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RESEARCH PAPER

Adaptive Strategy of Thermophilic *Oithona davisae* in the Cold Black Sea Environment

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Abstract

Annual dynamics of abundance and gender composition, seasonal variations in reproduction, respiration rate and locomotor activity of the new invasive cyclopoid species *Oithona davisae* were investigated in Sevastopol Bay (Black Sea) from January 2013 till July 2014. The abundance of *O. davisae* in Sevastopol Bay was highest in September – November at 15 – 23 ºC and decreased dramatically in winter – spring period at a temperature equal or less than 8ºC. From the end of February (8 ºC) till the middle of May (17.5 ºC) the population of *O. davisae* was represented only by adult females. Copepodites were observed first only when the water temperature increased to 17.5 ºC, and males appeared only in late May at 22 ºC. The revealed seasonal trends in copepod abundance and reproduction from field and experimental data suggest that winter population of *O. davisae* survives the cold season in the Black Sea at the stage of fertilized females which give the birth to the next generation in favorable spring conditions. To save energy resources, overwintering females have significantly lower temperature-related weight-specific respiration rate and moving activity than females from summer population. Such unique adaptation strategy facilitated the invasion and successful development of this thermophilic species in the cold Black Sea environment.

Keywords: Oithona davisae; adaptive strategy; population dynamics; respiration; locomotion, Black Sea

Soğuk Karadeniz Ortamına Termofilik *Oithona davisae*'nin Uyum Stratejisi

Özet

Karadeniz'de yeni yayılmacı siklopoid tür olan *Oithona davisae*'nin yıl içindeki bolluk dinamikleri, cinsiyet kompozisyonu, mevsimlik üreme ve solunum oranları ile lokomotor aktiviteleri Sivastopol Körfezi'nde Ocak 2013'dan Temmuz 2014'e kadar incelenmiştir. Körfezdeki en yüksek bolluk deniz suyu sıcaklığının 15-23 ^{o}C olduğu Eylül-Kasım aylarındadır ve bolluk, sıcaklığın $\leq$8 ^{o}C olduğu kış-ilkbahar aylarında önemli ölçüde düşer. Şubat sonundan (8 ^{o}C) Mayıs ortalarına (17.5 ^{o}C) kadar *O. davisae* populasyonu yalnızca ergin dişilerce temsil edilmektedir. Kopepoditler ilk kez su sıcaklığının 17.5 ^{o}C'ye çıktığında görülmeye başlanmıştır ve erkek bireyler yalnızca su sıcaklığının 22 ^{o}C ye ulaştığı Mayıs sonlarında ortaya çıkmıştır. Saha ve deneysel verilerden açığa çıkarılan kopepod bolluk ve üremelerindeki mevsimsel eğilim, elverişli ilkbahar şartlarında bir sonraki jenerasyonu v1erebilmek için *O. davisae* populasyonunun Karadeniz'in soğuk kış koşullarında döllenmiş dişi evresinde canlılığını koruduğunu göstermiştir. Kışlayan dişilerde, enerji kaynaklarını korumak için sıcaklıkla ilgili olarak ağırlığa mahsus solunum oranı ve hareket aktivitesi yaz populasyonuna göre önemli ölçüde düşüktür. Böyle eşsiz uyum stratejisi bu termofilik türün soğuk Karadeniz ortamına yayılımını ve başarılı gelişimini kolaylaştırmıştır.

Keywords: *Oithona davisae*; uyum stratejisi; populasyon dinamikleri; solunum; hareket, Karadeniz

Introduction

Oithona davisae Ferrari and Orsi, 1984 (Copepoda: Cyclopoida) is a new copepod species recently entered into the Black Sea presumably with ballast waters. The first few individuals of this species (ovigerous females, males and late copepodites – maximum 18 ind.m^{-3}) were found in Sevastopol Bay in December 2001 and identified initially as *Oithona brevicornis* (Zagorodnyaya 2002). However, later this species was re-examined and proved to be *O. davisae* (Temnykh and Nishida 2012). Since October 2005 *O. davisae* occurred regularly in Sevastopol Bay where its number in summer-autumn season (42667 ind m^{-3})

reached 99 % of total copepod abundance (Gubanova and Altukhov 2007; Altukhov *et al.,* 2014). In 2005 *O. davisae* was found in the north-western Black Sea (Selifonova 2011), and only in September 2009 it was registered along the Bulgarian coast of the Black Sea (Mihneva and Stefanova 2013). Small cyclopoids are the most abundant copepods (Gallienne and Robbins, 2001) and considered to be a suitable prey for the early fish larvae of numerous species (Turner, 2004; Islam *et al*., 2006). Before 1989 cyclopoid *Oithona nana*, similar in size to *O. davisae* was widespread throughout the Black Sea all year round and abundant in the surface layers. The number of *O. nana* amounted to 21000 ind m^{-3} in the open area of the Black Sea near Sevastopol (Greze *et al.,* 1971) and to 11000 ind m^{-3} in Sevastopol Bay (Gubanova *et al.,* 2001). However, *O. nana* totally disappeared from the zooplankton community in 1989 after the invasion and mass development of the predatory ctenophore *Mnemiopsis leidyi* in the Black Sea (Shushkina *et al.,* 1990; Kovalev *et al.,* 1999). *Oithona nana* was thought to have a crucial importance as a food source for many species of fish larvae due to its small size and high abundance before 1989 in the Black Sea. They constituted up to 70 % of the fish larvae ration (Tkach *et al.,* 1998), but totally disappeared from the larval guts since 1989. Disappearance of the smallest copepod fraction in the Black Sea resulted in starvation of more than 50% of the early fish larvae as was evident from their empty guts.

Further transformation of the Black Sea zooplankton community (since 1999); reduction of predator pressure due to the introduction of ctenophore *Beroe ovata* preying exceptionally on *M. leidyi* and changes in phytoplankton community structure -increase of the number of the small flagellates (Nesterova *et al.,* 2008) seemed to facilitate successful development of alien copepod *O. davisae* mainly feeding on small flagellates (Uchima 1988). However, in contrast to eurythermal *O. nana*, *O. davisae* is a thermophylic species (Uye and Sano 1995) because its maximum abundance is observed during warm seasons. Females predominate in the population of *O. davisae* in the areas of their permanent residence (the Sea of Japan) (Uye and Sano 1995, 1998) apparently due to low survival and short life duration of males. Therefore, wide distribution of *O. davisae* in the Black Sea (where salinity and inter-seasonal/average annual temperature are lower than in the Sea of Japan) seems to be the result of its life cycle adaptation to more severe environment. In the previous study (Svetlichny and Hubareva 2014) we have shown that *O. davisae* possessed a broad salinity tolerance range (3 - 40 psu).We have suggested that the maintenance of *O. davisae* population in the Black Sea during a long cold period depended on the ability of the fertilized females to keep the sperm alive in a spermatheca during long cold winter period until the spring temperature rise (Hubareva and Svetlichny 2013). Till now, the life cycle of *O.davisae* in more variable conditions and colder winters in the Black Sea (in comparison with the warmer Sea of Japan) was not investigated at all.

