

Research Article

Parasite infection of the non-indigenous round goby (*Neogobius melanostomus*) in the Baltic Sea

Henn Ojaveer^{1,2,*}, Aleksei Turovski³ and Kristiina Nõomaa⁴

¹University of Tartu, Ringi 35, 80012 Pärnu, Estonia

²National Institute of Aquatic Resources, Technical University of Denmark, Kemitorvet Building 201, 2800 Kgs. Lyngby, Denmark

³Tallinn Zoological Gardens, Paldiski Road 145, 13522 Tallinn, Estonia

⁴Estonian Marine Institute, University of Tartu, Mäealuse 14, 12618 Tallinn, Estonia

Author e-mails: henn.ojaveer@ut.ee (HO), mattias.turovski@hotmail.com (AT), kristiina.noomaa@ut.ee (KN)

*Corresponding author

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Abstract

Parasites may play several critical functions in marine ecosystems, including possibly influencing introduction success or modifying the roles of non-indigenous species. Based on seasonally replicated sampling, we have investigated parasite communities and infection rates of the non-indigenous round goby *Neogobius melanostomus* in two localities in the NE Baltic Sea, characterised by different invasion trajectories. The parasite community of the fish was very rich, consisting of at least 24 native parasite species, with moderate mean infection intensity – 9.4 parasites per host. In total 78% of fish were infected with parasites, most frequently hosting 1–3 parasite species per fish. The trematode *Diplostomum spathaceum* had the highest prevalence (46%), while the acanthocephalan *Corynosoma strumosum* and the trematode *Tylodelphys clavata* had the highest infection intensity (mean 6.8 and 7.2, respectively). The seasonal dynamics of prevalence were similar in both localities, with the lowest number of infected fish being found immediately after winter with no clear patterns/differences between other seasons. Broadly similar patterns appeared both for species richness and infection intensity. Both localities displayed very similar patterns of occurrence frequency: both had a few parasite species which were specific to one locality and five species that occurred more frequently in one of the two localities. Binomial regression of the probability of infection identified season, total body length, and sex as significant predictors, but not the locality of sampling. The quantitative model revealed that infection intensity was positively linked to total body length and parasite species richness, and was on average 2.7 individuals higher in summer and autumn than in winter and spring.

Key words: species richness, prevalence, infection intensity, temporally replicated sampling, rarefaction curve, factors affecting infection

Introduction

Parasites are ubiquitous components of natural plant and animal communities, and their importance in their hosts' ecology is evident (e.g., Dobson and Hudson 1986). Among other functions, parasites may play important roles in shaping host population dynamics, alter interspecific competition, influence community functioning, affect energy flow and appear to be important drivers of biodiversity (e.g., Torchin and Mitchell

2004; Hudson et al. 2006; Johnson et al. 2010; Lagrue et al. 2011 and references therein). According to the hypothesis of enemy release, introduced species often leave behind predators and parasites in their native habitats, leading to a decrease in the number of parasite species and lower infection intensity in the recipient ecosystem compared to the native distribution area (Mitchell and Power 2003; Torchin et al. 2003). This has been seen as one of the contributing factors behind the increased demographic performance of invasive species (Torchin and Mitchell 2004).

However, such an advantage over native species can be of short duration (Gendron et al. 2012) and undoubtedly calls for more research on this topic from a management perspective. This need is even more obvious in light of a contrasting finding in the snail *Batillaria attramentaria* (G.B. Sowerby I, 1855), where prevalence of parasite infections did not differ between populations with different invasion histories (10 vs. 80 years; Grason et al. 2018). Although the introduction of a potential new host species may have little effect on the parasite community at the ecosystem level (Thieltges et al. 2008), the general paucity of information availability on the parasites of introduced marine fishes should be seen as a major gap not only in fundamental knowledge (e.g., evolutionary marine bioinvasion ecology or trophic interactions in marine ecosystems), but also in applied science and management (e.g. preventing future introductions or conserving marine biodiversity) (Vignon and Sasal 2010). Specifically, relatively low parasite infection has been suggested as one of the likely contributing factors for the introduction and establishment success of the round goby *Neogobius melanostomus* (Pallas, 1814) (Ondračková et al. 2010; Kvach et al. 2017).

The round goby, a demersal fish species of Ponto-Caspian origin, was first found in the Baltic Sea in Puck Bay (Poland) in the early 1990s (Skora and Stolarski 1993). Since then, the species has succeeded in colonizing virtually the whole sea basin (Kotta et al. 2016 and references therein). This fish dominates commercial fish catches in several coastal areas, and several of its key ecological features are fairly well-studied at the pan-Baltic scale, including colonisation and spread, growth, trophic interactions and ecological impact (for an overview see Puntila et al. 2018 and references therein). Unfortunately, this is not the case for all key aspects of the invasion ecology of the species. A notable knowledge gap exists for parasite infections, about which there is only very limited spatial evidence available based on solid and temporally replicated sampling from the southern Baltic Sea which was collected over ten years ago (Rolbiecki 2006; Kvach and Skóra 2007).

The aim of the current study was to: i) describe the parasite infection of non-indigenous *N. melanostomus* in two spatially distinct localities in the Baltic Sea characterised by different invasion trajectories (Muuga located at the southwestern Gulf of Finland and Jaagupi situated in the northeastern Gulf of Riga), and ii) reveal any seasonal and spatial patterns in parasite infection of the fish.



Figure 1. Map of the study area with sampling locations in Muuga and Jaagupi.

