Impact of round goby on native invertebrate communities - An experimental field study

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ABSTRACT

This experimental field study provides first insights into the impact of a widely spread non-native fish species, round goby *Neogobius melanostomus* (Pallas 1814), on the diversity of native epifaunal macroinvertebrate communities in the Baltic Sea. A cage experiment was conducted in a macrophyte habitat in the Åland islands located in the northern Baltic Sea. Round gobies (13.5 ± 0.8 cm) affected macroinvertebrate biodiversity from a taxonomic and a trait-based point of view. Specifically, round goby decreased overall abundance, biomass and taxon richness of epifaunal invertebrates. Additionally, taxonomic and trait-based composition were affected, as the gobies reduced abundances of common bivalve (*Cerastoderma* spp. and *Mytilus* sp.) and gastropod species (*Hydrobia* spp.), and thereby modified the relative trait composition of the invertebrate assemblages. Round gobies consumed mainly larger epifaunal individuals leading to an overall decrease in invertebrate body size. Such alterations in taxonomic and trait-based diversity and composition of invertebrate communities through round goby predation may have implications for native fish species and other trophic levels in the respective food webs through food competition and trophic cascades. Round gobies might therefore affect ecosystem processes in invaded areas, and thus influence ecosystem functioning and services.

1. Introduction

Non-native organisms can have severe ecological impacts in invaded areas at a species-, community-, as well as an ecosystem-level. Effects of non-native species on the biodiversity of native communities can be both negative and positive, and manifest through direct biological interactions such as predation, competition and grazing, but also indirect impacts through the modification of hydrographic variables and habitats (Gallardo et al., 2016). Since the biodiversity of communities, including species abundance, richness and trait properties, are closely linked to ecosystem processes, non-native organisms can affect the functioning of food webs and entire ecosystems and therefore also ecosystem services (Chapin III et al., 2000; Gallardo et al., 2016; Tilman et al., 1997). For instance, non-native ecosystem engineers in marine and estuarine environments can strongly influence ecosystem functions by negatively affecting growth and metabolic rates of native organisms, and positively affecting nutrient fluxes, sedimentation and decomposition (Guy-Haim et al., 2017). Consequences of species invasions for

ecosystem services are mostly interpreted as negative (Charles and Dukes, 2007). Nevertheless, the impact of non-native organisms in invaded ecosystems is complex and context-dependent, amongst others, determined by both the trophic and functional group of the invader and the native community (Ricciardi et al., 2013; Thomsen et al., 2014). Whereas non-native species negatively affect the biodiversity of communities that have a similar trophic/functional level as the invader, impacts on higher trophic levels and different functional groups are generally positive (Thomsen et al., 2014).

The round goby (*Neogobius melanostomus* [Pallas 1814]) represents a successful invader that has colonized numerous habitats worldwide. Originating from the Ponto-Caspian region, it can be found in a large array of brackish and freshwater ecosystems, such as the Great Lakes in North America, the Baltic Sea, and several European river- and canal systems like the Rhine and the Danube (Kornis et al., 2012; Kotta et al., 2016). Round goby has become an established component of local food webs in its non-native range (Herlevi et al., 2018; Oesterwind et al., 2017) by feeding on a wide variety of macroinvertebrates and, less

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commonly, other fish and their fry, concurrently serving as prey for various organisms including predatory fish and birds (e.g. Almqvist et al., 2010; Rakauskas et al., 2013; Skora and Rzeznik, 2001; Vašek et al., 2014; Wiegleb et al., 2018). As round gobies can reach high densities and increasingly dominate fish communities in invaded areas (e.g. Jůza et al., 2018; Sapota and Skóra, 2005), this species has frequently been suspected to have an influence on native organisms and their ecological functions. Round goby has, for instance, been connected to the decline of native fish species (Janssen and Jude, 2001; Jůza et al., 2018; van Kessel et al., 2016) and is assumed to be causing diet shifts in fish and birds (Skabeikis et al., 2019; Ustups et al., 2016). Lower trophic levels, such as macroinvertebrate communities, might be affected through direct predation (Barton et al., 2005; Gallardo et al., 2016; Houghton and Janssen, 2015).

Several studies have investigated the impact of round gobies on native fish species, which comprises competition for food and space, preying on fry and juveniles, and serving as food source for predatory fish (Hirsch et al., 2016). However, experimental studies examining how round goby affects macroinvertebrate communities are surprisingly scarce. Nurkse et al. (2018) studied the effects of round gobies on common benthic invertebrate species from the Baltic Sea in aquaria, discovering that this fish species is capable of significantly reducing abundances of its prey organisms. Studies conducted under natural conditions, i.e. field experiments, stem mostly from the Great Lakes, where round goby impacts have been examined by means of cage experiments (Kornis et al., 2014; Kuhns and Berg, 1999; Mikl et al., 2017) and by comparing invertebrate communities amongst sites where round goby is present or absent (Kipp et al., 2012; Kipp and Ricciardi, 2012; Krakowiak and Pennuto, 2008; Lederer et al., 2006). Results have shown that round gobies substantially alter invertebrate community structure by reducing densities of certain species, such as bivalves (e.g. zebra mussels *Dreissena polymorpha*), crustaceans, gastropods and chironomids. Yet, not all of these studies reported a significant impact of round goby on invertebrates, suggesting that interactions between this non-native fish species and its prey organisms might be complex and context-dependent.

Due to their predation on specific organisms, high round goby densities may not only cause shifts in invertebrate community biodiversity and composition, but also alter the functional properties of invaded ecosystems and thus influence ecosystem functioning, as has been shown for non-native ecosystem engineers (Guy-Haim et al., 2017). This could be the case if round gobies would negatively affect organisms with a set of key traits that are strongly linked to ecosystem processes, leading to an alteration in trait composition of local invertebrate communities (cf. Chapin III et al., 2000. However, studies on the link between round goby predation and trait properties of prey communities are lacking, although they give a more in-depth insight into the consequences of round goby invasion for ecosystems and their functioning.

The aim of this study is to examine the impact of round goby predation on native epifaunal invertebrate communities in the Baltic Sea. By means of a field experiment, we study how round gobies affect the taxonomic and trait diversity and composition of invertebrate communities in a macrophyte habitat, where round gobies have established themselves in the local food web (Herlevi et al., 2018). Understanding the impact of non-native species may ultimately contribute to finding adequate management strategies for newly colonized areas.

