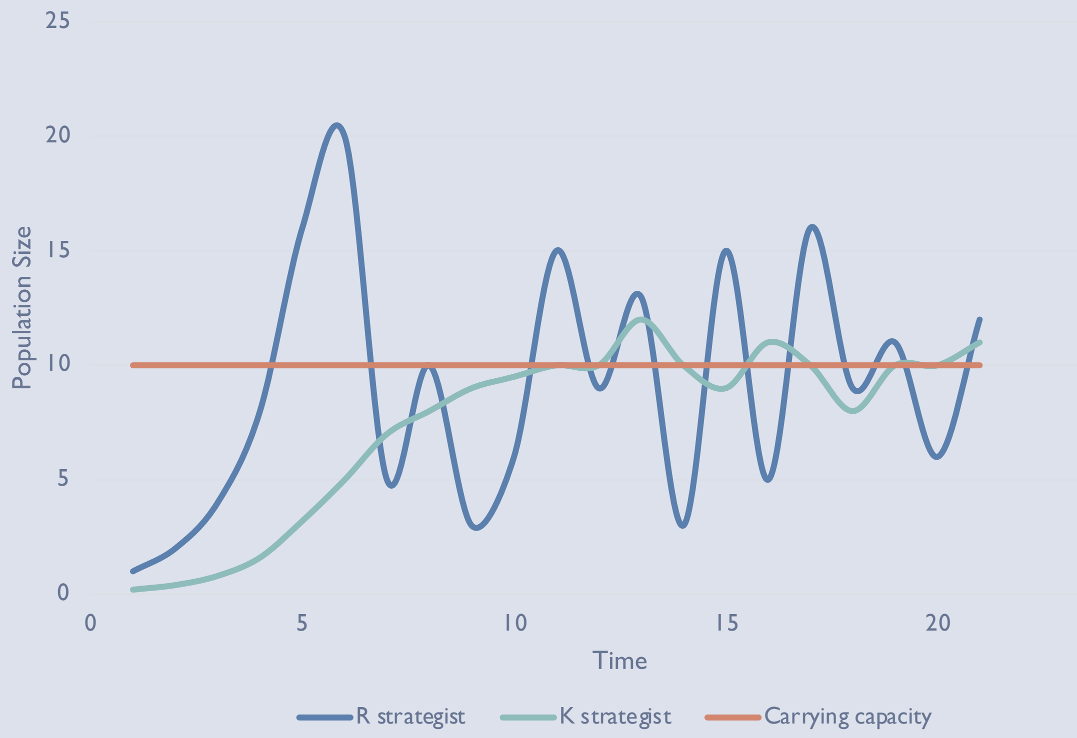
PELAGIC BIOLOGICAL PROCESSES

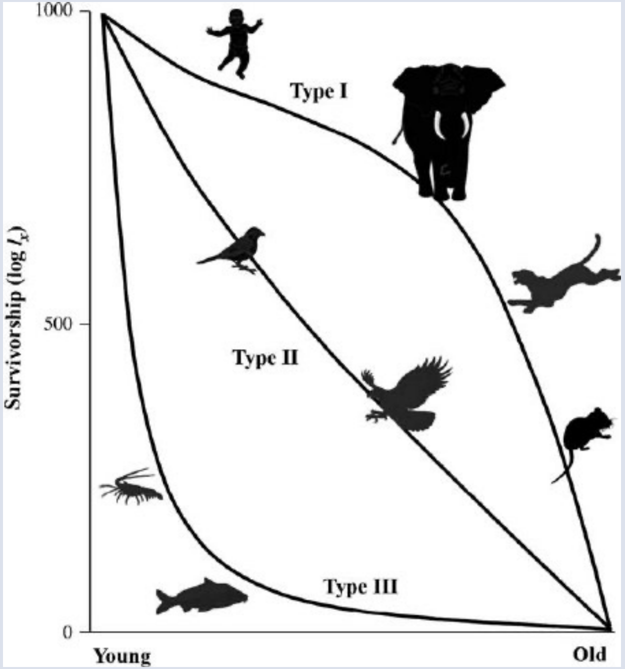
RECAPS

R AND K STRATEGIST



r-organisms	K-organisms
short-lived	long-lived
small	large
weak	strong or well-protected
waste a lot of energy	energy efficient
less intelligent	more intelligent
Have many offspring	Have few offspring
reproduce at an early age	reproduce at a late age
fast maturation	slow maturation
little care for offspring	much care for offspring
small size at birth	large size at birth

SURVIVOR SHIP CURVE



OCEAN CIRCULATION

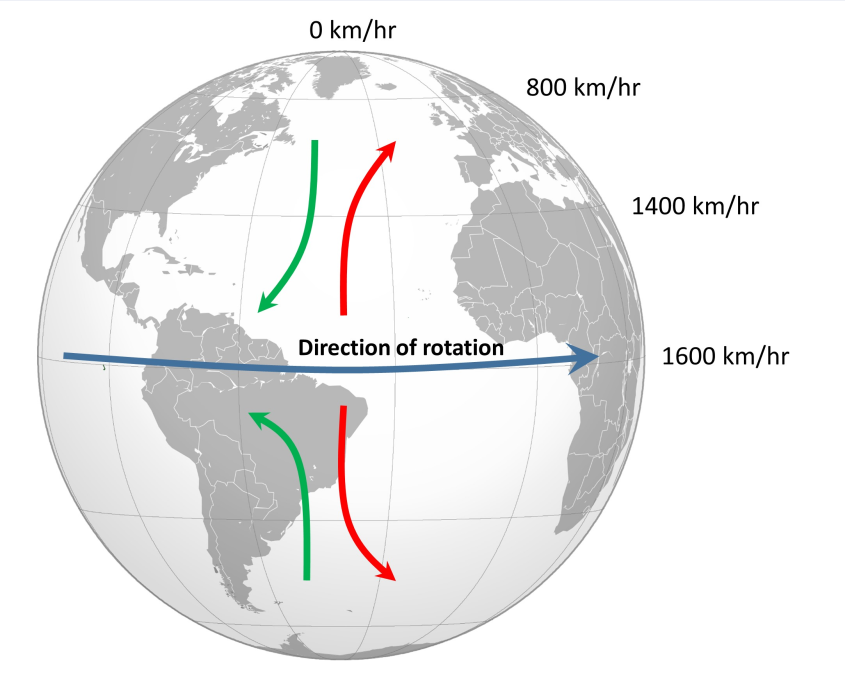
- *Surface circulation*
- *Thermohaline circulation*

SURFACE CIRCULATION

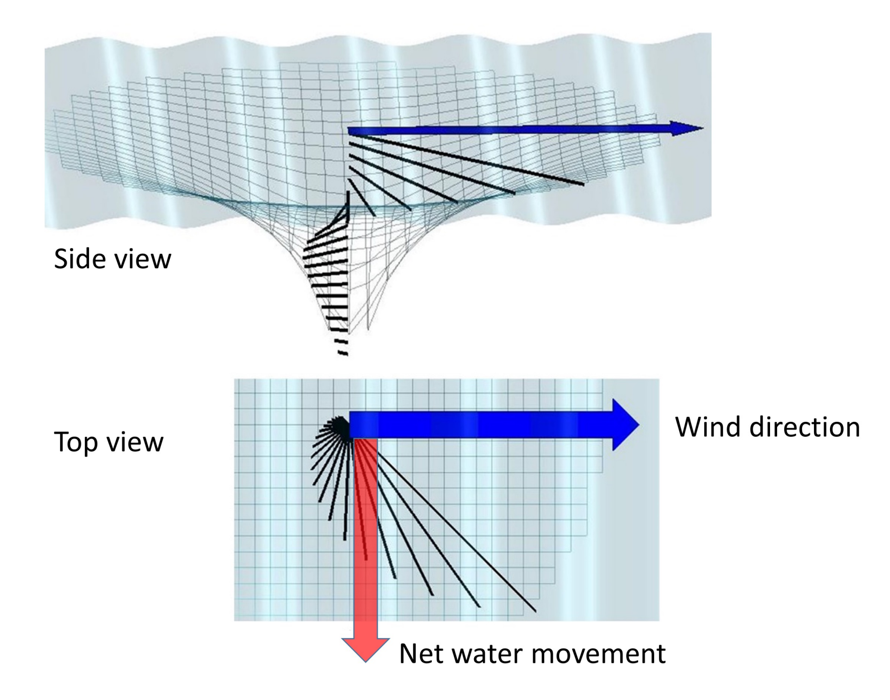
- *Surface currents*
- *Coriolis effect*
- *Up- and downwelling*

SURFACE CIRCULATION

- *Surface currents*
- *Coriolis effect*
- *Up- and downwelling*



EKMAN TRANSPORT



THERMOHALINE CIRCULATION

- *Mechanisms and conveyor belt*
- *Consequences of disruptions of the thermohaline circulation*

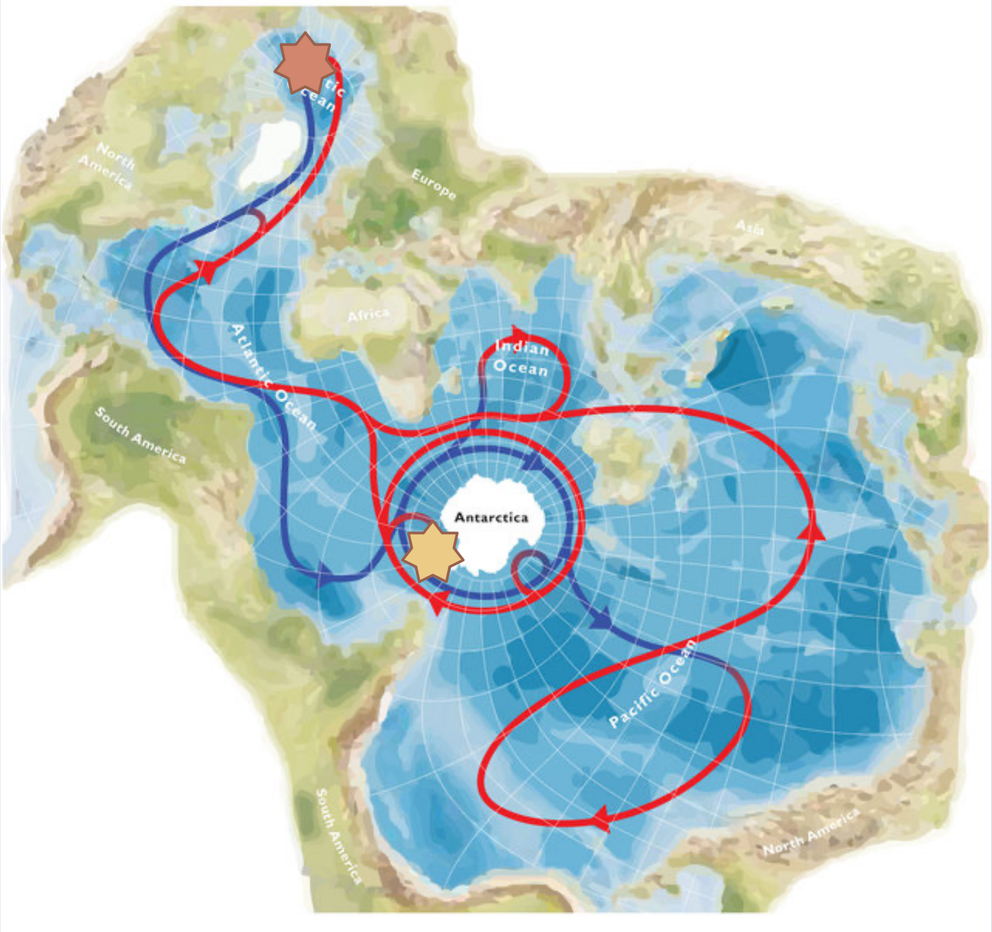
MIXING

- Different scales
- Molecular scale (salt fingers)
- Mechanical forces
  - Wind
  - Tides
- Destabilizing buoyancy forces
  - Cooling
  - Ice freezing

- 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.

NABW

ABW



NABW

ABW

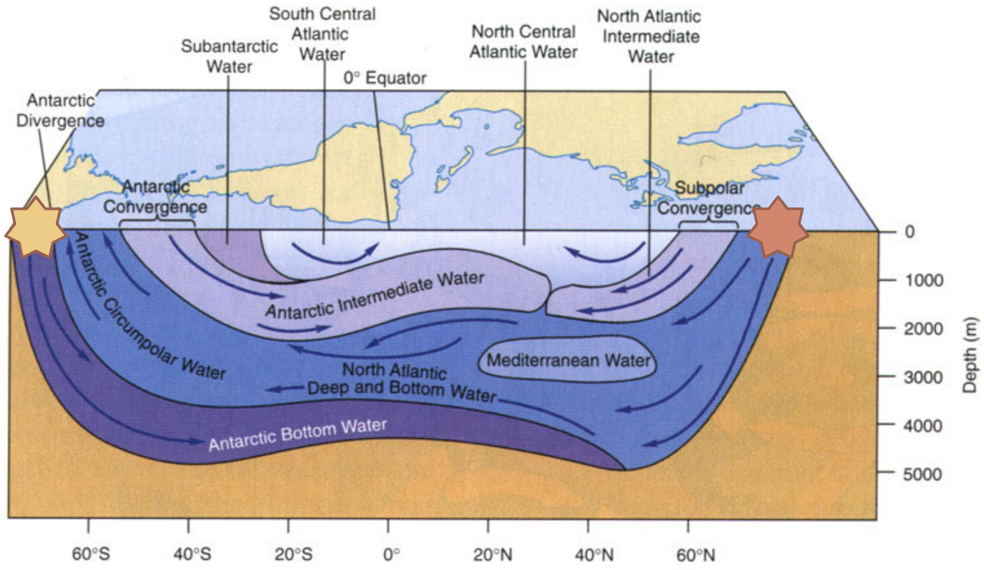
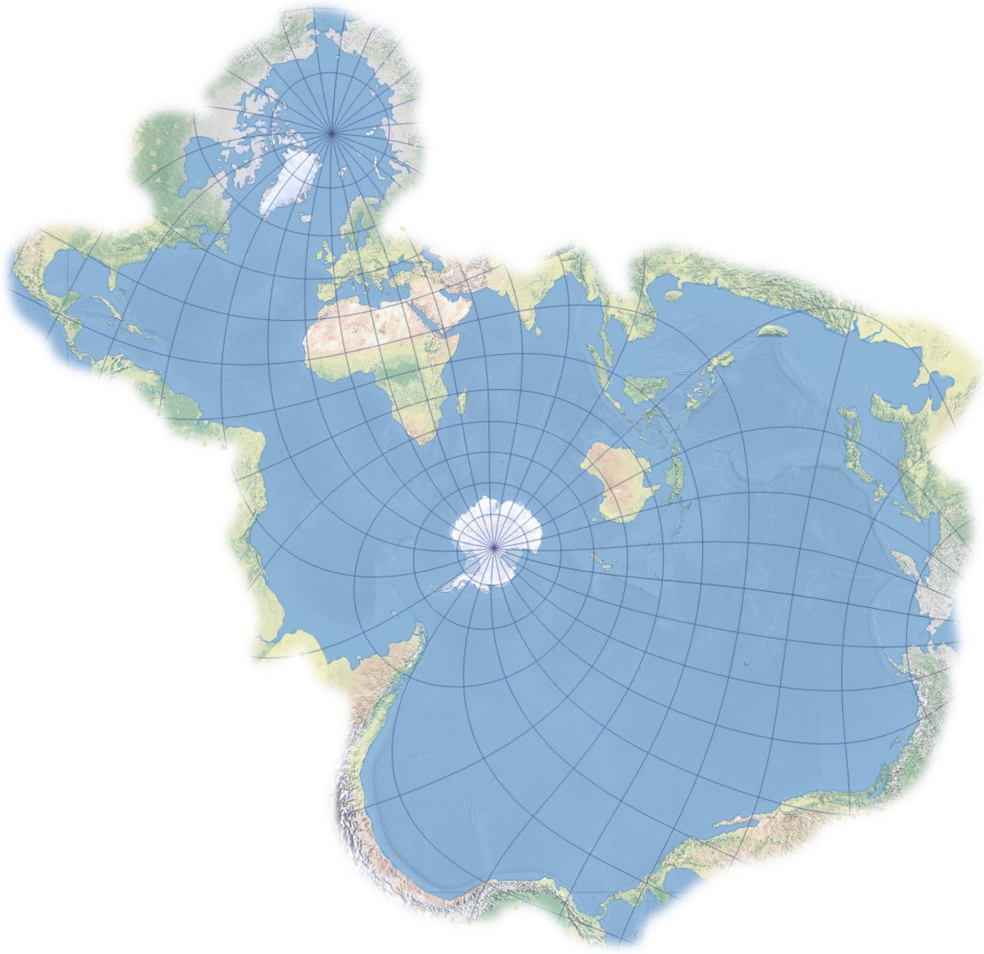


FIGURE 8–27 A vertical cross section of the Atlantic Ocean shows the various water masses that form layers at different depths. Antarctic Bottom Water is the densest water mass and it flows northward from around Antarctica. North Atlantic Bottom Water sinks near Greenland and flows southward over the 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.

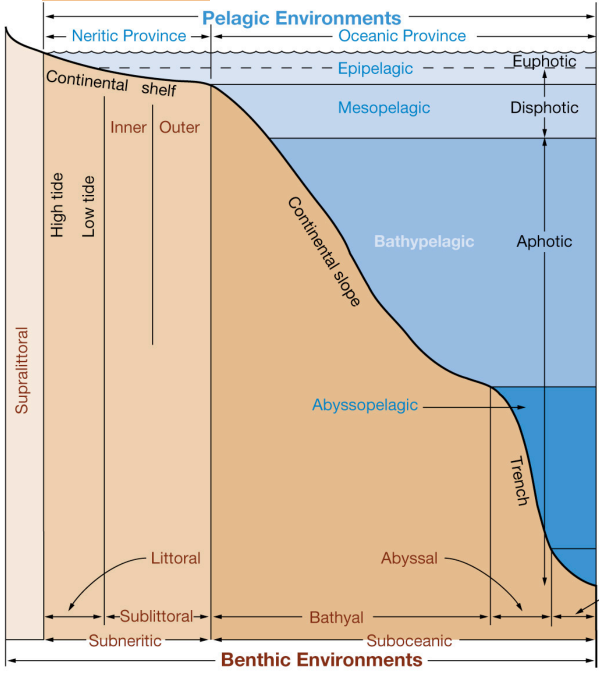
Segar 2007

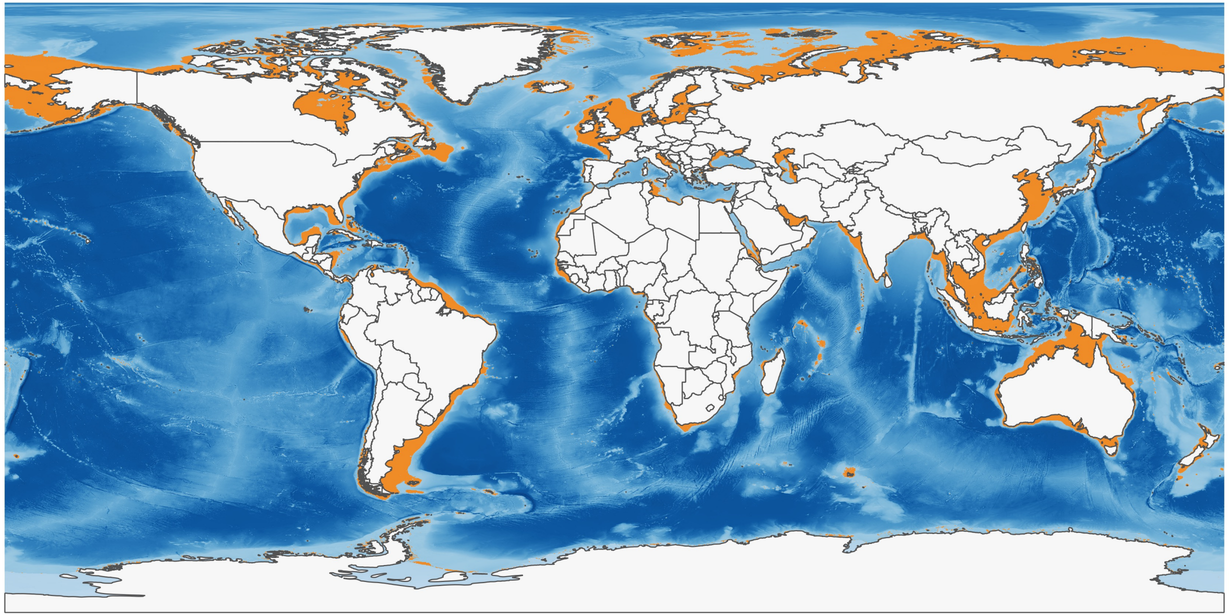


I. DIVISIONS OF THE MARINE ENVIRONMENT

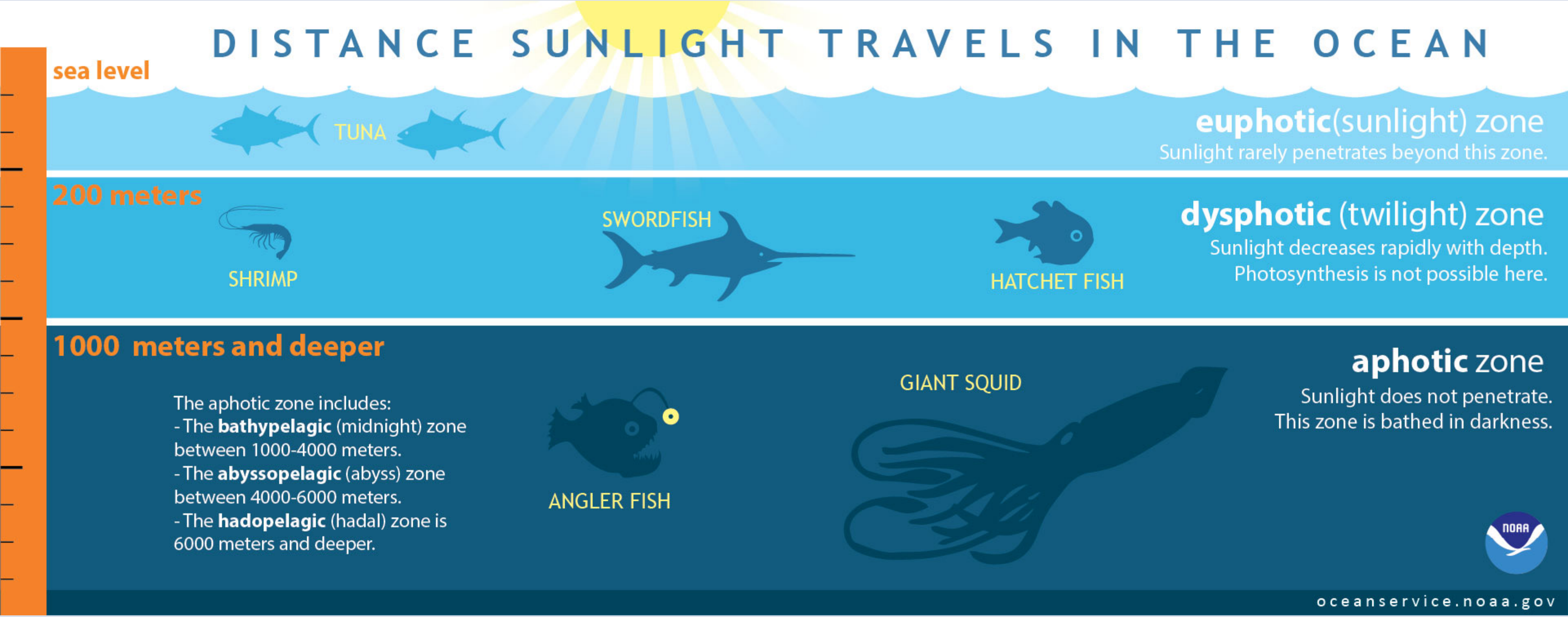
πέλαγος
(pélagos)
'open sea’

