Impacts of the invasive round goby (*Neogobius melanostomus*) on benthic invertebrate fauna: a case study from the Baltic Sea

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Short running title: Round goby impacts on benthic fauna

Abstract

Non-indigenous animals can impact native fauna via predation and competition for food and habitat. The round goby (*Neogobius melanostomus*) was first observed in the Baltic Sea in 1990 and has since displayed substantial secondary dispersal, establishing numerous dense populations where they may outcompete native fish and negatively impact prey species. There have been multiple round goby diet studies from both the Baltic Sea and the North American Great Lakes where they are similarly invasive. However, studies that quantify their effects on recipient ecosystems and, specifically, their impacts on the benthic invertebrate macrofauna are rare, particularly from European waters. In this study, we conducted the first before-after study of the potential effects of round goby on benthic invertebrate macrofauna taxa in marine-brackish habitats in Europe, focusing of two sites in the Western Baltic Sea, Denmark. Results were in line with those from the Great Lakes, indicating negative impacts to be focused on specific molluscan taxa, particularly gastropods, while other groups appeared to be largely unaffected or even show positive trends following invasion. Round goby gut content data was available at one of our study sites from the period immediately after the invasion. This data confirmed that round goby had in fact been preying on the subset of taxa displaying negative trends.

Keywords: anthropogenic change, infauna, invasion impacts, invasive species, non-indigenous species, predation, predator-prey interactions

Article (Brief communication format)

The impacts of non-indigenous invasive animals can be closely related to their feeding behaviour, via increased predation pressure and resource competition for native species (Olenin et al. 2017). The round goby, *Neogobius melanostomus* (Pallas 1814), is native to the Caspian, Black, Azov and Marmara Seas. From there it was introduced to the Baltic Sea, via ballast water, where it was first observed in the Gulf of Gdansk in 1990 (Kotta et al. 2015). At the same time the species was also observed in the North American Great Lakes (Kornis et al. 2012). Today, three decades after these first observations, the species has displayed pronounced secondary dispersal in both regions and is now common throughout large parts of the Baltic Sea (Kotta et al. 2015; Puntila et al. 2018) and in three of the four Great Lakes (Corkum et al. 2004; Kornis et al. 2012).

Round goby is a bottom-dwelling fish that occurs in a wide range of seabed habitats, from soft substrates (e.g. mud and sand, both with and without vegetation) to hard substrates (e.g. natural boulder reefs or man-made structures like harbor walls and jetties; Young et al. 2010; Kornis et al. 2012). Round gobies possess several invasive characteristics such as high competitiveness for territory, a broad diet, dispersal ability, and broad temperature and salinity tolerances (Kornis et al. 2012; Azour et al. 2015; Behrens et al. 2017; Christensen et al. 2021). As such, the round goby is generally thought to have negative impacts on recipient ecosystems and indigenous taxa.

A handful of studies from freshwater systems in the Great Lakes Region have found evidence that round gobies outcompete indigenous fish species for space and food, and may predate on both fish eggs and offspring (e.g. Chotkowski and Marsden 1999; Balshine et al. 2005). Competition with native fish has also been described in European waters (Karlson et al. 2007; Matern et al. 2021). Although, other studies have not detected effects on other fish species (e.g. Janac et al. 2016; Piria et al. 2016). In relation to benthic invertebrate macrofauna, studies available from the freshwater Great Lakes system have investigated invertebrate abundances before and after invasion or compared tributaries with and without round goby populations (Lederer et al. 2008; Kipp & Ricciardi 2012; Barrett et al. 2017; Pennuto et al. 2018), often finding that round goby invasion has the capacity to alter species composition and reduce the biomass of certain species.

