

Ctenophores—Invaders and Their Role in the Trophic Dynamics of the Planktonic Community in the Coastal Regions off the Crimean Coasts of the Black Sea (Sevastopol Bay)

G. A. Finenko^a, Z. A. Romanova^a, G. I. Abolmasova^a, B. E. Anninsky^a, T. V. Pavlovskaya^a, L. Bat^b, and A. Kideys^c

^a *Kovalevskii Institute for Biology of the Southern Seas, National Academy of Sciences of Ukraine, Sevastopol, Ukraine*

^b *Samsun University, Faculty of Fishery, Sinop, Turkey*

^c *Institute for Marine Sciences, Near East Technical University, Erdemli, Turkey*

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Abstract—The abundances, biomasses, and population structures of two introduced ctenophore species—*Mnemiopsis leidyi* and *Beroe ovata*—were monitored along with mesoplankton in the near-shore waters of the northern Black Sea (Sevastopol Bay and adjacent regions) over a period of four years (2000–2003), after the *B. ovata* invasion. The annual dynamics of the *M. leidyi* population were similar in these years: very low abundances and biomass values were observed during the major part of the year (unlike previous years) with a short-term peak in the summer–early autumn. *B. ovata* development during the growth in the *M. leidyi* biomass resulted in a sharp fall in the *M. leidyi* biomass down to extremely low values. The interannual differences in the populations of both ctenophore species were reflected by their quantitative parameters: the maximum biomass of *M. leidyi* varied from 790 g/m² in 2001 to 211–266 g/m² in other years. The maximum biomass values of *B. ovata* (38.9 and 32.5 g/m²) were observed in 2001 and 2003, respectively. In 2000–2003, from July to September, during the peak in *Mnemiopsis* development, the population consumed from 1.9 ± 0.4 to 13.4 ± 5.7% of the mesoplankton biomass per day, while in the years of *B. ovata* absence, these values were as high as 30–40%. For the first time, the grazing rate of microzooplankton by *M. leidyi* larvae was estimated. In August 2003, the maximum daily consumption rate was as great as 23–25% of the microzooplankton biomass. The daily rations of the *Mnemiopsis* larvae on microzooplankton were close or even higher than those on mesoplankton.

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INTRODUCTION

At the end of the 1980s, a new factor appeared in the Black Sea, which affected its ecosystem—the invasion of the North Atlantic ctenophore *Mnemiopsis leidyi*, which started to control the abundance of zooplankton, its biological diversity, the structure of the community, and the regularities of the functioning of the pelagic ecosystem. The invasion of the *M. leidyi* changed the direction of the energy flux in the planktonic community of the Black Sea. Instead of the trophic chain “zooplankton–fishes–planktophages,” the energy flux was driven over another chain: “zooplankton–*M. leidyi*.” In so doing, the trophic chain directed to fishes was sharply reduced, which resulted in serious economic damage.

At the end of the 1990s, the appearance of a new invader, the lobeless ctenophore *Beroe ovata*, induced new changes in the planktonic community [2, 3, 12, 13, 15, 21, 22, 24, 32, 33]. Being a monophage, which, under the conditions of the Black Sea, consumes exclusively *M. leidyi* (and, to a lesser extent, Pleurobrachia),

it regulates its abundance and, this way, controls other components of the ecosystem [34].

This paper is aimed at the quantitative estimation of the role of ctenophores–invaders in the trophic dynamics of the planktonic community in the inshore areas of the Crimean coast of the Black Sea (Sevastopol Bay and adjacent waters) based on the studies of the seasonal and interannual dynamics of the abundance, biomass, and population structure of the invaders and of mesoplankton (the principal food of *M. leidyi*).

MATERIALS AND METHODS

The collection of gelatinous zooplankton was performed either every month (in the winter–spring period) or two–three times a month (in the summer and fall). The samples were taken in the first part of the day with a Bogorov–Rass net with a diameter of 80 cm and a mesh size of 500 μm [8] at five stations (at three stations in Sevastopol Bay and at two stations in the shelf areas of the sea adjacent to the bay. This survey lasted from September 1999 to December 2003. The bay is 7 km long at a mean width of 850 m; its

mean depth comprises 12 m, and the water salinity is about 18‰.

At all the stations, the standard 0- to 10-m layer was hauled. In June–August, at the two stations of the shelf area with sea depths of 50 and 45 m, a thermocline was observed, whose upper boundary (10–12 m) coincided with the lower limit of sampling. Therefore, at these stations, only the community of the mixed layer the Black was analyzed. At all the stations, the surface water temperatures were measured.

Immediately after sampling, counting of all the gelatinous animals and their length measurements (total length of *B. ovata* and oral–aboral length of *M. leidy*) were performed. Small animals (<5 mm) were counted and measured at the laboratory under microscope at a magnification of $\times 16$. The abundances of different size groups of ctenophores were estimated with a size interval of 5 mm.

The biomass was calculated as the product of the abundance and the mean wet weight of each size group using the following regression equations [19]:

$$Beroe\ ovata: W = 0.85 L^{2.47} \quad 10 < L < 120$$

$$Mnemiopsis\ leidy: W = 1.07 L^{2.76} \quad 2 < L < 10$$

$$M. leidy: W = 1.31 L^{2.49} \quad 11 < L < 70,$$

where L is the body length, mm, and W is the wet weight, mg.

The total biomass was calculated as the sum of the biomasses of all the size groups in the population. In selected cases, a significant variability was observed in the ctenophore abundance between the stations; meanwhile, the annual dynamics were identical and, therefore, for all the stations, we used the mean values.

