Benthic biological processes

1

Benthic Zone

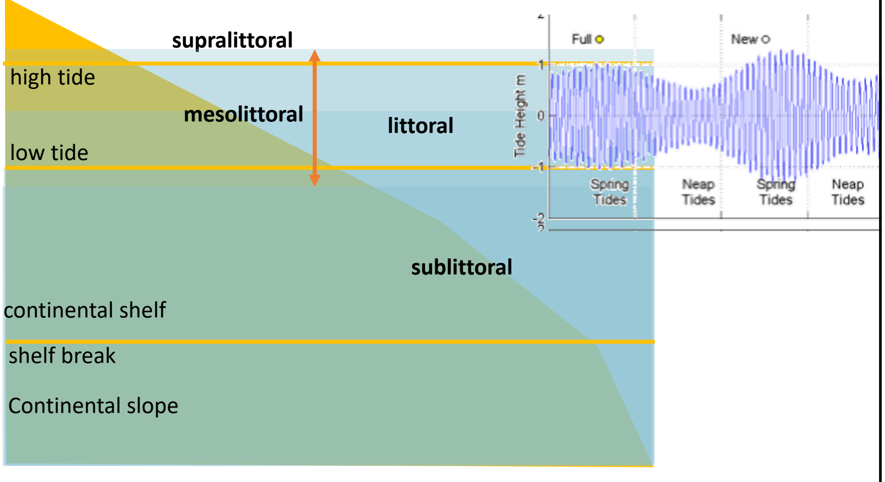
- Bénthos: 'the depths’
- lowest level: the sediment surface and some sub-surface layers

2

1. Characteristics of the benthic domain

- Position on the shore
- Available Light
- Depth
- Substrate

3



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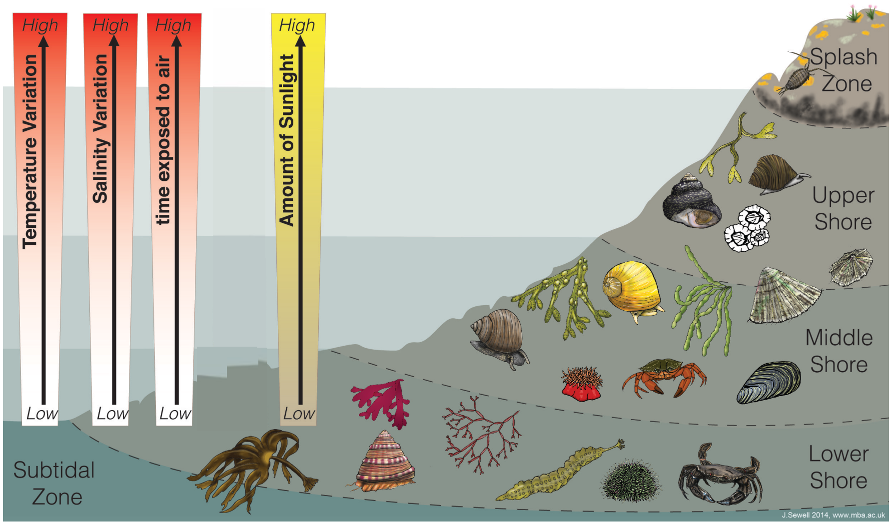

A schematic diagram of a rocky shore in the British Isles, showing the basic 'zones' and how environmental conditions change with height up the shore. © Marine Biological Association

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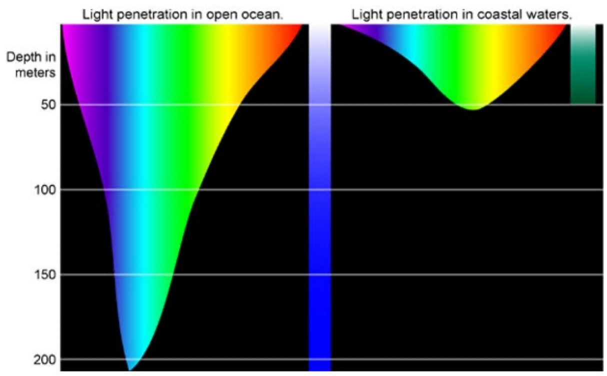
1. Characteristics of the benthic domain



Comparison of light penetration in open ocean and coastal water, showing the penetration depths of each colour (By NOAA – National Oceanic and Atmospheric Administration [Public domain], via Wikimedia Commons).

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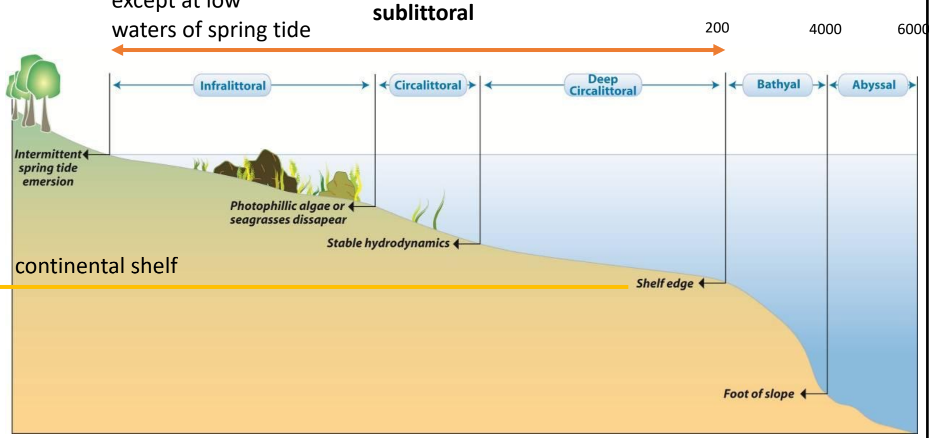
Circalittoral:
Compensation depth of the algae tolerating the lowest light intensities (150-200m)

Sublittoral:
Continuous immersion except at low waters of spring tide



EMODnet Phase 2 – Annual report

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1.1. Zones of the benthic domain

Tide level or depth	Zone	Characteristics
	Supralittoral	Saline moistening Continuous emersion except at extreme high waters of spring tide
Mean high water of spring tide		
	Mesolittoral	Daily cycles of immersion and emersion
Mean low water of neap tide		
	Infralittoral	Continuous immersion except at low waters of spring tide
Compensation depth of seagrasses or photophilic algae 15-20m at high lat. 30-40 m Mediterranean 80 m intertropical regions		
	Circalittoral	
Compensation depth of the algae tolerating the lowest light intensities (150-200m)		
	Bathyal	Continental slope and its foothills
3500-4000m		
	Abyssal	Abyssal plains Hydrothermal vents
6000-6500m		
	Hadal	Deep trenches

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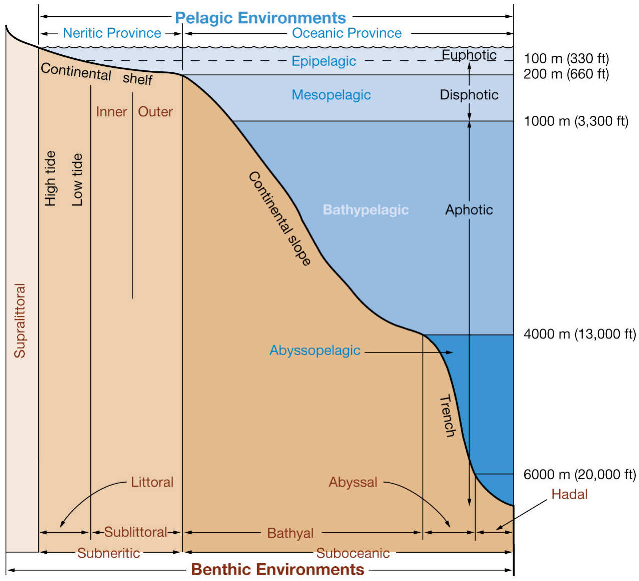
1. Characteristics of the benthic domain



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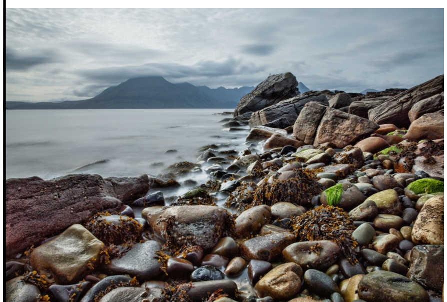
1.2. The substrate

- Hard substrate (immobile) vs. Soft subtrate (possible resuspension)
  - Depends on
    - Hydrodynamism and particle size
    - Slope of the substrate



https://pxhere.com/en/photo/1347376

Hard substrate

https://pixabay.com/photos/gravel-beach-stone-marine-texture-3873008/

Soft substrate

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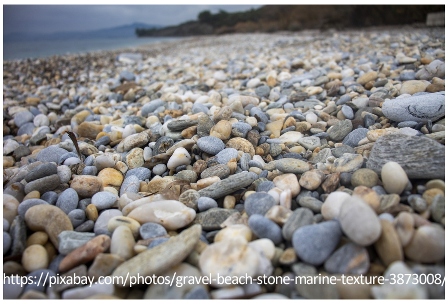
1.2. The substrate

- Hard substrate (immobile) vs. Soft subtrate (possible resuspension)
  - Depends on
    - Hydrodynamism and particle size
    - Slope of the substrate



Soft substrates

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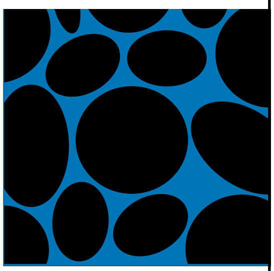
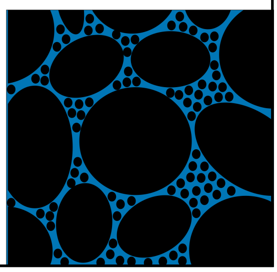
1.2. The substrate

Soft substrate

- Inorganic particles
- Organic particles
- Interstitial water

- Physical characteristics
  1. Size = function of hydrodynamism
     - Coarse sediments: few organic particles
     - Very fine sediments: instable for macrofauna
  2. Homogeneity
     - Well sorted: homogenous grain size
     - Poorly sorted: heterogenous grain size
  3. Porosity: $V_{interstitial} / V_{total}$
     - Depends on grain size and homogeneity of the sediment
     - Oxygen level
     - Important for meiofauna





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1.2. The substrate

Classification according to grain size

Particle sizes

φ scale	Size range (metric)	Aggregate class (Wentworth)	Other names
< -8	> 256 mm	Boulder	
-6 to -8	64–256 mm	Cobble	
-5 to -6	32–64 mm	Very coarse gravel	Pebble
-4 to -5	16–32 mm	Coarse gravel	Pebble
-3 to -4	8–16 mm	Medium gravel	Pebble
-2 to -3	4–8 mm	Fine gravel	Pebble
-1 to -2	2–4 mm	Very fine gravel	Granule
0 to -1	1–2 mm	Very coarse sand	
1 to 0	0.5–1 mm	Coarse sand	
2 to 1	0.25–0.5 mm	Medium sand	
3 to 2	125–250 μm	Fine sand	
4 to 3	62.5–125 μm	Very fine sand	
8 to 4	3.9–62.5 μm	Silt	Mud
> 8	< 3.9 μm	Clay	Mud
>10	< 1 μm	Colloid	Mud

