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HISTORY OF DISPERSION OF THE NORTH AMERICAN POLYCHAETE *MARENZELLERIA NEGLECTA* SIKORSKI & BICK, 2004 (ANNELIDA: SPIONIDAE) IN THE NORTHEASTERN SEA OF AZOV

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In the early 2010s, the alien polychaete worm *Marenzelleria neglecta* Sikorski & Bick, 2004 invaded the Sea of Azov. In few years, the species has widely spread over the desalinated sea area. Moreover, it was recorded in the Don delta and in the Sea of Azov–Kuban estuaries. This alien species formed a stable and numerous colony localized in the northeastern Sea of Azov; the history of this formation is traced based on material of complex hydrobiological and hydrological surveys of 2010–2020. The colony of this species developed against the backdrop of an increase in water salinity. Obviously, this factor had a decisive effect on the invasive process. An outbreak of abundance observed in the western Taganrog Bay in 2012 and 2013 was followed by a sharp decrease in abundance – down to complete absence of this polychaete worm in the samples. A drop in abundance was accompanied by a reduction of its range and a shift in the core of abundance towards sea areas with the lowest salinity. To date, there is a stable *M. neglecta* population in the central and eastern Taganrog Bay. Changes in the structure of prevalence in benthic communities during invasion were analyzed. As shown, the ratio of alien polychaetes in the periods of their mass development reached 92 % of the total abundance of benthos at individual stations.

Keywords: Polychaeta, alien species, benthic communities, macrozoobenthos, estuaries, Sea of Azov

A polychaete worm *Marenzelleria neglecta* Sikorski & Bick, 2004 is native to coastal and estuarine ecosystems of North America (Sikorski & Bick, 2004). Since the mid-1980s, it actively spreads in the northern seas of Eurasia – the Baltic and North ones (*Marenzelleria neglecta*, 2021). *Marenzelleria* species are quite difficult to identify morphologically. Initially, *M. neglecta* was not considered in the Baltic Sea, and the first polychaetes were identified as *Marenzelleria viridis* (Verrill, 1873). After the genus revision, those were assigned to a new species – *M. neglecta*. Later, two more *Marenzelleria* representatives – *M. viridis* and *M. arctia* (Chamberlin, 1920) – were found in the Baltic (Michalek, 2012). At present, *Marenzelleria* spp. group is considered as the most successful one out of the invaders to the Baltic Sea (Maximov, 2011 ; Zettler et al., 2002). The invasion of these worms significantly affected the structure of benthic and planktonic biocenoses (Ezhova et al., 2005 ; Kotta et al., 2006 ; Maximov, 2011 ; Zmudzinski et al., 1993). In the Gulf of Finland, their bioturbation and bioirrigation activity resulted in alterations in the entire ecosystem (Maksimov, 2018).

Being connected with the Sea of Azov by a network of canals and forming a single transport system, the Baltic could become a secondary donor area for *M. neglecta* invasion into the Sea of Azov basin (Boltachova & Lisitskaya, 2019). For the first time, *Marenzelleria* spp. was recorded there in 2014 (Syomin et al., 2016b). Later, adult worms were found at several stations in the Taganrog Bay and the Don delta, and larvae were registered in the bay plankton (Syomin et al., 2016a, b). In one of the first reports, high dispersion of the invader in the upper Taganrog Bay was highlighted: the occurrence of worms reached 90–100 % (Syomin et al., 2016a). Based on the specimens found, two morphotypes were described corresponding to characteristics of two species – *M. arctia* and *M. neglecta*. Further studies, with genetic analysis methods involved, showed as follows: in the Sea of Azov, there is only one *Marenzelleria* species – *M. neglecta* (Syomin et al., 2017).

In the AzNIIRKh samples, representatives of the family Spionidae, new for the Sea of Azov, were recorded in 2010. Those spionids differed morphologically from other, known representatives of the family, but were not identified. Subsequent processing of the material revealed that the registered polychaetes correspond to the described morphotypes of the genus *Marenzelleria*. Since 2016, alien spionids were confidently diagnosed as *Marenzelleria* sp.; later, as *M. neglecta*. Thus, the available material of surveys allows to trace *M. neglecta* invasion in the Sea of Azov since 2010. Our own data, as well as information on the invader occurrence in the Sea of Azov (Boltachova & Lisitskaya, 2019 ; Bulysheva et al., 2020 ; Syomin et al., 2016a ; Frolenko & Maltseva, 2017 ; Syomin et al., 2016b, 2017), show that the species formed a stable colony in the water area with a dynamic salinity regime.

