生物安全学报 2013，22(4)：229－236
JOURNAL OF BIOSAFETY http：// www. jbscn. org

DOI：10.3969/j. issn. 2095-1787.2013.04.002

Acartia tonsa（Copepoda）in the Black and Caspian Seas：Review of its success and some lessons

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Abstract：The variety of aquatic nonindigenous animals in marine habitats worldwide includes more than 16 planktonic Copepoda species. *Acartia tonsa* is a very successful one，distributed in many seas. Its invasion into European seas was analyzed before（Brylinski，1981），but from that time *A. tonsa* extended its range in European aquatic habitats. The author describes the history of the *A. tonsa* invasion into the Ponto-Caspian basin as well as some misleading earlier publications. Morphologic differences between *A. clausi* and *A. tonsa*，the neglect of which led to the wrong identification，were examined. The data on *A. tonsa* and total copepod dynamics in the Sevastopol Bay during the period of 1976～1996 and the same data on the Caspian Sea since 1981 were analyzed. The average size of *A. tonsa* in new habitats decreased，and its relative density in the Black and Caspian Seas gradually increased.
Key words：*Acartia tonsa*；Black Sea；Caspian Sea；aliens

Introduction

Alien species invasions are now recognized as one of the greatest ecological threats to human well-being（Leppäkoski *et al.*，2002；MacNeel，2001；Richardson，2011）. Alien species often cause enormous damage to biodiversity and the valuable natural ecosystems upon which we depend. Successful alien species can transform the species composition of ecosystems by repressing or excluding native species，either directly or indirectly（Leppäkoski *et al.*，2002；Richardson，2011）. Aliens can also have cascading effects on insect-eating birds and on plants that rely on insects for pollination or seed dispersal. The calculated damage from invasive species worldwide is total more than US＄1.4 trillion annually — 5% of the global economy — with impacts across a wide range of sectors（Pimentel *et al.*，2001）.

In past ecosystems changed and evolved in relative isolation；there were slight possibilities of a natural exchange with each other. Early human migration led to the first intentional introductions of alien species. Increase in human migratory movements，as well as flows of goods，directed introduction of exotic species have led to a huge increase in the intensity of anthropogenic transfers of alien species on a global scale（Grigorovich *et al.*，2002；Leppäkoski *et al.*，2002；Richardson，2011）. It is therefore not surprising that human-induced transfer of exotic species considered as the main reason for the growth of invasions at a global level. Based on this paradigm，we try to understand and explain current invasions，predicting new the possibility of invasions，to develop management approaches to mitigate the unwanted invasions and their results. To develop a scientific background of environmental management for preventing and mitigating damages from alien species we need to extract and analyze the lessons from the different seas. The Black sea gives us a lot of such lessons（Leppäkoski *et al.*，2002；Shadrin，2000）.

The Black Sea is a sea in south-eastern Europe（Zaitsev，2008），surrounded by dryland of Europe，Anatolia and the Caucasus. The sea is ultimately connected to the Atlantic Ocean via the Mediterranean and the Aegean Seas and various straits. The Black Sea is the world's largest meromictic basin where the deep waters have a very limited mixing with the upper

Received：2013－06－05 **Accepted**：2013－10－17
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layers of oxygenated waters, as a result, over 90% of the Black Sea volume is anoxic waters (Zaitsev, 2008). The sea area is 436400 km^2. 22 countries are entirely or partly located in the catchment area of the Black Sea, and more than 170 million humans live within this area of 2.3 mln · km^{-2} (UNDP, 1997, 2007). The ratio of the catchment basin surface to the surface of a recipient water body, the so-called specific catchment for the Black Sea $SC > 5$; which is a very high value. This indicates a high anthropogenic impact on the Black Sea ecosystem. A high anthropogenic impact disturbs the ecosystem and promotes to open a door for invasive species; currently more than hundred alien species were recorded in the Black Sea (Grigorovich *et al.*, 2002; Shadrin, 2000). Some of those had the catastrophic effects on the Black Sea ecosystem and human activities (Leppäkoski *et al.*, 2002; Shadrin, 2000; Shadrin *et al.*, 2012).

