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REVIEW

Disentangling the potential effects of four non-indigenous species on commercially and recreationally used fish stocks in the Baltic Sea—a review

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Abstract Non-indigenous species (NIS) are on a rise globally. They can pose strong impacts on ecosystems in their non-native range and can therefore be a serious threat to biodiversity. Here, we compile the existing information available regarding the extent to which commercially and recreationally used fish stocks (exploited fish species) are affected by NIS. To do so, we conducted a literature review to summarize the known and presumed impacts of four case study NIS with already known strong effects on the Baltic Sea ecosystem: round goby, *Neogobius melanostomus*, sea walnut, *Mnemiopsis leidyi*, mud crab, *Rhithropanopeus harrisii*, and fishhook water flea, *Cercopagis pengoi.* We found that round goby, mud crab and fishhook water flea are documented to serve as a new food source for native fish species, while sea walnut and fishhook water flea are supposedly affecting planktivorous fish through resource competition. Round goby is very likely a strong competitor for the benthivore fish community. There are also indications that it feeds on juvenile fish and fish eggs. Generally, our results show that large knowledge gaps exist, while the published impacts on exploited fish species are often solely based on correlations (e.g. decreasing abundances of native species

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with cooccurring increasing abundances of NIS), regionally restricted studies or expert judgements. In addition, many studies are older and the current population size of the NIS, which is obviously associated with their impact, is unknown. Thus, the majority of described impacts of NIS on commercially and recreationally used fish stocks seems to stem from assumptions. Therefore, more field observations and experimental studies are needed to be able to scientifically evaluate the impact of NIS. Nevertheless, in this review, the available information was summarized, even if they are speculative, and specific knowledge gaps were identified. Moreover, we outline further investigations that are needed to advance our mechanistic understanding of the interactions between NIS and exploited fish species in the Baltic Sea. This knowledge is essential for the sustainable management of aquatic resources and management of NIS of the Baltic Sea.

Keywords Invasive species · Fisheries · Impact · Management

Introduction

Invasions of non-indigenous species (NIS) can pose threats to global biodiversity with significant impacts on local ecosystem functions (Pyšek et al 2020). In this context, we define NIS with a negative effect on the invaded ecosystem, and with the potential to spread further, as invasive species. Negative effects on native organisms include interactions such as predation on native species or competition for common resources including habitat and food (e.g. Ericsson et al. 2021; Ojaveer et al. 2021). Competition with native organisms can result in the displacement of native species, sometimes even in their extinction, which can ultimately lead to economic losses with social cascading effects on different sectors including tourism and fisheries (Pyšek et al 2020; Warziniack et al. 2021; Haubrock et al. 2022; Kourantidou et al. 2022; Galil et al. 2015). However, not all NIS are documented to negatively affect invaded ecosystems, but might only have negligible or even positive impacts (Ojaveer et al. 2021).

Our study area, the Baltic Sea, is a semi-enclosed brackish water body with a comparatively low species diversity. It is characterized by an extended salinity gradient with nearly fresh water conditions in the north-east and marine conditions in the transition zone to the North Sea in the west. Populations of species inhabiting the Baltic Sea have been shown to either harbor special adaptations to cope with the large salinity range or they are restricted to certain areas along the salinity gradient (e.g. Snoeijs-Leijonmalm and Andrén 2017). Intermediate saline waters are documented to be especially prone to the introduction of new species, not only in the Baltic Sea, but also in other seas with extended salinity gradients (Paavola et al. 2005). In recent decades, the number of new NIS has increased alarmingly due to the intensification of global trade, increasing human mobility and the dismantling of former customs barriers (Seebens et al. 2017; Jensen et al. 2023). Thus, a continuous net immigration of species into the Baltic Sea has been observed, resulting from both natural dispersal and human-induced species introductions (Olenin et al. 2017), leading to "a sea of invaders" (Leppäkoski et al. 2002a, b).

Ojaveer et al. (2017) lists a total of 440 separate invasion events of 132 NIS and cryptogenic species for the Baltic Sea since the beginning of the nineteenth century. Furthermore, they mention that 78 of these 132 NIS and cryptogenic species were established before 2016. However, studies on their general impacts are lacking or are very incomplete for more than half of the most invasive species of the Baltic (Ojaveer et al. 2021). NIS with the potentially greatest impact on ecosystem structure and functioning in the Baltic Sea include: the ctenophore *Mnemiopsis leidyi*, the cladoceran *Cercopagis pengoi*, the mussel *Dreissena polymorpha* (recently also *D. bugensis*), the shrimp *Palaemon elegans*, the fish *Neogobius melanostomus*, the clam *Mya arenaria*, the polychaete *Marenzelleria* spp, the crab *Rhithropanopeus harrisii*, the amphipod *Gammarus tigrinus* and the barnacle *Amphibalanus improvisus* (Jensen et al. 2023; Ojaveer et al. 2021).

In general, several ecosystem components in the Baltic Sea, such as the native fish fauna, are exposed to a variety of stressors including climate change, eutrophication and fisheries (Reusch et al. 2018). This has led to drastic declines in several commercially exploited fish stocks, such as cod (*Gadus morhua*) (Eero et al. 2023). However, the relative contribution of different stressors and their interacting effects are, in many cases, far from being well understood. Likewise, effects of NIS on commercially used fish stocks are poorly documented, partly because the multiple pathways linking ecological processes and fish stock dynamics are difficult to quantify. It is often assumed, sometimes with little evidence, that NIS have negative impacts on the native fauna and flora, and thus also on native commercially and recreationally used fish species. Nevertheless, as the Baltic Sea is a relatively young, species poor brackish water ecosystem (c.f. Snoijs-Lejonmalm and Andrén 2017) colonized by organisms originating either from freshwater or marine systems, certain ecological niches may still be unoccupied and therefore easier to colonize by NIS (Paavola et al. 2005). Any NIS taking up residence in such niches would not need to hold the particular characteristics of an invasive species and should rather be acknowledged as a neutral newcomer in a developing natural community.

