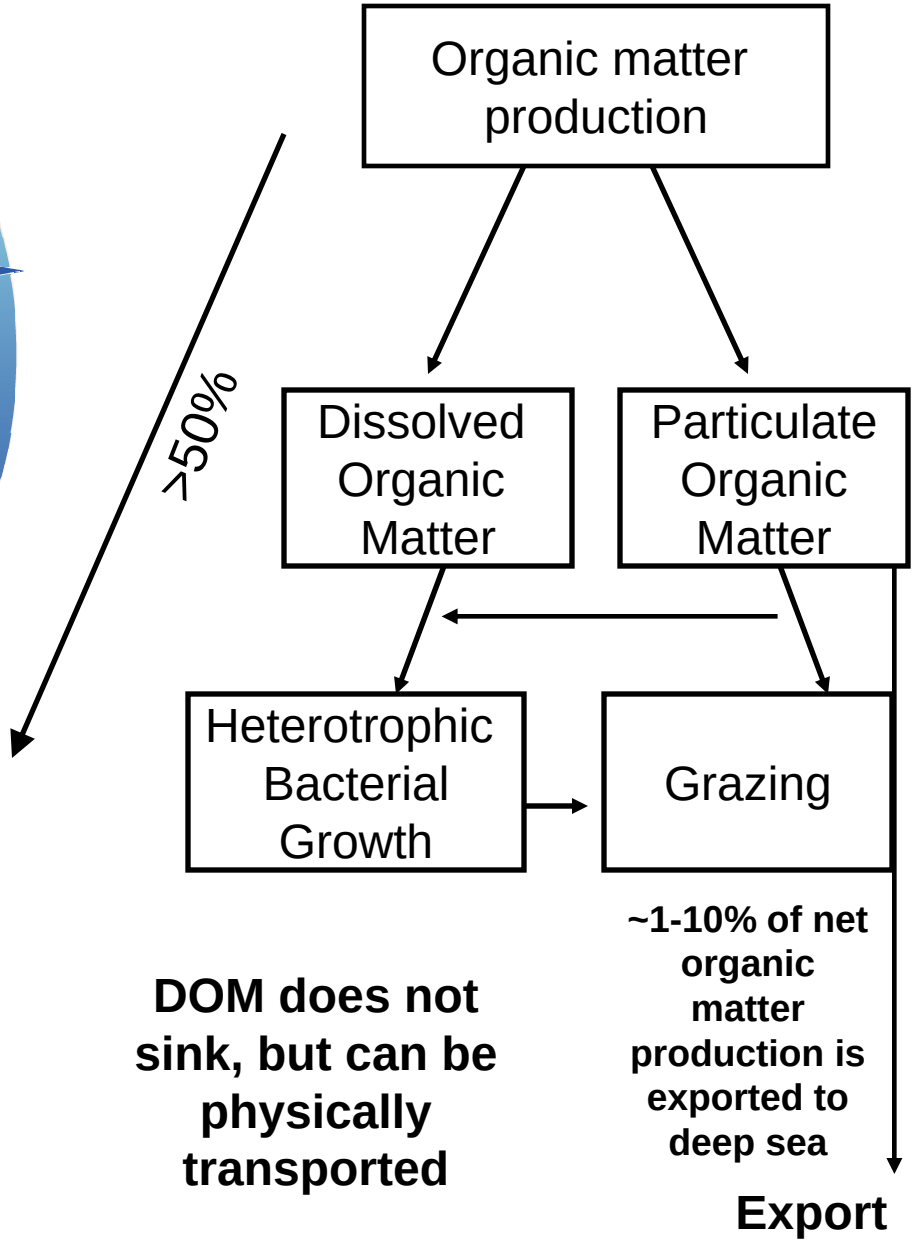
Bacterial growth regulates fluxes of carbon and nutrients, and dictates energy flow in marine ecosystems.



Respiration and remineralization

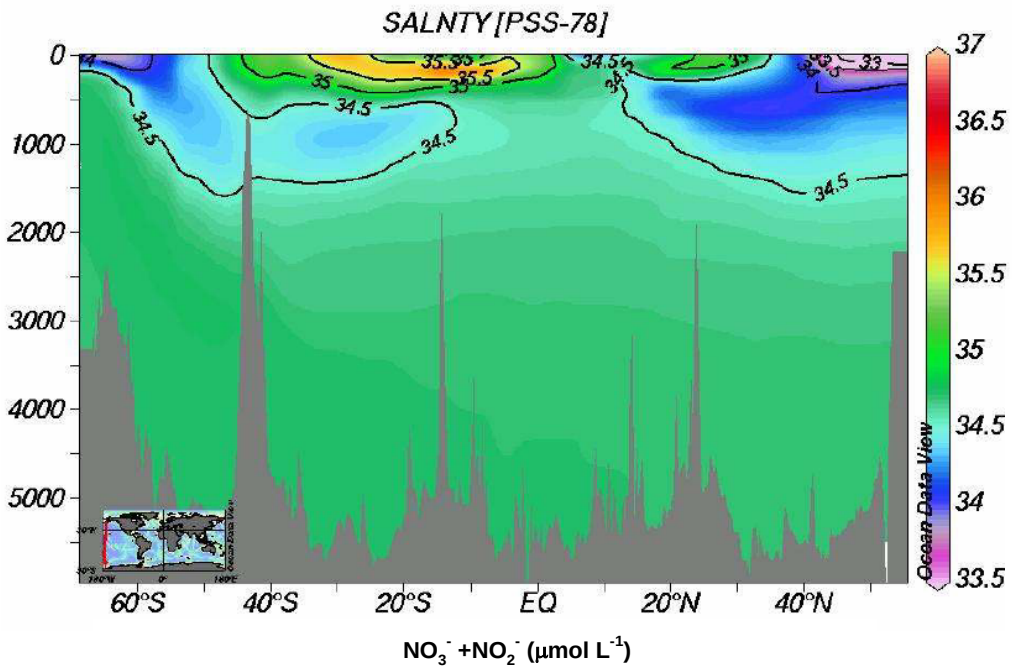
- **Organic matter production**
- **Organic matter consumption and remineralization**
- **Heterotrophic respiration and metabolism**
- **Processes controlling heterotrophic consumption of organic matter**

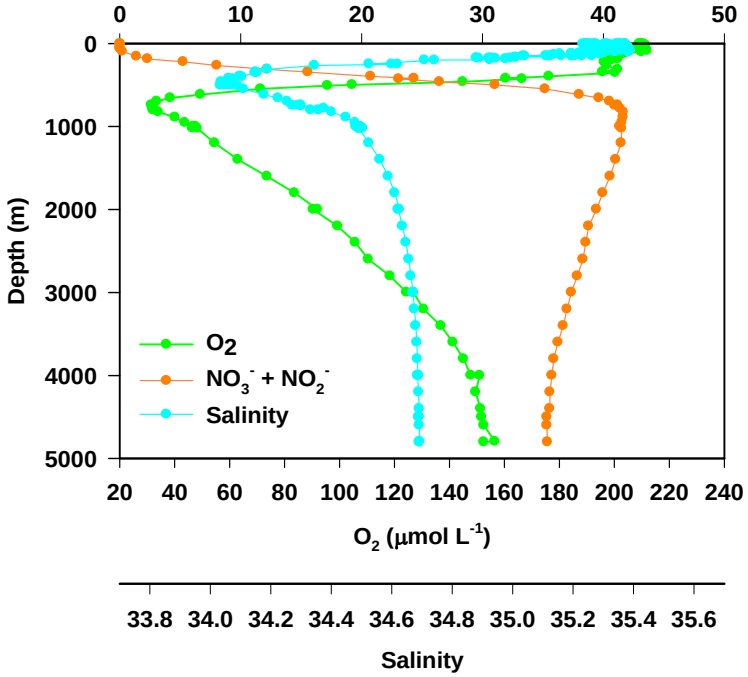


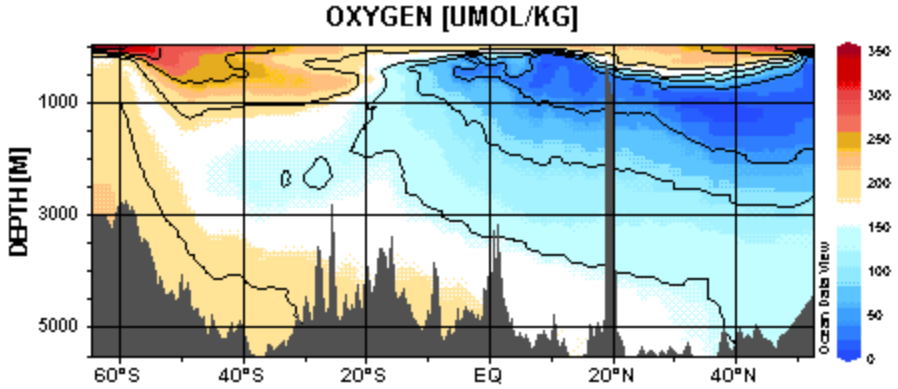


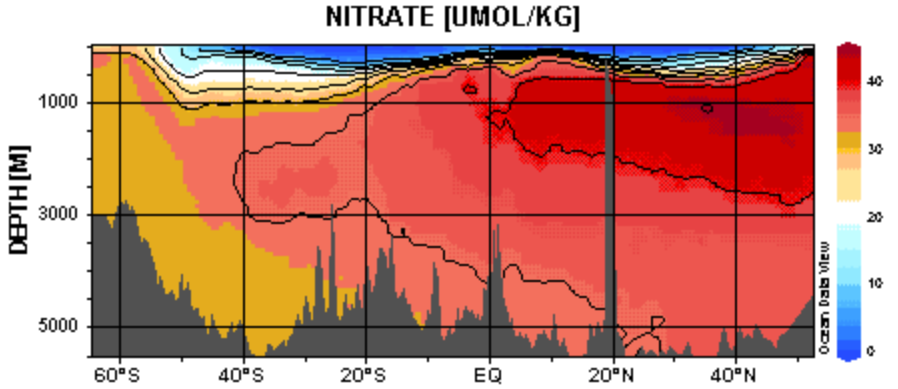
What happens to the 90-99% of organic matter production that does not get exported as particles?

