Université de Nantes Faculté des Sciences

STUE – M1 Bioproduction

Support de cours Bioproduction

PG Beninger

M1 STUE Bioproduction

Objectifs

- Décrire les principes régissant la bioproduction dans les différents écosystèmes marins.
- Indiquer comment la bioproduction de ces systèmes peut être augmentée ou davantage orientée vers les besoins anthropiques.

<u>Contenu</u>

- La colonne d'eau: la 'couverture productive' de tous les écosystèmes marins.

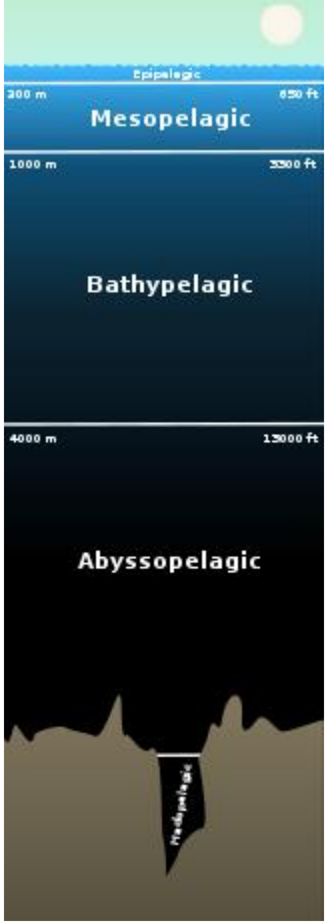
- La zone intertidale: un écosystème accessible, sous fortes contraintes. Côtes rocheux et meubles

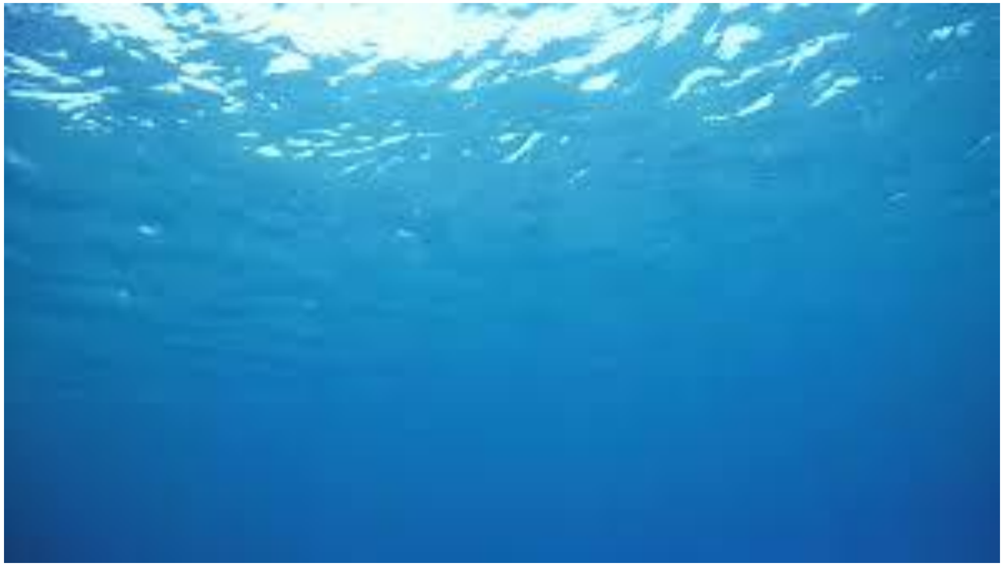
- La zone sublittorale: importance du couplage bentho-pélagique. La bioproduction des fonds rocheux et meubles ; les herbiers marins

- Les estuaires et les forêts de palétuviers : convergence de la bioproduction terrestre et de la bioproduction marine

- Les récifs coralliens: des oasis de bioproduction exceptionnels

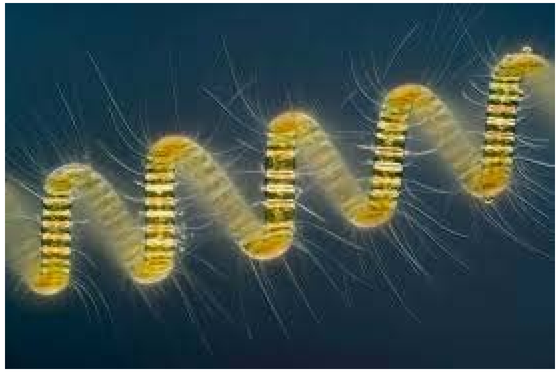
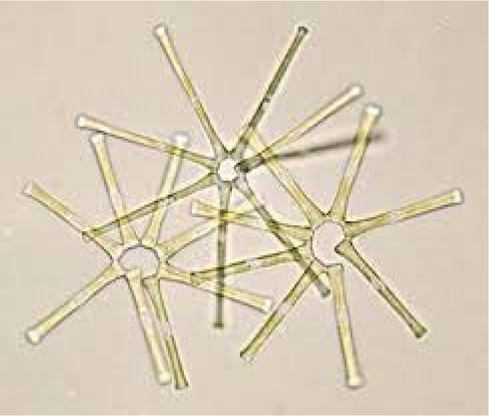
1 - La colonne d’eau: la ‘couverture productive’ de tous les écosystèmes marins



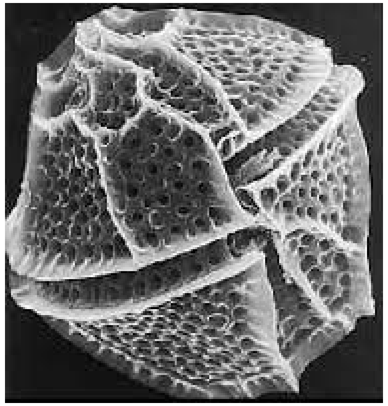


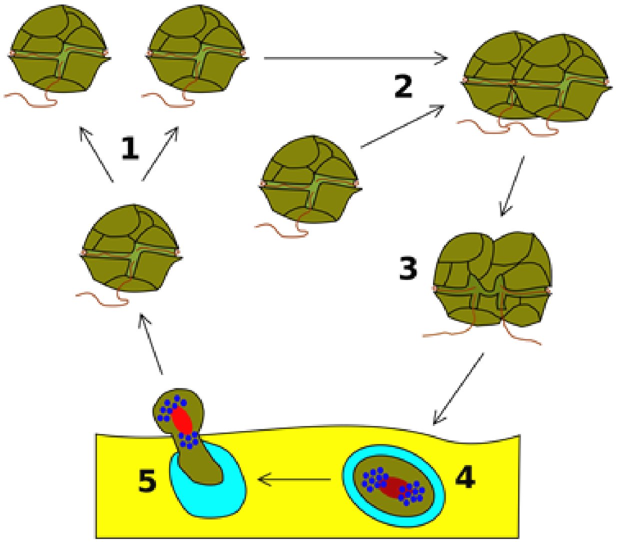
Le phytoplankton: les diatomées (Bacillariophyta)



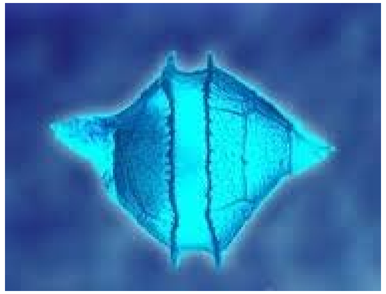




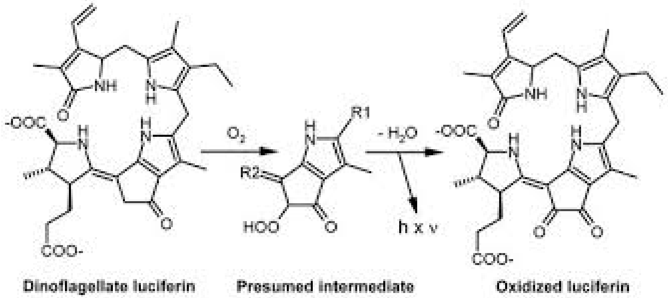
Le phytoplankton: les dinoflagellés (Dinoflagellata)





Dinoflagellés: bioluminescence et…

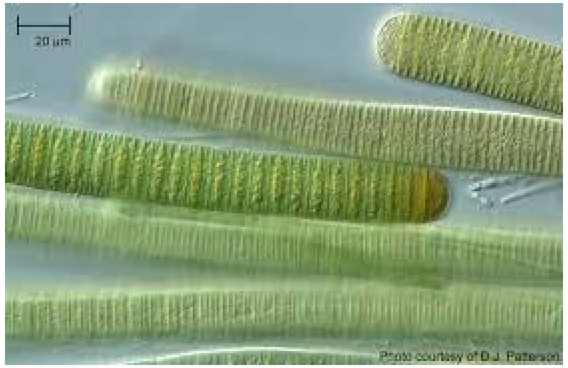


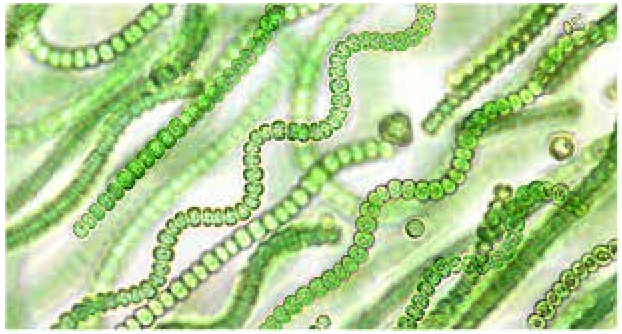
toxines

Known and Suspected Toxic Dinoflagellates

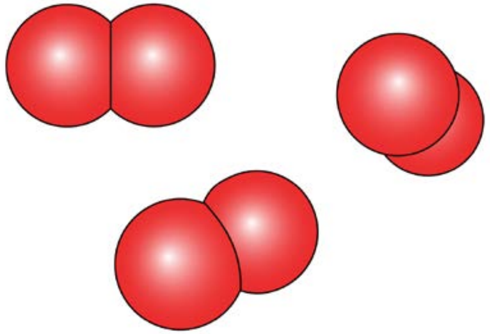
- *Alexandrium (Gonyaulax) tamarense*
- *A. catenella*
- *Amphidinium carterae*
- *Dinophysis acuta*
- *D. acuminata*
- *D. norvegica*
- *Cochlodinium polydridoides*
- *Gambierdiscus toxicus*
- *Gyrodinium estuariale*
- *Gymnodinium*
- *Karenia brevisulcata*
- *Karenia brevis (Gymnodinium)*
- *Pyrodinium bahamense*
- *Pfiesteria piscicida*
- *P. shumwayae*
- *Prorocentrum minimum*

Le phytoplankton: cyanobactéries (Cyanobactéria)

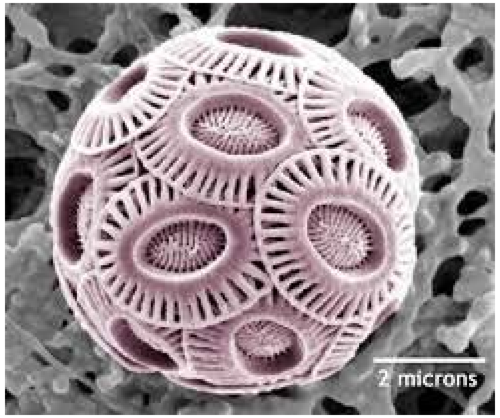




Stromatolithes

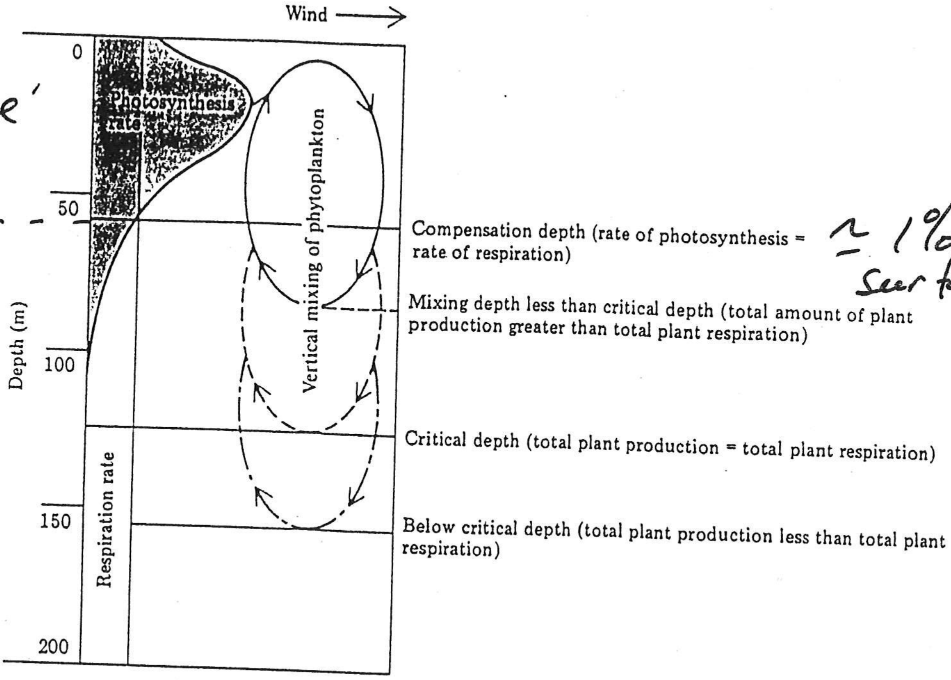


Le phytoplankton: les coccolithophores (Haptophyta)



Zone 'euphotique'

Zone 'aphotique'



≈ 1% hν de surface

Figure 2.21 The relationship between the compensation depth and the critical depth. Critical depth is the depth to which the total phytoplankton biomass may be circulated and still spend enough time above the compensation depth to have a total production equal to its total respiration during the same time period. (Modified from D. H. Cushing, Productivity of the sea, Oxford biology reader no. 78, Oxford University Press, 1975. Reprinted with permission from Carolina Biological Supply Co.)

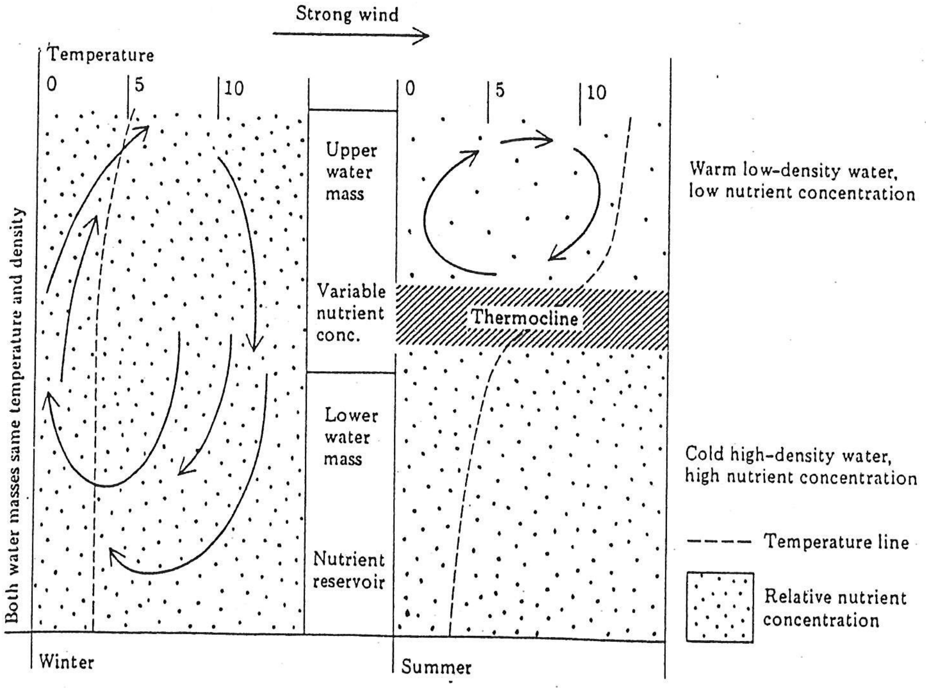
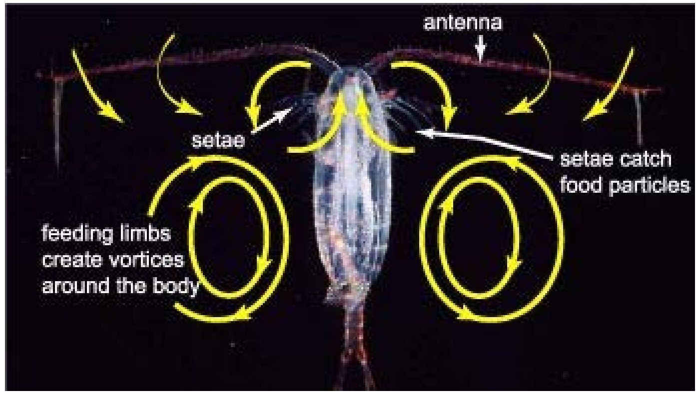


Figure 2.20 Thermal structure of temperate ocean water masses in two seasons, winter and summer, showing the relationships between nutrient concentration, temperature, density, and wind-induced mixing.

Zooplancton: Copepodes (Copepoda)



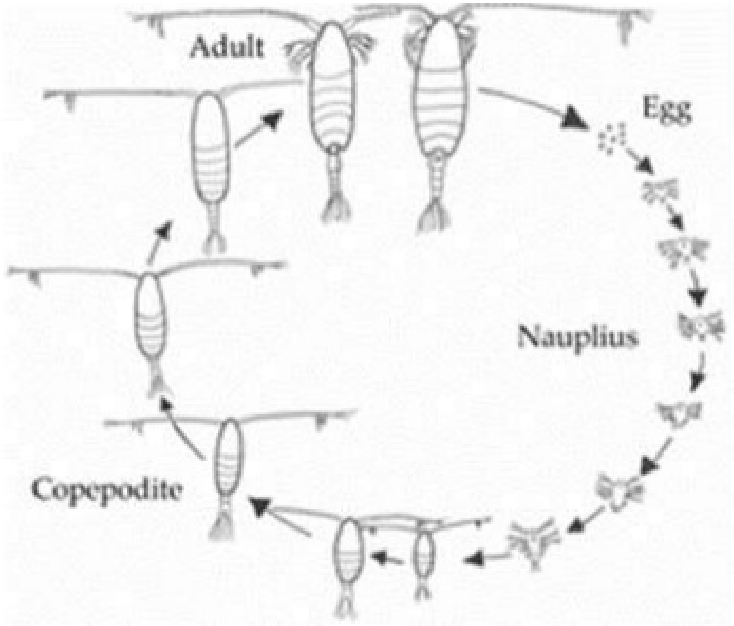
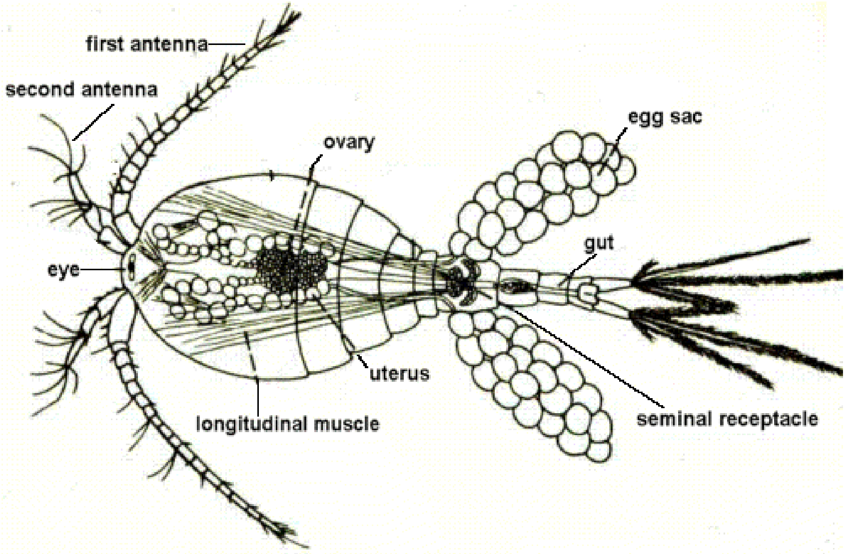
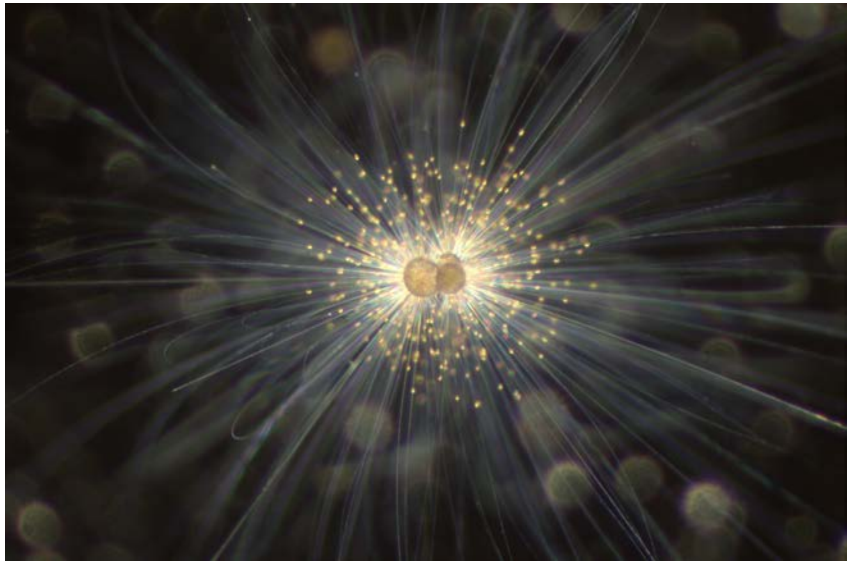
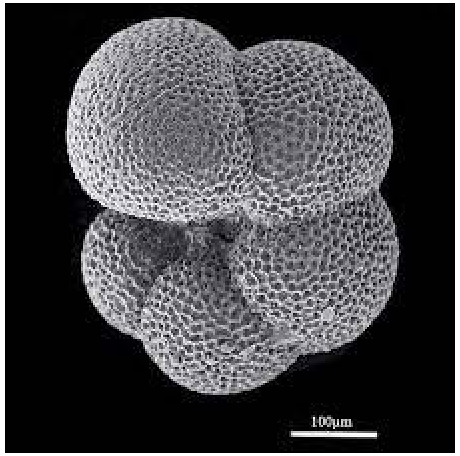


Fig : life cycle of copepod.

