

Making sense of ocean biota: How evolution and biodiversity of land organisms differ from that of the plankton

VICTOR SMETACEK

*Alfred Wegener Institute for Polar and Marine Research, Bremerhaven 27570, Germany
and*

CSIR National Institute of Oceanography, Dona Paula, Goa, India

(Email, Victor.Smetacek@awi.de)

The oceans cover 70% of the planet's surface, and their planktonic inhabitants generate about half the global primary production, thereby playing a key role in modulating planetary climate via the carbon cycle. The ocean biota have been under scientific scrutiny for well over a century, and yet our understanding of the processes driving natural selection in the pelagic environment – the open water inhabited by drifting plankton and free-swimming nekton – is still quite vague. Because of the fundamental differences in the physical environment, pelagic ecosystems function differently from the familiar terrestrial ecosystems of which we are a part. Natural selection creates biodiversity but understanding how this quality control of random mutations operates in the oceans – which traits are selected for under what circumstances and by which environmental factors, whether bottom-up or top-down – is currently a major challenge. Rapid advances in genomics are providing information, particularly in the prokaryotic realm, pertaining not only to the biodiversity inventory but also functional groups. This essay is dedicated to the poorly understood tribes of planktonic protists (unicellular eukaryotes) that feed the ocean's animals and continue to run the elemental cycles of our planet. It is an attempt at developing a conceptually coherent framework to understand the course of evolution by natural selection in the plankton and contrast it with the better-known terrestrial realm. I argue that organism interactions, in particular co-evolution between predators and prey (the arms race), play a central role in driving evolution in the pelagic realm. Understanding the evolutionary forces shaping ocean biota is a prerequisite for harnessing plankton for human purposes and also for protecting the oceanic ecosystems currently under severe stress from anthropogenic pressures.

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1. Introduction

The oceans are the cradle of life on this planet and have shaped and maintained the environmental conditions that made evolution of complex life forms possible. Thus, oxygenation of the atmosphere commenced with the invention of oxygenic photosynthesis by prokaryotic cyanobacteria (blue-green algae) that grew suspended in the sunlit surface layer and used water as the hydrogen source to convert CO₂ into organic matter. The waste product – molecular oxygen – was left behind to accumulate in the surface ocean and subsequently in the atmosphere. Oxidation of organic matter

to CO₂ and H₂O released the enormous energy required to split water. This additional energy was necessary to drive evolution of complex life forms (Falkowski *et al.* 2004). It took several billion years for oxygen levels to accumulate to the present levels, but while this was happening, new kinds of organisms – the eukaryotes – were created by different prokaryote lineages merging into single entities: the process known as evolutionary or serial endosymbiosis (Margulis 1981). Two of these lineages evolved multicellular organisms – higher plants and animals including fungi – that were able to colonize the land less than 500 million years ago, but the vast majority remained unicellular and stayed in the

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water. Various new lineages of planktonic protists (unicellular eukaryotes) with unique properties made their first appearance long after the land had been colonized (e.g. dinoflagellates, diatoms, coccolithophorids): but unlike the situation on land where new lineages tended to displace older ones, exemplified by the progression from algal carpets to mosses, ferns, gymnosperms and flowering plants, the new protistan lineages tend to coexist with older ones resulting in a high phylogenetic diversity in the plankton. Obviously, the forces driving evolution of protistan plankton will be different from those shaping evolution in the terrestrial realm.

Planktonic and terrestrial ecosystems also differ radically in their quantitative relationships. Although the oceans generate about half the annual net primary production on the planet – a total of around 100 gigatonnes carbon (Gt=10⁹ tonnes) – they harbour only a tiny fraction of total biomass: ~ 3 Gt C in the oceans versus ~600 Gt C on land (Falkowski *et al.* 1998). However, the comparison is deceptive because by far the bulk of the land ‘biomass’ is contributed by the cellulose and lignin infrastructure (wood) of plants, which is essentially dead tissue. Were one to compare only the mass of plasma in living cells, i.e. use nitrogen or phosphorus as the biomass currency, the difference between the two biomes would be much smaller. Nevertheless, on land, there would still be much more (living) biomass in plant tissue than in that of heterotrophs – microbes, fungi and animals, from worms to mammals – than is the case in the oceans; here, phytoplankton biomass is on average several-fold less than that of their dependents: the bacteria, heterotrophic protists (protozooplankton) and animals inhabiting the water column (from metazooplankton to whales) and the sea floor (from protists to worms and fish).

If one compares only the biomass of the chloroplasts – the organic carbon factories of both ecosystems – the difference between land and oceans shrinks much further, with overlap in the impoverished parts of both systems. Nevertheless, chloroplast biomass in a forest at the peak of the growth season would still be many times that of the densest phytoplankton bloom. However, if we consider only those chloroplasts that are working close to maximum capacity – those in the outermost leaves of the canopy – the ‘active photosynthetic biomass’ in blooms and forests will be fairly similar. This explains why such little biomass in the ocean can generate almost as much organic carbon as on land. One also has to remember that, although the oceans cover 70% of the planet, most of the area is occupied by the clear blue waters of the subtropical gyres – the ocean’s deserts.

The chloroplasts of land plants – once free-living cyanobacteria – divert most of their products into infrastructure, the production of which – on a global scale – is limited by the supply of water delivered by rainfall. Massive depletion of vegetation by herbivores – ranging from insects to elephants – in natural ecosystems is at best event-scale and clearly the exception. Hairston *et al.* (1960) reasoned

convincingly that the land is green because herbivore populations are limited by their predators and not their food. This theory is strongly supported by observation of natural ecosystems compared with those impacted by human intervention, e.g. overgrazing of vegetation by artificially high levels of livestock. Its implication is that the predators will be exercising natural selection on the herbivores, because the herbivores that survived are the ones that successfully evaded predators. These will be the best protected individuals, whether by camouflage, speed or defences, and not the ones with the highest conversion efficiency of plant into animal biomass, i.e. the ones that managed to occupy the most resource space. The latter condition applies to land plants, implying that species selection here is by competition within the trophic level, i.e. amongst the plants, for resource space (Hairston *et al.* 1960).

The situation in the plankton must be very different to account for the much lower autotroph/heterotroph biomass ratio mentioned above. Over most of the ocean and most of the year, photosynthesis of autotrophs is limited by the availability of an essential element: generally nitrogen or phosphorus, as well as iron, in the open ocean. Under these conditions, by far the bulk of phytoplankton growth is directly fuelled by nutrients remineralized by respiration and excretion of the heterotrophs (bacteria, proto- and metazooplankton), implying much heavier grazing pressure on the phytoplankton as compared to land plants. Thus, the products of planktonic photosynthesis are channelled into biomass of the heterotrophs of the ecosystem, which, in a sense, can be considered the equivalent of the terrestrial plant infrastructure providing nutrients to the chloroplasts. As such, planktonic ecosystems are ideally self-contained and only require a continuous supply of light energy to carry on. On land, biological interactions do not suffice to maintain structure of the ecosystem, because a continuous supply of water (the one-way transport system of plants), not provided by the heterotrophs but by rain, is required in addition to the nutrients recycled by heterotrophs (Smetacek and Pollehne 1986).

Only during phytoplankton blooms, which arise when resources (both light and nutrients) are not limiting, can phytoplankton accumulate sufficient biomass to perhaps exceed that of the heterotrophs (Assmy and Smetacek 2009). However, blooms are short-lived (a few weeks) because they are terminated by nutrient exhaustion after which phytoplankton growth largely depends on nutrients regenerated by the heterotrophs – the planktonic ‘infrastructure’. Thus, phytoplankton cells have a much shorter life span (days to weeks) than the photosynthesizing plant cells on land (several months), i.e. pelagic ecosystems have a higher turnover rate than their terrestrial counterparts (Smetacek and Pollehne 1986; Steele 1991). It follows that the course of evolution by natural selection of phytoplankton species will be influenced to a much greater extent by herbivores than is

the case in land plants. This must lead to selection of avoidance traits in the phytoplankton, including grazer deterrents (attack and defence mechanisms), just as is the case amongst land herbivores. However, this ‘top-down’ facet of marine plankton ecology has attracted much less research effort than the study of traits affecting growth rates of phytoplankton, such as nutrient uptake or acclimation to the light field, i.e. ‘bottom-up’ factors (Verity and Smetacek 1996).

The efficiency of recycling of limiting elements determines the rate at which the new nutrients, initially introduced by upward transport of deep, nutrient-rich water to the surface layer and taken up by the ensuing bloom, are lost from it by sinking out of organic particles. Eventually, in the course of weeks or months, the bulk of the new nutrients settles out in particles, but their composition and the depth they reach before being broken down (e.g. their size and C:N:P:Fe ratios) will be determined by the biology of the surface layer. This rain of organic particles, known as the biological carbon pump, depletes the surface layer of nutrients and impoverishes planktonic ecosystems. Furthermore, it not only fuels all life below the surface layer but also sequesters carbon in the deep water column and sediments (Falkowski *et al.* 1998). Interestingly, the amount of excess CO₂ (relative to equilibrium with today’s atmosphere) delivered to the deep ocean by this pump over the turnover time of the deep ocean (ca. 1,000 years) is about the same as that sequestered in the land vegetation, around 500 Gt, which, again, is about the average amount of CO₂ in the atmosphere over glacial–interglacial cycles. A further 200 Gt are estimated to be sequestered in the ocean sediments in the same period (0.2 Gt year⁻¹), albeit for geological time scales. Clearly, in terms of bulk turnover, ocean biota are key players in the global carbon cycle and hence must continue to play a role in regulating planetary climate via their potential impact on atmospheric CO₂ levels.

Unfortunately, our understanding of the driving forces underlying structure and functioning of planktonic ecosystems and their respective impacts on the carbon cycle (the relationship between ecology and biogeochemistry) has been progressing in a fragmentary manner ever since the underlying concept of ‘metabolism of the sea’ was postulated by Hensen (1887). This is reflected in the fundamental nature of the questions that continue to be debated for over a century; examples are the relationship between form and function in protists, or the factors driving seasonal species succession in plankton ecosystems. I maintain that this lack of directed progress is mainly due to the virtual absence of an evolutionary framework that links together the principle factors driving the evolution of protists into a coherent Big Picture. Such a framework will need to be tailored to the conditions specific to planktonic ecosystems, i.e. based on the mechanisms of natural selection, and equivalent, in its explanatory power, to the one under development for terrestrial ecosystems. It will have to be distinctly different because the oceans

are not green but blue – the colour of marine deserts – implying that phytoplankton, unlike land plants, are by and large under mortality control exerted by their predators, parasitoids and pathogens (the 3 Ps). It follows that more research effort needs to be focussed on the mortality environment *sensu* Smetacek *et al.* (2004) than on the much-studied growth environment.

