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Large-Scale Invasion of *Marenzelleria* spp. (Polychaeta; Spionidae) in the Eastern Gulf of Finland, Baltic Sea

A. A. Maximov
Zoological Institute, Russian Academy of Sciences, Universitetskaya nab. 1, St. Petersburg, 199034 Russia
e-mail: alexeymaximov@mail.ru

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Abstract—Polychaetes of the genus *Marenzelleria* are among the most successful introduced species in the Baltic Sea. Invading it for the first time in 1985, they rapidly colonized the entire sea, where they are currently represented by three closely related species. They have been recorded in the Russian waters of the Gulf of Finland since 1996. Until 2009, the introduction of polychaetes (identified as *Marenzelleria neglecta*) in the Gulf of Finland was not accompanied by any considerable changes in bottom communities. High biomass of *M. neglecta* was observed only in shallow-water areas of limited size above the summer thermocline. In 2009, polychaetes first occupied deep-water areas, which was related to the invasion of *M. arctia*, an arctic member of the genus, new to the eastern Gulf of Finland. Abundant reproduction of this species led to a multiple increase in the biomass of the macrozoobenthos. The role of polychaetes was especially considerable in areas of the bottom periodically affected by hypoxia, where macrozoobenthos was previously absent or extremely depleted. Because of the invasion, a large area of the gulf became occupied by almost single-species macrozoobenthos. *M. arctia* is characterized by considerable bioturbation and bioirrigation activity, and the introduction of this species has given the deep-water areas of the gulf a new functional group of benthos. The polychaete invasion, owing to its considerable impact on the biogeochemical processes and trophic relations in the eastern Gulf of Finland, will probably lead over the next few years to a cardinal reorganization at the scale of the entire ecosystem.

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INTRODUCTION

The geologically young Baltic Sea is considered one of the waterbodies most sensitive to biological invasions in the world (Leppäkoski et al., 2002, 2002a; Olenin, 2005; Paavola et al., 2005). This is also quite true of the Russian waters of the Gulf of Finland, where invaders make up about 5% of the total number of species and often dominate communities (Panov et al., 2003; Orlova et al., 2006). However, most alien species originate from the warm-water Ponto-Caspian Basin, and their distribution is mainly restricted to the well-heated surface waters above the summer thermocline. In bottom communities, consequently, visible changes took place only in littoral areas of relatively small size, where the proportion of alien organisms in the total benthos biomass at particular stations sometimes reached 96% (Orlova et al., 2006; *Ekosistema*..., 2008).

The fauna of open areas is qualitatively depleted and until recently largely retained its natural aspect. Over large areas of the bottom in the deep-water zone, macrozoobenthos was represented almost exclusively by cold-loving crustacean glacial relicts: *Saduria entomon* (L.), *Monoporeia affinis* (Lindstöm), and *Pontoporeia femorata* Kröyer. Until the mid-1990s, the bottom fauna of deep-water areas was undergoing considerable quantitative development (Maximov, 1997). Subsequently, considerable depletion or in some years even complete disappearance of the macrozoobenthos was observed owing to hypoxia and anoxia periodically emerging at the bottom, mainly related to the strengthening advection of oxygen-depleted salty deep waters from the Baltic Sea proper into the upper part of the Gulf of Finland, caused by large-scale variation in hydrometeorological processes in the region (Maximov, 2003; Maximov, 2006, 2008).

In this study, on the basis of collections made in 2008 and 2009, dramatic changes in the fauna of deep-water areas related to the abundant reproduction of the alien polychaetes *Marenzelleria* spp. are described. The uncertainty in the species name is due to the following reason. Molecular methods have shown that the Baltic Sea is currently actively colonized by several morphologically very similar species of this genus; two of these have been recorded within the boundaries of the Gulf of Finland: *M. neglecta* Sikorski et Bick and *M. arctia* (Chamberlin) (Bastrop and Blank, 2006; Blank et al., 2008). The identification of these closely related species based on morphological characters requires examining large intact individuals (Sikorski

