

The role of grazing in structuring Southern Ocean pelagic ecosystems and biogeochemical cycles

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Abstract: This review examines the links between pelagic ecology and ocean biogeochemistry with an emphasis on the role of the Southern Ocean in global cycling of carbon and silica. The structure and functioning of pelagic ecosystems is determined by the relationship between growth and mortality of its species populations. Whereas the key role of iron supply in conditioning the growth environment of land-remote oceans is now emerging, the factors shaping the mortality environment are still poorly understood. This paper addresses the role of grazing as a selective force operating on the structure and functioning of pelagic ecosystems within the larger conceptual framework of evolutionary ecology. That mortality due to grazing decreases with increasing cell size is widely taken for granted. We examine the impact of this principle across the range of size classes occupied by Southern Ocean plankton and show that relatively few species play crucial roles in the trophic structure and biogeochemical cycles of the Southern Ocean. Under iron-sufficient conditions, high growth rates of weakly silicified diatoms and *Phaeocystis* result in build-up of blooms that fuel “the food chain of the giants” (diatoms-krill-whales) and drive the carbon pump. In contrast, high grazing pressure of small copepods and salps on the regenerating microbial communities characteristic of the iron-limited Southern Ocean results in accumulation of large, heavily silicified diatoms that drive the silicon pump. The hypotheses we derive from field observations can be tested with *in situ* iron fertilization experiments.

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Introduction

The Southern Ocean (SO) is the largest upwelling region in the world ocean but it is also the only one where the bulk of the upwelling macronutrients nitrate and phosphate is returned with downwelling surface water to the ocean interior. In striking contrast, the bulk of the upwelling silicic acid is taken up by diatoms in the surface mixed layer across the Antarctic Circumpolar Current (ACC) and sinks to the deep ocean as biogenic silica (Falkowski *et al.* 1998). Most of it dissolves underway and accumulates as silicic acid in Circumpolar Deep Water (CDW). A fraction is buried as diatom ooze in the underlying sediments. This opal belt is the largest single sink for Si in the ocean (Tréguer *et al.* 1995). The decoupling between N and P cycles from that of Si is reflected in declining silicic acid concentrations, but not nitrate, in the winter-mixed upper layer across the ACC with Si:N ratios ranging from about 2 in the Antarctic Zone (AZ) in the south, to 0.3 in the Polar Frontal Zone (PFZ) between the Antarctic Polar Front (APF) and the sub-Antarctic Front (SAF) (Falkowski *et al.* 1998). So the contemporary SO is a strong silicon sink (Boyle 1998) with significant effect on nutrient inventories and ratios in the entire world ocean (Brzezinski *et al.* 2003, Sarmiento *et al.* 2004). This implies that the ecology of the surface layer of the ACC has a strong effect on the global silicon cycle but

little effect on carbon, nitrogen and phosphorus cycles.

The inefficient utilisation of N and P is due to the low productivity of Antarctic phytoplankton for which three independent but interacting factors are held responsible: growth limitation due to unfavourable light climate because of deep mixing or trace element deficiency, and high mortality due to grazing pressure by proto- and metazooplankton in excess of the growth rate of phytoplankton (Hart 1942, Chisholm & Morel 1991). The relative importance of these mutually inclusive explanations is still under debate but in recent years evidence has accumulated indicating that iron availability is a key factor. Extensive measurements of iron concentrations (de Baar & Boyd 2000) and the results of all *in situ* iron fertilization experiments (Boyd *et al.* 2000, Gervais *et al.* 2002, Coale *et al.* 2004) have confirmed that phytoplankton growth rates in the areas of the SO remote from land are limited by iron availability. Similarly, the higher productivity of coastal and shelf waters can be attributed to iron input from land run-off and contact with the sediments (Martin 1990).

The Si:N ratio is reported to be up to twofold higher in iron-deficient as compared to iron-sufficient diatoms (Takeda 1998, Hutchins & Bruland 1998) which implies that the former make thicker frustules (Boyle 1998) or that their cells contain relatively less plasma than iron-sufficient

diatoms (Franck *et al.* 2003), or both. Such a physiological mechanism could conveniently account for the decoupling between N and Si in the iron-limited ACC (Sarmiento *et al.* 2004) but it is a proximate explanation that needs to be examined in an ultimate or evolutionary framework. Thus, frustule thickness, manifested in the Si:N ratio, is an intrinsic morphological property of diatom species (Brzezinski 1985) that can vary fivefold, even between species of the same genus. So frustule thickness will have to have some ecological significance.

Interestingly, diatom biomass in the iron-depleted, open ACC, although low, tends to be dominated by species that are larger and have thicker frustules or stouter spines than the species that dominate the much higher diatom biomass in productive coastal waters (Hasle & Syvertsen 1996). This difference in diatom community composition is reflected in the underlying sediments. Whereas biogenic silica (BSi), dominated by the thick frustules of a few species, contributes about 50–70% of the sediments underlying the low productive areas of the ACC, the sediments under the productive regions have lower BSi (<10%) (Tréguer 2002) but twofold higher organic carbon percentage of bulk sediment (Berger & Herguera 1992). Most of the diatom frustules in coastal sediments are resting spores of the cosmopolitan diatom genus *Chaetoceros* (Crosta *et al.* 1997). Clearly, the differences in sediment geochemistry and frustule composition between the high and low productive regions will be due to differences in the ecology and hence community structure of the overlying water in these regions.

It is now well established that most of the primary production and biomass in the low productive ocean is in the smaller size fractions (pico- and nanoplankton) that are part of the microbial food web. Biomass increase over the stable background level of this ubiquitous recycling community is due to blooms of larger phytoplankton - diatoms and *Phaeocystis* colonies - whose occurrence is regionally and seasonally restricted (Smetacek *et al.* 1990, Waters *et al.* 2000). So we are left with a paradox: an ocean dominated by the microbial community which happens to be a major global silicon sink (Tréguer 2002, Pondaven *et al.* 2000). The demonstration of iron limitation resolved the earlier paradox of low productivity in the presence of high nutrients. But the silicon paradox cannot be resolved within the same framework. This will have to be extended to explain how the large, robust diatoms that take-up and sink the silicon in the regions where blooms are rare or absent fit into the two-system view of iron-limited, recycling microbial communities and iron-replete diatom blooms.

In this review we identify the features of SO pelagic ecology that are likely to shape its biogeochemistry. The causal links are traced within the framework of evolutionary trends within pelagic organisms. These hypotheses can now be tested with the aid of new methods ranging from

molecular tools to large-scale *in situ* fertilization experiments. New insights into adaptive strategies followed by the various organisms will emerge that will enable the quantification of ecosystem functioning at the genome level. This information can be used to formulate new kinds of models linking biodiversity and ecology with biogeochemistry. The intention of this review is to stimulate thinking at the broad-brush, big-picture scale where exceptions define the rules.

Pelagic ecology and biogeochemistry

Ecological principles

The processes that drive global biogeochemical cycles are structured according to ecological principles that emerge from the evolution of species interacting with one another within physico-chemical constraints of the environment. Little is known about the evolutionary ecology of plankton because its fossil record is highly selective, quite unlike the rich legacy left behind by terrestrial assemblages (Falkowski *et al.* 2004). The morphological evolution of land plants - from algal mat to moss carpet and eventually forest - is clearly shaped by resource competition, whereas speciation, demonstrated impressively by angiosperms, is also shaped by animal vectors. Land plants are susceptible to various pathogens (viruses, bacteria, fungi) and grazed by animals ranging from nematodes and insects to ungulates and elephants against whose depredations a variety of defences from mechanical to chemical have evolved. In contrast to the detailed, species-specific information available on the roles of resource competition versus mortality factors (bottom-up vs top-down) in shaping the structure and functioning of terrestrial systems, comparable knowledge from marine pelagic systems is scant (Verity & Smetacek 1996).

The much greater research effort focussed on factors controlling growth rates of phytoplankton has resulted in neglect of the other side of the coin - the factors regulating mortality rates. The disparity in treatment is reflected in the common usage of the term “growth environment” and the unfamiliarity of its equivalent “mortality environment”. Yet it is the balance between growth and mortality that determines the survivorship of species populations, the accumulation rate of biomass and eventually its fate. The causes of mortality, apart from internal programming (death at old age), are due to external agents: pathogens (viruses and bacteria), parasitoids (parasites that kill their hosts) and predators (proto- and metazooplankton). Each of these groups plays a significant but very different role in structuring the mortality environment, whereby their relative roles will vary within the seasonal cycle. These mortality factors determine biomass accumulation by phytoplankton and the fate of the produced material, so it is they that determine food chains and biogeochemical cycles (Banse 1995).

