

4. FUNCTIONAL ROLE OF THE CTENOPHORE INVADERS *Mnemiopsis leidyi* AGASSIZ AND *Beroe ovata* MAYER IN INSHORE PLANKTONIC COMMUNITIES

Finenko G.A.¹, Anninsky B.E.¹, Abolmasova G. I.¹, Romanova Z. A.¹,
Bat L.², Kideys A. E³

¹ *Institute of Biology of the Southern Seas, Sevastopol, Ukraine,*

² *University of Sinop, Fisheries Faculty, Sinop, Turkey,*

³ *Permanent Secretariat, Black Sea Commission, Istanbul, Turkey*

4.1 Introduction

In recent decades the numbers of alien species and their introduction rate to aquatic systems have been increasing over the world. Most extend biodiversity of the system and most of them don't have negative influence on its functioning. Only some of them can attain massive occurrence, suppressing or totally replacing the native species due to food competition and consumption. As a result the community structure is simplified, tolerance to external impact decreases and the system becomes open to injury. Ability to successful invasion of alien species, along with other factors, is determined with their ecological–physiological features. The characteristics of these species are short life cycle, high fecundity and growth rate, earlier maturation, wide food spectrum, eurybotics and high tolerance to pollution.

The North Atlantic ctenophore *Mnemiopsis leidyi* Agassiz A., 1865 (Ctenophora, Lobata) introduction of which caused real catastrophe in the Sea of Azov and the Black Sea in the late 80-s, have the most of these traits. The consequence of introduction of this species was changing of energy pathway in the plankton pelagic system (Vinogradov *et al.*, 1989; Shushkina *et al.* 1990; Shushkina and Vinogradov, 1991; Kideys, 1994). Instead of the trophic chain “zooplankton – planktivorous fish” the energy flow has been directed to “zooplankton – *M. leidyi*” chain that resulted in fishery collapse and great economic damage of the Black Sea countries. *M. leidyi* invasion has brought to reconstruction of the structure and functioning of different food levels of the Black Sea

ecosystem. Feeding on herbivorous zooplankton, egesting the nutrients and mucus it defined to significant extent the phytoplankton and microzooplankton dynamics in summer. High *Mnemiopsis* pressure on herbivorous zooplankton resulted in phytoplankton bloom occurred to be more often in inshore waters. Uneaten superfluous phytoplankton sinking has lead to oxygen deficiency and demise of fish, mussels and other valuable bottom species.

The first appearance of *M. leidy* in the Black Sea was recorded in November 1982 near Sudak, the south-eastern Black Sea (Pereladov, 1988); massive occurrence in different regions of the sea was observed in 1988–1989. Such long period between its appearance and bloom possibly is a result of extremely low water temperature in the Black Sea that years (Oguz, 2005): the coldest and severe winters of the last century were noted in 1985–1987 with mean winter (December – March) surface water temperature about 7.2°C.

At the end of 80-s there was a bloom of this ctenophore: in July – September 1989 its biomass in the open Black Sea was on average about 1.5 kg m⁻², in the inshore waters and on the northwestern shelf it was more than 3 kg m⁻² with maximum of 5.2 kg m⁻² (Shushkina *et al.*, 1990; Bogdanova and Konsulov, 1993) The total *M. leidy* stock in the sea was as high as 780 billion tons. In parallel with the other factors that destabilised the Black Sea ecosystem (eutrophication, various types of pollution) massive occurrence of this ctenophore has changed sharply species structure and biodiversity of mesozooplankton, the main food of *M. leidy* (Vinogradov *et al.*, 1992; Kovalev *et al.*, 1998). By the beginning of 90-s biomass of previously numerous warm water crustaceans – Copepoda *Paracalanus parvus* and Cladocera *Penilia avirostris*, *Pleopis polyphemoides* – has decreased some times, *Sagitta* – more than tenfold, *Aurelia aurita* – three times as compared to the previous period while *Acartia clausi* and *Acartia tonsa* became dominant in inshore regions.

Being the food competitor and consumer of fish eggs and larvae the ctenophores have caused tremendous damage to pelagic fish stock and as a result the catches of mass planktivorous fish and, first of all, *Engraulis encrasicolus ponticus* and *Trachurus mediterraneu ponticus* sharply

4. FUNCTIONAL ROLE OF THE CTENOPHORE INVADERS *Mnemiopsis leidyi* AGASSIZ AND *Beroe ovata* MAYER IN INSHORE PLANKTONIC COMMUNITIES

diminished (Niermann *et al.*, 1994; Gücü, 1997). Economical losses for all the countries around the Black Sea amounted to 240 billion dollars per year (Caddy and Griffith, 1992).

The role of the ctenophores in the Black Sea ecosystem degradation in the whole and in catch decreases in particular, is a point at issue. Quite a number of factors like over fishing (Gücü and Oguz, 1998; Gücü, 2002), natural climate fluctuations due to change of North Atlantic water circulation at the beginning of 1990-s (Niermann *et al.*, 1999; Bilio and Niemann, 2004; Oguz, 2005), eutrophication and anthropogenic pollution (Zaitsev and Alexandrov, 1997) may have been the reason but *M. leidyi* invasion is considered as a main factor that induced such sharp shifts in the Black Sea ecosystem (Zaika, 1994; Kideys, 2002; Kideys *et al.*, 2005).

As a result of lack of natural predators food and temperature conditions only have controlled *M. leidyi* abundance in the Black Sea. Here it showed the typical features of a new colonizer: after blooming during the initial period of settling (1989–1990) with biomass of $3\text{--}4\text{ kg m}^{-2}$, its biomass and abundance have decreased to moderate level. The reason of this decrease in 1991–1993 may have been colder climatic period: that years were very specific for the Black Sea ecosystem with the most cold winters with temperature 1.8°C below the average value (Oguz, 2005). In parallel with *M. leidyi* biomass the biomass of zooplankton also dropped sharply: from 17 g m^{-2} in 1990 to $2\text{--}4\text{ g m}^{-2}$ in 1991–1993. It coincided with the lowest level of fish stock and the highest phytoplankton biomass when compared to 1960-s. After the period of decrease a new peak of *M. leidyi* abundance followed in 1995, that was comparable with the peak of the late 1980-s. Like the first bloom the significant decrease of the biomass has followed for the successive years (1996–1997) that may have been the result of food lack. As Anninsky *et al.*, 1998a showed content of glycogen, the main storage compound in autumn 1996 in the *M. leidyi* population in the southern Black Sea corresponded to its content in 2 days starveling ctenophores. *M. leidyi* decreased pressure resulted in zooplankton and ichthyoplankton biomass

restoring. That years when the general ecological situation became better because of economic collapse in the former social countries some positive changes in the Black Sea pelagic ecosystem in the whole were observed: zooplankton biomass in the Central Black Sea started to increase since 1994, some zooplankton species that had disappeared in the recent years appeared again. During 1996–1998 *M. leidy* average biomass stabilized on the level of 200–300 g m².

In October 1997 a new invader ctenophore *Beroe ovata* Mayer 1912 a known feeder on *M. leidy* in native North Atlantic waters, appeared in shallow waters of Bulgaria (Konsulov and Kamburska, 1998) and in August – September 1999 it was observed in other regions of the Black Sea (in Sevastopol Bay and in the northeastern Black Sea). They believe that *B. ovata* massive occurrence in August – September 1999 was a result of abnormal warm winters of 1997–1998 and 1998–1999 as well as very hot summer of 1999 (Shushkina *et al.*, 2000).

Beroe introduction had initiated some new changes in the plankton community (Finenko *et al.*, 2000, 2001, 2003; Shiganova *et al.*, 2000, 2001, 2004; Shushkina *et al.*, 2004; Vinogradov *et al.*, 2000; Vinogradov and Shushkina, 2002). Being a monophage, which under the conditions of the Black Sea consumes almost exclusively *M. leidy* it regulates its abundance and, in this way, controls other components of the ecosystem (Finenko *et al.*, 2000, 2001; Shiganova *et al.*, 2000, 2004; Vinogradov *et al.*, 2000).

This chapter aims to analyze ecological–physiological features of both alien ctenophores, that enabled their massive occurrence under the conditions of the Black Sea, the seasonal and inter annual dynamics as well as trophic interactions in the planktonic community at the new stage of its development.

4. FUNCTIONAL ROLE OF THE CTENOPHORE INVADERS *Mnemiopsis leidyi* AGASSIZ AND *Beroe ovata* MAYER IN INSHORE PLANKTONIC COMMUNITIES

4.2 Chemical composition and elements of *M. leidyi* energy budget

4.2.1 Chemical composition

M. leidyi dry weight in the Black Sea amounts 2.0 -2.2% of wet weight (Finenko and Romanova, 2000; Vinogradov *et al.*, 2000; Vostokov *et al.*, 2001), that is significantly lower than in the other regions due to low salinity of the Black Sea.

Organic matter content in *M. leidyi* ranges from body ranges from 0.060 to 0.15% wet weight and depends on the ctenophore size, being maximal in small ctenophores with length less than 10 mm (Vinogradov *et al.*, 2000; Shushkina *et al.*, 2004). The energy content in adult *M. leidyi* with size range of 15–70 mm on average is 6.7 ± 1.0 cal g⁻¹ wet weight (Anninsky *et al.*, 2005). Predominant fraction is protein that forms about 80% of the total organic matter, lipids amount to about 8.7–10.0%. Carbohydrates and amino acids separately make up less than 6.5% of the total organic matter. Polysaccharides dominate in carbohydrates (4.4%) and the glycogen content reaches 3.0%. Phospholipids and sterins prevail in lipids amounting to 3.1% and 2.7% respectively. The main storage compound in *M. leidyi* is glycogen, which content is 4 times as great as all storage lipids (triacylglycerols and waxes). Glycogen content, as it was noted earlier, is an index of ctenophore food supply (Anninsky and Gubanova, 1998). Using this carbohydrate as a main source of accumulated energy is a characteristics of the species with low activity.

4.2.2 Feeding

The food of *M. leidyi* is the most of zooplankton species with size from tens and hundreds microns to 10–15 mm; their share in the ration depends on their mobility, predator and prey size as well as on time and place. According to Zaika and Revkov (1998), in summer in the coastal

regions off the Crimea and the Caucasus Coasts Cladocera *Pleopis polyphemoides*, *Oikopleura dioica*, Bivalvia larvae, Copepoda and their eggs may amount to 85–90% of the total number of prey in gut content of the ctenophores while tintinnids, Cirripedia nauplii, *Noctiluca scintillans*, Polychaeta, *Sagitta setosa* and Gastropoda and fish larvae are less than 1%. In offshore waters off the Caucasus coasts Copepoda and Cladocera prevailed in the ration in summer and winter (75 and 56%; 23 and 20% respectively), in inshore regions in winter eggs of invertebrates composed up to 85% of the total ration (Tsikhon–Lukanina *et al.*, 1993). Phytoplankton that was found sometimes in gut contents may have been originated from the Crustacean guts. In the experiments it was revealed that *M. leidyi* was starving when algae and detritus were the only food offered (Baker and Reeve, 1974). Survival rate of the ctenophores feeding on phytoplankton is similar to this on the filtered water.

It seems that small number of ciliates in the gut contents is not result of their low ingestion but of poor conservation and difficulties of identification. The ingestion rate of Cirripedia nauplii that can be observed into *M. leidyi* gut content probably is low. In our experiments ctenophores lost their weight when Cirripedia nauplii were ordered as a food in the same numbers as adult *Acartia clausi* (Finenko *et al.*, 1995). Low moving activity of these nauplii may not stimulate the lobes to such an extent as Copepoda do due to their higher vibration rate.

It is worth noting that fish larvae have been found rarely into *M. leidyi* gut content in the sea (only in 2.6% of total ctenophore number) (Tsikhon–Lukanina *et al.*, 1993) but predatory effect of *M. leidyi* population on them is possible to be high in the period of ctenophore maximum (more than 70% of total larvae abundance per day).

The daily rhythm in *M. leidyi* feeding was observed in nature: feeding intensity is significantly higher at night. Zaika and Revkov (1998) have revealed that at night the share of Ctenophores with some food in gut content was 4 times as high as during the day that may be a result of their migration to the surface sea layers with high food concentration at night (Vereshchaka, 2002).

4. FUNCTIONAL ROLE OF THE CTENOPHORE INVADERS *Mnemiopsis leidyi* AGASSIZ AND *Beroe ovata* MAYER IN INSHORE PLANKTONIC COMMUNITIES

An important characteristic of lobate ctenophore nutrition is continuous feeding, and therefore digestion rate is one of the factors that define their feeding rates. According to Reeve, 1978, Larson, 1987, Tsikhon-Lukanina *et al.*, 1995 digestion time values in *M. mccradyi* and *M. leidyi*, feeding on Copepoda, vary in wide range from 0.33 to 6.6 h and depend on temperature and prey number in gut content. Besides digestion time is a function both prey and predator sizes. Small prey (< 1 mm – Copepoda and Cirripedia nauplii, *Oitona* sp.) are digested by 50-mm *M. leidyi* for 0.3 - 0.6 h at 10-50 prey in their gut content (Larson, 1987). Large Copepoda (*Pontella mediterranea*, *Calanus ponticus*) were digested in the experiments much slowly than small ones (*A. clausi*), and digestion time decreased as *M. leidyi* size increased (Tsikhon-Lukanina *et al.*, 1995). For instance, 10- mm ctenophores digested *P. mediterranea* for 6.6 h, while in 70-mm *M. leidyi* the digestion time reduced by half under the same temperature conditions. All sized Ctenophores digested *A. clausi* of 1–2 mm for 1.0–1.7 h, that is 2 -3 times faster than digestion of *P. mediterranea* and *C. ponticus* (3–3.5 mm length). *Artemia salina* nauplii of 1 mm length were digested with the same rate as *A. clausi*. There was no a significant difference in digestion time at different prey number in the gut content (1.0–1.7 h), but the difference in the average digestion times of *A. salina* nauplii in two size groups of predators was significant: 0.86 ± 0.32 h in 20-30-mm ctenophores and 1.29 ± 0.38 h in 35–50 mm ($p < 0.01$) (Fig. 4.1.).

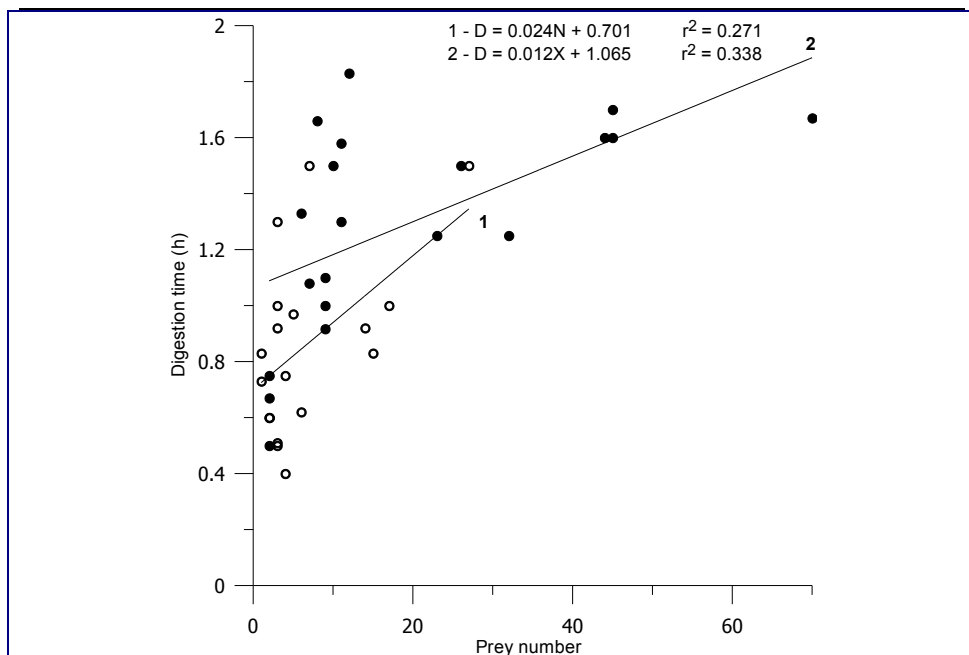


Figure 4.1. Relationship between digestion time (D) and prey number in gut content (N) in *M. leidy*: 1 = 20-30mm, 2 = 35-50mm

Digestion time of fish larvae (length of 3–32 mm) by adult *M. leidy* are close to digestion time of large planktonic Crustacea and range from 1.0–4.7 h (mean value is 2.8 h at 18–20°C) (Tsikhon–Lukanina *et al.*, 1993).

Ability for food selectivity of *M. leidy* is not clear. Although some authors revealed that *Acartia* sp., Bivalvia veligers, Cirripedia nauplii and Polychaeta larvae were more numerous in the diet than in environment (Burrell and Van Engel; 1976; Larson, 1987), our calculations from Zaika and Revkov (1998) data showed that ingestion rate of different prey species in the sea was proportional to their share in total zooplankton abundance.

Daily ration value - number or weight of prey ingested for a day - and clearance rate - volume that ctenophore have to process to get certain amount of food - are two important indices of feeding intensity of *M. leidy*. The feature of food behavior of lobate ctenophores is a linear

4. FUNCTIONAL ROLE OF THE CTENOPHORE INVADERS *Mnemiopsis leidyi* AGASSIZ AND *Beroe ovata* MAYER IN INSHORE PLANKTONIC COMMUNITIES

relationship between ingestion and prey number over a wide range of food concentrations, i.e. there is no critical (threshold) concentration under which food saturation is reached (Bishop, 1968; Reeve, 1980; Gibbson and Painting; 1992; Finenko *et al.*, 1995).

In the experiments the maximum concentration of Copepoda up to which the ration of *M. leidyi* increased was more than 3000 ind l^{-1} (Reeve *et al.*, 1978). Zaika and Revkov (1998) revealed also that in the Black Sea the food ingestion of *M. leidyi* of 20–40 mm increased in parallel with the food concentration increasing (Cladocera *P. polyphemoides* and Bivalvia larvae) in the range of 125–1100 ind m^{-3} . The same character of ration dependence we found when *M. leidyi* was fed on *A. salina* nauplii of much higher densities from 5 to 50 ind l^{-1} or 0.1–1.0 mg l^{-1} (Fig. 4.2). Under such effect of prey concentration on the ration value the clearance rate is constant and does not depend on food density.