To address knowledge gaps regarding the implications of species invasions in the Baltic Sea, this study aims to summarize the current scientific knowledge on the impacts and presumed effects of NIS on commercially and recreationally exploited fish stocks in the Baltic Sea by conducting an extensive literature review. To this end, we selected four case study species that are considered to be the best studied in the Baltic and have been identified as NIS with major impact on the Baltic Sea ecosystem (Ojaveer et al. 2021). These comprise the benthic fish species *Neogobius melanostomus* (round goby), the ctenophore *Mnemiopsis leidyi* (sea walnut), the crustacean *Rhithropanopeus harrisii* (mud crab), and the cladoceran crustacean *Cercopagis pengoi* (fishhook water flea). Information on the documented impacts of these four species was (i) summarized and used as a basis to (ii) discuss scenarios for the potential future spread of these species, to (iii) identify knowledge gaps regarding their effects on fish stocks and to (iv) suggest recommendations for the future management of NIS in the Baltic Sea. Our results will contribute to a better understanding of the role of NIS in the Baltic Sea ecosystem, which is essential for an efficient management of NIS in general and thus an integral part of ecosystem-based management of marine resources.

Material & methods

Based on the ICES Fisheries Overview for the Baltic Sea ecoregion (ICES 2022a), we considered 26 commercially and recreationally used fish stocks in our review (Supplement Table S1). Both grey and peer-reviewed literature were included in the literature review. The search for grey literature was conducted by all authors by checking local and national databases in the respective languages, as well as ResearchGate and Google Scholar. References were added to a systematic review protocol and information on the impacts of the four selected NIS on commercially used fish stocks and their associated fisheries were completed. To search for and retrieve information from peer-reviewed literature, a systematic literature search was conducted following the PRISMA (Preferred Reporting Items for Systematic Reviews and Meta-Analyses) approach (O'Dea et al. 2021). For each of the four case study species, a literature search was conducted in Scopus and Web of Science, using combinations of relevant keywords (Table 1) using the 'AND' operator, e.g. 'Baltic AND round gob* AND impact*' or 'Baltic AND round gob* AND effect*'.

Duplicate reference records were removed and the remaining references were added to the final systematic review protocol. Papers were first screened for relevance regarding the study aims using specific inclusion/exclusion criteria (Table 2). If articles were judged to be relevant (see supplement Table S2-5), the entire content was read and the information entered into the review protocol. Based on the information in the protocols, the impact of

Table 1 Keywords used in the systematic literature review. Each invasive species was combined with each of the specificsearch terms

Region	Invasive species	Specific search term
Baltic	Round gob*	Impact*
	Neogobius melanostomus	Effect*
	Comb jell*	Affect*
	Mnemiopsis leidyi	Influenc*
	(Harris) mud crab*	Competition
	Rhithropanopeus harrisii	Predation
	fishhook water flea*	Food web*
	Cercopagis pengoi	Interacti*

Table 2 Criteria and coding used to decide whether papers were included or excluded i.e., relevant or not relevant, from the literature review regarding the impacts of the four case study NIS on commercially and recreationally used fish species in the Baltic Sea

In/Exclusion coding	In/Exclusion reasoning	Explanation
yes	None of the below	The study fits the search criteria
no_A	Not dealing with/mentioning impact of case study species on exploited fish/fisheries	The study does not deal with/mention the impact of the respective case study species on commercial fish stocks/fisheries
no_B	Outside geographic scope	The study does not focus on the Baltic Sea
no_other	Other reason for excluding the paper	

each NIS on commercially and recreationally used fish species was summarized.

To obtain a general overview of the areas within the Baltic Sea, for which scientific information regarding the impacts of the case study NIS are available (and thus also to detect regional knowledge gaps), geographical areas, within which specific studies had been conducted, were noted at the level of the subdivisions (SD) defined by the International Council for the Exploration of the Seas (ICES).

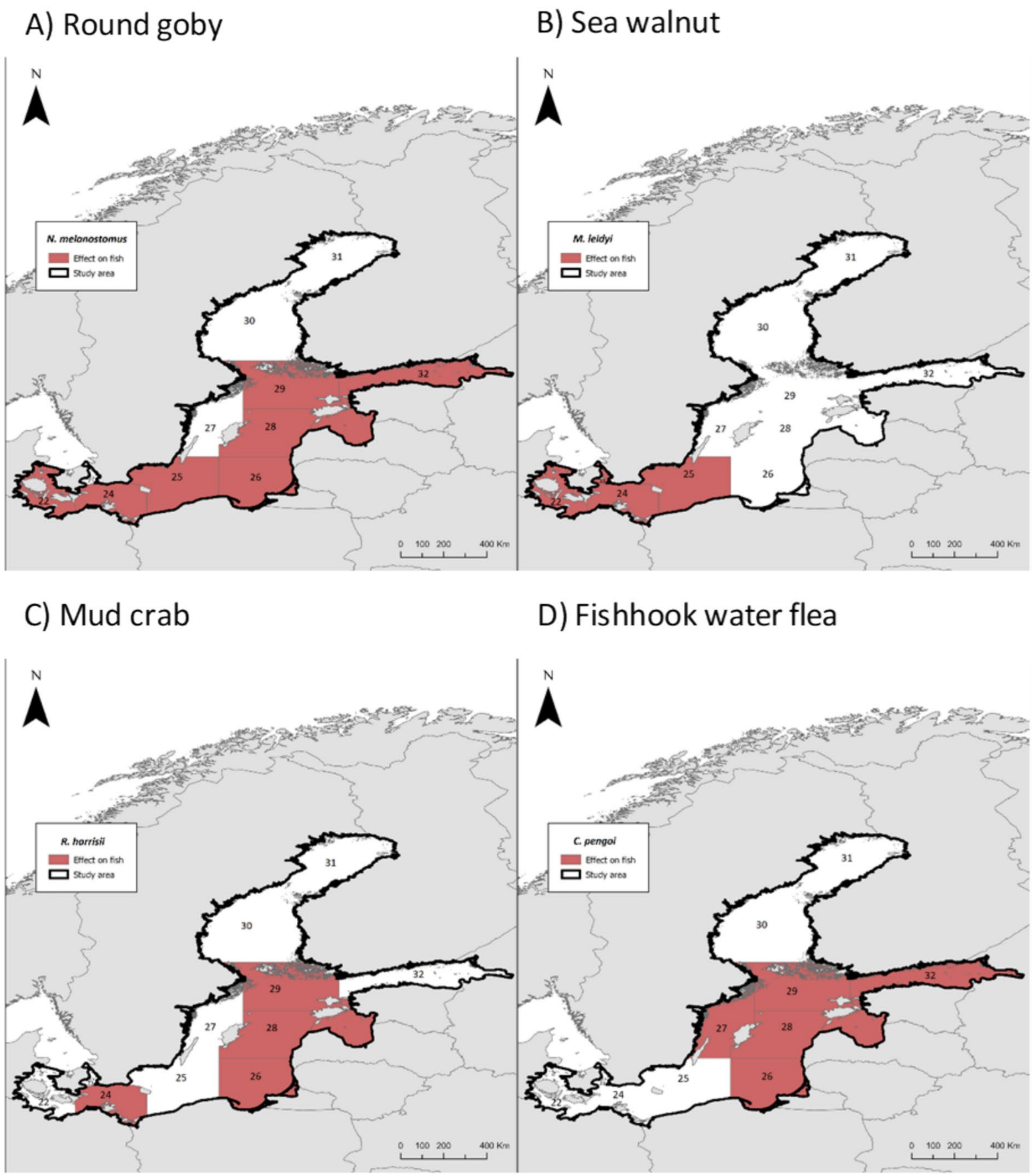
Available knowledge and its geographical origin

