Intraspecific variability in the filter mesh size of suspension feeding organisms: the case of invasive Ponto-Caspian corophiids (Crustacea: Amphipoda)

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Abstract

Suspension feeders play pivotal roles in the nutrient cycling of almost all aquatic ecosystems. Since sufficiently large differences in the filter mesh size (FMS) can lead to different food web positions, the inter- and intraspecific variability of this trait might be of community-level importance. The aim of this study was to quantify the range of FMS variation within the three invasive Ponto-Caspian Chelicorophium species based on a large material representing various conditions (1,224 specimens from 40 samples across Central Europe), characterize the components of variation within populations, identify the main factors determining intraspecific differences, and reveal how intraspecific variation affects the FMS overlaps among species. The FMS of the most widespread invader, C. curvispinum, varied within the broadest range (between 2.34–8.28 μm, compared to 2.51–5.97 μm in C. robustum and 1.08–3.23 μm in C. sowinskyi); nevertheless, the contribution of intraspecific plasticity to the invasion success of the species is not evident based on the present study. The within-individual variability of FMS increased with the individual mean of the trait and decreased with body size; however, it showed little differences among samples. The among-individual variation within samples could be partitioned into components related to body size (ontogenetic niche shift/differences among cohorts) and sex (ecological sexual dimorphism) as well as a seemingly random component (individual specialization), varying widely in extent and relative contributions. The FMS of C. curvispinum was significantly larger in the presence of C. sowinskyi than in allopatry, likely reflecting character displacement; however, it did not show further increase when C. robustum was also present. Similar differences could not be observed in C. sowinskyi. The FMS ranges of C. curvispinum and C. robustum never overlapped with that of C. sowinskyi in co-occurrence despite the considerable intraspecific differences among sites, suggesting that their interaction can be seen as a clear case of niche differentiation by food particle size. On the contrary, the strong overlaps observed between C. curvispinum and C. robustum indicate that other factors might play the primary role in their coexistence. The studied species appear to be suitable model organisms for identifying the drivers and mechanisms of FMS variability.

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INTRODUCTION

Suspension feeders play pivotal roles in the nutrient cycling of almost all aquatic ecosystems by virtue of their often high biomass and central position in food webs (Higgins & Vander Zanden, 2010; Atkinson et al., 2013, 2014). Therefore, revealing the dynamics of their trophic interactions is an important research objective especially in the context of local and global anthropogenic disturbances—such as climate change, invasive species, eutrophication, and microplastics—affecting the quantity, quality, as well as the size distribution of suspended matter substantially (Barnett, Adam & Lettenmaier, 2005; Higgins & Vander Zanden, 2010; Lewandowska et al., 2014; Abonyi et al., 2018, 2020; Germanov et al., 2018).

Comparing traits directly linked to resource acquisition offers a straightforward way for studying the trophic interactions and niche differentiation among functionally similar species. Nevertheless, even deeper insights might be gained by taking the intraspecific variation of the traits into account, as well (Bolnick et al., 2011; Violle et al., 2012; Des Roches et al., 2018). For example, the range (i.e., niche breadth) and components (i.e., within/among individuals, sexes, or size classes) of trait variation within species might influence the strength of interspecific interactions substantially (Bolnick et al., 2003, 2011). In addition, the spatial or temporal variability of the traits might be informative of the adaptive capacity and dynamics of the species (e.g., Jourdan et al., 2019; Santi et al., 2020).

Suspension feeders use several different methods for capturing food particles; nevertheless, most of these include regular meshes (i.e., filters; Riisgård & Larsen, 2010). In the simplest case, the filters are used for the mechanical retention of particles the size of which must be larger than the filter mesh size (henceforth ‘FMS’). Since sufficiently large differences in FMS among species can lead to qualitatively different diets and thus food web positions, the trait can be indicative of niche differentiation (Suh & Choi, 1998; Kang et al., 2009; Borza et al., 2018). Even if more complex mechanisms (e.g., adhesive forces) are involved, implying a less direct link with the size of the captured particles, FMS might still allow informative intra- or interspecific comparisons (Alstad, 1987).

