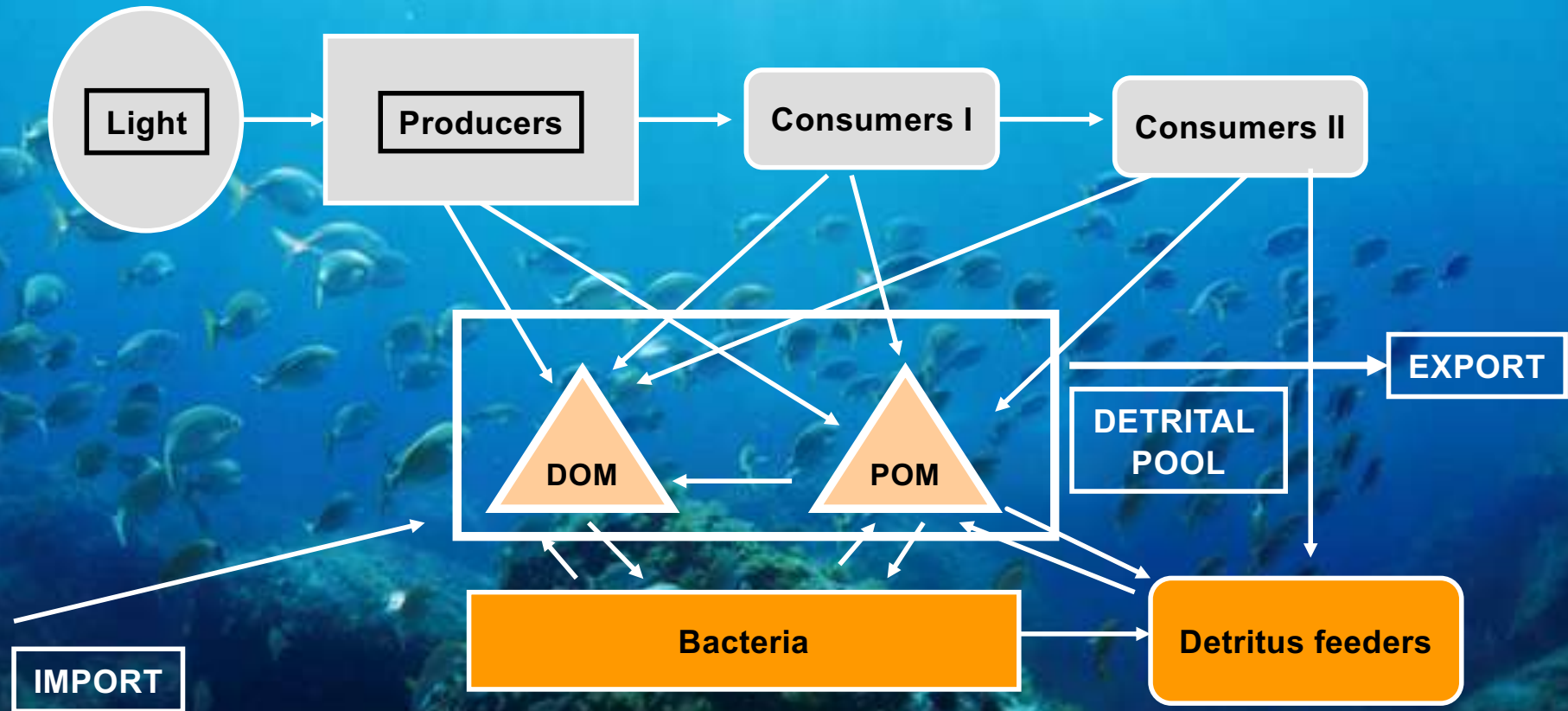


# Trophic chains and the importance of detritus

Detritus (90% of primary production)



# 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

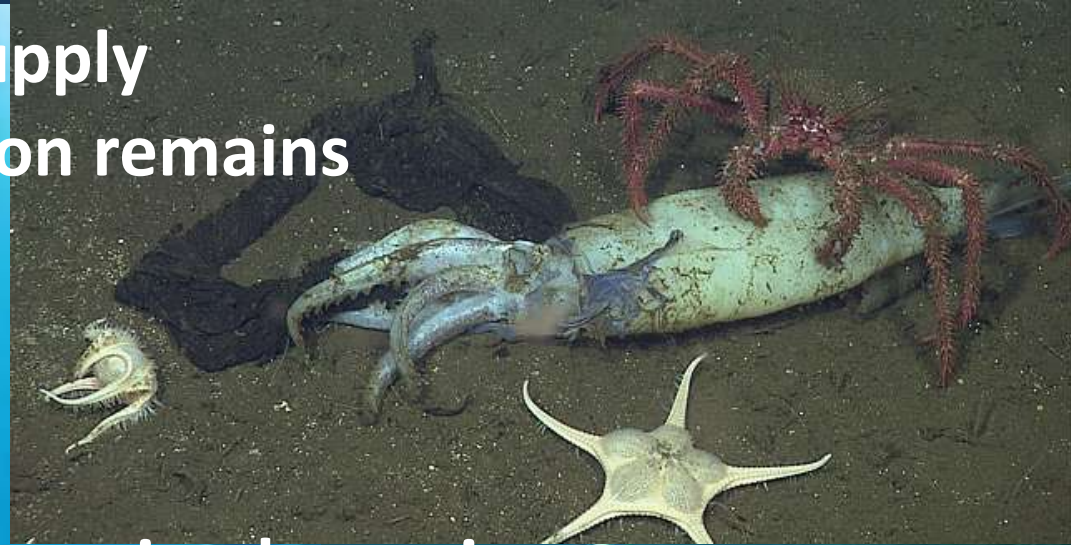




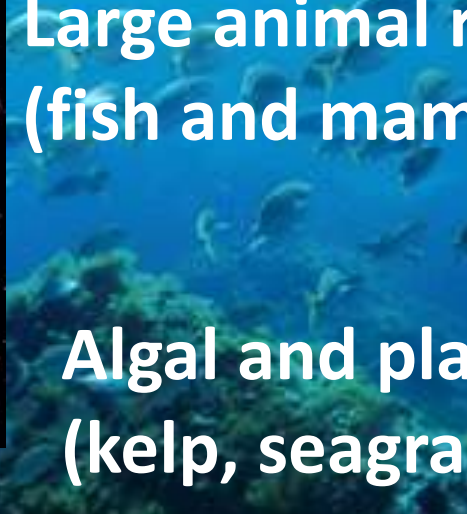
# Origin



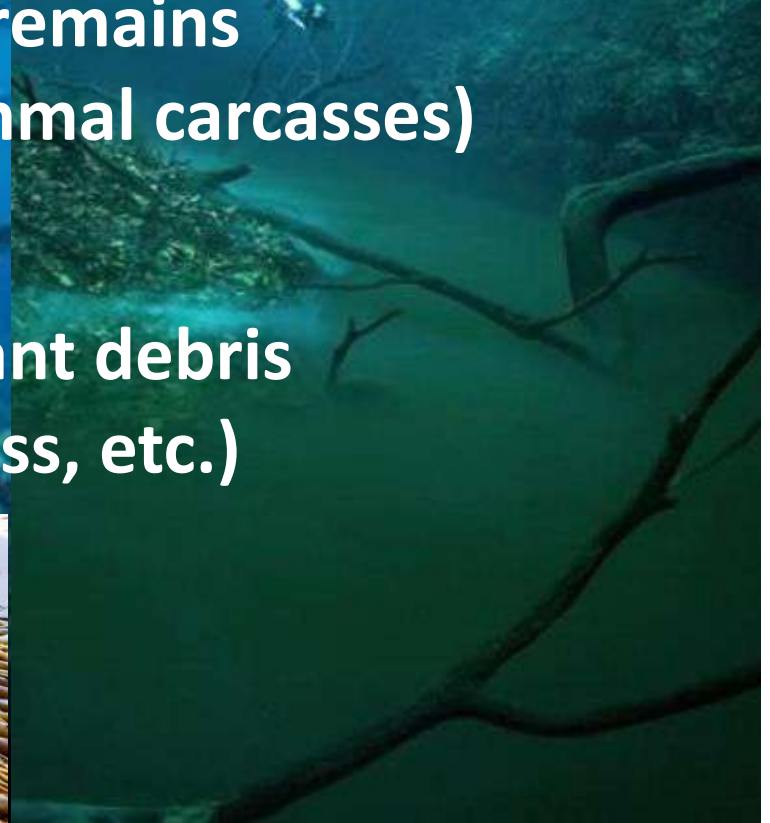
Terrestrial supply  
Small plankton remains  
Moulted  
Fecal pellets



Large animal remains  
(fish and mammal carcasses)

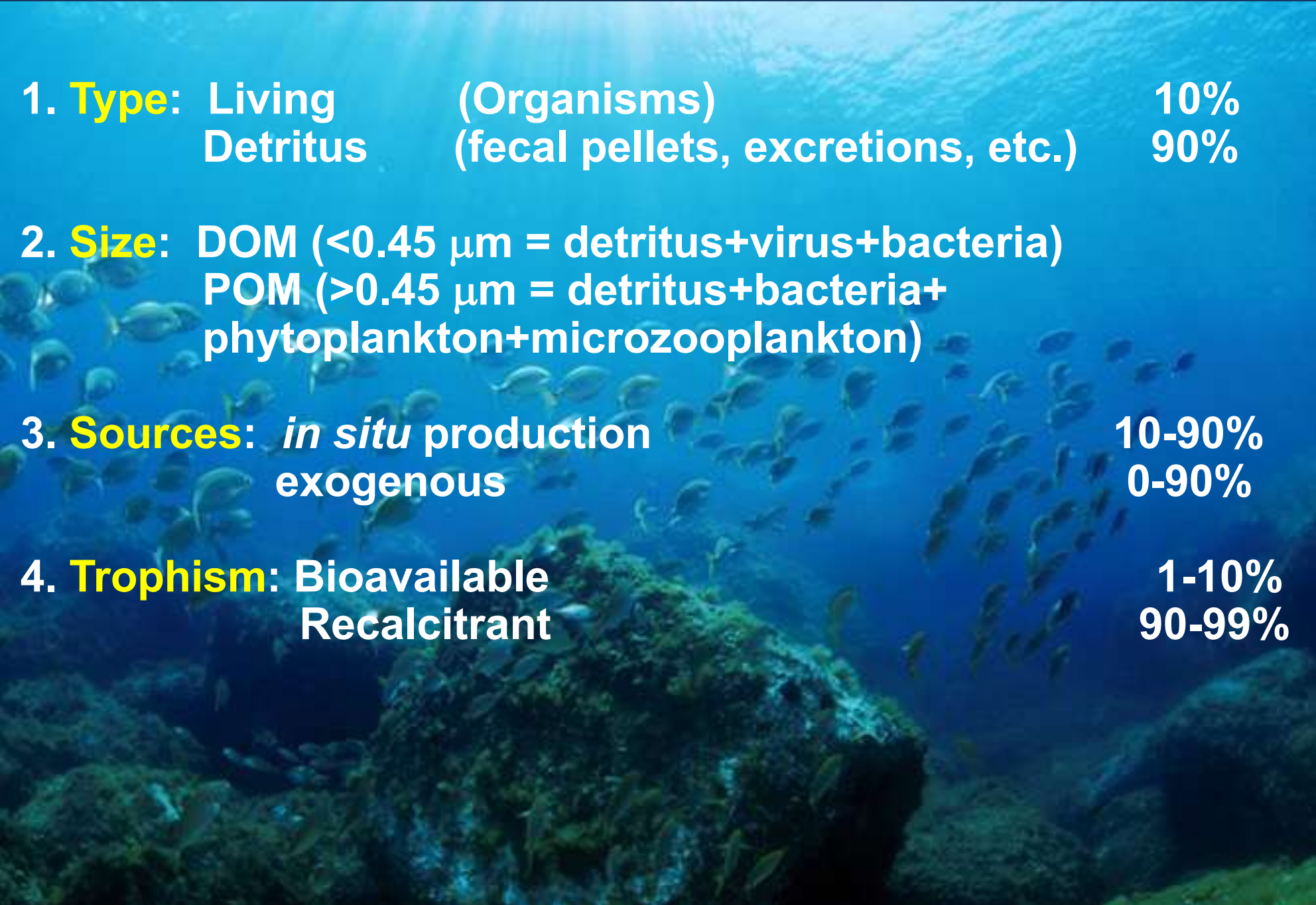


Algal and plant debris  
(kelp, seagrass, etc.)





# Classification of organic matter

- 
1. **Type:** Living (Organisms) 10%  
Detritus (fecal pellets, excretions, etc.) 90%
2. **Size:** DOM (<0.45  $\mu\text{m}$  = detritus+virus+bacteria)  
POM (>0.45  $\mu\text{m}$  = detritus+bacteria+phytoplankton+microzooplankton)
3. **Sources:** *in situ* production 10-90%  
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, microzooplankton 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  $\mu\text{m}$  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

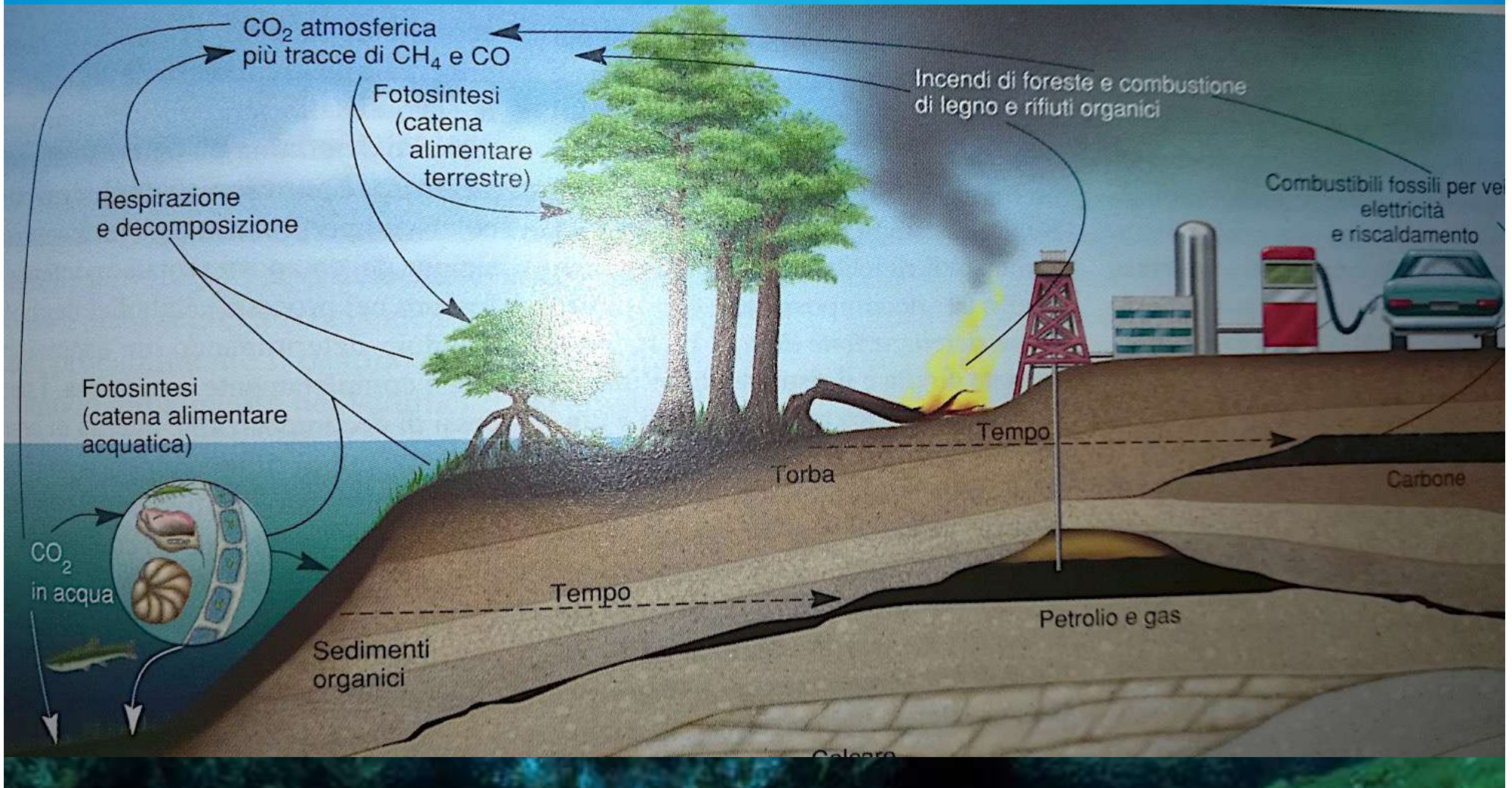
Labile organic matter is easily and rapidly available to be remineralized by organisms, whereas recalcitrant organic matter is formed during decomposition and other processes (agglomeration), and is difficult to be degraded by bacteria unless during long periods.

