

# THE EFFECTS OF HOST INTRODUCTION ON THE RELATIONSHIPS BETWEEN SPECIES RICHNESS AND AGGREGATION IN HELMINTH COMMUNITIES OF TWO SPECIES OF GREY MULLET (TELEOSTEI: MUGILIDAE)

V. SARABEEV<sup>1\*</sup>, J. A. BALBUENA<sup>2</sup>, S. MORAND<sup>3,4</sup>

<sup>1</sup>Department of Biology, Zaporizhzhia National University, Zhukovskogo 66, 69063 Zaporizhzhia, Ukraine

<sup>2</sup>Cavanilles Institute of Biodiversity and Evolutionary Biology, University of Valencia, PO Box 22 085, 46071 Valencia, Spain

<sup>3</sup>Institut des Sciences de l'Evolution – CNRS, CC065, Université Montpellier, Montpellier Cedex, France

<sup>4</sup>CIRAD ASTRE, Faculty of Veterinary Technology, Kasetsart University, 10400 Bangkok, Thailand

\* Corresponding author: vosa@ext.uv.es, volodimir.sarabeev@gmail.com

LIZA HAEMATOCHEILUS  
MUGIL CEPHALUS  
AGGREGATION  
COMMUNITY  
SPECIES RICHNESS

**ABSTRACT.** – Empirical parasitological surveys typically report multiple parasite species infections in hosts. Among the different factors that affect parasite communities within a host individual or population, interspecific interactions are of fundamental significance. Dependence of parasite aggregation on interspecific competition in parasite communities has been documented for several host-parasite systems. In this study we tested the effect of community size on parasite aggregation in native and introduced fish populations of two species of grey mullets (*Liza haematocheilus* and *Mugil cephalus*). We investigated the relationships between community heterogeneity and parameters characterizing species richness and both similar and different patterns for invasive and native hosts were revealed. The degree of aggregation of parasites decreased with parasite community size, except for monogeneans from the invasive host, thereby supporting findings of previous studies. Monogenean parasites, which were introduced in the new area together with their host, showed a positive relationship between the degree of aggregation and parasite community size. This suggests unregulated interactions in the introduced host-monogeneans system. The absence in the new host range of at least two monogenean species from the native range may have disturbed the evolutionary interaction established among them, which could have resulted in decreased interspecific competition. Multiple regression analysis showed that both species-rich communities and host introduction have a negative effect on species aggregation in parasite communities. Differences in helminth species richness, abundance and aggregation between native and invasive hosts support the idea that interspecific interaction is predominantly mediated by the host defense system.

## INTRODUCTION

Empirical parasitological surveys typically report multiple parasite species infections in hosts. Parasite species assemblages are referred to as infra- and component-communities depending on the level at which the observation is made, individual or population (Bush *et al.* 1997, Zander 2001). Among the different factors, which affect parasite communities within a host individual or population, parasite species interaction is of fundamental importance (Ferrari *et al.* 2016). Since Holmes & Price (1986) classified communities as interactive or non-interactive, depending on whether interaction takes place or not between the parasite species, there is a debate about the role of interactive vs. isolationist processes (Morand *et al.* 1999, Krasnov *et al.* 2006, Ferrari *et al.* 2016). Recently, Ferrari *et al.* (2016) summarized that interactive communities are structured by interactions between co-occurring species, whereas non-interactive communities are mostly organized by processes independent of the presence of other parasite species, such as host defense mechanisms and intraspecific competition. Species coexistence may

be explained by spatiotemporal aggregation patterns in populations and communities (Kilpatrick & Ives 2003). Intraspecific aggregation (or population abundance distribution) describes the degree to which a parasite species is clumped among a set of available hosts, whereas interspecific aggregation (or species abundance distribution (SAD)) is the degree to which different species co-occur in the same host individual or population (Ives 1991, Morand *et al.* 1999, Ma 2015). In other words, individuals coexist and interact with each other in space, time, population and community concurrently (Ma 2015).

In nature, parasites are not randomly distributed among hosts, but are often aggregated in both population and community simultaneously (Shaw & Dobson 1995, Krasnov *et al.* 2006, Poulin 2013, Yakob *et al.* 2014, Ferrari *et al.* 2016, Sarabeev *et al.* 2017). The aggregated distribution of parasites is caused by a variety of factors such as heterogeneity in host populations and/or infection pressure, which can act independently or together and might increase or decrease the observed level of parasite aggregation (Shaw & Dobson 1995, Wilson *et al.* 2002, Gourbière *et al.* 2015). The dependence of aggregation

on interspecific competition in parasite communities was noted by Krasnov *et al.* (2006). That pioneering study, which applied the slope  $b$  of Taylor's power law (Taylor 1961) to measure dispersion, revealed that aggregation level decreases with parasite community size (Krasnov *et al.* 2006). However, an earlier investigation of the effect of interspecific aggregation on the level of intraspecific aggregation, using Ives (1988) framework, found no obvious relationship between parasite dispersion and richness (Morand *et al.* 1999). More recently, Ferrari *et al.* (2016) proposed to use a new infra-community crowding index to measure the degree of interactivity of a parasite community within a host individual. In this work it was shown that the majority of abomasal parasites formed interactive communities and were influenced by the host species.