DOM does not sink, but can be physically transported









Without biology, distributions of nutrients would be controlled exclusively by physical transport

Stoichiometry of organic matter production

$$106\ CO_2 + 16\ HNO_3 + 1\ H_3PO_4 + 122\ H_2O + \text{trace elements (e.g. Fe)}$$

$$\text{light} \Downarrow$$

$$(\ C_{106}H_{263}O_{110}N_{16}P\ )\ +\ 138\ O_2$$

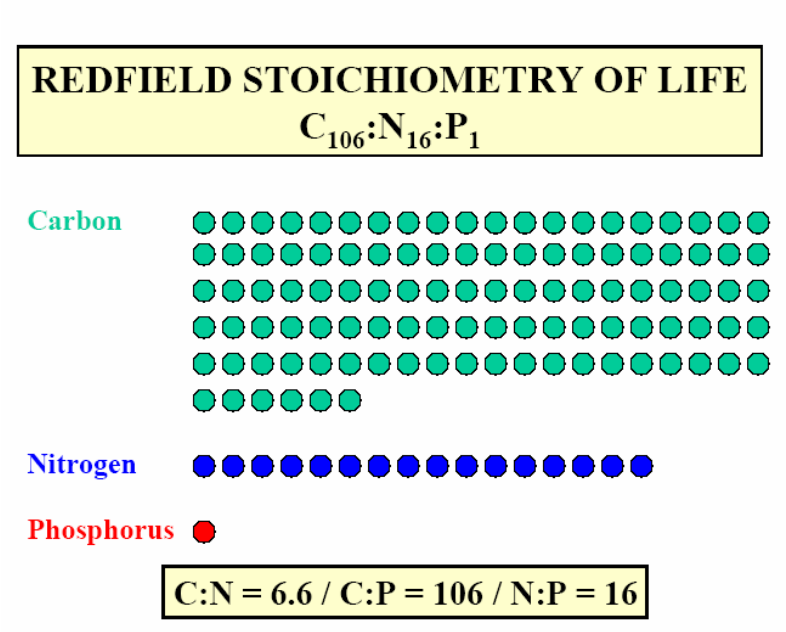
Or

$$(CH_2O)_{106}\,(NH_3)_{16}\,(H_3PO_4) + 138\ O_2$$

Atomic Ratios of the Principal Elements Present in Plankton

	C	N	P
Zooplankton	103	16.5	1
Phytoplankton	108	15.5	1
Average	106	16	1

from Redfield, Ketchum and Richards (1963)
The Sea Vol. 2



Growth rate influence on the chemical composition of phytoplankton in oceanic waters

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The chemical composition of oceanic phytoplankton (by atoms) typically occurs in the proportions $C_{106}N_{16}P_1$. Yet, in laboratory growth conditions these proportions are only observed for marine phytoplankton at high growth rates when non-nutrient limitation is approached. Thus growth rates of natural phytoplankton populations in oceanic waters may be near maximal and hence non-nutrient limited. The uniformly low biomass and residual nutrient levels in such waters does not preclude the possibility of high growth rates because zooplankton grazing and nutrient regeneration within the euphotic zone may keep this highly dynamic system in a balanced state.

An evaluation of the dependence of elemental stoichiometry on growth rate

Conclusion:

Redfield stoichiometry is approached when plankton growth rates are near maximum, and nutrients are not limiting growth…

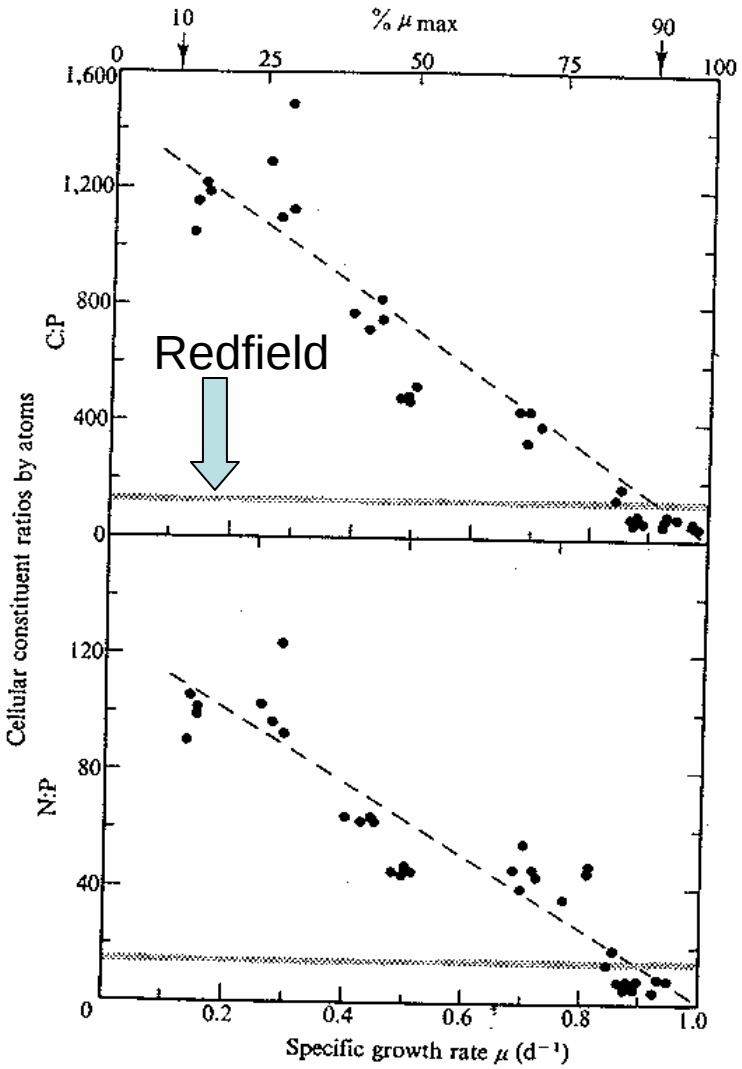
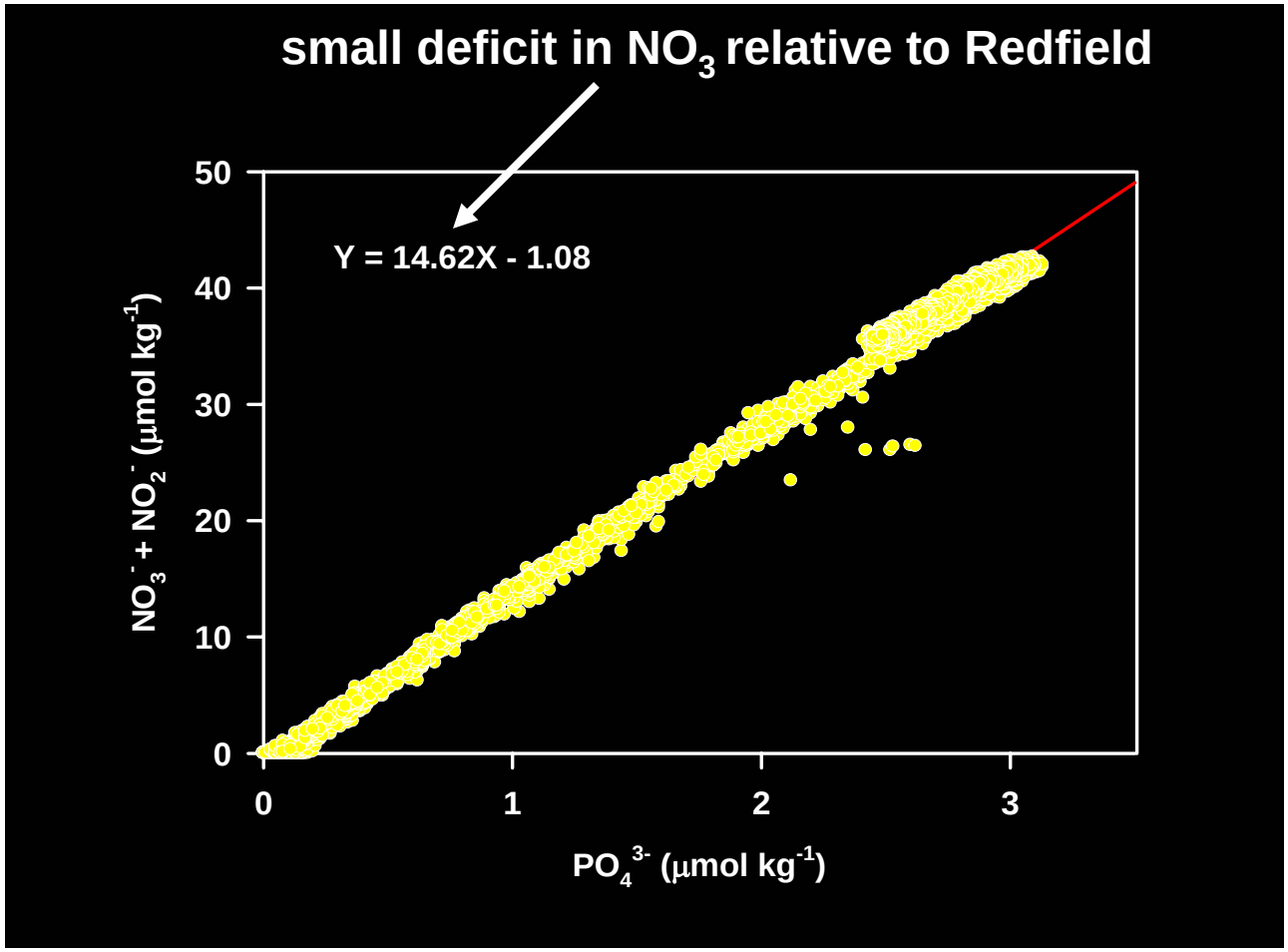


Fig. 1 The effect of specific growth rate on the carbon:phosphorus and nitrogen:phosphorus ratios of *Monochrysis lutheri* under phosphorus limitation in continuous culture at 18 °C and 0.03 cal cm^{-2} min^{-1} light intensity. Medium N:P ratios = 87:1 to 412:1. Shaded lines in Figs 1–3 represent C:P and N:P components of Redfield ratio ($C_{106}N_{16}P$). All dashed lines in these figures were drawn by eye and represent trends not absolute relationships between the respective cellular chemical ratios and growth rates. $\mu_{max} = 0.95\ d^{-1}$.

