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Invasion dynamics of the alien ctenophore *Mnemiopsis leidyi* and its impact on anchovy collapse in the Black Sea

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The mechanisms governing the unprecedented 1989–90 anchovy–Mnemiopsis shift event in the Black Sea were evaluated with a coupled model of bioenergetic-based anchovy population dynamics and lower trophic food web structure. Simulations showed that a combination of direct and density-dependent effects of overfishing, eutrophication-induced nutrient enrichment, climate-induced over-enrichment and temperature-controlled Mnemiopsis spring production were involved in the shift. Eutrophication made the system vulnerable to further enrichment through the change of regional climate to a severe winter regime during 1985–87. While Mnemiopsis was acclimating to its new environment, increasing nitrate flux into the euphotic layer enhanced the carrying capacity of the system, but a disproportionate Mnemiopsis biomass increase was delayed until spring temperature conditions returned to normal in 1988–89. Enhanced carrying capacity provided a competitive advantage of food consumption to Mnemiopsis compared with anchovy, and warm spring temperature conditions promoted their spring–summer production. Prevalent high fishery pressure and increasing impact of Mnemiopsis on the food web further induced the anchovy stock collapse. However, the shift event did not result in alternation of the system to a new totally Mnemiopsis-invaded quasi-stable regime. Instead, anchovy started recovering when the subsequent strong 1991–93 cooling regime limited the Mnemiopsis population growth. Our analysis indicated that the switch of a large marine ecosystem to a totally gelatinous invader-dominated state requires extremely strong environmental perturbations. More often, environmental disturbances create a suitable niche for an alien gelatinous invader to become a member of the food web structure, and to share food resources with the native small pelagic fish community.

INTRODUCTION

Invasions of marine habitats by native and/or non-indigenous gelatinous (medusae, ctenophores and siphonophores) species, which are occurring throughout the world, are a major ecological concern. The cumulative effects of mounting global warming, ocean acidification, eutrophication and risk of accidental spread worldwide through shipping traffic favour their settlement and sometimes domination of local food webs that are heavily stressed by pollution, eutrophication and overfishing (Mills, 2001; Byers, 2002). In some cases, their extent and impacts on ecosystems may be rather detrimental, such as diminishing the size of native populations and even extinctions, as well as significant alterations in community structure and ecosystem functioning (Moller, 1984; Purcell and Grover, 1990; Cohen and Carlton, 1998; Brodeur *et al.*, 1999; Purcell and Sturdevant, 2001; Lynam *et al.*, 2005).

Among gelatinous organisms, the ctenophore *Mnemiopsis leidyi* is known to be a highly opportunistic

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species with rapid linear growth and high reproduction ability under a wide range of environmental conditions. They consume mainly zooplankton ranging from protists to mesozooplankton depending on their life stages (Purcell *et al*., 2001; Rapoza *et al*., 2005). To a lesser extent, their diet also includes ichthyoplankton of planktivorous fish such as anchovy, sardine and herring during their spawning periods (Tsikhon-Lukinana *et al*. 1994; Vinogradov *et al*., 1996; Shiganova and Bulgakova, 2000; Purcell *et al*., 2001). Therefore, *Mnemiopsis* is a potential competitor of planktivorous fish as well as a predator during certain periods of the year. Its native habitat is the eastern coastal waters of the North and South American continents (Purcell *et al*., 2001) and it has been introduced into the Black, Marmara, the northern Aegean Seas in the early 1980s (Shiganova *et al*., 2001) as well as into the Caspian Sea (Finenko *et al*., 2006a). It was recently observed at growing quantities in western and northern European coastal waters as well as the Baltic Sea (Faasse and Bayha, 2006; Javidpour *et al*., 2006; Boersma *et al*., 2007; Haslob *et al*., 2007; Lehtiniemi *et al*., 2007; Oliveira, 2007; Riisgård *et al*., 2007; Viitasalo *et al*., 2008). Its establishment and population outbreak in the Black Sea was regarded as one of the most dramatic gelatinous invasion events with profound implications for ecosystem functioning (Kideys, 2002). This was partly due to the lack of any *Mnemiopsis* predators in the Black Sea prior to their predation by the accidentally introduced ctenophore *Beroe ovata* during 1998 (Vinogradov *et al*., 2000) in contrast to several fish species preying on them in American waters (Mianzan *et al*., 1996). The Black Sea experience during 1989–99 may be considered a natural laboratory in terms of attempting to understand the mechanisms that control the large-scale gelatinous invasion process and its likely ecosystem-wide detrimental effects.

Interest in ecological dimensions of alien species invasions has been increasing (Boxshall, 2007), yet there is no formal analysis and mechanistic understanding of invasions (Byers, 2002). In fact, how a non-indigeneous species gains competitive advantage over native species constitutes a fundamental question in ecology. Their population explosions exhibit non-linear dynamical behaviour involving prey–predator–consumer interactions in response to direct impacts of different external stressors as well as non-linear internal feedbacks. Therefore, invasion dynamics warrant a mechanistic insight by hypothesis-driven, process-oriented model studies that complement more traditional data-driven interpretations. The present work addresses this issue and focuses on the 1989–90 population outbreaks of *Mnemiopsis* and the simultaneous stock collapse of the top predator anchovy (*Engraulis encrasicolus*) in the Black Sea as a modelling case study of global relevance.

Observed features in relation to anchovy–Mnemiopsis interactions

An extensive number of publications has already dealt with various aspects of anchovy–*Mnemiopsis* interactions in the Black Sea. Bilio and Niermann (Bilio and Niermann, 2004) and Niermann (Niermann, 2004) reviewed all the available work and different views and hypotheses on the anchovy–*Mnemiopsis* interactions in depth. According to the virtual population analysis-based stock estimate by Prodanov *et al*. (Prodanov *et al*., 1997), the exploitable anchovy standing stock in October (i.e. prior to the beginning of the fishing season) experienced a significant increase from ~300 000 tonnes in the 1960s to 1 500 000 tonnes in the late-1970s. The increase was promoted simultaneously by favourable bottom-up resource supply due to increasing eutrophication (Humborg *et al*., 1997; Oguz and Gilbert, 2007) and weakening top-down pressure due to overfishing of piscivores and top predators (Daskalov *et al*., 2007; Oguz, 2007). The basin-scale signature of the nutrient enrichment was manifested itself in the change of peak nitrate concentration in the chemocline (the layer below the base of the euphotic zone) from 2–3 μM in the late 1960s to 7–8 μM in the mid-1980s (Fig. 1). This nitrate resource supported progressively more enhanced biological production in the system. This was evident by the change in water-column integrated May–November mean phytoplankton biomass of the interior basin from $<5\,\mathrm{g\,m^{-2}}$ in the early 1970s to $>15\,\mathrm{g\,m^{-2}}$ in the mid-1980s (Fig. 1).