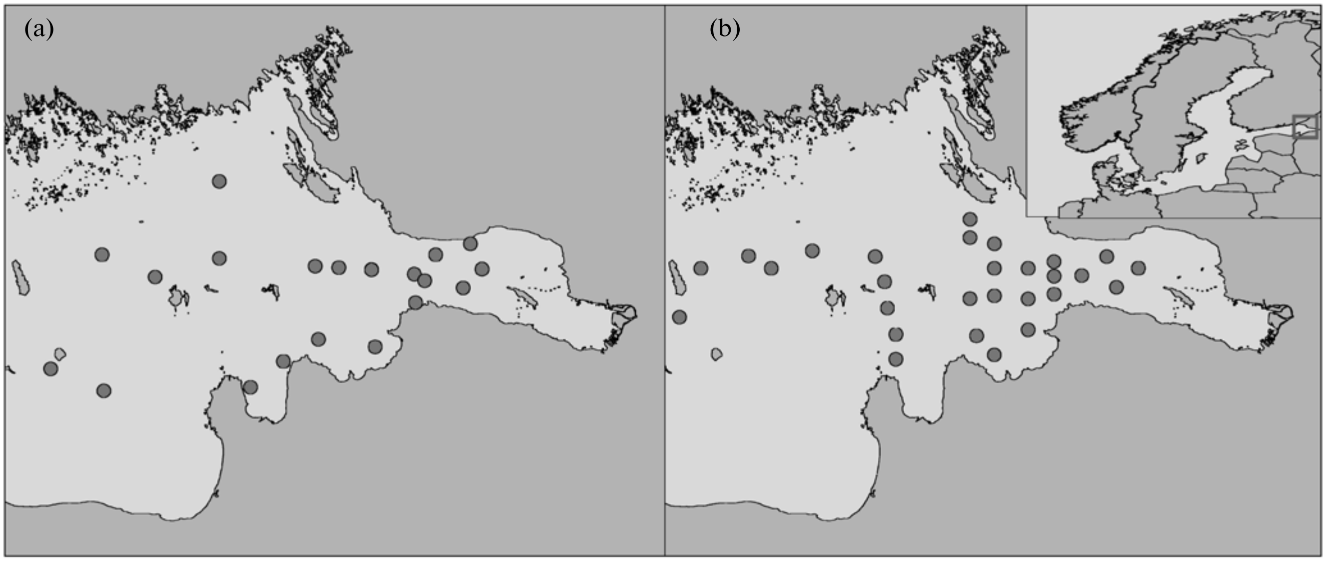

Fig. 1. Position of sampling stations in the eastern part of the Gulf of Finland in 2008 (a) and 2009 (b).

and Bick, 2004; Bastrop and Blank, 2006). Thus, a large proportion of the material in samples is in principle unidentifiable.

MATERIALS AND METHODS

The Gulf of Finland, one of the largest gulfs of the Baltic Sea, reaches deep into the land, stretching 420 km from west to east. The eastern part of the Gulf of Finland is usually understood as the water area confined between the islands of Kotlin and Gogland. In the east, this brackish waterbody is currently separated from the freshwater Neva Bay by a complex of constructions protecting the city of St. Petersburg from floods; in the west, it is limited by the meridian 27° E (Gogland Island). Detailed hydrological, hydrochemical, and hydrobiological descriptions of the area can be found in a recently published monograph (*Ekosistema...*, 2008).

Macrozoobenthos was collected in July–August 2008 and 2009 in open areas of the eastern Gulf of Finland at 51 stations (Fig. 1). The depth at the sampling stations varied from 13 to 75 m. The samples were taken with Van Veen grabs with surface area of 0.025 and 0.1 m^2. In 2008, in the open parts of the gulf at some stations, the DG-0.08 hydraulic grab (surface area 0.08 m^2) developed by the Northern State Scientific-Production Company of Marine Geological Prospecting (SEVMORGEO) was used. This grab is similar in design to the Van Veen grab, but is provided with a more convenient (especially for work in windy weather) hydraulic closing mechanism triggered immediately after the instrument touches the bottom. Usually two or three samples were taken at each station. The samples were washed through a nylon sieve with mesh size of 0.4 mm and preserved in 4% formaldehyde. Subsequent processing of the material was carried out in the laboratory according to the standard procedure.

