Science of the Total Environment 786 (2021) 147375

Contents lists available at ScienceDirect

Science of the Total Environment

journal homepage: www.elsevier.com/locate/scitotenv

Meta-analysis on the ecological impacts of widely spread non-indigenous species in the Baltic Sea

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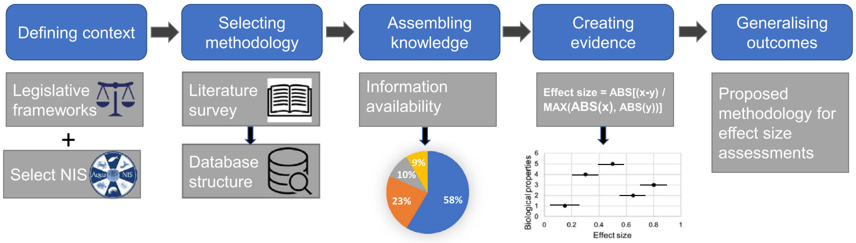
HIGHLIGHTS

- Effects of widespread NIS on ecosystem features and properties were quantified.
- Most impactful NIS, processes underlying the changes and sources of uncertainty were identified.
- Among communities, fish have been impacted the most while the pelagic realm is more affected than the benthic.
- Significant effects were evident on the entire food web.
- The effect size method offers a robust approach for general applications on quantification of the effects of NIS.

GRAPHICAL ABSTRACT



ARTICLE INFO

Article history:
Received 24 January 2021
Received in revised form 20 March 2021
Accepted 22 April 2021
Available online 28 April 2021

Editor: Martin Drews

Keywords:
Meta-analysis
Widespread non-indigenous species
Baltic Sea
Effect size
Biological properties
Trophic guilds

ABSTRACT

The introduction of non-indigenous species (NIS) is a major driver for global change in species biogeography, often associated with significant consequences for recipient ecosystems and services they provide for humans. Despite mandated by several high-level international legislative instruments, comprehensive quantitative evaluation on ecosystem impacts of marine NIS is scarce and lack a robust and data-driven assessment framework. The current study is aiming at fulfilling this gap, through quantitative assessment on the effects of the widespread NIS of the Baltic Sea on multiple ecosystem features and components including direct food-web effects. The outcomes of this study allowed identifying the most impacting widespread NIS, together with defining the processes underlying the most significant changes and outlined major sources of uncertainty. Lack and/or bias in the availability of evidence of impacts was recorded for several (both recent and early) introductions. Realizing a sophisticated, data and information-hungry framework for the evaluation of ecosystem impacts of NIS is not pragmatic for management purposes in the foreseeable future. Instead, simple approaches, such as application of common statistical parameters like absolute effect size, are more likely to result in tangible outcomes. As bearing no unit, effect sizes can be later easily aggregated across taxa, affected ecosystem features or spatial scales. The proposed approach enables performing systematic comparisons on the severity of impacts of different NIS along different study disciplines and ecosystems.

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https://doi.org/10.1016/j.scitotenv.2021.147375
0048-9697/

1. Introduction

Over recent centuries, the frequency at which human actions facilitated the movement of species into habitats outside their natural range has markedly increased (Seebens et al., 2017). This has made the introduction of non-indigenous species (NIS) a major driver for global change in species biogeography. The unprecedented rate of species introductions into new environments has far-reaching consequences, including threats to human health, impacts on human wellbeing and the economy, and alterations of recipient ecosystems (e.g. Perrings, 2002; Katsanevakis et al., 2014).

The invasions of NIS can have important effects on the structure and integrity of native communities extending beyond their often most frequently documented direct ecological effects (Feit et al., 2020). The environmental impacts of NIS can be multidimensional and often differ among environmental conditions, habitats and communities in the affected environments (Strayer, 2010). NIS can also cause rapid and long-lasting changes to the structure and function of ecosystems - so-called regime shifts, with major implications for biodiversity, the supply of ecosystem services, and human wellbeing and livelihoods (Shackleton et al., 2018). The ecological impacts of NIS in marine ecosystems include but are not limited to alteration of food-webs and habitat structures, disruption of native species via competition and predation, as well as spread of disease agents (e.g. Bax et al., 2003). However, the evidence of impacts of NIS across trophic levels in the marine environment remains greatly under-studied in comparison to the terrestrial realm (Pyšek and Richardson, 2010).

Efforts have been undertaken to synthesise impacts of marine NIS based on meta-analysis from published literature sources, at different spatial/regional scales (Ruiz et al., 1999; Katsanevakis et al., 2014; Guy-Haim et al., 2018; Anton et al., 2019). These studies have utilised different criteria for selecting NIS and applied different analytical approaches and evaluation frameworks. In the Baltic Sea, two basic impact assessment approaches have been applied so far: the biopollution level assessment method (Olenin et al., 2007) and literature review sensu Ruiz et al. (1999) for the most wide-spread NIS (Ojaveer and Kotta, 2015). While these works undoubtedly provide an insight into theoretical and methodological issues related to NIS impacts, they do not deliver a robust and empirical data-driven framework for quantifying ecosystem effects of NIS. The current study is aiming at fulfilling this gap.

The understanding and documenting of ecological consequences of NIS introductions is prerequisite for the objectives of several legislative instruments at various hierarchical levels; such as United Nations Convention on the Law of the Sea (UN, 1982), Convention on Biological Diversity (UN, 1992), the International Convention for the Control and Management of Ships' Ballast Water and Sediments (IMO, 2004), EU Marine Strategy Framework Directive (EC, 2008) and EU Invasive Alien Species Regulation (EU, 2014). Thus, advanced knowledge on the ecological impacts of NIS is a prerequisite, both to be used in national reporting to international legislative frameworks as well as in informing regional/local decision makers for marine ecosystem management.

The objective of the current study was to quantify impacts of the most widespread NIS of the Baltic Sea on various biological and ecological properties, including direct food-web effects, using meta-analysis of published literature on the ecological impact of NIS in the Baltic Sea and other European marine ecosystems. Here, we used 'absolute effect size' as a quantitative measure of impact. This approach is considered robust in meta-analysis as it avoids aggregating impacts across important opposing processes and methodologies and does not underestimate impacts, thereby adequately identifying the underpinning processes (Thomsen, 2020). Specifically, we aimed at: i) reviewing and analysing available data on the effects of NIS on biological properties; ii) quantifying the impact of NIS at different ecosystem levels, populations, communities and trophic guilds; iii) identifying the most impacting NIS, and iv) evaluating the significance of the effect size. Such an audit on the availability of the nature, type and magnitude of effects helps in developing an inclusive and a robust framework for assessing the impacts of NIS, as well as outlining the future science and monitoring needs to fill in the gaps in the impact assessment framework.