1. DIVISIONS OF THE MARINE ENVIRONMENT

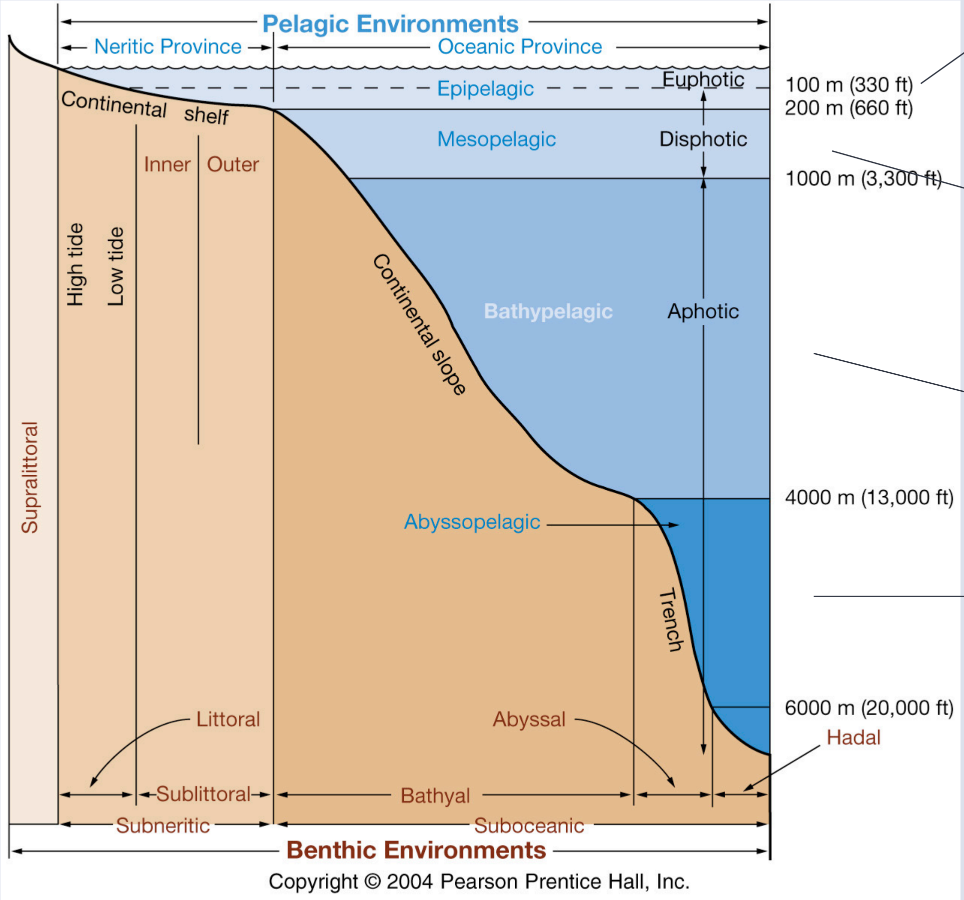




I. DIVISIONS OF THE MARINE ENVIRONMENT



1.1. ZONES OF THE PELAGIC DOMAIN



Epipelagic zone (0-200m):

- Euphotic
- Mixing zone
- Superficial water masses

Mesopelagic zone (200 - 1000m):

- Disphotic
- Intermediate water masses

Bathypelagic zone (1000 - 4000m):

- Aphotic
- Deep water masses

Abyssopelagic zone (below 4000m):

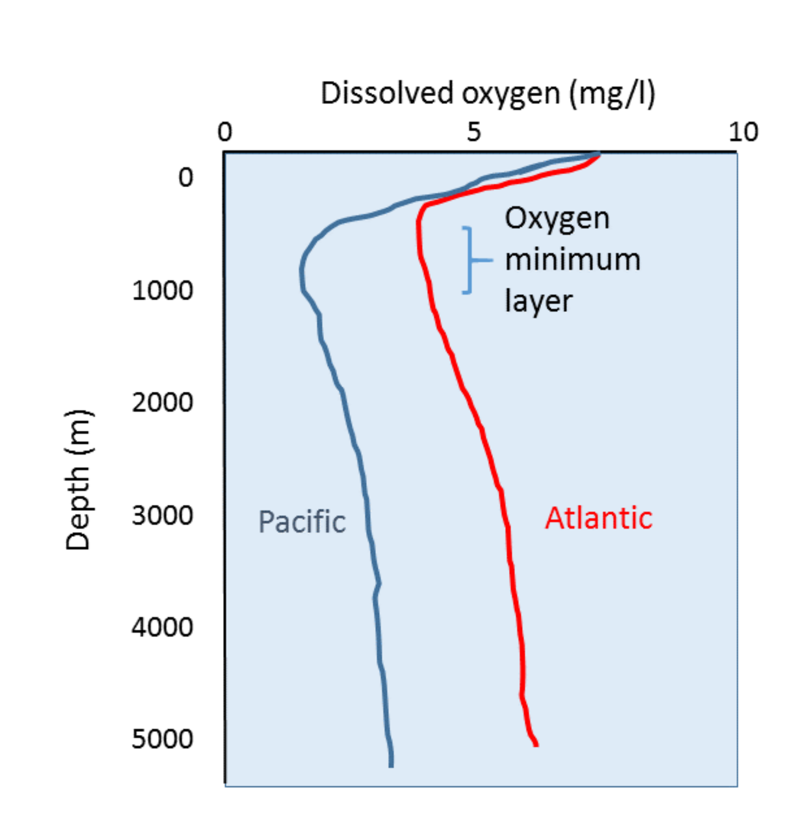
- Aphotic
- Bottom water masses
- Originating from high latitude sinking water

GASSES IN THE OCEANS

- Gasses
  - oxygen (O_2)
  - carbon dioxide (CO_2)
  - nitrogen (N_2)
- Solubility
  - Pressure
  - Temperature
  - Salinity

	Air	Total Ocean	Surface Ocean
N_2	78%	11%	48%
O_2	21%	6%	36%
CO_2	0.04%	83%	15%
Total	99.04%	100%	99%

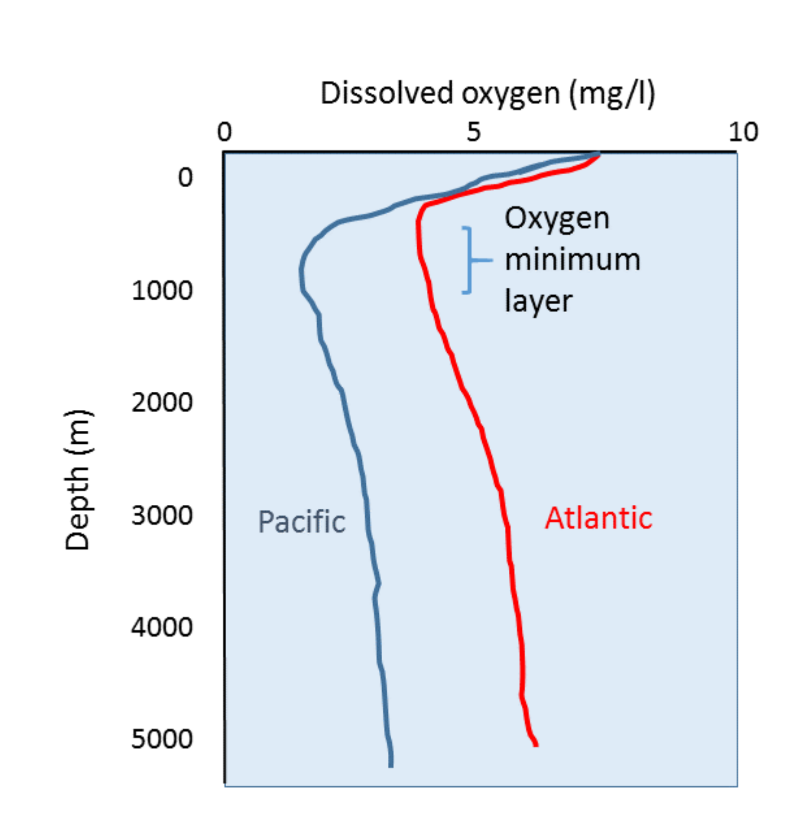
OXYGEN



Dissolved oxygen (mg/l)
0
5
10
0
1000
2000
3000
4000
5000
Depth (m)
Oxygen
minimum
layer
Pacific
Atlantic

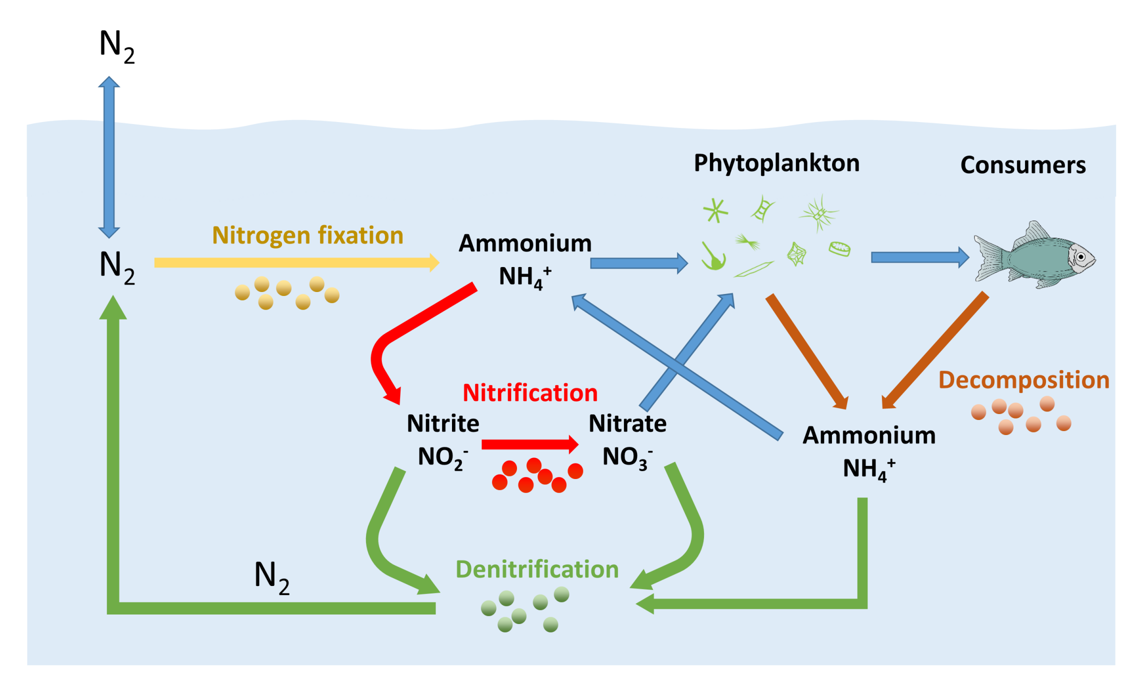
OXYGEN

- Surface
  - exchange from atmosphere
  - Produced by primary productivity
- Oxygen minimum layer
  - No exchange
  - No primary productivity
- Deep water
  - Cold
  - high pressure
  - Ocean circulation



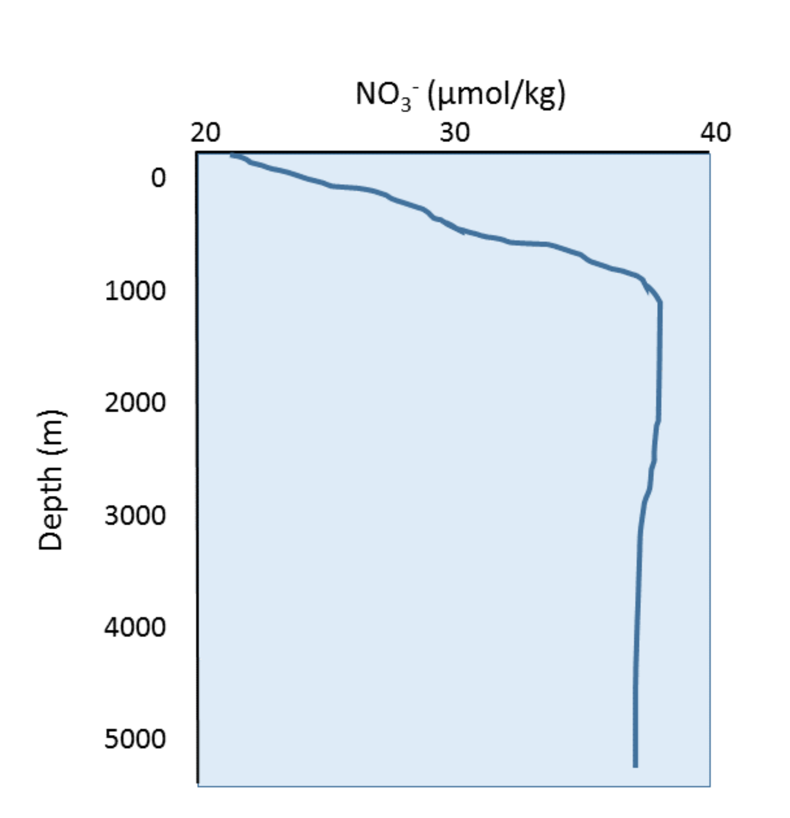
NITROGEN AND NUTRIENTS

- Nitrogen fixation
  - Cyanobacteria
  - Ammonium NH_4+
- Nitrification
  - bacteria
  - Nitrite NO_2-
  - Nitrate NO_3-
- Decomposition
- Denitrification
  - bacteria
  - N_2



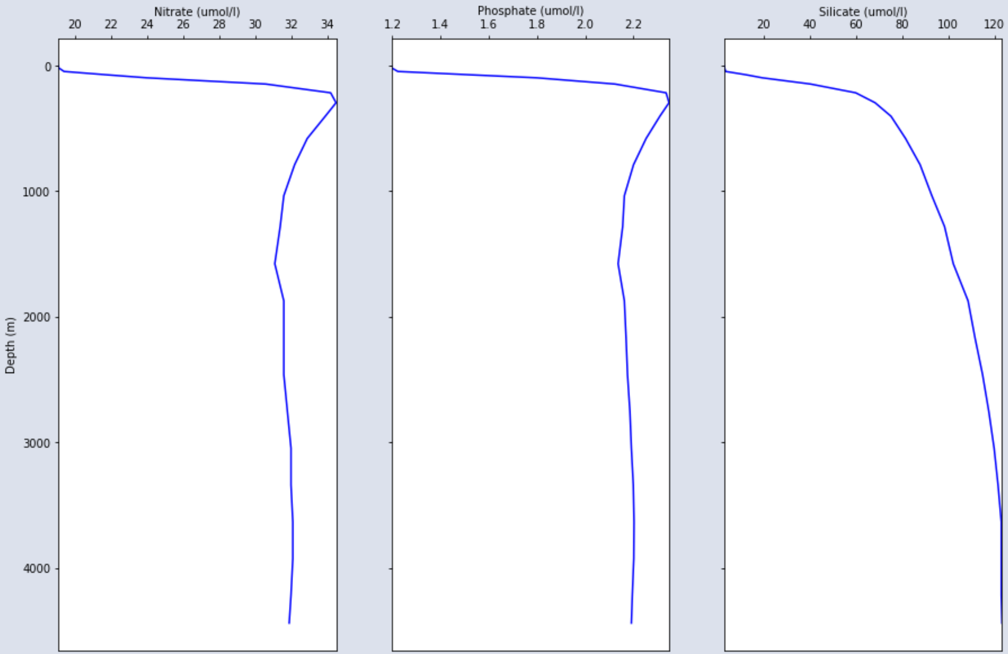
NITROGEN AND NUTRIENTS

- Surface
  - used by primary producers
- Increase with depth
  - No longer consumed
  - No primary productivity
- Deep water
  - Regenerated through decomposition



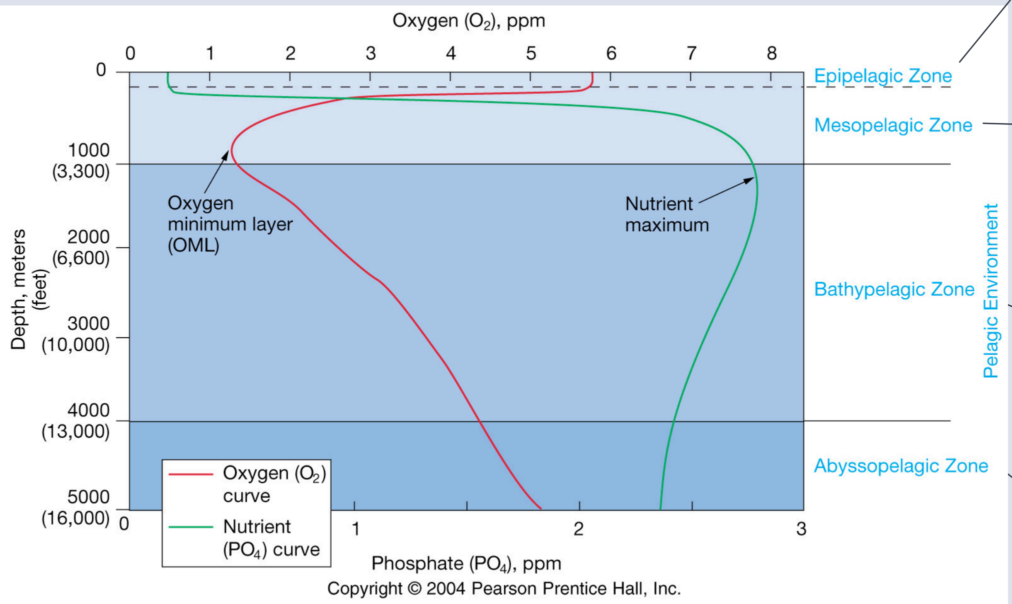
NITROGEN AND NUTRIENTS

- Nitrate
- Phosphate
- Silicate



Nitrate, phosphate, and silicate profiles from an open-ocean location in the South Atlantic (52º S, 35º13'58.8" W), north of South Georgia Island (image by PW, data from 2014, World Ocean Database).

1.2. VERTICAL DISTRIBUTION OF O_2 AND NUTRIENTS



Epipelagic zone (0-200m):

- Low nutrients
- High pO_2

Mesopelagic zone (200 - 1000m):

- ↓ pO_2 (min. ca 700m)
- ↑ nutrients

Bathypelagic zone (1000 - 4000m):

- ↑ pO_2 (>bottom waters)
- ± constant nutrients

Abyssopelagic zone (below 4000m):

- ↑ pO_2 (>bottom waters)
- ± constant nutrients

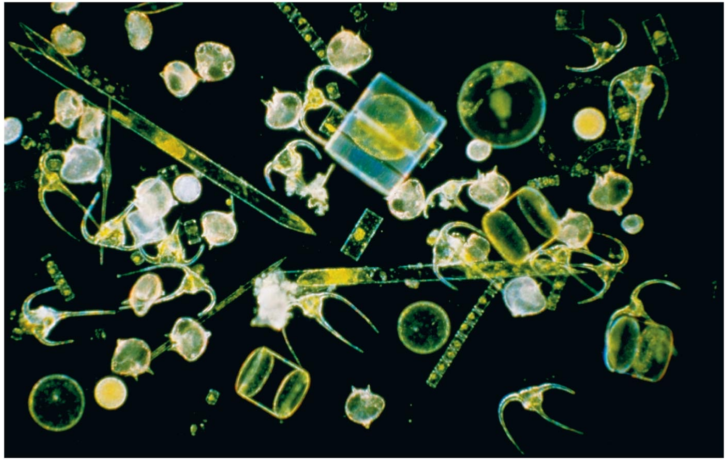
2. PELAGIC BIOLOGICAL PROCESSES

- 2.1 Definitions

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

PLANKTON

- Seston
  - Plankton: Unable to move against currents (dependent on the water mass)
  - Tripton: Particulate organic matter (POM) / marine snow



A.

"Marine snow" Photo: Henk-Jan Hoving/GEOMAR

NEKTON

Nekton:

Able to swim against currents (independent on water masses)

© Bruno de Giusti. An underwater picture taken in Moofushi Kandu, Maldives, showing predator bluefin trevally sizing up schooling anchovies

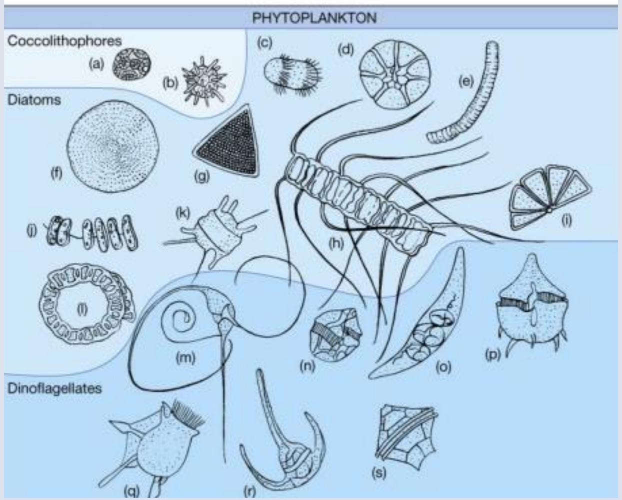
PLANKTON

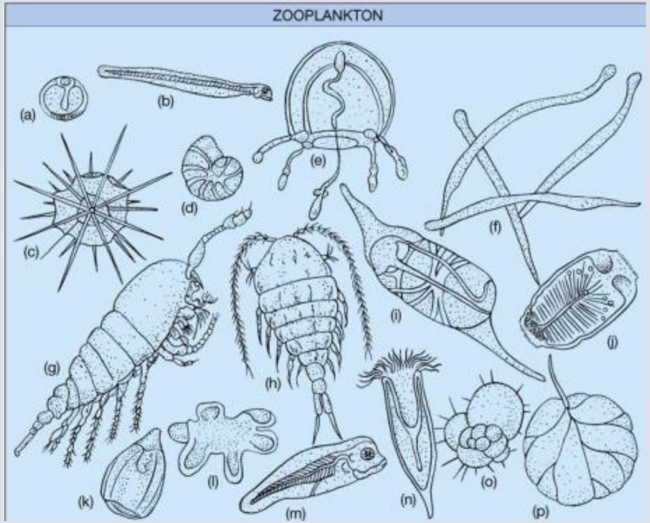
Plankton

Phytoplankton
(autotroph)

Mixoplankton
(Mixotroph)

Zooplankton
(heterotroph)





PLANKTON

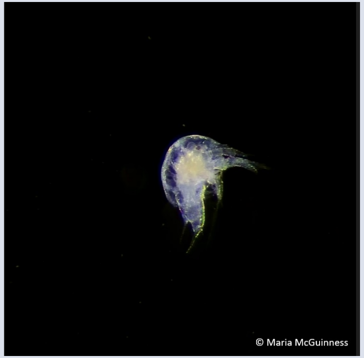
- **Holoplanktonic**: spend their entire life in the plankton, drifting wherever the currents take them.
- copepods, certain jellyfish species, some diatoms and amphipods.

PLANKTON

- **Meroplanktonic** spend only a portion of their life cycle in the plankton.
- larval crabs and lobsters live in the plankton for the first portion of their life until they are large enough to settle on the seafloor.
- copepods, certain jellyfish species, some diatoms and amphipods.
- Larval fish

PLANKTON

- Meroplankton
  - seastar
  - barnacles



2.1. DEFINITIONS

	Ultraplankton	< 2µm
	Nanoplankton	2 – 20 µm
Net Plankton	Microplankton	20 – 200 µm
	Macroplankton	200 – 2000 µm
	Megaloplankton	> 2000 µm
	Mesoplankton	200 – 20000 µm 1000 – 5000 µm

Aquaticlivefood.com.au

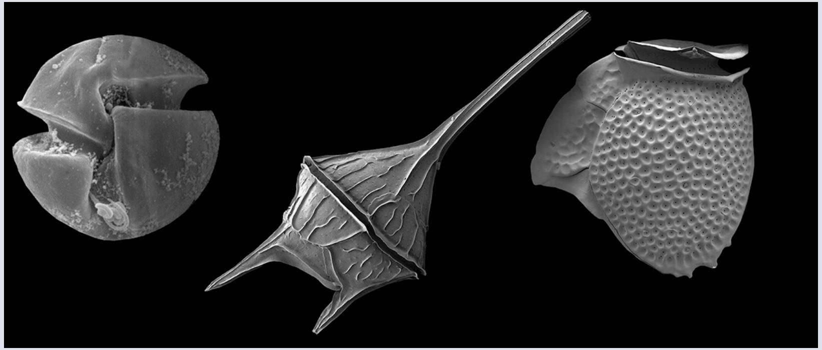
Daylymail.co.uk

Diatoms

- Silicon dioxide box (frustulae)
- Generally larger

dinoflagellates

- Two flagella
- Generally smaller



2.2. PRIMARY PRODUCTION

photosynthesis →

$$6CO_2 + 6H_2O \rightarrow C_6H_{12}O_6 \text{ (carbohydrate)} + 6O_2$$

respiration ←

conversion of inorganic compounds into organic compounds.

Mostly photosynthesis
Some chemosynthesis

2.2. PRIMARY PRODUCTION

- Gross primary productivity: total amount of organic material synthesized during photosynthesis or chemosynthesis.
- Net primary productivity: difference between the gross productivity and the amount of organic material used during respiration.
- Respiration: energy required for metabolic activity

- Net productivity = Gross productivity - Respiration

LIGHT AND DARK BOTTLE TECHNIQUE

14C METHOD

- A known amount of radioactive carbon in the form of bicarbonate is added to a water sample.

- The uptake of carbon by the primary producers is determined by measuring their radioactivity.

STANDING CROP OF PHYTOPLANKTON

- Phytoplankton are free-floating microscopic plants which are the primary producers of the oceanic system.

- In this method, either the number of plankton or the total weight of plankton per unit volume or unit area is measured.

2.2. PRIMARY PRODUCTION

- What are limiting factors?