The Caspian is variously classed as the world's largest lake or a full-fledged sea (Kosarev & Yablonskaya, 1994). It is situated where the South-Eastern Europe meets the Asian continent, between latitudes 47°07′N and 36°33′ N and longitudes 45°43′E and 54°20′ E. It is approximately 1030 km long and its width ranges from 435 km to a minimum of 196 km. It has no connection to the world's oceans and its surface level at the moment is around — 26.5 m below MSL. At this level, its total coastline is some 7000 km in length and its surface area is 386400 km^2. The water volume of the lake is about 78700 km^3. The water of the Caspian Sea is slightly saline; if we compare the Caspian water with oceanic water, it contains 3 times less salt. The Caspian Sea is a remnant of the ancient ocean, Tethys, more precisely of its Paratethys Bay. About 50 ~ 60 million years ago the Tethys Ocean connected the Atlantic and the Pacific Oceans. However, due to gradual shift of continental platforms it lost its connection with the Pacific Ocean and later on with the Atlantic Ocean. As a result, the water body became isolated. Today the Black and Caspian Seas are connected by Volga-Don Chanel. There are a lot of alien species in the Caspian Sea and almost all of them reached it via the Black Sea (Grigorovich *et al.*, 2002; Leppäkoski *et al.*, 2002; Shadrin, 2000).

Acartia tonsa invasion in the Black Sea

The copepod *A. tonsa* Dana, 1846 was first found and described as a specific morphotype of *A. clausi* Giesbrecht, 1889 (A-form) from 1976 ~ 1989 year samples taken in the Sevastopol Bay (the Black Sea) (Popova & Shadrin, 1992; Shadrin & Popova, 1994). Later, *A. tonsa* was identified from samples near Karadag (SW Crimea) (Belmonte *et al.*, 1994). Description of the A-form of *A. clausi* was based on morphological features that have not been used in the key for identification of copepods; in 1997, the misidentification was realized. The same mistake was made for the Caspian Sea specimens (Prusova *et al.*, 2002).

Because *A. tonsa* and *A. clausi* were not separately identified in the Black Sea before the late 1990s, we only have long-term data on *A. tonsa* for Sevastopol Bay (Shadrin *et al.*, 1999).

A. tonsa was absent in samples taken in 1968. By the next sampling, 1976 it was rather abundant. Unfortunately no samples were taken between these two dates. *A. clausi* is present year round whereas *A. tonsa* occurs only from May/June to October/January (Sazhina & Shadrin, 1993). In 1989 ~ 1996 *A. clausi* was absent in 22% ~ 38% of summer samples. In 1976, 20% of the samples had more than 50% individuals of *A. tonsa*. In 1989 ~ 1990, during a period when *A. tonsa* and *A. clausi* jointly occurred, *A. tonsa* clearly prevailed in about 50% of samples; it was 90% ~ 100% of the total density of both species.

In 1976 there were four *Acartia* species present in Sevastolpol Bay: *A. clausi*, *A. tonsa*, *A.* (*Paracartia*) *latisetosa* (Kritchagin, 1873) and *A. margalefi* Alcaraz, 1976. *A. margalefi* at that time was identified as small form of *A. clausi*. The total numbers of all *Acartia* spp. was 27% ~ 28% of the total density of Copepoda (Prusova & Shadrin, 1983). *A. margalefi* was dominant (Table 1, Fig. 1). *A. latisetosa* decreased after 1954, and after 1976, neither *A. latisetosa* nor *A. margalefi* were present.

