Pelagic Biological Processes

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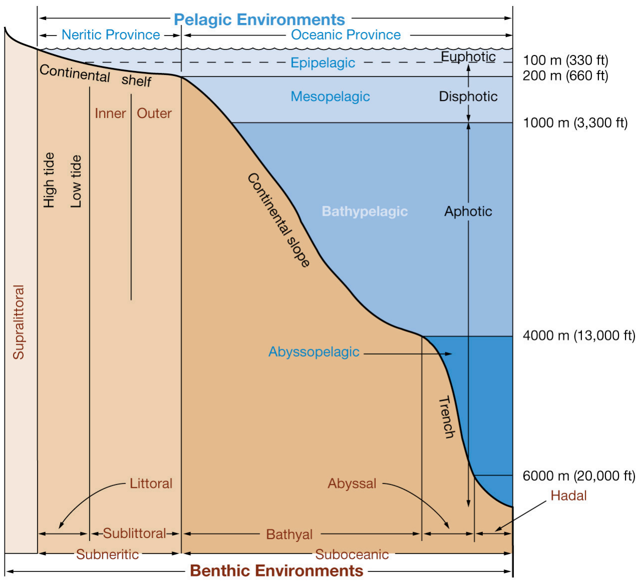
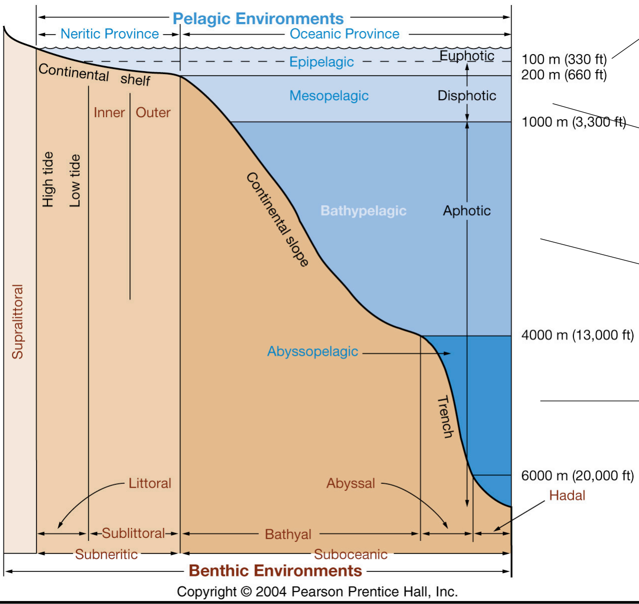
1. Divisions of the marine environment



2

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

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1.1. Zones of the pelagic domain

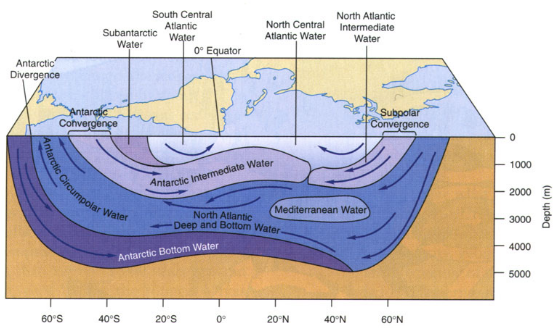

FIGURE 8–27 A vertical cross section of the Atlantic Ocean shows the various water masses that form layers at different depths. Antarctic Bottom Water is the densest water mass and it flows northward from around Antarctica. North Atlantic Bottom Water sinks near Greenland and flows southward over the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

Segar 2007

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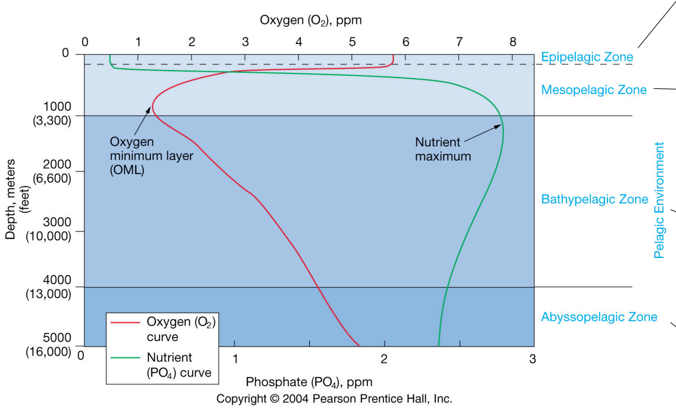
1.2. Vertical distribution of O_2 and nutrients



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

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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

Seston:

Plankton:

Unable to move against currents (dependent on the water mass)

Tripton:

Particulate organic matter (POM)

Nekton:

Able to swim against currents (independent on water masses)

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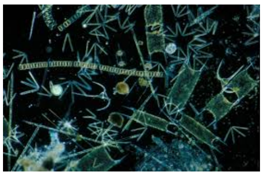
2. Pelagic biological processes

- 2.1 Definitions

Plankton

Phytoplankton (autotroph)	Mixoplankton (Mixotroph) Relative importance?	Zooplankton (heterotroph)



Natureasia.com

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2.1. Definitions

- Classification according to size

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

Aquaticlivefood.com.au

Daylymail.co.uk

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2.2. Primary production

- 2.2.1. Factors limiting P1

Light (bottom-up control)

