

Who am I

- Royal Belgian Institute for Natural Sciences
 - Université Libre de Bruxelles
 - Coordinator of the SCAR Antarctic Biodiversity Portal
-
- Main Interests
 - Open Biodiversity data
 - Bringing data to policy

Contact

- E-mail: anton.van.de.putte@ulb.be

SCAR Antarctic Biodiversity Portal

- SCAR: Scientific Committee for Antarctic Research
- www.biodiversity.aq
- Publication of data to
- Ocean Biodiversity Information System,
www.obis.org
- Global Biodiversity information Facility,
www.gbif.org

Teaching supports

- Slides of the course

Books

- At the « Bibliothèque des Sciences et Techniques »
- Both ULB and VUB students have access (for the latter, contact the desk in the library)
- Advanced course: not covered by a single book, even not by multiple ones; several parts based on original scientific literature
- « Framework »: Valiela I. 2015. Marine Ecological Processes. Springer (on line version available).

Books

- « Framework »: Valiela I. 2015. **Marine Ecological Processes**. Springer.
- Thurman HV. 1990. **Essentials of oceanography** 3rd ed. Columbus, Ohio : Merrill Pub. Co
- Segar DA 2007. **An introduction to ocean sciences 2nd edition**. Minneapolis/St. Paul, MN: West Pub.
- Levinton JS 1995. **Marine biology : function, biodiversity, ecology**. New York : Oxford University Press 420 p.
- Sheppard Ch 2000. **Seas at the millennium : an environmental evaluation** New York : Pergamon
- Steele, John H. 2001 **Encyclopedia of ocean sciences vol 1-6**

English

- Taught in English but
 - Most of us are not native speakers
 - Not an English language course
 - Do not hesitate to ask questions (rather small audience)
- Exam
 - In English (preferred)
 - But you have the right to have it in French (ULB students) or in Dutch (VUB students) (NB: Tropimundo in English, mandatory)

The course within your Master

- Marine Biology does not stop at the end of the course!
- Depending on your cursus further excursions during your Master on temperate or tropical shores: you'll need what you learned in this course!
- (ULB MA-BIOR A-D: BIOL-F-416 Stage de Biologie marine)

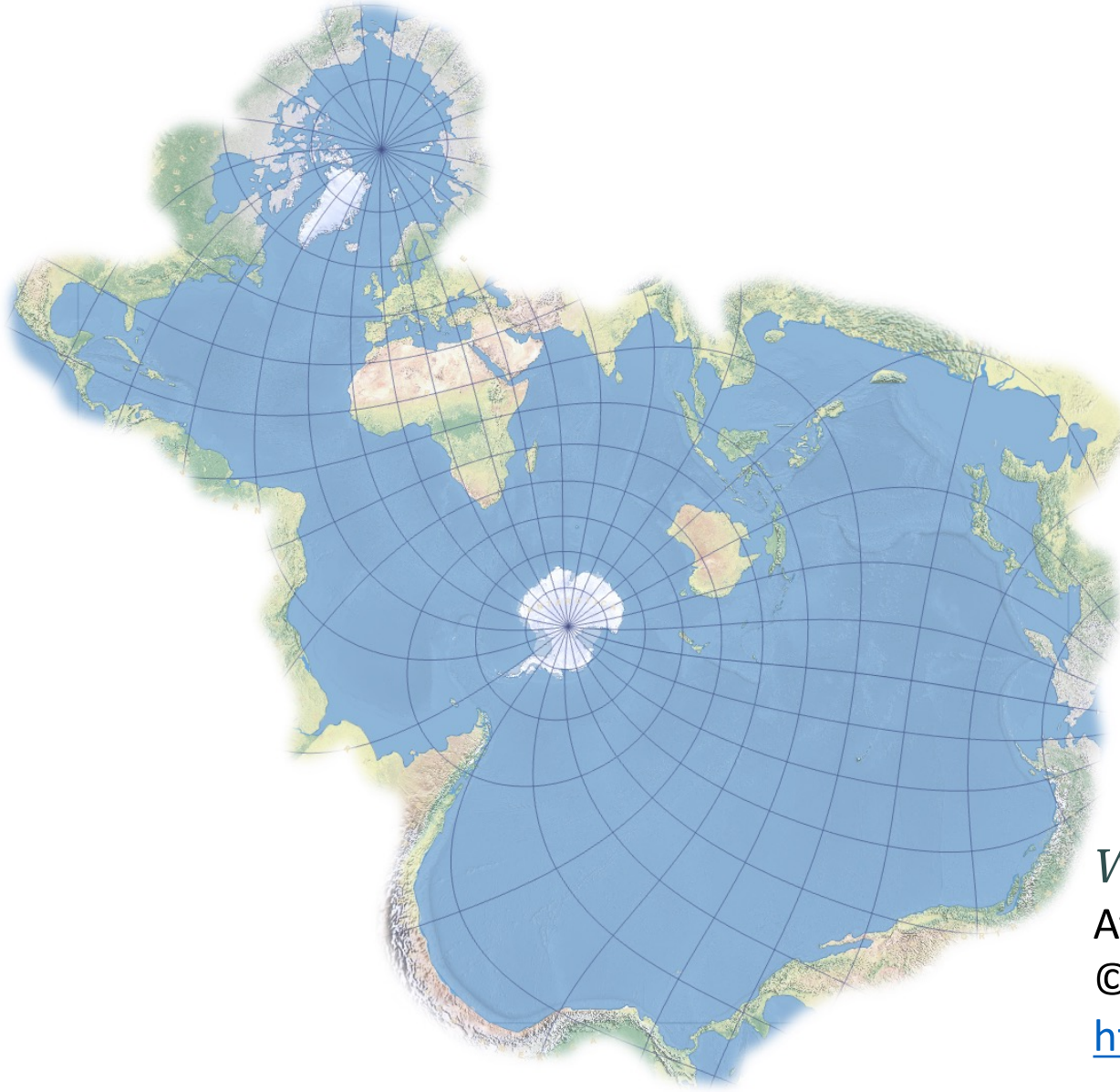
Pelagic Biological Processes

Anton Van de Putte

pelagic zone

- *Pélagos*: 'open sea'
- Water column
- V_s
- Benthos: 'the depths'
- lowest level: the sediment surface and some sub-surface layers

1. Divisions of the marine environment



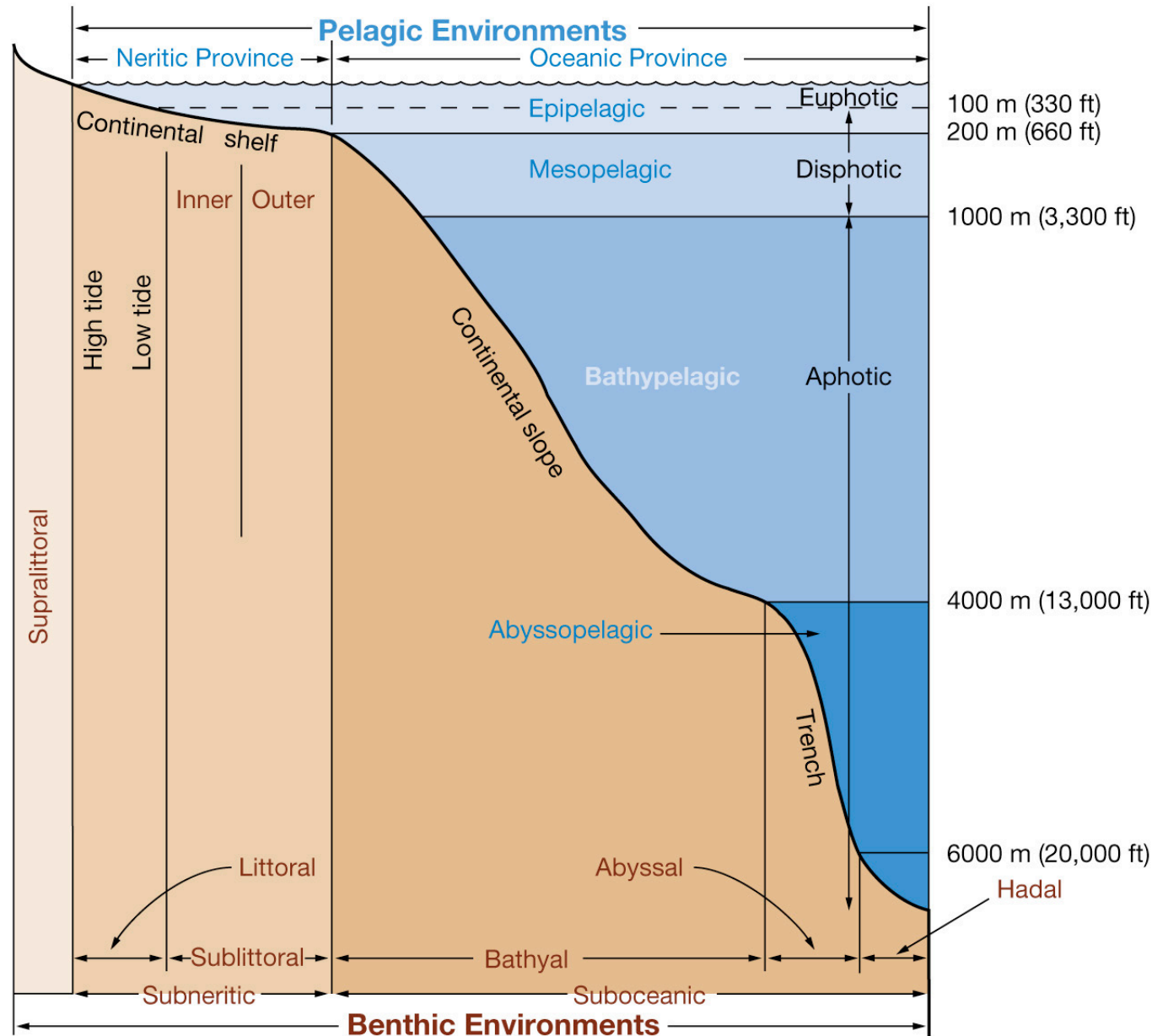
World Ocean Map in a Square

Athelstan Spilhaus

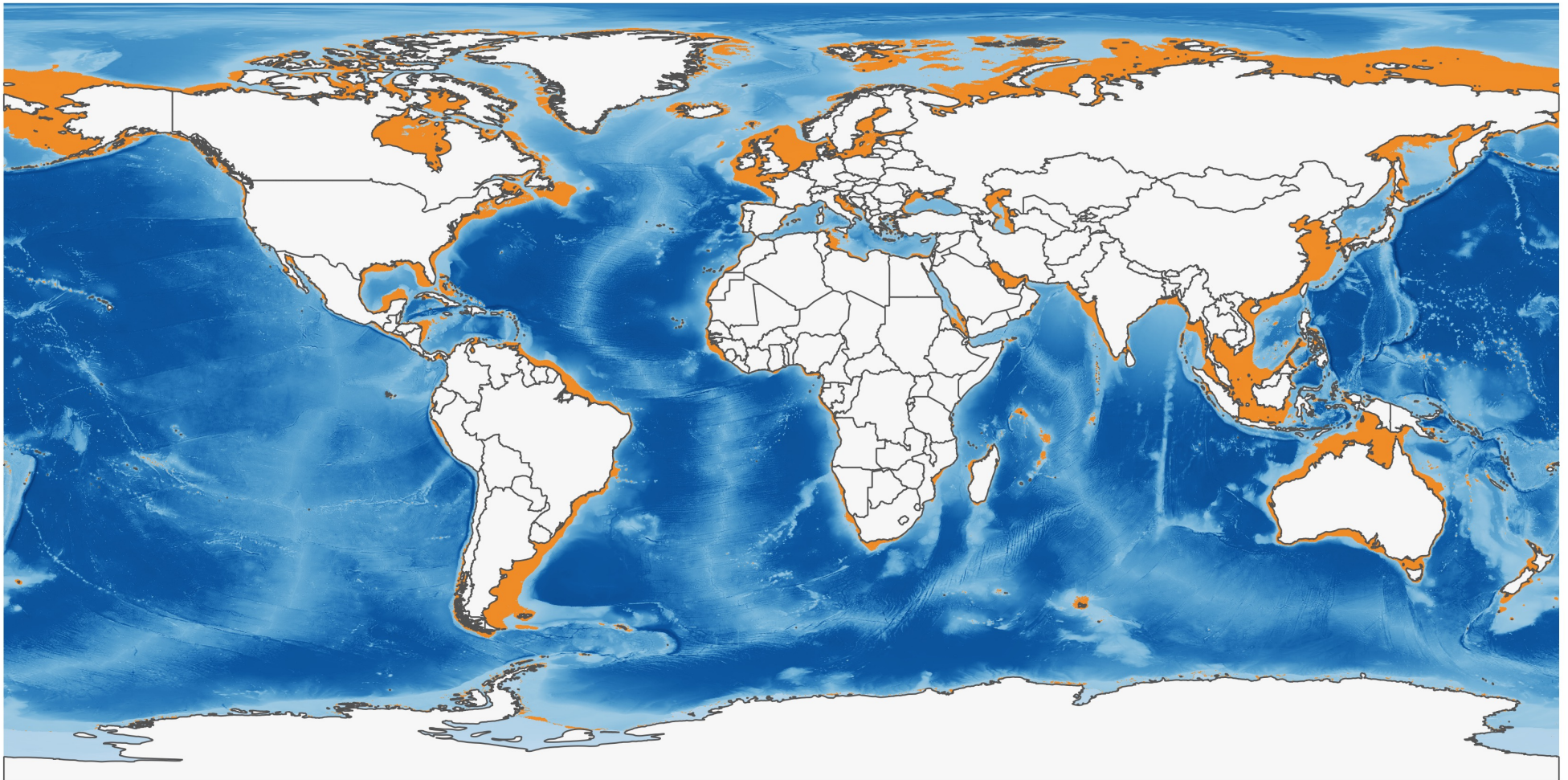
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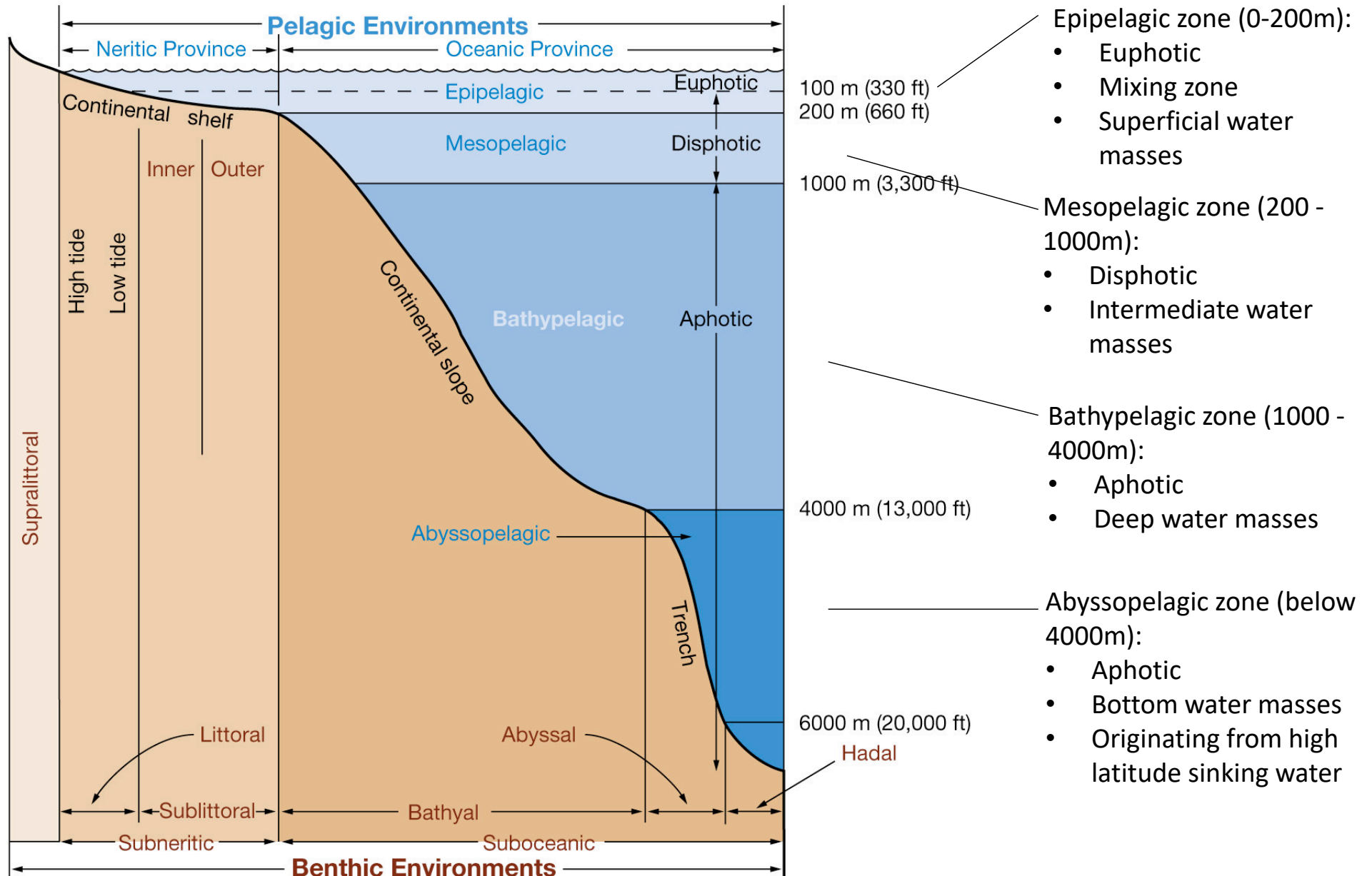
1. Divisions of the marine environment



