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Fate of the Black Sea *Acartia clausi* and *Acartia tonsa* (Copepoda) penetrating into the Marmara Sea through the Bosphorus

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Abstract

In October 2005 spatial distribution of live and dead *Acartia clausi* and *Acartia tonsa* was studied in the Black and Marmara Seas and near the Marmara Sea inlet of the Bosphorus, in order to understand their fate upon transportation between two seas. The morphometric characteristics in both species from all studied areas, and the decreased abundance of *A. clausi* and *A. tonsa* from the Black Sea towards the Marmara Sea indicate that the Marmara Sea *Acartia* populations are formed by recruitment from the Black Sea. We observed mass mortality of *A. clausi* in the Marmara Sea near the Prince Islands. The majority of carcasses (66% of total *A. clausi* numbers in the Marmara Sea) were found in the salinity gradient layer.

Laboratory experiments showed that during a gradual salinity increase (3.5–4 h) from 18.9 (salinity of the Marmara Sea surface layers) to 39.8 (Marmara Sea salinity at depths >25 m) *Acartia clausi* began to die at a salinity of 30 and that all copepods were dead at 39.8. In comparison with *A. clausi*, *Acartia tonsa* was more tolerant to short-term salinity increase. Despite the high salinity tolerance of *A. tonsa* however, the abundance of this species was estimated to be very low in the offshore Marmara Sea. Respiration rate and frequency of jumps in *A. tonsa* were 1.3–1.5 and 1.77 times higher, respectively, than those in *A. clausi*.

Keywords: *Acartia clausi*; *Acartia tonsa*; distribution; salinity tolerance; metabolism; Black Sea; Marmara Sea

1. Introduction

Copepods of the genus *Acartia* inhabit many coastal and offshore environments where they are usually among the most abundant zooplankton species. Two or more species may coexist simultaneously (Lee and McAlice, 1979; Gaudy et al., 2000), but frequently winter species alternate with summer ones (Conover, 1956; Jeffries, 1962). Local populations of Acartiidae can be formed due to highly variable conditions of temperature, salinity and food availability. In the Black Sea two mass species occur during the most of the year, i.e. the permanently eurythermic *Acartia clausi* and the recent warm-water species *Acartia tonsa* which has replaced the stenothermic *Acartia latisetosa* since the 1970s (Gubanova, 2000).

Acartia tonsa possesses a wide range of tolerance to salinity and oxygen concentration whilst *Acartia clausi* is considered a more stenohaline species which is extremely sensitive to hypoxia (Stalder and Marcus, 1997; Gaudy et al., 2000; Chinnery and Williams, 2004). *Acartia tonsa* is adapted to high food concentration (Paffenhöfer and Stearns, 1988) which is abundant in nearshore environments and estuaries.

Due to a positive water balance in the Black Sea, its water masses are transferred into the Marmara Sea through the Bosphorus Strait forming a brackish surface layer (15–20 m) with a salinity of 18–24 and temperature ranging from 20–24 °C

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in summer to 8–9 °C in winter. Below this brackish layer lies more densely saline (about 39) Mediterranean Sea water with a constant temperature of about 15 °C throughout the year (Besiktepe et al., 1994). According to the distribution of water masses, the structure of the zooplankton community in the Marmara Sea has been established whereby the species originating from the Black Sea inhabit the upper strata and the Mediterranean species are found in the deep layers (Tarkan et al., 2005). *Acartia* usually aggregate in the upper phytoplankton-rich layers, however, in the Black Sea they can migrate down to 50–70 m due to diel feeding rhythm (Kovalev, 1993; Besiktepe, 2001). In the Marmara Sea such vertical migrations may result in salinity shock and death of the organisms. Although the *Acartia* species dominate the copepods in the Marmara Sea (Tarkan and Erguven, 1988; Benli et al., 2001; Yuksek et al., 2002), little is known about the mechanisms of formation of the *Acartia* group in the Marmara Sea and the fate of the Black Sea *Acartia* species after their transportation through the Bosphorus.

The aim of this paper was to study the spatial and vertical distribution, size structure, abundance of live and dead *Acartia clausi* and *Acartia tonsa* near the Bosphorus Strait in the Black and Marmara Seas. We also analysed species-specific differences in respiration rate, activity and response to salinity change in order to estimate the adaptability of the Black Sea *Acartia* to the Marmara Sea environment.

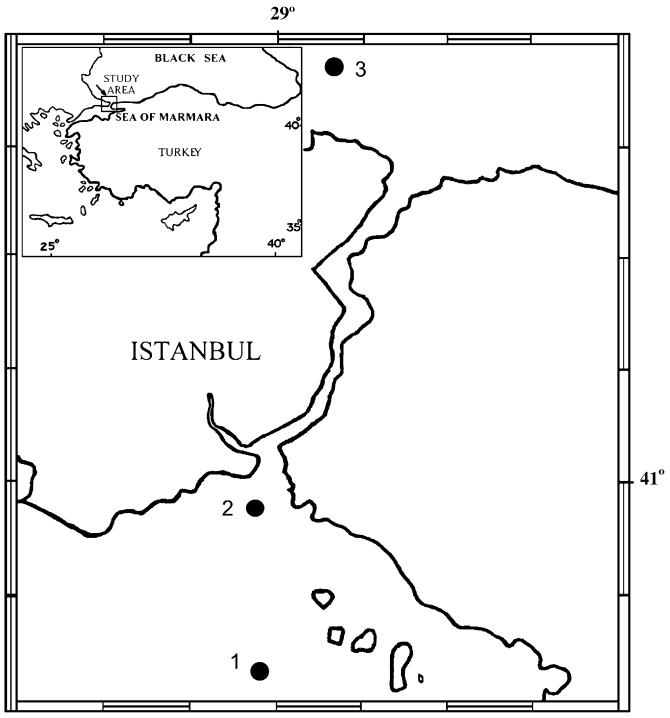

Fig. 1. Location of sampling stations in the Marmara and Black Seas in October 2005.

