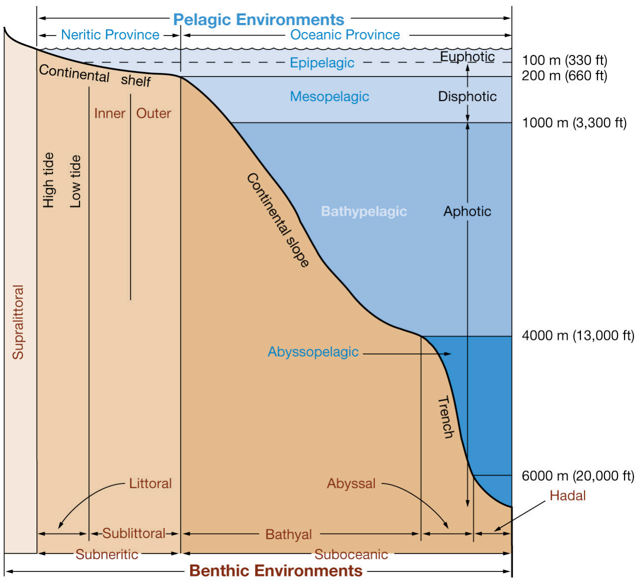
Benthic biological processes

1

1. Zones of the benthic domain



2

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
2500-3000m		
	Abyssal	Abyssal plains Hydrothermal vents
6000-6500m		
	Hadal	Deep trenches

3

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

4

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	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

5

2.1. Primary production

2.1.2. Factors controlling benthic P1

Light (bottom-up control)

Wikipedia.org

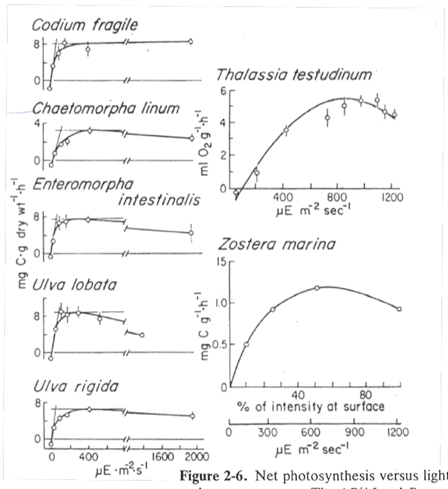


Figure 2-6. Net photosynthesis versus light intensities for five green macroalgae and two seagrasses. The $\Delta P/\Delta I$ and P_{max} are shown in the macroalgal graphs as straight lines. Points are mean and standard deviations, shown as vertical lines. Adapted from Arnold and Murray (1980), Buesa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

Inpn.mnhn.fr

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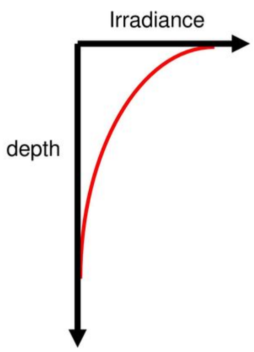
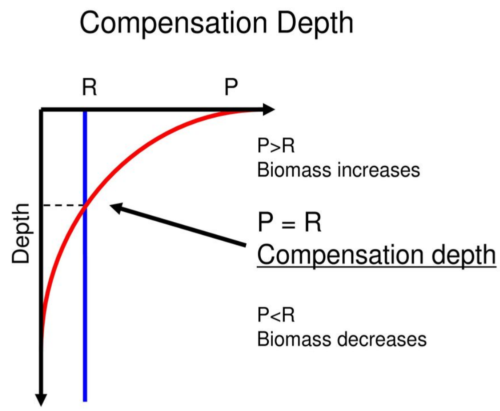
2.1. Primary production
2.1.2. Factors controlling benthic P1
Light intensity





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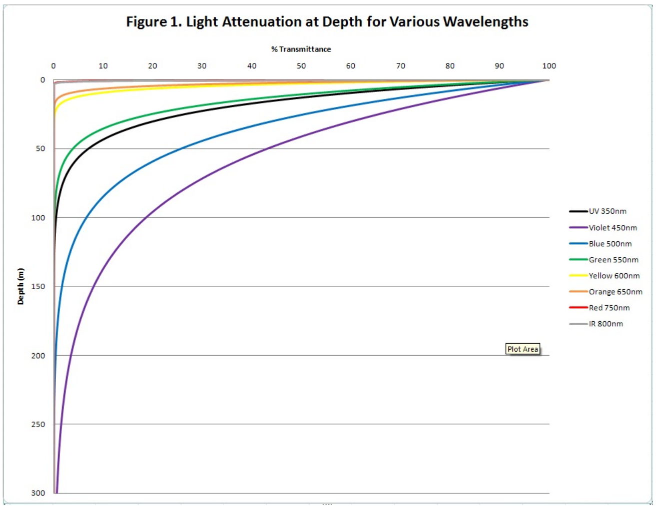
7

