Woods Hole Oceanographic Institution
Modeling and Synthesis of Southern Ocean Natural Iron Fertilization

Pelagic iron fertilization and the structure of planktonic communities in high nutrients environments of the Southern Ocean

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Since the late 90's many experiments at sea have been conducted to better understand the effect of iron fertilization on the structure of the pelagic ecosystem and its efficiency to export organic carbon.

⟶ An unambiguous demonstration of the limiting role of iron in HNLC areas.

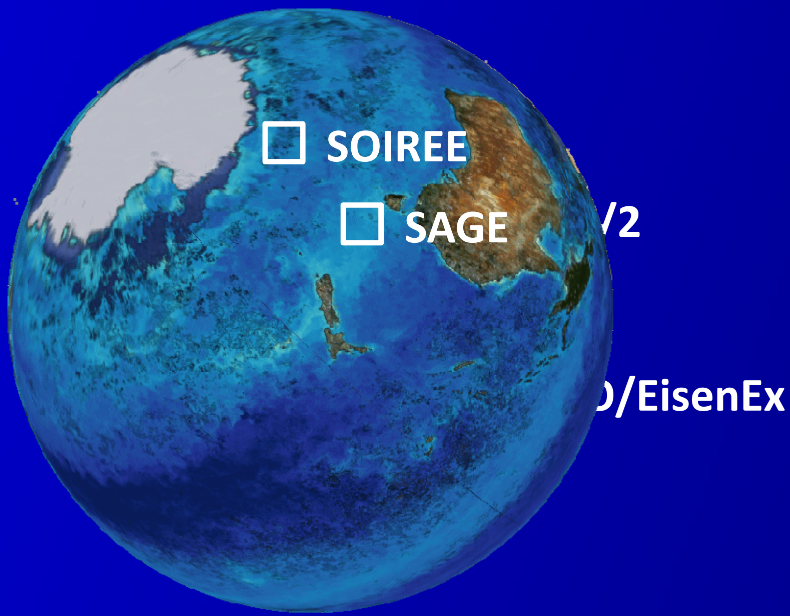
⟶ A reasoned skepticism as to their representativeness and their scaling up and extrapolation to the natural ecosystems.

- ⟶ Recurrent lack of observations of any significant vertical particulate flux at the end of blooms originated from artificial additions of iron.
- ⟶ Emerging question: Have ecosystems naturally enriched with iron developed, on long (geological?) time scales, a natural adaptation in the form of specific pelagic communities ?

In other words: It may not be enough to bring an element, as limiting as it can be, to radically transform the whole food web and/or make an ecosystem effective in terms of vertical export …

OBJECTIVE: To answer the question: What are the fundamental differences in terms of community structure between ecosystems limited by iron and ecosystems receiving inputs of iron, either permanently or temporarily?

METHOD: Examining the differences and similarities in the structure of the pelagic ecosystem, based on some studies of natural fertilization and artificial fertilization experiments that have been carried out in different sectors of the Southern Ocean.



Plankton community structure in the Southern Ocean

The HNLC area – Permanently Open Ocean Zone (POOZ)

⟶ Most of the time, the POOZ pelagic ecosystem is based upon low primary production by small phytoplankton fueling an inefficient biological pump, characterized by high protistan grazing, and efficient remineralization of fixed carbon and nutrients.

⟶ The mesozooplankton, even when present, plays a weak role in phytoplankton grazing although salps or appendicularians can sometimes have a much more significant impact than copepods.

⟶ Among copepods, small microphagous species such as *Oithona similis* are commonly found as dominants contributing to to the conservation of matter and the efficient recycling of biogenic elements in the surface layer.

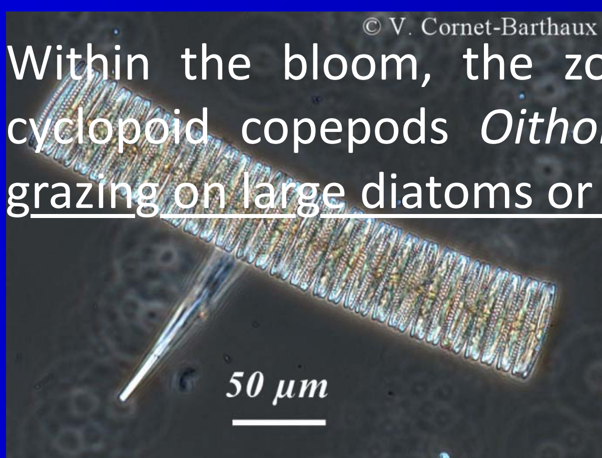
⟶ At times, occasional salp swarms, often represented by *Salpa thompsoni*, can be efficient grazers able to remove an amount of organic carbon almost equivalent to all of the primary production.