In the present paper we investigate the relationships between helminth species richness and community aggregation in two mullet fish, one of those is a native species, the flathead mullet *Mugil cephalus* L. (Whitfield *et al.* 2012), the other one, the so-iy mullet *Liza haematocheilus* (Temminck & Schlegel), native to the Amur River estuary and the Sea of Japan, which was deliberately introduced in the Black and the Azov Seas in 1972-1980 and in 1978-1984, respectively (Starushenko & Kazansky 1996, Occhipinti-Ambrogi & Savini 2003). The recent studies of Sarabeev (2015a) and Sarabeev *et al.* (2017) have shown that parasite communities, in the introduced species *L. haematocheilus*, are characterized by a low infra-community species richness and mean number of helminth individuals per fish and thus conform with isolationist communities as per Holmes & Price (1986). However, helminth communities were found to be less aggregated in the invasive population, as revealed by the lower values of the slope  $b$  (although this result has not been observed in all communities) (Sarabeev *et al.* 2017), which may indicate the presence of interactive communities in this host.

Herein we adopt the framework of Kilpatrick & Ives (2003), which was further applied to parasite communities by Krasnov *et al.* (2006). Whereas Krasnov *et al.* (2006) examined the relationship between the slope  $b$  of Taylor's power law and parasite species richness, we investigate here the dependence of aggregation, expressed as the exponent  $k$  of the negative binomial distribution (NBD) and the slope  $b$ , from both the overall parasite species richness per sample (PSR) and the mean of individual parasite species richness per host individual in the sample (MIPSR). We were particularly interested in testing whether parasite aggregation would be reduced relative to interspecific interactions and whether native and introduced species show the same pattern of relationship between community aggregation and species richness. We assume that the structure of parasite communities in both invasive and native host affects aggregation, being dependent on negative interactions among parasite species within each community. Our prediction is that aggrega-

tion in parasite communities should decrease as the number of species increases. This will further support the hypothesis that large parasite communities are less stochastic than poor-species communities (Morand & Krasnov 2008). Moreover, as species richness differed among native and invasive populations, the effect of host introduction on SAD in communities will be tested here after controlling for species richness. Our prediction is that the species introduction affects SAD and, in accordance with the hypothesis of Sarabeev *et al.* (2017), the community aggregation level in the invasive host is expected to be lower than in native ones.

## MATERIAL AND METHODS

*Parasite datasets:* This work is based on recently published results of our studies of SAD and helminth community size of two mullet fish across 14 localities in the Mediterranean, the Azov-Black Seas and the Sea of Japan (Sarabeev 2015a, Sarabeev *et al.* 2017). Forty-two datasets from two host species and 1,255 host individuals were analyzed. A comparative analysis of helminth communities from the introduced population of *L. haematocheilus* in the Azov-Black Seas with native population of the same species in the Sea of Japan and populations of *M. cephalus* across three regions was performed. We focused here on the relationships between aggregation indices and measurements of parasite community size. These relationships were examined for three groups of helminth parasites based on taxonomy and developmental stage, namely monogeneans, adult digeneans and larval digeneans. In addition, digeneans, acanthocephalans and nematodes were pooled in one data set and referred to as endoparasitic helminths, or endohelminths as opposed to ectoparasitic monogeneans. This was done to show differences between newly acquired parasites by *L. haematocheilus* in the new distribution area and those which were carried by the invasive host. Parasitic nematodes and acanthocephalans, as a separate taxonomic group, were not considered in the analyses because they were represented each by a single species in the introduced host (Appendix A) and, as such, did not form communities. Gill and/or skin monogeneans all are monoxenous and oioxenous species, except for species of *Metamicrocotyla* and *Solostamenides*. The monogenean species richness ranged from 2 to 7 per sample in the grey mullets examined. Endoparasitic helminths represented a more diverse group that included digeneans, nematodes (adult and larval stages in both groups) and acanthocephalans. All have heteroxenous life cycles and are stenoxenous (predominantly adult digeneans and nematodes, acanthocephalans) or euryxenous (larval digeneans and nematodes) (Appendix A). The size of the endohelminth community varied from 7 to 16 species (Sarabeev 2015a). In *L. haematocheilus* introduced in the Azov-Black Seas, ecto- and endohelminths have a different nature of origin. Monogeneans were carried to the introduced area together with *L. haematocheilus*, whereas endoparasitic species of the native area were lost and new species, mostly related with native grey mullets,

were acquired in the introduced area (Miroshnichenko & Maltsev 1998, Domnich & Sarabeev 1999, Balbuena *et al.* 2006, Dmitrieva *et al.* 2007, Kostadinova 2008, Pankov *et al.* 2009, Sarabeev *et al.* 2013, Sarabeev 2015a, b).