2. Material and methods

2.1. Study site

To examine the impact of the non-native round goby on native invertebrate communities, a field experiment was carried out in a macrophyte habitat in the northern Baltic Sea (Fig. 1) from 27 July until 7 September 2017. The experiment site was situated in the Åland archipelago at the north-eastern coast of an island close to Mariehamn (60° 3′ 15.84″ N, 19° 57′ 52.2″ E; salinity around 6; Fig. 1b). In the Åland Islands, the first round goby was caught in 2011 in the harbour of
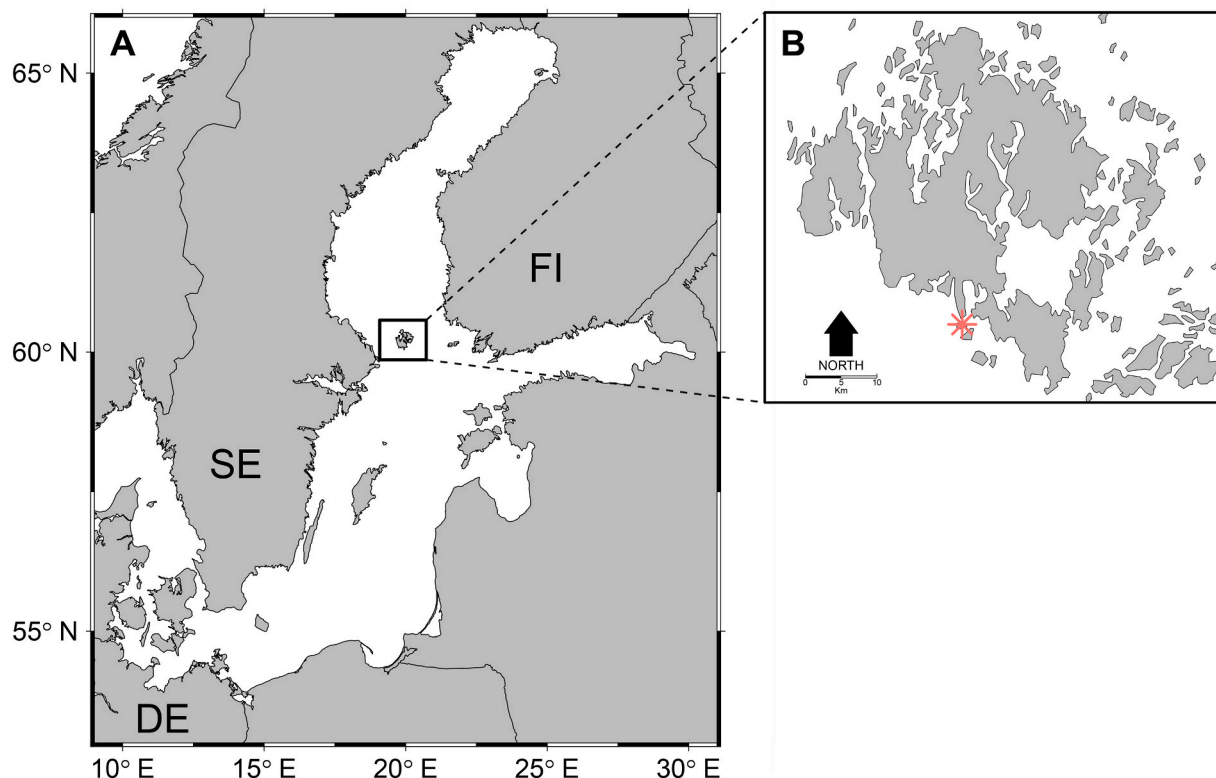
Fig. 1. Map of the (A) Baltic Sea with the (B) Åland Islands located at the entrance of the Gulf of Bothnia. A red asterisk marks the location of the experiment site in the Åland archipelago.

Mariehamn ([Herlevi et al., 2018](#)). The macrophyte habitat was within 10 m proximity to shore in a softbottom area with sandy to muddy sediment. Macrophyte and algae species in the habitat included *Stuckenia pectinata/Potamogeton pusillus*, *Chorda filum*, *Potamogeton perfoliatus* and *Myriophyllum* spp.. The experiment was conducted in 1.7 to 2.7 m water depth in an area where round goby presence had already been documented to avoid potentially contributing to a further spread of the species.

2.2. Round goby collection and holding

To collect round gobies for the experiment, fishing was conducted continuously over a time period of six weeks (20 July until 31 August 2017) before round gobies were used in the experiment, using baited eelfykes (length: 10 m, height: 40 cm, mesh sizes: 11, 14 and 17 mm) in the harbour of Mariehamn. During this time, gobies were held at densities of around 10 individuals in well-oxygenated holding tanks (1 m length x 1 m width x 60 cm height) at Husö Biological Station. The bottom of the tanks was covered with sand, while stones, flowerpots and pipes provided shelter for the fish. Tanks were subjected to ambient natural light conditions and additional artificial light during daytime (12 h artificial light during the day). Holding tanks were cleaned, and the water was exchanged regularly (every two to three days). Sand-filtered seawater was obtained directly from the bay near the station. Water conditions (e.g. temperature, salinity, oxygen concentration) therefore reflected ambient natural conditions, and were monitored regularly (overall mean values ± SD for holding tanks: temperature = $16.8 \pm 1.0\ °C$, salinity = 5.3 ± 0.1, oxygen saturation = $97.1 \pm 4.2\%$). Gobies were fed once a day with a mix of live, natural food items i.e. macroinvertebrates, such as amphipods and blue mussels, that naturally occur at the experiment site. Thus, round gobies were kept in aquarium conditions resembling natural field conditions as closely as possible. Fish were left without feeding the day before including them in the cages.

2.3. Experimental design

To examine how round goby predation affects native invertebrates, a cage experiment was conducted, in which taxonomic and trait-based diversity measures of invertebrate communities were compared between cages including round gobies and cages excluding fish. The experiment was carried out by SCUBA diving. Round rubber tubs served as cages (volume = 65 l, height: 45 cm, diameter at the opening: 60 cm, diameter at the bottom: 45 cm, $n = 12$). Four big holes in the sides and another hole in the bottom of the tub were covered with a white nylon net (mesh size = 4.5 mm), which could be opened and closed at the bottom of the tub. At the study site, tubs were set upside down onto the seafloor with their open side facing downwards (cage area: $0.28\ m^2$). Each cage was fastened to the bottom by a thick sand-filled fabric hose around the cage edges and attached with ropes to prevent cage dislocations and round goby escapes. Twelve cages were placed centrally in the macrophyte habitat in a random order with a distance between 0.5 and 3 m between any two cages.

