

**Marine snow, mucus aggregates and bottom anoxias: Consequences for benthic-pelagic coupling**

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In the years 1988 and 1989 floating carpets of gelatinous substances ("mucilage") covering great parts of the Northern Adriatic shocked fishermen, tourists, politicians and scientists alike. At least the latter had known large mucus aggregates as an episodic feature of the summer water column for many years and fishermen's tales of nets clogged by gelatinous masses ("mare sporco") are known from several places for the last century.

Several conflicting hypotheses have been put forward for the observed phenomena and a collaborative research project in the framework of the ARGE Alpen Adria has been implemented involving research groups from Italy, Croatia, Slovenia and Austria. We want to review here the state of knowledge of the effect of this phenomenon on the benthos and on exchange processes between the sea bottom and the water column.

Towards the end of spring phytoplankton blooms small flakes appear derived from extracellular released organic matter by phytoplankton algae. In a well mixed water column these flakes settle to the bottom and are consumed and remineralized by benthic biota. When the end of the spring bloom and the production of the initial flakes extend into the stratified period typical of the North Adriatic summer, the flakes are prevented to settle through the pycnocline into the cold and dense bottom water and remain in the superficial water column. Colliding flakes may merge into larger aggregates, forming "stringers" and "clouds" constituting spatial heterogeneities within the water column, showing enrichment factors for nutrients, phytoplankton, bacteria and flagellates of several orders of magnitude whereas the ambient water appears to be depleted in nutrients and biota. Larger aggregates efficiently trap inorganic (e.g. clay) or organic particles (such as fecal pellets) on their way to the bottom and prevent their sedimentation, effectively closing off the bottom from the input of organic matter. Towards the end of the summer the "clouds" - having attained a size exceeding 1 m - collect at the pycnocline in depths between 15 and 20 m. They are laden with trapped particulate organic and inorganic matter, their interior is anoxic with high concentrations of hydrogen sulfide. Within a few days they settle through the pycnocline and arrive on the bottom of this shallow sea.

Settling clouds suffocate filter feeding epibenthic fauna, such as sponges and ascidians. The ensuing hypoxic or even anoxic conditions, due to the oxygen consumption during the breakdown of this pulse of organic matter in the confined bottom water layers, leads to mass mortalities of the macrobenthos over hundreds and even thousands of square kilometers within a few days. The consequence of the formation of the mucus aggregates thus becomes the cause of bottom anoxias. The regeneration of these bottom communities consisting of large perennial species takes many years and has not been completed in many locations affected within the last decade due to recurrent oxygen crises, thus depriving the system of a possible regulatory mechanism for pelagic biomass production through the grazing action of the benthic suspension feeders. In this way the consequences of bottom anoxias may contribute to the causes of further blooms and mucus aggregate formation in a vicious circle.

Although Marine Snow is an ubiquitous phenomenon in all seas, mucus aggregates of the size and extent as those described above have rarely been described outside the Northern Adriatic. Its origin lies in the pelagic system. Microphytobenthos production - which has been suspected as the cause of the "mare sporco" cannot account for the observed large scale phenomena due to its small magnitude. The generation of extensive subpycnocline anoxias - which is also typical for other areas experiencing similar water column conditions (Skagerrak, Gulf of Mexico, Chesapeake Bay) - interrupts the usual pathways coupling the pelagic and benthic systems. The previously existing regulatory feedback between pelagic production and benthic consumption by large sized suspension feeders is replaced by a one-way forcing of the benthic biota by escalating pelagic processes.