

Population dynamics of the copepod invader *Oithona davisae* in the Black Sea

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Abstract: During 2013–2016 in Sevastopol Bay, seasonal and interannual dynamics of the population density, age and sex composition, fecundity, and mortality of males and females of *O. davisae* were studied. A maximum population number (up to 554 ind × 10³ m⁻³) was registered at the end of summer–end of autumn. In this period, the nauplii and early copepodite stages constituted up to 95% of the *O. davisae* population. During 1–2.5 cold winter–spring months, the population consisted only of females, who were not numerous. The phase of latent population development was recorded from April until July–August, with a high share of ovigerous females, maximum clutch size, and high egg production rate but low population density, which may be due to predator pressure from lobate ctenophores. The average share of adult males amounted to 32% at the end of spring and 27% at the beginning of winter, while the share of dead males reached maximum values (20.7%) during the winter degradation period for the population. On the basis of the studied successions of the population's developmental stages, from ovigerous females through nauplii and early copepodites to adults, the number of generations produced by *O. davisae* during the reproductive period (10–11) was determined.

Key words: *Oithona davisae*, population dynamics, generation time, life cycle, egg production, Black Sea

1. Introduction

Oithonids are small cyclopoid copepods under 1 mm in size that are distributed throughout the world's oceans (Nishida, 1985). They are primary consumers in marine ecosystems and provide a food source for higher trophic-level animals. *Oithona davisae* Ferrari and Orsi, 1984 occasionally inhabits eutrophic bays and coastal areas (Nishida, 1985; Uye and Sano, 1995). Although it is indigenous to the seas of Japan and China and other coastal areas (Hirakawa, 1988), it is an invasive species along the west coast of the United States (Ferrari and Orsi, 1984).

Oithona davisae (Copepoda: Cyclopoida) is an alien species recently introduced to the Black Sea. Several specimens were first found in Sevastopol Bay in 2001 (Zagorodnaya, 2002). Since 2005, this species has been routinely observed and has even dominated (during warm seasons) in Sevastopol Bay and the nearest coastal ecosystems (Gubanova and Altukhov, 2007; Selifonova, 2009; Altukhov et al., 2014). It was registered later along the Romanian (Timofte and Tabarcea, 2012), Bulgarian (Mihneva and Stefanova, 2013), Georgian (Shvelidze, 2016), and Turkish (Üstün and Terbiyik Kurt, 2016; Yıldız et al., 2017) coasts of the Black Sea. In 2014, *O. davisae* was first found in the subsurface layers of the Sea of Marmara,

which are formed by Black Sea water (Doğan and İşinibilir, 2016). The assumption that *O. davisae* has been transferred from the Black Sea to the Sea of Marmara can be confirmed by the coincidence of morphological and physiological characteristics of females; in addition, the same population structure of this species was synchronically studied in both seas (İsinibilir et al., 2016). Since *O. davisae* did not occur in European seas until 2003 (Saiz et al., 2003), one can suggest that the species was transported into the Black Sea with ship ballast waters, probably from southeastern Asia (Gubanova et al., 2014), where this copepod is prevalent (Ohtsuka and Nishida, 2017). Despite the fact that *O. davisae* is a warm-water species (Uye and Sano, 1995), it has successfully acclimatized in the cold Black Sea due to its ability to survive low temperatures in the state of fertilized quasi-diapausing females (Hubareva and Svetlichny, 2013; Svetlichny et al., 2016), which can produce a new generation after the spring rise in temperature. The periods of seasonal succession of the *O. davisae* population in Sevastopol Bay were determined by Altukhov et al. (2014), Seregin and Popova (2016), and Svetlichny et al. (2016). The first period, from the middle of May until August–September, was characterized by an increase in the percentage of offspring at a low

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population density for *O. davisae*. During the second later summer–autumn period, the abundance of this species reached the maximum value; during winter–early spring, the population density sharply decreased. It was shown that exclusive use of plankton nets did not allow proper analysis of the population dynamics of the small cyclopoid *O. davisae* due to pronounced underestimation of the number of early copepodite stages (Svetlichny et al., 2016). A quantitative analysis of the abundance of nauplii may only be carried out by using bottle sampling.

In the present paper, the results of long-term (2013–2016) weekly studies of the dynamics of all developmental stages of *O. davisae*, sex composition of late developmental stages, fecundity, and mortality in Sevastopol Bay are reported. On the basis of these field data, an attempt to reveal the main seasonal and interannual relationships of population dynamics and to determine the duration and number of generations produced by *O. davisae* during the year was made. Adaptive changes in the life cycle of this species after its introduction into the Black Sea are discussed.