A total of 249 peer-reviewed articles were found, of which 57 were considered relevant for our study. The majority of papers (n = 95) dealt with *N. melanostomus* (of which 27 were relevant for this study), whilst fewer articles were found for *C. pengoi* (in total: n = 61, relevant: n = 12), *M. leidyi* (in total: n = 56, relevant: n = 10) and *R. harrisii* (in total: n = 37, relevant: n = 8). A general overview of the results is presented in Supplementary Tables S2-5. Impacts of the four case study NIS on commercially and recreationally exploited fish species are described for the western and central Baltic Sea, while no information is available for the Bothnian Sea and Bay (SD 30, 31), the two most northern basins (Fig. 1). Knowledge for the Gulf of Finland (SD 32) only exists for the impacts of *N. melanostomus* and *C. pengoi*. Information regarding the impact of *M. leidy* is restricted to the most western parts of the Baltic Sea (SD 22–25), while studies on the impact of *N. melanostomus* cover the majority of Baltic Sea regions with the exceptions of SD 23, 27, 30 and 31 (Fig. 1).

Potential impact of *Neogobius melanostomus*

Neogobius melanostomus is a bottom-dwelling fish, native to the Ponto-Caspian region, which has invaded various areas, such as the North American Great Lakes, several European inland waterbodies, and the Baltic Sea (Kornis et al. 2012; Azour et al. 2015; Behrens et al. 2022; Cerwenka et al. 2023). It has a maximum life span of about seven years and can reach a maximum adult length of 25 cm in the Baltic Sea (Sokołowska and Fey 2011; Azour et al. 2015). The species has a high reproduction rate and shows a high tolerance towards various environmental factors i.e., it can be categorized as eurythermal and euryhaline (Corkum et al. 2004; Kornis et al. 2012; Behrens et al. 2017; Christensen et al. 2021). Furthermore, *N. melanostomus* shows more aggressive behavior than the majority of other fish species with a similar lifestyle in invaded areas, such as native gobies, sculpins and eelpouts or juveniles of larger demersal fish species (e.g. Kornis et al. 2012; Ericsson et al. 2021). Moreover, *N. melanostomus* possesses high flexibility in its feeding habits (Kornis et al. 2012; Borcherding et al. 2013; Nurkse et al. 2016; van Deurs et al 2021).

Although top-down pressure of *N. melanostomus* is relatively well studied, records of the species feeding directly on commercially and recreationally used fish species are rare. At the German coast, small *N. melanostomus* (< 10 cm) have been observed in shallow vegetated areas, which serve as important spawning grounds for herring *Clupea harengus* (Henseler et al. 2020). Stomach content analyses of field samples showed that, in contrast to larger individuals (> 10 cm), small *N. melanostomus* feed on *C. harengus* eggs. Yet, supplementary feeding experiments in the laboratory revealed a low preference for these eggs, suggesting that predation on *C. harengus* eggs by *N. melanostomus* is likely to have a lower negative



A) Round goby

B) Sea walnut

C) Mud crab

D) Fishhook water flea

Fig. 1 ICES subdivisions in the Baltic Sea. Red colored areas illustrate ICES subdivisions for which an impact of the case study NIS (**a**–**d**) on commercially and recreationally exploited fish stocks has been reported based on the literature review

impact than predation by native species, such as *Gasterosteus aculeatus* and *Perca fluviatilis* (Kotterba et al. 2017; Wiegleb et al. 2018;). However, the specific impact likely depends on *N. melanostomus* abundances in the environment, as well as on the available food resources. Consumption of small *Platichthys flesus* (≤ 38 mm TL) by *N. melanostomus* has only been observed under laboratory conditions

(Schrandt et al. 2016). However, a recent study based on metabarcoding of stomach contents showed that, besides feeding on *G. aculeatus, Zoarces viviparus* and *Rutilus rutilus, N. melanostomus* also prey on the early life stages of various commercial species including *Gadus morhua*, *Esox lucius*, *Sander lucioperca*, *P. fluviatilis*, *C. harengus*, *Sprattus sprattus* and salmonid species along the Swedish and Ålandish coast (Wallin Kihlberg et al. 2023).