Adaptation to the growth environment is shaped by competition and expressed in mechanisms of resource acquisition and population growth rate. If competitive exclusion were the major driving force in the plankton, picophytoplankton would dominate, because basic physical principles dictate that nutrient uptake and light absorption efficiencies increase with decreasing size, i.e. increasing surface/volume (s/v) ratio of the cell. Smaller cells divide faster, so population growth and dispersal rates in the mixed layer will outstrip those of larger cells. On the other hand, adaptation to the mortality environment expressed in defence mechanisms requires the diversion of resources away from growth metabolism, i.e. investment in defence slows down the growth rate. The relative cost of defence increases with decreasing cell size. For instance, a small cell will have to divert a greater proportion of its metabolites to build the same thickness of cell wall as compared to a larger cell. So the decreasing s/v ratio which accompanies increasing size is advantageous in the mortality environment. Clearly, the size spectrum of phytoplankton represents a trade-off gradient between adaptation to growth and mortality environments of the various species.

The mortality environment is determined by the resource acquisition techniques of the range of pathogens, parasitoids and predators (3Ps) present in it. So the response to them by their potential hosts and prey can range from avoidance strategies to mechanisms of mechanical and/or chemical protection. Avoidance (decreasing encounter rate) can be achieved by various means such as by low population density, by being small, by camouflage (being invisible to visual, or neutral to chemical, sensory systems) or by flight (swimming away with flagella, cilia or various other propulsion techniques). Organisms protect themselves by means of armour, immune systems, large size, toxic chemicals or weapons. None of these defence mechanisms will be equally effective against all the 3Ps but any reduction in mortality rate has the same effect on population size as a corresponding increase in growth rate. The question is not whether a species is eaten or not, but how often and by how many of the 3Ps, i.e. how effective are its avoidance and defence mechanisms at lowering its mortality rate. The interaction between attack and defence mechanisms - the "evolutionary arms race" (Dawkins 1982) - is often species-specific and is likely to be as much a major driving force for species diversity in the plankton (Smetacek 2001, Hamm *et al.* 2003, Irigoien *et al.* 2003) as it is in terrestrial and benthic systems where it has been studied systematically. An ecosystem in which the arms race has developed to a high degree of sophistication will select for defended species, which in turn will accumulate until their specialized pathogens or predators have built up their respective population size and so on. It is likely that species-specific, pathogen-host and predator-prey interactions are a powerful force in driving annual species succession, an ubiquitous, albeit poorly explained phenomenon

characteristic of all pelagic systems (Margalef 1978). In the discussion below we examine the various components of SO pelagic ecosystems in the light of this evolutionary arms race.

Iron limitation

Throughout most of the warm water sphere, nitrogen and phosphate clearly limit biomass accumulation but in the oceanic upwelling regions, where these macronutrients are supplied from deep water, iron has been shown to be the limiting nutrient. These are the high-nutrient, low-chlorophyll (HNLC) regions of the world ocean, of which the SO is the largest. The other HNLC regions are located in the sub-Arctic and equatorial Pacific (Falkowski *et al.* 1998). In all three regions iron fertilization experiments have demonstrated that conversion of the available macronutrients into biomass is limited by iron availability (Coale *et al.* 1996, Boyd *et al.* 2000, Tsuda *et al.* 2003). The supply of a trace element present in nanomolar concentrations has a similar effect in structuring pelagic ecosystems as the macronutrients present at concentrations three orders of magnitude higher.

Macronutrients provide the building blocks of biomass and the C:N:P ratio of particulate organic matter in the surface layer corresponds closely with that of dissolved nutrients in deep water (the Redfield ratio) world-wide and over a wide range of concentrations. This indicates that deep water chemistry is conditioned by the supply and eventual breakdown of sinking particulate matter (Falkowski *et al.* 1998). However, silicon and iron do not follow the Redfield rule for different reasons. Whereas the silicon cycle is influenced mainly by diatoms (Tréguer *et al.* 1995) that of iron is more complex. Its insolubility in oxygenated, alkaline ocean water implies a short residence time and hence selective loss relative to the dissolved macronutrients, reflected in its low concentrations in deep water. Although only trace amounts of iron are required by plankton, its involvement and indispensability in many key enzyme systems (chlorophyll synthesis, nitrate utilisation, redox systems, etc.) results in its playing as much a "building block" role as the macronutrients (Morel & Price 2003). The extent to which iron is recycled with the macronutrients by the surface community and eventually lost to deeper layers via sinking particles, is currently not well known. Protozoan grazing has been shown to recycle iron together with macronutrients (Barbeau *et al.* 1996) but there are no studies yet on the role of metazooplankton. Indirect evidence, discussed below, indicates that their grazing also contributes to the regenerating system.

Phytoplankton blooms are restricted in the modern SO to waters receiving an adequate iron supply from landmasses and sediments. Evidence is mounting that wind-blown dust is a major supply route of iron to the land-remote SO (Gao *et al.* 2001, Erickson *et al.* 2003). How much of this mineral

iron enters the pelagic ecosystem and how plankton access it is under debate. The chemistry of iron is complex and planktonic organisms will have developed mechanisms to deal with it. Since much of the atmospheric dust is settled out by precipitation, the aggressive chemistry of cloud droplets should render the iron bound in mineral form more accessible to plankton uptake. Indeed, Edwards & Sedwick (2001) have shown that 10–90% (average of 32%) of the iron in dust settled out by snow is bio-available following melting. It follows that snow-deposited dust released by icebergs melting in iron-limited waters is another significant source of iron, depending on the dust content and volume of the icebergs.

The development of distinct blooms with different dominant species was recorded in the land-remote PFZ of the Atlantic Sector (along 10°W) over a period of six weeks in 1992 (Smetacek *et al.* 1997). Throughout this period, iceberg concentrations ranged between 5–60 icebergs in a 22 km range around the ship (van Franeker 1994) and iron concentrations in the mixed layer north of the APF were consistently $> 1 \text{ nmol l}^{-1}$, well above limiting concentrations (de Baar *et al.* 1995). This year was clearly exceptional as icebergs are normally rare to absent in the ACC (Smetacek *et al.* 2002). Interestingly, the first voyage of RRS *Discovery* in 1925–27 happened to be an iceberg year, graphically described by Hardy (1967) in “*Great Waters*”. The ship encountered phytoplankton blooms also in the land-remote ACC including one dominated by *Phaeocystis*, the first and only such report from the land-remote ACC. Could Hardy’s impression of the great productivity of Antarctic waters have been shaped by this first encounter in an exceptional year?

Southern Ocean ecology and biogeochemistry

The enormous catches of diatoms in net tows from Antarctic waters, as compared to their veritable absence in subtropical and sub-Antarctic waters, was the basis for the earlier view of a highly productive SO (Hardy 1967). The productivity was reflected by the large populations of conspicuous, warm-blooded top predators and verified by their phenomenal growth rates. Blue whales were found to reach sexual maturity within 3–4 years of egg fertilization (Hardy 1967). The findings of the RRS *Discovery* cruises from 1925–39 were summarized by Hart (1934, 1942), whose insights regarding the role of bottom-up factors in determining seasonal and regional productivity are remarkably close to the modern view. He compared neritic with open ocean regions and speculated that iron availability limited production in the latter. He was also aware that silicic acid concentrations could limit diatom growth north of the APF. The role of grazing was considered to be important in reducing phytoplankton stocks during the summer months but not more. A major finding of this era was that whales fed almost exclusively on krill and that

“The food of these Euphausiids consists very largely, if not entirely of diatoms and other phytoplankton organisms. Thus we have here one of the simplest food chains possible, the building up of the vast body of the whale being only one stage removed from the organic fixation of the radiant energy of the sun by the diatoms” (Hart 1934). Hart (1942) was well aware that this simple food chain was restricted to a few productive regions, particularly the SW Atlantic Sector. We now know that this view is overly simplistic and does not explain why such a simple system prevails in the Antarctic. So the impact of grazing on ecosystem structure remains as obscure as in his time. The questions remain although the motivation for carrying out productivity studies has radically changed: from a food-chain, hence grazer-oriented approach to one where biogeochemistry occupies centre stage.