Congruence between NO_3^- : PO_4^{3-} and plankton composition indicates that photosynthesis, respiration, and remineralization control variability in nutrient concentrations



Organic material is produced in approximately the same elemental stoichiometry that inorganic nutrients are available. There are important exceptions…

TABLE 4.2.1

Stoichiometric ratios of phytoplankton organic matter and oxygen released during synthesis of the organic matter or consumed during remineralization.

The first line gives the traditional Redfield ratio. The second line is a revision of the hydrogen and oxygen content in the Redfield ratio based on a reevaluation of the range of composition of organic matter. The third line is based on an analysis of the remineralization ratio in the deep ocean below 400 meters.

	Organic Matter					*Oxygen*
	C	*H*	*O*	*N*	*P*	O_2
Redfield et al. [1963]	106	263	110	16	1	138
Anderson [1995]	106	164–186	26–59	16	1	141–161
Anderson and Sarmiento [1994]	117 ± 14	–	–	16 ± 1	1	170 ± 10

TABLE 4.2.2

Mean composition of primary components of marine phytoplankton.

From Anderson [1995]. Proteins and lipids were taken by him from the study of Laws [1991], carbohydrates from Strickland [1965], and nucleic acid from Adams et al. [1986]. Shown in parentheses are the mean compositions used by Hedges et al. [2002] in their study. Their carbohydrate composition was identical to Anderson [1995] and they did not include nucleic acid in their analysis.

Organic Matter Component	*Composition*	*H/C_{org} ratio*	*C_{org}/O ratio*
Carbohydrate	$C_6H_{10}O_5$	1.67	1.2
Lipid	$C_{40}H_{74}O_5$	1.85	8.0
Protein	$(C_{18}H_{34}O_2)$ $C_{3.83}H_{6.05}O_{1.25}N$	1.58	3.1
Nucleic acid	$(C_{106}H_{168}O_{34}N_{28}S)$ $C_{9.625}H_{12}O_{6.5}N_{3.75}P$	1.25	1.5

Another intersection of microbes and ocean chemistry

- **Heterotrophic bacteria consume organic matter:**
  - **1) production of biomass**
  - **2) respiration**
- **Respiratory activities of heterotrophic bacteria also return nutrients to mineral form--completing the cycle from inorganic to organic and back to inorganic--thus the final turn of this cycle is termed *remineralization***

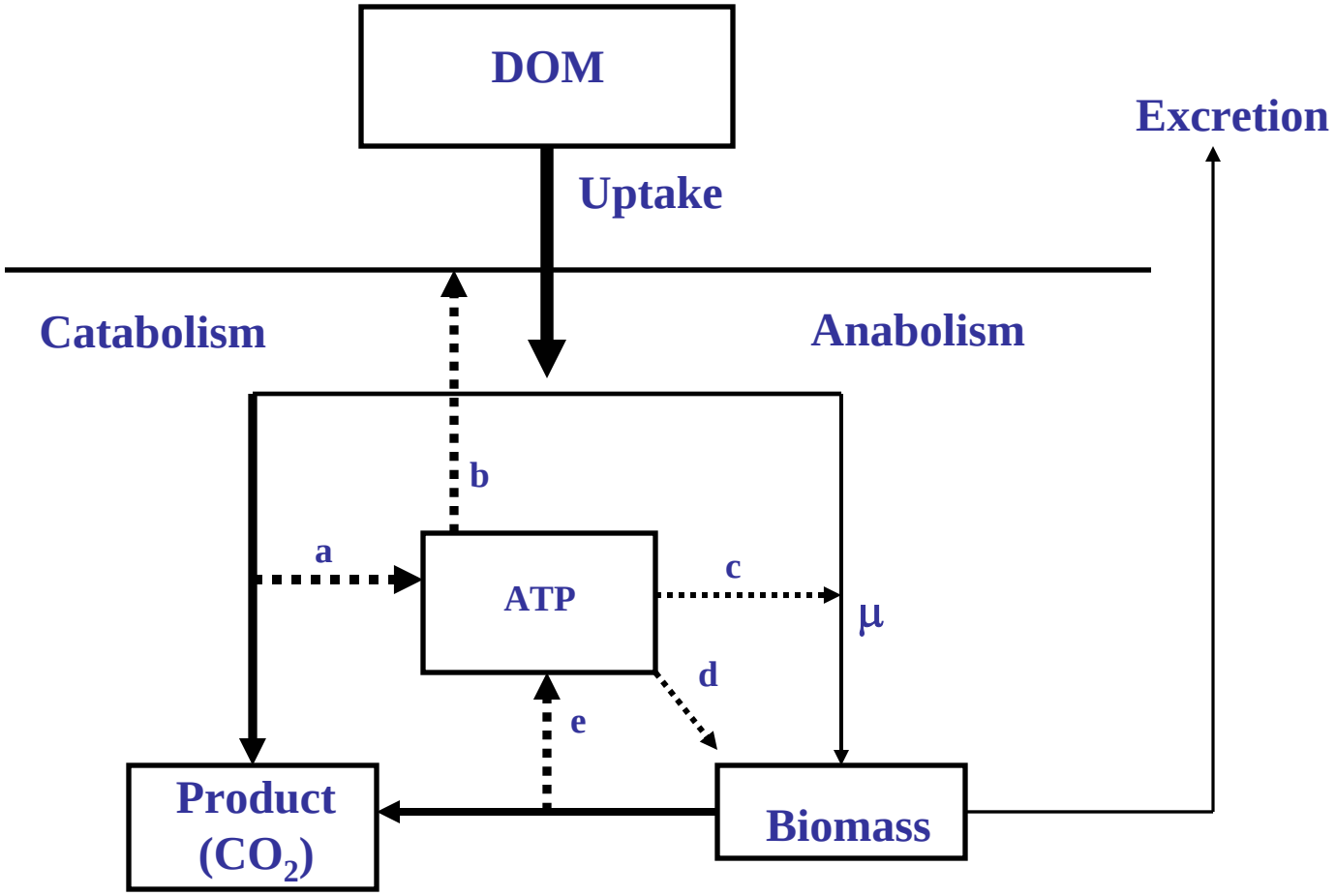
Complete remineralization of "average" organic matter by aerobic respiration:

$$(CH_2O)_{106}(NH_3)16H_3PO_4 + 138\ O_2 \Rightarrow 106CO_2 + 122H_2O + 16HNO_3 + H_3PO_4$$

Consumes O_2 | Produces CO_2 | Produces nutrients

- To understand remineralization, we need to understand:
  - Processes controlling bacterial growth
  - Controls on bacterial remineralization

Energetic costs of growth



del Giorgio and Cole (2001)

a. Oxidation of organic matter to form ATP, b. energy expense of active transport, c. anabolic reactions utilize energy, d. maintenance energy expenditures, e. degradation of biomass via endogenous metabolism.

Major energy consuming processes for growth

- **Solute transport**
- **Maintenance**
- **Growth and reproduction**
- **Regulatory**

We can estimate biomass production…
but we really need to know the total carbon flux required to support bacterial growth

- **Total amount of carbon that supports growth includes carbon used for biomass synthesis and carbon metabolized.**

- **Total flux of carbon supporting growth or**

Carbon demand = Production + Respiration

Respiration by various plankton size classes

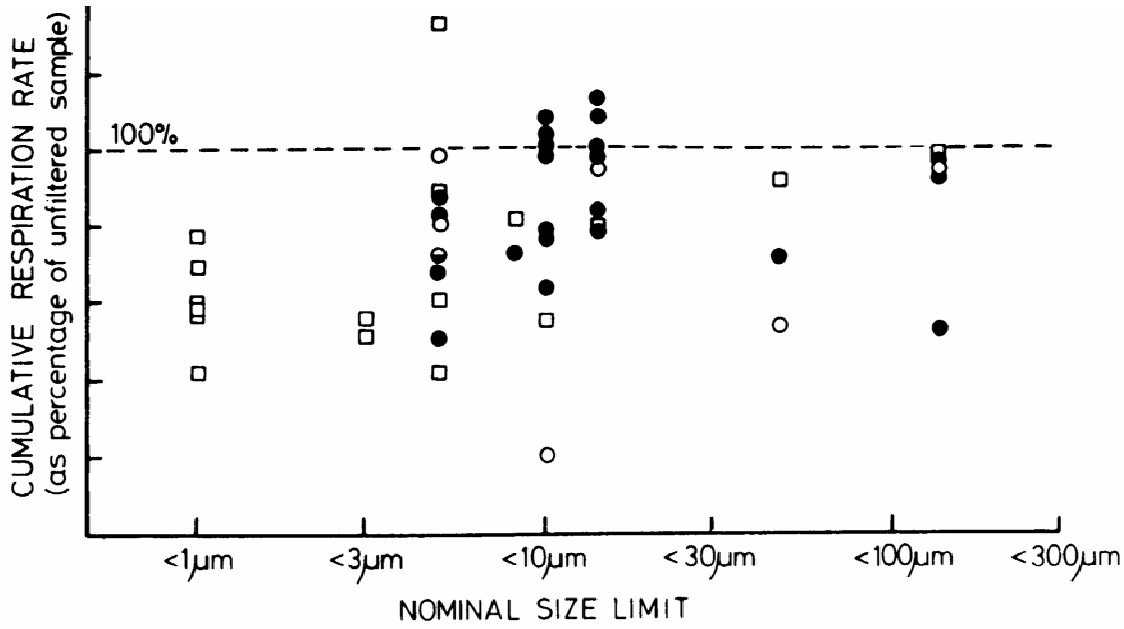


Figure 6. Distribution of respiratory activity with size. (□) CEPEX, samples from bag; (○) Loch Ewe, samples from bag; (●) Loch Ewe samples from outside bag. Data are expressed as cumulative respiration up to various size limits, normalized against the rate in the unfiltered sample. All the data points are for a single size horizon and are not replicates.

Williams (1984)

Note that 50-100% of plankton respiration in this example passes through a 10 μm filter; ~60% of the total respiration is by organisms <1 μm.