In the Sea of Azov, salinity averages 11–12 ‰. In the Taganrog Bay, which is characterized by the maximum spatial heterogeneity related to the effect of the Don runoff and the nature of water circulation, salinity varies within 1–9 ‰ (Ekologicheskii atlas Azovskogo morya, 2011). Interannual fluctuations in the sea salinity are irregular: desalinization periods of varying duration are replaced by salinization periods. In the sea, interannual fluctuations in salinity can reach 1 ‰; in the Taganrog Bay, the range is even higher – up to 3.6 ‰ (Gidrometeorologiya, 1991). Since 2007, a steady increase in the sea salinity was observed. In 2010–2020, the mean salinity in the open sea increased from 11.5 to 15.0 ‰, and in the Taganrog Bay, from 8.5 to 11.0 ‰.

The aim of this work is to describe the history of *M. neglecta* colony formation in the northeastern Sea of Azov, to determine the role of abiotic environmental factors in this process, and to assess the current state of the invader population in the Sea of Azov basin.

MATERIAL AND METHODS

Complex surveys in the Sea of Azov were performed according to the standard grid of stations applied in AzNIIRKh since 1952 (Metody rybokhozyaistvennykh, 2005). Annually, 1–4 cruises on the RV were carried out. The article presents the results of the summer survey in 2010, when alien spionids were revealed in the Sea of Azov for the first time, as well as the results of autumn surveys in 2012–2020. Based on them, interannual dynamics of *M. neglecta* abundance is analyzed (Table 1). Sampling was carried out with a Petersen grab with a capture area of 0.1 m^2, in duplicate. The material was processed according to the methodological recommendations (Metody rybokhozyaistvennykh, 2005). Benthos was washed through sieves with a filtration mesh diameter of 5.0 and 0.3 mm (upper and lower sieve, respectively). As a fixative, we used 4 % neutralized formalin or 76 % ethanol with formalin added to prevent maceration of worm tissues.

Table 1. Number of sampling stations carried out in the northeastern Sea of Azov

Month and year	Number of sampling stations	Month and year	Number of sampling stations
July 2010	21	October 2016	17
October 2011	25	September–October 2017	17
October 2012	21	September–October 2018	17
October 2013	16	October 2019	17
October 2014	21	October 2020	18
October 2015	17	**In total**	**207**

Benthic samples were analyzed under a binocular. With high abundance of juvenile worms, a sample was taken, and the individuals were counted in a Bogorov chamber. When analyzing the species population structure, two indicators of specific abundance were used – mean abundance and ecological abundance. Mean abundance (number of worms *per* unit area) was calculated considering all stations. Ecological abundance (abundance in a colony) was determined as the number of worms *per* unit of habitat, *i. e.*, excluding stations with zero values.

To determine salinity, samples were taken at 18 standard stations with a Niskin bathometer: in the bay and in the sea at depths less than 7 m, at two horizons (surface and bottom layer); at depths over 7 m, at three horizons (surface, 5 m, and bottom layer). Maps were generated with Surfer v15. The data were statistically processed using the PAST software (Hammer, 2012).

RESULTS

Spatial distribution. For the first time, alien polychaetes were recorded in samples in July 2010. The colony of worms occupied the eastern Sea of Azov and the western Taganrog Bay (Fig. 1). The core of the population, with the abundance reaching 6,000 ind.·m^{-2}, was localized in the silted shell rocks of the Yeleninsky banks. There, salinity was of 11.5 ‰.

