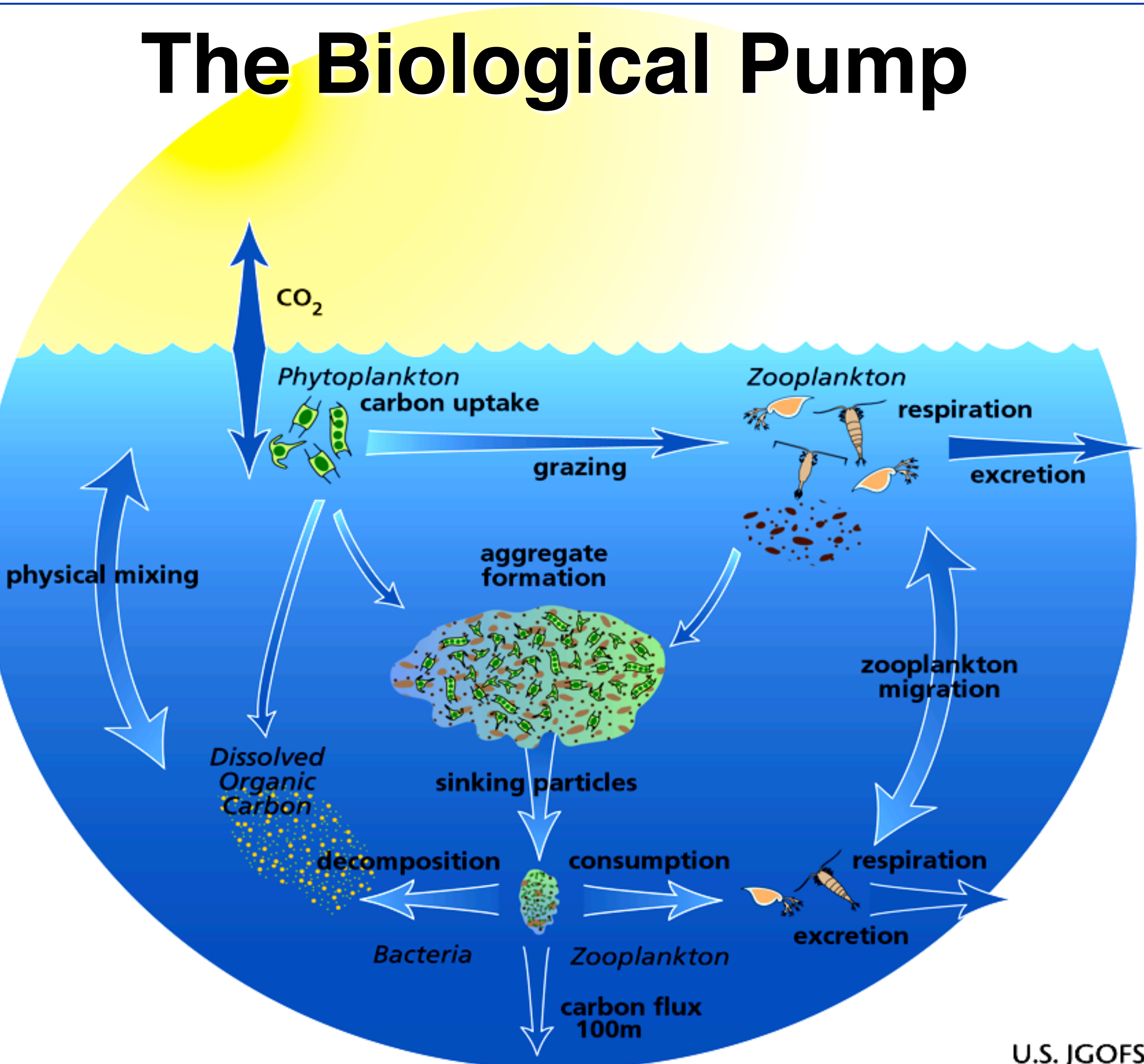
The biological pump: fueling the deep sea

I. Definition/Importance of pump
II. Components
   - Sinking particles (rates, communities, etc.)
   - Active transport
   - DOC advection
III. Other fuel- Chemoautotrophy

The issue:

How do organisms living in the dark ocean below the zone of primary food production fuel themselves?

The Biological Pump

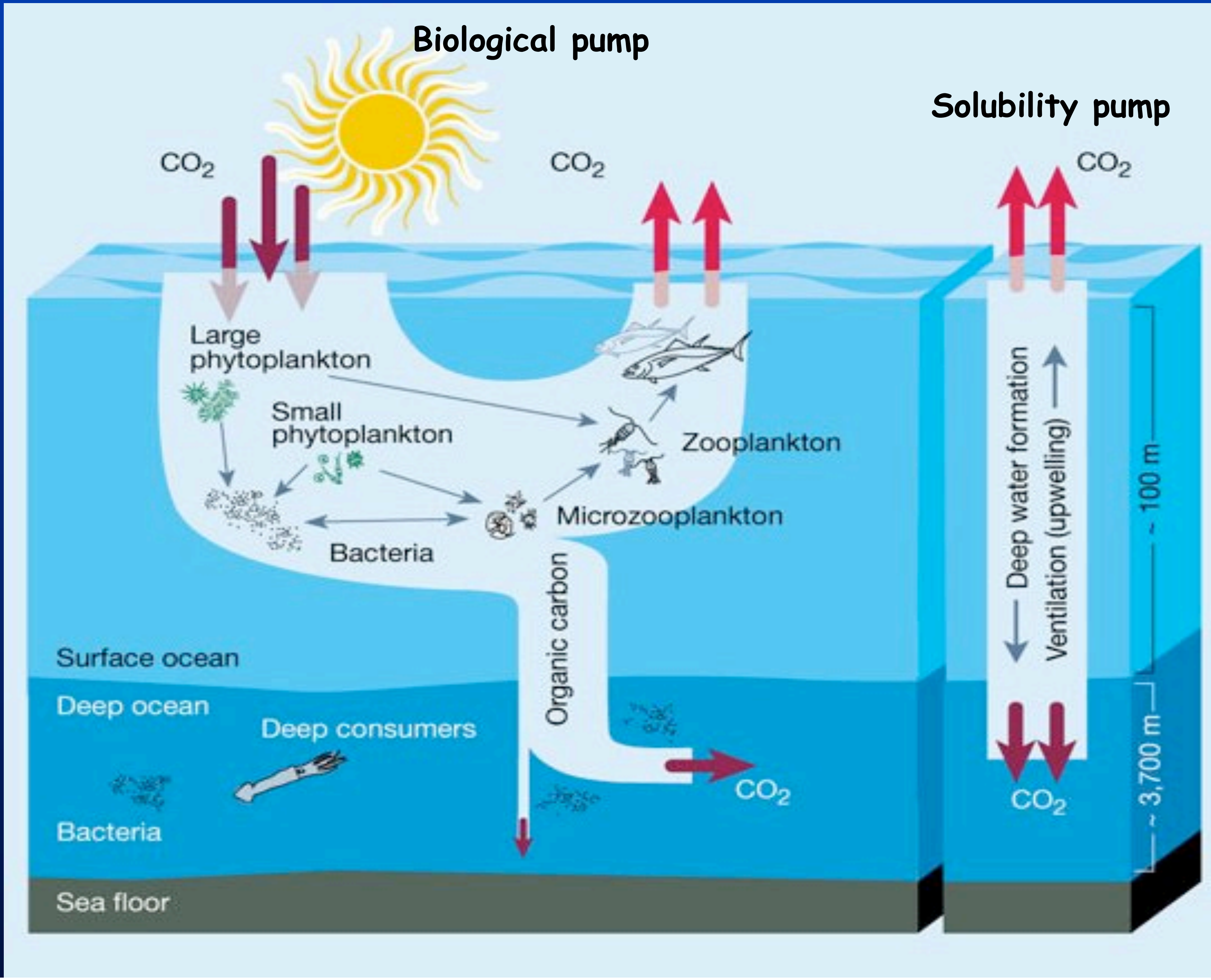


Process by which net community production from the ocean surface is transferred down into the ocean interior.

Various processes:

- aggregate sinking
- fecal pellet sinking
- zooplankton vertical migration
- physical mixing of DOM

are responsible for transforming dissolved inorganic carbon (CO_2) into organic biomass and pumping it in particulate or dissolved form into the deep ocean.


Biological pump
Solubility pump
CO_2
CO_2
CO_2
Large phytoplankton
Small phytoplankton
Zooplankton
Microzooplankton
Bacteria
Organic carbon
Deep water formation
Ventilation (upwelling)
~ 100 m
~ 3,700 m
Surface ocean
Deep ocean
Deep consumers
Bacteria
CO_2
CO_2
Sea floor

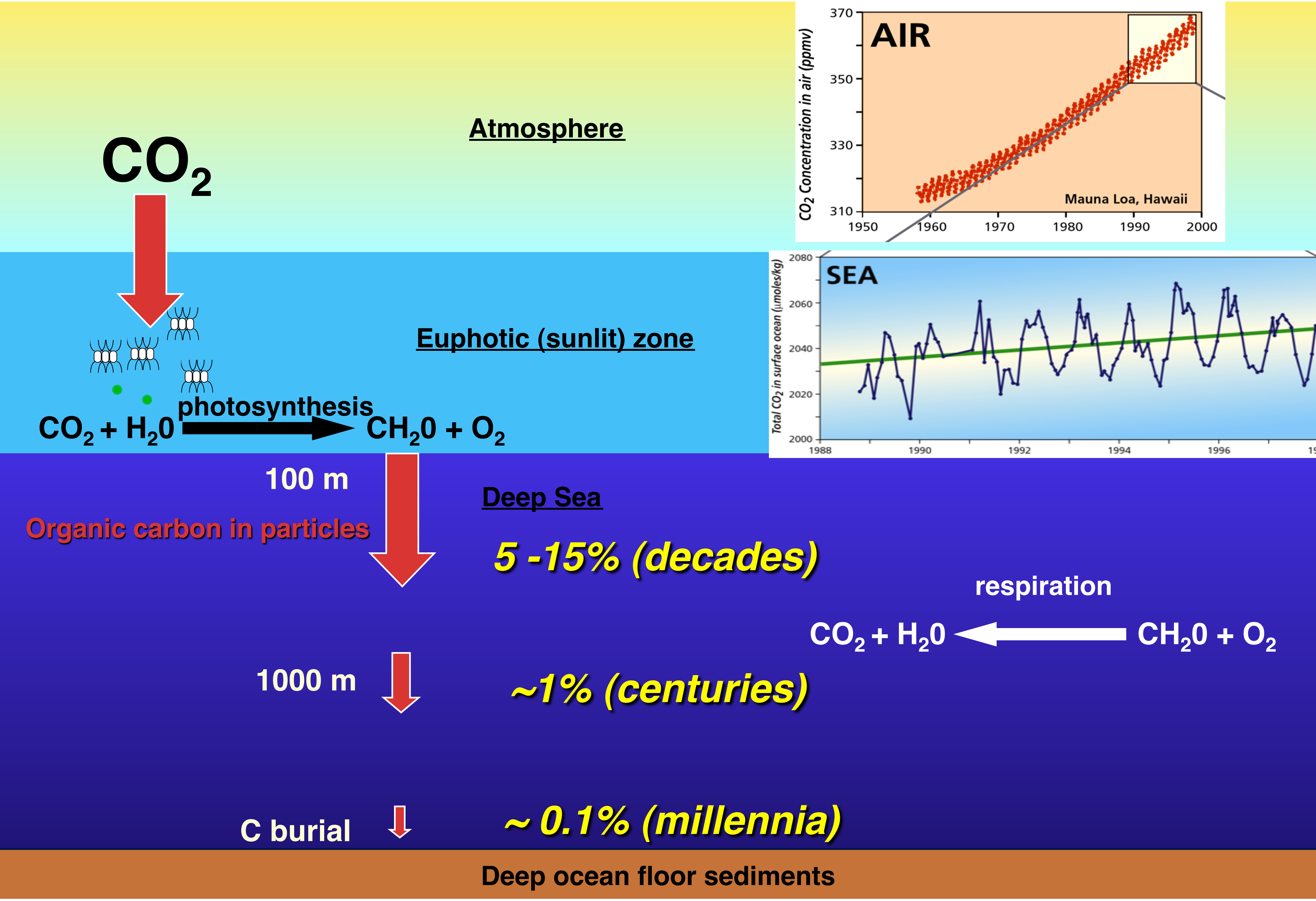
Biological pump vs. Solubility pump

1. Solubility pump

Because the solubility of CO_2 in seawater increases with decreasing temperature, the SOLUBILITY PUMP transfers CO_2 to the deep sea as the formation of cold deep waters at high latitudes acts as a temperature-dependent sink for atmospheric CO_2.

2. Biological pump

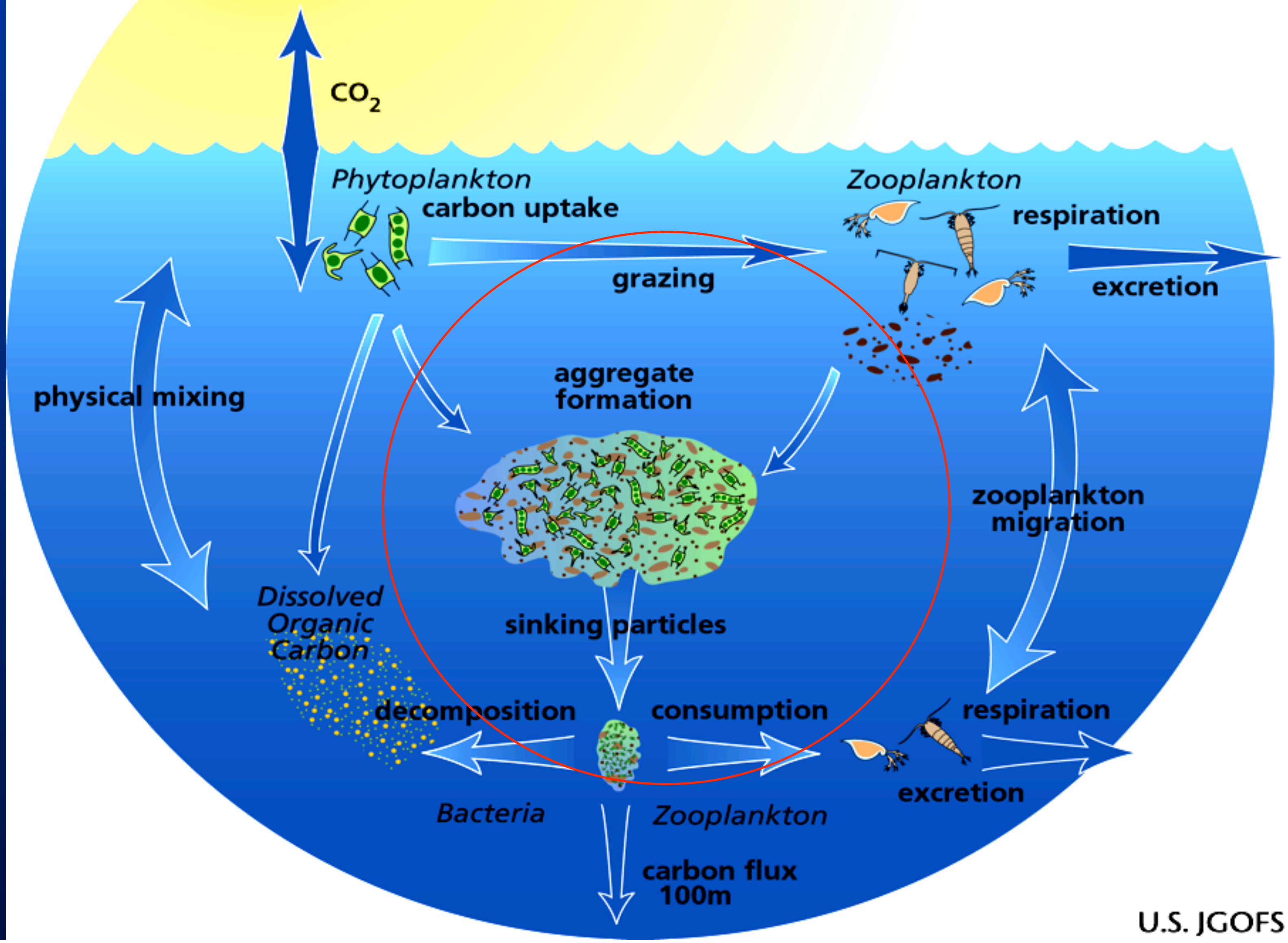
The BIOLOGICAL PUMP removes carbon from surface waters by gravitational settling, advection, and active biotransport of organic and inorganic carbon derived from biological production.