Bacterial production and respiration

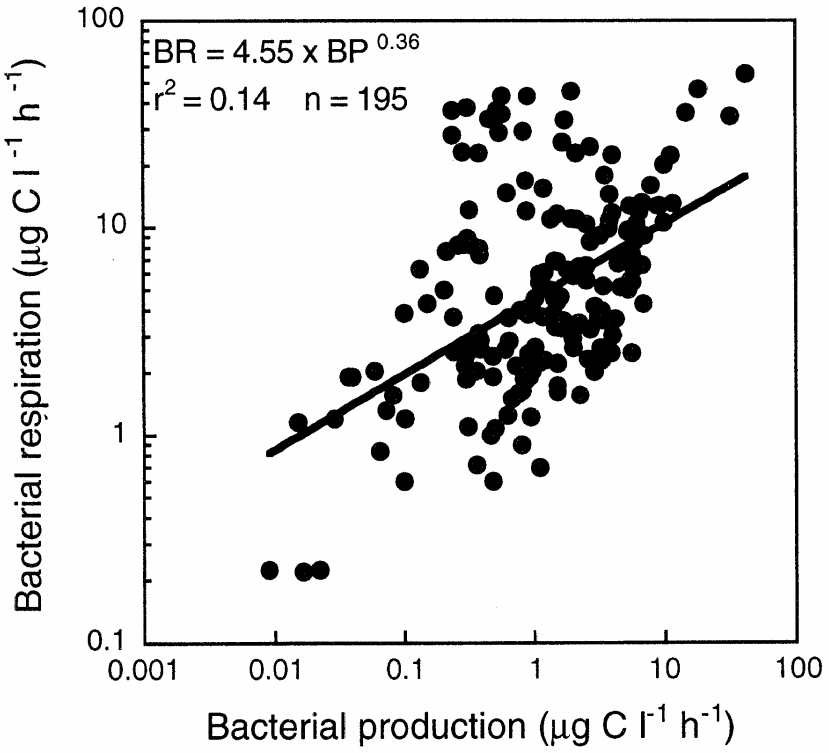


Figure 4. Bacterial respiration as a function of bacterial production in aquatic ecosystems. The data are paired observations of bacterial respiration (*BR*) and production (*BP*); the sources of these data appear in Table 1. The line is the least-squares fit to the log-transformed data.

del Giorgio and Cole (1999)

Estimates of BR and BP for marine (including estuarine) ecosystems. Note larger variation in BP relative to BR. The large variability in the relationship indicates measurements of BP are fairly poor indicators of BR. Also note the non-zero intercept, implying BR may proceed in the absence of measurable production.

The bacterial growth efficiency (BGE) is the growth yield or the amount of biomass synthesized relative to total carbon required for growth.

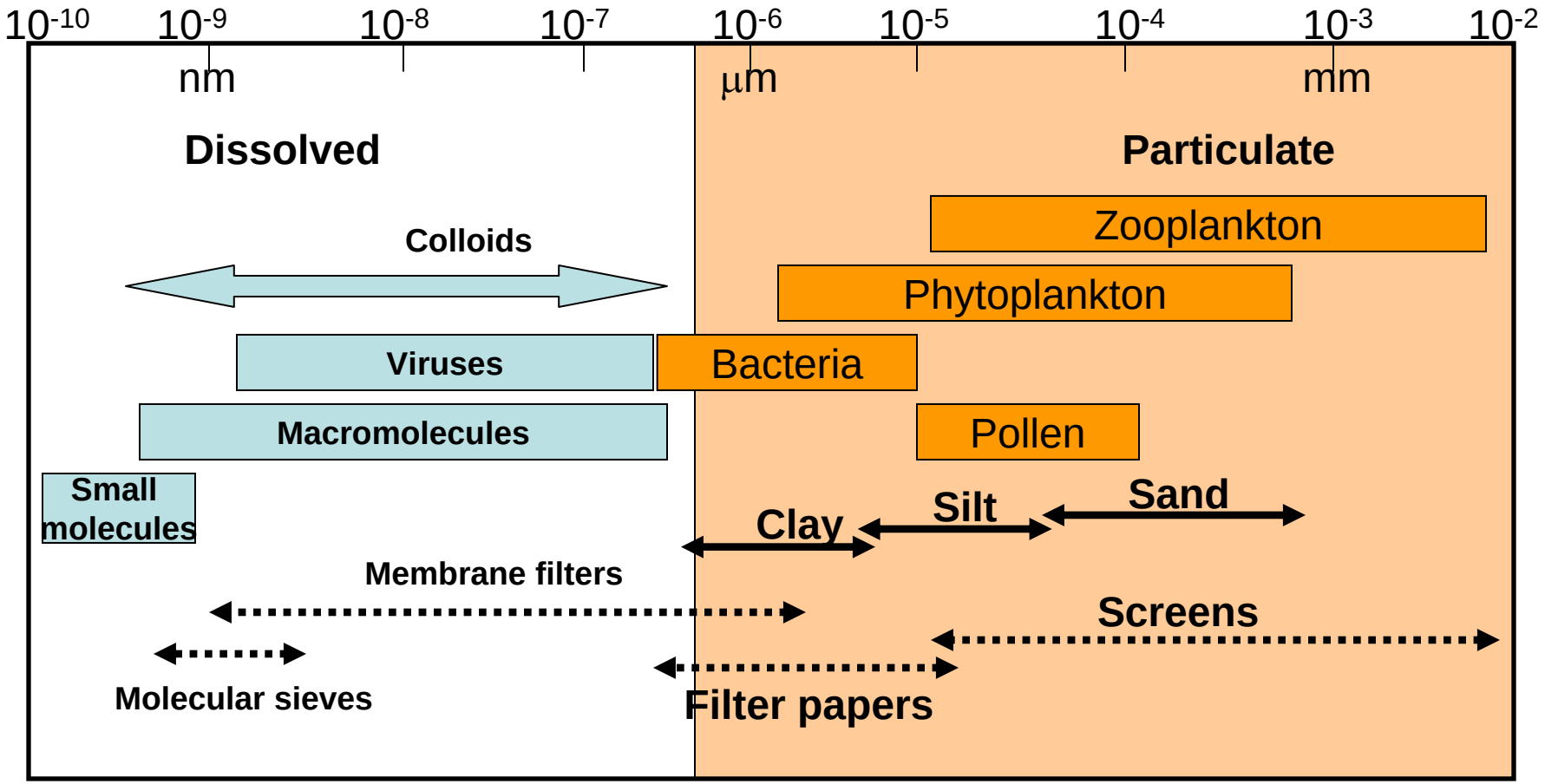
= BGE = BP / (BP + Respiration)

If we can constrain BGE, then we can place boundaries on total carbon demand

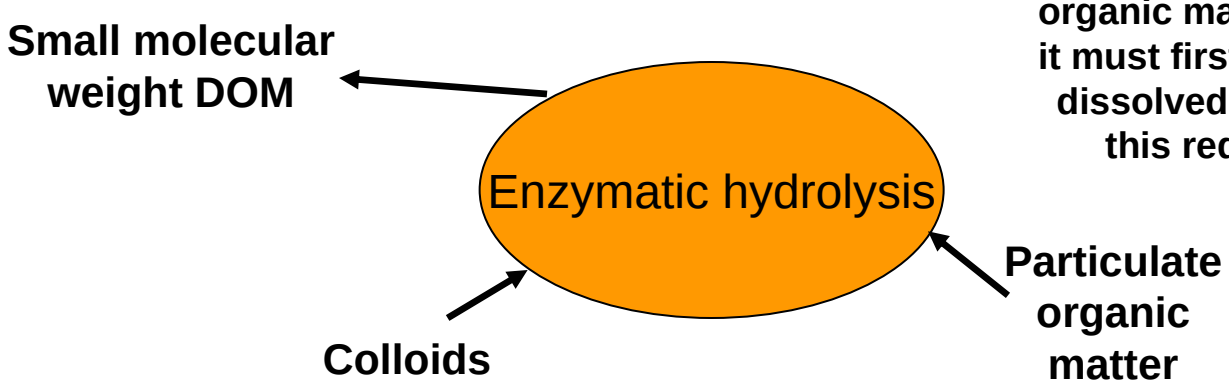
BP/ BGE = Carbon demand

Growth efficiency and carbon fluxes

- **The lower the growth efficiency = higher flux of carbon respired than into biomass.**
- **Higher growth efficiency = greater amount of carbon into biomass relative to total carbon flux.**



Bacteria do not use particulate organic matter for growth--- it must first be converted to dissolved organic matter; this requires energy



The type of substrates available and utilized for growth partly determine whether bacteria form a link or sink. Components of the DOM pool often require specialized ectoenzymes to breakdown polymers into transportable substrates. This process can be energetically expensive and directly influences bacterial growth efficiencies.

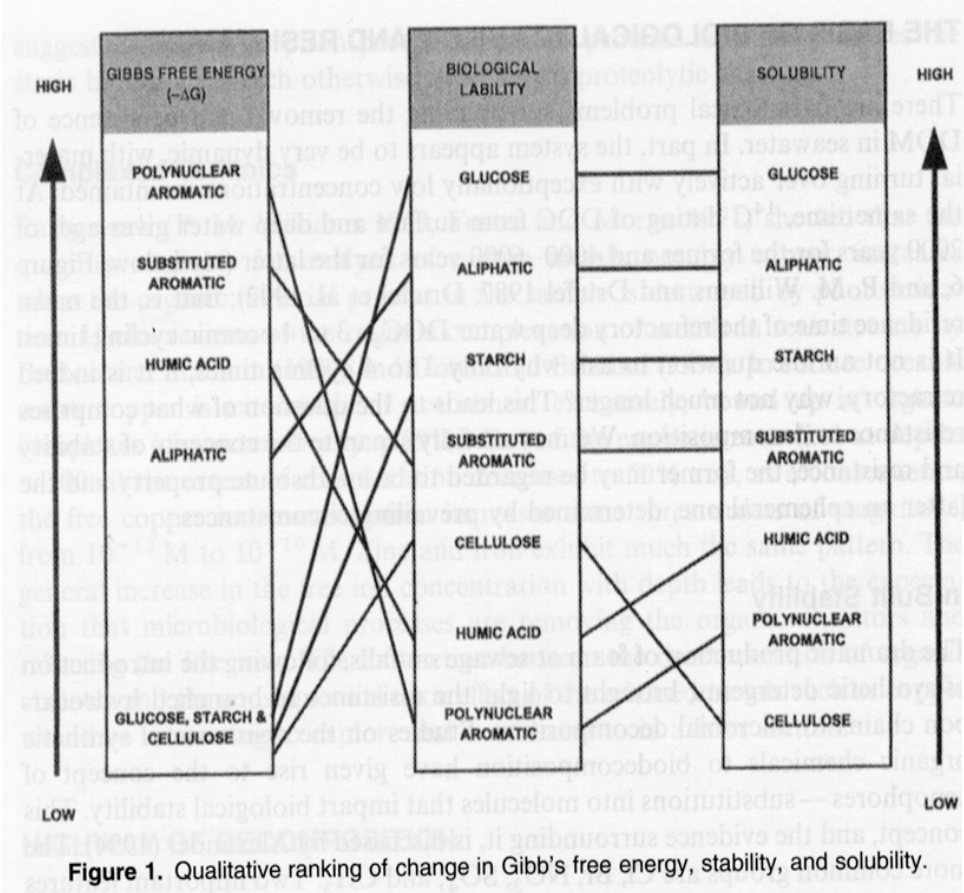


Figure 1. Qualitative ranking of change in Gibb's free energy, stability, and solubility.