Example: CRAM (carboxyl-rich alicyclic molecules) amino-sugars, amino acids, terpenoids, lignin)



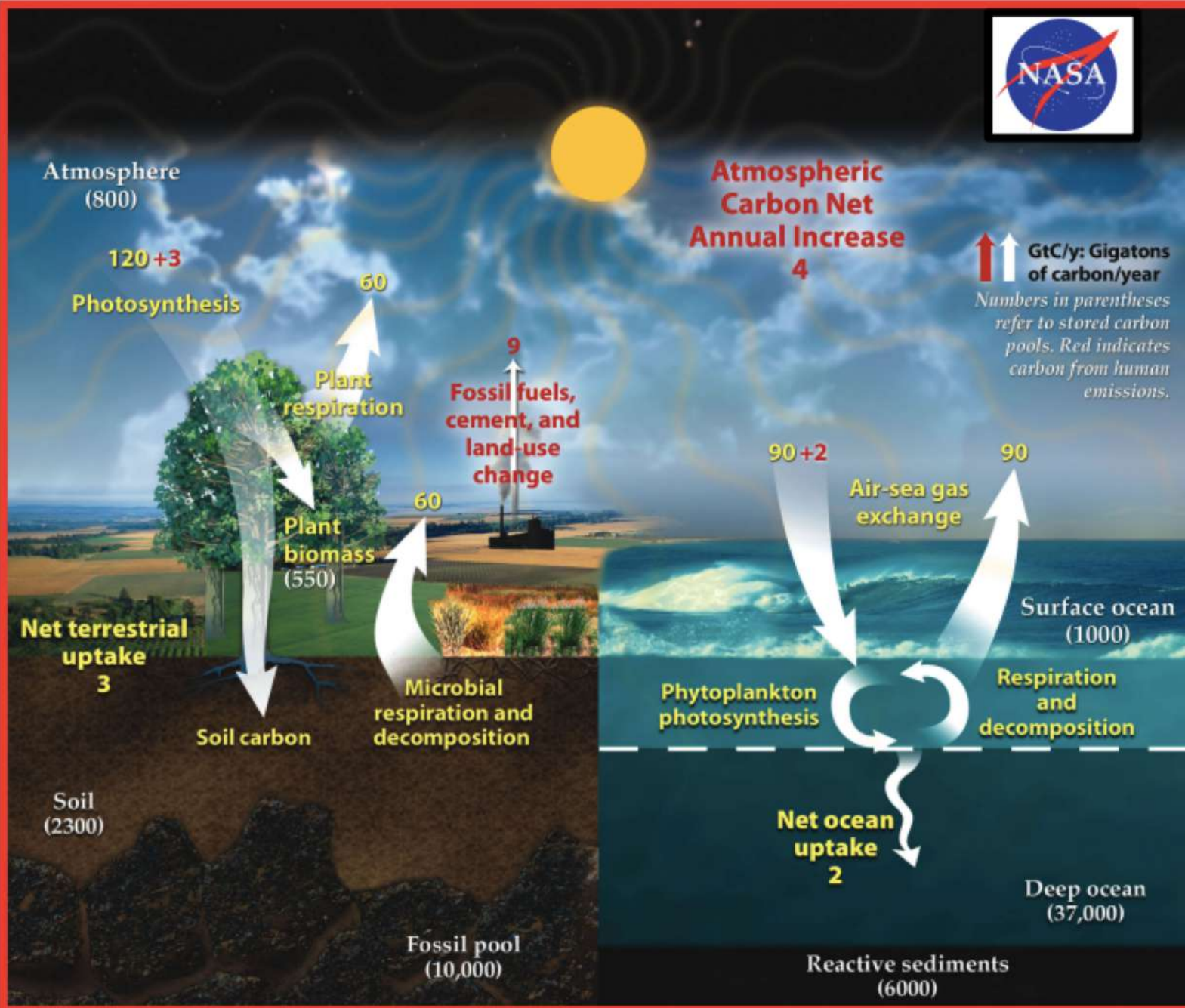
# Carbon

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<sup>3</sup>y).

The second part of the whole cycle consists of a long term cycle (10<sup>4</sup>-10<sup>3</sup>y), through weathering, volcanic activities, subduction of sediments and rocks, huge stocks in soil.



# BCP, ML, and MCP

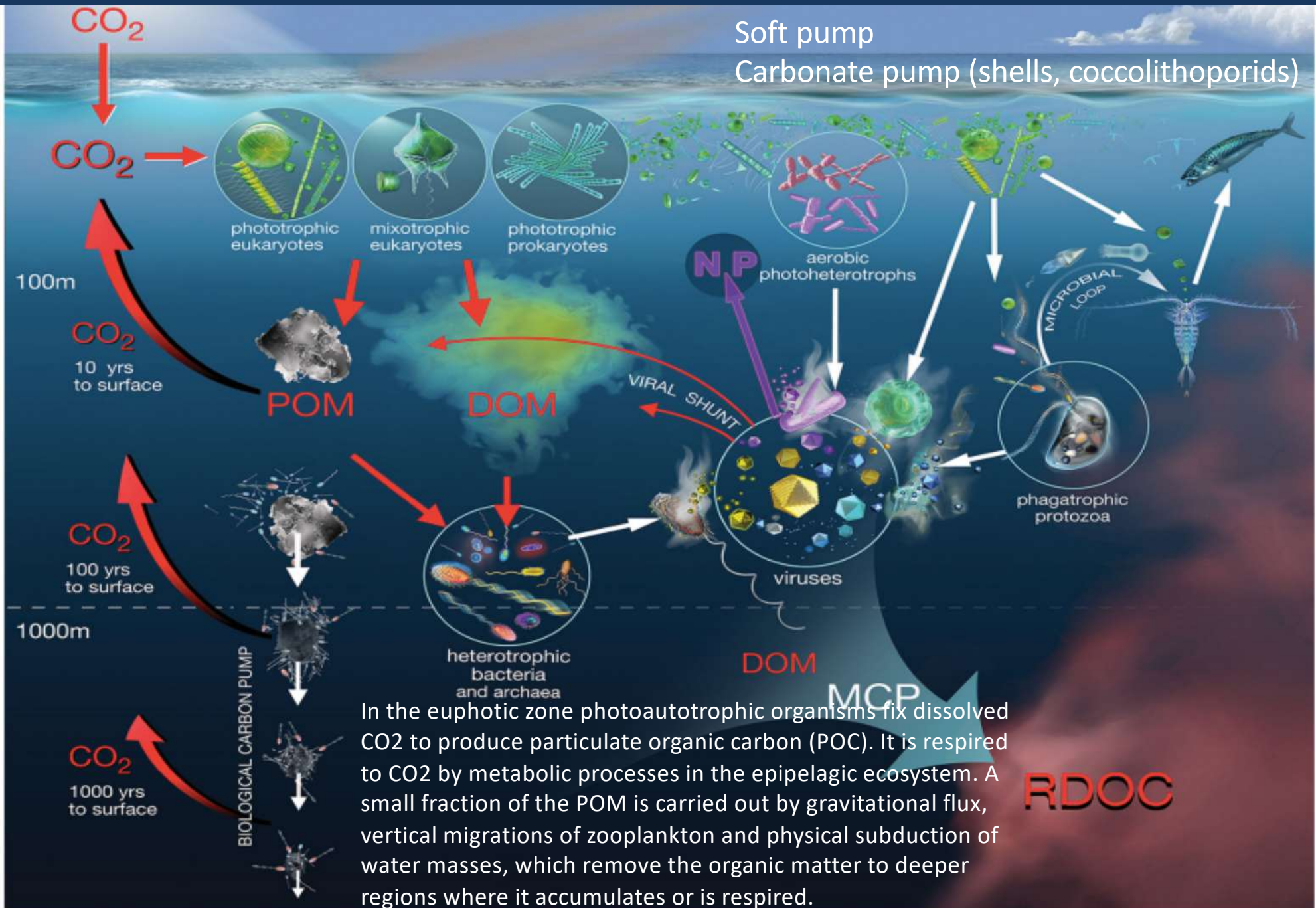
**Table 1.** Definitions and major impacts of the BCP, ML and MCP.

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 <sub>2</sub> 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 <sub>2</sub> through transformation of labile organic matter to recalcitrant organic matter; focusing on capacity of the ocean to store atmospheric CO <sub>2</sub>





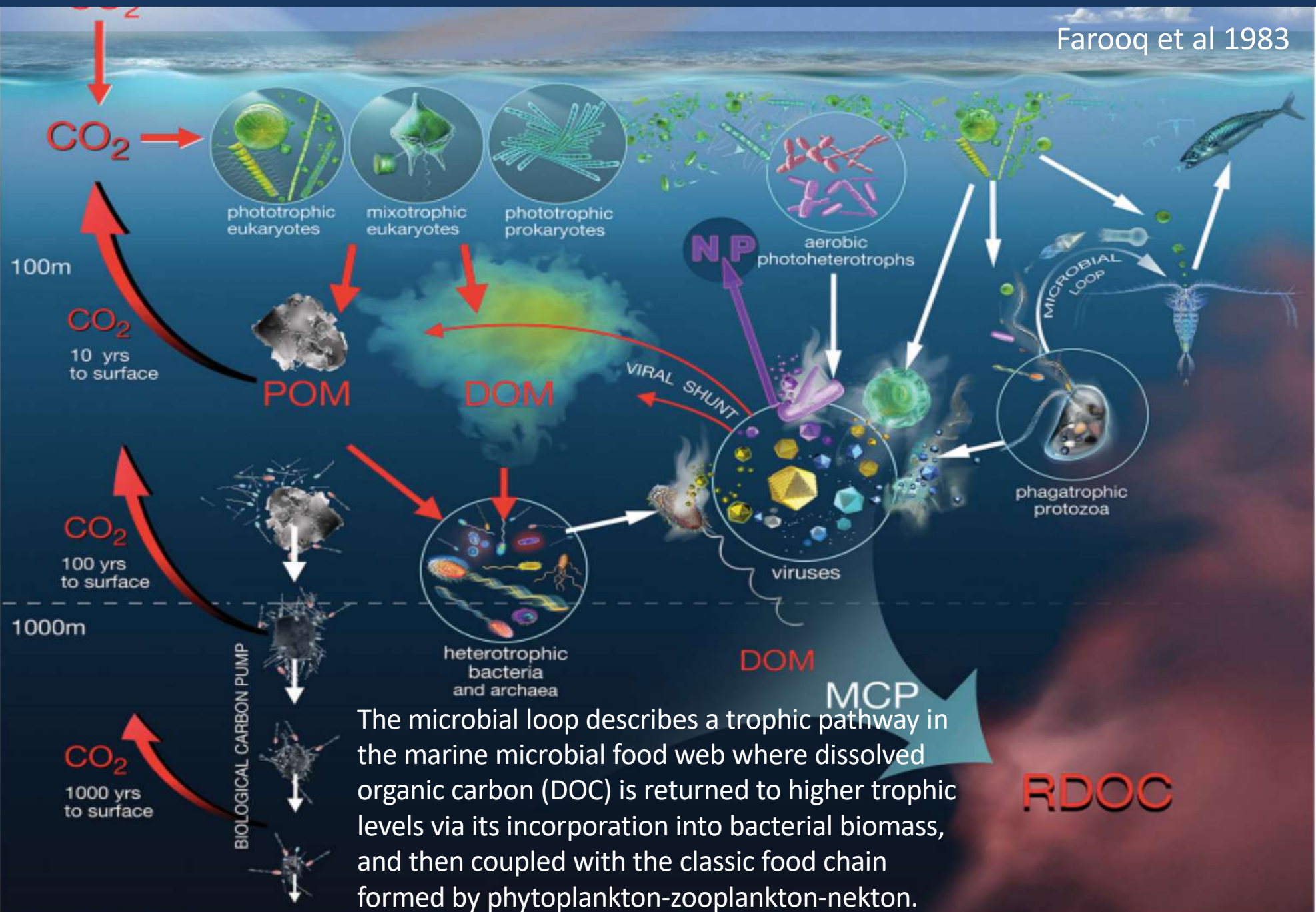
# Biological Carbon Pump





# Microbial loop

Farooq et al 1983

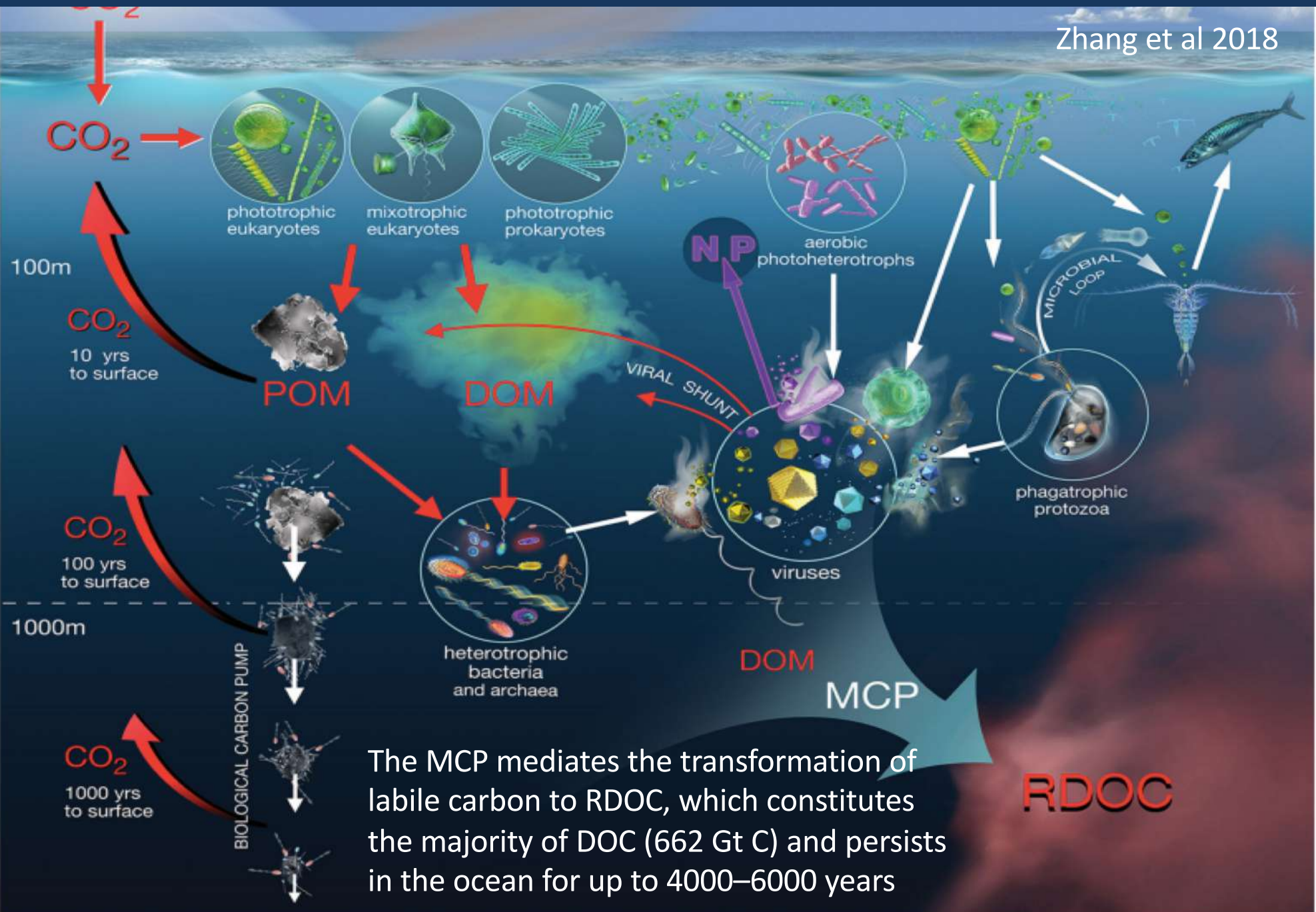


The microbial loop describes a trophic pathway in the marine microbial food web where dissolved organic carbon (DOC) is returned to higher trophic levels via its incorporation into bacterial biomass, and then coupled with the classic food chain formed by phytoplankton-zooplankton-nekton.