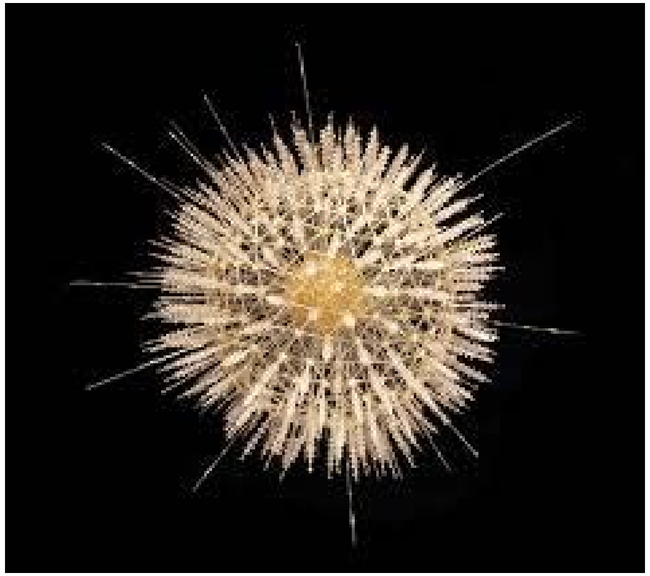
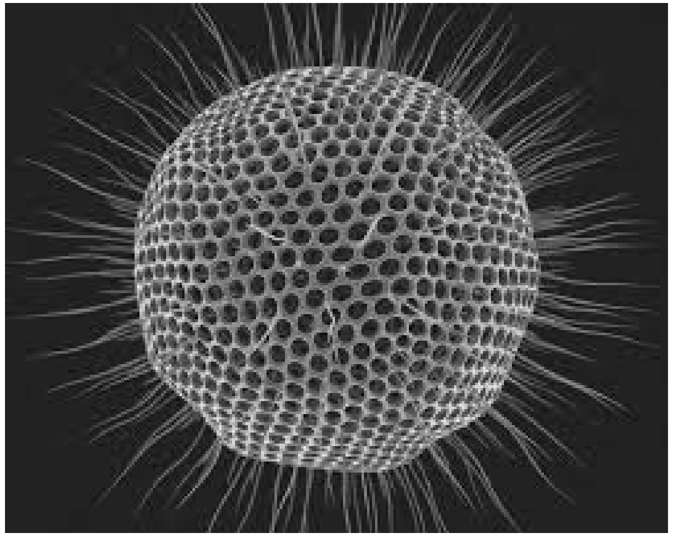
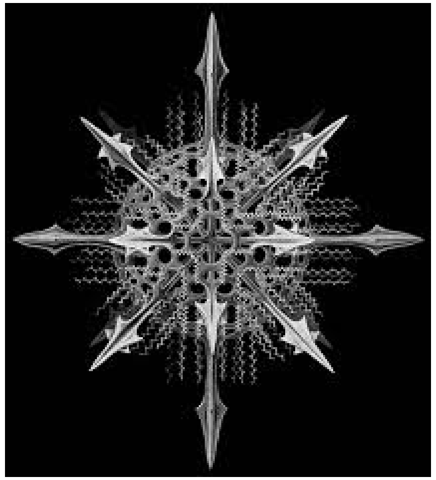


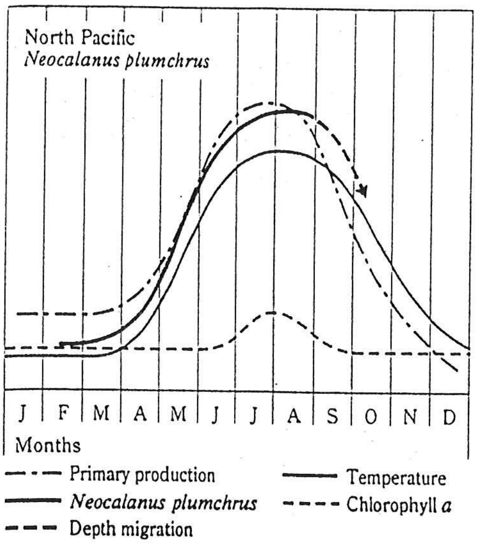
Zooplancton: Foraminifères (Foraminifera)





Zooplancton: Radiolaires (Radiolaria)

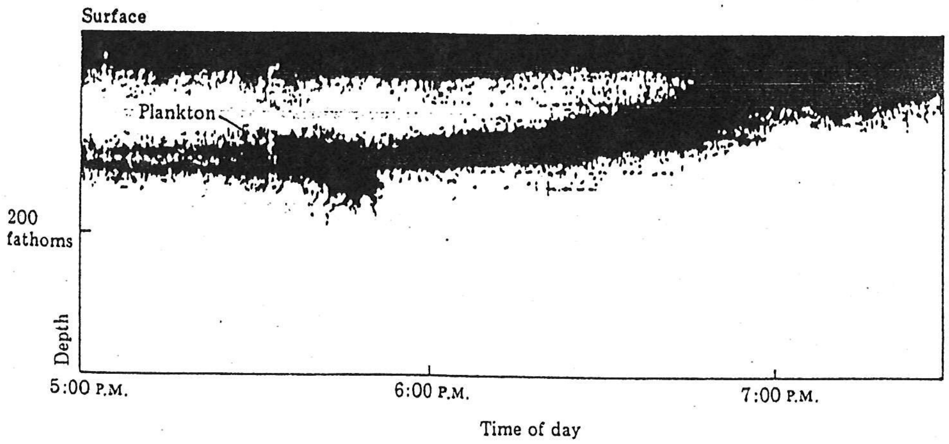
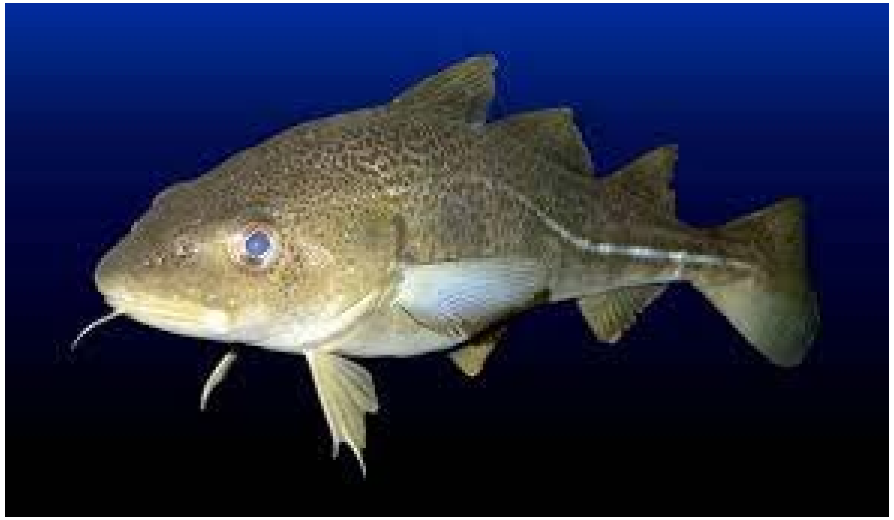


Figure 2.26 Sonogram record of movement of vertical migrating plankton. (After G. B. Farquhar, ed., Proceedings of an international symposium on biological sound scattering in the ocean, 1970, U.S. Government MC Report 005.)

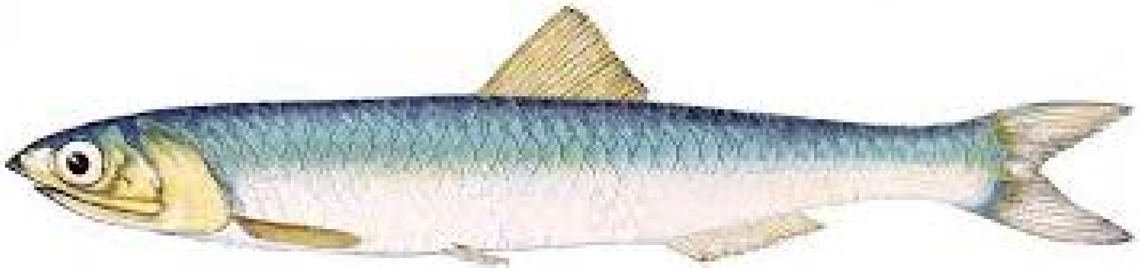
Necton épipélagique



Gadidae –
Gadus morrhua

Clupeidae –
Sardines, harengs, pilchards

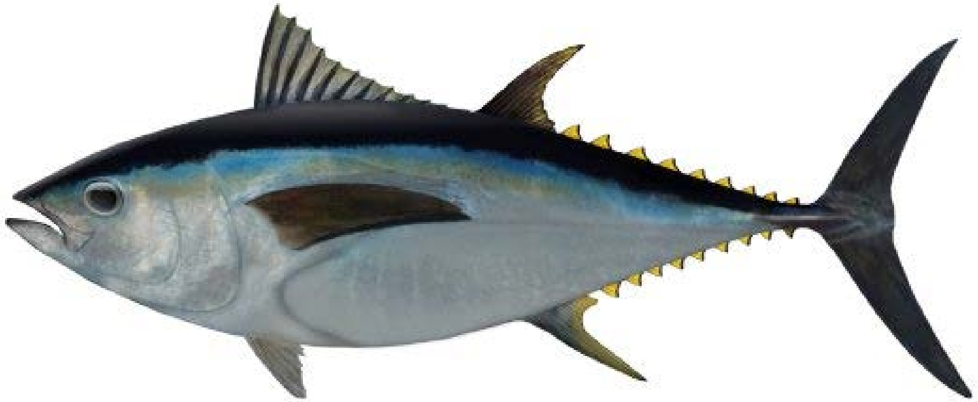
Necton épipélagique



Engraulidae - Anchois

Necton épipélagique

Scomber spp.
maquereau



Thunnus spp. Thon

Necton épipélagique

Elasmobranches

Reptiles

Mammifères

Oiseaux

Necton épipélagique

Calmar - Cephalopoda

Necton épipélagique

Biologie trophique :
les plus gros mangent les plus petits




Vol. 356: 239–250, 2008
doi: 10.3354/meps07286

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published March 18

Endothermy, ectothermy and the global structure of marine vertebrate communities

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ABSTRACT: Birds and mammals are the leading marine predators at high latitudes, while sharks and other large fish occupy top positions in tropical waters. The present study proposes that temperature-dependent predation success (TPS) explains global patterns of marine vertebrate community structure. Burst speed increases with temperature in ectotherms but is independent of temperature in endotherms. If capture success depends on relative swimming speeds of predator and prey, ectothermic prey will be more vulnerable to attack by endothermic predators at low temperatures. Conversely, high temperatures should enhance the ability of ectothermic predators to prey on endotherms. Pursuit-diving seabirds (penguins, auks and some cormorants) and pinnipeds (seals and sea lions) are ubiquitous in ocean waters with summer surface temperatures cooler than the mid-teens to low 20s (°C) but are virtually absent in warmer regions. We suggest that the near-absence of these animals at low latitudes is due to TPS, as warm water increases the difficulty of capturing fish prey and increases vulnerability to predation by large ectothermic and partially endothermic sharks. Pursuit-diving birds and pinnipeds are virtually absent from warm temperate and tropical waters, even where primary productivity and fisheries data suggest that food supplies are ample. This indicates that the low productivity that prevails in much of the tropical zone cannot explain the world-wide distributional patterns of pursuit-diving birds and pinnipeds. Endothermy in marine communities increases with cooler temperatures and with animal size. Pursuit-diving birds and pinnipeds are sensitive to temperature limits and may suffer important range contractions as oceans warm.

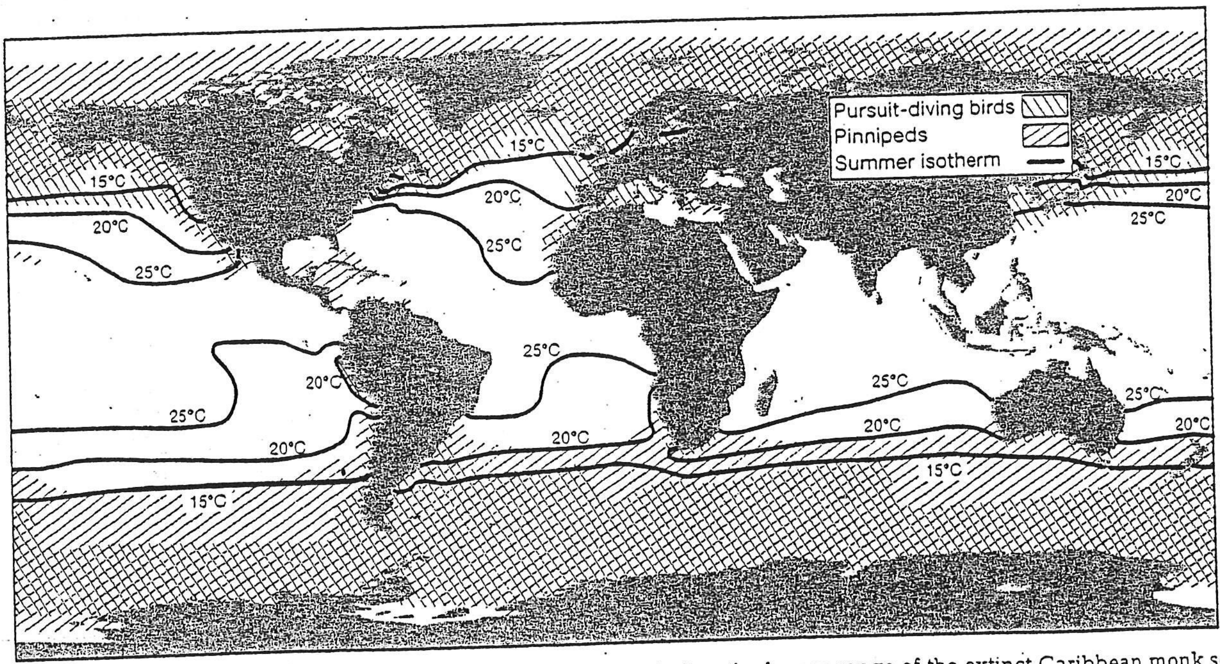

Fig. 1. World distributions of pursuit-diving birds and pinnipeds, including the former range of the extinct Caribbean monk seal, and summer (July and January) sea surface temperature (SST) isotherms

Vol. 188: 305–309, 1999
MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser
Published November 3

NOTE

A tropical bird in the Arctic (the cormorant paradox)

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[2]Institut für Meereskunde Kiel, Abteilung Meereszoologie, Düsternbrooker Weg 20, 24105 Kiel, Germany

ABSTRACT: Seabirds, like all marine endotherms, have to compensate for the extensive cooling effect of water when diving. Alone among them, cormorants (Phalacrocoracidae) have a wettable plumage and are predicted to require disproportionately large amounts of food to balance heat losses. These piscivorous birds are thus thought to have a detrimental impact on fish stocks. However, we show here that even in great cormorants from Greenland, which dive in water at 3 to 7°C, daily food intake is lower than for well-insulated European seabirds. Despite their wettable plumage, cormorants thus appear to manage their energy budgets in a remarkably efficient way. Nevertheless, the specific foraging strategies which enable this performance make cormorants dependent on high prey density areas, a feature that should be taken into account by future management plans.

KEY WORDS: Diving endotherms · Cormorants · Insulation · Food requirements · Prey

The ancestors of contemporary diving endotherms (seabirds and marine mammals) faced major adaptative challenges as they returned to a semi- or fully aquatic lifestyle some 50 to 30 million years ago. In particular, the high thermal conductivity of water compared to air led to a series of adaptations regarding insulation, for example thick layers of sub-cutaneous fat, water-proof fur and plumage. A remarkable exception to this can be found in cormorants (Phalacrocoracidae), diving birds whose plumage is wettable (Rijke 1968). Consequently, heat loss to the water, daily food requirements and predation pressure on prey stocks are all thought to be proportionately higher in great cormorants than in other diving endotherms (Draulans 1988). Present concerns regarding the potentially detrimental effect of the great cormorants *Phalacrocorax carbo*, and of the closely related double-crested cormorant *P. auritus*, on commercial fish populations throughout Europe and Northern America exemplify this (Glahn & Brugger 1995, Kirby et al. 1996). However, recent investigations of great cormorants breeding in Normandy showed that the food requirements of these birds were surprisingly low when compared to other (fully water-proof) seabirds from the same climatic zone (Grémillet 1997, Grémillet & Argentin 1998). A reason for this may be that, far from being archaic, plumage wettability in cormorants represents an excellent adaptation to diving in shallow, temperate waters (Lovvorn & Jones 1991, Wilson et al. 1992). The plumage, which is only partially permeable and thus keeps a thin insulating air layer at the water/skin interface (Grémillet et al. 1998a), enables the birds to become water-logged and to manoeuvre easily at depths without incurring buoyancy problems as do diving ducks, which are vigorously pushed back to the water surface (Wilson et al. 1992). This adaptation is appropriate as long as the birds hunt in relatively warm, shallow waters, and, not surprisingly, the cormorants' radiation started some 34 million years ago from tropical lagoons (Mourer-Chauviré 1982). Subsequently, this extremely cosmopolitan bird family has scattered over all 6 continents, with the breeding range of great cormorants extending from equatorial Africa to the high Arctic (Fig. 1; Johnsgard 1993, Russell et al. 1996) while that of double-crested cormorants extends from Cuba to Alaska (Johnsgard 1993). However, minimal body insulation is at odds with the survival of these birds through the European and North American winter or when breeding at high latitudes, as energy costs of swimming may then be 600% higher than during the European summer (Grémillet et al. 1998a). We infer that these situations should at least lead to increased fish consumption to compensate for and recognise concerns about the

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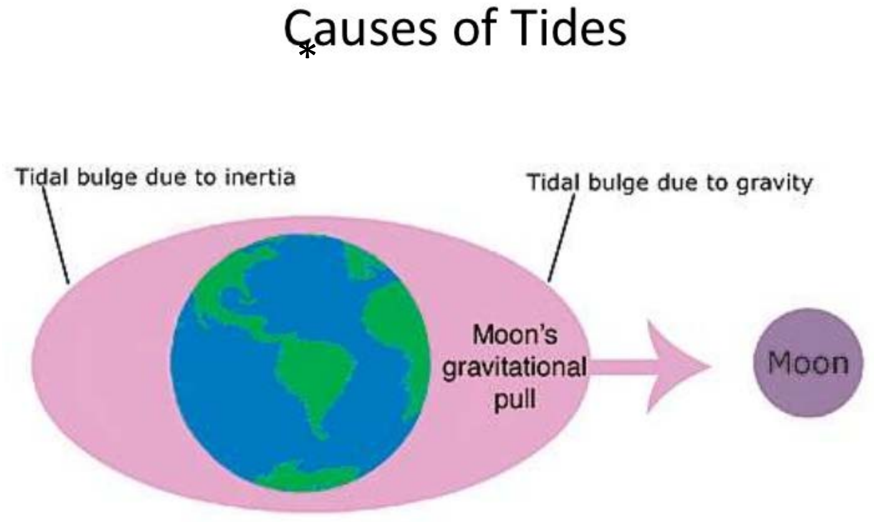
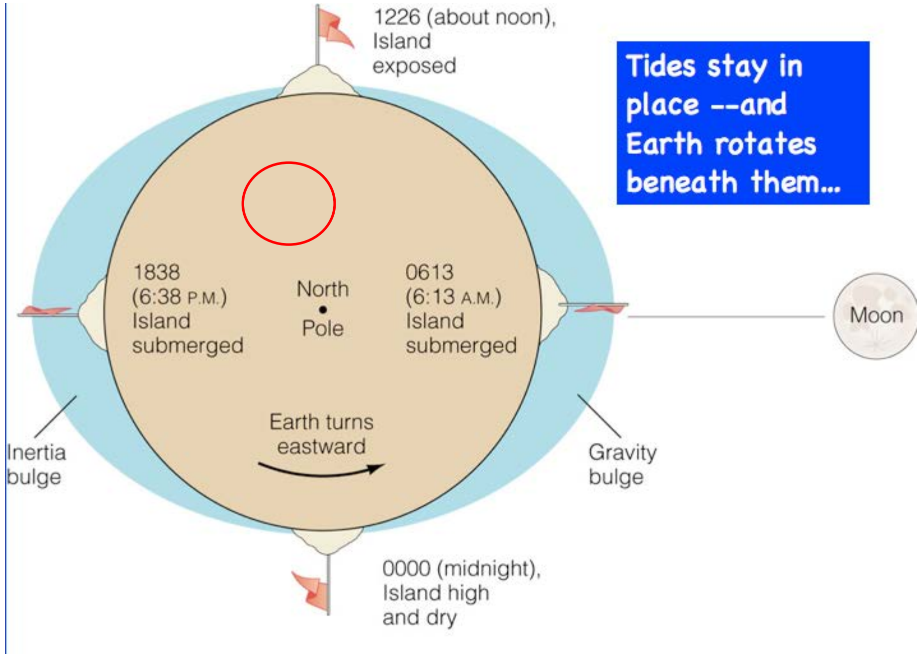
2 - La zone intertidale: un écosystème productive et accessible, sous fortes contraintes. Côtes rocheux et meubles

La zone intertidale: les marées, facteur structurant



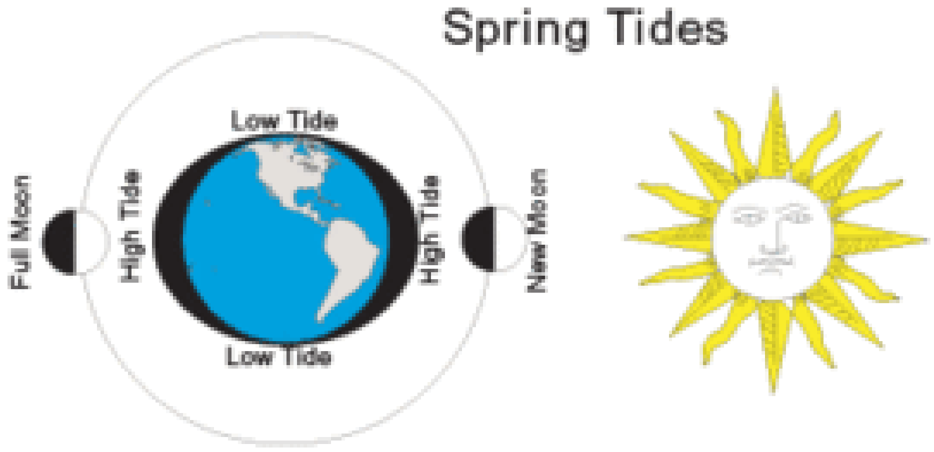


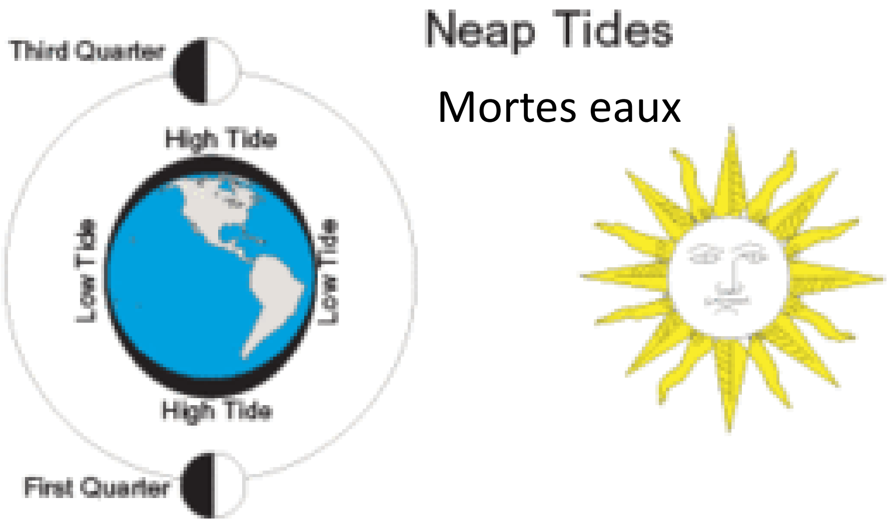
Tides stay in place --and Earth rotates beneath them...