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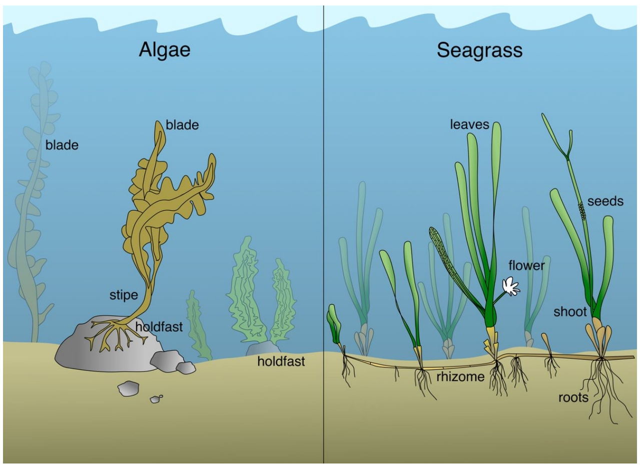

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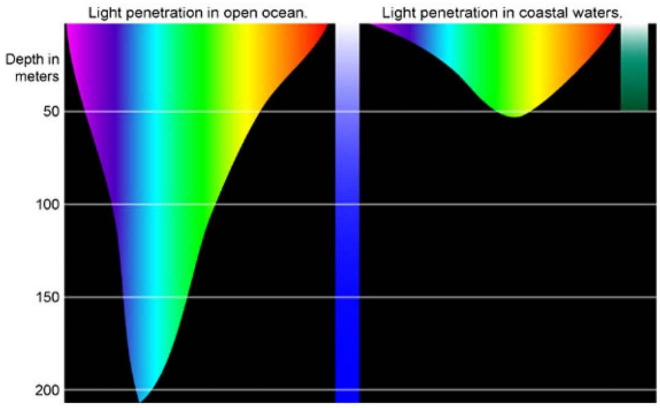
2. Benthic biological processes

2.1. Primary producers

2.1.1. Photosynthetic primary producers



Light penetration in open ocean and coastal water, showing the different depths to which each colour will penetrate (By NOAA – National Oceanic and Atmospheric Administration [Public domain], via Wikimedia Commons).

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2. Benthic biological processes

2.1. Primary producers

2.1.1. Photosynthetic primary producers

Domain	Kingdom	Phylum	
Bacteria			Cyanobacteria • Chla, phycocyanin, phycoerythrin • Able to fix N2 • Mats on tidal mudflats (anoxic interstitial water)

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Cyanobacteria

- Chla, phycocyanin, phycoerythrin
- Able to fix N2
- Mats on tidal mudflats (anoxic interstitial water)

Seasonal development of a coastal microbial mat. Cardoso et al. 2019

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2.1. Primary producers

2.1.1. Bacterial chemoautotrophic primary producers

Table 1-1. Major Electron Donors, Acceptors, and End Products for the Three Major Types of Primary Production[a]

	Electron donor (reductants)	Electron acceptor (oxidants)	Oxidized end products
Photosynthesis			
Oxygenic	H_2O	CO_2[b]	O_2
Anoxygenic	H_2S, H_2	CO_2[b]	S^0, SO_4^{2-}
Chemosynthesis			
Nitrifying bacteria[c]	NO_2^-, NH_4^+, NH_2OH	O_2, NO_3^-	NO_3^-, NO_2^-
Sulfur bacteria[c]	H_2S, S^0, $S_2O_3^-$	O_2	S^0, SO_4^{2-}
Hydrogen bacteria[c]	H_2	O, SO_4	H_2O
Methane bacteria[c]	CH_4	O_2	CO_2
Iron bacteria[c]	Fe^{2+}	O_2	Fe^{3+}
Carbon monoxide bacteria[c]	CO	H_2	CH_4

[a] From Fenchel and Blackburn (1979) and Parsons et al. (1977). There are many other possible chemosynthetic reactions and end products (see Tables 10-7, 10-8).
[b] Takes place if light furnishes the large amounts of energy needed to reduce the CO_2.
[c] These groups may also live heterotrophically, using a variety of organic compounds manufactured by other organisms as sources of energy (or electron donors), and with CO_2, H_2O, or more oxidized organic compounds as the end products.

- Interfaces oxic and anoxic zones
  - Sediments (RPD)
  - Decomposing organisms (whale carcasses)
  - Hydrothermal vents

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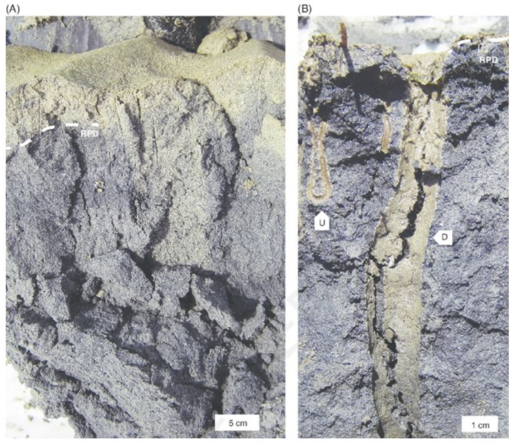
- Redox potential discontinuity (RPD). Redox potential discontinuity (RPD, dashed line) note a small U-shaped burrow (U: Arenicolites) and a decapod burrow (D. Parmaichnus or Thalassinoides).
- © Baucon & Felletti 2016



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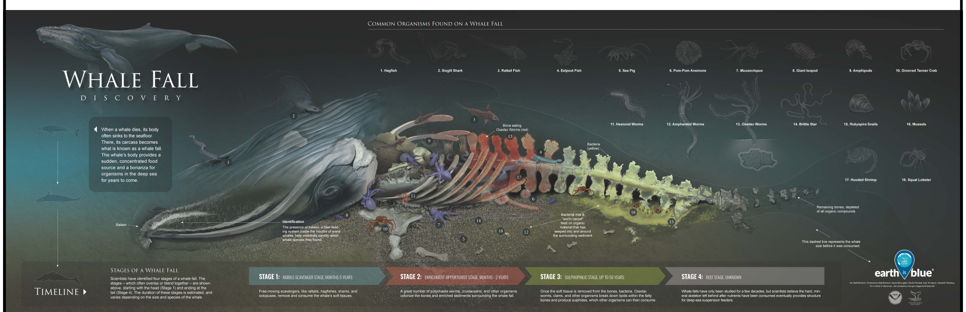

- **STAGE 1:** MOBILE-SCAVENGER STAGE, MONTHS-5 YEARS
- **STAGE 2:** ENRICHMENT-OPPORTUNIST STAGE, MONTHS - 2 YEARS
- **STAGE 3:** SULPHOPHILIC STAGE, UP TO 50 YEARS

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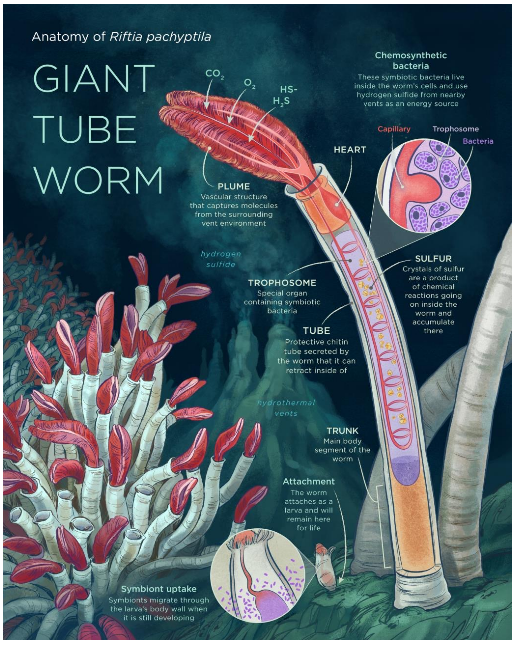

https://www.biointeractive.org/classroom-resources/how-giant-tube-worms-survive-hydrothe

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2. Benthic biological processes

2.1. Primary producers

2.1.1. Photosynthetic primary producers

Domain	Kingdom	Phylum	
Bacteria			Cyanobacteria • Chla, phycocyanin, phycoerythrin • Able to fix N2 • Mats on tidal mudflats (anoxic interstitial water)
Eukaryota	Chromista Chla, c abs green, yellow	Heterokontophyta	Microphytobenthos : principally pennate diatoms • Frequently mixotroph • Mats on tidal mudflats
			Phaeophyceae (brown algae) • Fucoxanthin, xantophyll, carotene • rocky shores
		Dinophyta	Zooxanthellae (Symbiodinium sp) Symbiont of cnidarians (incl reef-building corals)
	Plantae Chl a, b abs red, blue	Chlorophyta	Chlorophyceae (green algae) • Poor ability to store nutrients → eutrophic habitats
		Rhodophyta	Red algae Chl d, phycoerythrin (abs green), phycocyanin (abs blue)
		Spermatophyta	Flowering plants (soft bottom) • Seagrasses (Zostera, Posidonia, Thalassia…) • Saltmarsh plants (Spartina, Salicornia, …) • Mangroves

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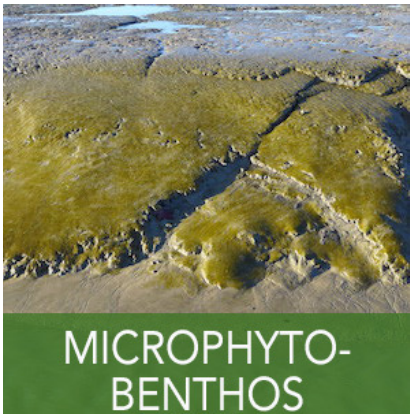
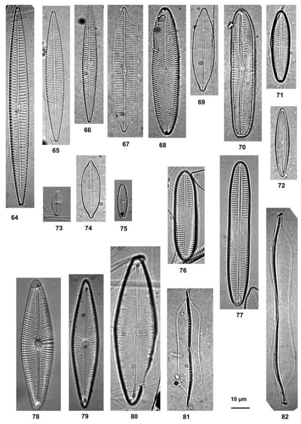
Microphytobenthos



Microphytobenthos : principally pennate diatoms

- Frequently mixotroph
- Mats on tidal mudflats



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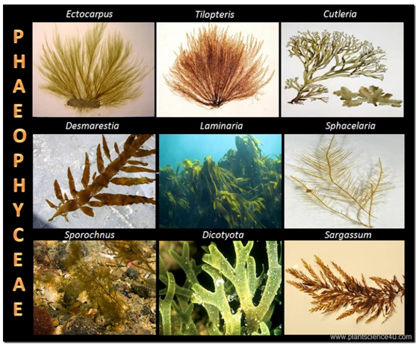
Phaeophyceae (brown algae)

- Fucoxanthin, xantophyll, carotene
- rocky shores
- dominant algae of intertidal zones and rocky infralittoral



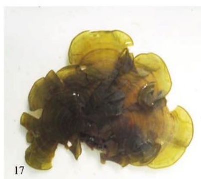


Fig. 15: *Turbinaria* sp. Fig. 17: *Padina pavonica*.

