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Aggregation patterns of helminth populations in the introduced fish, *Liza haematocheilus* (Teleostei: Mugilidae): disentangling host–parasite relationships

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ABSTRACT

A number of hypotheses exist to explain aggregated distributions, but they have seldom been used to investigate differences in parasite spatial distribution between native and introduced hosts. We applied two aggregation models, the negative binomial distribution and Taylor's power law, to study the aggregation patterns of helminth populations from *Liza haematocheilus* across its native (Sea of Japan) and introduced (Sea of Azov) distribution ranges. In accordance with the enemy release hypothesis, we predicted that parasite populations in the introduced host range would be less aggregated than in the native host area, because aggregation is tightly constrained by abundance. Contrary to our expectation, aggregation of parasite populations was higher in the introduced host range. However, the analyses suggested that the effect of host introduction on parasite aggregation depends on whether parasite species, or higher level taxonomic groups, were acquired in or carried into the new area. The revealed similarity in the aggregation parameters of co-introduced monogeneans can be attributed to the repeatability and identity of the host–parasite systems. In contrast, the degree of aggregation differed markedly between regions for higher level taxa, which are represented by the native parasites in the Sea of Japan versus the acquired species in the Sea of Azov. We propose that the host species plays a crucial role in regulating infra-population sizes of acquired parasites due to the high rate of host-induced mortality. A large part of the introduced host population may remain uninfected due to their resistance to native naïve parasites. The core concept of our study is that the comparative analysis of aggregation patterns of parasites in communities and populations, and macroecological relationships, can provide a useful tool to reveal cryptic relationships in host–parasite systems of invasive hosts and their parasites.

1. Introduction

Biological invasions have received increasing attention over the past decades as they represent a major threat to biodiversity and an important element of global environmental change (Dukes and Mooney, 1999; Simberloff, 2013). Invasive species may affect native populations and communities through different mechanisms including competition, predation, habitat alteration and changes in disease dynamics, while parasites play important roles in mediating such effects (Lymbery et al., 2014). For instance, escape from the effects of parasites is a frequent explanation given for the success of an introduced species (Keane and Crawley, 2002; Torchin and Lafferty, 2009). However, despite considerable research effort, many aspects of the host–parasite relationships and parasite spatial distribution related with species translocation remain poorly understood (Lymbery et al., 2014; Sarabeev, 2015a; Keogh et al., 2017; Sarabeev et al., 2018).

Abundance–variance (AVR) and abundance–occupancy (AOR) relationships are two of the most general macroecological patterns that describe the spatial distribution of free-living and parasitic species in populations and communities (Morand and Guégan, 2000; Gaston et al., 2006; Morand and Krasnov, 2008; Pérez-del-Olmo et al., 2011). The rationale is that the local abundance of a given species is expected to be positively related to its variance (AVR), and its probability of occurrence (i.e. prevalence) (AOR) (Gaston et al., 2006). AORs and AVRs have important implications in biological invasion theory because they may help in understanding the spatial distribution of invasive species within ecosystems (Gaston et al., 2000, 2006; Rigal et al., 2013). Sarabeev et al.

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(2018) examined AORs for helminth parasite populations of the introduced so-iuy mullet, *Liza haematocheilus* (Temminck & Schlegel), across its native and introduced distribution range in the Sea of Japan and the Azov Sea, respectively. The study showed that the AOR model fits the parasite data extremely well, irrespective of whether the parasite species are native or invasive. However, acquired parasite species, in contrast to co-introduced, use only a small portion of the introduced host population. Therefore, invasive and co-introduced parasite species can be separately identified based on their AORs (Sarabeev et al., 2018).

However, the AVR of this host–parasite system still remains to be explored. The AVR depends on the spatial distribution of parasite infra-populations among sampled hosts. In a Poisson (random) distribution, the variance theoretically equals the mean; whereas in aggregate distributions, often described by a negative binomial distribution (NBD), the variance increases more rapidly than the mean but less than the squared mean. Thus aggregation can be described by a Taylor's power law, in which the variance is proportional to a fractional power of the mean (Pérez-del-Olmo et al., 2013). In fact, the dispersion parameters *k* of the NBD and *b* of the Taylor's power law have been the most intensively used measures of parasite aggregation in epidemiological and evolutionary ecological studies of parasites (reviewed by Wilson et al., 2002; Morand and Krasnov, 2008; Pérez-del-Olmo et al., 2013). The distribution of parasite infra-populations in host individuals is typically highly skewed to the right, with most individuals harbouring low numbers of parasites, while a few individuals host many (Anderson and Gordon, 1982; Shaw and Dobson, 1995; Poulin, 2013). Recently, application of AVR in parasitological and epidemiological studies has received much attention, as comparative data on aggregation patterns offer a powerful tool in understanding regulation processes and epidemiological features (Keeling and Grenfell, 1999; Krasnov et al., 2006b,c; Morand and Krasnov, 2008; Sarabeev et al., 2017a). However, we still know very little about aggregation patterns of parasite populations from introduced hosts (Sarabeev et al., 2017b). A number of hypotheses exist to explain aggregated distributions, but those have not been frequently investigated to explain the differences in parasite spatial distribution between native and introduced hosts (Hodasi, 1969; Hudson et al., 1992; Poulin and Morand, 2000; Newey et al., 2005; Krasnov et al., 2006c; Pérez-del-Olmo et al., 2011; Poulin, 2013; Sarabeev, 2015a; Sherrard-Smith et al., 2015).

