

ORIGINAL ARTICLE

New invasive copepod *Oithona davisae* Ferrari and Orsi, 1984: seasonal dynamics in Sevastopol Bay and expansion along the Black Sea coasts

Denis A. Altukhov, Alexandra D. Gubanova & Vladimir S. Mukhanov

Department of Plankton, Institute of Biology of the Southern Seas, Sevastopol, Ukraine

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D. A. Altukhov, Department of Plankton, Institute of Biology of the Southern Seas, Nakhimova ave. 2, 99011 Sevastopol, Ukraine.

E-mail: dennalt@gmail.com

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Abstract

Seasonal and interannual dynamics of abundance of the recent invader *Oithona davisae* (Copepoda: Cyclopoida) were investigated in Sevastopol Bay from October 2005, when the species appeared in the plankton, to December 2009. The study was based on bi-weekly plankton sampling at three stations located within and adjacent to Sevastopol Bay, Crimea, Northern Black Sea. The abundance of *O. davisae* increased steadily in Sevastopol Bay in 2006–2009. The species was more abundant at the centre of the bay than at its mouth. During the investigated period, an absolute maximum of the invader abundance at the centre of Sevastopol Bay was observed in early December 2008 (91,650 ind. m⁻³) and at the mouth of the bay in late October 2007 (46,200 ind. m⁻³). The maximum contribution of *O. davisae* to the total copepod abundance was about 99%. Expansion of the invasive copepod along the Black Sea coasts is reported. Changes in structure of the zooplankton community for the last 20 years that preconditioned the invasion of the new copepod species in the Black Sea as well as the changes in the community structure caused by *O. davisae* are discussed.

Introduction

The unique hydrological conditions of the Black Sea predetermined a poor diversity of its zooplankton fauna. Although the Black Sea fauna is mostly of Mediterranean origin, a combination of low winter temperatures, rather low salinity, and an anoxic layer below about 200 m depth represents an insurmountable ecological barrier for the bulk of the Mediterranean zooplankton species against penetration of the Black Sea (Zaika 2000; Isinibilir *et al.* 2011).

From time to time, Mediterranean species of copepods have been recorded in the Black Sea plankton near the Bosphorus area (Pavlova 1965; Kovalev *et al.* 1976; Yuksek *et al.* 2002). However, none of these species has established in the Black Sea during the last decades. On the contrary, the recent zooplankton invaders are long-distance aliens (Gubanova *et al.* 2013). The copepod *Acartia tonsa* Dana, 1849, the ctenophores *Mnemiopsis leidyi* A. Agassiz, 1865 and *Beroe ovata*

Bruguiere, 1789 (Pereladov 1983, Belmonte *et al.* 1994; Konsulov and Kamburska 1998, Gubanova 2000) were most probably brought into the Black Sea in ballast waters of ships.

All the invasive species mentioned above have changed the structure of the Black Sea plankton community considerably. *Acartia tonsa* appeared in the plankton of Sevastopol Bay in the early 1970s and replaced the native species *Acartia latisetosa* Krichagin, 1873. Since 1976, this new species has been reported as the dominant copepod species in the coastal areas during summer (Gubanova *et al.* 2001). *Mnemiopsis leidyi* invasion increased the grazing pressure on zooplankton in late 1980s and early 1990s, especially during summer and autumn (Kamburska *et al.* 2003; Lebedeva *et al.* 2003). The invasion of *B. ovata*, preying on *M. leidyi*, reduced the abundance of the latter, the period of their reproduction and thus the overall grazing pressure on plankton during summer and autumn (Fienko *et al.* 2003; Hubareva *et al.* 2004; Gubanova *et al.* 2013).

The mesozooplankton of Sevastopol Bay, like that of other areas of the Black Sea, is represented by a relatively small number of taxonomic groups (Zernov, 1904; Greze *et al.* 1971). As few as seven species of Copepoda were found regularly in zooplankton samples from Sevastopol Bay until 2005: *Acartia clausi* Giesbrecht, 1889; *A. tonsa* Dana, 1849; *Calanus euxinus* Hulsemann, 1991; *Centropages ponticus* Karavaev, 1894; *Oithona similis* Claus, 1866; *Paracalanus parvus* Claus, 1863; and *Pseudocalanus elongatus* Boeck, 1865. With the exception of *A. tonsa*, all of these species are indigenous to the Black Sea.

Some specimens of a cyclopoid copepod new to the Black Sea were first found in Sevastopol Bay in December 2001. The species was identified as *Oithona brevicornis* (Zagorodnyaya, 2002). However, this discovery appears to represent an isolated record.