Bhagyaraj & Vijaya 2016

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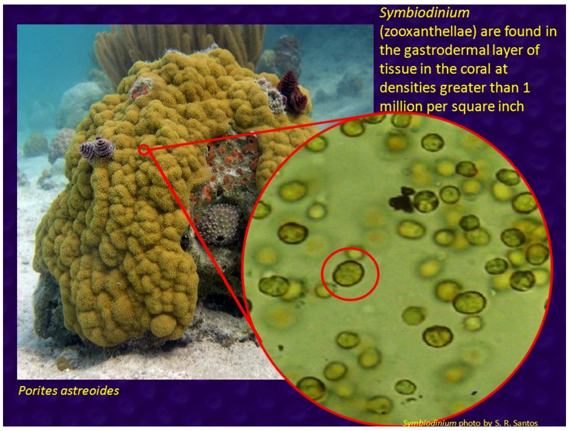
Zooxanthellae (Symbiodinium sp)



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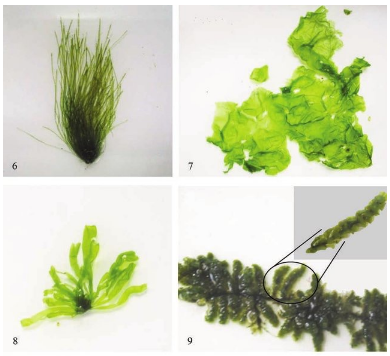
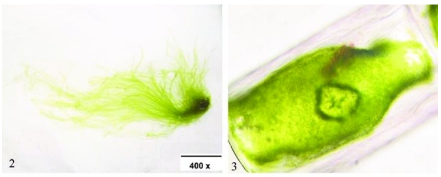
Chlorophyceae (green algae)

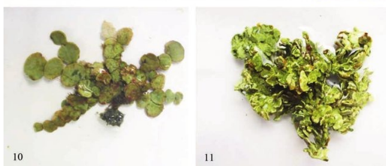


Chlorophyceae (green algae)

- Poor ability to store nutrients → eutrophic habitats

Fig. 2: *Ulva prolifera*.
Fig. 3: microphotograph of *Ulva prolifera* showing cellular contents.
Fig. 6: *Chaetomorpha linum*.
Fig. 7: *Ulva lactuca*.
Fig. 8: *Enteromorpha intestinalis*.
Fig. 9: *Caulerpa racemosa* and trumpet shaped ramuli of *C. racemosa*.
Fig. 10: *Halimeda tuna*.
Fig. 11: *Halimeda gracilis*. Bhagyaraj & Vijaya 2016





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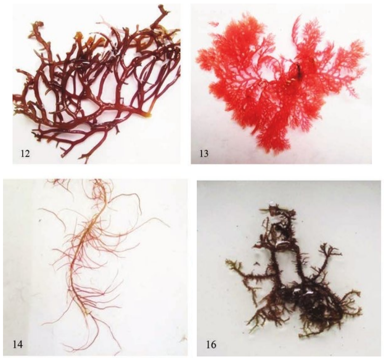
Rhodophyta (Red Algae)

- Fig. 12: *Kappaphycus alvarezii*.
  Fig. 13: *Portieria hornemannii*.
  Fig. 14: *Gracilaria verrucosa*.
  Fig. 16: *Hypnea musciformis*.

  Bhagyaraj & Vijaya 2016



Chl d, phycoerythrin (abs green), phycocyanin (abs blue)

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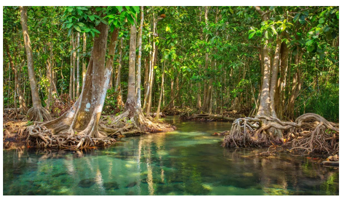
Flowering plants

Eelgrass *Zostera sp.*
© Project Seagrass

Common Cord-grass
Spartina anglica
© Bruno Nef, Waarnemingen.be



Mangrove © VUB

Flowering plants (soft bottom)

- Seagrasses (Zostera, Posidonia, Thalassia…)
- Saltmarsh plants (Spartina, Salicornia, …)
- Mangroves

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2. Benthic biological processes

2.1. Primary producers

2.1.1. Photosynthetic primary producers

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2.1. Primary production

2.1.2. Factors controlling benthic P1

Light (bottom-up control)

Wikipedia.org

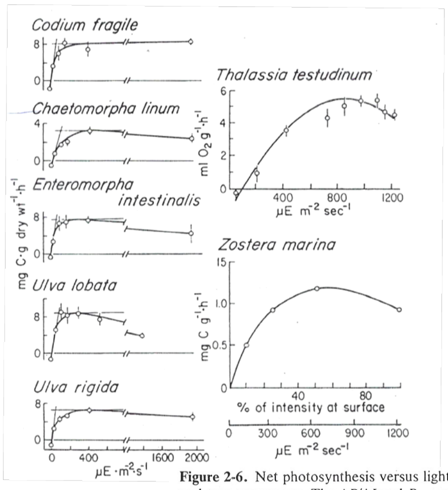

Figure 2-6. Net photosynthesis versus light intensities for five green macroalgae and two seagrasses. The $\Delta P/\Delta I$ and P_{max} are shown in the macroalgal graphs as straight lines. Points are mean and standard deviations, shown as vertical lines. Adapted from Arnold and Murray (1980), Buesa (1975), and McRoy (1974).

Inpn.mnhn.fr

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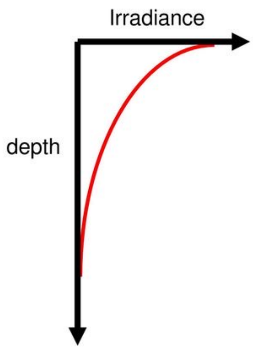
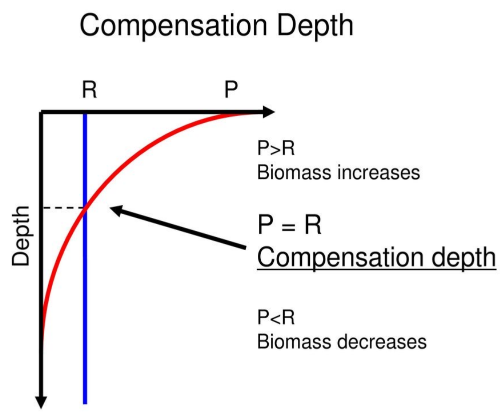
2.1. Primary production

2.1.2. Factors controlling benthic P1

Light intensity





https://player.slideplayer.com/79/13031396

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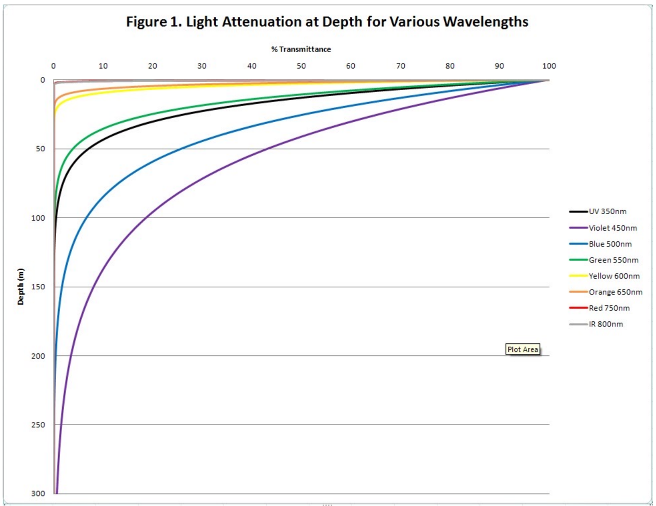
2.1. Primary production

2.1.2. Factors controlling benthic P1

Light: wave length



- Different taxa have different compensation depths
- Flowering plants, green algae: absorb red
- Red algae: absorb blue (+ adapted pigments)

http://oceanographyclay1987.blogspot.com/2010/10/light-attenuation-in-ocean.html

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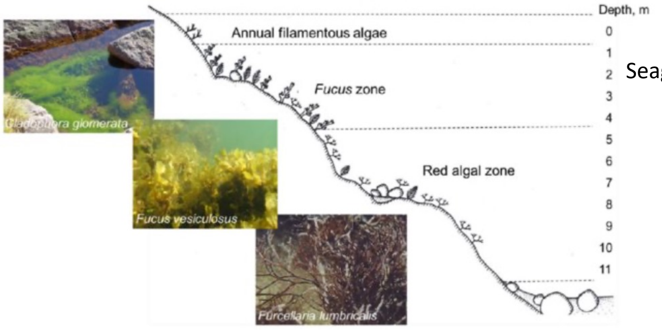

Seagrasses and green algae

red algae

Figure 3. General zonation of macroalgal groups in northern Baltic rocky shores with species examples. Photos by Elina Leskinen.

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2.1. Primary production

2.1.2. Factors controlling benthic P1

Nutrients (bottom-up control)

http://www.corpi.ku.lt/nemo/codium.html

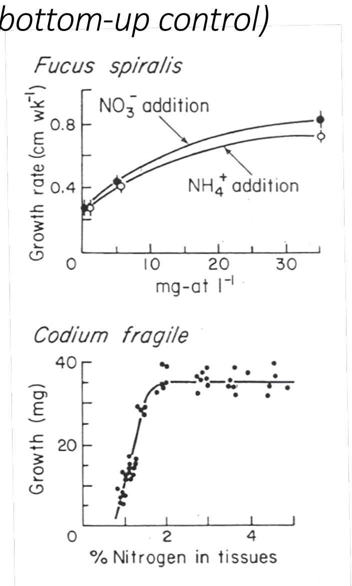

Figure 2-27. Top: Growth rate (elongation of fronds) of the brown alga *Fucus spiralis* in ambient concentrations (1.2 μg atom NO_3^- liter^{-1} and 1.7 μg atom NH_4^+ liter^{-1} and in cultures where additional NH_4^+ and NO_3^- were furnished. Adapted from Topinka and Robbins (1976). Bottom: Growth in weight of the green alga *Codium fragile* in relation to the percentage nitrogen in the tissues. Adapted from Hanisak (1979).