The introduction of new methods in the latter third of the last century revealed that phytoplankton stocks, as reflected in chlorophyll concentrations, were low over much of the land-remote SO and more similar to the nitrate-limited, warmer waters of lower latitudes, the so-called “deserts of the ocean” (Karl 2002). The structure of the communities was also found to be similar and dominated by pico- and nanoplankton with autotrophs, bacteria and heterotrophic protists (protozoa) each contributing roughly a third of the total biomass (Knox 1994). Investigation of this thriving, previously overlooked community, dubbed the microbial loop initially (Azam *et al.* 1983), was accompanied by a vigorous debate on whether it represented a sink or a link to higher trophic levels. The issue of how much organic matter produced by pico- and nanoplankton is indeed channelled by protozoa to the familiar top predators (big fish, mammals etc.) has yet to be resolved but the debate faded out with the shift of focus from the food chain to the biogeochemical context of plankton ecology which occurred in the course of the nineties. Attention was now focussed on the role of the microbial community in the global cycles of carbon and other biogenic elements (Azam 1998). In a sense, this was the link-sink debate revisited, albeit in the context of atmosphere, surface and deep oceans. In contrast to the trophic link-sink debate, this one now appears to be resolved. The contemporary SO plays a minor role in the global carbon cycle (Tréguer & Pondaven 2002), because its characteristic microbial community recycles the bulk of organic matter within the winter mixed layer.

The biogeography of SO plankton was documented during the first half of the last century and the patterns of productivity in the second half. The two approaches - species analyses and quantitative measurements of bulk properties and rates - now need to be linked within a unified ecological framework. The SO lends itself to the development of a conceptual framework linking the evolution of its biota and their ecological interactions with its biogeochemistry. Firstly, it is evolutionarily young, because its biota have evolved during the cooling phase

over the last 20 million years from those of the warm-water realm. The question arising here is: Have the same ecological structures been maintained or are there critical differences between the warm- and cold-water pelagic ecosystems? Secondly, Antarctica is the only continent whose entire margin lies more or less within the same climate zone, surrounded by an ocean consisting of broad, concentric bands of water rotating within their respective climate regimes. The “closed circle” nature of Antarctic ecosystems ensures circumpolar continuity of its species populations (Baker 1954) and guarantees them evolutionary continuity within a narrow range of environmental properties. The effect of glacial-interglacial cycles will have been minimal as the respective physical environments in relation to sea-ice cover were maintained and merely shifted north and south by about 5° latitude (Gersonde & Zielinski 2000). There are many cosmopolitan species but the SO has the largest percentage of endemic diatom species of any ocean region (Priddle & Fryxell 1985), indicating specific adaptation to the environment.

One can hypothesize that continuity coupled with predictability will result in tighter gearing between ecosystem components. The role of top-down factors should accordingly be greater in shaping form and function of individual organisms, the life cycles of species and the patterns of interaction within the community. These “merry-go-round ecosystems” of the SO are temporally more stable (in terms of carry-over of one year’s success to the next), and their biota less prone to expatriation than, for example, in the “one-way-street ecosystems” of the North Atlantic where species populations reach the end of their “ecological tether” due to advection from temperate to Arctic regimes and vice versa.

Inter-ocean comparisons of the structure and functioning of the respective pelagic ecosystems can improve our ability to identify trophic cascades, assess palaeoceanographic conditions and forecast future climate scenarios. Thus, the iron-replete North Atlantic plays a major role in the global carbon budget compared to the SO. The former receives much more iron from its extensive shelves, rivers and from North African dust which is why a spring phytoplankton bloom terminated by exhaustion of macronutrients is a prominent and regular feature of its annual cycle (Falkowski *et al.* 1998). However, annual levels of new production in both oceans, based on nitrate uptake within the mixed surface layer, are similar (Jennings *et al.* 1984, Campbell & Aarup 1992, Levitus *et al.* 1993), indicating that it is not the magnitude of production but presence or absence of a distinct bloom which determines the strength of the biological carbon pump. Apparently blooms developing under iron-replete conditions activate the carbon pump whereas iron-limited production has little effect on it.

In contrast the effect on the silicon pump appears to be the reverse. The biogenic silica content of North Atlantic sediments is low (< 10%) (Tréguer 2002) although layers of

phytodetrital fluff have been found to accumulate on the abyssal plain following sinking out of a significant portion of the spring diatom bloom (Beaulieu 2002). The North Atlantic sediments have more in common with the sediments underlying the productive Antarctic Peninsula plume than the latter have with the adjacent opal belt. So the higher silicic acid concentrations in ACC waters compared to the North Atlantic can not be the decisive factor. It follows that the species characteristic of these two types of ecosystem - the carbon and silicon sinking systems - are responsible for the major differences in biogeochemical cycles of the two system types. The species will have evolved under differing suites of selective pressures.

Two questions arise from this ocean comparison:

- 1) Did iron fertilization of the SO by elevated levels of glacial dust input (Petit *et al.* 1999, Mahowald *et al.* 1999) induce North Atlantic conditions similar to those reported from the North Pacific (Sancetta 1992) and, if so, will artificial fertilization be an effective mechanism to sequester atmospheric CO₂?
- 2) What was the effect of iron-replete conditions on the structure of glacial SO food webs and what could be the effect of artificial iron fertilization on the current ecosystems? Would the krill and subsequently whale populations increase in size?

Whereas the lively debate on the first question has received much publicity (Chisholm *et al.* 2001, Schiermeyer 2003), the second has not yet been given serious consideration. Yet the answers to both questions ultimately converge on the fate of the organic matter produced by iron-replete vs iron-limited systems. There is no ecological reason to assume a linear relationship between productivity and the amount exported to the deep sea. Nor should one expect a linear response of the food chain to increasing productivity with all trophic levels increasing proportionately. The point is that we do not yet know the answers to these fundamental questions.

In the following section we compare selected features of the major ecosystem components: phyto-, bacterio-, proto- and metazooplankton with those of other oceans and comment on the similarities and seek explanations for the differences. Emphasis is on the silicon cycle, but we point out some other interesting features as well that pertain to the relationship between growth and mortality environments of SO pelagic ecosystems. These examples illustrate possible links between ecology and biogeochemistry. We commence with the multi-compartmental microbial food web and move on to the major biomass producers - diatoms and *Phaeocystis* - and end with an overview of the zooplankton.

Structure of Southern Ocean pelagic ecosystems

Microbial network

The microbial network (Smetacek *et al.* 1990), comprising

bacteria, phytoplankton and protozoa smaller than about 10 μm , dominates the plankton under nutrient-limiting conditions. These organisms recycle and hence maintain essential elements in the surface layer. Cosmopolitan bacterial taxa also occur in the SO (Morris *et al.* 2002) and bacterial abundances during the growth season (Lochte *et al.* 1997, Arrieta *et al.* 2004) are the same as in other oceans (Fenchel 2002). Their division rates are a function of resource supply but higher growth rates are marginally reflected in abundance, because growth is balanced by mortality. Bacterial numbers are kept in check by grazing of heterotrophic nanoflagellates (HNF) (kinetoplastids and choanoflagellates) that in turn are eaten by larger ciliates and flagellates (Fenchel 2002). These groups are represented by the same taxonomical groupings oceanwide. Bacteriophages (viruses) exert effective control on bacterial numbers, also in the SO (Marchant *et al.* 2000, Pearce & Wilson 2003). The relative roles of pathogens and predators in constraining bacterial numbers will vary but there is little doubt that both will be working in tandem (Pearce & Wilson 2003). The near-constant bacterial numbers of about one million cells ml^{-1} throughout the ocean apparently represent a threshold maintained by density-dependent grazing pressure and infection by pathogens (Smetacek 2002).

All major lineages except cyanobacteria (Waters *et al.* 2000, Wright & van den Enden 2000) are well represented in the pico- and nanophytoplankton of the SO (Lopez-Garcia *et al.* 2001) with flagellates and small diatoms together maintaining biomass at chlorophyll *a* concentrations around 0.2 mg Chl *a* m^{-3} during the growth season. Primary production rates in the HNLC ACC range around 200 mg C $\text{m}^{-2} \text{d}^{-1}$ (Bracher *et al.* 1999, Strass *et al.* 2002) and increase significantly in the presence of adequate resources (light and nutrients) but biomass of pico- and nanophytoplankton does not. It follows that microbial phytoplankton populations, like the bacteria, are also constrained by mortality and that the growth rates of grazer populations must keep pace with that of their food.

The major grazers of the HNF and nanophytoplankton comprise small ciliates and dinoflagellates ranging around 5–15 μm in size. Not much is known about interaction within the small flagellates, and a sizeable proportion of primary production could well be burnt up within the HNF. However, ciliate and dinoflagellate biomass can increase substantially when productivity of the microbial food web is boosted (Klaas 1997, Landry *et al.* 2002). They in turn are grazed by still larger protozoa of the microzooplankton (20–200 μm) but also by the larvae of copepods and the adults of the ubiquitous small species which also feed directly on HNF (Juergens *et al.* 1996, Turner *et al.* 2001). So while much of the microbial biomass production is remineralised within the small size classes, some of it will indeed be passed up to higher trophic levels primarily by ciliates and dinoflagellates that play different ecological roles. Ciliates are ubiquitous grazers of small flagellates in

all aquatic environments; they ingest food items whole so there is an upper limit to prey size. Besides, they are deterred by spines and bristles (Verity & Villareal 1986). In contrast heterotrophic dinoflagellates have evolved an array of formidable techniques to capture and feed on prey of similar size and even much larger than themselves (Jacobsen 1999). Both groups can equal or even exceed the growth rates of phytoplankton so they contribute significantly to diversifying the mortality environment. However, both groups are preyed upon by the same predators dealt with further below. Protozoan grazing rates on phytoplankton are often higher than those of metazooplankton (Landry *et al.* 2002).

