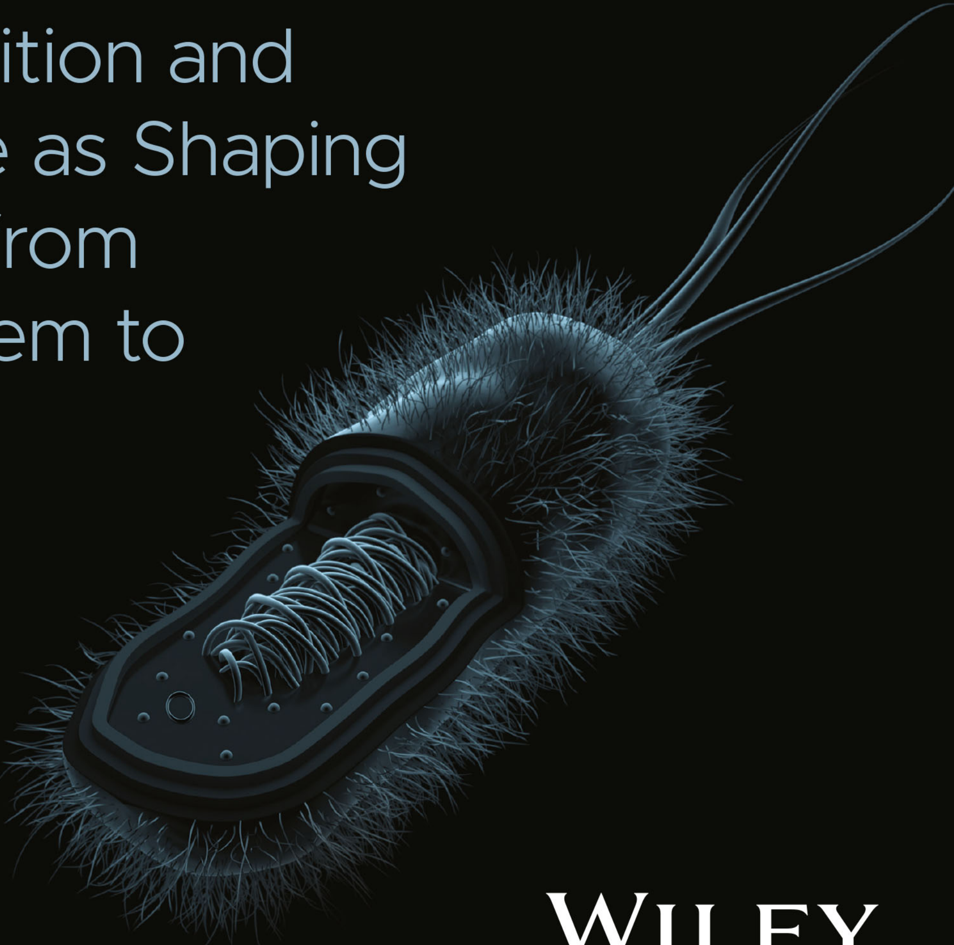
Tron Frede Thingstad

The Marine Microbial Food Web

Competition and Defence as Shaping Forces from Ecosystem to Genes



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Competition and Defence as Shaping Forces from Ecosystem to Genes

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About the Author

Tron Frede Thingstad received a degree in biophysics from the University of Oslo in 1973 with a thesis analysing stability properties in bacterial chemostat cultures. This was a time when computers had recently become strong enough to run ecosystem models. This evoked an optimistic spirit in ecologists, hoping that this could be the tool needed to generate the holistic ecosystem descriptions then advocated in ecology. An opportunity for pursuing such ideas suddenly arose in marine microbial ecology when there was an uncontrolled blow-out from one of the new oil fields in the North Sea, raising the politically urgent question of whether the natural bacterial community in sea water would degrade the pollution. With colleagues at the University of Bergen, Norway, sharing common interests and complementary expertise on microbial ecology, this path led into laboratory work with artificial microbial food webs, field work in Norwegian fjords, the Arctic and, in the context of European research programs, the Mediterranean Sea. In this book, Thingstad summarizes his view of what a modern 'holistic description of the marine microbial food web' could be.