**Data analysis:** The data on parasite aggregation was drawn from Sarabeev *et al.* (2017), in which SAD was characterized by using slope  $b$  accounted for both infra- and component-community levels. However, following Krasnov *et al.* (2006), component communities were the focus of the present study. In addition, the dispersion parameter  $k$  was also used at component community level as an inverse measure of aggregation (Lloyd-Smith 2007). The data on infra-population abundance, including zero observations, of the detected parasite species in the host sample were pooled across community (mixed species-population data sets of Ma (2015)), *i.e.* population abundance per sample of all detected parasite species was rearranged from a matrix to a column form to count values of  $k$  in the fish sample. The exponent  $k$  of the negative binomial distribution (NBD) was obtained using maximum-likelihood estimates (Rózsa *et al.* 2000).

Initially, to test for the effect of helminth community size on aggregation indices, we regressed the values of  $k$  and  $b$  calculated for each component-community across both the invasive and native host against the PSR and the MIPSR. The relationships were considered significant when  $P$ -values associated to Pearson's correlations coefficients were  $< 0.05$ . Next, we used one-way analysis of variance (ANOVA) and analysis of covariance (ANCOVA) to determine the relative explanatory power of host type (invasive *vs.* native) and community size in variation of the aggregation indices. In ANCOVA values of  $k$  and  $b$  were defined as dependent variables, host type as a fixed factor and PSR and MIPSR as covariates. The parallelism assumption (*i.e.* interaction with the covariate) was checked using an ANCOVA homogeneity-of-slopes model. Consequently, we performed a multiple additive ANCOVA model, which accounts for the absence of interaction. Statistical tests were carried out in PAST v3.0 (Hammer & Harper 2005). Because values of  $k$  did not fit normal distributions (Kolmogorov-Smirnov test for one sample),  $\log$  transformations before ANOVA and ANCOVA was applied to conform to assumptions of normality.

## RESULTS

### *Relationships between species richness and aggregation*

Parasite aggregation in native host populations decreased with the size of parasite communities. The regression was significant for negative relations of the slope of Taylor's law and the MIPSR for endohelminths from native and invasive hosts (Fig. 1D). The dependence of  $k$  on the MIPSR also indicated a decreasing aggregation level (the aggregation decreases, as  $k$  approaches 20 (Wilson *et al.* 2002)) with increasing community size in all studied groups of helminths from native hosts (Fig. 1A,

C, E, H). Significant positive relationships between  $k$  and MIPSR were found for endohelminths and larval digeneans from the invasive host (Fig. 1C, H) indicating that the aggregation decreased as helminth community size increased. The significant effect of the PSR on helminth aggregation in communities was only found for values of  $k$  counted for monogeneans from the invasive host. However, this relationship strongly supports a positive dependence of aggregation on the size of helminth communities (Fig. 2). The slopes for relationship between PSR and  $k$  from invasive and native hosts were significantly different (Table I, ANCOVA, test on the equality of slopes), indicating that the size of helminth communities had opposite effects on  $k$  for different types of hosts. The same trend was observed for the effect of MIPSR on both indices  $k$  and  $b$  for monogeneans, but these relationships were non-significant (Fig. 1A, B). Although slopes of the linear regressions were significantly different for relationship of MIPSR and  $k$  for endohelminths and larval digeneans, the same trend of relationships for invasive and native hosts was observed.

### *Effect of host introduction on aggregation indices*

Host type had a significant effect on  $k$  for endohelminths and larval digeneans (Table I, ANOVA). Additionally, the significant effect of host type on  $b$  was found for all helminth groups considered, after controlling for MIPSR (Table I, ANCOVA). Moreover, host type had a significant effect on  $b$  for adult digeneans, after controlling for PSR. The ANCOVA revealed significant negative effect of both the high rate of MIPSR and the host introduction on  $b$  for endohelminths.