Atmosphere
CO2
AIR
CO2 Concentration in air (ppmv)
370
350
330
310
1950
1960
1970
1980
1990
2000
Mauna Loa, Hawaii
SEA
Total CO2 in surface ocean (µmoles/kg)
2080
2060
2040
2020
2000
1988
1990
1992
1994
1996
Euphotic (sunlit) zone
photosynthesis
CO2 + H20 → CH20 + O2
100 m
Deep Sea
Organic carbon in particles
5 -15% (decades)
respiration
CO2 + H20 ← CH20 + O2
1000 m
~1% (centuries)
C burial
~ 0.1% (millennia)
Deep ocean floor sediments

The Biological Pump

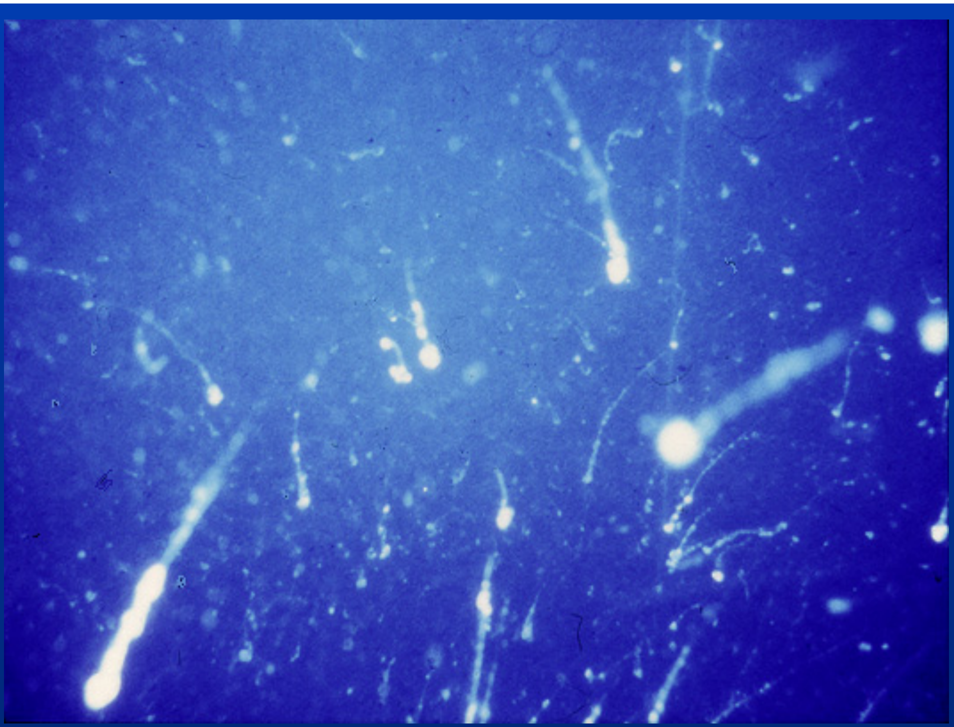
1. Vertical particle flux

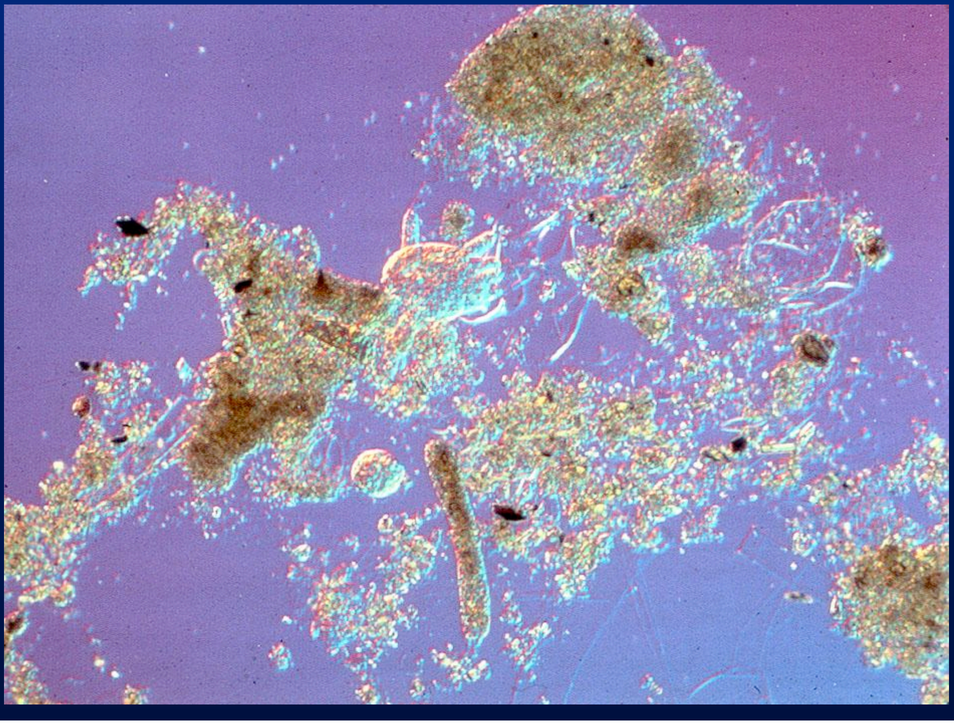


Vertical Particle Export

Marine Snow: non-living organic particles visible to the naked eye (> 0.5 mm)

- **1940's: Japanese looking at fish behavior from a submarine, hard to do due to high abundance of small aggregates**
- **1950's: named marine snow after passage in book "The sea around us" by Rachel Carson (long snowfall)**
- **1970's: collection of marine snow by BW diving**





Why is marine snow important?

1. transport of surface-derived organic matter to depth – marine snow is major component found in sediment traps - enrichment of Trace metals too

2. microhabitat for associated organisms: generally microorganisms are found at concentrations many orders of magnitude higher than in surrounding seawater - food source

Origins of Marine Snow

1. dead organisms: mostly planktonic, in coastal waters more diverse (bits of kelp, pollen, insects, wood ash)

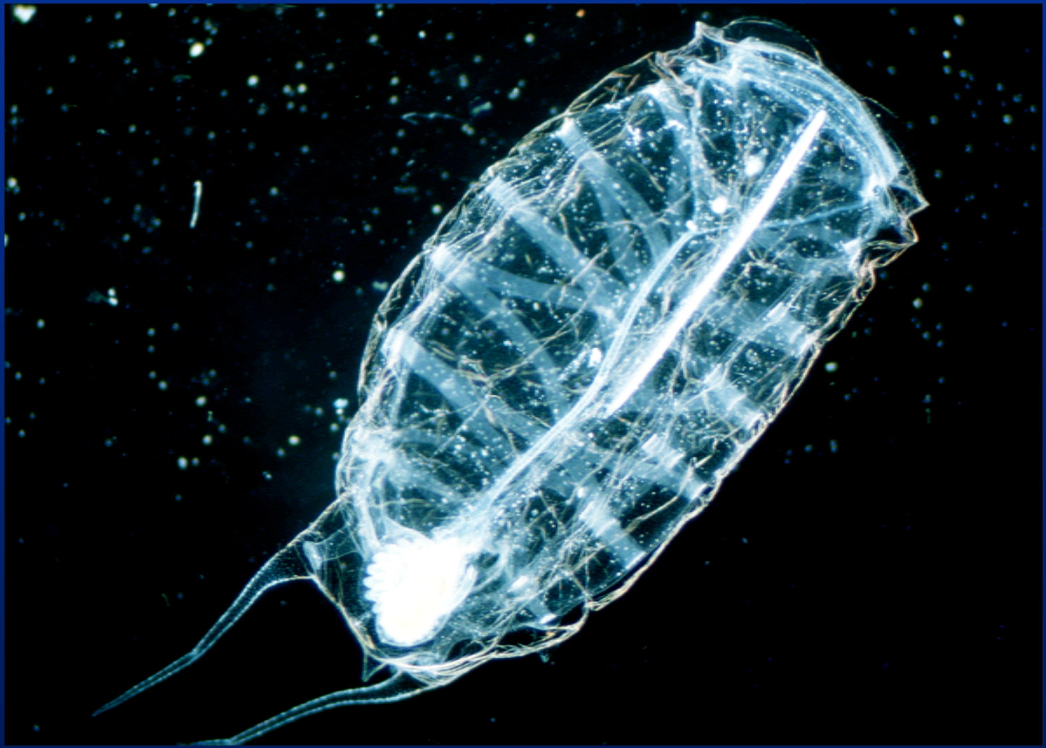
2. fecal pellets: crustacean pellets are covered with a layer of polysaccharides (peritrophic membrane), dense package that can sink rapidly to depth

3. mucous products: filter structures secreted by zooplankton (pteropod feeding webs, larvacean houses)

4. secretions by organisms: extracellular polymers cementing bacterial cell walls, mucus sheats produced by diatoms, cyanobacteria colonies

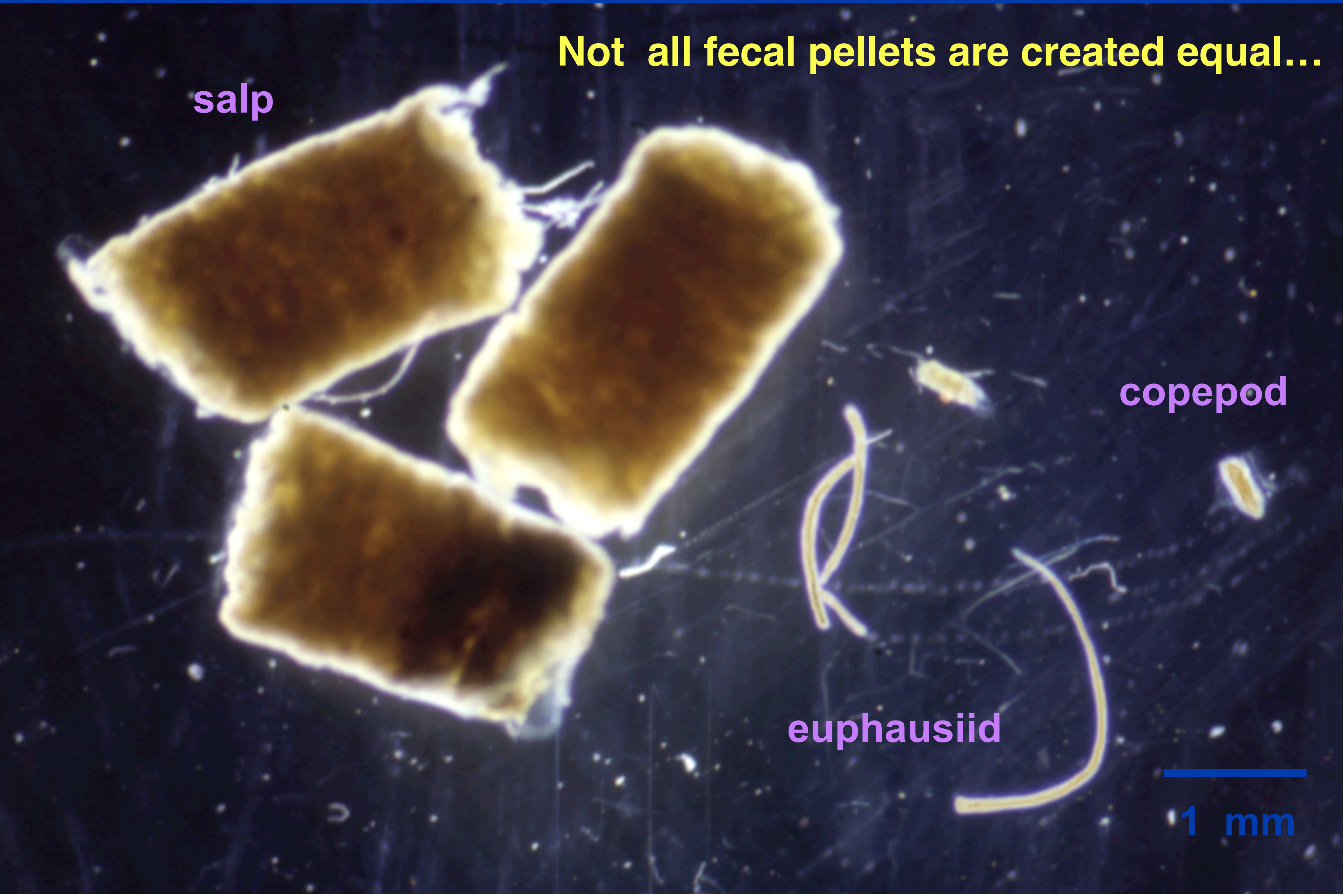
5. bubbles - DOC gets absorbed to bubbles and when they burst they condense to POC

Role of surface community composition

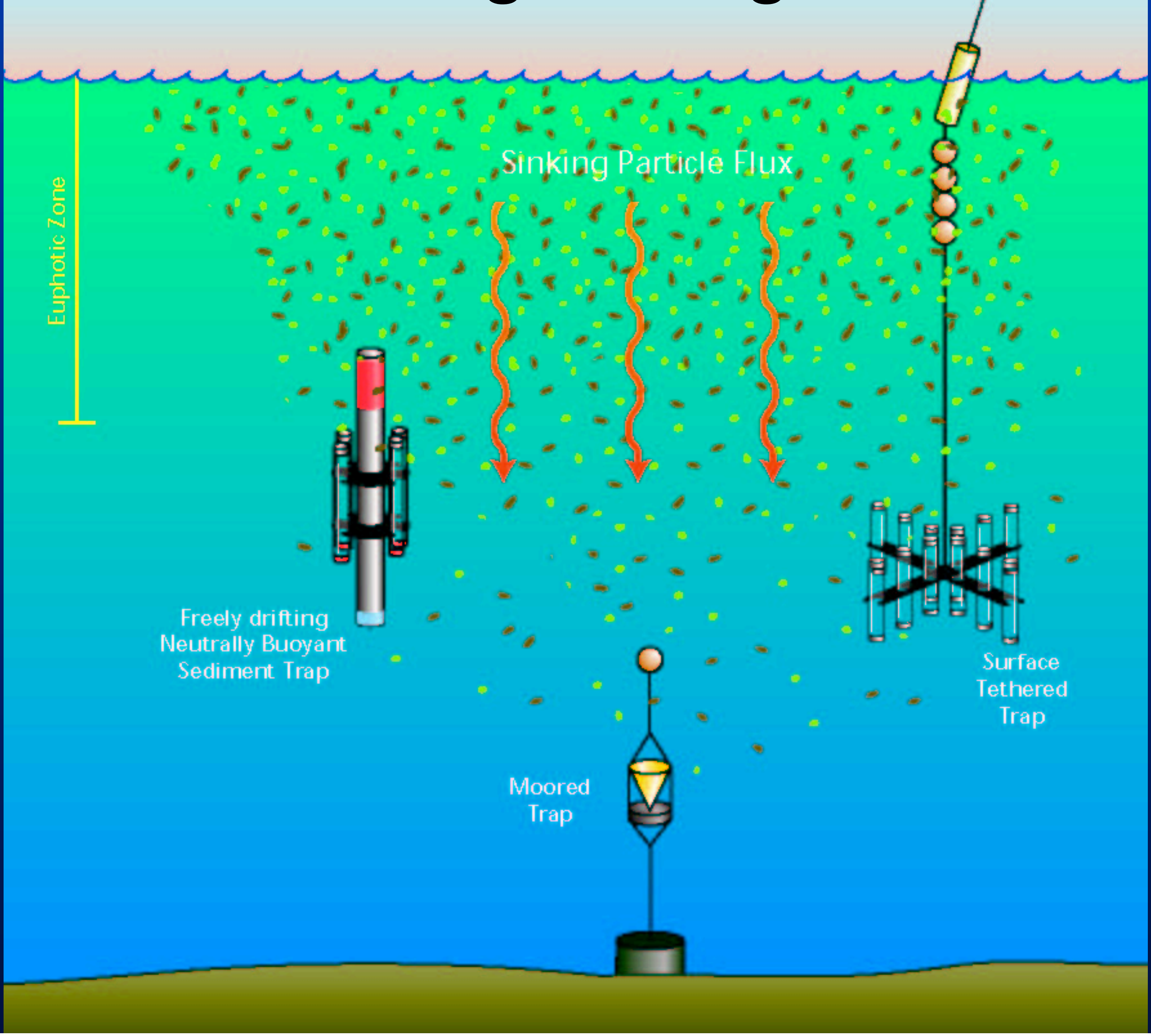


Salp

Copepod


Not all fecal pellets are created equal…
salp
copepod
euphausiid
1 mm

Collecting Sinking Particles

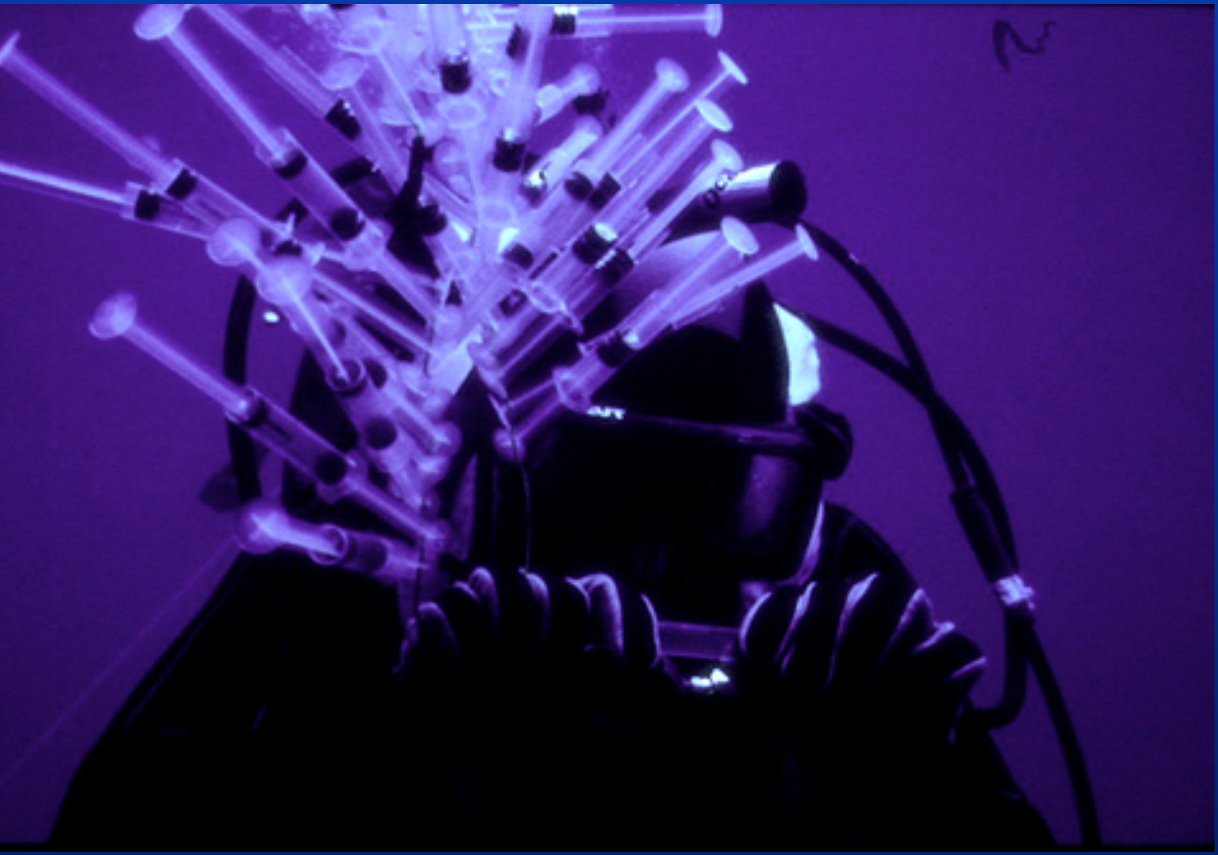


Sediment trap design

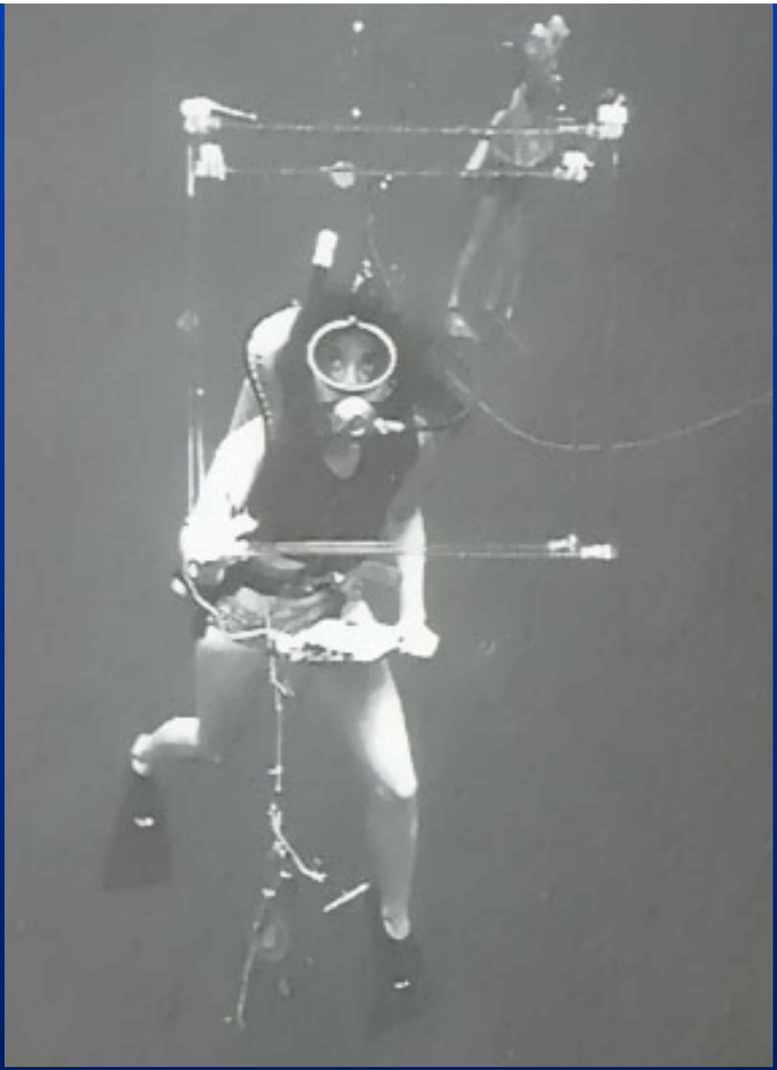
Particle Interceptor trap (PIT)

