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The impact of nuisance planktonic invaders on pelagic communities: a review of the Baltic Sea case studies

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Summary

The article focuses on the effects of planktonic nonindigenous species on pelagic communities in the Baltic Sea that can be assessed using the basic principles of invasion biology, ecological physiology, trophic dynamics in food chains, and production hydrobiology. The ecosystem effects of nuisance unicellular species (the potentially toxic bloom-forming dinoflagellates *Prorocentrum cordatum*) and multicellular invaders (the carnivorous fishhook water flea *Cercopagis pengoi*) are reviewed and illustrated by the data from the Baltic estuaries and coastal lagoons. The putative effects of trophic interactions in plankton on the possible new protistan alien species introductions and the magnitude of harmful dinoflagellate blooms are suggested to occur in the future Baltic Sea due to the ongoing desalinization process under the changing climate.

Key words: biological invasions, *Cercopagis pengoi*, harmful algal bloom, Impact index, *Prorocentrum cordatum*, protists

Do non-indigenous species always affect native communities?

The penetration of alien species into new environments is currently one of the major drivers for global change in species biogeography and ecosystem health, which is linked tightly with multiple environmental alterations due to the onslaught of human activities (Simberloff, 2011; Darling and Carlton, 2018; Ojaveer et al., 2021; Ricciardi et al., 2021). Many invaders cause adverse effects and/or pose an elevated risk of impact to native species, communities and ecosystems, or economic implications (Ojaveer et al., 2021; Vilizzi et al., 2021). Other nonindigenous species invade new environments without noticeable effects, or the effect is delayed, sometimes because of multidimensional niche differentiation, which buffers the impact of invasion (Telesh et al., 2016; Borza et al., 2021). Negligible effect of an invader can be observed also due to occupation of available and vacant ecological niches, although empty niches are extremely rare in the diverse and species-rich aquatic communities (Chesson, 2000; Elliott, 2003; Telesh et al., 2011a, 2011b, 2013; Litchman et al., 2012).

At microorganisms' level, the introductions of alien species are often "invisible", and because of the fewer dispersal barriers for microbes, compared

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with macroorganisms, environmental change might play a disproportionately large role in allowing microorganisms to spread (Litchman, 2010). Alternatively, microbial introductions can have evident nuisance ecosystem consequences. A good example of the microbial invasion with the delayed though devastating effects is the peculiar history of invasion of the Baltic Sea by the bloom-forming potentially toxic dinoflagellates *Prorocentrum cordatum* (Ostenfeld) J.D.Dodge, 1975 in the 1980-s (Telesh et al., 2016). Nowadays, these unicellular planktonic protists form harmful blooms (red tides) in this sea and in the marine coastal waters globally (Glibert, 2020).

In the brackish-water Baltic Sea, which has been the area of intensive ongoing invasion processes (Leppäkoski and Olenin, 2000; Olenin et al., 2017), *P. cordatum* is generally accepted as the only one truly invasive phytoplankton species because the dynamics and importance of only this unicellular alien meets the major established requirements of the ''invader'' (discussed in details by Olenina et al., 2010). Currently, the multiple negative ecosystem effects of red tides caused by *P. cordatum* are well identifiable. Moreover, the fine mechanisms of their invasive success, such as mixotrophic feeding mode, high adaptability of cells to external stresses, and intrapopulation heterogeneity in the uptake of different nutrient substrates, have been largely unveiled (Matantseva et al., 2016, 2018; Knyazev et al., 2018; Skarlato et al., 2018a, 2018b; Anderson et al., 2019; Glibert, 2020; Pechkovskaya et al., 2020; Telesh et al., 2020, 2021). However, linkage of this knowledge with predictive invasion theories and forecasts of nuisance ecosystem effects is still in its infancy because the integration of microbial biology into invasion science has been insufficient so far (Ricciardi et al., 2021).

For many multicellular planktonic invaders, the impact assessment can be even a greater challenge than for the unicellular aliens. For example, the carnivorous fishhook water flea *Cercopagis pengoi* (Ostroumov, 1891), native to the Ponto-Caspian region, is one of such invaders in plankton of the Baltic Sea. It was discovered there for the first time in 1992 (Ojaveer and Lumberg, 1995), and during the following several years these nonindigenous cladocerans successfully colonized the entire Baltic Sea, including the Vistula and Curonian lagoons (Naumenko and Polunina, 2000; Telesh and Ojaveer, 2002; Telesh, 2018, and references therein). Nowadays, *C. pengoi* is the only one multicellular alien species in plankton of the Baltic Sea, which is likely to have a strong impact on ecosystem functions (Olenin et al., 2017), particularly, on the pelagic food-web dynamics, which backs up fish feeding and fisheries. Specifically, the recent results suggested that in certain regions of the Baltic Sea, naturalization of *C. pengoi* might have caused population decline of the common pelagic copepods *Eurytemora affinis* (Poppe, 1880) that are the essential food for planktivorous fish (Naumenko and Telesh, 2019).