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

8

2.1. Primary production

2.1.2. Factors controlling benthic P1

Nutrients (bottom-up control)

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

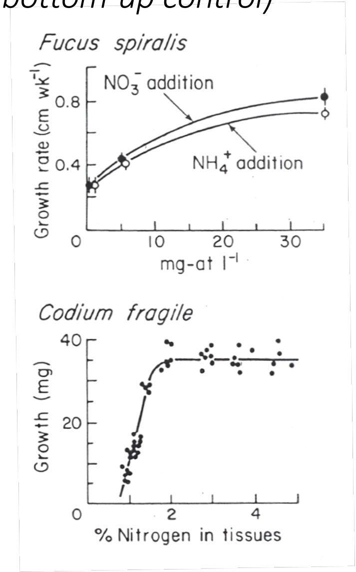


Figure 2-27. Top: Growth rate (elongation of fronds) of the brown alga *Fucus spiralis* in ambient concentrations (1.2 μg atom NO_3^- liter^{-1} and 1.7 μg atom NH_4^+ liter^{-1} and in cultures where additional NH_4^+ and NO_3^- were furnished. Adapted from Topinka and Robbins (1976). Bottom: Growth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

joshfecteau.com

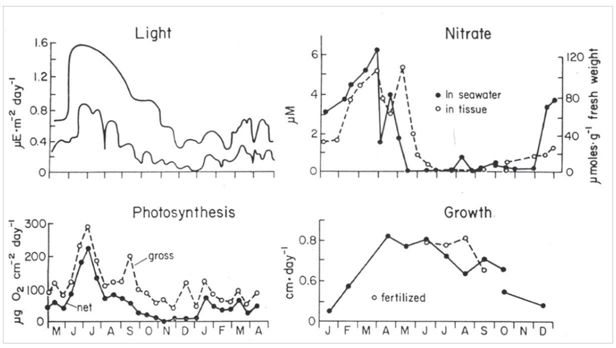

Figure 14-16. Seasonal cycle in growth and photosynthesis in the kelp *Laminaria longicruris* on the Nova Scotia coast. Left: Maximum and minimum light intensities (top) and rate of photosynthesis (bottom) during the year. Adapted from Hatcher et al. (1977). Right: Nitrate content in seawater and in 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).

- 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

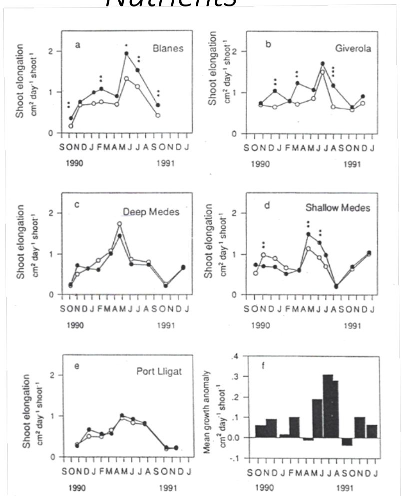

Fig. 1. *Posidonia oceanica*. (a to e) Seasonal changes in shoot elongation in control (o) and fertilized (•) plots at the 5 sites studied. (f) Mean growth anomaly relative to control (average growth in fertilized plots minus average growth in control plots). Asterisks indicate values significantly different 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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2.1. Primary producers

2.1.2. Factors controlling benthic P1: intertidal algae

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

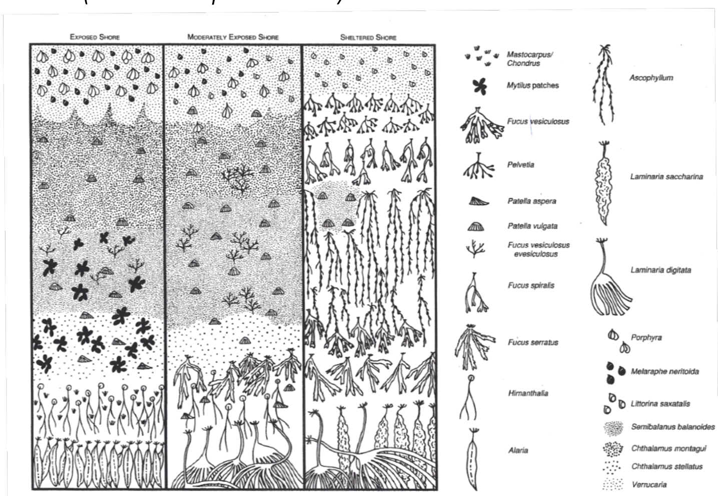

Fig. 5. Generalised diagram of a sheltered shore, a moderately exposed shore and an exposed shore on the west coast, showing the main zones of important shore organisms. (*After Ballantine, 1961*). Compare with Plate 1.