Phytoplankton of productive regions

Along the continental margins and in island plumes, iron concentrations are much higher than in land-remote oceanic water (Martin *et al.* 1990). Under these iron-replete conditions, phytoplankton biomass is much higher than in the microbial system. With a few exceptions which prove the rule, the bulk of excess biomass is contributed by large-celled phytoplankton - medium-sized diatoms and the colonial stage of *Phaeocystis*. The secular hypothesis of Cullen (1991) explains this ecological principle with the rule of decreasing mortality rate with increasing size: only larger phytoplankton escape the continuous heavy grazing pressure exerted on the microbial assemblages and are able to convert all macronutrients into their biomass. For reasons explained above, this general rule based on the mortality environment (larger cells enable better defences) does seem to apply but it does not explain why only relatively few key species tend to dominate biomass in their respective ecological groups and size classes. It should be mentioned that we are referring to species differentiated under the microscope, i.e. on the basis of their morphology. Genetic analyses are yielding “cryptic” species within morphologically similar frustules. These will represent environmental adaptation in various forms, e.g. to temperature or low light levels, at the physiological but not the morphological level. A reason why morphology is conserved in some cases but not in others can be sought in adaptation to the mortality environment.

The biomass of blooms around Antarctica, as also in other ocean margins, tends to be dominated by relatively few diatom species from disparate genera, comprising < 10% of the total species assemblage. These key species are medium-sized (10–50 μm), many have long chitin bristles or silica spines and grow in long chains (Smetacek *et al.* 1990). Many of the background species belong to the same genera as the dominants and occur in reasonably predictable seasonal and regional patterns. So evolution of the genera contributing bloom-forming species cannot be regarded as having been driven by selection for fast growth rates. Indeed, there is no obvious reason why episodic, dramatic

increases in population size of any species should confer greater evolutionary fitness or be regarded as ecologically more “successful”. So the widespread belief that bloom-forming species out-compete the background ones is meaningless in an evolutionary context because both survive equally well, implying that the much lower abundance of all the other species is still well above that necessary to maintain a viable population in the pelagial. It follows that only some species have evolved “boom-and-bust” life cycles defined by the annual range in population size.

The following diatom species contribute the bulk of biomass in iron-replete SO blooms, although their relative proportions vary considerably: *Thalassiosira antarctica*, *T. gravida*, *Chaetoceros socialis*, *C. curvisetus*, *C. debilis*,

C. neglectus, *Rhizosolenia hebetata*, *Proboscia alata*, *Corethron pennatum*, *Fragilariopsis cylindrus* and *F. curta*.

With the exception of the two *Fragilariopsis* species and *Phaeocystis antarctica* none of the others contribute substantially to the assemblage growing within the ice habitat, although many of them have stages capable of overwintering in it. The bloom-forming *Chaetoceros* species belong to the subgenus *Hyalochaetae* and are much smaller than the giant *Phaeoceros* species prominent in iron-limited assemblages. Several of the bloom-forming species are bipolar and also contribute to blooms in temperate shelf areas. *Chaetoceros socialis*, *C. debilis* and *C. curvisetus* are cosmopolitan. *Chaetoceros socialis* grows in spherical colonies that bear a superficial resemblance to those of *Phaeocystis*. Interestingly, the two species dominate blooms in the Arctic and Hart (1934) classifies them together as indicative of open ocean, melt-water associated blooms in the Antarctic. All bloom-forming *Chaetoceros* species are capable of converting vegetative cells into thick-walled resting spores that overwinter on the sediment surface in shallow environments, inside the sea-ice in the seasonal sea ice zone (SIZ) (Ligowski *et al.* 1992) and in the pycnocline in the open ocean (McQuoid & Hobson 1996). *Chaetoceros debilis* contributed 90% of the cell densities induced in the iron fertilization experiment SEEDS carried out in the North Pacific HNLC region (Tsuda *et al.* 2003).

The question that arises is why only some species express high growth rates when resources are replete whereas most other species do not react in the same way. Possibly, internal controls restraining high growth rates operate in the “background” species. The presence of such internal controls geared, for instance to seasonality, can be inferred from the predictable annual cycles of species succession. Since bloom-forming species belong to the same genera as many background species it would appear unlikely that the latter lack the physiological potential to achieve high growth rates. Some species have the ability to flood the newly established, favourable growth environment with large numbers of seeding cells which leads to dominance of

blooms even with mediocre growth rates. This seems to apply to *Fragilariopsis cylindrus* and *F. curta* and possibly also *Phaeocystis* which build up large stocks in the ice habitat which are then released to the water column following large-scale melting where they continue to grow (Scharek *et al.* 1994, Gleitz *et al.* 1996).

The case of *Phaeocystis* can shed light on the relationship between growth and mortality environments in speciation. At least six species have been identified worldwide based on morphological and genetic characteristics but only three species - *P. pouchetii* (Arctic), *P. globosa* (warm waters), *P. antarctica* (Southern Ocean) - dominate blooms (Medlin *et al.* 1994). These are also the only species thus far observed to form colonial stages comprising many hundreds of cells. The others occur only as the solitary nanoflagellate stage. Clearly, the flagellates have much higher mortality rates than the cells in large colonies simply because the former are part of the microbial network and hence susceptible to a much larger range of potential grazers and pathogens than the latter. Although *Phaeocystis* colonies are a widespread feature of iron-replete blooms, their contribution to bloom biomass varies widely and has yet to be explained. In the North Sea, *P. globosa* tends to attain dominance in the later spring, in the aftermath of the diatom bloom following Si exhaustion. So it has been argued that as long as Si is available, diatoms out-compete *Phaeocystis* for N and P but following Si exhaustion, the latter utilizes the remaining nutrients (Lancelot 1998). However, field observations do not support this scenario as *Phaeocystis* often dominates also in the presence of high Si concentrations, particularly in the SO. Indeed, given the wide range of growth conditions under which *Phaeocystis* blooms have been observed, it is not evident that a specific attribute of the growth environment, such as nutrient concentrations and ratios, or depth of the mixed layer, is a prerequisite for bloom development. Besides, solitary *Phaeocystis* and various stages of colony formation including individual large colonies are ubiquitous from the ACC to the Coastal Current even though blooms dominated regularly by *Phaeocystis* occur only in the Ross Sea (Arrigo *et al.* 1999). Bottom-up control on the size of the *Phaeocystis* population would not explain why some colonies do manage to develop but the majority not. We sketch a scenario in which variation in the mortality, rather than the growth environment, in the early stages of colony growth determines the build-up of blooms.

Solitary *Phaeocystis* flagellates initiate colony formation by shedding their flagellae and secreting a capsule-like structure around themselves. The cells divide within this capsule which grows simultaneously such that the individual cells maintain much the same distance from each other in a single peripheral layer regardless of the colony size achieved. It is widely believed that this “capsule”, and the colony matrix, is gelatinous, i.e. colonies are balls of jellies that grow outward. Hamm *et al.* (1999) have shown

that this is not the case in *P. globosa* and that the colonies are more analogous to distended balloons of water in which the cells are suspended in an endocolonial, peripheral network attached to the internal colony surface. The colony surface is in reality a skin which is extremely tough and plastic but, unlike a balloon, it is not elastic, i.e. it cannot be distended but is malleable. Considerable force is required to break the skin but once pierced the colony loses its organisation and disintegrates. These mechanical properties require that the skin grow over the entire surface area and from a chemical standpoint this is entirely feasible given that the building blocks of the skin are protein-carbohydrate complexes (Hamm *et al.* 1999) that can be inserted into the matrix of the skin anywhere over the surface. The skin is highly permeable to ions and dissolved molecules up to the size of large carbohydrates (< 2 nm diameter) and possibly digestive enzymes. The fact that colony cells have similar or even higher growth rates than solitary cells indicates that the nutrient supply to colony cells, despite their crowdedness, is not lower than in the case of solitaries. This rule should also apply to diatom cells in chains.