According to the concept introduced by Kilpatrick and Ives (2003) and Ma (2015), our recent studies of aggregation patterns in introduced and native fish hosts have been carried out at the community level (Sarabeev et al., 2017a,b). We found that the aggregation pattern in communities for the acquired higher level taxonomic groups (acanthocephalans, adult and larval digeneans) tended to be lower in the introduced fish population than for those in native fish, whereas the level of aggregation of the co-introduced group (monogeneans) was similar in native and introduced fish. However, the effect of host introduction on aggregation of the parasite populations was not considered in these studies. Here, we will study the spatial distribution pattern of the single-species populations (i.e. population abundance distribution) of helminth parasites of the introduced host across localities and seasons/years as opposed to the multi-species distribution pattern analysis of parasites in a single host individual or host sample (i.e. species abundance distribution) performed by Sarabeev et al. (2017b).

We applied two aggregation models, NBD and Taylor's power law, to study the aggregation patterns of helminth species in populations from *L. haematocheilus* across its native and introduced distribution range. According to the enemy release hypothesis (ERH), which predicts that in a new environment an introduced host population lacks natural enemies such as pathogens, parasites and predators (Keane and Crawley, 2002; Torchin and Lafferty, 2009), we expect that the level of helminth aggregation would be lower in the introduced host population relative to the native host population, because aggregation is tightly constrained by abundance (Poulin, 2013). Considerable reductions in parasite infection parameters (i.e., parasite escape) have been documented for the introduced population of the so-iuy mullet in the Azov Sea, thereby lending support to the ERH (Sarabeev et al., 2017b, 2018). However, the high abundance and prevalence of co-introduced parasites and rich helminth species diversity have been reported in *L. haematocheilus* from the new distribution range (Sarabeev, 2015b, 2018), which suggests that patterns observed for the studied host–parasite associations are far from universal. Therefore, our second hypothesis is that, according to the single-species population model considering aggregation as an evolutionary property and species-specific feature (Taylor, 1961; Krasnov et al., 2006b; Pérez-del-Olmo et al., 2011), aggregation patterns of highly host-specific parasites, which were carried to the new distribution range, will remain unchanged. Finally, we propose that, analogous to parasite population distribution in the abundance–occupancy plot for the introduced host (Sarabeev et al., 2018), the difference in parasite spatial distribution will be also detectable by comparison of the AVRs.

In the present study, the population abundance distribution of helminth parasites across the native and introduced ranges of *L. haematocheilus* is examined with the aim of discovering host–parasite relationships and testing the ERH. Interregional variations in aggregation parameters of helminth populations were assessed here to compare the spatial distribution of parasites from the so-iuy mullet across its native and introduced distribution ranges. We are particularly interested in establishing whether co-invasive and acquired parasite species differ in their AVRs, in order to gain insight on how parasite species from different origins use introduced hosts. According to Krasnov et al. (2006c) and Pérez-del-Olmo et al. (2011), we evaluate interspecific variations in both measured parameters of population aggregation among species, addressing the question of whether *k* and *b* are true characters of species and higher level taxonomic groups. Given that estimators of aggregation can be significantly biased by host sample size (HSS), prevalence and abundance (Wilson et al., 2002; Lloyd-Smith, 2007), the effects of these factors on *k* and *b* are also evaluated here.

2. Materials and methods

2.1. Materials

The present study is based on the same host–parasite database used by Sarabeev et al. (2018). It comprises 336 population samples from 40 helminth species, including 124 samples from the Sea of Japan, and 212 from the Sea of Azov.

2.2. Data analysis

Two measures to quantify aggregation of the helminth populations in the fish host, *L. haematocheilus*, were used: exponent *k* of the NBD and the slope *b* of Taylor's power law. Because the NBD and Taylor's power law models cover a wide range of parasite distributions and supplement each other (Wilson et al., 2002; Morand and Krasnov, 2008; Pérez-del-Olmo et al., 2013), we argue that the use of *k* and *b* is not redundant, but provides a more complete picture about dispersion patterns of parasites. The former was estimated by maximum-likelihood, because it has been shown to be more accurate than other methods (Gregory and Woolhouse, 1993; Lloyd-Smith, 2007). A web-based tool provided by Reiczigel and Rózsa (http://www.zoologia.hu/qp/) was used to compute *k* and its associated χ^2 *P* value, determining whether or not the parasite data fit a NBD. When *k* is large (>~20), the distribution approaches a Poisson distribution, and as *k* gets smaller, species aggregation increases (Wilson et al., 2002). For most macroparasite species of wildlife hosts, *k* is less than 1 (Shaw and Dobson, 1995).