Table 1 Total abundance of all copepods and *Acartia* spp. in the Sevastopol Bay, Black Sea, in 1976 (data from Prusova & Shadrin, 1983)

Date	Abundance (ind · m^{-3}) *			Relative density (%)	
	Copepods, total	*Acartia*, total	*A. clausi* (small form)	*Acartia* in total copepods	Small form of *A. clausi* in total *Acartia*
20 Jan 1976	2275	153.4	105	6.7	68
11 Feb 1976	3488	55.6	28	1.6	50
25 Feb 1976	3051	112.7	0	3.7	0
10 Mar 1976	1852	40.5	0	2.2	0
14 Apr 1976	2686	223.8	40	8.3	18
28 Apr 1976	6744	559.3	461	8.3	82
12 May 1976	3181	861.1	736	27.1	85
26 May 1976	2197	778.0	695	34.5	89
09 Jun 1976	5608	1131.5	632	20.2	56
23 Jun 1976	8020	5697.4	4750	71.0	83
14 Jul 1976	2448	1197.4	790	48.9	66
28 Jul 1976	803	368.6	158	45.9	43
11 Aug 1976	6724	4960.9	1829	73.8	37
28 Aug 1976	5065	3631.7	2395	71.7	66
15 Sep 1976	18836	6420.9	4605	34.1	72
27 Oct 1976	9790	1052.7	355	10.8	34
17 Nov 1976	14336	2527.7	2056	17.6	81
26 Nov 1976	6198	2624.4	2444	42.3	93
10 Dec 1976	8309	2250.2	2195	27.1	98
22 Dec 1976	5403	134.2	111	2.5	83
Average	5669	1660	1178	26.8	61
CV	0.78	1.18	1.22	0.91	0.48

CV — variation coefficient; * Average for 2 samples, 4 ~ 5 m^3 of water were filtrated for every sample (horizon 0 ~ 10 m).

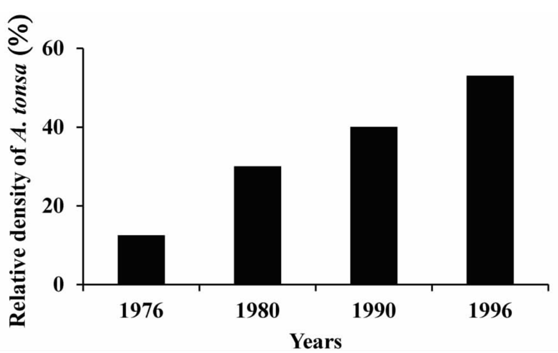

Fig. 1 Long-term changes of average year % of *A. tonsa* in total Copepoda density (the Sevastopol Bay)

From 1976 to 1996, *A. tonsa* density increased: it was 37% in 1976; 70% in 1989 ~ 1990 and 88.5% in 1995 ~ 1996. This was paralleled with an increase of *Acartia* spp. in all Copepoda: 14% (1954); 27% (1976); 46% (1979 ~ 1980); 60% (1989 ~ 1990) and 62% (1995 ~ 1996) (Petipa, 1959; Shadrin *et al.*, 1999). Changes, which occurred between 1954 and 1976, show that the introductions of *A. tonsa* and ctenophore *Mnemiopsis leidyi* A. Agassiz, 1865 are not the only reasons of the decline of Copepoda taxocene in the Sevastopol Bay. The ecosystem destabilization due to anthropogenic impact on the Bay may also have had an impact (Shadrin, 2000).

After 1976 the intra-annual variability of densities in *Acartia* species as well as of whole copepod taxocene increased (Table 2). Changes in the character of variability may be early-warning signals of a system drift to tipping points at which a sudden shift to a contrasting dynamical state may occur (Scheffer *et al.*, 2009) and indicate a destabilization in copepod taxocene and *Acartia* spp. populations. This increase was accompanied by a decrease in total copepod density and an increase in the relative contribution of *Acartia* to the total copepod density (Tables 1, Table 3 ~ 4). In 1999 ~ 2000 some samples were collected from Sevastopol Bay without any Copepoda, indicating a local collapse of copepods. In the summer of 1998, the mesozooplankton of the Sevastopol Bay was dominated by two alien species — *A. tonsa* and the cirripede *Balanus* (*Amphibalanus*) *improvisus* (Darwin, 1854) (Pavlova & Kemp, 1999).

