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"Carbon Cycling in the Pelagic Ecosystem"

A. PUDDU
IRSA/CNR
Rome
Italy

Earth Systems Science Course in Watersheds & Coastal Zone Simulation Modeling

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Carbon cycling in the pelagic ecosystem

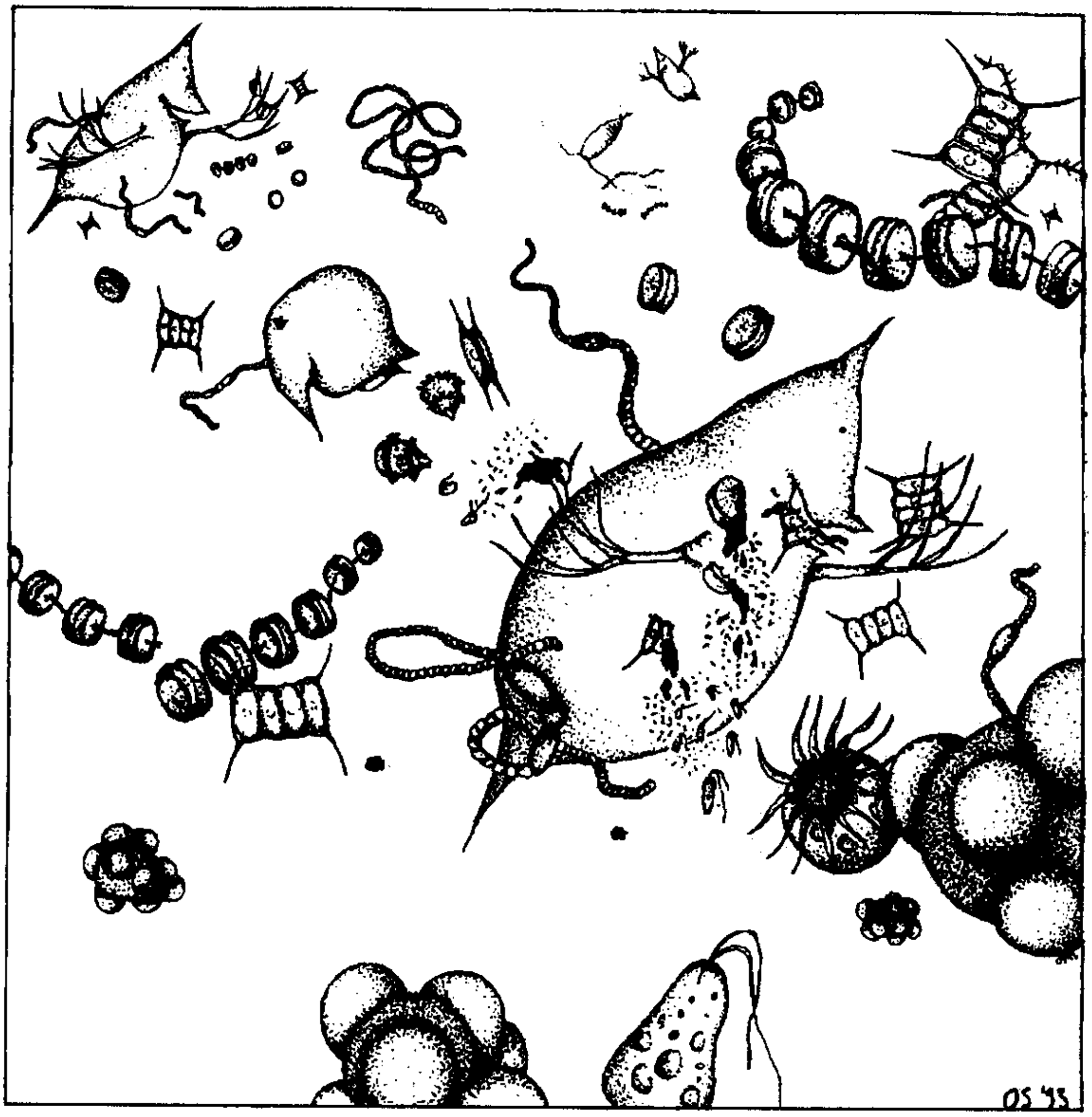
Alberto Puddu
Istituto di Ricerca Sulle Acque - CNR, Roma
puddu@irsa.rm.cnr.it

The ecological modeling needs various information regarding biological processes that are derived from *in situ* measurements or experiments in the lab

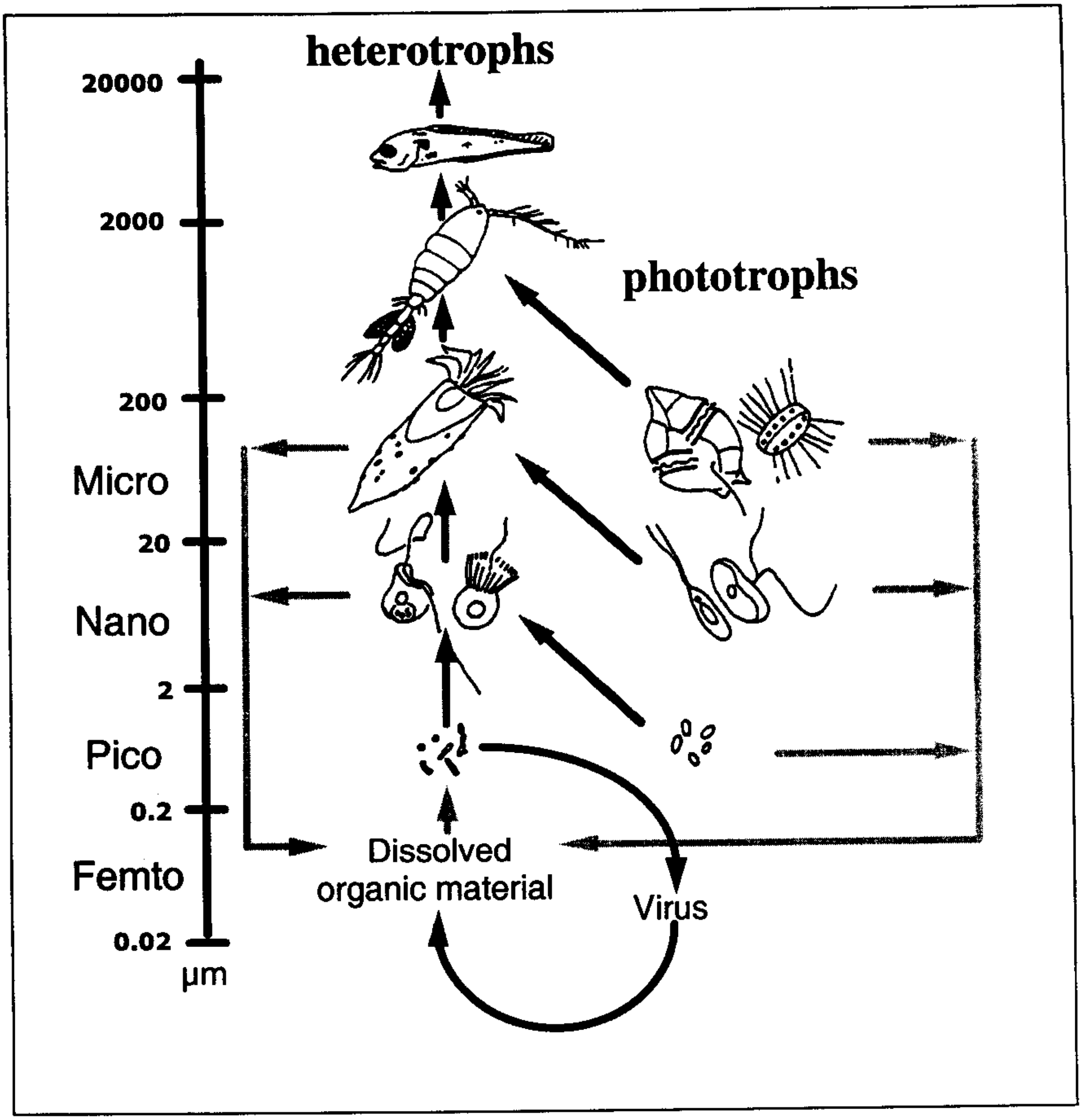
The need is for constant numbers applied to extended areas and periods

The main biological processes relevant to C and nutrients cycling, and, in general, to the ecosystem productivity, are:

- rates of primary productivity, affecting the particulate (POM) and dissolved organic (DOM) and inorganic matter (DIN, DIP)
- rates of bacterial productivity, affecting the dissolved organic (DOM) and inorganic matter (DIN, DIP)
- the grazing rates
- the efficiency in biomass transfer through the trophic chain



Many different organisms are living in the column water (fig.1). They are strictly interdependent, linked by trophic connections along the trophic chain.