Potential resource competition or other niche overlap in geographically overlapping distribution ranges of *N. melanostomus* and other fish species have been observed in several studies (e.g. Karlson et al. 2007; Kornis et al. 2012; Behrens et al. 2022). Karlson et al. (2007) documented a significant diet overlap between *N. melanostomus* and small *P. flesus* in addition to negative correlation between *N. melanostomus* and *P. flesus* abundances with a reverse depth distribution of the two species along the Polish coast, indicative of mutual avoidance behavior. Negative repercussions of *N. melanostomus* invasion for *P. flesus* are therefore assumed to be caused by competition for habitat and food availability. Generally, there seems to be a major overlap in the geographic distribution (up to 70%) of the two species, as revealed by a field study covering large parts of the Baltic Sea (Behrens et al. 2022). Potential food competition with (small) *P. flesus* has been suggested in several Baltic Sea regions (Corkum et al. 2004; Järv et al. 2011, 2015; Schrandt et al. 2016; Ustups et al. 2016; Rakauskas et al. 2020; Henseler et al. 2021). Additional indications for competition between *N. melanostomus* and native fish species have been reported along the Latvian and Swedish coasts. Field observations showed that both abundances and feeding success (e.g. proportion of filled stomachs) of juvenile *Scophthalmus maximus* decreased after the invasion of *N. melanostomus* (Ustups et al. 2016; Knospina and Ustups 2016), and that spawning stock biomass of *S. maximus* had been three times lower since 1997 (Ustups 2022). However, whether both negative trends can be solely attributed to the invasion of *N. melanostomus* has not been verified. A significant trophic niche overlap has been identified between *N. melanostomus* and *Pleuronectes platessa* and *P. flesus* in spring at the Lithuanian coast (Rakauskas et al. 2020). Accordingly, it was suggested that *N. melanostomus* competes for food resources with native fish species, such as S. *maximus*, *P. flesus* and *P. platessa* along the Latvian and Lithuanian coast (Aigars et al. 2018; Rakauskas et al. 2020; Ustups 2022). In addition, the modelled habitat overlaps between *N. melanostomus* and juvenile *E. lucius* at the Swedish south coast is assumed to negatively affect *E. lucius* through both competition and predation (Florin et al. 2018). Indeed, *N. melanostomus* has been documented to reduce abundances of benthic prey organisms common to the two species (e.g., *Cerastoderma* spp., *Hydrobia* spp., *Mytilus* spp.) (Henseler et al. 2021; Van Deurs et al. 2021).

Besides its negative effects on similar or lower trophic levels, *N. melanostomus* has been reported to serve as prey for higher trophic levels, such as birds and piscivore fish (Kornis et al. 2012; Liversage et al. 2019; Reckermann et al. 2022; Herlevi et al. 2023). For instance, medium-sized *G. morhua* and *P. fluviatilis* in the Gulf of Gdańsk rely heavily on *N. melanostomus* as a primary food source (Almqvist et al. 2010). Next to *G. morhua* and *P. fluviatilis*, several other commercially exploited fish species prey on *N. melanostomus* in the Baltic Sea including *S. lucioperca*, *S. maximus* and *E. lucius*, which is why positive effects of *N. melanostomus* on large predatory fish have been suggested (Järv et al. 2011, 2018; Oesterwind et al. 2017; Liversage et al. 2017; Rakauskas et al. 2020; Więcaszek et al. 2020; Funk et al. 2021; Herlevi et al. 2023). In Puck Bay, along the Polish coast for example, *N. melanostomus* is the main food source for *E. lucius* (Psuty et al. 2023). Since *N. melanostomus* represents the first mussel-feeding fish species in the Baltic Sea, it has been suggested that *N. melanostomus* might provide a new energetic pathway from mussels to large piscivores (Almqvist et al. 2010). Accordingly, along the Lithuanian coast, *N. melanostomus* might have strengthened the trophic pathway of organic matter and energy flow from the lower benthic levels up to piscivores, which could enhance predator production and thus commercially important fish species, benefiting coastal fisheries (Rakauskas et al. 2008). In contrast, the new trophic link might potentially reduce the quality of fish resources due to a lengthening of food chains (Rakauskas et al. 2020).

Due to its position in the food web of the Baltic Sea, the presence of *N. melanostomus* might benefit native commercially exploited fish species as they are released from predation pressure. In the Gulf of Gdańsk, for example, cormorants (*Phalacrocorax carbo*) shifted their diet from *Anguilla anguilla* and

S. sprattus to *N. melanostomus* (Bzoma and Stempniewicz 2001). Similar observations have been documented in the western Baltic Sea, where *N. melanostomus* represented about 35% of the estimated pellet biomass of the cormorant, while the contributions of *R. rutilus* and *Z. viviparus* substantially decreased within a five-year period (Oesterwind et al. 2017).

Another positive aspect of the presence of *N. melanostomus* is directly related to fisheries, as it has become a commercially used fish species itself in the eastern parts of the Baltic Sea (ICES 2022b). In Latvia, a specialized *N. melanostomus* fishery has been ongoing since 2015 with landings of over 1,000 tons in 2018. With regard to landings, *N. melanostomus* represents the second most important commercial species following *C. harengus* in the Latvian coastal fishery. In Lithuania, *N. melanostomus* was first observed in commercial catches in 2010 with the highest landings (above 200 tons) reported in 2016 and 2017. In Estonian coastal fisheries, *N. melanostomus* has been caught since 2007 with the highest landings of 256 tons documented in 2021 (ICES 2022b). Based on the current poor condition of many commercially exploited fish species, *N. melanostomus* might be a future alternative for small scale fisheries.

