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Long-Term and Seasonal Dynamics of the Population of *Cercopagis pengoi* (Ostroumov 1891) (Cladocera, Onychopoda) in the Eastern Part of the Gulf of Finland, Baltic Sea

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Abstract—Long-term seasonal studies of the population of *Cercopagis pengoi* (Ostroumov 1891) (Cladocera, Onychopoda) in the eastern Gulf of Finland were carried out for the first time. Material was collected every two weeks from mid-May to mid-October in the years 2009–2019, and only one species of the genus *Cercopagis* Sars 1897 (*C. pengoi*) was registered. Individuals of the first generation were found only during the first month of population development, from mid-May to mid-June. The second and subsequent generations developed from mid-June to mid-October. The appearance of the first generation in plankton in the spring occurred a month later than that observed in the Ponto-Caspian basin. In autumn, the disappearance of *C. pengoi* occurred at the same time as in the native range, in mid-October. The fecundity of parthenogenetic females was higher at the beginning of the growing season. In some years, individuals of the gamogenetic generation were not observed at all in the population. Compared to the populations inhabiting the Ponto-Caspian region, the duration of the growth season of the *C. pengoi* population was shorter, but the population density of this species was higher in the eastern part of the Gulf of Finland.

Keywords: Cladocera, *Cercopagis pengoi*, the eastern part of the Baltic Sea, population structure, peculiarities of reproduction

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INTRODUCTION

In recent decades, the large planktonic cladoceran *Cercopagis pengoi* (Ostroumov 1891) (Cladocera, Onychopoda, Cercopagididae) has become dispersed outside its native range, which is located in the Ponto-Caspian basin. In the Baltic Sea, this species was first found in the Gulf of Riga in 1992 (Ojaveer et al., 2000), then it was recorded in other regions of the Baltic Sea (Avinski, 1997; Żmudziński, 1998; Uitto et al., 1999; Bielecka et al., 2000; Gorokhova et al., 2000; Naumenko and Polunina, 2000). In subsequent years, *C. pengoi* naturalized in the Baltic Sea and became abundant here (Krylov et al., 1999; Antsulevich and Välipakka, 2000; Gorokhova et al., 2000; Ojaveer et al., 2000, 2004; Telesh et al., 2001; Litvinchuk et al., 2001; Polunina, 2005; Litvinchuk and Telesh, 2006; Litvinchuk, 2007; Golubkov et al., 2010; Bielecka et al., 2014; Golubkov and Litvinchuk, 2015; Rowe et al., 2016; Naumenko, 2018; Naumenko and Telesh, 2019).

Seasonal changes in the population of *C. pengoi*, starting from the first days of spring water warming, were studied in Pärnu Bay (Ojaveer et al., 2004). Reproductive peculiarities contribute to the dispersal and naturalization of this species in new water bodies. Resting (wintering) eggs, covered with a hard shell that protects against the effects of adverse factors, retain their viability during long-distance transportation; in addition, when sinking to the bottom of a waterbody, they are able to withstand a water temperature decrease in winter. During the growing season, along with the onset of favorable temperature conditions, the population size may rapidly increase as a result of intensive parthenogenetic reproduction (Mordukhai-Boltovskoi and Rivier, 1987; Rivier, 1998). Studies of the nature of the distribution of resting eggs in the bottom sediments of different parts of the Baltic Sea show that viable resting eggs of *C. pengoi* were covered by bottom sediments at great depths, and hatching of young individuals from such eggs was difficult in spring (Katajisto et al., 2013). The largest proportion of juveniles of *C. pengoi* hatched from the resting eggs was observed in shallower areas of the Baltic Sea, including the eastern part of the Gulf of Finland.

It seems important to take into account the details and possible changes in the formation of the *C. pengoi* population under new environmental conditions. This study aims to analyze the long-term seasonal timing and developmental characteristics of the *C. pengoi* population over 11 years of observations in the eastern part of the Gulf of Finland, a region located northwards off the current range of this species.

MATERIALS AND METHODS

Material for the study was collected biweekly from early May to mid-October in the years 2009–2019 in Katerlahti Bay, near the city of Primorsk, which is located onshore from this bay (60°36′ N, 28°61′ E, Vyborgskii district, Leningrad region) using a plankton net with a 0.25-m mouth diameter, mesh size 50 mm). Samples were taken in seven replicates. Upon each sampling, the water temperature (°C), salinity (‰), and transparency (m) were determined. The material was fixed with a 4% formalin solution and subsequently studied using standard techniques. A total of 2106 individuals of *Cercopagis pengoi* were analyzed.