Taking the words of Dobzhansky (1973) ‘Nothing in biology makes sense except in the light of evolution’ to heart, I examine in this essay the likely driving forces of planktonic evolution against the background of the fundamental differences between planktonic and terrestrial ecosystems presented above. The arguments are based on what is known but under-appreciated about the biology of plankton, but also on what is not known, i.e. the gaps in the Big Picture that require dedicated study. The intention is to generate debate on development of a conceptual framework of plankton evolution based on the concept that protection against grazers, as well as pathogens and parasitoids, i.e. competition for survival rather than for resource space, rules evolution of phytoplankton (Smetacek 2001). I present examples from various perspectives to show how the relationship between form and function in the protistan realm can possibly be explained by natural selection of prey by their predators – the evolutionary arms race (Dawkins and Krebs 1979) – than by competitive exclusion amongst the phytoplankton (Hamm and Smetacek 2007).

2. Life in the plankton

The open water inhabited by drifting plankton (bacteria, protists and various small animals up to jellyfish size that feed on them and each other) and free-swimming nekton (all large animals from fish to squid and whales) is known as the pelagial. For reasons mentioned above, but primarily because of the fundamental differences in the physical environment, pelagic ecosystems function very differently from the familiar terrestrial ecosystems of which we are a part. The underlying sea floor (the benthal) is inhabited by the benthos, which includes all organisms that spend most of their lives on, or in close proximity to, the bottom. This is again a different type of environment but shares one major characteristic with terrestrial systems that does not apply to the pelagial. On the surface of land and the sea floor, organisms compete with each other for space, with fitness expressed in the ability to hold space and to expand the range of their species by overgrowing the previous inhabitants, i.e. evolution favours competitive exclusion. In contrast, the waters of the surface ocean together with the organisms suspended in them (the plankton) are being renewed at scales of months to years, so space-holding in the same water parcel is selected for only in surface waters with a long history: the vast sub-tropical gyres, which are

also the ocean's deserts. Maintenance of a population in the same geographic region depends on how organism life cycles are geared to vertical circulation patterns of that region. This does not apply to the motile organisms of the nekton, which, by definition, can swim against the currents and are able to choose their habitat, i.e. space-holding in this group can be selected for.

We humans live in a world in which shape is dictated by the gravitational field, but in the water, overcoming gravity does not cost much energy or infrastructure. Thus, we intuitively understand why trees have to be strong, require roots to anchor them and a trunk to support the crown of leaves, because we sense, with our own bodies, the same forces they have to withstand. Indeed, our body is the template, via proprioceptive and vestibular sensory systems, with which we make sense to ourselves (Smetacek and Mechsner 2004). We can watch, visualize and embody the relationship between organism form and function in animals that occupy our space and time scales; thus, we can observe and understand locomotion in land animals and why large aquatic animals, whether sharks, fish or whales, have streamlined shapes. Using the scientific method, we can also relate form and function to other large animals like squid and jellyfish that differ from familiar fish in modes of propulsion and lifestyle. In short, organisms living at our scales make sense to us as also the space-holding ecosystems of which we are a part.

However, life at the scales of unicellular organisms, where viscosity of the medium becomes as important as gravity, is difficult for us to comprehend. Imagining oneself in a swimming pool filled with honey has been suggested as an analogue but this is deceptive because our bodies are made for moving in air and not in honey. Thus, one cannot imagine oneself zipping around at 700 km/h in honey, merrily bumping into objects without suffering any damage. But this is what many motile pelagic bacteria are doing, if we convert their speed measured in body lengths per second to our spatial scales. Yet, the energy required to rotate the flagellum which propels them is so little and their mass is so small that collisions leave them unfazed, i.e. the energy released by the collision is not enough to harm their cells (Purcell 1977). Even more difficult to imagine, let alone understand intuitively, is how molecular diffusion affects the environment of unicellular organisms (Smetacek 2002). Thus, it makes little difference to uptake efficiency of a cell whether the entire surface or only a small part of it is capable of capturing the nutrients provided by molecular mixing. This explains why organisms covered with impermeable armour with comparatively few pores, such as diatoms, are not handicapped relative to 'naked' ones. Since unicellular plankton does not make sense to us, we have to construct mental models of how they function under natural conditions. This is a prerequisite to understanding ecology and natural selection in the pelagial.

3. The lightness of life

A measure of how little we really understand about the life of unicellular plankton is our ignorance of how the cells manage to stay afloat. A prerequisite for oxygen to accumulate in the sunlit surface layer was its separation from organic matter, which had to be sequestered elsewhere. In other words, the production of organic matter had to be higher than its remineralization in the surface layer. This was ensured by the gravitational field as the organic matter that forms the substance of life – proteins, carbohydrates, lipids and DNA – is intrinsically denser than the water it displaces. Only lipids (hydrocarbons) are lighter, but large amounts (about two-thirds of total carbon) would be required to maintain the other building blocks in suspension. Thus, organic particles inherently sink and, if not remineralized in the water column, settle out on the sea floor, where reduced carbon can be sequestered for geological time scales from the oxygen released to produce it. Clearly, a huge amount of organic matter must have been buried in the sediments and subsequently transported into the earth's interior by tectonic subduction of the sea floor to compensate for the oxygen in the atmosphere and that bound as oxides in the crust. Indeed, the planet would be very different if organic matter did not happen to be denser than the water it displaces.

But what is not known is how cells without any obvious means of locomotion, such as cyanobacteria and many eukaryote lineages, remain suspended in the surface layer as long as they are alive but sink when they die. No doubt, some species of cyanobacteria secrete gas vacuoles within their cells which enable them to form scum on the surface, but many lack these or any other known flotation devices. Indeed, the enigma deepens when one considers that the mineral shells and skeletons of non-motile groups such as diatoms, radiolaria or foraminifera sink rapidly when empty but are maintained in suspension as long as the organisms are alive. In other words, their cells can afford to carry heavy armour. Where does the positive buoyancy of the living cell come from? None of the mechanisms cited in the textbooks (such as lipids, protrusions to increase drag, even turbulence, etc.) hold water because they do not explain why live cells stay in suspension but dead cells sink out of the surface layer. Shape does not seem to play a role in maintaining buoyancy, given the wide variety present in the plankton that ranges from spherical to needle-like, from smooth to flamboyant and even grotesque, at least to our eyes. Similarly, exchange of heavy ions (Na^+ , K^+ , SO_4^{2-}) against lighter ones (NH_4^+ , Cl^-) only works in a large vacuole (equivalent to a hot-air balloon), which is lacking in most species. Besides, freshwater plankton also manage to stay afloat. Is there something in the environment occupied by organisms between 0.002 and 2 mm that enables them to regulate their

buoyancy easily and that, like radioactivity, is outside our sensory abilities? Most biologists simply overlook the problem; so, it is time that physicists and chemists took up the challenge and tackled this fundamental property of life that has changed the face of our planet so radically.

Given that the mechanism enabling buoyancy regulation has been around from the gray beginnings of life, it would be parsimonious to assume that it is shared by all planktonic organisms and is located at the molecular level. A possible mechanism that comes to mind is modification of the tertiary structure of proteins (about 50% of cellular carbon), but also that of interstitial water (80% of plasma volume) in order to increase the volume occupied by the living cell. The resultant decrease in density of the cell relative to the water displaced could allow buoyancy control. Ice is an analogy that I am suggesting here: water molecules bound in ice crystals occupy more space than in their liquid state, and hence ice floats because it is lighter than water. Protein chemistry could also allow such an ‘inflated’ structure that would, however, cost energy to maintain and would revert to a denser, thermodynamically stable state on cell death. A rough estimate of the increase in cell volume required (the density of organic matter is ~ 1.1) ranges between 10% and 30% depending on the amount of ballast (from carbohydrates to mineral skeletons) carried by the cell and should not be too difficult to measure.

4. Historical background

The scientific study of protistan plankton commenced in the 1840s and within a few decades most of the common, large species ($>50 \mu\text{m}$), particularly those with mineral skeletons, had been described. The early workers confined their attention to morphology and taxonomy with little regard to trophic relationships because it was believed at the time that the food of the oceans was provided as a thin soup by the coasts and by rivers. One of the most influential biologists of that era – Ernst Haeckel – started his career by describing 2000 species of radiolaria collected during the Challenger expedition. The elaborate siliceous skeletons made by this enigmatic group are eye-catching, and Haeckel went to great pains to draw even the smallest details, barely visible under the microscope at his disposal. Clearly, he and his fellow taxonomists recorded the details in order to separate species but could not think of a function for them. Since he lacked an explanation, Haeckel decided that the intricate shapes had no real meaning and that they were produced by properties inherent to organic matter for which he coined the term ‘organic crystallography’. Haeckel was a man of strong beliefs. He was a talented draughtsman and prolific writer equipped with a forceful style; he was also the champion of Darwinian evolution in Germany and left a lasting impression on his field. One can speculate that his world view,

permeated with intricate patterns produced by organic matter quasi-independent of outside shaping forces, was formed by his early exposure to organisms whose lifestyles he was unable to imagine. How could he think up functions for intricate, symmetrical structures arising in creatures inhabiting a vast and featureless environment? They simply did not make sense to him (Smetacek *et al.* 2002).

