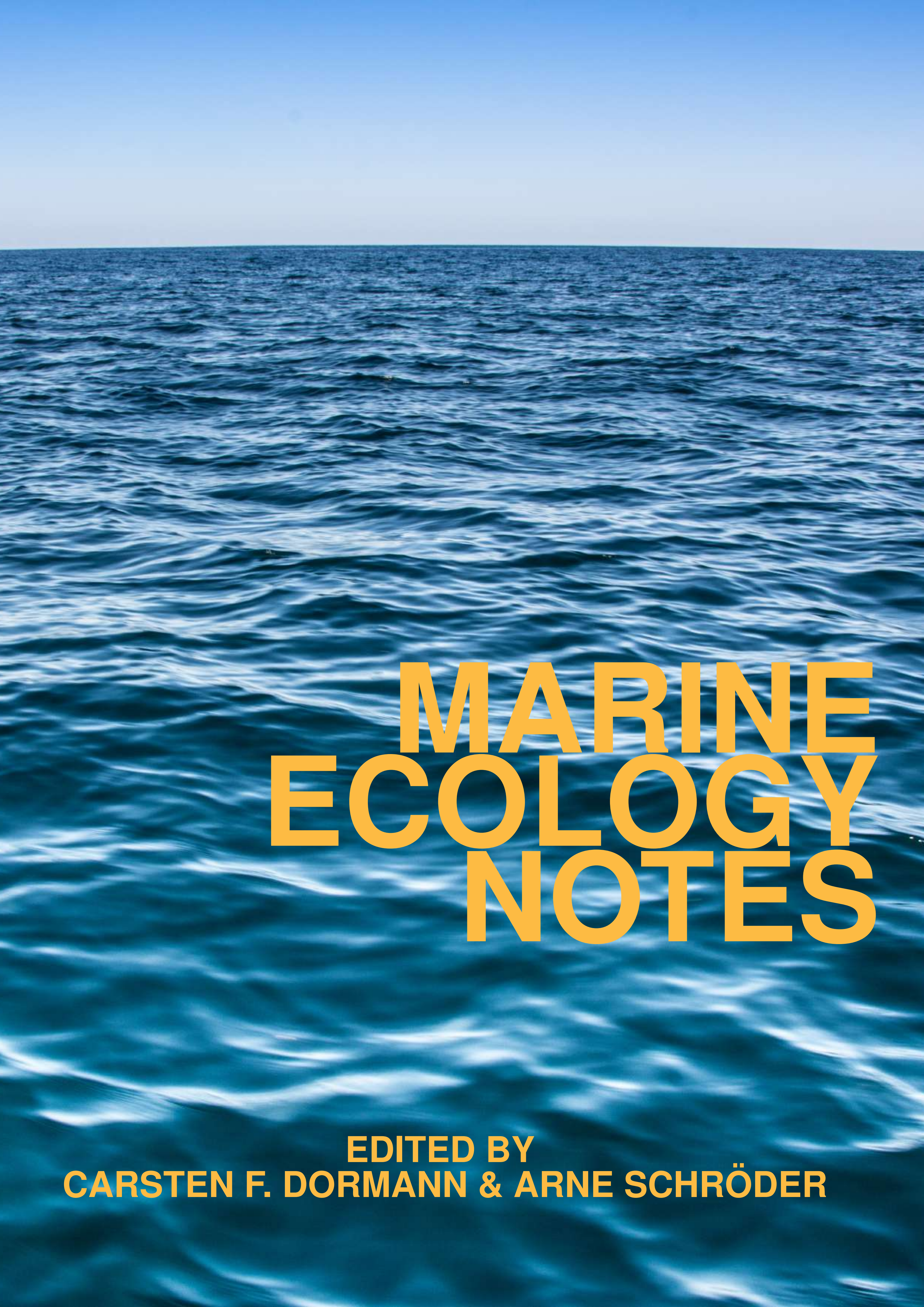

MARINE ECOLOGY NOTES

EDITED BY
CARSTEN F. DORMANN & ARNE SCHRÖDER

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PUBLISHED BY NO-ONE SPECIFICALLY, EXCEPT THE AUTHORS, REALLY.

Title picture cropped from “Ocean” by Apasciuto (`https://www.flickr.com/photos/apasciuto/32972768576`)

Images are hyperlinked to their websource *not* themselves, but through the first words of the caption. The sources of the text are typically hyperlinked through the chapter/section/subsection/paragraph title. Words in *italics* (except species names) are hyperlinked to Wikipedia for further reading. All these features are obviously only available in the PDF.

This book was typeset in LaTeX, using the Tufte-book class. Compression of the resulting massive PDF was carried out by the online service `ilovepdf.com`. Some images were taken from Flickr, as long as they were published under a Creative Commons license (photographer acknowledged in the caption).

First typesetting, June 2021

Contents

Preface

The go-to textbook "Marine Biology" by Levinton[1] leaves little to ask for, except for affordability (over €150,-, even as ebook!). This is in sharp contrast to Kaiser et al.'s "Marine Ecology",[2] whose nonchalant and scientifically sloppy writing does not appeal (e.g. referring to vascular plants as "real plants", which then algae are not, or the non-explanation of PSU) and cannot outweigh its low price. The actual content also becomes unreadable by a profusion of boxes and tables and figures that typographically disrupt the text. Also, this latter book is very thin on oceanography and unnecessarily expands on "biodiversity" and "ecosystem services" as topical points far too dominantly.

Evidently, everyone has their little pet topics, and here we indulge in emphasising ours. The text was edited overall by CFD, but the long chapter 3 was edited by AS.

This text heavily preys on Wikipedia. In fact, *all* text must be assumed to be copy-pasted from Wikipedia, except if indicated by a (subtly) different font. The current font indicates CFD and AS writing. *Text in italics* (other than Latin species names) includes an invisible link to the relevant web page accessible by clicking.

This (the default) font indicates text of Wikipedia origin.

The reason to so heavily rely on Wikipedia is simple: it is a very good resource for many scientific topics not under current political debate. So while we would not take the entries for biodiversity or climate change at face value, we found sea water chemistry[3] and plate tectonics[4] to be excellently resourced.

The text here may be different from the current Wikipedia, as that resource is changing continuously. We did not time-stamp each bit of text, so in a way we take responsibility for the quality of the selection we made. Also, we deleted and altered Wikipedia entries without indicating (e.g. removed non-SI units such as Fahrenheit or references and footnotes). All non-Wikipedia sources are indicated.

Of course, while we were lazy enough to copy-paste text from Wikipedia, we still strived for scientific accuracy. Two things helped us with that: (1) Long ago, CFD studied biology with minor in marine biology and physical oceanography at the University of Kiel in Germany. That "long ago" means that we can rely neither on our memory nor on the state of knowledge at that time. Hence, (2) the excellent book of Levinton cited above as well as many other books on the subject at hand are heavily thumbed references to

[1] Levinton, J. (2017). *Marine Biology: Function, Biodiversity, Ecology*. Oxford University Press, Oxford, UK, 5th edition

[2] Kaiser, M. J., Attrill, M. J., Jennings, S., and Thomas, D. (2020). *Marine Ecology: Processes, Systems, and Impacts*. Oxford University Press, New York, 3rd edition

[3] `https://en.wikipedia.org/wiki/Seawater`

[4] `https://en.wikipedia.org/wiki/Plate_tectonics`

back-up Wikipedia claims. In particular the Open University series on oceanography,[5,6,7,8,9,10,11] although also some years old, is a set of high-quality, authoritative and didactically exemplary textbooks.

Other open textbooks in the field can be found around the internet.[12]

We like to thank all the contributors to common good initiatives such as Wikipedia and photographers making their images available under a Creative Common license! The spirit of creating, maintaining and sharing knowledge about our plant is very heartening, and we hope this compilation of knowledge is seen in the same spirit.

Comments and corrections please to `carsten.dormann@biom.uni-freiburg.de`.

Freiburg, Oldenburg, Spring 2021

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[5] Open University (1989). *Seawater: Its Composition, Properties and Behaviour*. Pergamon, Oxford, U.K., 2nd edition

[6] Open University (1997). *Biological Oceanography: An Introduction*. Elsevier

[7] Open University (1998). *The Ocean Basins: Their Structure and Evolution*. Butterworth-Heinemann, Oxford, 2nd edition

[8] Open University (2000). *Waves, Tides and Shallow-Water Processes*. Butterworth-Heinemann, Oxford, 2nd edition

[9] Open University (2001). *Ocean Circulation*. Butterworth-Heinemann, Boston, 2nd edition

[10] Open University (2005). *Marine Biogeochemical Cycles*. Butterworth-Heinemann, Oxford, 2nd edition

[11] Open University (2013). *Case Studies in Oceanography and Marine Affairs*. Pergamon, Oxford

[12] e.g.: Introduction to Oceanography: `https://open.umn.edu/opentextbooks/textbooks/732`; with the same title: `https://rwu.pressbooks.pub/webboceanography`; or a student-written textbook on Tropical Marine Biology: `https://open.umn.edu/opentextbooks/textbooks/a-student-s-guide-to-tropical-marine-biology`

1

The Abiotic Environment

The marine physico-chemical environment is *extremely* different to our land-based experience.[1] This chapter given an overview of the main constraints to life in the oceans.

Oceans cover 71% (or 361 Gm^2) of our planet's surface and contain 97% of its water, some 1.34 Gm^3 (of a total of 1.386 Gm^3, see Fig. 1.1). While small in comparison to the entire earth, this "little" sphere contains enough seawater to yield an average ocean depth of 3000 m.

Interestingly, the *origin of water on earth* is not entirely clear. After the impact with Theia that created the moon,[2] no surface water remained. Yet, by 4 Gyr ago, water was present. The three sources currently discussed, and not mutually exclusive, are (1) chemical release from the mantel, (2) import by asteroids and (3) from Theia. Near-earth space rock may contain as much or more water as we currently have on earth.[3]

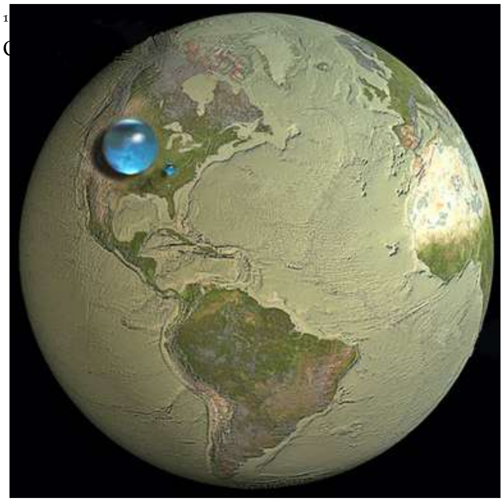

Figure 1.1: All the world's water would be a sphere with a radius of about 700 km (as a Gm^3 is a million km^3.). The picture is somewhat misleading, as the atmosphere extends to (roughly) 100 km, so the blue seawater sphere actually reaches far into outer space.

1.1 *Salt water properties*

Salinity On average, seawater in the world's oceans has a salinity of about 3.5% (35 g/l, 599 mM [4]). This means that every kilogram (roughly one litre by volume) of seawater has approximately 35 g of dissolved salts (predominantly sodium (Na^+) and chloride (Cl^-) ions).[5]

The salt in the seawater originates approximately half from the ocean floor at the time when the oceans formed, and half from river discharge.[6] The influx of new salts from rivers is more than counteracted by Cl^- deposition into the mantel, yielding a slight but somewhat surprising *decrease* of ocean salinity from around 50‰ to the current 35‰ over the last 500 Myr.[6]

Seawater contains more dissolved ions than any type of freshwater. Also, the ratios of solutes differ dramatically. For instance, although seawater contains about 2.8 times more hydrogen carbonate than river water, the percentage of hydrogen carbonate in seawater as a ratio of all dissolved ions is far lower than in river water. Hydrogen carbonate ions constitute 48% of river water solutes but only 0.14% for seawater. Differences like these are due to the varying residence times of seawater solutes; sodium and chloride have very long residence times, while calcium (vital for carbonate formation) tends to precipitate much more quickly. The most abundant dissolved ions in seawater are sodium, chloride, magnesium, sulfate and calcium. Its osmolarity is about 1000 mOsm/l (Fig. 1.2).

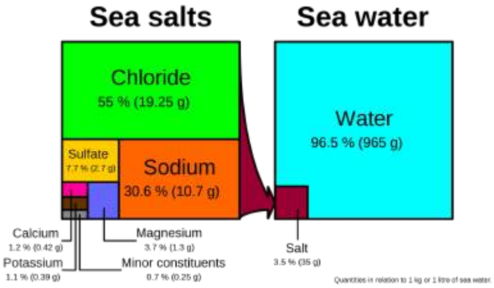

Figure 1.2: Concentrations of various salt ions in seawater (weight/weight). The composition of the total salt component is: Cl^- 55%, Na^+ 30.6%, SO_4^{2-} 7.7%, Mg^{2+} 3.7%, Ca^{2+} 1.2%, K^+ 1.1%, other 0.7%.

Solubility of most salts is, among other things, temperature-dependent. For two substances this is particularly important in this context. *Calcium carbonate* ($CaCO_3$) solubility doubles as water cools from 25°C to 10°C. This puts a chemical limit to the use of calcium carbonate as building material for marine life. *Hydrated silica* ($SiO_2 \cdot nH_2O$), in contrast, still has a very low solubility in cold waters, making it a more attractive biogenic structural material in

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[2] The *Theia impact*, some 4.5 Gyr ago.

[3] Rivkin, A. S. and DeMeo, F. E. (2019). How many hydrated NEOs are there? *Journal of Geophysical Research: Planets*, 124(1):128–142

[4] "mM" means "milli molar", i.e. 1 thousands mol/l = 1mol/m^3. If all salt was NaCl, which is a good approximation, with a molar mass of 23 g/mol + 35.4 g/mol = 58.4 g/mol, then 35 g/l would be 35/58.4 mol/l = 0.6 mol/l= 6 mM.

[5] Historically, several salinity scales were used to approximate the absolute salinity of seawater. A popular scale, still frequently found even in modern textbooks, was the "Practical Salinity Scale" where salinity was measured in "practical salinity units (psu)". The current standard for salinity is the "Reference Salinity" scale with the salinity expressed in units of "g/kg".

[6] Hay, W. W., Migdisov, A., Balukhovsky, A. N., Wold, C. N., Flögel, S., and Söding, E. (2006). Evaporites and the salinity of the ocean during the phanerozoic: Implications for climate, ocean circulation and life. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 240(1):3–46

cold waters. We shall return to this when investigating types of marine algae.

Ocean surface salinity varies substantially across the world (Fig. 1.3). Mixing with freshwater from rivers and ice shields reduces salinity, while high evaporation increases it (e.g. in the Mediterranean Sea).

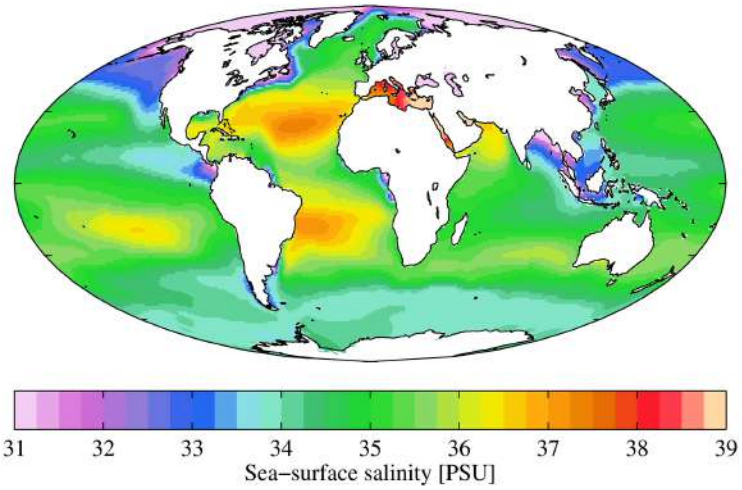

Figure 1.3: Annual mean of the sea surface salinity distribution (World Ocean Atlas, 2009).

Sea water density Average density at the surface is 1.025 kg/l. Seawater is denser than both fresh water and pure water (density 1.0 kg/l at 4°C) because the dissolved salts increase the mass by a larger proportion than the volume. In oceanographic context, sea water density is often expressed as a unitless parameter ϱ, computed as "density $- 1\text{g/kg} \cdot 1000$". As a result, we see sea water densities given as $\varrho = 32$, indicating an actual density of 1.032 g/kg.

Note that, unlike fresh water, seawater does not have a density maximum at 4°C but gets denser as it cools all the way to its freezing point of approximately −1.8°C.[7] This freezing point is however a function of salinity and pressure and thus −1.8°C is not a general freezing temperature for sea water. The freezing point of seawater decreases as salt concentration increases. The coldest seawater still in the liquid state ever recorded was found in 2010, in a stream under an Antarctic glacier: the measured temperature was −2.6°C.

pH Seawater pH is typically limited to a range between 7.5 and 8.4. However, there is no universally accepted reference pH-scale for seawater and the difference between measurements based on different reference scales may be up to 0.14 units.

Sound in water The speed of sound in seawater is about 1,500 m/s (whereas speed of sound in air is usually around 330

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[7] Icebergs do not contradict this statement: they are (largely) freshwater, hence less dense than sea water and with lower density even than freshwater warmer than 0°C.

m/s at roughly 101.3 kPa pressure, 1 atmosphere), and varies with water temperature, salinity, and pressure. Typical frequencies associated with underwater acoustics are between 10 Hz and 1 MHz. The propagation of sound in the ocean at frequencies lower than 10 Hz penetrates deep into the seabed,[8] whereas frequencies above 1 MHz are rarely used because they are absorbed very quickly. Due to its excellent propagation properties, underwater sound is used as a tool to aid the study of marine life, from microplankton to the blue whale. Echo sounders are often used to provide data on marine life abundance, distribution, and behaviour information. Echo sounders, also referred to as hydroacoustics is also used for fish location, quantity, size, and biomass.

Thermal properties The thermal conductivity of seawater is 0.6 W/mK at 25°C and a salinity of 35 g/kg. Thermal conductivity decreases with increasing salinity but increases with temperature. More importantly, water has a very high specific heat capacity of 4181 J kg^{-1} K^{-1} at 25°C, compared to air's 1006 J kg^{-1} K^{-1} (at 0°C). Given its roughly thousandfold higher density, a kg of water can absorb 4000 times the heat of a kg of air. This is important when considering the flow of radiation-induced heat from the tropics to the polar region, i.e. the driver of atmospheric circulation and ocean currents.

Gases in sea water The solubility of gases in seawater, in particular O_2 and CO_2, depends on temperature. At 0°C, O_2 solubility is at 8.1 ml/l, but at 20°C is is down to 5.3 ml/l. CO_2 is vastly more soluble (see next but one paragraph) and less affected by temperature: from 8,700 ml/l at 0°C down to 7,350 ml/l at 20°C.

Another interesting case is methane, CH_4. It is, as gas, very soluble (around 558 ml/l at 0°C). More interestingly, at the high pressures between 500 - 1000 m depth (> 50 bar) and temperatures below 4°C, methane is stable as so-called *methane clathrate*, which is a crystal structure of water trapping methane (chemically: $CH_4 \cdot 5.75\,H_2O$; Fig. 1.4). Methane clathrate formed over long periods in the past, possibly from organic substances, and is not in a chemical equilibrium with dissolved CH_4. The compound releases easily inflammable methane as it melts. Since methane is a potent greenhouse gas, the dozens of deposits discovered in the world's oceans[9] may contribute to a positive feedback loop if sea water temperature increases.

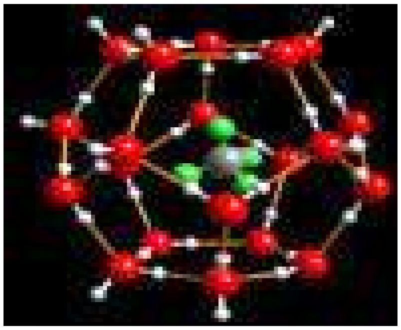

Figure 1.4: A single methane clathrate (= methane hydrate, "fire in ice"). Note the silvery C-atom with its four green H-atoms in the centre, surrounded by many H_2O molecules forming the cage ("clathrate").

CO_2 in the ocean Because of its importance for both atmosphere and ocean, CO_2 is worth closer examination. In water carbon dioxide forms carbonic acid, H_2CO_3, which dissociates into $H^+ + HCO_3^-$, i.e. a proton and hydrogen carbonate (= bicarbonate in old terminology), and further into $2H^+ + CO_3^{2-}$, i.e. two protons and carbonate:

$$CO_2 + H_2O \rightleftharpoons H_2CO_3 \rightleftharpoons H^+ + HCO_3^- \rightleftharpoons 2H^+ + CO_3^{2-}$$

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[8] Kuna, V. M. and Nábělek, J. L. (2021). Seismic crustal imaging using fin whale songs. *Science*, 371(6530):731–735

[9] *Map of methane clathrate sites.*

Under ocean pH and temperatures, most CO_2 in seawater will be present as HCO_3^- (Fig. 1.5). Only at very low or very high pH will the dissociation equilibrium shift substantially towards the left or the right hand side of the above chemical equation, respectively.

Overall, the ocean is a huge CO_2 buffer system. Under current atmospheric CO_2 increases, oceans take up more CO_2, store it as hydrogen carbonate, thereby releasing a proton. The result is *ocean acidification*. Such process will continue until very low pH (<6, see Fig. 1.5), before more CO_2 is released than taken up. Because of its huge volume, the ocean bicarbonate buffer plays an important role in the overall carbon balance of the world, even if pH changes only mildly (approx. from 8.25 to 8.14 since the 1750s).

In biological systems, e.g. within cells, the enzyme carbonic anhydrase upsets the equilibrium of the first step and catalyses the release of CO_2 from the dissociated hydrogen carbonate: $CO_2 + H_2O \rightleftharpoons H^+ + HCO_3^-$. This is the physiological mechanism through which heterotrophic organisms get rid of CO_2.

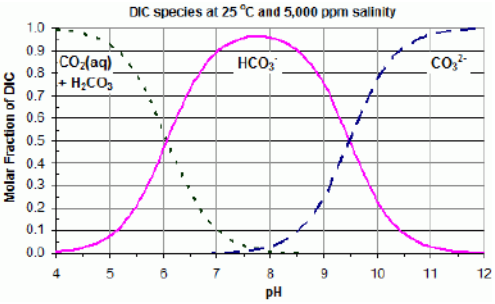

Figure 1.5: Bjerrum plot for carbonate speciation in seawater. DIC refers to dissolved inorganic carbon.

Viscosity A final important physico-chemical point of (sea) water is its viscosity, i.e. the resistance to movement within a medium. The ratio of inertia and viscosity is called the *Reynolds number*, Re. If inertial movement is low, Re will be high.

As the size of an organism and the strength of the current increases, inertial forces will eventually dominate, and the flow becomes turbulent (large Re). As the size and strength decrease, viscous forces eventually dominate and the flow becomes laminar (small Re).

As a rule of thumb, drifting plankton are small and, if they swim at all, do so at biologically low Reynolds numbers (0.001 to 10), where the viscous behaviour of water dominates and reversible flows, drag and eddies are the rule. Actively swimming nekton, on the other hand, are larger and swim at biologically high Reynolds numbers (around 100), where inertial flows are the rule and eddies (vortices) are easily shed. In human terms, life as phytoplankton at low Reynolds number is like swimming in honey ($Re \approx 10^{-3}$), while life at high Re is swimming in water as we know it ($Re \approx 10^6$, actually similar to fast cycling[10]). Big fish, whales and submarines experience values of around 10^8.

1.2 *Ocean geography*

Bathymetry A look at a map of ocean depths (Fig. 1.6) reveals the bathymetric structure of the (three to) five *oceans* (Arctic, Atlantic, Indian, Pacific and Southern Ocean). Beyond the green (for an average depth of 3500 m), mid-ocean ridges are noticeable, running through Atlantic, Indic and southern Pacific. Note the subduction zones (in blue) of the Pacific plate from Alaska along the east Asian sea board down to Samoa and New Zealand. Those along the Pacific coast of South America cannot be identified by deep trenches, while

[10] Terra, W., Sciacchitano, A., and Scarano, F. (2020). Cyclist Reynolds number effects and drag crisis distribution. *Journal of Wind Engineering and Industrial Aerodynamics*, 200:104143

those south of Sumatra and Java, east of South Georgia, and along the Caribbean crescent can be. Also note the large continental shelf area north of Russia and, somewhat smaller, north of Australia.

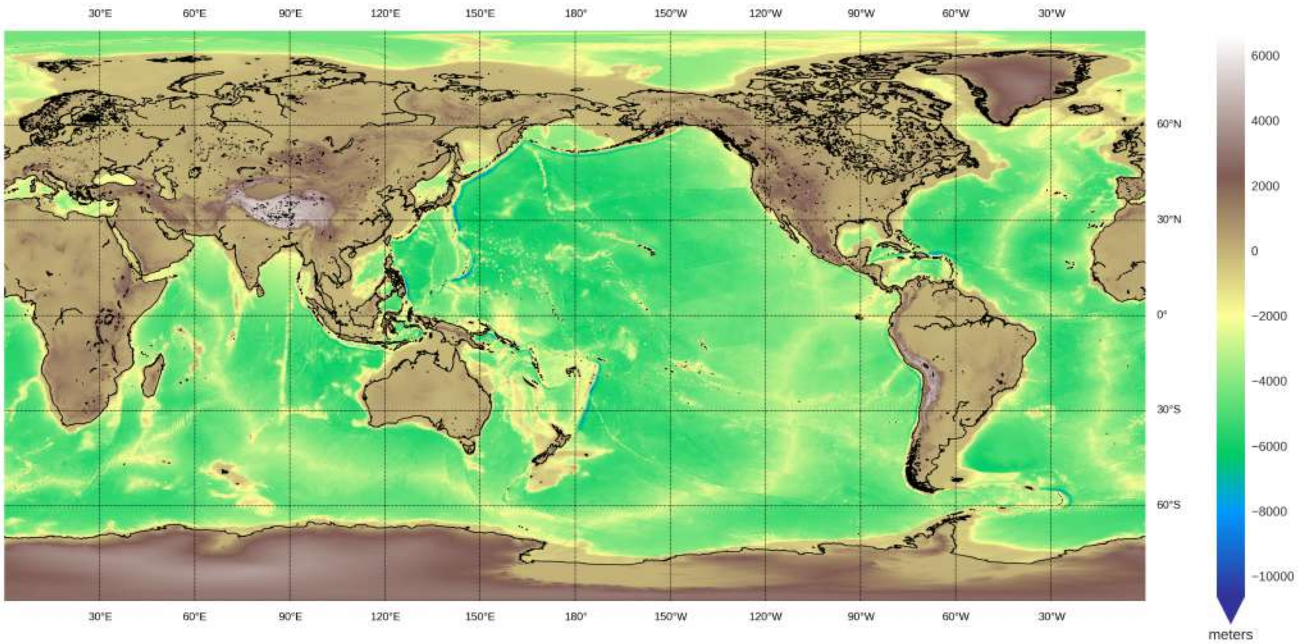

Figure 1.6: Ocean basin bathymetry (the ocean equivalent of topography, where "bathos", *βαθός*, means "deep").

The current locations of the tectonic plates are geologically just a transient arrangement, and earthquakes and volcanos remind us of their constant, if slow, movement.

While it is tempting to view the Atlantic and Indic as richer structured than the Pacific, this is a rather academic point of view. All three ocean basins are deep, islands and underwater sea mounts are clustered in archipelagos (which are largely far apart), and the typical impression of any organisms looking under water is as in Fig. 1.7.

Figure 1.7: The ocean, by and large, looks empty.

Ocean straits Important oceanic features are the straights, narrow passages among continents and islands: the Bering Strait (connecting the Pacific and the Arctic Ocean; only 50 m deep); the Gibraltar Strait (connecting the Mediterranean and the Atlantic; some 300 m deep); the Malacca Straight (connecting the Pacific and the Indic between Malaysia and Sumatra; 25 m deep); the Sunda Straight (between Sumatra and Java; 20 m); and the Davis Straight (between Greenland and Nunavut's Baffin Island; >1000 m deep). We need to remember that over geological times the sea level fluctuated over several hundred meters, connecting the land masses on either side of some straights. The Mediterranean was on the edge of drying up completely when the connection to the Atlantic was closed some 6 Myr ago.[11]

Locally, and at much shorter time spans, glaciation changes the face of the sea, too. During the last glaciation, the Canadian lakes and bays were covered in ice, as was the Barents, Baltic and large parts of the North Sea in Europe. Ever since the retreat of

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[11] This is the so-called *Messinian salinity crisis*, ended 5.3 Myr ago by the similarly spectacularly named *Zanclean flood*.

the glaciers, some 10,000 yr ago, the land masses and sea floor are rising some millimetres per year due to the relief from the weight of ice (*post-glacial rebound*).

Ocean provinces The Longhurst biogeographic provinces give a bit more structure to the oceans.[12] They distil both oceanographic and pelagic ecology into a categorical regions. While any categorisation of continuous changes is awkward, this scheme enjoys large practical advantages.

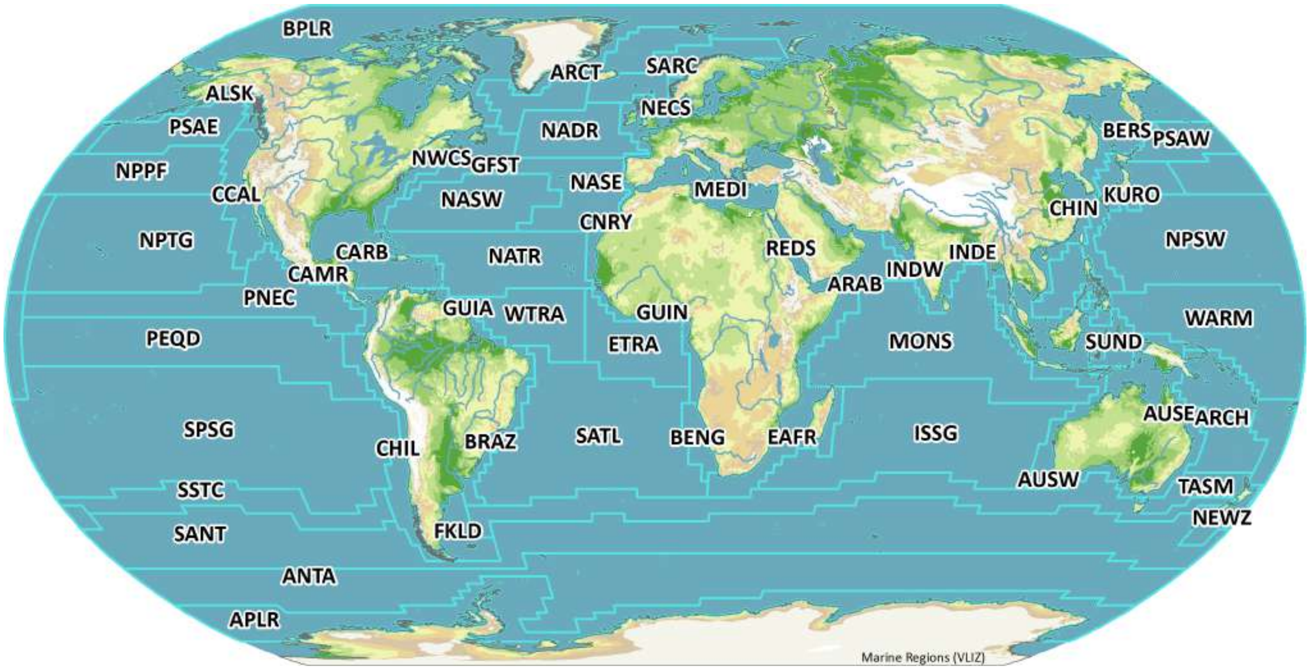

Figure 1.8: Longhurst biogeographic provinces, including the four-letter *Longhurst code*. Map from Flanders Marine Institute (2009). Longhurst Provinces. Available online at `https://www.marineregions.org`.

Ocean zonation

Starting at the water's edge is the littoral zone (Fig. 1.9). The part of it that is occasionally not inundated is called the intertidal (in itself again subdivided into supra- to subtidal). Here the bottom of the sea is typically not distinguished from the water phase.

The zone further out to sea, but still on the continental shelf (which is above 200 - 500 m water depth), is called the neritic zone. It is proper sea, but not the high seas and open ocean of the "oceanic" zone. In all these, the ocean bottom zone is called the benthos, or benthic zone, while the water column is referred to as the pelagic.

The depth layers also have Greek names, starting at the light-penetrated photic zone, going down into the bathyal (which includes the mesopelagic of Fig. 1.9), then abyssal and finally the hadal zone.

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[12] Longhurst, A. (2007). *Ecological Geography of the Sea*. Elsevier, Dordrecht, 2nd edition

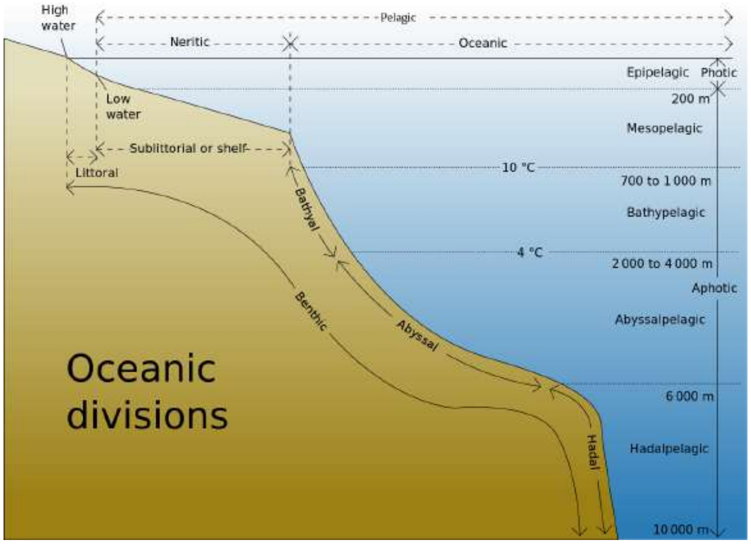

Figure 1.9: Nomenclature of oceanic divisions.

Along this depth gradient, the physico-chemical environment changes (Fig. 1.10). In tropical waters, there is often a strong stratification with a warm layer on top, which is broken up and remixed in autumn and winter. In contrast, temperate and polar waters remain well-mixed throughout the year.

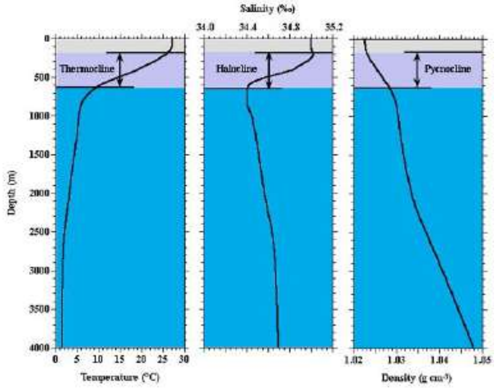

Figure 1.10: Idealised depth profiles of temperature, salinity and density in the tropics. In grey, at the top, the photic zone, below which there is a layer of warm surface water, called thermo-, halo- or pycnocline depending on what the focus of the study is. Below that, physical conditions vary more smoothly and predictably.

Light in the ocean Depth is probably the single most relevant gradient in the oceans. Apart from its physico-chemical gradients, and its gradient in salt solubility, it also has a gradient in light penetration (Fig. 1.11). Red and yellow are absorbed within a few meters, explaining why all diver suits look blue or black underwater. Chlorophyll has two absorption regions, one in the blue and one in the red, so half of the energy is lost to phytoplankton once they are below a dozen or so meters.

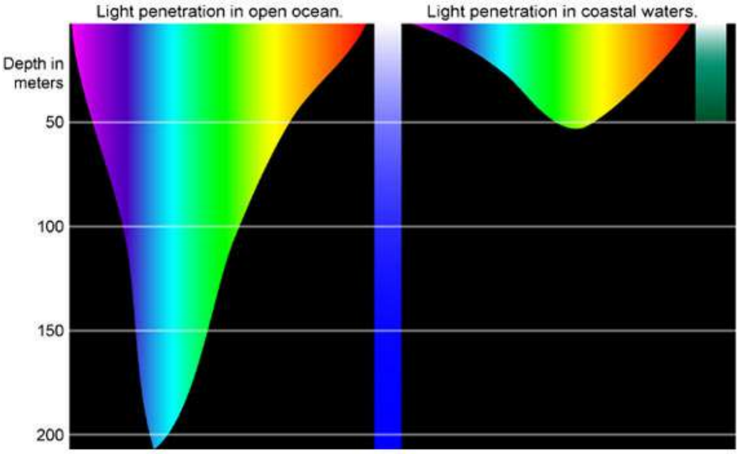

Figure 1.11: Light penetration. Depths to which different colours of light penetrate open ocean waters and the murkier coastal waters. Reflectance limits penetration in the latter.

Below 200 m, less than 1% of incoming light remains, but below 1000 m it is pitch dark. It is estimated that 90% of all marine life lives in the photic zone, thus while there is life all the way down to the deepest trench, there is not much of it in the dark.

Sea-level history

Global or eustatic sea level has fluctuated significantly over earth's history. The main factors affecting sea level are the amount and volume of available water and the shape and volume of the ocean basins. The primary influences on water volume are the temperature of the seawater, which affects density, and the amounts of water retained in other reservoirs like rivers, aquifers, lakes, glaciers, polar ice caps and sea ice. Over geological time scales, changes in the shape of the oceanic basins and in land/sea distribution affect sea level. In addition to eustatic changes, local changes in sea level are caused by tectonic uplift and subsidence. Over geologic time sea level has fluctuated by more than 300 m, possibly more than 400 m. The main reasons for sea level fluctuations in the last 15 million years are the Antarctic ice sheet and Antarctic post-glacial rebound during warm periods.

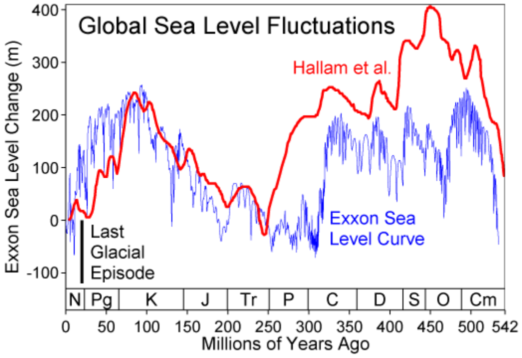

Figure 1.12: Comparison of two sea level reconstructions during the last 500 million years. The scale of change during the last glacial/interglacial transition is indicated with a black bar. (Hallam et al. and Exxon use very different techniques to measuring global sea-level changes. Hallam's approach is qualitative and relies on regional scale observations from exposed geologic sections and estimates of the areas of flooded continental interiors. Exxon's approach relies on the interpretation of seismic profiles to determine the extent of coastal onlap in subsequently buried sedimentary basins.)

The current sea level is about 130 m higher than the historical minimum. Historically low levels were reached during the Last Glacial Maximum (LGM), about 20,000 years ago. The last time the sea level was higher than today was during the Eemian, about 130,000 years ago.

Sea-level fluctuations at the scale of 100,000 years are at least in part also due to the orbital eccentricity of the earth around the sun (one of the *Milankovitch cycles*).

Over a shorter time scale, the low level reached during the LGM rebounded in the early Holocene, between about 14,000 and 6,000 years ago, and sea levels have been comparatively stable over the past 6,000 years. For example, about 10,200 years ago the last land bridge between mainland Europe and Great Britain was submerged, leaving behind salt marsh. By 8000 years ago the marshes were drowned by the sea, leaving no trace of former dry land connection. Observational and modelling studies of mass loss from glaciers and ice caps indicate a contribution to a sea-level rise of 2 to 4 cm over the 20th century.

1.3 *Ocean water movement*

Ocean circulation

An ocean current is a continuous, directed movement of sea water generated by a number of forces acting upon the water, including wind, the Coriolis effect, breaking waves, cabbeling, and temperature and salinity differences. Depth contours, shoreline configurations, and interactions with other currents influence a current's direction and strength. Ocean currents are primarily horizontal water movements.

An ocean current flows for great distances and together they create the Global Conveyor Belt (Fig. 1.13), which plays a dominant role in determining the climate of many of earth's regions. More specifically, ocean currents influence the temperature of the regions through which they travel. For example, warm currents travelling along more temperate coasts increase the temperature of the area by warming the sea breezes that blow over them. Perhaps the most striking example is the Gulf Stream, which makes northwest Europe much more temperate than any other region at the same latitude. Another example is Lima, Peru, where the climate is cooler, being sub-tropical, than the tropical latitudes in which the area is located, due to the effect of the Humboldt Current.

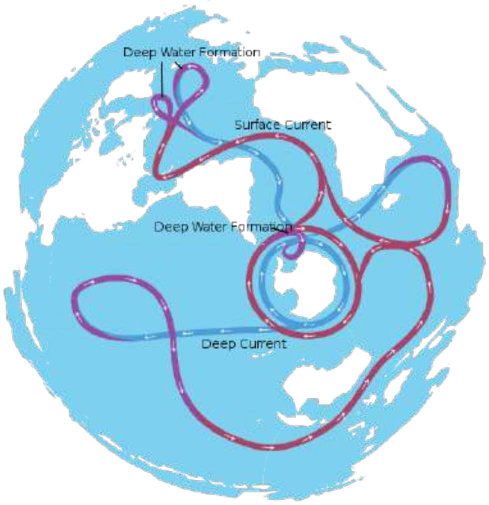

Figure 1.13: The global conveyor belt on a continuous-ocean map.

The technical term for the Global Conveyer Belt is "*thermohaline circulation* (THC)". It is largely driven by global density gradients created by low-latitude surface heat excess. The adjective thermohaline derives from "thermo-", referring to temperature, and "-haline" referring to salt content, factors which together determine the density of sea water.

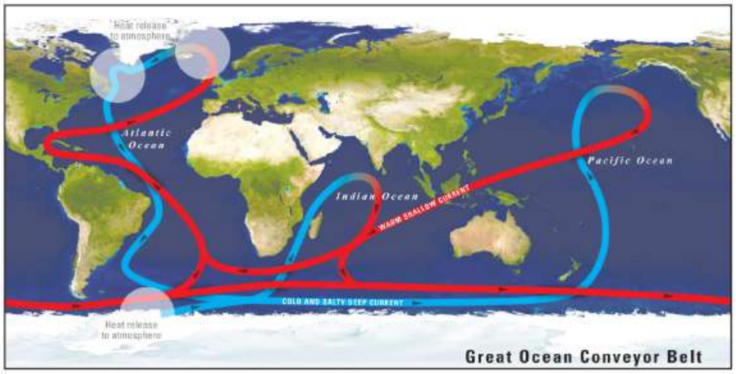

Figure 1.14: Ocean conveyer belt.

Arbitrarily, we can go through the THC (Fig. 1.14) by starting where the wind-driven surface currents (such as the Gulf Stream) travel polewards from the equatorial Atlantic Ocean, cooling en route, and eventually sinking at high latitudes (forming North Atlantic Deep Water). This dense water then flows into the ocean basins. While the bulk of it upwells in the Southern Ocean, the oldest waters (with a transit time of about 1000 years) upwell in the North Pacific. Extensive mixing therefore takes place between the ocean basins, reducing differences between them and making the Earth's oceans a global system. The water in these circuits transport both energy (in the form of heat) and mass (dissolved solids and gases) around the globe. As such, the state of the circulation has a large impact on the climate of the Earth.

Formation of deep water masses The dense water masses that sink into the deep basins are formed in quite specific areas of the North Atlantic and the Southern Ocean. In the North Atlantic, seawater at the surface of the ocean is intensely cooled by the wind and low ambient air temperatures. Wind moving over the water also produces a great deal of evaporation, leading to a decrease in temperature, called evaporative cooling. Evaporation removes only water molecules, resulting in an increase in the salinity of the seawater left behind, and thus an increase in the density of the water mass along with the decrease in temperature. In the Norwegian Sea evaporative cooling is predominant, and the sinking water mass, the North Atlantic Deep Water (NADW, Fig. 1.15), fills the basin and spills southwards through crevasses in the submarine sills that connect Greenland, Iceland and Great Britain which are known as the Greenland-Scotland-Ridge. It then flows very slowly into the deep abyssal plains of the Atlantic, always in a southerly direction. Flow from the Arctic Ocean Basin into the Pacific, however, is blocked by the narrow shallows of the Bering Strait. Effect of temperature and salinity upon sea water density maximum and sea water freezing temperature.

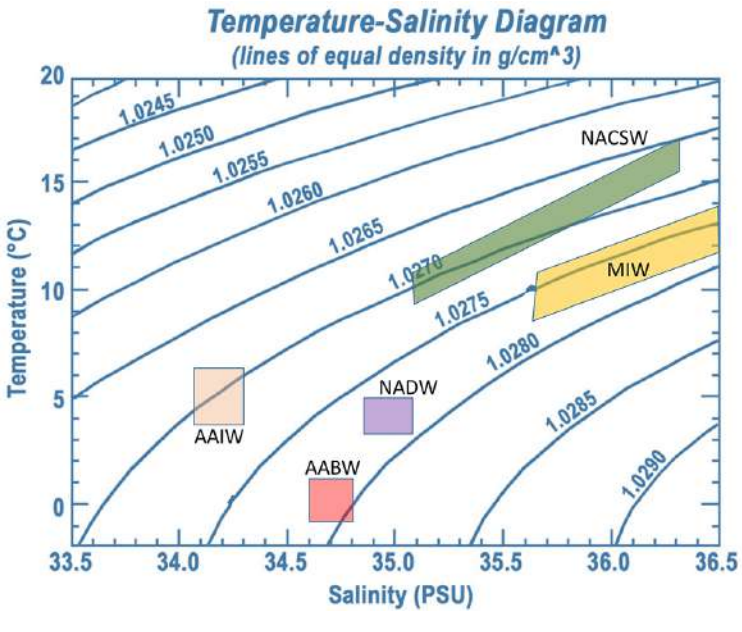

Figure 1.15: Characteristic ranges of temperature and salinity for the major Atlantic water masses. North Atlantic Central Surface Water (NACSW), Mediterranean Intermediate Water (MIW), Antarctic Intermediate Water (AAIW), North Atlantic Deep Water (NADW), and Antarctic Bottom Water (AABW). NADW is formed off Greenland (see Fig. 1.14) and is more saline and thus denser than the AAIW, but not as cold and dense as the AABW, leading to a layering of these three water bodies in the south Atlantic.

In the Southern Ocean, strong katabatic[13] winds blowing from the Antarctic continent onto the ice shelves will blow

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[13] Meaning "downhill"; here: from the continent onto the sea.

the newly formed sea ice away, opening polynyas[14] along the coast. The ocean, no longer protected by sea ice, suffers a strong cooling. Meanwhile, sea ice starts reforming, so the surface waters also get saltier, hence very dense. In fact, the formation of sea ice contributes to an increase in surface seawater salinity; saltier brine is left behind as the sea ice forms around it (pure water preferentially being frozen). Increasing salinity lowers the freezing point of seawater, so cold liquid brine is formed in inclusions within a honeycomb of ice (see also section 4.3.1). The brine progressively melts the ice just beneath it, eventually dripping out of the ice matrix and sinking. This process is known as brine rejection.

The resulting Antarctic Bottom Water (AABW) sinks and flows north and east, but is so dense it actually underflows the NADW. AABW formed in the Weddell Sea will mainly fill the Atlantic and Indian Basins, whereas the AABW formed in the Ross Sea will flow towards the Pacific Ocean.

The dense water masses formed by these processes flow downhill at the bottom of the ocean, like a stream within the surrounding less dense fluid, and fill up the basins of the polar seas. Just as river valleys direct streams and rivers on the continents, the bottom topography constrains the deep and bottom water masses.

Movement of deep water masses Surface water flows north and sinks in the dense ocean near Iceland and Greenland. It joins the global thermohaline circulation into the Indian Ocean, and the Antarctic Circumpolar Current.

Formation and movement of the deep water masses at the North Atlantic Ocean, creates sinking water masses that fill the basin and flow very slowly into the deep abyssal plains of the Atlantic. This high-latitude cooling and the low-latitude heating drives the movement of the deep water in a polar southward flow. The deep water flows through the Antarctic Ocean Basin around South Africa where it is split into two routes: one into the Indian Ocean and one past Australia into the Pacific.

At the Indian Ocean, some of the cold and salty water from the Atlantic—drawn by the flow of warmer and fresher upper ocean water from the tropical Pacific—causes a vertical exchange of dense, sinking water with lighter water above. It is known as overturning. In the Pacific Ocean, the rest of the cold and salty water from the Atlantic undergoes haline forcing, and becomes warmer and fresher more quickly.

The out-flowing undersea of cold and salty water makes the sea level of the Atlantic slightly lower than the Pacific and salinity or halinity of water at the Atlantic higher than the Pacific. This generates a large but slow flow of warmer and fresher upper ocean water from the tropical Pacific to the Indian Ocean through the Indonesian Archipelago to replace

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[14] Ice-free patches in sea ice are called *polynya*.

the cold and salty Antarctic Bottom Water. This is also known as "haline forcing" (net high latitude freshwater gain and low latitude evaporation). This warmer, fresher water from the Pacific flows up through the South Atlantic to Greenland, where it cools off and undergoes evaporative cooling and sinks to the ocean floor, providing a continuous thermohaline circulation.

Hence, the recent and popular name for the thermohaline circulation, emphasizing the vertical nature and pole-to-pole character of this kind of ocean circulation, is the meridional overturning circulation (MOC).

El Niño: a break for an ocean current Hundreds of currents together form the thermohaline circulation or ocean conveyer belt.[15] The *Humboldt Current* is a cold, nutrient rich northwards current along the Pacific coast of South America. Every 2 to 7 years (Fig. 1.16), this current wanes and is replaced by a warm current running the opposite direction, from the warm central Pacific southwards along the Chilean coast. This oscillation between cold and warm is the El-Niño-Southern Oscillation, ENSO, and the warm phase is called El Niño.[16]

The term El Niño refers to the warm and negative phase of the El Niño–Southern Oscillation (ENSO) and is the warming of the ocean surface or above-average sea surface temperatures in the central and eastern tropical Pacific Ocean. This warming causes a shift in the atmospheric circulation with rainfall becoming reduced over Indonesia, India and Australia, while rainfall and tropical cyclone formation increases over the tropical Pacific Ocean. The low-level surface trade winds, which normally blow from east to west along the equator, either weaken or start blowing from the other direction.

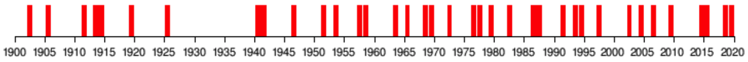

Figure 1.16: A timeline of all the El Niño episodes between 1900 and 2019. `https://en.wikipedia.org/wiki/El_Ni%C3%B1o`

It is believed that El Niño have occurred for thousands of years. For example, it is thought that El Niño affected the Moche culture in modern-day Peru. Scientists have also found chemical signatures of warmer sea surface temperatures and increased rainfall caused by El Niño in coral specimens that are around 13,000 years old. Around 1525, when Francisco Pizarro made landfall in Peru, he noted rainfall in the deserts, the first written record of the impacts of El Niño. Modern day research and reanalysis techniques have managed to find at least 26 El Niño events since 1900, with the 1982–83, 1997–98 and 2014–16 events among the strongest on record.

Currently, each country has a different threshold for what constitutes an El Niño event, which is tailored to their specific interests. For example, the Australian Bureau of Meteorology

[15] For a list see `https://en.wikipedia.org/wiki/Ocean_current`.

[16] In Spanish, the capitalized term El Niño means "the boy". In this phase of ENSO, the pool of warm water in the Pacific near South America is often at its warmest about Christmas. The original phrase, El Niño de Navidad, arose centuries ago, when Peruvian fishermen named the weather phenomenon after the newborn Christ. La Niña, chosen as the "opposite" of El Niño, i.e. cold phase of the ENSO, is Spanish for "the girl".

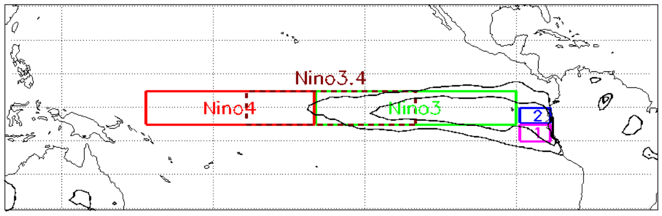

Figure 1.17: Niño3.4 and other index regions.

looks at the trade winds, SOI,[17] weather models and sea surface temperatures in the Nino 3 and 3.4 regions (Fig. 1.17), before declaring an El Niño. The United States Climate Prediction Center and the International Research Institute for Climate and Society looks at the sea surface temperatures in the Niño 3.4 region, the tropical Pacific atmosphere and forecasts that NOAA's Oceanic Niño Index (ONI) will equal or exceed +0.5°C for several seasons in a row. However, the Japan Meteorological Agency declares that an El Niño event has started when the average five month sea surface temperature deviation for the NINO3 region, is over 0.5°C warmer for six consecutive months or longer. The Peruvian government declares that a coastal El Niño is under way if the sea surface temperature deviation in the Niño 1 and 2 regions equal or exceed 0.4°C for at least three months.

There is no consensus whether climate change will have any influence on the occurrence, strength or duration of El Niño events, as research supports El Niño events becoming stronger, longer, shorter and weaker.

Global observations of El Niño events since 1950, show that regional impacts associated with El Niño events depend on what season it is (Fig. 1.18). However, while certain events and impacts are expected to occur during events, it is not certain or guaranteed that they will occur. The impacts that generally do occur during most El Niño events include below-average rainfall over Indonesia and northern South America, while above average rainfall occurs in southeastern South America, eastern equatorial Africa, and the southern United States.

Coastal upwelling In five regions of the world, a current is associated with coastal upwelling, remixing the water column, bringing nutrients from the deeper layers to the surface.

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[17] Southern Oscillation Index, a standardized index of observed sea level pressure differences between Tahiti and Darwin, Australia

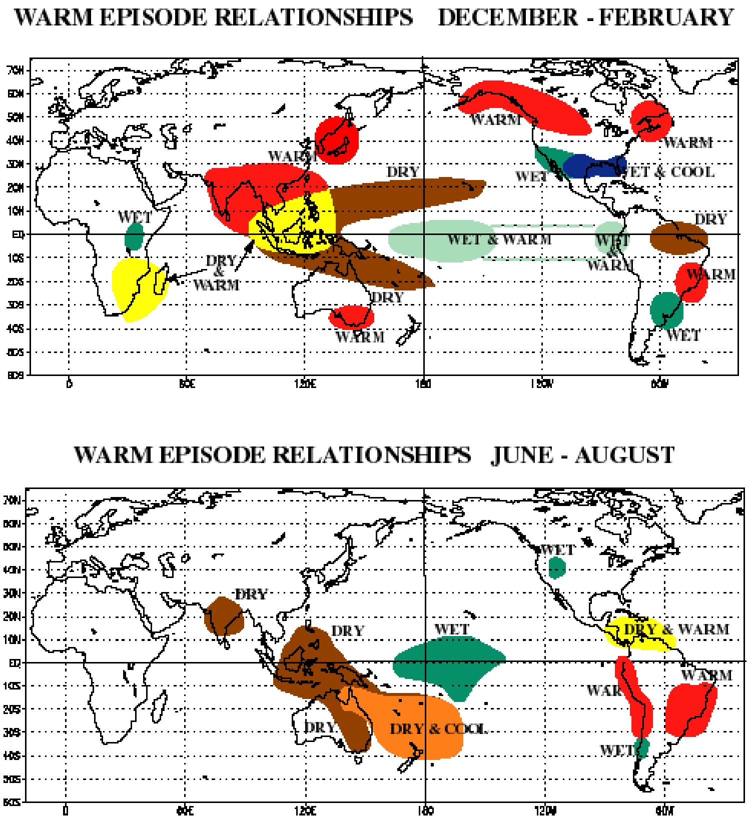

Figure 1.18: Regional impacts of warm ENSO episodes, demonstrating the far reach of El Niño.

The three main drivers that work together to cause upwelling are wind, Coriolis effect, and Ekman transport.[18] They operate differently for different types of upwelling, but the general effects are the same. In the overall process of upwelling, winds blow across the sea surface at a particular direction, which causes a wind-water interaction. As a result of the wind, Ekman transport causes the surface layer of water to move at about a 90° angle from the direction of the wind, and the friction between that layer and the layer beneath it causes the successive layers to move in the same direction. This results in a spiral of water moving down the water column. Then, it is the Coriolis forces that dictate which way the water will move; in the Northern hemisphere, the water is transported to the right of the direction of the wind. In the Southern Hemisphere, the water is transported to the left of the wind. If this net movement of water is divergent, then upwelling of deep water occurs to replace the water that was lost.

Worldwide, there are five major coastal currents associated with upwelling areas: the Canary Current (off Northwest Africa), the Benguela Current (off southern Africa, Fig. 1.19), the California Current (off California and Oregon), the Humboldt Current (off Peru and Chile), and the Somali Current (off Somalia and Oman). All of these currents support major fisheries.

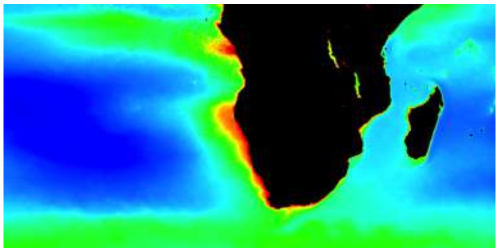

Figure 1.19: Chlorophyll a concentrations around southern Africa. The Benguela Current and its associated upwelling along the western coast is visible as extremely productive in red.

[18] *Ekman transport* occurs when ocean surface waters are influenced by the friction force acting on them via the wind. As the wind blows it casts a friction force on the ocean surface that drags the upper 10-100 m of the water column with it. However, due to the influence of the Coriolis effect, the ocean water moves at a 90°angle from the direction of the surface wind.

The Benguela Current is the eastern boundary of the South Atlantic subtropical gyre and can be divided into a northern and southern sub-system with upwelling occurring in both areas. The subsystems are divided by an area of permanent upwelling off of Luderitz, which is the strongest upwelling zone in the world.

Tides

Tides are the rise and fall of sea levels caused by the combined effects of the gravitational forces exerted by the Moon and the Sun, and the rotation of the Earth (Fig. 1.20).

The semi-diurnal range (the difference in height between high and low waters over about half a day) varies in a two-week cycle. Approximately twice a month, around new moon and full moon when the sun, moon, and earth form a line (a configuration known as a syzygy), the tidal force due to the sun reinforces that due to the moon. The tide's range is then at its maximum; this is called the spring tide.[19]

When the moon is at first quarter or third quarter, the sun and moon are separated by 90° when viewed from the earth, and the solar tidal force partially cancels the moon's tidal force. At these points in the lunar cycle, the tide's range is at its minimum; this is called the neap tide, or neaps.[20]

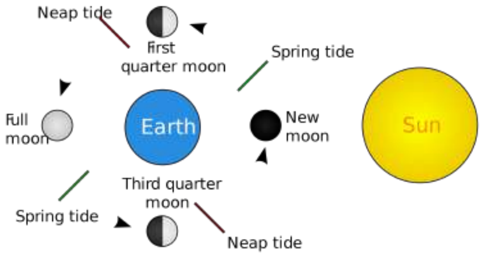

Figure 1.20: Tides schematic. Due to the bathymetry of some areas, neap and spring tides reach their maximum force 2 days after the first quarter moon, third quarter moon and new moon, full moon, respectively. In the absence of complications due to bathymetry, spring tides are exactly at the full and new moons and neap tides are exactly at the one-quarter and three-quarter moon.

Spring tides result in high waters that are higher than average, low waters that are lower than average, "slack water" time that is shorter than average, and stronger tidal currents than average. Neaps result in less extreme tidal conditions. There is about a seven-day interval between springs and neaps.

Tidal constituents are the multiple influences impacting tidal changes over certain periods of time. Primary constituents include the earth's rotation, the position of the moon and sun relative to the Earth, the moon's altitude (elevation) above the earth's equator, and bathymetry.

Tidal forces affect the entire earth, but the movement of solid earth occurs by mere centimeters. In contrast, the atmosphere is much more fluid and compressible so its surface moves by kilometers, in the sense of the contour level of a particular low pressure in the outer atmosphere.

In most locations, the largest constituent is the principal lunar semi-diurnal, also known as the M2 tidal constituent (Fig. 1.21). Its period is about 12 hours and 25.2 minutes, exactly half a tidal lunar day, which is the average time separating one lunar zenith from the next, and thus is the time required for the earth to rotate once relative to the moon. The lunar day is longer than the earth day because the moon orbits in the same direction the earth spins. This is analogous to the minute hand on a watch crossing the hour hand at 12:00 and then again at about 1:05.5.

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[19] As in "jump, burst forth, rise", not as in the season.

[20] "Neap" is an Anglo-Saxon word meaning "without the power".

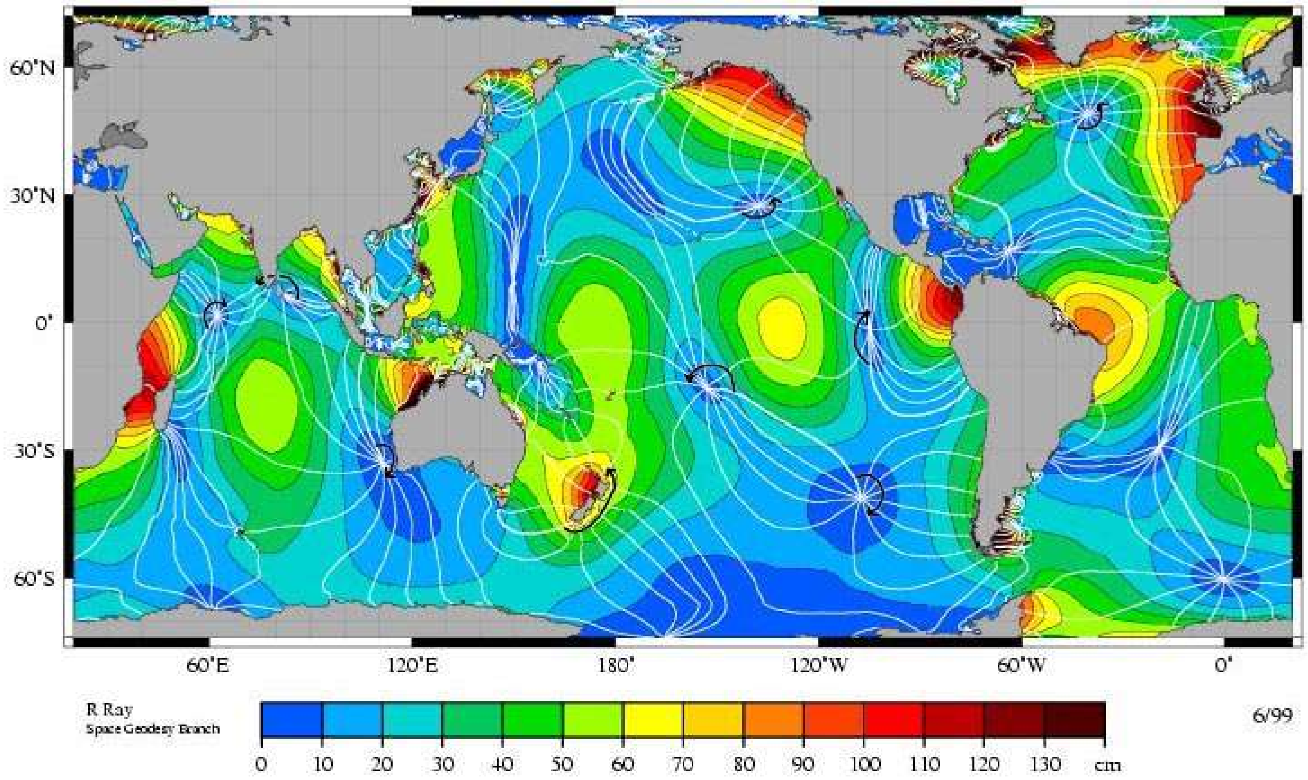


Figure 1.21: The amplitude of the lunar semi-diurnal tidal cycle (the so-called M2 tidal constituent). White "cotidal" lines indicate same tidal amplitudes and converge in blue areas of little or no tide ("amphidromic points"). Tide waves move around these points, generally counterclockwise in the northern hemisphere and clockwise in the southern hemisphere.

Mega-tides and amphidromic points Tidal ranges differ hugely across the globe. The largest tidal range can be found in the Bay of Fundy and in Ungava Bay (both Canada and ≈ 16 m tidal range) and the Severn Estuary (UK, ≈ 15 m). In these cases the coast formation increases the tidal amplitude, but similar ranges are observed at the French coast near St. Malo (≈ 13 m). Note that these height are an order of magnitude larger than the M2 tidal constituent depicted in Fig. 1.21, but the locations are in agreement.

Regions without noticeable tidal range are called "amphidromic points". Some amphidromic points are particularly noteworthy. The Caribbean Sea is without much tidal variation, thanks to the amphidrome near Hispaniola. The Mediterranean Sea lacks pronounced tides, as an amphidrome just east of the Strait of Gibraltar removes any triggering force of the north Atlantic tides. Similarly, an amphidrome in the Kattegat "removes" tidal effects from the Baltic Sea. The situation is much more complicated in the Southeast-Asian waters.

1.4 *Ocean weather and waves*

Wind waves, or wind-generated waves, are water surface waves that occur on the free surface of bodies of water. They result from the wind blowing over an area (or fetch) of fluid surface. Waves in the oceans can travel thousands of miles before reaching land. Wind waves on Earth range in size from small ripples, to waves over 30 m high, being limited by wind speed, duration, affected area and water depth.

Note that waves travel, but their water particles do not (much). They move in circles locally (orbital movement), with much less directional displacement as the surface wave might suggest (Fig. 1.22).

The more energy a wave contains, the larger becomes the amount of water that is moved in an orbital (rolling) movement, i.e. the larger the diameter of the circle in Figs 1.22 and 1.23. As a consequence, also the wavelength (distance between crests or troughs) increases. Energetic waves are thus barely visible in the open ocean, as they have long wavelengths. Reaching the shore, waves build up and break. It is here that their energy becomes visible (Fig. 1.23).

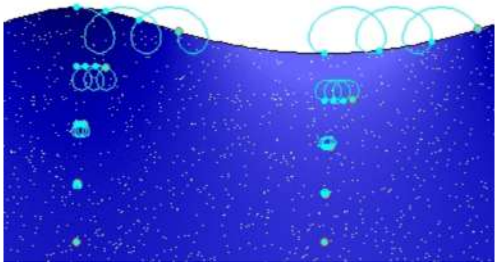


Figure 1.22: Water particle motion of a deep water wave.

