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Native and non-native ctenophores in the Gulf of Trieste, Northern Adriatic Sea

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Observations of ctenophore species were made in the Gulf of Trieste between 2003 and 2006. We examined native ctenophore species with special attention to representatives of the orders Lobata and Beroida, and we recorded among them two non-native ctenophores: Mnemiopsis leidyi A. Agassiz 1865 and Beroe ovata sensu Mayer, 1912. The validity of the Mediterranean species Beroe ovata is discussed. We determined that among the native species, it is not Beroe ovata but rather Beroe cucumis sensu Mayer, 1912 that occurs in the Mediterranean Sea.

INTRODUCTION

Over the last century, due to increased fishing pressure, anthropogenic eutrophication and global warming, many marine zooplankton communities have changed toward increasing dominance of harmful gelatinous species (Hays *et al.*, 2005; Dybas, 2006). Elevated populations of gelatinous species in their native habitats affect local ecosystems, but also raise the potential for spread to other areas either by natural expansions (Malej and Malej, 2004) or with ballast water (Dumont *et al.*, 2004).

A well-documented example of the introduction of the ctenophore *Mnemiopsis leidyi* A. Agassiz 1865 occurred in the Black Sea during the early 1980s, via ballast water (Vinogradov *et al.*, 1989). This species has shown explosive population growth since 1988, and subsequently expanded into the Sea of Azov (Studenikina *et al.*, 1991), the Sea of Marmara (Shiganova, 1993), and the eastern Mediterranean, including the Aegean Sea (Shiganova *et al.*, 2001). *Mnemiopsis leidyi* was first reported in the Caspian Sea in 1999, probably introduced in the ballast water of oil tankers (Ivanov *et al.*, 2000). Ctenophores preliminarily identified as *M. leidyi* were recorded in Berri lagoon and Marseille Bay (western Mediterranean Sea) during recent years (Francois Carlotti, personal communication). Its presence along the French coast was confirmed by the genetic study of a few specimens (Bayha *et al.*, 2004). In 2006, *M. leidyi* was recorded along the northern European coast, in the Baltic and North seas (Javidpour *et al.*, 2006; Faasse *et al.*, 2006; Viitasalo *et al.*, 2008).

The native habitat of *M. leidyi* includes estuaries and coastal regions along the eastern coast of North and South America (GESAMP, 1997). *Mnemiopsis leidyi* is polymorphic, with wide environmental tolerance; therefore, environmental conditions in the southern Eurasian seas seem suitable for the species' establishment in this area. The spread of *M. leidyi* is of particular concern since the species strongly affects all levels of most invaded ecosystems, including the fisheries in the Black, Azov and Caspian Seas, although effects were less pronounced in the Aegean Sea (Shiganova *et al.*, 2001; Shiganova *et al.*, 2004a, b, c).

In response to this situation, a group of experts from an international commission (GESAMP, 1997) proposed the introduction of potential predators for *M. leidyi*. Among the suggested species was another ctenophore *Beroe ovata*, which is an obligate predator on zooplanktivorous ctenophores, including *M. leidyi*. Although this suggestion was not intentionally implemented, *B. ovata*

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nevertheless appeared in the Black Sea in 1997, also likely introduced with ballast water (Konsulov and Kamburska, 1998). *Beroe ovata* established a large reproductive population in the Black Sea and began to control the population of *M. leidyi* by 1999 (Shiganova *et al*., 2000a). Detailed analysis of the morphology of the new Black Sea ctenophore indicated that it was *Beroe ovata sensu* Mayer, 1912 (Seravin *et al*., 2002). This identification was confirmed by Harbison (Harbison, 2001, personal communication) and molecular analyses by Bayha *et al*. (Bayha *et al*., 2004).

In October 1999, *Beroe ovata* was observed in the Sea of Azov (Shiganova *et al*., 2000b). It now appears regularly in the Sea of Azov in early autumn, as reported for *M. leidyi* (Mirzoyan *et al*., 2006). In 1999, two individuals of *B. ovata* were found near the Bosphorus Strait, in the Sea of Marmara (Tarkan *et al*., 2000). The species now occurs in this sea in the same season as in the Black Sea (Isinibilir *et al*., 2004). In November 2004, a *Beroe ovata* was found in the northern Evvoicos Gulf of the Aegean Sea (Shiganova *et al*., 2007a, b) with the source likely being the Black Sea.

Large blooms of gelatinous plankton, mainly Scyphomedusae, have been reported from the northern Adriatic Sea in the past (Avian and Rottini Sandrini, 1994; Purcell *et al*., 1999). On the other hand, Ctenophora were generally neglected due to difficulties with preservation and lack of taxonomic expertise in the region. Semi-quantitative data on a few Ctenophora species were reported in the early 20th century (Cori and Steuer, 1901; Issel, 1925; see Table I), but despite several observations of high ctenophore abundances during the last few decades, there have been no recent published reports on this gelatinous group.

In 2003, studies of gelatinous plankton, with special attention to Ctenophora, were initiated in the northernmost part of the Adriatic Sea within the framework of the Slovenian-Russian collaboration that has continued

Table I: List of Ctenophora species reported in the northern Adriatic

Phyl. Ctenophora (Class Tentaculata)	Other names	References
O. Cydippida		
F. Haeckeliidae		
Haeckelia rubra (Kölliker, 1853)	*Euchlora rubra* (Kölliker, 1853)	Krumbach, 1911
F. Lampeidae		
Lampea pancerina (Chun, 1879)	*Lampetia pancerina* (Chun, 1880)	Krumbach, 1911
F. Mertensiidae		
Callianira bialata (Della Chiaje, 1841)	*Eschscholtzia cordata* (Kölliker, 1853)	Steuer, 1903
F. Pleurobrachidae		
Hormiphora plumosa (L. Agassiz, 1960)		Riedl, 1991; Gamulin, 1979
Pleurobrachia pileus (O.F. Müller, 1776)		Issel, 1922, 1925; Gamulin, 1979
Pleurobrachia rhododactyla (L. Agassiz, 1860)		Mills, 2005
Pleurobrachia rhodopis (Chun, 1880)		Stiasny 1911, 1912; Krumbach, 1911; Gamulin, 1979
O. Lobata		
F. Bolinopsidae		
Bolinopsis vitrea (L. Agassiz, 1860)	*Bolina hydatina* (Chun, 1879)	This work
F. Mnemiidae		
Mnemiopsis leidyi (A. Agassiz, 1865)		This work
Deiopea kaloktenota (Chun, 1879)		Krumbach, 1911, Gamulin, 1979
F. Leucotheidae		
Leucothea multicornis (Quoy&Gaimard, 1824)	*Eucharis multicornis* (Eschscholtz, 1928)	Cori and Steuer, 1901; Steuer, 1903; Stiasny 1909, 1910, 1911, 1912, Krumbach, 1911, Issel, 1922, 1925, this work
O. Cestida		
F. Cestidae		
Cestum veneris (Lesueur, 1813)	*Cestus veneris* (Chun, 1879)	Krumbach, 1911, Gamulin 1979
O. Beroida		
F. Beroidae		
Beroe forskalii (Milne Edwards, 1841)		Steuer, 1903; Stiasny 1909, 1910, 1911, 1912; Krumbach, 1911, this work
Beroe ovata (Brown 1756)		Steuer, 1903, Gamulin,1979
Beroe sensu ovata (Mayer, 1912)	*Beroe ovata Chamisso* and *Tysenhardt*	This work: see discussion
Beroe sensu cucumis (Mayer, 1912)	*Beroe cucumis* Fabricius	This work: see discussion

within the EU-funded project SESAME. In this paper, we report on the Ctenophora fauna in this area and include new descriptions of, among others, two non-native species.