As the environmental deterioration progressed due to intensifying eutrophication, the food web structure started to be dominated by opportunistic and gelatinous species (*Noctiluca scintillans*, *Pleurobrachia rhodopis*, *Aurelia aurita*, *M. leidyi*, *Rhizostoma pulmo*). Among these, *Aurelia* and *Mnemiopsis* constituted typically more than 80% of the total gelatinous biomass (Kovalev and Piontkovski, 1998). The jellyfish *A. aurita* was rarely observed in the 1950s and 1960s but became a major gelatinous predator of the eutrophic Black Sea ecosystem with a typical biomass of $1\,\mathrm{g\ C\,m^{-2}}$ in coastal waters in the early 1980s (Fig. 2). However, the data were insufficient to monitor its biomass changes until 1988.

Mnemiopsis was first recorded along the Crimean coast in November 1982 (Pereladov, 1988), then observed in the north-western coastal waters in 1986 (Zaitsev *et al*., 1988) and in the north-eastern coastal waters in 1987 (Vinogradov *et al*., 1989) at low quantities

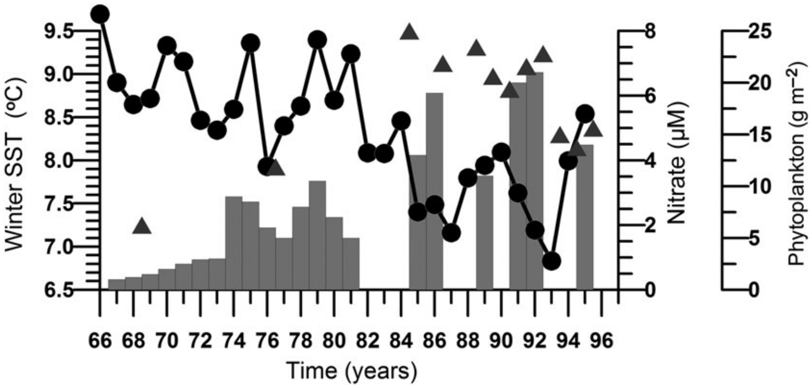

Fig. 1. Time series of winter-mean (December–March) sea surface temperature (SST) (filled circles), phytoplankton biomass of the May–November period averaged over all measurements within the basin deeper than 1500 m (grey bars) and peak nitrate concentration in the chemocline layer (triangles). Numbers on the horizontal axis represent the last two digits of the years. Phytoplankton data are taken from Mikaelyan (Mikaelyan, 1997), nitrate data from http://sfp1.ims.metu.edu.tr/ODBMSDB/, and the winter SST time series is constructed by the monthly mean data complied by Hadley Centre, UK. Meteorological Office (http://badc.nerc.ac.uk/data/hadisst) from all the available *in situ* measurements and the AVHRR satellite observations (Rayner *et al.*, 2003).

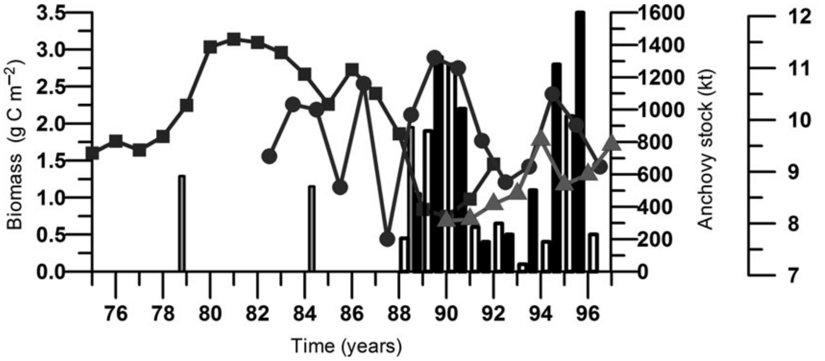

Fig. 2. Time series of the Black Sea anchovy exploitable stock (in kilotonnes) at the beginning of fishing season (October) (filled squares, triangles), the annual mean gelatinous biomass (in g C m^{-2}) that mainly represents *Aurelia aurita* prior to 1988 (gray bars) and *Mnemiopsis leidyi* afterwards in April (white bars) and in August (black bars), the monthly-mean April SST (in °C) averaged over the basin (filled circles). Numbers on the horizontal axis represent the last two digits of the years. The anchovy exploitable stock was estimated by Prodanov *et al.* (Prodanov *et al.*, 1997) (filled squares) and G. Daskalov (personal communications) (filled triangles). Gelatinous carnivore biomass data were provided by Shiganova *et al.* (Shiganova *et al.*, 2001) based on measurements in the north-eastern sector of the Black Sea. The April SST was retrieved from the monthly-mean 4.4 km Pathfinder night-time AVHRR data set provided by http://las.pfeg.noaa.gov/OceanWatch/servlets/dataset.

($<$0.5 kg ww m^{-2}) following its accidental introduction into the sea. According to data from the eastern basin, it reached an average biomass of 1 g C m^{-2} (1.0 kg ww m^{-2}) and was accompanied by ~1.5 g C m^{-2} *Aurelia* biomass in summer–autumn 1988 (Fig. 2). Its biomass then increased markedly to ~3.0 g C m^{-2} in offshore waters of the eastern basin (Fig. 2) and slightly higher in its coastal waters in 1989–90. The total *Mnemiopsis* biomass amounted to more than half a million tonnes when extrapolated over the whole basin, though this number is somewhat controversial (Vinogradov *et al.*, 1989; Mutlu *et al.*, 1994; Weisse *et al.*, 2002). Simultaneously with the sudden *Mnemiopsis* population outburst, the anchovy stock dropped from ~830 000 tonnes in 1988 to ~290 000 tonnes in 1990 (Fig. 2). At the same time, *Aurelia* biomass dropped to 10% of the *Mnemiopsis* biomass.

