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Population dynamics, ingestion, growth and reproduction rates of the invader *Beroe ovata* and its impact on plankton community in Sevastopol Bay, the Black Sea

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The impact of the introduced ctenophore Beroe ovata on its prey Mnemiopsis leidyi, another invader ctenophore voraciously feeding on mesozooplankton, and consequently on the mesozooplankton community, was evaluated by undertaking both laboratory and field studies in the northern Black Sea. Ingestion and growth rates as well as the gross growth efficiency of B. ovata were estimated from laboratory experiments. The daily ration of ctenophores was related to food abundance within a wide range of prey concentration and never reached saturation. Beroe ovata required high food rations (not less than 20% of body weight per day) for growth. The abundances, biomasses and population structures of these two introduced ctenophore species were also monitored, along with mesozooplankton, in inshore waters of the northern Black Sea (i.e. Sevastopol Bay and adjacent regions) over a period of 3 years (1999–2001) which is after B. ovata's arrival. The annual dynamics of the M. leidyi population were similar for the last 3 years: very low abundances and biomass values were observed during most of the year (unlike the previous years), with a sudden increase in summer–early autumn, but only for about a 2 month period. The B. ovata bloom during the peak M. leidyi biomass resulted in the M. leidyi biomass falling sharply to extremely low values. The predatory impact of M. leidyi on prey zooplankton was found to be reduced during the period of study compared with before.

INTRODUCTION

The accidental introduction of the northwestern Atlantic ctenophore *Mnemiopsis leidyi* in the early 1980s radically affected the Black Sea ecosystem (Vinogradov *et al.*, 1992; Shiganova, 1998; Shiganova *et al.*, 1998). Pronounced changes in plankton community structure took place during the peak occurrence of this ctenophore in the late 1980s. The *Aurelia aurita* biomass fell sharply because of competition for food with *M. leidyi*. The previously abundant zooplankton species like the copepod *Oithona nana* and the chaetognath *Sagitta setosa* were not found in samples taken in 1989; the abundance of the copepod *Paracalanus parvus* and cladocerans *Penilia avirostris* and *Pleopis polyphemoides* decreased dramatically while the copepod *Acartia clausi* became dominant in inshore waters. The total biomass of microzooplankton fell by 5- to 10-fold and mesozooplankton 6-fold (Kovalev *et al.*, 1998).

Mnemiopsis consumed a considerable proportion of the zooplankton (Finenko and Romanova, 2000) that had been the food for pelagic fish and their larvae in the years before the arrival of *M. leidyi*. In 1989 the fish catches decreased sharply for all the countries around the Black Sea (Kideys, 1994). Despite speculation about different possible reasons, e.g. climatic and hydrological fluctuations as well as anchovy population cycles (Niermann *et al.*, 1999), overfishing (Gücü, 1997) and anthropogenic pollution of the sea (Zaitsev and Alexandrov, 1997), the

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invasion of the exotic ctenophore *M. leidyi* might be considered as the main factor (Zaika, 1994).

The lack of natural predators feeding on *M. leidyi* resulted in temperature and food conditions being the only factors controlling the distribution and abundance of its population. In the Black Sea *Mnemiopsis* showed the typical pattern of a new colonizer: after its mass development in 1989 and 1990 (~2 kg m^{-2} biomass in the offshore waters) with a secondary increase in 1995, *M. leidyi* number and biomass fell to moderate (but still significant) levels of ~200 g m^{-2} (Mutlu *et al.*, 1994; Shiganova, 1998; Mutlu, 1999; Kideys and Romanova, 2001). During these years some positive changes in the pelagic ecosystem of the Black Sea occurred: the zooplankton biomass in the central Black Sea has been recovering since 1992, some species (*O. nana* and *S. setosa*) appeared again in inshore waters (Zagorodnyaya *et al.*, 2001). However, it is worth noting that during the second increase of *M. leidyi* levels in 1995, mesozooplankton biomass was again very low in the coastal waters of the Black Sea (Kovalev *et al.*, 1998).

The appearance of a new invader ctenophore *Beroe*, a known feeder on *Mnemiopsis* in native waters (Kremer, 1976), at the end of the 1990s in the Black Sea caused further improvements in the planktonic community. The consequence of this new invasion was positive for the recovery of the Black Sea ecosystem.

In autumn 1999 the first estimation of the predatory impact of *B. ovata* on the *M. leidyi* population was carried out in the Sevastopol and Blue Bays, the northern Black Sea. The *B. ovata* population appeared to graze from 5 to 80% of the *M. leidyi* population biomass daily and was found to be very effective in controlling the *M. leidyi* population in inshore waters of the Black Sea (Finenko *et al.*, 2000, 2001; Shiganova *et al.*, 2000; Shushkina *et al.*, 2000; Vostokov *et al.*, 2001). By analyzing the long-term distribution of *Mnemiopsis*, it has already been observed that the biomass of this ctenophore has been decreasing since the arrival of its predator *Beroe* in both Sevastopol and Blue Bays as well as in the southern Black Sea (Shiganova *et al.*, 2000, 2001; Finenko *et al.*, 2001; Kideys and Romanova, 2001). A reduction in the *Mnemiopsis* biomass and therefore decreased food competition with fish would result in future improvements of food conditions particularly for pelagic fish and hence fisheries.

The quantification of the top-down control mechanism exerted by *B. ovata* is important to understand ecosystem changes occurring in the pelagic ecosystem of the Black Sea. Therefore this investigation aimed (i) to study seasonal and inter-annual dynamics (1999–2001) of abundance, biomass and population structure of *M. leidyi* and *B. ovata* in Sevastopol Bay and adjacent water regions; (ii) to measure ingestion, growth and reproduction rates of *B. ovata* and the effects of food concentration and body weight on these parameters; and (iii) to estimate the grazing impact of *B. ovata* and *M. leidyi* on their prey populations.