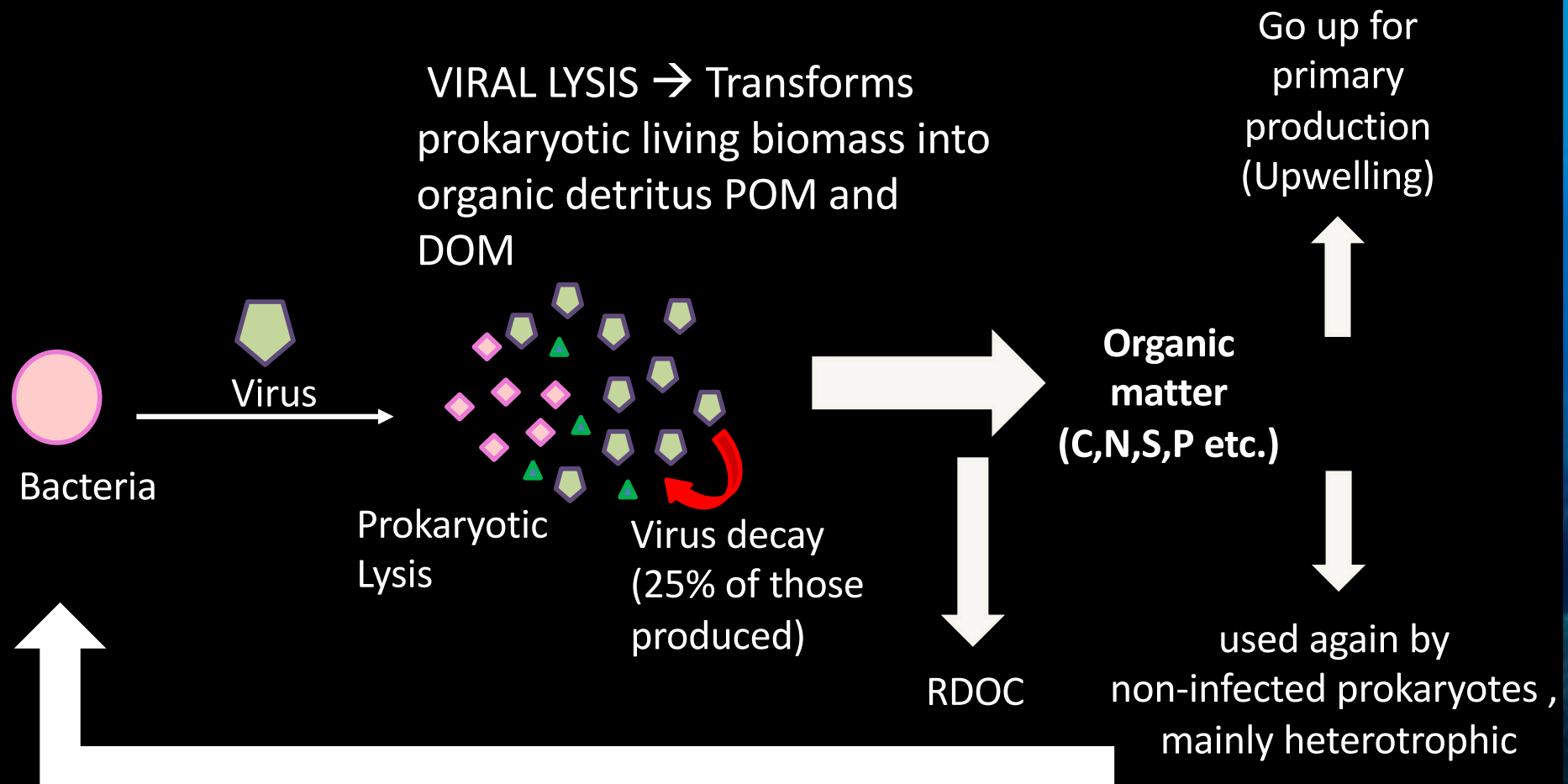
# Microbial Carbon Pump

Zhang et al 2018



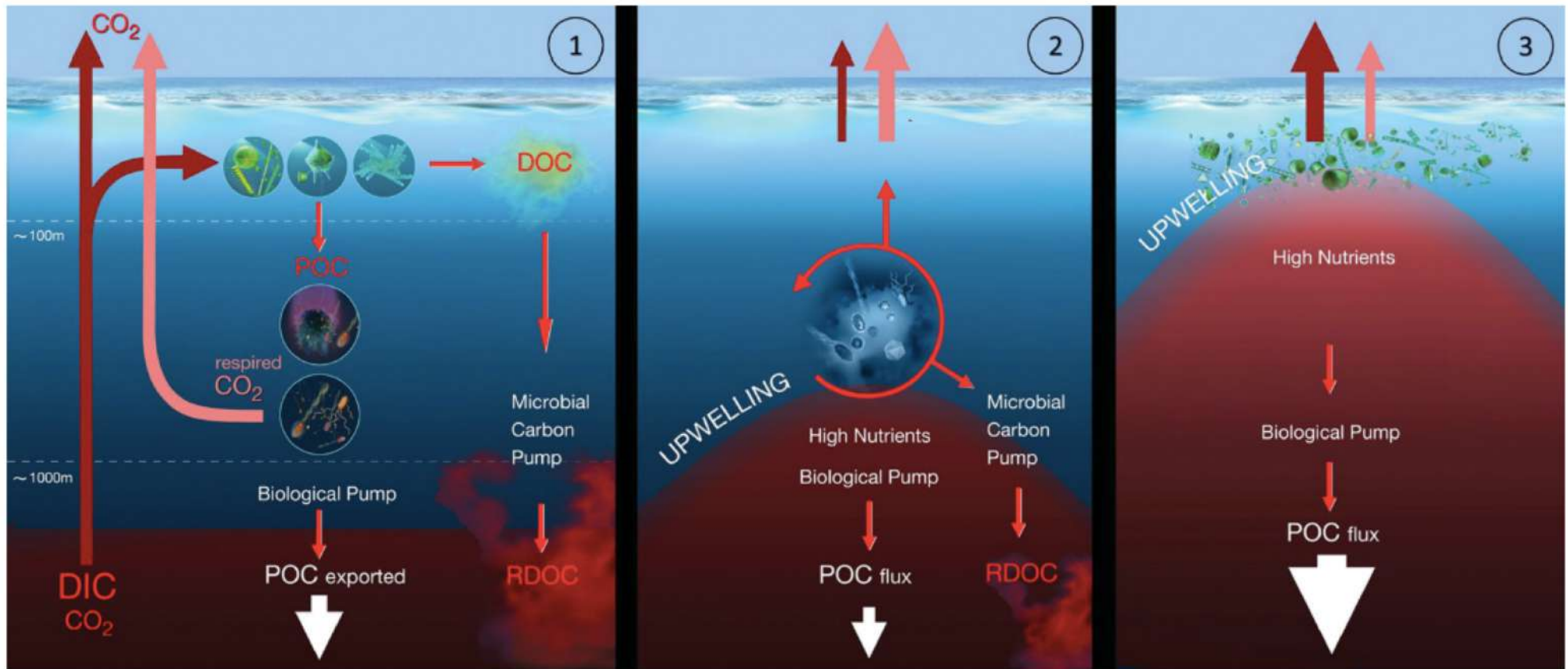
# Viral shunt

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 CO<sub>2</sub> flux exceeds downward POC export flux: nutrients are injected only into the lower layer of the euphotic zone; *Prochlorococcus* is dominant; CO<sub>2</sub> 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 CO<sub>2</sub> flux: nutrients are injected into the upper layer of the euphotic zone; diatoms are dominant; POC export exceeds CO<sub>2</sub> outgassing; the BCP is the prevailing mechanism for carbon sequestration.