The main aim of present study was to enhance understanding of adaptive strategy of thermophylic *O. davisae* in the cold Black Sea environment. To achieve this goal, we studied seasonal dynamics in abundance and gender composition, reproduction and respiration rates, and locomotor activity of *O. davisae* in Sevastopol Bay (the Black Sea). In order to assess the ability of *O. davisae* females to survive in fertilized state during long cold period and to give the birth to a new spring generation without males, we studied the effect of temperature on their reproductive activity and the length of low-temperature exposure on the delay of viable eggs laying in the long-term laboratory experiments.

Materials and Methods

Sampling

To study seasonal abundance of *O. davisae,* zooplankton samples were collected weekly by integrated horizontal tows of 20 m from the depth of 0.5 – 1.0 m with a speed of about 0.5 m s^{-1} by a plankton net (mouth diameter 0.3 m, mesh size 100 μm; volume of filtered water 1.43 m^{3}) from 14 January 2013 to 27 January 2014 at the permanent station (station 1; depth 3 m) located opposite the exit of Sevastopol Bay near the Institute of Biology of the Southern Seas (IBSS) embankment. The seawater temperature of the sampling date was recorded.

The samples were concentrated in 20 mL volume beaker using an inverse filtration through a sieve (mesh size 20 μm). Immediately after filtration the number of dead specimens (immobile individuals with the signs of decomposition) accumulated at the bottom of the beaker were counted and removed. To reduce motility of alive copepods and to prevent the discharge of the ovigerous sacs, they were anesthetized by magnesium chloride solution (final concentration of 9 g L^{-1}). After that the number of alive immobile *O. davisae* copepodites (CI - CV), adults (females and males), the number of ovigerous (with ovisacs) females and the number of eggs in the both egg sacs (clutch size) were counted in all samples, or 1/4 – 1/12 subsamples (depending on the abundance of animals, but not less than 200-300 individuals in each subsample) using Bogorov chamber under dissecting microscope. Nauplii of *O. davisae* were not counted as they were not retained quantitatively by the used net. Total number of *O. davisae* was calculated using the net retention coefficients of our plankton net for copepodites (CI - CV) and adult stages obtained in a separate experiment.

To calculate the net retention coefficients, we carried out 21 synchronous zooplankton samplings by

100 µm – mesh size plankton net tows and sea water sampling by plastic sampler of 6 L along the net track from the same depth, and compared them during May – July 2014. All available developmental stages of *O. davisae* were counted in both variants of sampling. The net retention coefficients (C_n) for copepodite stages and adults were calculated as the ratio between the number of individuals collected with the net (N_n, ind m^{-3}) and the number of organisms in the bottle container (N_b, ind m^{-3}): $C_n = N_n / N_b$.

To determine the size of copepods, the prosome length, total body length and width were measured dorsally to the nearest 5 µm in randomly selected anesthetized individuals under a light microscope using eyepiece micrometer at magnification x 210.

Sex differences of *O.davisae* at stage CV were determined similar to that in *O.brevicornis* (species with close to O. davisae morphology very close to *O.davisae*) after Uchima (1979).

To check whether our data on annual changes of abundance of copepodites and adults of *O. davisae* at station 1 obtained in 2013 - 2014 can be extended to the rest of the bay, we compared our data on interseasonal gender composition of *O. davisae* with the earlier data from the samples collected from October 2005 to December 2009 in the central point of Sevastopol Bay (station 2) known for the highest population number of this species in the area (referred as st.3 in Altukhov *et al.*, 2014). Samples at this station were taken bi-weekly by vertical hauls through the whole water column (from the bottom to the sea surface) using a Juday plankton net (mouth diameter 0.39 m, mesh size 150 µm).

Egg-Production of *Oithona davisae* Females in the Field

The average egg production rate (AEPR, eggs female^{-1} d^{-1}) *in situ* was calculated on the basis of the field net samples using the equation 6 of Uye and Sano (1995), modified from the equations 5 ($D=0.75+D_E$, where D is inter-clutch period, D_E is the embryonic development time) and 7 ($RF=OF*(D_E+0.75)/D_E$): $AEPR = CS\ OF\ TF^{-1}\ D_e^{-1}$, where CS is the clutch size (eggs female^{-1}), OF and TF are the numbers of ovigerous females and total number of females (females m^{-3}), respectively, and D_e is the time for embryonic development calculated as $D_E = 1.31\ 10^4\ (T + 12.3)^{2.6}$ (Uye and Sano, 1995, equation 4), where T is the temperature (°C).

Evaluation of Reproductive Potential of *Oithona davisae* Females in Experimental Conditions

To determine the reproductive potential of overwintering *O. davisae* females, copepods were collected from the st.1 in March 2013 at water temperature 8ºC. Vigorous and mature females without ovisacs were selected from the fresh samples and placed into the beakers (20 - 30 animals per 100 mL) filled with the 0.45 µm filtered Black Sea water (FSW) and gradually (during 1 - 2 h) acclimated to 5 different temperatures, 10, 11, 12, 16, 22, 23ºC (in 3 replicates). Females were incubated at these temperatures and at 8±0.5 ºC as a control temperature for 12 days. During the incubation, *O. davisae* were fed *ad libitum* heterotrophic dinoflagellates *Oxyrrhis* sp., and the number of females with ovisacs and the clutch size per female were monitored daily.

To assess the ability of *O. davisae* females to preserve viable sperm in their spermatheca during cold season in absence of males, females without ovisacs were selected from the field samples at the beginning of March 2014 at the ambient sea temperature of 9.5 ºC. Distributed at density of 50 individuals in 100 mL beakers (in 8 replicates), the overwintering females were incubated at 8 ºC (simulating cold season *in situ* conditions in the Black Sea) in a temperature-controlled camera under a 12 h light: 12 h dark cycle for the periods of different duration (17, 34, 56 and 71 days). We checked each beaker for survival and generative status of females every three days. Dead individuals if present were removed, and the water with food suspension was renewed. After the end of each incubation period (17, 34, 56, 71 days at 8 ºC) two beakers with copepods were used to check overwintering females for survival and possibility to realize their reproductive potential depending on longevity of exposure to low temperature conditions (8 ºC). To avoid the thermal stress, females were acclimated gradually (during several hours) from 8 to 20 ºC and, thereafter were incubated at 20 ºC in thermostatic chamber. From the start of incubation at 20 ºC the generative status of females was checked daily till appearance of the first ovisacs. The females with ovisacs were gently removed and transferred individually to separate beakers where they were observed daily till hatching of the viable nauplii from their ovisacs.