RESULTS

The quantitative distribution of macrozoobenthos in 2008 was extremely uneven (Fig. 2). In benthos abundance parameters, a decreasing trend with depth was observed. The highest biomass (66.5 g/m^2) was recorded in Koporye Bay at a depth of 13 m owing to the development of the marine bivalve mollusk *Macoma balthica* L. A relatively high level of quantitative development (up to 22.9 g/m^2) of the bottom macrofauna was typical also of shallow-water stations (depth less than 25 m) in the upper part of the Gulf of Finland near Kotlin Island, where the benthos consisted mostly of oligochaetes. At the same time, the biomass of bottom animals in the deep-water areas, which occupy most of the gulf's bottom, was usually very low because of hypoxia, which is typical of these areas. The fauna of areas with silty bottom was especially depleted, and at some of such stations, complete absence of macrozoobenthos was recorded.

By 2009, the distribution of macrobenthos had fundamentally changed (Fig. 3). This happened because of the sharp increase in biomass in the deep-water zone as a result of a surge in the abundance of alien polychaetes *Marenzelleria* spp.[1] These polychaetes colonized most of the gulf's area, taking a dominant

[1] According to G.N. Buzhinskaya's identification, all identifiable specimens from deep-water stations belonged to a single species, *M. arctia* (Chamberlin); however, since the samples included juvenile and fragmented worms that could not be safely identified, the term *Marenzelleria* spp. is used in this study.