Area description

The northern Adriatic basin is the northernmost protrusion of the Mediterranean Sea, and is strongly influenced by rivers discharging from the western coast (Fig. 1). The area is among the most productive regions in the Mediterranean Sea (Fonda Umani *et al.*, 1992; Harding *et al.*, 1999).

Increases in nutrient inputs during the latter half of the 20th century resulted in cultural eutrophication, although the effects have been alleviated over the past 15 years due to mitigation measures (Degobbis *et al.*, 2000). Approximately rectangular in shape, the Gulf of Trieste (Fig. 1) is the northernmost gulf of the enclosed Adriatic Sea, with an average depth of <20 m, a surface area of 600 km^2 and a volume of 9.5 km^3. Freshwater inputs are larger along the northern than the southern coast, approx. annual rate of flow of 90–130 m^3/s, and peaks of over 1000 m^3/s, when compared with 5–10 m^3/s and peaks up to 100 m^3/s (Mozetič *et al.*, 1998), respectively. The structure of the water column and water movements vary greatly with dominant seasonal influences. In winter, the waters of the Gulf are characterized by considerable homogeneity. In spring, heating of the surface layer and freshwater inflows begin to establish a pycnocline, which intensifies during the summer. Seasonal dynamics of thermal stratification are governed by the seasonal cycle of solar irradiance (Malačič, 1991). Autumnal cooling and wind mixing re-establish vertical water column homogeneity, although strong winds may cause destratification during summer. Mean surface temperatures in the summer months are well above 20°C, with maximum values above 26°C in July and August, while minima in February–March are below 10°C. The southeastern part of the Gulf shows variability in surface salinities ranging from slightly above 32 (in late spring and late autumn) to values close to 38 in winter and late summer. The Gulf is classified as a moderate eutrophic area (Flander-Putrle and Malej, 2003) with primary production ranging from 0.2 to 15.9 μmol C dm^{-3} day^{-1} (Malej *et al.*, 1995; Cantoni *et al.*, 2003) and mean mesozooplankton dry weight and ash-free biomass 18.5 and 13.6 mg m^{-3}, respectively (Benović *et al.*, 1984; Fonda Umani *et al.*, 1992).

METHOD

Observations of Ctenophora species were carried out during 2003–2007 in the southeastern part of the Gulf of Trieste using a video-camera operated from a research boat, during diving and/or while snorkeling. Observations *in situ* were made using a Sony DCR-VX200E video camera with an Ikellite underwater housing equipped with two 100 W lights and a depth gauge; the dimension of the imaged area was 2.3 m^2 (Malej *et al.*, 2007). Still pictures were taken with the Nikon D2X digital camera enclosed in a SEALUX CD2 underwater housing and operated by a diver. In addition, some specimens were hand-collected using plastic jars. Individuals of *M. leidyi* were hand-collected in the Bay of Piran in October 2005; similarly, *Beroe ovata* were hand-collected in autumn 2005. Individuals were maintained in a laboratory aquarium and photographed alive, while preservation in 2% neutralized formalin was not successful. Dimensions were assessed from photographs taken in the laboratory aquarium containing an object of known size. The Black Sea and the Mediterranean live individuals were put in Petri dishes with a small amount of seawater not completely covering the animal and then measured with a ruler. The same individuals were photographed and measured to make sure that measurements of individuals which

Fig. 1. Location of observations.

were available only from photos are comparable with others.

RESULTS AND DISCUSSION

Earlier works on zooplankton of the northern Adriatic reported occurrences of the following Ctenophora species: *Haeckelia rubra*, *Lampea pancerina*, *Callianira bialata*, *Hormiphora plumosa*, *Pleurobrachia rhodopis*, *P. pileus*, *P. rhododactyla*, *Bolinopsis vitrea*, *Deiopea kaloktenata*, *Leucothea multicornis*, *Cestum veneris*, *Beroe forskalii* and *Beroe ovata* (Table I). Special taxonomic studies of the ctenophores collected were not performed; therefore, identification of some these species is probably not reliable. In our observations during 2003–2007, we paid special attention to representatives of the Lobata and Beroidae, while other taxonomic groups were not studied.

Order Lobata L. Agassiz, 1860

Chun (Chun, 1880) described three species of Lobata in the Mediterranean (the Gulf of Naples): *Deiopea kaloktenota*, *Leucothea (Eucharis) multicornis* and *Bolinopsis (Bolina) hydatina*. The two first species are valid for the Mediterranean Sea, but species identification of the representatives of the genus *Bolinopsis* was uncertain for a long time. The presence of the genus *Bolinopsis* has been confirmed by several later authors, but species identification has not altered for a long time. Krumbach (Krumbach, 1925) noted one species, *Bolinopsis infundibulum*, in the Mediterranean. In contrast, other authors indicated *B. vitrea* (*Bolina hydatina*) as the sole species (Treguboff and Rose, 1957; Rossi, 1971; Cambell, 1982) and we also collected *B. vitrea* in the Aegean Sea (Shiganova *et al.*, 2004c). Mayer (Mayer, 1912) considered *B. infundibulum* as an Arctic and cold temperate water species, and *B. vitrea* as a warm water species, typical in the tropics, i.e. the West Indies, Florida and the Mediterranean. In the western Mediterranean close to the Strait of Gibraltar (Alboran Sea), Mills *et al.* (Mills *et al.*, 1996) found both species: *B. infundibulum* was observed in deeper waters (274–831 m) and *B. vitrea* found mostly in surface waters (upper 15 m). Most probably, only the warm water species (*B. vitrea*, L. Agassiz, 1860) occurs in other Mediterranean areas.

In the Gulf of Trieste two native species of Lobata, *Bolinopsis vitrea*, (L.Agassiz, 1860) and *Leucothea multicornis* (Quoy and Gaimard, 1824) were often found from October to March. In 2007, *Bolinopsis vitrea* was observed during summer (July). During 2004–2007, *Leucothea multicornis* individuals were frequently observed in swarms near the coast in December and April (Fig. 2B and C).

The representatives of the genus *Leucothea* are distinguished from all other Lobata by the two remarkable blind-ending sacs which form a pair of long narrow pits open to the exterior below and extending inward and upward above the tentacle-bulbs near to the level of the funnel (Fig. 2C). *Leucothea multicornis* is the largest member of the Lobata in the Mediterranean up to 25 cm long, covered with distinctive papillae. Its oral lobbies are large and contain complex winding chymiferous tubes (Mayer, 1912; Wrobel and Mills, 1998).