Mesoplankton was sampled simultaneously with the gelatinous organisms at a single monitoring station at the entrance to the bay using vertical hauls from 0 to 10 m with a Juday net with an opening of 37 cm and a mesh size of 120 μm . In 2003, mesoplankton was sampled at three stations: station 10 in the shelf area of the sea, station 7 at the entrance to the bay, and station 3 inside the bay. The samples fixed with a 4% formaldehyde solution were processed in a standard way in order to determine the abundance and size of each of the species and stage. The total biomass of mesoplankton was calculated from the abundance and weight of each group [9]. The fodder zooplankton was estimated as the difference between the total biomass and the biomass of gelatinous animals and dinoflagellates *Noctiluca scintillans*.

Only in 2003 was the microzooplankton examined together with the mesoplankton. The materials were collected using two methods: with a 10-l Niskin bottle sampler from depths of 0, 5, and 10 m and with an Upstein plankton net (Hydro-Bios GmdH, Germany) with a mesh size of 55 μm from the water column 0–10 m. In the bottle samples, ciliates and, in selected seasons, small rotifers were taken into account. Ciliates were counted in live samples in a Bogrov chamber with

isolated channels. The total volume of a sample examined was 20 ml and implied eight replications of 2.5 ml each. In the net samples, after their fixation with a Lugol solution, multicellular organisms, such as juvenile Copepoda and Cladocera stages, rotifers, mollusk larvae, nauplii of Cirripedia, and others, were counted. The biomasses of individual groups of organisms were determined using commonly accepted techniques from the body sizes and their similarity to various geometrical figures.

The intensity of the mesoplankton grazing by the *M. leidy* population was estimated by the formula $CR = 14.9 W^{-0.309}$, where CR is the filtration rate, l/g of dry weight per hour, and W is the energy equivalent of the body, cal/ind. [11]. When converting into energy units, we assumed that the caloric value of *M. leidy* equals 0.62 cal/mg of dry matter and the dry mass comprises 2.2% of the wet mass [11].

The calculations of the microzooplankton grazing by the larvae of *M. leidy* performed by us was based on an experimentally obtained equation which relates the filtration rate to the larva size [36]:

$$CR = 9.361 L + 4.541,$$

where CR is the filtration rate, ml/ind per hour, and L is the animal length, mm.

RESULTS

Seasonal Dynamics of the Abundance and Biomass of the Components of the Planktonic Community

Ctenophores. Monitoring studies of mesoplankton and ctenophores–invaders have been conducted by us since 1999 [12, 21, 22]. However, we will trace the annual development cycle of the heterotrophic links of the planktonic system only by the results of the surveys performed in 2003, which most completely covered the summer–fall period (the time of the mass development of both ctenophore species).

From January to May, only small amounts of *M. leidy* were observed in the plankton of the bay and adjacent regions of the shelf part of the sea (at abundances of 0.2–3.6 ind/m² and biomass values of 1–10 g/m²). This species was represented by large individuals with an oral–aboral length of 25–55 mm and individual wet weight of 5–35 g (Figs. 1a, 1b, 2). In the middle of May, the wintered fall–winter population started its reproduction (at a temperature of about 16°C and a biomass of zooplankton of 0.5 g/m²). Simultaneously, adult animals 30–55 mm long were presented in plankton as well as juveniles 0.25–0.3 mm long and eggs. Starting from this time, owing to the recruitment of the juveniles of the new generation, the population gradually, though insignificantly, increased its abundance. In so doing, the biomass was still low and ranged from 7 to 20 g/m². At the end of May–beginning of June, the core of the population (80% of the total abun-

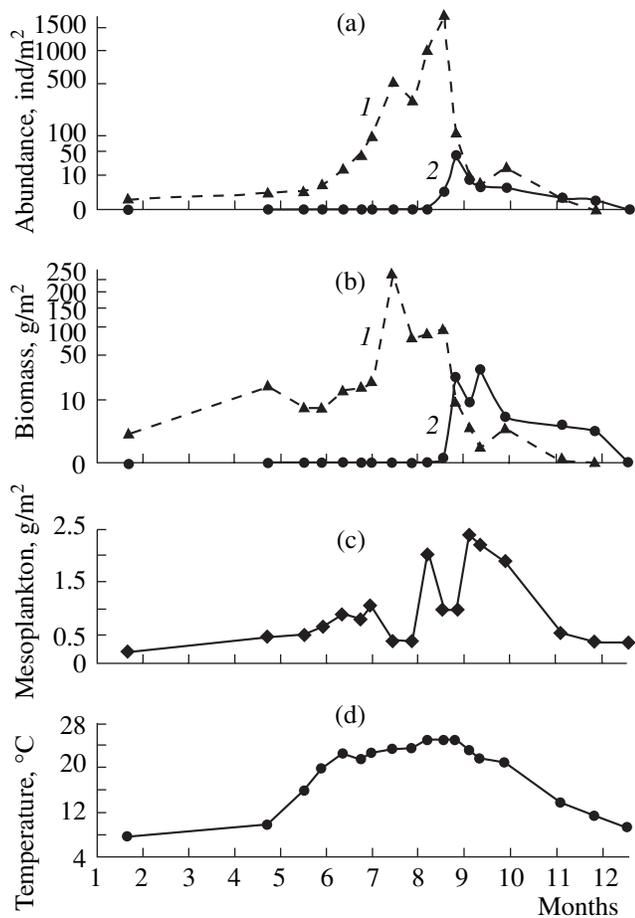


Fig. 1. (a) Abundance and (b) biomass of the ctenophores (1—*M. leidy*; 2—*B. ovata*); (c) mesoplankton biomass and (d) water temperature in Sevastopol Bay in 2003.

dance) consisted of the grown juveniles of the new generation 0.3–1.25 mm in length. The intensive reproduction in May was proved by our laboratory experiments; at this time, the fecundity of the sexually mature ctenophores was the greatest over the entire season (1600 ± 560 eggs in a clutch); in so doing, virtually all the adult animals reproduced. At the beginning of June, both the fecundity (206 ± 122 eggs) and the percentage of the reproducing animals (50–75%) decreased (Fig. 3).