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

13

2.1. Primary producers

2.1.2. Factors controlling benthic P1

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

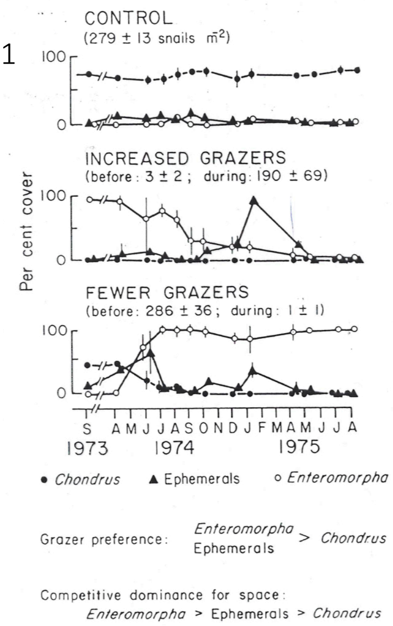

Figure 8-3. Experimental manipulation of a grazer snail (*Littorina littorea*) in tide pools in the higher reaches of the New England rocky intertidal zone. Adapted from Lubchenco (1978). © University of Chicago, reprinted by permission.

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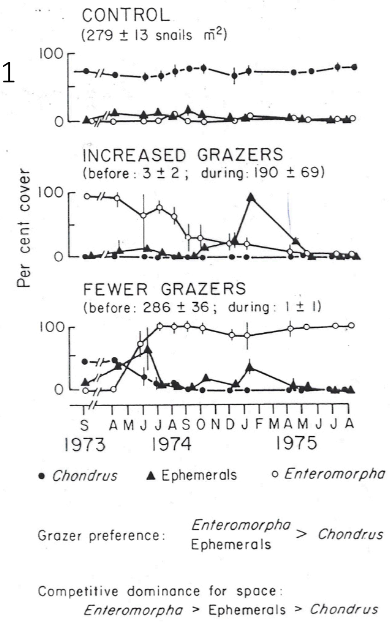
2.1. Primary producers

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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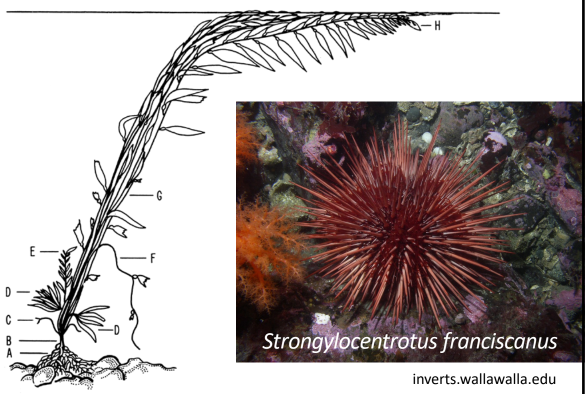
2.1. Primary producers

2.1.2. Factors controlling benthic P1

Biotic interactions: ex. giant kelp forest

Macrocystis pyrifera



inverts.wallawalla.edu

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.

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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

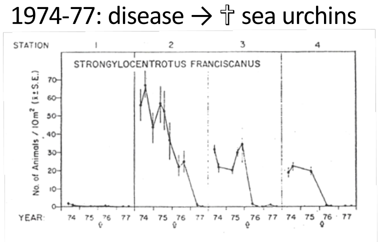

Fig. 1. *Strongylocentrotus franciscanus*. Changes in densities of sea urchins between 1974 and 1977 within the four stations (each 625 m^2) off Point Santa Cruz, California. Arrows indicate time of mass mortality of sea urchins