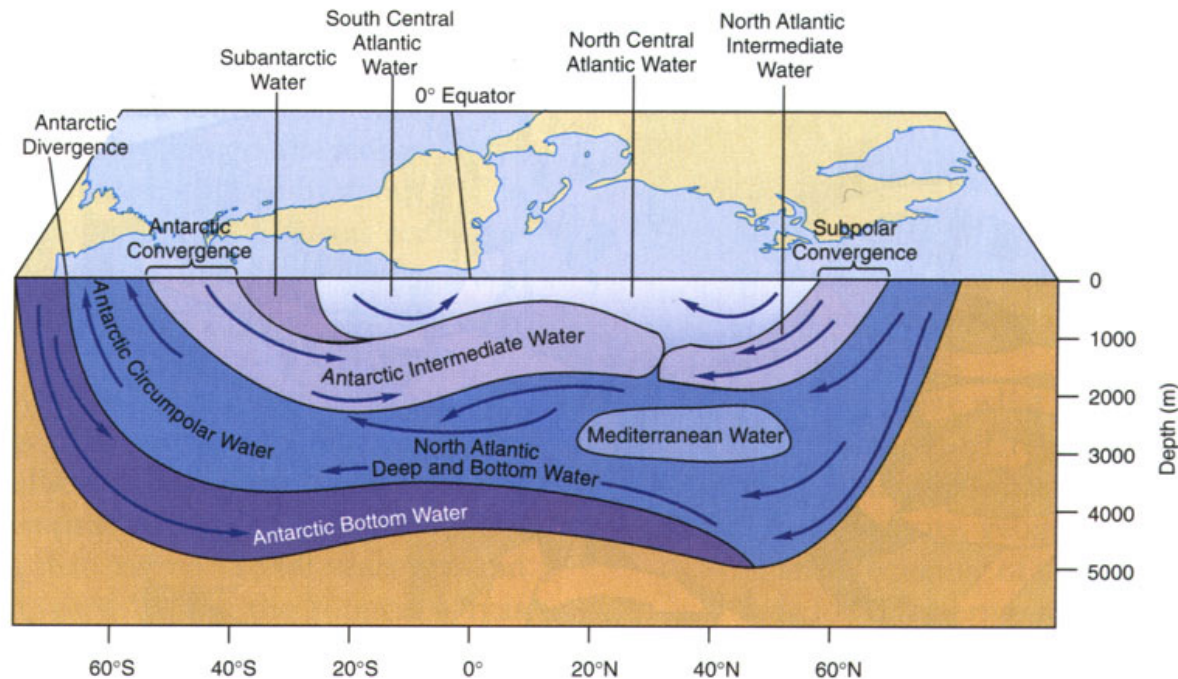
1. Divisions of the marine environment



1.1. Zones of the pelagic domain

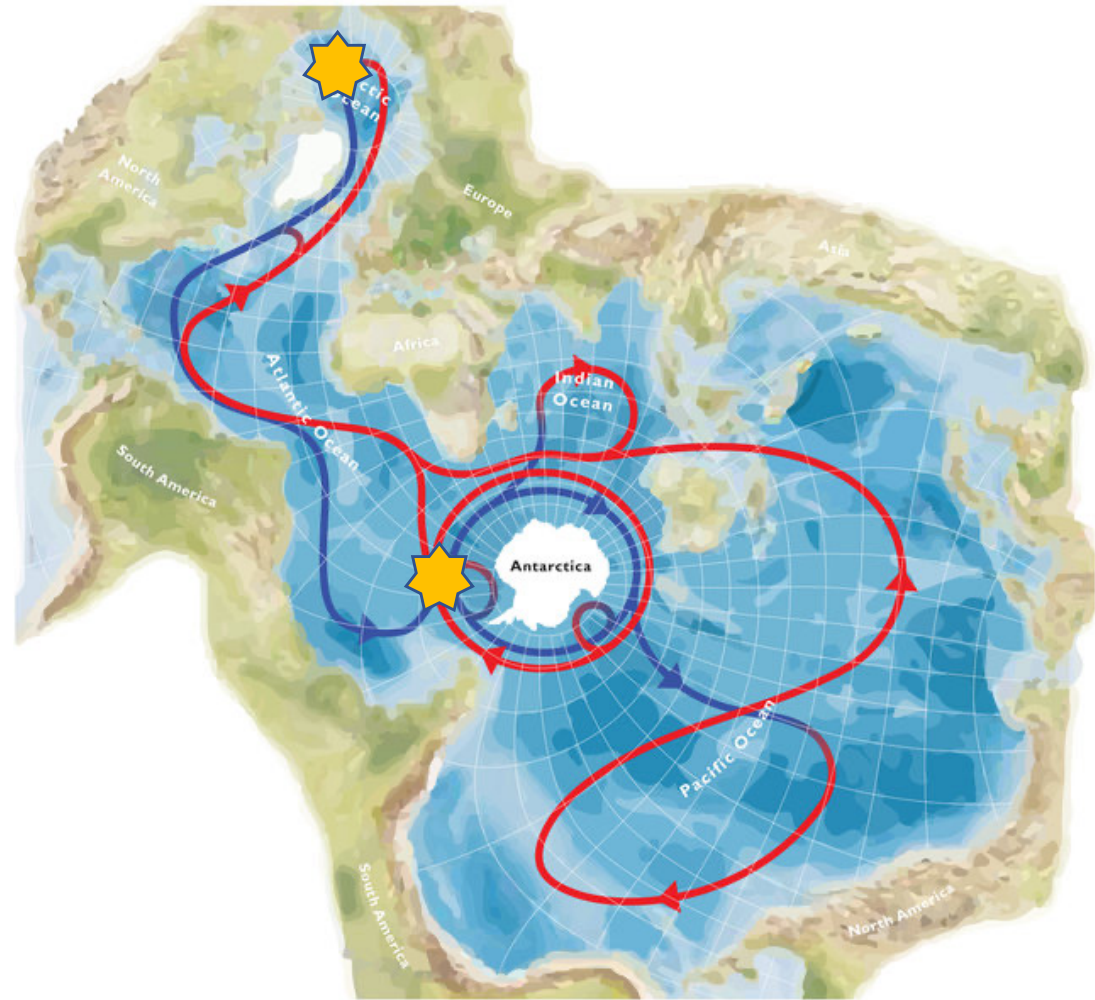


1.1. Zones of the pelagic domain



■ **FIGURE 8–27** A vertical cross section of the Atlantic Ocean shows the various water masses that form layers at different depths. Antarctic Bottom Water is the densest water mass and it flows northward from around Antarctica. North Atlantic Bottom Water sinks near Greenland and flows southward over the top of the Antarctic Bottom Water. Intermediate depth water masses are formed and sink at the Antarctic and subpolar convergences. The near surface layers are more complex. Note the tongue of Mediterranean Water that spreads across the North Atlantic Ocean from the Straits of Gibraltar at about 2–3,000 m depth between 20°N and 55°N.

- The globe viewed on a Spilhaus projection; in contrast to conventional projections, this portrays the ocean fringed by land. The global thermohaline circulation is shown in cartoon form, with upper-layer flow in red and lower-layer flow in blue.

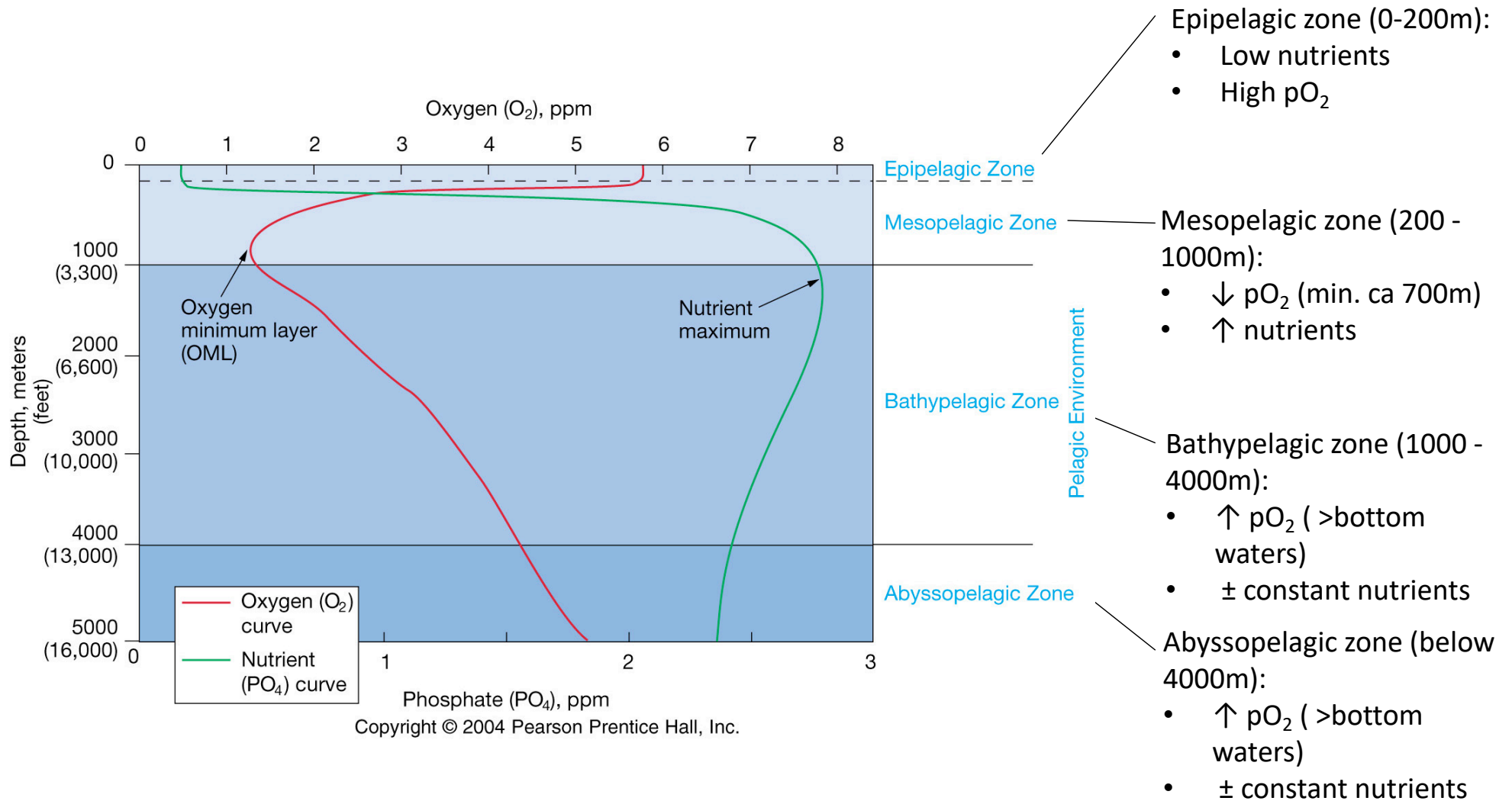


Gasses in the oceans

- oxygen (O₂)
- carbon dioxide (CO₂)
- nitrogen (N₂)

	Air	Total Ocean	Surface Ocean
N ²	78%	11%	48%
O ²	21%	6%	36%
CO ²	0.04%	83%	15%

1.2. Vertical distribution of O₂ and nutrients



2. Pelagic biological processes

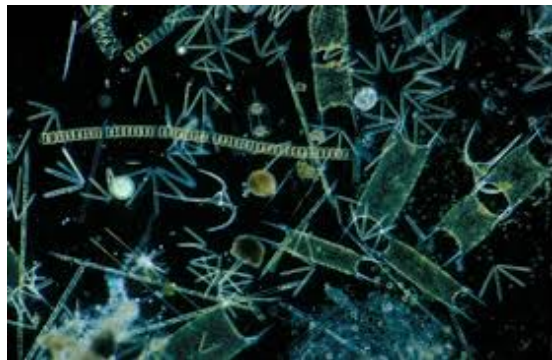
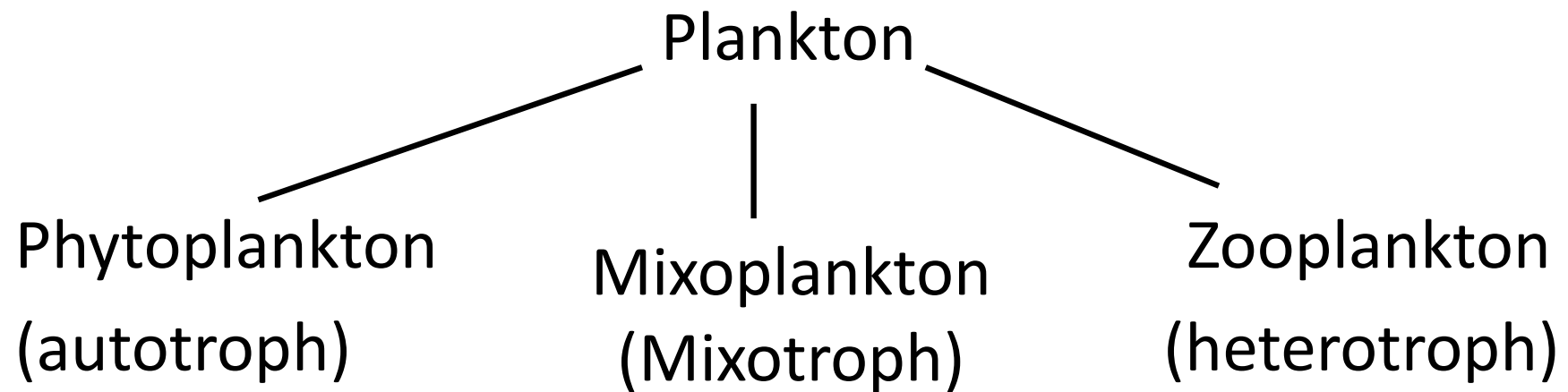
- 2.1 Definitions

Pelagos: organisms living in the water column without any contact with the bottom and which do not depend on the benthos for food

S e s t o n	{	<u>Plankton</u> :	<u>Nekton</u> :
		Unable to move against currents (dependent on the water mass)	Able to swim against currents (independent on water masses)
		<u>Tripton</u> :	
		Particulate organic matter (POM)	

2. Pelagic biological processes

- 2.1 Definitions



Natureasia.com

Relative
importance?



2.1. Definitions

- Classification according to size

Net Plankton	Ultraplankton	$< 2\mu\text{m}$
	<u>Nanoplankton</u>	$2 - 20 \mu\text{m}$
	Microplankton	$20 - 200 \mu\text{m}$
	Macroplankton	$200 - 2000 \mu\text{m}$
	Megaloplankton	$> 2000 \mu\text{m}$
	Mesoplankton	$200 - 20000 \mu\text{m}$ $1000 - 5000 \mu\text{m}$



Aquaticlivefood.com.au



Daylymail.co.uk

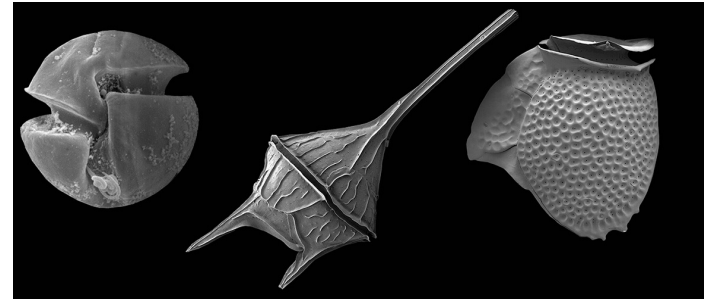
Diatoms

- Silicon dioxide box (frustulae)
- Generally larger



dinoflagellates

- Two flagella
- Generally smaller



2.2. Primary production

- The rate of formation of energy rich compounds from inorganic material.
- Mostly photosynthesis
- Some chemosynthesis
- What are limiting factors? (bottom-up vs top-down?)

2.2. Primary production

• 2.2.1. Factors limiting P1

Light (bottom-up control)

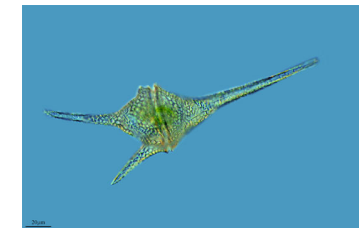
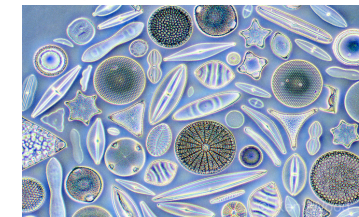
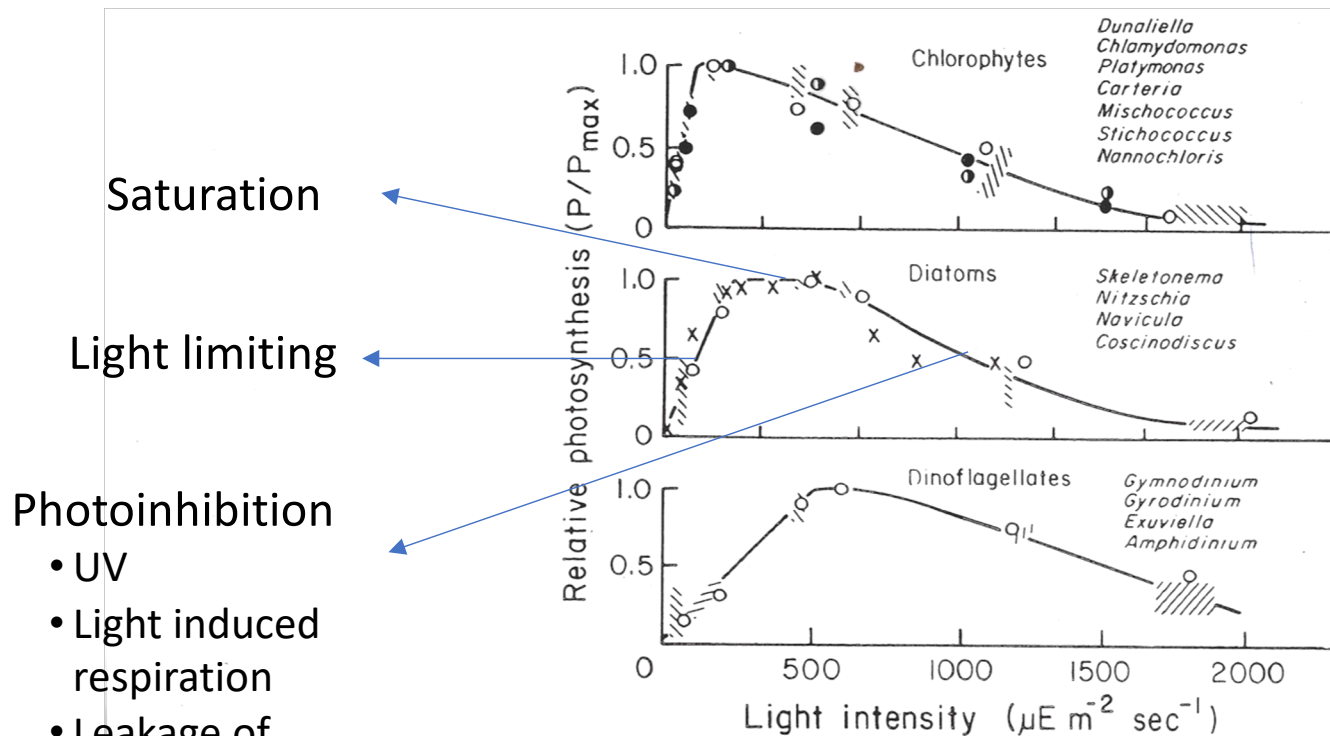


Figure 2-5. Curves of relative photosynthesis (P/P_{max}) versus light intensities for three algal groups. The chlorophytes include green and flagellated greens. Shaded rectangles represent the dispersion of points obtained experimentally using neutral filters in cultures grown with an irradiance of $1.3 \mu E m^{-2} sec^{-1}$; open circles correspond to cultures in natural light; solid and half-solid circles are cultures at 0.48 and $1.98 \mu E m^{-2} sec^{-1}$ and measured in the harbor at Woods Hole. Crosses correspond to the data of Jenkin (1937). Adapted from Ryther (1956).

Differs according to taxa

2.2. Primary production

- 2.2.1. Factors limiting P1

Light

- Sea water absorb the photosynthetic active radiation (PAR)

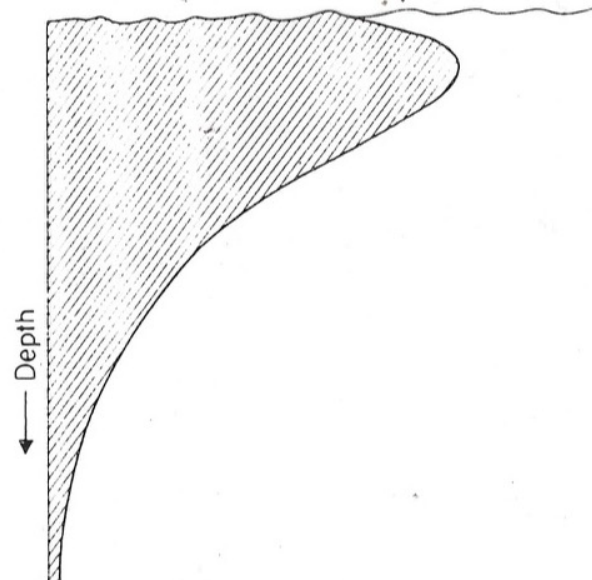
$$I_z = I_0 e^{-kz}$$

Where k: extinction coefficient

z: depth

I_0 : surface PAR

Fig. 2.3 The relationship between depth and photosynthetic production in the surface waters of the ocean.