In the middle of June, at a temperature of 21.5°C , a second wave of reproduction was observed and 94% of the population was represented by larvae smaller than 2 mm. Adult animals were represented only by the size group 40–45 mm, which made up only 6% of the total abundance. In July–August, the number of larvae was still sufficiently high (about 80% of the total abundance), while the size range of adult animals gradually decreased. This change was related to the dying out of the large animals of the preceding populations, whose proportion in the total abundance comprised only frac-

tions of a percent, and the bulk of the adult part of the population was composed of the grown juveniles of the new generation. The reproduction of *M. leidy*, which started in May, proceeded at different rates over the entire summer and led to a sharp increase in the abundance in the first half of August, when the individuals of the spring generation also started to reproduce. In the second half of August, the abundance dynamics changed sharply, which was caused by the appearance of another ctenophore—*B. ovata*—in plankton. During a short period (10–12 days), it reduced the abundance and biomass of *M. leidy* by an order of magnitude (Figs. 1a, 1b). With the further development of the *B. ovata* population, the population of *M. leidy* decreased up to December, when no ctenophores were available in plankton sampled with the methods available.

The scanty wintered population of *B. ovata* started to reproduce next to the peak of *M. leidy* development and rapidly reached the maximum abundance. In the middle of August, in the bay and adjacent regions of the shelf part of the sea, minor amounts of eggs and newborn juveniles were observed; by the end of August, 90% of the population was represented by juveniles smaller than 5 mm in size and only isolated adult animals with maximum sizes of 75 mm were noted (Fig. 4).¹ The adult individuals of the generation of the previous year seem to enter the coastal regions after wintering in the open part of the sea. At this time, intensive reproduction began: the average fecundity of the most actively reproducing part of the population with body lengths of 35–70 mm was 4500 ± 250 eggs in a clutch. All the eggs were viable and developed into larvae (Fig. 5). The high reproduction intensity of *B. ovata* provided a rapid increase in its abundance. The period of intensive reproduction was short-term (it lasted about two weeks); subsequently, the fecundity and the percentage of the reproducing ctenophores decreased significantly. The fecundity decreased from 4500 to 500 eggs in a clutch, only 50% of the adult population were involved into reproduction, and the proportion of resorbed eggs increased up to 15%.

In order to estimate the potential pressure of *B. ovata* on the *M. leidy* population, we used the data on the respiration rates [37] to calculate the minimum daily food demand of the *B. ovata* population. At the end of August and in first half of September, it comprised from 25 to 47% of the *M. leidy* biomass (in energy units). Taking into account the animal growth, which proceeded at that time, the grazing of *M. leidy* by the *B. ovata* population should be even greater. As early as in the second half of September, the *B. ovata* population faced a shortage of food: its respiration requirements were manifold (20–100 times) greater

¹ In Fig. 4, the data of hauls with a Bogorov–Rass net are presented. In parallel, eggs and larvae of *B. ovata* were counted in the samples taken with a Juday net (at three stations). In this case, the abundance of eggs and larvae was greater, though the dynamics was similar to that shown in the figure.