2. Material and methods

The study was performed for all non-indigenous and cryptogenic taxa (except parasites), currently established in over 50% of countries surrounding the Baltic Sea (AquaNIS, Editorial Board, 2015). Details on the species can be found in Table S1.

2.1. Identification of published sources

The published sources were identified from the ISI Web of Science and Scopus databases. The search terms within each term group (impact, taxonomy) were separated using the Boolean operator 'OR' and then combined using the Boolean operator 'AND' within a set of outer brackets.

In order to find a large majority of the relevant publications we kept the search terms very broad e.g. "Eriocheir sinensis" AND (impact OR effect OR role). In ISI Web of Science we selected the search criterion "TOPIC" and in Scopus we used "ALL FIELDS". Further, the two searches were integrated into a single search database.

The resulting hits were further screened based on the three inclusion criteria. Specifically, we included studies that (i) were carried out in the European seas, including off-shore, coastal, estuarine, and lagoon ecosystems; (ii) provided original data and involved a comparison between an affected state (NIS present) and a control state (NIS absent), such contrasts could involve spatial and temporal comparisons both in experimental and observational studies; (iii) reported a measure on the effect of NIS on biotic properties, communities, habitats and trophic guilds (e.g. native species biomass, mortalities or processes related to ecosystem fluxes).

The inclusion assessment was done at three successive steps. First, we evaluated the titles, and removed non-relevant studies. Second, we evaluated the abstracts. Several members of the review team independently assessed a subset of the studies ($n = 50$) and a multi-rater Kappa statistic relating to the assessments was calculated (Fleiss, 1971). The value of resulting statistics was far beyond 0.5; thus, the reviewers were considered consistent in their assessment and there was no need to discuss discrepancies and clarify or modify inclusion criteria. Third, we evaluated the remaining studies at full text. If it was not clear whether a study met our inclusion criteria at one of the levels of screening, it was evaluated at the next level.

2.2. Data extraction

When applying the above inclusion criteria, we were able to retain altogether 119 papers. Next, each paper was classified according to a set of properties as follows:

Study/method types: i) Correlative study, ii) Modelling study, iii) Controlled (field and laboratory) experiments.

Biotic properties affected: i) Population abundance/biomass (Pop. size), ii) Population distribution area/depth (Pop. distr.), iii) Population structure (Pop. str.), iv) Community productivity/biomass (Comm. prod.), v) Community structure (Comm. str.), vi) Phenology (Phen.), vii) Stomach/pellet content (Diet), viii) Consumption rate (Consumpt.), and ix) Individual performance, including growth, survival, etc. (Indiv.).

Community impacted: i) Plankton, ii) Benthos, iii) Fish, iv) Bird, v) Mammal.

Habitat impacted: i) Pelagic, ii) Benthic.

Trophic guilds impacted (EC, 2017, adjusted): i) Pelagic primary producers, ii) Benthic primary producers, iii) Pelagic secondary producers, iv) Benthic herbivores, v) Filter feeders, vi) Planktivores, vii) Deposit feeders, viii) Sub-apex pelagic predators, ix) Sub-apex demersal predators, and x) Apex predators.

Ultimately, the quantitative statistics of all measurements that were related to the effect of NIS were extracted. When possible, we extracted means with measurement unit, standard errors, standard deviations and sample sizes of control and impact values directly from tables and the text of the articles. Alternatively, we used ImageJ software to extract relevant comparisons from figures (Schneider et al., 2012). We also assessed if the differences between these comparisons were significant (at $p < 0.05$), insignificant or not studied.

When incomplete information was available, we attempted to obtain the missing information from the authors of the publication prior to excluding it. If we discovered that more than one publication reported the results of the same study (i.e. made the same comparison using the same data), we chose the publication that presented the data for the comparison most clearly, or we randomly selected one of the publications.

2.3. Calculation of effect size

The extracted quantitative data on the effects of NIS were then used to calculate respective effect sizes. Here, we defined the effect size as an absolute difference between two numbers (treatment vs control) divided by the maximum absolute value of the two numbers calculated as:

$$\text{Effect size} = \mathrm{ABS}((x-y)/\mathrm{MAX}(\mathrm{ABS}(x), \mathrm{ABS}(y))),$$

where x represents treatment (i.e. location or time with NIS) and, y is a respective reference value with no NIS present, ABS is the absolute value and MAX is the maximum value.

This formula is considered robust in meta-analysis, being not sensitive to the direction of effects. This is important because it avoids averaging impacts across important opposing processes, the latter being often defined by measurement unit (e.g. algal primary production vs respiration, mortality vs survival) rather than the effect of NIS per se. Consequently, when aggregating the effect size values along different covariates (e.g. study setting, biotic properties affected, community impacted) the formula does not systematically underestimate impacts and effectively identifies the underpinning processes of the effects of NIS (Thomsen, 2020). The formula yields effect sizes that vary between 0 and 1 with the former indicating no loss or gain and the latter a complete appearance or disappearance of the studied properties, respectively.

In order to assess the contribution of covariates to variation in the effects estimated in different studies, subgroup analyses were carried out. These subgroup analyses assessed the potential influence of NIS identity (i.e. the NIS under study), community (e.g. benthos), habitat type (e.g. benthic), biotic property (e.g. population abundance/biomass), trophic guild (e.g. pelagic primary producers) and study type (e.g. controlled experiment) on the estimated effects of NIS on biotic environments. Here, fitted linear model was used to assess statistical differences in the effect size between groups (e.g. NIS species, biotic property, community or trophic guild). Only groups that had at least 20 observations of effect sizes were assessed.

3. Results

3.1. Number of published papers and evidence of effects

In total, 119 papers contained information on the effects of NIS on biological properties with a total of 771 evidences. The majority of information comes from the Baltic Sea but for nine NIS, research evidence is also or only available from other European seas. These species are *Prorocentrum cordatum* (North Sea), *Mnemiopsis leidyi* (Black and Azov seas, Caspian Sea, North Sea, Mediterranean Sea), *Chara connivens* (Bay of Biscay and the Iberian Coast), *Acartia tonsa* (North Sea, Bay of Biscay and the Iberian Coast), *Palaemon elegans* (North Sea), *Amphibalanus improvisus* (Caspian Sea), *Mya arenaria* (North Sea) and *Chelicorophium curvispinum* (North Sea) (Table S1, Figs. 1 and 2). Most papers outside of the Baltic Sea are on *M. leidyi*.