Preface

Natural selection is a process that works at the level of individuals. These individuals have two possibilities to affect their fitness: to increase either their competitive or their defensive skills. As a result, competition and defence have worked together through more than four billion years of evolution as the main forces shaping the genes, organisms and food webs of today's ecosystems. Differences in physical and chemical conditions create differences in the constraints to these individual-level selection processes in different biotopes, reflected in the differences at the ecosystem level.

With this as a unifying perspective to diversity and complexity, this book is an attempt to summarize the present understanding, not only of what the contemporary Marine Microbial Food Web (MMFW) looks like but also how and why it became like this, and what consequences it has, from genome organization to basin scale biogeochemistry.

While this may sound as an abstract journey into the basic foundations of ecosystem organization, it comes with an urgent background of life's reality: the need to understand the properties of a biotope that covers 2/3 of the earth's surface and therefore constitutes a significant part of the complex socio-economic-ecological life support system in which we all live and on which our future depends.

Microbial ecology has the experimental advantage that whole ecosystems can be studied and manipulated at time and size scales feasible in a laboratory. Due to methodological developments, in particular the ability to sequence DNA, our ability to observe the MMFW at the resolution levels of species and strains, genomes and genes, has also changed dramatically over a few decades. With these tools, the MMFW, with its relatively simple organisms living in a relatively homogenous environment, may be one of the few(?) natural systems where a genes-to-ecosystem description may be a realistic goal within a reasonably near future.

Completion and future revisions of the genes-to-ecosystem story outlined here will depend on the co-operation of students from disciplines that differ in their scientific traditions, literature and terminologies; differences that easily hamper inter-disciplinary co-operation. The ambition has therefore been a text that is accessible to students of the MMFW starting with different backgrounds. An inevitable consequence is that parts of the text may appear trivial, while other may appear more difficult, depending on the reader's background education. Maybe this is inevitable when the ambition is a text that can serve to give students with different expertise a shared common platform of knowledge, hopefully facilitating the communication and co-operation needed for developing new ideas on the MMFW.

To keep the focus on ecology, experimental methods are not described in detail, neither are the technical aspects of computer programming. For those interested in pursuing the modelling aspects, Matlab® codes discussed in the text are available (see Appendix).

This book relies heavily on discussions and ideas developed through joint experimental and theory developments in the Research Group for Marine Microbiology at the University of Bergen, Norway. Without the collaborative spirit and the complementary expertise of members of this group and its collaborators, this book could not have been written.

Tron Frede Thingstad
Bergen, Norway, October 2024

About the Companion Website

This book is accompanied by a companion website.

www.wiley.com/go/Thingstad/marine_microbial_foodweb1e

This website contains:

- Codes

1

Setting the Scene

Intention: This chapter provides a basis for the biological and biogeochemical knowledge needed for the rest of this book.

To make the subsequent chapters accessible to readers with different backgrounds, this introductory chapter has three parts: (1) an introduction to the world's oceans and the role of microbes in its biogeochemical processes; (2) a brief introduction to the competitive and defensive traits of main functional groups of marine micro-organisms; (3) a short review of how the combination of new methodologies and new concepts has shaped contemporary ideas about the functioning of the marine microbial food web (MMFW).