2.2. PRIMARY PRODUCTION

- Light
- Nutrients

LIGHT

Saturation

Light limiting

Photoinhibition

- UV
- Light induced respiration
- Leakage of organic molecules

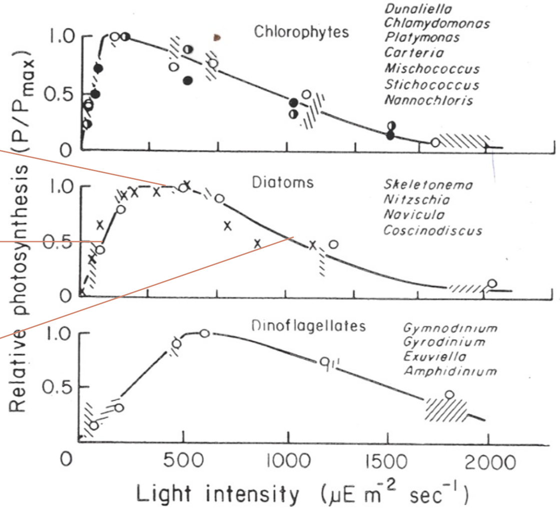
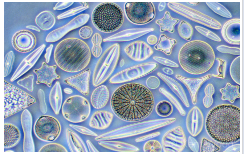
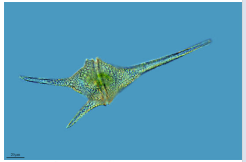


Figure 2-5. Curves of relative photosynthesis (P/P_{max}) versus light intensities for three algal groups. The chlorophytes include green and flagellated greens. Shaded rectangles represent the dispersion of points obtained experimentally using neutral filters in cultures grown with an irradiance of 1.3 μE 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 μE 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

LIGHT

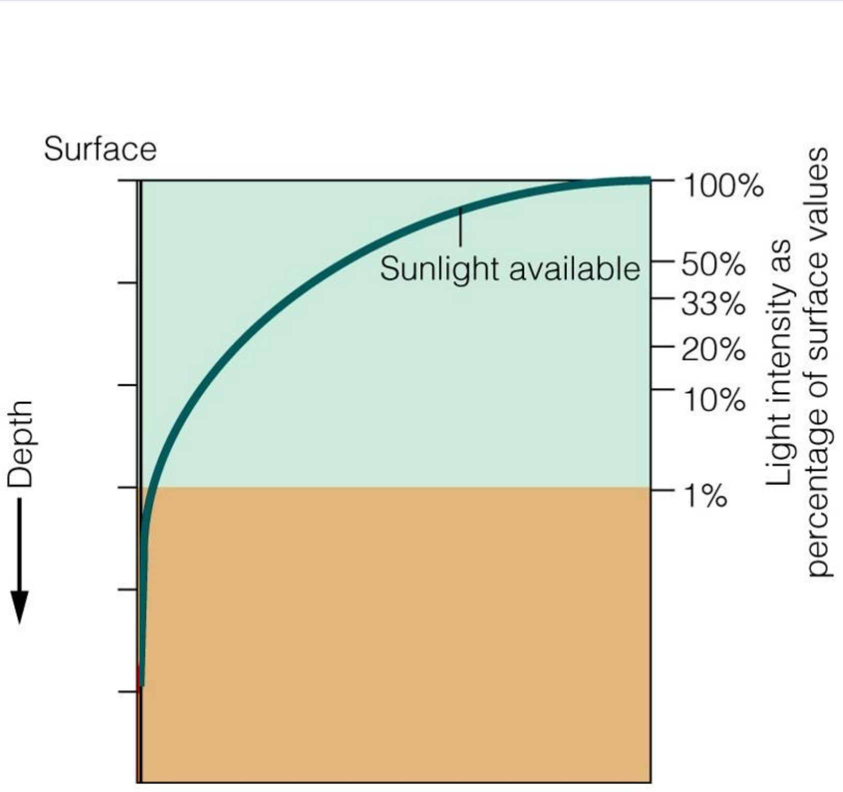
- Sea water absorb the photosynthetic active radiation (PAR)

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

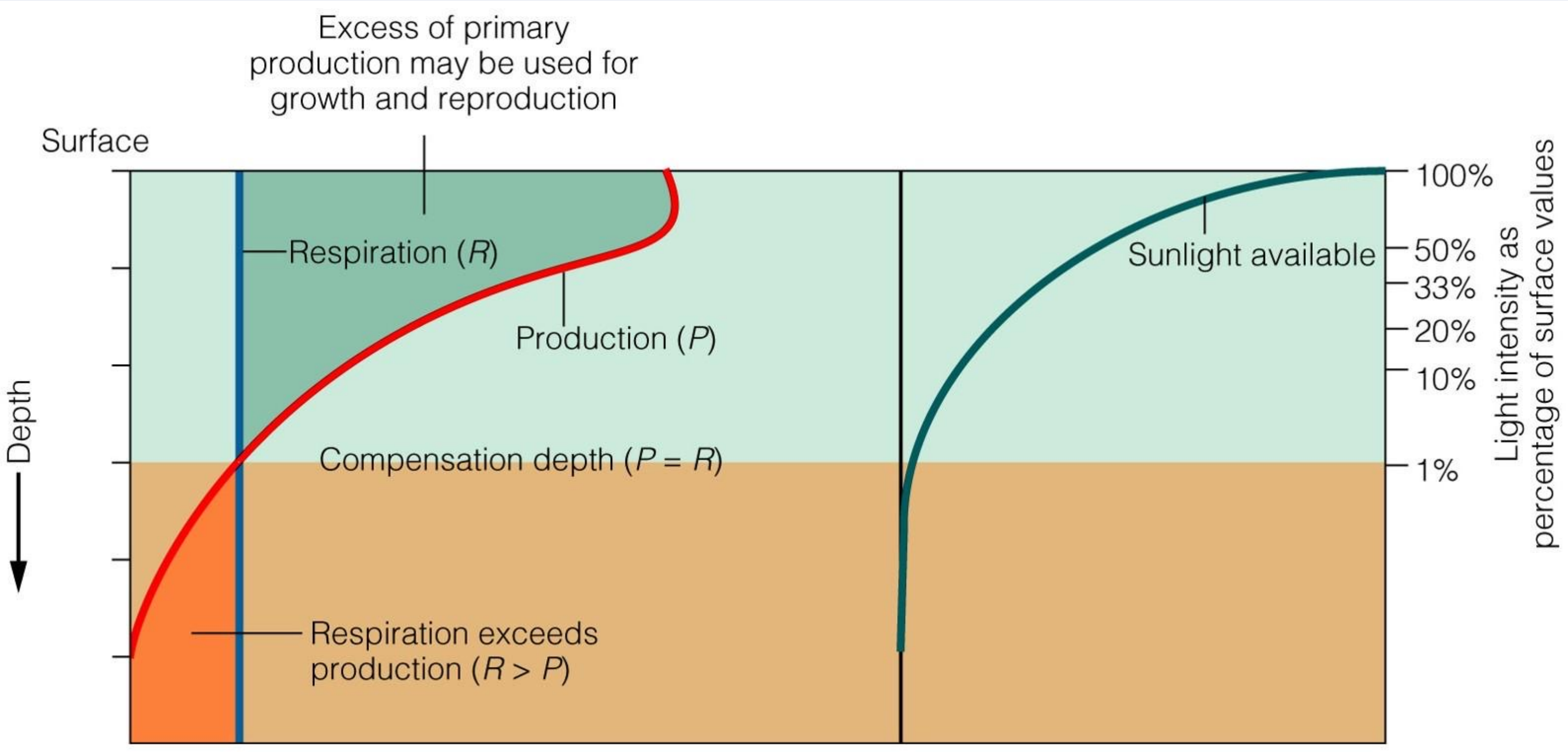
Where k: extinction coefficient

z: depth

I_0: surface PAR



LIGHT

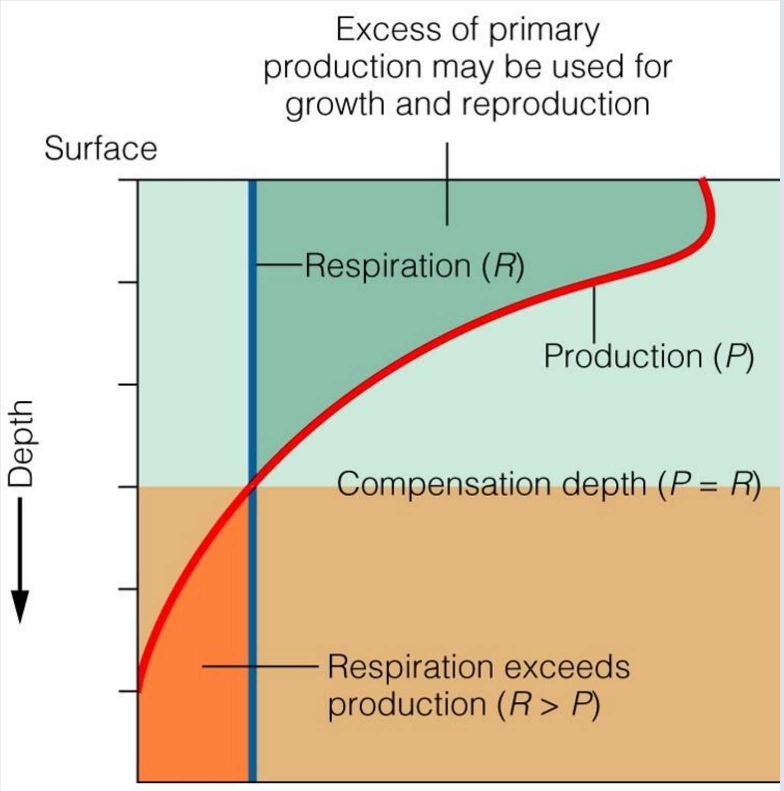


Excess of primary production may be used for growth and reproduction
Surface
Respiration (R)
Production (P)
Depth
Compensation depth (P = R)
Respiration exceeds production (R > P)
Sunlight available
100%
50%
33%
20%
10%
1%
Light intensity as percentage of surface values

LIGHT

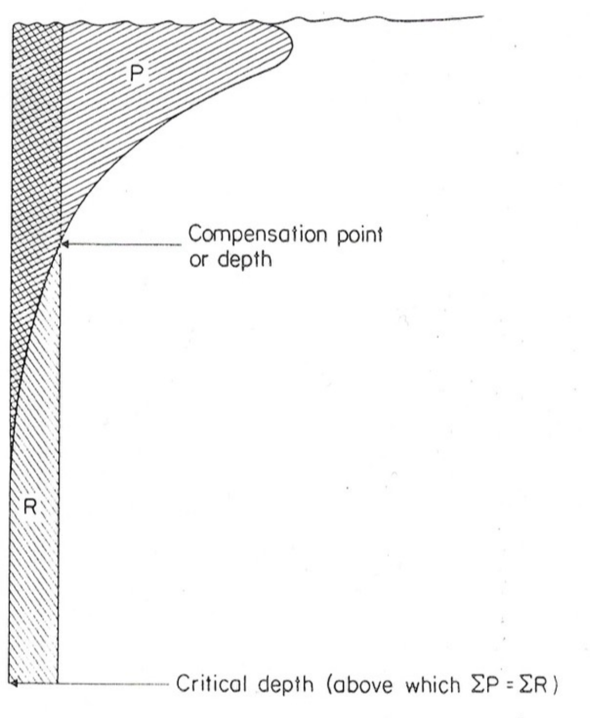
- Sea water absorb the photosynthetic active radiation (PAR)
- But respiration ≠ function of depth

➢ Compensation depth: R = Φ for a particular species



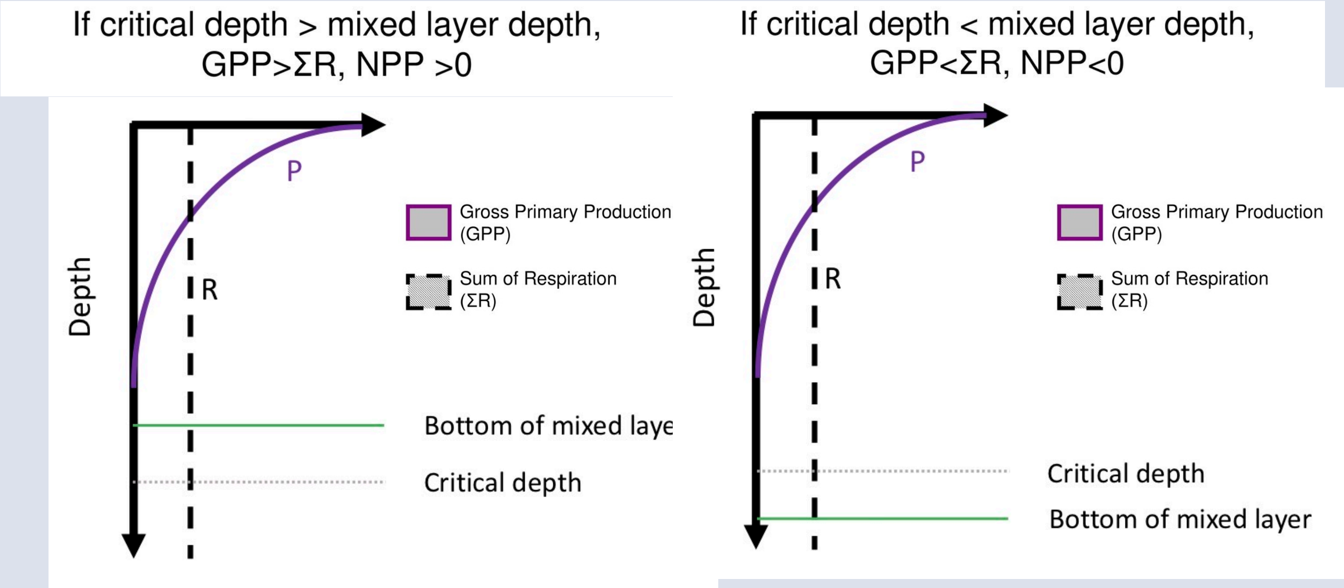
LIGHT

- Critical depth: ΣR = Σ Φ for the whole P1 community (net P1 of the community = 0)



LIGHT + MIXING

- Wind induces mixing of the water column ⟶ mixing depth



NUTRIENTS

- What is a nutrient ?
  - Only for P1, not for consumers !
  - Major nutrients: C, N, P, O, Si, Mg, K, Ca
    - N: proteins

      Inorganic forms in sea water:

      Abundant in sea water

      - NH_4^+ : no reduction necessary → most favorable
      - NO_3^-, $N0_2^-$: 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)

NUTRIENTS

- Uptake

Described by

Michaelis-Menten equation:

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

Vmax= Uptake velocity at saturation

C= nutrient concentration in SW

Ks= nutrient concentration in SW at which V=Vmax/2 (constant)

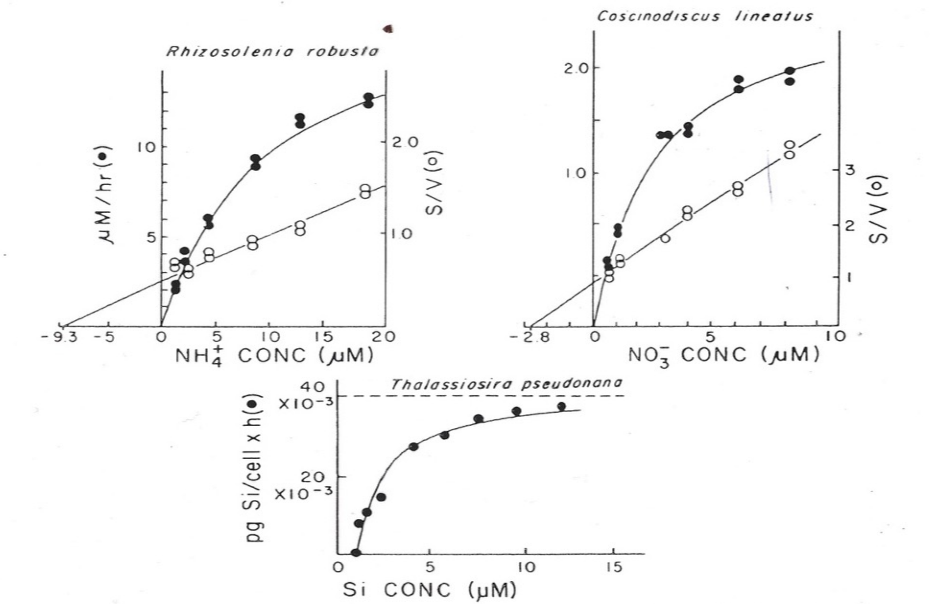
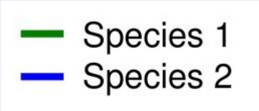


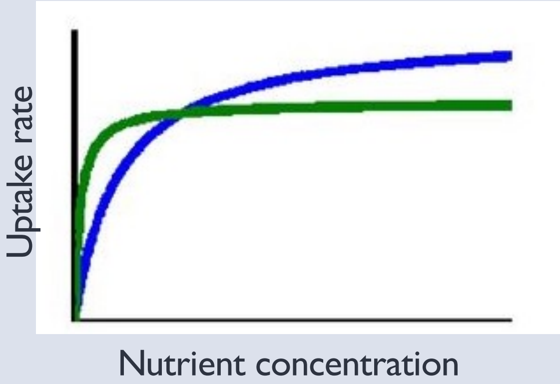
Figure 2-13. Michaelis-Menten curves (filled circles) and Woolf plots (open circles) fitted to data on uptake (μmole/hr) of ammonium, nitrate, and silica by three diatoms at different nutrient concentrations (μmole/liter). S is the concentration of nutrient being taken up, V is the uptake velocity. The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

NUTRIENTS

- Uptake: low and high Ks



Ks1 < Ks2
Vmax1 < Vmax2



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

NUTRIENTS

Ks depends on size

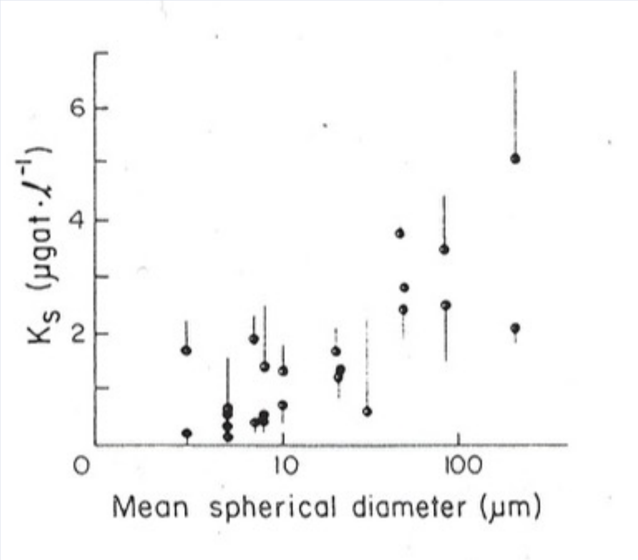


Figure 2-14. Half-saturation (K_s) values for nitrate uptake by phytoplankton of different size. The bars show the 95% confidence limits for the highest and lowest mean K_s reported. Adapted from Malone (1980).

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 ± 95% confidence interval)
Cyclotella nana	Moriches Bay	1.87 ± 0.48
	Edge of shelf	1.19 ± 0.44
	Sargasso Sea	0.38 ± 0.17
Fragilaria pinnata	Oyster Bay	1.64 ± 0.59
	Sargasso Sea	0.62 ± 0.17
Bellerochia spp.	Great South Bay	6.87 ± 1.38
	Off Surinam	0.12 ± 0.08
	Sargasso Sea	0.25 ± 0.18

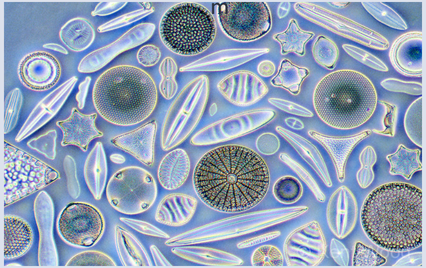
[a] From Carpenter and Guillard (1971). © Ecological Society of America, reprinted by permission.

Valiela 2009

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



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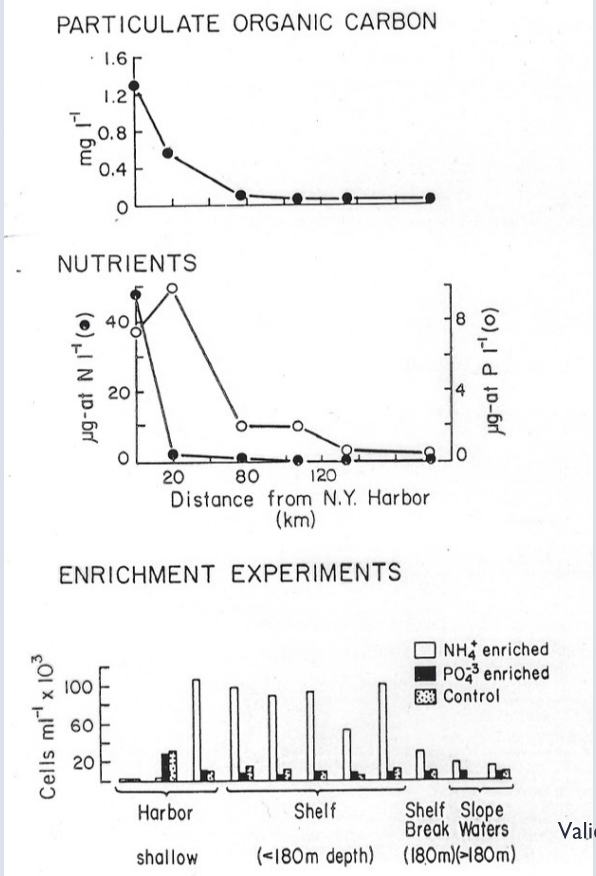
NUTRIENTS N AND P

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.