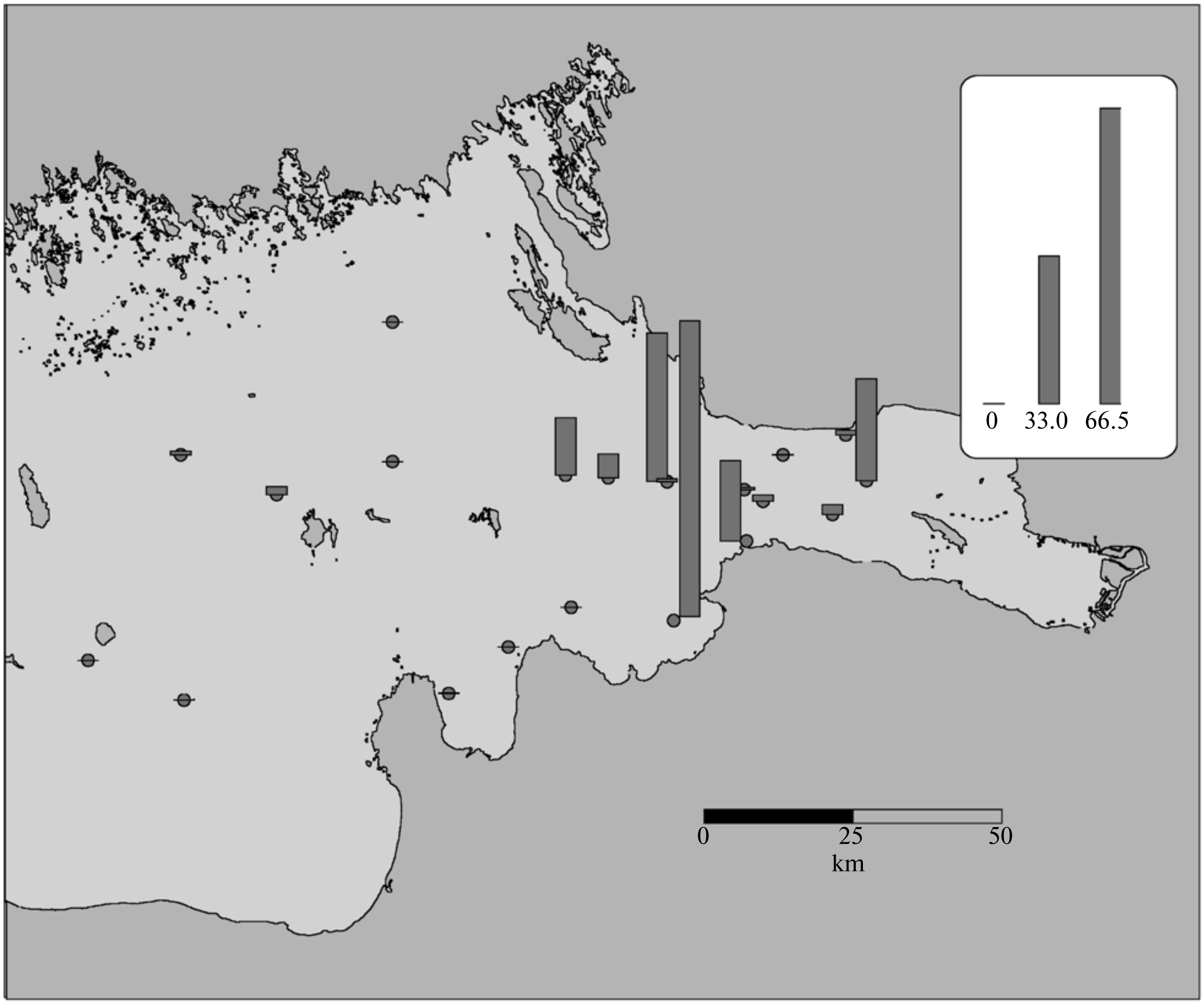

Fig. 2. Macrozoobenthos biomass (g/m^2) in the eastern part of the Gulf of Finland in 2008.

position in the benthos of almost all deep-water stations (Fig. 4). Only some areas of the bottom were dominated by *S. entomon*, mostly due to random sampling of scarce specimens of these large crustaceans. The role of polychaetes was especially great in parts of the bottom affected by hypoxia, where in 2008 macrozoobenthos was extremely depleted or absent. At such stations, *Marenzelleria* spp. was practically the only member of the macrofauna, making up over 99% of the total biomass (Fig. 4). In shallow-water areas of the Gulf of Finland, in contrast to deep-water areas, the composition and quantitative parameters of the benthos remained almost unchanged: these areas were still dominated by oligochaetes and the bivalve mollusk *Macoma balthica*. Consequently, the differences in benthos development level between different deep-water areas observed in 2008 had disappeared. Moreover, in 2009, even higher benthos biomass was typical of deep-water stations compared to shallow-water stations. It was in the deep-water zone, at a depth of 38 m, that the highest benthos biomass (94.1 g/m^2) was recorded.

DISCUSSION

Polychaetes of the genus *Marenzelleria* are among the most successful species recently introduced to the Baltic Sea (Zettler et al., 2002). They first appeared in the Baltic Sea in 1985, and quickly colonized large areas of the bottom in the South Baltic Sea, occupying a dominant position in the benthos of some areas (Rudinskaya, 2000; Zmudzinski et al., 1996; Ezhova et al., 2005; etc.). The polychaetes that had invaded the Baltic Sea were initially identified as *M. viridis* (Verill), a species of North American origin. Subsequently, following a revision of the genus, they were treated as a separate species, *M. neglecta*, also of North American descent (Sikorski and Bick, 2004). In the