The following NIS had more than ten papers published on their biological and ecological effects: *Cercopagis pengoi*, *M. leidyi*, *Marenzelleria* spp., *M. arenaria* and *Neogobius melanostomus*. *C. pengoi*, *D. polymorpha*, *Marenzelleria* spp. and *N. melanostomus* have the most substantial knowledge base with over 100 impact records.

In general, the evidence base was extremely limited until the early 2000s but has substantially grown since then (Fig. 2). No impact studies on biotic properties are available for nine widespread NIS and a very few evidences (1–2 papers) for the additional six species (Table S1). Thus, for the majority (60%) of wide-spread NIS of the Baltic Sea, our knowledge is still either lacking or extremely limited regardless of their first appearance in the invaded ecosystem. As evidenced by the invasion

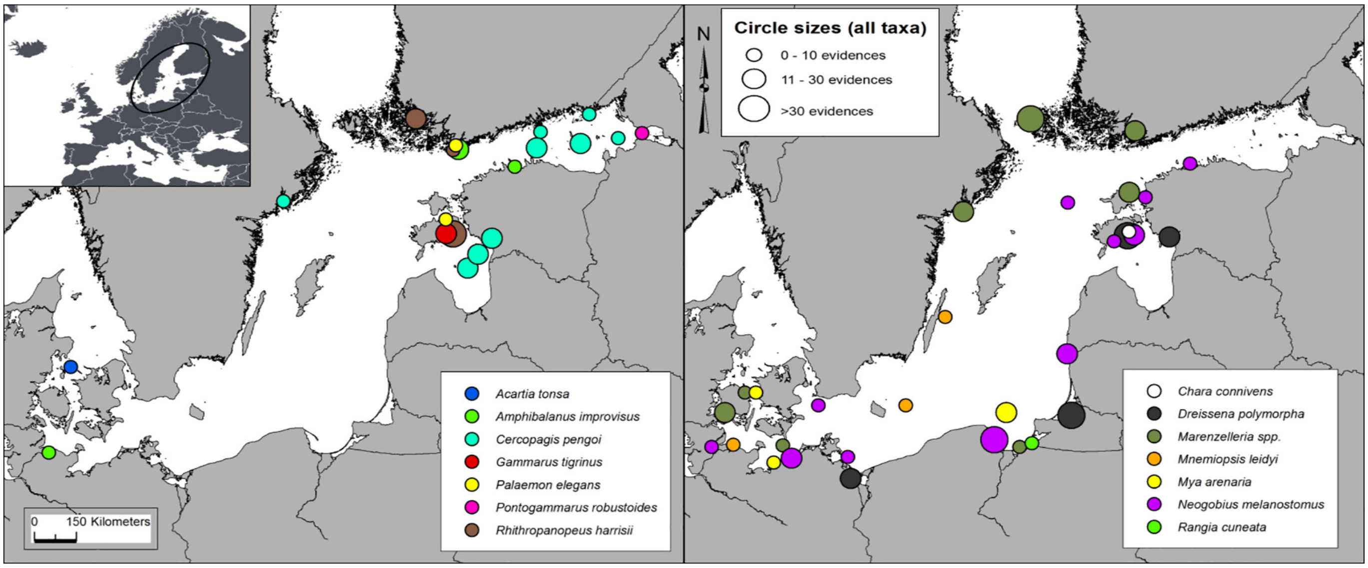

Fig. 1. Location of studies on the effects of the widespread NIS in the Baltic Sea on biotic properties.

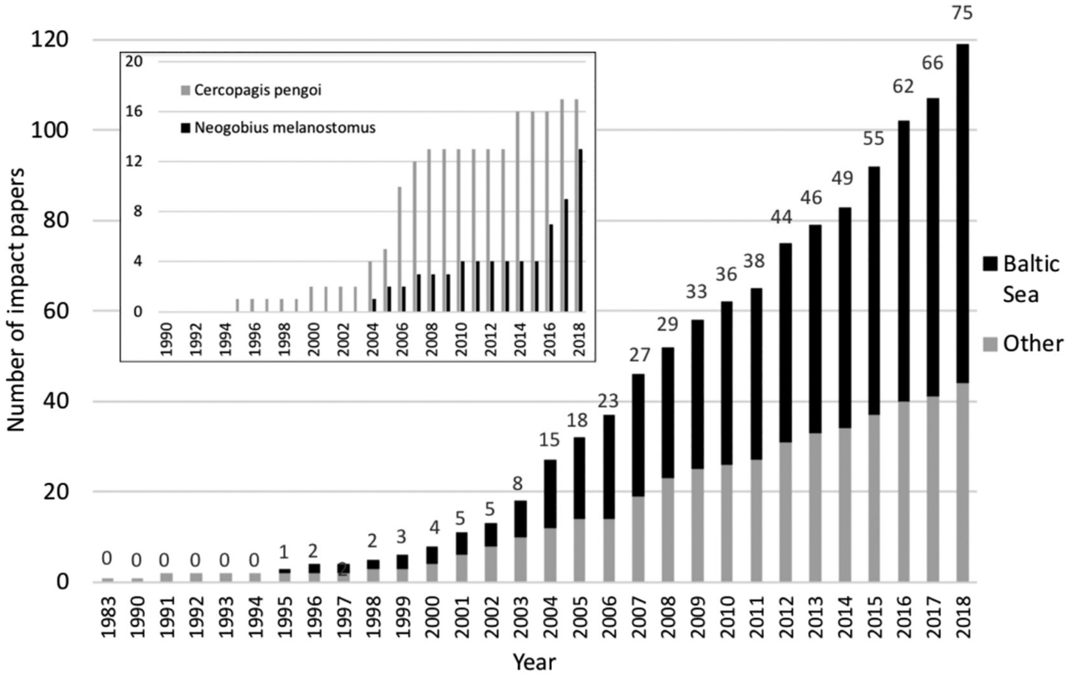

Fig. 2. Dynamics of the cumulative number of publications on the impacts of the wide-spread NIS of the Baltic Sea on the biotic properties. Grey bars: cumulative number of studies (papers) in other European seas; black bars and the numbers above them: cumulative number of studies in the Baltic Sea. The insert graph shows the breakdown of studies for two wide-spread Baltic NIS, *Cercopagis pengoi* and *Neogobius melanostomus*.

history of *C. pengoi* and *N. melanostomus* it took at least one decade until the knowledge base on their effects on biotic properties started to accumulate. Despite strong effects, the first evidence for the *N. melanostomus* was published 14 years after its invasion into the Baltic Sea (Fig. 2).