## DISCUSSION

The simulation model of Kilpatrick & Ives (2003) and further empirical studies of Krasnov *et al.* (2005, 2006) suggest that the value of  $b$  for Taylor's relationships for parasites is negatively affected by the number of co-occurring species. Kilpatrick & Ives (2003) demonstrated that they average 2 when there is a lack of interspecific competition, direct or apparent competition leads to values between 1 and 2, whereas the increase of competition between species decreases the  $b$  values from 2 to 1. This study showed that values of  $b$  assessed for helminth component-communities in native host populations decreased with community size, thus supporting the results of these previous studies. Moreover, the relationships observed herein between the size of helminth communities and the exponent  $k$  of the NBD indicate that helminth aggregation in native host populations decreased with an increase of the size of parasite community.

In the introduced host, negative or positive interactions between the degree of aggregation and the size of parasite

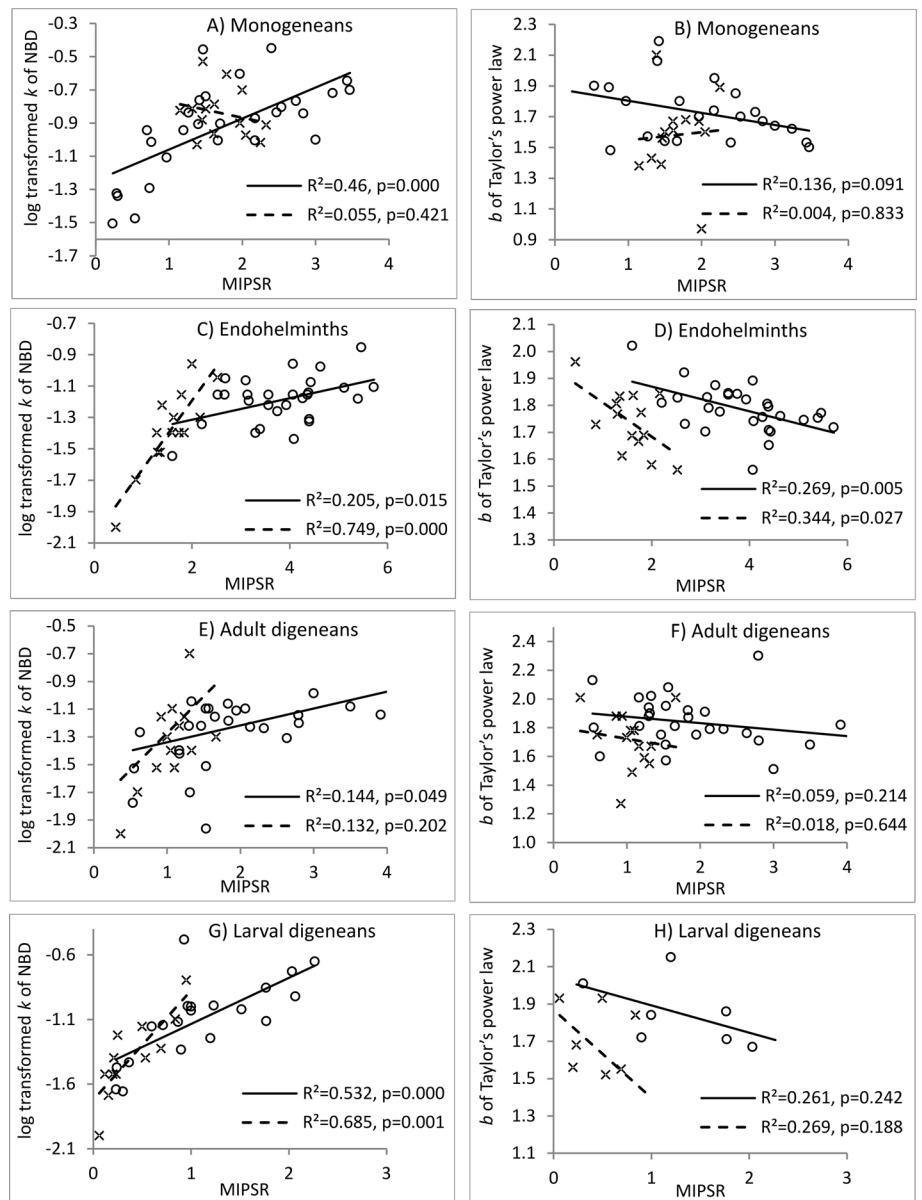


Fig. 1. – Relationship between mean individual parasite species richness (MIPSR) and the exponent  $k$  of the NBD (A, C, E, G), and the slope  $b$  of Taylor's power law (B, D, F, H) for four groups of helminth communities from invasive (dashed lines, crosses) and native (solid lines, open points) fish hosts

communities seem to be determined by the origin of the parasites, either acquired in the new area or introduced with their host. As expected, the negative relationships between the sizes of helminth communities occurred in the fraction of species acquired by *L. haematocheilus* in the Azov-Black Seas (endohelminths, adult and larval digeneans). Although the introduced host tended to exhibit lower values of MIPSR, total mean abundance and SAD indices (Sarabeev 2015a, Sarabeev *et al.* 2017, and the present study), its communities, nonetheless, remained interactive for the acquired helminth parasites. Monogenean communities, which were brought by the introduced species to the Azov-Black Seas from its native range, showed the opposite positive dependence of aggregation on the species richness. This finding does not support the hypothesis that aggregation should decrease as the parasite community size increases and rather suggests an