Saturation

Light limiting

Photoinhibition
- UV
- Light induced respiration
- Leakage of organic molecules

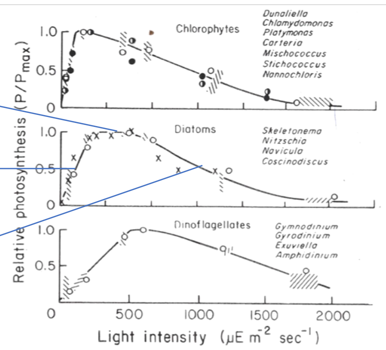
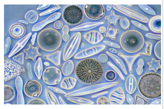
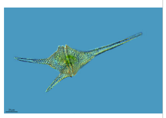


Figure 2-5. Curves of relative photosynthesis (P/P_{max}) versus light intensities for three algal groups. The chlorophytes include green and flagellated greens. Shaded rectangles represent the dispersion of points obtained experimentally using neutral filters in cultures grown with an irradiance of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

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2.2. Primary production

- 2.2.1. Factors limiting P1

Light

- Sea water absorb the photosynthetic active radiation (PAR)

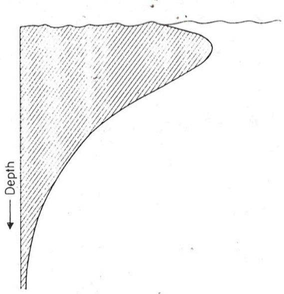
$$I_z = I_0 e^{-kz}$$

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.



Barnes & Hughes 1999

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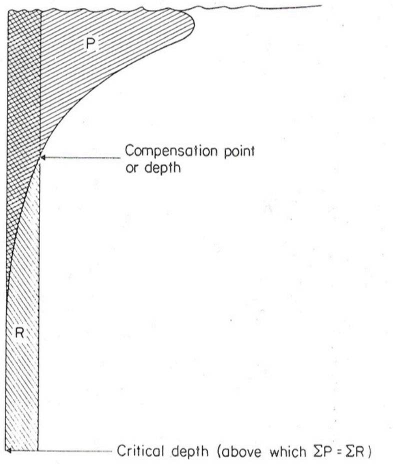
2.2. Primary production

- 2.2.1. Factors limiting P1

Light

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

➢ Compensation depth: R = Φ for a particular species
➢ Critical depth: ΣR = Σ Φ for the whole P1 community (net P1 of the community = 0)



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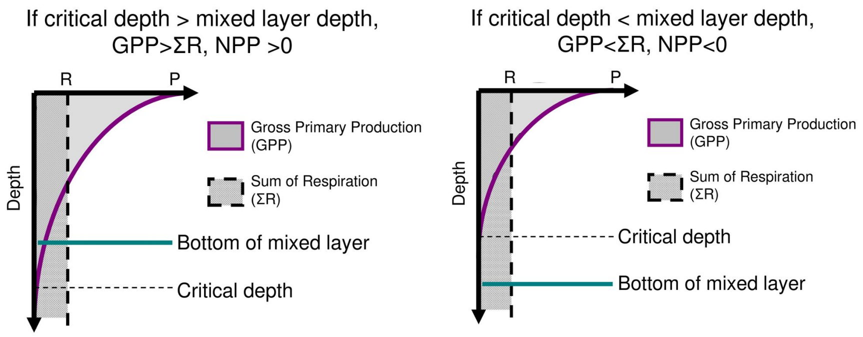
2.2. Primary production

- 2.2.1. Factors limiting P1

Light + Mixing

- Wind induces mixing of the water column → mixing depth



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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 ncessary → most favorable
      - NO_3^-, $N0_2^-$: have to be reduced (nitrate reductase)
      - Most marine inorganic N as NO_3^- (1µM 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)

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2.2. Primary production

- 2.2.1. Factors limiting P1

Nutrients

- Uptake

Described by

Michaelis-Menten equation:

$$V = \frac{Vmax \cdot C}{Ks + C}$$

Vmax= Uptake velocity at saturation

C= nutrient concentration in SW

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

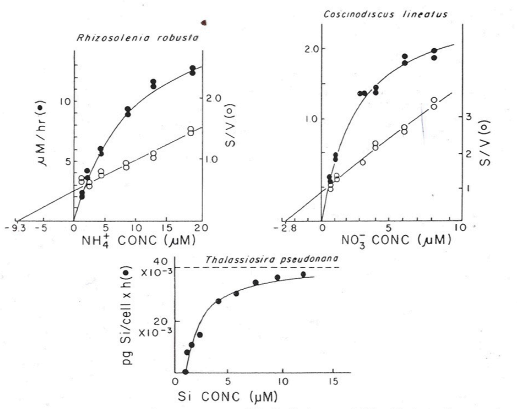

Figure 2-13. Michaelis-Menten curves (filled circles) and Woolf plots (open circles) fitted to data on uptake (µmole/hr) of ammonium, nitrate, and silica by three diatoms at different nutrient concentrations (µmole/liter). *S* is the concentration of nutrient being taken up, *V* is the uptake velocity.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