New specimens of the *Oithona* genus alien to the Black Sea were found in Sevastopol Bay only 4 years later (Gubanova & Altukhov 2007). The species was also identified as *O. brevicornis*. The same species has been routinely observed in samples taken since the mid-2000s (Altukhov & Gubanova 2006; Selifonova 2009). Recently, the species was re-identified as *Oithona davisae* (Temnykh & Nishida 2012). Thus, *O. brevicornis* and *O. davisae* are two different names for the same Black Sea species, but *O. davisae* is accepted as the correct name. From 2006 to 2009, the contribution of this species to the total copepod abundance in Sevastopol Bay increased to almost 99%, with its numbers rising up to about 90,000 ind. m⁻³.

The aim of the present study was to investigate the invasion patterns, interannual variability, seasonal dynamics and spatial expansion of the alien copepod *O. davisae* in the Black Sea, and the impact they had on the zooplankton community.

Material and Methods

Sevastopol Bay (SW Crimea, Ukraine) is about 7000 m long and 850 m wide, with an average depth of 12 m. Regular studies of plankton communities in the bay waters were performed in 1976, 1980, 1989, 1990, 1995 and 1996. They were resumed in 2002 and are ongoing. Samples were usually collected twice a month (with gaps due to technical or meteorological conditions) at three stations located within and adjacent to Sevastopol Bay (St. 1–3, Fig. 1), Crimea, Northern Black Sea. Samples were collected by vertical hauls through the whole water column (from the bottom to the sea surface) using a J-day plankton net (mouth area 0.1 m² and mesh size 150 µm). Samples were taken in the morning and fixed with formaldehyde solution (4% final conc.). Zooplankton counts were made under an MBS-9 stereomicroscope using a Bogorov counting chamber.

From 2006 to 2008, *O. davisae* was found episodically (in about 10% of the collected samples) at St. 1. The data obtained at this station in 2009 were not processed completely. For these reasons, the results obtained at St. 1 have not been included in the diagrams in this paper.

To study *O. davisae* expansion along the Black Sea coast in 2008–2010, samples were collected at St. 5–11 (Fig. 1) by vertical hauls through the whole water column (from the bottom to the sea surface) using a closing Epstein plankton net (mouth diameter of 10 cm and mesh size of 55 µm). The unpublished data from St. 4 were kindly provided by Kremena Stefanova (IO BAS, Bulgaria) (Fig. 1). The data on the appearance of *O. davisae* at St. 12 and 13 are cited from Selifonova (2009).

Copepods (I–VI copepodites) were identified using the taxonomic keys of Shuvalov (1980), Nishida (1985) and

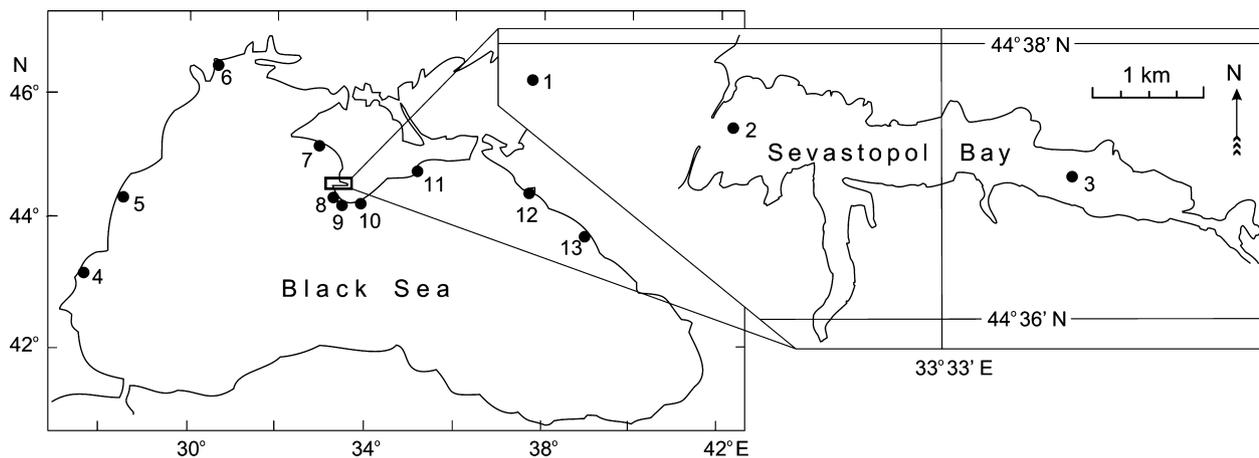


Fig. 1. Sampling stations in Sevastopol Bay and the Black Sea. Our data were obtained from St. 1–3 and 5–11; the data on the St. 4, 12 and 13 were obtained from other sources (see explanations in the text).