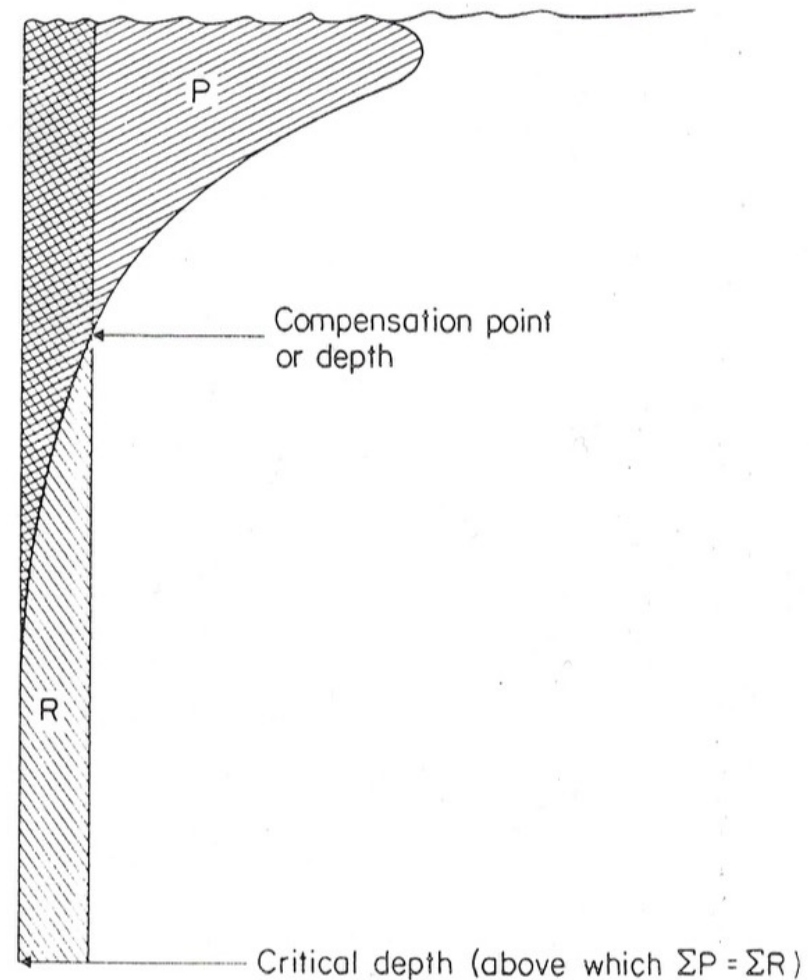


2.2. Primary production

• 2.2.1. Factors limiting P1

Light

- Sea water absorb the photosynthetic active radiation (PAR)
 - But respiration \neq function of depth
-
- Compensation depth: $R = \Phi$ for a particular species
 - Critical depth: $\Sigma R = \Sigma \Phi$ for the whole P1 community (net P1 of the community = 0)



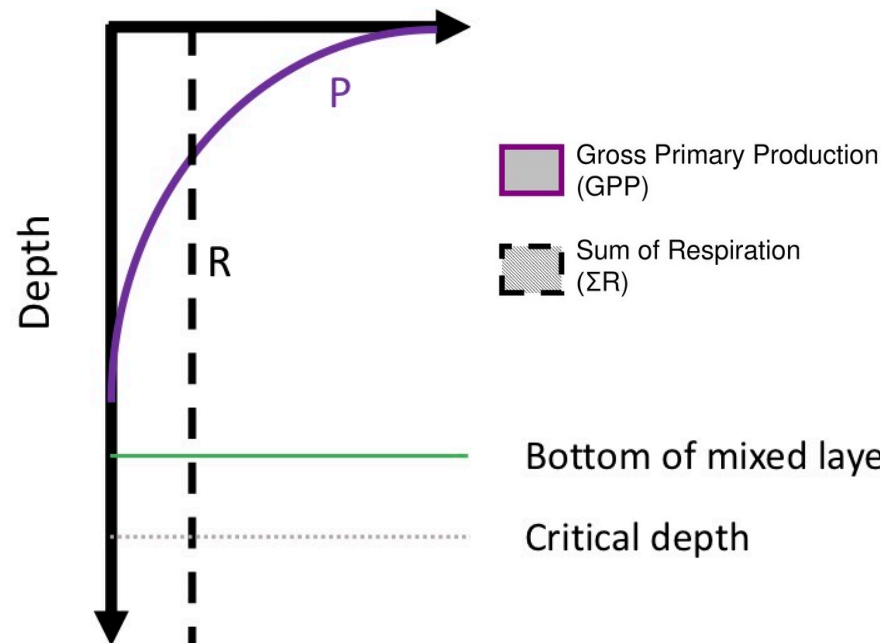
2.2. Primary production

• 2.2.1. Factors limiting P1

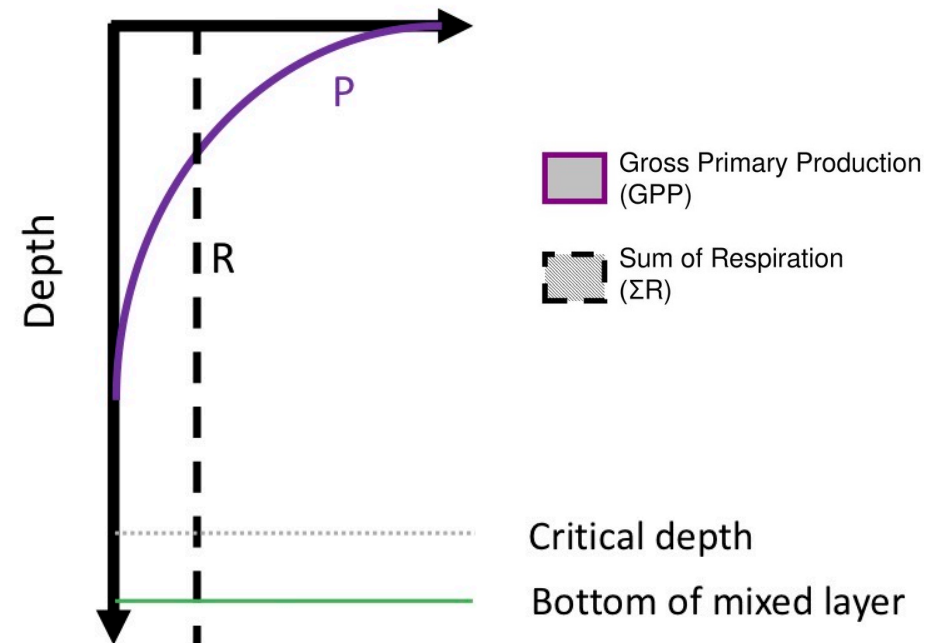
Light + Mixing

- Wind induces mixing of the water column → mixing depth

If critical depth > mixed layer depth,
 $GPP > \Sigma R$, $NPP > 0$



If critical depth < mixed layer depth,
 $GPP < \Sigma R$, $NPP < 0$



2.2. Primary production

• 2.2.1. Factors limiting P1

Nutrients (bottom-up control)

- What is a nutrient ?
 - Only for P1, not for consumers !
 - Major nutrients: C, N, P, O, Si, Mg, K, Ca Abundant in sea water
 - N: proteins
 - Inorganic forms in sea water:
 - NH_4^+ : no reduction necessary → most favorable
 - NO_3^- , NO_2^- : have to be reduced (nitrate reductase)
 - Most marine inorganic N as NO_3^- (1 μM to > 25 μM)
 - P: energy storage (ATP), enzyme phosphorylation
 - Inorganic forms in sea water:
 - Dissolved Inorganic Phosphate (PO_4^{2-}) (most favorable)
 - Dissolved Organic Phosphate
 - Si: diatom frustule
 - Trace nutrients: Fe, (Cu, V, Cd)

2.2. Primary production

• 2.2.1. Factors limiting P1

Nutrients

• Uptake

Described by

Michaelis-Menten equation:

$$V = \frac{V_{\max} \cdot C}{K_s + C}$$

V_{\max} = Uptake velocity at saturation

C = nutrient concentration in SW

K_s = nutrient concentration in SW at which $V = V_{\max}/2$ (constant)

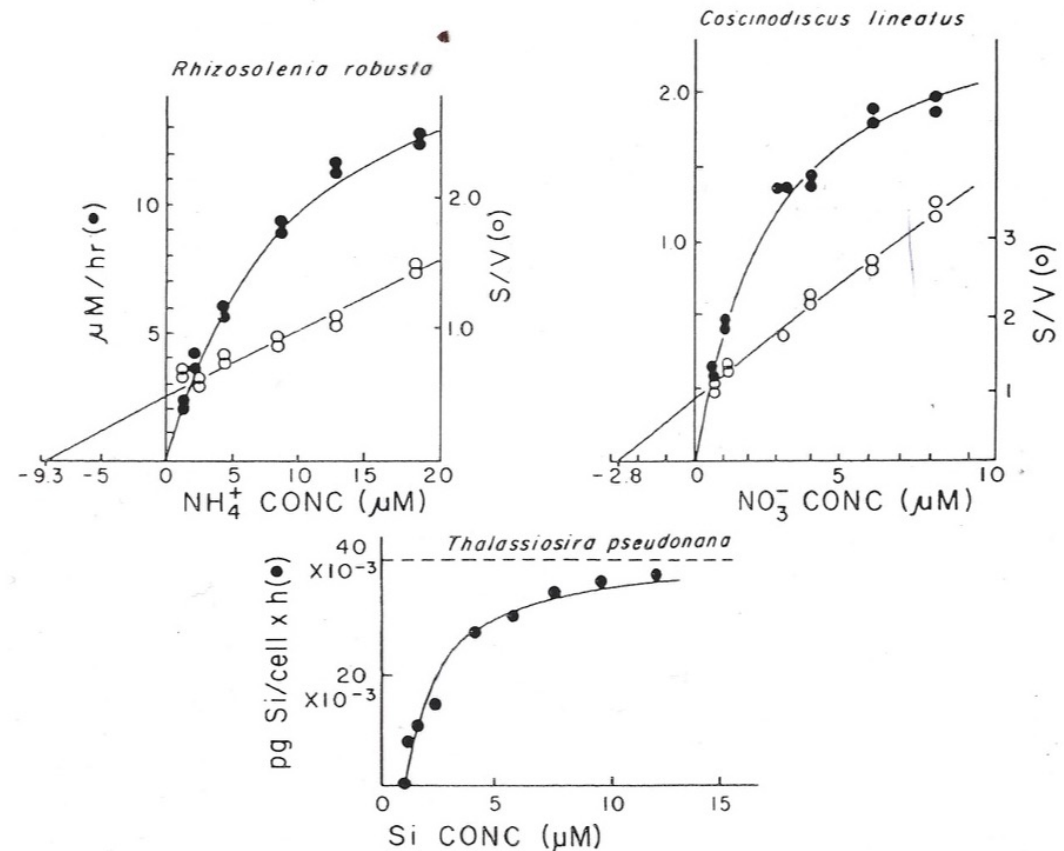


Figure 2-13. Michaelis-Menten curves (filled circles) and Woolf plots (open circles) fitted to data on uptake ($\mu\text{mole/hr}$) of ammonium, nitrate, and silica by three diatoms at different nutrient concentrations ($\mu\text{mole/liter}$). S is the concentration of nutrient being taken up, V is the uptake velocity. The x-intercepts of the top two graphs provide the estimate of K_s . Adapted from Eppley et al. (1969) and Paasche (1973).

2.2. Primary production

• 2.2.1. Factors limiting P1

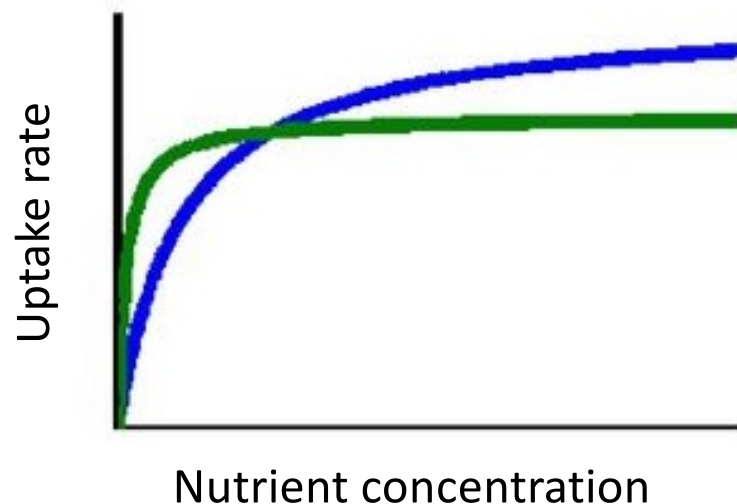
Nutrients

- Uptake: low and high K_s

— Species 1
— Species 2

$K_{s1} < K_{s2}$

$V_{max1} < V_{max2}$



- Species with a low K_s favoured in low nutrients concentrations but lower capacity \rightarrow no or limited blooms
- Species with a high K_s favoured in high nutrients concentrations and able to incorporate high amounts of nutrients \rightarrow blooms

2.2. Primary production

- 2.2.1. Factors limiting P1

Nutrients

- K_s depends on size

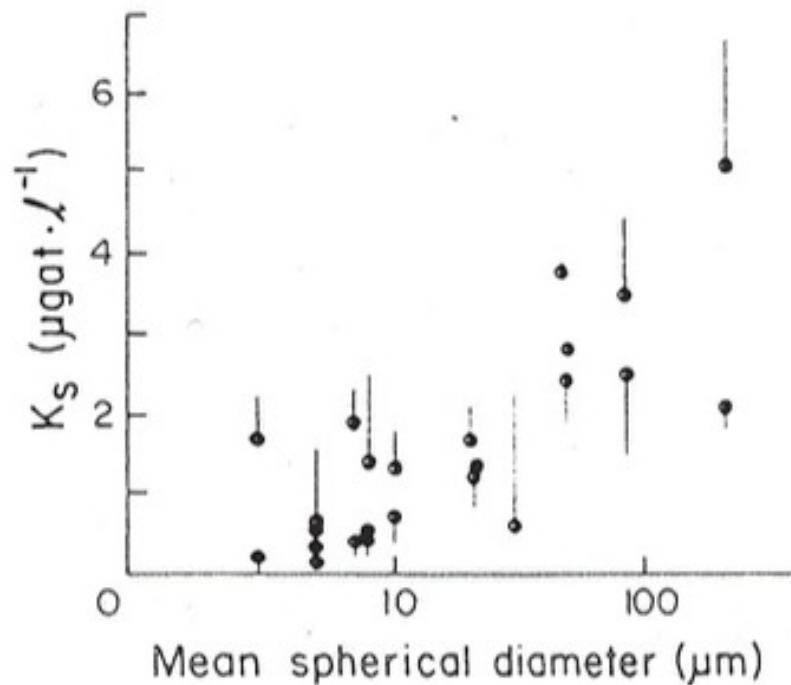


Figure 2-14. Half-saturation (K_s) values for nitrate uptake by phytoplankton of different size. The bars show the 95% confidence limits for the highest and lowest mean K_s reported. Adapted from Malone (1980).

2.2. Primary production

- 2.2.1. Factors limiting P1

Nutrients

- Ks differ according to habitat

Table 2-2. Half-Saturation Constants for Nitrate of Three Species of Algae Obtained from Coastal and Oceanic Environments in the Atlantic^a

Species	Source	K_s (Mean \pm 95% confidence interval)
<i>Cyclotella nana</i>	Moriches Bay	1.87 ± 0.48
	Edge of shelf	1.19 ± 0.44
	Sargasso Sea	0.38 ± 0.17
<i>Fragilaria pinnata</i>	Oyster Bay	1.64 ± 0.59
	Sargasso Sea	0.62 ± 0.17
<i>Bellerophia</i> spp.	Great South Bay	6.87 ± 1.38
	Off Surinam	0.12 ± 0.08
	Sargasso Sea	0.25 ± 0.18

^a From Carpenter and Guillard (1971). © Ecological Society of America, reprinted by permission.

2.2. Primary production

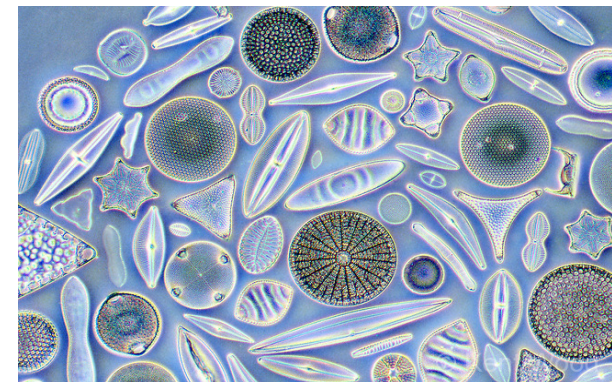
- 2.2.1. Factors limiting P1

Nutrients

- Ks
 - Usually lower in nano- (flagellates) than in microphytoplankton (diatoms)
- Usually higher in coastal communities rich in nutrients (selection for high Ks species)



Biology.kenyon.com



www.Labroots.com

2.2. Primary production

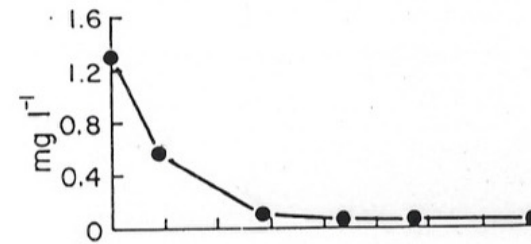
• 2.2.1. Factors limiting P1

Nutrients

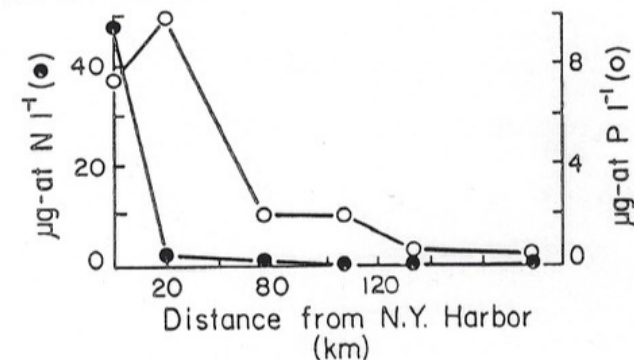
• N and P

Figure 2-24. Top and middle: Concentrations of particulate organic carbon and nutrients in surface water in a transect from New York Harbor to offshore. Bottom: Growth of *Skeletonema costatum* in water samples that were enriched with ammonium or phosphate and in unenriched samples. The sequence of stations is in relation to their distance from the source of nutrients in New York Harbor. The inoculum with which the experiments were started was of the same size as the left-most station in the graph. Adapted from Ryther and Dunstan (1971). © AAAS, reprinted by permission.

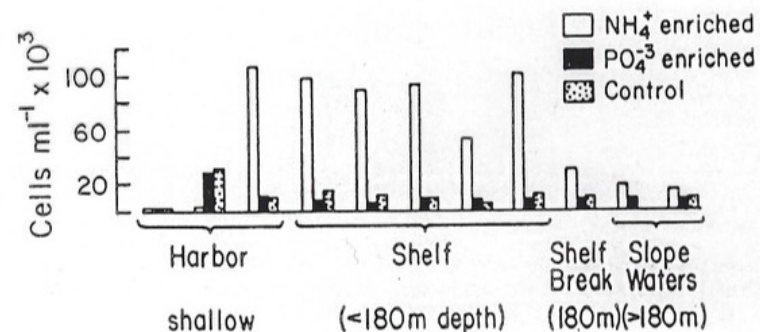
PARTICULATE ORGANIC CARBON



NUTRIENTS



ENRICHMENT EXPERIMENTS



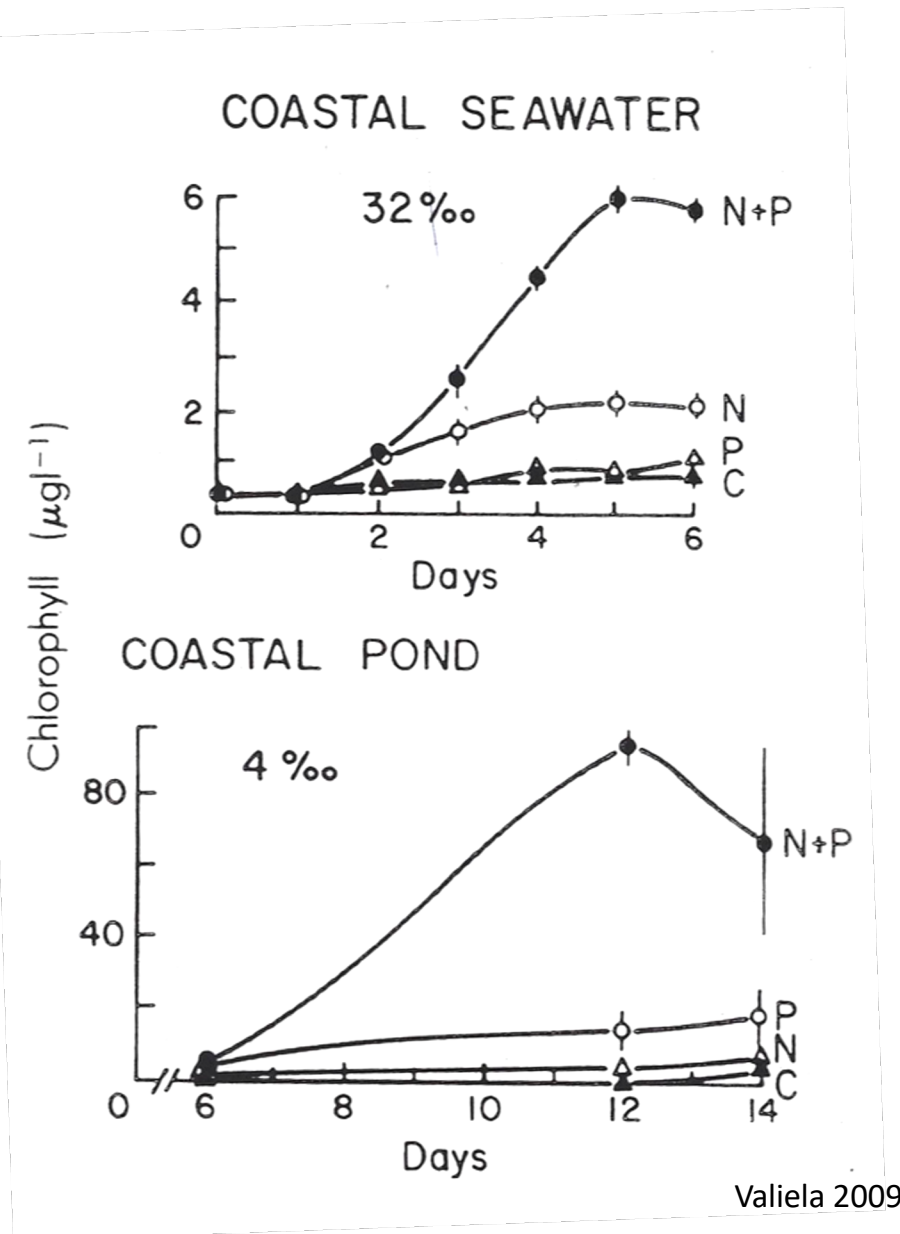
2.2. Primary production

• 2.2.1. Factors limiting P1

Nutrients

- N and P

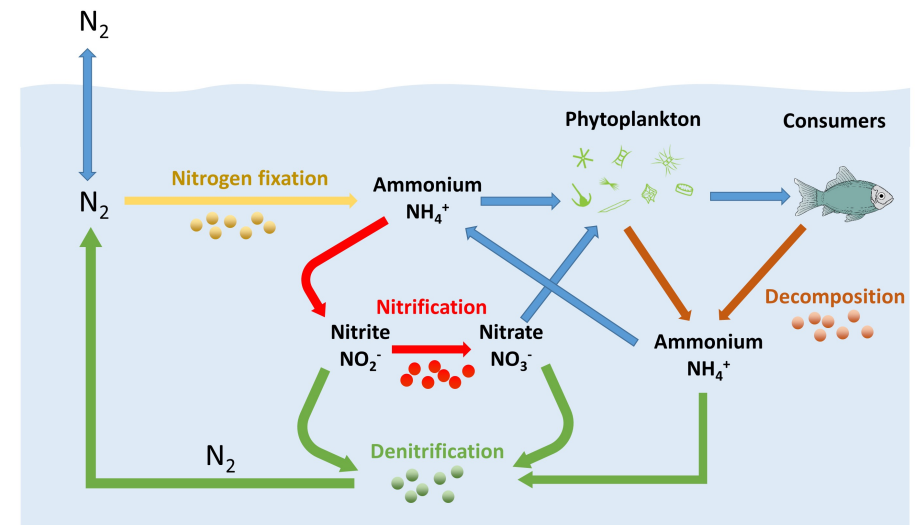
Figure 2-21. Enrichment experiments with coastal seawater of Vineyard Sound (salinity 32‰), Massachusetts, and a freshwater-dominated coastal pond (salinity 4‰) in Falmouth, Massachusetts. N+P, addition of nitrogen and phosphorus; P, addition of phosphorus; N, addition of nitrogen; C, control, no nutrient addition. Adapted from Vince and Valiela (1973) and unpublished data of Nina Caraco. Values are mean \pm standard error of several replicates.