Neutrally buoyant sediment trap

Neutrally buoyant sediment trap



Collecting marine snow by Blue - water diving



Counting particles

Using ^{234}Th to estimate export

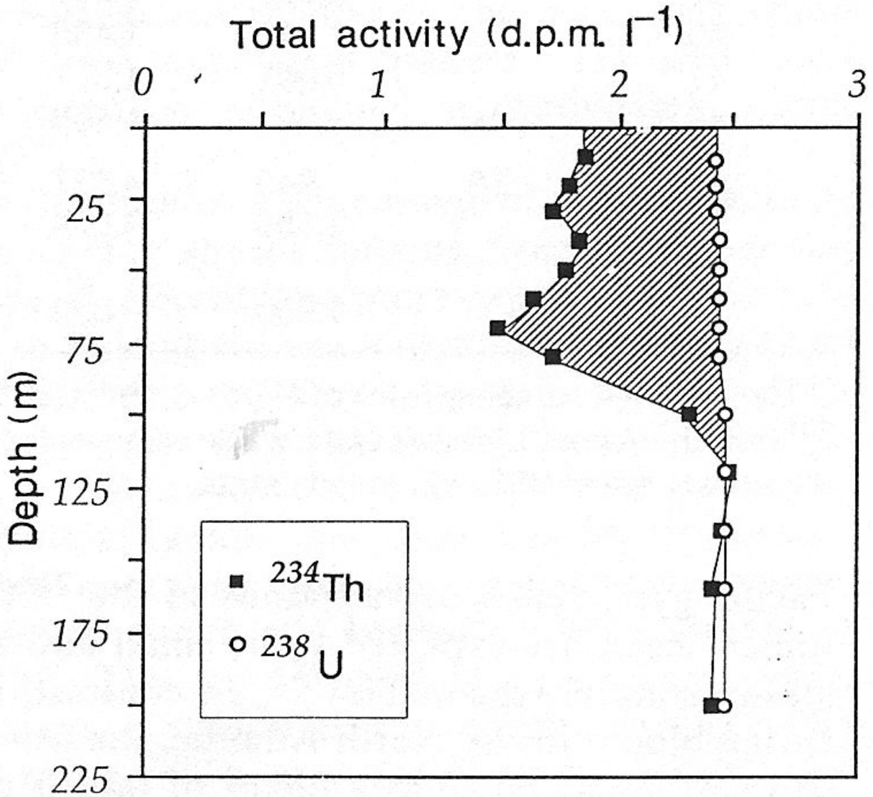


FIG. 1 Typical profile of ^{234}Th in the upper open ocean. Shaded area represents disequilibrium between total ^{234}Th and ^{238}U. Data taken from VERTEX 3 (ref. 11).

NATURE · VOL 353 · 3 OCTOBER 1991

^{234}Th supply:

via the decay of ^{238} U

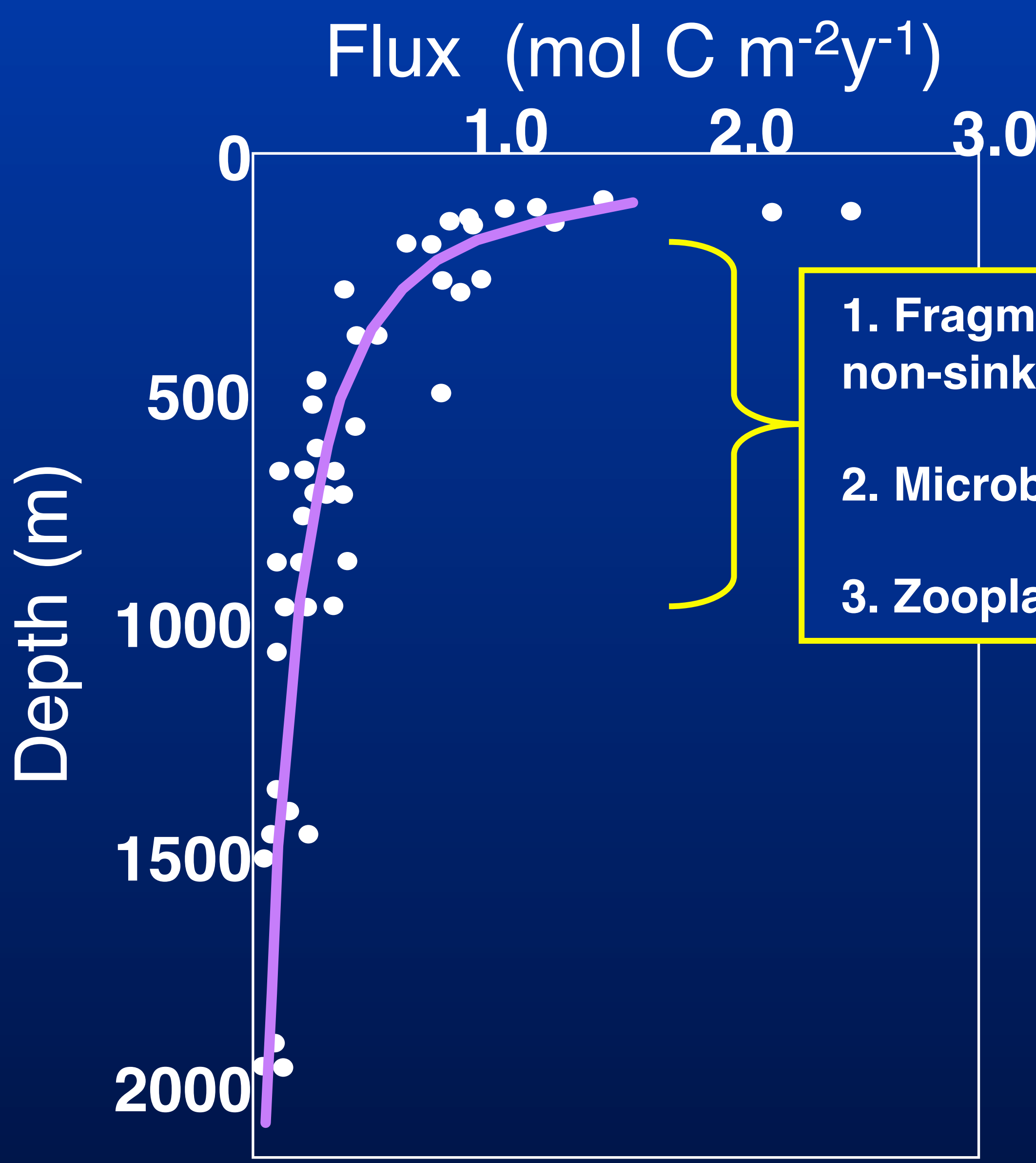
^{234}Th removal

- **radioactive decay**
- **sorptive removal on sinking particles**

Buesseler et al. (1991)

$$\partial^{234}\mathrm{Th}/\partial t = {}^{238}\mathrm{U} \times \lambda - {}^{234}\mathrm{Th} \times \lambda - P \qquad (1)$$

Sinking particle loss in the twilight zone



1. Fragmentation into smaller, non-sinking particles

2. Microbial decomposition

3. Zooplankton consumption

Martin et al. (1987)

Size distribution and Sinking rates

Stokes Law: describes the sinking behavior of a particle with a size of 1 μm - 1 mm

$$\text{sinking rate} = \frac{r^2 \; \frac{2}{9} \; g\,(dp - dsw)}{\mu}$$

r - particle radius

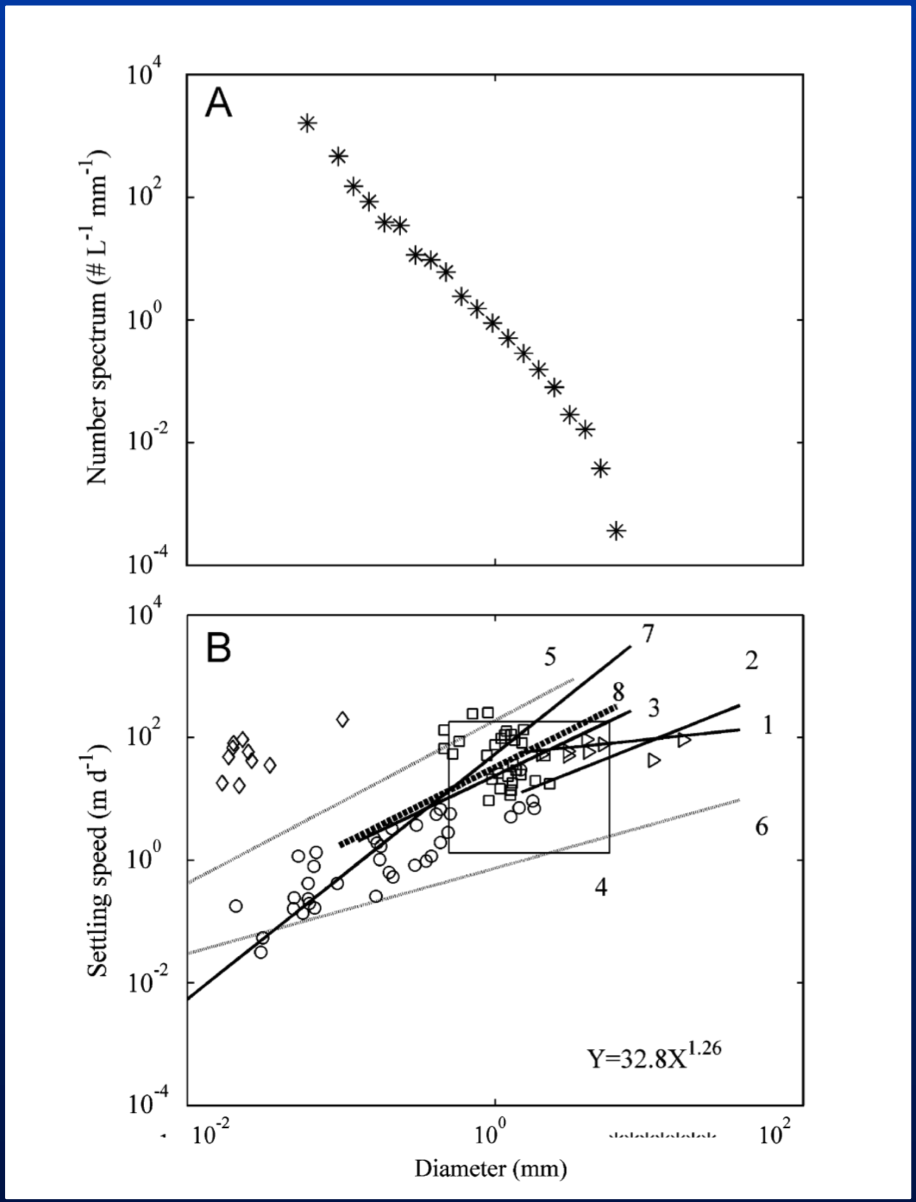
g - gravity

dp - particle density

dsw - density of seawater

μ - viscosity of seawater

Size distribution and Sinking rates



Aggregate settling velocity and mass flux based on size distribution. (A) Typical number spectrum from the UVP database profiles. (B) Particle settling velocity as a function of particle diameter measured by different authors

Guidi et al. (2008)

Evidence for fast sinking of Marine Snow/aggregates

• bomb testing in upper atmosphere - radioactive material in deep sea cucumber at several km's depth

• Chernobyl - 2-3 weeks later slug of radioactive material at Mediterranean seafloor

• diatom and sarcodine shells found in deep sea sediment directly below their surface populations

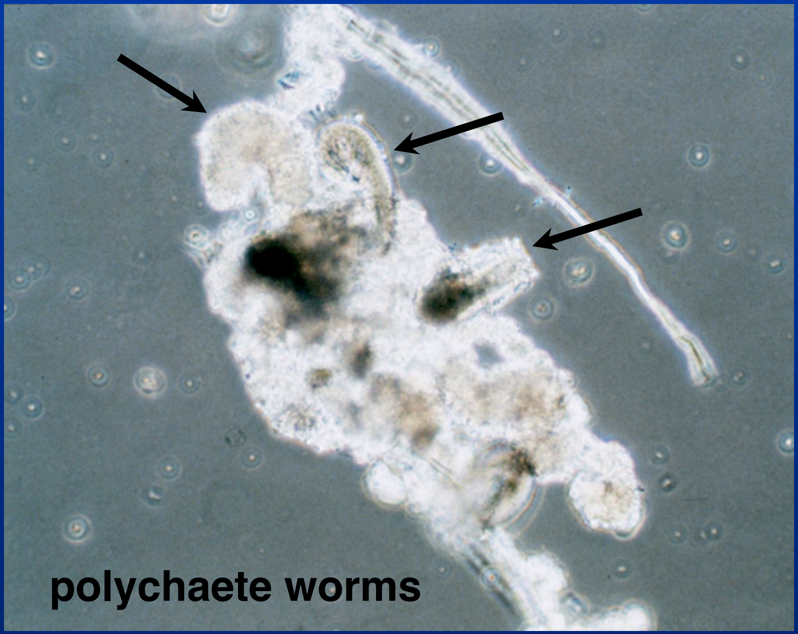
fecal pellet express!

some sinking rates: generally range 1-300 m / day

larvacean houses: ~ 25-300 m / day
giant larvacean houses: 800 m / day
salp fecal pellets: ~ 1000 m / day

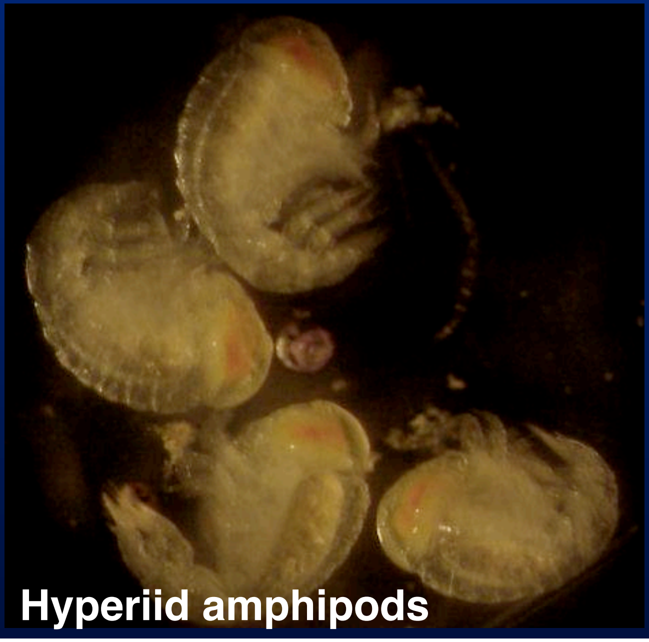
Zooplankton associated with detritus

Copepod (*Scopalatum*)