In our experiments clearance rate of 20–30 mm *M. leidyi* has not changed over a wide range of food concentrations (5–50 *A. salina* nauplii l^{-1}), being equal to 0.234 ± 0.076 l g $WW^{-1} h^{-1}$ and slightly increased in 40–50 mm ctenophores (Fig.4.3). Meantime *M. leidyi* weight (or energy content) affects on clearance rate value and correlation between these two values at 23°C is as follows:

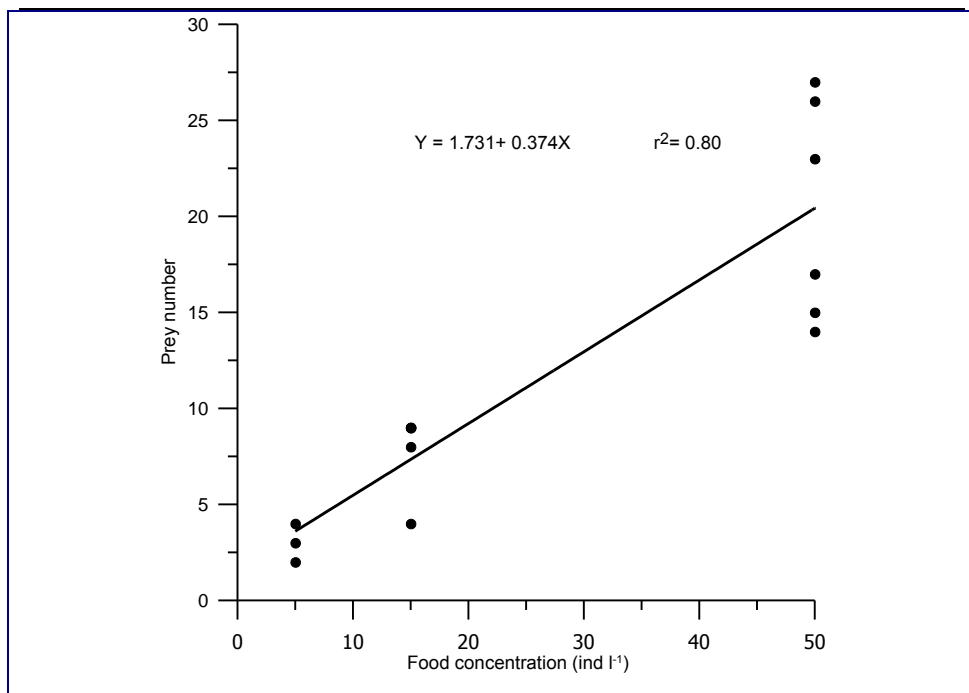


Figure 4.2. Effect of food concentration (ind l⁻¹) on ingestion rate in *M. Leidy*

$$CR/WW = 18.39WW_1^{-0.595} \quad 0.32 < WW_1 < 29.2, \quad n = 18, \quad r^2 = 0.616,$$

Where CR/WW is clearance rate, l·g⁻¹·h⁻¹; WW₁ is body energy content, cal·ind⁻¹ (Fig. 4.4).

Clearance rate depends also on prey size: it is twice as high when Ctenophore feed on Copepoda nauplii than on adult *A. clausi*: (Fig. 4.5)

4. FUNCTIONAL ROLE OF THE CTENOPHORE INVADERS
Mnemiopsis leidyi AGASSIZ AND *Beroe ovata* MAYER IN INSHORE
PLANKTONIC COMMUNITIES

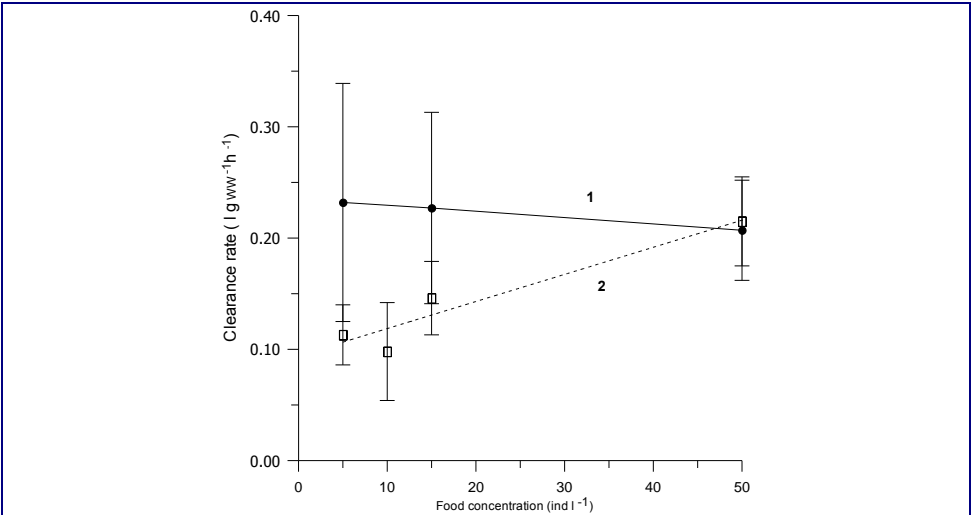


Figure 4.3. Effect of food concentration on clearance rate in 20 – 30 mm (1) and 40–50 mm (2) *M. leidyi*

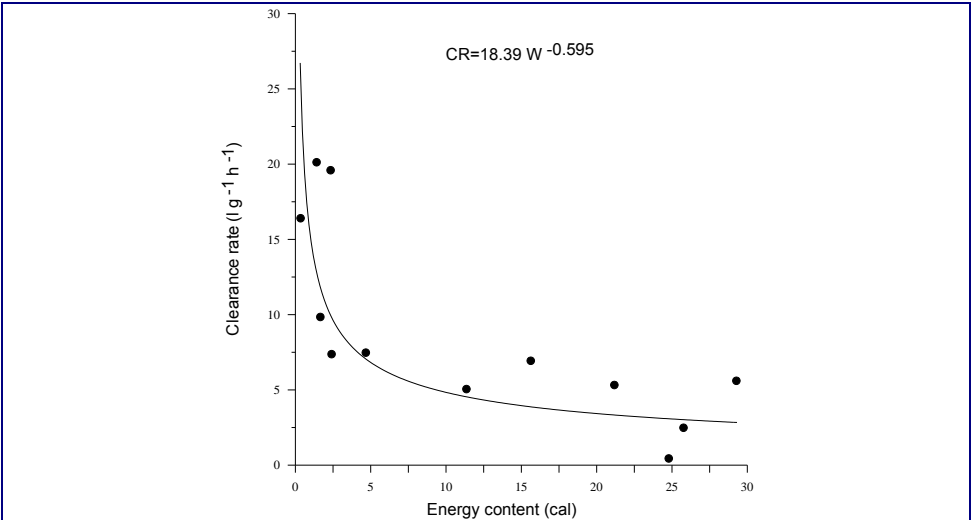


Figure 4.4. Relationship between specific clearance rate (l g⁻¹ DW h⁻¹) and body energy content (cal ind.⁻¹) in *M. leidyi*

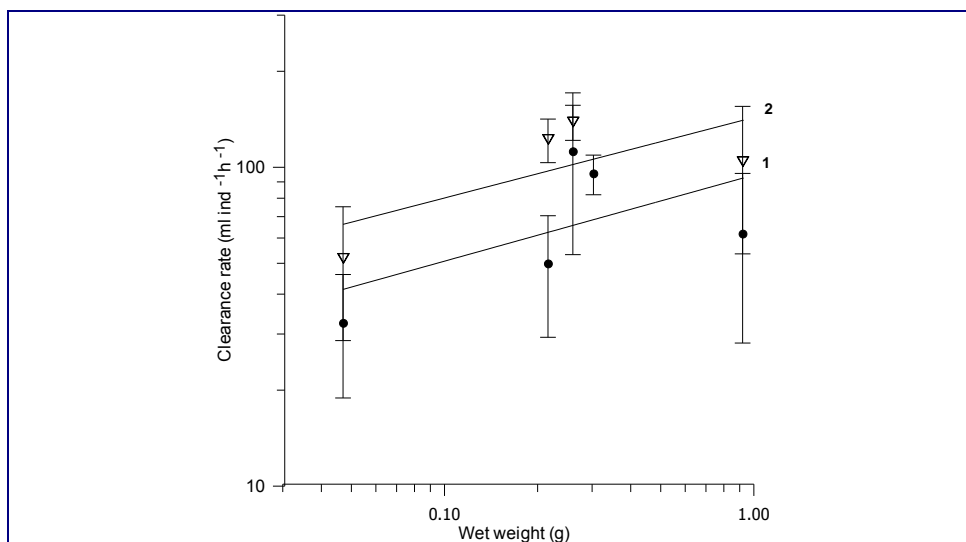


Figure 4.5. Relationship between clearance rate (ml ind. ⁻¹ h ⁻¹) and wet weight of *M. leidy* fed on *Acartia* sp. copepods and adult (1) or Copepoda nauplii (2)

$$\begin{aligned} CR_A &= 94.55 WW^{0.270} & r^2 &= 0.670 \\ CR_n &= 168.08 WW^{0.284} & r^2 &= 0.397 \end{aligned}$$

Where CR_A is clearance rate of *M. leidy* when they fed on adult and copepodites of *A. clausi*, CR_n is the same at feeding on Copepoda nauplii (ml ind⁻¹ h⁻¹) (Finenko *et al.*, 2006)

The feature of *M. leidy* is superfluous feeding when under high food concentration some share of prey is not digested, but it is covered with mucus and is released to water. So not only consuming but killing their prey *M. leidy* can decrease the prey abundance.

Growth

Our laboratory experiments on *M. leidy* growth at two food concentrations

(60 and 100 *A. clausi* l⁻¹ or 0.35 and 0.60 mg DW l⁻¹) revealed the different food provision of small and large ctenophores under the same food conditions: while both prey densities were sufficient for growth of

4. FUNCTIONAL ROLE OF THE CTENOPHORE INVADERS *Mnemiopsis leidyi* AGASSIZ AND *Beroe ovata* MAYER IN INSHORE PLANKTONIC COMMUNITIES

small *M. leidyi* with dry weight of less than 20 mg, they could not meet growth requirements of large ones (Finenko and Romanova, 2000). Under the same food concentration ($0.35 \text{ mg DW} \cdot \text{l}^{-1}$) the specific growth rate decreased six time: from 0.382 day^{-1} in the smallest (0.15 mg DW) to 0.06 day^{-1} in the ctenophores with dry weight of 13-18 mg. The same pattern was observed for gross growth efficiency values that were 0.50-0.88 in the former and 0.30 in the latter.

The large ctenophores of dry weight $> 20 \text{ mg}$ at both food concentrations consumed 21.1-4.6% of body energy content per day, but this energy was not sufficient to meet their growth requirements: they lost from 3 to 19% their weight in a day and these losses were proportional to ctenophore weights (Table 4.1).

Thus in the experiment the small *M. leidyi* of dry weight $< 20 \text{ mg}$ at food density of 60 ind l^{-1} could meet their food requirements as well as realize their high growth potential while for the ctenophore of $> 20 \text{ mg}$ dry weight even the experimental concentration of 100 prey l^{-1} was insufficient for their growth.

Table 4.1. Food consumption and growth rates of *M. leidy* at two food concentrations

Food concentration,(mg DW l ⁻¹)	Duration of experiment (day)	W _o	W _t	Body energy content (cal ind ⁻¹)	Weight specific growth rate (day ⁻¹)	Ration	Growth	K ₁	CR (l·g ⁻¹ ·h ⁻¹)
		(mg DW)				(cal·cal ⁻¹ ·day ⁻¹)			
0.35	8.6	0.15	4.0	1.38	0.38	0.43	0.21	0.50	20.15
- « -	5.8	0.76	5.2	2.31	0.31	0.74	0.27	0.36	19.62
- « -	8.6	1.02	5.6	2.38	0.20	0.29	0.16	0.55	7.40
- « -	5.7	13.74	19.7	11.33	0.06	0.24	0.07	0.29	5.08
- « -	5.7	17.92	27.2	15.60	0.07	0.28	0.08	0.30	6.96
- « -	4.7	47.27	27.9	24.76	-0.11	0.05	-0.11	-	0.47
- « -	5.7	48.39	26.1	25.74	-0.11	0.15	-0.08	- 0.56	2.51
0.60	8.0	20.40	15.5	11.39	-0.03	0.24	-0.03	- 0.14	4.35
- « -	7.0	40.60	22.9	21.15	-0.08	0.28	-0.08	- 0.03	5.35

W₀ = initial weight

W_t = final weight

K₁ = gross growth efficiency

CR = clearance rate

4. FUNCTIONAL ROLE OF THE CTENOPHORE INVADERS Mnemiopsis leidyi AGASSIZ AND Beroe ovata MAYER IN INSHORE PLANKTONIC COMMUNITIES

As our experiments showed the *M. leidyi* specific growth rate especially in early stages was very high under conditions of plenty of food and exceeded zooplankton growth rate. According to our observations, *M. leidyi* larvae in the laboratory during 9 days at temperature 23-24°C have grown from 0.7 to 9.5 mm, i.e. growth coefficient value was 1.2 per day that is close to phytoplankton growth rate.

Energy budget of small *M. leidyi* in the dry weight range of 2.1–22.6 mg, calculated from our experimental data at 23°C showed that under conditions of sufficient food abundance the daily ration was 40±20% of body energy content, assimilation efficiency was 58±14% and high gross and net efficiencies for growth were observed ($K_1 = 0.40 \pm 0.12$ and $K_2 = 0.69 \pm 0.10$) (Table 4.2).

Table 4.2. Daily energy budget of *M. leidyi* at 23°C (from Finenko and Romanova, 2000, Abolmasova, 2001)

DW	W	R	C	G	A	a	K_1	K_2	C/W
2.07	1.38	0.103	0.591	0.295	0.398	0.67	0.50	0.74	42.8
2.98	2.31	0.14	1.705	0.617	0.757	0.44	0.36	0.81	73.8
3.31	2.38	0.153	0.702	0.386	0.539	0.77	0.55	0.72	29.5
16.72	11.33	0.606	2.731	0.793	1.399	0.51	0.29	0.57	24.1
22.56	15.6	0.781	4.415	1.326	2.107	0.48	0.30	0.63	28.3
Mean ±SD						0.58 ±0.14	0.4 ±0.12	0.69 ±0.10	39.7 ±20.3

DW = dry weight (mg)

W = ctenophore body energy content (cal ind⁻¹)

R = respiration rate (cal ind⁻¹day⁻¹)

C = ration (cal ind⁻¹day⁻¹)

G = growth (cal ind⁻¹day⁻¹)

A = assimilated food (cal ind⁻¹day⁻¹)

a = assimilation efficiency (%)

K_1 = gross growth efficiency

K_2 = net growth efficiency

C/W = energy specific daily ration (% of body energy content)

In Sevastopol Bay the maximum population specific growth rate (0.092 day^{-1}) occurred in summer period of intensive reproduction of adult ctenophores and growth of larvae (Table 4.3). In spring and autumn when the population consisted from wintered large ctenophores it was minimal. Calculated average daily specific growth rate of the *M. leidy* population in a year in Sevastopol Bay was 0.039.

M. leidy can survive during the periods of food lack using their own body tissues for metabolic requirements (Anninsky *et al.*, 2005). Under experimental starving (8 days at 12.4°C) they lost 9.3% wet weight day^{-1} . The rate of organic matter loss was half as much (5.9%). While the percentage of four main biochemical components (proteins, lipids, carbohydrates and free amino acids) was practically constant during starvation, glycogen content in polysaccharides and monosaccharide content in total carbohydrates have reduced sufficiently (from 86.6% to $3\text{--}28.8\%$ and from 45.8% to $14.3\text{--}23.2\%$ from the start to the end of fasting correspondingly). This fact demonstrates once again that glycogen content is an indicator of ctenophore trophic status and can be used as an index of food provision in the sea (Anninsky *et al.*, 1989a).

Table 4.3. Daily specific production (μ) of *M. leidy* population in Sevastopol Bay in 1995

Period	Days	W_0	W_t	μ
10.08–11.09	31	0.015	0.126	0.092
26.09–30.10	35	0.020	0.126	0.073
26.09–21.12	85	0.020	0.280	0.031
30.11–28.03	120	0.007	0.460	0.035
28.03–29.06	60	0.460	1.020	0.013

W_0 = initial weight

W_t = final weight

Reproduction

In the Black Sea *M. leidy* reproduces the year round in temperature range from 8 to 28°C (Vinogradov and Shushkina, 2002; Romanova *et al.*, 2005). In winter ctenophore fecundity is low ($300\text{--}500$ eggs in a clutch); due to low abundance of adults and long embryonic period ctenophore eggs and larvae in plankton are very rare. Intensive

4. FUNCTIONAL ROLE OF THE CTENOPHORE INVADERS Mnemiopsis leidyi AGASSIZ AND Beroë ovata MAYER IN INSHORE PLANKTONIC COMMUNITIES

reproduction starts from the middle of April – early May and lasts until middle October – November. The most mass egg release is observed at surface water temperature of 23°C (Zaika and Revkov, 1994; Finenko *et al.*, 2006b). This time reproductive activity (share of reproduced ctenophores and egg number in a clutch) achieve their maximum (to 2000–3000 eggs in the largest *M. leidyi*). Reproduction takes place synchronously at night, the ctenophores are fully prepared for spawning after 3–4 h of darkness (Zaika and Revkov, 1994). Reproduction in the population is wavy with 1–14 day periodicity during the intensive reproduction and more prolonged intervals other time (Vinogradov and Shushkina, 2002). Egg number in a clutch is a function of trophic conditions. Effect of daily ration on a clutch size is described as $E = 0.052F^{1.69}$, where E is egg number and F is daily ration, joule ind⁻¹ (Vinogradov *et al.*, 2000).