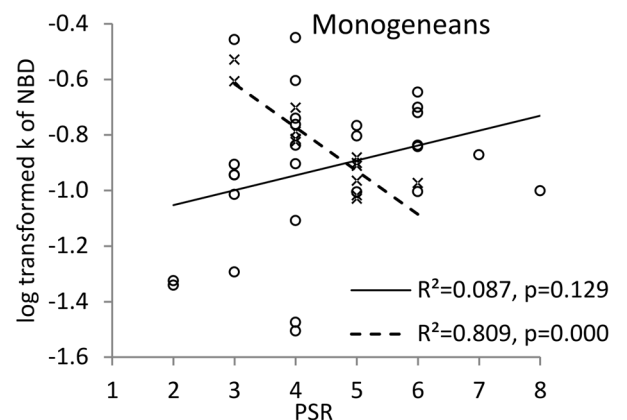


Fig. 2. – Relationship between parasite species richness (PSR) and the exponent  $k$  of the NBD for monogenean community from invasive (dashed lines, crosses) and native (solid lines, open points) fish hosts.

Table I. – Summary of ANOVA of the effects of host type (invasive vs. native) on exponent *k* of the negative binomial distribution and slope *b* of Taylor's power law, and ANCOVA with parasite species richness (PSR) and mean individual parasite species richness (MIPSR) as the covariates for four helminth communities (significant values are indicated in bold).

	ANOVA																							
	ANOVA				PSR x Host type				PSR				MIPSR x Host type				MIPSR				Host type			
	Mean squares	F	P		Mean squares	F	P		Mean squares	F	P		Mean squares	F	P		Mean squares	F	P		Mean squares	F	P	
Monogeneans	<i>k</i>	0.063	1.1	0.302	0.360	7.2	<b>0.011</b>	0.045	0.8	0.383	0.063	1.1	0.303	0.128	3.6	0.066	0.812	21.3	<b>0.000</b>	0.071	1.9	0.181		
	<i>b</i>	0.168	3.4	0.074	0.091	1.8	0.186	0.001	0.0	0.893	0.166	3.3	0.080	0.019	0.4	0.536	0.087	1.8	0.189	0.219	4.5	<b>0.041</b>		
Endohelminths	<i>k</i>	0.342	9.0	<b>0.005</b>	0.086	2.3	0.139	0.000	0.0	0.970	0.332	8.5	<b>0.006</b>	0.424	22.5	<b>0.000</b>	0.381	13.0	<b>0.001</b>	0.014	0.5	0.496		
	<i>b</i>	0.020	2.1	0.155	0.002	0.2	0.675	0.023	2.5	0.121	0.028	3.0	0.089	0.021	3.0	0.091	0.095	12.8	<b>0.001</b>	0.108	14.7	<b>0.000</b>		
Adult digeneans	<i>k</i>	0.004	0.0	0.862	0.002	0.0	0.910	0.000	0.0	0.991	0.004	0.0	0.864	0.209	1.7	0.195	0.511	4.2	<b>0.048</b>	0.078	0.6	0.430		
	<i>b</i>	0.130	3.9	0.056	0.038	1.1	0.294	0.046	1.4	0.249	0.137	4.1	<b>0.050</b>	0.002	0.1	0.805	0.056	1.7	0.203	0.184	5.6	<b>0.023</b>		
Larval digeneans	<i>k</i>	0.620	6.6	<b>0.016</b>	0.015	0.2	0.687	0.329	3.8	0.061	0.806	9.3	<b>0.005</b>	0.211	5.1	<b>0.032</b>	1.455	30.6	<b>0.000</b>	0.000	0.0	0.968		
	<i>b</i>	0.179	3.0	0.106	-	-	-	0.214	4.6	0.053	0.143	3.1	0.104	0.057	1.1	0.317	0.149	2.9	0.116	0.328	6.3	<b>0.027</b>		

