# Combining evolutionary and ecological approaches to make sense of pelagic ecosystems from phytoplankton to whales


Victor Smetacek

Alfred Wegener Institute for Polar and Marine Research

Bremerhaven, Germany


Advanced School on Complexity, Adaptation and Emergence in Marine Ecosystems,

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My talk is divided into the following sections:

1) With what do we „make sense“?

To understand „understanding“ we need to examine the evolutionary biology underlying physics.

2) What could have selected the many intriguing shapes of plankton.

3) Why are copepods and krill the dominant marine zooplankton today.

4) Why are Antarctic krill stocks declining and can we do anything about it?

5) How much carbon could ocean iron fertilization sequester?

The common denominator in my talk is the application of in situ experiments to test specific hypotheses about the structure and functioning of marine pelagic ecosystems.

Proprioception: Is the sensory system that supports body posture and movement also the root of our understanding of physical laws?

The body and vestibular organs as our major sense organs.

# Making sense

## Proprioception: is the sensory system that supports body posture and movement also the root of our understanding of physical laws?

Victor Smetacek and Franz Mechsner

Aristotle argued that human beings have five senses at their disposal. Although various other sense organs have come to light since then, this antique dogma still constrains popular imagination. The term 'sixth sense' resonates with instinct and metaphysics, implying that although the five 'regular' senses represent reality adequately, there is something else lurking in the subconscious. The search for the sensory system with which the blind guide their movements revealed that the body's sense of posture and movement relies on different types of tiny receptors densely packed in the muscles and tendons. In 1906 Charles Sherrington coined the term proprioception (perception of one's own) for the sensory modality based on these receptors and called it our 'secret sixth sense'. But this concept of the body as a major sense organ has failed to arouse the interest it deserves.

Proprioception functions in much the same way as the conventional senses. Proprioceptors precisely measure physical properties, such as muscle length, tendon tension, joint angle or deep pressure. Signals from this sensory orchestra are sent by afferent nerves through the spinal cord to the somatosensory, motor and parietal cortices of the brain, where they continuously feed and update dynamic sensory-motor maps of the body. So proprioception provides information on the physics of the body, the momentary distribution and dynamics of masses, forces acting on the limbs and their highly nonlinear interactions. The maps derived from these complex calculations not only guide body movement, they also (together with touch) sense the size and shape of objects and measure the geometry of external space. Weight — one's own and that of objects — is measured independently by pressure sensors and muscular tension. So subjective body consciousness provided by myriad networking proprioceptors is the basis of objective knowledge of fundamental physical properties — space, time and weight — of external reality.

Our daily doings are coordinated and run by a trinity of independent sensory systems: proprioception, vision and the vestibular organs of the inner ear (which sense balance, momentum and guide the eyes). Their signals are so tightly integrated that it is impossible to unravel them through introspection, a view which seems to favour vision as the primary sense organ of the mind. But whereas in the congenitally blind other senses more or less compensate for the loss, a child born without proprioception would not know it had a body and would be physically and mentally retarded as a result.



Effortless grace? A body's fine-tuned actions belie inner complexities.

Selective loss of proprioception in adults is rare. In the case of Ian Waterman, a rare disease caused degeneration of sensory nerves relaying information from the body to the brain from the neck down, but spared the motor nerves conveying signals in the other direction. He could see, but not feel, where his body was or whether it was moving or not. At the age of 19, he was left a helpless 'rag doll', who had to be fed, washed and dressed — attempts at movement elicited only uncontrolled jerks. However, his strong will and memory of his body enabled him to learn to gradually control and guide his movements with his eyes. But even after 30 years of intense practice, the simplest movement has not been automated, but requires concentrated visual attention so strenuous that he likens it to a daily marathon, and in the dark he still collapses like a rag doll. His case, and a few others, demonstrate that all purposeful movements, both conscious and unconscious, are controlled by proprioception.

The proprioceptive system is so efficient and reliable at granting us the freedom of movement we expect from our bodies that we unconsciously relegate it to a subconscious, background realm of reflexes below the sphere of the five 'primary' senses. This attitude is unjustified. Most of our movements are indeed automated and run, as in animals, by the more basic and evolutionarily older parts of the brain. But we easily forget, for good reason, the intense conscious attention required to learn complex skills, such as writing, skiing or driving. Learning a skill implies developing new patterns of movement by screening, coordinating and calibrating relevant information from the orchestra of signals supplied to the neocortex by the trinity of sensory systems. New neural programmes are computed, memorized by repetition and transferred to the more fundamental regions of the brain, from where they are run with less effort and relayed much faster than from the seat of conscious awareness. So mastering a skill amounts to automating it.

Human proprioceptive ability is far superior to that of animals, reflected in the range, variety and precision of our automated skills, and manifest in the tools we make and what we achieve with them. Just as tools are extensions of the body, so basic scientific instruments — the balance, pendulum and measuring rod — are extensions of body sense. Evolution of these instruments, together with optical ones, launched the scientific exploration of space and time domains outside those of the body experience. Interestingly, the models of external space based on mathematical language made sense before their confirmation by precise measurements. From where else could these models have come, if not from the neural correlates of internal models of the physical laws of motion which run our bodies automatically? So the rules and laws of science were in place, and obeyed blindly, before they were rediscovered in the external world. In short, the neural correlates of physics and mathematics did not evolve *de novo*, but are rooted in our 'subconscious' body sense. ■

*Victor Smetacek is at the Alfred Wegener Institute for Polar and Marine Research, Am Handelshafen 12, D-27570 Bremerhaven, Germany.*
*Franz Mechsner is at the Institute for Occupational Physiology, Ardeystr. 67, D44139 Dortmund, and the Institute for Advanced Study, Delmenhorst, Germany.*

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Is the mind‘s balance, and hence its functioning, derived from that of the body?

Is there an innate sense of justice?

How did it develop and where are ist neural correlates?

Relationship between material and abstract worlds.



# Mind-grasping gravity

Victor Smetacek

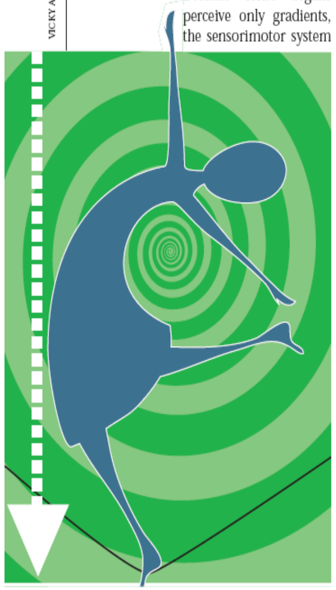
## Balance

*Is the mind's balance, and hence its functioning, derived from that of the body?*

Imagine yourself standing at the edge of a precipice, looking down at its foot, and then crouching at the same place on all fours. The difference between the two sensations is the difference between being human and being a quadruped. Clearly, latent anxiety is inherent in the precarious, human mode of bipedalism, which balances a vertical vertebral column on straight legs, with no tail for support.

Balance is so central to every activity, both of the body and the mind, that it is simply taken for granted. It is imbalance (disturbance, perturbation) that captures attention, be it fear of falling, the mental struggle to balance an equation, or the moral urge to right an injustice. As the concept of balance applies smoothly across the entire range of human endeavour, it would be parsimonious to assume a direct connection between the concrete and the abstract, on the basis of compatible neural hardware in the brain. Is the mind's balance, and hence its functioning, derived from that of the body?

Aristotle did not list balance as one of the explicit senses, although it is based on sensory organs. In contrast, Eastern philosophy is explicitly balance-based. Balance is to gravity as vision is to light, or hearing to sound; but whereas light and sound fields vary, Earth's gravitational field is constant. Because sense organs perceive only gradients, the sensorimotor system senses the gravitational field with great precision when the body moves.



VICKY ASKEW

Three independent organ systems enable the body to maintain balance. To experience how they interact with and compensate for each other, stand close to a wall, on one leg, with your arms dangling, and then shut your eyes; repeat the experiment but touch the wall lightly with a fingertip beforehand. Clearly, we rely on vestibular, visual and somatosensory systems to get our bearings in relation to gravity.

The vestibular organs of the inner ear sense gravity directly, but also as a deviation from the vertical and as self-motion. Balance and momentum signalled by this complex system are manifested in the body's centre of mass — the lower gut — as experienced on heaving ships and rollercoasters. These sensations can also be evoked, as in nightmares.

The eyes also sense and appreciate balance and mass. We enjoy watching dancers, athletes and acrobats (but also clowns), and the mass and symmetry of monumental buildings (or leaning towers) fill us with awe (or other emotions). Beauty, symmetry and balance evidently go hand in hand — there is more to the eye of the beholder than just vision.

The somatosensory system comprises a variety of receptors in the skin, muscles and skeleton which sense gravity as pressure and weight. Body awareness (proprioception) is part of this system. Although the arms are decoupled from locomotion, hand-held tools such as a cane (equivalent to touching the wall) or an acrobat's balancing rod significantly enhance the body's ability to balance.

Each sensory system provides independent, but integrated, coordinates for the body (including the hands) to orientate itself. Research on the vestibular cortex is in its infancy, but its multiple representation, its intimate interaction with visual and sensorimotor cortices and its right-hemispheric dominance distinguish it from other sensory systems. Recent studies indicate that the vestibular system is involved in self-perception and cognition. The human cerebellum, a central organ of balance and also of fine motor skills, contains five times as many neurons as the cerebrum but has received much less attention. Additional functions are only now coming to light.

As balance is central to every directed movement, evolving fine motor skills is synonymous with fine-tuning the sense of balance. Human evolution can be characterized as stages in differentiation and refinement of our balancing abilities. Our lineage first learned to balance bodies on feet, then tools in hands, and most recently, instruments and aircraft with eyes.

Refining balancing ability improved tool production and use, but also resulted in a form of perception that is linked to the hands and decoupled from the body. Whereas whole-body proprioception and personal viewpoint (the body's sense of balance) is subjective and private, the hands weighing different objects as the pans of a balance (say one big stone in the left, and two small ones in the right) create a demonstrable, verifiable quality (the balance between objects) that can be judged externally and objectively. With this 'disembodied' sense of balance, the principles of constancy and equivalence (the basis of common-sense logic) could be grasped, understood and communicated, in successive stages of evolution. Eventually, measuring rods, pendulums, levers and balances, which are mechanical projections of the body, could be transformed into abstract projections within the mind, unified by an innate understanding of gravity.

Just as there is a mind's eye and a mind's ear, there must also be a mind's gravity, based on each sensory system either on its own or in concert. This is the mind's space–time coordinating system, in which mass, balance and momentum — the substrates of science — are sensed. Archimedes, Newton and Einstein, among a host of others, have shown that there is more to insight than just vision or words.

The bipedal apes striding across the savannah with head held high evolved a very different proprioception and world view to their slouching cousins. Our ancestors dared to challenge gravity by standing up to it and we continue to do so, with our bodies and tools, minds and machines, balancing our way onwards and upwards, both literally and figuratively. ■

*Victor Smetacek is at the Alfred Wegener Institute for Polar and Marine Research, Am Handelshafen 12, 27570 Bremerhaven, Germany.*

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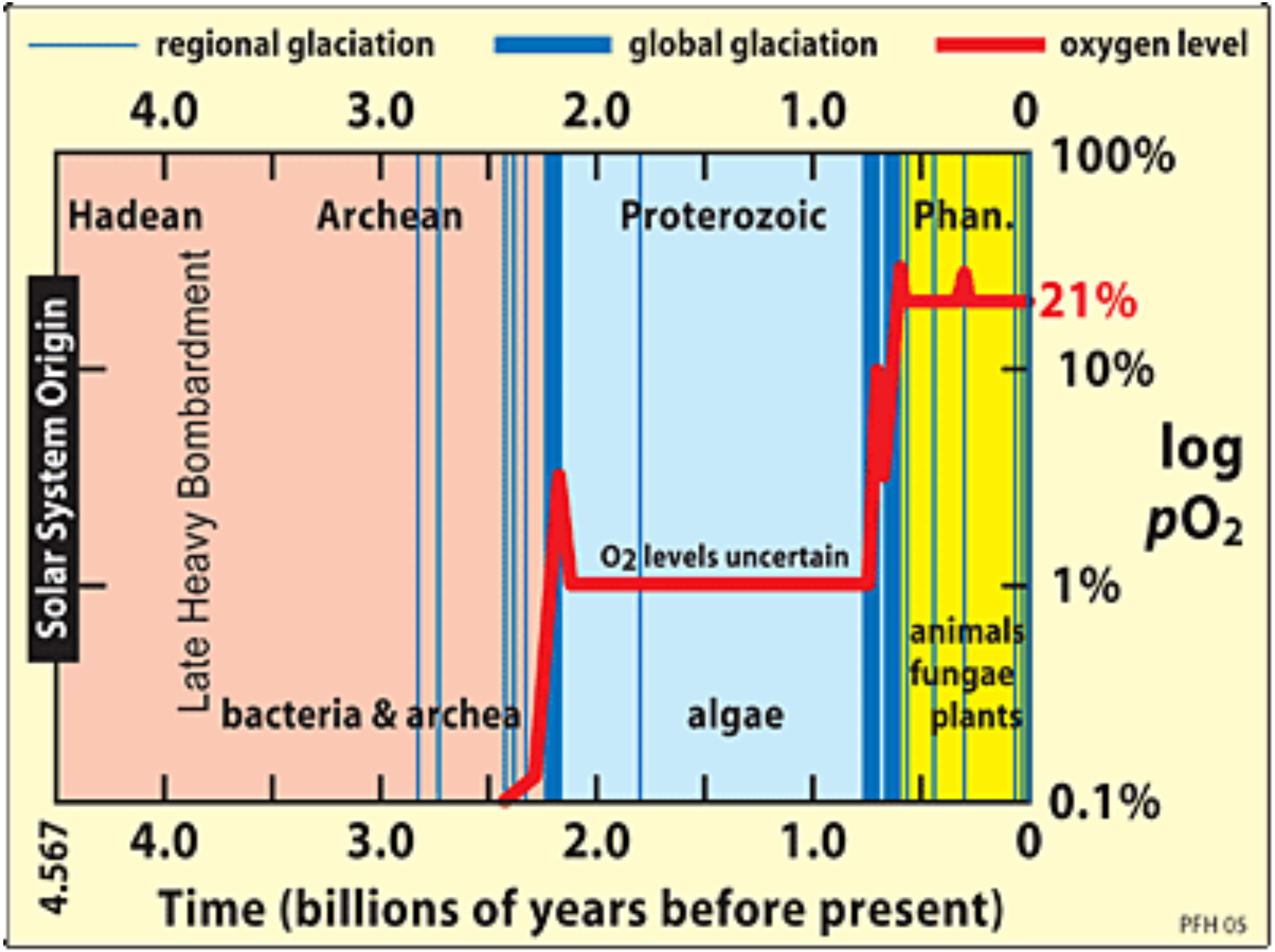
The earth is about 4.5 billion (10^9) years old

It has undergone dramatic shifts in climate in this period driven by changes in the composition of the atmosphere.

There have been periods of profound or moderate glaciations („snowball-earth phases“ and current glacial-interglacial cycles, respectively) interspersed with periods with virtually no ice on the planet (e.g. Mesozoic)

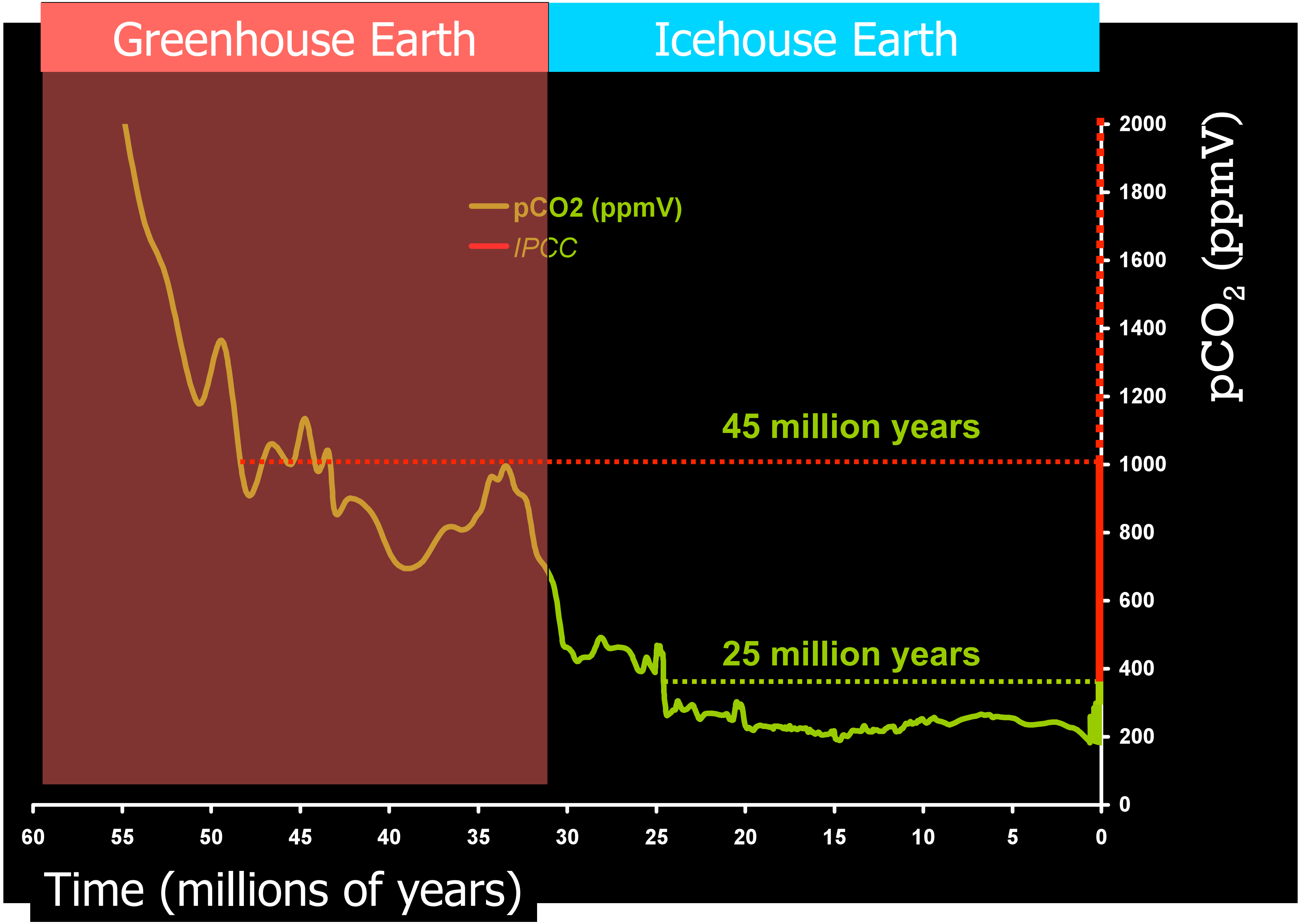
Cooling and warming of the earth is driven by feedback processes that operate on the earth‘s surface.

The timing can be set by processes outside the earth (planetary parameters) or underlying it‘s surface (plate tectonics).




http://www.snowballearth.org/

Courtesy: Henk Brinkhuis



Autotrophic organisms have changed the physics and chemistry of earth‘s surface drastically and continue to do so.

Their evolution is driven by natural selection which is essentially of 2 types:

1. Selection by the physico-chemical properties of the environment or „bottom-up selection“ whereby organism interactions are governed by competition for inorganic resources or light.

2. Selection by mortality due to grazers and predators, or „top-down selection“.

These two selection mechanisms are fundamentally different:

Bottom-up selection is according to fixed rules which constrain organisms within the bounds of physical and chemical „laws of nature“. These favour one or more „optimal solutions“ (e.g. shape of trees: palm trees and deciduous trees which have been reinvented many times). In phytoplankton, small (> 2µm) cells should be the most competitive but they contribute only marginally to biomass build-up.

Top-down selection is boundless, favours creativity and fosters diversity. Clearly, the „natural laws“ are obeyed but circumvented in various ways.

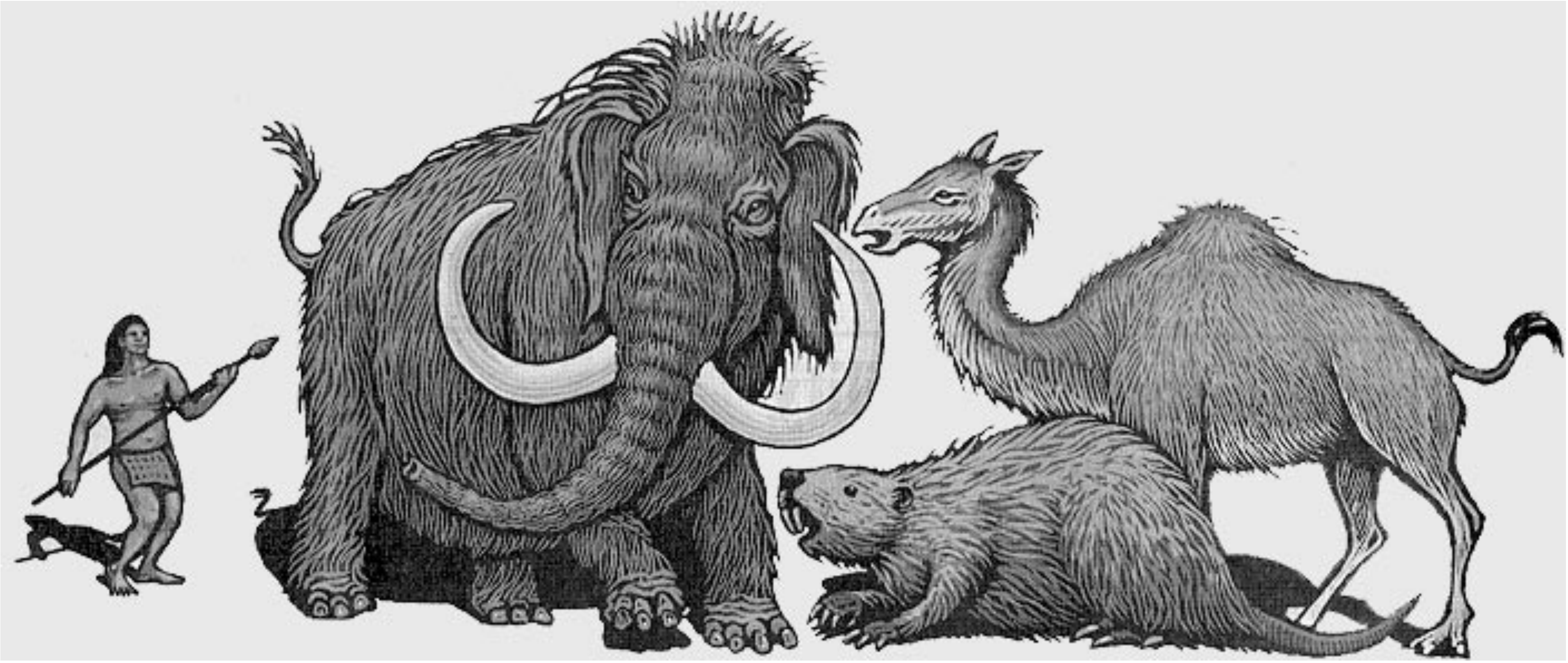
Evolution of animals is a case in point.



Tree ferns (top left), cycads (top) and palm tree (left) showing convergent morphology driven by bottom-up constraints

Form and function make sense here: selection of optimal solutions, because we are terrestrial organisms and live in a strong gravity field

Extinct Australian Megafauna



MAMMOTH LOSS— Animals such as mammoths, giant beavers and camels roamed the North American continent until about 10,000 years ago. What happened to them? Some scientists think human immigrants caused their extinction. WASHINGTON POST PHOTO

*Jeffrey Dorale*
*Department of Geosciences, The University of Iowa*

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# A mammoth murder mystery

**Twilight of the Mammoths: Ice Age Extinctions and the Rewilding of America**
by Paul S. Martin
University of California Press: 2005. 269 pp. $29.95, £18.95

**Alan B. Shabel**

M. LONG/NHMPL

Was climate change or hunting by humans to blame for the demise of large mammals in the Pleistocene?

In 1877, Richard Owen suggested that the great Pleistocene fossil mammals of Australia had been driven to extinction by "the hostile agency of man". Seven years later, C. S. Wilkinson replied that a reduction in rainfall, leading to the impoverishment of a once rich flora, was a more likely trigger for the loss of these beasts. And so it has always been in the study of late Quaternary extinctions: arguments for anthropogenic causes are countered by arguments in favour of climate change.

It is widely accepted that in the past 50,000 years, the world has lost a diverse array of reptiles, birds and mammals. A striking feature of this mass extinction event is that it disproportionately affected large-bodied vertebrates (more than 45 kg). With few exceptions, small vertebrates, plants and insects did not suffer dramatic losses. Another striking feature is the extinction event's geographic asynchrony: the extinctions occurred first in Australia (about 46,000 years ago) and much later in the Ameri-

wiped out the large vertebrates through direct predation pressure; although he acknowledges the potential role of less direct human influences, such as pathogen propagation and artificial fires, he focuses primarily on hunting. Second, he posits that the extinctions occurred extremely quickly; for example, he thinks the

of a widespread and biologically effective human population in the Americas before 13,000 years ago precisely because large, slow-moving, eminently huntable animals such as ground sloths continued to occupy their favorite dung caves in North and South America as late as they did." In other words, he takes the

All the major metabolic pathways, including oxygenic photosynthesis (Cyanobacteria), evolved in the Proterozoic under reducing conditions.

This is the phase of **chemical evolution w**hen physical and chemical properties of the environment dominated natural selection.

Organism interactions were simple and restricted to competition and protection against exoenzymes and (most probably) viruses. The latter is achieved by layers of slime and, possibly lipids.

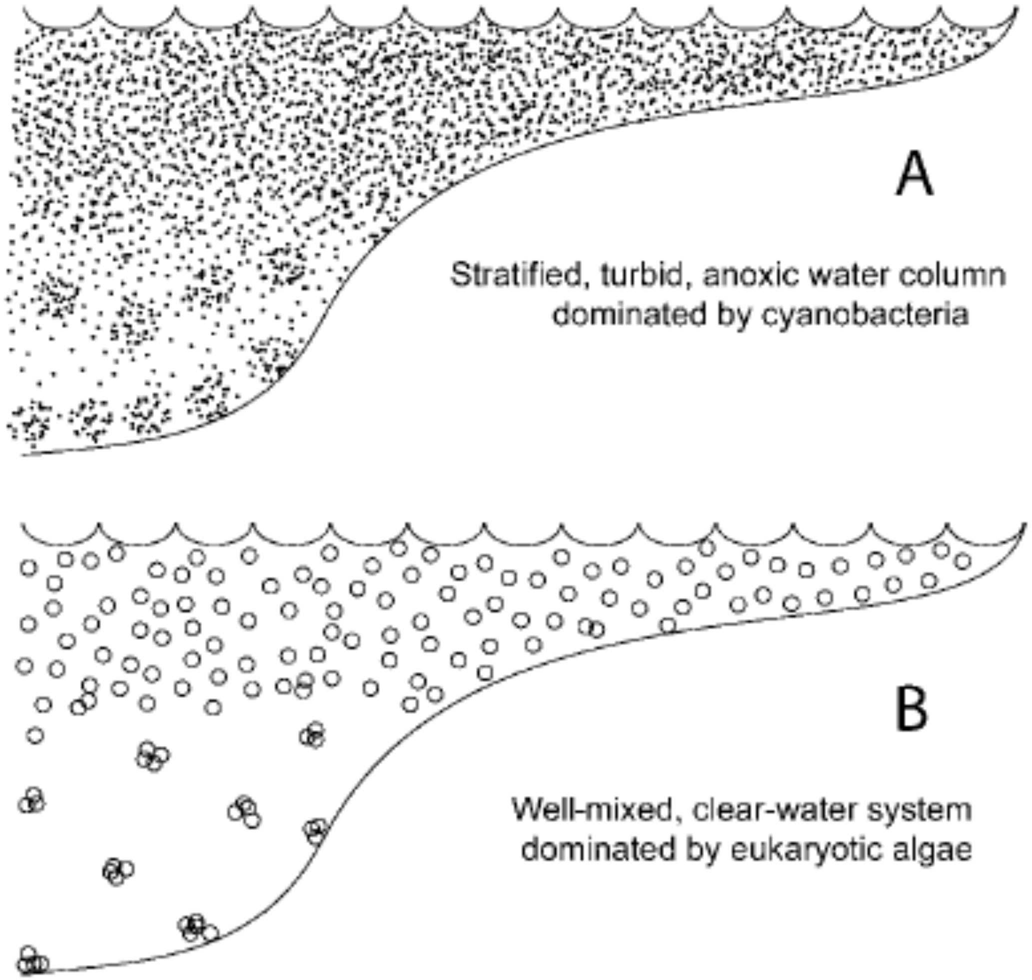
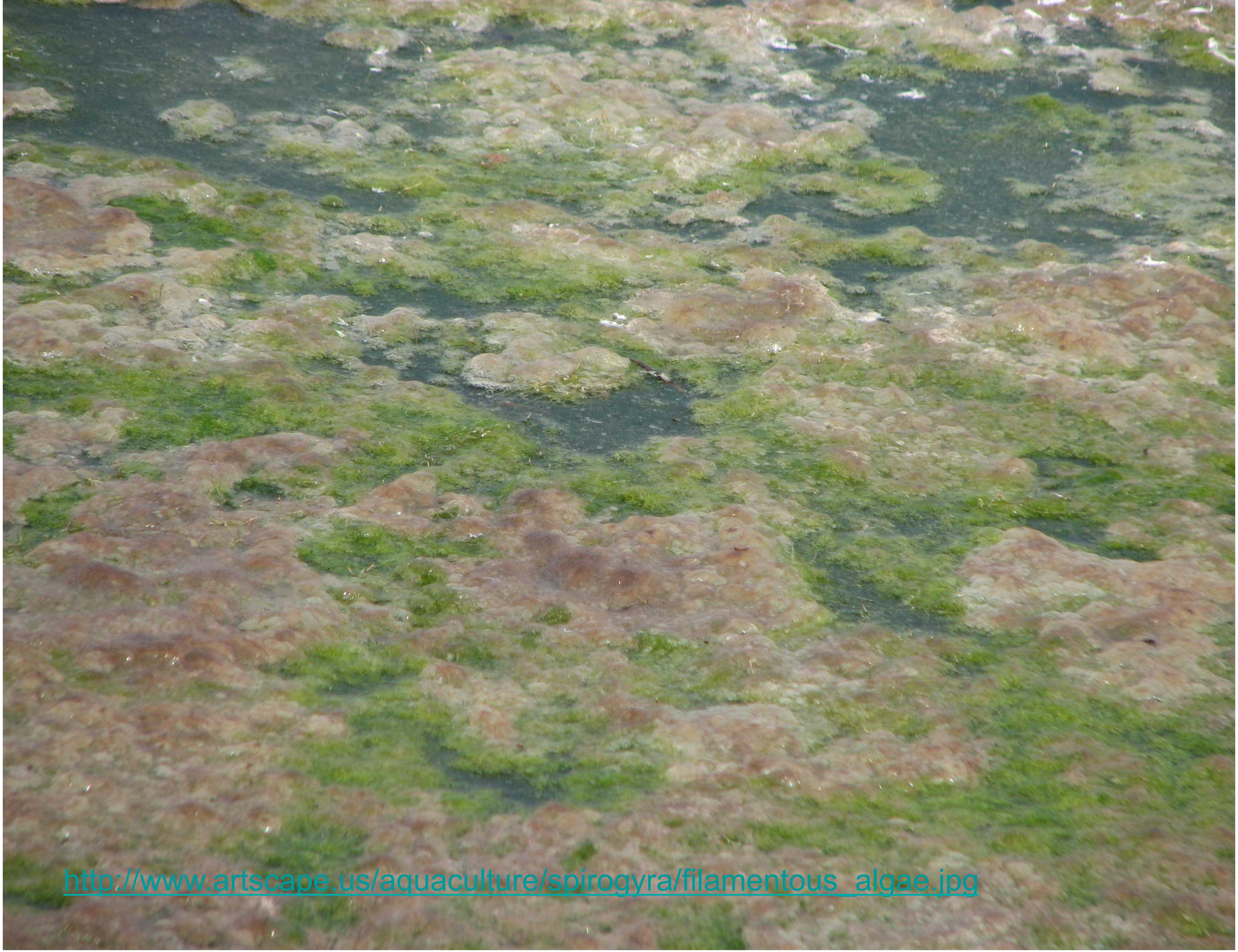



**Fig. 1** Schematic diagrams of two alternate stable states for the marine biological pump. (A) Dominance of shade-tolerant and shade-inducing cyanobacterial picoplankton in the absence of top-down selection for large net-phytoplankton, resulting in the stratified, anoxic/euxinic water column typical of pre-Cambrian oceans and Phanerozoic oceanic anoxic events. (B) Dominance of relatively large, export-prone eukaryotic net-phytoplankton in response to zooplankton grazing pressure, leading to increased light penetration and increased water-column ventilation.

N.J. Butterfield

Geobiology 7, 1-7 (2009)


http://www.artscape.us/aquaculture/spirogyra/filamentous_algae.jpg

Phagocytosis evolved only after the atmosphere had been sufficiently oxidised.

It facilitated endosymbiosis and hence the evolution of higher life forms (eukaryotes and later multicellular organisms) driven not only by tight coupling of endosymbiosis but also the looser relationships of co-evolution and ecosystem structure.

Bigger size improves defence ability (size escape), hence survival.

Since big cells of various shapes are responsible for most of the production, their lower growth rates must be balanced by lower mortality, i.e. they must be top-down selected.

Top-down selection is based on attack and defence systems. It is driven by the evolutionary arms race (Dawkins) or the „evolutionary olympics“. It initiated **mechanical evolution**: development of shape and later armour and the tools to crack them with.

The arms race had a profound effect on recent climate history at scales ranging from tens of millions of years (Cenozoic) to hundreds to thousands of years (transitions from glacial to interglacial stages).

# Individual and population

- The unit of natural selection in evolution is the individual organism.
- This is easily identified in metazoa and metaphytes because dividing cells stay together. The cells in a multicellular organism are attached, differentiated, organised in functional units that maintain integrity of the organism.
- Dividing cells of a unicellular organism, however, separate from one another and tend not to be differentiated. Nevertheless, all the cells emanating via vegetative division from a zygote belong to one clone hence represent one individual that is diffuse: The individual in unicellular organisms is a cloud.
- Individual cells can be sacrificed, like leaves of a plant, to maintain survival of the organism, whether a cloud of leaves, or a cloud of plankton cells.

Eukaryotes evolved from prokaryotes through endosymbiosis most probably via phagocytosis.

Phagotrophy became possible by increasing atmospheric oxygen levels emanating from prokaryote (cyanobacterial) photosynthesis.

Early eukaryotes engulfed cyanobacteria giving rise to chloroplasts, hence algae from which land plants evolved subsequently.

So far, attention has focussed on the endosymbiont. The exosymbiont („host cell“) has been neglected.

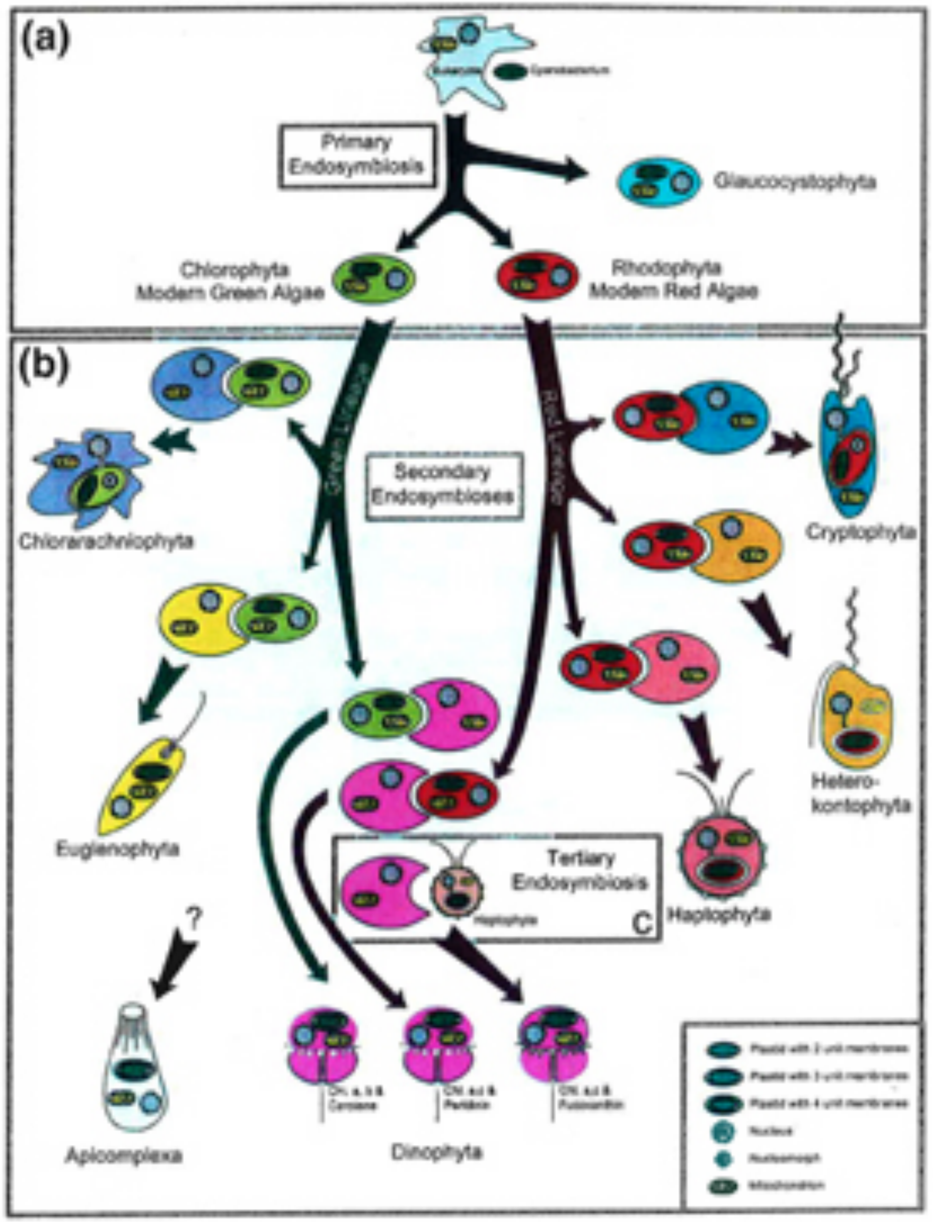
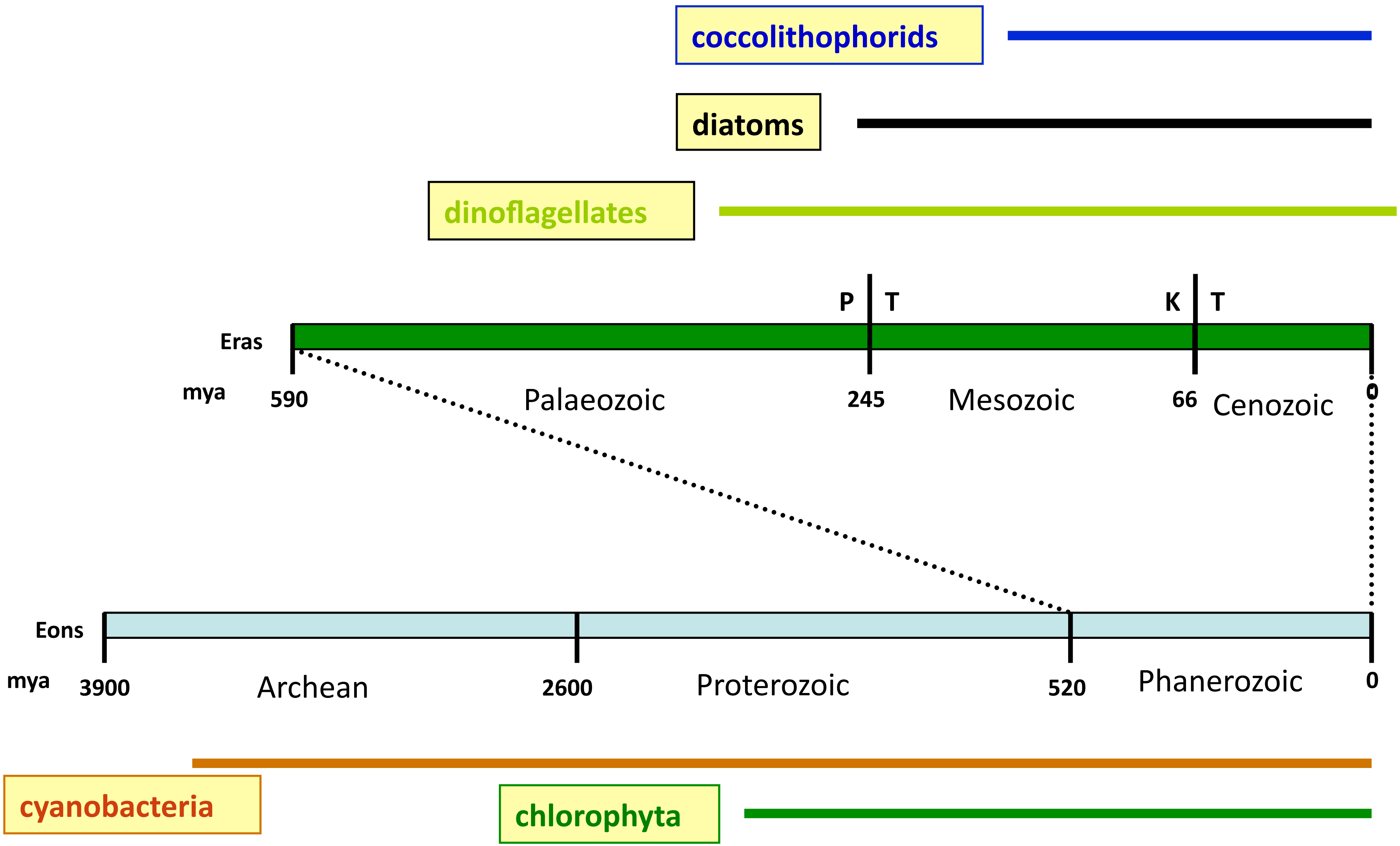



**Plate 12.1.** The basic pathway leading the evolution of eucaryotic algae. The primary symbiosis of a cyanobacterium with an apoplastidic host gave rise to both Chlorophyte algae and red algae. The Chlorophyte line, through secondary symbioses, gave rise to the 'green' line of algae, one division of which was the predecessor of all higher plants. Secondary symbioses in the red line with various host cells gave rise to all the chromophytes, including diatoms, cryptophytes and haptophytes. (From Delwiche, 2000 with permission.)

# Once upon a time........



Plankton evolution is ruled by protection and not competition. The many shapes of plankton reflect defence responses to specific attack systems ranging from pathogens, parasitoids to predators.



# A watery arms race

Victor Smetacek

## Plankton

*"Planktonic evolution is ruled by protection and not competition. The many shapes of plankton reflect defence responses to specific attack systems."*

Imagine yourself in a light forest looking upwards, seeing in your mind's eye only the chlorophyll-bearing cells of the canopy floating in mid-air, free from the attachment of leaves, twigs, branches and trunks. Now forget the forest and the trees, and see only blurred clouds of tiny green cells obscuring the blue sky beyond. You are looking at a phytoplankton bloom of a density typical of lakes and coastal oceans. Forests and algal blooms fix about the same amount of carbon — a few grams per square metre per day — because both are based on essentially the same photosynthetic machinery, fuelled by chlorophyll *a* in chloroplasts, the descendants of free-living cyanobacteria that have since evolved into plant organelles by endosymbiosis.

Chloroplasts provide their host cells with food in return for resources and protection. The land was colonized by one type of chloroplast/host cell, and the evolution of its various life-supporting systems is, from a human perspective, a straightforward success story: from algal slime to tropical rainforest. Indeed, the sole function of land plants, as considered in the thought experiment above, is to provide the chloroplasts with water and nutrients and give them access to light.

MICROFIELD SCIENTIFIC/SPL

Safe: diversity in plankton has its roots in defence.

Competition for resources and resource space has shaped the evolution of form and function in terrestrial vegetation. Can one apply the same evolutionary criteria to the other main plant life-form on our planet — the free-floating plankton of the pelagic realm? The phytoplankton bloom is suspended in a soup of resources, circulated by the wind within the sunlit surface layer. Its chloroplasts are provisioned by this viscous medium and do not require life-supporting hosts. Moreover, a striking feature of pelagic systems is the recurrent pattern of annual species succession. This is different from succession in land plants because the various stages, dominated by characteristic phytoplankton species, last for only a few weeks. There may be competition between species at the same stage for light and nutrients, but hardly at all between species of different stages. Apparently, space-holding plankton has not evolved.

So what other forces shape plankton cells, and are they the same as those that drive succession? Photosynthesis in plankton is spread across about ten different divisions, as separate from one another as land plants are from animals. Many of the lineages have species that function as algae ('plants') or as ingestors of particles ('animals'); many species do both. Generally, species with chloroplasts look no different to their relatives without them — cell shape does not reflect the mode of nutrition. Properties of the host cell, including shape, must do more than improve the photosynthetic efficiency of chloroplasts. Indeed, the enormous diversity of lineages and shapes present in unicellular plankton has defied explanation.

Although adoption by a host must have imposed many changes on the chloroplast, one main function of host cells is to protect chloroplasts against attack. The many mechanical and chemical defence systems evolved by land plants have elicited an equally heterogeneous arsenal of attack systems among their enemies, ranging from viruses to fungi, insects to elephants. Defence systems need to be deployed at the level of the leaf and are therefore not reflected in gross morphology, but they can be expensive. Hence there are fast-growing and slow-growing plants, all fuelled by chloroplasts, but differing in the degree of investment in defence.

The range of defence systems in plankton is only now coming to light. The size range of phytoplankton spans three orders of magnitude, but that of its predators spans five orders, from micron-scale flagellates to shrimp-sized krill. Pathogens (viruses and bacteria) pose a further challenge. Most predators and pathogens feed or infect selectively. Smaller predators hunt individual cells, whereas larger ones use feeding currents, mucous nets or elaborate filters to collect them *en masse*. Captured cells are pierced, ingested, engulfed or crushed, but have evolved specific defence measures. They can escape by swimming or by mechanical protection; mineral or tough organic cell walls ward off piercers or crushers. In adapting to deterring predators, cells have increased in size, formed large chains and colonies, or grown spines. Noxious chemicals also provide defence.

Obviously, none of these defence mechanisms conferred by host cells provides universal protection to chloroplasts. Most phytoplankton cells are eventually eaten or succumb to pathogens. Rapid fluctuation in population size favours survival fitness, more cycles and hence more adaptation to attack. If the carbon fixed by planktonic chloroplasts is invested mainly in this biological 'arms race', then planktonic evolution is ruled by protection and not by competition. The many different shapes and life cycles reflect responses to specific attack systems.

Suppose that competition for light rather than protection were the driving force in shaping pelagic ecosystems. Faced with a single, optimal solution, algae could well have evolved more efficient photosynthetic machinery. Improved energy use would favour production of hydrocarbons as both a buoyancy aid and a reserve substance. The ocean surface would then be covered with oily scum that would, as well as changing the planetary heat budget, severely reduce evaporation and hence rainfall on the continents, where life as we know it could not then have evolved. Luckily for us, this did not happen, and we have our blue, white and brown planet with its smudges of green, instead of dark green (or even black) oceans and bare, brown continents. ■

*Victor Smetacek is at the Alfred Wegener Institute for Polar and Marine Research, Am Handelshafen 12, 27570 Bremerhaven, Germany.*

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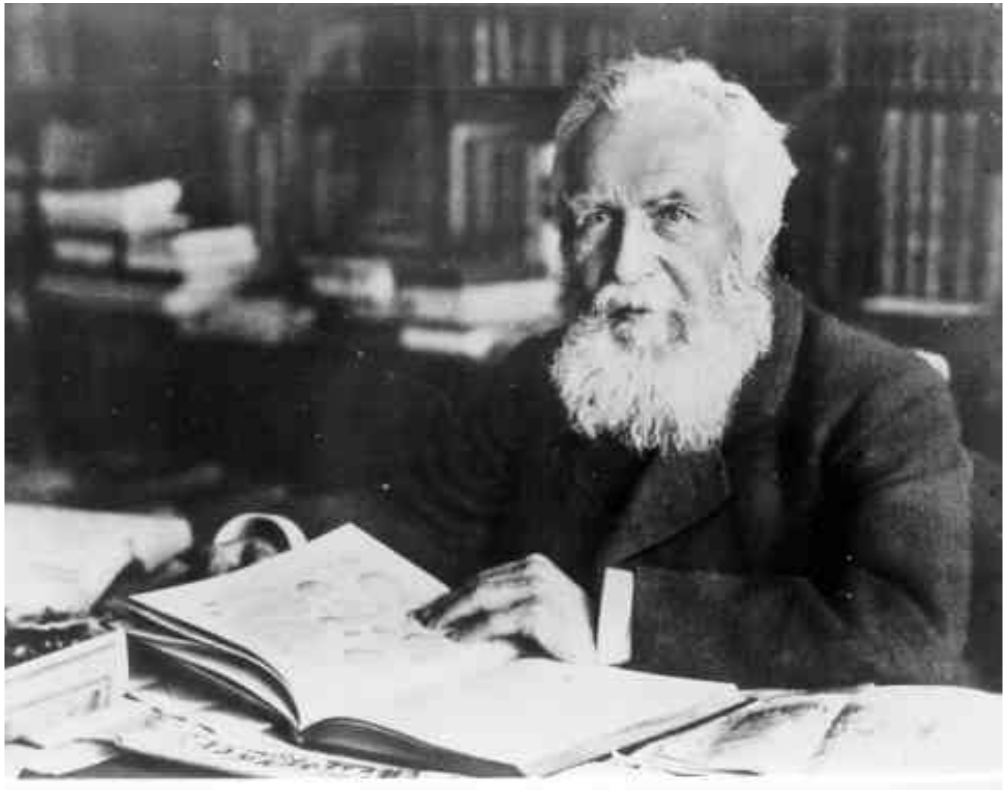


Ernst Haeckel (1834 – 1919) Professor at the University of Jena, Germany

Victor Hensen (1835 – 1924)

Professor at University of Kiel,Germany

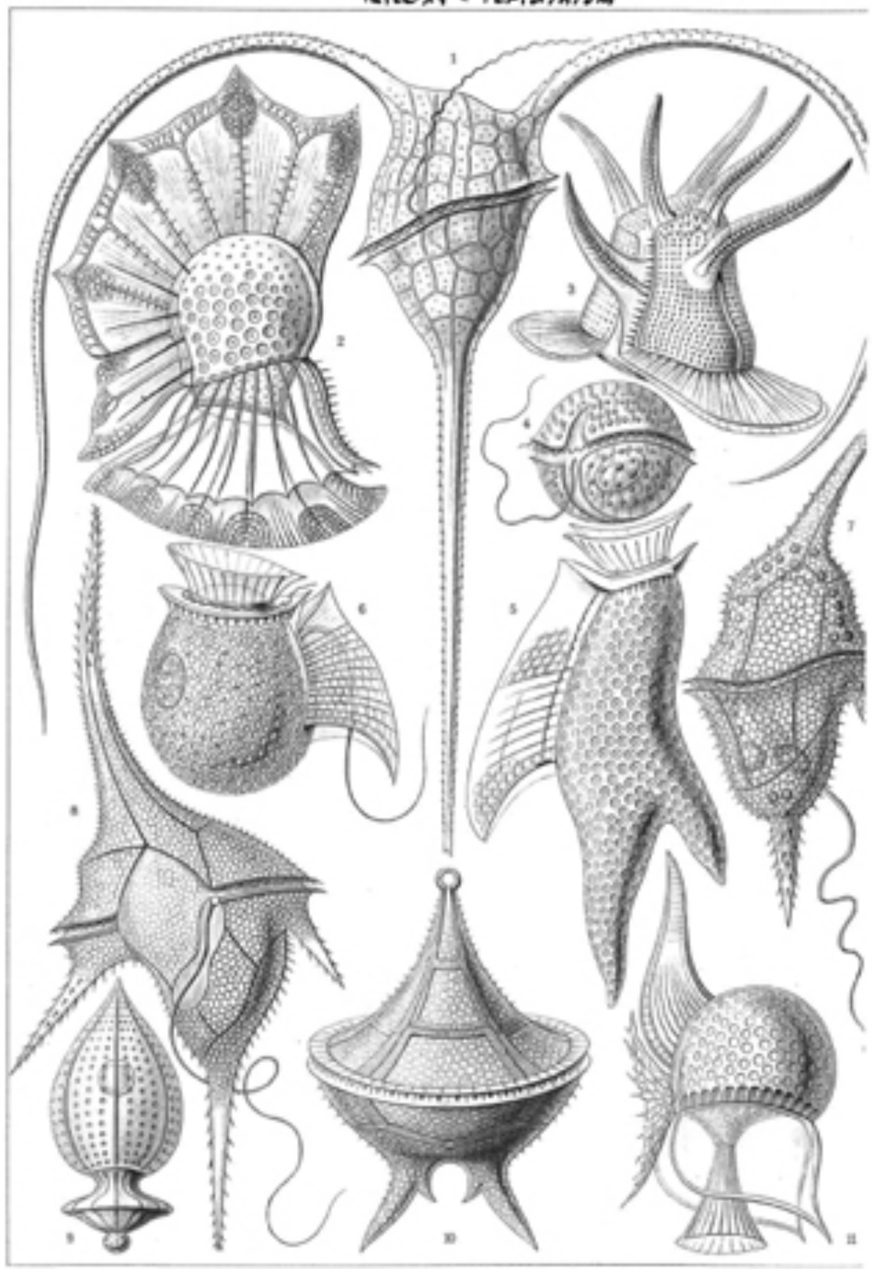
From Wikipedia, Feb. 2007

Dinoflagellates drawn by Haeckel

What is the function of these forms?

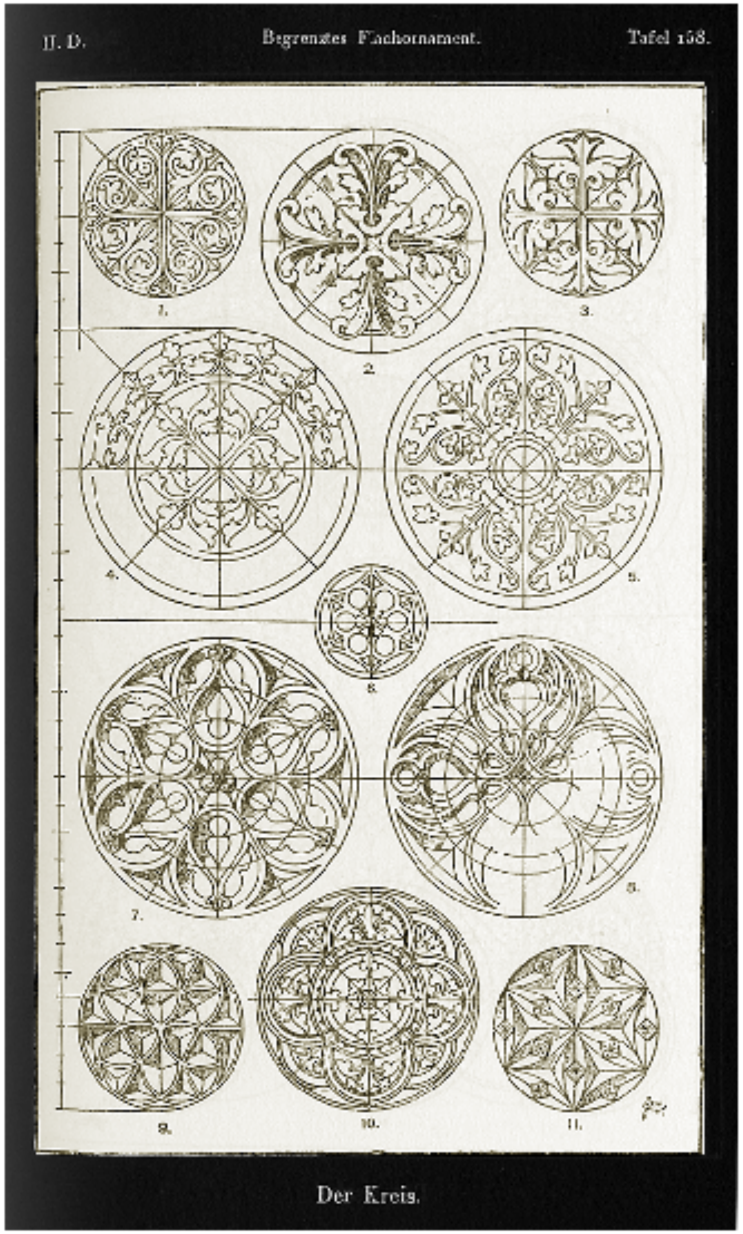
Shape does not determine whether an organism is photoauto- or phagotrophic.

Tafel XV - Peridinium



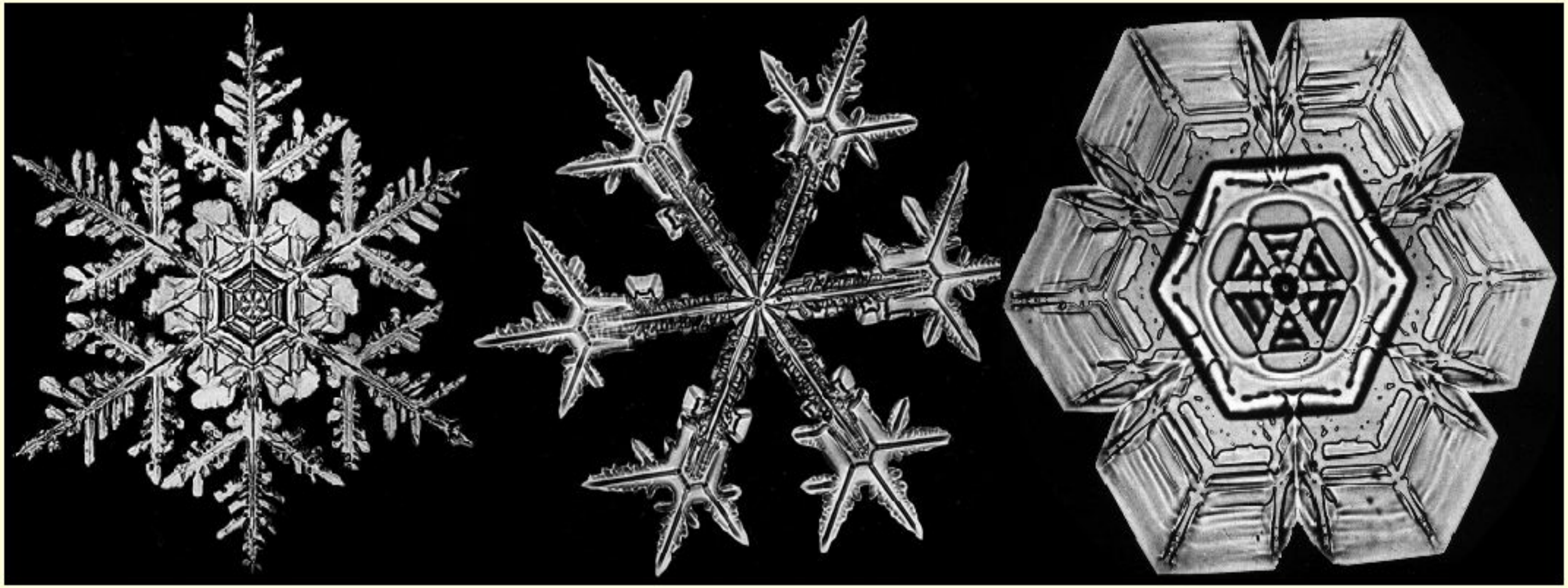
Peridinea. Geißelhütchen.

***Links***: Meyer, F.S. (Ed.) (1888). “Handbuch der Ornamentik : zum Gebrauche für Musterzeichner, Architekten, Schulen und Gewerbetreibende sowie zum Studium im Allgemeinen.” Seemann, Leipzig, 615 pp.  ***Rechts***: Haeckel (1904) Kieselalgen




Haeckel believed that plankton morphology arose according to the same inherent principles as these ice crystals: organic crystallography.

A coherent explanation for plankton morphology has yet to be formulated.

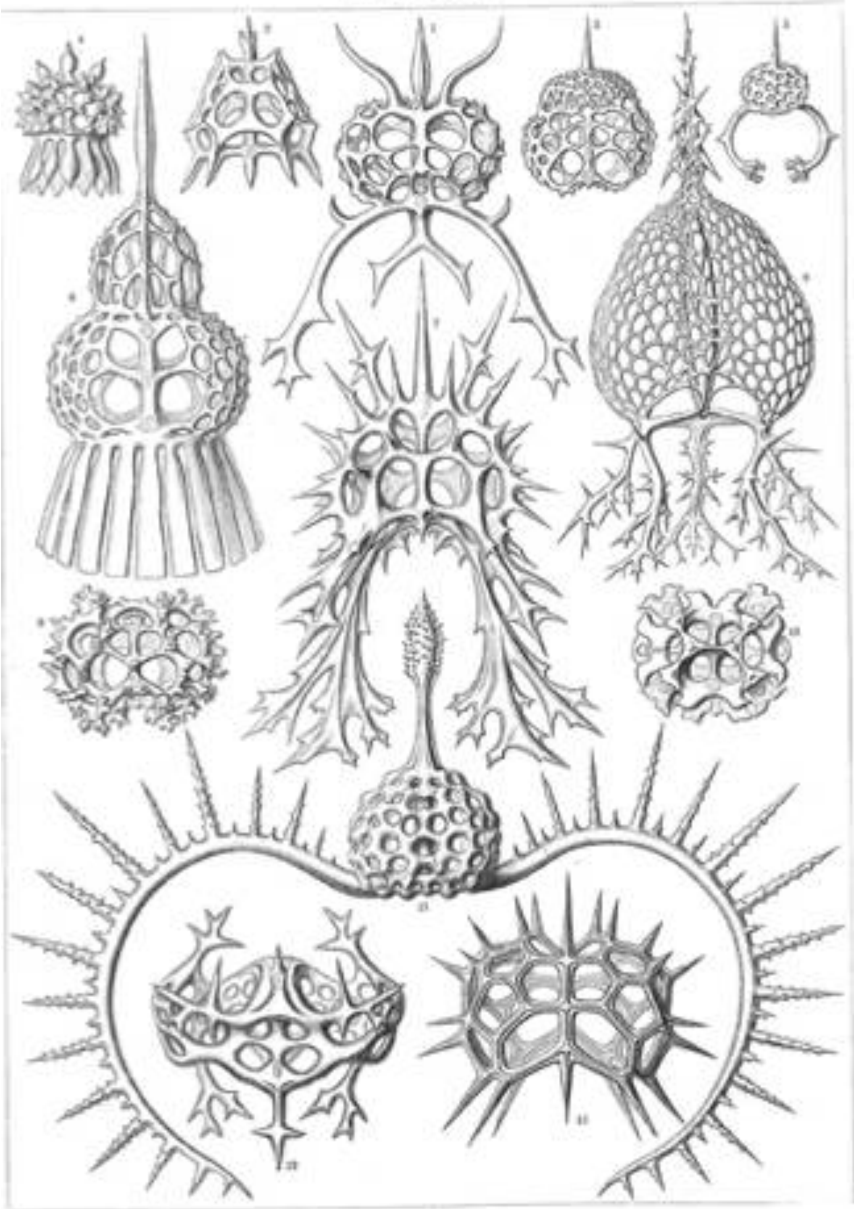


Bentley & Humphreys (1931) *Snow crystals*

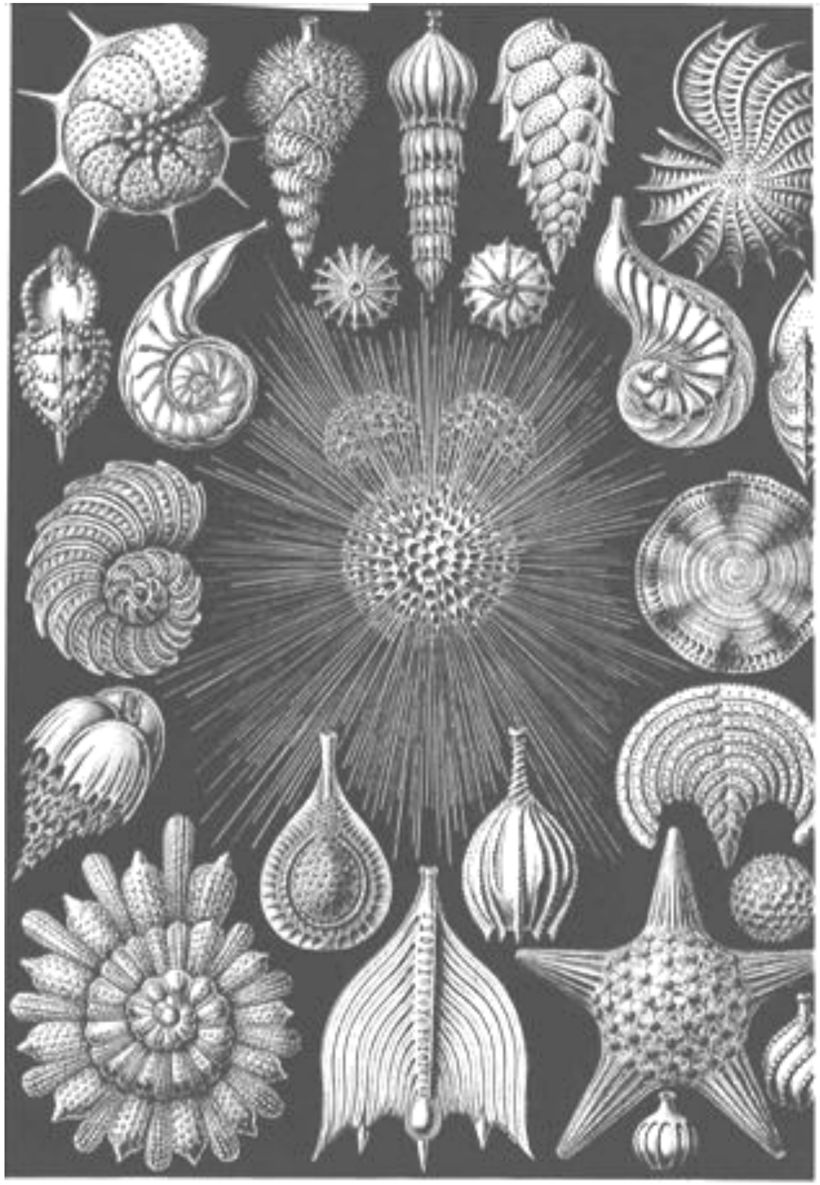
Ernst Haeckel, Kunstformen der Natur (1904)

Radiolaria shapes are baffling

But what about Foraminifera?
What do they remind us of?



Spyroidea. Nüßchenstrahlinge.



Thalamophora. Kammerlinge.

Drawing of plankton of Kiel Fjord by Hans Lohmann in 1908 to illustrate the importance of his discovery of „nannoplankton“.

The organisms are all drawn at the same scale and demonstrate the size differences between one of the smallest 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.

The adult copepod Oithona is about 1 mm long.