- Algae: no roots → nutrients > SW
- N possibly limiting

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2.1. Primary production
2.1.2. Factors controlling benthic P1
Nutrients

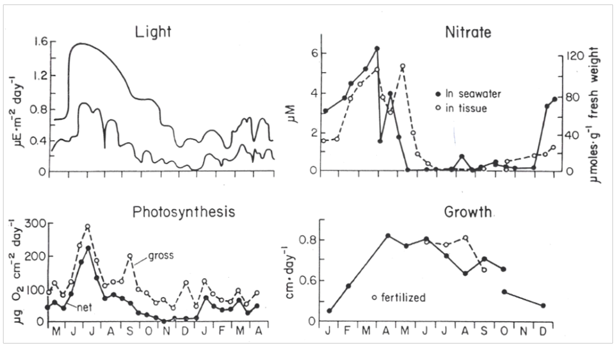

Figure 14-16. Seasonal cycle in growth and photosynthesis in the kelp *Laminaria longicruris* on the Nova Scotia coast. Left: Maximum and minimum light intensities (top) and rate of photosynthesis (bottom) during the year. Adapted from Hatcher et al. (1977). Right: Nitrate content in seawater and in tissues of kelp (top) and growth, as cm day^{-1} of blade elongation (bottom) in a kelp forest growing in water 18 m deep. Fertilization experiments done at site 9 m in depth; the growth rate of unfertilized kelp of 9 m was similar to that at 18 m. Adapted from Chapman and Craigie (1977).

joshfecteau.com

- Algae: no roots → nutrients > SW
- N possibly limiting if strong intra- or interspecific competition

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2.1. Primary production
2.1.2. Factors controlling benthic P1
Nutrients

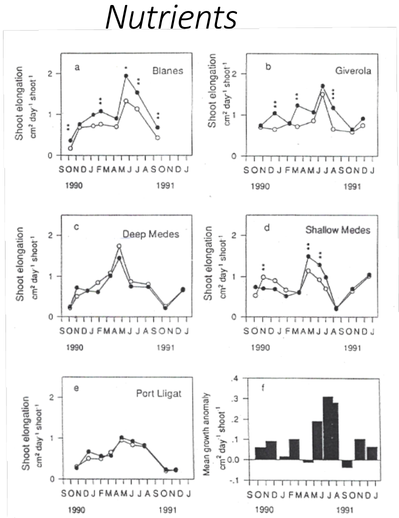

Fig. 1. *Posidonia oceanica*. (a to e) Seasonal changes in shoot elongation in control (o) and fertilized (•) plots at the 5 sites studied. (f) Mean growth anomaly relative to control (average growth in fertilized plots minus average growth in control plots). Asterisks indicate values significantly different from zero (***p < 0.001, ** p < 0.01, *p < 0.05)

Alcoverro et al 1995

- Phanerogams: roots → nutrients > sediment interstitial SW
- Anoxic sediment: inhibition of nutrient transporters → limitation

Posidonia oceanica

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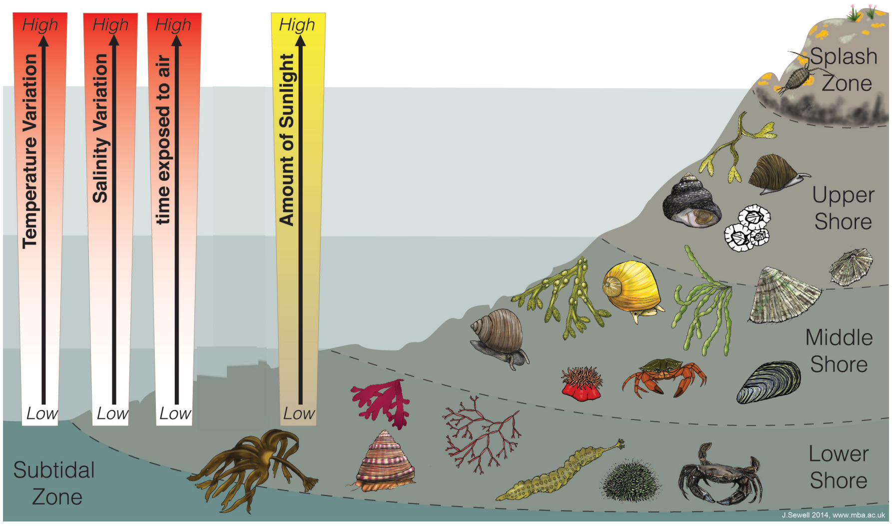

A schematic diagram of a rocky shore in the British Isles, showing the basic 'zones' and how environmental conditions change with height up the shore. © Marine Biological Association

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2.1. Primary producers

2.1.2. Factors controlling benthic P1: intertidal algae

Dessication, temperature, salinity, hydrodynamism (bottom-up controls)

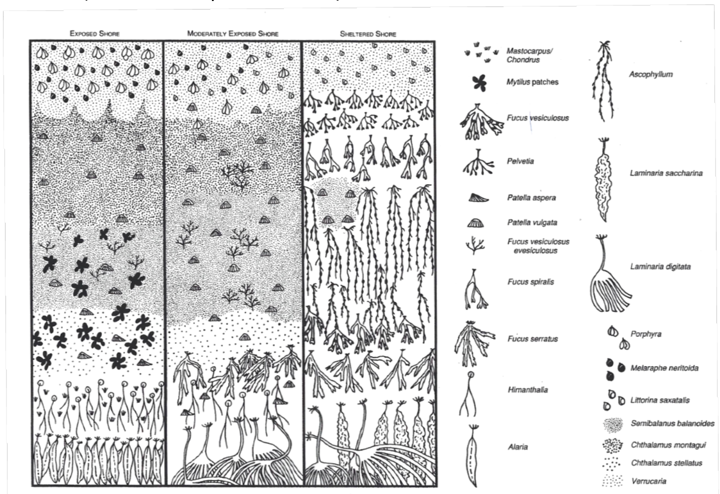

Fig. 5. Generalised diagram of a sheltered shore, a moderately exposed shore and an exposed shore on the west coast, showing the main zones of important shore organisms. (*After Ballantine, 1961*). Compare with Plate 1.

Intertidal zonation of algae

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2.1. Primary producers

2.1.2. Factors controlling benthic P1

Biotic interactions: ex. tide pools on rocky shores of New England

razottoli.wordpress.com/

Enteromorpha sp. islaynaturalhistory.blogspot.com

Littorina littorea Nozères Marinespecies.org

Chondrus crispus gulfofme.com

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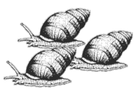
2.1. Primary producers

2.1.2. Factors controlling benthic P1

Biotic interactions: ex. tide pools on rocky shores of New England



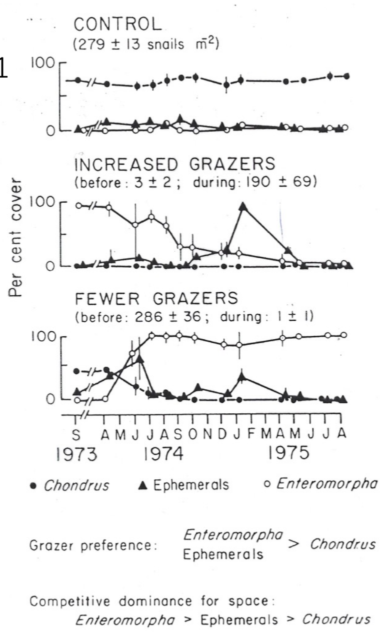


Figure 8-3. Experimental manipulation of a grazer snail (*Littorina littorea*) in tide pools in the higher reaches of the New England rocky intertidal zone. Adapted from Lubchenco (1978). © University of Chicago, reprinted by permission.

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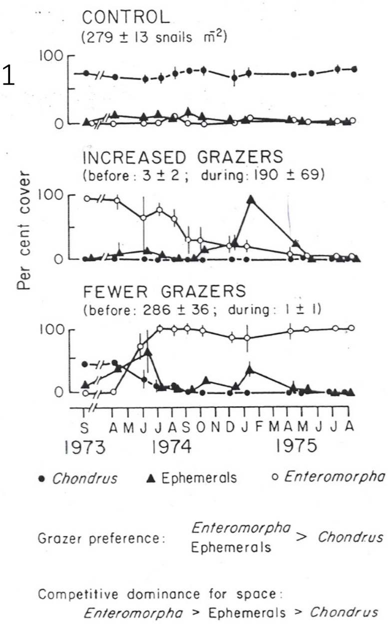
2.1. Primary producers

2.1.2. Factors controlling benthic P1

Biotic interactions: ex. tide pools on rocky shores of New England

- Grazer controls the composition of the P1 community, allowing the less competitive species to become dominant

➢ Top-down control by the grazer
➢ Competition for light/space between algae



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2.1. Primary producers

2.1.2. Factors controlling benthic P1

Biotic interactions: ex. giant kelp forest

Giant Kelp, Macrocystis pyrifera

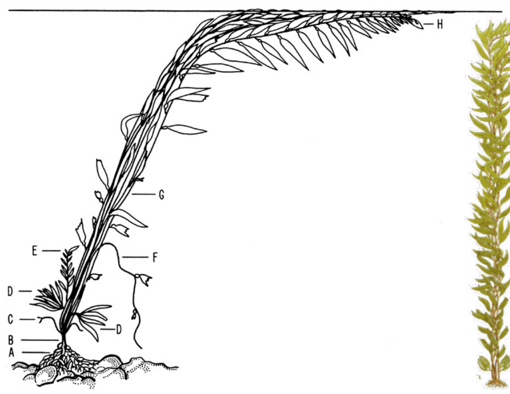

FIGURE 1. Diagram of a mature plant of the giant kelp, *Macrocystis pyrifera*, one to two years old, standing in 20 to 30 feet of water. A, holdfast; B, primary stipe; C, stub of an old frond; D, sporophyll clusters; E, juvenile frond; F, senile frond; G, stipe bundle; H, apical blade of mature frond, giving rise to additional blades.

© Andrea Dingeldein

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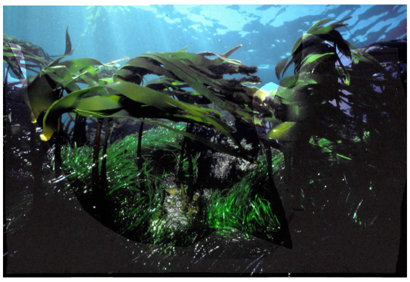
2.1. Primary producers

2.1.2. Factors controlling benthic P1

Biotic interactions: ex. giant kelp forest

© Andrea Dingeldein



Lovell and Libby Langstroth © California Academy of Sciences

Laminaria dentigera

Pterygophora californica

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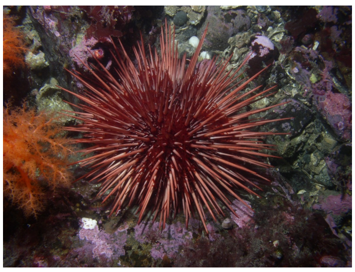
2.1. Primary producers

2.1.2. Factors controlling benthic P1

Biotic interactions: ex. giant kelp forest



inverts.wallawalla.edu

Strongylocentrotus franciscanus

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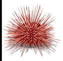
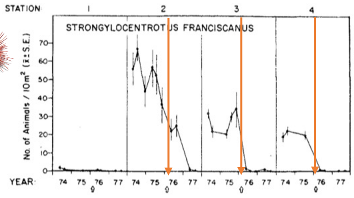
2.1. Primary producers

2.1.2. Factors controlling benthic P1

Biotic interactions: ex. giant kelp forest

1974-77: disease → ✝ sea urchins





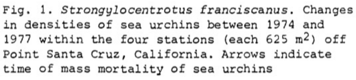


Fig. 1. *Strongylocentrotus franciscanus*. Changes in densities of sea urchins between 1974 and 1977 within the four stations (each 625 m²) off Point Santa Cruz, California. Arrows indicate time of mass mortality of sea urchins

- Release of the top-down control by the grazer

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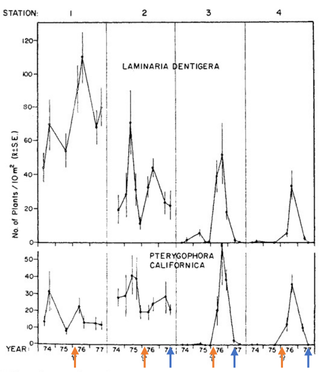
2.1. Primary producers

2.1.2. Factors controlling benthic P1

Biotic interactions: ex. giant kelp forest



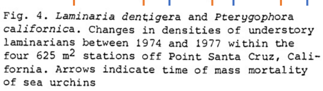


Fig. 4. *Laminaria dentigera* and *Pterygophora californica*. Changes in densities of understory laminarians between 1974 and 1977 within the four 625 m² stations off Point Santa Cruz, California. Arrows indicate time of mass mortality of sea urchins

Understory kelp plants, responded rapidly to the decreased in densities of sea urchins

in 1977 numerous dead and bladeless stipes of *L. dentigera* and *P.californica* were conspicuous at Stations 3 and 4, and nearly no live plants were found.