Apparently, the colony skin is an effective defence against a range of protozoa (small ingestors, peduncle and pallium feeders). However, smaller colonies will be susceptible to zooplankton grazing but the larger the colony, the smaller the number of potential grazers that can “get a grip” on them (Verity 2000). This “grazer gauntlet” through which the growing colonies have to pass determines how many “get through” and attain the relative safety of large colony size (> 500 µm diameter). The fact that colonies in their early stages are often found attached to the spines of diatoms (*Chaetoceros*, *Corethron*) also suggests that small colonies are vulnerable and find protection on these large diatoms. Constraints exerted by the mortality environment hence determine the occurrence of *Phaeocystis* blooms. This hypothesis can be tested by comparing the grazer communities of parts of the Ross Sea, where blooms are recurrent features, with the Weddell Sea, where *Phaeocystis* blooms tend to be sporadic (Arrigo *et al.* 1999).

The evolutionary success of diatoms has been attributed to their metabolically cheap and effective Si frustule (Smetacek 1999). *Phaeocystis* colonies bear superficial resemblance to the cells of large, rounded diatoms. Both are encased in tough outer coatings that provide protection against smaller grazers. These are lined on the inside with the cells and, in the case of diatoms, chloroplasts. One is tempted to suggest that *Phaeocystis* colonies are a flagellate’s way of copying the diatom strategy. Interestingly, *Phaeocystis* colony cells are immune to viral attack in contrast to the solitary cells (Brussaard *et al.* 1999). There is only one report of a virus infection of a diatom (Nagasaki *et al.* 2004). The virus in question is unusually small and is reported to be strain-specific indicating that diatoms too are protected against viral infection. Given this similarity, the question arises why

there are so many more diatom species but only three species of colony-forming *Phaeocystis*. Differentiation of the latter is estimated to have occurred 30 million years ago together with planetary cooling, which is ample time for speciation (Medlin *et al.* 1994). Hamm *et al.* (2003) suggest that a rigid shell, laid down following cell division, offers immense scope for form, hence species diversity, in contrast to a tough exoskeleton that grows with the colony. The spherical shape of the latter represents a single optimum solution given the properties required of it. The example of *Phaeocystis* and the various cosmopolitan bloom-forming species indicates that a single species can thrive in a wide range of growth environments ranging from shallow coastal to open ocean and even including sea ice. So the mortality environment is likely to play a greater role in governing abundance.

Diatoms of iron-limited systems

Whereas pico- and nanoflagellates contribute the bulk of phytoplankton biomass in the iron-limited Southern Ocean, microplankton diatoms (> 20 µm) are a universal feature. They are highly diverse in shape and size and comprise over 100 species from a broad range of the common diatom genera. In restricted regions along fronts where iron, albeit at low concentrations, is introduced to the surface in upwelling water, diatom biomass can exceed that of the microbial phytoplankton by a factor of two or more (Tremblay *et al.* 2002, Smetacek *et al.* 2002). About six species from disparate genera tend to contribute the bulk of biomass. They are all giants of their respective genera and of eye-catching appearance due to their extravagant use of silica (Si:N > 2). They can dominate diatom biomass in the PFZ at Si concentrations < 5 mmol m⁻³ indicating that high ambient concentrations are not a prerequisite for making thick frustules (Freier *et al.* 2000, Smetacek *et al.* 2002). Since it appears that these species are responsible for the bulk of Si depletion across the ACC, albeit in different ways, we shall describe their distinguishing features separately.

Some 13 species of *Fragilariopsis* occur in the Southern Ocean but *Fragilariopsis kerguelensis* is conspicuously different by virtue of its thickly ribbed frustules and its curved, ribbon-like chains that can be over 100 cells long under favourable growth conditions. It is most common in the Antarctic Zone (AZ) and along the APF with peak occurrence during spring and autumn (Hart 1934). At other times (winter and mid-summer) chains are shorter and up to 50% or more of randomly distributed frustules in a chain can be empty (El-Sayed & Fryxell 1993, Assmy 2004). The fate of the missing cell contents is unknown. Despite the extra ballast due to thick frustules and empty cells in the chains, chains with live cells manage to remain in suspension in the mixed layer. Observations during the iron fertilization experiment SOIREE even indicated positive

buoyancy of the population (Waite & Nodder 2001). This is truly an enigmatic species warranting further dedicated research. The frustules have been shown to be remarkably strong and can withstand five times higher pressure loads than those of a centric diatom of similar size (Hamm *et al.* 2003) suggesting that mechanical protection afforded against smaller and hence weaker crustacean zooplankton by the thick frustules is part of the survival strategy of this species. Its low abundance in the SIZ has been attributed to its inability to survive enclosure within the confines of the brine channels in sea ice (Scharek 1991). *Fragilariopsis kerguelensis* frustules are by far the most abundant in the silica ooze accumulating under the ACC (Zielinski & Gersonde 1997).

Thalassiothrix antarctica is a needle-shaped pennate that can be 5 mm long (the longest of all diatoms) but only 5 µm wide. It occurs singly or in bunches joined together at one end and has exceptionally thick frustules (1 µm wide) ornamented with prominent sharp barbs 1 µm long. The overall appearance reflects defence against grazers, although the function of the barbs is unknown but speculated on below. The frustules of this species are also prominent in surface sediments of the ACC but most are broken. In several regions of the ocean, layers of densely packed mats of intact *Thalassiothrix* spp. frustules have been found, identifying this genus as a major silica sinker (Kemp *et al.* 2000).

Thalassionema nitzschioides is a widely distributed pennate diatom in the ocean but the form common in the ACC has more robust frustules than those of the subtropical gyres. The rod-shaped cells are joined at the ends at perfect right angles giving the chains their characteristic zig-zag appearance. Its frustules are also common in the ooze belt (Fischer *et al.* 2002).

Corethron pennatum (formerly *criophilum*) is perhaps the most eye-catching diatom of the entire Southern Ocean. In striking contrast, its North Atlantic counterpart *C. hystrix*, albeit of similar morphology, is fragile and easily overlooked in plankton samples. The cells of *C. pennatum* range in diameter and length from 5–20 and 20–200 µm respectively. The cells carry rings of long, stout, barbed spines that sweep back like the ribs of a half-opened umbrella. The spines are hinged at the base and the function of the auxiliary ring of short, hooked spines at one end of the cell is to open the long spines following cell division so that they click into the desired angle of 45° set by the hinges (Crawford *et al.* 1997). This complex engineering demands a specialised function and deterrence of smaller ingestors (grazers) appears to be the most likely purpose. Because the spines are laid down inside the frustule of the parent cell, reduction of cell diameter proceeds more rapidly in the course of cell division than in other diatoms. The original size is restored by auxospore formation following a sexual phase where the cell contents are converted into gametes and the frustules discarded. Mass sinking of empty frustules

following a sexual phase was observed by Crawford (1995) who suggested that such events could explain the monospecific layers of this species found in the sediments of some regions of the Antarctic. Apart from such restricted layers, this species is generally absent from the ooze. Since this species occurs throughout the SO, including the SIZ, and frequently dominates diatom biomass, it must play a major role in transporting silica out of the surface layer.

Chaetoceros spp. of the subgenus *Phaeoceros* differ from those of the other subgenus *Hyalochaetae* dealt with above by their larger size and the presence of chloroplasts inside the long hollow spines that extend outward from the four corners of the rectangular cells. Several, morphologically similar species of *Phaeoceros* prominent in the ACC are again the largest of the genus with formidable spines up to 1 mm long that are covered with minute barbs. These species do not make resting spores and presumably survive the winter as vegetative cells. Because of their large size and long spines they will deter protozoan grazers and also smaller copepods (Verity & Villareal 1986). Their frustules are absent from the sediments but they are likely to be a significant component of vertical flux from the surface layer because the morphology lends itself to entanglement in sinking aggregates.

Thalassiosira lentiginosa is a large, heavily silicified species of this cosmopolitan centric genus. It is widespread in the ACC but has, to our knowledge, not been reported to contribute significantly to diatom biomass. However, its frustules are prominent in the ooze belt, indicating that they are exceptionally resistant to dissolution.

The cosmopolitan genus *Pseudo-nitzschia* spp. comprises many species that are difficult to differentiate under the light microscope. The cells are needle-shaped and joined at their tips to form long chains that can be over 1 mm long. This genus is prominent in the entire Southern Ocean and the largest species occur in the ACC (Hasle & Syvertsen 1996). The frustules are not thick but their high surface to volume (s/v) ratio will confer a Si:N ratio > 1. This genus is absent from the sediments but is likely to contribute significantly to silica flux from the surface layer because of its widespread dominance along frontal regions (Smetacek *et al.* 2002). *Pseudo-nitzschia lineola* contributed c. 25% of the total biomass (50% of abundance) at the end of the iron fertilization experiment EisenEx (Assmy 2004).

