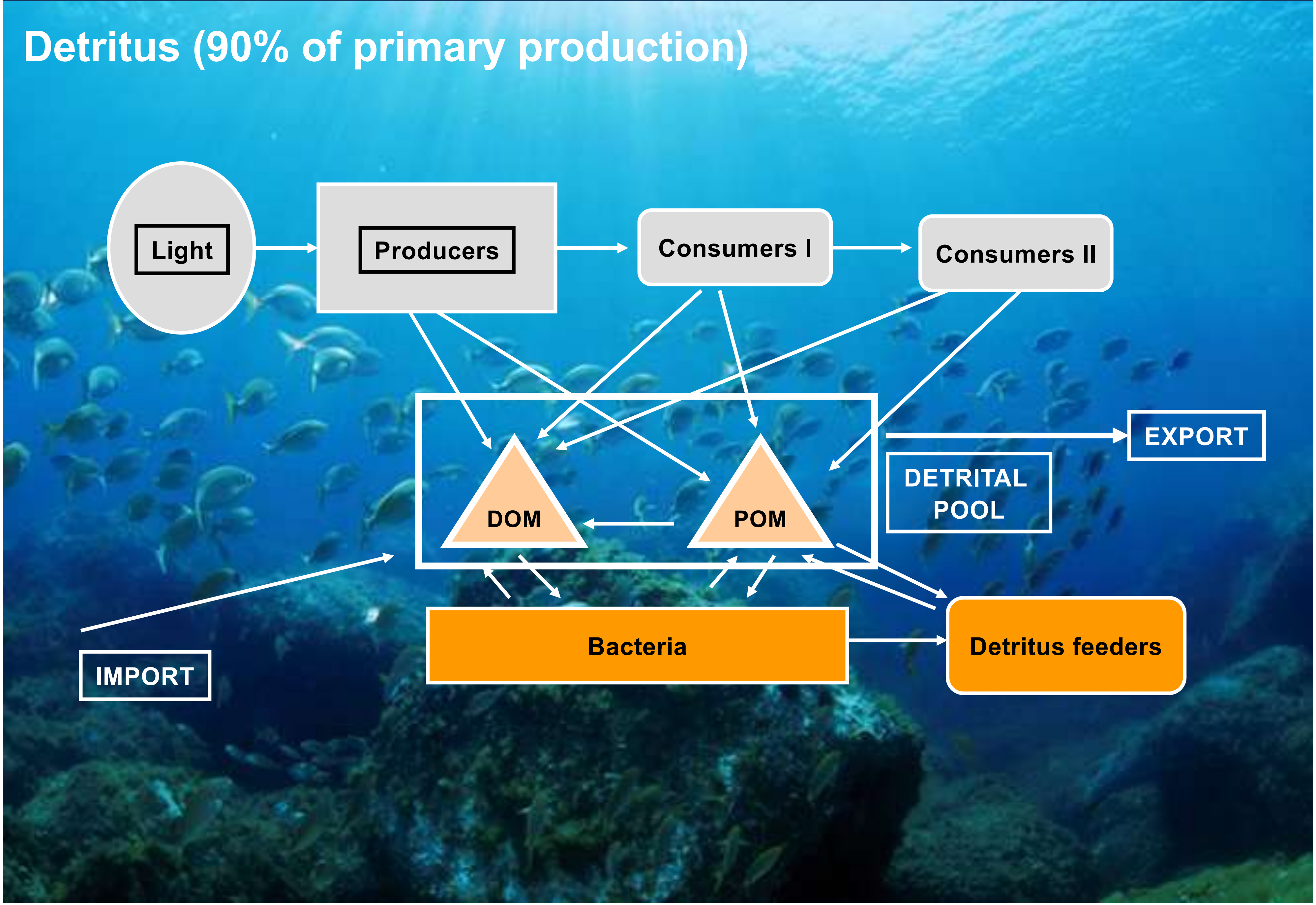
Trophic chains and the importance of detritus



Detritus

“non-predatory loss of organic carbon from each trophic level or inputs from external sources”
(Wetzel et al.,1972)

So, everything non-living and organic, irrespective of its size, composition and origin

Origin


Terrestrial supply
Small plankton remains
Moults
Fecal pellets
Large animal remains
(fish and mammal carcasses)
Algal and plant debris
(kelp, seagrass, etc.)

Classification of organic matter

1. **Type**: Living (Organisms) 10%
   Detritus (fecal pellets, excretions, etc.) 90%

2. **Size**: DOM (<0.45 μm)
   POM (>0.45 μm)

3. **Sources**: *in situ* production 10-100%
   exogenous 0-90%

4. **Trophism**: Bioavailable 1-10%
   Recalcitrant 90-99%

Type

Most of living organic matter in oceans comes from planktonic and benthonic bacteria, protists, phytoplankton, micro-zooplankton and meiofauna

Larger components are negligible in terms of amount and numbers

Microzooplankton are a group of heterotrophic and mixotrophic planktonic organisms between 20 and 200 µm in size. Important contributors to the group are phagotrophic protists such as flagellates, dinoflagellates, ciliates, radiolarians, foraminiferans, etc., and metazoans such as copepod nauplii, rotiferans and meroplanktonic larvae, among others.

Trophism

POM is composed by proteins, carbohydrates and fat acids

DOM is composed by a huge range of substances of molecular weight from very few until >100.000 d, and includes, for instance,

a. virus
b. carbohydrates (glucose, 50-60%)
e. aromatic compound (e.g., phenol, lignin, lipids)
f. amino acids
g. DNA and RNA

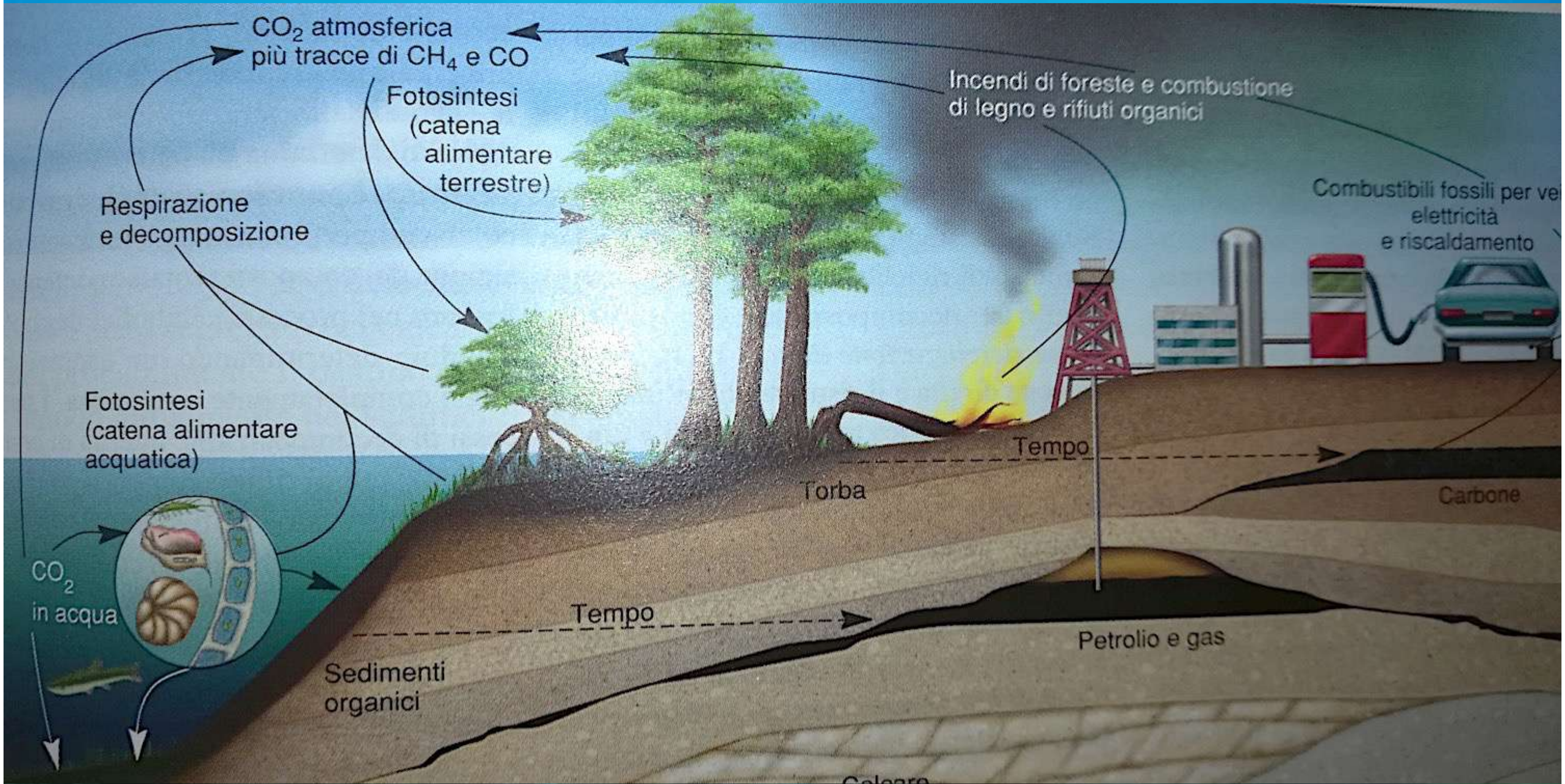
DOM pool is largely produced by phytoplankton and decomposition or bacterial and virus action

DOC/POC ratio 10-20:1 in the water column
DOC < 5% del TOC in sediments

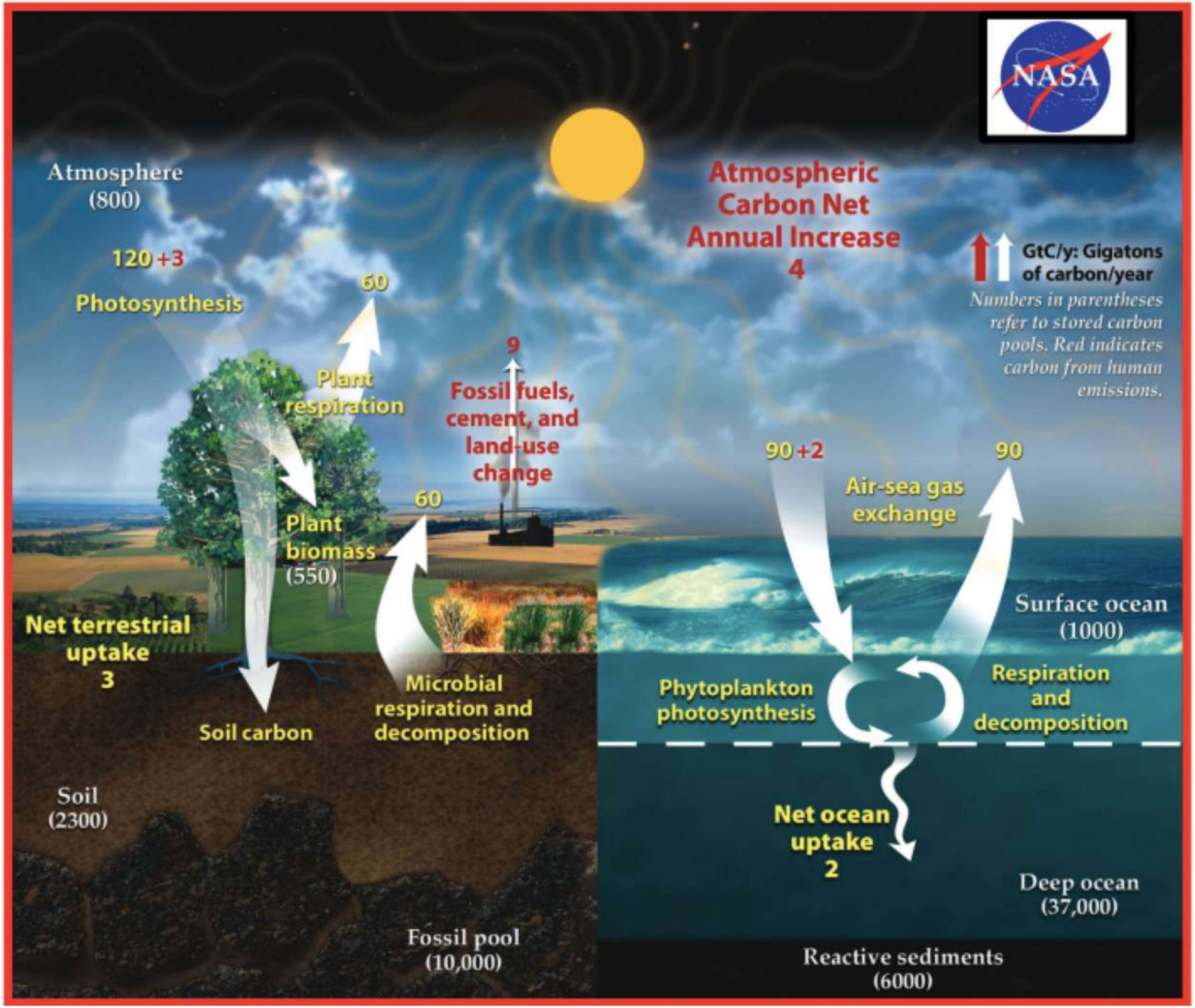
Labile organic matter is easily and rapidily available to be remineralized by organisms, whereas recalcitrant organic matter is formed during decomposition and other processes (agglomeration), and is difficult to be degraded by bacteria unless during long periods. Example: CRAM (carboxyl-rich alicyclic molecules) amino-sugars, amino acids, terpenoids, lignin)

Carbon

1,85 billions Gt on Earth. Only 44.000 Gt are on the surface of the planet, while the remaining is in the nucleus and the mantle. 94% of carbon on the surface is stocked into the ocean (water and sediments, mostly as bicarbonate and carbonate ions), 4.5% in the biosphere and 1.5% in the atmosphere.



Carbon cycle and balance



Short term cycle (1-10^3y).