Box 1.1 Important concepts of Chapter 1

Important concepts:

- *Marine microbial food web* (MMFW). The part of the marine food web consisting of unicellular organisms and their viruses. Only the pelagic part of the marine food web is discussed here.
- *Photic zone*. The upper layer where light is sufficient for photosynthesis to occur. With a maximum depth of 200 m, and 20 m a more typical value in coastal waters, the photic zone is a thin 'skin' on top of a vast ocean interior (an average depth of 3688 m).
- *Pycnocline*. A layer in the ocean with a steep gradient in water density. This can be either a *thermocline* where the density change is caused by a warm upper layer floating on top of cold deep-water or a *halocline* where low salinity water floats on top of high-salinity deep-water. Pycnoclines work as mixing barriers, reducing water exchange between the two layers.
- *Mixing depth*. There is a mixed layer extending from the surface to the mixing depth. It is not a mixing occurring at the mixing depth.
- *Compensation depth* and *critical depth*. Compensation depth is where phytoplankton's gross photosynthesis and respiration are equal. Critical depth is where gross photosynthesis and respiration, when integrated over the water column above, equals.
- *Limiting nutrient*. In the photic zone, photosynthetic production of biomass is linked to the consumption of elements other than carbon, needed to produce cells. When one of these is depleted, it limits the growth of phytoplankton and is referred to as the limiting nutrient. In some contexts, the element (e.g., N) is more important than its chemical forms (e.g., ammonium, nitrate, or urea), hence, we will use the term 'limiting element'. In the ocean, the growth-limiting element is typically N, but in some regions can also be P or Fe.

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- *Nutricline*. A layer in the ocean where the concentrations of limiting nutrient increases from the photic zone to the aphotic zone.
- *Upwelling*. When nutrient-rich deep-water is transported to the photic zone.
- *Redfield ratio*. The C:N:P molar ratio of 106 : 16 : 1 which is the average stoichiometry of particles in the upper ocean.
- *Photic zone nutrient content*. The total amount of limiting element available in the photic zone for sharing among all biologically active forms. This limits the total biomass that can be formed. In addition to the amount of the element incorporated into the organisms, it includes the summed concentration of the free forms of limiting nutrient (e.g., ammonium + nitrate + urea).
- *Import, regenerated and export production*. Imported production is the part of photic zone primary production based on imported limiting elements (also called *new production*). The other part, regenerated production, is based on limiting nutrients recycled within the photic zone. Export production is the amount exported to the photic zone.
- *Ocean conveyor belt*. A large-scale ocean circulation transporting deep-water from the North Atlantic to the North Pacific and returning to the North Atlantic as surface currents.
- *Ocean carbon sequestration*. The process whereby carbon is from the atmosphere and transported to the ocean's interior.
- *Biological pumps*. The biological mechanisms involved in ocean carbon sequestration.

1.1 The Physical and Chemical Environment of the MMFW

About two-thirds of the earth's surface is covered by ocean. Because of the conditions for life in water, primary producers in this biotope are micro-organisms. As a result, about 50% of the world's primary production occurs in the MMFW (Mattei and Scardi, 2021), not only feeding the world's large fisheries but also leading to an ocean sequestration of about 30% of the CO_2 emissions from our burning of fossil fuels (Gruber et al., 2019).

The solar energy absorbed by the earth is dissipated through two systems: physical and biological. Most of this energy is dissipated through the physical systems consisting of the circulations in the atmospheric and the ocean and the associated hydrological cycle. A small part of the energy (about 1–2% (Thompson et al., 2024)) enters photosynthesis where the organic material synthesized fuels the food webs that drive cycles of biologically active elements and oxidate the organic-C back to CO_2.

The physical dissipation system is a main driver of the biological systems. The key role of the hydrological cycle for terrestrial systems is demonstrated by the earth's large desert regions. In the ocean, where water is not a limiting factor, a main coupling comes from how dominant wind systems affect water circulation and the availability of growth-limiting elements, primarily N, P and Fe in the photic zone. When warm air rises along equator, it is replaced by air from higher latitudes. Deflected by the Coriolis force, this sets up an east-to-west wind along the equator. When this warm air is cooled in the upper atmosphere, it sinks back down at around 30° latitude, now forming a dominant west-to-east wind. In the Atlantic, these winds are known as the trade-winds because European traders used them to sail via West Africa to America along the Equator, returning at more northernly latitudes in the Atlantic. Where these dominant winds blow off the continents, surface water is transported away from the coast and replaced by nutrient-rich deep-water. The resulting combination of light and nutrients generates huge phytoplankton blooms, particularly visible off western Africa and Peru (Figure 1.1).