A bootstrapping technique developed by Boag et al. (2001) was used to calculate *b*, its associated S.D. and the coefficient of determination (R^2) of the model was used here with a slight modification. This technique provides accurate estimates of Taylor's power law parameters for each host sample. Differing from Boag et al. (2001) and Sherrard-Smith et al. (2015), higher numbers of bootstrap samples and replications were used, which yield more stable parameters from calculation to calculation. In the present study, 100 parasite infra-populations were sampled with replacement to obtain the variance-mean pair. In other words, Monte Carlo simulations were performed to model samples of helminth parasites by applying the extraction of many samples with replacement from the original sample, each much larger than the original dataset. This was repeated 500 times to estimate *b* and its associated statistics calculated from the linear regression of log (variance + 1) onto log (mean + 1). The bootstrapping technique was performed with the package 'boot' (https://cran.r-project.org/web/packages/boot/) in R. The expectation for Taylor's power law for variation between generated parasite populations is that the slope of the log variance versus log mean abundance ranges between 1 and 2 (Krasnov et al., 2006b,c). The fit of the data to the power model was assessed using the coefficient of determination (R^2).

The raw measures of aggregation parameters on parasite population samples and their associated statistics are provided in Supplementary Table S1 (Mendeley Data, DOI: 10.17632/fcngmddspx.1). The mean of *k* and *b* was calculated as an overall average of the species and taxonomic groups of species' *k* and *b* across distinct fish population samples. For each species and groups, we calculated mean *k* and *b*.

Interspecific variations in aggregation parameters among helminth species were tested with one-way ANOVA with 'species' as the testing factor. This test addresses the question of whether prevalence, abundance and aggregation parameters are true species characters. A significant effect of helminth species would result from repeatable within-species levels of infection and aggregation indices (Arneberg et al., 1997; Krasnov et al., 2006a; Pérez-del-Olmo et al., 2011). The repeatability analysis was also performed across five higher taxa. Moreover, one-way ANOVA was applied to test the effect of host introduction on aggregation parameters of helminth parasite species and higher level taxonomic groups. The sequential Holm-Bonferroni correction was applied to counteract the problem of multiple comparisons (Holm, 1979). A correction factor was used to compare higher level taxonomic groups and species which occurred in both regions (smallest P value = 0.05/4 = 0.0125 and 0.05/6 = 0.008, respectively).

Pearson's correlation coefficient (r) was used to test the relationship between host sample size (HSS), prevalence and mean abundance with *k* and *b*. Because values of *k* did not fit normal distributions (Kolmogorov–Smirnov test for one sample), log transformations were applied before ANOVA to conform to assumptions of normality. The ANOVAs were carried out with PAST v3.06 (https://folk.uio.no/ohammer/past). A significance level of 0.05 (two-tailed) was set for all statistical tests.

3. Results

3.1. Repeatability analysis and relationships between host sample size, prevalence, mean abundance and aggregation indices

Table 1 shows for each region (native and introduced) the mean, S.D. and range, accompanied by the numbers of localities and samples of *k* and *b* estimates for each species based on raw data (Supplementary Table S1, Mendeley Data, DOI: 10.17632/fcngmddspx.1). Although values of both aggregation indices varied considerably among samples within each region, their mean across populations revealed differentiation of species. This variation was not random with respect to the factor 'species', which had a significant effect on *k* and explained a significant part of its variation with a high percentage of variation among species (59% and 55% for the Sea of Japan and Azov Sea, respectively). Similarly, values of *b* estimated for helminth populations from the introduced host were also significantly affected by the factor 'species', but only 21–25% of the variation in *b* among samples was associated with differences among species (Table 2). Both parameter measures of aggregation, *k* and *b*, were also repeatable across helminth higher taxa. The percentage of variation among samples accounted for by differences among helminth taxa, as opposed to within taxa, was higher for the factor 'species' compared with higher taxa (Table 2).

There were weak but significant correlations between the HSS and both aggregation parameters, except in *k* from the Sea of Japan (r = 0.07, P = 0.48) (Supplementary Table S2 Mendeley Data, DOI: 10.17632/fcngmddspx.1). There were no significant relationships between the prevalence and *b* for any of the studied datasets. The correlation between the mean abundance and *b* for helminth populations from the Sea of Japan was not significant, while a weak but significant correlation was observed between these parameters from the Azov Sea. Pearson's correlations indicated that the prevalence and the mean abundance were highly and moderately correlated with *k*, respectively.

3.2. Regional variation in helminth aggregation

The Taylor's power function fit well with simulated values of the population variance-mean pair, as indicated by the high value of the coefficients of determination (between 0.5 and 1.0) (Supplementary Table S1, Mendeley Data, DOI: 10.17632/fcngmddspx.1). The slope *b* ranged between 0.6 and 4.6 with an average of 1.91 across all 336 samples. The standard errors of *b* were also small with an average of 0.032. Values of exponent *k* exhibited larger variation, ranging from 0.003 to 2.706. The degree of aggregation calculated was large: 288 of 293 estimates of *k* were less than 1, and 287 of 336 estimates of *b* were significantly higher than 1 (Supplementary Table S1, Mendeley Data, DOI: 10.17632/fcngmddspx.1). Although both random and highly aggregated distributions were observed among helminth populations within each region, the overall aggregation level tended to be significantly higher (Table 3) in the Azov Sea (the range of *k* and *b*-values were 0.003–2.706 and 0.71–4.56, with an average of 0.190 and 1.98, respectively) than in the Sea of Japan (k = 0.014–1.367, 0.235 and b = 0.56–3.3, 1.78). This is despite the fact that the population abundance distribution was close to a random distribution (*b* did not significantly deviate from 1 (Supplementary Table S1 Mendeley Data, DOI: 10.17632/fcngmddspx.1)) in most samples of *Solostamenides* sp. 1, *Haplosplanchnus pachysomus*, *Contracaecum* sp. 1 and *Neoechinorhynchus (Neoechinorhynchus) personatus* from the Azov Sea (Table 1). The introduced host was rarely infected by these four species, their abundance ranging from one to four per sample.