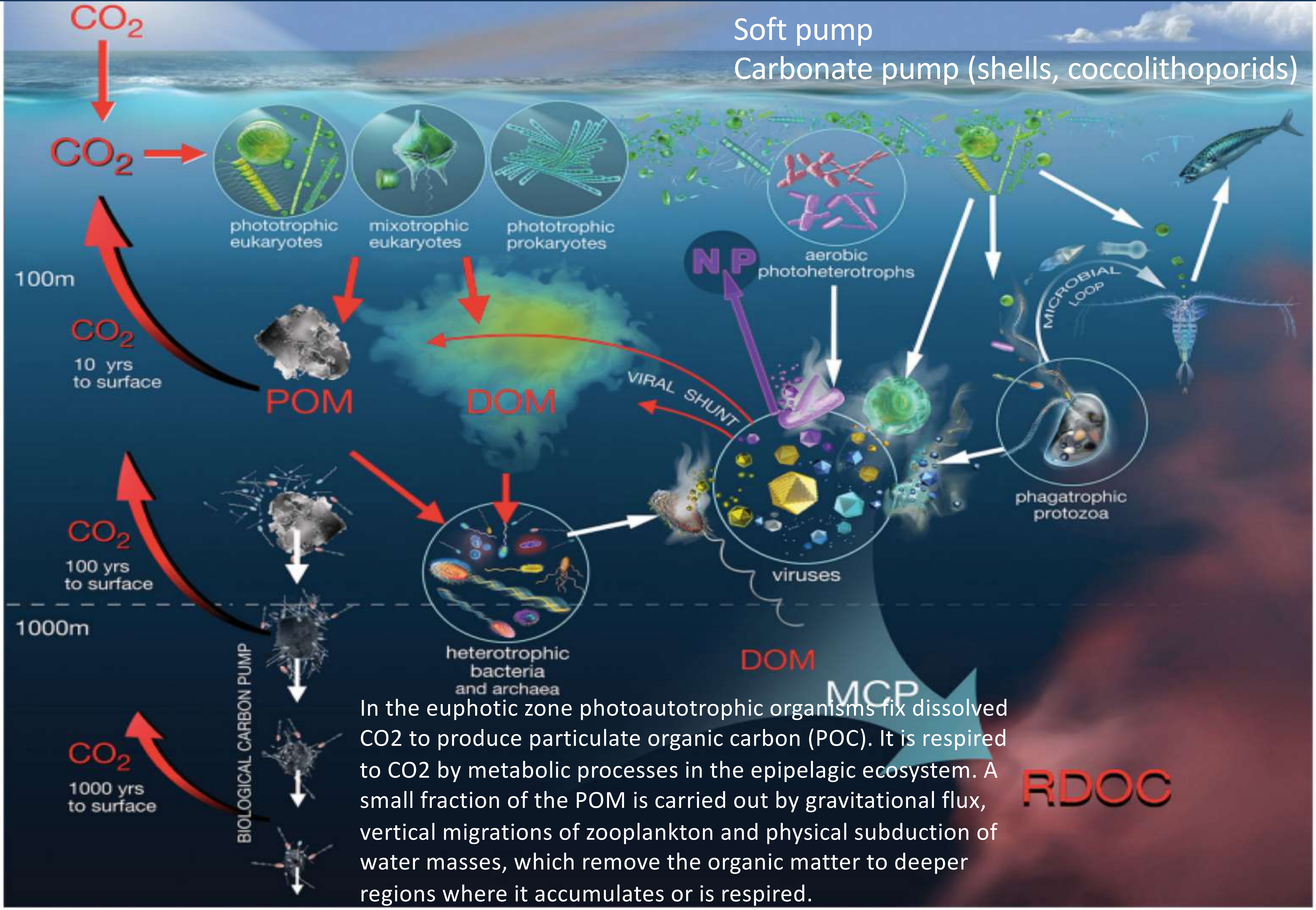
The second part of the whole cycle consists of a long term cycle (10^4-10^6y), through weathering, volcanic activities, subduction of sediments and rocks, huge stocks in soil.

BCP, ML, and MCP

Table 1. Definitions and major impacts of the BCP, ML and MCP.

Concept	Definition	Major impacts and focus
Biological pump	A complex ecosystem process that transports particulate organic carbon from the epipelagic zone to the deep interior of the ocean and further to the ocean floor	Sequestration of atmospheric CO_2 through vertical transportation of living biomass to marine sediments; focusing on sediment storage
Microbial loop	A 'feedback' pathway of loss of the primary production to the environment in the form of dissolved organic matter and the utilization of the latter by bacteria that feed the protozoa, which enter the food chain	The role of bacteria in sequestering nutrients from the environment, which are consumed by protozoa; focusing on organismal populations above thermocline
Microbial carbon pump	A conceptual framework for understanding the role of microbial processes in the production of recalcitrant dissolved organic matter in the ocean water column	Sequestration of atmospheric CO_2 through transformation of labile organic matter to recalcitrant organic matter; focusing on capacity of the ocean to store atmospheric CO_2

Biological Carbon Pump

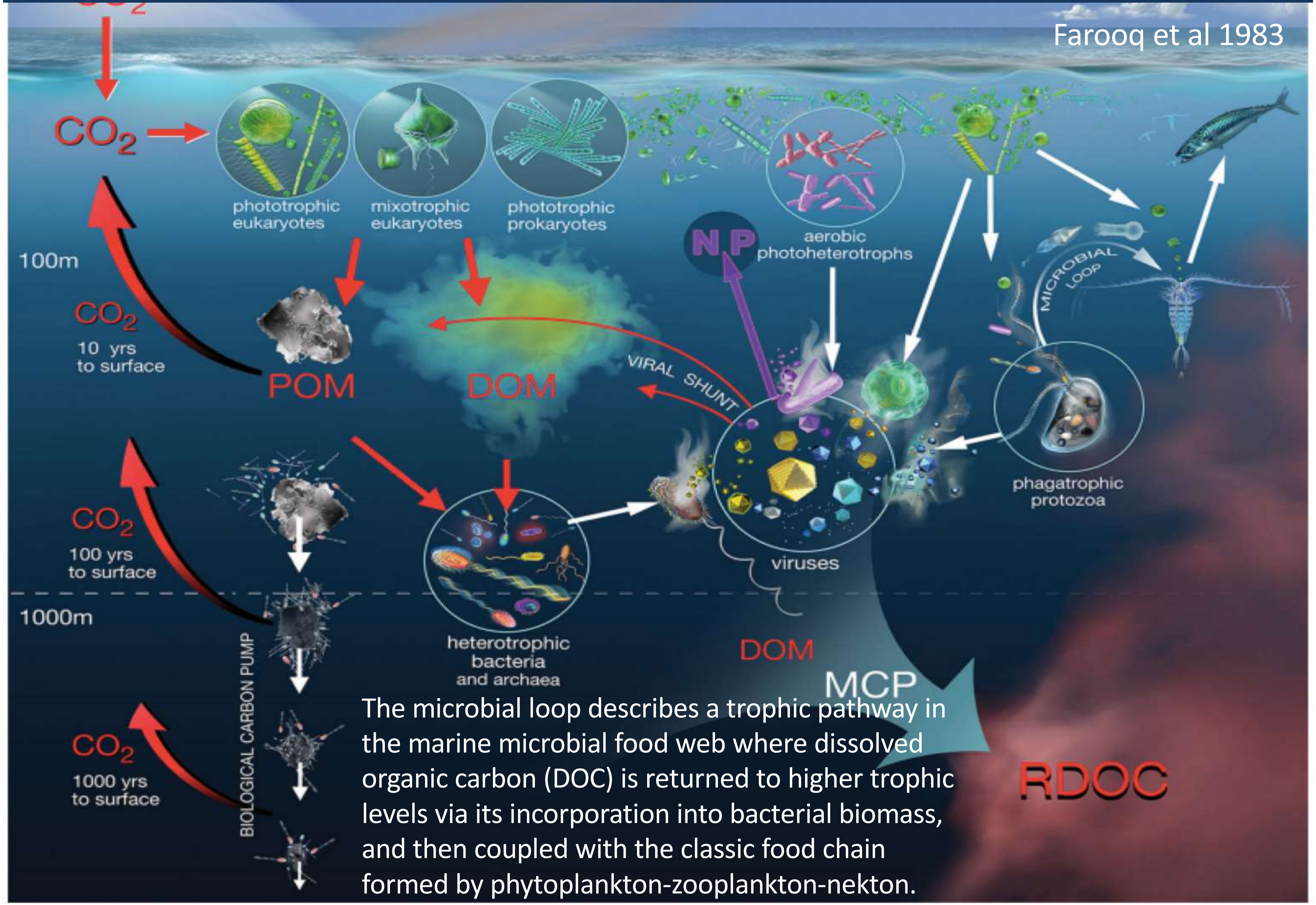


Soft pump

Carbonate pump (shells, coccolithoporids)

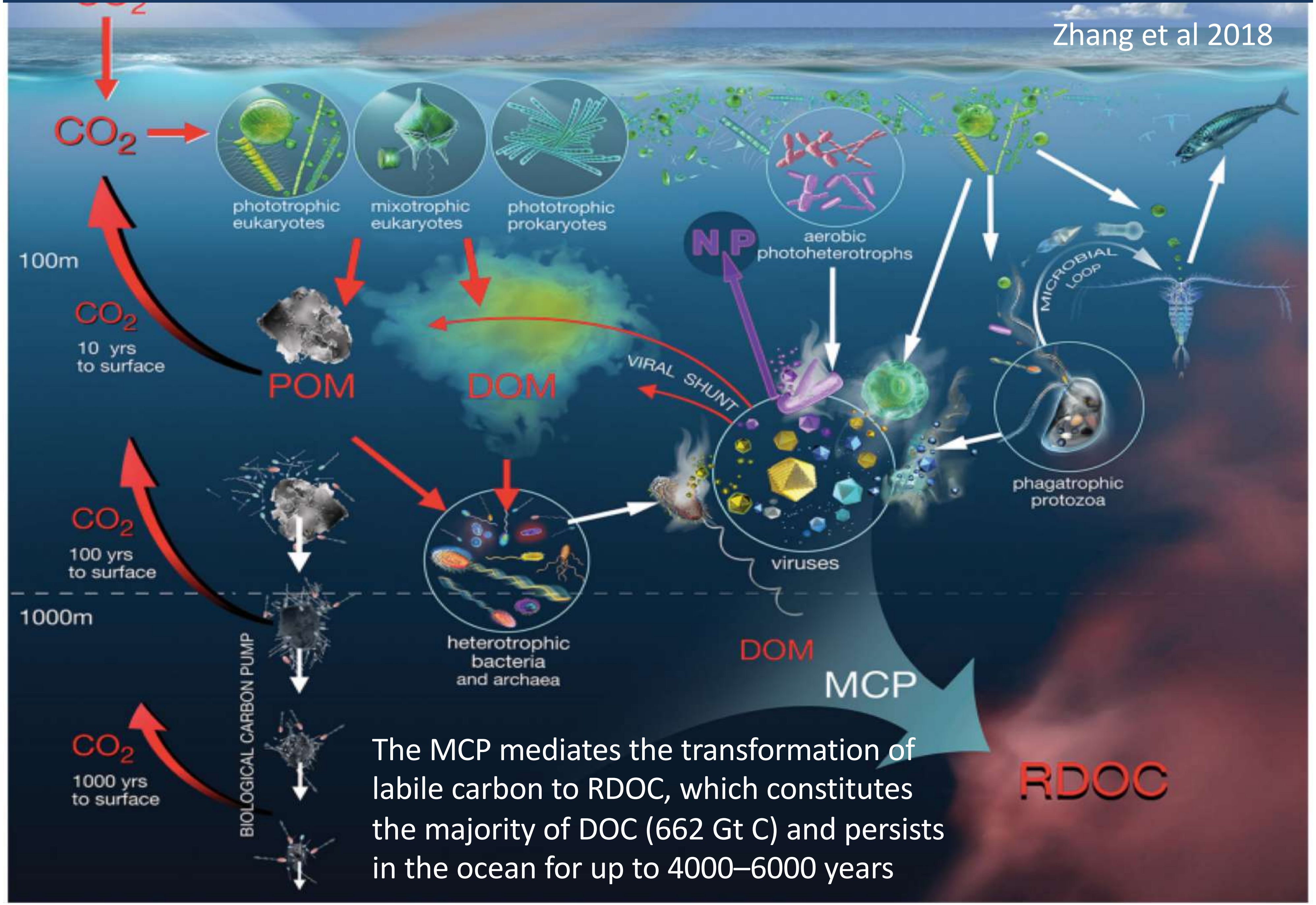
In the euphotic zone photoautotrophic organisms fix dissolved CO2 to produce particulate organic carbon (POC). It is respired to CO2 by metabolic processes in the epipelagic ecosystem. A small fraction of the POM is carried out by gravitational flux, vertical migrations of zooplankton and physical subduction of water masses, which remove the organic matter to deeper regions where it accumulates or is respired.

Microbial loop



The microbial loop describes a trophic pathway in the marine microbial food web where dissolved organic carbon (DOC) is returned to higher trophic levels via its incorporation into bacterial biomass, and then coupled with the classic food chain formed by phytoplankton-zooplankton-nekton.