Materials and methods

Study area

The round goby was sampled in two localities situated in the NE Baltic Sea: Muuga ($59^{\circ}31'24''\text{N}$; $24^{\circ}55'18''\text{E}$) and Jaagupi ($58^{\circ}3'24''\text{N}$; $24^{\circ}24'50''\text{E}$), located at the SW coast of the Gulf of Finland and NE coast of the Gulf of Riga, respectively (Figure 1). In Muuga, the fish was first observed in 2005, after which its presence in gillnet catches started to increase exponentially and exceeded 80% by 2010 (ICES 2017). Near Jaagupi, the fish was first observed in 2011, and its active colonisation process started in 2015 (H. Ojaveer unpubl. data).

Both localities are relatively shallow brackish environments with extensive seasonal ice-cover and overall low species diversity. Both areas experience strong anthropogenic impacts, including maritime transport, leisure boating, commercial/leisure fisheries and eutrophication. Several non-indigenous and cryptogenic species are very abundant in one or both localities, including the polychaete *Marenzelleria* spp., the predatory cladoceran *Cercopagis pengoi* (Ostroumov, 1891) the North American mud crab *Rhithropanopeus harrisii* (Gould, 1841), the cirriped *Amphibalanus improvisus* (Darwin, 1854), the gibel carp *Carassius gibelio* (Bloch, 1782) and the round goby (AquaNIS. Editorial Board 2015).

Sample collection, storage and laboratory analysis

Round goby were sampled across seasons from spring (June) 2016 to spring (June) 2017 (Table 1). Fish were collected from trapnet catches by commercial fishermen. In total 184 fish (89 from Muuga and 95 from Jaagupi)

Table 1. Time and location of sampling for the round goby *Neogobius melanostomus* with descriptive statistics of the samples and parasite infection in Muuga and Jaagupi, Baltic Sea, during 2016–2017.

Sampling time (Muuga / Jaagupi)	No. of fish	Mean TL (\pm SE), mm	% of males	Prevalence (%)	Mean species richness	Mean intensity
26.May / 2.Jun 2016	13/12	162.0 \pm 7.1 / 160.9 \pm 5.2	15.4/66.7	100.0/75.0	3.2/2.0	12.1/8.1
19.Aug / 9.Sep 2016	18/25	158.7 \pm 5.2 / 179.6 \pm 3.4	36.8/28.0	89.5/92.0	2.5/2.2	13.1/15.0
8.Dec 2016	12/12	118.5 \pm 3.7 / 154.1 \pm 4.8	36.4/16.7	81.8/100.0	2.2/2.4	8.8/13.9
21.Apr / 18.Apr 2017	23/26	139.3 \pm 6.2 / 138.6 \pm 5.5	43.5/26.9	31.9/57.7	1.7/1.4	3.6/2.9
14.Jun / 15.Jun 2017	23/20	148.2 \pm 4.7 / 169 \pm 5.2	47.8/35.0	87.0/80.0	2.1/1.9	5.6/7.3

were obtained. The collected fish were kept on ice until dissection (max. 12 hrs). Before dissection, they were measured for total body length, and the sex of each fish was determined.

The external body (including skin and fins) and gills were carefully examined visually for signs of ectoparasites (or larval stages of endoparasites like metacercaria of digenean trematodes), and all anomalies in appearance were noted. Both eyes, the entire digestive system (including the intestinal tract and gut contents) and the body cavity and organs (gonads, kidney, liver, mesenteries, spleen and pericardium) were inspected under a dissection microscope.

Unicellular parasites (ectoparasitic Ciliophora) were impregnated with 2% AgNO₃ (silver nitrate instant solution) on slides. Living diplostomid metacercaria were studied between two slides. *Cryptocotyle* metacercaria were isolated from cysts, fixed by heating in water with a drop of menthol solution added (24 g of menthol solution in 10 ml of 95% ethanol) and preserved prior to staining with acetic carmine in 70% ethanol (Vasilkova 1955). Cestodes and other trematodes were fixed in 70% ethanol and stained with carmine (Vasilkova 1955). Nematodes and acanthocephalans were stored in 70% ethanol and cleared in lactophenol for examination under the light microscope. Identification of trichodinoids was done according to Stein (1984), *Contracaecum* according to Fagerholm (1990) and *Eustrongylides* according to Karmanova (1968). All parasites were counted and identified to species or the lowest possible taxon level.

Data analysis

Rarefaction curves

Sampling efficiency assessment is important in parasite population studies such as this one (Blakeslee and Byers 2008). In order to establish our sampling size sufficiency and to assess total expected species richness in both populations and the entire sample, we used EstimateS 9.1.0 (Colwell 2013) to construct species accumulation and species richness estimator curves from our data. EstimateS uses Monte Carlo resampling (through randomization of sample order over a number of replicates [500 runs]) to determine the mean accumulation of species (Sobs) as samples are added over the full data set (Gotelli and Colwell 2001), while also providing standard deviations and 95% confidence intervals for each data point (Colwell 2013).

Sample-based rarefaction curves may not capture the total species richness within a population for a particular sampling effort, especially if these curves have not reached a stable asymptote. Thus, nonparametric estimators, such as Chao2, can be useful in predicting the eventual asymptote in species richness for a particular population (Gotelli and Colwell 2001); they do so by including the effects of rare species on the total species richness (Witman et al. 2004; Chao 2005). In addition, Walther and Morand (1998) advocated the use of Chao2 specifically for parasite species richness. Because a clearly asymptoting accumulation curve indicates complete capture of the total species richness in a population (Gotelli and Colwell 2001), estimator curves and species accumulation curves converging on the same asymptote reflect adequate sampling (Walther and Morand 1998). Therefore, we used this technique (with Chao2 as our estimator) to determine whether we had adequately sampled the round goby.