3.2. Study type/methods

Hereafter, as defined in the methodology chapter, we only report effect size comparisons (group means and standard errors) for groups that had at least 20 effect size observations. The most abundant were correlative and experimental studies almost equally contributing to the pool of impact evidence (ca. 52 and 47%, respectively) and involving effects of mostly the same NIS. Modelling approaches have been used rarely and with only a few NIS involved so far (*C. pengoi*, *M. leidyi*, *M. arenaria* and *N. melanostomus*, Table S2). The lowest effect size was recorded in modelling and experimental studies (0.50 ± 0.12 and 0.57 ± 0.02, respectively) followed by correlative studies (0.74 ± 0.02).

3.3. Effects on communities and biotic properties

As the majority of widespread NIS are demersal/benthic, the studies were addressing predominantly impacts on benthic communities (51% of evidence), followed by plankton and fish (30 and 17%, respectively, Fig. 3b, Table S3). The lowest mean effect size was recorded for benthic communities (0.58 ± SE 0.01), followed by plankton (0.70 ± 0.3) and fish (0.76 ± 0.03). Overall, pelagic communities were affected more than benthic ones (0.73 ± 0.02 and 0.59 ± 0.02, respectively).

Impact on the population size of native species was the most frequently addressed biotic property. It comprised nearly half of relevant evidence cases and involved 11 NIS, including few particularly well studied taxa, like *Marenzelleria* spp., *A. improvisus*, *M. arenaria*, *R. harrisii*, *D. polymorpha* and *G. tigrinus* (Fig. 3c, Table S4). Knowledge base on other key properties, such as individual performance, population distribution, population structure, phenology and community productivity were limited. It also appears that for six NIS (*P. cordatum*, *C. connivens*, *P. elegans*, *C. curvispinum*, *C. caspia* and *P. antipodarum*), impact knowledge is limited to only one biotic property. The largest documented effect size was due to changes in the diet of native taxa (0.82 ± 0.03) while the smallest was on individual performance of native biota (0.42 ± 0.06) (Fig. 4).

3.4. Effects on trophic guilds

All investigated trophic guilds were affected by at least one NIS, but the largest pool of evidence was available for deposit feeders (23%) and pelagic secondary producers (18%) (Tables 1 and S5). Trophic guilds related to the demersal/benthic realm always involved a higher number of NIS than their pelagic counterparts. The biggest effect size was documented for planktivores, followed by sub-apex demersal predators and pelagic primary producers.

3.5. Effect size of individual NIS

Effects of NIS on different biotic properties were all highly significant (Fig. 5, Table S6). Two relatively recently invaded pelagic NIS - *C. pengoi* and *M. leidyi* - had the highest effect size (0.88 ± 0.03 and 0.89 ± 0.02, respectively), followed by the zebra mussel (0.76 ± 0.03). The lowest effect was due to *A. improvisus* (0.32 ± 0.05).

3.6. Processes responsible

Consumption was the best studied process responsible (46% of evidences), followed by competition for habitat or food (19%), both involving a large number of NIS (Fig. 3d, Table S7). Some processes were due to one or two NIS taxa only e.g. bioturbation effects (11%) triggered by *Marenzelleria* spp. and partly by *R. harrisii*. The largest effect size was recorded for NIS that are a prey for native species, followed by facilitation of native species, as well as consumption, bioturbation and competition which all had very similar effect sizes (Fig. 6).

3.7. Certainty of effects in individual studies

Potential confounding factors affecting research outcomes of individual studies were acknowledged on average in about 41% of impact