- Release of the top-down control by the grazer
- Intraspecific competition

Exponential ↑ of kelp then ↓ density

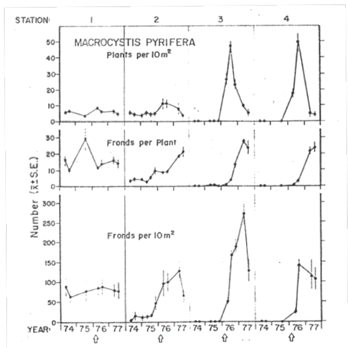

Fig. 2. *Macrocystis pyrifera*. Changes in plant densities, plant sizes, and frond densities of giant kelp between 1974 and 1977 within the four 625 m^2 stations off Point Santa Cruz, California. Arrows indicate time of mass mortality of sea urchins

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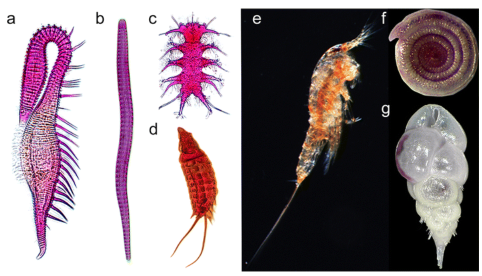
2.2. Consumers
2.2.1. Classification

- 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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2.2. Consumers

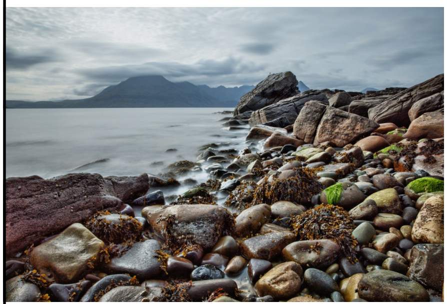
2.2.2. Controlling factors

Substrate

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

https://p

https://www.booking.com/hotel/to/sandy-beach-resort.fr.html



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

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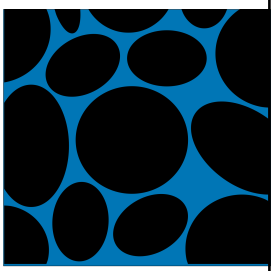
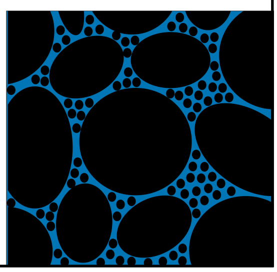
2.2. Consumers

2.2.2. Controlling factors

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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2.2. Consumers

2.2.2. Controlling factors

Soft 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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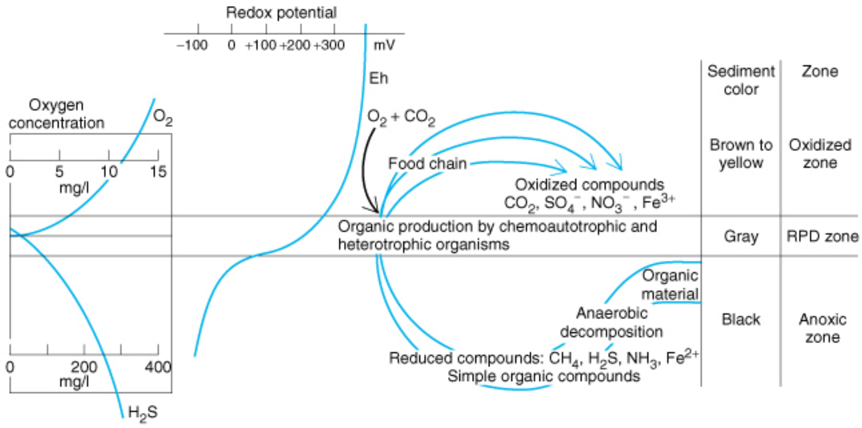
2.2. Consumers

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
anoxic	fermenting bacteria	anaerobic heterotrophs transform organic compounds into fatty acids and alcohols by glycolysis
	Sulfatoreducing bacteria	reduce SO_4^{2-} into H_2S
	Methane-producing bacteria	transform organic compounds into CH_4

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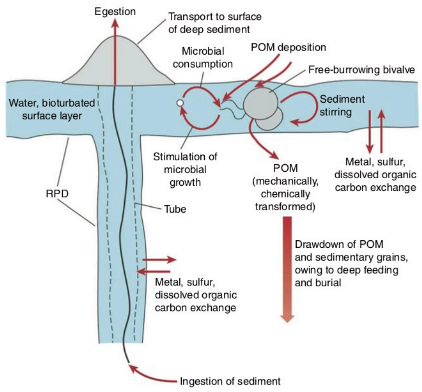
2.2. Consumers