2.2. Primary production

• 2.2.1. Factors limiting P1 *Nutrients*

- Sources of N (and P)
 1. Fixation of Atmospheric N_2
 2. Land run-off (rivers): principally NO_3^-
 3. Coastal bottom waters (upwelling!): principally NO_3^-
 4. Excretion/elimination by water column consumers: principally NH_4^+
- NO_3^- based P1: « new production »
- NH_4^+ based P1: « regenerated production »



*Simplified nitrogen cycle in the ocean.
Coloured dots represent the marine
bacteria responsible for nitrogen cycling*

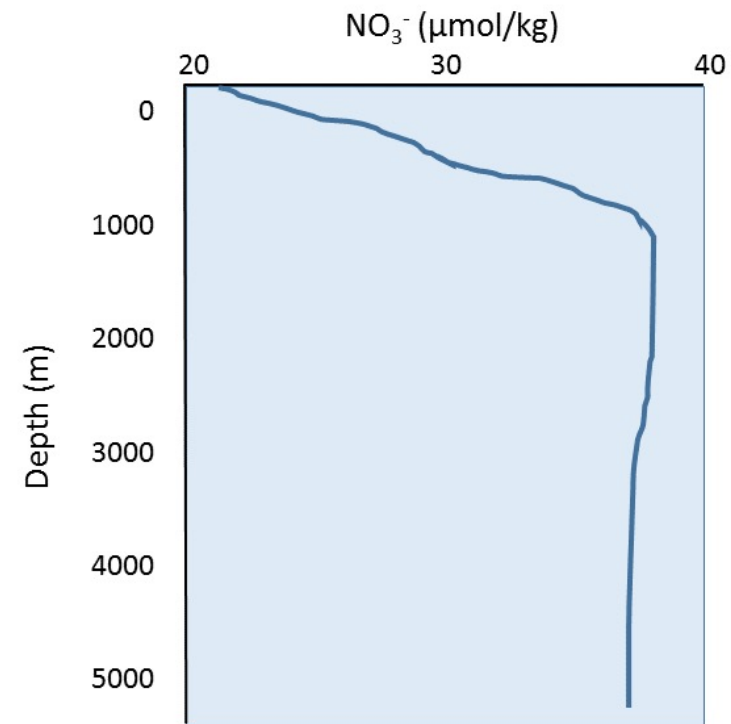
2.2. Primary production

- 2.2.1. Factors limiting P1

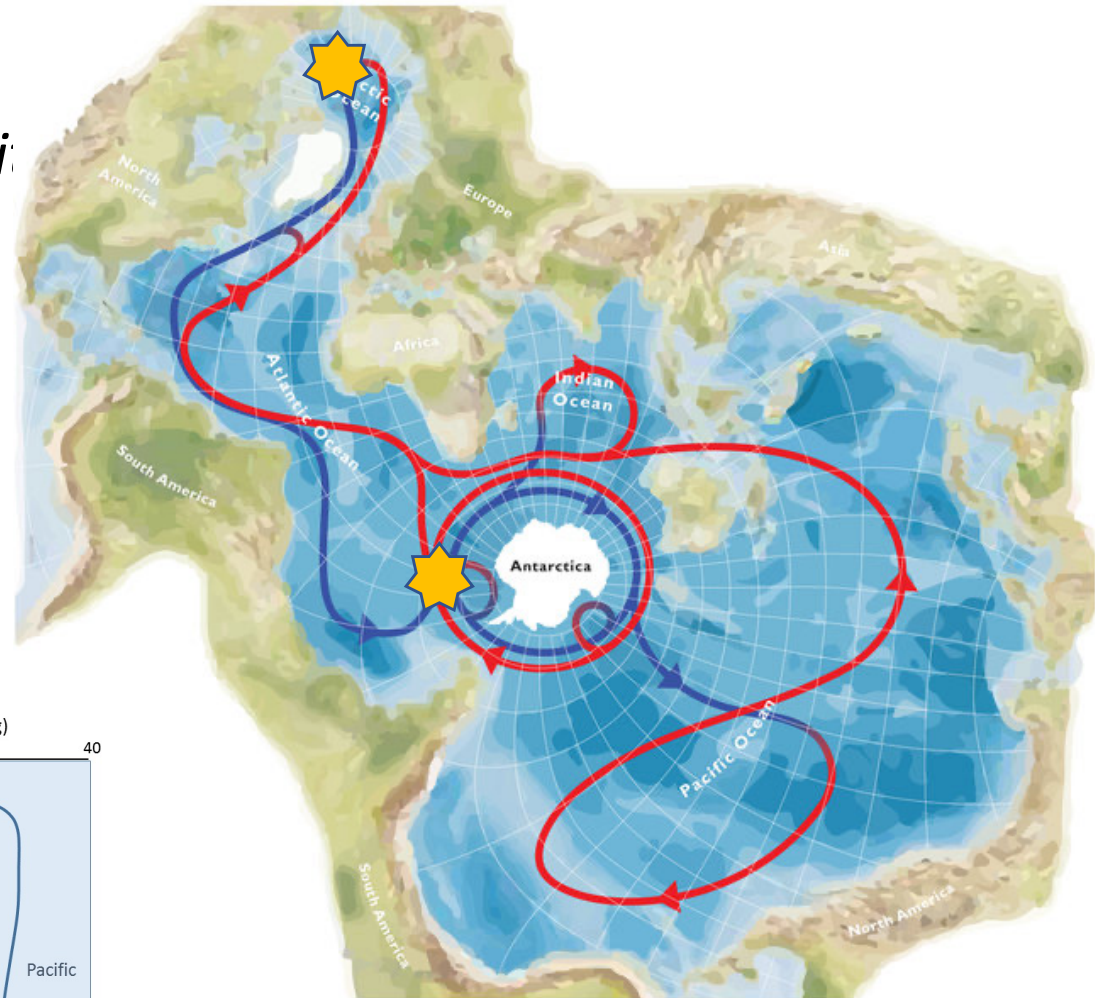
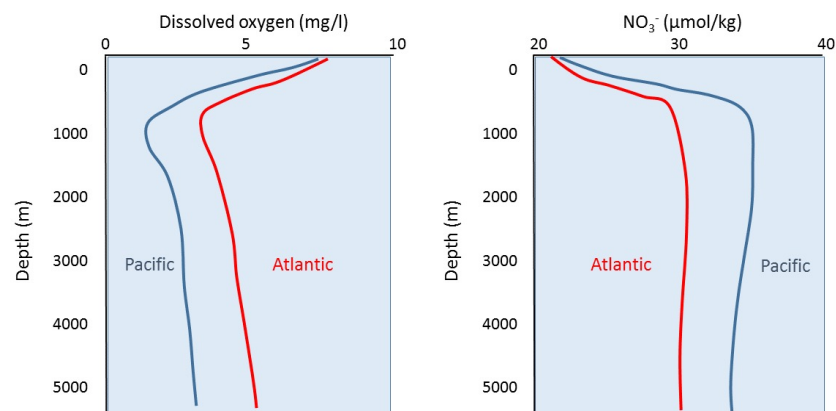
Nutrients

- low at the surface
 - rapidly consumed
 - do not have the chance to accumulate
- levels increase at depth
 - no longer consumed
 - regenerated through decomposition

Representative nutrient (nitrate) profile for the open ocean



Representative nutrient (nitrate) profile for the open ocean



2.2. Primary production

- 2.2.1. Factors limiting P1

Nutrients

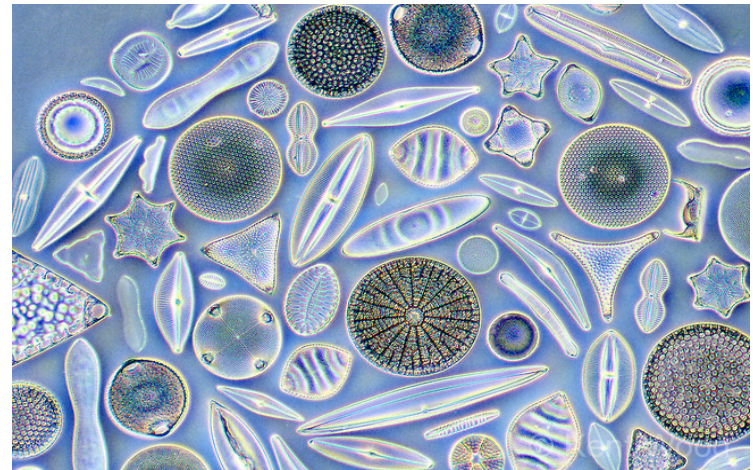
- N and P
 - In most marine environments, N is the main limiting nutrient
 - P is limiting in some eutrophicated environments (see later)
- C:N:P
 - In many phytoplanktonic primary producers, the C:N:P ratio is typically 106 : 16 : 1 = Redfield ratio
 - If Sea Water nutrient concentrations depart from this ratio, a limitation is very probable

2.2. Primary production

- 2.2.1. Factors limiting P1

Nutrients

- Si
 - Si limitation may terminate diatom blooms
 - Few clearly documented cases



2.2. Primary production

- 2.2.1. Factors limiting P1

Nutrients

- Fe
 - Component of ferredoxin involved in electron transfer from photosystem I to NADP⁺
 - From terrestrial origin (rivers, airborne) \leftrightarrow high concentrations (1 – 3 nM) in coastal zones, low to very low concentrations (<1 – 0.06 nM) in oceanic zones
 - Limiting in oceanic zones \rightarrow High Nutrients Low Chlorophyll (HNLC) regions

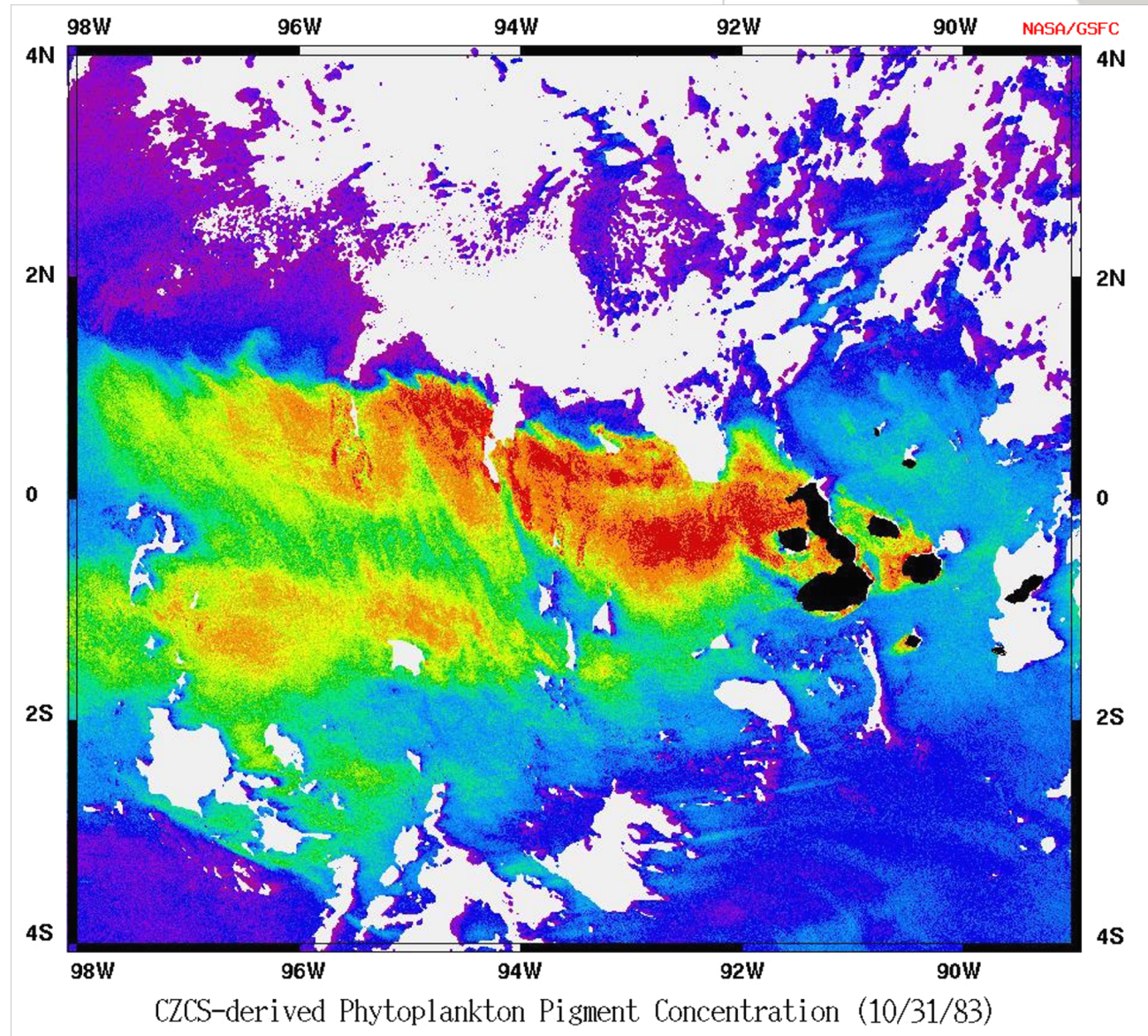
2.2. Primary production

- 2.2.1. Factors limiting P1

Nutrients

- Fe
 - First demonstrated as limiting in the equatorial Pacific

Ocean pigment concentration image obtained from the Nimbus-7 Coastal Zone Color Scanner on 31 October 1983 in the vicinity of the Galapagos Islands in the eastern equatorial Pacific Ocean. The concentrations in October 1983 were very high on the western side of the islands and extended for over 1000 kilometers to the west as a result of the westward flowing surface currents.



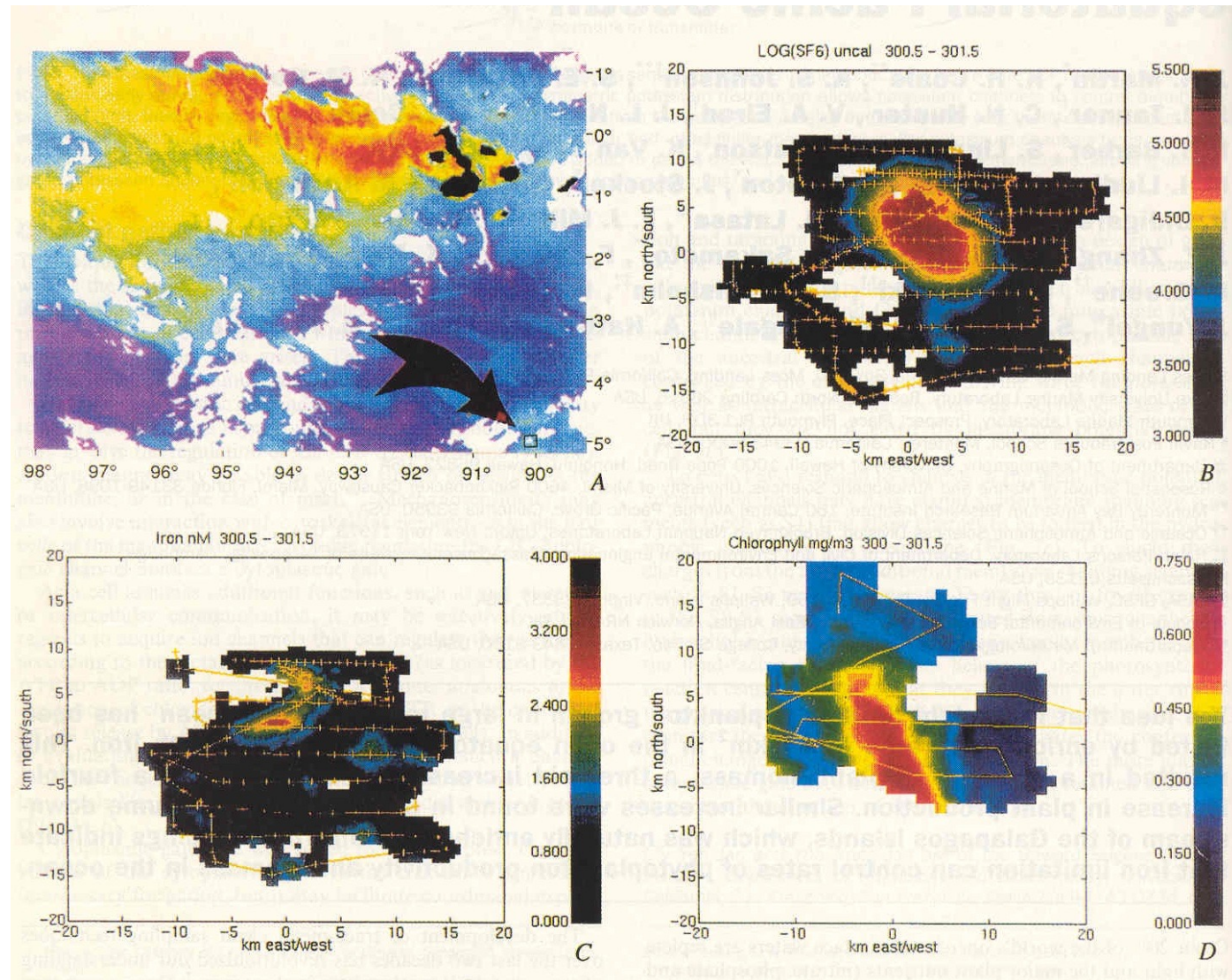
2.2. Primary production

• 2.2.1. Factors limiting P1

Nutrients

- Fe

Field Fe
enrichment
experiment (64
km²) IronEx1:
single enrichment



2.2. Primary production

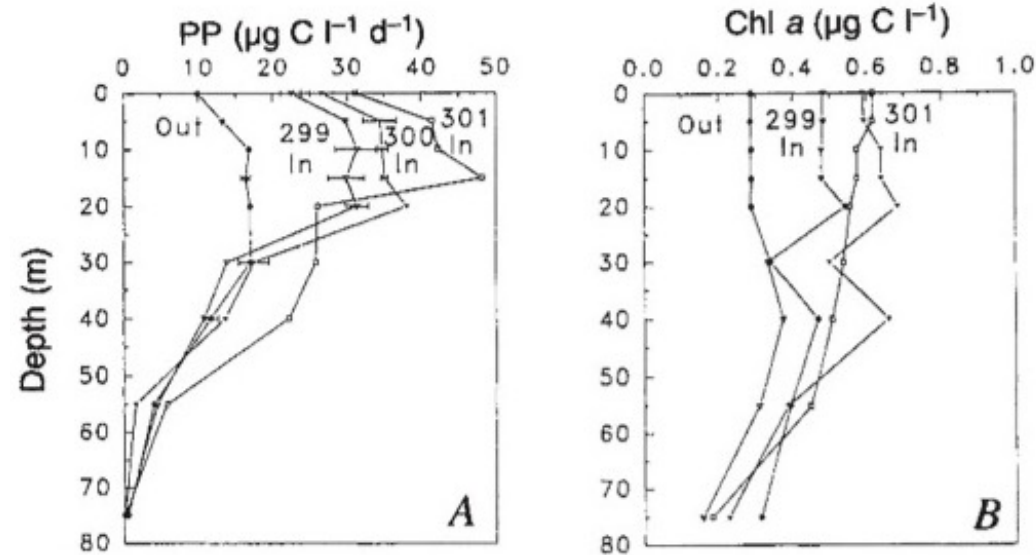
IronEx1

• 2.2.1. Factors limiting P1

Nutrients

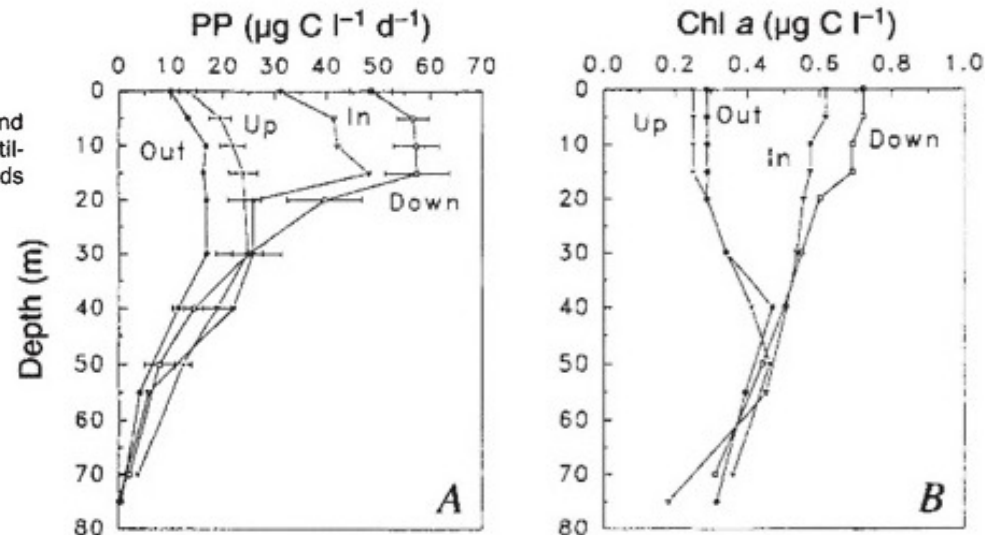
• Fe

FIG. 3 Vertical profiles, for the 3 days following fertilization, of primary production, PP, (A) chlorophyll *a* concentrations, Chl *a*, (B) as a function of time inside and outside the patch. Outside values are depicted for YD 299. Primary production was measured using $\text{H}^{14}\text{CO}_3^-$ uptake determined at various light levels, in incubations on board the ship. Chlorophyll was determined from filtered and extracted samples as in Fig. 1D. The errors associated with the chlorophyll analyses are generally $<0.02 \mu\text{g C l}^{-1}$. The depth to which the water column was enriched was ~ 35 m up to YD 301 (just before subduction). It is in the upper 35 m that the differences are most pronounced. Productivity and chlorophyll both converge by 75 m.