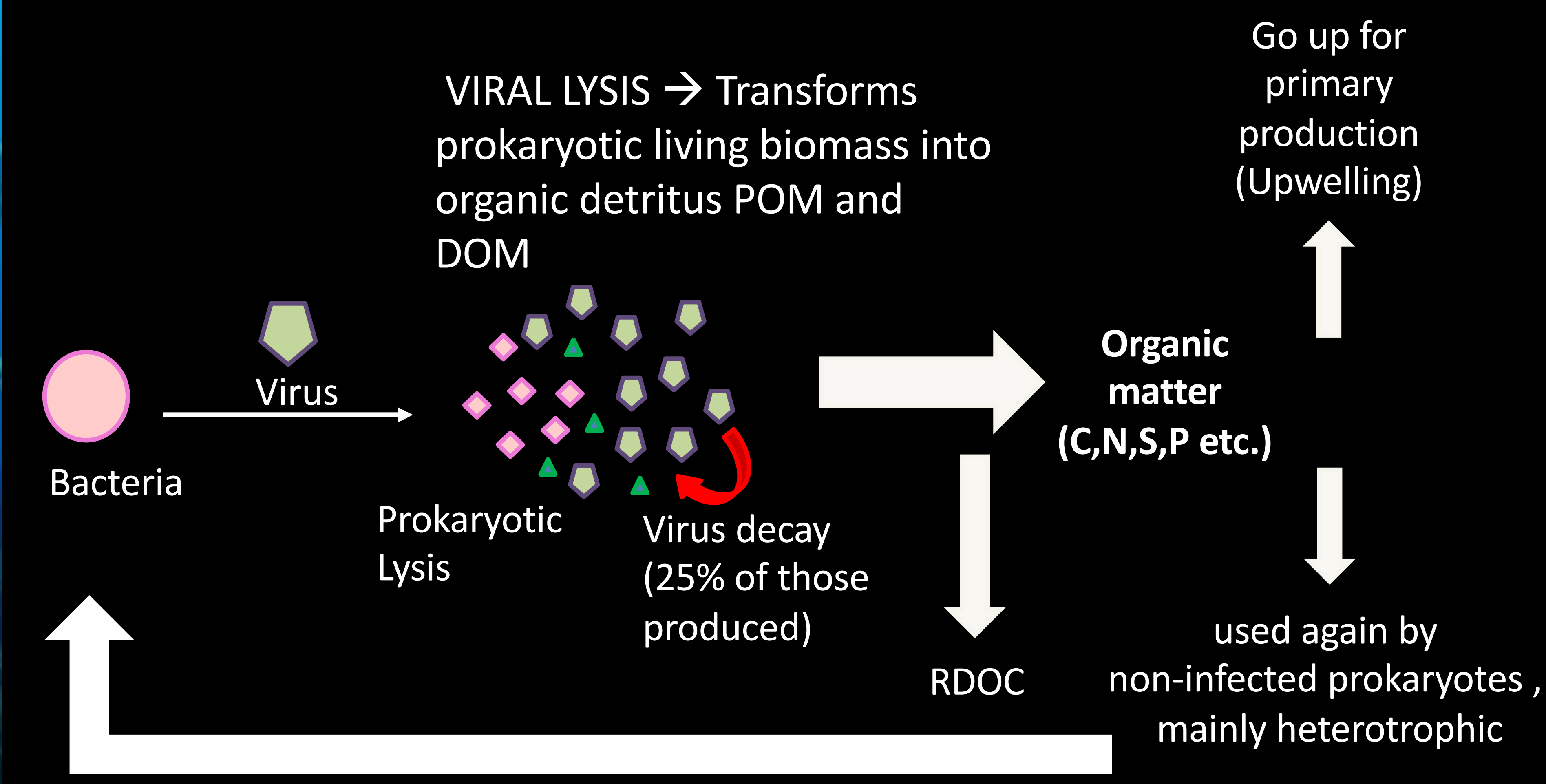
Microbial Carbon Pump



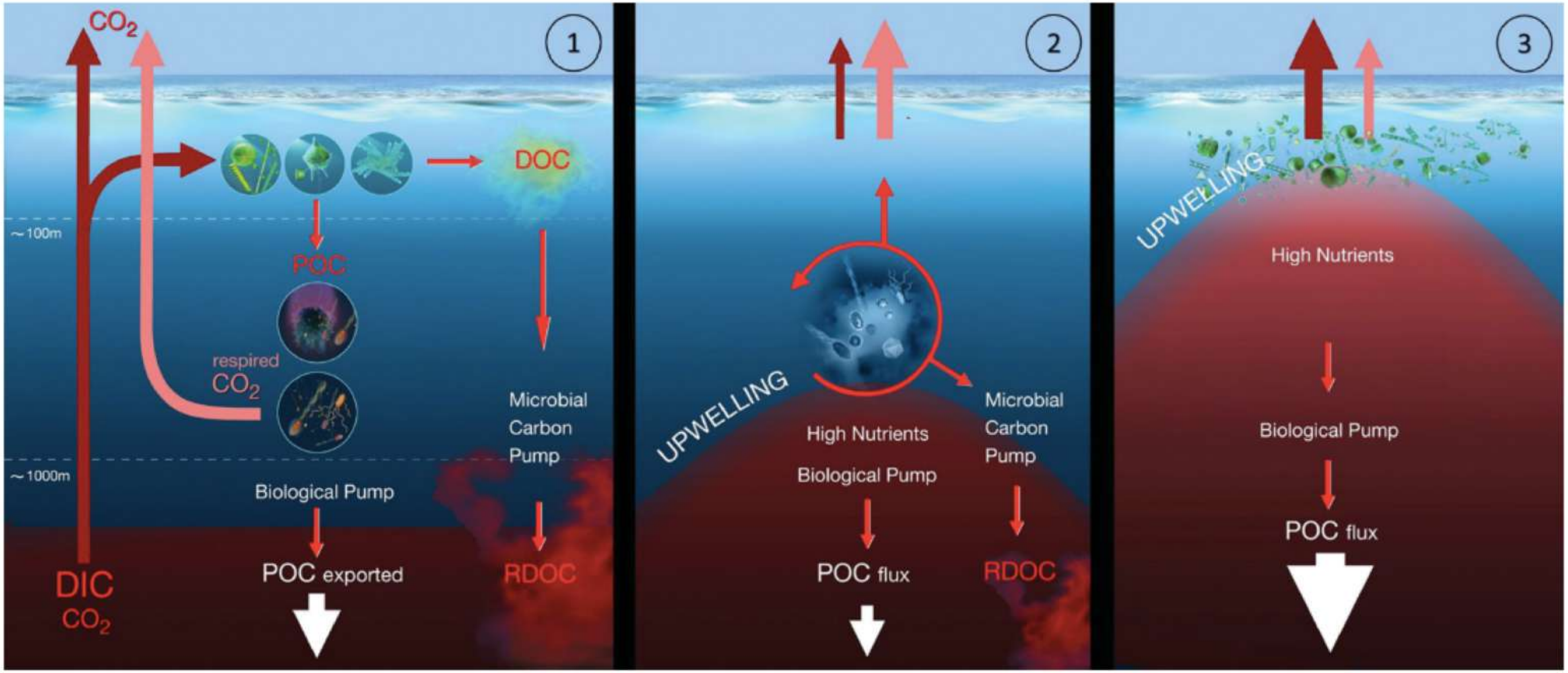
The MCP mediates the transformation of labile carbon to RDOC, which constitutes the majority of DOC (662 Gt C) and persists in the ocean for up to 4000–6000 years

Viral shunt

This process sustains a high prokaryotic biomass and provides an important contribution to prokaryotic metabolism, allowing the system to cope with the severe organic resource limitation of deep-sea ecosystems



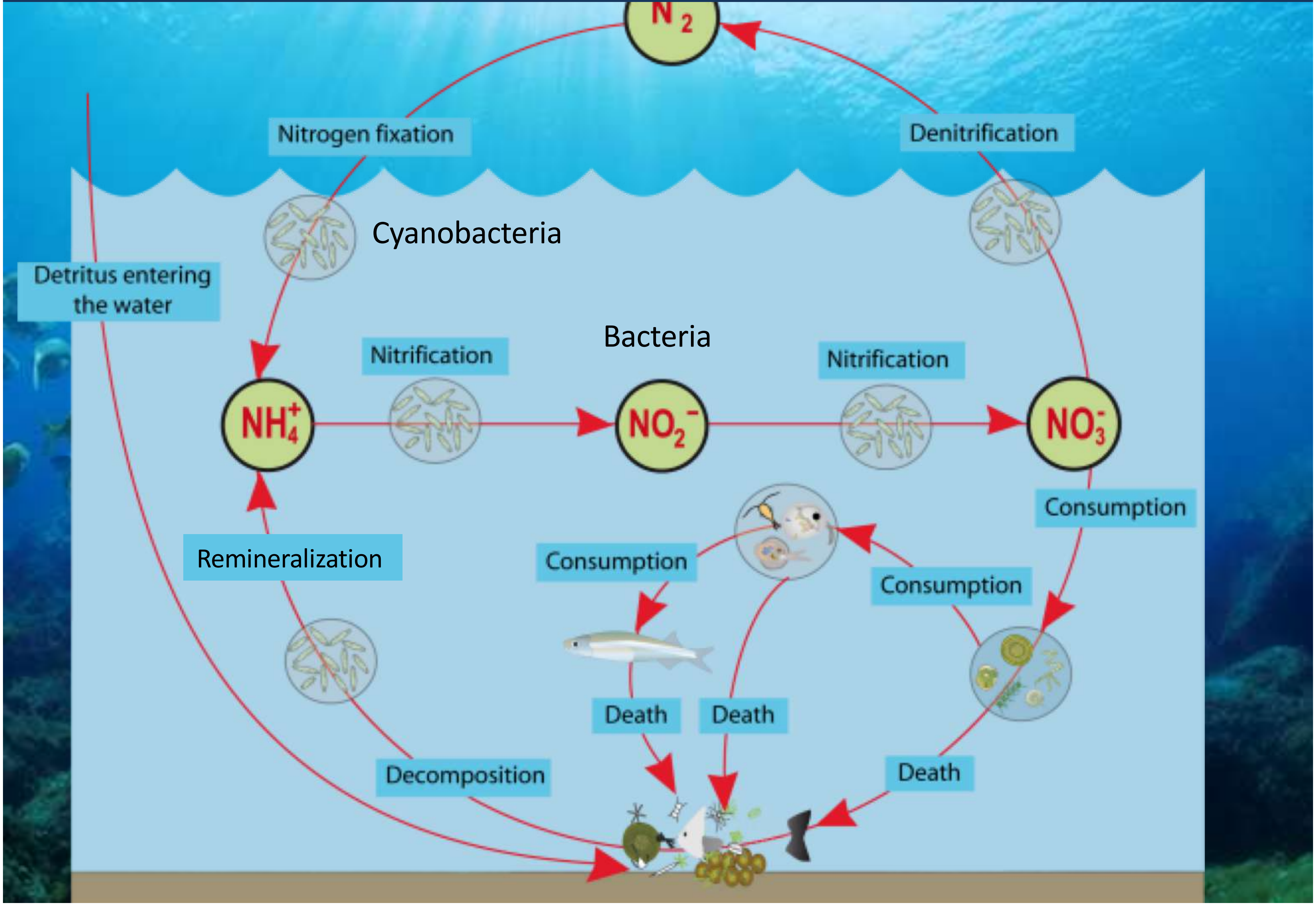
The viral shunt, releasing on a global scale , **37-50 megatons of carbon per year**, is an essential source of labile organic detritus in the deep-sea ecosystems



(1) Functioning of the BCP and the MCP in a non-upwelling region of the ocean. (2) Dominance of the MCP in scenario 1 where the total upward CO2 flux exceeds downward POC export flux: nutrients are injected only into the lower layer of the euphotic zone; *Prochlorococcus* is dominant; CO2 outgassing exceeds POC export; the MCP is the prevailing mechanism for carbon sequestration. (3) Dominance of the BCP in scenario 2 where the downward POC flux exceeds the total upward CO2 flux: nutrients are injected into the upper layer of the euphotic zone; diatoms are dominant; POC export exceeds CO2 outgassing; the BCP is the prevailing mechanism for carbon sequestration.

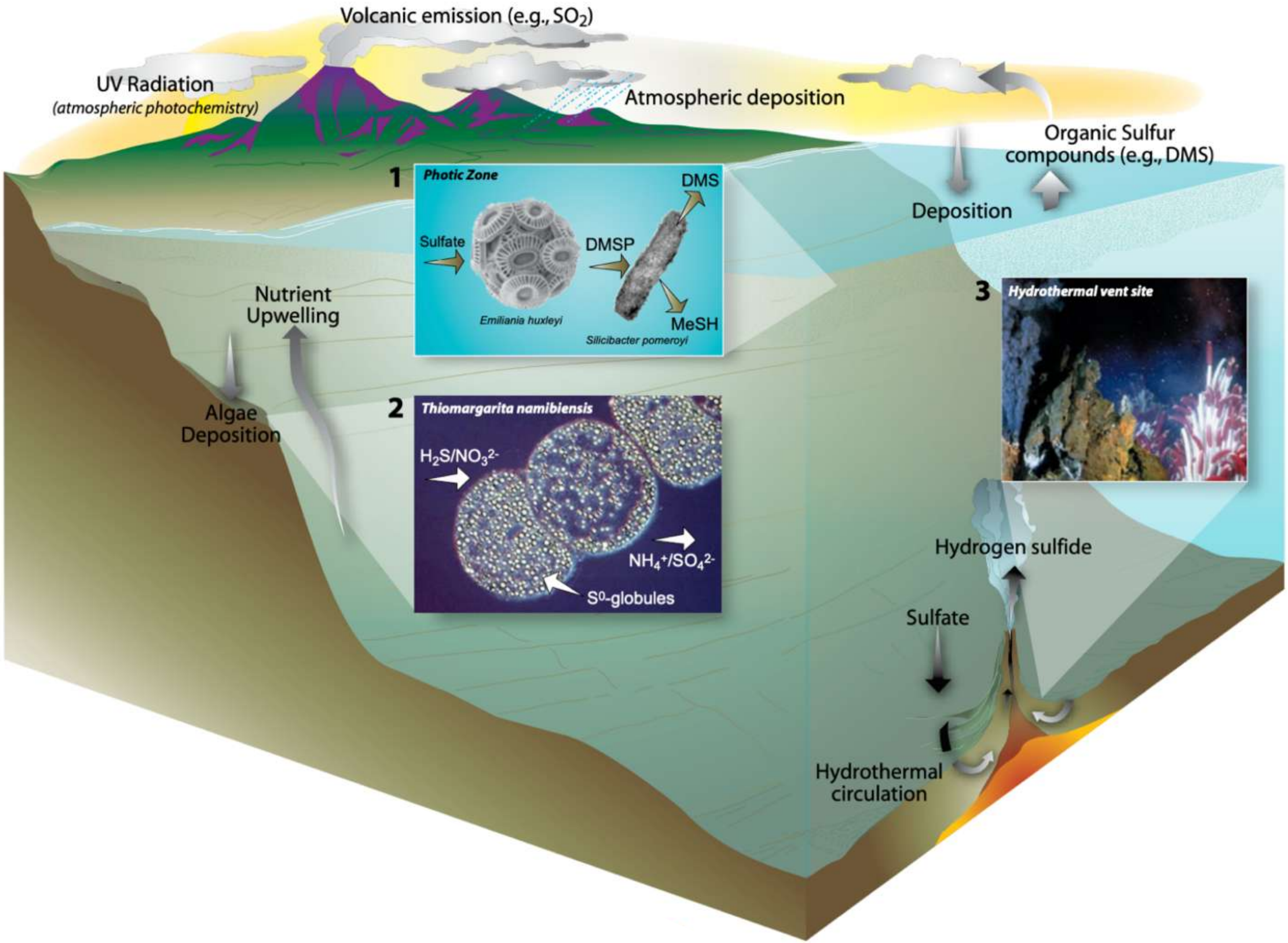
Terrestrial export of nutrients

N cycle



N2
Nitrogen fixation
Denitrification
Cyanobacteria
Detritus entering the water
Nitrification
Bacteria
Nitrification
NH4+
NO2-
NO3-
Consumption
Remineralization
Consumption
Consumption
Death
Death
Death
Decomposition

