

Modelling assessment of interactions in the Black Sea of the invasive ctenophores *Mnemiopsis leidyi* and *Beroe ovata*



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ABSTRACT

We analyzed the main factors that controlled the prey-predator dynamics of two invasive ctenophores, *Mnemiopsis leidyi* and *Beroe ovata* in the Black Sea using a demographic model. We assessed the bottom up cascading effect from edible zooplankton to its consumer *M. leidyi* and its predator *B. ovata*. For these purposes, we used life cycles of both ctenophores (ova, larva, juvenile, transitional and adult stages), variability of annual phenology and physiological features obtained from our field observations and experiments made in the north-eastern Black Sea over 27 years, combined with a long-term change in temperature and food availability for both ctenophores.

Model outputs were compared with field observations. Then, model scenarios were tested to understand which environmental conditions control *M. leidyi* and *B. ovata* development. Using our model, we found that the maximum annual abundances of *M. leidyi* and *B. ovata* increased with mean springtime temperature and development of spring-early summer zooplankton which is important for creation of *M. leidyi* abundance and consequently development of *B. ovata*. An assessment with changing concentration of the *M. leidyi* food (i.e. zooplankton) at the time of its annual development changed the maximum annual values reached by *M. leidyi*, and consequently *B. ovata*. It was found that time of appearance of *B. ovata* had changed to May since 2012 with increasing temperature, and as a result *M. leidyi* did not have time to reach high abundance, being grazed by *B. ovata* already since May. Model results were qualitatively the same as those from long-term field observations.

As a result, we obtained a model of two ctenophores interacting with total life structure: duration and scale of reproduction, growing from stage to stage, mortality, seasonal disappearance from water depending on temperature and prey availability. Similar analyses have never been done in the Black Sea and can be used for other seas where *M. leidyi* or both ctenophores invaded.

1. Introduction

The invasion of the carnivorous ctenophore *Mnemiopsis leidyi* A. Agassiz, 1865 in the Black Sea in the early 1980s (Vinogradov et al., 1989), and its dispersal to other seas of the Mediterranean basin and the Caspian Sea caused major, negative perturbations in these basins. This was a most dramatic example of non-native species effects on pelagic ecosystems (Shiganova et al. 2004; Finenko et al. 2003). A decade after the *M. leidyi* invasion, the arrival of its predator ctenophore *Beroe ovata sensu* Mayer 1912 in the Black Sea reversed the situation and the ecosystem started to recover (Shiganova et al. 2014). Understanding the mechanisms that control the size of the *M. leidyi* population in the Black Sea is especially important because *M. leidyi* is rapidly expanding around European seas and *B. ovata* follows it in many cases (Shiganova

et al., in press).

We analyzed field data for 27 years of observations of *M. leidyi*, before *B. ovata* and after its arrival, and edible zooplankton in the Black Sea. The same combined reproductive sequence of *M. leidyi* and *B. ovata* took place every year but with differences in value of abundance, time and duration of seasonal development of two species, determined by food concentration (edible zooplankton for *M. leidyi* and *M. leidyi* for *B. ovata*), temperature and other environmental parameters. Wind created different scale patchiness of distribution (Shiganova et al. 2014).

To better understand these processes, we used a population dynamics model to assess the mechanism of interaction at three trophic levels of the Black Sea ecosystem: the carnivorous ctenophores *Mnemiopsis leidyi* and *Beroe ovata*, which are strong drivers of ecosystem state now, edible zooplankton, and temperature.

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In the model, we analyze annual and seasonal variability of both invaders, as well as their relationships and bottom up cascading effects from edible zooplankton to its consumer *Mnemiopsis leidyi* and to *Beroe ovata* based on experimental and long-term field data from the north-eastern Black Sea.

Previous modelling assessments have been based mainly on published parameters obtained from *Mnemiopsis leidyi* in its native habitats, while *Beroe ovata* has never before been included in a modelling assessment (Kremer and Kremer, 1982; Oguz et al., 2008; 2012; Salihoglu et al., 2011). In addition there was no comprehensive study which describes bottom up effects of the two main drivers of the Black Sea, *Mnemiopsis leidyi* and *Beroe ovata*, which include their population capacity dynamics, phenology, interactions and control of *M. leidyi* development by *B. ovata*.

We assess the most important driving functions and test hypotheses that the availability of food (i.e. zooplankton for *M. leidyi*, and *M. leidyi* for *B. ovata*) and temperature have control over the duration of annual development and variability of interannual abundances. Our population dynamics model takes into account the life cycles and physiological features of the two ctenophores as a synthesis of field observations and eco-physiological laboratory experiments obtained in the north-eastern Black Sea over 27 years.