Total experiment time was six weeks starting with a four-week adaptation period, during which no fish were inside the cages and no fish could enter from the surrounding area ([Fig. 2](#)). The purpose of this adaptation period was to standardize cages as best as possible by accounting for the effect the cages might have on the benthic invertebrate community and the structure of the seafloor, and to allow invertebrate recolonization of the cages. During these four weeks, cages were inspected weekly for cleaning the outside of the nylon nets. After the adaptation period, epifaunal invertebrate samples were taken in all cages (Sampling 1; see below for sampling procedure). One week later, round gobies were randomly included in respectively half of the cages per habitat (Inclusion treatment, six replicates) whereas the other half remained empty (Exclusion Treatment, six replicates). For the Inclusion treatment, two round gobies were placed into the cages. Round goby
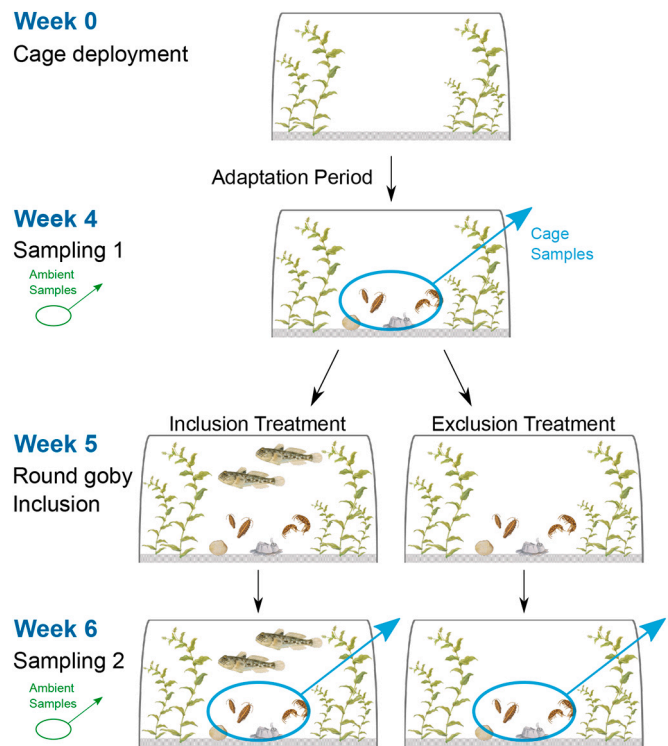

Fig. 2. Illustration of the experimental design in the macrophyte habitat.

density in the cages was therefore approximately seven individuals per m^2. Fish were sexed and measured for total length (TL) in the field directly before introducing them into the cages (mean size ± SD and female: male ratio = 13.5 ± 0.8 cm, 5:7). Round gobies were included in the cages for one week, after which the invertebrate community was sampled in all cages for the second time (Sampling 2). Due to poor visibility, it was not possible to retrieve hiding and fast-moving gobies from the cages for stomach content analyses without disturbing the sampling area i.e. the cage bottom and therefore compromising invertebrate samples. Additional to cage samples, invertebrates were sampled in untreated areas at the experiment sites (Ambient samples, 6 replicates) to get an unbiased picture of the invertebrate community at the study site. These samples were taken simultaneously with the cage samples at Sampling 1 and Sampling 2. On each field day, hydrographic conditions (temperature, salinity, pH, oxygen concentration) were recorded at the experiment site.

2.4. Invertebrate community sampling

Sampling of invertebrates followed the procedure of [Henseler et al. (2019)](#) with slight modifications. Invertebrate epifauna was sampled by collecting all macrophyte and algae material including attached organisms within a 25×12.5 cm area into net bags (mesh size: 0.5 mm). The two samples (at Sampling 1 and Sampling 2) were taken at opposite sides within each cage (e.g. first sample taken at the northern side, second one taken at the southern side of the cage). Invertebrate samples were sieved (mesh size: 0.5 mm) and stored in 70% Ethanol until further processing. Invertebrates were identified to the lowest possible taxonomic group, counted and weighed. Some organism groups were too light to be weighed, which is why the biomass presented here only takes into account weighable invertebrate taxa. For the trait analysis, the body size of individual invertebrates was measured under a light microscope to the nearest μm. When the number of individuals per taxonomic group was more than 50, body size was measured for a representative subsample of at least 50 individuals. Invertebrate density and biomass were standardized to sample volume to allow a direct comparison of samples.

Sample volume was measured with the water replacement method as the volume of macrophyte and algae material (mean sample volume $\pm$ SD: 12.8 ± 11.3 cm^3).

2.5. Invertebrate traits

For the biological trait analysis of the invertebrate community, eight categorical and one continuous traits were used (Table 1). Traits were chosen to describe the fundamental ecology of organisms, considering basic aspects of life-history including size, age, reproduction, feeding and morphology. Invertebrate traits and the construction of the species-trait matrix were adapted from Henseler et al. (2019). If body length was missing for a species in a sample due to non-intact individuals, the mean length of this species from all samples within the same treatment at the same sampling time (Sampling 1 or Sampling 2) was used.

2.6. Data and statistical analysis

All data analyses were conducted in the open source software R,

Table 1
List of invertebrate traits (8 categorical, 1 continuous) and trait categories used for the biological trait analysis. Labels correspond to the trait categories shown in Fig. 5. Table adapted from Henseler et al. (2019).

Trait	Category	Label	Relevance
Body size	Continuous[a]	–	Growth rate, productivity, metabolism, feeding interactions
Longevity	Very short (< 1 yr)	vsho	Life cycle/lifespan, productivity
	Short (1–2 yrs)	sho	
	Long (2–5 yrs)	lon	
	Very long (5–10 yrs)	vlon	
Reproductive frequency	Annual episodic	anep	Reproduction, productivity
	Annual protracted	anpr	
	Semelparous	sem	
Living habit	Attached	att	Living environment, dispersal, foraging mode
	Burrow dweller	budw	
	Free	free	
	Tube dweller	tub	
Feeding position	Suspension feeder	sus	Food acquisition, feeding mode
	Surface feeder	surf	
	Sub-surface feeder	susurf	
	Selection feeder	sel	
	Miner	min	
Resource capture method	Cirri	cirr	Food acquisition, complementary to *Feeding position*: summarize diet
	Jawed	jaw	
	Net	net	
	Pharynx	phar	
	Radula	rad	
	Siphon	siph	
Movement type	No movement	nom	Mobility, dispersal, ability to escape predation
	Swimmer	swim	
	Rafter-drifter	raft	
	Crawler	crawl	
	Byssus threads	byss	
	Tube	tube	
	Burrower	burr	
Body design	Articulate	art	Body structure, protection against predation
	Bivalved	biv	
	Conical	con	
	Turbinate	tur	
	Vermiform segmented	ves	
	Vermiform unsegmented	veun	
Sociability	Solitary	sol	Social behaviour
	Gregarious	greg	
	Aggregated	agg	

[a] Obtained from individual species measurements from the samples.

version 3.6.1 (R Core Team, 2019). Some samples were excluded from the analysis due to handling problems resulting in five Inclusion replicates at Sampling 1, and respectively five Inclusion and Exclusion replicates at Sampling 2. There were six replicates of the Exclusion treatment at Sampling 1. Only invertebrate taxa that were present in at least three samples were included in the analysis (cf. Supplement, Table S1 for a complete species list).

To compare the diversity of invertebrate communities between Exclusion and Inclusion treatments, different taxonomic and trait-based community measures were calculated. Taxonomic measures included invertebrate abundance and biomass, as well as the following indices: taxon richness, Pilou's evenness and the Shannon index (calculated with the vegan package; Oksanen et al., 2018). Trait indices - trait richness, trait evenness and trait dispersion - were computed with the FD package (Laliberté et al., 2014; Laliberté and Legendre, 2010). A more detailed description of the FD (functional diversity) calculation can be found in Henseler et al. (2019). Whereas trait richness refers to the number of trait categories expressed in a community, i.e. the trait space taken by species in a community, trait evenness describes the distribution of species abundances between expressed trait categories (described as functional richness and evenness in Mason et al., 2005). Trait dispersion can be perceived as a measure for trait diversity, as it represents the spread of the community in multidimensional trait space, and is defined as the abundance weighted mean distance of species to their weighted group centroid in trait space (described as functional dispersion in Laliberté and Legendre, 2010). To assess invertebrate community structure, both taxonomic (based on log-transformed abundances) and trait composition were computed. Trait composition was based on community-level weighted mean trait values (CWM), calculated by weighing expressed trait categories by relative abundances for each sample.