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

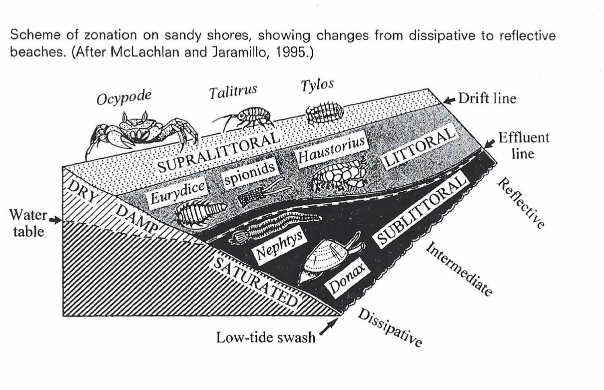
25

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

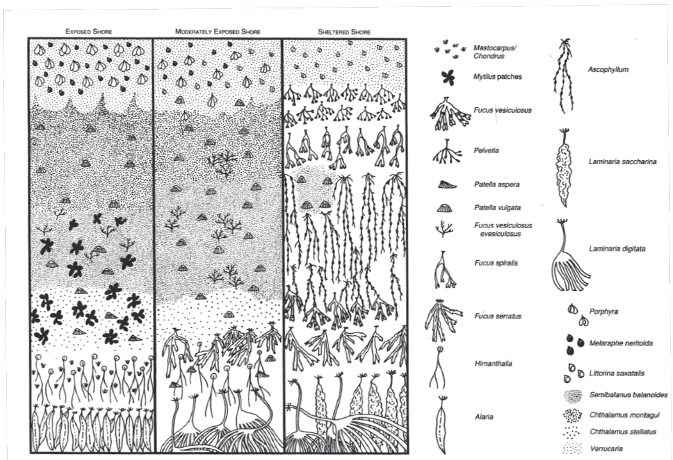

Fig. 5. Generalised diagram of a sheltered shore, a moderately exposed shore and an exposed shore on the west coast, showing the main zones of important shore organisms. (*After Ballantine, 1961*). Compare with Plate 1.

Intertidal zonation of metazoa

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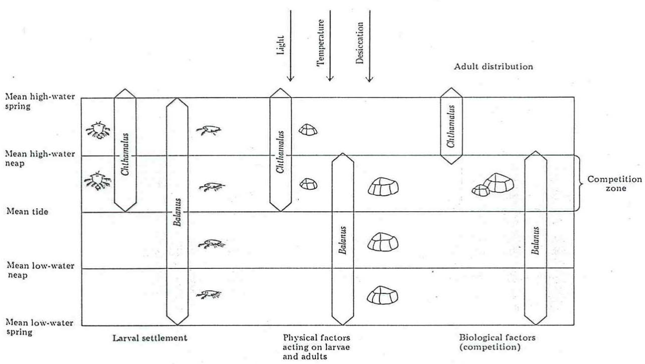
2.2. Consumers

2.2.2. Controlling factors

Rocky substrate

Abiotic factors and biotic interactions



Semibalanus balanoides

Chtamalus stellatus

- Larvae of two barnacles, *Chthamalus stellatus* and *Semibalanus balanoides*, settle out over a broad area
- Physical factors, mainly desiccation, 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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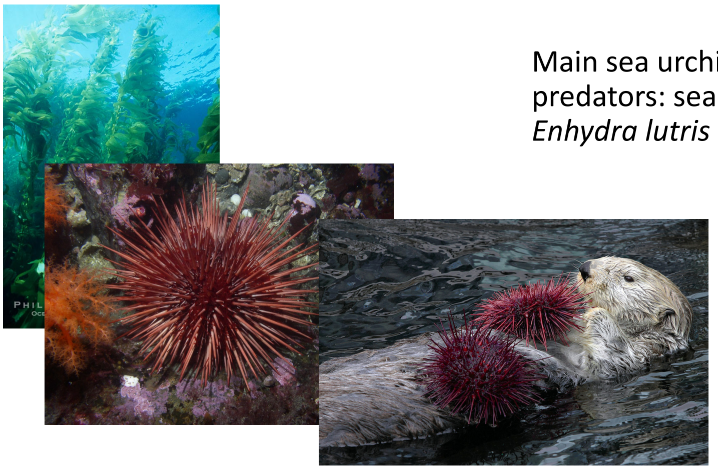
2.2. Consumers