2. Materials and methods

2.1. Sampling

Zooplankton samples were collected weekly by integrated horizontal tows of 20 m in warm seasons and 40 m in cold seasons, from a depth of 0.5–1.0 m with a speed of about 0.5 m s^{-1} using a plankton net (mouth diameter 0.3 m, mesh size $100 \mu\text{m}$) from 14 January 2013 until 27 December 2016 at a permanent station with a depth of 3 m located opposite the exit of Sevastopol Bay (Svetlichny et al., 2016). Beginning on 8 August 2014, synchronous seawater samplings were conducted by gradually filling a 6-L plastic bottle along the net track from the same depth to determine the precise number of nauplii and early copepodite stages of *O. davisae*.

The samples were concentrated in a 20-mL volume beaker using inverse filtration through a sieve (mesh size $20 \mu\text{m}$). After filtration, dead *O. davisae* (immobile specimens with signs of decomposition) that had aggregated at the bottom of the beaker were counted and removed. To reduce motility of live copepods and to prevent ovigerous females from dropping egg sacs, the individuals were anesthetized by magnesium chloride solution (final concentration of 9 g L^{-1}). After that, the numbers of live immobile ortho- and metanauplii, copepodites I–V (the sum of CI and CII and separately CIII, CIV, and CV), adult females and males, ovigerous (with ovisacs) females, and eggs in egg sacs (clutch size) were counted in all samples, or in 1/4–1/12 subsamples (if the number of animals exceeded ~800 and 2000 individuals in the sample, respectively) using a Bogorov chamber under a dissecting microscope.

2.2. Calculation of the population density of different developmental stages

The numbers of *O. davisae* copepodites and adults were calculated using the net retention coefficient (K) calculated as the mean bottle/net ratio ($K = N_b/N_n$) between the density of individuals collected with the bottle container (N_b , ind m^{-3}) and the density of individuals collected by the net (N_n , ind m^{-3}) for each stage during all studied periods. Using the mean net retention coefficient minimizes the effect of random factors (for example, nonuniform distribution of organisms in the water) on separate hauls using the net and bottles. Mean values of K ($n \approx 70$) amounted to 5.7 ± 2.9 for CI and CII, 2.8 ± 1.8 for CIII, 2.1 ± 1.1 for CIV, and 1.5 ± 0.4 for F, M, and CV with close body size. The propriety of using the constant net retention coefficients may be confirmed by the linear correlation ($R^2 = 0.89\text{--}0.95$) between N_n and N_b (Figure 1) within the wide range of densities ($200\text{--}200,000 \text{ ind m}^{-3}$) of different fractions of *O. davisae*.

The density of nauplii was calculated from the field samples collected with the bottles. To determine the size of copepods, the prosome length, total body length, and width were measured dorsally to the nearest $5 \mu\text{m}$ in randomly selected anesthetized specimens under a light microscope using an eyepiece micrometer at $210\times$ magnification.

Sex differences in *O. davisae* copepodites V were determined using the sex variations described in the closely related *O. brevicornis* (see Uchima, 1979).

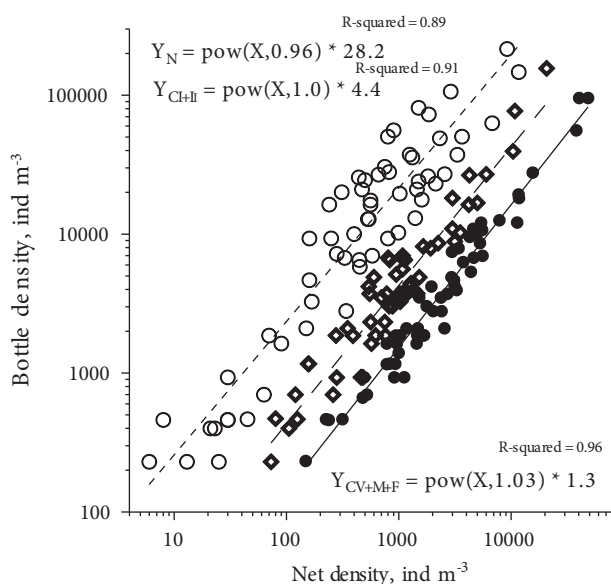


Figure 1. Relationships between the total densities (ind m^{-3}) of females, males, and copepodites V (●), early copepodites I–II (◇), and late nauplii (○) collected with the net and bottle sampler.

2.3. Estimation of the egg production of *O. davisae* females in the field

The average egg production rate (AEPR, eggs female⁻¹ day⁻¹) in situ was calculated on the basis of the field net samples using the modified equation of Uye and Sano (1995):

$$AEPR = CS \times OF \times TF^{-1} \times D_E^{-1},$$

where CS is the clutch size (eggs female⁻¹), OF is the number of ovigerous females, TF is the number of total females (females m⁻³), and D_E is the embryonic development time, calculated as:

$$D_E = 1.31 \times 10^4 \times (T + 12.3)^{2.6} \text{ (Uye and Sano, 1995),}$$

where T is the temperature (°C).

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

3. Results

According to the pronounced dynamics of the abundance of copepodite stages (Figure 2A), age composition,

physiological state of females, and egg production (Figures 2B–2D), and the numbers of ortho- and metanauplii (Figure 3) during the studied period, four phases of the annual cycle of *O. davisae* in Sevastopol Bay were recorded.