The El Niño phenomenon is when, in the Pacific, the equatorial east–west current changes the direction. The upwelling along the Peruvian coast then shifts to downwelling, nutrient-poor surface waters, reduced primary production, and a food chain that cannot support the plankton feeding anchovies.

North and south of the equator, there are large chlorophyll-poor regions (Figure 1.1) called the oceanic gyres. These are caused by a permanent thermocline that prevents mixing between the nutrient-poor photic zone and the nutrient-containing deep-water. The result is a permanently low photic zone nutrient content and therefore little biomass. The photic zone nutrient content does not only regulate how much biomass can be formed but is also an important driver for the structure of the MMFW: in the oligotrophic gyres, it is dominated by small (0.5–1.5 μm) picophytoplankton (Figure 1.2), while upwelling areas are typically dominated by large-celled (1–2 orders of magnitude larger, typically diatoms) species. The background for this can be understood from a simple steady-state argument: When the nutrient exchange between the photic and aphotic

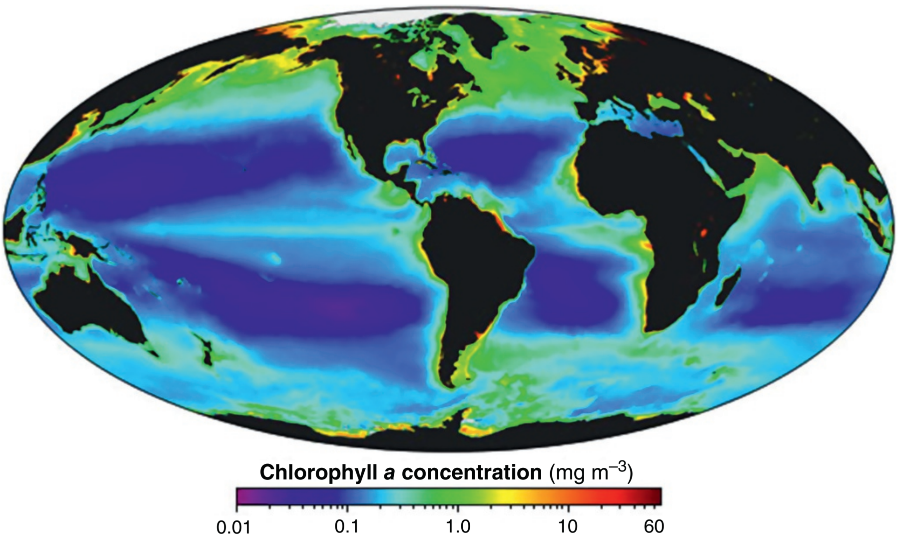

Figure 1.1 Global distribution of chlorophyll. Yearly average. From Global Chlorophyll (nasa.gov). *Source:* Figure from NASA/SeaWiFS Project.

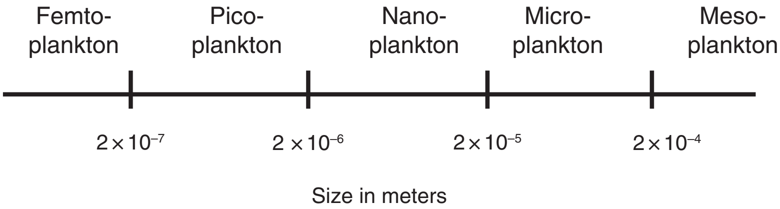

Figure 1.2 Traditional size-class divisions of plankton (logarithmic scale).

zones is in a steady state, import and export from the photic zone must be balanced. When the import is low, as in the gyres, the steady-state structure of the photic zone MMFW must produce little export. Sinking rates increase rapidly with size (as r^2 for a spherical particle). A food web dominated by free-living picoplankton will therefore produce much less export than one dominated by large diatoms ballasted with a heavy silicate frustule.