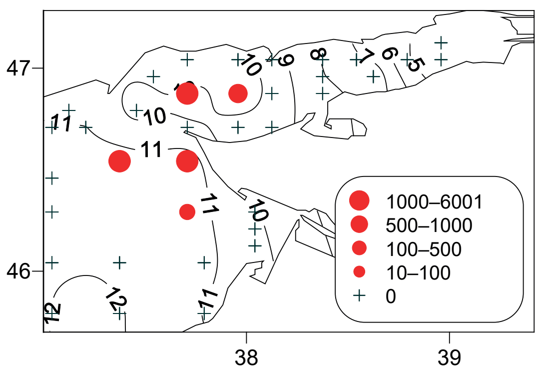

Fig. 1. *Marenzelleria neglecta* abundance, ind.·m^{-2}, in the northeastern Sea of Azov in July 2010 (isolines indicate salinity, ‰)

Since 2012, *M. neglecta* was regularly recorded in almost all surveys, and the polychaete colony occupied the estuarine area of the open sea and most of the Taganrog Bay (Fig. 2). The eastern boundary of the range, in comparison with that of the summer 2010, shifted towards east and ran along the line connecting the Beglitskaya Spit with Port-Katon. The core of the population, with the abundance of worms reaching 55,175 ind.·m^{-2}, was localized in the western bay. Mean water salinity in the western Taganrog Bay was 9.9 ‰. At the Yasensky Bay mouth, the abundance of worms was of 250 ind.·m^{-2}.

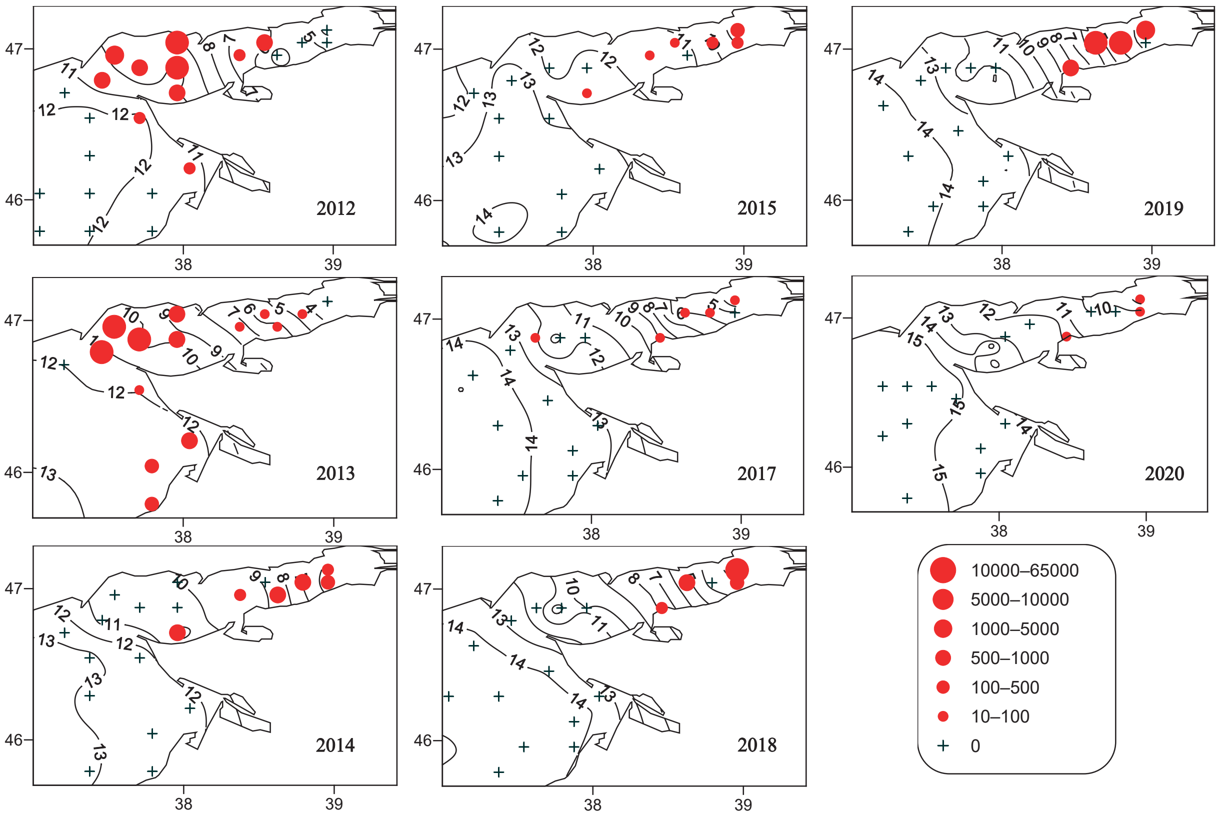

Fig. 2. *Marenzelleria neglecta* abundance, ind.·m^{-2}, in the northeastern Sea of Azov in 2012–2020 in autumn (isolines indicate salinity, ‰)