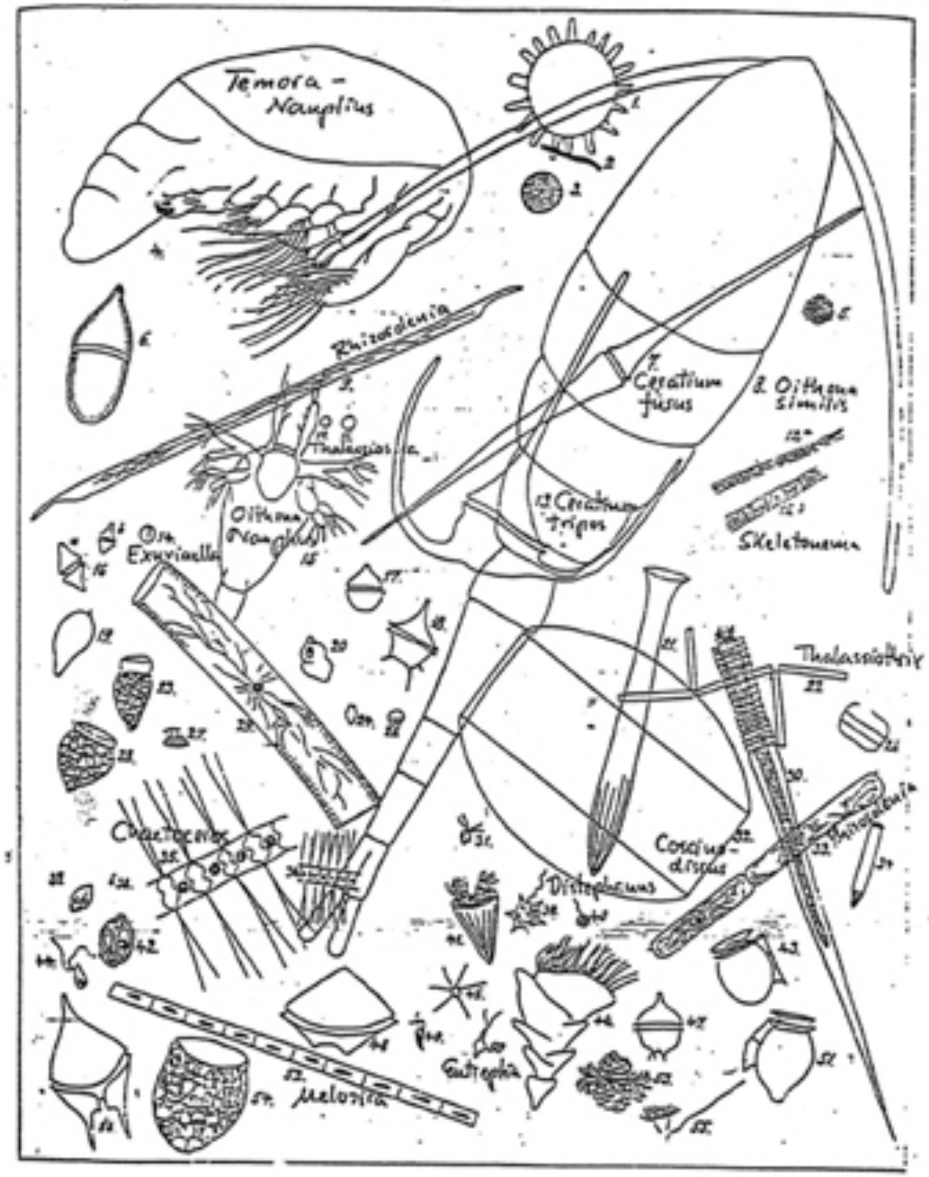
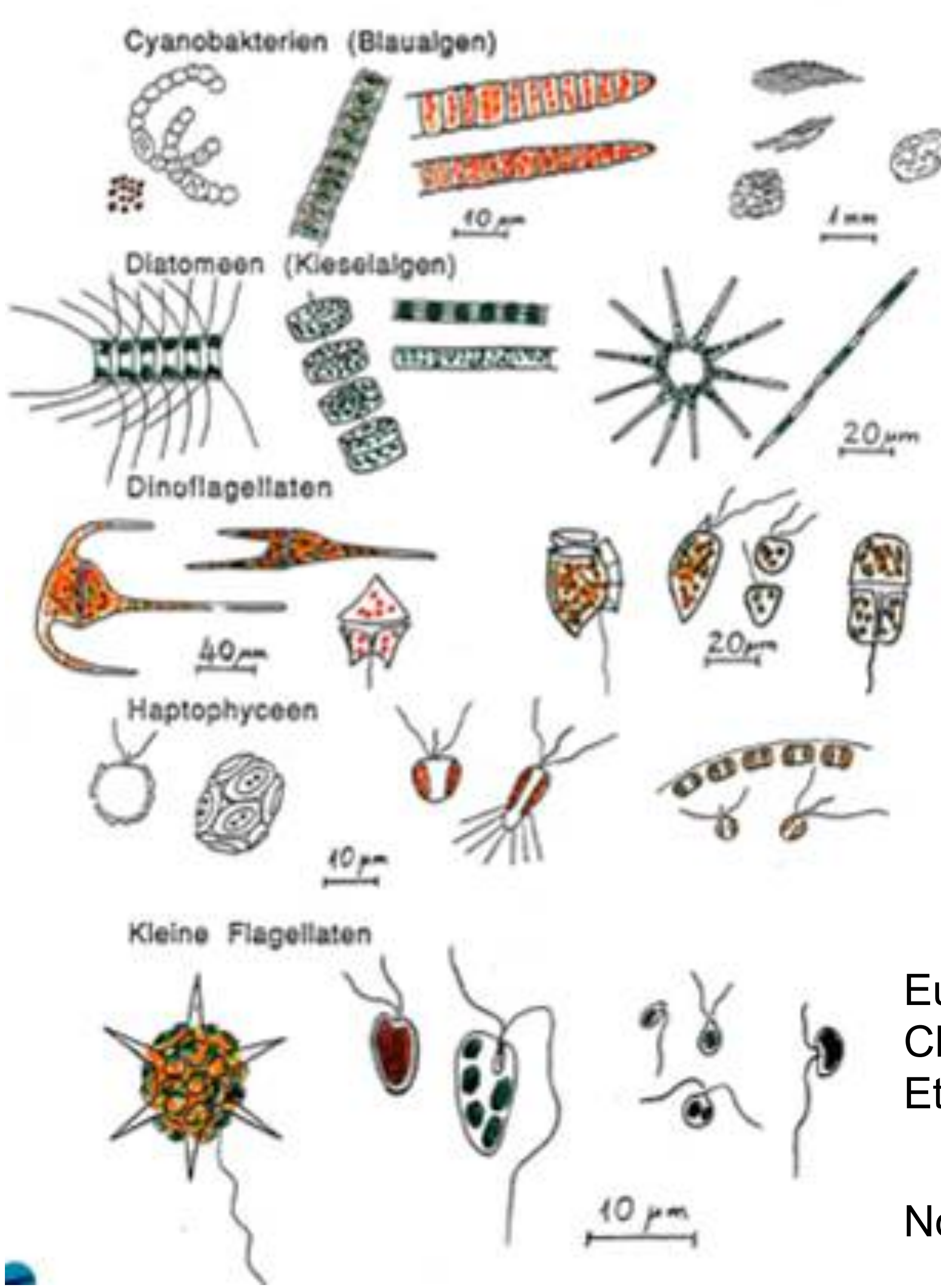



Abb. 25: Auswahl einer Reihe von Plankton-Organismen von Laboe, sämtlich bei 250facher Vergrößerung gezeichnet, um das gegenseitige Größenverhältnis zu zeigen (LOHMANN, 1908, S. 201).

Common genera of coastal phytoplankton




Colonial cyanobacteria, *Anabaena, Nostoc*

*Trichodesmium*, various colonies

Bloom-forming diatoms, *Chaetoceros, Thalassiosira*

*Skeletonema, Pseudo-nitzschia*

Bloom-forming dinoflagellates, *Ceratium* spp.

*Prorocentrum, Gymnodinium*

Coccolithophorids

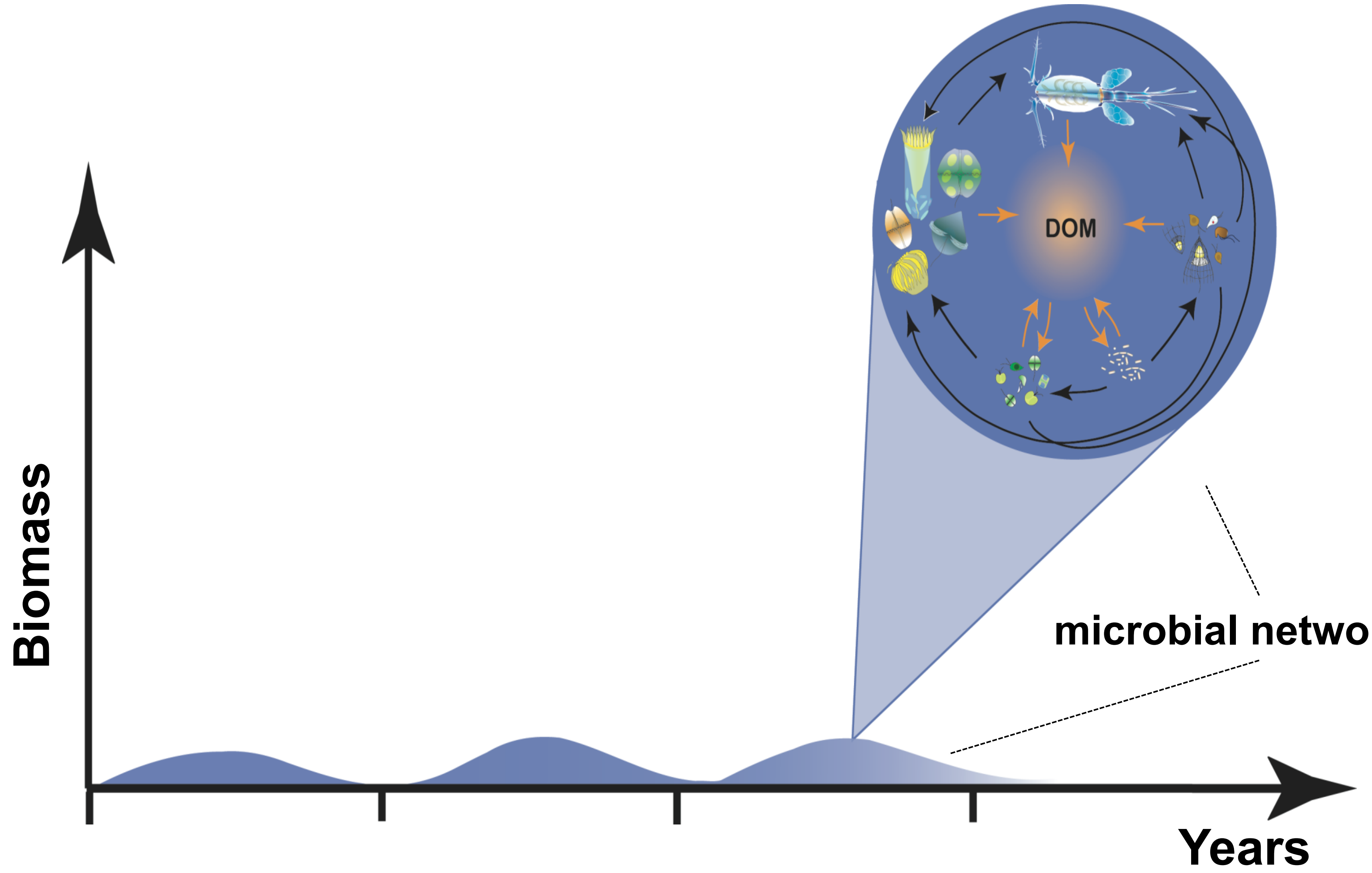
*Phaeocystis*

Nanoflagellates
Chrysophytes
Cryptophytes

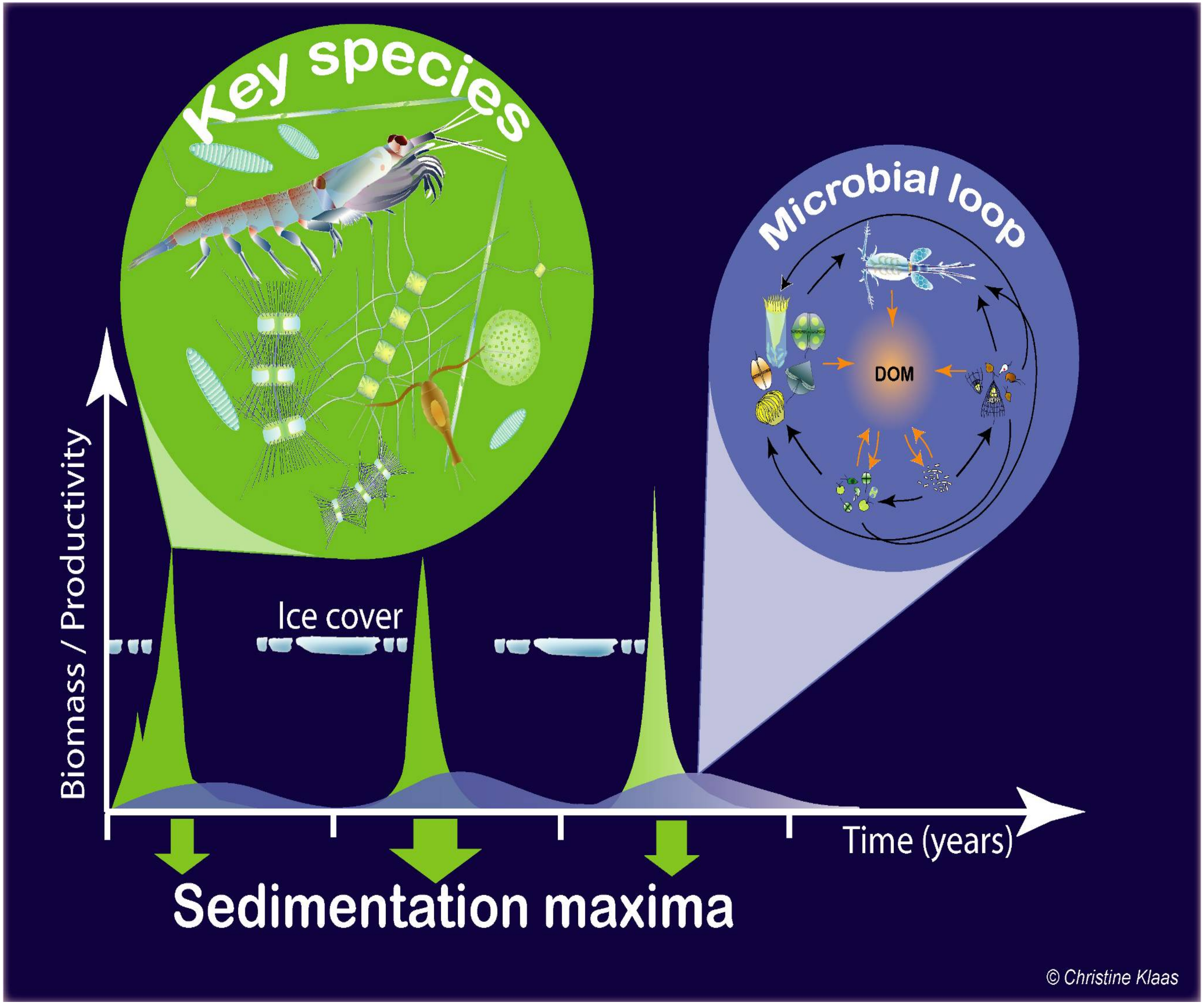
Euglenophytes,
Chlorophytes
Etc.

Note different scale bars

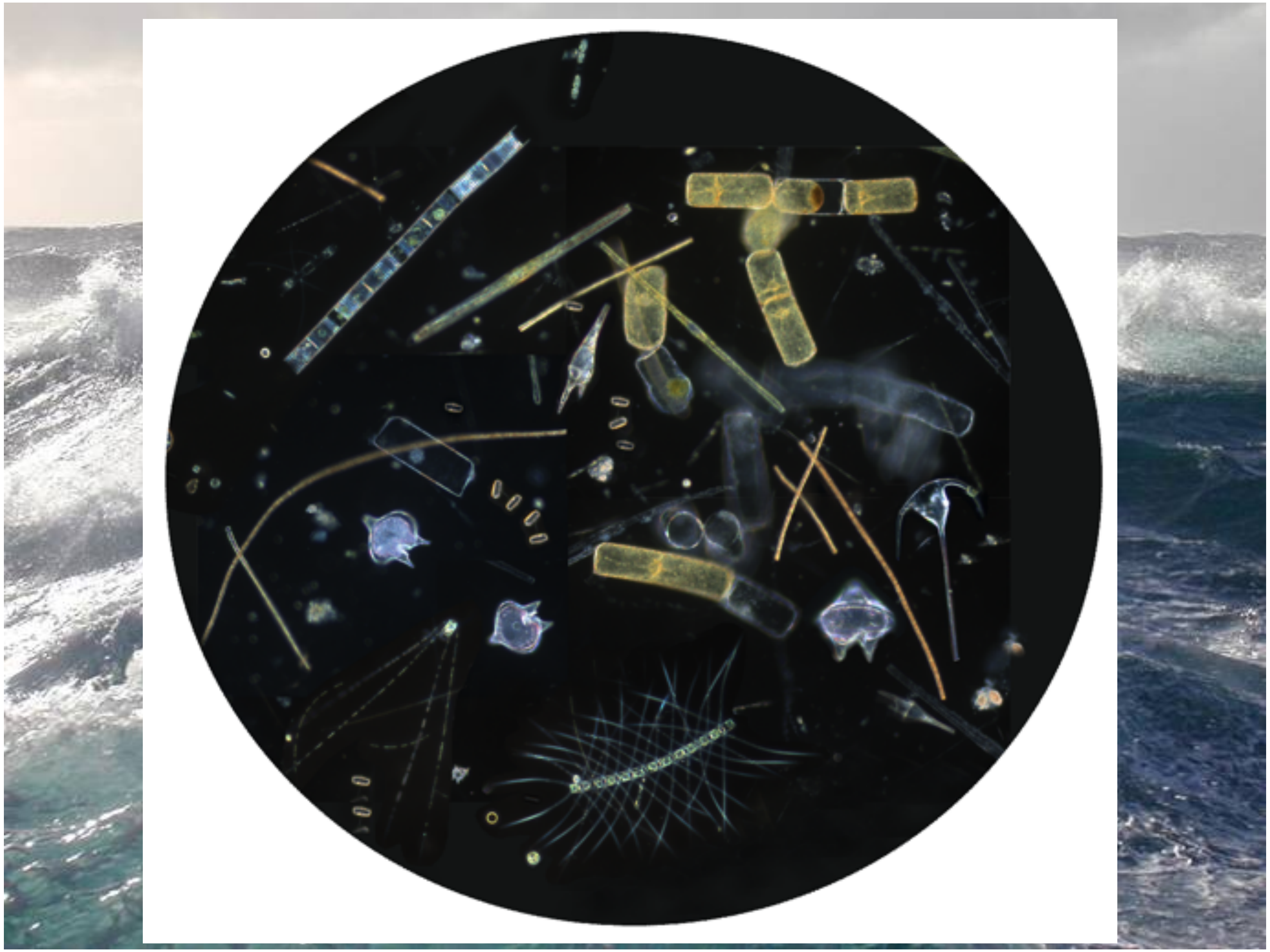
# Seasonal plankton cycle

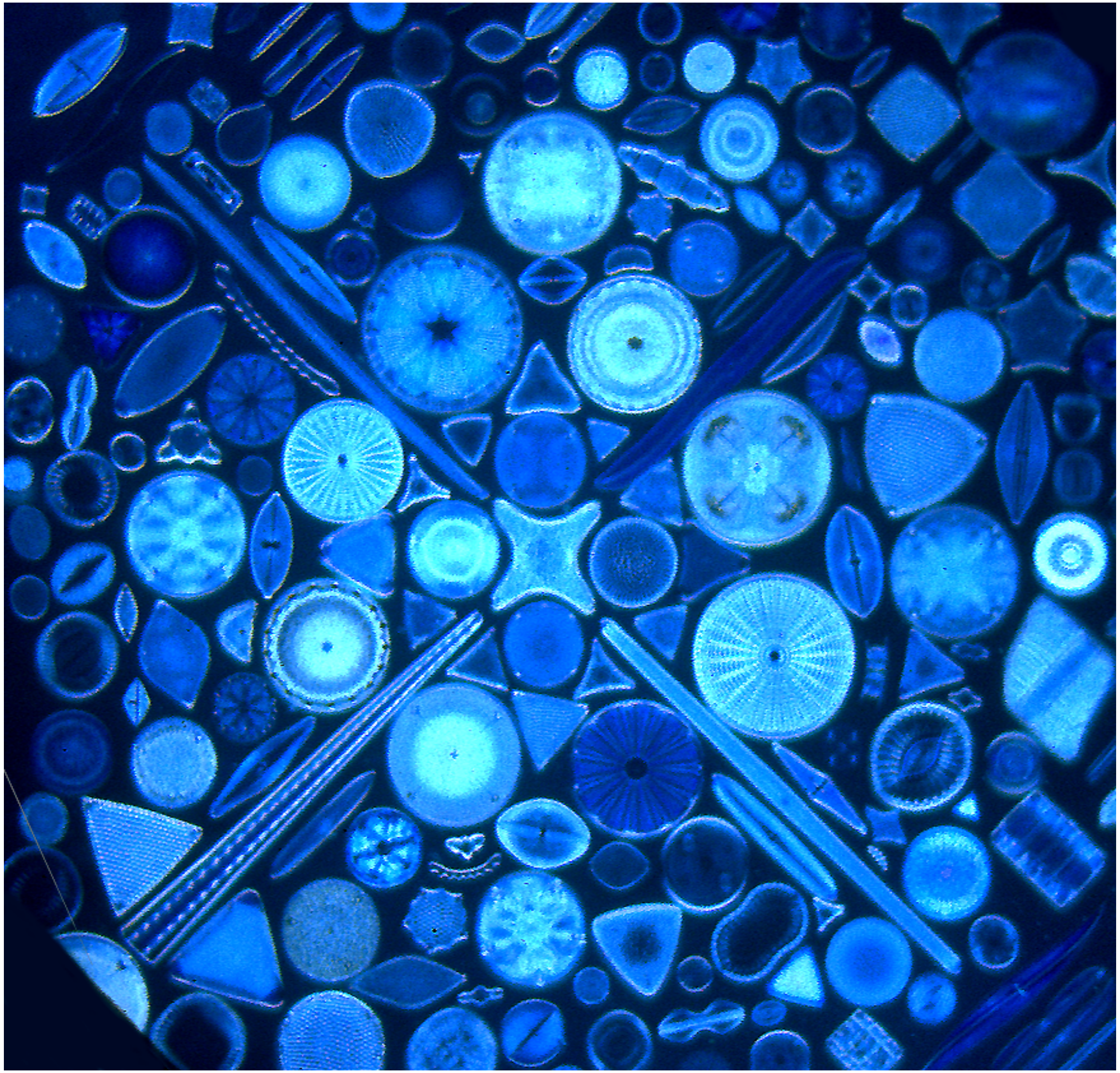



C. Klaas redrawn from
Smetacek et al. 1990


Key species
Microbial loop
DOM
Biomass / Productivity
Ice cover
Time (years)
Sedimentation maxima
© Christine Klaas

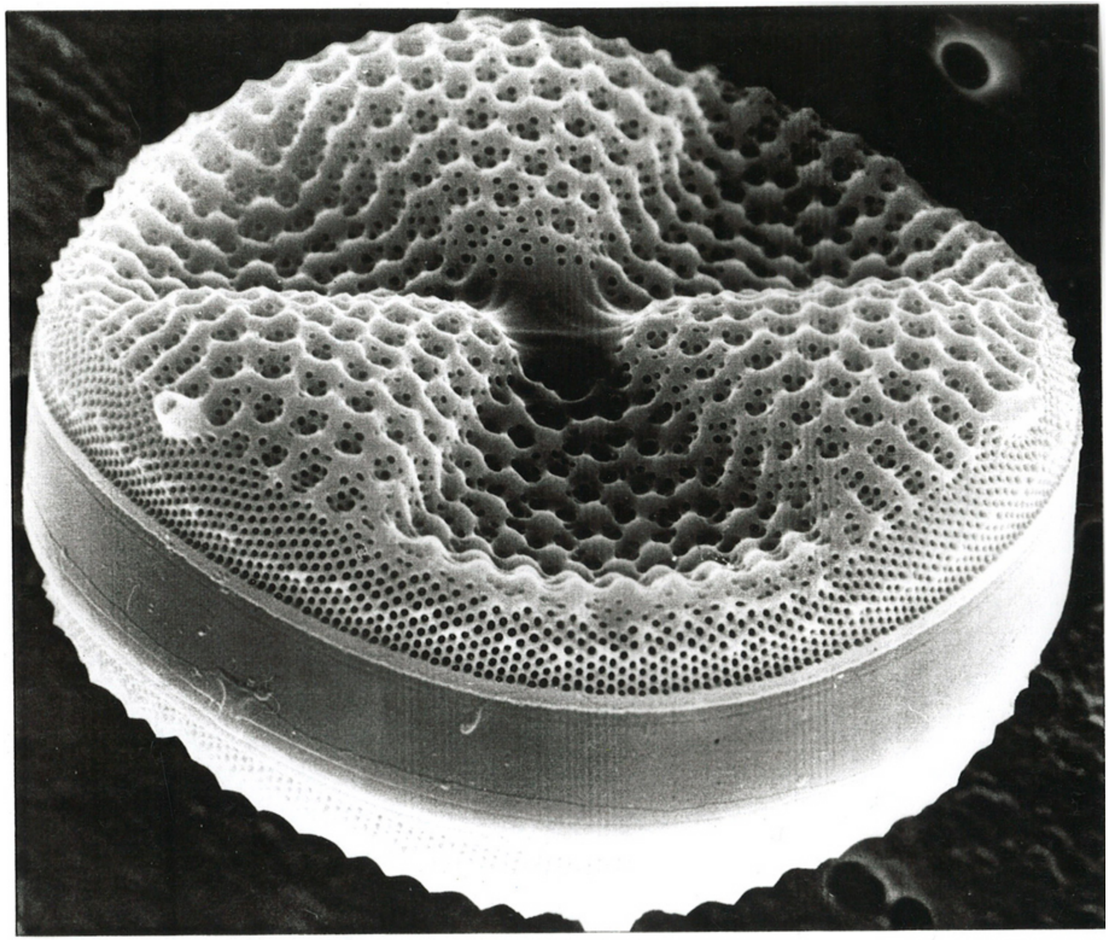
# Modern phytoplankton blooms are dominated by diatoms. Why?



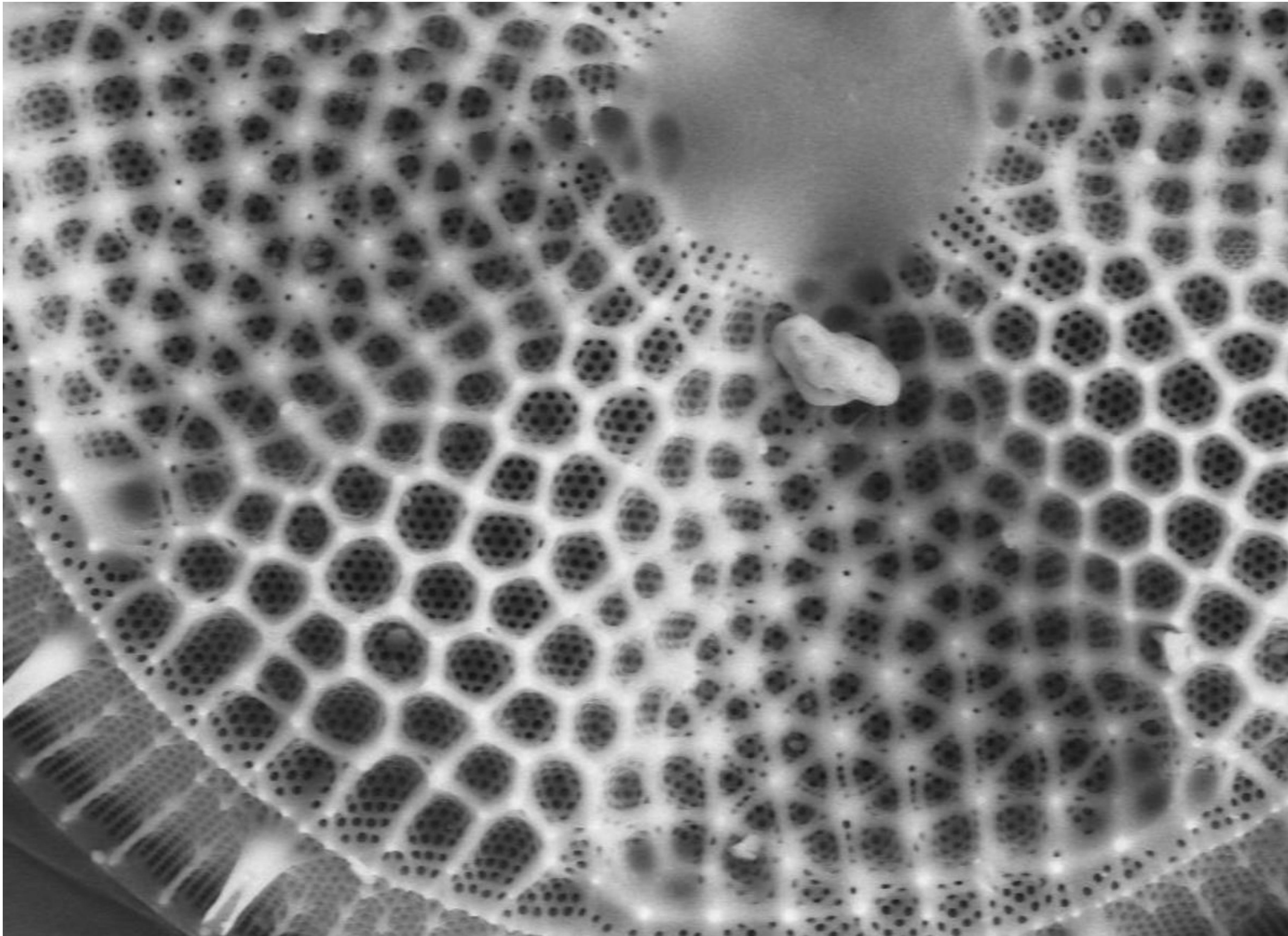


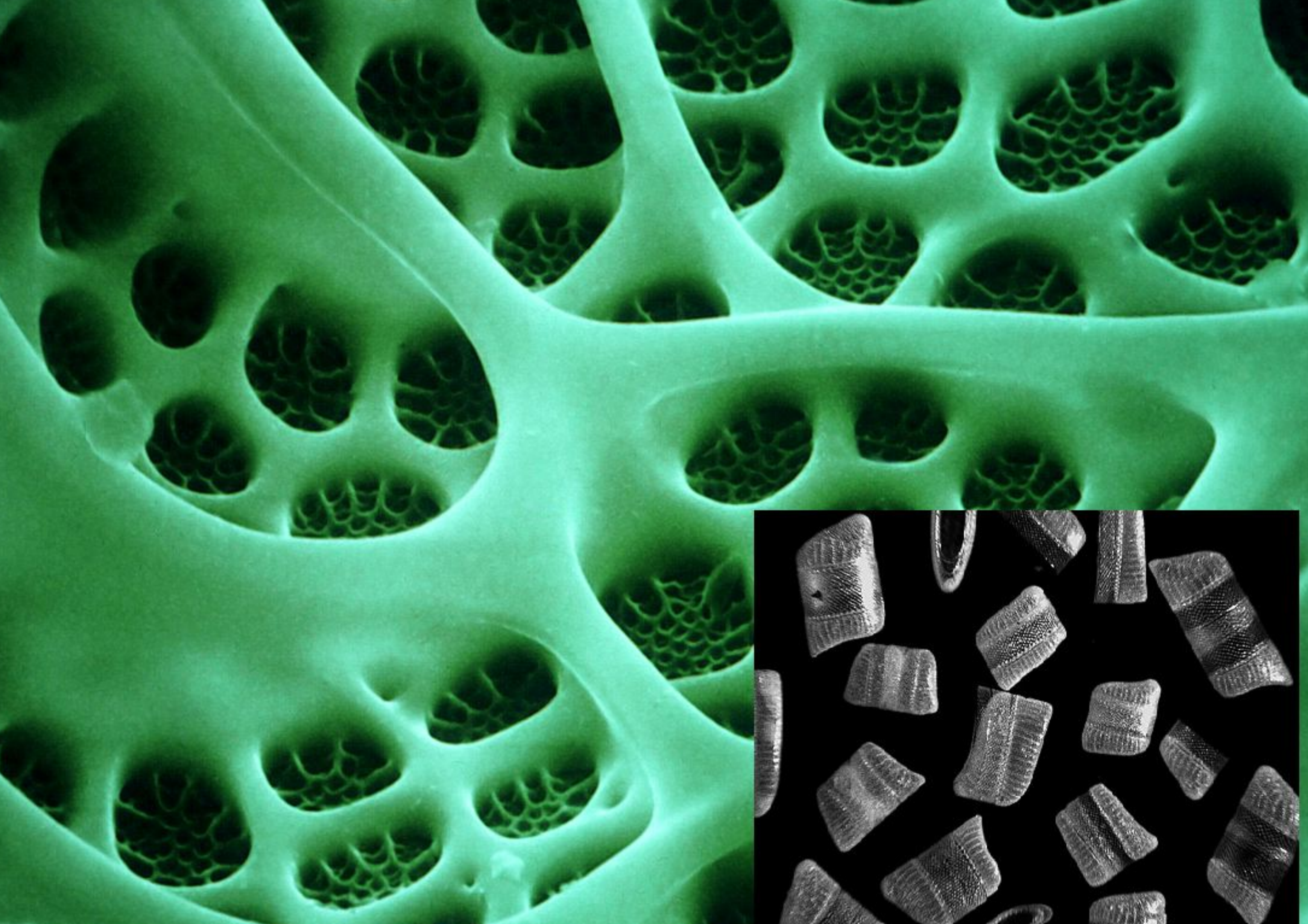
Crawford/Hinz

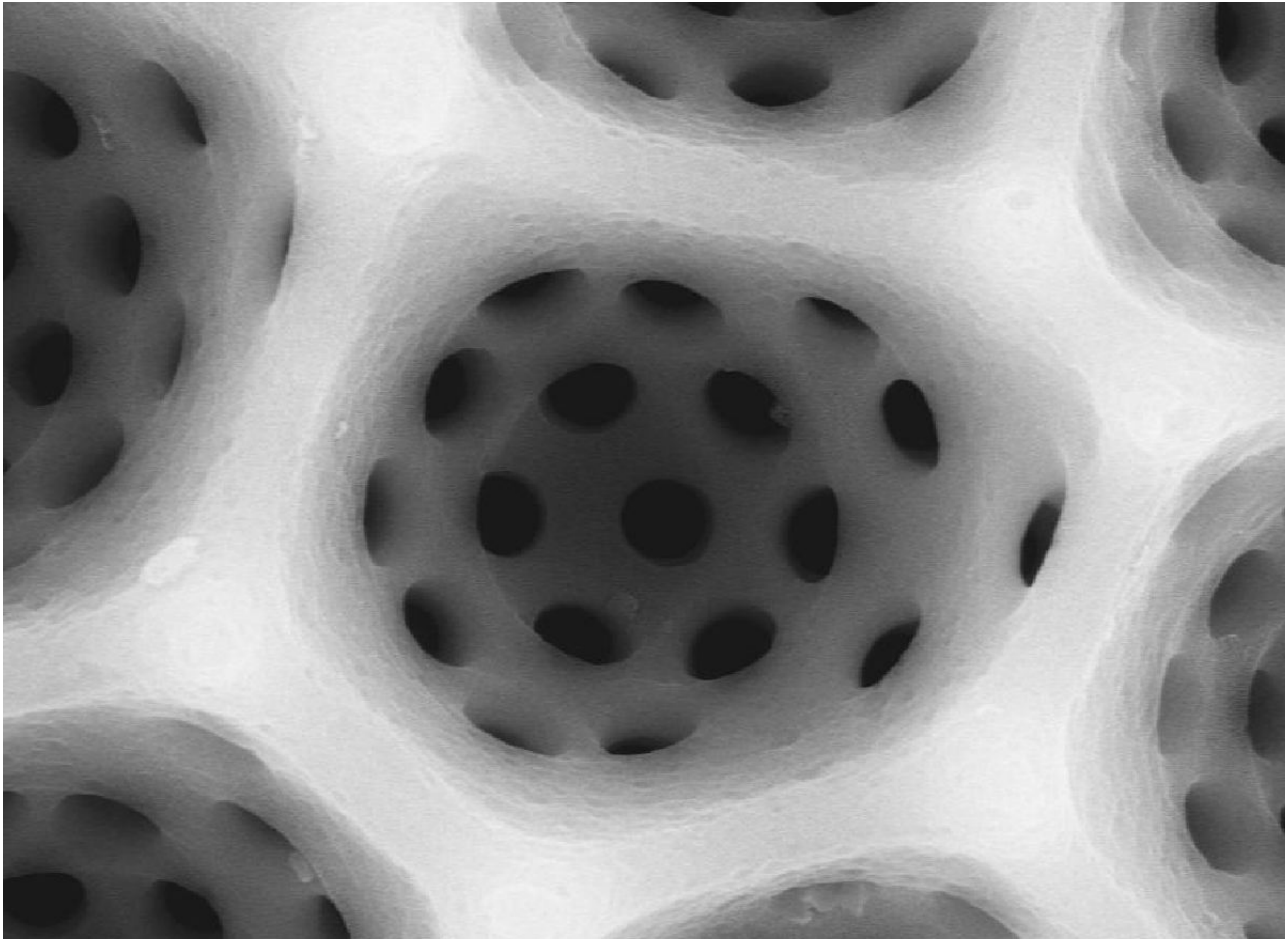
The function of diatom frustules is under debate today. Ehrenberg in the 1830s called them „Panzertierchen“ (armoured little animals).

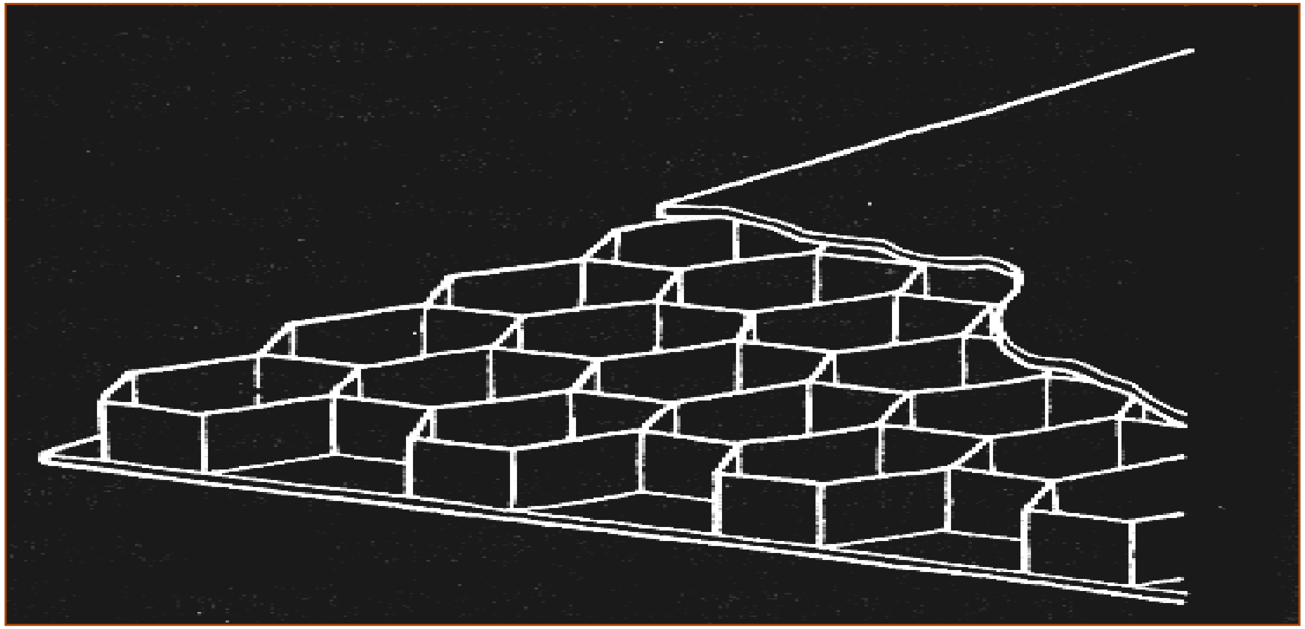


Bottom-dwelling diatom *Actinoptychus senarius* (Actino = ray; ptychus = fold); North West Shelf of Australia; diameter 30$\mu$m.

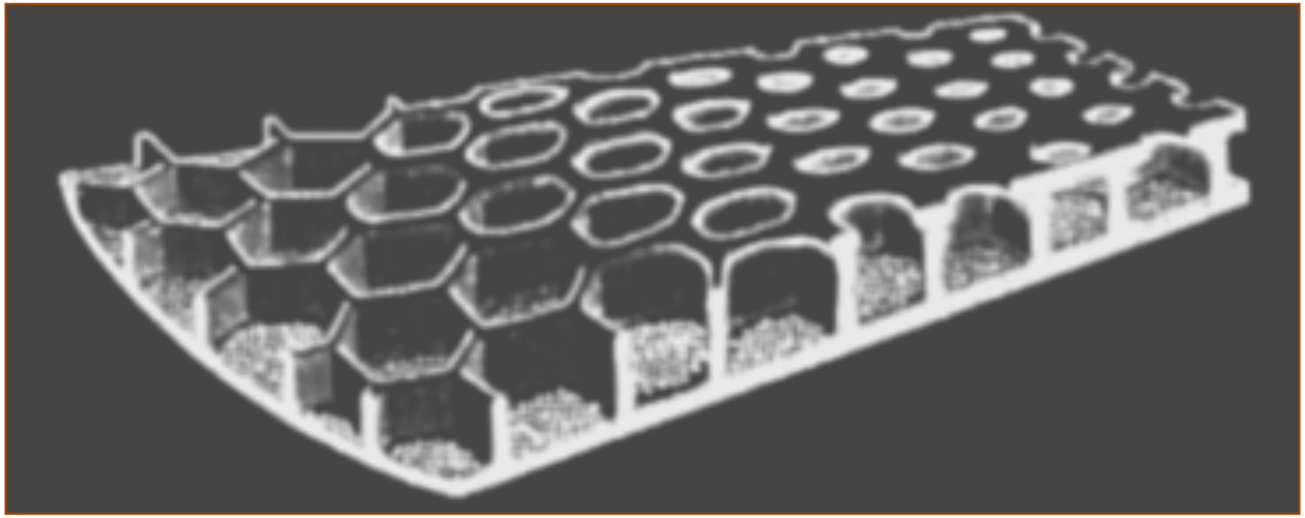






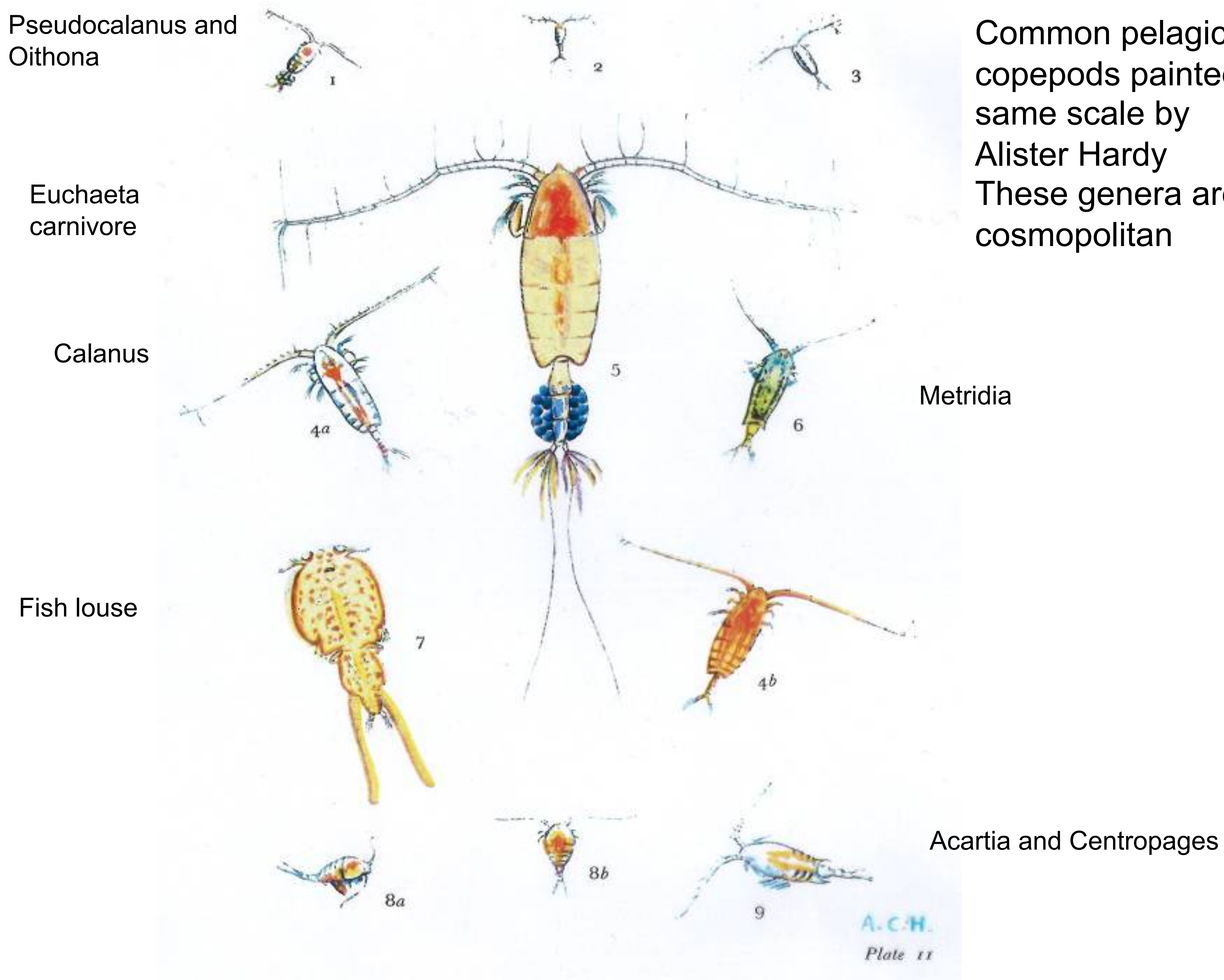


Hexcel Composites



Schmidt 1989

Common pelagic copepods painted at same scale by Alister Hardy
These genera are cosmopolitan



# Mouth of a copepod

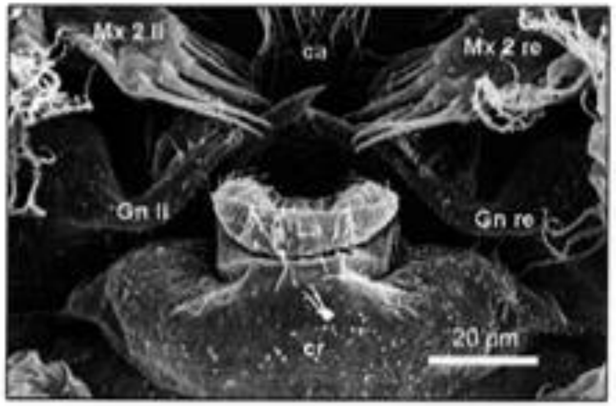
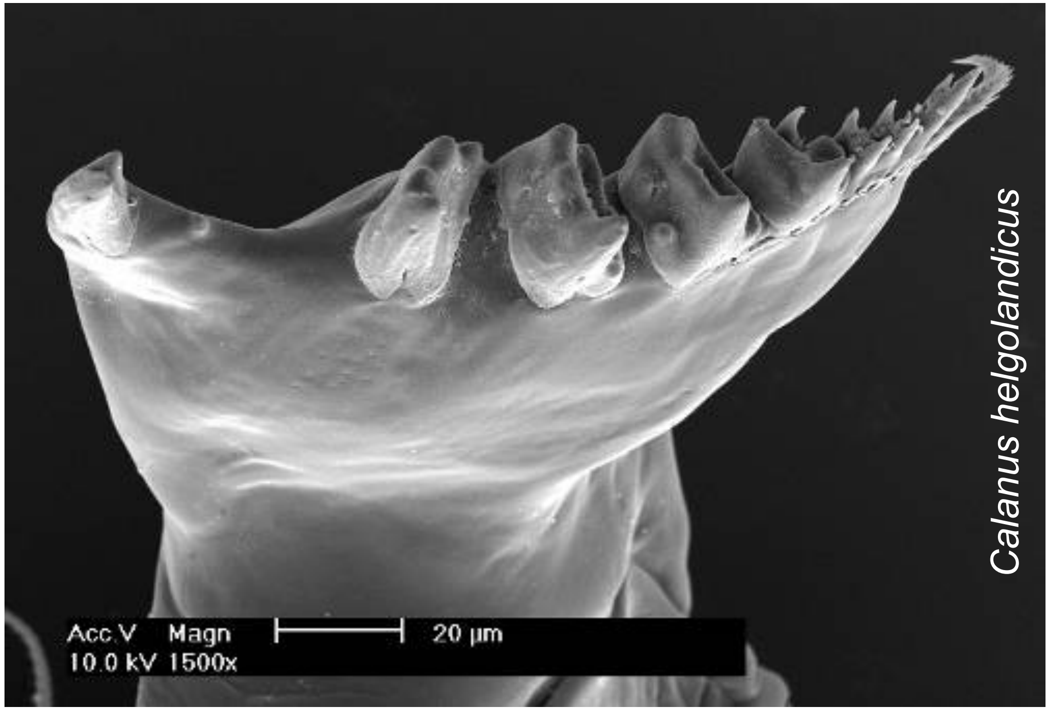
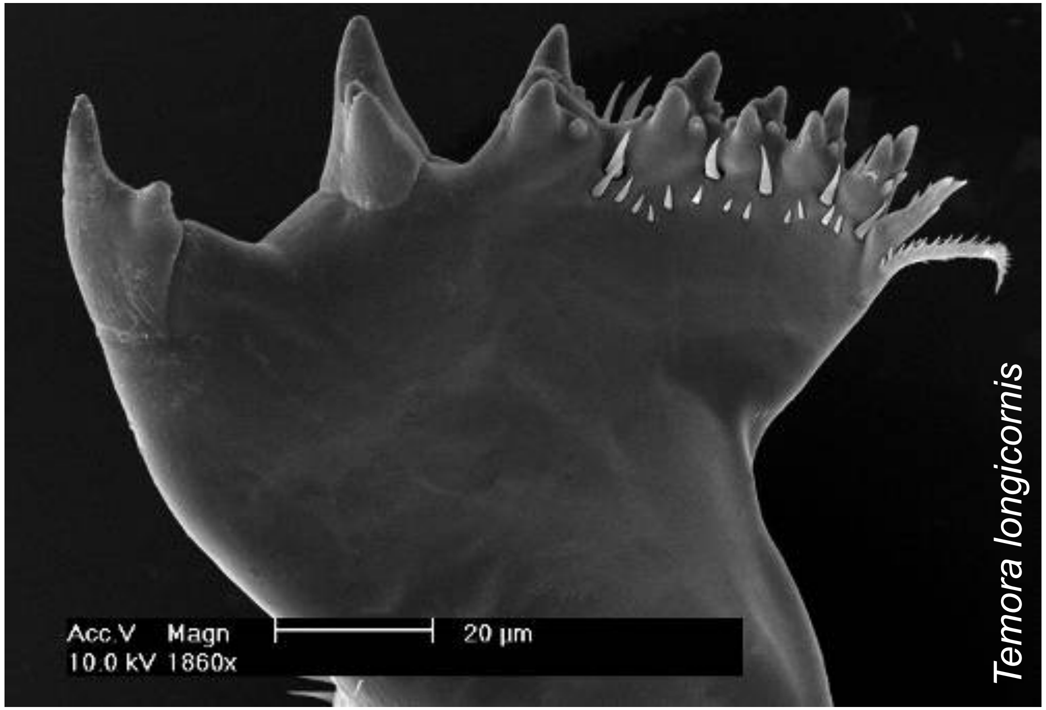


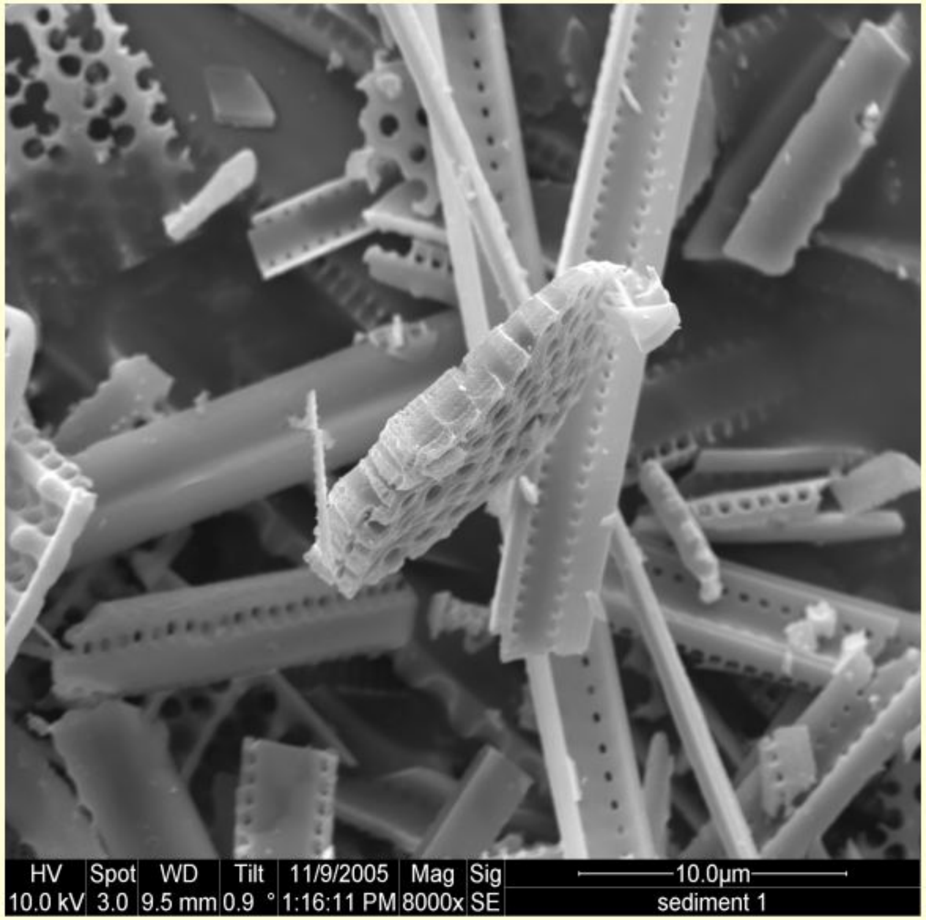

**Abb. 18:** Ansicht der Mundöffnungsregion auf der Ventralseite von *Microcalanus pygmaeus* C V. **Gn li** und **Gn re** linke und rechte Gnathobasen, **La** Labrum, **Mx 2 li** und **Mx 2 re** linke und rechte zweite Maxillen, **ca** caudal, **cr** cranial.

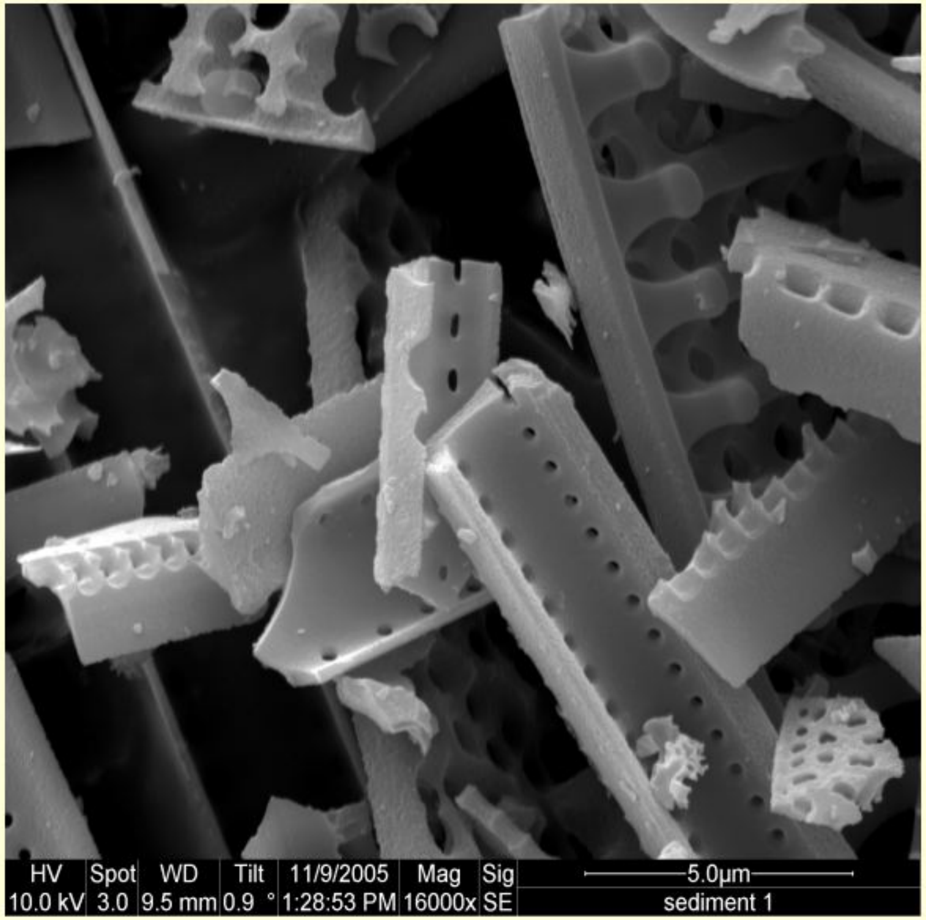



*Calanus helgolandicus*




*Temora longicornis*

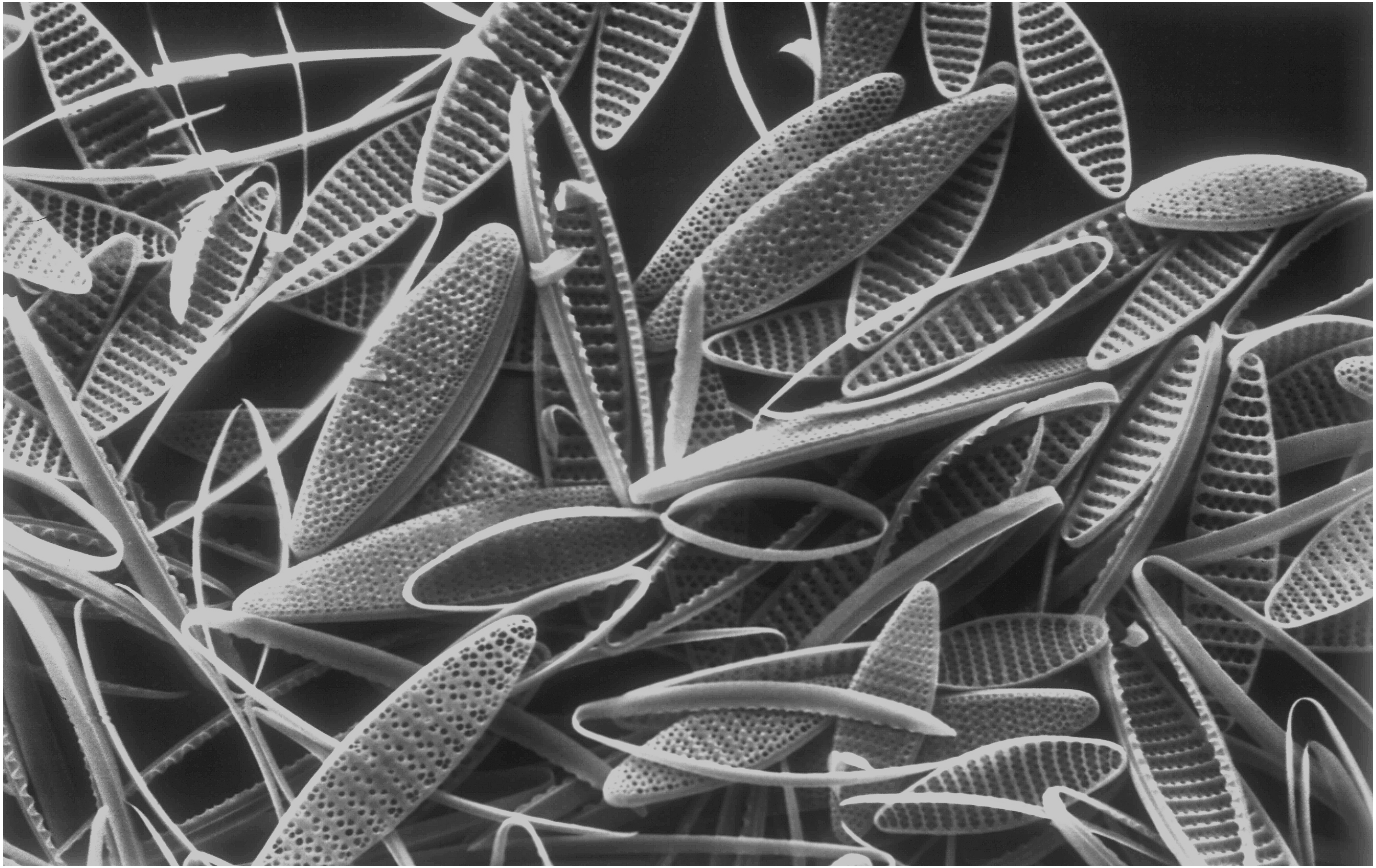



von Einem, nicht publiziert (2006)

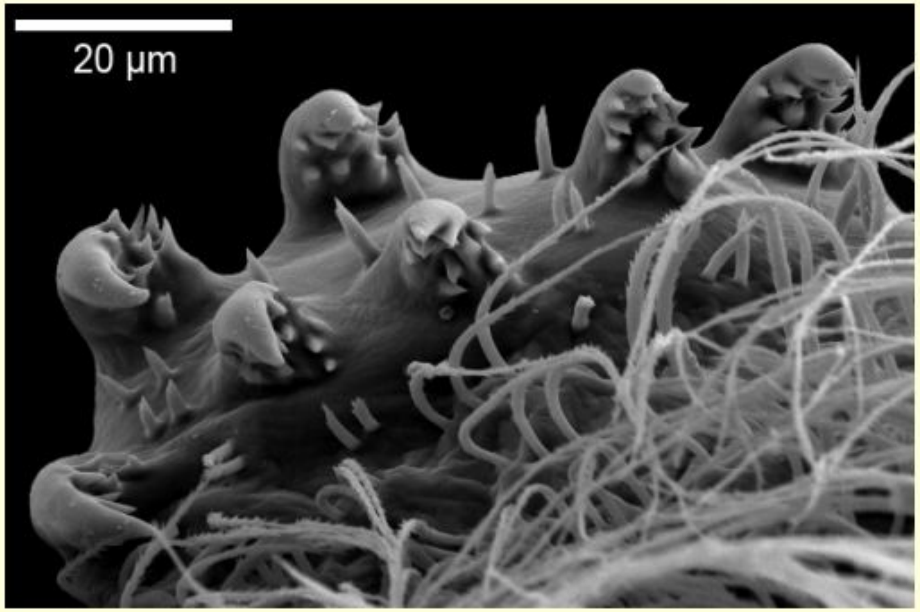
## REM - Bilder

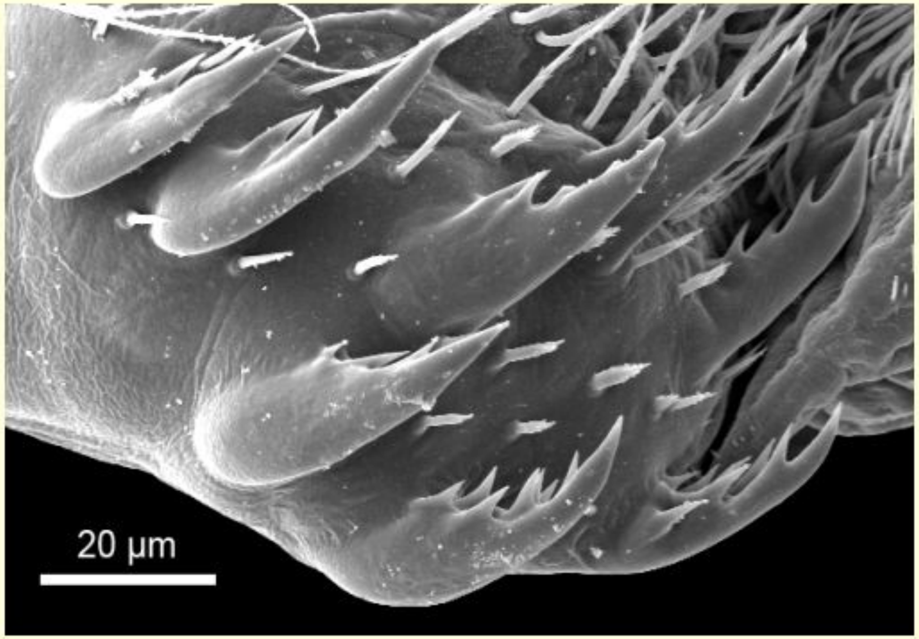
Antarktic Sediments are dominated by the pennate diatom *Fragilariopsis kerguelensis.* This is the largest global sink of silica.



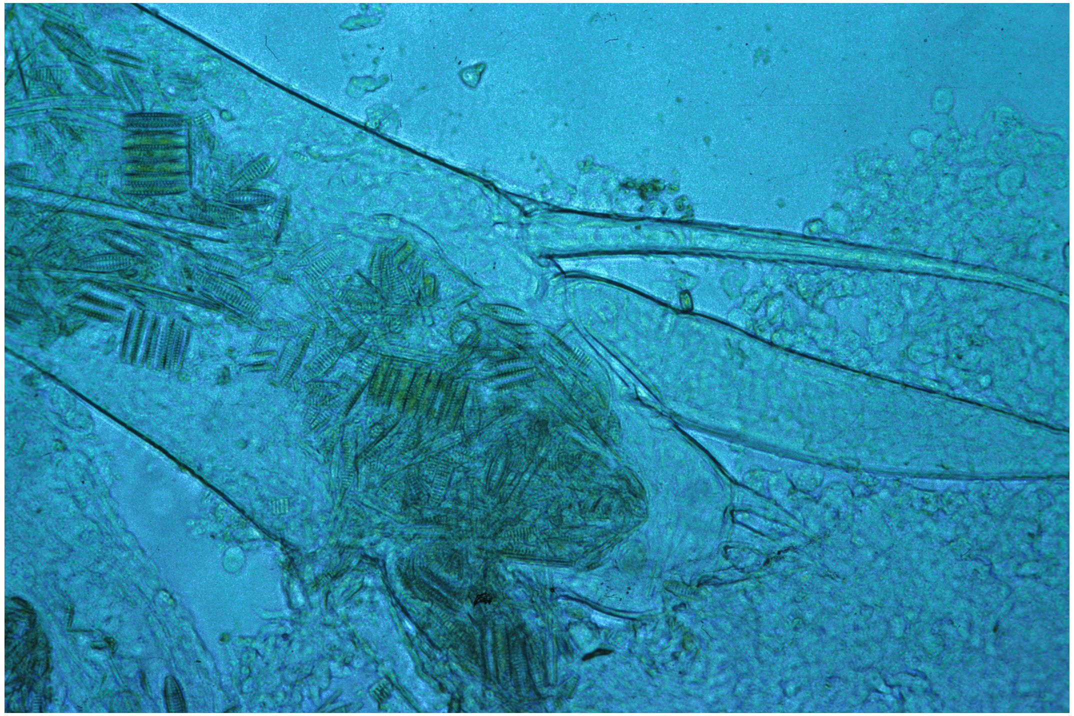
# Krill:
**mehrere Arten**

Mundwerkzeuge (Mandibeln) und
Kaumagen mit zahnartigen Strukturen

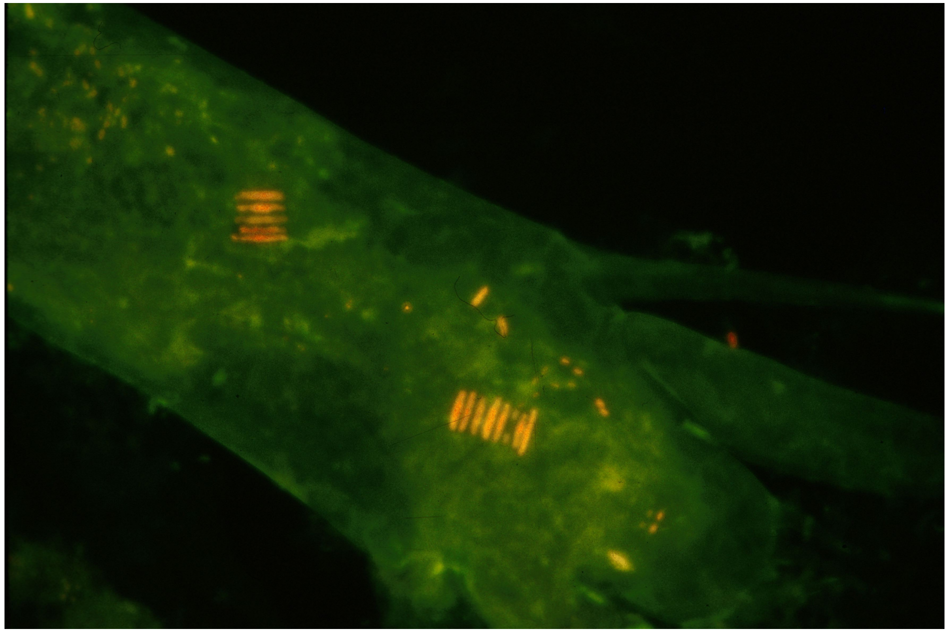


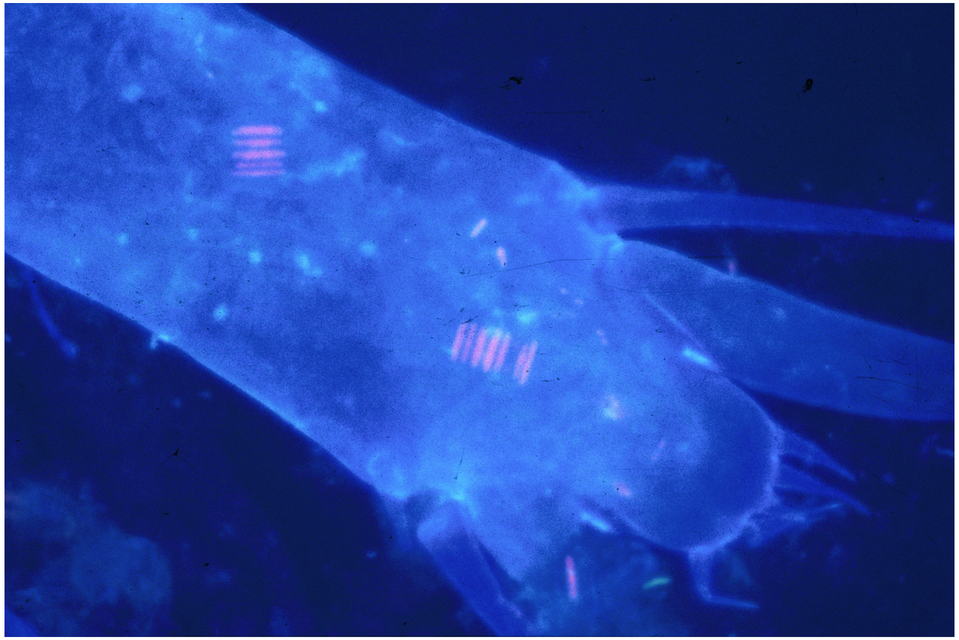
Hindgut of an euphausiid that has ingested numerous chains of *Fragilariopsis kerguelensis* of which many are intact, and some, as seen below, apparently still alive.



U. Freier



Intact chlorophyll *a* fluoresces red under UV



DAPI stained DNA fluoresces under UV

# Architecture and material properties of diatom shells provide effective mechanical protection

**Christian E. Hamm*, Rudolf Merkel†‡, Olaf Springer§, Piotr Jurkojc§, Christian Maier†, Kathrin Prechtel† & Victor Smetacek***

* *Alfred Wegener Institute for Polar and Marine Research, Am Handelshafen 12, 27570 Bremerhaven, Germany*
† *Technische Universität München, Physics Department (Biophysics Group E22), 85748 Garching, Germany*
‡ *Research Centre Jülich, Institute of Thin Films and Interfaces, 52425 Jülich, Germany*
§ *Hochschule Bremen – University of Applied Science, Neustadtswall 30, 28199 Bremen, Germany*

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Diatoms are the major contributors to phytoplankton blooms in lakes and in the sea and hence are central in aquatic ecosystems and the global carbon cycle[1]. All free-living diatoms differ from other phytoplankton groups in having silicified cell walls in the form of two 'shells' (the frustule) of manifold shape and intricate architecture[2] whose function and role, if any, in contributing to the evolutionary success of diatoms is under debate[3–5]. We explored the defence potential of the frustules as armour against predators by measuring their strength. Real and virtual loading tests (using calibrated glass microneedles and finite element analysis) were performed on centric and pennate diatom cells. Here we show that the frustules are remarkably strong by virtue of their architecture and the material properties of the diatom silica. We conclude that diatom frustules have evolved as mechanical protection for the cells because exceptional force is required to break them. The evolutionary arms race between diatoms and their specialized predators will have had considerable influence in structuring pelagic food webs and biogeochemical cycles.