METHOD

Abundance, biomass and population structure

Ctenophores (*M. leidyi* and *B. ovata*) were collected either monthly (in the winter–spring period) or twice a month (in summer–autumn) during the daytime with a Bogorov-Rass net (500 μm mesh size and 80 cm diameter) (Kiselev, 1969) at seven stations in Sevastopol Bay (stations 1–7) and at five stations in adjacent water regions (stations 7a–11) during September 1999–November 2001 (Figure 1). The Bay is 7 km long and on average 850 m wide with an average depth of 12 m. As in the Black Sea, the salinity of the Bay is ~18‰.

Maximum depths at stations 2–9 (except 6) varied from 10 to 18 m, at stations 10 and 11 depth reached 50 and 45 m. At stations 1 and 6, having a depth of <9 m, only horizontal samples were taken for analysis of population structure. At all other stations the standard layer of 10–0 m was sampled by vertical tows. There was a thermocline at the two deep stations (i.e. 10 and 11) during June–August, the upper boundary of which (10–12 m) coincided with the lower boundary of our sampling. There was not any halocline at these stations (Gordina *et al.*, 2001). The surface temperature was measured at each station.

Immediately upon retrieval, samples were examined, the ctenophores were counted and their lengths (total length of *B. ovata* and oral–aboral length without lobes of *M. leidyi*) were measured to the nearest 1 mm; the abundance of the ctenophores of different size groups (with intervals of 10 mm) was estimated.

The biomass was calculated from the abundance and the mean wet weight of each group using related regression equations (Finenko *et al.*, 1995, 2001):

$$\textit{B. ovata}: \quad W = 0.85\, L^{2.47} \qquad 10 < L < 120$$

$$\textit{M. leidyi}: \quad W = 1.07\, L^{2.76} \qquad 2 < L < 10$$

$$\textit{M. leidyi}: \quad W = 1.31\, L^{2.49} \qquad 11 < L < 65$$

where L is length in millimeters and W is wet weight in milligrams. The total biomass was computed as the sum of biomass of all size groups. Significant variability of ctenophore abundance could be observed between the stations in some cases but the annual dynamics was the

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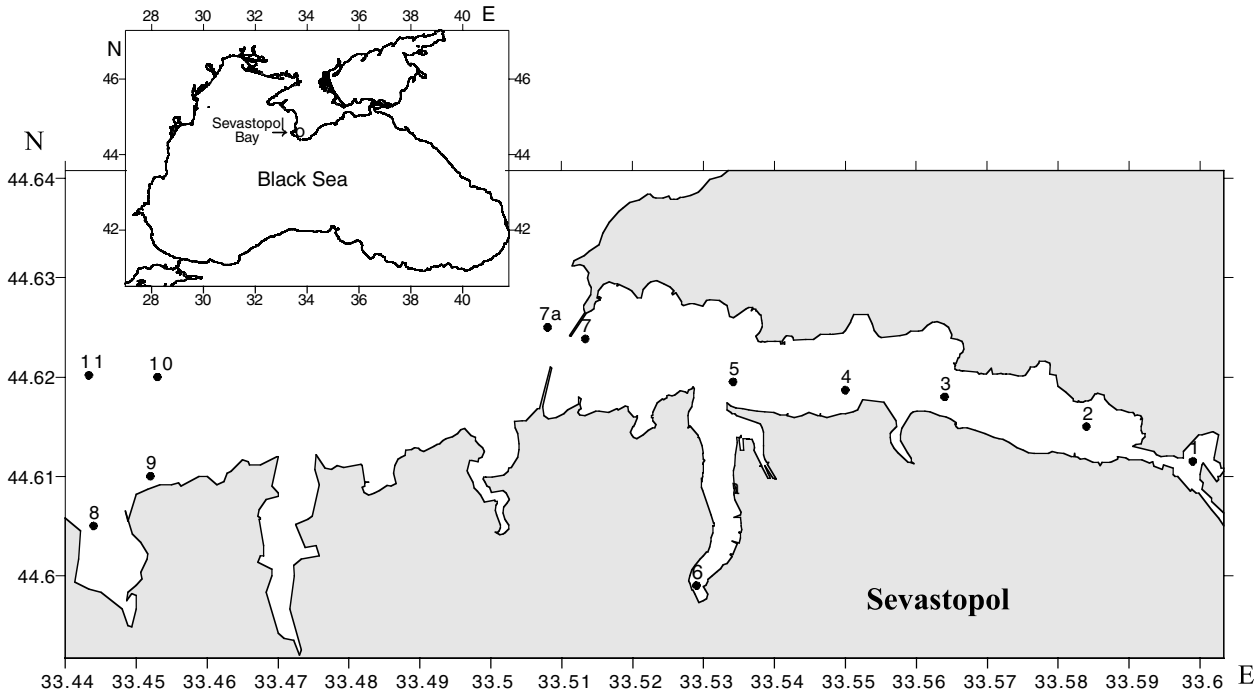


Fig. 1. Sampling locations 1–11 in Sevastopol Bay and adjacent water area.

same at all stations, so data obtained from all stations were integrated to calculate average number and biomass of ctenophores. The mesozooplankton samples were collected at similar time intervals from one monitoring station (station 7) using a Juday net (opening diameter 37 mm, mesh size 120 μm) by vertical hauls from near the bottom to the surface (10–0 m). At this station, zooplankton investigations have been undertaken during the last three decades by the IBSS and this enabled us to compare our data from previous years. Immediately after transportation to the laboratory, the samples were processed under a binocular microscope in Bogorov's counting chamber (Kiselev, 1969) for determining the abundance of each species and stage or size group. The biomass of total mesozooplankton was calculated by taking into account the abundance and weight of each of these groups (Petipa, 1957). Fodder zooplankton is evaluated separately without taking into account gelatinous species or the dinoflagellate *Noctiluca scintillans*.

The data from long-term (1976, 1989–1990 and 1995–1996) observations of zooplankton abundance and species composition in Sevastopol Bay were used for comparison (Gubanova *et al.*, 2001). The samples were collected at the same station (station 7 in our study) twice per month with the same sampling and calculation methods as we used. The annual averages were calculated by averaging the monthly means from January to December for each year.