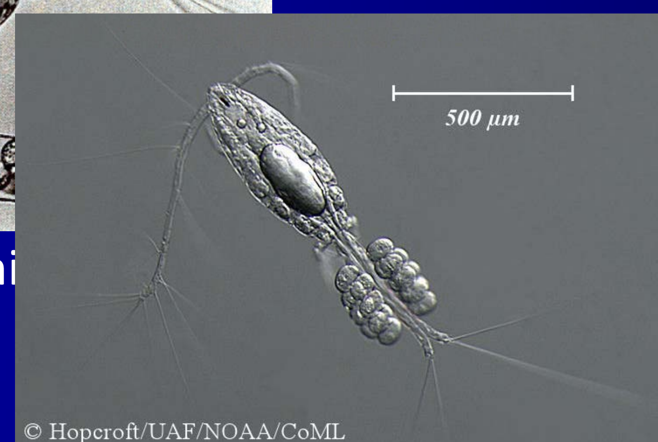
Plankton community structure in the Southern Ocean

Areas naturally fertilized by iron – The Antarctic Polar Frontal Zone (PFZ)

⟶ During ANT X/6, the iron–induced spring bloom of the PFZ was dominated by the large heavily silicified diatoms *Fragilariopsis kerguelensis*, *Corethron inerme* and *Corethron pennatum*, while the smaller *Pseudo–Nitzschia prolongatoides* and *Cylindrotheca closterium* were restricted to the South where no bloom developed at the same time.

⟶ Within the bloom, the zooplankton community was dominated by the cyclopoid copepods *Oithona similis* and *Oncaea* sp., and an important grazing on large diatoms or diatom colonies was unlikely.





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Plankton community structure in the Southern Ocean

Areas naturally fertilized by iron – The Antarctic Polar Frontal Zone (PFZ)

⟶ During ANT XIII/2, the ecosystem was operating at steady state. Primary production was fairly evenly distributed among the pico–, nano– and microphytoplankton. The accumulation of biomass by diatoms is not the simple result of increased growth but might reflects their resistance to grazing .

⟶ The dominant diatoms are represented by *Pseudo–nitzschia* cf. *lineola*, *Chaetoceros atlanticus*, and the 'giant' *Thalassiothrix antarctica*. This reflects either a different kind of community (compared to ANT X/6) or the existence of a seasonal succession may be related to the gradual establishment of a limitation by silicic acid.

⟶ The zooplankton population had extremely high biomass. The dominants are copepods: *Oithona similis*, *Oithona frigida*, and *Ctenocalanus citer* which were fed on delicate diatoms *Ps.* cf. *lineola* but not on large colonies of *Ch. atlanticus*, nor on giant cells of *Th. antarctica* .

Plankton community structure in the Southern Ocean

Areas naturally fertilized by iron – The Crozet Islands bloom

⟶ During CROZEX, early stages of the bloom under natural iron fertilization are dominated by large diatoms: *Corethron pennatum* and *Eucampia antarctica* were probably the first to develop, later giving way, probably due to limitation by silicic acid availability, to the succession of smaller *Thalassionema nitzschioides* and the prymnesiophyte *Phaeocystis antarctica* which tended to dominate the coastal assemblage.

⟶ Outside the fertilized area, in typical HNLC waters, *Fr. kerguelensis* and *C. pennatum* were dominants, together with *Dactyliosolen antarcticus* and the more delicate *Th. nitzschioides*, P*seudo–nitzschia* spp. together with *Chaetoceros* spp .

Plankton community structure in the Southern Ocean

Areas naturally fertilized by iron – The Crozet Islands bloom

⟶ During CROZEX, the mesozooplankton community was overwhelmingly composed by copepods which did not display any major temporal evolution over the 3–months survey from early November to late January.

⟶ A neritic assemblage was dominated by the medium–sized *Drepanopus pectinatus* and an oceanic assemblage was dominated by the large *Rhincalanus gigas* while *Oithona similis* was present in both communities.

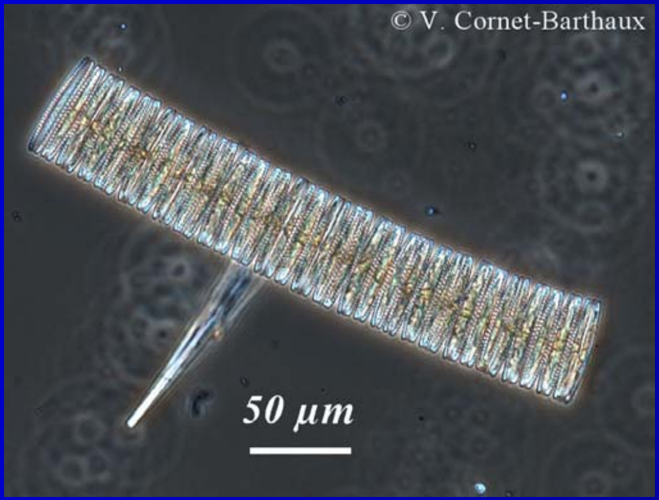
⟶ Grazing by copepods had little effect on the phytoplankton standing stock, regardless of the area.

⟶ Grazing by copepods had played an important role channeling more than 90% of primary production in the HNLC area, especially at the end of the productive period when primary production was dominated by picophytoplankton.