M. leidyi can reproduce being in larvae state. Already after 7–11 days after hatching at the length of 5–7 mm the first eggs appear. As larvae and juvenile ctenophores grow egg number increases and relation between *M. leidyi* length (L, mm) and egg number in a clutch (E) is described with power function (Romanova *et al.*, 2005).

$$E = 0.513 L^{1.86} \quad \begin{matrix} 5 \leq L \leq 20 \\ 5 \leq E \leq 178 \end{matrix} \quad (4.4)$$

Duration of embryonic development in the temperature range of 17–24°C reduces from 24 to 12 h with Q₁₀ of 2.34 (Zaika and Revkov, 1994; Romanova *et al.*, 2005).

Respiration.

M. leidyi respiration rate (R, ml O₂ ind⁻¹ h⁻¹) can be described as $R = 0.112 DW^{0.772}$ in a wide range of dry weights (0.0005 < DW < 0.41 g) at 23°C (Abolmasova, 2001). Similar relationship ($R = 0.11 DW^{1.02}$) was found also by other authors in the whole length range of adult ctenophores – 10–70 mm (Vinogradov *et al.* 2000; Vostokov *et al.* 2001). The most important factor affected on the respiration rate along

with their weight is a temperature. *M. leidy* is the most sensible to low temperature: in the range of temperature of 7–12°C Q_{10} coefficient was as high as 6.7 and decreased to 1.8 between 12–23°C (Abolmasova, 2001). The respiration intensity value depends on food supply not so much: the maximum value twice as high as minimum one (Finenko *et al.*, 1995). Under 8-day starving at 12.4°C respiration rate also was half as high as in freshly collected Ctenophora (Anninsky *et al.*, 2005).

4.3 Chemical composition and the elements of ctenophore *Beroe ovata* energy budget

4.3.1 Chemical composition

B. ovata dry weight amounts 2.4–2.5% of wet weight (Vinogradov *et al.*, 2000; Finenko *et al.*, 2001) that is close to the value in *M. leidy*. In the chemical composition *B. ovata* is also similar to *M. leidy* but organic matter content per unit of wet weight two times higher (Anninsky *et al.*, 2005). This determines its higher energy content $-14.8 \pm 2.8 \text{ cal g}^{-1}$ wet weight against $6.7 \pm 1.0 \text{ cal g}^{-1}$ in *M. leidy*. Protein, the main organic component, amounts to 80% of total organic matter; lipids, carbohydrates and free amino acids are 10 and 5.3–5.6%, correspondingly. Chemical composition is almost the same in the ctenophore size range of 17–43 mm, although in the *B. ovata* of the same size protein, carbohydrate and amino acid content can vary 2–3 fold, proteins and lipids – 3–4 times (Anninsky *et al.*, 2005).

4.3.2 Feeding

B. ovata is a monophage, that feeds almost exclusively on *M. leidy* in the Black Sea. Obviously, the another, indigenous Black Sea ctenophora *Pleurobrachia pileus* that is disconnected with *B. ovata* in space can be used as a supplementary food item during some periods of the population migration to the *B. ovata* inhabitation layers at night or in winter under extremely low *M. leidy* concentration.

The most important biotic factor that determines the *B. ovata* ration value is their weight (Finenko *et al.*, 2003). The effect of *B. ovata* wet

4. FUNCTIONAL ROLE OF THE CTENOPHORE INVADERS *Mnemiopsis leidyi* AGASSIZ AND *Beroe ovata* MAYER IN INSHORE PLANKTONIC COMMUNITIES

weight (WW, g) on specific daily ration (F/WW) in the experiments under food concentration of 2 g l^{-1} was described with power function:

$$F/WW = 25.9 \text{ WW}^{-0.703} \quad (3 < WW < 30 \text{ g})$$

and the ration value changed from 15 to 460% of wet weight (WW, g), being the maximum in the smallest ctenophores (Fig. 4.6).

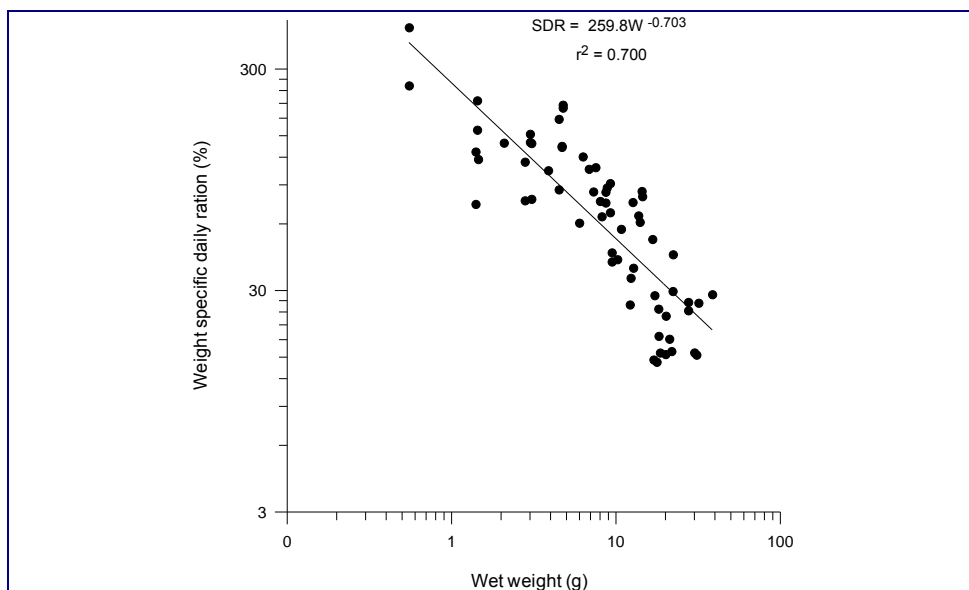


Figure 4.6. Relationship between weight-specific daily ration (SDR, %WW) and wet weight (g) in *B. ovata* at food concentration of 1 g l^{-1}

Probably such high ration values should be considered as a momentary greatest possible ration at high food concentration. But such situation is quite possible in the sea because as underwater observations showed *B. ovata* occur into *M. leidyi* aggregations. In such a way *B. ovata* can consume sufficient prey number to meet their food requirements for a long time and to minimize energy losses for food searching (Kideys *et al.*, 2004).

A periodicity in feeding is adaptation to sporadically food availability, it is not related to light conditions or to the time of day, but more to the intensity of the previous feeding: ingestion of a large portion of food is followed by a low feeding rate (Fig.4.7). All sizes of *B. ovata* consume intensively all sizes of *M. leidyi* but under conditions of possible selection and high prey density (number per volume), *B. ovata* preferred large and medium size *M. leidyi*. When there are no selection (the different size prey were offered in the experiment in the same biomass but various number separately) they could ingest the small *M. leidyi* too and ranges of specific daily rations were very close to each other upon feeding on different sizes of *M. leidyi*.

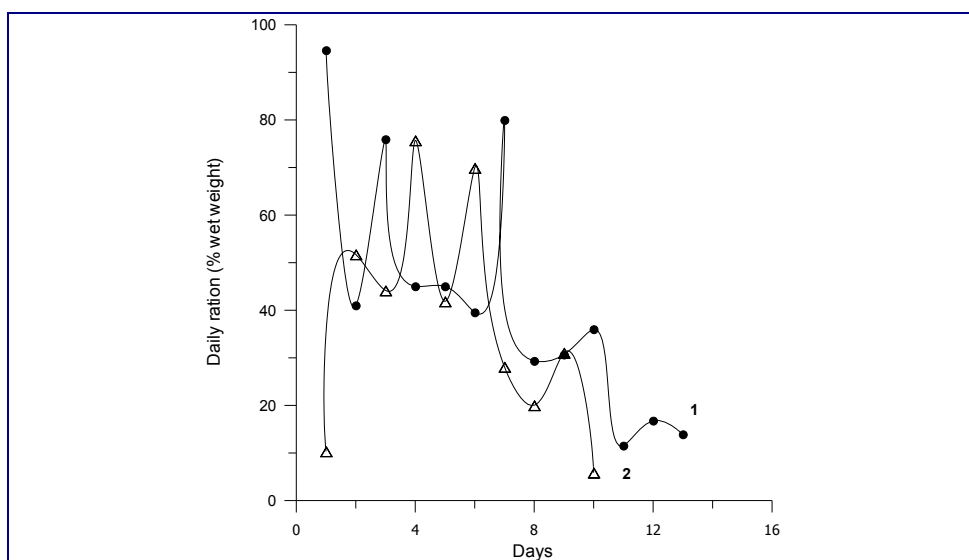


Figure 4.7. Dynamics of *B. ovata* feeding rate in long-term experiments at 26°C. 1 and 2 – *Beroe* specimens with initial length 30 mm. Average daily ration in *Beroe* 1 is $40.2 \pm 27.0\%$, in *Beroe* 2 is $37.9 \pm 23.4\%$

B. ovata digestion time varies from 0.75 to 5 hours at 20–22°C (Finenko *et al.*, 2000, 2001; Shiganova *et al.*, 2000) and the prey - predator weight ratio appeared to be effective on digestion time. It can be described by the following equation with a high coefficient of determination:

4. FUNCTIONAL ROLE OF THE CTENOPHORE INVADERS *Mnemiopsis leidyi* AGASSIZ AND *Beroe ovata* MAYER IN INSHORE PLANKTONIC COMMUNITIES

$$DT = 2.956 P^{0.59}$$

$$r^2 = 0.87$$

$$0.03 < P <$$

$$3.23$$

$$(4.6)$$

Where DT is digestion time, min, P is prey/predator weight ratio (Fig. 4.8).

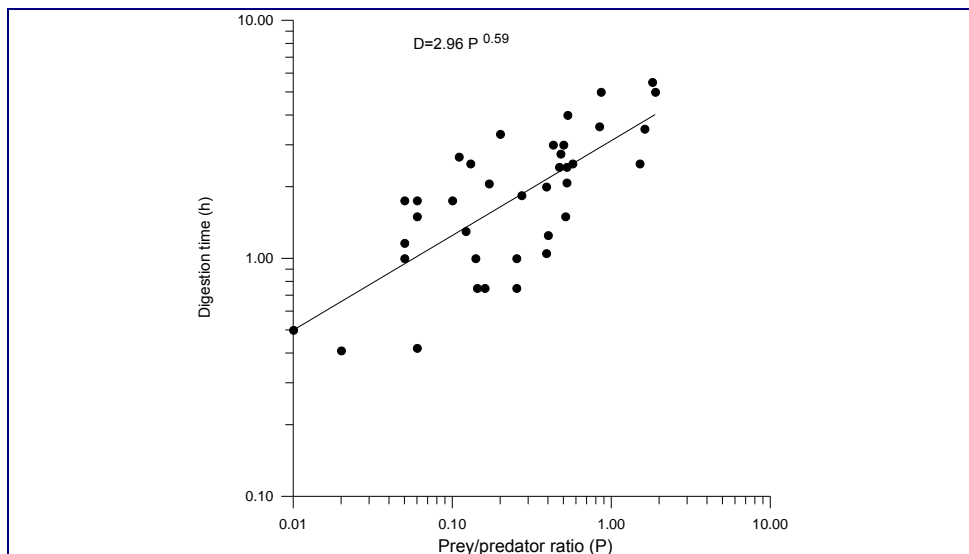


Figure 4.8. Effect of prey/predator weight ratio (P) on digestion time (D, h) in *B. ovata* at 21 °C

It is important because of different *M. leidyi* population structure throughout an year. In the Black sea *B. ovata* appear in plankton after *M. leidyi* reproduction and small ctenophores make up the most population. *B. ovata* ability to ingest small prey results in sharp decrease of *M. leidyi* abundance during the shortest period.

4.3.3 Growth

B. ovata high potential feeding rate can result in very high growth intensity: in Sevastopol Bay under maximum prey concentration and high temperature maximum daily specific population growth rate ranged

from 0.33 to 0.67, that is higher than the growth rate of planktonic Crustacea. It is a reason of explosive development of *B. ovata* population as well as *M. leidy* growth rate of which can be even higher than in *B. ovata*.

B. 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 disappearance of *B. ovata* from the plankton.

In our laboratory experiments the specific growth rate increased from -0.05 to 0.20 while the ration increased from 27 to 150% of body weight (Fig. 4.9). The same relation was found for gross growth efficiency (K_1) that was negative (about -0.26) at the ration value less than 27% of wet weight (Fig. 4.10). Increasing of the ration resulted in rise of the growth efficiency.

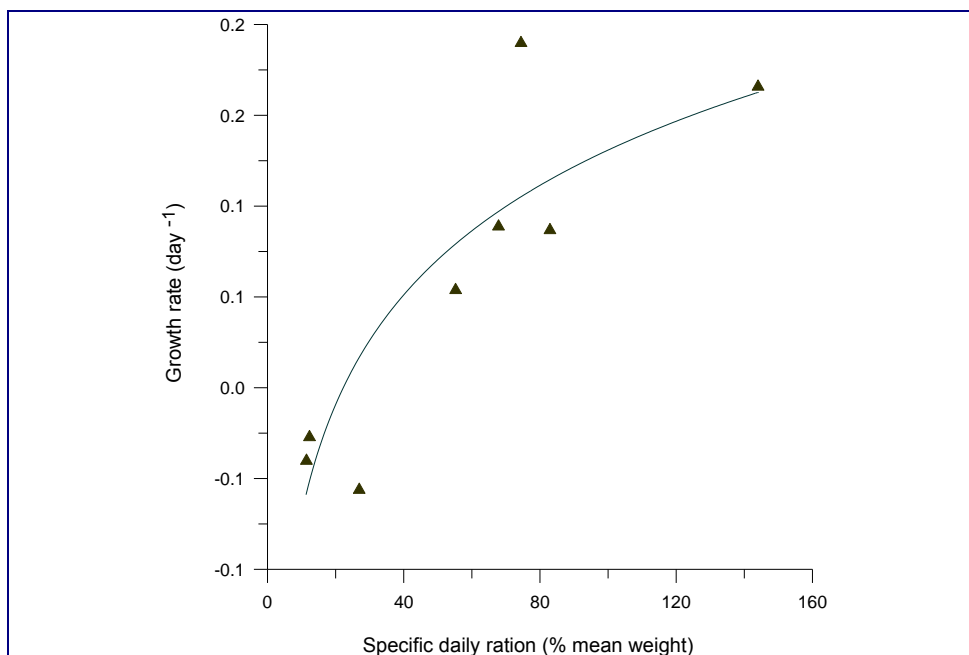


Figure 4.9. Effect of specific daily ration (%mean wet weight) on specific growth rate (day⁻¹) in adult *B. ovata*

4. FUNCTIONAL ROLE OF THE CTENOPHORE INVADERS Mnemiopsis leidyi AGASSIZ AND Beroe ovata MAYER IN INSHORE PLANKTONIC COMMUNITIES

Like *M. leidyi* *B. ovata* can endure long- term starving. Under 18- day experimental starving at temperature 16–18°C ctenophore wet weight have been decreasing by 9.4% in a day, while rate of organic matter decrease was half as much of that (5.9%) (Anninsky *et al.*, 2005). As our calculations showed at that rate of organic matter loss (with temperature correction) some *B. ovata* specimens are able to survive for rather long period (about 9 months when we don't find them in plankton) without any food.

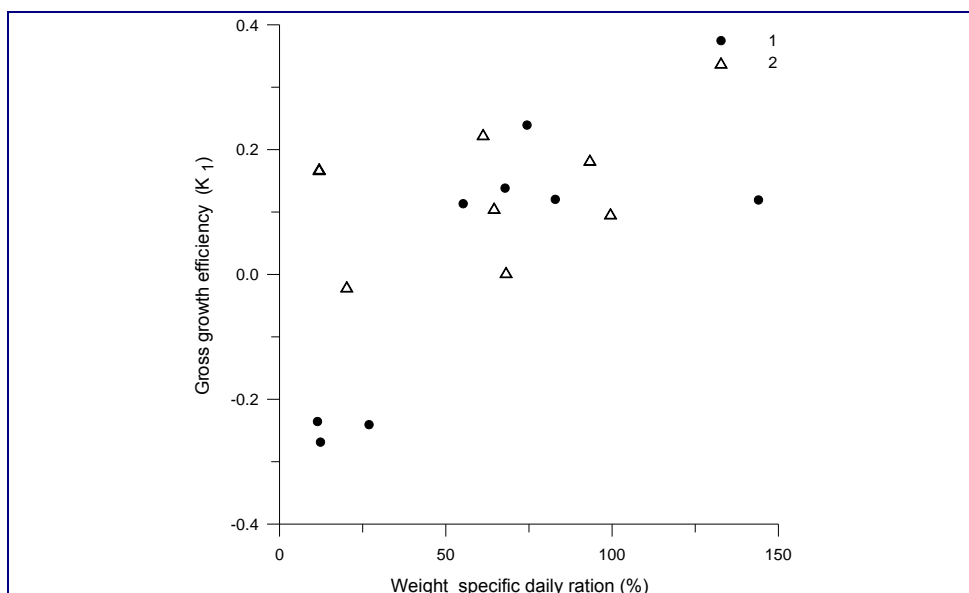


Figure 4.10. Effect of specific daily ration (% mean wet weight) on gross growth efficiency (K_1) at two food concentrations: $1.68 \pm 0.47 \text{ g l}^{-1}$ (1), $2.54 \pm 0.80 \text{ g l}^{-1}$ (2)

4.3.4 Respiration

The comprehensive researches of *B. ovata* energy metabolism in the Black Sea have been conducted by Svetlichny *et al.*, 2004, which cover their whole life cycle. As their experiments showed *B. ovata* had different relationship between respiration rate (R , $\mu\text{g O}_2 \text{ ind}^{-1} \text{ h}^{-1}$), and

wet weight (WW, mg) during ontogeny in contrast to most of marine invertebrates when these relations were unified for the whole life cycle. In small *B. ovata* with length of 0.4–3.0 mm and wet weight of 0.021–100 mg at 20°C it is expressed by the equation $R = 0.093 WW^{0.62}$, according which the weight - specific respiration rate reduces 20 times as wet weight raises; in ctenophores with length of 4–60 mm and wet weight of 100–30000 mg the expression $R = 0.016 WW^{0.99}$ shows that weight specific respiration rate is steady – state in this range of ctenophore size. The same character of relation between respiration rate and wet weight in adult *B. ovata* have been recorded earlier (Finenko *et al.*, 2001; Shiganova *et al.*, 2001; Vostokov *et al.*, 2001), but they have not conducted their researches on early stages of ctenophores.