The diverse assemblage of species comprising the background diatoms consist of smaller and more fragile forms than the giants described above. So iron-limitation does not necessarily lead to thick frustules. The reason why the largest and most robust cells accumulate the most biomass is most probably due to selective grazing pressure by large protozoa and smaller metazoa as well as salps on the smaller diatoms. The giants thus accumulate biomass by sequestering nutrients from the recycling pool in the course of time. This scenario was postulated to explain stable patterns of dominance of three of the giant species

maintained in the face of heavy grazing pressure of small copepods along the APF over a four week period of summer (Smetacek *et al.* 2002). Although each of the giant dominants contributed > 30% of total phytoplankton biomass in their respective zones, it was apparently the smaller size classes, including the background or recycling diatoms, that bore the brunt of the grazing pressure. This would be an extension of the principles balancing microbial food webs into the size class of microplankton and zooplankton, suggesting that the large majority of the weakly silicified ACC diatom species are part of the recycling system.

Interestingly, the same or morphologically similar species are prominent in the HNLC region of the North Pacific. The role of *Fragilariopsis kerguelensis* is played by the morphologically similar *Denticulopsis seminae* which, together with *Thalassiosira lentiginosa*, also contributes substantially to the diatom ooze accumulating under this region (Sancetta 1982). The genera *Corethron* and *Pseudonitzschia* are also prominent in the surface layer. The striking similarity in ecosystem structure of the two high-latitude HNLC regions is further evidence that nutrient uptake efficiency, hence growth rate, is not the decisive factor determining the contribution of the various genera to the microplankton component of recycling systems. That the frustules of these species are indeed the major contributors to vertical flux was demonstrated by sediment trap catches (Takahashi 1997).

Metazooplankton grazers

Up to the early nineties it was believed that phytoplankton biomass accumulation in HNLC regions was controlled by grazing pressure, implying that this factor alone could suppress bloom development (Parsons & Lalli 1988). Differences in the life cycles of the dominant copepods in the HNLC North Pacific and North Atlantic were suggested to be the prime cause for a recurrent spring bloom in one ocean and its absence in the other (Parsons & Lalli 1988). The differences in overwintering strategies of the copepods were related to differences in the depth of winter mixing (Evans & Parslow 1985). In a later version, Frost (1991) invoked protozooplankton as an added factor in the grazer-control hypothesis. Interestingly, the annual cycles of zooplankton biomass and the relative contribution of the different groups in the two oceans vary by less than a factor of two with biomass of the North Pacific zooplankton higher than in the North Atlantic (Parsons & Lalli 1988). This indicates that oceanic zooplankton are geared to the recycling system and that the diatom bloom does not have a lasting effect on them.

All major zooplankton groups are represented in the SO, implying that the grazer populations have adapted wholesale to the cooling process. As in other ocean regions, copepods are by far the most abundant zooplankton and

generally contribute > 50% to total metazoan biomass, followed by euphausiids and salps (Voronina 1998). Pteropods and appendicularians can be regionally and seasonally important but are not considered here. All these groups feed on phytoplankton and protozoa directly, albeit with widely differing feeding modes. Copepods are the most selective as they capture, examine and ingest prey items individually at rates faster than can be followed by the human eye (Strickler 1982). The other herbivores are much larger and collect suspended particles indiscriminately by using different techniques to concentrate them from the water.

Pelagic copepods span an order of magnitude in size and, despite the many species that occupy different ecological niches, they are of strikingly similar shape (Huys & Boxshall 1991). It has been argued that the evolutionary success of the copepod shape is due to its superior escape ability (Verity & Smetacek 1996). Approaching predators are sensed by the long antennae and powerful paddle-shaped thoracic appendages enable the copepods to jump out of the way (Yen 2000). Copepods crush their food prior to ingestion with powerful mandibles edged with silica that are suggested to have co-evolved with diatoms. Before the discovery of the important role of protozoa, it was believed that copepods were the main grazers of diatoms. But it has since been established that copepods preferentially prey on the larger protozoa (Stoecker & Capuzzo 1990, Gifford 1991, Sanders & Wickham 1993), particularly ciliates, based on the microbial community (Atkinson 1996, Lonsdale *et al.* 2000). Clearly, smaller diatoms will be a welcome addition to their diet. The fact that copepod faeces are generally packed with crushed but also whole diatom frustules does not mean that diatoms are the sole diet as most protozoa, with the exception of tintinnids and armoured dinoflagellates, do not leave identifiable remains in the faeces.

The cosmopolitan genus *Oithona* is the smallest and most ubiquitous (Paffenhöfer 1993). Its feeding apparatus indicates that it selects food items in the microplankton range, although its small size will set an upper limit to the particles it can handle and the frustules it can crack (Hamm *et al.* 2003). Although *Oithona* feed on a wide range of particles, they have been shown to also feed on faecal pellets of larger copepods (Gonzalez & Smetacek 1994). This behaviour will retard vertical flux from the mixed layer and contribute to the recycling system. Indeed, despite their high sinking rates, only a small percentage of copepod faeces sink out of the surface layer (Gonzalez *et al.* 1994, Dagg *et al.* 2003). Various small and medium-sized species contribute the bulk of copepod biomass south of the APF, although only one of these species (*Calanoides acutus*) has a life cycle in which the final copepodite (subadult) stage overwinters at great depth. Overwintering in the other species seems to be more flexible with parts of the population present in an active stage in the surface layer

throughout the winter (Schnack-Schiel & Hagen 1994).

Copepod biomass appears to vary widely and generalizations are difficult to draw (Voronina 1998). Foxton (1956) reported that average biomass was relatively high throughout the year, suggesting that recruitment more or less balanced mortality. Grazing pressure as a function of available food also appears to vary widely. By and large grazing pressure increases with decreasing food supply, implying that it is highest during HNLC conditions. The fact that the biomass of large, tough diatoms increases when iron limitation is alleviated, indicates that selective grazing pressure of copepods is a major factor shaping species dominance of the microphytoplankton assemblage. A survey carried out along the APF revealed copepod biomass of 7 g C m^{-2} (Pollard *et al.* 2002) which was in the same range as phytoplankton biomass of which 75% was contributed by giant diatoms (Smetacek *et al.* 2002).

Different euphausiid species are characteristic of the different water masses but only *E. superba* appears to play a major role as a grazer of phytoplankton. Euphausiids capture water parcels and filter them through sieve-like maxillipedes which can retain particles $> 6 \mu\text{m}$ efficiently. The ingested food is crushed in a muscular gizzard lined with teeth reminiscent of copepod mandibles (Suh & Toda 1992). Most of our knowledge of euphausiid ecology is based on *E. superba* which is reported to feed on a wide range of food items including microplankton, copepods and other euphausiids (Atkinson *et al.* 2002). Swarms of euphausiids are often encountered in the HNLC ACC but the percentage of the population present as solitary individuals or in swarms is not known (Dubischar & Bathmann 1997). Clearly, swarms will exert considerable local grazing pressure but, because of their patchy distribution, their effect on microplankton is also likely to be patchy. In any case, adult euphausiids are not likely to be deterred by the giant diatoms, with the possible exception of dense aggregations of *Thalassiothrix*.

The regions where blooms occur are the ones that support the proverbially large stocks of mammals, birds and squid based on the "food chain of the giants". However, even if we assume a very high transfer efficiency of 10:1 from phytoplankton to krill, the annual food demand is enormous as this simple calculation based on conservative estimates will show. Thus the food requirements of the whale stock prior to whaling (190 million tonnes of krill yr^{-1}) (Laws 1977) requires a total krill stock size of at least 600 million tonnes, equivalent to 12 g C m^{-2} for the high productive areas (5 million km^2 , the extent of the SIZ is 20 million km^2). This krill stock will require for its maintenance and recruitment an annual production of $\sim 1.5 \text{ g C m}^{-3}$ (ecological efficiency 10:1) over the 80 m mixed surface layer, equivalent to nitrate consumption of $\sim 19 \text{ mmol m}^{-3}$. But the nitrate content in the productive regions of today's ocean rarely sinks below 10 mmol m^{-3} , indicating that maximum new production averaged over the regions is

$c. 20 \text{ mmol m}^{-3}$ nitrate. Clearly much of the food of krill will be based on regenerated production, implying that much of the nitrate taken up is passed on in the surface layer as ammonia to the regenerating community.

Krill stock size estimated from net catches and acoustic surveys, and extrapolated over the known krill areas, range between 80 and 1000 million tonnes (Everson *et al.* 1990, Nicol *et al.* 2000). A recent assessment of krill net catches since the *Discovery* era indicate a drastic reduction in krill biomass in the SW Atlantic in the last 30 years (Atkinson *et al.* in press). The biomass of salps in contrast has increased in the same area. Since salps are more abundant in HNLC areas than in the high productive regions favoured by krill (Pakhomov *et al.* 2002), the trend could be due to a decline in productivity in the SW Atlantic. Clearly this alarming development requires dedicated investigation.