Different size fractions of the marine microplankton

microplancton
nanoplancton
picoplankton
femtoplancton

Fueled by solar energy, the balanced cycle of photosynthesis and respiration is the driving force of nearly all life on Earth

The products of ***photosynthesis*** are the source of energy for nearly all life on Earth.
Through this process, land plants and phytoplankton convert the sun's energy to chemical energy.
The net reaction is:

$$6CO_2 + 12H_2O \xrightarrow{\text{Chlorophyll \& sunlight}} 6O_2 + C_6H_{12}O_6 + 6H_2O$$

The reverse of this reaction is ***respiration***, a process carried out by all organisms, plants, bacteria and humans alike, that live in environments where molecular oxygen is present.
Energy is released in respiration, and this energy drives the biochemical reactions that constitute living systems

The Redfield Ratio

Phytoplankton to grow and reproduce, requires C, light and inorganic nutrients, particularly N & P The living biomass is then transferred to the higher levels of the trophic chain

The elemental composition of plankton "protoplasm" is relatively invariable:

106C : 16N : 1P

(by atoms)

276 atoms of O2 are required to completely oxidize (regenerate) organic matter to CO2, inorganic N & P

the equation for the oxidation of plant material

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

The amount of dissolved C, N & P in seawater, known to vary enormously in absolute concentration from place to place, should vary in a **constant proportion**

The pelagic bacteria

They exist

(1970s →, epifluorescence microscopy and fluorochrome stains: AO & DAPI)

They are:

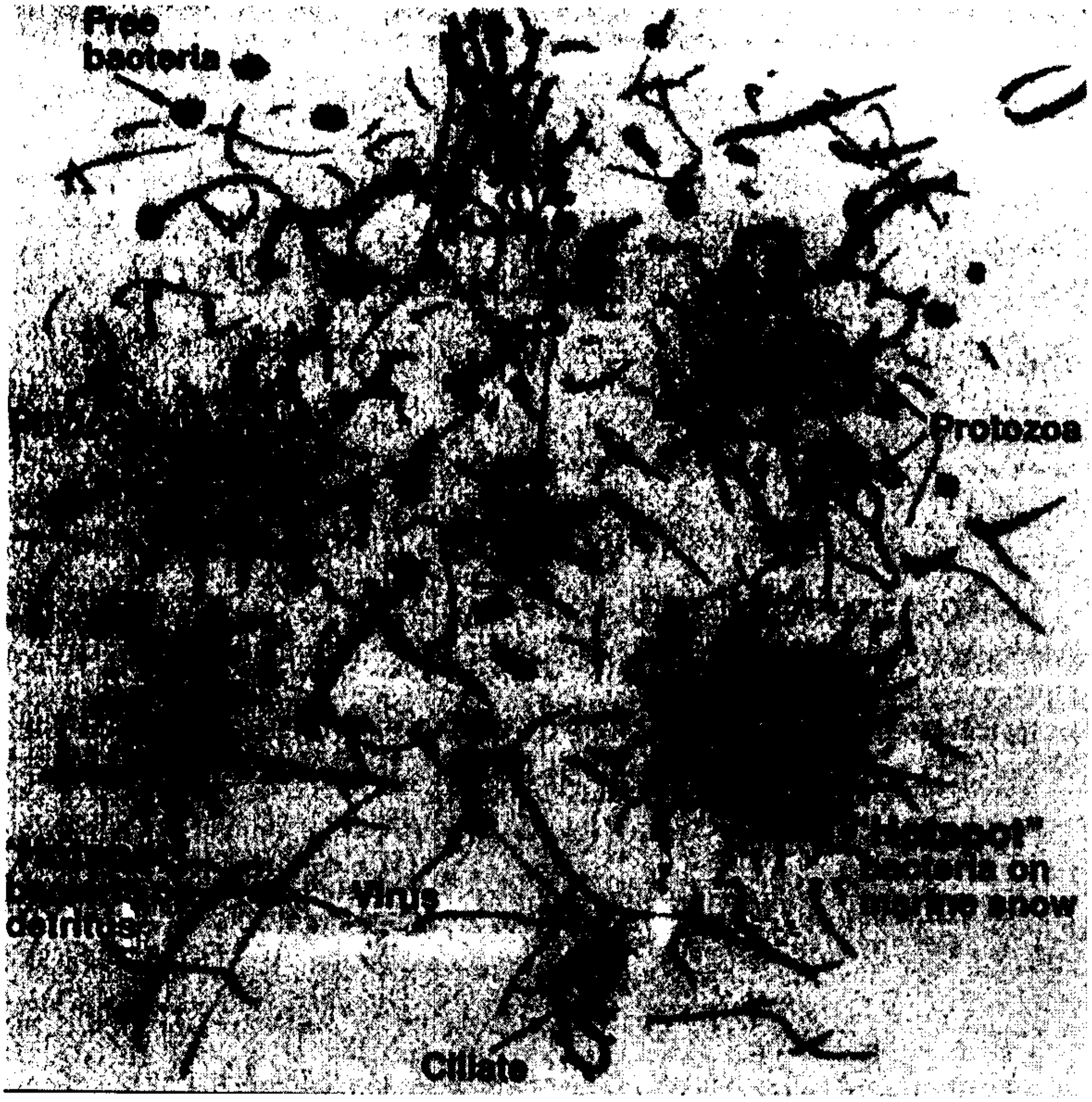
- small in size:
  (0.004-0.1μm^3)
- very abundant:
  10^9/L (1000 x phyto)
- there activity is relevant:
  0.01-10μgC/Lh (0.1-0.2 phyto)

The environment of marine bacteria

in a single µL of water:
- 1 algal cell
- 1000 bacteria
- 1-10 cyanobacteria
- 1 detritus particle
- 1 heterotrophic microflagellate
- 10^9 to 10^{12} molecules

in terms of C, in the same µL:
- 0.1 ng POC (1000µm distant)
- 1 ng DOC (only 50pg are immediately utilizable)

1 bacteria = 20fgC



A bacteria-eye view of the ocean's euphotic layer (from Azam, Science 1998)

Seawater is an organic matter continuum, a gel of tangled polymers with embebbed strings, sheets, and bundles of fibrils and particles, including living organisms, as "hotspots".

Bacteria (red) acting on marine snow (black) or algae (green) can control sedimentation and primary productivity; diverse microniches (hot spots) can support high bacterial diversity.

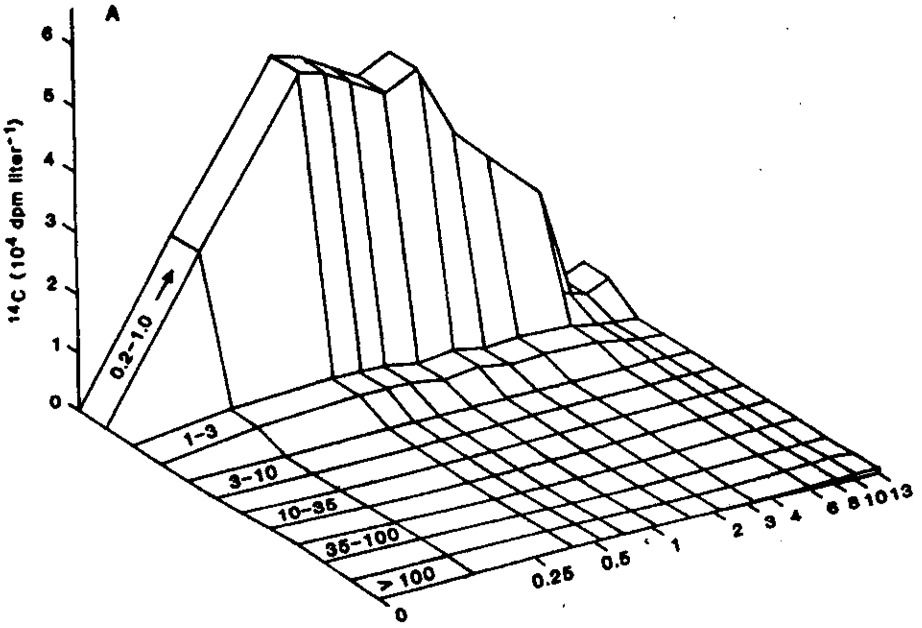
The Microbial Loop

(Azam et al. 1983)

Consortium of mechanisms whereby **O**rganic **C**arbon is diverted as **D**issolved **OC** from the upward flux of **P**articulate **OC** toward higher trophic levels and recycled to the bottom of the food chain

Bacterioplankton: a sink for C and not a link to higher orders consumers via a microbial loop

(Ducklow et al., Science 1986)



Experiment on a 300m^3 mesocosm

Results:

only a small amount of radiotracer initially fixed by the freeliving bacterioplankton was subsequently detected in size classes larger than 1μm;
at no point the Authors observed in the total POC larger than 1μm more than 4% of the label initially added to the system;
the major proportion of glucose carbon is fixed by bacteria and passed directly to CO$_2$ or to reformed DOC.

Conclusion:

bacteria are important principally as regenerators rather than as food for larger consumers.

What do bacteria eat ?

they are the only users of DOM

they can directly adsorb only small molecules (< 600 Dalton)

they must hydrolize bigger molecules

they can also hydrolize POM

DOC sources

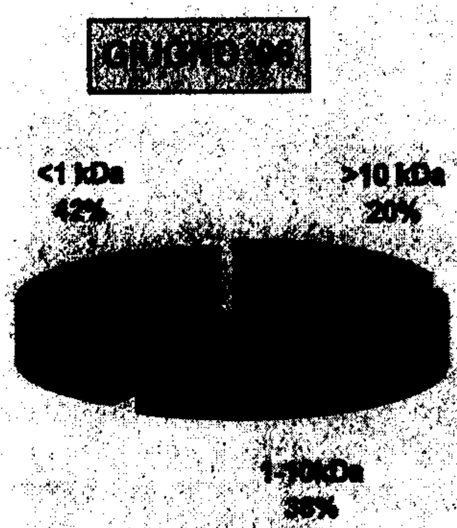
autochtonous

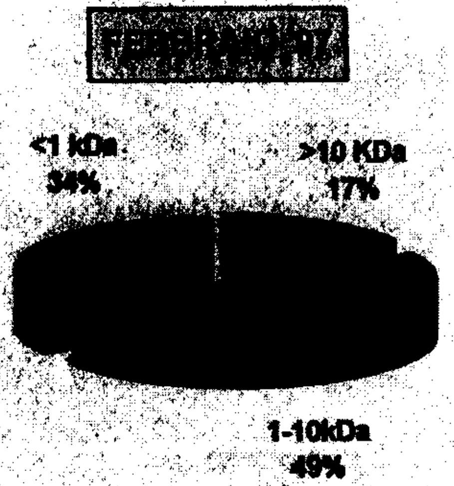
- **primary production**
- **grazing activity (sloppy feeding, etc.)**
- **viral lysis**

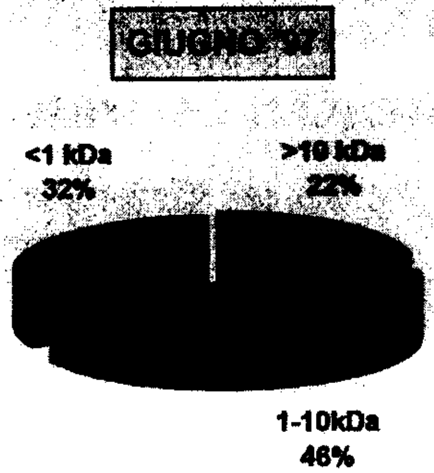
allochtonous

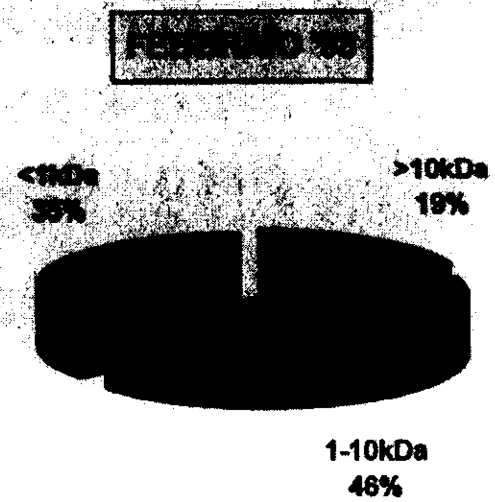
- **riverine inputs, whose distribution is influenced by water circulation**

DOC distribution in different size molecular fractions in the Northern Adriatic









Relevant questions ?