Williams (2000)

Macro-molecule	Elements contained	Hydrolytic enzymes	Action	Comments
Structural carbohydrates	C	Glucosidases	Polymers to oligo- and monomers	Rate dependent on sugar moities, type of linkages (α,β), branching, water solubility of carbo-hydrates
Proteins	C,N,	Proteases	Polymers to oligo- and monomers	
Nucleic acids	C,N,P	DNA'ses, RNA'ses,	Polymers to oligo- and monomers	
		Nucleo-tidases,	Orthophosphate from monomers	Primarily cellbound to bacteria
		Alkaline-phosphatases	Orthophosphate from monomers	Inhibited by free orthophosphate

Methods of determining BGE

- **Bacterial uptake and respiration of "model" DOM substrates (^{14}C-labeled DOC).**
- **Estimate increases in bacterial biomass relative to utilization of ambient DOC.**
- **Measure bacterial production in conjunction with respiration (changes in O_2 and/or CO_2 over time).**

Tracing heterotrophic utilization of model substrates

TABLE 2. *Percentage respired of the total uptake of various substrates. All samples from the Dairy Pond, Raleigh, N.C.; counted by liquid scintillation*

Date	Compound	Samples	Concn (mg/liter)	Avg % respired of total uptake	SD	Temp (°C)
22 Mar						
	Glucose-6	8	variable	23.9	4.35	10
	Glucose-6	8	variable	24.2	3.59	25
	Aspartic acid-U	8	variable	58.3	4.94	10
	Aspartic acid-U	8	variable	56.7	8.43	25
12 Sep						
	Glucose-6	3	0.033	18.1	0.616	24
	Glucose-U	3	0.007	31.6	8.28	24
	Acetate-U	3	0.018	38.1	2.50	24
	Glutamic acid-U	3	0.196	61.3	0.79	24
	Aspartic acid-U	3	0.218	60.0	1.16	24
	Methionine-U	3	0.042	39.9	3.15	24
	Serine-U	3	0.143	31.7	1.82	24
	Tyrosine-U	3	0.329	29.7	1.55	24
	Glycine-U	3	0.006	28.0	0.70	24
	Proline-U	3	0.140	27.6	2.28	24
	Isoleucine-U	3	0.150	26.7	5.89	24
	Phenylalanine-U	3	0.237	26.7	4.33	24
	Alanine-U	3	0.041	26.3	1.09	24
	Threonine-U	3	0.222	26.2	6.94	24
	Leucine-U	3	0.197	25.6	0.14	24
	Valine-U	3	0.169	25.1	3.42	24
	Lysine-U	1	0.240	11.6	—	24
	Arginine-U	3	0.406	8.4	6.14	24
3 Oct						
	Aspartic acid-U	8	variable	46.8	7.80	24

Growth efficiencies range ~60-80% using these model DOM substrates.

Hobbie and Crawford (1969)

Examples of bacterial growth efficiencies on model DOM substrates in several marine ecosystems

Region	Substrate	BGE (%)
N.E. Atlantic, Mediterranean Sea	Amino Acids Glucose	66-87 51-76
North Sea	Amino acids Glucose	16-50 20-50
Coastal California	Amino acids	60-90

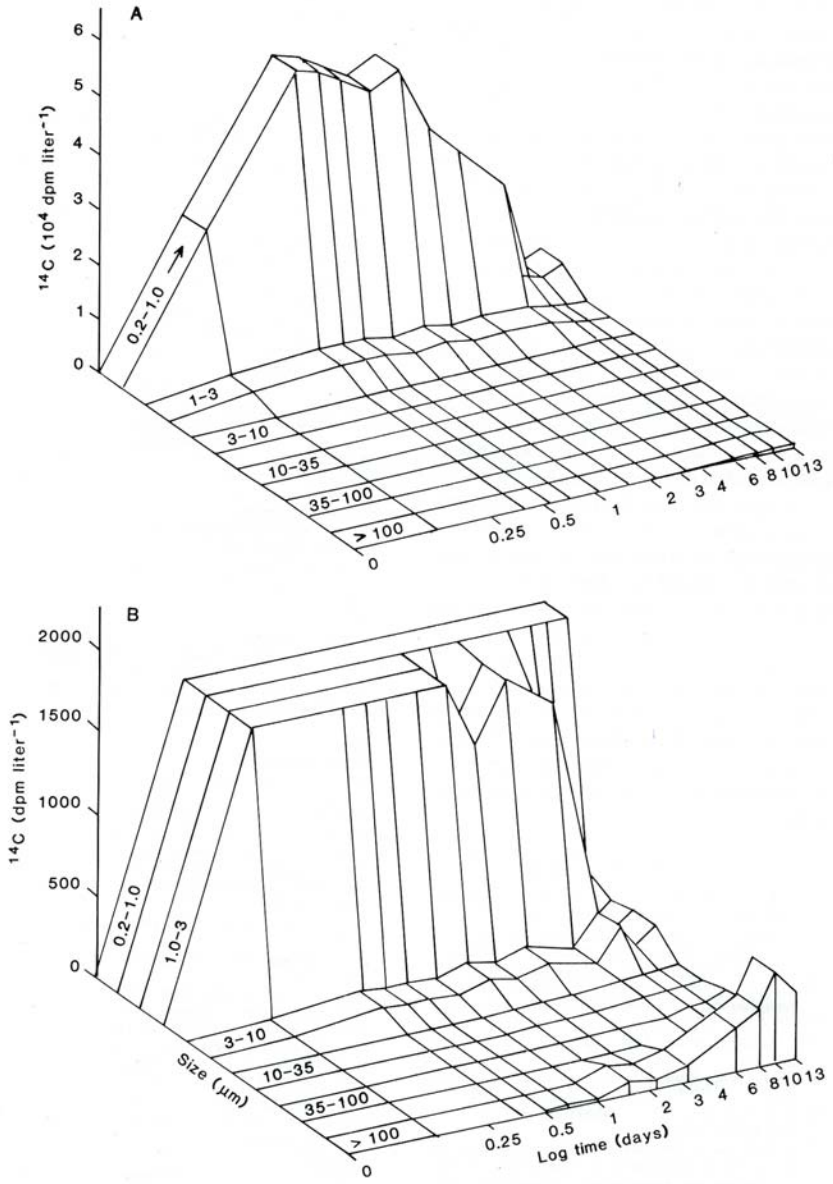


Fig. 2. (A and B) Redistribution of labeled carbon within the particulate pool at 5 m over the first 13 days of the experiment. (B) Rescaled version of the same data as in (A), showing only a very small, slow passage of label from the <1-μm bacterioplankton to larger organisms. With the whole-system data shown in Fig. 1, these results suggest that carbon removed from solution by the bacterioplankton did not pass to larger organisms, and instead was respired as CO_2 or released as DOC.

Ducklow et al. (1986)

Link vs Sink

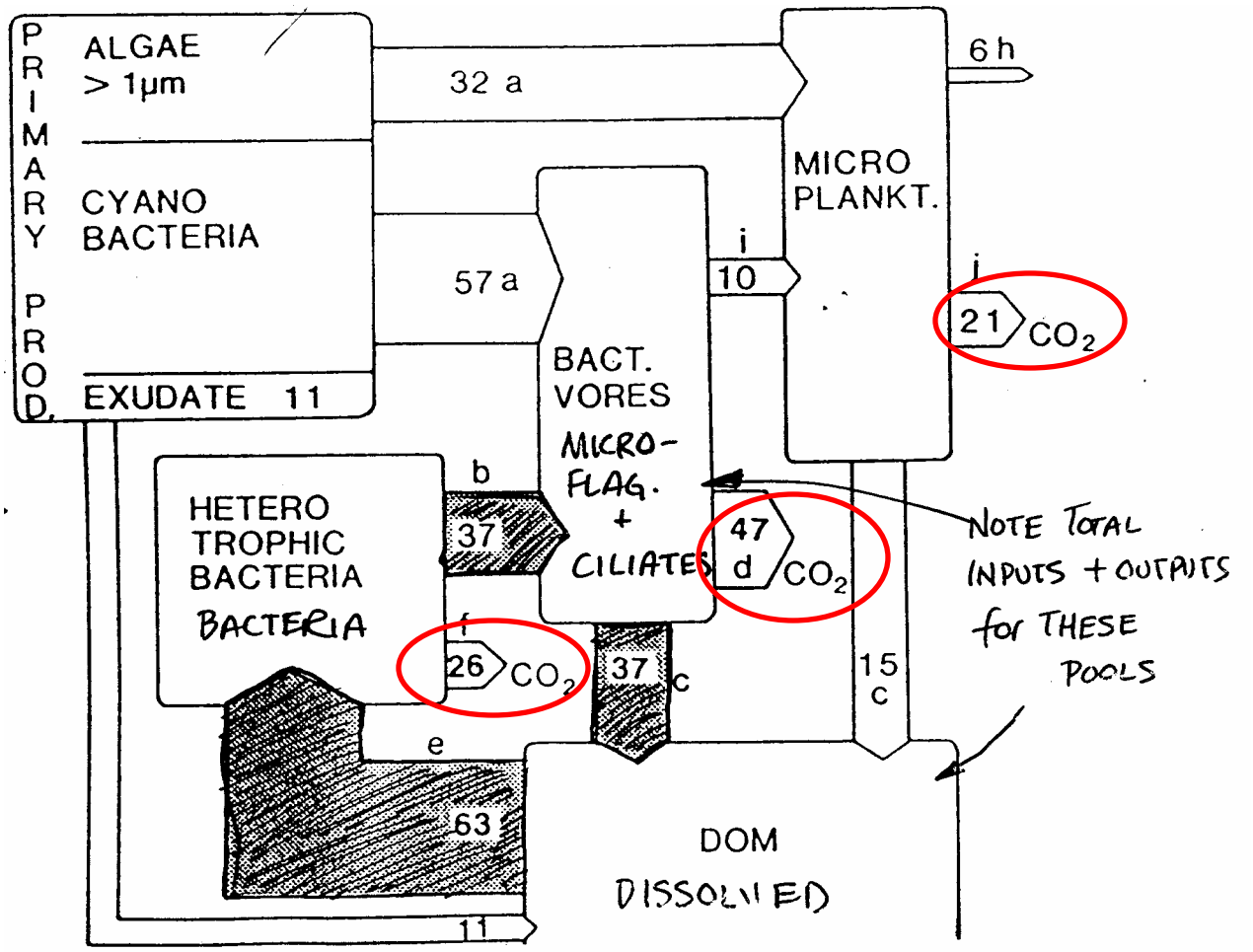
1. Measure growth efficiency.