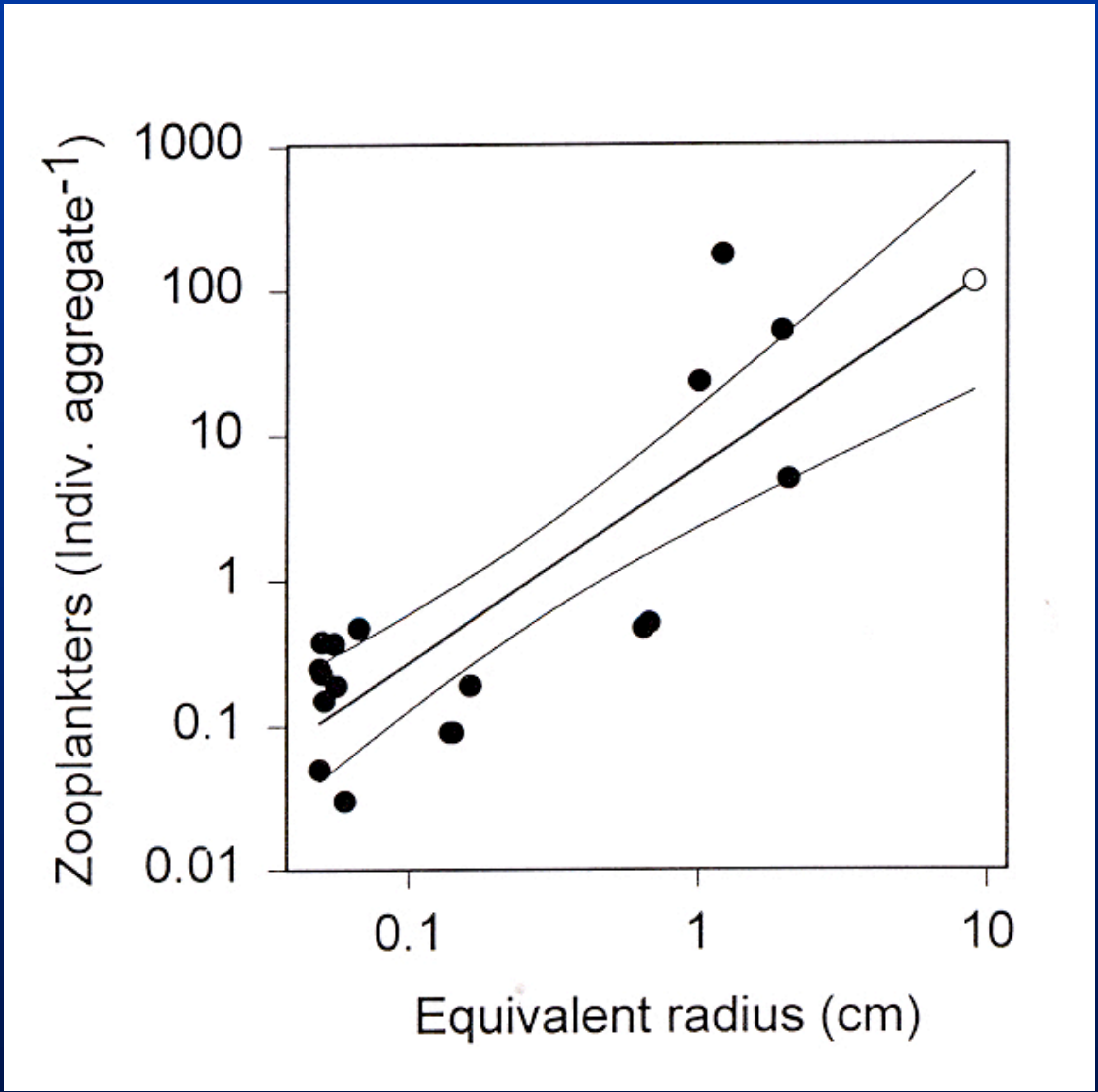
polychaete worms

Copepod *Oncaea* on larvacean house

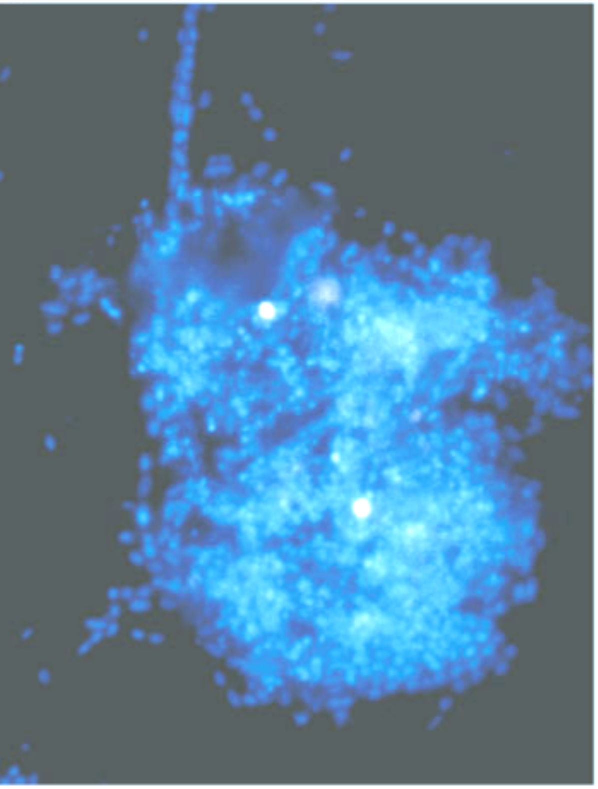


Hyperiid amphipods

Concentration of zooplankton on marine snow



Kiørboe (2000)



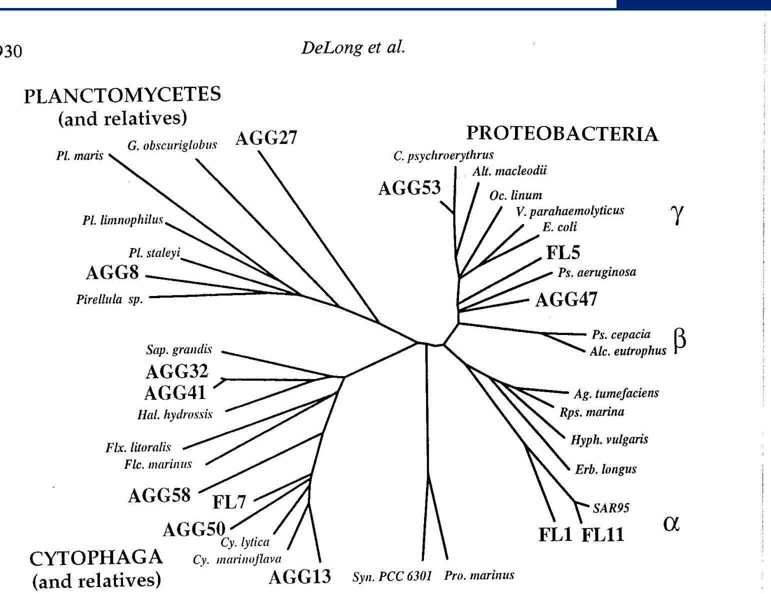
Attached Prokaryotes:

- Up to 3 orders of magnitude greater in abundance compared to surrounding water (i.e. 10^9 / ml)

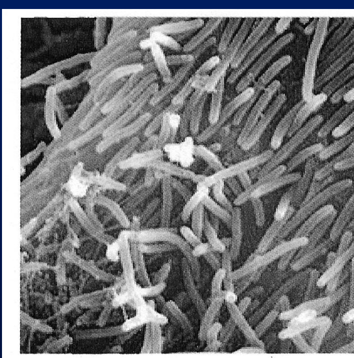
- predominantly *Bacteria*

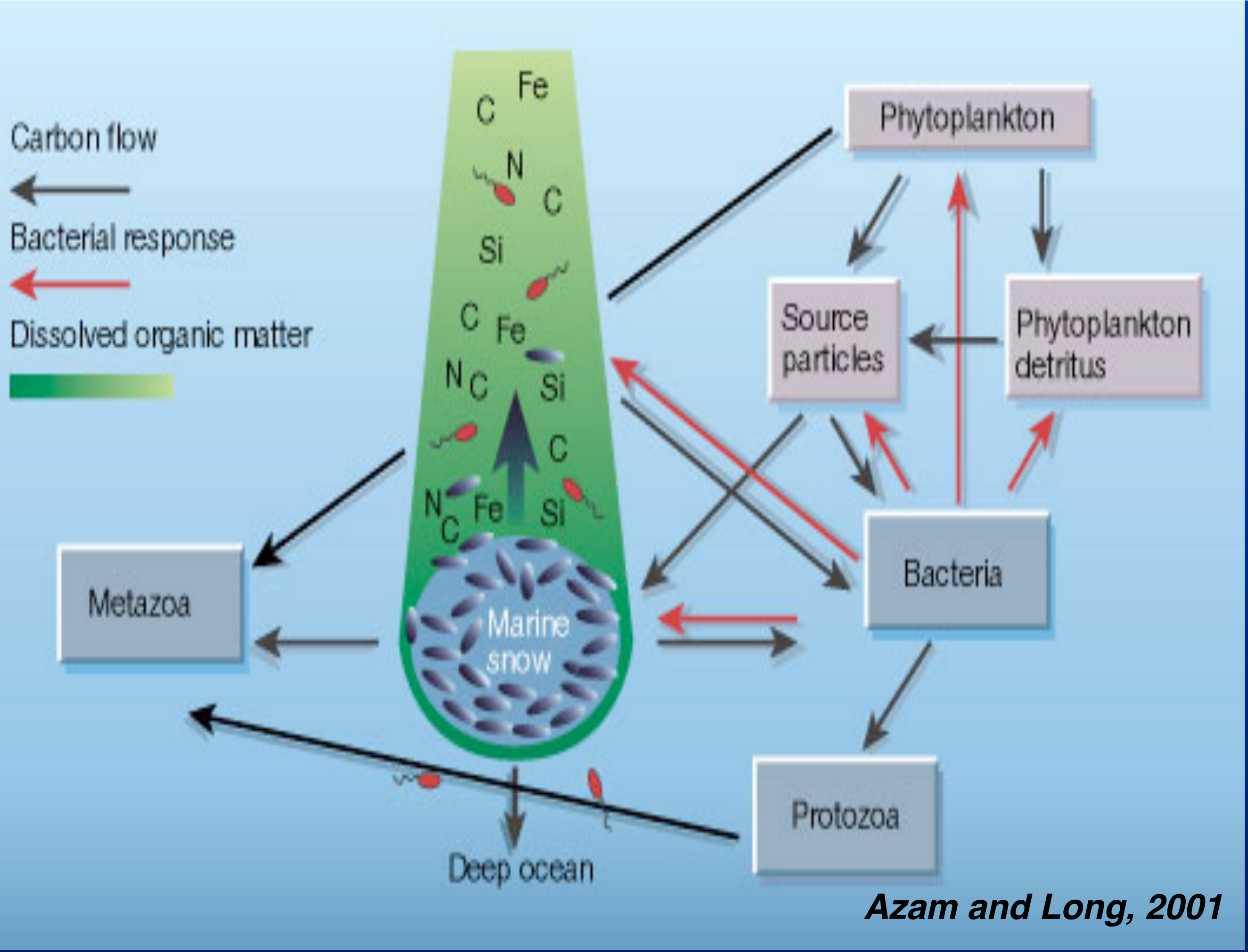
- Distinct differences in microbial assemblage of attached bacteria compared to free living

- High exoenzyme poduction



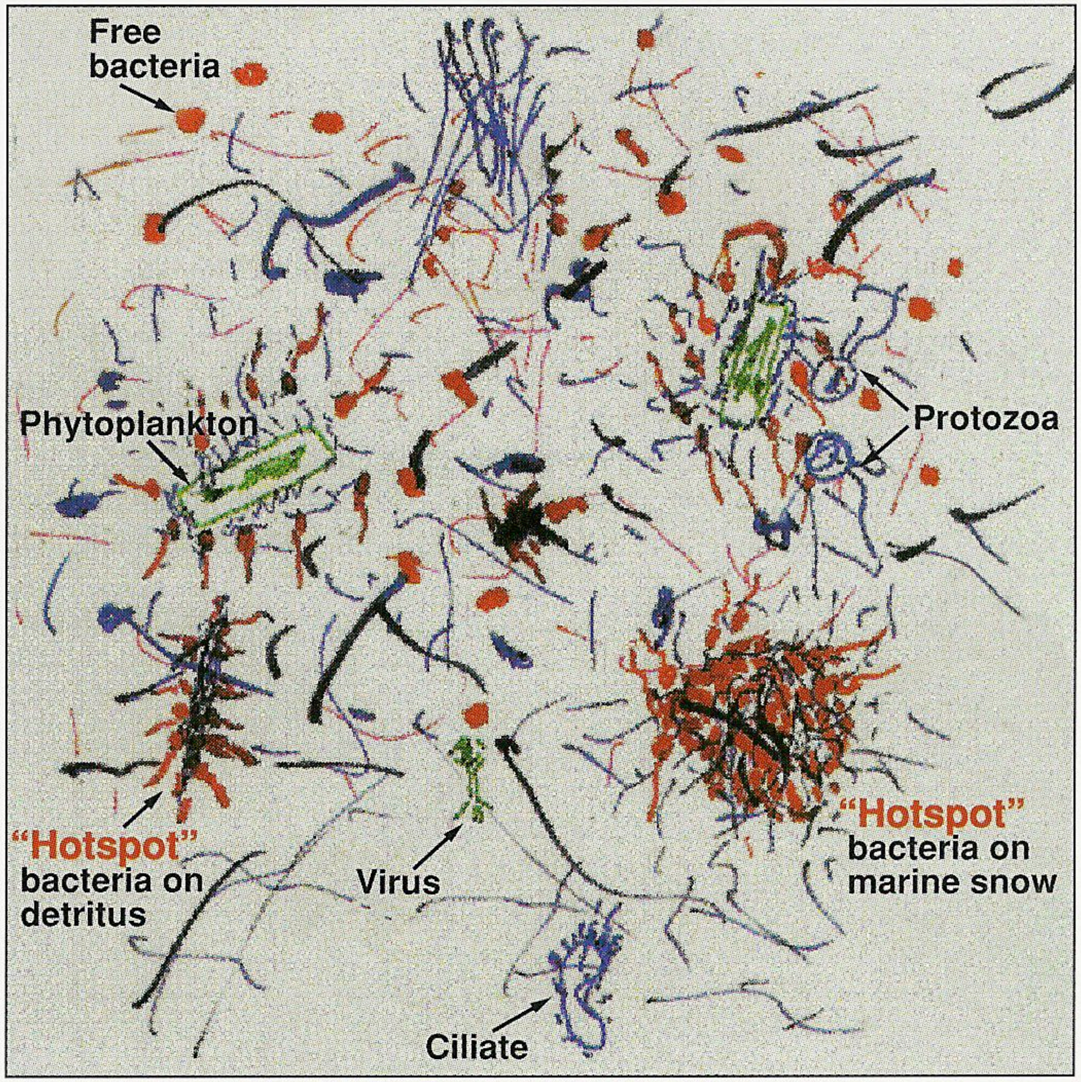
DeLong et al., 1993





Heterogeneity of the ocean interior – hot spots

- Solubilization of sinking particles released plume of organics and inorganics
- estimated that as much as 50% of bacterial carbon demand is met interaction with plume microenvironments (Kiorboe and Jackson 2001)



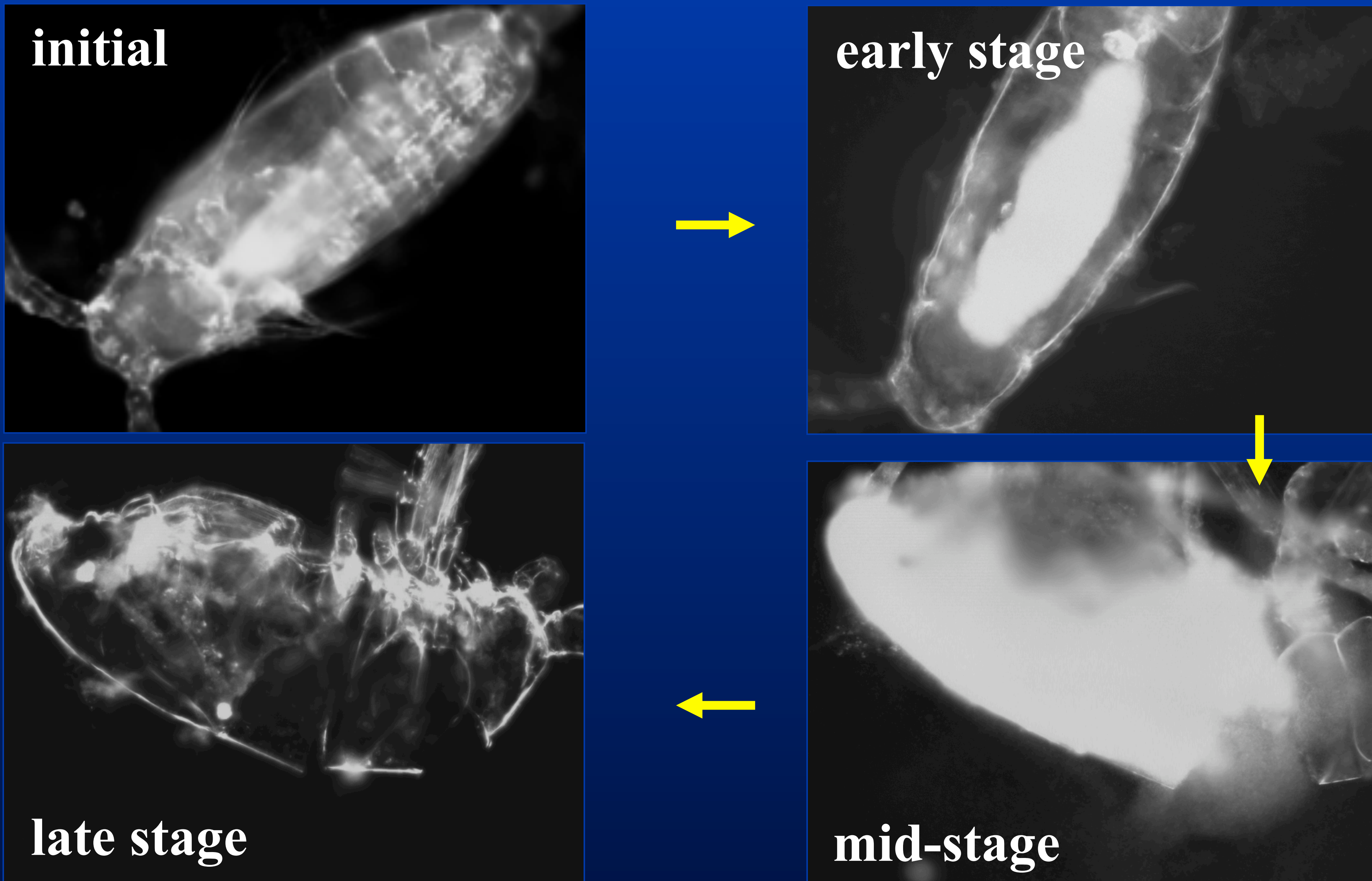
The microbial loop: impressionist version. A bacteria-eye view of the ocean's euphotic layer. Seawater is an organic matter continuum, a gel of tangled polymers with embedded strings, sheets, and bundles of fibrils and particles, including living organisms, as "hotspots." Bacteria (red) acting on marine snow (black) or algae (green) can control sedimentation and primary productivity; diverse microniches (hotspots) can support high bacterial diversity.