Haeckel published his attractive drawings of protists in a coffee-table book titled *Art Forms of Nature* (Haeckel 1904), which was very popular at the time and also influenced artists and architects (figures 1 and 2). He went to pains to emphasize the symmetry, whether bilateral or radial, of the organisms he drew, apparently swayed by his view of universal shapes in nature – the ‘art forms’. Perhaps he was influenced by ice crystals that can have many different patterns but are always symmetrical. It has been shown that

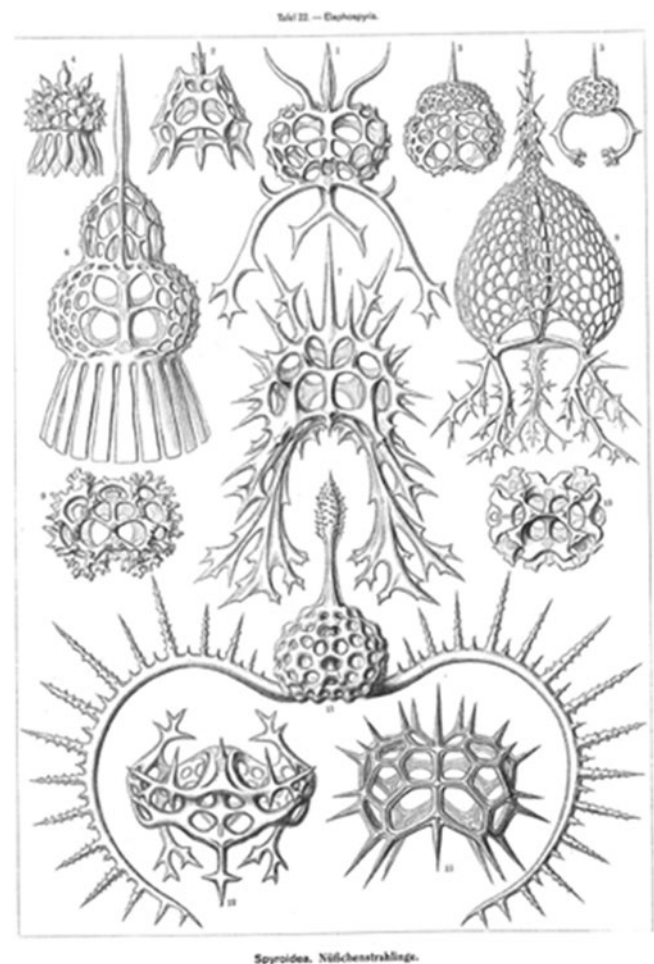


Figure 1. Silica endoskeletons of various species of radiolaria first described by Ernst Haeckel in the 1850s. The drawing was arranged for his highly influential coffee table book *Art Forms of Nature*, first published in 1904. The width of the figure is equivalent to about 0.1 mm.

Ernst Haeckel: Dinoflagellates

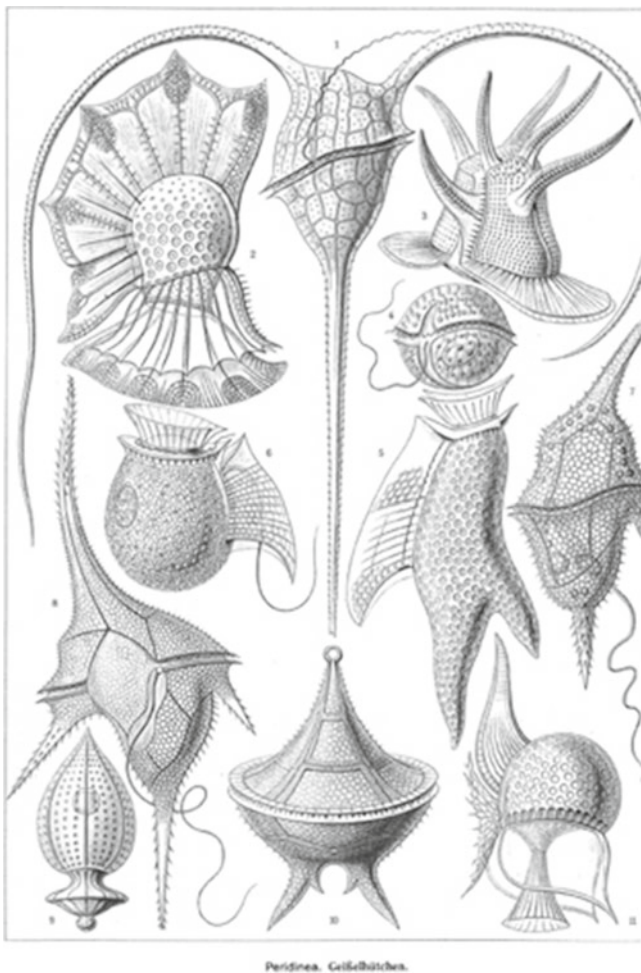


Figure 2. Various species of dinoflagellates armoured with cellulose plates drawn by Ernst Haeckel for *Art Forms of Nature*. He could not imagine that these bizarre shapes had any significance or function. The width of the figure is equivalent to about 0.1 mm.

Haeckel ‘fudged’ his drawings of vertebrate embryos in support of his proposal that ‘ontogeny recapitulates phylogeny’. This recapitulation hypothesis was rejected after much debate, but the underlying world view that there were structuring forces innate to biological systems that produced patterns, generally pleasing to the human eye, was not explicitly challenged. The implications of this belief are that searching for explanations for each and every morphological character is a futile undertaking (Hamm and Smetacek 2007).

Apart from the Haeckelian world view that form can evolve with little constraint by function, there are several other reasons why our understanding of the evolutionary forces driving speciation and the expression of such striking shapes in the plankton has languished for over a century. One of these was the diversion of attention to the role of

phytoplankton as the base of the food web leading to all animal life, including commercial fisheries, in the ocean. The field was launched by Haeckel’s contemporary – Victor Hensen – a physiologist who conceived the ground-breaking concept of ‘metabolism of the sea’, which could be quantified by the common currency carbon (Hensen 1887; Smetacek 1999a). In this world view there were organisms interacting with each other, with primary producers taking up nutrients and fixing energy and consumers doing the opposite, all suspended together in the same water mass. This was a grand vision of an ecosystem functioning like the physiology of an organism, and Hensen referred to the phytoplankton (a term he coined) as ‘the blood of the sea’ (Smetacek *et al.* 2002).

Because Hensen was concerned with ‘harvesting’ the sea, his terrestrial analogy was agriculture, which could be quantified. In contrast, natural terrestrial systems (forests) were not amenable to bulk measurements in terms of mass/area at the time because they were too heterogeneous and bulky to be sampled on foot. The world view of the agricultural paradigm consisted of food chains in which the links were trophic levels (plants, herbivores, carnivores) leading eventually to the organisms of interest (fish and other top predators). Rates of trophic transfer could be calculated as in agriculture. In this one-way-street scheme, the more trophic levels, the less food available to fish. The agricultural concept of limiting nutrient was introduced by Karl Brandt, a contemporary of Hensen, which meant that the total amount of biomass that could be built up in a given oceanic region was determined by the availability of fertilizer: the limiting nutrients nitrogen (nitrate and ammonia) and phosphate (Mills 1989). By the 1960s and 70s the methodology had vastly improved, and estimating the potential fisheries yield of a given ecosystem such as the North Sea from its rate of production and structure of the food chain appeared to be feasible (Steele 1974). However, before fish stocks could be predicted from production measurements, industrial fishing depleted them far below the carrying capacity of the ecosystem, greatly hampering the study of natural ecosystems.

In the terrestrial biome the central role played by bacteria as decomposers was appreciated by the beginning of the last century, but bacteria were not accorded much importance in the sea because most pelagic prokaryotes cannot be cultivated in the growth media offered to them by bacteriologists. It was the direct counting of bacterial cells by staining them with fluorescent dyes such as acridine orange in the 1970s that revealed their large numbers – 10^6 cells/mL – in every drop of surface water, with abundance dropping by about 2 orders of magnitude in the deep ocean. New techniques for indirectly assessing production rates using radioactively labelled substrates indicated that these cells were utilizing a significant share of the primary production and marine microbiology blossomed. Prior to these discoveries, pelagic ecosystems were thought to be dominated by zooplankton

grazing that recycled nutrients directly to phytoplankton. The discovery of the 'microbial loop' changed the simple food chain into a complex food web of organism interactions comprising prokaryotes which channelled dissolved organic carbon (DOC) to the eukaryotes. The application of molecular biology techniques has revealed the diversity of pelagic prokaryotes and their multiple relationships to the protists (Yooseph 2010). There is no doubt that increasing information on the quantitative structure of whole communities that genomics is now offering will vastly advance our understanding of the functioning of pelagic ecosystems from the community level to species-specific interactions and their resultant impact on biogeochemical cycles (Strom 2008).

Hensen quantified the carbon in organisms by counting them under a microscope, calculating their volumes and converting these into carbon units. The method went out of fashion, although it gives surprisingly reliable results of species biomasses, because it was supplanted by more convenient ways of quantifying phytoplankton using bulk properties such as pigments, in particular chlorophyll, organic carbon and other biogenic elements. Organisms, i.e. species, were literally lost from sight and all chlorophyll was considered equally good food. Hence, an unfortunate result of the agricultural paradigm was that little consideration was given to evolution of the organisms in relation to each other. The fact that the biomass of blooms was poorly grazed was explained by the match/mismatch hypothesis in which grazing copepods failed to time their crucial growth phase to that of the phytoplankton bloom. That the blooming species deterred their potential grazers was not considered until the late 1990s (Ianora *et al.* 2004) and has been under debate since then. The bottom-up trophic transfer model in which the nutrient supply governs plant production, the herbivores are limited by their life cycles and so on, is widely accepted as given. This is still the mainstream world view today in biogeochemistry and the global carbon cycle on which attention of bio-oceanographers converged, once interest in the agricultural paradigm waned with the decline of fisheries.

5. Terrestrial ecology and biodiversity

Another important reason why the study of the evolution of form and function in the protistan world has not received the attention it deserves is because evolutionary biology since its inception has been strongly influenced by the terrestrial, space-holding, competitive-exclusion paradigm in which plants are distinct from animals. Indeed, the last review of form and function in phytoplankton was that of Sournia (1982), who concluded that no relationship was discernible and advised phytoplankton ecologists to consult their children to obtain a fresh viewpoint. Had he included the non-photosynthetic protists in his review, he would have found that a relationship between form and function (form of

feeding) was equally elusive amongst the heterotrophs, implying that, in the pelagic realm, protistan shape is not generally related to a functional adaptation to maximize resource uptake, be it dissolved nutrients and light or suspended and swimming food particles. A comparison with the situation on land provides a background to assess the possible factors driving evolution of form and function in the protists.

All dominant life forms on land belong to only two disparate lineages: one leading from chlorophyte algae to the modern land plants and the other from choanoflagellate-like ancestors to animals, with fungi a related sideline. This clear-cut functional and phylogenetic dichotomy of land plants and animals is ancient and predates colonisation of the land some 500 million years ago. It also led to the dichotomy of Biology into botanists and zoologists who used the terms plant and animal kingdoms to delineate the respective realms over which they ruled. The protistan realm was disputed territory and most lineages were dealt with by both botany and zoology textbooks. The uncertain status of protists is exemplified by the exam question: is the flagellate *Euglena* a plant (it photosynthesizes with chloroplasts) or an animal (it ingests particles and can live without its chloroplasts)? This question poses a challenge to biology students brought up in the tradition of separate plant and animal kingdoms but it is irrelevant in the light shed by evolutionary endosymbiosis which shows that, in the protistan world, the form of nutrition matters little. As we shall see below, species of the same genus can be autotrophic or entirely heterotrophic; to separate them into plants and animals does not make sense.