Potential impact of *Mnemiopsis leidyi*

Mnemiopsis leidyi is a lobate ctenophore native to the east coast of North and South America which has been present in western Eurasian waters since the 1980s (Purcell et al. 2001; Faasse and Bayha 2006; Costello et al. 2012; Jaspers et al. 2018a). *M. leidyi* is characterized by high growth rates and great reproductive capacity (Jaspers et al. 2015a). Due to the difference in morphology, larvae and adults of *M. leidyi* have different prey preferences. While adults prey primarily on larger zooplankton such as copepods (Colin et al. 2010), larvae feed on microzooplankton < 100 µm (Sullivan and Gifford 2004). In the higher saline Kattegat, *M. leidyi* have been shown to produce $> 10{,}000$ eggs per day (Jaspers et al. 2015a), and even under starvation, animals keep daily egg production for up to 4 days (Jaspers et al. 2015b). Interestingly, reproduction rates of fed and 24h starved animals do not differ significantly (Jaspers et al. 2015b). Given food and temperature conditions are favorable, eggs are produced by *M. leidyi* on a daily basis (Costello et al. 2012; Jaspers et al. 2018b). Although, *M. leidyi* is known to feed primarily on zooplankton, the species also prey on fish larvae and occasionally on fish eggs (Hamer et al. 2011; Jaspers et al. 2011a). Yet, only one study has quantified the direct predation effects of *M. leidyi* on different developmental stages of cod eggs and larvae in the Baltic Sea (Jaspers et al. 2011a). Prey selection experiments conducted in the Baltic and North Sea confirmed that feeding by *M. leidyi* on different fish eggs was negligible and not significantly different from zero (Hamer et al. 2011; Jaspers et al. 2011a). However, other studies utilized field data to estimate temporal and spatial distribution overlaps to draw conclusions about possible interactions between *M. leidyi* and native fish species (e.g. Haslob et al. 2007; Schaber et al. 2011a, 2011b). Two years after the first recordings of *M. leidyi* in the southern Baltic Sea, no effects on juvenile *C. harengus and S. sprattus* along the German coast off Rügen could be determined based on temporal-spatial distribution patterns. Furthermore, no fish eggs were detected in the intestinal contents of *M. leidyi* in the Bay of Kiel, making it unlikely that it has a significant direct influence (Javidpour et al. 2009). In the Bornholm Basin, the spatial overlap between *M. leidyi* and *S. sprattus* was low in May 2007 (Haslob et al. 2007), most likely because *S. sprattus* eggs were distributed above the halocline, while *M. leidyi* was found well below the halocline (Schaber et al. 2011a; Haraldson et al. 2013). Thus, the overall spatial and temporal overlap with *S. sprattus* eggs is limited and no direct impacts are expected in the Bornholm Basin (Schaber et al. 2011a).

The most important spawning ground for eastern Baltic cod is located in the Bornholm Basin. *M. leidyi* and *G. morhua* eggs are found in the same depth range in this area, which could indicate a high predation risk, especially as *G. morhua* eggs have been observed in the stomachs of *M. leidyi* (Haslob et al. 2007). However, the direct impact of predation on *G. morhua* eggs has generally been estimated as low (Postel and Kube 2008; Schaber et al. 2011a, 2011b) due to low *M. leidyi* abundances in this area (Postel and Kube 2008; Haraldsson et al. 2013). In addition, laboratory experiments have shown that *M. leidyi* generally has low predation rates on *G. morhua* eggs (Jaspers et al. 2011a), and *M. leidyi* seems to select crustacean zooplankton over *G. morhua* eggs so that feeding rates on eggs are very low under environmental conditions representative of the spawning area in the Bornholm Basin (Hamer et al. 2011; Jaspers et al. 2011a).

In the laboratory, *M. leidyi* has been documented to directly feed on early *G. morhua* yolk sac larvae, although the spatio-temporal overlap has been shown to be negligible in the past (Jaspers et al. 2011b). However, recently feeding was also documented on herring yolk sac larvae (Stoltenberg et al. 2024). Hence, these impacts could magnify in the future if *M. leidyi* becomes more abundant in the Baltic Sea, in general, and in the Bornholm Basin, in particular, pointing to the importance of future monitoring of *M. leidyi's* population development.

Planktivorous fish and fish larvae might also be affected by the presence of *M. leidyi* through prey competition. Negative impacts and cascading effects of *M. leidyi* on calanoid copepods and diatoms, both representing prey for planktivorous fish and fish larvae, have been documented by comparing years with and without the presence of *M. leidyi* populations in higher saline areas of the Skagerrak and Limfjorden in Denmark (Riisgård et al. 2012; Tiselius and Møller 2017). While abundances may not be equally high in the Baltic Sea, the highest *M. leidyi* abundances have been observed in the southwestern Baltic Sea (Javidpour et al. 2009; Jaspers et al. under review), an area, where a high spawning stock biomass of *C. harengus* has been documented. Thus, we cannot exclude the possibility of indirect effects through food competition during *M. leidyi* population peaks in late summer/autumn (Haraldson et al. 2013). Therefore, autumn spawning *C. harengus* are especially expected to be negatively impacted, while spring spawning *C. harengus* may experience no direct or indirect effect by *M. leidyi* (Javidpour et al. 2009). Likewise, in November 2007, direct competition for food with juvenile fish in the Bornholm Basin was negligible due to very low *M. leidyi* abundances (Huwer et al. 2008). In general, *M. leidyi* is restricted to higher saline waters of the southwestern and deeper waters of the central Baltic Sea, where salinities are generally above 10 (Jaspers et al. 2018a) and do not occur in the more northern and eastern parts of the Baltic (Haraldsson et al. 2013; Lehtiniemi et al. 2012). Thus, given its current restricted environmental tolerance window in the Baltic Sea, no indirect effects on exploited fish populations through food competition can be expected in the Baltic Sea.

Another indirect impact on exploited fish populations could occur through the translocation of potential fish pathogens from *M. leidyi* to native fish (Jaspers et al. 2020). However, dedicated experiments are required to confirm the pathogen status and virulence of detected putative problematic microbial strains in the core microbiome of *M. leidyi* (Jaspers et al. 2020). In summary, no impacts of *M. leidyi* on commercially or recreationally exploited fish stocks occur in the lower saline areas of the Baltic Sea while, negative impacts on fish populations possibly through indirect effects such as prey competition may occur in areas with higher salinity such as the Kattegat and the southwestern Baltic Sea where *M. leidyi* occur in higher numbers.

Potential impact of *Rhithropanopeus harrisii*

Rhithropanopeus harrisii is native to the Atlantic coast of North America (Williams 1984; Projecto-Garcia et al. 2010) and possesses many characteristics of a successful invader. The species is omnivorous, euryhaline, eurytherm and occurs in a variety of habitats. Moreover, it has a high reproductive capacity and a long planktonic larval period (Costlow et al. 1966; Turoboyski 1973, Roche et al. 2007; Forward 2009, Fowler et al. 2013). These abilities have likely facilitated its wide spread (Roche et al. 2007; Kotta and Ojaveer 2012; Fowler et al. 2013). In both, its native and non-native range, it is found in different kinds of shelter on sandy, muddy, and rocky bottoms (Ryan 1956; Turoboyski 1973; Williams 1984; Petersen 2006; Fowler et al. 2013). Females are able to spawn at a carapace width of 4.8 mm in their native range and a width of 8 mm in invaded regions (Ryan et al. 1956; Turoboyski 1973). The maximum size of *R. harrisii* is bigger in invaded areas (26 mm) than in its native range (15.5 mm) (Ryan et al. 1956; Turoboyski 1973; Fowler et al. 2013).