Valiela 2009

NUTRIENTS N AND P

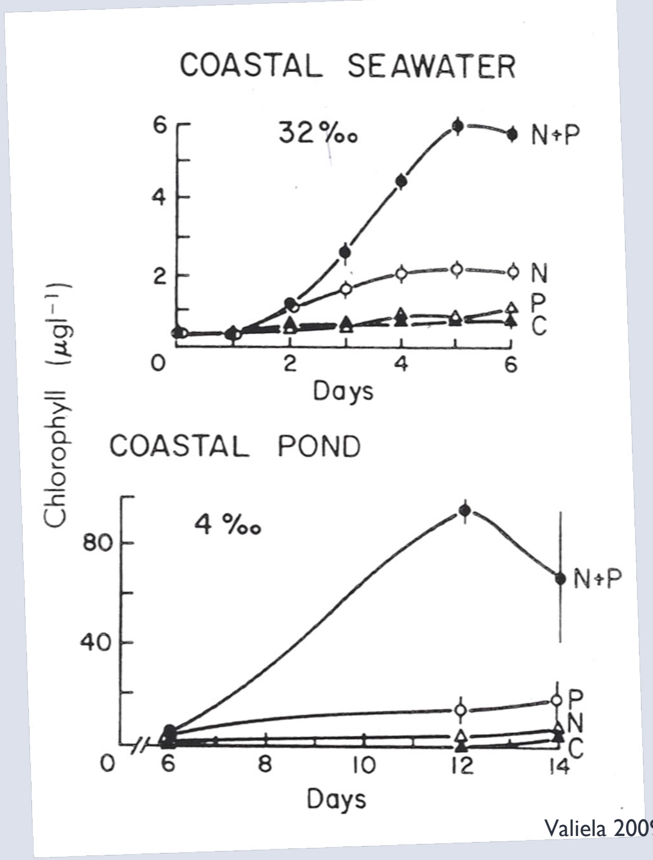
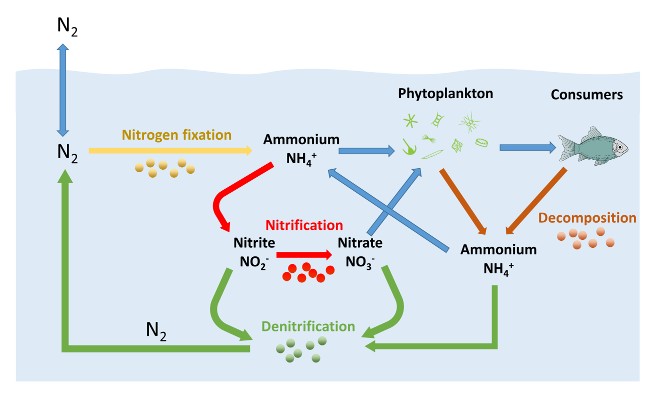


Figure 2-21. Enrichment experiments with coastal seawater of Vineyard Sound (salinity 32‰), Massachusetts, and a freshwater-dominated coastal pond (salinity 4‰) in Falmouth, Massachusetts. N+P, addition of nitrogen and phosphorus; P, addition of phosphorus; N, addition of nitrogen; C, control, no nutrient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

Valiela 2009

NUTRIENTS

- Sources of N (and P)
  1. Fixation of Atmosperic 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 PI: « new production »
- NH_4^+ based PI: « regenerated production »



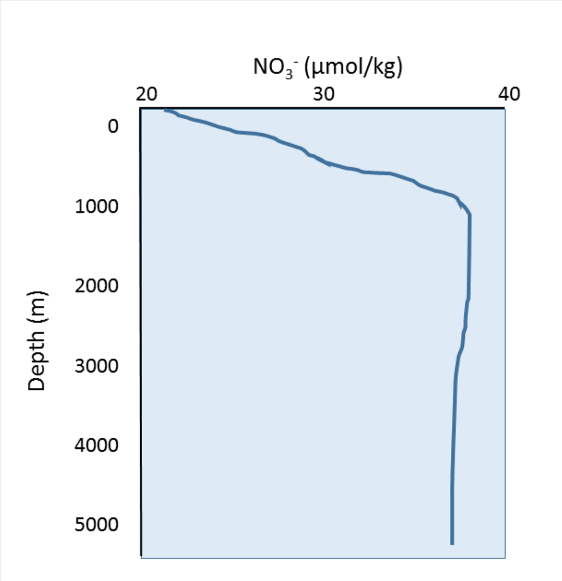
Simplified nitrogen cycle in the ocean. Coloured dots represent the marine bacteria responsible for nitrogen cycling

NUTRIENTS

low at the surface

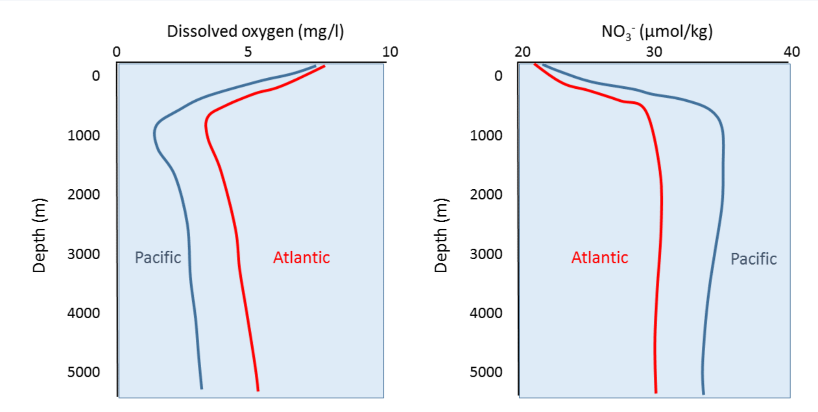
- rapidly consumed
- do not have the chance to accumulate

- 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



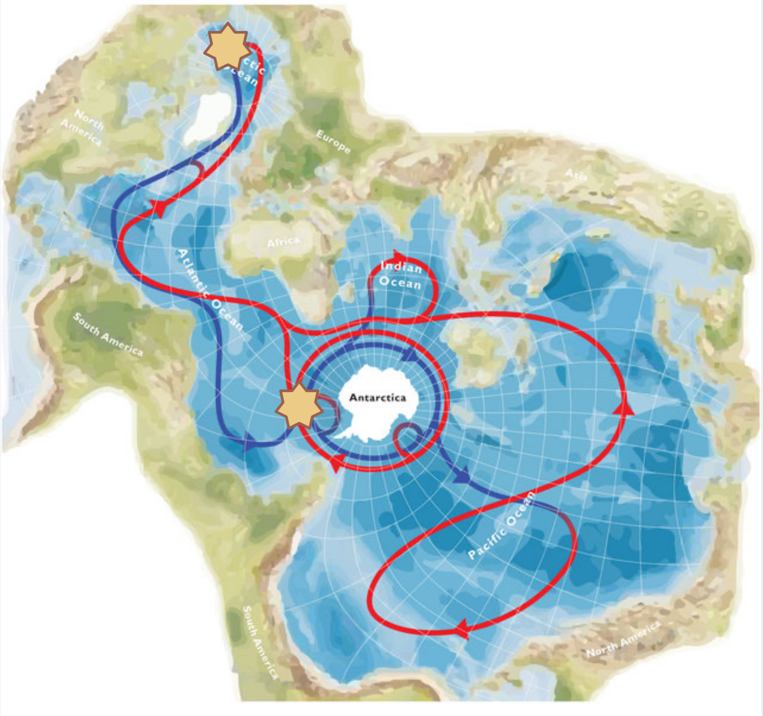
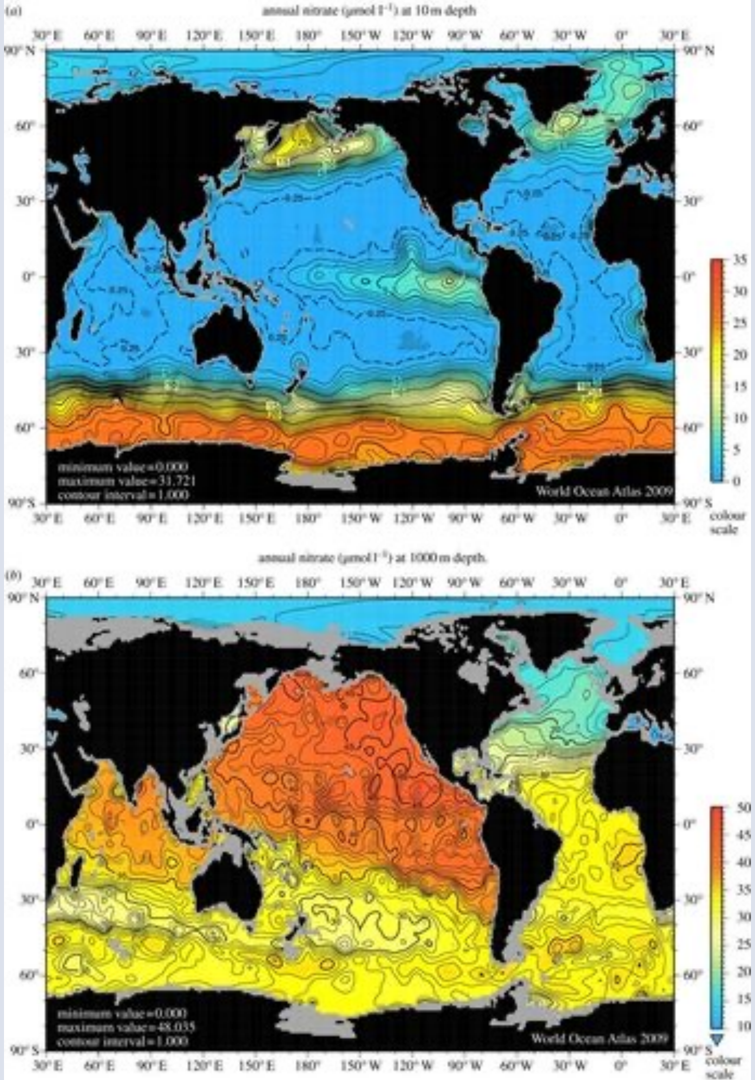


Figure 1. Nitrate concentrations in (*a*) surface waters of the ocean and (*b*) at 1000 m depth



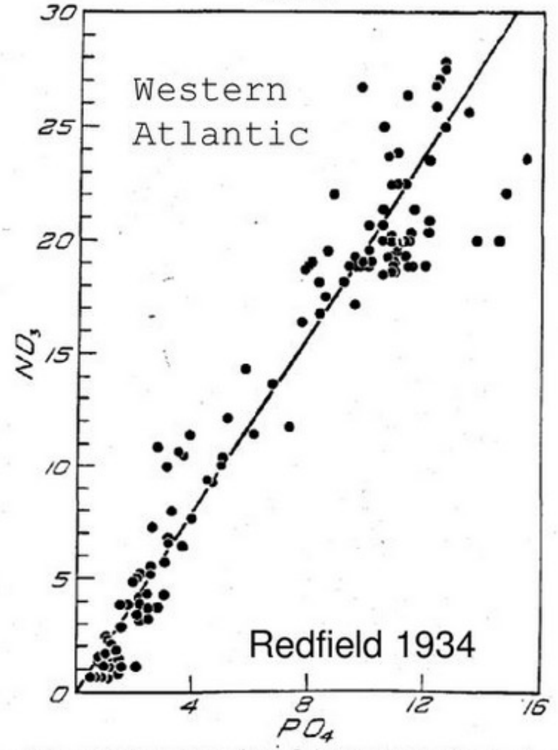
The marine nitrogen cycle: recent discoveries, uncertainties and the potential relevance of climate change, Volume: 368, Issue: 1621, DOI: (10.1098/rstb.2013.0121)

NUTRIENTS C:N:P

- N and P
  - In most marine environments, N is the main limiting nutrient
  - P is limiting in some eutrophicated environments (see later)

NUTRIENTS C:N:P

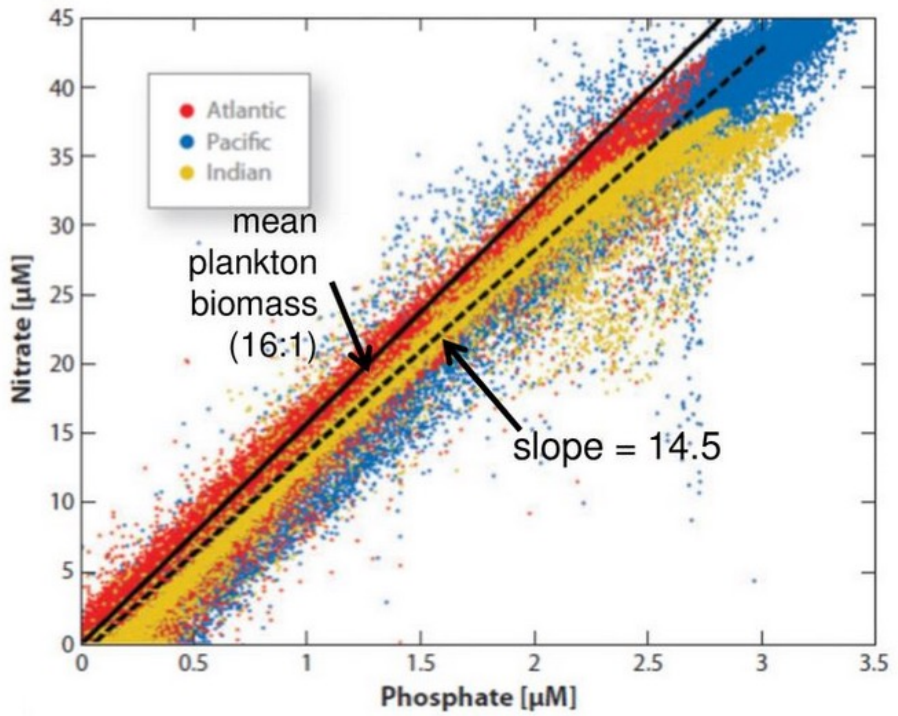
Fig. 1.



Correlation between concentrations of nitrate and phosphate in the waters of western Atlantic Ocean. Ordinate, concentration of nitrate, units 10^{-3} millimols per liter; abscissa, concentration of phosphate, units 10^{-4} millimols per liter. The line represents a ratio of $\triangle N : \triangle P = 20 : 1$ milligram atoms.

NUTRIENTS C:N:P

- 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



Webber & Dutch; Annu. Rev. Marine. Sci. 2012.4:113-141

NUTRIENTS C:N:P

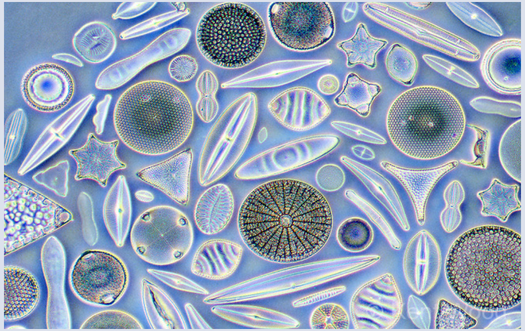
Nitrates (mg/l)

Phosphates (mg/l)	**0.1**	**1.0**	**2.0**	**3.5**	**5.0**	**7.5**	**10.0**	**12.5**	**15.0**	**17.5**	**20.0**	**25.0**	**30.0**	**35.0**	**40.0**	**45.0**	**50.0**
0.01	10.00	100.00	200.00	350.00	500.00	750.00	1000.00	1250.00	1500.00	1750.00	2000.00	2500.00	3000.00	3500.00	4000.00	4500.00	5000.00
0.05	2.00	20.00	40.00	70.00	100.00	150.00	200.00	250.00	300.00	350.00	400.00	500.00	600.00	700.00	800.00	900.00	1000.00
0.1	1.00	10.00	20.00	35.00	50.00	75.00	100.00	125.00	150.00	175.00	200.00	250.00	300.00	350.00	400.00	450.00	500.00
0.2	0.50	5.00	10.00	17.50	25.00	37.50	50.00	62.50	75.00	87.50	100.00	125.00	150.00	175.00	200.00	225.00	250.00
0.3	0.33	3.33	6.67	11.67	16.67	25.00	33.33	41.67	50.00	58.33	66.67	83.33	100.00	116.67	133.33	150.00	166.67
0.4	0.25	2.50	5.00	8.75	12.50	18.75	25.00	31.25	37.50	43.75	50.00	62.50	75.00	87.50	100.00	112.50	125.00
0.5	0.20	2.00	4.00	7.00	10.00	15.00	20.00	25.00	30.00	35.00	40.00	50.00	60.00	70.00	80.00	90.00	100.00
0.6	0.17	1.67	3.33	5.83	8.33	12.50	16.67	20.83	25.00	29.17	33.33	41.67	50.00	58.33	66.67	75.00	83.33
0.7	0.14	1.43	2.86	5.00	7.14	10.71	14.29	17.86	21.43	25.00	28.57	35.71	42.86	50.00	57.14	64.29	71.43
0.8	0.13	1.25	2.50	4.38	6.25	9.38	12.50	15.63	18.75	21.88	25.00	31.25	37.50	43.75	50.00	56.25	62.50
0.9	0.11	1.11	2.22	3.89	5.56	8.33	11.11	13.89	16.67	19.44	22.22	27.78	33.33	38.89	44.44	50.00	55.56
1	0.10	1.00	2.00	3.50	5.00	7.50	10.00	12.50	15.00	17.50	20.00	25.00	30.00	35.00	40.00	45.00	50.00
1.1	0.09	0.91	1.82	3.18	4.55	6.82	9.09	11.36	13.64	15.91	18.18	22.73	27.27	31.82	36.36	40.91	45.45
1.2	0.08	0.83	1.67	2.92	4.17	6.25	8.33	10.42	12.50	14.58	16.67	20.83	25.00	29.17	33.33	37.50	41.67
1.3	0.08	0.77	1.54	2.69	3.85	5.77	7.69	9.62	11.54	13.46	15.38	19.23	23.08	26.92	30.77	34.62	38.46
1.4	0.07	0.71	1.43	2.50	3.57	5.36	7.14	8.93	10.71	12.50	14.29	17.86	21.43	25.00	28.57	32.14	35.71
1.5	0.07	0.67	1.33	2.33	3.33	5.00	6.67	8.33	10.00	11.67	13.33	16.67	20.00	23.33	26.67	30.00	33.33
1.6	0.06	0.63	1.25	2.19	3.13	4.69	6.25	7.81	9.38	10.94	12.50	15.63	18.75	21.88	25.00	28.13	31.25
1.7	0.06	0.59	1.18	2.06	2.94	4.41	5.88	7.35	8.82	10.29	11.76	14.71	17.65	20.59	23.53	26.47	29.41
1.8	0.06	0.56	1.11	1.94	2.78	4.17	5.56	6.94	8.33	9.72	11.11	13.89	16.67	19.44	22.22	25.00	27.78
1.9	0.05	0.53	1.05	1.84	2.63	3.95	5.26	6.58	7.89	9.21	10.53	13.16	15.79	18.42	21.05	23.68	26.32
2	0.05	0.50	1.00	1.75	2.50	3.75	5.00	6.25	7.50	8.75	10.00	12.50	15.00	17.50	20.00	22.50	25.00
2.1	0.05	0.48	0.95	1.67	2.38	3.57	4.76	5.95	7.14	8.33	9.52	11.90	14.29	16.67	19.05	21.43	23.81
2.2	0.05	0.45	0.91	1.59	2.27	3.41	4.55	5.68	6.82	7.95	9.09	11.36	13.64	15.91	18.18	20.45	22.73
2.3	0.04	0.43	0.87	1.52	2.17	3.26	4.35	5.43	6.52	7.61	8.70	10.87	13.04	15.22	17.39	19.57	21.74
2.4	0.04	0.42	0.83	1.46	2.08	3.13	4.17	5.21	6.25	7.29	8.33	10.42	12.50	14.58	16.67	18.75	20.83
2.5	0.04	0.40	0.80	1.40	2.00	3.00	4.00	5.00	6.00	7.00	8.00	10.00	12.00	14.00	16.00	18.00	20.00

BREAK

NUTRIENTS: SI

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



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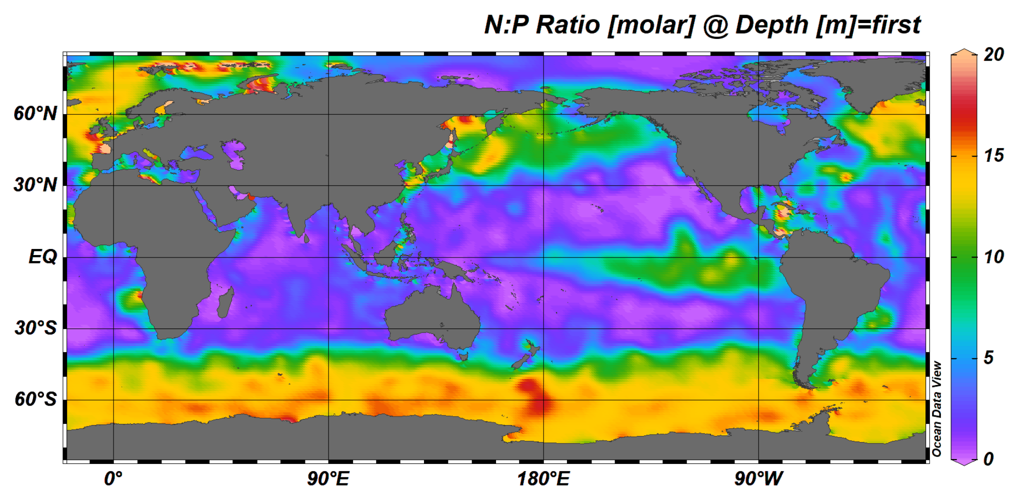
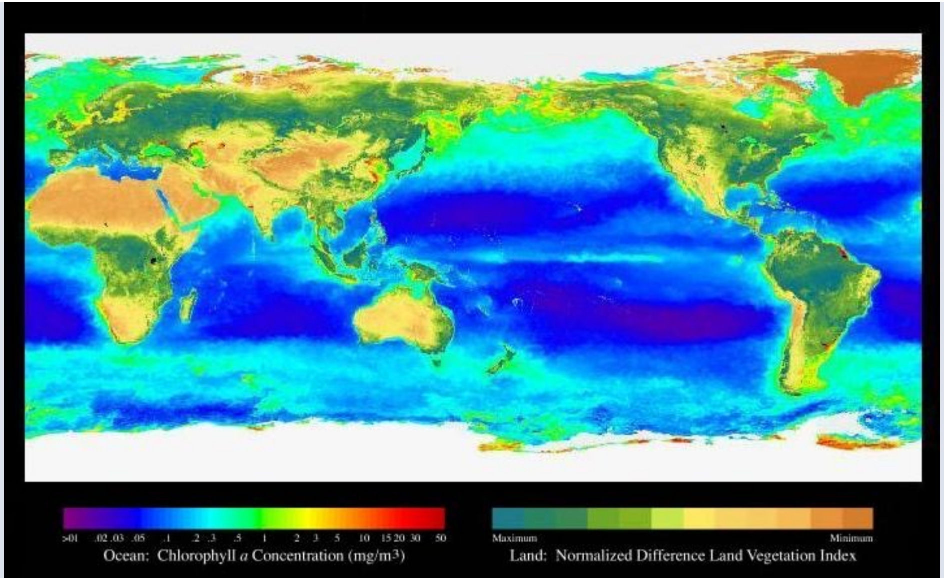
m

NUTRIENTS FE

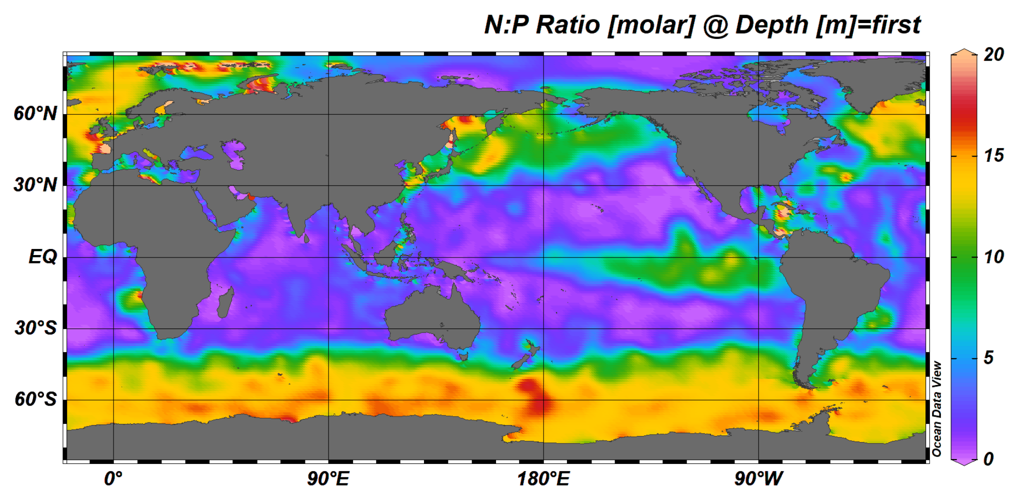
- Component of ferredoxin involved in electron transfer from photosystem I to $NADP^+$
- From terrestrial origin (rivers, airborne) ←→
  - high concentrations (1 – 3 nM) in coastal zones,
  - low to very low concentrations (<1 – 0.06 nM) in oceanic zones



Global nitrogen to phosphorus ratio is plotted for the global surface ocean



Global distribution of surface chlorophyll levels. Chlorophyll (a proxy for phytoplankton mass



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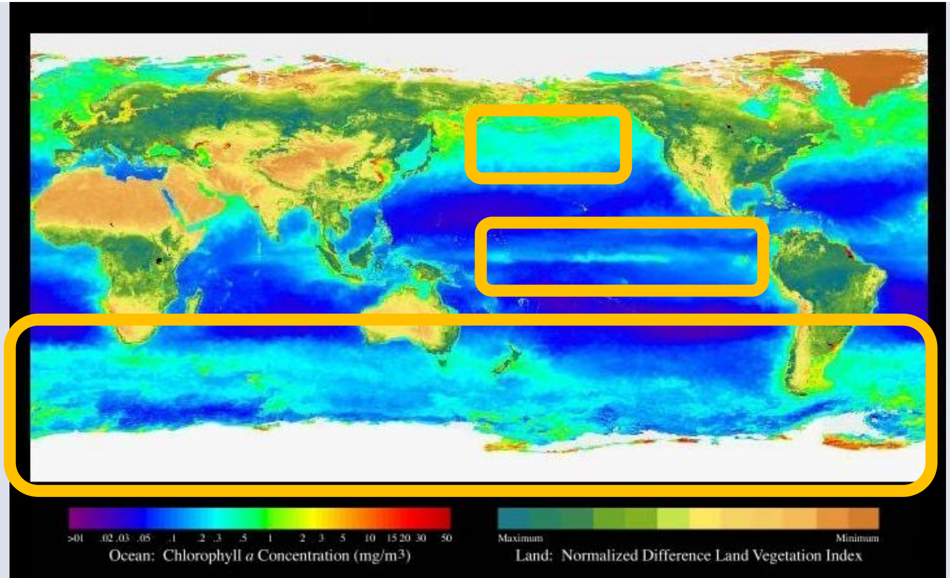


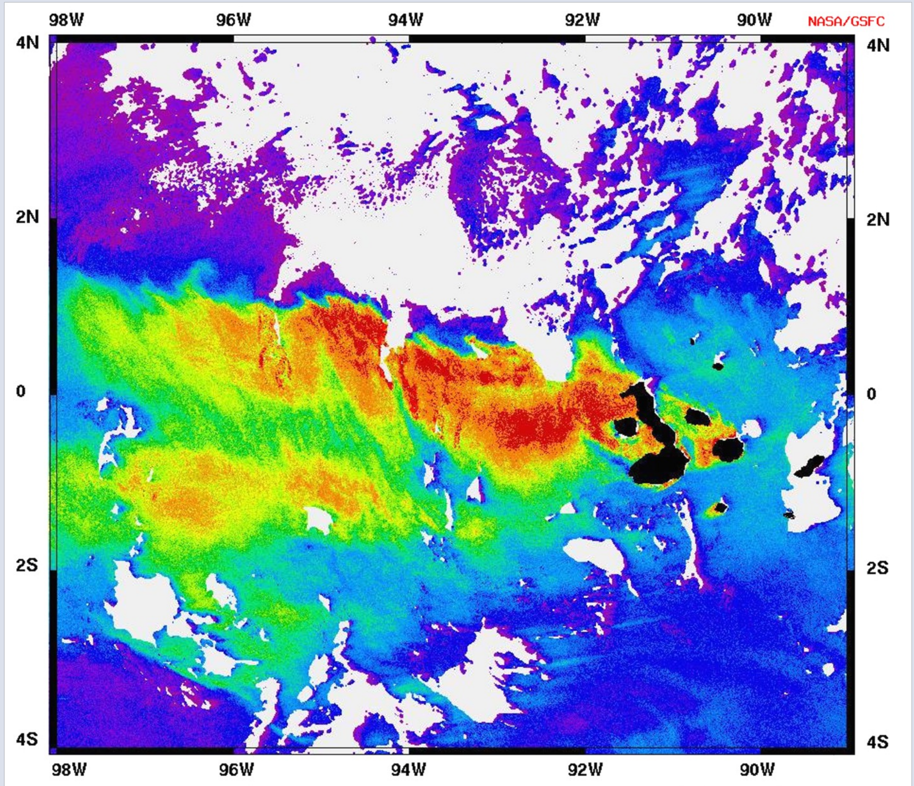
Global distribution of surface chlorophyll levels. Chlorophyll (a proxy for phytoplankton mass

NUTRIENTS FE

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

NUTRIENTS FE

- First demonstrated as limiting in the equatorial Pacific



CZCS-derived Phytoplankton Pigment Concentration (10/31/83)

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.