The structure and biomass of land ecosystems is determined by the availability of water. Where the water supply is in excess of demand, space is occupied by plants competing with each other for light. This is evident in the coverage and form of vegetation along the gradient from deserts to rain forests, which repeats itself on all continents. Everywhere, only two types of trees have emerged: the standard tree with a branching trunk and crown of small leaves, and the palm tree with its ring of large leaves atop a trunk, exemplified by tree ferns, cycads, palms and papaya trees. These shapes appear in size classes ranging from shrubs to trees with the height of the trunk often a function of water availability. Both shapes (morphotypes) have been invented repeatedly by successive plant lineages suggesting that their forms represent optimal solutions to competition for light in the air and water and nutrients in the ground. Similarly, the cactus-shape (xerophyte) as adaptation to arid conditions has evolved in a variety of plant families.

Grasses represent another type of shape and growth strategy to achieve competitive exclusion on the land. Grasslands (savannah and steppe) cover vast areas of the planet, indicating that they are excellent space-holders. However, as grasses are easily overgrown by trees and shrubs, they rely

on fire and mammalian grazers (ungulates and elephants) to overcome their competitors. They achieve this by growing at the base rather than the tip of the plant (as in trees and shrubs); so, grasslands provide a readily accessible, continuous supply of food to herds of grazing mammals, which also feed on the leaves and buds of young trees and shrubs, thereby preventing them from growing. Uneaten dry grass burns easily without damaging the grass base, whereas young trees and shrubs are killed; so, both grazing and fire maintain grassland and prevent forest cover. However, an assessment of savannah and forest habitats in Africa revealed that this top-down control of land vegetation functions only in regions where rainfall is below 650 mm/year; trees outgrow their grazers above that level and closed-canopy forests take over (Sankaran *et al.* 2005).

The relationship between form and function in overall shape of land plants is obvious; yet, within each of these morphotypes, a large variety of species has evolved, driven to a great extent by co-evolution with animals. This is reflected in the fact that plants are classified according to the structure of their sexual organs (flowers) and not by that of their vegetative body because herbs, shrubs and trees can be found within the same family. The fact that there are so many species of flowering plants is partly explained by selection by animals. Thus, evolution of intricate structures – flowers – to facilitate pollination resulted in the proliferation of species in land plants because of selection by their species-specific animal vectors whose own interests, payment in the form of food (nectar, pollen), also had to be met. Since land plants are anchored in their environment, another important driver of speciation is seed dispersal. Again, a huge variety of mechanisms evolved including the evolution of fruit pulp as payment for animal vectors. Not surprisingly, species diversity in angiosperms (flowering plants) is immense – some 250,000 species – compared to that in gymnosperms (wind-pollinated conifers) – <900 extant species. Interestingly wind pollination is more prevalent in colder temperatures where insect vectors are at a disadvantage compared to the tropics. However, grasses are also wind-pollinated but have large species diversity, nevertheless.

Co-evolution between plants and animals is also driven by the development of defence mechanisms (herbivore deterrents), whether mechanical (tough leaves, thorns, etc.), chemical (noxious secondary metabolites) or life style (phenology), against herbivores, in particular insects. Since these herbivore adaptations to plant defences (the arms race) tend to be species-specific, several tens of insect species are dependent on each tree species with the number rising with temperature. As a result there are many millions of insect species of which most evolved in the tropics. Summing up, the evolution of vegetation at the landscape level is driven by competitive exclusion amongst space-holders, whereas

speciation is largely driven by animals, whether pollen and seed vectors or herbivores. The evolution of animal shapes, on the other hand, knows no bounds. One only has to compare the shapes of major herbivores with one another – caterpillars with ants and aphids, or monkeys and squirrels with ungulates and elephants – to find out. However, one can relate the specific shape in each case to the style of food acquisition, whereby predators, via techniques of avoidance, defence and escape, are another major determinant.

6. Protistan lineages

In contrast to the two lineages on land, plankton are represented by a large number of lineages (clades) some of which are ancient (cyanobacteria, chlorophytes), while others (e.g. dinoflagellates, diatoms) made their first appearance only a few hundred million years ago; i.e. these radical new structural inventions are as recent as flowering plants and mammals. It has been relatively easy to trace evolution in land plant and animal lineages alike because both have left behind a coherent fossil record of descent from common ancestors, enabling the construction of phylogenetic trees. Unfortunately, the fossil record of protistan groups, apart from those with mineral skeletons, is meagre. Even less is known about the structure of past metazooplankton communities. Genomics is filling some aspects of the gap. Dating with molecular clocks allows rough estimates of first appearance as also the degree of relatedness between species or also between lineages. It is now clear that the genetic distance between plants and animals is as large as that between various protistan clades. Thus, the high phylogenetic diversity of the ocean compared to the land is due to the fact that the ocean has been inhabited for so much longer and many ancient lineages have survived. However, it is the new arrivals that are most intriguing because their novel structures seem to spring out of nowhere on first appearance. Attempts have been made to relate their appearance to changes in the chemistry of the ocean (Falkowski *et al.* 2004), but most newcomer lineages appear to thrive in both freshwater and seawater, from the poles to the tropics, implying that their physiology can adapt to a broader range of physico-chemical factors, in particular nutrient concentrations and alkalinity, than the ocean has undergone since the current oxygen levels were established.

Most protistan clades play a background role in terms of abundance and biomass and comparatively few contribute significantly to oceanic primary production and the biological carbon pump. Although they appear minute from our perspective, the size range between the smallest and largest protistan cells and colonies spans up to 4 orders of magnitude (μm – cm), the same as in land plants (from mosses to trees) and mammals (from mice to elephants) (figure 3). Their grazers, the protozoo- and metazooplankton, span an even larger size range. Thus, there are giants and dwarfs also

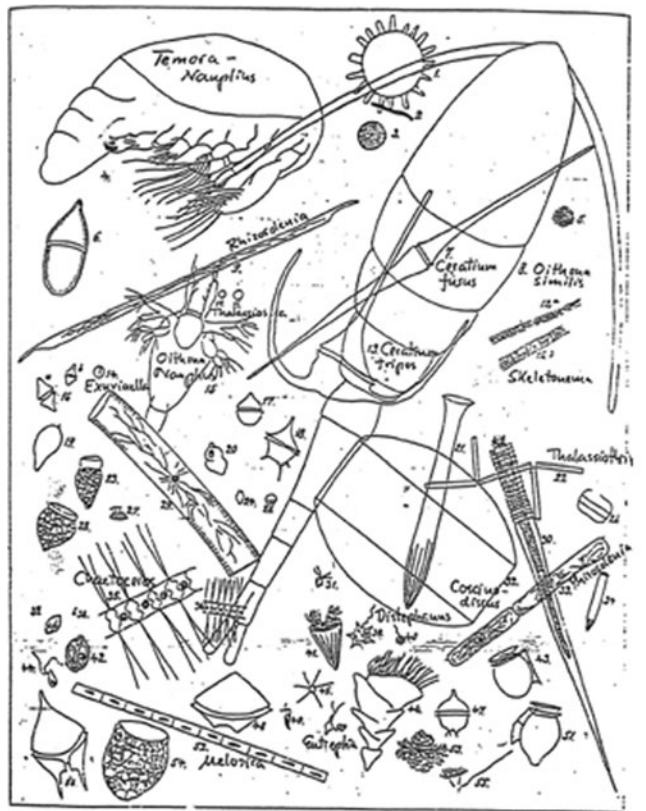


Abb. 25: Auswahl einer Reihe von Plankton-Organismen von Laboe, sämtlich bei 250facher Vergrößerung gezeichnet, um das gegenseitige Größenverhältnis zu zeigen (LOHMANN, 1908, S. 201).

Figure 3. Drawing of plankton from Kiel Fjord (Baltic Sea coast of Germany) by Hans Lohmann (1908) to illustrate the importance of his discovery of nanoplankton: cells $<20\ \mu\text{m}$, depicted at the bottom of the drawing. The organisms are all drawn at the same scale and demonstrate the size differences between one of the smallest marine planktonic copepods (*Oithona*) and various common species of diatoms, dinoflagellates, ciliates and other flagellates. Most of the species depicted here are cosmopolitan and ubiquitous in the coastal plankton. *Ceratium tripos* and *fusus* are superimposed on the cephalothorax of the copepod and *Mesodinium rubrum* is the round, hairy object in the bottom row (fourth object from the right). For scale, the copepod *Oithona* is about 1 mm long.

in the protistan world with representatives of both in most of the dominant clades. There are vast differences between the clades in terms of size, shape, nutrition, flagellation, mineral skeletons, etc. but also in the number of species. Diatoms are speciating rapidly; others have comparatively few, widely distributed, abundant species. Phyto- and protozooplankton merge into each other with mixotrophic forms such as the *Euglena* example in between. Both have comparable growth rates; indeed protozooplankton can have more divisions per day, as their growth is not restricted by the night. They thus have the potential to consume most of the phytoplankton

(Strom 2002); indeed, the fact that they do not succeed in curtailing build-up of phytoplankton blooms is mainly due to heavy grazing pressure on them by metazooplankton, in particular copepods (Sherr and Sherr 2009). It follows that, because protozooplankton, but not phytoplankton, is routinely controlled by copepods, the latter must represent less attractive food, implying that phytoplankton, in particular the bloom-forming species, have evolved more effective defences.

Bottom-up factors – the physics and chemistry of the water – will not suffice in explaining the diversity of traits (properties) as physics will be selecting for optimal size and shape. Indeed, the physics of the pelagial dictates that cells with the highest surface to volume (s:v) ratios, i.e. the smallest possible size of $1\text{--}2\ \mu\text{m}$ (picoplankton), will be the most efficient in taking up dissolved nutrients and light. So why have orders-of-magnitude larger eukaryotic cells taken over the chloroplasts and proliferated to such an extent that they dominate biomass in regions of high productivity? The obvious answer is protection from grazers by increasing size to deter predators, which is well known in the macroscopic world as ‘size escape’ (Smetacek 2001). A universal rule in the arms race is that smaller s:v ratio is advantageous because investment in defence decreases proportionally with increasing cell size.