In addition, in October 2005, we recorded a swarm of non-native *M. leidyi* A. Agassiz, 1865 (Fig. 2A) surrounded by the native *Beroe* species. A representative of *M. leidyi* can be easily distinguished morphologically from native *Bolinopsis vitrea* (Fig. 2A and B). Both species have an oval body with considerable lateral compression, two oral lobes on each side of the mouth and four smaller lobes, auricles, under the principal two oral lobes. However, the main difference is the position of the oral lobes. In *M. leidyi*, the oral lobes originate near the level of the infundibulum, whereas in *B. vitrea* they originate approximately half-way between the mouth and the level of the infundibulum (Fig. 2B) (Mayer, 1912). In addition, *M. leidyi* may have warts (papillae) on the body that have never been observed in *B. vitrea* (Fig. 2A and B).

Individuals of *M. leidyi*, which we observed with a video camera, were approximately 30–50 mm in length. The oral lobes and auricles were shorter than those observed in the Black Sea adult individuals of *M. leidyi* but longer than those found in the Azov and Caspian Seas (Shiganova *et al.*, 2007a, b). These could be juvenile individuals, or, more likely, they did not grow due to suboptimal conditions in the Gulf of Trieste. Usually, only adult individuals have warts on the body, although they were present on the observed individuals.

Most probably, individuals of *M. leidyi* were released with ballast water originating from the Black Sea, as there is a direct connection between the Port of Koper and various Black Sea ports (David and Perkovic, 2004; Alexandrov, 2004; Matishov *et al.*, 2005; David *et al.*, 2007).

Order Beroida Eschscholtz, 1829

During our observations, we identified three species which belong to the family Beroidae.

Two species of Beroidae inhabit the Mediterranean Sea, according to identification by Chun (Chun, 1880): *Beroe ovata* Brown 1756 and *Beroe forskalii* Chun. Perrier (Perrier, 1936); Treguboff and Rose (Treguboff and

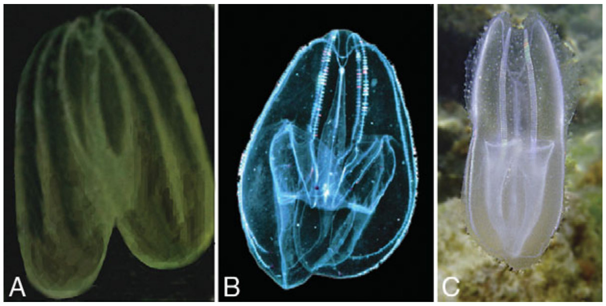

Fig. 2. (**A**) *Mnemiopsis leidyi* (photo of Janez Forte); (**B**) *Bolinopsis vitrea*, (**C**)-*Leucothea multicornis* (photo of Marjan Richter).

Rose, 1957) have followed Chun (Chun, 1880) for species identification. Mills has mentioned also *B. mitrada* as an infrequent visitor in the Mediterranean (Mills, 2005). *Beroe ovata* and *Beroe forskalii* occur in the Gulf of Trieste, but we discus below validation of the Mediterranean *Beroe ovata*.

Species of the family Beroidae are specialized predators on zooplanktivorous ctenophores and, occasionally, on salps (L. Agassiz, 1860). The body is mitten-shaped, egg-shaped or conical; extended laterally in the voluminous stomodeum. There are neither tentacles nor tentacular canals (Mayer, 1912) but eight meridional and two paragastric canals. The meridional canals lie under eight rows of ciliary combs. Meridional canals may communicate with each other by means of an anostomosing network of side branches (diverticulae), thus establishing a circum oral canal system. All species have a wide-flaring mouth and stomodeum with powerful cilia on the walls near the mouth, which help the ctenophore to bite and capture prey (Tamm and Tamm, 1993). The polar plate surrounding the sense-organ at the aboral pole is fringed and may have a row of branched papillae. These ctenophores generally have a pink color, while the largest adults are colored more intensely with a brown tinge (Mayer, 1912).

Beroe forskalii Milne Edwards (Fig. 3A and B) was the most abundant species in the Gulf of Trieste. Its body is conical in the aboral part while its aboral end is pointed (Fig. 4A) when viewed in the stomodaeal plane. The oral end is broad with a very large mouth. The mouth opening is wide, and has a large, half-circle shape. The body is strongly compressed. Diverticulae (lateral branches) of the meridional canals are very dense and anostomose with each other. There is axial funnel-tube. The aboral pole is fringed with a row of long branched papillae (Fig. 5A). Color varies from transparent to slightly pinkish in juveniles, becoming pink in adults.

Native "*Beroe ovata sensu* Chun" (Fig. 3C and D) was another species found during our surveys.

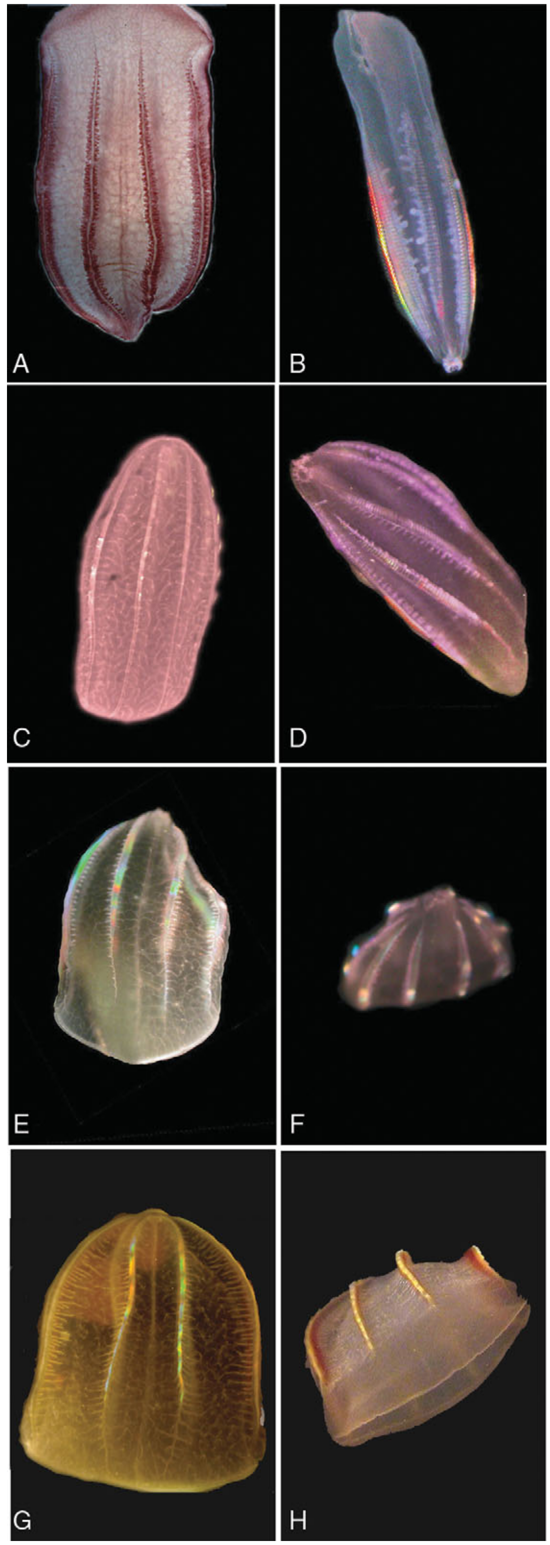

Fig. 3. (**A**) *Beroe forskaliI*; (**B**) its lateral view; (**C**) *Beroe ovata sensu Chun* from Mediterranean Sea; (**D**) lateral view; (**E**) *Beroe ovata sensu* Mayer from the Gulf of Trieste; (**F**) lateral view (photo of Tihomir Makovec); (**G**) *Beroe ovata sensu* Mayer from the Black Sea; (**H**) lateral view (photo of T. Shiganova).