1) The latent period was from April until July–August. The surface temperature increased from 8–10 °C up to the maximum values (27.5 °C in August 2014 and 2015); however, the population density was relatively low. Total abundance of copepodites and adults (TCS) did not exceed 8 ind × 10³ m⁻³, except at the beginning of summer 2016, when the number of TCS and total population abundance with nauplii (TP) rose to 28 and 124 ind × 10³ m⁻³, respectively. Nevertheless, during this initial annual cycle phase, the share of ovigerous females (up to 50%), clutch size (22 ± 3 eggs female⁻¹), and egg production rate (up to 6 eggs females⁻¹ day⁻¹) reached maximum levels. At the end of May–June, the first maximum of the share of males among adults (Figure 4A), varying from 33% in 2014 to 66% in 2015, was observed.

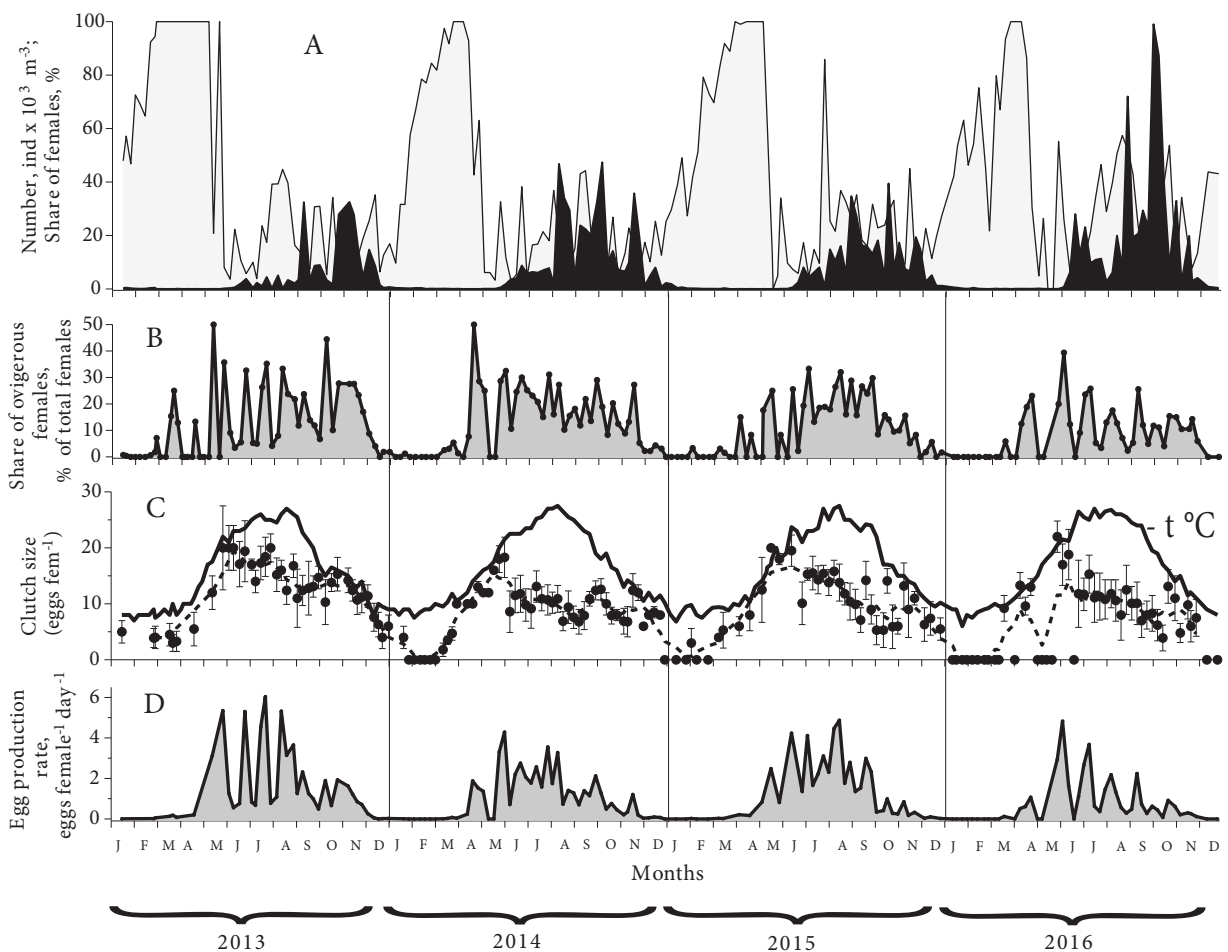


Figure 2. Interannual and seasonal population dynamics during 2013–2016: A) number of copepodites and adults, ind 10³ m⁻³ (■) and share of females, % of the total population number (□); B) share of ovigerous females, % of the total number of females; C) clutch size (eggs fem⁻¹) (●) and temperature (---); D) egg production rate (eggs female⁻¹ day⁻¹).