Immediately after the anchovy–*Mnemiopsis* shift, *Mnemiopsis* abundance decreased to a low level ($<$0.5 kg ww m^{-2}) in 1991–93. This decreasing trend reversed in 1994–95 with biomass increasing abruptly again to 3.5 g C m^{-2} in the deep interior basin (Fig. 2) and higher values (average 4.5 g C m^{-2}) in inshore waters (Shiganova *et al.*, 2001). The second peak was followed by a decrease in 1996–97. In 1998, one-third increase in offshore waters resulted in an average biomass of 0.9 g C m^{-2} (Shiganova *et al.*, 2001). Starting in 1999, *Mnemiopsis* biomass reduced considerably due to their predation by the new invader ctenophore *B. ovata*. Their large and abrupt inter-annual fluctuations indicate great sensitivity of growth and reproduction characteristics of *Mnemiopsis* to environmental influences and food availability.

The anchovy stock followed changes in *Mnemiopsis* biomass out-of-phase with a 1-year phase lag (Fig. 2). It first experienced a gradual trend of recovery during the low *Mnemiopsis* biomass period of 1991–93 up to ~800 000 tonnes in 1994 and a subsequent decline in 1995–96 and recovery again in 1997. The negative correlation ($r = -0.58$ with $P < 0.01$) between anchovy and *Mnemiopsis* biomass variations during the 1990s probably indicates a strong control by gelatinous zooplankton on the anchovy recruitment strength. A similar out-of-phase fluctuation also existed between *Aurelia* and *Mnemiopsis* (Kovalev and Piontkovski, 1998) and pointed to food competition in addition to their food competition with pelagic fish populations. When hydroclimatic conditions were favourable, *Mnemiopsis* constituted a major fraction of the total gelatinous biomass; otherwise, *Aurelia* dominated the gelatinous system (Kovalev and Piontkovski, 1998; Shiganova *et al.*, 2001). The ctenophore *Mnemiopsis* and scyphomedusan *Chrysaora quinquecirrha* system revealed a similar competition and fluctuation in Chesapeake Bay (Purcell and Decker, 2005).

Hypotheses proposed for the anchovy–*Mnemiopsis* shift

Essentially, two major and contrasting hypotheses have been proposed to explain the observed 1989–90 anchovy–*Mnemiopsis* shift. One of them states that overfishing caused the shift (Prodanov *et al.*, 1997; Gucu, 2002; Daskalov *et al.*, 2007). The other proposed excessive food competition and predation by *Mnemiopsis* as the main mechanism for the shift (Vinogradov *et al.*, 1989; Kideys *et al.*, 2000; Purcell *et al.*, 2001; Shiganova *et al.*, 2001). The role of climate-induced changes as an additional control on the shift process, however, attracted less attention (Niermann, 2004; Oguz, 2005).

The overfishing hypothesis promoted the fishery's role as a triggering mechanism of the shift. It related the anchovy stock collapse to an increasing rate of harvesting and subsequent development of recruitment failure after 1987. A significant increase in the Turkish fishing fleet capacity during the 1980s was thought to have caused the overfishing. According to this hypothesis, as the anchovy stock declined, food resources were preferentially diverted to *Mnemiopsis* and thus its biomass increased in the absence of predators and the lack of competitors. Using a tri-trophic level model of the small, medium and large pelagics, Oguz *et al.* (Oguz *et al.*, 2007) also emphasized the important role of increasing fishing effort for the collapse of small pelagics. However, the lack of a gelatinous group in the model precluded assessing the role of *Mnemiopsis* in the collapse. Overfishing may be a valid argument for the anchovy collapse, but whether it caused a concurrent *Mnemiopsis* population outbreak remains to be validated.

Alternatively, heavy food competition of the *Mnemiopsis* population with anchovy and their predation on anchovy eggs and larvae were suggested to cause the anchovy–*Mnemiopsis* shift (Vinogradov *et al.*, 1989; Kideys *et al.*, 2000; Purcell *et al.*, 2001; Shiganova *et al.*, 2001). Moreover, the decline in the anchovy stock may have been further accelerated by the selective feeding of *Mnemiopsis* on small copepods, which forced a shift in the diet of anchovy larvae to low caloric food such as Cladocera, Cirripedia, Ostracoda and Bivalvia, and thus resulted in less-efficient anchovy growth (Gordina *et al.*, 1998). This alternative hypothesis implicitly assumed that zooplankton biomass was more effectively consumed by *Mnemiopsis* in respect to anchovy during the shift phase. This assumption, however, also remains to be validated.

In regards to the anchovy–*Mnemiopsis* shift in the Black Sea, one of the critical questions is why the *Mnemiopsis* population outbreak was delayed until 1989–90 following its introduction during the early 1980s. A likely explanation for this delay may be the shift of the regional climate to a severe cooling regime in 1985 (Oguz *et al.*, 2006; Oguz and Gilbert, 2007). Severity of winter conditions was evident with ~2°C decrease in the winter-averaged (December–March) sea surface temperature (SST) from 1979–81 to 1985–87 (Fig. 1 and Table I). The severe winter climate regime was interrupted by a short-term warming phase in 1988–90, but continued during 1991–93.

On the basis of observations during the 1990s, Shiganova *et al.* (Shiganova *et al.*, 2001) noted an adverse effect of cold winter temperatures on the growth of the overwintering *Mnemiopsis* population and subsequent limitation of their spring and summer populations. In contrast, Sullivan *et al.* (Sullivan *et al.* 2001) and Costello *et al.* (Costello *et al.* 2006) found no clear correlation between winter (January, February) temperatures and the spring *Mnemiopsis* bloom date for Narragansett Bay, USA, but suggested a significant correlation with spring temperatures. A similar link was also reported in the Chesapeake Bay, USA (Purcell and Decker, 2005). Using the monthly sea surface winter and spring temperature data, we also looked for an indication of a similar correlation in the Black Sea.

Scope of the present work

The probable contributions of these hypotheses to the anchovy–*Mnemiopsis* shift are discussed below.

Table I: Basin-averaged sea surface temperature for the winter (December–March) season and for spring months (March, April and May) during 1985–90

Months/years	1985	1986	1987	1988	1989	1990
Winter-mean (December–March)	7.44	7.32	7.6	8.2	7.4	7.6
March	5.9 (6.3)	7.5 (7.5)	6.3 (6.3)	7.1 (8.0)	7.2 (7.7)	7.3 (7.8)
April	7.9 (8.7)	10.1 (10.7)	7.4 (7.7)	9.0 (10.1)	9.9 (11.2)	9.8 (11.0)
May	13.4 (14.5)	14.6 (15.1)	12.1 (11.7)	14.1 (14.2)	15.3 (15.7)	14.5 (15.0)
Spring type	Cold	Warm	Cold	Moderate	Warm	Warm

The data are retrieved from the monthly-mean 4.4 km Pathfinder-5 and 9 km Reynolds-NCEP (in parentheses) night-time global data sets.