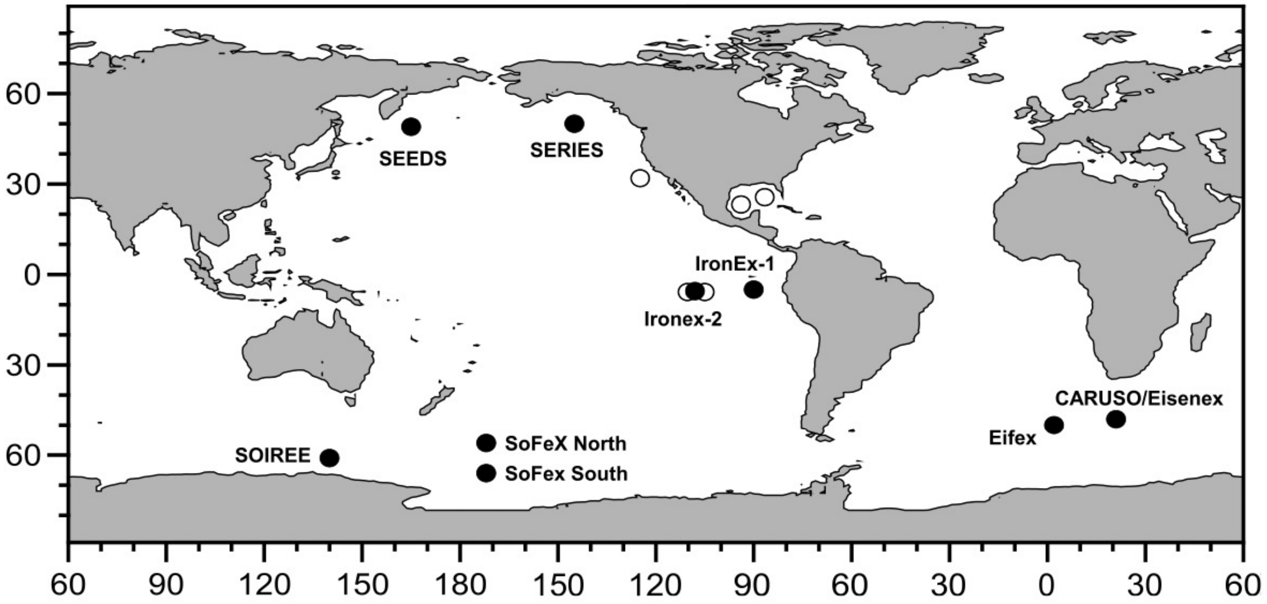
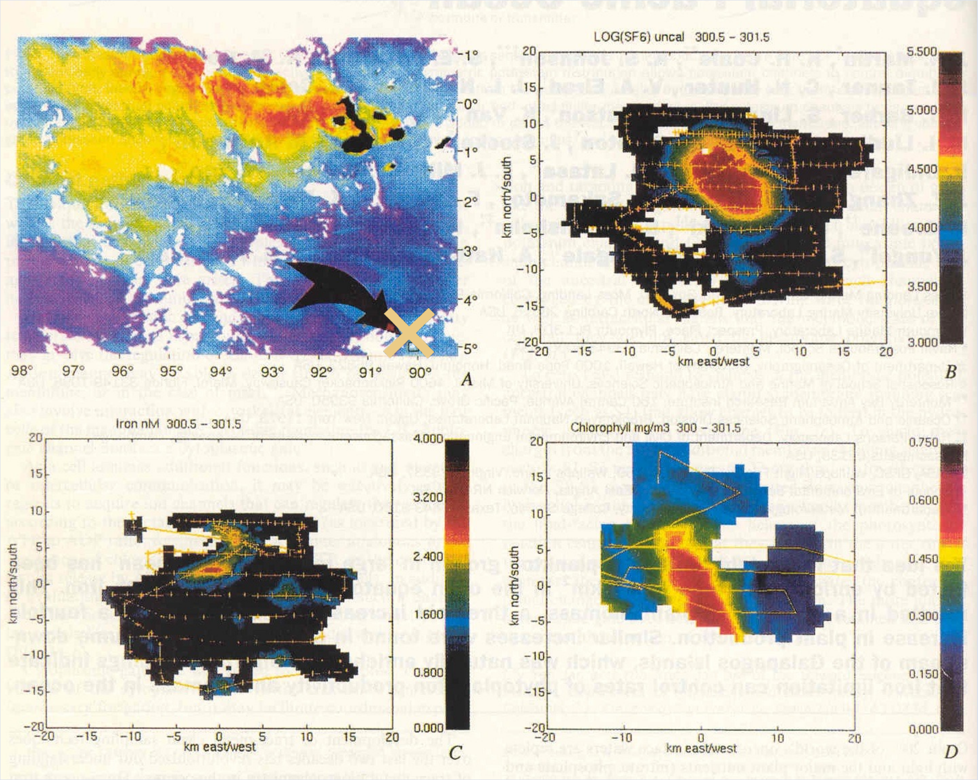


Figure 2. Chart showing the locations (filled circles) of the nine in situ Fe enrichment experiments conducted thus far. Moreover, also indicated are the open circle off California for the IronEx test site [*Coale et al.*, 1998], two open circles for two extra patches during IronEx-2 not further discussed here, and two experiments GreenSea 1 and 2 at unknown positions in the Gulf of Mexico [*Markels and Barber*, 2001].

NUTRIENTS FE

Field Fe enrichment experiment (64 km^2)
IronEx1: single enrichment

YD 301 = 28 oct



Nature 371: 124 (1994)

NUTRIENTS FE

IronEx1

P1: x4
Chla: X3

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 $H^{14}CO_3^-$ uptake determined at various light levels, in incubations on board the ship. Chlorophyll was determined from filtered and extracted samples as in Fig. 1*D*. The errors associated with the chlorophyll analyses are generally <0.02 μg 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.

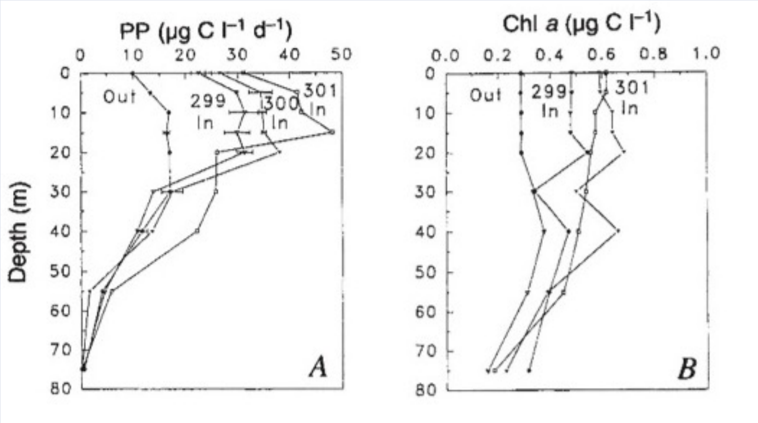
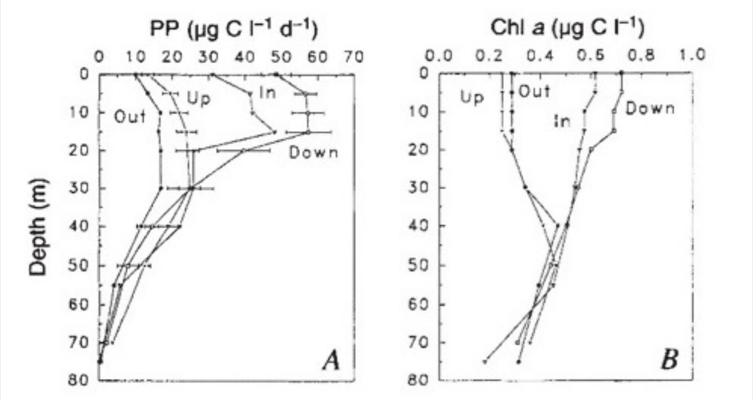


FIG. 4 Comparison of vertical profiles of primary production (*A*) and chlorophyll *a* concentrations (*B*) for stations inside and outside the fertilized patch, and stations upstream (westward) of the Galapagos Islands and downstream (eastward) of the Galapagos Islands.



Nature 371: 124 (1994)

NUTRIENTS FE

IronEx2

Chla: X27

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

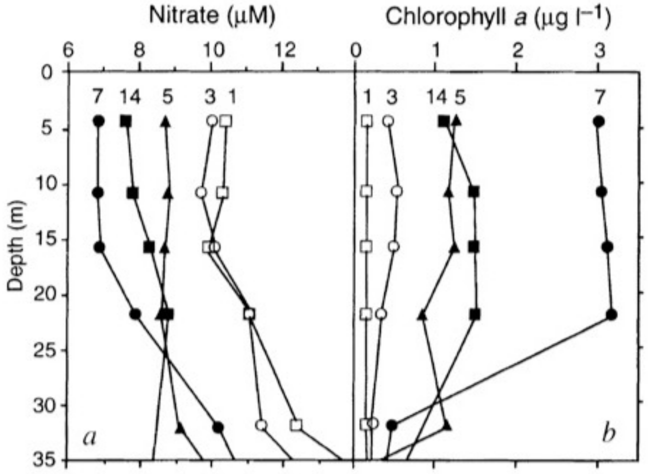


FIG. 3 *a*, Vertical profiles of mixed-layer nitrate from the daily 'inside-patch' stations of patch 1. Numbers at the top of each profile indicate the day of the patch 1 experiment. These plots illustrate the depletion of nitrate as the bloom reached its peak near days 7–9. The subsequent increase (day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

Nature 383: 495 (1996)

NUTRIENTS FE

IronEx2

And the winners are diatoms

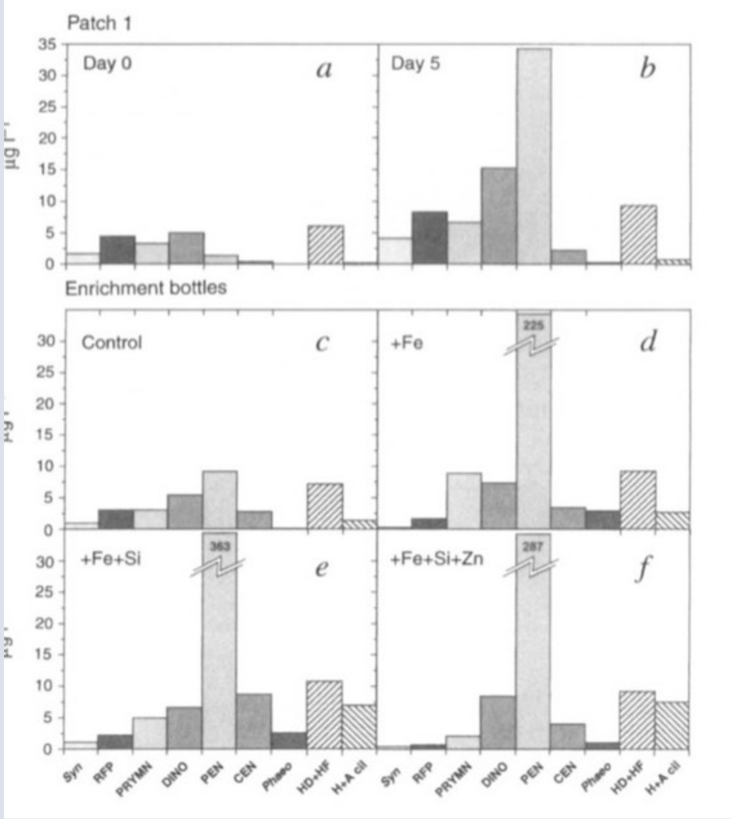
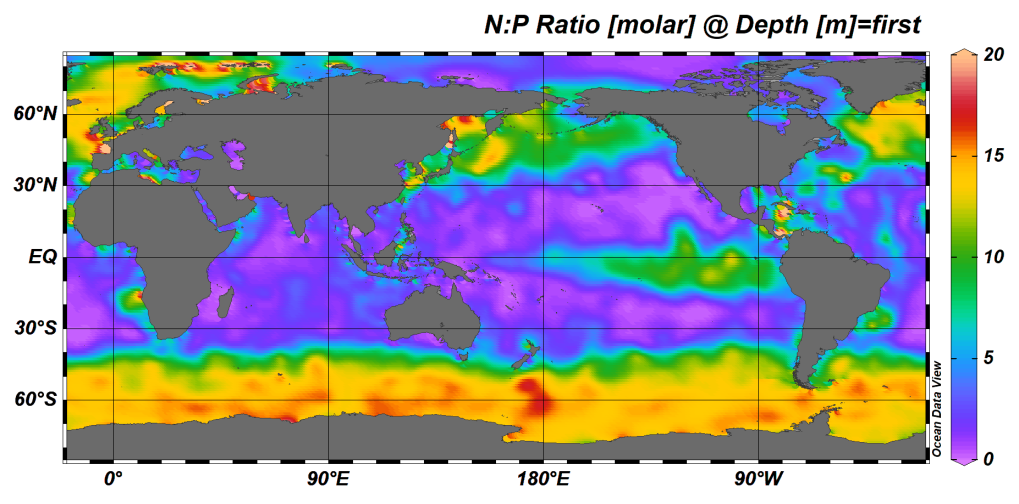
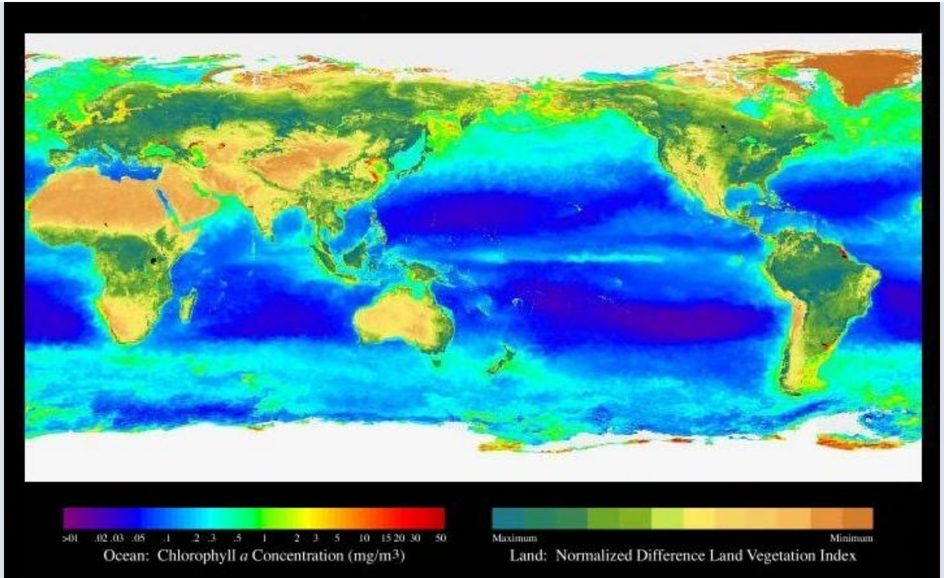


FIG. 4 *a*, Plankton community composition within patch 1 at day 0 of the experiment as expressed in μg C l^{-1}. This composition is similar to that observed at the 'outside-patch' stations over time. The groups represented include: *Syn*, *Synechococcus* spp.; RFP, red fluorescing picoplankton; PRYMN, 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 carboys[8] 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.

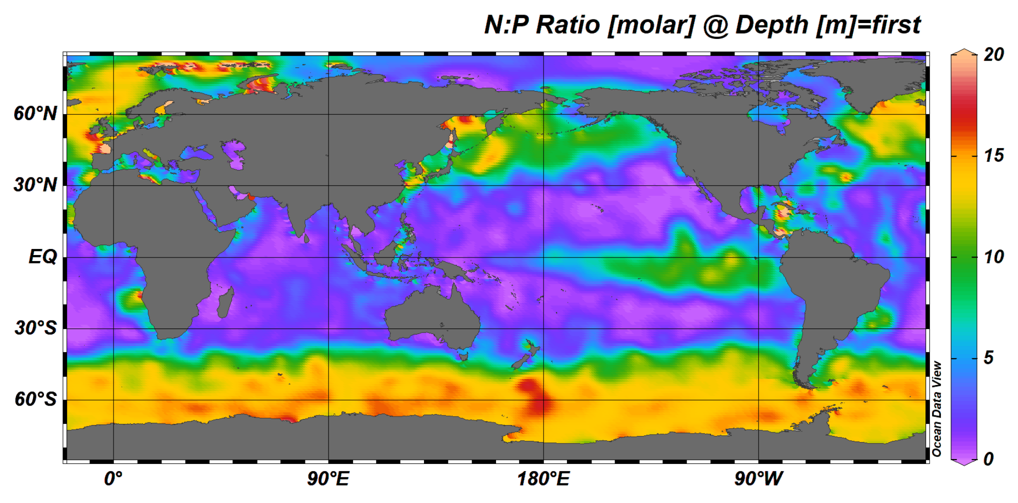
Nature 383: 495 (1996)



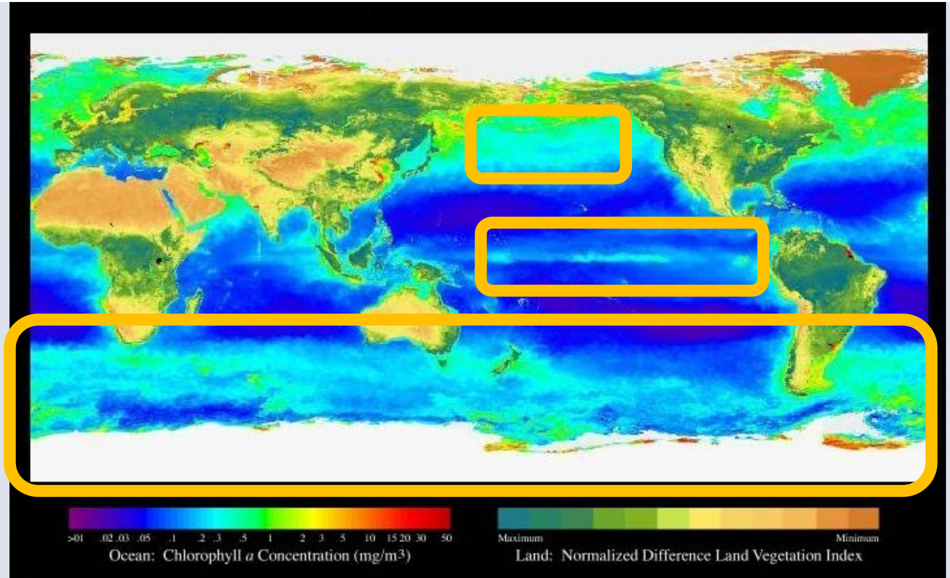
Global nitrogen to phosphorus ratio is plotted for the global surface ocean



Global distribution of surface chlorophyll levels. Chlorophyll (a proxy for phytoplankton mass



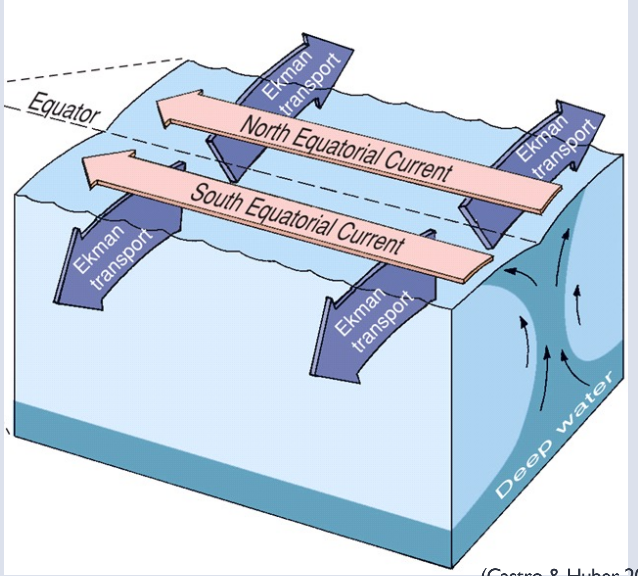
Global nitrogen to phosphorus ratio is plotted for the global surface ocean



Global distribution of surface chlorophyll levels. Chlorophyll (a proxy for phytoplankton mass

NUTRIENTS FE

- Principal HNLC Fe limited regions:
  - North Pacific
  - 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

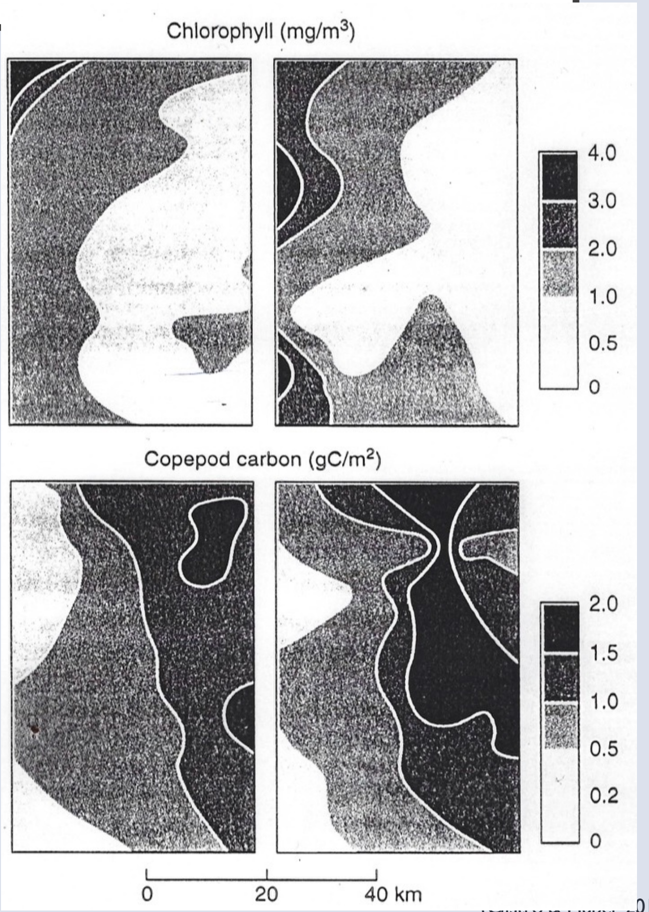


Fig. 9.13 Distribution of chlorophyll *a* and copepod carbon on a survey in the North Sea, showing an inverse relationship between phytoplankton and zooplankton standing stock. Phytoplankton are most abundant toward the left, whereas zooplankton are most abundant toward the right. (Modified from Steele,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

(Castro & Huber 2010)
Levinton 1995

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]

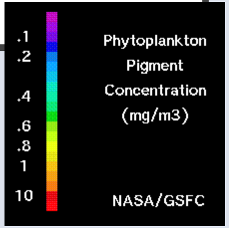
	Percentage of prod. eaten by herbivores	Number of trophic steps	Source
Phytoplankton			
Long Island Sound, USA	73[f]	4	Riley (1956)
Narragansett Bay, USA	0–30[g]	4	Martin (1970)
Cochin Backwater, India	10–40		Qasim (1970)
Beaufort Sound, USA	1.9–8.9		Williams et al. (1968)
Offshore California	7–52 (ave. 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)

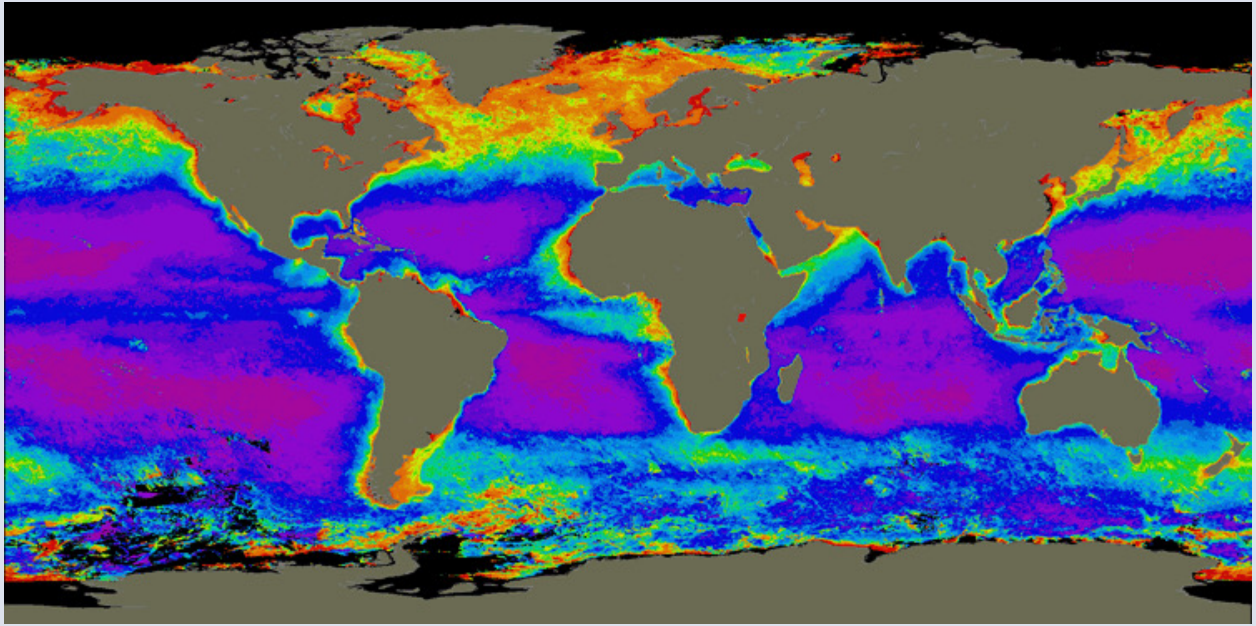
[a] Annual consumption except where indicated otherwise. These values are rough but best possible estimates based on many assumptions and extrapolations.
[b] Leaves only; 0.5–1.4% of total production is consumed by herbivores (Bray, 1961).
[c] This considers grass–cattle–man as the food chain.
[d] Includes 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.