Measurements of Respiration Rate of Active and Anesthetized Females

To compare the respiration rate of *O. davisae* overwintering females and those from summer population, the experiments were conducted on individuals collected at the st. 1 in the morning during March and August 2012. Prior to the experiments, actively swimming females without ovisacs were separated from the samples and placed into 100 mL beakers containing the aerated FSW of ambient temperature (8 º and ~ 25 ºC in March and August, respectively). Respiration rate (R, µgO_2 ind^{-1} h^{-1}) of copepods was determined using closed sealed chamber method, with all-glass experimental and control syringes used as the respirometers of 1.0 mL. About 60 - 80 active or about 100 anesthetized by MS-222 females were gently transferred by a pipette into an experimental syringe (filled with the FSW) supplied by protective sieve disc (mesh size 100 µm) at the confluent outlet. In order to obtain identical oxygen, salinity and seston content, we connected the control and experimental syringes with a plastic tube and pumped the water through it back and forth several times. Then the syringes were separated, closed by the stoppers and placed into the chamber with constant temperature. Incubation periods were about 2-3 and 3-4 h for active and anesthetized females, respectively, depending on experimental temperature. Incubation periods were as short as was consistent with a high analytical precision. We used short exposures (2-4 hrs) in the experiments because the significant decrease of respiration rate (in comparison with the first hours after the capture of copepods) during long-term exposures (8 – 40 hrs) was reported (Krishnaswamy 1959; Castellani and Altunbaş 2014) and also in order to prevent accumulation of metabolic products in the respirometers. At the end of the exposure, the water sample from experimental or control syringe was transferred to the small measuring flow chamber joined to luminescent dissolved oxygen sensor Hach LDO^{TM}.

To study the effect of temperature on the respiration rate of overwintering *O. davisae* females, the copepods collected at 8 ºC were acclimated gradually to 18 and 20, and then to 28 ºC during 24 h. To compare effect of short and long acclimation on respiration rate, the respiration rate of overwintering *O. davisae* was measured after one week of acclimation to 18 ºC in a separate experiment.

Swimming Activity

To determine the frequency of jumps per minute, freshly collected females in March and August were transferred into 100 mL beakers with FSW containing *Oxyrrhis* sp. *ad libitum*. After 24 h acclimation to 20 ºC, 10 active individuals (in 3 replicates) were transferred into 2 mL flat bottle with FSW and kept during about 0.5 h in the light for acclimation before the video registration. Lateral illumination from a 5 W light-emitting diode was guided through a collimator lens, antiglare shield and the aquarium towards the camera Nikon 1 V1, and copepods were video recorded at a rate of 30 frames s^{-1} during 5 min and 1200 frames s^{-1} during 3.3 s. Jumps frequency values for each individual was calculated basing on the total number of jumps for 5 min of exposure (at a rate of 30 frames s^{-1}) were multiplied by mean number of locomotor cycles in one jump determined by high speed videotaping (1200 frames s^{-1}). To study the crowding effect on moving activity, 1, 6, 16, 40, 60 and 80 females were placed into 1 mL flask and video recorded during 5 min at room temperature of 25 ºC. Jump frequency was measured for all individuals when the density was less than 10 ind mL^{-1}; and for randomly selected 10 animals when the density was higher than 10 ind mL^{-1}, in all cases minimum 10 animals were tested for jump frequency.

Statistical evaluation of data was conducted by 1-way analysis of variance and Student's *t*-test. Values presented in the figures and tables are means ± SD.

Results

Selective Retention of *Oithona davisae* Copepodite Stages by the Net Used

Mean net retention coefficients (C_n) for *O. davisae* females (prosome width 143 ± 4 µm) and males (prosome width 147 ± 14 µm), and copepodites V (CV) females (prosome width 126 ± 3 µm) and males (prosome width 138 ± 5 µm), calculated from the comparative synchronous net tows and sea water sampling by plastic sampler along the net track from the same depth carried out in 2014 (range of *O. davisae* population density of 3000 - 20000 ind m^{-3}) were 0.89 ± 0.3 for adults and 0.85 ± 0.3 for CV (Figure 1). For copepodites III and IV with the prosome width of 80 – 120 µm, C_n was significantly lower ($p < 0.05$, $n = 21$) (0.47 ± 0.2 and 0.57 ± 0.25, respectively). Mean C_n for copepodites I and II

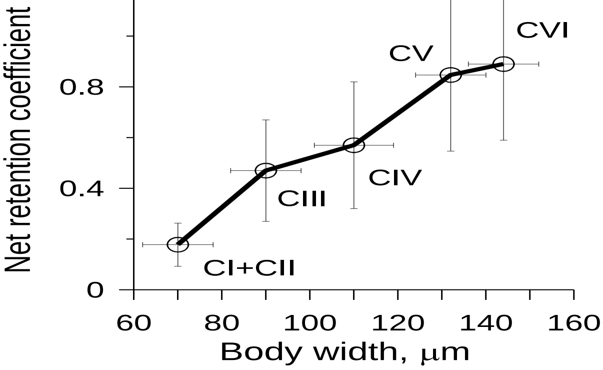

Figure 1. Net retention coefficients of *Oithona davisae* copepodite stages collected by the plankton net with the mesh size of 100 µm.

(prosome width of 60 – 80 μm) was found to be 0.17 ± 0.08.

Seasonal Variations in Abundance, Age and Sex Composition

In 2013 two main peaks of *O. davisae* abundance were observed (both about 35000 ind m^{-3}) at station 1, in the beginning of September and during October-November (Figure 2 A). Highest abundance (peaks) was associated mainly with high contribution of the earlier copepodites, CI - CIV accounting up to 96 % of the total number of *O.davisae* (Figure 2 B). In contrast, the decrease in *O. davisae* abundance was associated with the increase in relative abundance of females. In winter, when the sea water temperature decreased to 7 - 8 ºC, the share of females increased gradually within a month period, constituting from 42 % (14 January 2013) to 100 % (27 February 2013), and during the same period the share of males and copepodites I-V decreased from 19 and 39 %, respectively, to zero, and thereafter, the latter were totally absent from the winter - early spring samples. After a cold period, the copepodite stages were first observed only on 13 May when water temperature increased to 17.5 ºC, while the first males were found in the samples on 27 May 2013 at 22ºC in the post-overwintering population. The mean sex (male : female) ratio at CV stage (during the presence of this stage in *O. davisae* population) was 0.98 ± 0.26 (from May till December). However, the mean sex ratio of adults during the period of presence of both adult sexes in *O. davisae* population (from May till December). amounted to 0.24 ± 0.19 with two peaks in June (0.49 ± 0.22) after the appearance of males in the population, and in December (0.36 ± 0.12) prior their disappearance from the overwintering population due to their short life span (Kiørboe, 2007).