The vertical export of organic matter is an important biogeochemical function of the photic zone food web. It transports carbon, fixed by photosynthesis in the photic zone, to the ocean's interior (Figure 1.3). Most of this is oxidized to CO_2 in deep-waters, but the carbon will not be exposed to exchange with the atmosphere until the deep-water is returned to the surface by ocean circulation. The average age of dissolved organic carbon (DOC) as determined from the content of the radioactive ^{14}C isotope is 4000–6000 years (Druffel et al., 2016). This has traditionally been taken as evidence for recalcitrance of the material accumulating. An alternative hypothesis is that it is not the chemical nature, but the low concentration of individual components that limits the degradation rate (Arrieta et al., 2015). The two mechanisms are not mutually exclusive and may both contribute to the high observed age.

Central in this process is the ocean's conveyor belt. This is the large-scale ocean circulation whereby oxygen-rich deep-water formed in the cold North Atlantic is transported south through the deep Atlantic, into the Indian and Pacific Oceans, to surface again in the North Pacific. It then

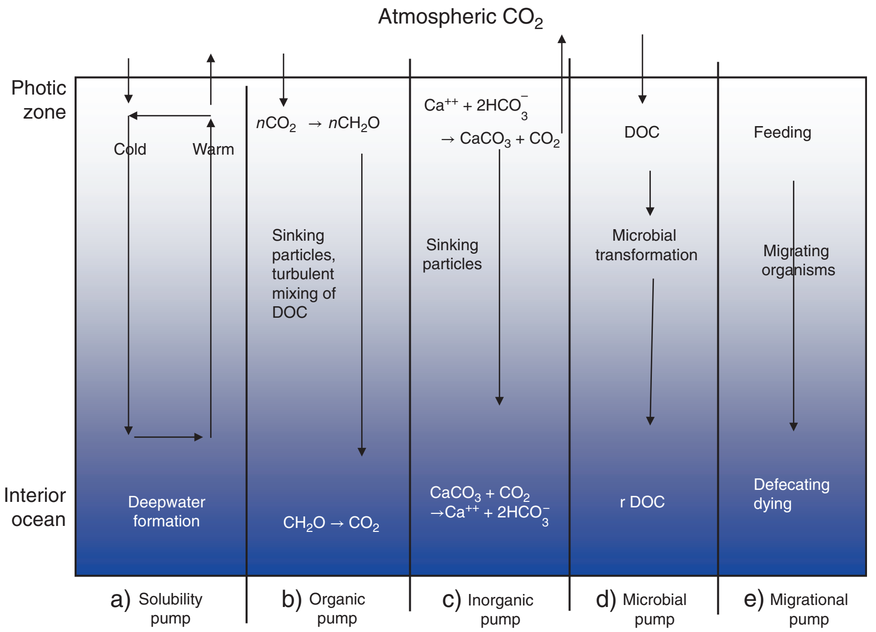

Figure 1.3 'Pumps' transporting C vertically in the ocean. (a) Solubility pump: since solubility of CO_2 is higher in cold than in warm water, deep-water formed in cold waters contains CO_2 that is released when upwelling in warm areas. (b) Organic biological pumps: organic material formed by photosynthesis in the photic zone is transported by sinking particles and vertical mixing of dissolved organic carbon (DOC). (c) When 1 mol of $CaCO_3$ is formed in the photic zone, 1 mol of CO_2 is released to the atmosphere. If the $CaCO_3$ sinks as, for example, coccoliths in faecal pellets, the reaction of $CaCO_3$ with CO_2 at depth will form bicarbonate (HCO_3^-) and Ca^{2+}, thereby also moving alkalinity from the surface to deep-waters. (d) Microbial transformation of DOC to recalcitrant forms (rDOC) will increase the turnover time of DOC in the ocean. This is referred to as the 'Microbial pump' in the literature. (e) Migrational pump. Vertically migrating organisms like copepods and mesopelagic fish that feed in the photic zone and defecate and die at depth, transport carbon from the upper layer to the ocean's interior.

