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Iron fertilization and the structure of planktonic communities in high nutrient regions of the Southern Ocean

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Abstract

In this review article, plankton community structure observations are analyzed both for artificial iron fertilization experiments and also for experiments dedicated to the study of naturally iron-fertilized systems in the Atlantic, Indian and Pacific sectors of the Southern Ocean in the POOZ (Permanently Open Ocean Zone) and the PFZ (Polar Frontal Zone). Observations made in natural systems are combined with those from artificially perturbed systems, in order to evaluate the seasonal evolution of pelagic communities, taking into account controlling factors related to the life cycles and the ecophysiology of dominant organisms. The analysis considers several types of planktonic communities, including both autotrophs and heterotrophs. These communities are spatially segregated owing to different life strategies. A conceptual general scheme is proposed to account for these observations and their variability, regardless of experiment type. Diatoms can be separated into 2 groups: Group 1 has slightly silicified fast growing cells that are homogeneously distributed in the surface mixed layer, and Group 2 has strongly silicified slowly growing cells within discrete layers. During the growth season, Group 1 diatoms show a typical seasonal succession of dominant species, within time windows of development that are conditioned by physical factors (light and temperature) as well as endogenous specific rhythms (internal clock), and biomass accumulation is controlled by the availability of nutrients. Group 1 diatoms are not directly grazed by mesozooplankton which is fed by protozooplankton, linking the microbial food web to higher trophic levels. Instead, successive dominant species of Group 1 are degraded via bacterial activity at the end of their growth season. Organic detritus fragments feed protozooplankton and mesozooplankton. The effective silicon pump leads to the progressive disappearance of silicic acid in surface waters. In contrast, Group 2 is resistant to grazing due to its strong silicification, and its biomass accumulates continuously but relatively slowly throughout the productive period. Group 2

diatoms are concentrated at or near the seasonal pycnocline and thus benefit from upward nutrient fluxes by diapycnal mixing. The decrease in light and the deep convective mixing in the fall produce both light and nutrient limitation leading to a massive carbon export of Group 2 diatoms, a major annual event of the biological pump. This scheme describes the seasonal evolution of plankton communities in surface waters of the Southern Ocean. The scheme could probably be extended to ecosystems that are characterized by a seasonal bloom under influence of iron or other nutrients.

Keywords: Plankton, Community composition, Trophic relationships, Southern Ocean, Limiting factors, Iron, Life cycle.

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1. Introduction

Since the mid 1990's many *in situ* experiments have been conducted in different parts of the oceans in order to better understand effects of iron fertilization on pelagic ecosystem structures and the efficiency of organic carbon export at depth (*i.e.* beyond the surface mixed layer). The first experiments of mesoscale artificial fertilization generated enthusiasm by showing unambiguously that iron plays a limiting role in high nutrient low chlorophyll (HNLC) areas (Martin *et al.*, 1994; Coale *et al.*, 1996). These results have progressively given way to skepticism about their representativeness and their applicability to full-scale natural ecosystems (Boyd *et al.*, 2007). A key source of doubt is the fact that recurrent observations show no significant increase in vertical flux of particulate organic carbon (POC) which could hypothetically be related to the artificial additions of iron to surface waters. It is within this context that a holistic approach to questions on iron fertilization has emerged in areas of the world ocean where HNLC waters are enriched with natural iron. This new approach also reveals a difference between artificial and natural iron fertilization systems: systems that are naturally enriched with iron have developed, on long (geological?) time scales, as a natural adaptation in the form of specific pelagic communities, while artificially disturbed systems have responded only on short time scales (Boyd *et al.*, 2007).

The biological carbon pump is a fast process which has played an important role in regulating atmospheric CO₂, and in turn climate (Bishop and Wood, 2009). Robinson *et al.* (2010) defines the biological pump as “the reprocessing and downward advection of dissolved organic matter, the sinking flux of particulate matter, and the active transport of organic matter and associated biominerals via vertical migration.” This definition underscores the unique role of pelagic plankton communities from bacteria to mesozooplankton. In these communities primary production, biotic processing or repackaging of POC, differential regeneration of major elements and zooplankton

vertical migration are primarily responsible for setting the export carbon flux out of the euphotic zone and controlling the magnitude and efficiency of carbon export that varies as a function of depth, season, and regional ecosystem structure (Buesseler and Boyd, 2009). In particular, the structure of a pelagic community determines the strength of its biological pump, defined as the magnitude of biogenic matter escaping the epipelagic domain, as well as its efficiency defined as its effectiveness in reducing surface nutrients relative to subsurface values (Sarmiento *et al.*, 2004). The efficiency of vertical export can be assessed through the vertical attenuation of POC below the euphotic zone, as discussed in detail by Buesseler and Boyd (2009). It is clear that regional differences exist in the strength, overall export efficiency and depth-dependent export efficiency of the biological pump, and these differences are driven by the structures of pelagic communities, which ultimately determine the magnitude of the biological sequestration of carbon in the deep ocean and sediments.

Table 1: General characteristics of the experiments considered in this synthesis (grey shading indicates artificial iron fertilization experiments).

Acronym	Region	Latitude	Longitude	Period of the year	Year
Antarktis X/6 ^a	Atlantic sector	47°S–60°S	6°W	September–November	1992
Antarktis XIII/2 ^b	Atlantic sector	49°S–52°S	6°E–12°E	December–January	1995–1996
SOIREE ^c	Australian sector	61°S	140°E	February	1999
CARUSO/EisenEx ^d	Atlantic sector	48°S	21°E	November	2000
SOFEX ^e	Pacific sector	56°S 67°S	172°W 172°W	January–February	2002
EIFeX ^f	Atlantic sector	49°S–51°S	1°E–4°E	February–March	2004
SAGE ^g	Pacific sector	47°S	172°E	March–April	2004
KEOPS 1 ^h	Indian sector	49°S–53°S	71°E–78°E	January–February	2005
CROZEX ⁱ	Indian sector	43°S–49°S	47°E–56°E	November–January	2004–2005
LOHAFEX ^j	Atlantic sector	47°S–49°S	14°W–16°W	January–March	2009

a, Smetacek *et al.* (1997); b, Strass *et al.* (2002a); c, Boyd *et al.* (2000); d, Smetacek (2001); e, Coale *et al.* (2004); f, Smetacek (2005); g, Harvey *et al.* (2011); h, Blain *et al.* (2007); i, Pollard *et al.* (2009); j, Smetacek (2010)

The Southern Ocean holds a special place in view of its possible impact on the

biogeochemistry of the world ocean. The Southern Ocean contains the largest HNLC area of the world ocean. The Polar Frontal Region (PFZ) is the site of Antarctic Intermediate Water (AAIW) formation. In the PFZ nutrient (nitrate, phosphate, silicic acid) signatures are known to be influenced by iron-regulated diatom blooms (de Baar *et al.*, 1995). The circulation of AAIW redistributes major nutrients to lower latitudes and controls the dynamics of primary producers over large regions of the world ocean, directly influencing the biological pump at the global scale. Changes in biogeochemical cycles of nitrogen and silicon, as a result of increased inputs of dissolved iron in the Southern Ocean, have been suggested to explain the difference in values of atmospheric $p\text{CO}_2$ between the last glacial maximum and the period just preceding the Anthropocene (Brzezinski *et al.*, 2002; Matsumoto *et al.*, 2002).