B. ovata respiration rate is 2–3 times as much as in *M. leidyi* at the same temperature. Thus, specific oxygen consumption by adult *B. ovata* at 20°C ranges from 0.010 to 0.020, while by *M. leidyi* from 0.003 to 0.007 $\mu\text{g O}_2 \text{ mg WW}^{-1} \text{ h}^{-1}$ (Shushkina *et al.*, 2000; Abolmasova, 2001; Shiganova *et al.*, 2001; Vostokov *et al.*, 2001; Svetlichny *et al.*, 2004; Anninsky *et al.*, 2005). Probably this is a result of larger locomotion activity as well as high organic matter content in *B. ovata* (Vostokov *et al.*, 2001; Anninsky *et al.*, 2005).

Respiration rate in adult ctenophores with length of 10–50 mm (200–12000 mg) in the temperature range of 10–28°C increases continuously and Q_{10} coefficient is equal to 2.17 ± 0.5 . The basal metabolism of ctenophores narcotized with chloral hydrate was 4.5 ± 0.9 times lower than total metabolism that is characteristics of aquatic animals with high locomotion activity (Svetlichny *et al.*, 2004).

The study of effect of food conditions on respiration rate revealed that *B. ovata* weight specific respiration rate after 18- days starving at $17 \pm 1^\circ\text{C}$ fell by 33%, while in *M. leidyi* it decreased almost 2 fold at 8-days starvation at 12.4°C , i. e. *B. ovata* tolerate to nutrition conditions and is able to survive without any food for more long time.

4. FUNCTIONAL ROLE OF THE CTENOPHORE INVADERS *Mnemiopsis leidyi* AGASSIZ AND *Beroe ovata* MAYER IN INSHORE PLANKTONIC COMMUNITIES

4.3.5 Reproduction

In the Black Sea *B. ovata* starts to produce eggs at length about 30–35 mm. Clutch size is related with ctenophore length and increases from 40 eggs in small to 5000–7000 eggs in 80–120 mm ctenophores (Arashkevich *et al.*, 2001). Besides it is related with feeding intensity and it is a good index of food supply of animals in the sea. At once after its appearance in plankton when *M. leidyi* is in abundance, *B. ovata* starts reproduction. This time *B. ovata* has maximum fecundity and all 100% of adult ctenophores reproduce (Table. 4.4). As early as in two weeks after fast exhausting of food (sharp decrease of *M. leidyi* abundance due to *B. ovata* consumption) the share of reproduced adult ctenophores in the population reduces to 50%, and egg number in a clutch decreases in two orders. Although hatching success is high, it is lower of it in the beginning of reproductive period. Attenuation of reproduction continues till October – November.

Thus, experimental data show that *B. ovata* in the conditions of high food supply can realize their food requirements, reach maximum growth rate and increase the population due to high fecundity.

Table 4.4. Dynamics of the reproductive indices of *B. ovata* in September 2003 (unpublished data of Finenko and Arashkevich)

Date	% of ctenophore reproduced	Egg number in a clutch	Hatching success (%)
12 – 14. 09	100	4498 ± 2652	96 ± 4
18 – 20. 09	86	1684 ± 543	95 ± 1
21 – 23. 09	67	525 ± 386	87 ± 15
24 – 26. 09	50	57 ± 17	83 ± 10

4.3.6 Feeding, respiration, growth and reproduction of *B. ovata* under low salinity.

We have studied an effect of lower salinity on survival and ecological-physiological characteristics of *B. ovata* in connection with the problem of its possible introduction to other seas, in particular to the Caspian Sea with its lower salinity.

As our experiments showed *B. ovata* larvae transferred from salinity of 18 to 6‰ without preliminary acclimation died immediately. When salinity was decreased step by step they were alive at 6‰ about a day. Survival and growth rate of larvae in the salinity range of 9–18‰ raised as salinity increased. Thus, survival time of 50% of larvae abundance was 3 days at 9‰, 5 days at 12‰ and 8 days at 18‰ at 24°C (Fig. 4.11). Growth rate ($\mu\text{m day}^{-1}$) at 1 ‰ was 1.5 times lower than at 18‰ but daily ration values were the same at both salinities (Table 4.5).

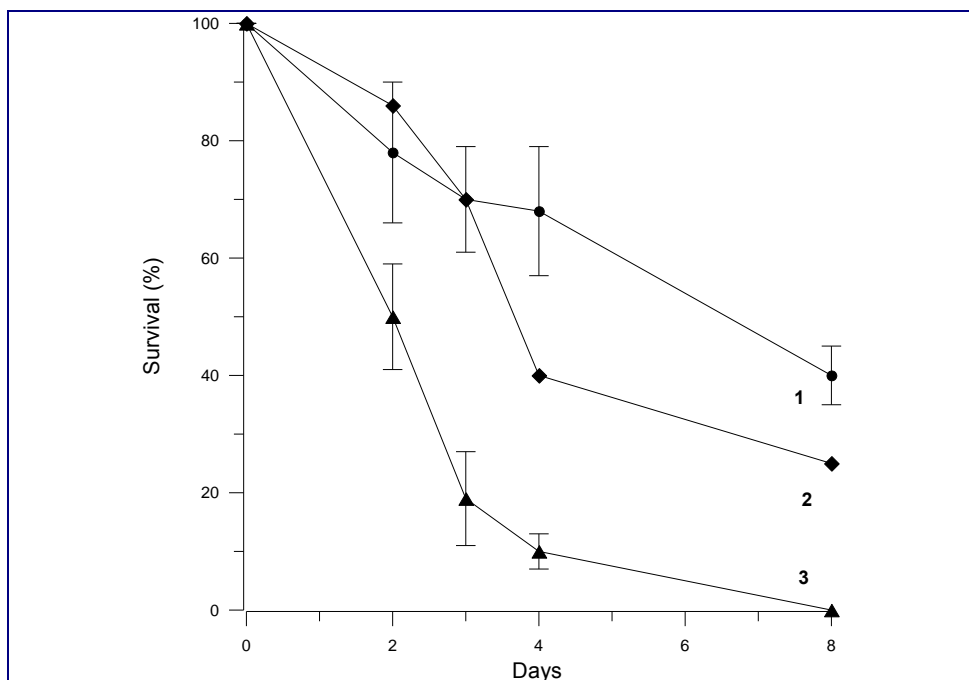


Figure 4.11. Survival of *B. ovata* larvae at different salinities (9, 12, 18‰)

4. FUNCTIONAL ROLE OF THE CTENOPHORE INVADERS Mnemiopsis leidyi AGASSIZ AND Beroe ovata MAYER IN INSHORE PLANKTONIC COMMUNITIES

Table 4.5. Growth, ingestion and survival rates of *B. ovata* larvae at salinities of 12 and 18 ‰ (unpublished data of Finenko, Romanova and Arashkevich)

Parameters	Salinity	
	12‰	18‰
Initial length (mm)	0.500 ± 0.075	0.500 ± 0.070
Initial number of larvae	40	40
Length at the end of the experiment (mm)	0.750	0.887 ± 0.327
Number of larvae at the end of the experiment	2	13
Days of growth	12	12
Growth rate (mm day ⁻¹)	0.021	0.032
Survival (%)	5.0	32.5
Daily ration (prey ind ⁻¹ day ⁻¹)	5.0	7±3

Adult *B. ovata* survived in the laboratory at 9‰ only for 3 days and on the second day there was 50% mortality (Fig.4.12). Ctenophores at 9‰ were inert, stayed near the bottom, did not feed and reproduce. At 12‰ salinity *B. ovata* were more active, swam in water column, their survival was higher than at 9‰, but lower than at 18‰, where during 8 days all ctenophores were alive. At the same salinity (12‰) survival was maximum (91%) in the smallest adults (10–19 mm), medium (62%) in size group of 20-29 mm and the lowest in large ctenophores > 30 mm during 5 days of the experiment (Fig.4.13).

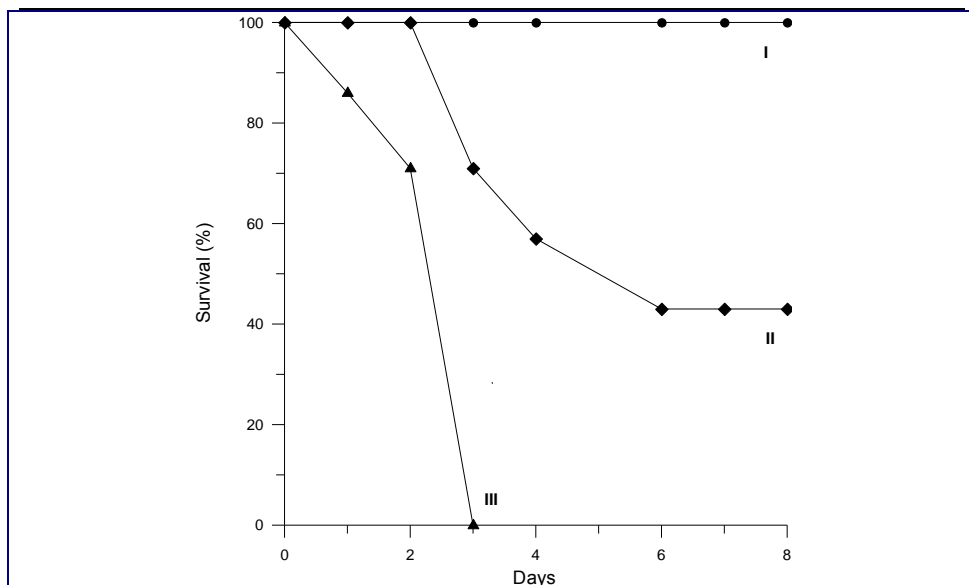


Figure 4.12. Survival of adult *B. ovata* at different salinities 18 (I), 12 (II), 9 ‰ (III)

The study of ecological-physiological indices of adult *B. ovata* that were acclimated to 12.5–13‰ salinity showed that they could feed intensively: daily ration values at high prey concentration were as high as 45–765% of wet weight, being maximum in small ctenophores (13–16 mm) (Fig. 4.14).

B. ovata growth in conditions of lower salinity was exponential during some or the largest part of life cycle ($L_t = L_0 e^{k \cdot t}$, where L_0 and L_t are initial and final length, k is growth coefficient, t is time). Daily weight specific rate of *B. ovata* at salinity of 12.5–13‰ was 0.07–0.11. These values were obtained for 30-mm ctenophores, when daily rations changed from 26 to 43% of wet weight.. The same growth rate was observed in our experiments in the Black Sea ctenophores at daily rations of 50% wet weight (Finenko *et al.*, 2003).

4. FUNCTIONAL ROLE OF THE CTENOPHORE INVADERS *Mnemiopsis leidyi* AGASSIZ AND *Beroe ovata* MAYER IN INSHORE PLANKTONIC COMMUNITIES

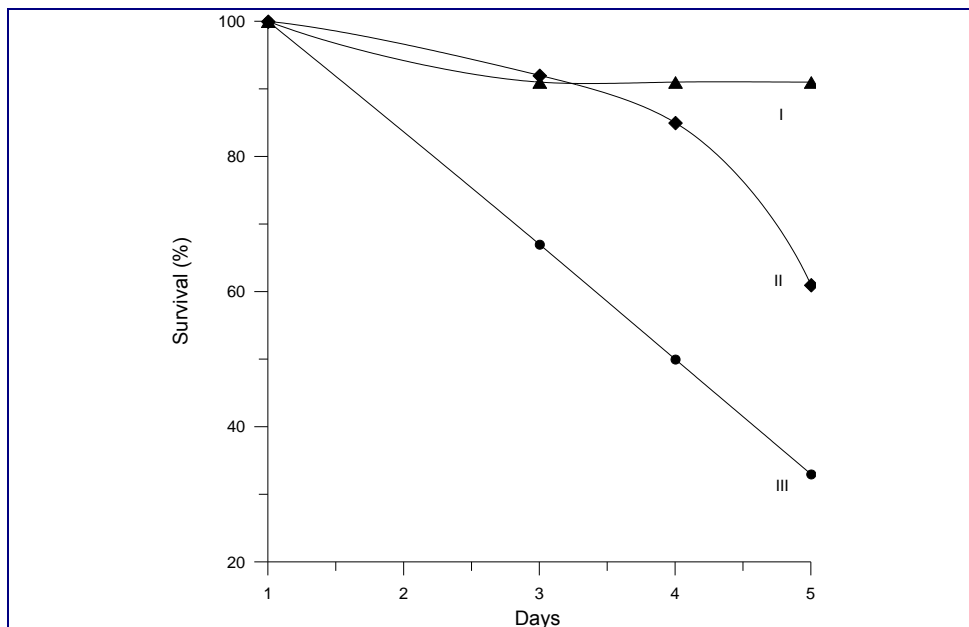


Figure 4.13. Survival of different size *B. ovata* at different salinities 12 ‰ (I – 10-19, II – 20-29, III – 30 –35 mm)

Even in conditions of lower salinity *B. ovata* assimilate food and use it for growth with high efficiency. These values calculated from ration, growth and respiration were as high as 0.72 for assimilation efficiency and 0.48 and 0.66 for efficiency of ingested and assimilated food utilization for growth, correspondingly (Table. 4.6).

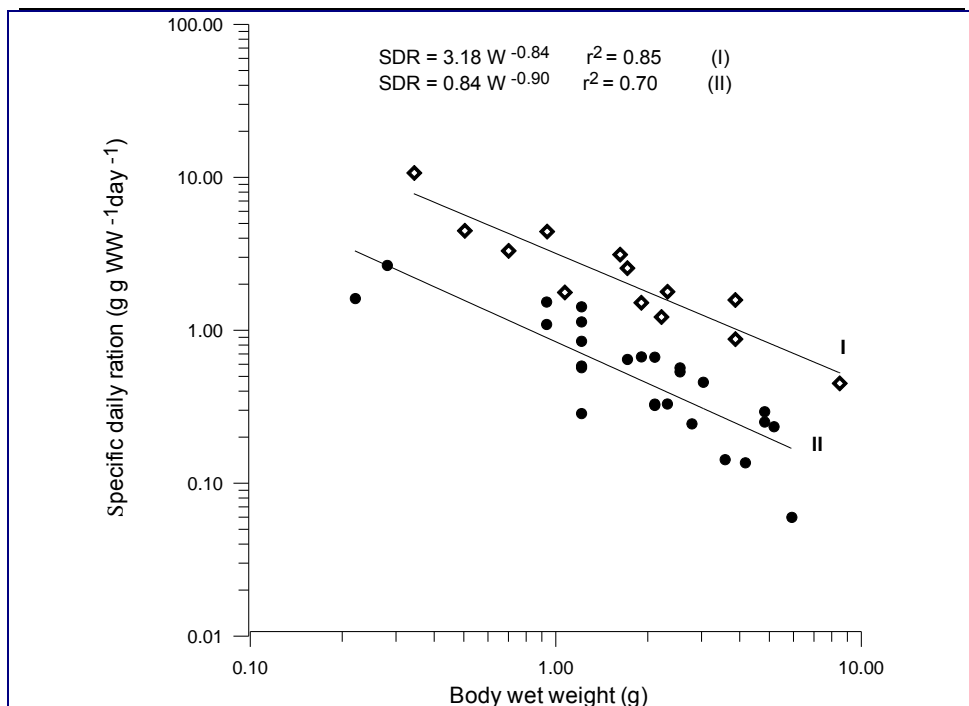


Figure 4.14. Effect of body wet weight (WW, g) on specific daily ration (SDR, g g⁻¹ day⁻¹) at two food concentrations (I – 1.66 г л⁻¹, $SDR = 3.18W^{-0.84}$, $r^2 = 0.85$; II – 1.00 г л⁻¹, $SDR = 0.84W^{-0.90}$, $r^2 = 0.70$). $t = 21^\circ\text{C}$

On the whole the rates of ecological-physiological processes in adult *B. ovata* adapted to suitable salinity conditions are rather close at salinities of 18‰ and 12.5–13‰ (Table 4.7). But *B. ovata* are less tolerate to lower salinity than *M. leidy*: lowest salinity value for *B. ovata* survival is about 7–9‰ (our data, Shiganova *et al.*, 2000) while *M. leidy* can live at salinity from 0.1 to 38‰ (Purcell, 2005).

B. ovata eggs appeared to be the most sensitive to lower salinity. During ontogenesis the salinity range as a rule is getting wider. *B. ovata* larvae were more sensitive to lower salinity than adult ctenophores. Meantime juvenile individuals (10–19 mm) were more resistant to reduced salinity from adult *Beroe* (> 30 mm).

4. FUNCTIONAL ROLE OF THE CTENOPHORE INVADERS Mnemiopsis leidyi AGASSIZ AND Beroe ovata MAYER IN INSHORE PLANKTONIC COMMUNITIES

Table 4.6. Daily energy budget of *B. ovata* (cal ind⁻¹ day⁻¹)

Initial weight, g	<i>C</i>	<i>R</i>	<i>G</i>	<i>A</i>	<i>a</i>	<i>K_I</i>	<i>K₂</i>
3.17	18.06	4.73	11.27	16	0.88	0.62	0.7
3.17	10.73	2.89	4.1	6.99	0.65	0.38	0.59
3.17	17.11	3.57	7.7	11.27	0.65	0.45	0.68
Average					0.72±0.13	0.48±0.12	0.66±0.06

C = daily ration

R = respiration rate

G = growth rate

A = assimilated food

a = assimilation efficiency

K_I = gross growth efficiency

K₂ – net growth efficiency

Table 4.7. Physiological characteristics of ctenophore *B. ovata* at the salinity of 12‰ (Caspian water) and 18‰ (the Black Sea)

Index	Caspian water (12 ‰)	The Black Sea (18 ‰)
Daily ration, % WW	14 - 380	5-460
Digestion time, h	0.5-7.5	0.5 –5.5
Respiration rate, ml O ₂ g ⁻¹ DW h ⁻¹	0.67	0.63 – 0.82

It seems possible to suppose that if to introduce *B. ovata* to water of lower salinity at the stages of early larvae the only small part of them could survive. But rather long preliminary acclimatization of juvenile animals (preferably with size of 10–20 mm) can affect upon the salinity resistance of both adult and embryos and larvae produced by them. As a result the survival range can be shifted towards lower salinity.