Similar seasonal trends in *O. davisae* were found during the winter – spring period of 2005 – 2009 (Figure 3) in the middle part of Sevastopol Bay where this species had the highest abundance (Altukhov *et al.*, 2014). From December to the end of February 2005 - 2009 when average monthly temperature decreased from 7.7 ± 1.6 to 6.2 ± 1.1ºC (Figure 3 A), the share of females in total population number increased from 69.8 ± 6.4 % to 100 %, whilst the share of males and copepodites V (22 ± 6 and 8 ± 6 %, respectively) declined to zero and completely disappeared from the population (Figure 3 B). Thereafter, in March and April *O. davisae* population consisted exceptionally of females (up to 2492 ind m^{-3} in March and April 2009). Through 2005 – 2009 males and V copepodites of *O. davisae* were registered first only in May. During January - April 2013 the egg-carrying females occurred rarely, however, at the end of March the share of females with the ovisacs containing 4.5 ± 2 eggs increased up to 25 % of the total number of females (27 ± 13 ind m^{-3}) (Figure 4 A, B). The first annual peak of ovigerous females (50 % of total female number) with the clutch size of 12 ± 3 eggs was recorded on 13 May. Maximum clutch size of 20 ± 7 eggs was observed during the period from the end of May till the end of July within the temperature range from 22 to 25 ºC. In August we found significant decrease in clutch size (12.4 ± 2.5 eggs) while the temperature increased up to 27 ºC. From October to December 2013 the temperature dropped from 20 to 9 ºC, and the clutch size decreased from 14.2 ± 2.5 to 4.2 ± 2.0 eggs. Maximum egg production rate up to 6 eggs female^{-1} day^{-1} was observed during the period from late May till start of August at temperatures 22 - 27 ºC (Figure 4 C). We recorded maximum share of dead

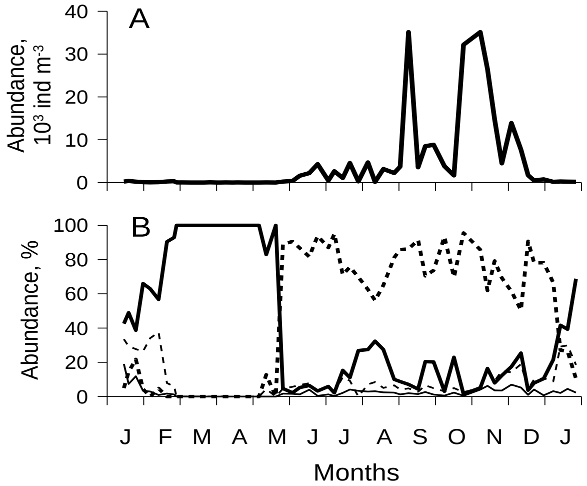

Figure 2. Seasonal variation in total abundance (A) and share (B) of copepodites I-IV (bold dashed line), copepodites V (thin dashed line), females (bold solid line) and males (thin solid line) of *Oithona davisae* in Sevastopol Bay at the station 1 in 2013.

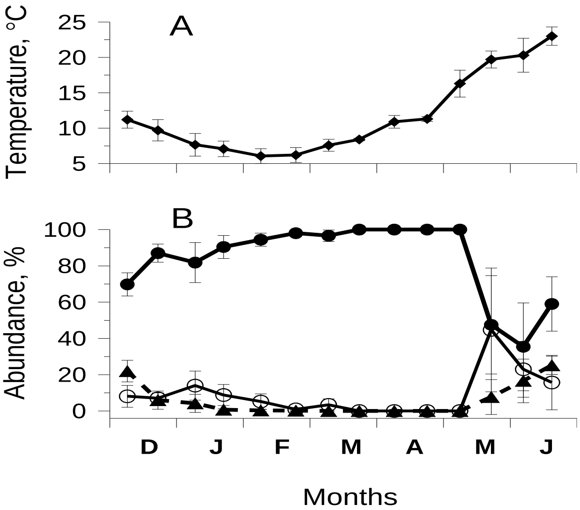

Figure 3. Seasonal variation in average annual temperature (♦, diamonds, solid line) (A) and the share of females (●, shaded circles), copepodites V (○, open circles) and males (Δ, triangles) of *Oithona davisae* in the central part of Sevastopol Bay (Altukhov et al,, 2014, station 3) during December – June 2006 -2009 (B).

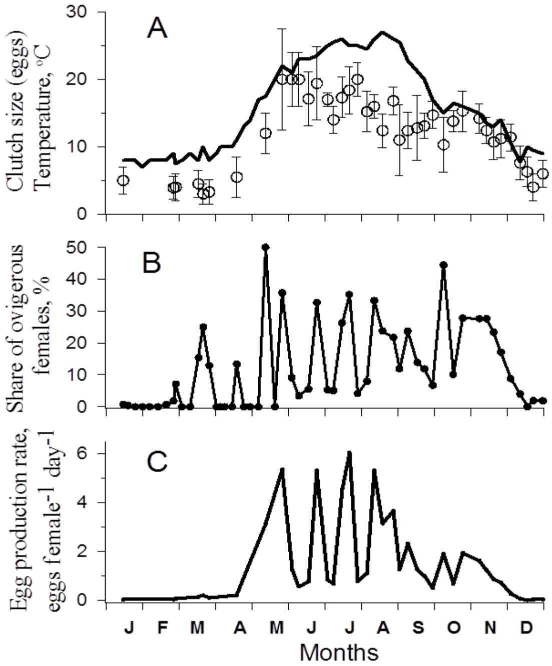

Figure 4. Seasonal variation in temperature (solid line) and clutch size (○, open circle) (A), share of ovigerous females (B) and egg production rate (C) of *Oithona davisae* in Sevastopol Bay at the station 1 during 2013. A: Temperature curve is denoted by solid line.

females (up to 18 % from the total number total abundance of this fraction) in October and December 2013 whilst the annual average value of dead individuals in the sample was about 6.3 ± 5 %. The maximum share of dead males was recorded in January and December 2013 (37 and 11 % of total abundance of males, respectively).

Effect of Temperature on Egg Production of Overwintering Females

When females collected in March 2013 at the sea temperature of 8°C were transferred to higher temperatures, they began to produce the eggs resulted in hatching of viable nauplii. Reproductive index as a share of ovigerous females (RI, %) positively correlated with temperature (Figure 5 A) following the equation: $RI = 5.6 * T - 46.2$ ($n = 27$, $r^2 = 0.81$). The duration from the beginning of reproductive activity up to maximum RI was also dependent on the temperature. No ovigerous females were recorded throughout the exposure at 8 and 10°C. Females transferred from 8 to 11 and 12°C began to produce egg sacs on days 5, 6 and maximum RI = 22 ± 17 %

was reached on day 12th. When females were transferred from 8 to 16 ºC, maximum RI 20 – 70 % was achieved between the days 3 and 8 whilst those transferred to 22 - 23ºC increased RI up to 60 – 97 % during the same period. Average clutch size, 4.4 ± 1.4 eggs female^{-1}, was not temperature-dependent.