2. Add ^{14}C DOM (glucose) and follow its transfer through the food web (into larger size fractions).

In this example, ^{14}C-glucose was added to seawater and passage of this DOC through the food web was monitored over time. Conclusion: very little of the DOC channeled into biomass passes to higher trophic levels—the vast majority is respired.

Bacteria appeared to be a SINK for carbon in this example.

Passage of organic carbon through microbial foods – losses at each trophic step



Hagstrom et al. (1989)

Carbon fluxes through an oligotrophic ocean food web. Note that 63% of the initial primary production passes to the DOM pool even with 89% of primary production removed via grazing. Also note that ~58% of the DOC uptake supports bacterial biomass and is available for trophic transfer—in this example, bacteria represent a link rather than a sink for carbon.

Measuring bacterial growth efficiency on naturally occurring DOC

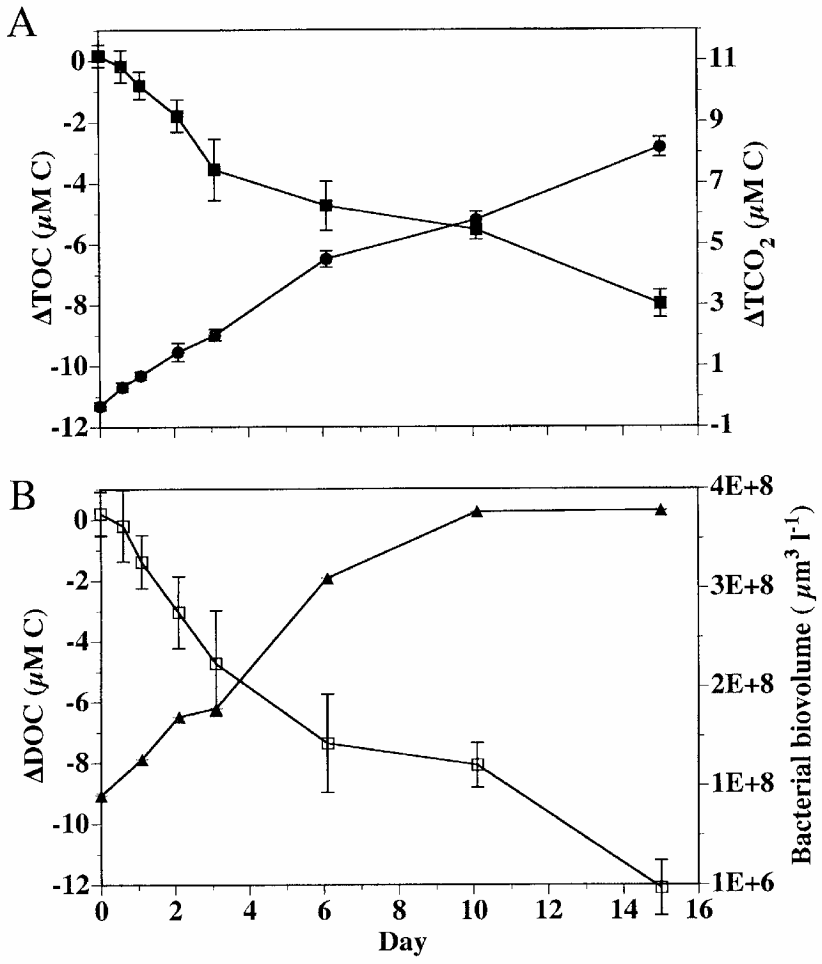


Fig. 3. AESOPS II bag 1 provides an example of time varying changes in (A) ΔTOC (■) and ΔTCO_2 (●) and (B) ΔDOC (□) and bacterial biovolume (▲). Error bars represent standard error of mean

Carlson et al. (1999)

Evaluating BGE based on changes in CO_2, DOC, and cell biomass. This approach requires eliminating the sources of DOM production in order to determine the net change over time.

BGE = ΔBB / ΔBB + ΔBR

or

BGE = ΔBB / ΔDOC

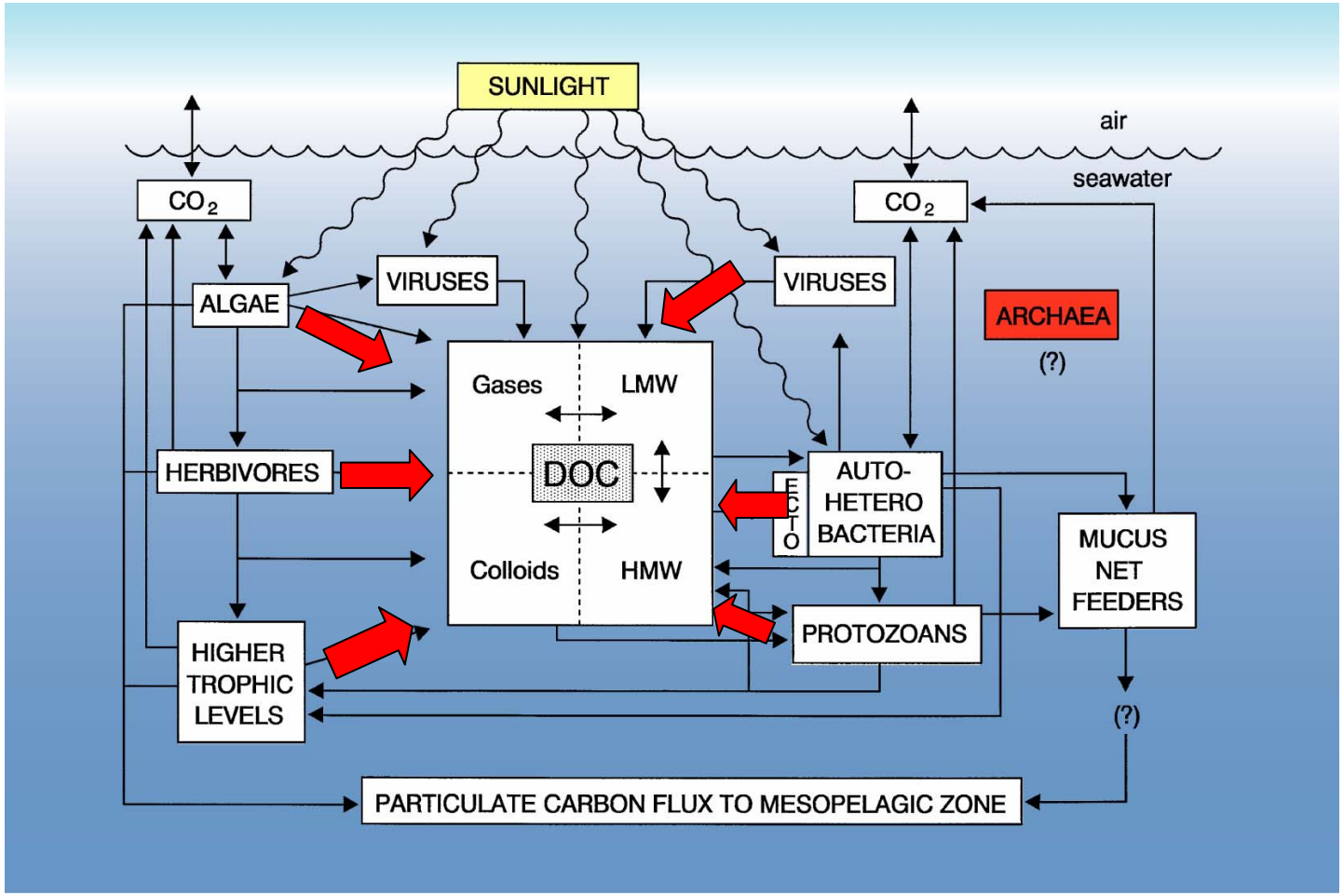
Estimates of BGE in various ocean ecosystems

Ecosystem	BGE (%)
Sargasso Sea	4-9
Coastal /Shelf waters	8-69
Central North Pacific	1-33
North Atlantic	4-6

Factors influencing BGE

- **Primary production**
- **DOM composition (compound classes and stoichiometry)**
- **Temperature**
- **Growth rate?? Several studies suggest μ is maximized at the expense of BGE.**

Sources of organic matter to microbial food webs



Contribution of different sources to marine DOC

Sources of DOM to ocean ecosystems

1. Direct algal excretion
2. Zooplankton (sloppy feeding, excretion)
3. Viral lysis
4. Bacterial release
5. Solubilization of POM