Community measures of invertebrates (taxonomic and trait-based indices and composition) were compared between treatments at Sampling 1 and Sampling 2 (same approach as in Kornis et al., 2014). For indices, differences between Exclusion and Inclusion treatments were analysed with Linear Models (LM) using Type II Sum of Squares (car package, Fox and Weisberg, 2011). LMs were conducted with indices as response variables, and treatment (2 levels: Exclusion and Inclusion) and sampling time (2 levels: Sampling 1 and Sampling 2) as fixed factors, including an interaction term of treatment and sampling time. Significant interaction terms indicate that the treatment effect differs with sampling time (i.e. before and after round goby inclusion). In this context, non-significant differences between treatments at Sampling 1 show that invertebrate communities were standardized sufficiently in all cages before round gobies were included, whereas significant differences between treatments at Sampling 2 can be related to the effect of round gobies on invertebrate communities. Abundances were analysed with Generalized Linear Models (GLM) using Type II Sum of Squares including abundance count data as response variable and an offset with the respective volume of each sample using a negative binomial distribution (MASS package; Venables and Ripley, 2002) and a log-link function. For taxon richness, we used a quasipoisson distribution and a log-link function. All other indices were modelled with the normal distribution and log-transformed as needed to meet model assumptions. Assumptions of data normality and homogeneous variances were checked by plotting residuals against fitted values. To compare indices between Exclusion and Inclusion treatments at Sampling 1 and 2, pairwise post-hoc comparisons were conducted using the lsmeans function (lsmeans package; Lenth, 2016). To test for differences in taxonomic and trait composition between treatments for Sampling 1 and Sampling 2, respectively, permutational multivariate ANOVAs (PERMANOVA) were conducted with 9999 permutations using the Bray-Curtis dissimilarity for taxonomic composition, and the Gower distance for trait composition. To check if multivariate dispersions were homogeneous between treatments, a permutational test of multivariate dispersion (PERMDISP) was applied prior to each PERMANOVA. Since PERMANOVA indicated a

significant result for the trait composition at Sampling 2, a SIMPER (similarity percentage) analysis was used to assess the dissimilarity between treatments regarding their invertebrate community trait composition, and to identify which traits contributed most to this dissimilarity. Since taxonomic composition showed significant differences between treatments at Sampling 2, abundances of specific species were analysed and compared between treatments. Only the most abundant species within a habitat (98% of the cumulative abundances) were compared between treatments, as they were well represented in the samples and therefore suitable for statistical analysis. To test whether invertebrate communities were similar between Ambient samples and Exclusion/ Inclusion cages before round goby inclusion, i.e. the starting point in cage and ambient communities was the same, taxonomic and trait-based indices and composition were statistically compared between Ambient samples and treatments (Exclusion, Inclusion) at Sampling 1 using LMs or GLMs. Maps were generated using the packages GISTools, rgdal, raster and oceanmap (Bauer, 2018; Bivand et al., 2017; Brunsdon and Chen, 2014; Hijmans, 2017).

3. Results

In total, 20 invertebrate species were found in the samples, of which 17 were considered in the analysis (Supplement, Table S1). Invertebrate communities did not differ between Ambient samples and Exclusion/ Inclusion treatments at Sampling 1 with respect to taxonomic or trait-based measures (indices and composition; analysis not shown; cf. Fig. 3), showing that invertebrate communities in the cages representatively reflected natural communities at the experiment start.

3.1. Taxonomic indices and composition of invertebrates

In the following section, we focus on the interaction effects of treatment and sampling time in the model results regarding taxonomic and trait-based indices, as these provide the necessary information to evaluate round goby predation effects on invertebrate communities (cf. section "Data and statistical Analysis"; cf. Supplement, Table S2 and S3 for complete model results). Regarding the taxonomic invertebrate community measures, a significant interaction between treatment and sampling time was found for total abundance ($p = 0.010$), biomass ($p = 0.004$) and taxon richness ($p = 0.010$), whereas no significant interaction existed for Pielou's evenness and the Shannon index ($p > 0.05$; Table 2; Fig. 3). Post-hoc comparisons showed that abundance, biomass and taxon richness were higher in the Exclusion than in the Inclusion treatment at Sampling 2 ($p < 0.05$; Exclusion vs. Inclusion [mean ± SD]: $44,200.0 ± 38,745.8$ vs. $5640.0 ± 3268.7$ n/dm^3; $159.9 ± 135.9$ vs. $5.5 ± 3.8$ g/dm^3; $7 ± 1$ vs. $4 ± 1$ taxa), but they did not differ between treatments at Sampling 1 ($p > 0.05$).

Based on PERMANOVA results, the taxonomic composition of invertebrate communities was similar between treatments at Sampling 1 ($p = 0.09$), but differed between Exclusion and Inclusion at Sampling 2 ($p = 0.008$; Table 2). Consequently, abundances of specific invertebrate taxa were analysed including *Amphibalanus improvisus*, *Cerastoderma* spp., *Hydrobia* spp. and *Mytilus* sp., which contributed 98% to the cumulative abundance of all samples (cf. Supplement, Fig. S1 for abundances of all species). Models on the abundances of *Cerastoderma* spp., *Hydrobia* spp. and *Mytilus* sp. showed a significant interaction between treatment and sampling time ($p < 0.05$; Table 3; Fig. 4), whereas the interaction was close to significant for *Amphibalanus improvisus* ($p = 0.054$). Post-hoc comparisons revealed no difference between treatments at Sampling 1 for any of the invertebrate taxa ($p > 0.05$). However, abundances were lower in the Inclusion than in the Exclusion treatment at Sampling 2 for *Cerastoderma* spp. ($p < 0.001$; $911.1 ± 859.4$ vs. $18,838.9 ± 15,171.1$ n/dm^3), *Hydrobia* spp. ($p = 0.017$; $860.0 ± 589.9$ vs. $2773.3 ± 1676.9$ n/dm^3) and *Mytilus* sp. ($p = 0.014$; $3626.7 ± 2463.0$ vs. $21,525.6 ± 26,568.7$ n/dm^3).