Valiela 2009

SPACE

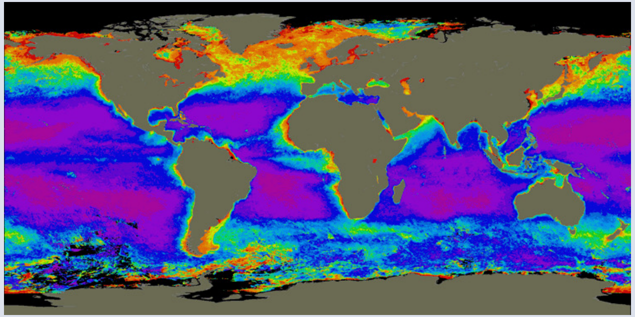
- Hydrographic factors

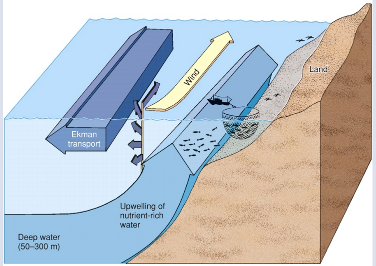


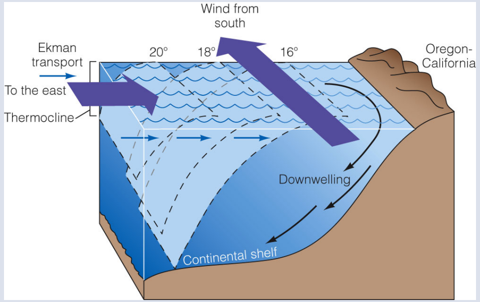


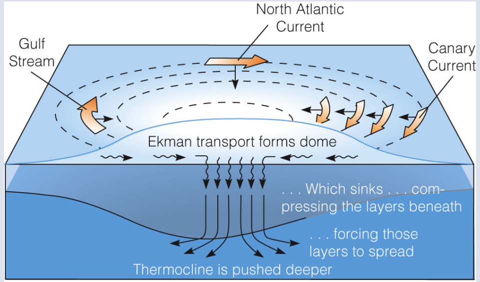
SPACE

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









(Castro & Huber 2010)

HARMFUL ALGAE BLOOMS

- Blooms can harm people, animals, and the environment when they
- Produce toxins (poisons)
- Become too dense
- Use up the oxygen in the water
- Release harmful gases

A harmful algal bloom offshore of San Diego County, California. (NOAA, With permisson from Kai Schumann)

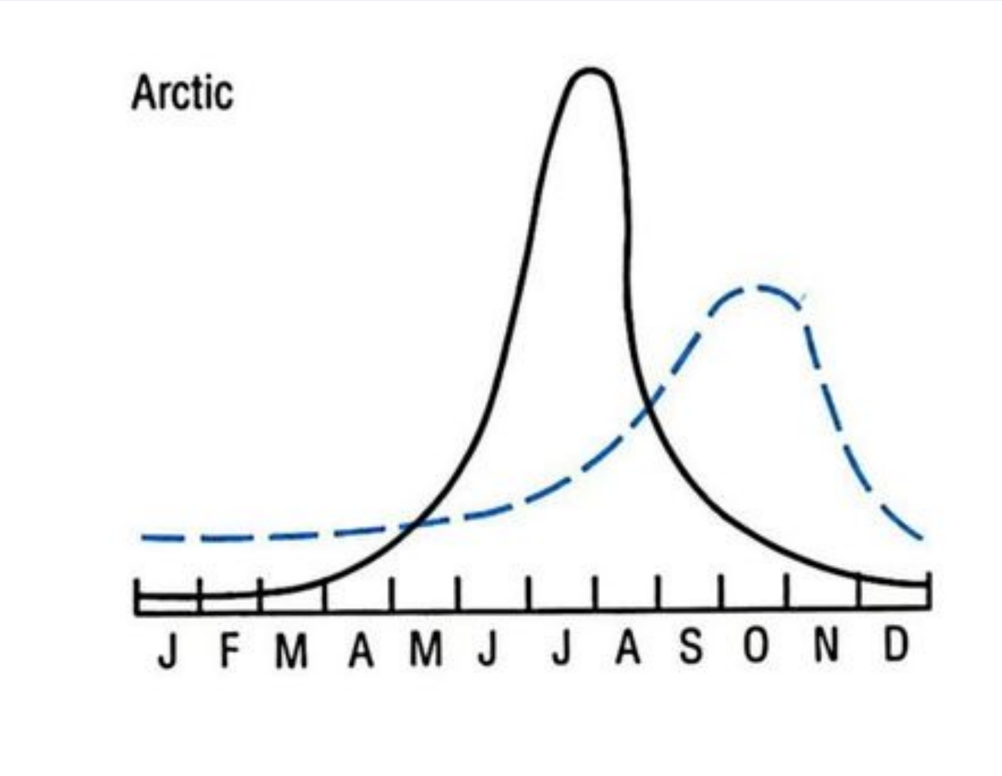
HARMFUL ALGAE BLOOMS

- Cyanobacteria (sometimes called blue-green algae) (freshwater)
- Dinoflagellates (sometimes called microalgae or red tide)
- Diatoms (sometimes called microalgae or red tide)

SEASONAL PATTERNS

Phytoplankton biomass

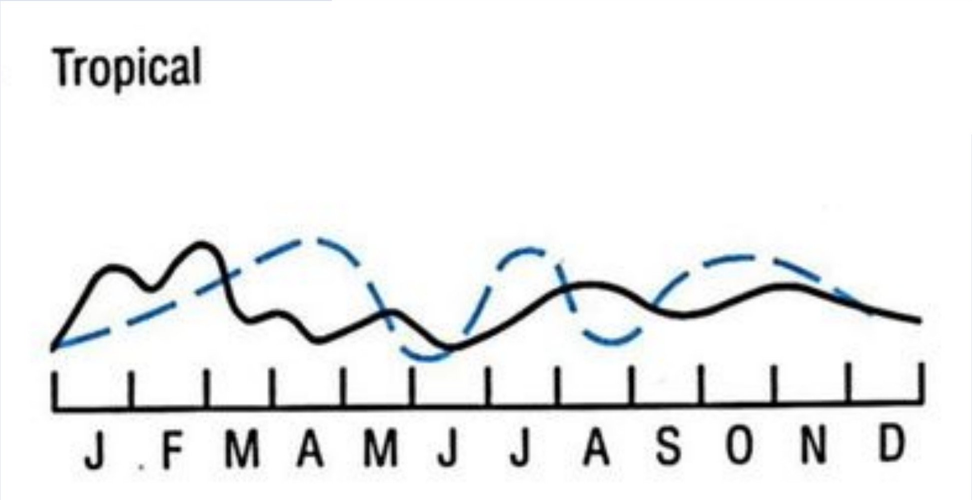
Zoooplankton biomass



SEASONAL PATTERNS

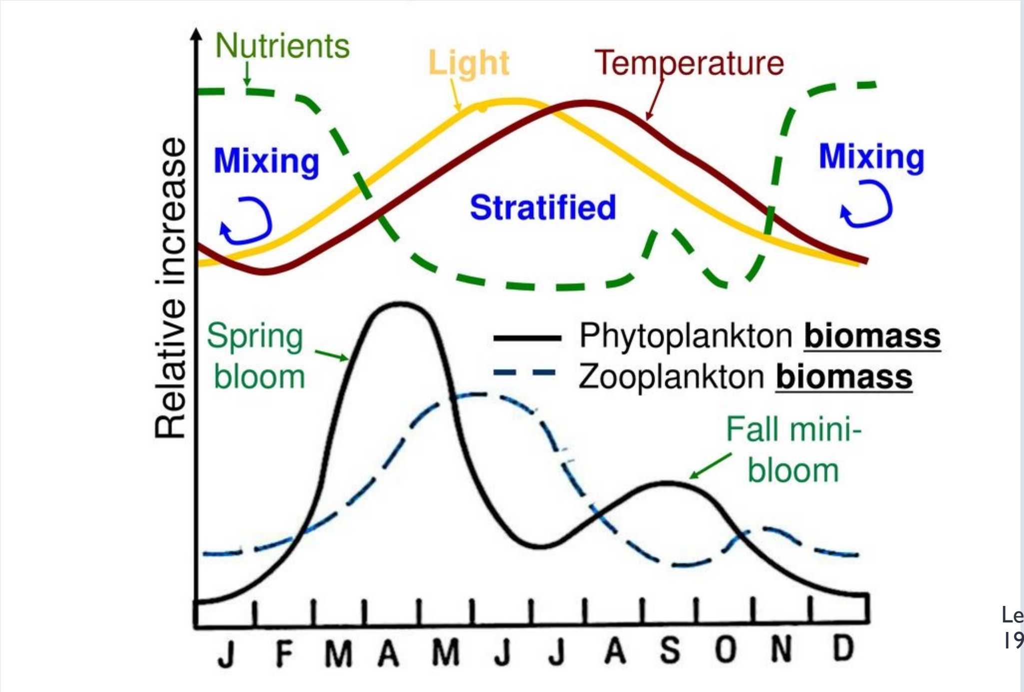
Phytoplankton biomass

Zoooplankton biomass



SEASONAL PATTERNS

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



Levinton 1995

SEASONAL PATTERNS

- Temperate North Atlantic (eutrophicated conditions)

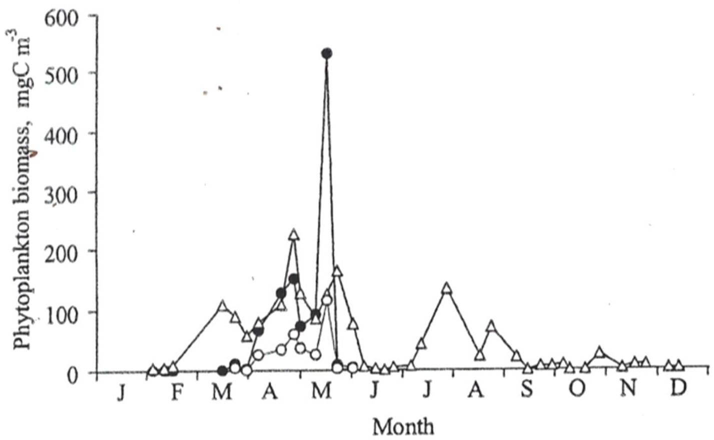


Fig. 1. Seasonal changes of diatoms (△), *Phaeocystis* colony (●) and cellular (○) C biomass measured at Stn 330 of Belgian coastal waters in 1995

Rousseau et al 2002

SEASONAL PATTERNS

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

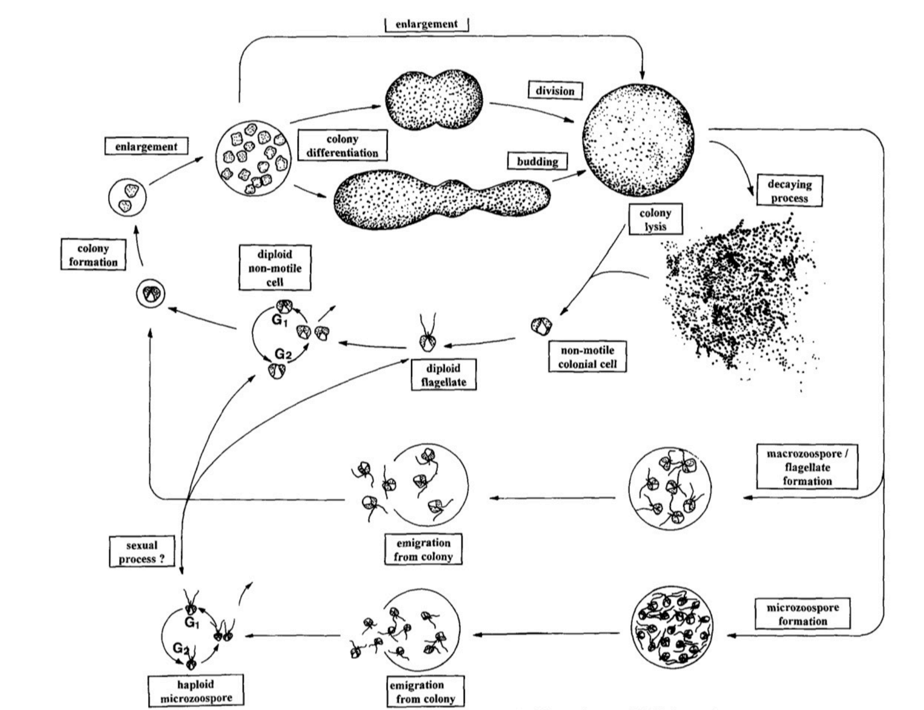


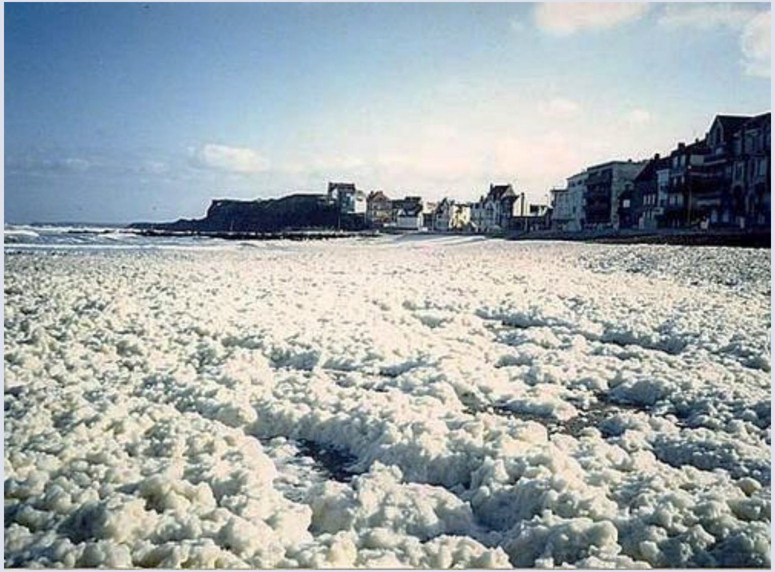
Fig. 9. Current status of *P. globosa* life cycle as compiled from culture and field observations.

Rousseau et al
1994

SEASONAL PATTERNS

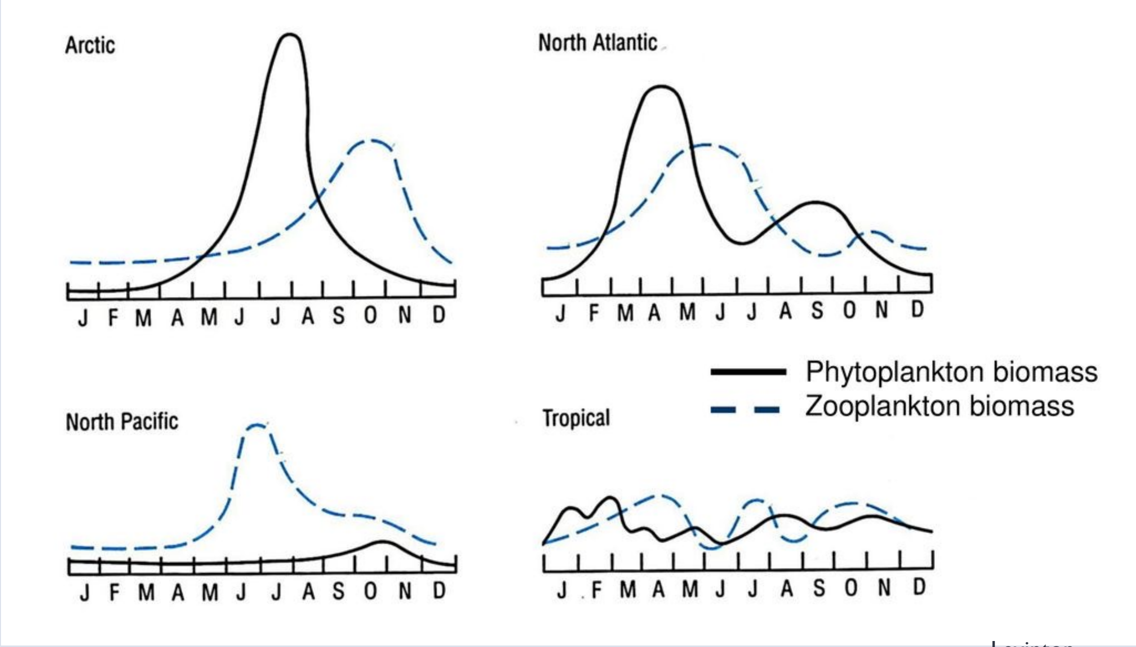
Time - Seasons

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



envlit.ifremer.fr

SEASONAL PATTERNS



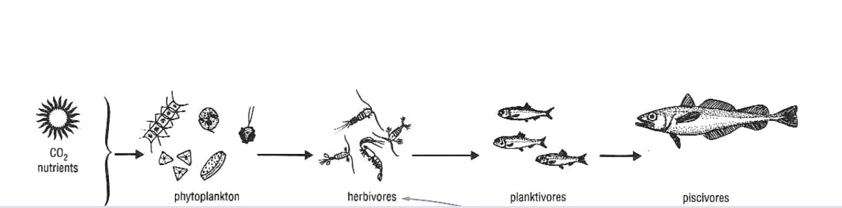
Levinton 1995

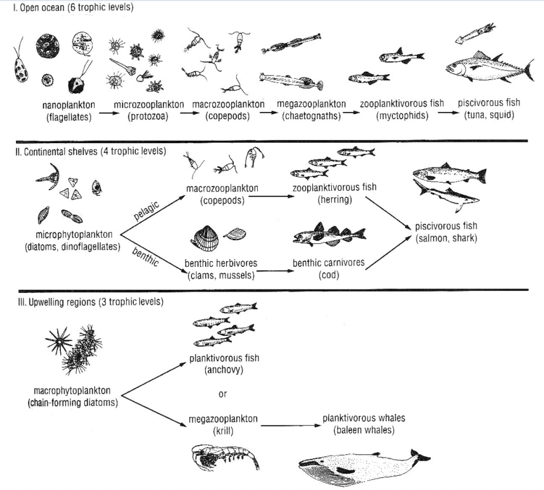
FOOD CHAINS

70's

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

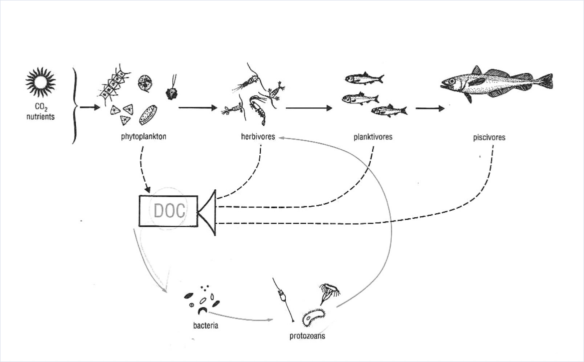
Based on net plankton

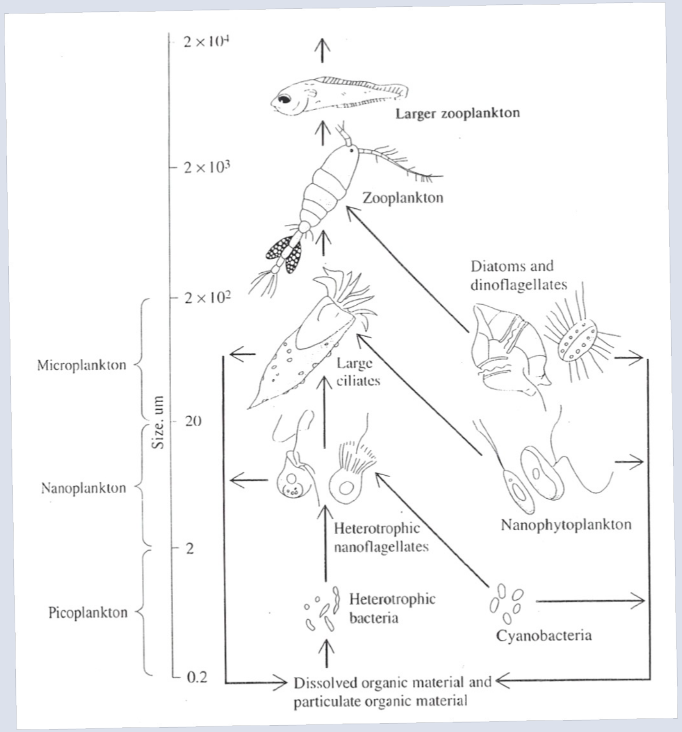




MICROBIAL LOOP

Finer Filters + fluorescent dyes





© Azam et al 1983

MICROBIAL LOOP

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

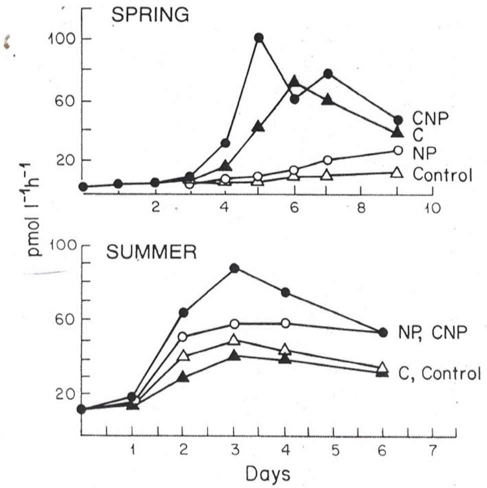
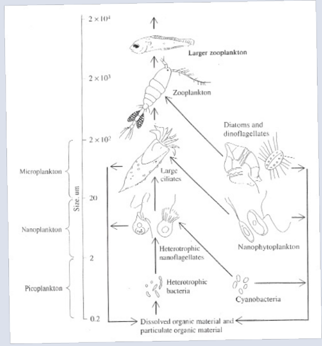


FIGURE 9-1. Thymidine incorporation rate in Baltic Sea bacteriplankton, in batch enrichment experiments done in early spring (top), and summer (bottom). Enrichments consisted of addition of sucrose (C), NH_4Cl (N), or KH_2PO_4 (P). control batches received no additions. Adapted from Kuparinen and Kuosa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