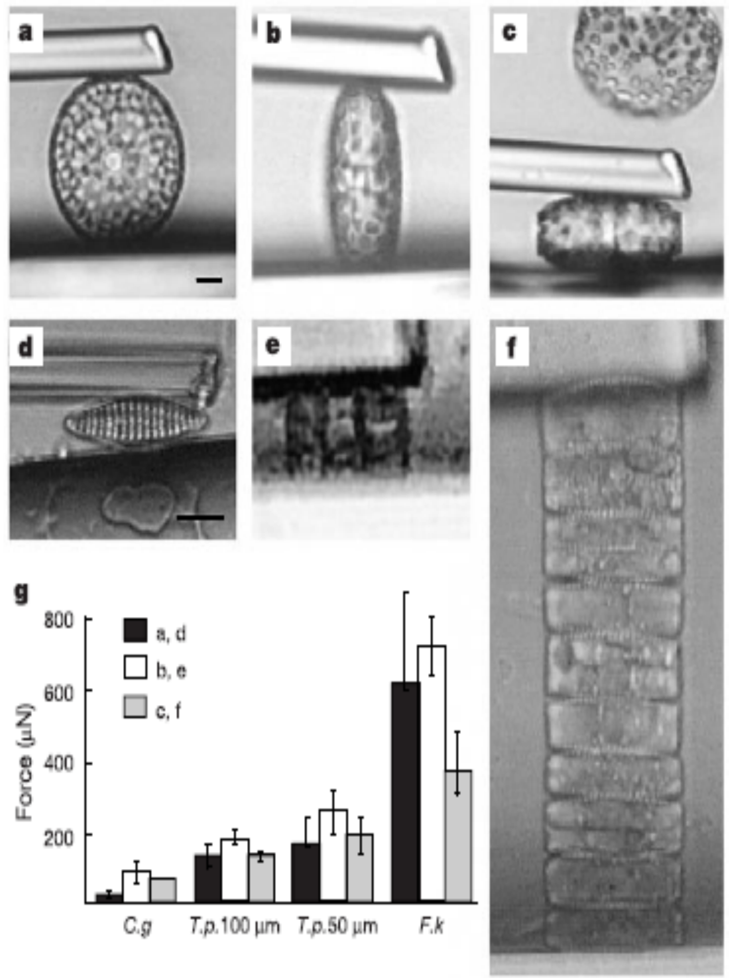



**Figure 1** Glass needle tests: Live single cells of *T. punctigera* (**a–c**) and *F. kerguelensis* (**d–f**), in chains (**e**, **f**). Pressures applied along the girdle bands, (**a**, **d**), across the girdle bands (**b**, **e**), and across the centre of the valves (**c**, **f**). **g**, Forces necessary to break *Coscinodiscus granii* (*C.g.*), *Thalassiosira punctigera* (*T.p.*) with diameters of 100 and 50 μm, and *Fragilariopsis kerguelensis* (*F.k.*). *C. granii* has a geometry similar to that of *T. punctigera*. Scale bars, 10 μm.

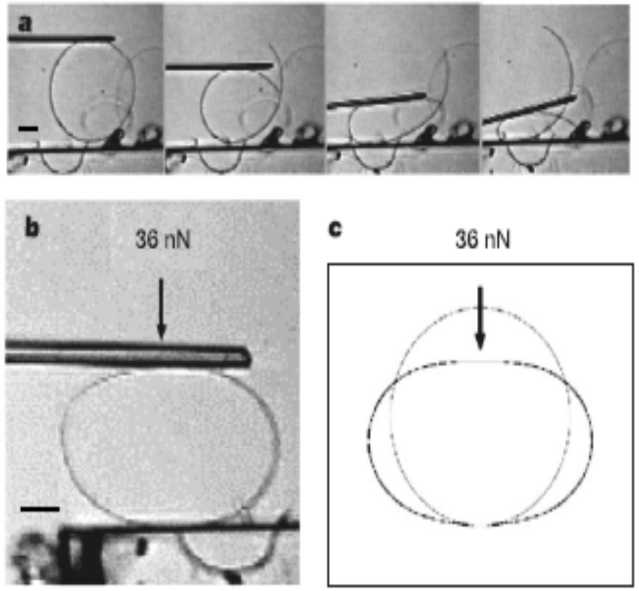


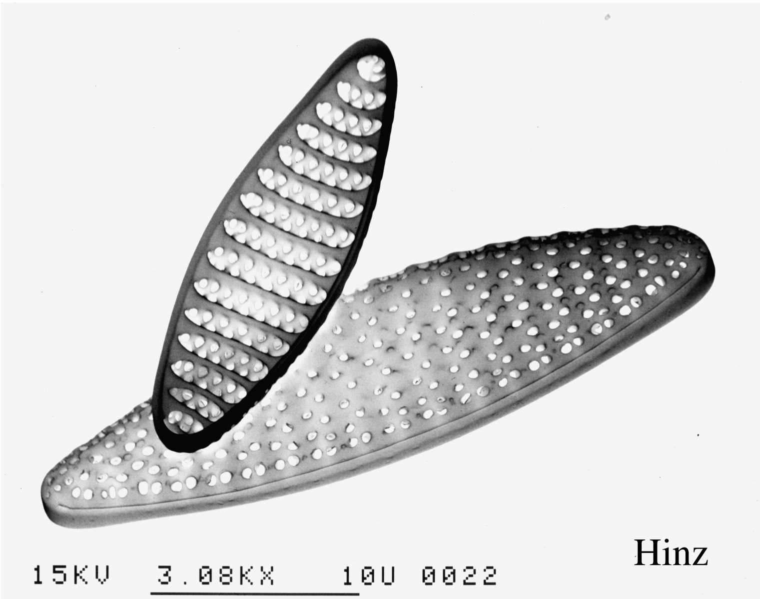

Figure 3 Properties of an isolated girdle band. **a**, Sequence showing strong elastic deformation of a girdle band as a function of increasing force. **b**, girdle band (pleura) deformed by a calibrated glass needle. **c**, FEM of the pleura, showing identical deflections as functions of the same force (36 nN). The Young's modulus $E$ of the silica in the FEM is 22.4 GPa. Scale bars, 10 μm.



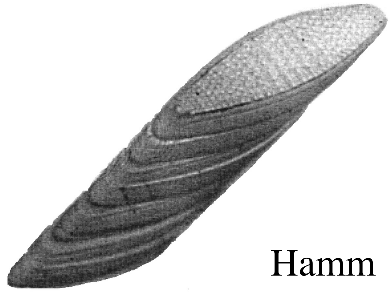


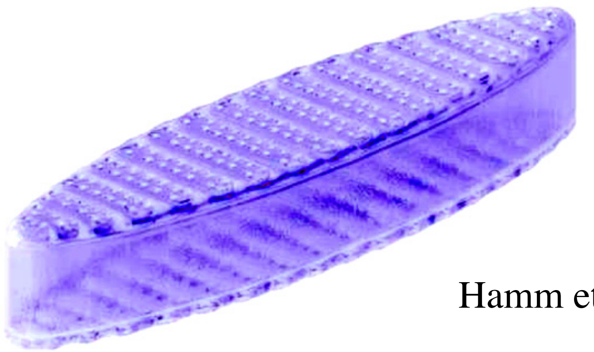
Hamm et al. 2003

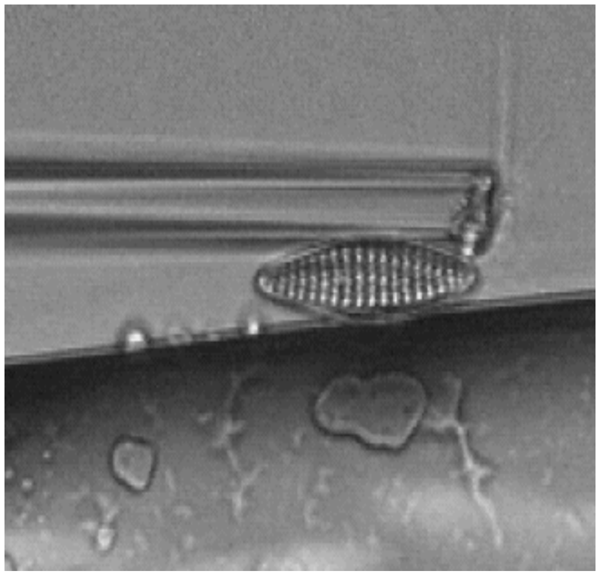
# SEM-pictures and FE-model of the Antarctic diatom *Fragilaiopsis kerguelensis*

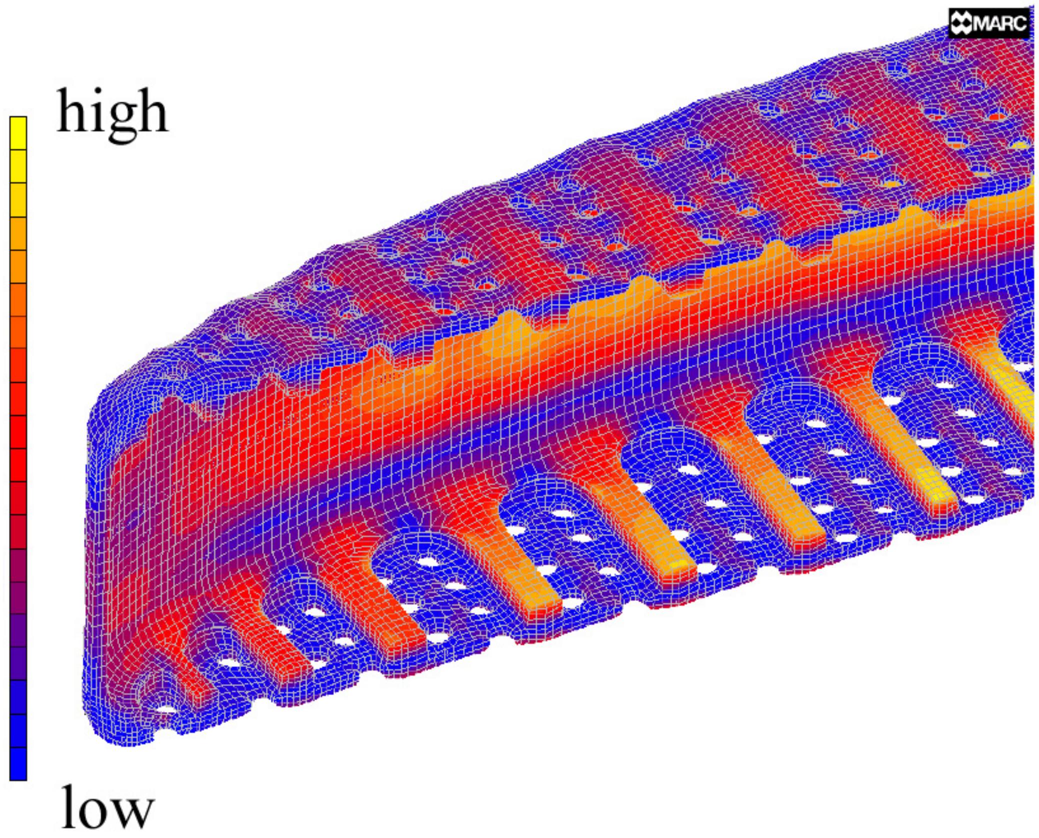


Hinz


Hamm

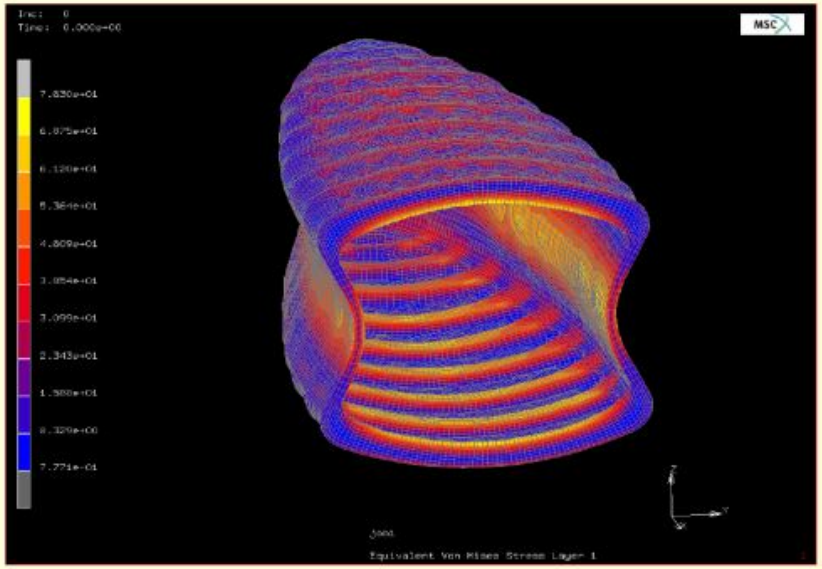

Hamm et al.

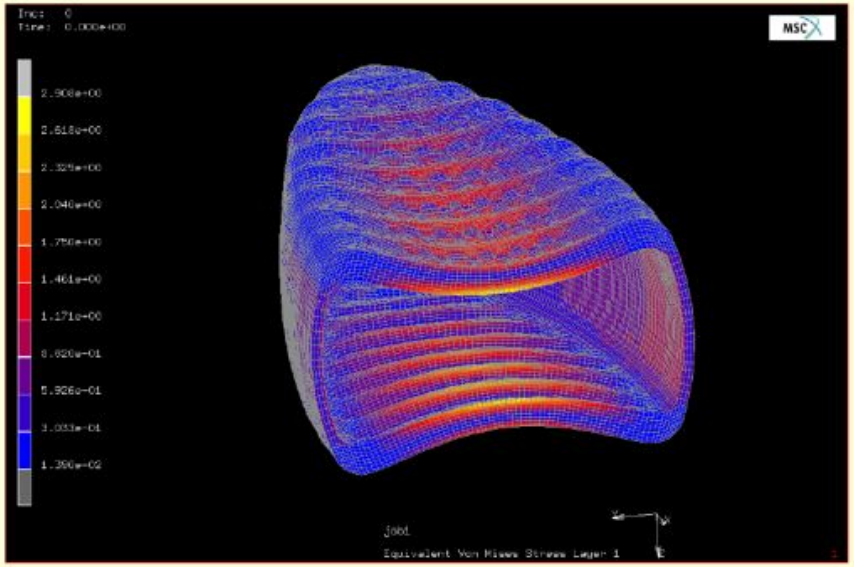


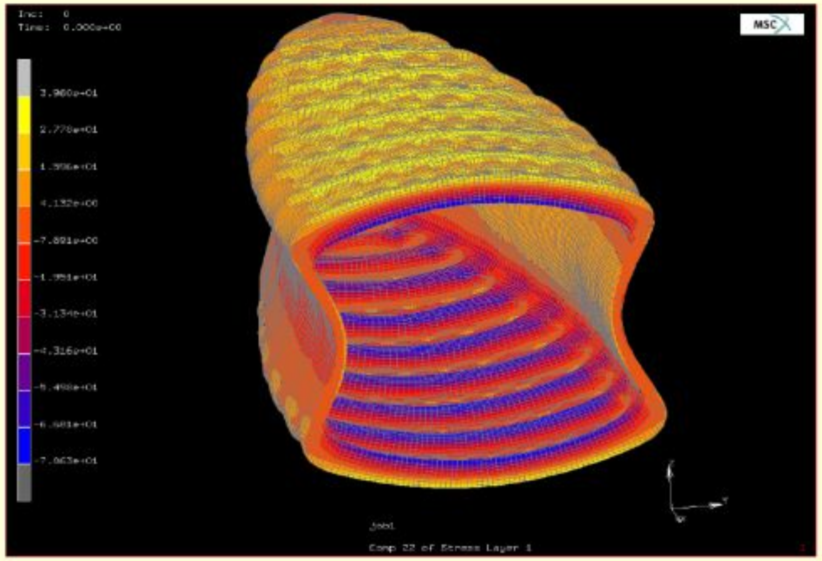


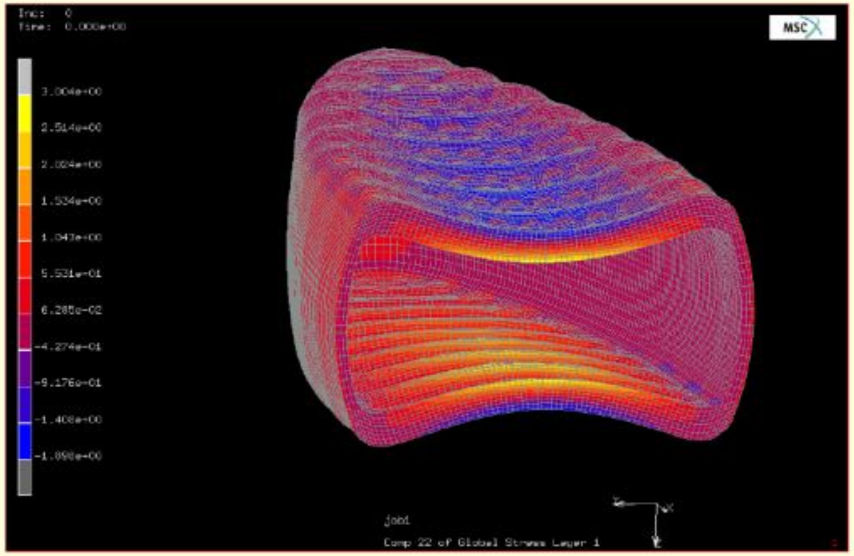

Equivalent van Mises Stress

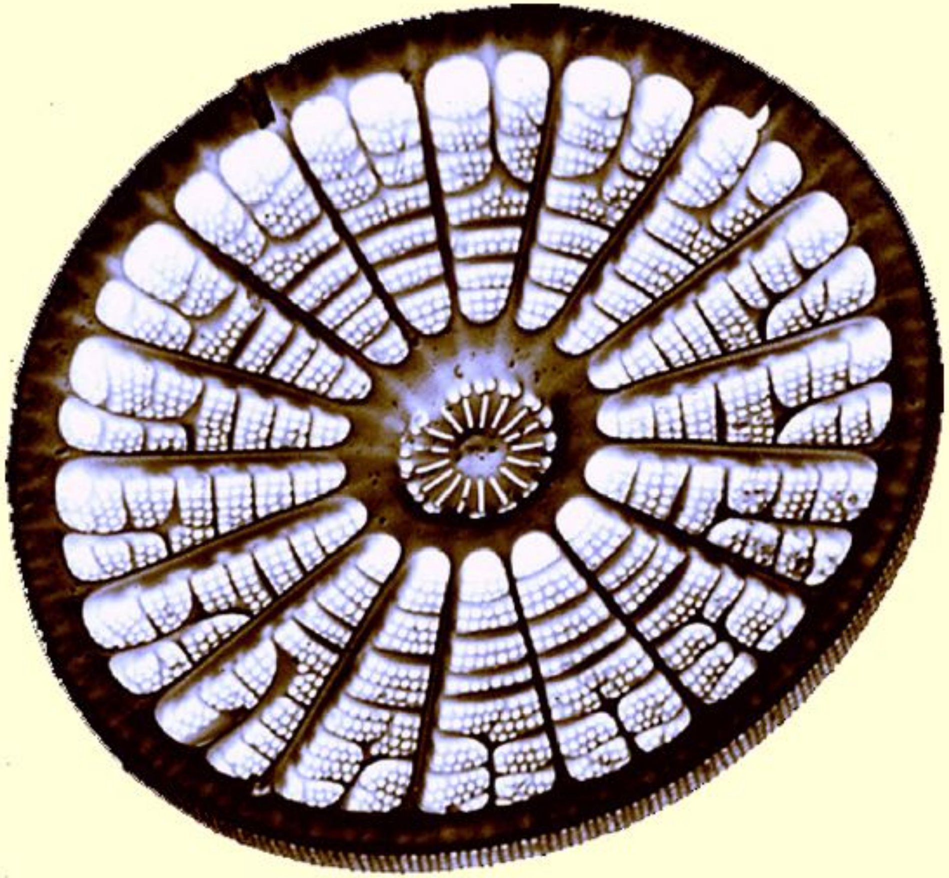
# FE- Berechnungen sagen Verbundwerkstoff voraus:



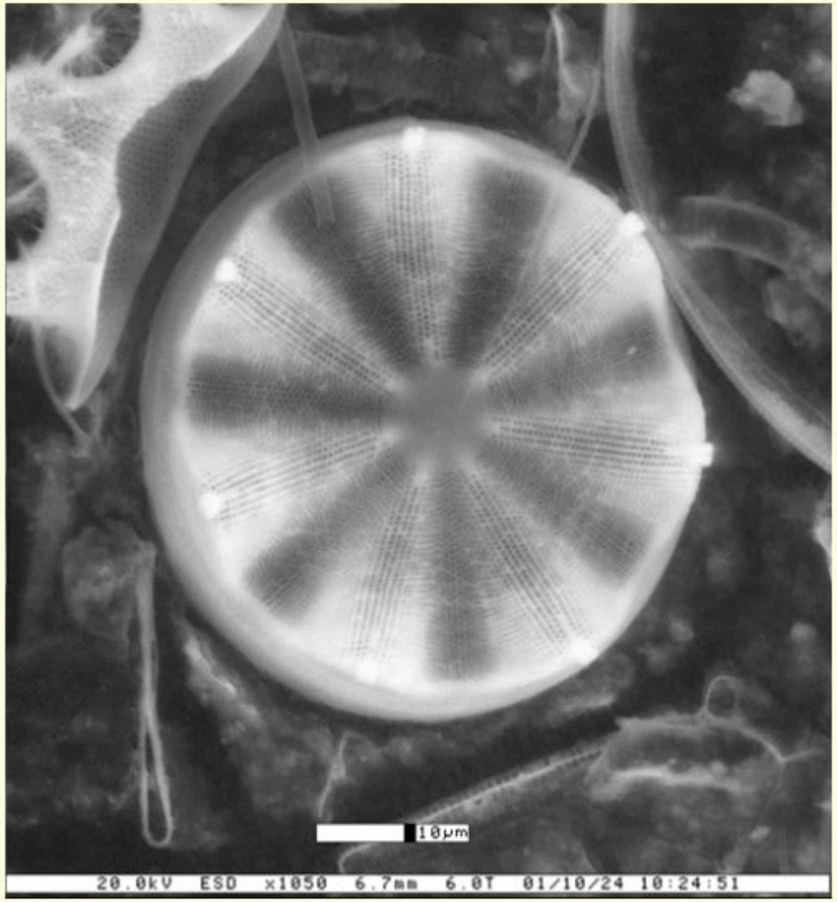



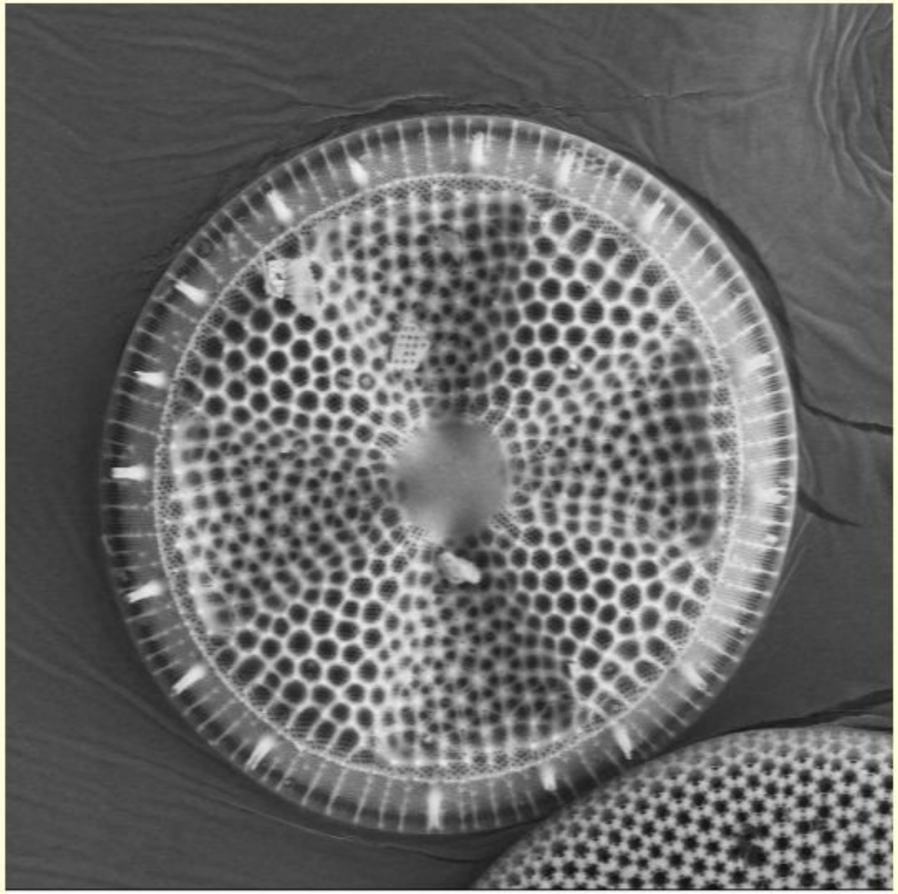



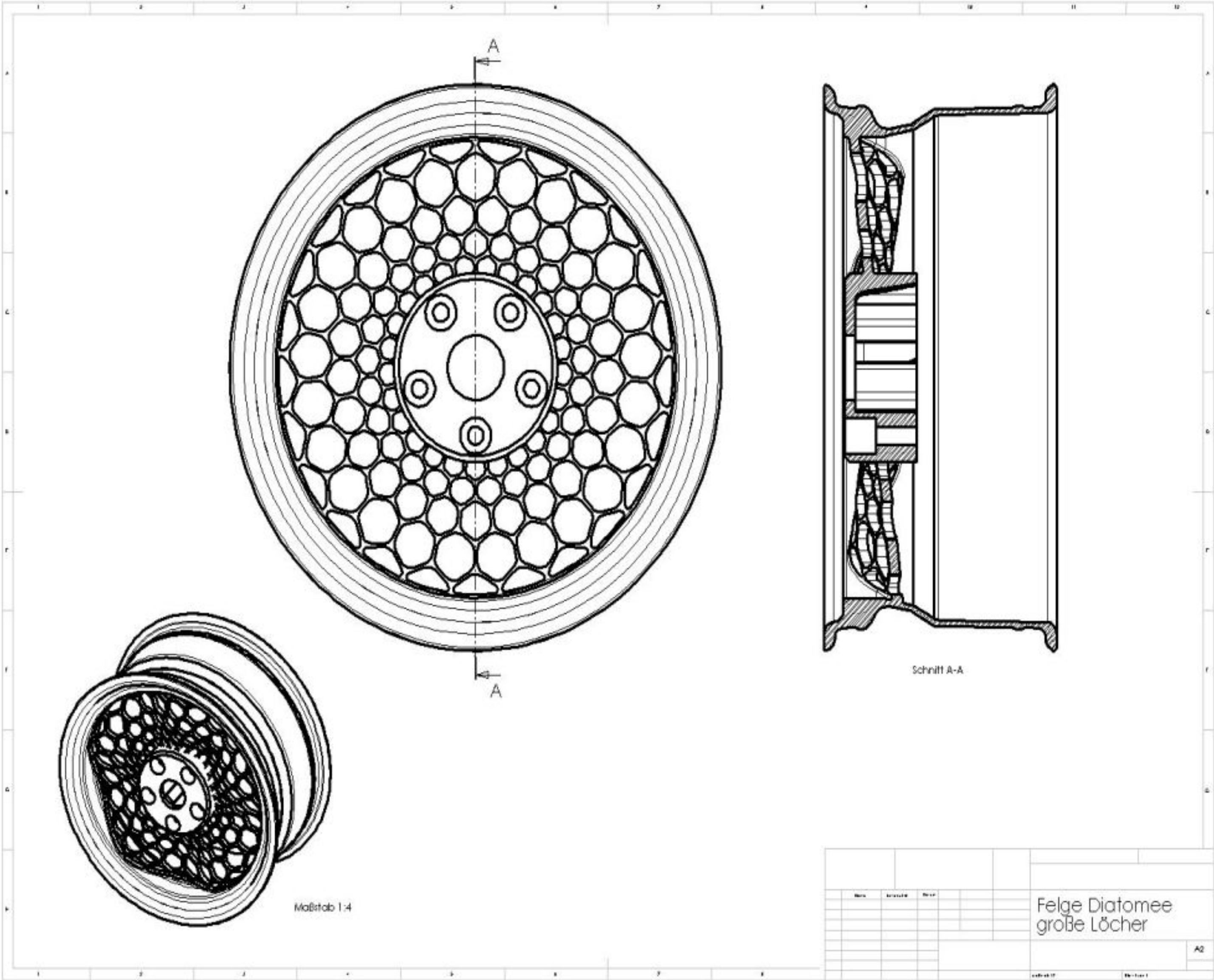


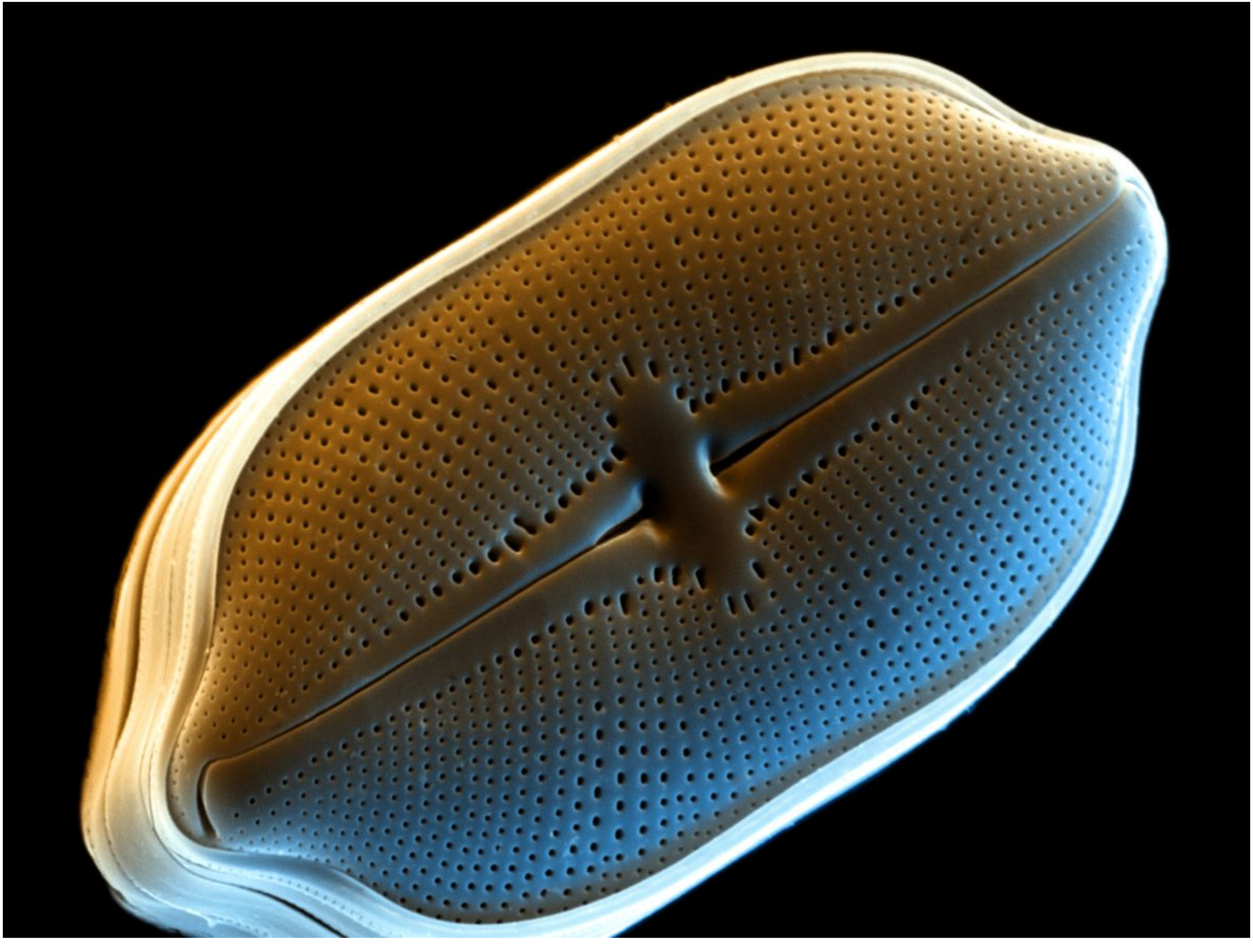
Schalenstrukturen sind skalierbar

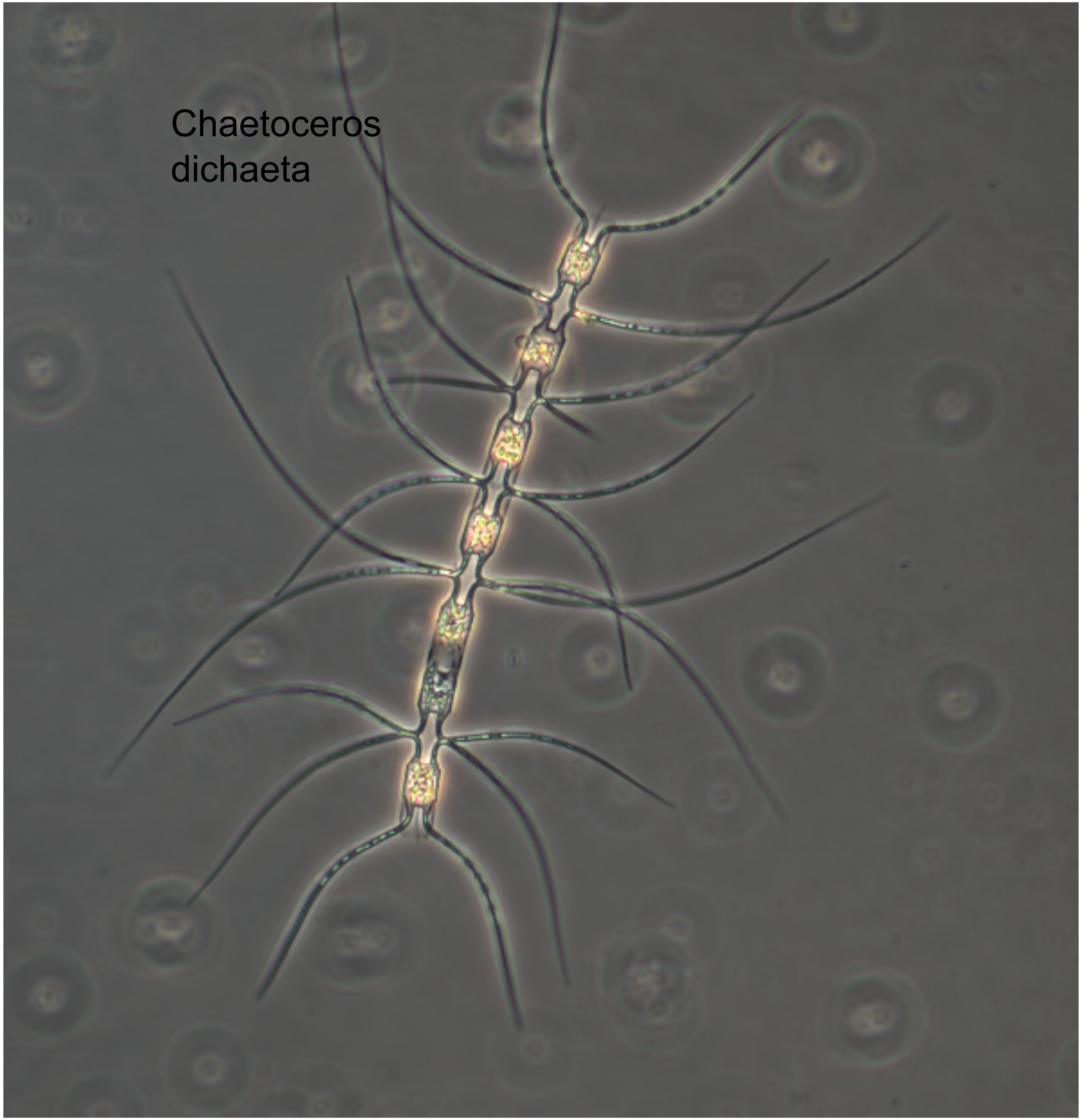
## Geometrien für Metalle

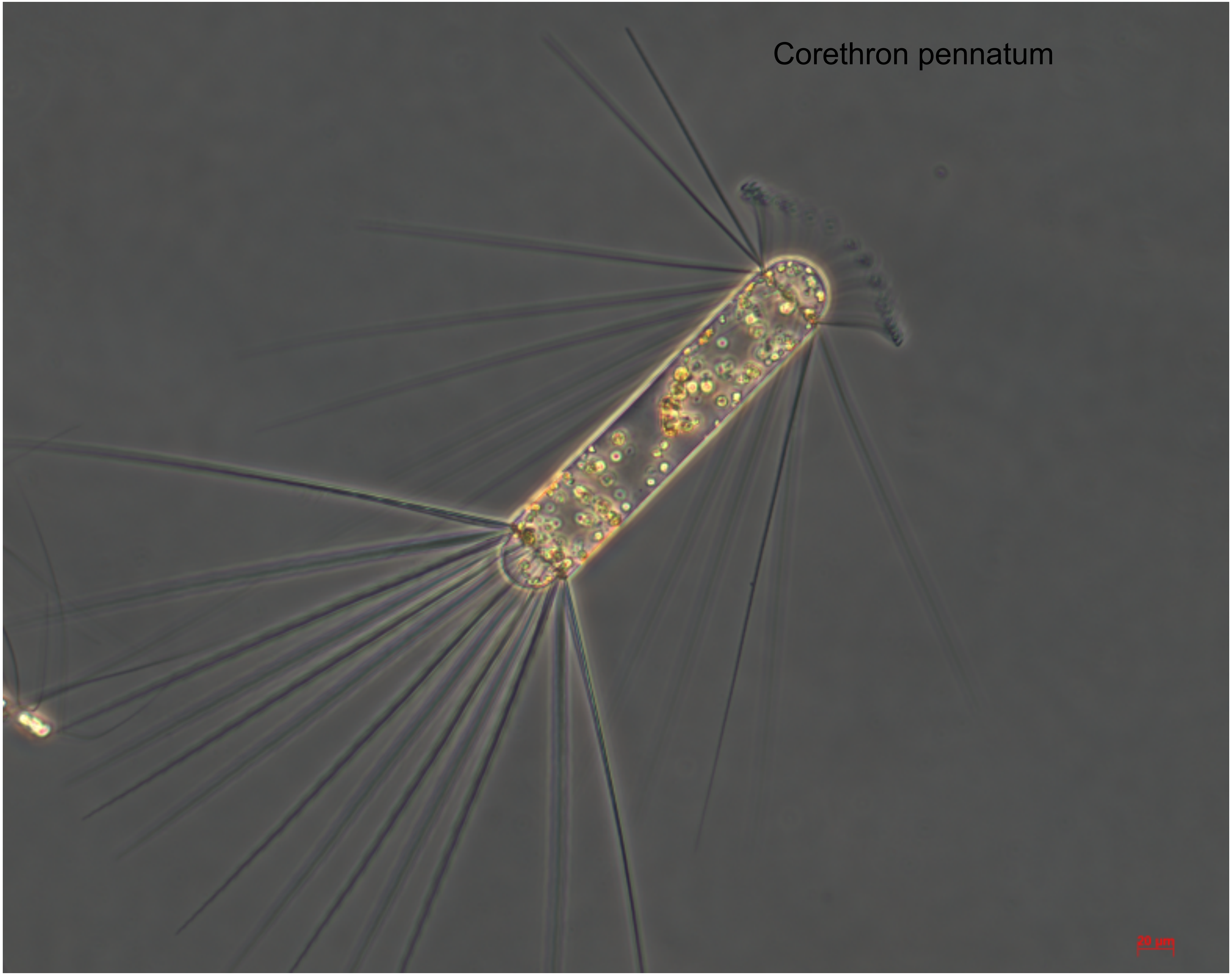


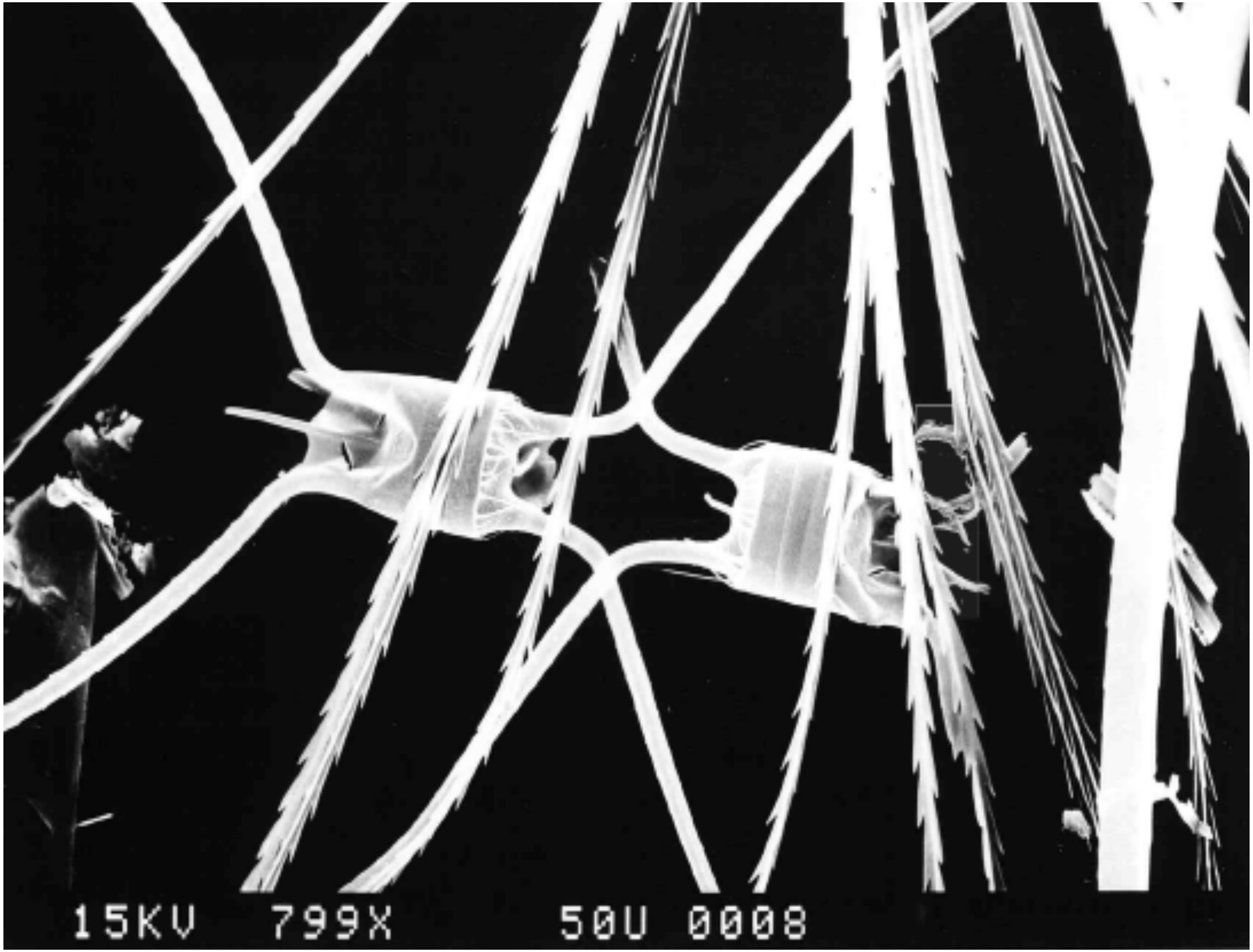

A
A
Schnitt A-A
Maßstab 1:4
Felge Diatomee
große Löcher
A2



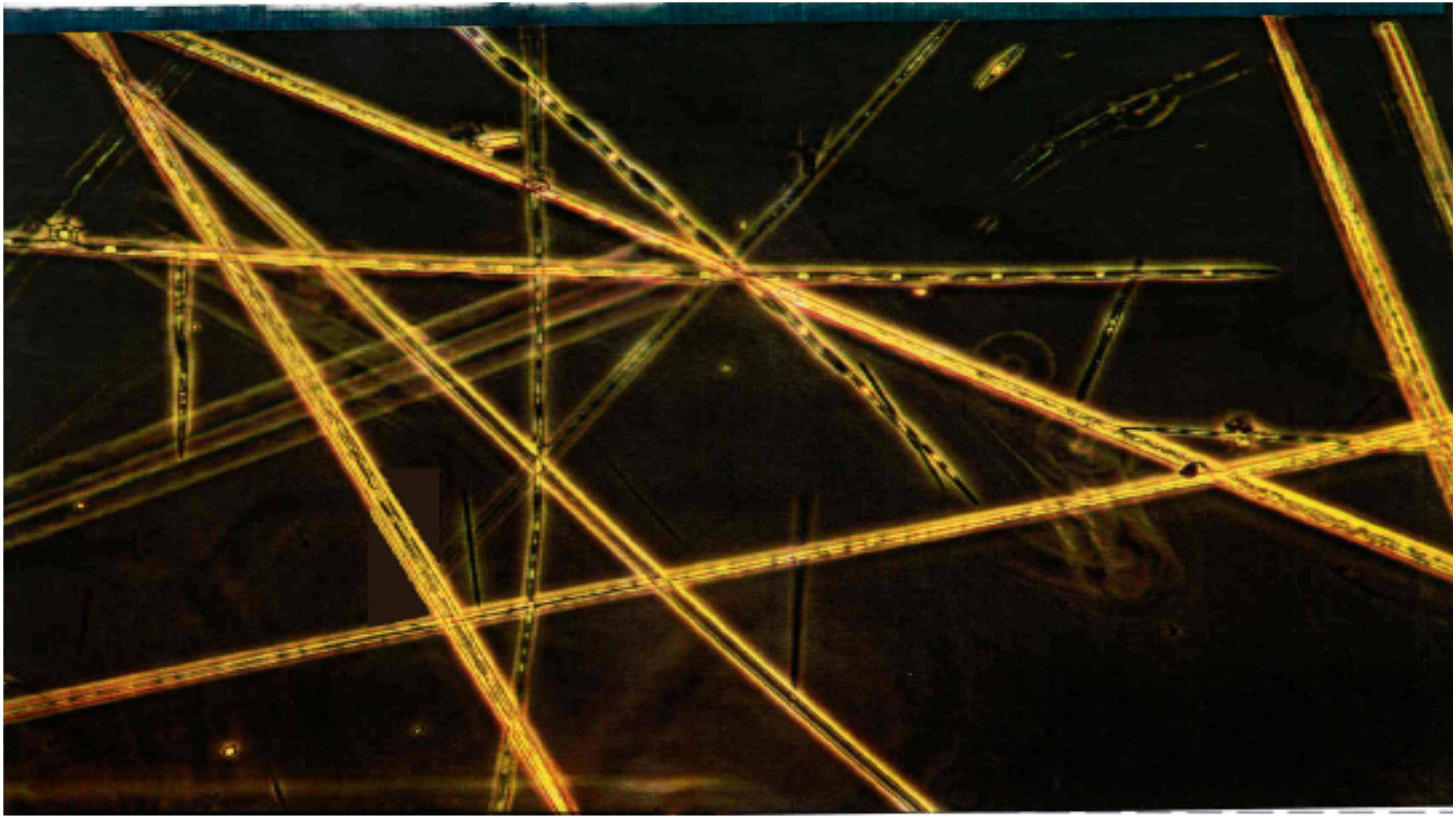

Chaetoceros
dichaeta


Corethron pennatum
20 µm

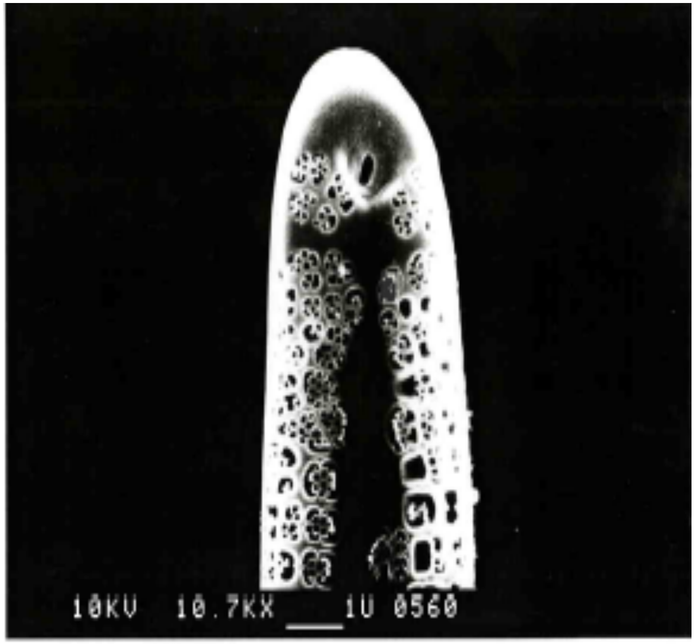
Chaetoceros chain and spines of Corethron pennatum. Note barbs.

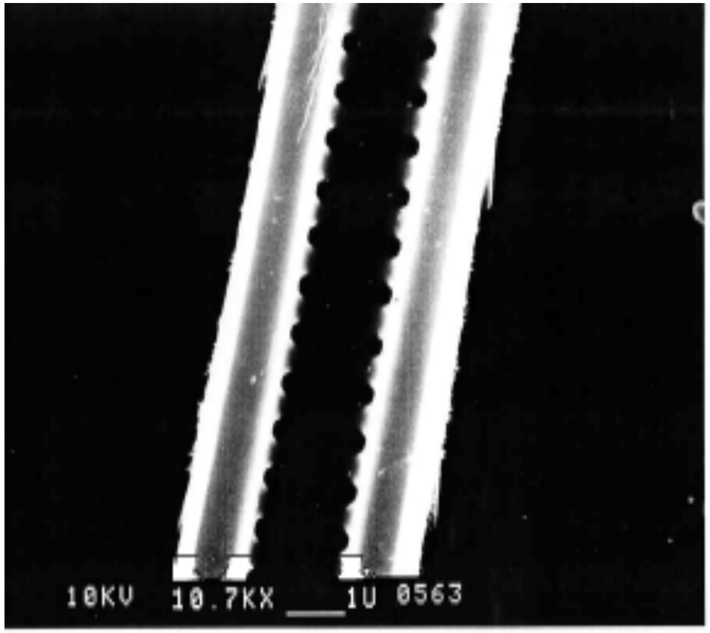


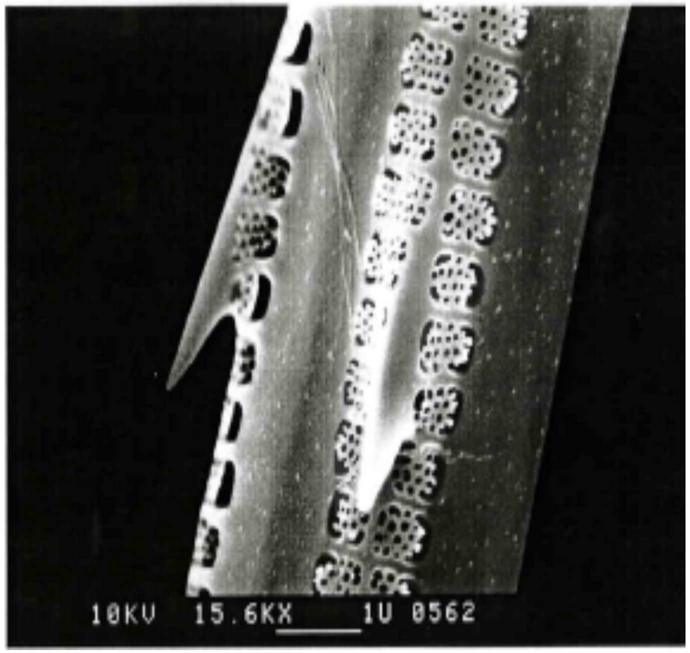
Needle-shaped ACC phytoplankton dominated by Thalassiothrix antarctica

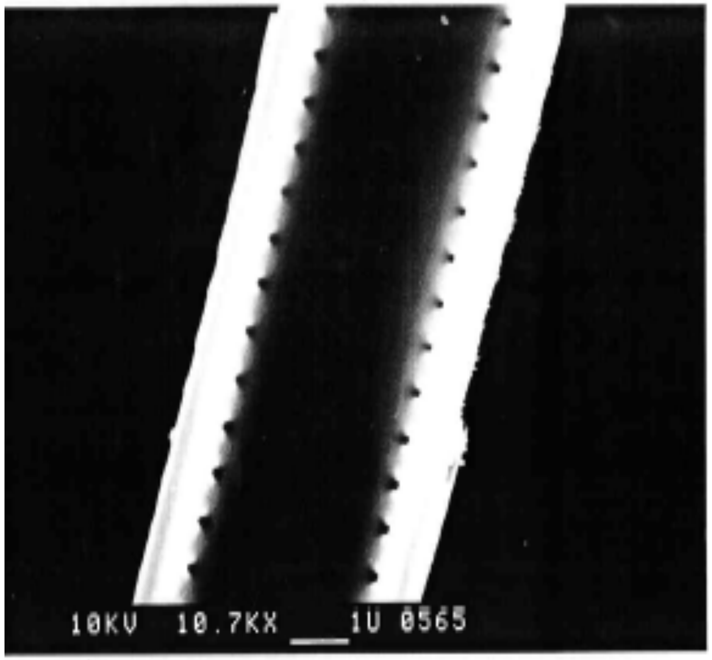


Thalassiothrix antarctica

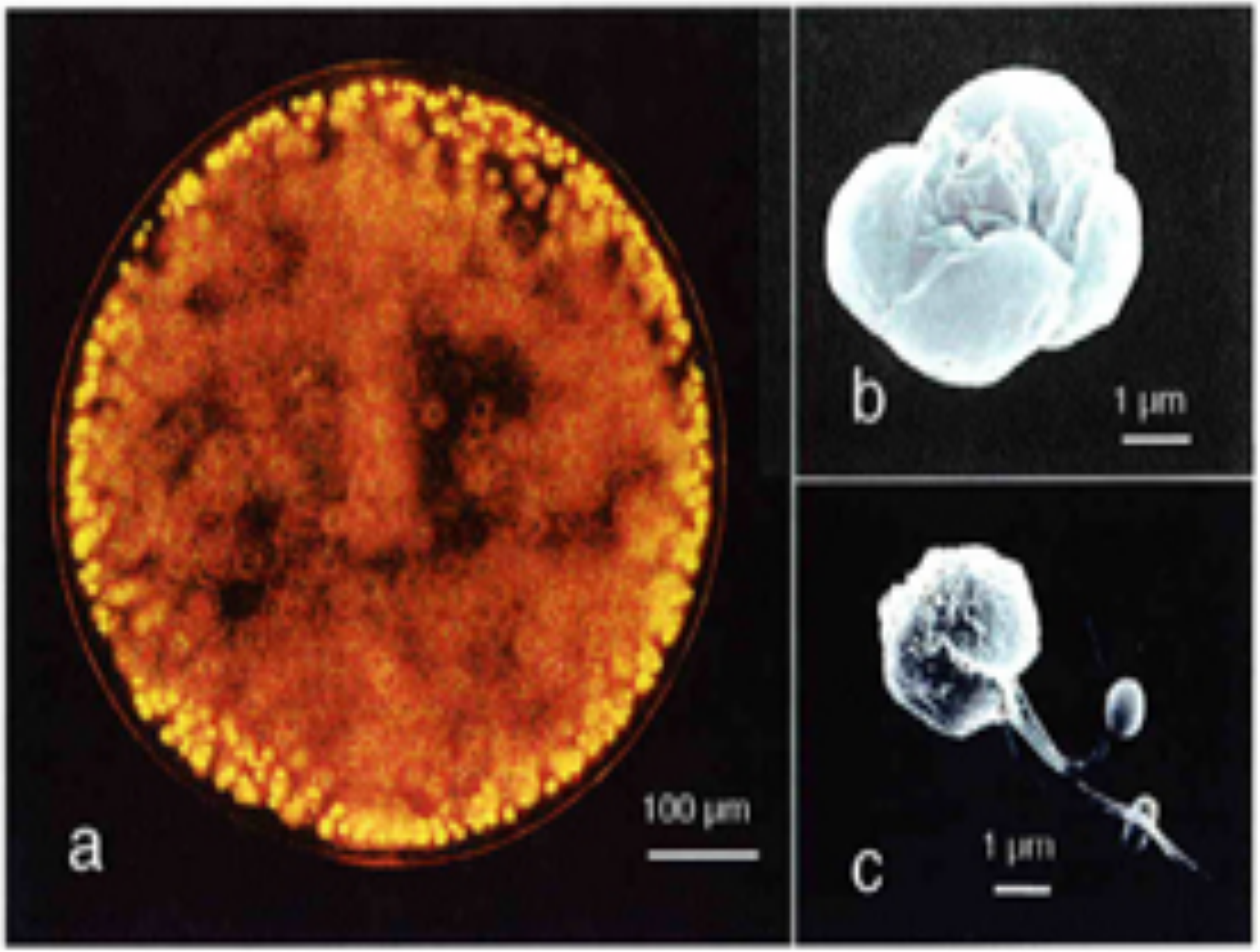


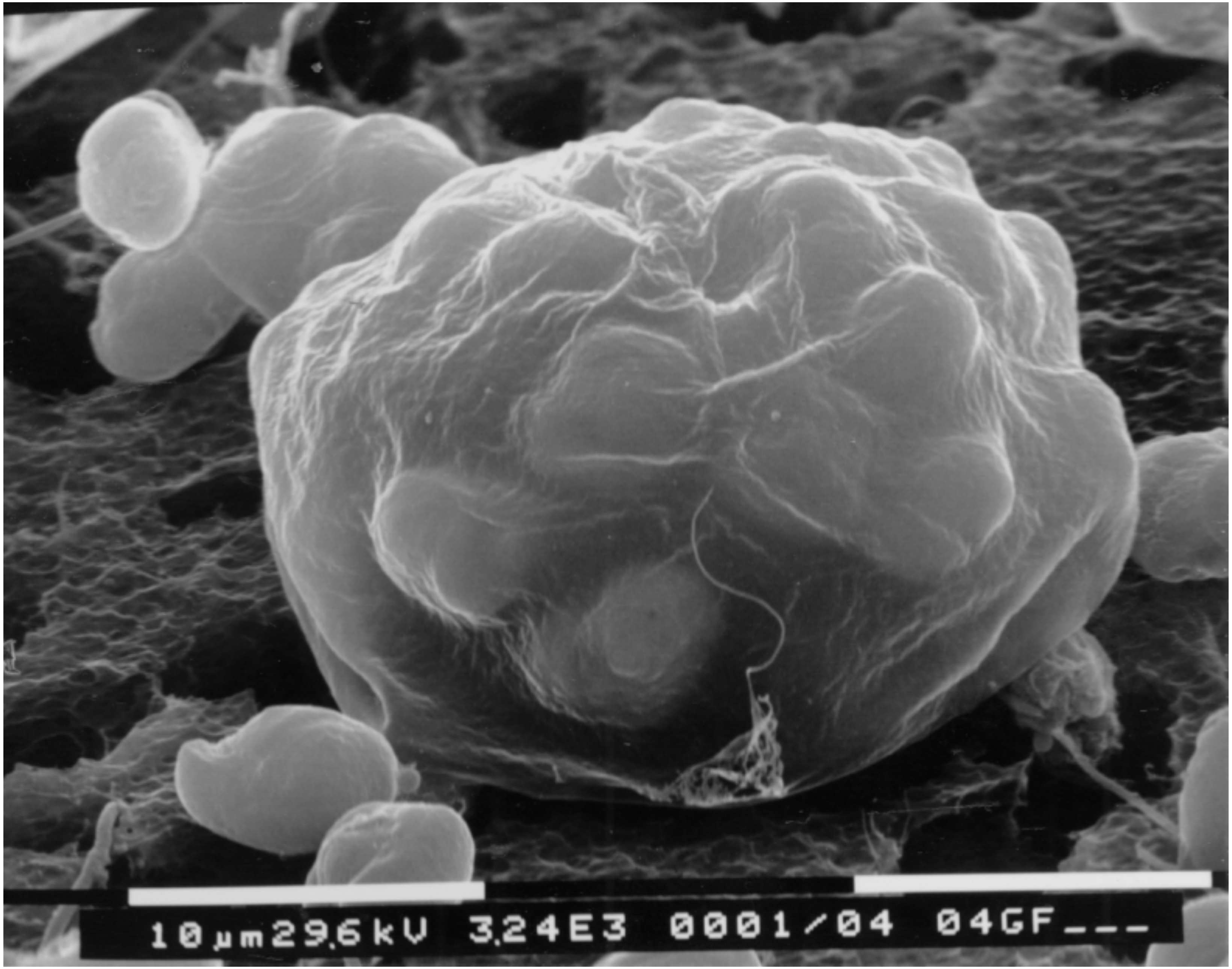



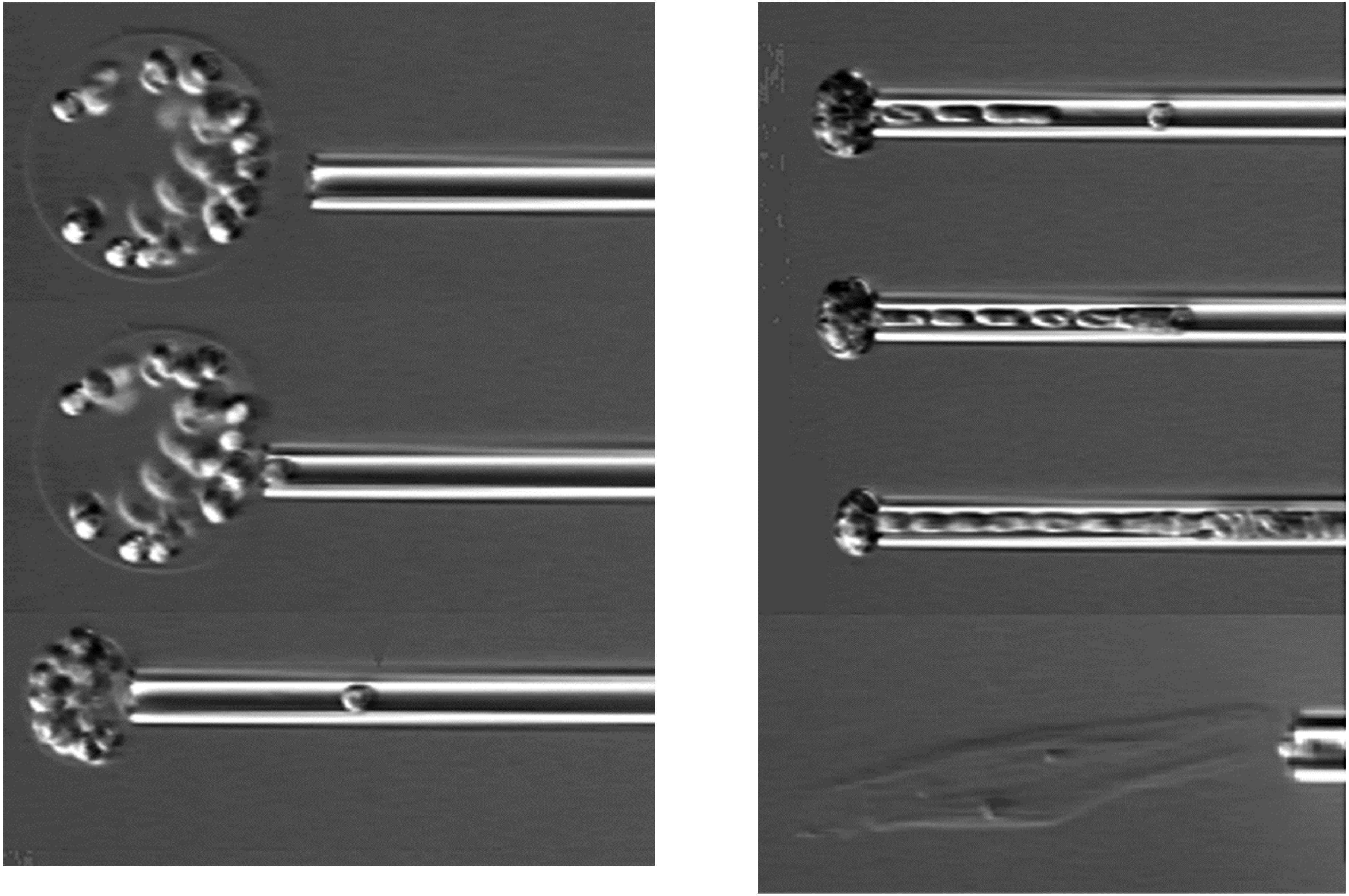



# *Phaeocystis*, colony and solitary cells



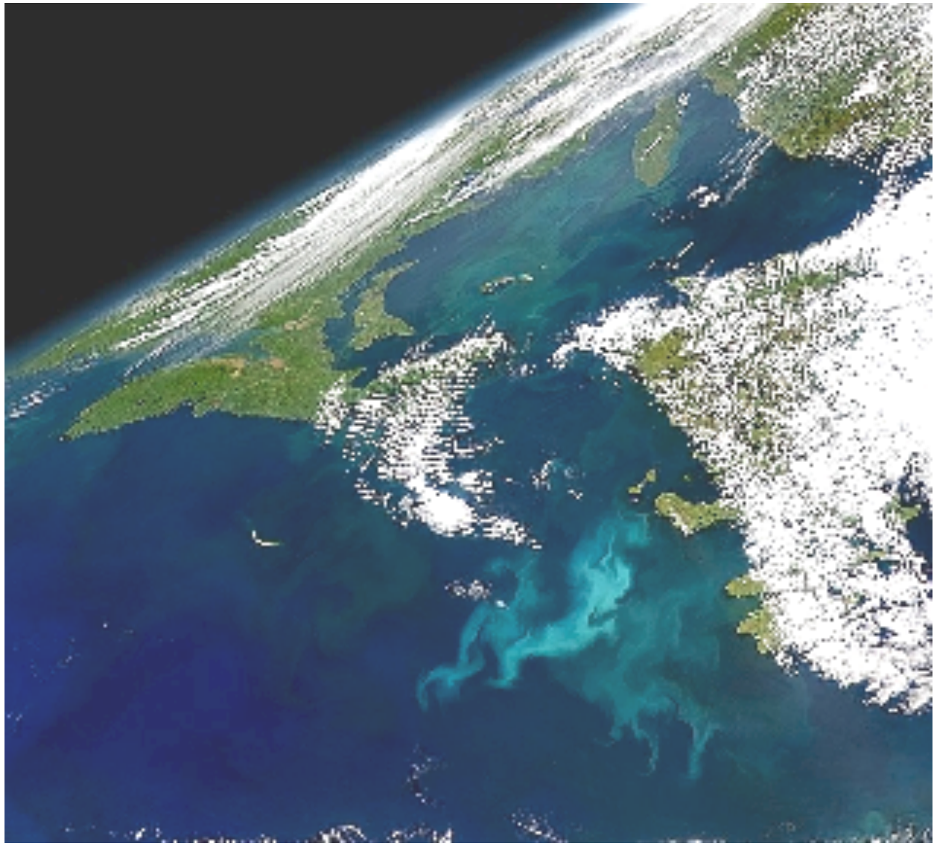
# *Phaeocystis* colony

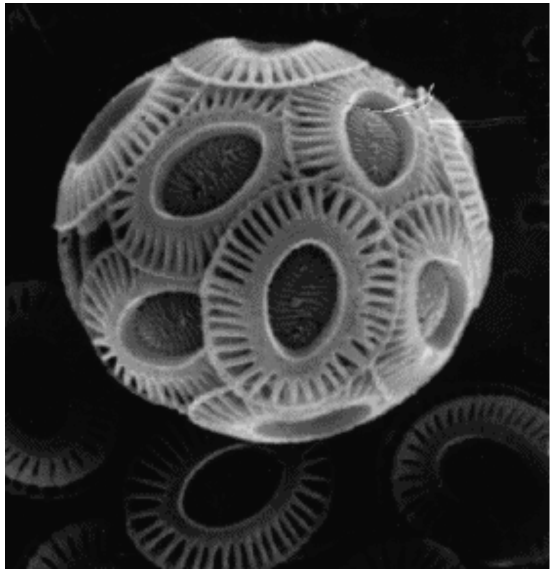




The tensile alternative: *Phaeocystis* colony under suction reveals that it is enclosed in a tough organic skin. Note extruded skin at right bottom.