Sazhina (1969). Abundance was calculated per cubic meter assuming that the net filtered with 100% efficiency over the depth range. Appendages were dissected under a stereomicroscope and mounted on microscope slides for detailed examination.

As *O. davisae* has a relatively small body size, its early developmental stages (I–III copepodites) are underestimated when using a net equipped with 150- μm mesh size (Kovalev *et al.* 1977). For this reason, only adults and the IV–V copepodites were counted in this study and the I–III stages ignored.

Results

Seasonal dynamics of *Oithona davisae* in Sevastopol Bay in 2005–2009

After the first appearance of *O. davisae* in the bay from October 2005 to March 2006, the species was not found in the samples in April–May 2006 at any of the stations, demonstrating unstable dynamics. For the next years, its abundance steadily increased and never dropped down to zero. In general, its seasonal dynamics at both the bay stations were similar, although every year had its own specific pattern (Fig. 2).

At the mouth of Sevastopol Bay (St. 2), *O. davisae* attained a density of 264 ind. m^{-3} in November 2005. Density then declined until late August 2006 (no individuals were found in April–May 2006), after which intensive development of the population started again. The maximum abundance (21,050 ind. m^{-3}) was reached in late October 2006. After this, the abundance of the population decreased sharply. In 2007, the intensive development began a bit later, in September. The maximal abundance (46,200 ind. m^{-3}) was observed in late October 2007. A similar trend was observed in 2008 but the peak (23,500 ind. m^{-3}) was recorded later, in early November 2008, and the following decrease in the species abundance was not as abrupt as those observed in 2006–2007.

In January–May 2009, the number of individuals was relatively low. In June 2009, the number exceeded 10,000 ind. m^{-3} , whereas it did not reach 1000 ind. m^{-3} during the summer months in 2006–2008. Some decrease in abundance was observed in July 2009. The peak was recorded in late August (35,550 ind. m^{-3}). Until the end of 2009, the numbers of *O. davisae* did not drop below 1000 ind. m^{-3} .

In general, the population of *O. davisae* was more abundant in the centre of the bay (St. 3) than at its mouth (paired *t*-test, $P < 0.001$, $n = 92$). In 2005, the maximal abundance (2311 ind. m^{-3}) was recorded in late December. Between January and August 2006, the invader had lower abundances, with a small peak (620 ind. m^{-3}) in March. No individuals were found in late March or in the middle

of May 2006. A few specimens were found in April, June and July 2006. The annual maximum observed in late October was almost 20 times greater (42,667 ind. m^{-3}) than in 2005. Three distinct peaks in January, March and June 2007 against a background of rather small values were followed by a rapid development of the population through September, with the maxima occurring in October (51,667 and 43,555 ind. m^{-3}). In 2008, the character of the species dynamics from January to October was almost the same as in 2006–2007, but no considerable fall of abundance was observed in November. The annual peak of *O. davisae* abundance was reached in early December, amounting to 91,650 ind. m^{-3} . Such an extremely high value had never been reported for planktonic copepods in Sevastopol Bay. These values seem to be the highest copepod abundances ever recorded in the Black Sea.

In January and early February 2009, the *O. davisae* population exceeded 10,000 ind. m^{-3} . The annual minimum (1856 ind. m^{-3}) was recorded in late February. Intensive development of the population started substantially earlier in 2009 than in 2006–2008. The maximal annual abundance was observed in mid-June (71,167 ind. m^{-3}) and *O. davisae* remained very numerous until the end of year. A decrease in the abundance (down to 4800 ind. m^{-3}) was observed in mid-November 2009.

From 2006 to 2009, outside Sevastopol Bay, *O. davisae* was observed at St. 1 episodically at rather low abundances. However, a slight increase in the species abundance and frequency of appearances was noticed. Analysis of the samples collected in autumn 2010 showed that at St. 1, the abundance of *O. davisae* increased sufficiently and exceeded 7000 ind. m^{-3} in October.

