

SIMULATION OF RECENT CHANGES  
IN THE BLACK SEA PELAGIC FOOD WEB STRUCTURE  
DUE TO TOP-DOWN CONTROL BY GELATINOUS CARNIVORES

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ABSTRACT

The immediate direct responses of the severe anthropogenic eutrophication in the Black Sea ecosystem were explosions in the productivity of pelagic microphytes, and stimulation of dinoflagellate growth as the diatom blooms were suppressed. These changes were accompanied by a sharp increase in the number of organisms feeding on mesozooplankton (e.g. *Noctiluca scintillans*, *Aurelia aurita*, *Pleurobrachia pileus*, *Mnemiopsis leidyi*) and a sudden drop in the diversity of zooplankton species in general. In the present work, a series of simulations are presented to explore such changes as took place in structure and functioning the Black Sea ecosystem within the last three decades. Our basic motivation is to understand, by combining the limited available data with model simulations, the nature of trophic interactions between components of the ecosystem at different stages of its evolution within the last three decades in response to nutrient enrichment and a change in the carnivore community.

Using a one dimensional, vertically resolved, coupled physical-biochemical model, the pelagic food web is represented by two groups of phytoplankton (diatoms and dinoflagellates), bacterioplankton, microzooplankton, omnivorous mesozooplankton, carnivorous mesozooplankton (dominated by medusae), the ctenophore *Mnemiopsis leidyi* and the giant omnivorous dinoflagellate *Noctiluca scintillans*. Dissolved and particulate organic nitrogen as well as nitrate, nitrite and ammonium constitute its other components. The model is set up to simulate the 1960's "eutrophication-free" pelagic food web conditions and its modifications during the late 1970's and the late 1980's. For the late 1960's ecosystem with lower nitrogen content and no mass development of gelatinous carnivores in the upper layer water column, the model suggests almost uniform structures for all components of the ecosystem throughout the year.

The phytoplankton community exhibits only its most robust features which are identified as the late winter-early spring bloom and the subsequent late spring bloom associated with the recycled production. The mesozooplankton blooms lag these events by a month. As compared to the forthcoming bloom events during the next decade, they are much weaker. The next simulation investigates how this "eutrophication-free" ecosystem could respond to mass development of gelatinous organisms which are the typical characteristic feature of the Black Sea zooplankton community under eutrophied conditions. When the growth and mortality characteristics of the carnivore group are modified to represent predominantly those of *Aurelia* and *Pleurobrachia*, the ecosystem responds to this change with a late spring-early summer and autumn biomass increase of the gelatinous species and a series of phytoplankton blooms as a result of top-down control on herbivores. The late winter-early spring phytoplankton bloom becomes more intensified. Two successive and longer-lasting phytoplankton blooms take place during the mid-summer and autumn periods. In other words, the phytoplankton blooms are not isolated events any more, but they become more extensive and regular features of the ecosystem.

A decade later, as the nitrate content in the water column builds up as a result of continuous nutrient supply from the anthropogenic sources, this response by the phytoplankton and zooplankton communities becomes even more pronounced. The shares of medusae and *Noctiluca* in the overall zooplankton community are increased. The early spring phytoplankton bloom is followed first by a mesozooplankton bloom of comparable intensity, which reduces the phytoplankton stock to a relatively low level and then by a medusae bloom that similarly grazes down the omnivores. The phytoplankton recover and produce a weaker late spring bloom, which triggers a steady increase in the *Noctiluca* biomass during the mid-summer. As the overall carnivore population decreases in August, the omnivores first and phytoplankton later give rise to two successive blooms during September-October period. This is followed by a secondary *Noctiluca* bloom. All these features are supported reasonably well by a set of in situ measurements performed during 1978 at a station off the Caucasian coast of the Black Sea. The success in the reproduction of many features of this specific data set justifies "optimum" complexity of the model structure and its capability for adequate representation of the Black Sea ecosystem.

Introduction of *Mnemiopsis* into the ecosystem leads to a new type of annual plankton distribution. The annual phytoplankton structure is characterized by three successive and extensive phytoplankton bloom periods in winter, spring and summer months. Winter blooms with that intensity were not reported until the 1990's. The other

interesting feature is the considerable reduction of the *Noctiluca* biomass. The *Noctiluca* peaks also take place two months earlier as compared to the "before- *Mnemiopsis*" period. It seems that the amount of food, which was consumed by *Aurelia* and *Noctiluca* before, is now used to a large proportion by *Mnemiopsis*. However, the numerical experiments indicate that the food competition between *Mnemiopsis* and *Aurelia* has a very delicate balance. One of them may dominate the ecosystem only by minor changes in their growth and reproduction characteristics. The data seem to suggest this is what is actually taking place in the Black Sea within the last ten years.

Overall this study demonstrates the combined effect of bottom-up forcing by antropogenic nitrogen enrichment and top-down control by gelatinous predators on the Black Sea plankton system. In general top-down control is paramount and the gelatinous predators, especially *Mnemiopsis*, might be considered as keystone species. Lower trophic levels exhibit similar annual cycles and amplitudes under low- and high nutrient levels in the absence of the top carnivores, but addition of the gelatinous species reduces mesozooplankton grazing and leads to increased phytoplankton blooms as observed throughout the 1980's-90's in the Black Sea.