One reason why the role of grazing is under-appreciated in the pelagic realm is the widespread belief that the individual cell is also the individual in the Darwinian sense, i.e. the unit of natural selection. This misconception has arisen because dividing cells of a unicellular organism separate from one another and appear as individual organisms, equivalent to individual multicellular land plants. Whereas the latter can sacrifice pieces (leaves) to the sampling herbivore to deter it from eating the whole individual, the sampled protistan cell is gone for good. This is a myth: all the cells emanating via vegetative division from a zygote belong to one clone and hence represent one diffuse individual. It follows that the individual in unicellular organisms is a cloud of cells that, in the case of marine plankton, can be spread over vast areas, intermingling with the cells of other individuals of the same species. Individual cells can be sacrificed, like individual leaves of a plant, to maintain survival of the individual organism, i.e. the entire clone.

In an ongoing arms race, it will be necessary for the selective grazer to recognize cells of a noxious or otherwise unpalatable species or newly mutated clone in order to avoid them. I suggest that shape is a signal to would-be predators, sensed by their proprioceptors – the sensory system that includes the sense of touch and allows discrimination of objects by the feel of a shape, in contrast to how it looks. In humans this is the sensory system that blind people rely on to lead relatively normal lives and that people who can see take for granted (Smetacek and Mechsner 2004). ‘Felt shape’ would be equivalent to the colour and ‘seen shape’

for visual predators that, because of the small size of the prey, cannot operate at the protistan size scale. If there is a shape, there must be something to sense it; otherwise it would have no evolutionary relevance. In this framework, conservation of shape by cryptic species makes sense. It follows that, if there are species equipped with effective grazer or predator defences, other species will mimic them, whether defenceless (Batesian mimicry) or also defended (Müllerian mimicry). Mimicry is well established in the animal kingdom but this might be the first time that it is invoked also for protists.

The cells in a multicellular organism are attached, differentiated and organized in functional units that maintain integrity of the organism. Protistan cells produced by vegetative cell division, with some exceptions (e.g. end-cells of some diatom chains), appear not to be differentiated. In many species all vegetative cells can turn into gametes, but this is not the case in others. Although the sexual phase of most protistan species has not yet been observed, there is enough information to assume that sex is a universal phenomenon. In most multicellular organisms sex and reproduction are obligatorily linked, but this is true only for very few protists such as foraminifera, which discard the parental shell instead of passing it on to the offspring. As a result, foraminifera shells dominate calcareous sediments in many places although their presence in the overlying water is modest. In most protists, sex leads to reduction in population size, simply because two haploid cells (most protists are haploid) fuse into one diploid zygote, often accompanied by mass death of vegetative cells that do not turn into gametes for whatever reason. Thus, with the exception of forams and some other groups, the term ‘sexual reproduction’ is a misnomer in the protistan world. Again, one can anticipate that genomic screening of large volumes of water will reveal new insights into the dynamics of protistan life cycles.

7. Exo- and endosymbiont

Eukaryotes evolved by the process of endosymbiosis whereby prokaryote cells became organelles to form new functional units; in the case of phytoplankton, cyanobacteria were transformed into plastids (chloroplasts). The idea that unrelated organisms could fuse together into new types of organisms with properties of both was first suggested at the turn of the nineteenth century but did not take hold. In modern times the concept of evolutionary endosymbiosis was introduced and vigorously defended in the 1970s by the late Lynn Margulis (1970, 1981). Initially, the concept that algal evolution was driven not only by mutations in single advancing lineages but even more so by separate lineages fusing together, was greeted with disbelief. But there were many holes and contradictions in the algal classification scheme based on pigment composition prevalent in the botany

departments of the time; further, there were striking examples of the ongoing process from the real world – ranging from facultative to obligate, organism to organelle relationships – to illustrate how it happens; so, the weight of evidence prevailed within a decade or two.

Molecular classification schemes of clades with phytoplankton members have focused primarily on the pigment-bearing endosymbionts with less regard paid to the origin and properties of the engulfing cells that are referred to as ‘host cells’, a term that smacks of a temporary or even parasitic relationship. However, in the arms race paradigm, it is the properties of the latter that define the new organism and set it apart from the engulfed endosymbionts. The logical term that sets the host cell on equal footing with the endosymbiont is ‘exosymbiont’ (Hamm and Smetacek 2007); indeed, one could as well term the entire process ‘evolutionary exosymbiosis’, which would draw attention to the arms race as the driving force behind protistan evolution. Closer examination revealed that endosymbiotic relationships arose not only between prokaryotes and eukaryotes but also amongst eukaryotes resulting in primary, secondary and tertiary symbioses, respectively. In the latter cases, properties of the exosymbiont, in addition to the modified chloroplasts, were selectively integrated into the new organism. A cyanobacterial cell on its own should have higher growth rates than a chloroplast because of its larger s:v ratio and because it can invest all its efforts in growth instead of contributing to the welfare of the exosymbiont. Since the genomes of both survive, the relationship is on even ground and terms such as enslavement misplaced. What the exosymbiont offers its endosymbionts is protection against the 3Ps by increasing size and deployment of mechanical (tough cell walls), chemical (toxins) and possibly immunological defences. I shall present some examples further below.

Another advantage of the intimate relationship between the symbionts is the short-circuiting of the recycling, microbial loop: the waste products of the heterotrophic partner can be fed directly to the chloroplasts of the same organism. This has been recently shown in diatoms where the presence of urea production genes initially raised surprise (Armbrust 2009). A closer look has shown that the exosymbiont has retained its entire nitrogen metabolism (required for making the frustule and maintaining intracellular structure) down to the final end-product urea, which is channelled to the endosymbionts (chloroplasts) via a biochemical pathway involving ornithine (Allen *et al.* 2011). This ‘tightening’ of ecosystem infrastructure can be regarded as a bridge between the conventional animal and plant kingdoms. In the ancient chlorophytes, genomes of exo- and endosymbiont are much more intimately integrated and they have produced, but only in freshwater, a broad range of disparate morphotypes, based, like their relatives the land plants, on cellulose. However, diatoms are comparatively recent, and so it is perhaps not surprising that

this extended form of exchange is still intact. Significantly, growth rates of some diatom species rank amongst the highest in the phytoplankton indicating that this drawn-out cycle is not much of a handicap. All sorts of implications for the exo- and endosymbiotic marriage arise in this connection such as how the formerly phagotrophic exosymbiont learned to provision its plastids with nutrients present at trace concentrations.

Ciliates are the most recent arrivals on the phytoplankton scene. Indeed there is only one species *Mesodinium rubrum* that has fine-tuned its interaction with its cryptophyte endosymbiont (a flagellate) to such an extent that it can form blooms dense enough to colour the water blood-red in the space of a few days. Nevertheless, it still has an obligate, but very modest, requirement for prey cells, presumably to obtain a growth factor, because its growth is fuelled primarily by photosynthesis of the endosymbiont (Fenchel and Hansen 2006a). This species occurs everywhere and blooms have been observed regularly, or sporadically, from the inner Baltic Sea at salinities <7‰ to the Arctic and equatorial oceans. Since pelagic ciliates are much faster swimmers than any flagellate, they can utilize nutrients from greater depths that can not be accessed by flagellates, thereby opening a new niche. Although described and understood by Lohmann (1908) from the Kiel Bight, *M. rubrum* did not attract attention until the 1970s when it played an important role in cementing the evolutionary endosymbiosis fact while it was still a hypothesis. The zoology/botany dichotomy is illustrated by this story from the 1960s told to me by one of the scientists involved (Thronsen, personal communication). One morning, the residents of Oslo were shocked at seeing the waters of the fjord blotched with patches of red water reminiscent of blood. Since this looked like an algal bloom, the botany department of the university organized a sampling foray and when they found that the culprit was the above-mentioned ciliate, they informed (apparently with some glee) the zoology department that it was their charge. After all, ciliates are not mentioned in botany textbooks. By the time the zoologists got their act together, the bloom was gone.

Since the 1980s a variety of other ciliate species have been shown to practise facultative phototrophy by means of 'kleptochloroplasts' (chloroplasts 'stolen' from ingested algae), which are retained for some time but subsequently digested or ejected. A prerequisite for *Mesodinium* symbionts to be permanent (Fenchel and Hansen 2006a) is provisioning with adequate amounts of N, P, Fe, etc., in the form of dissolved nutrients by the ciliate exosymbiont; these elements were acquired entirely in particulate food before that. Phytoplankton take up nutrients through arrays of element-specific entrance sites constructed out of proteins that are scattered over the cell membrane. These are also the sites on which viruses dock to inject their RNA into the cell and hence require protection. Developing such a sophisticated nutrient uptake system, quasi from scratch is, at

least to my imagination, quite an evolutionary feat for a former phagotroph: a much, much bigger jump than switching from carnivory to ungulate-style herbivory in a land animal or vice versa. So why has only one species managed this feat and how long did it take to develop the uptake system? Ciliates are, to my mind, the athletes of the protistan world but *Mesodinium* is reputed to be the fastest: it can attain velocities during jumps of 1.2 cm s^{-1} (Fenchel and Hansen 2006b) equivalent to about 500 body lengths s^{-1} . This is fast by any standard. This superior motility has two mutually inclusive benefits: it allows more efficient nutrient uptake because of the greater volume of water traversed during growth (*Mesodinium* makes regular jumps), but it also permits more effective escape from copepods than slower organisms (Fenchel and Hansen 2006b).

8. Plankton evolution and morphology

The term successful is often applied to species, groups or lineages that occur in higher abundances than others, implying that they are superior competitors for resources. However, the same effect can be achieved by reducing mortality; so, success here would mean better defences. The term successful is also applied to lineages with a high rate of speciation, implying successful adaptation to different niches, whether old or newly opened. Since the two overlap in some cases (grasses and diatoms) but not in others (gymnosperms, kinetoplastids), the term 'successful' can be confusing. Indeed, one needs to explain why there are some ubiquitous, cosmopolitan groups (from genus to lineage level) that have comparatively few species occupying vast ranges, with the recent arrival *Mesodinium rubrum* being a good example, while others have a large number of species also occupying large ranges, with some species generally more abundant than others (e.g. the diatom genus *Thalassiosira*). In the following I present some examples from the pelagic realm to show how the arms race paradigm can make sense of some otherwise inexplicable observations. Such a framework will have to explain the different types of evolutionary success mentioned above.