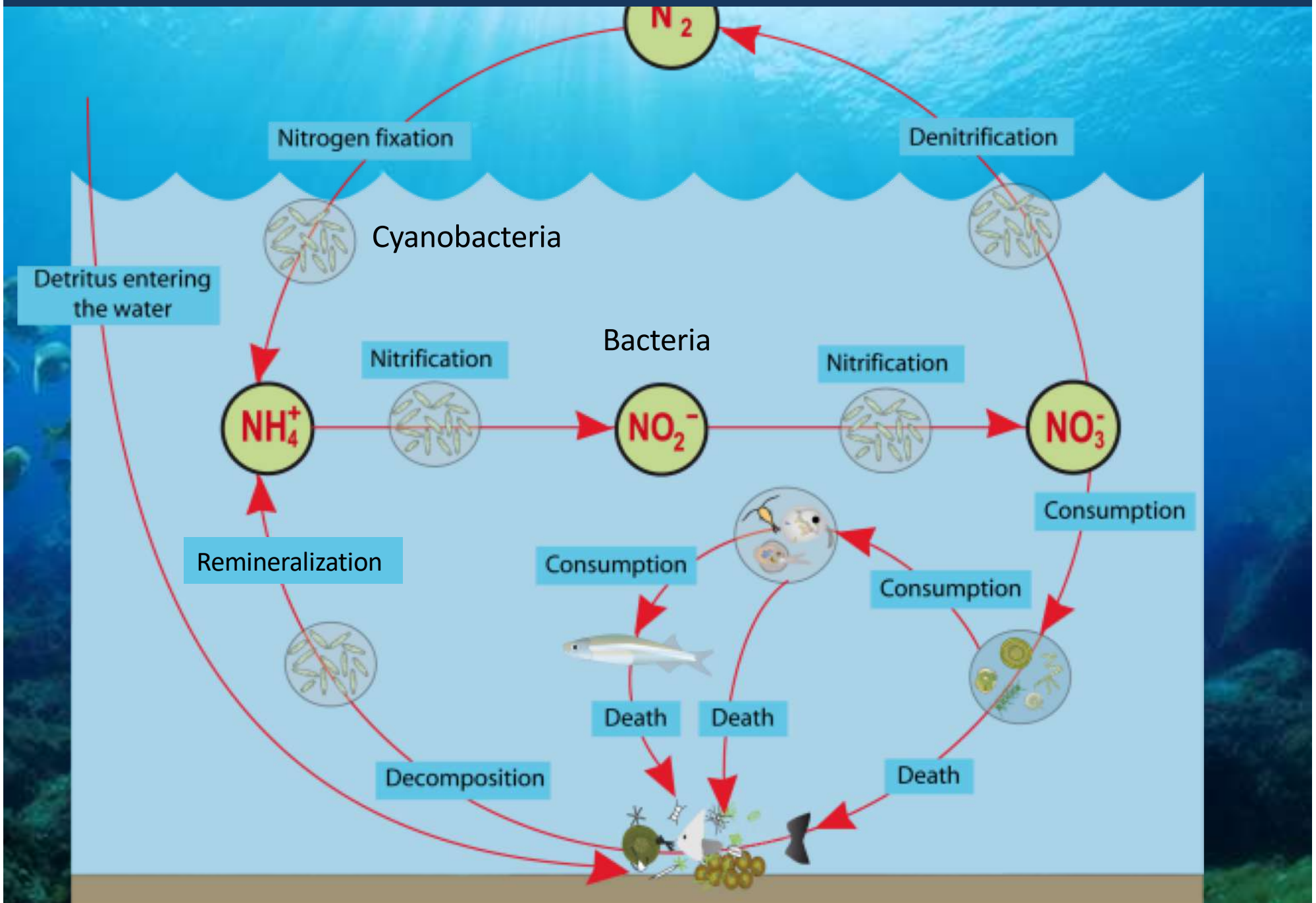


# Terrestrial export of nutrients

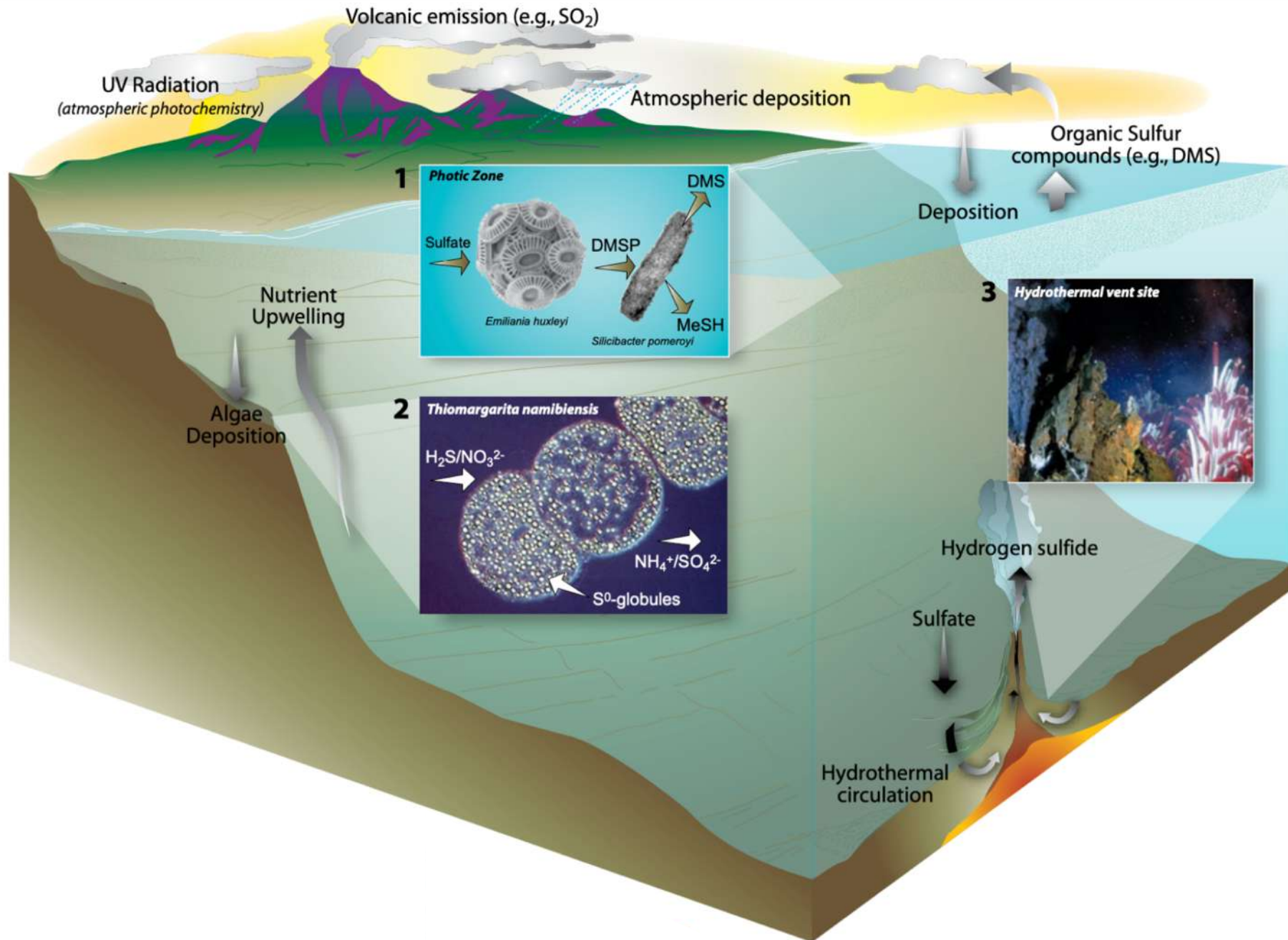




# N cycle



# S cycle

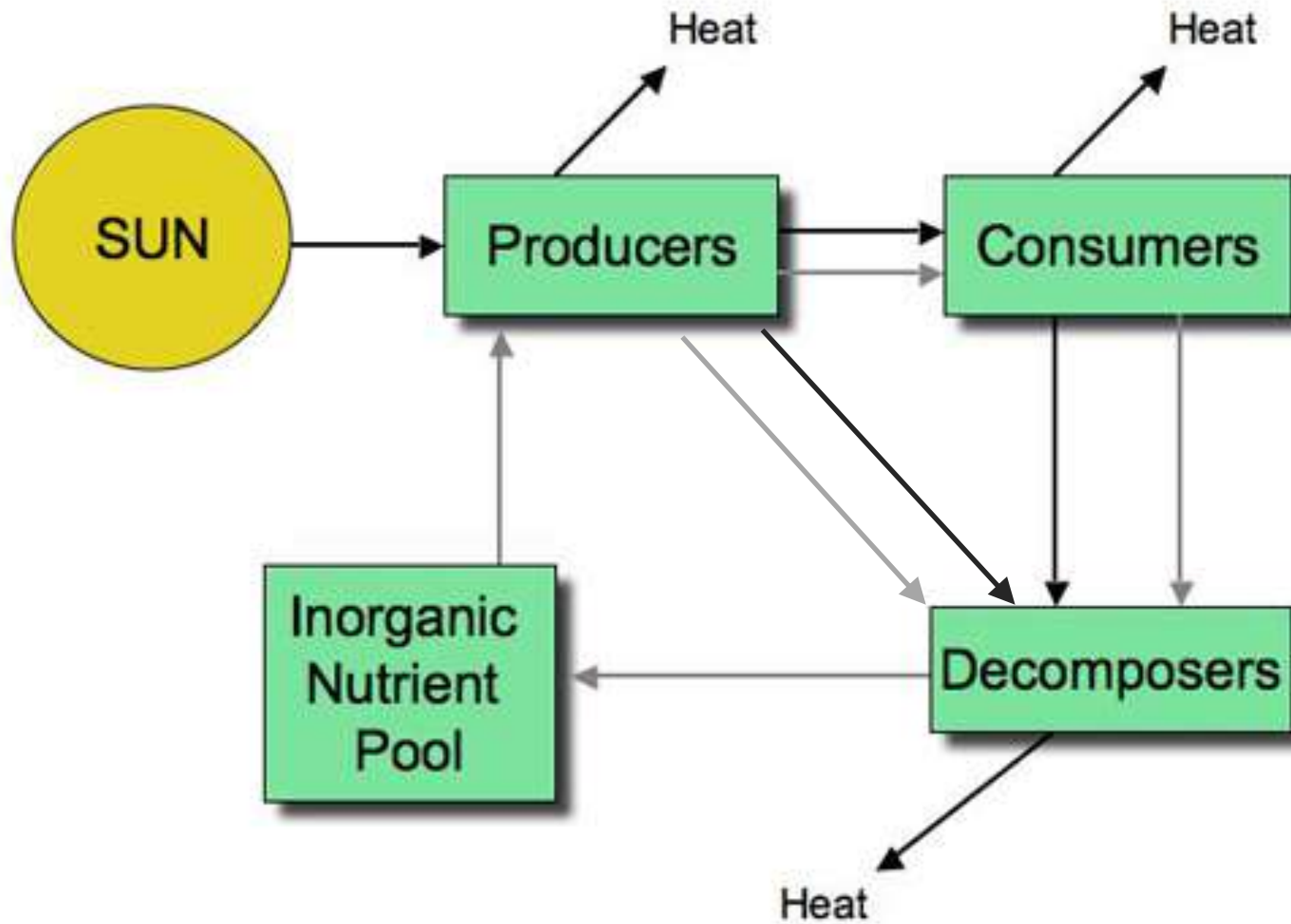




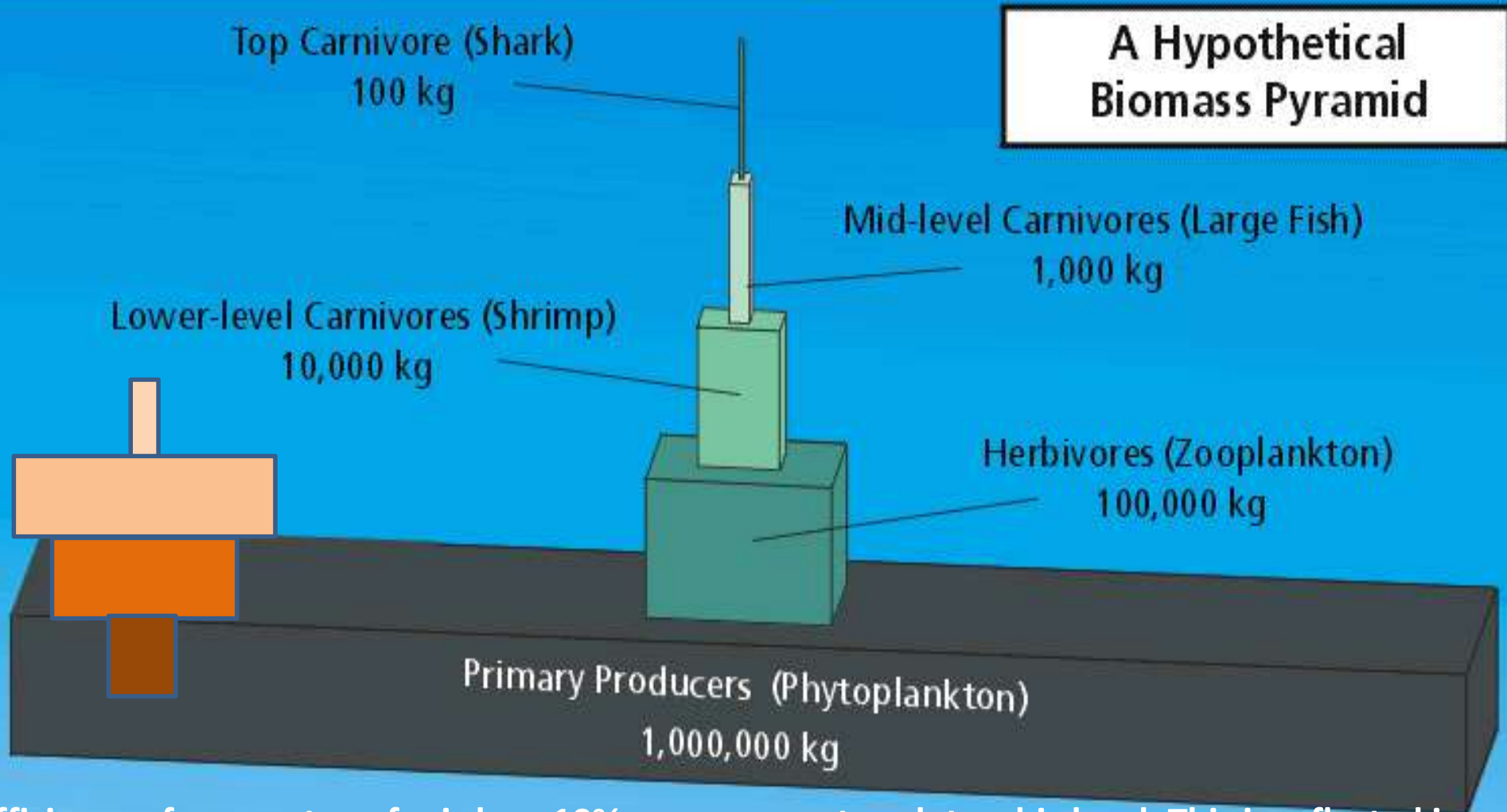
# Trophic webs

1 law of thermodynamics

2 law of thermodynamics



# Energy flow

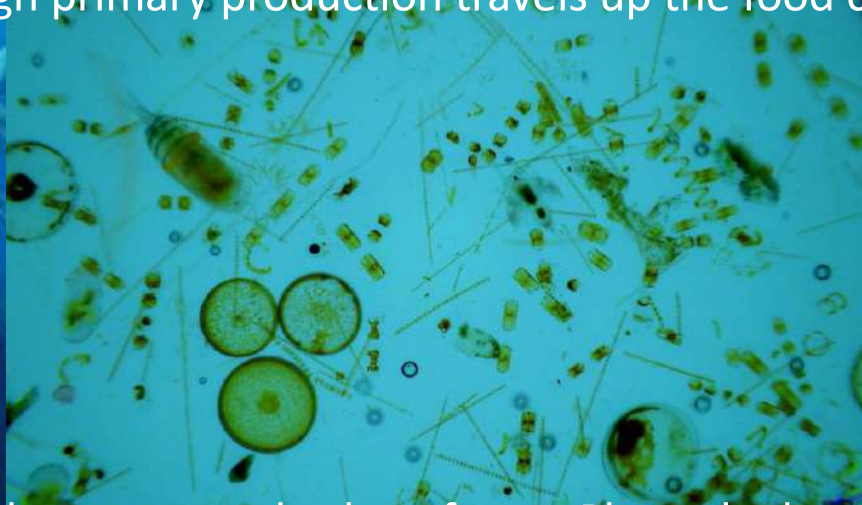


Efficiency of energy transfer is low, 10% on average at each trophic level. This is reflected in the biomass ratio between levels. Most of energy is lost in movement, excretions, fecal dejections, heat, so that moving from the basis (primary producers) to higher levels, the total sustainable biomass 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

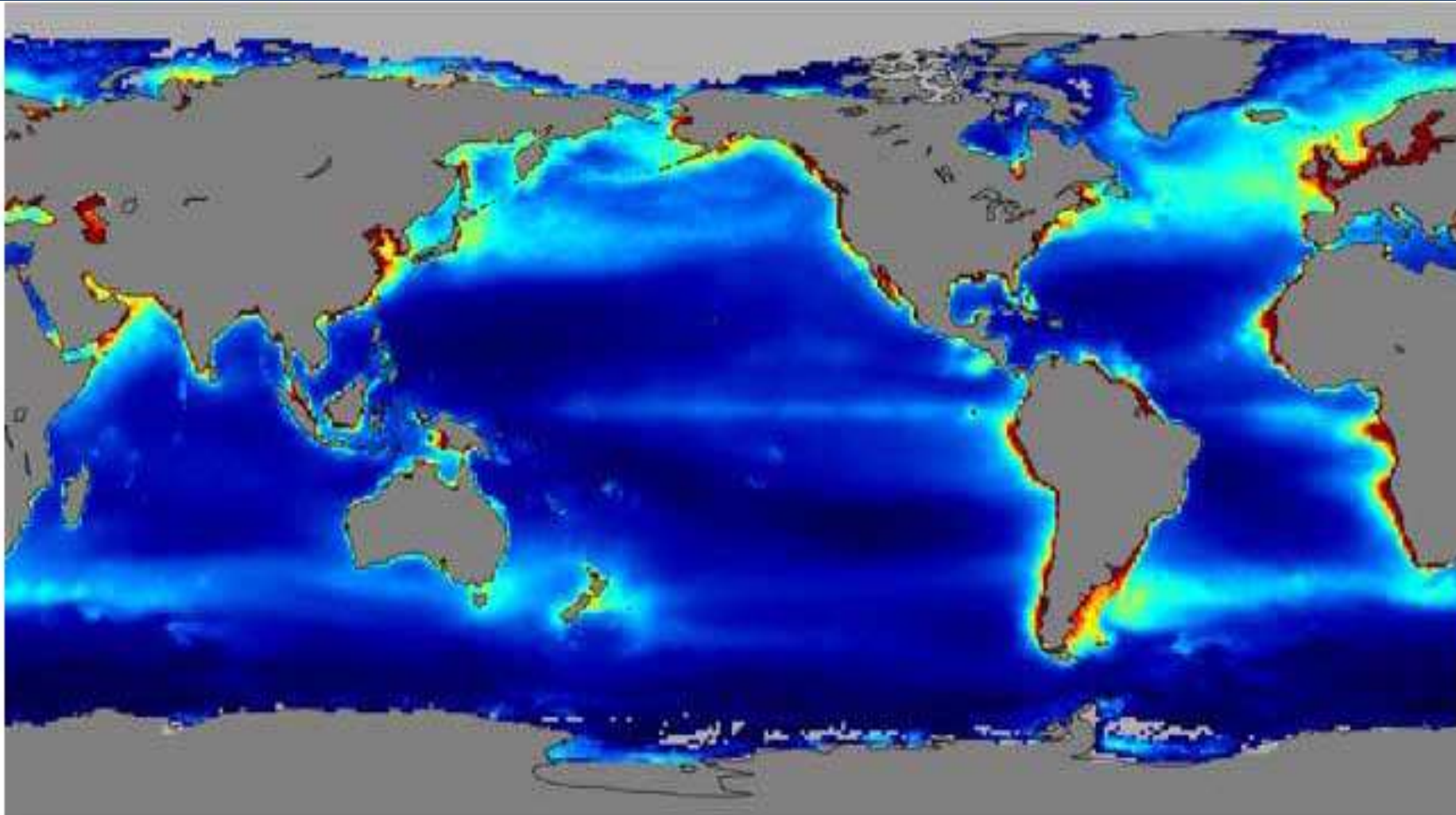
Because of these energy losses, most terrestrial ecosystems have no more than five trophic levels, and marine ecosystems generally have no more than seven. This is likely due to differences in the fundamental characteristics of land and marine primary organisms. In marine ecosystems, microscopic phytoplankton 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.



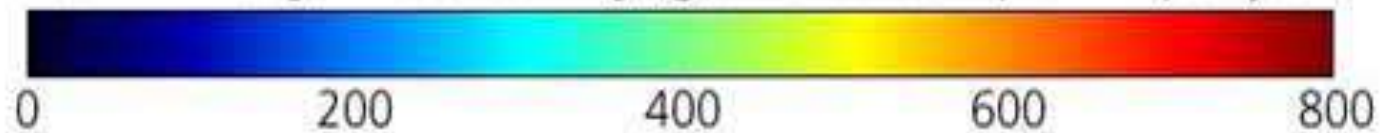
Growth rates may also be a factor. Phytoplankton are extremely small but grow very rapidly, so they support large populations of herbivores even though there may be fewer algae than herbivores at any given moment. In contrast, land plants may take years to reach maturity, so an average carbon atom spends 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