The estimated values of *k* did not show significant regional differences among higher taxonomic groups of helminth parasites. The highest aggregation level in both regions was found for adult digeneans, the lowest one for monogeneans. In contrast, the slope *b* exhibited significant regional differences among higher taxonomic groups, with the lowest aggregation level of larval digeneans in the native range of *L. haematocheilus* and the highest in its introduced range. Instead, acanthocephalans were the most aggregated groups in the former, and the lowest in the later (Fig. 1).

Table 1
Summary statistics describing two measures of aggregation of parasitic helminths, exponent *k* of the negative binomial distribution (NBD) and slope *b* of Taylor's power law, for samples of *Liza haematocheilus* examined from three and six localities in the Sea of Japan and the Azov Sea, respectively.

Helminth	The Sea of Japan							The Sea of Azov						
	No. of localities/samples	*k* of the NBD			*b* of Taylor's law			No. of localities/samples	*k* of the NBD			*b* of Taylor's law		
		Mean	S.D.	Range	Mean	S.D.	Range		Mean	S.D.	Range	Mean	S.D.	Range
MONOGENEA														
Gyrodactylus mugili	1/2	0.065	0.066	0.019–0.112	2.15	0.32	1.92–2.38	4/9	0.039	0.049	0.006–0.149	2.43	1.09	1.10–4.04
Gyrodactylus zhukovi	1/2	0.048	–	–	1.26	1.00	0.56–1.97	3/5	0.036	0.037	0.013–0.102	1.99	0.43	1.54–2.70
Ligophorus kaohsianghsieni	3/7	0.128	0.054	0.062–0.200	1.93	0.41	1.52–2.57	6/13	0.192	0.258	0.004–0.891	1.79	0.88	0.75–3.14
Ligophorus llewellyni	3/8	0.528	0.197	0.297–0.887	2.05	0.51	1.51–2.90	6/14	0.504	0.319	0.272–1.550	2.10	0.38	1.36–2.79
Ligophorus pilengas	3/8	0.491	0.294	0.190–0.938	1.68	0.39	1.00–2.39	6/14	0.567	0.183	0.409–1.092	2.02	0.46	1.27–2.88
Ligophorus triangularis	3/8	0.230	0.104	0.034–0.341	1.67	0.31	1.41–2.38							
Ligophorus miroshnichenki	3/8	0.249	0.090	0.116–0.377	1.77	0.39	1.18–2.35							
Solostamenides sp. 1	3/5	0.021	0.007	0.015–0.028	1.77	0.85	0.94–2.82	4/7	1.275	–	–	1.05	0.34	0.87–1.82
DIGENEA (adults)														
Dicrogaster contracta								6/14	0.078	0.052	0.016–0.183	2.02	0.72	0.86–3.12
Platydidymus flecterotestis	3/8	0.202	0.056	0.114–0.313	1.53	0.31	1.14–1.93							
Pseudohapladena mugili	3/8	0.143	0.082	0.068–0.325	1.54	0.25	1.16–1.86							
Saccocoelium sp. 1								1/2	0.082	–	–	1.74	1.12	0.95–2.53
Saccocoelium obesum								5/9	0.081	0.109	0.013–0.336	2.09	0.69	0.94–2.88
Saccocoelium tensum								6/14	0.126	0.079	0.020–0.330	2.09	0.42	1.45–2.98
Lecithobotrys putrescens								1/1	0.042	–	–	2.73	–	–
Haplosplanchnus bivitellosus	3/7	0.108	0.137	0.014–0.319	1.78	0.77	0.89–2.67							
Haplosplanchnus sp. 1	1/3	0.037	0.014	0.021–0.046	2.30	0.30	1.98–2.59							
Haplosplanchnus pachysomus								2/3	0.028	–	–	1.23	0.46	0.95–1.76
Schikhobalotrema sparisoma								2/3	0.029	0.037	0.003–0.055	2.70	1.80	0.95–4.56
Saturnius dimitrovi								6/14	0.133	0.220	0.015–0.870	1.92	0.60	1.18–3.12
Saturnius minutus								6/13	0.040	0.027	0.010–0.106	2.08	0.80	0.71–3.45
Saturnius overstreeti	2/2	0.037	–	–	1.84	1.55	0.75–2.94							
Saturnius papernai								4/11	0.084	0.094	0.012–0.305	2.28	0.79	1.27–3.76
Lecithaster galeatus								6/10	0.097	0.086	0.020–0.239	2.48	0.96	0.95–3.95
Lecithaster sp.	3/5	0.033	0.033	0.014–0.072	1.49	0.51	0.94–1.99							