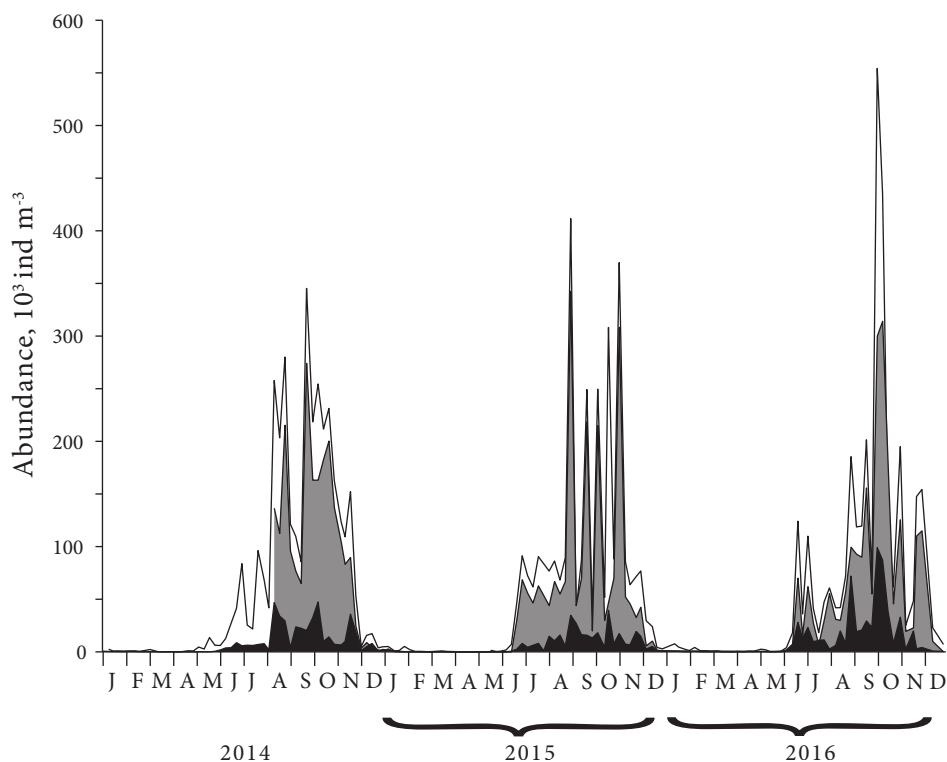


Figure 3. Seasonal dynamics of total population abundance (□), number of orthonauplii (⊞), and copepodites (■) during 2014–2016.

2) The phase of the maximum population growth from August–September until November–end of December was accompanied by a decrease in egg production characteristics (Figure 2C), while the temperature gradually reduced to 10–12 °C. Two or three annual peaks in the numbers of all copepodite developmental stages, associated with peaks in the numbers of nauplii, were registered during that period. In 2013, the maximum number of TCS reached $32.5 \text{ ind} \times 10^3 \text{ m}^{-3}$, while the mean number from September until December amounted to $14.5 \pm 10.6 \text{ ind} \times 10^3 \text{ m}^{-3}$. During the following 2 years, the maximum and mean numbers of TCS showed slight trends of increasing; in 2016, they elevated sharply up to 99.2 and $42.0 \pm 29.8 \text{ ind} \times 10^3 \text{ m}^{-3}$, respectively (Figure 2A), while the total population abundance including nauplii was equal to $554 \text{ ind} \times 10^3 \text{ m}^{-3}$, with the mean value of $216.3 \pm 167.4 \text{ ind} \times 10^3 \text{ m}^{-3}$ for the period of reproduction (Figure 3). At the end of this phase and the beginning of the following one, the maximum mortality of females, second peak of the share of males (about 40% of the number of adults), and maximum mortality of males (Figure 4B), varying from 15% in 2013 to 37.5% in 2014, were observed.

3) The degradation of the population from the end of November–beginning of December until the middle of February–March was followed by the dramatic decrease in the total abundance of *O. davisae* to $228 \pm 150 \text{ ind m}^{-3}$

and gradual elimination of adult males, copepodites, and nauplii from the population.

4) Survival of fertilized females (Svetlichny et al., 2016) occurred during the cold period of winter and the beginning of spring (7.5–9.5 °C). This phase of the life cycle decreased from 2.5 months (end of February–beginning of May) in 2013 to about 1 month (beginning–end of April) in 2016 (Figure 2A). During this period, ovigerous females with 1–6 eggs occurred rarely, while nauplii, copepodites, and adult males were absent.