In 2013, there were no significant changes in the spatial distribution of polychaetes. The main colony still occupied the estuarine sea area and the bay; the core was localized in the western bay (water salinity of 10.2 ‰); and the abundance remained high – up to 61,500 ind.·m^{-2}. The eastern boundary of the range shifted even further: the worms were found in the section Taganrog – the Semibalki village. The water area covered by the eastern aggregation increased, and this aggregation moved southward. Its maximum abundance was of 482 ind.·m^{-2}. Since 2014, changes in the spatial structure were recorded, and a drop in the population abundance was registered. The range of polychaetes began to decrease, and the species was no longer found in the considered sea area (salinity was of 12.3–12.9 ‰). The core of the colony shifted to the central Taganrog Bay (9.1 ‰), and maximum abundance decreased by an order of magnitude – down to 4,620 ind.·m^{-2}.

In 2015, the core of the polychaete aggregation shifted even further – to the eastern bay (9.1 ‰), and maximum abundance decreased to 640 ind.·m^{-2}. Salinity in the central Taganrog Bay reached 11.3 ‰, in the western bay, 12.5 ‰, and in the open sea, 13.3 ‰. In 2016, no polychaetes were found in the Sea of Azov. Salinity in the eastern Taganrog Bay, where the core of the aggregation was localized earlier, dropped to 3.5 ‰. In the central area, the value was 6.9 ‰, in the western area, 12.6 ‰, and in the open sea, 13.8 ‰. In 2017, single worms were recorded in the western Taganrog Bay (12.1 ‰); the main colony, with the abundance up to 640 ind.·m^{-2}, was registered on the border of the eastern and central Taganrog Bay (water salinity of 4.7 and 7.5 ‰, respectively).

In 2018–2020, worms completely disappeared from the western area (11.2–13.7 ‰). The range of the invader was limited to the central and eastern Taganrog Bay. In 2018, the core of the aggregation, with the abundance up to 1,890 ind.·m^{-2}, was found in the eastern bay (3.2 ‰). In 2019, the maximum (11,000 ind.·m^{-2}) was recorded in the central area, with its salinity reaching 7.0 ‰. In 2020, the abundance of worms decreased sharply: the maximum was 235 ind.·m^{-2}, and the species mainly occupied the eastern Taganrog Bay (9.7 ‰).

Dynamics of quantitative indicators. In 2012 and 2013, the mean abundance of *M. neglecta* was high – 4,628 and 7,084 ind.·m^{-2}, respectively. High values were recorded for ecological abundance as well – 9,719 and 8,720 ind.·m^{-2}, respectively. The next two years, 2014 and 2015, were characterized by a decrease in both indicators by an order of magnitude (Fig. 3). In 2017, mean and ecological abundance of polychaetes remained at a low level – 98 and 334 ind.·m^{-2}, respectively. Then, the population abundance began to increase gradually. By 2018, the mean abundance of worms was 274 ind.·m^{-2}; by 2019, the value reached 1,050 ind.·m^{-2}. A more noticeable growth was observed within the colony: in 2018, ecological abundance was 933 ind.·m^{-2}; by 2019, it was 4,464 ind.·m^{-2}. In 2020, the lowest values for the entire period were registered – the mean abundance of 16 ind.·m^{-2} and ecological abundance of 98 ind.·m^{-2}.