RESULTS

In the period 2009–2019, only one species of the genus *Cercopagis*, *C. pengoi*, was found in the eastern part of the Gulf of Finland, as well as earlier in 1997 and 1999 (Litvinchuk, 2001). The individuals of the first generation hatched from resting (wintering) eggs were identified in the total pool of specimens studied (Fig. 1a); these individuals were previously attributed to *Apagis ossiani* Mordukhai-Boltovskoi 1968, with one to four pairs of caudal claws and a characteristic feature of a shortened and straight caudal appendage. The individuals of the second and subsequent generations, i.e., the offspring of parthenogenetic females, included young females with one pair of caudal claws without eggs in the brood chamber (it was impossible to determine whether they belonged to the parthenogenetic or gamogenetic generations), parthenogenetic females with one to three pairs of caudal claws with eggs or embryos in the brood pouch (Fig. 1b), gamogenetic females with two or three pairs of caudal claws with or without resting eggs in the brood pouch, and males with one or three pairs of caudal claws. The pool studied also included the warm-water form "gracillima" of *C. pengoi*, which was characterized by an elongated brood pouch and caudal claws. Individuals with an abnormal body shape were noted; they had a deformed abdomen or smaller distance between the caudal claws comparing to "typical" individuals, which might have been caused by a distortion of the molting process. From 2009 through 2019, individuals of the first generation accounted for 0.71% of the total number of specimens studied; individuals of the second and subsequent generations of the typical form of *C. pengoi* made up 94.50%; the representatives of "gracillima" form, 4.65%; and individuals with an anomalous body shape, 0.14%.

Individuals of the first generation of *C. pengoi* were found only in the initial period of population development from mid-May to mid-June during the period of the lowest water salinity (0.7–1.8 ‰) at a water temperature of 11.9–15.7°C (Table 1). The water transparency in mid-May was relatively high, 1.6 ± 0.3 m; then, it decreased down to 1.1 ± 0.2 m in mid-June. These individuals were recorded in the plankton a month earlier than the individuals of the second and subsequent generations. The number of individuals of the first generation was low and amounted to 0.97–5.83 ind./m^3.

Parthenogenetic individuals of the second and subsequent generations, as well as gamogenetic individuals of *C. pengoi*, were recorded in plankton from mid-June through mid-October (Table 1). In 2009, 2010, and 2015, the *C. pengoi* population developed only in the summer months. In 2011, 2012, 2013, 2017, and 2019, individuals of *C. pengoi* were found in plankton from late June through mid-August, and, after a short break in autumn, in mid-September and mid-October. In 2014, 2016, and 2018, *C. pengoi* developed from late June through mid-September. In 2018, individuals of the second and subsequent generations of *C. pengoi* appeared at the earliest dates within the study period, in mid-June (Table 1). The number of individuals of the second and subsequent generations during the studied period varied within wide limits. Significant differences in the abundance of this species were noted both during the growing season and in different years of research (Table 1). The lowest abundance of *C. pengoi* (<15 ind./m^3) was observed in 2010, 2012, 2017, and 2019. High values (>100 ind./m^3) were recorded in 2009, 2014, 2015, and 2016. The population of *C. pengoi* reached its maximum development in mid-July of 2016 (836 ind./m^3).

Individuals of the second and subsequent generations of *C. pengoi* appeared in mid-June at the water temperature of 15.7 ± 1.7°C; the highest average abundance was recorded in mid-July, when the water warmed up to 19.0 ± 2.9°C (Fig. 1c). As the water temperature increased at the end of July up to 20.4 ± 3.6°C, the abundance of *C. pengoi* decreased. In mid-October, individuals of the second and subsequent generations were found in insignificant numbers at the water temperature of 10.9°C. During the period of mass development of *C. pengoi* from late June to mid-August, the water salinity was 2.3–2.8 ‰ and the water transparency was relatively low (1.1–1.5 m).