Table 1 (*continued*)

Helminth	The Sea of Japan							The Sea of Azov						
	No. of localities/ samples	*k* of the NBD			*b* of Taylor's law			No. of localities/ samples	*k* of the NBD			*b* of Taylor's law		
		Mean	S.D.	Range	Mean	S.D.	Range		Mean	S.D.	Range	Mean	S.D.	Range
DIGENEA (larva)														
Stephanostomum sp	2/2	0.018	–	–	1.66	1.03	0.94–2.39							
Diplostomum spp								5/12	0.138	0.238	0.007–0.780	2.20	0.93	0.86–3.44
Posthodiplostomum brevicaudatum								3/5	0.039	0.033	0.009–0.080	2.36	0.75	1.55–3.23
Tylodelphys clavata								1/3	0.018	0.006	0.014–0.022	2.13	1.11	0.86–2.92
Timoniella imbutiforme								1/2	0.052	0.007	0.047–0.057	2.07	0.10	2.00–2.14
Ascocotyle (*Phagicola*) *longa*								5/11	0.340	0.787	0.029–2.706	1.99	0.60	0.92–2.83
Heterophyidae gen. sp. 1	3/8	0.335	0.198	0.071–0.623	1.27	0.30	0.78–1.72							
Heterophyidae gen. sp. 2	2/3	0.122	0.115	0.018–0.247	1.76	0.55	1.35–2.38							
Cardiocephalus longicollis								3/3	0.020	0.007	0.014–0.028	2.36	0.62	1.76–2.99
NEMATODA														
Contracaecum sp. 1 (larva)								5/9	0.150	0.147	0.045–0.254	1.03	0.28	0.73–1.66
Cucullanus mugili	3/8	0.249	0.185	0.035–0.633	1.78	0.49	1.34–2.81							
Philometra biglobocerca	3/6	0.154	0.098	0.076–0.338	2.22	0.89	1.02–3.30							
ACANTHOCEPHALA														
Neoechinorhynchus (Hebesoma) yamaguti	3/8	0.215	0.114	0.086–0.402	2.13	0.69	1.27–3.22							
Neoechinorhynchus (Neoechinorhynchus) personatus								6/11	0.263	0.258	0.111–0.765	1.32	0.52	0.90–2.39
Neoechinorhynchus (Neoechinorhynchus) tylosuri	3/8	0.350	0.460	0.060–1.367	1.99	0.65	0.77–2.97							

Table 2
Effect of species and higher level taxonomy on aggregation indices, exponent *k* of the negative binomial distribution (NBD) and slope *b* of Taylor's power law, from *Liza haematocheilus* across its native and introduced ranges in the Sea of Japan and the Azov Sea (significant values are indicated in bold).

		k of the NBD					*b* of Taylor's power law			
Factor	R^2	Mean squares	*F*	df	*P*	R^2	Mean squares	*F*	df	*P*
The Sea of Japan										
Species	0.59	0.72	6.89	20, 95	**0.000**	0.21	0.43	1.37	20, 103	0.154
Higher level taxonomy	0.12	0.70	3.61	4, 111	**0.008**	0.09	0.92	2.96	4, 119	**0.023**
The Sea of Azov										
Species	0.55	1.36	7.76	24, 152	**0.000**	0.25	1.30	2.56	24, 187	**0.000**
Higher level taxonomy	0.15	2.28	7.82	4, 172	**0.000**	0.12	3.90	7.30	4, 207	**0.000**

Table 3
Summary of one-way ANOVA of the effect of host introduction on helminth aggregation indices, exponent *k* of the negative binomial distribution (NBD) and slope *b* of Taylor's power law, from *Liza haematocheilus* across its native and introduced ranges in the Sea of Japan and the Azov Sea (significant values are indicated in bold).

Population/species grouping	*k* of the NBD				*b* of the Taylor's power law			
	Mean squares	*F*	df	*P*	Mean squares	*F*	df	*P*
Species occurred in both regions								
Gyrodactylus mugili	0.19	0.70	1, 9	0.424	0.13	0.12	1, 9	0.741
Gyrodactylus zhukovi	0.06	0.43	1, 4	0.548	0.76	2.17	1, 5	0.201
Ligophorus kaohsianghsieni	0.03	0.12	1, 15	0.732	0.09	0.15	1, 18	0.703
Ligophorus llewellyni	0.01	0.31	1, 20	0.582	0.02	0.08	1, 20	0.782
Ligophorus pilengas	0.07	2.04	1, 20	0.169	0.58	3.02	1, 20	0.098
Solostamenides sp. 1	2.45	122.21	1, 2	**0.008**	1.52	4.25	1, 10	0.066
Higher level taxonomy[a]								
Monogeneans	0.14	0.40	1, 96	0.529	0.49	1.18	1, 108	0.279
Adult digeneans	0.52	2.86	1, 110	0.093	4.69	9.09	1, 125	**0.003**
Larval digeneans	2.03	6.40	1, 43	0.015	4.86	10.28	1, 47	**0.002**
Acanthocephalans	0.00	0.01	1, 20	0.942	3.54	9.74	1, 25	**0.005**
Whole helminth community	5.03	17.56	1, 291	**0.000**	3.07	6.15	1, 334	**0.014**

[a] Effect of introduction was not assessed for parasitic nematodes, as they were represented by different stages of the life cycle from different distribution ranges.