*

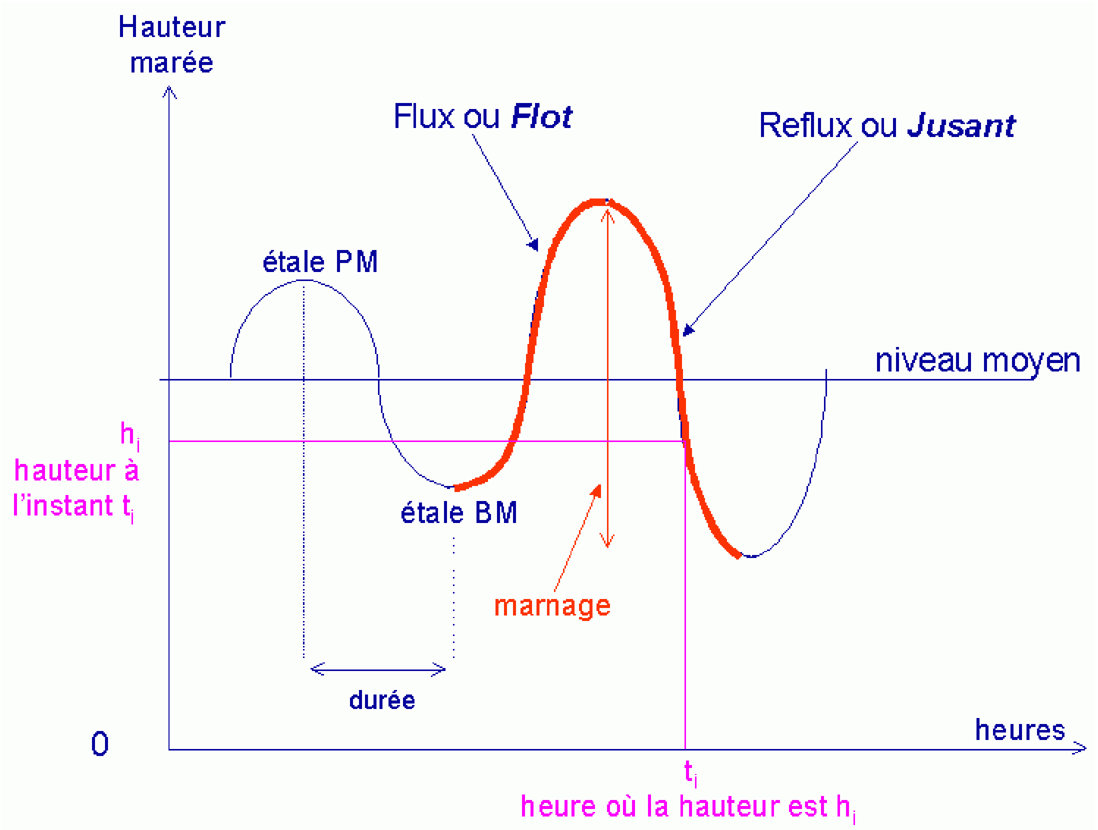
- Davantage de force centrifuge
- Plus loin de la lune
- Bourrelet *de facto* puisque moins de hauteur au N et S

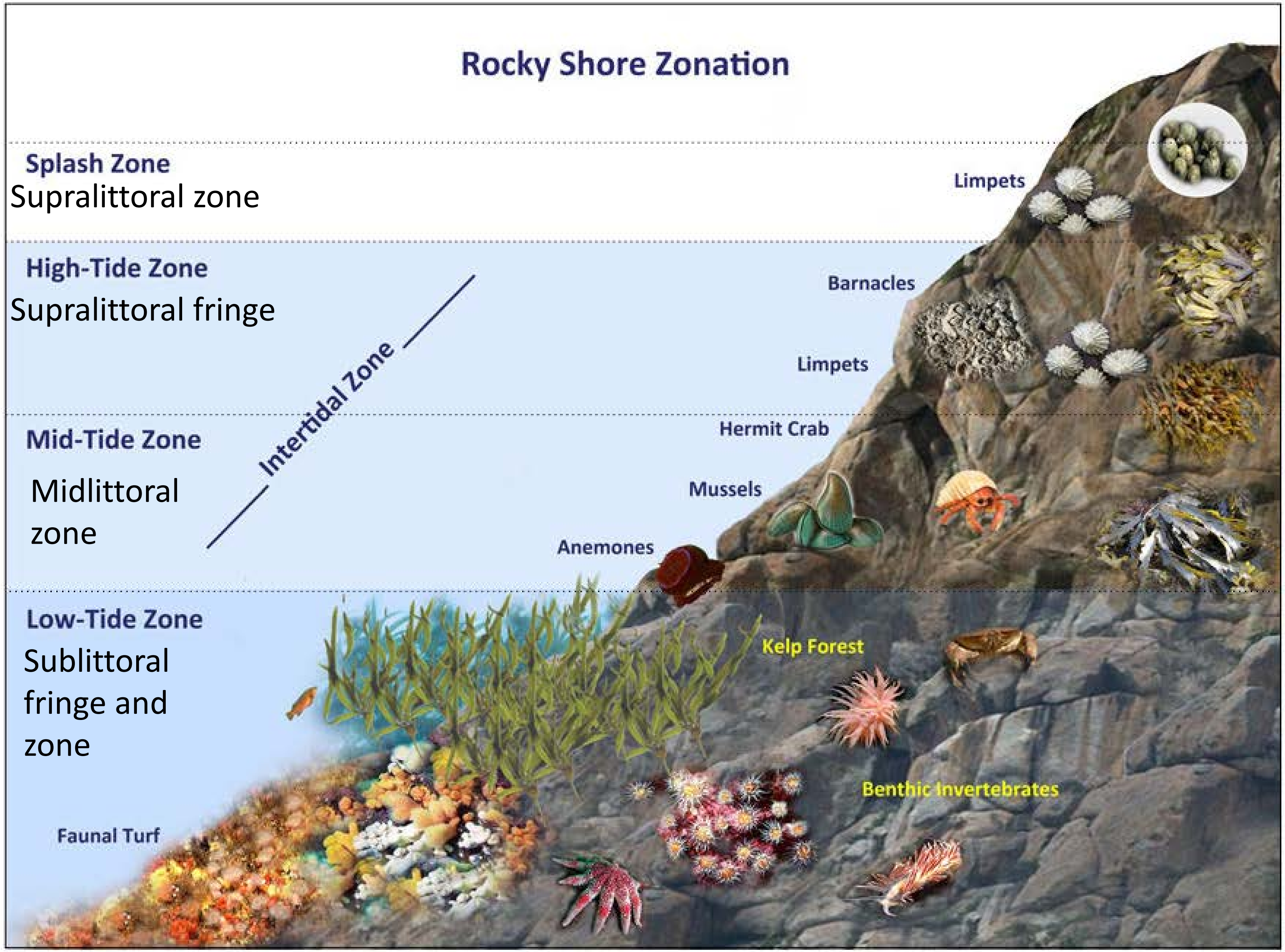
Vives eaux





Mortes eaux





Supralittoral zone

Supralittoral fringe

Midlittoral zone

Sublittoral fringe and zone

Periwinkles	*Littorina spp.*
Spiral Wrack	*Fucus spiralis*
Bladder Wrack	*F. vesiculosis*
Saw Wrack	*F. serratus*

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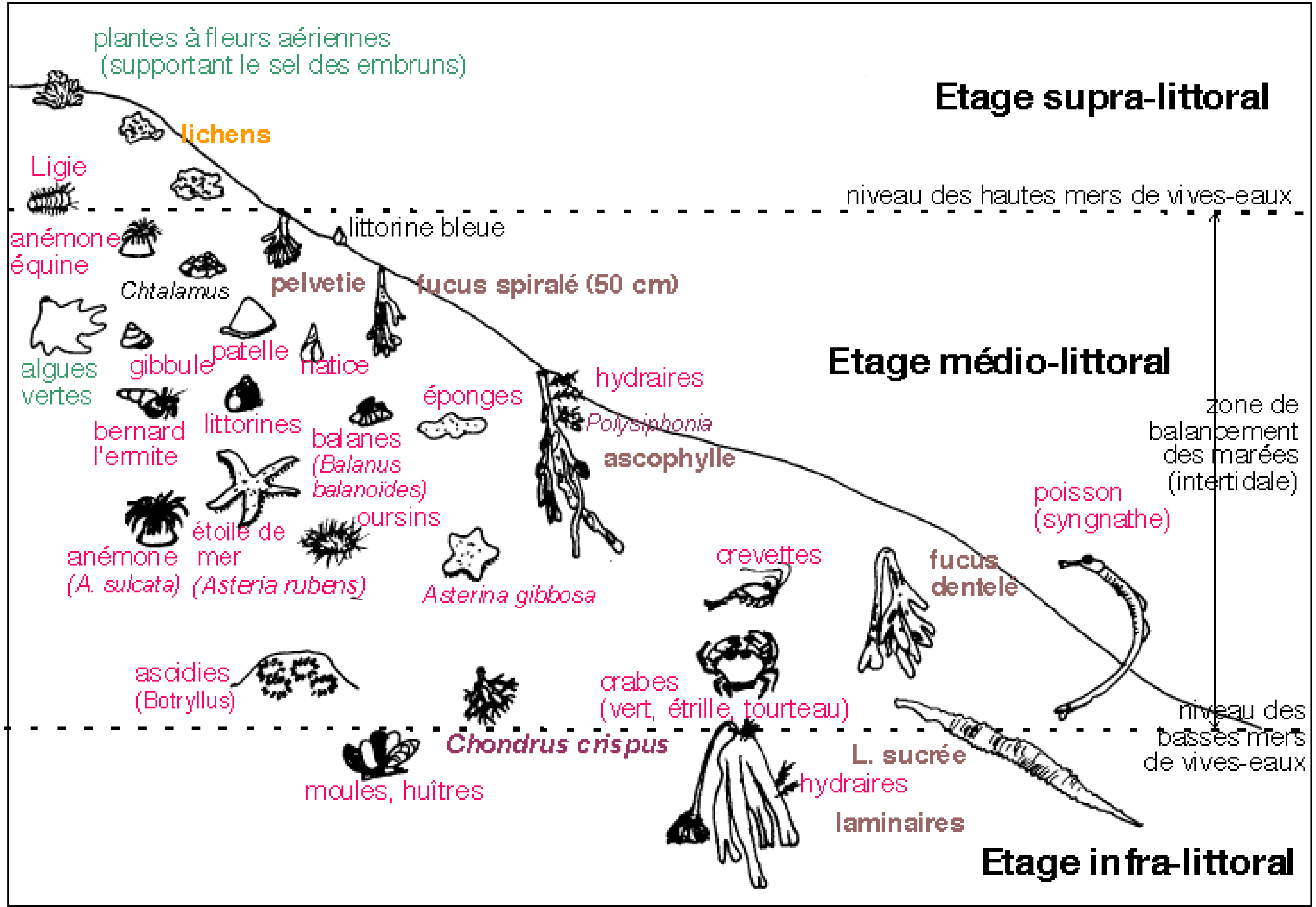
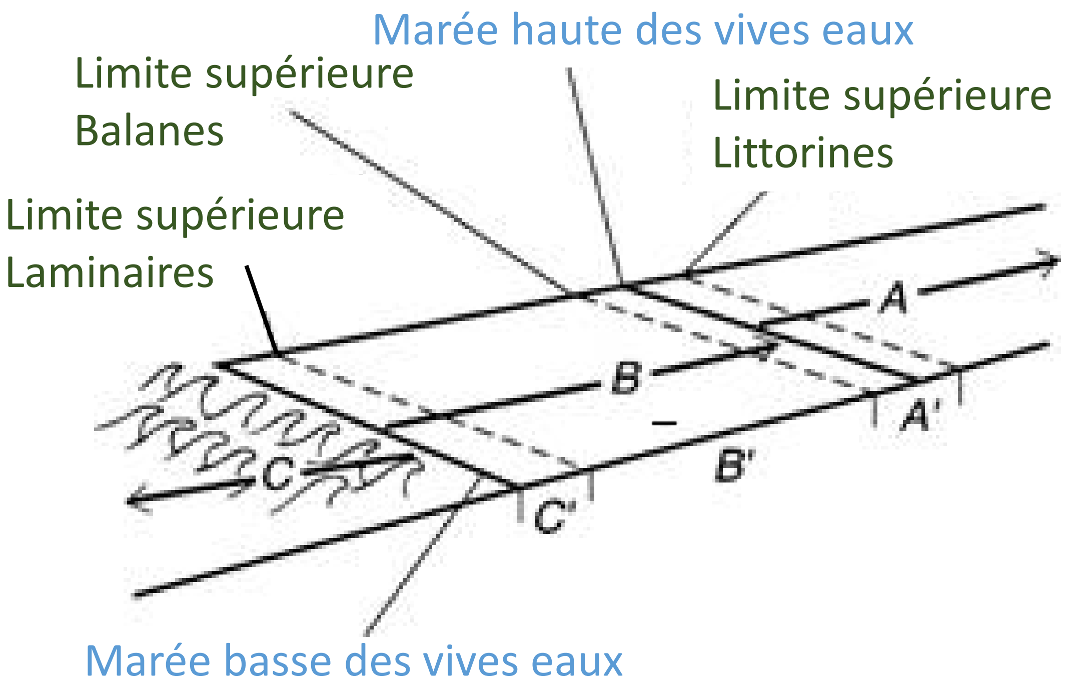
Zone intertidale rocheuse – zonation verticale



Zonation intertidale - Classification ‘universelle’ de Stephenson



Marée haute des vives eaux

Limite supérieure
Balanes

Limite supérieure
Littorines

Limite supérieure
Laminaires

Marée basse des vives eaux

A – Zone* supralittorale
A’ – Frange supralittorale
B – Zone littorale (intertidale)
B’ – Zone médiolittorale
C – Zone infralittorale (sublittorale)
C’ – Frange infralittorale (sublittorale)

* = ‘Etage’ dans ouvrages plus anciens

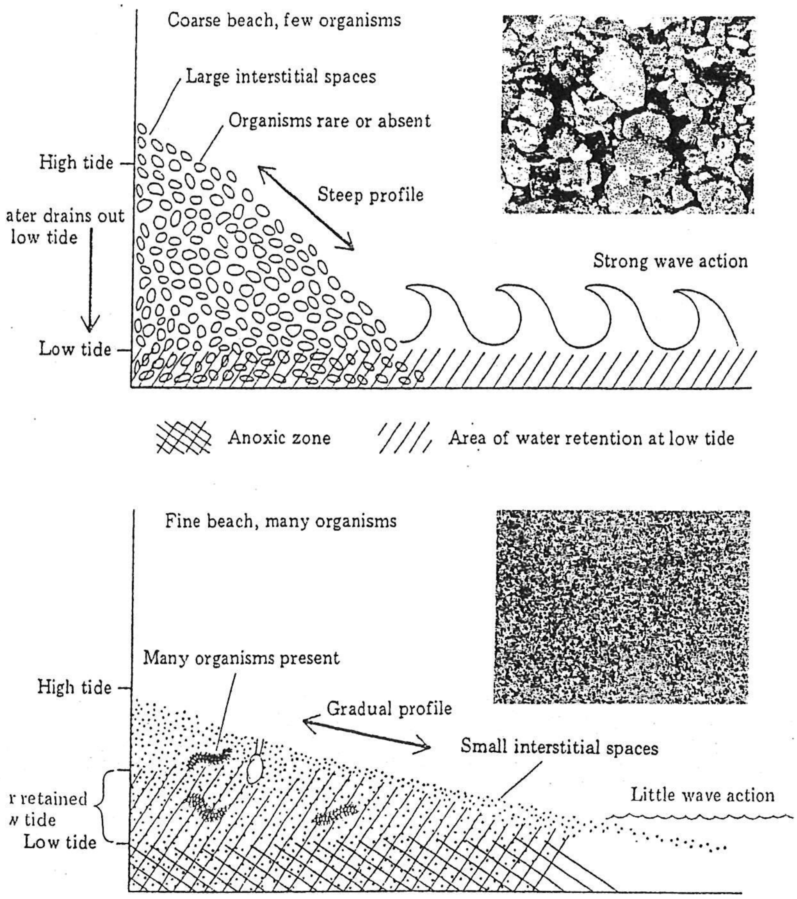


Figure 6.25 Comparison of the physical conditions found in fine-grained and coarse-grained beaches.

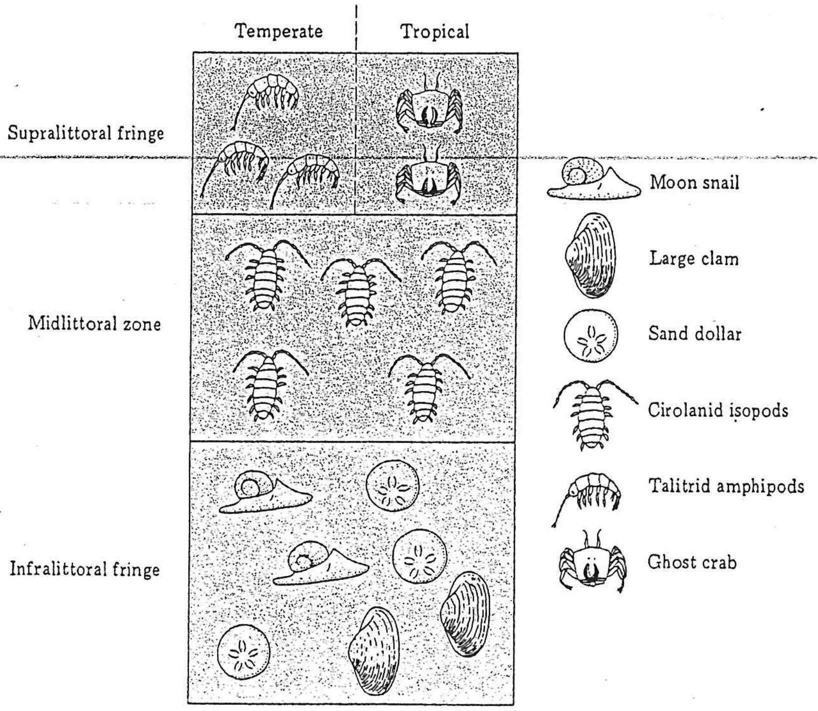


Figure 6.33 Generalized patterns of organism distributions for sandy beaches.

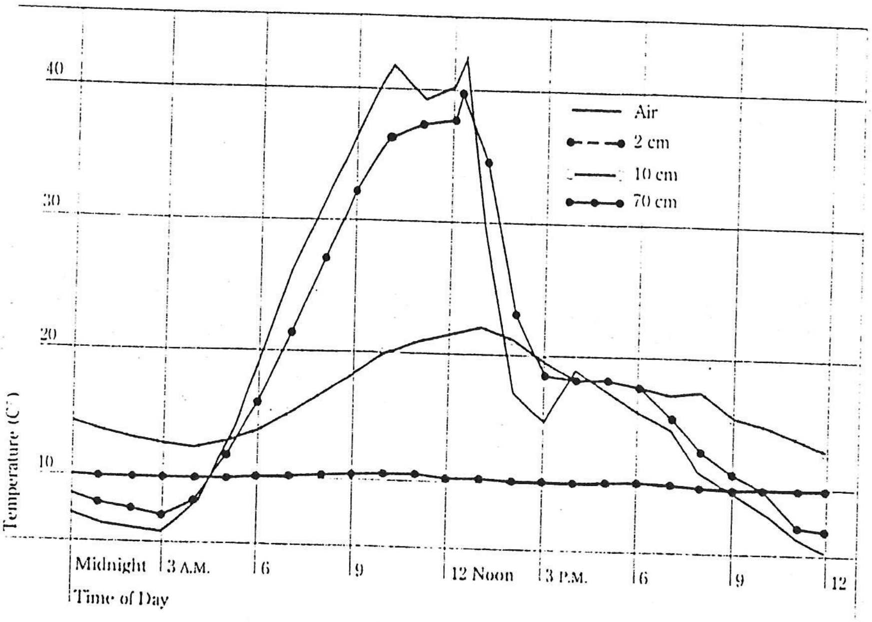


Figure 7.2 Graph showing the change in temperature at different depths in a sand beach in Denmark during a spring day. (From B. O. Jansson, Diurnal and annual variations of temperature and salinity of interstitial water in sandy beaches, Ophelia 4:173–201, 1967.)

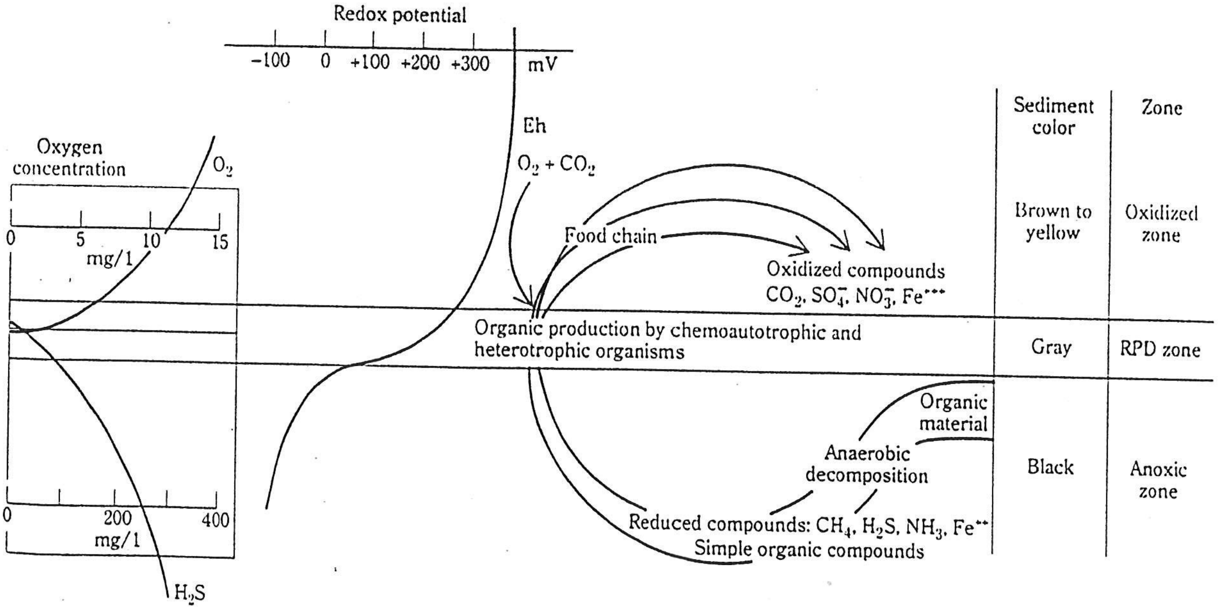


Figure 6.37 Diagrammatic representation of the physical and chemical characteristics of sediments across the redox discontinuity layer and the biological processes occurring in each. (From various sources.)

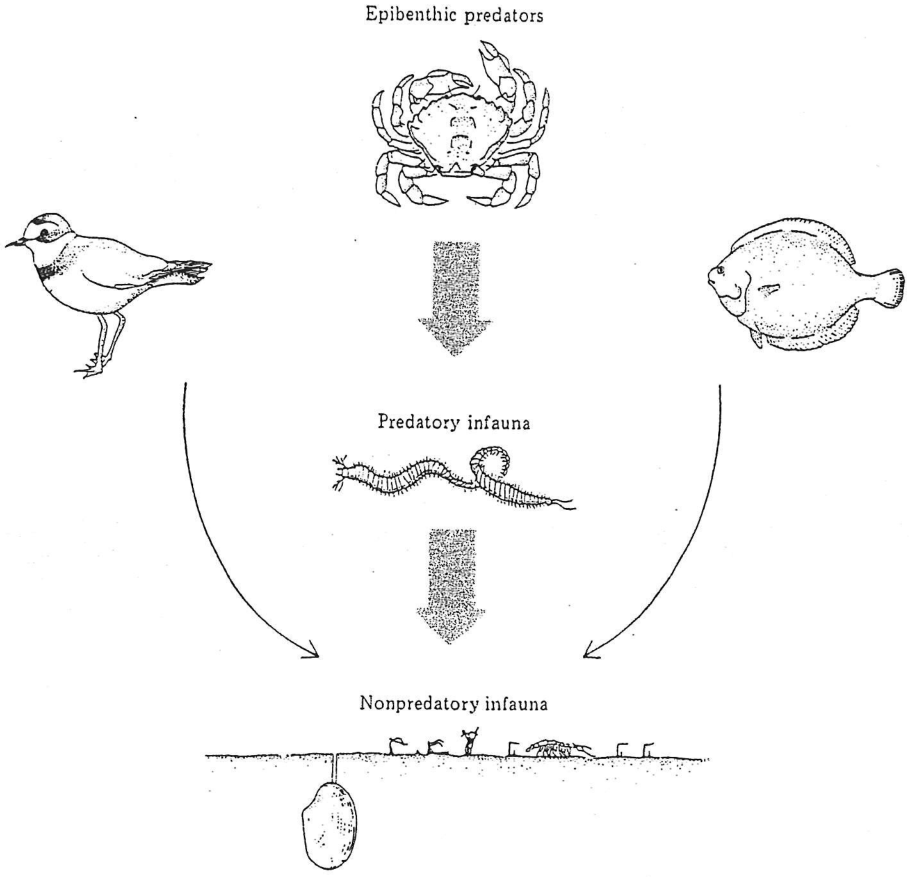


Figure 6.46 Diagrammatic representation of the interactions between various epibenthic predators and the infauna of sedimentary shores. Broad arrows indicate relations that may be particularly important. (From W. G. Ambrose, Role of predatory infauna in structuring marine soft bottom communities, Mar. Ecol. Prog. Ser. 17:102–115, 1984.)