Estimation of ingestion, growth and reproduction rates

The long-term experiments (8–11 days) with adult *B. ovata* were conducted to estimate digestion time, ingestion, growth and reproduction rates. Undamaged animals after careful selection were measured, weighed and placed in 5 l vessels containing 112 μm filtered seawater. The lengths and wet weights of *B. ovata* in the experiments ranged from 16 to 65 mm or from 0.55 to 40 g. *Mnemiopsis leidyi* specimens of 5–10 mm length (5–30 individuals per container) or 10–35 mm (1–7 individuals per container) were offered as food. Water in the containers was changed daily, the number of uneaten *M. leidyi* was counted and new prey specimens were added to maintain the specified food concentration. The *B. ovata* specimens were measured and weighed every 2–3 days. To examine the reproduction rate, water from each experimental vessel was filtered through a 112 μm mesh daily, and eggs (with a size of 830 ± 0.80 μm) retained on the mesh were transferred into 100 ml glass Petri dishes and counted in Bogorov's counting chamber under a binocular microscope. The *Beroe* feeding was tested at three food concentrations: I, 0.75; II, 1.40; III, 2.4 g wet wt l^{-1}. The consumption rates (R, g wet wt ind.$^{-1}$ day^{-1}) were calculated from the measured difference in concentration and total weight at the beginning and the end of observations. Digestion time was studied in the same experiments.

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Once ingestion occurred the *B. ovata* specimens were monitored every 15 min until defecation was complete and the gut was empty.

The average specific growth rates (μ, day^{-1}) were estimated assuming exponential growth:

$$W_t = W_0 \, e^{\mu t}$$

where W_t and W_0 are final and initial weights in mg, and t = time in days.

All experiments were conducted at a temperature of 18 ± 1°C.

To calculate the gross growth efficiency of *Mnemiopsis* and *Beroe* the dry:wet weight ratios of 0.022 and 0.024, caloricity of 0.64 and 0.68 cal mg^{-1} dry weight and carbon content of 6.5 and 6.6% of dry weight were taken, respectively (Anninsky, 1994, 2000; Finenko and Romanova, 2000; Finenko *et al.*, 2000).

RESULTS

Abundance, biomass and population structure of ctenophores

The annual dynamics of the *M. leidyi* population were similar during the 3 years: usually very low abundance and biomass during the winter–spring period and a sharp increase in summer–early autumn (early September in 2000 and mid-July–early August in 2001) (Figure 2A and B). Maximum biomasses on average were as large as 211.5 g m^{-2} in 2000 and 790.3 g m^{-2} in 2001. The appearance of *Beroe* during high levels of *M. leidyi* resulted in a sharp decrease of *Mnemiopsis* biomass down to 0.20 g m^{-2} in 2000 and to 0.02 g m^{-2} in 2001 and remained at this level for the next few months. After the disappearance of *B. ovata* in late autumn the *M. leidyi* biomass displayed a secondary peak, which was lower than the major one. In 1999 a summer peak of *M. leidyi* biomass was not found (it appeared to have occurred before sampling began), but in September–October, when *B. ovata* was still present in the plankton, the *M. leidyi* biomass (2.1–8.1 g m^{-2}) was lower than in previous years (Finenko and Romanova, 2000) but higher than secondary peaks in the next 2 years.

Beroe ovata was found in the plankton of Sevastopol Bay during 3 months: from September to November in 1999–2000 and from August to October in 2001. It appeared ~2 weeks after the maximum *M. leidyi* biomass (Figure 2A and B). In late September 1999, when *B. ovata* was first found in Sevastopol Bay the population consisted of animals measuring from <10 to 110 mm in length, whilst ctenophores of 10–50 mm size range were dominant (54%) (Figure 3). Reproduction was almost

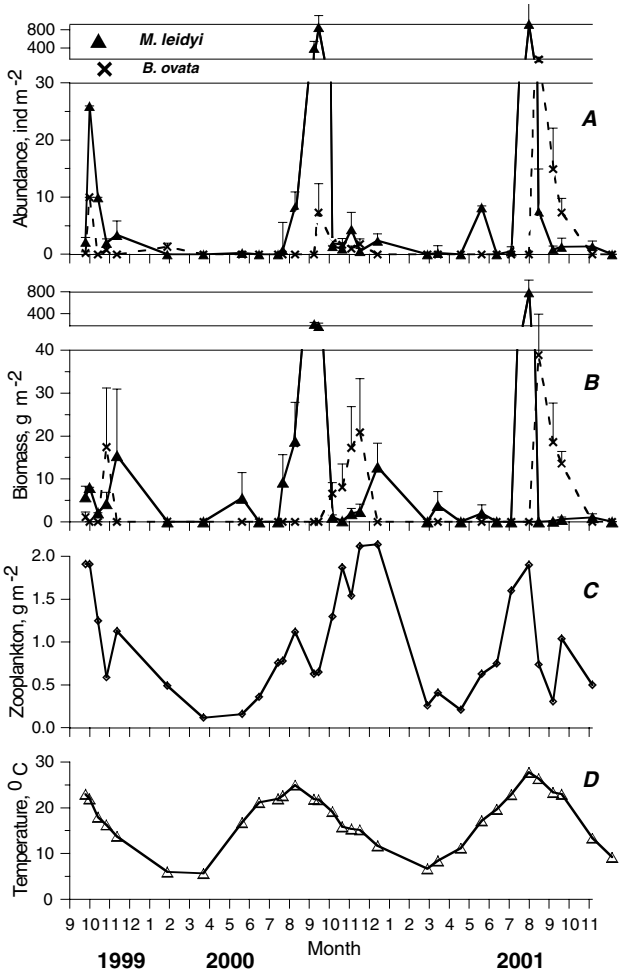


Fig. 2. (**A**) Abundance and (**B**) biomass of *M. leidyi* and *B. ovata*, (**C**) zooplankton biomass and (**D**) temperature (°C) in Sevastopol Bay in 1999–2001.

complete by this time. In September 2000, juvenile *Beroe* of <10 mm were the only size group, whilst in October–November ctenophores of 10–50 mm dominated (97 and 70% of total number). In August 2001, 90% of the population consisted of individuals of <10 mm, most of which were as large as 10–30 mm in September.