2. Methods

Copepods were sampled with a closing Nansen net (opening diameter 50 cm, mesh size 200 μm) on board a small fishing boat (Hedef-1) at a permanent station in the Marmara Sea (Fig. 1) near the Prince Islands (40°51′715 N, 28°57′901 E) on 13 October 2005. They were collected separately from the surface layer (0–25 m) consisting of the Black Sea water (salinity of 23.2 and temperature of 18.3 °C), intermediate layer (25–50 m) and the layer below the halocline (50–200 m) formed by the Mediterranean Sea water (salinity of 39.8 and temperature of 15.4 °C). One total vertical haul was also made on 16 October in the 0–50 m layer with surface water salinity of 18.9 and temperature of 18.4 °C near the Marmara Sea inlet of the Bosphorus. The zooplankton sample, collected by Dr Boris Anninsky from the layer of 70–0 m with a temperature of 19.1 °C near the Bosphorus in the Black Sea on 14 October 2005 during the R/V "Parshin" cruise, was used for comparison. The vertical profiles of temperature and salinity which are typical for October in the Black and Marmara Seas are shown in Fig. 2.

The samples were immediately preserved in 4% borax-buffered formaldehyde. In the laboratory the numbers of live and dead *Acartia* specimens were determined under a dissecting microscope. Dead organisms were identified by the condition of chitinous covering and internal organs. Dimness of exoskeleton and destruction of muscles were considered as attributes of death. We separated adults and copepodite stages V of *Acartia clausi* and *Acartia tonsa* basing on their morphological characteristics. To distinguish between early copepodite

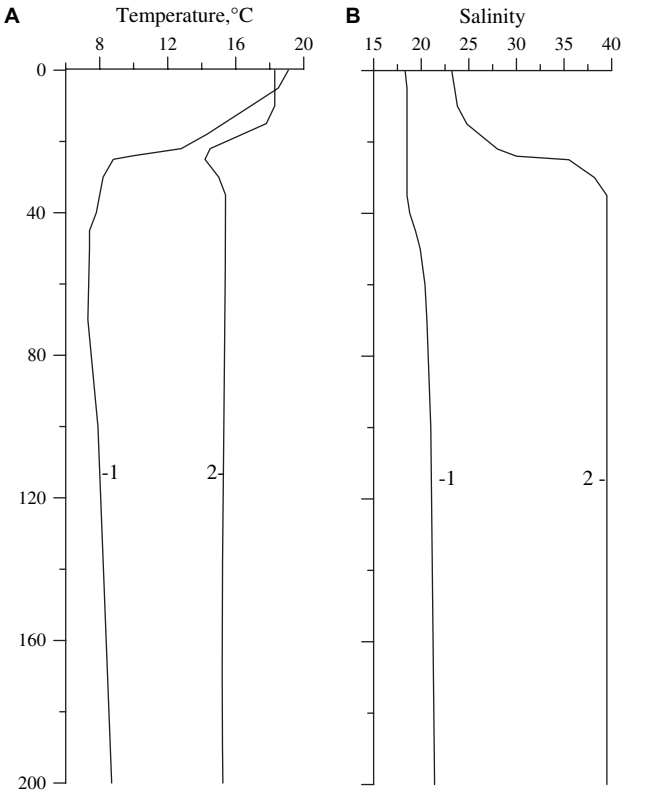

Fig. 2. The profiles of temperature (A) and salinity (B) typical for October in the southwestern Black Sea (1) and northeastern Marmara Sea (2).

stages of these two species, we used size ranges obtained during our study.

Live copepods collected near the Prince Islands and Bosphorus were used in physiological laboratory experiments. To determine the salinity tolerance ranges of *Acartia clausi* and *Acartia tonsa*, we studied their behavioural response to gradual salinity increase. In our experiments salinity was increased gradually from 18.9 and 23.2 to 39.8 over 3.5–4 h. The salinity-changing regime was chosen taking into account that the minimum rate of gravity sinking in the Black Sea *A. clausi* amounts to 2.5 m h^{-1} (Stepanov and Svetlichny, 1981) whilst the thickness of the salinity gradient layer in the Marmara Sea is about 10 m. A total of 40–50 females of either species were placed in the separate beakers of 50 ml volume with the initial salinity and then transported to the next chambers with a higher salinity of 2–3 every half an hour. At the end of every 0.5 h exposure the numbers of actively swimming and immobile animals were counted. We kept the motionless individuals in the beakers with given salinity for several hours under observation. If the muscles of these animals became opaque, we considered such *Acartia* dead. Three identical experiments were run for each species. The densely saline water was obtained by adding the Marmara Sea water from deep layers (39.8) to the surface Black Sea water (18.9 and 23.2 near the Bosphorus and Prince Islands, respectively). Water salinity was measured by a salinity meter ''pIONeer 65'' using the Practical Salinity Scale.