The form "gracillima" was recorded in the population of *C. pengoi* (abundance of 1.94–19.43 ind./m^3) in the middle of the growing season, during the period of the greatest water warming, from late June through late August (17.2–20.4°C). At the end of June 2013 and in the middle of July 2016, only a part of the population was represented by this form. At the end of August 2016, in mid-June 2018, mid-July 2018, and late July 2018, at the end of June 2019, and in mid-July 2019, only individuals of the "gracillima" form were found in the samples. By the end of June 2018, indi-

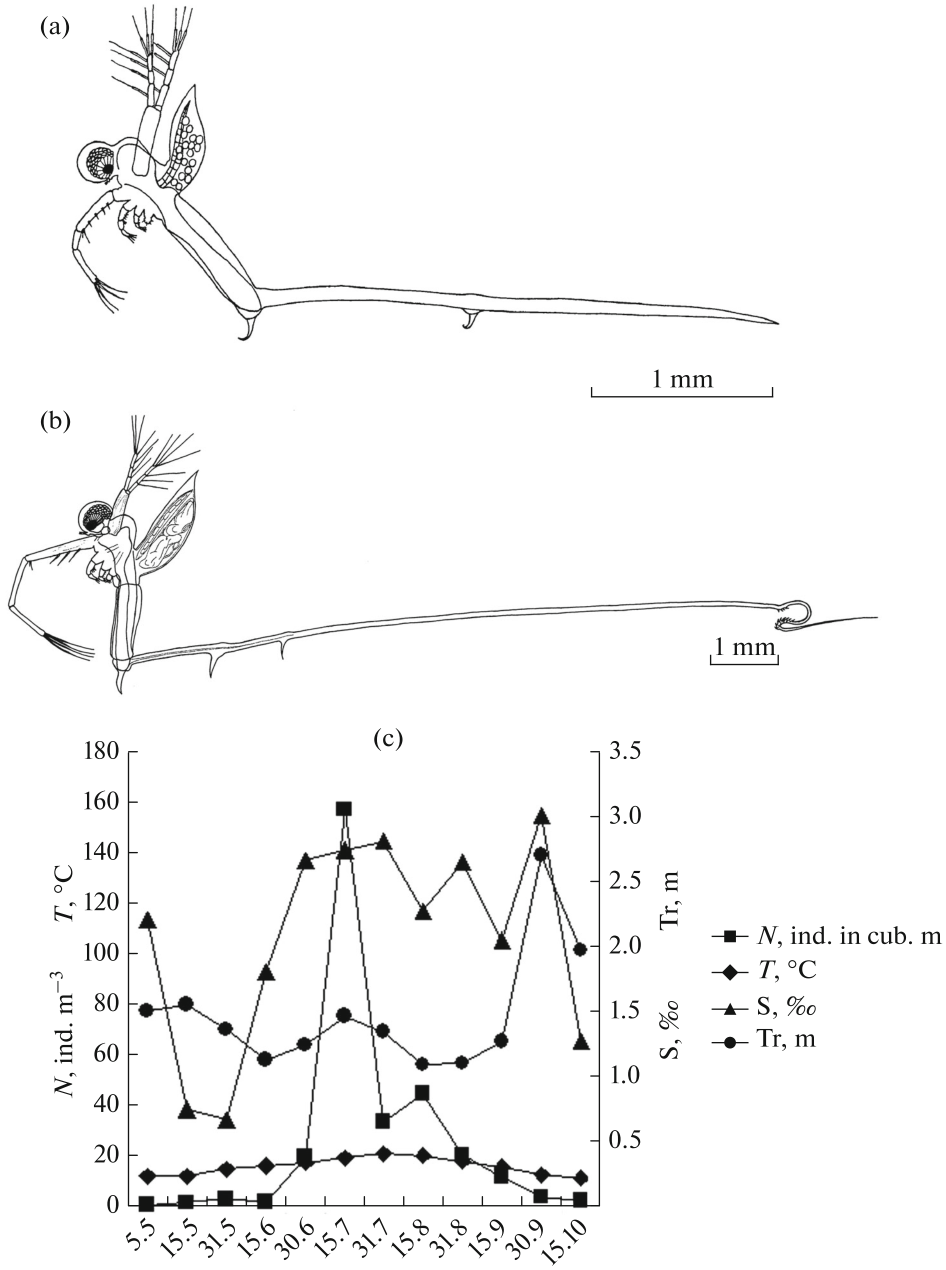

Fig. 1. Images of females of various generations and long-term dynamics of *Cercopages pengoi* and abiotic environmental factors: (a) an individual of the first generation with two pairs of caudal claws, born from a resting (wintering) egg; (b) parthenogenetic female of the second and subsequent generations with three pairs of caudal claws; (c) long-term average seasonal changes in the abundance of *C. pengoi* (*N*) and abiotic environmental factors (water temperature (*T*), water salinity (S), and water transparency (Tr)) in the eastern part of the Gulf of Finland from early May to mid-October of the years 2009–2019. The *X*-axis shows the dates from early May to late October.

viduals were characterized by intermediate traits between this form and the typical form of *C. pengoi*.