P1: x4
Chla: X3

FIG. 4 Comparison of vertical profiles of primary production (A) and chlorophyll *a* concentrations (B) for stations inside and outside the fertilized patch, and stations upstream (westward) of the Galapagos Islands and downstream (eastward) of the Galapagos Islands.



2.2. Primary production

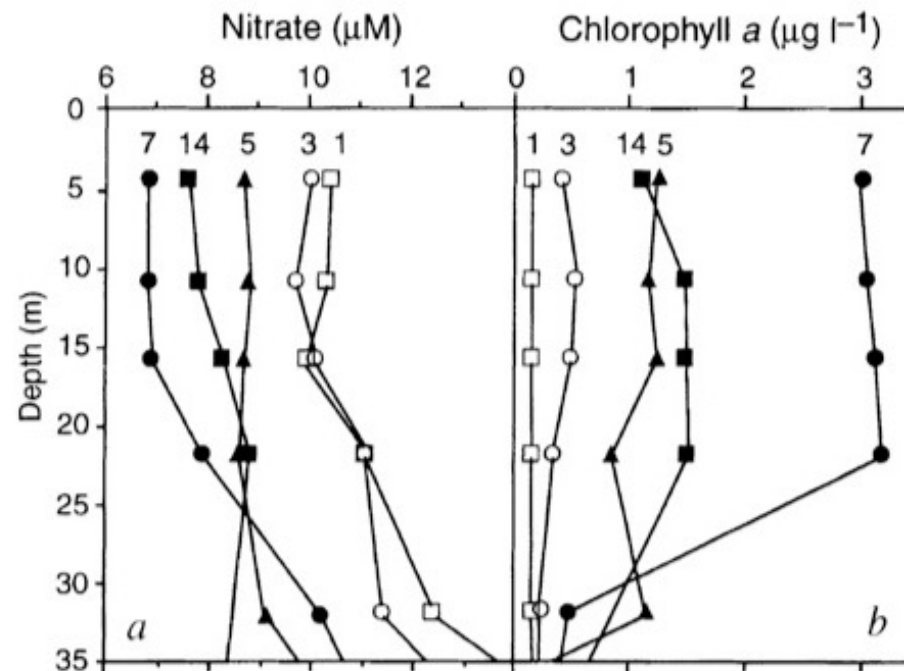
IronEx2

• 2.2.1. Factors limiting P1

Nutrients

• Fe

Second field Fe
enrichment
experiment in
the Eq Pacific
IronEx2:
multiple
enrichments



B: x85
Chla: X27

FIG. 3 a, Vertical profiles of mixed-layer nitrate from the daily 'inside-patch' stations of patch 1. Numbers at the top of each profile indicate the day of the patch 1 experiment. These plots illustrate the depletion of nitrate as the bloom reached its peak near days 7–9. The subsequent increase (day 14) is thought to be the result of mixing. Nitrate concentrations both inside and outside the patch converged to about $10 \mu\text{M}$ by $\sim 50 \text{ m}$. b, As a but for mixed-layer chlorophyll a.

2.2. Primary production

IronEx2

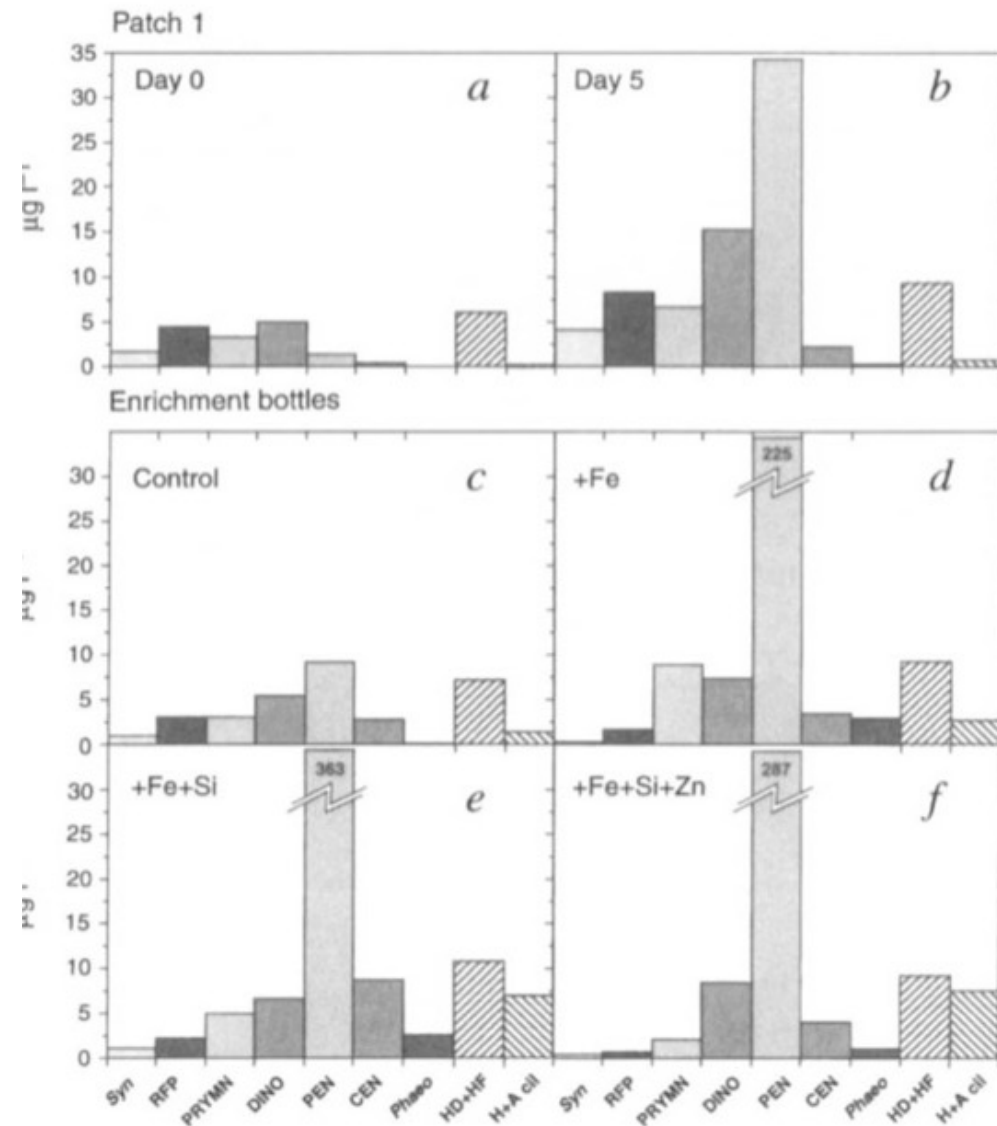
• 2.2.1. Factors limiting P1

Nutrients

• Fe

And the winners are diatoms

FIG. 4 a, Plankton community composition within patch 1 at day 0 of the experiment as expressed in $\mu\text{g C l}^{-1}$. This composition is similar to that observed at the 'outside-patch' stations over time. The groups represented include: *Syn*, *Synechococcus* spp.; RFP, red fluorescing picoplankton; PRYMN, Prymnesiophytes; DINO, autotrophic dinoflagellates; PEN, pennate diatoms; Phaeo, *Phaeocystis*; HD + HF, heterotrophic dinoflagellates + heterotrophic flagellates; H + A cil, heterotrophic + autotrophic ciliates. Shaded bars indicate autotrophic biomass and diagonally hatched bars indicate heterotrophic biomass (the most likely grazers on the smaller size fraction of autotrophs). *b*, Taxonomic composition of patch 1 on day 5 of the experiment indicating increases in all classes of phytoplankton, especially the diatoms. *c–f*, Results of the bottle enrichment experiments performed on deck in 20-litre carboys⁸ to test the effects of other potentially limiting nutrients. Water was collected using 30-litre Go Flo bottles deployed on Kevlar hydrowire and tripped with a Teflon messenger. Water was transferred to acid-cleaned, 20-litre polycarbonate bottles within a class 100 clean lab. chained to the deck of the ship. Treatments include: *c*, control, nothing added; *d*, +2 nM iron added; *e*, +2 nM iron, +10 μM silicic acid; *f*, +2 nM iron, +10 μM silicic acid, +2 nM zinc. Results indicate that diatoms in bottle enrichments with added iron outperformed the mesoscale experiment and that bottles with added silicic acid enhanced diatom growth relative to those without silicic acid. Zinc did not appear to have a positive effect on growth. Note the scale break in the diatom bar. Numbers at the top of the bar indicate the micrograms of carbon per unit volume attained in this group.

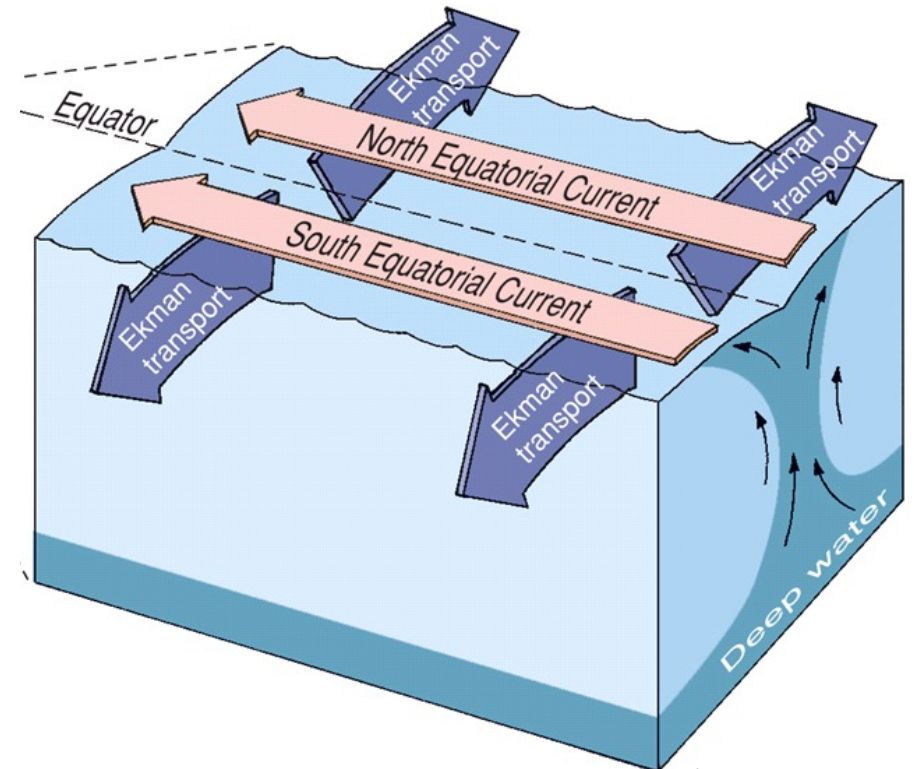


2.2. Primary production

- 2.2.1. Factors limiting P1

Nutrients

- Principal HNLC Fe limited regions:
 - Equatorial Pacific
 - Antarctica
- Linked to the presence of an offshore upwelling with no land runoff



(Castro & Huber 2010)

2.2. Primary production

- 2.2.1. Factors limiting P1
Grazing (top-down control)
- Some indications
 - Inverse horizontal spatial distributions

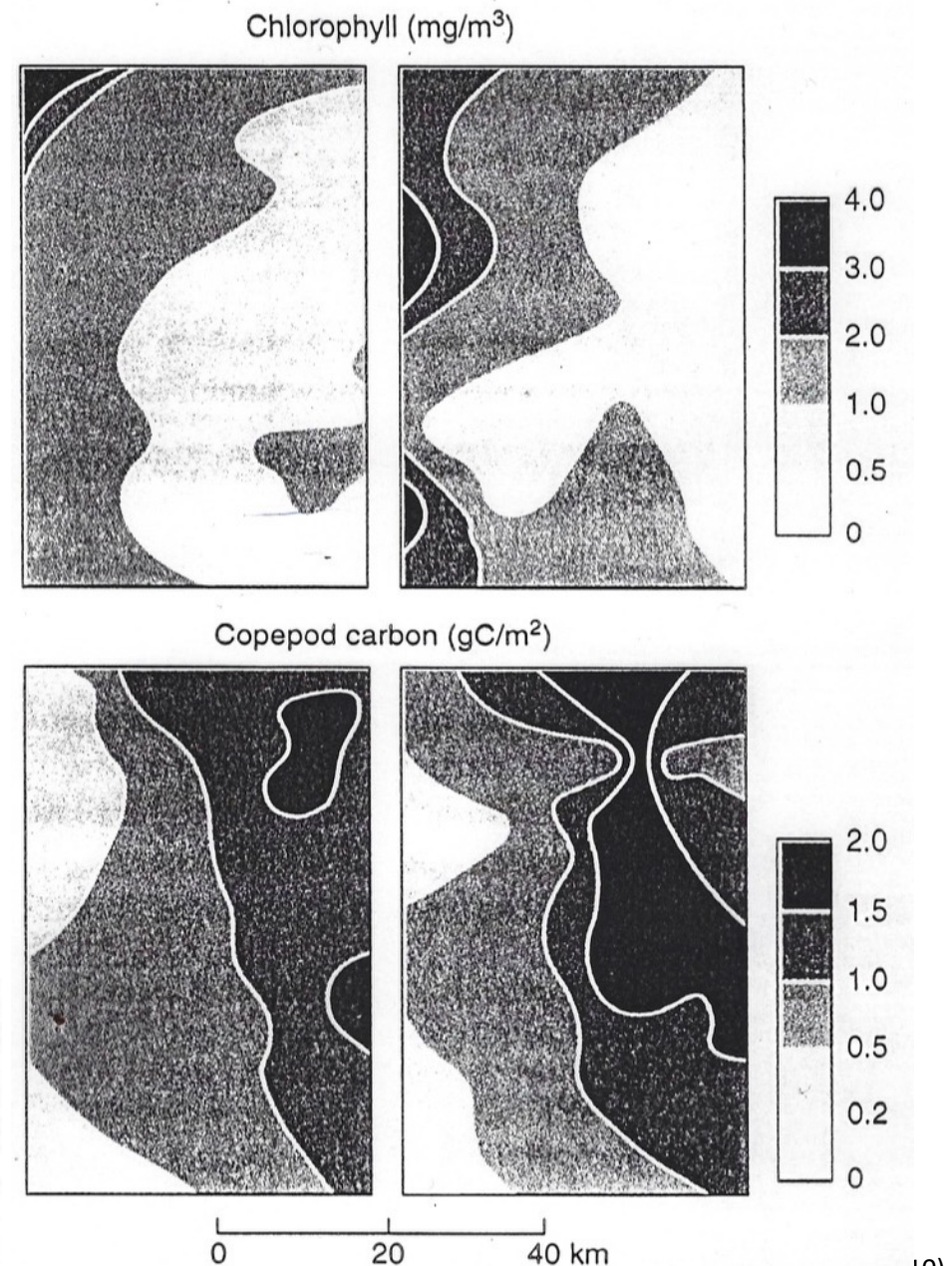


Fig. 9.13 Distribution of chlorophyll *a* and copepod carbon on a survey in the North Sea, showing an inverse relationship between phytoplankton and zooplankton standing stock. Phytoplankton are most abundant toward the left, whereas zooplankton are most abundant toward the right. (Modified from Steele, 1974.)

2.2. Primary production

- 2.2.1. Factors limiting P1

Grazing

- Highly variable according to regions and seasons: 0 -100%

Table 8-1. Percentage of Primary Production Consumed by Herbivores in Marine and Terrestrial Environments^a

	Percentage of prod. eaten by herbivores	Number of trophic steps	Source
Phytoplankton			
Long Island Sound, USA	73 ^f	4	Riley (1956)
Narragansett Bay, USA	0–30 ^g	4	Martin (1970)
Cochin Backwater, India	10–40		Qasim (1970)
Beaufort Sound, USA	1.9–8.9		Williams et al. (1968)
Offshore California	7–52 (ave. 23)		Beers and Stewart (1971)
Peruvian upwelling	92, 54–61	3	Walsh (1975), Whitledge (1978)
Open Seas (all phytoplankton)			
Georges Bank	50–54	4	Riley (1963), Cohen et al. (1981)
North Sea	75–80	4–6	Crisp (1975)
Sargasso Sea	100	5	Menzel and Ryther (1971)
Eastern Tropical Pacific	39–140 (ave. 70) ^h	5	Beers and Stewart (1971)

^a Annual consumption except where indicated otherwise. These values are rough but best possible estimates based on many assumptions and extrapolations.

^b Leaves only; 0.5–1.4% of total production is consumed by herbivores (Bray, 1961).

^c This considers grass–cattle–man as the food chain.

^d Includes above- and below-ground production and consumption.

^e Leaves and buds only.

^f This is an estimate of consumption of organic matter in the water column. Larger zooplankton consume about 20%, microplankton and bacteria an additional 43%. In the bottom, benthic animals use an estimated 31% of net primary production.

^g Of standing stock of algae.