Azam 1998

Factors that control community structure and OM use…

- nutrient field
- DOM quality
- Gels and hot spots

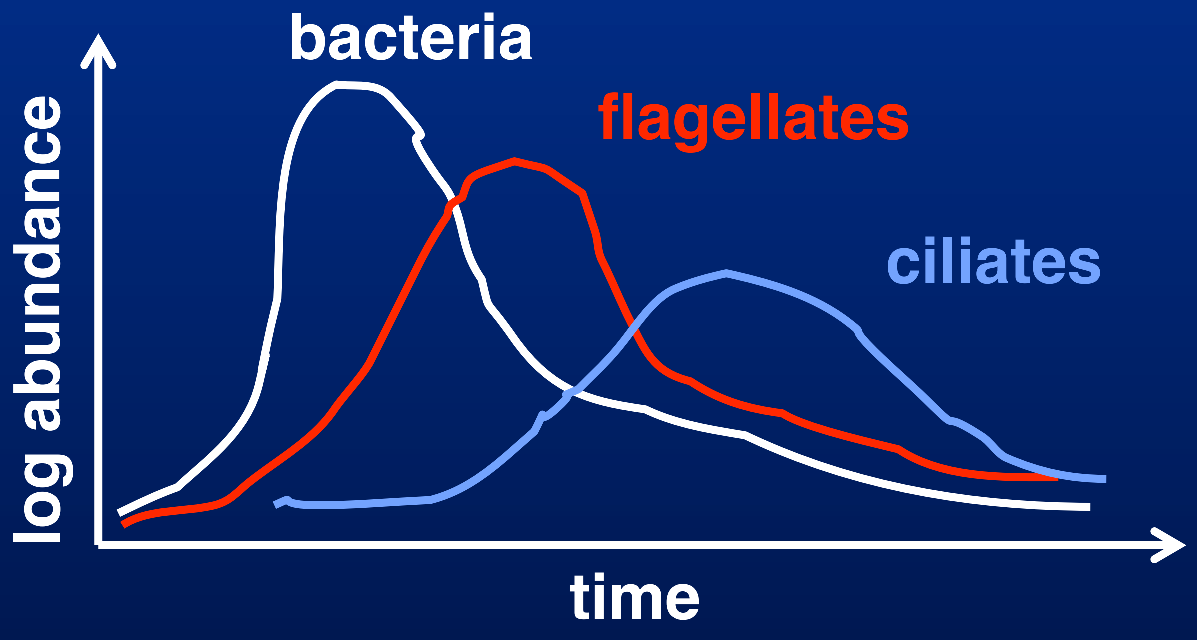
Bacterial action on zooplankton carcasses



Tang et al. (2006) Estuar. Coast. Shelf Sci

Associated Organisms

Succession in number and kind of organisms inhabiting aggregates



advantages:

- **food**

- **habitat**

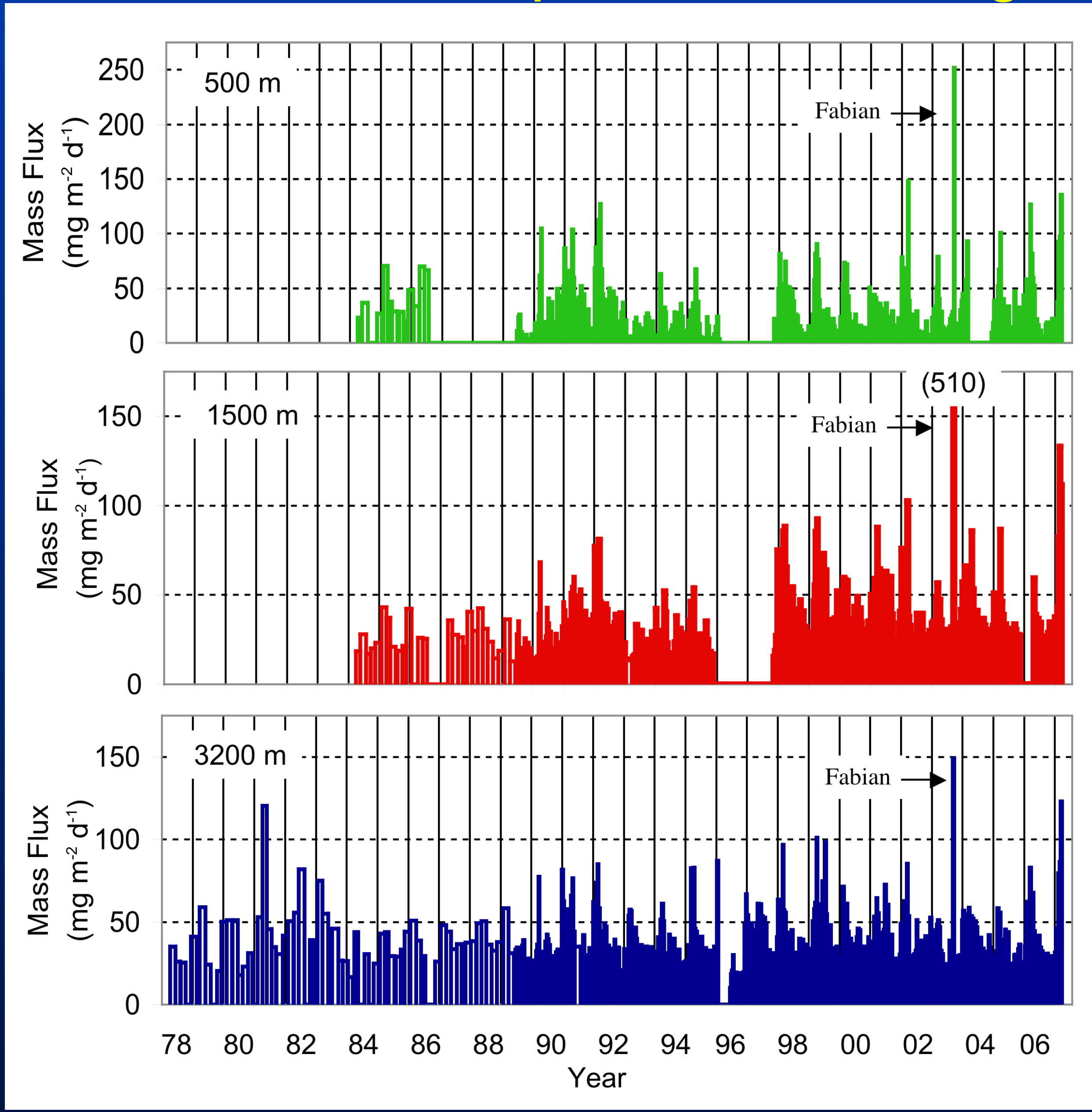
- **transport on aggregate guaranteeing dispersal (invertebrate larvae)**

Based on Duval and Silver

Deep-ocean sediment trap flux in the Sargasso Sea

Transformed the long-held view that the deep sea was a relatively stable, invariable environment

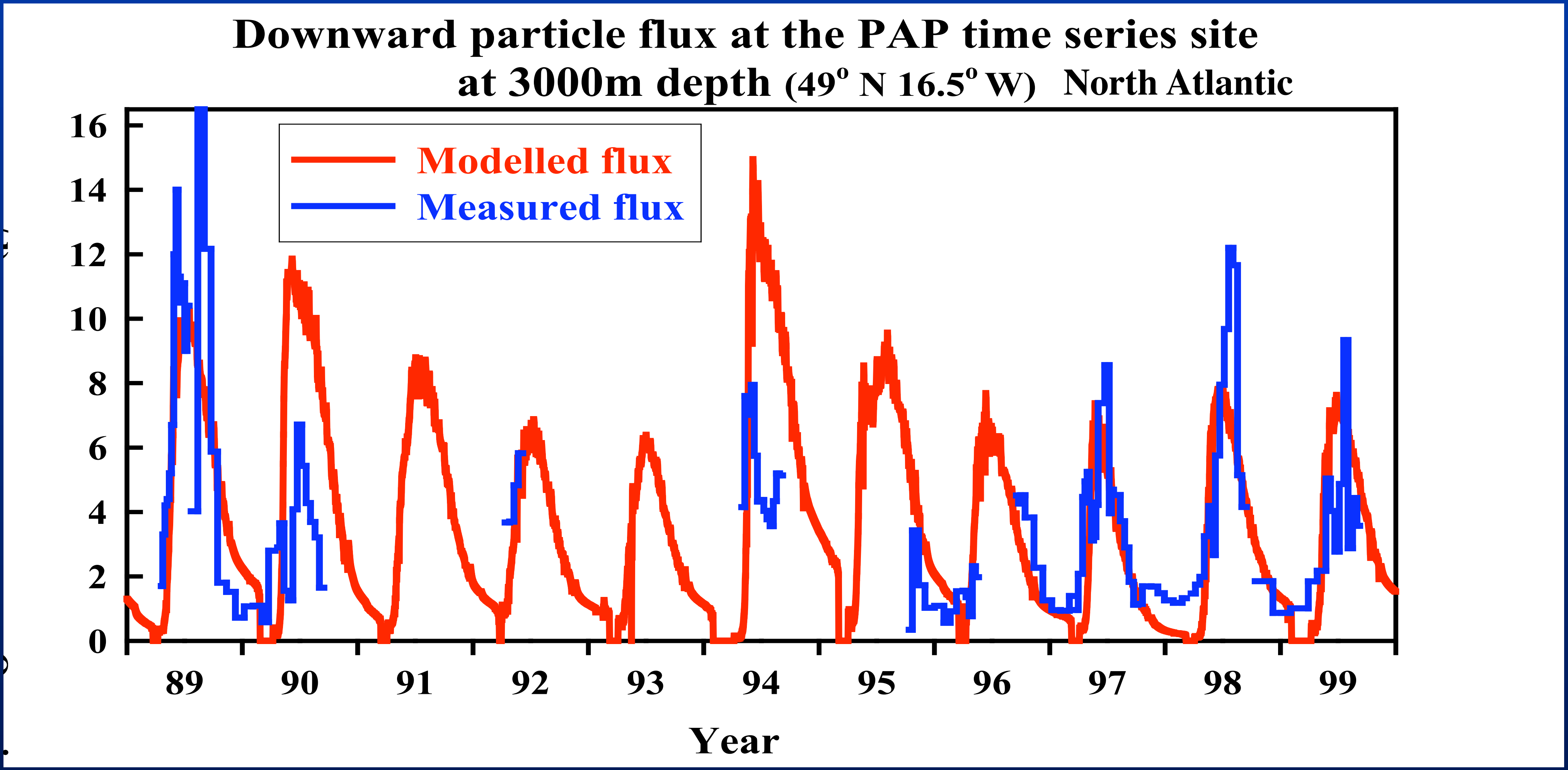
- **Seasonality**
- **Also, short-lived episodic events**



Extreme fluxes due to an advected plume of detrital carbonates during passage of Hurricane Fabian in Sep 2003.

Oceanic Flux Program

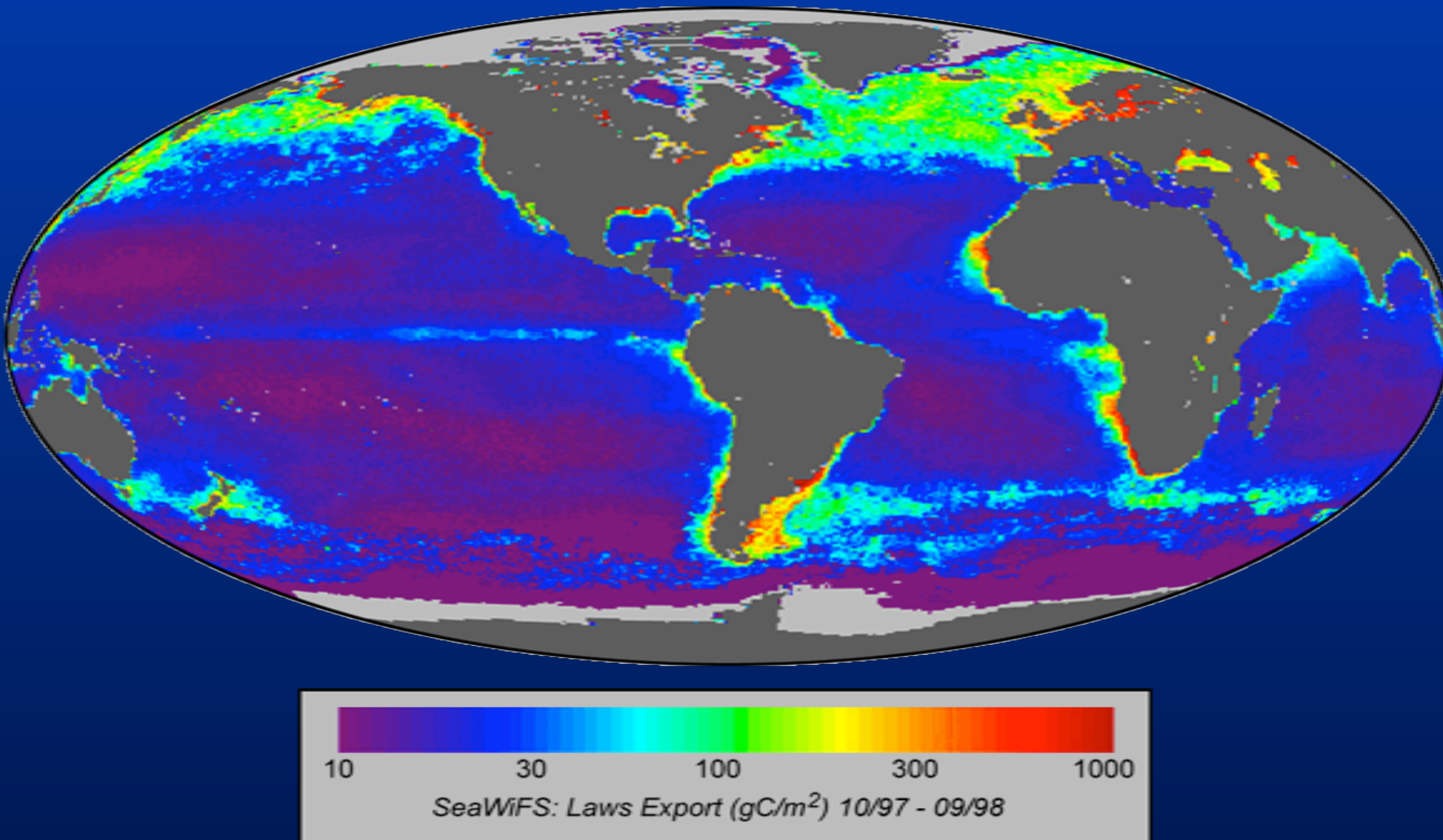
Conte and Weber (submitted)



Lampitt et al 2001

15cm long specimen of *Benthogone rosea* (sea cucumber) feeding on the phytodetrital layer at 2000m depth N. Atlantic