Although *R. harrisii* has been reported to consume soft tissues of *P. flesus* under laboratory conditions (Hegele-Drywa and Normant 2014), there does not seem to be any evidence of direct effects of *R. harrisii* on commercially exploited fish species in the Baltic Sea. However, it is an omnivore predator feeding on various benthic invertebrate grazers (Nurkse et al. 2016, 2018) in the Baltic Sea and has been reported to affect local communities through direct predation. For example, *R. harrisii* reduced the abundance, richness and diversity of native invertebrates associated with bladder wrack (*Fucus vesiculosus*) on a rocky littoral shore in the inner Archipelago Sea of Finland (Jormalainen et al. 2016; see also Forsström et al. 2015). Stable isotope analyses have shown that large *R. harrisii* (> 12 mm carapace width) can be grouped as secondary consumers together with fish, and are thus competing for prey (Aarnio et al. 2015). Therefore, it can be assumed that potential competition for food resources occur with other secondary consumers like *P. fluviatilis*, *R. rutilus*, *Abramis brama* and other fish species with a similar diet. Through this predation on macroinvertebrate communities, *R. harrisii* might possibly affect these afore mentioned exploited fish stocks by altering feeding conditions in the environment. An increase of *R. harrisii* abundance in partially empty ecological niches of vegetated soft-bottom and hard bottom habitats will likely increase the predation pressure on important seagrass *Zostera marina* grazers (Gagnon and Boström 2016) and grazers feeding on filamentous algae on bladderwrack. Along with a reduced availability of invertebrate prey, the subsequent decline of grazer such as amphipods may also lead to trophic cascades resulting in the deterioration of spawning habitats of certain fish species due to an increase of filamentous algae (Liversage et al. 2019, 2021).

Similar to *N. melanostomus*, *R. harrisii* can have positive direct effects on the local fish community by serving as a new prey source. Several native fish species, such as *Myoxocephalus quadricornis*, *P. fluviatilis*, *Gymnocephalus cernuus*, *S. lucioperca*, *R. rutilus* and other cyprinids consume *R. harrisii*, although the contribution of *R. harrisii* in fish stomach contents varies greatly among fish species and depends on the size of crabs and fish predators (Fowler et al. 2013; Puntila-Dodd et al. 2019). In summary, there are no known effects of *R. harrisii* on commercially exploited fish stocks in the Baltic Sea, while impacts on species important for recreational fisheries (e.g. *P. fluviatilis*) are more likely due to indirect effects through grazer depletion in key spawning habitats.

Potential impact of *Cercopagis pengoi*

Cercopagis pengoi is a cladoceran crustacean native to the Ponto-Aralo-Caspian region. It is a eurytherm and euryhaline generalist predator feeding on a variety of prey species of different sizes (Pichlová-Ptáčníková and Vanderploeg 2009; Gorokhova et al. 2000). The length of the species ranges from 1 to 3 mm without the hooked tail and from 6 to 13 mm including the tail (Benson et al. 2018). As other cladocerans, *C. pengoi* reproduces asexually during the summer and sexually during undesirable conditions (Benson et al. 2018). Sexual reproduction leads to the production of rugged resting eggs resistant to e.g. desiccation and ingestion by predators (Katajisto et al. 2013; Benson et al. 2018). The first documentation of the species in the Baltic Sea stems from 1990. Since then, it has become a prominent member of the zooplankton community in the Baltic proper, Gulf of Finland and Gulf of Bothnia (Katajisto et al. 2013). It is present in the northern Baltic proper from July to October but is most abundant in warm waters in August and September (Gorokhova et al. 2004).

The invasion of *C. pengoi* in the Baltic Sea seems to affect mainly three exploited important fish species, *C. harengus*, *S. sprattus* and *Osmerus eperlanus*, because it feeds on the same zooplankton prey as these planktivorous fish and is able to affect the zooplankton community substantially. For example, since abundances of *C. pengoi* reached high levels in the Gulf of Riga (by 85% in the eastern Gulf of Finland; Lehtiniemi and Gorokhova 2008), the abundances of the dominant copepod *Eurytemora affinis* have declined by 90% and the maximum abundances of the cladoceran *Bosmina* spp. have shifted to a period earlier in the season in the Gulf of Riga (Einberg et al. 2020). Both species are important prey of adult *C. harengus*, *S. sprattus* and *O. eperlanus* in the Baltic Sea (Lankov et al. 2010; Livdāne et al. 2016; Peltonen et al. 2004). Importantly, in the Gulf of Riga, Einberg et al. (2020) suggest that the changes in *C. pengoi* abundances were particularly conspicuous at higher temperature (> 15 °C), which may indicate that the effects of *C. pengoi* on herring, sprat and smelt may be accentuated in a future, affected by climate change.

However, the impact may be limited to adult fish because larval *C. harengus* feed almost exclusively on copepod nauplii larvae, and data from the Gulf of Riga indicate that the presence of *C. pengoi* affected neither timing nor maximum abundance of copepod nauplii during the *C. harengus* larvae feeding period between May and July (Arula et al. 2014).

C. pengoi is expected to have a positive effect on commercially used fish species by contributing significantly to the diets of *C. harengus*, *S. sprattus* and *O. eperlanus* in the Baltic Sea (Gorokhova et al. 2004; Lankov et al. 2010; Antsulevich and Välipakka 2000). In fact, it has been argued that the invasion of *C. pengoi* in the Gulf of Finland has allowed the herring stock to recover from the detrimental effects of declining copepod abundances during the 1980's (Antsulevich and Välipakka 2000). At the Swedish coast, *C. pengoi* becomes a major prey constituent from August until September complementing herring diet during the time when abundances of native zooplankton prey decrease and the major zooplanktivores are young-of-the-year clupeoids and mysids (Rudstam et al. 1992). *C. pengoi* contributes up to 60% of the prey biomass in stomachs of *C. harengus* sized 10–15 cm and accounted for ca. 10% of the stomach content in 10–15 cm *S. sprattus* (Gorokhova et al. 2004). In the Gulf of Riga, *C. pengoi* also constitutes a larger fraction of the diet of *C. harengus* during warmer months, when *C. pengoi* occurs in higher abundances (Ojaveer et al. 2004). Between 1999 and 2006, it also contributed up to 60% of the diet (stomach content wet weight) in adult *C. harengus* but comprised only a few percent of the diet of juvenile *C. harengus*, *S. sprattus* and *O. eperlanus* in the Gulf of Riga (Lankov et al. 2010).

