
13 Abiotic and Biotic Forcing on Vertical Particle Flux in the Southern Ocean

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13.1 THE SCENARIOS

The objective of this paper is to show the importance of physical, chemical and biological constraints for structuring the pelagic ecosystems (Priddle et al., 1992) and determining the eventual fate of the organic matter (Bathmann, 1991) and the role of zooplankton thereby (Bathmann, 1992). For this, data collected by the author on pelagic system structure, on mechanisms and fluxes within the pelagic realm are, reviewed for various scenarios from different sites in the Weddell Sea in the course of a year. I will start with the description of copepod biology in winter along a transect across the ice covered Weddell Sea and continue by presenting three scenarios for pelagic system structure during austral spring and summer (November to January). An autumn situation completes the course through the annual succession within pelagic Antarctic ecosystems of the Weddell Sea.

13.2 WINTER

Seasonal cycles of the biota in the Southern Ocean are strongly influenced by the dynamics of the $20 \times 10^6 \text{ km}^2$ of sea ice, as $16 \times 10^6 \text{ km}^2$ reform and melt each year. In the Weddell Sea these figures are 10 and $8 \times 10^6 \text{ km}^2$, respectively (Viehoff et al., 1994). Thus, nearly the entire Weddell Gyre is covered by sea ice in winter. Life under sea ice especially when it is covered by snow is limited by light which should result in low or no primary production (Nöthig et al., 1991). However, observations reveal the importance of phytoplankton production in the sea ice which is thought to be $200\text{--}2800 \text{ mg C m}^{-2} \text{ d}^{-1}$ and therefore as much as or even double, the amount which is produced in the open water during this time (Gleitz et al., 1994). New results on zooplankton distribution in winter demonstrate that a great percentage of the copepod population of the central Weddell Sea

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is actively feeding in the winter water directly under the sea ice with grazing rates similar to those of the summer population (Bathmann et al., 1991). Vertical particle fluxes under such conditions in the central Weddell Sea are reported to be the lowest in the world oceans (Wefer and Fischer, 1991). Protozoan grazing and, thus, the production of minipellets in this situation may also be responsible for effective recycling of organic material in the water column (Nöthig and Gowing, 1991). Thus, winter active copepods (*Calanus propinquus*) appear to be an important component to structure the pelagic food web by effectively recycling algae, protozooplankton and other organic material in the upper water column under the sea ice during winter. This might result in a reduced vertical particle flux (Figure 13.1).

13.3 SPRING

During the austral spring, varied circumstances pertaining in different portions of the Weddell Sea basin result in varied ecosystem responses. Three such systems of response have been identified and are described below.

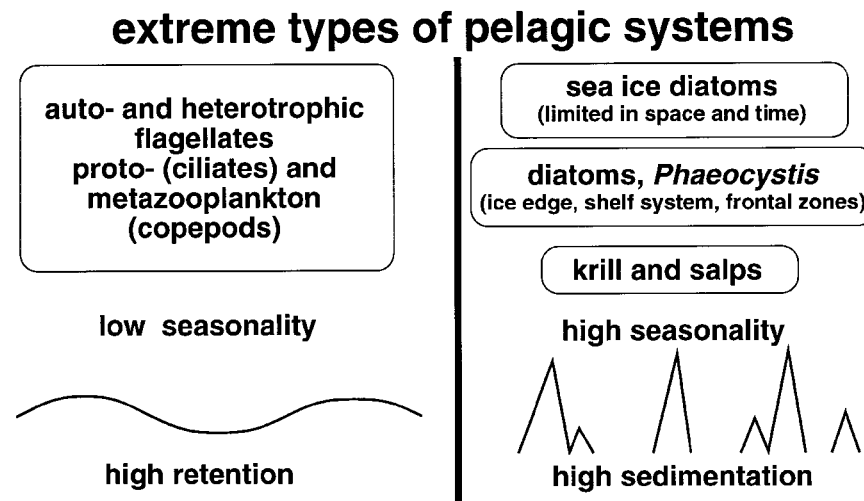


Figure 13.1 Conceptual models of two extreme organizational structures of pelagic ecosystems. Left hand side: recycling system with low annual variability in total biomass and low sedimentation output. Right hand side: export system with large sized organisms creating high biomass blooms which results in high vertical flux.