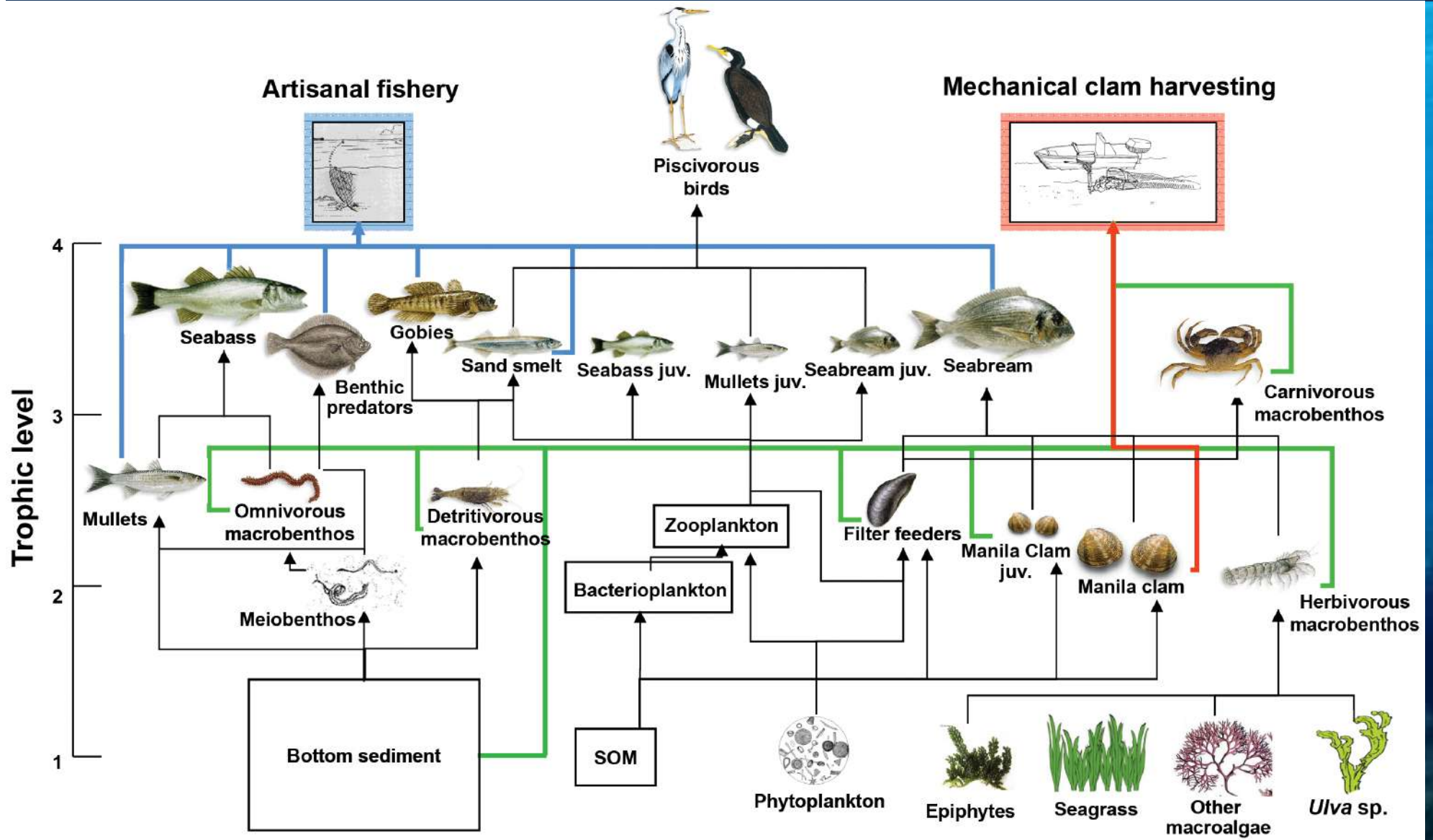


**Net Primary Productivity** (grams Carbon per m<sup>2</sup> per year)

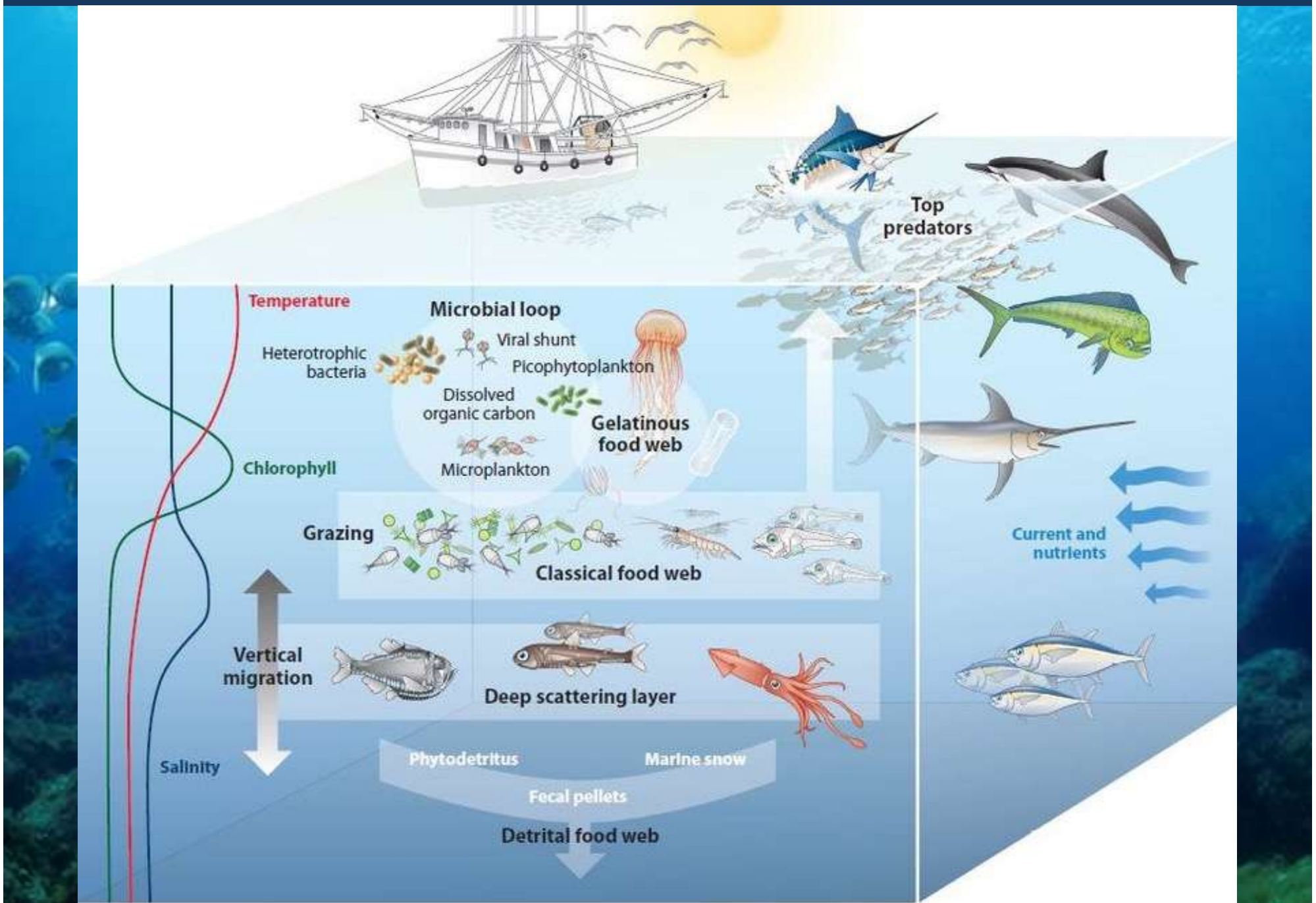




# Trophic webs: coastal Mediterranean

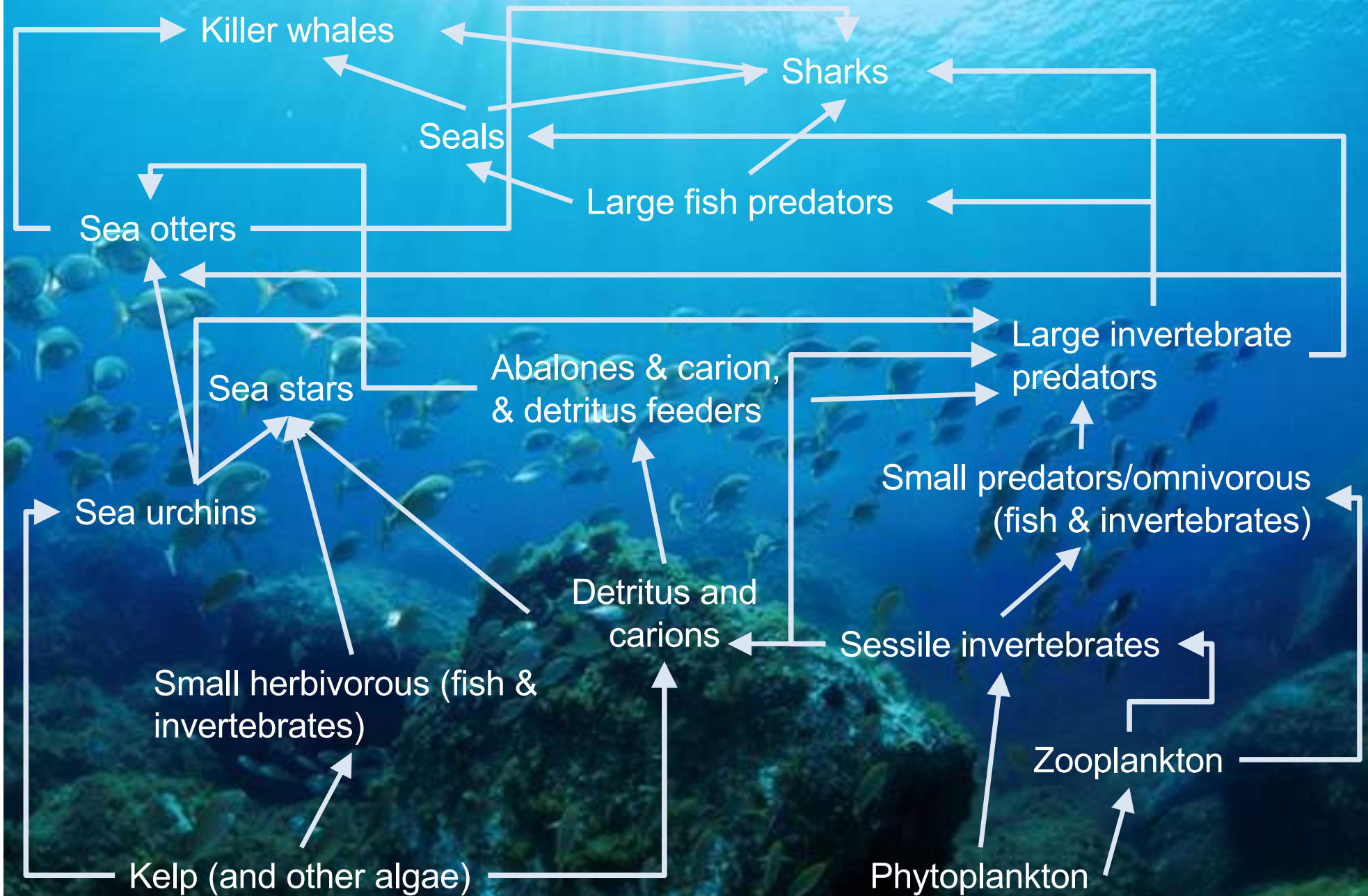


# Trophic webs: pelagic

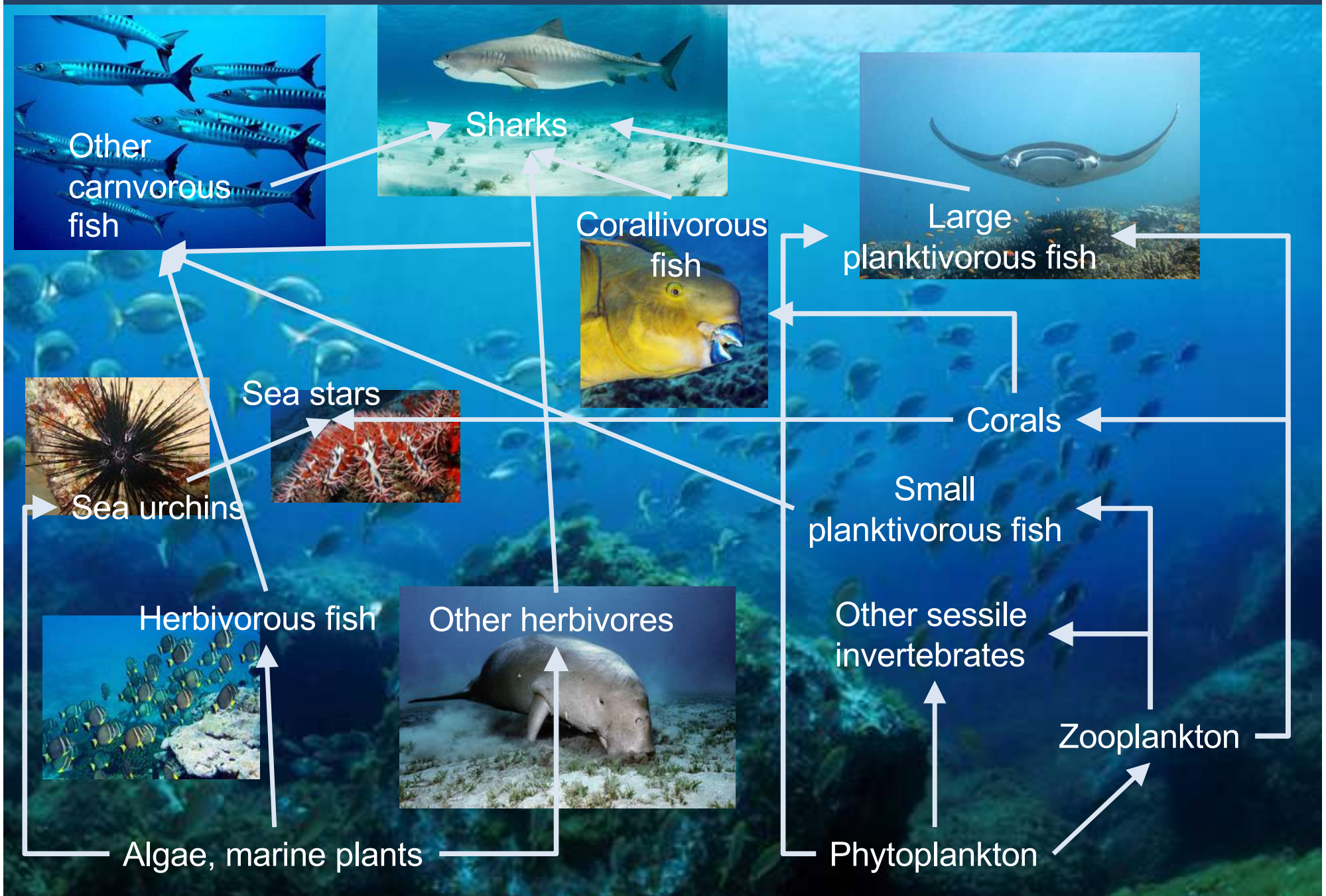




# Trophic web: kelp forests



# Trophic web: coral reefs





# 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 ecosystems.



# 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 Pacific Northwest. 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.



Pisaster



Thais

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.



Gooseneck  
Barnacles



Limpets



Bivalves



Acorn  
Barnacles



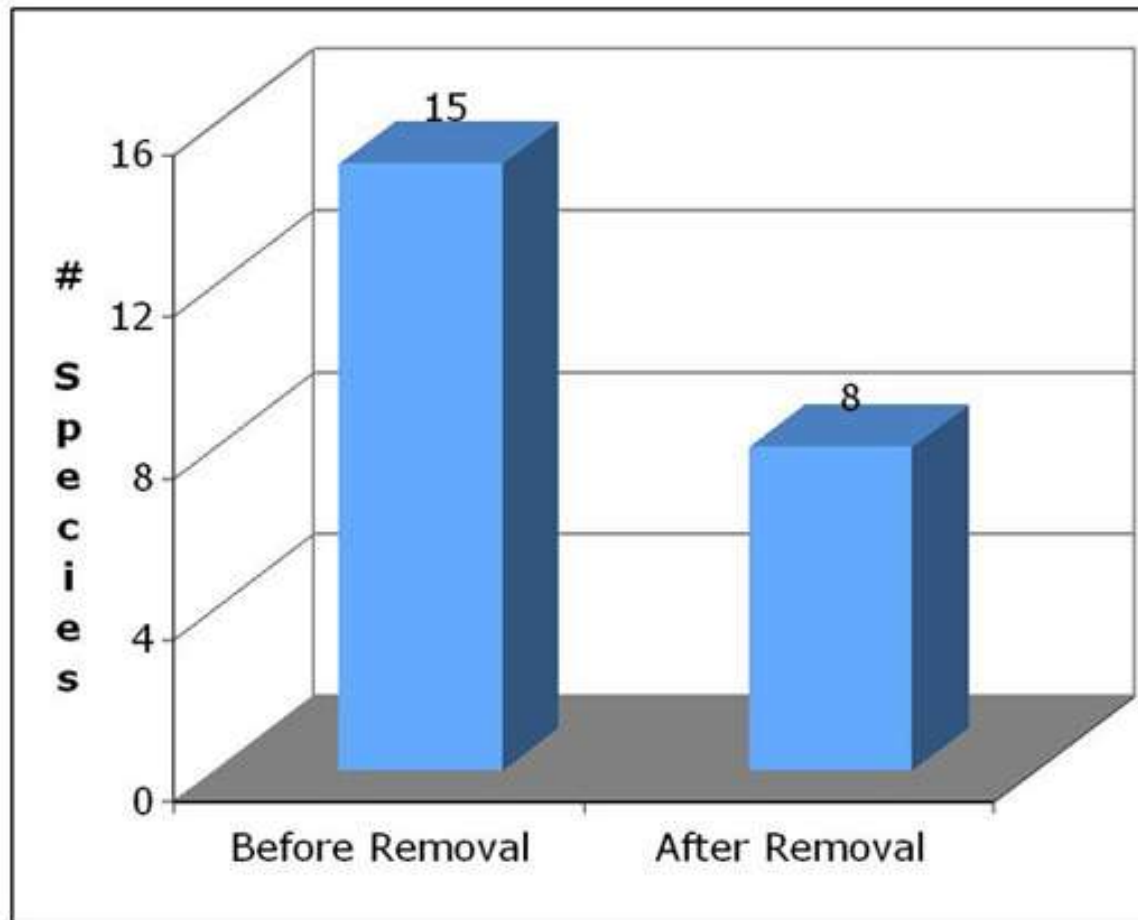
Chitons



# Paine's experiment

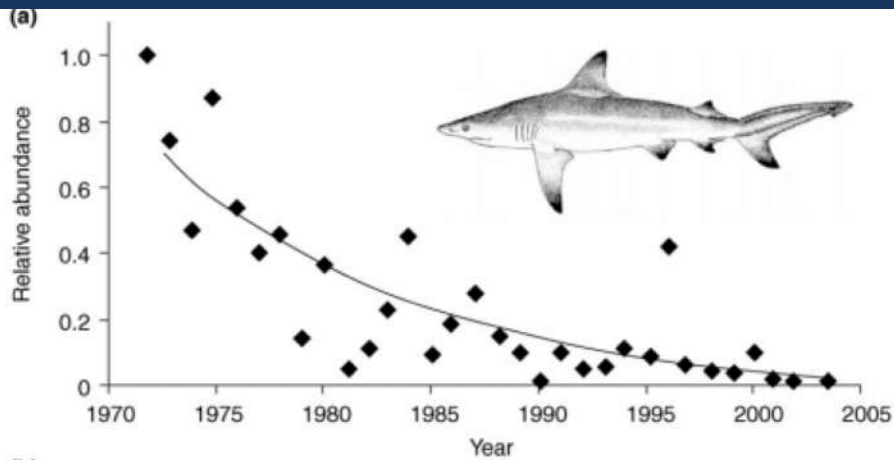
He tested his hypothesis in an experiment in which an area of the intertidal was kept free of starfish, comparing them with an undisturbed control area of equal size.

He observed dramatic changes after *Pisaster* was artificially removed compared with the control area that remained unchanged in its species number and distribution. After removal of starfishes the other species began to compete.