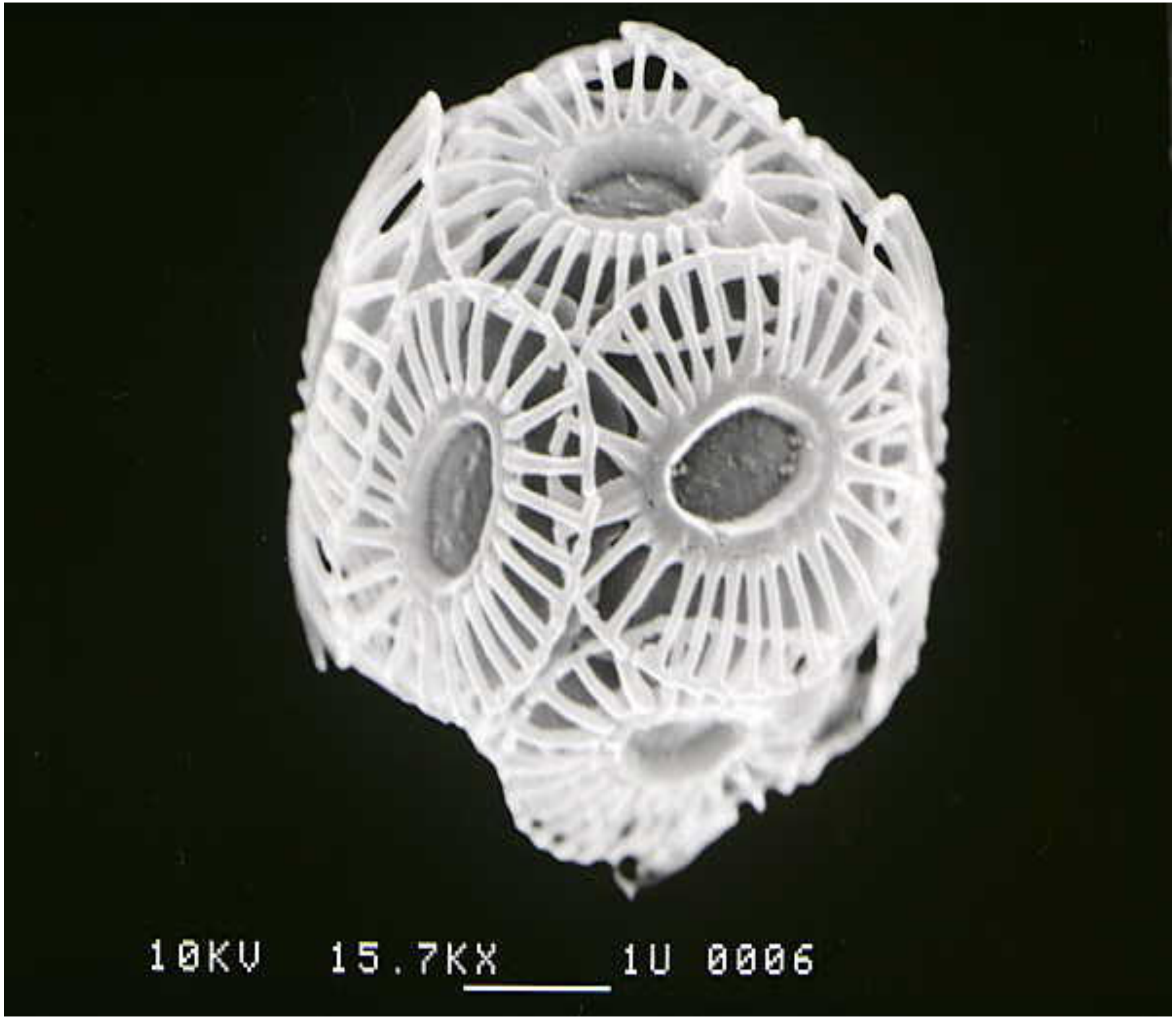
Hamm et al. MEPS 1999



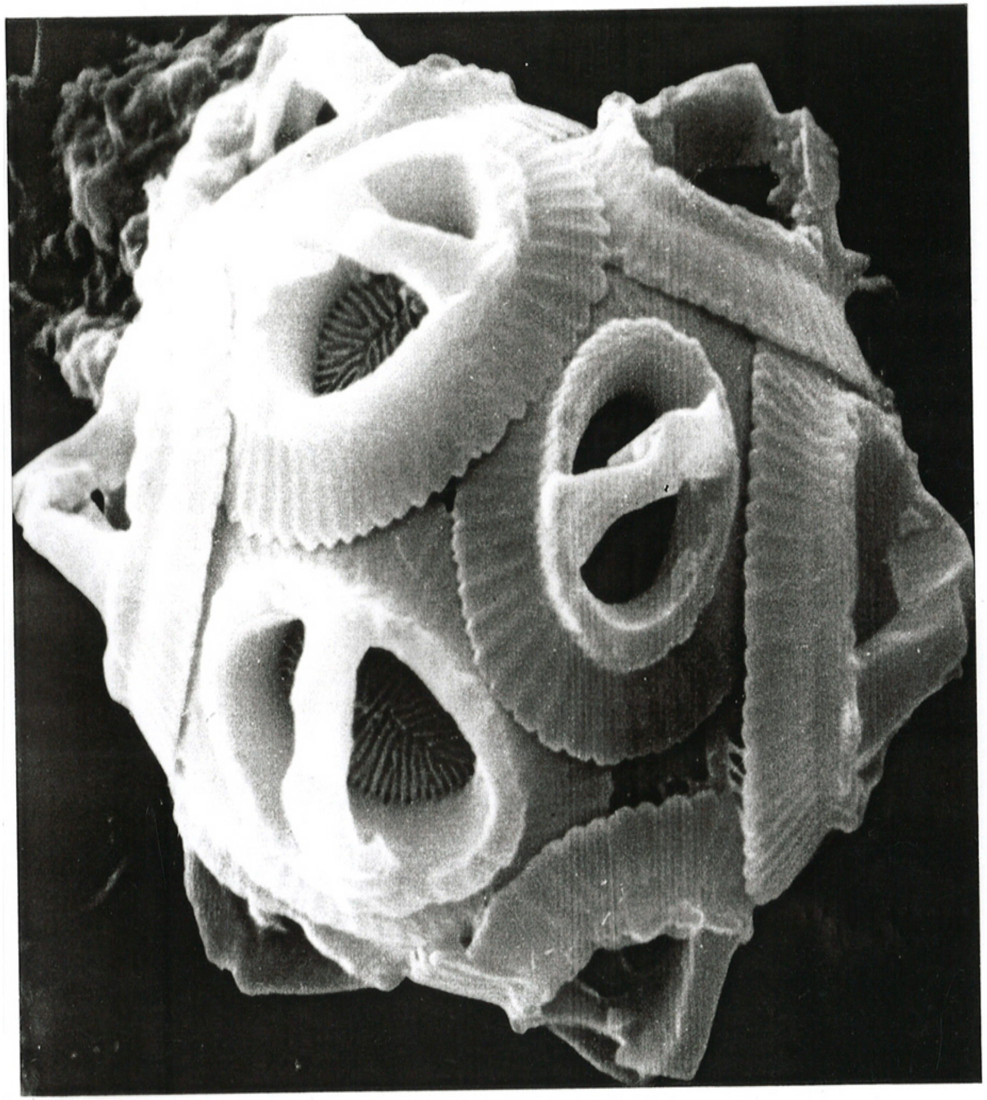


Coccolithophorids: Calcite plates (coccoliths)
*Emiliania huxleyi*

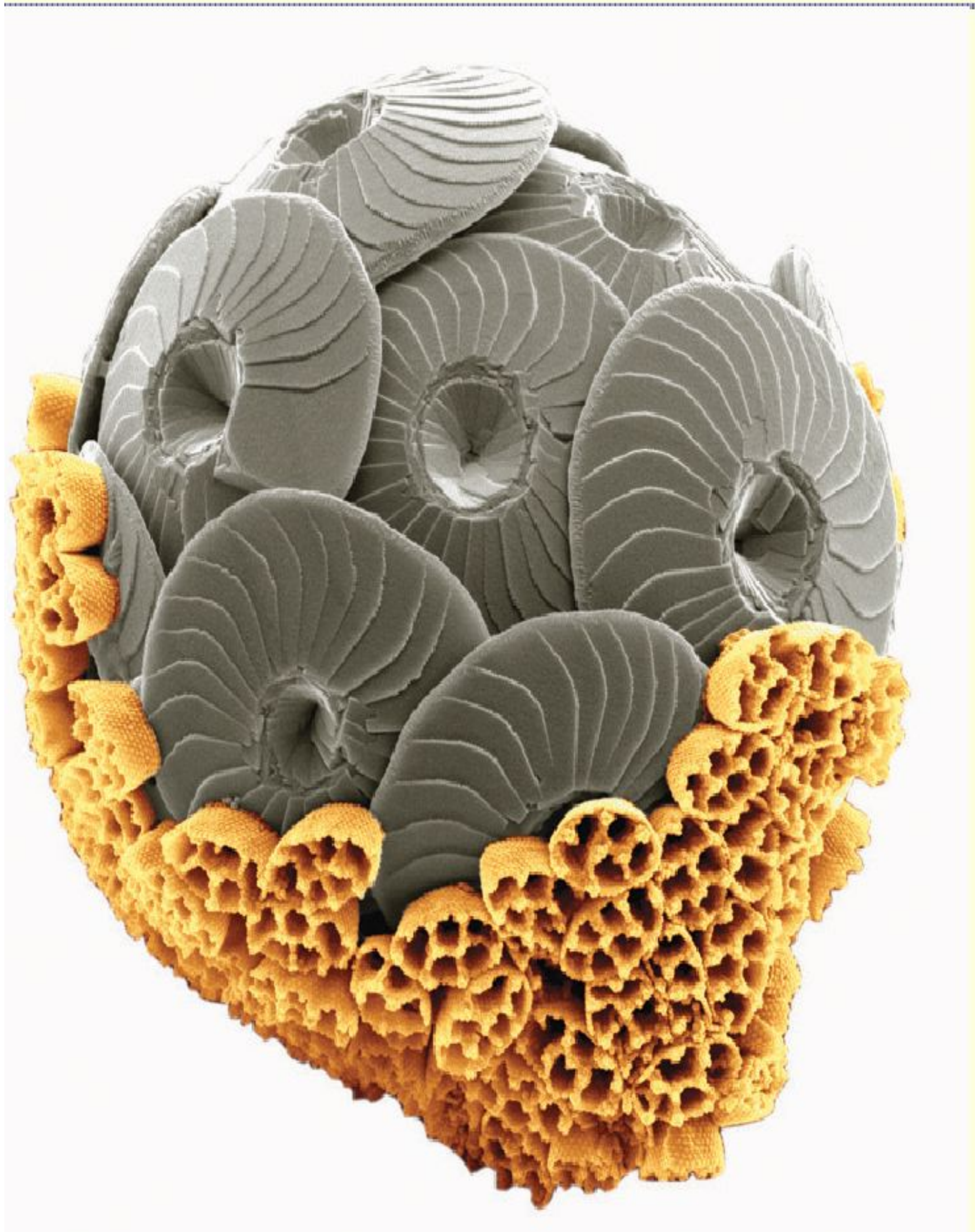
# Emiliania huxleyi (Coccolithophorid)

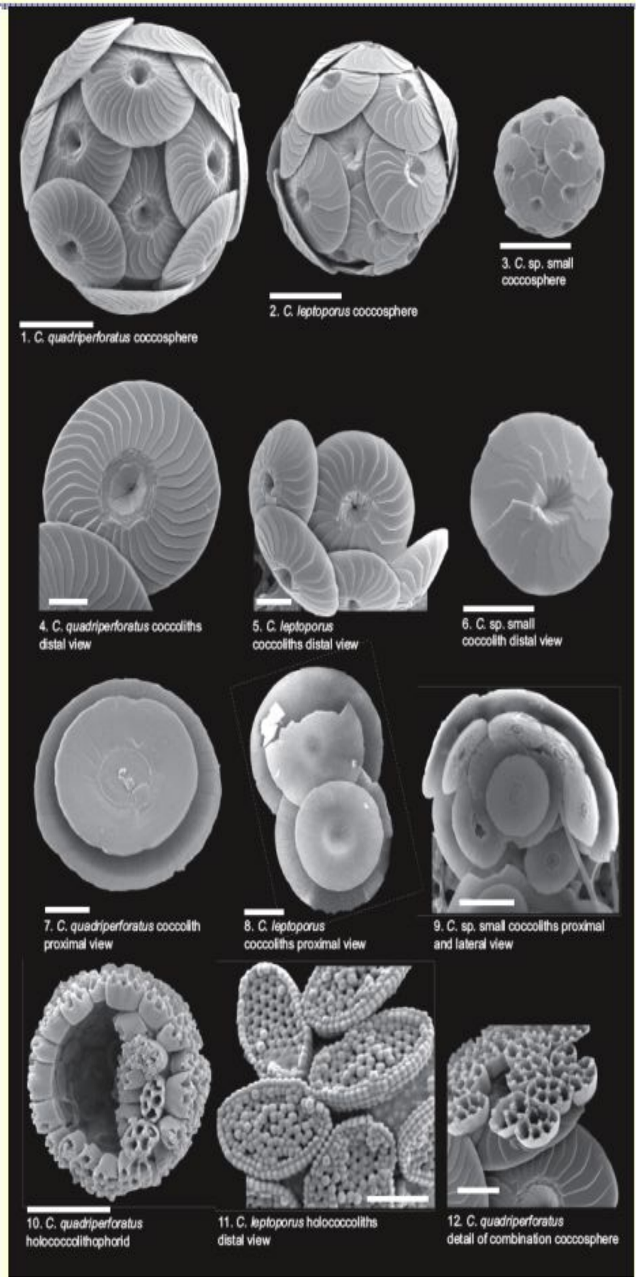


# Coccolithophord: *Gephyrocapsa*



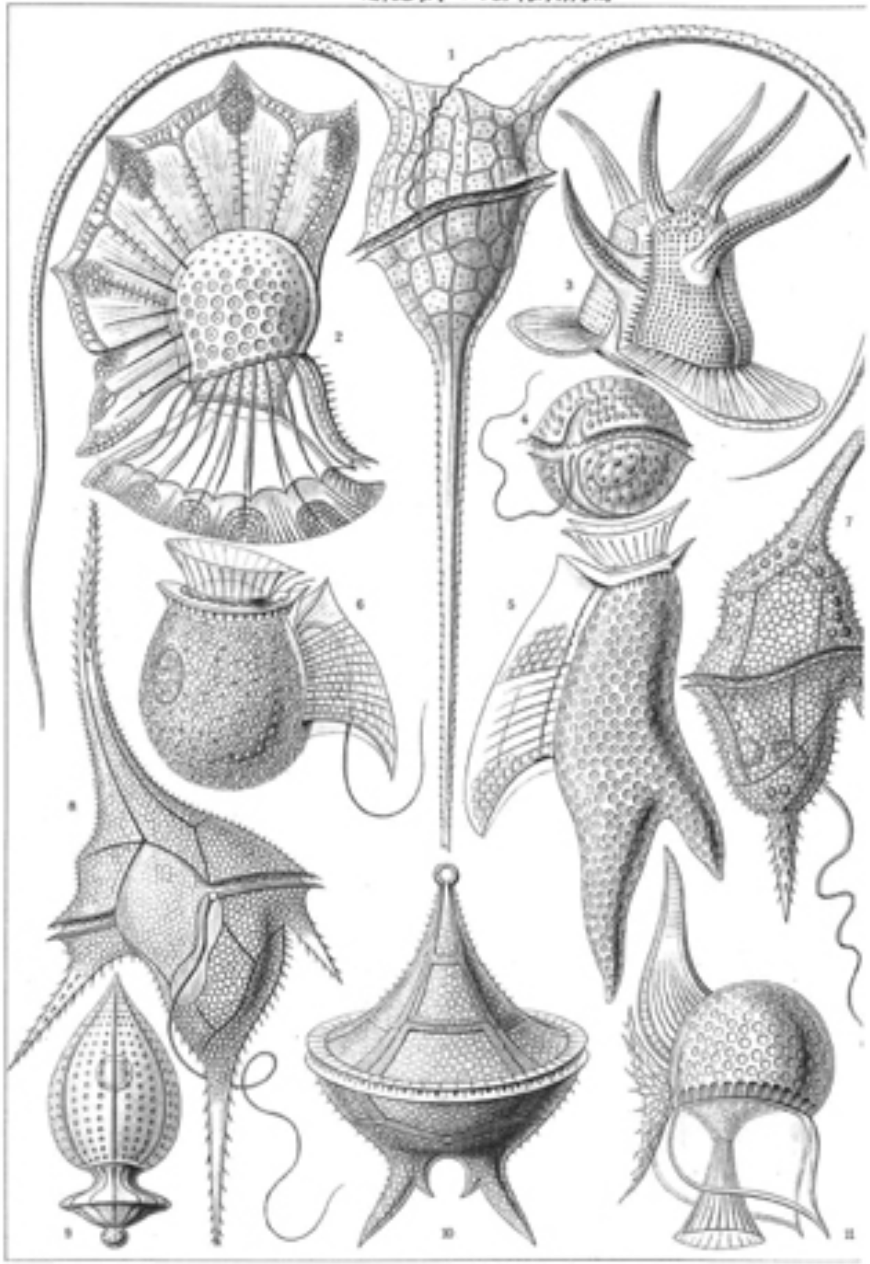
Coccolithophorid *Gephyrocapsa oceanica* covered by coccoliths with two bridge-like elements arching across a central pore; Sydney coastal waters; diameter 15$\mu$m.



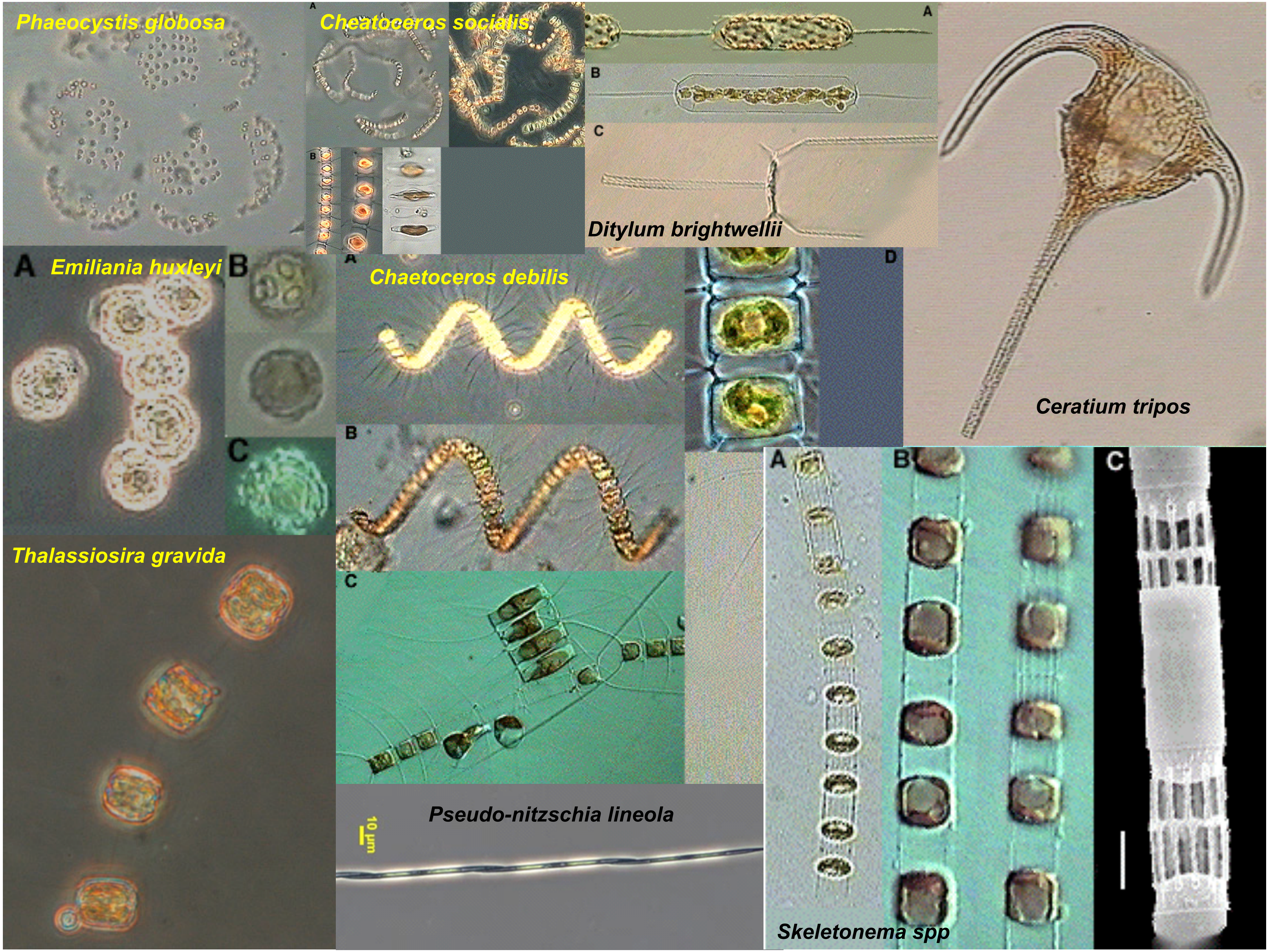

1. C. quadriperforatus coccosphere
2. C. leptoporus coccosphere
3. C. sp. small coccosphere
4. C. quadriperforatus coccoliths distal view
5. C. leptoporus coccoliths distal view
6. C. sp. small coccolith distal view
7. C. quadriperforatus coccolith proximal view
8. C. leptoporus coccoliths proximal view
9. C. sp. small coccoliths proximal and lateral view
10. C. quadriperforatus holococcolithophorid
11. C. leptoporus holococcoliths distal view
12. C. quadriperforatus detail of combination coccosphere

What is the function of these forms?

Tafel 14 - Peridinium

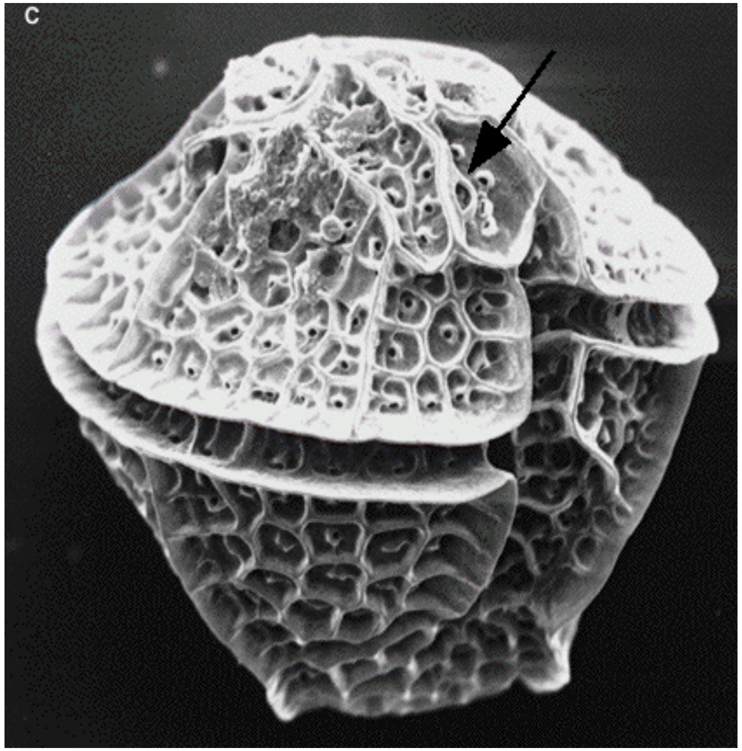


Peridinea. Geißelhütchen.



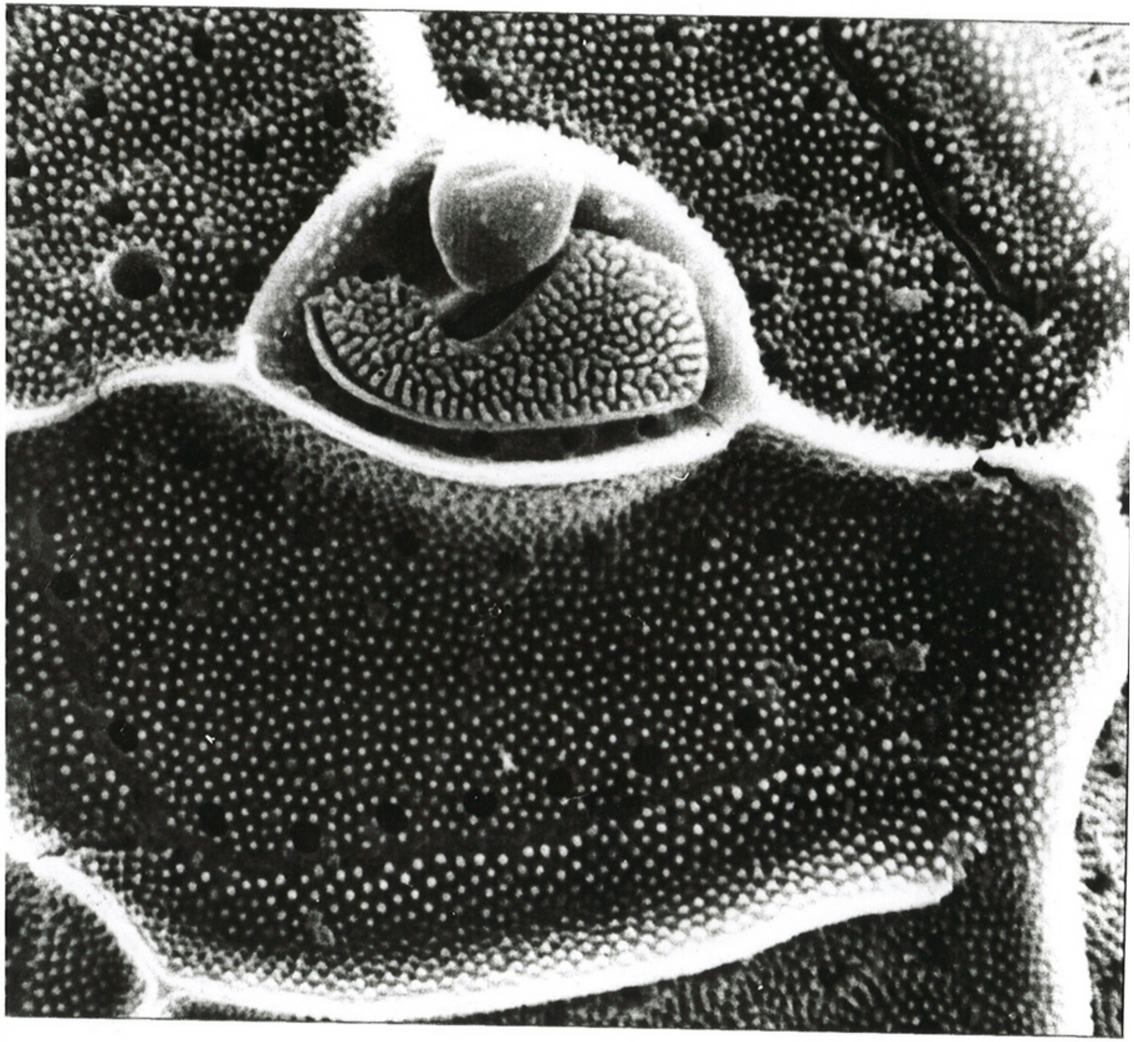
Phaeocystis globosa
A
Cheatoceros socialis
B
A
B
C
Ditylum brightwellii
A
Emiliania huxleyi
B
C
A
Chaetoceros debilis
B
C
D
Ceratium tripos
Thalassiosira gravida
Pseudo-nitzschia lineola
10 µm
A
B
C
Skeletonema spp

# Thecate dinoflagellates carrying armour of thick cellulose plates




Kuylenstierna and Karlson

# Close-up of dinoflagellate armour



Detail of thecal ornamentation and apical pore of the dinoflagellate *Pyrodinium bahamense.*

# Chemical defences (toxins or herbivore deterrants)

- The molecules comprising an organism fall into two categories:
- Primary metabolites are part of the life-supporting and reproductive machinery.
- Secondary metabolites (SMs) have other functions, primarily defence.
- The exact function of most SMs are unknown. Their occurrence varies even wirhin species and many are induced.
- A large variety of SMs have been identified in phytoplankton of which molecules toxic to humans have attracted most attention.
- These are neurotoxins that cause paralysis or amnesia, metabolic toxins that affect various organs such as lungs or alimentary canal. Their function is largely unknown but their effect on higher trophic levels, including humans, can be devastating.
- Recently, polyunsaturated aldehydes have been found in some diatom species that are produced from structural fatty acids by the action of a specific enzyme that is activated when the cell is crushed. Their role is under debate.

# Aldehyde suppression of copepod recruitment in blooms of a ubiquitous planktonic diatom

Adrianna Ianora[1], Antonio Miralto[1], Serge A. Poulet[2], Ylenia Carotenuto[1], Isabella Buttino[1], Giovanna Romano[1], Raffaella Casotti[1], Georg Pohnert[3], Thomas Wichard[3], Luca Colucci-D'Amato[4], Giuseppe Terrazzano[5] & Victor Smetacek[6]

[1]*Ecophysiology Laboratory, Stazione Zoologica "A. Dohrn", Villa Comunale, 80121 Naples, Italy*
[2]*Station Biologique de Roscoff, CNRS, Place Georges Teissier, 29682 Roscoff, France*
[3]*Max Planck Institute for Chemical Ecology, Hans Knöll Strasse 8, D-07745 Jena, Germany*
[4]*Institute of Endocrinology and Experimental Oncology, CNR, Via Pansini 5, 80131 Naples, Italy*
[5]*Department of Cellular and Molecular Biology and Pathology, University of Naples, Via Pansini 5, 80131 Naples, Italy*
[6]*Alfred Wegener Institute for Polar and Marine Research, Am Handelshafen 12, 27570 Bremerhaven, Germany*

The growth cycle in nutrient-rich, aquatic environments starts with a diatom bloom that ends in mass sinking of ungrazed cells and phytodetritus[1]. The low grazing pressure on these blooms has been attributed to the inability of overwintering copepod populations to track them temporally[2]. We tested an alternative explanation: that dominant diatom species impair the reproductive success of their grazers. We compared larval development of a common overwintering copepod fed on a ubiquitous, early-blooming diatom species with its development when fed on a typical post-bloom dinoflagellate. Development was arrested in all larvae in which both mothers and their larvae were fed the diatom diet. Mortality remained high even if larvae were switched to the dinoflagellate diet. Aldehydes, cleaved from a fatty acid precursor by enzymes activated within seconds after crushing of the cell[3], elicit the teratogenic effect[4]. This insidious mechanism, which does not deter the herbivore from feeding but impairs its recruitment, will restrain the cohort size of the next generation of early-rising overwinterers. Such a transgenerational plant–herbivore interaction could explain the recurringly inefficient use of a predictable, potentially valuable food resource—the spring diatom bloom—by marine zooplankton.

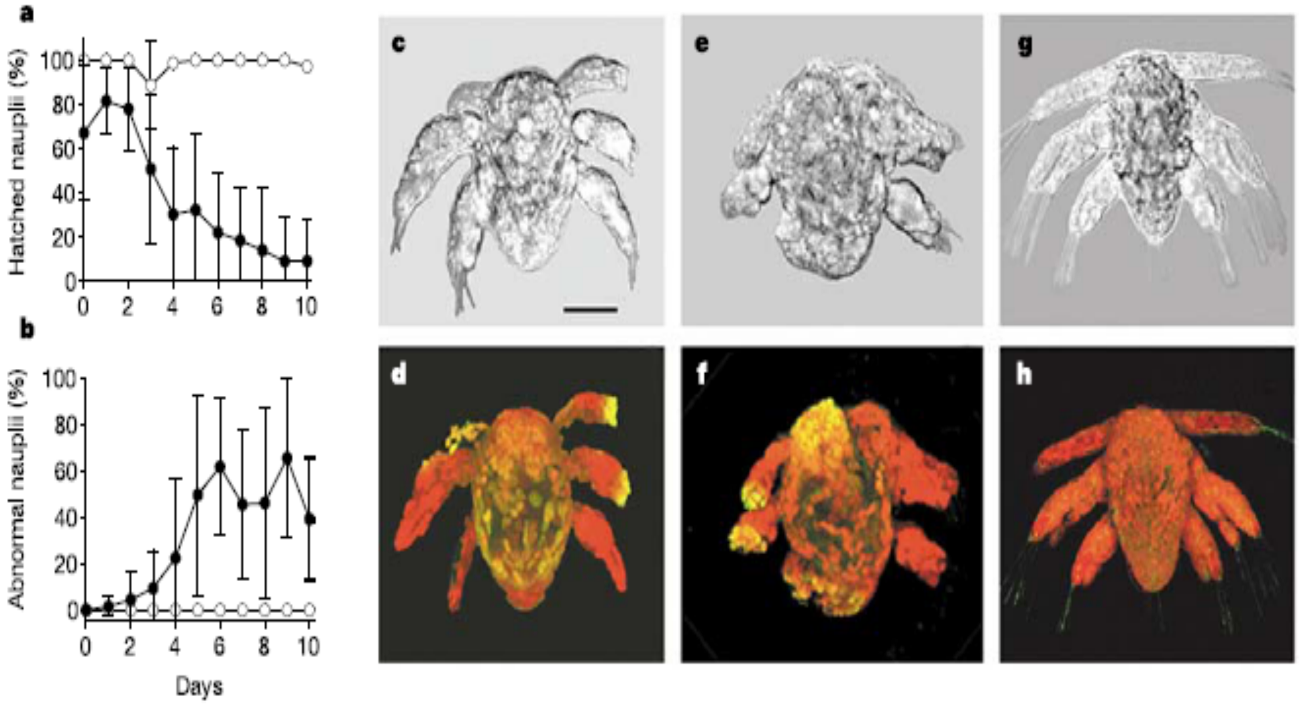



**Figure 3** Effects of diet on *C. helgolandicus* offspring fitness. **a**, After ten days of feeding, the viability of eggs spawned by *C. helgolandicus* females fed the diatom *S. costatum* SKE (filled circles) dropped to <20% compared with >95% with the control dinoflagellate *P. minimum* PRO (open circles). **b**, After five days of feeding on SKE, 45–65% of the hatched nauplii were abnormal. **c**, **d**, Such nauplii had deformed limbs that were positive for TUNEL staining (yellow, **d**) specific for apoptosis. **e**, **f**, After nine days of feeding on SKE, the degree of teratogenesis increased and nauplii were strongly deformed. **g**, **h**, Nauplii generated from females fed the control PRO diet appeared normal and stained negatively with TUNEL (**h**), indicating that nuclei were not apoptotic. Scale bar, 90 μm.

Ianora et al. 2004

## Example of carnivore deterrant

*Clione*, a carnivorous pteropod (sea butterfly) without a shell

An amphipod (crustacean) carries Clione on its back with 2 legs modified for the purpose.

Why?

Jim Mastro

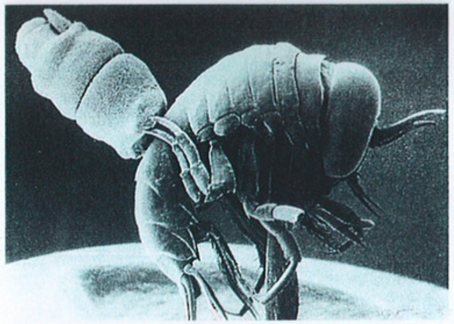


**Figure 3.** Intrigued by the chemical interactions found between sponges and their predators on the sea floor, the authors searched for interactions farther up the water column. There they found the sea butterfly, *Clione antarctica*, a snail without a shell (*top*). Sea butterflies were also observed in an unusual configuration on the backs of the small amphipod crustacean, *Hyperiella dilatata*, as shown in the electron micrograph. In some locations up to 74 percent of the amphipods was carrying a sea butterfly.

J.B. McClintock & B.J. Baker (1998)
Chemical Ecology in Antarctic Seas
American Scientist, Vol. 86: 254-263

# Amphipod capturing or kidnapping a *Clione* to carry on its back

a b c

**Figure 4.** Association between the sea butterfly and the amphipod is not accidental. Rather, the amphipod actively abducts the sea butterfly. First the amphipod grasps the sea butterfly *(a)*, then it throws the butterfly onto its back *(b)* and secures it there *(c)* before swimming off. Such an arrangement slows down the amphipod and makes maneuvering more cumbersome.

J.B. McClintock & B.J. Baker (1998)
Chemical Ecology in Antarctic Seas
American Scientist, Vol. 86: 254-263

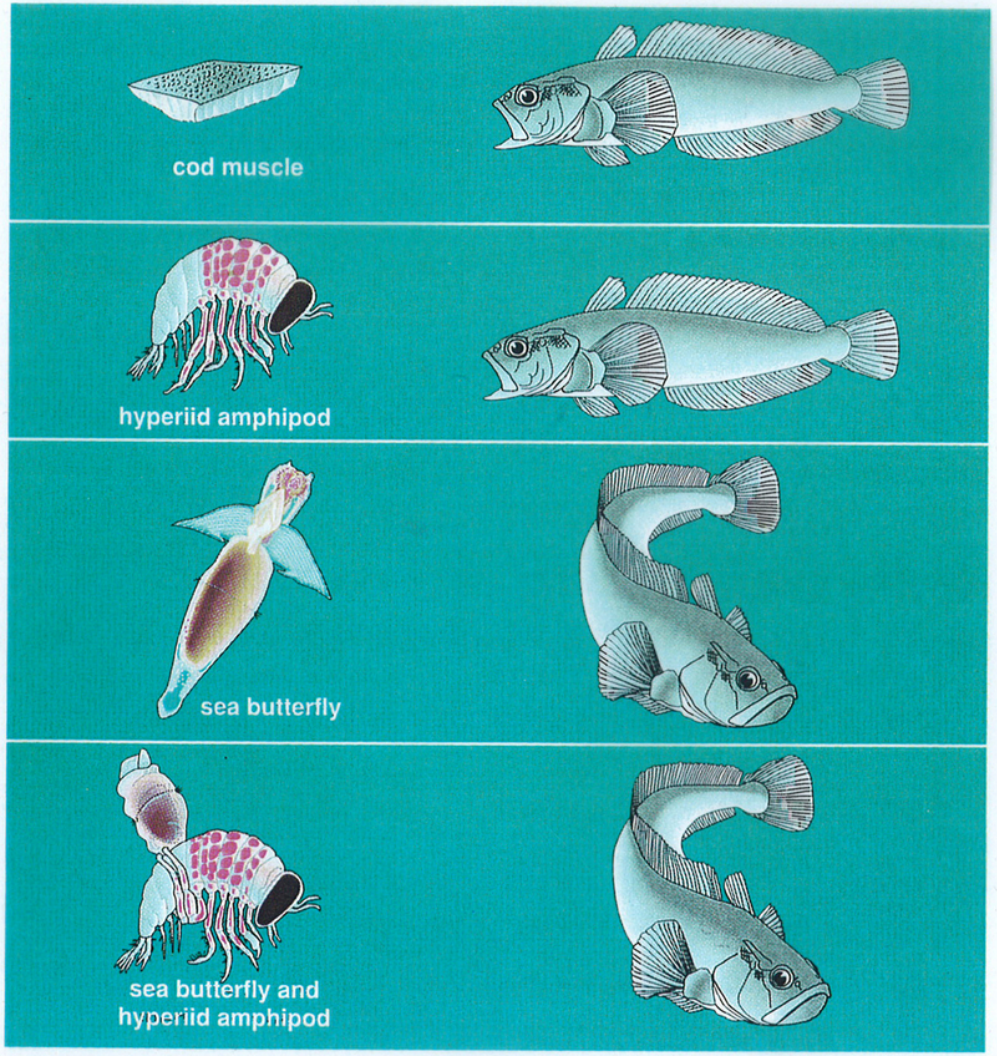



Figure 5. Sea-butterfly abduction by the hyperiid amphipod *H. dilatata* might make sense if the butterfly contains a chemical that deters predators. To test this hypothesis, the authors offered a variety of foods to fish that are the natural predators of the amphipod. As a control, cod-fish muscle was offered to the fish, which accepted it readily. They also ate the amphipod when it was offered alone. But the fish would not eat the sea butterfly, whether it was alone or in combination with the amphipod. (Drawings are not done to scale.)



J.B. McClintock & B.J. Baker (1998)
Chemical Ecology in Antarctic Seas
American Scientist, Vol. 86: 254-263

Fish are deterred by amphipods carrying the *Clione*.

It has been easier for the amphipod to modify 2 legs than to produce toxins itself.

The toxins are aldehydes.

Escape by flight, evolutionary Olympics

or by

Increasing size (size escape), but there is always „room at the top“, predators can simply grow bigger.

Bacteria can escape from their predators the nanoflagellates at various stages of attempts at capture.

Mechanisms of grazing resistance in aquatic bacteria
Dissertation von Carsten Matz

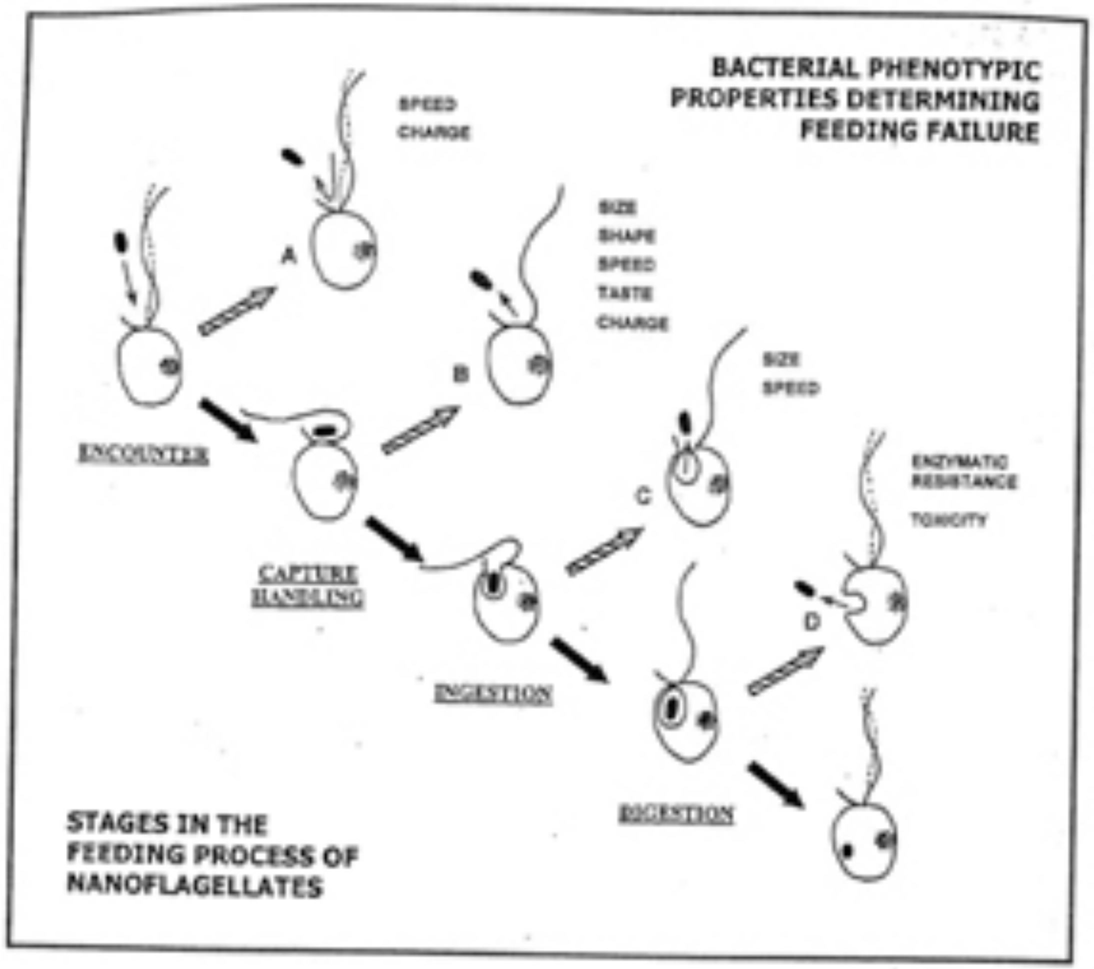



Figure 1. Predator-prey interactions in the feeding process of a heterotrophic nanoflagellate based on video microscopy. Sequence of salient stages in the feeding behaviour (*below*) and the respective bacterial phenotypic traits determining stepwise feeding failure and prey resistance (*above*, A–D).

## Prey handling time by pallium-Feeding dinoflagellate

## Prey escape and capture



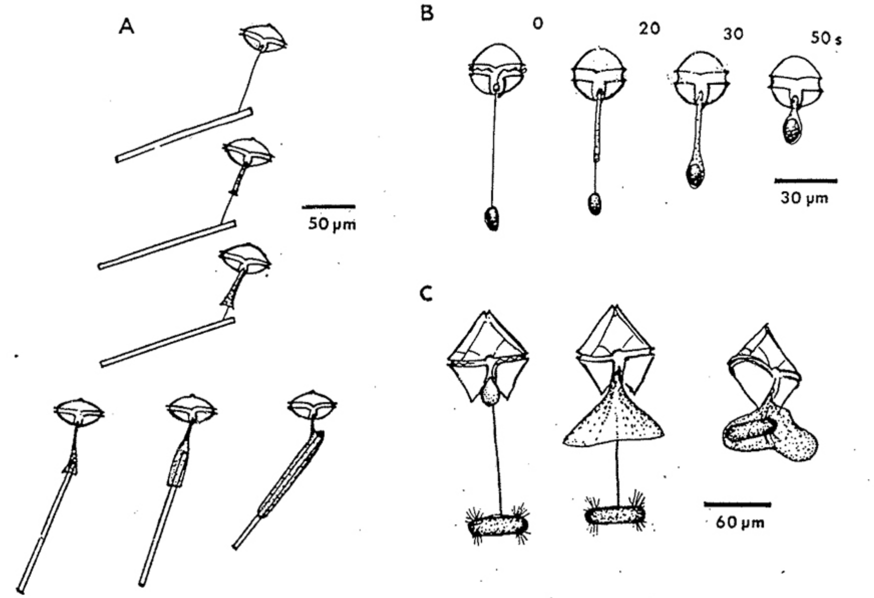



FIG. 2A–C. Pseudopod deployment in thecate heterotrophic dinoflagellates. (A) Sequence of approx. 3 min duration showing pseudopod deployment of *Zygabikodinium lenticulatum* feeding upon *Leptocylindrus danicus*. Note primary attachment filament. (B) Similar sequence of *Oblea rotunda* feeding on *Pyramimonas* sp., with times given. (C) *Protoperidinium conicum* feeding on *Corethron hystrix*. Note broadness of emerging pallium.

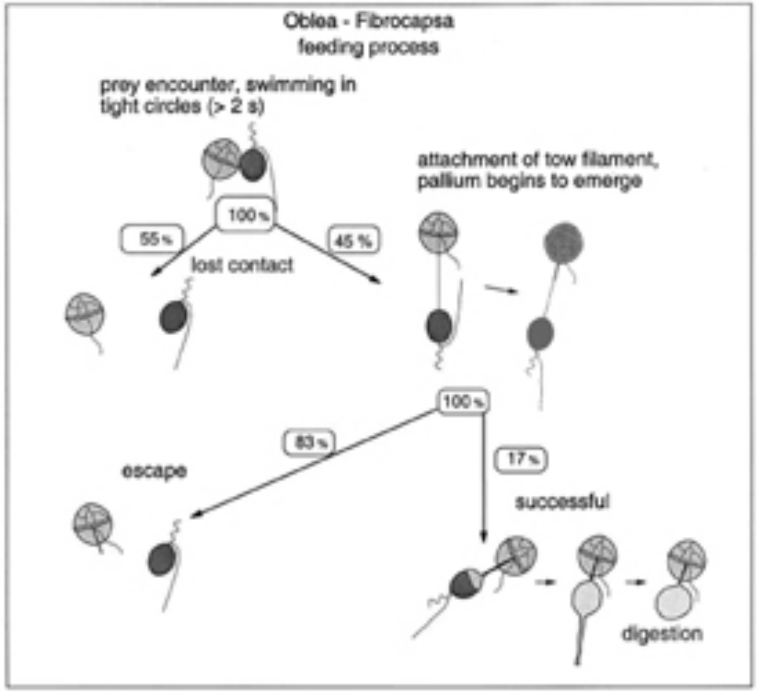
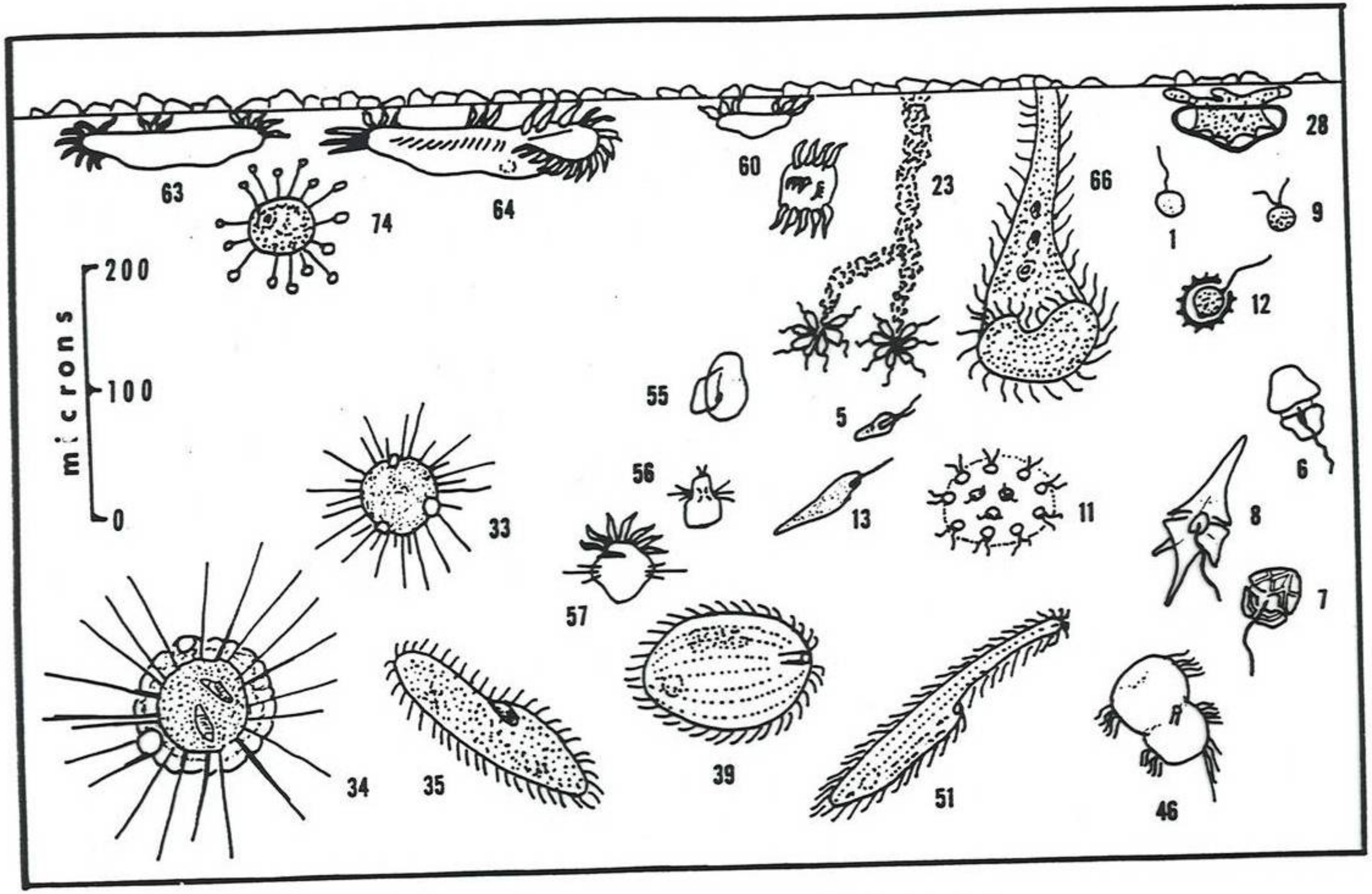



Fig. 10. *Oblea rotunda*. Observational quantification of different steps in the feeding process. Total numbers of observations were 471 and 606 for quantifying 'lost contact' or 'escape', respectively

Tillmann, U. & Reckermann, M. (2002): Dinoflagellate grazing on the raphidophyte *Fibrocapsa japonica*. Aquat. Microb. Ecol., 26: 247-257

Neuston and plankton from eutrophic fresh water

They are slow-swimming, less defended organisms than their marine counterparts

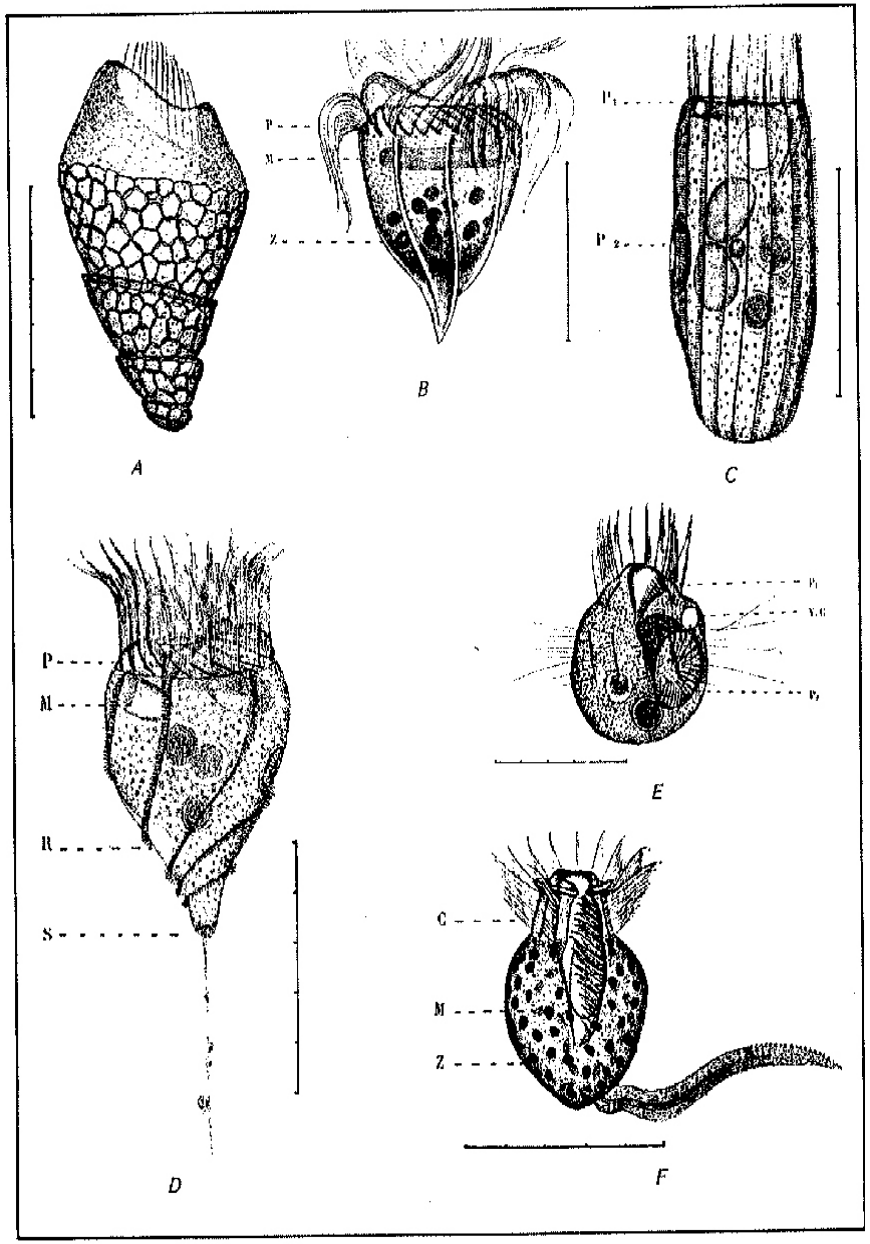



NEUSTON AND PLANKTON

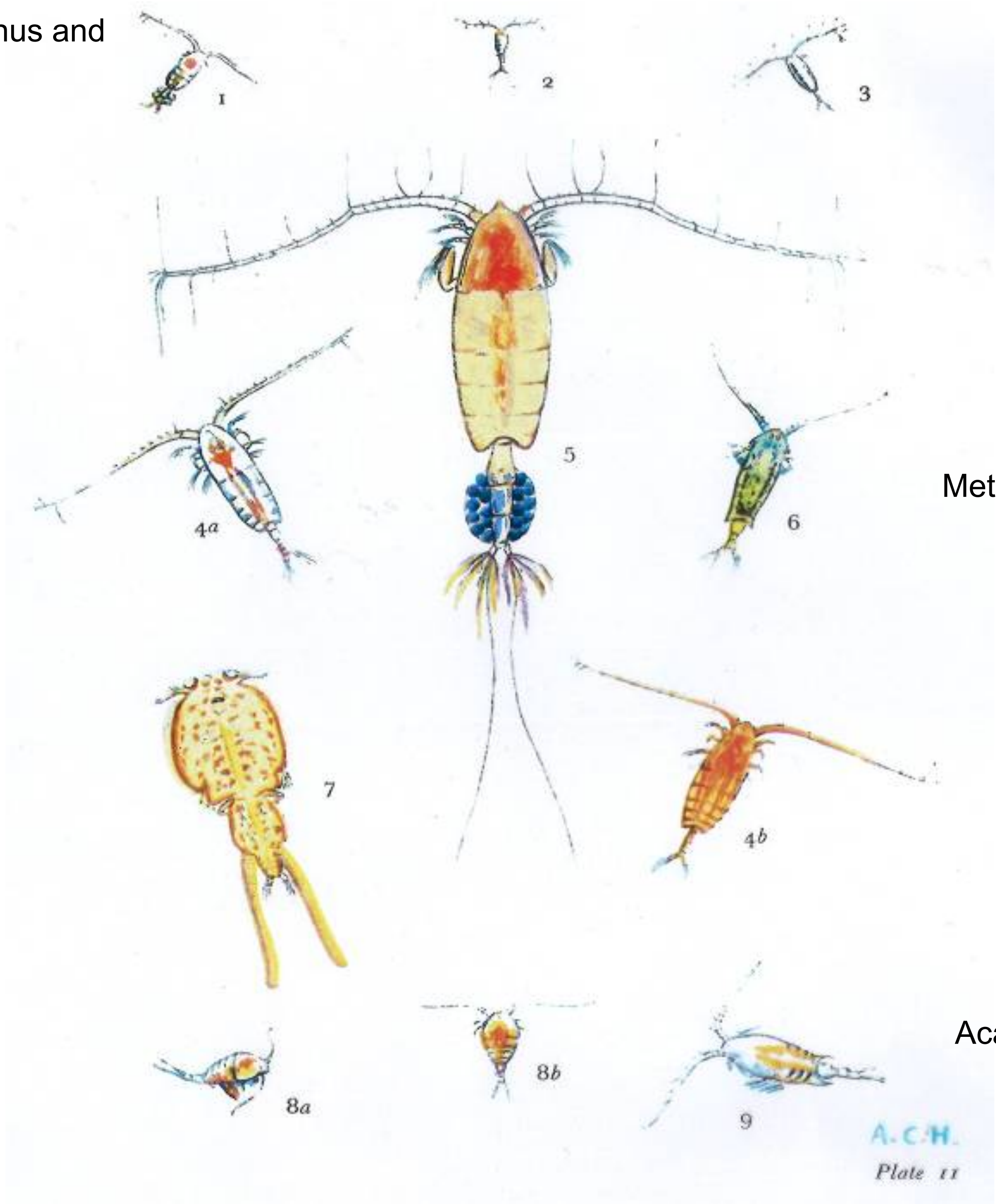
Choreotrichs
formerly oligotrichous ciliates are fast swimmers with a tough cell wall
Typical ciliates of the marine pelagial. Many are cosmopolitan.

Scale bars are 50 microns.

PLATE 24-19. Some examples of oligotrichous ciliates (Spirotricha) from the plankton (bars=50 µm, with 10 µm divisions). (A) *Laboea strobila*; (B) *Strombilidium velox*; (C) *Strombidinopsis claparedei*; (D) *Strombilidium adherens*; (E) *Halteria grandinella*; (F) *Tontonia gracillima*. From E. Fauré-Fremiet, 1924, *Bull. Biol. France Belgique* Suppl. 6, 171 p.



Common pelagic copepods painted at same scale by Alister Hardy These genera are cosmopolitan



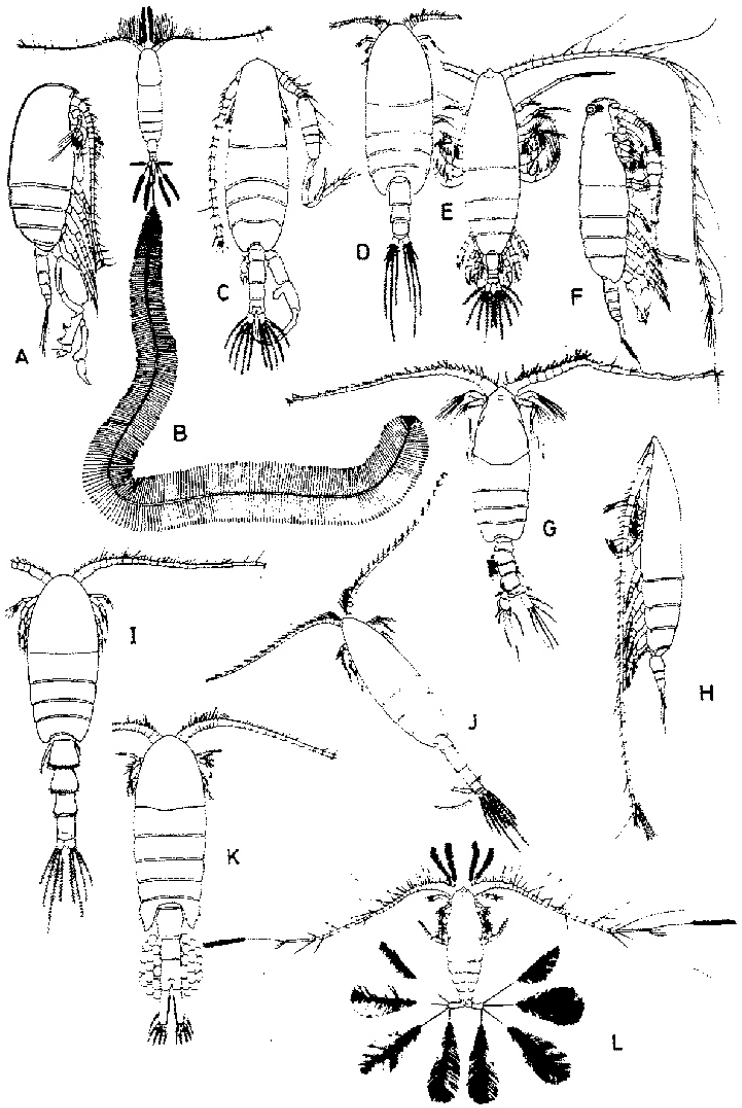



**Figure 2.2.1.** The diversity of calanoid body form. **A.** Diaixidae. **B.** Calocalanidae. **C.** Acartiidae. **D.** Pseudocyclopidae. **E.** Augaptilidae. **F.** Pontellidae. **G.** Metridinidae. **H.** Eucalanidae. **I.** Stephidae. **J.** Euchaetidae. **K.** Temoridae. **L.** Calocalanidae. The range of gross body morphologies exhibited within the Calanoida is relatively small compared to that found in the other large orders.

Calanoids are the common pelagic copepods. Note torpedo-shaped bodies



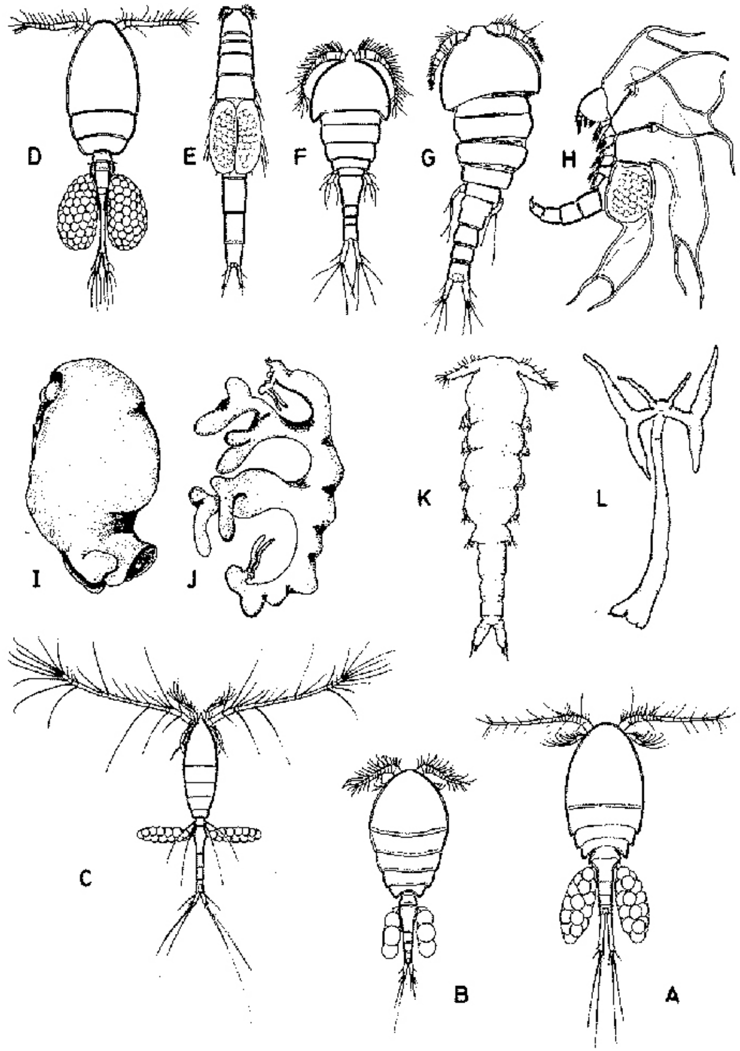
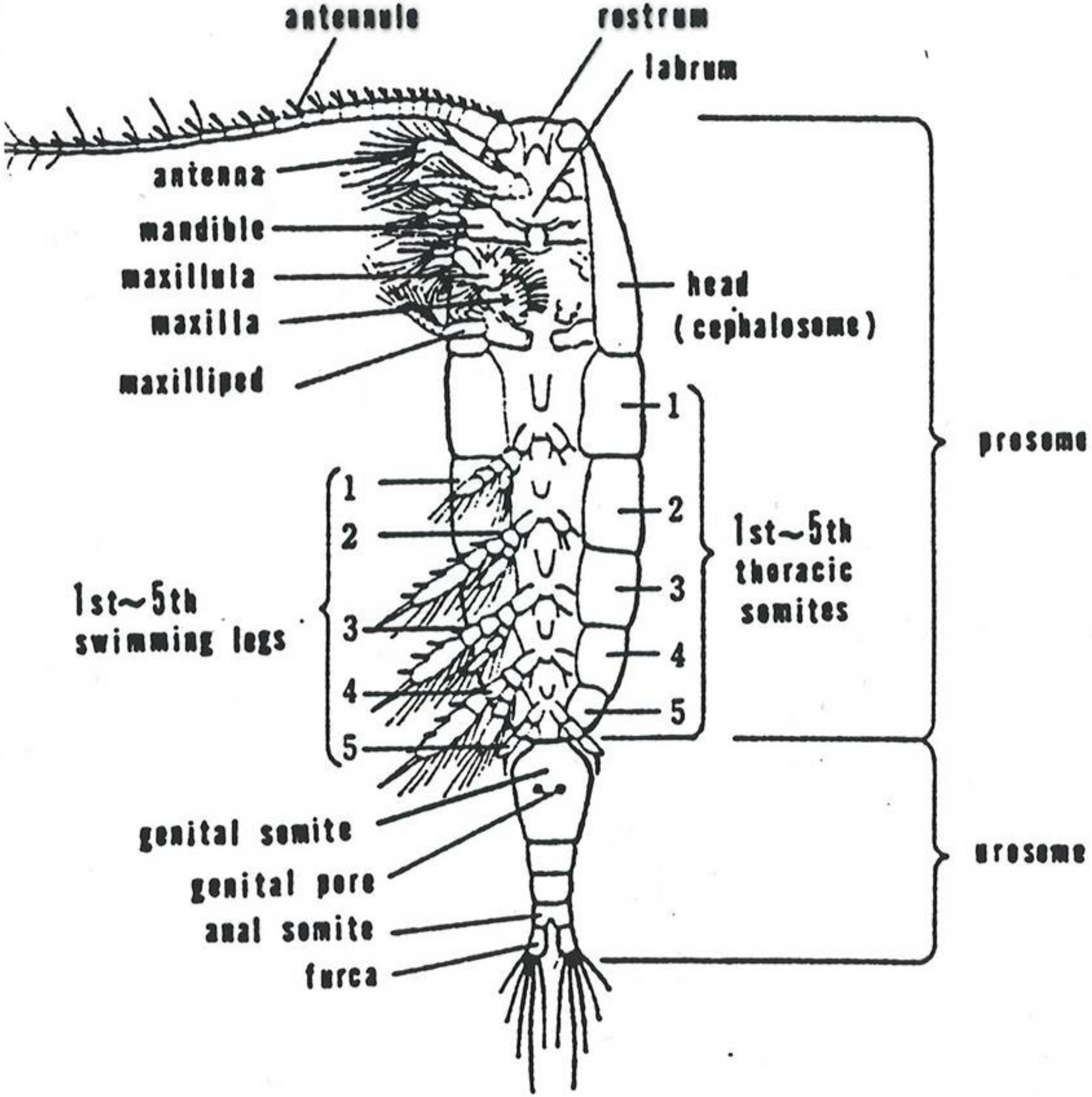



**Figure 2.8.1.** The diversity of cyclopoid body form. **A.** Cyclopidae. **B.** Cyclopinidae. **C.** Oithonidae. **D.** Thespesiopsyllidae. **E.** Ascidicolidae. **F.** Archinotodelphyidae. **G.** Mantridae. **H.** Notodelphyidae. **I.** Chordeumiidae. **J.** Cucumaricolidae. **K.** Ozmanidae. **L.** Lernaeidae.

Some cyclopoids are pelagic but many are parasites. Note differences in shape.

Morphology of a pelagic copepod, note investment in muscle



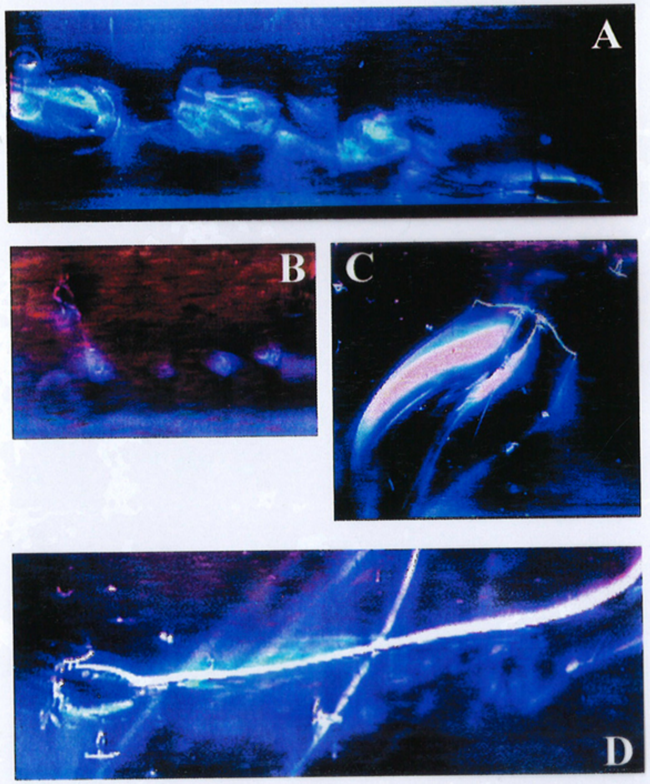


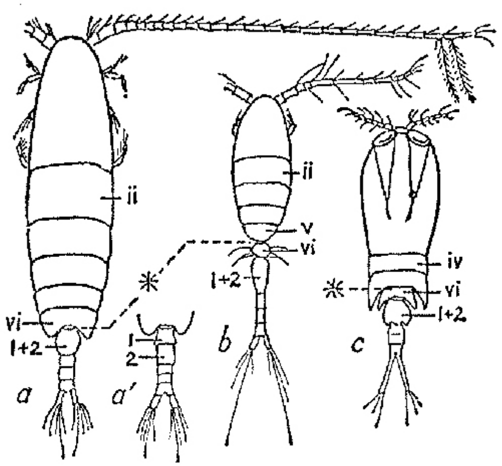

**Fig. 3. A.** Three toroidal vortices (30 Hz) shed by the escape movements of an adult copepod, *Euchaeta rimana* (cephalothorax 2.4 mm long; copepod is the dark silhouette in the lower right corner). **B.** Four vortices (100 Hz) of clock-wise sense shed by the escape movements of a juvenile copepod, *E. rimana* (cephalothorax 1.5 mm long; copepod is seen in profile in the upper left area of the videoimage). **C** and **D.** Wakes of free-swimming copepods, *E. rimana* (cephalothorax 2.4 mm long), swimming through seawater. **C.** Plan view of copepod swimming upward. **D.** Profile view of copepod swimming to the left. Note how smooth and thin the hydrodynamic trail is. The density gradient in the seawater, necessary for Schlieren photography, is enhanced visually with the color gradient. The white image shows the water moved by the copepod into an adjacent layer of water of differing density.

signal is that of a predator. Like a spider and its web, the copepod and its feeding current can be examined as a unit, as recommended by Strickler (1985). Vibrations transmitted along the web inform the spider of the position of the signal source within its web. Signals entrained along the streamlines and intersecting certain receptors inform the copepod of the position of the source within the volume of its feeding current.

