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An indicator-based evaluation of Black Sea food web dynamics during 1960–2000

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ABSTRACT

Four Ecopath mass-balance models were implemented for evaluating the structure and function of the Black Sea ecosystem using several ecological indicators during four distinctive periods (1960s, 1980–1987, 1988–1994 and 1995–2000). The results exemplify how the Black Sea ecosystem structure started to change after the 1960s as a result of a series of trophic transformations, i.e., shifts in the energy flow pathways through the food web. These transformations were initiated by anthropogenic factors, such as eutrophication and overfishing, that led to the transfer of large quantities of energy to the trophic dead-end species, which had no natural predators in the ecosystem, i.e., jellyfish whose biomass increased from 0.03 g C m^{-2} in 1960–1969 to 0.933 g C m^{-2} in 1988–1994. Concurrently, an alternative short pathway for energy transfer was formed that converted significant amounts of system production back to detritus. This decreased the transfer efficiency of energy flow from the primary producers to the higher trophic levels from 9% in the 1960s to 3% between 1980 and 1987. We conclude that the anchovy stock collapse and successful establishment of the alien comb-jelly *Mnemiopsis* in 1989 were rooted in the trophic interactions in the food web, all of which were exacerbated because of the long-term establishment of a combination of anthropogenic stressors.

1. Introduction

The Black Sea ecosystem underwent significant trophic transformations over the second half of the 20th century (Oguz and Gilbert, 2007). The history of these changes can be classified into four distinct periods: 1) the 1960s — pre-eutrophication, 2) 1980–1987 — intense eutrophication years, 3) 1988–1994 — the *Mnemiopsis leidyi* (Agassiz, 1865) — anchovy shift, and 4) 1995–2000 — the post-eutrophication phase (Fig. 1). The principal reasons for these transformations have long been debated (Bilio and Niermann, 2004; Kideys et al., 2000; Kovalev and Piontkovski, 1998; Kovalev et al., 1998; McQuatters-Gollop et al., 2008; Oguz and Gilbert, 2007; Oguz et al., 2003; Shiganova, 1998; Yunev et al., 2002, 2007; Zaitsev, 1992). When primarily focusing on the anchovy — *Mnemiopsis* shift in 1989 (Kideys, 2002), studies sought answers to enhance the comprehension of the mechanisms underlying the observed changes (Berdnikov et al., 1999; Daskalov, 2002; Daskalov et al., 2007; Gucu, 2002; Llope et al., 2011; Oguz, 2007; Oguz et al., 2008a,b). The roles of the trophic cascade because of overfishing (Daskalov, 2002; Gucu, 2002), *M. leidyi* (hereafter called *Mnemiopsis*) predation on anchovy eggs and larvae (Kideys, 2002; Lebedeva and Shushkina, 1994; Shiganova and Bulgakova, 2000) and the combination of bottom-up and top-down controls (Bilio and Niermann, 2004; Oguz, 2007; Oguz et al., 2008a) were all suggested as significant processes catalysing the observed ecosystem changes.

The pre-eutrophication phase of the 1960s characterised a healthy mesotrophic ecosystem with primary production values between 100 and 200 mg C m^{-2} y^{-1} (Oguz et al., 2012). In the 1960s, relatively rich biological diversity of the Black Sea comprised fishes from large demersal fish species, such as turbot (*Psetta maeotica*; Pallas, 1814), Black Sea striped mullet (*Mullus barbatus ponticus*; Essipov, 1927), spiny dogfish (*Squalus acanthias*; Linnaeus, 1758), and Black Sea whiting (*Merlangius merlangus euxinus*; Nordmann, 1840), to piscivorous pelagic fish, such as Atlantic bonito (*Sarda sarda*; Bloch, 1973), bluefish (*Pomatomus saltator*; Linnaeus, 1776), and Atlantic mackerel (*Scomber scombrus*; Linnaeus, 1758), as well as small pelagic fish, predominantly the Black Sea anchovy (*Engraulis encrasicolus ponticus*; Alexandrov, 1927), Black Sea horse mackerel (*Trachurus mediterraneus ponticus*; Aleev, 1956), and Black Sea sprat (*Sprattus sprattus phalaericus*; Risso, 1827). Three cetacean species, the Black Sea common dolphin (*Delphinus delphis ponticus*; Barabash-Nikiforov, 1935), the Black Sea bottlenose dolphin (*Tursiops truncatus ponticus*; Barabasch, 1940), and the Black Sea harbour porpoise (*Phocoena phocoena relicta*; Abel, 1905) represented the top predators of the system. During the subsequent two decades, the stocks of both pelagic piscivorous fishes and marine mammals were overexploited and primary and secondary pelagic production increased