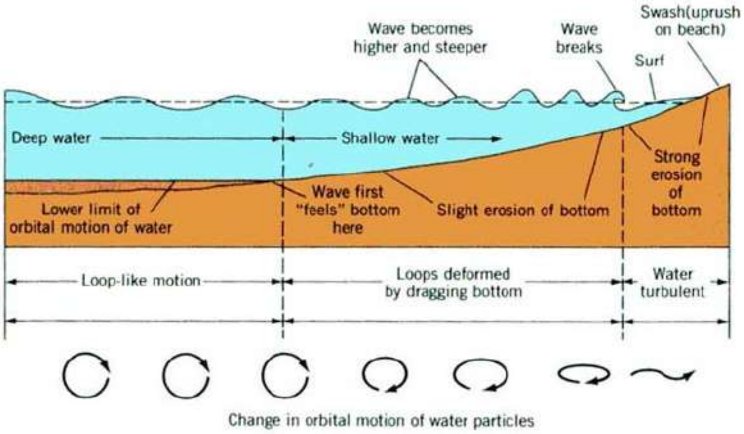
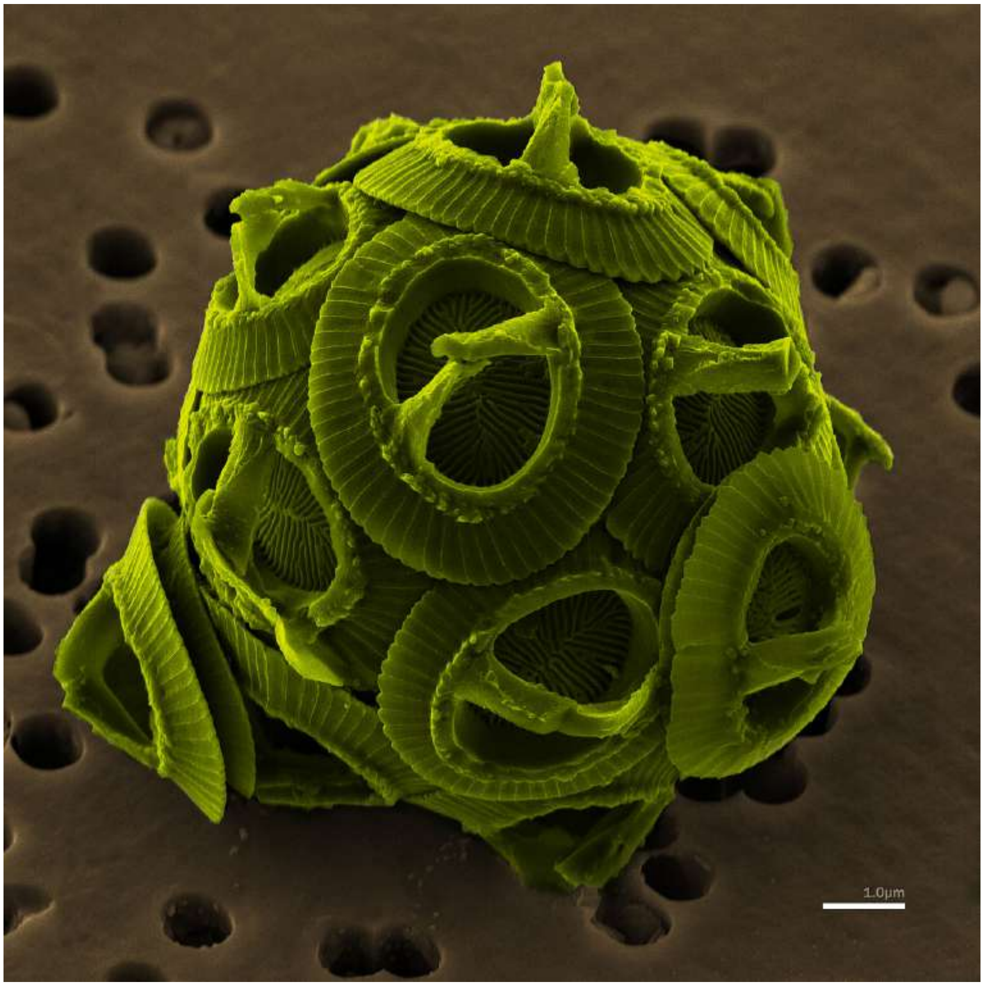


Figure 1.23: An ocean wave making landfall (*shoaling*). Notice that in the open ocean little of the wave's orbital motion is visible as actual wave. Reaching land, the sea bottom deforms the wave (*refraction*), causing it to (*break*).

When directly generated and affected by local waters, a wind wave system is called a "wind sea" (or wind waves). Wind waves will travel in a great circle route after being generated – curving slightly left in the southern hemisphere and slightly right in the northern hemisphere. After moving out of the area of fetch, wind waves are called swells and can travel thousands of miles. A noteworthy example of this are waves generated south of Tasmania during heavy winds that will travel to southern California producing desirable surfing conditions. More generally, a swell consists of wind-generated waves that are not significantly affected by the local wind at that time. They have been generated elsewhere or some time ago. Wind waves in the ocean are called "ocean surface waves".

2

Primary Productivity



False-color scanning electron micrograph of the coccolithophore *Gephyrocapsa oceanica*

> The assimilation of carbon by algae and marine vascular plants is, arguably, the basis of all oceanic life. In this chapter we learn about the biochemical basis, photosynthesis, and the most important groups of plant life that carry it out.

Primary productivity is the amount of carbon assimilated by plants (and cyanobacteria) per unit of time and space. In the ocean, most primary productivity is due to phytoplankton, i.e. largely unicellular, short-lived algae of less than 200 µm diameter, living in the top 50 m of the water column.

In contrast to life on land, **standing biomass is no good proxy for primary productivity**, as phytoplankton are intensively grazed by their zooplanktonic herbivores (see next chapter). As a result, most assimilated carbon is turned into animal tissue within a few hours to days. That, in turn, means that maps of chlorophyll concentration (Fig. 2.1) need not be good indicators of primary productivity, but are merely easily observable.

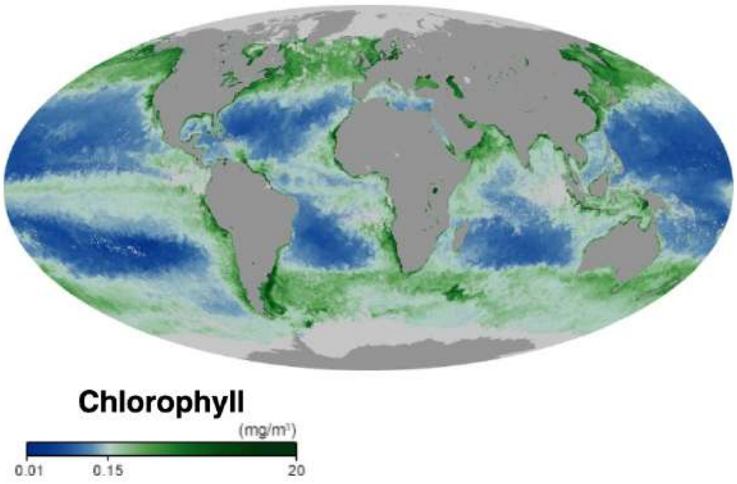


Figure 2.1: Map of ocean primary productivity (NASA). Note (sub)tropical waters are typically stably stratified, while polarwards of 40° nutrients from lower in the water column are regularly mixed into the top layer. High productivity along coasts is often, but not always, an effect of continental runoff bringing nutrients. Exceptions are upwelling regions such as off Namibia and Chile.

2.1 *Photosynthesis - the algal way*

Photosynthesis is the process of plants and some bacteria to convert light energy into chemical energy that can later be released to fuel the organisms' activities. This chemical energy is stored in carbohydrate molecules, such as sugars, which are synthesized from carbon dioxide and water – hence the name photosynthesis.[1]

Photosynthesis occurs in two stages. In the first stage, light-dependent reactions capture the energy of light and use it to make the energy-storage molecules ATP and NADPH. During the second stage, the light-independent reactions use these products to capture and reduce carbon dioxide.

The chemistry of photosynthesis In plants and algae, photosynthesis takes place in organelles called chloroplasts. A typical

[1] From the Greek (*φως*), "light", and synthesis (*σύνθεις*), "putting together".

plant cell contains about 10 to 100 chloroplasts, enclosed by a membrane. Plants absorb light primarily using the pigment chlorophyll. The green part of the light spectrum is not absorbed but is reflected, which is the reason that most plants have a green colour. Besides chlorophyll, plants also use pigments such as carotenes and xanthophylls to absorb light of different wavelengths. Algae also use chlorophyll, and various pigments, such as phycocyanin, carotenes, and xanthophylls in green algae, phycoerythrin in red algae (rhodophytes) and fucoxanthin in brown algae and diatoms resulting in a wide variety of colours.

In the light-dependent reactions, one molecule of the pigment chlorophyll absorbs one photon and loses one electron. This electron is passed down a series of molecules, starting the flow of electrons down an electron transport chain that leads to the ultimate reduction of NADP to NADPH. In addition, this creates a proton gradient (energy gradient) across the chloroplast membrane, which is used by ATP synthase in the synthesis of ATP.[2] The chlorophyll molecule ultimately regains the electron it lost when a water molecule is split in a process called photolysis, which releases a dioxygen (O_2) molecule as a waste product.[3]

In the light-independent (or "dark") reactions, the enzyme RuBisCO captures CO_2 from the atmosphere and, in a process called the *Calvin-Benson-Bassham cycle*, it uses the newly formed NADPH and releases three-carbon sugars, which are later combined to form sucrose and starch.[4]

RuBisCO RuBisCO (Ribulose 1,5-bisphosphate carboxylase-oxygenase) is probably the most common enzyme on Earth. It is large, in itself consisting of two large and two small subunits (Fig. 2.2), but assembles as 4 units into a larger complex (Fig. 2.3) of about 540 kDa.[5] Also, RuBisCO is slow, fixing only 3-10 carbon dioxide molecules each second per molecule of enzyme (in contrast to some enzymes that carry out thousands of reactions per second). Thus, in plant assimilatory tissue (leave, fronts and alike) RuBisCo easily comprises 30-50% of all protein.

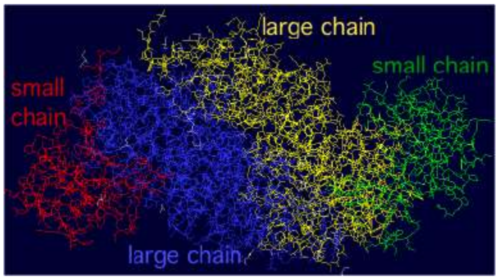


Figure 2.2: The structure of a RuBisCO unit, consisting of 2 large and 2 small subunits.

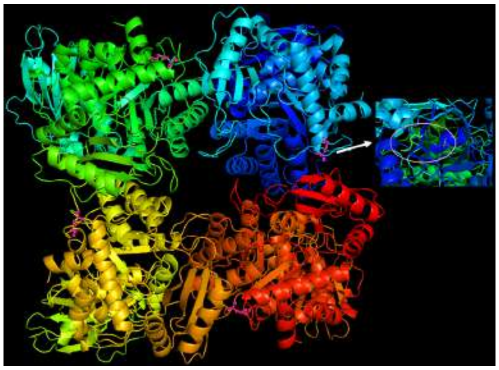


Figure 2.3: The structure of a full RuBisCO assembly, consisting of four units. Each colour range indicates the 4-piece RuBisCO unit of Fig. 2.2. The substrate binding sites are indicated in pink and zoomed in in the inset.

C-fixation by RuBisCO is slightly more effective for the lighter ^{12}C isotope,[6] leading to a change in the C-isotope ratio of organic matter over anorganic C. Isotope fractionation due to RuBisCO's carboxylation alone is predicted to be a 28‰ depletion.[7] However, fractionation values vary between organisms, ranging from an 11‰ depletion observed in coccolithophorid algae to a 29‰ depletion observed in spinach, as C-concentration mechanisms such as the pyrenoid (next paragraph) reduce depletion.

Carbon concentration mechanism and the pyrenoid Algae are restricted to aqueous environments, even in aquatic habitats, and this has implications for their ability to access CO_2 for

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[2] The *details* and the history of discovery is fascinating (Morton, 2009)!

[3] The light-dependent reaction in total: 2 H_2O + 2 $NADP^+$+ 3 ADP + 3 P_i+ light $\longrightarrow$ 2 NADPH + 2 H^++ 3 ATP + O_2, where P_i refers to phosphate.

[4] In sum, the dark reaction is:
3 CO_2+ 9 ATP + 6 NADPH + 6 H^+ $\longrightarrow$ $C_3H_6O_3$-phosphate + 9 ADP + 8 P_i + 6 $NADP^+$ + 3 H_2O, where the first product is called *3-phosphoglycerate*, or 3PG

[5] A *Dalton* gives mass in C-atom equivalents. As reference, carbonic anhydrase, mentioned in section 1.1, has 29 kDa.

[6] A phenomenon called the *kinetic isotope effect*.

[7] Depletion refers to the ratio of ^{12}C to ^{13}C, which decreases if more ^{12}C is fixed. This is typically indicated by the $\delta^{13}C$ value, which becomes more negative under depletion (CO_2 in the air: $\delta^{13}C = -4.4\%$). Note that ‰ isotope fractioning is **not** the same as $\delta^{13}C$ in %!

photosynthesis. CO_2 diffuses 10,000 times slower in water than in air, and is also slow to equilibrate. The result of this is that water, as a medium, is often easily depleted of CO_2 and is slow to gain CO_2 from the air. Finally, CO_2 equilibrates with bicarbonate (HCO_3^-) when dissolved in water, and in sea water is mainly found in the form of HCO_3^- (see section 1.1). Marine macrophytes, including seagrass, use both CO_2 and HCO_3^- (hydrogen carbonate) for photosynthetic carbon reduction, but the latter needs to be converted to the former in the cell. The net result of this is a low concentration of free CO_2 that is barely sufficient for an algal RuBisCO to run at a quarter of its maximum velocity, and thus, CO_2 availability may sometimes represent a major limitation of algal photosynthesis.

In algae (and hornworts) a special structure, the *pyrenoid*, establishes a carbon concentration mechanism (CCM). It centres the chloroplast's thylakoid stacks around the place of active CO_2 enrichment (employing, among other enzymes, the carbonic anhydrase of section 1.1), partly overcoming the CO_2 limitations of the medium water.[8]

Chlorophyll and pigments The light-dependent reaction requires energy, which is provided by light. The light-absorbing compound is chlorophyll (Fig. 2.4), with a Mg^{2+} ligand essential for its functioning.

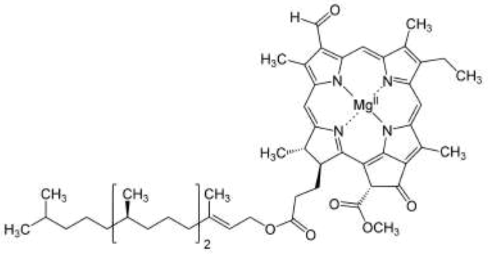

Figure 2.4: The general structure of chlorophyll, showing the important Mg-porphyrin structure common to all of them.

Chlorophyll molecules are arranged in and around photosystems that are embedded in the thylakoid membranes of chloroplasts. In these complexes, chlorophyll serves three functions. The function of the vast majority of chlorophyll (up to several hundred molecules per photosystem) is to absorb light. Having done so, these same centres execute their second function: the transfer of that light energy by resonance energy transfer to a specific chlorophyll pair in the reaction center of the photosystems. This pair effects the final function of chlorophylls, charge separation, leading to biosynthesis (see section 2.1, light-dependent reactions). The two photosystem II and I have their own distinct reaction centres, named P680 and P700, respectively.[9] These centres are named after the wavelength (in nanometers) of their red-peak absorption maximum. Both chlorophyll a and b are present in both photosystems, but b predominantly in PS II.

The spectral behaviour (i.e. which light frequencies are absorbed by a chloroplast; see Fig. 2.5) are heavily influenced by (1) the chlorophyll type (a is universal; b in vascular plants; various c subtypes in algae; d and f in cyanobacteria); (2) the specific physico-chemical configuration; and (3) the activity of other light-absorbing pigments such as *carotenes*[10] and *xanthophylls*.[11] Not all pigments are involved in light harvesting; *anthocyanins*[12] for example rather protect chloroplasts from light overexposure.

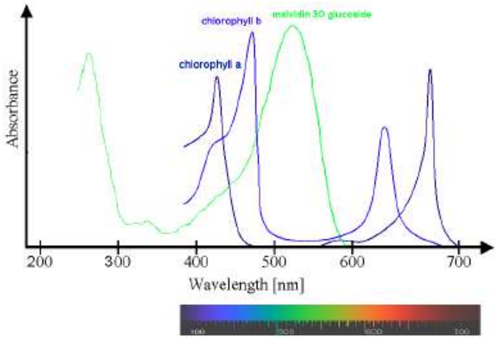

Figure 2.5: Superposition of spectra of chlorophyll a and b with oenin, a typical anthocyanidin, showing that, while chlorophylls absorb in the blue and yellow/red parts of the visible spectrum, oenin absorbs mainly in the green part of the spectrum.

Pigments, chlorophyll, many proteins and cofactors, and a photosystem are arranged in a large *light-harvesting complex*

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[8] A similar organelle exists in cyanobacteria, the *carboxysome*.

[9] The numbering has historic reasons. Only much after their discovery was it realised that PS II is the first photosystem of the so-called *Z-scheme*.

[10] E.g. the orange in carots.

[11] E.g. the yellow in egg yolk.

[12] The blue-red of red cabbage and aubergines.

(LHC, or antenna complex) in the thylakoid membrane. The antenna pigments' spectra are non-overlapping and broaden the range of light that can be absorbed in photosynthesis.

Light compensation depth Photosynthetic assimilation of CO_2 drives most metabolism on earth, including that of plants themselves. The amount of light that yields just as much assimilates as are respired by the organism is called the *light compensation point*. For marine algae, depth imposes a light compensation depth, obviously driven by the penetration depth of blue light (see Fig. 1.11). Pelagic algae occur down to 50 m, while benthic, *coralline red algae* hold the record at 270 m depth, thanks to a photopigment called phycoerythrin and a highly adapted metabolism.

2.2 *Chemoautotrophy*

Chemoautotrophs (or chemotrophic autotroph) (Greek: *χημεία* = chemical, *αντός* = self, *τροφή* = nourishment) derive their energy from chemical reactions rather than sunlight. All chemoautotrophs are bacteria and archaea.

While all animals do that too, chemo*auto*trophs do not rely on other organisms to have fixed the energy in the first place, as animals do for plants; that is, they do not rely on organic sources of C. Like plants, they fixate CO_2 to build complex organic molecules, using (variations of) RuBisCO in the Calvin-Benson-Bassham cycle.

Where plants use light as energy source and H_2O as electron donor, chemoautotrophs (typically) oxidise some substrate, which provides the energy, and reduce e.g. O_2 for its electrons. Chemically, it is thus interesting to investigate where in chemoautotrophy the (a) energy and (b) electrons come from.

Chemoautotrophs can use inorganic electron sources such as hydrogen sulfide (H_2S), elemental sulfur (S), ferrous iron (FeO), molecular hydrogen (H_2), and ammonia (NH_3) or organic sources. For historical reasons they generally are grouped sometimes by their substrate, sometimes by their main product:

Methanogens emit CH_4 rather than H_2O; they all belong to the archaea. The leading reaction here is the CO_2-based oxidation of diatomic hydrogen.[13] Since this reaction carries a fair amount of energy, methanogens can grow rapidly.

Sulfur oxidizers and reducers use H_2S and S, respectively, as substrate. Under aerobic conditions, the energy comes from the oxidation of hydrogen sulfide.[14] Under anaerobic conditions, the most common reaction uses nitrate as oxidising agent.[15] Also here the high energy release of the reaction allows for population doubling times of hours.

Nitrifiers oxidise NH_3 to NO_2^- and further on to NO_3^-. Nitrification is the process by which ammonia (NH_3) is converted

[13] $CO_2 + 4\ H_2 \rightarrow CH_4 + 2\ H_2O$

[14] $H_2S{+}0.5\ O_2 \rightarrow S_0{+}H_2O$

[15] $4\ H_2S{+}NO_3^- + 2\ H^+ \rightarrow 4\ S_0{+}NH_4^+ + 3\ H_2O$

to nitrate (NO_3^-). Nitrification is the net result of two distinct processes: oxidation of ammonia to nitrite (NO_2^-) by nitrosifying bacteria (e.g. the ubiquitous *Nitrosomonas*) and oxidation of nitrite to nitrate by the nitrite-oxidizing bacteria (e.g. the similarly omnipresent *Nitrobacter*). Both of these processes are extremely energetically poor leading to very slow growth rates for both types of organisms. Oxygen is required in both ammonia and nitrite oxidation, meaning that both nitrosifying and nitrite-oxidizing bacteria are aerobes.

Anammox bacteria combine $NH_4^+ + NO_2^-$ into $N_2 + 2H_2O$. This anaerobic process was only discovered in 1999 and is surprising in that it is a major processes yielding diatomic nitrogen. Also, by taking up two limiting nitrogen compounds, this process actually limits N-availability in the oceans. Again the energy gain is small and the bacterial growth rate pathetic (1 - 3 week doubling time).

Thermoacidophiles are defined by living in a hot and acidic environment rather than any specific chemical reaction; they are a special case of *extremophile* life forms more generally.

Most chemoautotrophs are bacteria or archaea that live in hostile environments (such as deep-sea vents) and are the primary producers in such ecosystems. [16]

2.3 Algal growth

Limiting resources Phytoplankton rely on a suite of nutrients for cellular function. Macronutrients (e.g. nitrate, phosphate, silica) are generally available in higher quantities in surface ocean waters, and are the typical components of common garden fertilizers.[17] Micronutrients (e.g. iron, zinc, cobalt) are generally available in lower quantities and include trace metals. Macronutrients are typically available in millimolar concentrations, while micronutrients are generally available in micro- to nanomolar concentrations. In general, nitrogen tends to be a limiting ocean nutrient, but in so-called High-Nitrogen, Low-Chlorophyll (HNLC) regions it is never significantly depleted. Instead, these regions tend to be limited by low concentrations of metabolisable iron. Iron is a critical phytoplankton micronutrient necessary for enzyme catalysis and electron transport.

Between the 1930s and '80s, it was hypothesized that iron is a limiting ocean micronutrient, but there were not sufficient methods to reliably detect iron in seawater to confirm this hypothesis. In 1989, high concentrations of iron-rich sediments in near-shore coastal waters off the Gulf of Alaska were detected. However, offshore waters had lower iron concentrations and

[16] A rare example of an 'extremophile' eukaryote would be the red algae *Galdieria sulphuraria*, whose genome revealed that its environmental adaptations likely originated from horizontal gene transfer from thermoacidophilic archaea and bacteria.

[17] The molecular ratio of 106 carbon : 16 nitrogen : 1 phosphorus is known as the *Redfield ratio*.

lower productivity despite macronutrient availability for phytoplankton growth. This pattern was observed in other oceanic regions and led to the naming of three major HNLC zones: the North Pacific Ocean, the Equatorial Pacific Ocean, and the Southern Ocean.

The discovery of HNLC regions has fostered scientific debate about the ethics and efficacy of iron fertilization experiments which attempt to draw down atmospheric carbon dioxide by stimulating surface-level photosynthesis. It has also led to the development of hypotheses such as grazing control which poses that HNLC regions are formed, in part, from the grazing of phytoplankton (e.g. dinoflagellates, ciliates) by smaller organisms (e.g. protists).

Resource limitation through the seasons Turbulent storms churn the ocean in winter, adding nutrients to sunlit waters near the surface. This sparks a assimilation frenzy each spring that gives rise to massive blooms of phytoplankton. Zooplankton reproduces slower and requires some weeks to catch up with primary producers (Fig. 2.6). Chlorophyll absorption enables scientists to monitor algal blooms from space. Observations show blooms typically last until late spring or early summer, when nutrient stocks are in decline and predatory zooplankton start to graze.

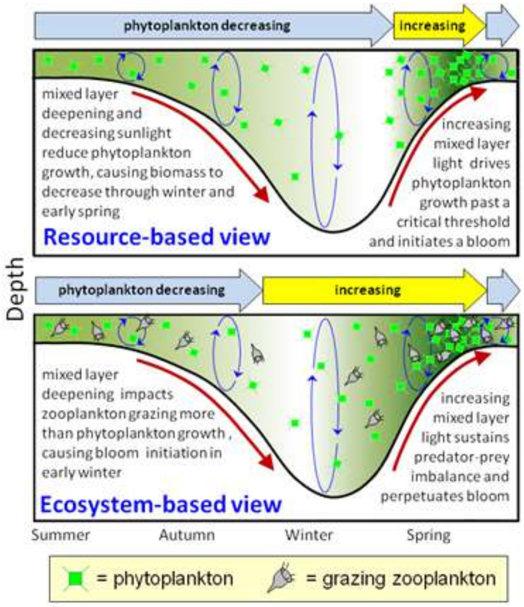

Figure 2.6: Hypotheses of plankton variability; resources and grazing are not mutually exclusive, however, and likely to both be responsible for the end of algal blooms in spring/summer. In higher latitudes, a second, smaller algal bloom may occur with the onset of autumn storm-induced remixing.

Grazing & defence It is important to realise that the typical cause of death for phytoplankton is being grazed by zooplankton. Morphological and chemical defence strategies exist, but of course require energy investment not available for growth. Thus, at low grazing pressure (e.g. in early spring), defended phytoplankton are outgrown by edible species. Only under late-spring grazing pressure will species with long spines or toxins have a competitive advantage.

Both long spines (preventing ingestion) and chemical defences (e.g. DMSP[18] in coccolithophores) are likely to be side effects of a different function. For example, long spines also increase buoyancy, keeping the individually longer in the photic zone, while DMSP primarily is an osmolyte.

2.4 Growth forms and types of primary producers

The principal marine primary producers are cyanobacteria, algae and marine plants. In a reversal of the pattern on land, in the oceans almost all photosynthesis is performed by algae and cyanobacteria, with a small fraction contributed by vascular plants and other groups. Algae encompass a diverse range of organisms, ranging from single floating cells (Fig. 2.7) to attached seaweeds (Fig. 2.8). They include photoautotrophs from a variety of groups. Bacteria are important photosynthetizers in both oceanic and terrestrial ecosystems, while no archaea utilise oxygen-evolving photosynthesis. A number of eukaryotes are significant contributors to primary production in the ocean, including green algae, brown algae and red algae, and a diverse group of unicellular groups. Vascular plants are also represented in the ocean by groups such as the seagrasses (Fig. 2.9).

Figure 2.7: *Emiliania huxleyi*, a ubiquitous coccolithophore in all ocean ecosystems, as a nicely prepared electron microscope specimen, and what it actually looks like through the optical microscope. Each transparent shield (coccolith) is about 2 µm, making *E. huxleyi* cells about 3-10 µm large.

Figure 2.8: *Laminaria digitata*, or oarweed, against a backdrop of *Ascophyllum nodosum.* This specimen may be 3 m, but they grow larger.

Figure 2.9: *Cymodocea nodosa*, or lesser Neptune grass, off the Spanish Mediterranean coast. Plants grow about 40 cm tall.

Unlike terrestrial ecosystems, the majority of primary production in the ocean is performed by free-living microscopic organisms called phytoplankton. It has been estimated that half of the world's oxygen is produced by phytoplankton. Larger autotrophs, such as the seagrasses and macroalgae (seaweeds) are generally confined to the and adjacent shallow waters, where they can attach to the underlying substrate but still be within the photic zone. There are exceptions, such as the 300 *Sargassum* species, but the vast majority of free-floating production takes place within microscopic organisms.

The factors limiting primary production in the ocean are also very different from those on land. The availability of water, obviously, is not an issue (though its salinity can be). Similarly, temperature, while affecting metabolic rates (see Q_{10}), ranges less widely in the ocean than on land because the heat capacity of seawater buffers temperature changes, and the formation of sea ice insulates it at lower temperatures. However, the availability of light, the source of energy for photosynthesis, and mineral nutrients, the building blocks for new growth, play crucial roles in regulating primary production in the ocean.

Plankton Size Phytoplankton is often referred to by its size (Table 2.10). *Macroplankton* refers to anything that can be seen by eye (e.g. the drifting *Sargassum*), as opposed to *microplankton* of <200 µm. Microplankton includes most phytoplankton, e.g. most coccolithophores, diatoms and dinoflagellates.

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[18] Dimethylsulfoniopropionate is an organosulfur compound with the formula $(CH_3)_2S^+CH_2CH_2COO^-$.

Nanoplankton is somewhat a misnomer, as it is merely very small, but not as small as the prefix suggests: 2 - 20 µm. It includes the smaller cousins of the microplankton, and a motley assortment of tiny algae with one or two flagella allowing modest movement. Smaller still is the *picoplankton* (2-0.2 µm), which is largely bacterial. *Femtoplankton* (<0.2 µm) comprises marine viruses.

Table 2.10: Size classes of plankton. *Slanted prefixes* refer primarily to zooplankton.

Prefix	Size
mega	> 20 cm
macro	2 - 20 cm
meso	0.2 - 20 mm
micro	20 - 200 µm
nano	2 - 20 µm
pico	0.2 - 2 µm
femto	<0.2 µm

2.4.1 *Cyanobacteria*

Cyanobacteria are a phylum (division) of bacteria,[19] ranging from unicellular to filamentous and including colonial species, which fix inorganic carbon into organic carbon compounds. They are found almost everywhere on earth: in damp soil, in both freshwater and marine environments, and even on Antarctic rocks. In particular, some species occur as drifting cells floating in the ocean, and as such were amongst the first of the phytoplankton. Crucially, many cyanobacteria (but not *Prochlorococcus*!) can fix nitrogen from the atmosphere or dissolved in the seawater, thereby substantially enriching the unproductive open seas.

The tiny marine cyanobacterium *Prochlorococcus* (Fig. 2.11), discovered only in 1986, forms part of the base of the ocean food chain and accounts for more than half the photosynthesis of the open ocean and an estimated 20% of the oxygen in the Earth's atmosphere. It is possibly the most plentiful genus on Earth: a single millilitre of surface seawater may contain 100,000 cells or more.

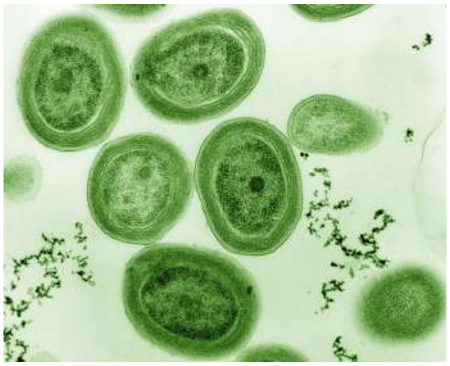

Figure 2.11: Transmission electron microscopic image of the world's most common photosynthesizer, *Prochlorococcus marinus*, with overlay green colouring. Size about 0.6 µm.

In addition to chlorophyll, cyanobacteria also use bacterial form (bacteriachlorophyll) and, more surprisingly. the purple pigment retinal, i.e. the same pigment found in the rods of animal vision. Only in 2000 was its main protein, rhodopsin, discovered in bacteria, although its colouring effect can be striking (e.g. in archaea: Fig. 2.12).

Figure 2.12: Halobacteria (archaea) in salt evaporation ponds coloured purple by bacteriorhodopsin. San Francisco Bay area.

2.4.2 *Green Algae*

The division of algae by colour is a pragmatic, not a phylogenetic choice. Typically these divisions are paraphyletic, i.e. have a common ancestor, but exclude some relatives. In the case of the green algae, vascular plants are also derived from their common ancestor but are not included in the "green algae", making that group paraphyletic.

The green algae include unicellular and colonial flagellates, most with two flagella per cell, as well as various coenobial (= colonial), coccoid and filamentous forms, and macroscopic, multicellular seaweeds. There are about 22,000 species of green algae. Green algae have chloroplasts that contain chlorophyll a and b, giving them a bright green color, as well as the accessory pigments β-carotene (red-orange) and xanthophylls (yellow) in stacked thylakoids. The cell walls of green algae

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[19] Originally, biologists thought cyanobacteria were algae, and referred to it as "blue-green algae". The more recent view is that cyanobacteria are bacteria, and hence are not even in the same Kingdom as algae. Most authorities exclude all prokaryotes, and hence cyanobacteria from the definition of "algae".

Figure 2.13: Composite image to illustrate the diversity of Ulvophyceae. Top left: *Ulva*, top right: *Caulerpa*, bottom left: *Bornetella*, bottom right: *Dictyosphaeria*.

usually contain cellulose, and they store carbohydrate in the form of starch.

The largest subgroup are the chlorophyta (aka prasinophyta), of which most are unicellular. They appear rather basic, in the sense that their growth form, pigmentation, life style is often simple compared to other algae. For example, unicellular green algae are simple, round blobs with or without flagella, without apparent shields or fancy structures (Fig. 2.14). As colonies, green algae form simple structures, such as filaments or hollow spheroids. Even the most complex seaweeds in this group, e.g. the Ulvophyceae, are flat sheets or simple conical, or spherical structures (Fig. 2.13). Some species adopted an endosymbiontic lifestyle (Fig. 2.15).

Some relevant green algae: *Blidingia minima*, *Codium fragile*, *Euglena* spp., *Ulva lactuca*

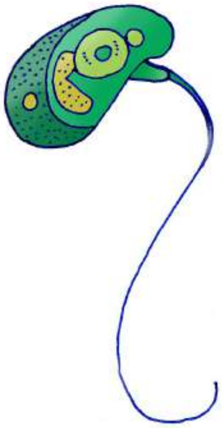

Figure 2.14: Schematic drawing of picoplankton *Micromonas pusilla*, with its single chloroplast (dotted, enclosing a starch granule), single mitochondrium (beige, dotted) and long flagellum.

2.4.3 *Red Algae - Rhodophyta*

The Rhodophyta are one of the oldest groups of eukaryotic algae. They also comprises one of the largest phyla of algae, containing over 7,000 currently recognized species with taxonomic revisions ongoing. The majority of species (6,793) are found in the class Florideophyceae, and mostly consist of multicellular, marine algae, including many notable seaweeds.

The red algae form a distinct group characterized by having eukaryotic cells without flagella and centrioles, chloroplasts that lack external endoplasmic reticulum and contain unstacked (stroma) thylakoids, and use phycobiliproteins

Figure 2.15: The ciliate *Paramecium bursaria*. It has a mutualistic endosymbiotic relationship with green algae called *Chlorella*. The algae are clearly visible in ciliate cytoplasm.

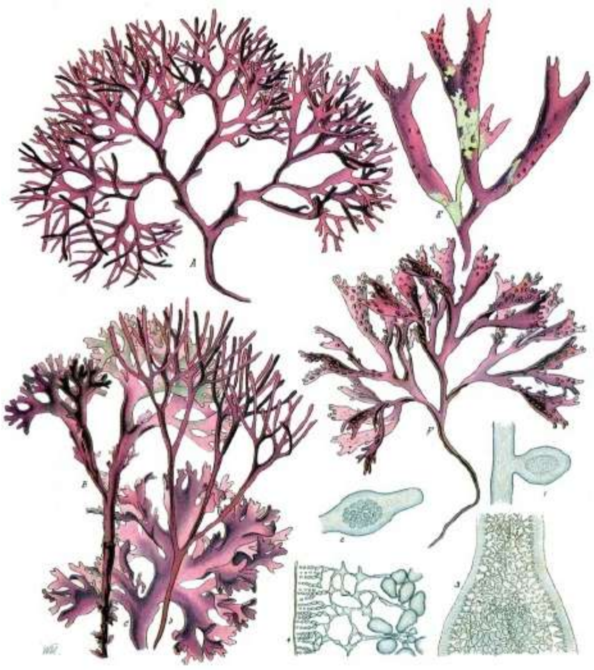

Figure 2.16: Irish Moss and False Irish Moss. Left top and bottom (A-D): various forms of Irish Moss *Chondrus crispus*; Right (E, F) forms of *Mastocarpus stellatus*; 1-4 sections through these species.

as accessory pigments, which give them their red color. Red algae store sugars as floridean starch, which is a type of starch that consists of highly branched amylopectin without amylose, as food reserves outside their plastids. Red algae have double cell walls. The outer layers contain the polysaccharides agarose and agaropectin that can be extracted from the cell walls by boiling as *agar*. The internal walls are mostly cellulose.

Most red algae are also multicellular, macroscopic, marine, and reproduce sexually. The red algal life history is typically an alternation of generations that may have **three generations rather than two**. For botanists, this is a big deal. Parasitic animals may have weird life cycles, but plants are much more catholic: diploid sporophyt, haploid gametophyt (in terrestrial plants reduced to pollen). Rhodophyta have two sporophyts (illustrated in Fig. 2.17).

The coralline algae, which secrete calcium carbonate and play a major role in building coral reefs, belong here. Grazed red algae may alter their growth form from lobes into crusts, as in the case of *Corallina officinalis*. Red algae such as dulse (*Palmaria palmata*) and laver (Jap.: nori; Kor.: gim: *Pyropia* and *Porphyra*) are a traditional part of European and Asian cuisines and are used to make other products such as agar, carrageenans and other food additives.

Some relevant species: *Ceramium virgatum*, *Chondrus crispus*, *Corallina officinalis*, *Delesseria sanguinea*, Gelidium spp., *Mastocarpus stellatus*, *Palmaria palmata*, *Polysiphonia ceramiaeformis*, *Porphyra* spp.

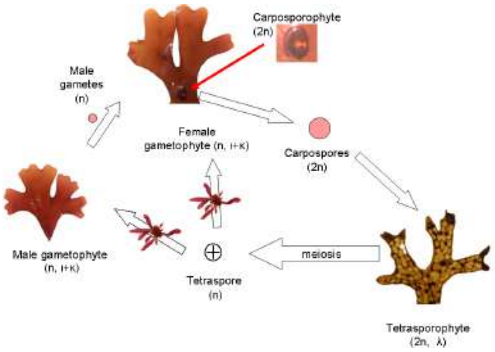

Figure 2.17: Life cycle of *Chondrus crispus*, with carpo- and tetrasporophyte. (ι, κ and λ refer to three types of carrageenan, forming rigid, soft or no gels, respectively.)

2.4.4 Brown Algae - Phaeophyceae

The brown algae are a large group of multicellular algae, including many seaweeds located in colder waters within the northern hemisphere, where they play an important role both as food and as a potential habitat. For instance, *Macrocystis*, a kelp of the order Laminariales, may reach 60 m in length and forms prominent underwater kelp forests. Kelp forests like these contain a high level of biodiversity. Another example is *Sargassum*, which creates unique floating mats of seaweed in the tropical waters of the Sargasso Sea that serve as the habitats for many species. Many brown algae, such as members of the order Fucales, commonly grow along rocky seashores.

Between 1,500 and 2,000 species of brown algae are known worldwide. Some species, such as *Ascophyllum nodosum*, have become subjects of extensive research in their own right due to their commercial importance.

Brown algae belong to the group Heterokontophyta, a large group of eukaryotic organisms distinguished most prominently by having chloroplasts surrounded by four membranes, suggesting an origin from a symbiotic relationship between a basal eukaryote and another eukaryotic organism. Most brown algae contain the pigment fucoxanthin, which is responsible for the distinctive greenish-brown color that gives them their name (Fig. 2.18). Brown algae are unique among heterokonts in developing into multicellular forms with differentiated tissues, but they reproduce by means of flagellated spores and gametes that closely resemble cells of other heterokonts.

Typical kelp (e.g. Fig. 2.8) uses a *holdfast* as root-like structure to anchor the plant in the substrate. The stem-like *stipe* holds the leaf-equivalent *fronds*. They can grow at the tips to the tune of cm per day. Sugar kelp, *Saccharina latissima* (Fig. 2.19), is grown commercially in aquaculture on floats as food and ingredient in cosmetics.

Some relevant species: *Alaria esculenta*, *Ascophyllum nodosum*, *Desmarestia viridis*, *Ectocarpus* spp., *Fucus vesiculosus*, *Fucus serratus*, *Himanthalia elongata*, *Macrocystis pyrifera*, *Laminaria hyperborea*, *Laminaria digitata*, *Pelvetia canaliculata*, *Saccharina latissima*, *Saccorhiza polyschides*, *Sargassum* spp.


Figure 2.18: Bladder wrack, *Fucus vesiculosus*, showing the stipe with surrounding cortex and epidermis, and, more characteristically, the gas-filled bladders (pneumatocytes) to yield buoyancy. Grows to 1 m.


Figure 2.19: Sugar kelp, *Saccharina latissima*, showing its characteristic wavy frond. Grows to 5 m.

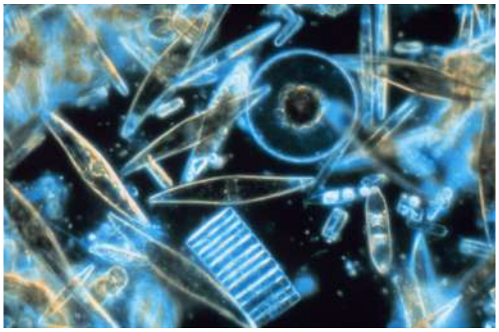
Figure 2.20: Assorted diatoms as seen through a microscope. These specimens were living between crystals of annual sea ice in McMurdo Sound, Antarctica.

2.4.5 Diatoms - Diatomea

Diatoms (Greek: *diá-tom-os* 'cut in half') are a major group of microalgae (Fig. 2.20), make up a significant portion of the earth's biomass: they generate about 20 to 50% of the oxygen produced on the planet each year, take in over 6.7 billion metric tons of silicon each year from the waters in which they live, and constitute nearly half of the organic material found in the oceans. The shells of dead diatoms can form a layer as thick as a 800 m on the ocean floor, and the entire Amazon basin is fertilized annually by 27 million tons of diatom shell dust transported by transatlantic winds from the African Sahara, much of it from Chad's *Bodélé Depression*, which was once made up of a system of fresh-water lakes.

Diatoms are unicellular: they occur either as solitary cells or in colonies, which can take the shape of ribbons, fans, zigzags, or stars (Fig. 2.21). Individual cells range in size from 2 to 200 µm. In the presence of adequate nutrients and sunlight, an assemblage of living diatoms doubles approximately every 24 hours by asexual multiple fission; the maximum life span of individual cells is about six days. The cell itself consists of two halves, each containing an essentially flat plate, or valve and marginal connecting, or girdle band: together, the are called frustule (Fig. 2.22). One half, the hypotheca, is slightly smaller than the other half, the epitheca. Diatoms have two distinct shapes: a few (centric diatoms) are radially symmetric, while most (pennate diatoms) are broadly bilaterally symmetric. A unique feature of diatom anatomy is that the frustules are made of **silica** (hydrated silicon dioxide). These frustules have structural colouration due to their reflective nanostructure, prompting them to be described as "jewels of the sea" and "living opals". This siliceous wall can be highly patterned with a variety of pores, ribs, minute spines, marginal ridges and elevations; all of which can be used to delineate genera and species.

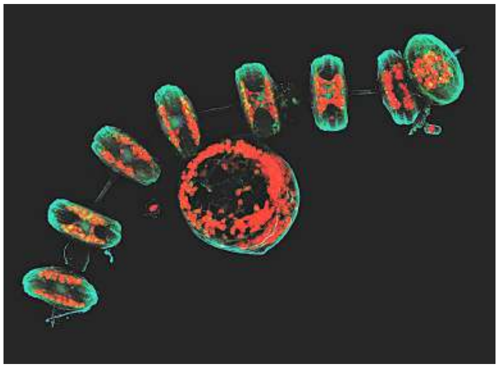

Figure 2.21: *Thalassiosira* diatoms form chain-like colonies. This confocal image shows the diatoms' cell wall (cyan), chloroplasts (red), DNA (blue), membranes and organelles (green).

Figure 2.22: Shape classification of diatom frustules (images of 3D models). The actual sizes of the frustules are about 10–80 µm.

As plankton, movement in diatoms primarily occurs passively as a result of both water currents and wind-induced water turbulence; however, male gametes of centric diatoms have flagella, permitting active movement for seeking female gametes. Unusually for autotrophic organisms, diatoms possess an *urea cycle*, a feature that they share with animals, although this cycle in diatoms facilitates rapid recovery from prolonged nitrogen limitation (while in animals it converts toxic NH_3 to harmless urea).[20] The family Rhopalodiaceae also possess a cyanobacterial endosymbiont called a "spheroid body". This endosymbiont has lost its photosynthetic properties, but has kept its ability to perform nitrogen fixation, allowing the diatom to fix atmospheric nitrogen.

Diatoms are used to monitor past and present environmental conditions, and are commonly used in studies of water quality. Diatomaceous earth (diatomite) is a collection of diatom shells found in the earth's crust. They are soft, silica-containing sedimentary rocks which are easily crumbled into a fine powder and typically have a particle size of 10 to 200 µm. Diatomaceous earth is used for a variety of purposes including for water filtration, as a mild abrasive, in cat litter, and as a TNT stabilizer (dynamite).

[20] Allen, A. E., Dupont, C. L., Oborník, M., Horák, A., Nunes-Nesi, A., McCrow, J. P., Zheng, H., Johnson, D. A., Hu, H., Fernie, A. R., and Bowler, C. (2011). Evolution and metabolic significance of the urea cycle in photosynthetic diatoms. *Nature*, 473:203–207

Diatom Ecology Planktonic diatoms in freshwater and marine environments typically exhibit a "boom and bust" (or "bloom and bust") lifestyle. When conditions in the upper mixed layer (nutrients and light) are favourable (as at the spring), their competitive edge and rapid growth rate enables them to dominate phytoplankton communities ("bloom").

When conditions turn unfavourable, usually upon depletion of nutrients, diatom cells typically increase in sinking rate and exit the upper mixed layer ("bust"). This sinking is induced by either a loss of buoyancy control, the synthesis of mucilage that sticks diatoms cells together, or the production of heavy resting spores. Sinking out of the upper mixed layer removes diatoms from conditions unfavourable to growth, including grazing and high temperatures. Cells reaching deeper water or the shallow sea floor can then rest until conditions become more favourable again. In the open ocean, many sinking cells are lost to the deep, but refuge populations can persist near the thermocline.

Ultimately, some diatom cells in these resting populations re-enter the upper mixed layer when vertical mixing entrains them. In most circumstances, this mixing also replenishes nutrients in the upper mixed layer, setting the scene for the next round of diatom blooms.[21] In the open ocean (away from areas of continuous upwelling), this cycle of bloom, bust, then return to pre-bloom conditions typically occurs over an annual cycle, with diatoms only being prevalent during the spring and early summer. In some locations, however, an autumn bloom may occur, caused by the breakdown of summer stratification and the entrainment of nutrients while light levels are still sufficient for growth. Since vertical mixing is increasing, and light levels are falling as winter approaches, these blooms are smaller and shorter-lived than their spring equivalents.

Diatom blooms are typically ended by a shortage of silicon. This can be seen in maps of surface nutrient concentrations – as nutrients decline along gradients, silicon is usually the first to be exhausted (followed normally by nitrogen then phosphorus). Because of this bloom-and-bust cycle, diatoms are believed to play a disproportionately important role in the export of carbon from oceanic surface waters

Some relevant genera: *Chaetoceros*, *Coscinodiscus*,

2.4.6 Coccolithophorids - Coccolithophyceae

Coccolithophyceae (= Prymnesiophyceae; Fig. 2.23) are single-celled phytoplankton distinguished by special **calcium carbonate** plates (or scales) called coccoliths, which are also important microfossils. Coccolithophores are almost exclusively marine and are found in large numbers throughout the sunlight zone of the ocean.

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[21] Behrenfeld, M. J. and Boss, E. S. (2014). Resurrecting the ecological underpinnings of ocean plankton blooms. *Annual Review of Marine Science*, 6(1):167–194

The most abundant species of coccolithophore, *Emiliania huxleyi*, is found in temperate, subtropical, and tropical oceans. This makes *E. huxleyi* an important part of the planktonic base of a large proportion of marine food webs. It is also the fastest growing coccolithophore in laboratory cultures. It is studied for the extensive blooms it forms in nutrient depleted waters after the reformation of the summer thermocline and for its production of molecules known as alkenones that are commonly used by earth scientists as a means to estimate past sea surface temperatures.

Coccolithophores are of particular interest to those studying global climate change because as ocean acidity increases, their coccoliths may become even more important as a carbon sink. Furthermore, management strategies are being employed to prevent eutrophication-related coccolithophore blooms, as these blooms lead to a decrease in nutrient flow to lower levels of the ocean.

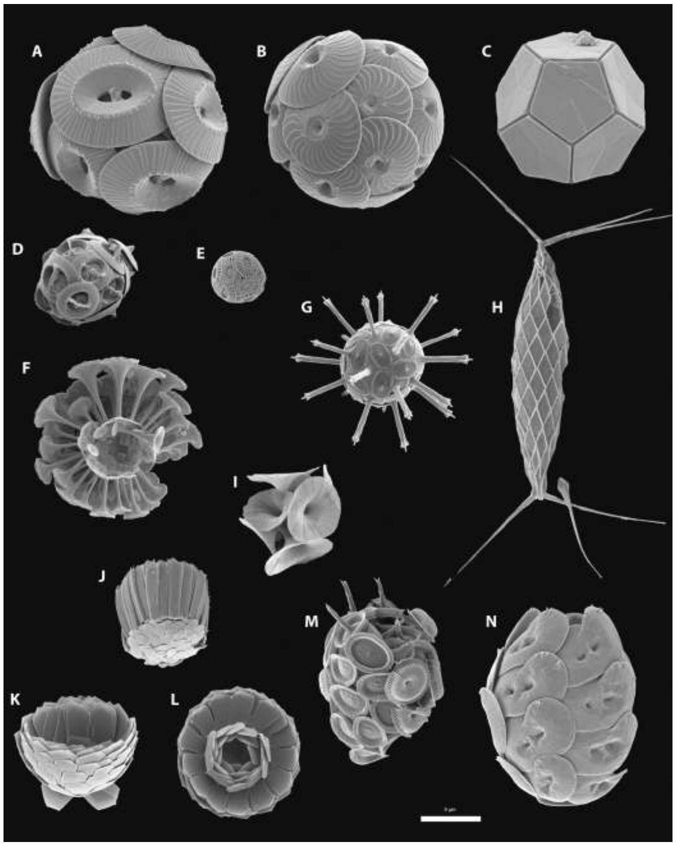

Figure 2.23: Diversity of coccolithophores: *Emiliania huxleyi* (E), the reference species for coccolithophore studies, is contrasted with a range of other species spanning the biodiversity of modern coccolithophores. All images are scanning electron micrographs of cells collected by sea-water filtration from the open ocean. (A to N) Species illustrated: (A) *Coccolithus pelagicus*, (B) *Calcidiscus leptoporus*, (C) *Braarudosphaera bigelowii*, (D) *Gephyrocapsa oceanica*, (F) *Discosphaera tubifera*, (G) *Rhabdosphaera clavigera*, (H) *Calciosolenia murrayi* (one spine broken off), (I) *Umbellosphaera irregularis*, (J) *Gladiolithus flabellatus*, (K and L) *Florisphaera profunda*, (M) *Syracosphaera pulchra*, and (N) *Helicosphaera carteri*. Scale bar: 5 µm.

Each cell contains two brown chloroplasts which surround the nucleus. The coccoliths are created inside the cell and while some species maintain a single layer throughout life only producing new coccoliths as the cell grows, others continually produce and shed coccoliths. Calcite formation begins in the Golgi complex where protein templates nucleate the formation of $CaCO_3$ crystals and complex acidic polysaccharides control the shape and growth of these crystals. As each scale is produced, it is exported in a Golgi-derived vesicle and added to the inner surface of the coccosphere. This means that the most recently produced coccoliths will lie beneath older coccoliths.

While the exact function of the coccosphere is unclear, many potential functions have been proposed. Most obviously coccoliths may protect the phytoplankton from predators. It also appears that it helps them to create a more stable pH. During photosynthesis carbon dioxide is removed from the water, making it more basic. Also calcification removes carbon dioxide, but the chemistry behind it leads to the opposite pH reaction; it makes the water more acidic. The combination of photosynthesis and calcification therefore even out each other regarding pH changes. In addition, these exoskeletons may confer an advantage in energy production, as coccolithogenesis seems highly coupled with photosynthesis.

Coccolithophores occur throughout the world's oceans. Their distribution varies vertically by stratified layers in the ocean and geographically by different temporal zones. While most modern coccolithophores can be located in their associated stratified oligotrophic conditions, the most abundant areas of coccolithophores where there is the highest species diversity are located in subtropical zones with a temperate climate. While water temperature and the amount of light intensity entering the water's surface are the more influential factors in determining where species are located, the ocean currents also can determine the location where certain species of coccolithophores are found.

The ratio between the concentrations of nitrogen, phosphorus and silicate in particular areas of the ocean dictates competitive dominance within phytoplankton communities. Each ratio essentially tips the odds in favour of either diatoms or other groups of phytoplankton, such as coccolithophores. A low silicate to nitrogen and phosphorus ratio allows coccolithophores to outcompete other phytoplankton species; however, when silicate to phosphorus to nitrogen ratios are high coccolithophores are outcompeted by diatoms. The increase in agricultural processes lead to eutrophication of waters and thus, coccolithophore blooms in these high nitrogen and phosphorus, low silicate environments.

One of the Prymnesiophyceae without coccoliths, *Phaeocystis*, is the organism forming the foam washed up on beaches after a bloom (Fig. 2.24).

Figure 2.24: *Phaeocystis* bloom in Nord-Pas-de-Calais.

Also, this may be as good a place as any other to mention that phytoplankton also suffers from viral attacks (Fig. 2.25). Their relevance for population dynamics, let alone biogeochemistry, is unclear.

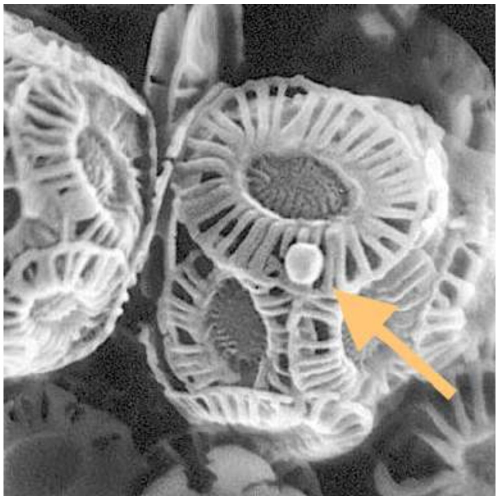

Figure 2.25: A coccolithovirus, *Emiliania huxleyi virus 86* (arrowed), infecting an *Emiliania huxleyi* coccolithophore. This giant marine virus possesses one of the largest known virus genomes.

2.4.7 *Dinoflagellates*

The dinoflagellates (Greek *δινος* "whirling" and Latin *flagellum* "whip"; Figs. 2.26, 2.27) are single-celled eukaryotes, mostly marine plankton, but they also are common in freshwater habitats. Many dinoflagellates are known to be photosynthetic, but a large fraction of these are in fact mixotrophic, combining photosynthesis with ingestion of prey (phagotrophy and myzocytosis).

In terms of number of species, dinoflagellates are one of the largest groups of marine eukaryotes, although this group is substantially smaller than diatoms. Some species are endosymbionts of marine animals and play an important part in the biology of coral reefs. Other dinoflagellates are unpigmented predators on other protozoa, and a few forms are parasitic (for example, *Oodinium* and *Pfiesteria*). Some dinoflagellates produce resting stages, called dinoflagellate cysts or dinocysts, as part of their life cycles.About 1,555 species of free-living marine dinoflagellates are currently described, of which all but some 200 are marine (free-living, as well as benthic).

A rapid accumulation of certain dinoflagellates (e.g. of *Gymnodinium* spp.) can result in a visible colouration of the water, colloquially known as "red tide" (a harmful algal bloom), which can cause shellfish poisoning if humans eat contaminated shellfish. Some dinoflagellates also exhibit bioluminescence (e.g. *Noctiluca scintillans* in the North Sea, Fig. 2.28).

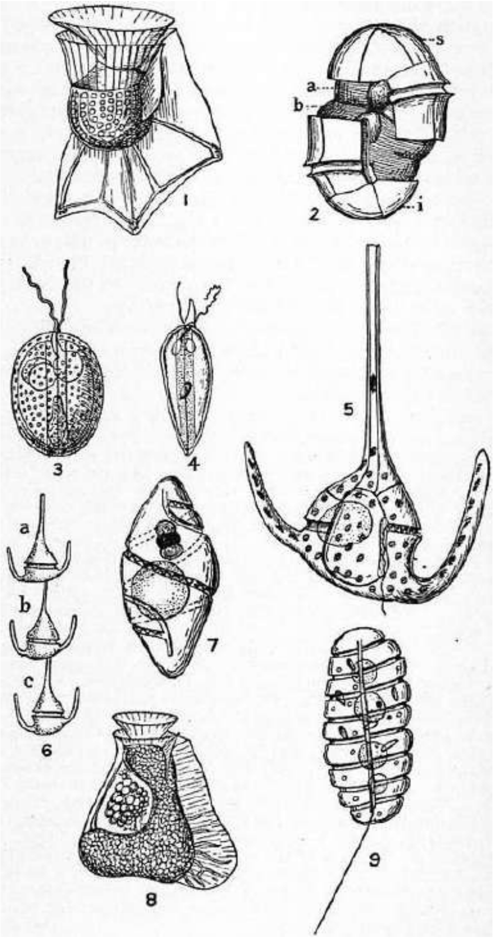

Figure 2.26: Some dinoflagellates: 1. *Ornithocercus*; 2. diagram; 3. *Exuviaeella*; 4. *Prorocentrum*; 5, 6. *Ceratium*; 7. *Pouchetia*; 8. *Citharistes*; 9. *Polykrikos*.

Figure 2.27: *Dinophysis acuminata*.

Dinoflagellates are unicellular and possess two dissimilar flagella arising from the ventral cell side. They have a ribbon-like transverse flagellum with multiple waves that beats to the cell's left, and a more conventional one, the longitudinal flagellum, that beats posteriorly. In armoured dinoflagellates, the complex cell coverings of overlapping **cellulose** plates create a sort of armour called the "theca" or "lorica". Although classified as eukaryotes, the dinoflagellate nuclei are not characteristically eukaryotic, as some of them lack histones and nucleosomes, and maintain continually condensed chromosomes during mitosis. This group, however, does contain typically eukaryotic organelles, such as Golgi bodies, mitochondria, and (three-membraned) chloroplasts.

The chloroplasts in most photosynthetic dinoflagellates are bound by three membranes, suggesting they were probably derived from some ingested algae. Most photosynthetic species contain chlorophylls a and c2, the carotenoid β-carotene, and a group of xanthophylls that appears to be unique to dinoflagellates, typically peridinin, dinoxanthin, and diadinoxanthin. These pigments give many dinoflagellates their typical golden brown color.

Three nutritional strategies are seen in dinoflagellates: phototrophy, mixotrophy, and heterotrophy. Phototrophs can be photoautotrophs or auxotrophs. Mixotrophic dinoflagellates are photosynthetically active, but are also heterotrophic. Facultative mixotrophs, in which autotrophy or heterotrophy is sufficient for nutrition, are classified as amphitrophic. If both forms are required, the organisms are mixotrophic sensu stricto. Some free-living dinoflagellates do not have chloroplasts, but host a phototrophic endosymbiont. A few dinoflagellates may use alien chloroplasts (cleptochloroplasts), obtained from food (kleptoplasty). Some dinoflagellates may feed on other organisms as predators or parasites.

Dinoflagellates of the Zooxanthellae are themselves endosymbionts inhabiting a great number of other invertebrates and protists, for example many corals, sea anemones, jellyfish, nudibranchs, the giant clam *Tridacna*, and several species of radiolarians and foraminiferans.

Figure 2.28: *Noctiluca scintillans*, a heterotrophic dinoflagellate that exhibits bioluminescence. Approx. 0.5 mm.

2.4.8 Others

The two remaining important groups of marine primary producers are both vascular plants, and thus strictly speaking in the same lineage as the green algae (which are paraphyletic, remember?): sea grasses and mangroves. Both occur only at the coast, but then so do many brown algae. While sea grasses are entirely under water, mangroves are not; indeed they are forest trees with their roots in the sea and show many adaptations common to trees of freshwater habitats (such as pneumatophores).

Seagrass

Seagrasses are the (only) flowering plants which grow in marine environments. There are about 60 species of fully marine seagrasses which belong to four families (Posidoniaceae, Zosteraceae, Cymodoceaceae and Hydrocharitaceae[22]), all in the order Alismatales (in the class of monocotyledons). Seagrasses evolved from terrestrial plants which recolonised the ocean 70 to 100 million years ago.

The name seagrass stems from the many species with long and narrow leaves, which grow by rhizome extension and often spread across large "meadows" (Fig. 2.29) resembling grassland; many species superficially resemble terrestrial grasses of the family *Poaceae*.

Figure 2.29: Turtle grass *Thalassia testudinum*, South Pigeon Creek estuary, southeastern San Salvador Island, eastern Bahamas.

To photosynthesize, seagrasses live in the submerged photic zone, and most occur in shallow and sheltered coastal waters anchored in sand or mud bottoms. Most species undergo submarine pollination and complete their life cycle underwater.

Genome analysis revealed that *Zostera marina* lost the entire repertoire of stomatal genes, genes involved in volatile compound biosynthesis and signaling (such as ethylene and terpenoids) as well as genes for ultraviolet protection and

[22] The first having only marine members, while that last also comprises several freshwater plants such as Canadian Waterweed *Elodea canadensis* or Common Frogbit *Hydrocharis morsus-ranae*.

phytochromes used for far-red sensing. Besides these gene losses, also gene gain events have been described, mostly involving the adjustment to full salinity and ion homeostasis.

Seagrass, sub- and intertidal Seagrasses occurring in the intertidal and subtidal zones are exposed to highly variable environmental conditions due to tidal changes. Seagrasses in the intertidal zone are regularly exposed to air and consequently experience extreme high and low temperatures, high photoinhibitory irradiance, and desiccation stress relative to subtidal seagrass. Such extreme temperatures can lead to significant seagrass dieback when seagrasses are exposed to air during low tide. Desiccation stress during low tide has been considered the primary factor limiting seagrass distribution at the upper intertidal zone.

In contrast, seagrasses in the subtidal zone (e.g. eelgrass, Fig. 2.30) adapt to reduced light conditions caused by light attenuation and scattering due to the overlaying water column and suspended particles. Seagrasses in the deep subtidal zone generally have longer leaves and wider leaf blades than those in the shallow subtidal or intertidal zone, which allows more photosynthesis, in turn resulting in greater growth. Seagrasses also respond to reduced light conditions by increasing chlorophyll content and decreasing the chlorophyll a/b ratio to enhance light absorption efficiency by using the abundant wavelengths efficiently.

Some relevant species: *Cymodocea nodosa*, *Halophila* spp., *Poseidonia oceanica* (Mediterranean Sea), , *Zostera marina*

Figure 2.30: Eelgrass *Zostera marina*, the most wide-ranging marine flowering plant in the Northern Hemisphere. Up to 1 m long.

Mangroves

Mangroves are salt-tolerant trees, also called halophytes, and are adapted to life in harsh coastal conditions. They contain a complex salt filtration system and complex root system to cope with salt water immersion and wave action. They are adapted to the low oxygen conditions of waterlogged mud.

Of the recognized 110 mangrove species, only about 54 species in 20 genera from 16 families constitute the "true mangroves", species that occur almost exclusively in mangrove habitats (Fig. 2.31). Demonstrating convergent evolution, many of these species found similar solutions to the tropical conditions of variable salinity, tidal range (inundation), anaerobic soils and intense sunlight. Plant biodiversity is generally low in a given mangrove. The greatest biodiversity occurs in the mangal of New Guinea, Indonesia and Malaysia.

Figure 2.31: Above and below water view at the edge of the mangal.

Adaptations to low oxygen Red mangroves (*Rhizophora mangle*, Fig. 2.32), which can survive in the most inundated areas, prop themselves above the water level with stilt roots and can then absorb air through pores in their bark (lenticels). Black mangroves (*Avicennia germinans*) live on higher ground and make many pneumatophores (specialised root-like structures which stick up out of the soil like straws for breathing) which are also covered in lenticels. Pneumatophores typically reach heights of 30 cm, and in some species over 3 m.

Figure 2.32: Free-standing red mangrove growing in shallow water in the Everglades National Park, Florida, USA.

Nutrient uptake Because the soil is perpetually waterlogged, little free oxygen is available. Anaerobic bacteria liberate nitrogen gas, soluble iron, inorganic phosphates, sulfides and methane, which make the soil much less nutritious. Pneumatophores allow mangroves to absorb gases directly from the atmosphere, and other nutrients such as iron, from the inhospitable soil. Mangroves store gases directly inside the roots, processing them even when the roots are submerged during high tide.

Limiting salt intake Red mangroves exclude salt from their xylem by having impermeable roots which are highly suberised (impregnated with the waxy suberin), acting as an ultra-filtration mechanism to exclude sodium salts from the rest of the plant. Analysis of water inside mangroves has shown 90% to 97% of salt has been excluded at the roots. Red mangroves can also store salt in cell vacuoles. White (*Laguncularia racemosa*) and grey mangroves (*Avicennia marina*) can secrete salts directly (Fig. 2.33); they have two salt glands at each leaf base (correlating with their name—they are covered in white salt crystals).

Figure 2.33: Salt crystals formed on *Avicennia marina* leaf.

Increasing survival of offspring In this harsh environment, mangroves have evolved a special mechanism to help their offspring survive. Mangrove seeds are buoyant and are therefore suited to water dispersal. Unlike most plants, whose seeds germinate in soil, many mangroves (e.g. red mangrove) are viviparous, meaning their seeds germinate while still attached to the parent tree (Fig. 2.34). Once germinated, the seedling grows either within the fruit (e.g. *Aegialitis*, *Avicennia* and *Aegiceras*), or out through the fruit (e.g. *Rhizophora*, *Ceriops*, *Bruguiera* and *Nypa*) to form a propagule (a ready-to-go seedling) which can produce its own food via photosynthesis.

The mature propagule then drops into the water, which can transport it great distances. Propagules can survive desiccation and remain dormant for over a year before arriving in a suitable environment. Once a propagule is ready to root, its density changes so the elongated shape now floats vertically rather than horizontally. In this position, it is more likely to lodge in the mud and root. If it does not root, it can alter its density and drift again in search of more favourable conditions.

Figure 2.34: Vivipary in *Rhizophora mangle*: seeds germinate while still on the parent tree.

3

Secondary (and higher) production

Copepod with eggs, by Kat Masback (NOAA)

In contrast to primary producers, secondary and higher producers of biomass use the organic matter already generated (directly or indirectly) by the primary producers to obtain matter and/or energy for their growth and reproduction. In short, secondary producers need to feed, i.e. they have to ingest (consume) dead or live organic matter (Fig. 3.1) into their bodies to get their energy and their carbon, fats, proteins, vitamins, and trace elements. They are therefore also called *heterotrophs*.[1]

Secondary productivity is than the amount of biomass produced by heterotrophs per unit time and space. In marine environments, secondary productivity is due to bacteria, archaea, protists, fungi, and animals all the way up to the largest, still extant species, the Blue Whale (*Balaenoptera musculus*).

Figure 3.1: A barracuda preying on a smaller fish.

3.1 Biochemistry of secondary production

After ingestion, secondary producers digest and assimilate the organic compounds into their bodies, and either synthesise from the broken-down parts (carbohydrates, amino acids, fatty acids) macromolecules for new tissue and cell processes (anabolism), or (2) channel them into the redox reactions of the biochemical pathways involved in the *catabolism* (Fig. 3.2) to utilise their stored energy.