Respiration rate was studied in *Acartia clausi* females collected from the Marmara Sea near the Bosphorus (salinity 18.9), Prince Islands (salinity 23.2) before and after one-day acclimation to 39.8, in females and males of *Acartia tonsa* sampled near the Bosphorus (18.9), and before and after one-day acclimation to 39.8 (in females only). To determine oxygen consumption, the sealed chamber method was used with experimental and control syringes of 2.0 ml filled with seawater. A total of 10–20 females or males of *Acartia* were transferred by pipette into an experimental syringe with a protective sieve disc (mesh size 200 μm) over the outlet. To obtain identical initial oxygen concentrations in control and experimental syringes from each pair, we connected the syringes with a plastic tube and pumped the water through them several times. The syringes were then separated, closed by the stoppers and incubated for 1–2 h at 20 ± 0.5 °C. For *A. clausi* and *A. tonsa* 10 experiments were conducted separately at each salinity value. Oxygen concentration was measured using a polarographic membrane oxygen sensor joined with the chamber (all-glass syringe) of 0.5 ml volume, with a magnetic stirrer inside (Svetlichny and Hubareva, 2005). The water sample from the experimental or control syringe was transferred to the chamber in six portions through the needle. Four last portions were used to calculate the average oxygen concentration.

Wet weight (WW, mg) of *Acartia clausi* and *Acartia tonsa* was calculated as $WW = kL_{pr}d_{pr}^2$, where L_{pr} and d_{pr}, (mm) are the length and width of prosome, respectively, k is the empiric coefficient being equal to 0.63 in females and 0.49 in males of *A. clausi* (Svetlichny, 1983). Dry weight (DW) of *A. clausi* was determined as $DW = 12.37L_{pr}^{3.63}$ (Durbin and Durbin, 1978). Dry weight of *A. tonsa* was calculated from the equation: $\log DW = 0.86L_{tot}$ (Heinle, 1966), where L_{tot} is total body length. L_{pr} was measured in lateral view as the distance separating the anterior-most margin of the forehead to the line demarcating the hinge separating the prosome from urosome. L_{tot} was determined as the distance from anterior-most margin of the forehead to the distal end of the furcal ramis.

The swimming properties of *Acartia clausi* and *Acartia tonsa* females were investigated at 20 °C and salinity of 18.9. One individual of each species was placed into a 50 ml glass container, and left in the experimental filming set-up for 30 min for acclimation. Activity of five individuals of every species was then filmed continuously during 5 min in five replicates over one hour. During the experiments, the copepods were fed with the algae *Thalassiosira weisflogii* and *Monochrysis lutheri*. The behaviour of the copepods was recorded at a rate of 25 frames s^{-1} using a digital camera facing the experimental container. Swimming paths were subsequently analysed and the mean number of jumps per minute was calculated.

For statistical analysis of the data one-way ANOVA was used. The comparisons of the parameters were made using the Student's *t*-test. Average values presented in the Figures and Tables are the means ± standard deviation.

3. Results

3.1. Field observations

Prosome length (L_{pr}), total body length (L_{tot}), body width (d) and total body length: body width ratio in females and males of *Acartia clausi* and *Acartia tonsa* from the Marmara and Black Seas are presented in Table 1. We did not find significant regional differences in the morphometric parameters of these species. In *A. clausi* mean L_{tot} amounted to 1.136 ± 0.06 and 1.158 ± 0.04 mm for females and 1.071 ± 0.032 and 1.064 ± 0.038 mm for males in the Black and Marmara Seas, respectively. Mean L_{tot} of *A. tonsa* amounted to 1.049 ± 0.047 and 1.066 ± 0.046 mm in females and 0.941 ± 0.027 and 0.959 ± 0.025 mm in males from the Black and Marmara Seas, respectively. However, the L_{tot}/d ratio for *A. clausi* (4.17 ± 0.038 mm) was significantly (Student's test, $t = 32$, $n = 120$, $p < 0.001$) higher than that for *A. tonsa* (3.83 ± 0.11 mm) reflecting morphological differences between these two species.

During the study period the abundance of both species decreased greatly in the direction from the Black Sea towards the Marmara Sea (Fig. 3A). The abundance of *Acartia clausi* in the Black Sea (87,263 ind. m^{-2}) was 7.4 times higher than that near the Marmara Sea inlet of the Bosphorus (11,750 ind. m^{-2}) and 7.7 times higher than that in the Marmara Sea near the Prince Islands (11,291 ind. m^{-2}). Live individuals constituted only 34% of the number of *A. clausi* captured in the Marmara Sea. Near the Prince Islands live *A. clausi* aggregated mainly in the subsurface layers formed by low-saline Black Sea water (Fig. 3B). In deeper strata consisting of the

Table 1
Morphometric parameters in *Acartia clausi* and *Acartia tonsa* collected in the Black Sea, in the Bosphorus region of the Black Sea and in the Marmara Sea (near the Prince Islands)