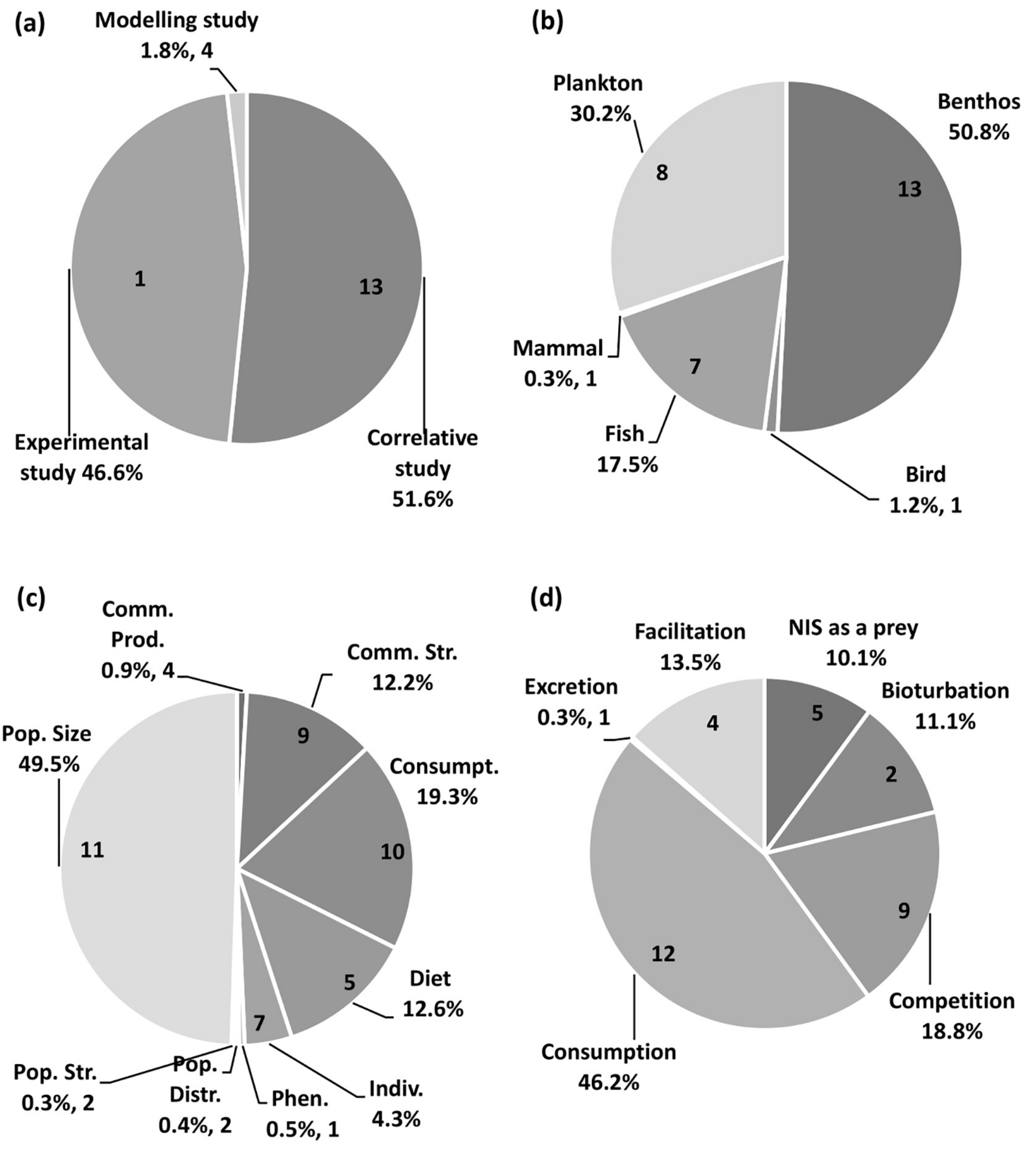

Fig. 3. Percentage of: (a) study type/methods employed in NIS impact investigations, (b) evidence of impact of NIS on a broad range of native communities, (c) evidence of impact of NIS on different biotic properties (population size, population distribution, population structure, community productivity, community structure, phenology, diet, consumption rate and individual performance), and (d) processes responsible for the observed effects of the most wide-spread NIS of the Baltic Sea. The numbers inside or adjacent the pie indicate the number of NIS involved.

evidences. For four NIS - *Marenzelleria* spp., *R. harrisii*, *N. melanostomus* and *P. elegans*, confounding factors were discussed or identified in 50% of the cases (Table 2).

Across analysed studies, about 32% of evidence of considered impacts was significant. For six NIS (*C. pengoi*, *M. leidyi*, *P. elegans*, *M. arenaria*, *R. harrisii* and *N. melanostomus*) the proportion of significant impacts exceeded that of insignificant ones (Table 2). Overall, the significance of impacts was not studied in around 39% of cases (47% of cases in the Baltic Sea), making the underlying knowledge base of individual studies rather uncertain.

4. Discussion

4.1. Information availability

The human-mediated introduction of marine NIS is at least centuries-old phenomenon, and has been actively facilitated by man in the past. However, NIS were only relatively recently acknowledged as a potential driver of change in the sea, following deleterious effects

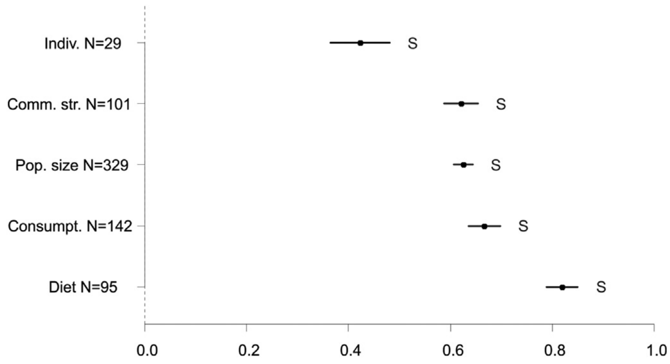

Fig. 4. The effect size (group mean and standard error) of the wide-spread NIS of the Baltic Sea on biotic properties (individual performance, community structure, population size, consumption rate and diet). Effect size was analysed for biotic properties that had at least 20 observations (*N* indicates number of observations). S denotes statistically significant difference from 0 (i.e. no effect) at $p < 0.05$.

Table 1

Impact evidence of NIS on trophic guilds: percentage of impact evidence (relevant studies), number and list of NIS affecting a particular trophic guild, and effect size. Effects on all trophic guilds were significant at $p < 0.001$. Trophic guilds followed by an asterisk displayed slightly lower mean effect size in the Baltic Sea compared to all evidence in the dataset. Effect size on apex predators was not evaluated because the number of observations was below the qualification criterion ($n = 20$).

Trophic guild affected	Evidence (%)	Number and list of affecting NIS	Effect size (mean ± SE)
Pelagic primary producers	11.8	6: *A. improvisus*, *D. polymorpha*, *Marenzelleria* spp., *M. leidyi*, *M. arenaria*, *R. harrisii*	0.70 ± 0.04
Benthic primary producers*	8.6	7: *A. improvisus*, *C. connivens*, *G. tigrinus*, *Marenzelleria* spp., *P. elegans*, *P. robustoides*, *R. harrisii*	0.51 ± 0.04
Pelagic secondary producers*	17.7	5: *A. tonsa*, *A. improvisus*, *C. pengoi*, *Marenzelleria* spp., *M. leidyi*	0.69 ± 0.04
Benthic herbivores*	11.4	6: *D. polymorpha*, *G. tigrinus*, *Marenzelleria* spp., *N. melanostomus*, *P. elegans*, *R. harrisii*	0.62 ± 0.04
Planktivores	9.1	4: *C. pengoi*, *M. leidyi*, *N. melanostomus*, *R. harrisii*	0.86 ± 0.04
Filter feeders*	5.6	8: *A. improvisus*, *D. polymorpha*, *Marenzelleria* spp., *M. leidyi*, *M. arenaria*, *N. melanostomus*, *P. cordatum*, *R. harrisii*	0.52 ± 0.06
Deposit feeders*	22.5	8: *C. curvispinum*, *D. polymorpha*, *Marenzelleria* spp., *M. leidyi*, *M. arenaria*, *N. melanostomus*, *P. robustoides*, *R. harrisii*	0.57 ± 0.03
Sub-apex pelagic predators	2.8	1: *N. melanostomus*	0.67 ± 0.08
Sub-apex demersal predators	10.2	7: *A. tonsa*, *D. polymorpha*, *M. leidyi*, *M. arenaria*, *N. melanostomus*, *R. cuneata*, *R. harrisii*	0.74 ± 0.04
Apex predators	0.3	1: *N. melanostomus*	Not evaluated

of a few notorious invasions (Ojaveer et al., 2018). This explains why published evidence on impacts posed by NIS started to accumulate only about 25 years ago but exhibited an exponential increase thereafter. Thus, empirical evidence of impacts of species introductions is largely unavailable prior to the 1990s, due to unawareness and partly associated to the lack of relevant pre-invasion data.

There are currently 72 NIS established in the Baltic Sea, out of which about one third are widespread (AquaNIS, Editorial Board, 2015). It appeared that quantitative data on impacts is either lacking or very incomplete for 60% of the widespread NIS. This suggests that potential or realised impacts of NIS on biotic properties for most of the established NIS in one of the best globally studied marine ecosystems remains largely unquantified.