When *classified by their energy*, electron acceptor, and carbon source, most secondary producers are **chemoorganoheterotrophs**[2] This classification includes many procaryotes, but also very many unicellular eukaryotes (protists), fungi, and of course all animals.[3]

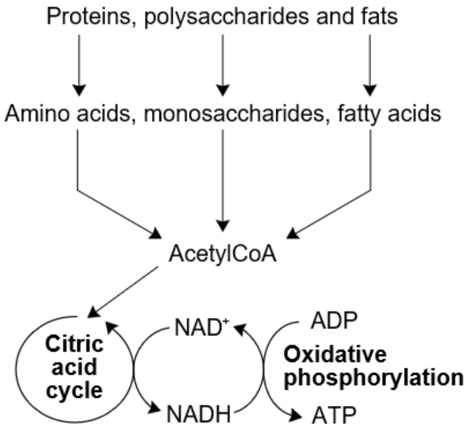

Figure 3.2: Schematic diagram of the catabolic pathways.

Citric acid cycle The citric acid cycle (CAC) – also known as the TCA cycle (tricarboxylic acid cycle) or the Krebs cycle[4] – is a series of chemical redox reactions used by all aerobic organisms including autotrophs) to release stored energy through the oxidation of acetyl-CoA derived from carbohydrates, fats, and proteins (Fig. 3.3). In addition, the cycle provides precursors of certain amino acids, as well as the reducing agents NADH and $FADH_2$, that are used in numerous other reactions. Its central importance to many biochemical pathways suggests that it was one of the earliest components of metabolism and may have originated abiogenically.

The name of this metabolic pathway is derived from the citric acid (a tricarboxylic acid, often called citrate, as this ionized form predominates at biological pH 7) that is used up and then regenerated by this sequence of reactions to complete the cycle. The CA cycle takes acetate (in the form of acetyl-CoA) and water, reduces the oxidising agents nicotinamide adenine dinucleotide (NAD^+) to NADH and flavin adenine dinucleotide (FAD) to $FADH_2$, and releases carbon dioxide. The NADH and $FADH_2$ generated by the citric acid cycle is fed into the oxidative phosphorylation (electron transport) pathway. The net result of these two closely linked pathways is the oxidation of nutrients to produce usable chemical

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[1] From Ancient Greek ἕτερος héteros = "other", because they feed on other organisms.)

[2] *chemo*: the energy source are organic compounds, *organo*: the electrons come from an organic source, *hetero*: the carbon source is also organic.

[3] *Photoheterotrophic* bacteria use light as energy source but ingested organic material for carbon.

[4] After Hans Adolf Krebs (⋆1900, †1981), one of the scientists involved in the cycles' description at the University of Sheffield.

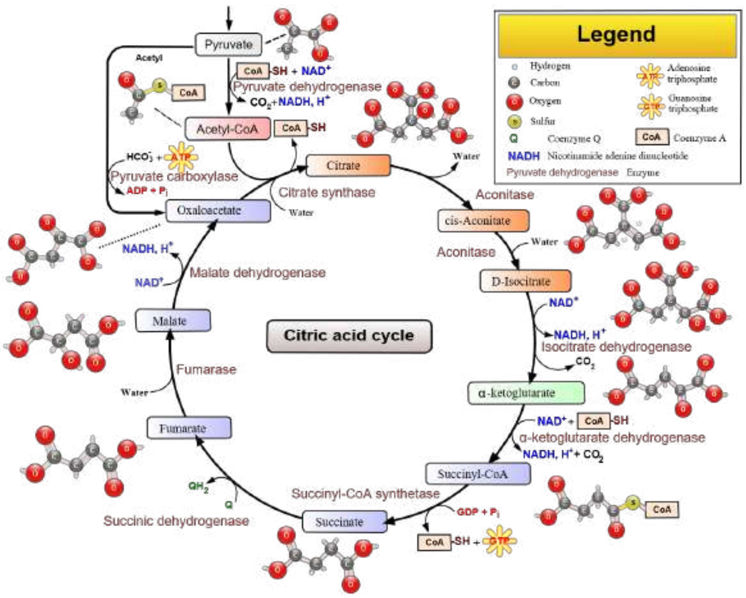

Figure 3.3: Overview of the citric acid cycle.

energy in the form of ATP (Fig. 3.2).

In eukaryotic cells, the citric acid cycle occurs in the matrix of the mitochondria. In prokaryotic cells, such as bacteria, which lack mitochondria, the citric acid cycle reaction sequence is performed in the cytosol with the proton gradient for ATP production being across the cell's surface (plasma membrane) rather than the inner membrane of the mitochondria.

The molecules NADH and $FADH_2$ can not only store a lot of energy but also release it very easily, making them efficient carriers to transfer electrons and energy from the organic compounds entering the citric acid cycle to the next step of the catabolism:

Oxidative phosphorylation Re-oxidation of NADH to NAD^+ by the NADH dehydrogenase and the transport of the donated electrons across the cell (prokaryotes) or mitochondrial inner (eukaryotes) membrane via the enzymes of the *respiratory electron transport chain* establishes a difference in electric charges between the mitochondrial matrix and intermembrane space (Fig. 3.4).

The electrical potential than allows the controlled diffusion of protons from the cytoplasm or the mitochondria matrix into inter membrane space. The electrons end up reducing O_2 to H_2O.

$$O_2 + 2\,NADH + 2\,H^+ \longrightarrow 2\,H_2O + 2\,NAD^+ \tag{3.1}$$

The potential difference between these two redox pairs is 1.14 volt, which is equivalent to ≈ -2600 kJ per 6 mol oxygen available energy from the oxidative phosphorylation. To not release that amount of energy in one go (which would be rather explosive and damaging to the cell)[5], the electron transfer to O_2 and the proton transfer across the membrane is a stepwise process involving four different reductase/oxidase enzyme complexes (Fig. 3.4) and up to eight redox reactions, of which three have enough redox potential to transfer electrons and protons.

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[5] Similar to a Knallgas reaction: 2 H_2 + O_2 → 2 H_2O

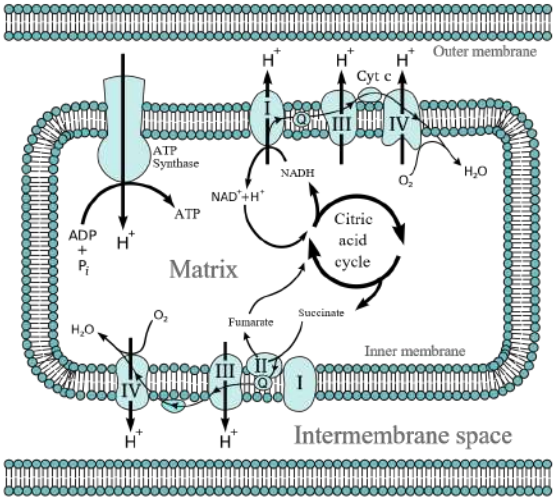

Figure 3.4: The electron transport chain in the cell is the site of *oxidative phosphorylation*. The figure depicts a mitochondrium within an eucaryotic cell.

As the protons flow back across the inner mitochondrial membrane through the pore of the *ATP synthase* (Fig. 3.5), the enzyme catalyses the phosphorylation of adenosine **di**phosphate (ADP) to adenosine **tri**phosphate (ATP).[6]

Some more ATP and NADH production already occurs in the steps of the *glycolysis*, the catabolic pathway that prepares glucose by transforming it into pyruvate and than acetate to enter the citric acid cycle.

The theoretical maximum yield of ATP through oxidation of one molecule of glucose in glycolysis, citric acid cycle, and oxidative phosphorylation is 38. In eukaryotes, two equivalents of NADH and four equivalents of ATP are generated in glycolysis, which takes place in the cytoplasm. Transport of two of these equivalents of NADH into the mitochondria consumes two equivalents of ATP, thus reducing the net production of ATP to 36. Furthermore, inefficiencies in oxidative phosphorylation due to leakage of protons across the mitochondrial membrane and slippage of the ATP synthase/proton pump commonly reduces the ATP yield to less than the theoretical maximum yield. The observed yields are, therefore, closer to ≈ 2.5 ATP per NADH and ≈ 1.5 ATP per UQH_2 (inside the respiration chain), further reducing the total net production of ATP to ≈ 30. An assessment of the total ATP yield with newly revised proton-to-ATP ratios provides an estimate of 29.85 ATP per glucose molecule.

ATP is an universal energy currency within cells for anabolic processes. The chemical energy bound in a ATP molecule by the ATP synthase during the oxidative phosphorylation can be released again in endergonic redox reactions,[7] which from assimilated organic food synthesise new macromolecules, cell components, and finally lead to the growth and reproduction of heterotroph organisms (Fig. 3.6).

Note though, that anabolism and catabolism are not strictly separated because many intermediary steps that prepare the assimilated food compounds to enter the citric acid cycle produce macro-

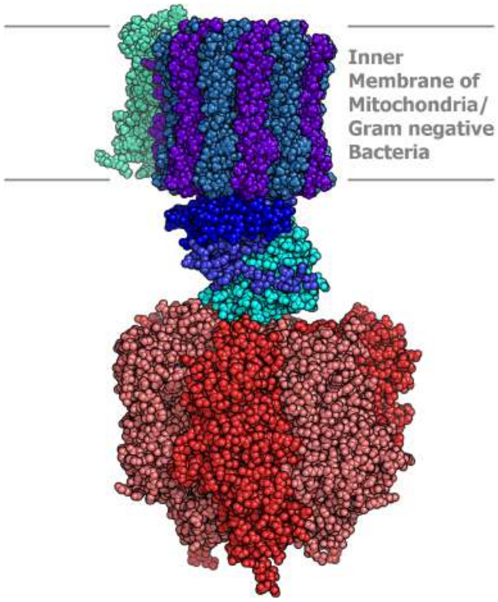

Figure 3.5: Molecular model of ATP synthase determined by X-ray crystallography. ADP binds to the reddish part of the enzyme that is sticking into the mitochondria matrix. Flow of H^+ ions (protons) through the bluish part (the pore) lets the reddish part rotate and this kinetic energy is used to bind a phosphor atom to ADP, synthesising ATP, which is then released from the binding sites.

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[6] That is:

$$\mathrm{ADP} + \mathrm{P_i} \longrightarrow \mathrm{ATP} + \mathrm{H_2O},\ \Delta G^\circ = 30.5\mathrm{kJ/mol} \tag{3.2}$$

[7] Reversing eqn (3.2):

$$\mathrm{ATP} + \mathrm{H_2O} \longrightarrow \mathrm{ADP} + \mathrm{P_i},\ \Delta G^\circ = -30.5\mathrm{kJ/mol} \tag{3.3}$$

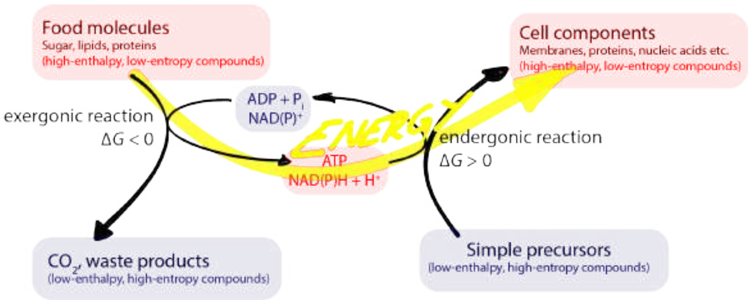

Figure 3.6: Use of ATP to drive the endergonic process of anabolism.

molecules for biosynthesis (especially amino acids and nucleotides for cellular protein and DNA/RNA synthesis).

In principle, together with the glycolysis and the citric acid cycle, the *oxidative phosphorylation* is a highly controlled and regulated, much slowed-down combustion reaction that releases the bound energy of the consumed biomass and makes it biologically available for further biochemical reactions within the cells.

Waste products Carbon dioxide and water (and nitrogen- and phosphorous-containing compounds from the respiration of amino acids, phospho-lipids and nucleotides) are the waste products of oxidative phosphorylation, in a reversed reaction to the photosynthetic one.

$$C_6H_{12}O_6 + 6\,O_2 \longrightarrow 6\,CO_2 + 6\,H_2O + \text{heat} \qquad (3.4)$$

The waste products are released into the water, where they may serve as the building blocks for primary production of biomass. The heat is respiratory loss of energy and usually dissipates irrevocably in the water, limiting the efficiency with which energy is transferred through the food web from primary producers to secondary and higher producers. Heterotrophy thus releases inorganic nutrients from organic matter in which it is biologically unavailable for primary producers and transports them along the global biogeochemical cycles, leading to re-mineralisation of biomass. Without the heterotrophs, algae would run quickly out of carbon dioxide and nutrients, or would have to rely on the much slower mobilisation of inorganic substances by physical processes alone (weathering of bedrock, volcanism).

Anaerobic secondary production Anaerobic organisms do not require oxygen for growth and as electron acceptor in the electron transport chain. Anaerobes may react negatively or even die when free oxygen is present. Anaerobes may be unicellular (e.g. protozoans, bacteria) or multicellular: Most fungi are obligate aerobes, requiring oxygen to survive, however some species, such as the Chytridiomycota that reside in the rumen of cattle, are obligate anaerobes; for these species, anaerobic respiration is used because oxygen will disrupt their metabolism or kill them. Deep waters of the oceans are a common anoxic environment in which the first true (obligate) anaerobic metazoans have been found

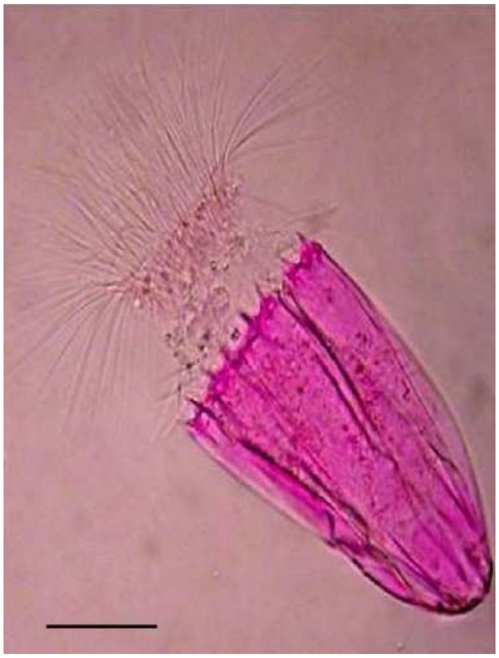

Figure 3.7: *Spinoloricus cinziae*, a metazoan that produces hydrogen, lacking mitochondria and instead using hydrogenosomes (Danovaro et al., 2010). Scale bar is 50 μm.

(Fig. 3.7).

Fermentation uses **organic** substances as electron acceptor instead of inorganic oxygen. Because organic compounds are of higher oxidative state and already store more energy, fermentation is usually yielding much less energy than oxidative phosphorylation.

There are many anaerobic fermentative reactions. Fermentative anaerobic organisms mostly use the lactic acid fermentation pathway (Fig. 3.10):

$$C_6H_{12}O_6 + 2\,\mathrm{ADP} + 2\,\mathrm{P_i} \longrightarrow 2\,\text{lactic acid} + 2\,\mathrm{ATP} + \text{heat} \quad (3.5)$$

The energy released in this equation is approximately 150 kJ per mol, which is conserved in regenerating two ATP from ADP per glucose. This is only 5% of the energy per sugar molecule that the typical aerobic reaction generates.

Plants and fungi (e.g., yeasts) in general use alcohol (ethanol) fermentation when oxygen becomes limiting:

$$C_6H_{12}O_6 + 2\,\mathrm{ADP} + 2\,\mathrm{P_i} \longrightarrow 2\,C_2H_5OH + 2\,\mathrm{ATP} + 2\,CO_2 + \text{heat} \quad (3.6)$$

The energy released is about 180 kJ per mol, which is conserved in regenerating two ATP from ADP per glucose. Anaerobic bacteria and archaea and some metazoa use these and also many other fermentative pathways, e.g., propionic acid fermentation, butyric acid fermentation, solvent fermentation, mixed acid fermentation, butanediol fermentation, Stickland fermentation, acetogenesis, or methanogenesis.

Several metazoan species that live in the sediments of the ocean bottoms (benthos) can use propionic and acetogenic fermentation processes facultatively,[8] such as the priapulid worm *Halicryptus spinulosus* (Fig. 3.8) or the bivalve mussels *Astarte borealis* (Fig. 3.9) and *Arctica islandica*. Facultative anaerobe species switch to anaerobic production in absence of oxygen, e.g. to survive anoxic intervals (periods of low oxygen concentrations) or to use anoxic habitats for shelter. Such anoxic conditions often arise in sediments when respiration of organic substances depletes O_2 but the slow diffusion from the water does not replenish it fast enough (Figs. 3.11 & 3.12). These organisms then trade off survival with growth and reproduction because of the low energy efficiency of the fermentation processes. Often, facultative anaerobe metazoans stay alive by using up stored metabolic products (in animals usually glycogen) and a slow but inefficient anaerobe metabolism allows a longer time in the anoxic sediment.

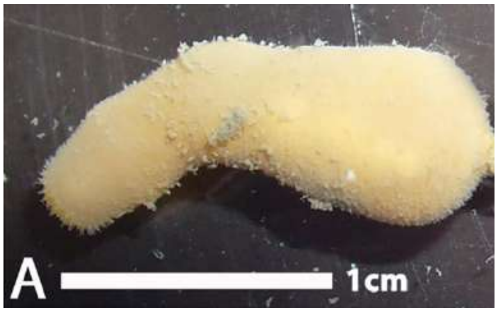

Figure 3.8: Adult with fully protruded introvert of the priapulid worm *Halicryptus spinulosus*.

Figure 3.9: *Astarte borealis*.

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[8] Oeschger, R. (1990). Long-term anaerobiosis in sublittoral marine invertebrates from the western baltic sea: *Halicryptus spinulosus* (priapulida), *Astarte borealis* and *Arctica islandica* (bivalvia). *Marine Ecology Progress Series*, 59:133–143; and Janssen, R., Wennberg, S. A., and Budd, G. E. (2009). The hatching larva of the priapulid worm *Halicryptus spinulosus*. *Frontiers in Zoology*, 6(1):8

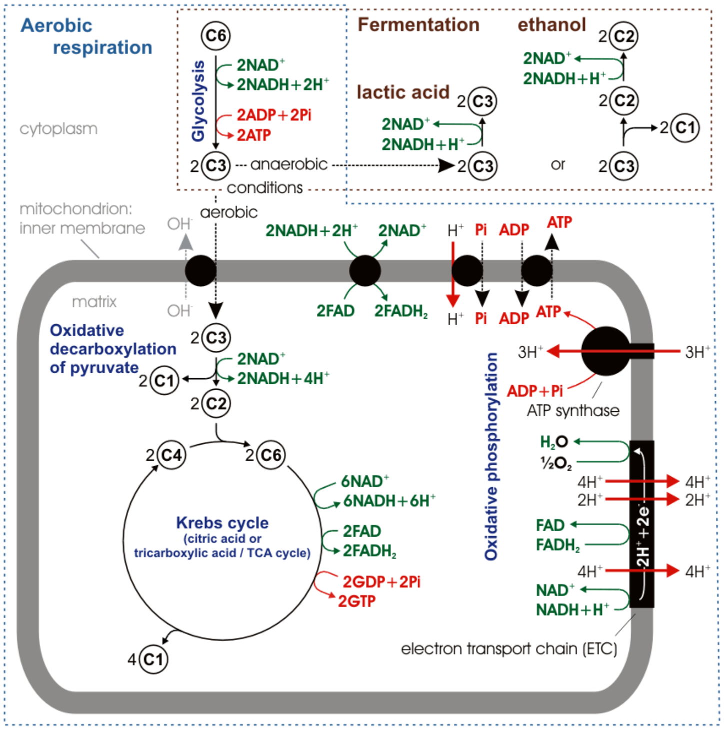

Figure 3.10: Comparison of a aerobic respiration and most known fermentation types in eukaryotic cells. Numbers in circles indicate counts of carbon atoms in molecules, C_6 is glucose $C_6H_{12}O_6$, C1 carbon dioxide CO_2. Mitochondrial outer membrane is omitted.

Anaerobic respiration is cellular respiration using **inorganic** electron acceptors other than molecular oxygen (O_2). Although oxygen is not the final electron acceptor, the process still uses a respiratory electron transport chain. Molecular oxygen is a high-energy oxidizing agent and, therefore, is an excellent electron acceptor. In **anaerobes**, other less-oxidizing inorganic substances such as nitrate (NO_3^-, *denitrification*,[9]) fumarate, sulphate (SO_4^{2-}, *sulphate respiration*), or sulphur (S) are used. These terminal electron acceptors have smaller reduction potentials than O_2, meaning that less energy is released per oxidized molecule. Therefore, anaerobic respiration is again less efficient than aerobic respiration via oxidative phosphorylation.

$$2\,NO_3^- + 10\,e^- + 12\,H^+ \longrightarrow N_2 + 6\,H_2O \tag{3.7}$$

$$SO_4^{2-} + 6\,e^- + 8\,H^+ \longrightarrow H_2S + 2\,H_2O + 2\,OH^- \tag{3.8}$$

The electrons e^- and protons H^+ come from the citric acid cycle via NADH.

Denitrifying and sulphate-reducing microorganisms (bacteria such as *Pseudomonas* spec., *Thiobacillus denitrificans*, *Paracoccus denitrificans* and *Desulfovibrio* spec., *Desulfotomaculatum nigrifans*, *Desulfobulbus propionicus*, *Desulfobacter postgatei*, *Desulfonema limnicola*, respectively) are important players in biogeochemical cycles and in ecosystems otherwise not very productive (see chapter 4).

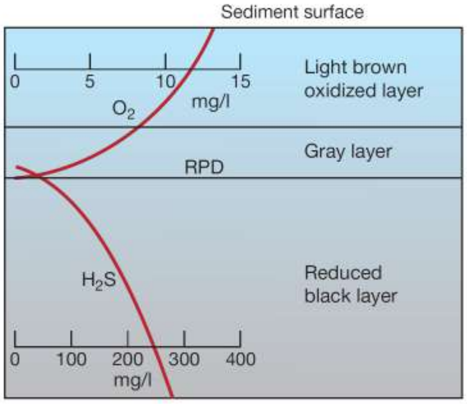

Figure 3.11: Cross section of the sediment near the sediment–water interface, showing the redox potential discontinuity (RPD), a boundary between oxidative and reducing processes. The diagram shows the concentration of oxygen and hydrogen sulphide. (from Levinton 2017)

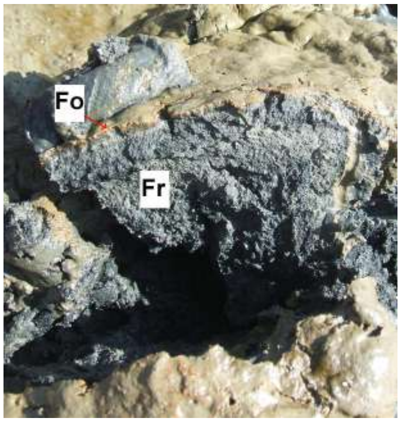

Figure 3.12: oxygenated (light-brownish, Fo) and anaerobe (dark-greyish, Fr) horizons in the Wadden Sea sediment. The lower horizon has high concentrations of hydrogen sulphite (H_2S), which produces the typical smell of rotten eggs when one digs into the sediment.

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[9] Middelburg, J. J., Soetaert, K., Herman, P. M. J., and Heip, C. H. R. (1996). Denitrification in marine sediments: A model study. *Global Biogeochemical Cycles*, 10(4):661–673

3.2 *Marine feeding ecology*

Heterotrophs require for their secondary production of biomass organic compounds to satisfy their metabolic demands for energy and matter (carbon hydrates, fat, proteins, trace elements, vitamins). They acquire this organic material by **feeding**, i.e. the ingestion of biomass generates by others into their own bodies.

Now, biomass can come in many different forms. It can be dead (e.g. faeces, corpses, plant litter eaten by detrivores)[10] or still alive, it can be dissolved in water (***dissolved*** *organic matter, DOM*) or exists in form of particles (***particulate*** *organic matter, POM*), i.e. in form of organisms or their left-overs. Living biomass can be algae and autotrophic bacteria (eaten by herbivores) or other heterotrophs (consumed by carnivores) or both (process of omnivory), living organisms can be consumed completely or only parts of them. Some heterotrophs may feed on everything (generalists), others have very specialised diets (specialists).

The possibility of classifying secondary producers by what, where, and how they feed is endless.[11] We here present three ways, but note that such typologies are not mutually exclusive.

3.2.1 *Osmotrophy vs. phagotrophy*

Osmotrophy[12] is a feeding mechanism involving the movement of ***dissolved*** *organic matter* (DOM) across the cell membrane for nutrition. Organisms that use osmotrophy are called osmotrophs. Osmotrophy is used by a diversity of organism, including bacteria, many species of protists and most fungi. Some macroscopic animals like molluscs, sponges, corals, brachiopods and echinoderms may use osmotrophic feeding as a supplemental food source.

Much organic material found in the oceans is of such a small size, between 0.22 - 7 µm, that it is dissolved in the water (Fig. 3.13). In the pelagial the concentration of dissolved organically derived carbon is roughly 0.4 to 2 g per litre sea water, in very nutrient-rich, productive ecosystems such as mangrove, estuary, tidal flat or upwelling regions often much higher (Fig. 3.15), resulting in a complex mosaic of DOM production in the oceans (Fig. 3.14), that of course also varies in time.[13]

However, much of DOM is not **biodegradable**, i.e. osmotrophs can either not ingest these substances or cannot metabolise them with their available enzymes. For example, the molecular structure of humic matter from eroded soils washed into the oceans (Fig. 3.15) is often too complex for osmotrophs' enzymes to break down and extract matter and energy from, at least not efficiently enough for a positive net energy balance. Other DOM substances such as polymers (conglomerations of organic and inorganic macromolecules) are too large for cell membrane enzymes to bind and transport into the cell. Sea-water concentrations of DOM compounds with a low molecular weight easily utilisable by bacteria (monomer sugars and

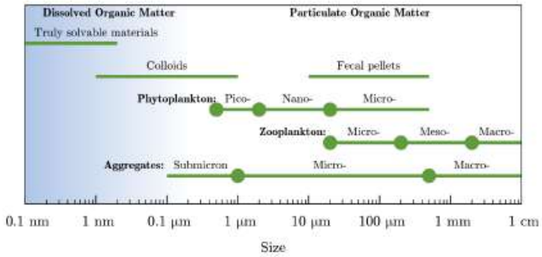

Figure 3.13: Size and classification of marine dissolved and particulate organic matter. DOM and POM are classified by size, but the demarcation is often quite variable. Sometimes whole organisms such bacteria or even crustacean zooplankton are included in POM.

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[10] Terminology often uses either the suffixes -vore, -vory, or -vorous from Latin *vorare*, meaning "to devour", or -phage, -phagy, or -phagous from Greek *φαγειν* (*phagein*), meaning "to eat".

[11] See here for a *List of feeding behaviours*

[12] Usually, the process is actively controlled and regulated by transport enzymes in the cell membrane and not purely passive diffusion along a concentration difference. The reference to osmosis in the Wikipedia article is thus quite misleading.

[13] DOM includes all dissolved organic matter, DOC only the fraction that contains carbon, which, to be honest, is probably near identical to DOM.

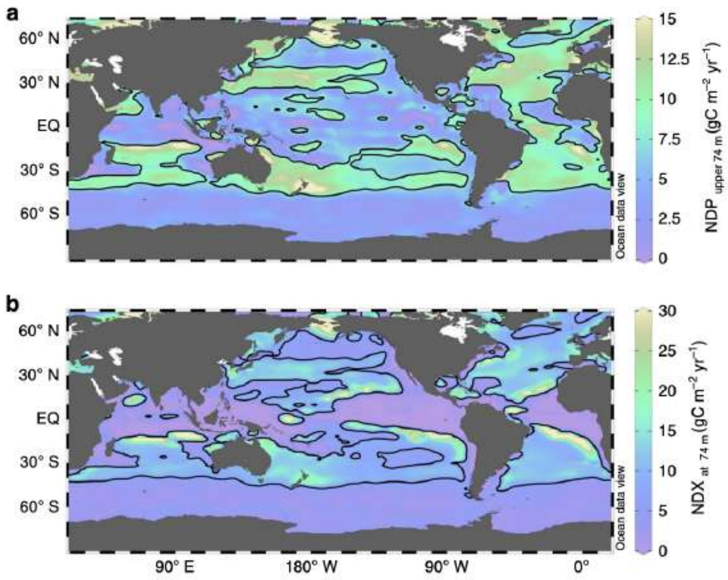


Figure 3.14: Net ocean DOC production and export fluxes: Net DOC production (NDP) in the upper 74 metres (a) and net DOC export (NDX) below 74 metres (b). At steady state, the global summation of NDX is equal to that of NDP, and is 2.31 ± 0.60 PgC yr.

amino acids mostly) occur more in the µg per litre range, polymer concentrations roughly in the mg range. To overcome the size limitation, several bacteria and protists but especially *marine fungi* secrete enzymes ("exoenzymes"; themselves contributing to DOM) into the surrounding water that break down organic substances outside the cells and then take in the smaller molecules.

The "autochthonous" (DOM produced **within** marine ecosystems) sources of DOM are many: phytoplankton (unicellular algae) exude carbon hydrates formed in excess during the dark reaction of photosynthesis, DOM leaches from macroalgae and sea grass, animals excrete it as waste from their metabolism or by *sloppy feeding* (e.g. when feeding releases body fluids or parts of the resource organism), viral lysis of bacteria cells produce DOM, and of course it arises during the decaying of dead organisms.

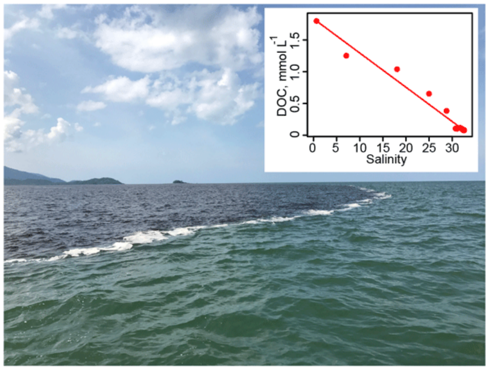


Figure 3.15: Peatland river water draining into coastal waters: The rivers carry high coloured dissolved organic matter (CDOM) concentrations, shown here interfacing with ocean shelf water. DOM produced **outside** and transported into marine ecosystems by rivers, groundwater and wind is called "allochthonous".

Osmotrophs ingest the dissolved organic compounds via *endocytosis* (Fig. 3.16). The process is controlled by enzymes in the cell membranes to which the food molecules bind and which transport substances from the surrounding water into the cytoplasm ("receptor-mediated endocytosis") or by proteins in the cell membrane that bud off small vesicles with the DOM-filled water into the cell ("pinocytosis"; Fig. 3.16).

Because of the involvement of proteins, these processes are often in a first approximation described by a *Michaelis-Menten enzyme reaction kinetic* (Fig. 3.17) for enzyme-substrate complexes:

$$v(S) = \frac{V_{max}S}{K_M + S}, \tag{3.9}$$

with S as the concentration of the dissolved food in the sea water (the "substrate" of the reaction), V_{max} is the maximal uptake (reaction) velocity, and K_M is the half-satiation constant, i.e. that

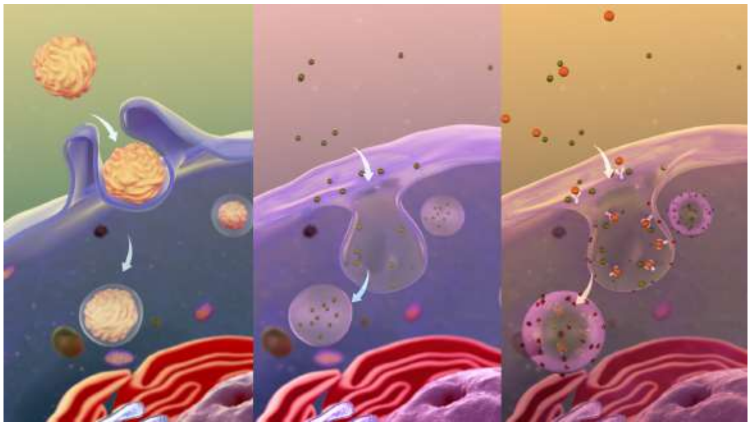


Figure 3.16: From left to right: phagocytosis, pinocytosis, receptor-mediated endocytosis. The latter two are used by osmotrophs, phagocytosis is the predominant ingestion form of protists. In phagocytosis, whole particles (the yellowish, rough-surfaced blobs) are surrounded by cell membrane protuberances and ingested. During pinocytosis ("cell drinking") the cell membrane engulfs small volumes of water with the DOM (the greenish dots) included, and the resulting vesicles bud off into the cytoplasm, where they dissolve, setting the dissolved organic matter free. In receptor-mediated endocytosis, some DOM molecules (the reddish dots) bind to proteins in the cell membrane (the whitish y-shaped forms), which induces the invagination of the cell membrane.

concentration of the food solution at half of V_{max}. This reaction is concentration-dependent and asymptotically approaches the maximum uptake velocity as the water DOM concentration[14] increases. At high food concentrations, the enzymes are satiated and more food does not lead to a higher ingestion.

The biochemical derivation of the Michaelis-Menten reaction (Eq. 3.9) makes several simplifying assumptions about how enzymes interact with their substrate. The first step in the derivation applies the law of mass action and thus of an equilibrium, which is reliant on free diffusion. However, in the environment of a living cell where there is a high concentration of proteins, the cytoplasm often behaves more like a viscous gel than a free-flowing liquid, limiting molecular movements by diffusion and altering reaction rates. Although the law of mass action can be valid in heterogeneous environments, it is more appropriate to model the cytoplasm as a fractal, in order to capture its limited-mobility kinetics. It is also important to remember that, while irreversibility is a necessary simplification in order to yield a tractable analytic solution, in the general case product formation is not in fact irreversible. The Michaelis–Menten equilibrium analysis is valid if the substrate reaches equilibrium on a much faster time-scale than the product is formed. The irreversibility assumption holds when the concentration of substrate is very much larger than the concentration of products and the energy released in the reaction is very large. In situations where neither of these conditions hold ((1) the concentration of the enzyme-substrate complex does not change on the time-scale of product formation, (2) the reaction is low energy, (3) a substantial pool of product exists), Eq. 3.9 breaks down, and more complex modelling approaches explicitly taking the forward and reverse reactions into account must be taken to understand the enzyme biology.

Phagotrophy[15] is the ingestion of ***particulate*** *organic matter, POM*, i.e. organic material in form of particles.[16] On the most basic level, particulate organic matter can be defined as both living and non-living matter of biological origin with a size of $\geq$ 0.2 μm in

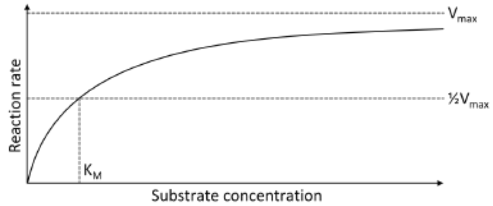


Figure 3.17: Michaelis–Menten saturation curve for an enzyme reaction showing the relation between the substrate concentration and reaction rate.

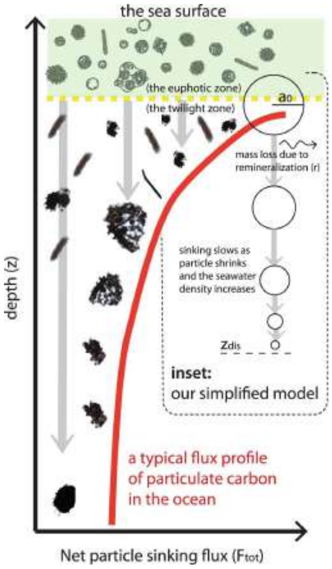
[14] The utilizable part of DOM.

[15] A term actually not very often used.

[16] Particulate organic carbon (POC) is a closely related term often used interchangeably with POM. POC refers specifically to the mass of carbon in the particulate organic material, while POM refers to the total mass of the particulate organic matter. In addition to carbon, POM includes the mass of the other elements in the organic matter, such as nitrogen, oxygen and hydrogen.

diameter, including anything from a small bacterium (0.2 µm) to blue whales (30 m) (Figs. 3.13 & 3.18).[17] Phagotrophs are thus all heterotrophs that feed on particles of dead or live biomass. That is a large group of organisms, ranging from protists that ingest particles with their *cytostome* or *pseudopodia* during phagocytosis (Fig. 3.16) to the Sperm Whale (*Physeter macrocephalus*), the largest toothed predator on Earth (Fig. 3.19).

Box 1: Marine Snow



In the deep ocean, *marine snow* is a continuous shower of mostly organic particulate detritus falling from the upper layers of the water column. Marine snow is made up of dead or dying animals and phytoplankton, protists, faeces. It is a significant means of exporting energy from the light-rich photic zone to the aphotic zone, a process which is referred to as the biological pump. Export production is the amount of organic matter produced in the photic ocean that is not recycled (remineralised) before it sinks into the aphotic zone. Because of the role of export production in the ocean's biological pump, it is typically measured in units of carbon (e.g. mg C m^{-2} d^{-1}).

As the origin of marine snow lies in activities within the productive photic zone, the prevalence of marine snow changes with seasonal fluctuations in photosynthetic activity and ocean currents. Marine snow can be an important food source for organisms living in the aphotic zone, particularly for organisms deep in the water column.

A simplified model of the flux of sinking POM is shown in the figure: Organic particles (spheres, initial radius a_0) produced within the sunlit euphotic zone (green region extending to z_{eu}) sink at a rate predicted by Stokes law. They slow as they reach greater depths due to their shrinking volume and increasing water density and would entirely disappear at z_{dis}.

Figure 3.18: Dead organic material formed in the photic zone ("marine snow") is falling from upper waters to the deep ocean.

Figure 3.19: A sperm whale and her calf off the coast of Mauritius. The calf has commensal remoras (suckerfish) attached to its body.

3.2.2 *The mode of ingestion*

Given the tremendous variability of forms that food resources[18] available to phagotrophic heterotrophs come in, it should not be surprising that how phagotrophs feed, i.e. their feeding mechanisms, are highly diverse, too. Here is an attempt to bring order to this diversity.[19]

Filter feeders They are a sub-group of suspension feeding animals that feed by straining suspended matter and food particles from water, typically by passing the water over and through a specialized filtering structure. Some animals that use this method of feeding are clams, krill, sponges, baleen whales, and many fish (including some sharks). Some birds,

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[17] And from the same Wikipedia article: "Particulate organic matter (POM) is a fraction of total organic matter operationally defined as that which does not pass through a filter pore size that typically ranges in size from 0.053 and 2 mm." We prefer and hence use here the more inclusive definition given in the text.

[18] A resource is a source or supply from which a benefit is produced and that has some utility, so food in whatever form is a resource required by protozoans and animals for survival, growth and reproduction. This contrasts with another, more narrow notion of resources in biology as inorganic substances required by autotrophs.

[19] List of aquatic feeding mechanisms in fish.

such as flamingos and certain species of duck, are also filter feeders. Filter feeders can play an important role in clearing water, and are therefore considered ecosystem engineers.

Filter feeding in the sense of holding a sieve into the water and **passively** catching everything that floats in there, is actually rather rare among marine organisms. One such examples are sea lilies or *Crinoids* (Fig. 3.20) that filter plankton and small particles of detritus from the sea water flowing past them with their feather-like arms. The arms are raised to form a fan-shape which is held perpendicular to the current. Mobile crinoids move to perch on rocks, coral heads or other eminences to maximise their feeding opportunities. The food particles are caught by the primary (longest) tube feet, which are fully extended and held erect from the pinnulae, forming a food-trapping mesh, while the secondary and tertiary tube feet are involved in manipulating anything encountered (Fig. 3.21).

Figure 3.20: Crinoid on the reef of Batu Moncho Island.

Figure 3.21: Two arms of a feather star (Echinmdermata: Crinoidea) with pinnules and tube feet outstretched.

More common to capture food particles is the **active** creation of water movement directed towards filtering structures or the active application of pressure to press some water through the filtering structures (Fig. 3.22). The latter mechanism is for examples used by *krill* (Euphausiacea, small decapod crustaceans of usually 1 - 2 cm sizes (some species can get up to 15 cm) that live predominantly pelagic in sometimes very large populations in all oceans.

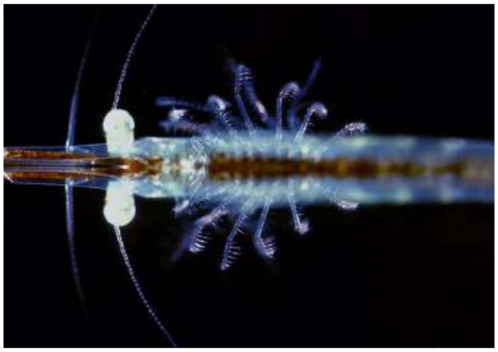

Figure 3.22: The filter basket of a mysid.

Krill has developed an extremely fascinating and in nature unique filtering apparatus: The anterior six legs (thoracopods) are very long and are carried in a defolded status below the body obliquely anterior/ventral, forming a fine meshed *feeding basket*. Under normal plankton concentrations the krill pushes its open feeding basket over some dm with high velocity of about 10 cm per second through the water, opened only a small slit on its front end. The plankton mass collected on its inner side is then under repeatedly opening and closing of the feeding basket "combed" towards the mouth opening. This is carried out with some rows of strong comb setae, interlocking in right angle into the filtering setae of the anterior thoracopods (Fig. 3.23). Under high plankton concentrations the krill is hovering at the spot and pumps continuously with its feeding basket.

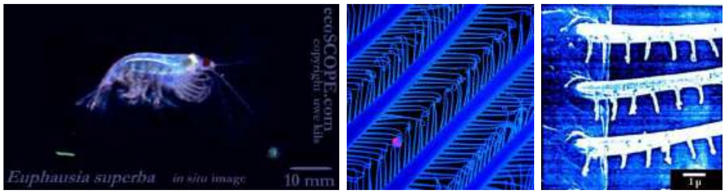

Figure 3.23: *Left*: *In situ* image of a fast swimming krill. Under the body the swimming legs (**pleopods**) are beating heavily, the feeding basket, formed by the **thoracopods**, is opened. In front of the feeding basket a red object is visible, probably a copepod. In the lower right corner you see a spit ball and in the left lower corner a faecal string. *Centre*: Magnified electron microscopic image of details of the feeding basket. On the 1st-degree filter setae in v-shape are 2nd degree filter setae. The small ball, probably a bacteria, is only 1 µm in size. *Right*: Again magnified. On the 2nd degree filter setae there are further 3rd degree setae arranged so that the distance left open in some areas is only 1 µm (Images by F. Alberti and U. Kils.)

There has been a lot of discussion whether the water in spite of its high viscosity (especially at the small sizes of µm range, see Reynolds number) can actually penetrate the finest filtering areas; probably the pumping and the high travel velocity deliver the necessary pressure for this feeding mode.

The same principle of pressing water with force through a mesh that krill uses to feed is also employed by their own predators: lunge-feeding *baleen whales*.[20] Lunge feeding is an extreme feeding method in which the whale accelerates from below a "bait ball" [21] to a high velocity and then opens its mouth to a large gape angle. This action generates the water pressure required to expand the whale's mouth and engulf and filter a huge amount of water and food. Lunge feeding by rorquals, a family of huge baleen whales that includes the blue whale, is said to be the largest biomechanical event on Earth. Lunge-feeders expand the volume of their jaw to a volume bigger than the original volume of the whale itself (Fig. 3.24).

To do this, the mouth inflates, which causes the throat pleats to expand, increasing the amount of water that the mouth can store. Just before they ram the bait ball, the jaw swings open at almost a 90° angle and bends which lets in more water. To prevent stretching the mouth too far, lunge-feeders have a sensory organ located in the middle of the jaw to regulate these functions. Then they must decelerate. This process takes a lot of mechanical work, and is only energy-effective when used against a large bait ball. Lunge feeding is more energy intensive than skim-feeding due to the acceleration and deceleration required.[22]


Figure 3.24: Pair of humpback whales lunge feeding.

Both lunge- and ram-feeding Baleen whales press than with the help of their tongue the gathered water through their filtering structures, the *baleen plates* (Fig. 3.25). The baleen plates are keratin structures of the gum that reach into the mouth and carry fine hairs which retain the prey suspended in the engulfed sea water.


Figure 3.25: Baleen hair is attached to each baleen plate.

Skim or ram filter feeding is a method of feeding underwater in which the predator moves forward with its mouth open, engulfing the prey along with the water surrounding it. During ram feeding, the prey remains fixed in space, and the predator moves its jaws past the prey to capture it. The motion of the head may induce a bow wave in the fluid which pushes the prey away from the jaws, but this can be avoided by allowing water to flow through the jaw. This can be accomplished by means of a swept-back mouth, as in baleen whales, or by allowing water to flow out through the gills with their *gill rakers* (Fig. 3.26) functioning as filtering structures, as in sharks and filter-feeding (often planktivorous) fish like the various herring species (*Clupeus* spec.). Herrings often hunt copepods. If they encounter copepods in high concentrations, the herrings switch to ram feeding. They swim with their mouth wide open and their opercula fully expanded. Every several feet, they close and clean their gill rakers for a few milliseconds.

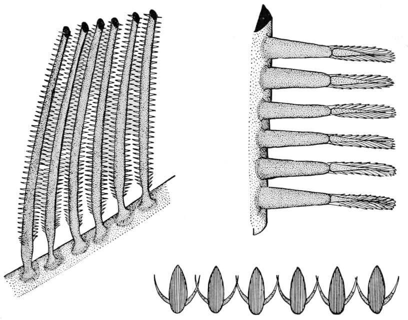
Figure 3.26: Top left: Gill rakers attached to the branchial arch, showing the projecting rows of hooks (×50). Top right: Hooks attached to the gill-raker (×180). Bottom: Gill rakers in cross section, showing angle at which hooks project from their point of attachment (water flow is downwards).

Many other marine filter feeders do not press gathered sea water through some filters but instead actively create water currents and direct that water towards their filtering structures. This **second** filter feeding mechanism is especially common among sessile or-

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[20] There are two types of feeding behaviours among Baleen whales: skim-(or ram) feeding and lunge-feeding but some species do both depending on the type and amount of food. Lunge-feeders feed primarily on swarms of krill, though some smaller lunge feeders (e.g. minke whales) also prey on schools of fish. Skim-feeders, like bowhead whales, feed upon primarily smaller plankton such as copepods.

[21] The term *bait ball* mainly describes a school of small fish, but can also mean a swarm of krill or zooplankton

[22] Skim- (ram-) feeders swim with an open mouth, filling it with water and prey. The "skimming" may take place on the surface, underwater, or even at the ocean's bottom, indicated by mud occasionally observed on right whales' bodies.

ganisms which can not move to engulf a volume of water, such as bivalves, tunicates or sponges.

Bivalves include the clams, oysters, cockles, mussels, scallops, and numerous other families that live in saltwater (see section 3.4, p. 91; Fig. 3.9), as well as a number of families that live in freshwater. The majority of bivalves are filter feeders. They feed mainly on phytoplankton and other microplankton free-floating (suspended) in seawater. Water is drawn into the shell from the posterior ventral surface of the animal. The water is then brought into the branchial chamber by the beating of cilia located on the gills for ciliary-mucus feeding. The water passes upwards through the gills, and doubles back to be expelled just above the intake. The labial palps finally funnel the food into the mouth, where digestion begins. In burrowing species, there may be two elongated, retractable siphons reaching up to the seabed, one each for the inhalant and exhalant streams of water. The gills of filter-feeding bivalves are known as **ctenidia** (Fig. 3.27) and have become highly modified to increase their ability to capture food.

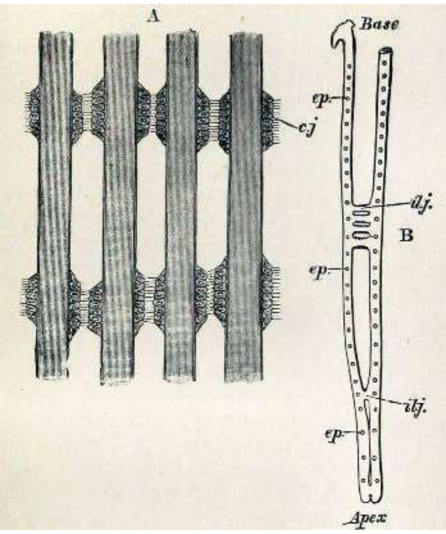

Figure 3.27: Four filaments of the gills (ctenidia) of the blue mussel (*Mytilus edulis*) a) part of four filaments showing ciliated interfilamentar junctions (cj) b) diagram of a single filament showing the two lamellae connected at intervals by interlamellar junctions (ilj) and the position of the ciliated interfilamentar junctions (cp)

For example, the cilia on the gills, which originally served to remove unwanted sediment, have become adapted to capture food particles, and transport them in a steady stream of mucus to the mouth. The filaments of the gills are also much longer than those in more primitive bivalves, and are folded over to create a groove through which food can be transported. The structure of the gills varies considerably, and can serve as a useful means for classifying bivalves into groups.

Sponges, the members of the phylum Porifera (meaning "pore bearer"), are a basal Metazoa (animal) clade (see p. 81). They are multicellular organisms that have bodies full of pores (called **ostia**) and channels allowing water to circulate through them, consisting of jelly-like mesohyl sandwiched between two thin layers of cells (Fig. 3.28). For feeding they most rely

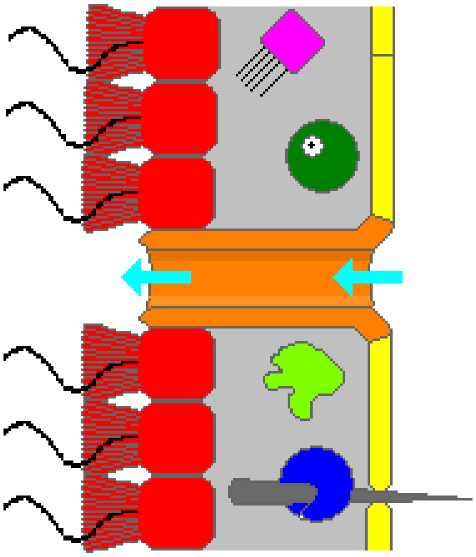

Figure 3.28: Main cell types of Porifera. The orange structure is an ostia, a pore between the inner part and the water.

on maintaining a constant water flow, created by the beating of the flagella of the inner *choanocytes*, through their bodies to obtain food and oxygen and to remove wastes. Sponges are predominantly detrivores and filter dead organic particles out of the water flowing through them. Particles larger than 50 µm cannot enter the ostia and *pinacocytes* (Fig. 3.28) consume them by phagocytosis (engulfing and intracellular digestion). Particles from 0.5 µm to 50 µm are trapped in the ostia, which taper from the outer to inner ends. These particles are consumed by pinacocytes or by archaeocytes, which partially extrude themselves through the walls of the ostia. Bacteria-sized particles, below 0.5 µm, pass through the ostia and are caught and consumed by choanocytes. Since the smallest particles are by far the most common, choanocytes typically capture 80 of a sponge's food supply. Archaeocytes transport food packaged in vesicles from cells that directly digest food to those that do not.

Tunicates are marine filter feeders with a water-filled, sac-like body structure and two tubular openings, known as siphons, through which they draw in and expel water (Fig. 3.29; see p. 100). During their respiration and feeding, they take in water through the incurrent (or inhalant) siphon and expel the filtered water through the excurrent (or exhalant) siphon.

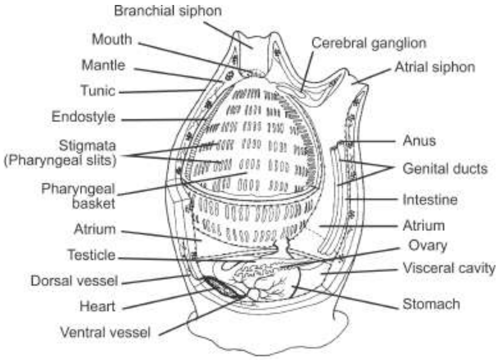

Figure 3.29: Internal anatomy of a generalised tunicate.

Nearly all tunicates are suspension feeders, capturing planktonic particles by filtering sea water through their bodies. Ascidians are typical in their digestive processes, but other tunicates have similar systems. Water is drawn into the body through the buccal siphon by the action of cilia lining the gill slits. To obtain enough food, an average ascidian needs to process one body-volume of water per second. This is drawn through a net lining the pharynx which is being continuously secreted by the endostyle. The net is made of sticky mucus threads with holes about 0.5 µm in diameter which can trap planktonic particles including bacteria. The net is rolled up on the dorsal side of the pharynx, and it and the trapped particles are drawn into the oesophagus. The gut is U-shaped and also ciliated to move the contents along. The stomach is an enlarged region at the lowest part of the U-bend. Here, digestive enzymes are secreted and a pyloric glandy adds further secretions. After digestion, the food is moved on through the intestine, where absorption takes place, and the rectum, where undigested remains are formed into faecal pellets or strings. The anus opens into the dorsal or cloacal part of the peribranchial cavity near the atrial siphon. Here, the faeces are caught up by the constant stream of water which carries the waste to the exterior. The animal orientates itself to the current in such a way that the buccal siphon is always upstream and does not draw in contaminated water.

The filtering performance and thus their impact on their food source and the ecosystem of filter feeders is often described by the filtration or **clearance rate** (Fig. 3.30), which expresses the volume of water cleared of food particles (non-food particles are often expelled before ingestion) per unit time and biomass of filter feeders, e.g. in $\mathrm{l\,h^{-1}\,g^{-1}}$.

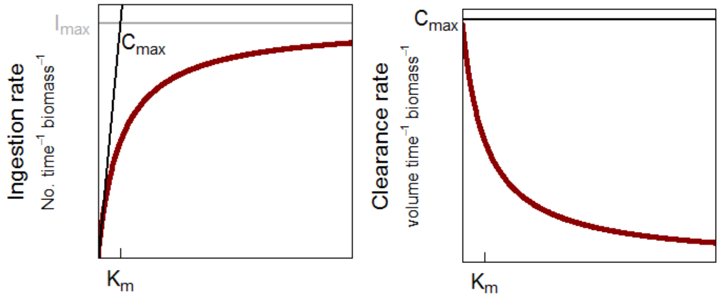

Figure 3.30: Ingestion and clearance rates of filter feeders as function of food particle concentration, R. *Left*: Ingestion rate $I(R)$ (red) can be described by a Michaelis-Menten formula (eq. 3.9) with I_{max} as the maximal ingestion rate at high food densities and K_m as the food concentration where $I_{max}/2$. *Right*: The clearance rate is the ingestion rate divided by the food particle concentration, $I(R)/R$. At high particle densities, the filtering apparatus and/or the digestive tract are working at maximum capacity and many food particles are simply egested or the filtering structures work slower.

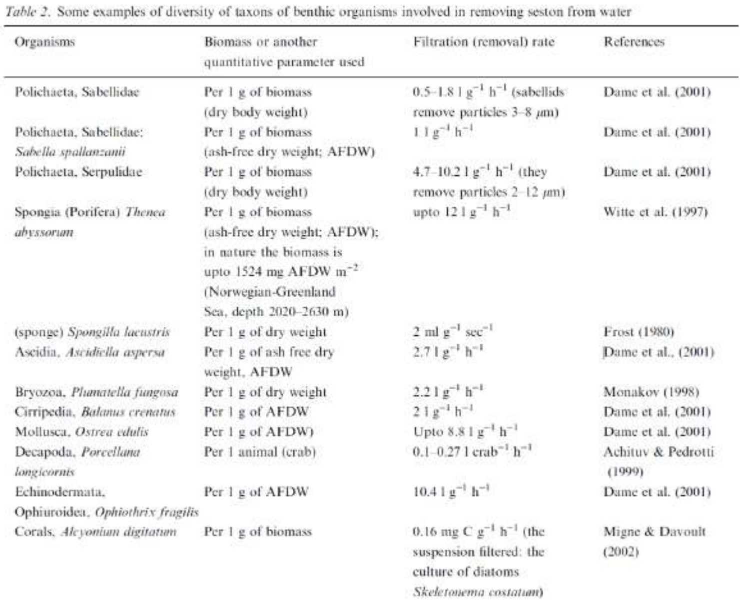

Table 2. Some examples of diversity of taxons of benthic organisms involved in removing seston from water

Organisms	Biomass or another quantitative parameter used	Filtration (removal) rate	References
Polichaeta, Sabellidae	Per 1 g of biomass (dry body weight)	0.5–1.8 l g^{-1} h^{-1} (sabellids remove particles 3–8 μm)	Dame et al. (2001)
Polichaeta, Sabellidae: *Sabella spallanzanii*	Per 1 g of biomass (ash-free dry weight; AFDW)	1 l g^{-1} h^{-1}	Dame et al. (2001)
Polichaeta, Serpulidae	Per 1 g of biomass (dry body weight)	4.7–10.2 l g^{-1} h^{-1} (they remove particles 2–12 μm)	Dame et al. (2001)
Spongia (Porifera) *Thenea abyssorum*	Per 1 g of biomass (ash-free dry weight; AFDW); in nature the biomass is upto 1524 mg AFDW m^{-2} (Norwegian-Greenland Sea, depth 2020–2630 m)	upto 12 l g^{-1} h^{-1}	Witte et al. (1997)
(sponge) *Spongilla lacustris*	Per 1 g of dry weight	2 ml g^{-1} sec^{-1}	Frost (1980)
Ascidia, *Ascidiella aspersa*	Per 1 g of ash free dry weight, AFDW	2.7 l g^{-1} h^{-1}	Dame et al., (2001)
Bryozoa, *Plumatella fungosa*	Per 1 g of dry weight	2.2 l g^{-1} h^{-1}	Monakov (1998)
Cirripedia, *Balanus crenatus*	Per 1 g of AFDW	2 l g^{-1} h^{-1}	Dame et al. (2001)
Mollusca, *Ostrea edulis*	Per 1 g of AFDW)	Upto 8.8 l g^{-1} h^{-1}	Dame et al. (2001)
Decapoda, *Porcellana longicornis*	Per 1 animal (crab)	0.1–0.27 l $crab^{-1}$ h^{-1}	Achituv & Pedrotti (1999)
Echinodermata, Ophiuroidea, *Ophiothrix fragilis*	Per 1 g of AFDW	10.4 l g^{-1} h^{-1}	Dame et al. (2001)
Corals, *Alcyonium digitatum*	Per 1 g of biomass	0.16 mg C g^{-1} h^{-1} (the suspension filtered: the culture of diatoms *Skeletonema costatum*)	Migne & Davoult (2002)

Figure 3.31: Clearance rates of various selected filter feeders (Ostroumov, 2005).

Even if a single filter feeder may only clear a few millilitre per hour[23] (Fig. 3.31), the sheer mass of all animals together can lead to impressive clearance rates of whole filter feeder communities, highlighting the important role of filter feeding in marine ecosystems. The net primary production (BPP − respiration) of phytoplankton in the Southern North Sea is reduced by about 10% by the filtration of the blues mussel population alone[24] and historically, the *now much reduced oyster populations* of Chesapeake Bay/USA could filter the whole Bay volume (68,137,200,000,000 ≈ 68 trillion l) in 2-4 days.[25] Filtration by filter feeders improves water quality by the removal of suspended organic particles that make water turbid (and increase light attenuation, limiting primary productivity). Also non-ingested particles are often removed from the water, when for example bivalves form pellets of unwanted material that more quickly sink down.

Overall, filter feeding is a very common feeding mode in marine

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[23] The clearance rate varies of course with species and body mass, it depends on food particle size and density, on external conditions like water temperature, salinity, pH, the presence of natural enemies of the filter feeder etc.

[24] Lemmen, C. (2018). North Sea ecosystem-scale model-based quantification of net primary productivity changes by the benthic filter feeder *Mytilus edulis*. *Water*, 10:1527

[25] I assume the US source means trillion = 10^{12}, i.e. on the short scale as it is used in the US. A trillion in Germany is 6 zeros longer = 10^{18}.

environments due to the often high concentrations of POM found there. Generally, filter feeders are rather non-selective in what food particles they capture. Food selection comes either later during ingestion (e.g. many bivalves can sort through the filtered material with their cilia to discard unwanted material) or before the attack, i.e. they base the decision to filter on the presence and density of desired food items (whales only show lunge-feeding behaviour when bait balls like krill swarms or fish schools actually occur).

Grazers and scrapers These are marine animals that feed by rasping (scraping) algae and other organisms from stones and other surfaces, they are also called "grazer-scrapers".[26] Scraper-grazers are, among many others, marine gastropods molluscs (sea snails and slugs) but also some bivalves,[27] large zooplankton such krill that scrape algae off ice covering the water, and echinoderms such as sea urchins.

Marine *gastropod* molluscs (as most molluscs) have muscular mouths with *radulae*, "tongues", bearing many rows of chitinous teeth, which are replaced from the rear as they wear out (Fig. 3.32). The radula primarily functions to scrape bacteria and algae off rocks, and is associated with the odontophore, a cartilaginous supporting organ. The radula is unique to the molluscs and has no equivalent in any other animal. Molluscs' mouths also contain glands that secrete slimy mucus, to which the food sticks. Beating cilia (tiny "hairs") drive the mucus towards the stomach, so the mucus forms a long string called a "food string".

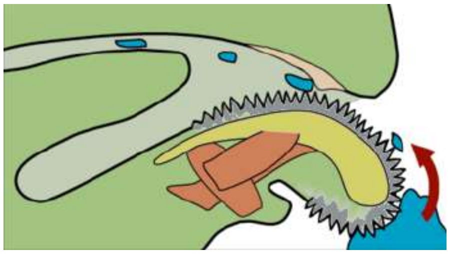


Figure 3.32: Diagrammatic transverse view of the buccal cavity of a gastropod, showing the radula and how it is used. The rest of the body of the snail is shown in green. The food is shown in blue. Muscles that control the radula are shown in brown. The surface of the radular ribbon, with numerous teeth, is shown as a zig-zag line.

Antarctic krill (*Euphausia superba*) have six rows of unusually strong, conical setae at the distal parts of the anterior thoracopods. They can swim in an upside down position obliquely under the ice or are working the side and bottom areas of ice caves to scrape off algae growing here with these setae (Fig. 3.33).

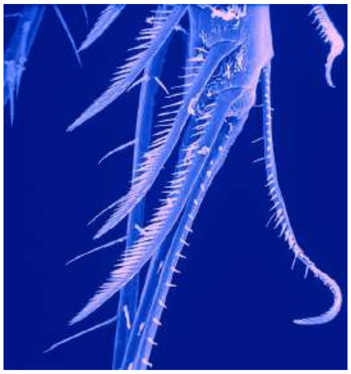


Figure 3.33: Three comb setae at the distal part of a thoracopod, strong formed setae, used by krill to scrape off ice algae from the undersurface of ice floes (Image: F. Alberti and U. Kils).

The jaw apparatus of *sea urchins* consists of five strong arrow-shaped plates known as pyramids, the ventral surface of each of which has a tooth band with a hard tooth pointing towards the centre of the mouth (Fig. 3.34). Specialised muscles control the protrusion of the apparatus and the action of the teeth, and the animal can grasp, scrape, pull and tear periphyton, bacteria, macroalgae such as kelps and slow moving or sessile animals from surfaces to feed upon.

Figure 3.34: Dentition of a sea urchin, known as the "Aristotle's Lantern".

Grazer-scrapers live necessarily where their non-motile or sessile food lives, i.e. close to or on surfaces such as rocky, sandy or muddy sediments of the benthos, on corals, or on artificial substrate like the foundations of offshore wind turbines or harbour quays. But they also occur close to or on free-floating substrates like *driftwood* or ship hulls etc.

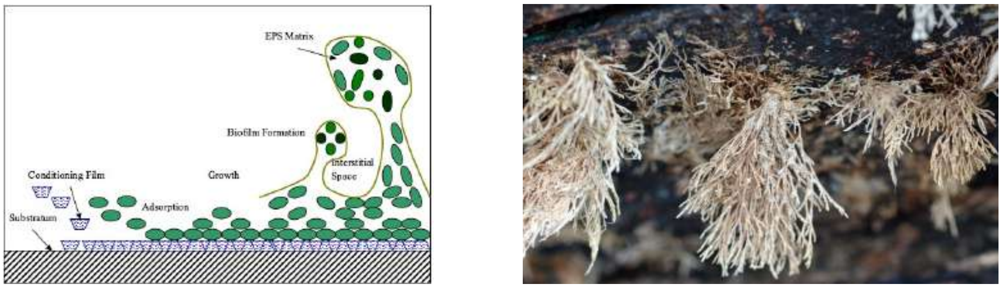
[26] Again the terminology is confusing: in terrestrial ecology, grazers are animals that feed on grasses and herbs, in limnology (freshwater ecology) grazers are herbivorous zooplankton that ingest whole phytoplankton cells, and in marine ecology grazers are those heterotrophs that feed on organisms growing on surfaces, e.g. bacterial or algal biofilms, mats or stands of macroalgae (e.g. kelps) and seagrass etc.

[27] The primitive bivalves of the *Protobranchia* scrape detritus from the seabed, and this may be the original mode of feeding used by all bivalves before the gills became adapted for filter feeding.

Box 2: Biofouling

Biofouling is the accumulation of microorganisms, plants, algae, or small animals where it is not wanted on surfaces, devices such as water inlets, pipework, grates, ponds, and rivers that cause degradation to the primary purpose of that item. Some gastropod species are exclusively found living on the baleen plates of baleen whales, where they scrape off algae and bacteria films.

About 1,700 species are responsible for biofouling. Biofouling is divided into microfouling — biofilm formation and bacterial adhesion — and macrofouling — attachment of larger organisms. Due to the distinct chemistry and biology that determine what prevents them from settling, organisms are also classified as hard- or soft-fouling types. Calcareous (hard) fouling organisms include barnacles, encrusting bryozoans, molluscs, polychaete and other tube worms, and zebra mussels. Examples of non-calcareous (soft) fouling organisms are seaweed, hydroids, algae and biofilm "slime". Together, these organisms form a fouling community.



Left: Biofouling initial process: Coating of submerged substrate with polymers. Bacterial attachment and extracellular polymeric substance (EPS) matrix formation. *Right:* Dead biofouling, under a wood boat.

Marine fouling is typically described as following four stages of ecosystem development. Within the first minute the van der Waals interaction causes the submerged surface to be covered with a conditioning film of organic polymers. In the next 24 hours, this layer allows the process of bacterial adhesion to occur, with both diatoms and bacteria (e.g. *Vibrio alginolyticus*, *Pseudomonas putrefaciens*) attaching, initiating the formation of a biofilm. By the end of the first week, the rich nutrients and ease of attachment into the biofilm allow secondary colonizers of spores of macroalgae (e.g. *Enteromorpha intestinalis*, *Ulothrix*) and protozoans (e.g. *Vorticella*, *Zoothamnium sp.*) to attach themselves. Within 2 to 3 weeks, the tertiary colonizers- the macrofoulers- have attached. These include tunicates, molluscs, crustaceans (barnacles), and cnidarians.

Raptorial feeders Phagotrophic heterotrophs live by killing and eating other animals, especially by catching living prey. Raptors actively attack and seize their living food items with specialised mouth parts (including teeth), extremities, or other body appendages. Another common term for raptorial feeders is "predators".[28]

In marine environments, fish and mammals but also most cnidarians (e.g. jellyfish, hydroids), ctenophora (comb jellies), echinoderms (e.g. sea stars, sea urchins, sand dollars, and sea cucumbers) and flatworms are raptorial feeders. Among crustaceans, copepods, lobsters, crabs, shrimps and barnacles are predators, and in turn crustaceans are preyed on by nearly all cephalopods (including octopuses, squid and cuttlefish). Among marine zooplankton, whether single-celled or multi-cellular, predatory grazing[29] on phytoplankton and smaller zooplankton is common, and found in many species of nanoflagellates, dinoflagellates, ciliates, rotifers, a diverse range of meroplankton animal larvae, and copepods. Many species of protozoa (eukaryotes) and bacteria (prokaryotes) prey on other microorganisms; the feeding mode is evidently ancient, and evolved many times in both groups.