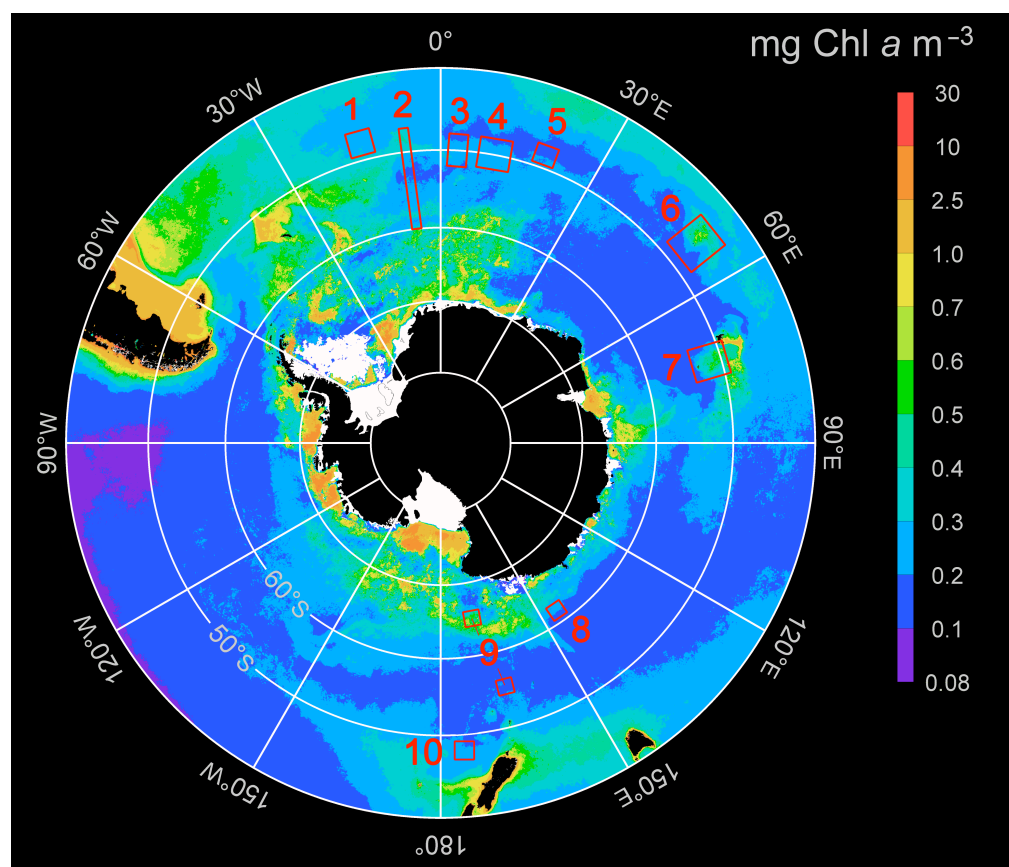


Figure 1 : July 2002 to March 2012 MODIS composite of chlorophyll in the Southern Ocean. Approximate locations of the natural and artificial fertilization experiments discussed in this paper are superimposed (red rectangles): 1, LOHAFEX; 2, Antarktis X/6; 3, EIFeX; 4, Antarktis XIII/2; 5, CARUSO/EisenEx; 6, CROZEX; 7, KEOPS 1; 8 SOIREE; 9, SOFeX (North and South patches); 10, SAGE. Although satellite data are lower by a factor of approximately 2 in the bloom areas (Venables *et al.*, 2007) the composite image clearly shows elevated chlorophyll a concentrations within regions of shallow or complex topography.

In this review paper, results are analyzed from several experiments that were conducted in recent years (see Table 1 and Figure 1) in the Atlantic, Indian, and Pacific sectors. The goal of this paper is to extract key information about the role of iron in structuring pelagic communities at the first trophic levels. This review is restricted to ice-free regions of the Southern Ocean, which are characteristic of the Permanently Open Ocean Zone (POOZ) and the Polar Frontal Zone (PFZ), regions where no large krill swarms have been reported. The objective of the exercise is to summarize the observations which were made in several major studies of natural or artificial iron fertilizations in order to 1) gain insights into the causes of productive ecosystems in the Southern Ocean, 2) build a conceptual framework, and 3) identify avenues of research priority to be tested in the future by a next generation of either natural or artificial iron fertilization experiments.

2. Plankton community structures in the Southern Ocean

2.1. The HNLC area

POOZ of the Southern Ocean is the largest HNLC area of the world ocean. Phytoplankton blooms are rare in the POOZ and most of the time (*i.e.* in the absence of significant iron inputs to surface waters) the POOZ pelagic ecosystem shows low primary production, with small phytoplankton fueling a weak biological pump that is characterized by high protistan grazing, and efficient remineralization of fixed carbon and nutrients (Landry *et al.*, 2002). Consequently, the mesozooplankton, even when present, play a weak role in phytoplankton grazing although salps or appendicularians can sometimes have a much more significant impact than copepods (Mayzaud *et al.*, 2002). 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 (Pakhomov *et al.*, 2002; Atkinson *et al.*, 2004). The dominant copepods are commonly small species such as *Oithona similis* (Takahashi *et al.*, 2010), and these contribute to the conservation of mass and the recycling efficiency of biogenic elements in the surface layer (Pond and Ward, 2011).

2.2. Areas naturally fertilized by iron

Within the HNLC environment of the Southern Ocean a few oases of greenery can be distinguished (Figure 1). Phytoplankton blooms are frequently observed in areas where fronts interact with large bathymetric features, such as ridges, islands, and plateaux. The first *in situ* monitoring of a bloom associated with the natural fertilization by iron was conducted, more or less accidentally, during the experiment Antarktis-X/6 'Frühling am Eisrand' in 1992. Under the combined effects of mixed-layer shallowing due to mesoscale structures driven by the interaction between Antarctic Circumpolar Current (ACC) and the bathymetry, and the increase of day length in the spring, a diatom bloom developed in the Antarctic Polar Front (APF) under the iron-replete

initial condition. The blooms at the PFZ were dominated by the large heavily silicified *Fragilariopsis kerguelensis*, *Corethron inerme* and *Corethron pennatum*, while the smaller *Pseudo-nitzschia prolongatoides* and *Cylindrotheca closterium* were restricted to the south of the PFZ where no bloom developed at the same time (Bathmann *et al.*, 1997). Although the vertical fluxes were not measured, the maximum penetration depth of the biogenic silica suggested an export of biomass out of the surface layer towards deep waters (Quéguiner *et al.*, 1997, Smetacek *et al.*, 1997). This was supported by the evolution of the $^{234}\text{Th}/^{238}\text{U}$ ratio (Rutgers van der Loeff *et al.*, 1997, 2002). Within the bloom, the zooplankton community was dominated by the cyclopid copepods *Oithona similis* and *Oncaea* sp. (Fransz and Gonzalez, 1997), and their grazing on large diatoms was therefore unlikely, as mentioned by Rutgers van der Loeff *et al.* (2002). The observation of many empty frustules and the possible role played by microzooplankton (Klaas, 1997) suggest that the vertical export of such a bloom is related to massive diatom sinking instead of stemming from mesozooplankton grazing. It is also worth mentioning the presence, close to the bloom area, of *Salpa thompsoni* that have a significant capacity to feed on microzooplankton and may be an important link from microbial food webs to macrozooplankton and vertical export (Gowing, 1989; Dubischar *et al.*, 1997).