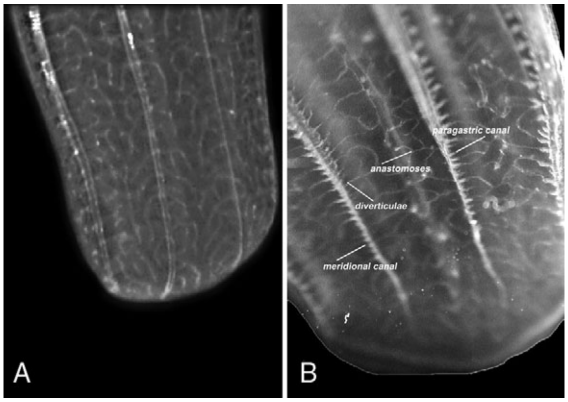

Fig. 4. (**A**) Lateral canals of the native Mediterranean *"Beroe ovata"sensu* Chun; (**B**) lateral canals of the non-native *Beroe ovata sensu* Mayer from the Gulf of Trieste.

This species is native to the Mediterranean Sea, described by Chun. But it is remarkably different from *B. ovata*, which occurs along the northeastern and southeastern American coast (Mayer, 1912; Harbison *et al*., 1978; Mianzan, 1999; Oliveira and Migotto, 2006) and was recently introduced into the Black Sea (Seravin *et al*., 2002). It has an oval egg-shaped body and is much less flattened in the paragastric plane (the large diameter of the ellipse is only twice or less than the small diameter) (Fig. 4B). In our video survey observations in the Gulf of Trieste, and measurements from these pictures, this native ctenophore has ratio of length to width (l/w) 2.1 ± 0.2 (Table II).

In measurements of individuals from pictures taken in other areas of the Mediterranean Sea, l/w values ranged from 2.16 ± 0.045 (Table II). The lateral canals have numerous diverticulae, which may branch out in adult ctenophores, but they do not anostomose with each other, and do not connect with the paragastric canals (Fig. 5A). The eight rows of cilia extend about three-quarters of the distance from the apical sense-organ to the mouth. There is no ring-canal around the mouth and the peripheral canal systems of the two broad sides are separated from each other. It has an axial funnel-tube. The polar-plate surrounds the sense organ at the aboral pole, which is fringed with a row of long-branched papillae (Fig. 5B). The oral part is rather rounded. These features are not characteristic for *Beroe ovata*, but rather of *Beroe cucumis* (Mayer, 1912).

Beroe ovata sensu Mayer, 1912 individuals (Fig. 3E and F) were also observed in autumn 2005, which are most probably non-native for the Mediterranean Sea. These individuals could originate from the Black Sea and, likewise, as with *M. leidyi* could be released with ballast water. The body of non-native *Beroe ovata* is mitten-shaped, wider at the oral end and not tapered at the aboral end (Fig. 3E and F, Tables II and III).

The lateral compression of the body is remarkable, being not less than three times compressed in the paragastric plane (Fig. 3F). Eight meridional canals are interconnected with each other by a loose network of numerous diverticulae, with anostomoses forming a wide meshwork (Fig. 4B), which is characteristic for *Beroe ovata*. The meridional canals lie under the eight rows of ciliary combs, which extend about three-quarters of the distance from the apical sense organ towards the mouth. Among them, there are four subsagital comb rows on the lateral part of the body and four subtentacular comb rows on the middle part of the body. In addition to the meridional canals, there are two lateral paragastric canals, which arise from the funnel and extend down the middle of the broad sides of the animal. There is no axial funnel-tube, but instead there are two lateral tubes which extend upward from the funnel to the two halves of the pole plate. Each of these tubes opens by an excretory pore on alternate opposite sides of the figure "8" shaped pole-plate. The sense organ at the aboral pole is not fringed with a row of long-branched papillae (Fig. 5C). The aboral end is rounded, while the oral end is almost straight and can be wider than the body width.

Individuals which we observed in the northern Adriatic had a ratio 1.3 ± 0.03 (Table II), similar to the non-native species *B. ovata* from the Black Sea that have a length to width (l/w) ratio of 1.2 ± 0.1 (Table III). From the measurements of individuals from the Black Sea (Fig. 3G and J) (Seravin *et al*., 2002) the length of the *B. ovata* body does not exceed 1.5 times its width; therefore, our individuals from the northern Adriatic

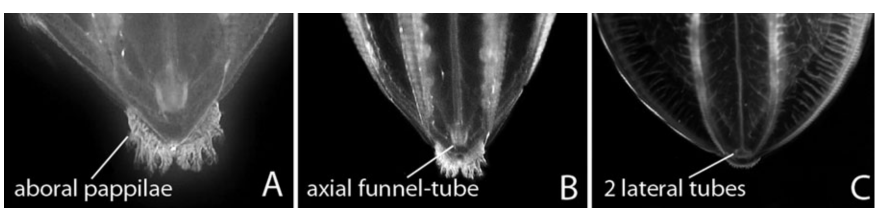

Fig. 5. Aboral part of the body. (**A**) *Beroe forskalii*; (**B**) *Beroe ovata sensu* Chun (photo of Tihomir Makovec); (**C**) *Beroe ovata sensu* Mayer (photo of T. Shiganova).

Table II: Body measurements of Beroe ovata sensu Mayer, 1912 and Beroe ovata sensu Chun from the Gulf of Trieste and the Mediterranean Sea

Organism/location	Length (mm)	Width (mm)	Ratio *l/w*
Beroe ovata sensu Mayer, 1912, Gulf of Trieste, Adriatic Sea	70.3	48.2	1.4
	64	47	1.3
	62	47	1.3
			Average 1.3 ± 0.03
Beroe ovata sensu Chun, Gulf of Trieste, Adriatic Sea	110	48.2	2.3
	96	44.3	2.2
	72	35.8	2.0
	63	32.8	1.9
			Average 2.1 ± 0.2
Beroe ovata sensu Chun, Mediterranean Sea	32	15	2.14
	92	42	2.13
	93	43	2.21
			Average 2.16 ± 0.045

Table III: Body measurements of Beroe ovata sensu Mayer, 1912 from the Black Sea

Length (mm)	Width (mm)	No. measured individ.	Ratio *l/w*
18–20	16.5–18	2	1.1 ± 0.02
30–40	32–45	2	1.1 ± 0.01
42–50	32–45	5	1.0 ± 0.4
51–60	48–51	9	1.1 ± 0.1
61–70	46–65	12	1.1 ± 0.1
71–78	52–68	8	1.2 ± 0.1
82–90	70–79	10	1.3 ± 0.1
99–100	72–85	3	1.3 ± 0.1
102–110	81–94	5	1.3 ± 0.1
120–121	90–103	2	1.2 ± 0.1
			Average 1.2 ± 0.1

have all the features consistent with those of the non-native *B. ovata*.