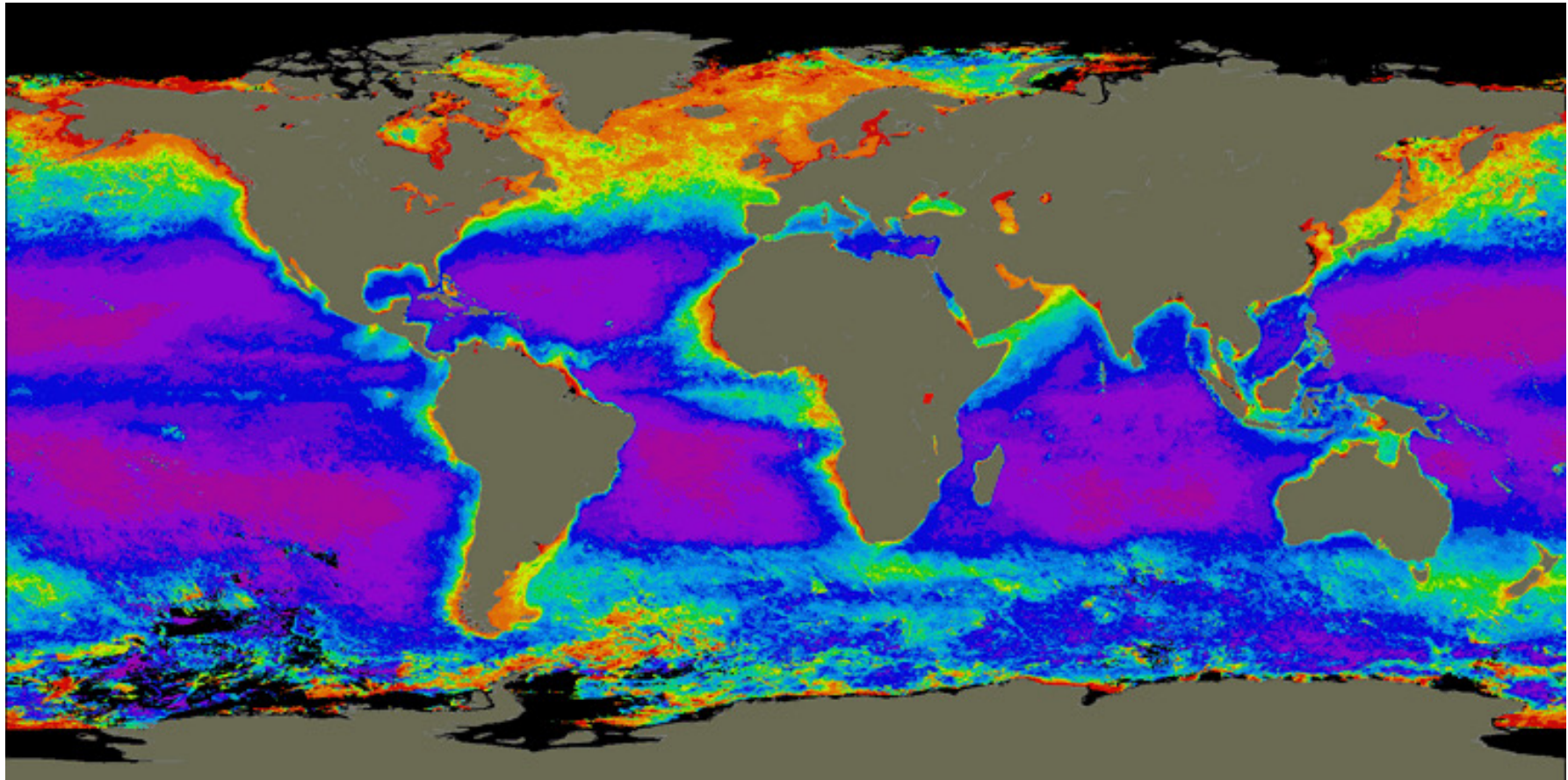
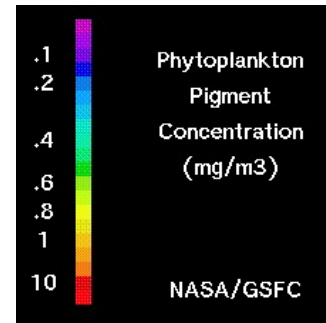
^h Includes only microzooplankton that passed through a 202 μ mesh. The biomass of these small species was about 24% of that of the larger zooplankton. Total consumption could easily be larger than reported if any of the larger species are herbivorous.

2.2. Primary production

- 2.2.2. Variations of P1 in space and time

Space

- Hydrographic factors

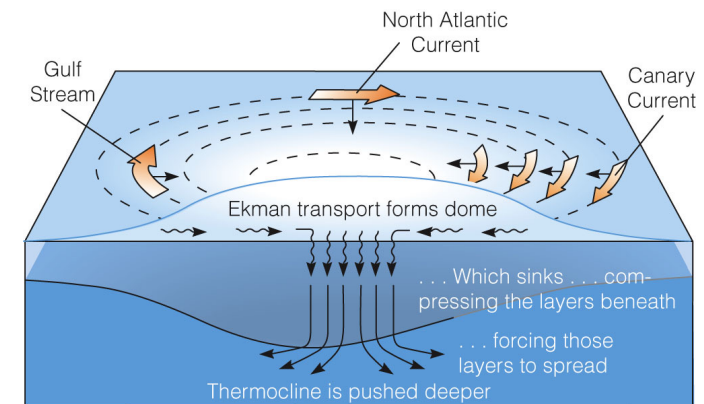
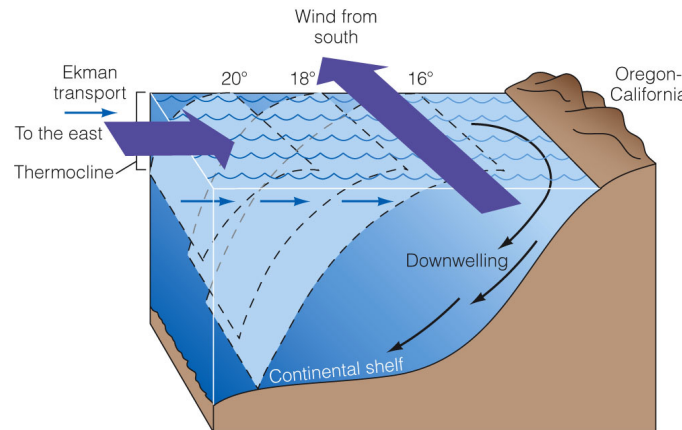
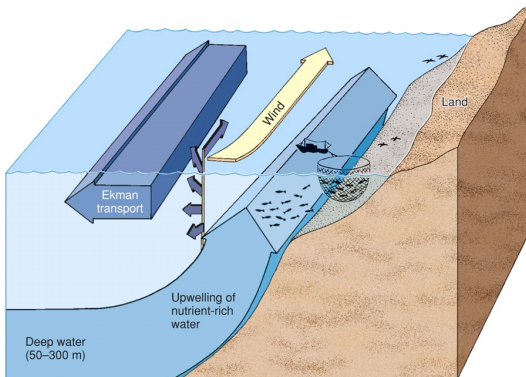
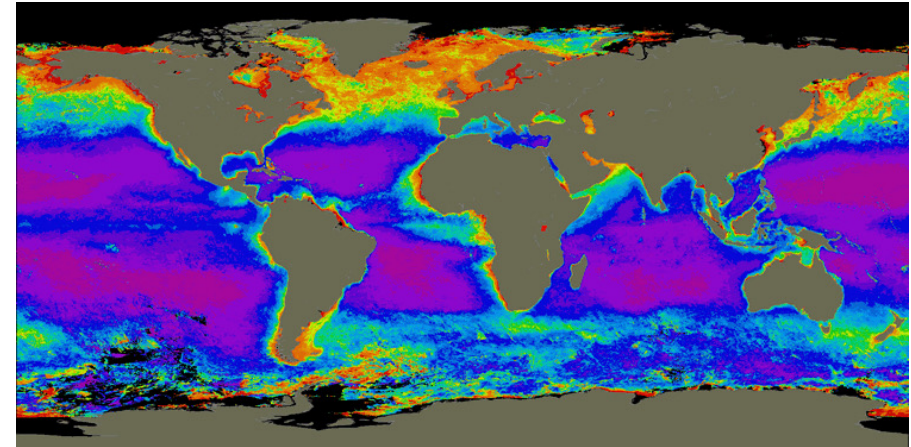


2.2. Primary production

• 2.2.2. Variations of P1 in space and time

Space

- Hydrographic factors:
 - Coastal upwellings
 - Coastal zones with mixed water column
 - Offshore upwellings
 - Downwellings:
 - Centre of oceanic gyres
 - Coastal downwellings

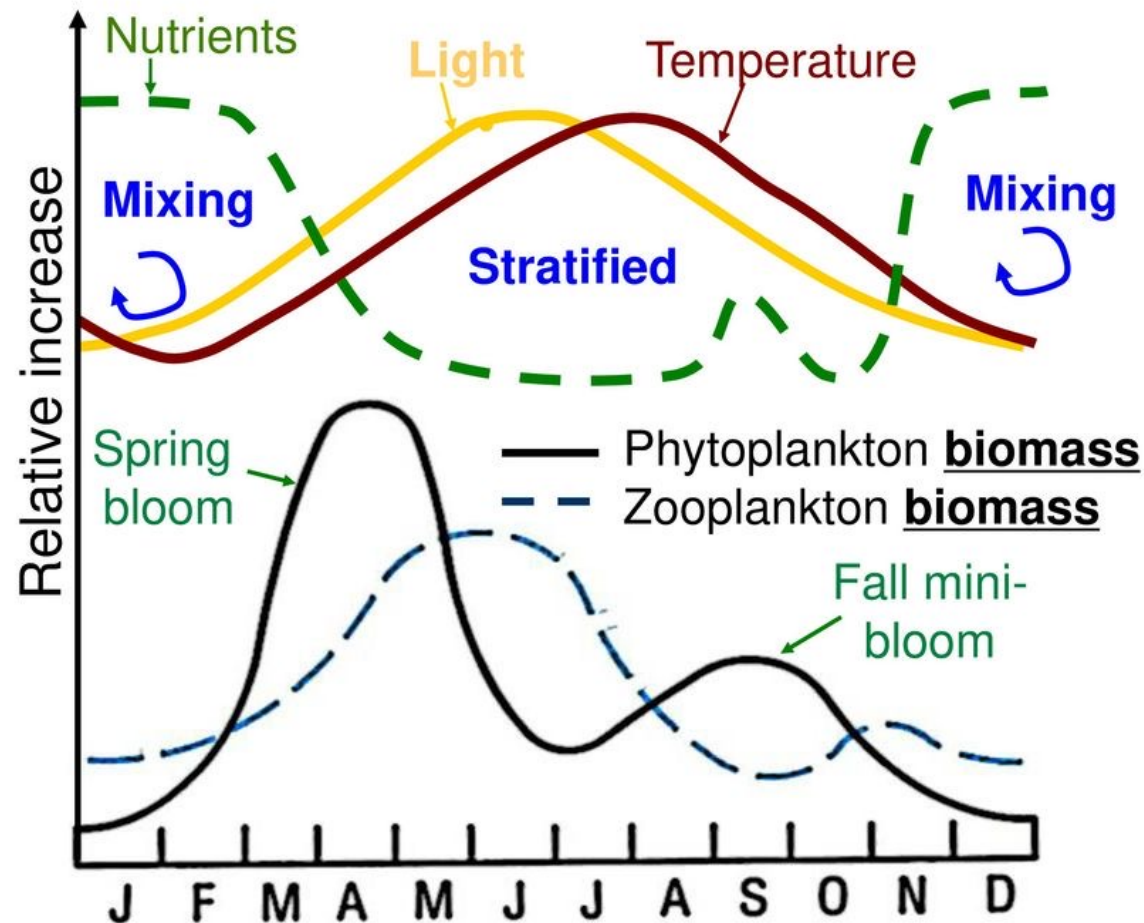


2.2. Primary production

- 2.2.2. Variations of P1 in space and time

Time - Seasons

- Temperate – Boreal North Atlantic (« natural » conditions)

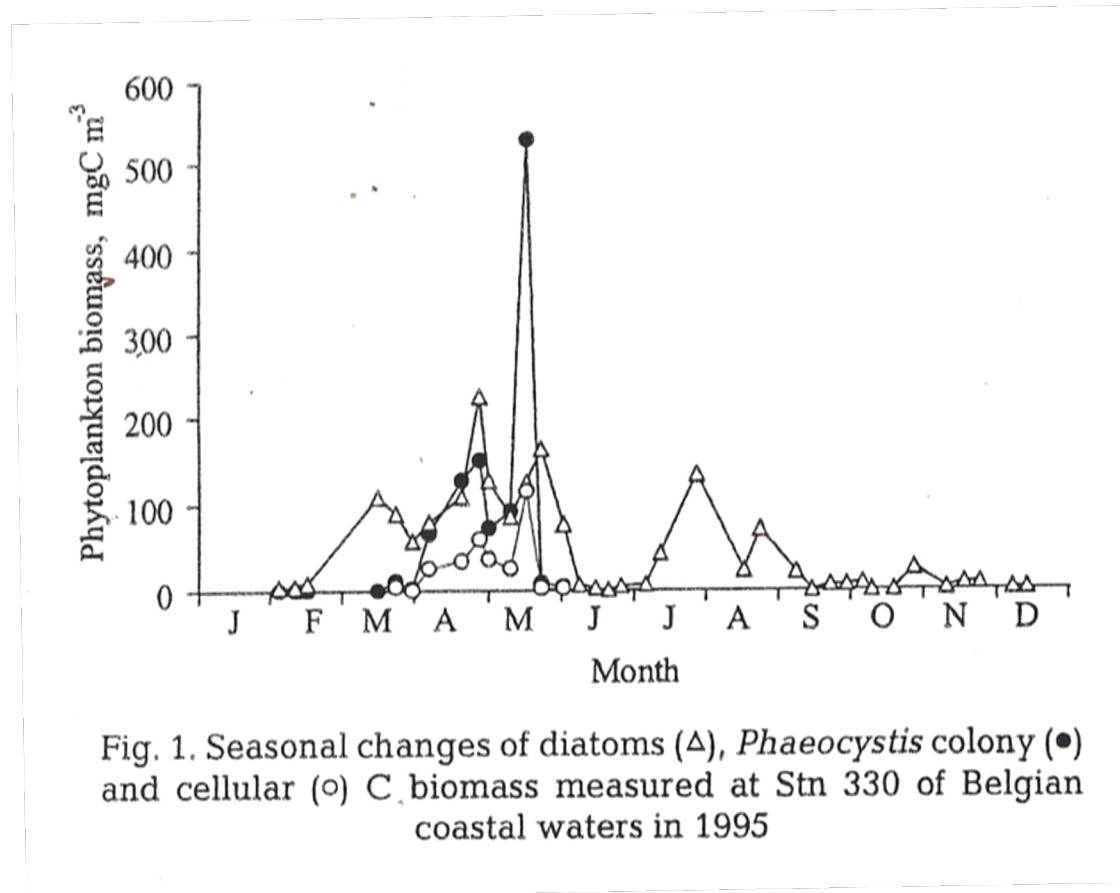


2.2. Primary production

- 2.2.2. Variations of P1 in space and time

Time - Seasons

- Temperate North Atlantic (eutrophicated conditions)



2.2. Primary production

- 2.2.2. Variations of P1 in space and time

Time - Seasons

- Temperate North Atlantic (eutrophicated conditions)
- Phaeocystis globosa* cycle

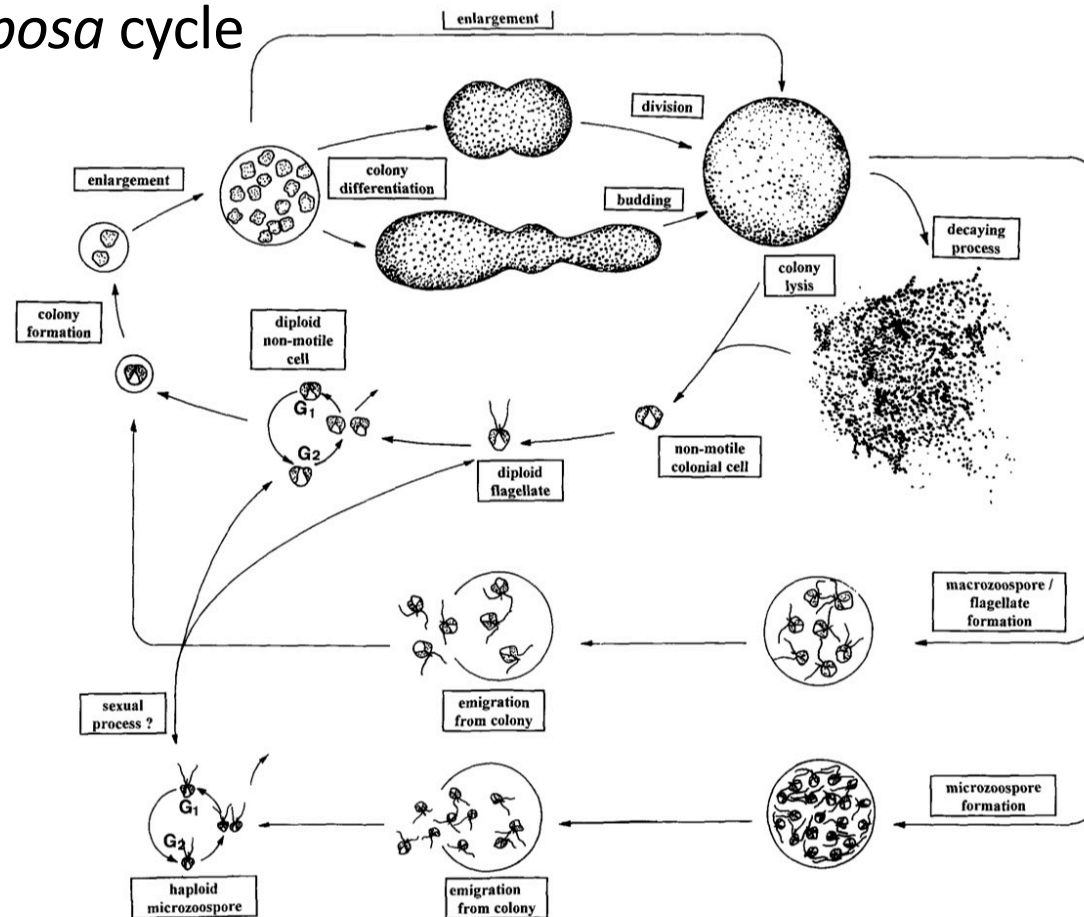


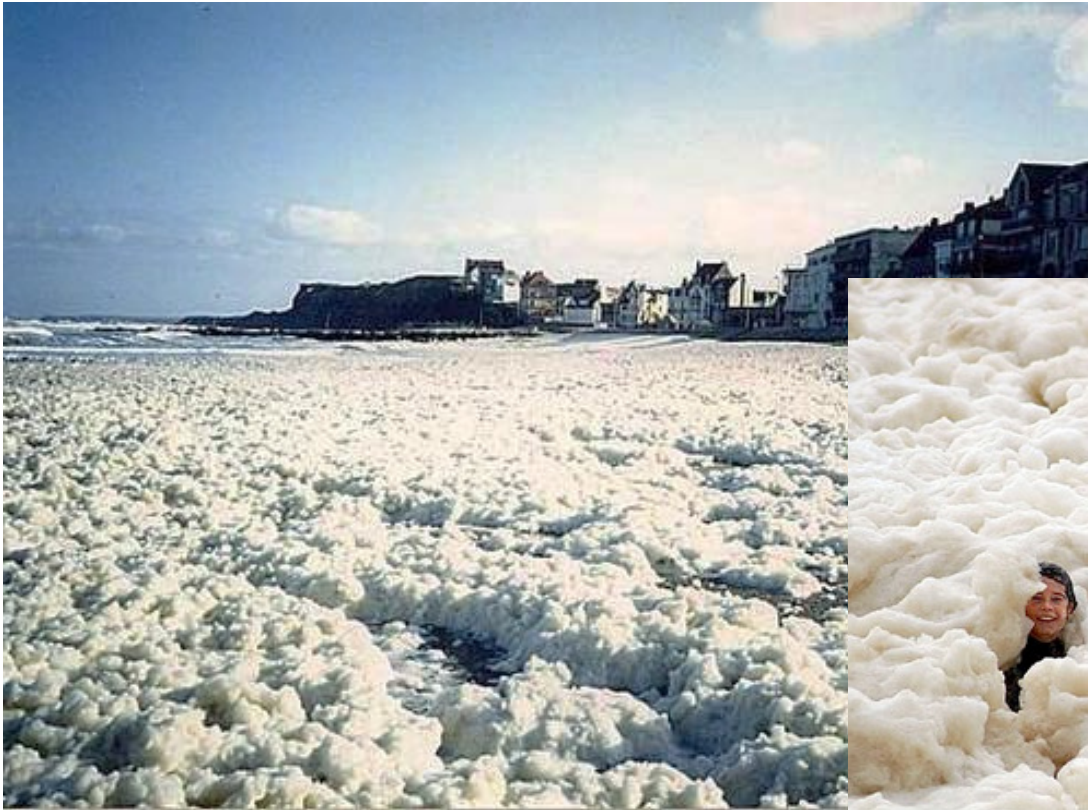
Fig. 9. Current status of *P. globosa* life cycle as compiled from culture and field observations.