The abundance characteristics of *Beroe* were consistent from year to year with maximum values occurring at the beginning of population development. In 2001, *B. ovata* abundance and biomass were much higher than in the previous 2 years.

The annual dynamics of the prey zooplankton biomass in 1999–2001 were characterized by one summer–autumn maximum (1.9–2.0 g m^{-2}) generated by the copepoda *Acartia clausi*, a few cladoceran species (60–90% of total biomass) and meroplankton (especially nauplii of *Balanus*) (Figure 2C). The increase in mesozooplankton biomass by late autumn with the sharp

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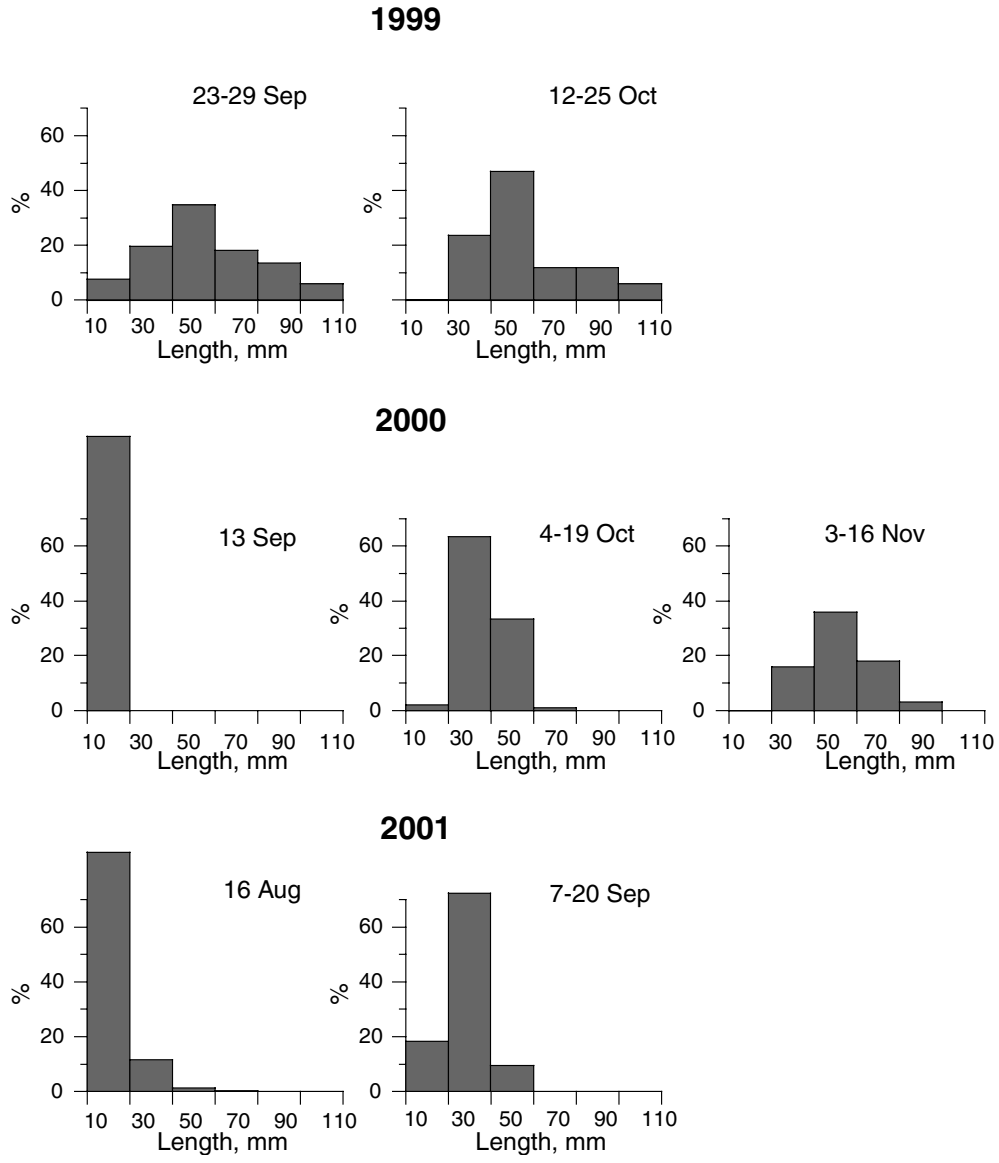


Fig. 3. Size structure of *B. ovata* population in 1999–2001 in Sevastopol Bay.

decrease in *M. leidyi* was particularly notable for the year 2000.

Digestion time, ingestion, growth and reproduction rates of *B. ovata*

Digestion time of adult *B. ovata* at 19 ± 10°C varied from 0.75 to 5 h at the tested wet weight range of both ctenophores (*Beroe* 0.55–27.5 g, *Mnemiopsis* 0.39–6.88 g). *Beroe ovata* of every size consumed both large and small *M. leidyi*, and the ratio between weight of prey and predator (*p*) affected the digestion time (*DT*) (Figure 4). The relationship between these values could be expressed as:

$$DT = 2.956\ p^{0.59}\ (n = 17,\ r^2 = 0.61,\ P < 0.01)$$

for a prey–predator weight ratio range of 0.03–3.24.