The assessments are made using a bi-directionally coupled model of lower trophic level and bioenergetics-based anchovy population dynamics (Oguz *et al.*, 2008) whose main features and the assumptions are summarized prior to the presentation of model results and their implications. We then present a new conceptual description of the anchovy–*Mnemiopsis* shift by connecting its climate, fishery and food competition and predation aspects. We conclude by placing the *Mnemiopsis* population outburst event into a global context in terms of the conditions leading to invasion success of alien gelatinous species.

METHOD

Brief description of the model structure

An extensive description of the model formulation, the parameters setting and validation aspects has been given in Oguz *et al.* (Oguz *et al.*, 2008). Here, we provide only an overview over the main features of the model relevant to this work. The lower layer food web structure was modelled with three phytoplankton groups (diatoms, dinoflagellates and nanophytoplankton), three zooplankton groups (micro-, mesozooplankton and gelatinous carnivores) and a simplified particulate and dissolved nitrogen cycle. The total gelatinous biomass mainly represented the contribution of *Mnemiopsis* during the shift period and *Aurelia* prior to the shift. This structure is a simplified version of the model described by Oguz *et al.* (Oguz *et al.*, 2001). Equilibrium solutions were obtained by integrating the model until steady state of the system with repeating yearly cycles of all state variables.

The 50-m deep euphotic zone was resolved by the annually varying surface-mixed layer and the sub-thermocline layer. An additional, biologically inactive nitrate source layer below supplied nitrate flux into the euphotic zone to drive year-long new and recycled biological production. This layer constituted the upper part of the chemocline where the nitrate available can efficiently be supplied into the euphotic zone by vertical mixing and advection. The nitrate available in even higher concentrations within the rest of the chemocline, however, cannot take part in this process because of strong stratification and weak turbulent mixing conditions in the Black Sea (Oguz *et al.*, 2003). Consistent with observations (Fig. 1), the nitrate concentration (N_c) of the source layer was set to half of the peak chemocline concentration. The model prescribed daily values of the mixed layer depth, temperature and photosynthetically available radiation in the layers, and the entrainment rate during the deepening phase of the mixed layer depth that was provided by Kraus–Turner type entrainment and mixed layer computations (Oguz *et al.*, 2001).

The anchovy weight growth was formulated following Rose *et al.* (Rose *et al.*, 1999) but tuned for Black Sea anchovy with some simplifications. Anchovy reduced during maturation through the losses due to basal mortality, predation by the gelatinous group and large pelagics and harvesting. The predation by large pelagics was not formally modelled but parameterized with a quadratic function of the anchovy population. Female adult anchovies spawned daily during June–August depending on their reproduction rate, total female adult biomass and some other environmental factors. After hatching, each daily population was followed as a specific cohort for 4 years. The basal mortality, consumption and respiration rates varied according to the life stages. The fishing mortality rate (expressed in per year) represented the total rate of anchovy harvesting each year from the beginning of October to mid-March.

Micro- and mesozooplankton consumption of anchovy were parameterized by a Holling-III (sigmoidal) function that provided a linear growth rate at low food concentrations and a slower and then saturated growth rate at increasing food concentrations. Consumptions of zooplankton and anchovy eggs and larvae by the gelatinous group were modelled by a linear function of prey biomass that implies no satiation of jellies at high prey concentrations. The model assigned equal rates of

Mnemiopsis feeding on zooplankton and anchovy eggs and larvae, which were set to 0.2 m^3 (mmol N day)$^{-1}$ consistent with observations (Purcell *et al.*, 2001). When expressed in terms of per capita consumption rate (per day), it is smaller than the anchovy consumption rate of zooplankton. Thus, the difference between the sigmoidal and linear food consumption formulations sets anchovy as a superior competitor at low food concentrations and the gelatinous group at high food concentrations.

The model distinguished two basic food chains with different food preferences: the first one is dominated by large phytoplankton, mesozooplankton and anchovy, and the second one is by small phytoplankton, microzooplankton and gelatinous group. Such a distinction was proposed by Parsons (Parsons, 1979) and supported later by observations (Purcell *et al.*, 2001). The model, however, allows interaction between these two basic food chains and thus allows complex trophic interactions within the food web.

As observed in the Black Sea prior to the introduction of *Beroe* in 1998, the model considered no predation on the *Mnemiopsis* population. Furthermore, the model does not incorporate interannual variations of the nitrate entrainment rate and of the mixed layer temperature that were likely introduced by the climatic changes. Their annual structures were biased to represent a stronger cooling regime of the mid-1980s that favoured a higher nutrient supply into the euphotic zone during the winter but more strongly limited the spring gelatinous biomass increase. The former assumption was not critical for the model since we covered the entire range of likely nitrate flux conditions in our simulations. On the other hand, the model simulations with different exponential and Q_{10}-type temperature control functions of *Mnemiopsis* growth did not resolve the delicate difference between the cold and warm temperature conditions well enough that apparently controlled the intensity of spring *Mnemiopsis* reproduction rate. This was due to the lack of any reported temperature control function of the growth based on measurements.

The relative roles of anchovy stock over-exploitation and nutrient enrichment of the system were examined by a set of simulations in which nitrate concentration of the subsurface source layer (N_c) was varied in the range of 1.0–10.0 μM at different anchovy fishing mortality rates. The rest of the parameters that were kept unchanged were previously optimized according to their observed ranges through sensitivity studies. The simulations with the low fishing mortality rate $m_f = 0.3$ year^{-1} (referred to as the low fishing pressure, LFP, simulations) and $N_c \leq 4.0$ μM represented the changes in the observed ecosystem structure from 1960s to the early 1980s. They, therefore, identified the prevailing environmental conditions that sustained high anchovy stock prior to the overfishing and the *Mnemiopsis* invasion phase. Whether overfishing alone could drive the anchovy–*Mnemiopsis* shift was then tested by repeating the LFP simulations with the higher fishing mortality of $m_f = 0.8$ year^{-1} (high fishing pressure, HFP, simulations) and $m_f = 1.3$ year^{-1} (very HFP, EFP, simulations) but keeping all other conditions similar. Additionally, the gelatinous and anchovy biomass versus N_c changes at higher enrichment regime ($N_c > 4.0$ μM) were used to identify the conditions that gave rise to the observed anchovy collapse and the marked gelatinous biomass increase.