Salps are very different to the crustacean zooplankton because, for their size (0.5–10 cm and up to 1 m in chain), they are slow-moving and have high reproductive rates achieved by vegetative budding of adults. Although this ability should have its greatest advantage in developing blooms, salps are most abundant under the impoverished conditions prevailing in the AZ (Pakhomov *et al.* 2002). They maintain their barrel-like shape by means of a hydroskeleton and an external cellulose-like cuticle made of tunicin and are wrongly regarded as gelatinous (Godeaux *et al.* 1998). They swim, breathe and feed by pumping water through their body by rhythmic contraction of transversal bands of muscles lining the cuticle (Madin 1974). Particles down to the picoplankton size class are collected by pressing the water through their feeding net. This feeding mode is highly effective at collecting small particles indiscriminately (Le Fèvre *et al.* 1998) but its major drawback is that increasing particle loads result in clogging of the fine meshed sieve. Salps can reverse flow and flush out the unwanted particles but long cells with barbs might well be difficult to dislodge. High concentrations of large diatoms (e.g. *Corethron* spp. and *Thalassiothrix* spp.) are likely to deter salps as clogging of the pharynx will eventually result in starvation (Harbison *et al.* 1986).

Metazoan predators

All the major invertebrate carnivore groups - coelenterates, ctenophores, chaetognaths, polychaetes, amphipods and gastropods - are present throughout the SO, each group represented by a few species (Boltovskoy 1999). Hence, the overall invertebrate zooplankton assemblage is similar to that of other oceans, although the adults tend to be larger than elsewhere. However, it is the vertebrate carnivores that are very different. Surface-living planktivorous fish characteristic of the Arctic such as clupeids, capelin and polar cod are absent (Rodhouse & White 1995) and their potential food - crustacean zooplankton - is eaten by baleen whales and squid. Since all the phyla are represented, even

in the coldest water around the continent, temperature *per se* does not appear to be the limiting factor.

Not much is known about the trophic fate of the abundant salp populations in the ACC (Pakhomov *et al.* 2002) but their remarkable transparency suggests camouflage against highly effective visual predators. Salps are too voluminous to be ingested whole by predators of similar size but, once shredded, can be ingested by a predator of the same size range. The muscles and gut will be valuable food but not the cellulose cuticle. A major predator of salps in the ACC is the hyperiid amphipod *Themisto gaudichaudii* (Hopkins 1985). This robust carnivore is abundant in the ACC (Kane 1966) and its large eyes and grappling appendages are well suited to hunting and handling salps. The most abundant squid *Illex argentinus* of the South Atlantic is reported to feed almost exclusively on *T. gaudichaudii* (Ivanovic & Brunetti 1994) off the Patagonian shelf. Squid are well equipped with beak and tentacles for coping with the robust amphipods. The role of squid in the SO is enigmatic but there is no question that this group is much more abundant than in the Arctic, which may be related to the absence or presence of large fish stocks respectively (Rodhouse & White 1995). The magnitude of this trophic link from microbes, salps, to amphipods and squid needs to be investigated. Such a food chain would be of low efficiency but could explain the presence of top predators in the iron-limited ACC.

Implications for biogeochemistry

The fact that microbial systems limited by macronutrients or iron have similar qualitative and quantitative structures and function at much the same rates ocean wide, suggests that organism interactions in the mortality environment, rather than the chemistries and physiological functions of the respective limiting nutrients, govern the ecology of balanced systems. The high degree of phylogenetic diversity reflected in the many lineages present in this system apparently has a stabilizing function on its structure. Its ubiquity suggests that this system represents an optimal solution to life in a viscous environment and is hence evolutionarily conserved. The interesting point is that the overall slowdown in physiological rates and the increase in viscosity with declining temperature down to the freezing point is not reflected in a corresponding trend in the relative proportions of the components of the microbial community, including the pools of dissolved and non-living, particulate organic matter, the latter expressed in the particulate organic carbon:chlorophyll ratio (Bathmann *et al.* 1997, Lochte *et al.* 1997).

The efficiency of remineralisation of organic matter by SO microbes, protozoa and metazoa is reflected, at the most general level, in the efficiency of retention of nutrients in the mixed layer and the corresponding weakness of the biological carbon pump across the ACC. Only about 15% of

the nitrate but > 75% of silicic acid upwelling along the southern divergence is lost to the deeper ocean in the course of its northward transport across the ACC and subsequent subduction as Antarctic Intermediate Water (Falkowski *et al.* 1998). The amount of organic carbon produced only by those diatoms whose frustules sink out in this 2–4 year period, assuming a Si:N ratio of 2, is equivalent to the entire nitrate inventory, i.e. *c.* 100 g C m⁻² (assuming a 60 m mixed layer depth). The total production, i.e. including that of diatoms whose frustules are recycled and the non-diatom phytoplankton of the microbial network, will be several times this figure. These rough calculations indicate that the magnitude of turnover by the microbial network and zooplankton is substantial, and that a significant amount of biomass should be available for channelling to higher trophic levels.

This conclusion does not necessarily imply that the fate of SO blooms is to be recycled in the surface layer, in contrast to the situation in the North Atlantic and along continental margins with their high carbon export production. Mass sinking of living cells, spores and phytodetritus is the common fate of iron-replete blooms in these regions (Smetacek 1985) and similar sinking events are reported from the SO (Bodungen *et al.* 1986, Wefer 1989). Fluff layers containing intact phytoplankton cells have also been found on the SO floor (Beaulieu 2002). However, blooms in other oceans are generally terminated by nitrate or silicate exhaustion. This is the exception in the SO and has only been reported from situations where shallow surface layers promoted high accumulation rates (Smetacek *et al.* 1992). So the effect of deep mixed layers in iron-replete, unprotected waters would be to lower accumulation rates and prolong the residence time of Antarctic blooms, which might be one of the reasons why a greater percentage of bloom biomass is eventually channelled up to higher trophic levels.

Another reason discussed by Verity & Smetacek (1996), can be sought in the biology of krill which enables it to gear such exceptionally high standing stocks to the regions of high productivity. The bulk of krill faeces tend to be recycled in the surface layer, despite their potentially high sinking rates (Gonzalez 1992). However, substantial amounts of krill faeces have been collected in sediment traps below the mixed layer suggesting that their faeces can contribute to flux, possibly when the capacity of faeces utilizers is saturated (Bodungen *et al.* 1987, Gersonde & Wefer 1987). Since krill is capable of easily handling all diatoms, including the giants and large colonies of *Phaeocystis*, accumulation of the latter could well reflect the extent of krill grazing pressure. This is probably the reason why the giant diatoms and *Phaeocystis* do not accumulate in the surface layers of productive regions where krill are the dominant grazers.

In striking contrast to the diatom ooze underlying the HNLC ACC, which is dominated by the frustules of giants,

the sediments underlying the productive waters of the continental margin have higher carbon contents and are dominated by the small resting spores of the bloom-forming *Chaetoceros* species (Crosta *et al.* 1997). These spores are also prominent in sediments throughout the productive regions of the ocean. Clearly by virtue of their resistance, these spores are by and large the only microfossils that document the presence of iron-replete blooms in overlying waters and are hence of value in palaeoceanographic research (A. Abelmann *et al.* unpublished data). The association between *Phaeocystis* and *Chaetoceros socialis* mentioned above would suggest that spores of the latter are also a proxy for *Phaeocystis* blooms, although the relationship is not obligatory.

The biomass produced by blooms drives the ocean's biogeochemical pumps. Hence a quantitative understanding of the mechanisms selecting species composition of bloom biomass is a prerequisite to modelling the role of productivity in regulating atmospheric carbon dioxide levels. The species composition of the bloom is bound to have an effect on the amounts and ratios of biogenic elements exported from the surface layer. For instance, species that form resting spores following nutrient exhaustion and sink out of the surface layer will export much more carbon than species that maintain their presence in the mixed layer throughout the year. The better defended of the latter will maintain higher stocks than the less defended that are vulnerable to attack by a greater range of grazers. The persistence of the bloom induced by the iron-fertilization experiment SOIREE for over a month (Boyd *et al.* 2000) could well be due to the *F. kerguelensis* population. Cell shape, size and other properties such as presence or absence of spines affects the composition and nature of vertical flux (e.g. algal aggregates or faecal pellets). Obviously grazing must play a decisive role in determining the fate of biomass and its role in

biogeochemical cycles.