2.2. Primary production

- 2.2.2. Variations of P1 in space and time

Time - Seasons

- Temperate North Atlantic (eutrophicated conditions)
- *Phaeocystis globosa*

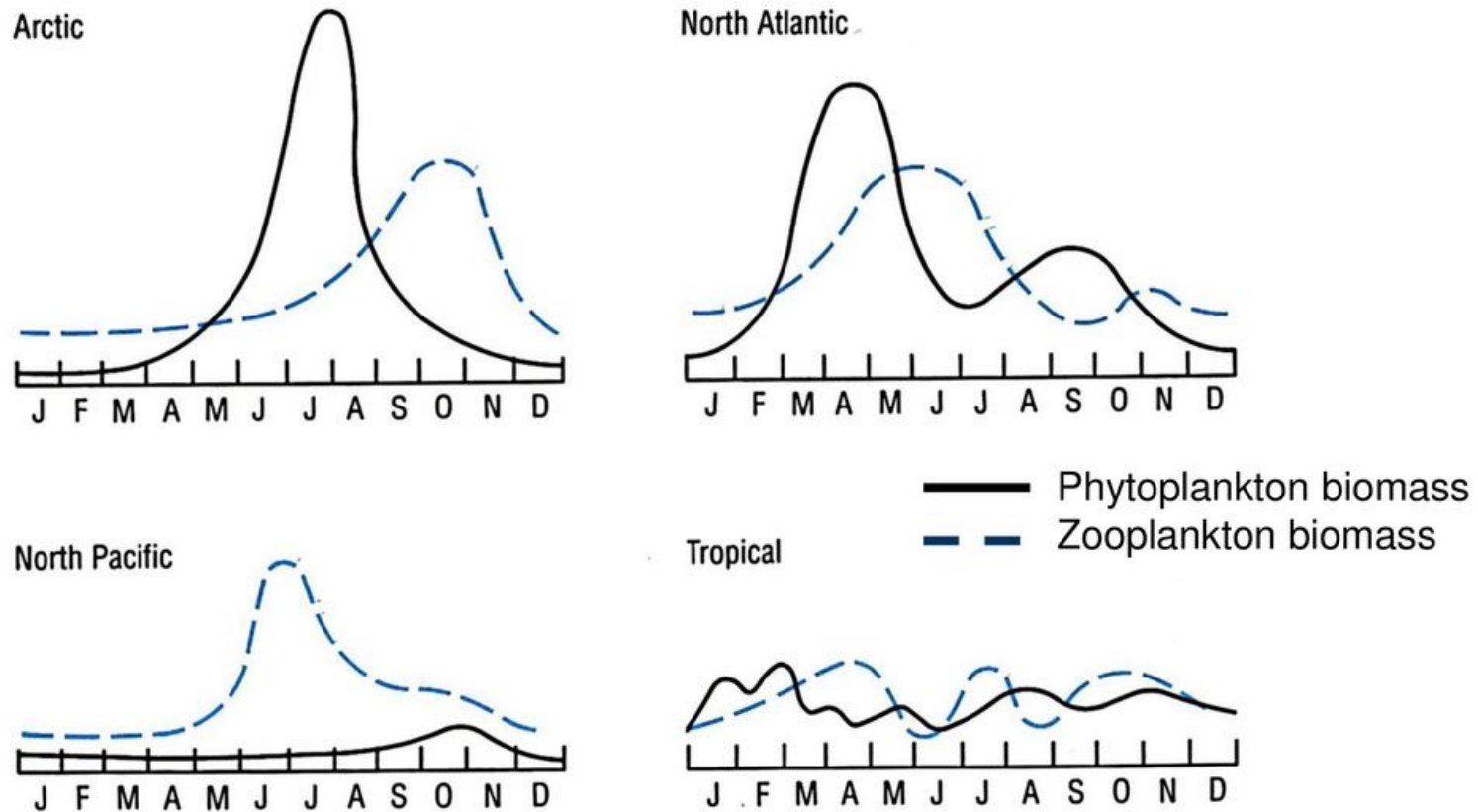


2.2. Primary production

- 2.2.2. Variations of P1 in space and time

Time - Seasons

- Other oceans



2.3. Consumers

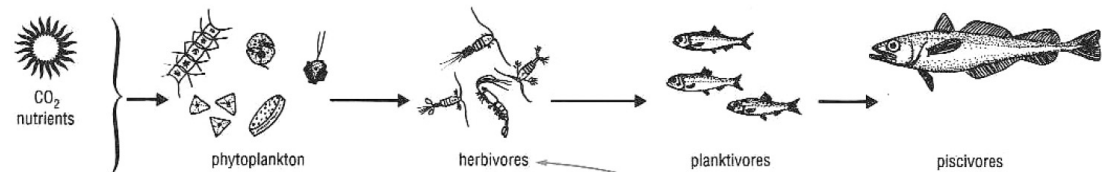
food chains

70's

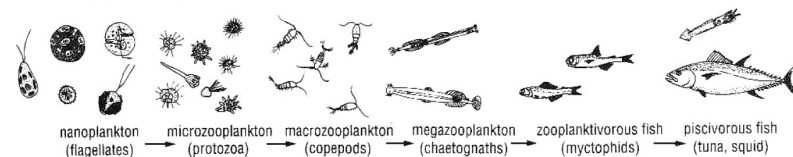
Dinoflagellates + diatoms ->
copepods -> herring -> mackerel -
> tuna

Based on net plankton

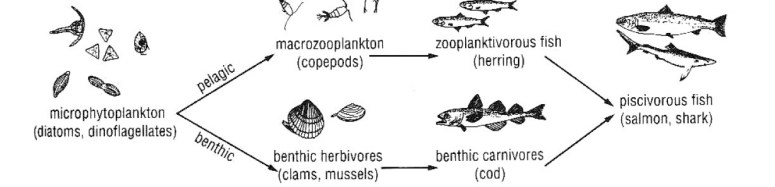
Finer Filters + fluorescent dyes



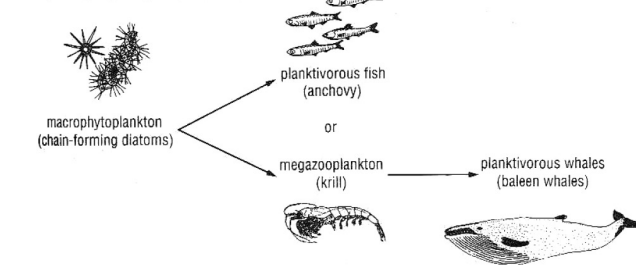
I. Open ocean (6 trophic levels)



II. Continental shelves (4 trophic levels)

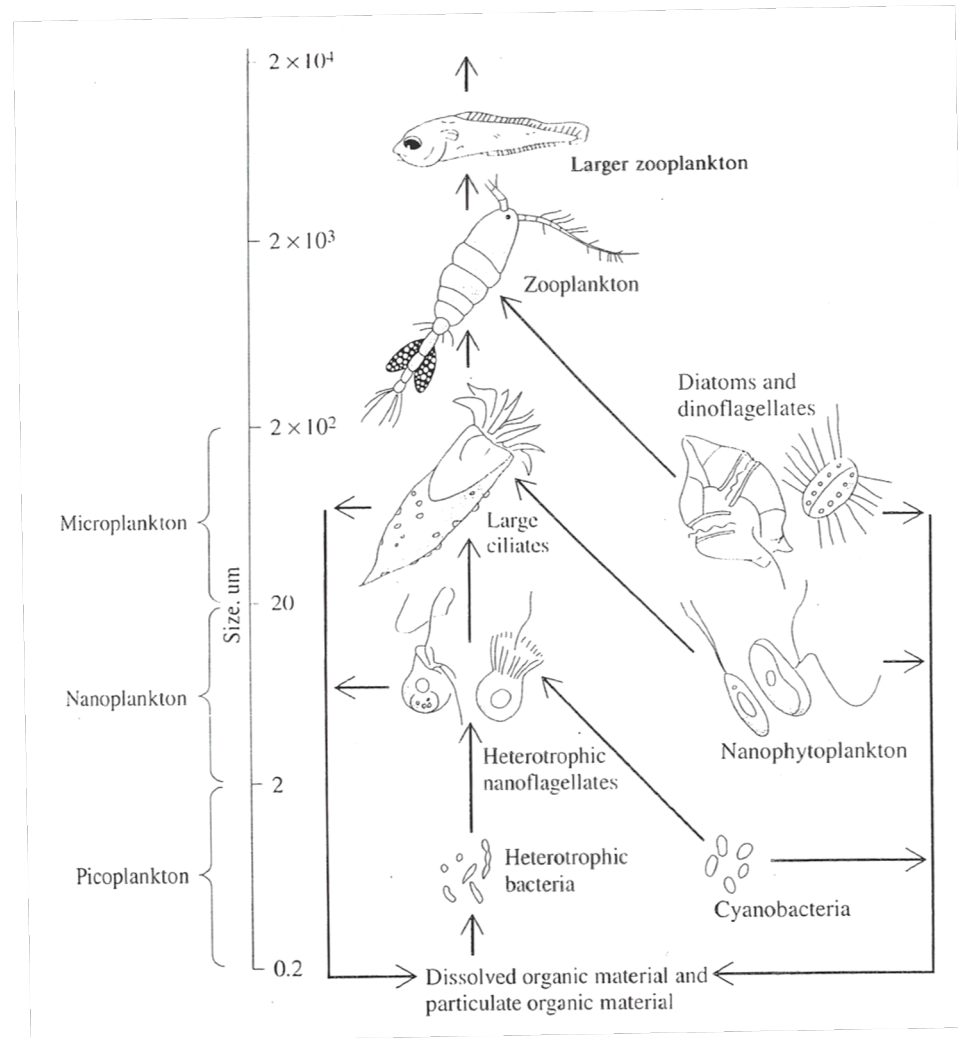
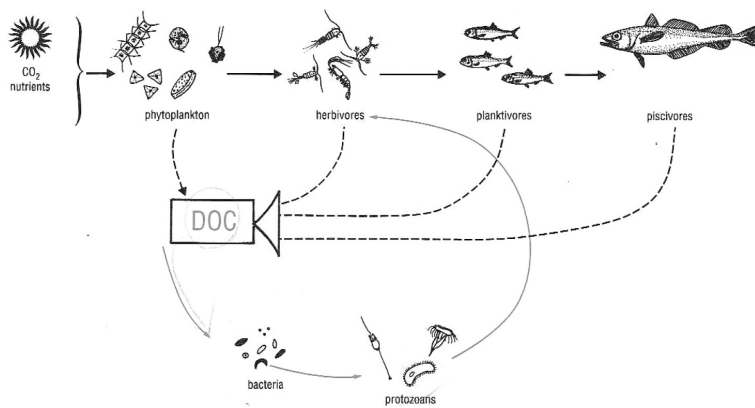


III. Upwelling regions (3 trophic levels)



2.3. Consumers

- 2.3.1. Microbial loop



© Azam et al 1983

2.3. Consumers

• 2.3.1. Microbial loop

Bacteria: bottom-up control by nutrients (inorganic and organic)

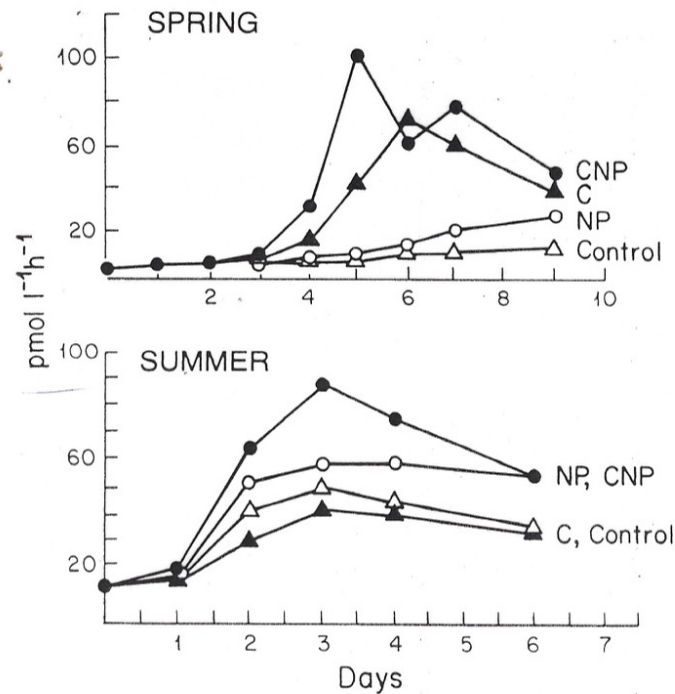


FIGURE 9-1. Thymidine incorporation rate in Baltic Sea bacterioplankton, in batch enrichment experiments done in early spring (top), and summer (bottom). Enrichments consisted of addition of sucrose (C), NH_4Cl (N), or KH_2PO_4 (P). control batches received no additions. Adapted from Kuparinen and Kuosa (1993).

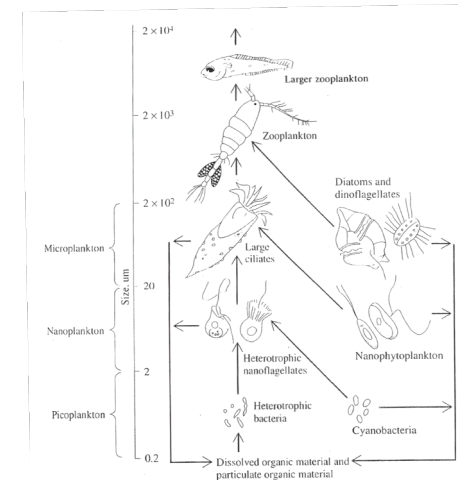


Table 2.4 Carbon: nitrogen ratios in various organisms.

Terrestrial tracheophytes	> 100:1
Marine tracheophytes	17–70:1
Macroalgae	10–60:1
Fungi	10:1
Phytoplanktonic algae	6–10:1
Bacteria	< 6:1

2.3. Consumers

• 2.3.1. Microbial loop

Bacteria: top-down control by nanoflagellates

In the lab

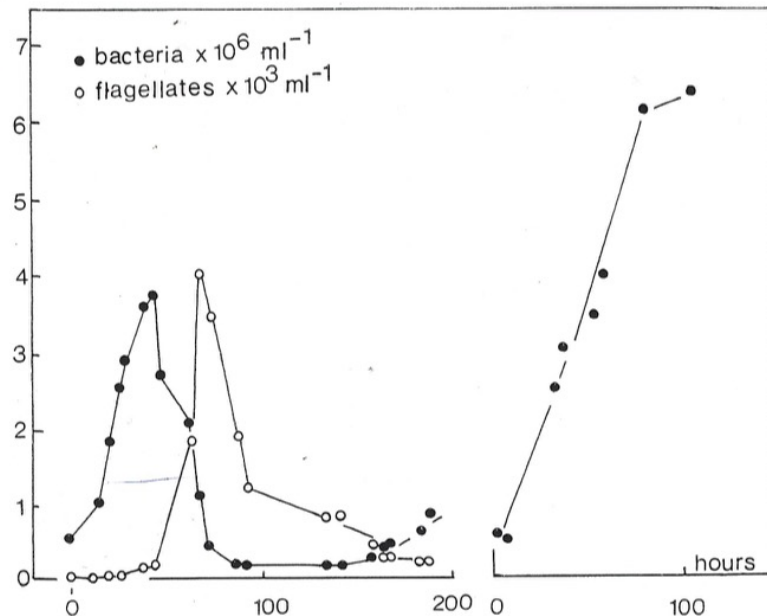
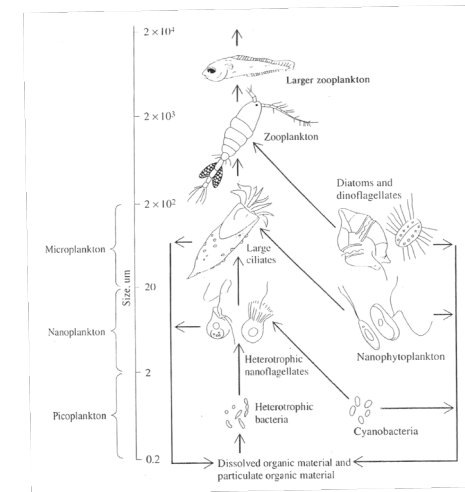
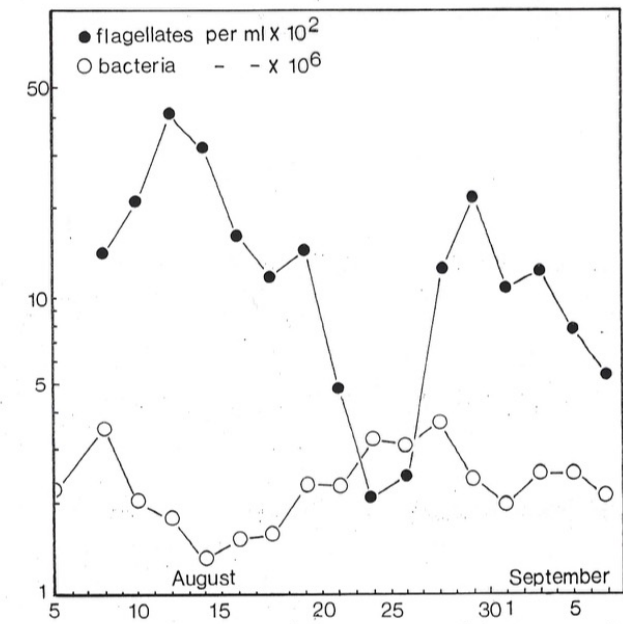


Fig. 58. Left: development of numbers of bacteria and of bacterivorous flagellates in a seawater sample filtered to remove larger plankters. Right: same water sample, but with the flagellates being removed as well. Redrawn from Fenchel [136]

Fig. 59. Numbers of bacteria and bacterivorous flagellates in the surface waters of Limfjorden, Denmark, over one month. Redrawn from Fenchel [136]



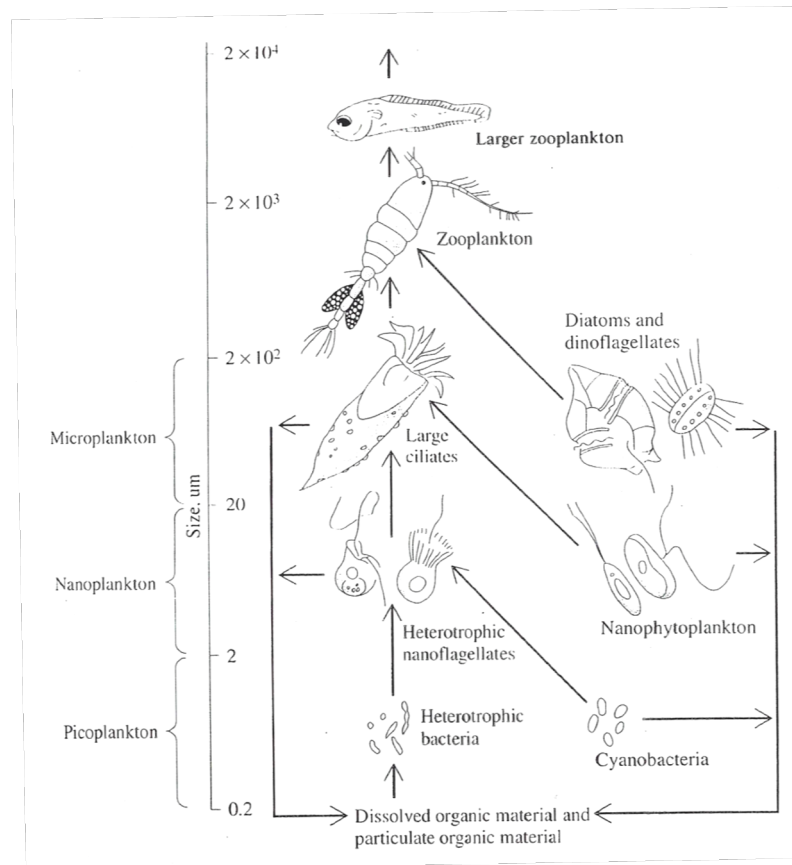
In the field



2.3. Consumers

- 2.3.1. Microbial loop

Nanoflagellates (auto- and heterotrophs):
top-down control by ciliates



2.3. Consumers

- Energy flow:

$$P_n = P_1 \cdot E^n$$

Where

P_n : production of trophic level n

P_1 : primary production of the community

E : ecological efficiency = $\frac{\text{Energy absorbed by level } n}{\text{Energy ingested by level } n}$

$E < 1$ (0.1 – 0.5)

n : trophic level

Much more trophic levels are involved than previously assumed

→ Energy/C from P_1 entering the microbial loop almost totally dissipated in the loop

→ Energy/C transfer between the microbial loop and the linear food chain is low

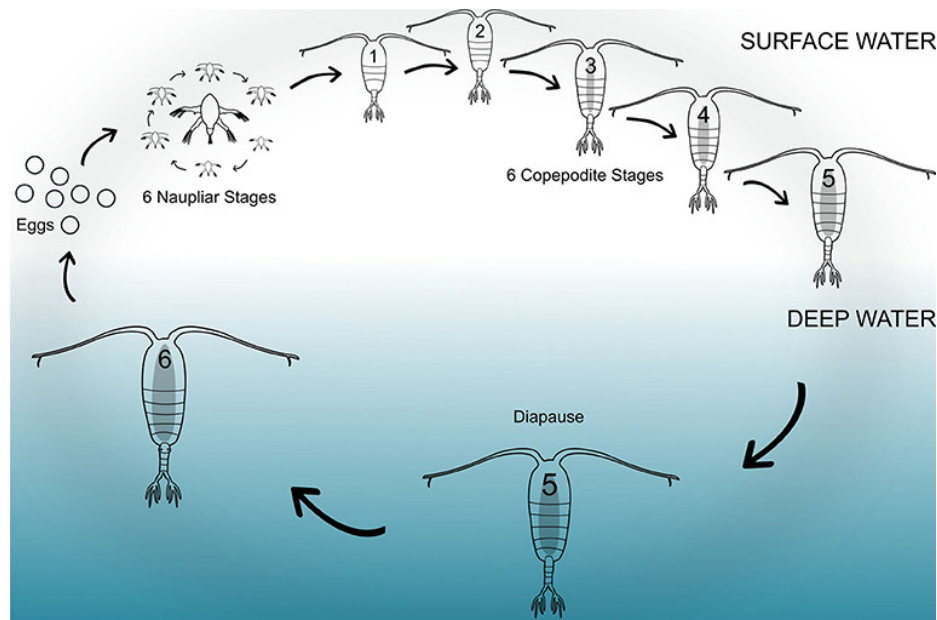
2.3. Consumers

- 2.3.2. Linear food-chain: nekton

Marine copepods from a single drop of water collected off Melbourne, Florida.