S cycle

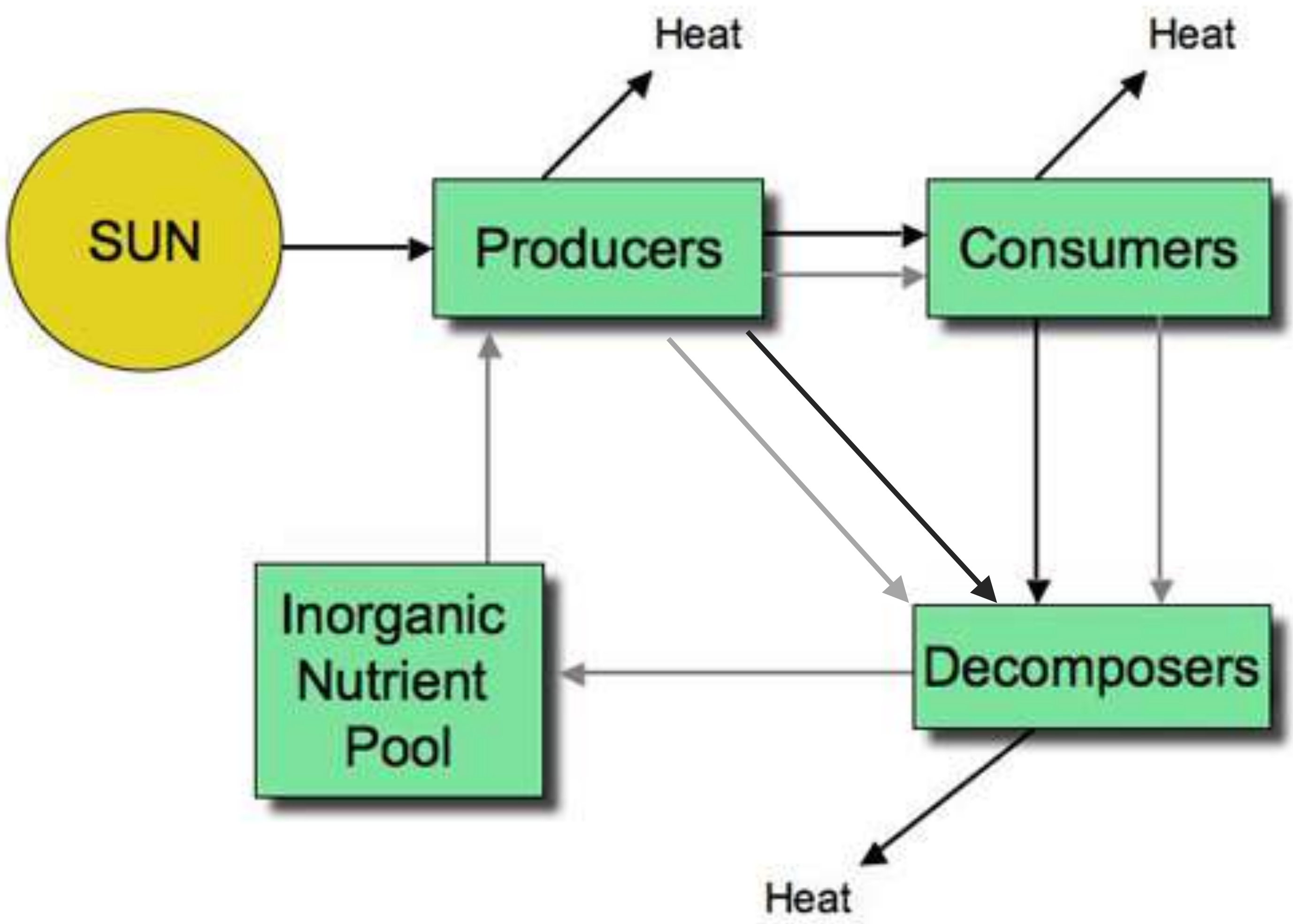


Volcanic emission (e.g., SO_2)
UV Radiation
(atmospheric photochemistry)
Atmospheric deposition
Organic Sulfur compounds (e.g., DMS)
Deposition
1
Photic Zone
DMS
Sulfate
DMSP
MeSH
Emiliania huxleyi
Silicibacter pomeroyi
Nutrient Upwelling
Algae Deposition
2
Thiomargarita namibiensis
H_2S/NO_3^{2-}
NH_4^+/SO_4^{2-}
S^0-globules
3
Hydrothermal vent site
Hydrogen sulfide
Sulfate
Hydrothermal circulation

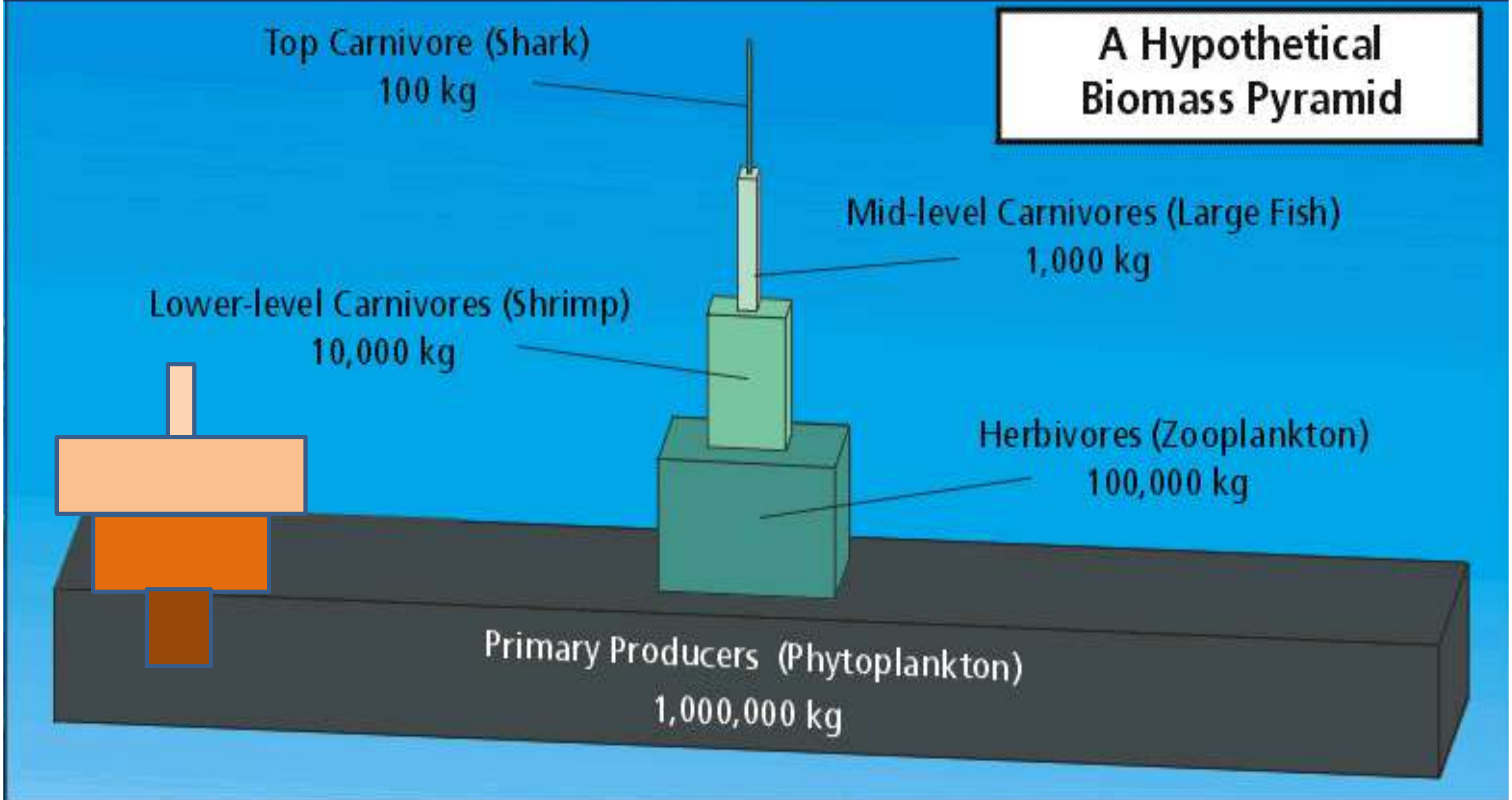
Trophic webs

1 law of thermodynamics

2 law of thermodynamics



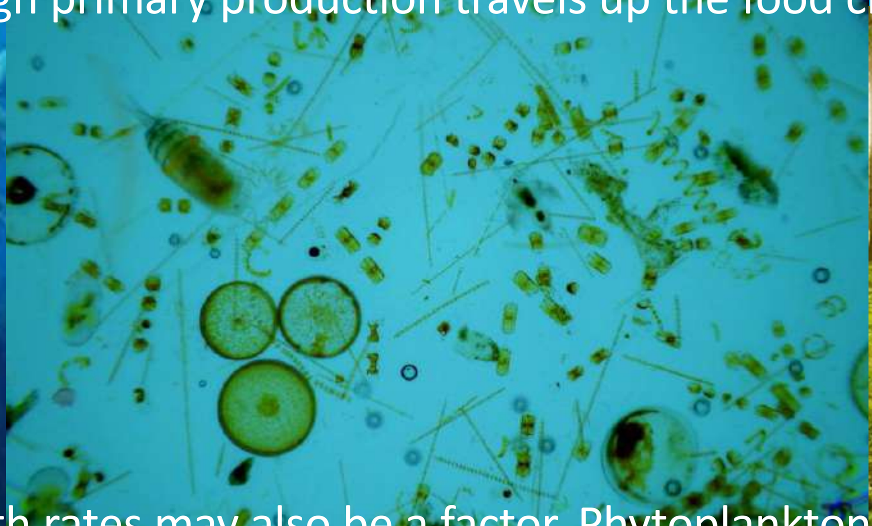
Energy flow

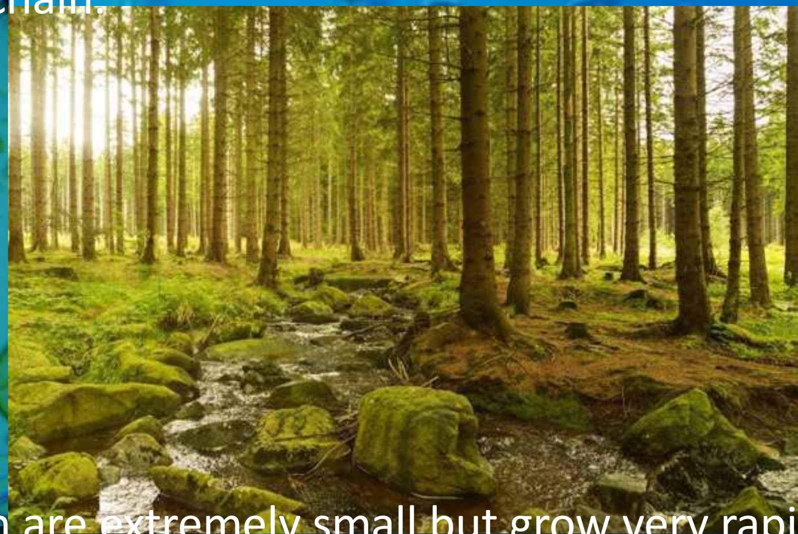


Efficiency of energy transfer is low, 10% on average at each trophic level. This is reflected in the biomass ratio between levels. Most of energy is lost in movement, excretions, fecal dejections, heat, so that moving from the basis (primary producers) to higher levels, the total sustainable biomass is drastically reduced. In some cases, in marine environments, the pyramid can be inverted because of differences in temporal turnover of organisms across levels

Differences between land and sea

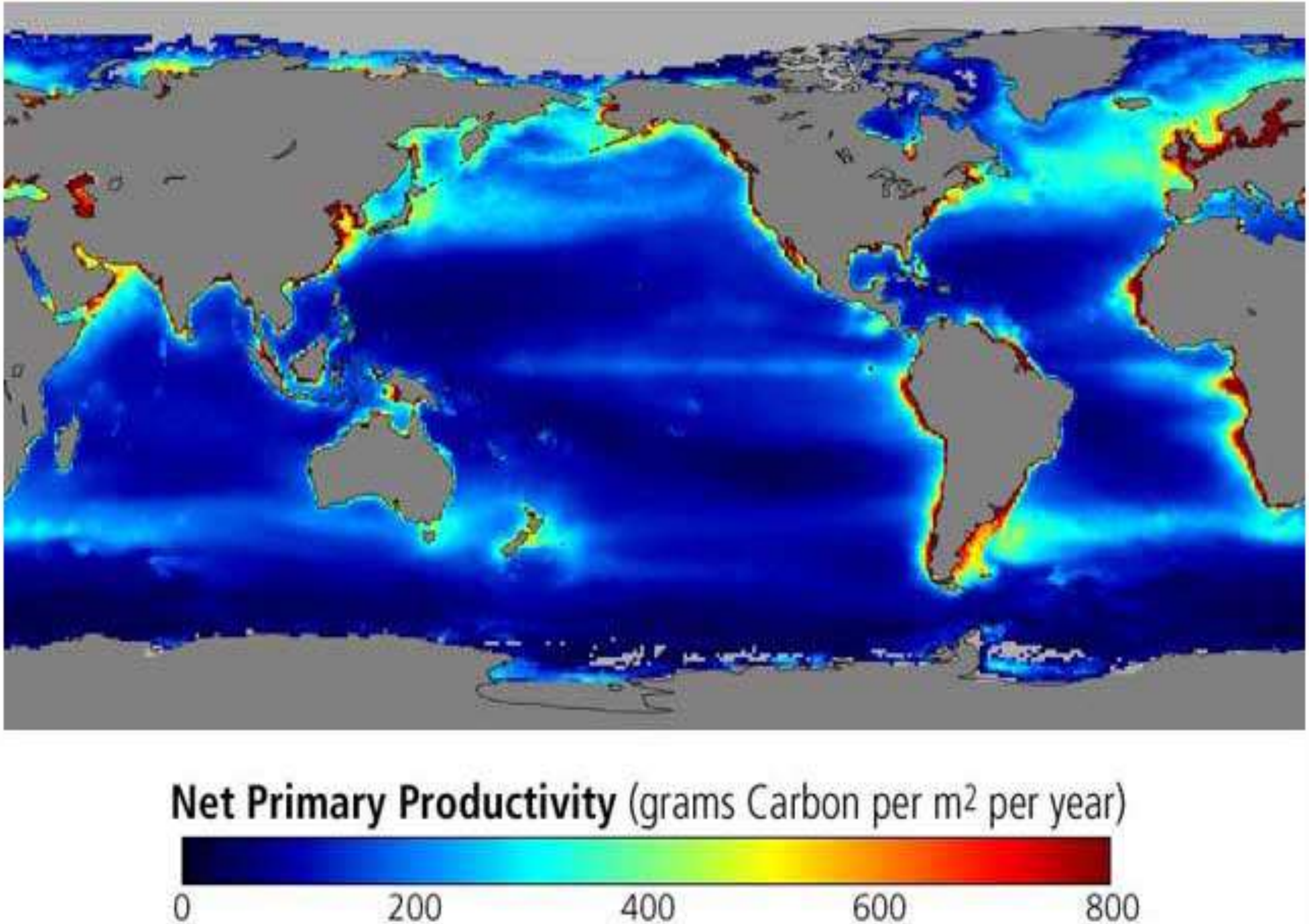
Because of these energy losses, **most terrestrial ecosystems have no more than five trophic levels**, and **marine ecosystems generally have no more than seven**. This is likely due to differences in the fundamental characteristics of land and marine primary organisms. In marine ecosystems, microscopic phytoplankton carry out most of the photosynthesis that occurs, while plants do most of this work on land. Phytoplankton are small organisms with extremely simple structures, so most of their primary production is consumed and used for energy by grazing organisms that feed on them. In contrast, a large fraction of the biomass that land plants produce cannot be used by herbivores for food, so proportionately less of the energy fixed through primary production travels up the food chain.