4.4 State of Ctenophore invader populations after *B. ovata* introduction

4.4.1 Seasonal dynamics

Extensive monitoring studies of the seasonal and interannual dynamics of ctenophores during recent decade after *B. ovata* introduction to the Black Sea have been conducting in the coastal regions off the Crimean Coast (Sevastopol Bay and adjacent waters) and in the northeastern Black Sea (Blue Bay near Gelendzhik) (Finenko *et al.*, 2001, 2003, 2006a; Shiganova *et al.*, 2000, 2003; Vinogradov *et al.*, 2000, 2005, 2006).

The typical seasonal dynamics of both alien species in both areas is the same and we will examine it as exemplified by the ctenophores in Sevastopol Bay.

In winter - early spring (January – April) *M. leidyi* is not abundant ($0.2\text{--}3.6 \text{ ind}\cdot\text{m}^{-2}$ and $1\text{--}10 \text{ g}\cdot\text{m}^{-2}$) and is represented by large individuals of an oral – aboral length of 25–55 mm and individual wet weight of 5–35 g (Figs. 4.15, 4.16). In spring (April – May) the wintered population started its reproduction (at temperature about 16°C) and in plankton adult animals (30–55 mm), as well as larvae (0.25–0.3 mm) and eggs are presented simultaneously. From this time, owing to the recruitment of the juveniles of the new generation, the population gradually, though insignificantly, increases its abundance but biomass is still low and ranges from 7 to 20 $\text{g}\cdot\text{m}^{-2}$. At the end of May – early June, the grown juveniles of the new generation of 0.3–1.25 mm length form the most population (80% of total abundance). Mainly reproduction takes place in bays and inshore waters where share of larvae (< 10 mm) in the time of maximum reproduction can exceed 90% of the total population abundance. In deeper waters (>100 m depth) there are no the individuals < 10 mm often, and large *M. leidyi* with length > 50 mm make up 20–30% of population (Vinogradov *et al.*, 2005). In the whole population size range is greater in open and shallow waters when compared to bay. Thus, in the bay *M. leidyi* maximum length is about 40 mm, and in adjacent shallow waters it is as long as 80 mm (our data).

4. FUNCTIONAL ROLE OF THE CTENOPHORE INVADERS *Mnemiopsis leidyi* AGASSIZ AND *Beroe ovata* MAYER IN INSHORE PLANKTONIC COMMUNITIES

Mnemiopsis reproduction starting in spring has been lasting over the entire summer at different rates with 2 week intervals between peaks (Vinogradov and Shushkina, 2002), that results in sharp increase of abundance in July – August at surface water temperature 23°C. This time the individuals of spring generation start reproduction also. The abundance dynamics changes sharply with appearance of another ctenophore – *B. ovata* – in plankton: *M. leidyi* abundance and biomass decrease one order of magnitude during short period (10–12 days) (Fig.4.15a,b). With the further development of the *B. ovata* population, the population of *M. leidyi* decreases until December when no ctenophores can be found in the bay or other shallow regions. Probably in winter *M. leidyi* makes aggregations near bottom in deep waters with temperature of 8–9°C (Mutlu, 1999; Zaika, 2005). Sufficient food supply of this non – numerous wintered population results in high individual growth rate and fecundity of the ctenophores in spring, so maximum abundance and biomass in summer can reach values that were observed in the years before *B. ovata* introduction

The population of *B. ovata* starts reproduction next to the peak of *M. leidyi* and rapidly reaches the maximum abundance. In this time mean fecundity of adult *B. ovata* with length of 35–70 mm is as high as 4500 ± 250 eggs in a clutch, all eggs are viable and they develop to larvae (Fig. 4.17). The high reproduction intensity of *B. ovata* provides a rapid increase in its abundance. The period of intensive reproduction is very short (about 2 weeks); later, the fecundity and the share of reproducing ctenophores decrease significantly. *B. ovata* is available in plankton during rather short period (2–3 months): from August – September till November – December in different years, then possibly like other *Beroe* species do in the northern seas the individuals of new generation sink to the near bottom waters and stay there until maximum of *M. leidyi* develops (Sieferd and Conover, 1992; Falkenhaug, 1996). As shown above, *Beroe* is tolerant to a fluctuating food supply and can survive without any food for relatively long periods of time (Anninsky *et al.*, 2005). However, in winter, it may use another ctenophore species, *P. Pileus*, as its food source.

This seasonal dynamics of ctenophores – invaders is typical for all shallow regions. Thus, in the northeastern Black Sea ctenophore development had the same pattern in the whole shallow zone up to region of continental slope but with some temporal shift in separate years particularly pronounced in 2004 (Shiganova *et al.*, 2004; Shushkina *et al.*, 2004; Vinogradov and Shushkina, 2002; Vinogradov *et al.*, 2005, 2006).

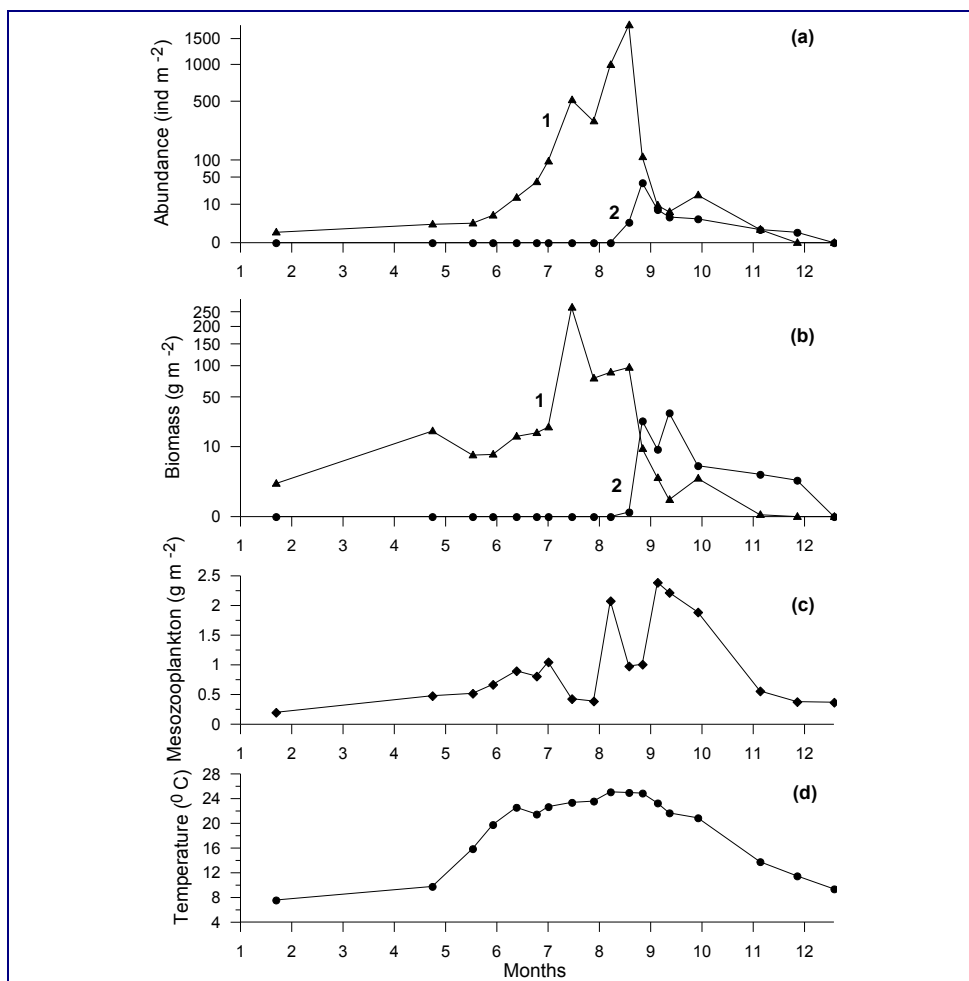


Figure 4.15. Abundance (a), biomass (b) of ctenophores *M. leidyi* (1) and *B. ovata* (2), mesozooplankton biomass (c) and water temperature (d) in Sevastopol Bay in 2003

4. FUNCTIONAL ROLE OF THE CTENOPHORE INVADERS *Mnemiopsis leidyi* AGASSIZ AND *Beroe ovata* MAYER IN INSHORE PLANKTONIC COMMUNITIES

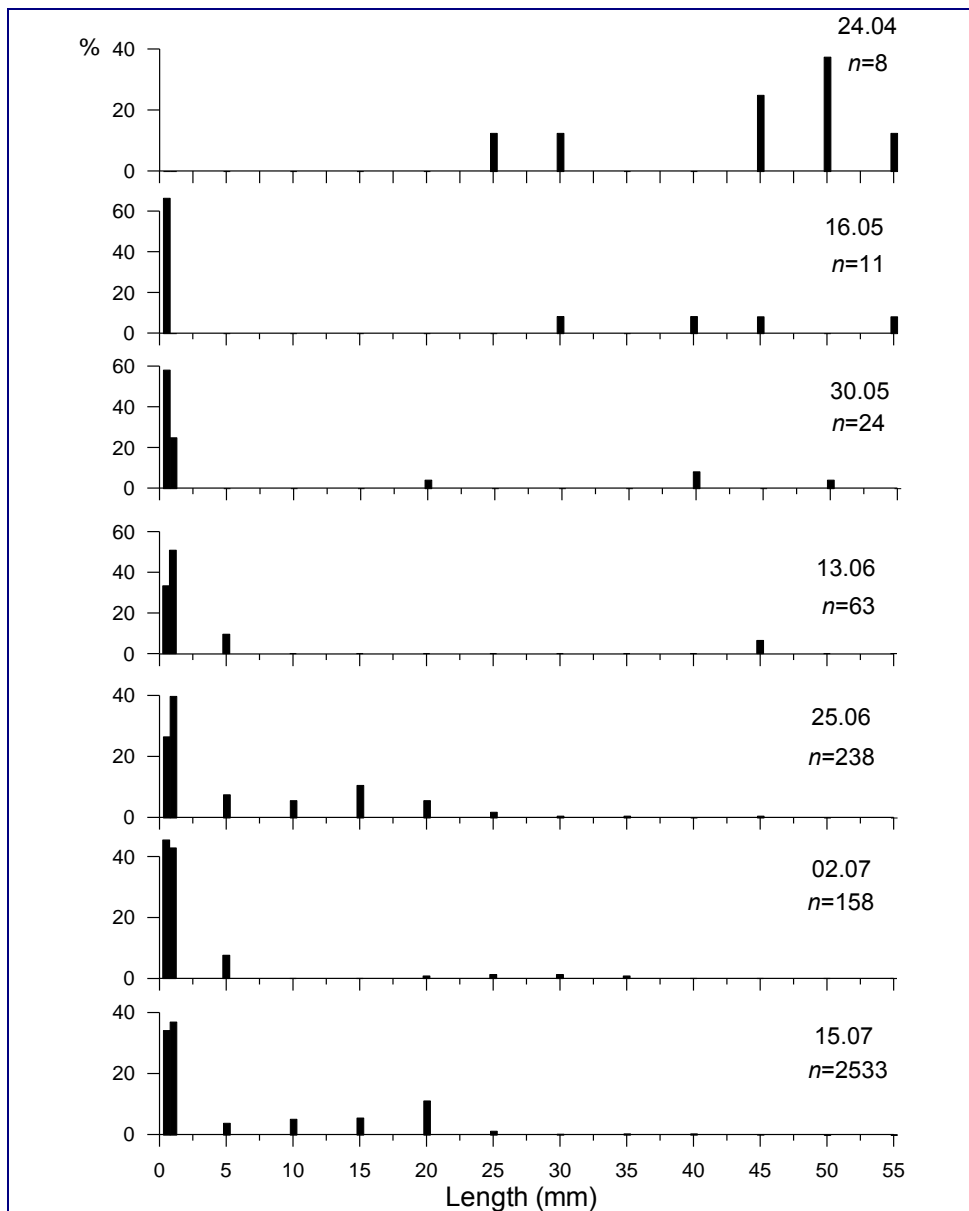


Figure 4.16. Population size structure of *M. leidyi* in Sevastopol Bay in 2003

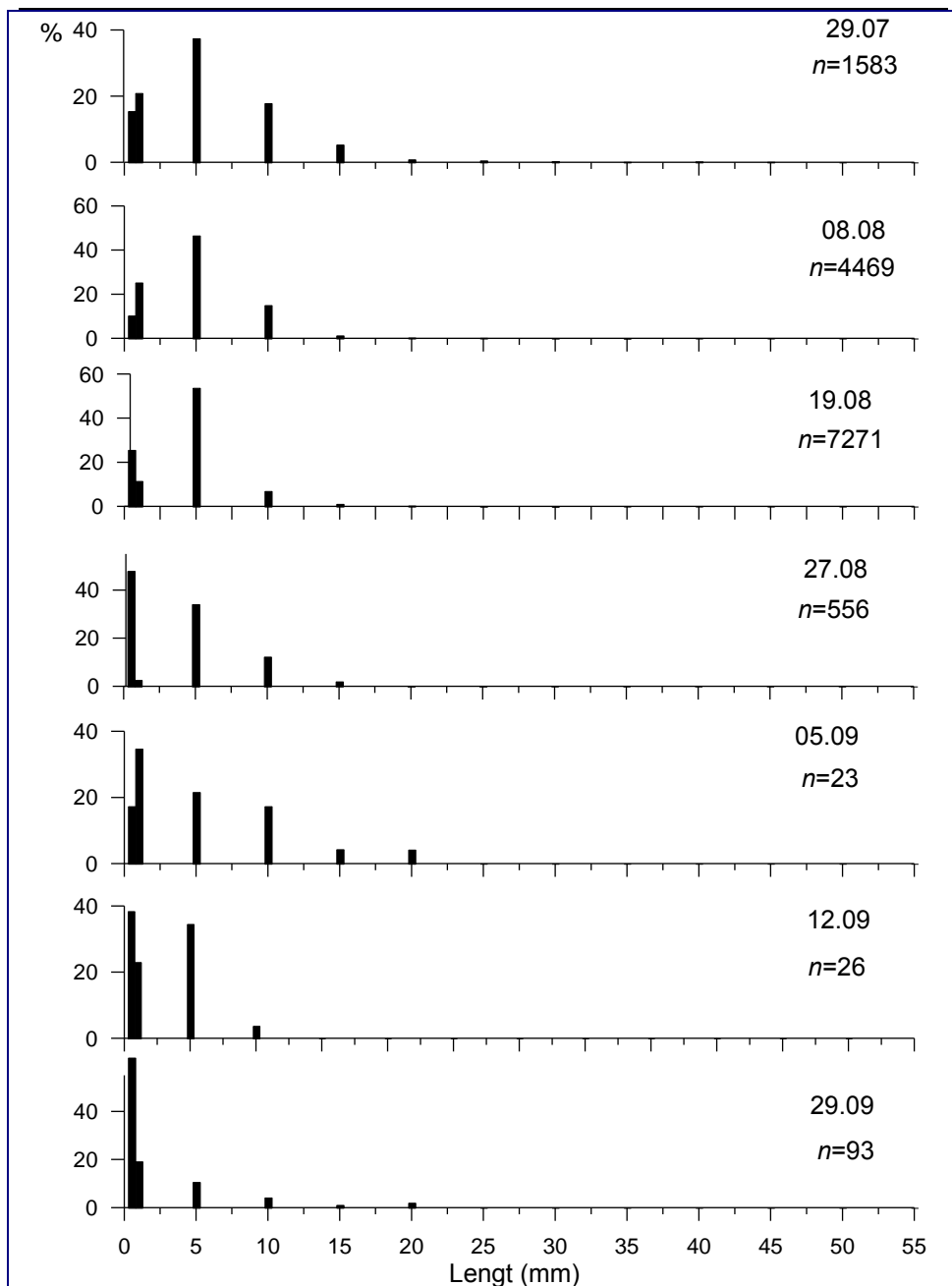


Figure 4.16 (cont'd).
Sevastopol Bay in 2003

Population size structure of *M. leidyi* in

4. FUNCTIONAL ROLE OF THE CTENOPHORE INVADERS *Mnemiopsis leidyi* AGASSIZ AND *Beroe ovata* MAYER IN INSHORE PLANKTONIC COMMUNITIES

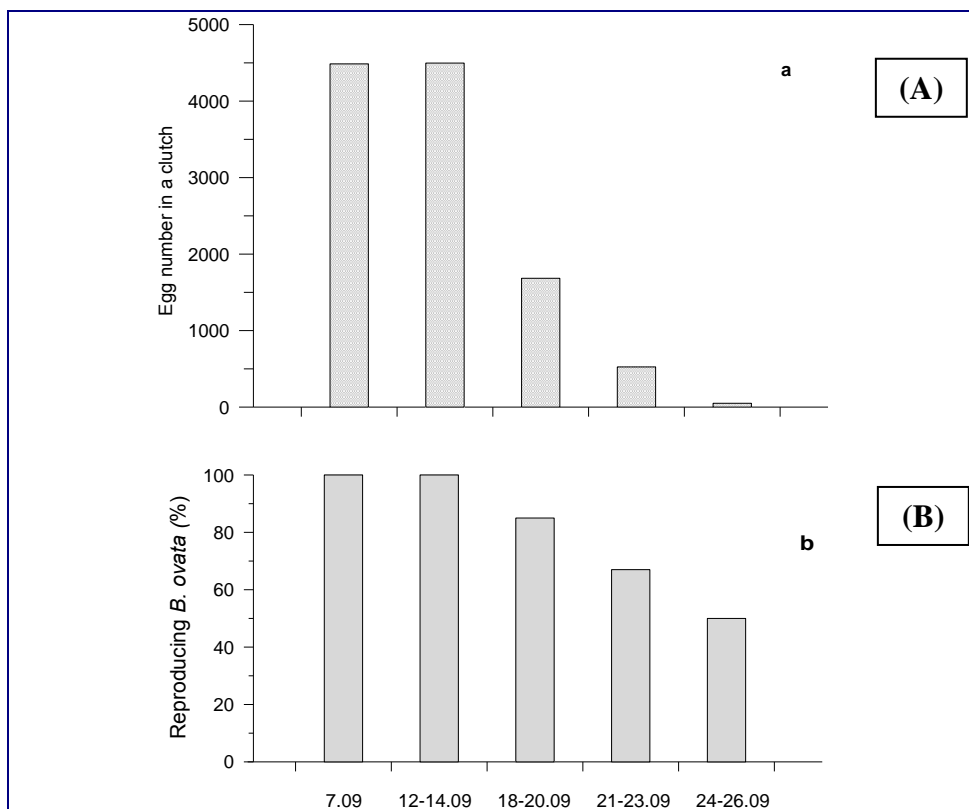


Figure 4.17. Clutch size of *Beroe* (A) and percentage of ctenophore reproduced (B) in September 2003

4.4.2 Interannual dynamics of the ctenophore invaders in different regions of the Black Sea.

During the entire study period after *B. ovata* appearance the patterns of population dynamics of both species are similar, though the timing of mass development and abundance differed in different years (Fig. 4.18). For example, the timing of maximum abundance of *M. leidyi* in the bay can be shifted for a month or more and it is governed by summer temperature. Thus, in 2000 at the lowest temperature in July for the recent 5 years (21.2°C) maximum abundance was observed in

September (temperature 23.5°C), and opposite, in 2002 it was in July at 25°C. As it was shown above, *M. leidy* maximum reproduction rate in the Black Sea occurs at 23°C, and it determines timing of seasonal maximum abundance in different years and in different sea areas as well. Maximum abundance value probably is a function of food conditions. As a rule, two – three weeks later of *M. leidy* peak a maximum of *B. ovata* is observed followed by a subsequent decrease in its abundance. *M. leidy* is very scarce over the whole autumn (0.4–6 ind m⁻² or <0.1–2.4 g m⁻² in different years in inshore areas). The peaks of abundance and biomass of both species do not coincide in time, since the main contribution to the biomass is made by large adult ctenophores, 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 populations of both ctenophore species consisted in their quantitative parameters: the maximum biomass of *M. leidy* in Sevastopol Bay (1100 g·m⁻²) was observed in 2001, while during the other years it was almost constant (160–230 g·m⁻²). Comparison between the values of the mean biomass of fodder zooplankton during the two – month 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·m⁻²); 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.