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2.1. Primary producers

2.1.2. Factors controlling benthic P1

Biotic interactions: ex. giant kelp forest

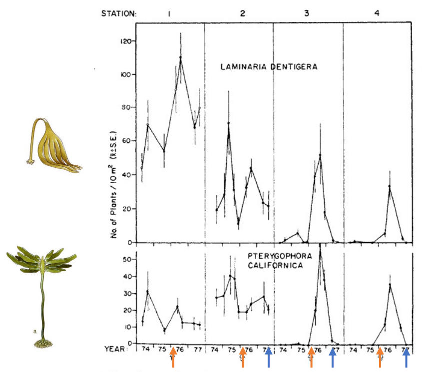

Fig. 4. *Laminaria dentigera* and *Pterygophora californica*. Changes in densities of understory laminarians between 1974 and 1977 within the four 625 m^2 stations off Point Santa Cruz, California. Arrows indicate time of mass mortality of sea urchins

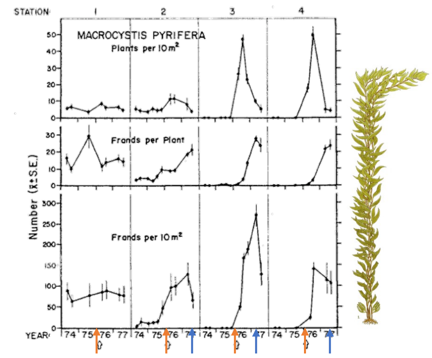

Fig. 2. *Macrocystis pyrifera*. Changes in plant densities, plant sizes, and frond densities of giant kelp between 1974 and 1977 within the four 625 m^2 stations off Point Santa Cruz, California. Arrows indicate time of mass mortality of sea urchins

Inter and Intraspecific competition

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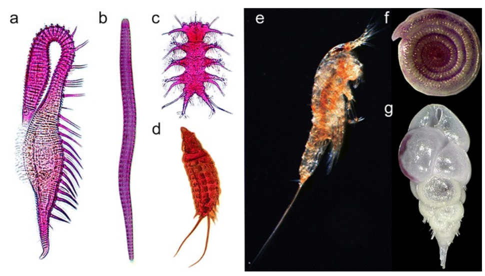
2.2. Consumers

2.2.1. Classification

- According to localization
  - Epifauna
  - Endofauna
    - Burrowers
    - Perforators
    - Interstitial fauna
- According to size

	Macrofauna
2- 0.5 mm	
	Meiofauna
100 – 40 µm	
	Microfauna



Zeppilli et al 2015

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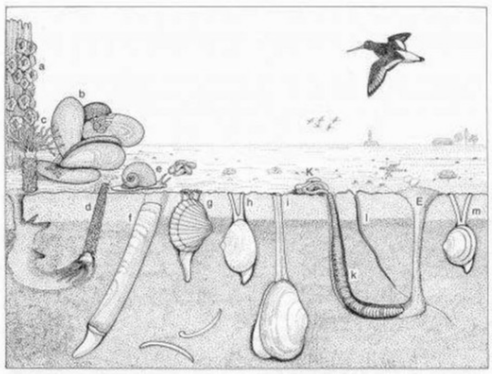

Profile of the sea floor showing typical **infaunal/epifauna** organisms (from Pierre Tardent).

a) Barnacles (Balaniden)
b) Blue mussels (*Mytilus edulis*)
c) Polychaete *Lanice conchilega*,
d) Polychaete *Lagis koreni*,
e) Snail *Littorina littorea*,
f) Rasor clam (*Ensis americanus*),
g) Bivalve *Cerastoderma edule*,
h) Bivalve *Scrobicularia plana*,
i) Bivalve *Mya arenaria*
k) Polychaet *Arenicola marina*,
l) Polychaete *Hediste diversicolor*,
m) Bivalve *Macoma balthica*

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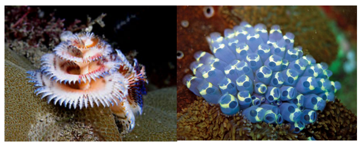
According to feeding type

- - suspensivorous: feeding on particles caught in the water column
- - depositivorous: feeding on sediment
- - herbivorous: feeding on primary producers
- - carnivorous: feeding on consumers
- - detritivorous: feeding detritus



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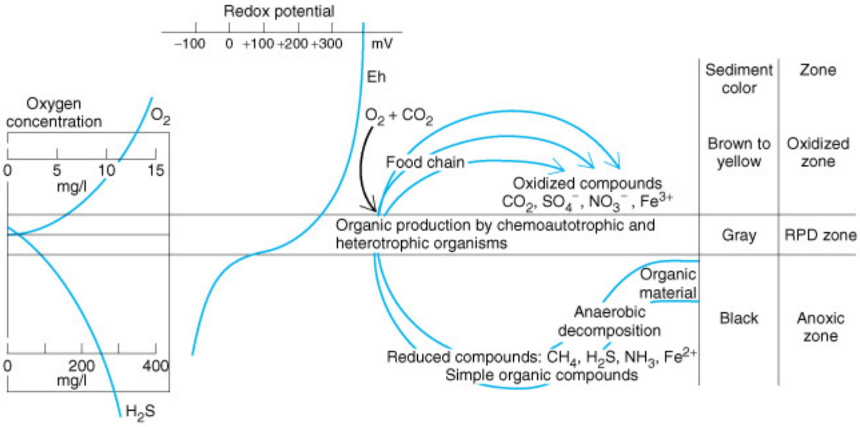
2.2. Consumers

2.2.2. Controlling factors

Soft substrate

- Chemical characteristics



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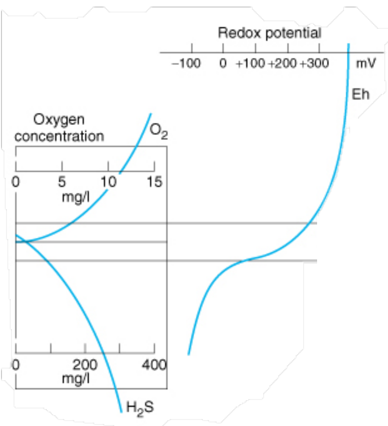
2.2. Consumers

2.2.2. Controlling factors

Soft substrate

- Chemical characteristics
  - Diffusion of O_2 from the interface SW - sediment
  - Consumption of O_2 in the superficial layers by aerobic bacteriae
  - → progressive ↓ of $[O_2]$ in interstitial water
  - → brutal change in oxydo-reduction potential: redox potential discontinuity (RPD) = interface aerobic – anaerobic layers
  - Depth of the RPD will depend on:
    - Hydrodynamism
    - Grain size and sorting



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2.2. Consumers

2.2.2. Controlling factors

Soft substrate

- Chemical characteristics
  - Vertical zonation of microorganisms

Sediment	Bacteria	Characteristics
oxic	aerobic (some photosynthetic)	
RPD	chemosynthetic sulfur bacteria	oxidize H_2S
	fermenting bacteria	anaerobic heterotrophs transform organic compounds into fatty acids and alcohols by glycolysis
anoxic	Sulfatoreducing bacteria	reduce SO_4^{2-} into H_2S
	Methane-producing bacteria	transform organic compounds into CH_4

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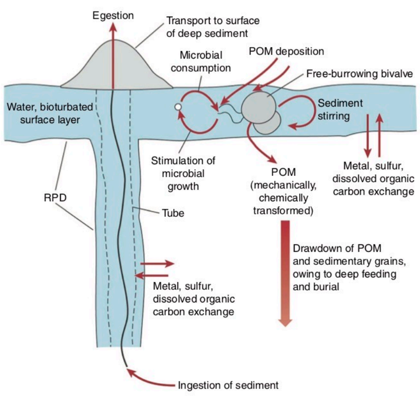
2.2. Consumers

2.2.2. Controlling factors

Soft substrate

- Chemical characteristics
  - Vertical zonation of eucaryotes
  - Meiofauna temporarily below RPD
  - Some protozoa able to live below the RPD (symbiotic bacteria)
  - Most of the meiofauna and all the macrofauna above the RPD
  - But… the RPD is not always horizontal! = bioturbation



Levinton 1995

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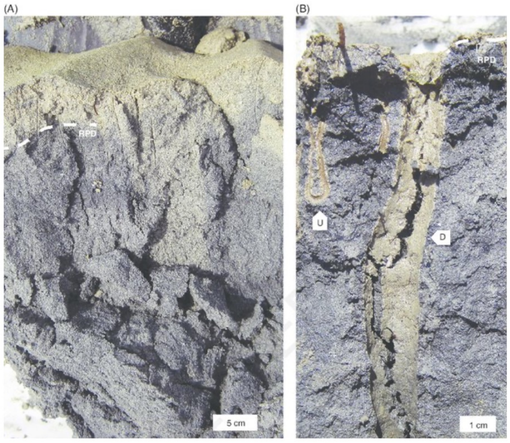
- Redox potential discontinuity (RPD). Redox potential discontinuity (RPD, dashed line) note a small U-shaped burrow (*U. Arenicolites*) and a decapod burrow (*D. Parmaichnus* or *Thalassinoides*).
- © Baucon & Felletti 2016



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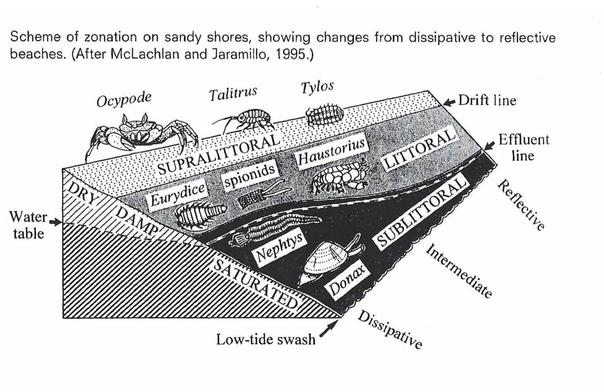
2.2. Consumers

2.2.2. Controlling factors

Soft substrate

Dessication, temperature, salinity, hydrodynamism



Intertidal zonation of metazoa

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2.2. Consumers

2.2.2. Controlling factors

Rocky substrate

Dessication, temperature, salinity, hydrodynamism

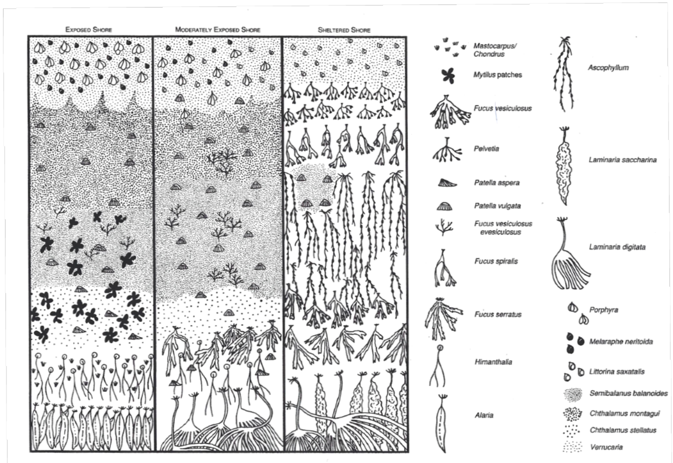

Fig. 5. Generalised diagram of a sheltered shore, a moderately exposed shore and an exposed shore on the west coast, showing the main zones of important shore organisms. (*After Ballantine, 1961*). Compare with Plate 1.