Within the copepod feeding current, flow velocities remain relatively stable. Using metabolic energy to

←

oviducts in the translucent body of the copepod are deep blue. **B** and **C.** Isotachs (lines of equal speed) of fluid flow surrounding a tethered copepod, *Euchaeta rimana* (cephalothorax 2.4 mm long). Each isoline represents increments of 1 mm $s^{-1}$ of flow speed (except for the 1.5 to 2.0 mm $s^{-1}$ isolines). **B.** Dorsal view of flow: The innermost yellow isoline of the plan view represents a maximum velocity of 20 mm $s^{-1}$. The blue isoline crossing the distal tip of each antennule represents 1.5 mm $s^{-1}$ flow. These are separated by only 2 mm. **C.** Lateral view of the flow: The innermost yellow isoline on the dorsal side of the copepod body (at left) represents 17 mm $s^{-1}$ flow. **D.** Schlieren videoimage of *Pareuchaeta* sp. showing the hydrodynamic imprint left by oscillatory movements of the locomotory appendages, the second antennae. The frequency of the movement is 30 Hz. The distance between ripples (9 ripples per cephalothorax length) is approximately 500 μm. The density gradient in the seawater, necessary for Schlieren photography, is enhanced visually with the color gradient. The white image shows the water moved by the copepod into an adjacent layer of water of differing density.





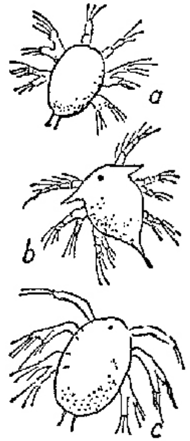




FIG. 49 (*left*). Showing how to distinguish the two main types of planktonic copepod: *a Calanus*, a typical member of the Gymnoplea, compared with *b* and *c*, *Oithona* and *Corycaeus*. members of the Podoplea. The movable articulation between the front and back divisions of the body is marked by an asterisk; the roman and arabic numerals mark some of the segments of the true thorax and abdomen. The first and second segments of the abdomen are always fused together in the females but distinct (as shown in *a*′) in the males.
FIG. 50 (*right*). Showing the similarity of the early larvae, the *Nauplius* stage, in three widely different groups of Crustacea: *a*, copepod; *b*, barnacle (*Balanus*); and *c*, euphausiid.

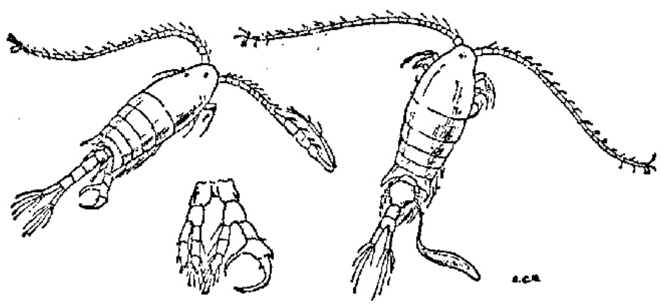
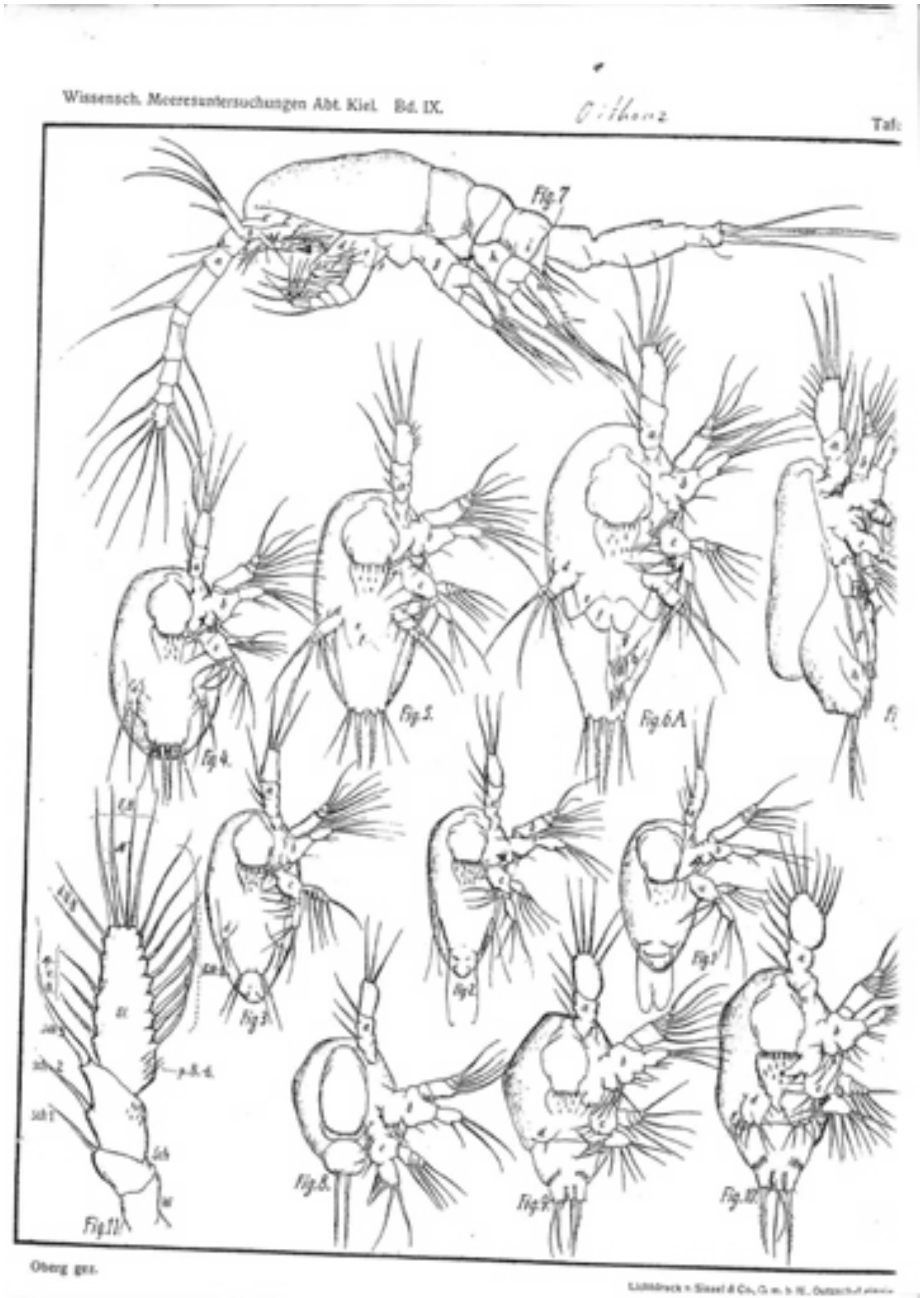


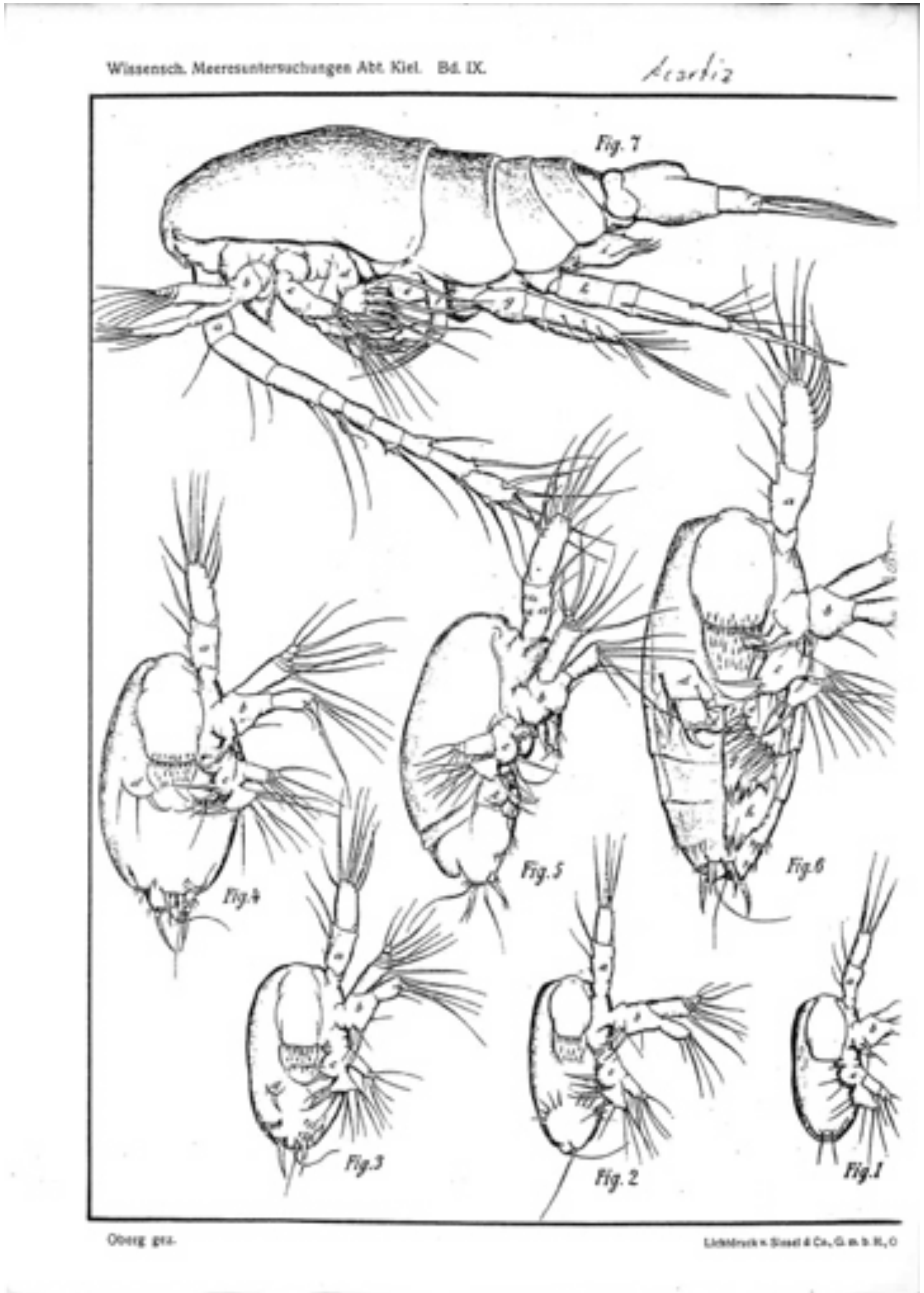
FIG. 51
Male and female of the copepod *Centropages hamatus*. Note the hinged antenna of the male for embracing the female and the last pair of his limbs (also shown enlarged) modified as a pair of forceps for attaching his sperm sac to her; the female is shown just after pairing with the sperm sac safely attached.

Natural history of copepods. Note that the copepod with eyes (c.) has short antennae. The long ones function as mechanoreceptors and apprise the animals of movements, whether prey or predators, in their surroundings.

from A. Hardy „The open sea“

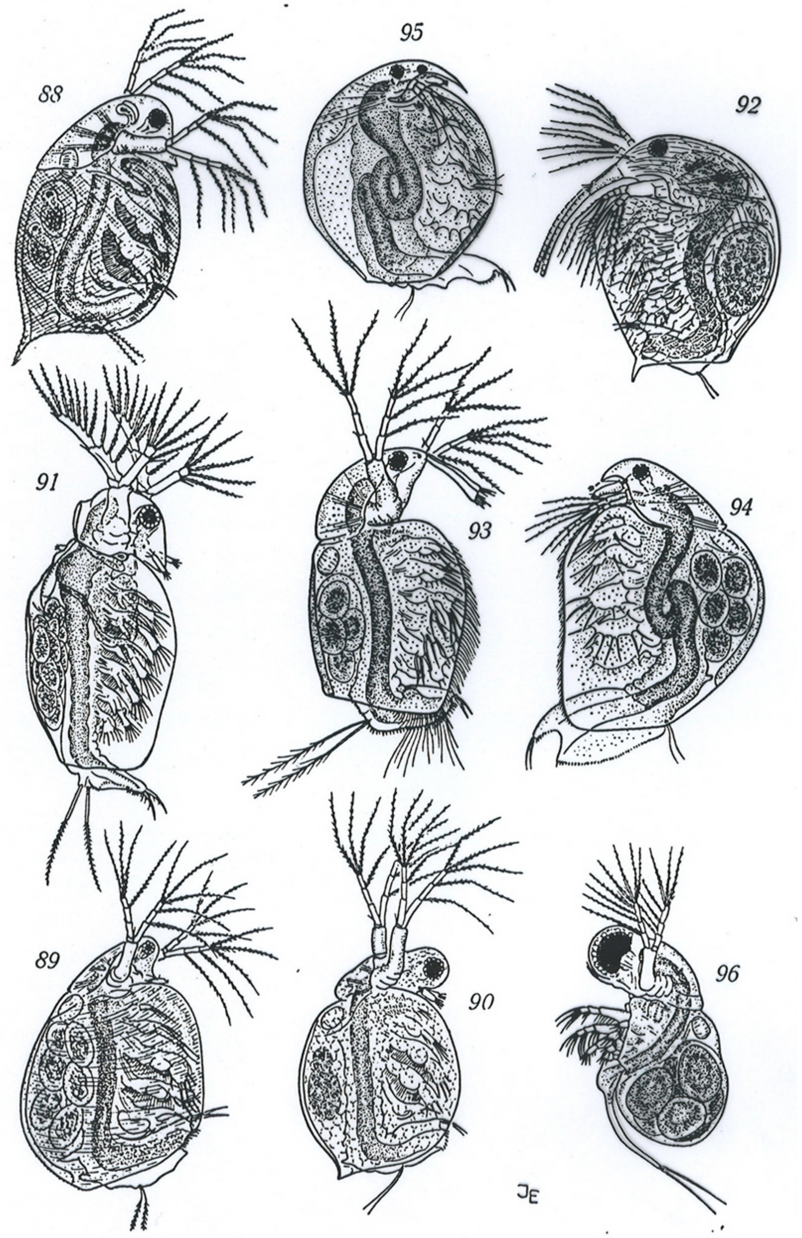



The copepod genus *Oithona* is present in the surface layer of the entire ocean and appears not to have a seasonal cycle, i.e. it breeds whenever sufficient food is available.




The copepod genus *Acartia* is present in all coastal waters except around Antarctica. The various species have strong seasonality, many species have benthic eggs.

Tafel 14




Cladocerans (Daphnids) are the typical zooplankton of eutrophic lakes. They feed with high efficiency on suspended particles by filtering water and multiply rapidly by growing new individuals in their brood pouches on their backs (by parthenogenesis).

They are slow swimmers represented in the marine environment by only 3 genera with a few species (*Penilia*, *Evadne*, *Podon*). Although they can form „blooms“ in coastal areas, their feeding habits are still unknown.

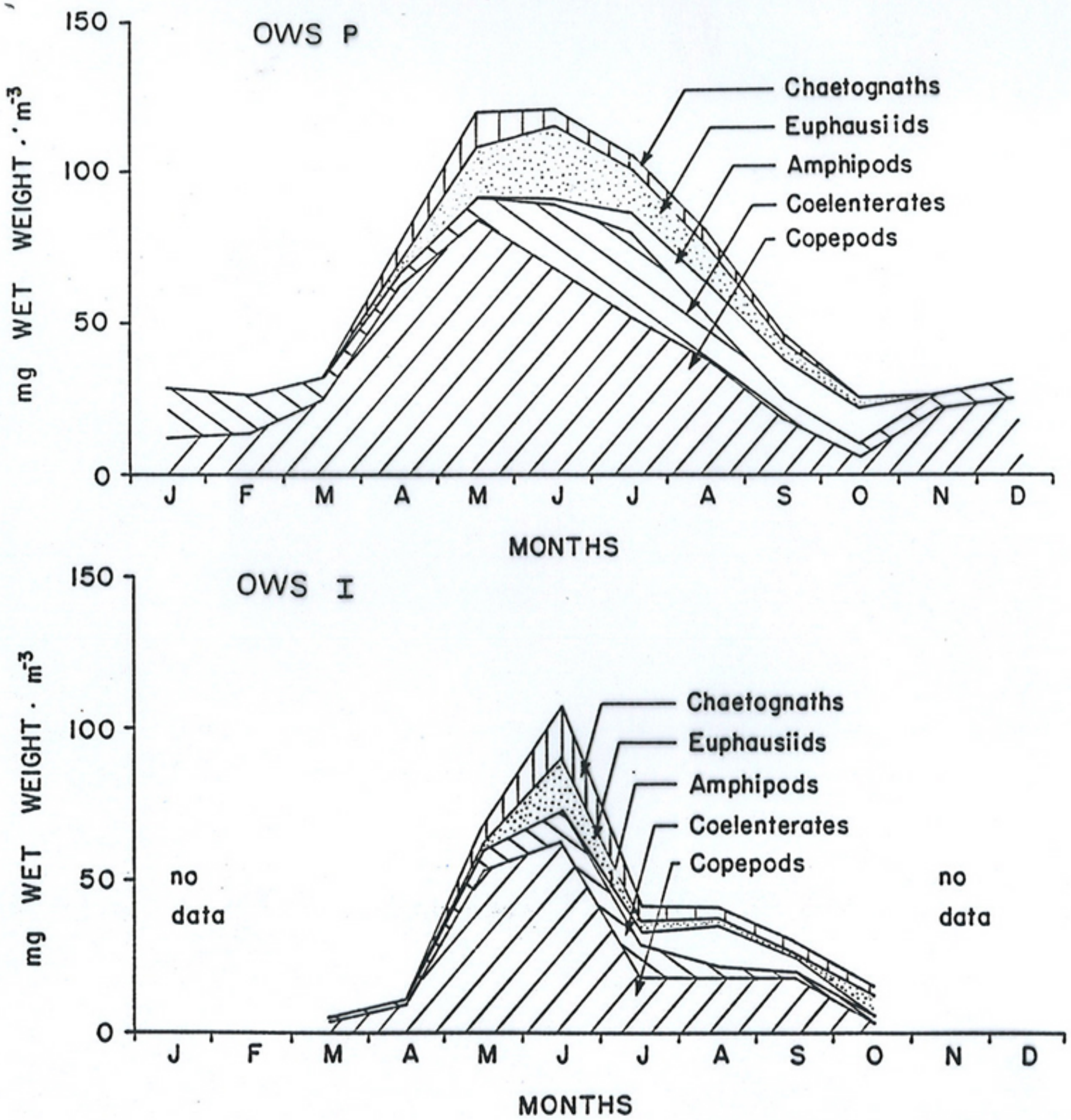



Fig. 7.—Changes in the total biomass of net zooplankton (minus salps) at OWS P (1971–1974) and OWS I (1971–1974).

Ocean weather station „Papa“, in the HNLC North Pacific

OWS „India“ in the North Atlantic. Note similarity in annual zooplankton biomass composition in both sites.

100 mg wet weight =
~20 mg dry weight =
~ 10 mg carbon biomass
Concentration m-3 x 100 m =
Stock m-2.

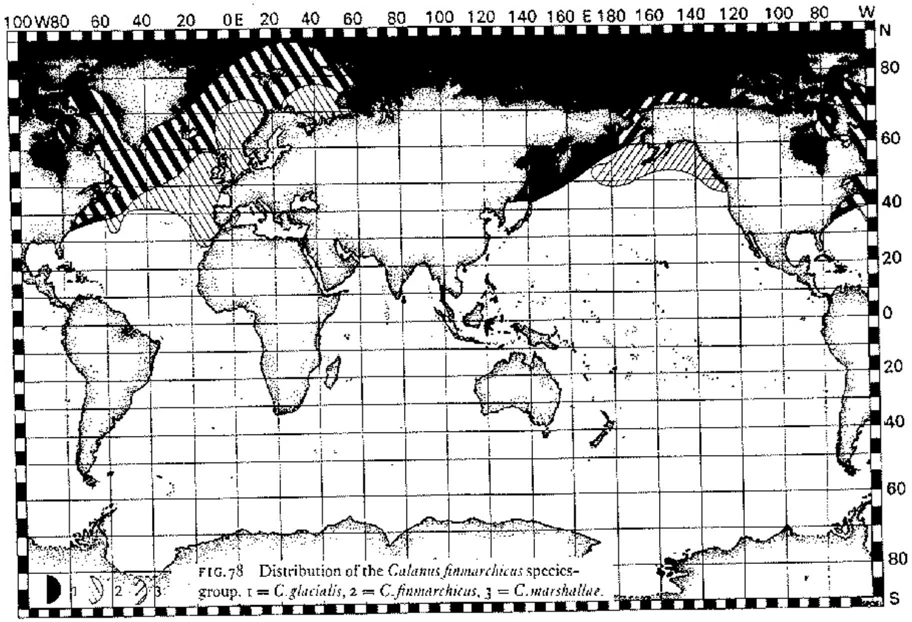


FIG. 78 Distribution of the *Calanus finmarchicus* species-group. 1 = *C. glacialis*, 2 = *C. finmarchicus*, 3 = *C. marshallae*.

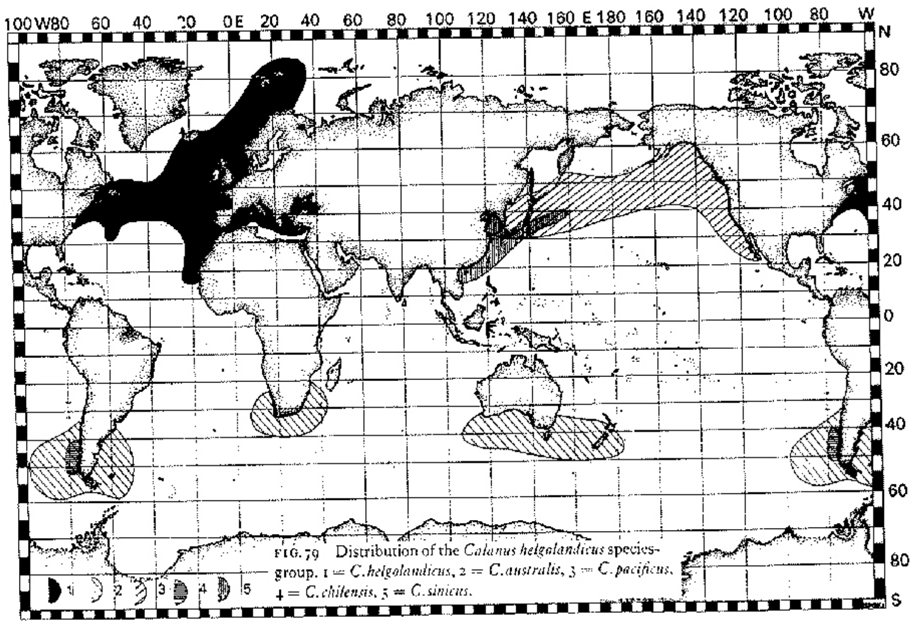


FIG. 79 Distribution of the *Calanus helgolandicus* species-group. 1 = *C. helgolandicus*, 2 = *C. australis*, 3 = *C. pacificus*, 4 = *C. chilensis*, 5 = *C. sinicus*.

Van der Spoel & Heymann (1983)

Most copepod species have distinct biogeographical ranges which partly overlap.

Related species can differ in their life cycles which gear them to specific oceanographical regimes, e.g. to polar, boreal, temperate waters, or to upwelling regimes.

# Shrimp-like zooplankton

Euphausiids and mysids painted at same scale by Alister Hardy


*Plate* 13. SHRIMP-LIKE CRUSTACEANS OF THE PLANKTON: MYSIDS (1, 4, 5, 6 AND 7) AND EUPHAUSIIDS (2 AND 3)

1. *Leptomysis gracilis* (G.O. Sars), adult male (×5) taken off the Lizard, August 1952
2. *Meganyctiphanes norvegica* (×2) from Loch Fyne, August 1951
3. *Thysanoessa raschii* (×2) Millport, Firth of Clyde, August 1951

4 and 5. *Anchialina agilis* (G.O. Sars), females (×5), *a*, adult carrying eggs, *b*, immature, showing remarkable range of colour characteristic of this species. Falmouth Bay, August 1952

6. *Gastrosaccus normani* (G.O. Sars), adult male (×5) taken off the Lizard, August 1952
7. *Praunus flexuosus* (Müller), female carrying eggs (×2), from Plymouth, October 1954

(The mysids were kindly identified for me by Mrs. O. S. Tattersall)

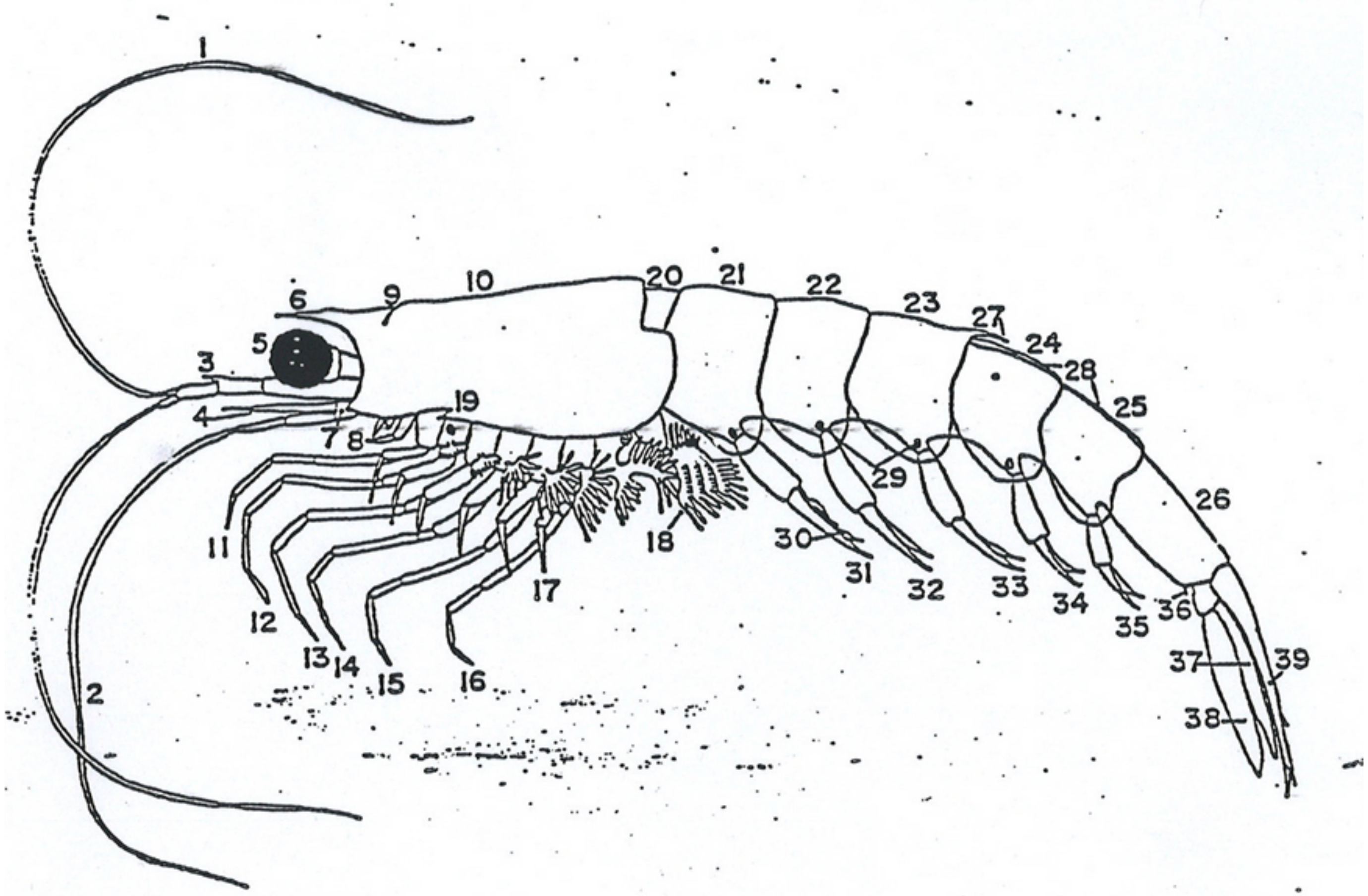


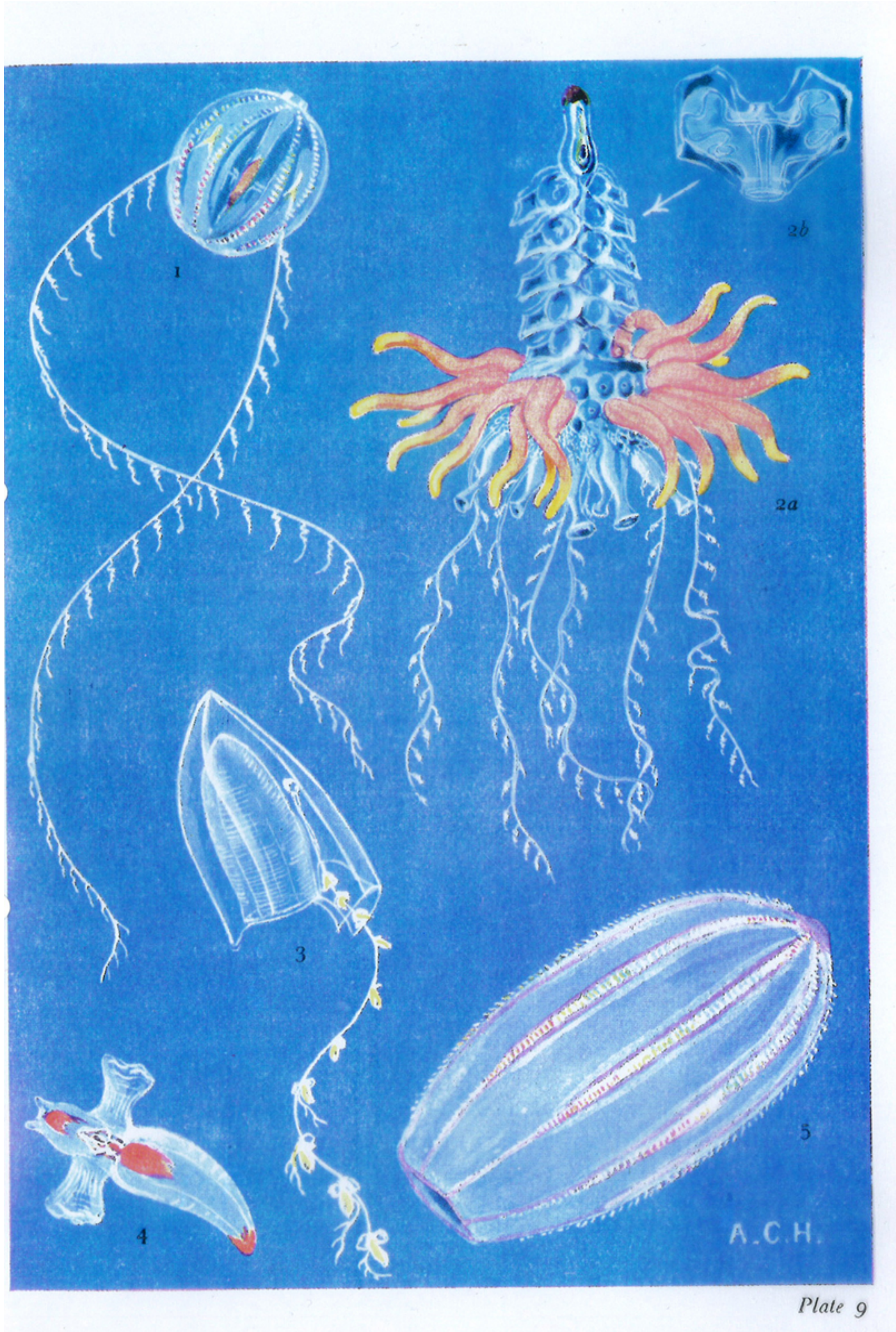

Figure 1. External morphology of an euphausiid (setae omitted). 1, flagellae of antennule; 2, flagellum of second antenna; 3, antennule lappet; 4, antennal scale (scaphocerite); 5, compound eye; 6, rostrum; 7, antennal peduncle; 8, mouthparts; 9, cervical groove; 10, carapace; 11-16, thoracic legs I-VI (endopods); 17, exopod of thoracic appendage VI; 18, gills (podobranchiae); 19, spine; 20, intermediate plate; 21-26, abdominal segments I-VI; 27, dorsal spine; 28, dorsal keels; 29, photophores (luminescent organs); 30, petasma (males only); 31-35, pleopods; 36, pre-anal spine; 37, endopod of uropod; 38, exopod of uropod; 39, telson.

The zebra‘s muscles have evolved to escape predators. Their teeth reflect adaptation to grinding grasses.

Gelatinous organisms painted by Alister Hardy.

Top left (Pleurobrachia) and bottom right (Beroe) are Ctenophores or comb jellies. Beroe feeds exclusively on other Ctenophores.

Bottom left is a heteropod (gastropod), the others are coelenterates or jellyfish.

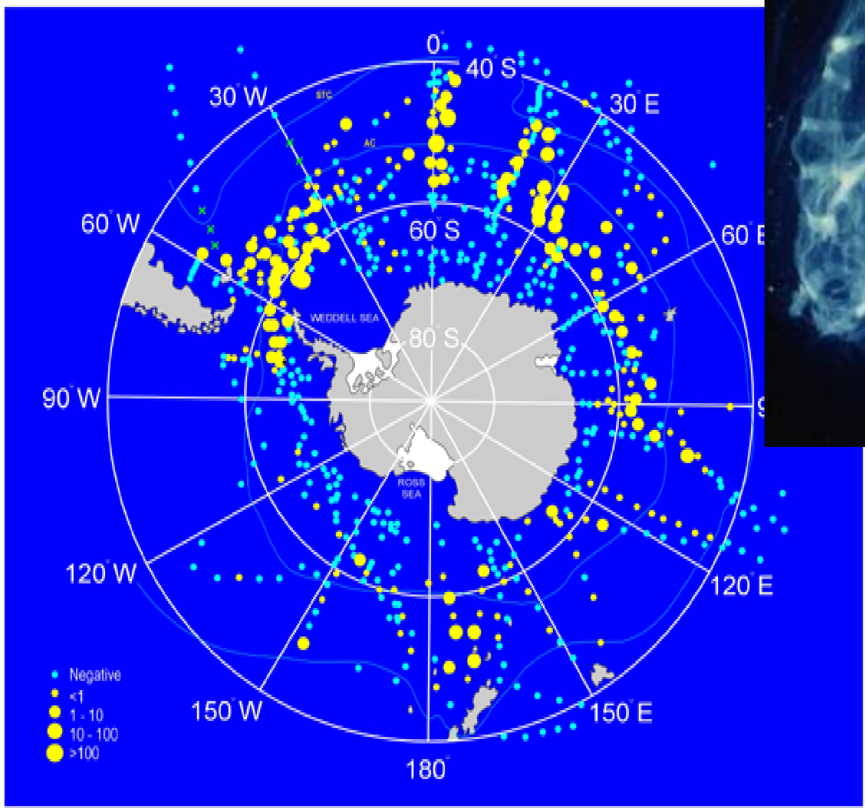


Salps are highly transparent (except for the stomach), filter-feeders that multiply by budding and can build huge stocks in some regions, such as the Southern Ocean.

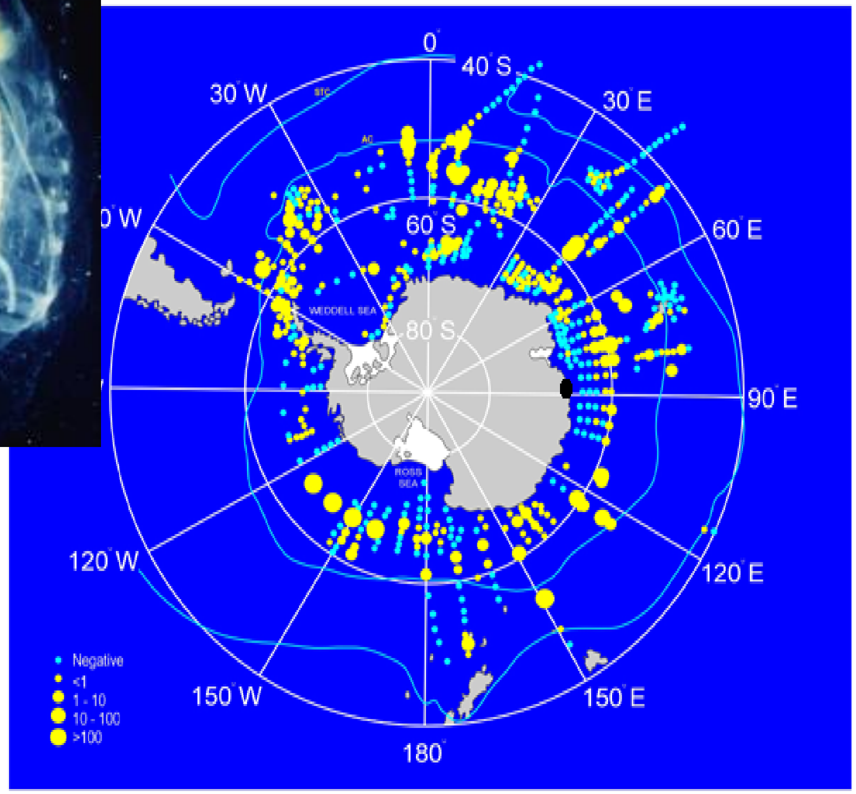
They are oceanic animals whose fliters can clog at high particle densities.

Their major predators are amphipods that have grappling mouth parts.

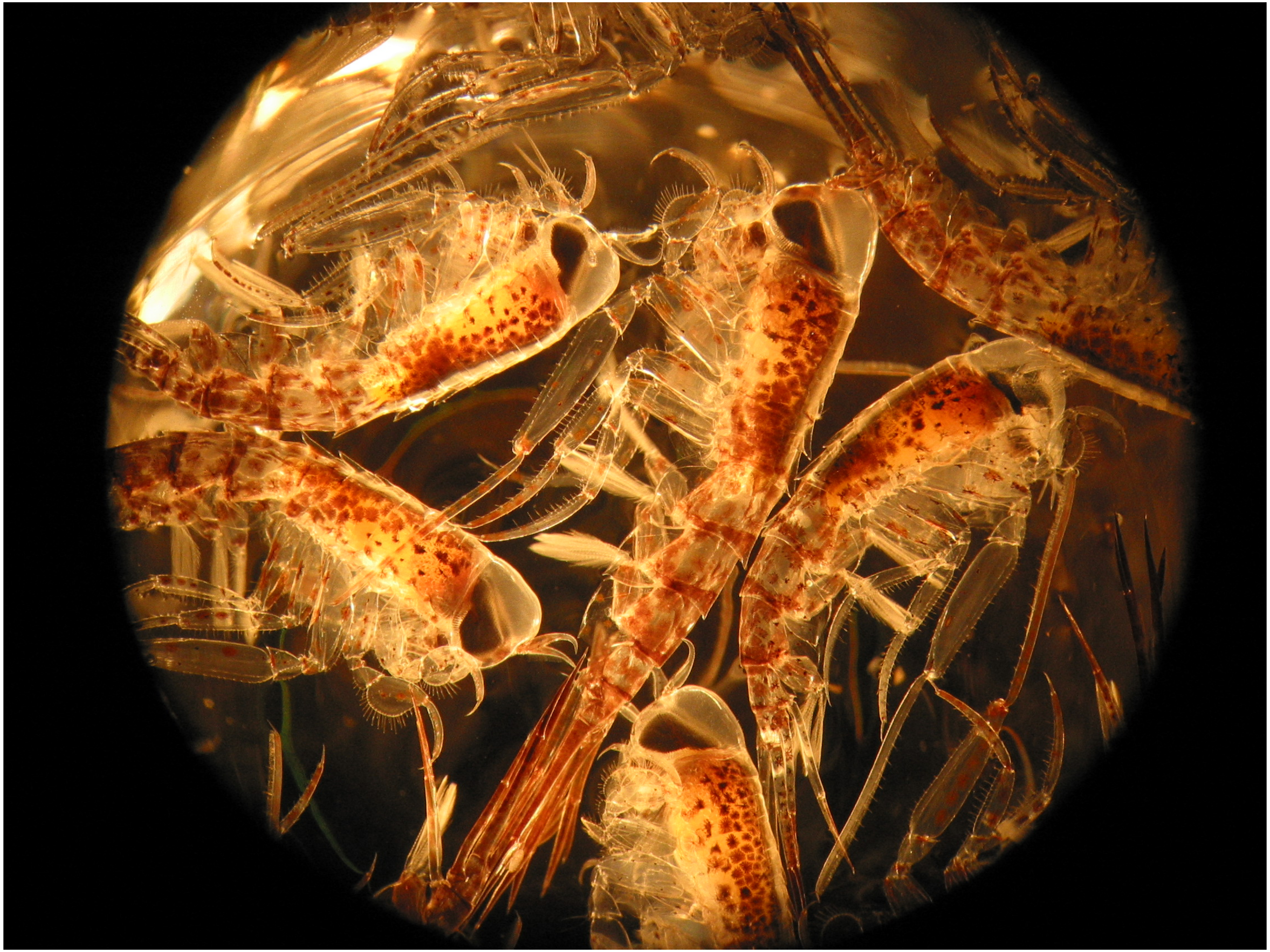
Salp range is moving southward since the last 50 years particularly in Indian and Pacific Sectors. Salps do not thrive in high productive areas so their spread is an indication of declining productivity.




1900-1952




1980-2000



Hyperiid amphipods are major predators of watery zooplankton: Note their large eyes and grappling appendages suited to tear apart their prey. (H. Gonzalés).

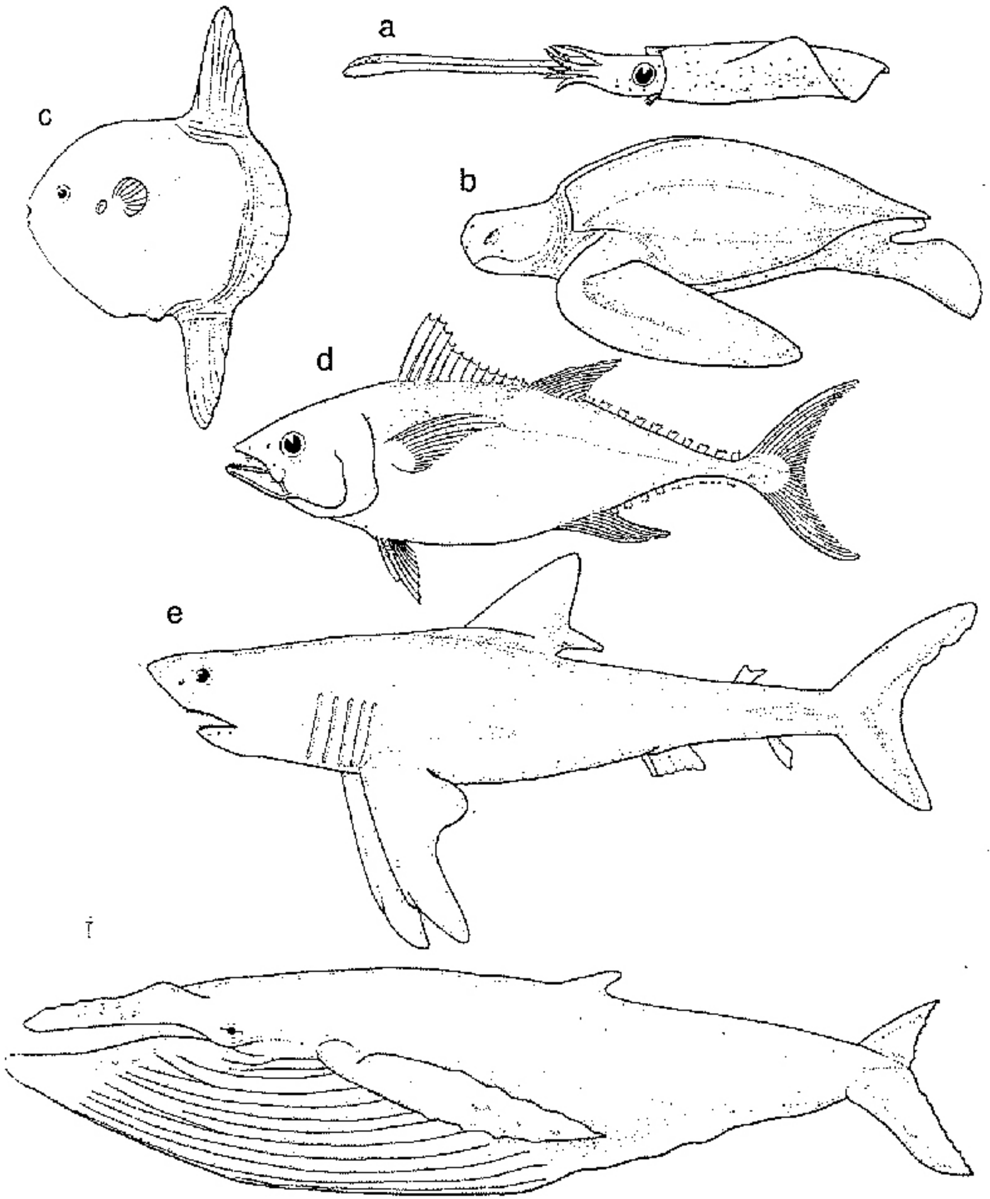



Abb. 54. Vertreter des Nektons. a) Kalmar (*Loligo*, Körperlänge 30 cm); b) Lederschildkröte (*Dermochelys coriacea*, 1 m); c) Mondfisch (*Mola mola*, 50 cm); d) Thunfisch (*Thunnus thynnus*, 1 m); e) Menschen- oder Weißer Hai (*Carcharodon carcharias*, 5 m); f) Buckelwal (*Megaptera novaeangliae*, 12 m).

Examples of nekton. The well-defended moonfish (c.) and turtle (b) feed primarily on jellies.

„You can‘t run with a belly full of jelly“.

## Consequences of natural selection of defences (arms race) for elemental cycles.

Cycles of biogenic elements depends on their ratios (C:N:P:SI:Fe, etc) in the bodies (cells), armour (exoskeletons) and waste products of the dominant organisms.

This will influence air/sea exchange of gases: $CO_2$, $N_2O$, DMS, etc.

The arms race will slow growth rates because energy and materials are diverted away from reproduction to defence. As in human societies.

Sediment surface is determined by the nature of the war fought in the overlying water.

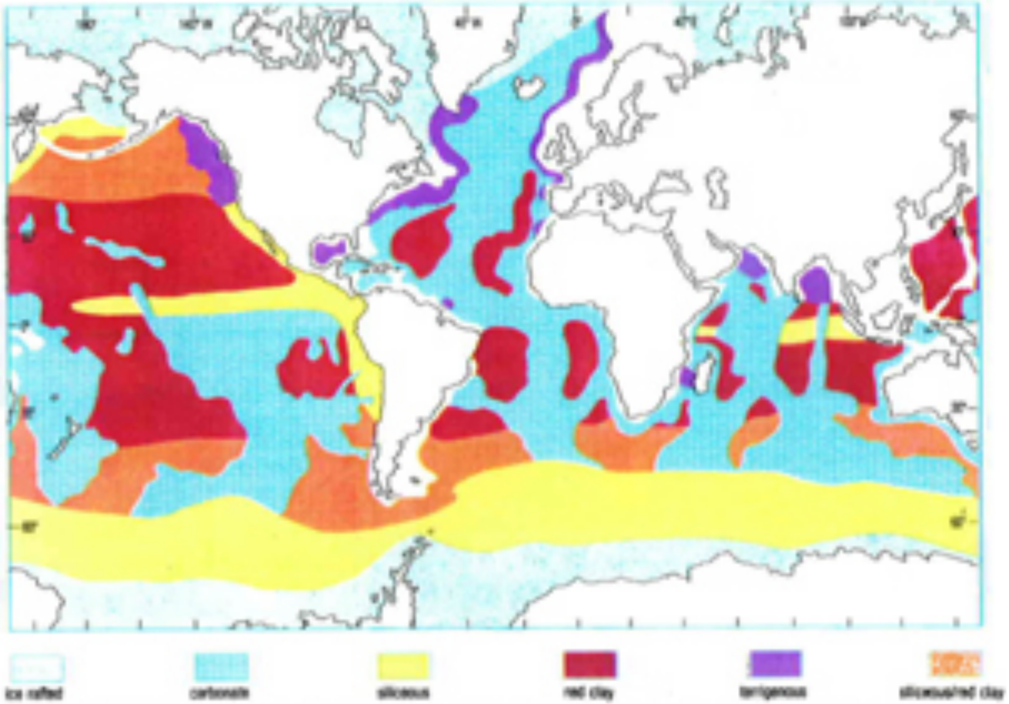



Figure 1.4 Distribution of dominant sediment types on the floor of the present-day oceans. Note that red clays are also terrigenous sediments.

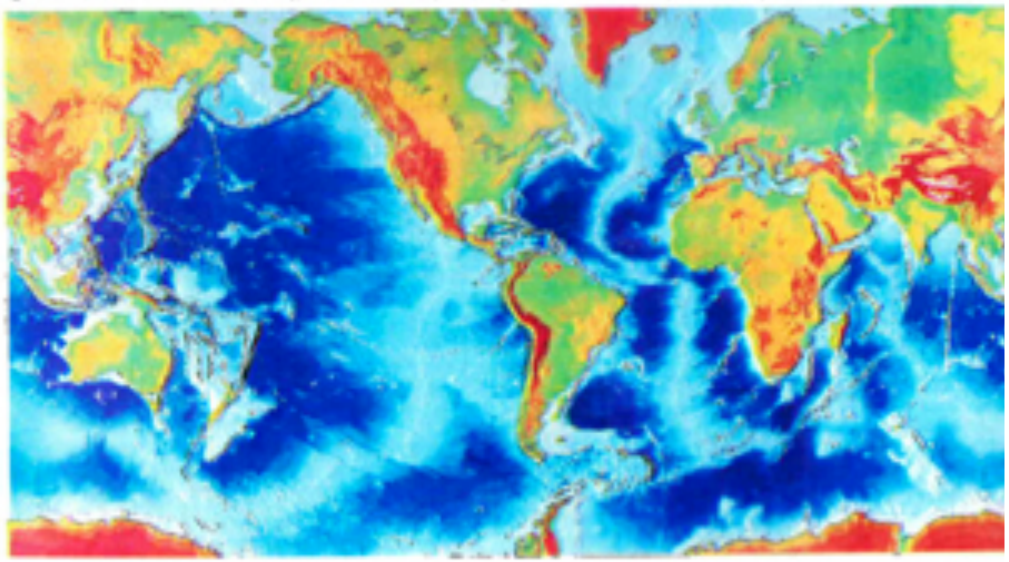
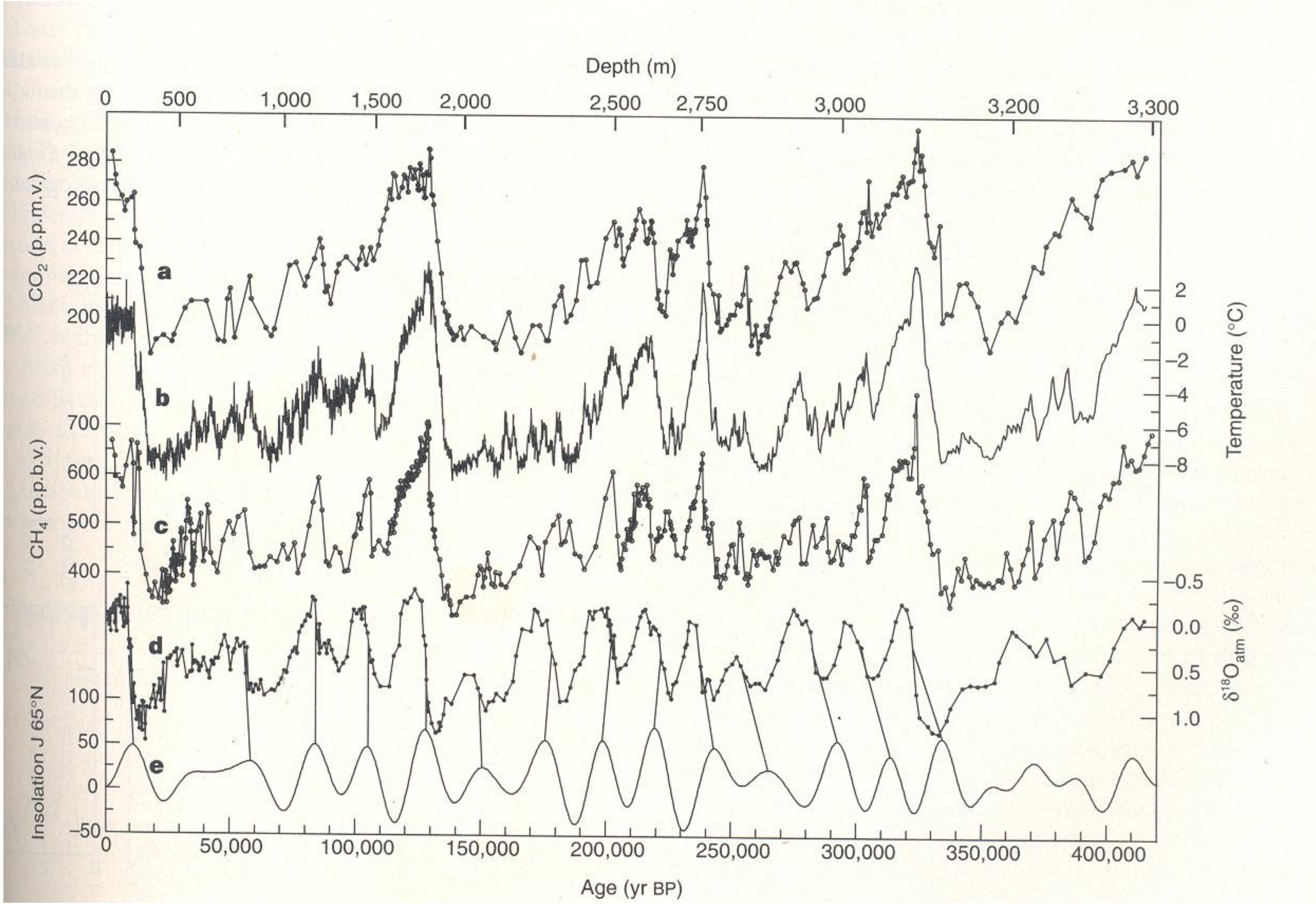


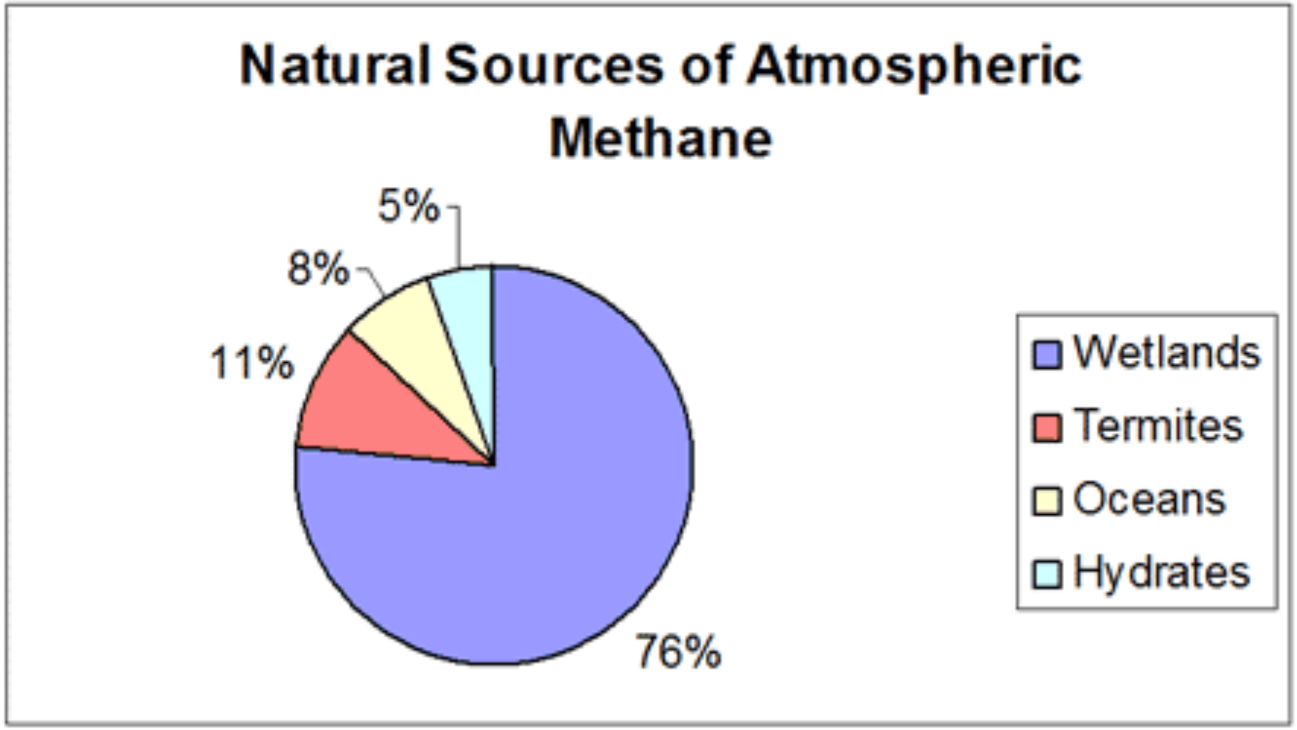
Figure 1.5 Shaded relief map of the Earth's solid surface. In oceanic areas, the deeper the blue, the deeper the water.

Distribution of dominant sediment types on the sea floor: pale blue: ice rafted sediments. Blue: carbonate (note effect of water depth and age). Yellow: siliceous (note no relation to depth). Red: Red clay (note strong relation to depth). Violet: terrigenous. Orange: siliceous/red clay.

Shaded relief map showing abyssal plains and mid-oceanic ridges.




From Petit et al. Nature 1999




EXIT Disclaimer

Source: Prepared from data contained in IPCC, 2001c .

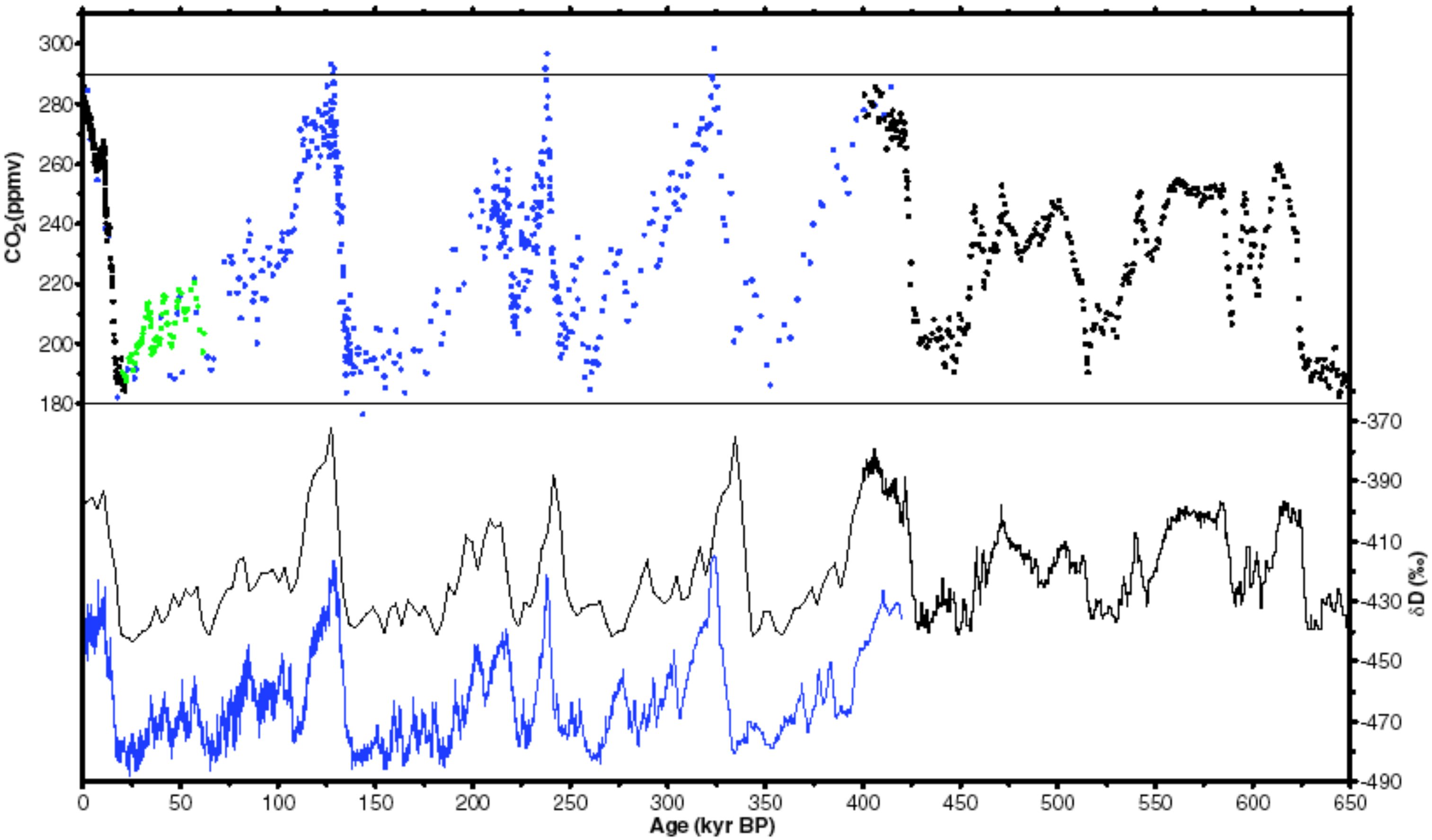



**Fig. 4.** A composite $CO_2$ record over six and a half ice age cycles, back to 650,000 years B.P. The record results from the combination of $CO_2$ data from three Antarctic ice cores: Dome C (black), 0 to 22 kyr B.P. (*9*, *11*) and 390 to 650 kyr B.P. [this work including data from 31 depth intervals over termination V of (*1*)]; Vostok (blue), 0 to 420 kyr B.P. (*5*, *7*), and Taylor Dome (light green), 20 to 62 yr B.P. (*8*). Black line indicates δD from Dome C, 0 to 400 kyr B.P. (*1*) and 400 to 650 kyr B.P. (*18*). Blue line indicates δD from Vostok, 0 to 420 kyr B.P. (*7*).



# Stable Carbon Cycle–Climate Relationship During the Late Pleistocene

Urs Siegenthaler,[1] Thomas F. Stocker,[1*] Eric Monnin,[1] Dieter Lüthi,[1] Jakob Schwander,[1] Bernhard Stauffer,[1] Dominique Raynaud,[2] Jean-Marc Barnola,[2] Hubertus Fischer,[3] Valérie Masson-Delmotte,[4] Jean Jouzel[4]

# Magic numbers in the biosphere

Glacial/interglacial CO2 concentrations (180 – 290 ppmv)

Glacial/interglacial methane concentrations (350 – 650 ppbv)

Redfield ratios (Pelagic C:N:P 106:16:1)

Deep-sea DOC concentrations (42 µmol $l^{-1}$)

Surface ocean bacterial numbers ($10^6$ $ml^{-1}$)

Virus:Bacteria ratio (10:1)

# Southern Ocean sea-ice extent, productivity and iron flux over the past eight glacial cycles

E. W. Wolff[1], H. Fischer[2], F. Fundel[2], U. Ruth[2], B. Twarloh[2], G. C. Littot[1], R. Mulvaney[1], R. Röthlisberger[1], M. de Angelis[3], C. F. Boutron[3], M. Hansson[4], U. Jonsell[4], M. A. Hutterli[1,5], F. Lambert[5], P. Kaufmann[5], B. Stauffer[5], T. F. Stocker[5], J. P. Steffensen[6], M. Bigler[5,6], M. L. Siggaard-Andersen[6], R. Udisti[7], S. Becagli[7], E. Castellano[7], M. Severi[7], D. Wagenbach[8], C. Barbante[9,10], P. Gabrielli[10] & V. Gaspari[9]

**Sea ice and dust flux increased greatly in the Southern Ocean during the last glacial period. Palaeorecords provide contradictory evidence about marine productivity in this region, but beyond one glacial cycle, data were sparse. Here we present continuous chemical proxy data spanning the last eight glacial cycles (740,000 years) from the Dome C Antarctic ice core. These data constrain winter sea-ice extent in the Indian Ocean, Southern Ocean biogenic productivity and Patagonian climatic conditions. We found that maximum sea-ice extent is closely tied to Antarctic temperature on multi-millennial timescales, but less so on shorter timescales. Biological dimethylsulphide emissions south of the polar front seem to have changed little with climate, suggesting that sulphur compounds were not active in climate regulation. We observe large glacial–interglacial contrasts in iron deposition, which we infer reflects strongly changing Patagonian conditions. During glacial terminations, changes in Patagonia apparently preceded sea-ice reduction, indicating that multiple mechanisms may be responsible for different phases of $CO_2$ increase during glacial terminations. We observe no changes in internal climatic feedbacks that could have caused the change in amplitude of Antarctic temperature variations observed 440,000 years ago.**

Vol 440|23 March 2006|**doi:10.1038/nature04614**

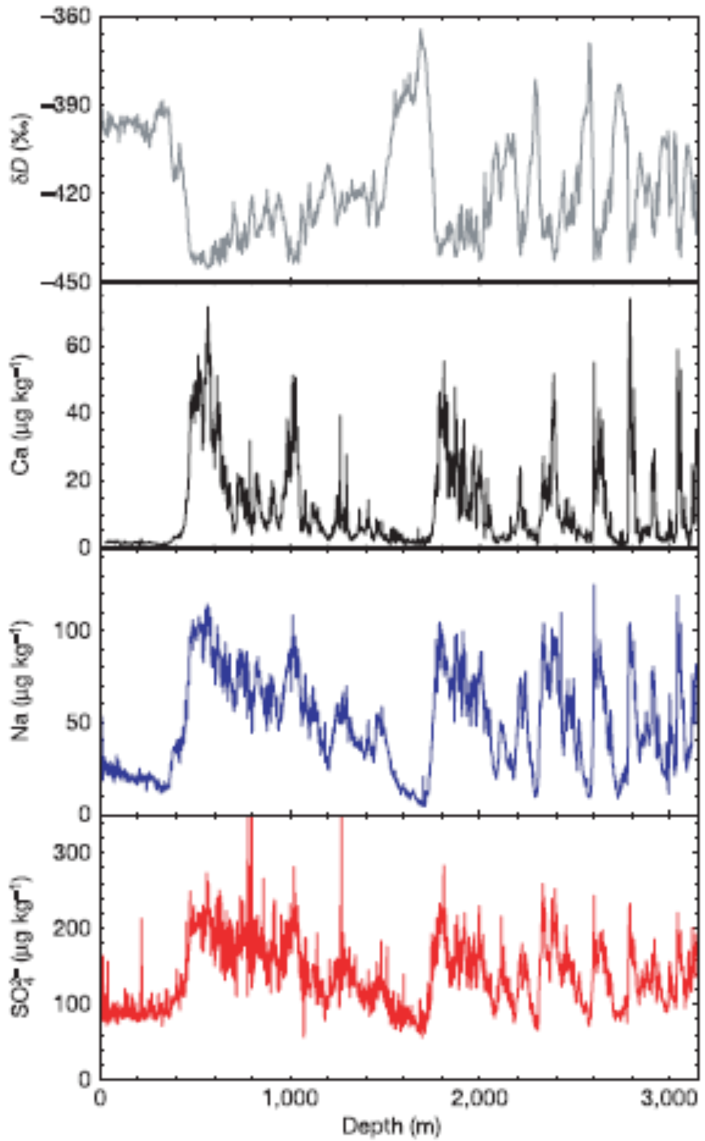



**Figure 1 | Measured concentrations from the EPICA Dome C ice core.** Data are on an ice depth scale. $\delta D$ are averaged over 3.85-m sections[6]; chemical concentrations are averaged over 2.2-m sections.

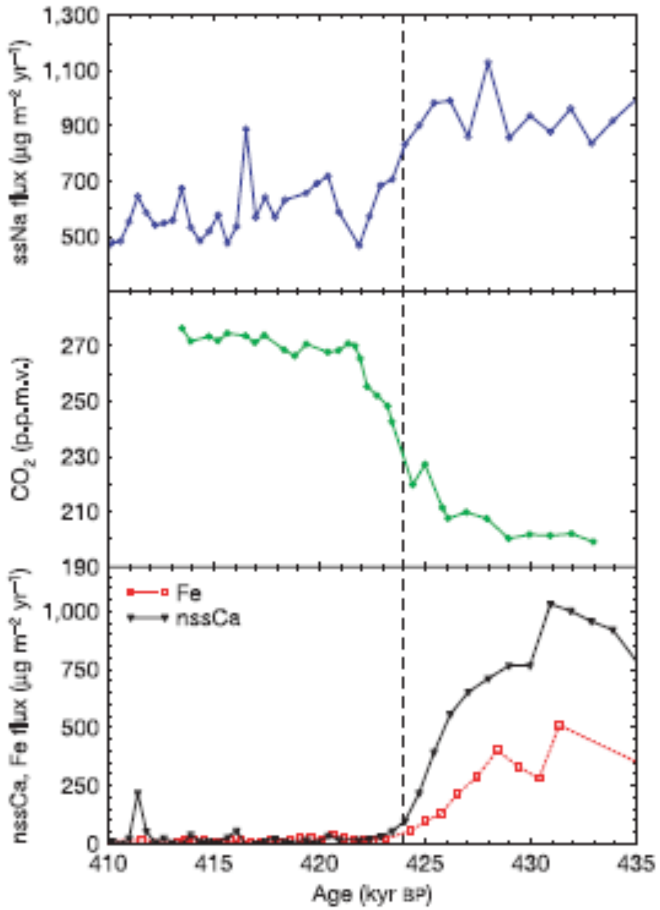



**Figure 4 | Chemistry and $CO_2$ across Termination V.** Chemical fluxes (averaged over 1.1 m depth increments, equivalent to a few hundred years at this depth, except for Fe, which consists of spot values at irregular intervals), and $CO_2$ concentration[6], across Termination V, between MIS12 and MIS11. Uncertainty in the alignment of the timescales for the $CO_2$ and chemical records is caused by the calculation of the gas-age/ice-age difference[6], and could be several centuries. The vertical dashed line indicates 424 kyr BP (see text).