An example of a group with comparatively few, wide-spread species is provided by the ancient group of minute flagellates (kinetoplastids or bodonids) with few, cosmopolitan species that are major consumers of the bacterioplankton, from lakes to the ocean (Fenchel 2005). They have small, unadorned cells (2–5 μm), with one large flagellum with which they wriggle through the water, capturing bacteria by means of a miniature 'trunk'. As mentioned above, pelagic bacteria are amongst the smallest organisms on the planet ($\sim 1 \mu\text{m}$) and evenly distributed at 10^6 cells/mL throughout the surface ocean. About half are immotile and the other half equipped with flagella which they use to seek food and to escape from predators (Smetacek 2002). It is

unclear what percentage of the cells are dormant cysts, which would serve to camouflage them from predators. Whereas bacterial cell numbers vary as little as 50%, the abundances of protists can vary by orders of magnitude. However, bacterial production (cell division) rates can vary several-fold over the course of the seasonal cycle and from region to region, implying that the constancy of numbers is maintained by mortality: due to viral infection and grazing by small flagellates and ciliates of which the kinetoplastids tend to contribute the bulk. It has been shown that larger bacteria are preferentially grazed and so it is likely that the small size is a form of reverse size escape. Viral infection is widely known to be a function of host density; so, this form of mortality is likely to set the upper limits of bacterial cell numbers. It follows that the lower level is set by predation. Quantification of the bacteria–virus–kinetoplastid relationship over a wide set of environmental conditions will provide insight into the set of rules governing metabolism and shifts in species composition of these components of the microbial community. The study by Yooseph *et al.* (2010) has shown what type of new information is in the offing.

Needless to say, almost nothing is known about the evolutionary history of kinetoplastids, but their simple morphology and lifestyle does not reflect a high degree of sophistication comparable to that achieved by the more recent ciliates. It is tempting to suggest that, because there is not much scope for refining techniques to locate and capture minute, suspended bacteria individually, the morphology of the kinetoplastid species has also stabilized, i.e. they represent optimal solutions for that function. New mutations can no longer increase fitness in terms of resource acquisition, i.e. optimal solutions to constraints posed by the physical and chemical environment have been reached for that size class. The ensuing ‘evolutionary spaceholding’ is due to ‘functional perfection’. An example of ‘functional perfection’ from day-to-day life is the bicycle. It is ideally geared to the human body for the purpose it serves. So, its basic morphology has not changed despite technological advances. In striking contrast, multifarious techniques to collect small, suspended particles indiscriminately have evolved in the metazooplankton (see Hardy 1956): mucous nets (pteropods) and sieves made of tissue (salps), or of mucous houses (appendicularians), or of stiff chitin bristles (crustacea), not to mention the many more techniques developed by benthic organisms. Unlike the omnipresent microbial community, the above metazooplankton invariably exhibit strong seasonality and/or patchiness in their occurrence, and hence are unlikely to exert a strong influence on speciation within the microbes. The major grazers of the kinetoplastids are other flagellates and ciliates but their numbers; hence, grazing pressure also varies seasonally due to trophic cascades exerted by their grazers, in particular copepods.

Interestingly, the other important group of bacterial grazers lumped together as heterotrophic nanoflagellates (HNF) – the choanoflagellates – are recent arrivals compared to the kinetoplastids with superficially similar cells but enlarged overall size due to stiff rods projecting out from the cells that range in shape and size, relative to the cell, from a mere collar to an elaborate parachute. The function of these external skeletons is not clear and it has been suggested that they improve the feeding rate by acting as a ‘drag’. Another, mutually inclusive explanation is that they are a form of size escape in order to deter small ingesting predators – in this case small ciliates that feed on HNF. The view is supported by some species that link their skeletons into colonies, which would deter also larger ingestors. As in the case of the kinetoplastids, comparatively few species have been described so far (Fenchel and Finlay 2006).

9. Diatoms

The opposite case, comparatively large number of species in a dominant clade, is represented by the diatoms. Their success is reflected in their domination of phytoplankton blooms worldwide, although only relatively few species participate in them (Assmy and Smetacek 2009). Diatoms contribute substantially to ocean primary production and play a central role in the biological carbon pump and hence the global carbon cycle. Ongoing evolution of diatoms is reflected in their rate of speciation, which is as rapid as that of the grasses. Species numbers of pelagic diatoms used to be estimated at around 1000, based on morphological traits alone. Genomic techniques have revealed that some species previously considered cosmopolitan actually comprise several distinct species. The increasing number of cryptic species coming to light indicates conservation of morphology, implying that the respective form must be fulfilling some function; otherwise, why would it be retained in such fine detail from the tropics to the poles, or from the coasts to the open ocean? A comparison with the benthic can shed some light on this issue. There are orders of magnitude more species of benthic than pelagic diatoms. The majority are pennate, and their shape and tough cell walls are obvious adaptations to life on a surface battered by waves and sediment particles. The large number of species is easily explained by adaptation to the broad range of habitats they inhabit – from mangrove trunks and sandy beaches to the sea floor at tens of metres depth. Benthic populations along the coasts of the continents are segregated from one another, enabling allopatric speciation by random gene drift. This mechanism of speciation is constrained in the pelagic by the mixing rate of surface water, which is orders of magnitude shorter than that required for gene pool segregation (Fenchel and Finlay 2006). No doubt, future genetic analyses will reveal more cryptic species, but the point is that the total number of pelagic species will still be small compared to

benthic species, although the latter colonize only a small fraction of the area occupied by plankton.

The diatoms appeared some 250 million years ago (Armbrust 2009), long after the tree morphotypes had been established on land. Indeed, forests of recognizable relatives of the living tree fossil *Ginkgo* were already present 280 million years ago. Another common protistan lineage, the dinoflagellates, appeared 300 million years ago. Both these lineages are as different from each other as they are from land plants. They occupy the size range between 2 μm and 1 mm with generally the larger cells, or small cells in long chains, dominating the biomass of phytoplankton blooms. Diatoms are entirely autotrophic, because the cells are enclosed in tightly sealed, intricately designed silica (glass) boxes that allow only uptake of dissolved substances (nutrients) and prevent phagotrophy. When the cells divide, each new box half is made inside the parent; so, successive divisions lead to decreasing size of daughter cells. Initial cell size is restored by a zygote that rapidly expands, bubble-like, to form an auxospore within which the new, vastly enlarged silica box is made. Since the diatom cell is always encased within the silica box, except when it is opened to allow the sperm to enter in the sexual phase and when the growing auxospore expands to restore cell size, the shell must play an important role in the success story of the diatoms. Indeed, at ocean scales, diatom growth is limited by the availability of dissolved silicon (silicate). It should be pointed out that auxospore formation often takes place at the end of a prolonged growth phase when gamete density will be at its highest but nutrient concentrations at their lowest. The ability of the germinating auxospore to increase its biomass several-fold in such a short time under these conditions is amazing and begs the question as to whether vegetative cells express growth rates close to their maximum potential most of the time.

A variety of functions pertaining to bottom-up factors have been attributed to the unique silica shell but the most likely core function is protection, particularly against pathogens and parasitoids (small flagellates that invade larger cells and feed on them). This is indicated by the fact that, in contrast to flagellates that are susceptible to viral attack, only a few cases of infection of diatoms have been reported so far. Apparently, the trade-off for giving up phagocytosis by the glass-box exosymbiont is reducing exposure to pathogens. Decimation of diatoms by parasitoids does occur, but the cases reported tend to be species-specific, indicating co-evolution between prey and parasitoids. Major grazers of diatoms are various protists, in particular dinoflagellates, which are able to digest the cell contents without breaking or opening the shells. Other important grazers are crustacean zooplankton – copepods and shrimp-like euphausiids – as well as filter-feeding fish like anchovies and sardines. All these grazers have developed techniques to crush the frustules: silica-lined mandibles for individual

crushing in the case of copepods and gizzards in the others (Hamm and Smetacek 2007).

The fact that so many organisms, including protists, feed on diatoms has earned them the epithet of ‘pastures of the sea’, but this is not at odds with co-evolution between diatoms and their zooplankton and fish grazers as it is analogous to the situation between mammalian grazers and grasses, where the latter also use silica as protection. The silica phytoliths that lend stiffness and sharpness to grasses, wear down the teeth and ultimately control the age of the grazers. Indeed, the favourite food of Indian elephants is bamboo, and they have partially overcome the problem by renewing the grinding part of their molars several times in their lifetime. It should be pointed out that grasses are highly diverse in terms of edibility and there are even toxic species. Do the grasses of the terrestrial realm, which depend on top-down factors to facilitate their dominance, have a message for pelagic ecologists?

Thus, crustacea will be faced with the same problem as terrestrial grazers, but they renew their silica-laced ‘teeth’ at each moult, which occurs between the various life cycle stages – 12 in copepods – perhaps also to compensate for the wear and tear involved in crushing diatom frustules. Actually, diatoms are more comparable to nuts or seeds than blades of grass because the edible part is encased in a shell, or an ear of wheat, and so eating diatoms whole is like eating nuts with the shells, or the grains with the husks and their spines. One can easily imagine the ballasting effect of eating peanuts with their shells, not to mention almonds. Here one would have to think twice before exerting the force required to crack an almond with one’s teeth because it could cost one a tooth. Given the range of shell thicknesses in diatoms, easily comparable to the range between peanuts and almonds, the copepods will be posed with a similar range of choices. Examples of the frustules of thick-walled species reduced to ‘rubble’ by crustacean grazers are depicted in figure 4. The architecture and material properties of diatom frustules make them surprisingly strong (Hamm *et al* 2003); so, it is not surprising that viable diatoms are commonly found in copepod and euphausiid faeces; these grazers will thus be selecting for stronger, thicker-shelled diatoms (Hamm and Smetacek 2007). It should be pointed out that selection by the arms race is the exact opposite of agricultural selection practised by *Homo sapiens*.