### 3.2. Trait-based indices and composition of invertebrates

Trait indices (trait richness, trait evenness and trait dispersion) did not have a significant model interaction of treatment and sampling time ($p > 0.05$; Table 2; Fig. 3). Thus, trait indices did not differ between Exclusion and Inclusion cages at either of the sampling times. The relative invertebrate trait composition based on weighted trait values differed significantly between treatments at Sampling 2 ($p = 0.044$; Table 2; Fig. 5), whereas it was similar for Exclusion and Inclusion cages before round goby inclusion at Sampling 1 ($p = 0.209$; cf. Supplement, Fig. S2 for trait composition based on absolute trait values). SIMPER results revealed an 18%-dissimilarity between invertebrate communities from Exclusion and Inclusion cages at Sampling 2. The trait categories explaining most of this dissimilarity were *Body size*, *Resource capture method - siphon*, *Body design - bivalved* and *Living habit - attached* contributing together 29% to the between-treatment dissimilarity (cf. Supplement, Table S4 for SIMPER results). Community-level weighted mean values (CWM) of *Body size* were relatively smaller in the Inclusion treatment than in the Exclusion treatment, whereas the other trait categories had relatively higher values in the Inclusion cages (Fig. 5). Mean *Body Size* based on absolute values of invertebrates was similar in Exclusion ($2.6 ± 1.7$ mm) and Inclusion ($2.1 ± 1.3$ mm) cages at Sampling 1 before round goby inclusion (ANOVA: $p = 0.266$, $F_{1,58} = 1.26$). At Sampling 2, invertebrates were comparatively smaller in the Inclusion ($1.8 ± 0.8$ mm) than in the Exclusion treatment ($2.6 ± 1.9$ mm; ANOVA close to significant: $p = 0.088$, $F_{1,52} = 3.02$; Supplement, Fig. S3).

4. Discussion

To examine the impact of a widely distributed, non-native fish species, round goby, on the biodiversity of epifaunal, native invertebrates, a field experiment was conducted in the northern Baltic Sea. There was a clear difference in taxonomic and trait properties of invertebrate communities between Exclusion and Inclusion treatments indicating that round goby predation affected invertebrate communities. This impact of round goby on the taxonomic and trait-based biodiversity of native organisms might have repercussions for ecosystem processes, and impair ecosystem functioning in invaded areas.

4.1. Round goby impact on invertebrate communities regarding taxonomic measures

Round goby affected the invertebrate community in the studied macrophyte habitat in the Åland Islands, both regarding taxonomic and trait-based measures. In the presence of fish, total abundance and biomass, as well as taxon richness of invertebrates were lower than in round goby absence, indicating that round goby predation negatively affected the taxonomic biodiversity of epifaunal macroinvertebrate communities. Similar results have been found in experimental studies from the Great Lakes area, which report decreased invertebrate densities (abundance and biomass) and lower Shannon diversity due to round goby (Kipp and Ricciardi, 2012; Krakowiak and Pennuto, 2008; Kuhns and Berg, 1999; Lederer et al., 2006). Taxonomic composition of invertebrates differed between Exclusion and Inclusion cages after fish inclusion, suggesting that round gobies also had an effect on community composition based on species abundances. Specifically, abundances of *Cerastoderma* spp., *Hydrobia* spp. and *Mytilus* sp. were lower in the presence of round gobies, implying that these species were targeted as prey organisms. This result is not surprising, as round gobies naturally feed on these bivalve and gastropod species in different parts of the Baltic Sea (Järv et al., 2011; Karlson et al., 2007; Oesterwind et al., 2017; Rakauskas et al., 2008). Round gobies generally undergo an ontogenetic diet shift comprising an increasing incorporation of molluscs in the diet with increasing body size. Correspondingly, individuals within the size range used in the cage experiment ($13.5 ± 0.8$ cm) feed
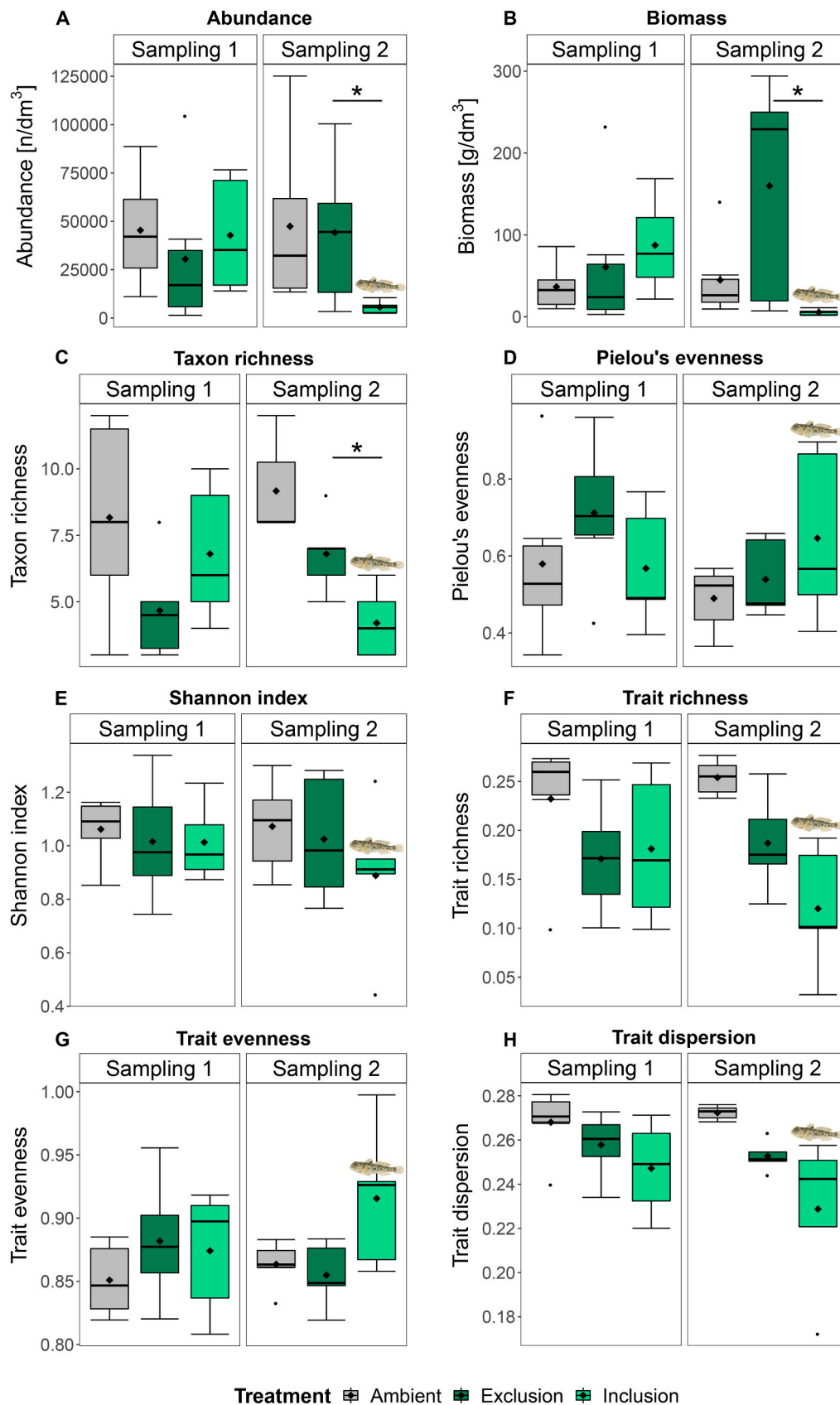
Fig. 3. Taxonomic and trait indices of the invertebrate community: (A) abundance, (B) biomass, (C) taxon richness, (D) Pielou's evenness, (E) Shannon index, (F) trait richness, (G) trait evenness and (H) trait dispersion. Indices are shown for Sampling 1 (before round goby inclusion) and Sampling 2 (after round goby inclusion) for Ambient samples, Exclusion and Inclusion treatments. Box whiskers indicate the lowest/highest values still within 1.5 times the interquartile range from the box and therefore represent minima and maxima when no outliers exist. Outliers are displayed as dots and mean values as diamonds. Asterisk indicate significant differences between Exclusion and Inclusion treatments. Significance levels lie at 0.05.