Plankton community structure in the Southern Ocean

Areas naturally fertilized by iron – The Crozet Islands bloom

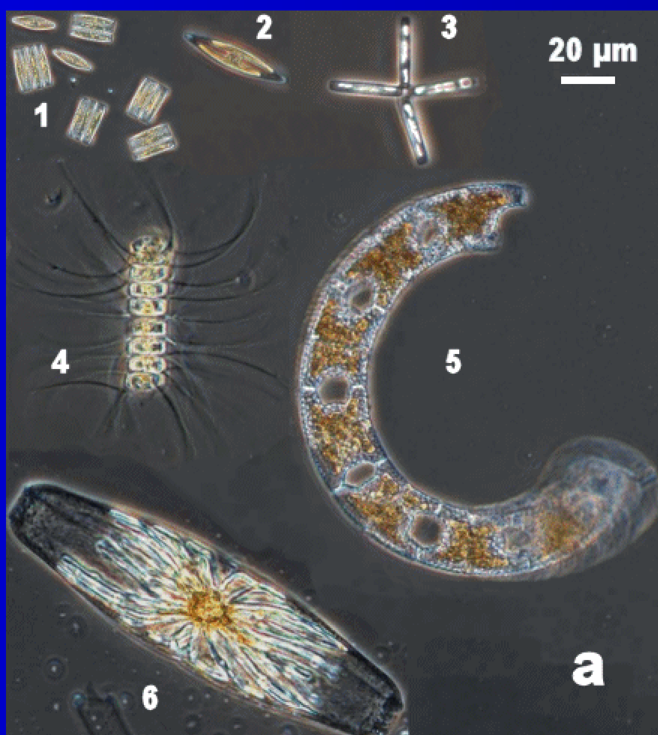
→ With regard to the vertical export of biogenic material, *E. antarctica* seemed to act as a particularly important player. While the vertical flux is enriched in *Fr. kerguelensis* compared to surface water in the HNLC area, that of the iron–enriched bloom area tends to be dominated by *E. antarctica*, which still accounts for a small fraction of organisms in suspension in the surface mixed layer .

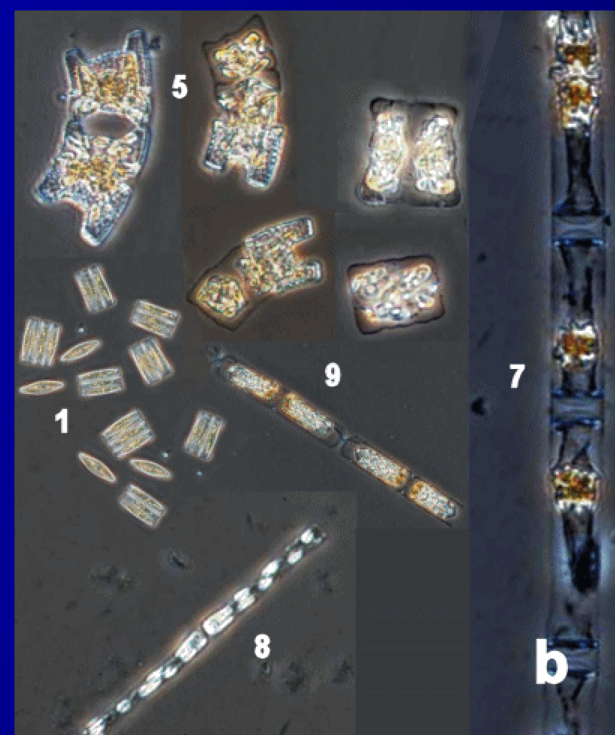


Plankton community structure in the Southern Ocean

Areas naturally fertilized by iron – The Kerguelen Islands SE bloom

⟶ Seasonal succession matters: During KEOPS, repeat analyses at the bloom station revealed an evolution from a *Chaetoceros* subgenus *Hyalochaete* species to a remnant *Eucampia antarctica* assemblage.

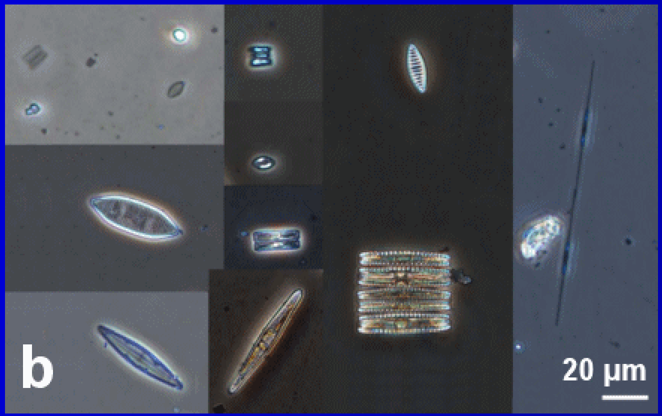




Plankton community structure in the Southern Ocean

Areas naturally fertilized by iron – The Kerguelen Islands SE bloom

→ In contrast the HNLC station, C11, remained dominated by *Fragilariopsis pseudonana* and *Fragilariopsis kerguelensis* throughout the survey.



Plankton community structure in the Southern Ocean

Areas naturally fertilized by iron – The Kerguelen Islands SE bloom

→ During KEOPS, at the center of the bloom, the comparison of phytoplankton samples collected from the rosette with those collected by net tows indicated the presence of two different kinds of diatom populations.

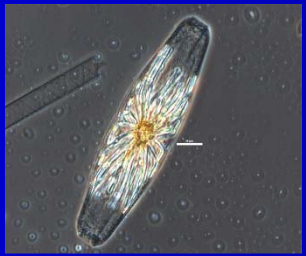
→ Questions:

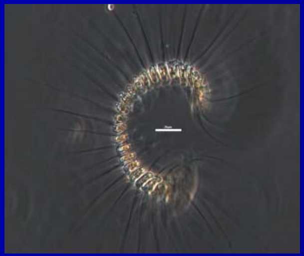
- Do they represent different ecological niches in the epipelagic domain?
- Could the two kinds of communities result into different carbon transfer pathways to the bottom waters, associated to different efficiencies?