Prior to the 1980s it was believed that copepods indiscriminately filtered particles out of their medium and ate them. Observations of tethered copepods with high-speed cinematography in the 1980s provided surprising insight into their food capturing and handling ability. Copepods pick particles selectively out of the feeding current they generate, occasionally lunging forward to chase a fleeing ciliate, evidently a choice food item. All this is happening much faster than the human eye can follow. Given the degree of

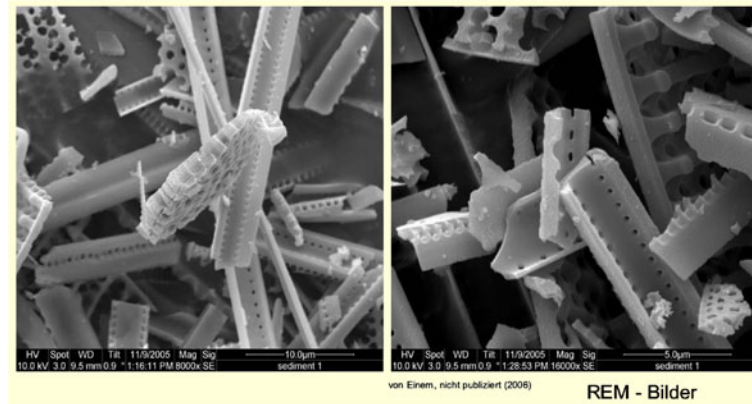


Figure 4. Scanning electron micrographs of surface sediment from the diatom ooze underlying the southern half of the Antarctic Circumpolar Current showing silica frustules of diatoms crushed by copepod mandibles and euphausiid (krill) gizzards. The cement-girder-like structures belong to *Thalassiothrix* ('sea hair') *antarctica*, the cells of which can be 2 mm long, making it the longest diatom in the world. It is a major contributor to the sediments, second only to *Fragilariopsis kerguelensis*. Photos Jessica Björk.

selectivity practised by the copepod, prey edibility will be defined by a range of subtle factors that influence how many cells of a particular species are eaten in a particular time period in relation to all potential prey items in the environment. The factors include (a) handling time and effort, (b) risk to hard parts, (c) relation between prey volume (enhanced by water, slime, mineral skeletons) and its food content and (d) toxic or noxious secondary metabolites, amongst others. In all these cases, the nature of the herbivore deterrents in the prey could potentially be signalled by its shape. This would require commensurate sensory systems and performance in the predators.

Since it is not yet possible to observe copepods directly in the wild the way one can observe insects or elephants on land, one tends to underestimate their abilities. Since crustaceans are the aquatic versions of insects and spiders (all are arthropods), there is no reason yet to credit them with inferior sensory performance. One only has to watch the complex behaviour of butterflies (I was a passionate butterfly collector as a boy) or watch a dragonfly prowling the air for prey on the wing, not to mention the established intelligence of bees and ants, to appreciate what complex lives copepods could well be leading. Whatever copepods are doing in detail, they are extremely good at it and dominate the ocean's zooplankton the way insects dominate on land (Verity and Smetacek 1996). In fact, there will inevitably be at least a few individuals of the smallest genus *Oithona* in every cubic metre of surface water from the poles to the tropics. Copepods are also extremely fast. Mating in the widespread copepod genus *Acartia* entails the male attaching a bag of sperm (spermatophore) with pincer-like male sex organs to the genital opening of the female. The act occurs while the male and female spin in a tight circle with such speed that even slowed-down video recordings cannot capture the

actual transfer (Bagøien and Kiørboe 2005). Clearly, this is a case of female selection of male fitness in terms of speed and agility: properties required to flee from attacking predators but also to capture fast-swimming prey, in particular ciliates. Clearly, *in situ* observation of copepods is sorely required to test the shape-selection by predation hypothesis.

10. Dinoflagellates

Despite their ubiquity, the numbers of dinoflagellate species is much smaller than that of diatoms and the majority are pelagic. Compared to the simple anatomy of diatoms, which can be characterized as shell-making machines, dinoflagellates are highly sophisticated, almost sentient beings. Some genera even have an ocellus equipped with a lens; because of its refractive properties, the lens is very prominent under the microscope. It can occupy up to 25% of cell volume, a delicious lump of protein for any predator, so it must fulfil an important function. However, no one knows what the cell is seeing or how the information is being processed. All dinoflagellates possess two characteristic flagella and a nucleus (the dinokaryon) with a structure quite unlike that of any eukaryotes. Some groups have thin, elastic cell walls capable of python-like distension, and others are rigid due to thick armoured plates made of cellulose, but all are capable of feeding on particles in a variety of novel ways (Jacobson 1999). However, many species are largely photoautotrophic and second only to the diatoms in their contribution to marine photosynthesis. A variety of shapes and sizes are represented in the bloom-forming species, indicating that bottom-up factors selecting for optimal shapes for nutrient and light uptake are not of central importance in building up biomass to bloom proportions (Assmy and Smetacek 2009).

In striking contrast to diatoms which carefully guard their dividing cells within the parental silica cell wall, dinoflagellates divide by tearing the cell into two unprotected halves which are at the mercy of pathogens, parasitoids and predators for some time until the new cell wall half is made. One way to reduce mortality is synchronous division which, like the gnus of the African savannah giving birth to their vulnerable babies at the same time, will swamp the feeding capacity of the predators and ensure that a significant number of offspring survive. Indeed, synchronous cell division is well established in bloom-forming dinoflagellates.

On the other hand, heterotrophic dinoflagellates contribute a significant fraction of pelagic grazers and some are voracious predators, feeding on prey much larger than themselves. They have evolved a variety of sophisticated feeding techniques: peduncles to pierce and suck out the contents of their prey and externally deployed 'stomachs' in which the prey is wrapped and digested outside the armour-plated cell. Dinoflagellates have been observed to 'inspect' a diatom chain by circling around it in tight loops several times before deciding to deploy the feeding apparatus (Jacobson and Anderson 1986). It follows that they not only have memory but also freedom of choice. The biochemical correlates of this sophisticated, decision-making process, analogous to the neural correlates of multicellular animals, await elucidation. It has also been shown that the success rate of dinoflagellates attempting to capture and eat another, similar-sized flagellate following first encounter is about 10%. The flagellate manages to escape most of the time (Tillmann and Reckermann 2002). This success rate of a hunting predator is not very different from that of a tiger hunting deer in the grasslands of India. If the success rate increases, the deer population goes down and there is more straw available for burning in the summer and vice versa with correspondingly different effects on vegetation at the landscape level. This type of trophic cascade has only recently been realized in pelagic ecosystems (Verity and Smetacek 1996) and it is likely that a web of species-specific interactions will come to light if looked for. Will principles of the arms race with regard to speciation and structure of the ecosystem apply across the entire gamut of planetary ecosystems?

The form of nutrition does not play a central role in the success story of the dinoflagellates as they have developed so many. Equally futile will be attempts at interpreting cell shape as adaptations to a particular lifestyle when the same shape is practising auto- and heterotrophy equally well. Thus, the bloom-forming large dinoflagellate species *Ceratium tripos*, *furca* and *fusus* play similar roles in the coastal plankton of regions as different as the Baltic Sea, the Gulf of Maine and the coastal waters of India. They are also common in the temperate open North Atlantic Ocean. *C. tripos* and *fusus* are depicted in figure 3; *C. furca* is slightly smaller and shaped like a two-pronged fork with unequal

prongs. Although strikingly dissimilar in shape, these species tend to occur together, often forming blooms, with their relative proportions varying inter-annually and regionally. Closer examination of the genome will in all likelihood reveal cryptic species hiding behind their identical shape, which will merely shift the question as to the factors maintaining the same morphology over such a broad range of environmental factors: light regime and intensity, temperature and salinity range, nutrient concentrations, etc. Since there are many other species of *Ceratium*, mostly in the tropical oceans, that are fairly easily separated on the basis of overall morphology, the constraint on shape of coastal species cannot be attributed to intrinsic limitations of the genus. Indeed, malformations quickly arise in laboratory cultures, indicating genetic plasticity in morphogenesis. We are left with the arms race as the shaping factor: the only common property of the geographical range of these species is the suite of potential grazers of *Ceratium*, ranging from ciliates and other dinoflagellates to various genera (but not species) of coastal copepods. Compared to other genera that are voraciously eaten by copepods, *Ceratium* species, including freshwater ones, are only sparingly eaten for unknown reasons. The bulky, strong armour of cellulose plates could be one reason, but it is likely that chemical defences will also come to light if searched for. Could their shapes, or the ability to recognize them, be genetically programmed in their grazers leading to their being selectively avoided, implying that deviating shapes would be eaten. Such an avoidance mechanism could possibly explain conservation of the bloom-forming *Ceratium* shapes.

Dinoflagellates are notorious for making harmful algal blooms that can have deleterious effects on higher trophic levels, in particular marine birds and mammals including sea-food eating humans, via the food chain. The blooms are natural, but can be exacerbated by eutrophication and aquaculture. The harm is caused by neurotoxins that lead to paralysis, or metabolic toxins that affect various organs such as lungs or alimentary canal. The immediate grazers of the harmful algae are barely, if at all, affected: indeed, they need to eat large quantities of the toxin in order to pass it up the food web. Despite several decades of intense research, the function of these peculiar molecules remains largely unknown. They are classic secondary metabolites and certainly not a side product of primary metabolism. As such these dinoflagellates are not unusual: other phytoplankton groups also produce a range of secondary metabolites of unknown function. Clearly these organisms are leading secret lives of greater complexity than we are willing to accord them. There are surprisingly large variations in toxin production between species or strains otherwise so similar that they have to be differentiated on the basis of detailed morphological studies of the minute cellulose plates covering their only opening through which food particles and gametes enter the cell. This

opening is equivalent to the genitals (flowers and sex organs) of multicellular organisms and the mouth of animals. Interestingly, but perhaps not surprisingly, these organs are also the basis of species differentiation in morphologically similar groups of plant and animal species by their respective botany and zoology taxonomists. Assuming that the toxins do play a role in defence, could the similarity in morphology at the scale accessible to the sensing predator be a case of Batesian mimicry?

Relatively few, albeit abundant, species are also found in other protistan clades such as the haptophyte flagellates, which include the chalk-bearing coccolithophorids and the colony-making, bloom-forming genus *Phaeocystis*. Blooms of the latter are recorded from many coasts and oceans, and yet genomic analysis could differentiate only three species: one each from the Arctic and Antarctic and the other everywhere else in between. The ciliates are perhaps the most remarkable in this regard: they are prominent inhabitants of all bodies of water from puddles to the open ocean, and many are highly adapted to life in the benthic or the open ocean, yet species numbers based on morphological criteria are estimated at around only 3000 (Fenchel and Finlay 2006). Low diversity in the microbial world is explained by the principle 'Everything is everywhere', which implies that dispersion is not a problem (Finlay 2002). However, this view is being debated and attention to the causative factors will perhaps lead to more differentiation as in the case of pelagic and benthic diatoms. Nevertheless, as discussed by Fenchel and Finlay (2006), the point is that there are surprisingly few protistan species (excepting diatoms) when compared to larger organisms. Similarly, zooplankton lineages, with the exception of tropical copepods, are also characterized by comparatively few species (generally <100), with one or a few dominating distinct biogeographical zones. As in the case of kinetoplastids, there appears to be little scope for speciation within the respective zooplankton clades in striking contrast to the case of insect/plant relationships on land.