Beroe species with such morphology are distributed along the Atlantic coast of North and South America (Harbison *et al*, 1978; Mianzan, 1999; Oliveira and Migotto, 2006), in the same areas as *M. leidyi*. Both species have been introduced and established in the Black Sea.

There is some controversy over the describing authority for this species. Mayer (Mayer, 1912) suggested it was Chamisso and Eysenhardt, 1821. Seravin *et al.* (Seravin *et al*., 2002) wrote that the descriptions of Chamisso and Eysenhardt (Chamisso and Eysenhardt, 1821) were so uncertain it was not clear what species they had, therefore, he suggested putting Mayer, 1912 as the identifier of *B. ovata*. Scientists from South America still use the name *B. ovata* Chamisso and Eysenhardt, 1821 thus following Mayer (1912) (Mianzan, 1999; Oliveira and Migotta, 2006). Harbison *et al.* (Harbison *et al*., 1978) first mentioned this species as *Beroe ovata* Bosc, but afterwards the first author (2001) indicated that it was *Beroe ovata sensu* Mayer, 1912 which was introduced into the Black Sea.

Based on the molecular phylogenetic analysis of the individuals from the Bosphorus region of Turkey, the western Mediterranean and the western Atlantic Bayha *et al.* (Bayha *et al*., 2004) concluded that *Beroe ovata sensu* Mayer, 1912, which seemed to be restricted to the eastern seaboard of North and South America, much like *M. leidyi*, was then introduced into the Black Sea. So, these authors use *Beroe ovata sensu* Mayer, 1912 as the species name.

The Mediterranean species described by Chun as *Beroe ovata* is in reality *Beroe cucumis*, according to the features described by Mayer (Mayer, 1912). Rossi (Rossi, 1971) also considered that *Beroe cucumis* Fabricium (=*B. ovata* Esch. Bosc) occurred in the Mediterranean Sea. Cambell (Cambell, 1982) showed that *Beroe cucumis* Fabricium inhabited the Mediterranean Sea as well. On the basis of comparison of the morphological features *B. ovata* from the Black Sea with individuals named *B. ovata* from the Mediterranean Sea Seravin *et al.* (Seravin *et al*., 2002) concluded that *Beroe cucumis* Fabricius (1780) occurs in the Mediterranean Sea.

Mills *et al.* (Mills *et al*., 1996) pointed out the incorrect identification of the Mediterranean *Beroe ovata*, but they just put *Beroe ovata* in inverted commas and wrote that that species, which was illustrated and called *B. ovata* Eschscholtz 1829 by Chun (1880), was also illustrated and called *Beroe cucumis* Fabricius 1780 by Mayer (1912). However, they added that the ctenophore that Mayer illustrated and called *Beroe cucumis* is not the same species as that first described from Greenland by Fabricius (1780), which appears to be restricted to Polar Regions and mesopelagic depths (Mills *et al*., 1996; Seravin, 1998). Later Harbison (Harbison, 2001, personal communication) suggested the name *Beroe cucumis sensu* Mayer, 1912 for this species. Bayha *et al.* (Bayha *et al*., 2004) also concluded that it was prudent to use the name *B. cucumis sensu* Mayer (*B. ovata sensu* Chun) for *B. ovata (sensu* Chun) from the Mediterranean as well as *B. cucumis* from the eastern Pacific and the western Atlantic indicating one widespread species instead of the several isolated ones.

Thus, using the main morphological features, we can subdivide three species of the genus *Beroe*, which we found in the Gulf of Trieste:

Phylum Ctenophora Eschscholtz 1829; Order Beroida Eschscholtz 1829; Genus *Beroe* Browne 1756. We provide descriptions that may useful for the identification of these species for researchers, even those not familiar with ctenophore morphology.

The body is conical, strongly compressed with a pointed aboral end and a broad oral end. Oval,

half circle-shaped large mouth. Ratio of length to width (l/w) more than 2. Meridional canals with very dense diverticulae, which may anastomose with each other. Comb rows all the same length and extending three-quarters to five-sixths of the body length. There is an axial funnel-tube. The aboral pole is fringed with a row of long branched papillae. Size is up to 200 mm. The Mediterranean, western Atlantic and Pacific oceans:
Beroe forskalii Milne Edwards, 1841.

The body is oval, egg-shaped and its aboral end is oval. Lateral compression is not strong, much less flattened in the paragastric plane (the large diameter of the ellipse is only twice or less that of the small diameter). Oval shape of mouth. Ratio of length to width (*l/w*) is more than 2. Meridional canals with numerous diverticulae, which may branch out in adult specimens but they do not anostomose with each other, and do not connect with paragastric Canals. There is an axial funnel-tube, the aboral pole is fringed with a row of long-branched papillae. Size is up to 150 mm. The Mediterranean, western Atlantic and Pacific oceans:
Beroe cucumis sensu Mayer, 1912 (*Beroe cucumis* Fabricius).

The body is mitten-shaped, wider at the oral end and rounded at the aboral end. Lateral compression is very strong (the large diameter is three to four times greater than the smaller). Almost straight or slightly oval shape of the mouth can be wider than body width. Ratio of length to width (*l/w*) is from 1.1 to 1.4 (less than 1.5). Meridional canals are interconnected with each other by a loose network of numerous diverticulae, with anostomoses forming a wide meshwork. Comb rows extend only about half of the body length. There is no axial funnel-tube, but instead there are two lateral tubes which extend upward from the funnel to the two halves of the pole plate. Each of these tubes opens by an excretory pore on alternate opposite sides of the figure “8” shaped pole-plate. The aboral pole is not fringed and without a row of long-branched papillae. Size is up to 160 mm. The north-eastern and south-eastern Atlantic, has invaded the Black Sea:
Beroe ovata sensu Mayer, 1912 (*Beroe ovata* Chamisso and Tysenhardt).

We assign preliminarily the name of the describer of *Beroe cucumis* and *B. ovata sensu* Mayer, 1912, following Harbison (Bayha *et al.*, 2004) and to Seravin in the case of *B. ovata* (Seravin *et al.*, 2002), because our conclusion is based on the small set of data, not collected from all areas of the species distribution. We left the name of the describer for *B. forskalii* (*B. forskali* in Mayer, 1912) as Milne Edwards, 1841, following Mills *et al.* (Mills *et al.*, 1996; Mills, 2005), Mianzan (Mianzan, 1999), Greve *et al.* (Greve *et al.*, 1976), Costelo *et al.* (Costelo *et al.*, 2001), although other authors have used Chun (Chun, 1880; Treguboff and Rose, 1957) for the Mediterranean species.