3.3. Effect of host introduction on aggregation parameters

Host translocation was not found to significantly affect aggregation parameters of helminth species in both the native and introduced distribution ranges, which were represented by carried monogeneans, except for *k*-values of *Solostamenides* sp. 1 (Table 3), in which the aggregation level was higher in the native host range (Table 1). Similarly, a comparison of the population abundance distribution over all monogeneans did not reveal any significant effect of host introduction on helminth aggregation. By contrast, *b* differed significantly in aggregation patterns between regions in acanthocephalans, adult and larval digeneans. Values of *k* for larval digeneans also showed significant differences in parasite aggregation across native and introduced ranges of the host (Table 3). Application of the Holm-Bonferroni correction of *P* values for multiple comparisons showed no significant effect of region in all cases for *k* in the four compared higher level taxonomic groups. Both indices agreed with each other in revealing higher aggregation levels of adult and larval digeneans in populations for the introduced host, while acanthocephalans showed an opposite pattern of dispersion. According to *b*, aggregation was significantly lower for acanthocephalan populations in the introduced host compared with the native one (Fig. 1). Populations of native naïve parasite species were weakly integrated compared with co-introduced monogenean species in the parasite communities of the introduced host such that they are mostly detectable by the study of the AVR (Fig. 2).

4. Discussion

Although *L. haematocheilus* appears to have lower infection parameters in the introduced host (Sarabeev, 2015b; Sarabeev et al., 2017b, 2018), the present results suggest that aggregation of helminth populations is higher in the introduced range. This observation rejects our first hypothesis assuming lower parasite population aggregation in the introduced hosts than in the native one. Thus, despite the positive relationships between aggregation and infection parameters (Poulin, 2013 and present study), the aggregation level did not arise from low infection levels in the introduced host. The evidence brought forward herein rather suggests that aggregation of higher level taxonomic groups depends on whether the species were acquired in or carried into the new area. Both measures of population abundance distribution agreed with each other, providing strong evidence for the revealed aggregation patterns for parasite species and higher level taxa from the native and introduced hosts. Aggregation was similar in the co-introduced monogeneans to that shown in the native range, whereas the acquired higher level taxa of helminth parasites in the new range mainly exhibited a higher level of aggregation than those in the native host area, except for acanthocephalans (nematodes were not compared, see Table 3). These findings agree with our second hypothesis, and reveal a different effect of host introduction on aggregation patterns for co-introduced and acquired groups of helminth parasites. Moreover, low values of abundance and its variance for acquired groups of helminth parasites in contrast to the high values found for co-introduced monogeneans and parasites of the native host range probably indicate that these parasitic groups occupy a different spatial distribution space. This pattern is clearly reflected in the study of AVRs where populations of acquired helminths are mainly aggregated in the lower left quadrant of the plot as opposed to co-introduced monogeneans and those from the native host, which stretch across the entire plot area or are allocated in its upper right quadrant (Fig. 2). Although aggregation of populations of acquired groups of parasites was higher, their mean abundance and its variance showed low values,

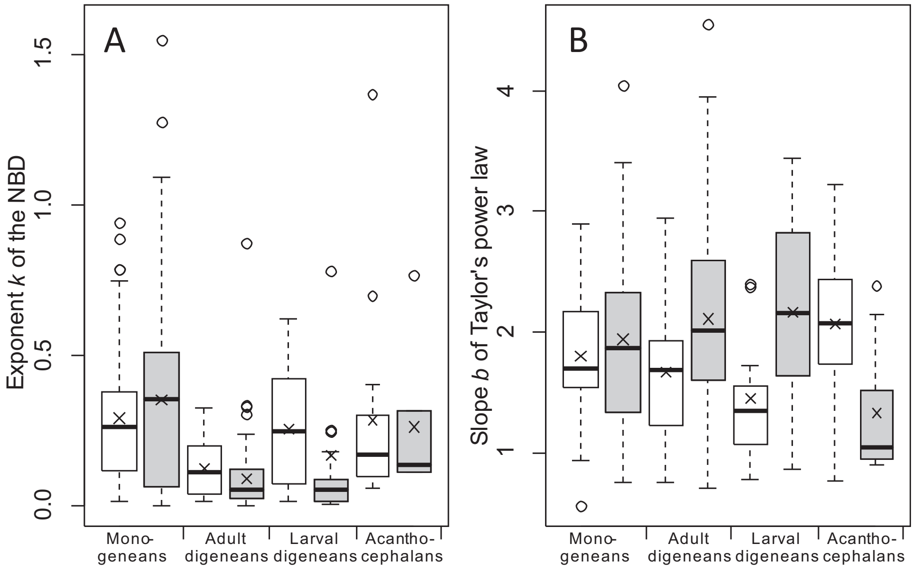

Fig. 1. Boxplots with mean values (crosses) of the exponent *k* of the negative binomial distribution (NBD) (A) and slope *b* of Taylor's power law (B) counted over species and samples for higher level taxonomic groups of parasites from *Liza haematocheilus* across its native (empty boxes) and introduced (filled boxes) ranges in the Sea of Japan and the Azov Sea, respectively. A significant difference between regions ($P < 0.05$) was observed for larval digeneans as estimated by *k* and for adult and larval digeneans, and acanthocephalans as estimated by *b* (Table 3). Nematodes were not compared, as they were represented by different stages of the life cycle from native and introduced distribution ranges.