The seasonal evolution of pelagic ecosystems in the Atlantic sector was studied four years later during the experiment Antarktis–XIII/2 “*Frontendynamik und Biologie*,” which extended the observations to the early summer, probably under iron–enrichment conditions that differed from the previous cruise (Strass *et al.*, 2002b). The PFZ was still productive at this time of the year, diatoms were still the main phytoplankton components in terms of biomass, and the system appeared to operate at steady–state. The production was fairly evenly distributed among the pico–, nano– and microphytoplankton, indicating that the accumulation of diatom biomass is not only the simple result of increased growth but also reflects their resistance to grazing (Tremblay *et al.*, 2002). *Fragilariopsis kerguelensis* and *Corethron pennatum* occurred in low numbers, and the dominant diatoms were represented by different species (*Pseudo-nitzschia* cf. *lineola*, *Chaetoceros atlanticus*, and *Thalassiothrix antarctica*) than in spring (Smetacek *et al.*, 2002). This reflects the existence of a seasonal succession related to the gradual establishment of a limitation by silicic acid (Quéguiner *et al.*, 1997; Tremblay *et al.*, 2002). Healthy *Thalassiothrix antarctica* was the dominant species responsible for the accumulation of biogenic silica. This accumulation was sometimes restricted to the lower part of the mixed layer, in areas where silicic acid was depleted in surface waters. This observation shows that, under conditions of growth limitation, even by silicic acid, some heavily silicified large-sized diatoms, so-called “giant diatoms,” can dominate the phytoplankton biomass (Kemp *et al.*, 2000). The low growth rates of these giant diatoms in the form either long-chain (*e.g.* *Fragilariopsis kerguelensis*) or large individuals cells (*e.g.* *Thalassiothrix antarctica*) promote an

increased silicification of their frustules. The longer duration of their cell cycles produces a longer duration of opal deposition (Claquin *et al.*, 2002). In turn, this strong silicification allows them to be particularly resistant to grazing by mesozooplankton (Hamm *et al.*, 2003). The accumulation of these diatoms occurs over a time scale on the order of several months, much longer than the duration of any artificial iron fertilization experiment accomplished in the past. The summer zooplankton populations in the PFZ had extremely high biomass, of the same order of magnitude as that of phytoplankton. The dominant copepods were again the small *Oithona similis*, *Oithona frigida*, and *Ctenocalanus citer* which fed on delicate *Ps. cf. lineola* but apparently not on large colonies of *C. atlanticus*, nor on giant cells of *Thalassiothrix antarctica* (Dubischar *et al.*, 2002; Pollard *et al.*, 2002; Smetacek *et al.*, 2002). *Oithona* feeding must however be considered with caution: its gut contents may not necessarily reflect its real food regime, because this copepod can eat fecal pellets of other species which could include nanoplankton and protozoans (Atkinson, 1998).

The two experiments, Kerguelen Ocean and Plateau compared Study (KEOPS 1) (Blain *et al.*, 2007) and Crozet Natural Iron Bloom and Export Experiment (CROZEX) (Pollard *et al.*, 2009) provided further information about the pelagic ecosystem structure in naturally iron-fertilized areas of the ACC downstream of Kerguelen and Crozet Islands, respectively. These experiments covered a critical portion of a seasonal cycle: KEOPS 1 characterized the end of the productive period while CROZEX characterized the late spring and early summer.

The results obtained during CROZEX confirmed that the early stages of the bloom under natural iron fertilization are dominated by large diatoms: *Corethron pennatum* and *Eucampia antarctica*. They were probably the first to develop, and their growth lasted till the limitation of silicic acid availability. Smaller *Thalassionema nitzschioides* and the prymnesiophyte *Phaeocystis antarctica* tended to dominate the coastal assemblage (Poulton *et al.*, 2007). Outside the fertilized area of typical HNLC waters, *Fragilariopsis kerguelensis* and *C. pennatum* were of dominant species, together with the large colony-forming *Dactyliosolen antarcticus* and *T. nitzschioides*, *Pseudo-nitzschia* spp. and *Chaetoceros* spp. (Poulton *et al.*, 2007; Salter *et al.*, 2007). The mesozooplankton community was overwhelmingly composed of copepods, which did not display any major temporal evolution over the 3-month study period from early November to late January. Fieldings *et al.* (2007) have distinguished a neritic assemblage dominated by the medium-sized *Drepanopus pectinatus* and an oceanic assemblage dominated by the large *Rhincalanus gigas*, while *Oithona similis* was present in both communities. One major finding is that grazing by copepods had little effect on the phytoplankton standing stock, regardless of the area, but it played an important role in consuming more than 90% of the primary production in the HNLC area, especially at the end of the productive period when primary production was essentially dominated by picophytoplankton (Fieldings *et al.*, 2007; Seeyave *et al.*, 2007). With regards to the vertical export of biogenic

materials, *E. antarctica* seemed to act as a particularly important player (Salter *et al.*, 2007). The vertical flux collected by sediment traps was dominated by *Fr. kerguelensis* in the HNLC area and by *E. antarctica* in the iron-enriched bloom areas, although the latter species only accounted for a small fraction of the phytoplankton observed in the surface mixed layer (Salter *et al.*, 2007).

During KEOPS 1, at the end of the plateau bloom, successive water samples at the bloom reference station revealed an evolution of the plankton community from an assemblage dominated by delicate *Chaetoceros*, subgenus *Hyalochaete*, to a remnant assemblage dominated by *Eucampia antarctica* (Quéguiner *et al.*, 2011). The initial assemblage was dominated by *Chaetoceros debilis*, *Fragilariopsis kerguelensis*, *Navicula* sp., *Thalassionema nitzschioides*, *E. antarctica*, and *Membraneis* sp. In the final assemblage *E. antarctica* was often present as resting stages and accompanied by *Fr. kerguelensis*, *Corethron inerme*, *Leptocylindrus danicus*, and *Guinardia cylindrus* (Armand *et al.*, 2008a). This diatom assemblage was similar to that observed previously in early spring within a phytoplankton plume northeast of Kerguelen where *Fr. kerguelensis* was dominant together with *Pseudo-nitzschia* spp. and *Thalassiosira* spp. (Blain *et al.*, 2001). In contrast with the situation on the plateau and the importance of large centric diatoms, the phytoplankton assemblages observed during the successive visits to the HNLC reference station always showed the dominance by heavily silicified diatoms, *Fr. kerguelensis*, the large *Thalassiosira lentiginosa* and *Thalassiosira antarctica*, and the very small *Fragilariopsis pseudonana* with varying, elevated proportions of dead cells (Armand *et al.*, 2008a). During KEOPS 1, at the center of the bloom of the naturally fertilized area, the comparison between water samples and net tows revealed the presence of two different diatom communities. By contrast to the assemblages described above, net tows were dominated by large colonies of the heavily silicified pennate diatoms *Fr. kerguelensis* accompanied by the giant *Thalassiothrix antarctica* (Armand *et al.*, 2008a). There is limited information about the nature of vertical export during KEOPS 1. Examinations of some surficial sediment thanatocoenoses indicated a predominance of the heavily silicified diatoms, which are probably the major players in the vertical flux (Armand *et al.*, 2008b). Over the plateau, the siliceous sediments were dominated by remnants of *Fr. kerguelensis*, *T. nitzschioides*, and *Chaetoceros Hyalochaete* resting spores, and to a lesser extent by frustules of *Thalassiosira antarctica* and *E. antarctica*. The HNLC sediments reflected the surface water assemblages and were dominated by *Fr. kerguelensis*, *T. lentiginosa* and *Thalassiothrix antarctica*. The zooplankton community was dominated by copepods. In the HNLC area, calanoid copepods of large size (*Calanus simillimus*, *Calanus propinquus*, *Metridia lucens*, *Paraeuchaeta* sp., *Pleuromamma robusta* and *Rhincalanus gigas*) and medium size (late copepodite and adult stages of *Clausocalanus* spp. and *Microcalanus* spp.) as well as small size (*Oithona similis*, *Oithona frigida* and *Oncaea* sp.) composed the bulk of the biomass (Carlotti *et al.*, 2008). Over the Kerguelen Plateau the composition of the copepod assemblage was still the same but with a

higher biomass, a high proportion of nauplii and a significant fraction of mesozooplankton sporadically associated with pteropods. Direct grazing on phytoplankton by mesozooplankton seemed low (Carlotti *et al.*, 2008). It is possible that the mesozooplankton fed on microzooplankton, since microzooplankton biomass was found to be particularly low in both the iron-enriched area and the HNLC area (Christaki *et al.*, 2008).