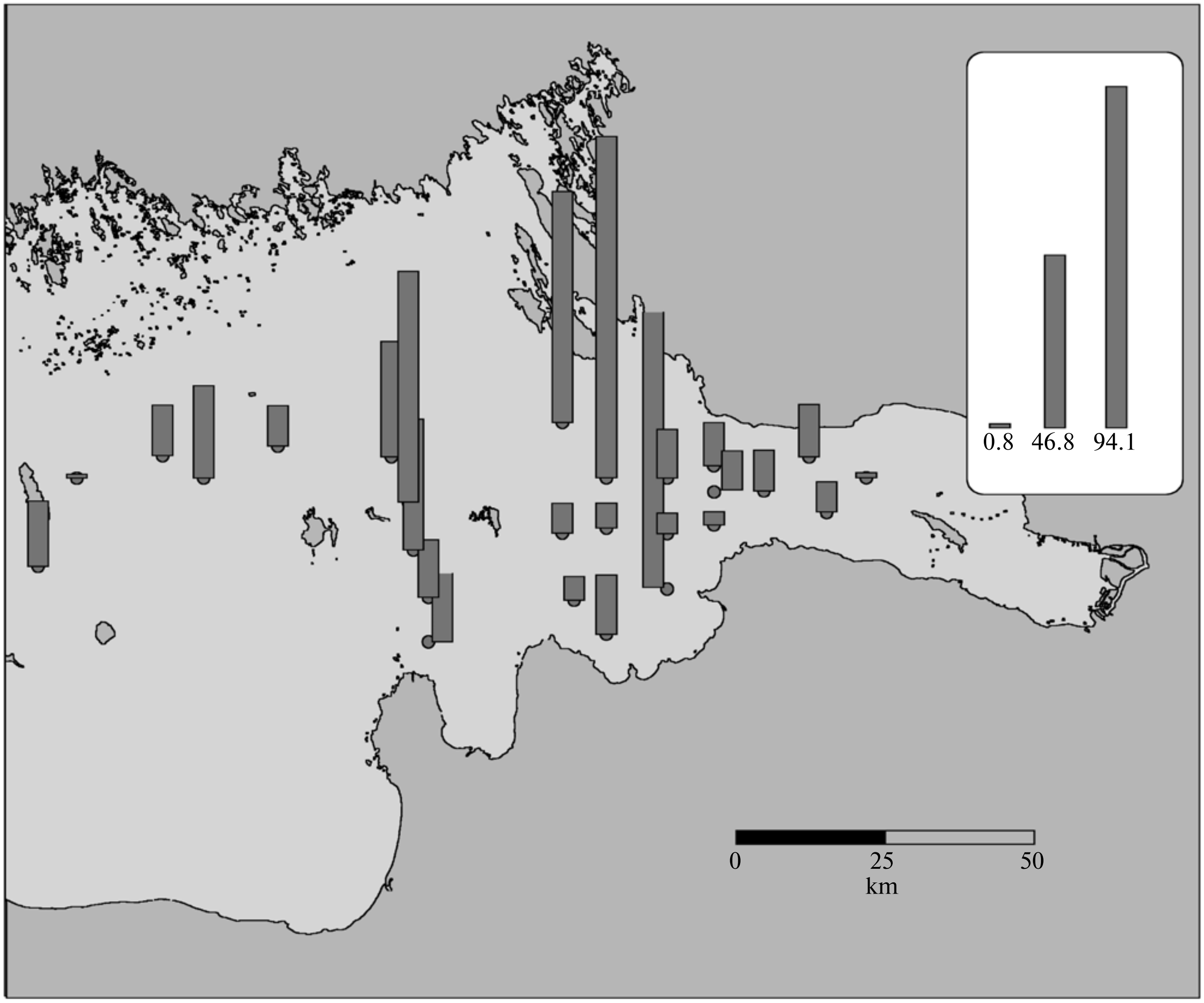

Fig. 3. Macrozoobenthos biomass (g/m^2) in the eastern part of the Gulf of Finland in 2009.

first half of the 1990s, these polychaetes became distributed in the Estonian and Finnish waters of the Gulf of Finland (Norkko et al., 1993; Stigzelius et al., 1997; Kotta and Kotta, 1998). In 1996, *M. neglecta* was first found in the Russian part of the gulf (Lyakhin et al., 1997), where it soon became a common component of the bottom fauna (Maximov and Panov, 2003). In the mid-2000s, the introduction of two more members of the genus *Marenzelleria* was recorded in the Baltic Sea: the aforementioned *M. viridis* and *M. arctia* (Chamberlin) (Bastrop and Blank, 2006; Blank et al., 2008). The latter species was known earlier only from the Arctic Basin (Sikorski and Buzhinskaya, 1998). Thus, the presence of three species of the genus in the Baltic Sea has been confirmed to date: *M. arctia, M. neglecta*, and *M. viridis.*

The introduction of *M. neglecta* was not accompanied by any considerable changes in the bottom communities of the eastern Gulf of Finland. Although at some stations considerable accumulations of polychaetes were observed, on the whole, in comparison with the South Baltic Sea, their abundance and biomass in the study area remained low until 2009, and the distribution of quantitatively developed polychaete populations was restricted to shallow-water areas of relatively small size lying above the summer thermocline (Maximov, 2009). In deeper areas, the episodic emergence of bottom hypoxia that led to mass mortality of macrozoobenthos and formation of large dead zones has become a typical feature during the last 15 years (Maximov, 2008). *M. neglecta* has planktonic larva and is, therefore, capable of quickly colonizing vacant areas of the bottom when oxygen-related conditions improve. In some years, abundant settling of young polychaetes was observed in such dead zones (Maximov and Panov, 2003). However, this species was for a long time unable to establish itself in deep-water areas. The reasons for this are not completely clear. In some