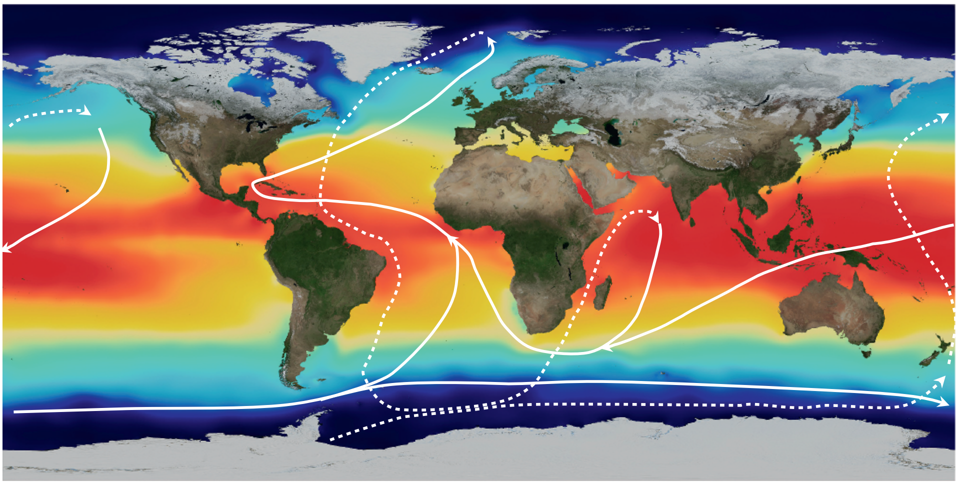

Figure 1.4 The oceanic conveyor belt. Cold, oxygen-rich water sinking in the North Atlantic floats southward in the deep Atlantic, into the Indian and Pacific oceans where the water returns as warm surface currents to the North Atlantic. The average circulation time is in the order of 1000 years. Surface currents in solid lines, and bottom currents in broken lines. The background map is surface salinity from NASA. *Source:* NASA / Public Domain.

returns to the North Atlantic as surface currents (Figure 1.4). As sinking material is degraded in the deep parts of the conveyor belt, oxygen is consumed, and the water is enriched in C, N, and P. This leads to an increasing gradient of CO_2, nitrate and phosphate (Figure 1.5) in the deep-water from the North Atlantic to the North Pacific, and high concentrations where this water up-wells in the North Pacific. The interaction between the MMFW and ocean circulation thus shapes the chemistry of the ocean.

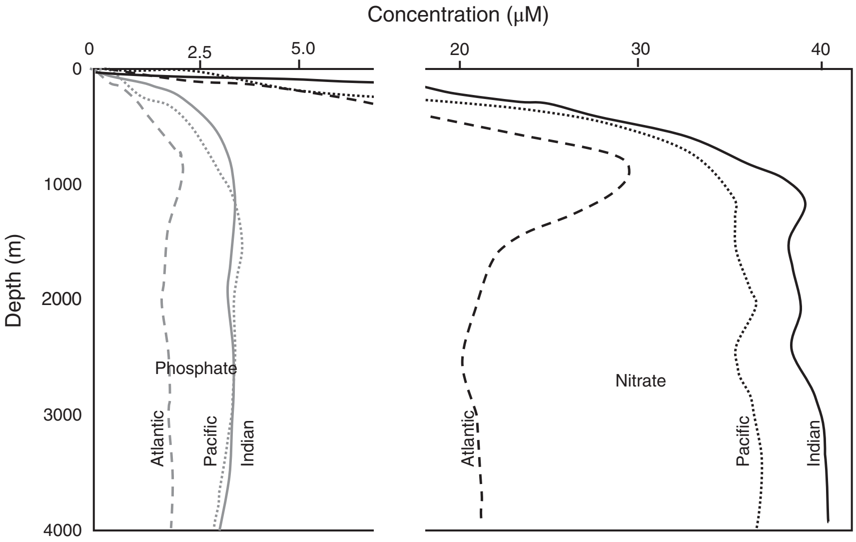

Figure 1.5 Vertical profiles of phosphate and nitrate in the Atlantic, Pacific and Indian oceans. The nitrate-N to phosphate-P ratio is close to 16 in all three oceans. *Source:* Adapted from Sverdrup and Johnson (1942) / Pearson.