2.3. Artificial iron fertilization experiments

During the Southern Ocean Iron Enrichment Experiment (SOIREE), two haptophyte groups, with pigment signatures respectively typical of *Phaeocystis* sp. and coccolithophores increased steadily during the first 8–10 days, and then decreased somewhat. On day 13, the in-patch community was dominated by diatoms notably the chain-forming pennate *Fragilariopsis kerguelensis*, and also *Rhizosolenia* sp. and *Pseudo-nitzschia* sp. (Gall *et al.*, 2001). Various very large diatom species were present, albeit with low numbers. However, they exerted a large impact on total biomass given their size. These included in particular *Thalassiothrix antarctica*, *Asteromphalus flabellatus*, *Trichotoxon reinboldii*, *Nitzschia* cf. *sicula*, *Coscinodiscus* spp., *Eucampia antarctica*, and various *Navicula* spp. (Waite and Nodder, 2001). The zooplankton community was composed of the late larval stages of the large copepods, *Calanoides acutus* and *Rhincalanus gigas*, which accounted for the bulk (87%) of the biomass, small copepodites of *Ctenocalanus* spp. and *Calanoides acutus*, as well as copepodites and adults of the small *Oithona similis*, which were the most numerically abundant (Zeldis, 2001).

During the initial phase of the EisenEx/CARbon dioxide Uptake by the Southern Ocean (CARUSO) Experiment, the microplanktonic diatoms were dominated by *Fragilariopsis kerguelensis* with a mean depth-integrated abundance of 5,737 cells L⁻¹ at day 0 of the experiment. This species increased up to 22,146 cells L⁻¹ inside and 9,389 cells L⁻¹ outside the patch by day 21. Chain lengths on the order of 4–30 cells per chain were indicative of favorable growth, with maximum observed lengths up to 160 cells/chain (de Baar *et al.*, 2005). The dominant diatom species at the initial phase of the experiment were: *Dactyliosolen antarcticus*, *Fr. kerguelensis*, *Haslea trompii*, *Corethron pennatum*, and *Guinardia delicatula*, as well as unidentified discoid diatoms (Assmy *et al.*, 2007). Two delicate diatom species, the centric *Chaetoceros debilis* and the pennate *Pseudo-nitzschia lineola*, increased their population concentrations exponentially throughout the experiment to 150-times and 90-times initial values, respectively. Because *C. debilis* initial abundance was one tenth that of *P. lineola*, the two contributed 1% and 21% to bloom biomass at the end of the experiment, respectively, highlighting the role of seeding in a bloom formation (Assmy *et al.*, 2007). There was some evolution of the >50 µm protozooplankton assemblages although no clear differences could be observed between assemblages inside and outside the patch, and the

biomass did not show any major evolution in both environments (Henjes *et al.*, 2007a). Grazing pressure by copepods, especially nauplii 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. Henjes *et al.* (2007b) concluded that this trophic cascade favored dominance of the bloom by large diatoms.

Only limited information on the structure of plankton communities is available for the Southern Ocean Iron Experiment (SOFeX). Under high nitrate, low silicic acid, conditions of the northern fertilized patch, Coale *et al.* (2004) and Peloquin and Smith (2007) reported an increase of larger (> 5 µm) cells within a mixed phytoplankton community composed of prymnesiophytes (incl. *Phaeocystis* sp.), pelagophytes, dinoflagellates, and the delicate diatom *Pseudo-nitzschia* sp. In the southern fertilized patch, otherwise characterized by high nitrate and high silicic acid concentrations, the phytoplankton community was dominated by diatoms, and the iron addition apparently did not modify the structure of the community (Coale *et al.*, 2004) which primarily consisted of *Corethron* spp., *Chaetoceros* spp., *Rhizosolenia* spp., *Fragilariopsis* spp. and *Asteromphalus* spp. (Peloquin and Smith, 2007).

During the European Iron Fertilization Experiment (EIFeX), the biomass distribution of the total diatom community showed a relative decrease in large *Chaetoceros* species, while *Thalassiothrix antarctica*, *Corethron inerme*, and large rhizosolenoids (including *Guinardia*, *Proboscia*, and *Rhizosolenia* species) increased. Other species, like *Fragilariopsis kerguelensis*, *Pseudo-nitzschia* spp., and *Dactyliosolen antarcticus*, were important in terms of biomass throughout the whole experiment, with only minor changes in their relative contribution to the total diatom biomass (Hoffmann *et al.*, 2006). Inside the iron-enriched patch the mesozooplankton were dominated by the large-sized *Rhincalanus gigas* and *Calanus simillimus* and the medium-sized *Ctenocalanus citer*, while outside the patch the mesozooplankton were predominantly medium sized. Grazing had a moderate impact on the phytoplankton standing stock, with grazing occurring at a rate up to ~1/3 of the primary production in the bloom (Krägfesky, 2008).

The SOLAS Air-sea Gas Exchange (SAGE) experiment has proven unique because fertilization resulted in only a small increase in biomass (doubled) resulting from the growth of non-siliceous phytoplankton (Peloquin *et al.*, 2011). 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, the microzooplankton biomass doubled as a result of active predation on picoeukaryotes and possibly the absence of grazing by copepods.

During the Indo-German iron fertilization experiment (LOHAFEX), the initial phytoplankton assemblage was dominated by small flagellates including prymnesiophytes, e.g. *Emiliana huxleyi*, solitary cells of *Phaeocystis antarctica* and other unidentified species, and unidentified prasinophytes, cryptophytes, choanoflagellates and coccoid cells (Assmy *et al.*, 2010). After iron fertilization, a slight increase in cell numbers was observed for some diatoms such as *Fragilariopsis kerguelensis*, *Corethron pennatum*, *Thalassionema nitzschioides*, and species of the genera *Thalassiosira* and *Pseudo-nitzschia*. However, this development stopped very quickly, and biomass concentrations measured inside and outside of the fertilized patch did not differ significantly (Assmy *et al.*, 2010). The study also showed that protozooplankton were co-dominated by heterotrophic dinoflagellates of *Proto-peridinium* and naked species, and tintinnids. The presence of many empty and crushed tintinnid loricae in water samples and copepod fecal matter is interpreted as an indication of the high grazing pressure on protozooplankton, such that the flagellate biomass was rapidly transformed into the larger mesozooplankton community (Assmy *et al.*, 2010). The mesozooplankton community was dominated by late copepodite stages of *Calanus simillimus* outside the patch, and adults and juveniles of *Oithona similis* and *Ctenocalanus citer* inside the patch (Mazzocchi *et al.*, 2010). Finally, LOHAFEX stands out relative to other fertilization experiments because of the presence in the study area of abundant amphipod *Themisto gaudichaudii*, an efficient predator of copepods, especially inside the fertilized patch (Mazzocchi *et al.*, 2010).

3. Iron and other environmental factors shaping the plankton community structure in the Southern Ocean

Synthesizing a complete dataset for seasonal community structures is difficult, given that the data were acquired during many experiments conducted at different times of different years in different geographic locations, in different nutritional environments, and under varied physical conditions. However by comparing the results of artificial fertilization experiments and studies of natural fertilization, it may be possible to identify major features of the dynamics of pelagic communities in the Southern Ocean POOZ and the PFZ. This is the goal of this section.