Meanwhile, usually it is problematic to demonstrate clearly the adverse ecosystem effects of certain invasive species (Simberloff, 2011; Vilizzi et al., 2021), mainly due to multiple external stressors as well as sheer complexity and low predictability of biotic interactions in plankton that are nonlinear, multidimensional, and even chaotic (Telesh et al., 2019). Therefore, it is often difficult to determine whether there was a reduction in the community/ecosystem integrity or damage at one or more levels of biological organization (cell, individual, population, community and ecosystem) because of nonindigenous species, or whether the invaders have been assimilated without any considerable effect (Elliott, 2003; Jeschke et al., 2014).

Searching for frameworks to predict ecosystem susceptibility to invasions: biotic interactions versus external stressors

The role of biotic interactions in transformations of pelagic communities caused by biological invasions has been a hot research issue during the recent decades. Particularly, it was shown by experiments and imitation modeling that population dynamics of planktonic cladocerans is regulated mainly by predation and competitive interactions; moreover, competition for food prevents invasion of the community by the alien species (Dgebuadze and Feniova, 2009). The latter conclusion can be supported by the discovery of the two decades-long delay in the bloom formation by *P. cordatum* after its introduction to the Baltic Sea, which was likely caused by the competition of this alien with four native congeneric species since their ecological niches largely overlapped (Telesh et al., 2016).

Unicellular eukaryotes in plankton are highly sensitive to both local and global environmental changes, such as composition and concentration of nutrient substrates, irradiance, water temperature and others, reacting to them by structural transformations of the communities as well as by the alterations in species' abundance, biomass, and productivity (Litchman et al., 2012; Schubert and Telesh, 2017; Schubert et al., 2017). The Baltic Sea studies revealed significant influence of water salinity on the structure and functions of natural phytoplankton communities (Olli et al., 2011) and the bacterial plankton (Herlemann et al., 2011, 2014; Dupont et al., 2014). At the same time, it was discovered that, unexpectedly, the concentration of dissolved and suspended nutrient substrates in the Baltic waters, which reflects the level of eutrophication, demonstrated only a weak correlation with the changes in phytoplankton community composition in this brackish-water sea (Olli et al., 2011). Meanwhile, the mesocosm experiments proved that salinity is another effective environmental factor, which defines species diversity of phytoplankton, since the algal species number in mesocosms was decreasing with the increasing salinity, while the tendency was the opposite when the concentration of nutrients was increasing (Larson and Belovsky, 2013). Thus, the complex and (often) controversial effects of different environmental factors on the structure of pelagic communities as well as the effects of trophic interactions on ecosystems' invasibility, including their susceptibility to harmful, bloom-forming non-indigenous phytoplankton species, need to be unveiled and evaluated for the prognostic purposes (Barton et al., 2013).

In the last 30 years, a number of impact assessment frameworks that allowed for evaluating the environmental and/or socio-economic effects of invasive species were developed (Blackburn et al., 2014; Crystal-Ornelas and Lockwood, 2020; Ricciardi et al., 2021, and references therein). Specifically, the comparative functional response approach was introduced, whereby the impacts of invasive species were compared with analogous native species as eco-evolutionary baselines, and the Invader Relative Impact Potential was suggested as a metric for understanding the ecological impacts of alien species (Dick et al., 2017). This approach has been recognized as a reliable tool for explaining the effects of existing alien species and predicting the potential future invaders from a plethora of taxa under a wealth of different contexts such as habitat complexity, temperature and dissolved oxygen regimes, water chemistry gradients, higher order predators, and parasites (reviewed by Dickey et al., 2020).

A large array of studies also attempted at finding traits to predict invasiveness (i.e. establishment and spread of new aliens); many of those, however, have failed to robustly predict ecological impact of species spanning diverse taxonomic and trophic groups, and no correlations between invasiveness and ecological impact were detected (Dickey et al., 2020; Ricciardi et al., 2021, and references therein).

Thus, the general predictive understanding of the ecological impacts of non-native species in aquatic ecosystems has been slow to mature (Ricciardi et al., 2013; Dickey et al., 2018; Vimercati et al., 2020). Therefore, for the variable, species-rich and heterogeneous plankton communities, simple and user-friendly metrics for the invaders' impact assessment are still rather scarce (Telesh et al., 2001; Laxson et al., 2003; Dick et al., 2017; Dickey et al., 2020; Ricciardi et al., 2021).

Trophic dynamics and invasion theory allow for evaluating the impact of carnivorous alien zooplankters on pelagic communities

Planktonic predators provide top-down control of grazers thus affecting directly the productivity of herbivorous zooplankton, which serves as basic food for pelagic fish, and indirectly influencing the primary productivity of phytoplankton, including the development of harmful blooms of various protistan species and the cyanobacteria. Therefore, evaluation of the impact of carnivorous planktonic aliens is of utmost importance for both predicting the fish forage supply and forecasting harmful algal blooms.