4. Discussion

Among the great number of cyclopoid copepods inhabiting the European seas and inner water bodies, only two species, *Oithona similis* and *O. nana*, occurred in the Black Sea up to the end of the 20th century. According to the model of the formation of copepod species composition in the Black Sea by its Mediterraneanization (Puzanov, 1967; Kovalev et al., 1999), the prognosis of possible changes in the biodiversity of copepods from this region at the present time did not include the invasion of other cyclopoid copepod species from the Mediterranean Sea to the Black Sea, at least not the stenohaline and osmoconformic representatives of the genus *Oithona* (Monchenko, 2001). In fact, *O. davisae*, transported into the Black Sea from the Indo-Pacific region (Gubanova et

al., 2014), has turned out to be a widely euryhaline species capable of osmoregulation within a salinity range of 12–40 psu (Svetlichny and Hubareva, 2014). However, *O. davisae* is a typical estuarine thermophilic copepod. In the areas of its native habitat, the water temperature decreases to 10 °C only for short periods (Uye and Sano, 1995), while in the Black Sea, the mean temperature does not exceed 8 °C from February until the end of April. Since cyclopoid copepods are not able to produce resting eggs (Aleksiev and Starobogatov, 1996), they cannot survive the cold season at the stage of diapausing eggs, as the invader *A. tonsa* (Gubanova, 2000) or other seasonal calanoid species can. No evidence of any diapause stage exists for copepods from the family Oithonidae (Marcus, 1996). Nevertheless, the unique ability of females of *O. davisae* fertilized in winter to keep the sperm alive in a spermatheca for 2.5 months (Svetlichny et al., 2016) allows the birth of new generations at the spring temperature increase. The formation of such a type of reproduction may be due to, on the one hand, an adaptation to the periods when the population densities decrease to the critical minimum below which mate encounters are too rare to allow population maintenance (Kiørboe, 2006), and on the other hand the likely shorter lifespans of males, based on the high energetic cost of mating (Kiørboe, 2007; Ceballos and Kiørboe, 2011; Saiz et al., 2017).

During 2013–2016, we established the trends of changes in population abundance and the duration of the overwintering period in females (Figure 2), which can be explained by the interannual variations in seasonal

temperature dynamics (Figure 5). From January to the middle of April 2013, the minimum temperatures (not higher than 8 °C) were recorded, which were close to 2005–2009 values (Svetlichny et al., 2016). In 2014–2016, the winter–spring temperatures were 1.2 ± 0.8 °C higher than those in 2013, which seemed to result in slower elimination of early developmental stages, decrease in the duration of the wintering phase of fertilized females, and earlier start of spring–summer latent phase in the population development. At the end of July–beginning of August 2014–2016, and from the middle of September to the middle of October, the water temperatures were 1.7

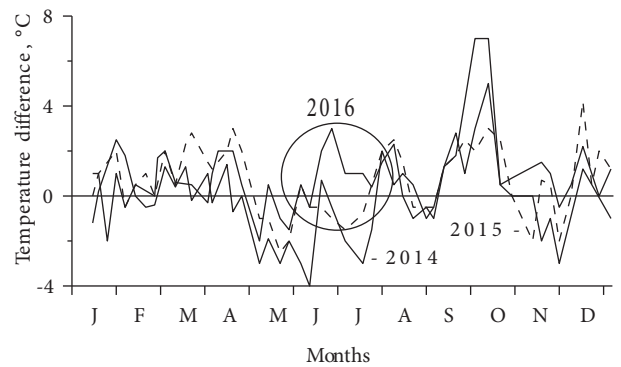


Figure 5. Seasonal temperature deviations in the Sevastopol Bay during the period 2014–2016 compared with the seasonal temperature trend in 2013. The circle marks an abnormal water temperature in June 2016.

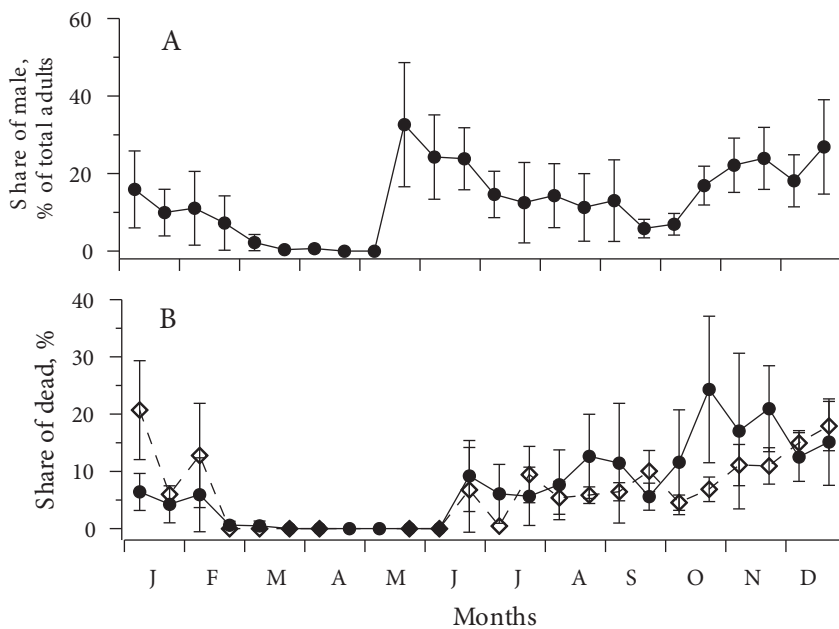


Figure 4. Seasonal dynamics of the mean (2013–2016) shares of males among adult males and females (A) and dead individuals (B) among females (●) and males (◇).