In Estonian coastal waters, the contribution of *C. pengoi* to the diet of *C. harengus* and *O. eperlanus* was high when the cladoceran was present in the water column (June–September). In general, *C. harengus* starts feeding on *C. pengoi* at a length of 4.1 cm, and *O. eperlanus* at a length of 7.3 cm. Thus, the consumption of *C. pengoi* by *C. harengus* is size-dependent and the share of *C. pengoi* in the diet of large *C. harengus* (15–16 cm) can reach over 10% by wet weight, thus exceeding that of smaller individuals by a factor of 2–3 (Kotta et al. 2006).

Overall, impacts of *C. pengoi* on planktivorous fish have been demonstrated to be among the strongest effects among Baltic NIS (Ojaveer et al. 2021). However, since its trophic role is complex, the direction of the impacts on planktivorous fish is difficult to predict. An increasing *C. pengoi* biomass may serve as an additional food source but may also impose significant competition for prey. Our review shows that impacts on commercial fish are obvious but also likely on recreational fish stocks, even if those studies are presently missing.

Due to its special morphology (its long caudal appendage i.e., hook), *C. pengoi* can also influence the efficiency of fisheries when thousands of individuals become entangled and thus form a paste-like substance which, when it gets caught on fishing lines and in nets, can reduce gear effectiveness (Panov et al. 1999).

Potential spreading and distribution of the case study NIS in the future

Due to different physiological tolerances, each of the four case study species has unique dispersal and reproductive requirements. Additionally, environmental conditions (e.g., salinity, temperature, oxygen concentration, depth, photoperiod, bottom substrate, etc.) differ greatly between regions in the Baltic Sea (Jaspers et al. 2021), which to a large degree influences the future spread of NIS (Holopainen et al. 2016; Snoijes-Lejonmalm and Andrén 2017; Quattrocchi et al. 2023). Therefore, the following section will differentiate between three regions with differing environmental conditions: the Danish Straits, the central Baltic Sea and the Gulf of Bothnia. The Danish Straits are located in the southwestern Baltic Sea, where salinity is highest and above 10 psu even in surface waters due to the connection with the North Sea (Hagen and Feistel 2005). The Straits are characterized by relatively strong currents (She et al. 2007), which may favor the passive dispersal of organisms and possibly the colonization of new areas. Shallow sills in the western Baltic Sea limit the inflow of saltier and oxygen-rich water from the North Sea/Skagerrak/Kattegat to the east. Therefore, the salinity decreases to around 7 psu in near-surface waters in the central Baltic Sea (Hagen and Feistel 2005). The offshore area of the central Baltic Sea is characterized by three deep basins (Bornholm Basin, Gdansk Deep, Gotland Basin) separated by shallow sills, further hindering water exchange with the North Sea, and differing in their water balance and hydrographic conditions (MacKenzie et al. 2000). These hydrographic conditions depend heavily on the renewal of bottom water by inflowing highly saline and oxygenated water masses from the North Sea and the Skagerrak/Kattegat (Möllmann et al. 2000). Within the last decades, oxygen depletion has been observed in the deeper basins since the exchange between bottom and surface waters is restricted by a permanent halocline. Salinity and temperature near the surface are influenced by freshwater runoff from rivers (Launiainen and Vihma 1990). The Gulf of Bothnia in the northern Baltic Sea is characterized by low salinity (3–4 psu) in surface waters (Hagen and Feistel 2005) and a strong freshwater influence from river systems. Winter periods are long and relatively cold with seasonal ice covers lasting up to several months (Seinä and Peltola 1991).

Based on the information gathered in the literature review, the Danish Straits in the western Baltic Sea appear to be affected most severely by the four case study species, while the Gulf of Bothnia seems to experience the lowest impact.

Since *N. melanostomus* already occur in all areas of the Baltic Sea with suitable environmental conditions, further distribution is only possible into freshwater or to the most northern areas where temperatures are, however, likely too cold for the species to thrive and be competitive (Christensen et al. 2021; Quattrocchi et al. 2023). Due to its flexible diet and high tolerance towards various environmental conditions, abundances may continue to increase throughout the Baltic Sea (Borcherding et al. 2013; Nurkse et al. 2016), but in the southern Baltic the population seems to have reached a stable state by now. A different trajectory was observed in Latvian waters, where the population increased exponentially since 2006, peaked in 2018, and then declined sharply, likely due to increased commercial fishing pressure (Kruze et al. 2023). Limiting factors for the dispersal of *N. melanostomus* could be competition with fish sharing the same ecological niche (Kornis et al. 2012) or predation by piscivores (Kornis et al. 2012; Rakauskas et al. 2013; Liversage et al. 2017; Happel et al. 2018; Herlevi et al. 2023). When present in large numbers, competition for food could either be a limiting factor or a driver for further spread (Azour et al. 2015). However, range expansions of *N. melanostomus* into the high saline North Sea are probably limited by salinity (Kornis et al. 2012; Behrens et al. 2017; Green et al. 2021).

Mnemiopsis leidyi still has the potential to further spread into the central Baltic Sea. However, decreasing salinity towards the north and east drastically affects reproduction, with egg production being drastically reduced at intermediate salinities (below 20 psu) and ceases at low salinities < 10 psu (Jaspers et al. 2011b). Hence, there is currently little risk that the species will expand its distribution into the main basin or the northern Baltic Sea. But salinity tolerance might change if the southern *M. leidyi* population is introduced to the Baltic Sea, as this population thrives in low saline areas of the Caspian Sea and Sea of Azov (Ivanov et al. 2000; Shiganova et al. 2001). Additionally, the introduction of the southern population could lead to hybridization and thereby impact salinity tolerance. Hybrid populations have lately been detected in the native range of the species and are suggested to be positively selected in extreme low saline environments (Pujolar et al. 2023). Hence, molecular monitoring of population structure and origin is important for management actions (Pujolar et al. 2022).