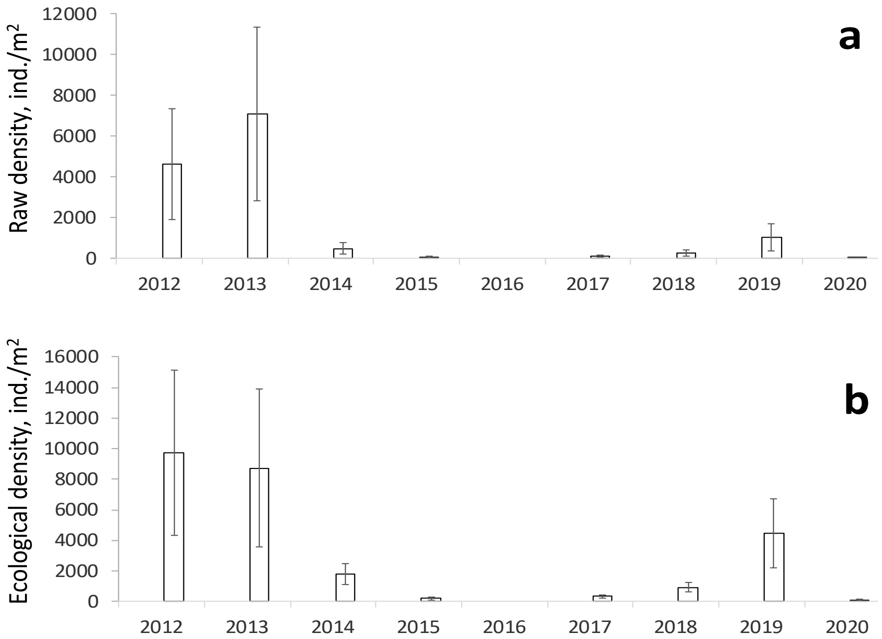

Fig. 3. Dynamics of mean abundance (number of individuals *per* unit area) (a) and ecological abundance (number of individuals *per* unit of habitat) (b) of *Marenzelleria neglecta* in the northeastern Sea of Azov in 2010–2020. Error bars indicate standard error

The structure of prevalence in communities. The main outbreak of the invader abundance was recorded in the western Taganrog Bay. There, *prior* to its beginning (in 2010 and 2011), mass and common benthic species – those with frequency of occurrence ≥ 50 % – were oligochaetes, two polychaetes (*Alitta succinea* (Leuckart, 1847) and *Polydora cornuta* Bosc, 1802), gastropods *Hydrobia* spp., and bivalves *Cerastoderma glaucum* (Bruguière, 1789). The total abundance of macrobenthos in the area averaged 8,953 ind.·m^{-2} in 2010 and 13,358 ind.·m^{-2} in 2011. The listed species and groups accounted for more than 90 % of the total population abundance. In 2012 and 2013, the polychaete *M. neglecta* was registered at all stations. Out of other representatives of the benthic fauna, *A. succinea*, *Hydrobia* spp., and oligochaete worms maintained high frequency of occurrence. The abundance of benthos increased threefold and amounted to 33,848 and 38,944 ind.·m^{-2} in 2012 and 2013, respectively.

In 2012, *M. neglecta* accounted for an average of 38 % of the total abundance in the western area; in 2013, the value was 58 %. During this period, the ratio of the invader in the communities reached 92 % of the total abundance at some stations (Fig. 4).

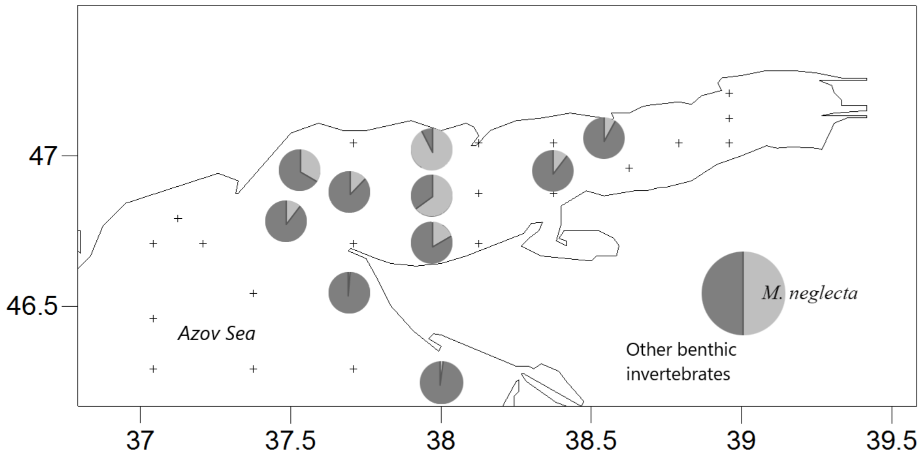

Fig. 4. *Marenzelleria neglecta* ratio in the total abundance of zoobenthos in the Sea of Azov in autumn 2012