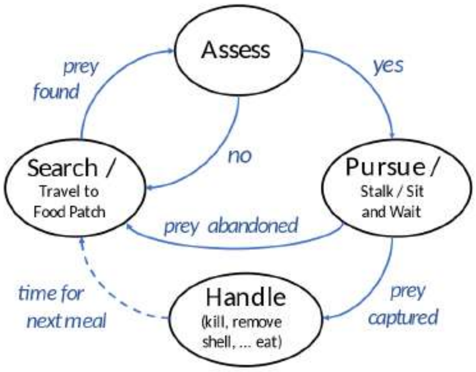


Figure 3.35: A basic foraging cycle for a predator.

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[28] Although that term is also (and more strictly) used for the ecological interaction of *predation*, see below.

[29] As I said, the terminology can be confusing

Seizing prey is a complex, multi-step process for a predator individual between encountering a prey item and finally ingesting it. At each step, natural selection can favour morphological, behavioural or physiological adaptations that optimise either the chance of a prey to ultimately avoid death or the chance of a predator of getting food.[30] Because raptorial feeders are mobile and feed on mobile prey, they must search for, pursue and kill its prey to feed. This is the process of *foraging*. These actions form a foraging cycle (Fig. 3.35). The predator must decide when and where to look for prey based on the prey's temporal and spatial distribution; and once it has located prey, the predator must assess whether to pursue it or to wait for a better choice. If it chooses pursuit, its physical capabilities determine the mode of pursuit (e.g., ambush or chase). Having captured the prey, it may also need to expend energy handling it (e.g., subduing it, killing it, removing any shell or spines, and ingesting it).

Predators have a choice of **search** modes ranging from "sit-and-wait" (*ambush predation*) to active or widely foraging. The sit-and-wait method is most suitable if the prey are dense and mobile, and the predator has low energy requirements. Wide foraging expends more energy, and is used when prey is sedentary or sparsely distributed. There is a continuum of search modes with intervals between periods of movement ranging from seconds to months. Sharks are almost always moving while many aquatic invertebrates rarely move longer distances. In between, others, like plovers and other shorebirds for example, alternate between actively searching and scanning the environment. Prey distributions are often clumped, and predators respond by looking for patches where prey is dense and then searching within patches. Where food is found in patches, such as rare shoals of fish in a nearly empty ocean, the search stage requires the predator to travel for a substantial time, and to expend a significant amount of energy, to locate each food patch (Fig. 3.36). With static prey, some predators can learn suitable patch locations and return to them at intervals to feed.

Figure 3.36: For example, the black-browed albatross (*Thalassarche melanophris*) regularly makes foraging flights to a range of around 700 km, up to a maximum foraging range of 3,000 km for breeding birds gathering food for their young.

Having found prey, a predator **assesses** it to decide whether to pursue it or keep searching. The decision depends on the costs and benefits involved. One of the factors to consider is size. Prey that is too small may not be worth the trouble for the amount of energy it provides. Too large, and it may be too difficult to capture. There is generally a positive correlation between the size of a predator and its prey.

Many *copepods* use mechanical and chemical sensors on their first (large) antennae pair not only to detect their food (individual phytoplankton cells and small zooplankton such as rotifers and ciliates) but also to assess the type of food particles and the size of it.[31]

Calanus helgolandicus is a planktonic herbivore, although

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[30] Lima, S. L. and Dill, L. M. (2011). Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology*, 68:619–640

[31] Copepods are in contrast to what marine ecologists believed for a long time, not filter feeders but raptorial feeders instead. They attack and capture individual prey items. Their body appendages produce a water current from anterior to posterior. As soon as food receptors (mechanical and chemical) detect the approach of a suitable algal cell the maxillae are opened. Water with the cell is sucked into the chamber between the maxillae. When the chamber is closed the water is pressed out again. The algal cell is trapped between the setae and even smaller "hairs" on them ("setules") of the maxillae. In this chamber particles of 5 µm diameter can be retained.

it has been shown to eat both dead diatoms and faeces from other members of its species ("detritivore"). This copepod seems to select particles based on their structure; marine snow (which is unstructured), is rejected, whereas dead diatoms and objects such as polystyrene (when given as beads 30 µm in diameter) are accepted as food. Faecal pellets are generally not accepted in whole (possibly due to the difficulty in handling very large particles). When the pellets are fragmented, they are generally ingested with alternate food. Many raptorial feeders can also adjust their feeding style after they assessed the prey. The copepod *Acartia tonsa* feeds on phytoplankton as well as on planktonic ciliates and rotifers. It acts as a suspension feeder when feeding on phytoplankton. When feeding on motile prey it acts as an ambush feeder; it stays nearly motionless in the water, detects movement of its prey, and then jumps toward the prey using a quick and strong beating of their first antennae. This movement serves also as the predominant escape mechanism of copepods from their predators, mainly fish. Copepod-hunting jelly fish can overcome this escape response. Moderate amounts of turbulence improve rates of ambush feedings. Like many raptorial feeders, copepods as more selective in which prey they attack and seize, in contrast to the more non-selective filter-feeding zooplankton such as Cladocera (water fleas) *of which only three genera exist in marine environments.*

To **capture** prey, predators have a spectrum of pursuit modes that range from overt chase (pursuit predation) to a sudden strike on nearby prey (ambush predation).

Ambush or sit-and-wait predators are carnivorous animals that capture prey by stealth or surprise. In animals, ambush predation is characterized by the predator's scanning the environment from a concealed position until a prey is spotted, and then rapidly executing a fixed surprise attack.

Some ambush predators use burrows etc. in which to hide, improving concealment at the cost of reducing their field of vision (Fig. 3.37). Some ambush predators also use lures to attract prey within striking range (Fig. 3.38).

The capturing movement has to be rapid to trap the prey, given that the attack is not modifiable once launched.

In pursuit predation, predators chase fleeing prey. If the prey flees in a straight line, capture depends only on the predator's being faster than the prey. If the prey manoeuvres by turning as it flees, the predator must react in real time to calculate and follow a new intercept path, such as by parallel navigation, as it closes on the prey. Many pursuit predators use camouflage to approach the prey as close as possible unobserved (stalking) before starting the pursuit. Pursuit predators include marine predators such as dolphins, orcas and many predatory fishes, such as tuna.

Once the predator has captured the prey, it has to **handle** it to finally subdue, kill, and ingest it. Handling has to be very

Figure 3.37: A moray eel *Echidna nebulosa* hiding in a live coral reef, located in Sabang, Philippines. Morays are opportunistic, carnivorous predators and feed primarily on smaller fish, crabs, and octopuses. The pharyngeal jaws of morays are located farther back in the head and closely resemble the oral jaws. When feeding, morays launch these jaws into the mouth cavity, where they grasp prey and transport it into the throat. Moray eels are the only known animals that use pharyngeal jaws to actively capture and restrain prey in this way. Also, morays' mouth openings extend far back into the head, compared to fishes which feed using suction. In the action of lunging at prey and biting down, water flows out the posterior side of the mouth opening, reducing waves in front of the eel which would otherwise displace prey.

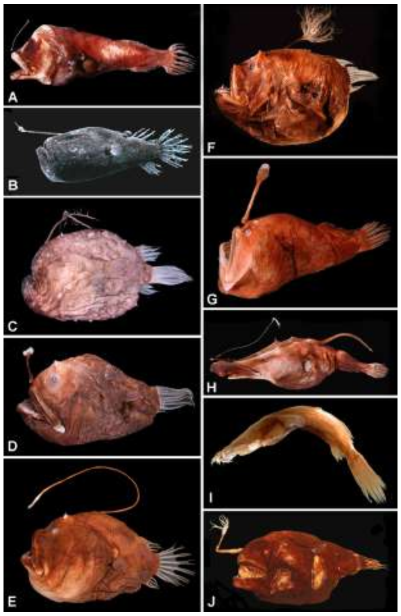

Figure 3.38: Various species of angler fish. The anglerfish are bony fish named for its characteristic mode of predation, in which a modified luminescent fin ray (the "esca") acts as a lure for other fish. Anglerfish can wiggle the esca to make it resemble a prey animal, which lures the anglerfish's prey close enough for the anglerfish to devour them whole. Some deep-sea anglerfish of the bathypelagic zone also emit light from their esca to attract prey.

carefully if the prey is dangerous to eat, if it possesses sharp or poisonous spines, as in many prey fish such as the Sohal surgeonfish (*Acanthurus sohal*) (Fig. 3.39), living on coral reefs in the Red Sea. These fish have a sharp scalpel-like spine on the front of each of their tail fins, able to inflict deep wounds. The area around the spines is often brightly coloured to advertise the defensive capability; predators often avoid the Sohal surgeonfish. Defensive spines may be detachable, barbed or poisonous. Some fish-eating birds like the osprey avoid the danger of spines by tearing up their prey before eating it (Fig. 3.40). Other prey may use some form of deterrents to prevent handling by predators (Fig. 3.41).

Figure 3.39: *Acanthurus sohal*, Sohal surgeonfish

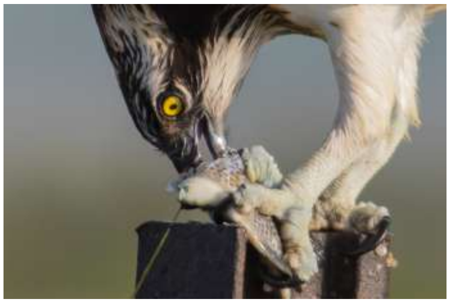

Figure 3.40: Osprey *Pandion haliaetus* tears its fish prey apart, avoiding sharp spines.

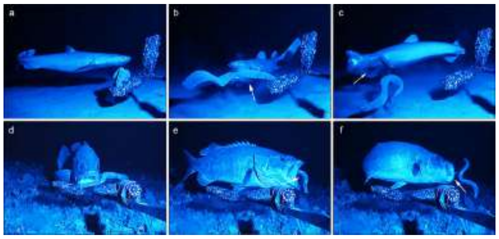

Figure 3.41: Anti-predator adaptation in action: the seal shark *Dalatias licha* (a–c) and the wreckfish *Polyprion americanus* (d–f) attempt to prey on hagfishes. As the predators seize their potential prey, the hagfishes project jets of slime (arrows) into the predators' mouths. Choking, the predators gag in an attempt to remove slime from their mouths and gill chambers and stop handling the hagfishes, which escape.

An important aspect of predation, as for osmotrophs, filter feeders and all other heterotrophs is the amount of prey items a predator can ingest per time depending on the prey density. This relationship is described by the *functional response* (Fig. 3.42). The functional response is associated with the numerical response, which is the reproduction rate of a consumer as a function of food density. Following C.S. Holling, functional responses are generally classified into three types, which are called Holling's type I, II, and III.

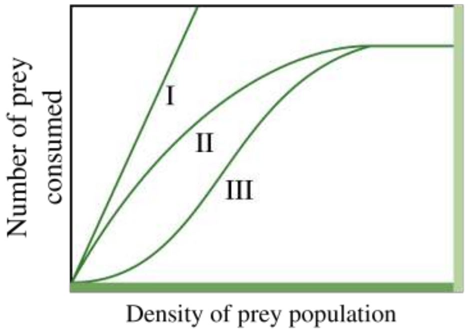

Figure 3.42: Types I, II, and III functional responses as relationships between the ingestion rate of a single predator (consumer) and the prey (resource) density it experiences.

Type I functional response assumes a linear increase in ingestion rate with food density, either for all food densities, or only up to a maximum, beyond which the ingestion rate is constant. The linear increase assumes that the time needed by the consumer to process a food item is negligible, or that consuming food does not interfere with searching for food. It was the first kind of functional response described and is also the simplest of the three functional responses currently detailed.

The **Type II** functional response is characterized by a decelerating ingestion rate, which follows from the assumption that the consumer is limited by its capacity to handle and digest food. The type II functional response is often modelled by a rectangular hyperbola, for instance as by Holling's disc equation, which assumes that processing of food and searching for food are mutually exclusive behaviours. The equation[32] is

$$\text{Type II: } I(R) = \frac{aR}{1+ahR}, \tag{3.10}$$

where $I(R)$ denotes ingestion rate and R denotes food (or prey or resource) density. The rate at which the consumer encounters food items per unit of food density is called the attack rate, a.[33] The average time spent on processing (handle, digest) a food item is called the "handling time", h.[34]

For example, as the number of phytoplankton cells increases the number of cells ingested per time by a single copepod first increases, but the proportion of cells ingested declines, because of the more cells in the water. Explained slightly differently, at very high phytoplankton densities, copepods need very little time to

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[32] Note that with $V_{max} = 1/h$ (or $h = 1/V_{max}$) and $K_M = 1/ah$ (or $a = V_{max}/K_M$), the Michaelis-Menten equation and the Functional Response Type II equation can be transformed into each other. Both equations are equivalent and differ only in their parametrisation.

find phytoplankton and spend almost all their time handling prey and very little time searching. Copepods are then satiated and the total number of algae cells reaches a plateau. The copepod is **satiated** and simply cannot ingest more given its feeding strategy and morphology (Fig. 3.43).

A **Type III** functional response is similar to type II in that at high levels of prey density, saturation occurs. But at low prey density levels, the relationship of number of prey consumed and the density of the prey population is a more than linearly increasing function of prey consumed by predators. This accelerating function is largely descriptive, and often justified by learning time, prey switching, or a combination of both phenomena, but the type III functional response lacks the rigorous theoretical underpinning of the type II functional response. "Learning" time is defined as the natural improvement of a predator's searching and attacking efficiency or the natural improvement in their handling efficiency as prey density increases. Imagine a prey density so small that the chance of a predator encountering that prey is extremely low. Because the predator finds prey so infrequently, it has not had enough experience to develop the best ways to capture and subdue that species of prey. Often, predators also develop a "search image" and cannot find items of a rare prey, because they are unfamiliar with identifying it.[35] "Prey switching" involves two or more prey species and one predator species. When all prey species are at equal prey densities, the predator will indiscriminately select between prey species. However, if the density of one of the prey species decreases, then the predator will start selecting the other, more common prey species with a higher frequency.

The functional response is **trait-dependent**. It varies with among predator species, within predators with prey species, and within predator and prey species with individual traits. One important determinant of handling time h and attack rate a and thus the feeding relationship (interaction) between consumer and resource is body size. Everything equal, attack rate goes up and handling time rises as prey size increases, because larger prey are often more easily detected and less finicky to handle for a predator of a given size. Many predators actively select larger prey when given the choice because they offer more energy and matter per ingestion. But than these patterns reverse: as prey get even larger predators may avoid them due to fear of injuries of a back-fighting powerful prey, too low chances of capture, too high costs of subduing, and/or too time-consuming handling. Notice how in Fig. 3.43 the straight rising part (the attack rate) gets shallower and the maximum ingestion rate declines ($I_{max} = h^{-1}$) as prey size increases.

3.2.3 *The type of food*

The third and final part of this brief typology of marine feeding behaviours considers shortly the type of food heterotrophs ingest.

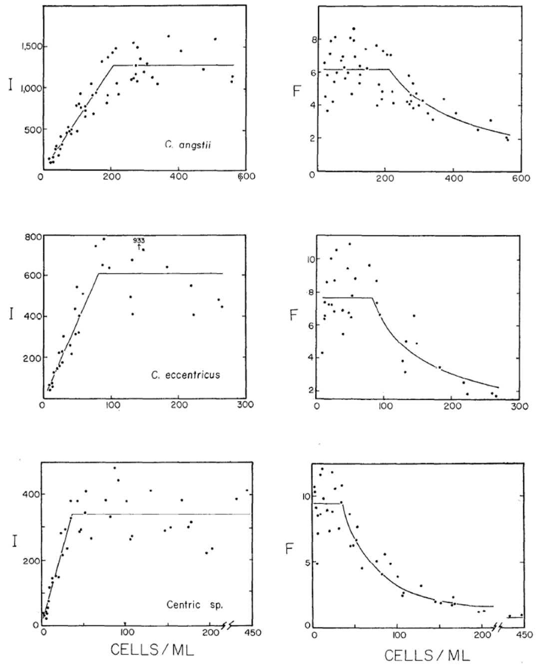

Figure 3.43: Effect of cell concentration on ingestion rate, I (cells eaten copepod^{-1} h^{-1}), and volume cleared, F (l copepod^{-1} h^{-1}), of equal-sized adult females of *Calanus pacificus* feeding on various diatom species: *Coscinodiscus angstii* (top graphs), *Coscinodiscus eccentricus* (center graphs) and centric sp. (lower graphs). Cell size of diatom prey increases from top to lower graphs (Frost, 1972).

[33] Encounter and thus the attack rate a depend on predator search strategies and the traits of prey that decrease the chance of encounters, e.g. feeding only during the night like daily vertical migrating copepods. Any traits that make a predator reject a prey during assessment or let a prey escape a capture also decrease a.

[34] Any prey traits that make handling after capture more difficult for the predator increase h and lower $I(R)$.

[35] I find it quite difficult to simultaneously look for two rare Lego pieces in my daughter's Lego box because I can focus efficiently on one shape only.

Detritivores (also known as detrivores, detritophages, detritus feeders, or detritus eaters) are heterotrophs that obtain nutrients by consuming detritus (decomposing plant and animal parts as well as faeces). By doing so, all these detritivores contribute to decomposition and the nutrient cycles. They should be distinguished from other decomposers, such as many species of bacteria, fungi and protists, which are unable to ingest discrete lumps of matter, but instead live by absorbing and metabolizing on a molecular scale (or osmophagy as described above). However, the terms detritivore and decomposer are often used interchangeably but they are different organisms.[36,37] Detritivores perform the first stage of re-mineralization, by fragmenting the dead matter, allowing for decomposers to perform the second stage of re-mineralization. The activity of detritivores are the reason why we do not see an accumulation of dead matter in nature. Typical marine detritivorous animals include sea stars, sea cucumbers, fiddler crabs, and some sedentary polychaetes such as worms of the family Terebellidae. Scavengers are detritivores that generally eat large quantities of organic matter, especially the carcasses of fish or marine mammals. Marine scavenger species are sea gulls, some shark species and many bony fish. Scavengers fragment large carcasses into smaller pieces by biting junk out of them, by sloppy feeding, and by excretion (see also section 4.2 for the spectacular example of "whale falls").

Herbivory is a form of consumption in which a heterotroph organism principally eats autotrophs such as plants, algae, and photosynthesising bacteria. More generally, organisms that feed on autotrophs in general are known as primary consumers. The largest group of herbivores in the oceans are crustacean zooplankton such as the raptorial copepods and filter-feeding krill (see above) and the phagotrophic ciliates (Fig. 3.44). Other herbivorous species are phytoplankton-filtering bivalves and grazing gastropods but also herbivorous fish (Fig. 3.45) and even the mammalian "sea cows" such as the dugong (Fig. 3.46).

A *Carnivore*, meaning "meat eater"[38], is an animal whose food and energy requirements derive solely from animal tissue or meat. This definition is more narrow than just eating other heterotrophs, which would include feeding on non-metazoan prey like protozoans and bacteria. Carnivory occurs in all higher marine organismal groups. Carnivores include but are not restricted to the mammalian order "Carnivora" which include *Pinnipeds*, i.e the three families of seals living semiaquatic[39] in marine habitats.

An *Omnivore* is an organism that has the ability to eat and survive on both autotroph and heterotroph living organic matter i.e. omnivory is the process of feeding on more than one trophic level. Often, omnivores have the ability to incorporate food sources such as algae, fungi, and bacteria into their

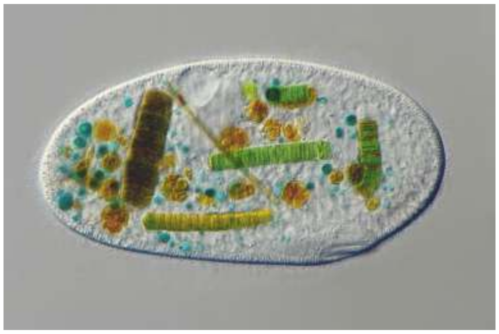

Figure 3.44: A ciliate (*Frontonia* sp.) digesting blue-green algae (cyanobacteria). The cytostome (the "mouth" of the cell) is seen on the right, facing down. Ciliates are found in concentrations of about 1 per ml and are important herbivores in the sea, constituting the first link in the food chain.

Figure 3.45: Mixed feeding shoal of herbivorous fish on a coral reef.

Figure 3.46: Dugong *Dugong dugon* feed mainly on seagrass. When eating they ingest the whole plant, including the roots, although when this is impossible they will feed on just the leaves.

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[36] Deposit feeders are animals that ingest sediment (mud, sand) and live off the organic matter in there. The organic matter can be dead, that is why the terms deposit feeder and detritivore are often used interchangeable, or alive, for example bacteria, protists, or rotifers living in there. One prime example is the lugworm *Arenicola marine* whose habitat are sandy Wadden Sea.

[37] A *bottom feeder* is an aquatic animal that feeds on or near the bottom (benthos) of a body of water such as shellfish, crabs, crayfish, sea anemones, starfish, snails, bristleworms, sea cucumbers and demersal (ground) fish. Again, organic matter can be dead or alive, but the use of terminology is once again not consistent. Sometimes, bottom feeder refers to benthic detritivores only.

[38] Latin, *caro*, genitive *carnis*, meaning "meat" or "flesh" and *vorare*, meaning "to devour"

diet. Although cases exist of herbivores eating meat and carnivores eating plant matter, the classification "omnivore" refers to the adaptation and main food source of the species in general, so these exceptions do not make either individual animals or the species as a whole omnivorous. A true omnivore obtains substantial matter and energy from both autotrophic and heterotrophic tissues. Many deposit or bottom feeders are omnivore, but also *pelagic mysids* that feed on algae, detritus and zooplankton, and some copepods and fish.

An important phenomenon is **life history omnivory**, when organisms feed on different trophic levels over their life cycle (ontogeny). For example, the juveniles of many fish species feed on crustacean zooplankton while later as adults they are piscivore and feed on planktivorous fish, often fish species that are competitors of their own young (Figs. 3.47 & 3.48). Due to their smaller size, copepod nauplii (the juvenile stages) may prefer smaller prey like heterotrophic bacteria and small algae cells whereas adults preferentially select larger prey that also include protists and even copepod nauplii (Fig. 3.49).

Life history omnivory is closely related **ontogenetic niche shifts** and ***metamorphosis***.

Due to the wide spread of complex life cycles (i.e those life cycles that consists of several distinct life history stages, e.g. planktonic larvae and sessile adults) in marine organisms, life history omnivory is likely to be very common in oceans. Its implications for marine food web structures and dynamics and how marine ecosystems respond to human impacts is an active research field of marine ecology.[40]

Figure 3.47: A cod (*Gadus* spec.) larvae.

Figure 3.48: A full-grown adult Atlantic Cod (*Gadus morhua*).

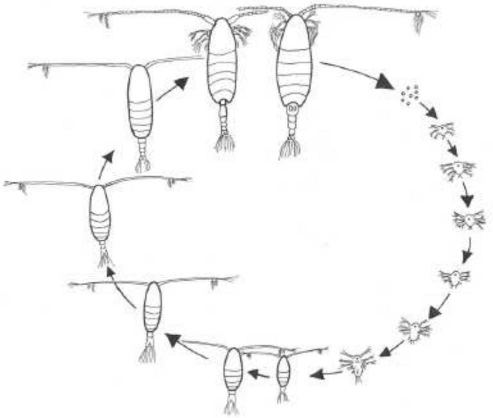

Figure 3.49: *Illustration of the copepod life cycle and its life stages.* (from NOAA Fisheries COPEPOD Project)

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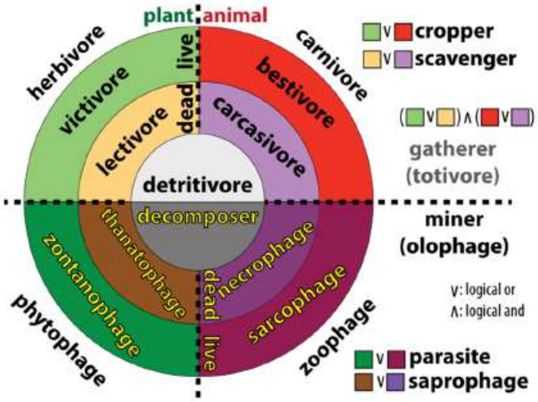
[39] They spend most of their lives in the water where they feed on fish and cephalopods, followed by crustaceans and bivalves, and then zooplankton and sea birds, but come ashore to mate, give birth, molt or escape from predators, such as sharks and killer whales.

[40] *Complex life cycles* are by no means restricted to heterotrophs. They are very common among protists, fungi, and algae.

Box 3: The Getz Categorisation

Another way of categorizing consumers is based on a biomass-transformation-web formulation that organizes resources into five components: live and dead animal, live and dead plant, and particulate (Getz, 2011). It distinguishes between mobile and sessile consumers.

In Getz's scheme, words for miners are of Greek etymology and words for gatherers are of Latin etymology. Thus, a "bestivore", such as a cat, preys on live animals (Latin: *bestia* = animal), while a "sarcophage", such as a botfly larva, mines live flesh, and a "zontanophage" (Greek: *ζοντανος* = alive), such as a leaf miner, mines live plant material. A "carcasivore" (Latin: *carcasium* = carcass), such as white-backed vulture, scavenge animal carcasses, while a "necrophage" (Greek: *νεκρος* = dead), such as a blowfly, mines dead flesh. "Victivores" (Latin: *victus* = living) gather live plant material and thus include frugivores, nectivores, graminivores, granivores and folivores as subcategories. "Lectivores", such as many termites, gather dead plant material (Latin: *lectus* = bed, which is the root of the word "litter", as in leaf-litter) and "thanatophages" (Greek: *θανατος* = death), such as pillbugs mine piles of dead plant material. Carnivore and herbivore are generic multigroup categories.



Wayne Getz's consumer categories are based on material eaten (plant: green live, brown dead; animal: red live, purple dead; or particulate: grey) and feeding strategy (gatherer: lighter shades; miner: darker shades).

3.3 *Marine food webs*

Marine ecology focuses strongly on from what resources (inorganic or organic, dead or alive) both primary and secondary producers obtain energy and matter, i.e. who ingests whom or what.[41] Ingestion thus couples consumers and resources to ***consumer-resource interactions***. Consumer-resource interactions are the core motif of *ecological food webs*, and are an umbrella term for a variety of more specialized types of biological species interactions including prey-predator *stricto sensu*, host-parasite/pathogen, detritus-detritivore, and plant-herbivore systems.

Food webs are the interconnection of several consumer-resource interactions of who-eats-whom in an ecological community. The linkages in a food web illustrate the ingestion pathways, such as where heterotrophs obtain organic matter by feeding on autotrophs and other heterotrophs. The food web is a simplified illustration of the various methods of resource ingestion that links an ecosystem into a unified system of exchange of energy and matter (Fig. 3.50).[42]

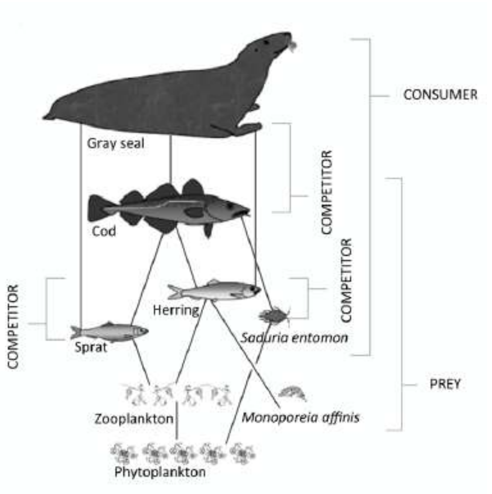


Figure 3.50: Classic food web for grey seals in the Baltic Sea containing several typical marine food chains.

[41] This explicitly includes autotrophs who have to ingest their inorganic resources, e.g. CO_2 and nutrients.

[42] The coupling between resource and consumer in models occurs via the functional response, which describes the effect a single consumer has on the density of the resource population. The functional response is therefore sometimes used as a measure for the interaction strength between consumer and resource.

Box 4: A secondary production model

Marine biologist have a long tradition of using mathematical models to understand consumer-resource systems and how they influence marine ecosystems. The well-known *Lotka-Volterra predator-prey model* was partially inspired by Volterra's discussions with the marine biologist D'Ancona. D'Ancona studied the fish landings in the Adriatic Sea and had noticed that the proportion of piscivorous fish caught had increased during World War I despite that the fishing effort had been very much reduced during the war. Later, more complex yet realistic models include e.g. density dependence, satiating feeding relationships, mortality (e.g. from fishing) etc. One recent development (de Roos, 2020) focuses on the differences between juveniles J and adults A in their ecological interaction with a resource R both life stages share:

$$\begin{aligned}\frac{dR}{dt} &= G(R)R - \omega_J(R)J - \omega_A(R)A\\ \frac{dJ}{dt} &= (\sigma\omega_A(R) - T)A + (\sigma\omega_J(R) - T)J - \gamma(\sigma\omega_J(R) - T, \mu)J - \mu J\\ \frac{dA}{dt} &= \gamma(\sigma\omega_J(R) - T, \mu)J - \mu A\end{aligned}$$

In the absence of consumers, the resource R grows dependent on its own density (note the (R) part!) with rate $G(R)$ and is diminished by consumption from juveniles J and adults A, with stage-specific and resource-dependent ingestion rates $\omega_J(R)$ and $\omega_A(R)$, respectively. Consumed resources are converted with efficiency σ into juvenile biomass J via somatic growth, minus some costs T for maintaining already existing biomass. J also increases through adult reproduction, again after some loss due to respiration etc. (σ) and after paying maintenance costs T. Juvenile and adult biomass declines with mortality, which is resource-independent and represented by the rate parameter μ. Finally, $\gamma(R, \mu)$ describes the rate with which juvenile biomass matures into adult biomass. This maturation rate depends on juvenile growth and mortality. Biomass that matures leaves the juvenile stage and increases the adult biomass.

One strong assumption of this model is that adults don't grow, they only reproduce. Juveniles and adults differ from each other only in the amount of resources they ingest per unit of their biomass. The resource conversion efficiency, σ, the costs of maintaining body functions etc., T, and mortality rate, μ, are assumed to be equal for juveniles and adults. Note that only the ingestion rate functions have lower indices $_J$ and $_A$. In principle, any or all demographic rates could be stage-specific. With $\omega_J(R) = \frac{aR}{a + ahR}$ and $\omega_A(R) = q\frac{aR}{1 + ahR}$ one can model the juvenile and adult ingestion rates as Holling Type II functional responses with attack rate a and handling time h.

The scaling factor q in these formulations represents the biomass-specific differentiation between the two life stages. For $q = 1$, juveniles and adults are equivalent in their biology (they are ecologically "symmetric"). The term "equivalent" here refers to biomass-specific rates, i.e. per unit biomass and not per individual. Larger individuals still have a higher intake in absolute terms. Then the stage-structured model collapses to a unstructured one in which the presentation of consumer biomass by two differential equations would be unnecessary. For $q < 1$, juveniles are superior foragers on the shared resource; when $q > 1$, adults are competitively superior, and the model is truly stage-structured. Accounting for stage structure and stage-specific differences into consumer-resource systems, e.g. life history omnivory or ontogenetic niche shifts, can increase the realism of mathematical models and lead to interesting effects (Persson and de Roos, 2013).

Species at the bottom of the food web (basal species), such as algae and other autotrophs, consume non-biological (inorganic) resources, such as minerals and nutrients of various kinds, and they derive their energy from sun light (photosynthesis) or chemical sources (chemosynthesis).Species higher up in the food chain survive by consuming other species and can be classified by what they eat and how they obtain or find their food, which was a big part of this chapter. Decomposers ingest the dead organic material and recycle it so that after re-mineralisation the pool of inorganic resources for primary production is renewed (Fig. 3.51).

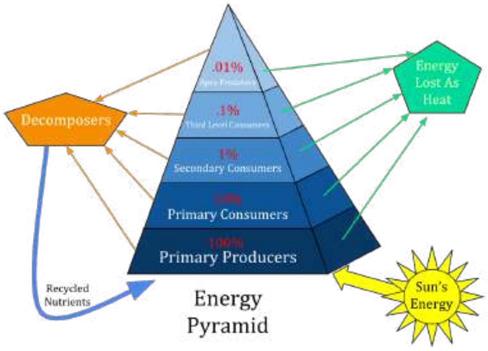


Figure 3.51: A pyramid of energy represents how much energy, initially from the sun, is retained or stored in the form of new biomass at each trophic level in an ecosystem. Typically, about 10% of the energy is transferred from one trophic level to the next, thus preventing a large number of trophic levels. Primary consumers feed on autotrophs, consumers above that level (secondary to tertiary) up to apex predators are carnivores.

A ***marine food web*** typically starts with energy from the sun powering phytoplankton growth (see chapter 2).Zooplankton constitute the 2^{nd} trophic level in the food chain, and include microscopic protozoa, small crustaceans such as copepods and krill, and the larvae of most if not all other organism groups. As primary consumers, zooplankton are the crucial link between the primary producers (mainly phytoplankton) and the rest of the marine food web (secondary consumers). In turn, the smaller herbivorous zooplankton are consumed by larger carnivorous zooplankters, such as larger predatory protozoa and krill, and by forage (planktivorous) fish, which are small, schooling, filter-feeding fish. Baleen whales belong into this 3^{rd} trophic level as well, despite their enormous size. The 4^{th} trophic level consists of predatory (piscivorous) fish, marine mammals and seabirds that consume forage fish. Examples are swordfish, seals and gannets. Apex predators, such as orcas, which can consume seals, and shortfin mako sharks, which can consume swordfish, make up a 5^{th} trophic level (Figs. 3.51 & 3.50).

In practice, trophic levels are not usually simple integers because the same consumer species often feeds across more than one trophic level. For example a large marine vertebrate may eat smaller predatory fish but may also eat filter feeders; the stingray eats crustaceans, but the hammerhead eats both crustaceans and stingrays. Animals can also eat each other; the cod eats smaller cod as well as crayfish, and crayfish eat cod larvae. The feeding habits of a juvenile animal, and, as a consequence, its trophic level, can change as it grows up, with sometimes counter-intuitive consequences for the ecological community. For example, juvenile cod are planktivore and compete as juveniles with sprat and herring, their adult prey. Cod thus undergoes an ontogenetic resource (niche) shift[43] and performs life-history omnivory[44] and interacts with herring and sprat via **stage-specific** *intraguild predation*. Intraguild predation, or IGP, is the killing and sometimes eating of a potential competitor of a different species. This indirect interaction represents a combination of predation and competition, because both species rely on the same prey resources and one also benefits from preying upon the other. The stage-specific IGP between cod and its *clupeid prey* may lead to *depensatory population growth*.[45] In population dynamics, "depensation" is the effect on a population (such as a fish stock) where a decrease in the breeding population (mature individuals) leads to *reduced* production and survival of eggs or offspring.[46] When large, adult cod are abundant, they exert a strong top-down effect on herring and sprat by predation. Few of those allow copepod zooplankton to thrive and cod juveniles can survive and grow to adulthood. However, when cod stock density is reduced, e.g. due to overfishing, their planktivorous prey are plenty, suppress zooplankton density, and thus outcompete their later predator's young. The cod stock suffers a recruitment bottleneck and can not, counter-intuitively, return to high densities, without reducing its adult prey fish populations first. Note, how this interaction is absent in Fig. 3.50 because the cod population is not separated into juvenile and adult fish as in the model in Box 3 (p. 68).

Such or other size- or stage-structure effects may be more prominent in marine than in terrestrial food webs because most if not all

[43] Feeding on different prey in different life cycle stages.

[44] Feeding on different trophic levels in different life cycle stages.

[45] Walters, C. and Kitchell, J. F. (2011). Cultivation/depensation effects on juvenile survival and recruitment: implications for the theory of fishing. *Canadian Journal of Fisheries and Aquatic Sciences*, 58:39–50

[46] The more common, but by no means universal, pattern is "compensation", where low adult densities lead to a higher offspring survival.

invertebrates in the oceans *have very distinct body forms as adults than as juveniles* and thus occupy often very different niches over their life (Fig. 3.52). More, the higher-level producers (mainly forage and predatory fish but also many of those metamorphosing invertebrates) grow substantially over their life. In contrast, on land, most secondary and tertiary consumers plus apex predators are avian or mammalian, which do not change much in body size and resource use once they become independent of their parents (usually soon after fledging or weaning off).

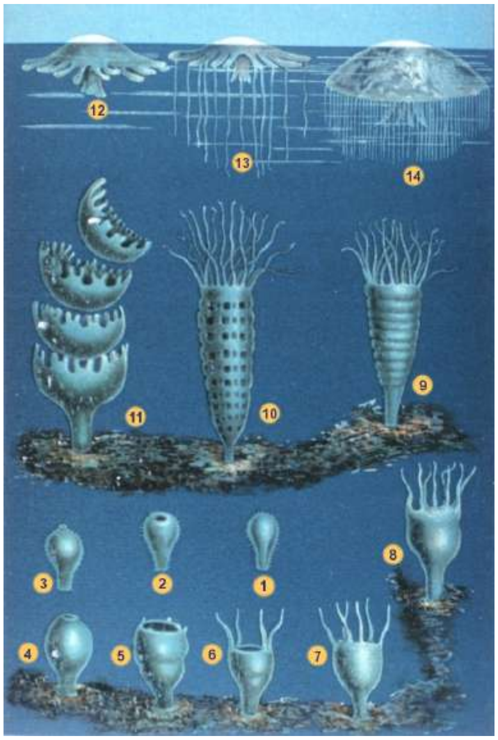


Figure 3.52: Life cycle of a Scyphozoa (Cnidaria): 1–3 Larva searches for site, 4–8 polyp grows, 9–11 polyp strobilates, 12–14 medusa grows. Such a biphasic life cycle between pelagic larva and benthic/sessile adult is very common in marine invertebrate organisms.

There exist more **differences between marine and terrestrial food webs**: Compared to land, marine environments often have *ecological biomass pyramids* which are inverted at the base (Fig. 3.53). In particular, the biomass of consumers (copepods, krill, shrimp, forage fish) is larger than the biomass of primary producers. This happens because the ocean's primary producers are tiny phytoplankton which grow and reproduce very rapidly (within hours to days even), so a small mass can have a fast rate of primary production.

In contrast, many significant terrestrial primary producers, such as mature forests, grow and reproduce slowly, so a much larger mass is needed to achieve the same rate of primary production. Because of this inversion, it is the zooplankton that make up most of the marine animal biomass. The rate of production divided by the average amount of biomass that achieves it is known as an organism's Production-Biomass ratio (P/B ratio). Production is measured in terms of the amount of movement of mass or energy per area per unit of time. In contrast, the biomass measurement is in units of mass per unit area or volume. The P/B ratio utilizes inverse time units (example: 1/month). This ratio allows for an estimate of the amount of energy flow compared to the amount of biomass at a given trophic level, allowing for demarcations to be made between trophic levels. The P/B ratio most commonly decreases as trophic level and organismal size increases, with small, ephemeral organisms containing a higher P/B ratio than large, long-lasting ones.

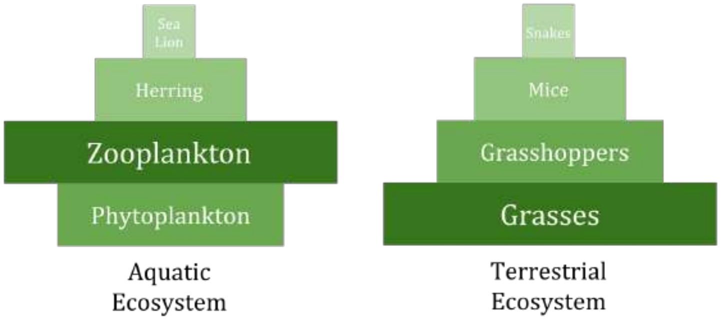


Figure 3.53: A pyramid of biomass shows the total biomass of the organisms involved at each trophic level of an ecosystem. These pyramids are not necessarily upright. There can be lower amounts of biomass at the bottom of the pyramid if the rate of primary production per unit biomass is high.

Marine algae or plants lack the secondary growth the

the woody trees of terrestrial ecosystems. However, they are able to reproduce quickly enough to support a larger biomass of grazers. This inverts the pyramid. Marine primary consumers have longer lifespans and slower growth rates that accumulates more biomass than the marine primary producers they consume. Phytoplankton live just a few days, whereas the zooplankton eating the phytoplankton live for several weeks and the fish eating the zooplankton live for several years. Aquatic predators also tend to have a lower death rate than the smaller consumers, which contributes to the inverted pyramidal pattern. The small size and lack of structural tissues in phytoplankton mean that aquatic primary producers achieve faster growth rates and are more nutritious to heterotrophs than their terrestrial counterparts.

Marine food webs also rely very strongly on microorganisms, possibly more than terrestrial ones. First, as mentioned above, the base of marine food webs are autotrophic bacteria and protists (phytoplankton) (Figs.3.50 & 3.53), but also many primary and secondary consumers are microscopic, including heterotrophic bacteria and protists, most crustacean zooplankton and invertebrate larvae. Especially the heterotrophic bacteria play an important role in *the microbial loop* (Figs.3.54 & 3.55).

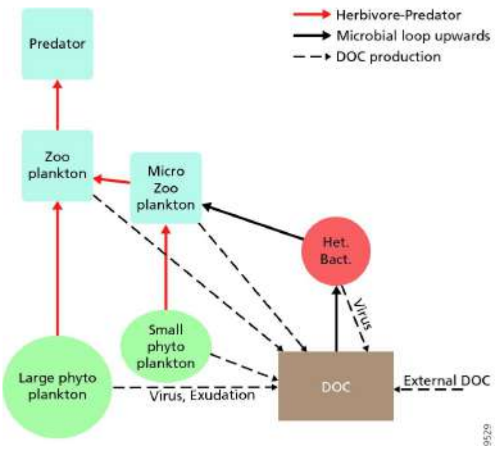


Figure 3.54: Food web structure in the euphotic zone: The linear food chain "large phytoplankton-herbivore-predator" (on the left with red arrow connections) has fewer levels than one with small phytoplankton at the base. The microbial loop refers to the flow from the dissolved organic carbon (DOC) via heterotrophic bacteria (Het. Bac.) and microzooplankton to predatory zooplankton (on the right with black solid arrows). Viruses play a major role in the mortality of phytoplankton and heterotrophic bacteria, and recycle organic carbon back to the DOC pool. Other sources of dissolved organic carbon (also dashed black arrows) includes exudation, sloppy feeding, etc. Particulate detritus pools and fluxes are not shown for simplicity.

The microbial loop describes a marine trophic pathway where dissolved organic carbon (DOC) is returned to higher trophic levels via its incorporation into bacterial biomass, and then coupled with the classic food chain formed by phytoplankton-zooplankton-nekton (Figs. 3.54 & 3.55). In general, DOC is introduced into the ocean environment from bacterial lysis, the leakage or exudation of fixed carbon from phytoplankton (e.g., mucilaginous exopolymer from diatoms), sudden cell senescence, sloppy feeding by zooplankton, the excretion of waste products by marine animals, or the breakdown or dissolution of organic particles from terrestrial plants and soils.

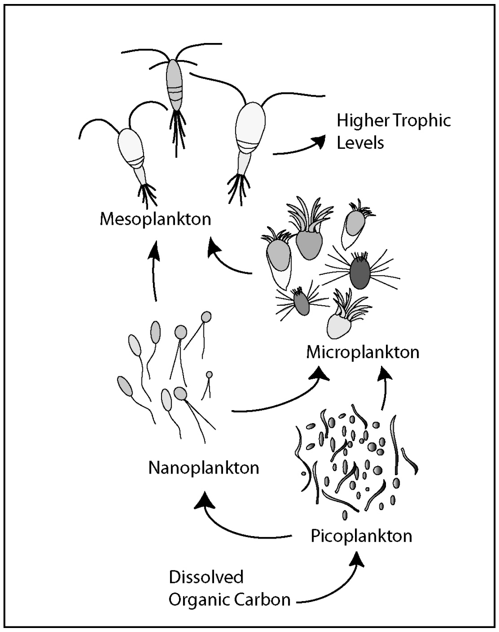


Figure 3.55: The microbial loop is a marine trophic pathway which incorporates DOC into the food web.

Since more than 95% of organic matter in marine ecosystems consists of polymeric, high molecular weight compounds (e.g. protein, polysaccharides, lipids), only a small portion of total DOM is readily utilizable to most marine organisms at higher trophic levels. This means that dissolved organic carbon is not available directly to most marine organisms; marine bacteria introduce this organic carbon into the food web, resulting in additional energy becoming available to higher trophic levels.[47] Without the microbial loop, DOC and its energy would be lost to the food webs. The microbial loop increases the efficiency of the marine food web via the utilization of DOM, aids in recycling of organic matter and nutrients and mediates the transfer of energy above the thermocline, stimulates phytoplankton growth,[48] and accelerates mineralization through regenerating production in nutrient-limited environments (e.g. oligotrophic waters). In general, the entire microbial loop is

[47] Recently the term "microbial food web" has been substituted for the term "microbial loop".

[48] More than 30% of DOC incorporated into bacteria is respired and released as carbon dioxide, available for carbon fixation during photosynthesis.

to some extent typically five to ten times the mass of all multicellular marine organisms in the marine ecosystem. Therefore, the microbial loop, together with primary production, controls the productivity of marine systems in the ocean.

Many heterotrophic bacteria accumulate within just a few minutes at small, local source patches of DOC. Therefore, the water column can be considered as a spatially organized place on a small scale rather than a completely mixed system. This patch formation affects the biologically-mediated transfer of matter and energy in the microbial loop.

The viral shunt can shortcut the microbial loop. The viral shunt is a mechanism that prevents marine microbial particulate organic matter (POM) from migrating up trophic levels by recycling them back into dissolved organic matter, when viruses infect microorganisms in the microbial loop. Prokaryotic and eukaryotic mortality contribute to carbon nutrient recycling through cell lysis.[49]

Another important aspect of marine food webs is their strong spatial structure. Vertical spatial heterogeneity arises from the light attenuation with depth and from the inevitable sinking of organic matter to the benthic. Horizontal variation in food webs often arises via dispersal of organisms between the pelagic and the littoral ocean habitats.

The biological pump is the ocean's biologically driven sequestration of carbon from the atmosphere and land run-off to the ocean interior and sea floor sediments. It is the part of the oceanic carbon cycle responsible for the cycling of organic matter formed mainly by phytoplankton during photosynthesis (Figs. 3.56 & 3.57).

The biological pump can be divided into three distinct phases, the first of which is the production of fixed carbon by planktonic phototrophs in the euphotic (sunlit) surface region of the ocean. In these surface waters, phytoplankton use carbon dioxide (CO_2), nitrogen (N), phosphorus (P), and other trace elements (barium, iron, zinc, etc.) during photosynthesis to make carbohydrates, lipids, and proteins. Some plankton, (e.g. coccolithophores and foraminifera) combine calcium (Ca) and dissolved carbonates (carbonic acid and bicarbonate) to form a calcium carbonate ($CaCO_3$) protective coating.

Once this carbon is fixed into soft or hard tissue, the organisms either stay in the euphotic zone to be recycled as part of the regenerative nutrient cycle or once they die, continue to the second phase of the biological pump and begin to sink to the ocean floor. The sinking particles will often form aggregates as they sink, greatly increasing the sinking rate. It is this aggregation that gives particles a better chance of escaping predation and decomposition in the water column and eventually making it to the sea floor.

The fixed carbon that is decomposed by bacteria either on the way down or once on the sea floor then enters the final

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[49] As much as 25% of the primary production from phytoplankton in the global oceans may be recycled within the microbial loop through the viral shunt. The DOM produced by the viral shunt pathway is comparable to the amount generated by the other main sources of marine DOM.

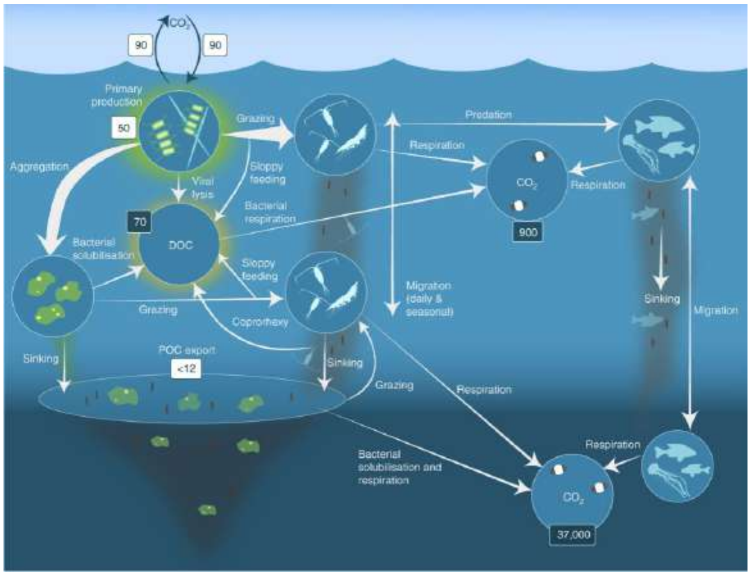

Figure 3.56: **The biological pump** is responsible for transforming dissolved inorganic carbon (DIC) into organic biomass and pumping it in particulate or dissolved form into the deep ocean. Inorganic nutrients and carbon dioxide are fixed during photosynthesis by phytoplankton, which both release DOM and are consumed by herbivorous zooplankton. Larger zooplankton - such as copepods - egest fecal pellets which can be re-ingested and sink or collect with other organic detritus into larger, more-rapidly-sinking aggregates. DOM is partially consumed by bacteria (black dots) and respired; the remaining refractory DOM is advected and mixed into the deep sea. DOM and aggregates exported into the deep water are consumed and respired, thus returning organic carbon into the enormous deep ocean reservoir of DIC. About 1% of the particles leaving the surface ocean reach the seabed and are consumed, respired, or buried in the sediments. There, carbon is stored for millions of years. The net effect of these processes is to remove carbon in organic form from the surface and return it to DIC at greater depths, maintaining the surface-to-deep ocean gradient of DIC. The thermohaline circulation returns deep-ocean DIC to the atmosphere on millennial timescales.

phase of the pump and is remineralized to be used again in primary production. The particles that escape these processes entirely are sequestered in the sediment and may remain there for millions of years. It is this sequestered carbon that is responsible for ultimately lowering atmospheric CO_2.

The biological pump is not so much the result of a single process, but rather the sum of a number of processes each of which can influence biological pumping. It is strengthened for example by vertical migration of zooplankton and the movement of fish which feed in the higher water layers but defecate deeper down or by whale falls that export significant organic material to the ocean bottoms. The biological pump is counteracted, among others, by marine mammals and birds like whales or penguins that feed deeper down[50] and transport the ingested matter upwards. Physical processes like mixing above the thermocline or large vertical water currents from the bottom to the surface in the various upwelling regions counteract the biological pump and bring carbon and nutrients back from the deep sea ocean floors to the productive euphotic zone.

Some of these processes have their own names, e.g. the *Whale Pump* or the *carbonate pump* for the sequestering of CO_2 as calcium carbonate via the shells of molluscs and some phytoplankton organisms like foraminifers and coccolithophores. Tectonic raising of deep calcium carbonate deposits and subsequent erosion can recycle the calcium back to where it can be biologically used (for example the chalk cliffs of the Baltic Sea islands Rügen (D) and Møn (DK)).

3.4 *Growth forms and systematics*

Marine life is the bacteria, archaea, fungi, protozoans, and animals that live in the salt or brackish water of the various marine habitats. Most life forms evolved initially in marine habitats, including probably life itself. Marine life is taxonomically and functionally very

[50] Sperm whales feed down to 5,000 m, and walruses feed on the benthos of the Arctic ocean.

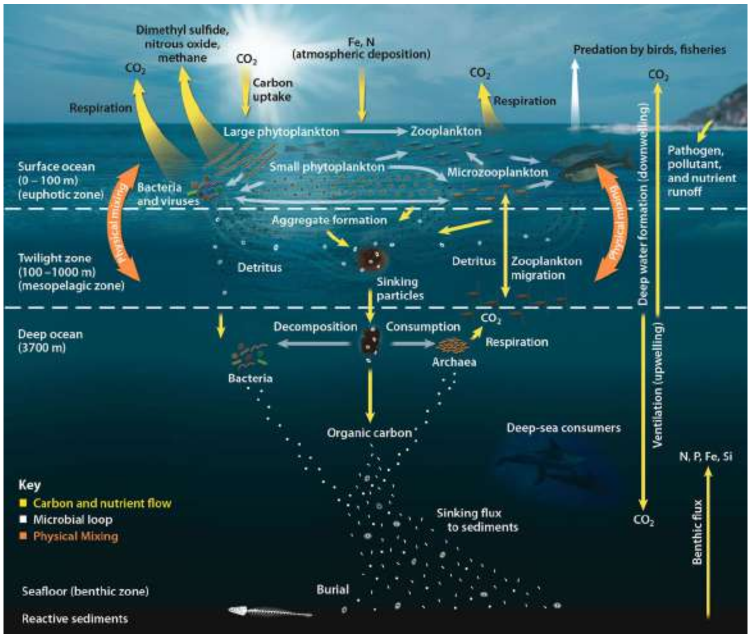

Figure 3.57: The pelagic food web, showing the central involvement of marine microorganisms in how the ocean imports nutrients from and then exports them back to the atmosphere and ocean floor. Pump processes vary with depth. Below 1,000 m carbon is considered removed from the atmosphere for at least 100 years.

diverse. In the following I will give a brief overview over the main heterotrophic organism (secondary producer) groups, although especially among bacteria, archaea, and protists, autotrophy, chemotrophy and heterotrophy[51] generally occur in the same taxonomic higher-order group.

Marine life forms can be classified by various of their features, leading to non-mutually exclusive groups:

A *prokaryote* is an organism that lacks a nuclear membrane-enclosed nucleus, mitochondria, or any other eukaryotic membrane-bound organelles. Prokaryotes are usually divided into two domains: Bacteria (formerly Eubacteria) and Archaea (formerly Archaebacteria). While typically being unicellular, some prokaryotes, such as cyanobacteria, may form large colonies (Fig. 3.59). Others, such as myxobacteria, have multicellular stages in their life cycles. Prokaryotes are asexual, reproducing without fusion of gametes, although horizontal gene transfer also takes place. ***Eukaryotes*** (Fig. 3.58) are organisms whose cells typically contain a cell nucleus enclosed within a nuclear envelope and other membrane-bound organelles such as mitochondria and Golgi apparatus; and chloroplasts can be found in plants and algae. The domain "Eukaryota" makes up third domain of life. The eukaryotes are usually now regarded as having emerged in the Archaea or as a sister of the now cultivated Asgard archaea. Eukaryotes represent a tiny minority of the number of organisms; however, due to their generally much larger size, their collective global biomass is estimated to be about equal to that of prokaryotes. Eukaryotes emerged approximately 2.1-1.6 billion years ago, during the Proterozoic eon, likely as flagellated phagotrophs. Eukaryotes may be either unicellular or multi-

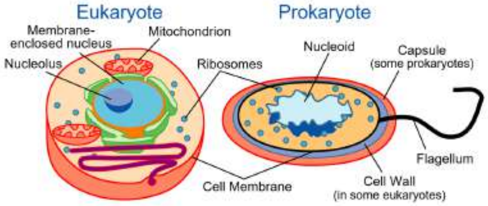

Figure 3.58: Comparison of eukaryote vs. prokaryote cells.

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[51] and *mixotrophy*

cellular, and include many cell types forming different kinds of tissue. Animals, plants, and fungi are the most familiar eukaryotes; unicellular eukaryotes are sometimes called protists or protozoa. Eukaryotes can reproduce both asexually through mitosis and sexually through meiosis and gamete fusion.

A *unicellular* organism, also known as a single-celled organism, is an organism that consists of a single cell (Fig. 3.60), unlike a (***multicellular***) organism that consists of multiple cells. Unicellular organisms fall into two general categories: prokaryotic organisms and eukaryotic organisms. All prokaryotes are unicellular and are classified into bacteria and archaea. Many eukaryotes are multicellular, but many are unicellular such as protozoa, unicellular algae, and unicellular fungi. Although some prokaryotes live in colonies, they are not specialised cells with differing functions. These organisms live together, and each cell must carry out all life processes to survive. In contrast, even the simplest multicellular organisms have cells that depend on each other to survive. Most multicellular organisms have a unicellular life-cycle stage. Gametes, for example, are reproductive unicells for multicellular organisms. Additionally, multicellularity appears to have evolved independently many times in the history of life. All species of marine animals (***metazoa***, Fig. 3.61), macroalgae, and most fungi are multicellular, whereas a few organisms are partially uni- and partially multicellular, such as slime moulds and social amoebae such as the genus *Dictyostelium*. Multicellular organisms arise in various ways, for example by cell division or by aggregation of many single cells. Colonial organisms are the result of many identical individuals joining together to form a colony. However, it can often be hard to separate colonial protists from true multicellular organisms, because the two concepts are not distinct; colonial protists have been dubbed "pluricellular" rather than "multicellular".

Figure 3.59: Stromatolites are formed from microbial mats as photosynthetic cyanobacteria slowly grow upwards to avoid being smothered by sediment. Unicellular organisms thus don't have to appear insignificant, which they definitely are not.

Figure 3.60: *Valonia ventricosa*, a species of alga with a diameter that ranges typically from 1 to 4 cm is among the largest unicellular species.

Marine microorganisms are any microscopic living organism or virus that are too small to see with the unaided human eye without magnification. Microorganisms are very diverse. They can be single-celled or multicellular and include bacteria, archaea, and most protozoa, as well as some fungi, algae, and certain microscopic animals such as rotifers. Many macroscopic animals and plants have microscopic juvenile stages. "Microorganism" is thus not a taxonomic term! Some microbiologists also classify biologically active entities such as viruses and phages as microorganisms, but others consider these as non-living.In contrast, **macroscopic** organisms are than those that humans can observed without a microscope or magnification lenses.

Plankton[52] are the diverse collection of organisms (Fig. 3.62) found in water that are unable to propel themselves against a water currentand simply drift with the current. Plankton organisms are still motile; within the water body they drift in they can actively move up or down or towards food or away from predators.

The individual organisms constituting plankton are called plankters. Marine plankton includes bacteria and archaea (*bacterioplankton*), algae (phytoplankton), fungi (mycoplankton), protozoa and drifting animals (*zooplankton*, Fig. 3.63) that inhabit the saltwater of oceans and the brackish waters of estuaries. Though many planktonic species are microscopic in size, plankton includes organisms over a wide range of sizes, including large organisms such as jellyfish. Plankton are defined by their ecological niche and level of motility rather than by any phylogenetic or taxonomic classification. Technically the term does not include organisms on the surface of the water, which are called pleuston — or those that swim actively in the water, which are called *nekton*.

Nekton[53] refers to the actively swimming aquatic organisms in a body of water. The term was proposed by German biologist Ernst Haeckel to differentiate between the active swimmers in a body of water, and the passive organisms that were carried along by the current, the plankton. As a guideline, nekton are larger and tend to swim mainly at biologically high Reynolds numbers ($> 10^3$ and up beyond 10^9, see also p. 1.1), where inertial flows are the rule, and eddies (vortices) are easily shed. Plankton, on the other hand, are small and, if they swim at all, do so at biologically low Reynolds numbers (0.001 to 10), where the viscous behaviour of water dominates, and reversible flows are the rule. Organisms such as jellyfish and others are considered plankton when they are very small and swim at low Reynolds numbers, and considered nekton as they grow large enough to swim at high Reynolds numbers. Many animals considered classic examples of nekton (e.g. *Mola mola*, squid, marlin) start out life as tiny members of the plankton and then, it was argued, gradually transition to nekton as they grow. Plankton are also often described in terms of size (Table 2.10, Figs. 3.13 & 3.64). Some of these terms may be used with very different size limits, especially on the larger end. The existence and importance of nano- and even smaller plankton was only discovered during the 80s, but they make up the largest proportion of all plankton in number and diversity.

Figure 3.61: The terms animals and metazoa are often used interchangeably.

Plankton and nekton organisms usually live in pelagic habitats, whereas *marine benthos*,[54] is the community of organisms that live on, in, or near marine sedimentary environments, also known as the benthic zone (see section 4.2, p. 129), from tidal pools along the foreshore, out to the continental shelf, and then down to the abyssal depths.[55]

Figure 3.62: Plankton species diversity: Diverse assemblages consist of unicellular and multicellular organisms with different sizes, shapes, feeding strategies, ecological functions, life cycle characteristics, and environmental sensitivities.

And finally there is of course the classification based on a common ancestry and characters of extent organisms by *systematics and taxonomy*. In biology, taxonomy is the scientific study of naming, defining (circumscribing) and classifying groups of biological organisms based on shared characteristics. Organisms are grouped into taxa and these groups are given a

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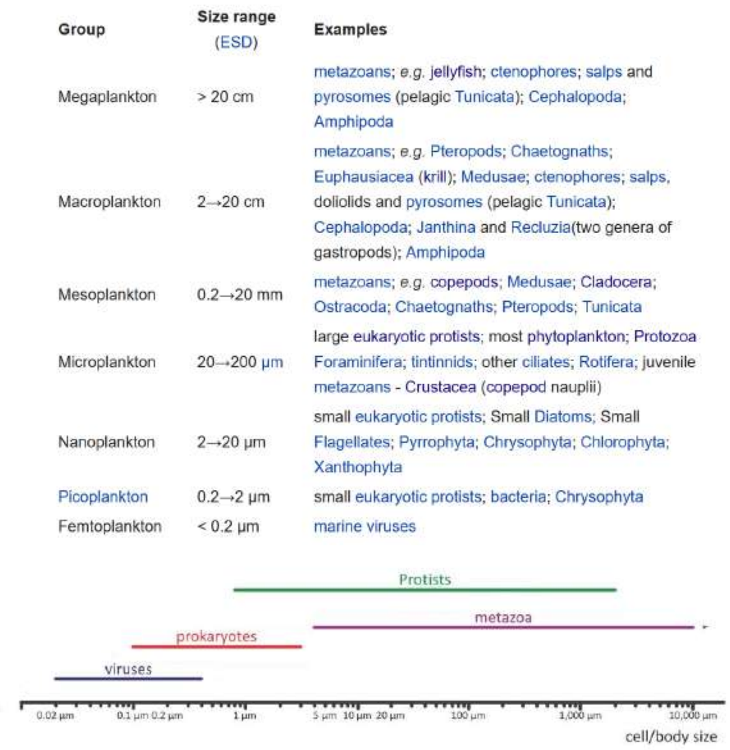
[52] From Greek πλανκτος, meaning "wanderer" or "drifter".



Group	Size range (ESD)	Examples
Megaplankton	> 20 cm	metazoans; *e.g.* jellyfish; ctenophores; salps and pyrosomes (pelagic Tunicata); Cephalopoda; Amphipoda
Macroplankton	2→20 cm	metazoans; *e.g.* Pteropods; Chaetognaths; Euphausiacea (krill); Medusae; ctenophores; salps, doliolids and pyrosomes (pelagic Tunicata); Cephalopoda; Janthina and Recluzia(two genera of gastropods); Amphipoda
Mesoplankton	0.2→20 mm	metazoans; *e.g.* copepods; Medusae; Cladocera; Ostracoda; Chaetognaths; Pteropods; Tunicata
Microplankton	20→200 µm	large eukaryotic protists; most phytoplankton; Protozoa Foraminifera; tintinnids; other ciliates; Rotifera; juvenile metazoans - Crustacea (copepod nauplii)
Nanoplankton	2→20 µm	small eukaryotic protists; Small Diatoms; Small Flagellates; Pyrrophyta; Chrysophyta; Chlorophyta; Xanthophyta
Picoplankton	0.2→2 µm	small eukaryotic protists; bacteria; Chrysophyta
Femtoplankton	< 0.2 µm	marine viruses

Figure 3.64: Plankton sizes by taxonomic groups.

taxonomic rank; groups of a given rank can be aggregated to form a more inclusive group of higher rank, thus creating a taxonomic hierarchy. The principal ranks in modern use are domain (Fig. 3.65), kingdom, phylum ("division" is sometimes used in botany in place of phylum), class, order, family, genus, and species. The Swedish botanist Carl Linnaeus is regarded as the founder of the current system of taxonomy, as he developed a ranked system known as Linnaean taxonomy for categorizing organisms and binomial nomenclature for naming organisms. With advances in the theory, data and analytical technology of biological systematics, the Linnaean system has transformed into a system of modern biological classification intended to reflect the evolutionary relationships among organisms, both living and extinct. Systematics is the study of the diversification of living forms, both past and present, and the relationships among living things through time. Relationships are visualized as evolutionary trees (synonyms: cladograms, phylogenetic trees, phylogenies). Phylogenies have two components: branching order (showing group relationships) and branch length (showing amount of evolution). Phylogenetic trees of species and higher taxa are used to study the evolution of traits (e.g. anatomical or molecular characteristics) and the distribution of organisms (biogeography). Systematics, in other words, is used to understand the evolutionary history of life on earth.

Figure 3.63: Sample of zooplankton which includes fish eggs, tunicates, several species of copepods, gastropod and decapod larva.

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[53] From Greek *νεκτον* = "to swim".

[54] From Greek *βενθος*, meaning "depth of the sea".

[55] And again, while any attempt of classifying the enormous diversity of life are useful for communication and delimitation in science, it is also doomed from the start. Many species referred to as "planktonic" occur frequently near the sea beds as well, for example copepods.

Marine bacteria *Marine bacteria* are, like all bacteria, unicellular (although they often form biofilms or colonies like filamentous cyanobacteria) and microscopic prokaryotes. They grow to a fixed size and then reproduce through binary fission, a form of asexual reproduction. Under optimal conditions, bacteria can grow and divide extremely rapidly, and bacterial populations can double as quickly as every 9.8 minutes. Bacteria are found in all marine habitats, and even in the air to where they are transported via sea spray.

Pelagibacter ubique and its relatives may be the most abundant micro-organisms in the ocean, and it has been claimed that they are possibly the most abundant bacteria in the world. They make up about 25% (estimated as about 10^{28} cells) of all microbial plankton cells, and in the summer they may account for approximately half the cells present in temperate ocean surface water.

Roseobacter is also one of the most abundant and versatile microorganisms in the ocean. They are diversified across different types of marine habitats, from coastal to open oceans and from sea ice to sea floor, and make up about 25% of coastal marine bacteria. Members of the *Roseobacter* genus play important roles in marine biogeochemical cycles and climate change, processing a significant portion of the total carbon in the marine environment. They form symbiotic relationships which allow them to degrade aromatic compounds and uptake trace metals. During algal blooms, 20-30% of the prokaryotic community are *Roseobacter*.

The largest known bacterium, the marine *Thiomargarita namibiensis*, can be visible to the naked eye and sometimes attains 750 µm.