1) how much POM is diverted to DOM

2) how efficiently bacteria incorporate DOC

3) what controls bacterial DOM uptake

How much POM is diverted to DOM ?

- **release of DOM by phytoplankton**:

direct Photosynthetic Extracellular Release (**PER**) range 5-40% (Lignell 1993) with an average of 13% (Nagata 2000)

mechanisms: overflow and leakage

- **release of DOM by grazers (Nagata 2000)**:

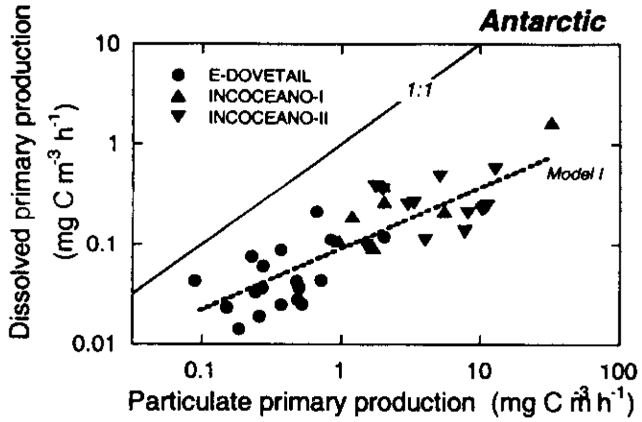
protozoa release as DOM 10-30% of ingested OM (small phytoplankton and bacteria)
metazoa (zooplankton) release as DOM 10-20% of ingested DOM (large phytoplankton)

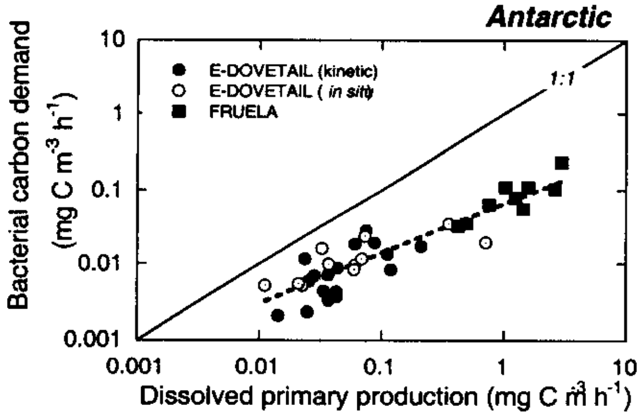
mechanisms: sloppy feeding, egestion of incompletely digested or unassimilated material, excretion of organic metabolites, fecal pellets (only zooplankton)

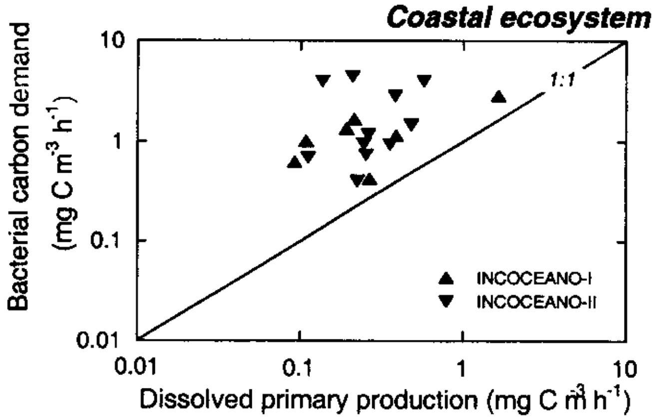
- **release of DOM mediated by viral infection**:

40% of host cell C during the declining phase of a phytoplankton bloom (Gobler et al. 1997)

About 50% of daily photosynthetic production is released as DOM





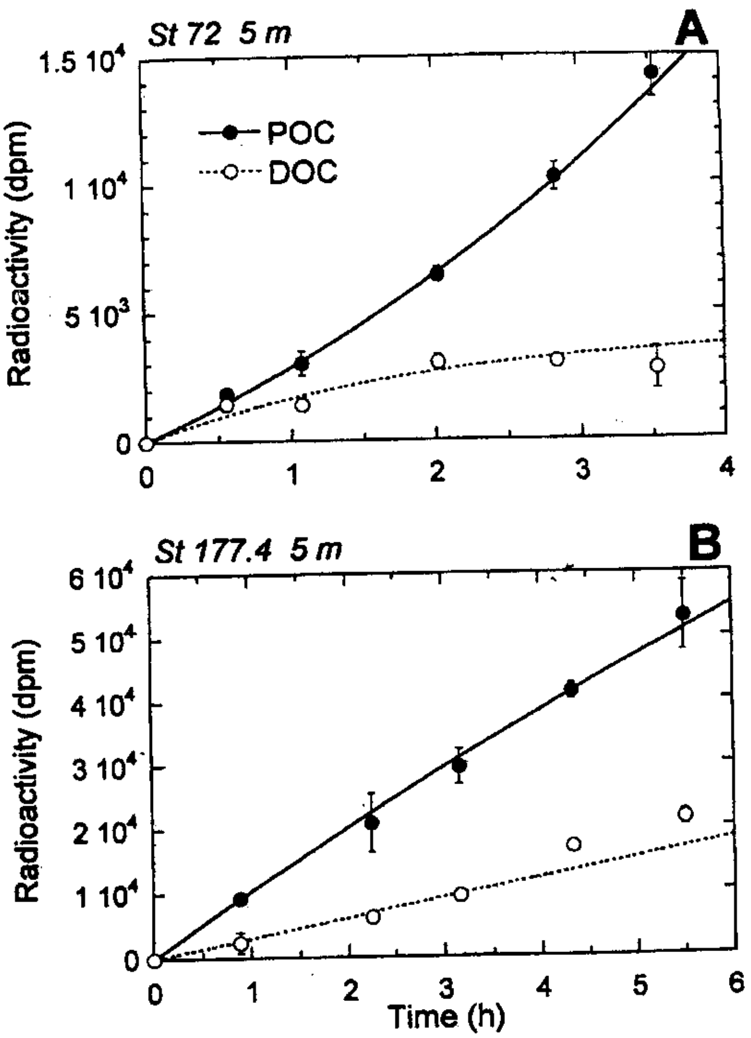


Morán et al. (submitted & in prep.)

DOC photosynthetic production correlates positively with POC production, with the percent extracellular release (PER) ranging 5-33%

In Antarctic waters, where PP is the only primary DOC source, BCD is strongly coupled with PP

In coastal waters, where other allochtonous DOC sources exist, BCP and PP are uncoupled



Time-course of labelled POC and DOC in different exeperiments. Particulate and dissolved C production can follows linear or non-linear patterns

(Moran & Estrada, in press)

How efficiently do bacteria incorporate DOC?

when transforming OM, bacteria:

- **produce new bacterial biomass (BP)**
- **respire organic C to inorganic CO_2 (BR) and remineralize nutrients**

Metabolic energy is expended for both processes.

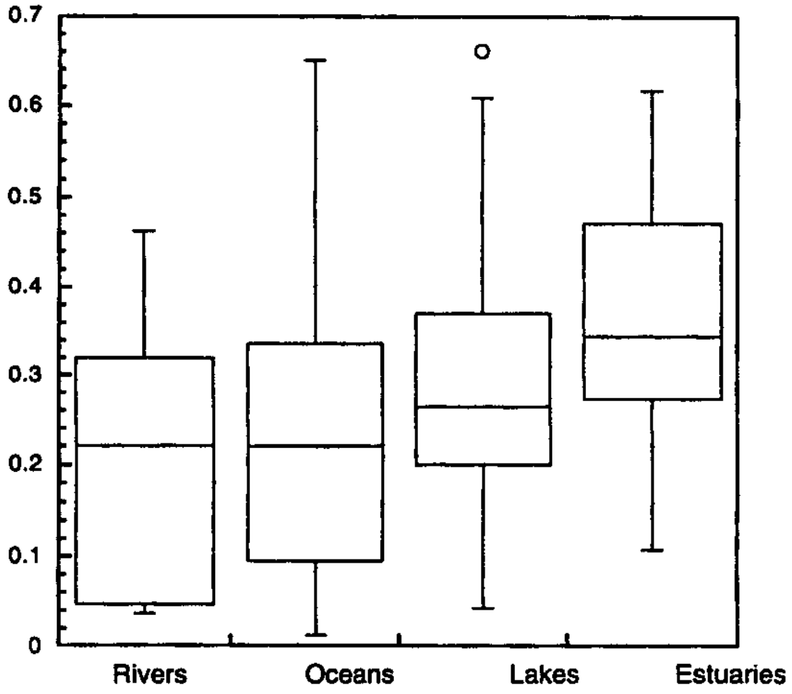
$$\frac{BP}{BP+BR} = BGE$$

Bacterial Growth Efficiency is the amount of new bacterial biomass produced per unit of organic C substrate assimilated.

Energy requirements are related to concentration, variety and nature of exogenous substrates as well to growth rate.

When growth is constrained by the supply of organic substrate or inorganic nutrients (both quantitative and qualitative) the BGE is reduced.