± 0.6 °C and 3.0 ± 1.9 °C higher, respectively, than those in 2013. This led to earlier attainment of the maximum population abundance and higher absolute total number of *O. davisae*, especially in early October 2016 ($554 \text{ ind} \times 10^3 \text{ m}^{-3}$), when due to an abnormally high water temperature ($25\text{--}26.5$ °C) from the middle until the end of June, the total population abundance amounted to $124 \text{ ind} \times 10^3 \text{ m}^{-3}$ while the number of copepodites and adults was equal to $27 \text{ ind} \times 10^3 \text{ m}^{-3}$, which was close to the peak abundance of these stages ($32.5 \text{ ind} \times 10^3 \text{ m}^{-3}$) during the September and November maximums in 2013.

A similar correlation between the rise in the mean temperature and the increase in the mean annual number of *O. davisae* was observed during 2010–2015 near the exit of Sevastopol Bay by Seregin and Popova (2016). Based solely on bottle sampling (1–6 L), the authors reported the 2-year cycle changes in the maximum seasonal numbers of *O. davisae* in Sevastopol Bay.

A maximum number of *O. davisae* was registered by Seregin and Popova (2016) in September 2014 ($1250 \text{ ind} \times 10^3 \text{ m}^{-3}$). In September 2014, we also recorded the peak abundance, which was significantly lower ($345 \text{ ind} \times 10^3 \text{ m}^{-3}$), probably due to the differences in location and depth of the stations. According to Seregin and Popova (2016), 88%–93% of the total population number in the period of its maximum development consisted of the nauplii. These data are in agreement with our results. Moreover, according to our study, among the nauplii the mean annual share of orthonauplii amounted to $77.8 \pm 19.1\%$, reaching 90% during the periods of maximum population abundance. Similar to this finding, among copepodites and adults the mean annual share of copepodite stages I–III constituted $47.6 \pm 29.4\%$ (taking into account the net retention coefficients) and increased up to 90% during the reproductive period.

One can suggest that during the earlier long-term studies in Sevastopol Bay (Altukhov et al., 2014) using net hauls with a mesh size of $150 \mu\text{m}$ (when only the adults and copepodites IV–V were registered), not more than 10% of the *O. davisae* population was analyzed. According to these authors, the maximum number of preadults and adults in 2005–2009 varied from 21 to $91 \text{ ind} \times 10^3 \text{ m}^{-3}$. Consequently, during that period, the population density of *O. davisae* may have exceeded 1 million $\text{ind} \text{ m}^{-3}$ due to uncounted nauplii and early copepodite stages.

The accelerated growth of the *O. davisae* population in the summer periods of 2014–2016 after a latent period of development was due to a sharp increase in the number of nauplii, which is an attribute of opportunistic species using the r-reproduction strategy. The r-strategists are characterized by higher fecundity rates. However, an egg-carrying species such as *O. davisae* has a relatively low egg production rate, which is a typical element of k-strategy.

That low egg production rate probably explains the sharp aging of the population and a decrease in density upon the arrival of winter.

A small number of fertilized females that had survived winter (not more than $300 \text{ ind} \text{ m}^{-3}$ in the studied area) began to produce eggs in egg sacs in the middle of March at the stable temperature of about 10 °C. After this peak in abundance, the first peak of the number of nauplii was observed in April, and then peaks in the numbers of all copepodite stages were registered. Since the period of laying eggs was synchronized with the temperature, we recorded the chain of consistent generations during all developmental periods. For example, based on the alternation of the peak numbers of different developmental stages shown in Figure 6, we distinguished three first generations of *O. davisae* in 2014.

The convenience of this approach is due to the fact that the contribution of any developmental stage to the population does not depend upon random variations in its number. The number of generations of *O. davisae* during 2014–2016 interpreted using the same approach is shown in Figure 7. Since the samples were collected every 7 days, the inaccuracy of the evaluation did not exceed ± 3.5 days.

The analysis conducted allowed distinguishing 4 generations in the latent period of 2014–2016 with a duration of 60 days at low temperatures from March until May, and with the duration of 21 days at the high temperatures before the beginning of the phase of maximum population growth (Figure 7), 3–4 generations in the peak number period from 3 to 4 weeks (probably less than 3 weeks, but the frequency of sampling prohibited more precise determination), and 2–3 generations in winter, with a duration of 76 days. According to our estimation, *O. davisae* produced 10–11 generations in Sevastopol Bay during the reproductive period. The mean generation time from egg to adult (Dg) significantly decreased from 61 ± 12 to 22 ± 3 days while the mean temperature when the generation developed increased from 9.1 ± 0.5 to 25.6 ± 0.9 °C, in accordance with the equation of Beleradek: $Dg = 39430(T+15)^{-2.05}$.