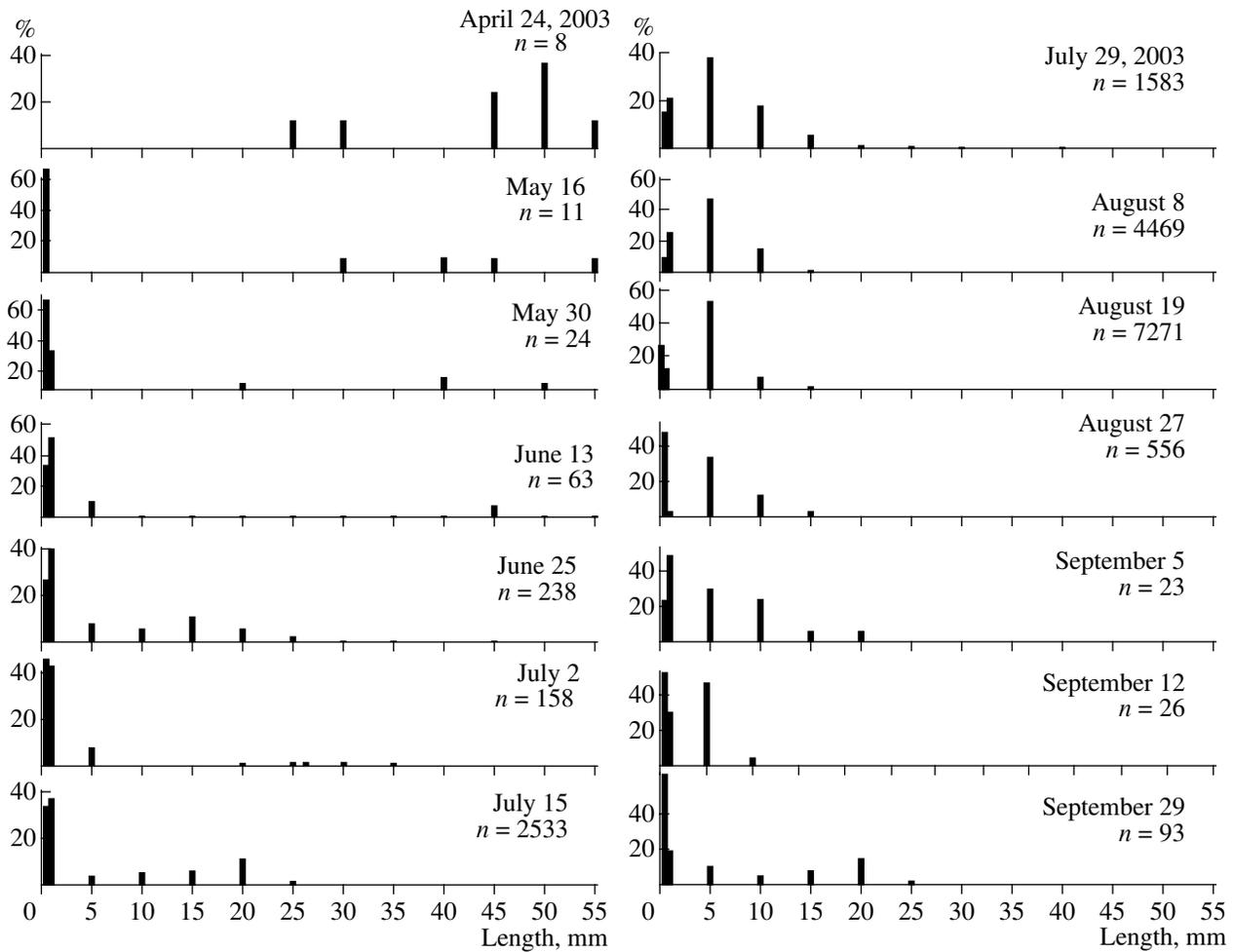


Fig. 2. Size structure of the *M. leidyi* population in Sevastopol Bay in April–September 2003.

than the *M. leidyi* biomass. Thus, the fodder base of *B. ovata* was exhausted over a very short period (10–12 days). Having almost completely destroyed the prey population, *B. ovata* stopped its reproduction and its abundance and biomass gradually decreased down its absolute disappearance in December.

Mesoplankton. In 2003, mesoplankton in Sevastopol Bay presented by copepods, mostly by *Acartia clausi*, which, in July and September, comprised up to 55 and 69% of the fodder plankton biomass, respectively. In August 2003, a mass development of the thermophilic Cladocera species *Penilia avirostris* was observed; it reached 82% of the fodder zooplankton biomass with a corresponding decrease in the proportion of *Acartia* down to 14% [6]. The particular feature of this year consisted of the relatively low biomass of meroplankton (less than 0.1 g/m² over the greater part of the year as compared to 1.8–2.0 g/m² in the preceding years) and of the growth in the contribution of *Sagittia setosa* (up to 7%) to the total biomass of the fodder zooplankton in September. The biomass of mesoplankton increased from January to the middle July and in the

second half of July decreased two- to threefold (Fig. 1c). Precisely during this period, the maximum biomass of *M. leidyi* was observed; its abundance increased more than fivefold, and the size spectrum of the population featured its maximum width. In July–August, the ctenophore population grazed from 4 to 11% (on average, $7.1 \pm 2.9\%$) of the zooplankton biomass per day. After the *B. ovata* appearance in the middle August, the biomass of zooplankton started to increase rapidly and reached its maximum (more than 2 g/m²) in September. Thus, the effect of *M. leidyi* on zooplankton was very short-term.

Microzooplankton. The seasonal variations in the abundance and biomass of microzooplankton at different stations were different. At the stations located in the shelf part of the sea and inside the bight (stations 10 and 3), the variations were characterized by two peaks (the early spring peak at the end of May–beginning of June and the summer peak in August–September). Meanwhile, at station 7 located at the entrance to the bay, no summer peak was observed: the early spring maximum at the end of May was followed by a decrease, and both

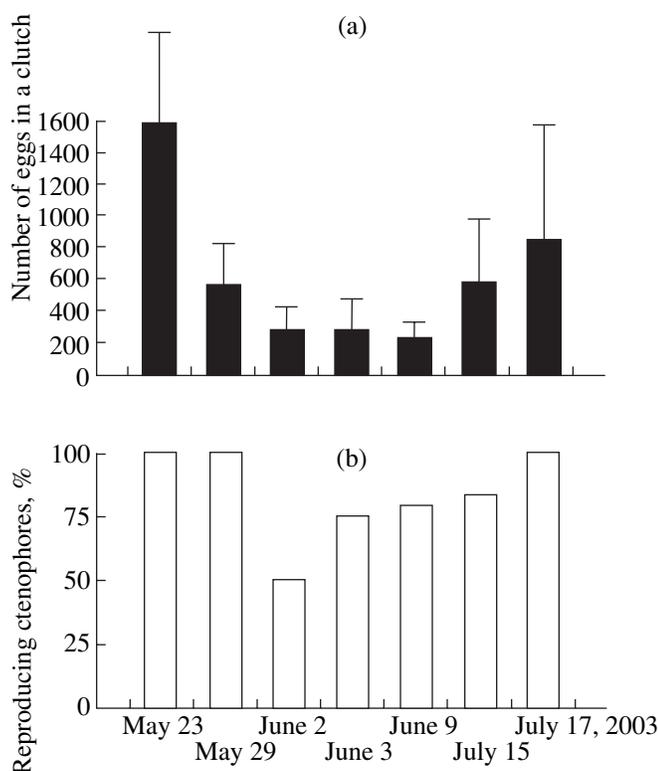


Fig. 3. (a) *M. leidy* fecundity and (b) percentage of reproducing ctenophores in Sevastopol Bay in 2003 (size group 60–80 mm).

the abundance and biomass were virtually constant until October averaging 10^6 ind/m² and 1 g/m², respectively (Fig. 6). During the period of the maximum development of microzooplankton, the bulk of its biomass was provided by ciliates, except for the spring peak at station 3 formed by rotifers. The maximum biomass values were observed at station 3 inside the bay, while the minimum values were confined to the shelf part of the sea.