Wolff et al. Nature 2006

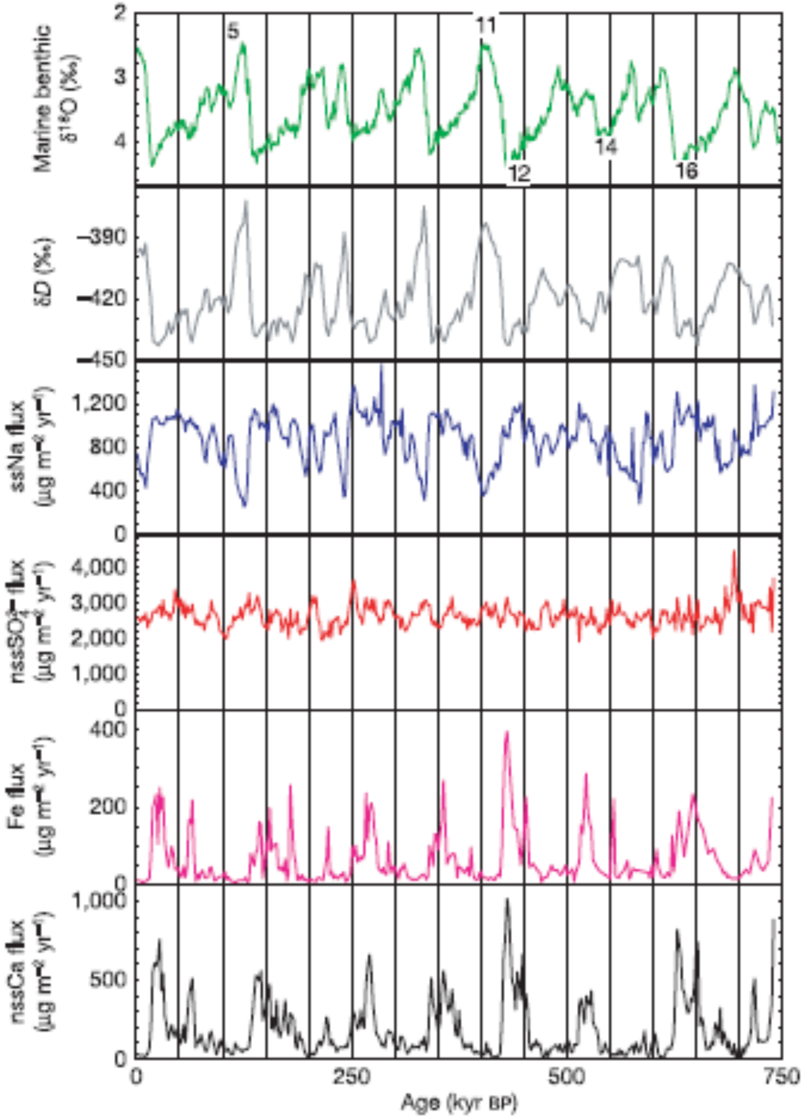



**Figure 2 | Chemical measurements from the EPICA Dome C core, on an age scale.** Chemical components (2-kyr averages) and $\delta D$ (3-kyr averages)[6] are from the EDC core; oxygen isotope values (1 kyr averages) from the marine benthic stack (on the LR04 timescale and with selected MIS numbers shown)[39]. While nssCa data represent almost continuous averages within each 2-kyr period, Fe data are averages of a few discrete samples. In the deeper ice, many 2-kyr periods have no Fe data, or are based on a single data point representing only a few decades. The obvious timing mismatch between EDC and the benthic stack around MIS14 is not yet resolved[39].

Wolff et al. Nature 2006

# Magic numbers in the biosphere

Glacial/interglacial CO2 concentrations (180 – 290 ppmv)

Glacial/interglacial methane concentrations (350 – 650 ppbv)

Redfield ratios (Pelagic C:N:P 106:16:1)

Deep-sea DOC concentrations (42 μmol $l^{-1}$)

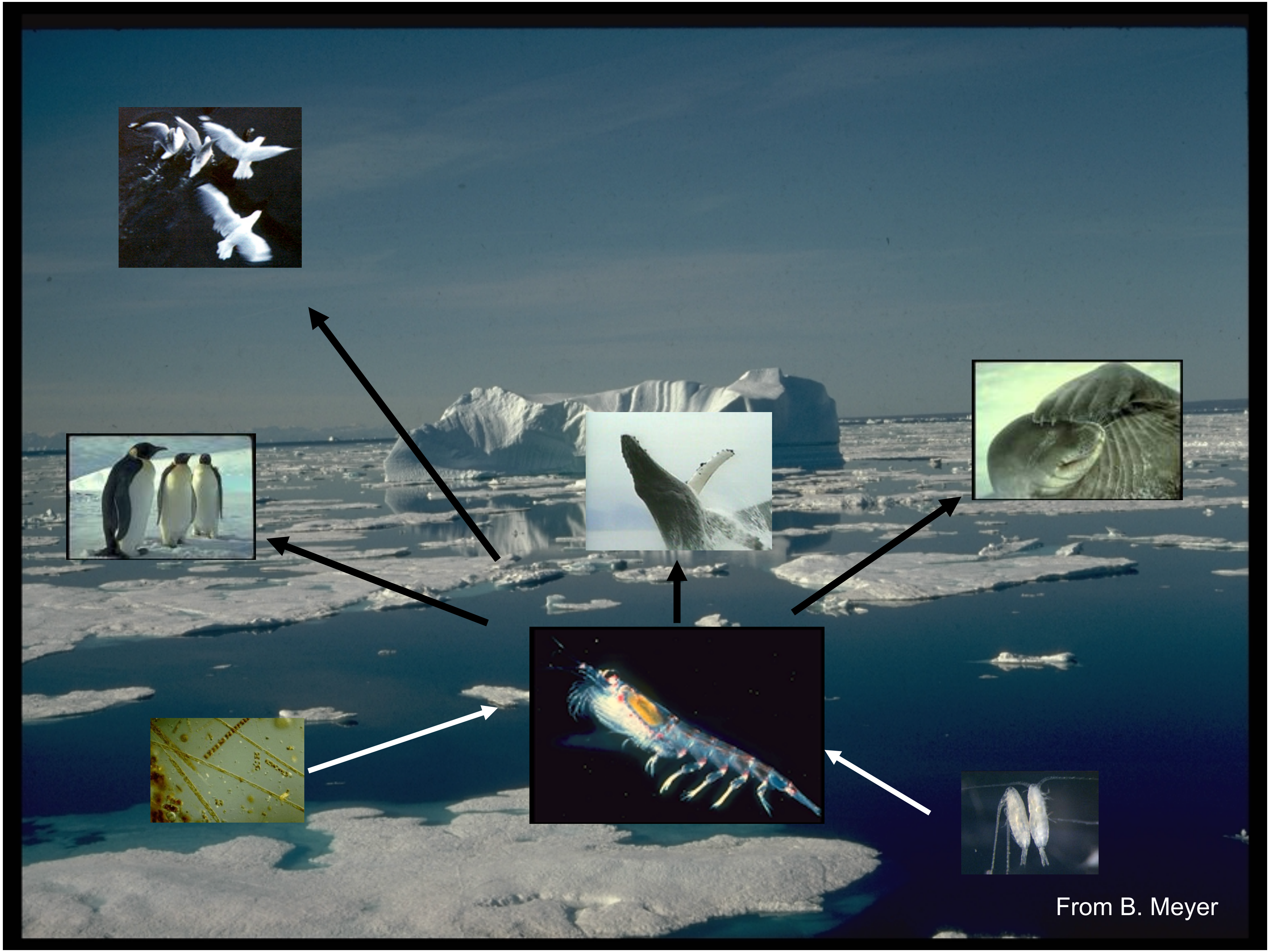
Surface ocean bacterial numbers ($10^6$ $ml^{-1}$)

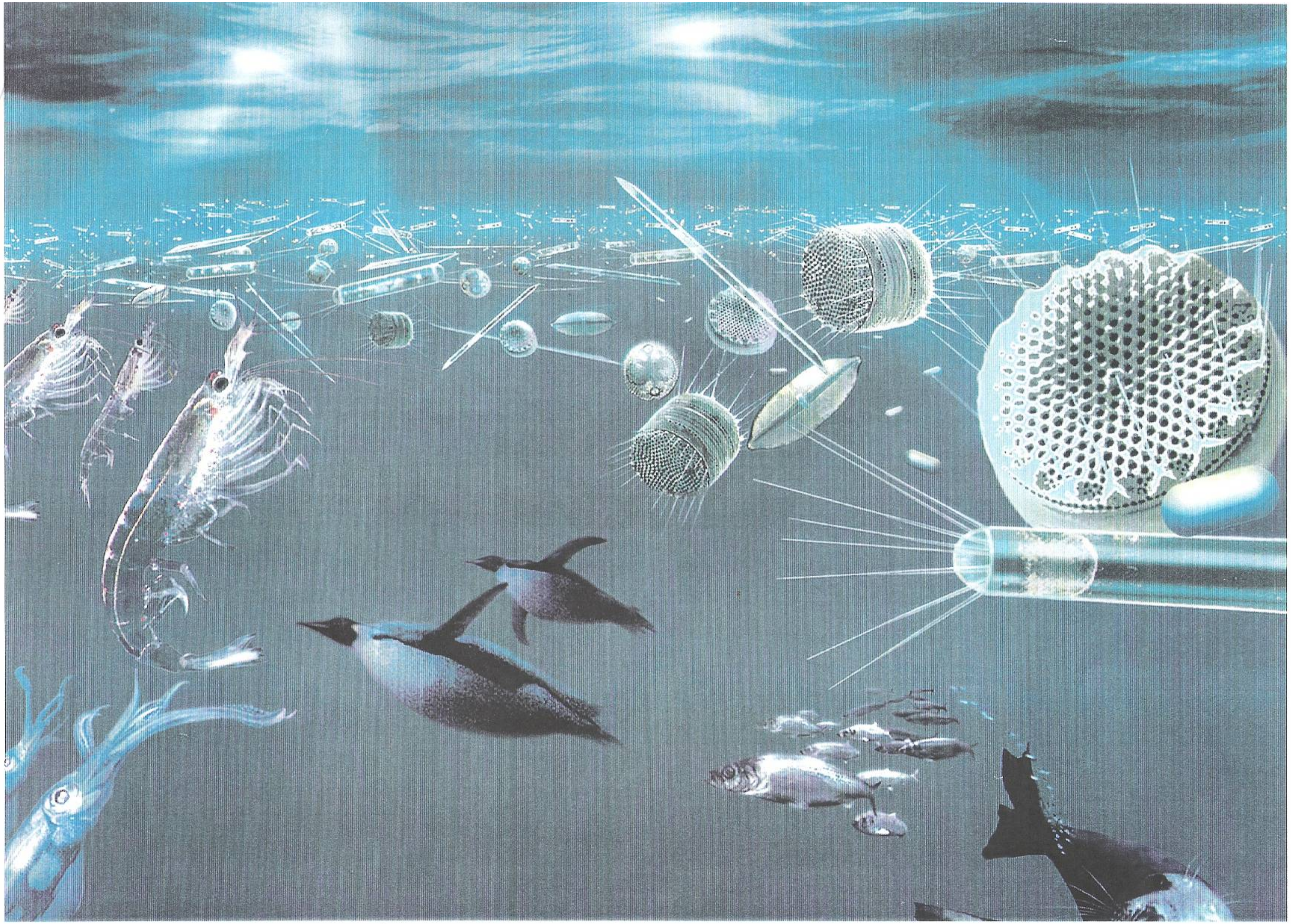
Virus:Bacteria ratio (10:1)

Non-sea-salt-sulphate (biogenic) flux to Antarctica (3 mg $m^{-2}$ $yr^{-1}$)

to

The Antarctic Blue Whale is the largest animal that ever lived. Their numbers have declined from 300,000 to less than 1,500 now. Their recovery is threatened by declining krill stocks.


From B. Meyer



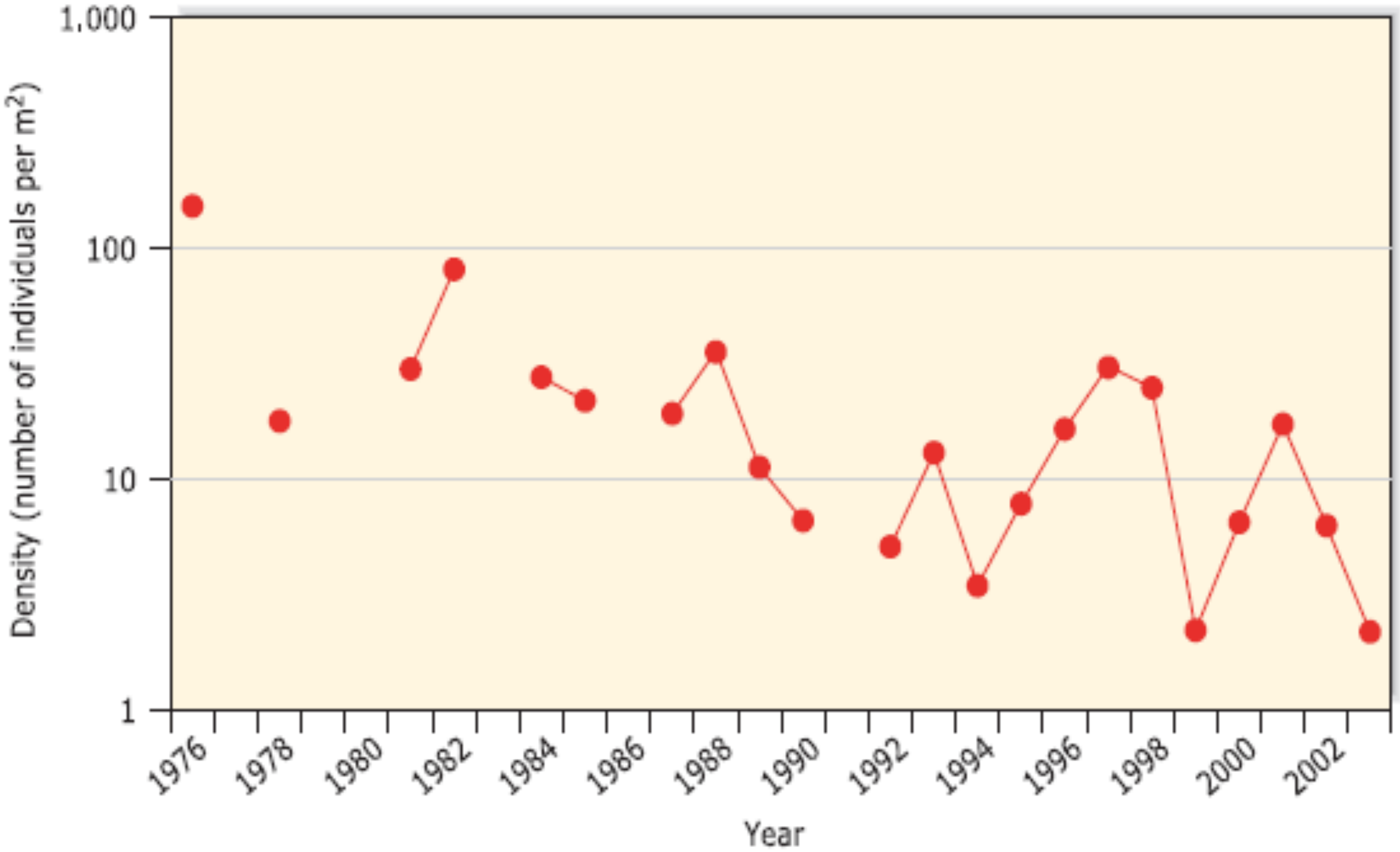
# Long-term decline in krill stock and increase in salps within the Southern Ocean

**Angus Atkinson[1], Volker Siegel[2], Evgeny Pakhomov[3,4] & Peter Rothery[5]**

[1]*British Antarctic Survey, Natural Environment Research Council, High Cross, Madingley Road, Cambridge CB3 OET, UK*
[2]*Sea Fisheries Institute, Palmaille 9, 22767 Hamburg, Germany*
[3]*Department of Earth and Ocean Sciences, University of British Columbia, 6339 Stores Rd, Vancouver, British Columbia, V6T 1Z4, Canada*
[4]*Department of Zoology, Faculty of Science and Technology, University of Fort Hare, Private Bag X1314, Alice 5700, South Africa*
[5]*NERC Centre for Ecology and Hydrology, CEH Monks Wood, Abbots Ripton, Huntingdon PE28 2LS, UK*

**Antarctic krill (*Euphausia superba*) and salps (mainly *Salpa thompsoni*) are major grazers in the Southern Ocean[1–4], and krill support commercial fisheries[5]. Their density distributions[1,3,4,6] have been described in the period 1926–51, while recent localized studies[7–10] suggest short-term changes. To examine spatial and temporal changes over larger scales, we have combined all available scientific net sampling data from 1926 to 2003. This database shows that the productive southwest Atlantic sector contains >50% of Southern Ocean krill stocks, but here their density has declined since the 1970s. Spatially, within their habitat, summer krill density correlates positively with chlorophyll concentrations. Temporally, within the southwest Atlantic, summer krill densities correlate positively with sea-ice extent the**

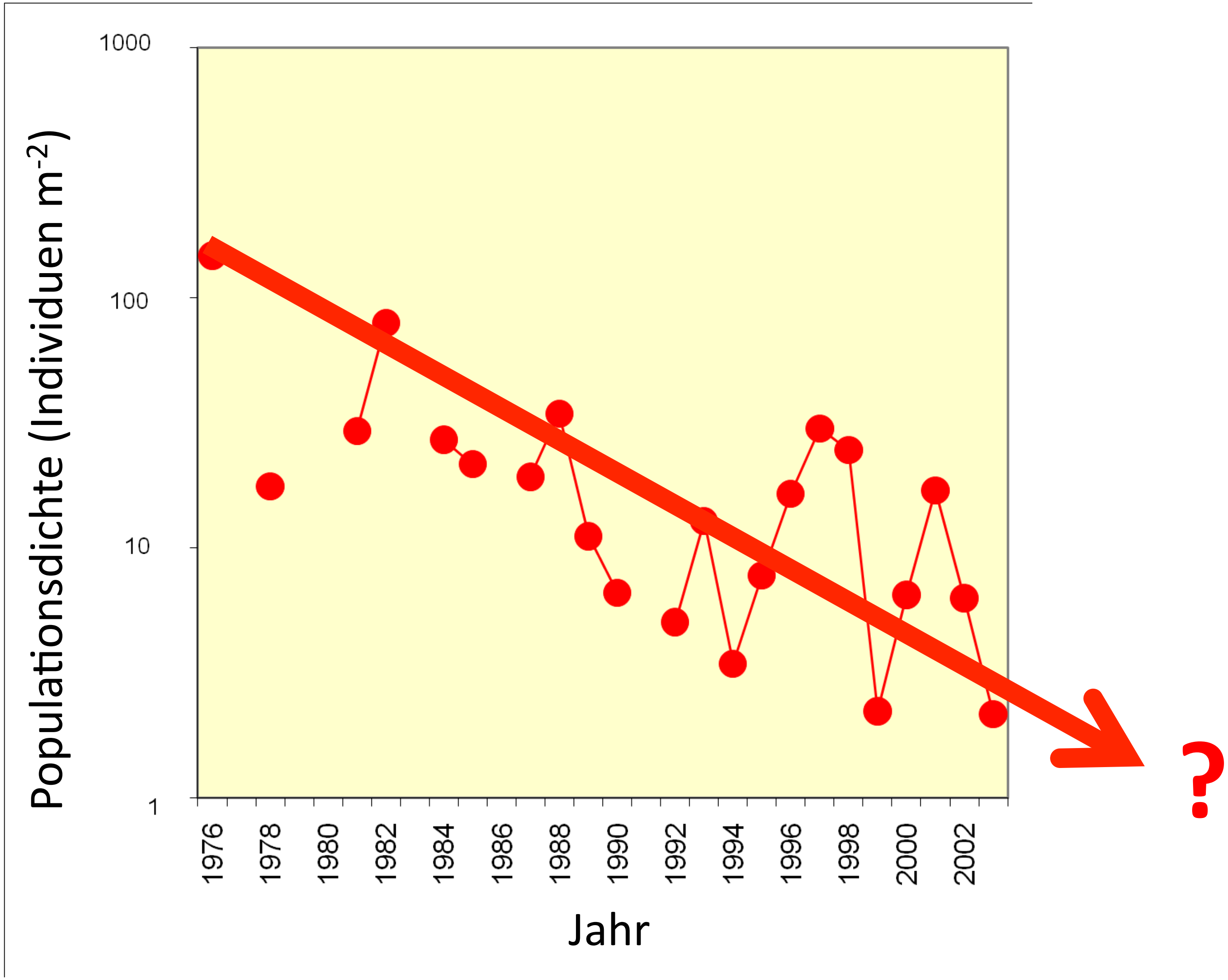
**Figure 2.3: Decline in krill stocks in the SW Atlantic from 1976 to 2003**




Krill density based on data from 4,984 stations.

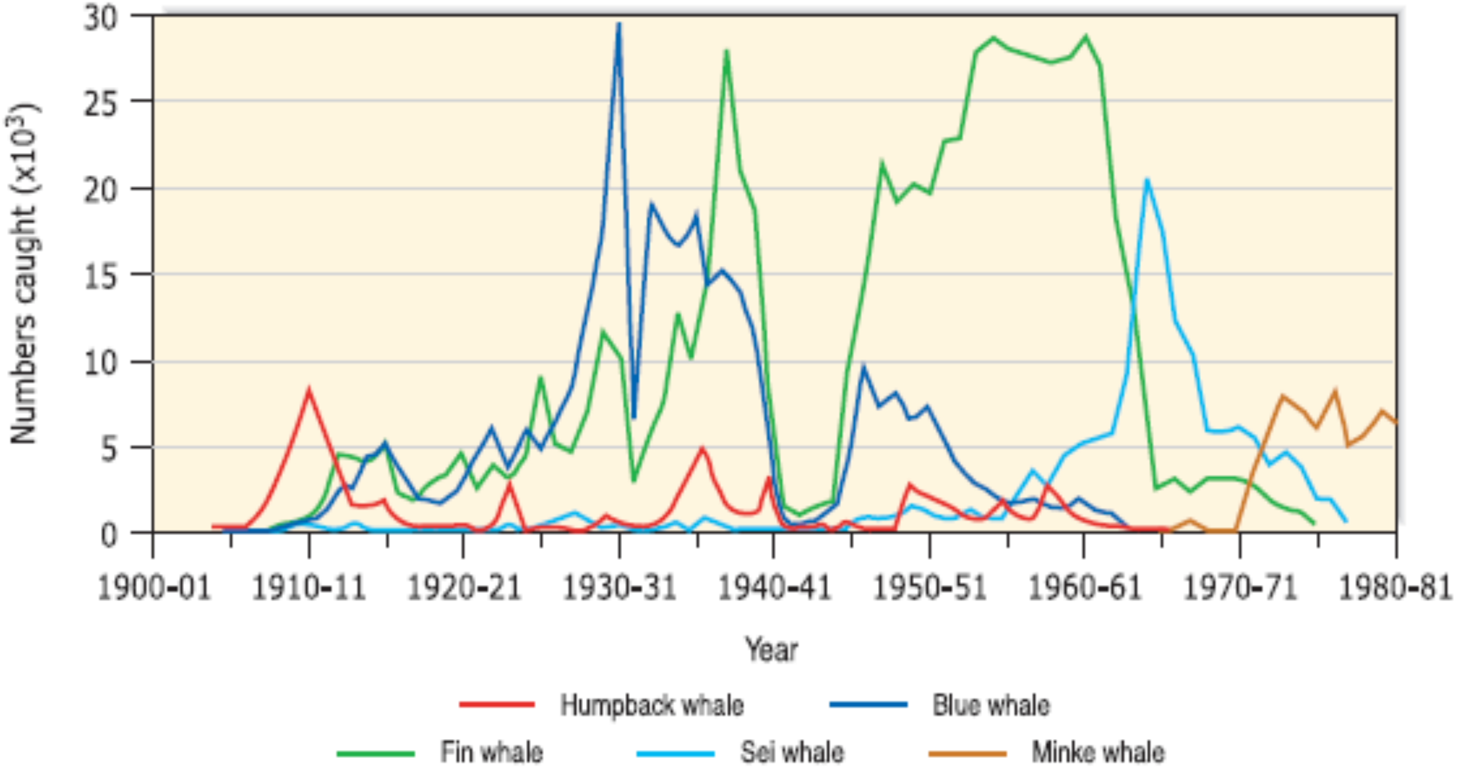
*Source*: Atkinson et al. 2004.

## Zusammenbruch der Krill-Bestände seit den 70er Jahren:
# Ein Paradoxon



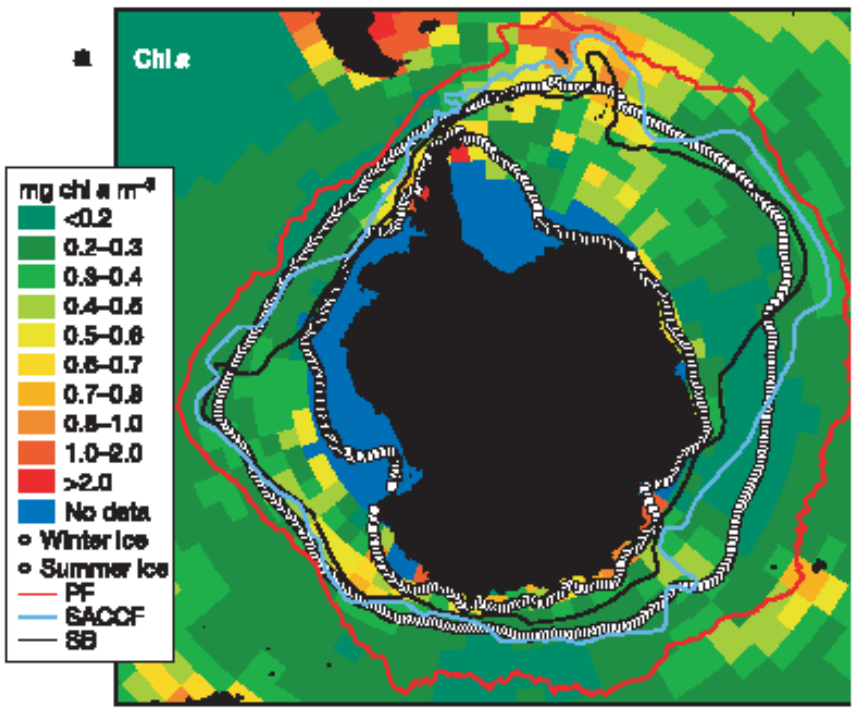

Atkinson et al. 2004

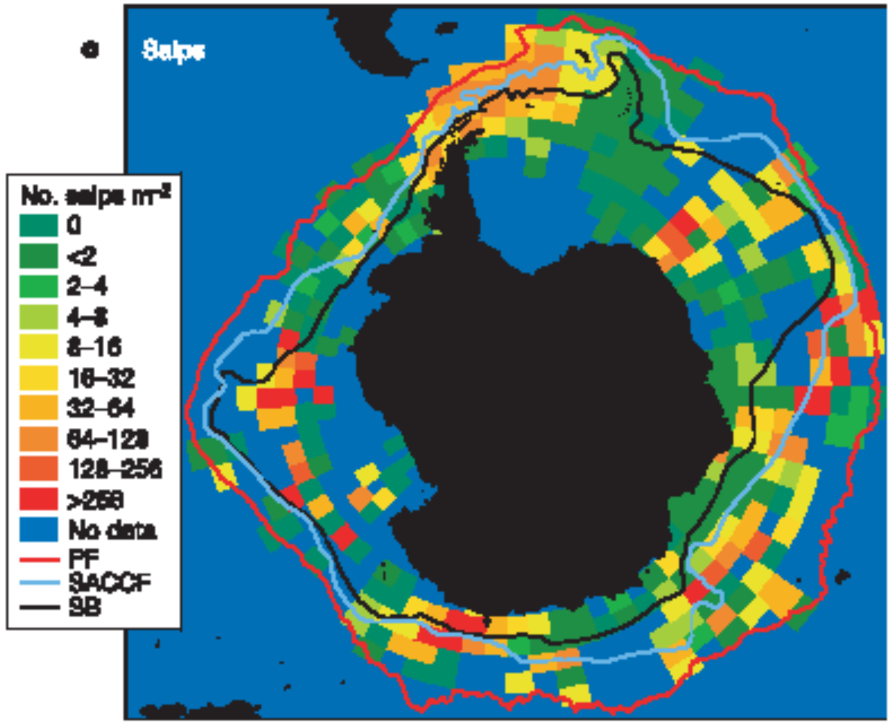
**Figure 2.1: Whale catches in Antarctic waters from 1904 to 1981**




Including data from land stations, moored factory ships and pelagic catches, though the numbers only represent whales landed.

*Source*: Laws 1977; Knox 1994.



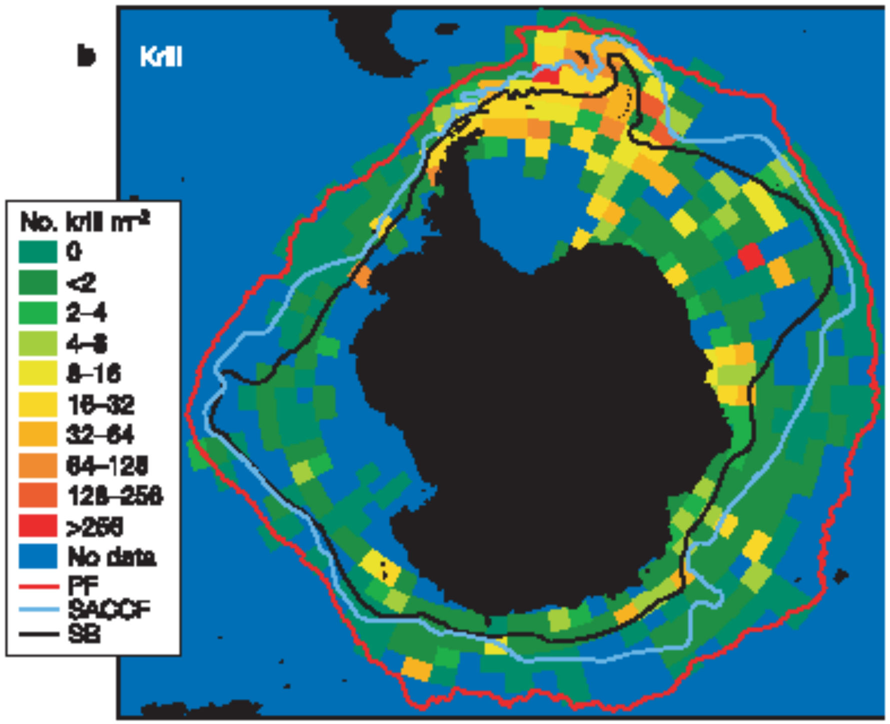




**Figure 1** Krill, salps and their food. **a**, Mean (November–April) chlorophyll *a* (chl *a*) concentration, 1997–2003. **b**, Mean krill density (6,675 stations, 1926–2003). **c**, Mean salp density (5,030 stations, 1926–2003). $\log_{10}$(no. krill m$^{-2}$) $= 1.2 \log_{10}$(mg chl *a* m$^{-3}$) $+ 0.83$ ($R^2 = 0.051$, $P = 0.017$, $n = 110$ grid cells). Historical mean positions are shown for the PF[29], Southern ACC Front (SACCF)[30], SB[30] and northern 15% sea-ice concentrations in February and September (1979–2004 means).

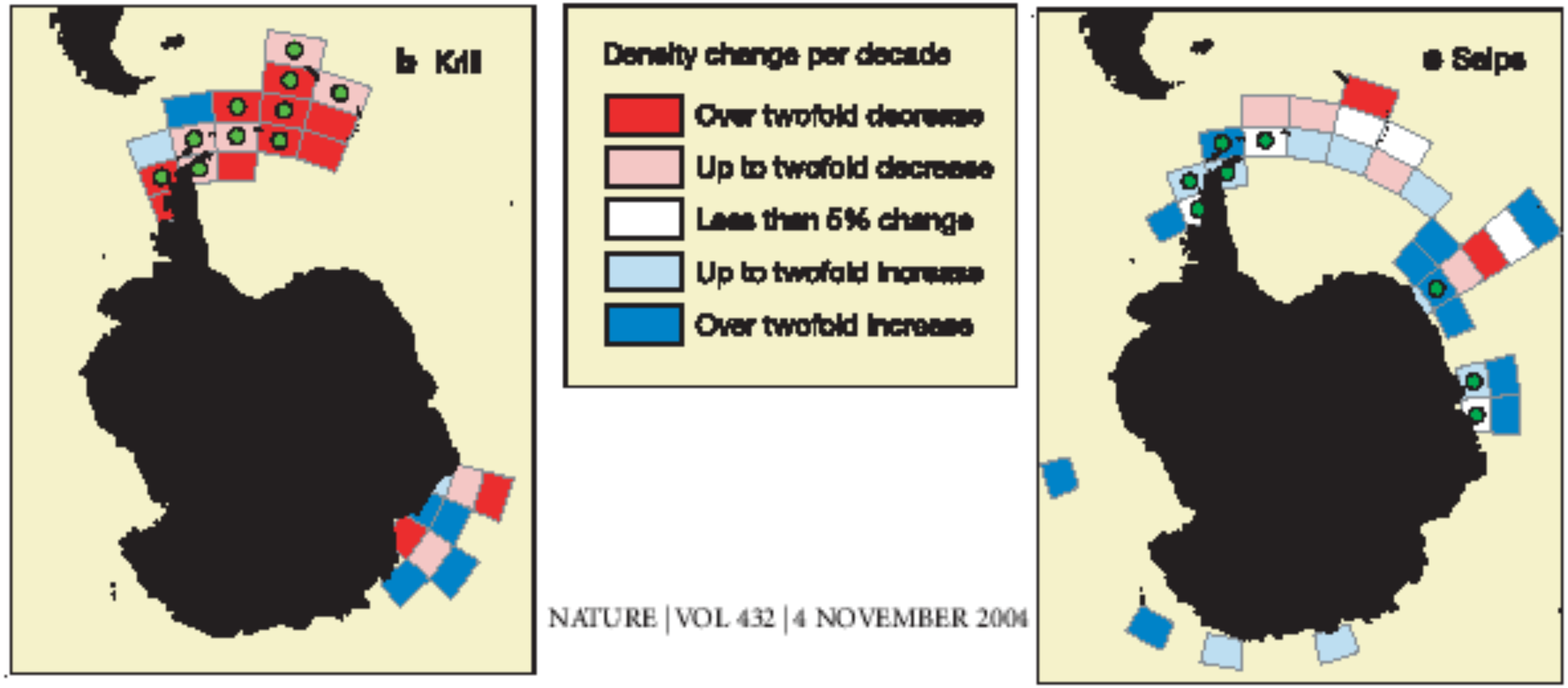





**Figure 2** Temporal change of krill and salps. **a**, Krill density in the SW Atlantic sector (4,948 stations in years with >50 stations). Temporal trends include **b**, post-1976 krill data from scientific trawls; **c**, 1926–2003 circumpolar salp data south of the SB. Regressions of $\log_{10}$(mean no. $m^{-2}$) on year were calculated for cells with ≥3 yr of data, weighted by number of stations in that year. One-sample $t$-tests supported a post-1976 decrease in krill density in the SW Atlantic (scientific trawls: $t = -3.4$, $P = 0.004$, 16 cells, smaller nets: $t = -2.5$, $P = 0.04$, 8 cells). Salp densities increased south of the SB after 1926 ($t = 3.1$, $P = 0.004$, 32 cells) Green spots denote cells usable in the spatio-temporal model.

A swarm of krill at the surface (Steve Nicol).

**Photo 2.3: Krill feeding on ice algae from the undersurface of sea ice**

Photo P. Marschall, AWI

**Photo 2.4: Two individuals of krill in an aquarium feeding on a dense culture of aggregated ice-algal diatoms.** Their voracity is reflected in the size of the food bolus and the continuity of the ingested food and faeces emanating from the tail end of the animal in the foreground.

# Adult Antarctic Krill feeding at abyssal depth Andrew Clark & Paul Tyler

Current Biology 2008

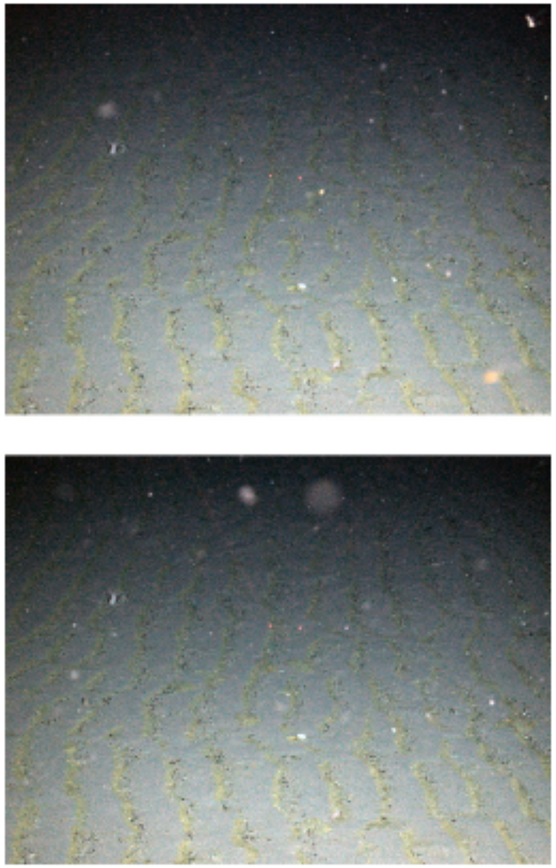


Figure S1. Phytodetritus at 3000 m, Photographed on *Isis* Dive 8

At this site, a steady bottom current has produced sediment ripples and winnowed the phytodetritus into the troughs between the ripples (images copyright Paul Tyler, National Oceanography Centre, Southampton).

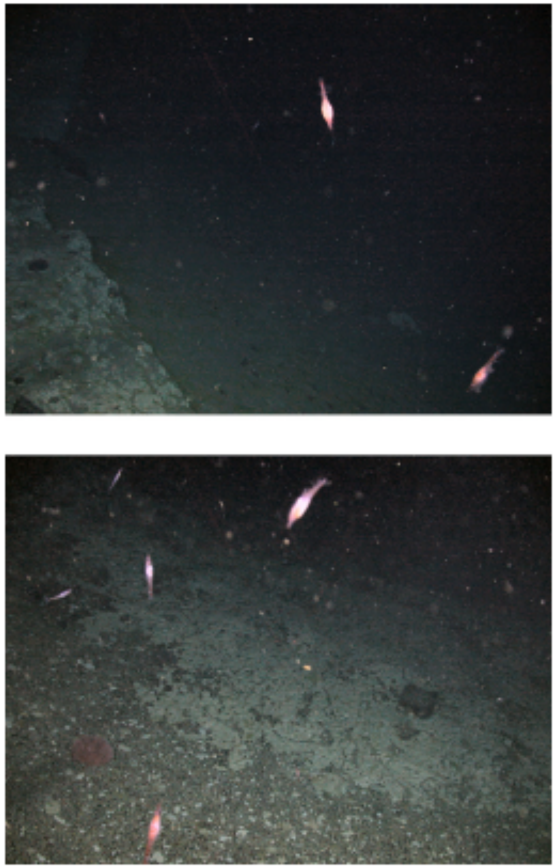


Figure S2. Adult Antarctic Krill, *Euphausia superba*, Photographed at 3000 m on *Isis* Dive 8

The swollen thorax of gravid females is clearly visible in both images (images copyright Paul Tyler, National Oceanography Centre, Southampton).

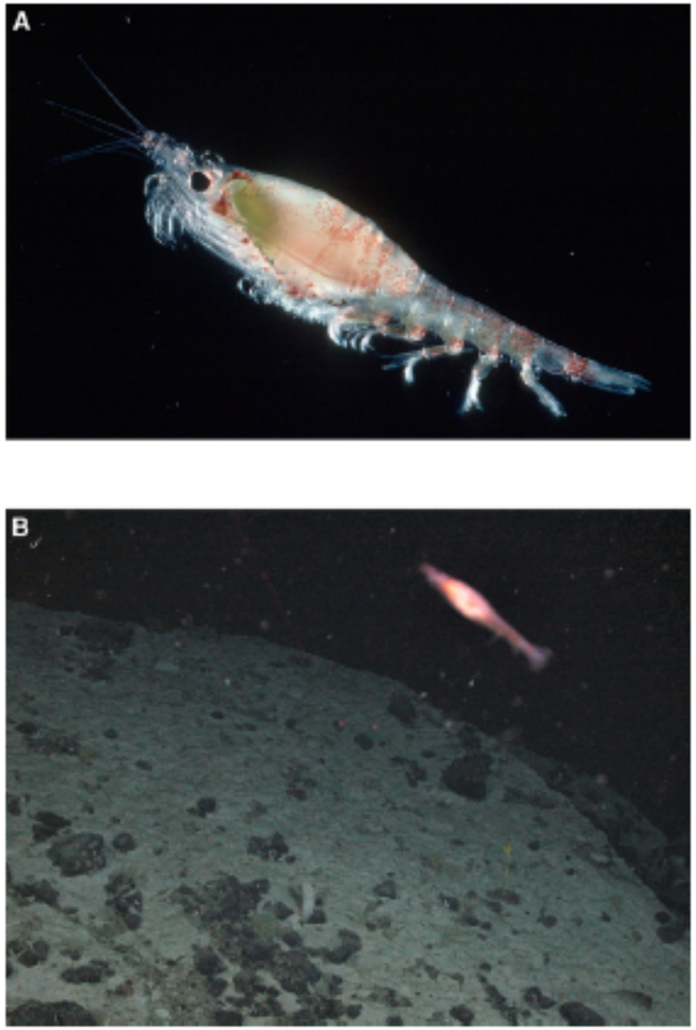


Figure 4. Antarctic Krill, *Euphausia superba*

(A) Gravid female *Euphausia superba* showing the markedly swollen thorax caused by the maturing ovary (image copyright British Antarctic Survey).
(B) Image taken from *Isis* at 3000 m (dive 8), showing adult Antarctic krill just above the seabed (image copyright Paul Tyler, National Oceanography Centre, Southampton).

# LITTLE EVIDENCE FOR INCREASE IN KRILL MORTALITY

Krill predator populations prior to decimation of the great whales were much larger than current stocks of krill predators such as seals, penguins and Minke whales.

Antarctic blue whales feed exclusively on Krill. About 300,000 were killed, equivalent to 30 Million tonnes. Food demand of all the great whales and other Krill predators prior to whaling is estimated at about 180 Million tonnes per year.

Annual global fish catch which resulted in current plight of fisheries world-wide was 70 Million tonnes per year since the 1970s.
Global human biomass is about 300 Million tonnes.

Blue whales are reportedly recovering but population size is still ~ 1% of original.
So it is highly unlikely that predation pressure alone is responsible for ongoing Krill decline.

Krill fishery plays a minor role

EVIDENCE FOR FOOD LIMITATION OF KRILL STOCKS

- Estimated former krill stock was at upper level of carrying capacity of the system (> 10 g C m-2, which is equivalent to that of phytoplankton biomass under bloom conditions)

- Release of Krill grazing pressure should result in correspondingly more chlorophyll. However, satellite data (comparison of CZCS with SeaWifs data) indicate the opposite (Gregg and Conkright 2002).

- Salps avoid phytoplankton blooms, so increase in their range is itself an indication of decreasing phytoplankton stocks, particularly diatoms.
- Caveat: Salp increase is indication of rising temperature in the new range.

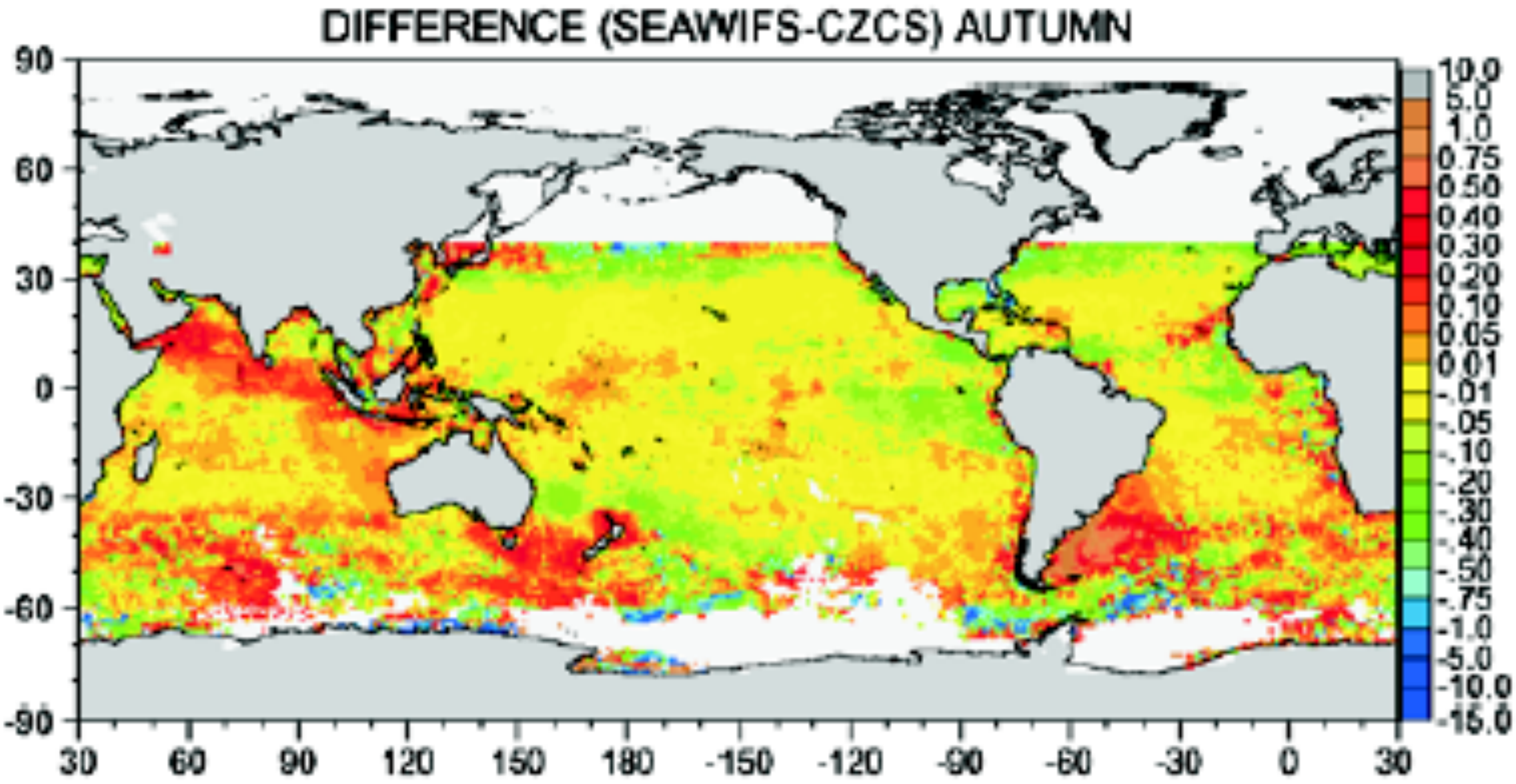
- Krill biology geared to maximise efficiency of available food uptake. particularly in sea ice habitat.

# POSSIBLE REASONS FOR DECLINE IN PRODUCTIVITY

- Southern Ocean productivity is controlled by supply of iron.

- Supply of „new“ iron to Antarctic Peninsula Plume is provided by:
- a) Contact of iron-impoverished surface water with land masses and sediments.
- b) Land run-off (in summer)
- c) Upwelling along continental slope
- d) Winter dust gathering on sea ice released during melting.

- In addition, recycling of iron in surface layer by heterotrophs.
- Whales will have contributed significantly to recycling of essential elements because they convert krill protein into blubber.
- Their feeding will condition the environment by increasing the pool of regenerated iron.




Differences in chlorophyll distribution between CZCS and SeaWiFS eras for Oct.-Dec.
Note reduction in the region along ACC.
From Gregg and Conkright GRL 29 (2002)

**Photo 2.9: A minke whale that had been feeding on krill, photographed in the Antarctic Peninsula Plume while defecating in surface water**

*Source*: Smetacek and Nicol 2005. Our thanks to Captain J. Brokowski II of RV *Nathaniel Palmer* for his kind permission to reprint this photo.

## Conclusions

The simple food chain of the giants: diatoms -> Krill -> whales is maintained by the giants There was much more iron in the animals than outside them.

Whales are top predators so their population size will be food regulated.

Populations of large, long-lived animals will stabilize the system on which they depend.

Blue whales are recovering but how long will it take for them to re-establish the system from which they have been slaughtered?

Artificial iron fertilization could be one way to speed-up the process.

Marine equivalent of ecosystem restoration and maintenance.

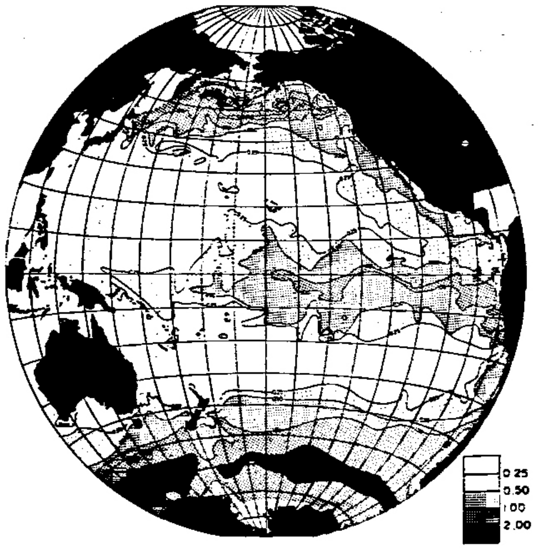
More details under www.beyondbluemag.com (October 2009)

LIMNOLOGY
AND
OCEANOGRAPHY

*December 1991*
Volume 36
Number 8

# WHAT CONTROLS PHYTOPLANKTON PRODUCTION IN NUTRIENT-RICH AREAS OF THE OPEN SEA?

The figure overleaf shows the distribution of inorganic phosphate-phosphorus ($\mu$g-atoms liter$^{-1}$) at the surface of the Pacific Ocean. It first appeared in *Limnology and Oceanography* in 1962 (Reid, J. L. 1962. On the circulation, the phosphate-phosphorus content, and the zooplankton volumes in the upper part of the Pacific Ocean. Limnol. Oceanogr. 7: 287–306).

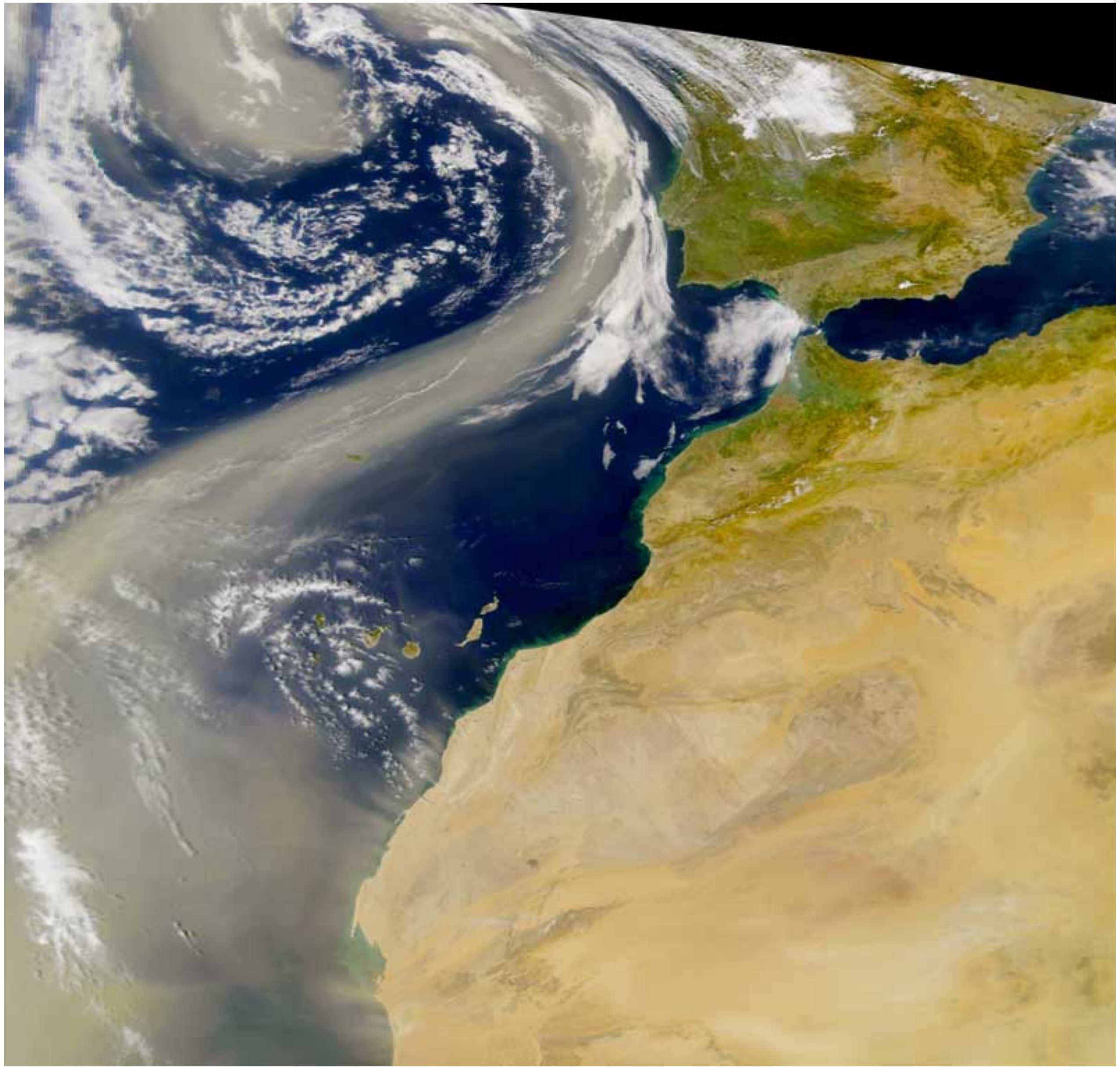


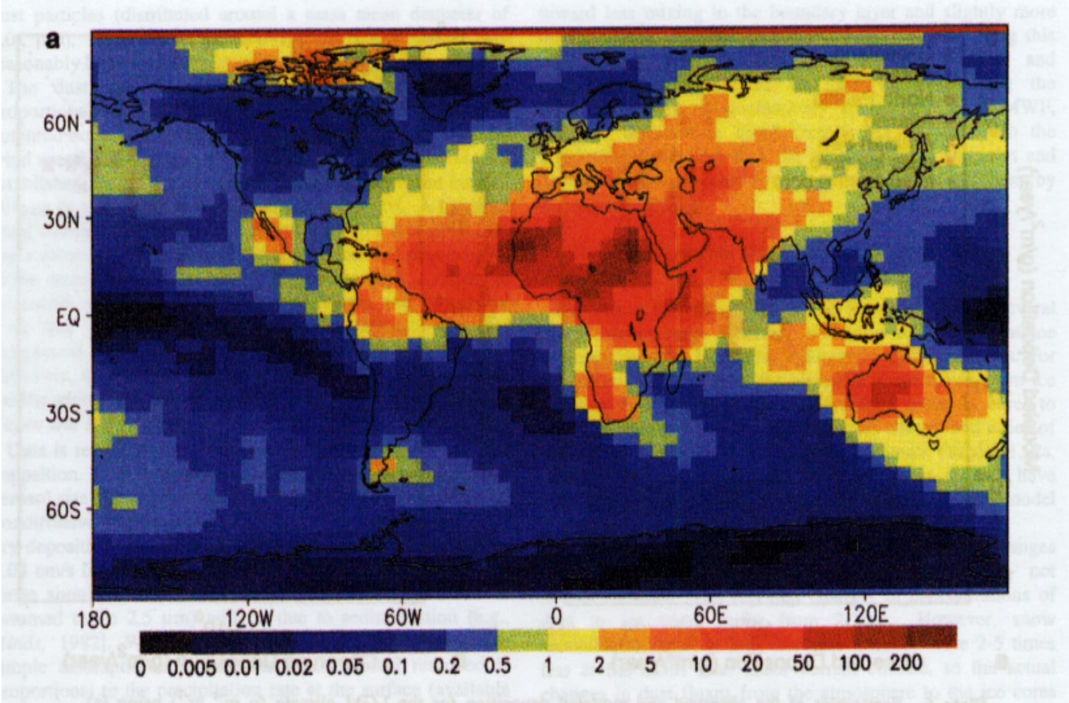

American Society of Limnology and Oceanography Symposium
22–24 February 1991
San Marcos, California

Sallie W. Chisholm and François M. M. Morel, Editors

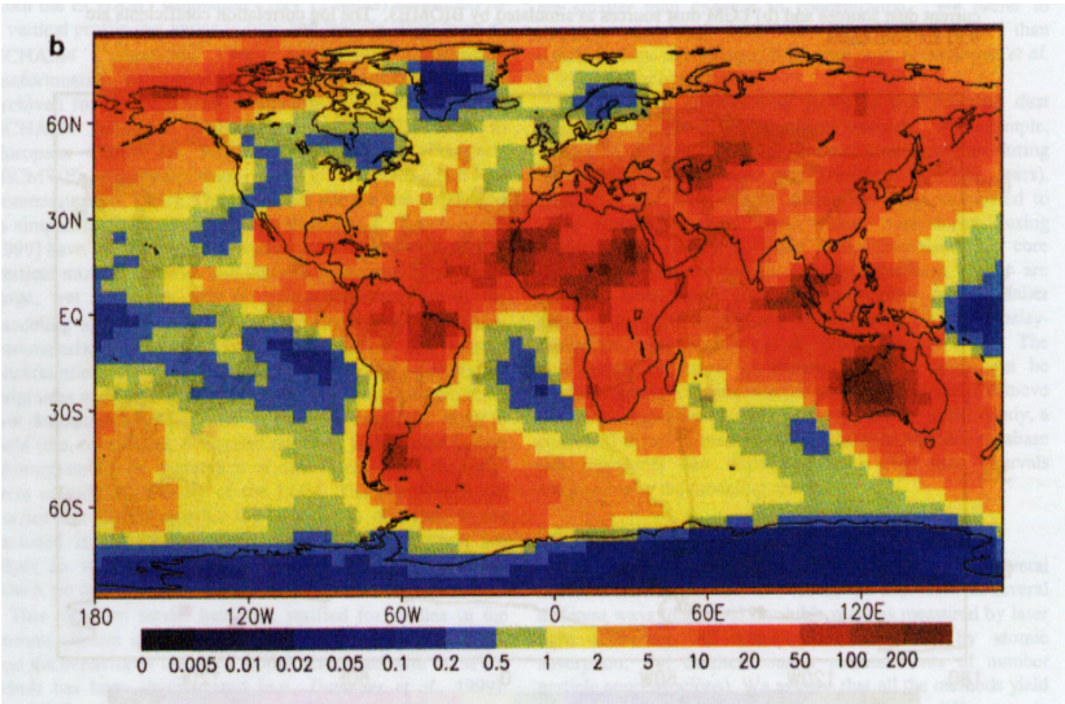
- deep mixed layers (light limitation)
- Iron availability
- heavy grazing pressure by zooplankton

Sahara sand and dust providing iron to the North Atlantic.






Dust input today




Dust input during glacials

Mahowald et al.

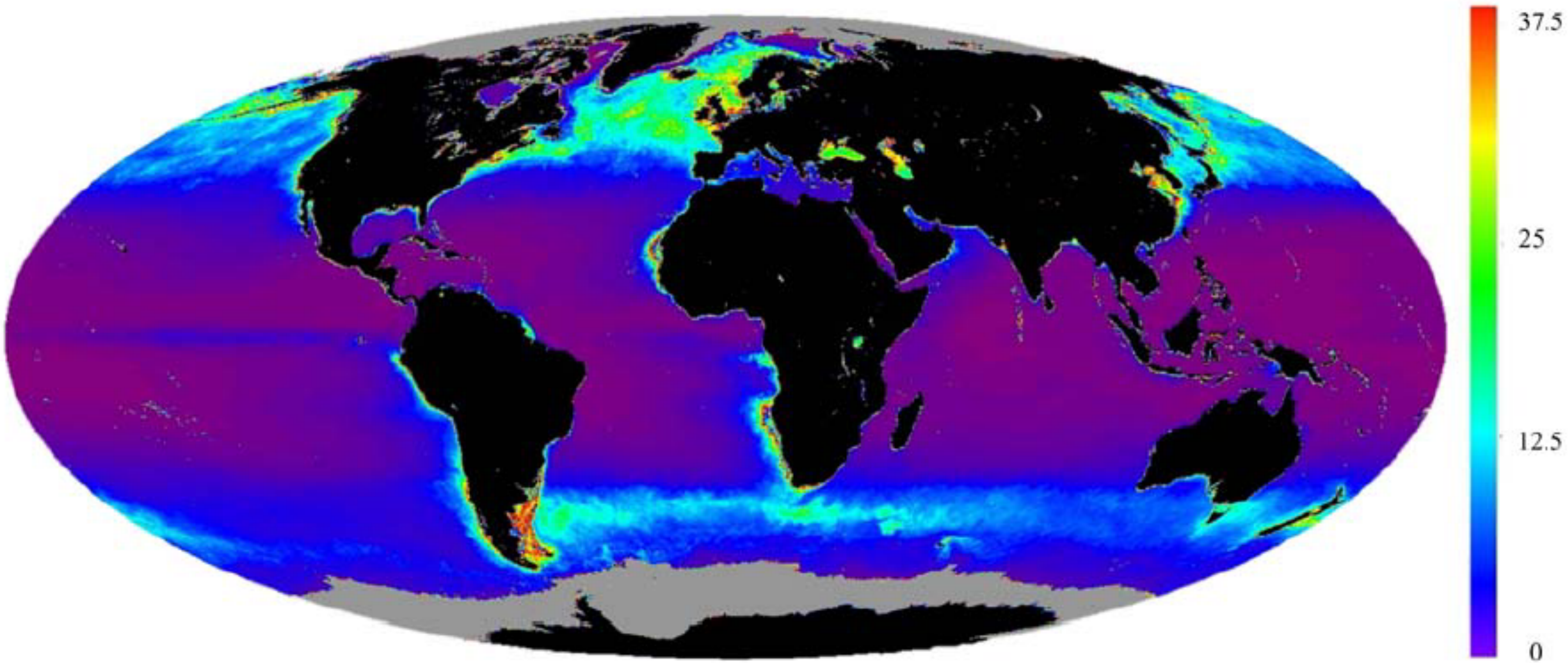
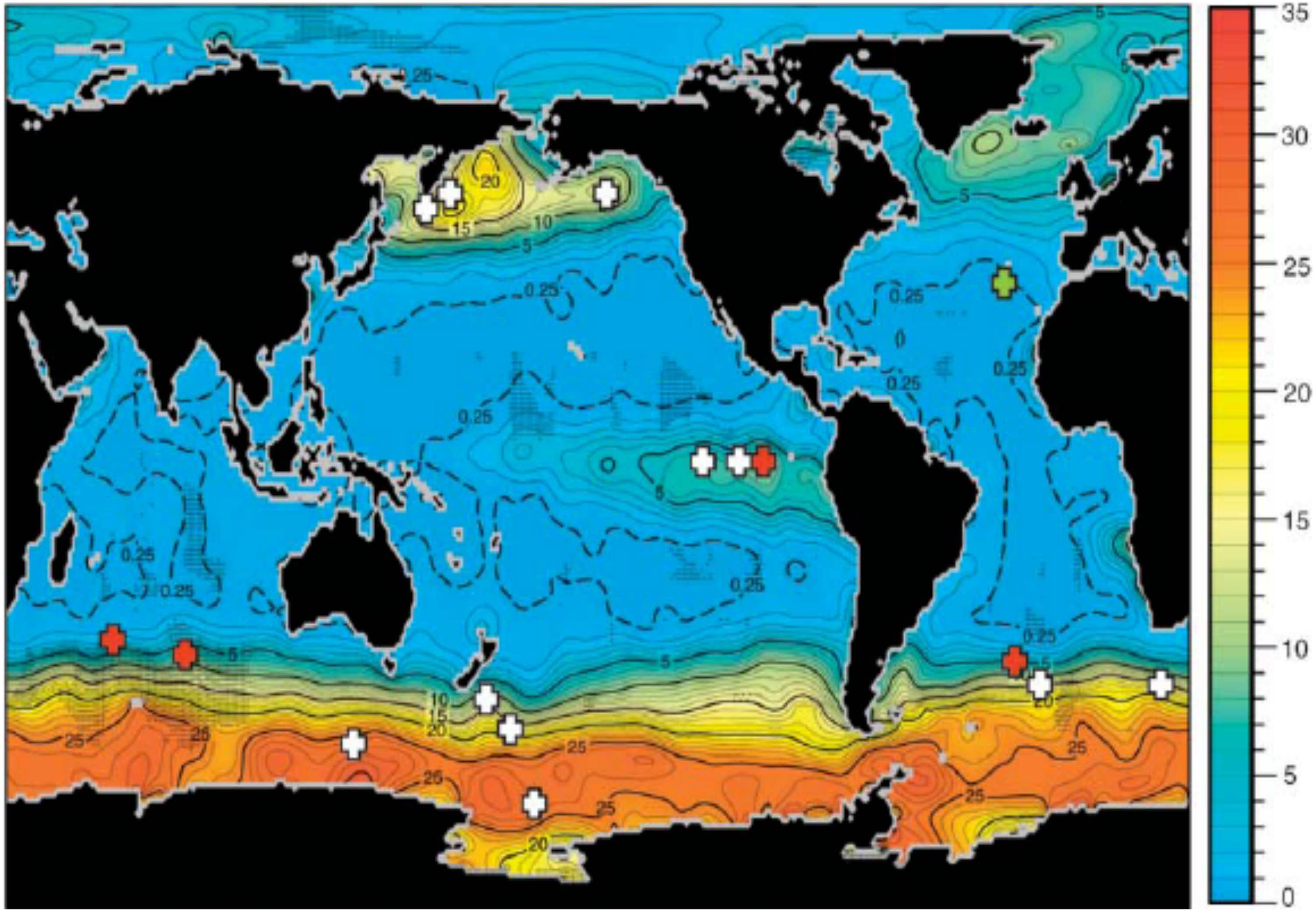



*Figure 3: Annual primary production (mol-C $m^{-2}$ $a^{-1}$) estimated using SeaWiFS data and model. Courtesy of P. Falkowski and D. Kolber, Environmental Biophysics and Molecular Ecology Laboratory, Institute of Marine and Coastal Sciences, Rutgers University, USA.*