By using the comparative functional response approach, a metric for evaluation of the effect of carnivorous invasive zooplankters on native communities was suggested two decades ago (Telesh et al., 2001). However, since this method was first presented in the national Russian-language journal, here we provide an additional, detailed description of the calculation algorithm for this authentic metric.

The impact of the *C. pengoi* population on the structure and functioning of plankton community was assessed by calculating the Impact index (here and after: *Ii*; in the original version: *I*), which was developed using the data on *C. pengoi* in the Neva Estuary (the Gulf of Finland, the Baltic Sea). This algorithm was elaborated using the basic principles of invasion biology (Parker et al., 1999) as well as ecological physiology, trophic dynamics in food cha-

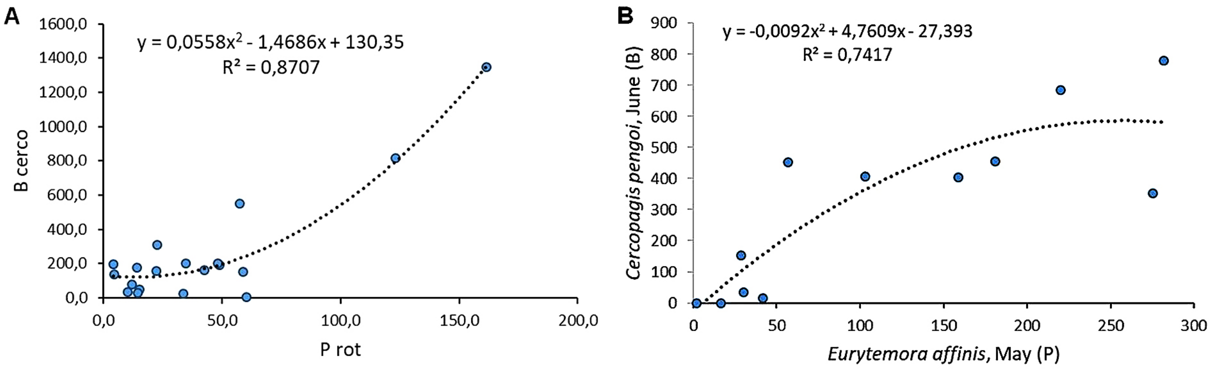

Fig. 1. The relations between biomass (B) of *Cercopagis pengoi* and production (P) of rotifers and copepods *Eurytemora affinis* in the Vistula Lagoon. A – Correlation of the biomass of *C. pengoi* (B_{cerco}, mg/m^3) with the average annual daily production rate of rotifers (P_{rot}, cal/m^3); B – shifted-data analysis correlates the *C. pengoi* biomass (B, mg/m^3) in June with the daily production rate (P, cal/m^3) of *E. affinis* during the preceding month, in May (calculated using the data from: Naumenko and Telesh, 2019).

ins, and production hydrobiology (Alimov, 2003). Applicability of the algorithm was verified by the data on the pelagic food-web dynamics in the Lake Ontario (Laxson et al., 2003).

Initially, Parker et al. (1999) proposed to view the impact (I) of an invader on the community of living organisms in a water body as the product of the invader's range (R), abundance (A) and *per capita* effect (E): $I = R \times A \times E$, later termed the "Parker-Lonsdale" equation. Telesh et al. (2001) suggested the assessment of the impact as a modification of the Parker-Lonsdale equation (Parker et al., 1999). Specifically, in the case when the population of *C. pengoi* inhabits the entire study region (e.g., in the Vistula Lagoon), in this modified calculation algorithm the parameter R (range) was skipped. Additionally, the authors infer that the share of the invader in the overall zooplankton abundance reflects the role of *C. pengoi* in plankton community more precisely than the absolute value of its abundance (A). The per capita effect (E) of *C. pengoi* was measured by calculating the ratio of its daily consumption rate to daily production rate of its preys. Thus, unlike the Parker-Lonsdale equation, the modified metric of the impact (Ii) considers not the absolute but the relative values of the parameters, namely: the contribution of *C. pengoi* to overall zooplankton abundance, and the ratio of the daily consumption rate of *Cercopagis* to the production rate of its potent prey organisms (Telesh et al., 2001):

$$Ii = (N_{cerco} / N_z) \times (C_{cerco} / P_{hz}), \quad (1)$$

where Ii is Impact index, a measure of predation pressure of *Cercopagis* on zooplankton (a dimensionless value); N_{cerco} is the maximum abundance of *C. pengoi* (ind/m^3); N_z is the total abundance of zooplankton (ind/m^3) at the date when N_{cerco} is maximal; C_{cerco} is the daily consumption rate of *C. pengoi* (cal/m^3), and P_{hz} is the daily production rate of herbivorous zooplankton that *C. pengoi* might feed on (cal/m^3).

Based on the data from the literature and own results described in Laxson et al. (2003), all non-predatory cladocerans, nauplia of copepods, copepodites I–III, and I–VI stages of the calanoid copepods (*Eurytemora affinis, Acartia tonsa*) were considered as potent prey organisms for *Cercopagis*. The index Ii is assessed for the periods (dates) of maximum population density of the invader during summer seasons.