The main difference between artificial and natural iron fertilization experiments is that in artificial iron experiments, the early development of all primary producers can be witnessed while in the natural iron fertilization observations depend on the stage of community development, not only of the phytoplankton but also of the entire pelagic food web at the beginning of the study. An iron fertilization experiment, whether natural or artificial, will at first result in the development of phytoplankton blooms. Following the classical paradigm illustrated by Margalef's (1978) mandala, these phytoplankton populations are often dominated by large size classes: microphytoplankton accumulate biomass most rapidly, and their potential vertical export of carbon is directly determined

by forming aggregates or indirectly through fecal pellets of grazers as the so-called classical food web (Buessler, 1998; Calbet and Landry, 2004). Although in every bloom, all size classes (pico-, nano-, and microphytoplankton) grow rapidly during the initial stage, biomass rapidly accumulates almost exclusively in diatoms (Gall *et al.*, 2001; Gervais *et al.*, 2002; Tsuda *et al.*, 2003; Marchetti *et al.*, 2006; de Baar *et al.*, 2005; Boyd *et al.*, 2007; Smetacek and Naqvi, 2008).

3.1. Iron, silicic acid, and light

Some experimental results, however, contradict the above scenario and illustrate the role also played by major nutrients. Several studies focused on the role of silicon in limiting the diatom growth, even in the HNLC waters of the Southern Ocean (Boyd *et al.*, 1999; Quéguiner, 2001; Nelson *et al.*, 2001; Mosseri *et al.*, 2008). Degrees of silicon limitation and iron availability are correlated pointing out the possibility of co-limitation (Quéguiner, 2001). In high nutrient, low silicic acid, low chlorophyll (HNLSiLC) waters, the SAGE experiment indicates that a major nutrient limitation is still likely to occur during the development of phytoplankton blooms after iron fertilization, and can lead to drastic changes in group dominance. Peloquin *et al.* (2011) showed that silicic acid limitation can stop diatom growth, thus shifting the dominance to other groups including picoeukaryotes. The low silicic acid of the LOHAFEX experiment also prevented diatom blooms, and instead the artificial iron fertilization stimulated development of a diversified assemblage of small nanoflagellates, which were the main contributors to the total phytoplankton biomass (Assmy *et al.*, 2010). Mosseri *et al.* (2008) indicated that diatoms of the KEOPS 1 study area were limited by silicic acid availability even within the bloom, which was at its final stage. Armand *et al.* (2008a) attributed the shift in diatom dominance at the end of the Kerguelen Plateau bloom to a progressive increase of silicon limitation. During CROZEX, a sharp decrease of silicic acid during the course of the bloom likely drove the species succession that ultimately resulted in *Phaeocystis antarctica* dominance (Poulton *et al.*, 2007). In the same vein, the dominance within the group of diatoms can also be affected by the concentration of added metal relative to the natural concentration of silicic acid. This is how Leblanc *et al.* (2005) explain the competition between large cells of the colony-forming *Pseudo-nitzschia* sp. and the small, less silicified solitary pennate *Cylindrotheca closterium*.

Shortly after the first experimental evidence of phytoplankton growth limitation by iron in the Southern Ocean (de Baar *et al.*, 1990; Martin *et al.*, 1990), the importance of vertical mixing in limiting the light field of a phytoplankton cell was also examined (Mitchell and Holm-Hansen, 1991). An inverse relationship between phytoplankton standing crop and the depth of the surface mixed layer was revealed. Mitchell *et al.* (1991) estimated that, for a minimum loss rate ($\sim 0.2 \text{ d}^{-1}$) and typical conditions of stratification and irradiance in the ACC, phytoplankton are unable to utilize more than 10% of the available macronutrients before they become light-limited by self-shading.

Nelson and Smith (1991) indicated that the highest chlorophyll *a* levels that can be sustained in summer in open waters not stabilized by melt water are $\sim 1.0 \mu\text{g L}^{-1}$ in the Weddell and Scotia Seas and probably less in areas experiencing stronger winds. Light limitation is not independent of iron limitation, as iron requirements are increased for photoacclimation under low light conditions (Venables and Moore, 2010). Several studies have documented the increase of photosynthetic competence of photosystem II (F_v/F_m ratio) in response to iron availability (Boyd *et al.*, 1999; Olson *et al.*, 2000; Boyd and Abraham, 2001; Sosik and Olson, 2002; Hiscock *et al.*, 2003; Moore *et al.*, 2007). During SOIREE, iron fertilization resulted in a two-fold increase of F_v/F_m within the fertilized patch (Boyd and Abraham, 2001). Hiscock *et al.* (2008) reported an immediate and sustained increase in the maximum quantum yield (ϕ_m) of total phytoplankton, an indicator of the photosynthetic efficiency, in response to iron addition during SOFeX. Moore *et al.* (2007) also concluded that interactions between iron and light availability influenced phytoplankton photophysiology and growth through the interplay between photochemical efficiency and photoinhibition, and potentially contributed to bloom longevity in the CROZEX area. The southward progression of the bloom was also controlled by light availability, but the spatial variability of the bloom was probably controlled by the iron supply. The bloom ends before light becomes a limiting factor (Venables *et al.*, 2007).

Iron and light play critical roles in mediating carbon export from the Southern Ocean mixed layer (Cassar *et al.*, 2011). Studies of the role of light have indicated that when deep mixed layers occur in the Southern Ocean, phytoplankton adapt poorly to low light due to the iron deficiency of surface waters. Under these conditions the early accumulation of biogenic matter in surface waters quickly leads to the self-shading of phytoplankton. In these circumstances, iron deficiency is probably responsible for the fact that surface diatoms have low affinity for silicic acid. In areas that are naturally iron fertilized, at the end of the productive season, lowered concentrations of silicic acid and iron deficiency severely limit the growth of diatoms in surface waters. Diatoms that accumulate at the base of the mixed layer transiently find a niche in the vertical gradient of iron and silicic acid where iron limitation is somewhat relieved, enabling some photoadaptation as well as an increase in the affinity to silicic acid. This situation lasts as long as daily light is sufficient to ensure minimum photosynthetic activity. Fall intensification of vertical mixing, combined with reduced incident irradiance, is prone to disperse these accumulations and to release a pulse of sediment into deeper water.

3.2. Does grazing matter?

The accumulation of biomass of phytoplankton is the result of the balance between growth and mortality. In the case of iron fertilization, biomass can accumulate because of increased

phytoplankton growth rates. If the biomass within some size classes is strongly limited despite a high growth rate, this implies a correspondingly elevated mortality rate. The trophic interaction through grazing and mortality makes the evolution of plankton community structure more complex than it would appear at first glance.

Because protozooplankton can grow and divide as rapidly as phytoplankton cells, they can control pico- and nanophytoplankton (Calbet and Landry, 2004; Peloquin *et al.*, 2011). Protozooplankton do not restrict their foraging activities to the small size classes of phytoplankton, and they can efficiently consume diatoms among microphytoplankton, ingesting prey several times larger than their body length (Calbet, 2008). For example, the increase in grazing pressure on *Chaetoceros debilis* by *Gyrodinium* sp. and *Gyrodinium spirale* was reported by Saito (2006) during SEEDS. For this reason several authors invoke selective grazing of faster-growing protozoa by copepods (Kleppel *et al.*, 1991; Christaki *et al.*, 2008; Saiz and Calbet, 2011) as a mechanism to relieve grazing pressure on large diatoms, enabling them to bloom (Assmy *et al.*, 2007). This reduction in grazing pressure from protozooplankton should also promote the increase in biomass of small size classes of phytoplankton, though it has not been observed *in situ*. We can hypothesize that a cascading effect arises fairly quickly (on time scales of weeks) after the start of the bloom, which drives a pelagic ecosystem with top-down controls of pico- and nanophytoplankton by protozooplankton and then by mesozooplankton. Carlotti *et al.* (2008) indicated that, during KEOPS 1, stocks of ciliates and heterotrophic nanoflagellates were probably controlled by mesozooplankton, especially during the later stage of a bloom, when they provided sufficient food to cope with the decrease in phytoplankton stocks. Nevertheless, microzooplankton grazing represents the major loss term for primary production across a broad range of marine regions and habitats from estuaries to open oceans and from tropical to polar areas (Calbet and Landry, 2004). Sherr and Sherr (2007) stress that some components of protozooplankton, *e.g.* heterotrophic dinoflagellates, are likely to be an important food resource for mesozooplankton, thereby linking the microbial network to the classical food web. Adding more complexity, in some occasions such as SEEDS II, copepod grazing controlled the food web structure at the lower trophic levels, keeping the diatom biomass at a very low level (Tsuda *et al.*, 2009). As summarized by Calbet (2008), more information is needed to better understand the roles played by protozooplankton in ecosystem dynamics.