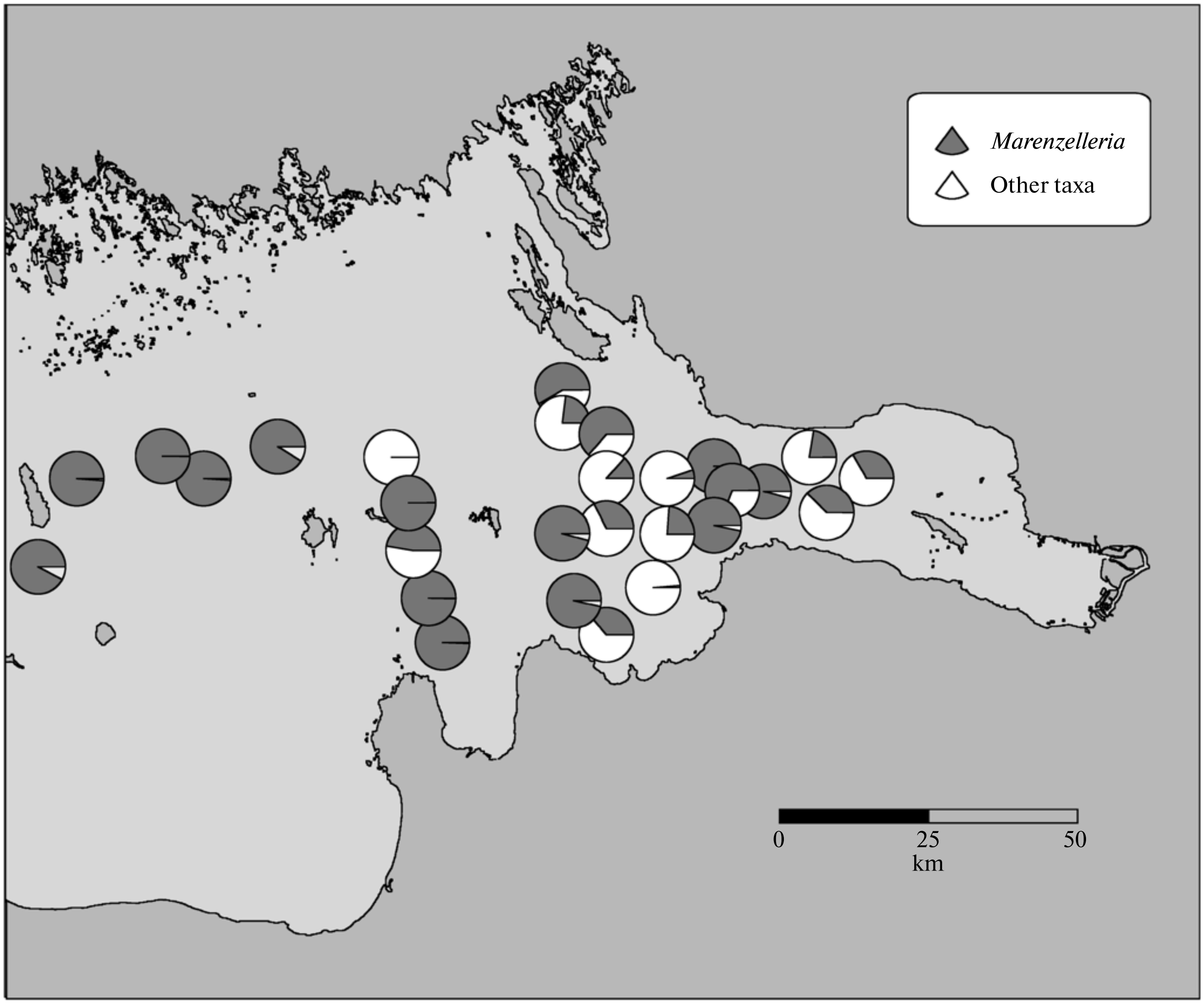

Fig. 4. Proportion of *Marenzelleria* spp. in the total macrozoobenthos biomass in 2009.

areas, repeated cases of hypoxia impeded polychaete colonization. However, even in parts of the deep-water zone with a favorable oxygen regime, *M. neglecta* was scarce. The factor that impeded the development of this relatively heat-loving Atlantic species was probably the low temperature of the bottom waters in the upper part of the Gulf of Finland. This factor is known to limit the distribution of many other marine animals in the North Baltic Sea (Segerstråle, 1972; Järvekülg, 1979; Elmgren, 1984). The abundant reproduction of alien polychaetes in the cold waters below the thermocline in 2009 was probably related to the invasion of an arctic member of the genus, *M. arctia*, better adapted to low temperature compared to the boreal *M. neglecta*. The introduction of *M. arctia* is considered to be related to the recent successful colonization of open areas of the North Baltic Sea by polychaetes (Bastrop and Blank, 2006; Blank et al., 2008). In the eastern part of the Gulf of Finland, the surge in polychaete abundance in 2009 may have been, at least partly, facilitated also by the high survival rate of their pelagic larvae owing to the conditions of that year favorable for planktonic organism development. For instance, according to L.F. Litvinchuk's unpublished data (personal communication), a sharp increase in the biomass of zooplankton was recorded in the Gulf of Finland in 2009.