Table 2

Comparison of taxonomic and trait-based indices and composition of invertebrate communities between treatments (Exclusion and Inclusion) and sampling times (Sampling 1 and Sampling 2) by means of Generalized/Linear models and F-tests for univariate analyses and PERMANOVA for multivariate analyses. Only results of the interaction effects of treatment and sampling time are shown. For complete model results, cf. Table S2 in the Supplementary Material.

| Variable	df	F	p
Abundance	1	1.61	0.222
Biomass	1	0.13	0.720
Taxon richness	1	0.73	0.405
Pielou's evenness	1	2.70	0.119
Shannon index	1	2.29	0.149
Trait richness	1	0	0.999
Trait evenness	1	0.47	0.505
Trait dispersion	1	2.38	0.142
Taxonomic composition			
treatment at Sampling 1	9	0.12	0.953
treatment at Sampling 2	10	1.90	0.101
Trait composition			
treatment at Sampling 1	9	0.52	0.853
treatment at Sampling 2	10	1.60	0.183

Table 3

Comparison of abundances of the most abundant invertebrate species (contributing 98% to the cumulative abundance of all samples) between treatments (Exclusion and Inclusion) and sampling times (Sampling 1 and Sampling 2) by means of Generalized Linear models and F-tests. Only results of the interaction effects of treatment and sampling time are shown. For complete model results, cf. Table S3 in the Supplementary Material.

Species	df	F	p
Amphibalanus improvisus	1	4.30	0.054
Cerastoderma spp.	1	12.18	0.003*
Hydrobia spp.	1	6.89	0.018*
Mytilus sp.	1	4.85	0.042*