Plankton community structure in the Southern Ocean

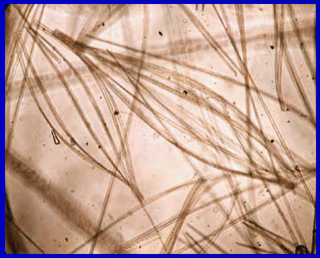
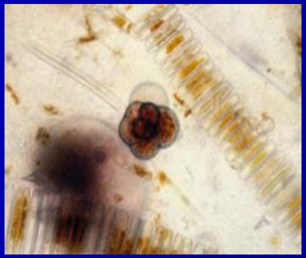
Areas naturally fertilized by iron – The Kerguelen Islands SE bloom

⟶ a population dominated by *Membraneis* spp., small *Chaetoceros* spp., and *Eucampia antarctica* in samples from the rosette





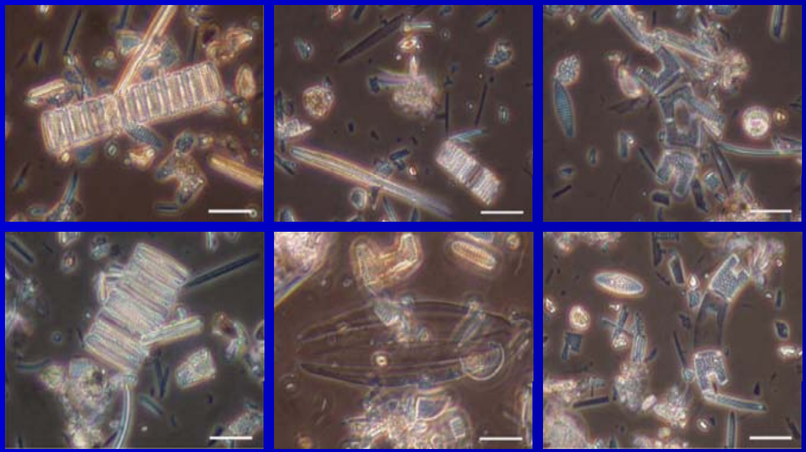
⟶ Large colonies of *Fragilariopsis kerguelensis* accompanied by the giant diatom *Thalassiothrix antarctica* in net samples.

Plankton community structure in the Southern Ocean

Areas naturally fertilized by iron – The Kerguelen Islands SE bloom

→ Empty frustules of *Fragilariopsis kerguelensis* represent 31% of the remains of diatoms in the surface sediment of the Kerguelen Plateau, and 57% in the HNLC area.



→ The superficial sediment thanatocoenose indicates a predominance of the heavily silicified diatoms, selectively exported to depth, and which are probably the major players of the vertical flux .

Plankton community structure in the Southern Ocean

Areas naturally fertilized by iron – The Kerguelen Islands SE bloom

→ The KEOPS zooplankton community was dominated by copepods.

→ In the HNLC area, calanoid copepods of large size (*Calanus simillimus*, *Calanus propinquus*, *Metridia lucens*, *Paraeuchaeta* sp., *Pleuromama robusta* and *Rhincalanus gigas*) and medium size (late copepodite and adult stages of *Clausocalanus* spp. and *Microcalanus* spp.) as well as small copepods (*Oithona similis*, *Oithona frigida* and *Oncaea* sp.) composed the bulk of the biomass .

→ Over the Kerguelen Plateau the composition of the copepod assemblage was the same but with a higher biomass, a high proportion of nauplii and a significant fraction of mesozooplankton sporadically associated with pteropods (another microphagous organism).

→ Grazing on phytoplankton was low. The mesozooplankton was either fed from the microzooplankton which biomass was found particularly low in the iron–enriched area and the HNLC area as well.

Plankton community structure in the Southern Ocean

Overview of artificial iron fertilizations

⟶ SOIREE : Two haptophyte groups at the beginning, with pigment signatures typical of *Phaeocystis* sp. and coccolithophores, respectively, increased steadily during the first 8–10 days, and then decreased somewhat. On day 13, the in-patch was later dominated by *Fragilariopsis kerguelensis*, followed by Rhizosolenia sp. then *Pseudo-nitzschia* sp. Various very large diatom species were abundant, notably *Thalassiothrix antarctica*, *Asteromphalus flabellatus*, *Trichotoxon reinboldii* and *Eucampia antarctica*.

⟶ Grazing by copepods had little effect on the phytoplankton standing stock, and accounted for only few percents of primary production, either inside or outside the patch.

⟶ The zooplankton community was composed by the large copepods *Calanoides acutus*, and *Rhincalanus gigas* which accounted for the bulk (87%) of the biomass, small copepodites of *Ctenocalanus* spp., *Calanoides acutus*, as well as copepodites and adult of the small *Oithona similis* which were the most numerically abundant.

Plankton community structure in the Southern Ocean

Overview of artificial iron fertilizations

⟶ EisenEx : During the initial phase, the microplanktonic diatoms were dominated by the heavily–silicified *Fragilariopsis kerguelensis* whose numbers increased inside and outside the patch.

⟶ Two delicate diatom species, the centric *Chaetoceros debilis* and the pennate *Pseudo-nitzschia lineola*, increased their population con–centrations exponentially throughout the experiment and Ps. Lineola dominated the biomass at the end of the experiment.

⟶ Grazing pressure by copepods, especially nauplii of of *Ctenocalanus* spp. and *Oithona* spp., and copepodite stages of *Oithona similis*, was responsible for the decline of aplastidic dinoflagellates and ciliates, resulting in a decreased grazing pressure over diatoms. This trophic cascade favored dominance of the bloom by large diatoms.