CONCLUSION

Two non-native comb-jelly species, *M. leidyi* and *Beroe ovata*, were recorded in the Gulf of Trieste in 2005 in addition to species known to occur from past records. It is presently difficult to say with certainty whether these two species have established viable populations in the northern Adriatic, since no population studies of Ctenophora have been carried out in this area. Thermohaline conditions and high prey abundance may favor establishment of *M. leidyi* in the northern Adriatic Sea; however, the concomitant presence of two species of Beroidae, which prey on *M. leidyi*, may prevent its explosive growth as has been observed in other new localities. *Beroe ovata* may not establish because salinity in the area may be too high and because it may compete with two native Beroe species for prey.

Beroe species eat their prey by engulfing it if size allows or, if it is too large, by biting pieces out with the use of macrocilia, compound ciliary-feeding organelles found inside the mouth opening. The macrocilia are different from one species of *Beroe* to another, seemingly adapted to a preferred prey (Tamm and Tamm, 1993). *Beroe ovata* occurs with *M. leidyi* as a prey in its native habitat along the eastern American coast (Mianzan, 1999; Purcell *et al.*, 2001; Oliveira and Migotto, 2006). *Beroe cucumis* occurs with the prey species *Bolinopsis*; therefore, we do not know if native *Beroe* species will consume *M. leidyi* or not in the Adriatic Sea. We observed that native *Beroe* species tried to swallow individuals of *M.leidyi* but then spat them out, indicating that the native *Beroe* probably does not prey on *M.leidyi*.

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REFERENCES

Agassiz, L. (1860) *Contribution to the Natural History of the United States of America*. Vol. 3. Little, Brown, 1-301, Boston.

Alexandrov, B. G. (2004) Problem of aquatic organisms released by ships and some approaches for risk assessment of new invasions. *Mar. Ecol. J.*, **3**, 5–17 (in Ukrainian).

Avian, M. and Rottini Sandrini, L. (1994) History of Scyphomedusae in the Adriatic Sea. *Boll. Soc. Adriat. Sci. Nat.*, **1**, 5–12.

Bayha, K. M., Harbison, G. R., Mcdonald, J. H. *et al*. (2004) Preliminary investigation on the molecular systematis of the invasive ctenophore Beroe ovata. In Dumont, H., Shiganova, T. and Niermann, U. (eds), *The Ctenophore Mnemiopsis leidyi in the Black, Caspian and Mediterranean Seas and other aquatic invasions—NATO ASI Series, 4*. Vol. 35. Kluwer Acadic Publication, Dordrecht, pp. 167–175.

Benović, A., Fonda Umani, S., Malej, A. *et al*. (1984) Net-zooplankton biomass of the Adriatic Sea. *Mar. Biol.*, **79**, 209–218.

Cantoni, C., Cozzi, S., Pecchiar, I. *et al*. (2003) Short-term variability of primary production and inorganic nitrogen uptake related to environmental conditions in a shallow coastal area (Gulf of Trieste, N. Adriatic Sea). *Oceanologica Acta*, **26**, 565–575.

Cambell, A. C. (1982) *The Hamkyn Guide to the Flora and Fauna of the Mediterranean Sea*. The Hamlin Publication Group, Middlesex, UK, p. 320.

Chamisso, A. and Eysenhardt, C. G. (1821) De animalibus quibusdam a classe vermium Linneana in circum navigatione terrae, auspicante N Romanzoff, duce Ottone de Kozebue, annis 1815-1818 peracta, observatis, fasc. II. *Nova Acta Acad. Caes Leopoldinae.*, **10**, 543–574.

Chun, C. (1880) Die Ctenophoren des Golfes von Neapel. *Fauna und Flora des Golfes von Neapel*, **1**, 1–313.

Cori, C. J. and Steuer, A. (1901) Beobachtungen über das Plankton des Triester Golfes in den jahren 1899 und 1900. *Zool. Anz.*, **24**, 111–117.

Costello, M. J., Emblow, C. and White, R. (ed.) (2001) European Register of Marine species. *A check list of the marine species in Europe and a bibliography of guides to their identification*. *Patrimoines naturels*, **50**, 463.

David, M. and Perkovic, M. (2004) Ballast water sampling as a critical component of biological invasions risk management. *Mar. Pollut. Bull.*, **49**, 313–318.

David, M., Golasch, S., Cabrini, M. *et al*. (2007) Results from the first ballast water sampling study in the Mediterranean Sea—the Port of Koper study. *Mar. Pollut. Bull.*, **54**, 53–65.

Degobbis, D., Precali, R., Ivančić, I. *et al*. (2000) Long-term changes in the Northern Adriatic ecosystem related to anthropogenic eutrophication. *Int. J. Environ. Pollut.*, **13**, 1–6.

Dumont, H., Shiganova, T. and Niermann, U. (2004) The Ctenophore *Mnemiopsis leidyi* in the Black, Caspian and Mediterranean Seas and other aquatic invasions. *NATO ASI Series 4*. Vol. 35. Kluwer Academic Publisher, Dordrecht, pp. 1–314.

Dybas, C. L. (2006) On a collision course: ocean plankton and climate change. *BioScience*, **56**, 642–646.

Faasse, M. A., Ligthart, A. H. M. and Bayha, K. M. (2006) The first record of the ctenophore *Mnemiopsis leidyi* in Dutch estuaries: an unrecognized invasion? *Aquat. Invasion*, **4**, 270–277.

Flander Putrle, V. and Malej, A. (2003) The trophic state of coastal waters under the influence of anthropogenic sources of nutrients (fish farm, sewage outfalls). *Periodicum Biologorum*, **105**, 359–365.

Fonda Umani, S., Franco, P., Ghirardelli, E. *et al*. (1992) Outline of oceanography and the plankton of the Adriatic Sea. In Colombo, G., Ferrari, E., Ceccherelli, V. U., Rossi, R. *et al*. (eds), *Marine Eutrophication and Population Dynamics*. Olsen and Olsen, Fredensborg, pp. 347–365.

Gamulin, T. (1979) Zooplankton of the eastern Adriatic Sea. *Prir. Istr. JAZU*, **43**, 177–270 (in Croatian).

GESAMP (IMO/FAO/UNESCO-IOC/WMO/WHO/IAEA/UNEP Joint Group of Experts on Scientific Aspects of Marine Environmental Protection). (1997) Opportunistic settlers and the problem of the ctenophore *Mnemiopsis leidyi* invasion in the Black Sea. *Rep. Stud. GESAMP,* **58**, 84.

Greve, W., Stockner, J. and Fulton, J. (1976) Towards a theory of speciation of *Beroe. Comp. Ecol. Behav.* In Meckie, G. *et al*. (eds), *Coelenterate ecology and behaviour.* Plenum Press, New York, pp. 251–258.