In European inlet waters and the marine and brackish habitats of the Baltic Sea, before-after studies of their impacts on the invertebrate macrofauna appear to be non-existent. In contrast, studies of their diet are quite common (e.g. Polacik et al. 2009; Skabeikis 2015; Nurkse et al. 2016; Piria et al. 2016; Oesterwind et al. 2017; Schwartzbach et al. 2018), along with a recent valuable experimental field study tested effects of goby presence on native fauna using caged areas (i.e. goby presence v absence, Henseler et al. 2021). The rareness of before-after studies may be due to the difficulties and costs of obtaining site specific abundance data of benthic fauna communities immediately prior to and after an invasion. This lack of studies is concerning as the limited knowledge of round gobies impacts on Baltic Sea ecosystems and communities has been identified as key a barrier to their management (Ojaveer and Kotta 2015). Therefore, aim of this study was to test the hypothesis that round goby invasions in the Baltic Sea impact these recipient ecosystems by reducing the abundance of prey taxa.

We focus on two sites in south-eastern Denmark, Guldborgsund and Stege Bugt (see specific locations in supplementary material S1, Figure S1). The first round goby observation along the main coastline of Denmark was made in Guldborgsund in 2009. By 2010, they were abundant throughout Guldborgsund, and by 2013 had reached an average density of 1.9 individuals.m^{-2} (Azour et al. 2015). Round gobies were not observed at Stege Bugt until later, in 2011 (Azour et al. 2015), which was likely colonized via secondary dispersal from Guldborgsund. Both are shallow brackish areas where local fishermen continue to catch large quantities of round goby as bycatch (Brauer et al. 2020).

Benthic invertebrate macrofauna data from fixed sampling stations in Guldborgsund and Stege Bugt, collected as part of the Danish national NOVANA marine monitoring program database (Surface Water Database, ODA: https://odaforalle.au.dk) were mined. All fauna samples were collected in spring using a HAPS core sampler (seabed area: 0.0143 m^2) and multiple samples was taken in each sampling-year (Table 1; Hansen et al. 2017; McLaverty et al. 2020). Species/taxa count data was extracted for the period 2006-2015 from areas (i.e. c. four years prior to and four years after invasion), including at least one sampling-year immediately prior to the first goby sighting and at least two sampling-years in a 2-to-5 year period following their first sighting. In Stege Bugt, invertebrate data was available in spring 2011 (also the year of the first round goby sighting), so for the purposes of this analysis we considered data from spring 2011 to represent pre-impact abundances. NOVANA data is recorded to species, genus, or occasionally higher taxonomic levels, therefore for our analysis we defined 20 broader taxonomic groups to aggregate the raw data to order and family levels where possible (see supplementary material S2 and Table S1 for full details of our taxonomic groupings). Species that were rarely detected in samples (in < 5% of cores) and could not be combined into order or family level groupings were excluded from analysis. All groupings were monophyletic, except Littorinimorpha, which were separated based on morphological distinctions into two groups: larger periwinkle species (e.g. *Littorina* sp., as 'Littorinimorpha (large)') and several species of much smaller sea snails (e.g. *Hydrobia* sp. and *Rissoa* sp., as 'Littorinimorpha (small)', generally <5 mm).

Gut content data from Guldborgsund (54°43'24.55"N, 11°52'49.70"E) was collected in the year immediately following their first arrival at the site (November 2010). A total of 289 Round gobies measuring 7.5-17 cm were collected with eel traps set over night in shallow waters (1-5 m). Gobies were frozen (-20 °C) until processed. The presence/absence and count data for prey detected in gut samples were identified to species where possible. Given the few hours from capture until freezing, there is a risk that soft bodied and very small food items might have been underestimated.

Count data per core sample (aggregated to our taxa groupings) was analyzed using general linear mixed effect models for each site ('brms' package v 2.14.4, Bürkner, 2017; negative binomial distribution, log-link function with default non-informative priors, chains = 2 chains, iterations = 6000, warmup = 2000). A round goby before-after impact fixed effect ('BA') was included, with taxonomic groupings included as a random effect with random slopes (i.e. 'BA|TaxaGroup'). Taxa-specific *BA* slopes were extracted from posterior distributions with 95% credible intervals to infer positive and negative impacts of goby invasion on each taxa's abundance. Sampling year and core sample ID was also included as random effects to account for non-independence within samples and sampling seasons. Separate models were used for each site (for full model specifications, see supplementary material S3 and Table S2). Despite all sampling occurring in spring, samples were taken in March in 2015 while in previous years sampling occurred in May, so a sensitivity analysis was conducted to ensure that this difference in timing did not influence our conclusions (see supplementary material S4).