Plankton community structure in the Southern Ocean

Overview of artificial iron fertilizations

→ EIFEX: a relative decrease in large *Chaetoceros* species was observed, while *Thalassiothrix antarctica*, *Corethron inerme*, and Rhizosolenoids, large diatoms increased their relative contribution. Other species, like *Fr. kerguelensis*, *Pseudo-nitzschia* spp., and *Dactyliosolen antarcticus*, were important in terms of biomass throughout the experiment, with only minor changes.

→ The mesozooplankton was dominated by the large *Rhincalanus gigas* and *Calanus simillimus* and the medium–sized *Ctenocalanus citer* in the iron–enriched patch while the latter species dominated outside.

→ Grazing impact by copepods was moderate on the phytoplankton standing stock and amounted up to ~1/3 of the primary production in the bloom .

Plankton community structure in the Southern Ocean

Overview of artificial iron fertilizations

→ SAGE experiment has proven unique because fertilization resulted in only a small increase in biomass (a doubling) resulting from the growth of non–siliceous phytoplankton.

→ Fertilization enabled a unique development of picoeukaryotes which was interpreted as reflecting a persistent limitation of diatoms by iron and silicic acid, associated with significantly lower iron needs of the picoplankton community.

→ Under these conditions, while it has generally little impact most of the time, the microzooplankton biomass doubled as a result of active predation on picoeukaryotes. No data on mesozooplankton but grazing was certainly low.

Environmental factors shaping the plankton community structure in the Southern Ocean

→ It still remains difficult to synthesize the complete community structure data set which has been acquired during many experiments conducted at different times of the year, in contrasted nutritional environments, and under varied physical conditions.

→ Comparison of artificial fertilization experiments and studies of natural fertilization may, however, renders possible to extract some major aspects of the dynamics of pelagic communities in the Southern Ocean POOZ. It is this exercise which is attempted here.

→ A major difference between artificial and natural fertilization experiments is that in the first case, the early development of all primary producers can be witnessed, while in the other case observations depend on the stage of development, not only of the phytoplankton, but also of the pelagic food web as a whole, at the beginning of the study.

Environmental factors shaping the plankton community structure in the Southern Ocean

→ Iron fertilizations, either natural or artificial, firstly result in the development of bloom phytoplankton populations. As so often, following the classical paradigm illustrated by the mandala of Margalef (1978), these populations are dominated by the larger size class.

→ The microphytoplankton grows the most rapidly, with a potential for vertical export directly by aggregation or indirectly inside faecal pellets associated to the so–called classical food web.

→ However, as in every bloom, all size classes (pico–, nano–, and microphytoplankton) grow rapidly during the initial stage although biomass finally accumulate almost exclusively in diatoms.

→ Some experimental results, however, contradict the above scenario and illustrate the role also played by major nutrients.

Environmental factors shaping the plankton community structure in the Southern Ocean

Iron and silicic acid

→ SAGE experiment: Although it was not conducted in typical HNLC waters, but rather in 'high nutrient / low silicic acid / low chlorophyll' waters, the experiment indicates that a major nutrient limitation, still likely to occur during the development of phytoplankton after iron fertilization, can lead to drastic changes in group dominance.

→ Peloquin *et al.* (2011) show that the limitation by silicic acid can results in the cessation of diatom growth, which yield their dominance to other groups including picoeukaryotes.

→ The dominance within diatoms can also be affected by the ratio between the addition of metals and the natural concentration of silicic acid, a process by which Leblanc *et al.* (2005) explained the competition between large cells of colony–forming *Pseudo–nitzschia* sp. and the small less silicified solitary pennate *Cylindrotheca closterium*.

Environmental factors shaping the plankton community structure in the Southern Ocean

Does grazing matter?

⟶ Because they can grow and divide as rapidly as phytoplankton cells, protozooplankton can be responsible for a rapid control of the pico– and nanophytoplankton (Calbet & Landry, 2004).

⟶ The protozooplankton does not restrict its foraging activity to the smaller size classes but can be very efficient in the consumption of diatoms from the microphytoplankton, being able to ingest preys several times larger than their body length (Calbet, 2008); for example, increase in grazing pressure on *Chaetoceros debilis* by *Gyrodinium* sp. and *Gyrodinium spirale* was reported by Saito (2006) during SEEDS.

⟶ Several authors invoke the selective grazing on the faster–growing protozoa by copepods (Kleppel *et al.*, 1991; Saiz & Calbet, 2011) as a mechanism able to release grazing pressure on large diatoms thus enabling them to bloom (Assmy *et al.*, 2007).

Environmental factors shaping the plankton community structure in the Southern Ocean

Does grazing matter?

→ Smetacek & Naqvi (2008) challenge the importance of grazing. They enlighten the fact that all Southern Ocean iron fertilization experiments induced blooms in a range of mixed layer depths and from spring to late summer which they consider as indicative that iron availability and nor light nor grazing controlled the build–up of biomass.

→ in all the experiments described above, the low grazing pressure of zooplankton on diatom standing-stock is a leitmotiv. Diatoms, even weakly silicified, tend to accumulate because the protozooplankton itself is under top–down control by the mesozooplankton.

→ Such accumulations generally result in a depletion of nutrients leading to the establishment of a network in which small microphagous copepods like *Oithona similis* play a central role.