2.2.2. Controlling factors

Rocky 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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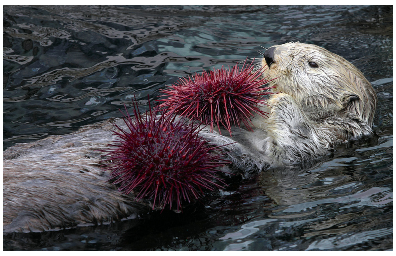
2.2. Consumers

2.2.2. Controlling factors

Rocky shores

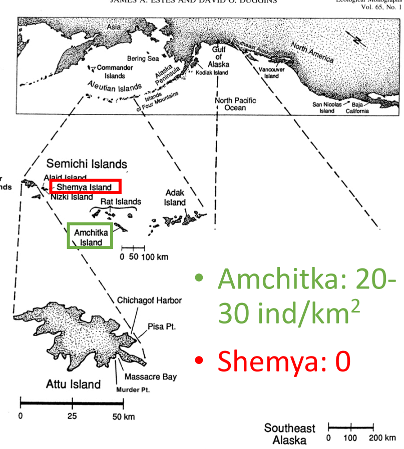
Biotic interactions: ex giant kelp forests



Enhydra lutris

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

78 JAMES A. ESTES AND DAVID O. DUGGINS Ecological Monographs Vol. 65, No. 1



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

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

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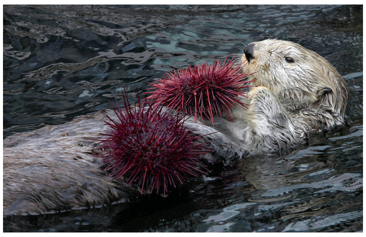
2.2. Consumers

2.2.2. Controlling factors

Rocky shores

Biotic interactions: ex giant kelp forests



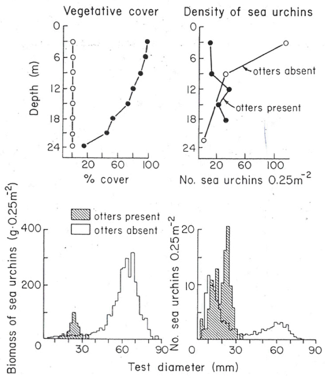


Figure 9-1. Interactions among sea otters, sea urchins, and vegetative cover in kelp beds off the Alaskan coast. Sea otters are present in Amchitka Island and absent in Shemya Island. Symbols on top left are the same as top right. Size of sea urchins is shown as the diameter of the test not including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

- Otters present:
  - Sea urchin density low
  - % cover kelp high
- Otters absent:
  - Sea urchin density high
  - % cover kelp = 0

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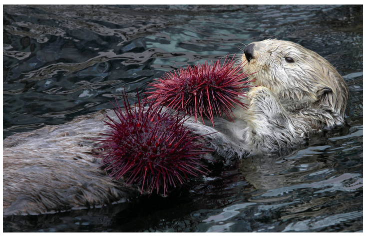
2.2. Consumers

2.2.2. Controlling factors

Rocky shores

Biotic interactions: ex giant kelp forests



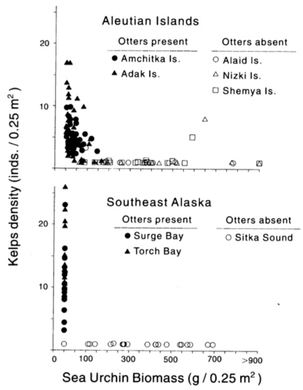


FIG. 7. Epibenthic kelp density (inds./0.25 m^2) plotted against estimated sea urchin biomass (g/0.25 m^2) for the Aleutian Islands and southeast Alaska. Points represent averages for sites within locations. Sea urchin biomass was estimated from samples of population density, size–frequency distribution, 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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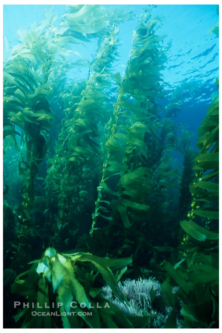
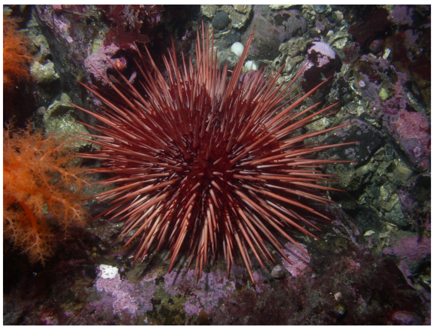
2.2. Consumers

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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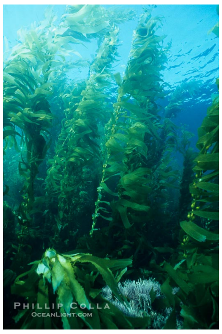
2.2. Consumers