Gut content data from Guldborgsund was summarized as the percentage of gut samples that each taxa group was detected within. Further exploratory analysis was also conducted to measure whether a taxa's prevalence in gut contents influenced the BA effect. First, taxa were categorized as present or absent based on their detection (or not) within gut samples. To test whether the BA effect was more negative in the taxa detected in gut samples than those not detected, we tested for an interaction between BA and taxa presence ('BA*Presence', Guldborgsund data only, using model specifications as above, also see supplementary material S3). To test if there was an overall positive or negative BA impact in each category of taxa, two separate models were used to estimate the BA effect for present and non-present subsets of taxa (Guldborgsund data only).

All credibility intervals below are 95% intervals. Statistically significant effects are inferred from credibility intervals not overlapping zero. Model performance was assessed by checking diagnostic plots to ensure chains were well mixed, and convergence was confirmed (Rhat = 1.00, zero divergent transitions after warmup). Conditional R^2 values ('R^2_{cond}') were estimated as a measure of the total amount of variance explained by each model (function 'r2_bayes', 'performance' package v 0.7.0, Lüdecke et al., 2021). Additionally, sensitivity analyses were conducted to check whether our results were sensitive to zero-inflation (see Supplementary Material S4). All data, models, and code are available at the Open Science Framework (https://osf.io/t5r4f/, doi: 10.17605/OSF.IO/T5R4F).

Taxa-specific *BA* effects showed non-zero negative responses for Cardiidae bivalves, and Neritidae gastropods at both sites, while Bryozoa was the only grouping with positive responses at both sites (Figure 1). Site specific changes at Guldborgsund were negative responses in Littorinimorpha (large) and Littorinimorpha (small) gastropods, and positive responses in Capitellidae and Orbiniidae polychaetes (Figure 1a). Site specific changes at Stege Bugt were negative responses in Lymnaeidae gastropods and Chironomidae insects, and positive responses in crustacean groups Isopoda and Amphipoda, as well as Spionidae polychaetes (Figure 1b). Overall BA effect estimates across all taxa were close to zero on both sites (Gulborgsund: BA: -

0.04 [-4.09, 4.05], intercept = -1.12 [-4.78, 2.31], R^2_{cond} = 0.51 [0.46, 0.56]; Stege Bugt: BA: -0.07 [-3.58, 3.54], intercept = -1.12 [-3.85, 1.27], R^2_{cond} = 0.31 [0.22, 0.42]).

Of our twenty taxa groupings, seven were found in gut samples from Guldborgsund (Fig 2a), of which Littorinimorpha (small)) was the most common group detected. Several bentho-pelagic species (e.g. *Palaemon* spp., *Gasterosteus aculeatus*) were detected in the gut content but were obviously not represented in core samples. The *BA* effect was influenced by an interaction with prey presence (BA*Presence: -2.66 [-4.63, -0.91], intercept = -2.04 [-5.85, 1.31], R^2_{cond} = 0.52 [0.46, 0.56]), i.e. the BA effect was more negative for taxa found in gut samples than in taxa that were absent from gut samples. The overall BA effect estimate for taxa present in gut contents was negative but overlapped zero (BA: -1.91 [-5.86, 2.23], intercept = 0.43 [-3.28, 4.08], R^2_{cond} = 0.50 [0.39, 0.58], Figure 2b), while the estimate for taxa absent from in gut contents was slightly positive but also overlapped zero (BA: 0.72 [-3.80, 4.87], intercept = -1.95 [-5.80, 1.95], R^2_{cond} = 0.56 [0.51, 0.61], Figure 2b).