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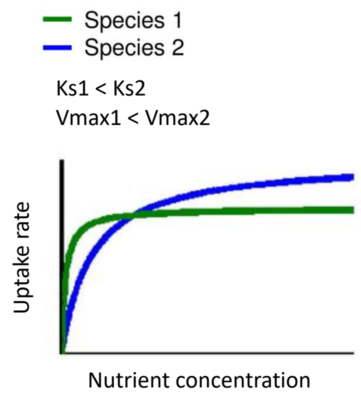
2.2. Primary production

- 2.2.1. Factors limiting P1

Nutrients

- Uptake: low and high Ks



- 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

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2.2. Primary production

- 2.2.1. Factors limiting P1

Nutrients

- Ks depends on size

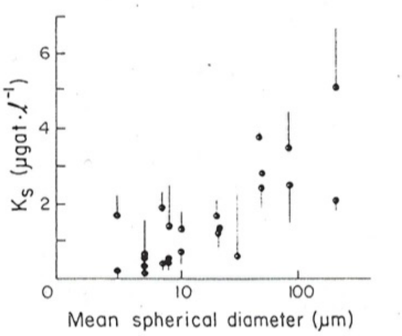

Figure 2-14. Half-saturation (K_s) values for nitrate uptake by phytoplankton of different size. The bars show the 95% confidence limits for the highest and lowest mean K_s reported. Adapted from Malone (1980).

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2.2. Primary production

- 2.2.1. Factors limiting P1

Nutrients

- Ks differ according to habitat

Table 2-1. Half-Saturation Constants (K_s) for Uptake of Nitrate and Ammonium by Cultured Marine Phytoplankton at 18°C[a]

	K_s (μg-atoms liter)		Cell diameter (μm)
	Nitrate	Ammonium	
Oceanic coccolithophores and diatoms	0.1–0.7	0.1–0.5	5
Neritic diatoms	0.4–5.1	0.5–9.3	8–210
Neritic or littoral flagellates	0.1–10.3	0.1–5.7	5–47
Oligotrophic, Tropical Pacific	0.1–0.21	0.1–0.62	—
Eutrophic, Tropical Pacific	0.98	—	—
Eutrophic, Subarctic Pacific	4.21	1.3	—

[a] From MacIsaac and Dugdale (1969) and Eppley et al. (1969). The Pacific data from natural mixed phytoplankton.

Valiela 2009

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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 ± 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.

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2.2. Primary production

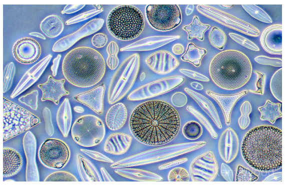
- 2.2.1. Factors limiting P1

Nutrients

- Ks
  - Usually lower in nano- (flagellates) than in microphytoplankton (diatoms)

Biology.kenyon.com

  - Usually higher in coastal communities rich in nutrients (selection for high Ks species)



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2.2. Primary production

- 2.2.1. Factors limiting P1

Nutrients

- N and P

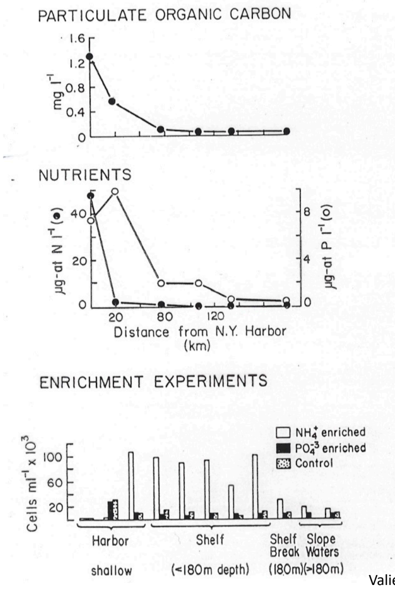

Figure 2-24. Top and middle: Concentrations of particulate organic carbon and nutrients in surface water in a transect from New York Harbor to offshore. Bottom: Growth of *Skeletonema costatum* in water samples that were enriched with ammonium or phosphate and in unenriched samples. The sequence of stations 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.

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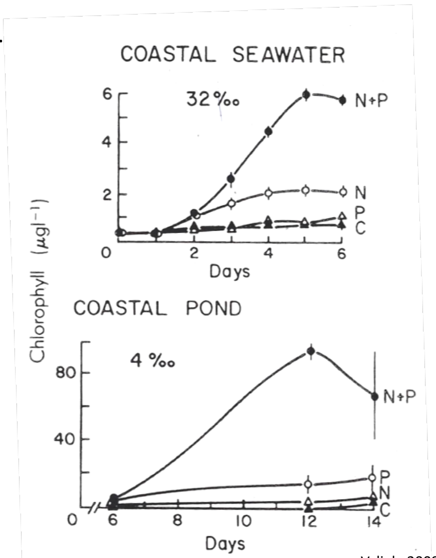
2.2. Primary production

- 2.2.1. Factors limiting P1

Nutrients

- N and P



Valiela 2009

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.