Ecological parameters of parasite infection

The following ecological parameters of parasite infection were used: prevalence (defined as the percentage of infected fish in a sample), infection intensity (number of parasites per infected fish; mean and total), intensity range (highest and lowest number of parasites per fish), species richness (number of parasite species per infected fish), and frequency of occurrence (percentage of samples containing the focal parasite).

Modeling

The probability of infection (coded as 0 or 1 for non-infected or infected fish, respectively) was analysed with a logistic regression (generalized linear model with binomial error distribution and logit link function), using the data from 183 fish. Explanatory variables in the probability model were the categorical variable “season” (with winter as the base level), area of sampling (Jaagupi or Muuga), total body length and sex.

The intensity of infection was modelled as a linear function of two continuous variables (parasite species richness and fish body length), and three categorical variables (sex, season and area), including only data from infected fish ($n = 142$). Full models included all explanatory variables in both localities with the best model identified with backward selection until only significant terms were retained in the model. Model diagnostics indicated that the variance of the number of parasites increased with the mean, violating the assumption of homogeneity, hence the linear model was replaced with a weighted linear regression in which the observations were weighted with the inverse of the number of parasites. Based on Akaike Information Criterion, weighted linear regression ($AIC = 788$) notably outperformed the unweighted linear regression ($AIC = 908$).

Table 2. List of parasites identified in the round goby *Neogobius melanostomus* with their habitat, prevalence, mean infection intensity and intensity range in Muuga (M) and Jaagupi (J). Legend: l. – larvae, met. – metacercaria larvae, cysth. – cystacanth larvae, ad. – adult, juv. – juvenile.

Parasites	Habitat	Prevalence (%) (M/J)	Mean intensity (M/J)	Intensity range (M/J)
CILIOPHORA				
<i>Trichodina acuta</i> Lom, 1961	external body, gills	1.1/2.1	5.0/2.5	5/2–3
<i>Trichodina domerguei</i> (Wallengren, 1897)	eyes, gills	21.4/3.2	3.9/2.0	1–18/1–3
<i>Trichodina jadratica</i> Raabe, 1958	external body, gills	10.1/10.5	1.6/1.4	1–4/1–2
<i>Trichodina nigra</i> Lom, 1960	external body, gills	5.6/1.1	2.6/2.0	2–6/2
TREMATODA				
<i>Bunodera luciopercae</i> (Müller, 1776), ad.	digestive system	0.0/2.1	0.0/3.5	0/3–4
<i>Cryptocotyle concava</i> (Creplin, 1825), met.	external body, gills	22.5/8.4	4.1/5.4	1–8/1–14
<i>Cryptocotyle lingua</i> (Creplin, 1825), met.	external body, gills	3.4/3.2	7.7/5.3	2–18/2–9
<i>Cryptocotyle</i> spp., met.	external body, gills	2.5/0.0	5.5/0.0	4–7/0
<i>Diplostomum baeri</i> Dubois, 1937, met.	eyes	5.6/5.3	3.6/4.8	1–10/1–15
<i>Diplostomum spathaceum</i> (Rudolphi, 1819), met.	eyes	48.3/44.2	4.9/7.6	1–15/2–31
<i>Tylodelphys clavata</i> (von Nordmann, 1832), met.	eyes	2.3/6.3	5.5/8.8	4–7/2–19
<i>Ichthyocotylurus pileatus</i> (Rudolphi, 1802) Odening, 1969, met	pericardium	1.1/2.1	4.0/5.0	4/5
CESTODA				
<i>Proteocephalus cernuae</i> (Gmelin, 1790), ad.	digestive system	0.0/1.1	0.0/2.0	0/2
<i>Proteocephalus percae</i> (Müller, 1780), ad.	digestive system	0.0/1.1	0.0/2.0	0/2
<i>Proteocephalus</i> spp., imm.	external body	0.0/3	0.0/1.0	0/1
NEMATODA				
<i>Camallanus lacustris</i> (Zoega, 1776), ad.	digestive system	13.5/7.4	2.3/5.0	1–4/2–11
<i>Contracaecum osculatum</i> (Rudolphi, 1802) Baylis, 1920, l.	liver	1.1/1.1	2.0/2.0	2/2
<i>Cucullanus heterochrous</i> (Rudolphi, 1802), ad.	digestive system	6.7/16.8	2.7/3.8	2–4/2–11
<i>Dichelyne</i> (<i>Cucullanellus</i>) <i>minutus</i> (Rudolphi, 1819), ad.	digestive system	9.0/9.5	4.0/4.2	1–8/2–8
<i>Eustrongylides excisus</i> Jägerskiöld, 1909, l.	external body	5.6/0.0	2.2/0.0	1–3/0
<i>Eustrongylides mergorum</i> (Rudolphi, 1809), l.	external body	2.3/0.0	2.0/0.0	2/0
Nematoda gg. spp., l.	digestive system	0.0/2.1	0.0/2.0	0/2
ACANTHOCEPHALA				
<i>Corynosoma semerme</i> (Forssell, 1904), acanthella cysth.	pericardium	6.7/7.4	3.0/2.7	2–4/2–4
<i>Corynosoma strumosum</i> (Rudolphi, 1802) Lühe, 1904, acanthella cysth.	pericardium	2.3/1.1	4.5/9.0	2–7/9
<i>Echinorhynchus gadi</i> Zoega in Müller, 1776, ad.	digestive system	1.1/5.3	2.0/3.8	2/2–7
<i>Echinorhynchus</i> sp., ad.	digestive system	1.1/0.0	2.0/0.0	2/0
<i>Pomphorhynchus laevis</i> (Zoega in Müller, 1776), ad.	digestive system	6.7/13.7	2.5/4.0	2–4/2–9

There were three cases in which species-level identification was impossible. These were designated by genus (*Cryptocotyle* spp., *Proteocephalus* spp.) or as nematode larvae, and likely included some individuals of species that were identified to species in this study (Table 2). None of these cases were included in the species list counts or in the analysis/modeling where species-level information was required.