Intertidal zonation of metazoa

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2.2. Consumers

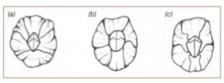
2.2.2. Controlling factors

Rocky substrate

Abiotic factors and biotic interactions

Chthamalus stellatus

Semibalanus balanoides



(a) Semibalanus balanoides
(b) Chthamalus stellatus
(c) Chthamalus montagui

Three British barnacle species; note that, in ***Chthamalus****, the central lines cross at right angles.*

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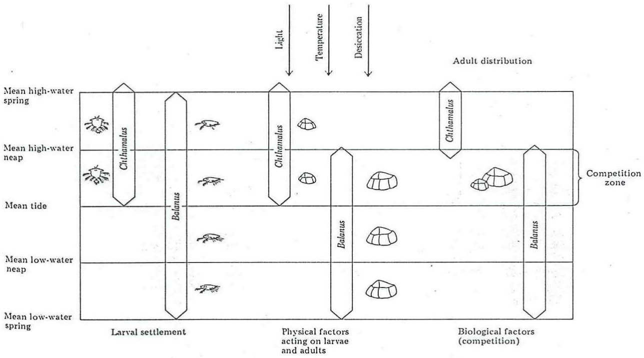
2.2. Consumers
2.2.2. Controlling factors
Rocky substrate
Abiotic factors and biotic interactions



Chthamalus stellatus

Semibalanus balanoides

- Larvae of two barnacles, *Chthamalus stellatus* and *Semibalanus balanoides*, settle out over a broad area
- Physical factors, mainly dessiccation, limit survival of *S. balanoides* above mean high water of neap tides
- Competition between *S. balanoides* and *C. stellatus* in the zone between mean tide and mean high water of neap tides eliminates *C. stellatus*.

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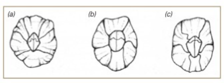
2.2. Consumers
2.2.2. Controlling factors
Rocky substrate
Abiotic factors and biotic interactions

Chthamalus stellatus



(a) Semibalanus balanoides
(b) Chthamalus stellatus
(c) Chthamalus montagui

Three British barnacle species; note that, in **Chthamalus**, the central lines cross at right angles.

Semibalanus balanoides

Chthamalus montagui

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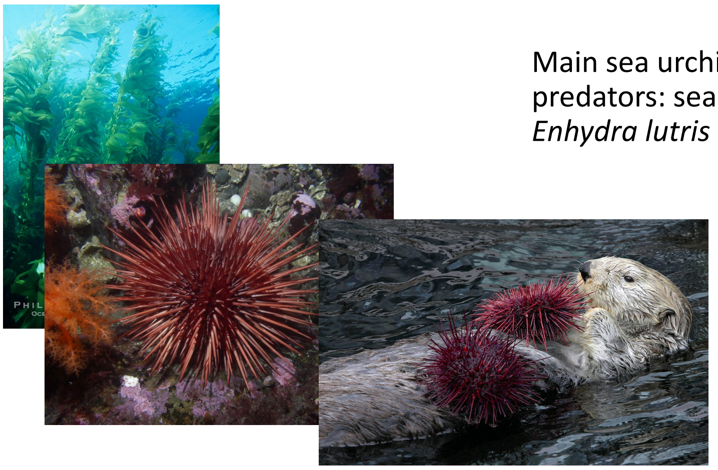
2.2. Consumers

2.2.2. Controlling factors

Rocky shores

Biotic interactions: ex giant kelp forests



Main sea urchin predators: sea otter *Enhydra lutris*

https://www.climate.gov/sites/default/files/otter_urchin_lrg.jpg

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2.2. Consumers

2.2.2. Controlling factors

Rocky shores

Biotic interactions: ex giant kelp forests

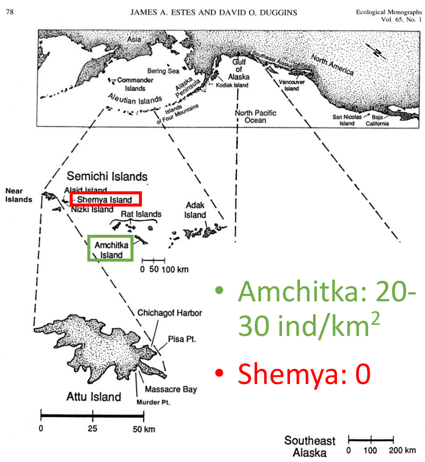

FIG. 1. Map of North Pacific Ocean showing study locations, sample sites, and place names referred to in the text.

- Amchitka: 20-30 ind/km^2
- Shemya: 0

Enhydra lutris

- Historical distribution: Aleutian Is - S California
- Quasi extinction beginning of 20th century (hunting)

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2.2. Consumers

2.2.2. Controlling factors

Rocky shores

Biotic interactions: ex giant kelp forests

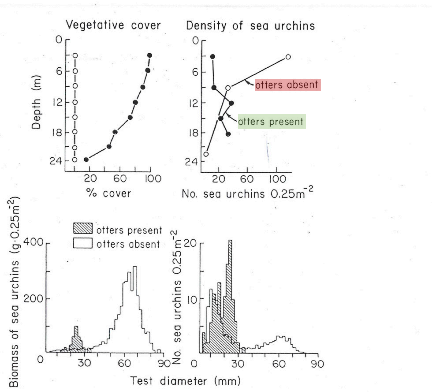

Figure 9-1. Interactions among sea otters, sea urchins, and vegetative cover in kelp beds off the Alaskan coast. Sea otters are present in Amchitka Island and absent in Shemya Island. Symbols on top left are the same as top right. Size of sea urchins is shown as the diameter of the test not including spines. Adapted from Estes and Palmisano (1974). © AAAS, reprinted by permission.

- Amchitka: Otters present:
  - Sea urchin density low
  - % cover kelp high
- Shemya: Otters absent:
  - Sea urchin density high
  - % cover kelp = 0
  - Higher biomass
  - Bimodal size distribution

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2.2. Consumers

2.2.2. Controlling factors

Rocky shores

Biotic interactions: ex giant kelp forests

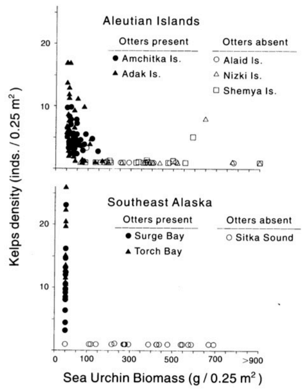

FIG. 7. Epibenthic kelp density (inds./0.25 m²) plotted against estimated sea urchin biomass (g/0.25 m²) for the Aleutian Islands and southeast Alaska. Points represent averages for sites within locations. Sea urchin biomass was estimated from samples of population density, size–frequency distribution, and the functional relation between test diameter and wet mass.

- Otters present:
  - Necessary for high kelp cover
- Otters absent:
  - Kelp cover always low

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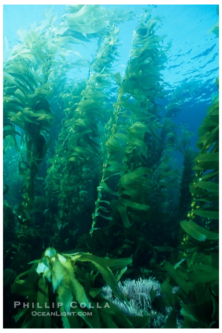
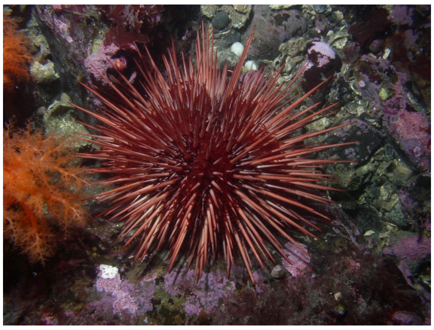
2.2. Consumers

2.2.2. Controlling factors

Rocky shores

Biotic interactions: ex giant kelp forests





Kelp and sea urchins have an indirect development:
Presence/absence also depends on recruitement of propagules or larvae

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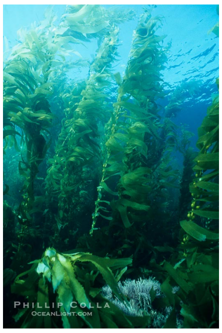
2.2. Consumers

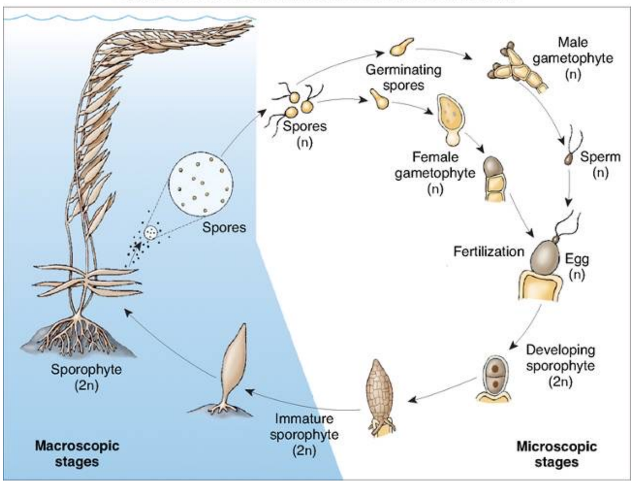
2.2.2. Controlling factors

Rocky shores

Biotic interactions: ex giant kelp forests



Planktonic stages



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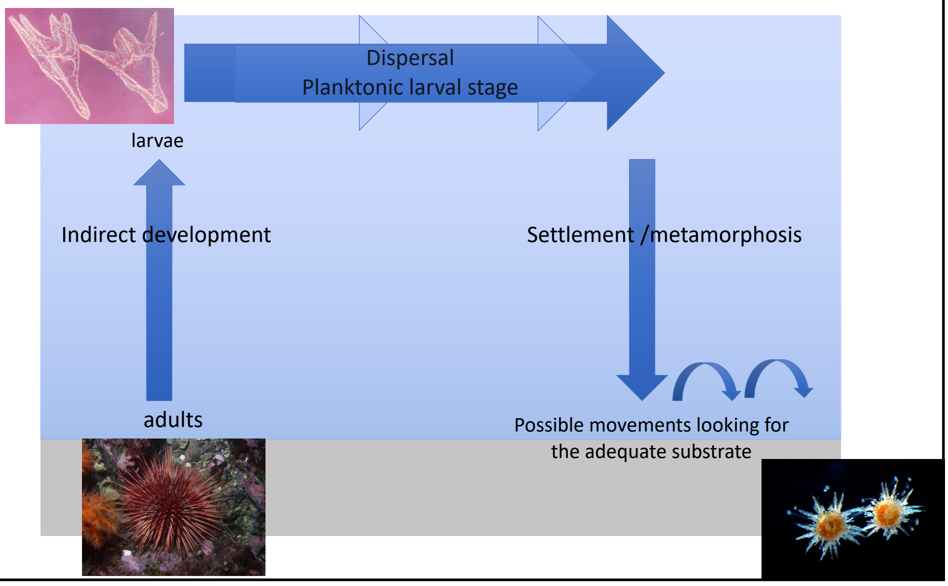
2.2. Consumers
2.2.2. Controlling factors
Rocky shores
Biotic interactions: ex giant kelp forests