Species	Sex	Area	Total length, L_{tot}, mm	Prosome length, L_{pr}, mm	Maximum body width, d, mm	L_{tot}/d
Acartia clausi	Females	Black Sea	1.136 ± 0.060	0.869 ± 0.034	0.270 ± 0.013	4.21
		Bosphorus	1.144 ± 0.061	0.889 ± 0.035	0.276 ± 0.008	4.14
		Marmara Sea	1.158 ± 0.040	0.880 ± 0.025	0.278 ± 0.005	4.17
	Males	Black Sea	1.071 ± 0.048	0.803 ± 0.032	0.254 ± 0.009	4.22
		Bosphorus	1.074 ± 0.054	0.822 ± 0.024	0.258 ± 0.009	4.16
		Marmara Sea	1.064 ± 0.038	0.813 ± 0.019	0.258 ± 0.013	4.12
Acartia tonsa	Females	Black Sea	1.062 ± 0.031	0.847 ± 0.023	0.271 ± 0.010	3.92
		Bosphorus	1.049 ± 0.047	0.844 ± 0.047	0.272 ± 0.010	3.86
		Marmara Sea	1.066 ± 0.046	0.838 ± 0.041	0.266 ± 0.012	4.01
	Males	Black Sea	0.949 ± 0.039	0.731 ± 0.035	0.256 ± 0.009	3.71
		Bosphorus	0.959 ± 0.025	0.723 ± 0.022	0.254 ± 0.009	3.78
		Marmara Sea	0.941 ± 0.027	0.725 ± 0.021	0.251 ± 0.006	3.75

Mediterranean Sea water we found a large percentage of dead copepods (77.5% at 25–50 m and 94.1% at 50–250 m). The maximum number of dead *A. clausi* (6125 ind. m^{-2}) was found in the salinity gradient layer.

The abundance of *Acartia tonsa* was lower than that of *Acartia clausi* in all studied areas. Although the number of *A. tonsa* individuals collected near the Prince Islands was 15 times lower than those collected near the Marmara Sea inlet of the Bosphorus (5500 ind. m^{-2}), we did not find mass mortality in this species.

3.2. Laboratory experiments

During a gradual salinity increase up to 39.8 some individuals of *Acartia clausi* (collected from the Marmara Sea near the Bosphorus at 18.9) stopped swimming and descended to the bottom of aquarium at about 30, and died at 39.8. In contrast, more than 90% of *Acartia tonsa* captured near the Marmara Sea inlet of the Bosphorus survived under the same treatment (Fig. 4A).

In *Acartia clausi* sampled near the Prince Islands (surface salinity of 22.3), the number of live individuals after a gradual salinity increasing to 39.8 was more than 90% (as in *Acartia tonsa* from the Bosphorus), but decreased to only 20–30% survival (Fig. 4B) during long-term high salinity treatment.

Respiration rate in *Acartia clausi* females varied in limits of 0.064–0.069 μg O_2 ind^{-1} h^{-1} independent of sampling location and salinity concentration. In females of *Acartia tonsa* collected near the Bosphorus in the Marmara Sea, respiration rate at 18.9 also did not differ from that after one-day acclimation to 39.8 (Fig. 5). In comparison with *A. clausi*, respiration rate of *A. tonsa* was significantly greater ($p < 0.001$) by 1.27 and 1.51 fold at 18.9 and 39.8, respectively.

Mean jump frequency (69.4 ± 16.5 min^{-1}) in *Acartia tonsa* was 1.77 times higher than that (39.2 ± 4.9 min^{-1}) in *Acartia clausi* (Fig. 5). According to our observations, two *Acartia*

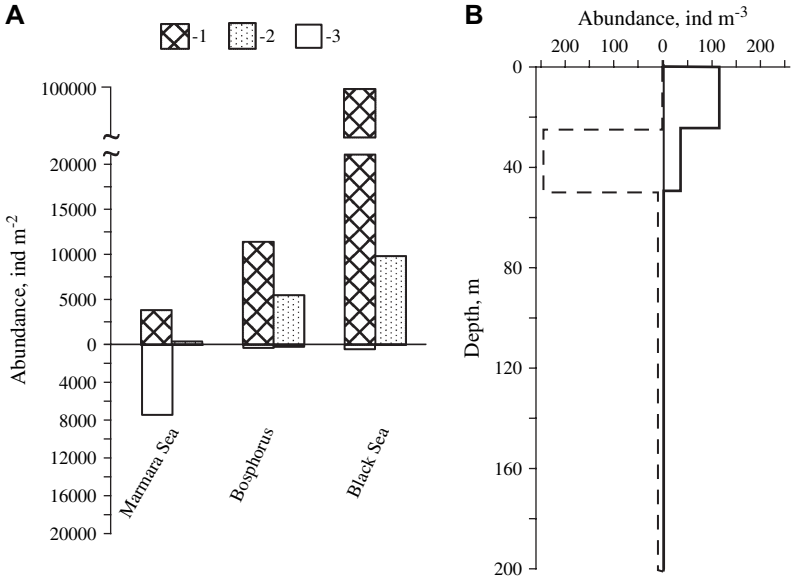

Fig. 3. (A) The number of live *Acartia clausi* (1) and *Acartia tonsa* (2) and their carcasses (3) from the Marmara Sea (near the Prince Islands), near the Marmara Sea inlet of the Bosphorus and in the Black Sea (near the Bosphorus), and (B) vertical distribution of live (—) and dead (- - -) *A. clausi* in the Marmara Sea (near the Prince Islands).