Cyanobacteria (Fig. 3.66) were the first primary producers to evolve an ability to turn sunlight into chemical energy about 2.3 billion years ago. They form a phylum (division) of bacteria which range from unicellular to filamentous and include colonial species. Some species occur as drifting cells floating in the ocean where they often produce algal blooms (Fig. 3.67). Unlike other prokaryotes, cyanobacteria have internal membranes, flattened sacs called thylakoids where photosynthesis is performed. Some filamentous cyanobacteria can differentiate into several different cell types: vegetative cells – the normal, photosynthetic cells that are formed under favourable growing conditions; akinetes – climate-resistant spores that may form when environmental conditions become harsh; and thick-walled heterocysts – which contain the enzyme "nitrogenase", vital for nitrogen fixation (N_2) in an anaerobic environment due to its sensitivity to oxygen.

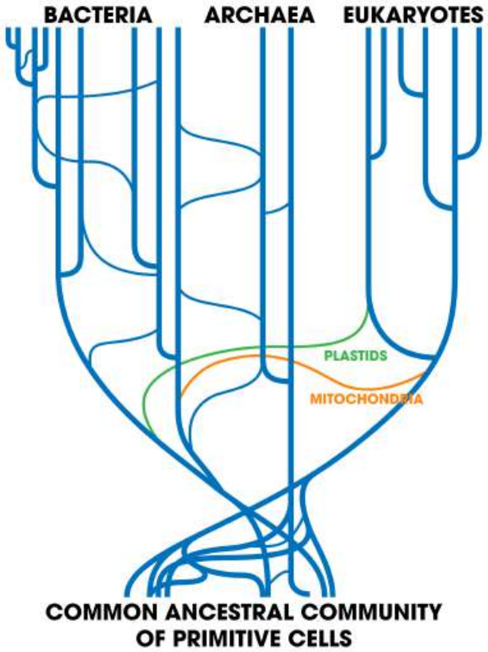

Figure 3.65: A 2005 tree of life showing horizontal gene transfers between branches, giving rise to an interconnected network rather than a tree. The figure also shows the three domains of life, bacteria, archaea, and eukaryotes (which include the autotrophic and heterotrophic protists, animals and the higher plants.)

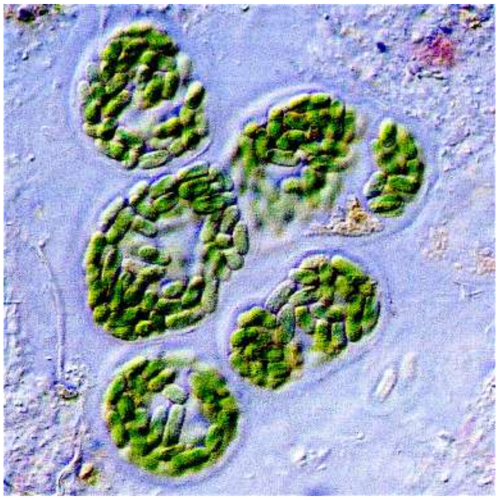

Figure 3.66: Cyanobacteria from a microbial mat. Cyanobacteria were the first organisms to release oxygen via photosynthesis.

Archaea Marine archaea constitute a domain of single-celled organisms. These microorganisms lack cell nuclei and are therefore prokaryotes. Archaea and bacteria are generally

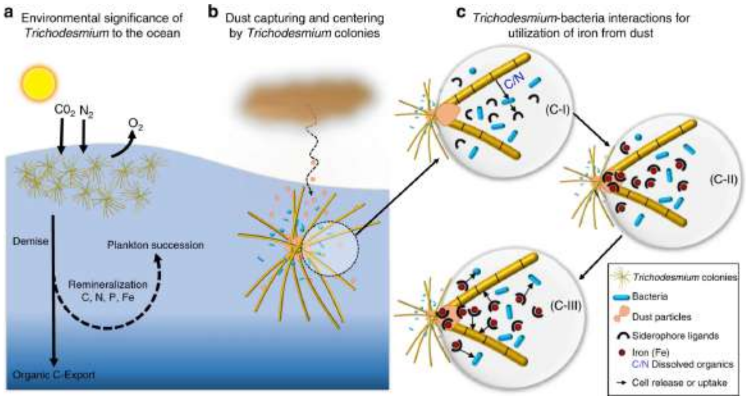

Figure 3.67: Colonies of marine cyanobacteria *Trichodesmium* interact with associated bacteria to acquire iron from dust. a) The N_2-fixing marine cyanobacterium *Trichodesmium* spp., commonly occurs in tropical and sub-tropical waters. b) *Trichodesmium* can establish massive blooms in nutrient poor ocean regions with high dust deposition, partly due to their unique ability to capture dust, centre it, and subsequently dissolve it. c) Bacteria residing within the colonies produce siderophores (c-I) that react with the dust particles in the colony core and generate dissolved Fe (c-II). This dissolved Fe, complexed by siderophores, is then acquired by both *Trichodesmium* and its resident bacteria (c-III), resulting in a mutual benefit to both partners of the consortium.

similar in size and shape, although a few archaea have very strange shapes, such as the flat and square-shaped cells of *Haloquadratum walsbyi*. Despite this morphological similarity to bacteria, archaea possess genes and several metabolic pathways that are more closely related to those of eukaryotes, notably the enzymes involved in transcription and translation. Other aspects of archaeal biochemistry are unique, such as their reliance on ether lipids in their cell membranes, such as archaeols. Archaea exhibit a great variety of chemical reactions in their metabolism and use many sources of energy: these range from organic compounds, such as sugars, to ammonia, metal ions or even hydrogen gas. Salt-tolerant archaea (the Haloarchaea) use sunlight as an energy source, and other species of archaea fix carbon; however, unlike plants and cyanobacteria, no known species of archaea does both. Archaea reproduce asexually by binary fission, fragmentation, or budding; unlike bacteria and eukaryotes, no known species forms spores. The first observed archaea were extremophiles, living in extreme environments, such as hot springs and salt lakes with no other organisms. Improved molecular detection tools led to the discovery of archaea in almost every habitat. Archaea are particularly numerous in the oceans, and the archaea in plankton may be one of the most abundant groups of organisms on the planet. Archaea are a major part of Earth's life and play important roles in many if not all biogeochemical cycles.

Figure 3.68: *Cladococcus abietinus*, a radiolarian protist. Radiolarians are 0.1 and 0.2 mm in size, with a round shell usually made of silica. They catch prey by extending parts of their body through the shell holes.

Marine "protists" These are the functionally and taxonomically very diverse marine eukaryotes that cannot be classified as plants, fungi or animals (Figs. 3.69, 3.68, 3.70). They are usually but far from always single-celled and microscopic. They are not a part of modern cladistics, because they are paraphyletic (lacking a common ancestor). Protists can be broadly divided into four groups depending on their nutrition mode. Autotrophic, photosynthetic protists are green algae, brown algae, diatoms and some dinoflagellates. Heterotrophic protists (also called "protozoans" because of their "animal-like"

Figure 3.69: Group of planktonic foraminiferans. Foraminiferans are predatory protists, protected with shells that have holes in them. The shells ("tests") are made of calcite, but are sometimes made of agglutinated sediment particles, or chitin, or (rarely) of silica. Most forams are benthic, but about 40 species are planktic.

energy and matter acquisition) feed on particulate organic matter (POM), dead or alive such as like bacteria, archaea, and other protists via their "cell mouths" or via phagocytosis. These include foraminiferans, amoebae, ciliates and flagellates. Saprotrophic protists ("slime moulds" and "slime nets") get their food from the remains of organisms that have broken down and decayed. Mixotrophic protists (especially ciliates and dinoflagellates) obtain their food from a combination of the above. Protists vary in size between a few µm up to 200 µm and sometimes even larger and are thus part of the nano- to micro-plankton or the microbenthos (often defined as < 0.1 mm).

Figure 3.70: The marine ciliate *Strombidium rassoulzadegani*. Marine ciliates are major grazers of phytoplankton and constitute an important component of the microzooplankton community with preference for small preys. Many ciliates are grazed by mesozooplankton. Thus, ciliates can be an important link to higher trophic levels.

Marine fungi Over 1500 species of marine fungi are known from marine environments. These are parasitic on marine algae or animals, or are saprobically feeding on dead organic matter. Spores of many fungal species have special appendages which facilitate attachment to the substratum. Marine fungi can also be found in sea foam and around hydrothermal areas of the ocean. A diverse range of unusual secondary metabolites is produced by marine fungi. Mycoplankton are saprotropic members of the plankton communities of marine and freshwater ecosystems. They are composed of filamentous free-living fungi and yeasts associated with planktonic particles or phytoplankton. Similar to bacterioplankton, these aquatic fungi play a significant role in heterotrophic mineralization and nutrient cycling. Mycoplankton can be up to 20 mm in diameter and over 50 mm in length. A typical milliliter of seawater contains about 100 fungal cells. This density is greater in coastal ecosystems and estuaries due to nutritional runoff from terrestrial communities. A higher diversity of mycoplankton is found around coasts and in surface waters down to 1000 metres, with a vertical profile that depends on how abundant phytoplankton is. This profile changes between seasons due to changes in nutrient availability. Marine fungi survive in a constant oxygen deficient environment, and therefore depend on oxygen diffusion by turbulence and oxygen generated by photosynthetic organisms.

Marine Porifera Sponges are animals of the phylum Porifera (Fig. 3.71). They are similar to other animals in that they are multicellular, heterotrophic, lack cell walls and produce sperm cells (Fig. 3.72). Unlike other animals, sponges lack true tissues and organs, and have no body symmetry. Sponges also do not have nervous, digestive or circulatory systems. Instead, most rely on maintaining a constant water flow through their bodies to obtain food and oxygen and to remove wastes. Their bodies are full of pores and channels allowing water to circulate through them, consisting of jelly-like mesohyl sandwiched between two thin layers of cells (Fig. 3.73). They

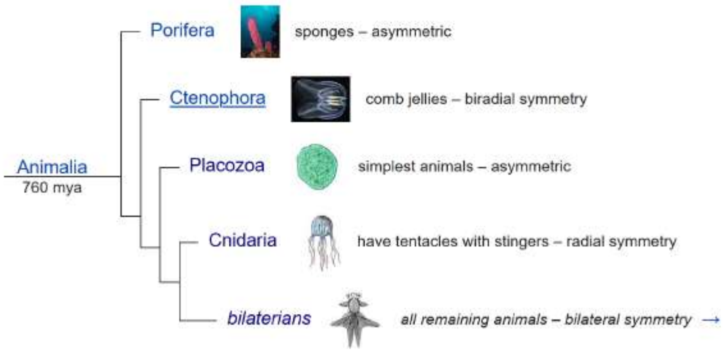

Figure 3.71: The most basal animal phyla, the animals that evolved first, are the Porifera, Ctenophora, Placozoa and Cnidaria. None of these basal body plans exhibit bilateral symmetry.

have unspecialized cells that can transform into other types and that often migrate between the main cell layers and the mesohyl in the process (see also Fig. 3.28). The shapes of their bodies are adapted for maximal efficiency of water flow through the central cavity, where it deposits nutrients, and leaves through a hole called the osculum. Many sponges have internal skeletons of spongin and/or spicules of calcium carbonate or silica. All sponges are sessile aquatic animals. Although there are freshwater species, the great majority are marine, ranging from tidal zones to depths exceeding 8,800 m. Some sponges live to great ages; the deep-sea glass sponge *Monorhaphis chuni* may live about 11,000 years.

Figure 3.72: Sponge biodiversity and morphotypes at the lip of a wall site in 20 m of water. Included are the yellow tube sponge, *Aplysina fistularis*, the purple vase sponge, *Niphates digitalis*, the red encrusting sponge, *Spirastrella coccinea*, and the gray rope sponge, *Callyspongia* sp.

While most of the approximately 5,000–10,000 known species feed on bacteria and other food particles in the water, some host photosynthesising micro-organisms as ~endosymbionts and these alliances often produce more food and oxygen than they consume (up to three times more). Such contributions to their habitats' resources are significant along Australia's Great Barrier Reef but relatively minor in the Caribbean. A few species of sponge that live in food-poor environments have become carnivores that prey mainly on small crustaceans. Many sponges shed spicules, forming a dense carpet several meters deep that keeps away echinoderms which would otherwise prey on the sponges. They also produce toxins that prevent other sessile organisms such as bryozoans or sea squirts from growing on or near them, making sponges very effective competitors for living space.

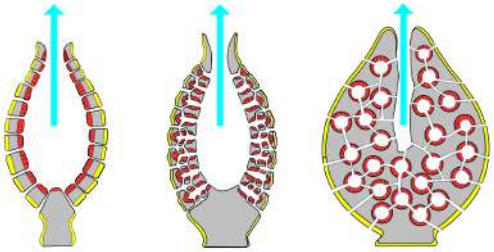

Figure 3.73: The three main sponge body structures. Left: Asconoid, middle: Syconoid, right: Leuconoid. Yellow = pinacocytes, red = choanocytes, gray = mesohyl.

Ctenophora Ctenophora (commonly known as comb jellies) comprise a phylum of invertebrate animals that live in marine waters worldwide (Fig. 3.74). They are notable for the groups of cilia they use for swimming ("combs"), and they are the largest animals to swim with the help of cilia. Most species have eight strips, called comb rows, that run the length of their bodies and bear comb-like bands of cilia, called "ctenes", stacked along the comb rows so that when the cilia beat, those of each comb touch the comb below.

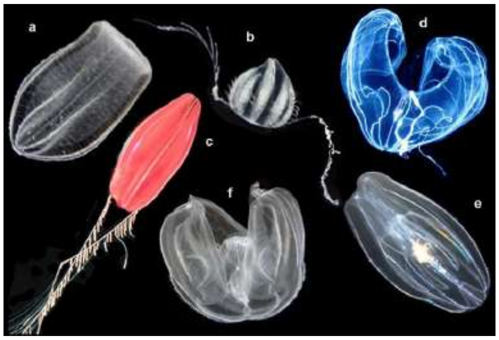

Figure 3.74: **Pelagic ctenophores:** (a) *Beroe ovata*, (b) *Euplokamis* sp., (c) *Nepheloctena* sp., (d) *Bathocyroe fosteri*, (e) *Mnemiopsis leidyi*, and (f) *Ocyropsis* sp.

Depending on the species, adult ctenophores range from a few millimeters to 1.5 m in size. Only 100 to 150 species have been validated, and possibly another 25 have not been fully described and named. The textbook examples are cydippids with egg-shaped bodies and a pair of retractable tentacles fringed with tentilla ("little tentacles") that are covered with colloblasts, sticky cells that capture prey. Their bodies consist of a mass of jelly, with a layer two cells thick on the outside, and another lining the internal cavity. The phylum has a wide range of body forms, including the egg-shaped cydippids, the flat generally combless platyctenids, and the large-mouthed beroids, which prey on other ctenophores. Like those of cnidarians, (jellyfish, sea anemones, etc.), ctenophores' bodies consist of a relatively thick, jelly-like mesoglea sandwiched between two epithelia, layers of cells bound by inter-cell connections and by a fibrous basement membrane that they secrete. Ctenophores have no central nervous system, but instead have a nerve net (rather like a cobweb) that forms a ring round the mouth and is densest near structures such as the comb rows, pharynx, tentacles (if present) and the sensory complex furthest from the mouth. The largest single sensory feature is the aboral organ (at the opposite end from the mouth). Its main component is a statocyst, a balance sensor (Fig. 3.75).

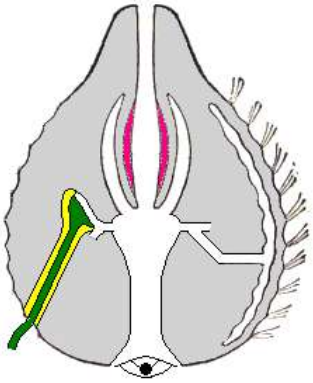

Figure 3.75: Section through a *Pleurobrachia*-like cydippid ctenophore. Left side shows canal from stomach to tentacle, right shows canal from stomach to comb-row.

Almost all ctenophores function as predators, taking prey ranging from microscopic larvae and rotifers to the adults of small crustaceans; the exceptions are juveniles of two species, which live as parasites on the salps on which adults of their species feed.

Despite their soft, gelatinous bodies, fossils thought to represent ctenophores appear in lagerstätten dating as far back as the early Cambrian, about 525 million years ago. The position of the ctenophores in the "tree of life" has long been debated. Biologists proposed that ctenophores constitute the second-earliest branching animal lineage, with sponges being the sister-group to all other multicellular animals. A 2020 analysis suggested that comb jellies are older than sponges. But in 2021, the latest study reaffirmed that sponges are the oldest among all animals.

Cnidaria Cnidaria (Fig. 3.76) is a phylum under kingdom Animalia containing over 11,000 species of aquatic animals found predominantly in marine environments. Their distinguishing feature is the "cnidocyte" (Fig. 3.77), specialized cells that they use mainly for capturing prey. Basic as their bodyplan may be, cnidocytes arguably are the most highly developed and specialised cell type in the animal kingdom, both in their mechanics and their potentially life-threatening venom. Their bodies consist of mesoglea, a non-living jelly-like substance, sandwiched between two layers of epithelium that are mostly one cell

Figure 3.76: **Four examples of Cnidaria.** Upper-left: The jellyfish *Chrysaora melanaster*, upper-right: the gorgonian *Annella mollis*, lower-left: the rocky coral *Acropora cervicornis*, lower-right: the sea anemone *Nemanthus annamensis*.

thick.

Cnidaria mostly have two basic body forms: swimming medusae and sessile polyps (Fig. 3.78), both of which are radially symmetrical with mouths surrounded by tentacles that bear cnidocytes. Both forms have a single orifice and body cavity that are used for digestion and respiration. Many cnidarian species produce colonies that are single organisms composed of medusa-like or polyp-like zooids, or both (hence they are trimorphic). Cnidarians' activities are coordinated by a decentralized nerve net and simple receptors. Several free-swimming species of Cubozoa and Scyphozoa possess balance-sensing statocysts, and some have simple eyes. Not all cnidarians reproduce sexually, with many species having complex life cycles of asexual polyp stages and sexual medusae (Fig. 3.52). Some, however, omit either the polyp or the medusa stage.

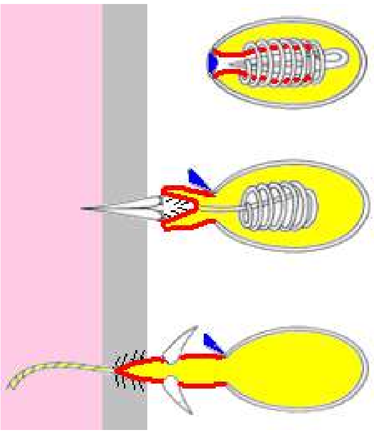

Figure 3.77: Firing sequence of the cnida in a hydra's nematocyst. Blue: operculum, red: "fingers" that turn inside out, yellow: to be injected venom, gray: victim's epidermis, pink: victim's tissues.

Cnidarians are classified into four main groups: the almost wholly sessile Anthozoa (sea anemones, corals, sea pens), swimming Scyphozoa (jellyfish), Cubozoa (box jellies), and Hydrozoa (a diverse group that includes all the freshwater cnidarians as well as many marine forms, and has both sessile members, such as *Hydra*, and colonial swimmers, such as the Portuguese Man o' War). The highly derived parasitic Myxozoa and Polypodiozoa were firmly recognized as cnidarians only in 2007.

Most cnidarians prey on organisms ranging in size from plankton to animals several times larger than themselves, but many obtain much of their nutrition from symbiontic dinoflagellates, and a few are parasites. Many are preyed on by other animals including starfish, sea slugs, fish, turtles, and even other cnidarians. Many scleractinian corals — which form the structural foundation for coral reefs — possess polyps that are filled with symbiotic photo-synthetic zooxanthellae. While reef-forming corals are almost entirely restricted to warm and shallow marine waters, other cnidarians can be found at great depths, in polar regions, and in freshwater.

Recent phylogenetic analyses support monophyly of cnidarians, as well as the position of cnidarians as the sister group of bilaterians. Fossil cnidarians have been found in rocks formed about 580 million years ago.

"Lower animals" have body bauplans that are not symmetric (Porifera) or radial-symmetric (Ctenophora, Cnidaria). In contrast, *Bilateria* have a bilaterian body (Fig. 3.79) that can be conceptualized as a cylinder with a gut running between two openings, the mouth and the anus. Around the gut it has an internal body cavity, a coelom or pseudocoelom. Animals with this bilaterally symmetric body plan have a head (anterior) end and a tail (posterior) end as well as a back (dorsal) and a belly (ventral); therefore they also have a left side and a right side.

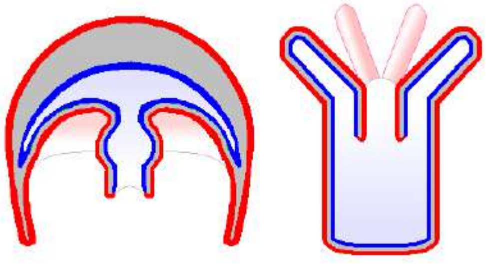

Figure 3.78: Medusa (left) and polyp (right). Medusae have the oral end down, polyps up towards the water. Red: exoderm, darkblue: endoderm, light blue: digestive cavity, gray: mesoglea.

Radial symmetry is often beneficial for sessile organisms in benthic habitats, where food and predators can come from all directions and organisms do not turn towards them.

For Bilateria, having a front end means that this part of the body encounters stimuli, such as food, favouring cephalisation, the development of a head with sense organs and a mouth. The body stretches back from the head, and many bilaterians have a combination of circular muscles that constrict the body, making it longer, and an opposing set of longitudinal muscles, that shorten the body; these enable soft-bodied animals with a hydrostatic skeleton to move by peristalsis. Most bilaterians (Nephrozoans) have a gut that extends through the body from mouth to anus, while Xenacoelomorphs have a bag gut with one opening. Many bilaterian phyla have primary larvae which swim with cilia and have an apical organ containing sensory cells. However, there are exceptions to each of these characteristics; for example, adult echinoderms are secondary radially symmetric (unlike their larvae), and certain parasitic worms have extremely simplified body structures.

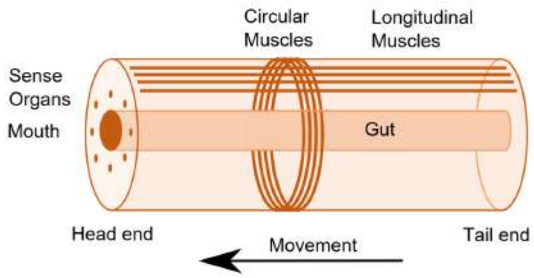

Figure 3.79: Idealised wormlike bilaterian body plan. With a cylindrical body and a direction of movement the animal has head and tail ends. Sense organs and mouth form the basis of the head. Opposed circular and longitudinal muscles enable peristaltic motion.

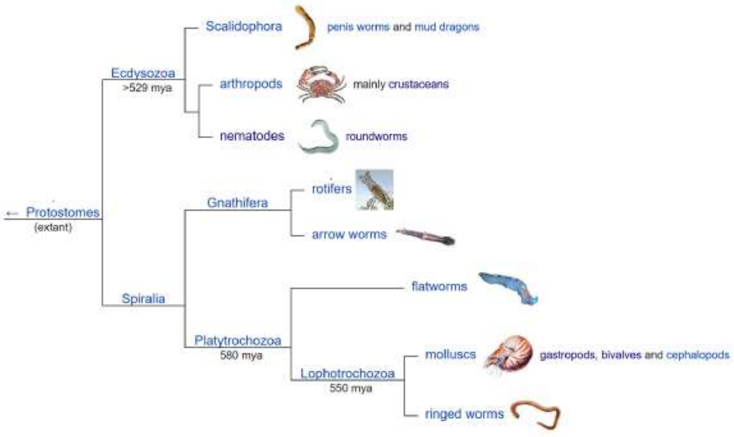

Figure 3.80: Protostomes (from Greek for "first mouth") are a superphylum of animals. It is a sister clade of the deuterostomes (from Greek for "second mouth"), with which it forms the Nephrozoa clade. Protostomes are distinguished from deuterostomes by the way their embryos develop. In protostomes the first opening that develops becomes the mouth, while in deuterostomes it becomes the anus.

The Bilateria are divided into Deuterostomes and Protostomes. The latter include (Fig. 3.80) Priapulida, marine Arthrodopa (mainly Crustaceans), Nematoda, Chaetognatha, Plathylminthes, marine Annelida, and the most commonly known invertebrate marine organisms, the Mollusca.

Priapulida Priapulida (after the Greek genitalia-exhibiting god Priapos; sometimes referred to for obvious reasons as "penis worms") is a phylum of unsegmented marine worms. Priapulids are cylindrical, ranging from 0.2–0.3 to 39 centimetres long, with a anterior mouth quite devoid of any armature or tentacles. The body is divided into a main trunk or abdomen and a somewhat swollen proboscis region ornamented with longitudinal ridges. The body is ringed and often has circles of spines, which are continued into the slightly protrusible pharynx. Some species may also have a tail or a pair of caudal appendages. The body has a chitinous cuticle that is moulted as the animal grows. Priapulids live in the mud and in comparatively shallow waters up to 90 metres deep. Some species show a remarkable tolerance for hydrogen sulfide and anoxia. They can be quite abundant in some areas. In an Alaskan bay as many as 85 adult individuals of *Priapulus caudatus* (Fig. 3.81) per square meter has been recorded, while the density of its larvae can be as high as 58,000 per square meter. Consistent morphological and molecular evidence supports their belonging to Ecdysozoa, which also includes arthropods and nematodes. They feed on slow-moving invertebrates, such as polychaete worms. About 20 extant species of priapulid worms are known, half of them being of meiobenthic size.

Figure 3.81: *Priapulus caudatus*, intertidal, boreal, circumpolar. The proboscis with the invisible mouth is the body part reaching up, down you see caudal appendages, probably for gas exchange and sensing the environment.

Nematoda Nematoda or roundworms constitute a phylum also called Nemathelminthes. They are a diverse animal phylum inhabiting a broad range of environments. Taxonomically, they are classified along with the Priapulida and the Arthropoda in the clade Ecdysozoa, and unlike flatworms (Platyhelminthes), have tubular digestive systems with openings at both ends (Fig. 3.82).

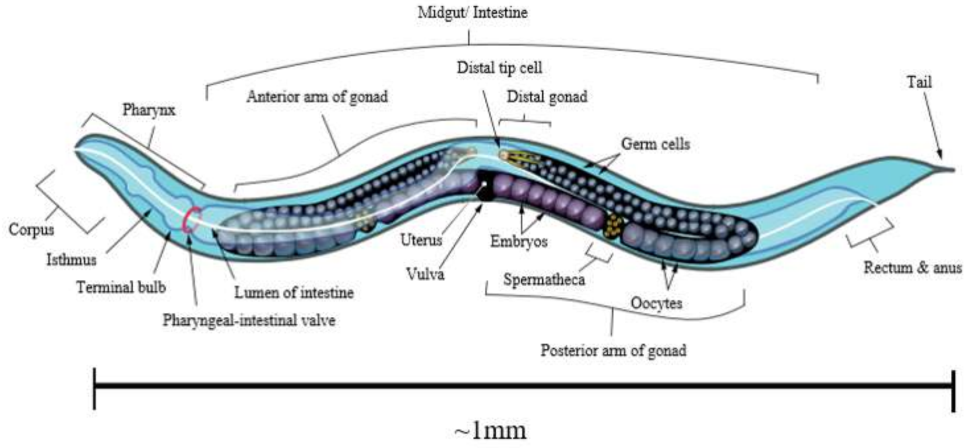

Figure 3.82: A lateral (left) side anatomical diagram of an adult-stage, hermaphroditic *Caenorhabditis elegans*.

Nematodes have successfully adapted to nearly every ecosystem: from marine (salt) to fresh water, soils, from the polar regions to the tropics, as well as the highest to the lowest of elevations. They are ubiquitous in freshwater, marine, and terrestrial environments, where they often outnumber other animals in both individual and species counts, and are found in locations as diverse as mountains, deserts, and oceanic trenches. They are found in every part of earth's lithosphere, even at great depths. They represent 90% of all animals on the ocean floor. Their numerical dominance, often exceeding a million individuals per square meter. They play crucial roles in polar ecosystems. The many parasitic forms include pathogens in most plants and animals. A third of the genera occur as parasites of vertebrates; about 35 nematode species occur in humans.

Figure 3.83: A group of marine nematods. Nematodes are ubiquitous cylindric worms which can parasite marine plants and animals.

Nematodes are very small, slender worms (Fig: 3.83): typically about 5 to 100 µm thick, and 0.1 to 2.5 mm long. The smallest nematodes are microscopic, while free-living species can reach as much as 5 cm, and some parasitic species are larger still, reaching over 1 m in length. The body is often ornamented with ridges, rings, bristles, or other distinctive structures. The head of a nematode is relatively distinct. Whereas the rest of the body is bilaterally symmetrical, the head is radially symmetrical, with sensory bristles and, in many cases, solid "head-shields" radiating outwards around the mouth. The mouth has either three or six lips, which often bear a series of teeth on their inner edges. An adhesive 'caudal gland' is often found at the tip of the tail. The epidermis is either a *syncytium* or a single layer of cells, and is covered by a thick collagenous cuticle. The cuticle is often of a complex structure and may have two or three distinct layers. Underneath the epidermis lies a layer of longitudinal muscle cells. The relatively rigid cuticle works with the muscles to create a hydroskeleton, as nematodes lack circumferential muscles. Projections run from the inner surface of muscle cells towards the nerve cords; this is a unique arrangement in the animal kingdom, in which nerve cells normally extend fibers into the muscles rather than vice versa. The mouth often includes a sharp stylet, which the animal can thrust into its prey. In some species, the stylet is hollow and can be used to suck liquids from plants or animals. In many marine nematodes, one or two unicellular "renette glands" excrete salt to maintain osmoregulation through a pore on the underside of the animal, close to the pharynx. A few aquatic nematodes possess what appear to be pigmented eye-spots, but whether or not these are actually sensory in nature is unclear.

Free-living species feed on particulate organic materials as varied as bacteria, algae, fungi, small animals, fecal matter, dead organisms, and living tissues. Free-living marine nematodes are important and abundant members of the meiobenthos. They play an important role in the decomposition process, aid in recycling of nutrients in marine environments. Many parasitic marine Nematoda infect bony fish and marine mammals.

Box 5: ***Marine worms***

Marine worms refer to all animals that typically have a long cylindrical tube-like body, no limbs, and no eyes (see *this list* of which taxa are included). Marine worms vary in size from microscopic to over 1 m in length for marine polychaete worms (bristle worms) and 58 m for the marine nemertean worm (bootlace worm), *Lineus longissimus*. Various types of worm occupy a small variety of parasitic niches, living inside the bodies of other animals. Free-living worm species live in marine environments. In biology, "worm" refers to an obsolete and paraphyletic taxon, *vermes*, used by Linnaeus and Lamarck for all non-arthropod invertebrate animals. *Parborlasia corrugatus* (see image on the right) is a ribbon worm in the family Cerebratulidae (Nemertea). It can grow to 2 m in length, and lives in marine environments down to 3,590 m. This scavenger and predator is widely distributed in cold southern oceans. Potential predators avoid it as it has a chemical defence: acidic mucus with a pH 3.5.

Arthropoda Arthrodopa (from Ancient Greek *arthron* "joint", and *pous*) "foot") are invertebrate animals having an exoskeleton, a segmented body, and paired jointed appendages (Fig. 3.84). They are distinguished by their jointed limbs and cuticle made of chitin, often mineralised with calcium carbonate. The arthropod body plan consists of segments, each with a pair of appendages. The rigid cuticle inhibits growth, so to keep growing, they have to go through moulting, which sheds their cuticula. Arthropods are bilaterally symmetrical. Some species have wings. They are an extremely diverse group, with up to 10 million species. The evolutionary ancestry of arthropods dates back to the Cambrian and is monophyletic.

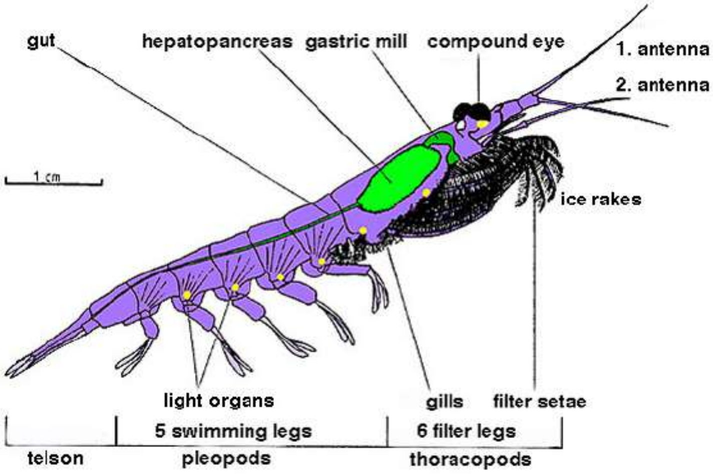

Figure 3.84: Body structure of a typical crustacean – Krill (Decapoda).

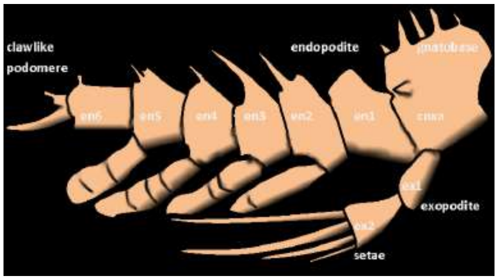

Figure 3.85: The biramous leg of a crustcean. The expodit often carries gills, while the endopodit may be adapted to walk on sediment or to swim.

Of the four main extant groups of Arthropoda (Insecta, Myriapoda, Arachnida and Crustacea), one is predominately aquatic and especially marine: the ***Crustacea*** (Fig. 3.84), which include copepods (and other crustacean zooplankton), Decapoda ("ten-footed" crustaceans, such as crabs, lobster, crayfish, shrimps, and krill), woodlice (Isopoda), and barnacles. The crustacean group can be treated as a subphylum under the clade Mandibulata; because of recent molecular studies it is now well accepted that the crustacean group is paraphyletic, and comprises all animals in the clade Pancrustacea other than hexapods. Some crustaceans are more closely related to insects and the other hexapods than they are to certain other crustaceans.

The 67,000 described crustacean species range in size from *Stygotantulus stocki* at 0.1 mm, to the Japanese spider crab with a leg span of up to 3.8 m and a mass of 20 kg. Crustaceans are distinguished from other groups of arthropods, such as insects, myriapods and chelicerates, by the possession of biramous (two-parted) limbs (Fig. 3.85), and by their larval forms, such as the nauplius stage of branchiopods and copepods.

Most crustaceans are free-living aquatic animals (pelagic like herbivorous amphipods (Fig. 3.89) or benthic like detritivore crabs), but some are parasitic (e.g. Rhizocephala; Figs. 3.87 & 3.88, fish lice, tongue worms) and some are sessile (e.g. barnacles, Fig. 3.86). The group has an extensive fossil record, reaching back to the Cambrian, and includes living fossils such as *Triops cancriformis*, which has existed apparently unchanged since the Triassic.

About 8 million tons of crustaceans per year are produced by fishery or farming for human consumption, most of it being shrimp and prawns. Krill and copepods are not as widely fished, but may be the animals with the greatest biomass on the planet, and form a vital part of the food chain.

Figure 3.86: Barnacles, which are crustacean suspension feeders, and limpets, which are molluscan grazer-scrapers, compete for space in the intertidal zone. Most barnacles are sessile and dwell continually in their shells, which are usually constructed of six plates. These plates are not moulted; however, like all ecdysozoans, the barnacle itself will still moult its cuticle. Barnacles reach into the water column with modified legs. These feathery appendages beat rhythmically to draw plankton and detritus into the shell for consumption.

Figure 3.87: Externa of a parasitical barnacle (Cirripedia), *Sacculina carcini* (highlighted), on a female swimming crab (*Liocarcinus holsatus*, Decapoda), from the Belgian coastal waters.

Figure 3.88: Specimen of the parasitical copepod *Acanthochondria cornuta* on the operculum, next to the gills of a European flounder (*Platichthys flesus).* Length of each egg sack approx. 4 mm.

Chaetognatha The Chaetognatha (meaning bristle-jaws) are a phylum of predatory marine worms that are a major component of plankton worldwide. Commonly known as "arrow worms" (Fig. 3.90), about 20% of the known Chaetognatha species are benthic, and can attach to algae and rocks. They are found in all marine waters, from surface tropical waters and shallow tide pools to the deep sea and polar regions. Most chaetognaths are transparent and are torpedo shaped, but some deep-sea species are orange. They range in size from 2 to 120 millimetres.

There are more than 120 modern species assigned to over 20 genera. Despite the limited diversity of species, the number of individuals is large.

Arrow worms are usually considered a type of protostome that do belong to neither Ecdysozoa nor Lophotrochozoa.

Figure 3.90: The chaetognath *Spadella cephaloptera*.

Chaetognaths are transparent or translucent dart (arrow)-shaped animals covered by a cuticle. The body is divided into a distinct head, trunk, and tail. There are between four and fourteen hooked, grasping spines on each side of their head, flanking a hollow vestibule containing the mouth (Fig. 3.91). The spines are used in hunting, and covered with a flexible hood arising from the neck region when the animal is swimming. All chaetognaths are carnivorous, preying on other planktonic animals. Some species are also reported to be omnivores, feeding on algae and detritus.

The trunk bears one or two pairs of lateral fins incorporating structures superficially similar to the fin rays of fish, with which they are not homologous, however: unlike those of vertebrates, these are composed of a thickened basement membrane extending from the epidermis. An additional caudal fin covers the post-anal tail. Two chaetognath species, *Caecosagitta macrocephala* and *Eukrohnia fowleri*, have bioluminescent organs on their fins.

Chaetognaths swim in short bursts using a dorso-ventral undulating body motion, where their tail fin assists with propulsion and the body fins with stabilisation and steering. Some species are known to use the neurotoxic tetrodotoxin to subdue prey.

Figure 3.89: Many crustaceans are very small, like this tiny amphipod, and make up a significant part of the ocean's zooplankton.

Figure 3.91: The "jaw" of the chaetognath *Sagitta* spec.

Platyhelminthes Flatworms or Platyhelminthes (from the Greek *πλατύ*, meaning "flat" and *ἑλμινς*, meaning "worm") are a phylum of relatively simple bilaterian, unsegmented, soft-bodied invertebrates. Unlike other bilaterians, they are acoelomates (having no body cavity), and have no specialized circulatory and respiratory organs, which restricts them to having flattened shapes that allow oxygen and nutrients to pass through their bodies by diffusion. The digestive cavity has only one opening for both ingestion (intake of nutrients) and egestion (removal of undigested wastes); as a result, the food cannot be processed continuously.

In traditional texts, Platyhelminthes are divided into "Turbellaria" (Fig. 3.92), which are mostly non-parasitic, and three entirely parasitic groups: Cestoda, Trematoda and Monogenea; however, since the turbellarians have since been proven not to be monophyletic, this classification is now deprecated.

Free-living flatworms are mostly predators, and live in water or in shaded, humid terrestrial environments. The name "Turbellaria" refers to the "whirlpools" of microscopic particles created close to the skins of aquatic species by the movement of their cilia. Cestodes (tapeworms) and trematodes (flukes) have complex life-cycles, with mature stages that live as parasites in the digestive systems of fish or vertebrates, and intermediate stages that infest secondary hosts. The eggs of trematodes are excreted from their main hosts, whereas adult cestodes generate vast numbers of hermaphroditic, segment-like proglottids that detach when mature, are excreted, and then release eggs. Unlike the other parasitic groups, the monogeneans are external parasites infesting aquatic animals, and their larvae metamorphose into the adult form after attaching to a suitable host.


Figure 3.92: The turbellarian flatworm *Pseudoceros dimidiatus* grows to be up to 8 cm. The bright and contrasting colours serve as a warning for predators to not eat this inedible species. These flatworms feed exclusively on colonial ascidians. The species is widespread on coral reefs in the Indian Ocean from the Red Sea to Australia and in the Western Pacific Ocean. It can reproduce both asexually, by dividing itself, and sexually. The species is a hermaphrodite. When two flatworms reproduce they battle over who gets to fertilize and who is fertilized.

Mollusca *Molluscs* (Latin for "soft") form a phylum with about 85,000 extant recognized species. They are the largest marine phylum in terms of species count, containing about 23% of all the named marine organisms. Molluscs have more varied forms than other invertebrate phyla (Fig. 3.93). They are highly diverse, not just in size and in anatomical structure, but also in behaviour and in habitat.


Figure 3.93: Diversity and variability of shells of molluscs (mainly Bivalvia and Gastropoda) on display in the Museum für Naturkunde Berlin/Germany.

The mollusc phylum is divided into 9 or 10 taxonomic classes. These classes include gastropods, bivalves and cephalopods, as well as other lesser-known but distinctive classes. Gastropods with protective shells are referred to as snails, whereas gastropods without protective shells are referred to as slugs. **Gastropoda** are by far the most numerous molluscs in terms of species. **Bivalvia** include clams, oysters, cockles, mussels, scallops, and numerous other families (see also p. 57 for feeding morphology). There are about 8,000 marine bivalves species (including brackish water and estuarine species). A deep sea ocean quahog clam has been reported as having lived 507 years making it the longest recorded life of all animals apart from colonial animals, or near-colonial animals like sponges. **Cephalopoda** include octopus, squid and cuttlefish. About 800 living species of marine cephalopods have been identified, and an estimated 11,000 extinct taxa have been described. They are found in all oceans, but there are no fully freshwater cephalopods.

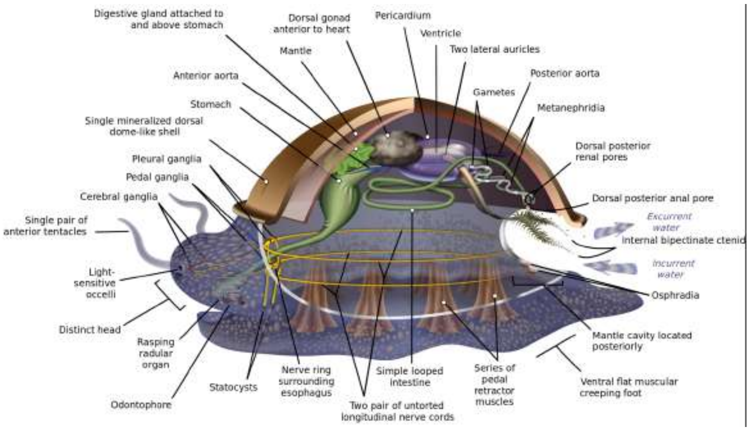

Figure 3.94: Anatomical diagram of a hypothetical ancestral mollusc.

Molluscs have such diverse shapes that many textbooks base their descriptions of molluscan anatomy on a generalized or hypothetical ancestral mollusc (Fig. 3.94). This generalized mollusc is unsegmented and bilaterally symmetrical with an underside consisting of a single muscular foot. Beyond that it has three further key features. Firstly, it has a muscular cloak called a mantle covering its viscera and containing a significant cavity used for breathing and excretion. A shell secreted by the mantle covers the upper surface. Secondly (apart from bivalves) it has a rasping tongue called a radula used for feeding. Thirdly, it has a nervous system including a complex digestive system using microscopic, muscle-powered hairs called cilia to exude mucus. The generalized mollusc has two paired nerve cords (three in bivalves). The brain, in species that have one, encircles the esophagus. Most molluscs have eyes and all have sensors detecting chemicals, vibrations, and touch.

Good evidence exists for the appearance of marine gastropods, cephalopods and bivalves in the Cambrian period 541 to 485.4 million years ago.

Figure 3.95: Some marine molluscs (from left to right): *Tonicella lineata* (Lined chiton), *Sepioteuthis lessoniar* *a, Nautilus* *en irradians* *ticus* (Blue se

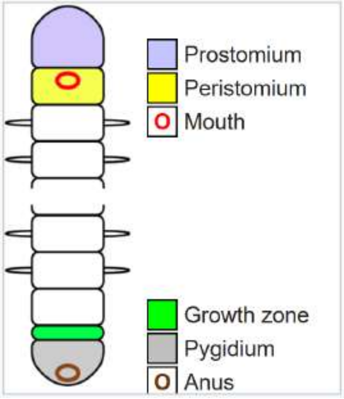

Figure 3.96: Diagram of segments of an annelid.

Annelida Annelida (from Latin *anellus*, "little ring"), also known as the ringed worms (Figs. 3.96 & 3.97), are a large phylum, with over 22,000 extant species including ragworms, earthworms and leeches. The species exist in and have adapted to various ecologies – some in marine environments as distinct as tidal zones and hydrothermal vents, others in fresh water, and yet others in moist terrestrial environments.

The annelids are bilaterally symmetrical, triploblastic, coelomate, invertebrate organisms. They also have parapodia for locomotion. Most textbooks still use the traditional division into *polychaetes* (almost all marine), *oligochaetes* (which include earthworms) and *leeches*. Cladistic research since 1997 has radically changed this scheme, viewing leeches as a sub-group of oligochaetes and oligochaetes as a sub-group of polychaetes. In addition, the Pogonophora, Echiura and Sipuncula, previously regarded as separate phyla, are now regarded as sub-groups of polychaetes. Annelids are considered members of the Lophotrochozoa, a "super-phylum" of protostomes that also includes molluscs, brachiopods, and nemerteans.

The basic annelid form (Figs. 3.96 & 3.98) consists of multiple segments. Each segment has the same sets of organs and, in most polychates, has a pair of parapodia that many species use for locomotion. Septa separate the segments of many species, but are poorly defined or absent in others, and Echiura and Sipuncula show no obvious signs of segmentation.

In species with well-developed septa, the blood circulates entirely within blood vessels, and the vessels in segments near the front ends of these species are often built up with muscles that act as hearts. The septa of such species also enable them to change the shapes of individual segments, which facilitates movement by peristalsis ("ripples" that pass along the body) or by undulations that improve the

Figure 3.97: Sea mouse *Aphrodita aculeata*, taken at the Marine Aquarium, Lyme Regis, Dorset, UK. This is a marine polychaete worm found in the North Atlantic, the North Sea, the Baltic Sea and the Mediterranean. The sea mouse normally lies buried head-first in the sand. It has been found at depths of over 3,000 m.

effectiveness of the parapodia. In species with incomplete septa or none, the blood circulates through the main body cavity without any kind of pump, and there is a wide range of locomotory techniques – some burrowing species turn their pharynges inside out to drag themselves through the sediment.

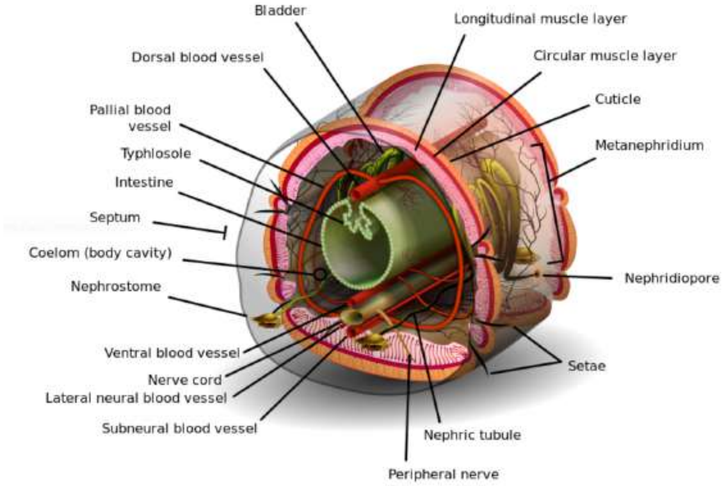

Figure 3.98: Diagram of segments of an annelid.

Feeding structures in the mouth region vary widely. Many polychaetes have a muscular pharynx that can be turned inside out to extend it. In these animals the foremost few segments often lack septa so that, when the muscles in these segments contract, the sharp increase in fluid pressure from all these segments everts the pharynx very quickly. Two families, the Eunicidae and Phyllodocidae, have evolved jaws, which can be used for seizing prey, biting off pieces of vegetation, or grasping dead and decaying matter. On the other hand, some predatory polychaetes have neither jaws nor eversible pharynges. Selective deposit feeders generally live in tubes on the sea-floor and use palps to find food particles in the sediment and then wipe them into their mouths. Filter feeders use "crowns" of palps covered in cilia that wash food particles towards their mouths. Non-selective deposit feeders ingest soil or marine sediments via mouths that are generally unspecialised. Some clitellates have sticky pads in the roofs of their mouths, and some of these can evert the pads to capture prey. Leeches often have an evertable proboscis, or a muscular pharynx with two or three teeth.

Figure 3.99: *Lamellibrachia* tube worms (here *L. luymes*) have no gut and gain nutrients from symbiontic chemoautotrophic bacteria living inside them.

Marine annelids may account for over one-third of bottom-dwelling animal species around coral reefs and in tidal zones. Burrowing species increase the penetration of water and oxygen into the sea-floor sediment, which encourages the growth of populations of aerobic bacteria and small animals alongside their burrows. Although the parasitic, blood-sucking leeches do little direct harm to their victims, some transmit flagellates that can be very dangerous to their hosts. Some small tube-dwelling oligochaetes transmit myxosporean parasites that cause whirling disease in fish.

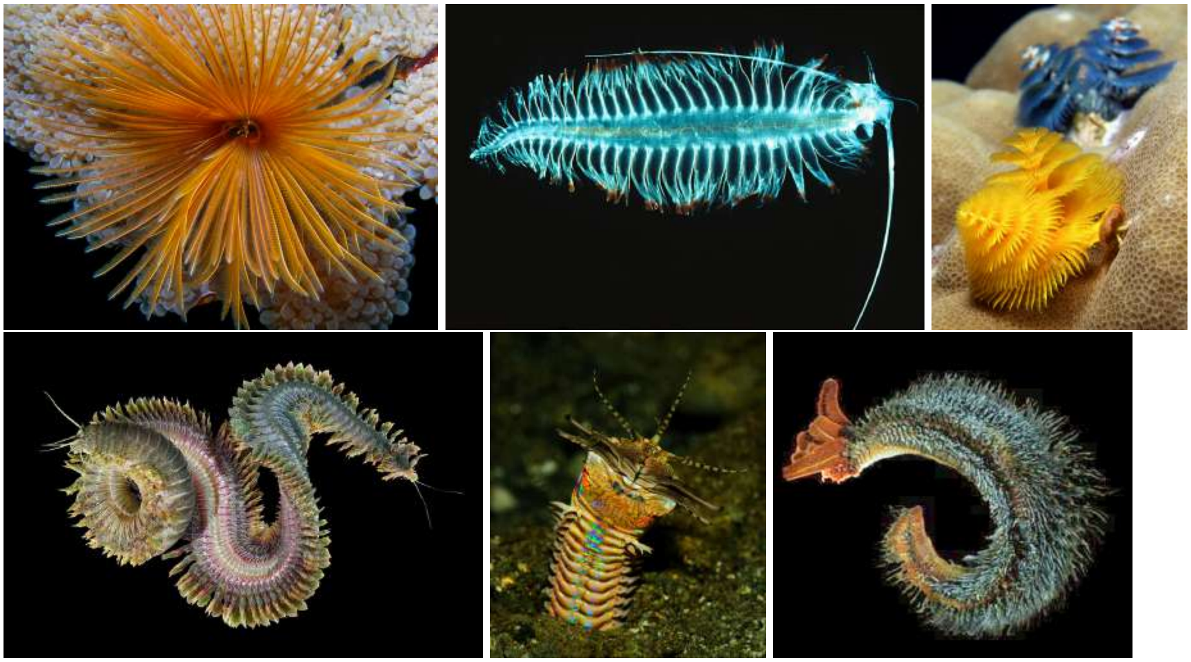

Figure 3.100: Some marine annelids, all polychaetes (from left to right): *Sabellaastarte* sp. (Feather duster worm), *Tomopteris* sp. (planktonic bristleworm), *Spirobranchus giganteus* (Christmas tree worm), *Alitta virens* (sand worm), *Eunice aphroditois* (sand striker), *Alvinella pompejana* (Pompeii worm)

DEUTEROSTOMES In deuterostomes the first opening that develops in the growing embryo becomes the anus, while in protostomes it becomes the mouth (Fig. 3.101). Deuterostomes form a superphylum of animals and are the sister clade of the protostomes. The deuterostomes include the echinoderms, hemichordates, tunicates and finally the vertebrates with fish and mammals (Fig. 3.102).

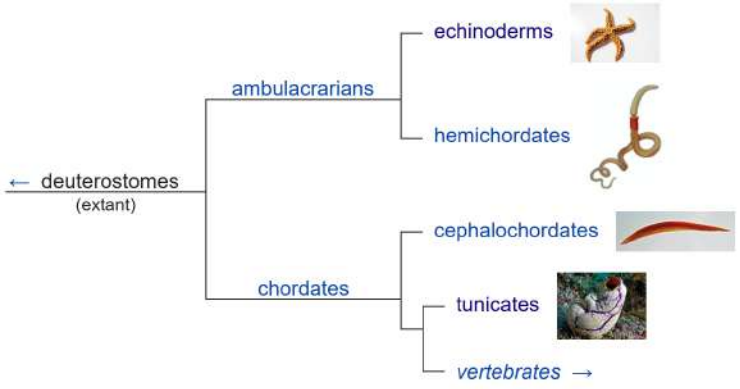

Figure 3.102: Phylogenetic relationships within deuterostomes.

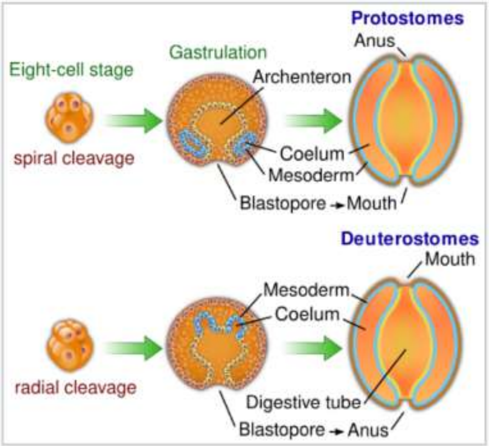

Figure 3.101: Early development differences between deuterostomes versus protostomes. In deuterostomes, blastula divisions occur as radial cleavage because they occur parallel or perpendicular to the major polar axis. In protostomes the cleavage is spiral because division planes are oriented obliquely to the polar major axis. During gastrulation, deuterostome embryo's anus is given first by the blastopore while the mouth is formed secondarily, and vice versa for the protostomes.

Echinoderms Echinodermata (Fig. 3.103) (from Ancient Greek εχῖνος "hedgehog" and δερμα "skin") is a phylum of purely marine invertebrates. The adults are recognizable by their (usually five-point, "penta") secondary radial symmetry, and include **starfish**, **sea urchins**, **bristle stars**, and **sea cucumbers**, as well as the **sea lilies**. Adult echinoderms are found on the sea bed at every ocean depth, from the intertidal zone to the abyssal zone. The phylum contains about 7000 living species, making it the second-largest grouping of deuterostomes. All echinoderms are marine and nearly all are benthic. Some sea-lilies can swim at great velocity for brief periods of time, and a few deep-sea sea cucumbers are fully floating. The "echinopluteus" larvae (Fig. 3.105) of echinoderms are pelagic and planktonic, and with the aid of ocean currents can be transported for great distances, reinforcing the global distribution of the phylum.

Following subdivisions are traditionally recognised (Fig. 3.104): the Asteroidea (starfish, 1,745 recent species), Ophiuroidea (brittle stars, 2,300 species), Echinoidea (sea urchins and sand dollars, 900 species), Holothuroidea (sea cucumbers, 1,430 species), and the Crinoidea (feather stars and sea lilies, 580 species).

Apart from their radial symmetry, echinoderms have a few other unique morphological characteristics, primarily their exosceleton of ossicles (Fig. 3.106) and their tube feet (Fig. 3.107), part of their internal water vascular (or "ambulacral") system.

Crinoids are suspension feeders and spread their arms wide into the water current to catch particles floating past.

Figure 3.103: The diversity of the Echinodermata.

These are caught by the tube feet on the pinnules, moved into the ambulacral grooves, wrapped in mucus and conveyed to the mouth by the cilia lining the grooves.

Also many brittle stars are suspension feeders, raising their branched arms to collect zooplankton. They secure food particles with mucus strands, spines or tube feet on their raised arms. Some are scavengers and feeders on detritus. Others again are voracious carnivores and able to lasso their waterborne prey with a sudden encirclement by their flexible arms.

Many sea urchins graze on benthic algae, often scraping off the thin layer of algae covering the surfaces of rocks with their specialised mouthparts. Other species devour smaller organisms, which they may catch with their tube feet. They may also feed on dead fish and other animal matter. Sand dollars may perform suspension feeding and feed on phytoplankton, detritus, algal pieces and bacteria surrounding grains of sand.

Many sea cucumbers are mobile deposit or suspension feeders, using their podia to actively capture food and then stuffing the particles individually into their mouths. Others ingest large quantities of sediment, absorb the organic matter and pass the indigestible mineral particles through their guts. In this way they disturb and process large volumes of substrate, often leaving characteristic ridges of sediment on the seabed. Some sea cucumbers live in burrows, anterior-end down and anus on the surface, swallowing sediment and passing it through their gut. Other burrowers live anterior-end up and wait for detritus to fall into the entrances of the burrows or rake in debris from the surface nearby with their podia.

Nearly all starfish are detritivores or carnivores, though a few are suspension feeders. Small fish may be captured and dead animal matter may be scavenged but the main prey items are living invertebrates, mostly bivalve molluscs. To feed on one of these, the starfish moves over it, attaches its tube feet and exerts pressure on the valves by arching its back. When a small gap between the valves is formed, the starfish inserts part of its stomach into the prey, excretes digestive enzymes and slowly liquefies the soft body parts. As the adductor muscle of the shellfish relaxes, more stomach is inserted and when digestion is complete, the stomach is returned to its usual position in the starfish with its now liquefied bivalve meal inside it. The same everted stomach process is used by other starfish to feed on sponges, sea anemones, corals, detritus and algal films.

Many echinoderms have remarkable powers of regeneration. They species routinely autotomise and regenerate arms and viscera (Fig. **??**). Sea cucumbers often discharge parts of their internal organs if they perceive themselves to be threatened. The discharged organs and tissues are regenerated

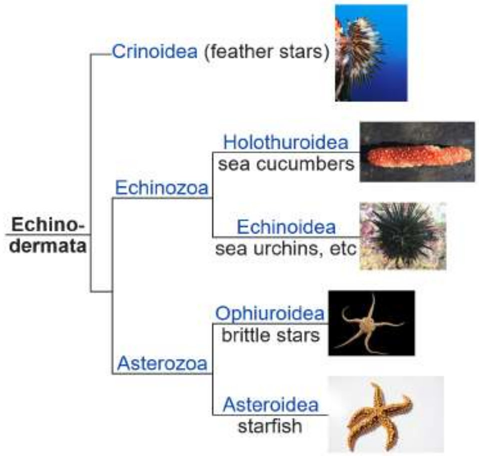

Figure 3.104: Phylogenetic relationships within the extant Echinodermata.

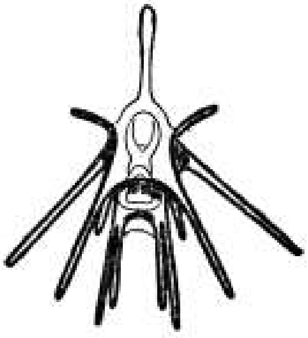

Figure 3.105: A bilaterally symmetric echinopluteus larva with larval arms. Although adult echinoderms possess pentaradial, or five-sided, symmetry, echinoderm larvae are ciliated, free-swimming organisms that organize in bilateral symmetry which makes them look like embryonic chordates. Later during metamorphosis, the left side of the body grows at the expense of the right side, which is eventually absorbed. The left side then grows in a pentaradially symmetric fashion, in which the body is arranged in five parts around a central axis. The secondary radial symmetry is an adaptation to their sessile existence. To stress this point: The mobile benthic sea cucumbers (Holothuridae) are, when adults, again **tertiary** bilateral symmetric!

over the course of several months. Sea urchins are constantly replacing spines lost through damage. Sea stars and sea lilies readily lose and regenerate their arms. In a few sea star species a single arm can survive and develop into a complete individual and in some species, the arms are intentionally detached for the purpose of asexual reproduction. During periods when they have lost their digestive tracts, sea cucumbers live off stored nutrients and even absorb DOM matter directly from the water.

Echinoderms are the prey of many organisms, such as crabs, sharks, sea birds and other echinoderms. Antipredator defences include the presence of spines, toxins, which can be inherent or delivered through the tube feet, and the discharge of sticky entangling threads by sea cucumbers. Because of their connective tissue, which can change rapidly to a rigid state, echinoderms are very difficult to dislodge from crevices. Certain sea cucumbers have a cluster of "Cuvierian" tubules which can be ejected as long sticky threads from their anus and entangle and permanently disable an attacker. Another defensive strategy sometimes adopted by sea cucumbers is to rupture the body wall and discharge the gut and internal organs. The animal has a great regenerative capacity and will regrow the lost parts later. Starfish and brittle stars may undergo autotomy when attacked, an arm becoming detached which may distract the predator for long enough for the animal to escape. Some starfish species can "swim" away from what may be danger, foregoing the regrowth by not losing limbs. It is not unusual to find starfish with arms of different sizes in various stages of regrowth.

Echinoderms play an important role in marine, benthic ecosystems. The grazing of sea urchins reduces the rate of colonization of bare rock by settling organisms but also keeps algae in check, thereby enhancing the biodiversity of coral reefs. The burrowing of sand dollars, sea cucumbers and some starfish stirs up the sediment and depletes the sea floor of nutrients. Their digging activities increases the depth to which oxygen can seep and allows a more complex ecological tier-system to develop. Some sea urchins can bore into solid rock and this bioerosion can destabilise rock faces and release nutrients into the ocean. Coral reefs are also bored into in this way but the rate of accretion of carbonate material is often greater than the erosion produced by the sea urchin. It has been estimated that echinoderms capture and sequester about 0.1 gigatonnes of carbon per year as calcium carbonate, making them important contributors in the global carbon cycle.

Echinoderms sometimes have large population swings which can cause marked consequences for ecosystems. An example is the change from a coral-dominated reef system to an alga-dominated one that resulted from the mass mortality

Figure 3.106: Ossicles are small calcareous elements embedded in the dermis of the body wall of echinoderms. They form part of the endoskeleton and provide rigidity and protection. They are found in different forms and arrangements in sea urchins, starfish, brittle stars, sea cucumbers, and crinoids. The figure shows two sea urchin skeletons atop each other.

Figure 3.107: Tube feet (more technically called podia) are small active tubular projections on the oral face of an echinoderm, whether the arms of a starfish, or the undersides of sea urchins, sand dollars and sea cucumbers. They are part of the water vascular system and function in locomotion, feeding, and respiration.

Figure 3.108: A sea star of the species *Linckia guildingi* regrowing from a single shed arm (the larger arm).

of the tropical sea urchin *Diadema antillarum* in the Caribbean Sea in 1983. Sea urchins are among the main herbivores on reefs and there is usually a fine balance between the urchins and the kelp and other algae on which they graze. A diminution of the numbers of predators (otters, lobsters and fish) can result in an increase in urchin numbers causing overgrazing of kelp forests with the result that an alga-denuded *urchin barren* forms (Fig. 3.109). On the Great Barrier Reef, an unexplained increase in the numbers of crown-of-thorns starfish (*Acanthaster planci*), which graze on living coral tissue, has had considerable impact on coral mortality and coral reef biodiversity.

Figure 3.109: Urchin barren: When predation of sea urchins by sea otters or orcas declines because of overfishing or pollution, sea urchin population growth is unchecked. Since sea urchins eat kelp, destructive sea urchin grazing of kelp beds initiates a regime shift from kelp forest to barren, in which one stable community state is shifted to another. A kelp bed can re-establish itself when urchin grazing intensity decreases again.

Echinoderms form part of the diet of many organisms such as bony fish, sharks, eider ducks, gulls, crabs, gastropod molluscs, sea otters, Arctic foxes and humans. Larger starfish prey on smaller ones and the great quantity of eggs and larvae produced form part of the zooplankton, consumed by many marine creatures. Crinoids are relatively free from predation. The body cavities of many sea cucumbers and some starfish provide a habitat for parasitic or symbiotic organisms including fish, crabs, worms and snails.

Hemichordata Hemichordata is a phylum of marine deuterostome animals, generally considered the sister group of the echinoderms. They appear in the Lower or Middle Cambrian and include two main classes: Enteropneusta (acorn worms), and Pterobranchia. A third class, Planctosphaeroidea, is known only from the larva of a single species, *Planctosphaera pelagica*.

Acorn worms are solitary worm-shaped organisms (Fig. 3.110). They generally live in burrows (the earliest secreted tubes) and are deposit feeders, but some species are pharyngeal filter feeders, while the family Torquaratoridae are free living detritivores. Pterobranchs are filter-feeders, mostly colonial, living in a collagenous tubular structure called a coenecium.

Figure 3.110: An acornworm.

Cephalochordata The Cephalochordata are the most basal Chordata taxon and share with the other taxa the five synapomorphies notochord, dorsal hollow nerve cord, endostyle, pharynx and post-anal tail. Cephalochordates are typically distributed in the sandy sediments of tropical and temperate shallow seas, although *Asymmetron inferum* has been found in the vicinity of whale falls at a depth of about 225 m. They can swim, but are mostly benthic as adults. They only expose the front end to the water and filter-feed on plankton by means of a branchial ciliary current that passes water through a mucous sheet. *Branchiostoma floridae* traps particles from microbial to small phytoplankton size, while *Branchiostoma lanceolatum* (Fig. 3.111) prefers bigger particles (>4 μm). Cephalochordata are especially interesting for evolutionary biologists for their role in the evolution of the chordata. Their ecological importance is rather limited.

Tunicata Tunicates are marine invertebrate animals of the subphylum Tunicata5. It is part of the Chordata, a phylum which includes all animals with dorsal nerve cords and notochords (including vertebrates). Their name derives from their unique outer covering or "tunic", which is formed from proteins and carbohydrates, and acts as an exoskeleton. In some species, it is thin, translucent, and gelatinous, while in others it is thick, tough, and stiff.

Some tunicates live as solitary individuals, but others replicate by budding and become colonies, each unit being known as a zooid. They are marine filter feeders with a water-filled, sac-like body structure (Figs. 3.29 & 3.112) and two tubular openings, known as siphons, through which they draw in and expel water. During their respiration and feeding, they take in water through the incurrent (or inhalant) siphon and expel the filtered water through the excurrent (or exhalant) siphon. Most adult tunicates are sessile, immobile and permanently attached to rocks or other hard surfaces on the ocean floor; others, such as salps, larvaceans, doliolids and pyrosomes, swim in the pelagic zone of the sea as adults.

Various species of the subphylum tunicata are commonly known as ascidians, sea squirts, sea pork, sea livers, or sea tulips.

Despite their simple appearance and very different adult form, their close relationship to the vertebrates is evidenced by the fact that during their mobile, planktonic larval stage, they possess a notochord or stiffening rod and resemble a tadpole (Fig. 3.113).