Individuals of *C. pengoi* with anomalies of development were found only in 2019, at the end of July and at the end of September, at a low population size and a relatively low water temperature, 15.2 and 13.5°C, respectively.

In 2010, 2012, and 2018, only parthenogenetic females were found in the populations of *C. pengoi*. The earliest dates for the appearance of representatives of the gamogenetic generation in plankton were noted at the end of June of 2013 and 2016. Moreover, both gamogenetic females and males appeared at this time. Gamogenetic females and males were found in plankton until mid-October (2011, 2014, and 2017). In other

Table 1. Average abundance (ind./m^3) of *C. pengoi* in the eastern part of the Gulf of Finland from early May to mid-October of the years 2009–2019 and in 1997

Year	Average abundance, dates (dd.mm)											
	05.05	15.05	31.05	15.06	30.06	15.07	31.07	15.08	31.08	15.09	30.09	15.10
1997*	–	–	–	–	56.5	419.00	50.00	8.00	321.00	–	–	–
2009	–	–	0.00	–	–	0.00	214.94	–	2.07	–	–	–
2010	–	–	0.00	–	0.00	0.00	2.90	0.00	–	–	–	–
2011	–	–	0.00	**1.13**	0.00	14.49	1.36	1.70	16.32	42.08	–	1.94
2012	0.00	0.00	**0.97**	0.00	0.00	0.00	4.86	10.69	0.00	0.97	–	–
2013	–	0.00	0.00	0.00	30.49	33.14	0.00	0.00	0.00	0.00	–	1.46
2014	–	**1.04**	**2.33**	0.00	1.94	294.34	2.33	139.89	2.08	–	–	2.27
2015	–	**0.97**	0.00	0.00	0.00	37.89	74.80	143.77	133.09	0.00	–	0.00
2016	0.00	–	**5.93**	0.00	50.51	836.40	2.91	1.94	5.83	6.80	0.00	0.00
2017	–	0.00	0.00	**1.94**	0.00	6.80	6.80	0.00	0.97	4.86	–	0.97
2018	–	0.00	0.00	1.94	10.69	19.43	12.63	11.66	1.94	–	–	–
2019	–	0.00	**0.97**	0.00	1.94	14.57	5.83	1.94	0.00	0.97	2.91	–

The asterisk * indicates data from Litvinchuk et al., 2001. The dash "–" indicates no survey carried out. Bold type indicates the samples in which specimens of the first generation, hatched from resting eggs, have been noted.

Table 2. Average body length (mm) of *C. pengoi* parthenogenetic females in the eastern part of the Gulf of Finland in early May–mid-October of the years 2009–2019

Year, parameter	Average body length, dates (dd.mm)											
	05.05	15.05	31.05	15.06	30.06	15.07	31.07	15.08	31.08	15.09	30.09	15.10
2009	–	–	–	–	–	–	–	–	–	–	–	–
2010	–	–	–	–	–	–	–	–	–	–	–	–
2011	–	–	–	**1.70**	–	1.80	–	–	1.60	1.61	–	–
2012	–	–	–	–	–	–	1.55	1.55	–	1.70	–	–
2013	–	–	–	–	1.88	1.80	–	–	–	–	–	–
2014	–	–	–	–	–	–	1.50	1.30	1.60	–	–	–
2015	–	–	–	–	–	1.50	1.45	2.00	–	–	–	–
2016	–	–	1.70	–	1.70	1.60	2.00	1.70	2.35	2.00	–	–
2017	–	–	–	–	–	1.77	1.80	–	–	–	–	2.00
2018	–	–	–	1.73	1.35	1.53	1.75	1.85	–	–	–	–
2019	–	–	–	–	2.00	1.80	1.50	–	–	–	–	–
Average body length (mm), all seasons ($X \pm SD$)	0.00	0.00	1.70	1.72 ± 0.02	1.73 ± 0.28	1.69 ± 0.14	1.65 ± 0.20	1.68 ± 0.27	1.98 ± 0.53	1.73 ± 0.19	0.00	2.00

The dash "–" indicates no survey carried out or the collected samples lacked adult females. The bold type indicates the average body length of specimens of the first generation (with four pairs of caudal claws) hatched from resting eggs.

years, gamogenetic individuals were found from mid-July. The age composition of the population varied widely. In 2011, 2013, 2017, and 2019, young females with one pair of caudal claws and without eggs formed the main part of the population from late September to mid-October.