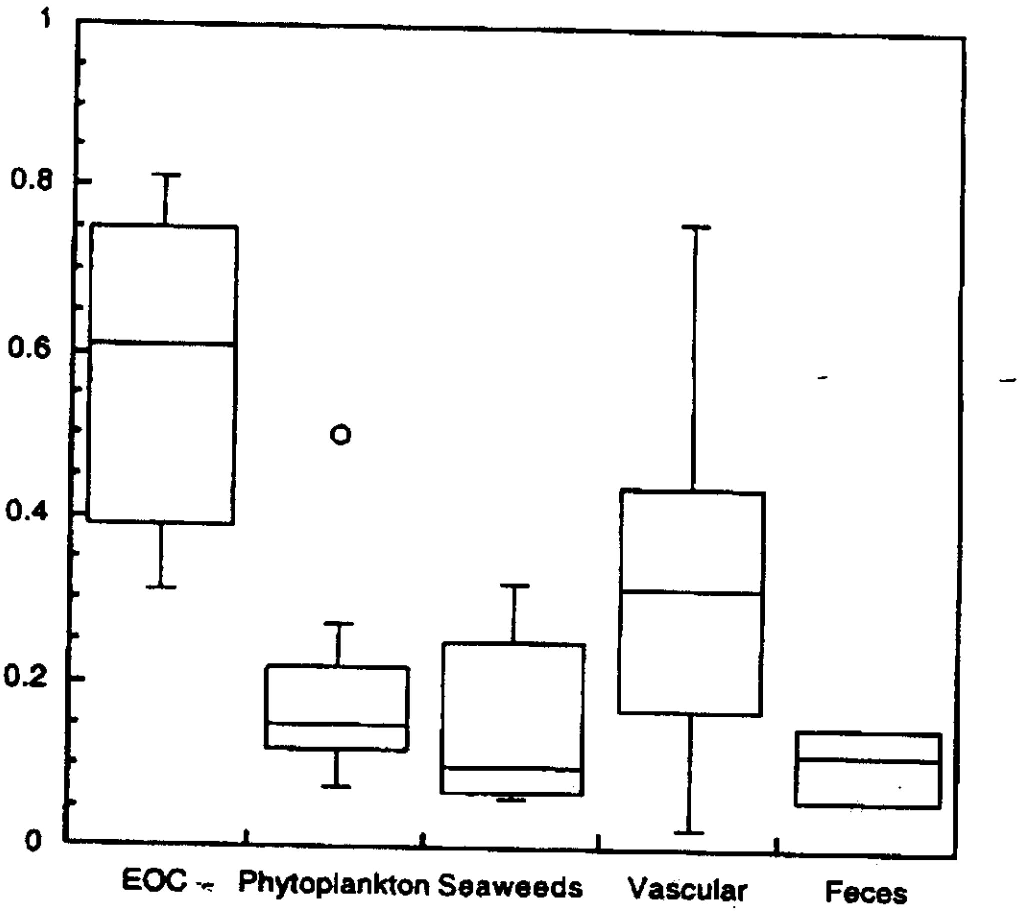
Maintaining the highest possible flow of energy would be advantageous even in conditions of severe constraints to growth for a rapid resumption of growth whenever environmental conditions change



Summary of literature data on direct measurements of BGE in natural aquatic systems, ranging from <0.05 to as high as 0.6.

BGE increases from marine areas to estuaries.

(Del Giorgio & Cole, 1998)

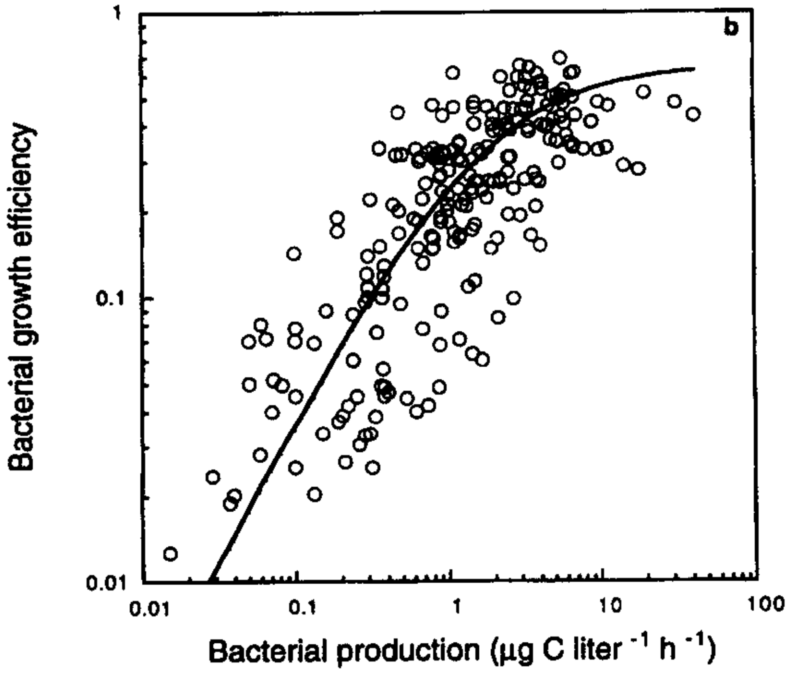


Summary of literature data on direct measurements of BGE for organic matter grouped according to the source.

The efficiency of conversion of detrital OM to bacterial biomass is generally low (<30%) for all categories except OM excreted by phytoplancton.

High bioavailability does not necessarily imply high BGE.

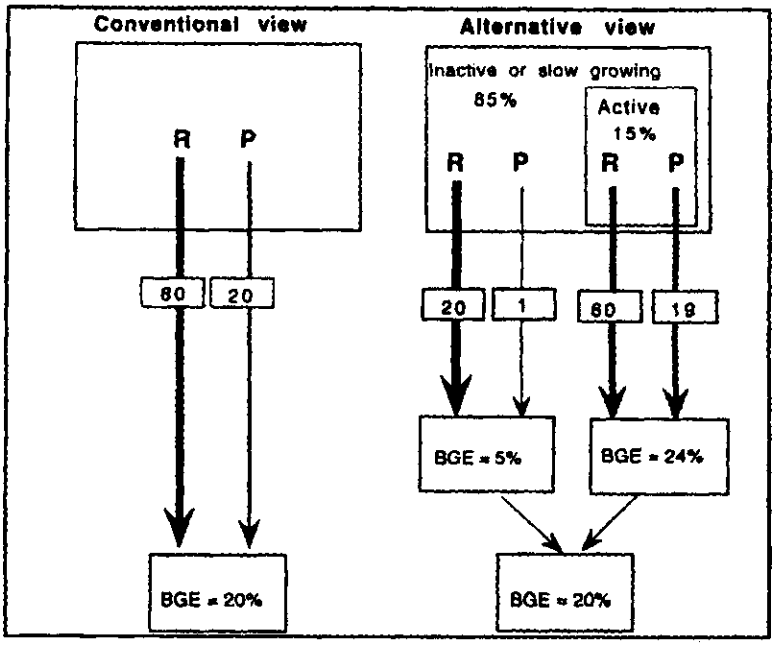
(Del Giorgio & Cole, 1998)



The pattern of increasing BGE vs increasing BP (positively correlated to primary production) describes a tendency for increasing BGE along trophic gradients of productivity in aquatic systems.

The large amount of variance in BGE for any given value of BP is the result of a large degree of uncoupling between bacterial production and respiration.

(Del Giorgio & Cole, 1998)



The bacterioplankton assemblage is composed both of highly active and growing bacteria (often a minor fraction) and dormant, slowly growing and even dead cells.

BGE commonly measured is the average of the BGE values of different subpopulations of bacteria.

The proportion of highly active bacteria increases along productivity gradients.

(Del Giorgio & Cole, 1998)

what controls bacterial DOM uptake?

main factors controlling bacterial activity are:

- temperature
- grazing (top-down control)
- virus (side-in control)
- substrates availability (bottom-up control) in terms of both quantity and quality

bottom-up control exerted by the substrate quantity

bacteria (45:9:1) needs more N & P than phytoplankton (106:16:1)

The elemental chemical composition of the <u>phytoplankton</u> biomass (Redfield Ratio)

106C : 16N : 1P

(by atoms)

The elemental chemical composition of the <u>bacterial</u> biomass (Goldman Ratio)

45C : 9N : 1P

(by atoms)

bacteria (> surf/vol) are better competitors for mineral nutrients than phytoplankton

bottom-up control exerted by the substrate quality

Bioreactivity strongly influences the uptake. The DOM pool includes molecules with highly variable reactivities.

In oceans the relative reactivity of different molecular size classes is:

POM > HMW DOM > LMW DOM

with LMW molecules representing the principal component of refractory DOC, 4000-6000 years old.

In eutrophied waters LMW, mainly composed of molecules freshly realeased, is highly bioreactive.

The incorporation efficiency (BGE) is influenced by the energy content of any specific organic molecule in the DOC pool.

The oceanic DOC pool: only a small amount of DOC is bioavailable

(Carlson & Ducklow, Deep-Sea Res. 1995)