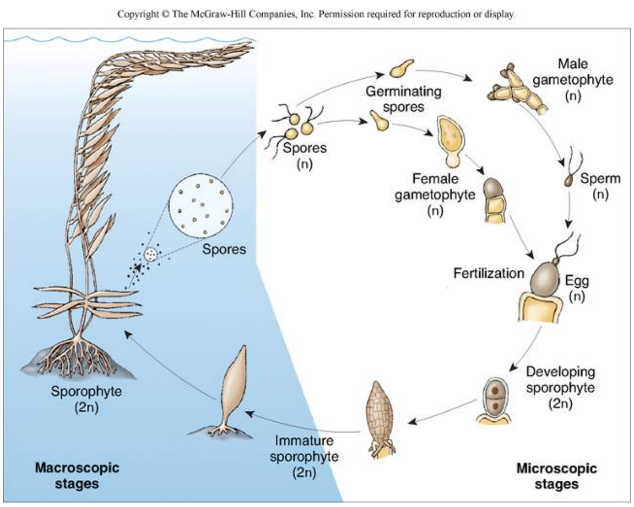
2.2.2. Controlling factors

Rocky shores

Biotic interactions: ex giant kelp forests



Planktonic stages



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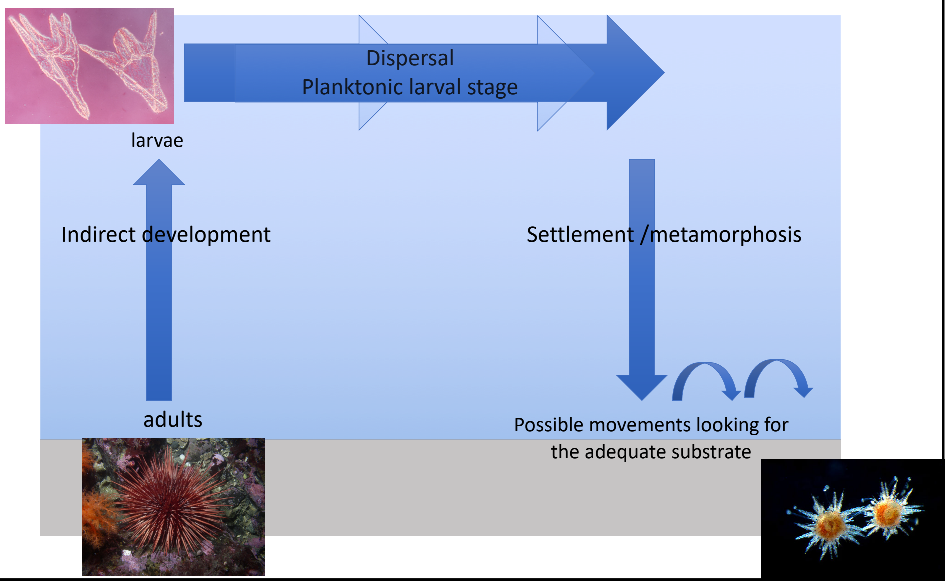
2.2. Consumers
2.2.2. Controlling factors
Rocky shores
Biotic interactions: ex giant kelp forests



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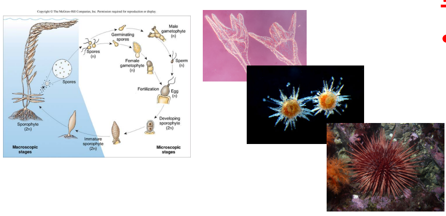
2.2. Consumers
2.2.2. Controlling factors
Rocky shores
Biotic interactions: ex giant kelp forests

<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/

Asterias forbesi

Thais lapillus

Mytilus edulis

Semibalanus balanoides

Chondrus crispus

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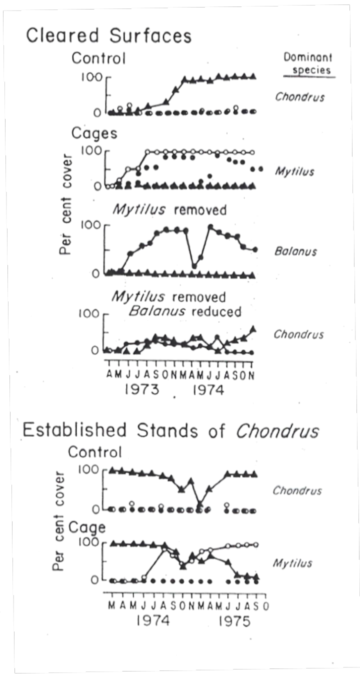
2.2. Consumers
2.1.2. Controlling factors
Rocky shores