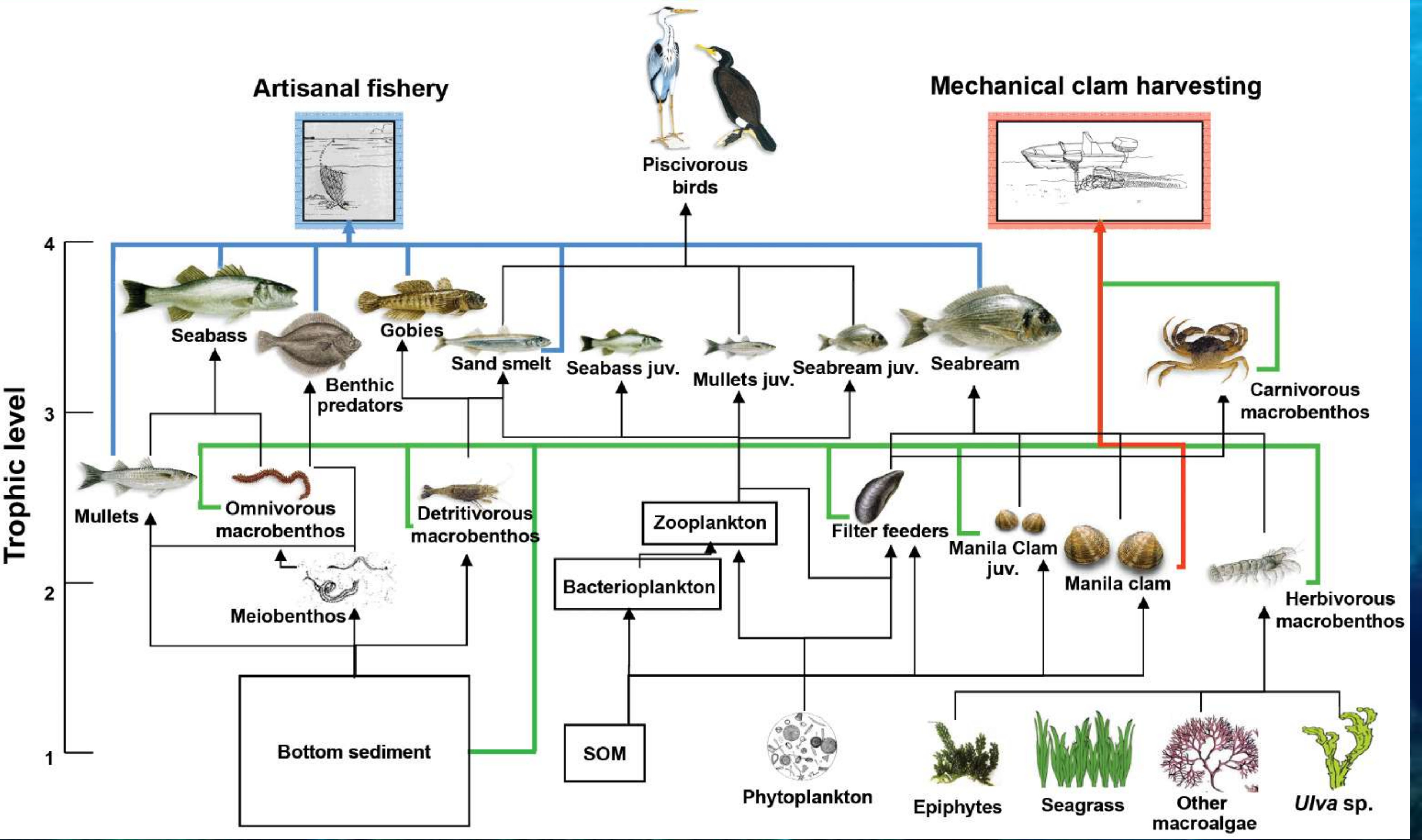


Growth rates may also be a factor. Phytoplankton are extremely small but grow very rapidly, so they support large populations of herbivores even though there may be fewer algae than herbivores at any given moment. In contrast, land plants may take years to reach maturity, so an average carbon atom spends a longer residence time at the primary producer level on land than it does in a marine ecosystem. In addition, locomotion costs are generally higher for terrestrial organisms compared to those in aquatic environments.

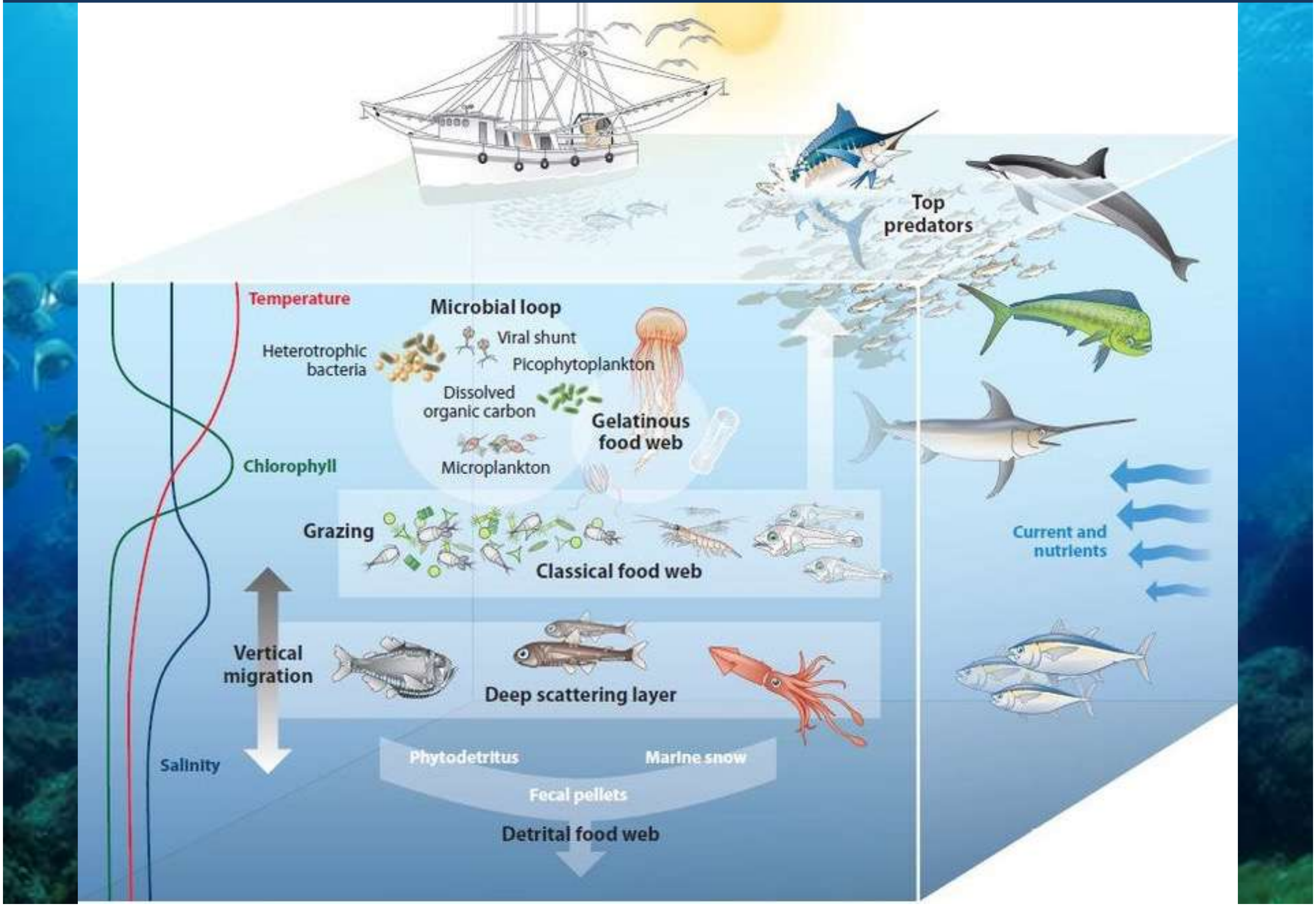
Total primary production in the ocean



Trophic webs: coastal Mediterranean



Trophic webs: pelagic



Keystone species

A keystone species is an organism that helps define an entire ecosystem. Without its keystone species, the ecosystem would be dramatically different or cease to exist.

Keystone species have low functional redundancy. This means that if the species were to disappear from the ecosystem, no other species would be able to fill its ecological niche.

They could be predators or herbivores (or producers).
Keystone can have either small population size or large number of individuals. Generally, in the case of predators, small numbers can have strong effects on ecosytems.

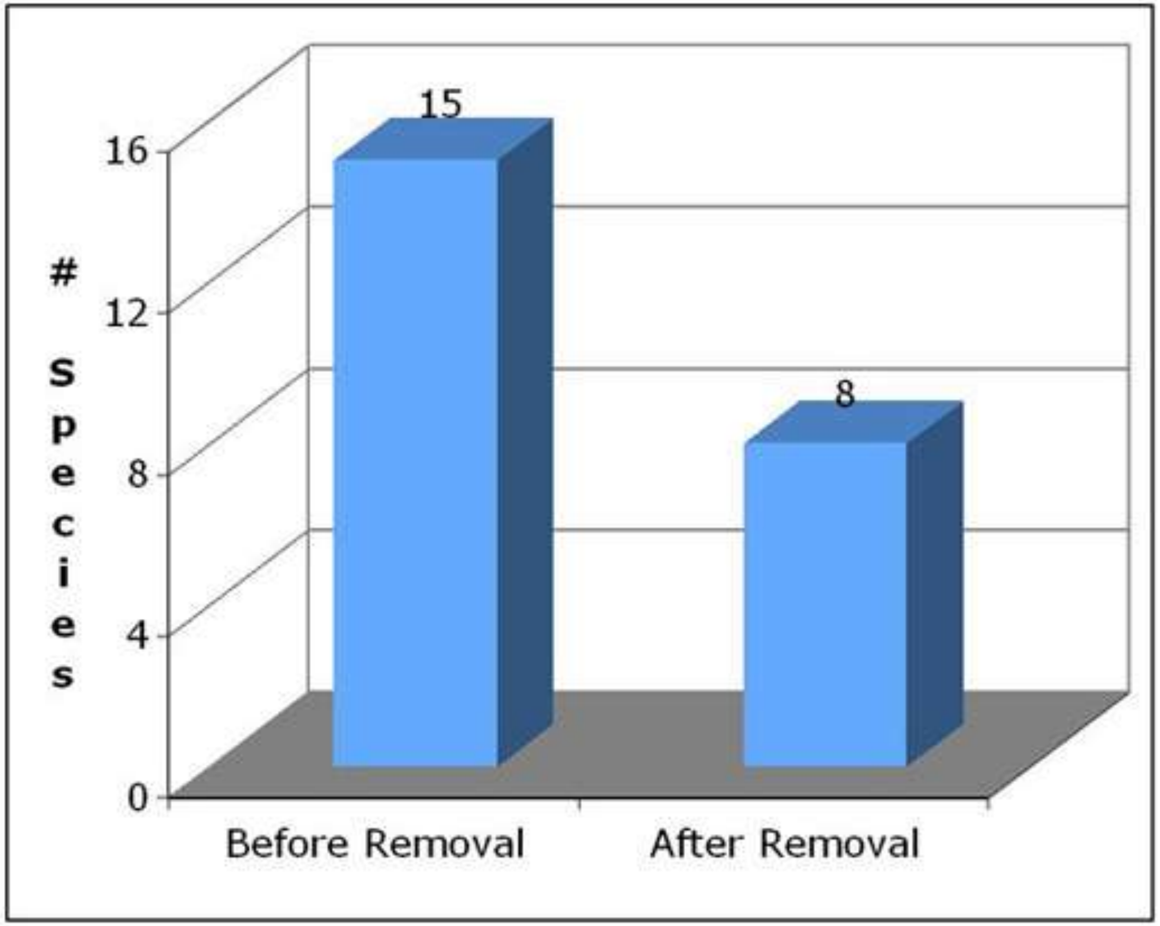
Paine's work

The term keystone species was first coined by Robert Paine (1966) after extensive studies examining the interaction strengths of food webs in rocky intertidal ecosystems in the Northwest Pacific. In his work, he studied a community dominated by the same species of mussels, barnacles, and the starfish, *Pisaster ochraceus*, which preys upon the other species as a top predator.

He had observed that the diversity of organisms in rocky intertidal ecosystems declined as the number of predators in those ecosystems decreased. He hypothesized that some of these consumers might be playing a greater role than others in controlling the numbers of species coexisting in these communities.