Results

Species richness

A total of 24 different native parasite species were observed in the round goby, with 21 species present in both localities. In total, we recorded four ciliate, seven digenean trematode, two cestode, six nematode and five acanthocephalan species. Besides the 23 identified species, *Echinorhynchus* sp. was also included in the species list (Table 2). There were a few differences

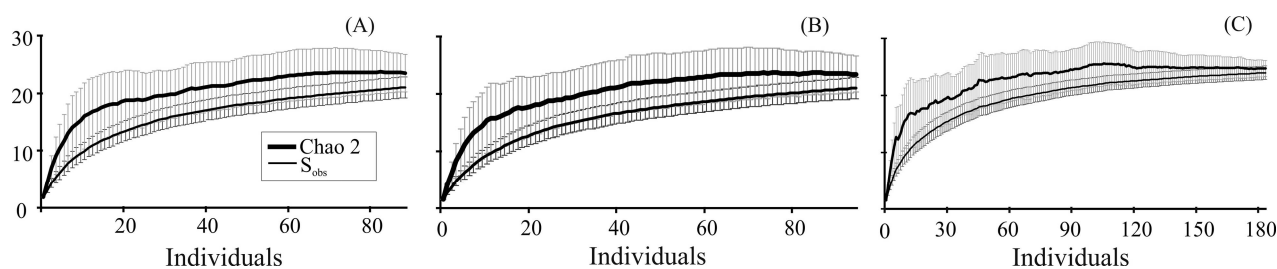


Figure 2. Parasite species richness, as a function of the number of round goby, *Neogobius melanostomus*, individuals examined, estimated using species accumulation and species estimator curves (Colwell 2013). Each panel shows Sobs and the Chao2 species richness (mean \pm SD) estimate in Muuga (A), Jaagupi (B) and cumulatively across both localities (C).

in presence/absence of species between the two localities studied. While *Eustrongylides excisus*, *E. mergorum* and *Echinorhynchus* sp. were only found in Muuga, *Bunodera luciopercae* and representatives of the genus *Proteocephalus* were only observed near Jaagupi.

Species accumulation (Sobs) and Chao2 species richness estimator analyses reached an asymptote at a parasite species richness of 21 and 23, respectively, in both localities indicating that we potentially underestimated parasite richness by around two taxa per location. This potential underestimation appears nearly significant from the confidence interval bands (Figure 2A, B). However, in cumulative analysis where data from both localities were merged together, Sobs and Chao2 both reached an asymptote at a parasite species richness of 24 with very narrow confidence interval bands (Figure 2C) suggesting adequate sampling size and no underestimation of cumulative parasite species diversity.

Infection rates

In total 78% of fish were infected with parasites (Muuga 77%, Jaagupi 79%), with most (> 50%) hosting 1–2 parasite species each (Figure 3A). Prevalence was highest for the eye fluke *Diplostomum spathaceum* (46% of all fish), which also had the third highest infection intensity (mean = 6.3). The second highest prevalence was recorded for the trematode *Cryptocotyle concava* at 22.5%. The highest mean infection intensity per locality was observed for the acanthocephalan *Corynosoma strumosum* (9.0), followed closely by the trematode *Tylodelphys clavata* (8.8) (Table 2). The overall mean infection intensity was 9.4 individual parasites per fish (Muuga 8.9, Jaagupi 9.9).

Across seasonal samples, the most stable component in the parasitofauna of the round goby was the trematode *D. spathaceum* with 100% frequency of occurrence (i.e. it was present in both localities in all seasons), followed by the freshwater nematode *Camallanus lacustris* (90%) and the trematode *C. concava*, the nematode *D. minutus* and the acanthocephalan *C. semerme* (80%). At the same time, 50% of parasites (i.e. 12 species) occurred only in one or two samples (Supplementary material Table S1). The seasonal dynamics of parasite prevalence were similar in both localities, with the