As a result of the *M. arctia* invasion, most of the gulf's area became occupied almost exclusively by this macrozoobenthos species (Figs. 3, 4), which replaced the community of glacial crustacean relicts that had existed there before, in which the role as important as that played currently by polychaetes was played by the amphipod *Monoporeia affinis*, which at some stations made up over 99% of the total abundance of macrozoobenthos (Maximov, 1993).

A sharp decrease in the abundance of *M. affinis*, a key species in the deep-water Baltic communities, was recorded in recent years also in other areas of the Baltic Sea. Some authors (Kotta and Olafson, 2003; Neideman et al., 2003; Kotta et al., 2006) explain this by competition with *Marenzelleria* spp., relying on results of experimental studies. However, the possibility of polychaetes replacing relict amphipods in natural conditions invokes strong doubts, since both species have long been occurring sympatrically in the estuaries of large Siberian rivers. For instance, *Marenzelleria*—which according to recent data is exactly *M. arctia* (Sikorski and Buzhinskaya, 1998; Sikorski and Bick, 2004)—and *M. affinis* constitute most of the macrozoobenthos in the Yenisei Gulf (Pirozhnikov, 1984, 1986). The presence of considerable competition between these animals is also unconfirmed by a number of experimental studies, the authors of which consider the decrease in the abundance of these crustaceans to be related to other processes (Eriksson Wiklund et al., 2008, 2009). Apparently, the polychaete invasion is not the reason for the *M. affinis* population decrease in the Baltic Sea. On the contrary, the decrease in the abundance of this species, which previously dominated Baltic communities, was probably caused by other factors and made the expansion of *Marenzelleria* spp. markedly easier. In the eastern part of the Gulf of Finland, the most important of these factors was probably the worsening oxygen regime of bottom waters, which led to the destruction of the earlier bottom communities (Maximov, 2003, 2008). The sharp increase in polychaete abundance took place only after the amphipod population disappeared because of hypoxia. This increase was especially pronounced in the areas that had suffered most from hypoxia.

It is, however, beyond doubt that the complex of hydrochemical conditions that has been established currently in the gulf is markedly more favorable to the invading opportunistic polychaete species than to the stenobiont native glacial relicts. A high degree of tolerance to hypoxia is typical of *Marenzelleria* species (Schiedek, 1997, 1999), while relict crustaceans are known for their special sensitivity to many unfavorable environmental factors, including oxygen deficiency (see, for example, (Sushchenya et al., 1986)). The high degree of tolerance to hypoxia in the invaders is probably a relatively widespread phenomenon. For instance, an increase in the role of invasive and cryptogenic species at low oxygen concentrations was observed in field experiments performed in the Chesapeake Bay (Jewett et al., 2005). In the strongly freshened eastern part of the Gulf of Finland, in addition to worsening oxygen-related conditions, the polychaetes probably benefited to some extent from an increase in salinity after the inflow of North Sea waters into the Baltic Sea (Eremina and Karlin, 2008). For instance, the first finding of *M. neglecta* in 1996 coincided with the entrance of salt waters into the upper part of the gulf from the Baltic Sea proper (Lyakhin et al., 1997).