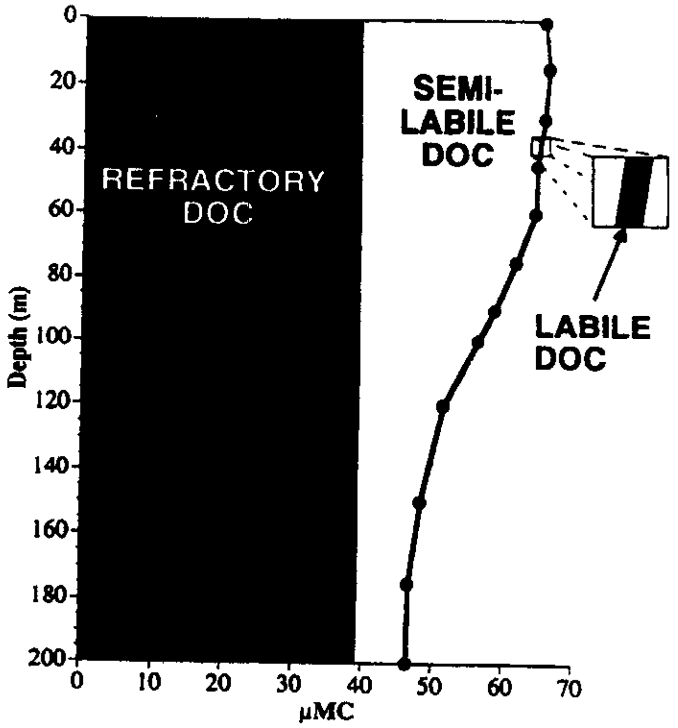
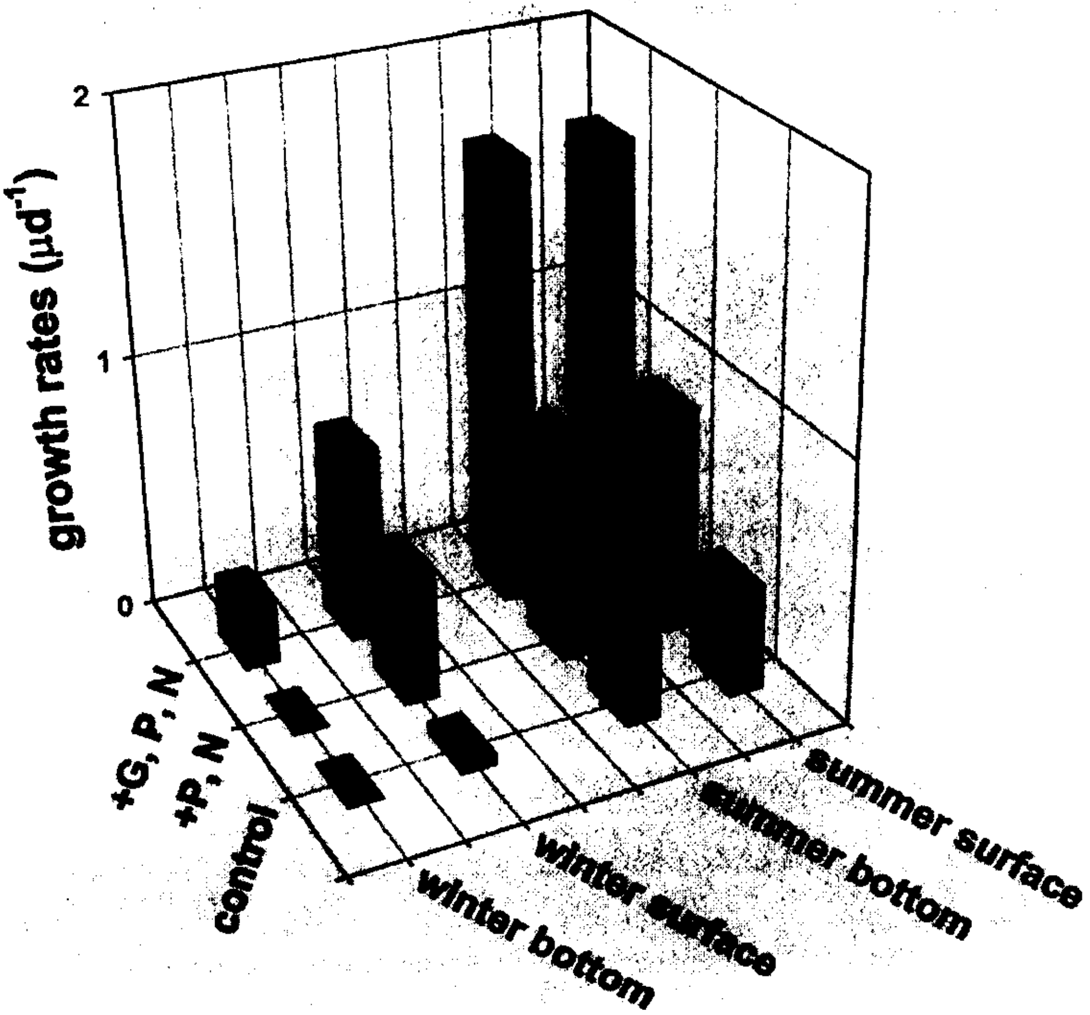


Fig. 6. Diagram of bulk DOC pool partitioned into refractory pool, semi-labile pool and labile pool.

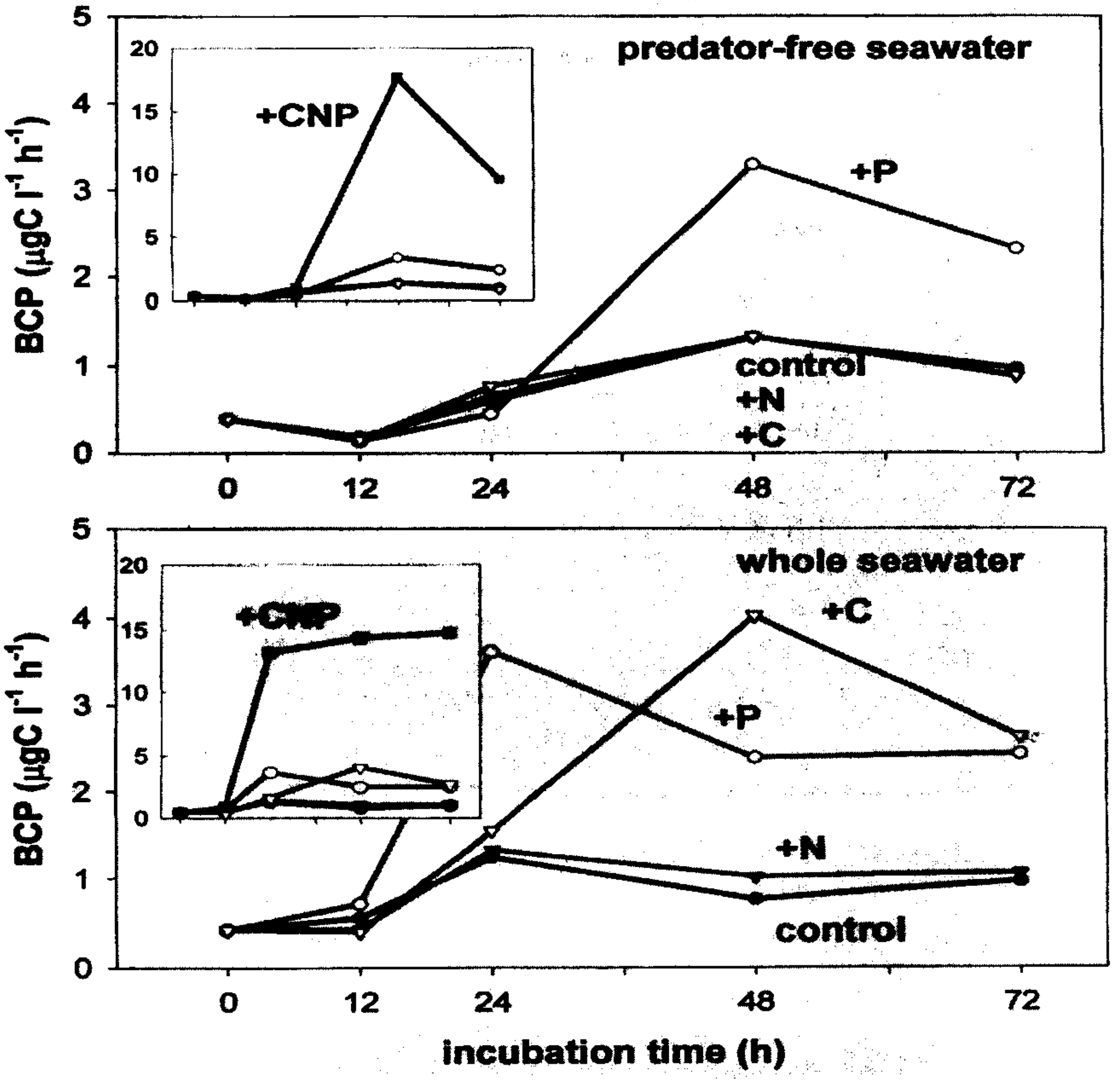
- DOC concentration in deep waters (>500m) is relatively constant (39.5μM C) indicating that this DOC is comprised of biologically resistant material
- assuming an equal distribution of this recalcitrant material throughout the water column, this is ~70% of bulk DOC in the upper 200m
- the remaining DOC consists of semi-labile portions which turn over on time scales of months to years and a small percentage (≤5%) comprised of labile DOC which turns over on the scale of hours to days



winter							
Feb. '97	st.12	-1m	36.0 psu	10°C	10^7 phyto	90µM DOC
	st. 5	-11m	34.3 psu	10°C	10^7 phyto	106µM DOC
summer							
June '97	st.19	-1m	37.3 psu	14°C	10^5 phyto	88µM DOC
	st.10	-23m	36.1 psu	22°C	10^6 phyto	103µM DOC