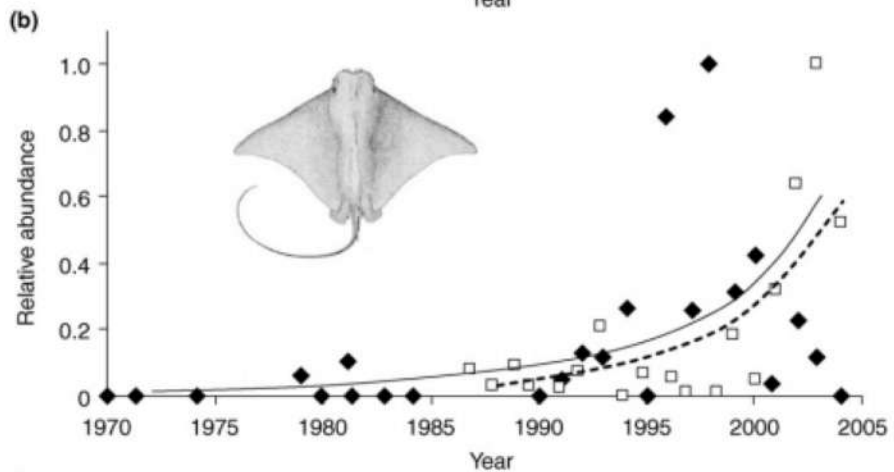


Within three months the barnacle, *Balanus glandula*, became dominant and after 9 months, it was replaced by another barnacle *Mitella* and the mussel *Mytilus*. The succession of species wiped out populations of benthic algae, causing some species, such as the limpet, to emigrate because of lack of 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

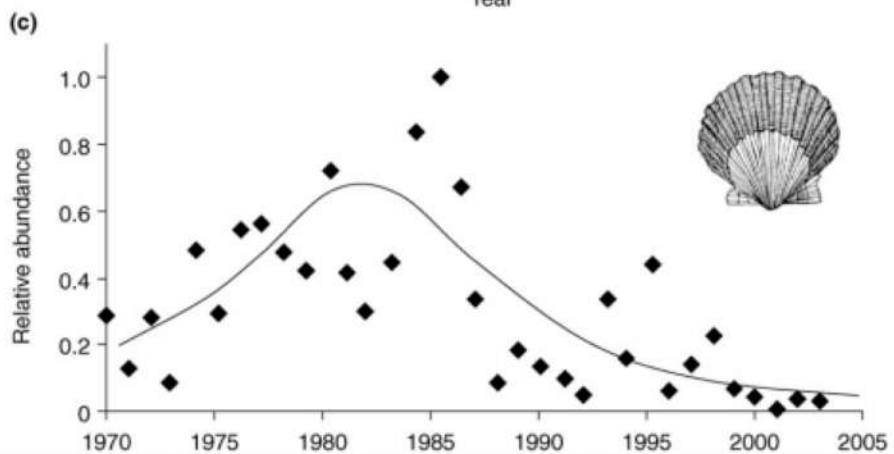
# Large predators



*Carcharhinus limbatus*



*Rhinoptera bonasus*



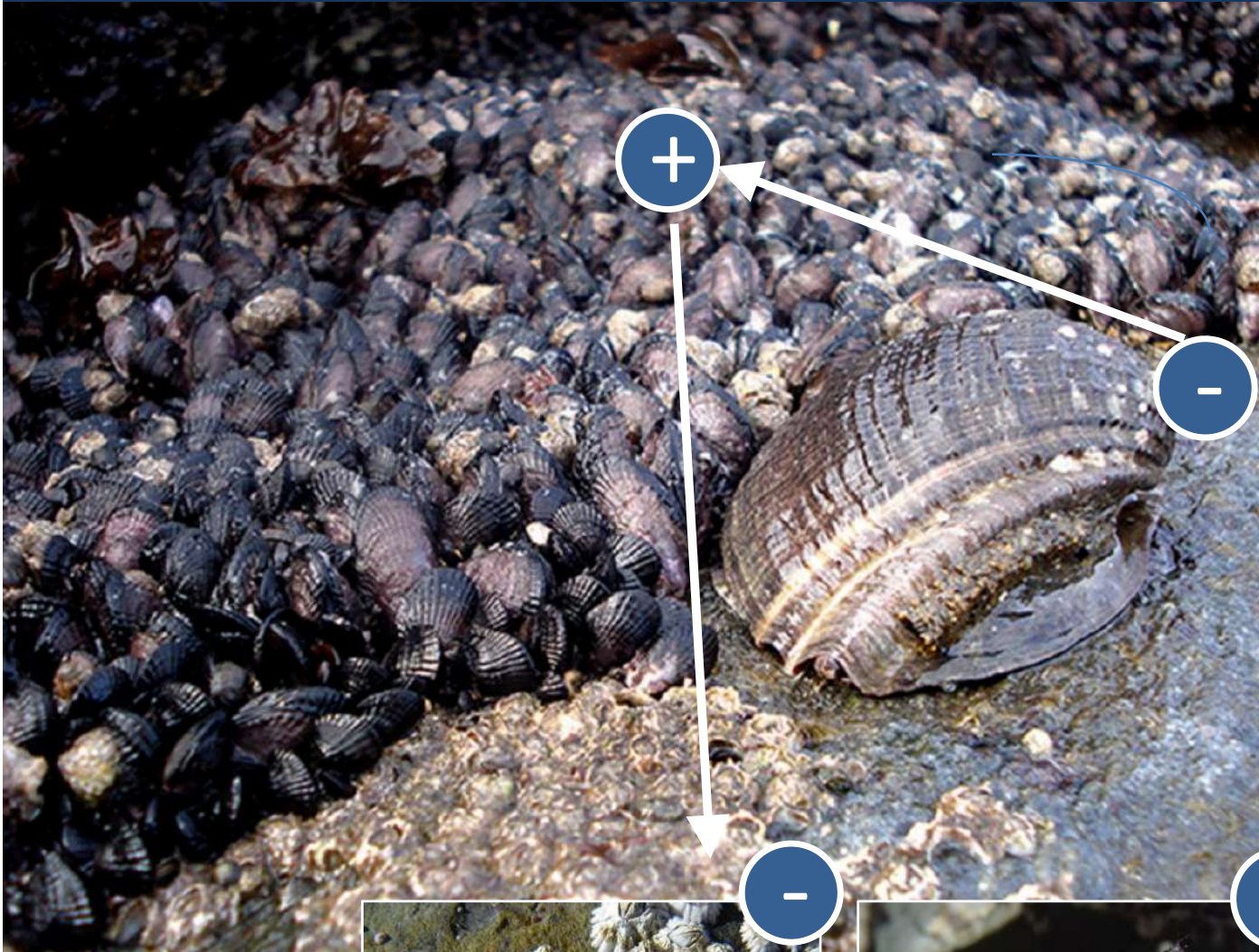
*Agropecten irradians*



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.



# Small predators

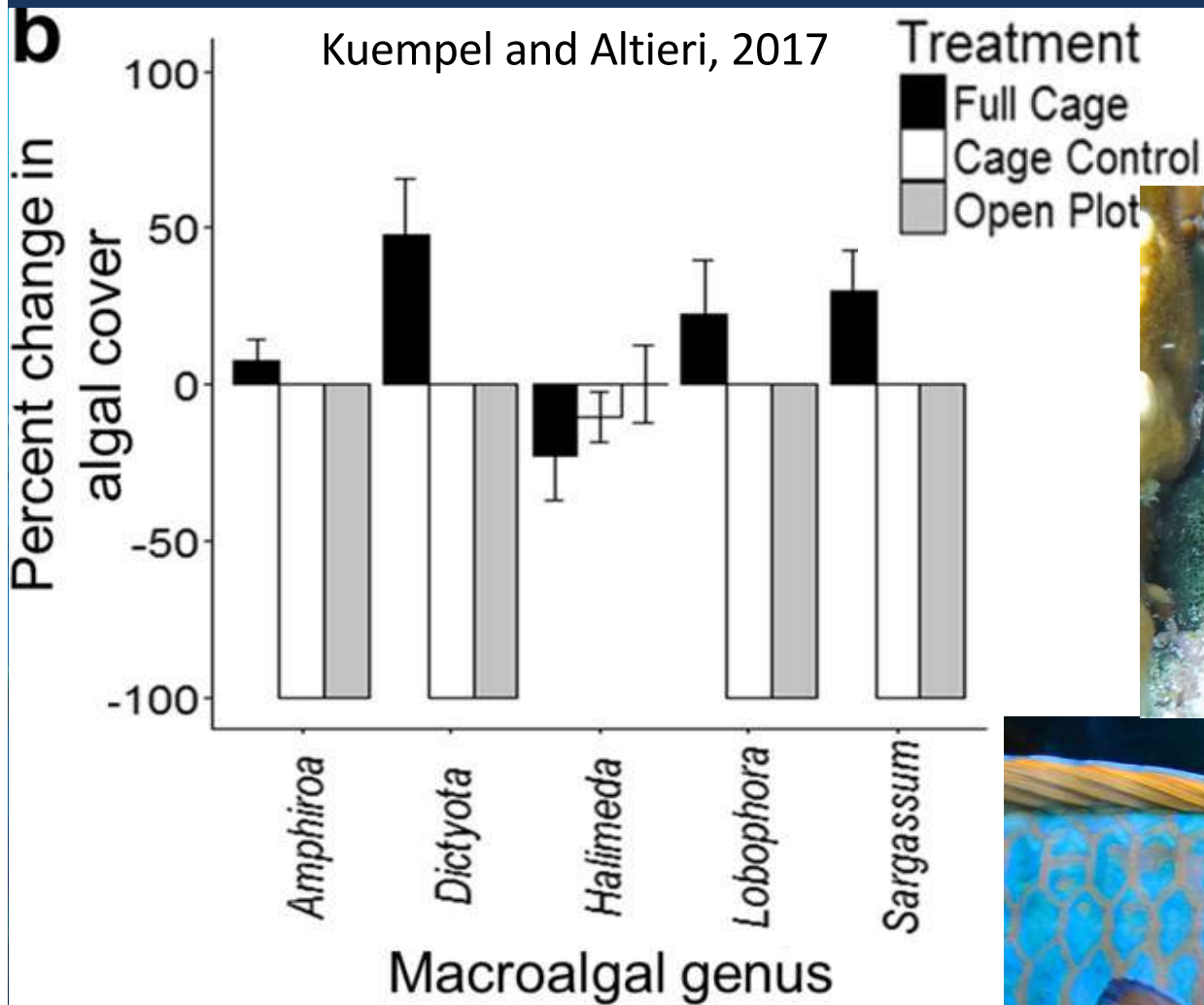


Decline in predator snails *C. concholepas* allows mussels *Perumytilus* to overcompete barnacles, macroalgae and herbivorous snails *Fissurella*.





# Herbivores

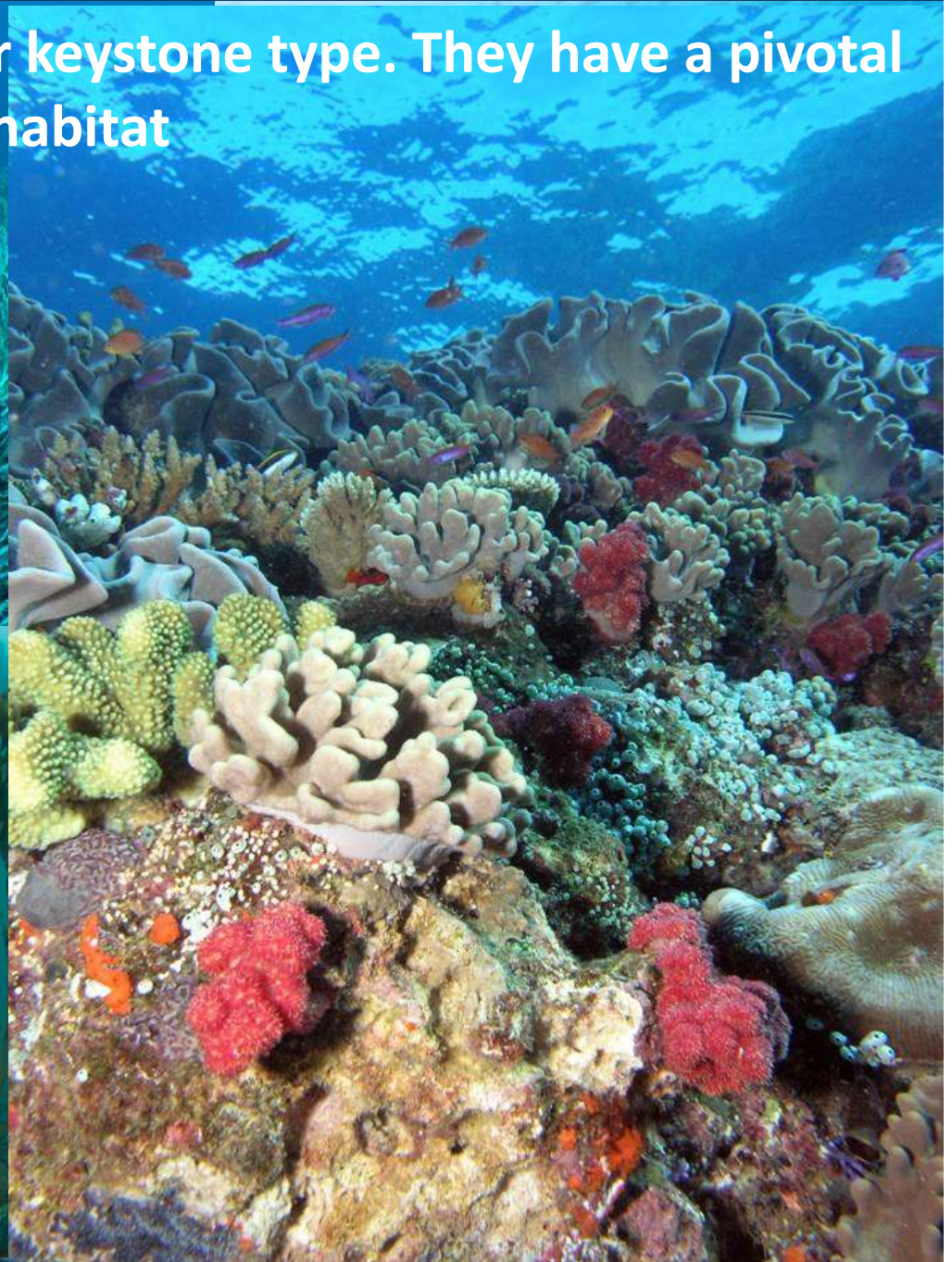


Key role in maintaining coral reefs healthy removing algal turf, dead corals and preventing the dominance of algae after disturbance



# Foundation species

Foundation species are a particular keystone type. They have a pivotal role in creating and maintaining a habitat





# Ecosystem engineering

## Box 1. Examples of marine ecosystem engineers categorized by structures formed

Coleman & Williams 2002

The following examples of widespread marine ecosystem engineers all increase the structural complexity of the habitat, the local biomass, and the local biodiversity, with additional ecological influences distinctive to each category.

- Corals, oysters, vermetid gastropods, sabellid worms and crustose coralline algae construct large solid mineralized reefs [a–d]. These provide settlement substratum for other organisms and provide refuge from predation.
- Marine plants (e.g. seagrasses and kelps) [a] form canopies of vegetation in nearshore waters. They modify water flow, entrain larvae and provide refuge from predation.
- Bivalve molluscs (e.g. mussels and clams) [a] build thick shellfish beds and mats on rocky shores and in soft sediments. The structure provided by shells and by byssal threads of molluscs serve to ameliorate environmental extremes, deposit organic matter, fertilize sediments and promote growth of marine plants [e,f].
- Tilefish, groupers, clams, amphipods, specific types of shrimps (callinassid, alpheid), sea cucumbers, fiddler crabs and worms form excavations and burrows [g], sometimes meters deep.
- While foraging, herbivorous sea turtles [h] and dugongs [i] create large gaps in seagrass beds. Dugongs 'bulldoze' through vegetation and sediments.