Journal of Experimental Marine Biology and Ecology 457 (2014) 128–134

Contents lists available at ScienceDirect

Journal of Experimental Marine Biology and Ecology

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Fine-scale spatial distribution of the temperate infaunal bivalve *Tapes* (=*Ruditapes*) *philippinarum* (Adams and Reeve) on fished and unfished intertidal mudflats

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ARTICLE INFO

Article history:
Received 26 February 2014
Received in revised form 1 April 2014
Accepted 2 April 2014
Available online xxxx

Keywords:
Spatial distribution
Tapes
Ruditapes
mudflat
Fractal
Autocorrelation

ABSTRACT

Temperate intertidal mudflats are important to both human and nonhuman foragers, the former for professional and recreational clam fishing, and the latter for food, especially for migratory shorebirds. Foraging strategy and success will depend to a large degree on the spatial distribution of the infaunal prey, which is very poorly-known at the scale at which these foragers exploit the resources. We characterized the fine-scale spatial distribution of the bivalve *Tapes philippinarum* on a chronically-fished and on an unfished (reference) mudflat, using autocorrelation, variogram, and fractal analyses. Two cohorts were identified at each site: one sub-legal and one legal size. Although both cohorts were clearly aggregated at the scale of $\leq$130 m, this aggregation was greatly attenuated at the fishing-impacted site, and most severely for the fished-size cohort. The fractal dimensions of the cohorts at the two sites corroborated the decreased spatial structure at the fishing — impacted site, and in particular for the fished-size cohort. Together with similar observations for other components of this mudflat ecosystem, these results underscore the need to incorporate the spatial aspect in assessments of both organism (prey or resource) distribution, its relationship to foraging strategies, and the effect of intertidal fishing on these processes.

1. Introduction

There is increasing awareness of the importance of spatial structure in population and community ecology (Fortin et al., 2002; Legendre and Legendre, 2012). Ecological processes occur within a spatially-ordered context, and failure to properly take account of spatial structure can generate misleading data and erroneous conclusions (Kühn, 2007; Lennon, 2000). In particular, spatial structure is critical to understanding predator–prey relations (Benoit-Bird and McManus, 2012; Benoit-Bird et al., 2013a; Humphries et al., 2010; Reynolds and Rhodes, 2009; Sims et al., 2008).

The geo-statistical techniques available for the study of spatial structure are widely used in the fields of geology and forestry, yet they are much less familiar in marine ecology (Boldina et al., 2014). The few marine studies were initially concentrated on benthic spatial structure, especially on the very 2-dimensional intertidal mudflat habitat (Blanchard, 1990; Guarini et al., 1998; Kostylev and Erlandsson, 2001; Seuront and Spilmont, 2002; Weerman et al., 2011), although recent work has begun to extend this to 3 and 4-dimensional contexts (Benoit-Bird and McManus, 2012; Benoit-Bird et al., 2013a,b).

Initial studies in benthic marine spatial ecology focused on large-scale spatial structure, i.e. hundreds of meters or kilometers (Andrew and Mapstone, 1987; Kraufvelin et al., 2011; Legendre et al., 1997; Underwood et al., 2000). However, recent studies support early work which showed that spatial patterning is evident at scales closer to the size of the organisms studied, e.g. meters or tens of meters for macroscopic organisms, and centimeters for meioscopic organisms (Blanchard, 1990; Boldina and Beninger, 2013; Boldina et al., 2014; Guarini et al., 1998; Seuront and Spilmont, 2002). In microphytobenthic communities, such patterning has been hypothesized to be the result of self-organization (Seuront and Spilmont, 2002; Weerman et al., 2010), and to be important for basic ecological processes such as feeding, reproduction, recruitment, and competition (Boldina and Beninger, 2013; de Jager et al., 2011) in marine animals. In particular, migratory shorebirds depend to a variable degree on infaunal bivalve resources (Beninger et al., 2011), and are considered to be sentinel species of environmental status (Huettmann and Czech, 2006; Piersma and Lindström, 2004).

To date, although fine-scale spatial studies on mudflats have covered the major ecological components of these ecosystems (Blanchard, 1990; Boldina and Beninger, 2013; Boldina et al., 2014; Guarini et al., 1998; Weerman et al., 2010), they are few in number, such that the knowledge base lacks sufficient depth to draw more general conclusions (Kraufvelin et al., 2011). Additionally, recent evidence suggests that

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http://dx.doi.org/10.1016/j.jembe.2014.04.001
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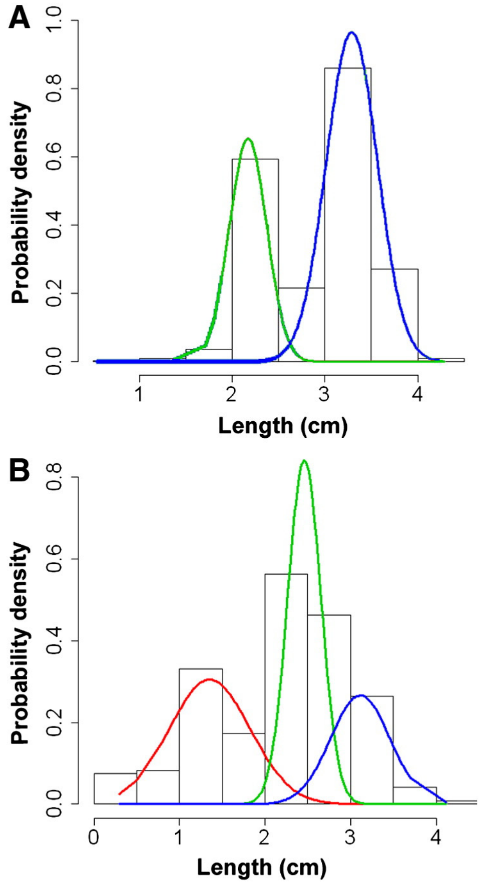


Fig 1. *Tapes philippinarum*. Length - probability density distributions. A. Reference site. B. Impacted site.

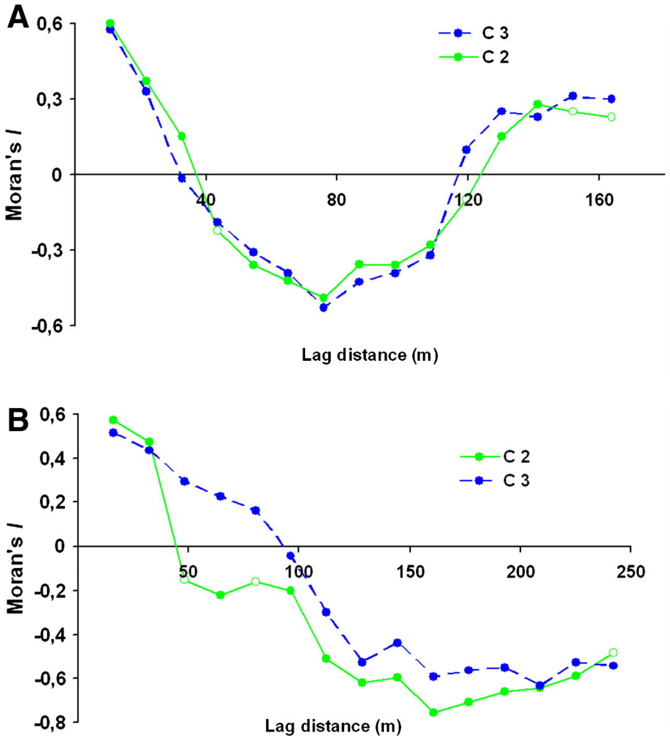


Fig 2. Spatial autocorrelograms for *T. philippinarum* densities. A. Reference site. B. Impacted site. C2 is presented by solid line, C3 by dashed line. Significant values are represented by solid circles, non-significant values are represented by empty circles.

there was more than one patch detected within the sampling transects. The observed inter-patch distances were almost identical for C2 and C3: 87 and 86 m, respectively.

3.2.2. Impacted site

The amplitude of the Moran's *I* values (0.57–0.76 for C2 and 0.5–0.63 for C3) demonstrated strong spatial autocorrelation. The patch size was approximately 45 m for C2 and 86 m for C3. The absence of a second peak on the correlograms indicates that the inter-patch distance was greater than the lengths of the transects (Fig. 2. B).

3.3. Variogram analysis and fractal dimension

3.3.1. Reference site

The points used for the calculation of fractal dimension from the variogram are shown in Fig. 3.

The spatial structure of *T. philippinarum* showed strong scaling behavior over the range < 80 m ($R^2 = 0.99$ and 0.98 for C2 and C3 cohorts respectively). A statistically significant difference of slopes of regression lines of the log–log plots of semivariance vs lag distance was not detected. In fact, the fractal dimension was nearly identical for both cohorts: 1.65 for C2 and 1.64 for C3 (Fig. 4).

3.3.2. Impacted site

The spatial structure of *T. philippinarum* showed scaling behavior over the range < 125 m ($R^2 = 0.97$ and 0.95 for C2 and C3 cohorts respectively) (Fig. 6). The points used for the calculation of fractal dimensions from the variogram are shown in Fig. 5. The resulting fractal dimensions were 1.78 (C2) and 1.83 (C3) (Fig. 6).

The fractal dimensions of C2 and C3 cohorts were significantly higher for the impacted site compared to the reference site (covariance analysis, $F = 65.08$, $P = 6E - 06$ and $F = 75.62$, $P = 2E - 06$ respectively) indicating that the spatial structure of the C2 and C3 cohorts at the impacted site was more homogeneous than that of the reference site. Furthermore, there was a much greater difference between the fractal dimensions of the sub-legal (C2) and legal — size cohorts (1.78 vs 1.83), compared to the nearly identical fractal dimensions of the reference site (1.65 and 1.64).

4. Discussion

T. philippinarum showed a clearly aggregated spatial distribution for both sites at distances < 130 m. Not surprisingly, this result contradicts the 'random' 2-dimensional spatial distribution previously reported for *T. philippinarum* (Lee, 1996), using the highly inadequate variance:mean method (Dale et al., 2002; Hurlbert, 1990). Aggregative prey spatial distributions can have effects disproportionate to the biomass of organisms in them, underscoring the importance of their detection and characterization in ecological studies (Benoit-Bird and McManus, 2012).

The high values of Moran's *I* autocorrelation coefficient for *T. philippinarum* on the impacted site fail to tell the complete

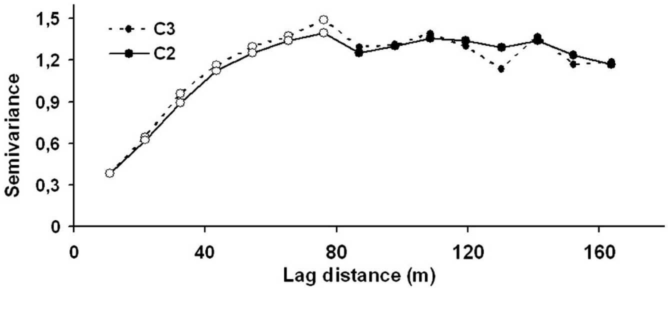


Fig 3. *Tapes philippinarum*, reference site. Experimental variograms for C2 and C3 cohorts. Open circles show the points used for calculating the fractal dimension.

Marine Biology (2005) 146: 1223–1234
DOI 10.1007/s00227-004-1521-5

RESEARCH ARTICLE

Robert W. Elner · Peter G. Beninger
Daniel L. Jackson · Tracy M. Potter

Evidence of a new feeding mode in western sandpiper (*Calidris mauri*) and dunlin (*Calidris alpina*) based on bill and tongue morphology and ultrastructure

Received: 21 April 2004 / Accepted: 29 October 2004 / Published online: 14 December 2004

Abstract Sandpipers of the genus *Calidris* tend to have similar body shapes and use narrow, tubular bills to feed on invertebrates in aquatic habitats over an extensive migratory range. Highly plastic foraging behaviours have been displayed but the associations between diet and feeding mechanics are less well understood. Here, scanning electron microscopy was used to relate the ultrastructure of the bills and tongues of two sympatric congeners, western sandpiper (*C. mauri*) and dunlin (*C. alpina*), to function and elucidate the sensory and mechanical basis to feeding. The morphology of the relatively larger, more robust bill of the dunlin suggests specialization for probing although both species are known to feed on epifaunal and infaunal prey. In general, external and internal bill features appear similar for the congeners and the microstructure of taste bud and salivary gland complexes in their mouth cavities correspond to descriptions for other birds. However, the tongues of the two species are remarkable for their distinctive microstructural details as well as copious mucus and extraneous material. In particular, each species has unique tongue papillae, and the keratinized lateral spines along the edges and at the tips of the western sandpiper tongue are markedly longer and denser than for those of the dunlin. Based on the unique features of the tongues and associated observations, inter-species differences in foraging performance can be inferred. Further, evidence suggests that the western sandpiper, and, to a lesser extent, the dunlin, deposit feed on surficial biofilm materials, as opposed to incidentally imbibing such materials while targeting epifaunal prey. Commensurate with the evidence, a novel functional and mechanistic case for unfiltered biofilm grazing in birds is proposed.

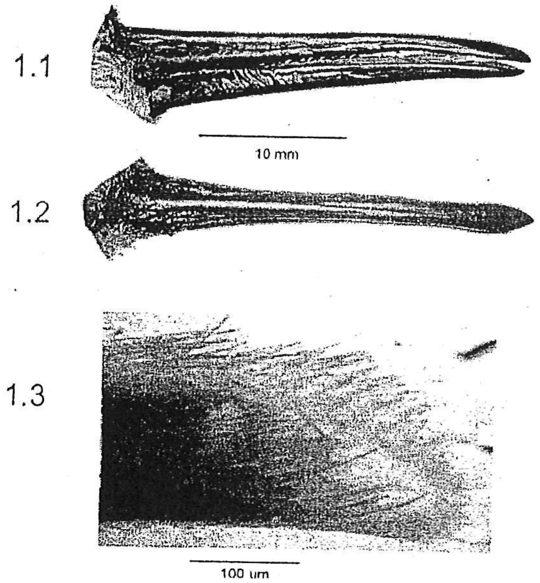
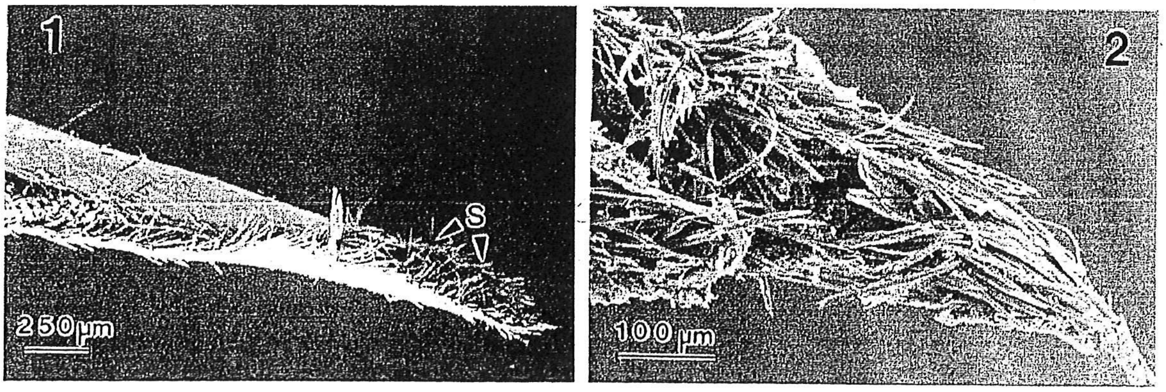


Fig. 1 Western sandpiper, *Calidris mauri*. Complete bill. *1.1* Side aspect, external surface of the maxilla and mandible (*scale bar* 10 mm). *1.2* Dorsal aspect, external surface of the maxilla (*scale bar* 10 mm). *1.3* Dorso-lateral aspect, distal section of tongue in water (*scale bar* 100 μm)



Ecology, 89(3), 2008, pp. 599–606

BIOFILM GRAZING IN A HIGHER VERTEBRATE: THE WESTERN SANDPIPER, *CALIDRIS MAURI*

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Abstract. We show that a higher vertebrate can graze surficial intertidal biofilm, previously only considered a food source for rasping invertebrates and a few specialized fish. Using evidence from video recordings, stomach contents, and stable isotopes, we describe for the first time the grazing behavior of Western Sandpipers (*Calidris mauri*) and estimate that biofilm accounts for 45–59% of their total diet or 50% of their daily energy budget. Our finding of shorebirds as herbivores extends the trophic range of shorebirds to primary consumers and potential competitors with grazing invertebrates. Also, given individual grazing rates estimated at seven times body mass per day and flock sizes into the tens of thousands, biofilm-feeding shorebirds could have major impacts on sediment dynamics. We stress the importance of the physical and biological processes maintaining biofilm to shorebird and intertidal conservation.

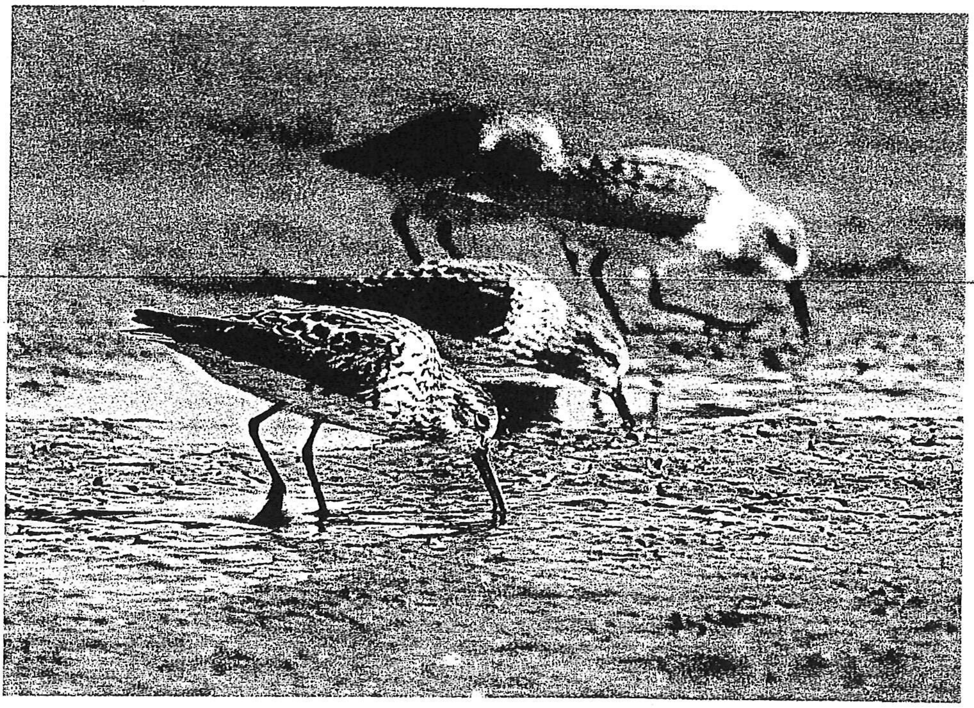

Plate 1. Western Sandpipers (*Calidris mauri*) grazing surficial biofilm on the Roberts Bank mudflat, British Columbia, Canada. For their feeding behavior, see movie files in the Appendices. Photo credit: T. Kuwae.

Vol. 428: 259–269, 2011
doi: 10.3354/meps09050

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published May 3

Downward trophic shift during breeding migration in the shorebird *Calidris mauri* (western sandpiper)

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ABSTRACT: The recent demonstration of mudflat surficial biofilm feeding by western sandpiper *Calidris mauri* has provided new insight into the feeding ecology of shorebirds. We assessed feeding modes over the migratory cycle, and specifically whether a downward shift in trophic position occurred during the 2004 northward migration from their overwintering areas to the Arctic breeding grounds. We used stable isotope composition and calculated trophic positions of adult western sandpiper at their northward migratory stopover on Roberts Bank, British Columbia, Canada, in 3 animal compartments with increasing turnover times (stomach contents, liver, and muscle). This allowed the retrospective determination of their major diet source types over time frames encompassing the geographical ranges of their previous migratory stopovers and arrival on the Roberts Bank stopover. Detailed taxonomic and photopigment determinations were also performed on stomach contents and surficial biofilm. The Roberts Bank biofilm showed high taxonomic homogeneity among sampling sites, suggesting a qualitatively consistent food source during western sandpiper stopover. A statistically significant downward shift in mean trophic position (TP) occurred between previous migratory stopovers (TP = 3.0 ± 0.5, mean ± SD) and arrival on the Roberts Bank stopover, where the maximum probability densities showed >70% dietary contribution of benthic diatoms, with a TP = 2.3 ± 0.4, close to the diet of the suspension-feeding bivalves *Tapes philippinarum* and *Mya* sp. (TP = 2). Advantages of biofilm over macrofaunal feeding during migration may include decreased handling and search time, as well as greater availability and digestibility of the high-energy carbohydrates needed for flight.