Table 2 Interannual coefficient of variation of some density parameters of Copepoda in the Sevastopol Bay, between 1976 ~ 1996

Years	Coefficient of variation		
	Total Copepoda density	*Acartia* taxocene density	*Acartia* part in total Copepoda density
1976	0.78	1.18	0.91
1979 ~ 1980	0.96	1.28	0.62
1989 ~ 1990	1.75	2.34	0.64
1995 ~ 1996	1.62	2.18	0.58

Table 3 Total abundance of all copepods and *Acartia* spp. in the Sevastopol Bay, Black Sea, in 1989 ~ 1990 (data from Popova & Shadrin, 1992)

Date	Abundance (ind · m^{-3})*		*Acartia* vs. total copepods (%)	Date	Abundance (ind · m^{-3})*		*Acartia* vs. total copepods (%)
	Copepods, total	*Acartia*, total			Copepods, total	*Acartia*, total	
13 Mar 1989	247.0	3.0	1.2	06 Feb 1990	298.0	30.0	10.1
03 Apr 1989	1542.5	275.0	17.8	14 Feb 1990	137.0	14.0	10.2
10 Apr 1989	2059.0	262.5	12.7	22 Feb 1990	583.0	13.0	2.2
24 Apr 1989	402.0	287.5	71.5	14 Mar 1990	407.0	48.0	11.8
15 May 1989	391.0	375.0	95.9	26 Mar 1990	161.0	21.0	13.0
22 May 1989	125.0	100.0	80.0	11 Apr 1990	363.0	43.0	11.8
03 Jul 1989	6691.0	6400.0	95.9	23 Apr 1990	226.0	96.0	42.5
05 Sep 1989	57.0	57.0	100.0	07 May 1990	632.0	337.5	53.4
11 Sep 1989	450.0	450.0	100.0	22 May 1990	504.0	392.0	77.8
18 Sep 1989	302.0	300.0	99.3	04 Jun 1990	393.0	350.0	89.1
09 Oct 1989	101.5	92.5	91.1	18 Jun 1990	2879.0	2800.0	97.3
16 Oct 1989	1013.5	1012.5	99.9	09 Jul 1990	760.0	537.5	70.7
30 Oct 1989	222.0	212.0	95.5	30 Jul 1990	31.0	29.0	93.5
20 Nov 1989	206.0	201.0	97.6	10 Sep 1990	1487.5	1487.5	100.0
12 Dec 1989	66.0	29.0	43.9	27 Sep 1990	217.0	215.0	99.1
09 Jan 1990	104.0	29.0	27.9	Average	721.0	516.0	60.2
30 Jan 1990	8.0	1.0	12.5	*CV*	1.75	2.34	0.64

CV — variation coefficient; * Average for 2 localities (4 ~ 5 samples); 4 ~ 5 m^3 of water were filtrated for every sample (horizon 0 ~ 10 m).

Table 4 Total abundance of all copepods and *Acartia* spp. in the Sevastopol Bay, Black Sea, in 1995 ~ 1996 (data from Shadrin *et al.*, 1999)

Date	Abundance (ind · m^{-3})*		*Acartia* vs. total copepods (%)	Date	Abundance (ind · m^{-3})*		*Acartia* vs. total copepods (%)
	Copepods, total	*Acartia*, total			Copepods, total	*Acartia*, total	
14 Jun 1995	30	29	96.7	12 Feb 1996	82	8	9.8
30 Jun 1995	2547	2537	99.6	28 Mar 1996	768	85	11.1
20 Jul 1995	122	122	100.0	29 Apr 1996	529	264	49.9
14 Aug 1995	158	158	100.0	28 May 1996	58	44	75.9
19 Sep 1995	231	128	55.4	Average	453.5	337.7	61.8
11 Dec 1995	10	2	20.0	*CV*	1.62	2.18	0.58

CV — variation coefficient; * Average for 2 ~ 4 samples; 4 ~ 5 m^3 of water were filtrated for every sample (horizon 0 ~ 10 m).

Currently *A. tonsa* occupies all the Black Sea area including its closed and semi-closed lagoons, with salinity to 55 ppt, (Shadrin & Anufriieva, 2013), and the Azov Sea including Sivash Bay (Prusova *et al.*, 2002; Zagotodnyaya *et al.*, 2008). Analyzing changes in the Black Sea zooplankton many authors blame on *M. leidyi* (Finenko *et al.*, 2003; Gubanova *et al.*, 2001; Murina *et al.*, 2003). Considering the vigorous invasion by *A. tonsa*, it seems those two new-comers have jointly influenced the zooplankton community.