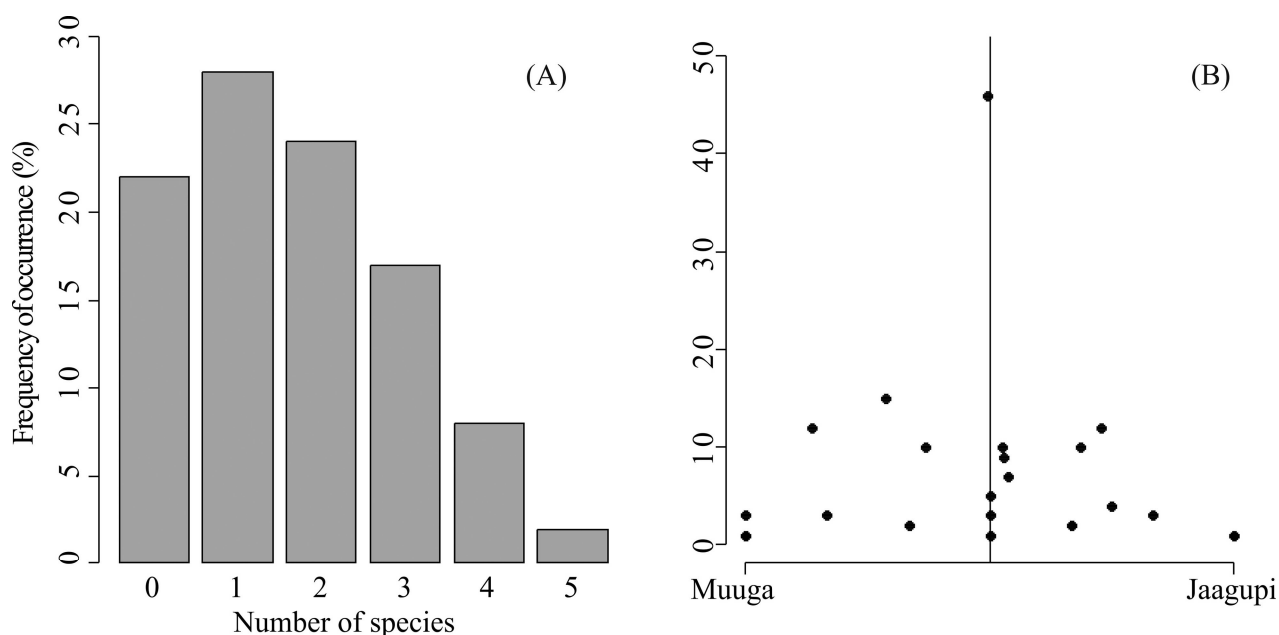


Figure 3. Frequency histogram showing the number of parasite species in the round goby, *Neogobius melanostomus* (A), and the spatial distribution of parasites in round goby in Muuga and Jaagupi (B) x axis – proportional occurrence of parasites in two localities, y axis – frequency of occurrence (%). The more frequently a given parasite species was observed either in Muuga or Jaagupi, the closer the respective black dot is located to either the “Muuga” or “Jaagupi” label. Points falling along the vertical line denote parasite species which were found in equal frequencies in both localities.

lowest number of infected fish found immediately after winter, and no clear patterns/differences between other seasons. Broadly similar patterns appeared both for the mean infection intensity and species richness (Table 1). Thus, several parasite taxa often found during other seasons were missing in samples collected immediately after winter, such as *Cryptocotyle lingua*, *Cucullanus heterochorus*, *Pomphorhynchus laevis*, *Trichodina domerguei* and *Tylodelphys clavata* (Table S1).

Both localities displayed very similar patterns of occurrence frequency for different parasite taxa. Both had a few parasite taxa which were specific to only one locality and five parasite taxa that occurred more frequently in a given locality (for species details see Table 2). In addition, both localities shared several parasites with almost equal infection levels (see vertical line on Figure 3B).

Factors affecting parasite infection

Binomial regression of the probability of infection identified the season, sex and total body length as significant predictors, but not the area of sampling (Table 3). To interpret the output of logistic regression, the slope (estimate) values were back transformed by taking the exponent; the resulting value quantified the change in the odds ratio of the infection probability as a response to a unit change in the explanatory variable. Hence, any positive slope coefficient means an increase in the proportion (however small the increase is), and any negative coefficient indicates a decrease in proportion. Probability of infection was lowest in winter (close

Table 3. Summary of the modeling. In both models, season was included as a categorical variable, with winter as the base level, so the effect of other seasons is given in contrast to winter. Sex was also included as a categorical variable, with female as the base level.

Model 1: probability of infection

glm(formula = infected ~ as.factor(season) + total body length + as.factor(Sex),
family = binomial(link = "logit"))

Coefficients:

	Estimate	Std. Error	z value	p-value
(Intercept)	-4.70	1.31	-3.60	< 0.01
Spring	1.41	0.51	2.78	< 0.01
Summer	1.60	0.69	2.34	< 0.05
Autumn	2.88	0.86	3.36	< 0.01
Total body length	0.37	0.01	3.95	< 0.01
Sex: male	-1.19	0.45	-2.67	< 0.01

Null deviance: 194.70 on 183 degrees of freedom.

Residual deviance: 138.77 on 178 degrees of freedom.

Model 2: infection intensity

lm(formula = number of parasites ~ species richness + total body length + season,
weights = 1/number of parasites)

Coefficients:

	Estimate	Std. Error	z value	p-value
(Intercept)	-6.63	1.81	-3.66	< 0.01
Spring	3.67	0.33	11.11	< 0.01
Summer	0.03	0.01	2.38	< 0.05
Autumn	0.27	0.63	0.43	0.67
Total body length	2.67	0.86	3.10	< 0.01

Residual standard error: 1.496 on 136 degrees of freedom

Adjusted R-squared: 0.578

to 0), and 4, 5 and 17 times higher in spring, summer and autumn, respectively. Infection probability was also much lower for males than females (the probability of a male being infected was 3 times lower than that of a female), and increased with the total body length of fish by 1.44 times with every added cm.

The quantitative model (Table 3) further revealed that among the infected fish, infection intensity was positively linked to parasite species richness with each additional parasite species increasing the overall infection intensity by 3.7 individuals on average. Further, it was established that one parasite individual was added with each 25 mm increase in total body length, and infection intensity was on average 2.7 individuals higher in summer and autumn than in winter and spring.