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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 SW nutrient concentrations depart from this ratio, a limitation is very probable

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2.2. Primary production

- 2.2.1. Factors limiting P1

Nutrients

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

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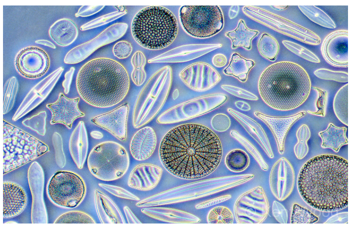
2.2. Primary production

- 2.2.1. Factors limiting P1

Nutrients

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



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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) ←→ high concentrations (1 – 3 nM) in coastal zones, low to very low concentrations (<1 – 0.06 nM) in oceanic zones
  - Limiting in oceanic zones → <u>H</u>igh <u>N</u>utrients <u>L</u>ow <u>C</u>hlorophyll (HNLC) regions

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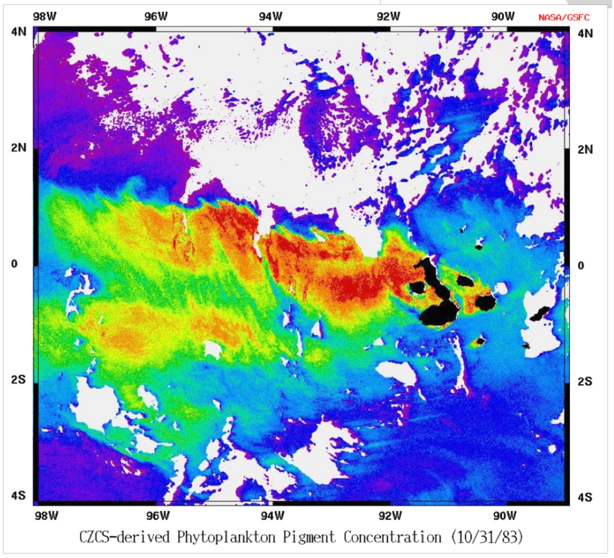
2.2. Primary production

- 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.



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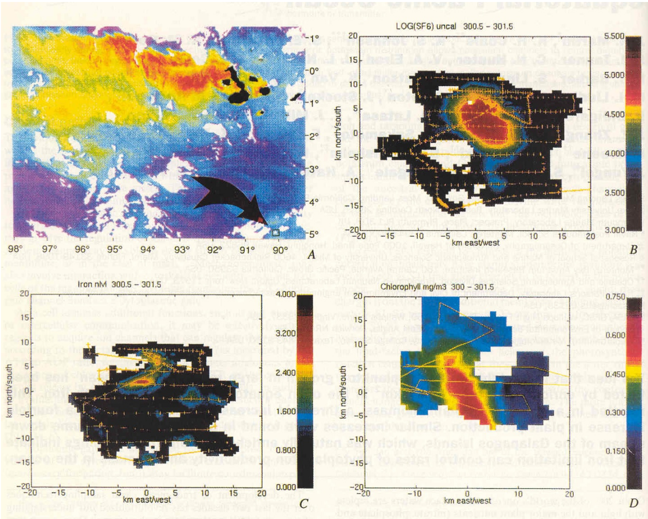
2.2. Primary production

- 2.2.1. Factors limiting P1

Nutrients

- Fe

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



Nature 371: 124 (1994)

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2.2. Primary production

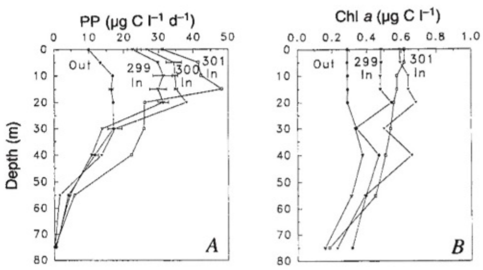
IronEx1

- 2.2.1. Factors limiting P1

Nutrients

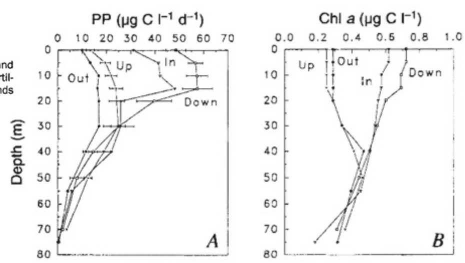
- Fe

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 $H^{14}CO_3^-$ 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.



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.



Nature 371: 124 (1994)

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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

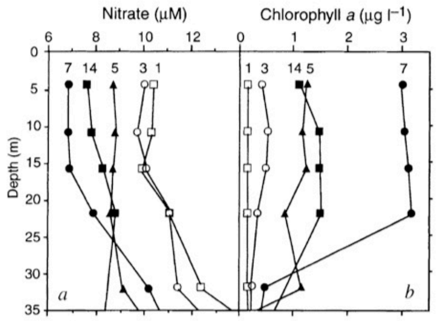

FIG. 3 *a*, Vertical profiles of mixed-layer nitrate from the daily 'inside-patch' stations of patch 1. Numbers at the top of each profile indicate the day of the patch 1 experiment. These plots illustrate the depletion of nitrate as the bloom reached its peak near days 7–9. The subsequent increase (day 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*.