Smetacek and Naqvi (2008) challenged the importance of grazing in artificial iron fertilization experiments. They indicated that all Southern Ocean iron fertilization experiments induced blooms in a range of mixed layer depths in seasons from spring to late summer. This fact indicates that “iron availability and not light or grazing controlled the build-up of biomass.” Nevertheless it remains unknown which processes at the scale of phytoplankton cells are directly impacted by the suppression of iron limitation. In the vast majority of artificial iron fertilization

experiments described above, the low grazing pressure of zooplankton on diatom standing stock is a leitmotiv. Diatoms, even weakly silicified, tend to accumulate in the surface mixed layer partly because protozooplankton are under top-down control by mesozooplankton, as described above. Other causes should nevertheless exist, because the blooms induced by artificial fertilization represent an early stage of new development stimulated by iron addition during which the mesozooplankton plays only a minor role (Zeldis, 2001; Schultes *et al.*, 2006). We can hypothesize that different control factors are set up, probably successively, in the course of the productive period to achieve a gradual sequestration of organic matter in the surface layer. Observations made during KEOPS 1 and CROZEX suggest that, along with a low grazing pressure on diatoms, nutrients are recycled or injected to allow the maintenance of phytoplankton populations. The results of Mosseri *et al.* (2008) show that the diatoms in the bloom of the Kerguelen Plateau largely use ammonium, which accounts for 39 to 77% of nitrogen requirements. The Crozet bloom is also supported largely by ammonium and, even at its maximum development, the nitrate accounts for less than 67% of requirements (Lucas *et al.*, 2007). Also nitrification in the euphotic zone appears to be an important process (Sanders *et al.*, 2007). Bacterial activity intensifies during the productive period, probably fuelled by dissolved organic matter that is produced by nutrient-limited phytoplankton as well as by other particulate organic matter stored in the upper ocean during the post bloom phase over several months in turn replenishing regenerated nutrients in the surface layer (Obernosterer *et al.*, 2008; Sanders *et al.*, 2007). The difference between faster regeneration of nitrogen (and probably phosphorus) and slower regeneration of silicon gradually leads to the emergence of silicic acid limitation at the very end of the productive season.

In blooms produced by either natural or artificial fertilization, mesozooplanktonic communities are frequently dominated by copepods belonging mainly to the orders of Calanoida (*Calanus propinquus*, *Rhincalanus gigas*, *Metridia lucens*, *Calanus simillimus*, *Calanoides acutus*, *Ctenocalanus citer*, *Paraeuchaeta* spp., and *Pleuromamma robusta*), Cyclopoida (*Oithona similis* and *Oithona frigida*) and Poecilostomatoida (*Oncoea* spp.). The presence of small copepods is reported by only a few authors, but their frequent absence in the samples is mainly due to the inefficiency of capture by coarse nets (see Svendsen *et al.*, 2011). Copepod diet is still not well understood. It varies at the seasonal and interannual scales in relation to the life cycles of organisms and to the availability of different food resources. Several studies have indicated that small organisms of the genera *Oithona* and *Oncoea* have a predominantly omnivorous/detritivorous diet (Atkinson, 1998). Adult *Oithona* spp. are omnivorous with a preference for moving prey such as ciliates, while their nauplii are non-selective feeders, feeding on particles <10 µm. Both link the classical food web to the microbial food web (Svendsen *et al.*, 2011). *Oithona similis* is reported to feed on diverse prey including autotrophic and heterotrophic flagellates and ciliates, as well as on

copepod nauplii (Nakamura and Turner, 1997). The majority of larger Calanoida also consume a predominantly omnivorous/detritivorous diet (Atkinson, 1998; Pasternak *et al.*, 2009). Only *Calanoides acutus* seem to have a preference for herbivory compared to omnivory (Atkinson, 1998; Pasternak and Schnack-Schiel, 2001), while *Calanus propinquus* and *Rhincalanus gigas* are sometimes identified as carnivores (Pasternak and Schnack-Schiel, 2001).

In the post-bloom period, zooplankton communities are likely to exert significant control on the fate of organic matter. Through complex interactions between different species and larval stages, organic matter is constantly recycled within the surface layer. In addition, by coprophagy and coprorhexy, copepods turn their fecal pellets into smaller particles that are retained within the surface layer and that can then be degraded by other organisms such as bacteria and protozooplankton (Iversen and Poulsen, 2007) or even ingested sporadically by microphagous pteropods (Carlotti *et al.*, 2008). This retention of matter is accompanied by two processes. First there is a gradual transfer of nutrients towards the mesozooplankton, a process which is the principal cause of a weak vertical export of nitrogen and phosphorus. Second the latter are decoupled from biogenic silica, which is gradually removed from the surface layer by a silicon pump that is particularly efficient at the low surface temperatures of the Southern Ocean (Dugdale *et al.*, 1995).

One of the remaining questions is the transfer of bacterial production to higher trophic levels, i.e., giving the low impact of grazing by protozooplankton on bacteria, Christaki *et al.* (2008) call this the “missing link”. Zeldis (2001) also discussed “the enigma of copepod nutrition” during SOIREE, referring to the apparent lack of high density detrital material which might have been the principal food source. They questioned the role of fine-scale (5 m) vertical structures (seen in density and transmissometer data) to act as accumulation layers for biogenic matter. Such discontinuity layers are difficult to sample without disturbance, and they also vary in depth spatially and temporally, in response to internal waves, currents, episodic weather events and seasonal mixing (Robinson *et al.*, 2010). We must therefore focus on investigating the transfer of biogenic matter between the microbial and the classical food webs, hence between the ‘regeneration system’ or the ‘export pathway’ as articulated by Sarmiento *et al.* (2004). This will need to incorporate a new dimension of vertical heterogeneity that seems to be present even in the Southern Ocean.