Calculation of the Impact index using the data from the Neva Estuary and the eastern Gulf of Finland (Telesh et al., 2001), the Vistula Lagoon (Naumenko and Telesh, 2019), the central Gulf of Finland and the open Baltic Sea (Litvinchuk and Telesh, 2006) demonstrated long-term dynamics of the effects of non-indigenous cladoceran *C. pengoi* on native zooplankton communities. Using the most recent data from the Vistula Lagoon (Naumenko and Telesh, 2019), it was possible to show that the biomass of *C. pengoi* strongly ($R^2 = 0.87$, $p < 0.05$) correlated positively with the daily production rate of rotifers, their potent preys, and this relation can be described by the binomial equation (Fig. 1, A). Moreover, the shifted-data meta-analysis of

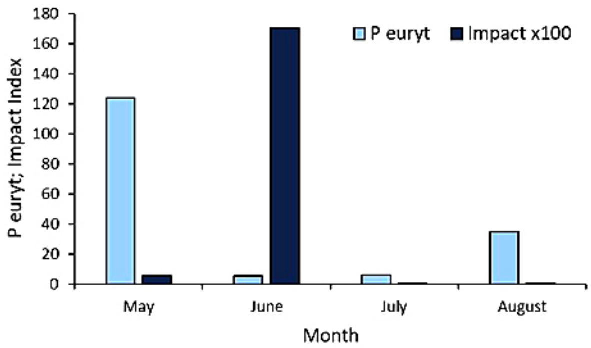

Fig. 2. The monthly average daily production rate of *Eurytemora affinis* (P_{euryt}, cal/m^3) and predation pressure of *Cercopagis pengoi* expressed as the Impact index during the same months in the Vistula Lagoon. Impact values (Impact ×100) were averaged for each month when the annual maxima of *C. pengoi* abundance were observed (n=2 in May, July and August; n=10 in June). Based on the data from Naumenko and Telesh (2019).

the same database (Naumenko and Telesh, 2019) demonstrated strong correlation ($R^2 = 0.74$, $p < 0.05$) between the biomass of *C. pengoi* in June and the daily production rate of *E. affinis* during the preceding month (May) in the Vistula Lagoon (Fig. 1, B).

Moreover, the results showed that the maximum Ii values were usually registered in June, and during the succeeding months, in July and August, i.e. after the highest predation pressure of *C. pengoi,* the productivity of *E. affinis* decreased substantially (Fig. 2).

These results allow suggesting that nauplial stages and juveniles of *E. affinis* were the preferable food for *Cercopagis* in the Vistula Lagoon. Importantly, the data also confirmed that the share of *C. pengoi* in the overall biomass of cladocerans has been increasing exponentially during the recent two decades; meanwhile, the specific daily production rate of *E. affinis* has been decreasing ($R^2 = 0.97$, $p < 0.05$) since 1999 (see Fig. 7 in Naumenko and Telesh, 2019). Thus, elimination of nauplia and younger copepodites of the grazer *E. affinis* by the planktonic predator *C. pengoi* impacted the pelagic community significantly and might have caused serious alterations in the overall plankton community structure, primary productivity of phytoplankton, production of copepods, and availability of fish food supply.

Biological invasions in plankton cause controversial effects that trigger ecosystem alterations

The unprecedented rate of human-mediated species introductions into new environments over recent centuries has numerous far-reaching consequences, including impacts on human health and the economy, and alterations of recipient ecosystems (Perrings, 2002; Ojaveer et al., 2021). Biological invasions can have important effects on the structure and integrity of native communities, and these effects often extend beyond their most frequently documented direct ecological modifications (Feit et al., 2018; Telesh et al., 2019). In particular, the invaders can cause rapid and long-lasting changes to the structure and functions of ecosystems — the so-called regime shifts, with major implications for biodiversity, ecosystem services, and human wellbeing and livelihoods (Shackleton et al., 2018; Ricciardi et al., 2021).

The impact of the invaders can differ in various environmental conditions, different habitats and communities, depending on the ecological niche dimensions of the alien species. The ecological niche of the predatory fishhook water flea *C. pengoi* is rather broad. For example, *C. pengoi* is highly tolerant to a wide range of salinities and can inhabit both fresh waters, e.g. the Great Laurentian Lakes (MacIsaac et al., 1999; Laxson et al., 2003), and marine environments such as the Southern Caspian Sea with salinity of 12[1] (Bagheri et al., 2014). Recent studies in the brackish-water Neva Estuary (eastern Gulf of Finland, the Baltic Sea) showed that biomass of *C. pengoi* was the highest at salinity ca. 2.6 and water temperature around 18 °C (Golubkov et al., 2020). These results are consistent with the earlier findings showing that *C. pengoi* has a broad ecological niche. Thus, in different areas of the Baltic Sea, this invader has been registered at salinities 0.3–6.0 in a wide range of temperatures: 4–24 °C (Krylov et al., 1999; Ojaveer et al., 2004; Litvinchuk and Telesh, 2006; Bielecka et al., 2014; Rowe et al., 2016; Helenius et al., 2017; Naumenko, 2018).