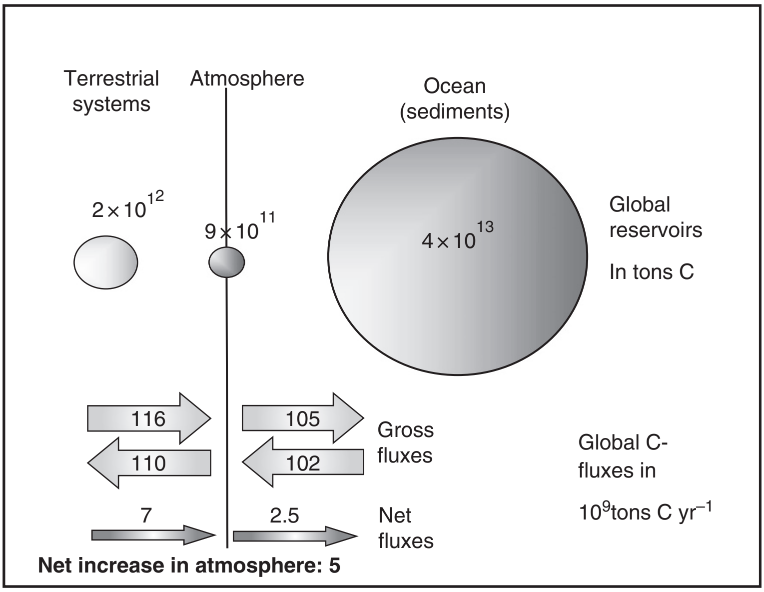

Figure 1.6 The main active pools and fluxes of the global carbon budget (geological reservoirs not included).

The circulation time of the conveyor belt is in the order of 1000 years (Primeau, 2005). The C transported into the deep-water is therefore sequestered (isolated from exchange with the atmosphere) for a sufficiently long time to influence climate change. About 50% of our present fossil fuel emissions are sequestered, with an estimated equal distribution between terrestrial and marine ecosystems (NOAA, 2015). The oceans' biological, chemical and circulation processes thus presently sequester about a quarter of the emissions. This net influx is the small difference between large exchange rates between the ocean and the atmosphere. While the greenhouse effect depends on the concentration of greenhouse gases in the atmosphere, the dominant dynamic reservoir of C is the pool of inorganic C in the ocean (Figure 1.6). Only a small shift in the balance between the ocean and the atmosphere reservoirs can therefore have large climate effects.

The geological importance of the coupling between ocean circulation and the MMFW (see Box 1.1) can be illustrated by the anoxic events in the earth's geological history. These are events where ocean circulation slowed down so much that large parts of the ocean's interior became anoxic. Under anoxic conditions, the degradation of organic matter is retarded and the burial of organic matter in the ocean's sediments increases. This buried organic matter is the source of the oil that we are burning today.

Micro-organisms need other elements than carbon (Figure 1.7). Particularly important in our discussion of the MMFW are nitrogen, phosphorous, and iron, the main elements known to potentially limit biological production in the photic zone. Also, because silicon is required by diatoms to form their frustules, it can limit the standing stock of this important group of phytoplankton.