Specific daily ration of adult ctenophores (*SDR*, %) in the experiments with food concentration 1.8 g wet wt l^{-1} ranged from 15 to 460% of body wet weight (*W*, g) from the largest to the smallest animals and could be described as (Figure 5)

$$SDR = 259\ W^{-0.703};\ (n = 64,\ r^2 = 0.70,\ P < 0.01)$$

The clearance rate (the water volume swept clear

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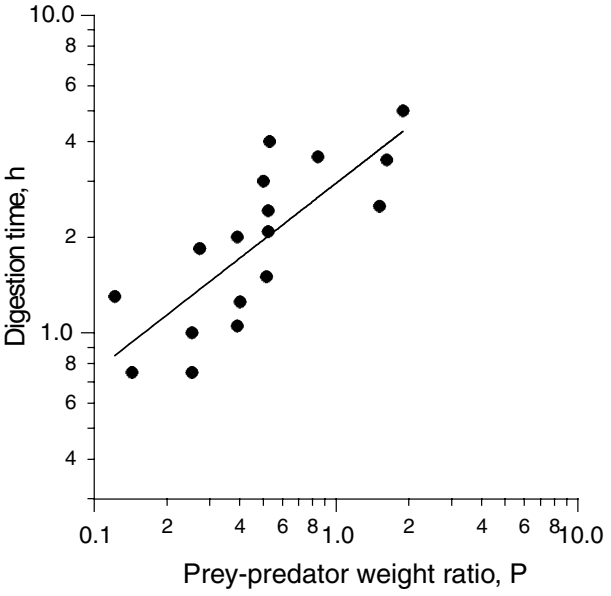


Fig. 4. Relationship between digestion time (h) and prey–predator wet weight ratio in *B. ovata*.

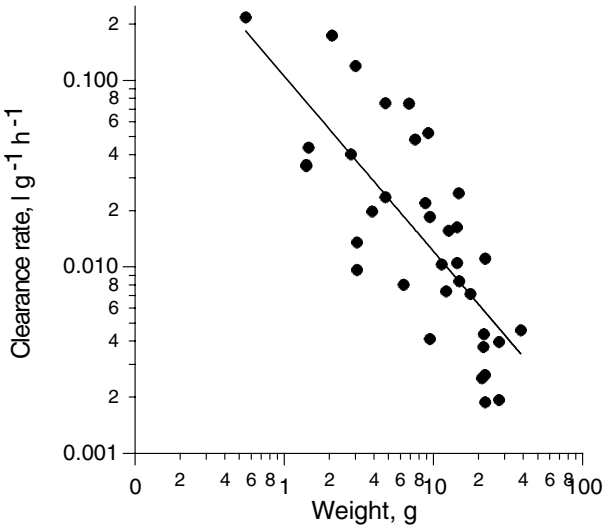


Fig. 6. Relationship between clearance rate (l g^{-1} h^{-1}) and wet weight (g) in *B. ovata*.

during a time period per unit body weight) did not depend on the density of *M. leidyi* in the range of 0.8–6.2 ind. l^{-1} or 0.47–7.36 g l^{-1} but the negative correlation between clearance rate (*CR*, l g^{-1} wet wt h^{-1}) and the wet weight of ctenophores (*W*, g) was evident (Figure 6); the equation describing this relationship was as follows:

$$CR = 0.105\ W^{-0.939}\ (n = 36,\ r^2 = 0.59,\ P < 0.01)$$

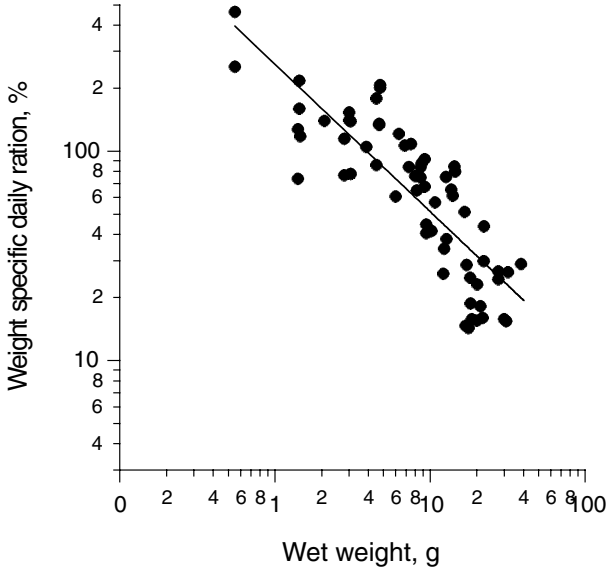


Fig. 5. Relationship between weight-specific daily ration (%) and wet weight (g) in *B. ovata*.

At exponential growth that is characteristic of ctenophores (Zaika, 1972), the specific growth rate does not depend on the size but on the specific ration. In our experiments the specific growth rate increased from –0.05 to 0.20 while the ration increased from 27 to 150% of body weight (Figure 7). The same relationship was observed for gross growth efficiency (*K*), which was negative (~–0. 26) at the ration value <27% of wet weight (Figure 8). As can be seen from Figure 5, under these food conditions large *Beroe* lost some weight. Increasing the ration improved growth efficiency.

In our experiments *B. ovata* started reproduction at a body length of 12–13 mm. Separate determinations of egg wet weight yielded a value of 0.153 mg egg^{-1}. Under controlled food conditions during 10 days when daily weight-specific rations averaged 20–108% of *B. ovata* wet weight, they had 4–6 clutches and the total number of eggs laid by one ctenophore ranged from 2066 to 4220 (Table I) or from 0.2 to 1.6% of body weight (0.02–0.16% per day).