RESULTS

Assessment of the overfishing hypothesis

Under the low fishing mortality conditions of ~0.3 year^{-1} (the LFP solutions), the change in anchovy standing stock biomass between the points A and B in Fig. 3 simulated its 5-fold proliferation from ~300 000 to ~1 500 000 tonnes in response to a 2-fold increase in N_c from 1.5 to 3.0 μM and 2-fold weakening of the predation pressure of piscivorous fishes. The corresponding gelatinous biomass, representing mainly the jellyfish *A. aurita*, increased from negligibly low biomass to ~0.7 g C m^{-2}. In accordance with the data shown in Fig. 2, these changes represent the transformation of the ecosystem from a low anchovy and no *Aurelia* regime of the 1960s to a high anchovy and low *Aurelia* regime of the late 1970s. The range of N_c between 3 and 4 μM sustained almost the same peak stock size (1 575 000 ± 75 000 tonnes) but supported increasing gelatinous biomass in the range of 0.7–1.3 g C m^{-2}. Therefore, the subsurface nitrate concentrations of 3–4 μM and an LFP of 0.3 year^{-1} marked optimum conditions prior to a strong control by the gelatinous group on anchovy as observed in the early and mid-1980s. That was because of their competitive disadvantage in prey consumption under moderate carrying capacity conditions.

Keeping these conditions the same, we next examined whether overfishing alone could drive the shift under the moderate enrichment conditions ($N_c = 4.0$ μM). According to the simulations, the observed collapse level (~300 000 tonnes) was attained at fishing mortality rate values around 1.3 year^{-1} as depicted by the arrow from the point B of the LFP solution to the point C2 of the EFP solution in Fig. 3. This collapse in anchovy stock, however, introduced only a slight increase in the gelatinous biomass up to ~1.5 g C m^{-2} (Fig. 3). Therefore, the overfishing simulations imply that under gradually increasing harvesting rate from

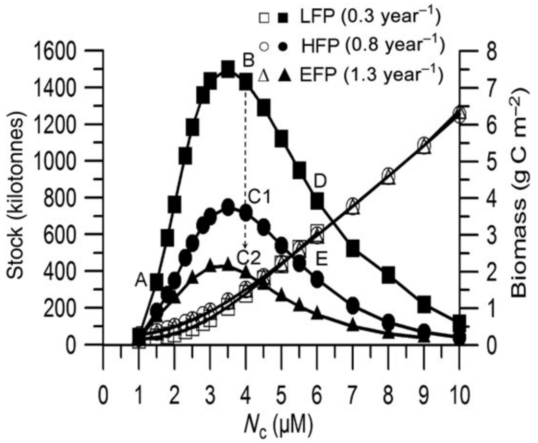

Fig. 3. Model estimates of exploitable anchovy stock (at the beginning of October) versus subsurface nitrate concentration, N_c, for the low (LFP; 0.3 year^{-1}), high (HFP; 0.8 year^{-1}), and very high (EFP; 1.3 year^{-1}) fishing mortality rates denoted by filled squares, filled circles, filled triangles, respectively. The corresponding estimates of the annual-mean gelatinous biomass are shown by open squares, open circles, open triangles, respectively. The capital letters A and B mark the likely states of the anchovy stock during the 1960s and early 1980s, respectively, when fishing mortality was low. C1 and C2 mark the likely state of the anchovy stock at the end of the 1980s under HFP and EFP conditions but without additional enrichment of the euphotic layer; thus, the transition from B to C2 represents the anchovy stock change in the case of an overfishing-only scenario. D marks the likely state of the anchovy stock at the end of the 1980s experiencing enrichment but low fishing pressure conditions; thus, the transition from B to D marks the likely path for the *Mnemiopsis* food competition scenario. The transition from C1 to E marks the likely path when anchovy experience both the overfishing and the *Mnemiopsis* food competition. The most likely scenario for the evolution of the anchovy–gelatinous system is the change from A to B during the 1970s, from B to C1 during the first half of the 1980s and from C1 to E at the end of the 1980s.

~0.3 to ~0.8 year^{-1}, but in the absence of an additional climate-induced enrichment of the system (i.e. N_c= 4 µM) the Black Sea would maintain a moderate anchovy stock (~750 000 tonnes) and a moderate biomass of gelatinous species *Aurelia* and *Mnemiopsis* (~1.5 g C m^{-2}).

Critique

The overfishing mechanism alone failed to explain the *Mnemiopsis* population outbreak. One of the reasons was the lowest level of zooplankton biomass over the year during the harvesting period of adult anchovies (October–March). Therefore, zooplankton biomass that was released from the anchovy predation pressure provided only a minor contribution to the *Mnemiopsis* overwintering population. The other reason was setting of the lowest allowable catch size to 7 cm in the model, consistent with data by Gucu (Gucu, 2002). Thus, the majority of the age 0 class population remained unfished and were able to produce sufficient offspring during the next spawning season. The new generation had a sufficient population to exert high predation pressure on the zooplankton population as it was still the superior competitor at moderate zooplankton biomass levels.

Assessment of the *Mnemiopsis* food competition and predation hypothesis

According to the simulations shown in Fig. 3, the observed gelatinous biomass size of 3.0 g C m^{-2} during the shift was possible for the choice of N_c= 6 µM, independent of the level of fishing mortality imposed on the anchovy stock. This implies a 50% increase in the nitrate flux supplied into the euphotic layer with respect to early 1980s without any further increase in the existing subsurface nitrate concentration. We assume that such an increased nitrate flux can be provided by 50% stronger entrainment and Ekman pumping rates introduced by the climate-induced changes prior to the anchovy–*Mnemiopsis* shift (Oguz *et al.*, 2001). This additional enrichment supported a high zooplankton biomass that made *Mnemiopsis* a superior competitor compared with anchovy because of its linearly increasing growth rate at high food conditions, whereas anchovy growth rate approaches a saturation level. This is indicated indirectly in Fig. 3 by the change in the slope of *Mnemiopsis* biomass.