unregulated relationship in the host-parasite system of the introduced host and its monogeneans. In other words, it may indicate that parasite species in a community do not exert negative effects on each other and that host subjected to multiple challenges from several monogenean species does not respond with stronger immune responses. The positive pattern of relationships between the level of aggregation and species richness for the introduced host supports several previous findings and indicates that fish gills are not likely saturated to form interactive communities (Morand *et al.* 2002). However, it raises the question why observed links between the level of aggregation and the size of monogenean communities in native and invasive host populations showed the opposite trend (*e.g.* Figs 1A, 2). Spatial interaction on fish gills among grey mullet's monogeneans was studied in *Ligophorus* spp. by Sanfilippo (1978) and Pron'kina *et al.* (2010). Both authors examined the same host-parasite system: *Liza aurata* (Risso) and its specific monogeneans *Ligophorus vanbenedenii* (Parona & Perugia) and *L. szidati* Euzet & Suriano. Sanfilippo (1978) argued that the position of monogeneans on fish gills depends on whether infections are mono or bi-specific. Pron'kina *et al.* (2010) postulated that interspecific competition is not an important factor determining species allocation on fish gills. The relationships between aggregation indices and the size of parasite communities of monogeneans of native host-parasite systems studied here indicate negative species interactions (Fig. 1A) thereby supporting Sanfilippo's (1978) view. We hypothesize that the absence in the new host range of at least two monogeneans species (Sarabev *et al.* 2013) disrupted the evolutionary interactions between the parasites resulting in the decrease of interspecific competition and change in their distribution. Moreover, interspecific competition might be latent in the case of bi-specific species co-occurring as showed by Pron'kina *et al.* (2010). The community aggregation measured by *b* was significantly lower in the invasive host for monogeneans than in the native hosts after controlling for IPSR (Table I). This suggests the existence of constraints on the degree of aggregation of monogeneans in the invasive host because the host-parasite system remains constant in time. One of these constraints can be the intraspecific regulation process that controls the levels of parasite aggregation and abundance depending on demographic factors such as intrinsic birth and death rates, mating behavior and mobility (Morand *et al.* 1999, Bagge *et al.* 2005, Krasnov *et al.* 2006).

The multiple regression analysis showed that both the size of helminth communities and the type of host had influences on the slope *b*. Krasnov *et al.* (2006) suggested that the efficiency of population regulation processes increases with community size due to interspecific competition, which could be direct or apparent, via the host. This competition would result in the increase of regulation in rich communities. The variance of abundance

increases less with increasing mean abundance under species interaction due to niche restriction. Moreover, interactions between parasite species are mainly mediated by the host, where the host defense system can be a primary mechanism of this mediation (Krasnov *et al.* 2006). In a new host-parasite system, both host and parasite did not get enough evolutionary time for displaying optimal virulence and adaptive defence. Sarabeev *et al.* (2017) assumed that the invasive host (at least adult individuals considered here) likely has a stronger regulation effect on the native range of parasites to operate at the infra-community level that resulted in lowering both abundance and community aggregation. The present study further supports the hypothesis of the negative effect of the invasive host on the SAD revealing significant differences in  $b$  between invasive and native host populations after controlling for MIPSRS, which agrees with the current theory on host resistance to native range parasites (*e.g.* Torchin *et al.* 2003, Emblidge Fromme & Dybdahl 2006, Kopp & Jokela 2007).

The rich species diversity of acquired parasites, both overall and in samples, reported in the introduced population of *L. haematocheilus* (see Domnich & Sarabeev 1999, Kostadinova 2008, Sarabeev 2015a), indicates that this host regularly faces native parasites in the introduced area. However, the invasive host was less heavily parasitized in terms of both individual parasite species richness and total mean abundance (Sarabeev 2015a, Sarabeev *et al.* 2017) with lower community aggregation (Fig. 1D, F and H; Table I). These observations suggest that the introduced host may act as a sink or dead-end for a large number of stenoxenic and euryxenic parasites and thus could reduce parasitism in native hosts via a dilution effect. This effect has been reported in a number of epidemiological studies of invasive hosts (Keesing *et al.* 2006, Johnson *et al.* 2008, Kelly *et al.* 2009, Johnson & Thielgtges 2010, Lettoof *et al.* 2013), but further studies are needed to confirm the density-dependent dilution effects of *L. haematocheilus* on the local parasite communities.

The present study showed that differences in the species number of helminth parasites per host population may explain up to 81 % of the variation in the aggregation indices estimated. However, this effect might result not only from species interactions, but also from species responses to environmental stochasticity (Kilpatrick & Ives 2003). Host plays a key role in determining the abundance, community structure and niche availability of parasites, and serves as mediator of both intraspecific and interspecific interactions (Krasnov *et al.*, 2006). Moreover, as stated above,  $b$ , MIPSRS and total mean abundance estimated for helminth communities from invasive host had lower values than those in native hosts. This result further supports the idea that the host can mediate interactions among helminth species via its defense system.