Taxonomic bias in bioinvasion ecology has been previously indicated as of concern (e.g. Jeschke et al., 2012). Our study conforms with that and provides further evidence of a very unequal knowledge base for different NIS as well as investigated features, i.e. biotic properties impacted and processes responsible. Among NIS, the most abundant evidence is available for a few relatively recently introduced species (*M. leidyi*, *C. pengoi*, *Marenzelleria* spp. and *N. melanostomus*), which together form over 50% of the published evidence. On the other hand, information about the impact on different trophic guilds was much more balanced, likely due to several NIS affecting the same guild.

Although NIS impacts are often context dependent (Robinson et al., 2017), we still sought information on the widespread Baltic Sea NIS from all European marine areas. Such search strategy enabled us to inform on i) the differential nature and magnitude of effects in the Baltic and other seas as well as ii) to complement the impact database with evidence of research carried out elsewhere if missing from the Baltic Sea region. Overall, information on the impacts of the widespread NIS of the Baltic Sea outside the basin is very limited. Substantial evidence appears to be available only for *M. leidyi*, mostly from the Black and Caspian Seas - the region of its first reported introduction outside of its native range (Shiganova, 1998). There is some additional evidence outside the Baltic Sea for two NIS (*A. tonsa* and *M. arenaria*). Information on the impact for *P. cordatum* and *C. curvispinum* originates from outside the Baltic Sea only. Our results suggest that experimental investigations should be encouraged to make better use of the impact studies. Specifically, laboratory experiments are less dependent on local ecosystem conditions and less impacted by likely confounding factors, and therefore allow establishing causality, also securing higher reliability and generality of the results.

Time-lags are inherent constituents in bioinvasion science. These can be related to delayed detections (Azzurro et al., 2016), species identifications (Bick et al., 2018) or evidence of impact since the first observation (current study). The latter is affected by multiple factors (e.g. research interest, funding, awareness or management relevance), and can be substantial. Time-lags in evidence of impact can be quantitatively estimated since the early 1990s when NIS started to attract wider attention due to their ecological impacts. The Baltic Sea case indicates that the time-lag between the first observation of a NIS and the first quantified impact evaluation can be around one decade, while accumulation of the evidence base required for performing an impact assessment may take much longer time. This has implications both for undertaking regional/local management actions as well as reporting to meet the requirements of international legislation.

More broadly, studies on NIS impacts are mostly confined to the period after the major climate-driven reorganisation of several marine

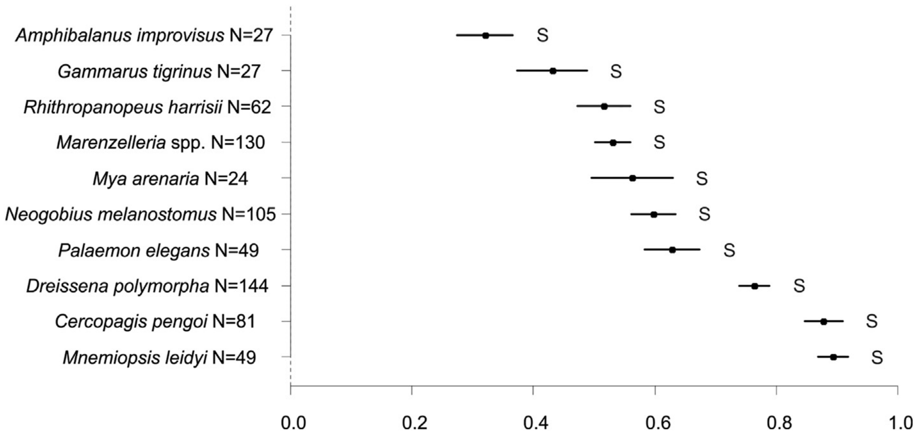

Fig. 5. Effect size (group mean and standard error) of ten widespread NIS of the Baltic Sea on biotic properties based on evidence in all European seas. *N* indicates number of observations. S denotes statistically significant difference from 0 (i.e. no effect) at $p < 0.05$.

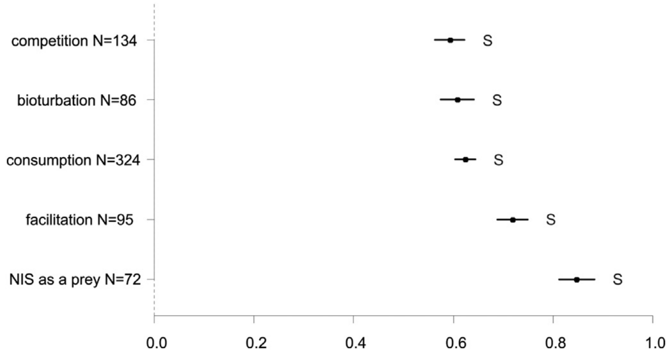

Fig. 6. Effect size (group mean and standard error) of the widespread NIS of the Baltic Sea on biotic processes based on evidence from all European seas. *N* indicates number of observations. S denotes statistically significant difference from 0 (i.e. no effect) at $p < 0.05$.

ecosystems globally in the late 1980s (e.g. Möllmann et al., 2011). For instance, in the Baltic Sea, substantial rise in water temperature and drop in salinity was reported since the early 1990s (Möllmann et al., 2009). Importantly, in recent decades marine ecosystems have been suffering from multiple severe anthropogenic stressors and thereby our knowledge on the effect of NIS largely originates from substantially modified ecosystems. This is especially relevant for several widespread early benthic introductions, such as *A. improvisus*, *M. arenaria* and *D. polymorpha*, where a lack of baseline knowledge in several ecosystem features and properties preceding their incursions is affecting our capability to quantify the effects of these NIS. However, these taxa are nowadays common constituents in coastal food webs that influence the functioning of both benthic and pelagic ecosystems (e.g. Foster and Zettler, 2004; Lauringson et al., 2007). Such a situation further stresses the need for adequately designed experimental studies not only to identify causal relationships and quantify the potential impacts, but also to interpret findings from field observations.

4.2. Species-specific effects and underlying mechanisms

Benthic NIS dominate among widespread NIS in the Baltic Sea and other European marine ecosystems (Galil et al., 2014). However, despite the strong positive bias towards the information availability on the effects of benthic NIS, the largest effect size was recorded for the fish community, followed by plankton and benthos. Similarly, among trophic guilds, planktivores and sub-apex demersal predators had largest effect sizes. Judging from the substantial effect size on pelagic primary producers, it can be concluded that NIS have significantly altered multiple food-web links with affected taxa belonging to different biotic communities. Importantly, the direct impact of a single NIS can extend to multiple trophic guilds and is not necessarily restricted to a particular community associated with an adult stage of that NIS. Therefore, the food-web interactions of NIS are extremely complex with simultaneous incorporation of effects of both pelagic and demersal NIS on multiple trophic levels. This at least partly explains why the pelagic realm is more affected than the benthic.