Discussion

In this study we examined the parasite communities of the round goby *Neogobius melanostomus* in two distinct locations in the northern Baltic Sea characterised by different invasion trajectories. We found a very rich parasite community (at least 24 species) consisting solely of native species. It appeared there were only marginal differences between the well-established population in Muuga and the population which is currently at the establishment phase near Jaagupi. While the infection intensity corroborated several previous findings in the Baltic Sea (Herlevi et al. 2017;

Kvach et al. 2017; Rolbiecki 2006; Kvach and Skóra 2007), the independence of parasitic infection from invasion history contradicted earlier research on this fish. Prior work established that parasite species richness and abundance in the non-native goby were associated with the time of introduction. Specifically, within 15 years of introduction to the Great Lakes region, parasite abundance and richness of the round goby had more than doubled, and the number of parasite species had increased to levels typical of indigenous fish (Gendron et al. 2012). Also, species richness increased by three times (from 4 to 12 species) within two years in the Gulf of Gdansk after about a decade since introduction (Kvach and Skóra 2007). This published evidence clearly stresses the importance of taking a short-term perspective on species introductions for studies focusing on parasite – non-native species interactions. However, despite the fact that many generalist parasites can adapt to utilize novel hosts very quickly, temporal scales of much longer than one decade should also be considered. Indeed, as host-parasite adaptation occurs across evolutionary time-scales (Lively and Dybdahl 2000), individual case studies performed so far indicate that generalizations should be avoided, and only tentative patterns and principles about hosts as aliens can be outlined (Taraschewski 2006).

There are at least two general patterns that characterize the parasite community of the round goby in its invaded range. First, non-native parasites with complex life cycles that use the goby as final hosts were either not introduced into the new area or were unable to complete their life cycles there (Kvach and Skóra 2007; Ondračková et al. 2015). As it has been suggested that the fish was introduced into the Baltic Sea in the egg or larval stage (Sapota and Skóra 2005), the introduction of host-specific non-native parasites appears unlikely. The second general pattern is that the parasite community of the introduced round goby appears to be dominated by a very few species. These include the acanthocephalan *Pomphorhynchus tereticollis* (Rudolphi, 1809) in the Elbe River (Kvach et al. 2017), *D. spathaceum* and *C. concava* in Puck Bay (Kvach and Skóra 2007), *Anguillicola crassus* (Kuwahara, Niimi and Itagaki, 1974) and *D. spaethacum* near Hel (Kvach and Skóra 2007), *Hysterothylacium aduncum* (Rudolphi, 1802) and *A. crassus* in the Vistula lagoon (Rolbiecki 2006), *P. laevis* in the Rhine River (Ondračková et al. 2015) and *P. laevis* and *D. spathaceum* in Klaipeda Strait (Rakauskas et al. 2008). Similar patterns were observed in this study, with a very strong dominance of basically one species—*D. spathaceum*—in the parasitofauna.

In its native range in the Black Sea and Sea of Azov, a total of 71 and 43 parasite species, respectively, have been recorded in the round goby (Rolbiecki 2006 and references therein). In the Baltic Sea, the total number of parasites recorded so far is 34, with the highest total number found in the Vistula Lagoon and delta (22 species; Herlevi et al. 2017 and references therein). In terms of mean infection intensity, most values in the native

Black Sea and invaded range (incl. our study) remained below 10 parasites per infected fish. However, a few deviations have been observed. For instance, the round goby was over 30 times more infected with a few common parasite species, including *C. concava* and *C. lingua*, in its native range (Kvach 2005) than we found in this study. Also, the mean infection intensity of *C. concava* and *D. spathaceum* in the round goby in the Gulf of Gdansk was substantially higher than in our study (around 14 and 3 times, respectively; Kvach and Skóra 2007). A similar pattern emerged from comparison of the mean intensity of *Pomphorhynchus* sp. infection of the fish in the newly colonised site in the Elbe River, which was over 5 times higher (Kvach et al. 2017) than we found in the NE Baltic Sea. Although we have not calculated total parasite abundance in our study, the mean values recorded for both native and non-native areas of the Danube River for autumn (100.7 and 79.3, respectively; Ondračková et al. 2010) appeared to be several times higher than the corresponding value in our study (ca. 12 parasites per fish).

As mentioned above, the parasite community of the round goby in our study appeared to be very rich, with a total of 24 parasite species recorded. Broadly similar results were obtained in studies performed in the Vistula Lagoon (20 parasites; Rolbiecki 2006) and the Danube River (16; Ondračková et al. 2010). However, the parasite richness of the round goby has been low in many other studies conducted in both freshwater and marine environments (e.g. 3 taxa in the Rhine River (Emde et al. 2014), 3–4 taxa per location in various localities of the Baltic Sea (Herlevi et al. 2017), 7 in the upper Elbe River (Kvach et al. 2017), and 7 in Klaipeda Strait (Rakauskas et al. 2008)). While infection with 7–9 parasite species shortly after introduction is characteristic of the invasive *Neogobius* genus (Ondračková et al. 2010), the round goby has been present for around a decade in some of study locations listed above. However, the sample size of fish in these studies differed by over 10 times (from 41 to 486). As none of these studies constructed species accumulation and species richness estimator curves (to analyse whether the sample size was sufficient to assess the total species richness; Blakeslee and Byers 2008), the reliability and certainty of these results cannot be estimated or compared. In fact, two studies suggested the possibility that rare species might not have been found due to small sample sizes (Kvach and Skóra 2007; Herlevi et al. 2017). However, based on our results, we can conclude that our sample size of 184 fish is slightly but insignificantly underestimating the overall parasite species richness.