The average body length of adult parthenogenetic females at the beginning and end of the growing season was greater than that in the middle of the season, 1.70–2.00 and 1.65–1.69 mm, respectively (Table 2). The length of an individual of the first generation hatched from a resting egg at the late stage of development (four pairs of caudal claws) was 1.7 mm.

The fecundity of individuals of the first generation was 5–12 embryos per female (Table 3). The number of embryos in parthenogenetic females varied widely

Table 3. Average fecundity of *C. pengoi* parthenogenetic females (number of embryos per female) in the eastern part of the Gulf of Finland in early May–mid-October, 2009–2019

Year, parameter	Average fecundity, dates (dd.mm)											
	5.05	15.05	31.05	15.06	30.06	15.07	31.07	15.08	31.08	15.09	30.9	15.10
2009	–	–	–	–	–	–	4.29	–	–	–	–	–
2010	–	–	–	–	–	–	6.00	–	–	–	–	–
2011	–	–	–	**12.00**	–	7.00	6.00	–	5.50	3.38	–	–
2012	–	–	**5.00**	–	–	–	6.00	6.00	–	6.00	–	–
2013	–	–	–	–	6.67	6.00	–	–	–	–	–	–
2014	–	–	–	–	20.00	4.25	4.50	5.50	5.50	–	–	–
2015	–	–	–	–	–	7.33	9.00	6.00	6.33	–	–	–
2016	–	–	10.33	–	7.40	5.93	–	6.00	10.33	6.00	–	–
2017	–	–	–	–	–	12.33	6.25	6.75	8.00	–	–	–
2018	–	–	–	12.00	5.75	9.75	6.40	9.75	4.00	–	–	–
2019	–	–	**11.00**	–	9.50	8.50	3.25	–	–	–	–	–
Average fecundity, all seasons ($X \pm SD$)	0.00	0.00	8.78 ± 3.29	12.00	9.86 ± 5.83	7.64 ± 2.53	5.93 ± 1.65	6.67 ± 1.56	6.61 ± 2.24	5.13 ± 1.51	0.00	0.00

The dash "–" indicates no survey carried out or the collected samples lacked adult females. Bold type indicates the fecundity of specimens of the first generation (with four pairs of caudal claws) hatched from resting eggs.

during the study period. The minimum number, two embryos, was noted in mid-September 2011. The maximum fecundity of parthenogenetic females, 20 embryos per female, was recorded at the end of June 2014. The average fecundity of parthenogenetic females of *C. pengoi* was higher at the initial stages of population development. From late May to late June, the average number of embryos per female was 9.86–12.00 (10.24 ± 4.83). In the subsequent periods, from mid-July to mid-September, fecundity was 5.13–7.64 (6.49 ± 2.04) embryos (Table 3).

Gamogenetic females with resting eggs were found in the *C. pengoi* population from late July to mid-October 2009, 2011, 2015–2017; all of them usually had one resting egg each. In 2015, two females had two resting eggs each in the brood chamber. The diameter of the resting eggs varied from 0.25 to 0.40 μm. In 2017, a gamogenetic female in the brood pouch had one "typical" resting golden egg with a diameter of 0.40 μm and two dark-gray small undeveloped resting eggs (0.15 and 0.20 μm).

DISCUSSION

In the central part of the Caspian Sea, earlier development of individuals of the first generation of *C. pengoi* was noted at the end of April (Mordukhai-Boltovskoi and Riv'er, 1987) compared to the middle of May in the Gulf of Finland (original data) and Pärnu Bay (Simm and Ojaveer, 2006). In these bays of the Baltic Sea, the development of individuals from resting eggs begins when the water warms up to 11–12°C and lasts for about one month, from mid-May to mid-June.