These results represent the first test for the effects of round goby invasion on benthic invertebrate macrofauna in marine/brackish environments. We found that only a subset of taxa (largely molluscs) appears to be negatively impacted by goby invasions is generally consistent with the handful of studies are available from the Great Lakes region (i.e. freshwater environments). A study from the upper St. Lawrence River concluded that gastropod richness and median size declined as goby numbers increased, whereas dreissenid bivalves were unaffected and mainly avoided by the round goby (Kipp and Ricciardi 2012). In contrast, in Lake Michigan, dreissenids declined after the invasion of round goby, together with isopods, amphipods, trichopterans, and gastropods (Lederer et al. 2008). The negative effect on dreissenids was found to be caused by predation, whereas the effect on the rest of the benthic invertebrate community may have been indirect (i.e. loss of microhabitat and dreissenids pseudo-faeces) (Lederer et al. 2008). Interestingly, some invertebrates, such as oligochaetes and chironomids increased in numbers in an invaded bay in Lake Ontario as the gastropods disappeared (Barrett et al. 2017). Increases in abundance were also observed at our sites, particularly in some polychaete groups. This may suggest that the goby can have indirect positive effects on certain taxa, for example by foraging selectively on certain groups, they may decrease the levels of resource competition for others.

The strong negative effect on gastropods (and to some extent bivalves) seems to be a recurring phenomenon in many of the Great Lakes studies (Kipp and Ricciardi 2012; Pennuto et al. 2018; Barrett et al. 2017). Similarly, previous gut content-based European studies and one field experiment support the notion that round goby show a preference for certain molluscs (e.g. Borza et al. 2009; Oesterwind et al. 2017; Henseler et al. 2021). The present study supports this, and especially for Neritidae and Cardiidae gastropods, strong negative effects were found that were clearly reflected in their observed densities before and after invasion. For example, the average observed density per square meter of both taxa fell by approximately 98% at Guldborgsund, with Stege Bugt showing similar but more modest decreases of 59% (Neritidae) and 75% (Cardiidae). A strong negative impact on certain gastropods in these areas is a particular concern, as several studies from the Great Lakes Region have highlighted the risk of trophic cascades leading to increased algal biomass as gastropod grazing pressure is reduced (Kipp and Ricciardi 2012; Pennuto et al. 2018; Barrett et al. 2017), potentially signaling a risk of broader changes to ecosystem function and community structure in invaded areas.

As there was a lack of appropriate control sites (i.e. we could not identify a comparable non-impacted site with similar physical parameters such as depth and salinity, and with comparable macrofauna sampling intensity), we therefore lack the ability to directly infer causality between the goby invasion and observed changes. As such, observed trends (negative or positive) should be viewed cautiously. An additional shortcoming of the NOVANA data is the poor detection of mobile taxa such as decapods (*Palaemon* spp.), which this and other studies in the Baltic have found to be a substantial component of round goby diets (Kornis et al. 2012). Single method monitoring programs will tend to produce blind spots for certain taxa and limit our ability to measure impacts across the full community.

To mitigate the negative impacts of anthropogenic pressures on our aquatic environments, empirical data is required to plan and prioritize management efforts (Liu et al. 2008). In the Baltic Sea there is a specific lack of knowledge on the impacts of non-indigenous species on native fauna (Ojaveer and Kotta 2015). Therefore, with this study we hope to highlight the utility (and some limitations) of environmental monitoring data to assess the impacts of non-indigenous species. In this context it is important to consider both positive and negative effects of non-indigenous species on ecosystems, and our broad analysis approach across a wide range of taxa suggests that while some groups appear to be severely impacted by this invasion, others may benefit from round goby presence. This also highlights the importance of reporting positive and negative findings (Fanelli 2012). In the anticipation that round goby will continue its secondary dispersal in the Western Baltic Sea, we suggest that further multi-year regional monitoring programs in advance of the invasion front would be valuable. Ideally ecosystem monitoring would include appropriate control areas allowing before-after-control-impact analysis (as in Conner et al. 2016), which would allow us to better estimate and thus mitigate the impacts of the round goby invasion in northern European waters.