In the period from 2006 to 2009, the average annual abundance of *O. davisae* increased from 1749 to 5543 ind. m^{-3} at the mouth of Sevastopol Bay (St. 2) and from 4347 to 22,284 ind. m^{-3} at the centre of the bay (St. 3). The average annual abundances of the other copepod species were less variable. At St. 2, the minimum (2138 ind. m^{-3}) and the maximum (3652 ind. m^{-3}) numbers were recorded in 2006 and 2008, respectively. At St. 3, the lowest (1968 ind. m^{-3}) and the highest (3377 ind. m^{-3}) values were obtained in 2008 and 2007, respectively. During the periods of maximum densities of *O. davisae*, its contribution to the total copepod abundance rose to 96.42% and 98.72% at St. 2 and 3, respectively. The contribution of the invader to the total average copepod abundance was considerably higher at the centre of the bay (St. 3) than at its mouth (St. 2) (Fig. 3).

Expansion of *Oithona davisae* along the Black Sea coasts

In autumn 2005, establishment of *O. davisae* in the Black Sea was reported simultaneously in Sevastopol Bay (our

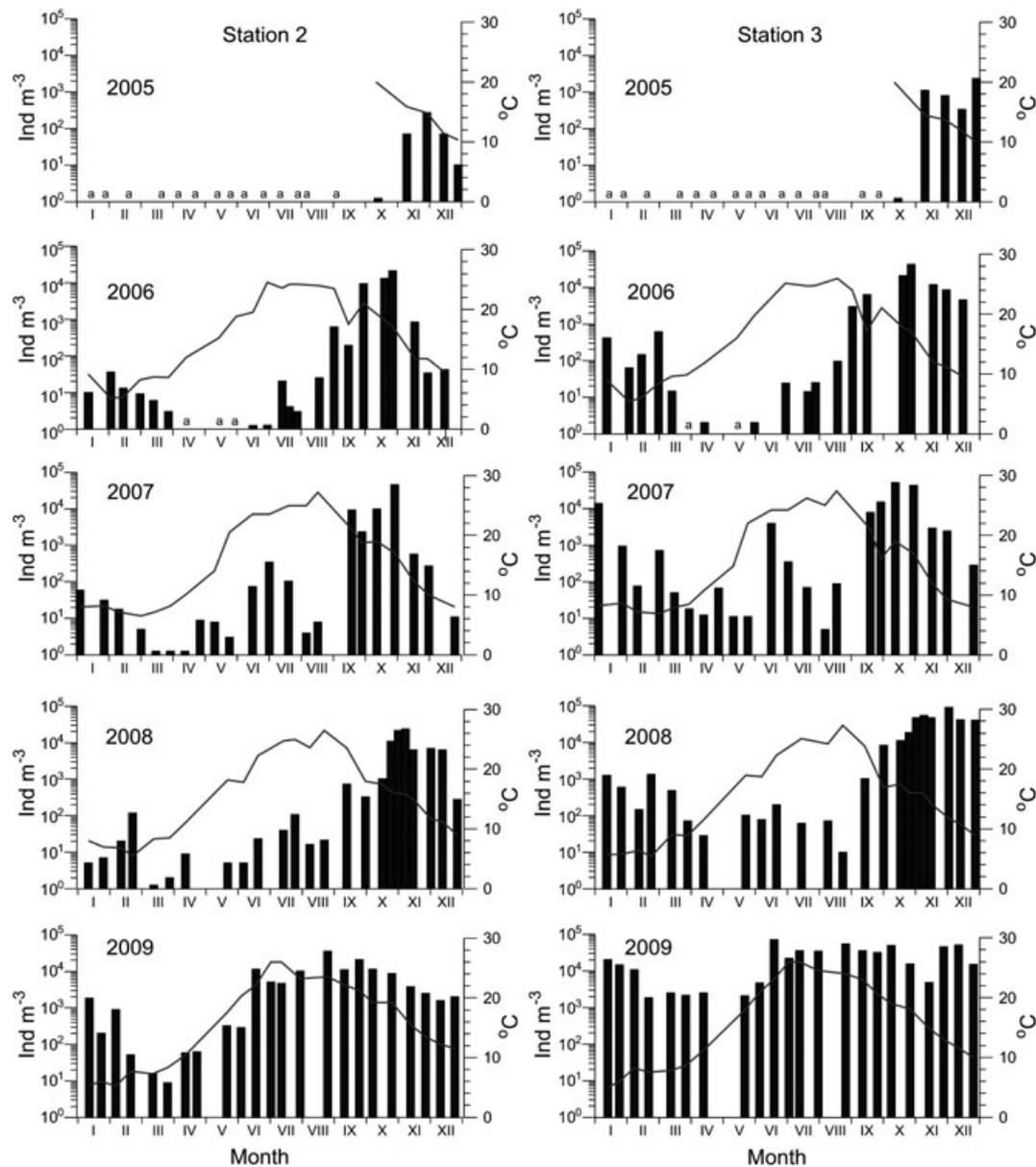


Fig. 2. Seasonal dynamics of *Oithona davisae* abundance (bars) and water temperature (lines) at the mouth (St. 2) and centre (St. 3) of Sevastopol Bay from 2005 to 2009. Samples marked 'a' are samples in which no individuals of *O. davisae* were found.