Keeping the fishing mortality rate ~0.3 year^{-1} as in the early 1980s (i.e. without the overfishing mechanism), the LFP simulations suggest that the gelatinous biomass attained its observed biomass level of 3.0 g C m^{-2} during the shift, but anchovy biomass decreased only by ~40% (to ~800 000 tonnes) as depicted by the stock change from the point B to D in Fig. 3. This result may also be interpreted in such a way that anchovy would be able to maintain a moderate stock regime even in the case high *Mnemiopsis* biomass (around 3.0 g C m^{-2}) in the absence of overfishing (i.e. under low-to-moderate fishing efforts). In fact, this was the case during the 1994–95 *Mnemiopsis* outbreak events. Our model findings, therefore, contradict the qualitative interpretation of the data by Daskalov *et al.* (Daskalov *et al.*, 2007) who related the origin of the *Mnemiopsis* bloom to the anchovy stock collapse.

Critique

This mechanism was also unable to fully explain the *Mnemiopsis* population outbreak–anchovy stock collapse event. The solutions shown in Fig. 3 suggest that (i) the *Mnemiopsis* biomass increase was not so sensitive to the changes in anchovy fishing pressure, but critically depended upon the rate of increase of carrying capacity of the system by increasing nitrogen flux and (ii) in addition to the change in carrying capacity increasing the fishing mortality to $\sim$0.8 year^{-1} brings the anchovy stock down to its collapse level of $\sim$300 000 tonnes along the arrow from the point B to E in Fig. 3.

A similar requirement of a higher carrying capacity was also implicitly included in the Gucu model (Gucu, 2002) by constraining the ECOPATH model with high phytoplankton biomass as it was observed during the collapse period. Therefore, his model ascribed an additional role of the over-enrichment mechanism in addition to the overfishing, and thus allowed a food competition advantage of *Mnemiopsis*. But he did not further elaborate on its dynamical implications, and interpreted the model results from the fishery perspective.

According to the model computations, the *Mnemiopsis* predation on anchovy eggs and larvae contributed to the anchovy stock loss only by $\sim$40 000 tonnes, which roughly corresponded to 10% of the loss due to food competition effect between anchovy and gelatinous zooplankton. Very low weights of anchovy eggs and larvae were responsible for such low stock loss in spite of its considerable impact on population level. Therefore, the model suggests the zooplankton consumption advantage of *Mnemiopsis* relative to anchovy at relatively high resources as the primary mechanism for its disproportionate biomass growth and reduction of anchovy recruitment biomass.

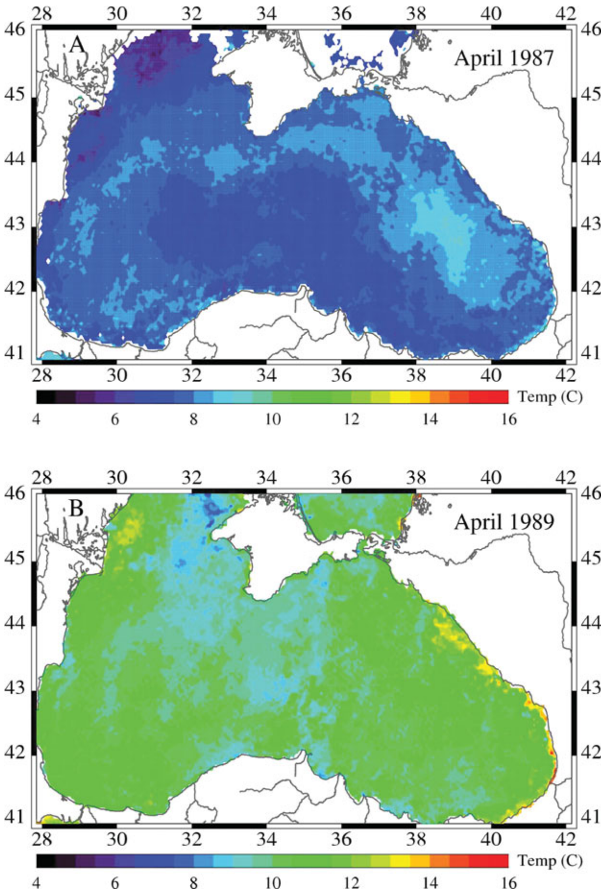

Fig. 4. Monthly-mean SST distributions for (**A**) April 1987 and (**B**) April 1989. The data are retrieved from the Pathfinder AVHRR, night time, 4.4 km resolution global data set provided by http://las.pfeg.noaa.gov/OceanWatch/servlets/. The main temperature range is 6.5–8.5°C in April 1987, and 10–13°C in April 1989.

Assessment of the temperature control hypothesis of *Mnemiopsis* invasion

The winter-average SST of the basin remained in the range of 7.3–8.2°C during 1985–90, and March monthly-mean temperature was $\sim$1.0°C colder prior to 1988 (Table I). The winter temperature during 1985–90 was therefore not warm enough to exert control on the timing of spring *Mnemiopsis* bloom as suggested by Shiganova et al. (Shiganova *et al*., 2001). However, the April and May basin-average SST difference before and after 1988 was more than 2.0°C (Table I), and even exceeded 4°C in coastal regions as indicated by the April monthly-mean SST fields for 1987 and 1989 (Fig. 4). For example, the temperature range of 10–13°C in April 1989 was attained approximately a month later during 1987 (not shown). Even April 1988 was characterized by cold temperatures ($\sim$9°C) and low *Mnemiopsis* biomass ($\sim$0.4 g C m^{-2}) along the north-eastern coastal waters in spite of exceptionally high zooplankton biomass of 18 g m^{-2} (Shiganova *et al*., 2001). In contrast, the *Mnemiopsis* biomass was close to 2.0 g C m^{-2} in April 1989 in the case of warmer temperatures around 10.5°C (Fig. 4) and a similar zooplankton biomass.

In addition, cold SSTs generally imply strong turbulence in the water column that may limit pursuit success and food capture ability of *Mnemiopsis* due to dispersion of prey patches (Wrobslewski 1984; MacKenzie and Kiorboe, 2000). Therefore, turbulence conditions during spring of 1989–90 may also result in a higher spring *Mnemiopsis* production with respect to the colder 1985–87 phase.

The years 1991–93 were also distinguished by cold (<10°C) April surface temperature and very low *Mnemiopsis* biomass, but followed by high biomass during the subsequent warm years 1994–95 when the April surface temperature exceeded 10°C (Fig. 2). This conjecture is further supported by a positive correlation ($r = 0.66$ with $P < 0.01$) between the Black Sea warmer spring surface mixed layer temperature and the

Mnemiopsis biomass increase. The mixed layer temperature of 10°C therefore seems to be a threshold for high spring *Mnemiopsis* production in the Black Sea.