B. ovata reached its maximum abundance and biomass values in Sevastopol Bay also in 2001 (140 ind m⁻² and 53 g·m⁻²); in 2000 and 2002 it was not higher than 14 g·m⁻².

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) (Finenko *et al.*, 2000; Shiganova *et al.*, 2000; Vinogradov *et al.*, 2000; Kideys and Romanova, 2001). Its further development in the regions studied was similar. The seasonal dynamics of the abundance of both species in the northeastern Black Sea off the Caucasian coast (Blue Bay and adjacent regions) in the years 1999–2004 featured the same patterns with certain time shifts in some years; this

4. FUNCTIONAL ROLE OF THE CTENOPHORE INVADERS *Mnemiopsis leidyi* AGASSIZ AND *Beroe ovata* MAYER IN INSHORE PLANKTONIC COMMUNITIES

was especially obvious in 2004 (Shiganova *et al.*, 2001, 2003; Vostokov *et al.*, 2001; Vinogradov *et al.*, 2002, 2005; Shushkina *et al.*, 2004). Here, similarly to Sevastopol Bay, the maximum *M. leidyi* biomass was observed in 2001 and was comparable with the values in the years before *B. ovata* invasion.

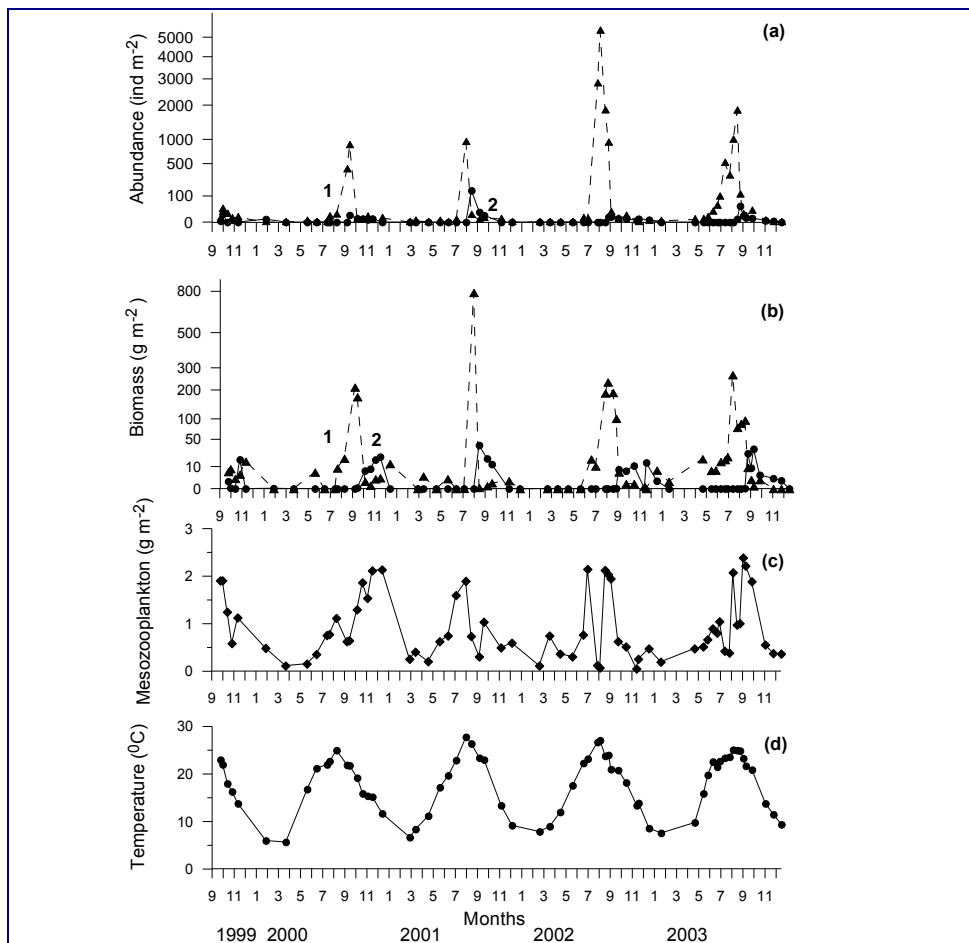


Figure 4.18. Abundance (a), biomass (b) of *M. leidyi* (1) and *B. ovata* (2), biomass of mesozooplankton (c) and water temperature (d) in Sevastopol Bay in 1999 – 2003.

The abundance and biomass of *B. ovata* in Blue Bay were higher than those in Sevastopol Bay; in August 2001 they reached 700–800 ind m⁻² and 500 g m⁻², respectively. In Sevastopol Bay during all the years the abundance and biomass of *B. ovata* did not exceed 140 ind m⁻² and 39 g m⁻² (August 2001). Such high difference between abundance and biomass values in different regions possibly is due not only their real distinctions but also to different methods of the calculations. We have not introduced correction coefficient for the net catch ability but in the studies of the Shirshov Institute of Oceanology in Blue Bay the authors applied various coefficients (2–4) for different size groups of ctenophores.

In the northwestern Black Sea off the Bulgarian coast, *B. ovata* was first founded in 1997 (two years before of the other regions) (Konsulov and Kamburska, 1998). During the surveys in 1998 and 1999 (in late September) *B. ovata* presented in plankton with abundance of 40–80 ind m⁻² but in the beginning of September 2000 and August 2001 it was absent in both the coastal and the open sea waters (Kamburska, 2004). About 90% of the *M. leidyi* population at that time was comprised by juvenile individuals, 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. 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 timing of development of two ctenophore populations and the rapid (avalanche -like) change in their abundance require frequent observations to estimate correctly the dynamics of both populations. Such kind of the research allows to obtain more valuable information even as compared to oceanographic cruises, when sampling is performed only a few times in an year.

So, 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, started to control *M. leidyi* abundance and reduced its pressure on other constituents of the ecosystem. It is worth noting that *M. leidyi* maximum abundance and biomass in some years can reach rather high

4. FUNCTIONAL ROLE OF THE CTENOPHORE INVADERS *Mnemiopsis leidyi* AGASSIZ AND *Beroe ovata* MAYER IN INSHORE PLANKTONIC COMMUNITIES

values. Probably the better food provision of this over-wintering not numerous population produces 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 *B. ovata*. Density of the *M. leidyi* population appeared to be a function of food abundance and the role of *B. ovata* consisted in a reduction of prey biomass in autumn but not in a limitation of the maximum biomass.

In recent years the *M. leidyi* mass development has been limited to a significantly shorter period (1–2 months) as compare to preceding years (5–6 months).

So *B. ovata* role in planktonic community of the Black Sea consists in sharp suppression of *M. leidyi* abundance and as a result shortening of the period of mass presence in the plankton.

4. 5 Quantification of trophic relations in food chain of *B. ovata* – *M. leidyi* – meso – (micro) zooplankton

4.5.1 Predatory pressure of ctenophores on zooplankton community

In a series of previous studies, an inverse correlation was established between Copepoda density and the biomass of lobate ctenophore, 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 (Burrell and Van Engel, 1976; Kremer, 1979; Larson, 1987; Purcell, 1994). Higher consumption rates (more than 20% of zooplankton biomass per day) result in a sharp reduction of the prey abundance (Deason, 1982; Matsakis and Conover, 1991).

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 were as high as 30–40%

of zooplankton biomass (Finenko and Romanova, 2000). From July to September in the years 2000–2003, after *B. ovata* appearance, *M. leidyi* pressure on zooplankton decreased significantly: in the period of its maximum development, the population consumed from 6.0 ± 0.4 to $13.2 \pm 57\%$ of zooplankton biomass per day (Table 4.8). In other periods of the year, consumption of mesozooplankton by ctenophores was insignificant (less than 1% biomass per day). The population rations in the periods of *M. leidyi* maximum changed from 0.4 to 9.2% of its energy content (Table 4.9). While the minimum food requirements, or sustaining daily rations calculated from population respiration rate data (Abolmasova, 2002) ranged from 3.3 to 6.4% of the population energy content. So, there are some periods when the *M. leidyi* population in Sevastopol Bay experiences a lack of food. This usually occurs when the forage mesozooplankton biomass is lower than 0.1 g m^{-3} .

Assuming that the daily consumption rate by the *M. leidyi* population should not exceed 10% of the zooplankton biomass and that the mean clearance rate is about $1.5 \text{ l ind}^{-1} \text{ day}^{-1}$ the calculated critical biomass of ctenophores that does not affect mesozooplankton abundance should not be greater than 4 g m^{-3} or 120 g m^{-2} (if the greater part of population dwells in the upper 30-m layer) (Mutlu, 1999; Vinogradov *et al.*, 2005). As it follows from our observations, in recent years, after *B. ovata* invasion in the inshore regions of the Black Sea overcritical values of *M. leidyi* biomass have been observed only during short periods and only during these periods does the *M. leidyi* population control the zooplankton community.

Table 4.8. Predatory impact of the *M. leidyi* population on mesozooplankton biomass (% loss per day) in 1995 – 2003

Month/year	1995	2000	2001	2002	2003
June-August	21.3 ± 15.8	0.2 ± 0.05	6.0 ± 6.1	13.2 ± 5.9	7.1 ± 2.9
September-November	9.0 ± 3.3	1.2 ± 0.9	0.01	0.06 ± 0.04	0.5 ± 0.4

M. leidyi larvae and juvenile can consume microzooplankton along with mesozooplankton (Stoecker, 1987; Sullivan and Gifford, 2004). In the period of maximum abundance larvae of <10 mm length make up to

4. FUNCTIONAL ROLE OF THE CTENOPHORE INVADERS *Mnemiopsis leidyi* AGASSIZ AND *Beroe ovata* MAYER IN INSHORE PLANKTONIC COMMUNITIES

90% of the total population numerical abundance in inshore waters. The potential maximum grazing of microzooplankton by *M. leidyi* larvae calculated from our experimental clearance rate data, ranged from 1.9 to 25% of prey biomass daily in Sevastopol Bay in July – September 2000–2005 while in adjusted water regions it was much less (0.3–5.1%) (Table 4.10). Meantime, even at such high grazing rate of *M. leidyi* larvae in the bay microzooplankton biomass have not only decreased but, in contrast, had had a trend to increase. Along with high growth rate of infusoria, that have been the main component of microzooplankton in the bay. One possible reason for this could be their mass development on mucus released by the ctenophores.

Table 4.9. Abundance, biomass, zooplankton grazing, respiration rate and daily ration of the *M. leidy* population in Sevastopol Bay during July –September 2000

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 ⁻¹	<i>R</i> , cal day ⁻¹	<i>Q/B</i> , %	<i>R/B</i> , %	<i>Q/R</i>
06.09.2000	21.9	40.7	21.1	266.5	0.52	0.063	1.6	9.51	4.29	3.3	1.6	2.0
03.09.2000	21.8	86.6	17.3	218.1	0.2	0.065	2.2	6.66	4.86	2.8	2.2	1.3
01.08.2001	27.8	93.8	79.0	995.7	0.842	0.19	27.0	26.6	41.6	2.5	4.2	0.6
30.07.2002	26.7	281.2	18.8	236.5	0.067	0.013	14.3	8.05	1.48	3.2	0.7	4.6
06.08.2002	27.1	535.7	23.3	294.0	0.044	0.008	20.3	10.01	1.30	3.2	0.4	8.0
20.08.2002	23.8	182.5	18.9	238.0	0.104	0.213	12.5	8.89	21.38	3.5	9.0	0.39
29.08.2002	24.0	92.2	10.1	127.5	0.11	0.20	6.6	4.81	10.75	3.5	5.4	0.65
15.07.2003.	23.4	51.2	26.6	335.4	0.512	0.043	10.7	10.83	3.68	2.2	1.1	2.94
29.07.2003	23.4	31.7	7.7	96.9	0.243	0.039	3.9	6.69	1.22	6.4	1.2	5.3
08.08.2003	25.1	99.3	8.7	110.1	0.088	0.208	6.1	4.17	10.13	3.5	9.2	0.38
19.08.2003	25	181.8	9.6	121.5	0.053	0.098	7.8	7.63	6.15	5.8	5.1	1.14

T = surface water temperature

N = abundance

B = biomass (wet weight and energy content)

W = mean wet weight of *M. leidy* in the population

ZB = zooplankton biomass

PI = zooplankton grazing rate

Q = respiration rate

R = population daily ration

4. FUNCTIONAL ROLE OF THE CTENOPHORE INVADERS Mnemiopsis leidyi AGASSIZ AND Beroe ovata MAYER IN INSHORE PLANKTONIC COMMUNITIES

Table 4.10. Microzooplankton grazing by *M. leidyi* larvae in inshore waters of the Black Sea

Date	N (larvae m ⁻³)	W _{avr} (mg)	CR (l day ⁻¹)	Grazing (% biomass)
Shelf				
06.09.00	20.8	251.2	21.75	2.17
01.08.01	16.1	253.0	16.92	1.69
30.07.02	106.0	69.2	51.44	5.14
08.08.02	87.2	61.1	40.18	4.02
19.08.03	117.8	25.2	41.23	4.12
21.07.04	11.7	40.1	4.65	0.46
06.08.04	16.5	36.0	6.34	0.63
20.08.04	4.6	151.2	3.37	0.34
31.08.04	6.6	213.2	6.14	0.61
03.08.05	10.0	94.0	5.64	0.56
Sevastopol Bay				
06.09.00	89.3	69.2	43.4	4.3
01.08.01	109.4	30.2	40.0	4.0
30.07.02	412.0	41.1	164.5	16.5
08.08.02	727.7	23.5	250.3	25.0
20.08.02	196.3	75.3	98.9	9.9
19.08.03	197.5	26.4	69.8	7.0
21.07.04	64.7	4.3	18.5	1.9
06.08.04	371.2	70.2	181.3	18.1
20.08.04	125.4	92.0	69.7	7.0
31.08.04	294.1	50.4	125.6	12.6
03.08.05	417.7	22.0	142.4	14.2

Predatory impact of *B. ovata* on *M. leidyi* population is short-term but very intensive. Minimum daily food requirements of *B. ovata* population in the peak abundance period ranged from 25 to 47% of *M. leidyi* population biomass (Svetlichny *et al.*, 2004). If to take account of growth and reproduction of ctenophores daily consumption rate of *M. leidyi* by the *B. ovata* population should be even higher. During some

short periods it could be well in excess of the prey biomass both off the Crimean and Caucasian coasts (Finenko *et al.*, 2000; Shushkina *et al.*, 2004a). As early as in 2–4 weeks after its appearance in the plankton the *B. ovata* population experiences a lack of food as its respiration demands exceed prey biomass by some 20–100 times (Abolmasova *et al.*, 2002). Using the model of Geritsen and Strickler (1977) we calculated that at an *M. leidy* biomass of $<7 \text{ g m}^{-2}$ encounters and captures of prey by *B. ovata* are so occasional that it practically can't consume *M. leidy* (Finenko, unpublished data). Probably it enables to *M. leidy* population to avoid full extermination. Another reason for the *M. leidy* population preservation is spatial disconnection of the species studied: while *B. ovata* inhabits in the upper mixed layer (0–15 m), some part of *M. leidy* population (mainly large animals of $> 30 \text{ mm}$ length) inhabits at the depths of $> 40\text{--}50 \text{ m}$ in sub-thermocline layer (Vinogradov *et al.*, 2002). Besides, *B. ovata* horizontal distribution is much more heterogeneous than that of *M. leidy*, and some of the depths inhabited by *Mnemiopsis* may not be occupied by its predator.

4.5.2 Effect of ctenophores on mesozooplankton and ichthyoplankton abundance

B. ovata introduction to the Black Sea resulted in the structural changes into zooplankton community. Decrease of *M. leidy* abundance as a consequence of *B. ovata* invasion has induced mesozooplankton biomass increasing especially the warm water species that have suffered greatly during the first years of *M. leidy* introduction (Lebedeva *et al.*, 2003; Shiganova *et al.*, 2004; Shushkina *et al.*, 2004; Hubareva *et al.*, 2005).