[1] Salinity is reported using the Practical Salinity Scale approved by the Joint Panel of Oceanographic Tables and Standards, according to which salinity is defined as a pure ratio, and has no dimensions or units.

The ecological impacts of nonindigenous species in marine ecosystems include but are not limited to alteration of biodiversity and food webs, habitats and community structure, displacement of native species due to competition and predation, as well as the spread of disease agents (Bax et al., 2003; Litchman, 2010; Telesh et al., 2016, 2020; Olenin et al., 2017). As shown recently, the diverse and highly productive mesozooplankton of the Vistula Lagoon harbors 74 species, including rotifers (36), cladocerans (16) and copepods (22 species) (Naumenko and Telesh, 2019). The latter study confirmed that in this shallow brackish lagoon, *C. pengoi* usually appeared in plankton in May when water warmed up to 15 °C, as shown earlier by Naumenko (2018), and reached their maximum in June, occupying a comfortable niche in the abundant, species-rich and productive community at temperatures not exceeding 20 °C. Moreover, the monthly averaged values of abundance, biomass and productivity of *E. affinis, C. pengoi,* and *A. tonsa* (another common and abundant non-indigenous species in the Vistula Lagoon, see Khanaychenko et al., 2019, and references therein) demonstrated a clear seasonal demarcation of their populations.

High Impact index values, calculated according to Telesh et al. (2001) during the maximum population development of *C. pengoi*, and sharp decline of daily production rate of *E. affinis* after the population peak of this invasive predator confirmed that nauplii and juveniles of *E. affinis* were the preferable food items for Cercopagis in the Vistula Lagoon (Naumenko and Telesh, 2019). Meanwhile, the copepods *A. tonsa* were on average 10 times less abundant, compared to *E. affinis*. However, the results allow assuming that during their maximum productivity in July, *A. tonsa* can also contribute significantly as prey and have a potential to sustain the population of *C. pengoi* later in the season, during July and August.

These results (Naumenko and Telesh, 2019) are consistent with the earlier studies that used stable isotopes to demonstrate food-web changes after the Baltic Sea invasion by *C. pengoi* (Gorokhova et al., 2005). The laboratory experiments revealed effective consumption of the nauplii and copepodites of *E. affinis* by *C. pengoi* (Simm et al., 2006; Lehtiniemi and Gorokhova, 2008). The recent findings in the Vistula Lagoon support those previous results by showing additionally that in certain regions of the Baltic Sea, naturalization of *C. pengoi* might have caused the population decline of the common pelagic copepods *E. affinis* that serve as prey not only for *Cercopagis* but also for planktivorous fish (Naumenko and Telesh, 2019). In this context, the latter results that demonstrated certain periodicity in the development of *C. pengoi* population and revealed the statistically reliable increase in the share of this predator in zooplankton of the Vistula Lagoon can inform the future prognostic modeling of the impact of this invader on the planktivorous fish stock and yield.

However, so far any forecasts of the putative long-term population development of *C. pengoi* face certain challenges because the effects of this introduction to the Baltic Sea have been multidirectional and sometimes controversial. Moreover, complexity of biotic interactions in plankton that are nonlinear and even chaotic as well as numerous confounding environmental factors act as strong external stressors that affect the invaders' impact on native communities (Telesh et al., 2019).

In Figure 3, we summarized the positive and negative ecosystem effects of *C. pengoi* on the recipient plankton communities and outlined its cumulative role as a nuisance ecosystem modifier.

The major positive effect of this invasion is the enrichment of plankton diversity by a new invertebrate predator, which restructured the pelagic food web thus enhancing stability of zooplankton community in stressful conditions (Naumenko and Telesh, 2019). This alien also increased food competition in the plankton and bentho-pelagic ecosystems between several invertebrates and fish species (Kotta et al., 2004; Ojaveer et al., 2004), stimulating energy turnover through the community and enhancing benthic-pelagic coupling. Another positive role of this invader is that in late summer and early autumn, it can constitute a large proportion in the diet of major planktivorous fish species of the Baltic Sea, e.g., the sticklebacks *Gasterosteus aculeatus* and *Pungitius pungitius*, the Atlantic herring *Clupea harengus* and the European sprat *Sprattus sprattus* (Gorokhova et al., 2004; Ojaveer et al., 2004). *C. pengoi* can make up to 83% of the diet of large (adult) herring (Ojaveer and Lumberg, 1995) and up to 100% of the diet of nine-spined stickleback and bleak in the Baltic Sea (Lankov et al., 2010).