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Author Contributions (CRediT taxonomy)

MVD: Conceptualization, Formal Analysis, Investigation, Methodology, Software, Validation, Writing – original draft

NPM: Formal Analysis, Funding acquisition, Investigation, Methodology, Software, Visualization, Writing – original draft

KSPH: Conceptualization, Methodology, Data curation, Software, Investigation, Writing - review & editing.

GD: Conceptualization, Methodology, Writing - review & editing.

FA: Investigation, Writing - review & editing.

HC: Methodology, Writing - review & editing.

PRM: Methodology, Writing - review & editing.

JWB: Conceptualization, Funding acquisition, Methodology, Supervision, Writing - review & editing.

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Tables

Table 1. Overview of NOVANA benthic fauna samples used in the present study.

Sampling site (latitude/longitude)	Pre-impact samples (n, year)	Post-impact samples (n, year)
Guldborgsund (54.70714 ° N, 11.86273 ° E)	20 (2007-May)	30 (2011-May); 42 (2013-May); 42 (2015-March)
Stege Bugt (54.99996 ° N, 12.22708 ° E)	20 (2009-May): 42 (2011-May)	42 (2013-May): 42 (2015-March)

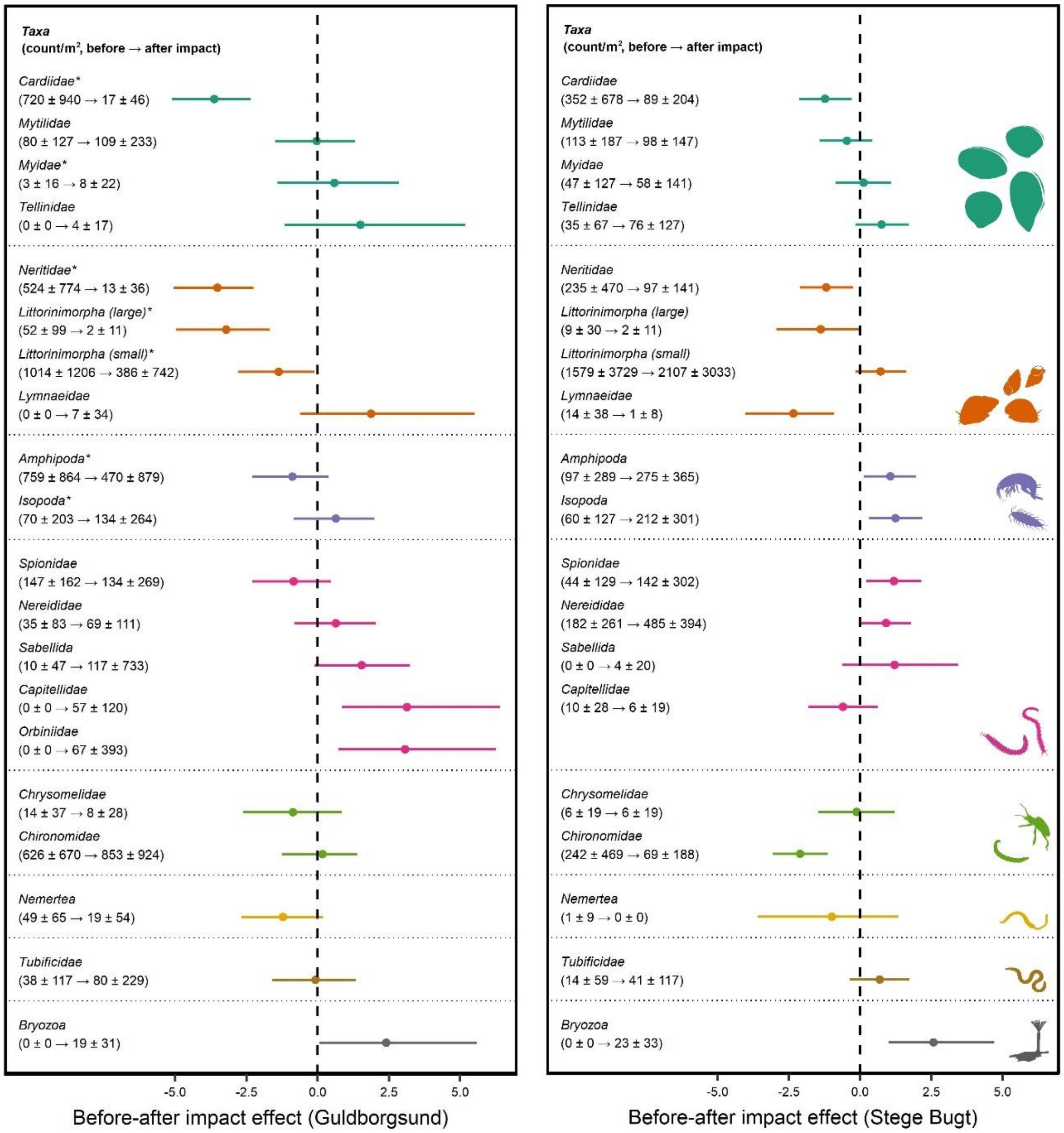
Figure Legends