JGOFS



35
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25
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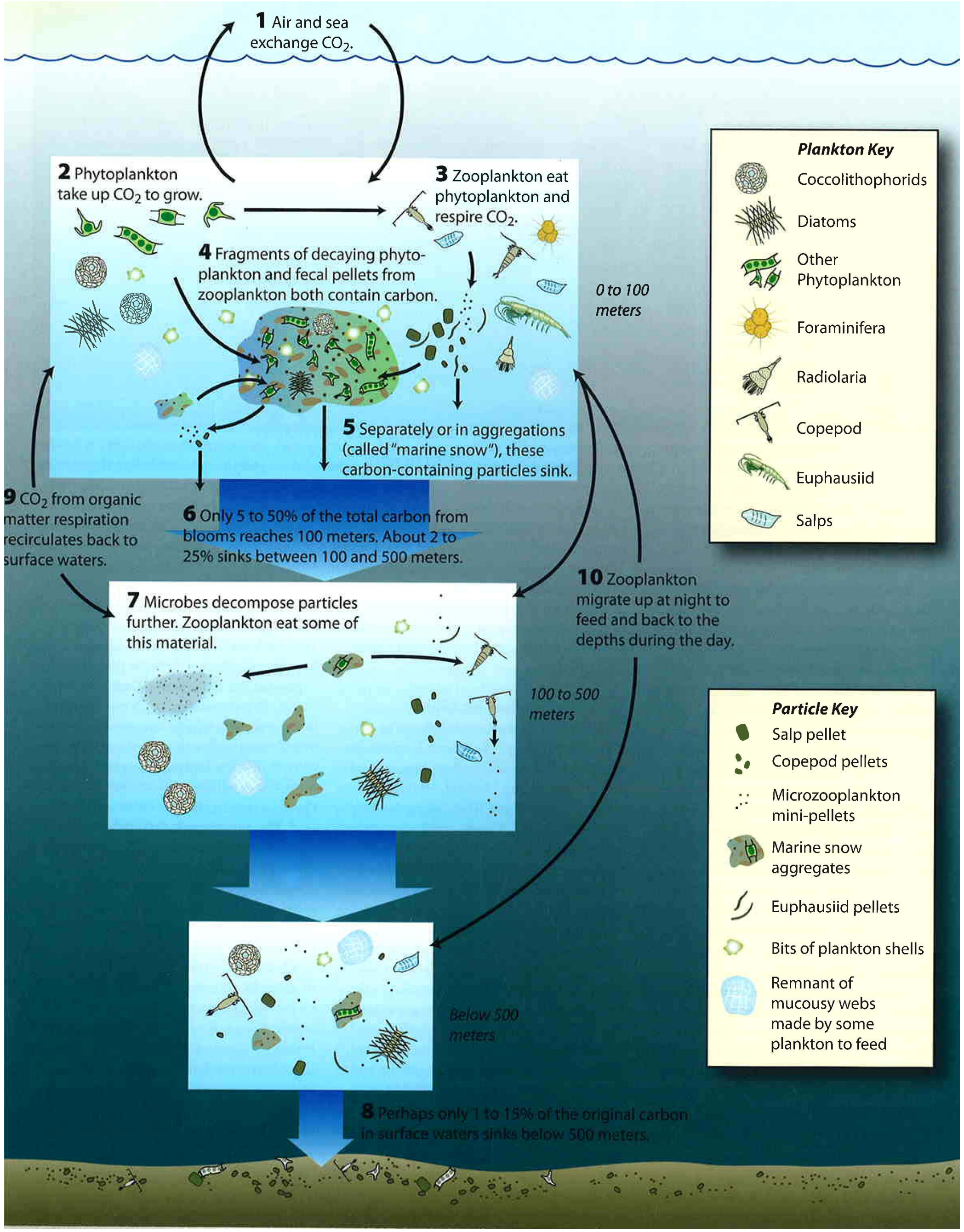
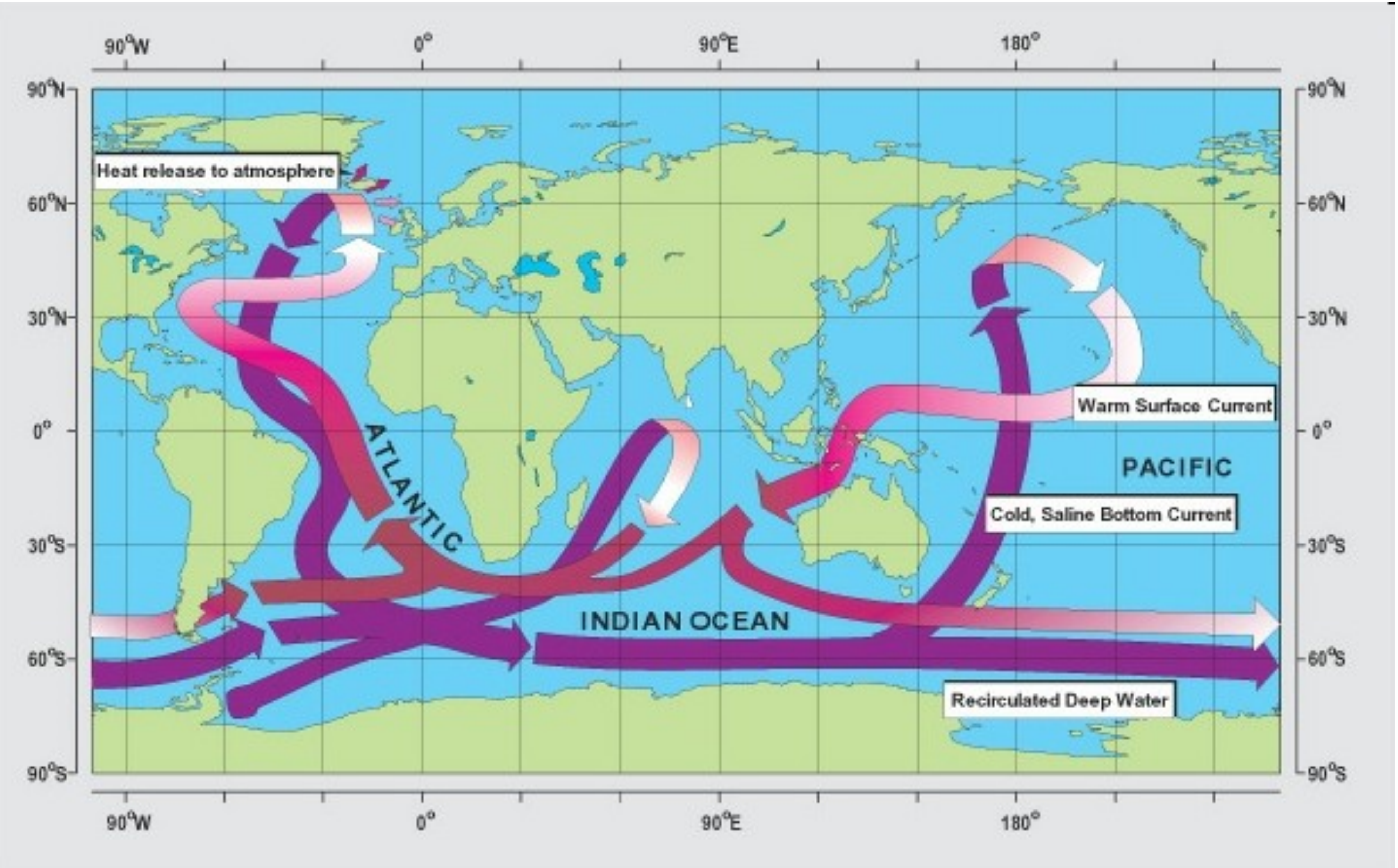
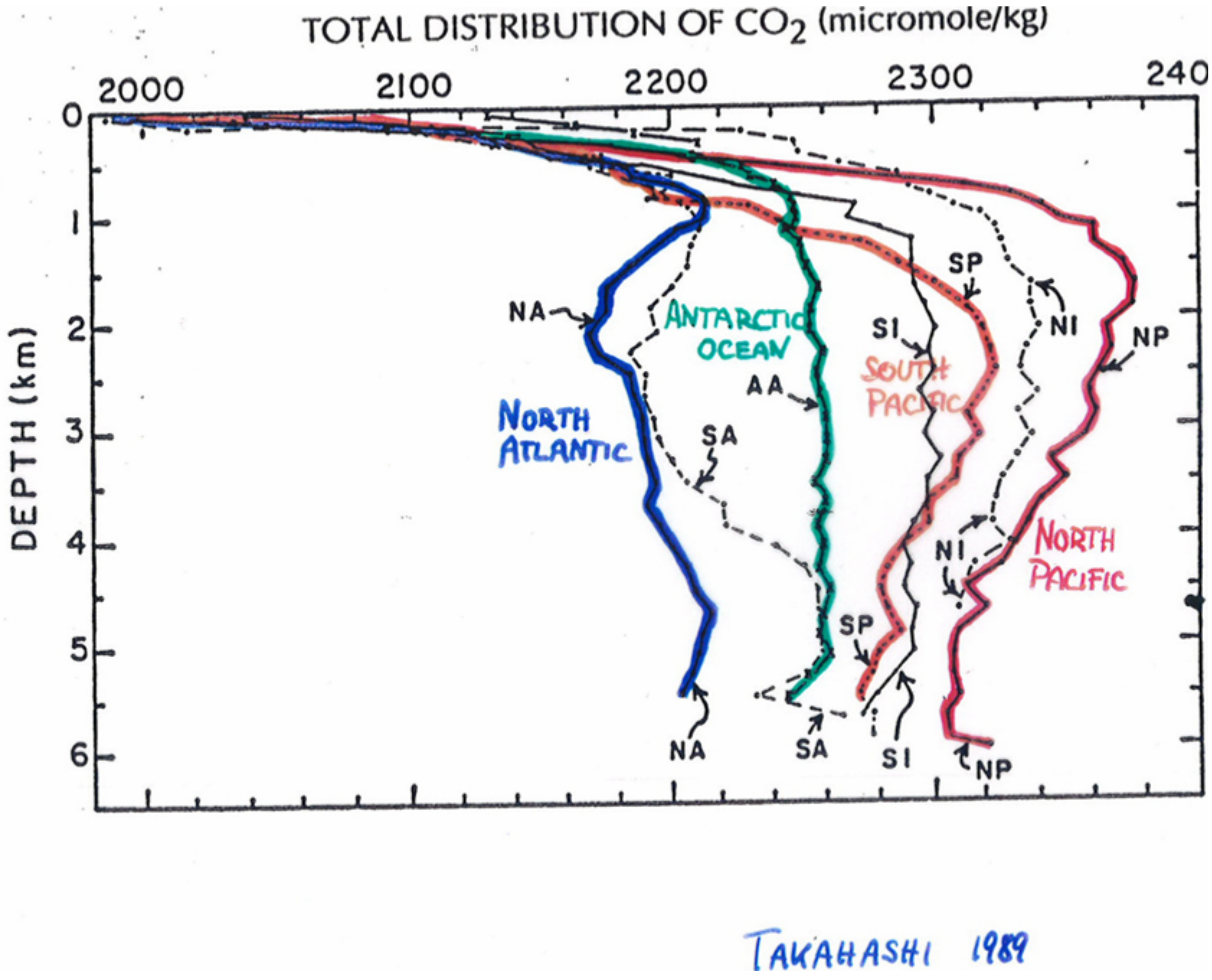
# The biological carbon pump



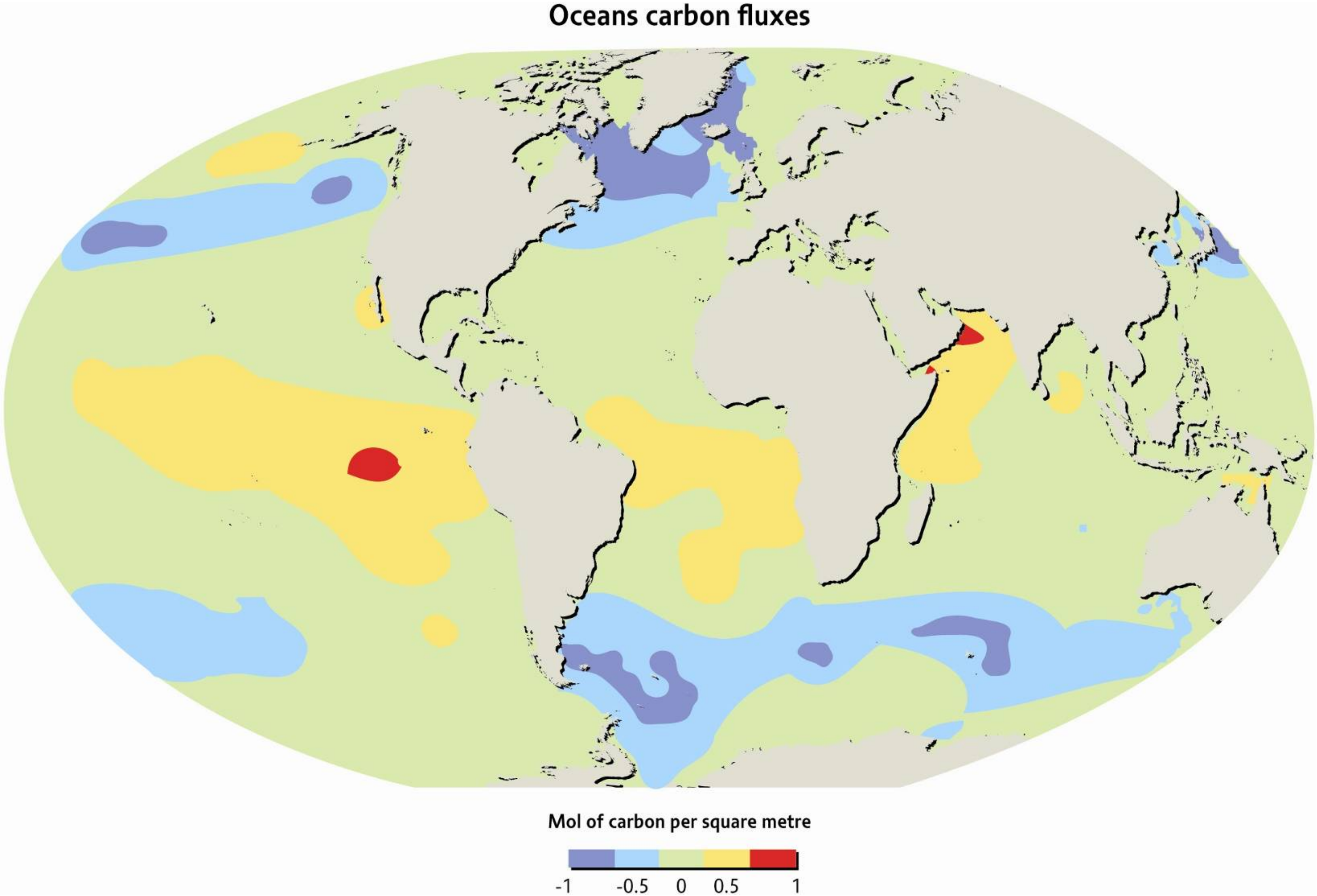

Powell 2008


90°W
0°
90°E
180°
90°N
60°N
30°N
0°
30°S
60°S
90°S
Heat release to atmosphere
Warm Surface Current
ATLANTIC
PACIFIC
Cold, Saline Bottom Current
INDIAN OCEAN
Recirculated Deep Water

Result of the biological carbon pump on the conveyor belt
Thermohaline circulation



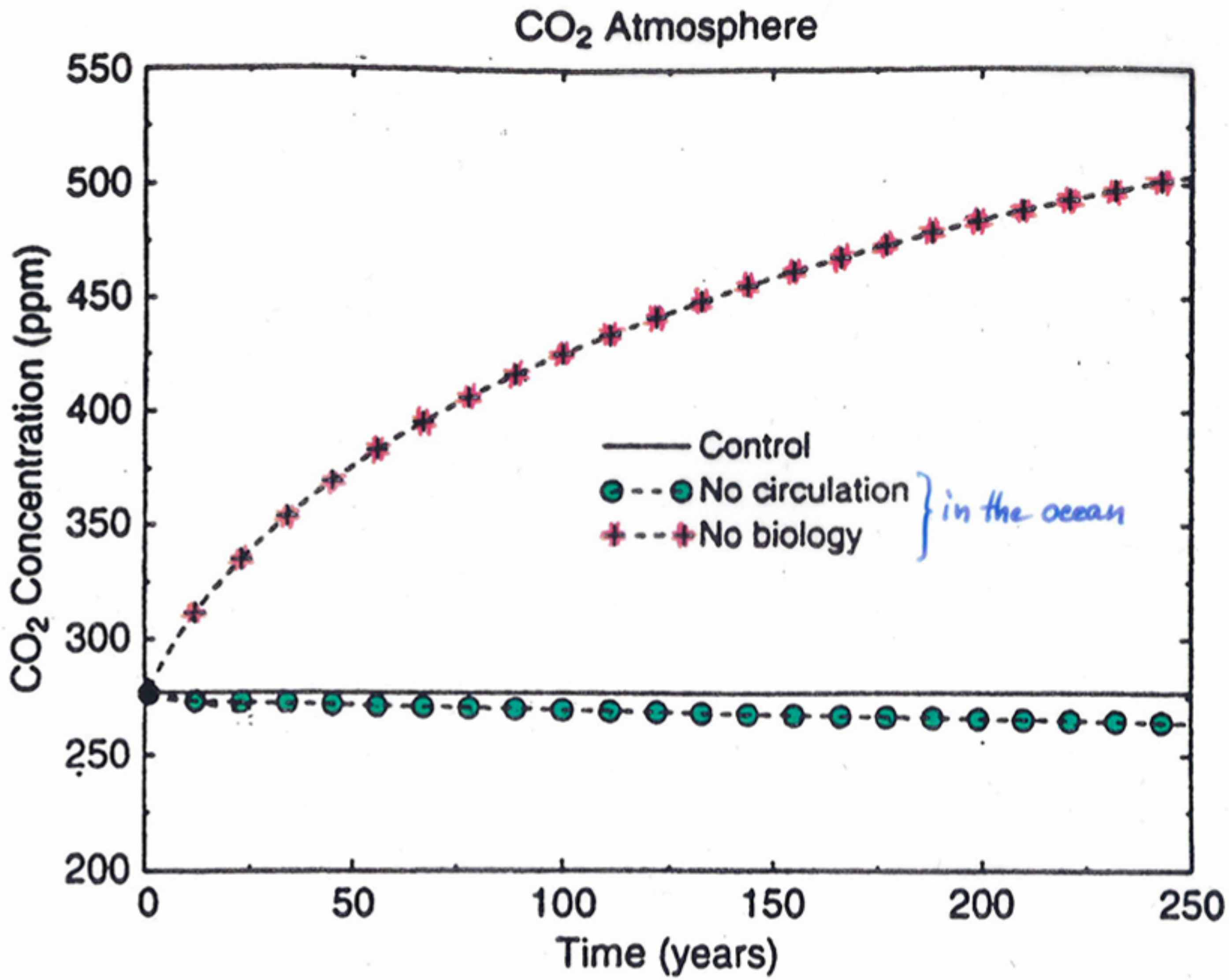
# Carbon fluxes in the oceans



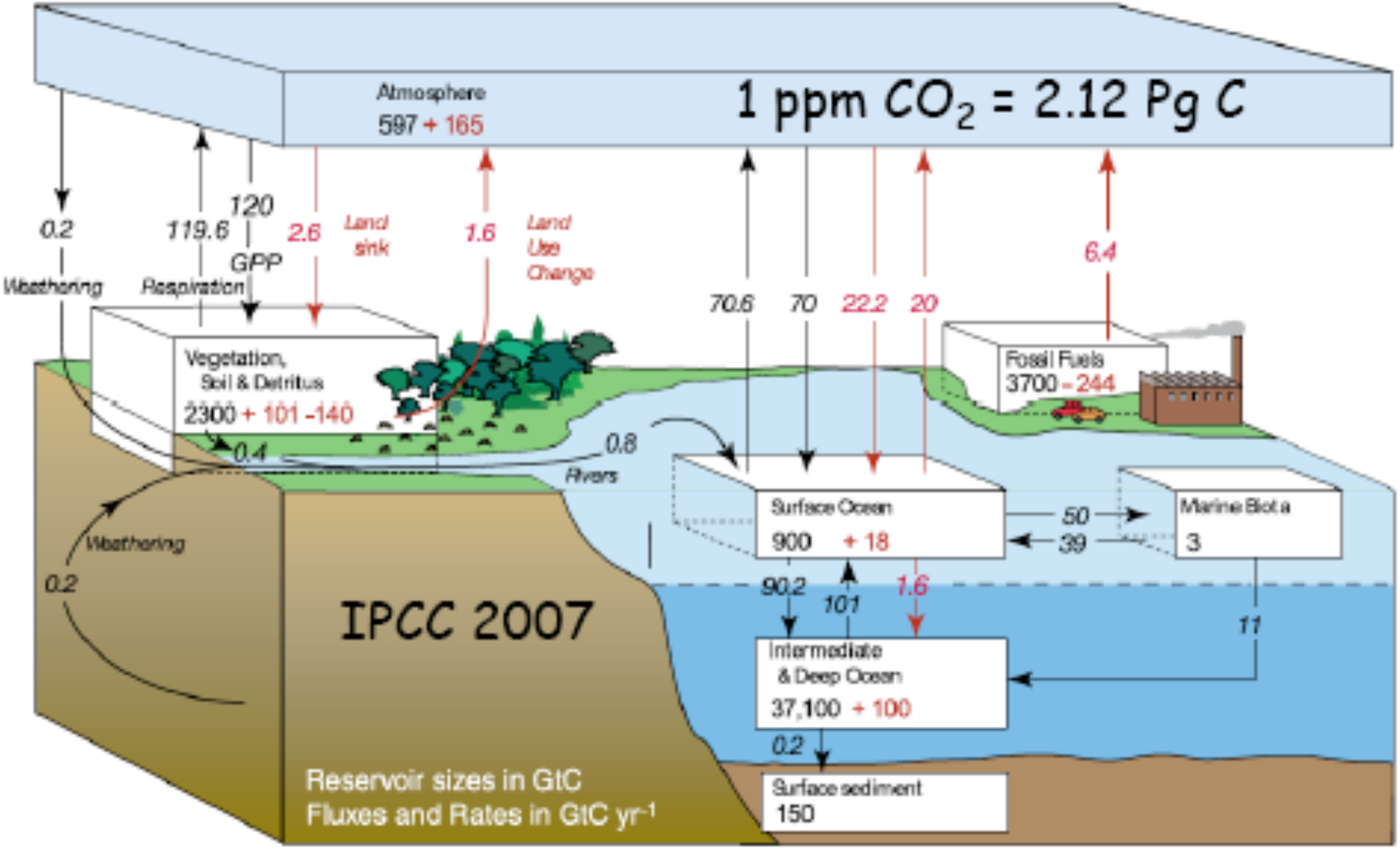

**http://maps.grida.no/go/graphic/oceans-carbon-fluxes**

Adapted from Takahashi et al., 2009. Marine Institute Ireland, 2009.

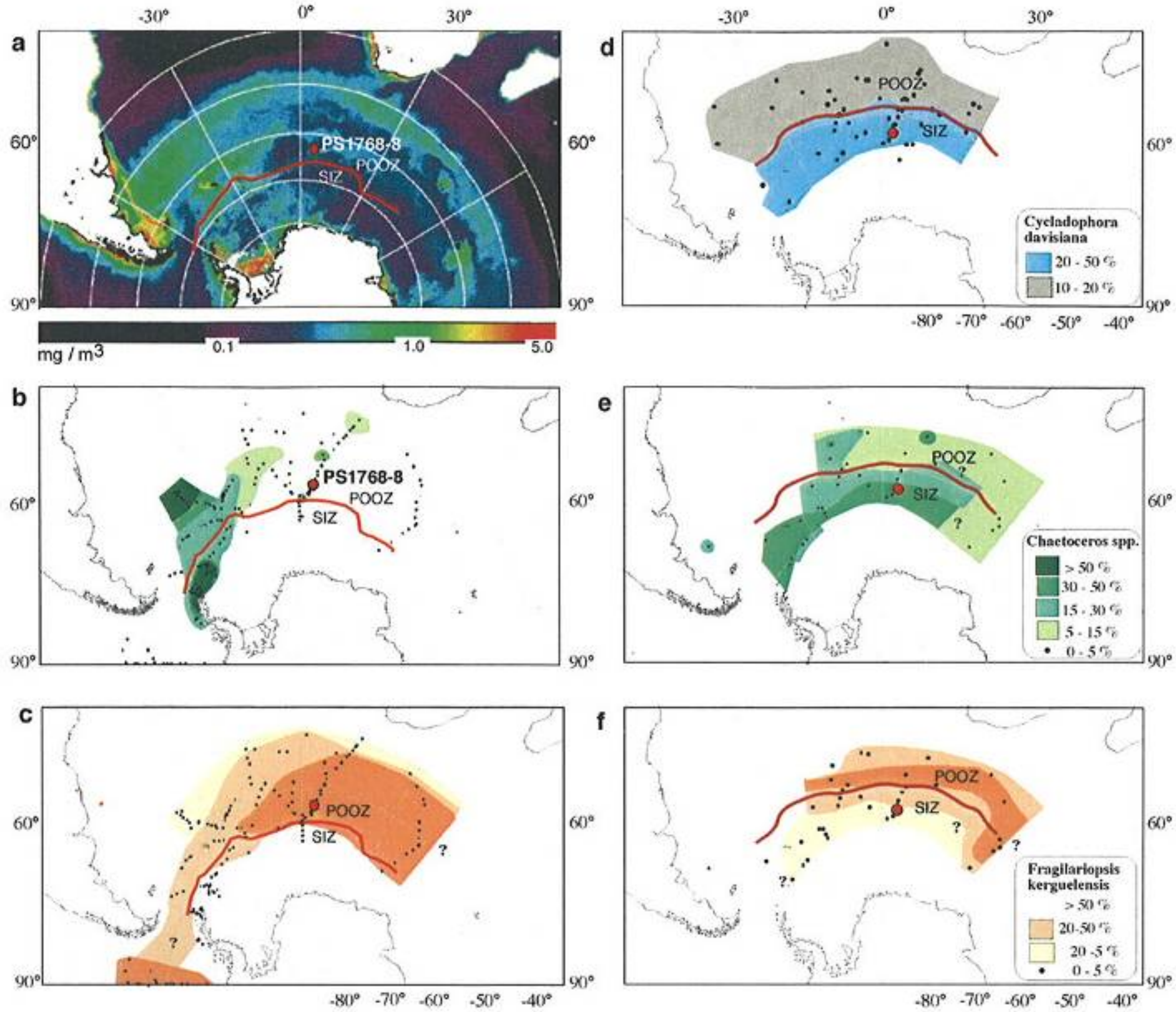
*Riccardo Pravettoni, UNEP/GRID-Arendal*




MAIER REIMER, MIKOLAJEWICZ, WINGUTH 1996

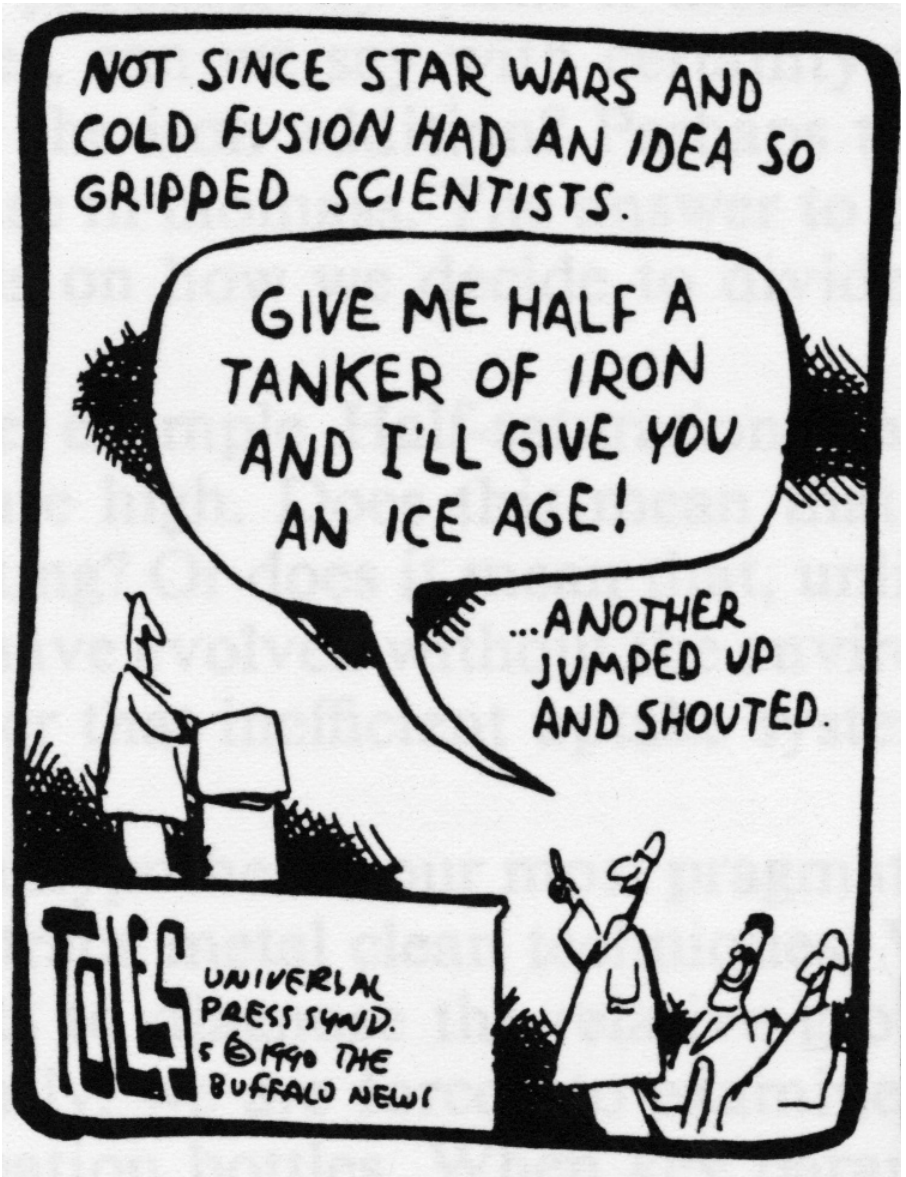



$1\ Gt\ C = 1\ Pg\ C = 10^{15}\ g\ C$




Abelmann, et al._Fig. 1

# Iron fertilization as a means to reduce atmospheric $CO_2$-Levels?



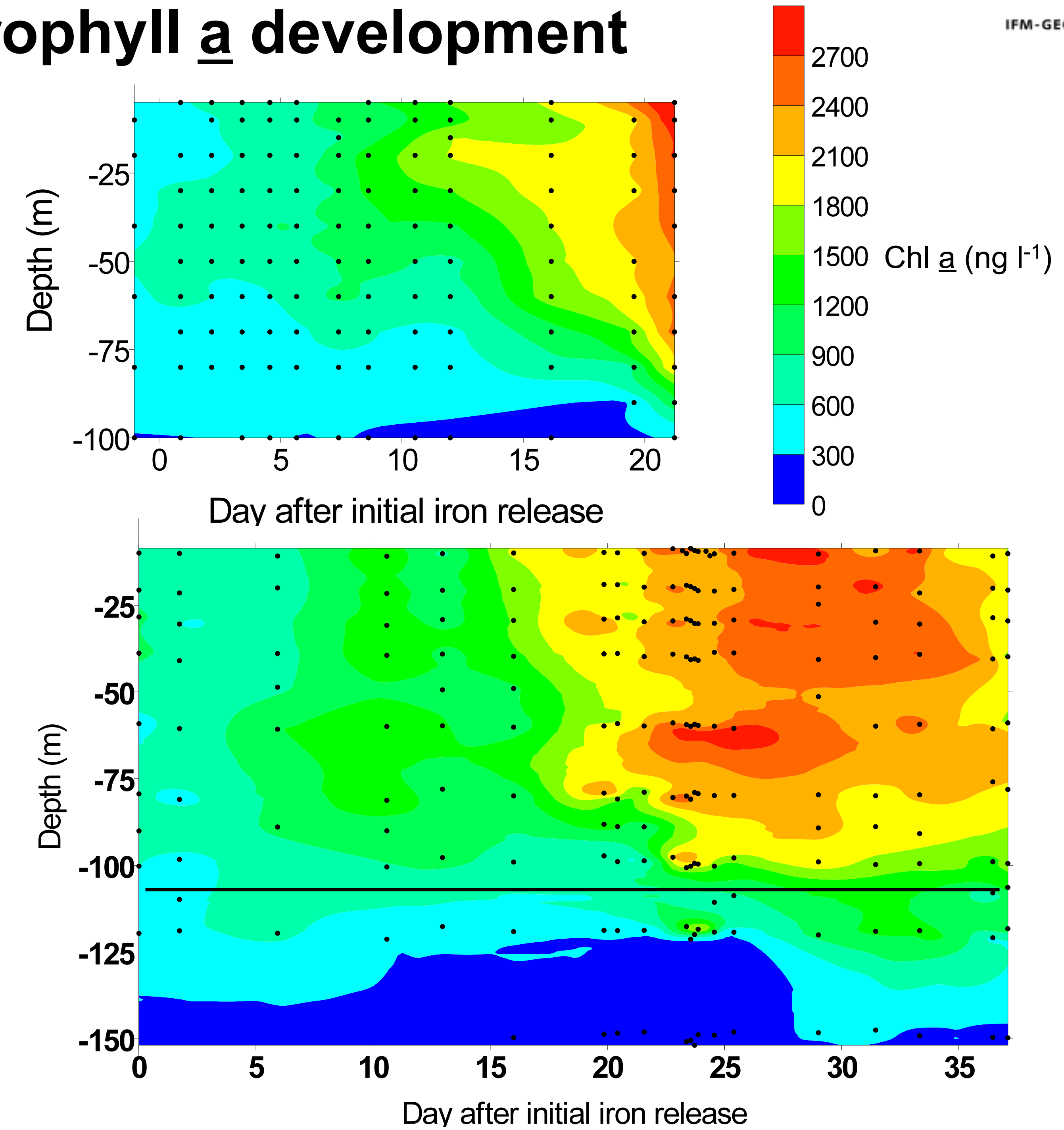
# Eisendüngung mit deutscher Beteiligung



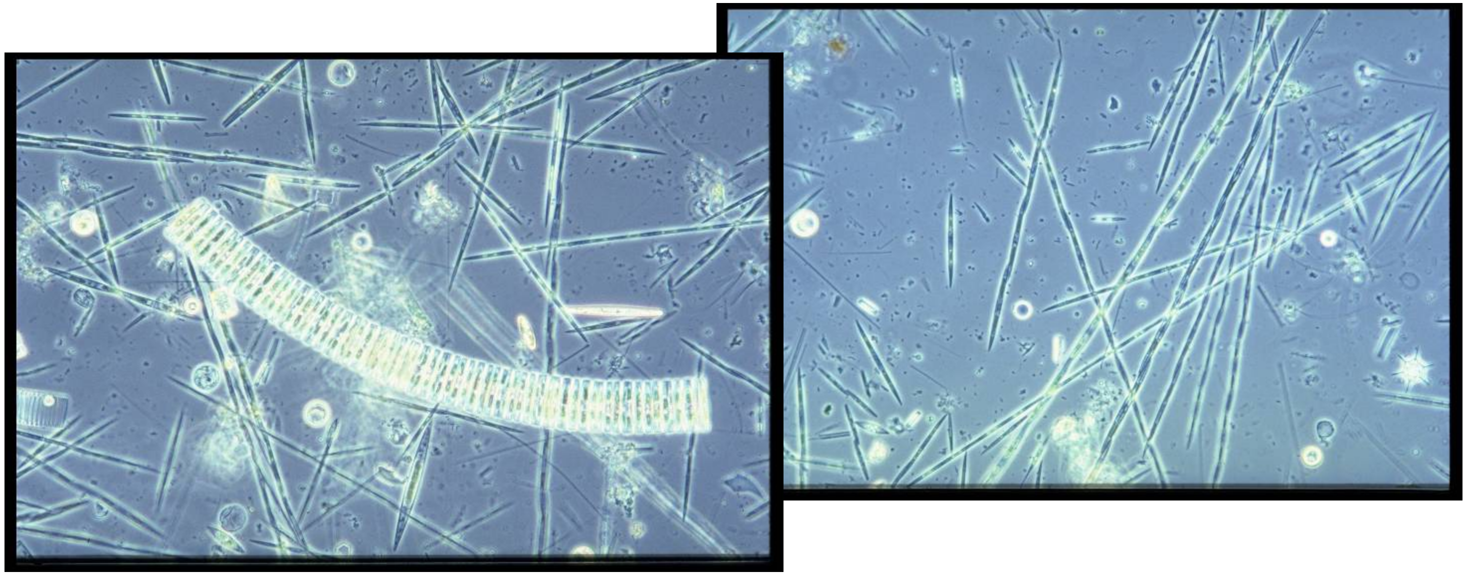

# Chlorophyll a development

EisenEx

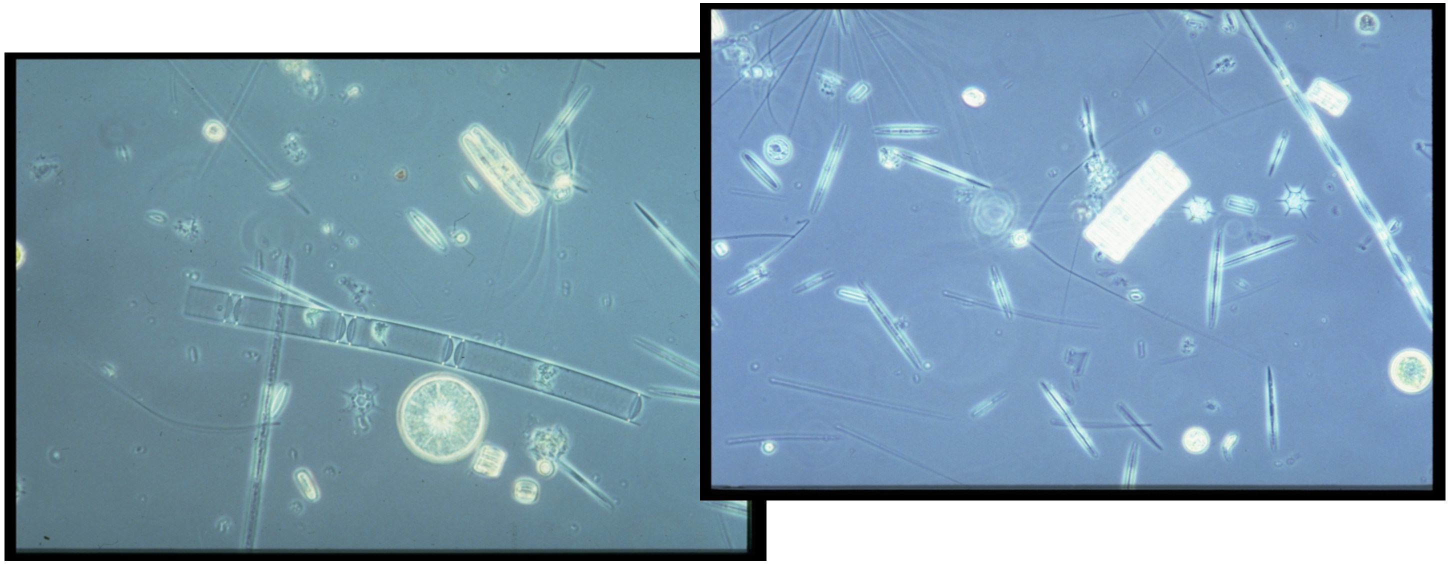
EIFEX

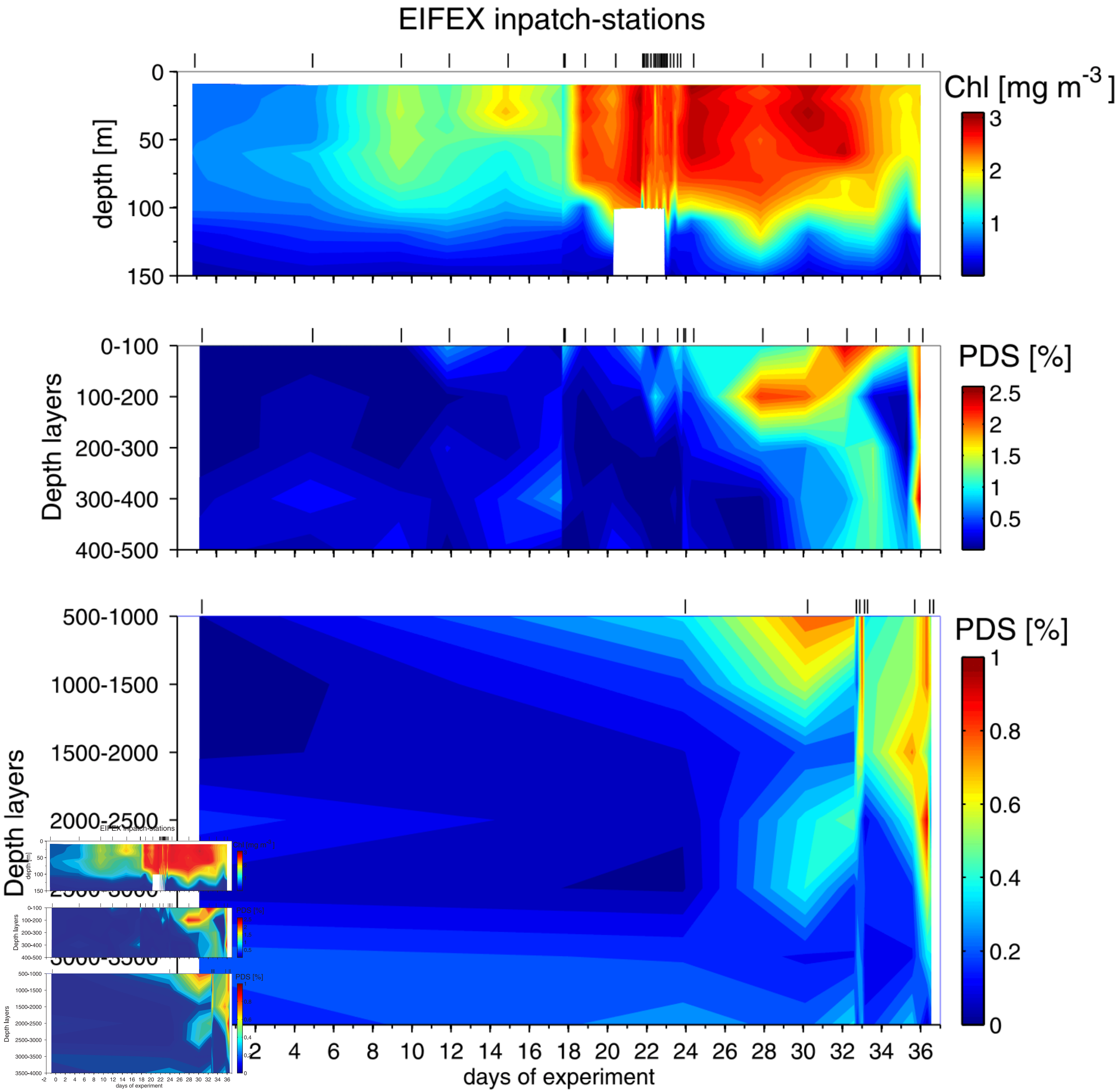


In patch station 21 days after first Fe-release

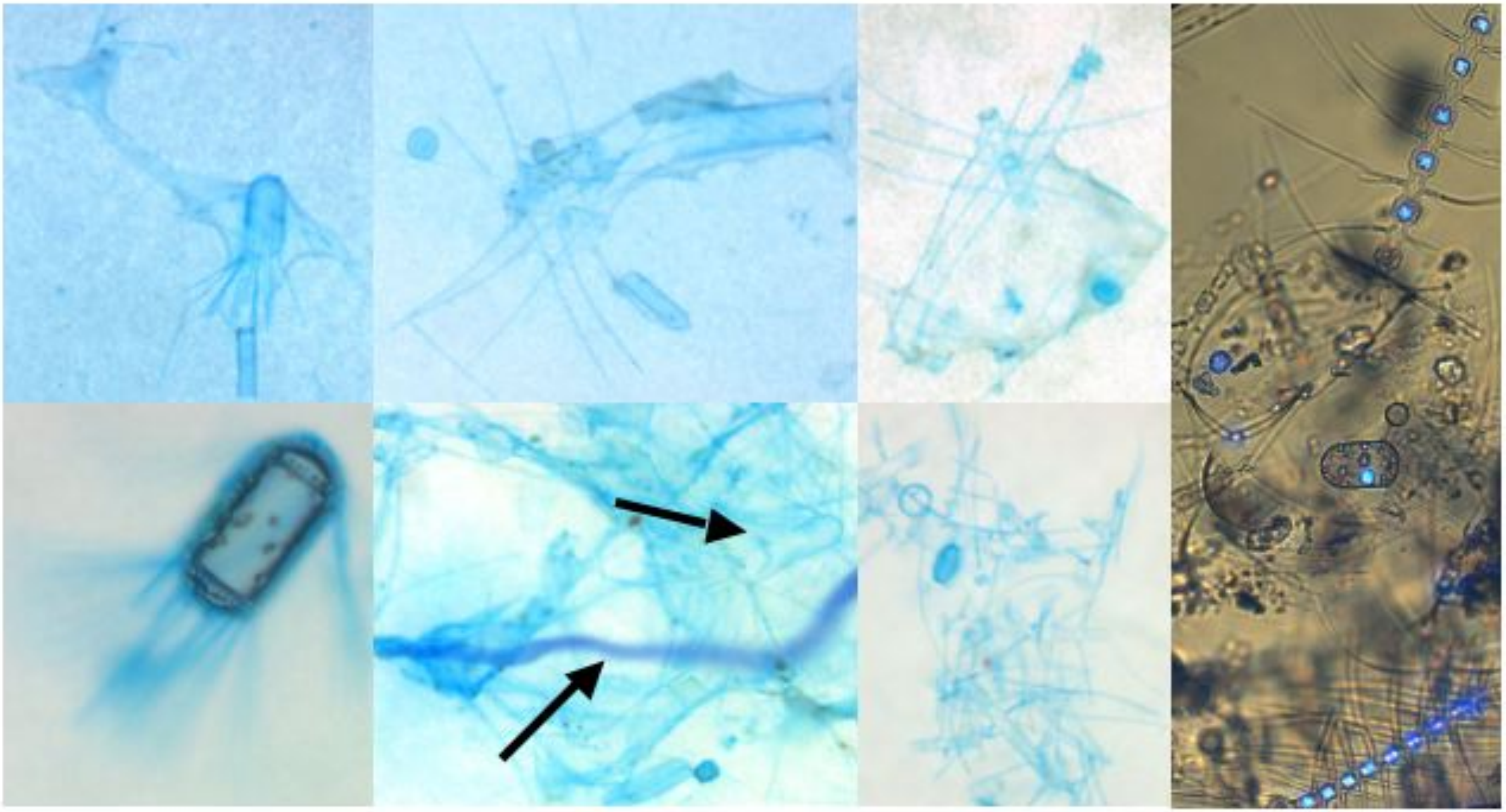


Out patch station 21 days after first Fe-release

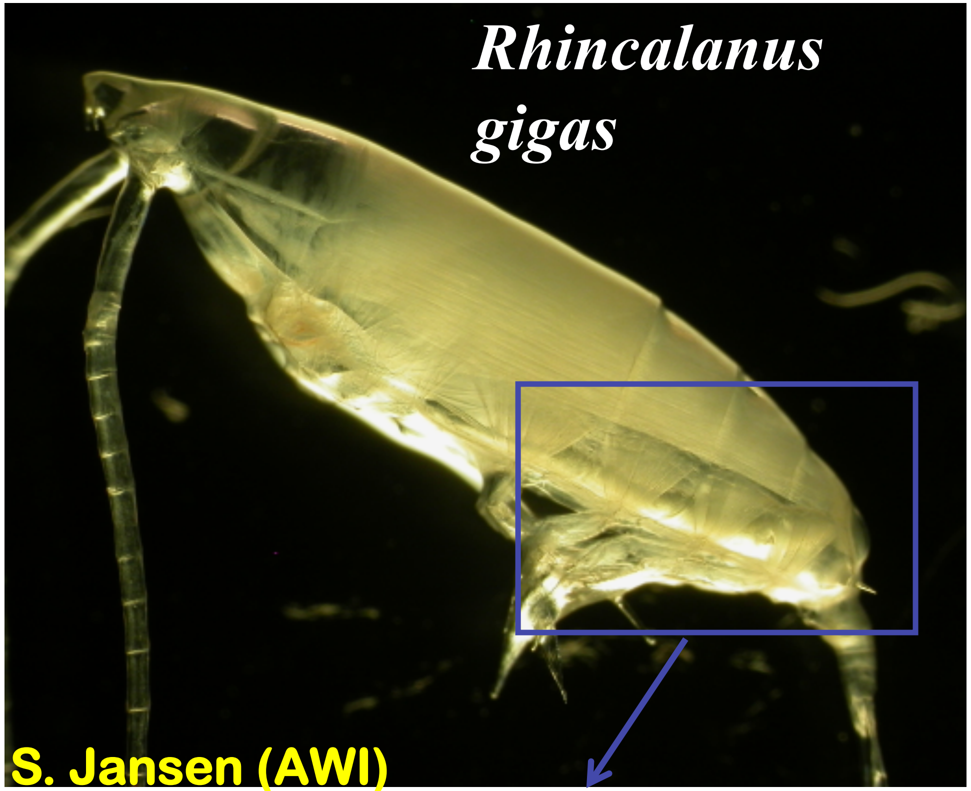


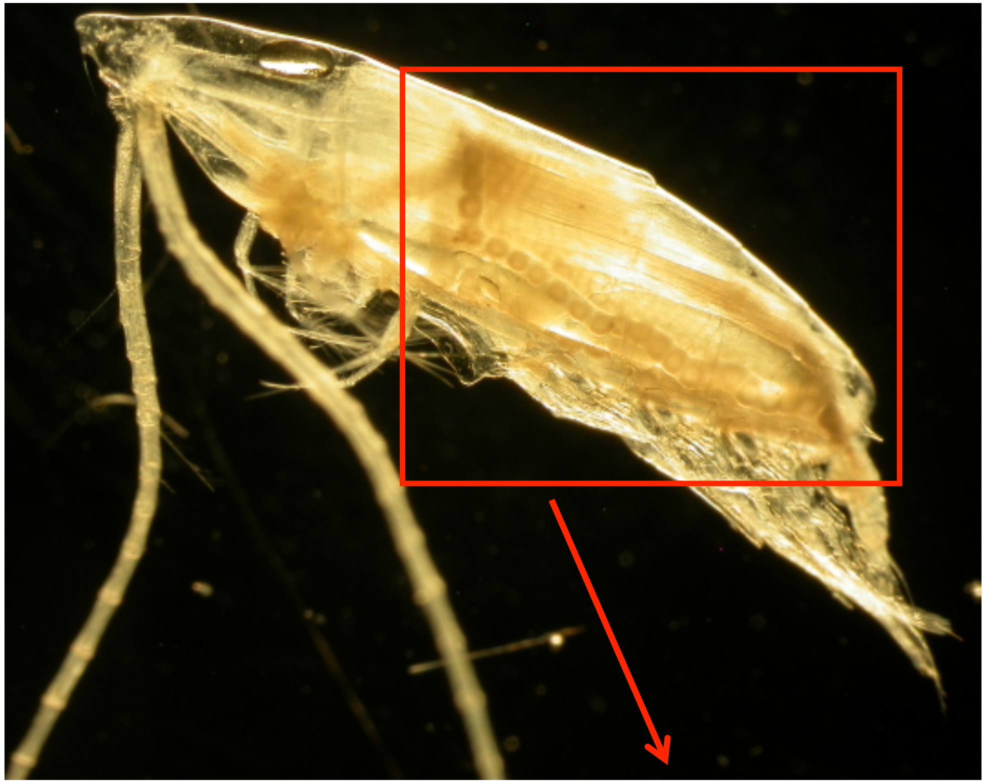


EIFEX inpatch-stations
depth [m]
Chl [mg m$^{-3}$]
Depth layers
PDS [%]
Depth layers
PDS [%]
days of experiment

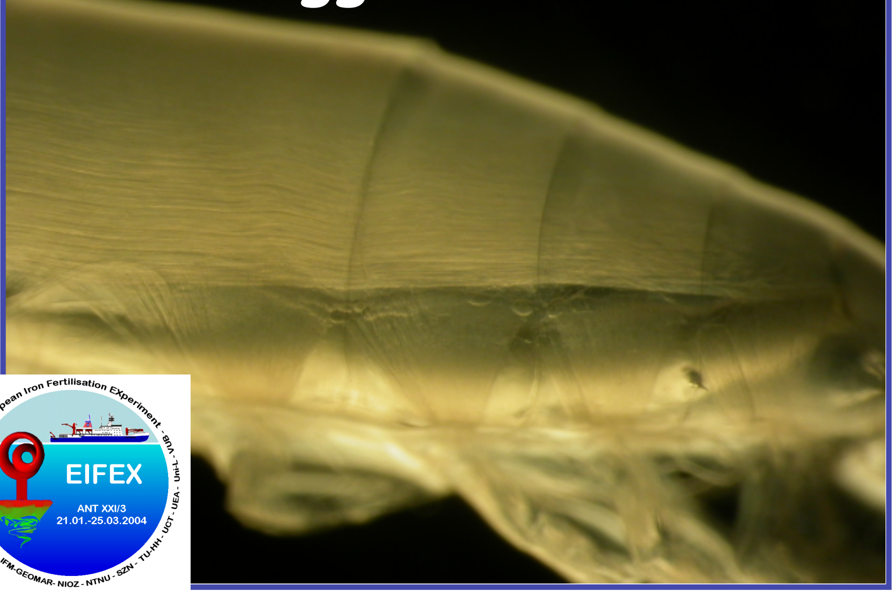


EIFEX: Aggregates collected during the sinking bloom from mesopelagial and stained with Alcian Blue (TEP) and DAPI (right)



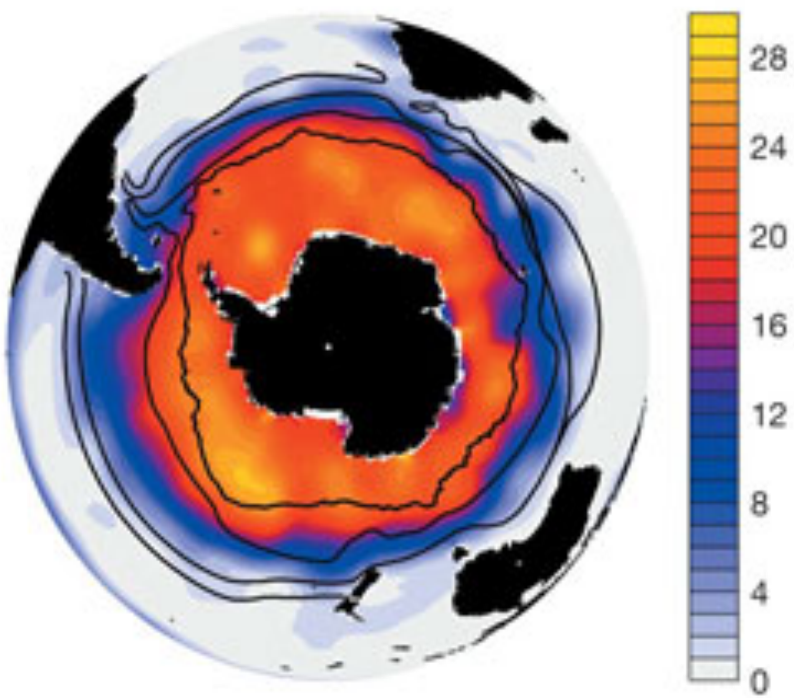
No eggs in low chl.



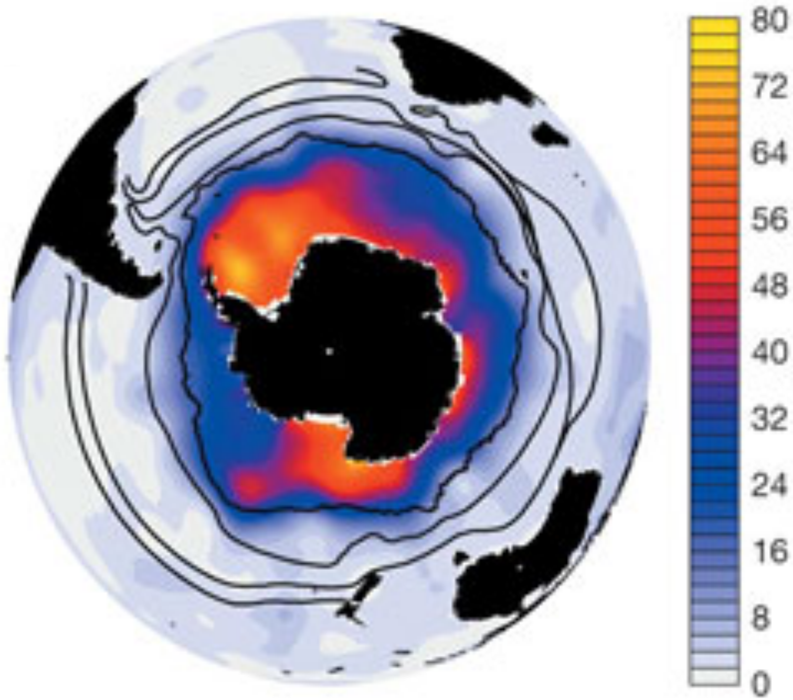
Egg production in iron + chl.

# Iron limitation prevents use of plant nutrients

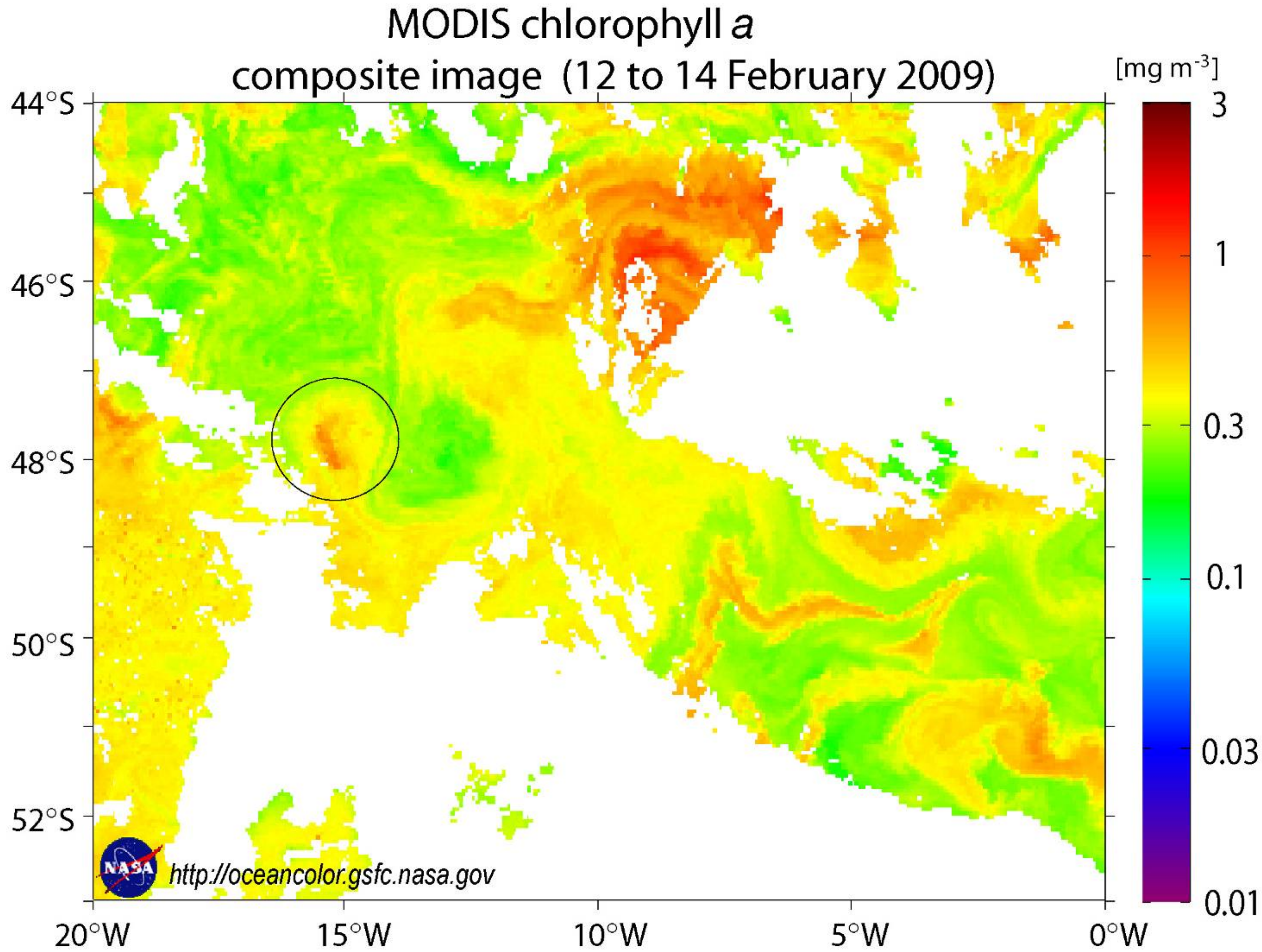
Nitrate ($\mu$M)

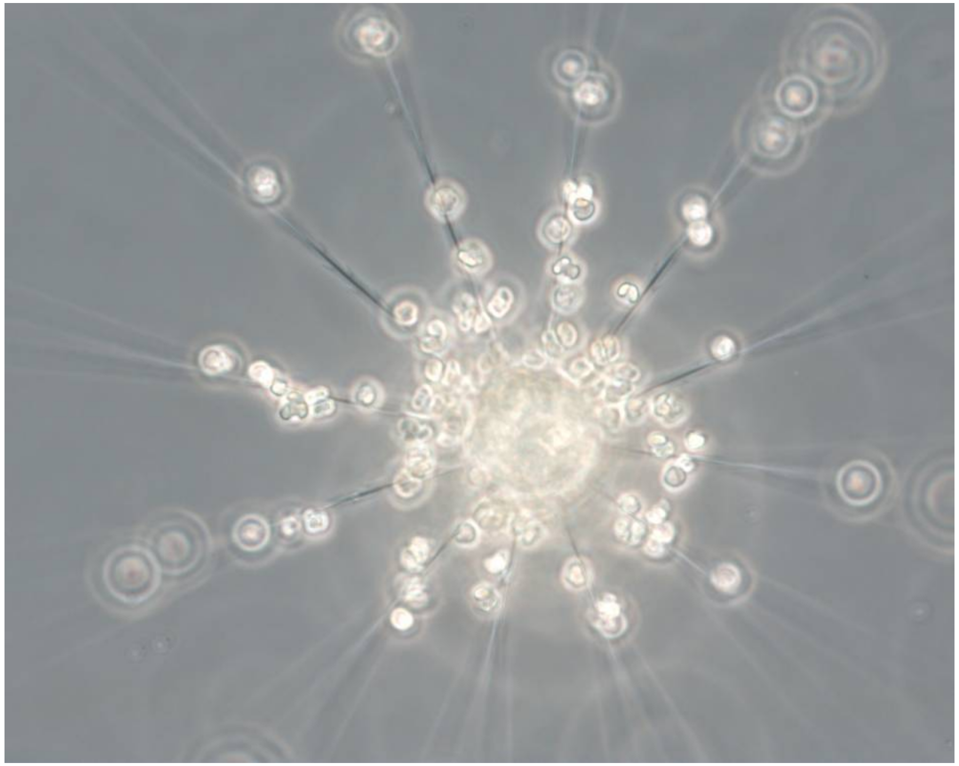


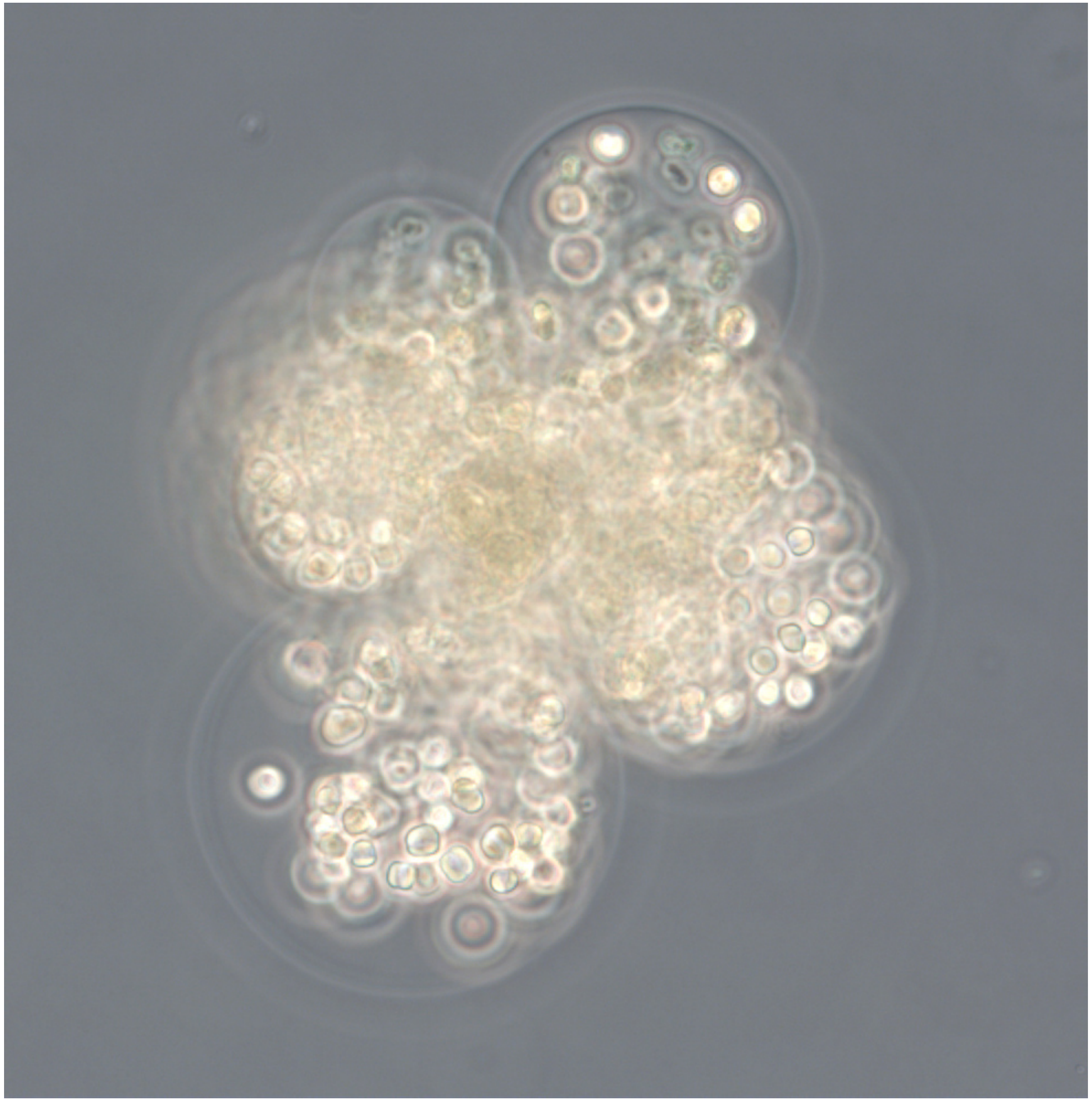

Dissolved silicon ($\mu$M)




Nitrate availability sets the upper limit for growth of ALL algae, silicon limits diatoms.


MODIS chlorophyll a
composite image (12 to 14 February 2009)
[mg m-3]
3
1
0.3
0.1
0.03
0.01
44°S
46°S
48°S
50°S
52°S
20°W
15°W
10°W
5°W
0°W
http://oceancolor.gsfc.nasa.gov





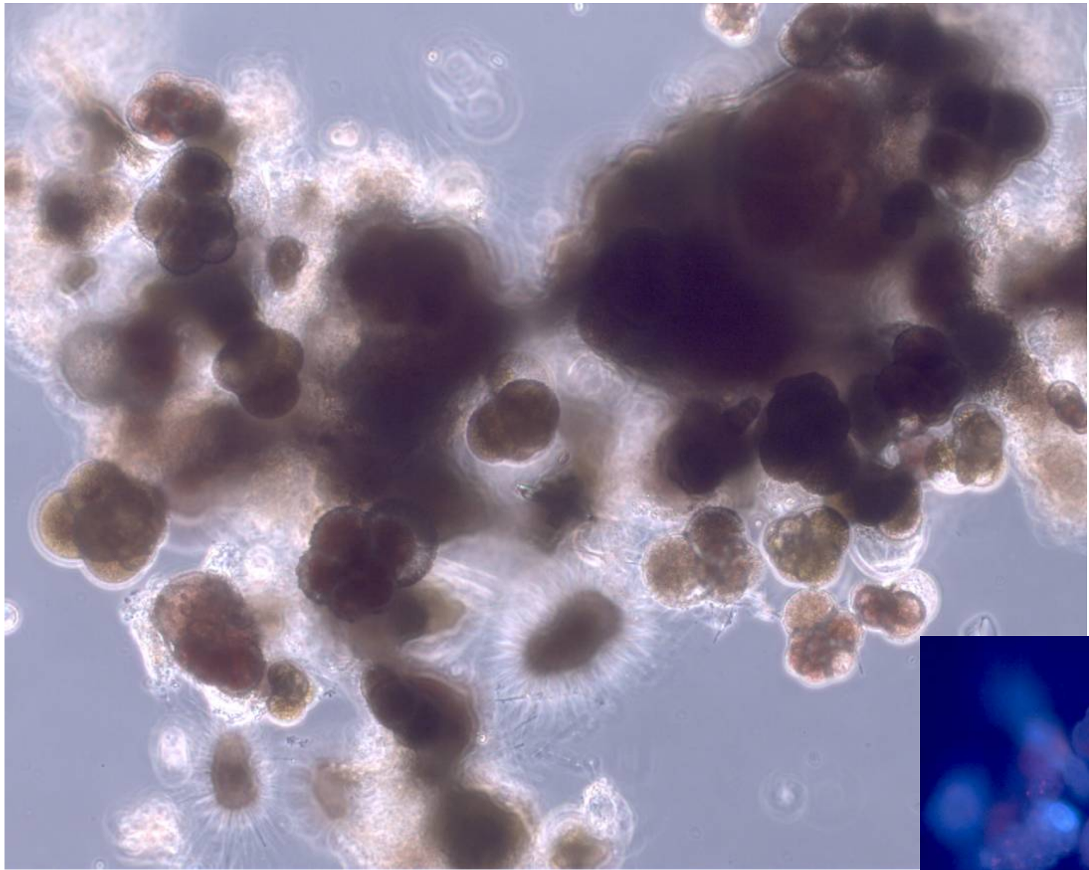
Colonies of *Phaeocystis* are covered by a tough skin, but they are vulnerable in their young stages.

Large dinoflagellates (*Ceratium*) are armour-plated but vulnerable when dividing.

# A typical picture of LOHAFEX zooplankton

*Calanus simillimus* (~ 2.7 mm CV), *Oithona similis* (~ 0.7 mm),

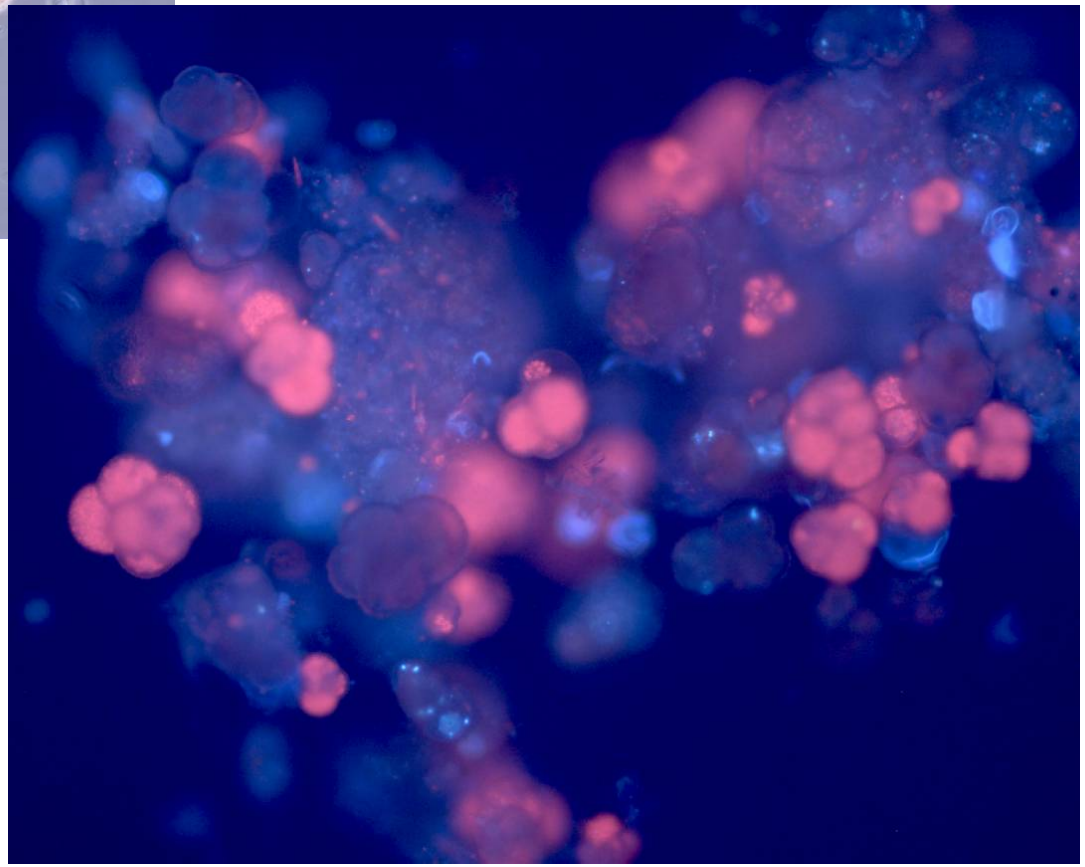
Copepods kept the bloom in check because diatoms could not grow



Foraminifera during LOHAFEX

Several species have algal symbionts, others not.