B: x85
Chla: X27

Nature 383: 495 (1996)

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2.2. Primary production

IronEx2

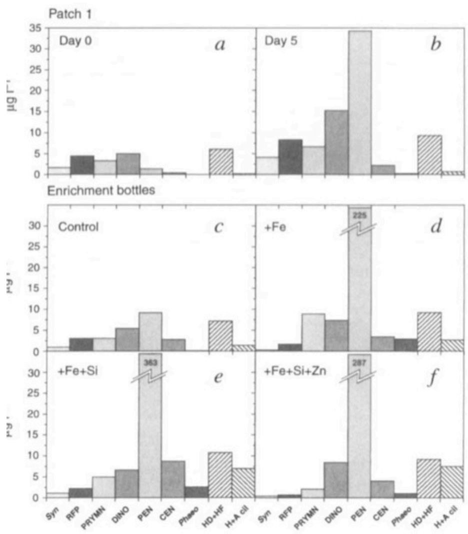
- 2.2.1. Factors limiting P1

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 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)

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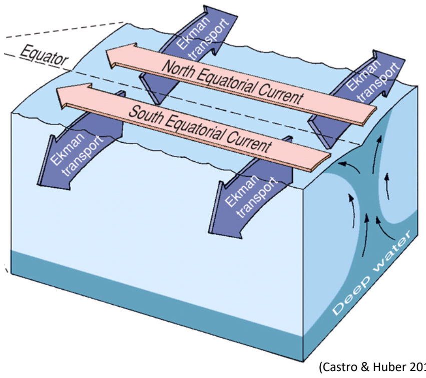
2.2. Primary production

- 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)

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2.2. Primary production

- 2.2.1. Factors limiting P1

Grazing (top-down control)

- Some indications
  - Inverse horizontal spatial distributions

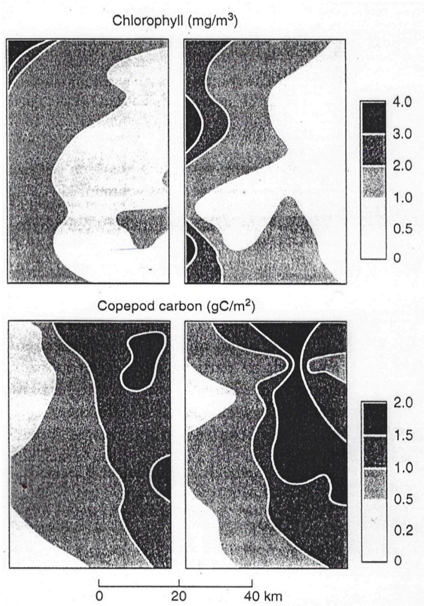

Fig. 9.13 Distribution of chlorophyll *a* and copepod carbon on a survey in the North Sea, showing an inverse relationship between phytoplankton and zooplankton standing stock. Phytoplankton are most abundant toward the left, whereas zooplankton are most abundant toward the right. (Modified from Steele,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

Levinton 1995

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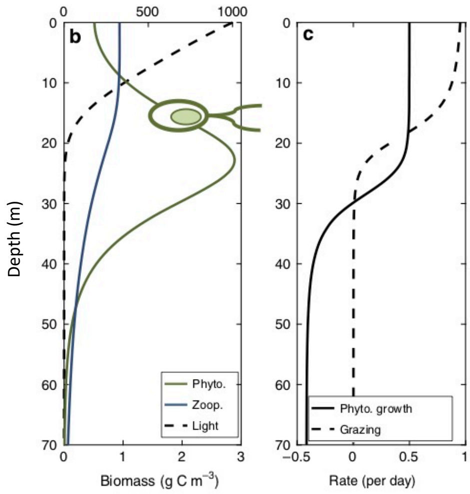
2.2. Primary production

- 2.2.1. Factors limiting P1

Grazing

- Some indications
  - vertical distribution: deep chlorophyll maxima



Light-dependent grazing drives deep chlorophyll maxima (DCM) formation in a one-dimensional model. **b** When light dependence is introduced, a deep phytoplankton biomass maximum corresponding to a deep chlorophyll maximum emerges. **c** Phytoplankton accumulation in a DCM arises from two processes: elevated grazing near the water column's surface, and depressed growth due to light limitation below the compensation depth.

Moeller et al 2019

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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.

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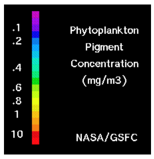
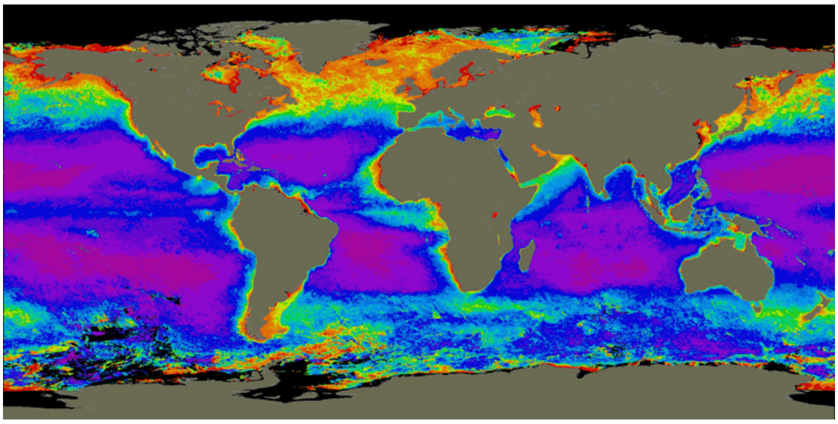
2.2. Primary production