3.3. Species successions and life cycles

The rapid temporal succession of species is another major feature of the phytoplankton ecosystem. Saito *et al.* (2006) pointed out that iron inputs modify the dominant diatom bloom species, which in turn determine the overall response of the entire community. The limited information about the long-term stability of phytoplankton community structure makes it difficult to scale up the findings of artificial iron fertilization experiments (Boyd *et al.*, 2007). During EIFeX the

collapse of initially dominant species, *Chaetoceros dichaeta* and *Chaetoceros atlanticus*, and their successors, *Fragilariopsis kerguelensis* and *Corethron inerme*, were not clearly related to grazing by large copepods, *Calanus simillimus*, *Rhincalanus gigas* and *Pleuromamma robusta* (Assmy *et al.*, 2005 ; Kruse *et al.*, 2009). No clear signs of mechanical breakage associated with crustacean grazing were observed that might have accounted for the disappearance of *C. dichaeta* and *C. atlanticus*. Both species were found intact in copepod guts, and this was considered to be indicative of resistance to grazing. In fact, Assmy *et al.* (2005) reported that *C. dichaeta* and *C. atlanticus* seemed senescent, with chains of many empty cells or cells with disintegrating cytoplasm, a phenomenon that could be related to cell death due to epidemic virus and bacterial infection or programmed apoptosis. These mechanisms of apoptosis and species-specific pathogenicity have also been raised by Smetacek *et al.* (2002), together with grazing 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 1 (Armand *et al.*, 2008a). Assmy *et al.* (2007) reported that empty frustules and broken frustules tended to increase in the course of the bloom development of EisenEx caused by several potential loss processes which are not easy to deconvolute. These include viral and bacterial infections, selective or non-selective grazing by protozoa to mesozooplankton, as well as natural mortality including apoptosis. During SEEDS II some heterotrophic bacteria of *Cytophaga-Flavobacteria-Bacteroides* closely related to the genus *Saprospira* were observed to be able to kill eukaryotic phytoplankton such as diatoms, dinoflagellates, and prymnesiophytes (Kataoka *et al.*, 2009). This suggested that pathogenic bacteria could also shape the community resulting from iron fertilization. Assmy *et al.* (2007) argued that the ratio of growth to mortality rates determines the success of a given species in an iron-induced bloom, because none of the observed individual species should be resource limited, and thus sinking losses should be decreased to their lowest level. One might therefore expect a high variability of dominant species and the success of a single species would depend on an ecological environment previously acquired, and an inoculum community of virus, bacteria, flagellates, ciliates and mesozooplankton more or less resulting from initial natural plankton populations. Within single species, growth and reproduction depend on many factors including cell size, temperature, light and nutrients (*e.g.* Drebes, 1966). It is therefore possible that the different species succeed one another during the productive season in successive time windows that are conditioned by physical factors such as light and temperature and probably also by their specific internal clocks. If this is true, then in terms of production and possibly of biomass accumulation, the timing of a given species development is constrained from one year to another in the open ocean by availability of nutrients, including iron, in the period corresponding to its own time window. For the smaller size classes of the pico- and nano-phytoplankton, species succession

could also play an important role, but taxonomic changes are still far from being resolved for these tiny microorganisms. Since we cannot control the initial state of the experimentally perturbed environment, this constitutes a major obstacle to generalizing results from artificial fertilization experiments, because no experiment could be repeated under strictly identical conditions.

During an artificial iron fertilization experiment in HNLC regions, the success of a given species (or taxonomic group) seems to result from a combination of controls by nutrient limitations, selective grazing on different size classes and initial seeding stocks, all of which could in turn be controlled directly by seasonality such as internal clocks triggering growth at maximal rates under some environmentally photoperiod-related conditions (Tsuda *et al.*, 2005; Smetacek and Naqvi, 2008). This makes artificial iron fertilization experiments very different from natural iron fertilization experiments which necessarily take into account the adjustment of various components of a food web and seasonal development of pelagic production.

4. Iron-induced or neritic blooms?

Smetacek and Naqvi (2008) argued that naturally iron fertilized blooms are extensions of coastal blooms, which are dominated by neritic species with a different life cycle from oceanic species, and have characteristics of heavily silicified, fast-sinking, grazing-resistant, resting spores. In a recent paper, Salter *et al.* (2012) also indicated that the vertical export in the iron fertilized area within the wake of Crozet Islands was primarily contributed by a rapid settling of *Eucampia antarctica* resting spores. They attributed the enhanced carbon export in naturally fertilized systems not to iron relief of open ocean diatoms, but rather to the advection and growth of diatom species with characteristics of island systems and subsequent flux of resting spores. This hypothesis may also apply for the Kerguelen Plateau bloom, where many *Chaetoceros Hyalochaete* resting spores as well as the final formation of *E. antarctica* resting spores were observed inside the surface mixed layer, while the surface sediment of the plateau was also characterized by the dominance of *Fragilariopsis kerguelensis*, *Thalassionema nitzschioides* and *Chaetoceros Hyalochaete* spores and the presence of *E. antarctica* and *Thalassiosira antarctica* (Armand *et al.*, 2008a, b).

Armand *et al.* (2008b) mentioned a great abundance of *Chaetoceros* spores on the Kerguelen plateau. They also showed that spores were not the dominant component of the surface sediments in the northeastern plateau. Indeed in the Atlantic sector of the Southern Ocean, *Chaetoceros* spores have a wider distribution in glacial sediments than in interglacial sediments. However, in the wakes of the Antarctic Peninsula and South Georgia *F. kerguelensis* is more abundant (20 to >50%) than *Chaetoceros* spores (15 to >50%), and it is even dominant at some locations in modern sediments. In last glacial diatom assemblages, *Chaetoceros* spores are a little less abundant (<50%) while *F. kerguelensis* retains the same overall importance (20 to >50%). This is a strong indication that the

two diatom assemblages occupy different niches and probably react in very distinct manners to iron input. The presence of *Fragilariopsis kerguelensis* in sedimentary thanatocoenoses throughout the POOZ thus suggests an alternative explanation that differs from Smetacek and Naqvi's (2008) hypothesis that naturally fertilized blooms are simply extensions of coastal blooms. In addition, some large species such as *Thalassiothrix antarctica* seem to thrive almost everywhere at background levels. Given their large size (length > 1 mm) they could be part of the 'shade flora' reviewed by Sournia (1982) representing species that occur preferentially or exclusively at some discrete depth below the surface (usually, around 100 m depth). These species form the 'knephoplankton' meaning the wanderers of twilight (Lo Bianco, 1903 in Sournia, 1982). These species may often be undersampled by conventional means, e.g. Niskin bottles, as discussed by Quéguiner *et al.* (2011). de Baar *et al.* (2005) also pointed that despite sporadic observations in fertilized patches, very large taxa such as *Rhizosolenia*, *Thalassiothrix*, *Trichotoxon*, *Asteromphalus*, and *Actinocyclus* should not be overlooked because, in terms of biomass, the giant diatoms may reach higher levels than the numerically more abundant smaller diatoms. In fact, these giant diatoms, known as "the thistles of the plankton meadows" (Smetacek, 2000), are observed in practically all natural and artificial iron fertilization experiments, and in some artificial fertilization experiments, such as SOIREE, their growth was more representative of iron relief of open ocean diatoms. Even during SAGE, despite the very low concentrations of silicic acid and dominance by picoeukaryotes, the genera *Thalassiothrix* and *Dactyliosolen* were still persistent.

On the other hand, a deep biogenic silica maximums (DSM), located at the base of the mixed layer, was found several times in remote areas far from islands. These DSMs correspond to the accumulation of large diatoms (Bathmann *et al.*, 1997; Kopczyńska *et al.*, 2001; Quéguiner *et al.*, 2011; de Salas *et al.*, 2011). These large diatoms probably find a compromised environment at depth where light limitation is not severe, major nutrients and iron are brought in small but sufficient amounts by diffusion through the pycnocline where their combined slow growth rates and resistance to grazing allow a progressive biomass build-up in the course of their productive season. *F. kerguelensis* is a good example of this type of organism with a heavily silicified architecture protecting it from grazing (Hamm *et al.*, 2003; Wilken *et al.*, 2011). At the onset of winter conditions, the deepening of the mixed layer is the major process responsible for a massive export of these giant players, by a process similar to the "fall dump" (Kemp *et al.*, 2000). In all cases, including a neritic bloom exported to deep oceanic areas or bloom development under typical HNLC conditions, inefficiency of grazing by copepods appears to be the key to the selective export of silica in the POOZ as well as in the PFZ of the Southern Ocean.