data, St. 1–3), Novorossiysk (St. 12) and Tuapse bays (St. 13) (Selifonova 2009). In October 2008, when *O. davisae* were extremely abundant in Sevastopol Bay, zooplankton samples were additionally taken in Balaklava Bay and the open waters outside it (St. 8) and no individuals of the species were found there. In October 2009, samples were taken at the same stations, *O. davisae* proving to be the dominant species in all of them. Then, in November–December 2009, *O. davisae* was found in all the samples from Yevpatoriya (St. 7), Yalta (St. 10) and Feodosiya (St. 11) coastal waters. The species was reported by

Kremena Stefanova (IO BAS, Varna, Bulgaria) from Varna Bay (St. 4) in August 2010. In autumn 2010, the invader was discovered in waters off Odessa (St. 6) and Constanta (St. 5).

Discussion

The present study has shown that *O. davisae* is very tolerant of variations in water temperature. For example, almost the same values of abundance (exceeding 10,000 ind. m⁻³) were observed at St. 3 in February 2009 and

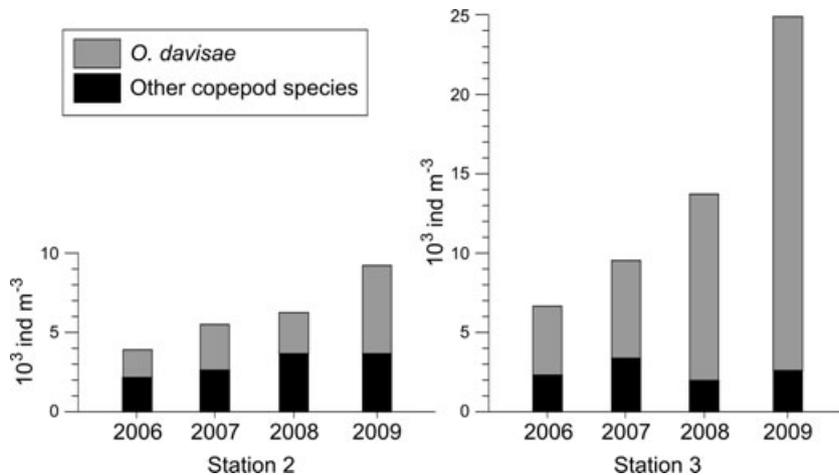


Fig. 3. Average annual contribution of *Oithona davisae* to the total copepod abundance at St. 2 and 3 in 2006–2009.

St. 2 in August 2009, with surface water temperatures of 8.2 °C and 23.2 °C, respectively. Maxima of abundances were also observed over a rather wide range of water temperatures (Table 1).

According to an experimental study, the salinity tolerance of *O. davisae* ranges from 3 to 40 psu (Svetlichny L. S. and Hubareva E. S., unpublished data). Thus, *O. davisae* has a high tolerance to different environment conditions, allowing it to survive and reproduce in the Black Sea. However, the success of the invasion was strongly influenced by the native community (Alimov *et al.* 2004). After occasional introduction, an invader must either find a niche that is not occupied or compete for an occupied one (Berg & Carton 1988; Di Castri 1990). Low resilience of the native zooplankton community to *O. davisae* invasion was possibly preconditioned by earlier invasions of the predatory ctenophores *M. leidyi* and *B. ovata* (Gubanova & Altukhov 2007). *Mnemiopsis leidyi* invasion resulted in a substantial increase in grazing pressure on zooplankton in the late 1980s and early 1990s, especially during summer and autumn (Kamburska *et al.* 2003; Lebedeva *et al.* 2003). One of the results of the destructive *M. leidyi* invasion was a complete disappearance of *Oithona nana*, which had dominated the copepod community until the 1990s (Gubanova *et al.* 2002).