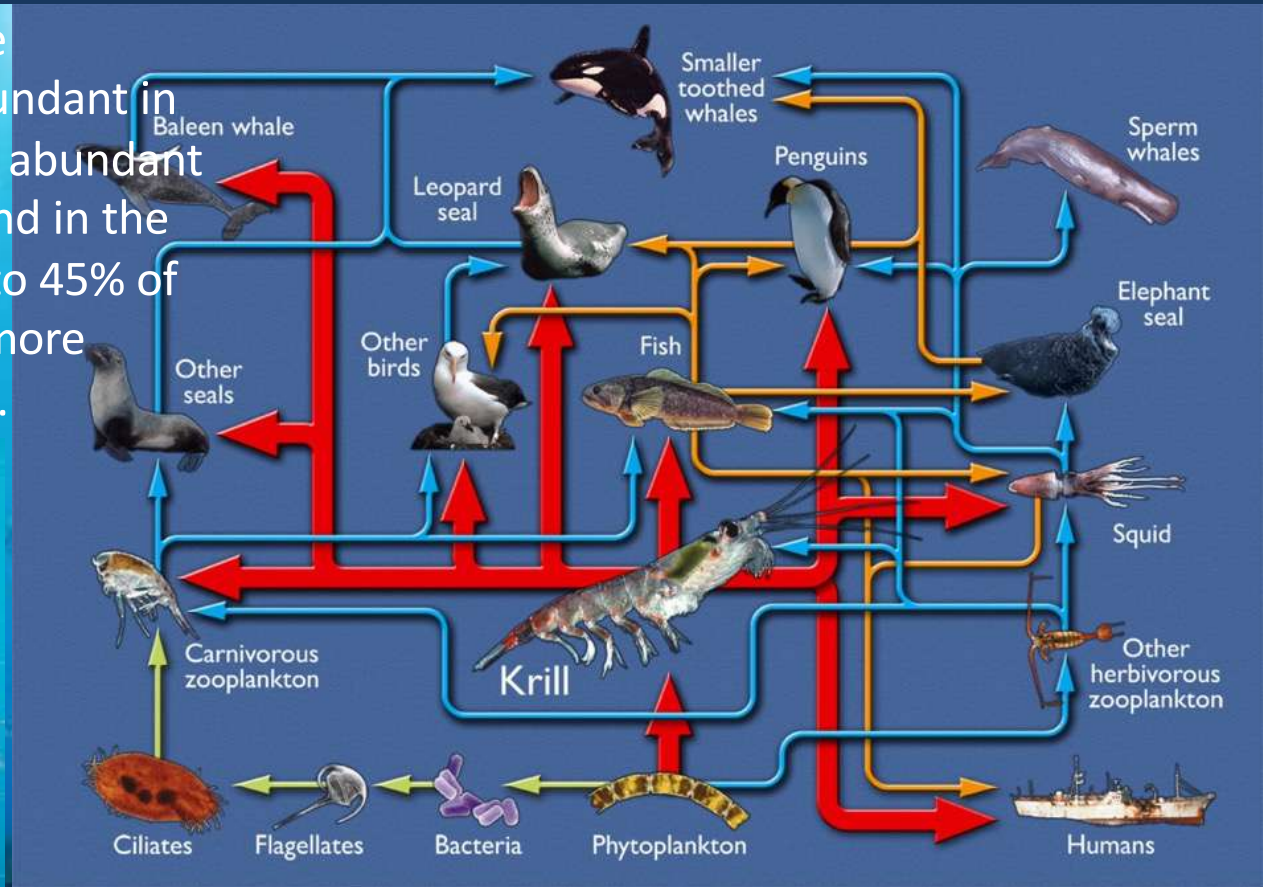
Ecosystem engineers are organisms that create, modify or maintain habitats (or microhabitats) by causing physical state changes in biotic and abiotic materials that, directly or indirectly, modulate the availability of resources to other species. They can be allogenic (modifying existing physical environment) or autogenic (providing physical structures)



# 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 Southern Ocean.

>10.000 ind m<sup>-1</sup>  
(William et al., 1983)



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).



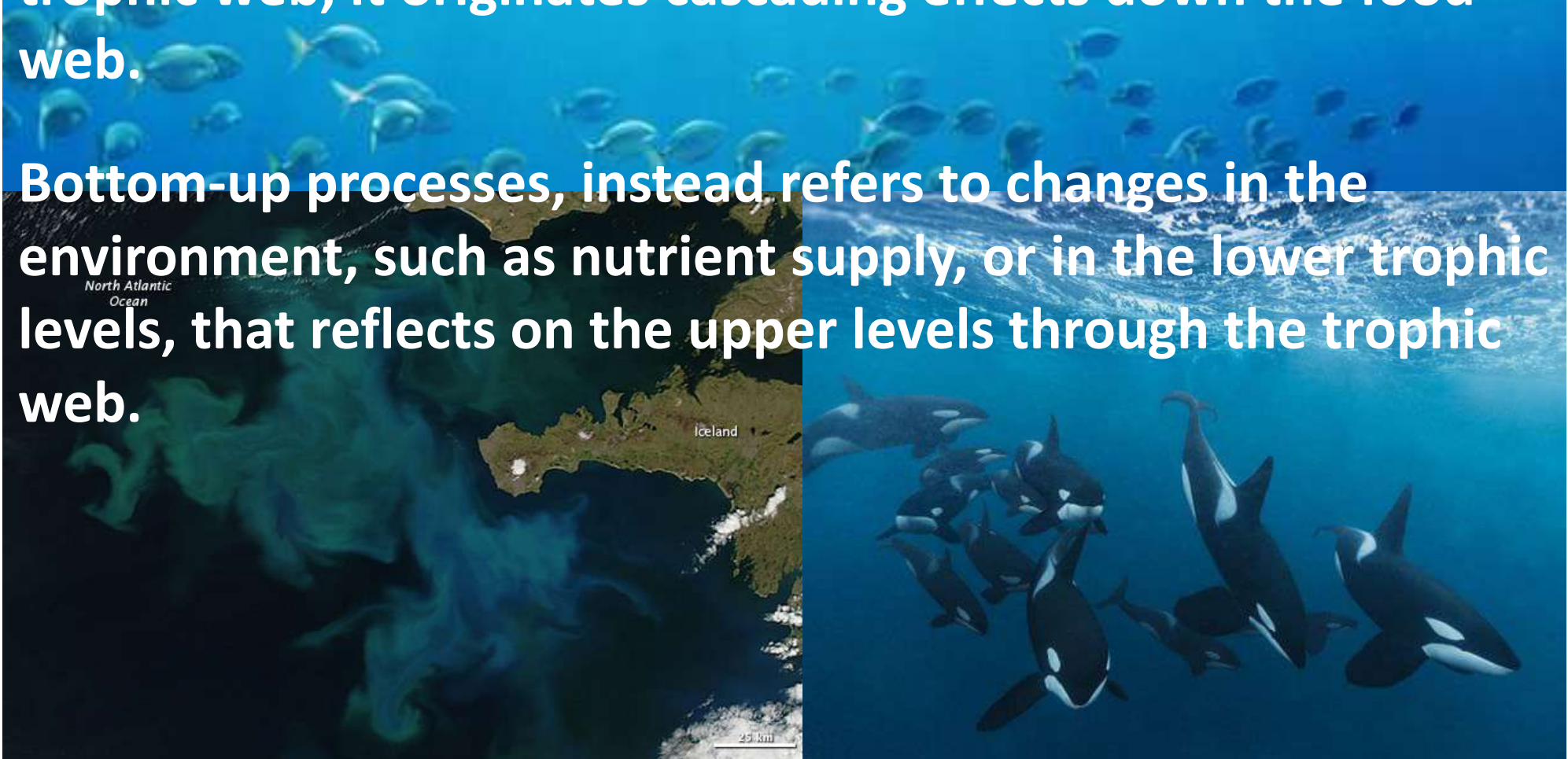
Crab-eater seal  
(*Lobodon carcinophaga*)



# Top-down and bottom-up

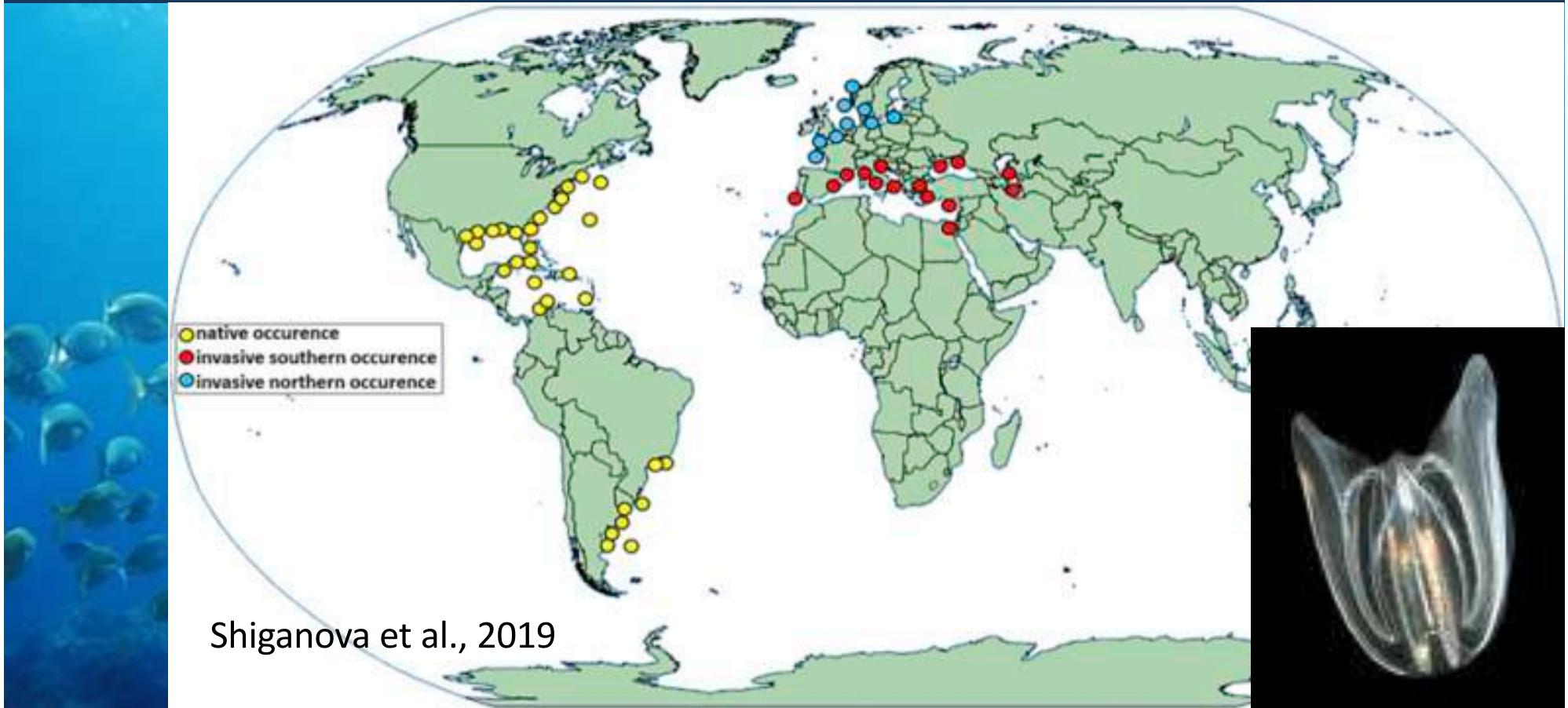
Top-down processes involve a predator/consumer that exert a control on populations of preys, which are at a lower trophic level. When this control propagate through the trophic web, it originates cascading effects down the food web.

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.



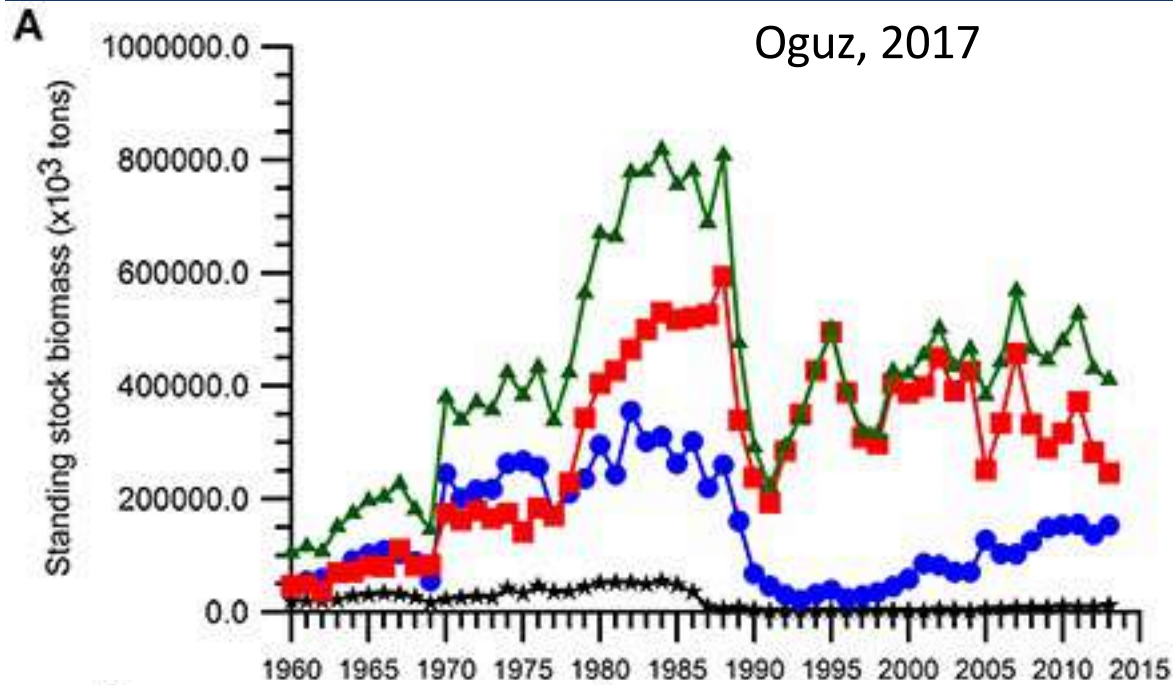


# Top-down from invasive predators

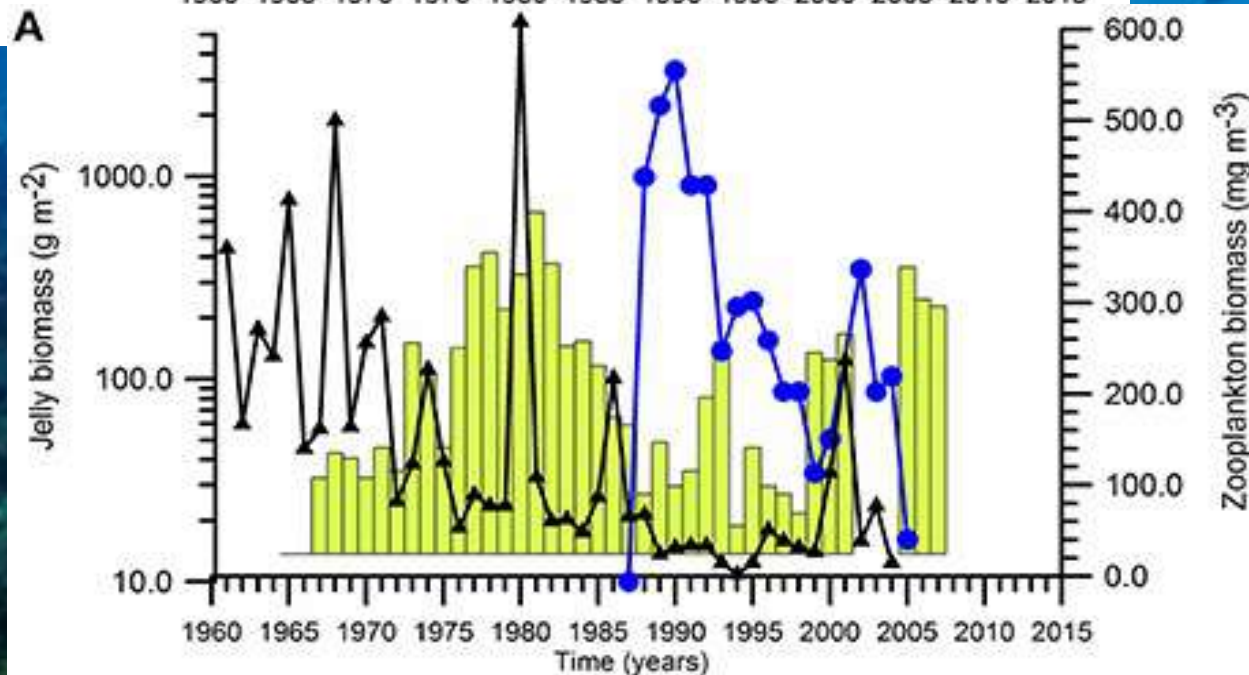


*Mnemiopsis leidyi* introduced in 1980 in the Black Sea. Blooms up to 7600 individuals per m<sup>3</sup>. Now spread in Mediterranean Sea, also in the Adriatic Sea. Wide range of tolerance to temperature and salinity. Predator of plankton, including fish eggs and larvae. Introduced with ballast waters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

