Biotic processes controlling vertical export of biogenic matter from marine pelagic systems

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Pelagic systems are potentially capable of retaining and recycling all biogenic material, although some losses due to sinking particles inevitably occur. However, in coastal areas and on shelfs a major proportion of the phytoplankton production is usually supplied to the sediments (e.g. Smetacek *et al.*, 1984). Relating primary production in the surface layers quantitatively to vertical particle flux is difficult in the open ocean because only a small percentage of the total production (e.g. large phytoplankton cells, various kinds of aggregates and faecal pellets) is lost annually via sinking. A "pelagic mill", grinding suspended and sinking particles in the mesopelagic zone of the ocean, is usually effective and regulates vertical flux. The physical environment determines nutrient availability (and consequently new production), influences the cell size of phytoplankton, the aggregation of sticky particles and hence the particles potentially available for sedimentation (Alldredge and Jackson, 1995). Thus there is a strong impact of *bottom-up regulation* of vertical flux, determined by abiotic control. However, there is also an obvious, but in marine ecosystems so far less considered, *top-down regulation* which is entirely determined by the biota. The strength and variability of top-down control is an important driving force for the fate of organic matter which is reflected in observed geographic and interannual variability. Differences in patterns and magnitude of export production in various pelagic ecosystems may be unexplained when exclusively regarded from an abiotic and bottom-up perspective.

The relationship between phyto- and zooplankton governs vertical flux seasonality, and zooplankters with different life cycles and feeding strategies further modify the principle patterns of export production (Wassmann *et al.*, 1991). The relationship between various zooplankton communities and life patterns of major forms has not been adequately studied in order to understand entirely the regulation of export of organic matter from the upper layer (Verity and Smetacek, 1996). For example, herbivores with life-cycle strategies which involve over-wintering of large biomass and predictable seasonal appearance (copepods, euphausiids) will have a different impact than opportunistic organisms with very low overwintering biomass (e.g. salps, pteropods). In some areas, predictable seasonal appearance by over-wintering zooplankton can be reduced, amplified or be stochastic due to inter-annual variations in advection. The role of omnivory and carnivory as well as the coupling between the microbial loop, meso-zooplankton and suspended biomass on vertical flux is poorly known. Also, the role of different zooplankton functional groups to promote (e.g. grazing and production of large faecal pellets) or remove sinking matter (e.g. grazing on aggregates and processes such as coprophagy) influence the export and retention efficiency of various pelagic ecosystems.

It is repeatedly assumed that large, ungrazed cells, aggregates and some faecal pellets dominate vertical export in the upper layers, in particular at the end of major phytoplankton blooms. This implies that the physical environment and phytoplankton primarily determine vertical export of biogenic matter. This opinion find support in the notion that so far a majority of vertical flux studies have been carried out in areas where meso-zooplankton is excluded from over-wintering or were other processes result in a mis match between phyto- and zooplankton production. The assumption that abiotic and bottom-up regulation of vertical flux predominates gains also support by the fact that many of the biogeochemically oriented vertical flux investigations with long-term deployed multitraps were rarely accompanied by extensive planktonic research. This implies that the vertical export of carbon is estimated, but less is known about the composition of the sedimented matter, let alone the plankton dynamics above the sediment traps which control the vertical flux. To understand the impact of top-down regulation on vertical export of biogenic matter suggests that greater emphasis on research focused on planktonic food webs is needed in basically biogeochemically oriented approaches.

The emphasis on biogeochemical focused, long-term measurements of vertical flux (e.g. Berger *et al.*, 1989) has not improved the understanding on the *regulation* of vertical flux, but indicates what orders of magnitude can be expected and what seasonal patterns. This implies that the conspicuous amounts of vertical flux data from all over the oceans are interpreted on the basis of a rather vague and insufficient theory of vertical flux regulation at present. Biological oceanographers may have a naive attitude in understanding transport and behaviour of biogenic elements in the ocean when it comes to physico-chemical processes. However, biogeochemical approaches easily ignore the implications of the term 'bio' preceding geochemistry. Retention and export food chains and in particular top-down regulation play a pivotal role for the regulation of vertical flux of biogenic matter (Wassmann, 1997) and much of the composition and seasonal cycling of biogenic fluxes may stay unexplained without a good knowledge of the evolved biotic control processes. This conclusion may have crucial consequences for future biogeochemical programmes investigating pelagic-benthic coupling in the ocean. Phyto- and zooplankton as well as process-oriented research endeavours have to be the focal point of future research if the current comprehension of export from and retention in the upper layers is going to make distinct progress.

The presentation considers the role of export and retention food chains for pelagic-benthic coupling by evaluating different food chain scenarios and processes such as aggregation, grazing and zooplankton-mediated fluxes. The consequences of grazing on phytoplankton by different zooplankton types for the vertical export of particulate organic matter from the euphotic zone are discussed. Reference is made to existing data and algorithms regarding primary production and vertical export of carbon from the euphotic zone, both on annual and daily time scales. Examples regarding the role of nutrient addition, removal of pelagic carnivores and zooplankton grazing for vertical flux are presented. It is speculated how variable grazing impact of micro- and meso-zooplankton, as well as herbivorous, omnivorous and carnivorous feeding strategies of meso-zooplankton could compete with aggregation during phytoplankton blooms and influence export fluxes. It is concluded that the transport of particulate organic matter to depth not only depends on bottom-up regulation as determined by abiotic control and physical forcing, but also on the structure and function of the prevailing planktonic food web. Scenarios are presented which indicate that biotic and top-down regulation play a pivotal role for the regulation of vertical flux and that some of the patterns of biogenic vertical export may remain unexplained when exclusively interpreted by abiotic and top-down regulation.

References

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