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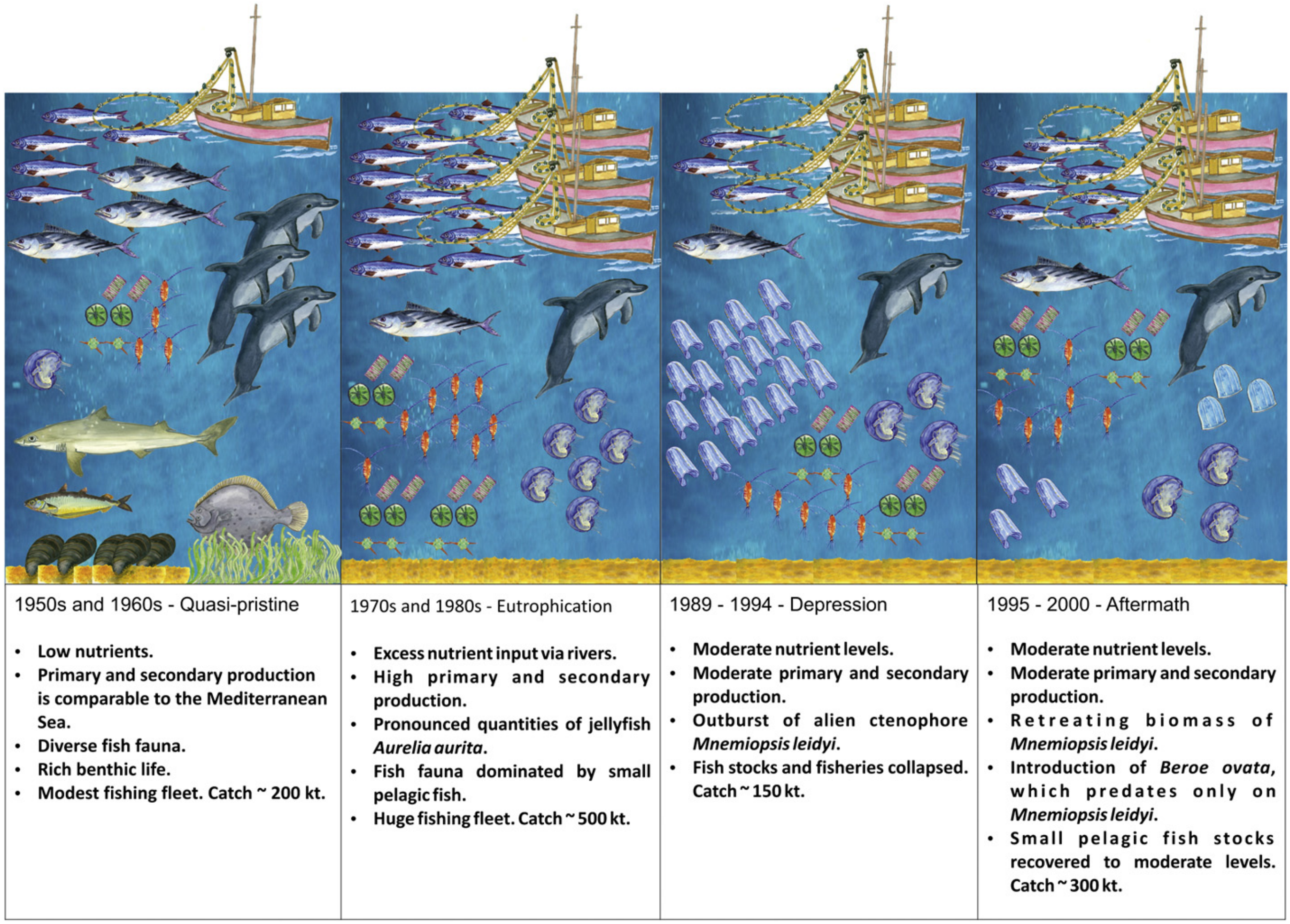