- 2.2.2. Variations of P1 in space and time

Space

- Hydrographic factors





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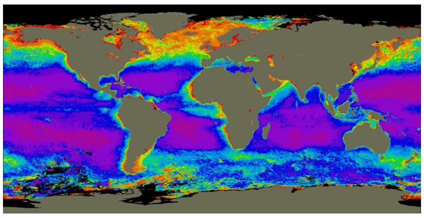
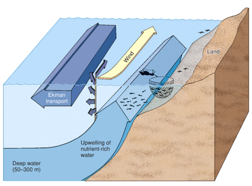
2.2. Primary production

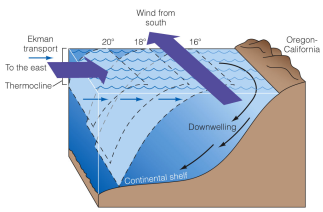
- 2.2.2. Variations of P1 in space and time

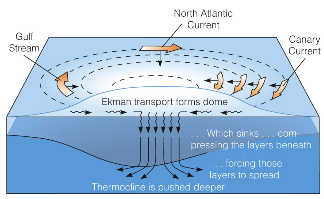
Space

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









(Castro & Huber 2010)

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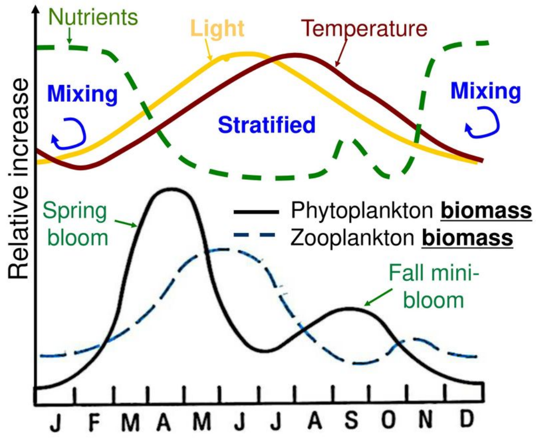
2.2. Primary production

- 2.2.2. Variations of P1 in space and time

Time - Seasons

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



Levinton 1995

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2.2. Primary production

- 2.2.2. Variations of P1 in space and time

Time - Seasons

- Temperate North Atlantic (eutrophicated conditions)

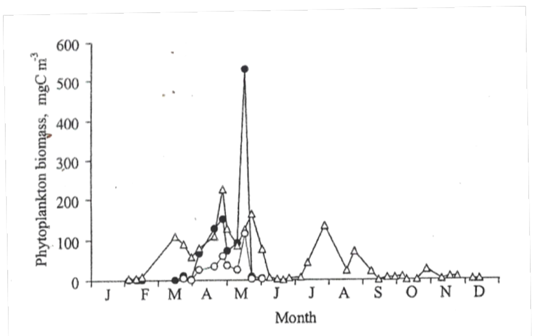

Fig. 1. Seasonal changes of diatoms (Δ), *Phaeocystis* colony (•) and cellular (○) C biomass measured at Stn 330 of Belgian coastal waters in 1995

Rousseau et al 2002

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2.2. Primary production

- 2.2.2. Variations of P1 in space and time

Time - Seasons

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

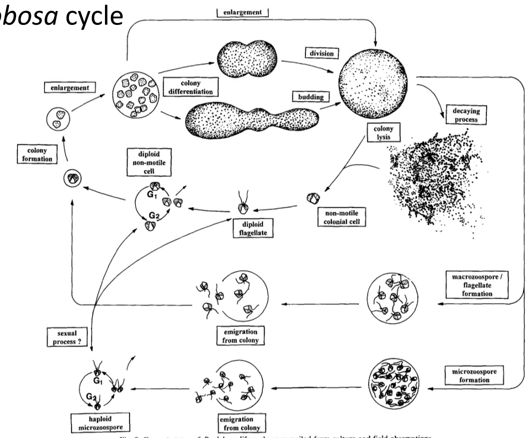

Fig. 9. Current status of *P. globosa* life cycle as compiled from culture and field observations.

Rousseau et al 1994

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2.2. Primary production

- 2.2.2. Variations of P1 in space and time

Time - Seasons

- Temperate North Atlantic (eutrophicated conditions)

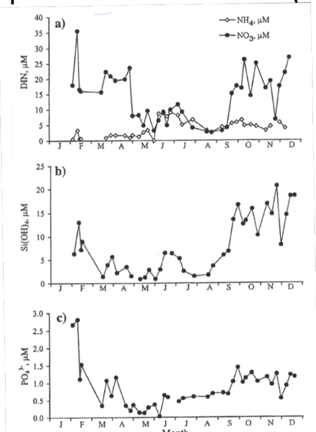

Fig. 3. Seasonal changes of major inorganic nutrient concentrations (µM): (a) Dissolved inorganic nitrogen, DIN (NO_3, NH_4); (b) $Si(OH)_4$; and (c) PO_4 recorded at Stn 330 in 1995

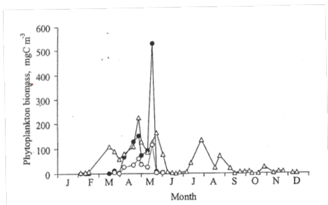

Fig. 1. Seasonal changes of diatoms (Δ), *Phaeocystis* colony (●) and cellular (○) C biomass measured at Stn 330 of Belgian coastal waters in 1995

Limitation by P and not by N !