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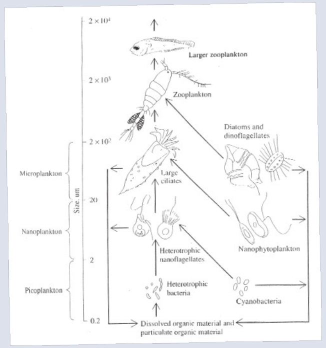
MICROBIAL LOOP

Bacteria: top-down control by nanoflagellates



In the lab

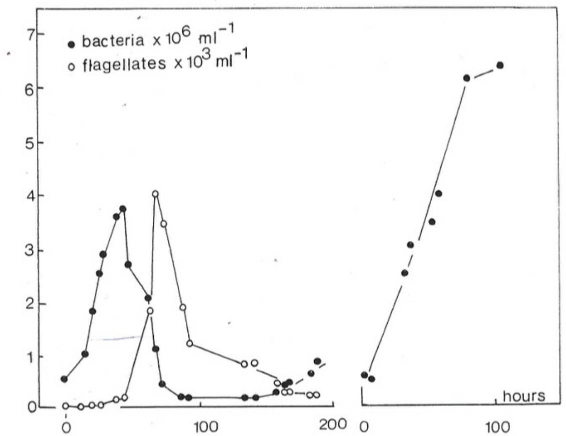


Fig. 58. Left: development of numbers of bacteria and of bacterivorous flagellates in a seawater sample filtered to remove larger plankters. Right: same water sample, but with the flagellates being removed as well. Redrawn from Fenchel [136]

In the field

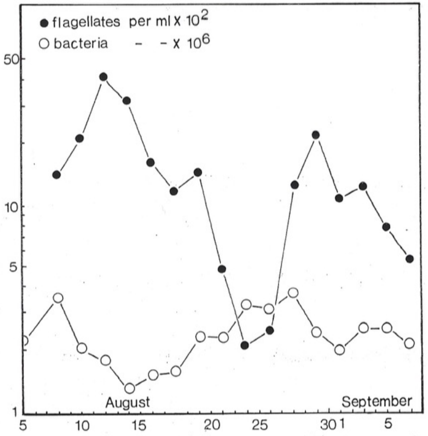
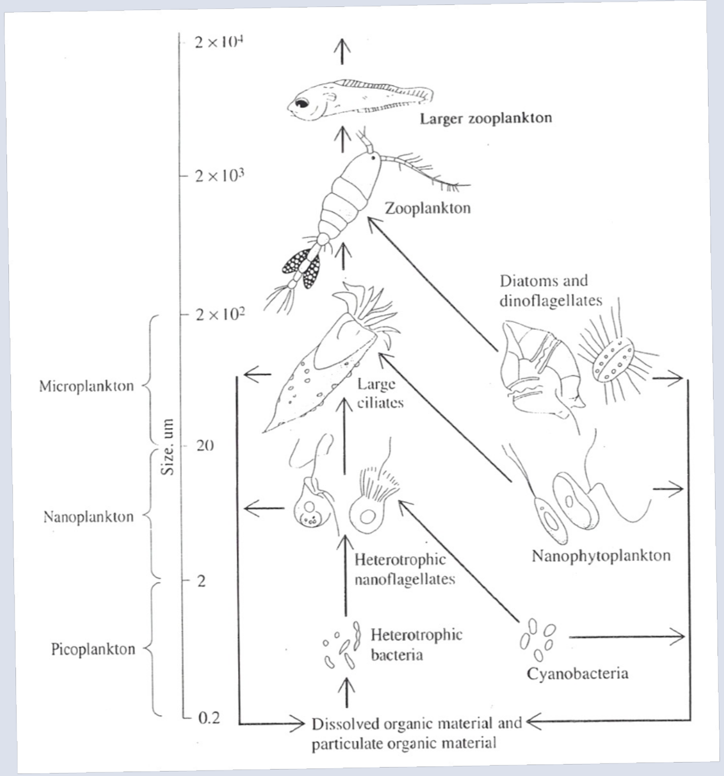


Fig. 59. Numbers of bacteria and bacterivorous flagellates in the surface waters of Limfjorden, Denmark, over one month. Redrawn from Fenchel [136]

. MICROBIAL LOOP

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



. MICROBIAL LOOP

- Energy flow:

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

Where
P_n: production of trophic level n
P_I: primary production of the community

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

$E < 1$ (0.1 – 0.5)
n: trophic level

Much more trophic levels are involved than previously assumed

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

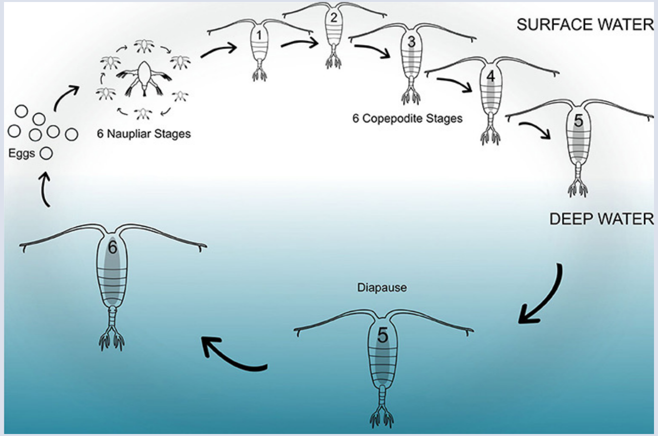
→ Energy/C transfer between the microbial loop and the linear food chain is low

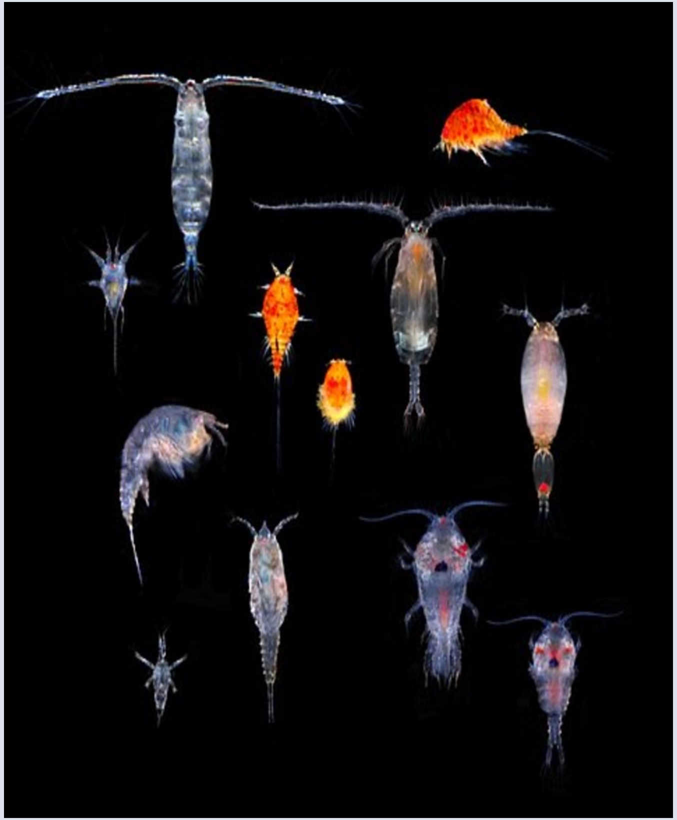
2.3. CONSUMERS

- 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)





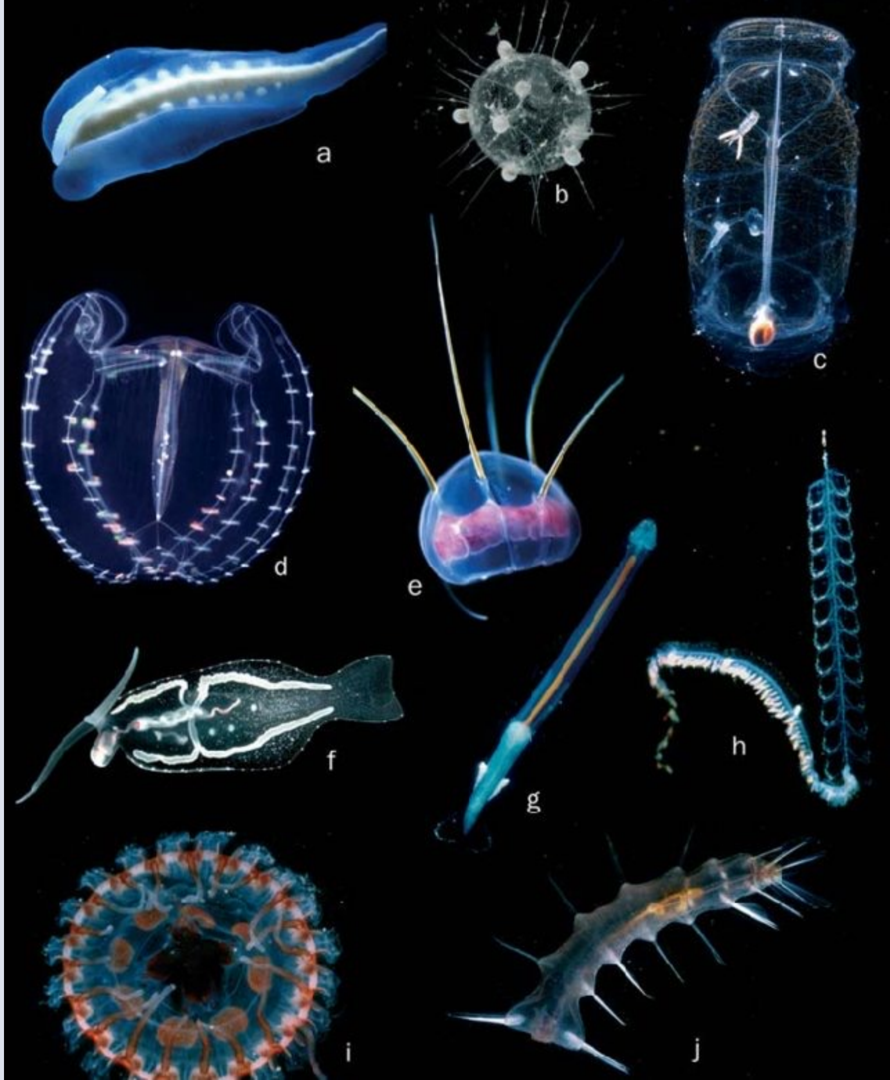
OTHER ZOOPLANKTON

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

NEKTON:FISH

Teleostean fishes

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

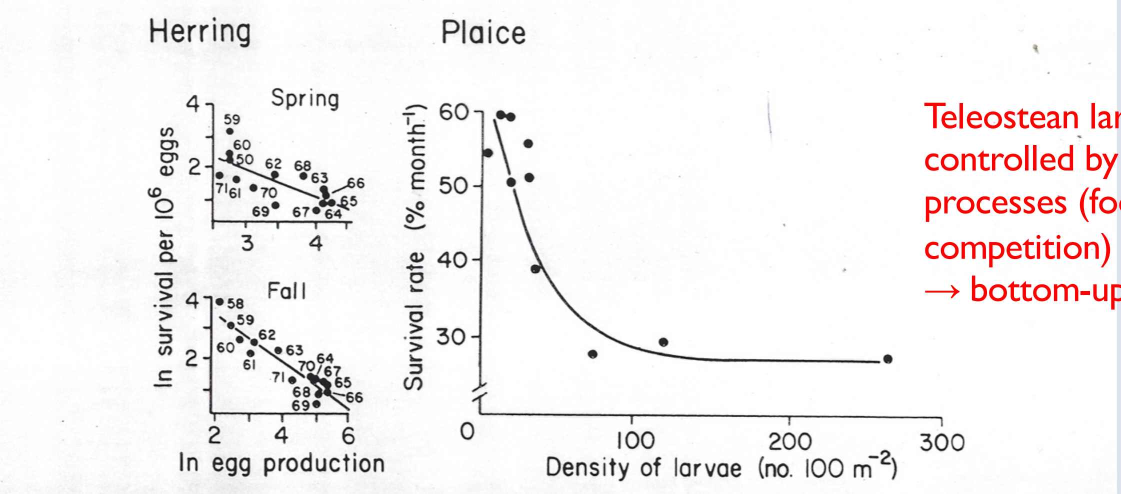


FIGURE 4-9. Survival of fish during the first year of life (age 0) at different densities. Data for spring and fall herring cohorts from Winters (1976). Plaice data from Lockwood (1978).

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

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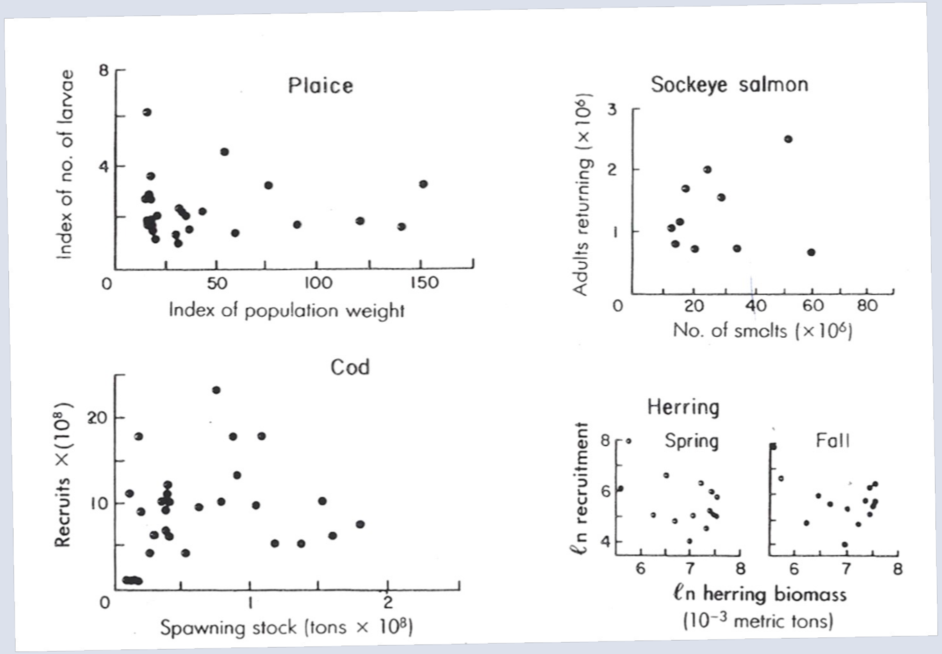
NEKTON:FISH

- 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.

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NEKTON: BIRDS AND MAMMALS

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

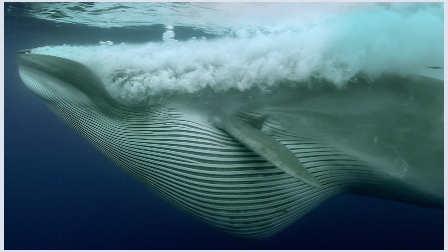

Table 9-3. Rough Estimates of Whale and Seal Stocks, Migratory Losses, and Food Consumption in Prepelagic Whaling and in Recent Times[a]

	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).

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

[a]Data 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

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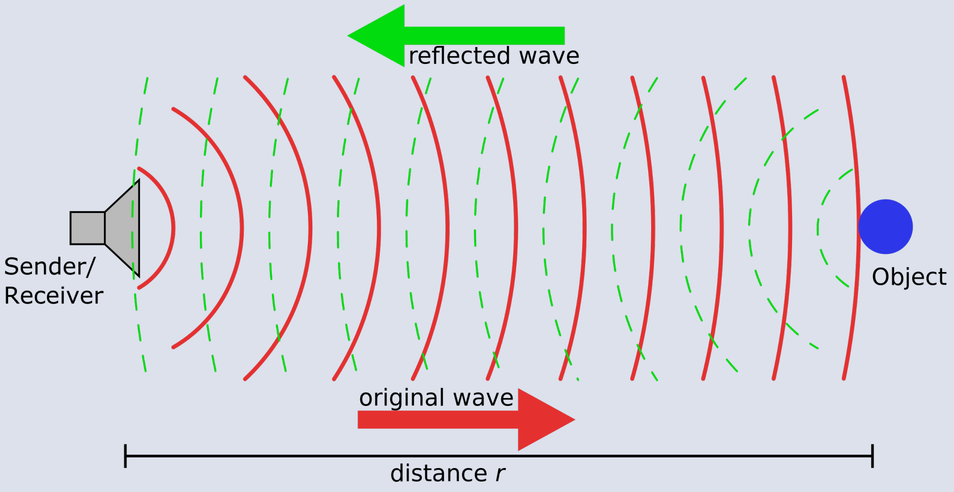
INTERACTIONS

SONAR



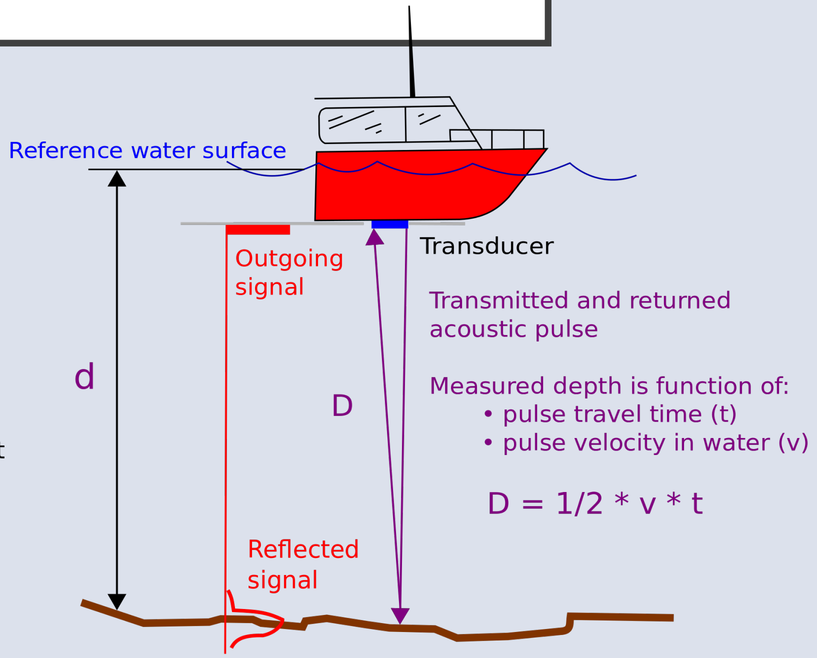
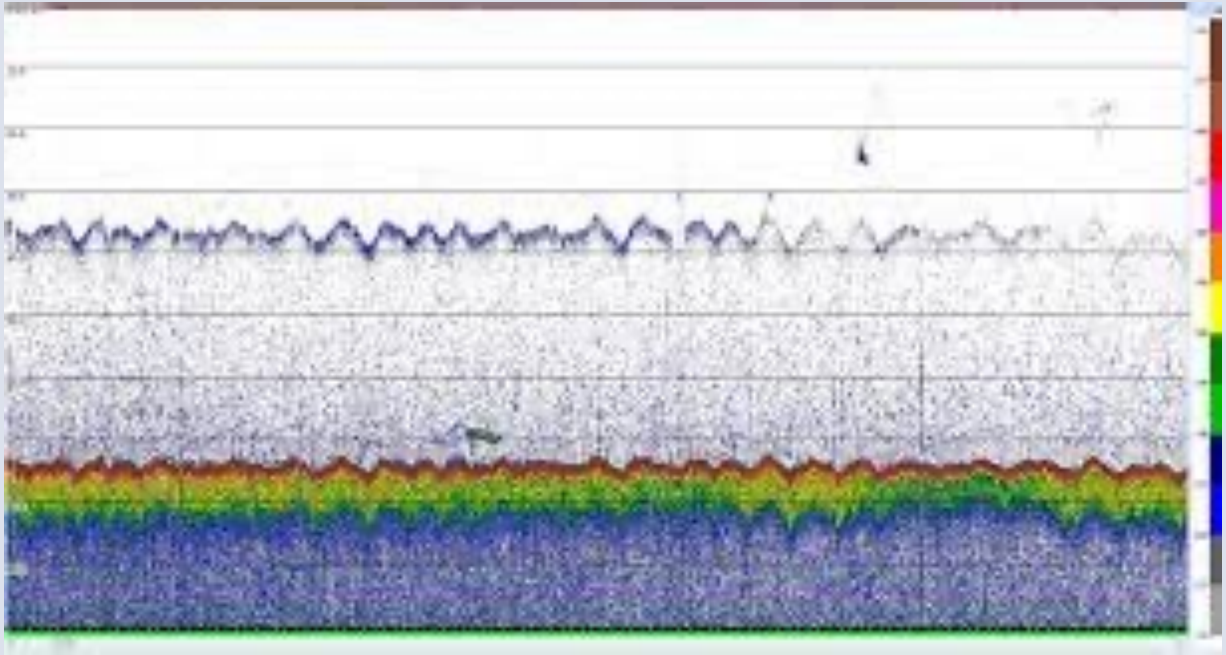
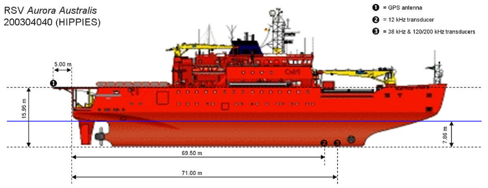