Negative effects of *C. pengoi* are also numerous and, therefore, alarming (Fig. 3). Predation of *C. pengoi* on herbivorous copepods and cladocerans eliminates the phytoplankton grazers and thus promotes modifications in the pelagic community structure favoring the enhanced primary production and

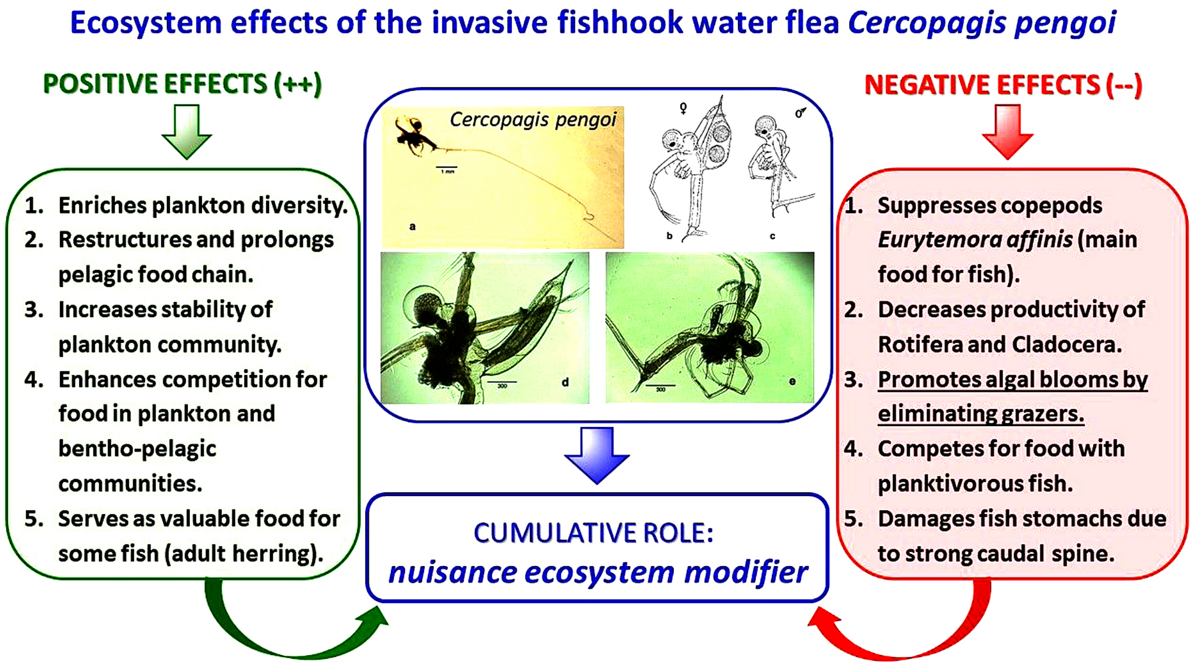

Fig. 3. Major positive and negative effects and cumulative role of *Cercopagis pengoi* in the recipient communities. Images: female of *C. pengoi* with one resting egg in the brood pouch (a); female with two resting eggs (b); male (c); female body, with embryos in the brood pouch (d); juvenile specimen at stage I (e). Photos I.V. Telesh (a, d-e), scales (d, e): µm. Drawings (b, c): modified from Telesh and Heerkloss (2004).

algal blooms in the low-salinity environments (Naumenko and Telesh, 2019). These devastating effects have a potential to initiate secondary (biological) pollution and cause water quality deterioration (Telesh, 2018).

To date, the most important negative effect of *C. pengoi* is the elimination of planktonic rotifers, cladocerans and juvenile copepods; this suppression deteriorates the food supply for planktivorous fish and, therefore, threatens fishery in the Vistula Lagoon. Moreover, even though *C. pengoi* is an acceptable food source for some fish, as mentioned above, many fish species avoid feeding on these cladocerans and demonstrate negative values of the electivity index (Lankov et al., 2010). Besides, as shown earlier, *C. pengoi* can injure fish stomachs by its long and sharp hooked caudal spine (Antsulevich and Välipakka, 2000; Leppäkoski and Olenin, 2000). Finally, they clog and foul fishing nets causing harm to fisheries accompanied by economic losses (Ojaveer and Lumberg, 1995; Krylov et al., 1999).

Due to the accumulated data, *C. pengoi* along with just a few other invaders (*Dreissena polymorpha, Marenzelleria* spp. and *Neogobius melanostomus*) was named as the nonindigenous species that has the substantial knowledge base with over 100 impact records and with more than ten papers published on their biological and ecological effects (Ojaveer et al., 2021). Meanwhile, it is worthy of note that despite being the only one nonindigenous species that is likely to have a strong impact on ecosystem functioning in the pelagic zone of the Baltic Sea (Olenin et al., 2017), according to the present knowledge, *C. pengoi* is not considered as a serious threat to aquatic ecosystems globally (Vilizzi et al., 2021).