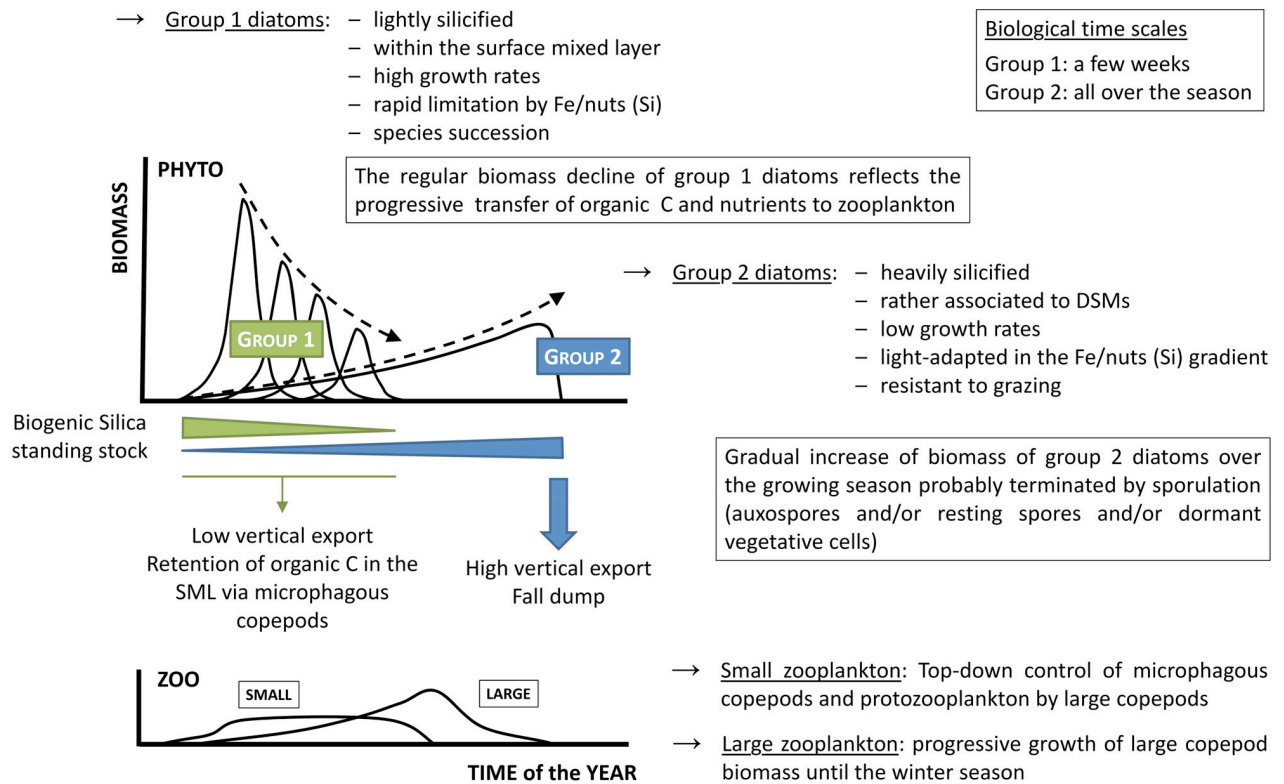


Figure 2 : Conceptual scheme of the development of planktonic communities within or at the base of the surface mixed layer (SML) of the Southern Ocean HNL. On this basic scheme, any further addition of the main limiting factor (Fe) is likely to induce responses of varying magnitude depending on the time at which it takes place (directly related to the amount of major nutrients remaining in the surface layer and not mobilized by zooplankton and higher trophic levels).

5. Conclusion

A general conceptual scheme for the development of pelagic ecosystems in the Southern Ocean is developed from the observations made both in artificial fertilization experiments and in those studies dedicated to naturally fertilized systems (Figure 2). A conceptual scheme should only offer a framework for future research: the hypotheses will need to be validated or rejected in future studies. In early spring, the increase in available light allows the development of diatoms at high growth rates, therefore slightly silicified, within the surface mixed layer. These diatom assemblages represent a group that will soon be affected by the availability of nutrients, including iron and silicic acid. Silicic acid will then be gradually eliminated by the operation of the silicon pump. The nutritional control along with the specificities of biological cycles and actions of pathogens cause a succession of dominant species. Succession time windows for each individual species are probably limited to a few weeks. Diatoms can be separated into 2 groups: Group 1 consists of slightly silicified fast growing cells homogeneously distributed in the surface mixed layer, and Group 2

consists of strongly silicified slowly growing cells within discrete layers. The Group 1 organisms can grow due to the high grazing of small zooplankton on pico- and nanoplankton and protozooplankton, which are primary grazers on diatoms. As the grazing on diatoms from Group 1 appears to be quite low, it is likely that diatom cell death due to nutrient limitation, pathogen action and/or bacterial degradation finally leads to a fragmentation of the organic matter which will then feed the group of omnivorous/detritivorous small zooplankton.

These omnivorous/detritivorous small zooplankton populations may later be consumed gradually by large carnivorous zooplankton, as manifested by a slow increase in large zooplankton biomass during the course of the productive season. In such a system, nutrient recycling and biomass transfer to the more temporally stable compartment of large zooplankton maintain vertical export of nutrients at very low levels. Silicon is the exception, since biogenic silica is unused by zooplankton and therefore is selectively removed by sinking out of the surface mixed layer.

Parallel to the development of diatoms in Group 1, diatoms in Group 2 are located within discrete layers and/or are heterogeneously distributed within the surface layer. They will also be able to develop as the light increases in the spring. Diatoms in this group have lower growth rates and, as a corollary, a strong silicification, which allows them to be very resistant to grazing. The importance of this Group 2 gradually increases as they accumulate biomass throughout the productive period. By gradual accumulation at the pycnocline discontinuity, these organisms benefit indeed from diffusive inputs of nutrients from the upper layer of the mesopelagic zone and gradually build up a deep silica maximum. In this system, the vertical export of organic matter remains low until the late fall and winter. The disappearance of the seasonal pycnocline and intensification of vertical mixing in the late fall and winter then lead to a dispersion of the deep silica maximum and a massive export of organic matter similar to the fall dump, most likely representing the major annual event of the biological pump. The Group 1 diatom community is frequently dominated by *Chaetoceros* species which are known to produce resting spores at the end of their cell cycle. It remains to be demonstrated that the increase in vertical export of carbon is due to the sedimentation of these *Chaetoceros* spores (as compared to that of giant diatoms) even if they can act as ballast carrying carbon-rich aggregates. In fact, since the two communities co-exist, albeit at different vertical levels, it is likely that the sedimentation of either of them at the end of their growing seasons, acts as a filter that moves vertically downward, sweeping almost all organic matter off the epipelagic zone to the deeper water and sediments.

This conceptual scheme will be further refined once we have better identified the discrete levels associated with the different organisms between the surface mixed layer and its base. We also will need a better assessment of the trophic relationships between bacteria, protozooplankton and

mesozooplankton. These relationships directly affect the regenerative capacity of nitrogen and phosphorus in pelagic systems and the processes that decouple silicon from these major cycles. More attention is needed for biological controlling factors, such as seasonal evolution of diversity of bacteria, flagellates, ciliates and diatoms, *in situ* growth rates of the dominant species, biological cycles related to endogenous rhythms and roles of pathogens in the future. It is obvious however, that in such a scheme, the artificial addition of a limiting factor is likely to induce very different responses depending on the initial development stage of a system, that explains the differences between observations made in different artificial iron fertilization experiments. Finally, the Southern Ocean offers us a unique case study for understanding the role of iron within a “natural laboratory”, and it gives the scientific community an opportunity to glean insight into plankton community processes that probably within most oceanic regions characterized by a seasonal bloom (Blain *et al.*, 2008).

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