All have tough shells and slow reproductive rates



Whole forams in copepod faecal pellet

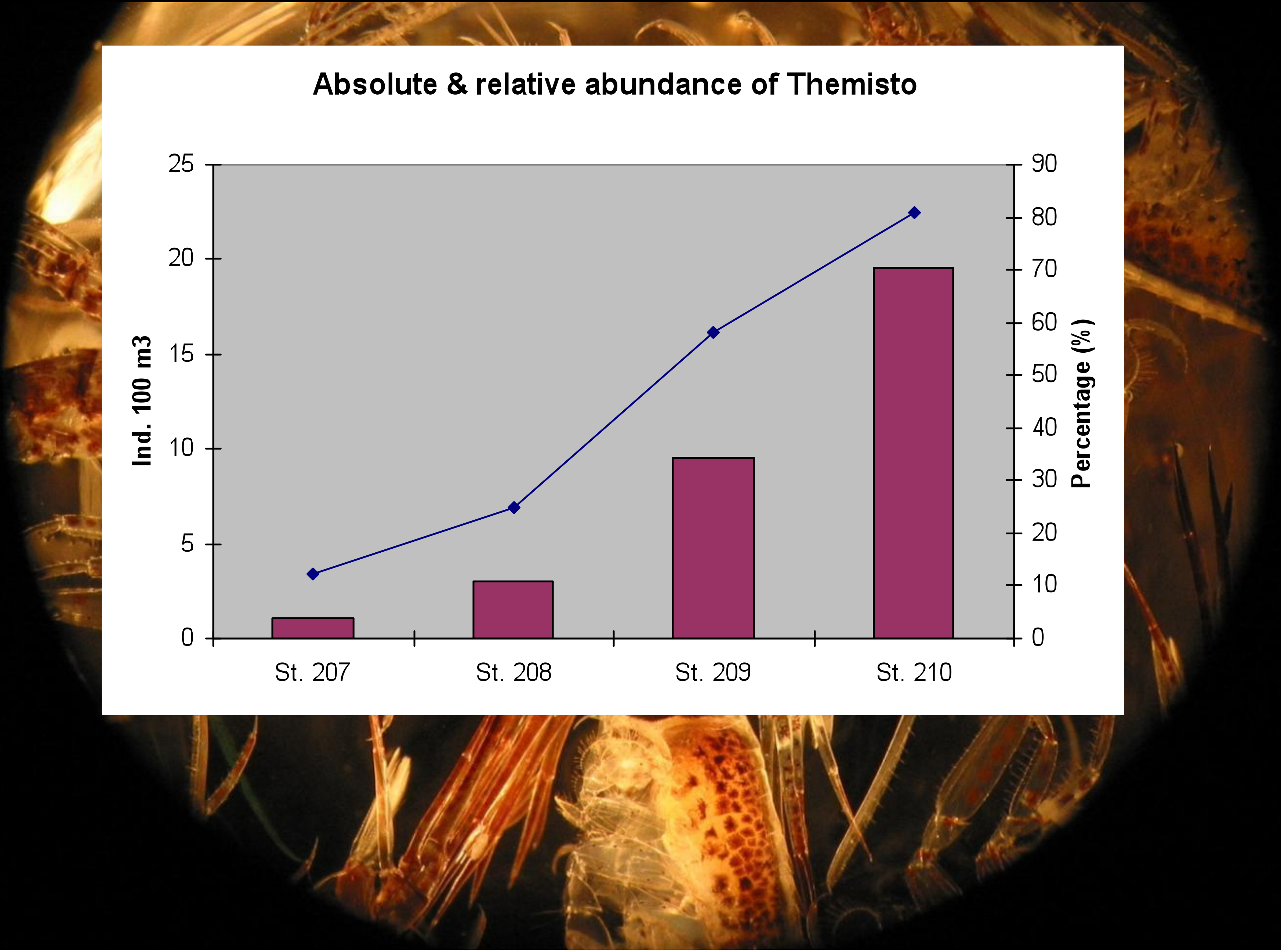
Foram with spines bitten off.

Piece of foram shell

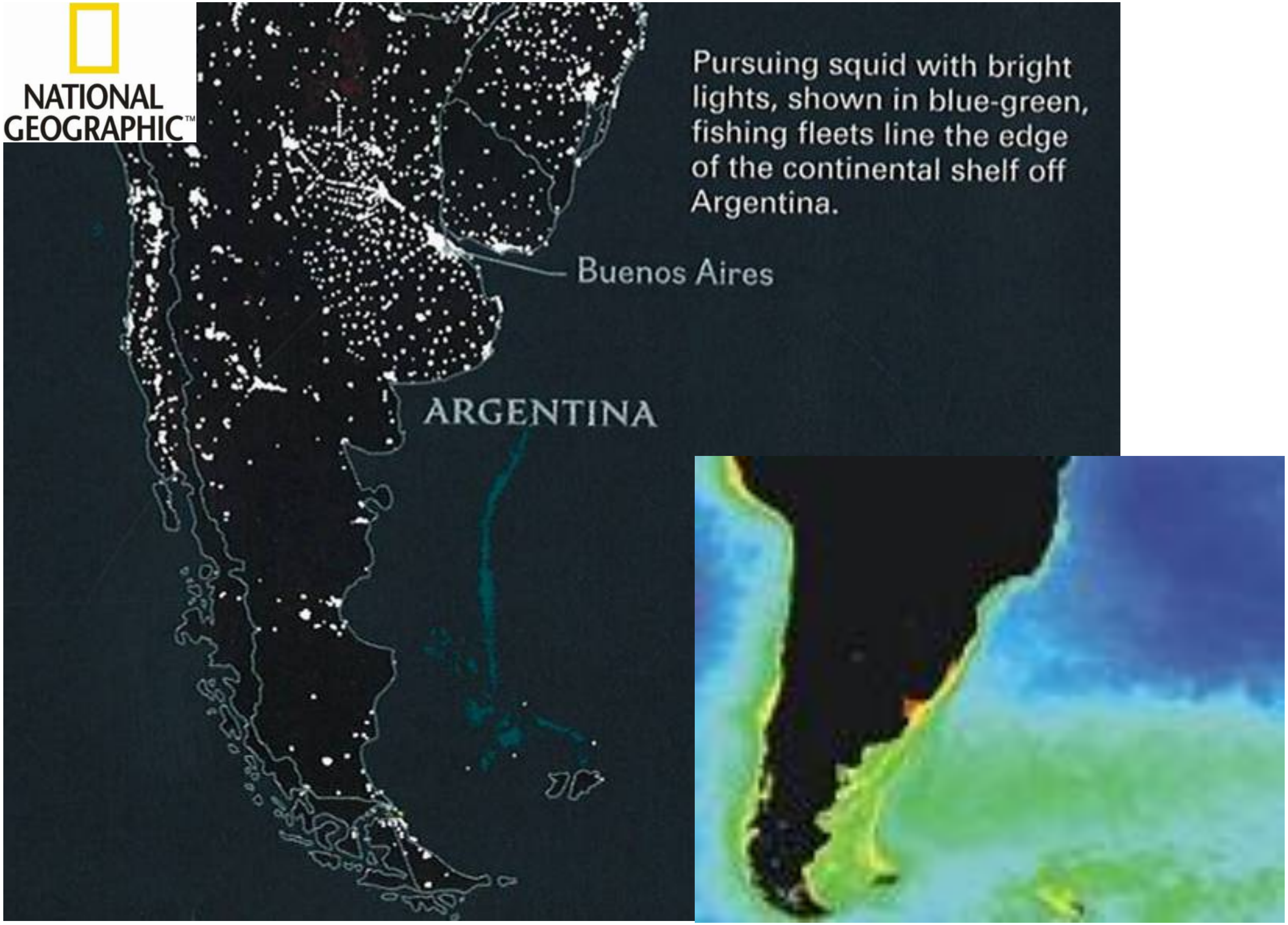
Photos by Assmy and Montresor

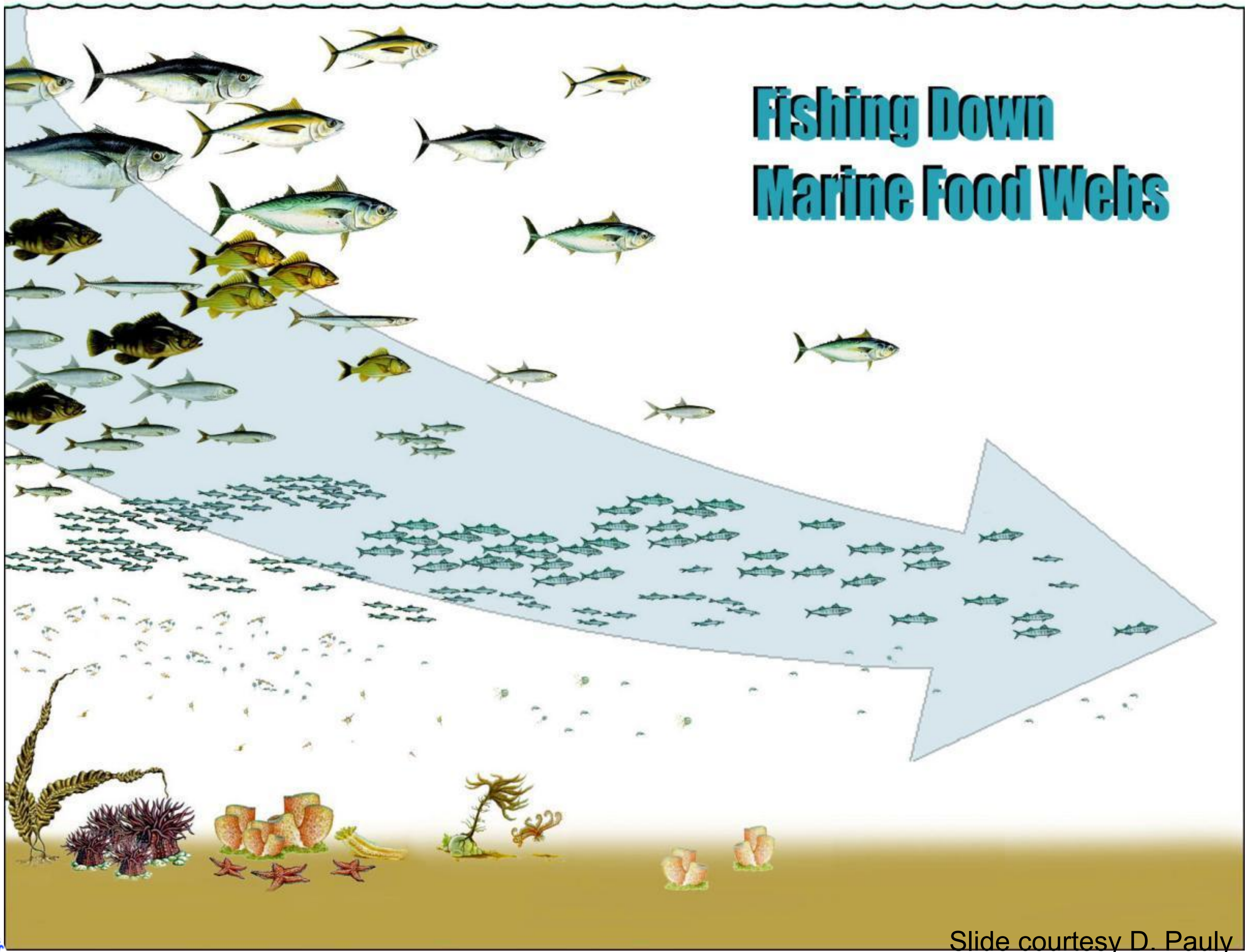
LOHAFEX 2009

# A voracious predator: The amphipod *Themisto gaudichaudii*



# Energy transfer to higher trophic levels




Fishing Down
Marine Food Webs
Slide courtesy D. Pauly

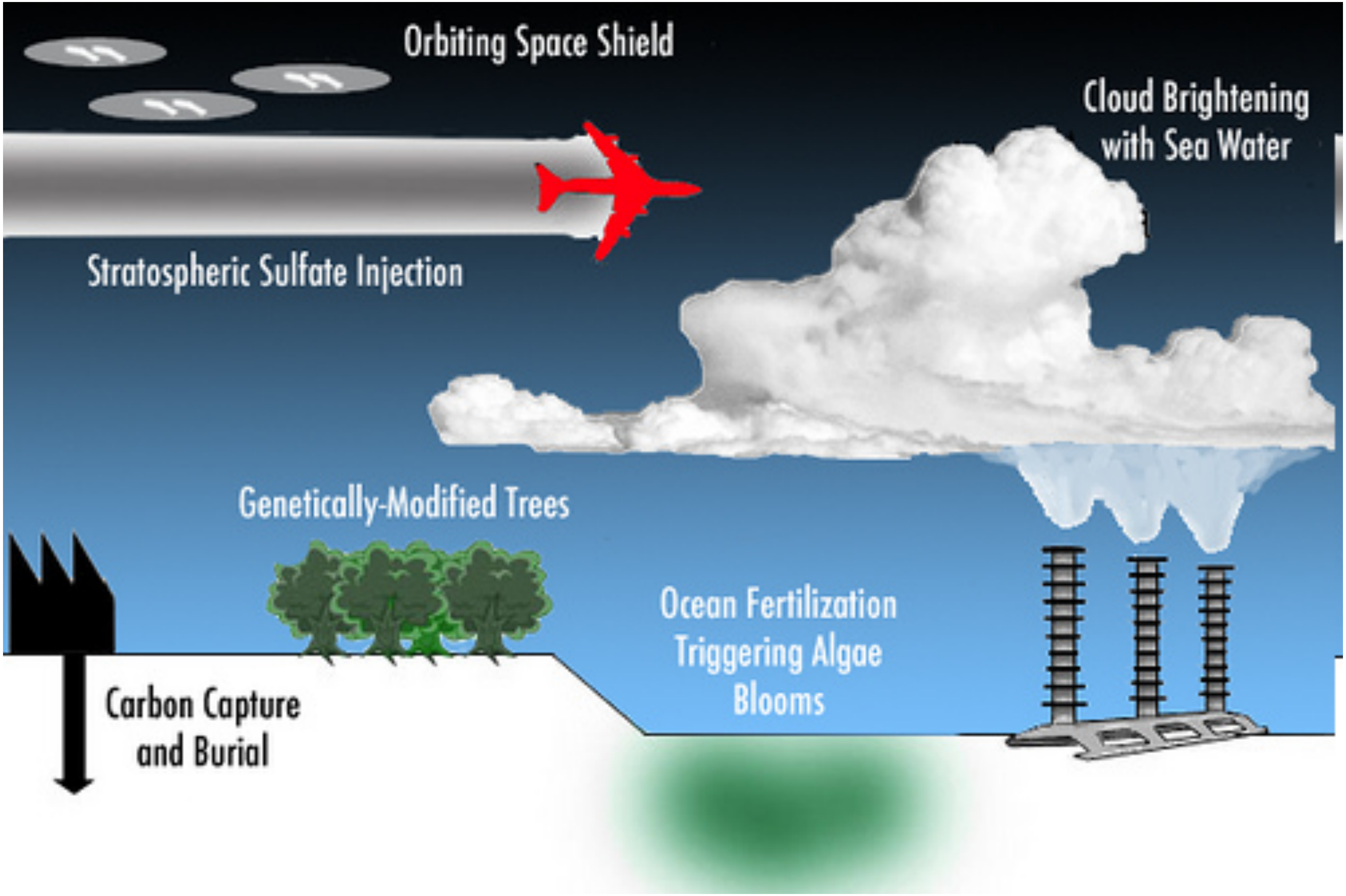
Homo sapiens first destroyed the terrestrial megafauna (except for Africa and only partly in south and southeast Asia) and now we have nearly wiped out the marine megafauna.

But there is hope. Perhaps we will learn.

I ended my talk here because of time constraints.

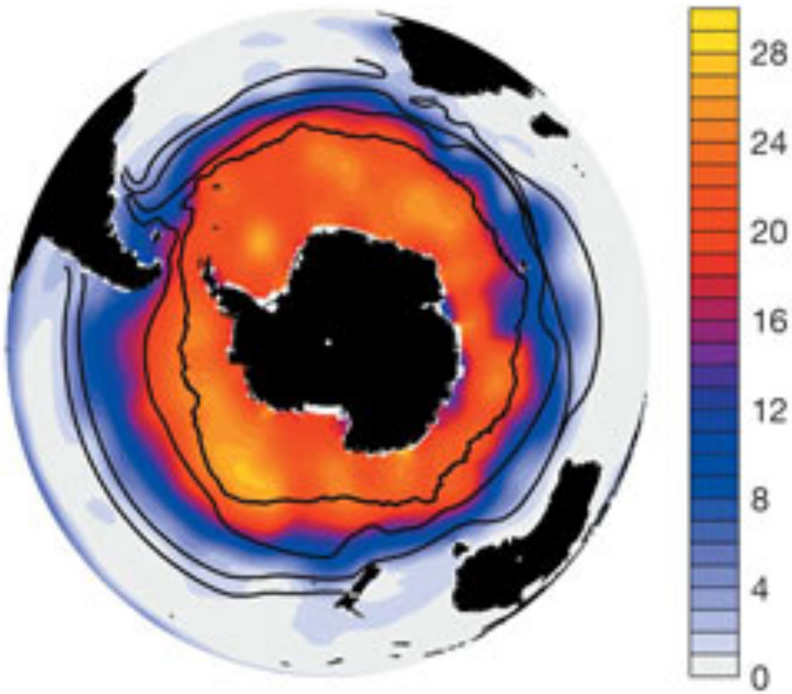
The following slides deal with geoengineering and the imminent threats of global warming.

# Geoengineering the climate

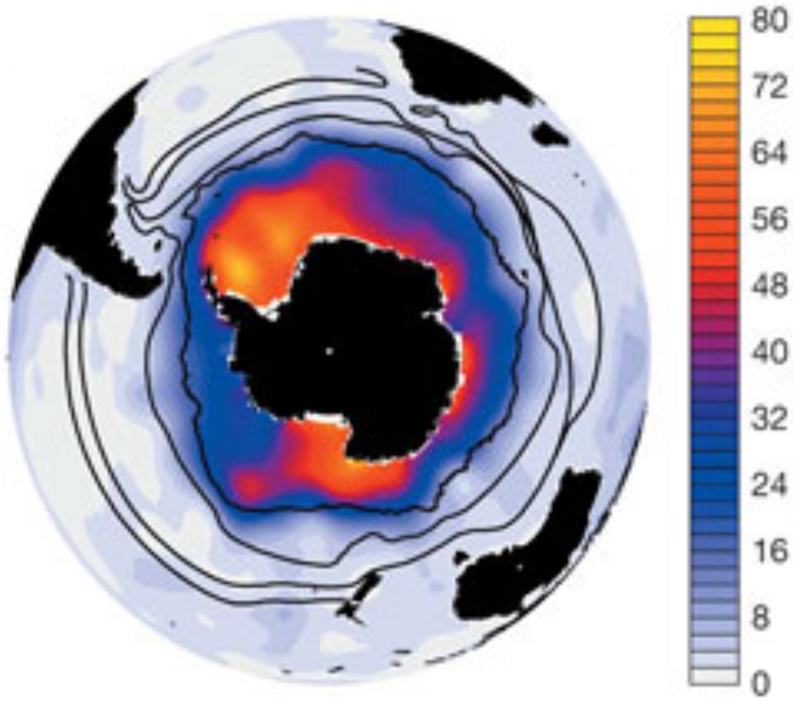


# Iron limitation prevents use of plant nutrients

Nitrate ($\mu$M)

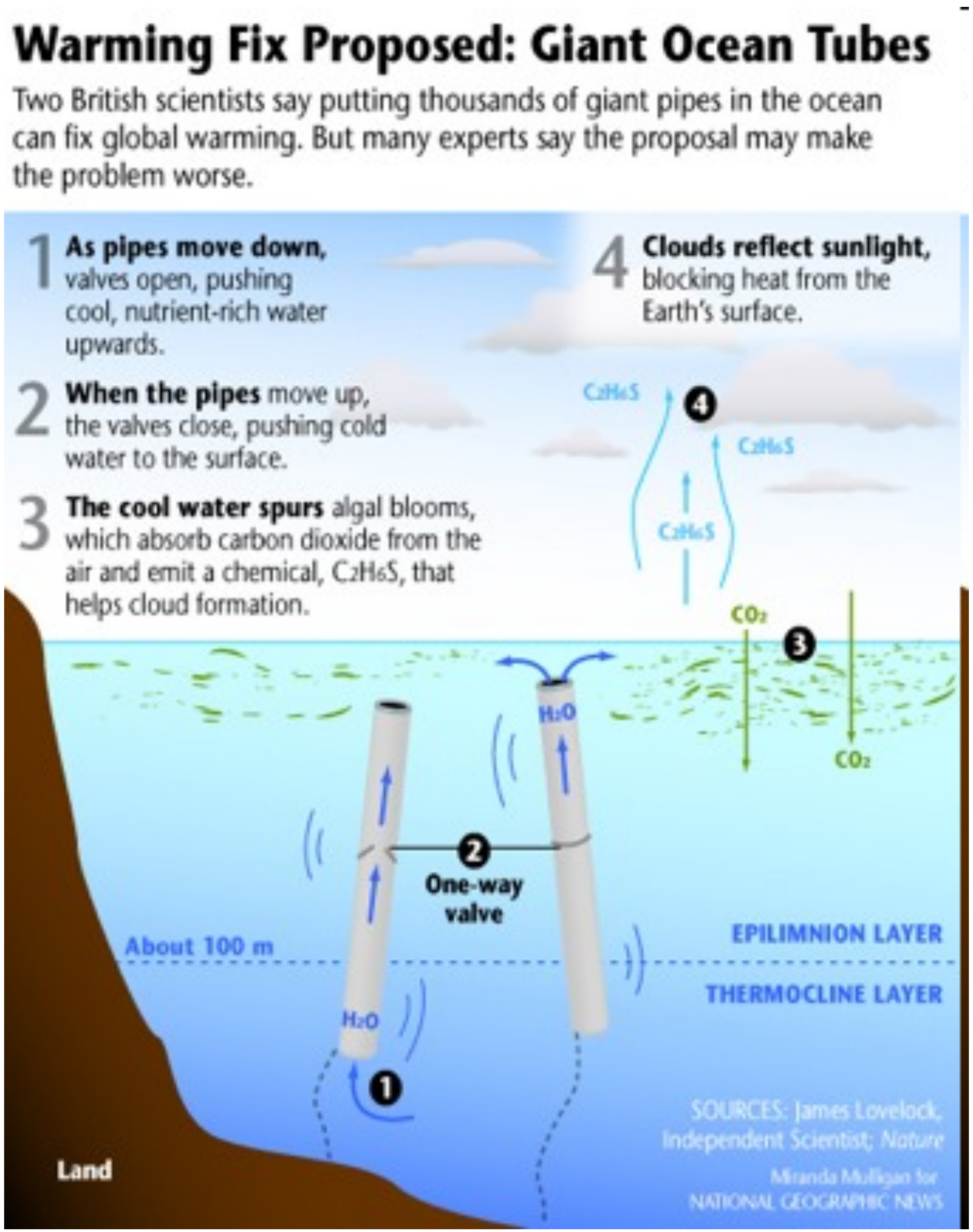



Dissolved silicon ($\mu$M)

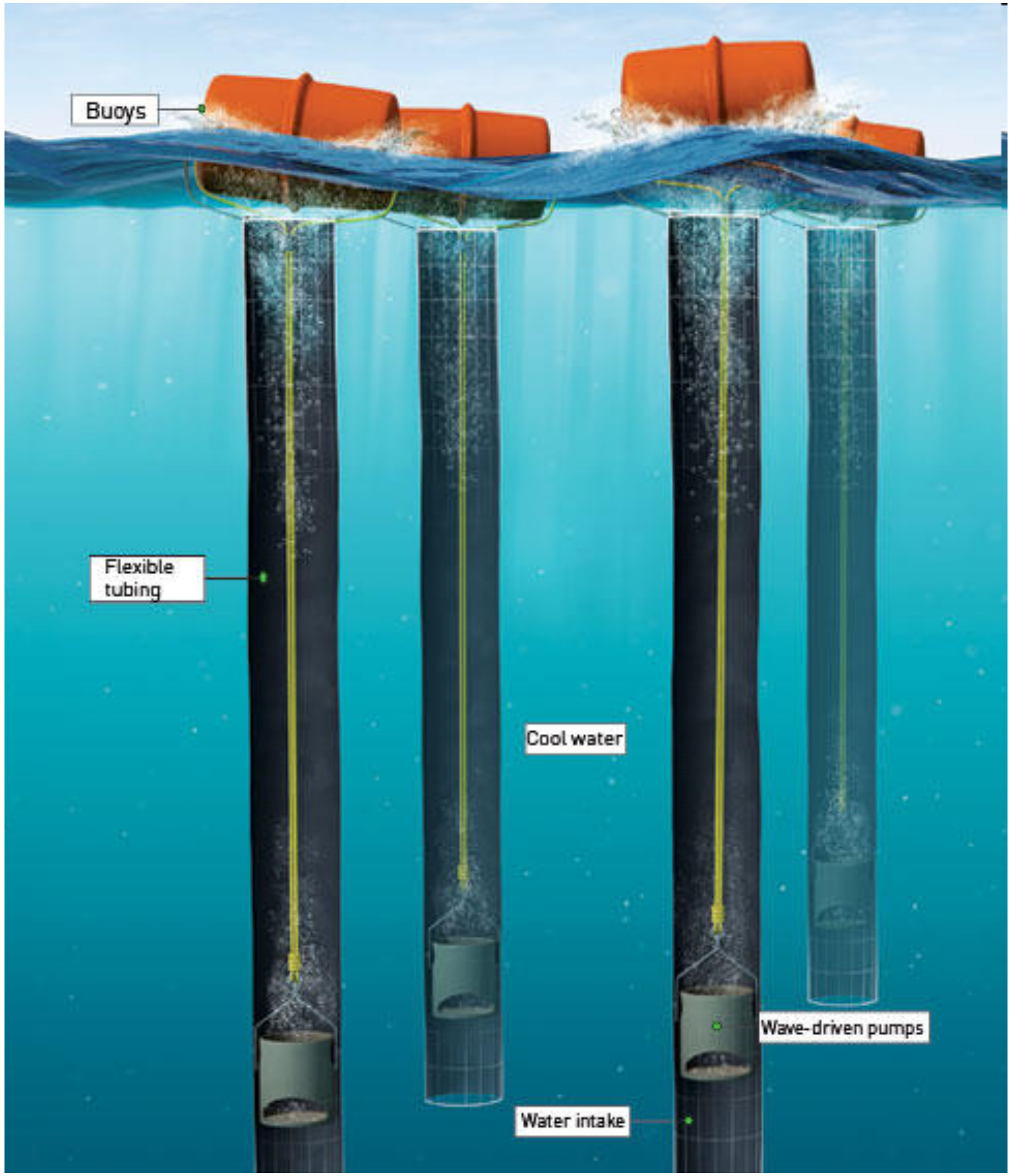



Nitrate availability sets the upper limit for growth of ALL algae, silicon limits diatoms, hence determines how much carbon can be sequestered in the oecans by iron fertilization becasue only diatoms seem to do the job.

Figure from Sarmiento et al. Nature (2004).

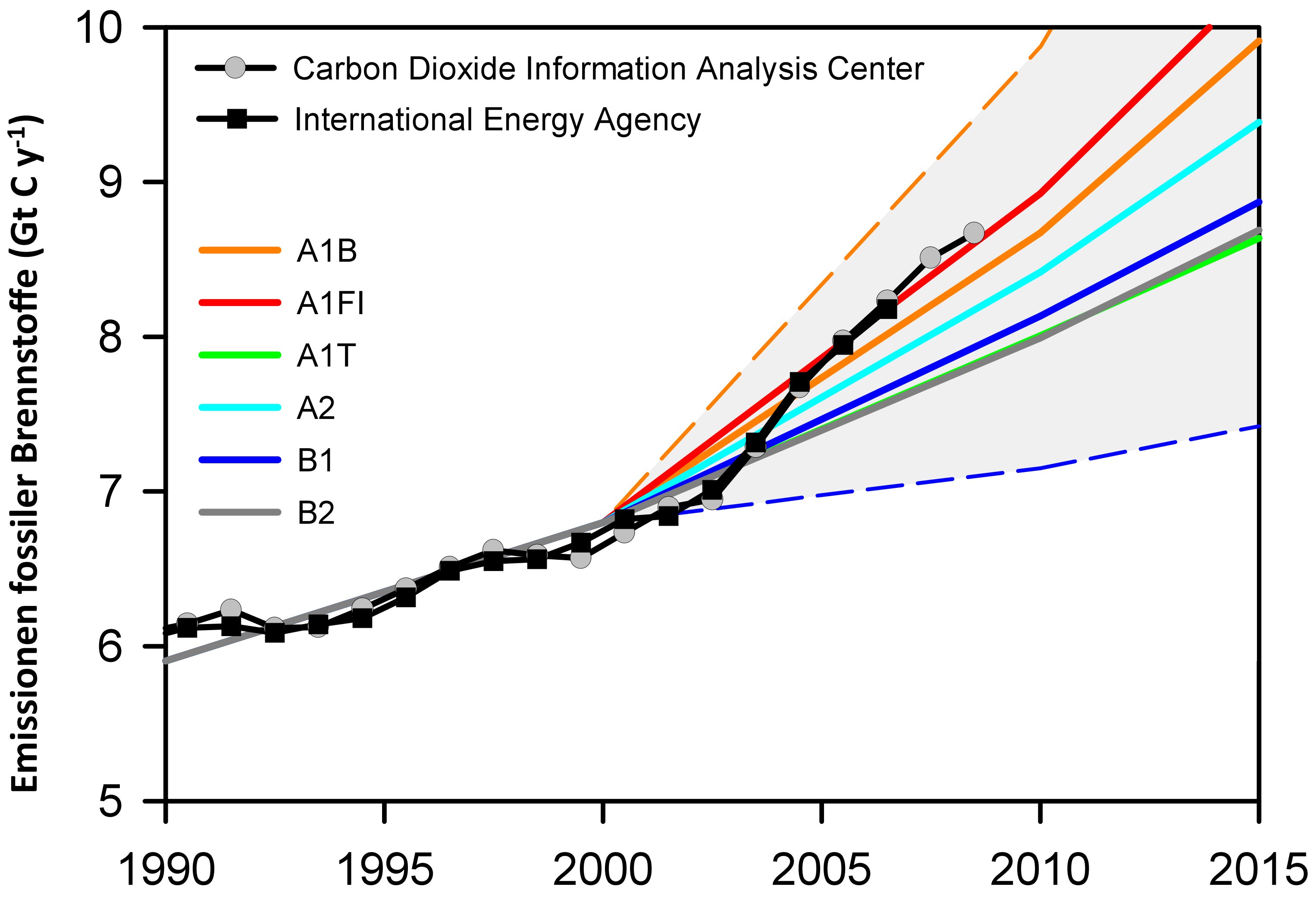



„The pipes“: proposed by Lovelock and Rapley.




gcaptain.com/maritime/blog/tubes-in-the-ocean

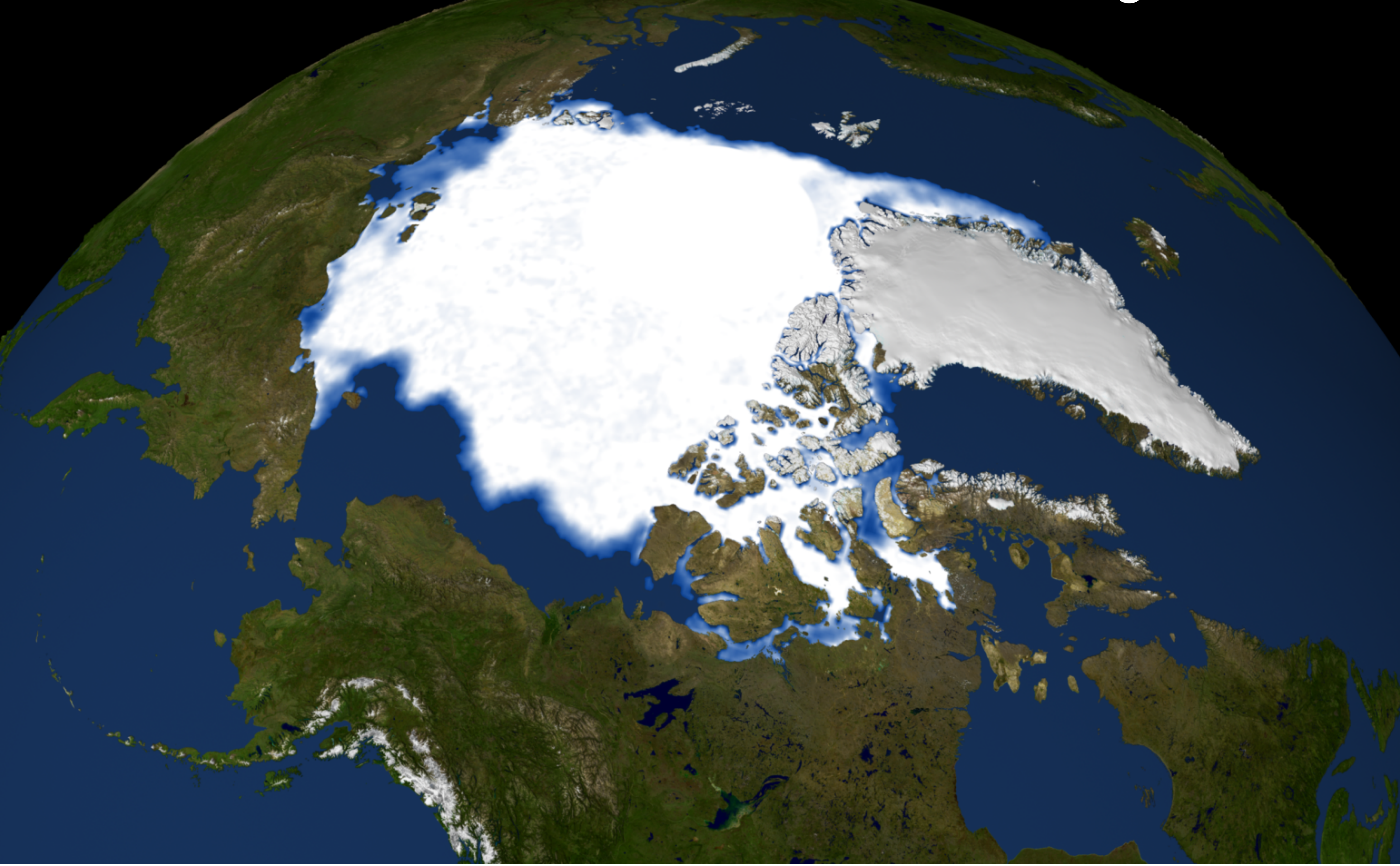
# $CO_2$ Emissionen folgen den pessimistischsten Prognosen des Klimarates



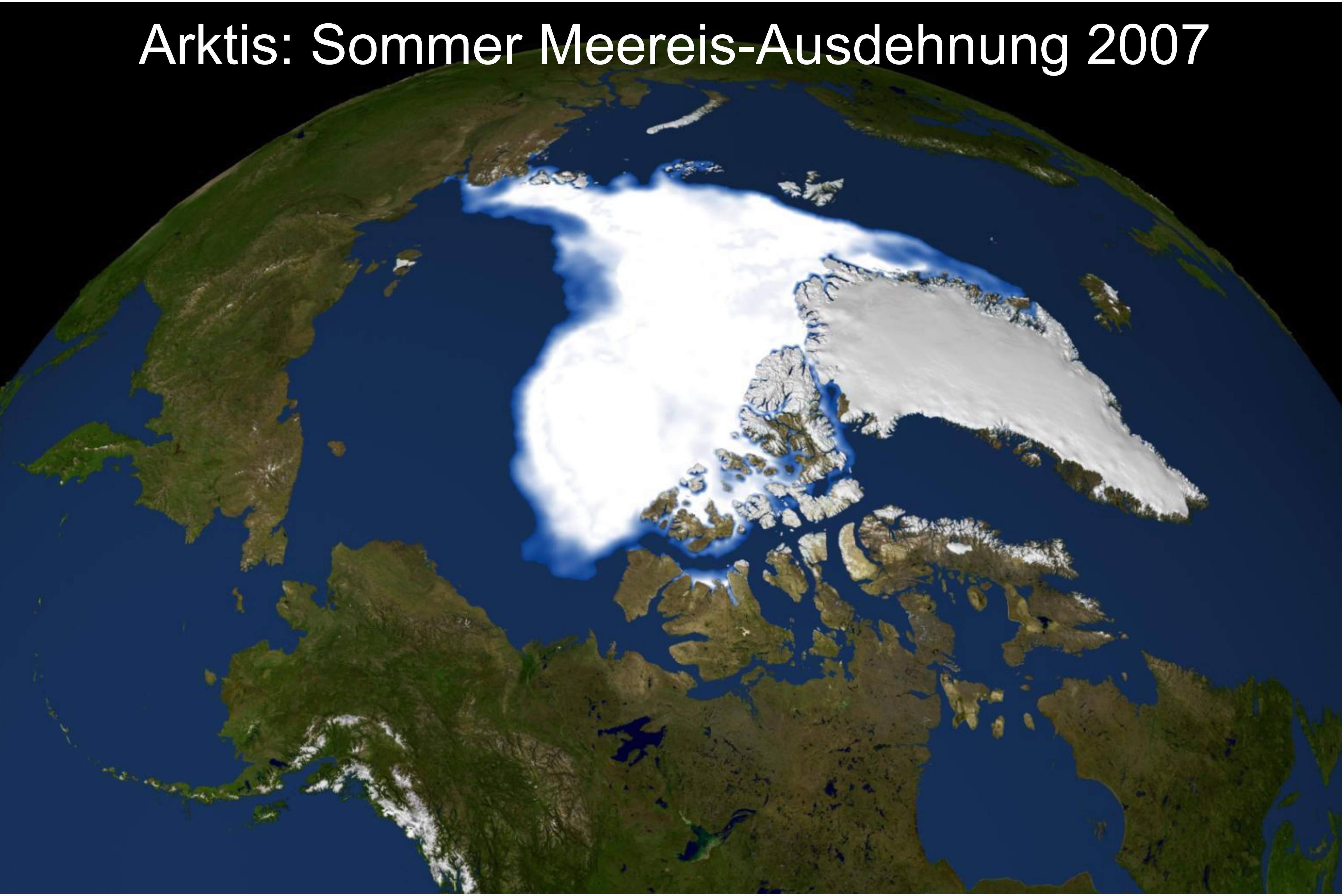

Raupach et al. 2007; Le Quéré et al. 2009


WEATHER WARFARE
GEO-ENGINEERING
THE HIDDEN TRUTH

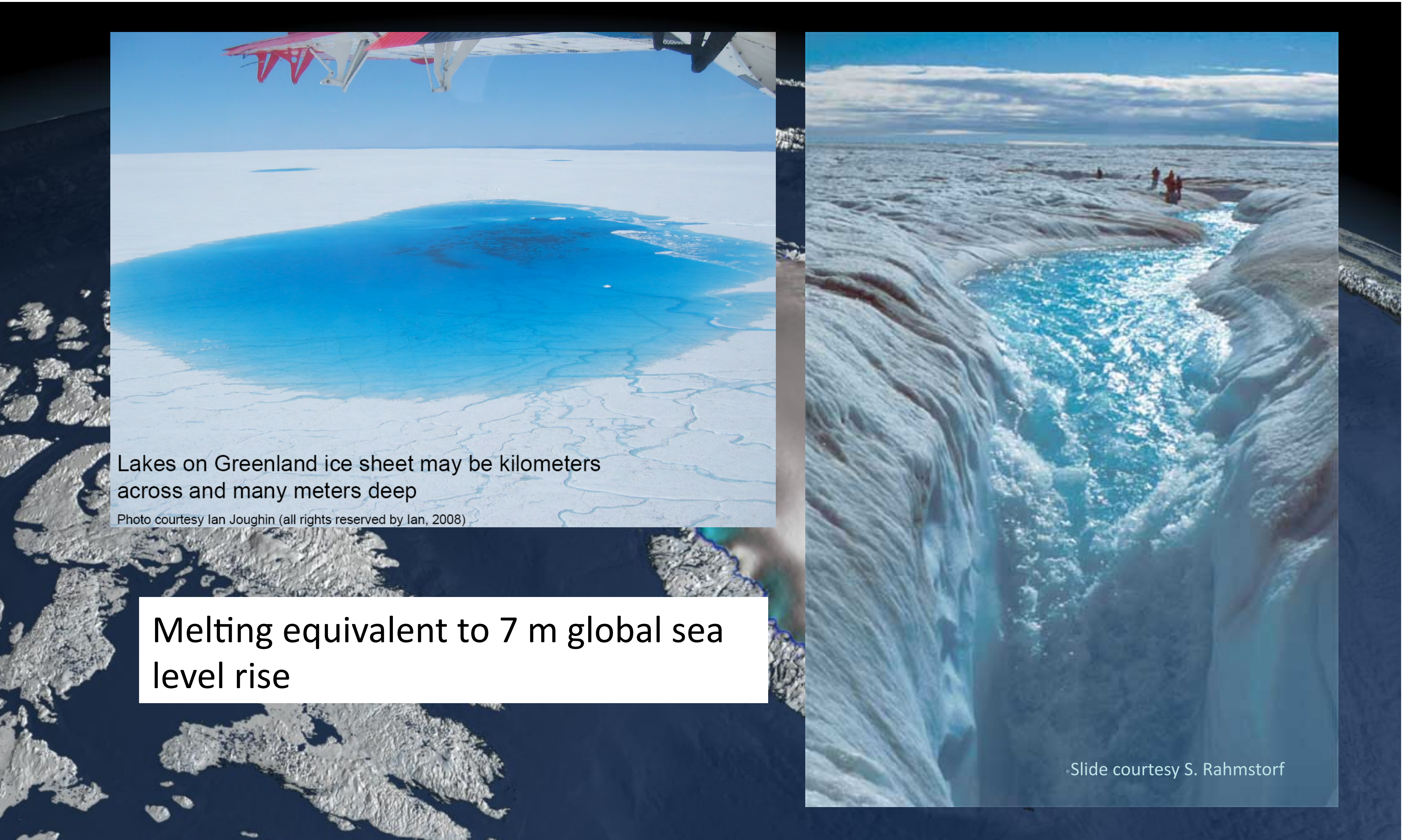
- Arktis: Sommer Meereis-Ausdehnung 1979



# Arktis: Sommer Meereis-Ausdehnung 2007

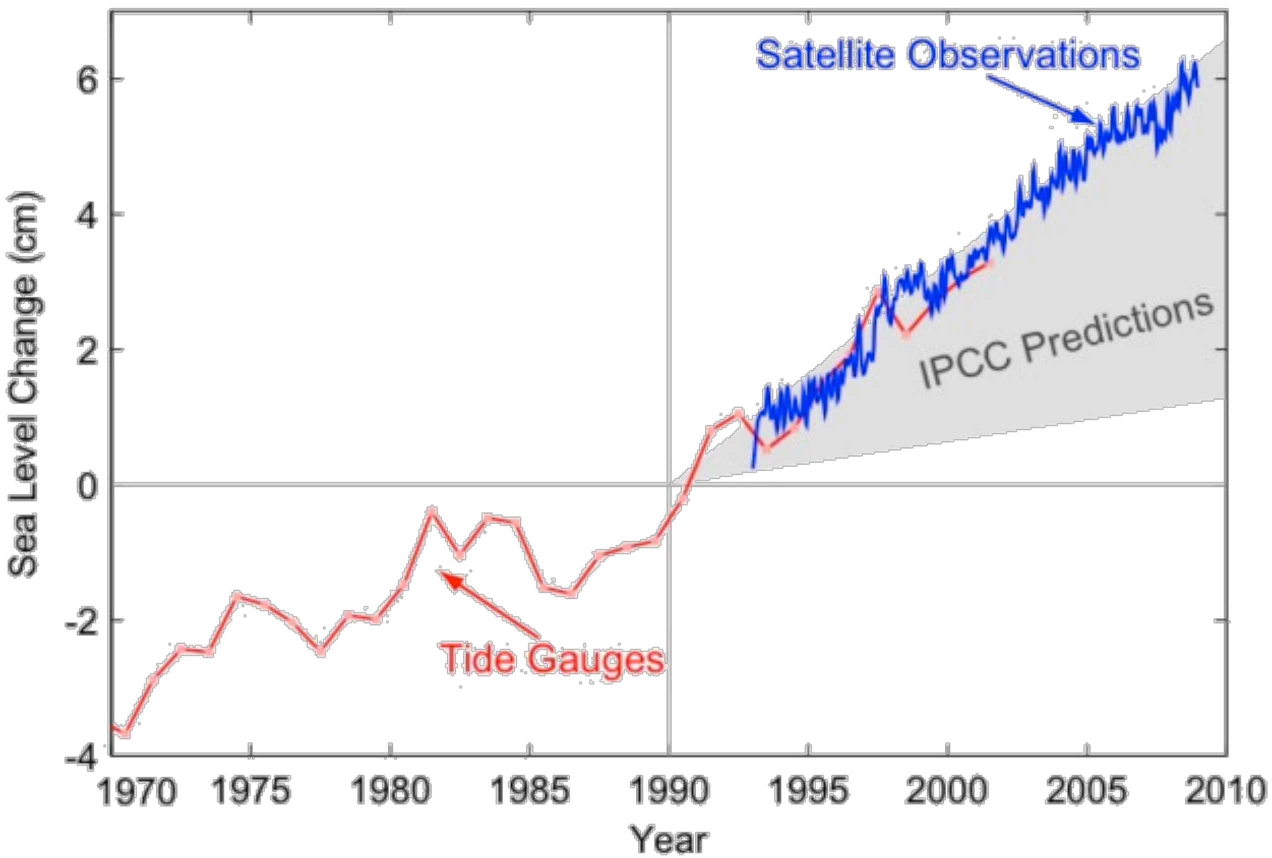


# Greenland




Melting equivalent to 7 m global sea level rise

# Sea-level rise




www.noaa.gov/features/climate/sealevelchanges.html

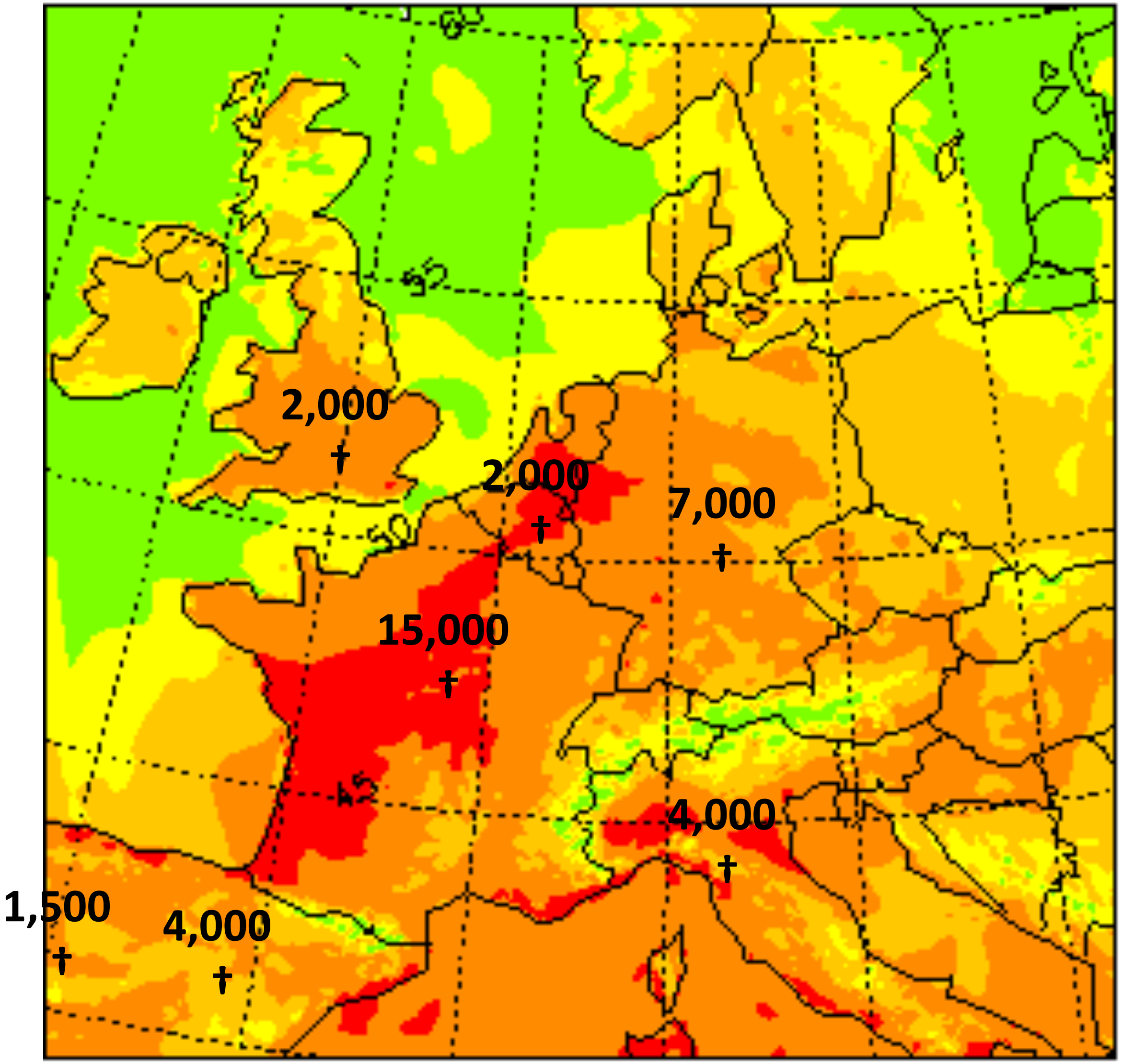
www.copenhagendiagnosis.com after

Church & White (Geophysical Research Letters 2006) and Cazenave et al. (Global and Planetary Change 2008)

Slide courtesy S. Rahmstorf

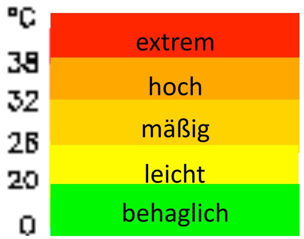
# Hitzewellen/Heat waves

**Hitzetote und Gefühlte Temperatur am 8. August 2003, 13 UTC**




**Summer 2003:**
**the biggest natural catastrophe in Europe since centuries**
**ca. 35.000 heat stroke victims**

Hitzebelastung

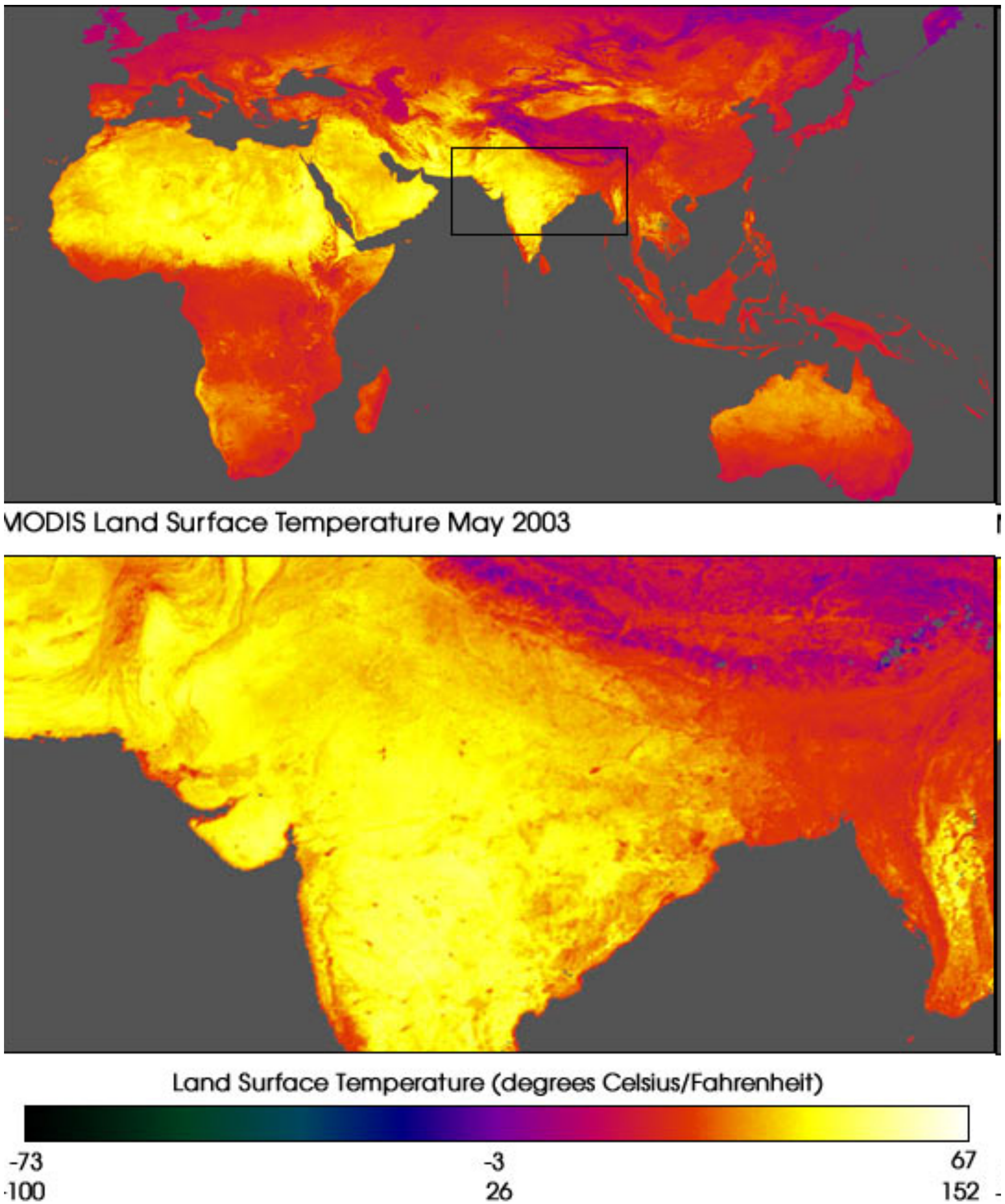



Mortalitätsdaten: Earth Policy Institute
Gef. Temp.: Deutscher Wetterdienst



Slide courtesy S. Rahmstorf

At the same time, this was happening in north Africa and south Asia



Participants of the LOHAFEX experiment

Dr. Syed Wajih Naqvi (NIO) Co-Chief Scientist of LOHAFEX on board Polarstern

My thanks to all the colleagues who accompanied me on the 3 fertilization experiments EisenEx, EIFEX and LOHAFEX, particularly Philipp Assmy, Christine Klaas, Marina Montresor and Joachim Henjes.

The captains and crews of RV Polarstern deserve unstinted praise for their professionality and support.

Thank you for your attention!

I have shown you just a few examples of the evolutionary arms race and evolutionary Olympics.

This is an aspect of evolutionary ecology of plankton organisms now slowly coming to light.

There is ample scope for research: We still do not know how and why the immense proliferation of planktonic shapes took place. But I feel that there is no other way to explain them than the evolution of protective mechanisms.

In situ experiments are the best way to test these hypotheses because it is impossible to simulate natural zooplankton communities, i.e. the mortality environment, in the lab or mesocosms, whereas the growth environment can.

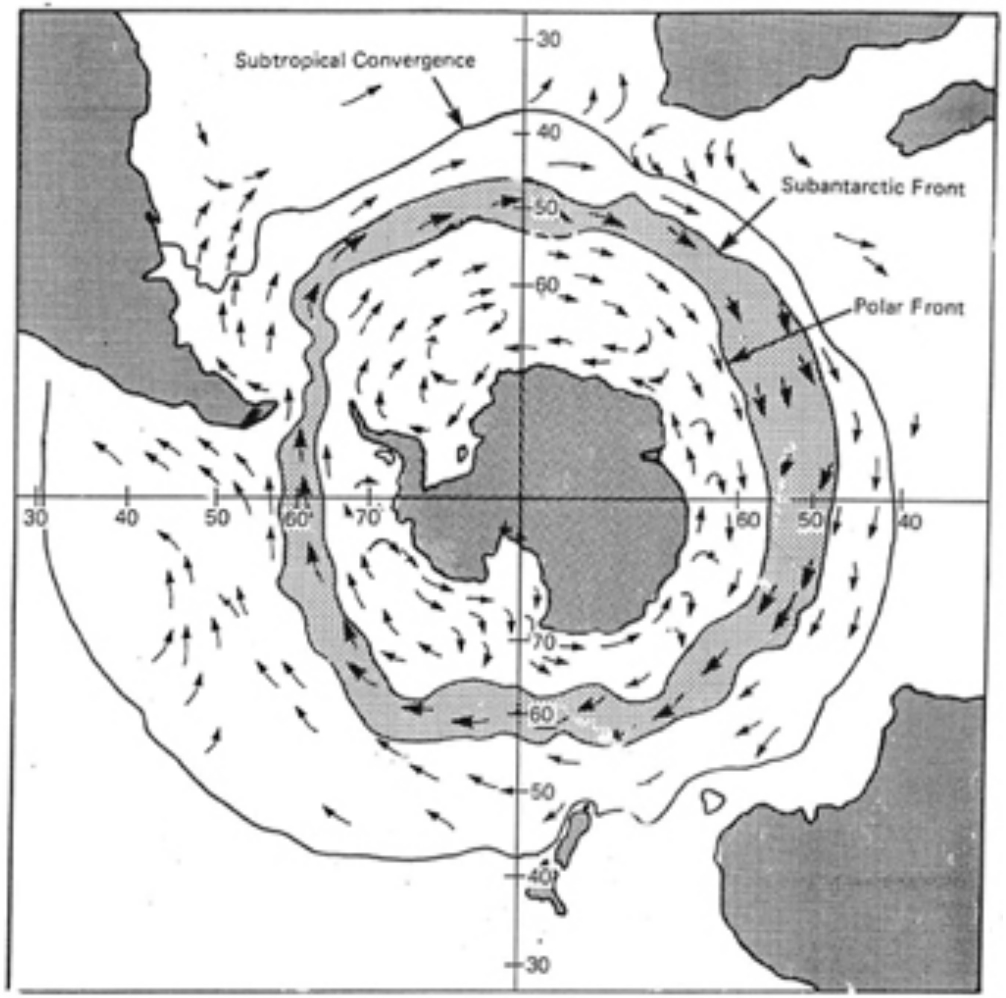



Fig. 5.2. The distribution and flow of surface water masses of the Southern Ocean. The Polar Frontal Zone (shaded) is bordered to the north by the Subantarctic Zone and to the south by the Antarctic Zone. A reverse, anticlockwise current flows in the Continental Zone which lies in the immediate vicinity of the coast. Modified from Heath (1981). Clifford (1983) and Deacon (1984).

VINCENT 1988

**Proposal :**

To carry out an iron fertilization experiment along the marginal ice zone of the Weddel-Scotia Confluence.

- **Aims:**
- To enhance magnitude and prolong duration of the ice edge bloom.
- Study the relationships between pelagic ecosystem structure and biogeochemical cycles of C, N, P, Si, Fe, etc.
- Follow species succession patterns (diatoms to Phaeocystis) and interactions within the pelagic food web
- Study the impact of an artificially enhanced phytoplankton bloom on krill feeding behaviour and reproductive physiology
- Measure composition and magnitude of vertical flux (ungrazed phytoplankton vs. zooplankton faeces)
- Validate various proxies for palaeoproductivity and glacial CO2 drawdown


30 July 2009 | www.nature.com/nature | £10
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# Observations of Biologically Generated Turbulence in a Coastal Inlet

Eric Kunze,[1*] John F. Dower,[1*] Ian Beveridge,[2] Richard Dewey,[1] Kevin P. Bartlett[1]

Measurements in a coastal inlet revealed turbulence that was three to four orders of magnitude larger during the dusk ascent of a dense acoustic-scattering layer of krill than during the day, elevating daily-averaged mixing in the inlet by a factor of 100. Because vertically migrating layers of swimming organisms are found in much of the ocean, biologically generated turbulence may affect (i) the transport of inorganic nutrients to the often nutrient-depleted surface layer from underlying nutrient-rich stratified waters to affect biological productivity and (ii) the exchange of atmospheric gases such as $CO_2$ with the stratified ocean interior, which has no direct communication with the atmosphere.

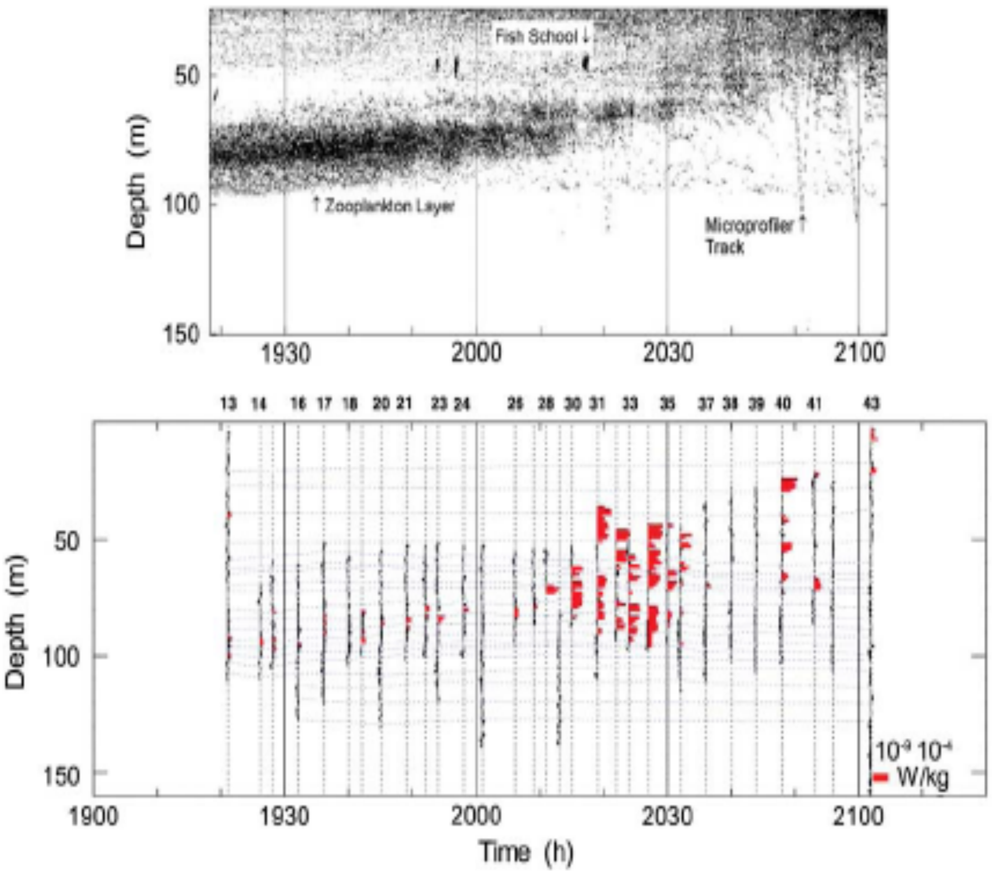


**Fig. 1.** Profile time series in Saanich Inlet spanning about 100 min during dusk on 28 April 2005. (**Top**) Acoustic backscatter data from a 200-kHz echosounder reveals vertical migration of the backscatter layer. The lowering and raising of the vertical microstructure profiler is also evident for some profiles. (**Bottom**) Turbulent dissipation rate log($\varepsilon$) (red, index lower right) with vertical dotted lines denoting profile times and horizontal dotted lines denoting salinity or density surfaces. For profiles 13 to 29, dissipation rates are on the order of $10^{-9}$ W $kg^{-1}$. For profiles 30 to 36, spanning 17 min, dissipation rates are two to four orders of magnitude higher before falling back to background levels of about $10^{-9}$ W $kg^{-1}$ for the remainder of the time series.

OCEAN SCIENCE

# Creatures Great and Small Are Stirring the Ocean

Explaining the forces that mix things up in the ocean has always been the province of the physical oceanographers. It seemed obvious that physics governs how the winds and tides drive the waters and thus how deep, cold, nutrient-rich seawater is mixed toward the surface. Marine life was clearly just along for the ride.

But recent evidence suggests that marine life may itself be helping stir the ocean, from local to global scales. "My initial reaction was, 'Preposterous,' " says physical oceanographer Carl Wunsch of the Massachusetts Institute of Technology in Cambridge. "Then you look at the numbers, and it's not so preposterous. The order-of-magnitude numbers suggest it's worth talking about." And the implications could be huge. Overfishing of the big whales, for example, could be changing global climate.

**Oceanic agitator.** This 2-centimeter krill, *Euphausia pacifica*, can mix the sea if it teams up with thousands of its kind.

size and swimming habits. By Huntley and Zhou's calculations, the turbulent mixing of schooling animals from krill and anchovies to whales "is equivalent to a pretty sustained storm at a local level," says Huntley.

Huntley imagines that schools of krill in the stratified Southern Ocean around Antarctica could be stirring water upward with each daily vertical migration, locally replenishing the nutrients depleted by the

Grander speculations will appear in the upcoming *Journal of Marine Research* (July 2006 issue). Physical and biological oceanographers led by William Dewar of Florida State University in Tallahassee calculated how much energy phytoplankton store in new organic matter each year: about $63 \times 10^{12}$ watts (63 terawatts, or TW). Perhaps something like 1% of that, or almost 1 TW, may go into swimming motions that stir ocean waters, they estimate from expected energy losses and from the amount of oxygen consumed in the ocean.

A TW of biomixing would be a lot. In 1998, Walter Munk of the Scripps Institution of Oceanography in San Diego, California, and Wunsch estimated that 2 TW of mixing is required to mix deep, cold waters to the surface. That completes the "conveyor belt" circulation of the world ocean, which is vital to the climate system. Dewar and his colleagues speculate that the decimation of stocks of big fish and whales over the past couple of centuries could have removed enough biomixing to have an effect on climate. **–RICHARD A. KERR**

**Proposal II**:

To extend the growth season in the Peninsula Plume region by supplementing the iron supply to the regenerating, summer system.

Location: Scotia Sea between Peninsula tip and South Georgia

- **Hypotheses to be tested:**

- Iron limits post-spring-bloom production in the region.

- Growth rates of Krill and copepods are food limited

- Zooplankton grazing feeds the regenerating system (carbon and iron in faeces is recycled within the surface layer).

# KRILL RECRUITMENT IS DEPENDENT ON A COMBINATION OF ADEQUATE FOOD SUPPLY AND PROTECTION FROM PREDATORS IN SEA ICE

- Gonads of adult Krill disappear in winter and only develop when sufficient food is available.
- Eggs are laid off the continental slope (>1000 m depth).
- Larval development on the way up occurs without feeding.
- First-feeding larvae require high food concentrations and cannot arrest development, i.e. they easily starve to death, unlike adults.
- Larvae survive best in melting sea-ice rich in ice biota where they also find shelter from predators..

- Caveats: Krill seem to spawn anytime, anywhere.
- Larvae are also found away from sea ice, so its presence
- is not obligatory but might reduce mortality.

All the major metabolic pathways, including oxygenic photosynthesis, evolved in the Proterozoic under reducing conditions

This is the phase of **chemical evolution w**hen physical and chemical properties of the environment dominated natural selection.

Only after the atmosphere had been sufficiently oxidised was it possible for phagocytosis to evolve.

This facilitated endosymbiosis and hence the evolution of higher life forms (eukaryotes and later multicellular organisms)

Phagocytosis had a dramatic effect on life forms as it initiated **mechanical evolution**: development of shape and later armour and the tools to crack them with.

Cyanobacteria as we know them, evolved deep in the Proterozoic, under reducing conditions. They have not changed their shape much since then.

Organism interactions were simple and restricted to competition and protection against exoenzymes and (most probably) viruses. The latter is achieved by layers of slime and, possibly lipids.

Evolution of eukaryotes was driven not only by tight coupling of endosymbiosis but also the looser relationships of co-evolution and ecosystem structure.

Thus diatoms achieved dominance in co-evolution with copepods and euphausiids.

The arms race had a profound effect on recent climate history at scales ranging from tens of millions of years (Cenozoic) to hundreds to thousands of years (transitions from glacial to interglacial stages).

# Pitfalls

- More is always better than less
- Variability is more interesting (hence publishable) than constancy.
- The search for understanding is the function of scientists, if you dedicate yourself to the search and not to the object of study you will lead satisfying, successful careers.
- Biologists are always in danger of identifying themselves with their object of study, thus creating territory which results in territoriality, unhealthy competition, stagnation.
- Plankton ecology has gone global. We should rise to the challenge and not wave team flags.

Global change in the Anthropocene is much more than just warming or acidification

Productivity patterns are changing as a result of anthropogenic global change

Nutrient imput to surface ocean will change due to climate change: vertical mixing, circulation patterns (El Nino, North Atlantic Oscillation)

Trophic cascades due to removal of top predators (megafauna)

Influence of upper trophic levels on productivity is poorly understood (top-down).

Environmental conditioning is established in terrestrial systems (from ants to elephants) and the benthos (bioengineering). What about the pelagic realm (copepods to whales)? Is „stirring“ by nekton important?

Crustacea increasing biomass in overfished continental margins (?)

Gelatinous zooplankton increasing in pelagial (?)

Introduction of exotic species are causing local imbalance.

Not to mention the unanticipated effects of geo-engineering schemes to avert impending disaster.

To understand the structure and functioning of pelagic ecosystems, and their effects on underlying benthos, we need to carry out more in situ experiments.

Ocean iron fertilization cannot be avoided, we as a community should control them.

# Growth and death are driving forces of evolution

In the growth arena, **competition** for resources (bottom up) determines fitness.

In the mortality arena, **defence** mechanisms against pathogens, parasites, predators (3Ps) (top-down) determine fitness.

Ultimately, **trade-offs** between the two determine species fitness.

Species properties improving competition are very different from those improving defence.

In terrestrial vegetation, competition is for light and water: space-holding. Plants also defend themselves, either mechanically (thick cell walls, thorns etc.) or chemically (herbivore deterrants, toxins, teratogens, etc.)

Space-holding cannot apply to plankton, because the environment changes faster than the life-time of the organisms.

Is this the reason why marine pelagic plants have not developed infrastructure (roots, trunk and crown) but stayed unicellular?

So what drives phytoplankton evolution, competition or defence?

# Chemical defences (toxins or herbivore deterrants)

- The molecules comprising an organism fall into two categories:
- Primary metabolites are part of the life-supporting and reproductive machinery.
- Secondary metabolites have other functions, primarily defence.
- The exact function of most SMs are unknown. Their occurrence varies even wirhin species and many are induced.
- A large variety of SMs have been identified in phytoplankton of which molecules toxic to humans have attracted most attention.
- These are neurotoxins that cause paralysis or amnesia, metabolic toxins that affect various organs such as lungs or alimentary canal. Their function is largely unknown but their effect on higher trophic levels, including humans, can be devastating.
- Recently, polyunsaturated aldehydes have been found in some diatom species that are produced from structural fatty acids by the action of a specific enzyme that is activated when the cell is crushed. Consensus is slowly emerging as to their role as a wound-induced defence mechanism.

## Attack and defence mechanisms in the plankton

Killing neighbouring cells by means of exo-enzymes probably the first form of attack, followed later by whole-sale ingestion (phagocytosis) of prey cells. There will have been a range of intermediate stages.

**Prey cells have evolved a range of measures to protect themselves:**

Avoidance by camouflage (in the open water by being motionless, odourless or transparent): e.g. cysts or spores.

Escape by rapid locomotion: bacteria from HNF, flagellates from other flagellates, ciliates from copepods by swimming away.

Resistence to ingestion by increasing size (size escape) e.g. excess water.

Resistence to penetration by strong cell walls, spines, barbs, slime.

Weapons: trichocysts etc.

Chemicals: External deterrants,or internal toxins coupled to external signals such as shape that is recognised by the predator,

None of these measures can provide universal protection and mortality will accordingly be selective. So many different shapes will co-exist and bloom-forming species come in a range of shapes.

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- Recently, polyunsaturated aldehydes have been found in some diatom species that are produced from structural fatty acids by the action of a specific enzyme that is activated when the cell is crushed. Their role is under debate.

There are 2 types of zooplankton in the sea:

Muscular zooplankton (copepods and krill) that flee predators and are hence particularly attractive because they pack a lot of protein.

Watery zooplankton (salps and jellies) that are eaten by specialized carnivores.

Commercial fish stocks are fed by all food chains.

Greatest transfer efficiency where nutrient concentrations high.

We really do not understand the relationship between magnitude of primary production and size of animal populations.