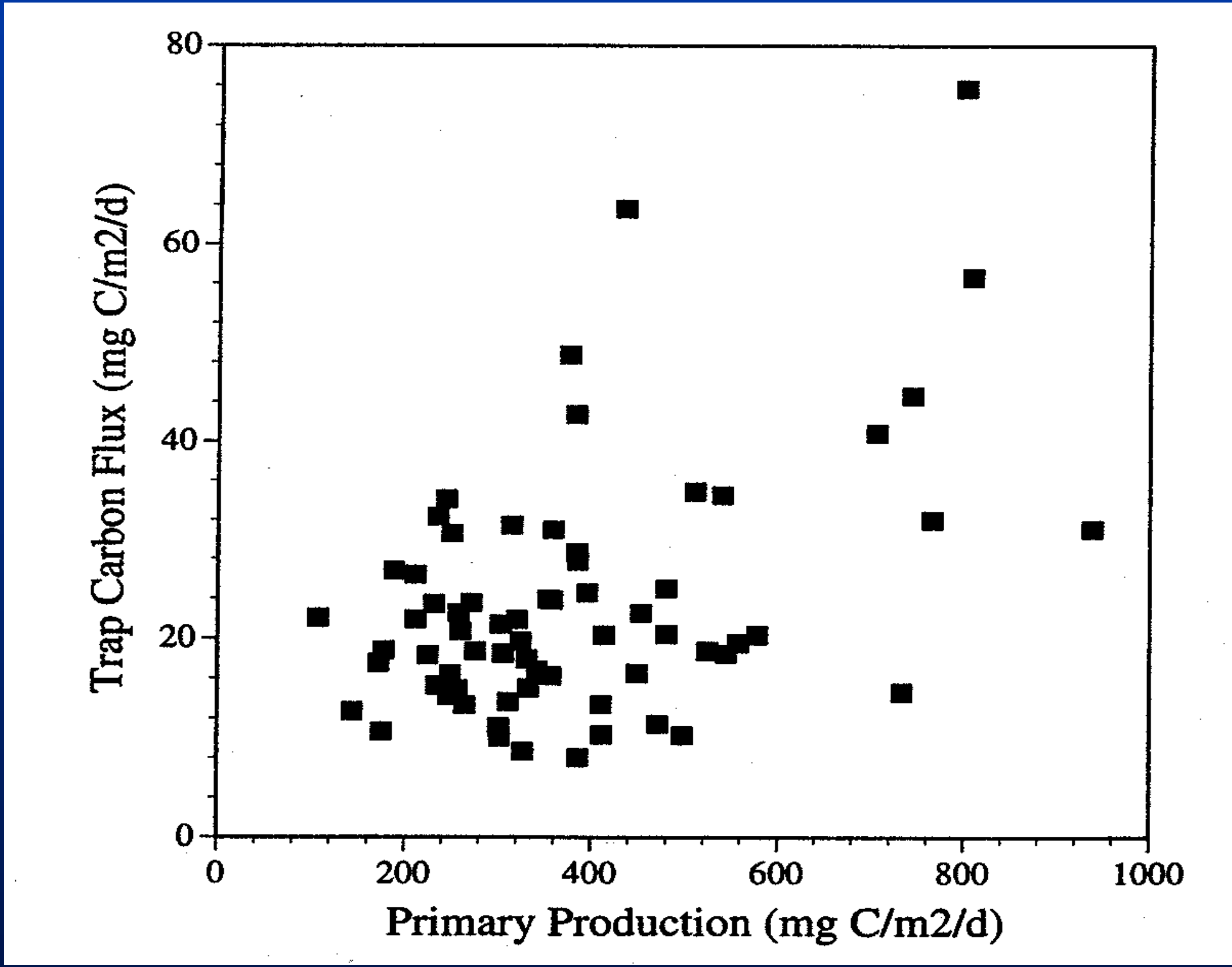
Global Export maps



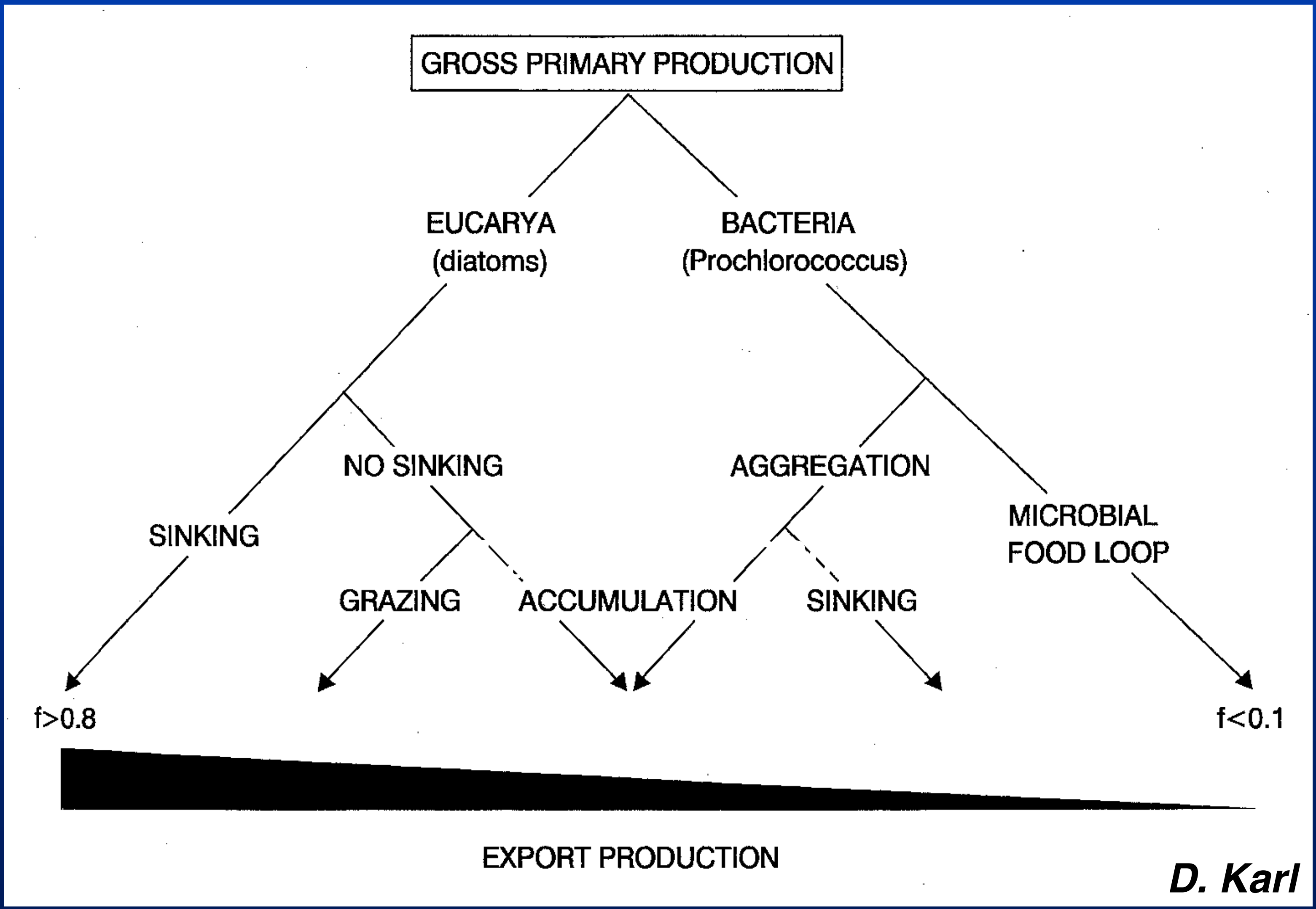
Annual export of organic carbon

as calculated from PTE model, temp and net PP. ***Laws et al 2000***

Relationship between PP and Flux



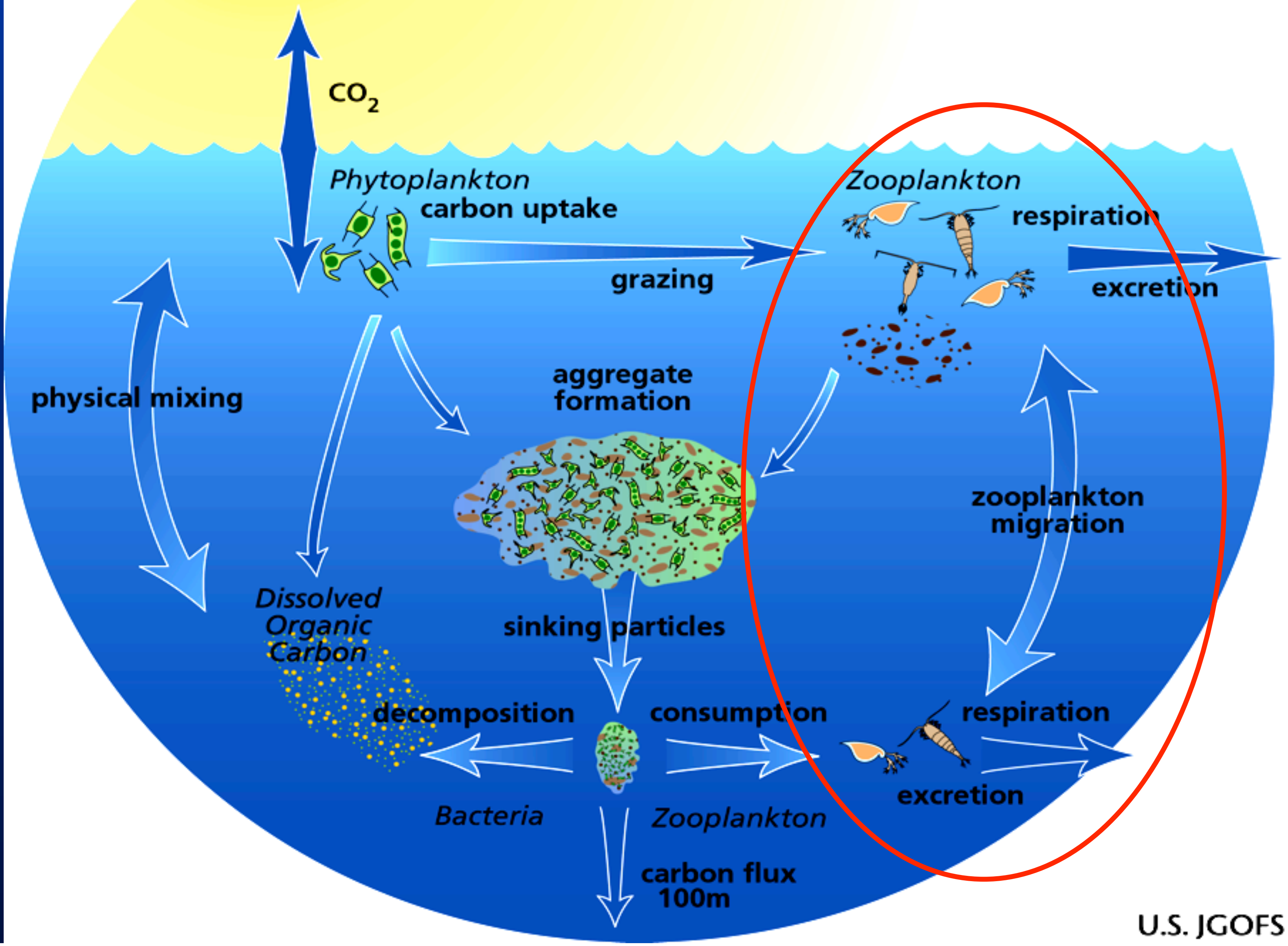
Bermuda Atlantic Time-series Study (Steinberg et al 2001)



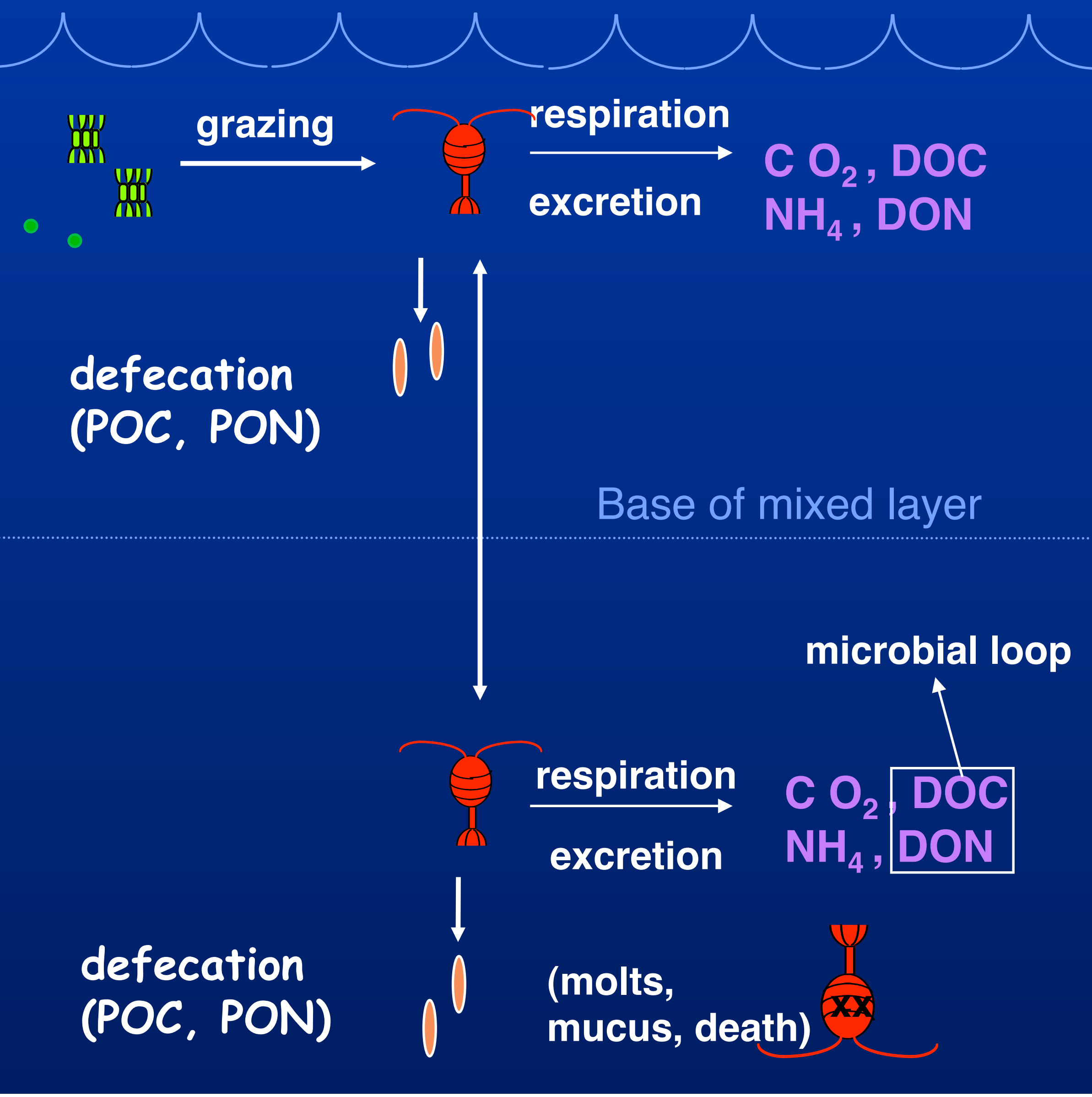
Export/vertical flux is not necessarily related to primary productivity in a positive and linear fashion, but likely is driven by short-term events and the biological composition of the surface assemblage.

The Biological Pump

2. Diel vertical migration



Vertical Migration and active transport

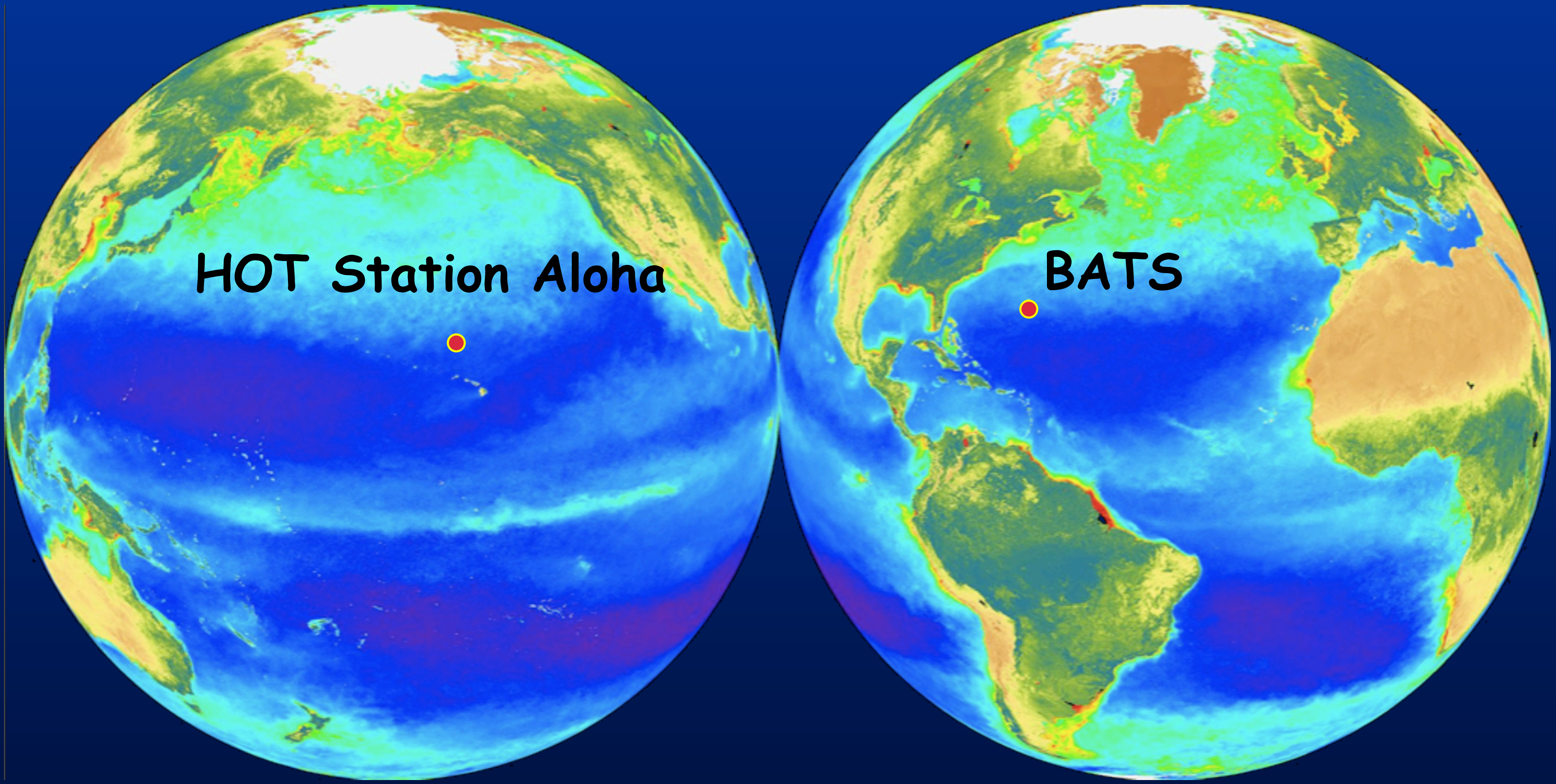


Vertical migrators

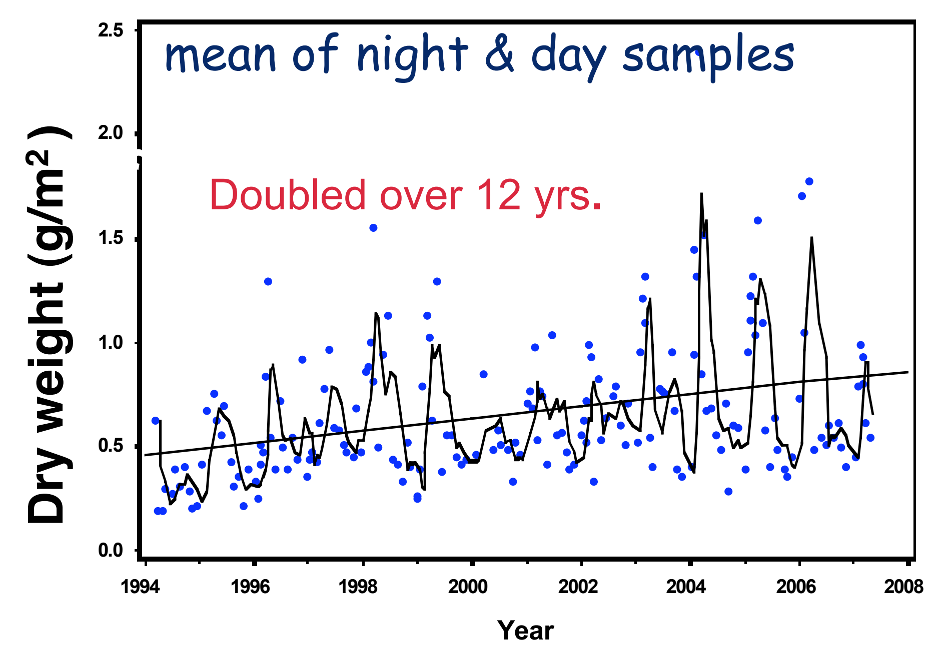
Some examples from U.S. JGOFS time-series sites