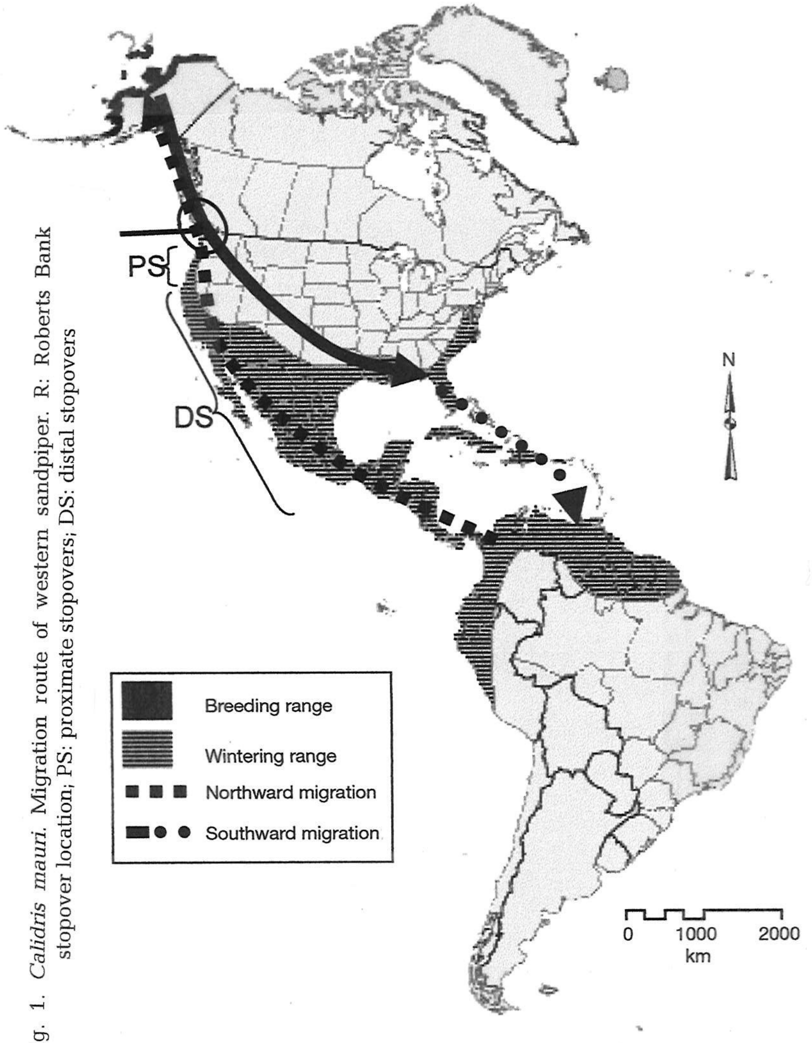

Fig. 1. *Calidris mauri.* Migration route of western sandpiper. R: Roberts Bank stopover location; PS: proximate stopovers; DS: distal stopovers

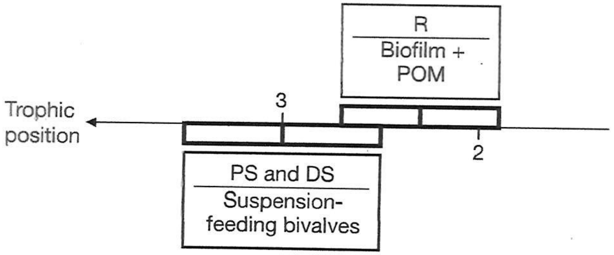

Fig. 4. *Calidris mauri.* Major components of western sandpiper diets and trophic positions at proximate and distal stopover grounds (PS and DS) prior to arrival at Roberts Bank stopover (R), as given by the $\delta^{13}C$ and $\delta^{15}N$ of muscle (DS), liver (PS), and stomach contents (R). Bold rectangles represent SD of the means

3 - La zone sublittorale: importance du couplage bentho-pélagique. La bioproduction des fonds rocheux et meubles; les herbiers marins

Vol. 356: 103–112, 2008
doi: 10.3354/meps07280

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published March 18

Live benthic diatoms from the upper continental slope: extending the limits of marine primary production

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ABSTRACT: Discovery of obligate benthic diatoms living as deep as 191 m substantially extends the known depth range of these primary producers and holds significant implications for oceanic productivity and biogeochemical cycling. Species of the epipsammic, monoraphid genus *Cocconeis* dominated the ≥35 species of living benthic diatoms identified from the North Carolina continental margin in samples collected at bottom depths from 67 to 191 m. A total of 126 species were identified from prepared samples, more than 90% of which are obligate benthic forms. Mid-day, near bottom, photosynthetically active radiation values recorded at the 191 m site averaged 0.106 µmol photons m^{-2} s^{-1}, representing about 0.028% of surface incident radiation and resulting from a water column attenuation coefficient of 0.0446 m^{-1}. The presence of active benthic microalgae in these extremely low light conditions suggests the development of special light-harvesting adaptations including elevated levels of the blue-light absorbing accessory pigment, fucoxanthin. Extending the limit of benthic microalgal production to upper slope depths offshore from North Carolina increases the estimated total benthic primary production in that area of the continental margin by about 14%. At present, extrapolating potential increases in benthic microalgal biomass and production resulting from extending the depth limits of viable benthic microalgae to a larger, global, oceanic scale is limited by paucity of data.

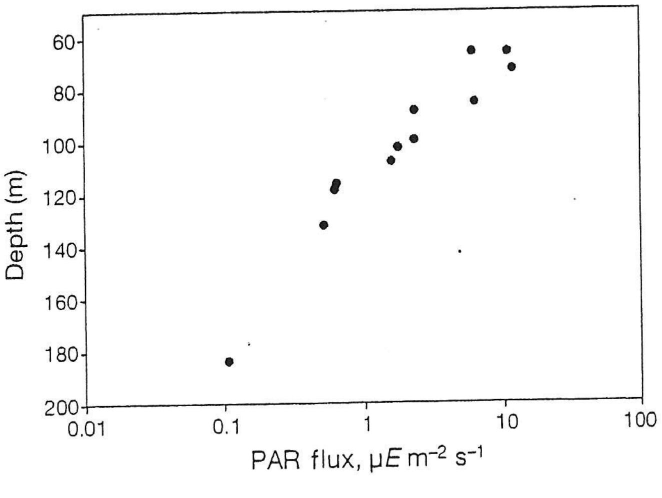


Fig. 2. Values of PAR observed (uncorrected for time of day effects on surface incident PAR flux) at near-bottom depths at each of 12 sites (excluding ROV Sites 4 and 5) in Onslow Bay, 16–17 October 2003 (transects 2003 I and 2003 II, Fig. 1). Linear regression yielded the relationship: log (near-bottom PAR) = 2.086 – 0.0177(depth); $r^2 = 0.925$; $F = 123.9$; df = 1,10; $p < 0.0001$

Bivalves benthiques sublittoraux - Pectinidae

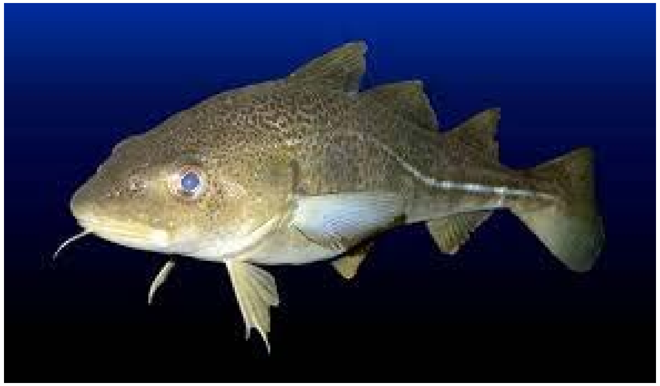
Crustacés sublittoraux- Décapodes

Cancridae

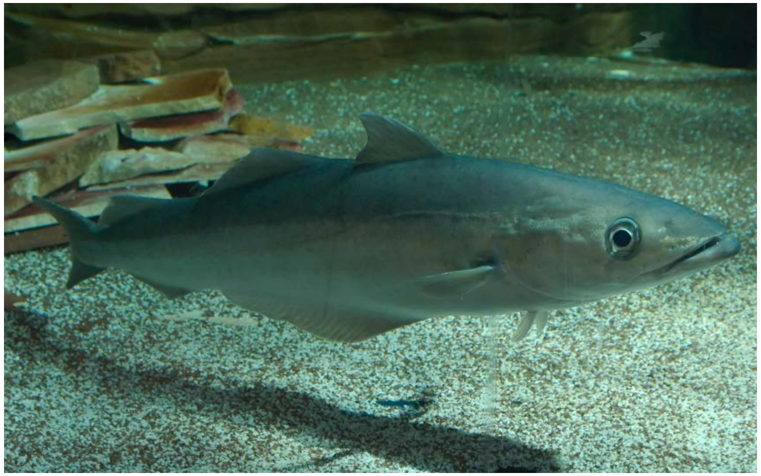
Homarus gammarus

Crevette Crangon sp.

Poissons sublittoraux démersaux (bentho-pélagiques)



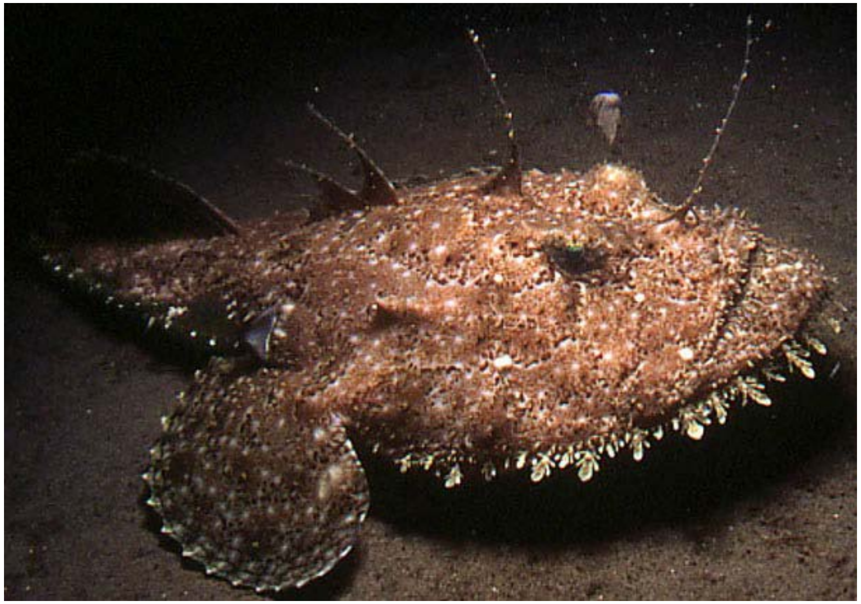
Cabillaud, *Gadus morhua* - rétrognathe



Lieu, *Pollachius virens* - prognathe

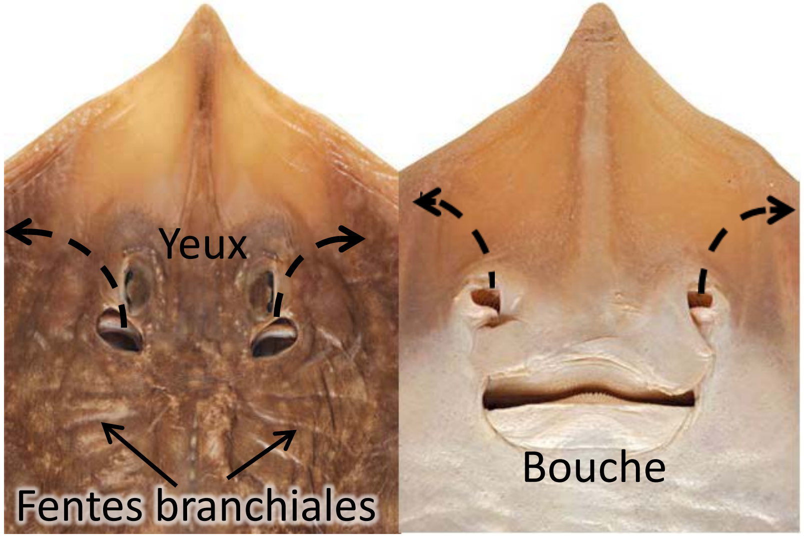
Merlu, *Merluccius merluccius*

Poissons de fond sublittoraux épibenthiques



Poissons de fond sublittoraux épibenthiques

Poissons de fond sublittoraux épibenthiques



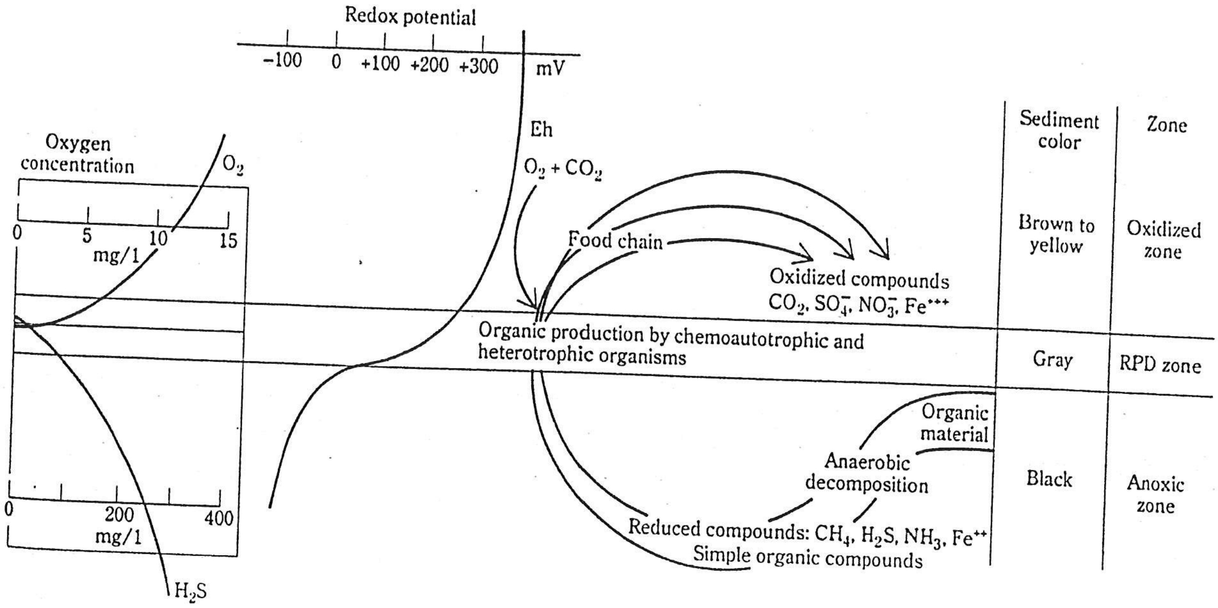


Figure 6.37 Diagrammatic representation of the physical and chemical characteristics of sediments across the redox discontinuity layer and the biological processes occurring in each. (From various sources.)

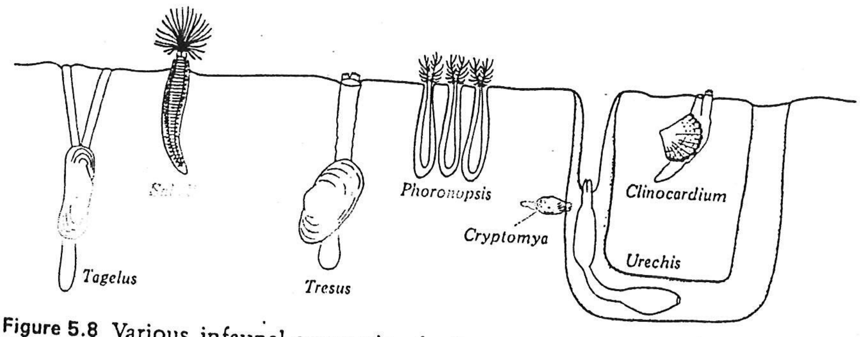


Figure 5.8 Various infaunal suspension-feeding types distributed at different depths in the substrate.

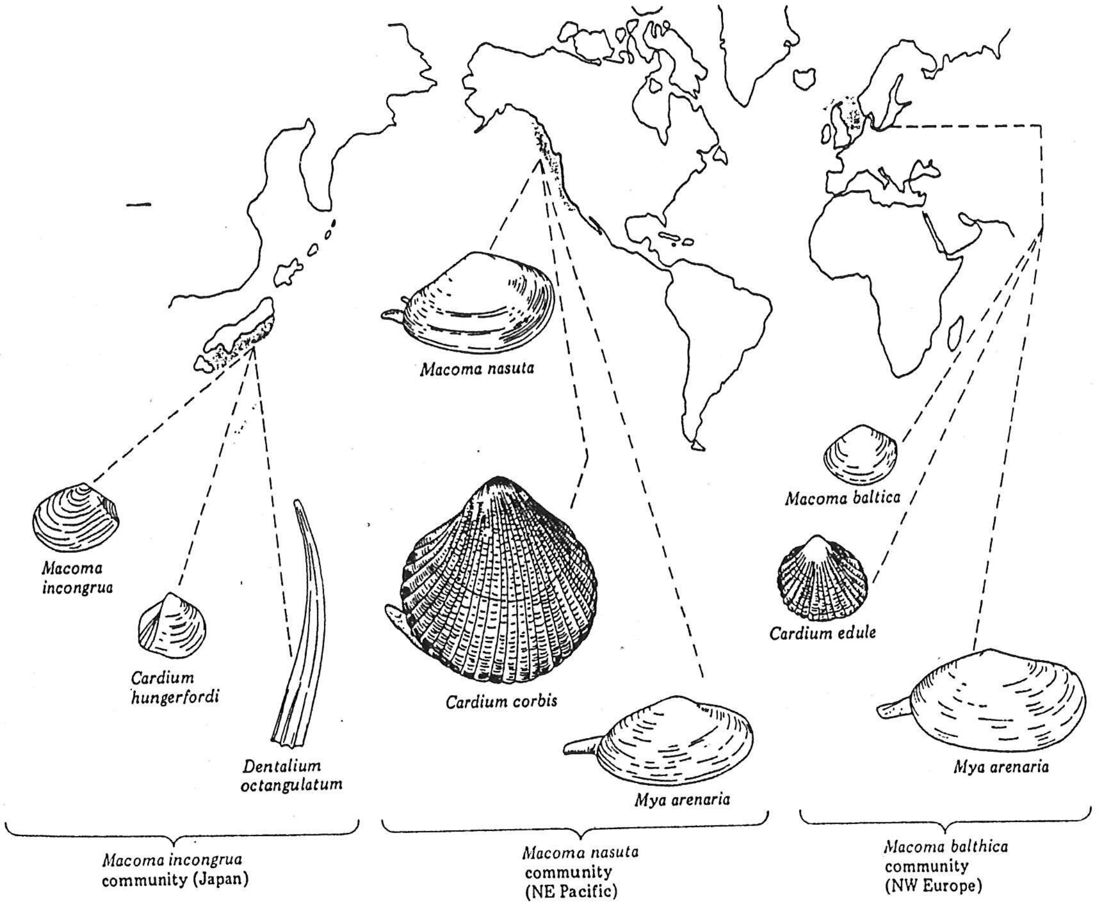
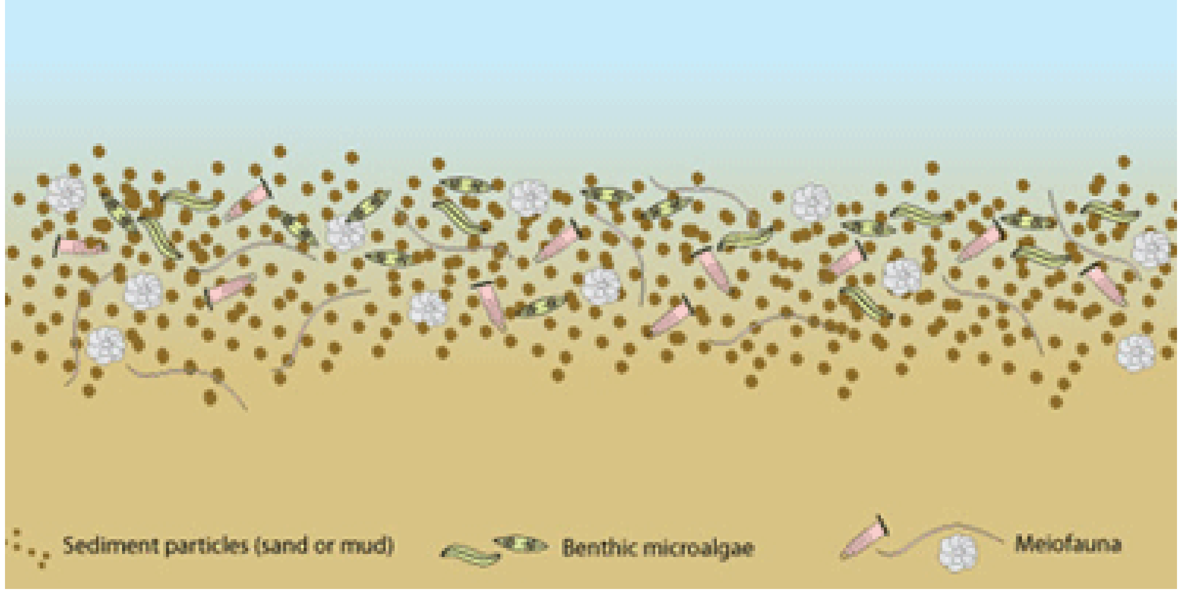


Figure 5.3 Diagram illustrating the parallel bottom communities dominated by the bivalve *Macoma* in three different areas in the North Temperate Zone. (Modified from G. Thorson, Bottom communities. *In:* The treatise on marine ecology and paleoecology, Vol. 1, Ecology, edited by J. Hedgpeth, The Geological Society of America, 1957.)

La méiofaune interstitielle



Nématodes

Copépodes harpactacoïdes

Foraminifères

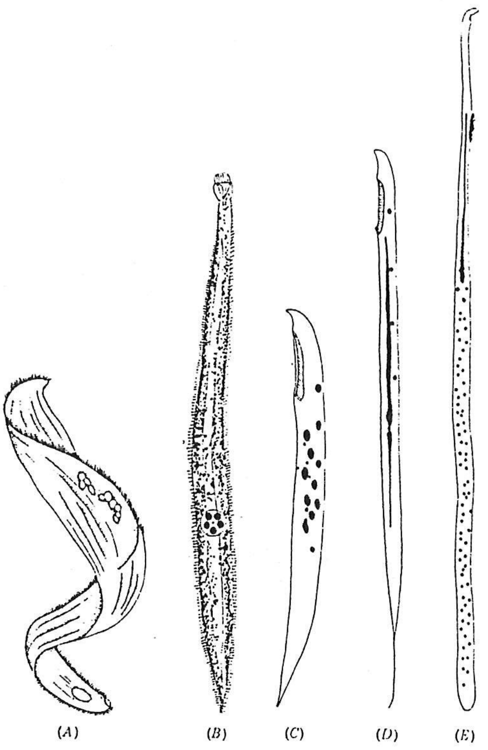


Figure 7.3 Types of interstitial ciliate protozoans, phylum Ciliophora. *(A) Loxophyllum vermifôrme* with a flattened body. *(B) Tracheloraphis remanei* with a cylindrical body. *(C) Remanella faurei* with a flattened elongated body. *(D) Remanella caudata* with an elongated body and tail. *(E) Geleia gigas* with a thread-like body. (From B. Swedmark, The interstitial fauna of marine sand, Biol. Rev. 39:1–42. Copyright © 1964 by Cambridge Philosophical Society; reprinted with permission of Cambridge University Press.)

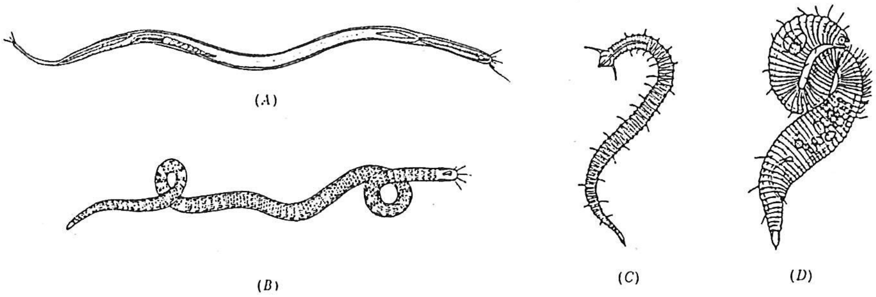


Figure 7.5 Some interstitial nematodes. *(A) Paramonohystera wieseri. (B) Cyttaronema reticulatum. (C) Tricoma hopperi. (D) Epsilonema.* (From various sources.)

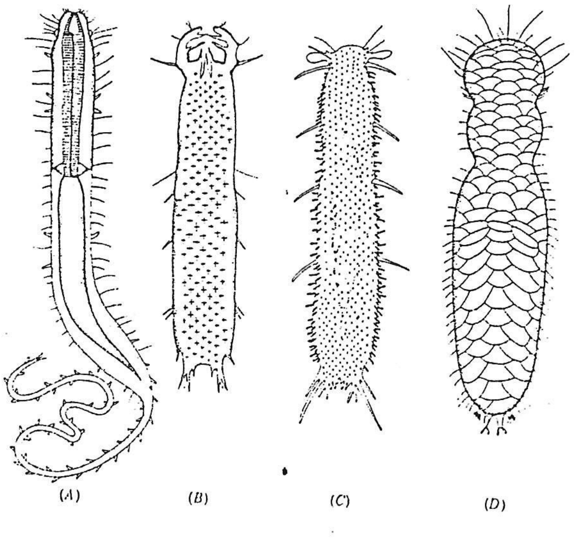


Figure 7.6 Some interstitial gastrotrichs. *(A) Urodasys viviparus. (B) Pseudostomella roscovita. (C) Thaumastoderma heideri. (D) Diplodasys ankeli.* (From B. Swedmark, The interstitial fauna of marine sand, Biol. Rev. 39:1–42. Copyright © 1964 by Cambridge Philosophical Society; reprinted with permission of Cambridge University Press.)