Rousseau et al 2002

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2.2. Primary production

- 2.2.2. Variations of P1 in space and time

Time - Seasons

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

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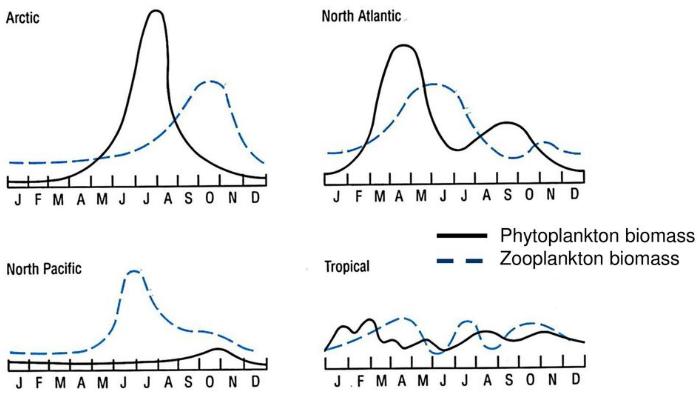
2.2. Primary production

- 2.2.2. Variations of P1 in space and time

Time - Seasons

- Other oceans



Levinton 1995

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2.3. Consumers

- 2.3.1. Microbial loop

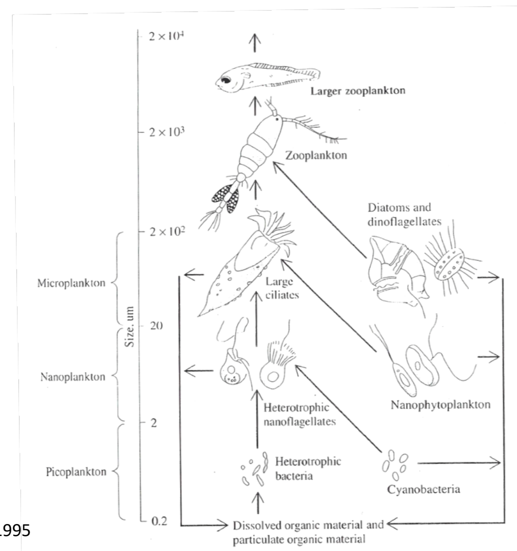

Figure 2.28 Diagrammatic representation of the microbial loop and its relationship to the "classical" plankton food web. Autotrophs are on the right and heterotrophs on the left. (Modified from T. Fenchel, Marine planktonic food chains, Am. Rev. Ecol. Sys. 19:19–38, 1988.)

Levinton 1995

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2.3. Consumers

- 2.3.1. Microbial loop

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

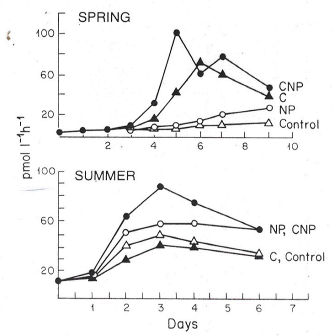

FIGURE 9-1. Thymidine incorporation rate in Baltic Sea bacteriplankton, in batch enrichment experiments done in early spring (top), and summer (bottom). Enrichments consisted of addition of sucrose (C), NH_4Cl (N), or KH_2PO_4 (P). control batches received no additions. Adapted from Kuparinen and Kuosa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

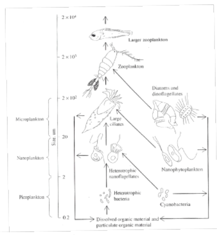

Table 2.4 Carbon: nitrogen ratios in various organisms.

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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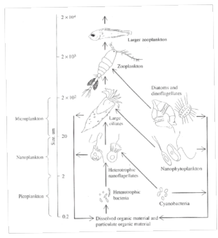
2.3. Consumers

- 2.3.1. Microbial loop

Bacteriae: top-down control by nanoflagellates



In the lab

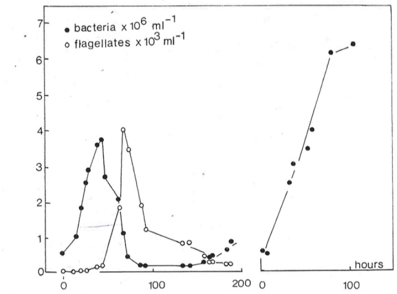


Fig. 58. Left: development of numbers of bacteria and of bacterivorous flagellates in a seawater sample filtered to remove larger plankters. Right: same water sample, but with the flagellates being removed as well. Redrawn from Fenchel [136]

In the field

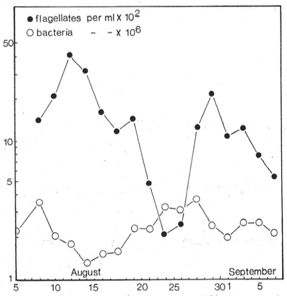


Fig. 59. Numbers of bacteria and bacterivorous flagellates in the surface waters of Limfjorden, Denmark, over one month. Redrawn from Fenchel [136]