Environmental factors shaping the plankton community structure in the Southern Ocean

Does grazing matter?

→ Microphagous copepods feed large copepods which biomass slowly and gradually increases until the return of winter conditions.

→ There is a gradual transfer of nutrients towards the larger mesozooplankton. This process is the principal cause of a weak export of biogenic matter, except for silica which is gradually removed from the surface layer by a silicon pump (Dugdale et al., 1995) particularly efficient at low temperatures.

Environmental factors shaping the plankton community structure in the Southern Ocean

Species successions and life cycles

⟶ During EIFEX the collapse of previously growing *Chaetoceros dichaeta* and *Chaetoceros atlanticus* and their replacement as dominant by *Fragilariopsis kerguelensis* and *Corethron inerme* was not related to grazing by the mesozooplankton (Assmy *et al.*, 2005 ; Kruse *et al.*, 2009).

⟶ Assmy *et al.* (2005) assigned the disappearance of *Ch. dichaeta* and *Ch. atlanticus* to their life history as no clear signs of mechanical breakage associated with crustacean grazing were observed.

⟶ *Ch. dichaeta* and *Ch. atlanticus* seemed senescent with chains with many empty cells or cells with disintegrating cytoplasm, a phenomenon that could be related to epidemic (virus or bacterial infection?) or programmed cell death (apoptosis).

Environmental factors shaping the plankton community structure in the Southern Ocean

Species successions and life cycles

→ Apoptosis and species–specific pathogenicity have also been raised by Smetacek *et al.* (2002), together with crushing by small copepods, to explain the senescent condition of early summer populations of the delicate *Pseudo–nitzschia* spp. in the Atlantic sector of the PFZ.

→ This could also have been the case for the decaying diatom population of the HNLC site during KEOPS (Armand *et al.*, 2008).

→ Assmy *et al.* (2007) report increase of empty and broken frustules during the EisenEx bloom, reflecting several loss processes not easy do deconvoluate (viral/bacterial infections, grazing, selective or not, by protozoo– to meso-zooplankton, 'natural mortality' including apoptosis).

→ During SEEDS II heterotrophic bacteria of the *Cytophaga-Flavobacteria-Bacteroides* were closely related to the genus *Saprospira*, able to kill eukaryotic phytoplankton such as diatoms, dinoflagellates, and prymnesiophytes (Kataoka *et al.*, 2009): Pathogenic bacteria could also shape the phytoplankton community.

Environmental factors shaping the plankton community structure in the Southern Ocean

Species successions and life cycles

→ For Assmy *et al.* (2007) it is the ratio of growth to mortality rates that determines the success of a given species in an iron–induced bloom because none of the individual species is anymore resource–limited, then sinking losses are decreased at their lowest level.

→ One might therefore expect a high variability of dominant species in that the success of a single species would depend on an ecological environment previously acquired, and an inoculum community (incl. virus, bacteria, flagellates, ciliates, mesozooplankton), resulting itself from the more or less recent history of initial natural plankton populations.

→ Since we cannot of course control the initial state of the experimentally perturbed environment, that constitutes a major obstacle to the generalization of the results obtained in artificial fertilization experiments because no experiment could be reproduced.

Environmental factors shaping the plankton community structure in the Southern Ocean

Species successions and life cycles

→ In artificial iron fertilization of HNLC environments, the success of a given species (or taxonomic group) then seems to result from a complex combination of:

- control by a major nutrient that could become progressively limiting,
- selective grazing pressure decrease or suppression on the different size classes,
- initial seeding stocks which in turn could be controlled directly by seasonality (internal clocks triggering growth at maximal rates under some environmentally photoperiod–related conditions) .

→ This makes artificial fertilization experiments very different from "natural experiments", which necessarily take into account the adjustment of the various components of the food web and the temporal dimension of the seasonal development of the pelagic production.

Iron–induced or neritic blooms?

→ some authors, like Smetacek &Naqvi (2008), argue that naturally iron fertilized blooms are extensions of coastal blooms dominated by neritic species with a life cycle different as compared to oceanic species, characterized by the production of heavily silicified, fast–sinking, grazing–resistant, resting spores.

→ In a recent paper, Salter *et al.* (2011) also indicate that the vertical flow of the iron fertilized area in the wake of Crozet Islands was mainly the result of a rapid sedimentation of *Eucampia antarctica* resting spores.

→ This hypothesis cannot be reject regarding the bloom of Kerguelen Plateau where many *Chaetoceros Hyalochaete* resting spores as well as the final formation of *E. antarctica* resting spores were observed in the mixed layer (Armand *et al.*, 2008a) and the surface sediment of the plateau was also characterized by the dominance of *Chaetoceros Hyalochaete* spores together with *Fragilariopsis kerguelensis* and *Thalassionema nitzschioides* (Armand *et al.*, 2008b).

Iron–induced or neritic blooms?

The knephoplankton

→ The presence of *Fragilariopsis kerguelensis* in sedimentary thanatocenoses of the entire POOZ suggests another explanation, not exclusive with respect to the previous one.

→ some large species such as *Thalassiothrix antarctica* seem to thrive mostly everywhere at background levels. Given their large size (length > 1 mm) they could be part of the 'shade flora' (Sournia, 1982), the 'knephoplankton' (Lo Bianco, 1903) representing species occurring preferentially or exclusively at some discrete depth below the surface (usually, around 100 m depth).