Fig. 1. The schematic illustration of the four periods in the Black Sea. The figure was depicted based on the classifications in the published literature and derived from an earlier work (Fig. 10) in Langmead et al. (2007).

excessively because of nutrient enrichment from rivers discharging mainly into the northwestern shelf of the Black Sea. The small pelagic fish species and the moon jelly, *Aurelia aurita* (Linnaeus, 1758), became dominant in the ecosystem. The benthic flora and fauna greatly deteriorated because of the frequent hypoxia events of the shelf waters (Mee, 2006; Zaitsev, 1992; Zaitsev and Mamaev, 1997). Simultaneously, the Turkish fishing fleet grew enormously in size and technology (Gucu, 2002), and the fishery yield attained 700 kt, a significant proportion (~500 kt) of which consisted of anchovy. In 1989, the non-indigenous comb jelly species *Mnemiopsis*, which was introduced to the Black Sea ecosystem in the early 1980s via the ballast waters of shipping vessels, flourished in both abundance and biomass. This same year also coincided with the collapse of the Turkish fishery yield from an average of 700 kt during the early 1980s to only 150 kt in 1989 (Oguz, 2007). Subsequently, the Turkish fishery yield recovered to approximately 300 $\pm$ 100 kt, whereas it remained at very low levels throughout the rest of the Black Sea (Oguz et al., 2012). During this recuperation period, blooms of *Mnemiopsis* were suppressed naturally because of the appearance of another non-indigenous gelatinous species, *Beroe ovata* (Mayer, 1912), a natural *Mnemiopsis* predator. By the end of the 1990s, the entire Black Sea ecosystem was characterised by moderate primary (200–400 mg C m^{-2} y^{-1}, Oguz et al., 2012) and secondary productivity (McQuatters-Gollop et al., 2008; Mee, 2006), although the ecosystem of the northwestern shelf and western coastal waters was still far from recovery and rehabilitation (Oguz and Velikova, 2010).

To investigate the changes summarised above and their underlying causes, the various aspects of the Black Sea lower trophic food web function were studied in terms of aggregated biogeochemical models (e.g., Grégoire and Friedrich, 2004; Gregoire and Lacroix, 2003; Gregoire and Soetaert, 2010; Gregoire et al., 2004, 2008; He et al., 2012; Lancelot et al., 2002; Oguz and Merico, 2006; Oguz et al., 2000, 2001, 2008b; Staneva et al., 2010; Tsiaras et al., 2008). Additionally, mass-balance models of different complexities were also set-up by Gucu (2002), Daskalov (2002), and Orek (2000). Gucu (2002) focused on the second half of the 1980s when examining the role of increased fishing pressure on the collapse of anchovy stocks, whereas Daskalov (2002) adopted a broader time frame, starting from the pre-eutrophication period, and noted that trophic cascades that were initiated by overfishing played a leading role in ecosystem changes. However, both of these studies lacked the quantification of ecosystem characteristics of the Black Sea during these changes. Here, we expand upon these previous studies by i) using a set of indicators that quantify the condition of the ecosystem to systematically analyse each defined ecosystem period and, ii) providing an understanding of the interactions between the food web components that led to the aforementioned changes in the Black Sea. The ecological analyses were performed within the framework of “ecosystem health”, which will ultimately provide reference points to evaluate the transformations of the Black Sea's ecosystem structure and function over recent decades based on quantitative ecosystem metrics. Here, ecosystem health was used to define the potential of an ecosystem under stress to sustain its structure and function over time (Costanza, 1992; Costanza and Mageau, 1999; Haskell et al., 1992; Schaeffer et al., 1988). The methodology that was adopted to assess ecosystem health comprised the application of ecological network