It is known that, along with mesoplankton, *M. leidy* at the early stages of its development can also consume microzooplankton [35, 36]. As was shown above (Fig. 2), in 2003, the maximum abundance of the *M. leidy* larvae (up to 10 mm in length) was observed in August. The larvae were represented by three size groups: <0.5, 0.5–5.0, and 5–10 mm with a mean length of each group of 0.25, 3, and 7.5 mm, respectively. Based on the above-presented formula (see Materials and Methods), using the abundance of larvae of each size group, we calculated the total water volume, which can be filtered by the larvae per day removing all the microzooplankton from it. At selected stations, the maximum potential daily grazing of microzooplankton by *M. leidy* larvae in August 2003 changed from 0.9 to 23–25% of its biomass; it was highest at station 3 with the maximum biomass of microzooplankton and *M. leidy* larvae (Table 1). Meanwhile, regardless of the grazing rate, the microzooplankton biomass showed a

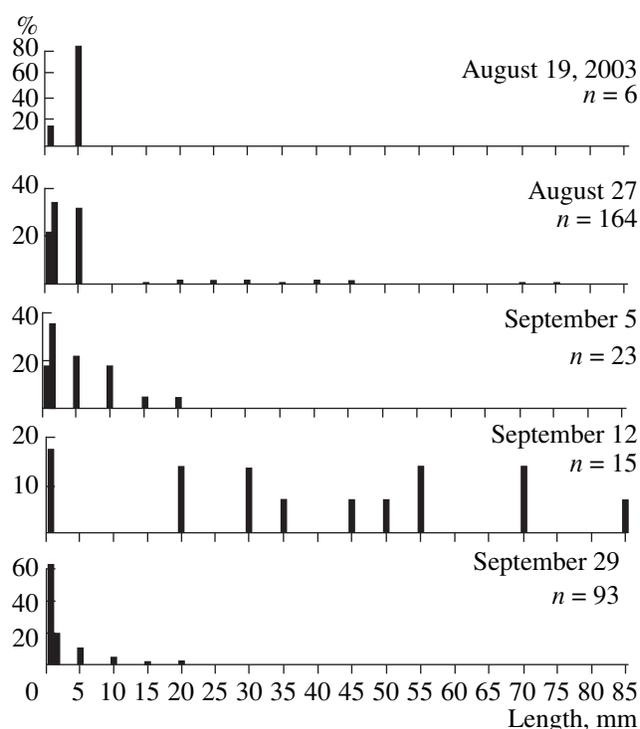


Fig. 4. Size structure of the *B. ovata* population in August–September 2003.

tendency to increase rather than decrease; in addition to the high growth rate of ciliates, this might also result from their intensive development on the mucus released by ctenophores.

Thus, the principal feature of the development of the populations of ctenophores and zooplankton in 2003 was presented by the longer period of reproduction of *M. leidy* (from May to November) as compared to preceding years. For a short time (the second half of July), *M. leidy* controlled the zooplankton biomass, which resulted in its twofold decrease. After *M. leidy* was suppressed by its predator *B. ovata*, the biomass of zooplankton was rapidly restored. This was a clear manifestation of the cascade effect in the population dynamics in the food chain zooplankton–*M. leidy*–*B. ovata*.

Features of the Interannual Dynamics of the Ctenophore–Invader Development

During the entire observation period after the *B. ovata* appearance (including September–December 1999, when *B. ovata* was first encountered in the plankton of the bay), the characteristics of development of the populations of both ctenophore species were similar, though the times of the appearances and the quantitative parameters of the species abundance differed in different years (Fig. 7). For example, the times of the appearance of *M. leidy* in the bay differed by almost a month: the end of July in 2001 and the second half of

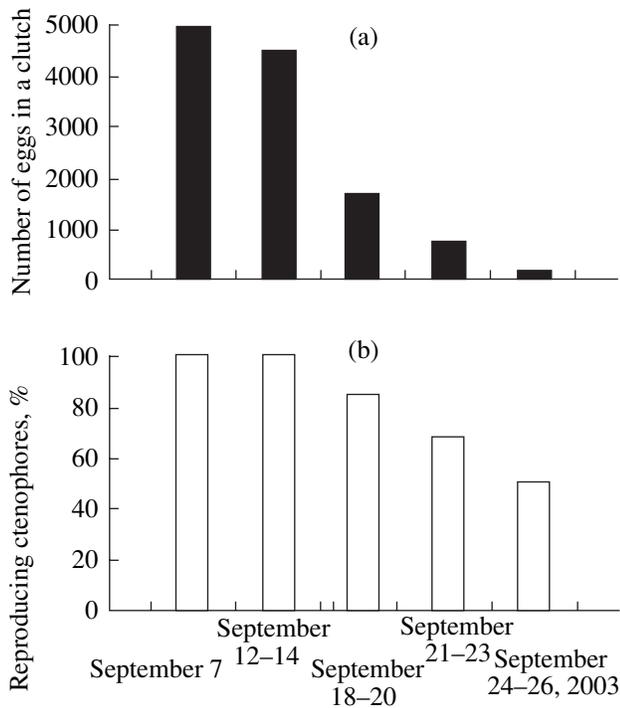


Fig. 5. (a) Fecundity of *B. ovata* and (b) percentage of reproducing animals in September 2003.