life cycle of *Calanus finmarchicus*

© Holly Jenkins (NOC)



Other zooplankton

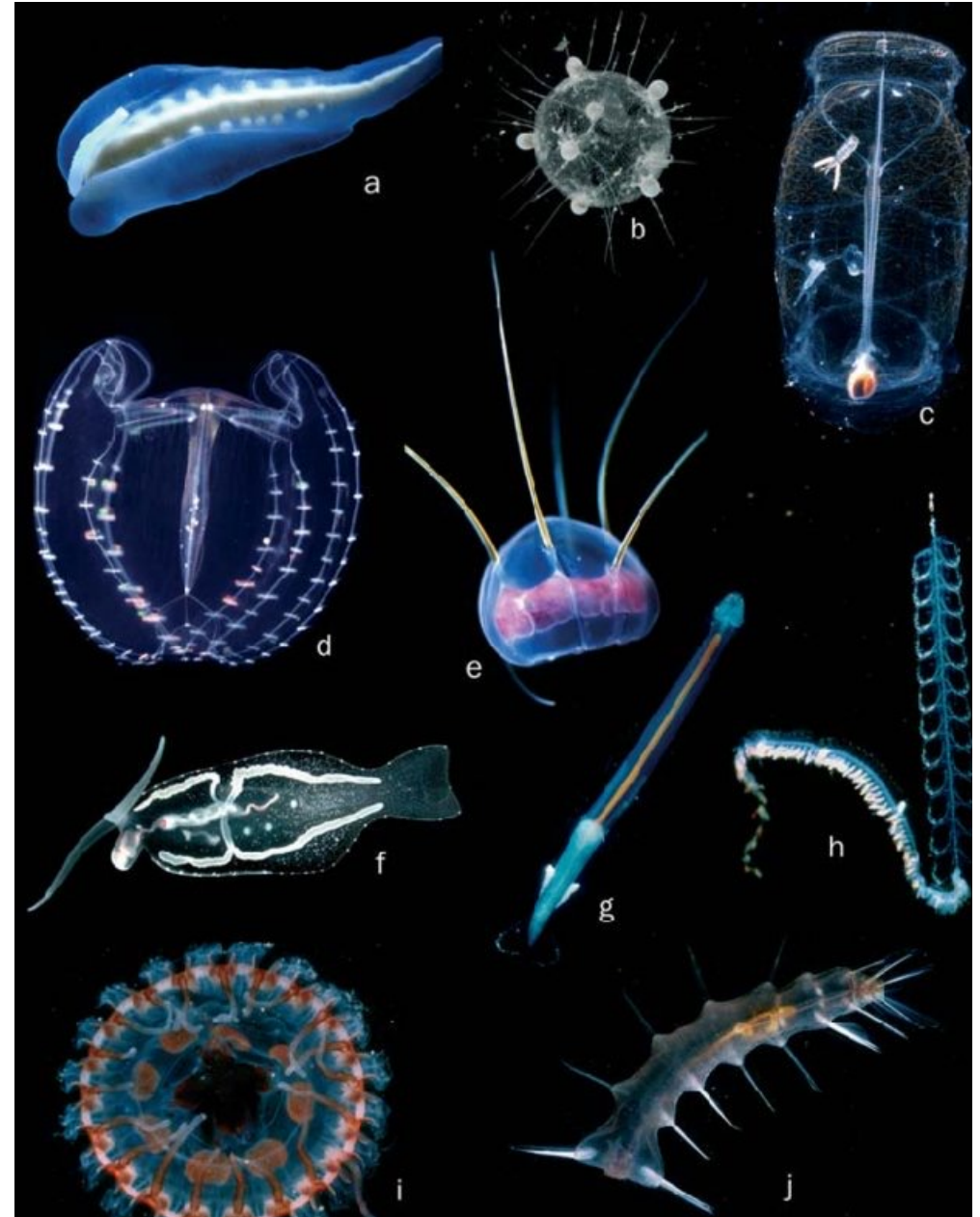
protists – diatoms,
dinoflagellates,
radiolarians, and
foraminifera

© *Christian Sardet,*
Plankton –
Wonders of the
Drifting World,
Univ. Chicago Press
2015



Other zooplankton

- Representative members of **gelatinous zooplankton**. Organisms from at least eight phyla are included among the gelata. (a) Nemertean. (b) Phaeodarian radiolarian. (c) Salp with parasitic copepod. (d) Lobate ctenophore. (e). Narcomedusan hydrozoan. (f) Nudibranch mollusc. (g). Chaetognath. (h) Physonect siphonophore. (i) Coronate scyphozoan. (j) Polychaete.



Other zooplankton

- **Cnidaria**
- **Jellyfish**
- **Ctenophora**
- **Beroe cucumis with**
Parasitic amphipod
Hyperia galba, ©
Alexander Semenov



Other zooplankton

- Pteropods
- Shelled, sea butterfly
© Steve Ringman
- Unshelled, sea snail
- Clione Limacina



Other zooplankton

- **Chordata**
- **Salps**



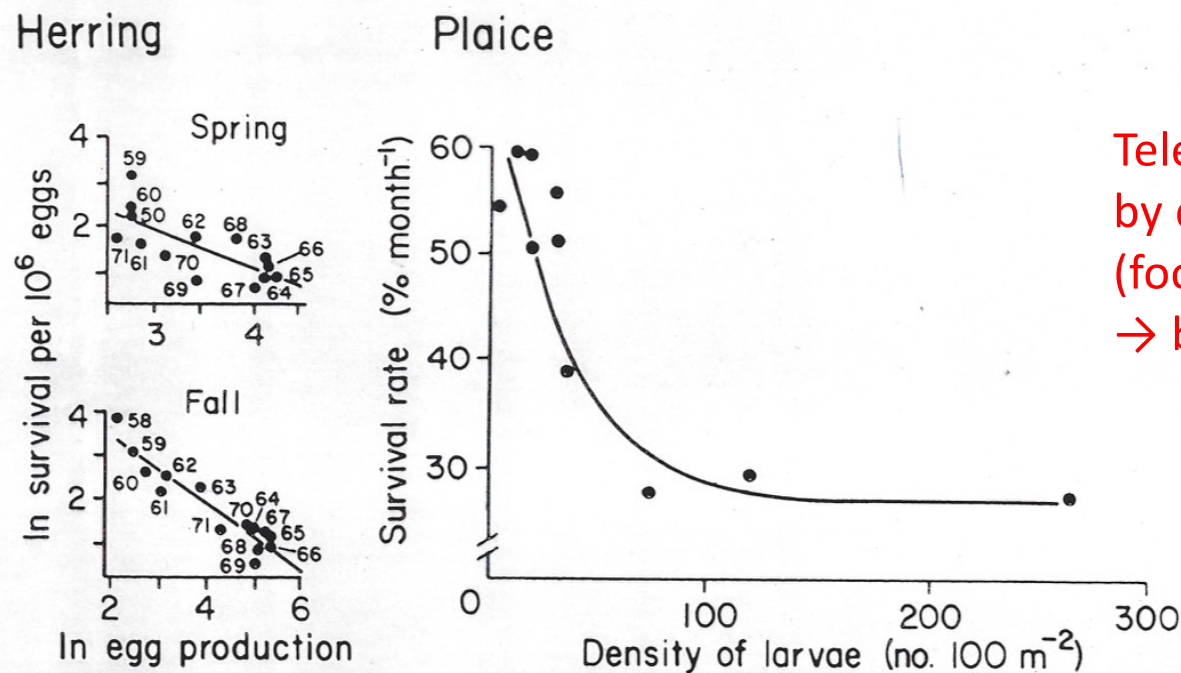
Photo: Mike Stukel / Florida State University

2.3. Consumers

• 2.3.2. Linear food-chain: nekton

Teleostean fishes

- Better studied (fisheries)
- Most = r strategists (many eggs/larvae with low energetic investment)



Teleostean larvae controlled
by d-dependent processes
(food competition)
→ bottom-up control

FIGURE 4-9. Survival of fish during the first year of life (age 0) at different densities. Data for spring and fall herring cohorts from Winters (1976). Plaice data from Lockwood (1978).

2.3. Consumers

• 2.3.2. Linear food-chain: nekton

Teleostean fishes

- Better studied (fisheries)
- Most = r strategists (many eggs/larvae with low energetic investment)



Recruitment in adult teleostean populations independent of population size → top-down control

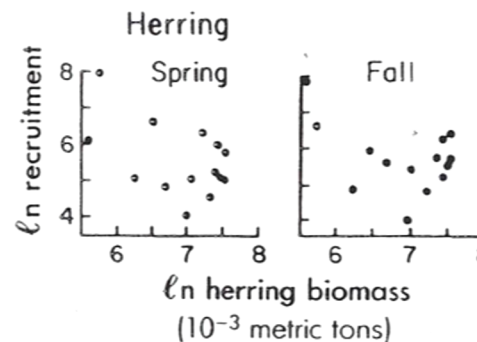
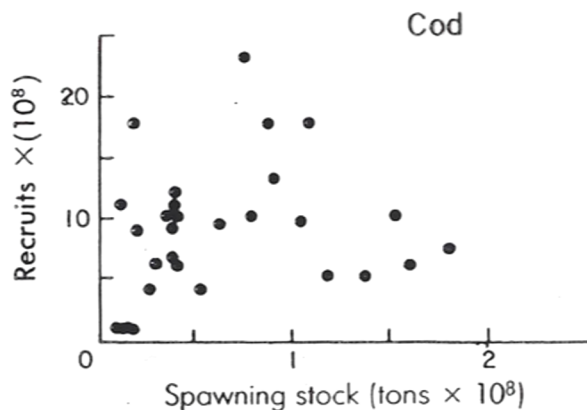
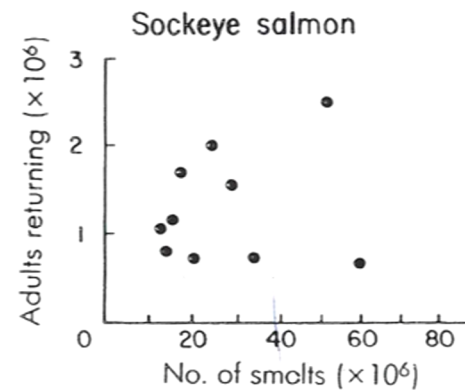
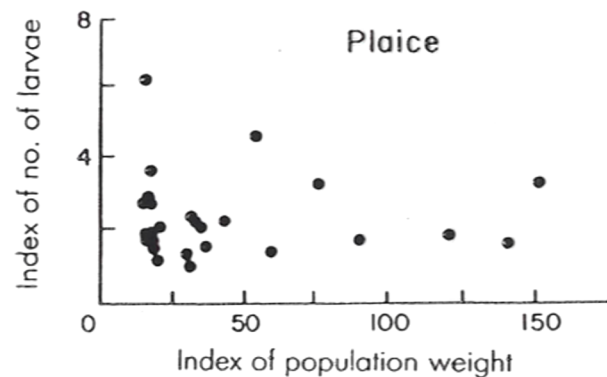


Figure 4-10. Recruitment in fish populations in relation to density. Top left: Recruitment of plaice in to the North Sea fishery in relation to stock density. The values are dimensionless indices obtained from catch statistics [adapted from Cushing (1975)]. Bottom left: Recruitment of cod in Arcto-Norwegian waters (1940–1969) in relation to the abundance of spawners [adapted from Garrod and Clayden (1972)]. Top right: Recruitment of sockeye salmon in Skeena estuary, British Columbia [adapted from Ellis (1977)]. Smolts refer to young fish leaving rivers for the sea. Bottom right: recruitment of herring in southern Gulf of St. Lawrence, Canada. Adapted from Winters (1976). © Canadian Journal of Aquatic and Fisheries Sciences, reprinted by permission.

2.3. Consumers

• 2.3.2. Linear food-chain: nekton

Birds and mammals

- k strategists (few youngs with high energetic investment)
- « full scale experiment »: whale hunting

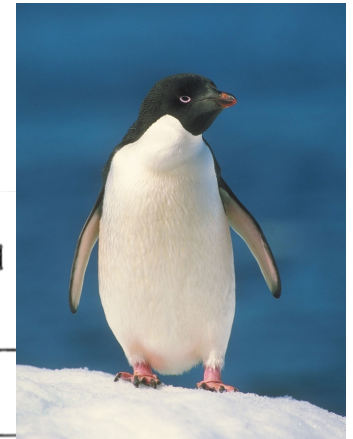
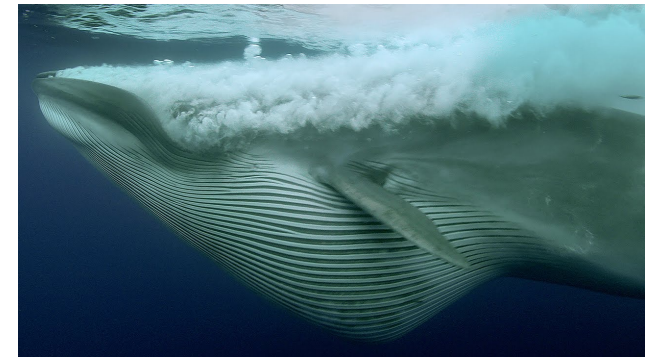


Table 9-3. Rough Estimates of Whale and Seal Stocks, Migratory Losses, and Food Consumption in Prepelagic Whaling and in Recent Times^a

	Whales			Seals
	Initial	Recent	Percent removed	Recent
Stock	46	8	83	3.5
Loss from Antarctic Ocean	19	3	84	Not migratory
Food consumption			Percentage left unconsumed	
Krill	190	43	77	64
Fish	4	1	75	6
Squid	12	5	58	7

^a Values are in millions of tons. Data on food consumption by penguins, other birds, and fish are not available. Adapted from Laws (1977a,b).

2.3. Consumers

• 2.3.2. Linear food-chain: nekton

Birds and mammals

- « full scale experiment »: whale hunting

TABLE 9-3. Recent Changes in Penguins and Seal Populations in Antarctica.^a

	Principal foods	Changes in population
Penguins		
Emperor (<i>Aptenodytes forsteri</i>)	Fish	No significant increase
King (<i>A. patagonica</i>)	Mainly squid	Marked increase ($5\% \text{ y}^{-1}$)
Adelie (<i>Pygoscelis adeliae</i>)	60% krill, 40% fish and other	<u>Local increases</u> ($2.3\% \text{ y}^{-1}$) in whaling areas
Chinstrap (<i>P. antarctica</i>)	Krill	<u>Marked increase</u> , extended range
Gentoo (<i>P. papua</i>)	Benthic fish, some krill	<u>Some increases</u>
Macaroni (<i>Endiptes chrysolophus</i>)	75–98% krill, 2–25% fish	(<u>Increases</u> of $9\% \text{ y}^{-1}$)
Seals		
Crabeater (<i>Lobodon arcinophagus</i>)	94% krill, 3% fish, 2% squid	Earlier maturity, <u>increase in numbers</u> ($7.5\% \text{ y}^{-1}$)
Fur (<i>Arctocephalus gazella</i>)	34% krill, 33% fish, 33% squid	<u>Population explosion</u> ($14\text{--}17\% \text{ y}^{-1}$) especially in overlap with range of baleen whales; appearance of new colonies

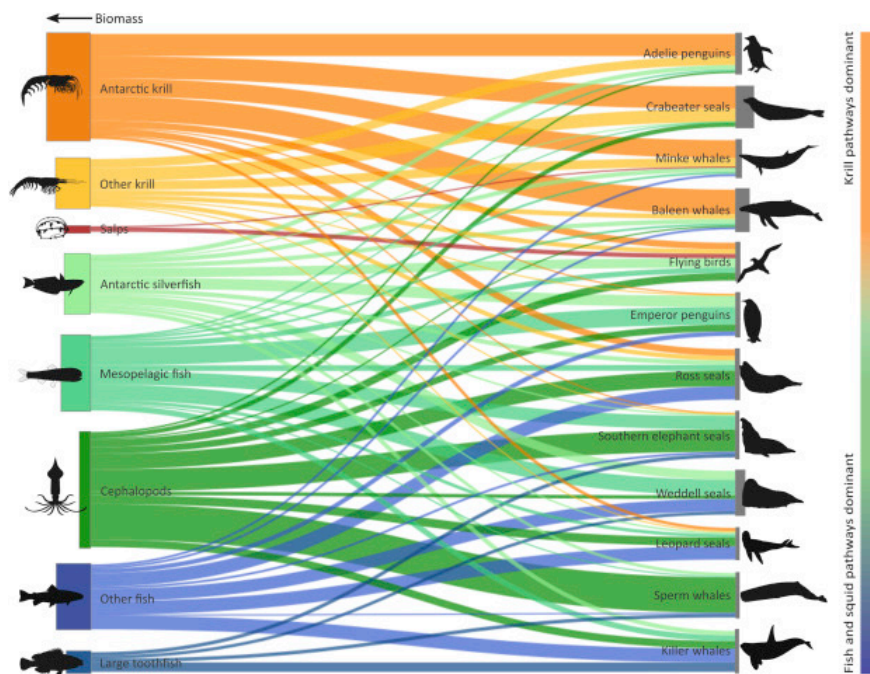
^aData from Conroy (1975), Stonehouse (1975), Laws (1977a,b), Payne (1977), Øritsland (1977), Croxall and Prince (1979), Hinga (1979), Laws (1985), and Cooper et al. (1990).



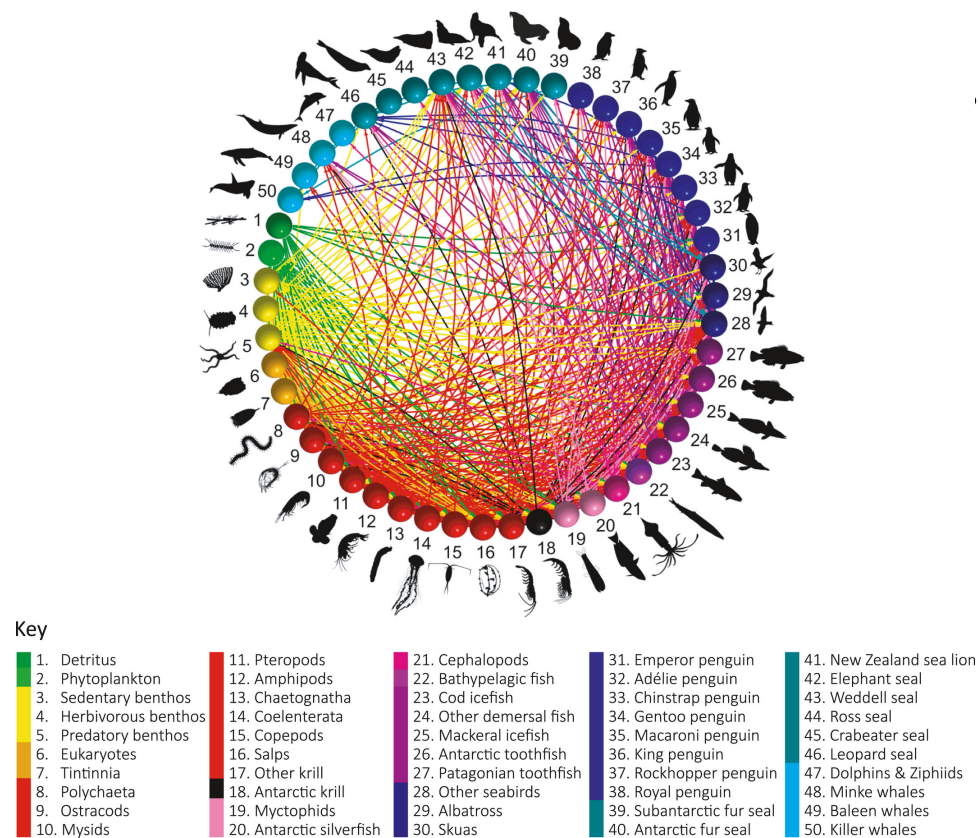
Populations of krill-eating penguins and seals increased in parallel with whale hunting → Bottom-up control of krill-eating vertebrates by food

2.3. Consumers

- Food webs
- Multiple and shifting interactions between organisms.



- Sankey diagram depicting predator-prey interactions between mid-trophic level groups of interest and [marine mammal](#) and bird functional groups within the Prydz Bay



- network diagram for the 50 trophic groups and their associated interactions

Nodes are colored according to broad taxonomic groups (e.g., yellow for benthic organisms, red for zooplankton) with numbers corresponding to the name of the group listed in the key. Silhouettes are representative of the types of organisms associated with each node. Edges (i.e., connections) are colored according to prey species/group and are directed toward the relevant predator node. This overall representation shows the complexity of trophic connections present in the database, which are more clearly resolved in regional food web configurations

- Food chains don't exist in real ecosystems
- Almost all organisms are eaten by more than one predator (and vice versa)
- Food webs reflect the multiple and shifting trophic interactions.
- Many species don't fit in convenient categories
- Omnivores
- Detrivores
- Parasites
- Cannibalism