After 17 days of incubation at 8ºC without males, up to 85 ± 13 % of females started production of eggs after temperature increase up to 20ºC. In case of the long-term exposures at 8 ºC during 34, 56 and 71 days, the maximum observed number of ovigerous females after the increase of temperature to 20 ºC was 57 ± 19, 87 ± 9 and 47 ± 12 %, respectively (Figure 5 B). The number of eggs in the ovisacs varied from 1 to 9 (mean value of 4.1 ± 1.5) and was independent of the duration of exposition at 8 ºC. In all experiments females began to lay eggs on the day 2 - 3 after the increase of temperature from 8 to 20 ºC, and the viable nauplii hatched on day 5. The mean mortality of females during low-temperature (8 ºC) exposures constituted 13 ± 8 % and was similar even after the temperature increase to 20 ºC. The high mortality was observed only in case of the longest exposure (71 days), where 80 % females died 5 days after the rise in temperature.

Respiration Rate in Spring and Summer Females

Respiration rate (R) of females collected in March was 0.00219 ± 0.00044 μg O_2 ind^{-1} h^{-1} at 8 ºC and increased up to 0.00925 ± 0.0020 μg O_2 ind^{-1} h^{-1} at 28 ºC (Figure 6) in accordance with the equation: $R = \exp(0.072 * T) * 0.0012$ ($r^2 = 0.81$). Within the range of 8 - 28ºC the average Q_{10} value amounted to 2.06 ± 0.18. Respiration rate of females from spring generation collected at 8ºC and acclimated during 24 h and one week to 18ºC did not differ significantly ($p < 0.001$). Respiration rate of anesthetized individuals collected from natural spring population and acclimated gradually to 18ºC (0.00135 ± 0.0003 μg O_2 ind^{-1} h^{-1}) was 3-fold lower than that of active copepods (Table 1). Respiration rates of females from summer population and that of spring females (both acclimated to 20ºC) and measured at the same temperature did not differ significantly. However, weight-specific respiration rate of summer females was significantly ($p < 0.05$) 1.32-fold higher than that of spring females because of the differences in body size and weight (see Table 1). The ratio between total and basal metabolism of both summer and spring females amounted to 3.

Moving Activity of Females from Spring and Summer Populations

General motility pattern in undisturbed active females of *O. davisae* included sinking with ventral side down and upward jumps. Each jump consisted of 1 - 5 multiple kicks (on average 1.2 ± 0.2) with the use of the antennules, thoracic legs and abdomen. Jump frequency distribution of spring and summer females was unimodal with strong differences in modal values (Figure 7 A). At the same density (5 ind mL^{-1}) and temperature (20 ºC) average jump frequency (37.3 ± 14.5 min^{-1}) of spring females was significantly ($p < 0.001$) lower than that of summer females (96.4 ± 16.7 min^{-1}). We recorded crowding effect in summer females at 25ºC only at the density more than 40 ind mL^{-1}, at 60 ind mL^{-1} jump frequency increased up to 210 ± 70 jump m^{-1} (Figure 7 B).

Discussion

Life Cycle of *O. Davisae* in Sevastopol Bay

O. davisae is perennial species. No records on producing diapausing eggs by cyclopoids are known (Alekseev and Starobogatov 1996). No evidence of any diapause stage exists for copepods from Oithonidae family (Marcus 1996). Therefore, population of *O. davisae* cannot be temporarily intermittent but depends on the presence of alive stages all year round, and its abundance significantly depends on seasonal temperature alterations.

Similar seasonal abundance patterns of *O. davisae* and environmental factors were observed in

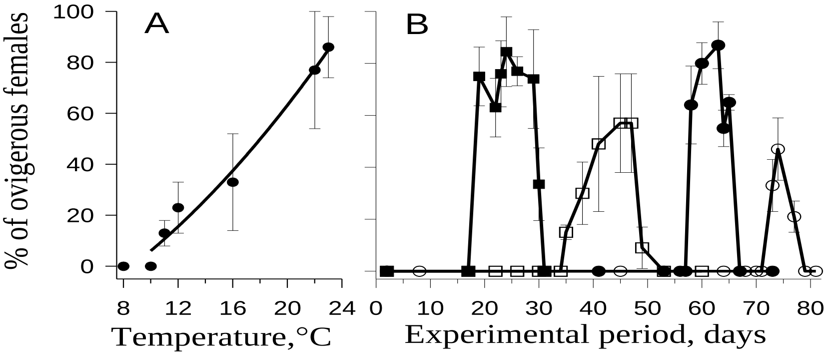

Figure 5. Effect of temperature on the reproductive activity of freshly collected overwintering females (A) and the share of ovigerous females at 20ºC after the incubation during 17 (■, shaded squares), 34 (□, open squares), 56 (●, shaded circles) and 71 (○, open circles) days at 8°C (B). All females used in experiments were collected at the beginning of March.

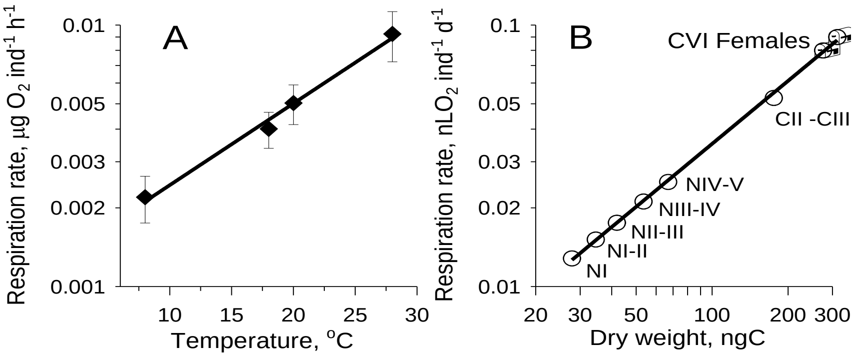

Figure 6. Effect of temperature on respiration rate of overwintering females of *Oithona davisae* (A) and ontogenetic changes of respiration rate of *Oithona davisae* (B) from nauplii through copepodite stages II and III (○, open circles; see Almeda *et al.,* 2011) till females (●, shaded circles, our data). Note. Respiration rates of nauplii, copepodites and females (R, nl O_2 ind^{-1} h^{-1}) on B were calculated in accordance with the relationship between R and carbon dry weight (CDW, ng C) following the equation: $R = 0.001\ CDW^{0.767}$ (Almeda *et al.*, 2011), where $CDW = 0.0021\ L^{2.14}$ for nauplii, L is body length and $CDW = 0.0318\ L_{pr}^{1.61}$ for copepodites and females.