on molluscs to a large extent (Hempel et al., 2019; Karlson et al., 2007; Skabeikis and Lesutienė, 2015; Skora and Rzeznik, 2001). Round gobies are assumed to possess an opportunistic feeding strategy, preying on organisms that are available in high abundances (Borcherding et al., 2013; Brandner et al., 2013), which corroborates our findings. *Cerastoderma* spp., *Hydrobia* spp. and *Mytilus* sp. were the most abundant invertebrate taxa in the cages in the beginning and at the end of the experiment, as well as in the Ambient samples (cf. Supplement, Fig. S1), indicating that round gobies in our experiment fed on the invertebrate species with the highest availability. Therefore, it is most likely that they also prey on these organisms under natural conditions at the study site. The effects of this non-native fish species might accordingly be strongest for taxa dominant in a specific environment. While the impact of round goby on invertebrate abundance and biomass in our study is likely a result of direct predation on the most abundant taxa, the decline in taxon richness might additionally be linked to a decrease in habitat structure and food availability, which is provided by bivalves, as suggested by Lederer et al. (2006). Due to a previous lack of experimental field studies on round goby impact from the Baltic Sea, a comparison of our results to findings from the same invaded region is not possible. However, lab studies conducted in the Baltic Sea have documented that round gobies are able to reduce abundances of gammarids and bivalves, including *Macoma balthica* and *Mytilus* sp. (Nurkse et al., 2018), which partly fits the results of our experiment. Experimental studies from the Great Lakes found a negative effect of round goby predation on the density of certain invertebrate taxa, such as gastropods, bivalves (dreissenids) and, to a large extent also, insects (Kipp and Ricciardi, 2012; Krakowiak and Pennuto, 2008; Kuhns and Berg, 1999; Lederer et al., 2006). As round gobies seem to have an impact on invertebrate taxa with the highest availability in the environment, their effect in an ecosystem may be context-dependent and vary conditional on dominating prey species in invaded areas. Contrary to their impact on epifaunal invertebrates, round gobies did not seem to affect infaunal macroinvertebrate communities in the same macrophyte habitat in Åland, based on a small-scale pilot study (Henseler, unpublished results; cf. Supplement, Table S5 for infaunal species considered in this study). Taxonomic indices (total abundance, biomass, taxon richness, Pielou's evenness and
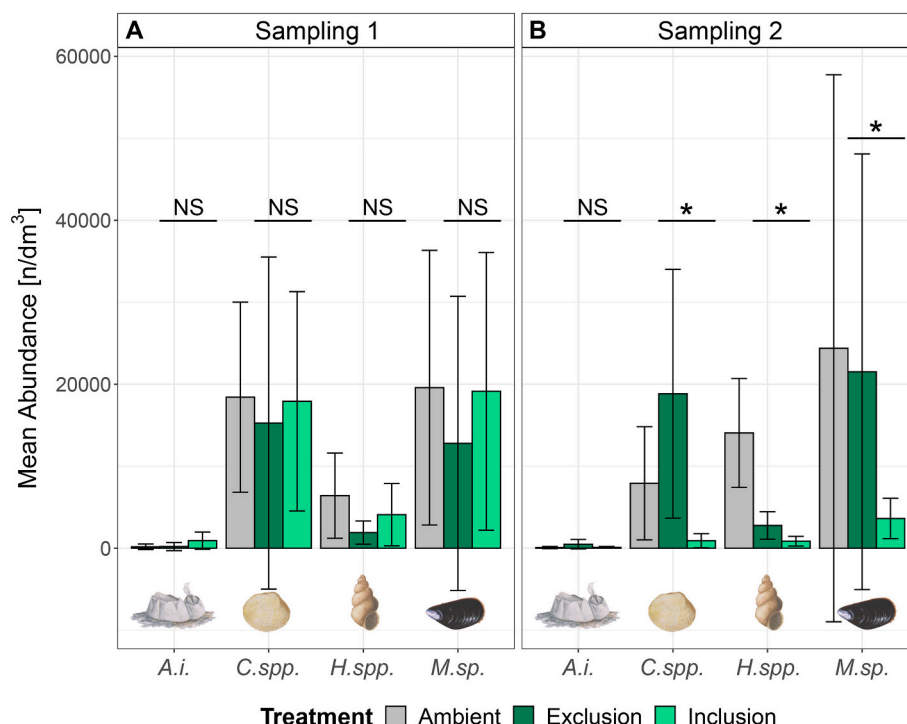
Fig. 4. Mean abundances and standard deviation of invertebrate species that were compared statistically between treatments: *Amphibalanus improvisus* (*A.i.*), *Cerastoderma* spp. (*C.spp.*), *Hydrobia* spp. (*H.spp.*), *Mytilus* sp. (*M.sp.*). Abundances are shown for (A) Sampling 1 (before round goby inclusion) and (B) Sampling 2 (after round goby inclusion), for Ambient samples, as well as for the Exclusion and Inclusion treatments. Asterisk indicate significant differences between Exclusion and Inclusion treatments, and "NS" point out non-significant differences. Significance levels lie at 0.05.
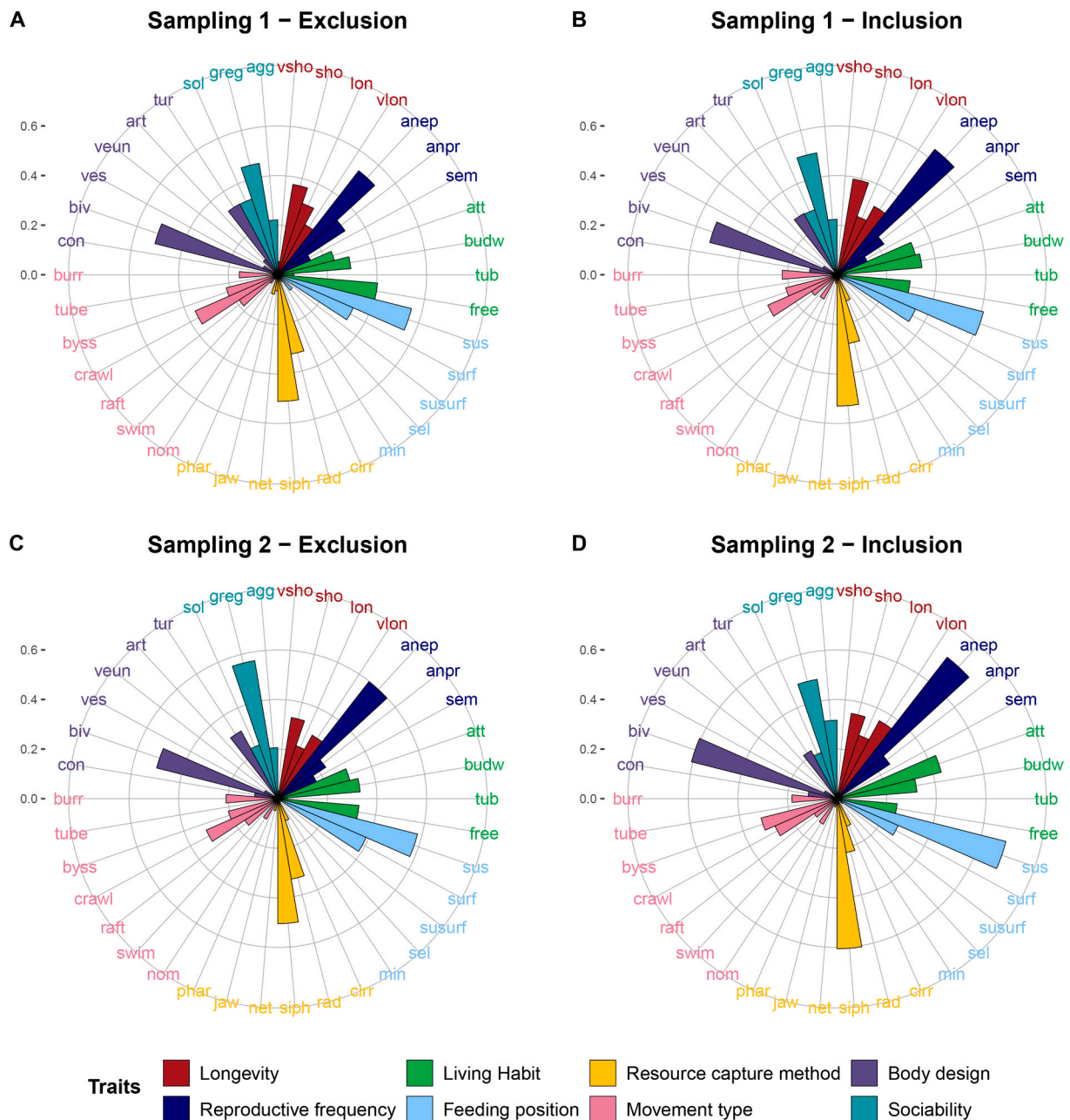
Fig. 5. Relative trait composition displayed as community-weighted means (CWM) i.e. weighted trait values, of the invertebrate community. CWMs are shown for (A) and (B) Sampling 1 (before round goby inclusion) and (C) and (D) Sampling 2 (after round goby inclusion) for the Exclusion (left column) and Inclusion (right column) treatments. Colour coding refers to the different traits. For label descriptions, cf. Table 1. *Body Size* was excluded from the plots due to disproportionally large CWM values.

Shannon index) and composition of infaunal invertebrate communities did not differ between round goby presence and absence. This indicates that the predation effect of round gobies is possibly higher for invertebrate epifauna than for infaunal communities, at least under small-scale experimental conditions. However, since other experimental studies (e. g. from the Great Lakes; see references above) have only considered the impact of round goby on epifaunal prey communities, this aspect requires further investigation.

4.2. Round goby impact on invertebrate communities regarding trait-based measures

Round goby predation did not only affect the taxonomic structure of the invertebrate community, but also the trait-based composition (based

on CWM i.e. weighted trait values), which differed between Exclusion and Inclusion treatments at the end of the experiment. The overall dissimilarity between the treatments was, however, comparatively low (18%). Nonetheless, the traits most responsible for this difference can be directly linked to the invertebrate species, which were most affected by round gobies regarding their abundances. Whereas *Resource capture method - siphon* and *Body design - bivalved* are associated with bivalves, *Living habit - attached* is additionally expressed by *Mytilus* sp.. Thus, round goby had the highest impact on trait categories that are linked to the taxa, which experienced an abundance decline through round goby predation. These trait categories had a higher contribution to the relative trait composition in the Inclusion cages (Fig. 5), which can be explained by the overall reduced taxon richness, making the traits of the most abundant organisms, *Cerastoderma* spp., *Hydrobia* spp. and *Mytilus*