→ de Baar *et al.* (2005) also stresses that point that, despite sporadic observations in fertilized patches, very large taxa such as *Rhizosolenia*, *Thalassiothrix*, *Thrichotoxon*, *Asteromphalus*, or *Actinocyclus* should not be overlooked because, in terms of biomass, the giant diatoms may reach higher levels than the numerically more abundant smaller diatoms.

Iron–induced or neritic blooms?

The Deep Silica Maximums

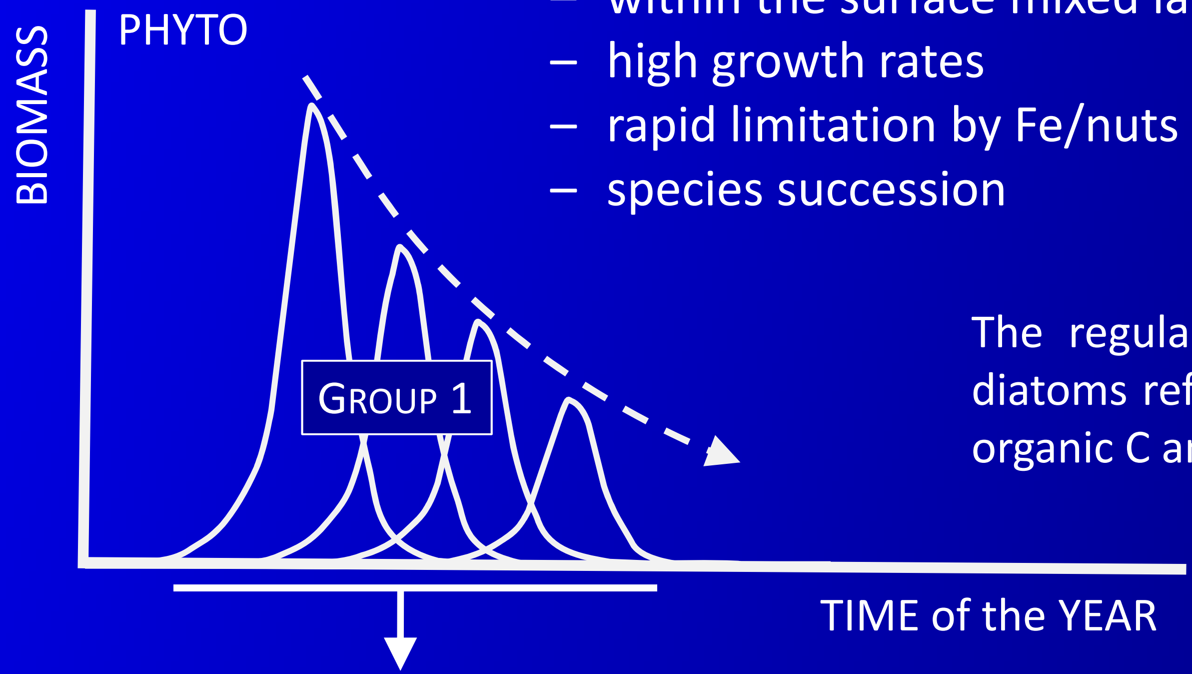
⟶ several times, a deep biogenic silica maximums (DSM), located at the base of the mixed layer, was found in areas remote from islands.

⟶ These DSMs correspond to the accumulation of large diatoms like *Fragilariopsis kerguelensis/Corethron inerme/Corethron pennatum* (Bathmann *et al.*, 1997), *Fr. kerguelensis/Dactyliosolen antarcticus* (Kopczyńska *et al.*, 2001), large Rhizosolenoids (Quéguiner *et al.*, 2011), *Trichotoxon reinboldii/Proboscia inermis/D. antarcticus/Membraneis challengeri* (de Salas *et al.*, 2011).

⟶ These large diatoms probably find a an environmental compromise at depth where light limitation is not that severe, major nutrients and iron are brought in small although sufficient quantities by means of diffusion through the pycnocline, and where their combined slow growth rates and resistance to grazing allow a progressive biomass build–up in the course of the productive season.

Pelagic iron fertilization and the structure of planktonic communities in high nutrients environments of the Southern Ocean

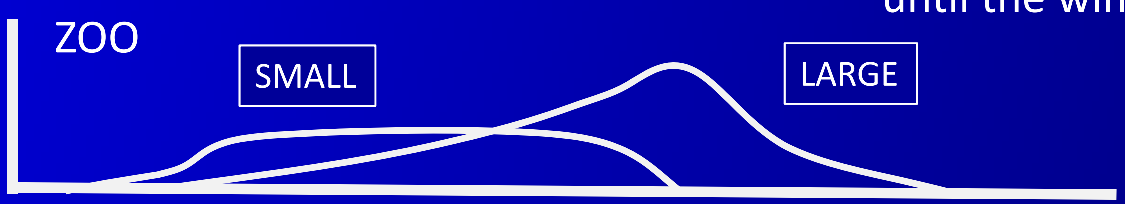
→ Group 1 diatoms :
- lightly silicified
- within the surface mixed layer
- high growth rates
- rapid limitation by Fe/nuts (Si)
- species succession