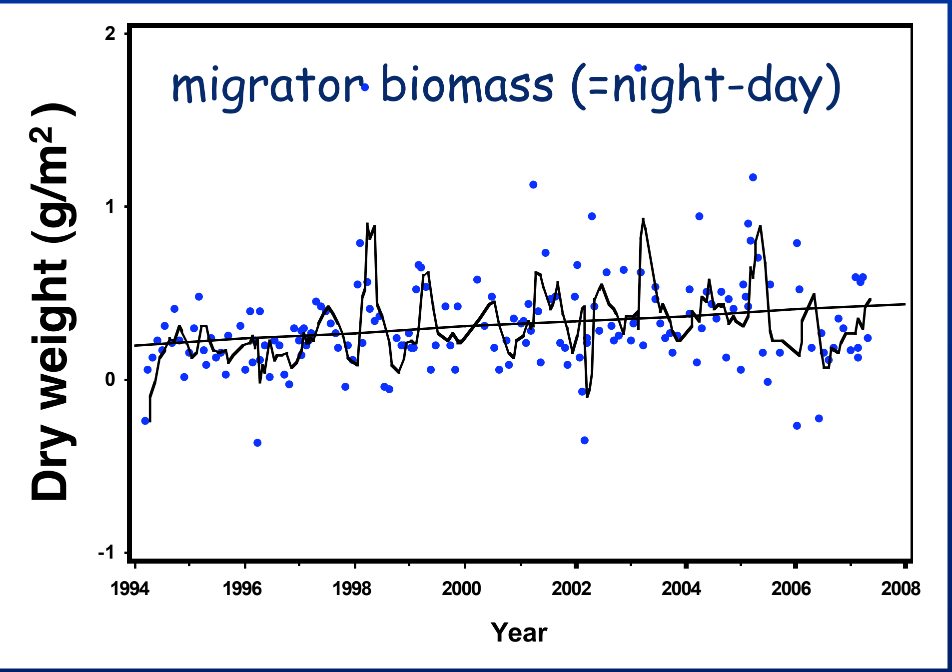
Hawaii Ocean Time-series

Bermuda Atlantic Time-series Study



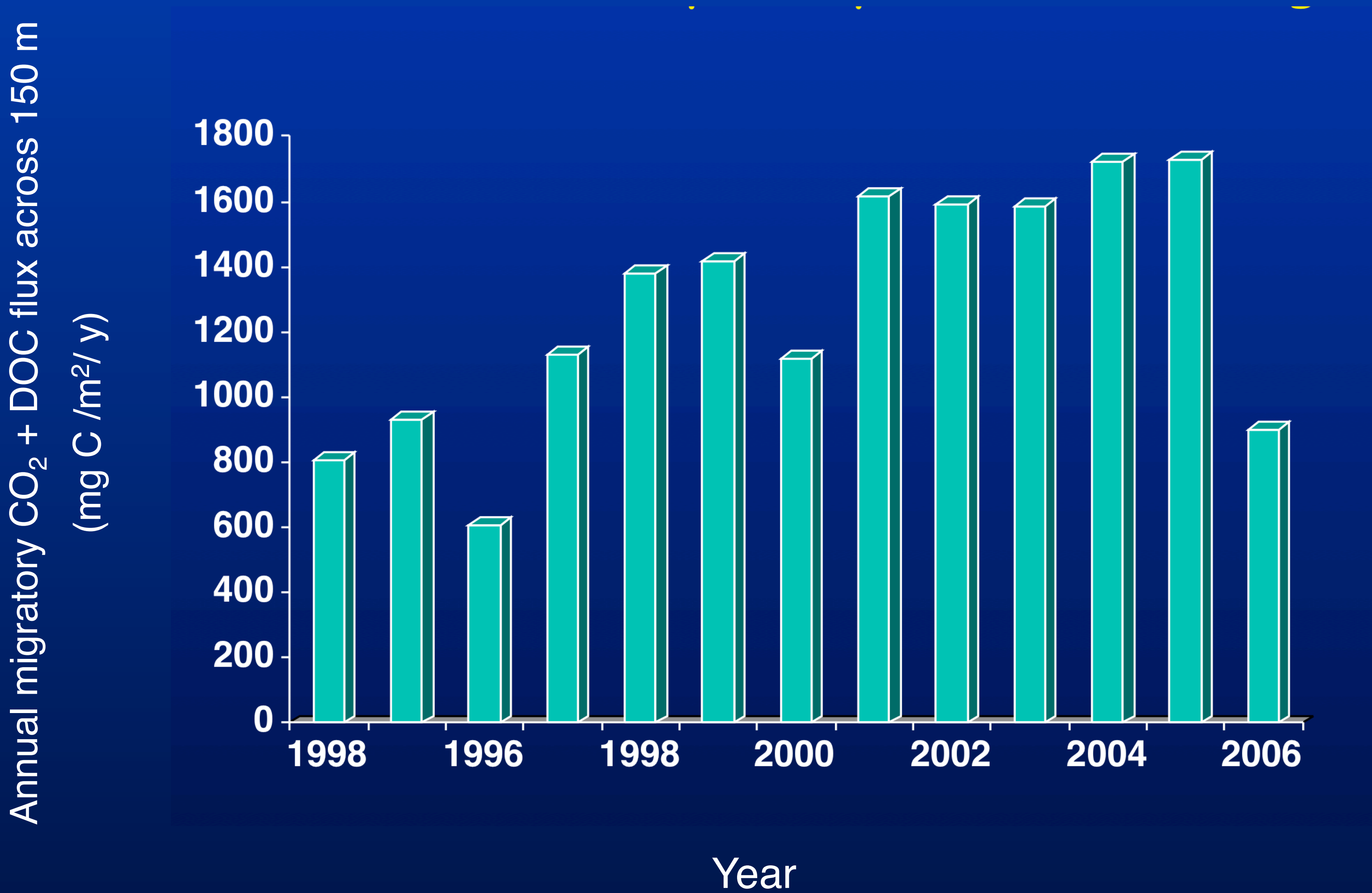
Increase in mesozooplankton biomass at BATS





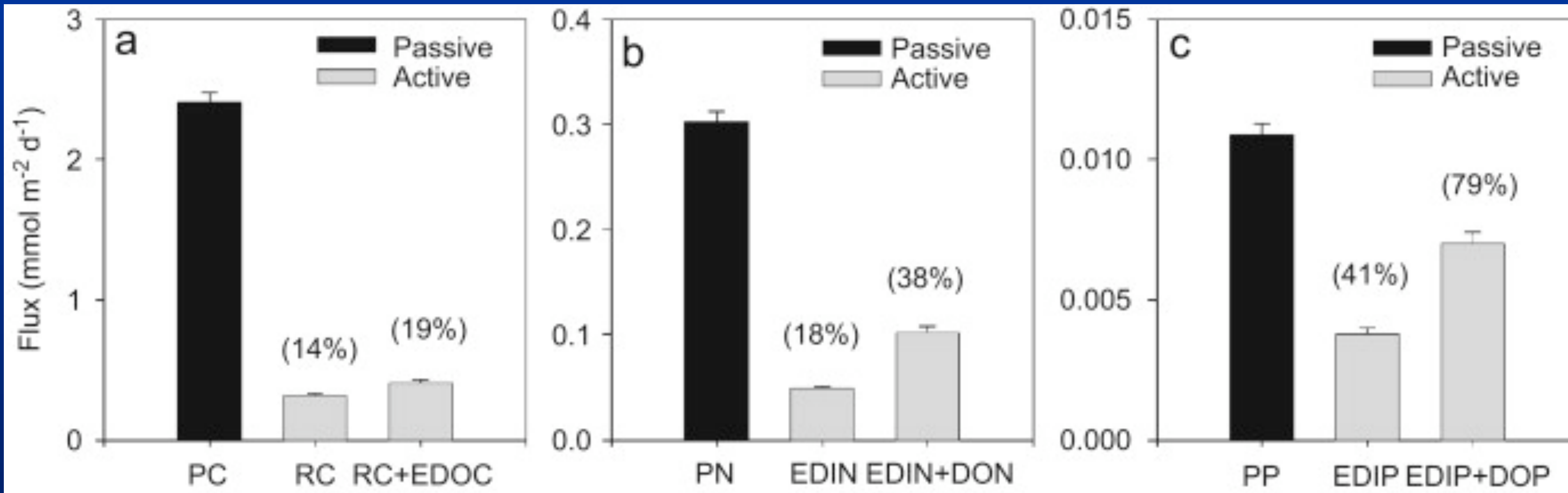
(same happening at HOT)

Increase in active transport by diel vertical migrators



Calculated as in Steinberg et al. (2000), Lomas et al. (2002)

Passive vs. active transport at station ALOHA

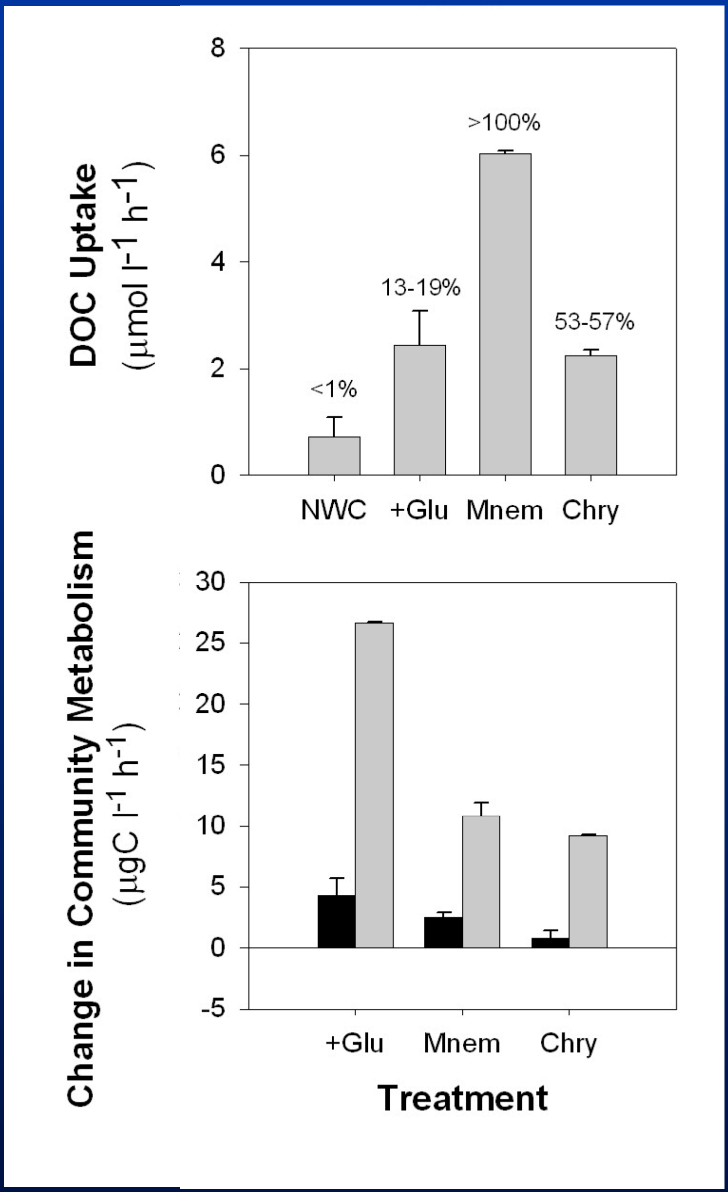


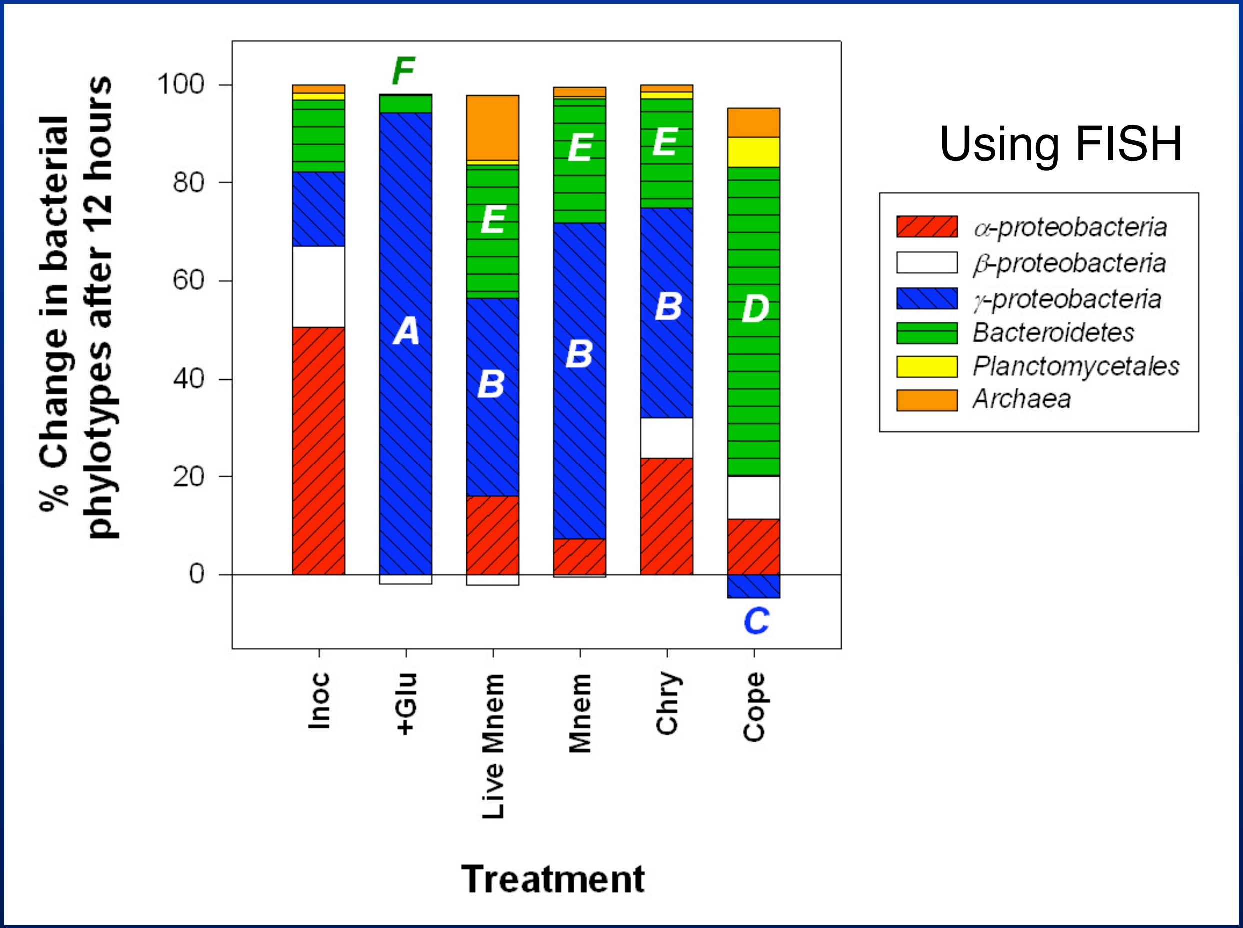
Percentages above active flux estimates are active fluxes as mean percentage of passive particle fluxes

Active transport is an especially important mechanism for phosphorus (P) removal from the euphotic zone
enhanced P-limitation of biological production in the N. Pacific subtropical gyre

(Hannides et al. 2008)

Links between zooplankton-DOM and microbial community





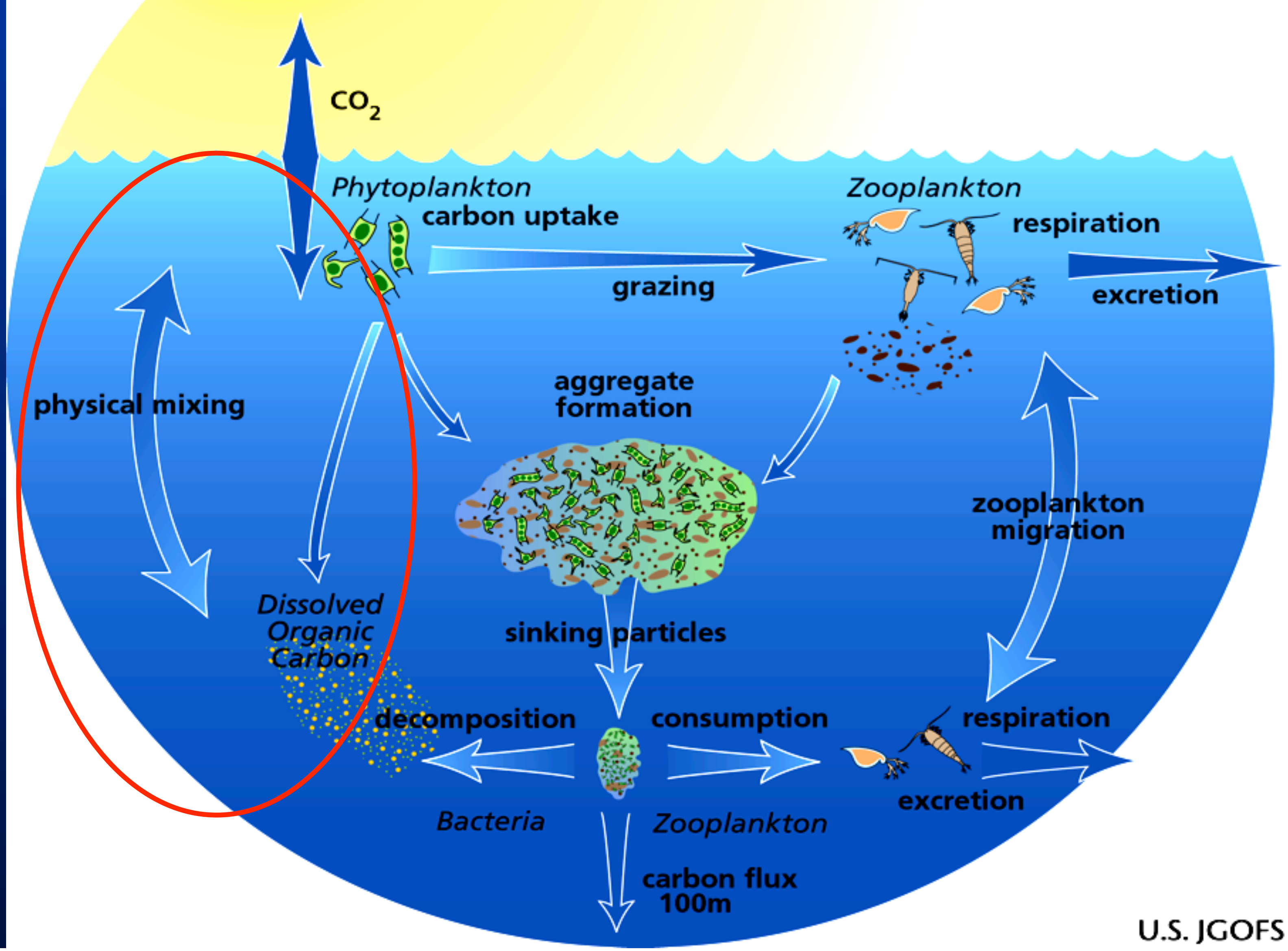
Rob Condon, in prep.