Conclusions and perspectives

The overall conclusion that can be drawn from this broad overview of the structure and functioning of pelagic ecosystems is that organism interactions played out in the mortality environment have a major role in shaping the evolution of plankton and hence biogeochemical cycles. The fact that only a few phytoplankton species, of widely differing shape and size and from widely disparate genera, express the growth rates necessary to break out of the grazer gauntlet and form blooms indicates that this type of boom-and-bust life cycle is one of several, if not many, life cycle strategies. In the bloom-forming life cycle, population size fluctuates annually over three or more orders of magnitude. In all the other plankton species, annual fluctuation in population abundance is constrained within two or less orders of magnitude. These life cycles can be differentiated along a gradient extending from fast-growing, heavily grazed species to slow-growing, because heavily defended ones. The bulk of the species fall somewhere in between, so it is the properties of the extreme species that accumulate biomass by virtue of fast growth rates or effective defences that need to be examined more closely if we are to gain an understanding of their mechanistic role in trophic transfer and biogeochemical cycles.

Small copepods and salps are the top grazers of the microbial food web that, in view of their high biomass in the HNLC ACC, must in turn support as yet unknown higher trophic levels. We postulate a food chain leading via amphipods to squid. Studies carried out in lakes indicate that the length of the food chain is a function of the area of the lake (Post *et al.* 2000). It follows that the vast areal extent of microbial communities of the Southern Ocean should be capable of supporting food chains extending to

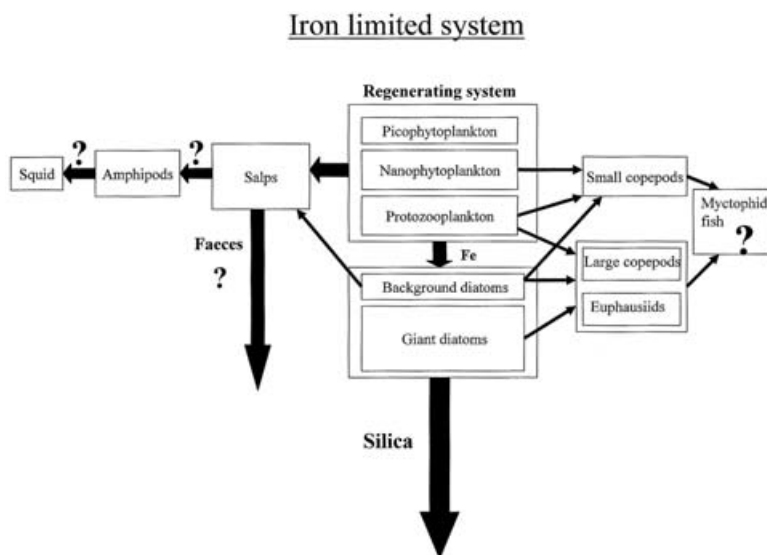


Fig. 1. Schematic representation of an iron-limited, silica-sinking, open ocean system. The regenerating system comprises bacteria (not shown) and piko- and nanophytoplankton together with their protozoan grazers. Salps and copepods graze on this system but also on the weakly-silicified “background diatoms”, whereas the “giant diatoms” are mainly grazed by large copepods and euphausiids. Vertical flux consists mainly of silica. The composition and quantitative role of salp faeces is unknown, as is also the fate of salp biomass. The magnitude of the food chain leading from salps to amphipods and squid relative to total production needs to be ascertained.

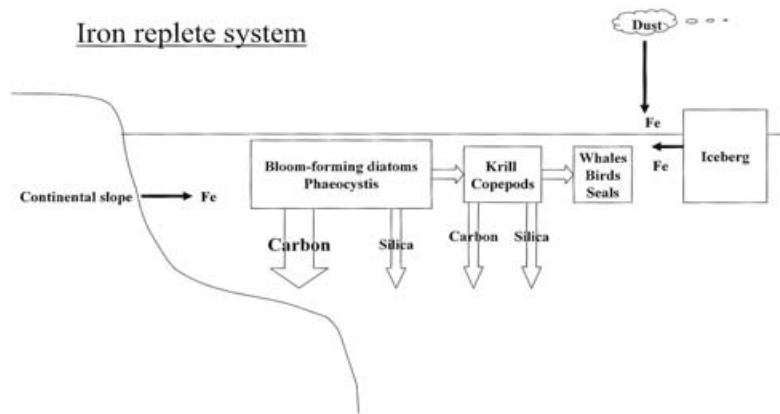


Fig. 2. Schematic representation of an iron-replete, carbon-sinking phytoplankton bloom system. Iron is supplied from land run-off and shelf sources and in land-remote areas from aeolian dust or melting icebergs. Vertical flux comprises diatom cells, phytodetritus or faeces of crustacean zooplankton with lower Si:C ratios than in iron-limited systems.

top predators such as squid, albeit at population sizes much lower than those in the krill-dominated, iron-replete regions.

The biomass of the giant, heavily silicified diatoms that accumulate by sequestering nutrients from the microbial network is eventually recycled in the surface layer, presumably by larger copepods and euphausiids. But their robust frustules sink out of the surface layer, resulting in retention of N and P but loss of Si. These species are the main silica sinkers. The mode of loss of biogenic silica can range from individually sinking frustules, aggregates bound together by mucus or compact faeces. It remains to be ascertained how the relative roles of these transport mechanisms vary with the species and what effect they have on the biogeochemistry of the water column and underlying sediments. It should now be clear that the differences in the Si:N ratio between iron-limited HNLC diatoms (Fig. 1) and their iron-replete counterparts in blooms (Fig. 2) is due to differences in the species composition and not the physiology of individual diatom species.

Chemical defences in plankton have not received much attention (Wolfe 2000), and SO plankton even less. It has been suggested that dimethylsulphoniopropionate (DMSP), produced in large quantities by haptophytes including SO *Phaeocystis*, is a herbivore deterrent (Wolfe *et al.* 1997). The active principle is acrylic acid which is lysed from DMSP following cell destruction. The volatile gas dimethylsulphide (DMS) derived from DMSP is reported to play a climate-active role when released to the atmosphere (Charlson *et al.* 1987). Further investigation is required to ascertain the relationship between *Phaeocystis* blooms and release of DMS to the atmosphere and this example highlights the need for species-specific studies of possible defence mechanisms.

A powerful new methodology to test the hypotheses outlined above are *in situ* iron fertilization experiments that enable the study of interactions within ecosystems with their full complement of grazers and pathogens. The SOIREE and EisenEx experiments carried out in the HNLC ACC indicate that the giant diatoms are the first to respond by virtue of their large stock size, but none of the

experiments lasted long enough to enable the fast-growing species to build-up significant biomass (Boyd 2002, Assmy 2004). In the EisenEx experiment, a single fast-growing species, *Pseudo-nitzschia lineola* contributed > 25% of bloom biomass by the end of three weeks. This species and another fast-growing, albeit weakly silicified one - the resting spore forming *Chaetoceros debilis* - had accumulation rates double those of all other species present (Assmy 2004). Interestingly, the same species *C. debilis* grew at exceptionally high growth rates during the SEEDS fertilization experiment in the North Pacific and contributed > 90% of bloom biomass. The experiment ended before the fate of the bloom could be ascertained, but it is very likely that it was followed by mass sinking (Tsuda *et al.* 2003).

It is too early to pass judgement on the fate of iron-induced biomass. Indeed, there is no reason to believe that an artificially induced bloom, if nurtured long enough and over a large enough area, will behave differently to the blooms that occur around the continental margins. The results of the iron fertilization experiment EisenEx indicated a significant increase in biomass of small copepods within three weeks, indicating that the zooplankton were food limited (Henjes 2004). The effect of iron fertilization on higher trophic levels will depend on the locality and duration of the experiment. Thus iron fertilization augmenting the natural iron supply around continental margins or along iron-rich island plumes is likely to increase phytoplankton biomass and attract krill. Clearly much can be learned from experiments carried out in various regions around the Southern Ocean. There is legitimate concern over plans by geo-engineering companies to exploit the HNLC ACC as a CO₂ sink (Chisholm *et al.* 2001). The international community will have to decide how best to deal with such issues. It is the task of scientists to ascertain the long-term effects of any such climate management scheme. For instance an areal intensification or extension of the productive Peninsula plume could well have a beneficial effect on populations of top predators (mammals and birds) if they are food-limited.

The current debate on productivity of the Southern Ocean during glacial times - the iron hypothesis of John Martin

(1990) - is based on interpretations of a range of geochemical proxies that provide conflicting evidence (Sigman & Boyle 2000, Anderson *et al.* 2002). From an ecological standpoint and in view of the well established higher iron supply during glacials (Petit *et al.* 1999), it is hard to imagine that productivity will not have been correspondingly higher. The current impasse between ecologists and geochemists is most likely to be broken by introduction of new and more reliable biological proxies that can best be validated in the context of iron fertilization experiments. An added incentive to carrying out more such experiments is the ideal training ground they offer for the kind of international, interdisciplinary research demanded by Earth System Science investigating global change.

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