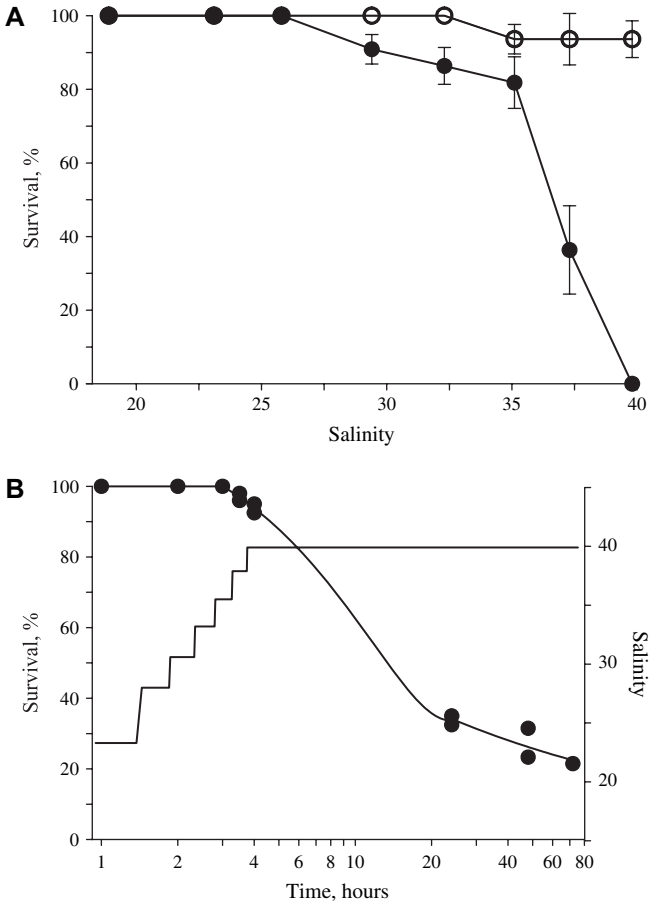

Fig. 4. Survival of *Acartia clausi* (●) and *Acartia tonsa* (○) collected near the Marmara Sea inlet of the Bosphorus during short-term (3.5 h) gradual salinity changing from 18.9 to 39.8 (A) and *A. clausi* sampled near the Prince Islands in the Marmara Sea after salinity changing from 22.3 to 39.8 (B). Note that the steps of salinity increase in the experiments with the individuals captured near the Bosphorus (A) are the same as during salinity acclimation of *A. clausi* from the Marmara Sea (B).

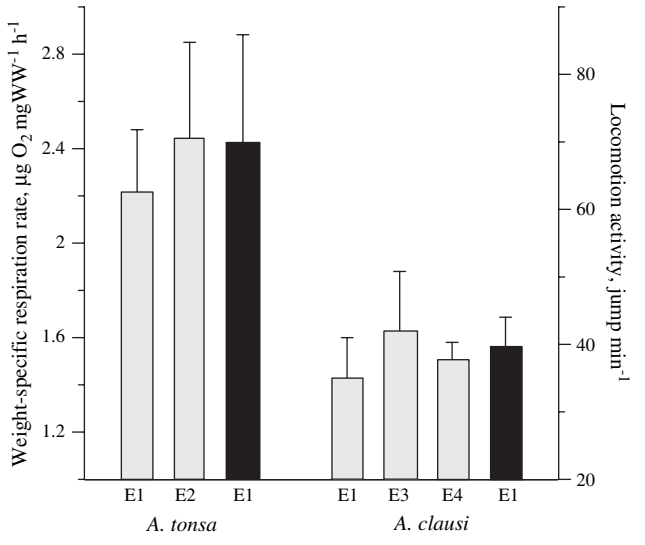

Fig. 5. Weight-specific respiration rate (□) and locomotion activity (■) of *Acartia clausi* and *Acartia tonsa* collected in the Marmara Sea near the Bosphorus at salinities of 18.9 (E1) and 39.8 (E2), and near the Prince Islands at salinities of 23.2 (E3) and 39.8 (E4).

species exhibit different behavioural patterns during locomotion. *Acartia clausi* use mainly "hop and sink" swimming whilst *A. tonsa* exhibit jumps and horizontal gliding (when filtering food by mouth appendages) as well.

4. Discussion

In coastal regions of the north-western Atlantic where *Acartia clausi* and *Acartia tonsa* are the native species, the total body length for females of *A. tonsa* varies between 1.15 and 1.3 mm (Steuer, 1923) exceeding that for *A. clausi* females. In contrast, in the Black Sea *A. tonsa* is smaller than *A. clausi* (Gubanova, 2000). Both species have coexisted in the Black Sea since the 1970s following the introduction and subsequent invasion of *A. tonsa*, probably in ship ballast waters (Gubanova, 1997). Body lengths of *A. tonsa* females collected in 1976 ranged from 0.96 to 1.2 mm with a mean value of 1.09 ± 0.07 mm (Gubanova, 2000). Belmonte et al. (1994) however reported body lengths in females of *A. tonsa* sampled in 1990 as 0.821–0.98 mm confirming the suggestion of Kovalev (1968) that adaptation of copepods to the Black Sea conditions may result in the reduction of body size. In October 1996 the mean body length of *A. tonsa* females in the Black Sea amounted to 0.879 ± 0.032 mm whilst that in the adjacent Marmara Sea was significantly higher (1.011 ± 0.027 mm), indicating the existence of the *A. tonsa* population indigenous to the Black Sea to be different from the Marmara Sea population (Kovalev et al., 1998). According to our data, in October 2005, body length of *A. tonsa* females from the south-western Black Sea ranged from 1.03 to 1.13 mm (with a mean value of 1.062 ± 0.031 mm) indicating the tendency of body size to increase in *A. tonsa*. In the Marmara Sea near the Bosphorus and Prince Islands body length values for females and males of *A. tonsa* did not differ significantly from those in the Black Sea (Table 1). We also found no regional differences in body lengths of females and males of *A. clausi*. During the period under study *Acartia* populations in the north-eastern Marmara Sea probably consisted of individuals which had penetrated from the Black Sea through the Bosphorus.