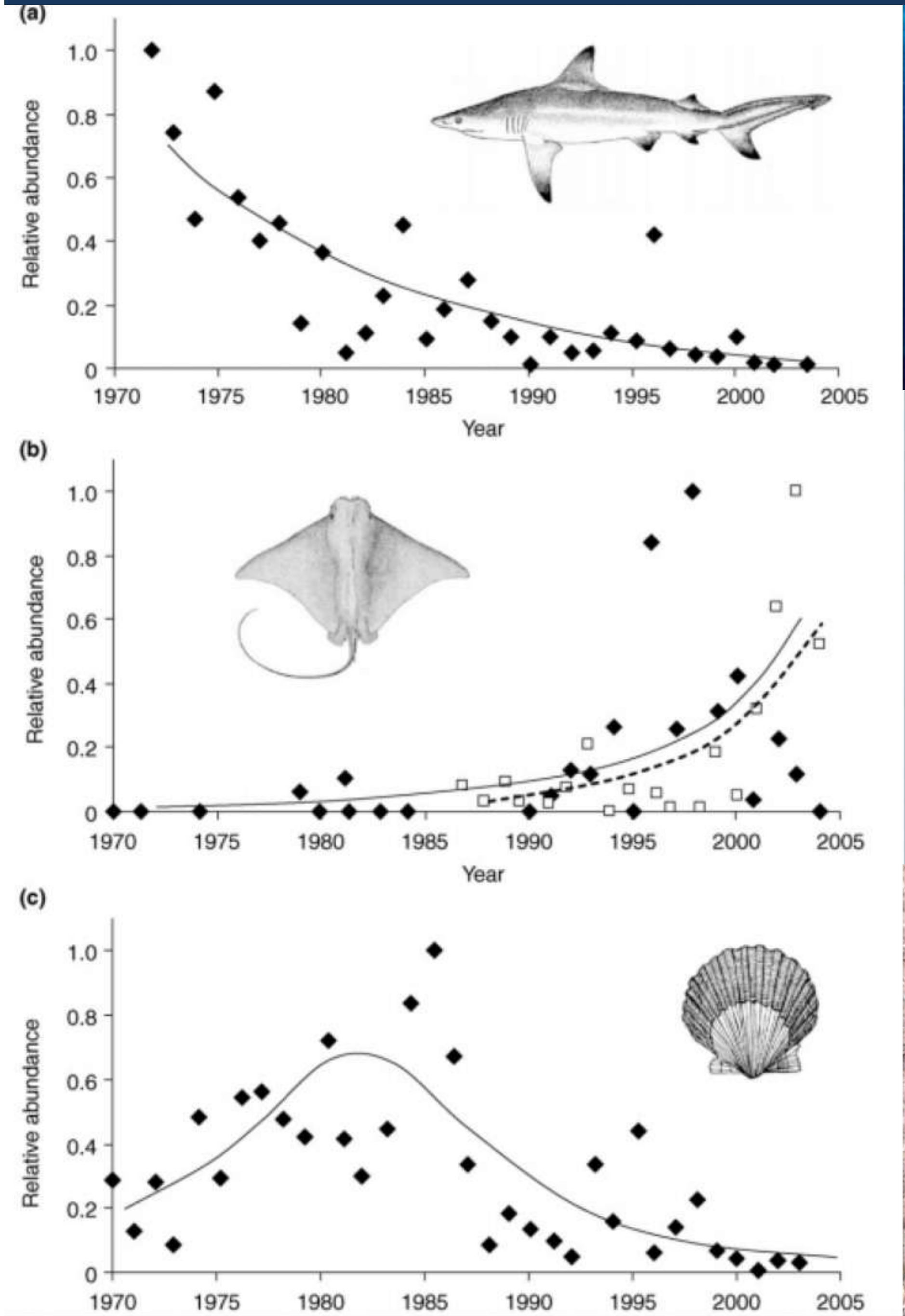
Paine's experiment

He tested his hypothesis in an experiment in which an area of the intertidal was kept free of the starfish, comparing them with an undisturbed control area of equal size.
He observed dramatic changes after *Pisaster* was artificially removed compared with the control area that remained unchanged in its species number and distribution. Aftern removal of starfishes the other species began to compete.



Within three months the barnacle, ***Balanus glandula***, became dominant and after 9 months, it was replaced by another barnacle ***Mitella*** and the mussel ***Mytilus***. The succession of species wiped out populations of benthic algae, causing some species, such as the limpet, to emigrate because of lack of food and/or space. After a year of the starfish's removal, species diversity significantly decreased in the study area from fifteen to eight species

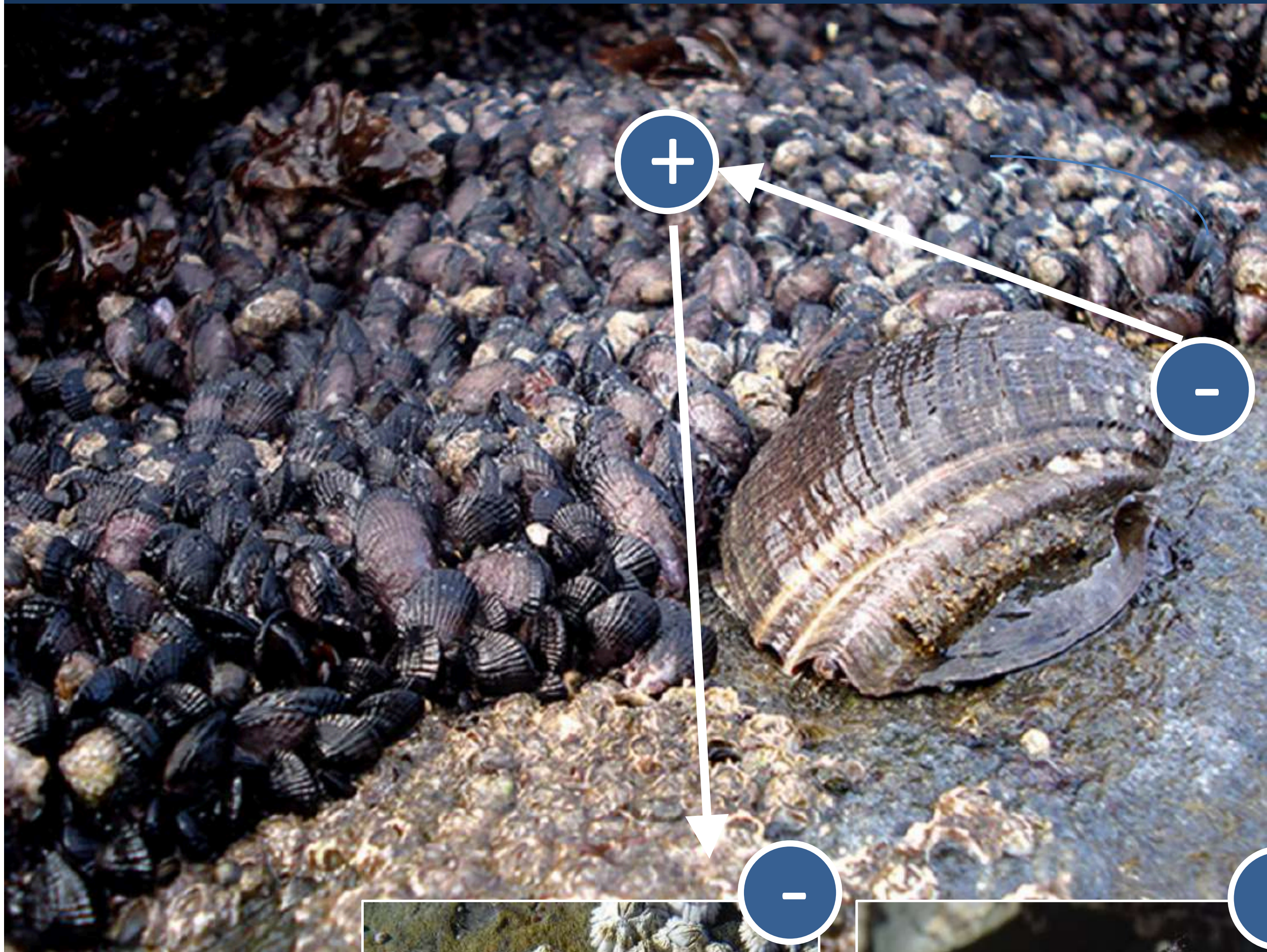
Large predators



Sharks play an important role, removing weak and/or sick fish. In this example, the decline of sharks in the eastern Atlantic (USA) lead to increasing population of rays (release of mesopredators), and to a decrease in scallops.

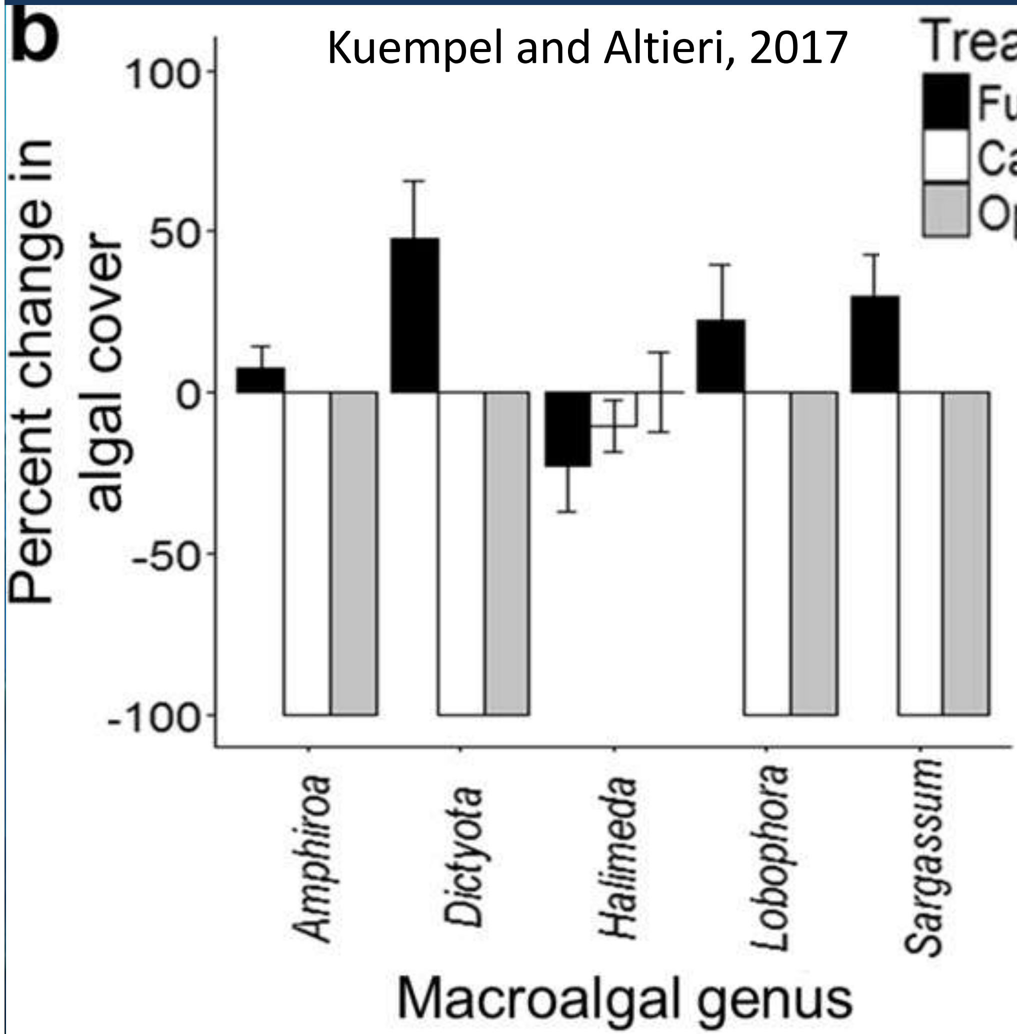
Heithous et al., 2007

Small predators



Decline in predator snails *C. concholepas* allows mussles *Perumytilus* to overcompete barnacles, macroalgae and herbivorous snails *Fissurella*.

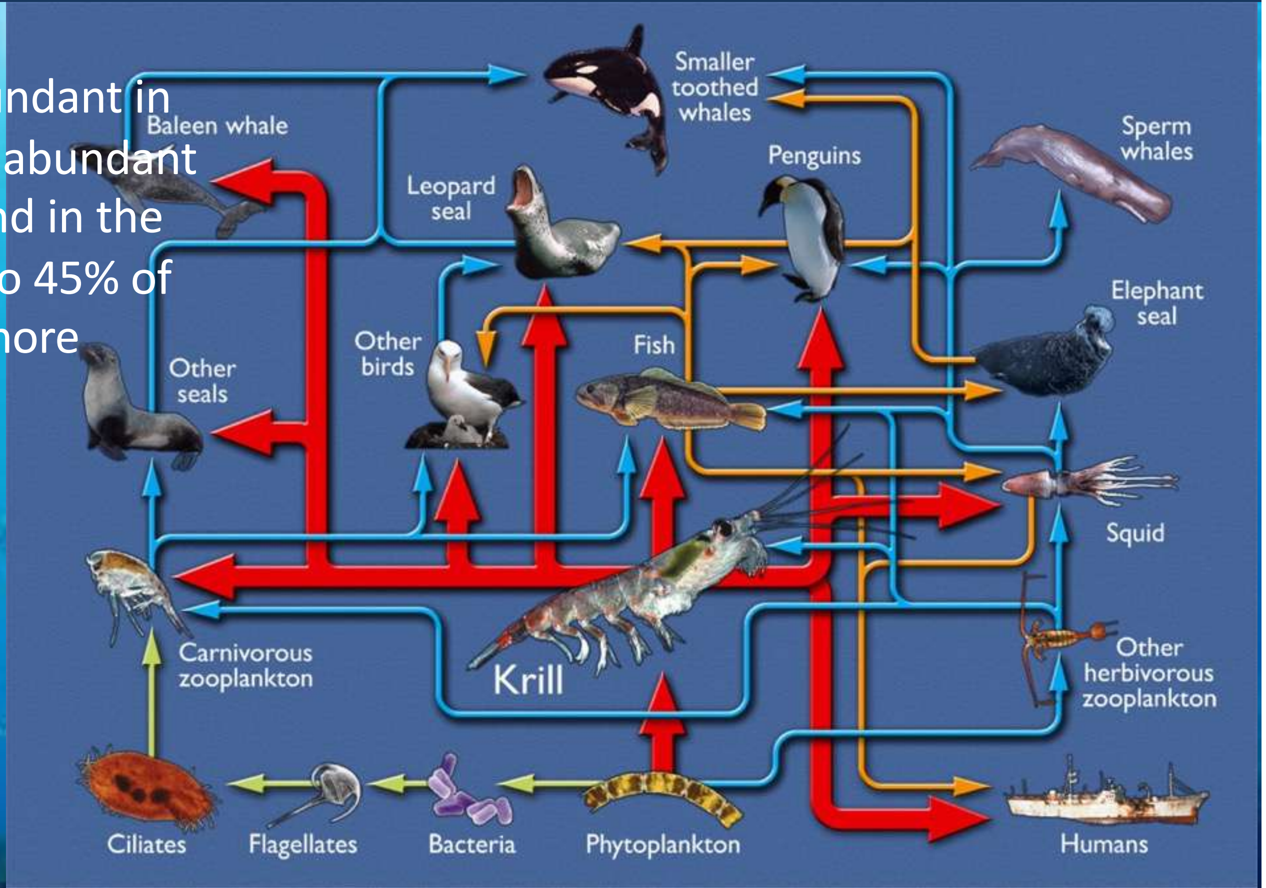
Herbivores



Key role in maintaing coral reefs healthy removing algal turf, dead corals and preventing the dominance of algae after disturbance

Keystone for trophic importance

Krill (Euphausiacea) are shrimp-like crustaceans that are extremely abundant in polar waters. In the Arctic they are abundant in waters on the Atlantic portion and in the Bering Sea. Krill can constitute up to 45% of zooplankton catches but krill are, more prominent in the Sourthern Ocean.