Final hosts may influence the host-parasite dynamics of *N. melanostomus* in its introduced range (Emde et al. 2014). For instance, several fish-eating birds (such as gulls and terns) are definitive hosts of the trematodes *Cryptocotyle* spp., *Diplostomum* spp. and *T. clavata* (Valtonen et al. 2001; Zander and Reimer 2002), and these bird species are currently very abundant in our study region. This is the likely reason for the high

prevalence/intensity rates of these trematodes. The fact that we did not detect *Anguillicoloides crassus*, for which the round goby serves as a paratenic host and which has been found in the fish in other areas of the Baltic Sea (Rolbiecki 2006; Kvach and Skóra 2007; Kvach et al. 2017), may be the result of stock depression in the definitive host of *A. crassus* – the European eel *Anguilla anguilla* (Linnaeus, 1758) (ICES 2018a).

For three parasites—the nematode *C. osculatum* and the two acanthocephalans *C. semerme* and *C. strumosum*—seals act as the primary definitive host in the Baltic Sea (Valtonen et al. 2001). Importantly, grey seals have recently been shown to consume the round goby (Scharff-Olsen et al. 2019), and seals are currently relatively abundant in the region after recovering from a deep depression (ICES 2018b). Thus, the round goby likely acts as an additional/alternative paratenic host for those three parasite taxa and facilitates the completion of their life cycles in the Baltic Sea.

Salinity is important for the presence of parasites. Given the geographic location of both study areas (low-salinity conditions in the NE Baltic Sea), a few brackish species including *D. spathaecum*, *C. concava* and *T. clavata* were amongst the most dominant in terms of either prevalence or infection intensity. However, several marine parasites (e.g., the nematodes *C. osculatum*, *C. heterochorus* and the acanthocephalans *C. semerme*, *C. strumosum* and *E. gadi*) were also present. In addition, we found a few species of freshwater origin, including the trematode *B. luciopercae* which requires a freshwater bivalve (*Dreissena polymorpha* (Pallas, 1771)) as an intermediate host and the nematode *C. lacustris* which uses cyclopoid copepods as intermediate hosts. Both of these freshwater parasites have also been found in estuary/lagoon conditions in the southern Baltic Sea (Rolbiecki 2006; Rakauskas et al. 2008).

Seasonal demography of parasite infection of the round goby has received relatively little attention (Ondračková et al. 2015; Kvach et al. 2017), and based on prior investigations no major conclusions can be drawn. While previous work has documented insignificant and/or no seasonal difference in ecological parameters of parasite infection for the round goby between spring and autumn (Ondračková et al. 2015; Kvach et al. 2017), our work points to a distinct seasonal difference in multiple parameters (including probability of infection, prevalence, infection intensity and parasite community richness). While some of the “missing parasites” in winter can be justified (e.g. *T. acuta* and *T. domerguei*, which prefer warm water), we might have simply missed several parasites due to generally lower prevalence/infection intensity in winter (see Table S1). Thus, to better capture the parasite community in winter, a larger sample size compared to other seasons should be secured. The generally lower prevalence/infection intensity in or immediately after winter stresses the importance of diet in shaping the parasitofauna of this fish. We suggest that diet breadth, which is wider for larger than younger individuals (e.g.

Skabeikis and Lesutienė 2015), is likely the main factor contributing to higher parasite diversity in larger fish. However, as it is only the total sample that confidently captures all parasite richness (because the rarefaction threshold was not reached for individual sampling events early in sampling for either locality), results about the seasonal demography of parasite infection should be treated with caution.

Host diet and host-parasite compatibility both contribute to the distribution of parasites in the fish community (Lagrue et al. 2011). Molluscs serve as first intermediate hosts for trematodes. Molluscs are very abundant in our study area and serve as important prey for the round goby (e.g. Järv et al. 2011; Skabeikis and Lesutienė 2015), which likely contributes to the frequently high prevalence and rate of infection by trematodes in the round goby. However, it should be noted that the infection of the fish by some flukes, e.g. *Diplostomum* spp. and *Tylodelphys clavata*, is a result of direct physical contact with parasite larvae rather than prey consumption (e.g. Barber et al. 2000 and references therein). Several amphipod species, which serve as the intermediate hosts of acanthocephalans, are readily available to the fish in the study area (e.g. Järv et al. 2011) and are actively consumed by the round goby both in the field (e.g. Skabeikis and Lesutienė 2015) and under experimental conditions (Nurkse et al. 2016). Thus, the finding of five acanthocephalan taxa in the round goby, one of which (*C. strumosum*) had the highest infection intensity we recorded (7.2), is unsurprising. Similarly, because the round goby is a benthic feeder, the importance of parasites that use planktonic crustacean copepods as intermediate hosts (e.g. the cestode *Proteocephalus* spp. and the nematodes *C. lacustris* and *D. minutus*) is rather low. However, juvenile round goby actively prey on copepods, and larger goby may consume planktivorous fish (Skabeikis and Lesutienė 2015). In addition, our as-yet unpublished research confirms that adult round goby can also directly consume copepods (K. Nõomaa *unpubl. data*). Prey composition of the round goby in the area (Järv et al. 2011) might also explain the rarity of the nematodes *E. exciscus* and *E. mergorum*, which use oligochaetes and chironomids as first intermediate hosts.