In the central and eastern Taganrog Bay, *M. neglecta* was found in mass since 2014. *Prior* to its invasion, oligochaetes, *A. succinea*, and the polychaete *Hediste diversicolor* (O. F. Müller, 1776) prevailed in the bottom communities of this water area. In the eastern Taganrog Bay, the relict polychaetes *Hypaniola kowalewskii* (Grimm in Annenkova, 1927), cumaceans *Pterocuma pectinatum* (Sowinsky, 1893), and insect larvae of the family Chironomidae had high frequency of occurrence. Together, these groups accounted for 88 % of the total abundance of benthic fauna in the central Taganrog Bay and 97 % in its eastern area. In the central area in 2010–2013, the mean abundance of benthos varied from 2,591 to 8,825 ind.·m^{-2}. In 2014, this indicator did not change significantly (3,320 ind.·m^{-2}). *M. neglecta* ratio in the community averaged 31 %. In 2010–2013 in the eastern Taganrog Bay, mean abundance varied from 5,310 to 26,995 ind.·m^{-2}. In 2014, it decreased to 2,393 ind.·m^{-2} due to a drop in the abundance of oligochaetes. *M. neglecta* ratio reached 36 %.

DISCUSSION

M. neglecta expansion into the coastal waters of continental Europe has been studied in detail (Ezhova et al., 2005 ; Maximov, 2011 ; Norkko et al., 1993 ; Zettler et al., 2002 ; Zmudzinski et al., 1993). The polychaete invaded the southern Baltic around the mid-1980s and rapidly distributed in the coastal sea areas; the species was recorded in the Netherlands, Germany, Poland, Russia, Lithuania, Latvia, and Estonia (*Marenzelleria neglecta*, 2021). In the early 1990s, *M. neglecta* reached the coast of Sweden where it was recorded at the Gulf of Finland mouth. In 1990–1993, it invaded the eastern Gulf of Finland and the southern Bothnian Bay. By 2000, the species distributed throughout the entire Gulf of Finland, up to the freshwater Neva Bay.

High rate of worm dispersion is due to its long larval stage. As shown, the pelagic stage of *M. neglecta* at +20 °C lasts for 4–5 weeks; at a lower temperature (+5 °C), the process can last for 2.5–3 months (Bochert, 1997). Juvenile polychaetes are also known to be highly motile and capable of staying in plankton (Dauer et al., 1980, 1982, cited from: Bochert et al., 1996). This provides the species with additional opportunities when colonizing new water areas.

In the Sea of Azov, worm dispersion was very rapid as well. In 3–4 years after the first record of polychaetes at the Taganrog Bay mouth, high-abundant aggregations of *M. neglecta* were registered throughout the northeastern sea, *inter alia* in the bay. According to both literature data and our own observations, *M. neglecta* was also found in other sea areas, up to the Kerch Strait (Boltachova & Lisitskaya, 2019 ; Bulysheva et al., 2020 ; Frolenko & Maltseva, 2017). In 2014, the invader was registered in the Don delta. In 2016 and 2017, worms were regularly recorded at a considerable distance from the mouth – in the upper Mokraya Kalancha channel (Zhivoglyadova & Elfimova, 2021). *M. neglecta* colonies were observed in the Azov estuaries of the Krasnodar Region. In 2015, an aggregation of polychaetes, with the abundance of 160 ind.·m^{-2}, was found in the Akhtarsky estuary.

As shown, with no restrictions on food resource which is typical for eutrophic water areas, polychaetes are capable of increasing their abundance rapidly. This is facilitated by high fecundity of *M. neglecta* (10–40 thousand of eggs *per* ind.) and early maturity which can be reached already during the first year of life (Bochert & Bick, 1995).

In the Sea of Azov, high abundance of the population (5–7 thousand ind.·m^{-2}) was revealed in 2012 and 2013. Comparable values were registered in some areas of the Baltic. Specifically, in the Darss-Zingst lagoons (Germany), a few years after the first record of *M. neglecta* population, there was an outbreak which resulted in a sharp increase of the abundance – from several hundreds to 5,000 ind.·m^{-2} – and a subsequent maximum of 10,000 ind.·m^{-2} (Zettler et al., 2002). An exponential increase in *M. neglecta* abundance and its high values were observed in the Vistula Lagoon as well: in 1988–1994, the abundance of polychaetes reached 5–7 thousand ind.·m^{-2} (Ezhova & Spirido, 2005).