supporting the ERH (Keane and Crawley, 2002; Torchin and Lafferty, 2009). Among the acquired parasites, the distribution was close to randomness in three species: *H. pachysomus*, *Contracaecum* sp. 1 and *N. (N.) personatus*. We suggest that low infection levels, together with the quasi-random distribution of these helminth species, result from the accidental nature of host encounter and non-compatible host–parasite interactions.

The repeatability analysis revealed that the aggregation of helminth parasites most likely represents true species characteristics and differs consistently between higher level taxonomic groups. The lack of, or weak correlation, between HSS and values of *k* and *b* suggests that sampling effort did not affect, or reasonably appear to affect, detectability and the estimation of aggregation parameters in the studied host–parasite systems. The slope of the Taylor's power law was not very sensitive to mean abundance, nor to the prevalence of helminth parasites and remains a robust and consistent ecological observation as was defined by Taylor (1961). By contrast, *k* values were greatly dependent on both infection parameters, the prevalence and the mean abundance. The influence of parasite infection parameters and sampling effort on the measurement of *k* has been discussed before (Gregory and Woolhouse, 1993; Poulin, 1996; Shaw et al., 1998), and it was expected in the present analysis. Comparing the variation in *k* values among samples with those of *b*, it has been found that the first index is less variable within species than the second one. At first glance it may seem that the NBD model fits the observed parasite distribution better than Taylor's power law model, but given the strong link between *k* and parasite infection parameters, it may alternatively simply reflect variance in prevalence and mean abundance among samples (Sarabeev et al., 2018). Our results are consistent with previous studies suggesting that the aggregation indices of the individual parasite species in a host are predictable among localities across its regional distribution, but also depended to some extent on local environmental parameters (Krasnov et al., 2006b; Pérez-del-Olmo et al., 2011).

The similarity in the aggregation parameters of monogenean species can be attributed to the repeatability and identity of the host–parasite systems. In contrast, the degree of aggregation differed markedly between regions for higher level taxa, which are represented by the native parasites in the Sea of Japan versus the acquired species in the Sea of Azov. Low prevalence (Sarabeev et al., 2018), coupled with high aggregation, could indicate that helminths tend to be aggregated in a small portion of the susceptible host individuals. We suppose that, for the acquired species, the host plays a crucial role in regulating their infra-population size due to the absence of evolutionary adaptation in naïve parasitic helminths and high host-induced parasite mortality rates, which is a common event observed for host–parasite relationships in an invasive host (Emblidge Fromme and Dybdahl, 2006; Kopp and Jokela, 2007). Both the encounter and the compatibility filters (see Combes, 2001) could act together in establishing new host–parasite systems, but the role of the filters could be different with respect to adult and larval digeneans. Grey mullets feed on a mudflat biofilm using a scrape feeding strategy (Odum, 1970), thus they become infected by passively encountering gastrointestinal digeneans. In this case, a host–parasite association could be established when the introduced host encounters a compatible digenean species. Parasite individuals tend to aggregate in a compatible host as an adaptation to mating opportunities (Krasnov et al., 2006c). The host encounter by directly transmitted larval digeneans may be largely dependent on host behaviour, which differs between the introduced and native Azov-Black Sea mullets; for instance, native mullets perform offshore migrations, whereas the introduced so-iuy mullet prefers to move to lagoons and rivers (Minos et al., 2010).

The aggregation assessed for the single-species population abundance in the present study and for community abundance data in Sarabeev et al. (2017a) revealed the same and paradoxical results when comparing parasite dispersion patterns between the native and introduced hosts. The absence of differences in aggregation between monogeneans in both regions was confirmed at the population and community levels (Sarabeev et al., 2017a,b and the present study) and was explained here by the repeatable infection and aggregation parameters for the same host–parasite species pair. Adult and larval digeneans acquired in the introduced host range were more aggregated in populations and less