Table 1. Respiration rate (R), weight-specific respiration rate (R WW^{-1}) and morphological characteristics of active and anesthetized *Oithona davisae* females collected during spring and summer periods. Values are presented as means ± SD

Total length (L), µm	Prosome length (l_{pr}), µm	Prosome width (d_{pr}), µm	Wet weight (WW), mg	Acclimation temperature ºC	Experimental temperature ºC	R, µg O_2 ind^{-1} h^{-1}	R WW^{-1}, µg O_2 mg^{-1} h^{-1}
Spring generation living at 8 ºC							
577 ± 21	303 ± 63	151 ± 9	0.00429 ± 0.00059	8	8	0.00219 ± 0.00044	0.539 ± 0.109
				8	18	0.00383 ± 0.00093	0.942 ± 0.229
				8	20	0.00504 ± 0.00087	1.237 ± 0.213
				8	28	0.00925 ± 0.0020	2.272 ± 0.494
				18[a]	18[a]	0.00401 ± 0.00058[a]	0.985 ± 0.208 [a]
				18[ab]	18[ab]	0.00135 ± 0.0003 [ab]	0.332 ± 0.075 [ab]
Summer generation living at 22 – 28 ºC							
511 ± 31	279 ± 30	132 ± 7	0.00288 ± 0.0004	20	20	0.00444 ± 0.0017	1.64 ± 0.636
						0.00149 ± 0.00016[b]	0.497 ± 0.054 [b]

[a] One week of incubation at 18ºC. [b] Anesthetized individuals.

Wet weight of a female (WW, mg) was calculated using the equation: $WW = \rho_b 0.47\ L^{0.21}\ l_{pr}^{0.93}\ d_{pr}^{1.86}$ (Svetlichny *et al.,* 2012a), where ρ_b is equal to 1.05 g cm^{-3} (Svetlichny and Hubareva 2014), L, lpr and d_{pr} are given in mm.

Fukuyama Harbor (Inland Sea of Japan) where it is considered to be aboriginal species, and in Sevastopol Bay (Black Sea) where this copepod is an alien species. In temperate Fukuyama Harbor two annual peaks (up to 5.98 x 10^5 adults and copepodites m^{-3}) were recorded for its population in June – July and September 1987 at maximum temperature of 20 - 28 ºC (Uye and Sano 1995). The mid-summer decline in *O. davisae* abundance correlated with high predation pressure of the lobate ctenophore *Bolinopsis mikado.* The similar seasonal abundance patterns was observed in Sevastopol Bay during 2013, two annual peaks of *O. davisae* number were recorded: one at the beginning of September (35147 ind m^{-3}) and the second - from 25 October to 14 November (with the maximum of 35140 ind m^{-3}). Decrease in *O. davisae* abundance during September and October 2013 was synchronized with the increase in population numbers of jellyfish *Mnemiopsis leidyi* and *Aurelia aurita* (typical for this season) in Sevastopol Bay (Anninsky *et al.*, 2013; Finenko *et al.*, 2013).

Both in Sevastopol Bay and in Fukuyama Harbor, the minimum abundance of *O. davisae* was observed between February and in the beginning of May, when the temperature was low. In Sevastopol Bay minimum *O. davisae* number ranged between 1

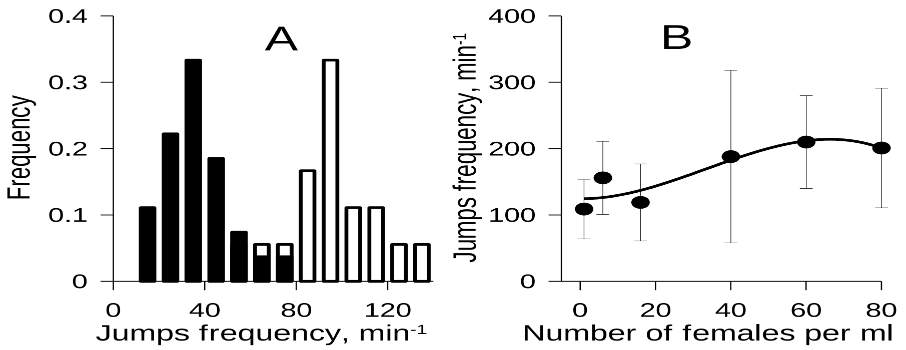

Figure 7. Frequency diagram of jump frequency in *Oithona davisae* females from spring (■, shaded squares) and summer (□, open squares) generations. Effect of crowding on jump frequency of females from summer population (B).

and 400 ind m^{-3} when the water temperature was around 6-8ºC, and in Fukuyama Harbor it was recorded up to 5 x 10^{3} ind m^{-3} when the surface temperature was around 10-13ºC. In both bays the skewed ratio for females in adult part of population of *O.davisae* was observed all year round. In Fukuyama Harbor the *O. davisae* population was mainly composed of adults (about 85 %) predominated by females during March and April (Uye and Sano 1995) while in Sevastopol Bay the population consisted of only adult females during the same period. No males were recorded in Sevastopol Bay between the end of February and the end of April in 2005 – 2009 and in 2013 while in total 64950 females were sampled during these periods. This finding cannot not be related to the catching efficiency of the nets, because the prosome width of the males and females are identical, and the escape reaction of both genders from the net are similar (Jiang and Kiorboe 2011) but can be related only to the total absence of males in winter population of *O. davisae* in Sevastopol Bay. Differences between the lowest winter temperatures in Fukuyama Harbor and Sevastopol Bay (10-13 ºC vs 6-8ºC) explain the minor presence of males and copepodites in the temperate environment of the Inner Sea of Japan and total absence of males in cold environment of the Black Sea.

The dynamics of copepodites and adults fractions in 2013 (Figure 2 B) indicated three periods of *O. davisae* population development in Sevastopol Bay. During the first, winter-spring (mean surface temperature of 8.4 ± 0.8 ºC) period males and copepodites disappeared, and only overwintering females remained in population. The elimination of males was accompanied by high share (up to 37 % of their abundance of their empty carcasses in Sevastopol Bay. The second, spring–summer period, from the middle of May to the middle of August (mean temperature 23.6 ± 2.6 ºC) was characterized primarily by the increase in the share of copepodites, up to 93.6 % and then by the increase in the share of females up to 32.4 % at low average density of *O.davisae* - 420 – 2200 ind m^{-3}. During the third period, from the middle of August till the end of December, the abundance of this species varied from 1700 to 35000 ind m^{-3} with high share of copepodites (85 ± 9 %). From May till December 8 pronounced peaks in number of ovigerous females with mean periodicity of 25 ± 5 d were observed (Figure 4 B), presumably corresponding to the number of generations of population during the reproductive period of *O. davisae*. In Fukuyama Harbor the share of ovigerous females in *O. davisae* adult part of population also varied greatly all year round (Uye and Sano 1995), but they did not show such pronounced periodicity in the share of ovigerous females as we found in Sevastopol Bay where the development of *O. davisae* is strictly synchronized with the temperature.