An example, from Northern Adriatic waters, of C or/and n&P limitation

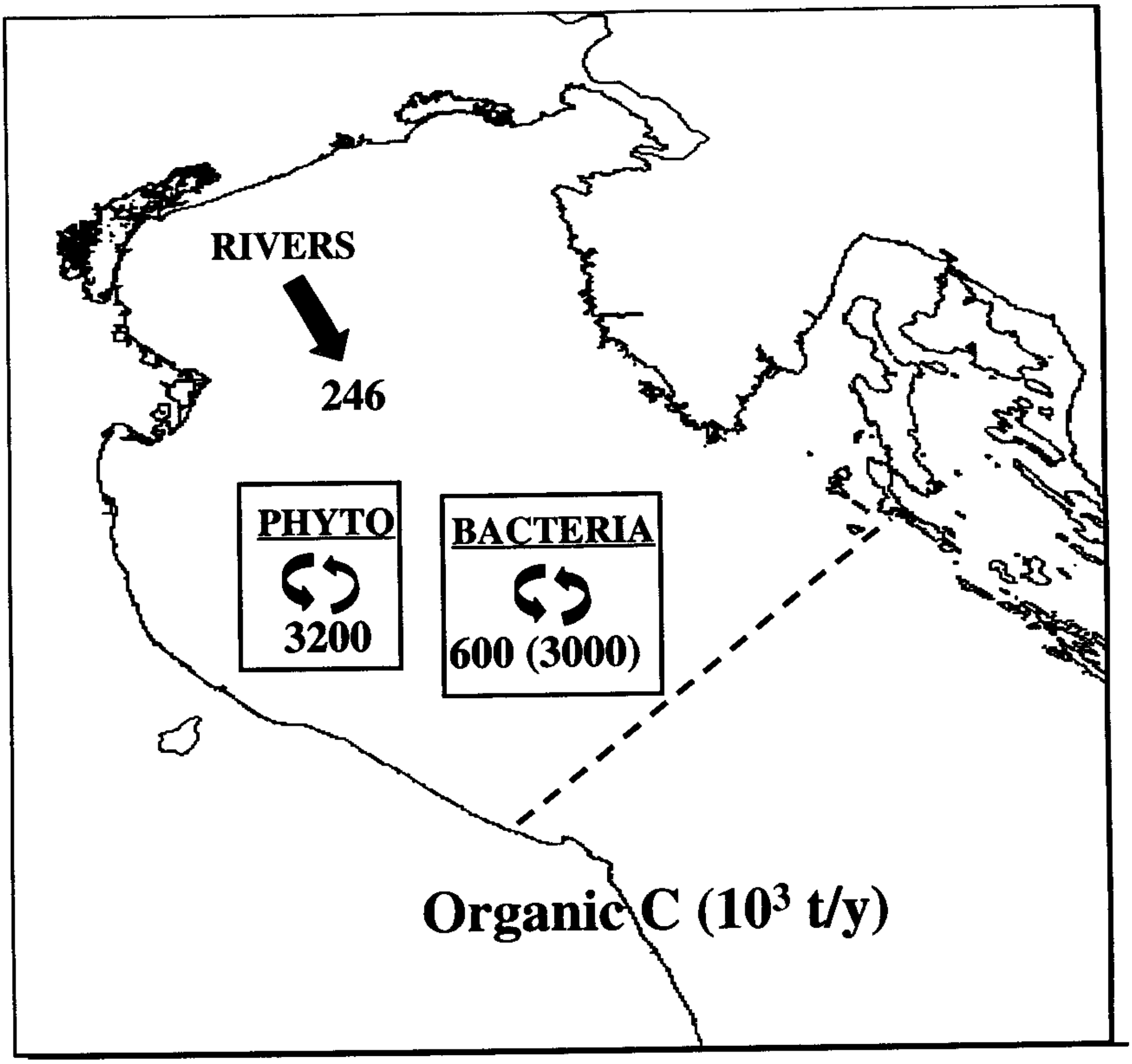
October 29, 1998



additons: +1.5 µM PO_4 + 8 µM NH_4 +125 µM Glucose
C:N:P = 80:5:1

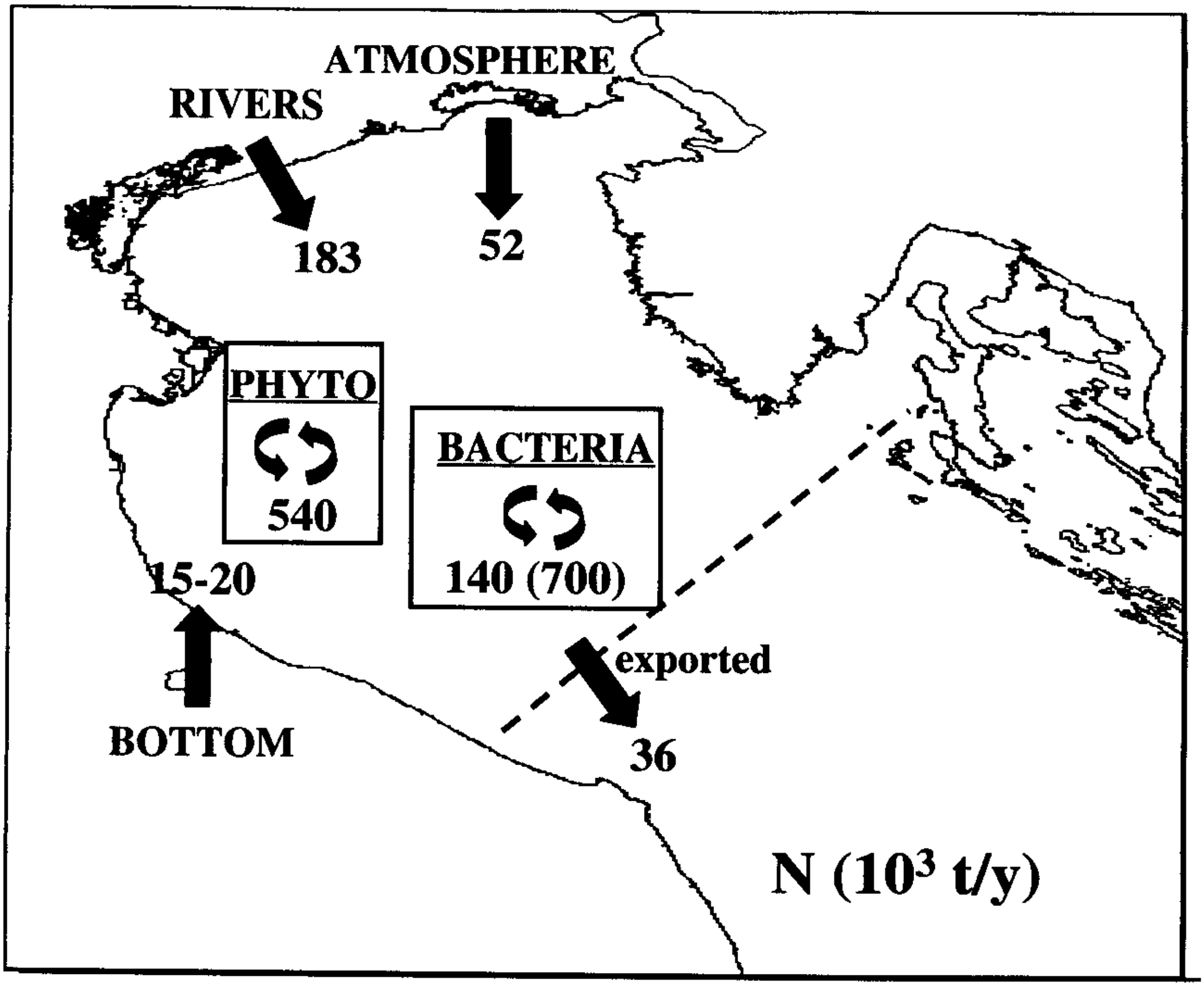
sampling: -5m 35.9 psu 19°C 112µM DOC

- **P limitation can control bacterial activities**
- **bacterivorous grazers stimulate P turnover**



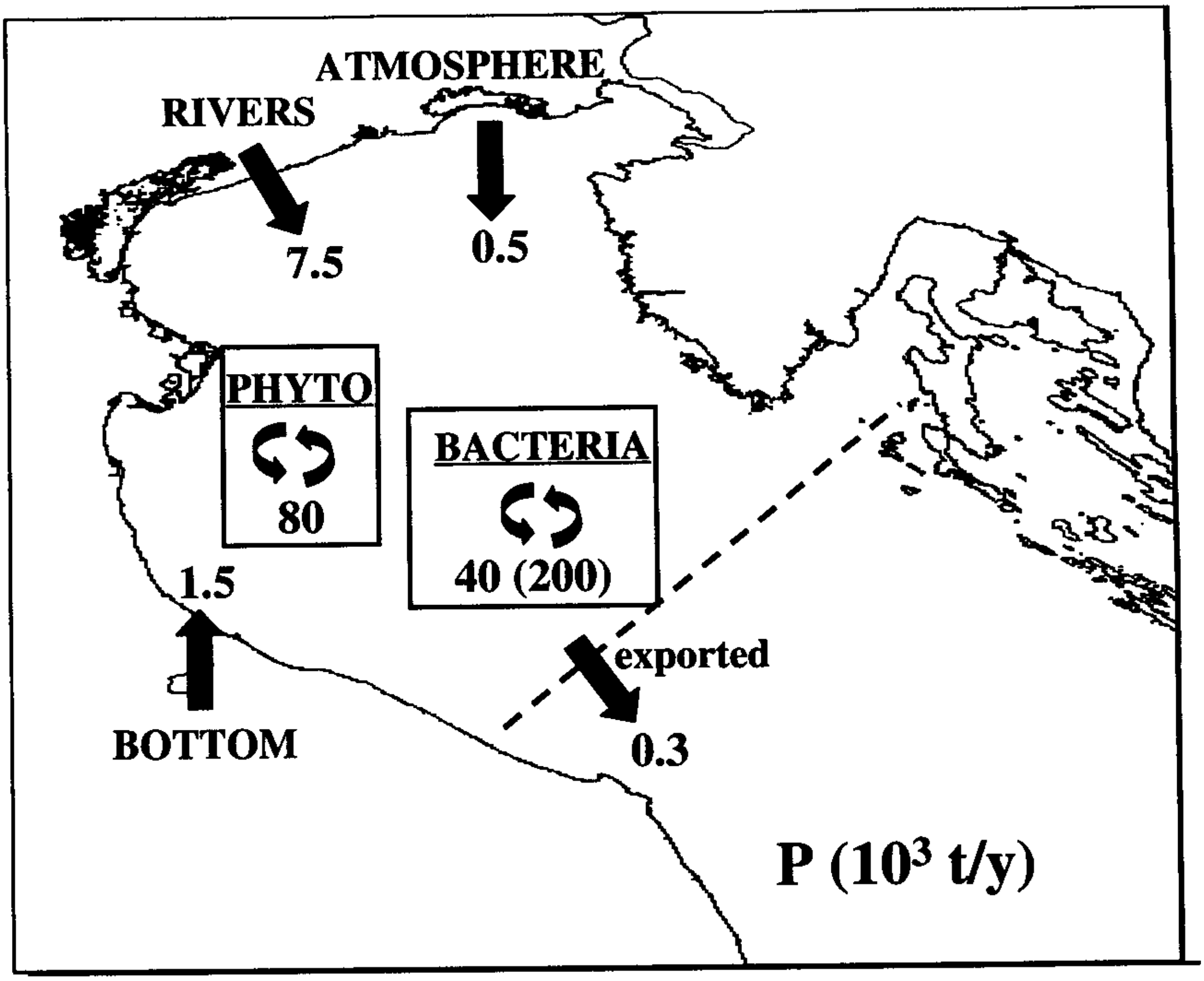
Annual OC inputs to the Northern Adriatic basin & C fluxes through fito- and bacterioplankton

rivers: measured as TOC (DOC is 50%)
phyto: estimated from PP measurements
bacteria: estimated from BCP, in brackets BCD