The putative effects of carnivorous planktonic aliens on the future invasions, community structure and harmful dinoflagellate blooms

Currently, we only can speculate that the greatest challenge for the future of the Baltic coastal lagoons, e.g., the eastern Gulf of Finland or the Vistula Lagoon, can be the potent invasion by the bloom-forming dinoflagellates *Prorocentrum cordatum* that so far have not yet populated these low-salinity environments (Golubkov et al., 2019; Kownacka et al., 2020; E. Naumenko, pers. com.). Meanwhile, the natural salinity tolerance range of *P. cordatum* is very broad: in the Baltic Sea waters, these flagellates prosper at salinities 2–22; however, their

Table 1. The minimum and maximum values of water temperature (T, °C) and salinity range of occurrence of *Prorocentrum cordatum* and *Cercopagis pengoi* in the Baltic Sea, and survival of *Acartia tonsa* in the experiments.

Species	T, °C	Salinity	References
Prorocentrum cordatum	3.0 – 24.0	2.0 – 22.0	Telesh et al., 2016
Cercopagis pengoi	4.0 – 24.0	0.3 – 6.0	Golubkov et al., 2020 (and references therein)
Acartia tonsa	5.0 – 34.0	6.0 – 30.0	Peck et al., 2015 (and references therein)

optimum salinity range, which allows for blooming, is much narrower: 6.1–9.7 (Telesh et al., 2016). The lower segment of the salinity tolerance range of *P. cordatum* partly coincides with that of *C. pengoi* in the Baltic Sea: 0.3–6.0 (Golubkov et al., 2020, and references therein) (Table 1).

Moreover, the common in the Baltic Sea and abundant non-indigenous calanoid copepods *A. tonsa* are known as effective grazers of *P. cordatum* (reviewed by Khanaychenko et al., 2019). This and other typical representatives of both graspers and filtrators among calanoid copepods can graze on *P. cordatum* either selectively or non-selectively. Importantly, the copepods do not avoid these dinoflagellates in the mixture with other food particles, perceiving them as non-toxic edible microalgae. Therefore, the trophic structure of plankton likely determines the harmful algal blooms' development, magnitude and duration due to the complex interplay of external triggers and internal driving forces of plankton dynamics within the communities (Telesh et al., 2019, 2021). Indeed, one should expect that, in the cases when the grazing pressure on the blooming dinoflagellates is high enough to restrict their excessive growth rate, the bloom does not develop or, once started, it terminates quickly. However, so far the evidences of the role of grazers in controlling the dynamics of *Prorocentrum* blooms are rare and largely controversial (Khanaychenko et al., 2019, and references therein).

Besides, the comparison of ecological niche dimensions of *A. tonsa* and *C. pengoi* in the Baltic Sea with environmental preferences of *P. cordatum* demonstrates low capacity of the latter population to be top-down controlled by the planktonic crustaceans. Specifically, we compared water temperature and salinity preferences, i.e. optimum values for population development of these nonindigenous species in the Baltic Sea; for *A. tonsa*, the same parameters during the optimum egg production rate in the experiments (Peck et al., 2015) were considered (Fig. 4).

This comparison allows concluding that the mixotrophic, potentially toxic bloom-forming dinoflagellates *P. cordatum* and the herbivorous calanoid copepods *A. tonsa* have similar ranges of preferable water temperatures (16–25 °C) that partly coincide with that of *C. pengoi*, and comparable lower temperature tolerance limits (Table 1, Fig. 4). However, the optimum salinities for all three species differ substantially and do not overlap at all. In particular, the range of salinity values allowing for bloom development of *P. cordatum* in the Baltic Sea is rather narrow: 7.9 ± 1.8 (Telesh et al., 2016). The optimum salinities for *C. pengoi* in this water body are 0.4–4.3 (Golubkov et al., 2020), and for *A. tonsa*, the preferable salinities are 10.0–20.0 (Peck et al., 2015). Thus, the co-occurrence and, consequently, the suppression of *P. cordatum* population by planktonic crustaceans nowadays is unlikely, neither through grazing by *A. tonsa* nor due to community restructuring effects caused by *C. pengoi*.

Nevertheless, the extreme survival ranges of the major abiotic characteristics of these planktonic invaders in the Baltic Sea are very wide, and their lower salinity tolerance limits are largely overlapping (Table 1). Thus, in the future the putative coexistence of *P. cordatum, C. pengoi* and *A. tonsa* in the shallow brackish-water Baltic coastal environments, e.g., in the Vistula Lagoon or in the eastern Gulf of Finland, is highly probable because of the ongoing desalinization of the Baltic Sea coastal waters due to changing climate (Rajasilta et al., 2014; Vuorinen et al., 2015). In the latter case, the elimination of herbivorous cladocerans and other grazers by *C. pengoi* would presumably favor phytoplankton proliferation, including the potentially toxic bloom-forming dinoflagellates, and could thus trigger the formation of devastating red tides in the oligohaline coastal waters and lagoons of the Baltic Sea.