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

- Top-down control by predators
- Competition for space

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



○ *Mytilus*
● *Semibalanus*
▲ *Chondrus*

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• Sheltered shores: predators present
➢ Algae dominant

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• Exposed shores: predators absent
➢ Barnacles and mussels dominant

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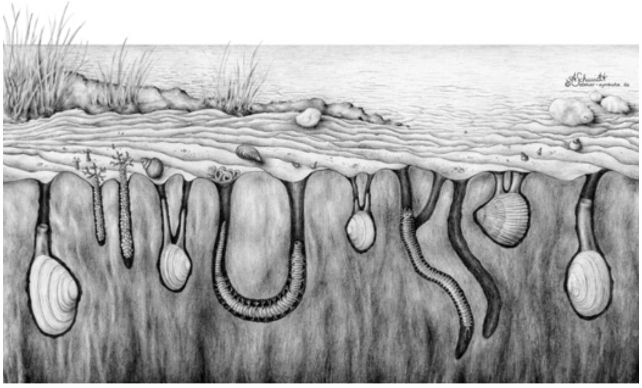
2.2. Consumers
2.1.2. Controlling factors
Sandy/muddy shores

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

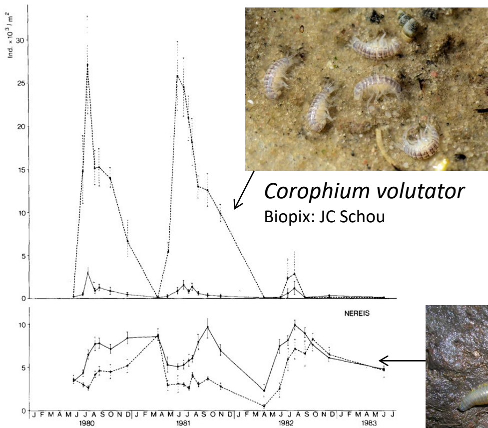

Fig. 2. Mean densities (± SE) of *Corophium volutator* (1980–1983) and *Nereis diversicolor* in the two sub-areas; solid line, 0–400 m (n = 15); broken line, 400–500 m (n = 5).

Olafsson & Persson 1986

Corophium volutator
Biopix: JC Schou

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

Nereis diversicolor
manayunkia.files.wordpress.com

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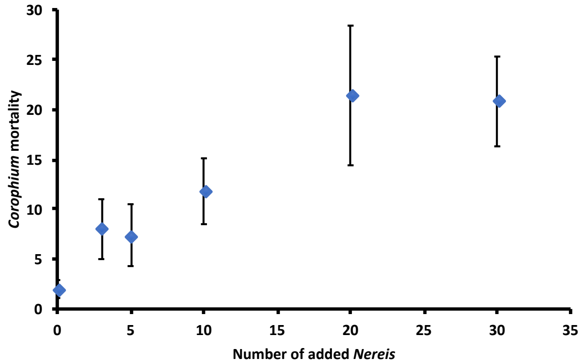
2.2. Consumers

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

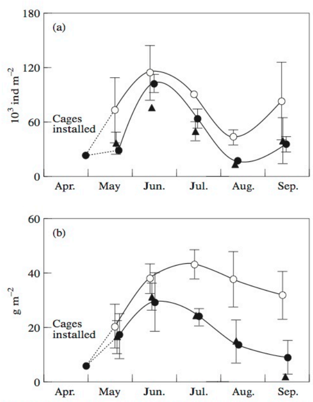

FIGURE 1. Monthly average density of macroinfauna inside complete cages (○), ambient sediments (●) and in partial cages (▲) (a) and the corresponding mean biomass (b). Vertical bars are standard errors of the mean.

Sarda et al 1998

🡅 density and biomass of infauna

- 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

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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

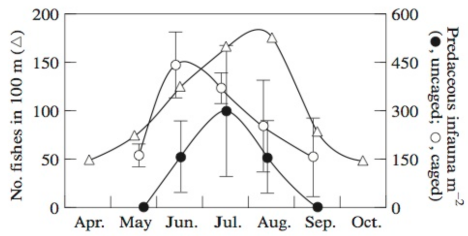

FIGURE 4. Density of predaceous infauna in complete cages and ambient sediments, and number of total fishes in a transect of 100 m in the tidal sandy channels of the marsh.

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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