The average C:N:P stoichiometry of particulate matter in the upper ocean is 106 : 16 : 1, referred to as the Redfield ratio (Redfield et al., 1963). This is also often used as an average ratio for phytoplankton consumption of the elements during growth. There are, however, large variations, both depending on growth conditions and between plankton groups (Geider and La Roche, 2002). Important examples include heterotrophic bacteria (Vrede et al., 2002) and diatoms (Arrigo, 2005) with N:P ratios around 8–10, about half the Redfield value. The capability of diatoms (Thingstad et al., 2008) and *Phaeocystis* spp. (Thingstad and Billen, 1994) to photosynthesize

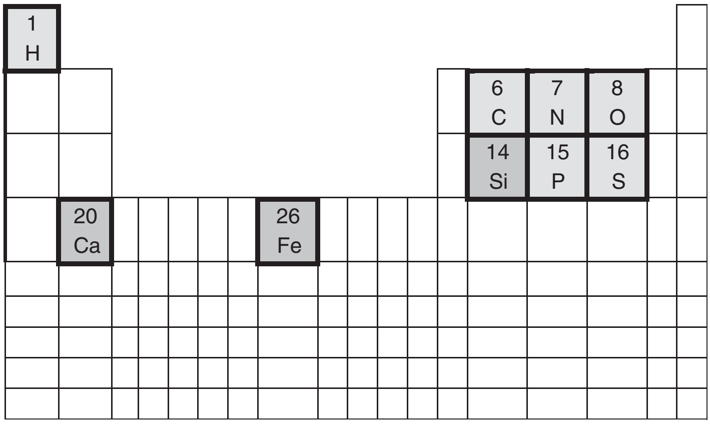

Figure 1.7 Elements with particularly important roles in marine pelagic microbes and their place in the periodic system. Marine microbes are primarily built from the reactive non-metals shown (light-shaded). Silicone is important for building diatom frustules and Ca for $CaCO_3$ structures such as the coccoliths of coccolithophores. N, P and Fe can limit primary production in the photic zone. The solubility of oxygen as O_2 in water is low. When oxygen-depleted, marine environments become dominated by microbes using oxidized forms of N and S (e.g., nitrate and sulphate) as terminal electron acceptors.

organic-C at ratios far above the Redfield ratio is also important. Related to this is the hypothesis that fast-growing organisms such as bacteria and diatoms need a high content of P-containing nucleic acids (Isanta-Navarro et al., 2022). The relative consumption and biomass content of potentially limiting nutrients thus depend to some extent on the structure of the MMFW.

The Redfield ratio is important for the C-cycle. If you have 16 atoms of bioavailable N limiting production in the photic zone, you can bind c. 106 atoms of C. If you want to sequester more C, you have to add or import 'new' N without adding or reimporting the exported C in a ratio of 106 : 16 or higher. For an efficient transport of C to the deep ocean, N and P must be released to non-sinking forms at shallower depths, allowing a faster reimport to the photic zone for the limiting nutrients than for C.

High-latitude regions have a pronounced yearly variation in the daily light cycle. In the extreme polar regions with 24 hours of darkness in winter and 24 hours of light in summer. This leads to a spring bloom when the light level in the upper layer, enriched in nutrients through winter mixing, reaches a level that allows primary production to exceed losses. The onset of this spring bloom depends not only on the increase in sunlight but also on the vertical stability of the water column. In an unstable water column, phytoplankton will be mixed into the deep and dark layers, delaying the spring bloom relative to sites where a shallow pycnocline restricts mixing and phytoplankton are kept within the photic zone. The traditional theory for this (Sverdrup, 1953) uses the concept of critical depth which is the depth above which depth-integrated daily gross photosynthesis equals the depth-integrated respiration. Without other losses such as sinking or grazing, a mixing depth shallower than the critical depth will allow positive net growth and a spring bloom is possible. As illustrated in Figure 1.8, a spring bloom can start once the mixing depth becomes shallower than the critical depth. In places with a shallow halocline such as Norwegian fjords (freshwater input) and along the polar ice edge (low-saline meltwater), the spring bloom therefore occurs early, as opposed to for example, the open North Atlantic, where a thermocline must be formed before the spring bloom can start. The only loss factor considered in Sverdrup's original theory is respiration. A more comprehensive analysis taking other losses such as grazing into account has been