Under "normal" conditions sea ice cover decreases in the Coastal Current (CC) on the north-eastern Weddell Sea shelves by breaking up and gradual melting. Bathmann et al. (1991) have described five stages in pelagic system succession associated with these conditions of ice retreat and biological production.

1. The first stage (shortly before ice melting) was similar to that described above for the ice covered Weddell Sea with copepods dominating and with little vertical flux mainly consisting of sinking copepod fecal pellets.
2. Shortly after the start of sea ice melting in beginning of January 1989, in the second stage, ice algae sank to at least 500 m water depth (which was the depth of a sediment trap recording sinking material in 2.5 days intervals).
3. Five to 8 days later, during the third stage, euphausiid pellets occurred in the sinking material indicating feeding of krill on released ice algae.
4. The next peak in vertical flux, the fourth stage, was attributed to phytoplankton. The $\delta^{13}\text{C}_{\text{org}}$ values of -32‰ indicated the pelagic origin of this material as opposed to the less negative $\delta^{13}\text{C}$ values (-23‰) of organic material released by the ice.

These latter three stages of enhanced vertical flux resulted in a sedimentation rate of about $100 \text{ mg C m}^{-2} \text{ d}^{-1}$ (Bathmann et al., 1991).

5. The three stages of high sedimentation were followed by low sedimentation of material dominated mainly by minipellets (detected by microscopical observations) and probably produced by protozooplankton (e.g., heterotrophic dinoflagellates, radiolaria, foraminifera; Nöthig and v. Bodungen, 1989) which comprises the fifth stage of pelagic succession.

Thus, ice melting in spring on a continental shelf in the eastern Weddell Sea may induce several stages in the pelagic system succession, with periods of regeneration and export (Figure 13.1) *sensu* Smetacek et al. (1991).

A completely different situation of spring plankton development under sea ice is reported for the south-eastern Weddell Sea in austral spring 1990/91. During the spring, melting of sea ice was very much reduced in the Weddell Sea (Viehoff et al., 1994) and strong northeasterly winds forced the remaining ice into the interior of the Weddell Sea. In the midst of this sea ice (strongly compressed and deformed) the research ice breaker *Polarstern* stuck for about 14 days, being incapable of moving out (Bathmann et al., 1992). Primary production was very low in the ice and in the surface waters of this area ($< 100 \text{ mgC m}^{-2}$; Gleitz et al., 1994). Microbial activity was nearly as high as primary production but only in the sea ice and in melt water pools on top of, and in-between, the ice (Grossmann et al., 1994). The vertical particle flux measured with sediment traps attached at 4 and 50 m below the sea ice showed a decrease in the vertical flux of carbon and nitrogen as well as in chlorophyll with depth. The composition of the material changed from ice algae (at 4 m) to krill fecal strings at 50 m indicating heavy krill grazing in the upper 50 m water column directly under the ice (Gonzalez et al.,

1994). These authors confirm their conclusions by presenting data demonstrating that the maximum concentrations of krill fecal string were dispersed in the upper 100 m of the water column. Cyclopoid copepods (of the genus *Oncaea*) probably were feeding heavily on these pellets, and reduced pellet sedimentation significantly, especially where the numbers of cyclopoid copepods exceeded some 30 ind. m⁻³ (Gonzalez et al., 1994). In this scenario of low primary production but heavy sea ice coverage in spring in the Southern Ocean, vertical particle flux was strongly controlled by zooplankton grazing activity either on ice algae, sinking algal material or fecal matter.

A third situation of spring bloom impacts on sinking matter was recorded from the ice free areas at the Polar Frontal zone (PFz) at about 48°S 6°W (Smetacek et al., 1994). The investigations were carried out within the framework of the JGOFS Southern Ocean Process Study and one of its main conclusions is briefly summarized below. The full details of the results will be presented elsewhere. The sedimentation within the three domains in the Marginal Sea Ice Zone (MIZ) at 60°S (i. at the northern border of the Weddell Gyre, ii. in the southern branch of the Antarctic Circumpolar Current (ACC) and, iii. in the PFz) was controlled by three different factors.