Harding, L. W., Degobbis, D. and Precali, R. (1999) Production and fate of phytoplankton: annual cycles and interannual variability. In Malone, T.C., Malej, A, Harding, L.W., Smodlaka, N., Turner, R.E. *Ecosystems at the Land-Sea Margin: Drainage Basin to Coastal Sea. Coastal Estuar. Stud.*, **55**, 131–172.

Harbison, G. R. (2001) The catastrophic invasion of the Black Sea by Mnemiopsis leidyi: only doing what other ctenophores did long ago? *CIESM Workshop Series*, **14**, 85–86.

Harbison, G. R., Madin, L. P. and Swanberg, N. R. (1978) On the natural history and distribution of oceanic ctenophores. *Deep-Sea Res.*, **25**, 233–256.

Hays, G. H., Richardson, A. J. and Robinson, C. (2005) Climate change and marine plankton. *Trends Ecol. Evol.*, **20**, 337–344.

Issel, R. (1922) Nuove indagini sul plancton nelle acque di Rovigno. *R. Comitato Talassogrfico Italiano, Memoria*, **102**, 1–36.

Issel, R. (1925) Ricerche sulle variazioni del Plancton nelle aque di Rovigno e di Quarto (1922–1923). *R. Comitato Talassogrfico Italiano, Memoria*, **115**, 1–41.

Isinibilir, M., Tarkan, A. N. and Kideys, A. E. (2004) Decreased levels of the invasive ctenophore *Mnemiopsis* in the Sea of Marmara. In Dumont, H., Shiganova, T. and Niermann, U. (eds), *The Ctenophore Mnemiopsis leidyi in the Black, Caspian and Mediterranean Seas and other aquatic invasions. NATO ASI Series 4, Vol. 35*. Kluwer Academic Publication, Dordrecht, pp. 155–175.

Ivanov, V. I., Kamakim, A. M., Ushivtzev, V. B. *et al*. (2000) Invasion of Caspian Sea by the comb jellyfish *M.leidyi* (Ctenophora). *J. Biol. Invasions*, **2**, 255–258.

Javidpour, J., Sommer, U. and Shiganova, T. (2006) First record of *Mnemiopsis leidyi* in the Baltic Sea. *Aquat. Invasion*, **1**, 299–302.

Konsulov, A. S. and Kamburska, L. T. (1998) Ecological determination of the new Ctenophora–*Beroe ovata* invasion in the Black Sea. *Tr. Ins. Oceanology.* Varna, pp. 195–197.

Krumbach, T. (1911) Notizen über die Dauna der Adria bei Rovigno. IV. Die Ctenophorenfauna von Rovigno nach den Novemberstürmen 1910. *Zool. Anz.*, **37**, 315–319.

Krumbach, T. (1925) Zweiter Unterstamm der Coelenterata; Acnidaria–Collaria- Greifzellentiere. *In Dr.Willy Kukenthal Handbuch der Zoologie*. Vol. 1. Walter de Gruyter and Co. Bd, Leipzig, Berlin, pp. 1–50.

Malačič, V. (1991) Estimation of the vertical eddy diffusion coefficient of heat in the Gulf of Trieste (Northern Adriatic). *Oceanol. Acta*, **14**, 23–32.

Malej, A. and Malej, A. (2004) Invasion of the Jellyfish *Pelagia noctiluca* in the Northern Adriatic: a non-success story. In Dumont, H., Shiganova, T. U. and Niermann, T. (eds), *Aquatic Invasions in the Black, Caspian and Mediterranean Seas and other aquatic invasions. NATO ASI Series. 4*. Vol. 35. Kluwer Academic Publication, Dordrecht, pp. 273–285.

Malej, A., Mozetič, P., Malačič, V. *et al*. (1995) Phytoplankton responses to freshwater inputs in a small semi-enclosed gulf (Gulf of Trieste, Adriatic Sea). *Mar. Ecol. Prog. Ser.*, **120**, 111–121.

Malej, A., Turk, V., Lučić, D. *et al*. (2007) Direct and indirect trophic interactions of *Aurelia* sp. (Scyphozoa) in a stratified marine environment (Mljet Lakes, Adriatic Sea). *Mar. Biol.*, **151**, 827–841.

Matishov, G. G., Selifonova, Z. h. P., Erygin, V. V. *et al*. (2005) Investigations of the water ballast in the harbour of Novorossiysk and some aspects of biological contamination of the Black and the Azov Seas. In Matishev, G. G. (ed.), *Ecosystem investigations of environment and biota of the Azov basin and the Kerch Strait.*. Vol. VII. Apatity, pp. 131–142.

Mayer, A. G. (1912) Ctenophores of the Atlantic coast of North America. *Publs. Carnegie Inst.*, **162**, 1–58.

Mianzan, H. (1999) Ctenophora. In Boltovskoy, D. (ed.), *South Atlantic Zooplankton*. BACKHUYS Publishers, Leiden, The Netherlands, pp. 561–573.

Mills, C. C. E. (2005) Ctenophora. La Checklist della fauna italiana (Rellini *et al.* ed.), Fasc. 3. http://www.sibm.it/CHECKLIST/menusxcheck.htm.

Mills, C. E., Pugh, P. R., Harbison, G. R. *et al*. (1966) Medusae, siphonophores and ctenophores of the Aboral sea, South western Mediterranean. *Sci. Mar.*, **60**, 145–163.

Mirzoyan, Z. A., Martynuk, M. L. and Vyazun, E. V. (2006) Development of ctenophores *Mnemiopsis leidyi* and *Beroe ovata* population in the Sea of Azov. *Proceedings of AZNIIRKH "The main problems of fishery in the Azov- Black Sea basin" (2004–2005)*. Postov-on-Don pp. 136–148 (in Russian).

Mozetič, P., Fonda Umani, S., Cataletto, B. *et al*. (1998) Seasonal and interannual plankton variability in the Gulf of Trieste (northern Adriatic). *ICES J. Mar. Sci.*, **55**, 711–722.

Oliveira, O. M. P. and Migotto, A. E. (2006) Pelagic ctenophores from the Sao Sebastiano Channal, southeastern Brasil. *Zootaxa*, **183**, 1–26.

Perrier, R. (1936) *La faune de la France.T.1.Paris*, 8–64.

Purcell, J., Malej, A. and Benović, A. (1999) Potential Links of Jellyfish to Eutrophication and Fisheries. In Malone, T.C., Malej, A, Harding, L.W., Smodlaka, N., Turner R.E (eds), *Ecosystems at the Land-Sea Margin: Drainage Basin to Coastal Sea*. *Coastal Estuar. Stud.*, **55**, 241–264.

Purcell, J. E., Shiganova, T., Decker, M. B. *et al*. (2001) The ctenophore *Mnemiopsis leidyi* in native and exotic habitats: U. S. estuaries versus the Black Sea basin. In Purcell, J. E., Graham, W. M. and Dumont, H. J. (eds). *Hydrobiologia*, 451, 145–176.