Acartia clausi dominates the *Acartia* genus in the off-shore Black Sea both in summer and winter (Kovalev et al., 1998). In the Marmara Sea *A. clausi* is also the most abundant species all year round (Tarkan and Erguven, 1988; Tarkan et al., 2005).

According to our results, in October 2005 the abundance of *Acartia clausi* and *Acartoa tonsa* in the Black Sea near the Bosphorus amounted to 87,263 ind. m^{-2} (1246.6 ind. m^{-3}) and 9800 ind. m^{-2} (140 ind. m^{-3}), respectively, exceeding the maximum numbers for these species in the south-western Black Sea in 1996 (Kovalev et al., 1998). This indicates favourable conditions for *Acartia* population development in October 2005 in the Black Sea. Nevertheless, in the Marmara Sea the abundance of *A. clausi* and *A. tonsa* diminished by 7.7 and 26.1 fold, respectively. A similar but less pronounced decrease in zooplankton numbers from the Black Sea towards the Marmara Sea was found by Tarkan et al. (2005) in 1999–2000. In contrast, Yuksek et al. (2002) based on the study

conducted during 1997–1998 reported higher total zooplankton abundance in the Marmara Sea compared with the Black Sea. One should take into account that these authors analysed zooplankton distribution only within the upper seasonal thermocline layer whilst in the Black Sea zooplankton aggregates mainly in the sub-thermocline deeper layers. Our study showed that simultaneously with the reduction of copepod abundance in the Marmara Sea the share of dead *A. clausi* increased and constituted 66% of *Acartia* numbers near the Prince Islands. Probably, the copepods descending below low-saline surface layers undergo severe salinity shock and die. In the Marmara Sea the maximum number of dead *A. clausi* was found in the salinity gradient layer. Furthermore, during death the mass density of *A. clausi* carcasses decreases from 1.059 ± 0.009 to 1.026 ± 0.002 g cm^3 (Stepanov and Svetlichny, 1981) which is lower than water density of the deep Marmara Sea layers (1.0296 g cm^3) with the temperature of 15.4 °C and salinity of 39.8. This may explain the reason for the aggregation of *A. clausi* carcasses in the salinity gradient layer.

Studies on zooplankton mortality have mainly focused on potential natural elimination in the populations due to predation and food availability (Heptner et al., 1990; Mauchline, 1998; Ohman et al., 2004). However, the copepods can suffer from mass mortality caused by marked changes in the environment. Tang et al. (2006) showed that in a front in the York and Hampton Rivers non-consumptive mortality of *Acartia tonsa* amounted to on average 33.8 and 28.6%, respectively, with a maximum of 53.6%. In the different regions of the Black Sea in summer 1967 zooplankton mortality varied between 25 and 20.6% whilst *A. clausi* mortality in May 1977 reached 60% in the northwestern part exposed to severe anthropogenic effects (Koval, 1984).

We suggest that mass mortality of *Acartia clausi* in the Marmara Sea in October 2005 is due to the abrupt salinity gradient (between the upper Black Sea water and deep Mediterranean Sea water), not man-made pollution, because during this period we have found low mortality in cladocerans *Pleopis polyphemoides* and *Evadne tergestina* (Svetlichny et al., 2006) which prefer surface layers. Moreover, in our experiments all *A. clausi* individuals collected in the Bosphorus Current died after gradual salinity increase from 18.9 to 39.8 over 3.5 h. The survival of *A. clausi* sampled far from the Bosphorus, near the Prince Islands was higher under short-term high salinity treatment. However, about 80% of these individuals died after being kept for one day in high-saline water.

Despite the fact that some zooplankton species possess a wide salinity tolerance range, local populations of these species cannot tolerate the whole range of salinities. *Acartia clausi* from the Gulf of Fos (French Mediterranean coast) is able to survive within the salinity range of 1–65 whilst its optimal range was between 24 and 30 (Cervetto et al., 1995). Anraku (1964) showed that acclimation success depends mainly on the gradient and rate of salinity changes. When the salinity decreased from 34.5 to 27, *Calanus* spp. from Kongsfjorden remained alive for several hours but, after a salinity reduction to 24, all individuals died within 1 h and at a salinity below 9 they all died within 15 min (Zajaczkowski and Legezynska, 2001). Therefore, the decrease in abundance and mass mortality of *A. clausi* sensitive to hyper-osmotic stress according to our results may be considered as a natural phenomenon when taking into account the extremely pronounced salinity gradient in the Marmara Sea amounting to 20 in the subsurface (20–30 m) layer.

It is however difficult to explain the dramatic decrease in abundance of *Acartia tonsa* in the Marmara Sea compared with its number in the Bosphorus Current because in our study *A. tonsa* showed higher tolerance to short-term salinity increase from 18.9 to 39.8 than *Acartia clausi*. A similar phenomenon was reported by Cervetto et al. (1999) for the northern Mediterranean, near Marseilles. Though *A. tonsa* living in the Berre Lagoon at the salinity of 10–12 were tolerant to high salinity and could withstand, at least for a period of several days, salinities higher than 35–38, they are absent in the neighboring Gulf of Fos with the salinity of 35–40 where *A. clausi* occur.