When comparing the timing of the appearance of representatives of the second and subsequent generations of *C. pengoi* in plankton, it has been reported that these individuals are found already in April and May in the southern parts of its native range, i.e., in the Bulgarian Gebedzhinskoe Lake (Beloslavskoe) located on the Black Sea coast, in the Caspian Sea, and in the Dnieper–Bug estuary (Valkanov, 1951; Markovskii, 1954; Rivier and Mordukhai-Boltovskoi, 1966). In the eastern part of the Gulf of Finland (original data) and in Pärnu Bay (Ojaveer et al., 2004), these individuals develop later, starting from mid-June.

In autumn, the disappearance of *C. pengoi* from plankton is noted in mid-October in the eastern part of the Gulf of Finland, similarly to that observed in the water bodies of the Black Sea basin and in the Caspian Sea (Valkanov, 1951; Mordukhai-Boltovskoi, 1967). In Pärnu Bay, the last individuals of the second and subsequent generations of *C. pengoi* are recorded at the end of September (Ojaveer et al., 2004).

In the eastern part of the Gulf of Finland, in mid-July 1997, the maximum abundance of *C. pengoi* was 419 ind./m^3 (Litvinchuk et al., 2001). In 2016, also in mid-July, the abundance reached 836 ind./m^3. In Pärnu Bay in mid-July 2001, the maximum abundance of this species was 550 ind./m^3 (Ojaveer et al., 2004).

In 2009–2019, in the eastern part of the Gulf of Finland, the individuals of the second and subsequent generations appeared at the beginning of the season at a water temperature of 15.7°C. The population reached its maximum development at 19.0°C, but when the water warmed up above 20.0°C, the abundance of *C. pengoi* decreased. The last individuals were recorded in plankton in autumn at 10.9°C. In Pärnu Bay, a similar pattern of development of the population of *C. pengoi* was noted: at the beginning of development of the population, the water temperature was 15°C; the abundance of *C. pengoi* reached its maximum at 17–19°C and then decreased as the water temperature exceeded 20°C. The last individuals were recorded in autumn at 12°C (Ojaveer et al., 2004).

The form "gracillima" of *C. pengoi* in the eastern part of the Gulf of Finland developed in insignificant numbers during the warmest season; these individuals were found both separately and together with the typical form and were reported for the northern part of the Caspian Sea (Mordukhai-Boltovskoi and Rivier, 1987).

Individuals with anomalies of development were found for the first time during the present study. The reasons for the appearance of such individuals in the population are not yet clear. Disruptions of the molting process may be related to environmental conditions, but it is still a question under discussion.

The structure of the *C. pengoi* population in different years (2009–2019) varied markedly. In some years, individuals of the gamogenetic generation were not recorded at all in the population. In other years, gamogenetic individuals developed in the population; they appeared in late June to mid-July. In 1997, in the eastern part of the Gulf of Finland, gamogenetic individuals developed from mid-July (Litvinchuk et al., 2001), and in Pärnu Bay, from early July (Simm and Ojaveer, 2006). In Gebedzhinskoe Lake (Black Sea basin), gamogenetic females and males appeared in the population in June (Valkanov, 1951), and in the Caspian Sea, in August (Mordukhai-Boltovskoi, 1967). In the Caspian Sea, representatives of the gamogenetic generation were rare (Mordukhai-Boltovskoi and Rivier, 1987) and they were not recorded at all in the water bodies of the Dnieper River basin (Glamazda, 1971; Mordukhai-Boltovskoi, 1965; Mordukhai-Boltovskoi and Galinskii, 1974).

In some years, in autumn (end of September–mid-October), young females with one pair of caudal claws without eggs dominated in the population of *C. pengoi*. It was impossible to determine whether these females belonged to the parthenogenetic or gamogenetic generation, but considering the timing of their development in late autumn, we assumed that these were young gamogenetic females.

The average body length of adult parthenogenetic females in the eastern part of the Gulf of Finland was maximum (1.98 ± 1.53 mm) at the end of the growing season. In Pärnu Bay, the average length of adult parthenogenetic females was 2.06 ± 0.04 mm (Simm and Ojaveer, 2006). In the southern parts of the range, i.e., in the Sea of Azov, the Caspian Sea, and the Tsimlyansk Reservoir, the body length of adult parthenogenetic females was 2.00 mm (Mordukhai-Boltovskoi and Rivier, 1987).

In the eastern part of the Gulf of Finland, the fecundity of individuals of the first generation was 5–12 embryos per female (9.3 ± 3.8). In Pärnu Bay, the fecundity of individuals of the first generation was higher and averaged 11.6 ± 1.0 embryos per female (Simm and Ojaveer, 2006).