Predatory impacts of *M. leidyi* on zooplankton and *B. ovata* on the *Mnemiopsis* population

Based on *M. leidyi* abundance, the individual wet weight of ctenophore in the population over the year and its clearance rate (*CR*, ml ind.$^{-1}$ h^{-1}) measured in laboratory experiments for animals of different wet weight (*W*, g), according to:

$$CR = 53.08\ W^{0.405}$$

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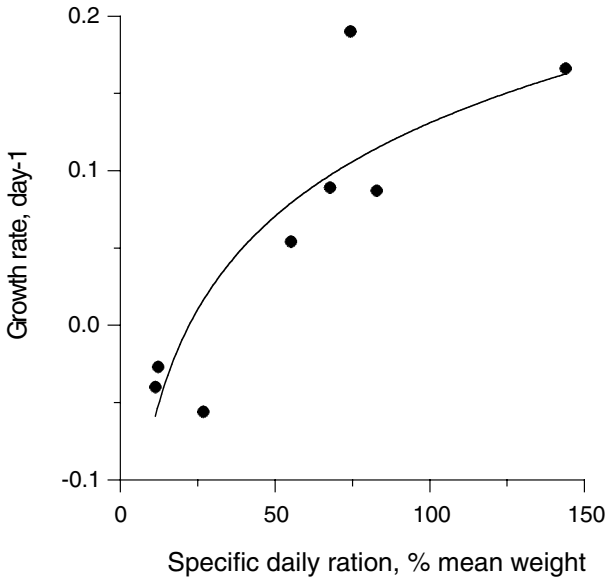


Fig. 7. Effect of specific daily ration (% mean wet weight) on specific growth rate (day^{-1}) in adult *B. ovata*.

at 22°C (Finenko and Romanova, 2000), the predatory impact of *M. leidyi* populations on zooplankton have been estimated. Being almost a non-selective predator *Mnemiopsis* could consume all types of zooplankton and remove 4–6% of the biomass daily in August–September 2000 and ~16% in early August 2001 when abundance peaks of the *M. leidyi* population occurred. Later the *Mnemiopsis* population was devastated due to the predation of *B. ovata* and the predatory effect became low (below 1% per day).

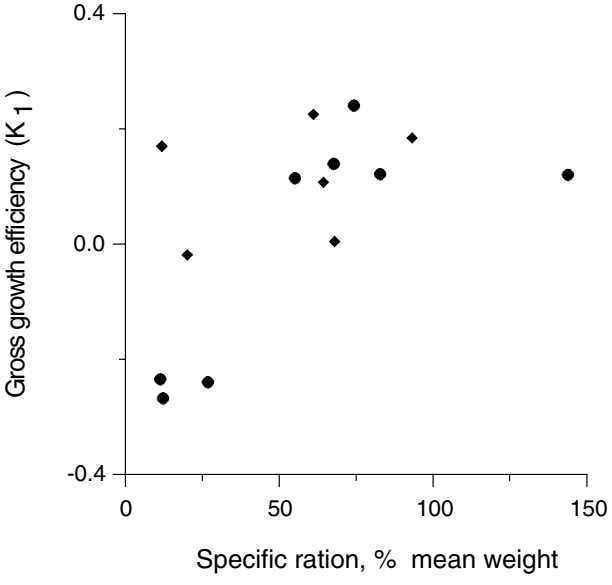


Fig. 8. Effect of specific daily ration (% mean wet weight) on gross growth efficiency (K_1) at two food concentrations: 1.68 ± 0.47 g l^{-1} (diamonds), 2.54 ± 0.80 g l^{-1} (circles).

Table I: Fecundity of B. ovata in long-term feeding experiments

No. of bottle	*Beroe* wet wt, (g)	Specific daily ration, (% wet wt)	Total egg number
1	4.68	108.3 ± 33.0	4007
2	10.7	97.7 ± 43.2	2066
3	17.0	70.1 ± 27.2	4220
4	21.8	20.1 ± 8.4	2525

DISCUSSION

Population dynamics

The ability of *Mnemiopsis* to adapt successfully to seasonal fluctuations in food abundance and temperature enables them to increase their population density very rapidly. Although the *Mnemiopsis* peak biomass is suggested to be governed by temperature in the northwestern Atlantic (Purcell *et al.*, 2001), in the past, high biomass and abundance values were often reported even in winter in the Black Sea. For example, studying distribution of *M. leidyi* in eight different cruises during 1991–1995, Mutlu (Mutlu, 1999) found peak values of biomass and abundance between January and March when the range of surface temperatures was 6.5–10°C in the southern Black Sea. Although monthly or more intensive data on *M. leidyi* are scarce, in the northern Black Sea, it shows a more seasonal distribution with lower values in winter (Shiganova, 1998). However, before the appearance of *B. ovata* the period in which *M. leidyi* notably occurs was wider: for example values >200 g m^{-2} were present from May till November (accounting for more than half a year) in 1995 in Sevastopol Bay (Finenko and Romanova, 2000). However, as revealed in this study, after the *B. ovata* invasion, occurrence of *M. leidyi* biomass is limited to only 2 months (i.e. July and August, Figure 2A and B). When it reaches peak values in a month or so, *B. ovata* starts to increase sharply and in the following 2 weeks this predator controls the levels of *M. leidyi* very effectively. In the southern Black Sea, too, in the last few years *M. leidyi* has not occurred until summer (A. E. Kideys, personal observation). Probably higher temperatures in summer 2001 resulted in the earlier seasonal maximum of *Mnemiopsis* (Figure 2A and B). The maximum biomass value increased from 1999 to 2001, being 211.5 g m^{-2} in 2000 and 790.3 g m^{-2} in 2001. *Beroe*

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ovata seemed to act even quicker in 2001 in reducing the *M. leidyi* peak. A similar event was also observed for 2002 (our personal observation).

After the disappearance of *B. ovata* in late autumn, the *M. leidyi* biomass again increased, but at a lower level than in previous years. Probably the better food provision of this over-wintering not numerous population produced fast growth and high fecundity so that in early summer the maximum abundance and biomass values of *M. leidyi* exceeded those in the years prior to the appearance of *Beroe*. In Narragansset Bay the annual population dynamics of *Mnemiopsis* were similar to those in Sevastopol Bay: the pattern of seasonal dynamics was identical during 3 years (1971, 1972, 1974) but differences in the timing and maximum biomass values occurred. In 1974 the population fell dramatically in September, whilst high biomasses were observed in this month in the other 2 years (Kremer, 1976). A reduction of the *Mnemiopsis* biomass coincided with an increase in *Beroe* abundance. Density of the *Mnemiopsis* population appeared to be a function of food abundance and the role of *Beroe* consisted in a reduction of prey biomass in autumn but not in a limitation of the maximum biomass.