Furthermore, respiration rate (at low and high salinities) and locomotor activity in *Acartia tonsa* females were higher than in *Acartia clausi* suggesting a higher energy metabolism level and, consequently, a higher expansion potential for *A. tonsa*. In our experiments weight-specific respiration rates of *A. tonsa* females accounted for 10.95 ± 1.4 (at salinity of 18.9) and 12.10 ± 2.1 μg O_2 mg DW^{-1} h^{-1} (at salinity of 39.8) whilst for *A. clausi* weight-specific respiration rates were 7.9 ± 1.1 and 8.04 ± 0.5 μg O_2 mg DW^{-1} h^{-1} at the same low and high salinities, respectively. Similarly, respiration rates of the Black Sea *A. tonsa* (Table 2) normalized to 20 °C were consistent with early observations by Klekowski and Sazhina (1980) in the Pacific Ocean (12.3 μg O_2 mg DW^{-1} h^{-1}), the data of Kiørboe et al. (1985) (13 μg O_2 mg DW^{-1} h^{-1}) and Calliari et al. (2006) at salinity of 20 (11.5 μg O_2 mg DW^{-1} h^{-1}) for *A. tonsa* in laboratory cultures originating from the North Sea. Our findings partially disagree with the results of Calliari et al. (2006) who found higher respiration rates in *A. clausi* at a salinity of 33 (Table 3). Conover (1956), Anraku (1964) and Gaudy et al. (2000) also reported higher respiration rates in *A. tonsa* in comparison with *A. clausi*.

The frequency of jumps in *Acartia tonsa* from the northwestern Atlantic at a salinity of 22 was reported as 61.0 ± 3.4 jumps min^{-1} (Saiz, 1994) being close to the level of 69.4 ± 16.5 jumps min^{-1} for the Black Sea *A. tonsa* found in this study. According to Seregin and Piontkovski (1998), the frequency of jumps obtained during two experiments in *A. clausi* from the Black Sea at the salinity of 17–20 amounted to 36 ± 5.7 and 41 ± 5.8 jumps min^{-1} while we estimated this parameter as 39.2 ± 4.9 jumps min^{-1} for the same species.

Within the same temperature and salinity tolerance ranges, *Acartia tonsa* as an opportunistic species possessed higher clearance and grazing rates (Conover, 1956; Anraku, 1964; Tiselius, 1998), spent more time actively feeding and produced more pellets and eggs (Tiselius et al., 1997), displayed

Table 2
Respiration rate in *Acartia tonsa* from different environments and expressed as the rate per capita (Q), wet weight-specific rate (Q/WW) and dry weight-specific rate (Q/DW) at experimental temperature and normalized to 20 °C (Q_{20}/DW). Dry weight of *A. tonsa* in our experiments was calculated as $DW = 0.0134L_{pr}^3$ (Kiørboe et al., 1985). Dry weight of *A. tonsa* in the study of Klekowski and Sazhina (1980) was determined using DW = 0.2WW (our results). Dry weight of *A. tonsa* for Calliari et al. (2006) was calculated according to the equation of Berggreen et al. (1988) taking into account the prosome length values by Calliari (personal communication) and carbon content: DW ratio of 0.4. *Females collected near the Bosphorus, **Females collected near the Bosphorus and acclimated to 39.8, ***Males

Area	Temperature (°C)	Salinity	Wet weight (WW, mg)	Dry weight (DW, mg)	Q (μg O_2 ind^{-1} h^{-1})	Q/WW (μg O_2 mg^{-1} h^{-1})	Q/DW (μg O_2 mg^{-1} h^{-1})	Q_{20}/DW (μg O_2 mg^{-1} h^{-1})	Reference
Near the Bosphorus	20	18.9	0.040 ± 0.004	0.0081	0.0876 ± 0.012*	2.20 ± 0.287		10.95 ± 1.4	Present study
		39.8			0.097 ± 0.017**	2.43 ± 0.424		12.10 ± 2.1	
		18.9	0.024 ± 0.004	0.0052	0.054 ± 0.006***	2.23 ± 0.269		10.40 ± 1.1	
Northwestern Atlantic	20	30		0.0076	0.129			17.01	Conover, 1956 (Fig. 13, 19)
				0.0071	0.124			17.59	
Northwestern Atlantic	22.5	31.5		0.0099–0.0127	0.092–0.119		9.5–11.62	8.0–9.8	Anraku, 1964 (Fig. 4)
Pacific Ocean	16	35	0.023	0.0046	0.043	1.87	9.35	12.33	Klekowski and Sazhina, 1980 (Fig. 1)
Laboratory culture	18	27		0.0074	0.087		11.76	13.5	Kiørboe et al., 1985 (Fig. 6)
Mediterranean Sea	20	15		0.005	0.012			2.4	Gaudy et al., 2000
		25			0.0136			2.72	
		35			0.0202			4.04	
North Atlantic	22			0.007	0.08		11.43	9.9	Ikeda et al., 2001
Laboratory culture	20	34		0.0113	0.26			23.01	Thor et al., 2002
Laboratory culture	18	34		0.0113	0.082		7.26	8.3	Thor, 2003
Laboratory culture	18	20		0.0111			10.0	11.5	Calliari et al., 2006
		33		0.0107			5.26	6.04	

Table 3
Respiration rate in *Acartia clausi* from different environments and expressed as the rate per capita (Q), wet weight-specific rate (Q/WW) and dry weight-specific rate (Q/DW) at experimental temperature and normalized to 20 °C (Q_{20}/DW). Q_{20} is respiration rate normalized to 20 °C. Dry weight of *A. clausi* in the experiments of Pasternak et al. (1983) was calculated using DW = 0.16WW (Petipa, 1966). Dry weight of *A. clausi* in the study of Calliari et al. (2006) was determined using the equation of Uye (1982) taking into account prosome length values by Calliari (personal communication) and carbon content: DW ratio of 0.4.
*Females, **Females + males