Colonies of tunicates occur in a range of forms, and vary in the degree to which zooids integrate with one another. In the simplest systems, the individual animals are widely separated, but linked together by horizontal connections called stolons, which grow along the seabed. Other species have the zooids growing closer together in a tuft or clustered together and sharing a common base. The most advanced colonies involve the integration of the zooids into a common structure surrounded by the tunic. These may have separate buccal siphons and a single central atrial siphon and may be organized into larger systems, with hundreds of star-shaped units. Often, the zooids in a colony are tiny but very numerous, and the colonies can form large encrusting or mat-like patches

By far the largest class of tunicates is the Ascidiacea. The body of an ascidian is surrounded by a test or tunic (Fig. 3.114). The tunic is composed of proteins and complex carbohydrates, and includes tunicin, a variety of **cellulose**. The tunic is unique among invertebrate exoskeletons in that it can grow as the animal enlarges and does not need to be

Figure 3.111: Lancelet (or amphioxus) *Branchiostoma lanceolatum*, approx. 22 mm.

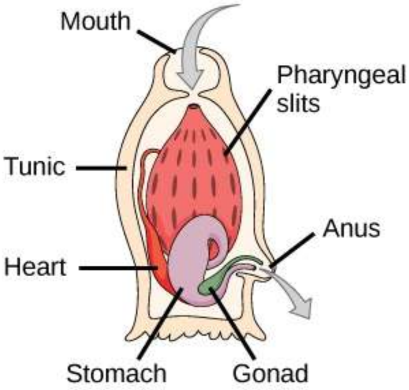

Figure 3.112: In the adult stage of the tunicate the notochord, nerve cord, and tail disappear.

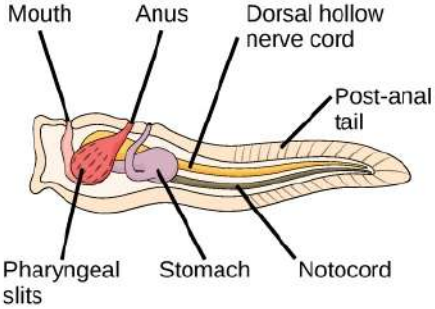

Figure 3.113: The larval stage of the tunicate possesses all of the features characteristic of chordates: a notochord, a dorsal hollow nerve cord, pharyngeal slits, and a post-anal tail.

Figure 3.114: *Polycarpa aurata*, the gold-mouth sea squirt.

periodically shed. Inside the tunic is the body wall or mantle composed of connective tissue, muscle fibres, blood vessels, and nerves. Two openings are found in the body wall: the buccal siphon at the top through which water flows into the interior, and the atrial siphon on the ventral side through which it is expelled. A large pharynx occupies most of the interior of the body. It is a muscular tube linking the buccal opening with the rest of the gut. It has a ciliated groove known as an endostyle on its ventral surface, and this secretes a mucous net which collects food particles and is wound up on the dorsal side of the pharynx. The gullet, at the lower end of the pharynx, links it to a loop of gut which terminates near the atrial siphon. The walls of the pharynx are perforated by several bands of slits, known as stigmata, through which water escapes into the surrounding water-filled cavity, the atrium. This is criss-crossed by various rope-like mesenteries which extend from the mantle and provide support for the pharynx, preventing it from collapsing, and also hold up the other organs.

The Thaliacea, the other main class of tunicates, is characterised by free-swimming, pelagic individuals. They are all filter feeders using a pharyngeal mucous net to catch their prey. The order Pyrosomida are bioluminous colonial tunicates with a hollow cylindrical structure (Fig. 3.115). The buccal siphons are on the outside and the atrial siphons inside. About 10 species are known, and all are found in the tropics. The 23 species of the order Doliolida are small, mostly under 2 cm long. They are solitary, have the two siphons at opposite ends of their barrel-shaped bodies, and swim by jet propulsion. The 40 species of the order Salpida are also small, under 4 cm long, and found in the surface waters of both warm and cold seas. They also move by jet propulsion, and often form long chains by budding off new individuals (Fig. 3.117).

A third class, the Larvacea (or Appendicularia), is the only group of tunicates to retain their chordate characteristics in the adult state, a product of extensive neoteny (Fig. 3.116). The 70 species of larvaceans superficially resemble the tadpole larvae of amphibians, although the tail is at right angles to the body. The notochord is retained, and the animals, mostly under 1 cm long, are propelled by undulations of the tail. They secrete an external mucous net known as a house, which may completely surround them and is very efficient at trapping planktonic particles.

VERTEBRATA The Vertebrata are chordates that have a vertebral column (backbone) and a cartilaginous or bony skull. The vertebral column provides the central support structure for an internal skeleton which gives shape, support, and protection to the body and can provide a means of anchoring fins or limbs to the body. The vertebral column also serves to

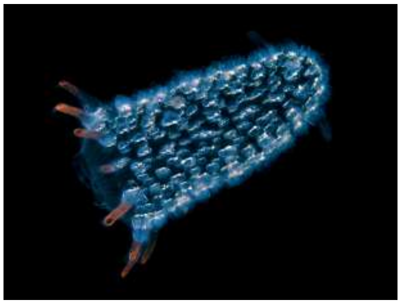

Figure 3.115: *Pyrosoma* are free-floating colonial tunicates. Colonies reach up to 18 m and consist of up to 100s to 1000s of individual “zooids”. Each zooid is a few mm long and is embedded in a common gelatinous tunic that joins all of them. Each zooid opens both to the inside and outside of the ”tube”, drawing in water from the outside to its internal filtering mesh, filtering the microscopic organisms on which it feeds, and then expelling the filtered water to the inside of the colony.

Figure 3.116: *Oikopleura dioica*, a small, cosmopolitan, solitary, and pelagic appendicularian. Every 3 - 4 hours, *O. dioica* creates a mucus net which surrounds its body. Water is pumped through it and food particles are filtered out and then transferred into the mouth. Once the gelatinous net is too clogged to allow further filtration, it is abandoned and drift down to the seabed as “marine snow”.

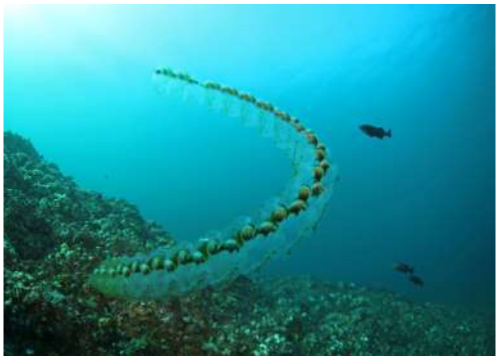

Figure 3.117: A salp chain: Salps have a very complex life cycle with alternating generations. The solitary phase, the “oozooid”, is a single, barrel-shaped animal that reproduces asexually and creates a chain of 10s to 100s of individuals. This salp chain is the “aggregate” stage of the life cycle. Each blastozooid in it reproduces sexually (the blastozooids are sequential hermaphrodites), with the growing embryo oozooid attached to the body wall of the parent. The oozooids are eventually released from the parent blastozooids, and continue to feed and grow as oozoid.

house and protect the spinal cord that lies within the vertebral column. Marine vertebrates can be divided into marine "fish" (which are not a taxonomic group!, Fig. 3.118) and marine tetrapods (which evolved from the lob-finned fishes within the bony fish (Fig. 3.127) and include marine birds, reptiles, and mammals; Fig. 3.131).

Marine vertebrates are due to their generally large sizes, rather close phylogenetic relationship to humans, their good fossil record (endoskeleton), and their high nutritional and economic importance for humans very well-studied. Many vertebrates are higher trophic level consumers and even apex predators (humans included) and thus have strong impacts on the structure of marine food webs. However, the wealth of information on marine vertebrates compared to marine microorganisms and most other taxa of higher animals does not mean at all that the latter are ecologically less relevant.

Fish The marine organisms which most people think of in association with ocean or sea are the various fish species. *Fishes*[56] typically breathe by extracting oxygen from water through gills and have a skin protected by scales and mucous. They use fins to propel and stabilise themselves in the water, and usually have a two-chambered heart and eyes well adapted to seeing underwater, as well as other sensory systems. About 20,000 species of marine fish have been described as of 2017. Fish are abundant in most bodies of water. They can be found in nearly all aquatic environments, from high mountain streams (e.g. char and gudgeon) to the abyssal and even hadal depths of the oceans (e.g. cusk-eels and snailfish), although no species has yet been documented in the deepest 25% of the ocean.

"Fish", a paraphyletic clade, are divided into the jawless fish (or *Agnatha*) and the jawed fish (*Gnathostomata*). The Gnathostomata comprise all jawed vertebrates, i.e. marine (and terrestrial) reptiles, birds, and mammals, too. The Agnatha are the hagfish and the lampreys:

[56] The plural for fish is fish, unless in a scientific context where fishes can be used when talking about several types or species of fish. More, the words "fishery", "fisherman" etc. can refer to many taxa that are not fish in any biological sense, e.g. molluscs (shellfish) or crustacans (crayfish, krill).

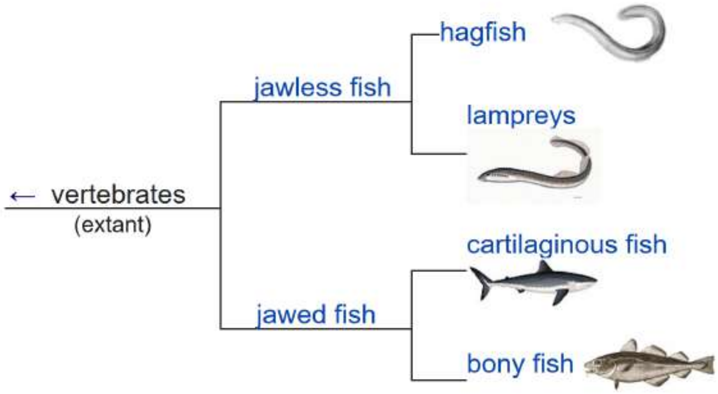

Figure 3.118: Phylogenetic relationships of extant "fishes".

Hagfish (Myxini), are worm-shaped, slime-producing marine jawless fish. They have cartilaginous skulls and tooth-like structures composed of keratin. Colours depend on the species, ranging from pink to blue-grey, and black or white spots may be present. Eyes are simple eyespots, not lensed eyes that can resolve images. Hagfish have no true fins and have six or eight barbels around the mouth and a single nostril. Instead of vertically articulating jaws such as Gnathostomata, they have a pair of horizontally moving structures with tooth-like projections for pulling off food. The mouth of the hagfish has two pairs of horny, comb-shaped teeth on a cartilaginous plate that protracts and retracts. These teeth are used to grasp food and draw it toward the pharynx. They have no vertebral column, although hagfish do have rudimentary vertebrae (Fig. 3.119).

Figure 3.119: Pacific hagfish *Eptatretus stoutii* at 150 m depth, California, Cordell Bank National Marine Sanctuary.

Hagfish are also called slime eels, because they can exude copious quantities of a milky and fibrous mucus from some 100 glands running along their flanks. The species *Myxine glutinosa* was named for this slime. When captured, they secrete the slime, which expands into up to 20 litres of sticky, gelatinous material when combined with water; one litre of slime has about 40 milligrams of mucus and proteins (Fig. 3.120).

Figure 3.120: Hagfish can tie themselves in an overhand knot (shown in the figure), which works its way from the head to the tail of the animal, scraping off the slime as it goes and freeing them from a captor. Rheological investigations showed that hagfish slime viscosity increases in elongational flow which favours gill clogging of suction feeding fish, while its viscosity decreases in shear which facilitates scraping off the slime by the travelling-knot. A vertebral column would not allow that.

Hagfish can survive months between feedings; their feeding behavior, however, appears quite vigorous. Analysis of the stomach content of several species has revealed a large variety of prey, including polychaetes, shrimp, hermit crabs, cephalopods, brittle stars, bony fishes, sharks, birds, and whale flesh. Hagfish can also feed upon and often even enter and eviscerate the bodies of dead and dying/injured sea creatures much larger than themselves. They are known to devour their prey from the inside. Hagfish have the ability to absorb dissolved organic matter across the skin and gill, which may be an adaptation to a scavenging lifestyle, allowing them to maximize sporadic opportunities for feeding. Hagfish have also been observed actively hunting the red bandfish, *Cepola haastii*, in its burrow, possibly using their slime to suffocate the fish before grasping it with their dental plates and dragging it from the burrow.

Hagfish are typically found in large clusters on and near the sea floor.

Lampreys (Petromyzontiformes) have scaleless, elongated bodies, and can range from 13 to 100 cm in length. Lacking paired fins, adult lampreys have large eyes, one nostril on the top of the head, and seven gill pores on each side of the head[57] (Figs. 3.121 & 3.122). Instead of true vertebrae, they have a series of cartilaginous structures called "arcualia" arranged above the notochord. The pharynx is subdivided; the ventral part forming a respiratory tube that is isolated from the mouth by a valve called the velum. This is an adaptation to how the adults feed, by preventing the prey's body fluids from escaping through the gills or interfering with gas exchange, which takes place by pumping water in and out of the gill pouches instead of taking it in through the mouth.

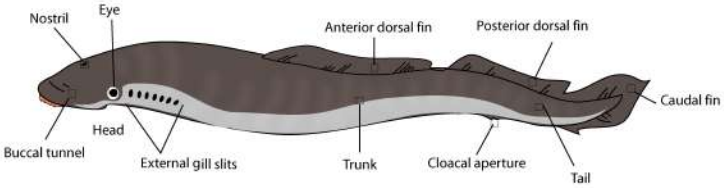

Figure 3.121: Basic external anatomy of a lamprey.

There are about 38 known extant species of lampreys. Parasitic carnivorous species are the most well-known, and feed by boring into the flesh of other fish to suck their blood (Fig. 3.123); but only 18 species of lampreys engage in this lifestyle. Of the 18 carnivorous species, nine migrate from saltwater to freshwater to breed (some of them also have freshwater populations), and nine live exclusively in freshwater.

Figure 3.122: Sea lamprey *Petromyzon marinus*.

Figure 3.123: Mouth of a sea lamprey *Petromyzon marinus*. Lamprey use their suction cup-like mouth to attach to the skin of a fish and rasps away tissue with its sharp, probing tongue and keratinized teeth. A fluid produced in the lamprey's mouth, called lamphredin prevents the victim's blood from clotting.

Lampreys live mostly in coastal waters and are found in most temperate regions. Some species (e.g. *Petromyzon marinus*) travel significant distances in the open ocean.

Marine lampreys are anadromous, i.e. they migrate between freshwater and marine habitats. The anadromous migration is tied to their life cycle: Anadromous lampreys spend up to four years in the sea before migrating back to freshwater, where they spawn. Adults create nests (called "redds") by moving rocks, and females release thousands of eggs, sometimes up to 100,000. The male, intertwined with the female, fertilizes the eggs simultaneously. Being semelparous, both adults die after the eggs are fertilized. After hatching, larvae burrow in the sand and silt bottom in quiet water downstream from spawning areas and filter-feed on plankton and detritus.[58] After metamorphosis which provides them with eyes, teeth,

[57] Lampreys are often called "nine-eyed eels". The name is derived from the seven external gill slits that, along with one nostril and one eye, line each side of a lamprey's head section. The German word for lamprey is Neunauge and in Japanese they are called yatsume-unagi ("eight-eyed eels"), which excludes the nostril from the count.

[58] Another example of an ontogenetic niche shift.

and a sucking mouth, they migrate to the sea, beginning to prey on other animals while still swimming downstream.

Chondrichthyes Jawed fish[59] fall into two main groups: fish with bony internal skeletons and fish with cartilaginous internal skeletons (Fig. 3.118). The *Chondrichthyes* or **cartilaginous** fish have jaws and skeletons made of cartilage rather than bone. They are divided into the Elasmobranchii (sharks, rays, skates, and sawfish) and into the Holocephali (chimaeras).

Well-known shark species such as the tiger shark, blue shark, great white shark, mako shark, thresher shark, and hammerhead shark are carnivorous apex predators. In contrast, basking sharks, whale sharks (Fig. 3.124), and megamouth sharks have independently evolved different strategies for filter feeding plankton: basking sharks practice ram feeding, whale sharks use suction to take in plankton and small fishes, and megamouth sharks make suction feeding more efficient by using the luminescent tissue inside of their mouths to attract prey in the deep ocean. This type of feeding requires gill rakers – long, slender filaments that form a very efficient sieve—analogous to the baleen plates of the great whales. The shark traps the plankton in these filaments and swallows from time to time in huge mouthfuls. Sharks are found in all seas. They generally do not live in fresh water, with a few exceptions such as the bull shark and the river shark which can swim both in seawater and freshwater. Sharks are common down to depths of 2,000 m, rarely beyond that).

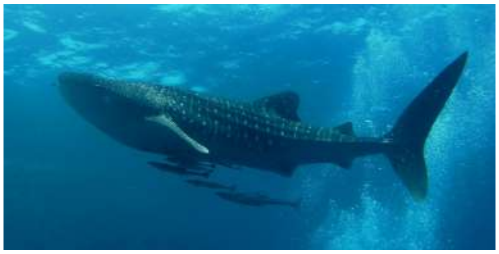
Figure 3.124: A whale shark *Rhincodon typus*.

Rays and skates (Batoidea) are distinguished by their flattened bodies (Fig. 3.125), enlarged pectoral fins that are fused to the head, and gill slits that are placed on their ventral surfaces. Most rays and skates have developed heavy, rounded teeth for crushing and grinding the shells of bottom-dwelling species such as snails, clams, oysters, crustaceans, and some fish, depending on the species. Manta rays feed on plankton and the sawfish uses its "saw" to feed on benthos (Fig. 3.126)


Figure 3.125: A devilfish *Mobula mobular* of the Mobulidae, a family of large rays incl. manta which live in the open oceans by filter-feeding on plankton.


Figure 3.126: A sawfish *Pristis pristis*.

Osteichthyes The bony fish (Fig. 3.127) is a diverse taxonomic group of fish that have skeletons primarily composed of bone tissue. They can be contrasted with the Chondrichthyes, which have skeletons primarily composed of cartilage. The vast majority of fish are members of Osteichthyes, which is an extremely diverse and abundant group consisting of 45 orders, and over 435 families and about 28,000 species. It is the largest class of vertebrates in existence today. The group Osteichthyes is divided into the ray-finned fish (Actinopterygii) and lobe-finned fish (Sarcopterygii).

Early bony fish had simple lungs (a pouch on either side of the esophagus) which helped them breathe in low-oxygen water. In many bony fish these have evolved into swim blad-

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[59] Note, the Gnathostomata are not all fish, because evolution led to the origin of the Tetrapoda from the lob-finned bony fish within them.

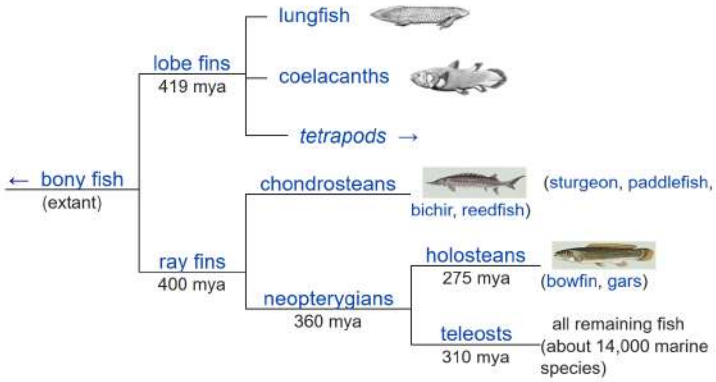

Figure 3.127: Phylogenetic relationships of the bony fish (Euteleostomi). Lungfish are also known as the order Dipnoi.

ders, which help the body create a neutral balance between sinking and floating, i.e. for better control of their buoyancy.[60] Osteichthyes have an operculum, which helps them breathe without having to swim. Bony fish have no placoid scales. Mucus glands coat the body. Most have smooth and overlapping ganoid, cycloid or ctenoid scales.

Actinopterygii, members of which are known as ray-finned fishes, is a clade (traditionally class or subclass) of the bony fishes. The ray-finned fishes are so-called because their fins are webs of skin supported by bony or horny spines (rays, Fig. 3.128), as opposed to the fleshy, lobed fins that characterize the class Sarcopterygii (lobe-finned fish, Fig. 3.129). The actinopterygian fin rays attach directly to the proximal or basal skeletal elements, the radials, which represent the link or connection between these fins and the internal skeleton (e.g., pelvic and pectoral girdles). The fins of lobe-finned fishes differ from those of all other fish in that each is borne on a fleshy, lobelike, scaly stalk extending from the body.

The Teleostei (Greek: *τέλειος* "complete" and *όστέον* "bone") is by far the largest infraclass in the class Actinopterygii, the ray-finned fishes, containing 96% of all extant species of fish. Teleosts are arranged into about 40 orders and 448 families. Over 26,000 species have been described. Teleosts range from giant oarfish measuring 7.6 m or more, and ocean sunfish weighing over 2 t, to the minute male anglerfish *Photocorynus spiniceps*, just 6.2 mm long. Including not only torpedo-shaped fish built for speed, teleosts can be flattened vertically or horizontally, be elongated cylinders or take specialised shapes as in anglerfish and seahorses (Fig. 3.130).

The difference between teleosts and other bony fish lies mainly in their jaw bones; teleosts have a movable premaxilla and corresponding modifications in the jaw musculature which make it possible for them to protrude their jaws outwards from the mouth. This is of great advantage, enabling them to grab prey and draw it into the mouth. In more derived teleosts, the enlarged premaxilla is the main tooth-

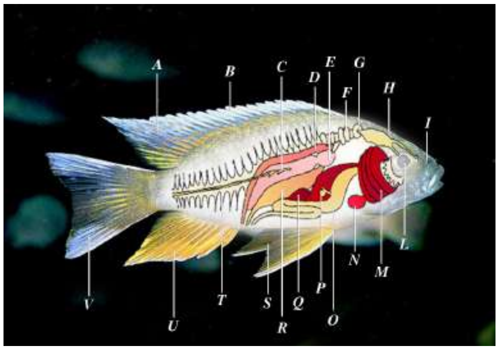

Figure 3.128: Anatomy of a typical ray-finned, teleost fish (cichlid). A: dorsal fin, B: fin rays, C: lateral line, D: kidney, E: swim bladder, F: Weberian apparatus, G: inner ear, H: brain, I: nostrils, L: eye, M: gills, N: heart, O: stomach, P: gall bladder, Q: spleen, R: ovaries or testes, S: ventral fins, T: spine, U: anal fin, V: caudal fin

Figure 3.129: The coelacanth *Latimeria* sp. was long considered a "living fossil" because scientists thought it was the sole remaining member of a taxon otherwise known only from fossils, with no close relations alive, and that it evolved into roughly its current form approximately 400 million years ago. However, several more recent studies have shown that coelacanth body shapes are much more diverse than previously thought.

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[60] The lungs of amphibians, reptiles, birds, and mammals were inherited from their bony fish ancestors.

bearing bone, and the maxilla, which is attached to the lower jaw, acts as a lever, pushing and pulling the premaxilla as the mouth is opened and closed. Other bones further back in the mouth serve to grind and swallow food. Another difference is that the upper and lower lobes of the tail (caudal) fin are about equal in size. The spine ends at the caudal peduncle, distinguishing this group from other fish in which the spine extends into the upper lobe of the tail fin.

Figure 3.130: Some of the large diversity of growth forms within the Teleostei.

Marine Tetrapoda A Tetrapoda (Greek for "four feet") are vertebrates with limbs (feet). Tetrapods evolved from ancient lobe-finned fishes about 400 million years ago during the Devonian Period when their earliest ancestors emerged from the sea and adapted to living on land. This required a change from a body plan for breathing and navigating in gravity-neutral water to a body plan with mechanisms enabling the animal to breath in air without dehydrating and move on land. Tetrapods can be divided into four classes: amphibians, reptiles, birds and mammals (Fig. 3.131). Marine tetrapods are tetrapods that **returned from land to the sea**. The first returns to the ocean may have occurred as early as the Carboniferous Period (358 - 299 Mya), whereas other returns occurred as recently as the Cenozoic (70 Mya to today), as in cetaceans (whales) and pinnipeds (seals).

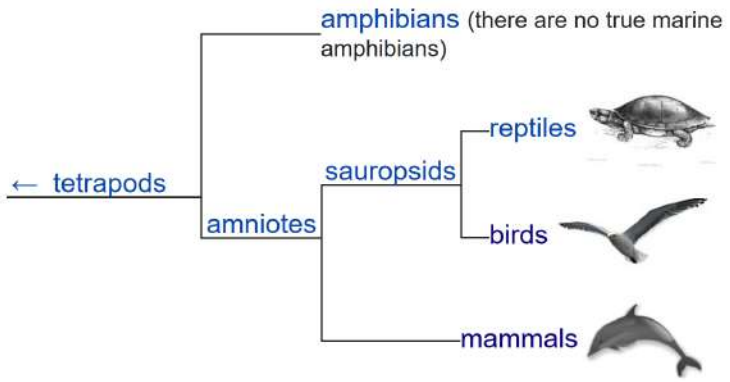

Figure 3.131: Phylogenetic relationships of the Tetrapoda.

Extant non-avian reptiles which inhabit or frequent the sea (**marine reptiles**) include **sea turtles**, **sea snakes**, the **marine iguana**, and the **saltwater crocodile**. Of the approximately 12,000 extant reptile species, less than 100 are marine. Except for some sea snakes, most extant marine reptiles are oviparous and need to return to land to lay their eggs. Apart from sea turtles, the species usually spend most of their lives on or near land rather than in the ocean. Sea snakes generally prefer shallow waters nearby land, around islands, especially waters that are somewhat sheltered, as well as near estuaries. Unlike land snakes, sea snakes have evolved flattened tails which help them swim.

Marine birds are adapted to life within the marine environment. They are often called seabirds. While marine birds vary greatly in lifestyle, behaviour and physiology, they often exhibit striking convergent evolution, as the same environmental problems and feeding niches have resulted in similar adaptations. Examples include albatross, penguins, gannets, and auks. In general, marine birds live longer, breed later and have fewer young than terrestrial birds do, but they invest a great deal of time in their young. Most species nest in colonies, which can vary in size from a few dozen birds to millions. Many species are famous for undertaking long annual migrations, crossing the equator or circumnavigating the Earth in some cases. They feed both at the ocean's surface and below it, and even feed on each other. Marine birds can be highly pelagic, coastal, or in some cases spend a part of the year away from the sea entirely. Some marine birds plummet from heights, plunging through the water leaving vapour-like trails, similar to that of fighter planes.

There are about 130 living and recently extinct **marine mammal**[61] species such as seals, dolphins, whales, manatees, sea otters and polar bear. They are unified by their reliance on the marine environment for feeding. Both cetaceans and sirenians are fully aquatic and therefore are obligate water dwellers. Seals and sea-lions (pinnipeds) are semiaquatic; they spend the majority of their time in the water, but need to return to land for important activities such as mating, breeding and moulting. In contrast, both otters and the polar bear are much less adapted to aquatic living. Their diet varies considerably as well: some may eat zooplankton; others may eat fish, squid, shellfish, and sea-grass; and a few may eat other mammals. In a process of convergent evolution, marine mammals, especially cetaceans such as dolphins and whales, redeveloped their body plan to parallel the streamlined fusiform body plan of pelagic fish. Front legs became flippers and back legs disappeared, a dorsal fin reappeared and the tail morphed into a powerful horizontal fluke. This body plan is an adaptation to being an active predator in a high drag environment. A parallel convergence occurred with the now extinct marine reptile ichthyosaur.

The marine mammals one may see in the North Sea are the Harbour seal (*Phoca vituina*, Fig. 3.133), the Grey seal (*Halichoerus grypus*, Fig. 3.132), and the Harbour porpoise (*Phocoena phocoena*, Fig. 3.134).


Figure 3.132: Grey seal *Halichoerus grypus*, female with pup.


Figure 3.133: Harbour seal colony on Heligoland.


Figure 3.134: A harbour porpoise off the coast of Denmark.

3.5 *Adaptations of higher animals*

Marine environments offer many possibilities for organisms to live in them. In fact, life likely originated in the earliest oceans.

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[61] *List of marine mammal species*

But the conditions in the seas also have their own challenges and these require many morphological, physiological and behavioural adaptations from the organisms living in them that are different from terrestrial habitats.

Problems to solve include finding food and avoid being food. This chapter already gave many examples of various adaptations of marine heterotroph consumers to feed. Each of these adaptations aim to make the successful completion of each ot the various stages in the foraging cycle (Fig. 3.35) as probable as possible. The other side of the coin, from a prey perspective, is of course, to minimise that chance.

Predator avoidance Anti-predator adaptations are mechanisms developed through evolution that assist prey organisms in their constant struggle against predators. Adaptations have evolved for every stage of the foraging cycle.

The first line of defence consists in avoiding detection, through mechanisms such as camouflage, masquerade, apostatic selection, living underground, or nocturnality.

One form of detection avoidance specific to the oceans (and deep enough lakes) is *diel vertical migration (DVM)*,[62] as the vertical distribution of light in the oceans creates permanently dark regions deep in water (see section 4.1.1, p. 126). The migration occurs when organisms move up to the uppermost layer of the sea at night and return to the bottom of the daylight zone of the oceans. In terms of biomass, it is the greatest migration in the world. It is not restricted to any one taxon as examples are known from crustaceans (copepods), molluscs (squid), and ray-finned fishes and more.

The most prominent cues for DVM are changes in light intensity during dusk and dawn and in fish predation intensity. While vertical migration is generally nocturnal, with the animals ascending from the depths at nightfall and descending at sunrise, the timing can be altered in response to the different cues and stimuli that trigger it. Some unusual events impact vertical migration: DVM is absent during the midnight sun in Arctic regions and vertical migration can occur suddenly during a solar eclipse.

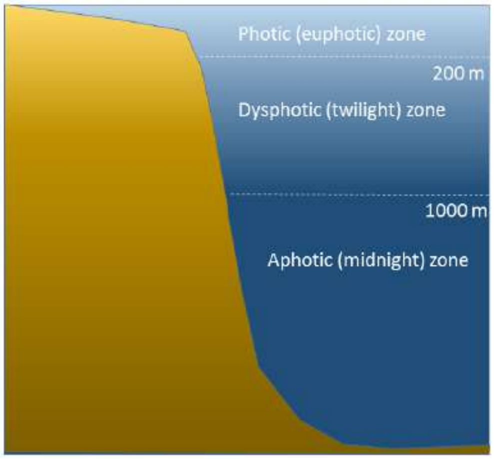

Figure 3.135: Zones of the water column as defined by the amount of light penetration. The depth of the photic zone is, by definition, where radiation is degraded down to 1% of its surface strength, so it's not a fixed depth.

There are many hypotheses as to why organisms would vertically migrate, and several may be valid at any given time. The most supported one is predator avoidance: because fish hunt visually and require light to detect their prey, a given body of water may be viewed as a risk gradient by a prey, e.g. various zooplankton species. The surface layers are riskier to reside in during the day than deep water, and as such promotes varied longevity among zooplankton that settle at different daytime depths. Indeed, in many instances it is advantageous for zooplankton to migrate to deep waters during the day to avoid predation and come up to the surface at night to feed (Fig. **??**).[63]

As a second, alternative line of defence, prey animals may,

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[62] The word diel comes from the Latin *dies* day, and means a 24-hour period.

[63] Other reasons for DVM may be protection from UV light, although organisms often migrate deeper than UV light penetrates and even respond (though less) to moon light, or higher energy conservation in cooler water, although studies show that migrating zooplankton often grow and reproduce less.

once detected, ward off attack, whether by advertising the presence of strong defences in aposematism, by mimicking animals which do possess such defences, by startling the attacker, by signalling to the predator that pursuit is not worthwhile, by distraction, by using defensive structures such as spines, and by living in a group. Members of groups are at reduced risk of predation, despite the increased conspicuousness of a group, through improved vigilance, predator confusion, and the likelihood that the predator will attack some other individual, i.e. there is safety in numbers. A **dilution effect** is seen when animals living in a group "dilute" their risk of attack, each individual being just one of many in the group. One common example is the shoaling of fish. Often, animals seek central positions in such a group, because the centre of the group has the lowest risk of danger, so animals are predicted to strive constantly to gain this position (**selfish herd concept**). Individuals living in large groups may also be safer from attack because the predator may be confused by the large group size. As the group moves, the predator has greater difficulty targeting a given individual prey. Such **predator confusion** can lead to a "Type IV" functional response, in which a predator's ingestion rate declines again at high prey densities. In larger groups, also the chance of an approaching enemy being detected by a member of the prey group, increases. **Predator satiation** occurs, when the growth in numbers of a predator ("numerical response") can not catch up with the numbers of its prey. The proportion of prey eaten decreases with prey density (Fig. 3.30)

Some prey species are capable of fighting back against predators, whether with chemicals, through communal defence, morphological features like spines etc., or by ejecting noxious materials (Fig. 3.119). Many animals can escape by fleeing rapidly, outrunning or outmanoeuvring their attacker.

One fighting-back strategy effective only in water due to its conductivity is electricity. *Electric fish* such as the Electric ray *Torpedo marmorata* (Fig. 3.136). They and other strongly electric fishes use modified neurons or muscle cells ("electrocytes") to produce electric discharges when attacked and than escape the stunned predator.


Figure 3.136: Electric ray *Torpedo marmorata*

Finally, some species are able to escape even when caught by sacrificing certain body parts: e.g., many echinoderms can shed their arms, often distracting predators long enough to permit the prey to escape.

Aquatic respiration Aerobe heterotrophs require oxygen (O_2) as an electron acceptor in their mitochondrial respiration chain and they need to get rid of the carbon dioxide (CO_2) produced in the Citric Acid cycle during the catabolic oxidation of assimilated food molecules (Figs. 3.3 & 3.4; Eqs. 3.4 & 3.4). *Respiration* is the process whereby an aquatic organism exchanges these respiratory gases with water, obtaining oxygen from oxygen dissolved in water and excreting carbon dioxide and some other metabolic waste products into the water.

In very small animals, plants and bacteria, simple diffusion of gaseous metabolites is sufficient for respiratory function and no special adaptations are found to aid respiration. Passive diffusion or active transport are also sufficient mechanisms for many larger aquatic animals such as many worms, jellyfish, sponges, bryozoans and similar organisms. In such cases, no specific respiratory organs or organelles are found.

In contrast, higher animals have such specialised respiratory organs or organelles for the gas exchange. Usually, these are ***gills***. Gills (Figs. 3.137 & 3.138) are characterised by (1) large surface area to allow as much oxygen to enter the gills as possible because more of the gas comes into contact with the membrane, (2) good supply of body fluids to maintain the concentration gradient needed, (3) thin membranes to allow for a short diffusion pathway, and (4) ways for increasing water flow across membranes.

Figure 3.137: A sea slug *Pleurobranchaea meckelii*: The gill (or ctenidium) is visible in this view of the right-hand side of the animal.

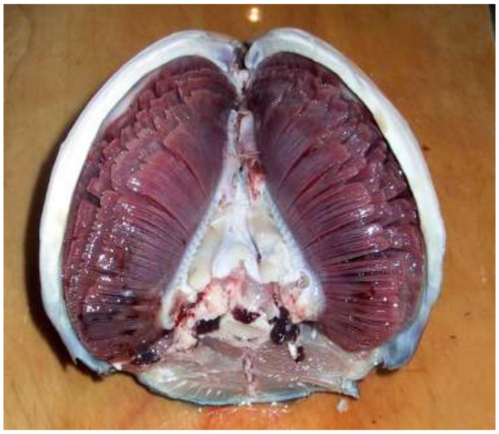

Figure 3.138: The red gills inside a detached tuna head (seen from posterior). In bony fish, the gills, carried by gill arches, lie in a branchial chamber covered by a bony lid, the operculum.

Bony fish use the long bony cover for the gill (the operculum) for pumping water through the gills to increase water flow. Others, like some species of sharks use "ram ventilation": only when they swim, water flows into the mouth and across the gills. Because they rely on this technique, they must keep swimming in order to respire.

Bony fish use countercurrent flow to maximize the intake of oxygen that can diffuse through the gill (Fig. 3.139). Countercurrent flow occurs when deoxygenated blood moves through the gill in one direction while oxygenated water moves through the gill in the opposite direction. This mechanism maintains the concentration gradient thus increasing the efficiency of the respiration process as well and prevents the oxygen levels from reaching an equilibrium.

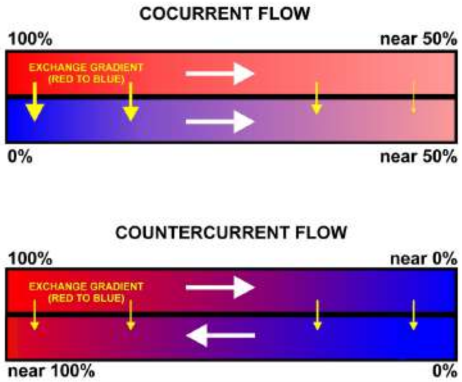

Figure 3.139: Concurrent and countercurrent flow exchange systems. Red represents a higher value of the partial pressure of a gas than blue so the gas being transported in the channels flows from red to blue. In bony fish in contrast to cartilaginous fish a countercurrent flow (lower diagram) of blood and water in the gills is used to extract oxygen from the environment.

Marine mammals, birds, and reptiles breath; i.e. they inhale and exhale air from and to the atmosphere, not the water. For this, they have to return to the surface regularly. Marine mammals are able to dive for long periods. Both pinnipeds and cetaceans have large and complex blood vessel systems which serve to store oxygen to support deep diving. Other important reservoirs for oxygen include muscles, blood, and the spleen[64] which all have the capacity to hold a high concentration of oxygen. They are also capable of bradycardia (reduced heart rate), and vasoconstriction (shunting most of the oxygen to vital organs such as the brain and heart) to allow extended diving times and cope with oxygen deprivation. If oxygen is depleted, marine mammals can access substantial reservoirs of glycogen that support anaerobic glycolysis of the cells involved during conditions of systemic hypoxia associated with prolonged submersion.

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[64] In German: "Milz".

Homoeostasis Homeostasis is the state of steady internal, physical, and chemical conditions maintained by living systems. This is the condition for optimal functioning of the physiological processes within organisms and includes many variables, such as body temperature and fluid balance, being kept within certain pre-set limits (homeostatic range). Other variables include the pH of extracellular fluid, the concentrations of sodium (Na^{2+}), potassium (K^{+}) and calcium ions (Ca^{2+}), as well as that of the blood sugar level, and these need to be regulated despite changes in the environment, diet, or level of activity.[65] Each of these variables is controlled by one or more regulators or homeostatic mechanisms, which together maintain life. The variables generally have a minimum and maximum value below and above which physiological functioning is not possible anymore and the organism dies. Between these critical thresholds there is often an optimum at which a physiological process is most efficient given the energy expended on it (Fig. 3.140).

In many parts of the oceans, external (environmental) conditions are rather stable, e.g. the warmth of the sun carried by infrared light does not penetrate deeply beyond the immediate surface waters (other light wavelength do, though). The same is true for rain water. Especially beyond the mixing depth, the environment changes only slowly compared to the life cycle of may organisms. Even conforming species experience near homoeostatic conditions. Other marine habitats are much more variable, especially in the littoral zone where due to tides organisms can be exposed to high fluctuations in temperature, oxygen levels, etc.

Osmoregulation is the active regulation of the osmotic pressure of an organism's body fluids, detected by osmoreceptors, to maintain the homeostasis of the organism's water and electrolyte content; that is, it maintains the fluid balance and the concentration of electrolytes (salts in solution which in this case is represented by body fluid) to keep the body fluids from becoming too diluted or concentrated.

Osmoconformers are marine organisms that maintain an internal environment which is isotonic to their external environment. This means that the osmotic pressure of the organism's cells is equal to the osmotic pressure of their surrounding environment. By minimizing the osmotic gradient, this subsequently minimizes the net influx and efflux of water into and out of cells. Even though osmoconformers have an internal environment that is isosmotic to their external environment, the types of ions in the two environments differ greatly in order to allow critical biological functions to occur (e.g. neurons require Na^{2+}, K^{+} and Ca^{2+} in specific concentrations, or the proton gradients in mitocondria must not be disturbed by external changes in osmolarity). Most osmoconformers are marine invertebrates such as echinoderms, mussels, crustaceans, jellyfish, ascidians. Some osmoconformers, such as echinoderms, are stenohaline, which means they

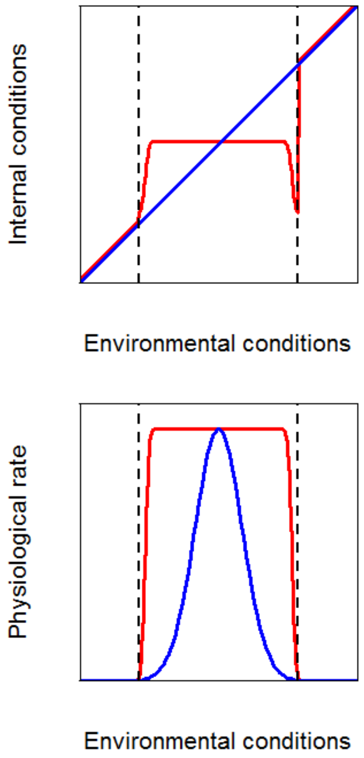

Figure 3.140: **Comparison of conformers (blue) and regulators (red).** *Upper panel:* Regulators can keep their internal (body) conditions homoeostatic over a range of external (environmental) conditions, whereas in conformers internal and external conditions equal each other. Beyond the critical values (dashed black lines), death occurs, and the conditions in dead regulators can of course not be held constant any more. *Lower Panel:* Physiological rates (ana- and catabolism, digestion, activity, etc.) in conformers have a more or less narrow optimum, while regulators (at higher energetic costs) have a wider range of environmental conditions over which they can maintain high rates. When dead, physiological rates are zero.

[65] Strictly, respiration is a mechanism to keep internal carbon dioxide and oxygen levels near-constant.

can only survive in a limited range of external osmolarities. The survival of such organisms is thus contingent on their external osmotic environment remaining relatively constant. On the other hand, some osmoconformers are classified as euryhaline, which means they can survive in a broad range of external osmolarities. Mussels are a prime example of a euryhaline osmoconformer. Mussels have adapted to survive in a broad range of external salinities due to their ability to close their shells which allows them to seclude themselves from unfavourable external environments. An advantage of osmoconformation is that such organisms do not need to spend much energy to regulate ion gradients. However, to ensure that the correct types of ions are in the desired location, a small amount of energy is expended on ion transport. A disadvantage to osmoconformation is that the organisms are subject to changes in the osmolarity of their environment.

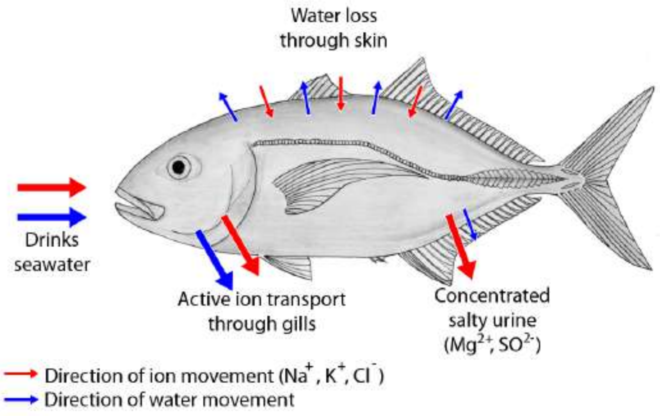

Figure 3.141: Movement of water and ions in saltwater fish.

In a strictly osmoregulating animal (fish, mammals, birds, reptiles), the amounts of internal salt and water are held relatively constant in the face of environmental changes. It requires that intake and outflow of water and salts be equal over an extended period of time. A marine fish has an internal osmotic concentration lower than that of the surrounding seawater, so it tends to lose water and gain salt. It actively excretes salt out from the gills and via its hyper salty urine and it drinks sea water (Fig. 3.141). Some marine fish, like sharks, have adopted a different, efficient mechanism to conserve water, i.e. osmoregulation. They retain urea in their blood in relatively higher concentration.

Thermoregulation is the ability of an organism to keep its body temperature within certain boundaries, even when the surrounding temperature is very different. A thermoconforming organism, by contrast, simply adopts the surrounding temperature as its own body temperature, thus avoiding the need for internal thermoregulation. The internal thermoregulation process is one aspect of homeostasis: a state of dynamic stability in an organism's internal conditions, maintained far from thermal equilibrium with its environment.

Thermoregulation is a specific problem for marine endotherms[66] (mostly mammals) because water has a high thermic conductivity and it is usually colder than mammal body temperatures ($\approx$ between 36°C and 38°C). Marine mammals are adept at thermoregulation using dense fur or blubber (Fig. 3.142), counter-current heat exchange systems in their respiratory and blood circulation systems (Fig. 3.139); and reduced appendages, and large size to prevent heat loss.

Fishes of the *Notothenioidei* living in Antarctic and Subantarctic waters (and a few other organisms) are able to survive in the freezing, ice-laden waters of the Southern Ocean because of the presence of an *antifreeze glycoprotein* in blood and body fluids. Antifreeze proteins (AFPs) bind to small ice crystals to inhibit the growth and recrystallization of ice that would otherwise be fatal. Their low concentration minimizes their effect on osmotic pressure. The unusual properties of AFPs are attributed to their selective affinity for specific crystalline ice forms and the resulting blockade of the ice-nucleation process. AFPs create a difference between the melting point and freezing point (busting temperature of AFP bound ice crystal) known as "thermal hysteresis" (Fig. 3.143). The addition of AFPs at the interface between solid ice and liquid water inhibits the thermodynamically favoured growth of the ice crystal. Ice growth is kinetically inhibited by the AFPs covering the water-accessible surfaces of ice.

Locomotion and buoyancy Moving in and through water is much different than moving on land. In aqueous environments friction becomes the major challenge to *aquatic locomotion*, with gravity being much less of a concern due to *buoyancy*.

The impact of friction on movement is related to the *Reynolds number* Re (see section 1.1, p. 6). Re is the ratio of inertial forces to viscous forces within a fluid which is subjected to relative internal movement due to different fluid velocities. A region where these forces change behaviour is known as a boundary layer (Fig. 3.144), such as the surface of an organism. A similar effect is created by the introduction of a stream of high-velocity fluid into a low-velocity fluid, such as the water movement through the pores of a sponge and out at the osculum[67]. This relative movement generates fluid friction, which is a factor in developing turbulent flow. Counteracting this effect is the viscosity of the fluid, which tends to inhibit turbulence. The Reynolds number quantifies the relative importance of these two types of forces for given flow conditions, and is a guide to when turbulent flow will occur in a particular situation.

When Re is low, viscosity dominates and organism behave like in honey: very small organisms need to overcome this force with

Figure 3.142: Blubber is a thick layer of vascularized adipose tissue under the skin of all cetaceans, pinnipeds, penguins, and sirenians. It functions as a thermal insulator and has the advantages over fur (as in sea otters) in that, though fur retains heat by holding pockets of air, the air expels under pressure (i.e., when the animal dives). Blubber, however, does not compress under pressure. While diving in cold water, blood vessels covering the blubber constrict and decrease blood flow, thus further increasing blubber's efficiency as an insulator. Blubber also aids buoyancy and streamlines the body, because the organized, complex collagenous network supports the noncircular cross sections characteristic of cetaceans (Fig. 3.146). Whale blubber is thus an example that adaptations can serve several purposes. It also tastes disgusting.

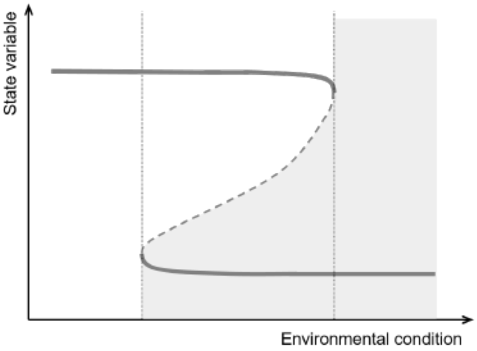

Figure 3.143: Hysteresis in any dynamic system (ecosystem, food web, population, cell physiology) occurs when the shift to one state of the system (e.g. concentration of ice crystals in body fluid) happens at a different value of an external (environmental) driver (e.g. sea water temperature). With AFPs body fluid freezes at the left threshold (dotted line) instead at the right one (sea water freezing temperature of -1.9°C) but de-freezes again at the right threshold (after Schröder et al., 2005).

[66] Endotherms create heat via metabolic processes. When the surrounding temperatures are cold, endotherms increase metabolic heat production to keep their body temperature constant, thus making the internal body temperature of an endotherm more or less independent of the temperature of the environment. One metabolic activity is that they possess a larger number of mitochondria per cell than ectotherms, enabling them to generate more heat by increasing the rate at which they metabolize fats and sugars (Eq. 3.4).

energy when they move within water or generate water movement, e.g. filter and suspension feeders. Also, close to the cell surface water hardly moves at all (Fig. 3.144), which creates problems for nutrient supply and gas exchange because molecules close to the cell are replenished only by diffusion which is very slow.

When Re is high, inertia dominates and turbulence occurs: the water breaks up into wakes behind the moving animal, creating pressure drag where due to to the turbulent flow behind the swimming organism water pressure is lower than in front. This drag pulls the animal back. The drag is the higher, the wider the cross-sectional area is. Streamlining the body minimises that drag and makes swimming of large organisms more efficient. Especially large pelagic species have this torpedo-like body form (Figs. 3.146 & 3.145). Fish species in habitats where fast, long swimming is less important have short, round bodies with high drag but reduced friction. The secretion of mucus along the organism's body surface, or the addition of long-chained polymers to the velocity gradient, can reduce frictional drag experienced by the organism, hence many fish have mucus-covered scales. Instead, sessile benthic organisms allow themselves (or their appendages) to bend with the current and when too strong (too fast water movement) they retract into shell or carapace (barnacles, mussels).

Buoyancy, or upthrust, is the upward force exerted by water (or any fluid) that opposes the weight of a partially or fully immersed object. Pressure increases with depth as a result of the weight of the overlying water. Thus, the pressure at the bottom of a submerged object is greater than at the top of the object. The pressure difference results in a net upward force on the object.

The magnitude of the force is proportional to the pressure difference, and is equivalent to the weight of the fluid that would otherwise occupy the submerged volume of the object, i.e. the displaced fluid. For this reason, an object whose average density is greater than that of the fluid in which it is submerged tends to sink. If the object is less dense than the liquid, the force can keep the object afloat.

Many aquatic/marine organisms have developed organs to compensate for their weight and control their buoyancy in the water. These structures, make the density of their bodies very close to that of the surrounding water. Some hydrozoans, such as Siphonophora, has gas-filled floats; the *Nautilus*, *Sepia* and Spirula (Cephalopoda) have chambers of gas within their shells; and most teleost fish and many lantern fish (Myctophidae) are equipped with swim bladders (Fig. 3.147). Many aquatic and marine organisms may also be composed of low-density materials (e.g. Fig. 3.142). Deep-water teleosts, which do not have a swim bladder, have few lipids and proteins, deeply ossified bones, and watery tissues that maintain their buoyancy. Some sharks' livers are composed of low-density lipids, such as hydrocarbon squalene or wax esters

[67] The total cross-sectional area of all choanocytes is much larger than the cross-section of the osculum (which the sponge can control, too). Because all the water entering has to leave again, the outflow velocity is high, higher than the water current outside the sponge. The exiting water with the waste products is thus ejected far away from the sponge

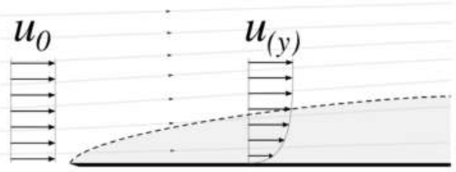

Figure 3.144: The laminar boundary layer velocity profile across a smooth surface.. When an object encounters a free water stream (to the left) a boundary layer occurs in which the velocity is linearly reduced. Exactly at the surface, it is zero. In the layer viscous forces are strong. The smaller Re, the thicker the boundary layer relative to the object.

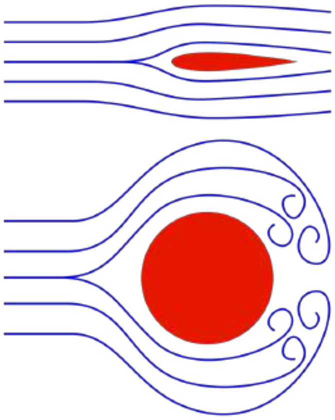

Figure 3.145: Water flow around a streamlined (foil) and non-streamlined object (sphere). The turbulence behind the sphere (the "wake") creates drag.

Figure 3.146: An adult blue whale *Balaenoptera musculus* from above. You can see the torpedo-like form of the body. Compare that to the foil in Fig. 3.145.

Figure 3.147: A swim bladder.

(also found in Myctophidae without swim bladders), which provide buoyancy.

Swimming animals that are denser than water must generate lift or adapt a benthic lifestyle. Movement of the fish to generate hydrodynamic lift is necessary to prevent sinking. Often, their bodies act as hydrofoils, a task that is more effective in flat-bodied fish. At a small tilt angle, the lift is greater for flat fish than it is for fish with narrow bodies. Narrow-bodied fish use their fins as hydrofoils while their bodies remain horizontal. In sharks, the heterocercal tail (Fig. 3.148) shape drives water downward, creating a counteracting upward force while thrusting the shark forward. The lift generated is assisted by the pectoral fins and upward-angle body positioning. It is supposed that tunas primarily use their pectoral fins for lift.


Figure 3.148: The heterocercal caudal fin of a shark.

Buoyancy maintenance is metabolically expensive. Growing and sustaining a buoyancy organ, adjusting the composition of biological makeup, and exerting physical strain to stay in motion demands large amounts of energy. It is proposed that lift may be physically generated at a lower energy cost by swimming upward and gliding downward, in a "climb and glide" motion, rather than constant swimming on a plane.

Vision Many marine organism perceive their environment at least partially by vision. Vision always requires a certain minimum of light, and the availability of light in the oceans is not only temporal (day - night, seasonal) but also spatially variable due to the light attenuation with depth. The organs animals developed to perceive light are *eyes*, which come in many different forms.

Pit ("pin hole") eyes are eye-spots which may be set into a pit to reduce the angles of light that enters and affects the eye-spot, to allow the organism to deduce the angle of incoming light. Found in about 85% of phyla, these basic forms were probably the precursors to more advanced types of "simple eyes". They are usually small, comprising up to about 100 cells covering about 100 µm. The resolution of pit eyes can be greatly improved by covering it with a material with refractive[68] index higher than the medium to form a "lens eye". As light passes through the lens it bends and, because lenses are convex, and is focused on the photoreceptor cells on other side of the eye. The most basic form, seen in some gastropods and annelids, consists of a lens with a refractive index of 1. A far sharper image can be obtained in a "refractive eye" using materials with a high refractive index.[69] Sea water has a rather high density, so lenses of marine organisms need to be denser than on land. Refractory indexes often decrease to the lens edges; this decreases the focal length and thus allows a sharp image to form on the retina. This also allows a larger aperture for a given sharpness of image, allowing more light to enter the lens; and a flatter lens, reducing spherical aberration.

The focused light is received by the receptor pigment molecules

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[68] Refraction is the change in direction of a light wave when it passes between media of different density.

[69] In vertebrate eyes, this structure consists of lens, iris and cornea.

in the cells of the retina, which excite when hit by photons. The excitation finally produces a neural signal in the ganglion or brain of the organism to be interpreted. Photoreceptor pigments differ in the wave length that excites them, and depending on the depth an organism lives, may differ among species or life history stage.

Those deep-sea fishes that are not blind have a large variety of different rhodopsin pigments to better receive the little light available. Rhodopsin is much more sensitive to light that many other pigments, but is also more quickly destroyed by light ("photobleaching").

Deep-sea fishes[70] also often produce their own light. Such *bioluminescence* is in some animals bacteriogenic, produced by symbiotic bacteria such as those from the genus *Vibrio*; in others, it is autogenic, produced by the animals themselves. The principal chemical reaction in bioluminescence involves a light-emitting molecule and an enzyme, generally called luciferin and luciferase, respectively. The uses of bioluminescence by animals include, apart from illumination, mimicry of other animals, for example to lure prey, and signalling to other individuals of the same species, such as to attract mates.

Reproduction, dispersal, and migration All organisms reproduce, i.e. they create new individuals from their own biomass. Without reproduction, populations could not grow and numbers of a species would only decrease through death. Most animal species reproduce at least once in their life via *sexual reproduction*, the exchange and mixture (combination) of genetic material among the parent individuals via gametes (Fig. 3.149).[71] Sex leads to genetic variation between parents and the produced offspring and among offspring. Higher genetic variation results in larger phenotypic variation, i.e. differences in traits among the offspring and thus a higher chance of survival and reproduction in changing environments. Sexually reproducing organisms thus usually have a higher fitness. This benefit is higher than the big costs of sex: only half the individuals in a population actually produce new organisms; the individual investing more biomass and energy (usually the egg-producing female) into new offspring only does so for 50% of its genetic material; males invest often much energy and survival chances into sexual traits; and individuals can only reproduce when they find a mate.

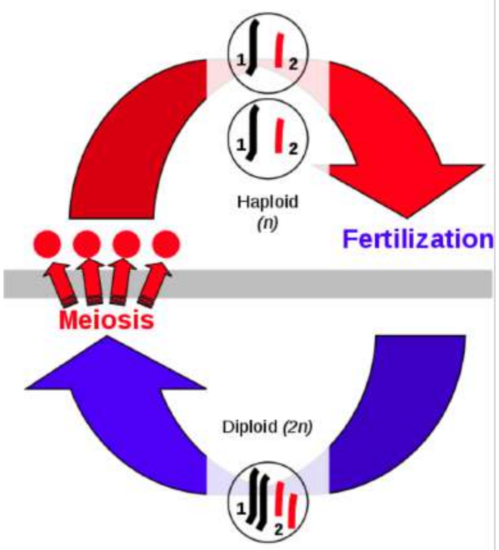

Figure 3.149: In the first stage of sexual reproduction, "meiosis", the number of chromosomes is reduced from a diploid number (2n) to a haploid number (n). During "fertilisation", haploid gametes come together to form a diploid zygote, and the original number of chromosomes is restored.

Figure 3.150: Clownfish are initially male; the largest fish in a group becomes a female.

Adaptations regarding reproduction in marine environment have to solve three problems: (1) Given the emptiness of many marine habitats (the open ocean, the deep sea) finding a mate is often difficult. (2) Survival to adulthood of enough offspring given the conditions of marine life. (3) Finding a good new space to live is especially important for sessile benthic organism.

Finding mates Without gametes of the opposite sex, sexual reproduction is not possible. Finding a mate that produces these gametes is hence a crucial first step in its process. However, finding a mate in the oceans can be difficult: in many marine habitats, especially

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[70] Deep-sea fishes have a range of complex adaptations to cope with the unique requirements of their habitat. Their protein structure and reaction criteria can still perform reactions under high pressure. Their cellular membranes favour phospholipid bilayers with a higher proportion of unsaturated fatty acids, which induce a higher fluidity than their surface counterparts. They have excessively large mouths to be less size-selective and increase the probability of ingesting the rare prey.

[71] Gametes are specialised reproductive cells carrying only half the genetic material of a parent and which fuse during fertilisation to make up a new diploid organism. Male gametes are sperm, female gametes eggs. In fact, the size of gametes defines the sex: small gametes - male. Most unicellular organisms do not produce gametes and exchange genetic material via different mechanisms, so still some from of "sex".

the open waters of the high sea (pelagic) at any depth and the benthic part of the deep sea are, compared to land, devoid of organisms owing to the low primary productivity here. Encounters between individuals of the opposite sex of a species are thus often rare and rely much on chance, possibly occurring when one or both individuals are ready for reproduction (the environmental conditions may be off, they my be too young or too old, not in the right phase of a reproductive cycle etc.). Sessile organisms in the benthic have the general problem of being stuck with the neighbour individuals that happen to settle close to them.


Figure 3.151: Five views of a shell of *Crepidula fornicata*. This marine gastropod is native to the western Atlantic Ocean and an invasive species in the North Sea. It is an sequential hermaphrodite.

One way of avoiding the problem of mate finding is to simply forego sexual reproduction and *reproduce asexually*. Asexual reproduction excludes the mixture of genetic material and the fusion of gametes of opposite sex. Asexually reproduced offspring are hence clones of each other and of their mother. For bacteria, archaea and protists (including phytoplankton) it is the typical form of reproduction where by binary fission of the single mother cell two daughter cells emerge. *Budding* is a type of asexual reproduction in which a new smaller organism develops from an outgrowth or bud due to cell division at one particular site. Marine animals that reproduce by budding include Cnidaria (Fig. 3.52), some sponges, some flat worms (e.g. *Convolutriloba* spec.), and echinoderm larvae. *Fragmentation* is an extreme form of asexual reproduction parental bodies split into parts and each fragment develops into a mature clone genetically and morphologically identical to its parent (Fig. 3.108).

Parthenogenesis is a natural form of asexual reproduction in which growth and development of embryos occur without fertilization by sperm. In animals, parthenogenesis means development of an embryo from an unfertilized egg cell. Parthenogenesis occurs in various marine invertebrates, e.g. nematodes, marine snails and crustaceans, and was observed in some shark species, although so far only in captivity.

Often, parthenogenesis alternates with sexual reproduction at least once per life. As environmental conditions deteriorate due to overexploitation of resources, the accumulation of waste products or simply an increasing density of conspecifics (crowding), asexually reproducing females[72] produce males which than fertilise eggs. This alternation of asexual/sexual procreation is often proximately triggered by the shortening of day lengths, a drop in water temperature etc., or shortage of resources.

Figure 3.152: *Osedax rubiplumus*

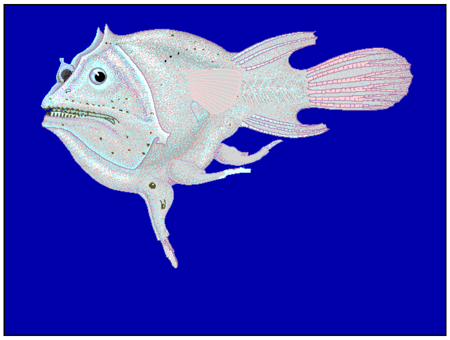
Figure 3.153: *Haplophryne molli*, with three males attached at the underside.

Hermaphroditism is a reproductive strategy where a single organism can produce both gametes associated with male and female sexes. Many taxonomic groups of animals (mostly invertebrates) do not have separate sexes. In these groups, hermaphroditism is a normal condition, enabling a form of sexual reproduction in which either partner can act as the "female" or "male". For example, the great majority of tunicates, pulmonate snails, opisthobranch snails, earthworms, and slugs are hermaphrodites. Hermaphroditism is also found in some fish species and to a lesser degree in other vertebrates.

[72] E.g. in some marine rotifers.

Sequential hermaphrodites occur in species in which the individual is born as one sex, but can later change into the opposite sex. This contrasts simultaneous hermaphrodites, in which an individual possess fully functional male and female genitalia at the same time. Sequential hermaphroditism is common in fish (particularly teleost fish, Fig. 3.150) and many gastropods (such as the common slipper shell, Fig. 3.151). Sequential hermaphrodites can only change sex once.

"Parasitic dwarf males" are an adaptation in many deep sea organisms such as *Osedax* worms, a polychaete living at whale carcasses (Fig. 3.152), whose females carry harems of dozens to hundreds tiny males in their bodies. Any eggs released by a female are already fertilised, i.e. fused with the male gametes, the sperm. Another example are some angler fish (order of *Lophiiformes*), where the tiny males attach to the much larger female and fuse to such a degree that the sexes share their blood systems and receives nutrients and oxygen from the female (Fig. 3.153).

Deep-sea fish also often use bioluminescence to attract mates in the darkness of their habitat.

Another common mechanism employed by many marine organisms to ensure that their gametes find another of the opposite sex is to *spawn*, i.e. to release and deposit the eggs and sperm into the sea water. Spawn consists of the reproductive cells (gametes) of many aquatic animals, some of which will become fertilized and produce offspring. The process of spawning typically involves females releasing ova (unfertilized eggs) into the water, often in large quantities, while males simultaneously or sequentially release spermatozoa (milt) to fertilize the eggs. Most aquatic animals, including fish, crustaceans, molluscs, echinoderms, cnidaria etc., except for aquatic mammals and reptiles, reproduce through the process of spawning.

Figure 3.154: The Pacific oyster *Crassostrea gigas* spawns at 20°C. It is very fecund, with females releasing about 50–200 million eggs in regular intervals (5–10 times a minute) in a single spawning. The eggs are pushed through the gill ostia into the mantle chamber, and are finally released in the water, forming a small cloud. In males, the sperm is released at the opposite end of the oyster, along with the normal exhalent stream of water. A rise in water temperature is the main cue in the initiation of spawning. The Pacific oyster is an invasive species in Europe, introduced in oyster aquaculture due to its high growth rate.

The chances for fertilisation among the released gametes are highest during synchronised mass spawning events, when groups of animals release sometimes huge numbers of gametes into the water, Mass spawning is often triggered by environmental stimuli like high phytoplankton densities, rise in water temperature (Fig. 3.154) or the lunar cycle.

Figure 3.155: A good catch of *Palolo viridis*.

A particular large and regular mass spawing with relevance for human culture occurs in the Samoan Palolo worm, *Palola viridis*. It is a Polychaeta species from the waters of some of the Pacific islands, including Samoa, Vanuatu, and the islands of the Malaysian Archipelago (Indonesia and the Philippines). Reproduction involves mass spawning at night in spring or early summer. The reproductive (and substantially larger) part of their body ("epitoke") autotomises and floats to the surface, there releasing sperm and eggs. The mechanisms or triggers which induce spawning such that it occurs during nights of a waning moon, continuing for several nights, are not completely known. Exposure to sunlight destroys this "tail" part of the worm's body afterwards. Several indigenous populations in regions where palolo occur use the reproductive portion of the worm as a food source. During their short-lived annual appearance in the last quarter of the moon in October and November, epitokes are gathered with nets or buckets, and are either eaten raw or cooked in several different ways (Fig. 3.155).

Offspring survival Without the survival of the offspring produced, the whole reproduction business would be a waste of time and effort. From a population point of view, at least as many juveniles have to make it to adulthood ("recruitment"[73]) as the number of parents involved in producing them to keep a population stable. From an individual parent's perspective, the rule is "the more, the better", because that will increase the relative contribution of the parental genes in the next generation.

In most if not all species juveniles (especially the early larval and juvenile stages) and adults have very different ecological requirements. Due to the differences in body size, morphology, behaviour, and physiology, they use different resources, have different natural enemies, and respond differently to abiotic conditions. To protect eggs, larvae and juveniles and to offer them the best possible conditions, many marine adult organisms (especially in fish, mammals, reptiles) regularly migrate between habitats most favourable for them in terms of feeding and survival, and habitats most beneficial for the survival and growth of their offspring.[74]

Among marine sessile invertebrates, *larval dispersal* by planktonic and pelagic larval stages is common to increase offspring survival to adulthood. The most widely accepted theory explaining the evolution of a pelagic larval stage is the need for long-distance dispersal. Sessile and sedentary organisms such as barnacles, tunicates, and mussels require a mechanism to move their young into new territory, since they cannot move long distances as adults. Many species have relatively long pelagic larval durations on the order of weeks or months. During this time, larvae feed and grow, and many species metamorphose through several stages of development. For example, barnacles moult through six nauplia stages before becoming a cyprid and seeking appropriate settlement substrate. This strategy can be risky. Some larvae have been shown to be able to delay their final metamorphosis for a few days or weeks, and most species cannot delay it at all. If these larvae metamorphose far from a suitable settlement site, they perish.