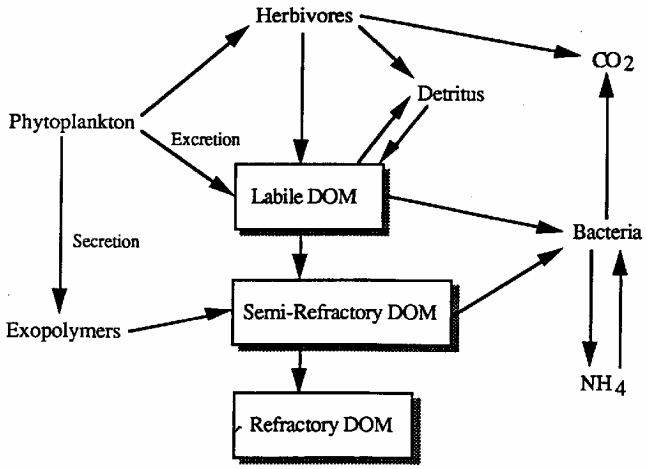
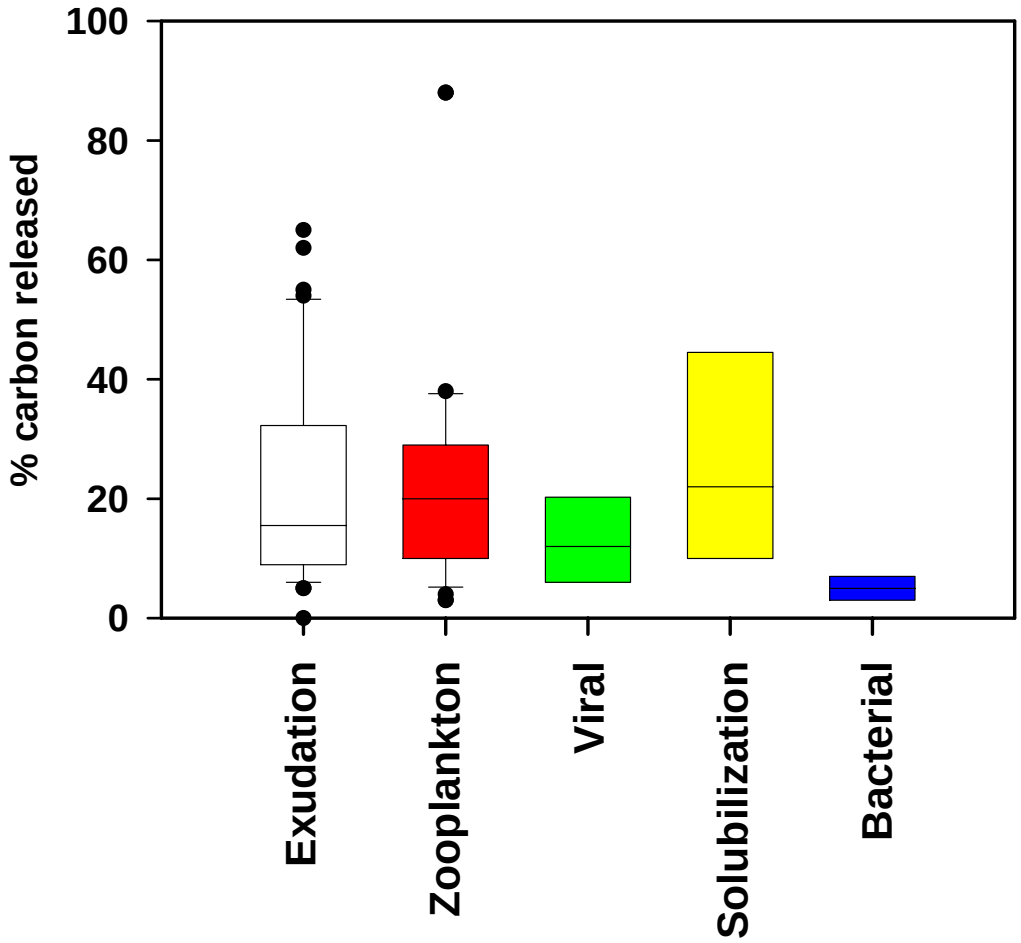


Figure 1 Three major pools of dissolved organic matter (DOM) and the processes contributing to them.



Exudation % ^{14}C primary production, zooplankton % carbon ingested, solubilization % C released from aggregates, bacterial % release from ^{14}C labeled organic substrate. Sources: Nagata (2001), Carlson (2002).

The source of the DOM influences BGE

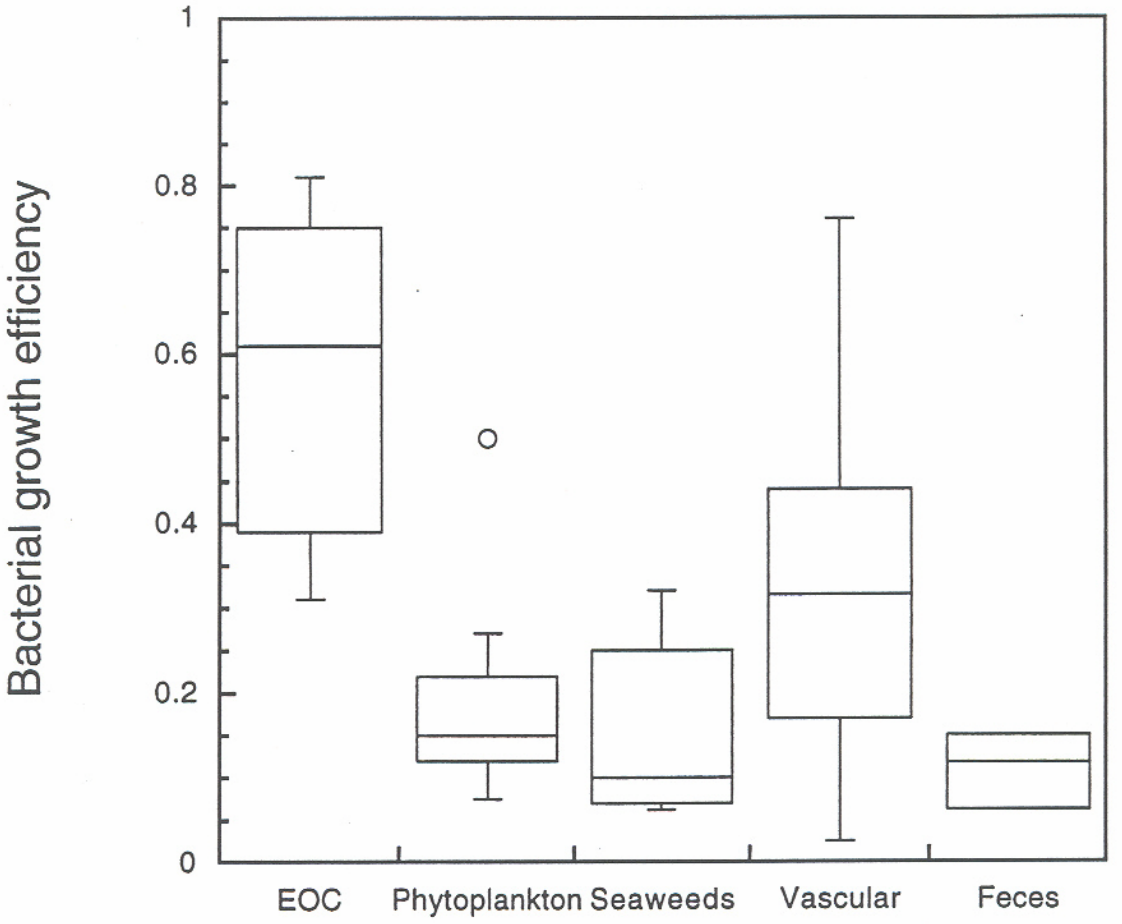


Figure 5 Summary of literature data on direct measurements of BGE for organic matter grouped according to source. Box-and-whisker plot shows median and upper/lower quartiles (box), and range of values (bars). Extreme outliers are marked as open circles. The sources of the data are in Table 2.

del Giorgio and Cole (1999)

Growth efficiencies vary widely depending on the DOC source. DOC exudates from actively growing cells appears to support higher growth yields (40-70%) than growth on cellular constituents. The source of the DOC partly determines its suitability as a growth substrate.

Substrate and temperature regulation of BGE

As C:N increases, BGE decreases – suggests N may limit bacterial growth

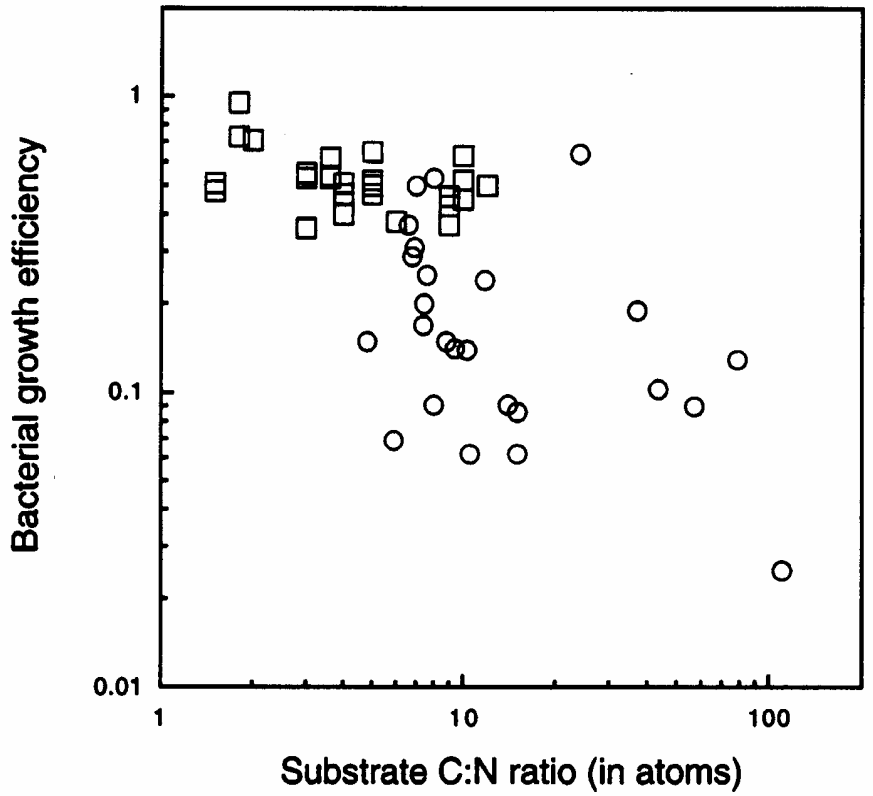


Figure 4 BGE as a function of the C:N ratio of the substrate. *Open circles* correspond to measurements of BGE on natural complex substrates. *Open squares* correspond to BGE in defined media (45, 46).

del Giorgio and Cole (2001)

BGE appears to have an inverse relationship with temperature.