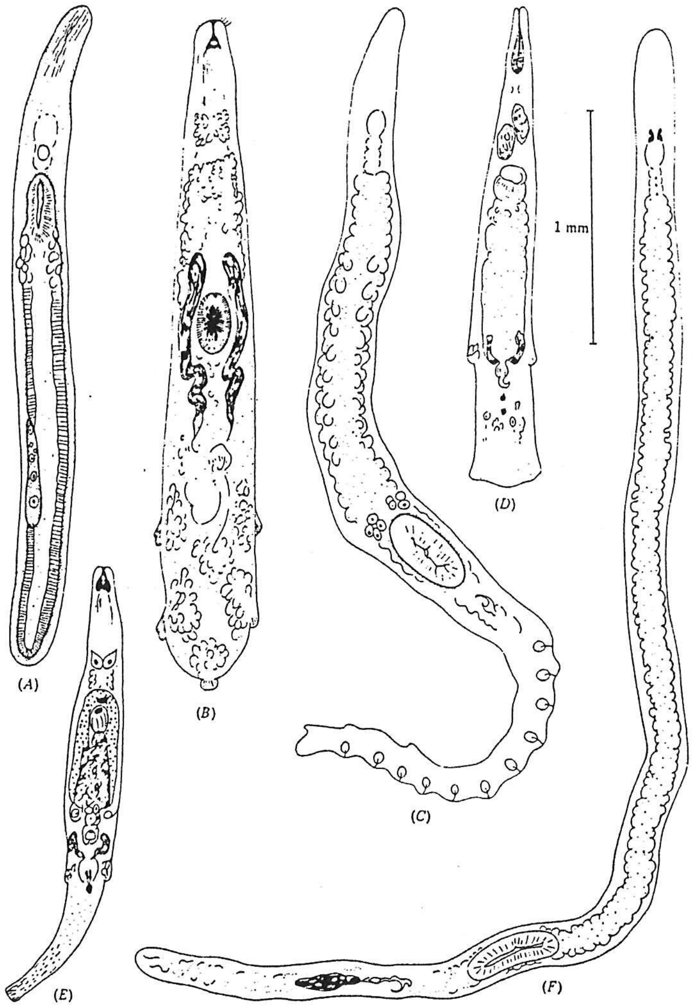


Figure 7.4 Examples of some turbellarian flatworms from an interstitial marine sand beach in Florida. *(A)* A member of the family Macrostomidae. *(B)* A member of the family Kalyptorhynchidae. *(C) Polystylophora* sp. *(D) Proschizorhynchus* sp. *(E) Cicerina* sp. *(F) Nematoplana* sp. (From L. Bush, Characteristics of interstitial sand turbellaria: The significance of body elongation, muscular development, and adhesive organs. Trans. Amer. Microsc. Soc. 87(2):244–251, 1968.)

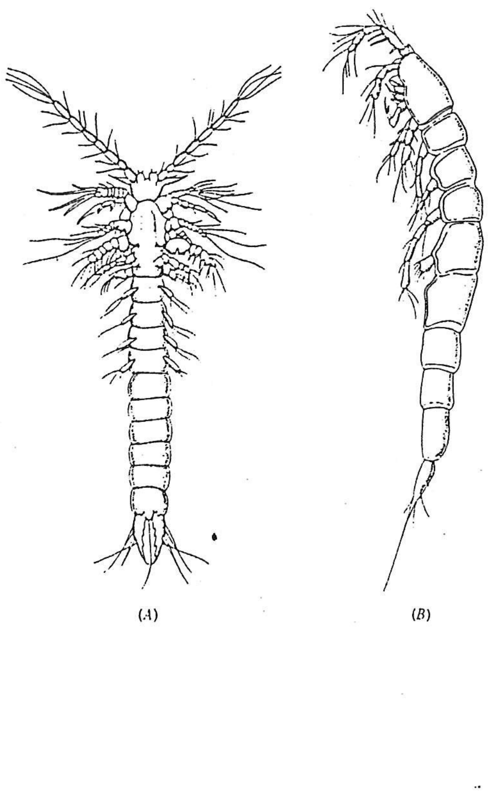


Figure 7.8 Some crustacea of the interstitial fauna. *(A) Derocheilocaris remanei* (Mystacocarida). *(B) Cylindropsyllis laevis* (Copepoda). (From B. Swedmark, The interstitial fauna of marine sand, Biol. Rev. 39: 1–42. Copyright © 1964 by Cambridge Philosophical Society; reprinted with permission of Cambridge University Press.)

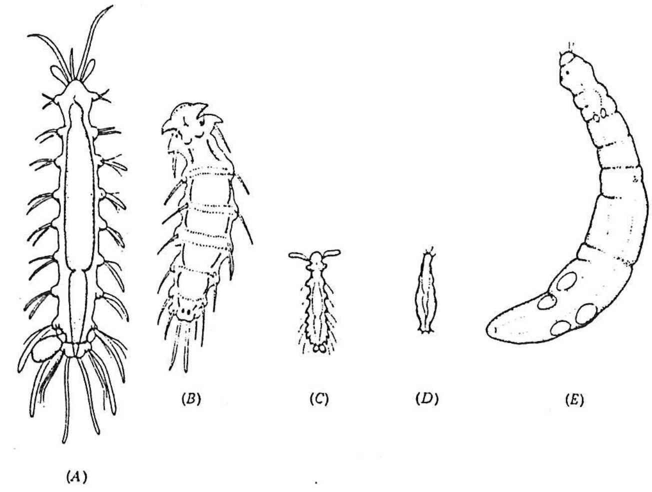


Figure 7.7 Some representative interstitial annelids of the class Polychaeta. *(A) Mesonerilla intermedia. (B) Paranerilla limnicola. (C) Nerillidium simplex. (D) Diurodrilus* sp. *(E) Trilobodrilus* sp. (From N. C. Hulings [ed.], Proceedings of the first international conference on meiofauna, Smithsonian Contributions to Zoology no. 76, 1971.)

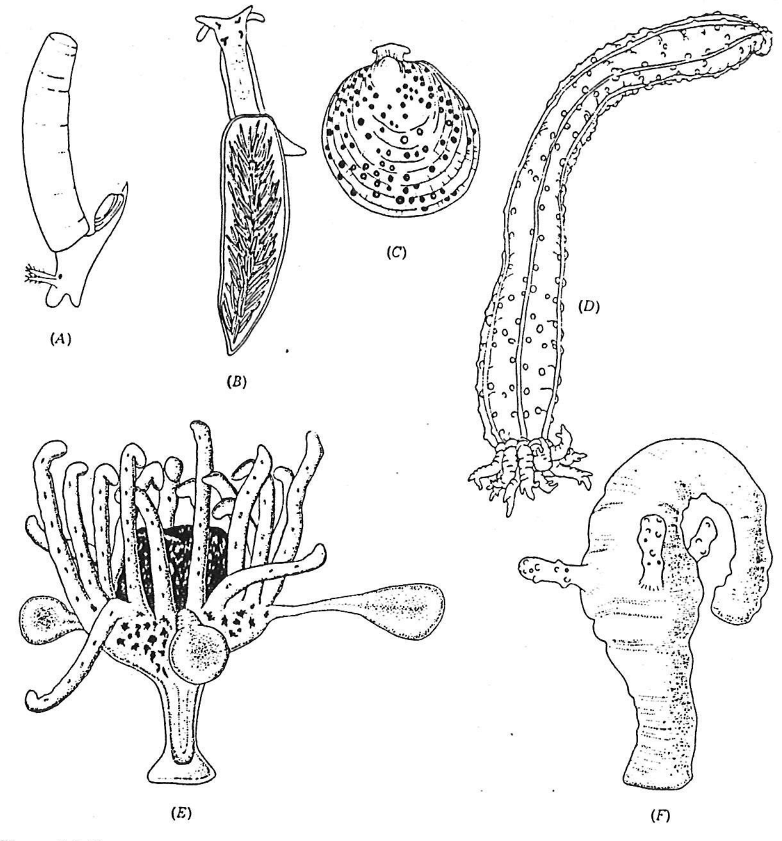


Figure 7.9 Representative interstitial Mollusca, Cnidaria, Echinodermata, and Brachiopoda. *(A) Caecum glabrum* (Mollusca, Gastropoda). *(B) Hedylopsis brambeli* (Mollusca, Gastropoda). *(C) Gwynia capsula* (Brachiopoda). *(D) Labidoplax buskii* (Echinodermata). *(E) Stylocoronella riedli* (Cnidaria, Scyphozoa). *(F) Psammohydra nanna* (Cnidaria, Hydrozoa). (From N. C. Hulings [ed.], Proceedings of the first international conference on meiofauna, Smithsonian Contributions to Zoology no. 76, 1971.)

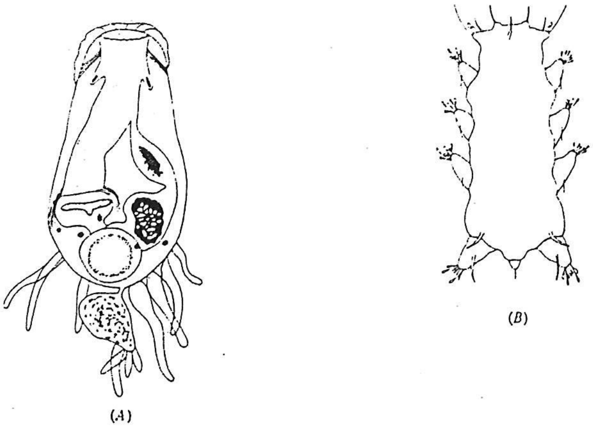


Figure 7.10 Sample interstitial Bryozoa and Tardigrada. *(A) Monobryozoon ambulans* (Bryozoa). *(B) Batillipes pennaki* (Tardigrada). (*A*, after N. C. Hulings [ed.], Proceedings of the first international conference on meiofauna, Smithsonian Contributions to Zoology no. 76, 1971. *B*, after L. W. Pollock, Distribution and dynamics of interstitial Tardigrada at Woods Hole, Massachusetts, U.S.A., Ophelia 7[2]: 145–165, 1970.)

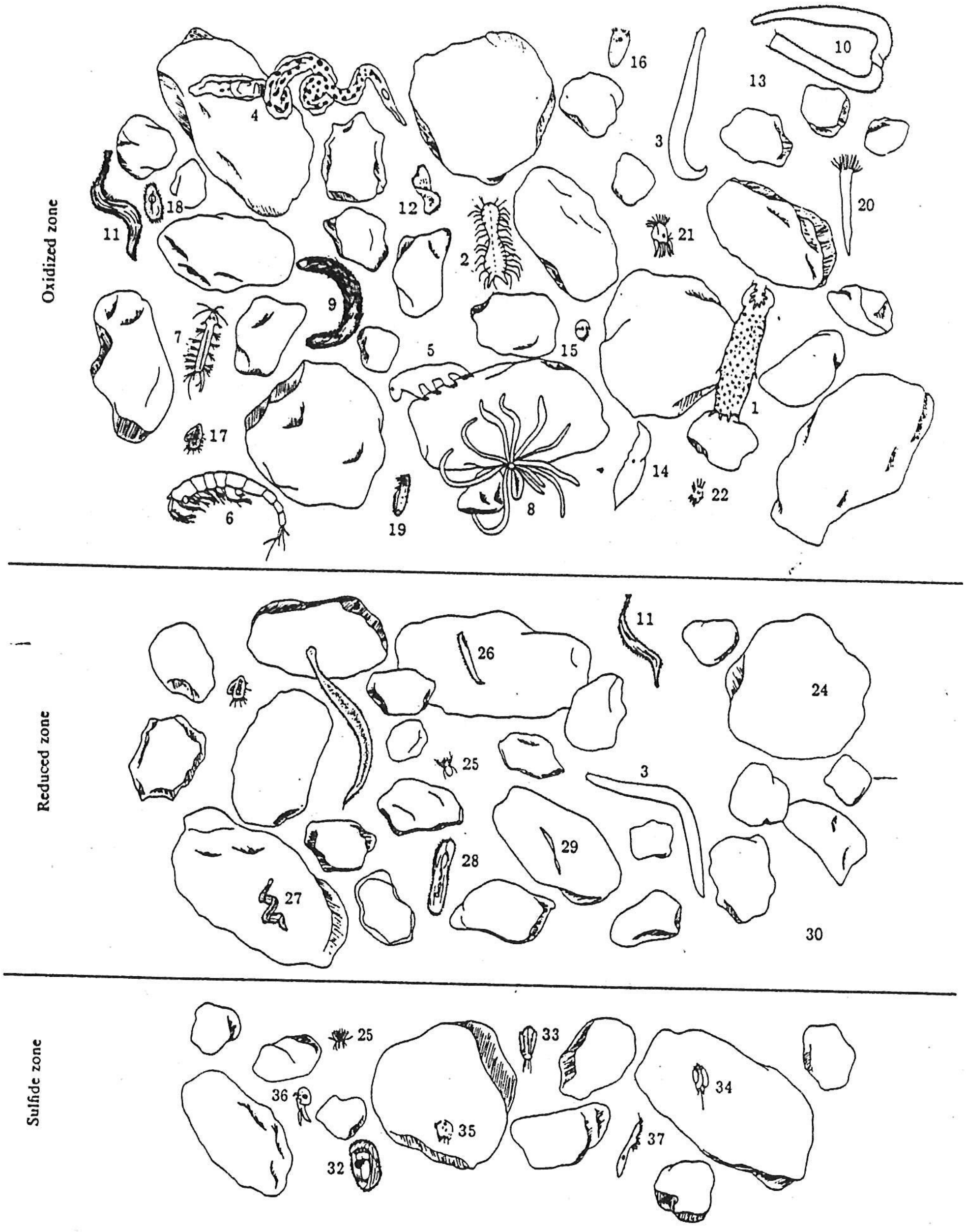

Oxidized zone
Reduced zone
Sulfide zone
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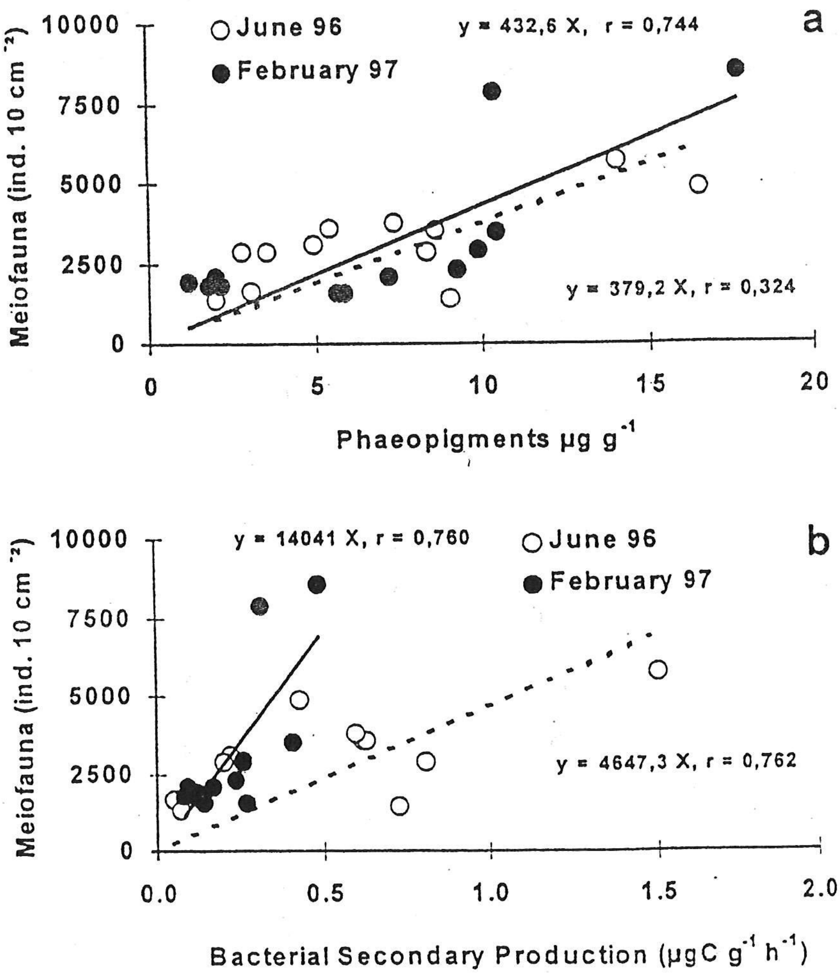
Fig. 5 Relationships between meiofaunal abundance and a phaeopigment concentration or b bacterial secondary production



Marine Biology (1999) 134: 419–427

A. C. Pati · G. Belmonte · V. U. Ceccherelli · F. Boero

The inactive temporary component: an unexplored fraction of meiobenthos

Received: 10 September 1998 / Accepted: 12 April 1999

Abstract Numerous morphotypes and great abundances of resting stages falling within the meiobenthic size-range were found in meiobenthos samples collected in a coastal lagoon of the North Adriatic Sea. Biodiversity, abundances and energetic values of both active and inactive meiobenthic organisms were analysed by the traditional techniques of meiobenthology. Inactive stages were represented by more than 100 morphotypes and formed 52% of the meiobenthos in terms of numbers of individuals. Inactive meiobenthos came mostly from plankton: the second and third most abundant groups of all meiobenthic organisms were the eggs of a rotifer and the cysts of a dinophyte, respectively. Resting stages of plankters fit the definition of temporary meiobenthos, making up the "inactive temporary meiobenthos", but they are usually not considered in meiobenthology. The diversity and abundance of the meiobenthos is, thus, currently underestimated; this leads to neglect of the role of meiobenthos in several processes linking different ecosystems. It is hypothesised, for instance, that the meiobenthic resting stages of planktonic organisms (besides being the "seeds" for the perpetuation of planktonic communities) might also be the prey of meiofaunal organisms with piercing mouth parts. If this proves correct, a regulatory role might be proposed for the meiofauna in respect to plankters with benthic stages.

Communicated by R. Cattaneo-Vietti, Genova

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Introduction

The meiobenthic dimensional range (from 31 to 1000 μm, Giere 1993) is a kind of "transit station" for many organisms whose adults belong to other compartments, both pelagic and benthic. Warwick (1989) proposed that organisms spending their whole life in the meiobenthos (permanent meiobenthos) intensely affect those species having only one or several life stages within this dimensional range (temporary meiofauna). Warwick et al. (1986) and Strathmann (1990) suggested that pelagic larvae and encapsulated eggs evolved in macrofauna to both escape predation from permanent meiofauna and to avoid resource competition with it.

Interactions between permanent meiofauna and meiobenthic macrofaunal settlers have been studied also from an ecological standpoint, with the proposal of the "meiofaunal bottleneck" (Bell and Coull 1980). This envisages a control of macrofauna by permanent meiofauna predation on newly settled juveniles of macrofauna having a meiofaunal size. Further studies, however, restricted the general value of this concept (see Zobrist and Coull 1992, 1994).

Some studies analysed the role of meiofauna on ecosystem structure and organisation, including pelagic compartments (Platt 1981; Warwick 1989), but the meiobenthos is not currently considered to have important ecological connections with pelagic compartments. The temporary meiobenthos, however, does not solely consist of the settled larvae of the macrofauna. Many planktonic organisms, in fact, have stages which rest in the sediments (for reviews see Boero 1994, 1996; Boero et al. 1996) and have sizes that fall within the dimensional range of meiobenthos. Several aspects of plankton ecology (e.g. response to adverse conditions, spatial and temporal segregation among potentially competitive species, and propagule storage for future recruitment) are involved in the production of benthic resting stages by planktonic organisms (Marcus and Boero 1998). The importance of resting stage banks, thus, must be further

Mar Biol (2007) 152:339–350
DOI 10.1007/s00227-007-0696-y

RESEARCH ARTICLE

Trophic importance of subtidal metazoan meiofauna: evidence from in situ exclusion experiments on soft and rocky substrates

Roberto Danovaro · Mariaspina Scopa ·
Cristina Gambi · Simonetta Fraschetti

Abstract In coastal marine ecosystems, predation might affect spatial distribution and population dynamics of benthic assemblages. Here, by means of experimental exclusion of potential predators, we compared the effects of epibenthic predation on metazoan meiofaunal assemblages on soft and rocky substrates. Different patterns of abundance were observed in uncaged versus caged plots, across habitats. In caged soft substrates, the abundance of Nematodes, Copepods and Polychaetes increased by 56, 45, 57%, respectively, in the first 3 months. An increase in the number of meiofaunal taxa was also observed. The exclusion of predators from rocky substrates showed less clear patterns. It did not affect the number of taxa while a decrease in meiofaunal abundance was observed. Our results suggest that the exclusion of epibenthic predators had clear effect on total metazoan meiofaunal abundance and on the number of taxa, only in soft bottoms. The different impact of predation across habitats can be potentially explained by differences in terms of spatial variability and substrate complexity. We estimated that, coarsely, more than 75% of total metazoan meiofaunal production can be channeled to higher trophic levels through predation on soft-bottoms. Among meiofaunal taxa, Polychaetes and Nematodes provided the major contribution to benthic energy transfers. These results suggest the trophic relevance of metazoan meiofauna in coastal food webs and claim for the refinement of further experiments for the quantification of its role in different ecological systems.

Table 2 Average abundance of the main taxa contributing to the Bray–Curtis dissimilarity value between control (uncaged) and caged plots at 45, 60 and 90 days respectively from the beginning of the experiment in soft sediments

Soft bottom	45 days				60 days				90 days			
	Average abundance		Contribution %	Cumulative %	Average abundance		Contribution %	Cumulative %	Average abundance		Contribution %	Cumulative %
	Control	Cage			Control	Cage			Control	Cage		
Nematodes	30.8	54.8	34.3	34.3	40.7	55.6	36.7	36.7	32.3	69.0	43.9	43.9
Copepods	10.5	25.4	21.5	55.7	12.6	12.5	5.7	71.3	9.2	13.1	4.5	89.1
Nauplii	6.9	16.3	13.3	69.0	10.4	9.7	5.8	65.5	13.7	21.9	9.8	71.1
Polychaetes	6.1	12.9	9.7	78.7	7.6	13.5	12.6	49.3	11.3	25.9	17.4	61.3
Others	2.9	6.3	4.9	89.6	1.1	5.9	10.4	59.7	0.0	2.5	3.1	92.2

Journal of Sea Research 85 (2014) 85–91

Contents lists available at ScienceDirect

Journal of Sea Research

journal homepage: www.elsevier.com/locate/seares

Effect of long-term mechanical perturbation on intertidal soft-bottom meiofaunal community spatial structure

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ARTICLE INFO

Article history:
Received 15 May 2013
Received in revised form 16 September 2013
Accepted 10 October 2013
Available online 21 October 2013

Keywords:
Meiofauna
Spatial distribution
Geostatistics
Mudflat
Fishing impact

ABSTRACT

Situated at the interface of the microbial and macrofaunal compartments, soft-bottom meiofauna accomplish important ecological functions. However, little is known of their spatial distribution in the benthic environment. To assess the effects of long-term mechanical disturbance on soft-bottom meiofaunal spatial distribution, we compared a site subjected to long-term clam digging to a nearby site untouched by such activities, in Bourgneuf Bay, on the Atlantic coast of France. Six patterned replicate samples were taken at 3, 6, 9, 12, 15, 18, 21 and 24 cm lags, all sampling stations being separated by 5 m. A combined correlogram–variogram approach was used to enhance interpretation of the meiofaunal spatial distribution; in particular, the definition of autocorrelation strength and its statistical significance, as well as the detailed characteristics of the periodic spatial structure of nematode assemblages, and the determination of the maximum distance of their spatial autocorrelation. At both sites, nematodes and copepods clearly exhibited aggregated spatial structure at the meso scale; this structure was attenuated at the impacted site. The nematode spatial distribution showed periodicity at the non-impacted site, but not at the impacted site. This is the first explicit report of a periodic process in meiofaunal spatial distribution. No such cyclic spatial process was observed for the more motile copepods at either site.