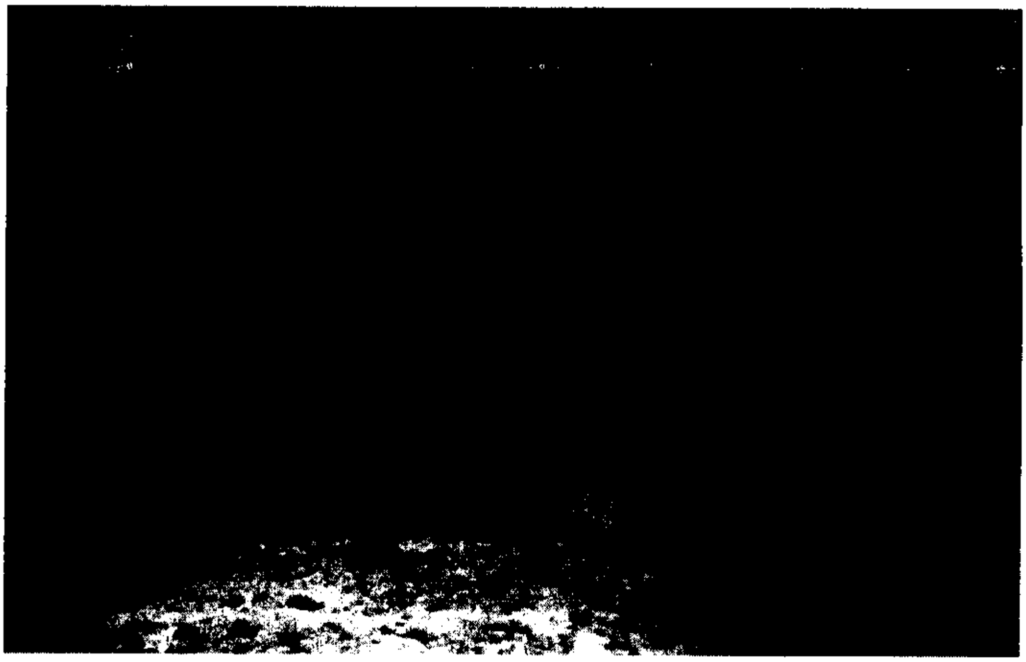
Annual N inputs to the Northern Adriatic basin & fluxes through fito- and bacterioplankton

rivers:	TN (DIN is 80%)
atmosphere:	TN
bottom:	$N\text{-}NO_3 + N\text{-}NH_3$
exported:	DIN
phyto:	estimated from fixed C
bacteria:	estimated from BCP and BCD



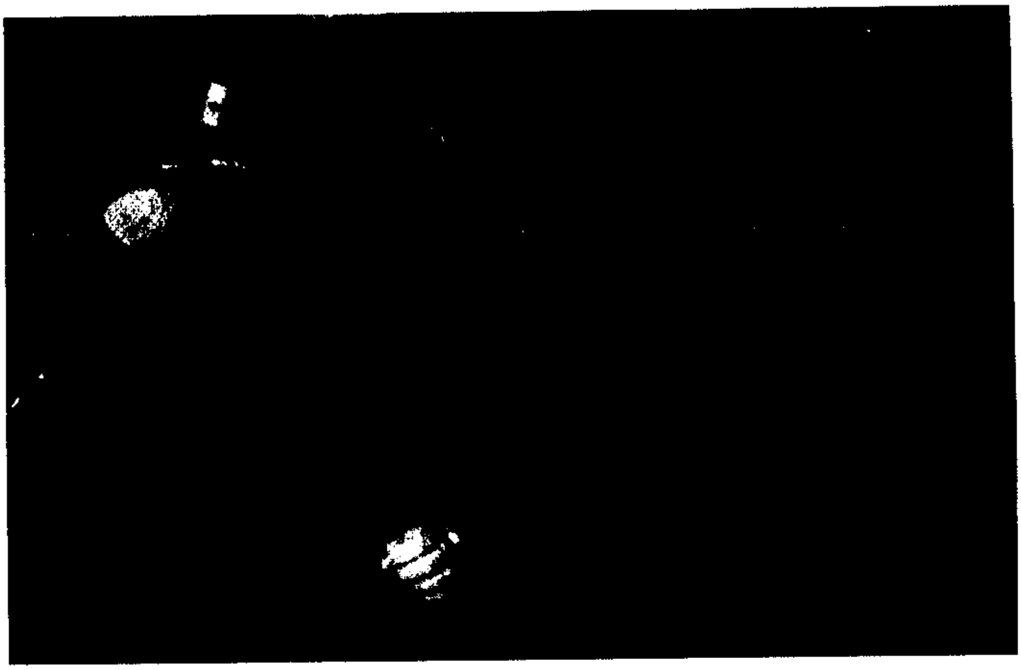
Annual P inputs to the Northern Adriatic basin & fluxes through fito- and bacterioplankton

rivers:	TP (DIP is 80%)
atmosphere:	TP
bottom:	P-PO_4
exported:	P-PO_4
phyto:	estimated from fixed C
bacteria:	estimated from BCP and BCD



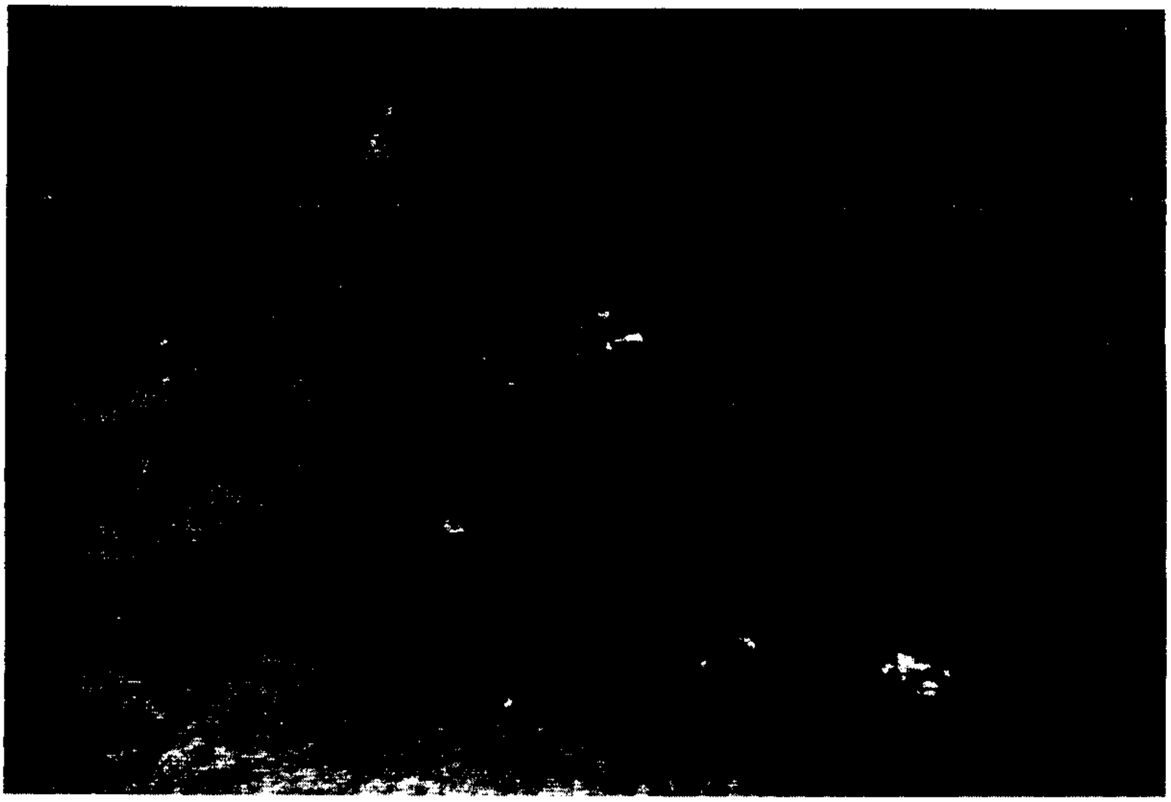
Elongate, amorphous cloud (lenght approx. 4m) and smaller cloud (1m) above bottom at the end of August 1983 in the eastern Adriatic Sea (Island Rab, depht 10m)

from Stachowitsch et al. 1990



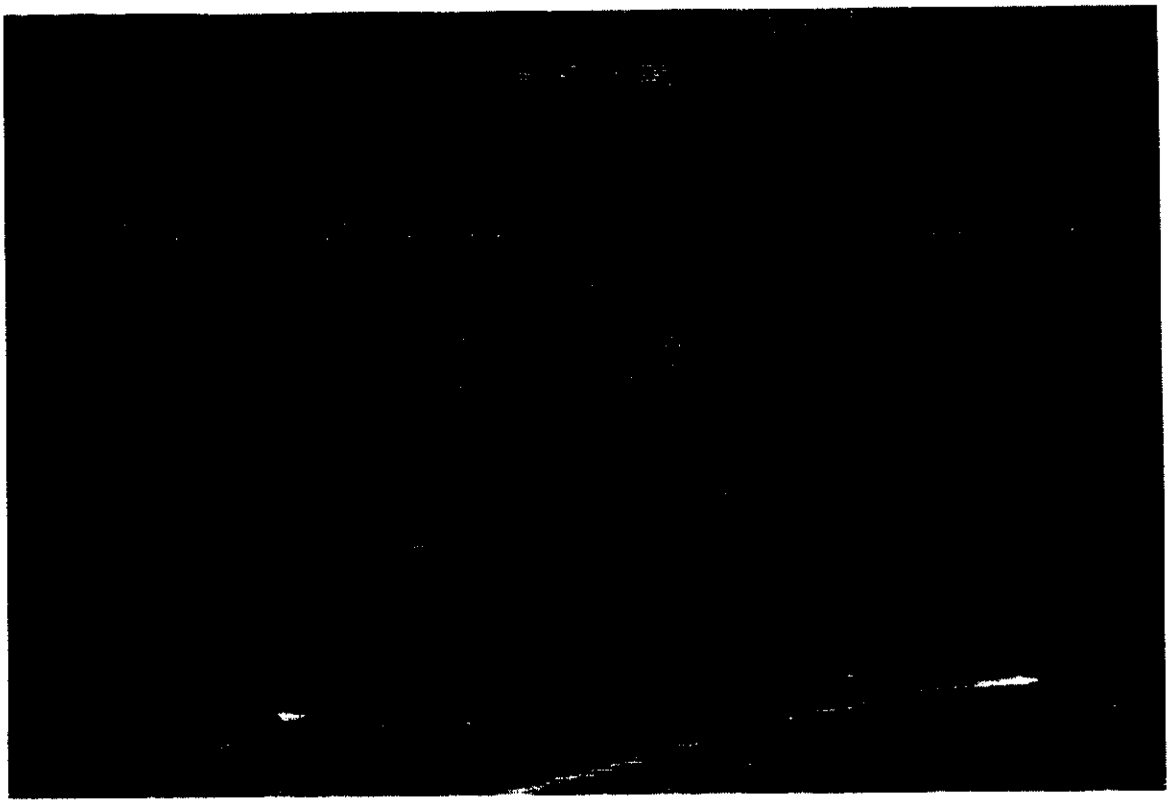
Dense network of clouds on June 1989, approximately 2 km off Piran, depht 4m