At the low temperature of 10 °C, the Dg obtained in our study slightly exceeded the Dg of *O. davisae* from Fukuyama Harbor and Tokyo Bay (56.2 and 44.4 days, respectively) (Uye and Sano, 1998), but was about 2-fold higher at the high temperature (Figure 8). This discrepancy may be explained on the one hand by overestimation at the high temperature in our study (due to an insufficient frequency of samplings), or on the other hand by the fact that the values reported by Uye and Sano (1998) were obtained using individuals of *O. davisae* reared at a stable temperature and under food-satiated laboratory conditions.

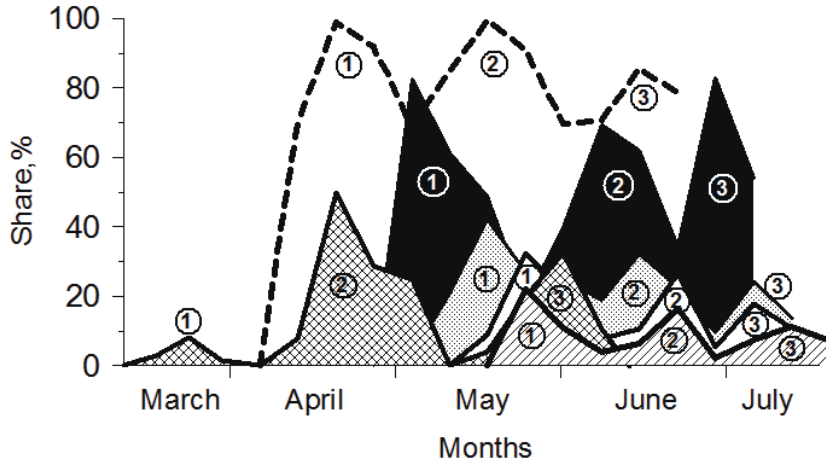


Figure 6. Shares (%) of females with egg sacs in the total number of females (▨), nauplii in the total population abundance (---), and CI + II (■), CIII (▤), CIV (□), and CV (▩) in the total number of copepodites during the first three generations of *Oithona davisae* in March–July 2014.

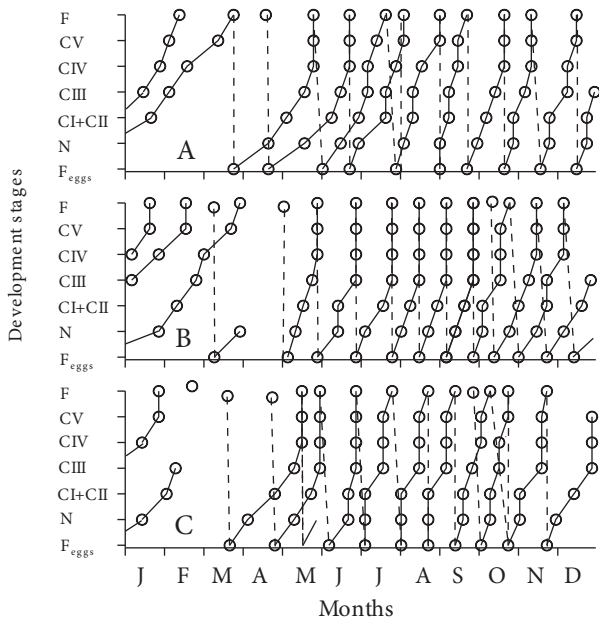


Figure 7. Number of generations in *Oithona davisae* in 2014 (A), 2015 (B), and 2016 (C) distinguished on the basis of the maximum share of ovigerous females (F_{eggs} , % of the total number of females), nauplii (N, % of the total population number), early copepodites of I and II stages (CI + II, % of the total number of copepodites), copepodites of III–V stages (CIII, CIV, and CV, respectively, % of the total number of copepodites), and females (F, % of the abundance of all copepodite stages). The solid lines show the succession of developmental stages within one generation (bold lines indicate the generations with the maximum numbers). The dotted lines show the relations between the generations.

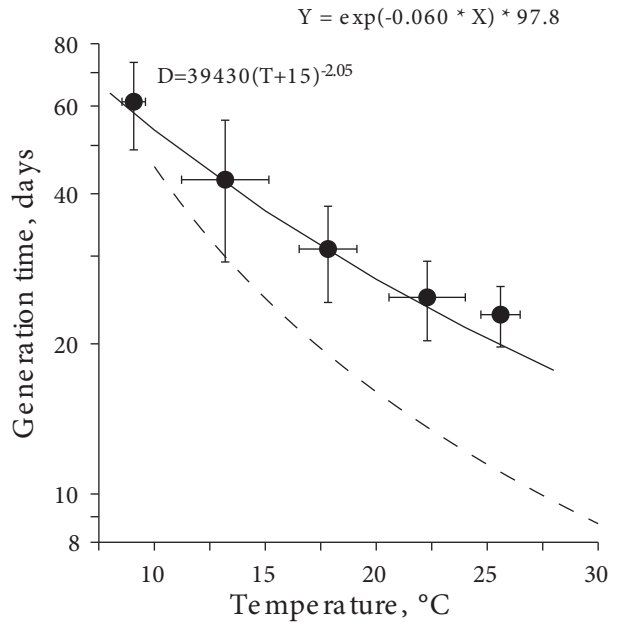


Figure 8. Relationships between the mean generation time and the mean development temperature in Sevastopol Bay (●) and Fukuyama Harbor (----) (Uye and Sano, 1998).