Figure 1. Taxa-specific before-after (BA) effects for (a) Guldborgsund and (b) Stege Bugt (with 95% credibility intervals). Positive or negative effects that do not overlap zero are interpreted as showing a change in abundance following the arrival of round gobies. Mean densities per square meter (± s.d.) in samples before and after invasion are also shown for each taxa group. Taxa groupings are arranged by class/phylum groupings by: (from top to bottom) class Bivalvia, class Gastropoda, class Malacostraca, class Polychaeta, class Insecta, phylum Nemertea, class Clitellata, class Bryozoa. Note, Orbiniidae were not detected at Stege Bugt, so were not included in analysis for that site.

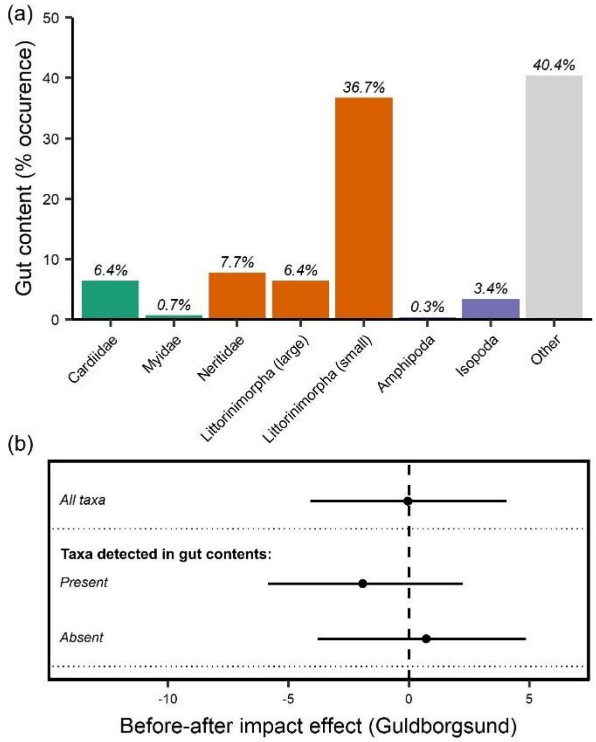
Figure 2. Gut content data for round gobies at Guldborgsund in 2011, including (a) the percentage occurrence of taxa groupings in gut content of (n = 297 fish), and (b) the overall *BA* effect estimates for Guldborgsund for all taxa (from the full site model), as well as present and absent subsets of taxa (with 95% credibility intervals). ‘Other’ taxa found in gut contents were primarily mobile taxa that are poorly detected in HAPS core data (e.g. *Palaemon adspersus, Palaemon elegans*) and fish (*Gasterosteus aculeatus*, round gobies scales).

Figures

Figure 1



397 *Figure 2*



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