This first study to indicate the impacts of long-term anthropogenic mechanical perturbation on meiofaunal spatial structure opens the door to a new dimension of mudflat ecology. Since macrofaunal predator search behaviour is known to be strongly influenced by prey spatial structure, the alteration of this structure may have important consequences for ecosystem functioning.

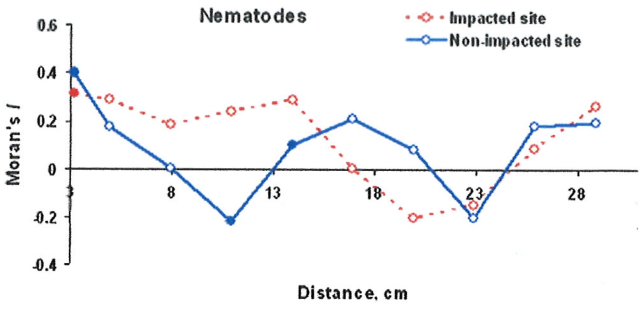


Fig. 3. Omnidirectional spatial autocorrelogram for nematode densities using 10 equidistant classes. Significant values are represented by solid symbols; non-significant values are represented by empty symbols.

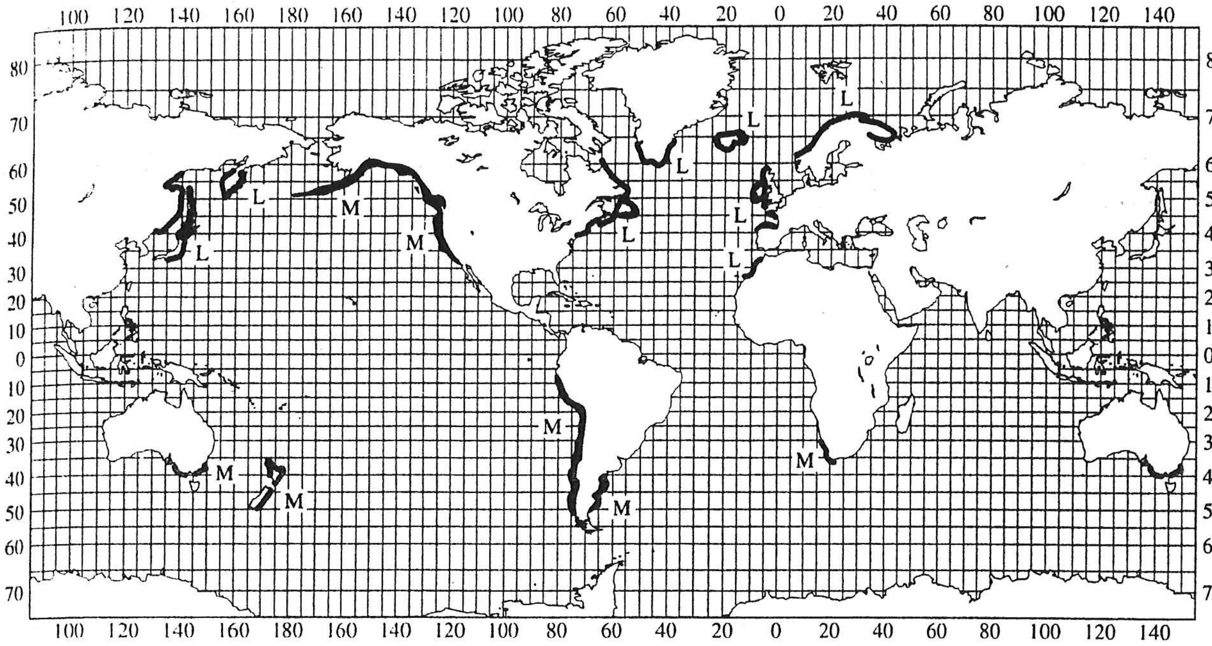
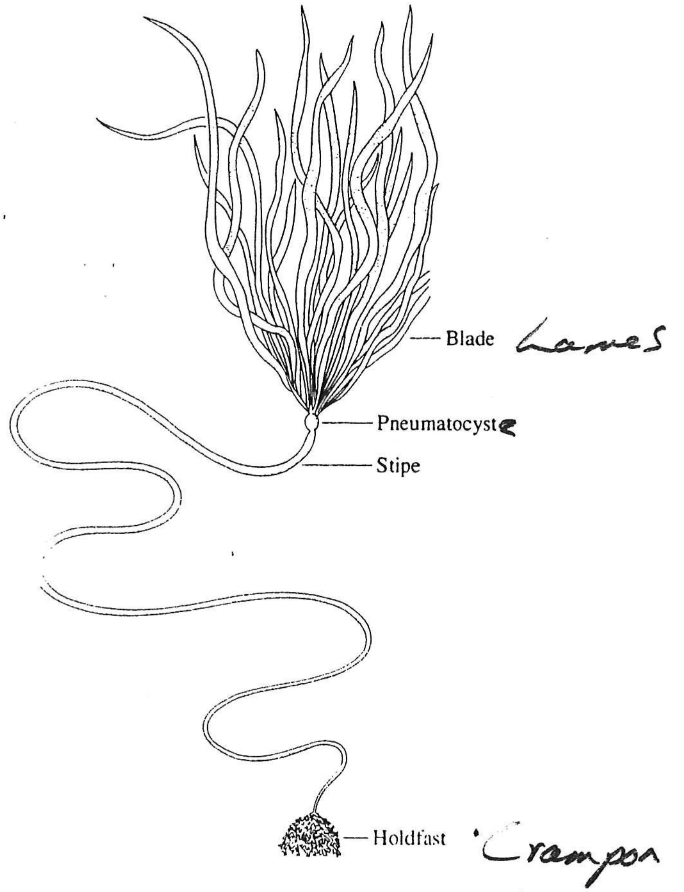
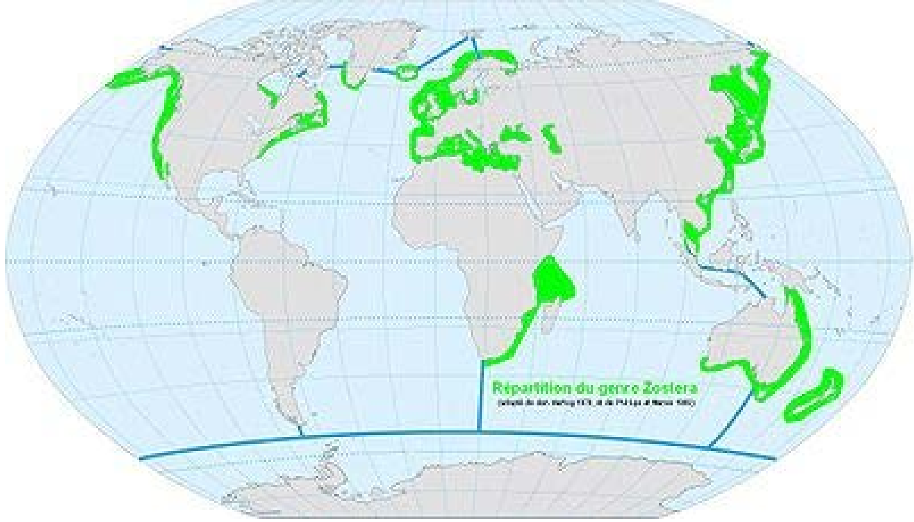
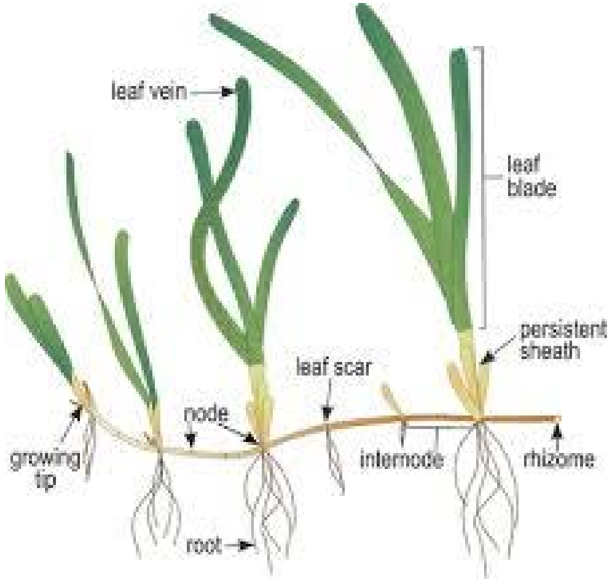


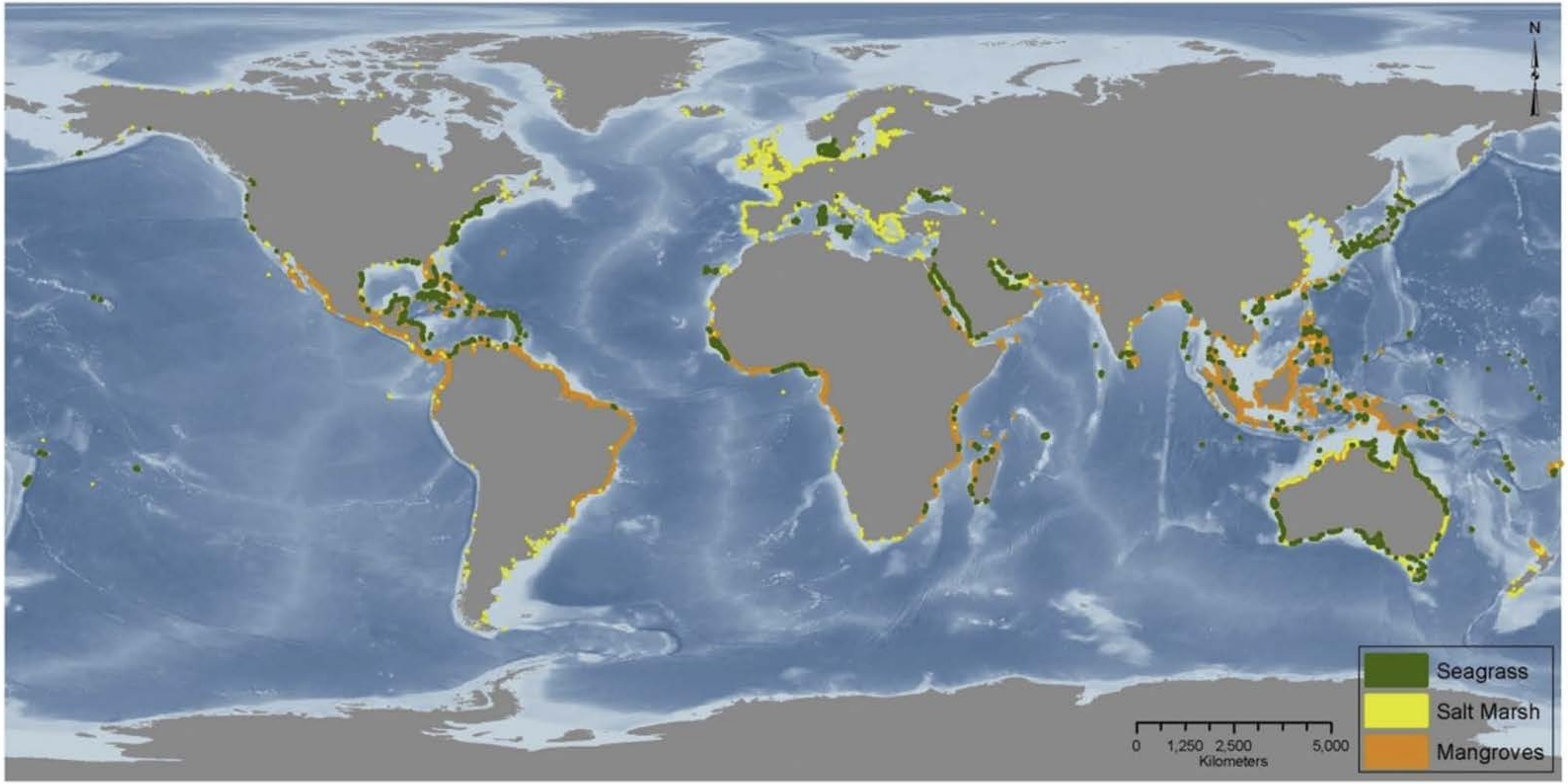
Figure 5.14 Distribution of kelp beds in the world, indicating the dominant genera. (L) *Laminaria*; (M) *Macrocystis*. (Modified from K. H. Mann, Seaweeds: Their productivity and strategy for growth, Science 182[4116]:975–983, 1973. Copyright © 1973 by the American Association for the Advancement of Science.)



Les champs de Zostères






N
Seagrass
Salt Marsh
Mangroves
0
1,250
2,500
5,000
Kilometers

Journal of Experimental Marine Biology and Ecology 394 (2010) 154–160

Contents lists available at ScienceDirect

Journal of Experimental Marine Biology and Ecology

journal homepage: www.elsevier.com/locate/jembe

Increasing density of juvenile Atlantic (*Gadus morhua*) and Greenland cod (*G. ogac*) in association with spatial expansion and recovery of eelgrass (*Zostera marina*) in a coastal nursery habitat

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ARTICLE INFO

Article history:
Received 6 April 2010
Received in revised form 4 August 2010
Accepted 5 August 2010

Keywords:
Cod
Disturbance
Recruitment
Seagrass
Vegetation

ABSTRACT

Global declines of eelgrass (*Zostera marina*) have major ramifications for the juvenile fishes for which this plant can provide nursery habitat. However, it is less clear how rapidly fishes can recover when habitat loss is reversed, either through natural growth or through habitat enhancement efforts. We investigated the consequences of natural expansion and recovery of eelgrass following disturbance, on the densities of juveniles of two cod species – Atlantic (*Gadus morhua*) and Greenland (*Gadus ogac*) cod – in a coastal nursery area in Newfoundland, Canada. Eelgrass has been expanding at this location, likely as a result of reduced disturbance from winter pack-ice in the past decade. We conducted bi-weekly sampling of juvenile fish densities at 12 sites from July to November annually, 1995–2006, by seine netting. Each site was designated as either 'natural', 'expansion', 'removal-recovery' or 'unvegetated' dependent on their recent eelgrass coverage and involvement in a manipulation study (1999–2000; Laurel et al. 2003b). We measured eelgrass percentage cover at each site by analysis of aerial photographs. Eelgrass cover had noticeably increased in the 1999–2000 'removal-recovery' sites and at the 'expansion' sites following 2000. Using randomized intervention analysis (RIA) we detected positive relationships between eelgrass cover and relative fish density during 2001–2006. These results suggested a significant and rapid increase in age-0 cod density associated with eelgrass habitat expansion. We suggest that juvenile cod density responds to annual expansion and contraction of eelgrass cover, illustrating the potential cascading effects of eelgrass loss associated with climate change, human disturbance, and disease and the potential benefits of eelgrass conservation and enhancement.

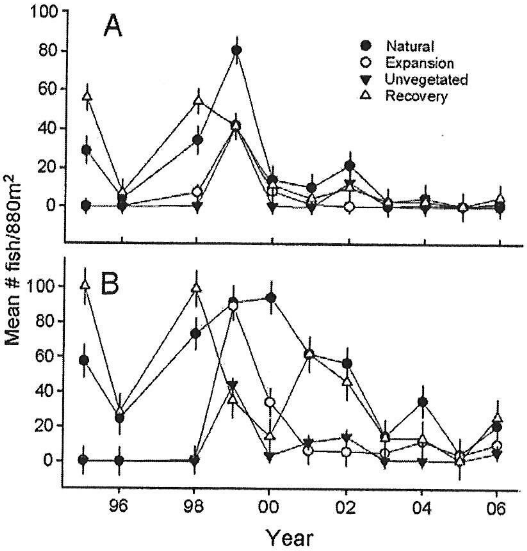
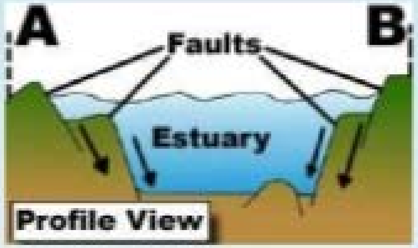


Fig. 3. Interannual mean density (±SE) of A *G. morhua* and B *G. ogac* at each of four conditions of vegetation in Newman Sound, Newfoundland 1995–2006. Natural eelgrass ($n=6$), eelgrass expansion ($n=3$), unvegetated ($n=1$), and recovery sites ($n=2$). Refer to Fig. 1 for site names.

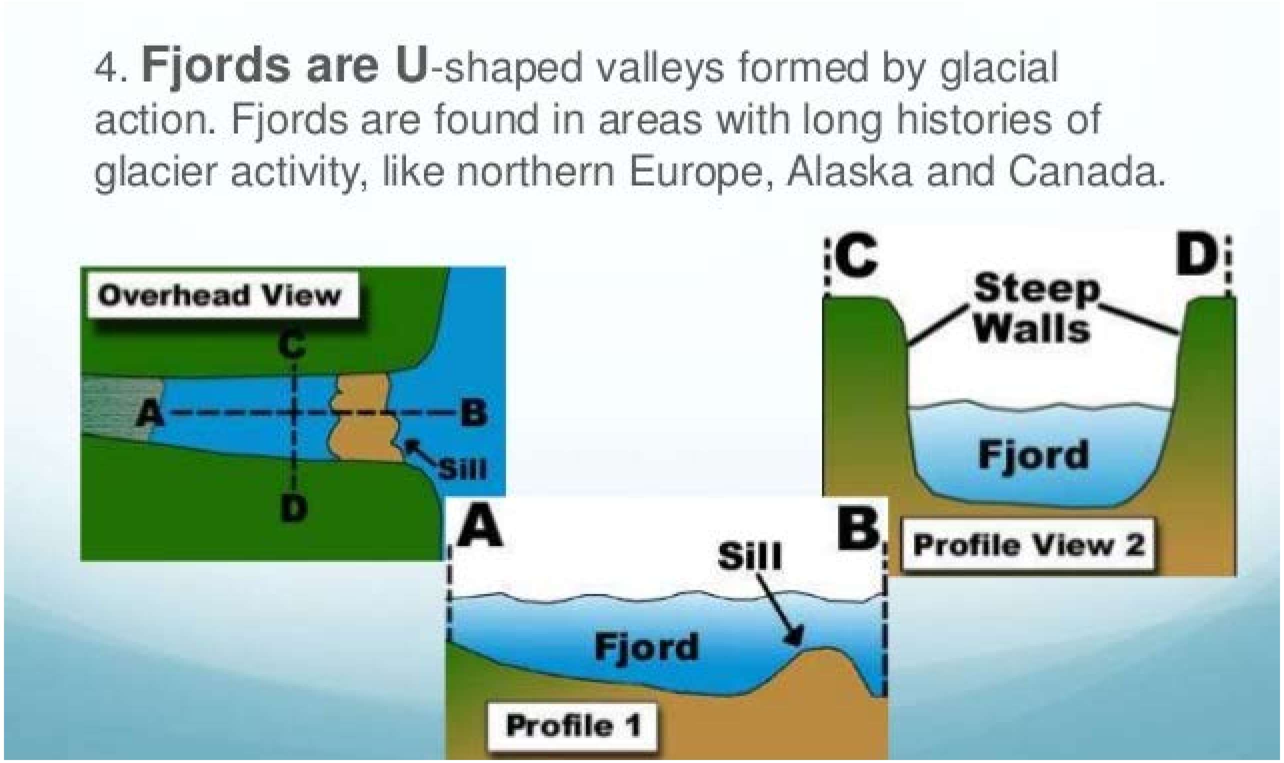
4 - Les estuaires et les forêts de palétuviers : convergence de la bioproduction terrestre et de la bioproduction marine

Tectonic Estuaries

- Tectonic Estuaries are formed by the movement of the Earth's crust. It can cause a section to sink or subside. This creates a depression or basin. Most of these estuaries form along the fault lines when earthquakes occur. The seawater and freshwater that pours into these estuaries after it's creation is the estuary. A good example would be the San Francisco Bay. It's right on a fault line and the area is known for it's earthquakes.



Estuaire de type fjord

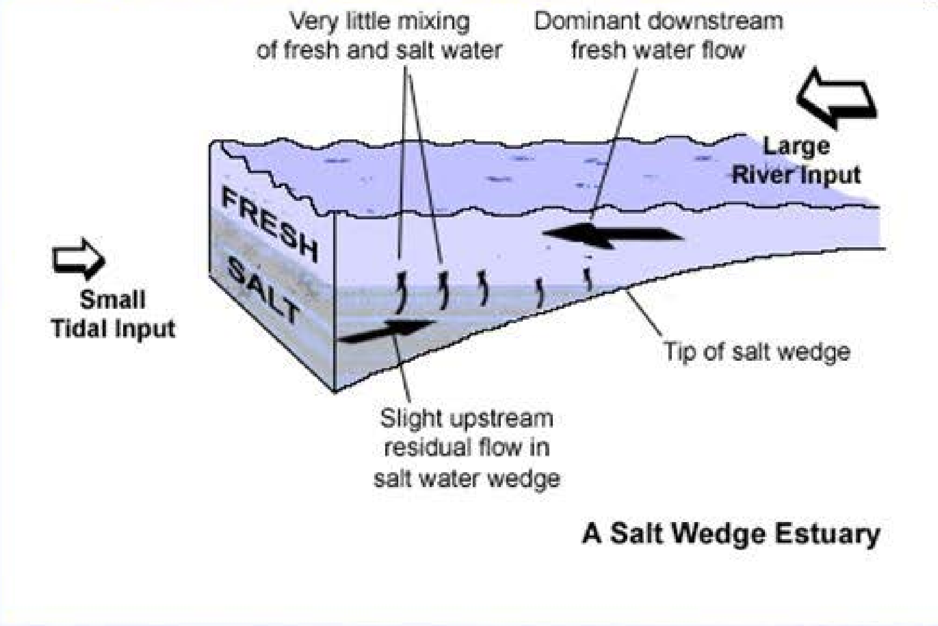


4. **Fjords are U**-shaped valleys formed by glacial action. Fjords are found in areas with long histories of glacier activity, like northern Europe, Alaska and Canada.