Many invertebrate larvae have evolved complex behaviours and endogenous rhythms to ensure successful and timely settlement. As larvae reach their final pelagic stage, they become much more tactile; clinging to anything larger than themselves. One study observed crab postlarvae and found that they would swim vigorously until they encountered a floating object, which they would cling to for the remainder of

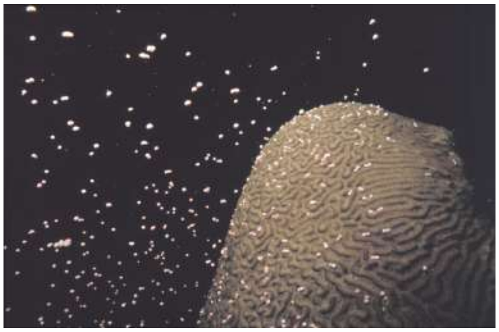

Figure 3.156: Brain coral *Diploria labyrinthiformis* spawning.

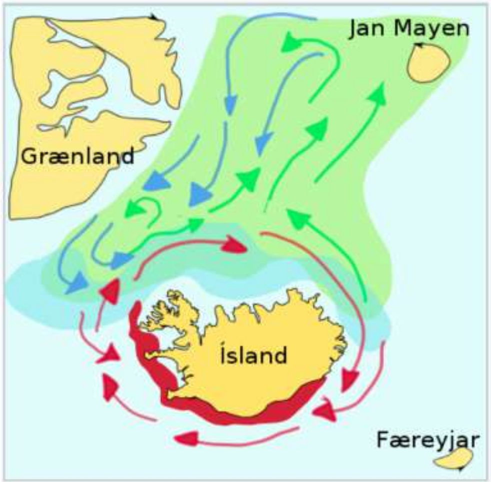

Figure 3.157: Seasonal migration of Icelandic capelin (*Mallotus villosus*) between adult feeding areas (green) and spawning grounds / larval habitats (red). Around Iceland, maturing capelin usually undertake extensive northward feeding migrations in spring and summer, and the return migration takes place in September to November. The migration is linked to the seasonal availability of plankton as food for non-larval capelin.

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[73] In population dynamics, recruitment is the process by which new individuals are added to a population, whether by birth and maturation or by immigration.

[74] When habitats of larval or juvenile fish have features very distinct from the adult habitats, one often speaks of a "*nursery habitat*". Mangroves, salt marshes, estuaries, seagrass beds and also the Wadden Sea are typical nursery habitats for a range of marine fish and invertebrate species.

the experiment. It was hypothesized that by clinging to floating debris, crabs can be transported towards shore due to the oceanographic forces of internal waves, which carry floating debris shoreward regardless of the prevailing currents. Once returning to shore, settlers encounter difficulties concerning their actual settlement and recruitment into the population. Space is a limiting factor for sessile invertebrates on rocky shores.[75] Settlers must be wary of adult filter feeders, which cover substrate at settlement sites and eat particles the size of larvae. Settlers must also avoid becoming stranded out of water by waves, and must select a settlement site at the proper tidal height to prevent desiccation and avoid competition and predation. To overcome many of these difficulties, some species rely on chemical cues to assist them in selecting an appropriate settlement site. These cues are usually emitted by adult conspecifics, but some species cue on specific bacterial mats or other qualities of the substrate.

Larval dispersal comes with high costs, not least among them the sometimes incredible high mortality rate during dispersal. Estimates are difficult and depend on species and conditions, but as few as 0.01% of released Pacific oyster eggs may survive long enough to find a new habitats. "Larval retention" is the opposite strategy in which larvae settle next or even on conspecific adults, given that this habitat must be almost by definition one that is beneficial for adult life.

Settling in new habitat Because they cannot actively move against the water, planktonic larvae have to rely on water currents and movement to transport them to new habitats. Adults may have some control over where their offspring may end up by choosing the time of spawning (e.g. during a tidal cycle) but also sensory adaptations by the larvae can increase the chance of finding a suitable habitat (see *marine larval ecology*).

Magnetic fields: Far from shore, some larvae are able to use magnetic fields to orient themselves towards the coast over large spatial scales. There is additional evidence that species can recognize anomalies in the magnetic field to return to the same location multiple times throughout their life. Though the mechanisms that these species use is poorly understood, it appears that magnetic fields play an important role in larval orientation offshore, where other cues such as sound and chemicals may be difficult to detect.

Light: Phototaxis (ability to differentiate between light and dark areas) is important to find a suitable habitat. Taxa that lack developed eyes, such as schyphozoans, use phototaxis to find shaded areas to settle away from predators. Phototaxis is not the only mechanism that guides larvae by light. The larvae of the annelid *Platynereis dumerilii* do not only show positive and negative phototaxis over a broad range of the light spectrum, but swim down to the center of gravity when they

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[75] Indeed, intraspecific competition among larva and adults for space is likely one big driving force for larval dispersal: large body sizes favour competition strength for space because larger organisms have higher growth rates and can outgrow smaller ones, so offspring have no chance in settling at their spawning sites, which are already occupied by their parents.

are exposed to non-directional UV-light. This behaviour is a UV-induced positive gravitaxis. This gravitaxis and negative phototaxis induced by light coming from the water surface form a ratio-metric depth-gauge. Such a depth gauge is based on the different attenuation of light across the different wavelengths in water. In clear water blue light (470 nm) penetrates the deepest. And so the larvae need only to compare the two wave length ranges UV/violet (< 420 nm) and the other wavelengths to find their preferred depth. Species that produce more complex larvae, such as fish, can use full vision to find a suitable habitat on small spatial scales. Larvae of damselfish use vision to find and settle near adults of their species.

Sound: Some marine larvae use sound and vibrations to find a good habitat where they can settle and metamorphose into juveniles. This behaviour has been seen in fish as well as in the larvae of scleractinian corals. Many families of coral reef fish are particularly attracted to high-frequency sounds produced by invertebrates, which larvae use as an indicator of food availability and complex habitat, where they may be protected from predators. It is thought that larvae avoid low frequency sounds because they may be associated with transient fish or predators and is therefore not a reliable indicator of safe habitat. The spatial range at which larvae detect and use sound waves is still uncertain, though some evidence suggests that it may only be reliable at very small scales. There is concern that changes in community structure in nursery habitats, such as seagrass beds, kelp forests, and mangroves, could lead to a collapse in larval recruitment due to a decrease in sound-producing invertebrates. Other researchers argue that larvae may still successfully find a place to settle even if one cue is unreliable.

Olfaction (chemical cues): Many marine organisms use olfaction (chemical cues in the form of scent) to locate a safe area to metamorphose at the end of their larval stage. This has been shown in both vertebrates and invertebrates. Research has shown that larvae are able to distinguish between water from the open ocean and water from more suitable nursery habitats such as lagoons and seagrass beds. Chemical cues can be extremely useful for larvae, but may not have a constant presence, as water input can depend on currents and tidal flow.

4
Ocean Habitats

Algae on coastal rocks at Shihtiping in Taiwan

The ocean is easiest defined through the large-scale presence of saltwater. Defining ecosystems *within* the marine realm is inevitably somewhat arbitrary, and their borders are not always clear. However, these habitat are extremely different. In this chapter we get to know the most important of them.

4.1 The pelagic zone

The open ocean is relatively unproductive because of a lack of nutrients, yet because it is so vast, it has more overall primary production than any other marine habitat (Fig. 4.1). Only about 10 percent of marine species live in the open ocean. But among them are the largest and fastest of all marine animals, as well as the animals that dive the deepest and migrate the longest. In the depths lurk animal that, to our eyes, appear hugely alien.

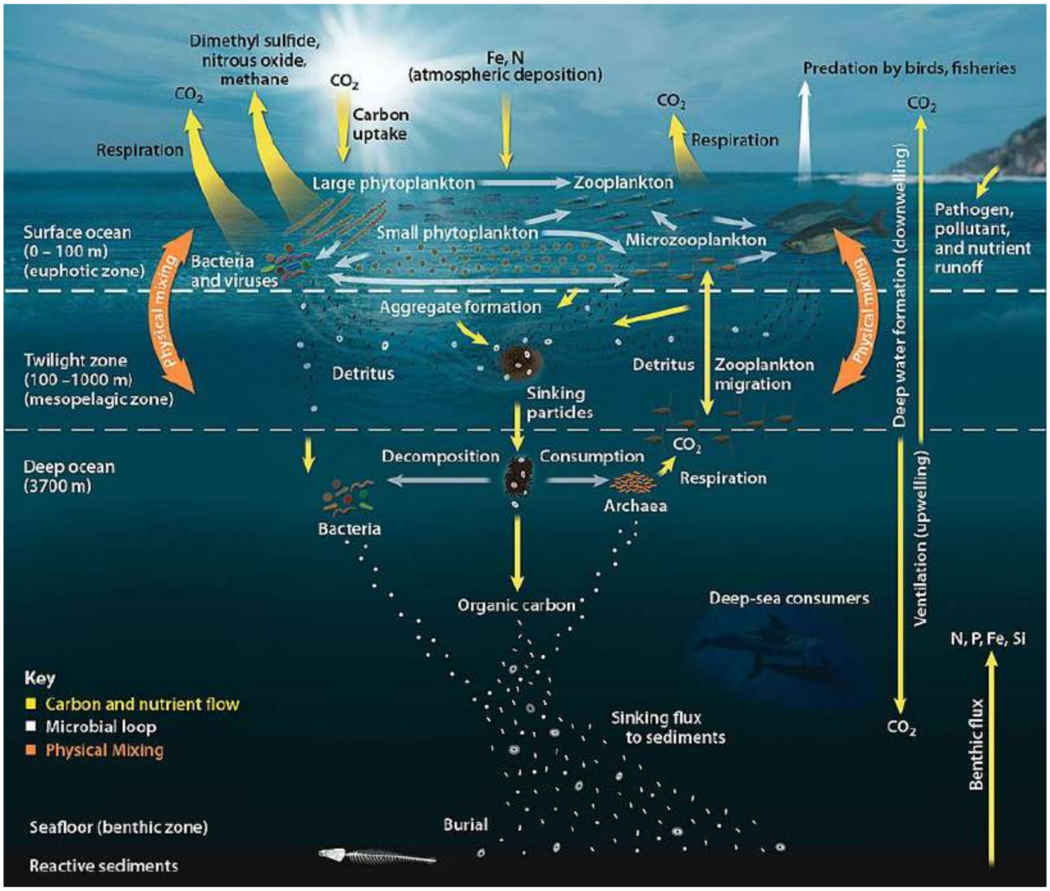

Figure 4.1: From top: The pelagic food web, showing the central involvement of marine microorganisms in how the ocean imports nutrients from and then exports them back to the atmosphere and ocean floor.

Much of the aphotic zone's energy is supplied by the open ocean in the form of detritus. In deep water, "marine snow" is a continuous shower of mostly organic detritus falling from the upper layers of the water column.[1] Its origin lies in activities within the productive photic zone. Marine snow includes dead or dying plankton, protists (diatoms), fecal matter, sand, soot and other inorganic dust. The "snowflakes" grow over time and may reach several centimetres in diameter, travelling for weeks before reaching the ocean floor. However, most or-

[1] See section 4.2 for whale falls and chemosynthesis as examples of point-based energy inputs.

ganic components of marine snow are consumed by microbes, zooplankton and other filter-feeding animals within the first 1,000 metres of their journey, that is, within the epipelagic zone. In this way marine snow may be considered the foundation of deep-sea mesopelagic and benthic ecosystems: As sunlight cannot reach them, deep-sea organisms rely heavily on marine snow as an energy source.

4.1.1 Surface Waters

The surface waters are sunlit. The waters down to about 200 metres are said to be in the epipelagic zone (Fig. 4.1). Enough sunlight enters the epipelagic zone to allow photosynthesis by phytoplankton. The epipelagic zone is usually low in nutrients. This is partially because the organic debris produced in the zone, such as excrement and dead animals, sinks to the depths and is lost to the upper zone. Photosynthesis can happen only if both sunlight *and* nutrients are present.

In some places, such as the edge of continental shelves, nutrients can upwell from the ocean depth, or land runoff can be distributed by storms and ocean currents. In these areas, given that both sunlight and nutrients are now present, phytoplankton can rapidly establish itself, multiplying so fast that the water turns green from the chlorophyll, resulting in an algal bloom. These nutrient-rich surface waters are among the most biologically productive in the world, supporting billions of tonnes of biomass.

Phytoplankton are eaten by zooplankton - the most abundant zooplankton species are copepods and krill: tiny crustaceans that are the most numerous animals on Earth. Other types of zooplankton include jelly fish and the larvae of fish, marine worms, starfish, and other marine organisms. In turn, the zooplankton are eaten by filter-feeding animals, including some sea birds, small forage fish such as herrings and sardines, whale sharks, manta rays, and the largest animal in the world, the blue whale. Yet again, moving up the food chain, the small forage fish are in turn eaten by larger predators, such as tuna, marlin, sharks, large squid, sea birds, dolphins, and toothed whales.

In response to the predatory pressures in the surface water food chain, many planktonic and nectonic organisms engage in diel[2] vertical migration (DVM), also known as diurnal vertical migration. The migration occurs when organisms move up to the uppermost layer of the sea at night and return to the bottom of the daylight zone of the oceans during the day (Fig. 4.2). In terms of biomass, it is the greatest migration in the world! It is not restricted to any one taxon as examples are known from crustaceans (copepods), molluscs (squid), and ray-finned fishes. The phenomenon may arise for a number of reasons, though it is most typically to access food and avoid

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[2] The word diel comes from the Latin *dies*, day, and means a 24-hour period.

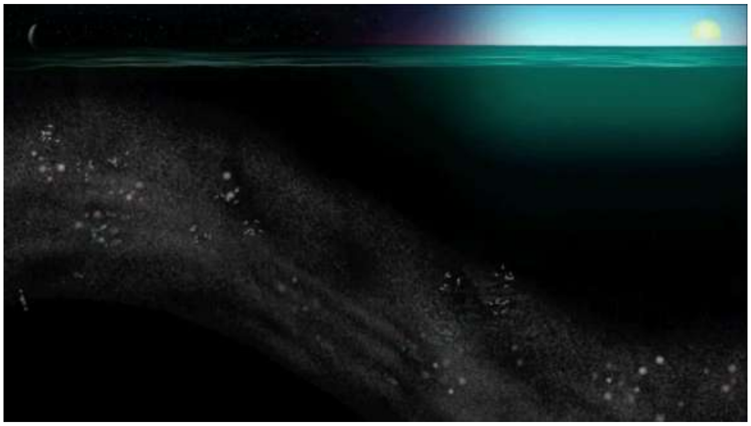

Figure 4.2: Daily migration of marine life to and from the twilight zone to the ocean surface. During day, much zooplankton and nekton stays deep in the water, returning to the surface layer at night. (Still of a NASA animation at `en.wikipedia.org/Diel_vertical_migration`.)

predators. While this mass migration is generally nocturnal, with the animals ascending from the depths at nightfall and descending at sunrise, the timing can be altered in response to the different cues and stimuli that trigger it. Some unusual events impact vertical migration: DVM is absent during the midnight sun in Arctic regions and vertical migration can occur suddenly during a solar eclipse.

4.1.2 *The Mesopelagic*

Somewhat a simplification, the mesopelagic is the zone where the microbial loop comes into its own. Although some light penetrates the mesopelagic zone, it is insufficient for photosynthesis (Fig. 4.1). The biological community of the mesopelagic zone has adapted to a low-light, low-food. This is a very efficient ecosystem with many organisms recycling the organic matter sinking from the epipelagic zone resulting in very little organic carbon making it to deeper ocean waters. The general types of life forms found are daytime-visiting herbivores, detritivores feeding on dead organisms and fecal pellets, and carnivores feeding on those detritivores. Many organisms in the mesopelagic zone move up into the epipelagic zone at night, and retreat to the mesopelagic zone during the day (Fig. 4.2). There is so much biomass in this migration that sonar operators in World War II would regularly misinterpret the signal returned by this thick layer of plankton as a false sea floor (Fig. 4.3).

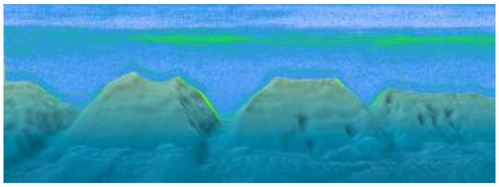

Figure 4.3: Underwater sonar 2D-slice through the water column: The green layer is the deep scattering layer of diel vertically migrating mesopelagic zooplankton and fish.

Microbes in the mesopelagic Very little is known about the microbial community of the mesopelagic zone because it is a difficult part of the ocean to study. Recent work using DNA from seawater samples emphasized the importance of viruses and microbes role in recycling organic matter from the surface ocean, known as the microbial loop.[3] These many microbes can get their energy from different metabolic pathways. Some are autotrophs, heterotrophs, and even some chemoautotrophs

[3] Viruses do not, of course, contribute directly to recycling of organic matter. However, they kill microbes, thereby cycling material even within the microbial loop.

(oxidising ammonium as their energy source).

Microbial biomass and diversity typically decline exponentially with depth in the mesopelagic zone, tracking the general decline of food from above. The community composition varies with depths in the mesopelagic as different organisms are evolved for varying light conditions. Microbial biomass in the mesopelagic is greater at higher latitudes and decreases towards the tropics, which is likely linked to the differing productivity levels in the surface waters.

Zooplankton in the mesopelagic The mesopelagic zone hosts a diverse zooplankton community. Common zooplankton include copepods, krill, jellyfish, siphonophores, larvaceans, cephalopods, and pteropods. Gelatinous organisms are thought to play an important role in the ecology of the mesopelagic and are common predators. Though previously thought to be passive predators just drifting through the water column, jellyfish could be more active predators (Fig. 4.4).

Mesopelagic zooplankton have unique adaptations for the low light. Bioluminescence is a very common strategy in many zooplankton (Fig. 4.5). This light production is thought to function as a form of communication between conspecifics, prey attraction, predator deterrence, and/or reproduction strategy. Another common adaption are enhanced light organs (read: eyes), which is common in krill and shrimp, so they can take advantage of the limited light. Some octopus and krill even have tubular eyes that look upwards in the water column.

Most life processes, like growth rates and reproductive rates, are slower in the mesopelagic. Metabolic activity has been shown to decrease with increasing depth and decreasing temperature in colder-water environments. For example, the mesopelagic shrimp-like mysid, *Gnathophausia ingens* (Fig. 4.6), lives for 6 to 8 years, while similar benthic shrimp only live for 2 years.

Fish in the mesopelagic The mesopelagic is home to a significant portion of the world's total fish biomass; one study estimated mesopelagic fish could be 95% of the total fish biomass. Another estimate puts mesopelagic fish biomass at 1 billion tons. This ocean realm could contain the largest fishery in the world and there is active development for this zone to become a commercial fishery.

The Gonostomatidae, or **bristlemouth**, are common mesopelagic fish (Fig. 4.7). The bristlemouth could be the Earth's most abundant vertebrate, with numbers in the hundreds of trillions to quadrillions. Another dominant family of fish in the mesopelagic zone are lanternfish (Myctophidae, Fig. 4.8 top), which include 245 species distributed among 33 different genera. They have prominent photophores along

Figure 4.4: Helmet jellyfish *Periphylla periphylla* is a luminescent, red-colored jellyfish of the deep sea. Size 30 cm. From: *Arctic Ocean Diversity*.

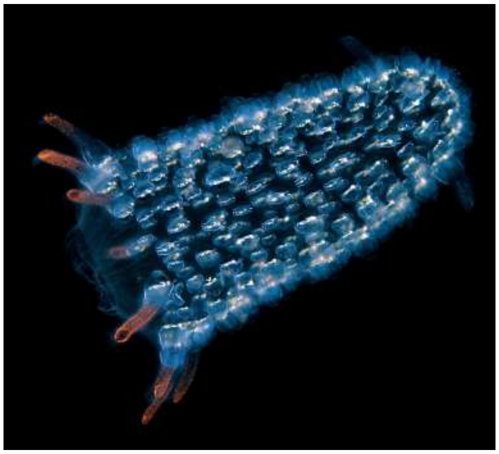

Figure 4.5: *Pyrosoma*, a colonial tunicate; each individual zooid in the colony flashes a blue-green light. Size 20 cm.

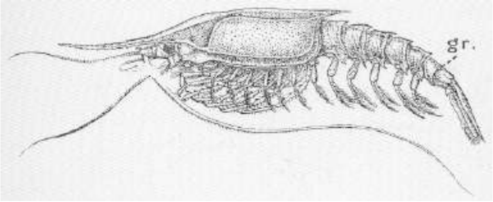

Figure 4.6: *Gnathophausia millemoesii*, one of the deep-sea mysidacea not unlike *G. ingens*. Size 3 cm. *gr*: a groove dividing the last abdominal somite.

their ventral side.

Food is often limited and patchy in the mesopelagic, leading to dietary adaptations. Common adaptations fish may have include sensitive eyes and huge jaws for enhanced and opportunistic feeding. Fish are also generally small to reduce the energy requirement for growth and muscle formation. Other feeding adaptations include jaws that can unhinge, elastic throats, and massive, long teeth. Some predators develop bioluminescent lures, such as the tasselled anglerfish, which can attract prey, while others respond to pressure or chemical cues instead of relying on vision.

Figure 4.7: Veiled anglemouth, *Cyclothone microdon*, a mesopelagic (to abyssopelatic) bristlemouth of the family Gonostomatidae. Size 10 cm.

4.1.3 *Deep Sea*

In the deep ocean, the waters extend far below the epipelagic zone (Fig. 4.1), and support very different types of pelagic life forms adapted to living in these deeper zones. Some deep-sea pelagic groups, such as the lanternfish, ridgehead, marine hatchetfish, and lightfish families (Fig. 4.8) are sometimes termed "pseudoceanic", because rather than having an even distribution in open water, they occur in significantly higher abundances around structural oases, notably seamounts and over continental slopes. The phenomenon is explained by the likewise abundance of prey species which are also attracted to the structures.

The fish in the different pelagic and deep water benthic zones are physically structured, and behave in ways that differ markedly from each other. Groups of coexisting species within each zone all seem to operate in similar ways, such as the small mesopelagic vertically migrating plankton-feeders, the bathypelagic anglerfishes, and the deep water benthic *grandiers*.

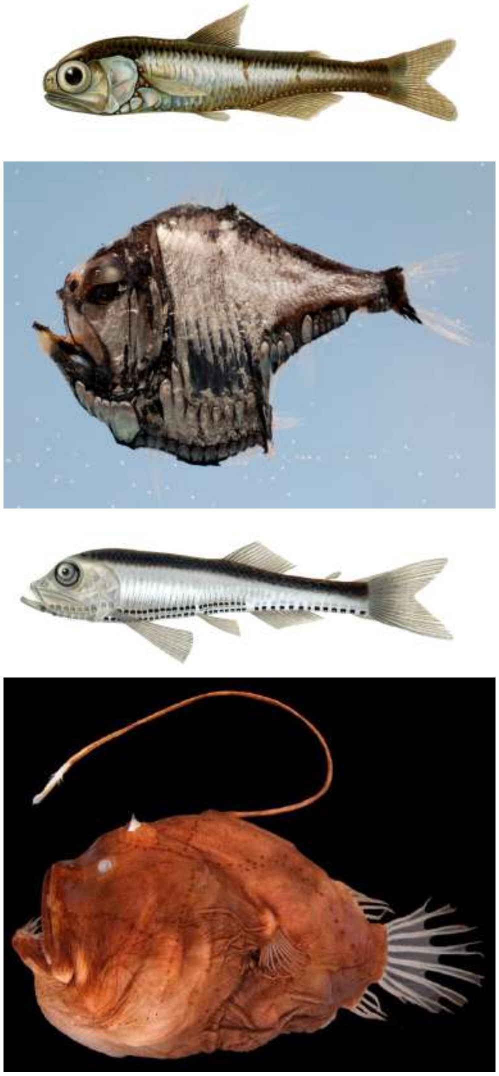

Figure 4.8: From top: Lanternfish *Myctophum punctatum* (10 cm); Atlantic silver hatchetfish *Argyropelecus aculeatus* (7 cm); Slender Lightfish *Vinciguerria attenuata* (4 cm); an anglerfish *Bufoceratias wedli* (10 cm). Note extreme eye size, easily larger than the brain itself.

4.2 *The Sea Floor - Benthos*

Terrigenous sediment is the most abundant sediment found on the sea floor, followed by biogenous sediment. The sediment in areas of the ocean floor which is at least 30% biogenous materials is labelled as an "ooze". There are two types of oozes: Calcareous oozes and Siliceous oozes. Plankton is the contributor of oozes. Calcareous oozes are predominantly composed of calcium shells found in phytoplankton such as coccolithophores and zooplankton such as the foraminiferans. These calcareous oozes are never found deeper than about 4,000 to 5,000 meters because at further depths the calcium dissolves. Similarly, siliceous oozes are dominated by the siliceous shells of phytoplankton such as diatoms and zooplankton such as radiolarians. Depending on the productivity of these planktonic organisms, the shell material that collects when these organisms die may build up at a rate anywhere from 1 mm to 1 cm every 1000 years.

"Benthos" (from Greek *βένθος* = "the depth") is the community of organisms which live on, in, or near the seabed. This community lives in or near marine sedimentary environments, from tidal pools along the foreshore, out to the continental shelf, and then down to the abyssal depths. The benthic zone is the ecological region on, in and immediately above the seabed, including the sediment surface and some sub-surface layers. Benthos generally live in close relationship with the substrate bottom, and many such organisms are permanently attached to the bottom.

In the euphotic zone, phytoplankton and algae contribute much of the energy input for benthic organisms. In the dark, food sources are any form of organic material, e.g. marine snow or detritus. Filter feeders, such as sponges and bivalves, dominate hard, sandy bottoms. Deposit feeders, such as polychaetes, populate softer bottoms. Fish as well as sea and brittle stars (Fig. 4.9), snails, cephalopods, and crustaceans are important predators and scavengers.

Due to the extremely low supply of the dark benthos with energy,[4] even invertebrate scavengers (many echinoderms, crustaceans but also snails and clams) have developed a fine sense of smell and aggregate on food sources from many kilometers. A particularly spectacular case is the succession of species scavenging on whale carcasses.

Figure 4.9: Common brittlestar *Ophiura ophiura*, a typical species of the benthos. Size 15 cm.

Whale falls

A whale fall occurs when the carcass of a whale has fallen onto the ocean floor at a depth greater than 1,000 m, in the bathyal or abyssal zones. On the sea floor, these carcasses can create complex localized ecosystems that supply sustenance to deep-sea organisms for decades. This is unlike in shallower waters, where a whale carcass will be consumed by scavengers over a relatively short period of time.

The bodies of most great whales (which includes sperm whales and many species of baleen whale) are slightly denser than the surrounding seawater, and only become positively buoyant when the lungs are filled with air.[5] When the lungs deflate, the whale carcasses can reach the sea floor quickly and relatively intact due to a lack of significant whale-fall scavengers in the water column. Once in the deep-sea, cold temperatures slow decomposition rates, and high hydrostatic pressures increase gas solubility, allowing whale falls to remain intact and sink to ever greater depths.

Deep-sea whale falls are thought to be hotspots of adaptive radiation for specialized fauna. Organisms that have been observed at deep-sea whale fall sites include giant isopods, squat lobsters, polychaetes, prawns, shrimp, lobsters, hagfish, the boneworm *Osedax* (an annelid, p. 93), crabs, sea cucumbers, and sleeper sharks (*Somniosus* spp.). New

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[4] Which is still an order of magnitude higher than in the water column: Ritzau, W. (1996). Microbial activity in the benthic boundary layer: Small-scale distribution and its relationship to the hydrodynamic regime. *Journal of Sea Research*, 36(3–4):171–180

[5] This is the reason why there are no "shark falls" or "tuna falls": their density is marginally lower than that of water.

Figure 4.10: A chemoautotrophic whale-fall community in the Santa Cruz basin off southern California at a depth of 1,674 m, including bacteria mats, vesicomyid clams in the sediments, galatheid crabs, polynoids, and a variety of other invertebrates.

species have been discovered, including some potentially specializing in whale falls.[6] Researchers estimate that 690,000 carcasses/skeletons of the nine largest whale species are in one of the four stages of decomposition at any one time. This estimate implies an average spacing of 12 km and as little as 5 km along migration routes. They hypothesize that this distance is short enough to allow decomposers' larvae to disperse/migrate from one to another.

Chemosynthesis - hydrothermal vents and cold seeps

A hydrothermal vent is a fissure on the sea floor from which geothermally heated water discharges. Hydrothermal vents are commonly found near volcanically active places, areas where tectonic plates are moving apart at spreading centres, ocean basins, and hotspots. Relative to the majority of the deep sea, the areas around submarine hydrothermal vents are biologically more productive, often hosting complex communities fuelled by the chemicals dissolved in the vent fluids. Chemosynthetic (rather than photosynthetic or organotrophic) bacteria and archaea form the base of the food chain, supporting diverse organisms, including giant tube worms, clams, limpets and shrimp.

The most spectacular, and most common, hydrothermal vent is the Black Smoker (Fig. 4.11). They appear as black, chimney-like structures that emit a cloud of black material. Black smokers are formed in fields hundreds of meters wide when superheated water from below Earth's crust comes through the ocean floor (water may attain temperatures above 400°C). This water is rich in dissolved minerals from the crust, most notably sulfides.

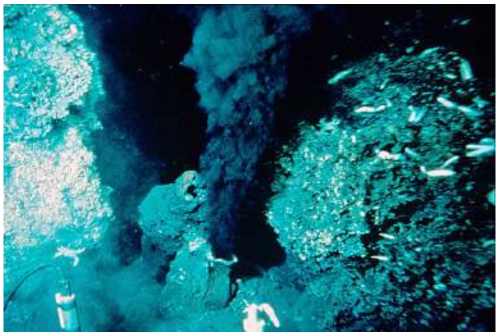

Figure 4.11: Black smokers were first discovered in 1979 on the East Pacific Rise at 21°north latitude at a depth below 2500 m.

The hydrothermal vents are recognized as a type of chemosynthetic-based ecosystems where primary productivity is

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[6] Have a look at a *Natural World Facts video* (8 min) on the topic.

fuelled by chemical compounds as energy sources instead of light (chemoautotrophy).[7] The chemosynthetic bacteria grow into a thick mat which attracts other organisms, such as amphipods and copepods, which graze upon the bacteria directly. Larger organisms, such as snails, shrimp, crabs, tube worms, fish (especially eelpout, cutthroat eel, ophidiiforms and *Symphurus thermophilus*), and octopuses (notably *Vulcanoctopus hydrothermalis*), form a food chain of predator and prey relationships above the primary consumers. The main families of organisms found around seafloor vents are annelida, tubeworms, gastropods, and crustaceans, with large bivalves and "eyeless" shrimp making up the bulk of non-microbial organisms.

Tube worms (Siboglinidae), which may grow to over 2 m tall in the largest species, often form an important part of the community around a hydrothermal vent (Fig. 4.12). They have no mouth or digestive tract, and like parasitic worms, absorb nutrients produced by the bacteria in their tissues. About 10 billion bacteria are found per g of tubeworm tissue. Tubeworms have red plumes which contain hemoglobin. Hemoglobin combines with hydrogen sulfide and transfers it to the bacteria living inside the worm. In return, the bacteria nourish the worm with carbon compounds.

Figure 4.12: Large concentrations of tubeworm *Riftia pachyptila*, with anemones and mussels colonizing in close proximity in the Galapagos Rift.

4.3 *The Polar Seas*

The Arctic and Antartic Ocean are not only geographical opposites. The Arctic is a sea surrounded by land, while the Antartic is a land surrounded by sea. Both host a similar area of sea ice, which is seasonally waxing and waning to a similar degree.

The Arctic sea The Arctic ice pack undergoes a regular seasonal cycle in which ice melts in spring and summer, reaches a minimum around mid-September ($\sim 5 \cdot 10^6$ km^2 = 5 Gm^2 or 1% or Earth's surface area), then increases during fall and winter (to $\sim 16 \cdot 10^6$ km^2). Summer ice cover in the Arctic is about 50% of winter cover. Some of the ice survives from one year to the next. Currently, 28% of Arctic basin sea ice is multi-year ice, thicker than seasonal ice: up to 3–4 m thick over large areas, with ridges up to 20 m thick. In the regular seasonal cycle there has been an underlying trend of declining sea ice in the Arctic in recent decades as well.[8]

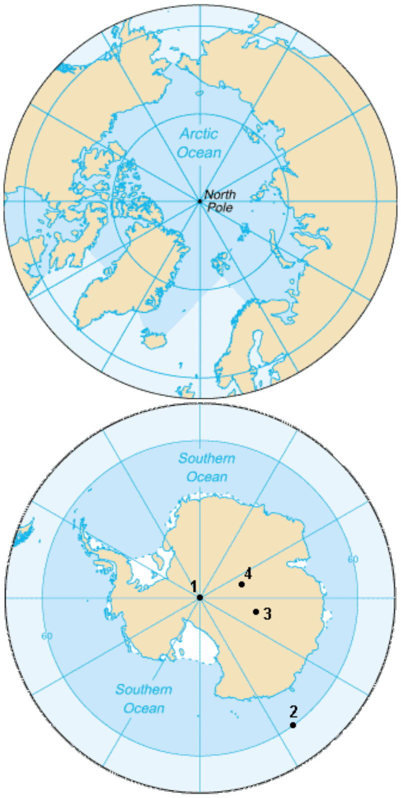

Figure 4.13: An azimuthal projection showing (*top*) the Arctic Ocean and the North Pole, and (*bottom*) the South Geographic Pole (1), South Magnetic Pole (2), South Geomagnetic Pole (3; not of our concern) and South Pole of Inaccessibility (4; ditto). Outermost blue lines are 60°.

The Antarctic sea The Antarctic sea ice cover is highly seasonal, with very little ice in the austral summer, expanding to an area roughly equal to that of Antarctica in winter. It peaks ($\sim 18 \cdot 10^6$ km^2) during September, which marks the end of austral winter, and retreats to a minimum ($\sim 3 \cdot 10^6$ km^2) in February. Consequently, most Antarctic sea ice is first year ice, a few meters thick. Since the ocean off the Antarctic coast

[7] Instead of releasing oxygen gas while fixing carbon dioxide as in photosynthesis, hydrogen sulfide chemosynthesis produces solid globules of sulfur in the process:
$18\ H_2S + 6\ CO_2 + 3\ O_2 \rightarrow C_6H_{12}O_6 + 12\ H_2O + 18\ S$

[8] Schofield, O., Ducklow, H. W., Martinson, D. G., Meredith, M. P., Moline, M. A., and Fraser, W. R. (2010). How do polar marine ecosystems respond to rapid climate change? *Science*, 328(5985):1520–3

usually is much warmer than the air above it, the extent of sea ice is largely controlled by the winds and currents that push it northwards. If it is pushed quickly, the ice can travel much further north before it melts. Most ice is formed along the coast, as the northward-moving ice leaves areas of open water (coastal latent heat polynyas), which rapidly freeze.

4.3.1 Sea Ice

Sea ice arises as seawater freezes. Because ice is less dense than water, it floats on the ocean's surface (as does fresh water ice, which has an even lower density). Sea ice covers about 7% of the Earth's surface and about 12% of the world's oceans. Much of the world's sea ice is enclosed within the polar ice packs in the Earth's polar regions: the Arctic ice pack of the Arctic Ocean and the Antarctic ice pack of the Southern Ocean.

In rough water, fresh sea ice is formed by the cooling of the ocean as heat is lost into the atmosphere. The uppermost layer of the ocean is supercooled to slightly below the freezing point, at which time tiny ice platelets (frazil ice) form. With time, this process leads to a mushy surface layer, known as grease ice. Frazil ice formation may also be started by snowfall, rather than supercooling. Waves and wind then act to compress these ice particles into larger plates, of several meters in diameter, called pancake ice. These float on the ocean surface, and collide with one another, forming upturned edges. In time, the pancake ice plates may themselves be rafted over one another or frozen together into a more solid ice cover, known as consolidated pancake ice. Such ice has a very rough appearance on top and bottom.

When sea water freezes, the ice is riddled with brine-filled channels which sustain "sympagic" (ice-associated) organisms. In fact, a number of varieties of algae such as diatoms engage in photosynthesis in polar regions of the earth. Other energy sources include Aeolian dust and pollen swept in from other regions. These ecosystems also include bacteria and fungi, as well as animals such as flatworms and crustaceans. A number of sympagic worm species are commonly called "ice worms".

Additionally, the ocean has abundant plankton, and prolific algal blooms occur in the polar regions each summer as well as in high mountain lakes, bringing nutrients to those parts of the ice in contact with the water. In spring, krill scrape off the green lawn of ice algae from the underside of the pack ice (Fig. 4.14). They in turn provide food for animals such as krill and specialised fish like the bald notothen, fed upon in turn by larger animals such as Emperor penguins and Minke whales.

Figure 4.14: ROV image of krill grazing under the ice. In this image most krill swim in an upside down position directly under the ice.

4.3.2 *Sea Ice Microbial Community*

The fluctuation of brine salinity, which is controlled by atmospheric temperatures, is the single-most influential factor on the chemistry of the sea-ice matrix. The solubility of carbon dioxide and oxygen, two biologically essential gases, decreases in higher salinity solutions. This can result in hypoxia within high heterotrophic activity regions of the sea ice matrix. Regions of high photosynthetic activity often exhibit internal depletion of inorganic carbon compounds and hyperoxia. These conditions have the potential to elevate brine pH and to further contribute to the creation of an extreme environment. In these conditions, high concentrations of dissolved organic matter (DOM) and ammonia and low concentrations of nutrients often characterize the ice matrix.

The concentration of nutrients such as nitrate, phosphate and silicate inside the sea ice matrix relies largely on the diffusive influx from the sea ice-water interface and to some extent on the atmospheric deposits on the sea ice-air interface.

The chemical properties of the sea-ice matrix are highly complex and depend on the interaction within the internal sea-ice biological assemblage as well as external physical factors. Winters are typically characterized by moderate oxygen levels that are accompanied by nutrient and inorganic carbon concentrations that are not growth limiting to phytoplankton (Fig. 4.15). Summers are typically characterized by high oxygen levels that are accompanied by a depletion of nutrients and inorganic carbon. Because of its diffusive interaction with seawater, the lower part of the sea ice matrix is typically characterized by higher nutrient concentrations.


Figure 4.15: Polar sea ice matrix covered in algae community showing a typical environment for sea ice microbial communities.

Microorganisms present in the surface seawater during fall are integrated in the brine solution during ice formation. Studies have shown that sea-ice microbial retention can be enhanced by the presence of extracellular polymeric substance/polysaccharides (EPS) on the walls of the brine channels. EPS are proteins expressed on the cell walls of microorganism such as algae. They improve the cell adherence to surfaces and when found in sufficient concentration, are thought to play a role in recruiting other organisms such as microbes. Airborne microorganisms make up a significant proportion of the microbial input to the ice matrix. Microorganisms located in the sea or in the ice matrix brine can be incorporated in falling snow or in aerosols.

Both the Antarctic and Arctic sea ice environments present strong vertical gradients of salinity, temperature, light, nutrients and DOM. These gradients were shown to induce strong vertical stratification in bacterial communities throughout the ice layer. Microbial abundance declines significantly with depth in the upper and middle ice, but not in the lowest, suggesting that much of the prokaryotic bacterial community is resistant to extreme environmental conditions. Heterotrophic bacteria were also shown to be more abundant at the bottom of the ice layer in zones of greater algae concentration, which characterized by higher DOM and nutrient concentrations.

Metagenomic studies of the Ross Sea illustrate the high abundance of aerobic anoxygenic phototrophic bacteria in sea ice environments. The predominance of Gammaproteobacteria in sea ice around the globe have been reported by many studies. A large proportion of the identified sea-ice microbial community in these studies were shown to belong to phylotypes associated with heterotrophic taxa.

Bacteria in all environments contribute to the microbial loop, but the roles of sea-ice microbial communities in the microbial loop differ due to the rapidly changing environmental conditions found in the Arctic and Antarctic. Sea-ice algae contribute 10%–28% of the total primary production in ice-covered regions of the Antarctic. Microalgae provide a vital source of nutrition for juvenile zooplankton such as the Antarctic krill *Euphausia superba* in the winter. DOM derived from phototrophic microalgae is crucial to the microbial loop, by serving as a growth substrate for heterotrophic bacteria.

4.4 Upwelling

Upwelling is an oceanographic phenomenon that involves wind-driven motion of dense, cooler, and usually nutrient-rich water from deep water towards the ocean surface, replacing the warmer, usually nutrient-depleted surface water. The nutrient-rich upwelled water stimulates the growth and reproduction of primary producers such as phytoplankton. Due to the biomass of phytoplankton and presence of cool water in these regions, upwelling zones can be identified by cool sea surface temperatures (SST) and high concentrations of chlorophyll a.

The increased availability of nutrients in upwelling regions results in high levels of primary production and thus fishery production. Approximately 25% of the total global marine fish catches come from five upwellings that occupy only 5% of the total ocean area. Upwellings that are driven by coastal currents (see section 1.3 and Fig. 4.16) or diverging open ocean have the greatest impact on nutrient-enriched waters and global fishery yields.

Coastal upwelling is the best known type of upwelling, and the most closely related to human activities as it supports some of the most productive fisheries in the world. Normally, this upwelling process occurs at a rate of about 5–10 meters per day, but the rate and proximity of upwelling to the coast can be changed due to the strength and distance of the wind.

Deep waters are rich in nutrients, including nitrate, phosphate and silicic acid[9], themselves the result of decomposition

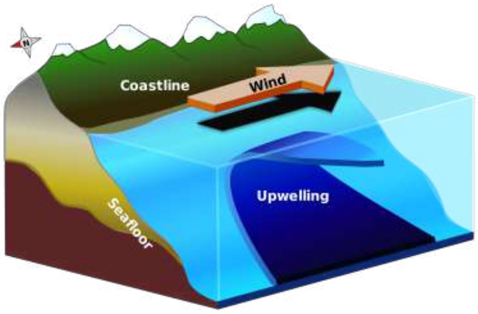

Figure 4.16: Coastal upwelling will occur if the wind direction is parallel to the coastline and generate wind-driven currents. These are diverted to the right of the winds in the Northern Hemisphere and to the left in the Southern Hemisphere due to the Coriolis effect. The result is a net movement of surface water at right angles to the direction of the wind. When this "Ekman transport" is occurring away from the coast, surface waters moving away are replaced by deeper, colder, and denser water.

[9] The term "silicic acid" has traditionally been used as a synonym for silica, SiO_2. Strictly speaking, silica is the anhydride of orthosilicic acid, $Si(OH)_4$. What is meant here is really silica, SiO_2.

of sinking organic matter (dead/detrital plankton) from surface waters. When brought to the surface, these nutrients are utilized by phytoplankton, along with dissolved CO_2 and light energy from the sun, to produce organic compounds, through the process of photosynthesis. Upwelling regions therefore result in very high levels of primary production (the amount of carbon fixed by phytoplankton) in comparison to other areas of the ocean. They account for about 50% of global marine productivity. High primary production propagates up the food chain because phytoplankton are at the base of the oceanic food chain.[10]

Coastal upwelling exists year-round in some regions, known as major coastal upwelling systems (Fig. 4.17), and only in certain months of the year in other regions, known as seasonal coastal upwelling systems (see section 1.3). Many of these upwelling systems are associated with relatively high carbon productivity and hence are classified as Large Marine Ecosystems.

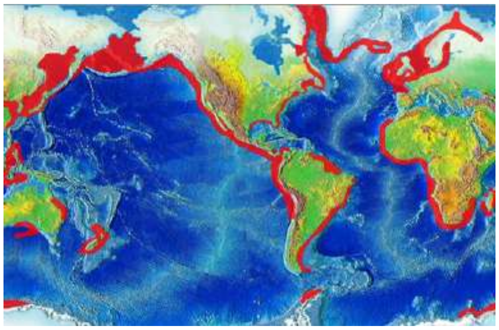

Figure 4.17: Areas of upwelling in red.

A major threat to both this crucial intermediate trophic level and the entire upwelling trophic ecosystem is the problem of commercial fishing. Since upwelling regions are the most productive and species-rich areas in the world, they attract a high number of commercial fishers and fisheries. On one hand, this is another benefit of the upwelling process as it serves as a viable source of food and income for so many people and nations besides marine animals. However, just as in any ecosystem, the consequences of over-fishing from a population could be detrimental to that population and the ecosystem as a whole.

The possibility of ecosystem collapse is the very danger of fisheries in upwelling regions. Unfortunately, the fish that are the most popular targets of fisheries, comprising about 64% of the entire catch), are pelagic predatory fish. Among those, the six main species that usually form the intermediate trophic layer represent over half of the catch. Depleting these stocks endangers the trophic level above, as well as the overall nutrient cycling (through reduced return of nutrients in faeces, carcasses and detritus).

The fisheries off the Pacific coast of South America is a particularly interesting case, due to the irregular El Niño Southern Oscillation events (see section 1.3). During the El Niño, waters are warmer and nutrient poor, leading to substantially lower primary and secondary productivity (Fig. 4.18). If fishing would extract the same amount of fish as during regular years, each El Niño event would result in a substantial depression of population sizes, which may take years to recover even without continued fishing pressure.[11] Such a pattern can be seen in the south-east Pacific (Fig. 4.19).

[10] Phytoplankton → zooplankton → predatory zooplankton → filter feeders → predatory fish → marine birds and mammals, incl. humans

[11] Bertrand, A., Lengaigne, M., Takahashi, K., Avadí, A., Poulain, F., and Harrod, C. (2020). *El Niño Southern Oscillation (ENSO) Effects on Fisheries and Aquaculture*. FAO, Rome

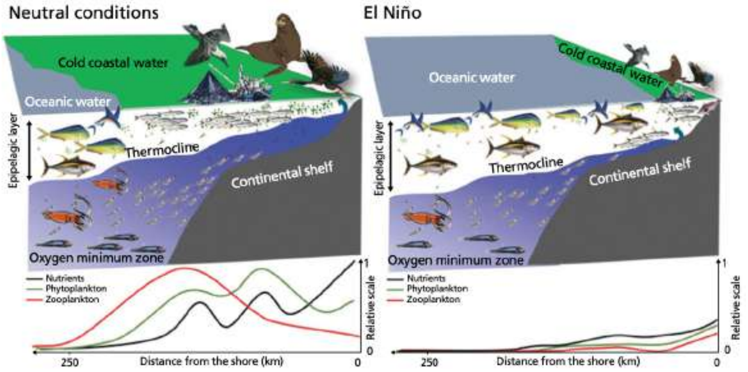

Figure 4.18: In non-El Niño years, the thermocline is shallow, so wind-driven upwelling is highly efficient in terms of nutrient supply, and the coastal ecosystem exhibits high biomass and primary productivity and extends far from shore. It is dominated by large phytoplankton, supports a food web with large zooplankton, small pelagic fish, seabirds, marine mammals and fishers. An oceanic low biomass and low primary productivity ecosystem is found offshore of the coastal ecosystem when nutrients are depleted. During extreme El Niño years the productive coastal area is reduced dramatically and the oceanic ecosystem impinges close to the shore. Source: Bertrand et al. (2020), p. 39.

4.5 *The Continental Shelf*

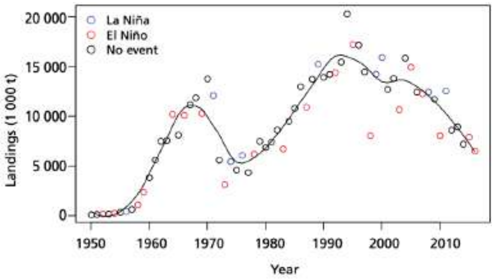

Figure 4.19: Fisheries landings in the south-east Pacific, and the effect of El Niño (red dots). Note that world wide, landings have stabilised in the 1990s, while here the signal of overfishing is clearly visible. Source: Bertrand et al. (2020), p. 38.

A continental shelf[12] is a portion of a continent that is submerged under an area of relatively shallow water known as a shelf sea. Much of these shelves were exposed by drops in sea level during glacial periods. The continental margin, between the continental shelf and the abyssal plain, comprises a steep continental slope, surrounded by the flatter continental rise, in which sediment from the continent above cascades down the slope and accumulates as a pile of sediment at the base of the slope. Extending as far as 500 km (310 mi) from the slope, it consists of thick sediments deposited by turbidity currents from the shelf and slope. The continental rise's gradient is intermediate between the gradients of the slope and the shelf.

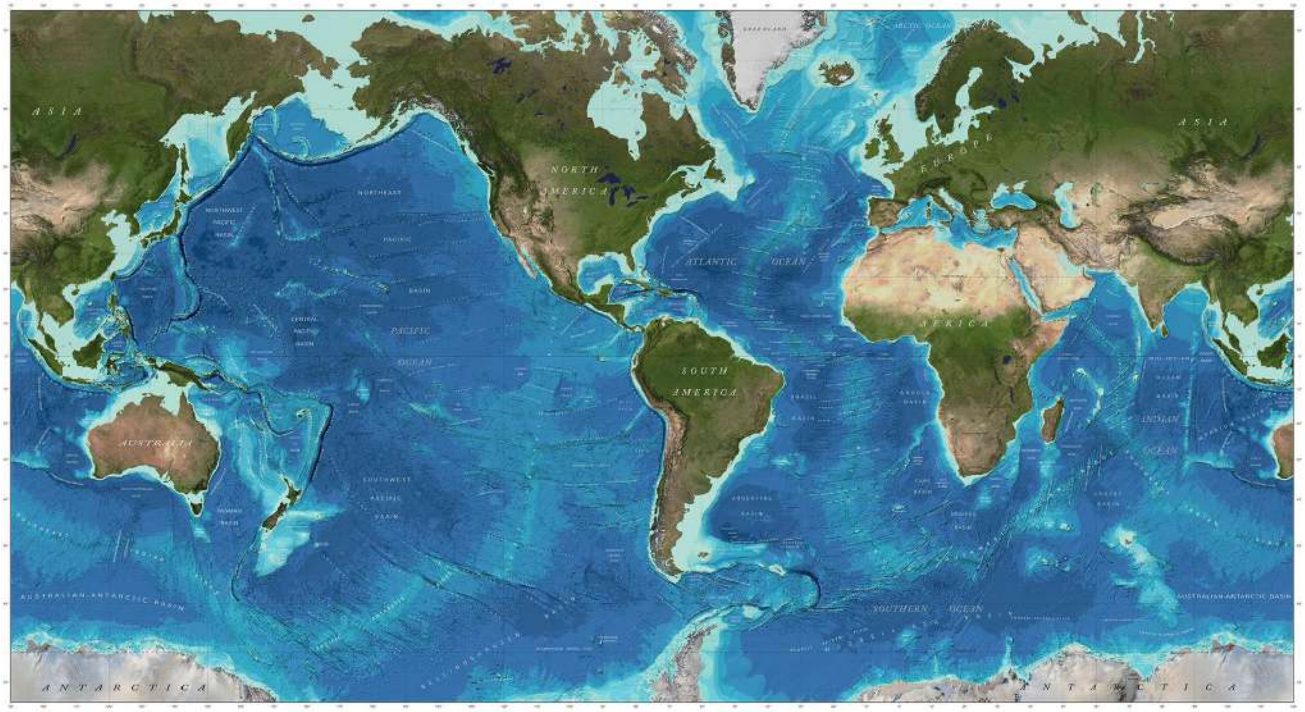

Figure 4.20: Global continental shelf, highlighted in light green.

The character of the shelf changes dramatically at the

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[12] Under the United Nations Convention on the Law of the Sea, the name continental shelf was given a legal definition as the stretch of the seabed adjacent to the shores of a particular country to which it belongs.

shelf break, where the continental slope begins. With a few exceptions, the shelf break is located at a remarkably uniform depth of roughly 140 m; this is likely a hallmark of past ice ages, when sea level was lower than it is now. The continental slope is much steeper than the shelf; the average angle is 3°, but it can be as low as 1° or as high as 10°. The slope is often cut with submarine canyons.

The width of the continental shelf varies considerably (Fig. 4.20) – it is not uncommon for an area to have virtually no shelf at all, particularly where the forward edge of an advancing oceanic plate dives beneath continental crust in an offshore subduction zone such as off the coast of Chile or the west coast of Sumatra. The largest shelf – the Siberian Shelf in the Arctic Ocean – stretches to 1,500 km in width. The South China Sea lies over another extensive area of continental shelf, the Sunda Shelf, which joins Borneo, Sumatra, and Java to the Asian mainland. Other familiar bodies of water that overlie continental shelves are the North Sea and the Persian Gulf. The average width of continental shelves is about 80 km.

Continental shelves teem with life because of the sunlight available in shallow waters, in contrast to the biotic desert of the oceans' abyssal plain. The pelagic environment of the continental shelf constitutes the neritic zone, and the benthic province of the shelf is the sublittoral zone. The shelves makes up less than ten percent of the ocean, and a rough estimate suggest that only about 30% of the continental shelf sea floor receives enough sunlight to allow benthic photosynthesis.

Though the shelves are usually fertile, if anoxic conditions prevail during sedimentation, the deposits may over geologic time become sources for fossil fuels.

4.6 Coral Reefs

A coral reef is an underwater ecosystem characterized by reef-building corals. Reefs are formed of colonies of coral polyps, helped by coralline algae and sponges, held together by calcium carbonate. Corals are the most prodigious reef-builders. However many other organisms living in the reef community contribute skeletal calcium carbonate in the same manner as corals. These include coralline algae and some sponges. Reefs are always built by the combined efforts of these different phyla, with different organisms leading reef-building in different geological periods.

Coral belongs to the class Anthozoa in the animal phylum Cnidaria, which includes sea anemones and jellyfish. Unlike sea anemones, corals secrete hard carbonate exoskeletons that support and protect the coral. Most reefs grow best in warm, shallow, clear, sunny and agitated water. Coral reefs first appeared 485 million years ago, at the dawn of the Early Ordovician, displacing the microbial and sponge reefs of the

Cambrian.

Sometimes called rainforests of the sea, shallow coral reefs form some of Earth's most diverse ecosystems. They occupy less than 0.1% of the world's ocean area, about half the area of France, yet they provide a home for at least 25% of all marine species, including fish, mollusks, worms, crustaceans, echinoderms, sponges, tunicates and other cnidarians. Coral reefs flourish in ocean waters that provide few nutrients. They are most commonly found at shallow depths in tropical waters, but deep water and cold water coral reefs exist on smaller scales in other areas.

4.6.1 Reef types

A "fringing reef" (Fig. 4.21), also called a shore reef, is attached to a shore or borders it with an intervening narrow, shallow channel or lagoon. It is the most common reef type. Fringing reefs follow coastlines and can extend for many kilometres. Fringing reefs are initially formed on the shore at the low water level and expand seawards as they grow in size. The surface of the fringe reef generally remains at the same height: just below the waterline. In older fringing reefs, whose outer regions pushed far out into the sea, the inner part is deepened by erosion and eventually forms a "lagoon". Fringing reef lagoons can become over 100 m wide and several metres deep. Like the fringing reef itself, they run parallel to the coast. The fringing reefs of the Red Sea are a typical example, occurring along all its shores except off sandy bays.

Figure 4.21: Fringing reef in the Red Sea, Eilat, Israel.

"Barrier reefs" (Fig. 4.22) are separated from a mainland or island shore by a deep channel or lagoon. Their lagoons can be several kilometres wide and 30 to 70 m deep. Above all, the offshore outer reef edge formed in open water rather than next to a shoreline. Like an atoll, it is thought that these reefs are formed either as the seabed lowered or sea level rose. Formation takes considerably longer than for a fringing reef, thus barrier reefs are much rarer. The best known and largest example of a barrier reef is the Australian Great Barrier Reef. Other major examples are the Belize Barrier Reef and the New Caledonian Barrier Reef.

Figure 4.22: Satellite image of part of the Great Barrier Reef adjacent to the Queensland coastal areas of Airlie Beach and Mackay. It is clearly removed from the shore by several dozen kilometres of water.

"Atolls" or atoll reefs (Fig. 4.24) are a more or less circular or continuous barrier reef that extends all the way around a lagoon without a central island. They are usually formed from fringing reefs around volcanic islands. Over time, the island erodes away and sinks below sea level. Atolls may also be formed by the sinking of the seabed or rising of the sea level. A ring of reefs results, which enclose a lagoon. Atolls are numerous in the South Pacific, where they usually occur in mid-ocean, for example, in the Caroline Islands, the Cook Islands, French Polynesia, the Marshall Islands and Micronesia. The entire Maldives consist of 26 atolls.

Zones Coral reef ecosystems contain distinct zones that host different kinds of habitats. Usually, three major zones are recognized (Fig. 4.23): the fore reef, reef crest, and the back reef (frequently referred to as the reef lagoon).

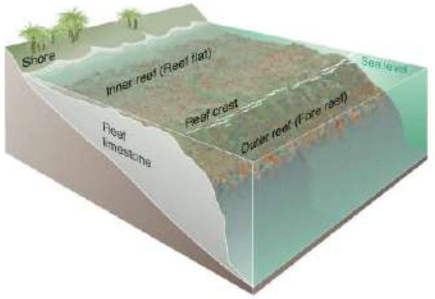

Figure 4.23: The three major zones of a coral reef: the fore reef, reef crest, and the back reef.

Reef formation Most coral reefs, particular fringe reefs, were formed after the Last Glacial Period when melting ice caused sea level to rise and flood continental shelves. Most coral reefs are less than 10,000 years old. As communities established themselves, the reefs grew upwards, pacing rising sea levels. Reefs that rose too slowly could become drowned, without sufficient light. Atolls are found in the deep sea away from continental shelves, around oceanic islands and atolls. The majority of these islands are volcanic in origin. Others have tectonic origins where plate movements lifted the deep ocean floor.

The archetypical formation of an atoll was postulated, as it happens, by Charles Darwin.[13] He theorized that uplift and subsidence of Earth's crust under the oceans formed the atolls. Coral atolls develop from reefs fringing volcanic islands. Reefs fringing volcanic islands build vertically to sea level, forming steep-walled barrier reefs. As a volcanic island subsides, or sinks, with time, the growing reef keeps pace with the rising water level. When the island eventually submerges, the ring-shaped reef forms an atoll with a central lagoon.

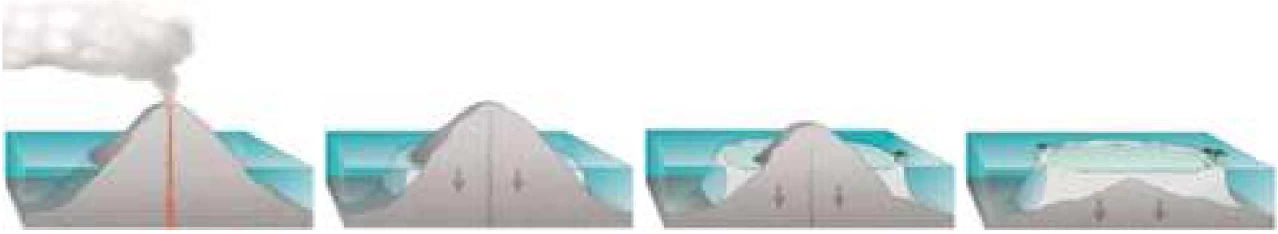

Figure 4.24: Atoll forming. From left: Volcanic island; fringing reef; barrier reef; atoll.

Reef-building or "hermatypic" corals live only in the photic zone (above 50 m), the depth to which sufficient sunlight penetrates the water. Healthy tropical coral reefs grow horizontally from 1 to 3 cm per year, and grow vertically anywhere from 1 to 25 cm per year. Above the water, and at its very surface, UV-radiation seems to damage the photosynthetic endosymbiontic algae of corals. Thus, while corals can grow substantially under optimal conditions, they always keep underwater.

4.6.2 Coral reef growth

Coral polyps do not photosynthesize, but have a symbiotic relationship with microscopic algae (dinoflagellates) of the genus *Symbiodinium*, commonly referred to as zooxanthellae. These organisms live within the polyps' tissues and provide organic nutrients that nourish the polyp in the form of glucose, glycerol and amino acids. Because of this relationship,

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[13] After encountering some during his voyage on the Beagle.

coral reefs grow much faster in clear water, which admits more sunlight. Without their symbionts, coral growth would be too slow to form significant reef structures. Corals get up to 90% of their nutrients from their symbionts. In return, as an example of mutualism, the corals shelter the zooxanthellae, averaging one million for every cubic centimeter of coral, and provide a constant supply of the carbon dioxide they need for photosynthesis.

The varying pigments in different species of zooxanthellae give them an overall brown or golden-brown appearance and give brown corals their colours (Fig. 4.25). Other pigments such as reds, blues, greens, etc. come from coloured proteins made by the coral animals. Coral that loses a large fraction of its zooxanthellae becomes white (or sometimes pastel shades in corals that are pigmented with their own proteins) and is said to be bleached, a condition which, unless corrected, can kill the coral.

Figure 4.25: The colour of corals depends on the combination of brown shades provided by their zooxanthellae and pigmented proteins (reds, blues, greens, etc.) produced by the corals themselves.

Reefs grow as polyps and other organisms deposit calcium carbonate, the basis of coral, as a skeletal structure beneath and around themselves, pushing the coral head's top upwards and outwards. Waves, grazing fish (such as parrotfish), sea urchins, sponges and other forces and organisms act as bioeroders, breaking down coral skeletons into fragments that settle into spaces in the reef structure or form sandy bottoms in associated reef lagoons.

Coralline algae are important contributors to reef structure. Although their mineral deposition rates are much slower than those of corals, they are more tolerant of rough wave-action, and so help to create a protective crust over those parts of the reef subjected to the greatest forces by waves, such as the reef front facing the open ocean. They also strengthen the reef structure by depositing limestone in sheets over the reef surface.

"Sclerosponge" is the descriptive name for all *Porifera* that build reefs. In the early Cambrian period, *Archaeocyatha* sponges were the world's first reef-building organisms, and sponges were the only reef-builders until the Ordovician. Sclerosponges still assist corals building modern reefs, but like coralline algae are much slower-growing than corals and their contribution is (usually) minor.

4.6.3 Cold-water reefs

The habitat of deep-water corals, also known as cold-water corals, extends to deeper, darker parts of the oceans than tropical corals, ranging from near the surface to the abyss, beyond 2,000 m, where water temperatures may be as cold as 2°C. Deep-water corals grow more slowly than tropical corals because there are no zooxanthellae to feed them. *Lophelia* (Fig. 4.26) has a linear polyp extension of about 10 mm/year (compared to tropical 100-200 mm/year).

While there are nearly as many species of deep-water corals as shallow-water species, only a few deep-water species develop traditional reefs. Instead, they form aggregations called patches, banks, bioherms, massifs, thickets or groves. Deep-sea reefs are sometimes referred to as "mounds", which more accurately describes the large calcium carbonate skeleton that is left behind as a reef grows and corals below die off, rather than the living habitat and refuge that deep-sea corals provide for fish and invertebrates.

Four genera (*Lophelia*, *Desmophyllum*, *Solenosmilia*, and *Goniocorella*) constitute most deep-water coral banks at depths of 400–700 m. The world's largest known deep-water *Lophelia* coral complex is the Røst Reef. It lies between 300 and 400 m deep, west of Røst island in the Lofoten archipelago, in Norway, inside the Arctic Circle. Discovered during a routine survey in May 2002, the reef is still largely intact. It is approximately 35 km long by 3 km wide.


Figure 4.26: *Lophelia pertusa* is a reef building, gonochoric (=dioecious), deep-water coral, which does not contain zooxanthellae.

Lophelia reefs can host up to 1,300 species of fish and invertebrates. Various fish aggregate on deep sea reefs. Deep-sea corals, sponges and other habitat-forming animals provide protection from currents and predators, nurseries for young fish, and feeding, breeding and spawning areas for numerous fish and shellfish species. Rockfish, Atka mackerel, walleye pollock, Pacific cod, Pacific halibut, sablefish, flatfish, crabs, and other economically important species in the North Pacific inhabit these areas.


Figure 4.27: The strong beak of humphead parrotfish *Bolbometopon muricatum* is able to grind the sturdiest corals off Borneo. Photo by Hectonichus.

Threats to coral reefs Since their emergence 485 million years ago, coral reefs have faced many threats, including disease, predation, invasive species, bioerosion by grazing fish (Fig. 4.27), algal blooms, geologic hazards, and recent human activity. This include coral mining, bottom trawling,[14] and the digging of canals and accesses into islands and bays, all of which damage marine ecosystems. Other localized threats include blast fishing, overfishing, coral overmining, and marine pollution, including use of the banned anti-fouling biocide tributyltin; although absent in developed countries, these activities continue in places with few environmental protections or poor regulatory enforcement. Chemicals in sunscreens may awaken latent viral infections in zooxanthellae and impact reproduction.


Figure 4.28: Bleached *Acropora* coral with normal coral in the background.

Greenhouse gas emissions present a broader threat through sea temperature rise and sea level rise, although corals adapt their calcifying fluids to changes in seawater pH and carbonate levels and are not directly threatened by ocean acidification. Corals respond to stress by "bleaching", i.e. expelling their colourful zooxanthellate endosymbionts (Fig. 4.28). Corals with deeper-water "Clade C"-zooxanthellae are generally vulnerable to heat-induced bleaching, whereas corals with

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[14] For an impression, see photos and video at *Blue Seals*.

the hardier, near-surface Clades A or D are generally resistant, as are tougher coral genera such as *Porites* and *Montipora*.

4.7 *The Intertidal: the Land-Sea Interface*

The intertidal zone is where sea and land meet. It is defined as the area within the tidal range, i.e. above water at low and under water at high tide.

The area above the high-tide mark is the supralittoral zone which is virtually a terrestrial environment impacted by salt spray. Between the high and low-tide marks is the intertidal or littoral zone. Below the low-tide mark is the sublittoral or subtidal zone.

There are several factors that make these systems special:

- Its organisms are exposed to the air at least some hours per day. This means exposure to UV-light, to high (and low) temperatures, to dessication and to land-based predation.
- Breaking waves pose a strong physical strain on the intertidal. In polar regions, ice scoring may occur.
- The system blends the euphotic zone, with its phytoplankton-derived carbon input, and the benthic zone, with its detritus-based food web.

Most importantly for ecologists, the intertidal zone is the part of the ocean most accessible to humans for scientific research, and accordingly it is the best known part of the ocean.

Four common intertidal ecosystems exist, two where the benthos "crawls" onto land (rocky shores and tidal flats[15]), and two where the land dips its feet into the ocean (mangroves and salt marshes).

Not every metre of coast line features an intertidal of interest. Without tidal amplitude it is "only" the waves and their salt spray that prevents terrestrial vegetation growing up to the shoreline. Or said shoreline may be a lifeless rock or rubble, frozen for months in polar regions and tossed around by waves at high exposure, crushing any macroscopic life (Fig. 4.29).


Figure 4.29: The rise and fall of tides on a rocky shore can define a volatile habitat for marine life. (Friendly Beaches, Tasmania, Australia; photo by J.J. Harrison)

4.7.1 *Rocky shores*

A rocky shore is an intertidal area of sea coasts where solid rock predominates. Rocky shores are biologically rich environments, and are a useful "natural laboratory" for studying intertidal ecology and other biological processes.

Many factors favour the survival of life on rocky shores. Temperate coastal waters are mixed by waves and convection, maintaining adequate availability of nutrients. Also, the sea brings plankton and organic matter in with each tide. The high availability of light (due to low depths) and nutrient levels means that primary productivity of seaweeds and algae

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[15] We shall omit the sandy shores here, which are a simple yet interesting system. Some turtles use it for breeding, waders for foraging, and plenty of interesting microscopic creatures live in amongst the sand grains. See also

McLachlan, A. and Defoe, O. (2017). *The Ecology of Sandy Shores*. Academic Press, Cambridge, MA, 3rd edition can be very high. Human actions can benefit or impair rocky shores due to nutrient runoff.