sp., dominate even more in the community. The expression of trait categories based on absolute trait values (i.e. not weighted by relative abundances for each sample) was overall lower in the Inclusion than in the Exclusion treatment (Supplement, Fig. S2), implying that round goby also affected the absolute expression of traits in the experiment. Thus, round goby predation reduces the overall contribution of invertebrate traits to ecosystem processes (due to changes in absolute trait expression) potentially leading to an overall decrease in ecosystem functions (quantitative effect). Additionally, the relative contribution of traits to these processes is altered (due to changes in relative trait expression) possibly causing a shift in magnitude of certain processes (qualitative effect). Round goby impacts on invertebrate communities might therefore have consequences for ecosystem functioning in invaded areas due to a modification in invertebrate trait expression (Chapin III et al., 2000). The trait *Body Size* contributed most to the difference in relative trait composition of invertebrates between Exclusion and Inclusion cages, and was smaller in the presence of round gobies (difference in mean size close to significant between treatments at Sampling 2). Thus, round gobies fed on larger individuals indicating that this fish species can affect the size structure of communities. This is in line with findings from other invaded areas, where round gobies likewise decreased the size of prey organisms (Kipp et al., 2012; Kipp and Ricciardi, 2012; Mikl et al., 2017). On the other hand, lab studies examining the impact of round goby feeding on different sizes of bivalves generally show that round gobies (ca. 10–15 cm TL) select for smaller individuals between 3 and 27 mm (Nurkse et al., 2016; Perello et al., 2015; Schrandt et al., 2016; Schwartzbach et al., 2019). However, invertebrates in our experiment were generally rather small (overall size range of invertebrates in the macrophyte habitat: 0.4–12.0 mm; Supplement, Fig. S3) and thus still lie within the documented preferred size range. As body size plays a significant role in food webs and ecological processes through its link to, amongst others, growth and metabolic rates, productivity and mortality (Brose et al., 2017; Brown et al., 2004; Woodward et al., 2005), the alteration of invertebrate size structure through round gobies could have implications for ecosystem functioning in invaded regions. Yet, it has to be considered that natural round goby populations also contain smaller individuals feeding on other, i.e. smaller, invertebrate sizes than fish in this experiment. This might result in an equal predation pressure for smaller and larger invertebrates under natural conditions. Hence, the main effect of round goby predation in natural systems might rather manifest through an overall abundance reduction than through a shift in the size structure of native invertebrate communities.

Round gobies are generally documented to favour structured rocky or stone habitats (e.g. Ramler and Keckeis, 2020; Ray and Corkum, 2001; Sapota and Skóra, 2005). Yet, high round goby abundances have been found in a variety of other habitats (Kornis et al., 2012), underlining the broad habitat use of this species. For instance, round goby presence in vegetated habitats on softbottom is known from the Baltic Sea, the Great Lakes and the Caspian Sea (Bogutskaya et al., 2004; Cooper et al., 2009; Cooper et al., 2007; Henseler et al., 2020; Jude and DeBoe, 1996). Additionally, at our study site, round gobies were observed in high numbers in the macrophyte habitat, rendering it appropriate to conduct this experiment in a vegetated area, even if this might not constitute the primary habitat of this fish species.

4.3. Ecological implications of round goby predation

For our experiment, the number of round gobies included in the cages was chosen to resemble abundances in nature. Densities of this species from the Danish and Polish coast in the Baltic Sea range from 1.9 up to 30 individuals per m^2 (Azour et al., 2015; Sapota, 2004; Sapota and Skóra, 2005). Round goby density in our experiment (7 per m^2) lay well within this reported abundance range, reflecting natural field conditions. Depending on whether round goby abundances are lower or higher in a specific invaded area than in our study, predation impacts of this species on invertebrate communities could accordingly be weaker or stronger. Another aspect worth considering in the impact assessment of non-native species is the health status of individuals in a population. In a parallel experiment with a similar set-up conducted at the German coast (data not shown), round gobies were in a poor body condition displaying infected spots on the skin and caudal fins (Supplement, Fig. S4). Additionally, many dead individuals were observed in the field. This was witnessed at various locations along the German coastline in addition to Danish, Swedish and Estonian coastal waters (Jane Behrens and Redik Eschbaum, personal communication). One year later, round gobies in the Åland archipelago showed similar disease symptoms (personal observation) indicating a Baltic Sea wide infection of this non-native species during the years 2017/2018. In the experiment in Germany, there was no predation effect of round gobies on invertebrate communities, which might potentially be linked to the poor body condition of the fish, although this can only be speculated. Yet, impact studies should take into account body condition of invaders when evaluating their effects on native organisms and ecosystems.

Through their predation on native invertebrates, round gobies could have an indirect impact on organisms of a similar trophic level i.e. native fish species, feeding on the same organisms. As a successful invader, round goby might be more efficient in preying on a wide spectrum of organisms, as it has been shown in laboratory experiments in the Great Lakes (Naddafi and Rudstam, 2014), making them competitively superior to native fish species regarding predation rates. As round gobies reduce abundances and overall body size of invertebrates, this could negatively affect native fish species in areas of high round goby density. Availability of invertebrates is likely lower and mostly small, possibly juvenile, individuals will prevail in invaded areas, which might be energetically less profitable prey for native fish. In the Baltic Sea, flounder *Platichthys* spp. represents one native species, which might experience food competition through round goby due to diet overlap. Flounder feeds on similar prey organisms as round goby, including bivalves (*Macoma balthica, Mytilus* sp.) and gastropods (*Hydrobia* spp.) (Järv et al., 2011; Karlson et al., 2007), which belong to the species affected most in our cage experiment, suggesting that round goby might reduce food availability for flounder.

Besides their impact on native invertebrate and fish communities, round gobies might affect other trophic levels, by inducing trophic cascades. By means of intense predation on invertebrate grazers, like small gastropods, high fish abundances can cause increased filamentous algal growth (Eriksson et al., 2009; Korpinen et al., 2007). Accordingly, high round goby densities have been linked to increased benthic algal biomass and chlorophyll-a concentrations, presumably through their consumption of grazing invertebrates (Kipp and Ricciardi, 2012; Kuhns and Berg, 1999). In our study, round gobies decreased abundances of *Hydrobia* spp., which is a grazing gastropod, expressing the traits *Feeding position - surface feeder* and *Resource capture method - radula*. The CWM-values of these categories were lower in the Inclusion than in the Exclusion treatment after fish inclusion at Sampling 2 (Fig. 5; Supplement, Table S4), indicating that invertebrate grazing might decline in the presence of round gobies, potentially leading to increased opportunistic algae growth in coastal areas invaded by this fish species. This could have implications for ecosystem functioning, and affect ecosystem services of coastal habitats, for example through increased filamentous algal blooms.

5. Conclusions

This field experiment provides novel insights into the impact of a non-native fish species, round goby, on the biodiversity of native macroinvertebrate communities in the Baltic Sea. Round gobies negatively affected abundance, biomass and taxon richness of epifaunal invertebrates in a macrophyte habitat in the northern Baltic Sea, and had an influence on taxonomic and trait-based composition. Abundances of common Baltic Sea bivalve and gastropod species were lower in round

goby presence, and, correspondingly, the expression of traits associated with these organisms was modified. Round goby seemed to influence the size structure of the invertebrate community by decreasing overall body size. Thus, this study offers information on the impact of round goby on trait properties of invertebrate communities, which can have consequences for ecosystem functioning in invaded areas. Effects of round goby on the diversity of native invertebrate communities in their invaded range might have consequences for other organisms through food competition or trophic cascades, which might entail repercussions for ecosystem functions and services.

Declaration of Competing Interest

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

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jembe.2021.151571.

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