A. tonsa, making its own niche, uses many of the resources previously used by *A. latisetosa*. These two species are very similar in size and ecological requirements. However, the degradation of the *A. latisetosa* population began a long time before the introduction of *A. tonsa* (1976) and *M. leidyi* (1986) into the Black

Sea. *A. latisetosa* and *A. margalefi* had vanished from Sevastopol Bay before the introduction of *M. leidyi* but several years after the introduction of *A. tonsa*. Possibly the main reason was sediment pollution, damaging the obligatory resting egg-stage of the original, native species (Shadrin *et al.*, 1999). Resting stage cannot survive in hard polluted sediments. *A. tonsa* also has resting eggs while *A. clausi* has not (Sazhina & Shadrin, 1993).

A comparison of *A. tonsa* and *M. leidyi* impacts on native zooplankton enables the conclusion that *A. tonsa* is mostly responsible for the changes in composition of copepod taxocene while *M. leidyi* is responsible for the drastic decrease of total copepod abundance. A competing alien invader influences the diversity of closely related species, but a predatory invader decreases the total density of its prey. *A. tonsa* and *M. leidyi* impacts transformed the Black Sea pelagic ecosystem to an alternative stable state. In the period 2001 ~ 2008, a new alien copepod *Oithona davisae* Ferrari and Orsi, 1984 (Gubanova & Altukhov, 2007; Temnykh & Nishida, 2012; Zagorodnyaya, 2002), became abundant and another transition started.

A. tonsa in the Caspian Sea

The article reporting *A. clausi* in the Caspian Sea (Kurashova & Abdullaeva, 1984) included pictures that more closely correspond to *A. tonsa* than *A. clausi*. We checked the samples taken in 1986 in the North and Central part of the Caspian Sea (kindly sent to us by Dr. Kurashova), and all specimens were identified as *A. tonsa* (Prusova *et al.*, 2002).

The history of the *A. tonsa* invasion into the Caspian Sea was given by several articles (e.g. Kurashova & Abdullaeva, 1984; Tinenkova *et al.*, 2000), except that these articles refer to it (erroneously) as *A. clausi* (Prusova *et al.*, 2002). In 1979 a single specimen of *Acartia* sp. was found in the Volga-Don Channel. In August 1981, several more individuals were sampled in the eastern part of the southern Caspian Sea. By August 1982, all life stages of *A. tonsa* were very abundant in the Central Caspian Sea (up to 30000 ind · m^{-3}). In 1983, *A. tonsa* had reached the Northern Caspian Sea, and by 1998, the species occupied the whole Caspian Sea including deepwater zones (where it reached 264 ind · m^{-3}) and hypersaline areas. Since 1986 *A. tonsa* is the dominant copepod in the Southern Caspian Sea (more 3000 ind · m^{-3}). It outcompeted a formerly dominant copepod *Eurytemora grimmi* (Sars G O, 1897) (whose density was about 2000 ind · m^{-3} before the introduction of *A. tonsa*, and 800 ind · m^{-3} thereafter). *Calanipeda aquaedulcis* Kritchagin, 1873 was a dominant copepod in the central part of the Caspian Sea. From 1981 (start of invasion of *A. tonsa*) *C. aquaedulcis* decreased in density, from a — 200 ~ 600 ind · m^{-3} in 1971 ~ 1981, to — 58 ~ 340 ind · m^{-3} in 1982 ~ 1993 (Tatarintseva *et al.*, 2000). In the Caspian as well as the Black Sea, *A. tonsa* was increasing in density approximately with same rate (Table 5).