In inshore waters of the northeastern Black Sea the mean annual biomass of forage zooplankton in 1999–2000 was five times higher than in 1992–1998 (Lebedeva *et al.*, 2003). Effect of *M. leidy* abundance reduction was most evident in biomass values of *Acartia* sp., *Paracalanus parvus* and Cladocera. The average *P. parvus* and Cladocera biomasses in 1999–2001 were higher 10 times of that in the years of *B. ovata* absence (1992–1998). In Sevastopol Bay average numerical abundance of planktonic Crustacea in spring – autumn 2000–2003 increased about 4 times compared to 1998 (Fig. 4.19), and Copepoda abundance raised ten – fold compared to 1995. The average *Mnemiopsis* biomass fell that time

4. FUNCTIONAL ROLE OF THE CTENOPHORE INVADERS *Mnemiopsis leidyi* AGASSIZ AND *Beroe ovata* MAYER IN INSHORE PLANKTONIC COMMUNITIES

from 119.5 ± 41.5 to 21.9 ± 16.9 g m⁻². Abundance and biomass of warm water Copepoda *Centropages ponticus* and Cladocera *Penilia avirostris* and *Pleopis polyphemoides* that have been affected by *M. leidyi* most strongly after *B. ovata* introduction increased from 6 to 20% and from 12 to 39% of total forage zooplankton abundance, respectively. In separate years (August 2003) Cladocera biomass especially *P. avirostris* reached up to 80% of total forage zooplankton biomass. However, it is worth noting that besides effect of *Beroe* climatic forcing could be a factor governing zooplankton development. In July – August 1999 – 2002 the highest water temperature on the sea surface and into Cold Intermediate Layer was observed for the last 13 years (Shushkina *et al.*, 2004), that stimulated development of warm water species with their short life cycle.

It was noted increasing of biomass of *Sagitta setosa*, food competitor of *Mnemiopsis* that have disappeared almost completely in the years of *M. leidyi* bloom. *S. setosa* maximum biomass in September – October 1999–2001 in the northeastern Black Sea near – shore waters was 8–9 mg m⁻³, in waters off Crimea coast its biomass raised up to 14 mg m⁻³ in September 2003. In autumn of 2000–2002 substantial share of mesozooplankton biomass (up to 16%) in the northeastern region and in Sevastopol Bay was formed by appendicularian *Oikopleura dioica* (Hubareva *et al.*, 2004).

Along with the general trend to increase forage zooplankton biomass after *B. ovata* introduction there are some inter annual differences that are caused by timing of *B. ovata* appearance in plankton and its food pressure on *M. leidyi*. As example, mean forage zooplankton biomass value in 2004 was lower than in previous years as in Sevastopol Bay as in the northeastern part of the sea that was a result of long presence of *M. leidyi* in plankton and later appearance of *B. ovata* (Vinogradov *et al.*, 2005).

B. ovata introduction did affect on neither *Oithona similis* no *Pseudocalanus elongatus* abundances that are low so far (Fig. 20). Effect of *M. leidyi* on mesozooplankton structure is the result of difference in

ecology of the species. Thus, *O. similis* and *P. elongatus* being the cold water species with reproduction peak at 7-15°C are disconnected with *M. leidy* in space and time (Gubanova *et al.*, 2002); that is a reason of no apparent effect on their abundance in the years after *B. ovata* introduction. In contrast, abundance of warm- water and eurythermal Copepod species – *C. ponticus*, *A. clausi* that have a reproductive peak in July – September, in the period of *M. leidy* reproduction and growth, revealed clear relation with *M. ovata* abundance.

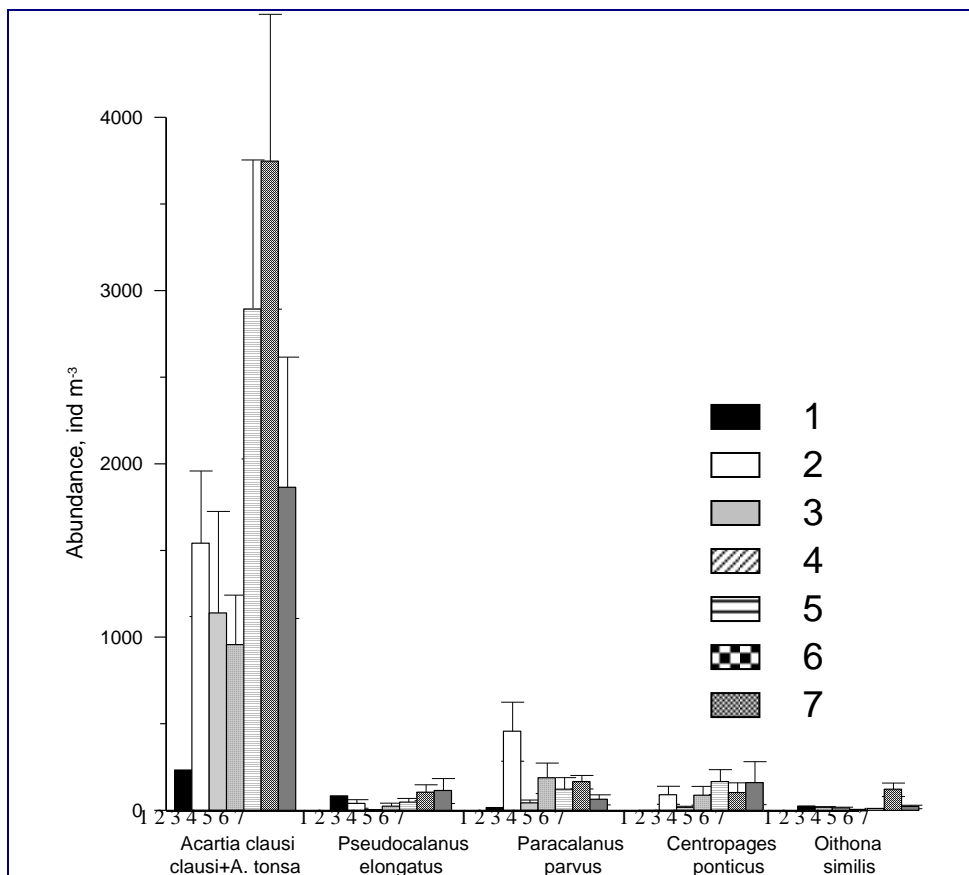


Figure 4.19. Inter annual dynamics of Copepod species abundance (ind m⁻³) in Sevastopol Bay during 1995- 2003 (bar is a standard error): 1-th column is 1995 –1996 (Gubanova *et al.*, 2002; 2, 3, 4 – 2000, 2001, 2002 - (Hubareva *et al.*, 2004), 5,6,7 – 2003, 2004, 2005 (our unpublished data).

4. FUNCTIONAL ROLE OF THE CTENOPHORE INVADERS *Mnemiopsis leidyi* AGASSIZ AND *Beroe ovata* MAYER IN INSHORE PLANKTONIC COMMUNITIES

In inshore waters off Crimea coast as well as in the northeastern Black Sea *Mnemiopsis* biomass decrease resulted also in some changes of meroplankton abundance: in recent years (2003–2005) in inshore waters off Crimea coast its share in total biomass of forage zooplankton decreased down to 14–28% of average annual values as compared with about 40% in 1999–2002 (Fig. 4.20). However while in the northeastern inshore waters some changes in species composition in meroplankton occurred – Bivalvia larvae became dominant constituent instead of Cirripedia nauplii in previous years in waters off Crimea coast the latter remains dominant.

In summer 2000–2001 a trend to increase species number, egg and larvae fish abundance in different areas of sea was shown (Shiganova *et al.*, 2004; Gordina *et al.*, 2005). In inshore waters near Sevastopol eggs and larvae of the Mediterranean Sea migrates Bonito and Bluefish have been found, that testifies to favourite conditions for their spawning and feeding. While in the years of before *B. ovata* introduction the percentage of larvae of summer – spawning fish without any food in their stomachs was as high as 80–100% (Tkach, 1993; Tkach *et al.*, 1998) in 2000–2001 54.5% of anchovy larvae and 73% of Blennidae and Gobiidae larvae had food in the stomach (Gordina *et al.*, 2005).

In late August 1999, the first year of *B. ovata* appearance off the Caucasian coast ichthyoplankton consisted of eggs and larvae of 24 species of summer – spawning fish. Maximum eggs (323 ind m⁻²) were observed for anchovy *Eugraulis encrasicolis ponticus*, abundances of *Trachurus mediterraneus ponticus*, *Mugil saliens* and *Diplodus annularis* eggs were about 1.2 ind m⁻². Such high abundance of anchovy and *T. mediterraneus* was not found since 1988 after *M. leidyi* introduction (Shiganova *et al.*, 2003). High abundances of early stages of these species were noted in 2001 also, the year with hot summer and earlier *B. ovata* appearance in plankton.

However, predatory impact of *M. leidyi* on micro- and mesozooplankton can be considerable in short period of its peak in summer. When this period synchronizes with fish larvae development in plankton, its

negative effect can be resulted in insufficient food supply and low survival of fish larvae, as it was observed in 2004, when *M. leidy* was abundant for a long time due to later appearance of *B. ovata* (Vdodovich *et al.*, 2007).

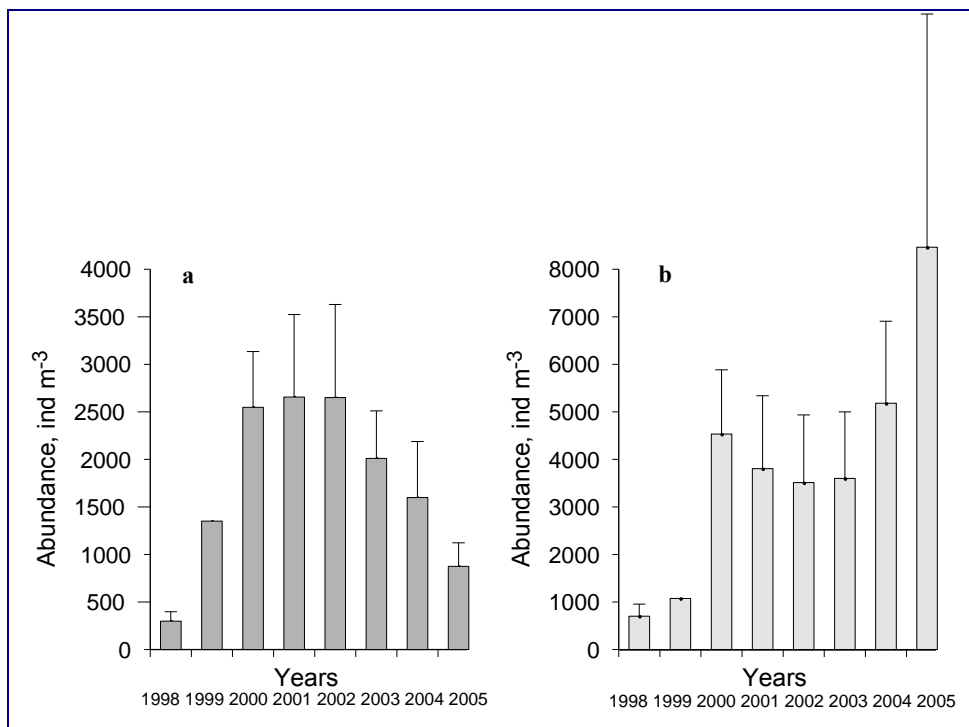


Figure 4.20. Average abundance (ind m⁻³) of meroplankton (A) and planktonic Crustacea (B) during spring – autumn period (May – September) of 1998 – (Gubanova *et al.*, 2002,) 1999 – (Gordina *et al.*, 2003), 2000 –2002 (Hubareva *et al.*, 2004)

Thus, after *B. ovata* introduction some features of recovery of the inshore Black Sea plankton community were evident: duration and predatory impact of *M. leidy* on mesozooplankton have been decreased, biodiversity and abundance of which have raised and food supply of planktivorous fish larvae improved. Meantime, mesozooplankton concentration remains lower than during the 1970s–80s. *B. ovata* impact does not result in absolute suppression of *M. leidy* and its pressure on forage zooplankton and fish larvae but essentially shortens this pressure.

4. FUNCTIONAL ROLE OF THE CTENOPHORE INVADERS *Mnemiopsis leidyi* AGASSIZ AND *Beroe ovata* MAYER IN INSHORE PLANKTONIC COMMUNITIES

Probably now as the Black Sea planktonic community as the ecosystem of inshore regions transferred to new dynamic equilibrium, that depends much on interrelations between the ctenophore-invaders.

References

- Abolmasova G.I., 2001. Energy metabolism in *Mnemiopsis leidyi* A. Agassiz in relation to temperature and food conditions. *Hydrobiol. Journal.*, 37 (2), 90–95 (in Russian).
- Abolmasova G.I., Romanova Z.A., Finenko G.A., 2002. Energy requirements of *Mnemiopsis leidyi* and *Beroe ovata* populations in relation to nutrition conditions in Sevastopol Bay. *In* Second Intern. Conf. Oceanography of the Eastern Mediterranean and Black Sea. Similarities and differences of two interconnected basins (14–18 Oct. 2002, Ankara, Turkey). Ankara, 146–147.
- Anninsky B.E., Gubanova A., 1998. Chemical composition and state of ctenophore *Mnemiopsis mccradyi* (Mayer) in the Black Sea. *Hydrobiol. Journ.*, 34 (3), 36–43 (in Russian).
- Anninsky B.E., Romanova Z.A., Abolmasova G.I., Gücü A.C., Kideys A. E. 1998. Ecological and physiological state of the ctenophore *Mnemiopsis leidyi* (Agassiz) in the Black Sea in autumn 1996. *In* Ivanov L & Oguz T. (eds.). Ecosystem Modelling as a Management Tool for the Black Sea. Symposium on Scientific Results. Klüwer Academic Publishers, Dordrecht/Boston/London. 1, 249–262.
- Anninsky B.E., Finenko G.A., Abolmasova G.I., Hubareva E.S., Svetlichny L.S., Bat L., Kideys A., 2005. Effect of starvation on the biochemical composition and respiration rates of ctenophores *Mnemiopsis leidyi* and *Beroe ovata* in the Black Sea. *J. Mar. Biol. Ass. U.K.* 85., 549–561.
- Arashkevich E.G., Anokhina L.L., Vostokov S.V. *et al.*, 2001. Reproductive strategy of *Beroe ovata* (Ctenophora, Atentaculata)

- Beroida) – a new invader to the Black Sea. *Okeanologiya* 41 (1), 116–120 (in Russian).
- Baker L.D., Reeve M.R., 1974. Laboratory culture of the lobate Ctenophore *Mnemiopsis mccradyi* with Notes on feeding and fecundity. *Mar. Biol.* 26 (1), 57–62.
- Bilio M., Niermann U., 2004 Is the comb jelly really to blame for it all? *Mnemiopsis leidyi* and the ecological concerns about the Caspian Sea. *Mar. Ecol. Prog. Ser.* 269, 173–183.
- Bishop J.W., 1968. A comparative study of feeding rates of tentaculate ctenophores. *Ecology*. 49, 996–997.
- Bogdanova D.P., Konsulov A.S., 1993. On the distribution of the new ctenophore species *Mnemiopsis mccradyi* in the Black Sea along the Bulgarian coastline in the summer of 1990. *Dokl Bulgarian Akad Nauk.* 46, 71–74.
- Burrell V.G., Van Engel W.A., 1976. Predation by and distribution of a Ctenophore, *Mnemiopsis leidyi* A. Agassiz. in the York River Estuary. *Estuar Coast Mar. Sci.* 4., 235–242.
- Caddy, J. F., Griffiths, R. C., 1990. A perspective on recent fishery-related events in the Black Sea. In: Recent trends in the fisheries and environment in the general fisheries for the Mediterranean (GFCM) area. *GFCM Stud. Rev.*, 63, 43–71.
- Deason E.E., 1982. *Mnemiopsis leidyi* (Ctenophora) in Narragansett Bay, 1975–1979: abundance, size composition and estimation of grazing. *Estuar Coast Shelf Sci.* 1, 121–134.
- Falkenhaus T., 1996. Distributional and seasonal patterns of ctenophores in Malangen, northern Norway. *Mar. Ecol. Prog. Ser.* 140, 59–70.
- Finenko G.A., Abolmasova G.I., Romanova Z.A., 1995. Intensity of the nutrition, respiration, and growth of *Mnemiopsis mccradyi* in relation to food conditions. *Marine Biology* (Vladivostok) 21 (5), 315–320 (in Russian).
- Finenko G.A., Anninsky B.E, Romanova Z.A., Abolmasova G. I., Kideys A. E., 2001 Chemical composition, respiration and

4. FUNCTIONAL ROLE OF THE CTENOPHORE INVADERS *Mnemiopsis leidyi* AGASSIZ AND *Beroe ovata* MAYER IN INSHORE PLANKTONIC COMMUNITIES

feeding rates of the new alien ctenophore, *Beroe ovata*, in the Black Sea. *Hydrobiologia* 451, 177–186.

Finenko G.A., Romanova Z.A., 2000. Population dynamics and energetic of the ctenophore *Mnemiopsis leidyi*. *Okeanologiya* 40 (5), 720–728 (in Russian).

Finenko G.A., Romanova Z.A., Abolmasova G. I., 2000. A new invader to the Black Sea – ctenophore *Beroe ovata*. *Ekologiya Moray* 50, 21–25 (in Russian).

Finenko G.A., Romanova Z.A., Abolmasova G.I., Anninsky B.E., Svetlichny L.S., Hubareva E.S., Bat L., Kideys A. E., 2003. Population dynamics, ingestion, growth and reproduction rates of the invader *Beroe ovata* and its impact on plankton community in Sevastopol Bay, the Black Sea. *J. Plankton Res.* 25 (5), 539–549.

Finenko G.A., Romanova Z.A., Abolmasova G.I., Anninsky B.E., Hubareva E.S., Bat L., Kideys A., 2005. Effect of food conditions on ingestion rate and digestion time in lobate ctenophore *Mnemiopsis leidyi*. *Morskoi ecologic. journal.* 4 (1), 75–83 (in Russian).