June in 2002. As a rule, the *M. leidy* population reached its maximum abundance a month and a half after its appearance. The smallest duration of the population development was observed in 2001, which was the warmest of all the years of observations. In this year, despite the late appearance of *M. leidy*, its abundance reached a maximum as early as in 25 days. Two–three weeks later, in all the years except for 2000, a peak of *B. ovata* development was observed followed by a subsequent decrease in its abundance. The coincidence of the maximums of the abundances of *B. ovata* and *M. leidy* observed in 2000 is related to the infrequent sampling of samples collected; because of this, we might have missed the true peak of *M. leidy* abundance. *M. leidy* retained its low abundance over the entire fall (0.4–6 ind/m² or <0.1–2.4 g/m² in different years). Note that the peaks of abundance and biomass

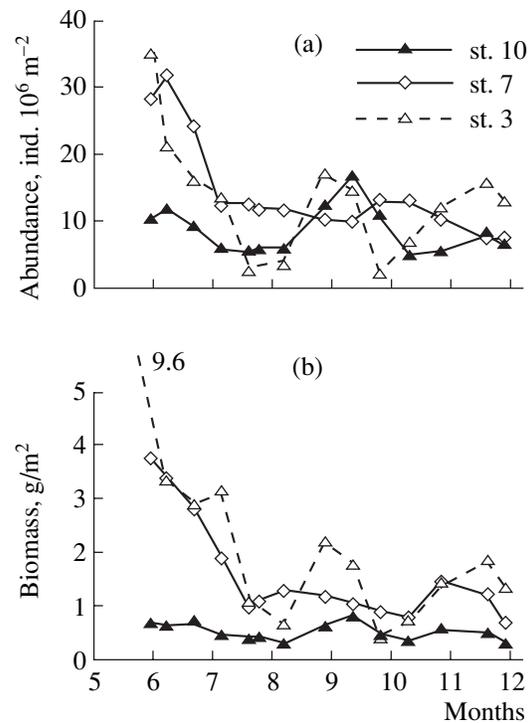


Fig. 6. (a) Abundance and (b) biomass of microzooplankton in Sevastopol Bay in 2003.

of both species do not coincide in time, since the main contribution to the biomass is made by large adult animals, while high abundance values are provided by larvae (for *M. leidy*) and juvenile individuals (for *B. ovata*). The interannual differences in the development of the population of both ctenophore species consisted in their quantitative parameters: the maximum biomass of *M. leidy* (790 g/m²) was noted in 2001, while during the other years it was virtually constant (211–266 g/m²). *B. ovata* reached its maximum biomass values in 2001 and 2003 (38.9 and 32.5 g/m², respectively), while in 2000 and 2002, it biomass did not exceed 11 g/m².

A comparison between the values of the mean biomass of fodder zooplankton during the two-month

Table 1. Daily rations on meso- and microzooplankton and percentages of grazing of both components of the planktonic community by the *M. leidy* population in August 2003. All the values are presented as percentage of the total biomass

Date	$T^{\circ}\text{C}$	Number of station	<i>M. leidy</i> biomass, (g/m ³)	Daily ration		Grazing	
				meso	micro	meso	micro
August 5	25.1	10	0.55	13.1	0.7	0.6	0.8
		7	2.79	9.3	9.1	5.0	9.7
		3	3.27	3.3	18.7	7.7	25.6
August 19	25.0	10	0.41	0.7	5.8	0.7	1.2
		7	1.37	5.1	15.3	6.5	11.6
		3	4.58	2.2	29.3	9.4	23.6

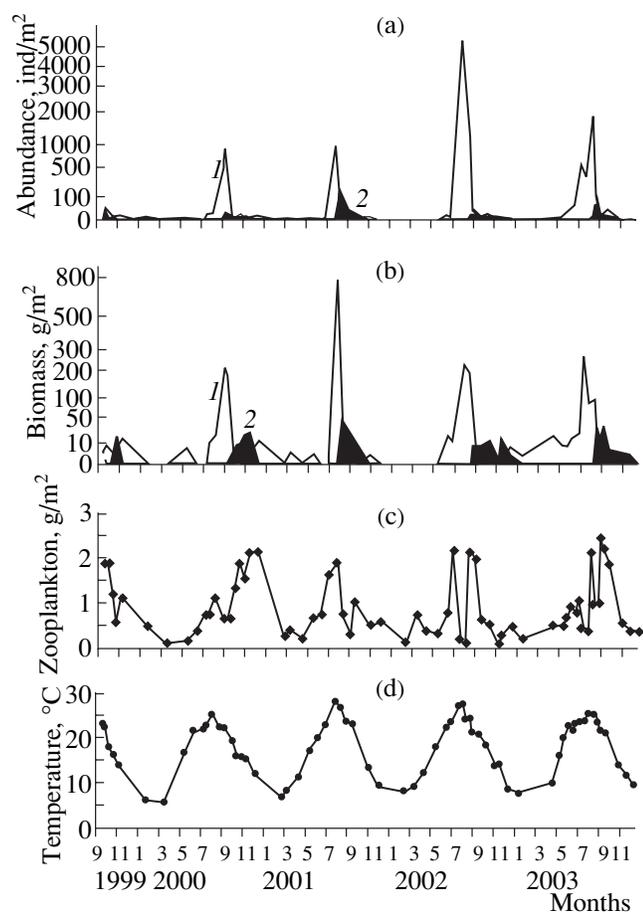


Fig. 7. (a) Abundance and (b) biomass of the ctenophores (1—*M. leidy*; 2—*B. ovata*); (c) mesoplankton biomass and (d) water temperature in Sevastopol Bay in 1999–2003.

period prior to maximum *M. leidy* development showed that, in 2001, it was almost twice as high as in other years (1.42 against 0.8–0.88 g/m²); this was probably caused by the high summer temperatures and sufficient food supply. These factors provided a high fecundity and, correspondingly, very high abundance of ctenophores.