Table 5 Changes of some average summer characteristics of *A. tonsa* population in the Caspian Sea (data from Prusova *et al.*, 2002; Tatarintseva *et al.*, 2000)

Part of the Sea	1981		1982		1983		1984		1987 ~ 1993	
	N/B	*K*	*N/B*	*K*	*N/B*	*K*	*N/B*	*K*	*N/B*	*K*
Southern	>0	>0	–	–	–	29	–	–	8900/56	51
Central	0	0	<30000	–	–	29	10800/211	–	5000/39	46
Northern	0	0	0	0	780/3	3	5900/30	17	4700/47	29

N — *A. tonsa* density (ind · m^{-3}), *B* — *A. tonsa* biomass (ind · m^{-3}), *K* — portion of *A. tonsa* in total Copepoda density (%).

From the Black Sea, *A. tonsa* also spread into the Marmara Sea between 1980 and 1990 and it is abundant there, especially near the entrance into the Bosphorus Channel (Zagorodnyaya *et al.*, 2000). *A. tonsa* was introduced through the Black Sea into the Mediterranean Sea as well (Farabegolli *et al.*, 1989).

Morphological changes of *A. tonsa* in the Ponto-Caspian Basin

After introduction into the Black and Caspian Seas, individuals of *A. tonsa* became smaller. In the native area, *A. tonsa* male body length is 1.0 ~ 1.3 mm and that of females is 1.3 ~ 1.5 mm (Steuer, 1926). In this area, where *A. tonsa* and *A. clausi* coexist, *A. tonsa* is longer than *A. clausi* (Conover, 1956). In the Sevastopol region *A. tonsa* became smaller: females were 1.09 mm in 1976 and 0.9 mm in 1995 ~ 1996, significant ($P = 0.001$) reduction. Comparable trends exist for male of *A. tonsa* in samples taken in the summer 1990 near Karadag (ES Crimea) (Belmonte *et al.*, 1994). In the Caspian Sea *A. tonsa* became smaller as well. In 1982 *A. tonsa* females had a body length of 0.900 ~ 0.975 mm, males — 0.750 ~ 0.850 mm (Kurachova & Abdullaeva, 1984). In 1986 *A. tonsa* females were 0.72 ~ 0.94 mm long, and males 0.71 ~ 0.82 mm (Prusova *et al.*, 2002).

In Sevastopol Bay, there was a step by step divergence in size between the two *Acartia* species and as a result there was a decrease in competition between these species (Table 6). It is important to note that the alien species caused this change in ratio. Many non-native species in the Black Sea underwent morphological modifications (Shadrin, 2000) and if a changed alien will come back in natural areal we can talk about "boomerang" invasion which may be more dangerous one than direct invasion (Shadrin, 2000). We don't know "boomerang" invasions among aquatic organisms now but some terrestrial changed aliens came back in native areal and led to drastic changes in former native communities (Brasier & Buck, 2001).

Table 6 Seasonal relative densities and sizes of *A. clausi* and *A. tonsa* in the Sevastopol Bay, Black Sea, in 1995 ~ 1996 (data from Shadrin *et al.*, 1999)

Date	*A. tonsa* in *A. tonsa* + *A. clausi* (%)	Length (mm) L_2 (*A. clausi*) Mean	*CV*	L_1 (*A. tonsa*) Mean	*CV*	L_1/L_2
03 Jun 1995	100.0	–	–	0.92	0.04	–
21 Aug 1995	93.7	1.105	0.02	0.915	0.03	0.83
20 Sep 1995	100.0	–	–	1.01	0.04	–
17 Oct 1995	90.8	1.22	0.06	1.05	0.04	0.86
04 Feb 1996	2.6	1.35	0.04	1.00	–	0.74
19 Feb 1996	0.0	1.34	0.02	–	–	–
20 Mar 1996	0.0	1.35	0.02	–	–	–
23 May 1996	46.4	1.17	0.02	0.93	0.025	0.795
19 Jun 1996	94.1	1.15	0.03	0.93	0.035	0.81
Average	58.62	1.24	0.03	0.96	0.04	0.81
CV	0.75	0.08	0.44	0.05	0.21	0.05

CV — variation coefficient.

Acknowledgments: The author is grateful to all those who over the years has been involved in his research. I thank two anonymous referees and my editor who helped to improve the manuscript.

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