Finenko G.A., Kideys A.E., Anninsky B.E., Shiganova T. A., Roohi A., Tabari M, Rostami H. , Bagheri S., 2006a. Invasive ctenophore *Mnemiopsis leidyi* in the Caspian Sea: feeding, respiration, reproduction and impact on zooplankton community. *Mar. Ecol. Prog. Ser.* 314, 171–185.

Finenko G.A., Romanova Z.A., Abolmasova G.I., Anninsky B.E., Bat L., Kideys A., 2006b. 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). *Okeanologiya.* 46 (4), 472–482 (in Russian).

Geritsen J., Strickler J., 1977. Encounter probabilities and community structure in zooplankton: a mathematical model. *J. Fish. Res. Board. Can.* 34, 73–82.

- Gibbson M.I., Painting S.J. 1992. The effects and implications of container volume on clearance rates of the ambush entangling predator *Pleurobrachia pileus* (Ctenophora: Tentaculata). *J. Exp. Mar. Biol.* 163 (2), 199–208.
- Gordina A.D., Zagorodnyaya JU. A., Kideys A.E. *et al.* , 2005. Summer ichthyoplankton, food supply of fish larvae and impact of invasive ctenophores on the nutrition of fish larvae in the Black Sea during 2000 and 2001. *J. Mar. Biol. Ass. UK.* 85, 537–548.
- Gubanova A.D., Polikarpov I.G., Saburova M.A., Prusova I.Yu., 2002. Long -term dynamics of mesozooplankton community in Sevastopol Bay (1976–1996) as exemplified by Copepoda. *Okeanologiya.* 42 (4), 537–545 (in Russian).
- Gücü A.C., 1997. Role of fishing in the Black Sea ecosystem. *In: Orzoy E. and Mikaelyan A (eds.). Sensitivity in Changes: Black Sea, Baltic Sea and North Sea.* Klüwer Academic Publishers. The Netherlands, pp. 149–162.
- Gücü A.C. 2002. Can overfishing be responsible for the successful establishment of *Mnemiopsis leidyi* in the Black Sea? *Estuar., Coast. and Shelf Science* 54, 439–451.
- Gücü A.C., Oguz T., 1998. Modelling trophic interrelationships in the Black Sea. *In: Ivanov L. and Oguz T. (eds.). Ecosystem Modelling as a Management Tool for the Black Sea.* 2, 359–371.
- Hubareva E.S., Svetlichny L.S., Romanova Z.A., Abolmasova G.I., Anninsky B.E., Finenko G.A., Bat L., Kideys A., 2004. Zooplankton community state in Sevastopol Bay after invasion of the ctenophore *Beroe ovata* into the Black Sea. *Mar. Ecological Journal* 3 (1), 39–46 (in Russian).
- Kamburska L., 2004. Effects of *Beroe cf ovata* on gelatinous and other zooplankton along the Bulgarian Black Sea Coast. *In: H. Dumont, T.A. Shiganova, U. Nierman (eds.) Aquatic Invasions in the Black, Caspian, and Mediterranean Seas.* NATO Science Series. IV. Earth and Environmental Sciences. 35. Klüwer Academic Publishers, 137–154.

4. FUNCTIONAL ROLE OF THE CTENOPHORE INVADERS *Mnemiopsis leidyi* AGASSIZ AND *Beroe ovata* MAYER IN INSHORE PLANKTONIC COMMUNITIES

- Kideys A., 1994. Recent dramatic changes in the Black Sea ecosystem. The reason for the sharp decline in Turkish anchovy fisheries. *J. Mar. Systems* 5, 171–181.
- Kideys A.E., 2002. Fall and rise of the Black Sea ecosystem. *Science* 297, 1482–1484.
- Kideys A.E., Romanova Z.A., 2001. Distribution of gelatinous macrozooplankton in the southern Black Sea during 1996–1999. *Mar. Biol.* 139, 535–547.
- Kideys A.E., Finenko G.A., Anninsky B.E., Shiganova T. A., Roohi A., Tabari M, Youseffyan M, Rostamian M., Rostami H, Negarestan H. 2004. Physiological characteristics of the *Beroe ovata* in Caspian Sea water. *Mar. Ecol. Prog. Ser.* 266, 111–121.
- Kideys, A. E., Roohi, A., Bagneri, S., Finenko, G., Kamburska, L., 2005. Impacts of Invasive ctenophores on the fisheries of the Black Sea and Caspian Sea. *Oceanography*. 18 (2), 76–85.
- Konsulov A., Kamburska L., 1998. Ecological determination of the new ctenophore *Beroe ovata* invasion in the Black Sea. *Oceanology*, IO BAS. 2, 195–198.
- Kovalev A.V., Gubanova A.D., Kideys A.E., Melnikov V.V., Nierman U., Ostrovskaya N.A., Prusova I.Yu., Skryabin V.A., Uysal Z., Zagorodnyaya J., 1998. Long-term changes in the biomass and composition of fodder zooplankton in coastal regions of the Black Sea during the period 1957–1996. *In*: Ivanov L.I., Oguz T. (eds). *Ecosystem Modelling as a Management Tool for the Black Sea*. Klüwer Academic Publishers. Dordrecht/Boston/London. 1, 209–221.
- Kremer P., 1979 Predation by the Ctenophore *Mnemiopsis leidyi* in Narragansett Bay, Rhode Island. *Estuaries* 2, 97–105.
- Larson R J. 1979. *In situ* feeding rates of the Ctenophore *Mnemiopsis mccradyi*. *Estuaries* 10 (2), 87–91.

- Lebedeva L.P., Shushkina E.A., Vinogradov M.E. *et al.*, 2003. Long – term transformation of mesoplankton community structure in the Northeastern Black Sea under impact of the alien ctenophores. *Okeanologiya* 43 (5), 710–715 (In Russian).
- Matsakis S., Conover R.J., 1991. Abundance and feeding of medusae and their potential impact as predators on other zooplankton in Bedford Basin (Nova Scotia, Canada) during spring. *Can J Fish Aquat Sci.* 48, 1419–1430.
- Mutlu E., 1999. Distribution and abundance of ctenophores and their zooplankton food in the Black Sea. II. *Mnemiopsis leidyi*. *Mar Biol.* 135, 603–613.
- Niermann U., Bingel F., Gorban A. *et al.*, 1994 Distribution of anchovy eggs and larvae (*Engraulis encrasicolus* Cuv.) in the Black Sea in 1991 and 1992 in comparison to former surveys. *ICES J. Mar. Sci.* 51, 395–406.
- Niermann U., Kideys A., Kovalev A.V. *et al.*, 1999. Fluctuation of pelagic species of the open Black Sea during 1980-1995 and possible teleconnection. In: Besiktepe S.T. *et al.*(eds). NATO Science Series. Environmental degradation of the Black Sea: challenges and remedies. Resulting from ARW, Constanta–Mamaya (Romania). 1997, Klüwer Acad. Publ., 143–147.
- Oguz T., 2005. Black Sea ecosystem response to climatic variations. *Oceanography. Black Sea special Issue.* 18, 122–133.
- Pereladov M.V., 1988. Some observations on biocenosis dynamics in Sudak Gulf of the Black Sea. III All- Union Conference in Marine Biology., 1. (Abstracts, Sevastopol, 18–20 October 1988). Kiev. Publishers IBSS. 1, 237–238 (in Russian).
- Purcell J.E., White J.R., Roman M.R., 1994. Predation by gelatinous zooplankton and resource limitation as potential controls of *Acartia tonsa* copepod populations in Chesapeake Bay. *Limnol. Oceanogr.* 39, 263–278.
- Purcell J.E., 2005. Climatic effects on formation of jellyfish and ctenophore blooms: a review. *J. Mar. Biol. Ass. U.K.* 85, 461–476.

4. FUNCTIONAL ROLE OF THE CTENOPHORE INVADERS *Mnemiopsis leidyi* AGASSIZ AND *Beroe ovata* MAYER IN INSHORE PLANKTONIC COMMUNITIES

- Reeve M.R., 1980. Comparative experimental studies on the feeding of Chaetognaths and Ctenophores. *J. Plankton Res.* 2 (4), 381–393.
- Reeve M.R., Walter M.A., Ikeda T., 1978. Laboratory studies of ingestion and food utilization in lobate and tentaculate Ctenophores. *Limnol. Oceanogr.* 23 (4), 40–51.
- Romanova Z.A., Abolmasova G.I., Finenko G.A., 2005. Reproductive strategy of *Mnemiopsis leidyi* in inshore waters of the Black Sea. *Proceedings of Volodimir Gnatyuk Ternopol National teacher's training University. Biology issue.* 4 (27), 197–198 (in Russian).
- Shiganova T., 2005. Changes in appendicularian *Oikopleura dioica* abundance caused by invasion of alien ctenophores in the Black Sea. *J. Mar. Biol. Ass. U.K.* 85, 477–494.
- Shiganova T.A., Bulgakova Yu.V., Sorokin P.Yu., Lukashev Yu.F., 2000. Results of study of *Beroe ovata*, a new invader to the Black Sea. *Proceedings of RAS.* 2, 581–590 (in Russian).
- Shiganova T.A., Bulgakova Yu.V., Volovik S.P. *et al.*, 2001. The new invader *Beroe ovata* Mayer 1912 and its effect on the ecosystem in the north – eastern Black Sea. *Hydrobiologia* 451, 187–197.
- Shiganova T.A., Musaeva E.I., Bulgakova Yu.V., Mirzoyan Z.A., Martynyuk M.L., 2003. New settlers comb jellies *Mnemiopsis leidyi* (A. Agassiz) and *Beroe ovata* Mayer 1912 and their influence on the pelagic system of northeastern Black Sea. *Proceedings of RAS. Issue Biology.* 2, 225–235 (in Russian).
- Shiganova T.A., Dumont H.J., Mikaelyan A. *et al.*, 2004. Interactions between the invading Ctenophores *Mnemiopsis leidyi* (A. Agassiz) and *Beroe ovata* Mayer 1912, and their influence on the pelagic ecosystem of the northeastern Black Sea. *In: H. Dumont, T.A. Shiganova, U. Nierman (eds). Aquatic Invasions in the Black, Caspian, and Mediterranean Seas. NATO Science Series. IV. Earth and Environmental Sciences.* 35. Kluwer Academic Publishers, 33–70.

- Shushkina E.A., Nikolaeva G.G., Lukasheva T.A., 1990. Changes in the Black Sea planktonic community structure under mass occurrence of *Mnemiopsis leidyi*. *Journal of General Biology* 51 (1), 54–60 (in Russian).
- Shushkina E.A., Vinogradov M.E., 1991. Long-term dynamics of planktonic biomass in the open Black Sea. *Okeanologiya* 31 (6), 973–980 (in Russian).
- Shushkina E.A., Musaeva E.I., Anokhina L.L., Lukasheva T.A., 2000. Role of the gelatinous macroplankton: jellyfish *Aurelia*, ctenophores *Mnemiopsis* and *Beroe* in the planktonic communities in the Black Sea. *Okeanologiya*. 40 (6), 859–866 (in Russian).
- Shushkina E.A., Vinogradov M.E., Lebedeva L.P., Lukasheva T.A., 2004. Zooplankton distribution on the shelf of the northeast Black Sea in the warm climatic period of 2000 –2002. *Okeanologiya*. 44 (4), 524–537 (in Russian).
- Shushkina E.A., Vinogradov M.E., Lebedeva L.P., Lukasheva T. A., 2004a. The structure of the coastal plankton communities at the beginning of the cooling cycle (2003) in the northeastern part of the Black Sea. *Okeanologiya* 44 (6), 892 – 900 (in Russian).
- Sieferd T.D., Conover R.J., 1992. An opening – closing plankton net for horizontal sampling under polar sea – ice. *Sarsia*. 76, 273–277.
- Stoecker D.K., Verity P.G., Michaels A.E., Davis L.H., 1987. Feeding by larval and post-larval ctenophores on microzooplankton. *J. Plankton Res.* 9, 667–683.
- Sullivan L.J., Gifford D.J., 2004. Diet of the larval ctenophore *Mnemiopsis leidyi* A. Agassiz (Ctenophora, Lobata). *J. Plankton. Res.* 26 (4), 417–431.
- Svetlichny L.S., Abolmasova G.I., Hubareva E.S., Finenko G.A., Bat L., Kideys A., 2004. Respiration rates of *Beroe ovata* in the Black Sea. *Mar. Biol.* 145, 585–593.

4. FUNCTIONAL ROLE OF THE CTENOPHORE INVADERS *Mnemiopsis leidyi* AGASSIZ AND *Beroe ovata* MAYER IN INSHORE PLANKTONIC COMMUNITIES

- Tkach A.V., 1996. Feeding of the Black Sea fish larvae. *In*: Konovalov S. M. (ed.). Recent state of the Black Sea ichthyofauna.– IBSS NASU, 153–168 (in Russian).
- Tkach A.V., Gordina A.D., Niermann U., Kideys A.E., Zaika V.E., 1998. Changes in the larvae nutrition of the Black Sea fishes with respect to plankton. *In*: Ivanov, L. and Oguz, T. (eds.). Ecosystem Modelling as a Management Tool for the Black Sea. Klüwer Academic Publishers, Dordrecht/Boston/London. 1, 171–188.
- Tsikhon–Lukanina E.A., Reznichenko O.G., Lukasheva T.A., 1995. Feeding of ctenophore *Mnemiopsis*. *Fish Industry*. No 4, 46–49 (in Russian).
- Tsikhon–Lukanina E.A., Reznichenko O.G., Lukasheva T.A., 1993. Predation rates on fish larvae by the ctenophore *Mnemiopsis* in the Black Sea inshore waters. *Okeanologiya*. 33 (6), 895–900 (in Russian).
- Vdodovich I.V., Gordina A.D., Pavlovskaya T.V., Finenko G.A., Klimova T.N., Abolmasova G.I., Romanova Z.A., Polikarpov I. G., 2007. Specific features of the feeding of larval fish of the families Blenniidae and Gobiidae in relation to changes in the coastal plankton community of the Black Sea. *Voprosy ichthyologii*, 47 (4), 542–554.
- Vereshchaka A.L., 2002. Microscale distribution pattern of gelatinous macroplankton in the Black Sea off the Gelendgik Coasts in August 2002. *Okeanologiya*. 42 (1), 91–98 (in Russian).
- Vinogradov, M. E., Sapozhnikov, V. V., Shushkina, E. A., 1992. Ecosystem of the Black Sea Nauka, Moscow, 112 pp. (in Russian).
- Vinogradov M.E., Shushkina E.A., Musaeva E.I., Sorokin P.Yu., 1989. A new invader to the Black Sea – ctenophore *Mnemiopsis leidyi* (A. Agassiz) (Ctenophora: Lobata) *Okeanologiya* 29 (2), 293–299 (in Russian).

- Vinogradov M.E., Sapoznikov V.V., Shushkina E.A., 1992. The Black Sea ecosystems. M. Nauka. 112 pp. (in Russian).
- Vinogradov M.E., Shushkina E.A., 2002. Dynamics of age structure of ctenophores *Mnemiopsis leidyi* and *Beroe ovata* populations off the Caucasus Coast of the Black Sea. In: Zatsepin A.G., Flint M.V. (eds.) Comprehensive studies of the Northeastern Black Sea. M. Nauka, 272–288 (in Russian).
- Vinogradov M.E., Shushkina E.A., Anokhina L.L., Vostokov S.V., Kucheruk N.V., Lukashova T.A., 2000. Dense aggregations of the ctenophore *Beroe ovata* (Eschscholtz) near the north-eastern shore of the Black Sea. *Okeanologiya* 40 (1), 52–55 (in Russian).
- Vinogradov M.E., Lebedeva L.P., Vinogradov G.M. *et al.*, 2005. Monitoring of the pelagic communities of the northeastern Black Sea in 2004: macro and mesoplankton. *Okeanologiya* 45 (3), (in Russian).
- Vinogradov M.E., Vinogradov G.M., Lebedeva L.P., Lukasheva T.A., Zasko D.N., 2006. Patterns of ctenophore populations in the north-eastern part of the Black Sea in 2005. *Okeanologiya* 46 (3), 406–414 (in Russian).
- Vostokov S.V., Arashkevich E.G., Drits A.V., Lukashev Yu.F., 2001. Ecological and physiological characteristics of the ctenophore *Beroe ovata* in the coastal waters of the Black Sea: quantity, biomass, size distribution, hunting behavior, feeding and metabolism. *Okeanologiya* 41 (1), 109–115 (in Russian).
- Waggett R., Castello T.H., 1999. Capture mechanisms used by the lobate ctenophore, *Mnemiopsis leidyi*, preying on the copepod *Acartia tonsa*. *J Plankton Res.* 21, 2037–2052.
- Zaika V.E., 1994. The drop in anchovy stock in the Black Sea: Result of biological pollution? Report of the Second Technical Consultation on Stock Assessment in the Black Sea. Ankara, Turkey, 15-19 February 1993. Rome, Italy, FAO. No 495, 78–83.

4. FUNCTIONAL ROLE OF THE CTENOPHORE INVADERS *Mnemiopsis leidyi* AGASSIZ AND *Beroe ovata* MAYER IN INSHORE PLANKTONIC COMMUNITIES

- Zaika V.E., 2005. Where and how the Black Sea population of the ctenophore *Mnemiopsis leidyi* is wintering? *Marine Ecological Journal*. 4 (1), P. 51—54 (in Russian).
- Zaika V.E., Revkov N.K., 1994. Anatomy of gonads and reproduction pattern of ctenophore *Mnemiopsis* sp. in the Black Sea. *Zool. Journ.* 73, (3), 5—11 (in Russian).
- Zaika V.E., Revkov N.K., 1998. Food of the Black Sea ctenophore *Mnemiopsis* in relation to zooplankton community composition. *Hydrobiol. Journal*. 34 (3), 29—35 (in Russian).
- Zaitsev Yu.P., Alexandrov B.G., 1997. Recent man-made changes in the Black Sea ecosystem. In: Örsoy E. and Mikaelyan A. (eds.) *Sensitivity to Change: Black Sea, Baltic Sea and North Sea*. Klüwer Academic Publishers, Dordrecht/Boston/London, 25—31.