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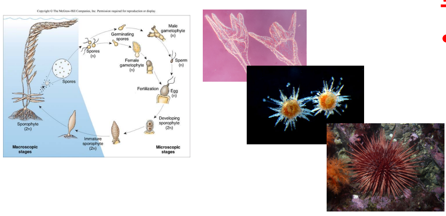
2.2. Consumers
2.2.2. Controlling factors
Rocky shores
Biotic interactions: ex giant kelp forests

<u>Top-down controls</u>
- Otters → sea urchins
- Sea urchins → kelp

= trophic cascade



<u>Recruitment of juveniles</u>
- Depends on the advection of competent larvae by hydrographic processes

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2.2. Consumers

2.1.2. Controlling factors

Rocky shores

Biotic interactions: ex. tide pools on rocky shores of New England

razottoli.wordpress.com/

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Biotic interactions: ex. tide pools on rocky shores of New England

Asterias forbesi

Thais/Nucella lapillus

Mytilus edulis

Semibalanus balanoides

Chondrus crispus

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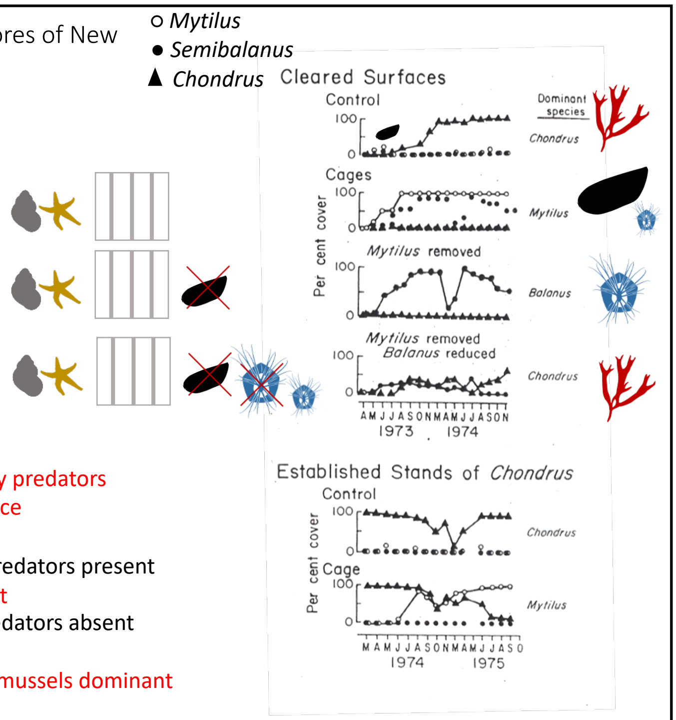
tide pools on rocky shores of New England



- Top-down control by predators
- Competition for space

- Sheltered shores: predators present
  - Algae dominant
- Exposed shores: predators absent (washed away)
  - Barnacles and mussels dominant

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- Sheltered shores: predators present
  - Algae dominant

72

- Exposed shores: predators absent
    - ➢ Barnacles and mussels dominant

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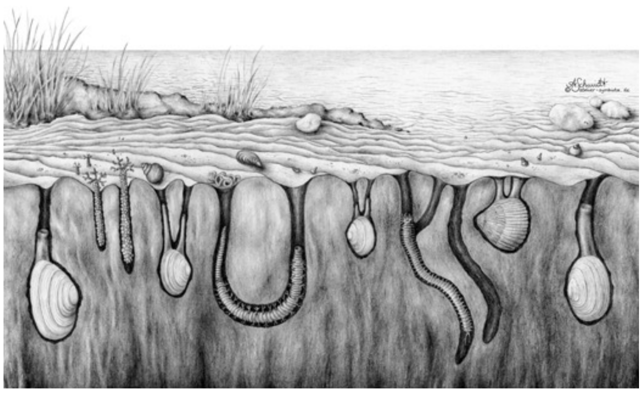
2.2. Consumers

2.1.2. Controlling factors

Sandy/muddy shores

Biotic interactions

- Effects much more variable than on rocky shores:
    - 3D environnement ➔ escape possibilities higher



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2.2. Consumers

2.1.2. Controlling factors

Sandy/muddy shores

Biotic interactions: competition

Olafsson & Persson 1986

Corophium volutator

- filter-feeder & detrivore
- burrows at sediment-water interface
- U-shaped

Nereis diversicolor

- filter-feeder & detrivore
- predator/scavenger
- burrows at sediment-water interface

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Sandy/muddy shores: Biotic interactions: competition

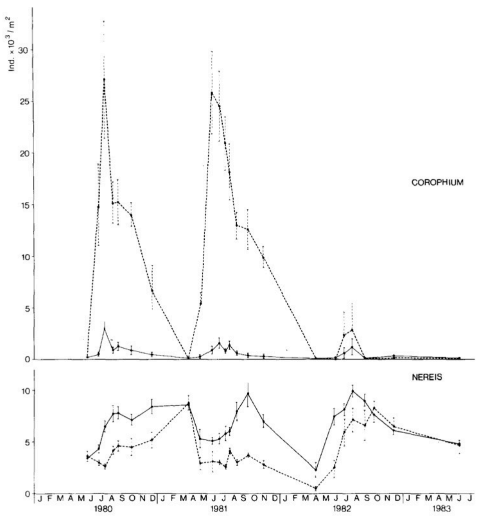

Fig. 2. Mean densities (± SE) of *Corophium volutator* (1980–1983) and *Nereis diversicolor* in the two sub-areas; solid line, 0–400 m (*n* = 15); broken line, 400–500 m (*n* = 5).

Olafsson & Persson 1986

Competition for space and exclusion: first come, first served <-> importance of recruitment

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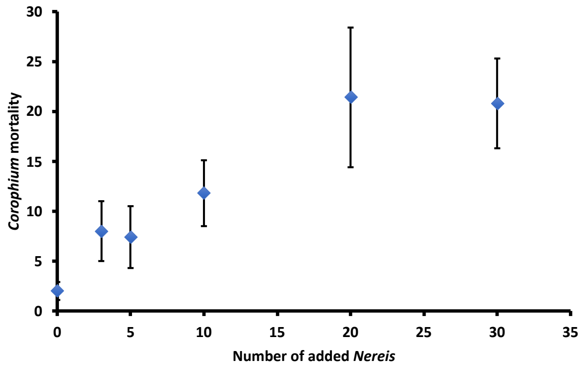
2.2. Consumers

2.1.2. Controlling factors

Sandy/muddy shores

Biotic interactions: competition

- Competition for space and exclusion: first come, first served <-> importance of recruitment



Olafsson & Persson 1986

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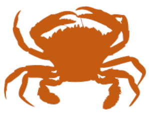
2.2. Consumers

2.1.2. Controlling factors

Sandy/muddy shores

Biotic interactions



- Predation: effects much more varied than on rocky shores:
  - More complex trophic networks ➔ mutiple trophic interactions mitigating the effects of excluding one predator
  - Ex: salt marsh NE USA

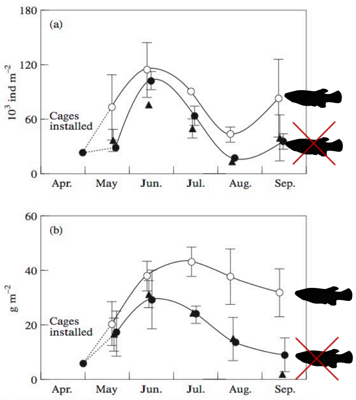


FIGURE 1. Monthly average density of macroinfauna inside complete cages (○), ambient sediments (●) and in partial cages (▲) (a) and the corresponding mean biomass (b). Vertical bars are standard errors of the mean.

Sarda et al 1998

↑ density and biomass of infauna

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2.2. Consumers

2.1.2. Controlling factors

Sandy/muddy shores

Biotic interactions

- Effects much more varied than on rocky shores:
  - Ex: salt marsh NE USA

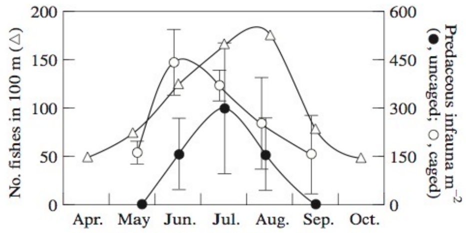

FIGURE 4. Density of predaceous infauna in complete cages and ambient sediments, and number of total fishes in a transect of 100 m in the tidal sandy channels of the marsh.

Sarda et al 1998

↑ predaceous infauna density

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2.2. Consumers

2.1.2. Controlling factors

Sandy/muddy shores

Biotic interactions

- Competition
  - Recruitment: first come, first served
  - Exclusion:
    - Modification of habitat (bioturbation)
    - Eradication of post-larvae
- Top-down control possible but:
  - More complex effects than on rocky shores
  - Not general: refuges
    - Burrowing
    - Protection by phanerogams (seagrass beds and mangroves)

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Evaluation

- **Method(s) of evaluation**
- Oral examination starting with the critical presentation of a scientific article in relation with the course (submitted for approval to the titular)
- Written reports for the practicals
- **Mark calculation method (including weighting of intermediary marks)**
- If the marks for the oral exam and practicals are both higher or equal to 8/20, then the final mark will be calculated as 70% for the oral exam and 30% for the practicals.If the mark of either the oral exam or the practicals is lower than 8/20, then the final mark will be the lower of these.