# Effects on fish populations



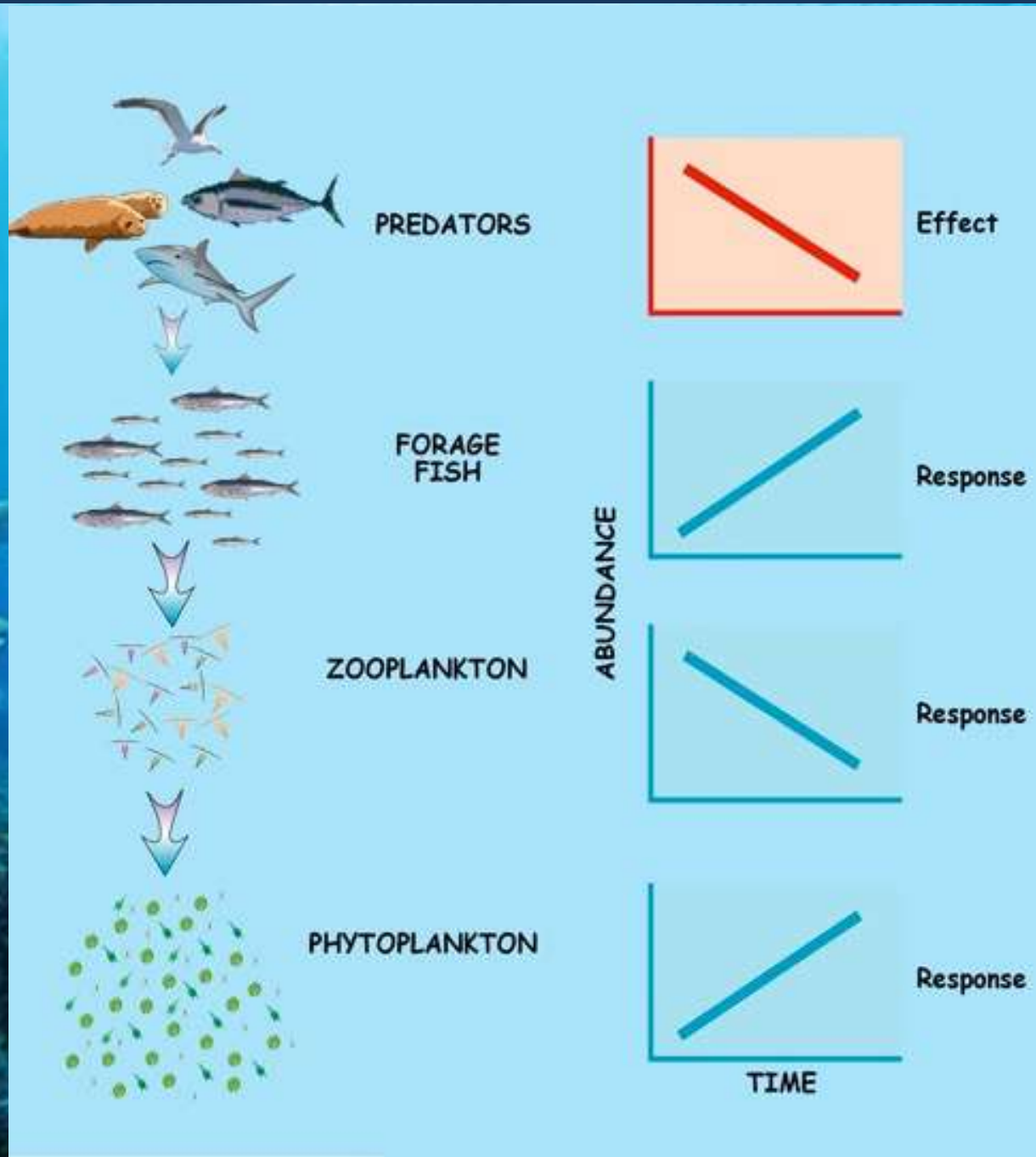
Concurrent effects due to pollution, overfishing and finally the introduction of the ctenophores lead fish stocks and fisheries to collapse. Double effect of predation of *Mnemiopsis*: direct reduction of recruitment of fish due to predation on egg and larval stages, and indirect effect through competition 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.



# Trophic cascades

## Cascading effects if sea otter are removed



Sea Otter

### Sea Otters: Their Role in Structuring Nearshore Communities

Abstract. A comparison of western Aleutian Islands with and without sea otter populations shows that this species is important in determining littoral and sublittoral community structure. Sea otters control herbivorous invertebrate populations. Removal of sea otters causes increased herbivory and ultimately results

SCIENCE, 1974.  
Vol. 185: 1058-1060

JAMES A. ESTES

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Sea urchins

Hughes et al., 2005  
**TREE**



Kelp forests



Barrens

Top-down control of sea urchins in  
kelp forest (Western Pacific, USA)

Vol. 136, No. 1

The American Naturalist

July 1990

### INFERENCE IN ECOLOGY: THE SEA URCHIN PHENOMENON IN THE NORTHWESTERN ATLANTIC

R. W. ELNER AND R. L. VADAS, SR.

Biological Sciences Branch, Department of Fisheries and Oceans, P.O. Box 550, Halifax,  
Nova Scotia B3J 2S7, Canada; Department of Botany and Plant Pathology,  
University of Maine, Orono, Maine 04469

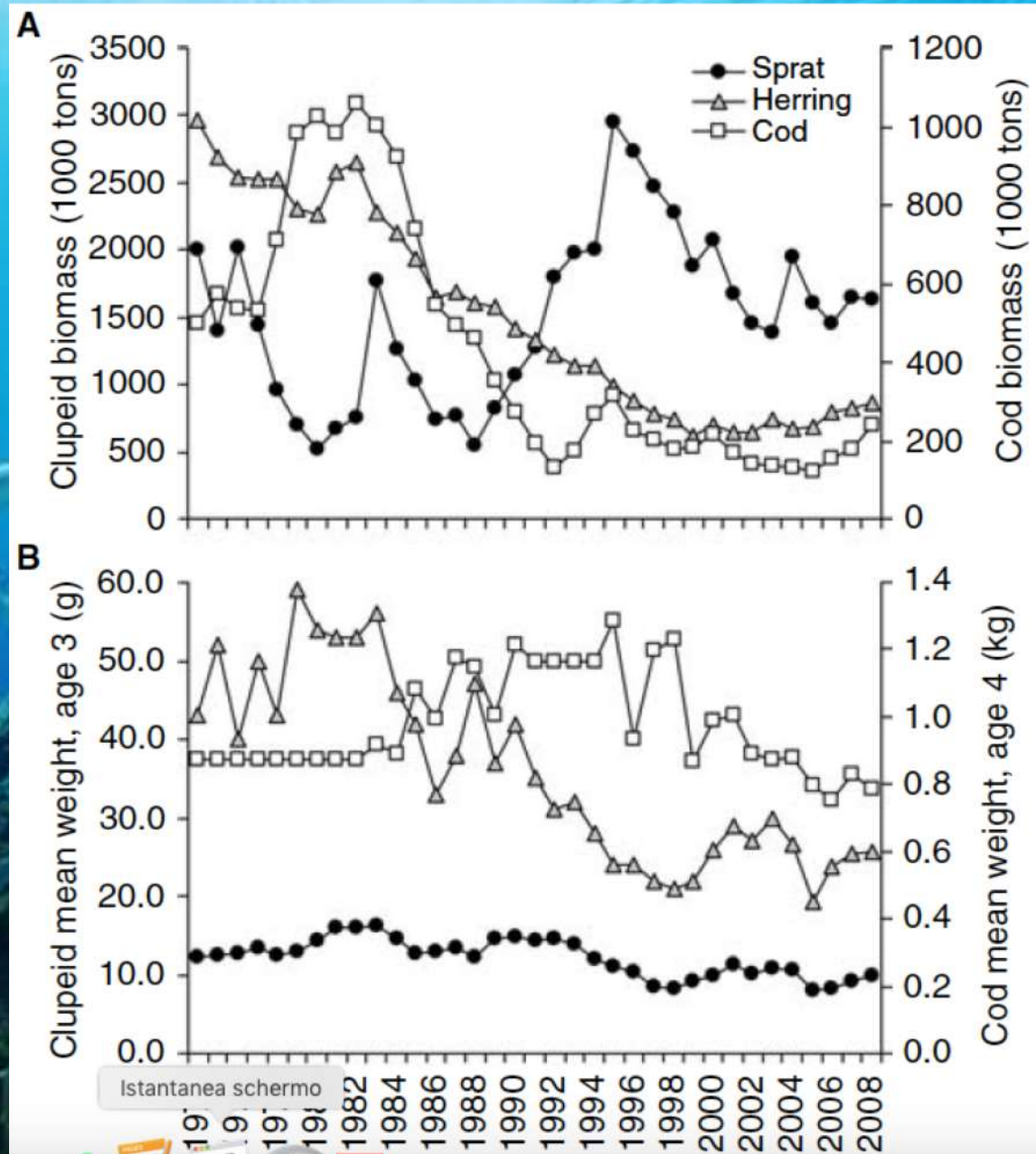
Submitted November 21, 1988; Revised July 17, 1989; Accepted October 12, 1989

A fundamental concern in ecology is the absence of a consensus on how to  
"do" this science. Over the past few years, diametrically opposed treatises have

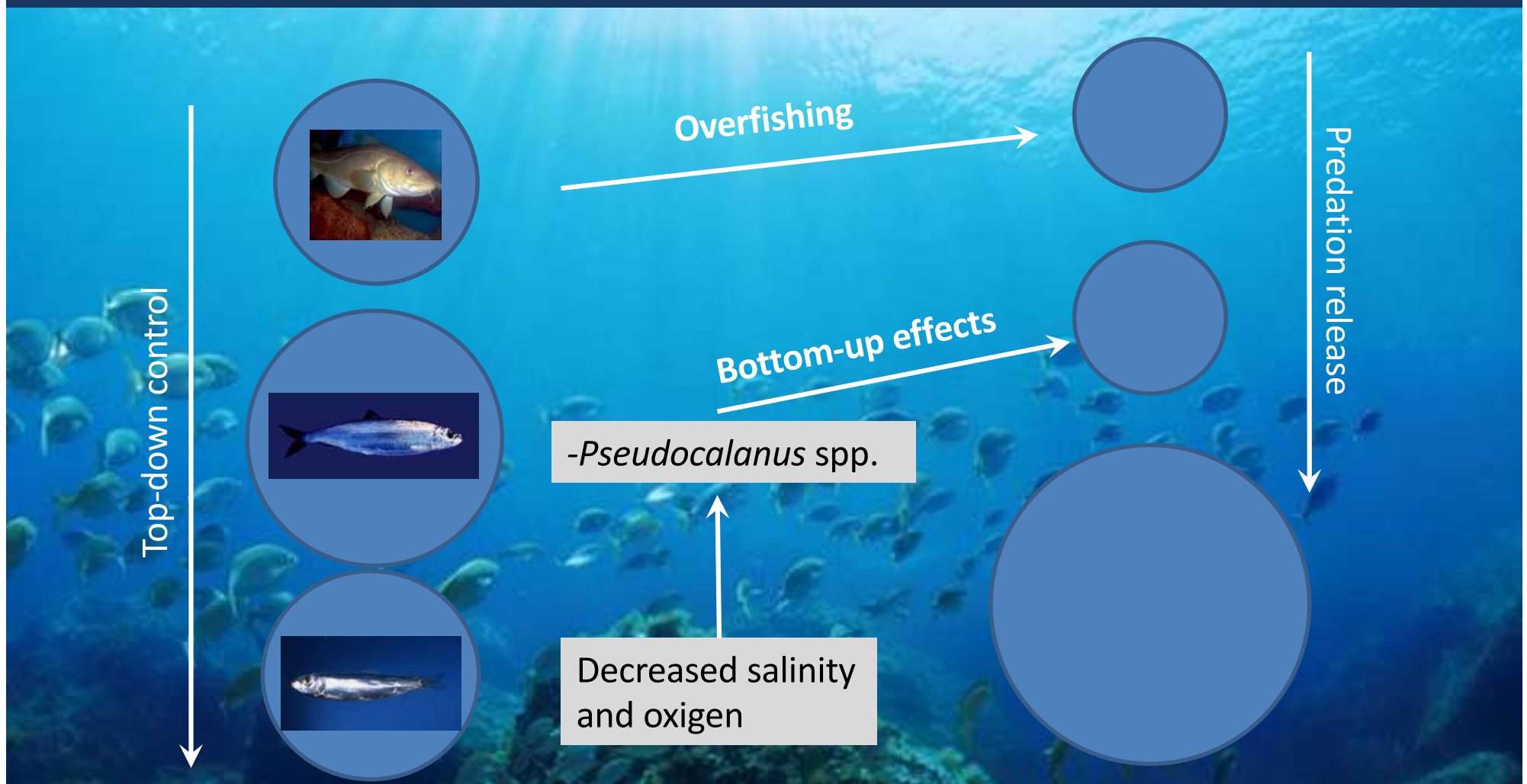


# Top-down and bottom up

Strong reductions in the abundance of a top predator (cod) has also been reported to cause a trophic 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

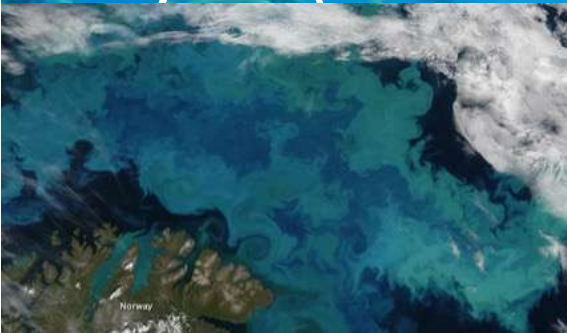


Changes in the Baltic Sea were primarily bottom-up, strongly structured by salinity, but top-down forcing related to changes in cod abundance also shapes the ecosystem. (Flinkman et al. 1998; Casini et al., 2011)



# 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

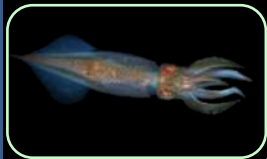
Predator diversity may dampen cascading effects

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



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

### Life cycles

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



Herbivores and predators from the water column feed on benthos

### Trophic webs

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



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

### Organic matter

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

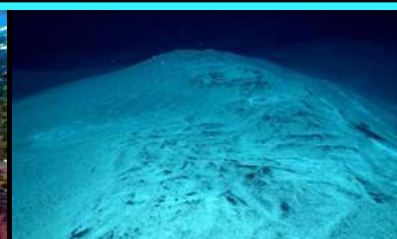


Nutrients and gases reach the bottom and can turn back as living matter or through upwelling

### Biogeochemical cycles



## Benthos

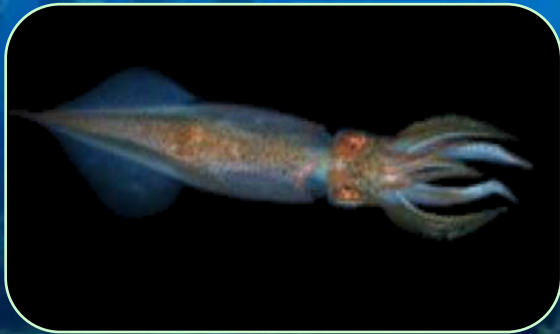




## Life cycles



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

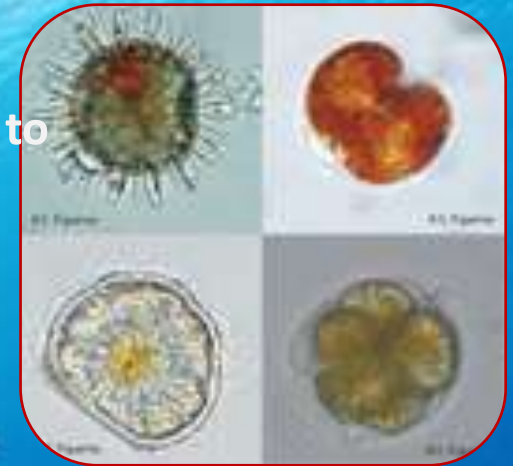
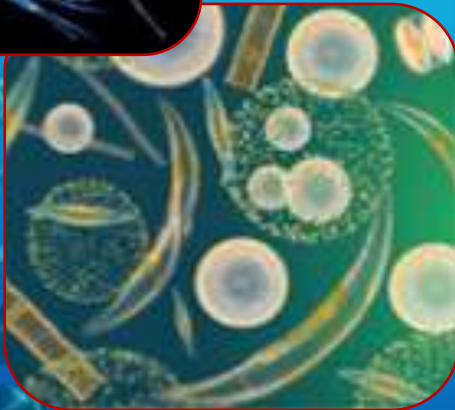




## Organic matter



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.