In the MIZ, deep water mixing overrode the small potential effect of water column stabilization induced by melt water from the sea ice (Bathmann et al., 1994) with the result that phytoplankton biomass accumulation (spring bloom at the ice edge) did not occur. This situation probably was prolonged until at least mid December (Lancelot and Veth, 1995). In the southern ACC, huge swarms of the aggregating form of *Salpa thompsonii* exploited the phytoplankton with grazing rates well above areal primary production (Dubischar and Bathmann, 1996). Phytoplankton biomass was dominated by small auto- and heterotrophic nanoplankters (Detmer and Bathmann, 1996); export of material from this system due to sedimentation was very limited (Rutgers van der Loeff et al., 1996). So we postulate that salp grazing in the southern ACC in spring was effectively structuring the pelagial toward a highly retentive system (Figure 13.1).

Zooplankton grazing in the area of the PFz was, in contrast, less than 5% of primary production. In the PFz three distinct phytoplankton blooms developed (Bathmann et al., 1996) which were at least partially favored by the naturally high concentrations of suspended iron (de Baar et al., 1995). The dissolved iron possibly was transported into the waters of the PFz by a jet stream (Veth et al., 1995). These blooms finally sank out of the surface ocean layers as intact senescent cells (Rutgers van der Loeff et al., 1996). The blooms were composed of different algae species of which the sinking of one (*Fragellariopsis kerguelensis*)

not only transported organic matter but also silicate (opal) in its thick frustules during sinking (Bathmann et al., 1996).

In conclusion, the spring situation of pelagic system structure and the pathways and magnitude of the flux of organic matter in the pelagic systems in the Weddell Sea, Antarctica very much depend on physical conditions (sea ice distribution; surface water mixing; light regime), chemical constraints (micronutrient concentrations), algal species composition (silicified versus non-silicified species), and the composition and impact of various zooplankton grazers. Superimposed and probably even more important is the gearing of those factors in space as well as in time for structuring of the pelagic ecosystems and determination of the eventual fate of the organic matter (recycled *versus* exported; Figure 13.1).

13.4 AUTUMN

Here I concentrate only on one of the various scenarios from the literature for biomass pathways at the end of the growing season in the Weddell Sea. Bathmann et al. (1992) reported a high phytoplankton accumulation ($> 4 \text{ mg chl a m}^{-3}$) in the Coastal Current (CC) over the shelves of the Lazarev Sea (eastern Weddell Sea). This high phytoplankton biomass could accumulate in the absence of strong zooplankton grazing and under stable hydrographical conditions. One of the numerous autumn storms eventually compressed the surface waters of the CC containing this biomass near the shelf ice coast and subsequently dispersed the surface water and its plankton biomass to greater water depths (shelf depth is between 250 and 500 m in this area). One consequence was a homogenous distribution of phytoplankton biomass throughout the entire water column with the subsequent input of most of this phytoplankton biomass to the benthos ($13 \text{ gC m}^{-2} \text{ week}^{-1}$; Bathmann et al., in prep.). There, plankton biomass was buried and partially utilized by the infauna. In part, the plankton material also was transported further down slope on the continental rise (F. Riemann pers. communication).

In the upper water column phytoplankton growth potential was still as high as during summer (Gleitz et al., 1994) but ice formation cleared the surface water of algae which were incorporated and concentrated in freshly forming sea ice (Grossmann et al., 1994). The growth rates of the new ice community were equally high compared to the rates measured from the planktonic algae (Gleitz and Thomas, 1993).

13.5 CONCLUSION

This short article compares some scenarios describing the variability of plankton succession and of the vertical particle flux observed in the Weddell Sea. These scenarios result from the interaction of various biological and physico-chemical factors which match or mismatch in space and time. It has to be stressed that the examples given are selected from the Weddell Sea, one of the many areas of the Southern Ocean. Similar conclusions were reported from nearby areas such as the Weddell-Scotia Sea (Bianchi et al., 1992). Very little information is available on the production and fluxes during winter and about biological patterns and processes from some regions of the Southern Ocean; one area of interest in this context is the south-western and permanently ice covered Weddell Sea. On the other hand, the biological processes we recently discovered at the Polar Front changed our paradigm of pelagic system organization in Antarctic waters that the melting sea ice positively influences biological production. We now have evidence to believe that superimposed on hydrographical and chemical constraints on phytoplankton blooming and sedimentation, the biological impact of grazers (micro- and macrozooplankton) plays a major role in pelagic system structuring in Antarctic waters.

13.6 ACKNOWLEDGMENTS

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