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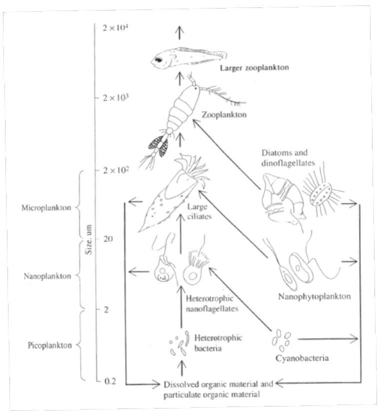
2.3. Consumers

- 2.3.1. Microbial loop

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



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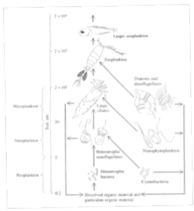
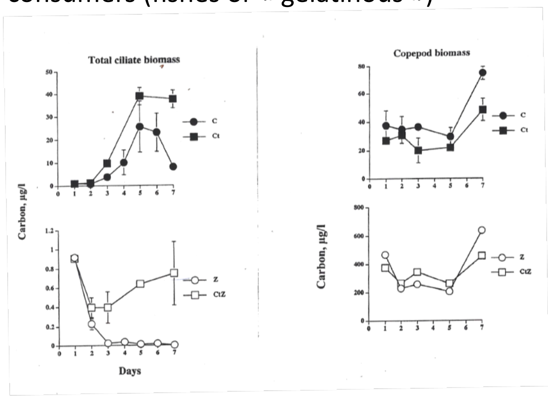
2.3. Consumers



- 2.3.2. Linear food-chain: plankton

Microplankton (diatoms and ciliates): top-down control by copepods

Copepods: top-down control by consumers (fishes or « gelatinous »)



Graneli & Turner 2002

Evolution of copepod and ciliate biomass during mesocosm studies using 90µm-filtered seawater from the Skagerrak (Sweden).

C: control: natural phytoplankton and zooplankton abundance

Z: zooplankton: natural phytoplankton + 10x natural zooplankton abundance

Ct: ctenophores: natural phytoplankton and zooplankton abundance + 10 ctenophores

CtZ: natural phytoplankton + 10x natural zooplankton abundance + 10 ctenophores

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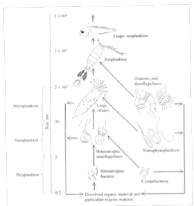
2.3. Consumers



Plankton:

- Succession of top-down controls:

Planktivorous fishes or « gelatinous »

↓

Copepods

↓

Ciliates

↓

Flagellates

↓

Bacteriae

= trophic cascade

- If copepods consumed by « gelatinous » (jelly-fishes, ctenophores) → impact on fisheries

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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

→ The highest the level number, the lowest the production of the level

→ 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

→ Fate of energy /C depends on the entry level of P_1

Diatoms → copepods = linear food chain
↘POM/DOM = microbial loop
Nanoflagellates → microbial loop

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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)

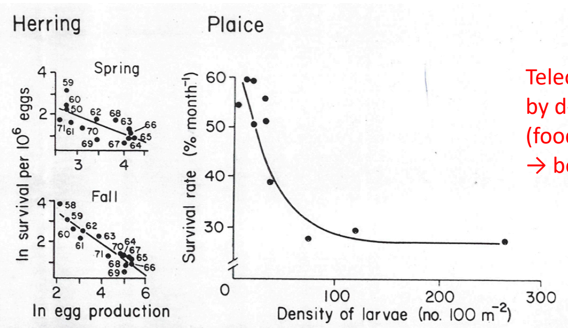

FIGURE 4-9. Survival of fish during the first year of life (age 0) at different densities. Data for spring and fall herring cohorts from Winters (1976). Plaice data from Lockwood (1978).

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

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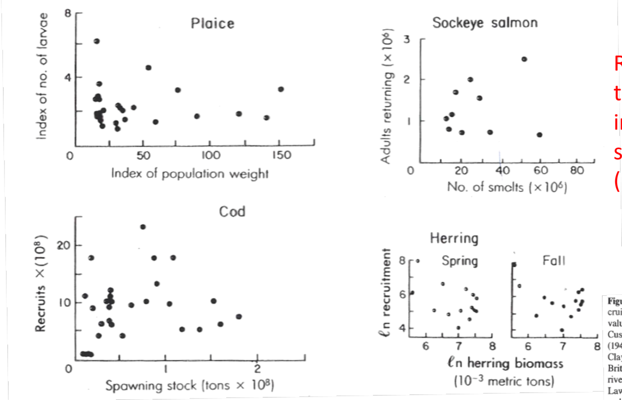
2.3. Consumers

- 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 (man!)

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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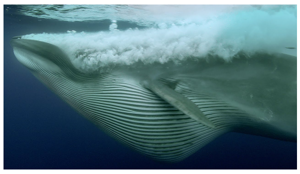
2.3. Consumers

- 2.3.2. Linear food-chain: nekton



Birds and mammals

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

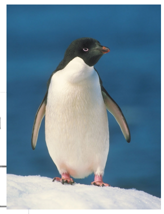


Table 9-3. Rough Estimates of Whale and Seal Stocks, Migratory Losses, and Food Consumption in Prepelagic Whaling and in Recent Times[a]

	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).

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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 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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