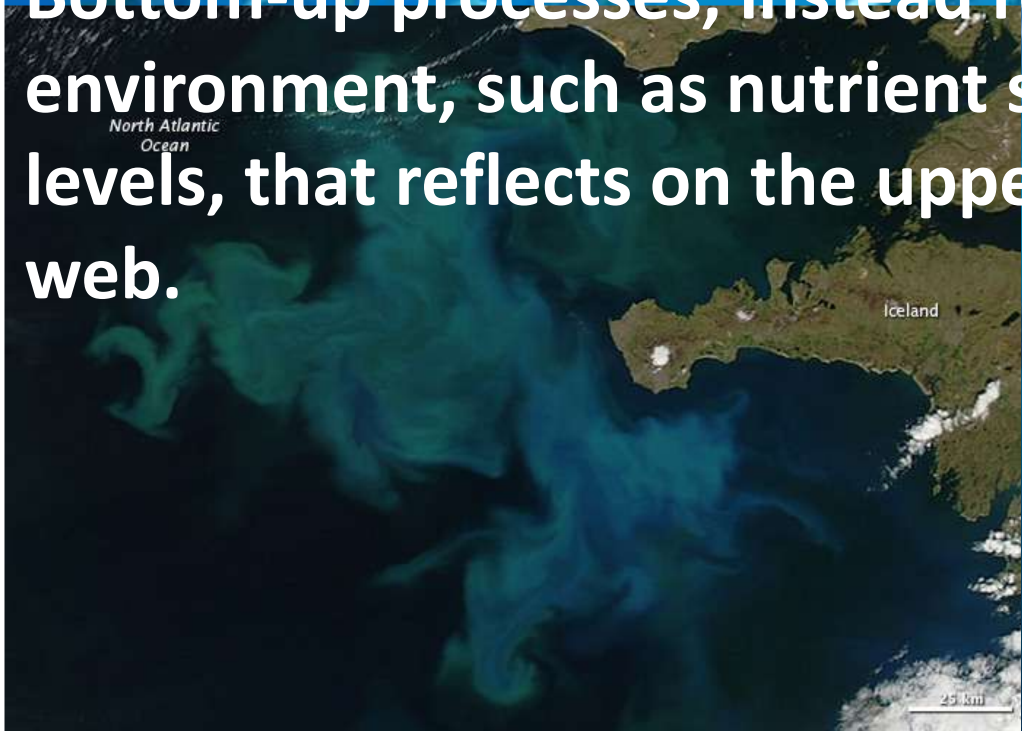


Antarctic krill *Euphausia superba* often dominates the zooplankton community in numbers and biomass.
Krill are highly influential organisms, capable of grazing as much as 55% of the net primary production and sustaining the functioning of the whole marine ecosystem in the Antarctic (Flores et al., 2012). Many polar organisms, from zooplankton to whales rely on krill as a primary food resource. Its estimated biomass Reach >400 million tons (Flores et al., 2012).

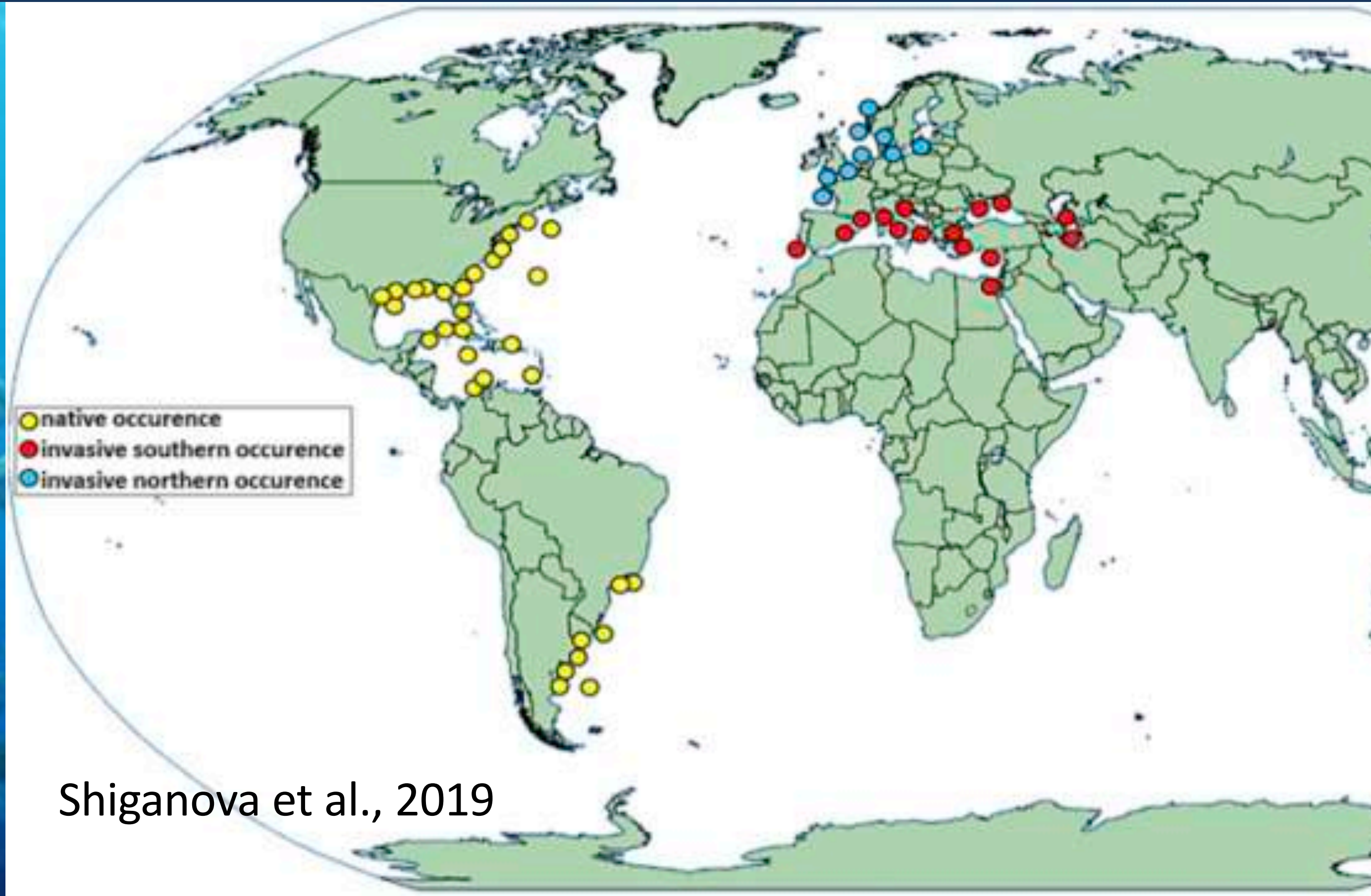
Top-down and bottom-up

Top-down processes involve a predator/consumer that exert a control on populations of preys, which are at a lower trophic level. When this control propagate through the trophic web, it originates cascading effects down the food web.

Bottom-up processes, instead refers to changes in the environment, such as nutrient supply, or in the lower trophic levels, that reflects on the upper levels through the trophic web.

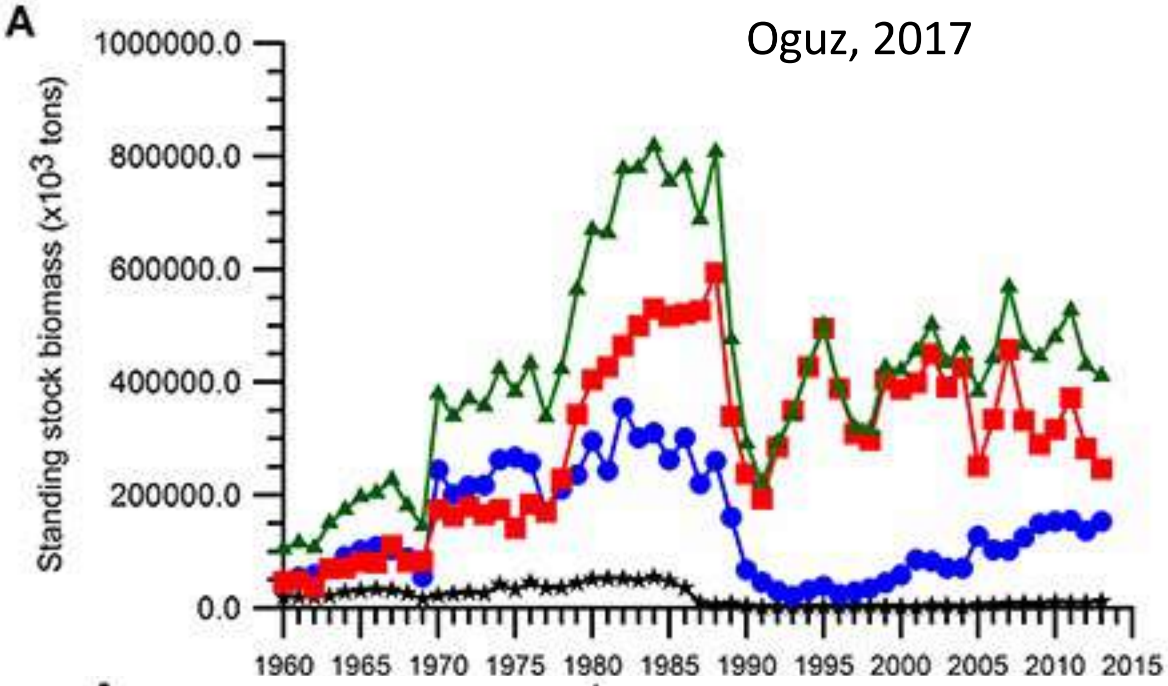


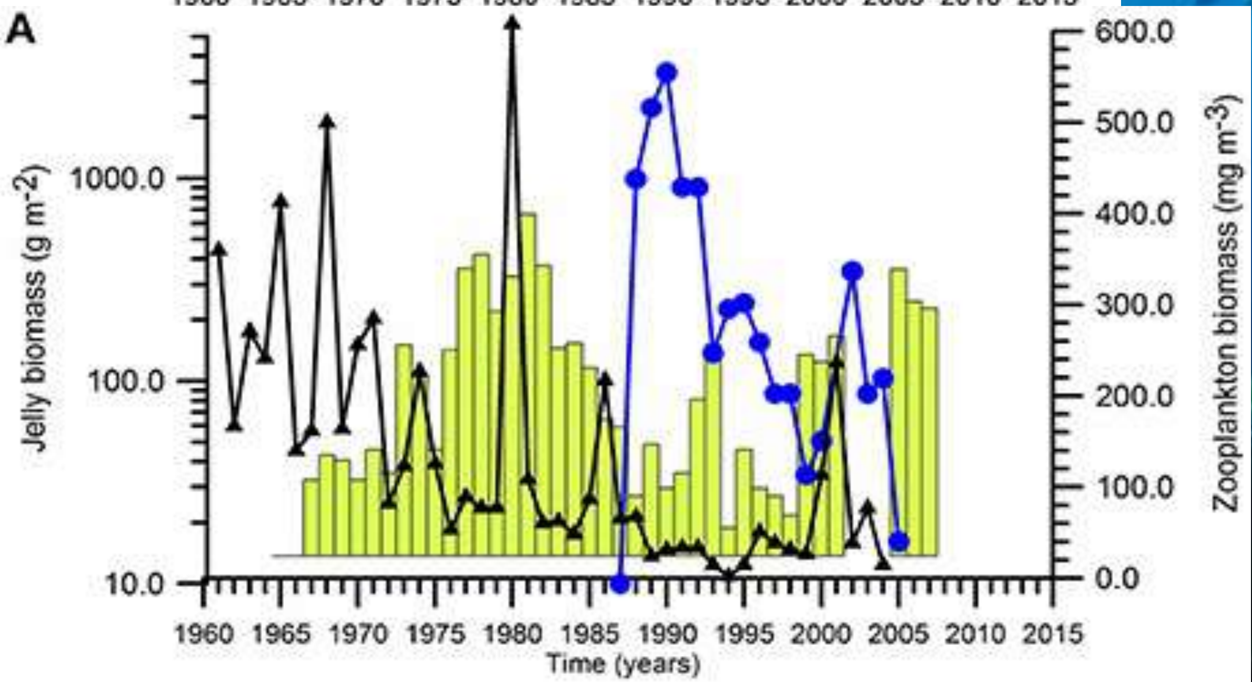
Top-down from invasive predators



Mnemiopsis leidyi introduced in 1980 in the Black Sea. Blooms up to 7600 individuals per m^3. Now spread in Mediterranean Sea, also in the Adriatic Sea.
Wide range of tolerance to temperature and salinity. Predator of plankton, including fish eggs and larvae. Introduced with ballast waters in ‘80s the Black Sea in , native from western Atlantic Ocean.

Effects on fish populations



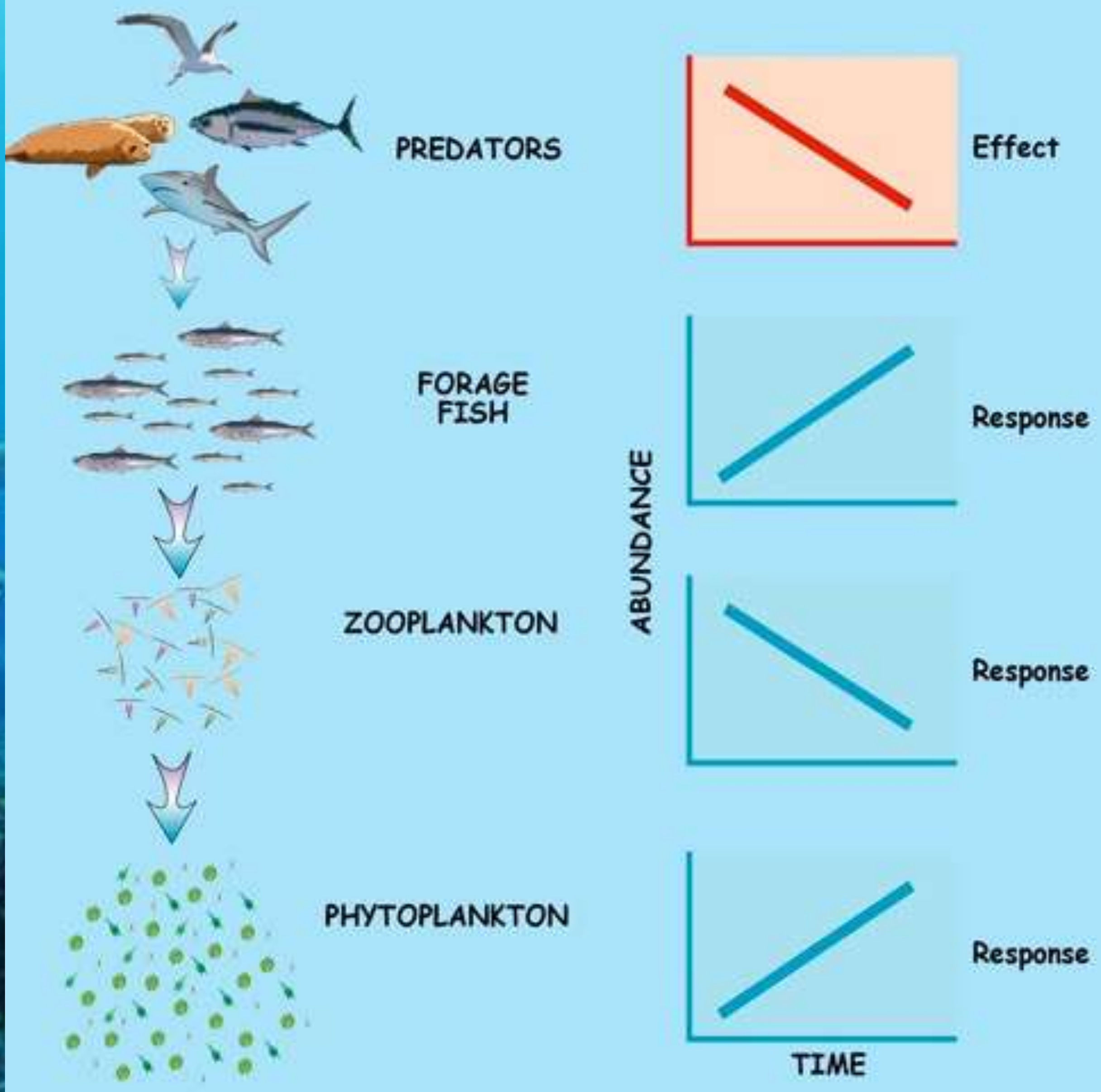


Concurrent effects due to pollution, overfishing and finally the introduction of the ctenophores lead fish stocks and fisheries to collapse.