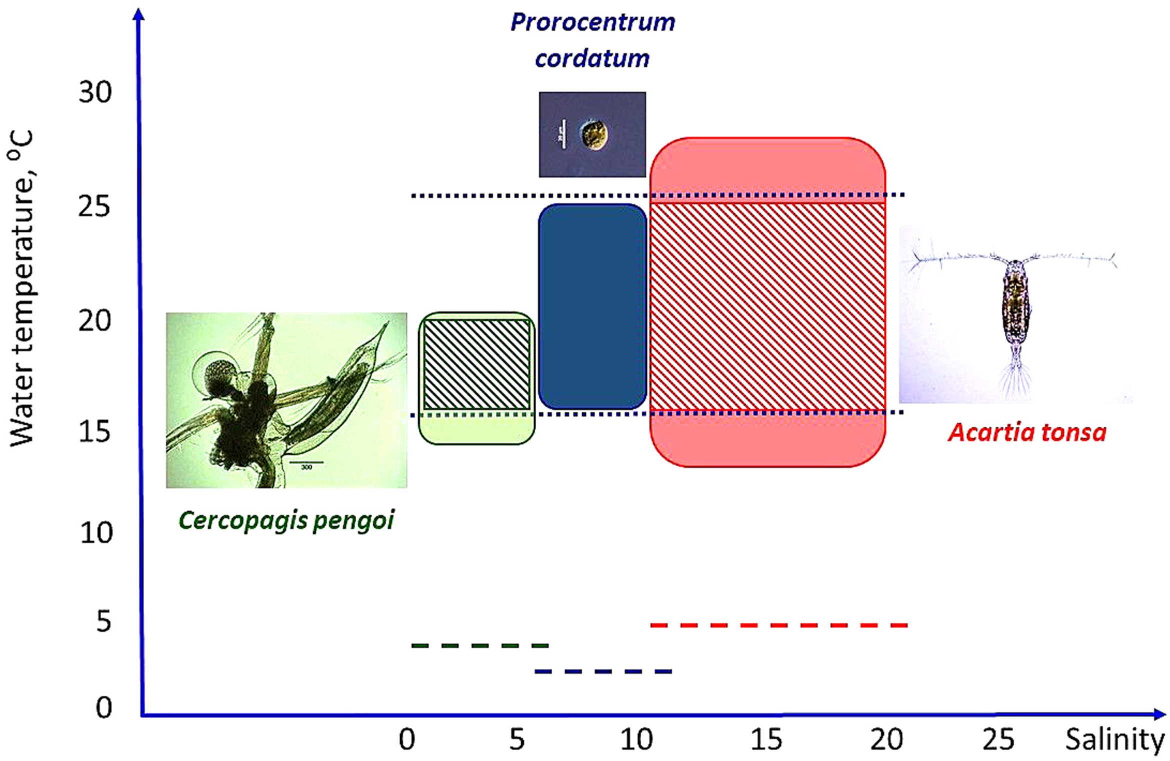

Fig. 4. Schematic representation of water temperature/salinity preferences (i.e. optimum values for population development) of three non-indigenous planktonic species in the Baltic Sea: the fishhook water flea *Cercopagis pengoi*, the dinoflagellates *Prorocentrum cordatum*, and the calanoid copepods *Acartia tonsa* (for *A. tonsa*, the egg production rate in the experiments was considered; data from: Peck et al., 2015). The dotted lines and the diagonally striped areas in the water temperature/salinity 'niches' of *A. tonsa* and *C. pengoi* indicate the water temperature range, which overlaps with the relevant characteristic for *P. cordatum*. The broken lines indicate the lower temperature tolerance limits. Images: *C. pengoi*, female body, with embryos in the brood pouch, scale bar 300 µm, photo I.V. Telesh; *P. cordatum*, live cell, scale bar 20 µm, from open sources; *A. tonsa*, photo courtesy of L.S. Svetlichny.

Outlook

The current knowledge of the ecosystem effects of the nuisance unicellular species (the potentially toxic bloom-forming dinoflagellates *Prorocentrum cordatum*) and multicellular invaders (the carnivorous fishhook water flea *Cercopagis pengoi*) allows concluding about the increasing role of invasive species in plankton of the Baltic Sea estuaries and coastal lagoons. Because of broad ecological niches of these aliens, biotic interactions rather than external environmental stressors can be considered as the primary drivers of plankton dynamics, composition, abundance, and productivity. The basic principles of invasion biology, ecological physiology, and production hydrobiology promote the current and future assessments of the impact of planktonic non-indigenous species on the native communities. Summarizing the multiple effects of *C. pengoi*, one of the most influential pelagic invaders in the Baltic Sea, we can conclude that its cumulative role is the nuisance ecosystem modifier. The recent data from the Vistula Lagoon show that the contribution of this alien species to the overall cladoceran biomass has been consistently increasing during the past two decades. Therefore, we can infer that in the future, top-down control of planktonic grazers by *C. pengoi* will possibly contribute to the deterioration of fish food supply and presumably restructure the pelagic community in a way, which can promote harmful algal blooms and new protistan alien species introductions to the Baltic coastal waters. The robust evaluation of trophic interactions in plankton by using the available impact assessment frameworks and reliable metrics, experimental results and field studies could inform the future prognostic modeling of the invaders' effects on the timing and magnitude of red tides as well as on the perspectives of fish stock and yield in the Baltic Sea and beyond.

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