In 2009–2019, in the eastern part of the Gulf of Finland, the fecundity of parthenogenetic females of *C. pengoi* was higher at the beginning of the growing season than later, in the middle and the end of season, when it was 10.2 and 6.5 embryos per female, respectively. The average seasonal fecundity was 7.2 ± 3.0 embryos per female. The maximum number of embryos per female (20) was recorded at the beginning of the summer of 2014. In the eastern part of the Gulf of Finland, in 1997, at the beginning of the season, the fecundity was also higher than in subsequent periods (16.6 embryos per female). The average fecundity for the season was 6.7 ± 4.2 embryos per female, and the maximum number of embryos per female (24) was noted at the beginning of July 1997 (Litvinchuk et al., 2001). In Pärnu Bay, in the years 1997–2003, the average fecundity of parthenogenetic females per season was 10.2 ± 0.3 embryos and the maximum fecundity (15 embryos per female) was recorded at the end of June (Simm and Ojaveer, 2006). In the Vistula Lagoon, in 1999, fecundity averaged 13.0 embryos per female; in 2006, this value was lower and was 7.0 embryos per female (Polunina, 2014). In the Caspian Sea, the average fecundity of parthenogenetic females was 13 embryos (Mordukhai-Boltovskoi and Riv'er, 1987). In Gebedzhinskoe Lake, up to ten embryos per female were recorded (Valkanov, 1951). Therefore, the highest fecundity of parthenogenetic females at the beginning of the season and the maximum number of embryos per female were noted in the eastern part of the Gulf of Finland in 1997. The highest average seasonal fecundity of parthenogenetic females was observed in the Vistula Lagoon in 1999; it was similar to the fecundity of parthenogenetic females from the Caspian Sea.

In the eastern part of the Gulf of Finland, in the period 2009–2019, gamogenetic females of *C. pengoi* with resting eggs were observed from late July through mid-October. The frequency of their occurrence during the season was low; these females were found for only five years of the entire study period. In other years, they were not found. Fecundity was equal to one or two, rarely three (one egg of normal size, two underdeveloped), resting eggs. In the eastern part of the Gulf of Finland, in 1997, gamogenetic females with eggs were found from mid-July. Most of the females carried one to two resting eggs in the brood pouch, and the maximum number of eggs per female was three (Litvinchuk et al., 2001). In Pärnu Bay, gamogenetic females with resting eggs were found from late June through late September in the years 1997–2003; their fecundity was one to two resting eggs per female (Simm and Ojaveer, 2006). In the Vistula Lagoon, in 2000, 2001, and 2006, females carried one to three resting eggs (Polunina, 2014). In the Caspian Sea and in Lake Ontario, one to two resting eggs per female were recorded (Mordukhai-Boltovskoi, 1967; MacIsaac et al., 1999), while in Gebedzhinskoe Lake and in the Aral Sea, it was one resting egg (Zernov, 1903; Valkanov, 1951). It is interesting to note that in the southeastern part of the Baltic Sea, in early August 1999, gamogenetic females of *C. pengoi* with four resting eggs in the brood pouch were registered (original unpublished data). This was the maximum number of eggs per female recorded for this species.

CONCLUSIONS

During the study of long-term seasonal changes in the population of *C. pengoi* in the eastern part of the Gulf of Finland, the timing and peculiarities of the development of particular stages and age groups were assessed. The duration of development of the *C. pengoi* population is shorter in the eastern part of the Gulf of Finland compared to that in the Ponto-Caspian region. The timing of the development and fecundity of individuals of the first generation has been specified. The species abundance is higher compared to the other parts of the range, despite the fact that more than 25 years have passed since the introduction of this species into the eastern part of the Gulf of Finland. Representatives of the gamogenetic generation were not recorded in the population in certain years. The fecundity of parthenogenetic females of *C. pengoi* in the eastern part of the Gulf of Finland was higher in the first years after invasion.

It is important to continue seasonal studies of the *C. pengoi* population in the eastern part of the Gulf of Finland. This will make it possible to estimate the changes in the timing of development and the peculiarities of the biology of this species in the northern parts of its range.

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COMPLIANCE WITH ETHICAL STANDARDS

Conflict of interest. The authors declare that they have no conflict of interests.

Statement on the welfare of animals. All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

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