One noticeable finding of our study is that the exponent  $k$  of the NBD was more sensitive to parasite species rich-

ness than the slope  $b$  of Taylor's law. In six out of eight cases the effect of MIPSRS on  $k$  was significant, while in only two out of eight the relationships between  $b$  and the species richness were significant. The observed patterns of relationships between the size of helminth communities and both indices agreed with each other. There are several benefits of using  $k$  in comparative analyses of helminth component-communities: this parameter was not affected by total mean abundance (results not shown), it could be applied to species-poor parasite communities, even with two species, and it can be calculated directly from multi-species data by applying maximum-likelihood techniques. In contrast, the slope  $b$  is less applicable to small species assemblages, especially with 2 and 3 species because species richness actually represents the sample size used to fit the model (Sarabeev *et al.* 2017). In addition, estimation of  $b$  requires the initial computation of mean and variance pairs for each species with subsequent logarithmic transformation and fit to regression model (Taylor 1961), which can be very time consuming. Our observation opens the possibility to apply the exponent  $k$  of the NBD in the study of parasite species interactions in communities. Therefore, further studies investigating regulation processes in host-parasite systems should pay more attention to the exponent  $k$  of the NBD.

In conclusion, size differences in parasite communities can explain a large proportion of variability in the values of aggregation indices. Our study of the relationships between community heterogeneity and parameters characterizing species richness suggested the existence of both same and different patterns for invasive and native hosts. Although the observed links were not all significant and all aggregation indices were not always significantly affected by the PSR or the MIPSRS in all studied cases, this holistic approach revealed clear trends in relationships. The degree of aggregation of parasites in hosts decreased with the increase in community size, except for monogeneans from the invasive host, thus supporting the results of previous studies. Monogenean parasites, which were introduced in the new area together with their host showed opposite (positive) relationship between the degree of aggregation and parasite community size. This suggests unregulated interactions in introduced host-monogeneans system. The absence in the new host range of at least two monogenean species might destroy the evolutionary established distribution of parasites, which resulted in decreased interspecific competition. This study suggests that both species-rich communities and host introduction have negative effect on the species aggregation in communities. Distinctions in the helminth species richness, abundance and aggregation between native and invasive host populations support the idea that interspecific interaction is likely predominantly mediated by the host defense system.

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## APPENDIX A

Parasite/host list of helminth species collected from two mullet hosts with information on their regional distribution and specificity.

	Speci- ficity*	<i>M. cephalus</i>			<i>L. haematocheilus</i>	
		Mediterranean	Azov-Black Seas	Japan Sea	Azov-Black Seas	Japan Sea
<b>MONOGENEA</b>						
<i>Ligophorus cephalis</i> Rubtsova, Balbuena, Sarabeev, Blasco-Costa & Euzet, 2006	O	+	+	-	-	-
<i>L. chabaudi</i> Euzet & Suriano, 1977	O	+	-	+	-	-
<i>L. cheleus</i> Rubtsova, Balbuena & Sarabeev, 2007	O	-	-	+	-	-
<i>L. domnichi</i> Rubtsova, Balbuena & Sarabeev, 2007	O	-	-	+	-	-
<i>L. abditus</i> Dmitrieva, Gerasev & Gibson, 2013	O	-	-	+	-	-
<i>L. kaohsianghsieni</i> (Gussev, 1962)	O	-	-	-	+	+
<i>L. llewellyni</i> Dmitrieva, Gerasev & Pron'kina, 2007	O	-	-	-	+	+
<i>L. mediterraneus</i> Sarabeev, Balbuena & Euzet, 2005	O	+	+	-	-	-
<i>L. pacificus</i> Rubtsova, Balbuena & Sarabeev, 2007	O	-	-	+	-	-
<i>L. pilengas</i> Sarabeev & Balbuena, 2004	O	-	-	-	+	+
<i>L. triangularis</i> Sarabeev, Rubtsova, Tingbao & Balbuena, 2013	O	-	-	-	-	+
<i>L. miroshnichenki</i> Sarabeev, Rubtsova, Tingbao & Balbuena, 2013	O	-	-	-	-	+
<i>Gyrodactylus mugili</i> Zhukov, 1970	O	-	-	-	+	+
<i>G. zhukovi</i> Ling, 1962	O	-	-	-	+	+
<i>Polyclithrum ponticum</i> Gerasev, Dmitrieva & Gaevskaya, 2002	O	-	+	-	-	-
<i>Metamicrocotyla cephalus</i> (Azim, 1939)	S	+	-	-	-	-
<i>Solostamenides</i> sp. 1	S	-	+	-	+	+
<i>Solostamenides</i> sp. 2	N	-	+	-	-	-
<b>DIGENEA (adults)</b>						
<i>Dicrogaster contracta</i> Looss, 1902	S	+	+	-	+	-
<i>D. perpusilla</i> Looss, 1902	S	+	-	-	-	-
<i>Platydidymus flecterostes</i> (Zhukov, 1971)	S	-	-	+	-	+
<i>Pseudohapladena mugili</i> (Zhukov, 1971)	S	-	-	+	-	+
<i>Haploporus benedeni</i> (Stossich, 1887)	S	+	-	-	-	-
<i>S. cephalis</i> Blasco-Costa, Montero, Gibson, Balbuena, Raga & Kostadinova, 2009	S	+	+	-	+	-
<i>Saccocoelium obesum</i> Looss, 1902	S	+	+	-	+	-
<i>S. tensum</i> Looss, 1902	S	+	+	-	+	-
<i>Lecithobotrys putrescens</i> Looss, 1902	S	+	+	-	+	-
<i>Haplospalchnus bivitellus</i> Zhukov, 1971	S	-	-	+	-	+
<i>Haplospalchnus</i> sp. 1	S	-	-	+	-	+
<i>H. pachysomus</i> (Eysenhardt, 1829)	S	+	+	-	+	-
<i>Schikhobalotrema sparisoma</i> (Manter, 1937)	S	+	+	-	+	-
<i>Saturnius dimitrovi</i> Blasco-Costa, Pankov, Gibson, Balbuena, Raga, Sarabeev & Kostadinova, 2006	S	+	+	-	+	-
<i>S. minutus</i> Blasco-Costa, Pankov, Gibson, Balbuena, Raga, Sarabeev & Kostadinova, 2006	S	+	+	-	+	-
<i>S. overstreeti</i> Blasco-Costa, Montero, Gibson, Balbuena, Raga, Shvetsova & Kostadinova, 2008	S	-	-	+	-	+
<i>S. papernai</i> Overstreet, 1977	S	+	+	-	+	-
<i>S. segmentatus</i> Manter, 1969	S	-	-	+	-	-