It is well-established that macrozoobenthic communities and the abundance and biomass of taxa vary at both temporal (season, year) and spatial scales. In addition to climate and multiple anthropogenic factors, predation by the round goby can result in the depletion of dominant prey species, thereby leading to drastic changes in the system (e.g. Skabeikis et al. 2019). Changes in available prey will ultimately affect the parasite community of the fish. Thus, a detailed interpretation of the presence and dynamics of different parasites requires detailed information on available prey populations and goby diet. In addition, the food web positioning of the fish might be site-specific (Herlevi et al. 2018), and this might vary over time (dependent on prey availability). The situation is further complicated

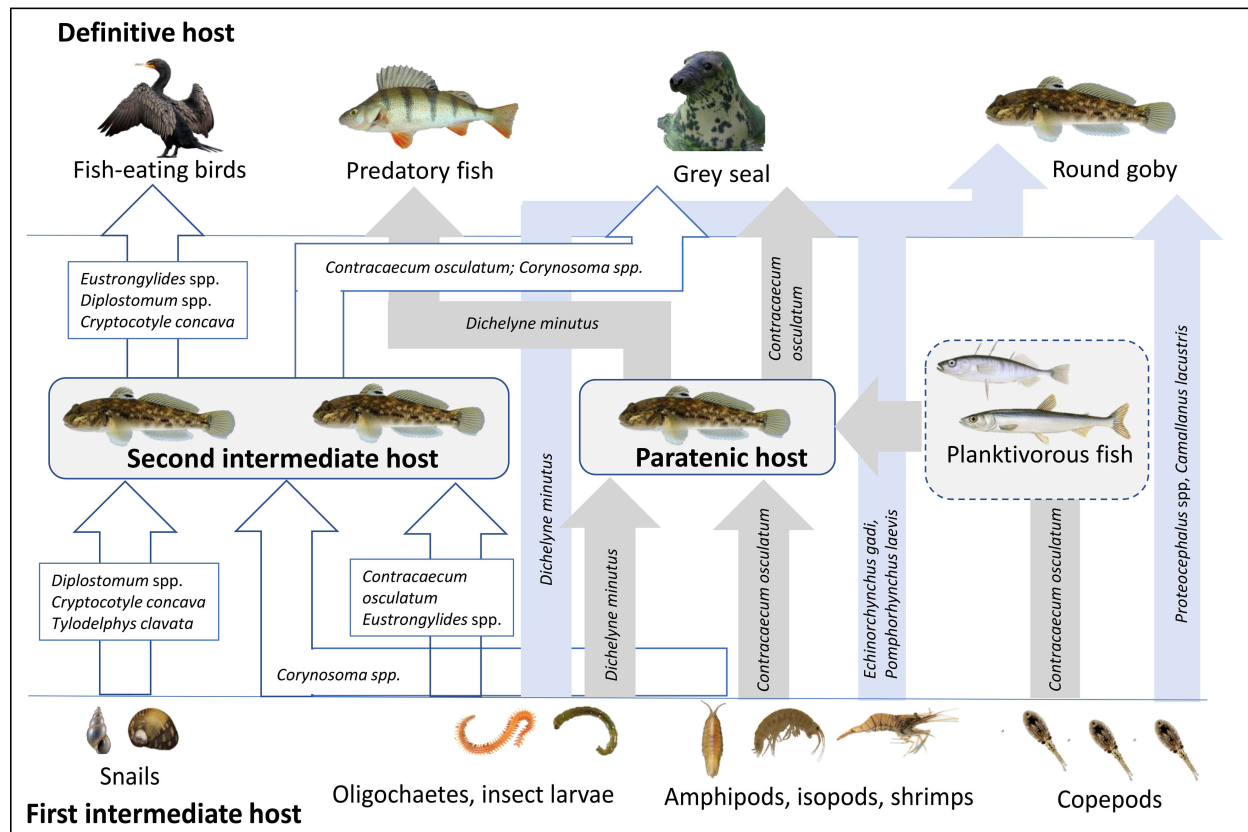


Figure 4. The role of the round goby *Neogobius melanostomus* in the transfer of parasites in the Baltic Sea (Kvach and Skóra 2007 updated), together with examples of parasites found in the current study for each transfer pathway. The infection of the round goby by *Trichodina* spp., *Diplostomum* spp., *Cryptocotyle concava* and *Tylodelphys clavata* is not directly through prey consumption but results from physical contact with parasite larvae released into the sea by their intermediate hosts (marine invertebrates).

by the fact that the round goby can migrate substantial distances (a few kilometres per day; K. Nõomaa *unpubl. data*) and thus can potentially consume prey far from where it is sampled. Thus, it is unlikely that we can explain the presence of all parasites in the fish, as substantial uncertainty is inherent in these studies.

Based on the findings of this study, and considering previous work on parasite-host relationships in the Baltic Sea and beyond (e.g. Kinne 1984; Bauer 1987; Valtonen et al. 2001; Zander and Reimer 2002; A. Turovski *unpubl.*) and on the food-web interactions of the round goby in various parts of the Baltic Sea (e.g. Rakauskas et al. 2008; Järv et al. 2011; Skabeikis and Lesutienė 2015, 2019; Herlevi et al. 2018; Scharff-Olsen et al. 2019; K. Nõomaa *unpubl.*), we have extended a schematic diagram on the role of the round goby in parasite life cycles and transfer in the system. This diagram does not necessarily illustrate the transfer pathways of all parasites either occurring in the system or infecting the round goby, but rather focuses on the role of the fish in parasite life cycles and transmission. It appears that in addition to previous knowledge (Kvach and Skóra 2007), this system also involves copepods as first intermediate hosts and seals as definitive hosts (Figure 4). Thus, the introduction of the round goby has resulted in additional or alternative pathways of parasite transmission in the Baltic Sea, likely affecting the parasite communities of definitive hosts in the system.

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Supplementary material

The following supplementary material is available for this article:

Table S1. Seasonal variation in parasite prevalence (%) in the round goby *Neogobius melanostomus* in Muuga and Jaagupi.

This material is available as part of online article from:

http://www.reabic.net/aquaticinvasions/2020/Supplements/AI_2020_Ojaveer_etal_SupplementaryTable.xlsx