11. Speculation on the sensory realm in the protistan world

There is little doubt that copepods have well-developed proprioceptors that enable them to differentiate and escape from approaching predators and recognize, capture and handle motile prey. However, proprioception in invertebrates has not received much attention, let alone in the protistan realm, although it has been invoked (Sheets-Johnstone 2007). There is no doubt that chemistry plays a central role in microbial interactions, implying that protists have an acute sense of smell (Wolfe 2000; Roberts *et al.* 2011). But in the arms race, chemical cues (e.g. pheromones) could also serve as signals to pathogens and predators, and so alternative

sensory systems will also be selected for. One only has to watch a video in real time of the ubiquitous freshwater ciliate *Paramecium* struggling to find its way out of a mat of algal filaments to appreciate the degree of complex locomotory behaviour it is capable of. Indeed, its attempts to squeeze through a loophole, find it too narrow, move backwards and choose another path are reminiscent of that of a mouse extricating itself from a dense bush. To my eyes the ciliate behaves like a sentient being equipped with proprioception (body sense) (Smetacek and Mechsner 2004) based on both locomotory and sensory cilia. It remains to be seen what abilities other protists have in this regard.

In this connection it is worth pointing out that sensory hairs tuned to the movement of water and objects lying on them are the functional basis of the vertebrate vestibular organs that sense gravity and body movement and fine-tune eye movements to those of the head. In other words, without sensory input from hair cells, vision would be constantly blurred and you would not be able to read at all. The cilia of ciliates are analogous sensory receptors (Sheets-Johnstone 2007). As mentioned above in connection with the ocelli of dinoflagellates and their apparent examination of prospective prey, we have no idea how sensory input is processed, but it can only be happening at the molecular level. We are left with the tantalizing question: Is there more to the animal brain than just neurons?

12. Concluding remarks

As we have seen, phylogenetic diversity in the plankton of the oceans is high but species diversity low. However, in a given body of water there will be tens or even hundreds of phytoplankton species present at any given moment. This co-occurrence of many species in what appears to be a homogeneous environment is known as Hutchinson's paradox of the plankton (Hutchinson 1961) and has been debated for many decades. The debate has, however, not questioned the underlying concept of space-holding: competitive exclusion by evolution of an optimal solution in the growth environment. In the arms race paradigm, survival and not growth is at stake, and so attention is shifted to the mortality environment (*sensu* Smetacek *et al.* 2004) where a broad range of pathogens, parasitoids and predators are exerting selective forces on their hosts and prey. This results in evolution of a corresponding range of defence measures, none of which can provide universal protection in the pelagic realm (Hamm and Smetacek 2007). Therefore, the mortality environment will always be heterogeneous and the paradox ceases to exist in the arms race paradigm.

The arms race has, in all probability, always been more important in driving speciation in the pelagic realm than bottom-up factors, but unfortunately, the fossil record of past zooplankton communities is extremely meagre. Nevertheless,

one can assume that invention of the silica box and its subsequent refinement by diatoms introduced a new form of defence to the plankton. The challenge of overcoming the silica box was met by dinoflagellates and some other protists, but particularly copepods and euphausiids seem to have co-evolved with diatoms (Hamm and Smetacek 2007). In an ongoing arms race, some species of prey can be expected to be a bit 'ahead' of their predators, enabling them to accumulate more biomass than other, more vulnerable species. In the case of bacteria and their pathogens and predators, total abundance of the former (the aforementioned 10^6 cells/mL) is invariably kept in check by mortality but this does not apply to protists, many of which regularly increase abundance by orders of magnitude. Diatoms are the best example because they are by far the most dominant members of phytoplankton blooms ocean-wide. The biomass build-up indicates that the respective species have outpaced their grazers and accumulated more biomass than the grazers can handle (Smetacek 1999b). The excess biomass, burdened by the heavy silica frustules, eventually sinks out rapidly and deep and provides food to the benthos and the deep-sea organisms. An additional function of the silica ballast suggested by Raven and Waite (2004) would be to rapidly remove cells killed by pathogen infection or invasion by parasitoids from the surface layer, thereby precluding proliferation of the pathogen or parasitoid and further infection of healthy prey cells. Most of the nutrients exported from the surface layer are ultimately returned to it in the course of deep-ocean circulation but a part is buried in the sediments for geological time scales, i.e. recycling of ocean sediments by tectonic activity.

Diatoms are thus major regulators of carbon dioxide levels in the atmosphere and ultimately climate. Indeed, the rise and diversification of the diatoms in the oceans coincides with steady cooling of the planet and growth of the Antarctic ice sheet between about 50 and 30 million years ago (Armbrust 2009). The high mountain ranges, including the Himalayas, also started rising in this period. The cooling coincides with declining atmospheric CO₂ levels for which burial of carbon by diatoms in the ocean and weathering of new rock exposed by the rising mountains are the major candidates. Weathering results in silicate being replaced by carbonate (from CO₂ in the atmosphere) in rocks crumbled by the wind and roots of plants. The silicate is ultimately washed into the oceans where it fuels diatom growth. Indeed, the oceans are hugely undersaturated in silicate and there are large regions rich in nitrate and phosphate where diatom growth is limited by lack of silicate. This example demonstrates how the great nutrient cycles of the planet are connected with one another by the evolving biosphere to regulate climate. Are humans now undoing, in the course of decades, what the diatoms took 20 million years to bring about and another 30 million years to maintain?

The CO₂ accumulating in the atmosphere that is responsible for ongoing global warming will stay there for thousands of years and ultimately be taken up by the ocean via acidification of the surface layer. The rise in CO₂ in the atmosphere from 280 to 390 ppm during the past 100 years is equivalent to 230 billion tonnes (Gt) of carbon: equivalent to one-third of the above-ground vegetation on all the continents. How much more forest cover will be required to take up this amount of carbon and where is the space for it? Technical means of removing CO₂ directly are burdened by the enormous energy costs required to capture and transport the CO₂, not to speak of the uncertain dump sites. The ocean, on the other hand, contains 38,000 Gt of dissolved carbon mostly in the form of bicarbonate and has already taken up half of the total CO₂ released by deforestation and fossil fuel burning. Regardless of the rate of CO₂ emissions, we must take steps now to explore ways and means of transferring CO₂ from the atmosphere into the deep ocean in as diffuse a manner as possible. Can we harness the ocean's biological carbon pump for this purpose?

It is now established that large nutrient-rich regions of the ocean in the subarctic and equatorial Pacific and the entire Southern Ocean have low phytoplankton biomass because their growth is limited by lack of iron, i.e. they suffer from anaemia to use a human analogy. A dozen field experiments have shown that adding trace amounts of iron (a few mg m⁻²) to the ocean surface stimulates large blooms of diatoms dominated by various, common species in the presence of sufficient silicate (Boyd *et al.* 2007). It is likely that the fate of the artificially stimulated blooms will be the same as that of natural diatom blooms: the bulk of the biomass will sink to great depths and a part will be buried in the sediments (Smetacek 1985, 1999b). Such *in situ* perturbation experiments provide the means to study the impact of intact 3P communities on phytoplankton, i.e. to test the hypotheses presented above (Assmy *et al.* 2007; Henjes *et al.* 2007a, b). Larger-scale and longer-term experiments will provide invaluable information on the impact of increasing production on the global carbon cycle (Smetacek and Naqvi 2008; Smetacek *et al.* 2012) but also on higher trophic levels (Smetacek 2008). They might also indicate whether diatoms can be harnessed to mitigate at least some of the harmful effects of global warming anticipated in this century, such as heat waves, the likes of which have not been experienced before. However, no matter how successful the technique, it can only be applied to the silicate-rich regions of the iron-limited oceans. The maximum amount of CO₂ that could be sequestered by this method is around 1 Gt per year (Coale *et al.* 2004), only a quarter of current accumulation rates; it is too little to provide a solution, but might also be too much to ignore.

The human imprint on the ocean has reached vast and deep proportions. The impacts range from ocean-wide decimation of top predators and commercial fish stocks to large-

scale deterioration of entire ecosystems as disparate as Arctic sea ice (due to melting), coral reefs (due to bleaching and acidification), fjords and estuaries (due to aquaculture, pollution and eutrophication). The biggest, long-term threat is sea level rise, which will, in the years to come, have devastating effects on human society and coastal ecosystems, i.e. unless we do something to avert it.

This is a time for bold new thinking regarding human use of the biosphere, in particular the oceans (Marra 2005). For instance, we need to develop new techniques of aquaculture based on organisms selectively bred contrary to the principles of the arms race: these would be the planktonic equivalent of vegetables, fodder plants and domesticated animals. The ‘vegetables’ and ‘fodder plants’ (fast-growing, nutritious phytoplankton) could be separated from wild grazers in large plastic enclosures and either used directly for human consumption or fed to ‘domesticated zooplankton’ that could in turn be fed to crustaceans, fish and squid. The doldrums of the subtropical gyres of the oceans would be ideal sites for such aquaculture farms established alongside artificial islands tethered to the sea floor. These could be submerged to avoid passing storms and nutrients could be obtained from deep water pumped to the surface with solar energy. This is just a vision but it could put to use the ocean’s deserts, which, in the form of subtropical gyres, cover a substantial area of the planet and abut the coasts of developing economies. Artificial iron fertilization could also be used to boost stocks of wild oceanic fish and squids in appropriate regions such as the subarctic Pacific or the northern half of the Southern Ocean, if the aforementioned experiments indicate that such an undertaking is feasible. Intensive, highly localized utilization of the ocean’s resources is the only way to take pressure off other regions so that they can recover from over-fishing. Indeed, there is an urgent need to establish large, protected regions of the ocean equivalent to the national parks on land but opposition from current users is, and will continue to be, formidable if alternatives are not offered. If humankind manages to successfully rise to the global challenges of this and coming centuries, future generations will be busy with atmospheric and ecosystem restoration; should we not be doing our best to lighten their burden?

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Corresponding editor: ROBERT M GREENBERG