The dinoflagellate *Oxyrrhis marina* and some ciliates are known to be the main components of *O. davisae*'s natural diet (Saiz et al., 2014). Therefore, successful development of this species in the Black Sea in the period when the share of the small phyto- and zooflagellates in the phytoplankton community increased (Nesterova et al., 2008) may not be accidental. Nevertheless, that component of the microplankton community seems not to be sufficient for *O. davisae* to gain the same rates of growth and production in the Black Sea as in Japan's inner seas (Uye and Sano 1995, 1998). Additionally, there are differences in the seasonal character of the population dynamics of *O. davisae* in Sevastopol Bay and Fukuyama Harbor. According to Uye and Sano (1995), the main period of *O. davisae* population development in Fukuyama Harbor starts in June, just after the phytoplankton bloom, while in the Black Sea the maximum number of the same species can be observed not earlier than August. The first maximums of the share of ovigerous females (about 50%) in both bays were registered in April–May. The maximum clutch size in Fukuyama Harbor was reported in May–June (about 30 eggs female⁻¹) and agreed with the maximum number of females, while in Sevastopol Bay two peaks were recorded, in May–June (22 ± 3 eggs female⁻¹) at the extremely low population density and in October (up to 15 ± 3 eggs female⁻¹) at the highest population density (Figure 2). The egg production rate of Black Sea *O. davisae* depended on the temperature (Figure 9) to the same extent as for the same species in Fukuyama Harbor (Uye and Sano, 1995). However, in Fukuyama Harbor, the egg production rate reached the highest value (up to 11.6 eggs female⁻¹ day⁻¹) at the maximum abundance of *O. davisae*, while in Sevastopol Bay the maximum egg production rate (up to 6 eggs female⁻¹ day⁻¹) was observed at an extremely low population number during the latent period (Figure 2).

The latent character of the development of *O. davisae* during the spring–summer period indicates a potential for increase in the development period for 5 months. However, to achieve this, an increase in the winter temperature up to 10 °C and a decrease in another environmental parameter that may inhibit the development of this species in spring and summer would be needed. Uye and Sano (1995) reported that in Fukuyama Harbor during midsummer, the *O. davisae* population is reduced due to predation by

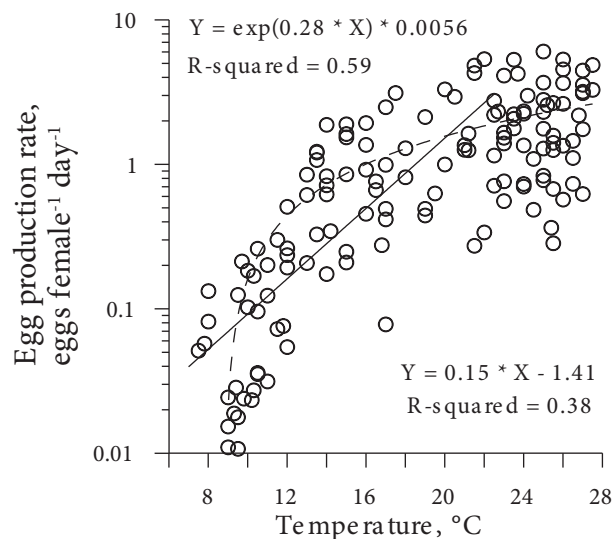


Figure 9. Relationship between the egg production rate and the temperature in Black Sea *Oithona davisae*, approximated by the exponential (----) and linear (—) equations within the range of 10–28 °C.

the lobate ctenophore *Bolinopsis mikado*. In the Black Sea, the population of *O. davisae* may be controlled by another lobate ctenophore, *Mnemiopsis leidyi*, which appeared in that region in the 1980s. This thermophilic species occurs in small numbers in the plankton even in winter and the beginning of spring. Depending on the time of seasonal increase in temperature, the development of *M. leidyi* begins in April (Louppova and Arashkevich, 2008) or May–June (Shiganova et al., 2014). The maximum annual abundance of this species near Sevastopol Bay was registered in July–August (Finenko et al., 2013). Such seasonal patterns in *M. leidyi*'s abundance may result in limiting the development of the *O. davisae* population in spring and summer or increasing the abundance of this copepod at the end of summer and autumn, when the population of *M. leidyi* is suppressed by the invasive predator ctenophore *Beroe ovata*.

Acknowledgments

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