From June through September in the years 2000 to 2003, after *B. ovata* appearance, the population of *M. leidy* in the period of its maximum development consumed from 1.9 ± 0.4 to $13.4 \pm 5.7\%$ of the zooplankton biomass per day; only in August 2001, when the *M. leidy* biomass showed a short-term period of biomass values comparable with those typical of the “pre-*B. ovata*” years, consumption increased up to 27%

(Table 2). During other periods of the year, the pressure of ctenophores on the planktonic community was insignificant (less than 1%) owing to the fact that *B. ovata* efficiently controlled the population of its prey. The ratios of the population in the peak periods comprised from 0.4 to 9.2% of the biomass expressed in energy units (Table 3). The minimum food demands or maintaining daily rations calculated from the respiration rates of the population [1] changed from 3.3 to 6.4% of the population biomass during the peaks of different years. A comparison between the daily rations and the minimum food demands showed that, at a fodder zooplankton biomass less than 0.1 g/m³, the *M. leidy* population experienced a shortage of food.

DISCUSSION

Seasonal and Interannual Population Dynamics

The four-year-long monitoring of the abundance and biomass of two ctenophore species—invaders, fodder zooplankton, and microzooplankton (only in 2003) allowed us to recognize the particular features of their annual cycles and the mechanisms of abundance regulation, and to quantitatively estimate the interrelations between the three subsequent trophic levels (mesoplankton (microzooplankton)—*M. leidy*—*B. ovata*).

While in the first years after *B. ovata* invasion, the issue of its ability for acclimatization under the conditions of the Black Sea was urgent, the observations of subsequent years made it clear that this species found its place in the composition of the Black Sea macrozooplankton, occupied its niche, and started to control development of the pelagic ecosystem.

The first *B. ovata* appearance in Sevastopol Bay coincided with its appearance in other regions of the Black Sea (the northeastern and southern parts of the sea) [2, 12, 13, 24]. Its further development in the regions studied was similar. The seasonal dynamics of the abundance of both species in the northeastern part of the Black Sea off the Caucasian coast (Golubaya Bay and adjacent regions) in the years 1999–2004 featured the same patterns with certain time shifts in selected years; this was especially clearly expressed in 2004 [3–6, 14–16, 33]. Here, similarly to Sevastopol Bay, the maximum *M. leidy* biomass was observed in 2001 and was comparable with the values observed before *B. ovata* invasion. The maximum *M. leidy* abundance observed in selected periods in other years (for example, in August 2002) reached very high values (4500–5000 ind/m²) both at some of the shallow-water

Table 2. Grazing of mesoplankton by the *M. leidy* population (% of the biomass per day) in 2000–2003

Month	2000	2001	2002	2003
June–August	0.2 ± 0.05	6.0 ± 6.1	13.2 ± 5.9	7.1 ± 2.9
September–November	1.2 ± 0.9	0.01	0.06 ± 0.04	0.5 ± 0.4

Table 3. Abundance, biomass, zooplankton consumption, respiration, and food consumption of the *M. leidy* population in Sevastopol Bay in July–September 2000–2003

Date	<i>T</i> , °C	<i>N</i> , ind/m ³	<i>B</i> , g/m ³	<i>B</i> , cal/m ³	<i>W</i> , g	<i>ZB</i> , g/m ³	<i>PI</i> , %	<i>Q</i> , cal/day	<i>R</i> , cal/day	<i>Q/B</i> , %	<i>R/B</i> , %	<i>Q/R</i>
September 6, 2000	21.9	40.7	21.1	266.5	0.52	0.063	1.6	9.51	4.29	3.3	1.6	2.0
September 3, 2000	21.8	86.6	17.3	218.1	0.2	0.065	2.2	6.66	4.86	2.8	2.2	1.3
August 1, 2001	27.8	93.8	79.0	995.7	0.842	0.19	27.0	26.6	41.6	2.5	4.2	0.6
July 30, 2002	26.7	281.2	18.8	236.5	0.067	0.013	14.3	8.05	1.48	3.2	0.7	4.6
August 6, 2002	27.1	535.7	23.3	294.0	0.044	0.008	20.3	10.01	1.30	3.2	0.4	8.0
August 20, 2002	23.8	182.5	18.9	238.0	0.104	0.213	12.5	8.89	21.38	3.5	9.0	0.39
August 29, 2002	24.0	92.2	10.1	127.5	0.11	0.20	6.6	4.81	10.75	3.5	5.4	0.65
July 15, 2003	23.4	51.2	26.6	335.4	0.512	0.043	10.7	10.83	3.68	2.2	1.1	2
July 29, 2003	23.4	31.7	7.7	96.9	0.243	0.039	3.9	6.69	1.22	6.4	1.2	5.3
August 8, 2003	25.1	99.3	8.7	110.1	0.088	0.208	6.1	4.17	10.13	3.5	9.2	0.38
August 19, 2003	25	181.8	9.6	121.5	0.053	0.098	7.8	7.63	6.15	5.8	5.1	1.14

Note: *T* [degree Celsius] is the surface temperature, *N* is the abundance, *B* is the biomass, *W* is the mean wet weight of *M. leidy* in the population, *ZB* is the zooplankton biomass, *PI* is the zooplankton grazing, *Q* is the respiration, and *R* is the daily ration of the population.

stations of the northeastern coastal zone [16] and in Sevastopol Bay (our data). The biomass was lower, since the population consisted of small individuals. The avalanchelike changes in the abundances of both species during the period of *B. ovata* development, which we traced over four years, is also confirmed by the results of the studies performed on September 2 and 11 and October 3 of 2001 in Golubaya Bay. On September 2, about two weeks after *B. ovata* appearance, both ctenophore species were represented in plankton (33 ind/m² and 2.6 g/m² of *M. leidy* and 48 ind/m² and 295 g/m² *B. ovata*). Meanwhile, already by September 11, *M. leidy* was absolutely consumed and only *B. ovata* was observed in plankton with a significantly smaller abundance (15 ind/m²) and biomass (147 g/m²). In our opinion, not only the temperature decrease [16], but also the destruction of the food stock resulted in the fact that, at the beginning of October, *B. ovata* was absent, while *M. leidy* was represented by larvae and small individuals with a low abundance (less than 60 ind/m²).