Thus, the subsequent development of the situation in the Gulf of Finland will largely depend on hydrometeorological conditions, especially on the frequency of hypoxia recurrence. The long-term dynamics of the dissolved oxygen content in the eastern part of the Gulf of Finland is essentially cyclic, and bottom hypoxia was repeatedly recorded in the past (Maximov, 2006). In the past, improvements of the oxygen regime led to complete recovery of the initial structure of the benthos, though the recovery process sometimes took as long as several years (Maximov, 2003, 2008). The introduction of *M. arctia* to deep-water areas fundamentally changed the type of recovery succession in the bottom communities of the eastern Gulf of Finland after hypoxia-related mortality. Polychaetes, because of their planktonic larva, as well as the high tolerance of adult worms to low concentrations of oxygen, are capable of colonizing free areas of the bottom markedly more rapidly that the indigenous bottom animals. The consequences of the invasion are probably irreversible. Stable improvement of oxygen-related conditions would probably lead to the recovery of the populations of relicts, and the formation of a bottom biocenosis that would include *M. arctia* and the glacial relict crustaceans *S. entomon* and *M. affinis*, similar to that existing in the estuaries of Siberia (Pirozhnikov, 1984), could be expected. In reality, however, the episodically recurring cases of hypoxia will maintain the advantage of polychaetes, and the prevalence of *M. arctia* in deep-water areas will continue to be observed in the future. In this case, their continued prevalence can even be viewed as a positive phenomenon, since the newly formed communities are more stable and viable under the hydrochemical regime that has been established. On the whole, it can be noted that the successful naturalization of *Marenzelleria* spp. is clearly related to changes in the state of the ecosystem of the entire Baltic Sea. Only 25 years ago, members of this genus were absent in the Baltic Sea, while currently the presence of three from five described *Marenzelleria* species has been confirmed (Sikorski and Bick, 2004).

The consequences of such a large-scale invasion are hard to assess unequivocally. However, they will definitely prove quite considerable and will affect the entire ecosystem of the gulf. The introduction of *M. arctia* has resulted in the emergence, in the deep-water areas of the eastern part of the Gulf of Finland, of a new functional group of bottom animals, which play here the role of so-called ecosystem engineers (Crooks, 2002; Mermillod-Blondin and Rosenberg, 2006; Wallentinus and Nyberg, 2007). These polychaetes are known to dig over the substrate to a markedly greater depth (up to 40 cm) compared to indigenous species of the Baltic Sea. Thus, the introduction of these polychaetes is leading to a strong intensification of exchange processes at the boundary between the water and the bottom, in particular, to an increase in the outflow of nutrients from bottom sediments (see, for example, (Karlson et al., 2005; Hietanen et al., 2007)), which increases eutrophication, one of the main environmental problems of the Baltic Sea. This process, however, is probably important mostly in shallow-water areas. In deep-water areas of the Baltic Sea, including the Gulf of Finland, the biogeochemistry of nutrients is largely determined by oxygen-related conditions (Pitkänen et al., 2001; Conley et al., 2009]. Bioturbation and bioirrigation activity of worms, which leads to the absorption of oxygen by deep layers of the substrate and to the formation of a thick oxygenated layer, will probably accelerate the processes of phosphate burial and denitrification in deep-water bottom sediments (see, for example, (Karlson et al., 2007)), which may have the opposite effect on the dynamics of nutrients, decreasing their outflow into the water and, thus, reversing the eutrophication and improving the environmental state of the upper part of the Gulf of Finland.

It is also very difficult to predict unequivocally the impact of this invasion on the food supply of fish. The hypoxia-related decrease in the abundance of relict crustaceans in the eastern part of the Gulf of Finland had negative impact on the supply of such commercially important fishes as the European smelt and the Baltic herring (Golubkov et al., 2010). The formation of strong polychaete populations in 2009 led to a multiple increase in the macrozoobenthos biomass up to the highest values recorded in the eastern part of the Gulf of Finland during the periods of favorable oxygen-related conditions of the mid-1980s and the first half of the 1990s (Shishkin et al., 1989; Maximov, 1997). Thus, a rich food supply has formed now in the open areas of the gulf. However, the potential of its usage by the native fishes requires special studies. According to Polish investigators, the ability of *Marenzelleria* spp. to dig deep into the bottom reduces their accessibility to benthophagous fish in the South Baltic Sea (Zmudzinski, 1996). For the most abundant commercial fishes of the Gulf of Finland, the European smelt and the Baltic herring, a switch to feeding on polychaetes also seems problematic, since these fishes are strongly connected trophically with glacial relicts, which they feed on seasonally in winter (Golubkov et al., 2010). At the same time, there are data indicating that migrating worms are consumed by predatory fishes, e.g., zander (Winkler and Debus, 1996). The author of this study believes that such dramatic changes in the benthos are bound to influence the composition of the fish population, which in turn may lead to corresponding cascade effects at other trophic levels. Thus, the invasion of *M. arctia* will probably lead over the next few years to cardinal restructuring of the entire ecosystem in the eastern part of the Gulf of Finland as a result of considerable changes in biogeochemical processes and trophic relations.

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