2. Materials and methods

2.1. Study area

The main ctenophore habitat is the coastal waters from where they spread with the current to open areas. Our observations were conducted in the north-eastern Black Sea with a starting sight in the coastal area of Blue Bay and offshore. Blue Bay is a small, semi-enclosed and shallow water body (depth between 7 and 14 m). There, temperature varies from 6 °C in winter to 27 °C and sometimes 30 °C in summer in last years, and salinity from 17 to 18. The major driving force for the Black Sea Rim current is cyclonic contour current on the continental slope of the Black Sea, which forms the two rings in the western and eastern parts of the Sea Meandering of the Rim Current frontal zone causes the formation of eddies, mainly anticyclonic, which migrate offshore and exchange waters and their fauna between the coastal and offshore areas. In addition, wind-driven Ekman transport, which is in a direction normal to the coastline, affects the concentration (numerical abundance and biomass) of plankton in the coastal zone (Zatsepin et al., 2010; Shiganova et al., 2014).

2.2. Field data

Most of the data on mesozoo- and gelatinous plankton were collected during expeditions of the P.P. Shirshov Institute of Oceanology of Russian Academy of Sciences, in the northeastern Black Sea from 1992 to 2004. In addition, in 2000 and up to the present time (2017) samples were collected within the Blue Bay and offshore in the north-eastern Black Sea, along a transect from the Blue Bay up to 1000 m. For present estimations we took into consideration the inshore waters where water depths ranged from 7 to 100 m in the Blue Bay and outside it (Fig. 1). In addition, samples of zooplankton and ctenophores were collected regularly around a year at monitoring station (7 m depth) in Blue Bay. The data for present model assessment were collected from stations ≤ 100 m depth. Some data for previous years were taken from Pasternak (1983), Khoroshilov and Lukasheva (1999), and Vinogradov et al. (2002, 2005, 2006). In the present study, temperature and salinity data were measured vertically with a CTD profiler. Zooplankton (including eggs and larvae of ctenophores) were collected with a Juday plankton net (0.1 m² opening, 180 μ m mesh size), and gelatinous plankton with a Bogorov Rass (BR) net (1 m² opening, 500 μ m mesh size) and a smaller size modification (0.2 m² opening, 500 μ m mesh size). All samples were collected using vertical hauls from the bottom to the surface in the area

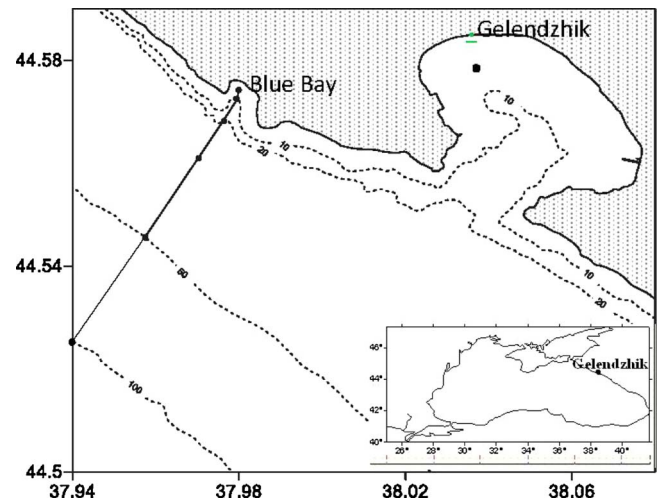


Fig. 1. Map of north-eastern Black Sea, showing the locations of Blue Bay and of the sampling transect.

where there was not anoxic layer yet. We did not use coefficient for insignificance catchability in our estimations, which was used by Vinogradov et al. (2002, 2005, 2006).

3. Demographic model

3.1. Model structure

We developed a model to explore the processes involved in the coupling of the prey *M. leidyi* and its predator *B. ovata*. These processes are included interactions between two species and forcing environmental variables.

We designed the model incorporating the known characteristics of the life cycles of two species. The timing and amplitude of the seasonal abundances depended on biological rates such as spawning, development, growth and mortality. In addition, we used forcing environmental variables such as temperature and food concentration effect on these biological rates of the two ctenophores. Among them timing of appearance ctenophores in the water column, start of reproduction, maximal reproduction rate, which coincided with maximum abundances of both ctenophores within the range of observations. As usual in modelling, the calibration of processes (feeding, spawning, growing, mortality) was based on the known ranges of parameters, which were either taken from unpublished field data and experiments conducted by one of the authors (T.A. Shiganova) or came from the literature.

The model considered the ontogenic development of the species, i.e. a period of time necessary for ovae to develop into larvae, for the latter to develop the characteristic features and properties of juveniles, and for juveniles to become adults. This period of time from hatching to mature spawning, is the generation time and it depended on the development rate at each step, which is influenced by temperature and food. This property is usually not considered in ecosystem models based on biomasses of species (Shiganova, 2009). Our field and experimental data taken into consideration were compared and verified with published data (Finenko et al., 2003; Kremer and Kremer, 1982; Kremer, 1976, 1979, 1994; Kremer and Reeve, 1989; Kremer et al., 1986; Reeve et al., 1989; Salihoglu et al., 2011).

Thus, our model considered four life-cycle stages for each of the two-ctenophore species (i.e. ova, larva, juvenile, and adult), and each stage comprised several age classes. A developmental time is ascribed to each stage, which set the average time required for an individual to acquire the characteristics of the next stage. The sum of time spent in each developmental stage gives the generation time. This is summarized in Fig. 2. On Fig. 2 each line corresponds to ctenophore life stages,

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