The introduction of *B. ovata* to the Black Sea has considerably shortened the time of *M. leidyi* availability in large numbers in the plankton and hence its predatory impact on the zooplankton.

Digestion time, ingestion, growth and reproduction rates of *B. ovata*

The digestion time in *Beroe* in the present study is comparable with those determined by other authors for ctenophores. The digestion times of *Mnemiopsis mccradyi* and *M. leidyi* feeding on copepods varied from 0.33 to 3.5 h depending on temperature and prey number in the stomadeum (Reeve and Walter, 1978; Reeve, 1980; Larson, 1987). According to Shiganova *et al.* (Shiganova *et al.*, 2000) the digestion time of *B. ovata* varied from 3 to 5 h at 24–26°C. Digestion times of *B. ovata* feeding on *M. leidyi* at 21 ± 1°C in our previous experiments varied within a wider range from 0.5 to 5.5 h depending on the prey–predator weight ratio (0.01–2.0) (Finenko *et al.*, 2001). In this study digestion time ranged from 0.75 to 5 h at 18°C when the prey–predator weight ratio changed from 0.03 to 3.24.

Like other gelatinous predators *Beroe* ingest their prey in proportion to the widely ranging prey concentrations (Reeve and Walter, 1978; Reeve *et al.*, 1978). In conditions of high food abundance ingested food could reach >400% of body wet weight per day. Such a high ingestion rate could produce a high growth rate of ctenophores. However, the maximum daily specific growth rate for adult *Beroe* in our experiments was ~0.2. This value is rather low compared with the values of 0.76 and 0.78 day^{-1} for *M. mccradyi* (Reeve and Baker, 1975) and *Pleurobrachia bachei* (Reeve and Walter, 1976), but close to Miller's value (0.25) for *M. leidyi* in a range of temperatures up to 20°C, at which the fastest growth rates were observed (Reeve and Walter, 1978). The *M. leidyi* growth rate was found to range from 0.06 to 0.38 per day, being dependent on the ctenophore weight (Finenko and Romanova, 2000). Greve (Greve, 1970) reported the maximum daily growth rate for *Beroe cucumis* as 0.4 and for *Bolinopsis infundibulum* as 0.2. The lowest ctenophore growth rates (0.02–0.04 day^{-1}) were reported by Kamshilov (Kamshilov, 1960) in the Barents Sea for *B. cucumis* at low temperatures.

In Sevastopol Bay in August 2001 under conditions of maximum prey concentration and high temperature, the maximum daily growth rate of the *B. ovata* population computed from field biomass data varied between 0.66 and 0.37. The maximum growth efficiency of adult *B. ovata* in our experiments was ~0.3–0.35 under a high specific daily ration value and was comparable with those of other gelatinous predators (Fraser, 1969; Reeve *et al.*, 1989). *Beroe ovata* demands both high food rations (not less than 20% of body weight per day) and a high prey biomass for growth. Probably the low prey abundance in late autumn is a major reason for the disappearance of *B. ovata* from the plankton.

Predatory impact of *M. leidyi* on zooplankton and *B. ovata* on *Mnemiopsis* population

During the first 2 years (1999–2000) after the arrival of *Beroe* in Sevastopol Bay its effect on the plankton community was very pronounced: the mean summer–autumn *Mnemiopsis* biomass fell by a factor of 4.6 in comparison with 1995 (Finenko and Romanova, 2000) when *Beroe* was absent (230 g m^{-2} in 1995 and 50 g m^{-2} in 2000). The predatory impact of *M. leidyi* on the forage zooplankton diminished sharply: even when *M. leidyi* were at their peak biomass, they were found to remove 4–6% of zooplankton standing stock daily, throughout most of the year this value was below 1% per day.

In 2001 the mean summer–autumn *M. leidyi* biomass (160 g m^{-2}) was close to that in 1995 (230 g m^{-2}) as well as its predatory impact on zooplankton (maximum daily grazing rates were 16 and 20% of the zooplankton biomasses in 2001 and 1995, respectively), but a very short *Mnemiopsis* bloom in 2001 resulted in high average annual zooplankton biomass values.

A decrease in the predatory impact of *Mnemiopsis* on zooplankton during the last 3 years is confirmed by the comparison of minimum food requirements of the

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Mnemiopsis population with its food supply (biomass of zooplankton, cal m^{-2}) (calorific content of zooplankton was taken as 4 cal mg^{-1} dry weight, dry:wet weight ratio as 0.2, and 1 ml of O_2 is assumed to be equal to 4.86 cal). Food requirements were calculated for station 7, where zooplankton and ctenophore have been sampled, from the relationship between oxygen consumption rate and mean weight of ctenophores in the population at different temperatures (Abolmasova, 2001). The daily energy requirements accounted for 29–39% of the zooplankton stock only in September 2000 and August 2001 (period of maximum *Mnemiopsis* biomass), for other months they were below 1%. In July 1995 these values ranged from 172 to 284% of the zooplankton stock, being in the range of 17–53% during the longest period (July–October). Another conclusion from these findings is that the *Mnemiopsis* in the bay might experience a lack of food, especially during the period of intensive growth in summer when fodder zooplankton biomass cannot meet their energy requirements. Either the animals fed in micropatches of zooplankton, or they had additional food sources. Two different mechanisms of prey encounter that are functioning simultaneously (directing the food into the mouth by using lobes or transport of prey through food canals along the body) enable them to capture a wide range of prey with different swimming speeds such as ciliates, copepod nauplii and bivalve larvae (Waggett and Costello, 1999). Stoecker *et al.* (Stoecker *et al.*, 1987) have shown that planktonic ciliates and copepod nauplii are preyed on by larval and post-larval *Mnemiopsis* and that they may be particularly important as food for newly hatched ctenophore larvae. In Sevastopol Bay *M. leidyi* larvae (wet weight 0.296 g) comprised up to 80% of population abundance on 1 August 2001 (the peak of *Mnemiopsis* biomass) and biomass of microzooplankton (infusoria and copepod nauplii) was 0.92 g m^{-2} (T. Pavlovskaya, unpublished data). If the clearance rate of the larvae was 1 l g^{-1} wet wt day^{-1} at 20°C (Stoecker *et al.*, 1987), the ctenophore population could remove ~4% of the microzooplankton biomass daily and cover 20% of their respiration requirements from that (microzooplankton caloricity is 0.5 cal mg^{-1} wet wt) (Khlebovich, 1979).