Positive or Salt Wedge estuary

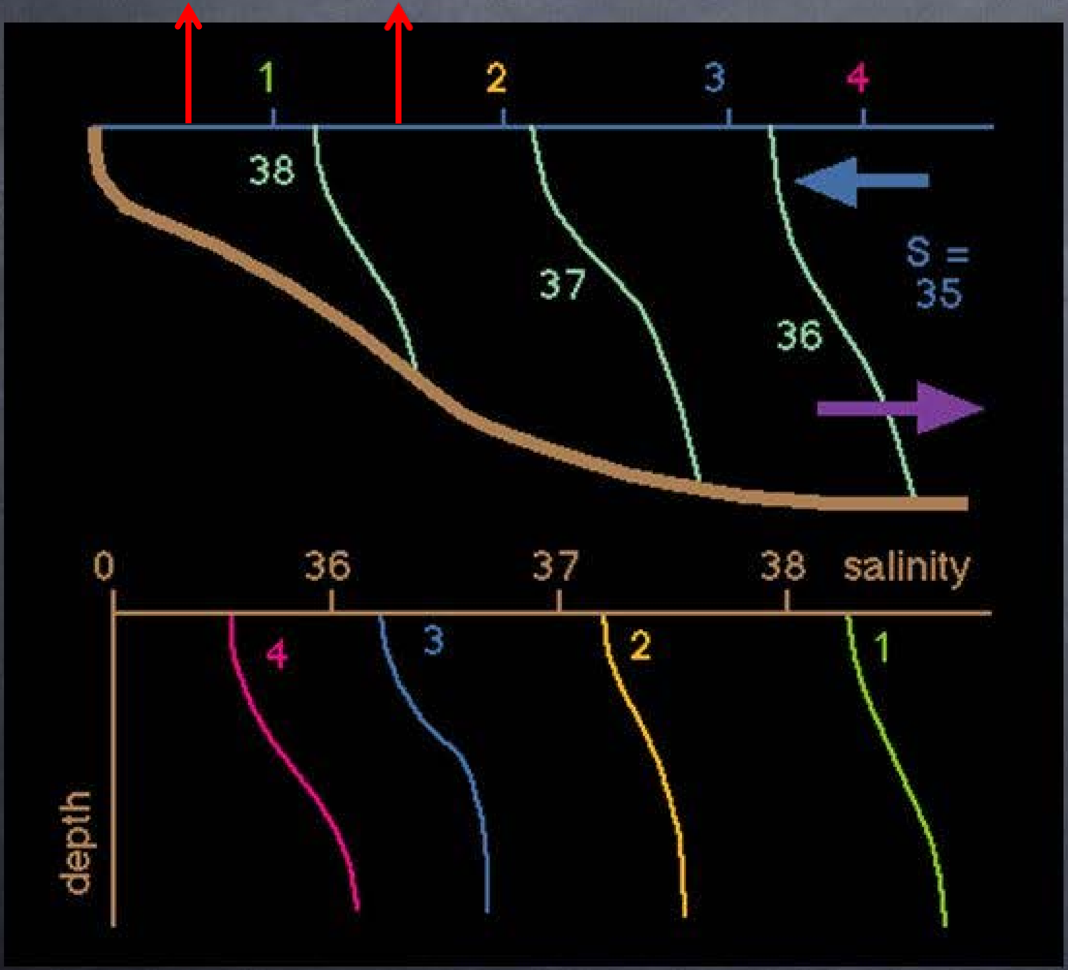
- Where FW input >>evap, FW moves across the surface, mixing with SW, dec salinity but leaving deep water unmixed
- Isohalines slant upstream at bottom
- Vertical profile: salinity always least at surface
- Horizontal –

decreasing upstream



A Salt Wedge Estuary

Inverse estuaries (hypersaline lagoons)



Inverse estuaries are a feature of hot arid climates. They include shallow regions with a large surface area such as hypersaline lagoons, but also gulfs of significant depth and extent. Evaporation becomes a dominant factor in the salt budget of the gulfs, and the salinity increases from the mouth to the head.

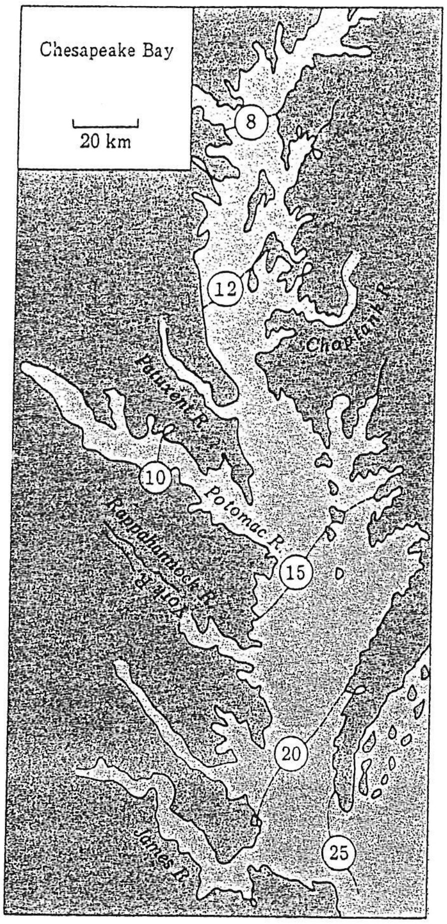


Figure 8.4 Result of Coriolis effect on salinity in the Chesapeake Bay estuary. Note the deflection of the isohalines to the right in this Northern Hemisphere estuary. Circled numbers refer to salinity values in parts per thousand. (After D. S. McLusky, Ecology of estuaries, Heinemann, 1971.)

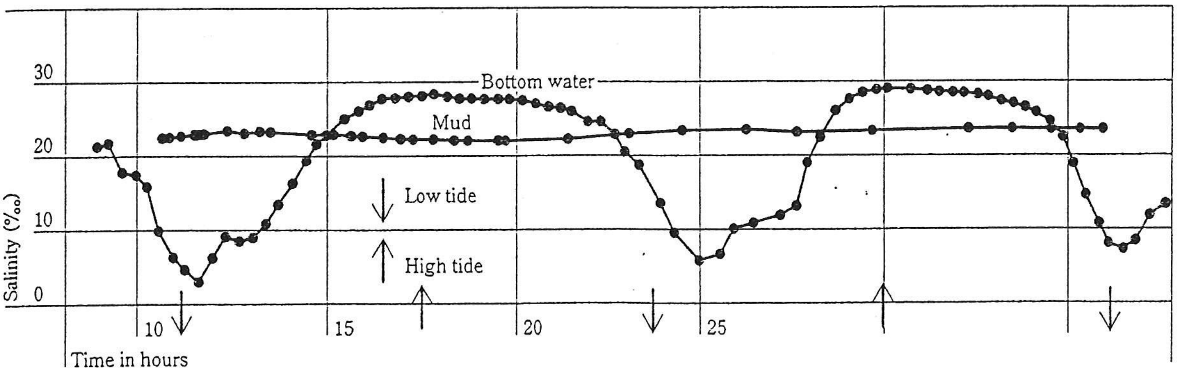


Figure 8.5 Comparison of salinity fluctuations in the water column with that interstitially in the bottom mud. Data from the Pocasset River estuary in Massachusetts. (After P. C. Mangelsdorf, Jr., Salinity measurements in estuaries, pp. 71–79. *In:* G. H. Lauff [ed.], Estuaries pub no. 83 AAAS, 1967.)

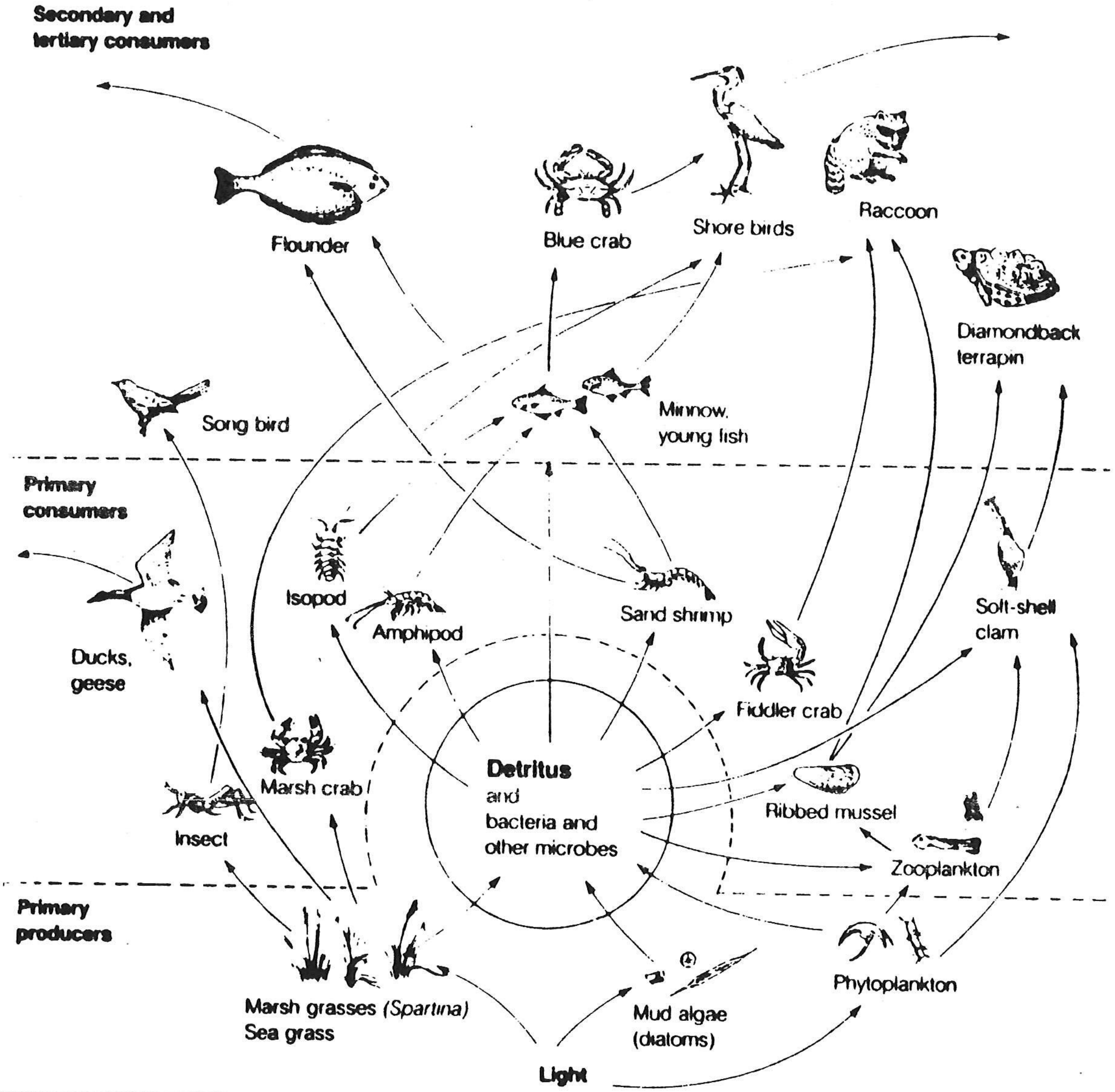
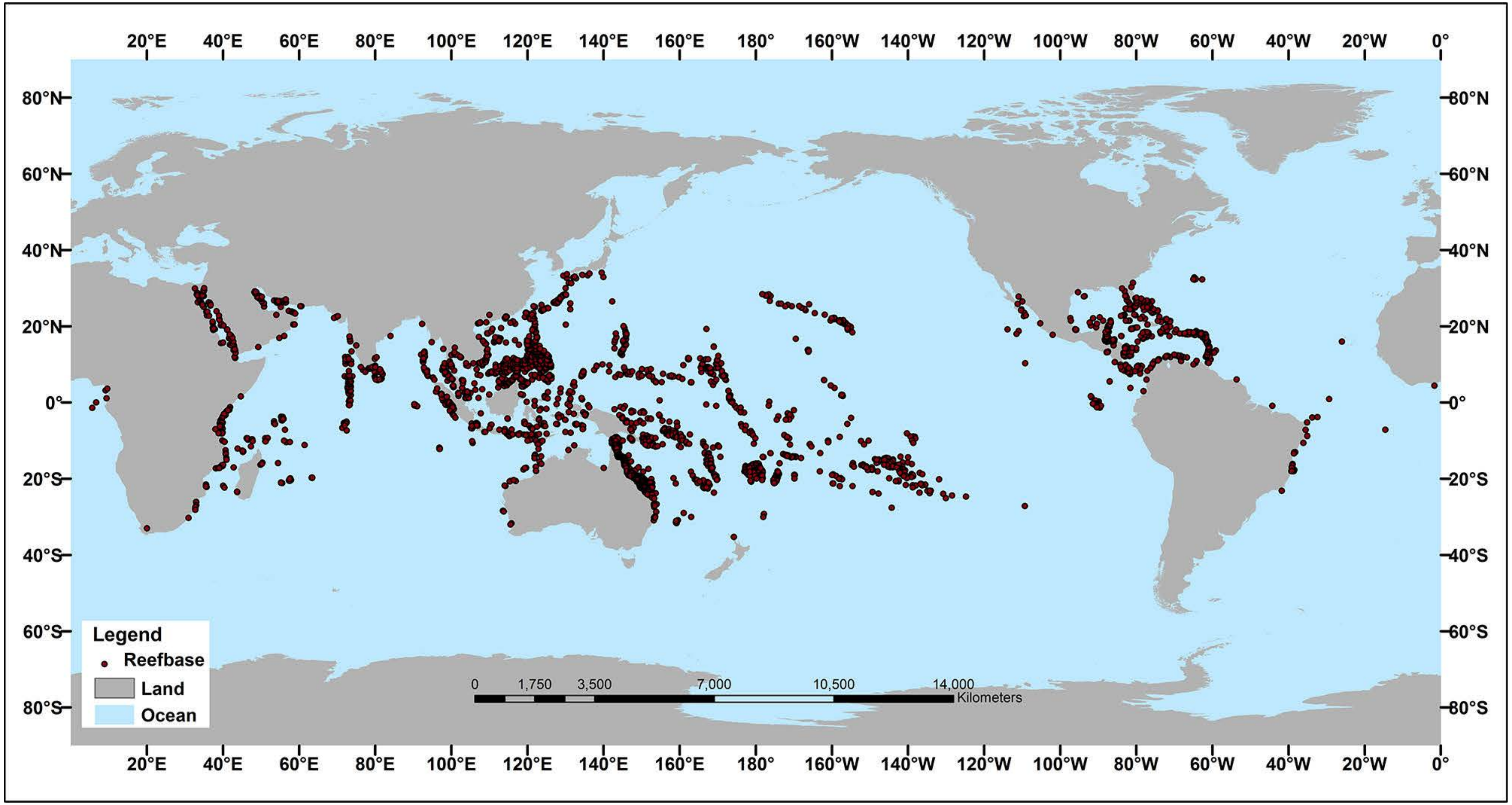
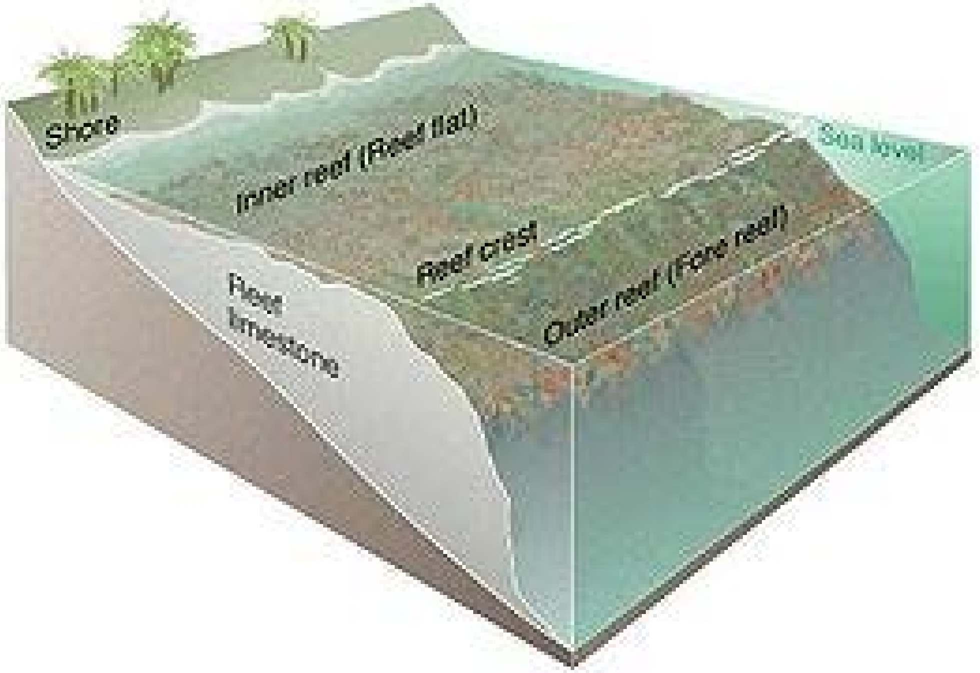


FIGURE 10-16

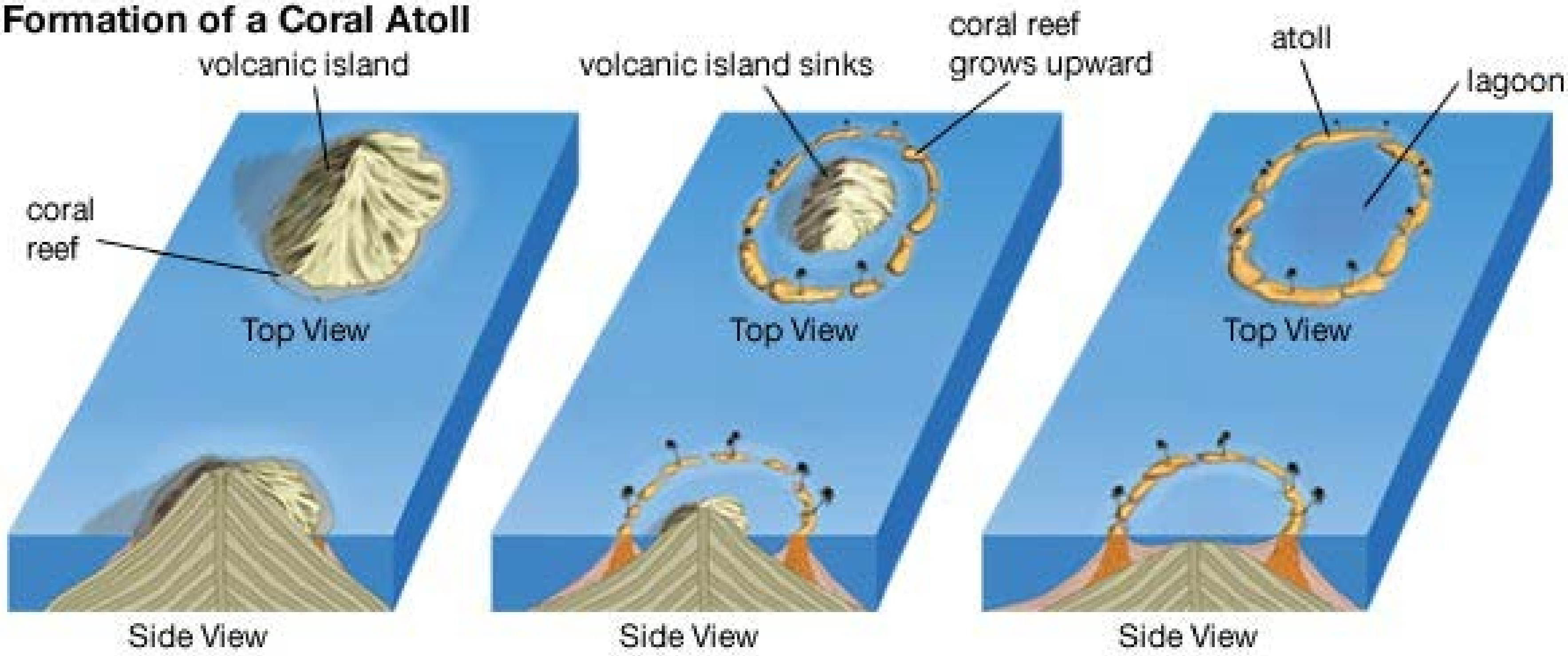
Estuarine food web. Only a small number of energy pathways are shown in the illustration. A large amount of energy is lost or exported from the estuary after it reaches migratory birds and fishes.

Distribution mondiale des récifs coralliens




Shore
Inner reef (Reef flat)
Sea level
Reef crest
Outer reef (Fore reef)
Reef limestone

Formation of a Coral Atoll



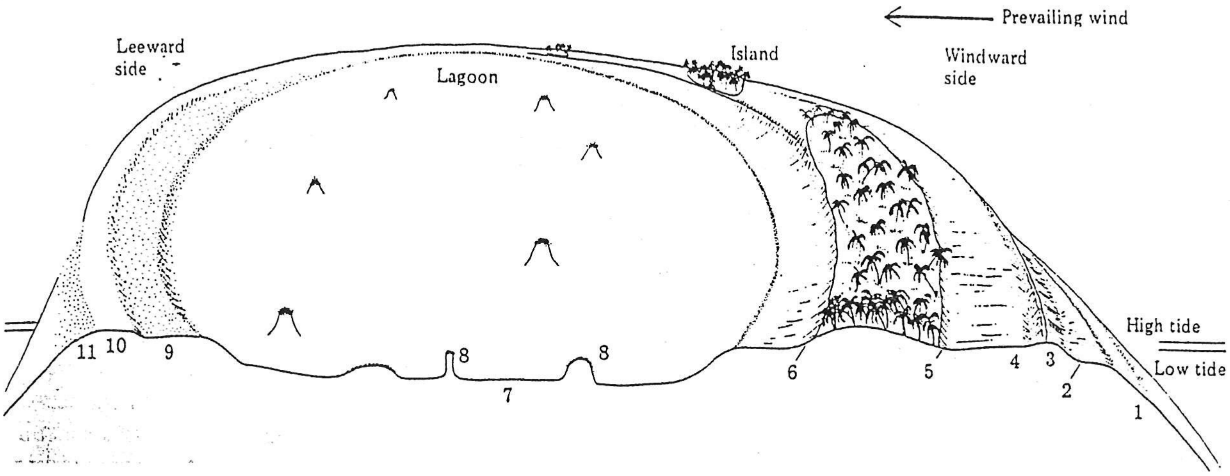


Figure 9.7 Diagrammatic cross section of a typical atoll: (1) outer seaward slope, (2) windward reef margin with spur and buttress zone, (3) algal ridge, (4) the reef flat, (5) seaward beach of the island, (6) lagoon beach of the island, (7) lagoon floor, (8) lagoon reefs, (9) leeward reef flat, (10) leeward reef margin, (11) leeward reef slope. (Modified from C. M. Yonge, The biology of coral reefs, Adv. Mar. Biol. 1:209–260, 1963.)

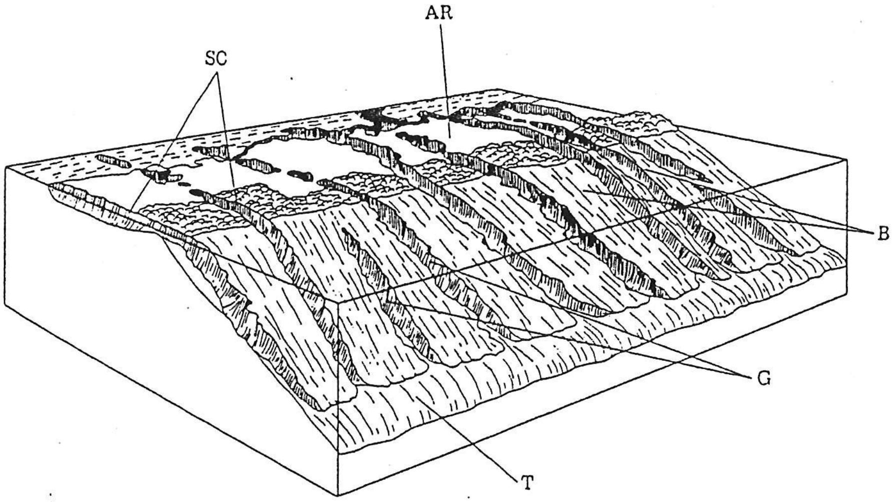


Figure 9.8 Generalized sketch of the spur and buttress zone of a windward reef. (AR) Algal ridge; (B) buttresses or spurs; (G) grooves; (SC) surge channels; (T) 18-m terrace. (After C. M. Yonge, The biology of coral reefs, Adv. Mar. Biol. 1:209–260, 1963.)

Les Atolls