R. harrisii has populated all major sub-basins of the Baltic Sea offering favorable conditions, however, there still seems to be available habitat for the species at a local scale. Since the species requires at least salinities around 2.5 psu for reproduction (Williams 1984), its distribution ends in the northernmost areas of the Baltic Sea (Bothnian Bay). Yet, it cannot entirely be ruled out that *R. harrisii* will migrate into the north, especially since it successfully settled in the low salinities of southern Baltic lagoons.

Cercopagis pengoi is most abundant in the Baltic zooplankton community in temperatures ranging between 13 and 25 °C and below a salinity of 5.8 psu, and will thus be expected to become more abundant and widespread in coastal and open sea areas of at least the northern Baltic in the future climate, with rising temperatures allowing for more parthenogenetic generations (Holopainen et al. 2016).

Knowledge gaps and recommendations for management

In general, reports of the presence of a specific NIS are limited to a particular point in time and space. Although the relationships between abundance of NIS and magnitude of impact are obvious, most studies do not report abundance data. Furthermore, changes in abundance during the invasion and establishment process, and consequently the magnitude of impacts, also vary. Yet, it is precisely this information that is often missing in order to be able to estimate the effects of NIS. For example, it is rarely reported how long a NIS has been present in the study area or whether it has already established a stable population or is still in the process of doing so. In this respect, most available studies are older and lack regular updates of details on occurrence, abundances, population status and dynamics of the NIS or ecosystem impacts in the invaded area, which hinders a scientific based evaluation of their impact.

Even though monitoring the presence and impacts of NIS is considered an important part of marine environmental management and despite the stated intention to focus on NIS in the EU Marine Strategy Framework Directive, only few monitoring programs exist specifically targeting NIS, leading to insufficient data and knowledge (Outinen et al. 2024).

One of the important key management objectives include early detection of NIS in dispersal centers and beachheads, as well as long-term monitoring to track the impact of NIS in recipient ecosystems that are particularly vulnerable to introductions (Lehtiniemi et al. 2015). For example, HELCOM's COMBINE monitoring program (Cooperative Monitoring in the Baltic Marine Environment, HELCOM 2017) is currently used to record the presence-absence and densities of NIS in phytoplankton, zooplankton and benthic animals in all Baltic sub-basins (HELCOM 2017). However, routine monitoring in many Baltic Sea states does not cover all invasion hotspots, habitats and taxonomic groups. In this context, especially, the Gulf of Finland, the Gulf of Riga, coastal lagoons and the German "Bodden" areas are regarded as "hotspots" and entrance gates for numerous invasions in the Baltic (Leppäkoski et al. 2002a, b). Furthermore, the extent of monitoring varies between different areas and is not standardized so that a comparison between areas and time is challenging. Knowledge of the occurrence of NIS at specific locations or depths, as well as the occurrence of NIS over time or within seasons, is critical for assessing the impacts of specific NIS on commercially and recreationally fish species, food webs, and ecosystems, which is why HELCOM suggests using other additional surveys and new methodologies to monitor NIS presence and spread (HELCOM 2021). Therefore, the future strategy should be double-edged, and although rapid assessment of target species in key invasive areas is important, it should not replace long-term monitoring programs. These monitoring programs should be based on environmentally friendly sampling methods to reduce the impact on the monitored ecosystem as much as possible (Hammerl et al. 2024). Another opportunity is the performance of tagging studies to investigate the migration pattern of NIS.

The link between NIS and ecological impacts, as well as changes in fish stocks, are difficult to quantify. Depending on the species, NIS can have a negative or positive impact on certain native commercially or recreationally used fish species. Most of the widely distributed NIS have either no or very incomplete overall impact data (Ojaveer et al. 2021) and often only one aspect of frequently multi-path interactions is considered.

One of the major knowledge gaps regarding the impact of NIS concerns the introduction and transmission of parasites. Accordingly, information on the four case study NIS acting as sources of parasites are scarce. In addition, little is known about the transfer and biomagnification of pollutants in the Baltic Sea food web by NIS. For example, Graca et al. (2022) suggested a possible transfer of mercury from beach wrecks to *R. harrisii*, but other studies have found low concentrations of mercury in their tissues (Wilman et al. 2019), indicating that local differences exist.

Filling these above-mentioned knowledge gaps would improve the ability to assess the impact of NIS on exploited fish species in the Baltic Sea. Besides a higher monitoring effort, more effort should be invested into regional and transnational impact studies covering the whole distribution area of the NIS and longer time periods.

Conclusion

In this review, we summarized the existing knowledge on the impact of four NIS (*Neogobius melanostomus*, *Mnemiopsis leidyi*, *Rhithropanopeus harrisii*, *Cercopagis pengoi*) on commercially and recreationally used fish species in the Baltic Sea. We show that most of the selected species have a potential impact on these fish stocks. However, despite our focus on NIS with most information available, no conclusive evidence was found suggesting that commercially or recreationally used fish stocks are currently severely impaired through the invasion of the four species. The majority of negative effects reported derive from correlative relationships, which suggest, but do not prove existing impact or the underlying mechanisms of interaction. Since the impact of NIS can vary on a very local scale due to differences in NIS abundances, and many areas of the Baltic Sea still lack impact studies, the four NIS might potentially have a considerable impact on exploited fish stocks in specific regions, which has, however, not yet been detected. It is therefore important to prove whether the described correlative relationships between NIS and native species represent actual interactions and to establish a mechanistic understanding by dedicated experiments. Moreover, it appears crucial to investigate cumulative impacts of multiple NIS, while improving our knowledge on the distribution and abundance dynamics of NIS at a higher geographic resolution, at the same time.

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Data availability The dataset used for this study is available by the corresponding author on reasonable request.

Declarations

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