The predatory impact of the *B. ovata* population in Sevastopol Bay, calculated from data on *Beroe* respiration rate (Svetlichny *et al.*, 2003), its size structure and abundance, could amount to 60% of *M. leidyi* biomass per day in October–November 2001. The minimal food requirements of the *Beroe* population in August–September 2001 far exceeded the energy content of their prey population.

In October 1999 the values of predatory impact ranged from 2 to 53% (Finenko *et al.*, 2001). In the northeastern Black Sea in September 1999 the *Beroe* population consumed 0.7–5.7% of *M. leidyi* biomass daily (Shiganova *et al.*, 2000). According to the calculations of Shushkina *et al.* (Shushkina *et al.*, 2000), the potential predatory impact of *Beroe* on a *Mnemiopsis* population in the same region could be as high as 30–80% of the biomass daily. The huge potential pressure of *B. ovata* on the *M. leidyi* population is supported by experimental data on the feeding behavior and ingestion rate of ctenophores. The daily ration of ctenophores grows in parallel with the food abundance within a wide range of prey concentrations and does not achieve any saturation (Reeve and Walter,

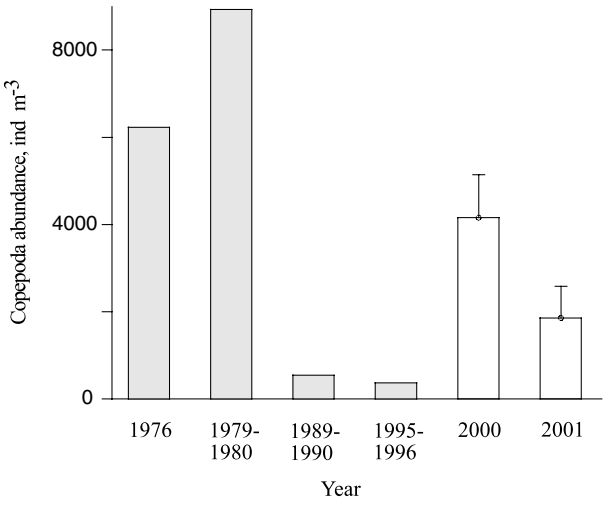


Fig. 9. Inter-annual dynamics of Copepoda abundance in Sevastopol Bay during 1976–1996 (Gubanova *et al.*, 2001) and 2000–2001 (our data; vertical bars denote SE).

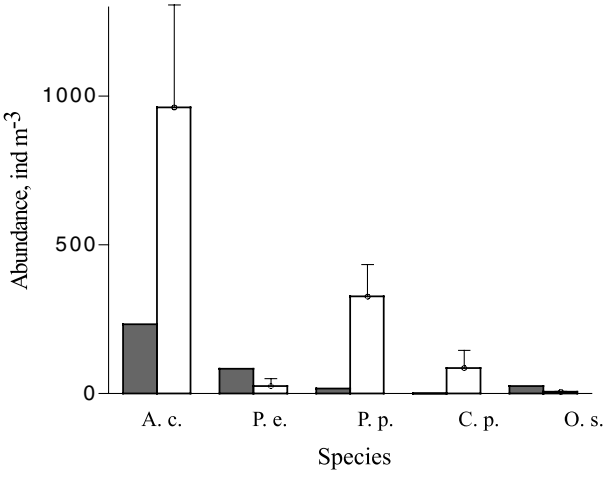


Fig. 10. Mean annual abundance of copepod species (ind. m^{-3}) during 1995–1996 (shaded columns) (Gubanova *et al.*, 2001) and 2000–2001(open columns) (our data; vertical bars denote SE). A.c., *Acartia clausi* + *A. tonsa*; P.e., *Pseudocalanus elongatus*; P.p., *Paracalanus parvus*; C.p., *Centropages ponticus*; O.s., *Oithona similis*.

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1978; Reeve *et al.*, 1978). In the sea in conditions of patchy prey distribution when the average biomass could be exceeded several times, *Beroe* are able to feed very intensively and thus reduce the *Mnemiopsis* population sharply for a short period. A keen decrease in *M. leidyi* abundance during the period of *B. ovata* availability in the bay supports the hypothesis that the predatory impact of this invader is an important factor determining the structure and functioning of the plankton community in inshore waters of the Black Sea.

Intensive predation on *Mnemiopsis* by *Beroe* should cause an increase in zooplankton biomass. In fact the mean annual prey zooplankton biomass (1.10 ± 0.65 g m^{-2}) in 2000–2001 increased by >2-fold compared with 1995 (0.42 ± 0.38 g m^{-2}). This difference is statistically significant at $P < 0.05$ (Student's *t*-test). Considerable increases in mean annual copepod abundance as a whole (Figure 9) and some species (*Acartia clausi*, *Paracalanus parvus*, *Centropages ponticus*) in particular (Figure 10) were also observed in the last 2 years as compared with previous years when *Mnemiopsis* bloom occurred and *Beroe* was absent. It means that the predatory impact of *Mnemiopsis* on prey zooplankton was reduced in the years of *Beroe* availability. The effectiveness of the ctenophore *B. ovata* in controlling high levels of the voracious plankton consumer *M. leidyi* and hence improvements in the pelagic ecosystem including the increase in the quantity of mesozooplankton presents an important step in dealing with invasive pelagic ctenophores, not only for the Black Sea but for other regions having similar problems.

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