



Nonlinear controls of anchovy stock and anchovy-gelatinous regime shift in the Black Sea: A modeling study

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*A one-dimensional bi-directionally coupled model of lower trophic food web and bioenergetics-based anchovy population dynamics for the Black Sea was used to elucidate the effects of fishing, environment and mechanisms that control three sharp changes of anchovy stock between the low, moderate and high quasi-stable regimes and accompanying changes of gelatinous predator zooplankton biomass. The first transition was a two-fold shift of anchovy stock from its low (~ 300 kt) to moderate (~ 700 kt) regime due to weakening piscivores predation pressure and competitive exclusion of gelatinous carnivores during the late 1960s. After maintaining the moderate regime until 1978, another two-fold shift to the high stock regime (~ 1400 kt) took place during 1979 – 1980 in response to moderate nutrient enrichment of the upper layer water column due to growing effect of eutrophication. This transition and subsequent high stock phase was accompanied with a low-to-moderate gelatinous biomass ($< 1 \text{ gC m}^{-2}$). This phase was ended by a third regime shift that brought anchovy stock temporarily back to the low regime during 1989-1990 and concurrently proliferated the gelatinous species, *Mnemiopsis*, biomass up to 3.0 gC m^{-2} as an alternative predator. The anchovy-*Mnemiopsis* regime shift was primarily linked to excessive nutrient enrichment of the system, but increasing fishing pressure further aggravated the anchovy stock collapse. As often observed at highly productive intraguild systems, the third shift identifies a transition from the resource (herbivory) – consumer (anchovy) - predator (gelatinous carnivory) coexistence regime to the resource - predator*

only regime. These transitions illustrate nonlinear response of the system to multiple density-independent exogenous controls and their density-dependent feedback mechanisms.