Double effect of predation of *Mnemiopsis*: direct reduction of recruitment of fish due to predation on egg and larval stages, and indirect effect through competition due to predation on zooplankton

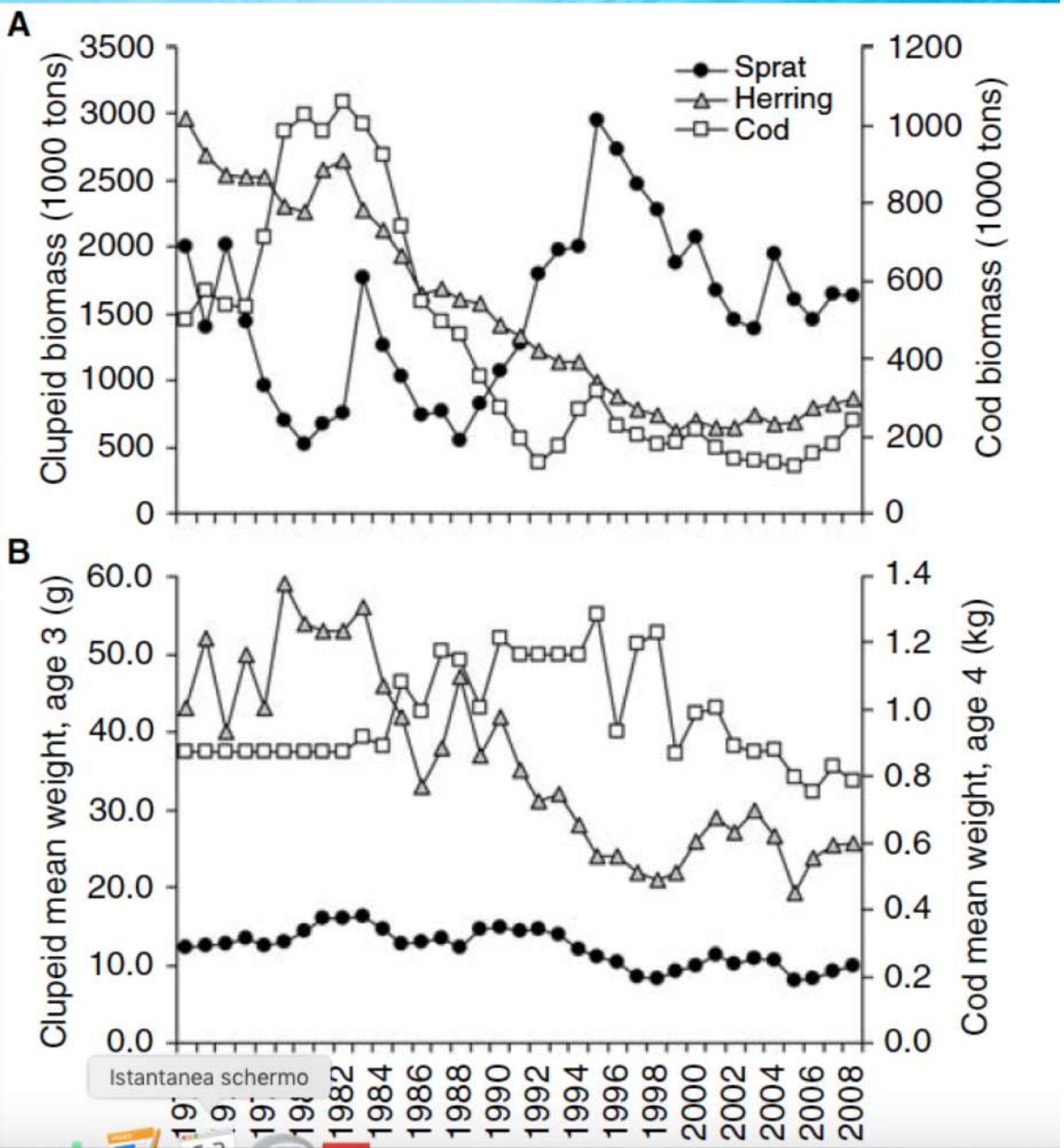
Trophic cascades

Trophic cascades occur when top-down control causes drastic changes in the ecosystem through effects that propagate downwards the food web (Pace et al. 1999).
In ecosystems that are strongly structured by predation, reducing top predator abundance can alter several lower trophic levels.

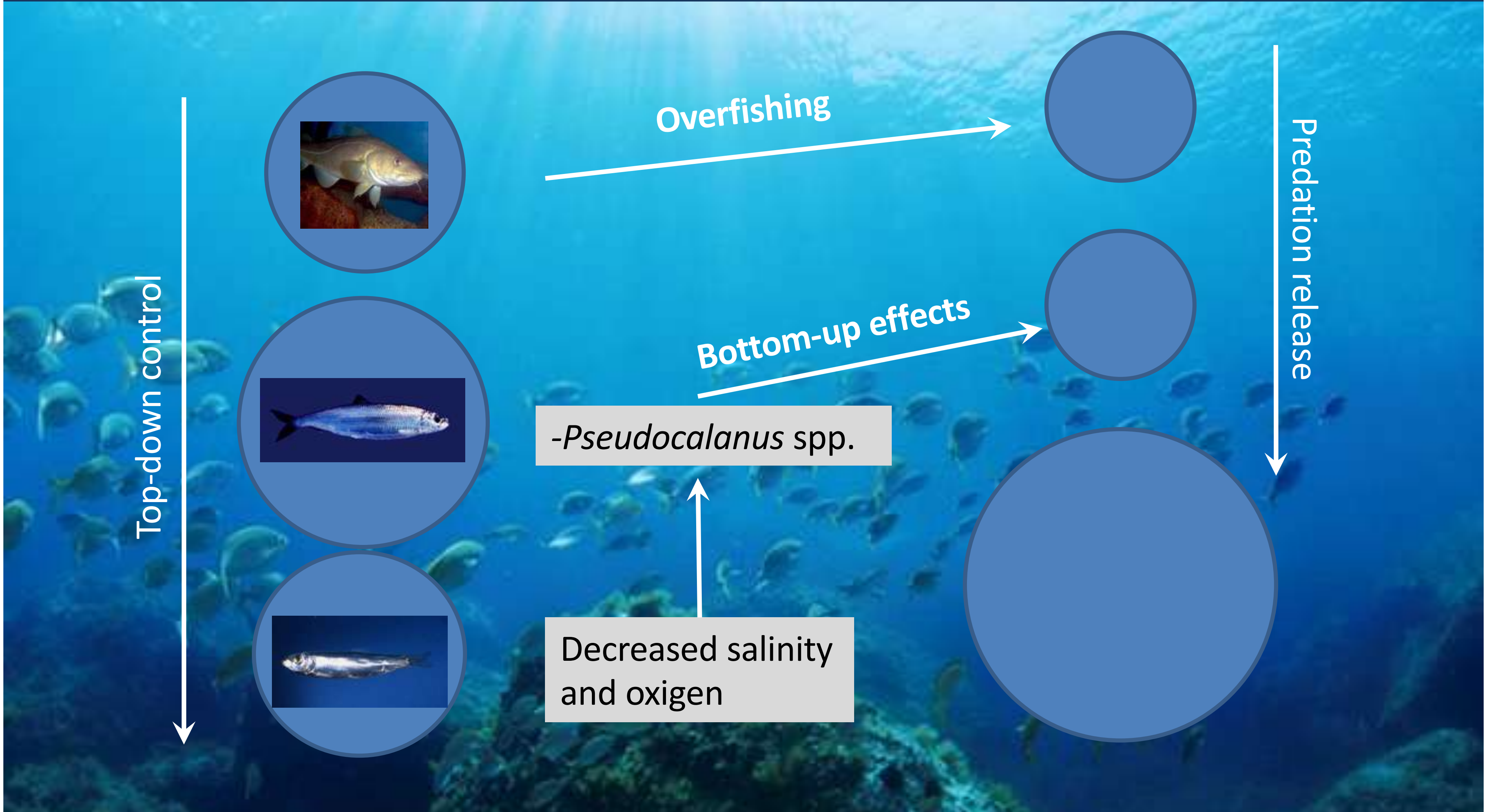


Top-down and bottom up

Strong reductions in the abundance of a top predator (cod) has also been reported to cause a tropic cascade in the relatively simple Baltic food chain, involving a subsequent increase in the zooplanktivorous sprat, which in turn affected the biomass, species and stage composition, as well as the vertical distribution of zooplankton (Casini *et al.*, 2008).



Top-down and bottom up



Changes in the Baltic Sea were primarily bottom-up, strongly structured by salinity, but top-down forcing related to changes in cod abundance also shapes the ecosystem. (Flinkman et al. 1998; Casini et al., 2011)

Bottom up prevailing

Top-down control is likely to occur in simple trophic webs, where there is a strong predation control on lower trophic levels. This process is more likely to occur in closed basins and coastal areas. In pelagic food webs and open sea the dominant process is likely to be related to bottom up effects. One possibility, in accordance with a predominant view of oceanographers, is that these ecosystems are structured from the bottom-up (resource limitation) and top-down control by oceanic predators is truly rare. (Baum and Worm, 2009)

High degree of connectance among and within species
Prevalence of omnivory and dietary breadth
Ontogenetic diet shifts
Predator diversity may dampen cascading effects
Simultaneous exploitation of predator and prey can inhibit prey responses

Trophic cascade leading to regime shifts could be rare in open ocean ecosystems

Benthic-pelagic coupling

Benthic – pelagic coupling

Life cycles

Pelagic or planktonic species lay eggs, or have larval or juvenile stages in benthos

Benthic species spent part of their life as adult, juvenile or larvae in plankton

Trophic webs

Herbivores and predators from the water column feed on benthos

Benthic species have adults or juveniles feeding on plankton or on larval - juveniles of nekton

Organic matter

Planktonic species have resting stages in benthos. Organic matter (fecal pellets, dead organisms, etc.) fall on the bottom

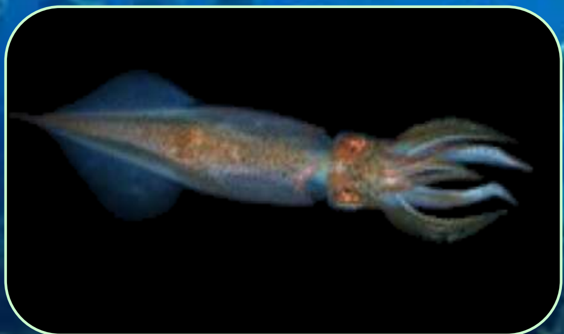
Resting stages disclose and turn back to the plankton. Benthic species feed on particles and could turn in the water column via life cycles

Biogeochemical cycles

Nutrients and gases reach the bottom and can turn back as living matter or through upwelling

Life cycles

Benthic species spent part of their life as adult, juvenile or larvae in plankton



Pelagic or planktonic species lay eggs, or have larval or juvenile stages in benthos

Life cycles connect pelagic and benthic domain as, depending on the life stage, species belong to benthos or plankton and pelagos

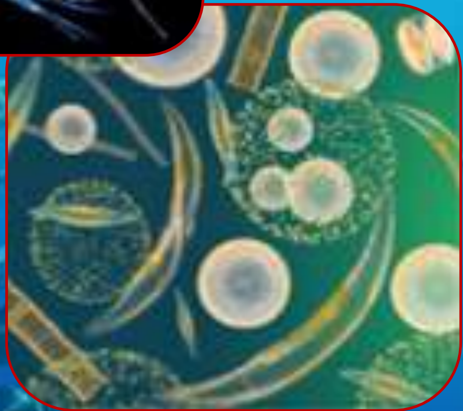
Trophic webs

Predator-prey relationships across different compartments connect benthos, nekton and plankton allowing energy flow from the bottom to the water column and viceversa

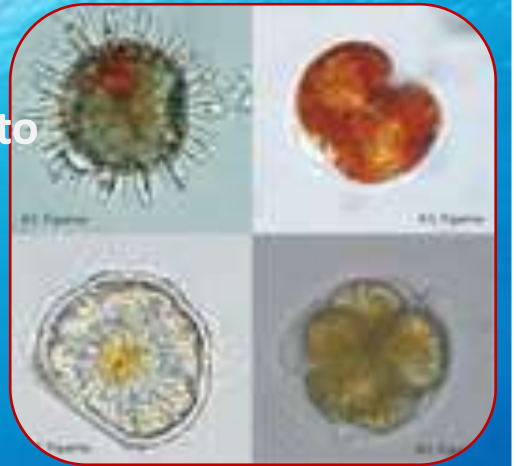
Herbivores and predators from the water column feed on benthos

Benthic species have adults or juveniles feeding on plankton or on larval -juveniles of nekton

Organic matter



Planktonic species have resting stages in benthos. Resting stages disclose and turn back to the plankton.



Organic matter (fecal pellets, dead organisms, etc.) fall on the bottom. Upwelling re-suspend nutrients in the upper layer triggering phytoplankton blooms

Biogeochemical cycles

Nutrients and gases reach the bottom and can turn back as living matter or through upwelling. Shells of calcifying organisms, or silica shells of diatoms also export elements to the sea bottom.