Critique
The lack of systematic laboratory experiments that are necessary for a realistic parameterization of the temperature control of the *Mnemiopsis* spring reproduction in the model hindered the resolution of the role of cold and warm spring temperature controls on the *Mnemiopsis* population outbreak. However, the observations reveal convincing evidence for the limitation of spring *Mnemiopsis* production when temperature was $<10°$C even in the case of sufficiently high food availability. Under these conditions, the spring *Mnemiopsis* production was likely delayed to May. But the delay might cause further reduction in adult overwintering population, and a mismatch between zooplankton and *Mnemiopsis* production might subsequently lead to less efficient spring and summer (July–September) *Mnemiopsis* production. This was indeed the case in Sevastopol Bay (Finenko *et al.*, 2006b) and Golubeya Bay along the north-eastern coast (Vinogradov *et al.*, 2005) during the cold year 2003 with comparable severity to the years 1985–87. The highest *Mnemiopsis* biomass level of ~250 g ww m^{-2} during the summer prior to their predation by *B. ovata* was an order of magnitude lower than in a typical warm year.

If the same spring temperature threshold concept was applied to the acclimation period, the years 1983, 1984 and 1986 emerge as favourable years for the settlement and spreading of *Mnemiopsis* over the basin (Fig. 2).

DISCUSSION

Simulating the first-order characteristics of the system fairly realistically, our analysis suggests the co-existence of moderate biomass of anchovy and jellies in the absence of climate-induced over-enrichment even if anchovy were overfished. Alternatively, anchovy would probably maintain a moderate stock level together with high gelatinous biomass in the case of over-enrichment but without overfishing. The anchovy collapse and the *Mnemiopsis* bloom coincided because these mechanisms took place simultaneously. Therefore, our analysis provides a new view of the shift event that involves complex interactions exerted by overfishing, eutrophication and climate, and combines some elements of three different scenarios described above. A new proposed conceptual synthesis (Fig. 5) identifies three particular phases; the "background-conditioning" phase (1970–84), the "pre-conditioning" phase (1985–87) and the "anchovy–*Mnemiopsis* shift" phase (1988–90). These correspond to three essential stages of invasions, with some additional features, suggested by community ecology theory (Shea and Chesson, 2002): transport of an organism to a new location, establishment and population increase in the invaded locality, and regional spread from initial successful populations.

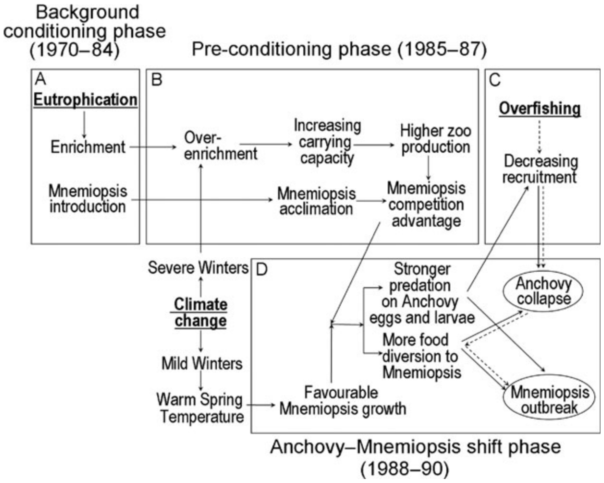

Fig. 5. Main features of the new conceptual description of the anchovy–*Mnemiopsis* shift. The boxes A and B represent the background- and pre-conditioning phases of the *Mnemiopsis* population invasion, respectively. The box C shows the additional contribution of overfishing and recruitment failure to the anchovy collapse. Box D relates the *Mnemiopsis* population outbreak and concurrent anchovy stock collapse to favourable spring temperature conditions, stronger *Mnemiopsis* predation on anchovy eggs and larvae and more food diversion to *Mnemiopsis* (arrows with continuous line) as well as overfishing (arrows with broken line).

During the 1970–84 "background-conditioning" phase (Fig. 5, Box A), the eutrophication-induced enrichment of the euphotic layer in response to increasing anthropogenic nitrate load provided increasing rates of primary and secondary productions and, at the same time, accumulated more nitrate concentration into the chemocline. *Mnemiopsis* was also introduced into the Black Sea during this phase. In the subsequent 1985–87 phase, the system was pre-conditioned by the acclimation of *Mnemiopsis* to the Black Sea conditions as well as the additional enrichment of the euphotic layer by means of climate-induced changes (Fig. 5, Box B). The latter provided more enhanced secondary production and diverted more food resources to the gelatinous group due to their competitive advantage of consuming prey under high resource conditions. The increasing fishery was also becoming critical for sustainability of the anchovy stock due to decreasing recruitment population (Fig. 5, Box C). The unfavourable winter–spring temperature conditions of the surface mixed layer,

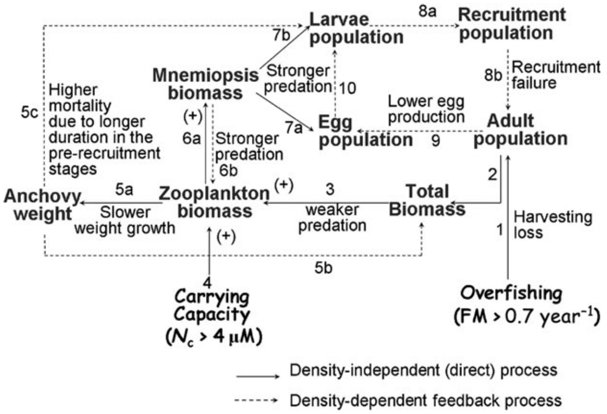

Fig. 6. Schematic description of density-independent processes (solid lines) and density-dependent processes (broken lines) exerted on anchovy stock by overfishing and *Mnemiopsis* food competition and predation. The changes in carrying capacity and fishing pressure conditions were the main drivers of the anchovy–*Mnemiopsis* shift. Plus sign marks a positive contribution. Negative contributions are unmarked. The numbers mark processes described in the text.

however, precluded *Mnemiopsis* responding favourably to the high zooplankton resource.