Area	Temperature (°C)	Salinity	Wet weight (WW, mg)	Dry weight (DW, mg)	Q ($\mu g\ O_2\ ind^{-1}\ h^{-1}$)	Q/WW ($\mu g\ O_2\ mg^{-1}\ h^{-1}$)	Q/DW ($\mu g\ O_2\ mg^{-1}\ h^{-1}$)	Q_{20}/DW ($\mu g\ O_2\ mg^{-1}\ h^{-1}$)	Reference
Marmara Sea	20	23.2	0.043 ± 0.005	0.0078	0.069 ± 0.014*	1.60 ± 0.28		8.62 ± 1.5	Present study
		39.8			0.0643 ± 0.005*	1.49 ± 0.09		8.04 ± 0.5	
Near the Bosphorus	20	18.9	0.043 ± 0.006	0.0078	0.0689 ± 0.009*	1.41 ± 0.19		7.9 ± 1.1	
Northwestern Atlantic	20	30		0.0047	0.069			14.6	Conover, 1956 (Fig. 13, 19)
				0.0048	0.064			13.4	
Northwestern Atlantic	22.5	31.5		0.005–0.0086	0.048–0.092*		9.5–11.3	7.9–9.5	Anraku, 1964 (Fig. 5)
Black Sea	20.5	17–18	0.054	0.0086	0.12**	2.23		13.9	Petipa, 1966
			0.054	0.0086	0.075**	1.39		8.7	
	23		0.04	0.0064	0.069*	1.73		10.8	
Northeastern Atlantic	18	34					1.6	1.8	Champalbert and Gaudy, 1972
	21						5.48	5.1	
Mediterranean Sea	13	37		0.0132			3.99	6.5	Mayzaud, 1973 (Table 7)
Sea of Japan	14.5–16.3	32.5		0.0101	0.049		4.76	6.7	Ikeda, 1974
	15.0–15.7			0.0108	0.063		6.11	8.3	
Mediterranean Sea	20	37		0.010	0.0563–0.0907			5.6–9.1	Gaudy, 1977
Black Sea	17–18	17–18		0.008	0.065		8.1	9.7	Pavlova, 1987 (Table 24)
	17–20			0.005	0.189		37.8	41.9	
Black Sea	21–25	17–18	0.0285	0.0054	0.035–0.100*	1.23–3.51		5.2–15.1	Pasternak et al., 1983
North Sea	12.5	22–32		0.0101			9.0–32.9	15.1–55.3	Båmstedt et al., 1990
		28–32		0.0061			9.3–17.3	15.6–29.1	
Mediterranean Sea	20	15		0.010	0.018		0.018	1.8	Gaudy et al., 2000
		25			0.017		0.017	1.7	
		35			0.016		0.016	1.6	
Laboratory culture	18	20		0.0077			7.6	8.7	Calliari et al., 2006
		33		0.0079			10.0	11.5	

a higher percentage of egg hatching rate success (Castro-Longoria, 2003; Chinnery and Williams, 2004), produced more generations and underwent a shorter development time (Jeffries, 1962; Gillooly, 2000) than *Acartia clausi*. However, Paffenhöfer and Stearns (1988) demonstrated that *A. tonsa* require high food concentration in the surrounding environment. The expansion of this species may therefore be a result of the drastic increase in eutrophication over the last few decades.

Moreover, the high adaptability of *Acartia tonsa* adults is accompanied by a low salinity tolerance of the juvenile stages. Tester and Turner (1991) reported maximum survival of *A. tonsa* nauplii at a salinity of 20–25. Naupliar survival declined rapidly at salinities greater than 25 and temperatures less than 20 °C. The eggs incubated at 10 °C hatched poorly and none of the nauplii survived.

In the Black Sea during October–November when the water temperature falls below 15 °C, the number of *Acartia tonsa* sharply decreases (Gubanova, 2000). In the Marmara Sea in 1997 the last peak of abundance in *A. tonsa* was observed at the beginning of October also at 15 °C (Yuksek et al., 2002). In this period the number of *A. tonsa* was even greater than that of *Acartia clausi*. During our sampling period the surface water temperature was 18.3 °C. We cannot therefore explain the absence of *A. tonsa* from its annual development patterns. Food availability seems not to affect strongly the number of *Acartia* because phytoplankton concentration near the Bosphorus in the Marmara Sea is higher than in the Black Sea (Yuksek et al., 2002). Probably, comparative studies of salinity tolerance in *A. clausi* and *A. tonsa* during the life cycle from eggs to adults will contribute to understanding of this phenomenon.

In conclusion, in October 2005 in the northeastern Marmara Sea the populations of *Acartia clausi* and *Acartia tonsa* seem to consist of the Black Sea individuals penetrating through the Bosphorus. Near the Prince Islands the numbers of *A. clausi* and *A. tonsa* were 7.7 and 26.1 fold lower, respectively, in comparison with those in the Bosphorus region of the Black Sea. The population density of *A. tonsa* in the Marmara Sea was found to be very low, despite high levels of energy metabolism and locomotion activity in this species and the ability to tolerate sharp salinity changes from 18.9 to 38.9. Due to their narrow salinity tolerance range (according to our experimental data), *A. clausi* penetrating into the Marmara Sea generally die, and their carcasses congregates in the salinity gradient layer contributing to the dietary intake by deep-sea planktonic community.

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