The invasion of *B. ovata* preying on *M. leidyi* reduced the abundance of the latter, curtailing the period of their

reproduction and thus reducing the overall grazing pressure on plankton during summer and autumn (Finenko *et al.* 2003; Hubareva *et al.* 2004; Gubanova *et al.* 2013). As a result, the abundances of the copepod species that reproduce in autumn increased in 2002–2004. The new copepod species, *O. davisae*, was introduced in the Black Sea in 2005. We suppose that it occupied the environmental niche of *O. nana* in Sevastopol Bay zooplankton. These related species are ecologically similar. They also have the same body size. Seasonal dynamics of *O. davisae* at St. 2 became more and more similar to those of *O. nana*, especially in the last years (2008 and 2009) (Fig. 4). Like *O. davisae*, *O. nana* is an eurythermic species present in the Black Sea plankton all year round. According to regular observations of the plankton dynamics in Sevastopol coastal waters between 1960 and 1970, the highest numbers of *O. nana* were recorded in September–November, and the minimal densities occurred between January and March (Greze *et al.* 1971). At the mouth of Sevastopol Bay in 1976 and 1980, the maximum abundances were observed in September. So, both the biological features of *O. davisae* and the susceptibility of the native zooplankton community to invasion favoured the success of the species' establishment in the Black Sea.

As the smallest planktonic copepod species in the Black Sea, *O. nana* was one of the preferred food items for fish

Table 1. *Oithona davisae* maximum abundances and water temperatures at the two stations in Sevastopol Bay from 2006 to 2009.

Year	Station 2			Station 3		
	Max value (ind. m ⁻³)	Date	T, °C	Max value (ind. m ⁻³)	Date	T, °C
2006	21,050	27 October	17.1	42,667	27 October	17.1
2007	46,200	29 October	17	51,667	12 October	19
2008	23,500	7 November	15.8	91,650	1 December	11.7
2009	35,550	26 August	23.5	71,167	19 June	23.1

T, temperature.

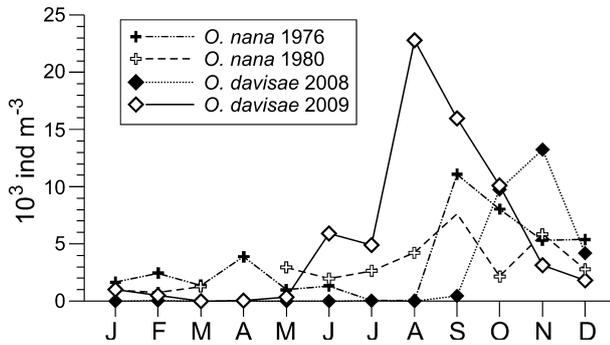


Fig. 4. Seasonal dynamics of *Oithona nana* in 1976 and 1980 and *O. davisae* in 2008 and 2009 at the mouth of Sevastopol Bay.

larvae in the early developmental stages. The disappearance of *O. nana* at the end of the 1980s resulted in a dramatic decrease in the abundance of fish larvae (Tkach 1995). According to our data, the duration of the population increase of *O. davisae* has been extended not only in the bay but also in open coastal waters (Altukhov 2010). The food stocks necessary for the survival of fish larvae have become more abundant. Thus, an increase in abundance of larvae of the fish species that are spawning in bays and the coastal waters during the second half of the year may be expected.

It was noted (Berezina 2004) that if an alien species tolerant of recipient environments does not encounter a strong grazing/predation pressure, its abundance rises sharply. Afterwards, the growth is limited and the abundance reaches a plateau. If *O. davisae* follows the same pattern, a stabilization of its numbers may be foreseen owing to elevated predation pressure.

Conclusion

The new invasive species *O. davisae* has become one of the most abundant copepod species in Sevastopol Bay since its first appearance there in 2005. *O. davisae* usually reached peaks of abundance in autumn. The period of dominance of the species in the bay is extending, with the highest abundances being recorded in the central part of the bay. Species abundance increased not only in the bay but also in the open coastal areas. The invader has expanded along the Black Sea coast since 2009. The success of the *O. davisae* invasion appears to have been preconditioned by the biological features of the species and the vulnerability of the native zooplankton community. We hypothesize that *O. davisae* has occupied the niche of the indigenous copepod *O. nana*, which vanished in the late 1980s.

As a result of the *O. davisae* invasion, the total abundance of fodder zooplankton increased considerably. Like *O. nana*, the invader seems to be a preferred food item for early stages of fish larvae. Long-term studies at basin

scale are still needed to monitor continuously the structural changes in the Black Sea zooplankton community.

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