The actual "anchovy–*Mnemiopsis* shift" phase was initiated during 1988 once spring temperature conditions were slightly more favourable for the spring *Mnemiopsis* production with respect to 1985–87. As soon as the spring temperature conditions reverted back to normal conditions in the subsequent warm year (1989), the food competition and reproduction advantage of *Mnemiopsis* against *Aurelia* and the weakening food competition advantage of anchovy triggered the population outbreak of *Mnemiopsis* (Fig. 5, box D). At the same time, the increasing of *Mnemiopsis* predation on anchovy eggs and larvae contributed to further recruitment failure and reduction of anchovy stock in addition to the loss due to harvesting.

In Fig. 6, we provide additional details on the processes controlling anchovy stock depletion. The direct effect of overfishing (arrows 1 and 2) was a reduction of the total anchovy biomass, while one of its feedbacks was to introduce lower total egg production of adult females and thus lower recruit populations (arrows 9, 10, 8a and 8b). Another feedback was a weaker predation pressure on zooplankton and thus a positive impact on its biomass (arrow 3). Zooplankton biomass was also affected positively by the high carrying capacity (arrow 4) and negatively by strong predation pressure of the gelatinous group (arrow 6b). The latter compensated or even exceeded the positive contributions, and their net effect was either no increase or some reduction in zooplankton biomass that then slowed down the anchovy weight growth (arrow 5a). Slower weight growth led to lower anchovy weight in all age classes (arrow 5b). At the same time, longer duration of early life stage populations caused higher mortality (arrows 5c and 8a) that further contributed to the recruitment failure (arrow 8b) and reduced the total biomass (arrow 2). A negative feedback loop was also imposed by growing predation pressure of the *Mnemiopsis* population on anchovy eggs and larvae (arrows 7a, 7b and 10), which subsequently reduced its total biomass (arrows 8a, 8b and 2).

The mechanisms proposed here for the invasion of *Mnemiopsis* into the Black Sea fit well with the "niche opportunity" concept of invasion ecology (Shea and Chesson, 2002) that defined the invader's high growth rate in terms of (i) its high resource consumption rate compared with the resident species at the same resource densities, (ii) low abundance of natural enemies (e.g. diseases, predators and parasites) that permits low maintenance cost and (iii) favourable physical environment (temperature, turbulence, etc.). These factors and their interactions determine whether invasion is promoted or inhibited. We have shown that the Black Sea climate-induced over-enrichment provided a favourable resource opportunity for invasion but, at the same time, the physical environment set by cold spring temperatures inhibited the invasion until conditions become favourable in terms of warm spring temperatures. Moreover, the lack of any predator of *Mnemiopsis* (prior to the settlement of *B. ovata* into the Black Sea 10 years later than its first population outbreak) as well as its low natural mortality rate compared with its competitor promoted its invasion success, although it may not be considered an entirely successful invasion process, as evaluated next.

The model simulations possess two alternate states of the anchovy–gelatinous system: the consumer-only regime of low carrying capacity conditions and the predator-only regime of high carrying capacity conditions that are separated from each other by a wide range of co-existence regime at moderate carrying capacity conditions (Holt and Polis, 1997; Diehl and Feibel, 2000; Mylius *et al.*, 2001). Referring to Fig. 3, the *Mnemiopsis* invasion and the accompanying anchovy collapse remained within the co-existence regime in which the zooplankton biomass was also almost half of, and the anchovy stock three times higher than, their likely values in the complete *Mnemiopsis* invasion regime. This implies that the system has not been enriched sufficiently strongly during the second half of the 1980s for the complete and persistent *Mnemiopsis* invasion.

The predator (*Mnemiopsis*)–consumer (anchovy) system within the co-existence regime responds faster to changing environmental conditions (e.g. the carrying capacity and winter-spring temperature of surface waters) and thus may be subject to considerable interannual fluctuations. An interesting example is the sharp *Mnemiopsis* biomass decrease to ~ 0.5 g C m^{-2} and the corresponding increase in anchovy stock to $\sim$800 000 tonnes 3 years after the 1989–90 invasion event (Figs 1 and 2). According to Fig. 3, these changes conform roughly to $N_c = 2.5$ μM under high fishing mortality rate of 0.8 year^{-1} and therefore point to a considerable reduction in the carrying capacity of the system in 2 years. Referring to Fig. 3 in Oguz and Gilbert (Oguz and Gilbert, 2007), the pronounced reduction in zooplankton biomass during the same period, the reason for which is unclear, justifies the reduction in the carrying capacity conditions. Apparently, the severe winter 1991–93 climatic conditions introduced a strong limitation on the invasion capacity of *Mnemiopsis*, allowed anchovy to recover immediately after the collapse and conditioned the system for the next (1994–95) *Mnemiopsis* population outbreak. The partial invasion success and the subsequent fluctuating *Mnemiopsis* biomass, therefore, prevented the Black Sea confronting an ecological disaster.

CONCLUDING REMARKS

The present study provided a quantitative modelling framework for invasion dynamics of the alien ctenophore species *M. leidyi* into the Black Sea. This invasion has so far been the most dramatic large-scale gelatinous zooplankton invasion event encountered globally. The analysis was designed to assess the basin-scale characteristics of the system that undoubtedly show differences at local scales (e.g. coastal versus offshore waters, the western versus eastern basin) due to the different importance of control mechanisms (e.g. temperature, patchiness of populations, mixing and transport) and their feedbacks on physiological characteristics (e.g. mortality, growth and reproduction). According to the parameter setting of the model, the anchovy–gelatinous system varied within their co-existence regime under changing carrying capacity conditions throughout the 1980s. Prior to the mid-1980s, this regime was identified by high anchovy–moderate gelatinous biomass due to the competitive advantage of anchovy on the zooplankton resource consumption. The climate-induced enrichment together with anchovy overfishing, however, reversed the system to high gelatinous–low anchovy biomass regime at the end of 1980s. The sensitivity studies showed that they are robust features of the model within 10–20% range of some critical parameters.

Perhaps, the most important message from the example of the Black Sea *Mnemiopsis* invasion may be the difficulty of a large marine ecosystem to flip to a totally invader-dominated state by replacement of a native small pelagic fish species with an invader gelatinous species. It seems to require extremely strong environmental perturbations that should be even stronger than what the Black Sea experienced during the 1980s and the early 1990s. Therefore, more often in the case of invasion the result may be the development of a suitable niche for an alien gelatinous invader in terms of its physiological adaptation to the local conditions. Then, it becomes a member of the food web structure, shares food resources with the native small pelagic fish community and may seriously alter community interactions depending on the level of environmental disturbances.

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