To our knowledge, this is the first study that proves the possibility of the long-term preservation of viable sperm after mating by overwintering *O. davisae* females in natural environment. Earlier the possibility to produce viable eggs in several months after fertilization was shown in diapausing females of *Cyclops strenuus* (Næss and Nilssen 1991) and harpacticoid copepod *Harpacticus uniremi* (Jewett and Feder 1977). Cyclopoid females as a rule need to be fertilized only once in the lifetime (Smyly 1970), and there is no evidence of any diapauses stage in cyclopoids (Alekseev and Starobogatov 1996; Marcus 1996).

We suggest that *O. davisae* population survives cold season in the Black Sea at the stage of fertilized females (Hubareva and Svetlichny 2013) basing on the fact that about 97 % of overwintering females started to produce viable eggs within 2-3 days after the transfer from the ambient sea water (8 °C) to the warm water (22 – 24ºC) (Figure 5 A). Females of *O. davisae* were found to live up to 80 - 120 days and to spawn eggs during 30 days after only one mating at 20°C in laboratory experiments (Ceballos and Kiørboe 2011). Consequently, at lower temperature of the Black Sea, the period of preservation of viable sperm after mating could be longer than that in the experiments of Ceballos and Kiørboe (2011). The long preservation of alive sperm by fertilized

O.davisae was proved also by the fact that according to our experimental results, 87 and 47 % of females collected in March at 8ºC and exposed in experimental conditions to prolonged (56 and 71 days, respectively) incubation at 8ºC were able to produce viable eggs.

However, in spite of high share of breeding overwintering females, their clutch size and egg production rate were low (about 4 eggs female^{-1} and 0.11 eggs female^{-1} day^{-1}, respectively), both in freshly collected *O. davisae* from the sea, and under experimental conditions where copepods fed *ad libitum*. The most probable explication of low egg production rate in overwintering females was their age (since they arrive in population in early winter, and the experimental results of Ceballos and Kjorboe (2011) proved our suggestion as they observed significant reduction in females reproduction rate from 15 days old onwards. On the contrary, in females developing in Sevastopol Bay in summer-autumn natural populations, clutch size and egg production rate reached 19.4 ± 5.5 eggs female^{-1} and 6 eggs female^{-1} day^{-1}, respectively, which however were 1.5 and 2 times, correspondingly, lower than maximum clutch size and egg production rate in *O. davisae* from Fukuyama Harbor (Uye and Sano 1995). The differences in fecundity of females from different environments may be due to different feeding conditions. However, our field and experimental data were in accordance with both production parameters of *O. davisae* from continuous in laboratory growth experiments of Zamora-Terol and Saiz (2013).

Therefore, since the last males of winter generation were observed on 25 February 2013 at 8°C, we assume that the first copepodites of spring generation collected in the sea on 13 May (in 76 d) originated from the eggs of overwintering females fertilized before the disappearance of males.

Respiration rate of *O. davisae* from spring and summer generations

Only few studies were devoted to respiration rates of adult *O. davisae*. Nakata and Nakane (1987, cited in Castellani *et al.*, 2005), reported respiration rate of *O. davisae* as 0.56 µl O_2 µgC^{-1} day^{-1} at 25 °C. Using gradient diver respirometer system, Hiromi *et al.*, (1988) found respiration rate of *O. davisae* adults (usually females) ranging from 4.6 to 5.9 nl O_2 ind^{-1} h^{-1}, or 0.35 – 0.48 µl O_2 µgC^{-1} day^{-1} at any temperature in wide temperature range. Later, metabolic rate of this species was determined using the Winkler method (Hiromi 1994), and at 20 °C respiration rate it was found 1.6-fold higher than that reported by Hiromi *et al.*, (1988). Nevertheless, in both studies respiration rates of *O. davisae* were almost constant within the range of 10 – 30 °C.

In our experiments respiration rate of overwintering females in temperature range from 8 to 28 °C increased from 0.0022 to 0.0092 µg O_2 ind^{-1} h^{-1}, with theoretically valid values of Q_{10} = 2.06 ± 0.18. Close temperature coefficients for respiration were obtained in the experiments on early developmental stages of *O. davisae* (Almeda *et al.*, 2010) and on other copepods (Ikeda *et al.*, 2001; Castellani and Altunbaş 2014 ; Svetlichny *et al.*, 2010).

Maximum weight-specific respiration rate of *O. davisae* summer females amounting to 0.42 µl O_2 µg C^{-1}day^{-1} in our experiments were close to the magnitudes obtained for other species of the genus *Oithona* (see Castellani *et al.*, 2005). According to our results, respiration rates of summer *O. davisae* females conformed to the general scaling relation to body carbon weight obtained for early development stages of *O. davisae* in the experiments of Almeda *et al.*, (2011) with theoretically valid slope of 0.78 (Figure 8 A). Based on comparative estimations of metabolic rates of different copepods, the metabolic requirements in *Oithona* genus were suggested lower than those in calanoids with the same body weight (Lampitt and Gamble 1982; Paffenhöfer 1993; Castellani *et al.*, 2005; Almeda *et al.*, 2011). Actually, the carbon body weight of *O. davisae* summer

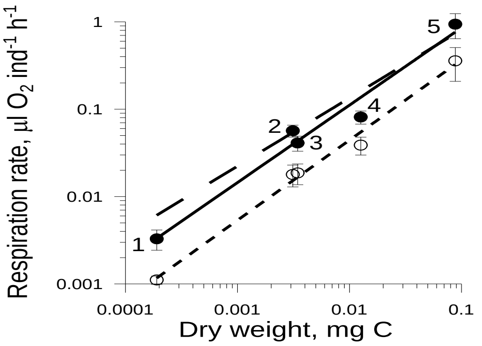

Figure 8. Respiration rate (R) of *Oithona davisae* and other Black Sea copepods at 20°C: 1 - *Oithona davisae* (our data); 2 – *Acartia clausi* (Hubareva et al., 2008); 3 - *Calanipeda aquaedulcis* and 4 – *Arctodiaptomus salinus* (Svetlichny et al., 2012b); 5 – *Calanus euxinus* (Svetlichny et al., 2010). Solid line and shaded circles and dashed line and open circles show total metabolism and basal metabolism of copepods, respectively. Long dashed line shows the relationship between R and carbon dry weight of calanoid copepods according to the equation: lnR = 0.124 + 0.78lnCDW + 0.073T, where T is temperature (Ikeda et al., 2001).