As evidenced by our meta-analysis only a few NIS (*M. leidyi* (outside the Baltic Sea), *Marenzelleria* spp., *R. harrisii*, *N. melanostomus* and *D. polymorpha*) had major roles in the food web processes at multiple trophic levels and affecting multiple habitats, stressing thereby the relevance of species identity. However, this species list could be more extensive if more species were tested for food-web effects. The Baltic Sea is a very dynamic ecosystem and the spatio-temporal patterns of the biota are largely set by multiple abiotic forcing (e.g. Segerstrale, 1969). The influential NIS are those that can exert significant control over resource availability via modulation of the physical, chemical and biotic flows among different habitats via multiple direct or indirect mechanisms, such as consumption and competition. And often they are those that introduce novel functions to the invaded communities, such as filter feeding (*D. polymorpha*), bioirrigation (*Marenzelleria* spp.) or predation (*R. harrisii*) (Lauringson et al., 2007; Bonaglia et al., 2013; Lokko et al., 2018).

4.3. Methodological considerations

The currently used standardised metric of absolute effect size can be considered robust in meta-analysis that compares studies lacking a common metric in impact measurements, including an unbalanced number of evidence and involving opposing ecological processes. Some earlier studies have also used metrics that not only quantify the magnitude of effect, but also provide information on its direction (Guy-Haim et al., 2018; Anton et al., 2019). However, the latter approach is not so robust. Individual studies mostly report positive or negative effects dependent on the ecological processes involved, and the direction of effect may help to understand both the nature and magnitude of individual effects. Nevertheless, in many circumstances the direction of effect is defined by the focus of the study (e.g. primary production vs. respiration) and when averaging effects across opposing processes the overall (cumulative) effect size may appear small and insignificant, providing an erroneous message of the little or moderate impact of NIS (Guy-Haim et al., 2018; Thomsen, 2020).

In ecology, rigorous experimentation is considered a particularly valuable tool to improve our understanding of key principles in the functioning of ecosystems. This is because experiments enable identifying cause-and-effect relationships and quantifying response functions through a systematic manipulation of the factors of interest, while controlling against the intrusion of other factors that might otherwise

Table 2
Information on the significance of the effects of individual studies (%) and confounding factors considered (%) in the biotic property impact studies by individual NIS (all evidences/Baltic Sea evidences). In case only one number is given, it applies to both all evidences and those from the Baltic Sea. Only NIS for which at least 20 evidence of impacts were available, were included in calculations (for details, see Table S1). Mechanisms responsible for effects on habitats are shown in italics.

Species name	Significance of effects			Main mechanisms	Confounding factors
	Yes	No	Not studied		
Amphibalanus improvisus	20.0/17.8	76.7/78.6	3.3/3.6	Biodeposition	16.7/10.7
Cercopagis pengoi	21.9	14.3	63.8	Predation, NIS as prey	19.0
Dreissena polymorpha	12.0	38.0	50.0	Biodeposition, *habitat engineering*	40.0
Gammarus tigrinus	0	0	100	Grazing, competition, NIS as prey	0
Marenzelleria spp.	33.1	50.0	16.9	Competition, *bioturbation*	78.5
Mnemiopsis leidyi	71.0/NA	9.7/NA	19.3/NA	Predation	27.4/NA
Mya arenaria	10.7/4.7	7.1/4.8	82.1/90.5	Biodeposition, competition	32.1/14.3
Neogobius melanostomus	42.8	22.9	34.3	Predation, NIS as prey	56.2
Palaemon elegans	66.0/NA	32.0/NA	2.0/NA	Predation, competition	78.0/NA
Rhithropanopeus harrisii	46.0	34.9	19.1	Predation, *bioturbation*	73.0
Average	32.4/22.3	28.5/30.4	39.1/47.3		42.1/36.5

confound the results and interpretation (Cooke et al., 2017). Correlative field studies are performed in realistic environments, but they do not allow the complete control of many potential confounding variables (Odum, 1977). Due to the abovementioned reasons we expected that the impacts of NIS assessed in experimental conditions would be stronger than correlative studies carried out in natural conditions. However, the results of our study were the opposite with effect sizes measured in experiments being systematically lower compared to correlative studies. This suggests that many experiments did not meet all important characteristics of the natural settings and the realised impact may be amplified by the synergetic effect of multiple stressors affecting the ecosystem. Often experiments were too short in relation to the studied processes and therefore differences among treatment and reference were weak. Field observations (despite involving many confounding variables) following the studied systems through a long period of time may enable researchers to quantify shifts that took place at a slow rate and/or involved time lags.

4.4. Uncertainty of estimates

There is always some uncertainty associated with quantitative estimates. In the current study, three main sources can be identified, all related to the individual papers: i) heterogeneity in different study types, ii) significance of each evidence of impact, and iii) potential confounding factors.

Despite the effect size of the studied NIS and affected parameters significantly differing from 0 (i.e. patterns were non-random), the certainty of underlying data calls for caution. This is because only about 1/3 of the documented impacts in individual papers were significant while significance was not tested in about 39% of cases. However, in studies where NIS had statistically non-significant outcomes (often interpreted as “no impact”), the species might still have large impacts that were missed due to small sample or effect sizes and/or high variation of data (Davidson and Hewitt, 2014). While the very large proportion of evidence with untested significance is certainly an issue, it should not undermine the overall conclusions of the current study.

It appeared that for the majority of cases, confounding factors were ignored. Wherever confounding factors were detected and reported, they appeared to be somewhat connected with the study type, location and properties investigated. For example, where population size and distribution were studied, often abiotic conditions, such as temperature, depth, salinity or seasonal variation affected measured response variables. Community level studies and evidences related to diet and consumption in turn, presented more confounding factors related to size of prey/predator, as well as presence of other organisms competing for the same resources. No further conclusions can be drawn from these findings as some papers studied and detected confounding factors, whereas others only provided speculations.

4.5. Relevance for assessment and management

The problem with the accelerating rate of introductions of NIS globally is not only in their high number, but also the effects these species cause to the recipient ecosystems. If the effect of a NIS is minimal, its management is not the priority. However, clear evidence of NIS impacts should support assessment of environmental status and guide management measures. The revised Commission Decision of the MSFD (EC, 2017) requests to use information on NIS impacts (D2) in the assessments of several criteria under EU MSFD D1 (Biological diversity) and D6 (Sea-floor integrity). Our work very clearly points to an obvious gap of knowledge in the decision as we largely did not know how NIS impact the D4 (Marine food webs). An integration of information and knowledge obtained through the current meta-analysis broadens the knowledge base and justifies incorporation of NIS into the assessment of MSFD D4, as almost all trophic guilds were shown to be affected by NIS.