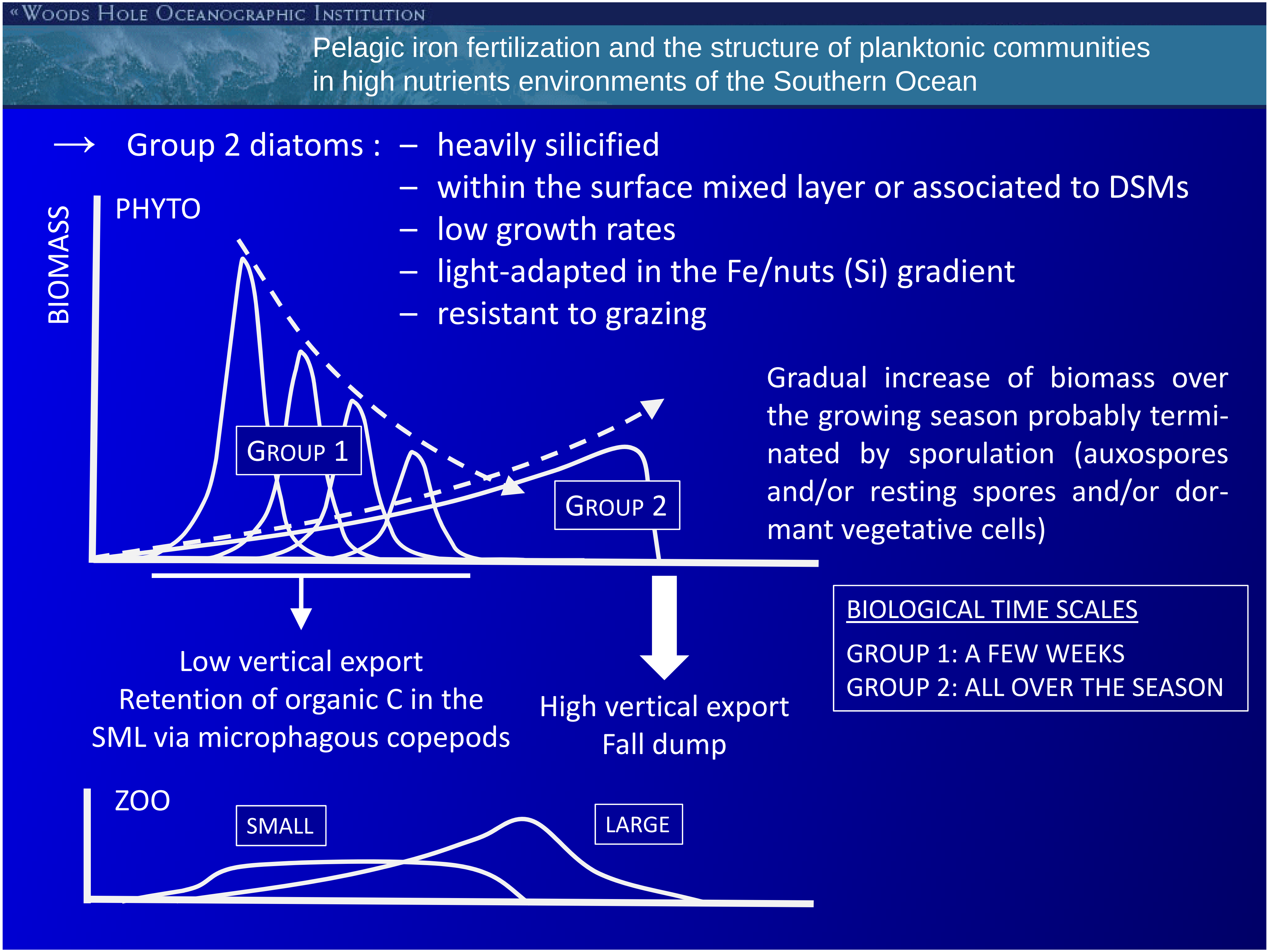


The regular biomass decline of group 1 diatoms reflects a progressive transfer of organic C and nutrients to copepods

Low vertical export
Retention of organic C in the
SML via microphagous copepods

1) Top-down control of microphagous copepods and protozooplankton by large copepods
2) progressive growth of large copepod biomass until the winter season





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Pelagic iron fertilization and the structure of planktonic communities
in high nutrients environments of the Southern Ocean
→ Group 2 diatoms :
– heavily silicified
– within the surface mixed layer or associated to DSMs
– low growth rates
– light-adapted in the Fe/nuts (Si) gradient
– resistant to grazing
BIOMASS
PHYTO
Group 1
Group 2
Gradual increase of biomass over the growing season probably terminated by sporulation (auxospores and/or resting spores and/or dormant vegetative cells)
Low vertical export
Retention of organic C in the
SML via microphagous copepods
High vertical export
Fall dump
BIOLOGICAL TIME SCALES
GROUP 1: A FEW WEEKS
GROUP 2: ALL OVER THE SEASON
ZOO
SMALL
LARGE

Opened questions regarding biodiversity control and its possible alterations

- ⟶ What controls the seasonal phytoplankton succession (incl. nanoflagellates) and how is it affected by iron inputs/additions at the different stages of ecosystem development?
- ⟶ What effects can be produced by iron inputs/additions on the structure of the pelagic food web under different temporal situations?
- ⟶ Has altering the biodiversity of pelagic communities major effects on the biogeochemical fluxes and the transfer of matter inside the food webs?
- ⟶ Are ecological functions sufficiently redundant so that iron inputs/ additions have a moderate impact on food webs as well as being efficient in terms of vertical export?
- ⟶ What is the fate of large zooplankton at the end of the productive period?
- ⟶ To be completed …