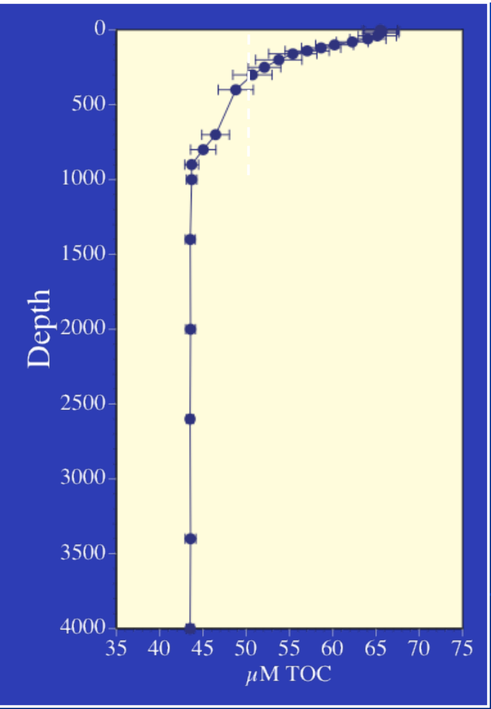
Location	Migratory flux (mg C/m^2/d)	Migratory flux as % of POC flux
Subarctic Atlantic (NABE)	?	?
Subtropical Atlantic (BATS)	4	12%
Subtropical & Tropical Atlantic	3-9	4-14%
Subarctic Pacific (K2)	16-46	26-200%
Subtropical Pacific (ALOHA)	2-8 5	11-44% 19%
Equatorial Pacific	4-7 4-8	18-25% 4-8%

Diel migratory active dissolved C flux vs. passive POC flux across 150 m. High and low latitude N. Atlantic and N. Pacific sites are compared. (Refs: Longhurst et al. 1990; Steinberg et al. 2000, 2008b; Zhang & Dam 1997, Rodier &Le Borgne 1997; Hannides et al. 2009)

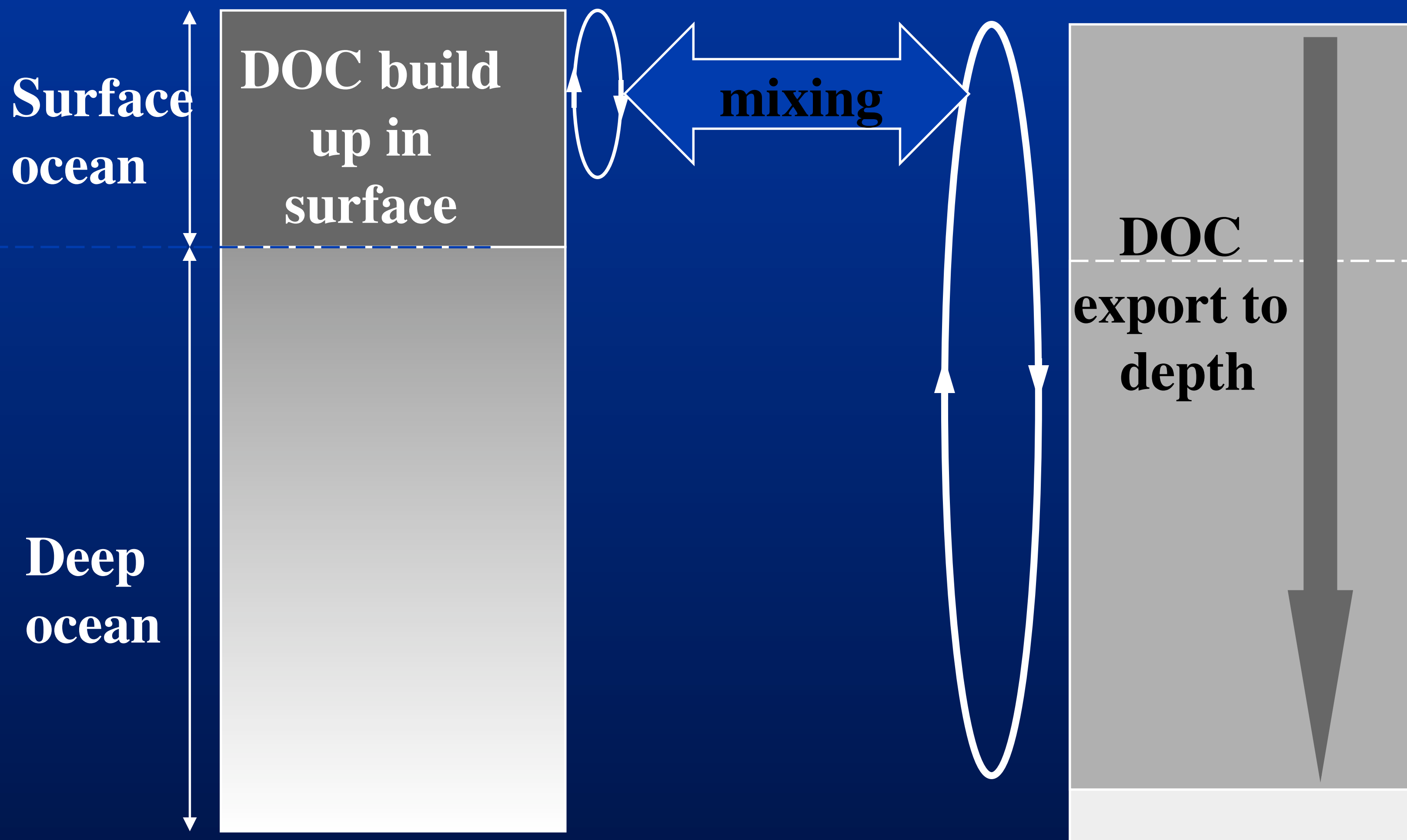
The Biological Pump

3. Vertical advection of DOC

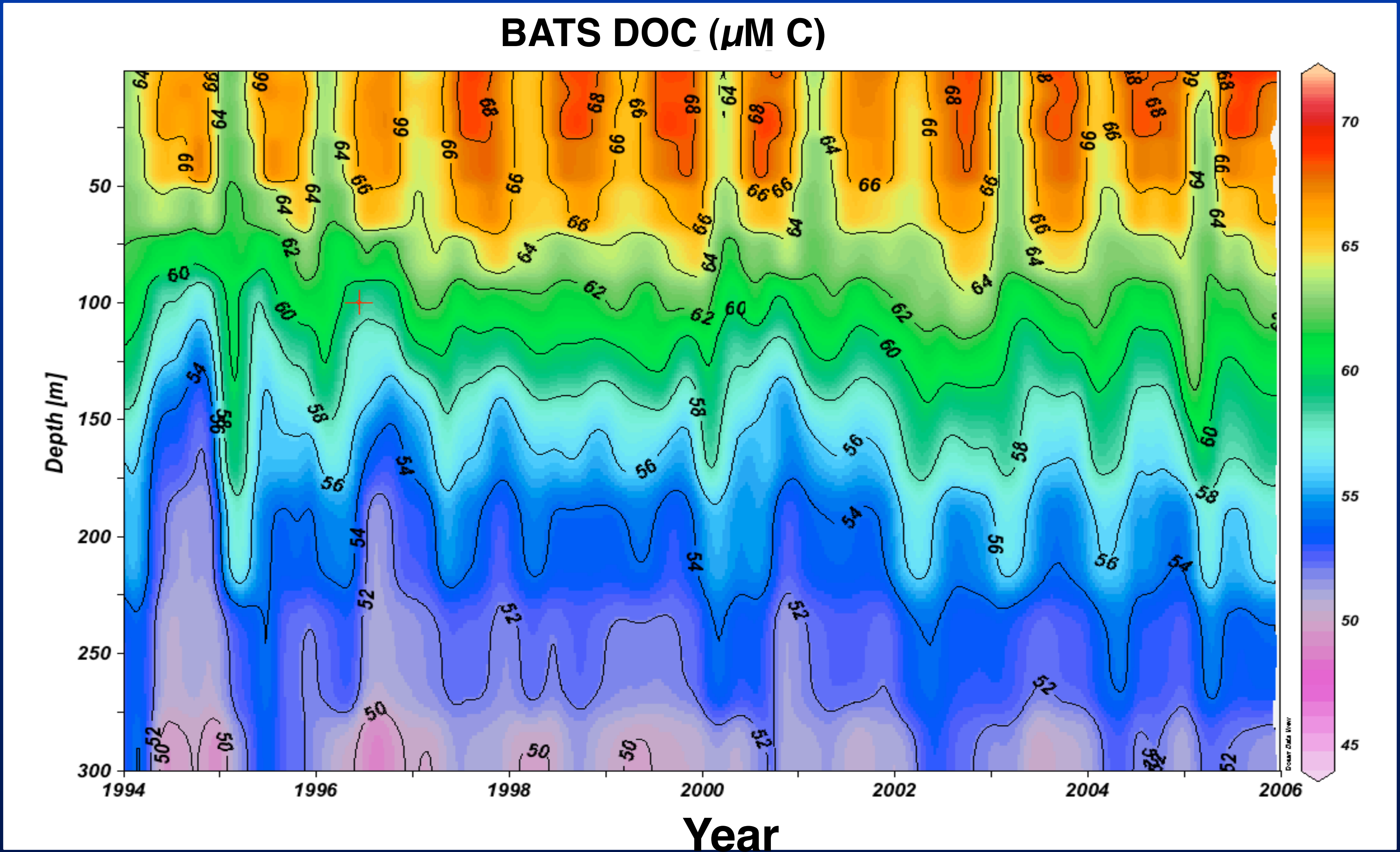



Depth
0
500
1000
1500
2000
2500
3000
3500
4000
35 40 45 50 55 60 65 70 75
μM TOC

DOC export

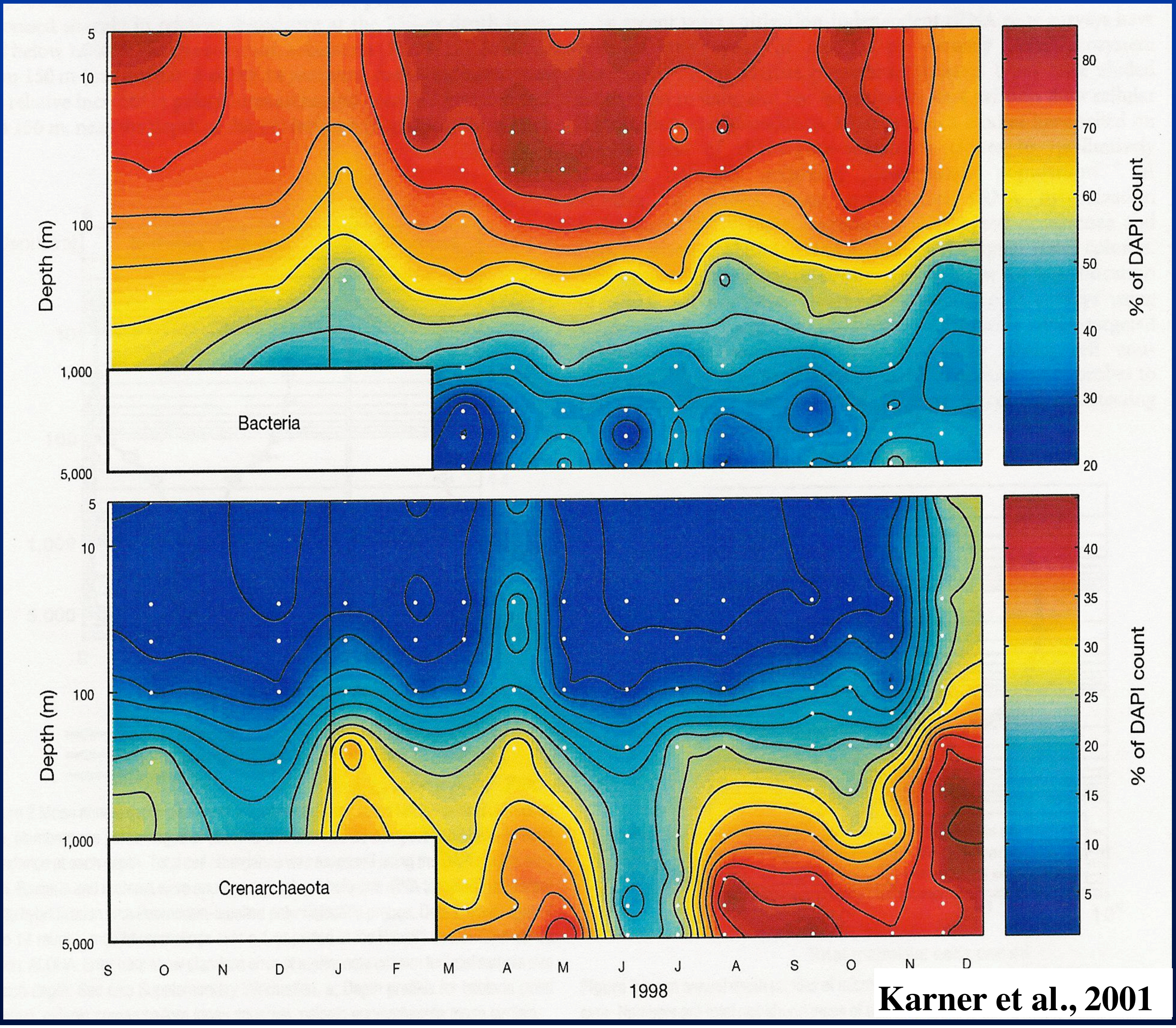

Surface ocean
Deep ocean
DOC build up in surface
mixing
DOC export to depth

Vertical export of DOC via seasonal advective overturn



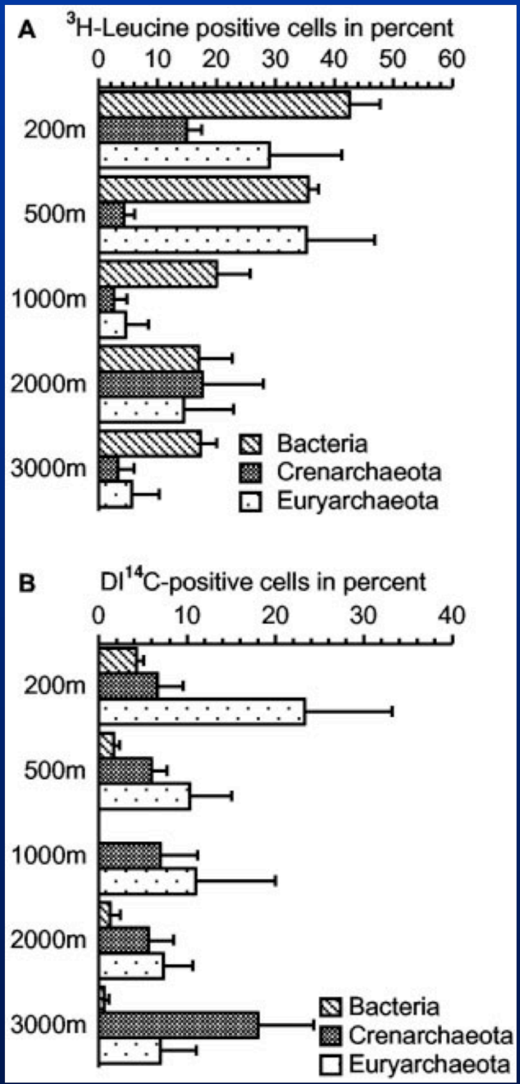
C. Carlson, updated from Hansell & Carlson 2001

Archaea abundance in N. Pacific Gyre



Karner et al., 2001

Meso- and bathypelagic Archaea & Chemoautotrophy



Percentage taking up leucine (A) and bicarbonate (B) at different depth horizons (MICRO-CARD -FISH)

(Herndl et al. 2005)

- Oxidize ammonia for energy

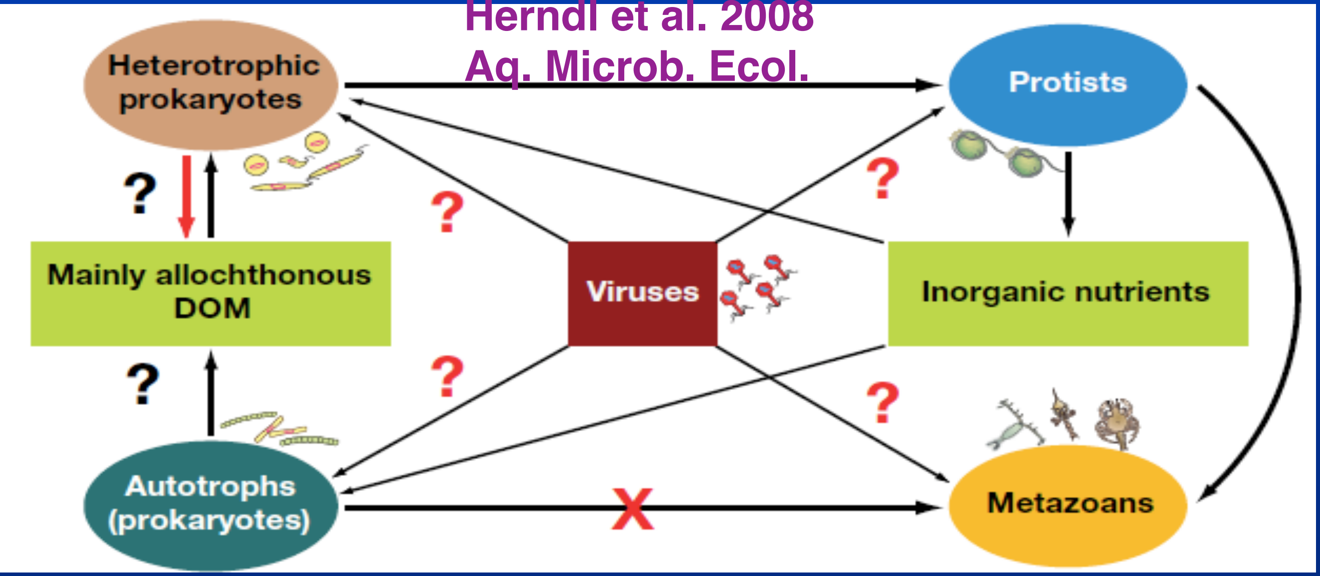
  (Nitrosopumilus maritimus)

- 1mmol C m^{-2} d^{-1} fixation in meso and bathypelagic (Herndl et al. 2005)

- new source of Organic C in the interior

Zooplankton and the Mesopelagic Microbial Loop: Recent Views

Herndl et al. 2008
Aq. Microb. Ecol.



- Microbial diversity
- Particle-associations
- Bottom-up control at depth vs. top-down control near surface

- Importance of vertical migrators in transporting C to depth and supplying mesopelagic C demand

Steinberg et al. 2008
Limnol. Oceanogr.