The abundance and biomass of *B. ovata* in Golubaya Bay were higher than those in Sevastopol Bay; in August 2001, they reached 700–800 ind/m² and 500 g/m², respectively. In Sevastopol Bay, during all the years considered, the abundance and biomass of *B. ovata* did not exceed 140 ind/m² and 39 g/m² (August 2001). In contrast to the northeastern part of the sea, the biomass in Sevastopol Bay never reached

values comparable to the *M. leidy* biomass values in the first years of its expansion in the Black Sea².

In the northwestern part of the sea off the Bulgarian coast, *B. ovata* was first encountered in 1997 [26]. During the surveys in 1998 and 1999 (in late September), *B. ovata* presented in plankton reaching an abundance of 40–80 ind/m², while in August–September of 2000 and 2001, it was absent in both the coastal and the open parts of the sea [23]. About 90% of the *M. leidy* population at this time was represented by juvenile individuals with a high abundance and biomass, which suggested a reproduction peak that preceded *B. ovata* appearance. The absence of *B. ovata* seems to be related to the time of the observations, when it simply had not reached the Bulgarian waters. Indeed, in these years, in Sevastopol Bay, we first observed *B. ovata* somewhat later—in the middle September in 2000 and in the middle August in 2001. In our opinion, the interannual variations in the times of development of two ctenophore populations and the rapid (avalanchelike) change in their condition require frequent observations in order to estimate correctly the dynamics of both populations. This kind of research allows one to obtain

² When calculating the abundance and biomass of zooplankton of both ctenophore species, we introduced no correcting coefficients for the hauling properties of the plankton net, while in the studies of the Shirshov Institute of Oceanology, Russian Academy of Sciences, in Golubaya Bay, the author applied various coefficients (2–4) for different species and size groups (Shushkina et al., 2004), which hampers comparison of the data from different regions.

more valuable information even as compared to oceanographic cruises, when sampling is performed only a few times during the year within a short interval of time.

Ctenophore Pressure on the Zooplankton Community

In a series of previous studies, an inverse correlation was established between the ctenophore density and the biomass of lobate ctenophores, which made the authors suggest that they control the copepod biomass. Meanwhile, gelatinous predators, which consume less than 10% of the zooplankton biomass per day, cannot reduce their abundance and biomass [19, 27, 28, 31, 32]. Higher consumption rates (more than 20% per day) result in a sharp reduction of the prey abundance [20, 29]. In the waters of Chesapeake and Narragansett bays, the maximum pressure of the *M. leidyi* population might reach 31% of the total zooplankton biomass per day [18, 20, 27]. In Narragansett Bay, the mean daily predatory index increased up to 20% of the zooplankton biomass, when larvae and juvenile individuals of *M. leidyi* were taken into account in the calculations; from 56 to 91% of the total consumption was provided by predator activity of ctenophores less than 10 mm in length. The higher specific clearance rate of larvae as compared to adult ctenophores led to a disproportion between the larva biomass and predatory impact on zooplankton.

In Sevastopol Bay in June–August 1995 and in the open waters of the Black Sea in September 1996, six–seven years after the *M. leidyi* “outburst,” the daily values of predatory impact on zooplankton were high reaching 30–40% of the zooplankton biomass [11, 17], which pointed to its insufficient food provision. From July through September in the years 2000–2003, after *B. ovata* appearance, the *M. leidyi* pressure on mesoplankton decreased significantly: in the period of its maximum development, the population consumed from 1.9 ± 0.4 to $13.4 \pm 5.7\%$ of the zooplankton biomass per day. In other periods of the year, the ctenophore pressure on the zooplankton community was insignificant (less than 1%), because *B. ovata* efficiently controlled the population of its preys. A high degree of food provision of the *M. leidyi* population (the ratio of the mesoplankton biomass to that of *M. leidyi* expressed in carbon units) was also observed in September–October 2001, when *B. ovata* presented in plankton, at the shallow-water stations in the northeastern part of the Black Sea [16].

Assuming that the daily consumption by the *M. leidyi* population should not exceed 10% of the zooplankton biomass and that the mean clearance rate obtained in experiments is about 1.5 l/ind per day, the calculated critical biomass of ctenophores that do not affect mesozooplankton should not be greater than 4 g/m³ or 120 g/m² (if the greater part of the population dwells in the upper 30-m layer) [5, 30]. As follows from our observations, in the recent years, after the *B. ovata*

invasion in the near-shore regions of the Black Sea, overcritical values of *M. leidyi* biomass are observed only during short periods and only during these periods does the *M. leidyi* population control the zooplankton community.

In selected years, the maximum abundance and biomass of *M. leidyi* may reach values greater than those before the *B. ovata* invasion owing to the better food provision of the compact wintering part of the population and, correspondingly, to its intensive growth and high fecundity. The density of the *M. leidyi* population is a function of the food availability and the role of *B. ovata* consists in reducing the *M. leidyi* biomass in the fall rather than of restriction of its maximum biomass. In recent years, the mass development of *M. leidyi* has been limited to a significantly shorter period (1–2 months) as compared to preceding years (5–6 months).

In the period of maximum development, the *B. ovata* pressure on *M. leidyi* is short-term though very intensive. According to our data, in Sevastopol Bay, the potential daily consumption rate of *M. leidyi* by the *B. ovata* population comprised 25–47% of its biomass (with no account for the energy expenditures for growth and reproduction); in selected years, off the Crimean and Caucasian coasts, it could even exceed the biomass of the prey [12, 16, 21].

Thus, the new component of the food web—*B. ovata*—started to control the abundance of *M. leidyi*; it reduced the pressure of *M. leidyi* on other components of the ecosystem and the related intensity of the matter and energy fluxes over the bottom-up and top-down food chain.

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