Quoy, J. R. C. and Gaimard, J. P. (1824) Zoologie. Deuxième partie. In Freycinet, L. (eds), *Voyage autour du Monde sur les corvettes de S.M.D'Uranie et la Physicienne, pendant les annes 1817, 1818, 1819 et 1820*. Chez Pillet Ainé, Paris, pp. 409–461.

Riedl, R. (1991) *Fauna e flora del Mediterraneo. Phylum Ctenophora. Franco Muzio & c. editore*. Italian edition. Padova and Verlag Paul Parey, Hambur-Berlin, pp. 175–180.

Rossi, L. (1971) Guida a Cnidari e Ctenofori della fauna Italiana. Rossi L. (ed.) *Quadreni della civica stazione idrobiologica di Milano. Milano. Civica stazione idrobiologica.*, **2**, 101.

Seravin, L. N. (1998) In Dobrovolsky, A. A. (ed.), *Ctenophora–comb-jellies (Methodology)*. St Perersburg, Omsk, p. 84 (in Russian).

Seravin, L. N., Shiganova, T. A. and Luppova, N. E. (2002) Investigation History of Comb Jelly *Beroe Ovata* (Ctenophora, Atentaculata, Beroida) and Certain Structural Properties of Its Black Sea Representative. *Zool. Zh.*, **81**, 1193–1201.

Shiganova, T. A. (1993) Ctenophore *Mnemiopsis leidyi* and ichthyoplankton in the Sea of Marmara in October of 1992. *Oceanology*, **33**, 900–903.

Shiganova, T. A., Bulgakova, Y. u. V. and Sorokin, P. Y. U. (2000a) Investigations of new settler *Beroe ovata* in the Black Sea. *Biol. Bull.*, **2**, 247–255.

Shiganova, T. A., Bulgakova, Y. u. V., Volovik, S. P. *et al*. (2000b) A new alien species *Beroe ovata* and its effect on ecosystems of Azov-Black Sea basin in August–September 1999. In Volovik, S. P. (ed.), *Ctenophore* Гребневик *Mnemiopsis leidyi (A.Agassiz) in Azov and Black Seas; its biology and consequences of its intrusion*. Rostov- on- Don, pp. 432–449 (in Russian).

Shiganova, T. A., Mirzoyan, Z. A., Studenikina, E. A. *et al*. (2001) Population development of the invader ctenophore *Mnemiopsis leidyi* in the Black Sea and other seas of the Mediterranean basin. *Mar. Biol.*, **139**, 431–445.

Shiganova, T. A., Dumont, H. J. D., Mikaelyan, A. S. *et al*. (2004a) Interaction 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 Dumont, H., Shiganova, T. and Niermann, U. (eds), *The Ctenophore Mnemiopsis leidyi in the Black, Caspian and Mediterranean Seas and other aquatic invasions. NATO ASI Series, 4*. Kluwer Academic Publication, Dordrecht, pp. 33–70.

Shiganova, T. A., Dumont, H. J. D., Sokolsky, A. F. *et al*. (2004b) Population dynamics of *Mnemiopsis leidyi* in the Caspian Sea, and effects on the Caspian ecosystem. In Dumont, H., Shiganova, T. and Niermann, U. (eds), *The Ctenophore Mnemiopsis leidyi in the Black, Caspian and Mediterranean Seas and other aquatic invasions. NATO ASI Series, 4*. Kluwer Academic Publication, Dordrecht, pp. 71–111.

Shiganova, T. A., Christou, E. D., Bulgakova, Y. u. V. *et al*. (2004c) Study on the distribution and biology of the invader *M.leidyi* in the northern Aegean Sea, comparison with indigenous species *Bolinopsis vitrea*. In Dumont, H., Shiganova, T. and Niermann, U. (eds), *The Ctenophore Mnemiopsis leidyi in the Black, Caspian and Mediterranean Seas and other aquatic invasions. NATO ASI Series, 4*. Kluwer Academic Publication, Dordrecht, pp. 113–135.

Shiganova, T. A., Christou, E. D. and Siokou-Frangou, I. (2007a) First finding of alien species *Beroe ovata* Mayer 1912 in the Aegean Sea. *Mediterranean Mar. Sci.*, **8**, 5–14.

Shiganova, T. A., Bulgakova, Y. u., Siokou-Frangou, I. *et al*. (2007b) Changes in ctenophore *Mnemiopsis leidyi* phenology and population dynamics linked to environmental variability and climate forcing in its recipient areas of the Southern Seas. Human and Climate forcing of Zooplankton Populations. International Zooplankton Production Symposium, Japan, Hiroshima, 28 May–1 June 2007, p. 91.

Steuer, A. (1903) Beobachtungen über das Plankton des Triester Golfes im Jahre 1902. *Zool. Anz.*, **27**, 145–149.

Stiasny, G. (1912) Beobachtungen über das Plankton des Triester Golfes während des Jahres 1911. *Zool. Anz.*, **39**, 604–610.

Stiasny, G. (1909) Beobachtungen über das Plankton des Triester Golfes im Jahre 1908. *Zool. Anz.*, **24**, 289–293.

Stiasny, G. (1910) Beobachtungen über die marine Fauna des Triester Golfes im Jahre 1909. *Zool. Anz.*, **35**, 583.

Stiasny, G. (1911) Beobachtungen über die marine Fauna des Triester Golfes während des Jahre 1910. *Zool. Anz.*, **37**, 517–523.

Studenikina, E. I., Volovik, S. P., Miryozan, I. A. *et al*. (1991) The ctenophore *Mnemiopsis leidyi* in the Sea of Azov. *Oceanology*, **31**, 722–725.

Tamm, S. L. and Tamm, S. (1993) Diversity of macrociliary size, tooth patterns, and distribution in *Beroe* (Ctenophora). *Zoomorphology*, **113**, 79–89.

Tarkan, A. N., Isinibilir, M. and Benli, H. A. (2000) An observation on distribution of the invader *Mnemiopsis leidyi* (Agassiz,1865) and the resident *Aurelia aurita* (Limm,1758) along the Strait of Istanbul. Azturk, B., Kadnoglu, M. and Ozturk, H. (eds) The Symposium of the Marmara Sea 2000. TUDAV, Istanbul, pp. 461–467.

Treguboff, G. and Rose, M. (1957) Manuel de planctonologie Mediterraneenne. Paris. *Centre Nat. Rech. Sci.*, **1**, 1–587.

Vinogradov, M. E., Shushkina, E. A., Musaeva, E. I. *et al*. (1989) Ctenophore *Mnemiopsis leidyi* (A.Agassiz) (Ctenophora: Lobata) — new settler in the Black Sea. *Oceanology*, **29**, 293–298.

Viitasalo, S., Lehtiniemi, M. and Katajisto, T. (2008) The invasive ctenophore *Mnemiopsis leidyi* overwinters in high abundances in the subarctic Baltic Sea. *J. Plankton Res.*, doi:10.1093/plankt/fbn088.

Wrobel, D. and Mills, C. (1998) *Pacific Coast Pelagic Invertebrates. A Guide to the Common Gelatinous Animals*. Monterey Bay Aquarium, Monterey, pp. 108.