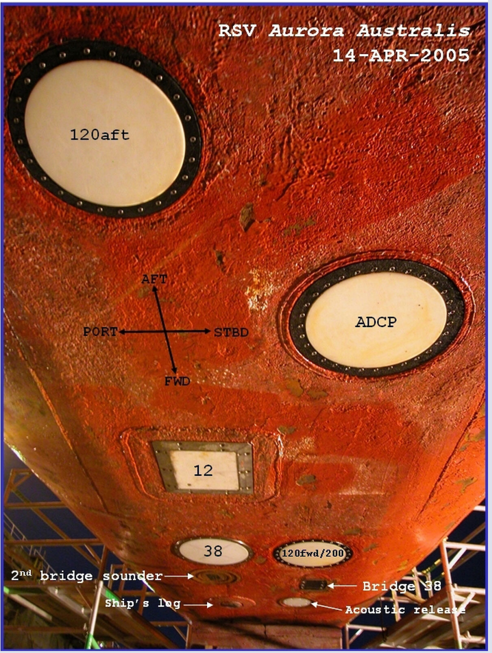
Figure 9-1. Acoustic depth measurement

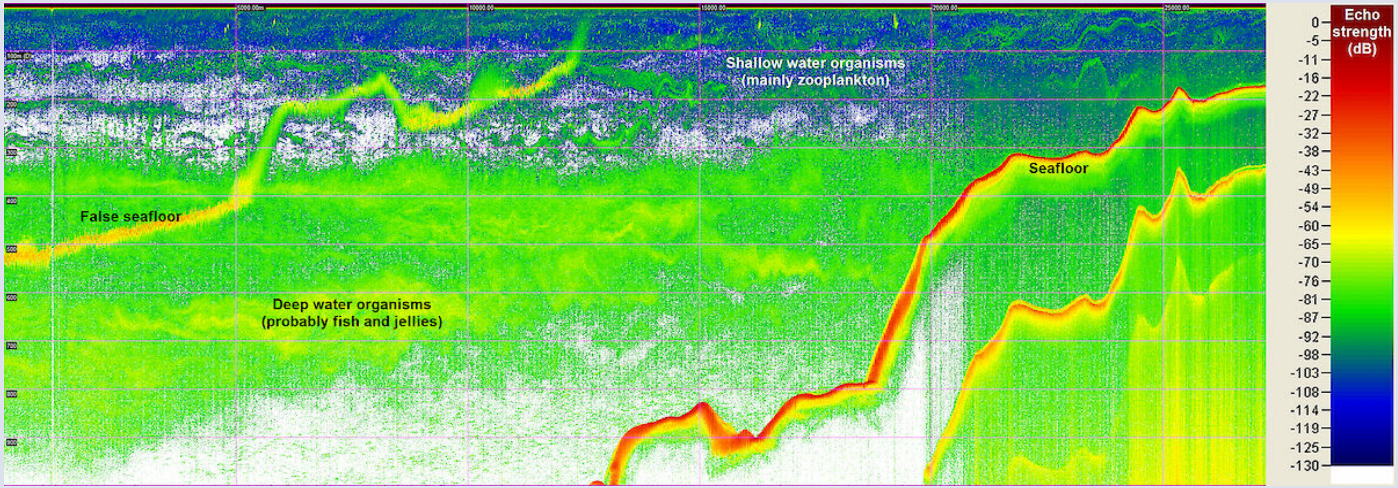
FALSE SEAFLOOR



SCATTERING LAYERS



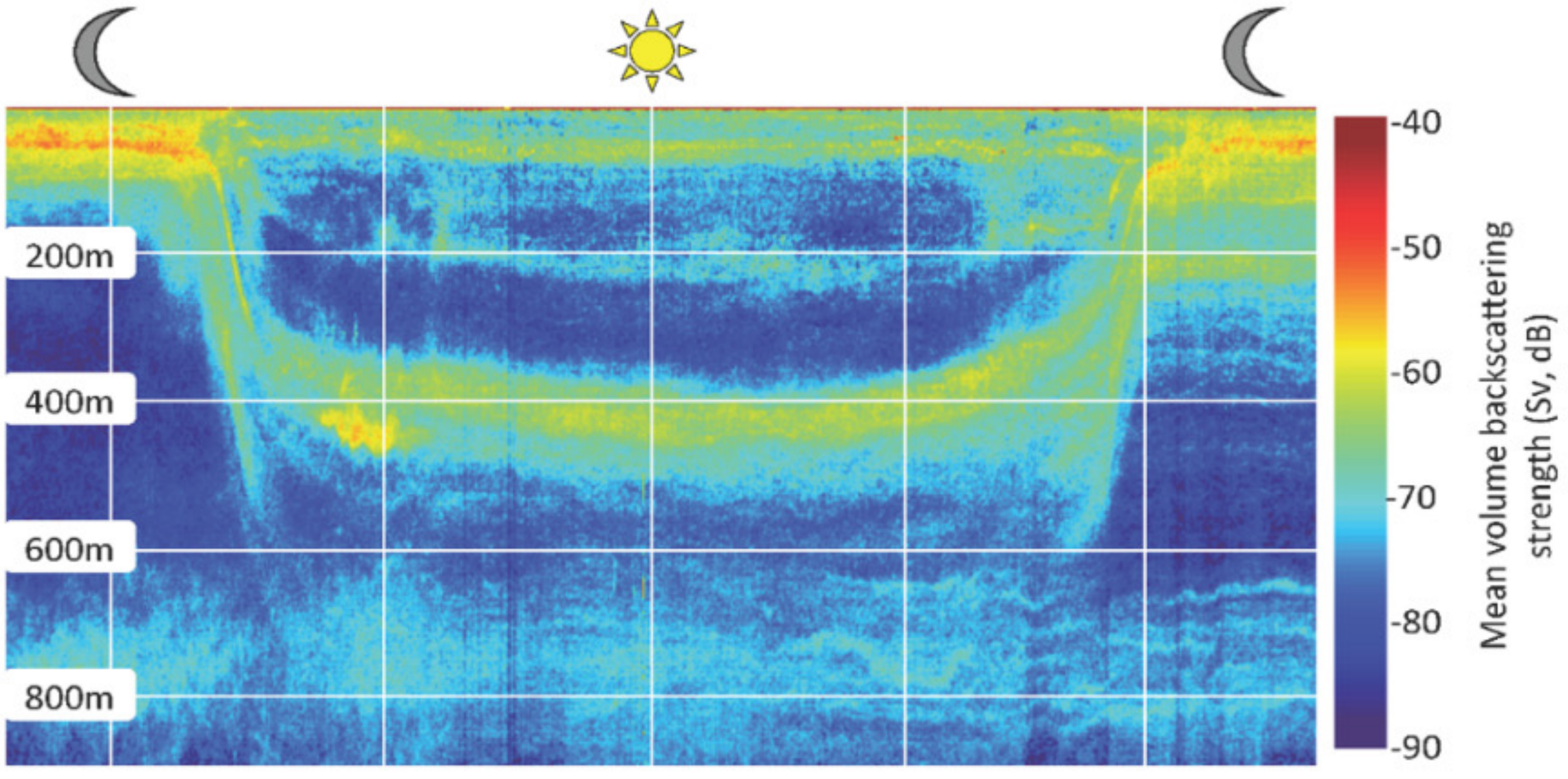




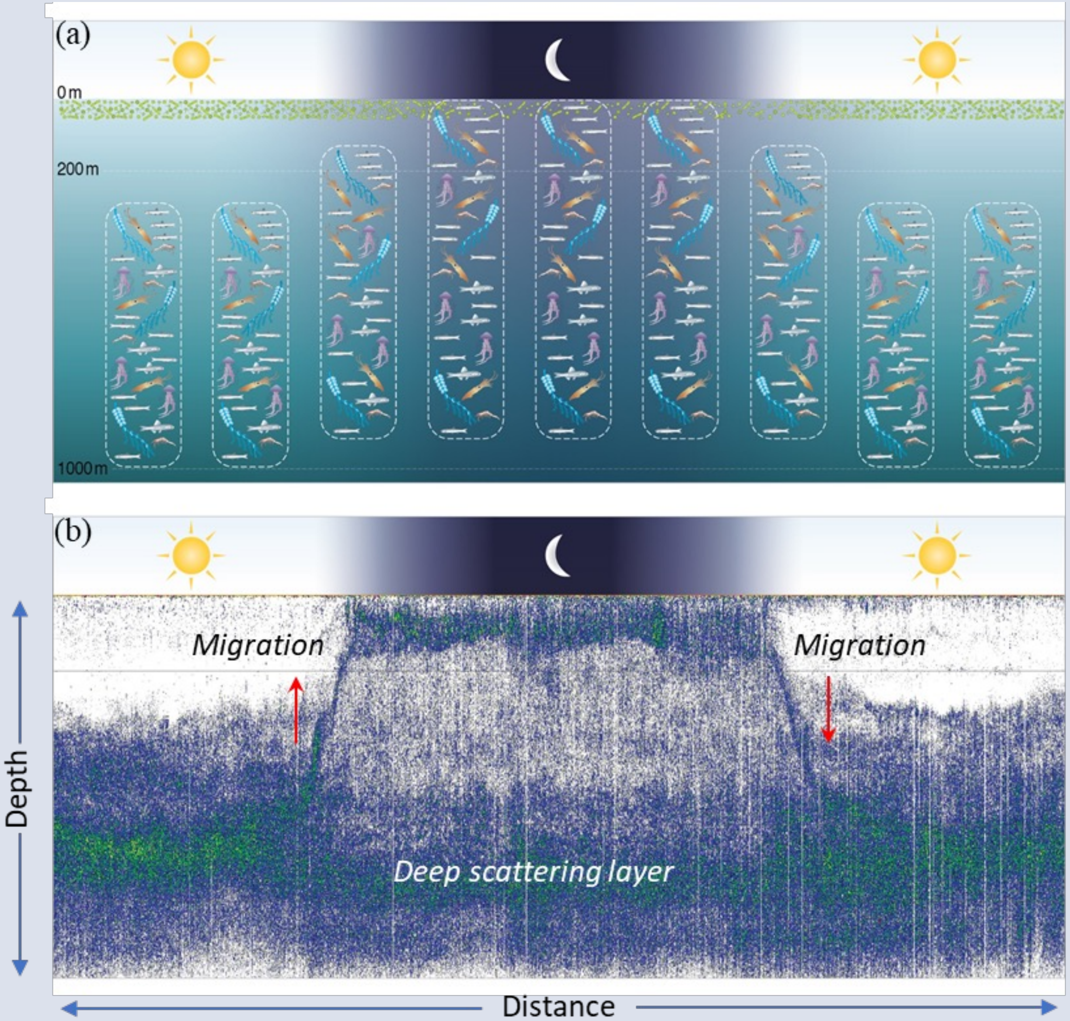
DIEL VERTICAL MIGRATION

- **(A)** sea butterfly (credit: R. Hopcroft, NOAA); **(B)** copepod (credit: U. Kils); **(C)** siphonophore (credit: K. Raskoff, NOAA); **(D)** amphipod (credit: E. A. Lazo-Wasem); **(E)** Hatchetfish feeding on a crustacean (credit: F. Costa); **(F)** glass squid (credit: E. Widder, NOAA); **(G)** comb jelly (credit: A. Semenov); **(H)** decapod (credit: S. Fielding); and **(I)** dragonfish (credit: E. Widder/HBOI, NOAA).

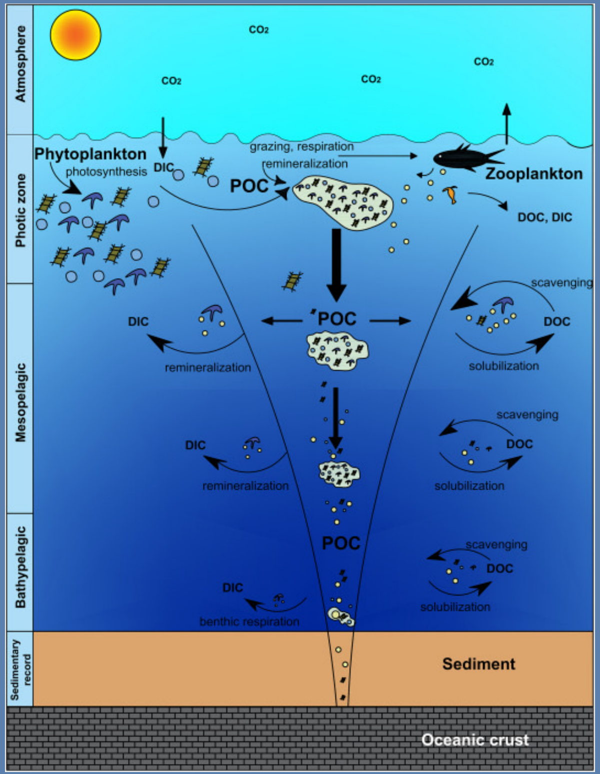
Freer J and Hobbs L (2020) DVM: The World's Biggest Game of Hide-and-Seek. Front. Young Minds. 8:44. doi: 10.3389/frym.2020.00044



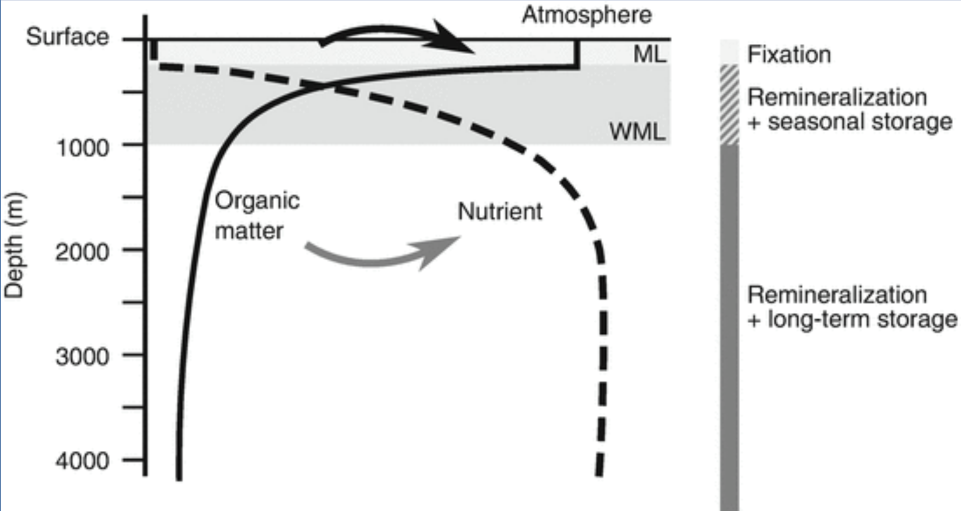
This echogram illustrates the ascending and descending phases of the diel vertical migration through the water column. The yellows and reds are indicative of the greatest density of animals. *Image courtesy of DEEP SEARCH - BOEM, USGS, NOAA.*


(a)
0 m
200 m
1000 m
(b)
Migration
Migration
Deep scattering layer
Depth
Distance

BIOLOGICAL CARBON PUMP



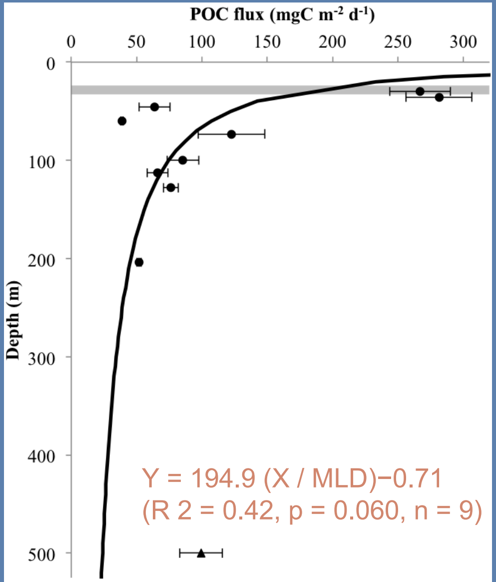
- Export
  - Sinking
  - Active Transport
  - Physical Transport
- Remineralization and Transfer
- Vertical Profiles



MARTINS LAW

$$Fz = Fz0e^{-(rz)/v}$$

$$Fz = Fz0(z/z0)^{-b}$$



- For sinking particles
- transfer efficiency is a function of sinking speed and remineralization rate:
- fast remineralization and slow sinking retains matter near the surface ocean,
- slow remineralization and fast sinking allow organic matter to be transported much deeper.
- Assuming that remineralization rate (r) and sinking speed (v) are constant with depth, flux (F z) at a depth (z) can be calculated from a reference flux (F z0) as:
- Observations of particle flux profiles suggest that particle flux is better described by an empirical power-law function known as the “Martin curve” (Martin et al. 1987):
- This power-law function implies that particle sinking speeds increase, and/or remineralization rates decrease, with depth.
- For carbon, “Martin’s coefficient” b varies regionally with a global average of 0.86, while other elements have different values due to varying remineralization and transfer rates

Anna Belcher, Morten Iversen, Sarah Giering, Virginie Riou, Stephanie A. Henson, Leo Berline, Loic Guilloux and Richard Sanders - [1] doi:10.5194/bg-13-4927-2016

MESOPELAGIC FISH

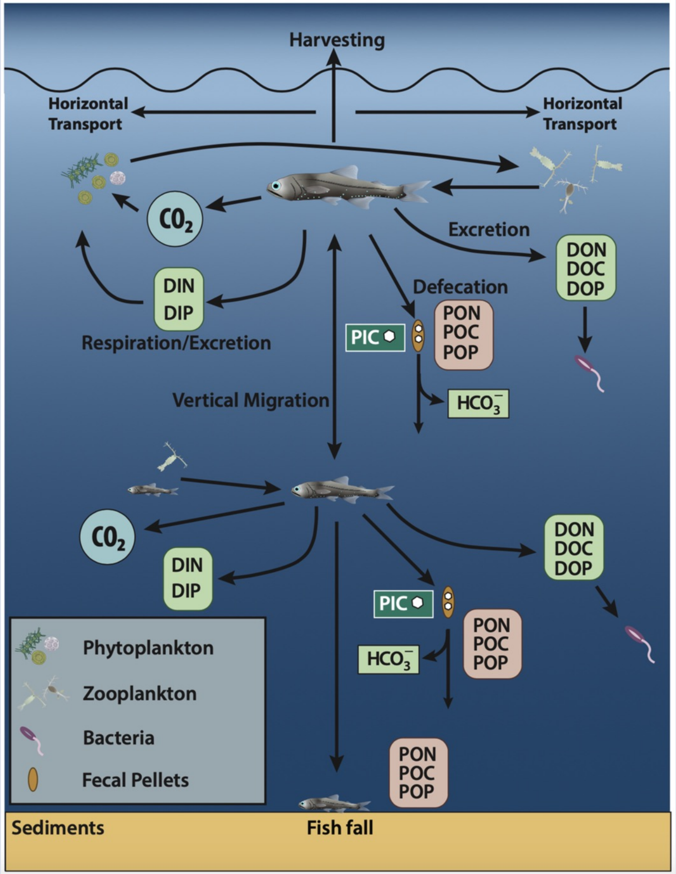
Lanternfish with blue bioluminescense (From Adobe Stock, Sam)

- small, abundant fish living in the mesopelagic zone between the depth of 200-1000m
- bioluminescence

GONOSTOMATIDAE

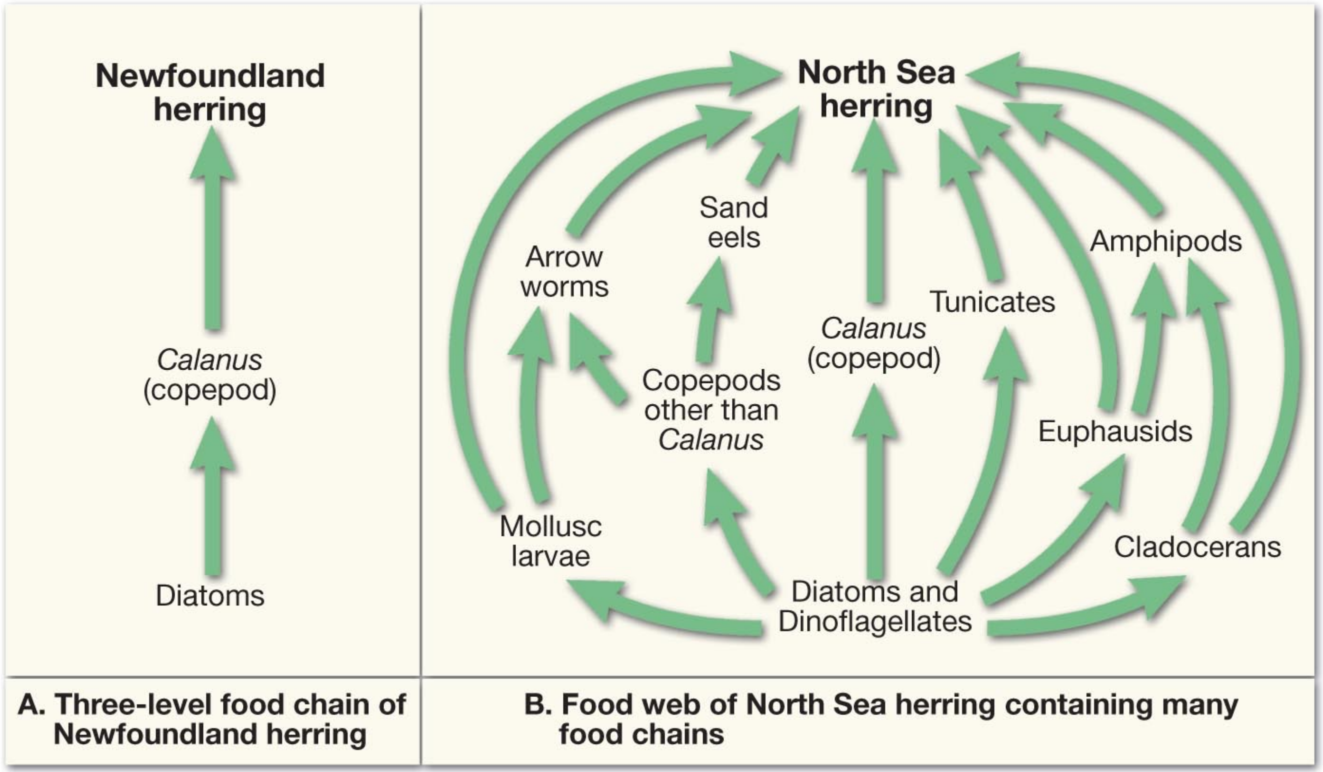
- Gnostomatidae AKA “Bristlemouths”
- most abundant of all mesopelagic fish
- most abundant vertebrate
  > humans, birds, and amphibians
- Up to one quadrillion individuals or 10^15 fish!

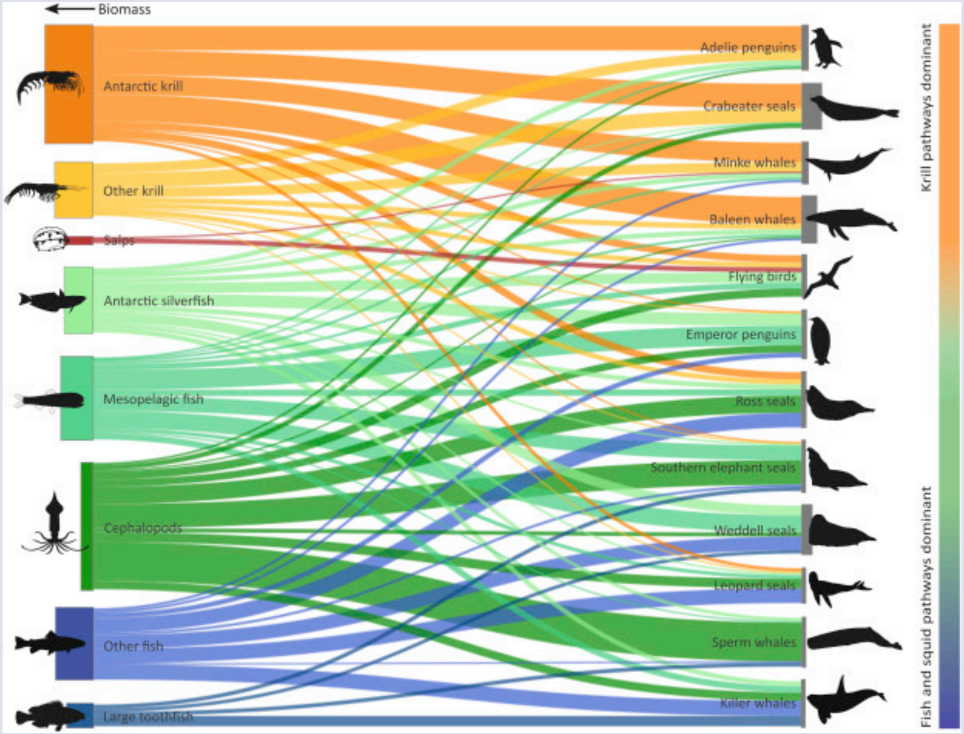
CARBON PUMP



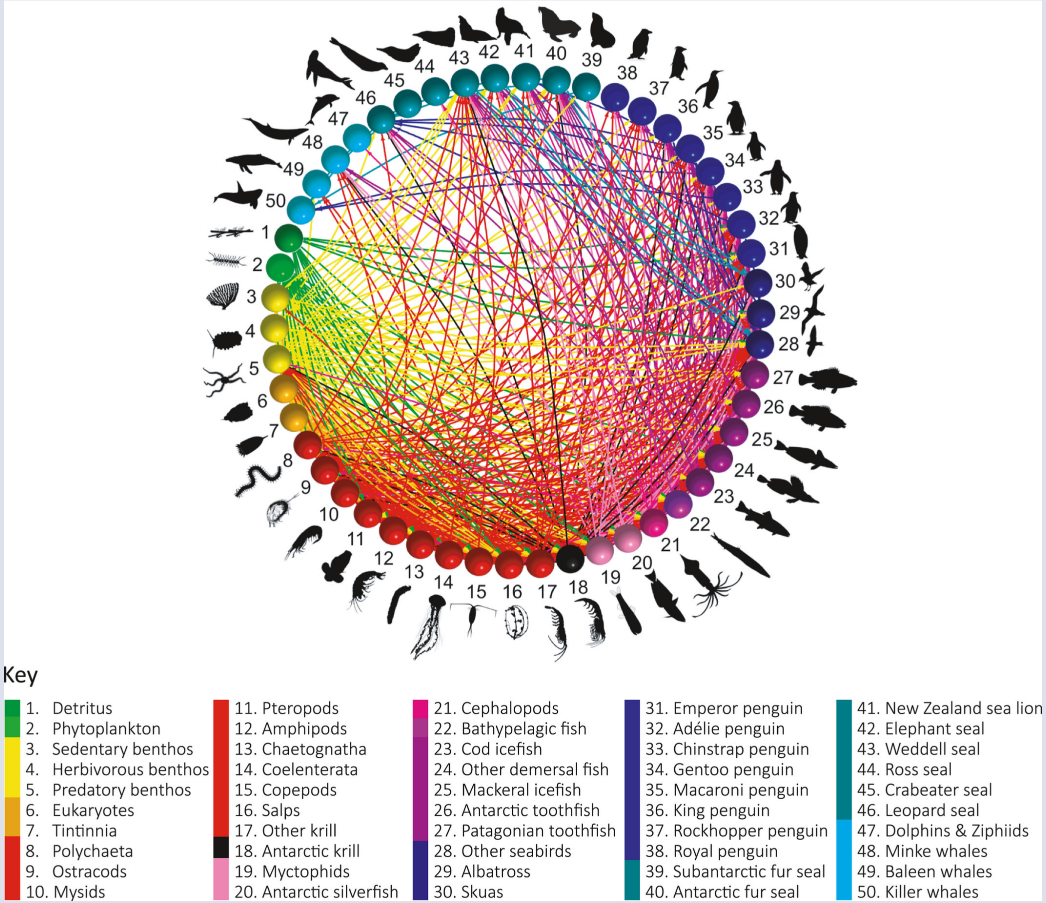
Limnology & Oceanography, Volume: 66, Issue: 5, Pages: 1639-1664, First published: 17 February 2021, DOI: (10.1002/lno.11709)

FOOD CHAINS AND FOODWEBS


Newfoundland herring
Calanus (copepod)
Diatoms
North Sea herring
Sand eels
Arrow worms
Amphipods
Tunicates
Calanus (copepod)
Copepods other than Calanus
Euphausids
Mollusc larvae
Cladocerans
Diatoms and Dinoflagellates
A. Three-level food chain of Newfoundland herring
B. Food web of North Sea herring containing many food chains



- 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

PRACTICAL: ONLINE RESOURCES FOR MARINE BIODIVERSITY DATA

Bring laptop

No special software needed

Work with same groups as other practical

Class

30 minutes intro to online resources

Work together to find information on a marine taxon

Small 'literature' report