Thus, at the initial stage of invasion, the reasons for the active development of *M. neglecta* population in the Sea of Azov seemed to be high trophic status of the water body and favorable salinity conditions. In 2010–2013 in the western Taganrog Bay, where polychaete colonies with the highest abundance were recoded, salinity averaged 9.7–10.0 ‰; in the northeastern sea, 11.4–12.2 ‰. Apparently, further dispersion of the population was determined by the dynamics of this factor.

The upper optimum limit for the polychaete is 10 ‰ (Sikorski & Bick, 2004). Worms were no longer found in the northeastern sea at mean salinity of 12.9 ‰ (2014); in the western Taganrog Bay, the abundance of colonies decreased by almost an order of magnitude with a rise in salinity to 12.5 ‰ (2015). Then, the population almost completely shifted to freshened areas of the bay – the central and eastern ones, with mean salinity of 10.2 and 7.6 ‰, respectively. Apparently, the eastern Taganrog Bay has unfavorable conditions for the species reproduction. The experiment showed that at salinity < 5 ‰, the survival of larvae is problematic: those cannot complete their development and switch to a benthic lifestyle (Bochert, 1997). According to our data, water salinity in the eastern area in different years varied from 1.4 to 9.1 ‰. Out of the entire observation period, salinity in the eastern Taganrog Bay was higher than the isohaline of 5 ‰ only in 2014 and 2015, and this should have contributed to successful reproduction of the species.

Conclusion. High salinity currently recorded in the Sea of Azov seems to limit the dispersion and to inhibit the large-scale invasion of *Marenzelleria neglecta* there. Despite the facts of worm registration throughout the entire water body, *M. neglecta* forms aggregations with the high abundance only in its desalinated areas. For this species, the optimum of water salinity varies between 7–12 ‰. Since 2017, a stable polychaete population exists within the central and eastern Taganrog Bay. At the same time, significant fluctuations in quantitative indicators are still observed in the colony. Apparently, the main reason for it is a dynamic salinity regime: the species reproduction depends on the hydrological situation. Evidently, further *M. neglecta* development in the Sea of Azov will be controlled by water salinity. Long-term positive trend of its values allows to assess the situation for the species development as unfavorable.

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ИСТОРИЯ ОСВОЕНИЯ СЕВЕРОАМЕРИКАНСКОЙ ПОЛИХЕТОЙ *MARENZELLERIA NEGLECTA* SIKORSKI & BICK, 2004 (ANNELIDA: SPIONIDAE) СЕВЕРО-ВОСТОЧНОЙ ЧАСТИ АЗОВСКОГО МОРЯ

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В начале 2010-х гг. чужеродная полихета *Marenzelleria neglecta* Sikorski & Bick, 2004 вторглась в бассейн Азовского моря. За несколько лет вид широко расселился по опреснённой акватории моря, а также был отмечен в дельте Дона и в азово-кубанских лиманах.

История формирования чужеродным видом устойчивого и многочисленного поселения, локализованного в северо-восточной части моря, прослежена по материалам комплексных гидробиологических и гидрологических съёмок 2010–2020 гг. Развитие популяции вселенца в водоёме-реципиенте происходило на фоне увеличения его солёности. Очевидно, этот фактор оказал решающее влияние на инвазионный процесс. За вспышкой численности, наблюдавшейся в западной части Таганрогского залива в 2012 и 2013 гг., последовало резкое уменьшение показателей обилия, вплоть до полного отсутствия полихет в пробах. Снижение численности червей сопровождалось сокращением ареала и смещением ядра плотности в наиболее распреснённые районы моря. В настоящее время постоянное поселение *M. neglecta* существует в границах центрального и восточного районов Таганрогского залива. Проанализировано изменение структуры доминирования в донных сообществах в ходе инвазии. Показано, что доля чужеродных полихет в периоды их массового развития на отдельных станциях достигала 92 % общей численности бентоса.

Ключевые слова: Polychaeta, чужеродные виды, донные сообщества, макрозообентос, эстуарии, Азовское море