Despite these favourable factors, there are also a number of challenges to marine organisms associated with the rocky shore ecosystem. Generally, the distribution of benthic species is limited by salinity, wave exposure, temperature extremes, desiccation and thus general stress. The constant threat of desiccation during exposure at low tide can result in dehydration. Hence, many species have developed adaptations to prevent this drying out, such as the production of mucous layers and shells. Many species use shells and holdfasts to provide stability against strong wave actions. There are also a variety of other challenges such as temperature fluctuations due to tidal flow (resulting in exposure), changes in salinity and various ranges of illumination. Other threats include predation from birds and other marine organisms, as well as the effects of pollution.

Zonation Because intertidal organisms endure regular periods of immersion and emersion, they essentially live both underwater and on land and must be adapted to a large range of climatic conditions. The intensity of climate stressors varies with relative tide height because organisms living in areas with higher tide heights are emersed for longer periods than those living in areas with lower tide heights. This gradient of climate with tide height leads to patterns of intertidal zonation (Fig. 4.30, 4.31), with high intertidal species being more adapted to emersion stresses than low intertidal species. These adaptations may be behavioural (i.e. movements or actions), morphological (i.e. characteristics of external body structure), or physiological (i.e. internal functions of cells and organs). In addition, such adaptations generally cost the organism in terms of energy (e.g. to move or to grow certain structures), leading to trade-offs (i.e. spending more energy on deterring predators leaves less energy for other functions like reproduction).

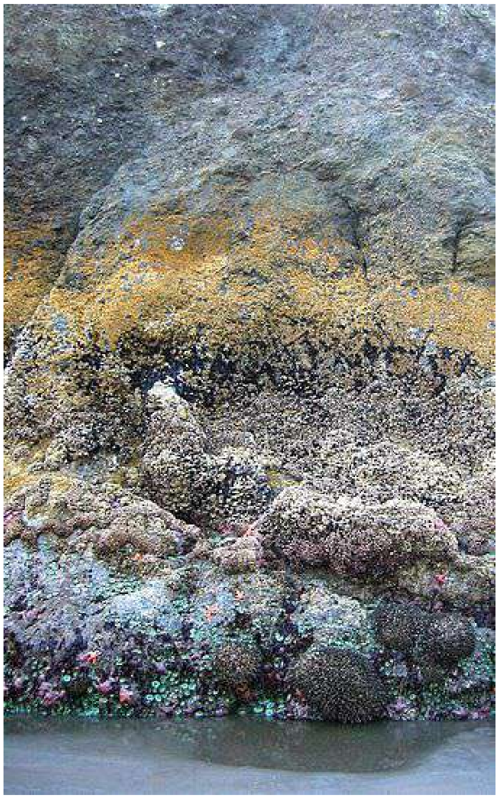

Figure 4.30: A rock, seen at low tide, exhibiting typical intertidal zonation. (Approx. 3 m wide strip.)

Intertidal organisms, especially those in the high intertidal, must cope with a large range of temperatures. While they are underwater, temperatures may only vary by a few degrees over the year. However, at low tide, temperatures may dip to below freezing or may become scaldingly hot, leading to a temperature range that may approach 30°C during a period of a few hours. Many mobile organisms, such as snails and crabs, avoid temperature fluctuations by crawling around and searching for food at high tide and hiding in cool, moist refuges (crevices or burrows) at low tide. Besides simply living at lower tide heights, non-motile organisms may be more dependent on coping mechanisms. For example, high intertidal organisms have a stronger stress response, a physiological response of making proteins that help recovery

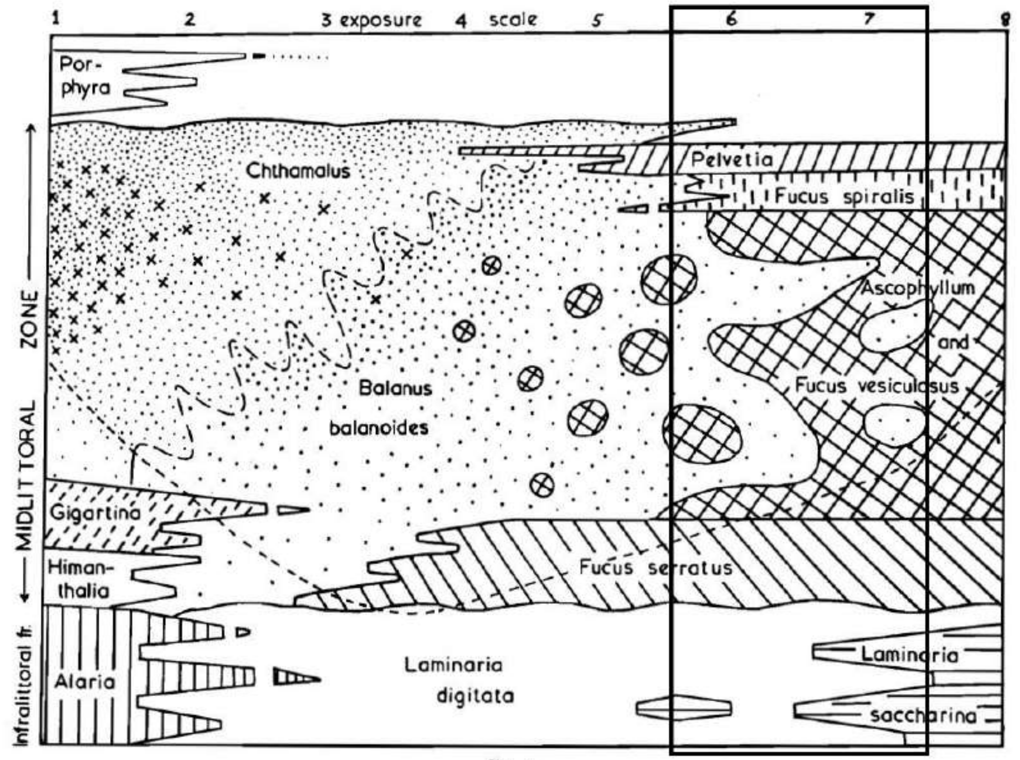

FIG. 1

The changes in distribution and zonation of the barnacles and algae with exposure. Based on shores in the Dale area, Pembrokeshire, except the extremely sheltered shore. Vertical scale according to Stephenson's universal scheme. Horizontal scale of exposure (sheltered to the right) with the approximate positions of the exposure scale given.

× = *Fucus vesiculosus* f. *evesiculosus*.

— — — = upper limit of "Lithothamnia".

Figure 4.31: Classic schematic drawing of rocky shore zonation at different wave explores, from exposed on the left to sheltered on the right.

from temperature stress just as the immune response aids in the recovery from infection.

Intertidal organisms are also especially prone to desiccation during periods of emersion. Again, mobile organisms avoid desiccation in the same way as they avoid extreme temperatures: by hunkering down in mild and moist refuges. Many intertidal organisms, including *Littorina* snails, prevent water loss by having waterproof outer surfaces, pulling completely into their shells, and sealing shut their shell opening. Limpets (*Patella*) do not use such a sealing plate but occupy a home-scar to which they seal the lower edge of their flattened conical shell using a grinding action (Fig. 4.32). They return to this home-scar after each grazing excursion, typically just before emersion. Still other organisms, such as the algae *Ulva* and *Porphyra*, are able to rehydrate and recover after periods of severe desiccation.

In addition to these exposure stresses (temperature, desiccation, and salinity), intertidal organisms experience strong mechanical stresses in locations of high wave action. To prevent dislodgement, many mollusks (such as limpets and chitons) have low-profile, hydrodynamic shells. Types of substrate attachments include mussels' tethering byssal threads (Fig. 4.33) and glues, sea stars' thousands of suctioning tube feet, and isopods' hook-like appendages that help them hold

Figure 4.32: Star barnacles (*Chthamalus stellatus* and *C. montagui*) and young limpets (*Patella vulgata*). Note how snug the lower left limpet fits to the rock. The right limpet noticeably "bulldozed" barnacles around its homepatch. Area approx. 7 cm wide.

on to intertidal kelps.

Figure 4.33: *Mytilus* mussel in California, showing the byssus threads. (The mussel is approx. 4 cm.)

Food-web structure During tidal immersion, the food supply to intertidal organisms is subsidized by materials carried in seawater, including photosynthesizing phytoplankton and consumer zooplankton. These plankton are eaten by numerous forms of filter feeders—mussels, clams, barnacles, sea squirts, and polychaete worms—which filter seawater in their search for planktonic food sources. The adjacent ocean is also a primary source of nutrients for autotrophs, photosynthesizing producers ranging in size from microscopic algae (e.g. benthic diatoms) to huge kelps and other seaweeds. These intertidal producers are eaten by herbivorous grazers, such as limpets that scrape rocks clean of their diatom layer and kelp crabs that creep along blades of the feather boa kelp *Egregia* eating the tiny leaf-shaped bladelets. Higher up the food web, predatory consumers – especially voracious starfish, but also whelks (Fig. 4.34) – eat other grazers (e.g. snails) and filter feeders (e.g. mussels). Finally, scavengers, including crabs and sand fleas, eat dead organic material, including dead producers and consumers.

Figure 4.34: Dog whelk *Nucella lapillus* on barnacles, one of its many prey. Picture by Martin Talbot (on flickr). (Each snail is approx. 1.5 cm.)

Species interactions In addition to being shaped by aspects of climate, intertidal habitats—especially intertidal zonation patterns—are strongly influenced by species interactions, such as predation, competition, facilitation, and indirect interactions. Ultimately, these interactions feed into the food web structure, described above.

One dogma of intertidal ecology – supported by several classic studies – is that species' lower tide height limits are set by species interactions whereas their upper limits are set by climate variables.[16] Classic studies by Robert Paine established that when sea star predators are removed, mussel beds extend to lower tide heights, smothering resident seaweeds.[17] Thus, mussels' lower limits are set by sea star predation. Conversely, in the presence of sea stars, mussels' lower limits occur at a tide height at which sea stars are unable to tolerate climate conditions.

Competition, especially for space, is another dominant interaction structuring intertidal communities. Space competition is especially fierce in rocky intertidal habitats, where habitable space is limited compared to soft-sediment habitats in which three-dimensional space is available. As seen with the previous sea star example, mussels are competitively dominant when they are not kept in check by sea star predation. Joseph Connell's research on two types of high intertidal barnacles, *Semibalanus balanoides*[18] and *Chthamalus stellatus*, showed that zonation patterns could also be set by competition between closely related organisms.[19] In this example, *Semibalanus* outcompetes *Chthamalus* at lower tide

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[16] Menge, B. A. and Farrell, T. M. (1987). Community structure and interaction webs in shallow marine hard- bottom communities: tests of an environmental stress model. *Advances in Ecological Research*, 19:189–259; and Menge, B. A. (1995). Indirect effects in marine rocky intertidal interaction webs: patterns and importance. *Ecological Monographs*, 65:21–74

[17] Paine, R. T. (1969). A note on trophic complexity and community stability. *The American Naturalist*, 103:91–93

[18] At that time still in the genus *Balanus*, despite having a membranous, not a *Balanus*-style calcareous base plate.

[19] Connell, J. H. (1961b). The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus*. *Ecology*, 42(4):710–723; and Connell, J. H. (1961a). Effects of competition, predation by *Thais lapillus*, and other factors on natural populations of the barnacle *Balanus balanoides*. *Ecological Monographs*, 31(1):61–104

heights but is unable to survive at higher tide heights. Similarly, *Chthamalus*, which occurs in a refuge from competition (similar to the temperature refuges discussed above), has a lower tide height limit set by competition with *Semibalanus* and a higher tide height limit is set by climate.

Although intertidal ecology has traditionally focused on these negative interactions (predation and competition), there is emerging evidence that positive interactions are also important. Facilitation refers to one organism helping another without harming itself. Mussels, although they are tough competitors with certain species, are also good facilitators, as mussel beds provide a three-dimensional habitat to species of snails, worms, and crustaceans.

Tide pools Tide pools or rock pools are shallow pools of seawater that form on the rocky intertidal shore (Fig. 4.35). As such, they provide a watery habitat amidst the sun and wind exposed intertidal during low tide. As a result, tide pools are a mixture of subtidal communities (as they are always under water) and intertidal refuges for species sensitive to the open air. As a consequence, predatory organisms such as crabs, neogastropod snails and of course fish may concentrate in tide pools, with intense but not necessarily representative trophic interactions.

Figure 4.35: *Top:* A tide pool in Porto Covo, west coast of Portugal. *Middle:* Tide pool on Gabriola Island, British Columbia, with purple sea star *Pisaster ochraceus* (approx. 30 cm) crowding to avoid the sun. *Bottom:* Beadlet anemones, whelks, limpets, jellyfish and *Corallina* in a rock pool on the rocky shore at Aberdour Bay, Scotland.

For example, algae grow better in rock pools than in the surrounding intertidal, luring in herbivorous snails and limpets. These, in turn, do not have the benefit of freedom from predation that they enjoy during low tide elsewhere, when dog whelk and crabs are taking refuge from the sun in cracks and the subtidal. In consequence, rock pool herbivores are typically suppressed by their predators, allowing algal growth to be more luxurious in tide pools than on the exposed rock.

Organisms of the subtidal that can be readily observed in tide pools are in particular sea anemones and starfish, but also algae and of course small fishes.

4.7.2 *Tidal flats*

Tidal flats, also known as mud flats, are coastal wetlands that form in intertidal areas where sediments have been deposited by tides or rivers. They are found in sheltered areas such as bays and estuaries and may be viewed geologically as exposed layers of bay mud, resulting from deposition of estuarine silts, clays and aquatic animal detritus. Most of the sediment within a tidal flat is within the intertidal zone, and thus the flat is submerged and exposed approximately twice daily (Fig. 4.36).

Figure 4.36: The mudflats of the Pilsumer Watt near Greetsiel, Germany. Green patches are the (invasive) cord grass *Sporobolus anglicus* (= *Spartina anglica*).

The bay mud is rich in animal life, much of which feeds either on the detritus in the sediment (or the bacteria that live off it) or filter-feeds on the particles in the water column. Sessile polychaetes as well as amphipods crustaceans build tubes and ducts in the sediment, while clams and mussels buried in the sediment for protection use their siphon, to suck in water from which they sift detritus and plankton.

Bay mud composition varies greatly with distance to river and topography. The "typical" bay mud is rich in silt and organic material (up to 30% each), and poor in sand. On its surface, diatoms form a dense, slimy layer grazed by *Littorina* snails and preventing water movement to reach into the sediment. Combined with high decomposition rates of the organic detritus by bacteria, only the top 1-2 cm is oxygenised, and below that anaerobic bacteria produce a deeply black anoxic layer exuding foul smell: H_2S. Bioturbation, i.e. the turnover of sediment by burrowing bivalves and polychaetes, locally leads to aerobic conditions, and overall dramatically increases the depth of the aerobic layer.

Sandier deposits, higher up towards the shoreline and further away from river influxes, host a noticeably different set of species of the same families. It is here that we find the lugworm, producing its characteristics casts (Fig. 4.37). Thanks to the absence of a closed diatom layer, a much higher pore volume and lower organic content, the aerobic horizon easily reaches 10-20 cm into the sediment.

Medium-sized (up to a few cm) predatory polychaetes roam the surface at high tide (Fig. 4.38), while seeking shelter in their burrows during low tide. Birds feed on all of these creatures at low, and fish (sand goby, sole, flounder, particularly in sandy areas) and crabs at high tide. During spring and autumn migration, the Wadden Sea hosts millions of waders, whose bill morphology gives away their foraging niche: sanderlings, sand pipers and dunlins (Fig. 4.39) pick off surface-dwelling amphipods and alike, while oystercatchers, godwits, snipes and curlews access polychaetes and bivalves up to a dozen centimetres into the mud.

Figure 4.37: Lugworms *Arenicola marina* are not typically visible, but the few cm tall casts produced by their burrowing make distinctive patterns in damp sand.

Figure 4.38: The polychaet ragworm *Hediste diversicolor* (= syn. *Nereis diversicolor*) forms an important part of the diet of many waders. Size up to 10 cm.

Figure 4.39: Dunlin *Calidris alpina* arrive in their thousands on tidal flats during migration. Size approx. 20 cm.

4.7.3 *Mangroves*

Mangroves can be found in over one hundred countries and territories in the tropical and subtropical regions of the world (Fig. 4.40). The largest percentage of mangroves is found between the 5°N and 5°S latitudes. Approximately 75% of world's mangroves are found in just 15 countries. Asia has the largest amount (42%) of the world's mangroves, followed by Africa (21%), Northern, Central America and the Caribbean (15%), Oceania (12%), and South America (11%).

The intertidal existence to which these trees are adapted represents the major limitation to the number of species able to thrive in their habitat. High tide brings in salt water, and when the tide recedes, solar evaporation of the seawater in the soil leads to further increases in salinity. The return of tide can flush out these soils, bringing them back to salinity levels comparable to that of seawater.

At low tide, organisms are also exposed to increases in temperature and reduced moisture before being then cooled

Figure 4.40: The world's mangrove forests in 2000.

and flooded by the tide. Thus, for a vascular plant to survive in this environment, it must tolerate broad ranges of salinity, temperature, and moisture, as well as a number of other key environmental factors—thus only a select few species make up the mangrove tree community.

About 110 species are considered "mangroves", in the sense of being a tree that grows in such a saline swamp, though only a few are from the mangrove plant genus, *Rhizophora* (Fig. 2.31). However, a given mangrove swamp typically features only a few tree species. For comparison, the tropical rainforest biome contains thousands of tree species, but this is not to say mangrove forests lack diversity. Though the trees themselves are few in species, the ecosystem that these trees create provides a habitat for a great variety of other species, including as many as 174 species of marine megafauna.

Mangrove tree size, within the a given species, shows a clear relation to solar energy input. *Avicennia marina* reaches several meters of height in northern New Zealand, but south of Auckland it is less than a meter tall.

Mangroves are an important source of *blue carbon*. Globally, mangroves stored 4.19 Pg of carbon in 2012, but they are lost at a rate of approx. 0.2% per year.[20]

4.7.4 *Salt marshes*

A salt marsh is a coastal ecosystem in the upper coastal intertidal zone between land and open saltwater or brackish water that is regularly flooded by the tides. It is dominated by dense stands of salt-tolerant plants such as herbs, grasses, or low shrubs. These plants are terrestrial in origin and are essential to the stability of the salt marsh in trapping and binding sediments (Fig. 4.41).

Plant species diversity is relatively low, since the flora must be tolerant of salt, complete or partial submersion, and anoxic mud substrate. The most common plants of the lower salt marsh are glassworts (*Salicornia* spp.) and cord grass

Figure 4.41: Salt marsh of the Jade Bight, Germany. Land reclamation through rows of wooden poles driven into the bay mud leads to a typical salt marsh zonation pattern.

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[20] Goldberg, L., Lagomasino, D., Thomas, N., and Fatoyinbo, T. (2020). Global declines in human-driven mangrove loss. *Global Change Biology*, 26:5844–5855; and Richards, D. R., Thompson, B. S., and Wijedasa, L. (2020). Quantifying net loss of global mangrove carbon stocks from 20 years of land cover change. *Nature Communications*, 11:4260

(*Spartina* spp.), which have worldwide distribution. They are often the first plants to take hold in a mudflat and begin its ecological succession into a salt marsh. Their shoots lift the main flow of the tide above the mud surface while their roots spread into the substrate and stabilize the sticky mud and carry oxygen into it so that other plants can establish themselves as well. Plants such as sea lavenders (*Limonium* spp.), plantains (*Plantago* spp.), and rushes (*Juncus geradii*) and grasses (*Puccinellia* spp., *Festuca rubra*) grow once the mud has been vegetated by the pioneer species. Woody plants (such as *Halimione portulacoides*), miniature mangroves if you wish, establish once the soil layer provides enough nutrients.

Salt marshes are quite photosynthetically active and are extremely productive habitats. They serve as depositories for a large amount of organic matter and are full of decomposition, which feeds a broad food chain of organisms from bacteria to mammals.

Figure 4.42: Río de la Plata estuary, Argentina/Uruguay, looking East. Water on the river is brown because of sediments carried from the Paraná and Uruguay rivers. The colour turns blue when approaching the South Atlantic Ocean. The exact location of the colour change (which also implies a change from fresh to salt water) depends on winds and currents.

Figure 4.43: The Venetian Lagoon, Italy. No ideal, but charismatic example of a lagoon-type estuary, as only 11% is permanently covered by open water, while around 80% consists of tidal shallows and salt marshes.

Figure 4.44: A fjord-type estuary: Svalbard's van Mijenfjorden, with the clear barrier island at its mouth. At this latitude, marine ecology is much simplified.

4.8 Estuaries

An estuary is a partially enclosed coastal body of brackish water with one or more rivers or streams flowing into it, and with a free connection to the open sea. Estuaries form a transition zone between river environments and maritime environments known as "ecotone". Estuaries are subject both to marine influences, such as tides, waves, and the influx of saline water, and to riverine influences, such as flows of freshwater and sediment. The mixing of seawater and freshwater provides high levels of nutrients both in the water column and in sediment, making estuaries among the most productive natural habitats in the world.

Most existing estuaries formed during the Holocene epoch with the flooding of river-eroded or glacially scoured valleys when the sea level began to rise about 10,000–12,000 years ago. Estuaries are typically classified according to their geomorphological features or to water-circulation patterns. "Drowned valleys", or ria, are coastal plain estuaries (Fig. 4.42). In places where the sea level is rising relative to the land, sea water progressively penetrates into river valleys and the topography of the estuary remains similar to that of a river valley. This is the most common type of estuary in temperate climates. The width-to-depth ratio of these estuaries is typically large, appearing wedge-shaped (in cross-section) in the inner part and broadening and deepening seaward. Water depths rarely exceed 30 m.[21] "Lagoon-type" or bar-built estuaries are found in a place where the deposition of sediment has kept pace with rising sea levels so that the estuaries are shallow and separated from the sea by sand spits or barrier islands (Fig. 4.43). They are relatively common in tropical and subtropical locations.[22] Fjords were formed where Pleistocene glaciers deep-

[21] Examples are the Severn (UK), Elbe (Germany), Chesapeake Bay (USA), Bahía Blanca (Argentina), Sydney Harbour (Australia) or Johor Strait (Singapore). Note that not every river mouth is automatically an estuary, as it may not experience tidal mixing with seawater.

[22] Examples include most of the coast of New Jersey or Florida (USA), Venice (Italy), Lake Maracaibo (Venezuela), Keta Lagoon (Ghana) or Chilika Lake (India).

ened and widened existing river valleys so that they become U-shaped in cross-sections. At their mouths there are typically rocks, bars or sills of glacial deposits, which have the effects of modifying the estuarine circulation. "Fjord-type" estuaries are formed in deeply eroded valleys formed by glaciers (Fig. 4.44). These U-shaped estuaries typically have steep sides, rock bottoms, and underwater sills contoured by glacial movement. *The estuary is shallowest at its mouth* (in contrast to ordinary fjords), where terminal glacial moraines or rock bars form sills that restrict water flow. In the upper reaches of the estuary, the depth can exceed 300 m. The width-to-depth ratio is generally small. In estuaries with very shallow sills, tidal oscillations only affect the water down to the depth of the sill, and the waters deeper than that may remain stagnant for a very long time, so there is only an occasional exchange of the deep water of the estuary with the ocean.[23]

Of the thirty-two largest cities in the world in the early 1990s, twenty-two were located on estuaries. Unsurprisingly, many estuaries suffer degeneration from a variety of factors including soil erosion, deforestation, overgrazing, overfishing and the filling of wetlands. Eutrophication may lead to excessive nutrients from sewage and animal wastes; pollutants including heavy metals, polychlorinated biphenyls, radionuclides and hydrocarbons from sewage inputs; and diking or damming for flood control or water diversion.

Water circulation The residence time of water in an estuary is dependent on the circulation within the estuary that is driven by density differences due to changes in salinity and temperature. Less dense freshwater floats over saline water, and warmer water floats above colder water (at temperatures greater than 4°C). As a result, near-surface and near-bottom waters can have different trajectories, resulting in different residence times.

Vertical mixing determines how much the salinity and temperature will change from the top to the bottom, profoundly affecting water circulation. Vertical mixing occurs at three levels: from the surface downward by wind forces, the bottom upward by boundary generated turbulence (estuarine and oceanic boundary mixing), and internally by turbulent mixing caused by the water currents which are driven by the tides, wind, and river inflow.

"Salt-wedge" estuaries are characterized by a sharp density interface between the upper layer of freshwater and the bottom layer of saline water. River water dominates in this system, and tidal effects have a small role in the circulation patterns (e.g. the Mississippi estuary). The freshwater floats on top of the seawater and gradually thins as it moves seaward. The denser seawater moves along the bottom up the estuary forming a wedge shaped layer and becoming thinner

[23] Fjord-type estuaries can be found along the coasts of Alaska, the Puget Sound region of western Washington state, British Columbia, eastern Canada, Greenland, Iceland, New Zealand, and Norway.

as it moves landward. As a velocity difference develops between the two layers, shear forces generate internal waves at the interface, mixing the seawater upward with the freshwater.

"Partially stratified" estuaries are less dominated by river discharge (e.g the Thames). Turbulent mixing induced by the current creates a moderately stratified condition. Turbulent eddies mix the water column, creating a mass transfer of freshwater and seawater in both directions across the density boundary. Therefore, the interface separating the upper and lower water masses is replaced with a water column with a gradual increase in salinity from surface to bottom. A two layered flow still exists however, with the maximum salinity gradient at mid depth. Partially stratified estuaries are typically shallow and wide, with a greater width to depth ratio than salt wedge estuaries.

In "vertically homogeneous" estuaries, tidal flow is greater relative to river discharge, resulting in a well mixed water column and the disappearance of the vertical salinity gradient. The width to depth ratio of vertically homogeneous estuaries is large, with the limited depth creating enough vertical shearing on the sea floor to mix the water column completely. If tidal currents at the mouth of an estuary are strong enough to create turbulent mixing, vertically homogeneous conditions often develop.

Challenging conditions for marine life Estuaries are incredibly dynamic systems, where temperature, salinity, turbidity, depth and flow all change daily in response to the tides. This dynamism makes estuaries highly productive habitats, but also make it difficult for many species to survive year-round. As a result, temperate estuaries large and small experience strong seasonal variation in their fish communities. In winter, the fish community is dominated by hardy marine residents, and in summer a variety of marine and anadromous fishes move into and out of estuaries, capitalizing on their high productivity.

Two of the main challenges of estuarine life are the variability in salinity and sedimentation. Many species of fish and invertebrates have various methods to control or conform to the shifts in salt concentrations and are termed osmoconformers and osmoregulators. Many animals also burrow to avoid predation and to live in a more stable sedimental environment. However, large numbers of bacteria are found within the sediment which has a very high oxygen demand. This reduces the levels of oxygen within the sediment often resulting in partially anoxic conditions, which can be further exacerbated by limited water flux.

Phytoplankton are key primary producers in estuaries. They move with the water bodies and can be flushed in and out with the tides. Their productivity is largely dependent upon the turbidity of the water. The main phytoplankton present is diatoms and dinoflagellates, which are abundant in the sediment. Still, the primary source of food for many organisms in estuaries, including bacteria, is detritus from the settlement of the sedimentation.

5

Human Effect

Fishermen in Sesimbra, Portugal

> Human activities affect every place on earth. As the human population size and our affluence grows, so does our impact on the natural world. We see it on land, where we live. We see it less when the ocean surface hides what is beneath as we fly over or float on it. And the coast, from which we watch the ocean waves break, overlooks only a tiny fraction of the actual biome. In this chapter we explore some of the effects human action has. We know of them, but we don't see them; we see them, but we do not want to know of them.

Humans affect on marine life is direct, e.g. through fisheries and habitat destruction, as well as indirect, through pollution. Pollution encompasses a wide range of effects: nutrient and agrochemical input through rivers; human waste products including plastics; oil spillage; drifting fishing gear ("ghost nets"); introduction of chemicals and heavy metals for oil and gas exploration; CO_2-induced ocean acidification; climate change-induced coral bleaching; sound pollution through intense shipping traffic, ocean drilling, military (and much less but locally significant scientific) soundings.

As with many human effects on ecosystems, the rapid expansion of the human population and their increasing affluence has stretched many marine ecosystem beyond breaking point. Stocks of several fish species have been depleted, species driven (close) to extinction, habitats destroyed, food webs altered and organisms poisoned.[1]

Roughly a third of the world population depends for its survival on marine production. More and more open-ocean fishery is supplemented by aquaculture.[2] Opportunities for win-win situations and symbiontic coexistence of humans and marine life are scarce; alterations of coastlines and destruction of fish nurseries (mangroves, coral reefs, sea grass meadows) are irreversible under continued use; local dependence on the ocean in low-income countries without alternative.

Finally, the open ocean, beyond the 370 km (= 200 nautical miles) exclusive economic zone around a countries coast, is subject to international legislation,[3] but its enforcement is both logistically nigh impossible and politically highly problematic. As a consequence, fishing, resource exploration and ocean dumping (of radioactive waste, sludge, and any form of liquid waste) are tackled only by public shaming through environmental NGOs.[4] The *Tragedy of the Commons* applies to the oceans at a scale second only to that of the atmosphere.

5.1 *Fishery & Aquaculture*

Commercial fishing is the activity of catching fish[5] and other seafood for commercial profit, mostly from wild fisheries. It provides a large quantity of food to many countries around the earth, but those who practice it as an industry must often pursue fish far into the ocean under adverse conditions. Large-scale commercial fishing is also known as industrial fishing.

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[1] Jennings, S., Kaiser, M., and Reynolds, J. D. (2009). *Marine Fisheries Ecology*. John Wiley & Sons, New York

[2] Naylor, R. L., Hardy, R. W., Buschmann, A. H., Bush, S. R., Cao, L., Klinger, D. H., Little, D. C., Lubchenco, J., Shumway, S. E., and Troell, M. (2021). A 20-year retrospective review of global aquaculture. *Nature*, 591(78517851):551–563

[3] The 1982 *United Nations Convention on the Law of the Sea*.

[4] Ringius, L. (1997). Environmental NGOs and regime change: the case of ocean dumping of radioactive waste. *European Journal of International Relations*, 3(1):61–104

[5] "Fish", in the context of fisheries, includes crustaceans, molluscs, echinoderms, turtles, whales and other non-fish marine animals.

Commercial fisheries harvest a wide variety of animals, ranging from tuna, cod, and salmon to shrimp, krill, lobster, clams, squid, and crab. However, a very small number of species support the majority of the world's fisheries: herring, cod, anchovy, tuna, flounder, mullet, squid, shrimp, salmon, crab, lobster, oyster and scallops. All except the last four provided a worldwide catch of well over a million tonnes in 1999, with herring and sardines together providing a catch of over 22 million metric tons in 1999.

As Fig. 5.1 shows, catch of wild fish has plateaued in the 1990s, despite a continuous increase in the amount of nets, vessels and kilometers covered by commercial fisheries.

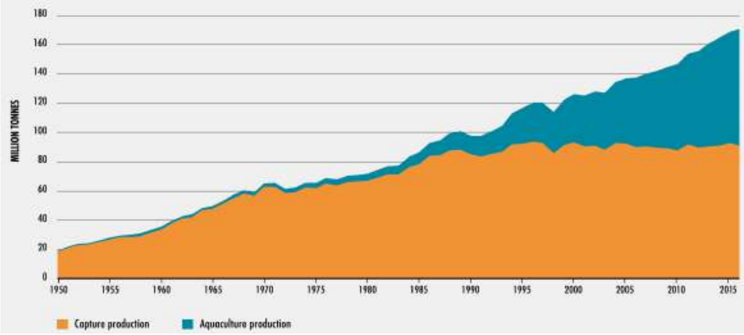

Figure 5.1: World capture fisheries and aquaculture production 1950–2015. By Food and Agriculture Organization of the United Nations (FAO).

In 2016, of the 171 million tonnes of fish caught, about 88% were utilized for direct human consumption. The greatest part of the 12% used for non-food purposes was reduced to fishmeal and fish oil, while the rest was largely utilized as material for direct feeding in aquaculture and raising of livestock, as bait, in pharmaceutical uses and for ornamental purposes (e.g. pearls).

Figure 5.2: Common, and spectacular bycatch. *Top:* Shrimp bycatch. The FAO estimated discard rates (bycatch to catch ratios) as high as 20:1 with a world average of 5.7:1. *Bottom:* Rescuing North Atlantic right whale from by-catching. The animal was observed entangled with gear wrapped around both flippers and encircling its entire body. The rescue team was able to remove enough gear to allow the whale to shed most of the remaining gear on its own.

"Bycatch" is the industry term for what they consider "unwanted or economically-worthless aquatic animals who are unintentionally caught using destructively indiscriminate fishing methods like longlines and driftnets, which generally target marketable marine creatures such as tuna and swordfish".[6] There are also billions of animals that are killed in this manner every year, including sea turtles, marine mammals, and sea birds (Fig. 5.2). Between 1990 and 2008, it was estimated that 8.5 million sea turtles alone were fatally caught in nets or on longlines as bycatch.

Overfishing occurs because fish are captured at a faster rate than they can reproduce. Both advanced fishing technologies and increased demand for fish have resulted in overfishing. The Food and Agricultural Organization has reported that "about 25 percent of the world's captured fish end up thrown overboard because they are caught unintentionally, are illegal market species, or are of inferior quality and size".[7] It should not go unnoticed that overfishing has caused more ecological extinction than any other human influence on coastal ecosys-

[6] Cited from `foodispower.org`.

[7] From DUJS.

tems. On the other hand, marine protected areas have shown to be effective in locally reversing overfishing trends.[8]

Dynamite fishing The effect of fisheries on fish stock, but also on local communities, on social and nutritional development, on political power struggles following sovereignty is complex, and often rather sad. As an example, take dynamite fishing.

Dynamite fishing or blast fishing is a destructive fishing practice using explosives to stun or kill schools of fish for easy collection. Although effective in killing or stunning the fish, a problem with dynamite fishing is the inefficiency of retrieval. For every ten fish killed, only one or two float to the surface (Fig. 5.3), while in all others the damage to the air bladder makes them denser than water and sink to the bottom.

Figure 5.3: Fish floating immediately after the blast.

This often illegal practice is extremely destructive to the surrounding ecosystem, as the explosion often destroys the underlying habitat (such as coral reefs) that supports the fish. The frequently improvised nature of the explosives used means danger for the fishermen as well, with accidents and injuries.

So why do fishermen,[9] particularly in the Indo-Pacific (Tanzania, Philippines, Indonesia), engage in a practice that is dangerous, destroys their own livelihoods and is illegal? Among other factors, fishermen face market competition from large industrial fishing fleets. To survive, literally, they have to harvest at ever lower costs, driving them into a *Tragedy of the Commons*. When Australia excluded fishing from its huge new marine protected areas, international fisheries experts worried that the demand for fish would now be covered by dynamite fishing in Indonesia, rather than the much environmental-friendlier and more efficient Australian industrial fisheries. This argument neglects the immense reduction in competition Indonesian fishermen now experienced, allowing for more traditional, less efficient but also less destructive fishing methods. In a final twist, any reduction of competition is immediately compensated for by local overpopulation's ever-rising demand for food.

Aquaculture Marine aquaculture, also known as mariculture (Fig. 5.4), is the farming of fish, crustaceans (e.g. shrimp), molluscs (e.g. oysters) and algae. Aquaculture involves cultivating populations under controlled conditions, in contrast with commercial fishing of wild fish. Aquaculture operations in 2015 supplied about half of the fish and shellfish that is directly consumed by humans (Fig. 5.1). Some forms of aquaculture, such as seaweed farming, have the opportunity to be part of climate change mitigation, while other forms of aquaculture have negative impacts on the environment, such as through nutrient pollution or disease transfer to wild populations.

Figure 5.4: Mariculture, in the form of fish farming, near Amarynthos, Euboea, Greece.

Raising marine organisms under controlled conditions in exposed, high-energy ocean environments beyond significant coastal influence is a relatively new approach to mariculture.

[8] Worm, B., Hilborn, R., Baum, J. K., Branch, T. A., Collie, J. S., Costello, C., Fogarty, M. J., Fulton, E. A., Hutchings, J. A., Jennings, S., Jensen, O. P., Lotze, H. K., Mace, P. M., McClanahan, T. R., Minto, C., Palumbi, S. R., Parma, A. M., Ricard, D., Rosenberg, A. A., Watson, R., and Zeller, D. (2009). Rebuilding global fisheries. *Science*, 325(5940):578–585

[9] Yes, they are overwhelmingly men.

Some attention has been paid to how open-ocean mariculture can combine with offshore energy installation systems, such as wind farms, to enable a more effective use of ocean space. The largest deep water open ocean farm in the world is raising cobia (Fig. 5.5) 12 km off the northern coast of Panama in highly exposed sites.

There are environmental hazards such as waste, damage to ecosystems, and negative effects on humans. Because they are so densely packed together, the faecal matter that accumulates can create algal blooms, or parasites and viruses that thrive in the polluted environment.

One of the primary concerns with mariculture is the potential for disease and parasite transfer. Farmed stocks are often selectively bred to increase disease and parasite resistance, as well as improving growth rates and quality of products. As a consequence, the genetic diversity within reared stocks decreases with every generation - meaning they can potentially reduce the genetic diversity within wild populations if they escape into those wild populations. Such genetic pollution from escaped aquaculture stock can reduce the wild population's ability to adjust to the changing natural environment. Species grown by mariculture can also harbour diseases and parasites which can be introduced to wild populations upon their escape. An example of this is the parasitic sea lice on wild and farmed Atlantic salmon in Canada and Scotland.

Figure 5.5: Cobia *Rachycentron canadum*, aka black bonito and black kingfish, is a fish of warm-temperate to tropical waters of the Atlantic, Indic and Pacific off Japan. It grows up to 2 m but in farming is harvested at half that size.

Algal aquaculture Global production of farmed aquatic plants (Fig. 5.6 and 5.7), overwhelmingly dominated by seaweeds for production of agar and carrageenan as well as human consumption, grew in output volume from 13.5 million tonnes in 1995 to just over 30 million tonnes in 2016. As of 2014, seaweed contributed 27% to all marine aquaculture. Seaweed farming is a carbon-negative crop, with some potential for climate change mitigation.

Figure 5.6: Underwater farming of gusô, *Eucheuma* spp., in the Philippines.

Figure 5.7: Look closely: aerial view of seaweed farms along the south coast of South Korea. Seaweed is often grown on ropes, which are held near the surface with buoys. This technique ensures that the seaweed stays close enough to the surface to get enough light during high tide but doesn't scrape against the bottom during low tide. About 90 percent of all the seaweed that humans consume globally is farmed. In comparison to other types of food production, seaweed farming has a light environmental footprint because it does not require fresh water or fertilizer.

There has been considerable discussion as to how mariculture of seaweeds can be conducted in the open ocean as a means to regenerate decimated fish populations by providing both habitat and the basis of a trophic pyramid for marine life. It has been proposed that natural seaweed ecosystems can be replicated in the open ocean by creating the conditions for their growth through artificial upwelling and through submerged tubing that provide substrate. Following the principles of permaculture, seaweeds and fish from marine permaculture arrays can be sustainably harvested with the potential of also sequestering atmospheric carbon, should seaweeds be sunk below a depth of one kilometer. As of 2020, a number of successful trials have taken place in Hawaii, the Philippines, Puerto Rico and Tasmania.

5.2 Shipping

The environmental impact of shipping includes air pollution, water pollution, acoustic, and oil pollution. The shipping industry's current and past attitude to pollution is captured by their mantra "In the ocean, the solution to pollution is dilution."[10]

Ballast water Cruise ships, large tankers, and bulk cargo carriers use a huge amount of ballast water,[11] which is often taken on in the coastal waters in one region after ships discharge wastewater or unload cargo, and discharged at the next port of call, wherever more cargo is loaded. Ballast water discharge typically contains a variety of biological materials, including plants, animals, viruses, and bacteria.[12] These materials often include non-native, nuisance, invasive, exotic species that can cause extensive ecological and economic damage to aquatic ecosystems along with serious human health problems.

Wildlife collisions Marine mammals, such as whales and manatees, risk being struck by ships, causing injury and death. For example, a collision with a ship travelling at only 15 knots has a 79% chance of being lethal to a whale.

One notable example of the impact of ship collisions is the endangered North Atlantic right whale, of which 400 or fewer remain (Fig. 5.8). The greatest danger to the North Atlantic right whale is injury sustained from ship strikes. Between 1970 and 1999, 35.5% of recorded deaths were attributed to collisions. From 1999 to 2003, incidents of mortality and serious injury attributed to ship strikes averaged one per year. From 2004 to 2006, that number increased to 2.6. Deaths from collisions has become an extinction threat. The United States' National Marine Fisheries Service (NMFS) and National Oceanic and Atmospheric Administration (NOAA) introduced vessel speed restrictions to reduce ship collisions with North Atlantic right whales in 2008, which expired in 2013. However, in 2017 an unprecedented mortality event occurred, resulting in the deaths of 17 North Atlantic right whales caused primarily from ship-strikes and entanglement in fishing gear.

Figure 5.8: Northern Right Whale *Eubalaena glacialis* breaching the surface near dolphins. The veil-like structure is its bow wave. Note that this species has no dorsal fin. Scratches suggest encounters with boats, the most common cause of death for this species.

Sound pollution Noise pollution caused by shipping and other human enterprises has increased in recent history. The noise produced by ships can travel long distances, and marine species who may rely on sound for their orientation, communication, and feeding, can be harmed by this sound pollution.

Oil spills Most commonly associated with ship pollution are oil spills. While less frequent than the pollution that occurs from daily operations, oil spills have devastating effects. While being toxic to marine life, polycyclic aromatic

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[10] As conveyed by *Science* writer Eric Stokstad in his podcast interview to his piece on the topic.

Stokstad, E. (2021). Shipping rule cleans the air but dirties the water. *Science*, 372(6543):672–673

[11] Insufficiently ballasted boats tend to tip or heel excessively in high winds.

[12] Wolff, W. J. (2005). Non-indigenous marine and estuarine species in The Netherlands. *Zoologische Medelingen Leiden*, 79(1):1–116

hydrocarbons (PAHs), components in crude oil, are very difficult to clean up, and last for years in the sediment and marine environment. Marine species constantly exposed to PAHs can exhibit developmental problems, susceptibility to disease, and abnormal reproductive cycles. One of the more widely known spills was the *Exxon Valdez* incident in Alaska. The ship ran aground and dumped a massive amount of oil into the ocean in March 1989. Despite efforts of scientists, managers and volunteers, over 400,000 sea birds, about 1,000 sea otters, and immense numbers of fish were killed.

In addition to oil spills, PAH are also released with so-called "scrubbing" waste. Scrubbing is an post-combustion process to extract sulfur from burning crude diesel in ship engines. Alongside the relatively harmless sulfur, PAHs and heavy metals are dumped and wreak substantial ecological havoc.[13]

5.3 *Pollution*

Marine pollution occurs when harmful effects result from the entry into the ocean of chemicals, particles, industrial, agricultural and residential waste, noise, or the spread of invasive organisms. Eighty percent of marine pollution comes from land. Air pollution is also a contributing factor by carrying off iron, carbonic acid, nitrogen, silicon, sulfur, pesticides or dust particles into the ocean.

The pollution often comes from nonpoint sources such as agricultural runoff, wind-blown debris, and dust. Pollution in large bodies of water can be aggravated by physical phenomena such as the biological effects of Langmuir circulation. Nutrient pollution, a form of water pollution, refers to contamination by excessive inputs of nutrients. It is a primary cause of eutrophication of surface waters, in which excess nutrients, usually nitrates or phosphates, stimulate algae growth. Many potentially toxic chemicals adhere to tiny particles which are then taken up by plankton and benthic animals, most of which are either deposit feeders or filter feeders. In this way, the toxins are concentrated upward within ocean food chains. Many particles combine chemically in a manner highly depletive of oxygen, causing estuaries to become anoxic.

When pesticides are incorporated into the marine ecosystem, they quickly become absorbed into marine food webs. Once in the food webs, these pesticides can cause mutations, as well as diseases, which can be harmful to humans as well as the entire food web. Toxic metals can also be introduced into marine food webs. These can cause a change to tissue matter, biochemistry, behaviour, reproduction, and suppress growth in marine life. Also, many animal feeds have a high fish meal or fish hydrolysate content. In this way, marine toxins can be transferred to land animals, and appear later in

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[13] Stokstad, E. (2021). Shipping rule cleans the air but dirties the water. *Science*, 372(6543):672–673

meat and dairy products.

5.3.1 Sources of pollution

Direct discharge Pollutants enter rivers and the sea directly from urban sewerage and industrial waste discharges, sometimes in the form of hazardous and toxic wastes, or in the form of plastics (see below, section *Types of pollution*).

Inland mining for copper, gold, etc., is another source of marine pollution. Most of the pollution is contaminated soil, which ends up in rivers flowing to the sea (Fig. 5.9). However, some minerals discharged in the course of the mining can cause problems, such as copper, a common industrial pollutant, which can interfere with the life history and development of coral polyps. Mining has a poor environmental track record. For example, according to the United States Environmental Protection Agency, mining has contaminated portions of the headwaters of over 40% of watersheds in the western continental US. Much of this pollution ends up in the sea.

Figure 5.9: Acid mine drainage in the Rio Tinto River, Spain.

Land runoff Surface runoff from farming, as well as urban runoff and runoff from the construction of roads, buildings, ports, channels, and harbours, can carry soil and particles laden with carbon, nitrogen, phosphorus, and minerals. This nutrient-rich water can cause fleshy algae and phytoplankton to thrive into algal blooms, which have the potential to create hypoxic conditions by using all available oxygen. In the coast of southwest Florida, harmful algal blooms have existed for over 100 years. These algal blooms have been a cause of species of fish, turtles, dolphins, and shrimp to die and cause harmful effects on humans who swim in the water.

Deep-sea mining Deep-sea mining is a relatively new mineral retrieval process undergoing research which takes place on the ocean floor. Ocean mining sites are usually around large areas of polymetallic nodules or active and extinct hydrothermal vents at about 3,000 – 6,500 m below the ocean's surface. The vents create sulfide deposits, which contain precious metals such as silver, gold, copper, manganese, cobalt, and zinc. The deposits are mined using either hydraulic pumps or dredging systems that take ore to the surface to be processed. As with all mining operations, deep-sea mining raises questions about potential environmental damages to the surrounding areas.

Because deep-sea mining is a relatively new field, the complete consequences of full-scale mining operations are unknown. However, experts are certain that removal of parts of the sea floor will result in disturbances to the benthic layer, increased toxicity of the water column, and sediment plumes from tailings. Removing parts of the sea floor disturbs the habitat of benthic organisms, possibly, depending on the type of mining and location, causing permanent disturbances. Aside from direct impact of mining the area, leakage, spills, and corrosion could alter the mining area's chemical make-up.

Among the impacts of deep-sea mining, it is theorized that sediment plumes could have the greatest impact. Plumes are caused when the tailings from mining (usually fine particles) are dumped back into the ocean, creating a cloud of particles floating in the water.

5.3.2 *Types of pollution*

Acidification The oceans are normally a natural carbon sink, absorbing carbon dioxide from the atmosphere. Because the levels of atmospheric carbon dioxide are increasing, the oceans are becoming more acidic (see section 1.1). Increasing acidity is thought to have a range of potentially harmful consequences for marine organisms such as depressing metabolic rates and immune responses in some organisms and, in combination with warmer waters, causing coral bleaching. By increasing the presence of free hydrogen ions, the additional carbonic acid that forms in the oceans ultimately results in the conversion of carbonate (CO_3^{2-}) into hydrogen carbonate (HCO_3^-). This net decrease in the amount of carbonate ions available may make it more difficult for marine calcifying organisms, such as coral and some plankton, to form biogenic calcium carbonate, and such structures become vulnerable to dissolution.

Eutrophication Eutrophication is an increase in chemical nutrients, typically compounds containing nitrogen or phosphorus, in an ecosystem. It results in an increase in the ecosystem's primary productivity (excessive plant growth and decay), and further effects including lack of oxygen and severe reductions in water quality, fish, and other animal populations.

The biggest inputs are rivers that empty into the ocean, and with it the many chemicals used as fertilizers in agriculture as well as waste from livestock and humans. An excess of oxygen-depleting chemicals in the water can lead to hypoxia and the creation of a dead zone.

Estuaries tend to be naturally eutrophic because land-derived nutrients are concentrated where runoff enters the marine environment in a confined channel (Fig. 5.10). In the ocean, there are frequent red tide algal blooms that kill fish and marine mammals and cause respiratory problems in humans and some domestic animals when the blooms reach close to shore.

Figure 5.10: Eutrophication and solid waste spoiling the shore of Lake Maracaibo, a brackish lagoon in Venzuela. Images by Wilfredor.

Plastic debris Plastic is different from most other pollutants in that it decays extremely slowly, over hundreds of years. Also, it is lighter than water, thereby affecting light penetration and surface-feeding organisms. When broken down and eroded, plastic is ingested by organisms from copepods to whales, obstructing their digestive systems and potentially causing death.[14]

Marine debris is mainly discarded human rubbish which floats on, or is suspended in the ocean. Eighty percent of marine debris is plastic – a component that has been rapidly accumulating since the end of World War II. The mass of plastic in the oceans may be as high as 100,000,000 tonnes.

With respect to plastics, it has been estimated that the 10 largest emitters of oceanic plastic pollution worldwide are, from the most to the least, China, Indonesia, Philippines, Vietnam, Sri Lanka, Thailand, Egypt, Malaysia, Nigeria and Bangladesh.[15]

Discarded plastic bags, six-pack rings, cigarette butts and other forms of plastic waste which finish up in the ocean present dangers to wildlife and fisheries. Aquatic life can be threatened through entanglement, suffocation, and ingestion (Fig. 5.11). Fishing nets, usually made of plastic, can be left or lost in the ocean by fishermen. Known as ghost nets, these entangle fish, dolphins, sea turtles, sharks, dugongs, crocodiles, seabirds, crabs and other creatures, restricting movement, causing starvation, laceration, infection, and, in those that need to return to the surface to breathe, suffocation.

Many animals that live on or in the sea consume flotsam by mistake, as it often looks similar to their natural prey. Plastic debris, when bulky or tangled, is difficult to pass, and may become permanently lodged in the digestive tracts of these animals. Especially when evolutionary adaptions make it impossible for the likes of turtles to reject plastic bags, which resemble jellyfish when immersed in water, as they have a system in their throat to stop slippery foods from otherwise escaping. Thereby blocking the passage of food and causing death through starvation or infection.

Figure 5.11: The unaltered stomach contents of a dead albatross chick include a variety of plastic marine debris, 2009.

Plastics accumulate because they don't biodegrade in the way many other substances do. They will photodegrade on exposure to the sun, but they do so properly only under dry conditions, and water inhibits this process. In marine environments, photodegraded plastic disintegrates into ever-smaller pieces while remaining polymers, even down to the molecular level. When floating plastic particles photodegrade down to zooplankton sizes, jellyfish attempt to consume them, and in this way the plastic enters the ocean food chain.

Plastic debris tends to accumulate at the centre of ocean gyres. The North Pacific Gyre, for example, has collected the so-called "Great Pacific Garbage Patch" (Fig. 5.12), which is estimated to be one to twenty times the size of Texas (700,000 to 15,000,000 km^2). There could be as much plastic as fish in

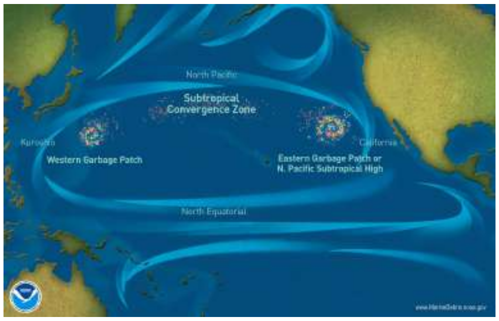

Figure 5.12: Great Pacific garbage patch; Pacific Ocean currents have created three patches of debris.

[14] Research into marine plastic debris is relatively young, and many quantifications of its impact are thus still unreliable.

[15] Jambeck, J. R., Geyer, R., Wilcox, C., Siegler, T. R., Perryman, M., Andrady, A., Narayan, R., and Law, K. L. (2015). Plastic waste inputs from land into the ocean. *Science*, 347(6223):768–771

the sea (but see side note above).

Toxic additives used in the manufacture of plastic materials can leach out into their surroundings when exposed to water. Waterborne hydrophobic pollutants including PCBs, DDT, and PAHs collect and magnify on the surface of plastic debris, thus making plastic far more deadly in the ocean than it would be on land. Hydrophobic contaminants are also known to bioaccumulate in fatty tissues, biomagnifying up the food chain and putting pressure on apex predators. Some plastic additives are known to disrupt the endocrine system when consumed, others can suppress the immune system or decrease reproductive rates.

Toxins Apart from plastics, there are particular problems with other toxins that do not disintegrate rapidly in the marine environment. Examples of persistent toxins are PCBs, DDT, TBT, pesticides, furans, dioxins, phenols, and radioactive waste. Heavy metals are metallic chemical elements that have a relatively high density and are toxic or poisonous at low concentrations. Examples are mercury, lead, nickel, arsenic, and cadmium. Such toxins can accumulate in the tissues of many species of aquatic life in a process called bioaccumulation. They are also known to accumulate in benthic environments, such as estuaries and bay muds: a geological record of human activities of the last century.

5.4 Sea-Floor Resource Exploration and Mining

Like all human activities, also sea-floor mining has multiple impacts: noise pollution during the drill, habitat destruction during the extraction, toxic spills during operation accidents. Acknowledging the inevitable simplification when presenting human impact for exploration and extraction activities at the sea floor, the following examples are meant as illustration of obvious and less obvious impacts.

Gas extraction Extraction of gas causes the reservoir sediment to compact and hence may cause the surface to subside, if only soft sediments overly the gas reservoir. This is the case in the northern Dutch Wadden Sea, where decades of gas extraction have cause a measurable subsidence of the mud flats.[16] The so-called *Groningen Gas Field* is the largest in Europe and extraction of gas from 3000 m depth started immediately upon discovery in 1959. Only in 2014 led the exponential increase in earthquakes to a cut in gas extraction, which led to a complete decommissioning by 2022.

"Manganese" nodules The deep sea contains many different resources available for extraction, including silver, gold, copper, manganese, cobalt, and zinc. These raw materials

[16] Fokker, P. A., van Leijen, F. J., Orlic, B., van der Marel, H., and Hanssen, R. F. (2018). Subsidence in the dutch wadden sea. *Netherlands Journal of Geosciences*, 97(3):129–181

are found in various forms on the sea floor. “Manganese nodules” are a shorthand for all of these lumps of ore found as surface deposits in the deep sea.

There are two predominant forms of mineral extraction being considered for full-scale operations: continuous-line bucket system (CLB) and the hydraulic suction system. The CLB system is the preferred method of nodule collection. It operates much like a conveyor-belt, running from the seafloor to the surface of the ocean where a ship or mining platform extracts the desired minerals, and returns the tailings to the ocean. Hydraulic suction mining lowers a pipe to the seafloor which transfers nodules up to the mining ship. Another pipe from the ship to the seafloor returns the tailings to the area of the mining site. Hydrolic suction avoids the vast deposit plume of the CLB tailing dumped in the ocean, and is much more selective on the sea floor. But it is also much more expensive to operate and inefficient for large deposit regions. There, CLB dredges many square kilometers indiscriminately, destroying all surface habitat.

Research shows that polymetallic nodule fields are hotspots of abundance and diversity for a highly vulnerable abyssal fauna.[17] Because deep-sea mining is a relatively new field, the complete consequences of full-scale mining operations on this ecosystem are unknown. However, some researchers have said they believe that removal of parts of the sea floor will result in disturbances to the benthic layer, increased toxicity of the water column and sediment plumes from tailings. Removing parts of the sea floor disturbs the habitat of benthic organisms, with unknown long-term effects. Preliminary studies on seabed disturbances from mining-related activities have indicated that it takes decades for the seabed to recover from minor disturbances. Minerals targeted by seabed mining activities take millions of years to regenerate, if they do so at all. Aside from the direct impact of mining the area, some researchers and environmental activists have raised concerns about leakage, spills and corrosion that could alter the mining area’s chemical makeup.

Oil extraction Deepwater drilling is the process of creating holes by drilling rig for oil mining in deep sea. There are approximately 3400 deepwater wells in the Gulf of Mexico alone with depths greater than 150 meters. It has not been technologically and economically feasible for many years, but with rising oil prices the deepwater gas and oil market is back on the rise after the 2010 *Deepwater Horizon disaster*.

Offshore oil production involves environmental risks, most notably oil spills from oil tankers or pipelines transporting oil from the platform to onshore facilities, and from leaks and accidents on the platform. Produced water is also generated, which is water brought to the surface along with the oil and gas; it is usually highly saline and may include dissolved or

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[17] Vanreusel, A., Hilario, A., Ribeiro, P. A., Menot, L., and Arbizu, P. M. (2016). Threatened by mining, polymetallic nodules are required to preserve abyssal epifauna. *Scientific Reports*, 6(11):26808

unseparated hydrocarbons.

Aquatic organisms invariably attach themselves to the undersea portions of oil platforms, turning them into artificial reefs (Fig. 5.13). In the Gulf of Mexico and offshore California, the waters around oil platforms are popular destinations for sports and commercial fishermen, because of the greater numbers of fish near the platforms. The United States and Brunei have active Rigs-to-Reefs programs, in which former oil platforms are left in the sea, either in place or towed to new locations, as permanent artificial reefs. In the US Gulf of Mexico, as of September 2012, 420 former oil platforms, about 10 percent of decommissioned platforms, have been converted to permanent reefs.

On the US Pacific coast, marine biologist Milton Love has proposed that oil platforms off California be retained as artificial reefs, instead of being dismantled (at great cost), because he has found them to be havens for many of the species of fish which are otherwise declining in the region, in the course of 11 years of research.

Figure 5.13: The Fujikawa Maru was a 132 metre-long aircraft transport ship. She was hit by a torpedo in 1944 and sank slowly, coming to rest upright at a depth of approx. 34 m. Ship's gun, Chuuk 2009. Foto credit: Stephen Masters, flickr

Bibliography

Allen, A. E., Dupont, C. L., Oborník, M., Horák, A., Nunes-Nesi, A., McCrow, J. P., Zheng, H., Johnson, D. A., Hu, H., Fernie, A. R., and Bowler, C. (2011). Evolution and metabolic significance of the urea cycle in photosynthetic diatoms. *Nature*, 473:203–207.

Behrenfeld, M. J. and Boss, E. S. (2014). Resurrecting the ecological underpinnings of ocean plankton blooms. *Annual Review of Marine Science*, 6(1):167–194.

Bertrand, A., Lengaigne, M., Takahashi, K., Avadí, A., Poulain, F., and Harrod, C. (2020). *El Niño Southern Oscillation (ENSO) Effects on Fisheries and Aquaculture*. FAO, Rome.

Connell, J. H. (1961a). Effects of competition, predation by *Thais lapillus*, and other factors on natural populations of the barnacle *Balanus balanoides*. *Ecological Monographs*, 31(1):61–104.

Connell, J. H. (1961b). The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus*. *Ecology*, 42(4):710–723.

Danovaro, R., Dell'Anno, A., Pusceddu, A., Gambi, C., Heiner, I., and Møbjerg Kristensen, R. (2010). The first metazoa living in permanently anoxic conditions. *BMC Biology*, 8:30.

de Roos, A. M. (2020). Effects of life history and individual development on community dynamics: A review of counterintuitive consequences. *Ecological Research*, 35(6):930–946.

Fokker, P. A., van Leijen, F. J., Orlic, B., van der Marel, H., and Hanssen, R. F. (2018). Subsidence in the dutch wadden sea. *Netherlands Journal of Geosciences*, 97(3):129–181.

Frost, B. W. (1972). Effects of size and concentration of food particles on the feeding behavior of the marine planktonic copepod *Calanus pacificus*. *Limnology and Oceanography*, 17(6):805–815.

Getz, W. M. (2011). Biomass transformation webs provide a unified approach to consumer–resource modelling. *Ecology Letters*, 14(2):113–124.

Goldberg, L., Lagomasino, D., Thomas, N., and Fatoyinbo, T. (2020). Global declines in human-driven mangrove loss. *Global Change Biology*, 26:5844–5855.

Hay, W. W., Migdisov, A., Balukhovsky, A. N., Wold, C. N., Flögel, S., and Söding, E. (2006). Evaporites and the salinity of the ocean during the phanerozoic: Implications for climate, ocean circulation and life. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 240(1):3–46.

Jambeck, J. R., Geyer, R., Wilcox, C., Siegler, T. R., Perryman, M., Andrady, A., Narayan, R., and Law, K. L. (2015). Plastic waste inputs from land into the ocean. *Science*, 347(6223):768–771.

Janssen, R., Wennberg, S. A., and Budd, G. E. (2009). The hatching larva of the priapulid worm *Halicryptus spinulosus*. *Frontiers in Zoology*, 6(1):8.

Jennings, S., Kaiser, M., and Reynolds, J. D. (2009). *Marine Fisheries Ecology*. John Wiley & Sons, New York.

Kaiser, M. J., Attrill, M. J., Jennings, S., and Thomas, D. (2020). *Marine Ecology: Processes, Systems, and Impacts*. Oxford University Press, New York, 3rd edition.

Kuna, V. M. and Nábělek, J. L. (2021). Seismic crustal imaging using fin whale songs. *Science*, 371(6530):731–735.

Lemmen, C. (2018). North Sea ecosystem-scale model-based quantification of net primary productivity changes by the benthic filter feeder *Mytilus edulis*. *Water*, 10:1527.

Levinton, J. (2017). *Marine Biology: Function, Biodiversity, Ecology*. Oxford University Press, Oxford, UK, 5th edition.

Lima, S. L. and Dill, L. M. (2011). Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology*, 68:619–640.

Longhurst, A. (2007). *Ecological Geography of the Sea*. Elsevier, Dordrecht, 2nd edition.

McLachlan, A. and Defoe, O. (2017). *The Ecology of Sandy Shores*. Academic Press, Cambridge, MA, 3rd edition.

Menge, B. A. (1995). Indirect effects in marine rocky intertidal interaction webs: patterns and importance. *Ecological Monographs*, 65:21–74.

Menge, B. A. and Farrell, T. M. (1987). Community structure and interaction webs in shallow marine hard-bottom communities: tests of an environmental stress model. *Advances in Ecological Research*, 19:189–259.

Middelburg, J. J., Soetaert, K., Herman, P. M. J., and Heip, C. H. R. (1996). Denitrification in marine sediments: A model study. *Global Biogeochemical Cycles*, 10(4):661–673.

Morton, O. (2009). *Eating the Sun: How Plants Power the Planet*. Harper Perennial, illustrated edition edition.

Naylor, R. L., Hardy, R. W., Buschmann, A. H., Bush, S. R., Cao, L., Klinger, D. H., Little, D. C., Lubchenco, J., Shumway, S. E., and Troell, M. (2021). A 20-year retrospective review of global aquaculture. *Nature*, 591(78517851):551–563.

Oeschger, R. (1990). Long-term anaerobiosis in sublittoral marine invertebrates from the western baltic sea: *Halicryptus spinulosus* (priapulida), *Astarte borealis* and *Arctica islandica* (bivalvia). *Marine Ecology Progress Series*, 59:133–143.

Open University (1989). *Seawater: Its Composition, Properties and Behaviour*. Pergamon, Oxford, U.K., 2nd edition.

Open University (1997). *Biological Oceanography: An Introduction*. Elsevier.

Open University (1998). *The Ocean Basins: Their Structure and Evolution*. Butterworth-Heinemann, Oxford, 2nd edition.

Open University (2000). *Waves, Tides and Shallow-Water Processes*. Butterworth-Heinemann, Oxford, 2nd edition.

Open University (2001). *Ocean Circulation*. Butterworth-Heinemann, Boston, 2nd edition.

Open University (2005). *Marine Biogeochemical Cycles*. Butterworth-Heinemann, Oxford, 2nd edition.

Open University (2013). *Case Studies in Oceanography and Marine Affairs*. Pergamon, Oxford.

Ostroumov, S. A. (2005). Some aspects of water filtering activity of filter-feeders. *Hydrobiologia*, 542:275–286.

Paine, R. T. (1969). A note on trophic complexity and community stability. *The American Naturalist*, 103:91–93.

Persson, L. and de Roos, A. M. (2013). Symmetry breaking in ecological systems through different energy efficiencies of juveniles and adults. *Ecology*, 94(7):1487–1498.

Richards, D. R., Thompson, B. S., and Wijedasa, L. (2020). Quantifying net loss of global mangrove carbon stocks from 20 years of land cover change. *Nature Communications*, 11:4260.

Ringius, L. (1997). Environmental NGOs and regime change: the case of ocean dumping of radioactive waste. *European Journal of International Relations*, 3(1):61–104.

Ritzau, W. (1996). Microbial activity in the benthic boundary layer: Small-scale distribution and its relationship to the hydrodynamic regime. *Journal of Sea Research*, 36(3–4):171–180.

Rivkin, A. S. and DeMeo, F. E. (2019). How many hydrated NEOs are there? *Journal of Geophysical Research: Planets*, 124(1):128–142.

Schofield, O., Ducklow, H. W., Martinson, D. G., Meredith, M. P., Moline, M. A., and Fraser, W. R. (2010). How do polar marine ecosystems respond to rapid climate change? *Science*, 328(5985):1520–3.

Schröder, A., Persson, L., and de Roos, A. M. (2005). Direct experimental evidence for alternative stable states: a review. *Oikos*, 110:3–19.

Stokstad, E. (2021). Shipping rule cleans the air but dirties the water. *Science*, 372(6543):672–673.

Stow, D. (2017). *Oceans: A Very Short Introduction*. Oxford University Press, 1. edition edition.

Terra, W., Sciacchitano, A., and Scarano, F. (2020). Cyclist Reynolds number effects and drag crisis distribution. *Journal of Wind Engineering and Industrial Aerodynamics*, 200:104143.

Vanreusel, A., Hilario, A., Ribeiro, P. A., Menot, L., and Arbizu, P. M. (2016). Threatened by mining, polymetallic nodules are required to preserve abyssal epifauna. *Scientific Reports*, 6(11):26808.

Walters, C. and Kitchell, J. F. (2011). Cultivation/depensation effects on juvenile survival and recruitment: implications for the theory of fishing. *Canadian Journal of Fisheries and Aquatic Sciences*, 58:39–50.

Wolff, W. J. (2005). Non-indigenous marine and estuarine species in The Netherlands. *Zoologische Medelingen Leiden*, 79(1):1–116.

Worm, B., Hilborn, R., Baum, J. K., Branch, T. A., Collie, J. S., Costello, C., Fogarty, M. J., Fulton, E. A., Hutchings, J. A., Jennings, S., Jensen, O. P., Lotze, H. K., Mace, P. M., McClanahan, T. R., Minto, C., Palumbi, S. R., Parma, A. M., Ricard, D., Rosenberg, A. A., Watson, R., and Zeller, D. (2009). Rebuilding global fisheries. *Science*, 325(5940):578–585.

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