This understanding was formed based on several species-specific evidences, such as *N. melanostomus*, *C. pengoi*, *R. harrisii*, *D. polymorpha*, and suggest that food-web impacts of NIS can compromise the D4 overall objective ‘*All elements of the marine food webs, to the extent that they are known, occur at normal abundance and diversity and levels capable of ensuring the long-term abundance of the species and the retention of their full reproductive capacity*’. Unfortunately, comprehensive knowledge on this is lacking so far. As the type and size of effects vary along spatial scales, and are often context specific, detailed results from this study cannot be extrapolated to other European regional seas, not even for the same species.

Our work explicitly contributes to the criterion 2 (D2C2) of the MSFD D2 (EC, 2008) by providing advanced understanding on NIS causing measurable impacts on native species and the magnitude of the effects by identifying the processes/mechanisms responsible. Such a process-based knowledge also helps managers in setting priorities for NIS data collection and improving national/regional monitoring programs presently lacking monitoring efforts on impacts (Lehtiniemi et al., 2015).

From the management perspective, results of the current work clearly support previous statements that management of marine NIS cannot be based on impacts (e.g. Ojaveer et al., 2015), due to multiple major gaps in our knowledge. While knowledge from other regions may indeed help us understand the effects of some NIS of the Baltic Sea (e.g. *M. leidyi* case in the Black Sea), there are only a very few widespread NIS common within the European seas.

The understanding of species-specific impacts of aquatic NIS is important due to several international legislative agreements on top of the MSFD. Agreeing with the BWM Convention requires identification of target species (TS), which are NIS that may have damaging impacts on the environment, human health or property and resources (Gollasch et al., 2020). Our study shows that at least the 9 NIS (Fig. 5, except *M. leidyi*) should be on the TS list of the HELCOM. Further, EU IAS Regulation (EU, 2014) and the national laws implementing the Regulation target to prevent and manage the introduction and spread of invasive alien species, yet only considering invasive alien species of the European Union concern. These species are pre-screened and risk assessed to demonstrate causing so significant damage that it justifies the adoption of dedicated measures applicable across the EU. Effect size might be a good option for the pre-screening exercises and our study helps to identify candidate species for the risk assessment for the purpose of the Regulation.

And finally, it is obvious that all meta-analyses rely on the studies conducted previously and are affected both by the quality and comprehensiveness of such studies. This should be taken into account when providing management advice, both in terms of the lack of evidence on particular NIS or impact types, as well as uncertainty of the evidence or existing confounding factors affecting the outcomes.

5. Conclusions

There are several recently developed frameworks that classify NIS based on their impacts (e.g. Blackburn et al., 2014; IUCN, 2019). Based on the evidence from one of the best studied marine ecosystems globally, the Baltic Sea, we reiterate the previous concern (Ojaveer et al., 2015) that these proposed ‘unified’ frameworks are not suitable for marine NIS, as most of them will qualify as data deficient. Specifically, the current study evidenced that we lack any evidence of impact for 28% of the widely distributed NIS and information on other 32% is extremely limited. The outcome of the present study re-stresses previous statements that ‘no evidence’ cannot be treated equal to ‘no impact’. Such species should be labelled as ‘data deficient’ and therefore conclusions on NIS impacts on the assessed ecosystem may be incomplete.

Despite continuous accumulation of impact evidence, we should be pragmatic and not expect exponential improvement in the underlying knowledge base. Instead, small and incremental advancement is more likely. Therefore, application of data and information-hungry frameworks for evaluation of ecosystem impacts of NIS for management purposes (including meeting obligations of international legislative instruments) is not pragmatic in the foreseeable future. Results of the current work suggest that instead, simple straightforward data-driven approaches, such as robust calculations of simple effect size of certain NIS in a particular area on particular biological features, can be quite handy for achieving tangible impact evaluation outcomes with the available knowledge base. As bearing no unit, effect sizes can be later easily aggregated across taxa, affected ecosystem features or spatial scales. The suggested methodology can be applied to other types of impacts caused by NIS, such as on physical or chemical features. Furthermore, it is evident that applicability of the proposed methodology (i.e. meta-analysis of existing studies) relies on the availability of previously conducted studies, and so, its usability might be limited to well-studied topics/ecosystems. However, in case the method is adopted, it will provide a clear guidance which data needs to be collected for the estimation of NIS effects.

As such, the proposed methodology requires searching for literature on available impact evidences of NIS and documenting the following information: 1) NIS for which impact is being evaluated, 2) geographical area where evidence was collected, 3) biological property impacted by NIS, 4) initial value of the impacted property, and 5) final value of the impacted property. Based on this information the absolute effect size and its significance can be calculated, including ready to be used for pre-screening purposes for legislative risk assessments (e.g. EU IAS Regulation or TS selection under BWMC).

CRediT authorship contribution statement

Henn Ojaveer: Conceptualization, Methodology, Resources, Writing – original draft, Project administration, Investigation. **Jonne Kotta:** Conceptualization, Methodology, Resources, Writing – original draft, Formal analysis, Investigation. **Okko Outinen:** Formal analysis, Writing – review & editing, Visualization, Investigation. **Heli Einberg:** Formal analysis, Visualization, Writing – review & editing. **Anastasija Zaiko:** Investigation, Writing – review & editing. **Maiju Lehtiniemi:** Conceptualization, Methodology, Resources, Writing – original draft, Investigation.

Declaration of competing interest

The authors declare that they have no known competing financial interest or personal relationship that could have appeared to influence the work reported in this paper.

Acknowledgements

The authors are grateful to two anonymous reviewers for their comments that improved the quality of the manuscript. The authors thank the Working Group on Introductions and Transfers of Marine Organisms (WGITMO) of the International Council for the Exploration of the Sea (ICES) for facilitating this research. This work resulted from the Joint Baltic Sea Research and Development Programme (BONUS) project 'Taking stock of Baltic Sea food webs: synthesis for sustainable use of ecosystem goods and services', XWEBS, which was supported by BONUS (Art 185), funded jointly by the European Union and Estonian Research Council (2012–20). This study was prepared within the project COMPLETE – Completing management options in the Baltic Sea region to reduce risk of invasive species introduction by shipping. The project is co-financed by the European Union's funding Programme Interreg Baltic Sea Region (European Regional Development Fund) (R069). JK was also supported by the Estonia-Russia Cross Border Cooperation Programme project "Adrienne".

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2021.147375.

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