	Speci- ficity*	<i>M. cephalus</i>			<i>L. haematocheilus</i>	
		Mediterranean	Azov-Black Seas	Japan Sea	Azov-Black Seas	Japan Sea
<i>Robinia aurata</i> Pankov, Webster, Blasco-Costa, Gibson, Littlewood Balbuena & Kostadinova, 2006	S	+	-	-	-	-
<i>Lecithaster galeatus</i> Looss, 1907	S	-	+	-	+	-
<i>L. confusus</i> Odhner, 1905	S	+	+	-	-	-
<i>Lecithaster</i> sp.	S	-	-	+	-	+
<i>Cardicola mugilis</i> Yamaguti, 1970	O	+	-	-	-	-
<b>DIGenea (larva)</b>						
Acanthocolpidae gen. sp.	E	+	-	-	-	-
<i>Stephanostomum</i> sp.	E	-	-	+	-	+
<i>Rhipidocotyle</i> sp.	E	+	-	-	-	-
<i>Diplostomum</i> sp.	E	-	+	-	+	-
<i>Posthodiplostomum brevicaudatum</i> (Nordmann, 1832)	E	-	-	-	+	-
<i>Tylodelphys clavata</i> (Nordmann, 1832)	E	-	-	-	+	-
<i>Timoniella imbutiforme</i> (Molin, 1859)	E	-	-	-	+	-
<i>Ascocotyle (Phagicola) longa</i> Ransom, 1920	E	+	+	-	+	-
<i>Galactosomum</i> sp.	E	+	-	-	-	-
Heterophyidae gen. sp. 1	E	-	-	+	-	+
Heterophyidae gen. sp. 2	E	-	-	+	-	+
<i>Cardiocephalus longicollis</i> (Rudolphi, 1819)	E	+	+	-	+	-
<b>NEMATODA</b>						
<i>Contraecum</i> sp. 1 (larva)	E	-	+	-	+	-
<i>Cucullanus bioccai</i> Orecchia & Paggi, 1987	S	+	-	-	-	-
<i>C. mugili</i> Belous, 1965	S	-	-	+	-	+
<i>Philometra biglobocerca</i> Belous, 1965	O	-	-	-	-	+
<b>ACANTHOCEPHALA</b>						
<i>Neoechinorhynchus (Hebesoma) yamaguti</i> Tkach, Sarabeev & Shvetsova, 2014	S	-	-	+	-	+
<i>N. (Neoechinorhynchus) personatus</i> Tkach, Sarabeev & Shvetsova, 2014	S	+	+	-	+	-
<i>N. (N.) tylosuri</i> Yamaguti, 1939	S	-	-	+	-	+

\* Specificity abbreviations: O, oioxenous; S, stenoxenous; E, euryxenous; N, specificity was not determined.