from Stachowitsch et al. 1990



Cloud snagged on multi-species clump on June 1989 in 25m off Piran

from Stachowitsch et al. 1990



Extensive gelatinous surface layer, interspersed with creamy material, 17 km off Cesenatico on July 1989. These mats extended more than 40 km out to sea

from Stachowitsch et al. 1990

Close-up of gelatinous surface layer 17 km off Cesenatico on July 1989. Top of floating spongy masses dries to leathery or crust-like consistency (approx. 1.5m^2)

from Stachowitsch et al. 1990

The mucilage phenomena

is the result of a 2 step processe:

1. the accumulation of refractory DOC, consisting of abundant polysaccharides and high weight molecular components

many factors contribute to these accumulation, both abiotic:
- **eddy circulation, vertical stratification, increased freshwater residence time**
- **chemical and physical transformation of DOC**

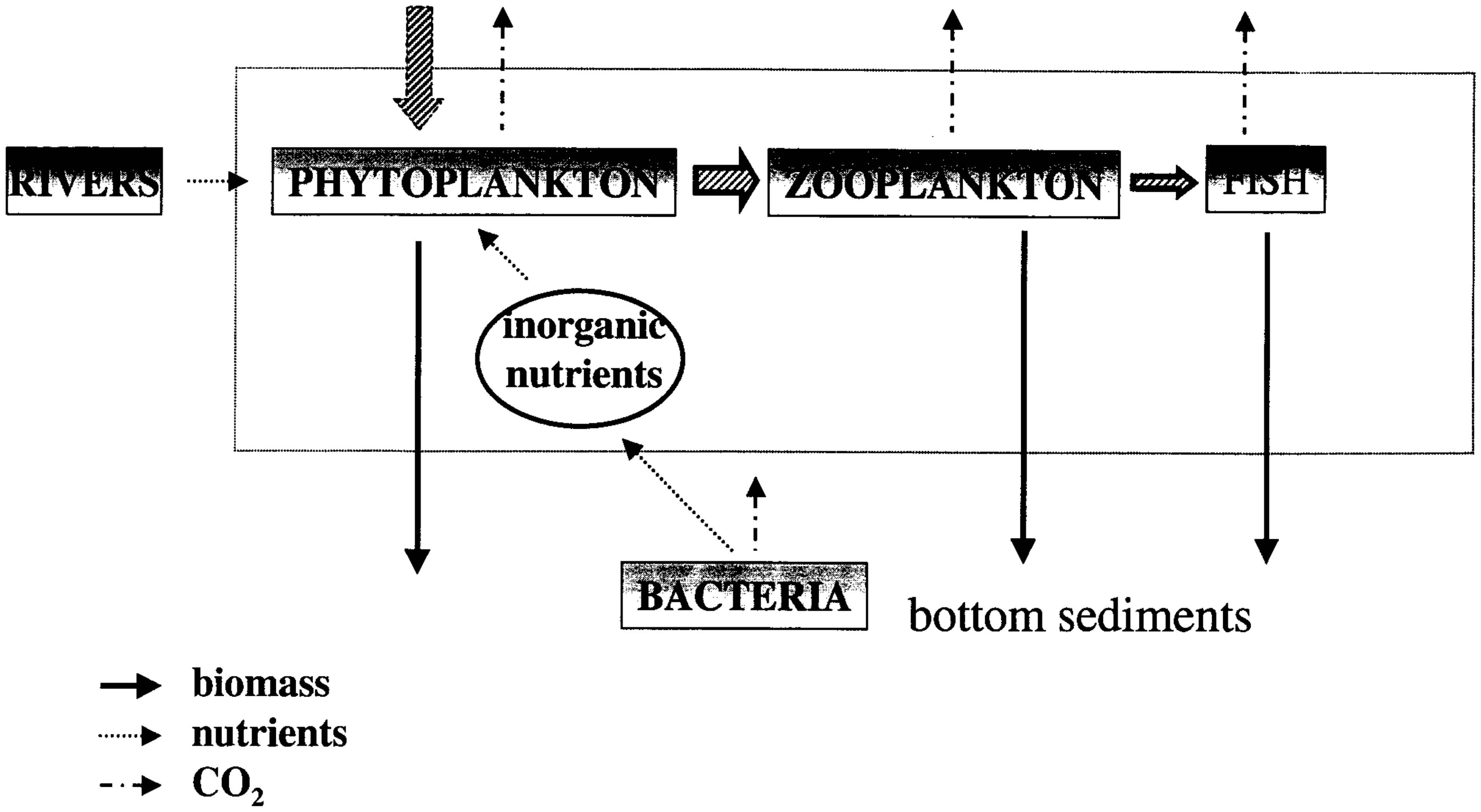
and biotic:
- **restricted DOC uptake by bacteria partially due to P limitation**
- **bacterial transformation of DOC**
- **bacterial production of refractory DOC**

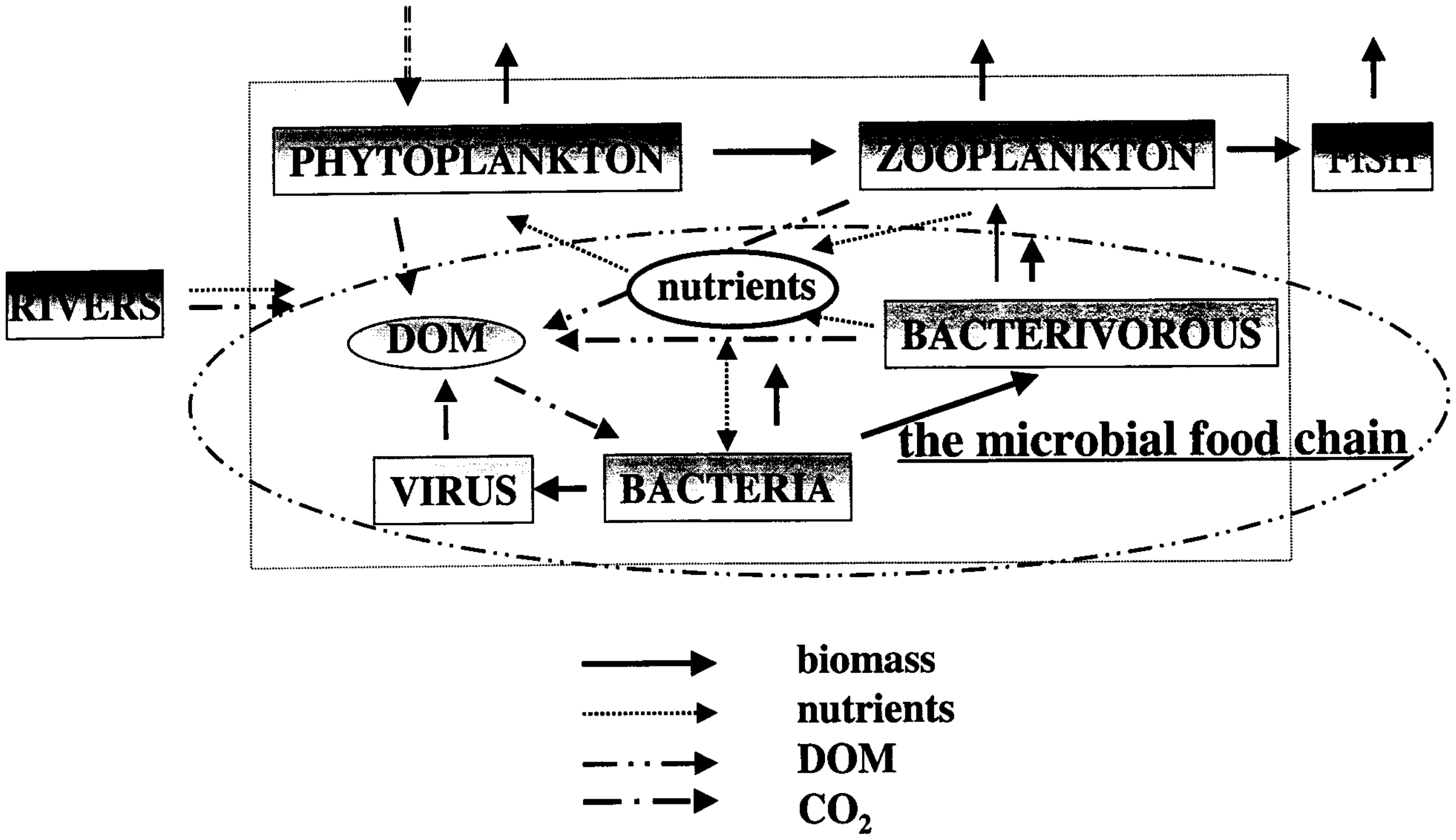
etc.

2. the transformation of dissolved colloids into polymer gels

causes and persistence of the above gelation are at this moment unknown

the "classic" grazing food chain





the "classic" & the microbial food chain