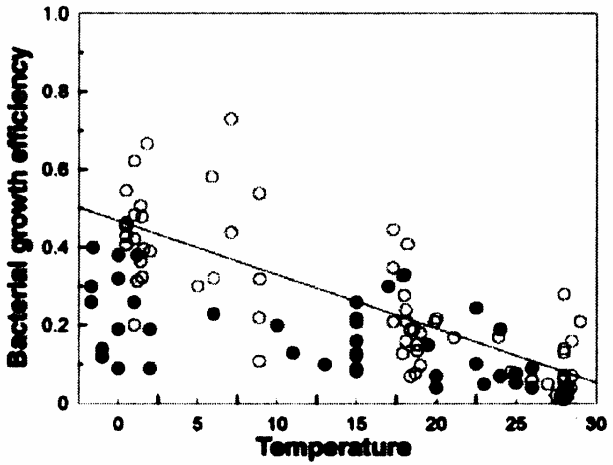


Fig. 1. Scatter plot of bacterial growth efficiency as a function of temperature for bacterioplankton from polar, temperate, and tropical oceans. Bacterial growth efficiency was determined from concurrent measurements of bacterial production and DOC uptake (open symbols) or of bacterial production and size-fractionated O_2 uptake (filled symbols). The ordinary least squares regression (regression line shown) between temperature (T) and bacterial growth efficiency (BGE) is: BGE = $0.374[\pm 0.04] - 0.0104[\pm 0.002]T$, ($r^2 = 0.54$, $n = 107$, $F = 84.27$, $P < 0.001$). Values in brackets are the 95% confidence intervals of the regression parameters.

Rivkin and Legendre (2001)

Bacterial growth efficiencies across aquatic ecosystems

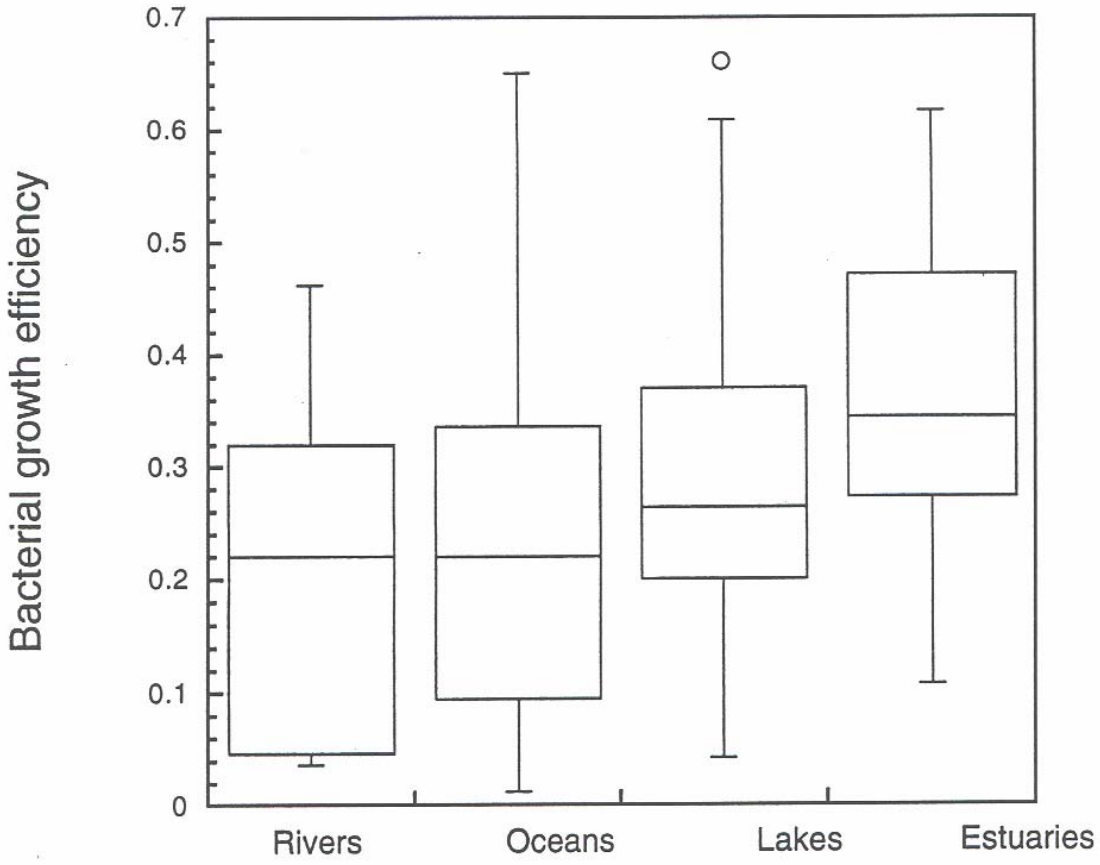


Figure 2 Summary of literature data on direct measurements of BGE in natural aquatic systems. Box-and-whisker plot shows median, and upper/lower quartiles (box), and range of values (bars). Extreme outliers are marked as open circles. The sources of the data are in Table 1.

del Giorgio and Cole (1999)

BGE in the open ocean ~10-30%. Growth efficiency tends to increase along a productivity gradient from oligotrophic to eutrophic environments.

BCD relative to PP (%) or

DOM uptake/Primary production (%)

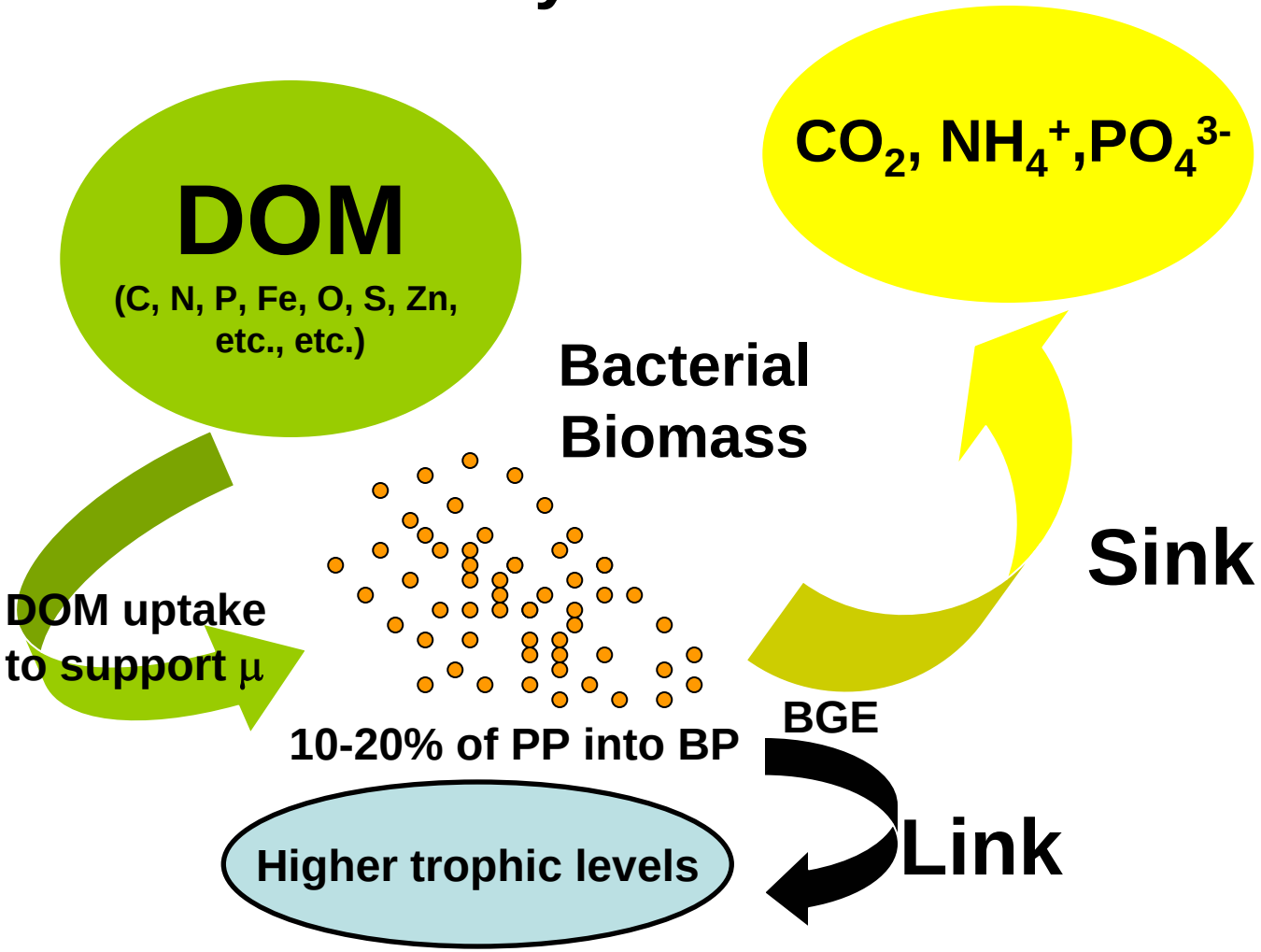
	BGE		
BP/PP	0.50	0.20	0.15
0.30	60%	150%	200%
0.20	40%	100 %	133%
0.10	20%	50%	67%

Initial estimates: BP/PP= 0.30 and BGE= 0.50

Current best guess: BP/PP= 0.20 and BGE= 0.15

Motivation

Bacterial growth regulates fluxes of carbon and nutrients, and dictates energy flow in marine ecosystems.



Main points of today's lecture

- **The total flux of carbon supporting bacterial growth includes respiration and production.**
- **Bacterial growth efficiencies in the open ocean range 10-30%, suggesting that 70-150% of particulate primary production sustains bacterial carbon demands, with the majority of this carbon respired.**
- **The role of bacteria in nutrient regeneration from DOM depends on the balance between substrate and biomass stoichiometry.**