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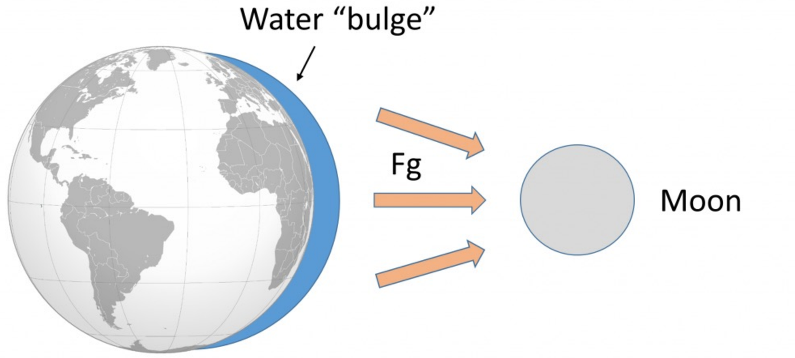
Tides

$$F_{grav} = \frac{G * m_1 * m_2}{d^2}$$

where G represents the universal gravitation constant

$(G = 6.67 \times 10^{-11}\ N{\cdot}m^2/kg^2)$



Gravitational forces between the Earth and moon cause a bulge of water to appear on the side of the Earth facing the moon (PW).

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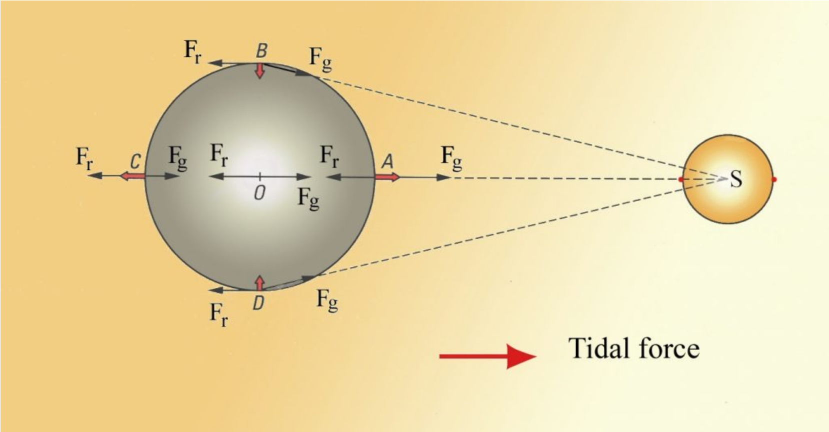
Gravitational forces vs inertial forces



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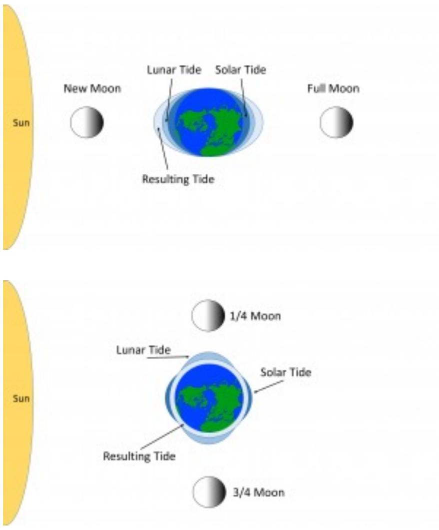
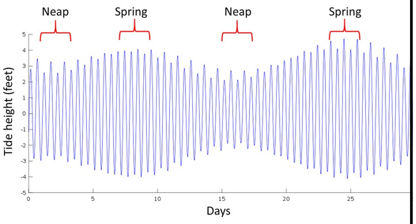
Sun





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- 400 variables influence tides
- Tidal day (24 hours 50 minutes)
- Declination of the moon
- continents and the bottom topograph

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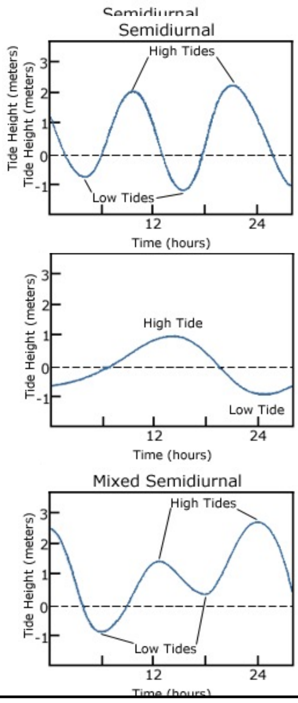

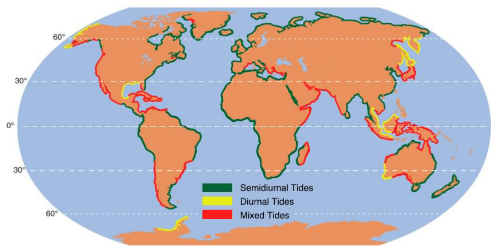

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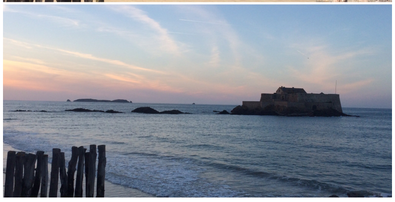

- St. Malo France
- Mediterranean

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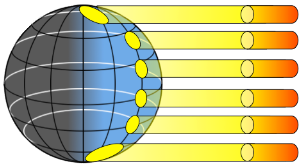

- *Because of the curvature of the Earth, the same amount of sunlight will be spread out over a larger area at the poles compared to the equator. The equator therefore receives more intense sunlight, and a greater amount of heat per unit of area (By Thebiologyprimer (Own work) [CC0], via Wikimedia Commons).*

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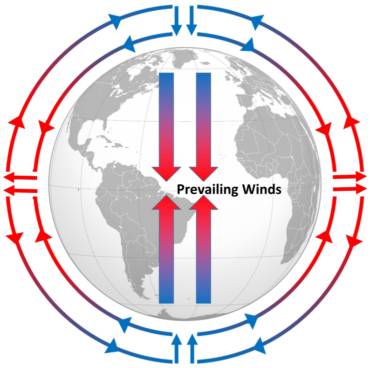
- *Hypothetical atmospheric convection cells on a non-rotating Earth. Air rises at the equator and sinks at the poles, creating a single convection cell in each hemisphere. The prevailing winds moving over the Earth's surface blow from the poles towards the equator in both hemispheres (Modified by PW from globe image by Location_of_Cape_Verde_in_the_globe.svg: Eddo derivative work: Luan fala! [CC BY-SA 3.0], via Wikimedia Commons).*



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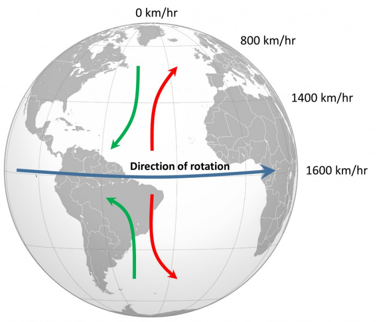

- *The Coriolis Effect. Objects moving from the equator towards the poles (red arrows) move into a region of slower rotational speed and their paths are deflected "ahead" of their point of origin. Movement from high latitudes to low latitudes (green arrows) goes from a region of low speed to a region of higher rotation speed, and there is deflection "behind" their point of origin. In the Northern Hemisphere this deflection is always to the right from the point of origin, and in the Southern Hemisphere the deflection is always to the left (Modified by PW from globe image by Location_of_Cape_Verde_in_the_globe.svg: Eddo derivative work: Luan fala! [CC BY-SA 3.0], via Wikimedia Commons).*

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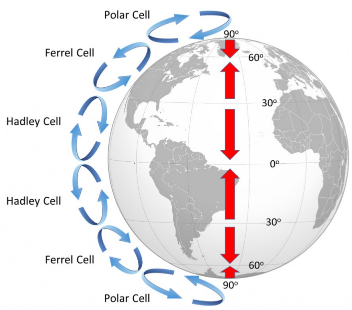
- *On a rotating Earth, there are three atmospheric convection cells in each hemisphere, leading to alternating bands of surface winds (red arrows) (Modified by PW from globe image by Location_of_Cape_Verde_in_the_globe.svg: Eddo derivative work: Luan fala! [CC BY-SA 3.0], via Wikimedia Commons).*



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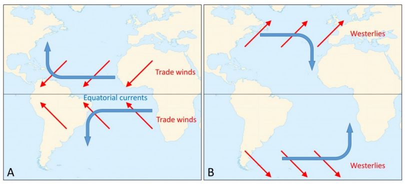
- *Generalized surface currents in the Atlantic Ocean. A) Surface water moving at 45° relative to the trade winds create the westward flowing equatorial currents. B) Between 30-60° latitude, the westerlies form eastward flowing surface currents (PW, map by Catrin (Own work, Using GMT) [CC BY-SA 3.0], via Wikimedia Commons).*



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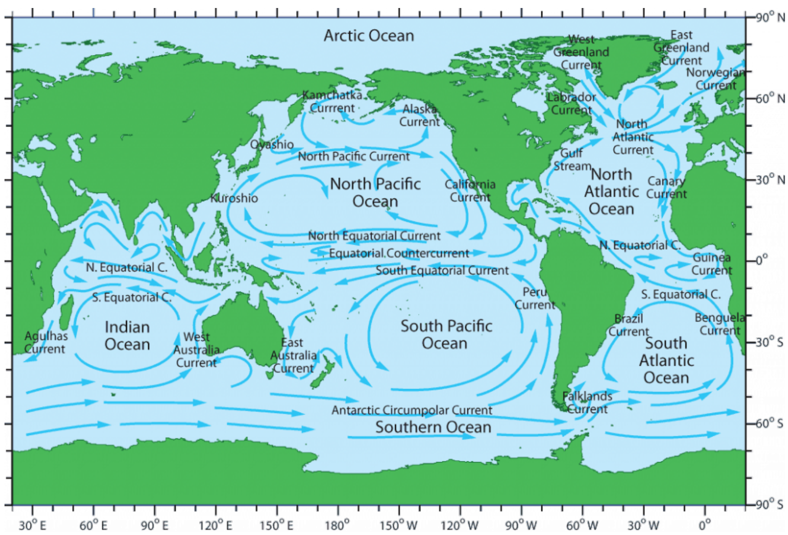

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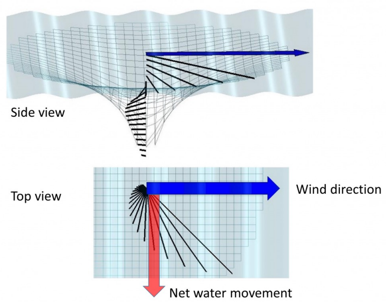

- *The Ekman spiral, shown for the Northern Hemisphere. Wind blowing over the water (blue arrow) creates a surface current 45º offset from the wind. Each successive layer of water is moved and deflected by the layer above, creating a spiraling pattern of water movement that diminishes with depth. The net movement of the water within the spiral is 90º relative to the wind direction (red arrow) (Modified by PW from Ekman spiral By Schlusenbach (unbekannt) [Public domain], via Wikimedia Commons).*

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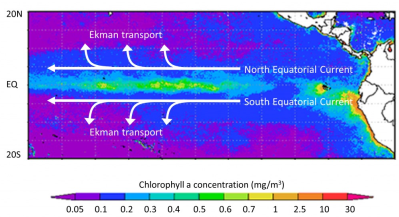

- *Equatorial upwelling and increased productivity as a result of divergence between the north and south equatorial currents (Modified by PW from image by NASA [Public domain], via Wikimedia Commons).*

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