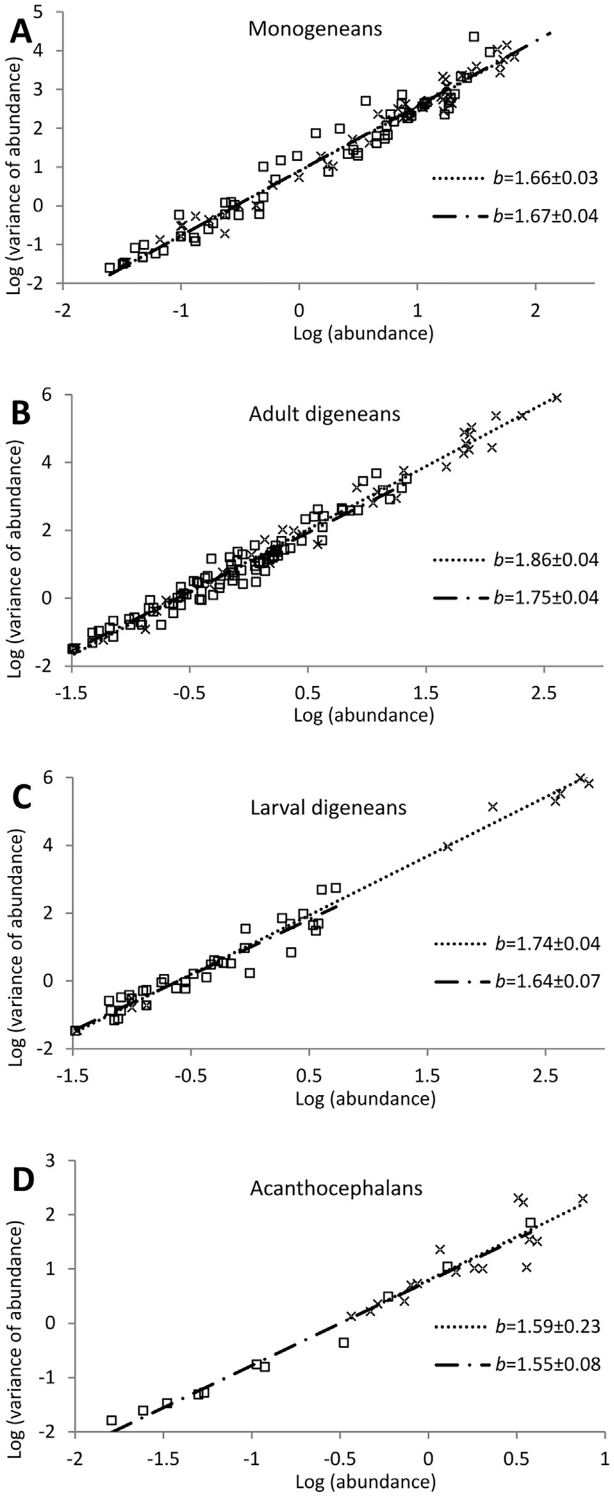

Fig. 2. Relationships between the log-variance and log-mean of abundance fitted to a power function in (A) monogeneans, (B) adult and (C) larval digeneans, and (D) acanthocephalans from *Liza haematocheilus* across its native (cross, dotted line) and introduced (open square, dash-dotted line) ranges in the Sea of Japan and the Azov Sea, respectively. A mixed population-species dataset was used. Nematodes were not compared, as they were represented by different stages of the life cycle from native and introduced distribution ranges.

aggregated in communities when compared with those from the native host area. It is interesting to note that the slopes of regression lines, obtained from mixed population-species data (Fig. 2), for acanthocephalans, adult and larval digeneans in the Azov Sea are below those of the Sea of Japan, indicating the smaller *b* value. This model corresponds to the mixed population-species spatial aggregation pattern of parasites in the host according to type III of the power law extension defined by Ma (2015). Aggregation estimated for populations, species and mixed population-species data actually was constructed with different types of sampling data, thus their parameters have different biological interpretations (Ma, 2015). Sarabeev et al. (2017a) assumed that there may be at least two reasons why helminth species are less aggregated in communities from introduced hosts: (i) the host individual has an approximately equal negative effect on any parasite species to be encountered; (ii) highly infected individuals could die and be lost from a population at the early juvenile stage due to parasite-induced host mortality. For instance, Sarabeev (2015b) showed that the absence of heavily infected fish among older age groups of fish was associated with mortality of juvenile individuals mostly propitiated by the larval digenean *Timoniella imbutiforme*. Assumptions inferred from different types of sampling data in the present and previous studies (Sarabeev et al., 2017a,b) agree well with each other, indicating that a large part of the introduced population may remain uninfected due to host resistance to parasites of the invaded range. In addition, encounter of an infected host with (i) the same parasite species will increase infra-population size, increasing population aggregation as an adaptation to mating opportunities (Krasnov et al., 2006c); (ii) another parasite species may not result in new infection due to the interspecific competition, strongly mediated by the host defence system (Krasnov et al., 2006c; Sarabeev et al., 2017a), thus decreasing community aggregation.

The results presented here, together with our recent studies (Sarabeev et al., 2017a,b, 2018), are, to our knowledge, the first attempts to document and analyse spatial distribution patterns of helminth parasites at both the population and community levels from an invasive host across its native and introduced distribution ranges. The diverse species composition representing five major higher taxa of helminths allowed estimation of the effect of host introduction on infection and aggregation parameters with respect to different taxonomical and ecological groupings. Our studies illustrate the importance of using different methodological approaches for various taxonomic groups in revealing the patterns of parasite spatial distribution to make important assumptions about the nature of host–parasite relationships. AVRs and AORs sharing infra-population size as a common currency are probably different expressions of the same phenomenon, describing the spatial distribution of parasites in populations and communities. We showed that AVRs and AORs provide a mechanistic explanation of the ERH, where co-invasive and acquired parasite species could be detectable using both relationships. Their interpretation sheds light on the population regulation processes in host–parasite systems underlying the success of introduced host species in the new area.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ijpara.2018.10.004.

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