females calculated from its size according to the equation of Uye and Sano 1995) was 0.19 µg C. Respiration rate of calanoid copepods with carbon body weight of 0.19 µg C following the equation of Ikeda (2001) at 20°C should be 6.1 nl O_2 ind^{-1} h^{-1} (Figure 8). Such respiration rate is about 2 times higher than the magnitude obtained for *O. davisae* in our experiments (3.3 ± 1.2 nl O_2 ind^{-1} h^{-1}). However, taking into account the difference in the used methods and in physiological state of animals, those differences may be insignificant. It should be noted also that crowding effect in O. davisae in our short-term experiments does not decrease the respiration rate of *O. davisae*. At least, in the Black Sea total respiration rates of cyclopoid *O. davisae* (summer generation) and calanoid *Acartia clausi* (Hubareva *et al.,* 2008), *Calanipeda aquaedulcis, Arctodiaptomus salinus* (Svetlichny *et al*., 2012b) and *Calanus euxinus* (Svetlichny *et al.,* 2010) fit a power regression model (Figure 8) approximated as $R = 6.2\ CDW^{0.87}$. The ratio between total and basal metabolism of cyclopoid *O. davisae* (3.0) was as high as in calanoids *A. clausi* (3.2) and *C. euxinus* (2.6). The difference between total and basal metabolism of *O.davisae* corresponded to sufficiently high (about medium) of their activity but does not reach the critical level when the ratio between the total and basal metabolism increase to 6 (Svetlichny and Umanskaya 1991; Buskey 1998). While *O. davisae* is considered a thermophilic (Uye, Sano, 1995) copepod, females of this species in Sevastopol Bay can withstand broad interseasonal variations in temperature from 5 – 8 °C in cold period to 26 – 28 °C in summer. In accordance with the temperature coefficient Q_{10} of 2.06 obtained from our experimental results, the respiration rate of *O. davisae* females during the cold period should be expected 4-5 times lower than that during the warm period. However, we revealed the more significant than expected shift in metabolic rate of overwintering females, which involved a further half-fold reduction in weight-specific respiration rate in comparison with that in summer females at the same experimental temperature (Table 1). This finding indicates the ability of females of this species to survive winter in a state of reduced metabolic activity which is similar to metabolic arrest, manifested in diapausing stages of some species of marine pelagic copepods (Svetlichny *et al.,* 1998, Auel *et al.,* 2005).

Swimming Activity

All types of swimming movements observed in *O. davisae* females (Uchima and Hirano 1988) are based on jumping mode resulting from the backward kicks by antennas, swimming legs and abdomen (Kiorboe *et al.,* 2009) Therefore, the frequency of repositioning jumps is considered to be an adequate characteristic of moving activity in this species. In our study jump frequency of overwintering females acclimated during one week to 20 °C at density 5 ind mL^{-1} was about 3-fold lower (37.3 ± 14.5 min^{-1}) than that in summer copepods (96.4 ± 16.7 min^{-1}) at the same temperature (Figure 7 A) and close to jump frequency of *O. davisae* females at 20 – 22 ºC in the studies of Uchima and Hirano (1988) and Heuschele and Kiorboe (2012) amounting to 35 – 48 min^{-1} and 57.9 min^{-1}, respectively. In our opinion, the inability of overwintering females *O. davisae* to increase the locomotor activity to the level of summer females with the temperature increase confirms our hypothesis about the metabolic shift allowing this thermophilic copepod to survive during the cold season. To increase measurement accuracy, the copepods were crowded artificially in our small respiration device, and that raises the question of the impact of crowding on our data. Special observations showed that the behavior (jump frequency) of *O. davisae* females remained unchanged in the density range of 1 - 40 ind mL^{-1} similar to the observations of Uchima and Hirano (1988). However, at the higher density (up to 80 ind mL^{-1}) the activity of *O. davisae* sharply increased due to the increase in frequency of the contacts between the individuals. In order to provide the required accuracy of measurements, in our respiration experiments we used the copepod density of 60 – 80 ind mL^{-1}. Consequently, taking into account high (3:1) ratio between total and basal metabolism, we suggest that the crowding did not reduce respiration rate of *O. davisae* in our experiments.

Conclusion Remarks

The invasion, successful establishment and expansion of thermophilic copepod *O. davisae* in the cold Black Sea is evidence of extremely high adaptive plasticity of this species. In fact, the specimens of *O.davisae* within the salinity tolerance range of 3 – 40 ‰ have constant body volume and mass density that indicates their ability to osmoregulate (Svetlichny and Hubareva 2014). In order to overcome unfavorable conditions, the females of this species can keep viable sperm in a spermatheca for a long period of time (according to our observations, up to 2 months after mating) and lay fertilized eggs after the increase in water temperature. The ability to reduce energy metabolism and locomotor activity facilitates the survival of *O. davisae* females during the cold season and, probably, during low food availability period. In general, high adaptation potential of females of *O. davisae* may promote a successive distribution of this species via ship ballast water in the estuaries with low salinity and temperature. In 1979 *O. davisae* was reported to be introduced from the western Pacific in the San Francisco Estuary (Ferrari and Orsi 1984) and in 1980 in the Chilean fjords (Hirakawa 1988). This species was found and established in the Mediterranean (Saiz *et al.,* 2003) and in the Black (Zagorodnayaya 2002; Gubanova *et al*., 2007;

Altukhov *et al*., 2014) Seas. It was registered for the first time in October 2010 in the northern Wadden Sea (the Northern Sea), and now became a permanent plankton species of this region (Cornils and Heckmann 2015). Therefore, the expansion of *O. davisae* through ballast waters continues at the present time. Cordell *et al.*, (2008) studied plankton samples collected from the ballast water of ships arriving to Puget Sound (Washington, USA) and found the number of *O. davisae* to be about 7000 ind m^{-3} in 80 % of samples (Lawrence and Cordell 2010). Successful establishment of *O. davisae* to the Black Sea seems to be related to phytoplankton structure changes including a prevalence of small flagellates due to climate-driven effects (Nesterova *et al.*, 2008; Mavrodieva 2012). Similar shift in phytoplankton dominance from diatoms toward small flagellates recorded in Tokyo Bay in 1960 brought to changes in the size structure of the copepod community in the 1970s from relatively large *Acartia omori* (referred as *A . clausi*), *Micrisetella norvegica* and *Paracalanus* sp. to small *O. davisae* (Uye 1994).

At present *O. davisae* successfully compete with larger copepods *A. tonsa* and *A. clausi* in Sevastopol Bay. *Oithona nana* (of the similar size and same feeding spectrum as *O. davisae*) previously having been inhabiting the Black Sea occurs nowadays in the neighboring Marmara Sea (Isinibilir *et al.,* 2008) and in the Bosphorus Strait (Isinibilir *et al.,*, 2011). This native Oithonidae species was found occasionly in some zooplankton samples in the Black Sea in 1997 (Kovalev *et al.,* 1999) and even during last years (Yu. Zagorodnyaya, pers. com.) but some reasons prevent it to occupy its former ecological niche and achieve a high population number. Therefore, still it is not clear why *O. davisae* successfully occupied the ecological niche of disappeared earlier *O. nana*, while the latter is not successful to return, and this question awaits further study.

Acknowledgements

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