



## **Trophic controls on the Black Sea ecosystem: A modelling study**

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A one-dimensional bi-directionally coupled model of lower trophic level and anchovy population dynamics was developed to analyse the mechanisms controlling sharp anchovy and gelatinous zooplankton biomass transitions during the critical period of radical ecosystem transformation from the late 1960s to the late 1980s in the Black Sea. A two-fold increase in anchovy stock from its low ( $\sim 300$  kt) to moderate ( $\sim 700$  kt) regime at the end of the 1960s was related to weakening piscivore predation pressure, slight nutrient enrichment of the basin during early eutrophication phase and competitive exclusion of gelatinous carnivores. After maintaining the moderate stock regime during the 1970s, the next transition to the high anchovy stock regime ( $\sim 1500$  kt) during 1979–1980 was caused by additional nutrient enrichment of the water column due to growing influence of eutrophication. As the enrichment was building up, jellies started to coexist with anchovy at low biomass levels ( $< 1.0$  gC m<sup>-2</sup>) but they did not yet exert a strong control on anchovy because of their competitive disadvantage of consuming prey at low carrying capacity conditions. The high stock regime ( $> 1000$  kt) persisted until the third transition (1989–1990) that brought anchovy stock back to the low regime ( $\sim 300$  kt) and proliferated the biomass of the alien gelatinous species *Mnemiopsis* up to 3.0 gC m<sup>-2</sup>. The anchovy-*Mnemiopsis* shift was pre-conditioned by eutrophication-induced nutrient accumulation in the subsurface layer and triggered by their more effective transport into the productive surface layer following the switch of regional climate into a severe winter phase during 1985–1987. The resulting enhanced resource carrying capacity together with decreasing adult anchovy stocks due to overfishing led to competitive advantage of *Mnemiopsis* in food exploitation relative to anchovy, growth and reproduction advantages relative to the native gelatinous species *Aurelia aurita*, and stronger predation on anchovy eggs and larvae. Approximately 50% of the anchovy stock depletion was caused by increasing fishing pressure beyond its threshold 1.5 y<sup>-1</sup> and the rest by competition with and predation by *Mnemiopsis*. Nonlinear coupling of these two independent processes amplified the anchovy collapse; neither of them however would be able to impose individually such a severe anchovy stock change under the observed environmental conditions of the Black Sea.