Although the intraspecific variability of FMS might have community-level implications in several cases, especially when keystone species are involved, it has received relatively little attention so far. The most well-known in this regard are hydropsychid caddisflies which nonetheless represent a special case with respect to the adhesive nature of the silk material they use for constructing their nets and the possibility of repeated net spinning during the life of a single individual. Loudon & Alstad (1992) demonstrated experimentally that individual Hydropsyche sp. larvae decrease the mesh size and increase the total area of their nets as ambient current velocity increases (although this pattern was not observable in Cheumatopsyche sp. larvae). The plasticity of FMS has also been studied in Daphnia spp., where Lampert & Brendelberger (1996) found that individuals experimentally adapted to low food density have larger filter screens and finer meshes.
Corophiids are small (<10 mm) crustaceans, filtering suspended particles actively by pumping water through their self-constructed tubes attached to hard surfaces or burrowed into soft sediments. They are distributed worldwide in oceans and seas reaching high density especially in tidal mudflats (Ger dol & Hughes, 1994); however, some of the species also occur in freshwater, including three invasive Chelicorophium species (C. curvispinum (G.O. Sars, 1895), C. robustum (G.O. Sars, 1895), and C. sowinskyi (Martynov, 1924)) originating in the Ponto-Caspian region (Borza et al., 2015). Very few data have been published on their FMS and even less is known about the intraspecific variability of the trait. Borza et al. (2018) found that FMS showed body length and sex dependency within populations in the invasive Chelicorophium species within their native range (Lower Danube), and the proportion of unexplained within- and among-individual variation was different per species. Borza et al. (2018) found no evidence for site-related intraspecific differences; however, another study focusing on the oligohaline corophiids of the Baltic Sea revealed significant differences in the FMS of all three native species among sampling sites, and the FMS of the invasive Baltic population of C. curvispinum also differed considerably from that of the native population in the Lower Danube (Borza, Arbačiauskas & Zettler, 2021).

The aim of this study was to (1) quantify the range of FMS in the three invasive Chelicorophium species based on a large material representing a wide range of conditions, (2) characterize the components of variation within populations, (3) identify the main factors determining intraspecific differences, and (4) reveal how intraspecific variation affects the niche differentiation among species.

**MATERIALS & METHODS**

**The studied materials**

Altogether 1,224 specimens (N = 715 for C. curvispinum, N = 202 for C. robustum, and N = 307 for C. sowinskyi) from 40 samples (stored in ethanol) across Central Europe were included in the analysis (Table 1, Fig. 1). The samples were chosen to represent various conditions regarding the locality and type of the waterbody, and season of year. Special emphasis was put on representing different species combinations.

The specimens included in the analysis were selected from the samples to represent a body length range as broad as possible in both sexes. In most cases slightly more females were included since they grow larger. Small specimens (<~2 mm) without recognizable secondary sexual features were considered juveniles.

**Morphological measurements**

The morphological measurements were done conforming to the procedure described by Borza et al. (2018). After the measurement of standard body length (from the tip of the rostrum to the end of the telson; using ocular micrometer), microscopic preparations were made from the filtering setae. The part of the 2nd gnathopods bearing the setae was dissected, mounted on a slide, and covered in Canada balsam. The measurements were made on
digital photographs (Fig. 2) taken under light microscope (DIC, 1,000× magnification) using the ImageJ2 software (Rueden et al., 2017). To decrease measurement error, the distance between the centers of six bristles (spanning five gaps) near the basis of the setae was
### Table 1  The samples included in the analysis.

| Sample no. | Site                  | Water body | Date              | Geographic coordinates          | Species present | Studied materials |
|------------|-----------------------|------------|-------------------|---------------------------------|-----------------|-------------------|
| 1          | Fonyód                | Lake Balaton | not available     | 46°45'07.8"N 17°33'16.4"E   | C               | 24 (11/12/1) 1.8–5.2 |
| 2          | Paloznak              | Lake Balaton | not available     | 46°58'32.7"N 17°56'59.5"E   | C               | 23 (12/10/1) 2.2–4.7 |
| 3          | Tihany                | Lake Balaton | not available     | 46°54'47.8"N 17°53'37.2"E   | C               | 24 (14/9/1) 1.8–4.2 |
| 4          | River Zala mouth      | Lake Balaton | not available     | 46°42'33.6"N 17°15'57.3"E   | C               | 24 (14/10/0) 2.2–5  |
| 5          | Peenestrom            | Baltic Sea  | 20.06.1998        | 53°51'00.0"N 13°49'59.9"E   | C               | 35 (19/16/0) 2.3–6.5 |
| 6          | River Nemenas mouth   | Baltic Sea  | 05.09.2015        | 55°20'12.1"N 21°14'53.4"E   | C               | 30 (16/13/1) 2–5.5  |
| 7          | Zecherin              | Baltic Sea  | 25.09.2018        | 53°51'54.0"N 13°49’51.6"E   | C               | 27 (13/10/4) 1.9–4.7 |
| 8          | Budapest              | Middle Danube| 20.04.2018        | 47°25'42.2"N 19°03'00.1"E   | C-R-S           | 30 (15/15/0) 2.7–6.2 14 (8/6/0) 4-7.5 |
| 9          | Barcs                 | Middle Drava | 09.11.2009        | 45°57'03.4"N 17°26'50.1"E   | C-S             | 16 (8/8/0) 2.2–5   |
| 10         | Vrbovka               | Middle Drava | 18.02.2017        | 45°49'41.5"N 17°44'05.6"E   | C-S             | 24 (13/11/0) 3.2–5.1  |
| 11         | Göd                   | Middle Danube| 30.03.2007        | 47°40'40.3"N 19°07'29.2"E   | C-S             | 24 (13/10/1) 2–6  |
| 12         | Göd                   | Middle Danube| 12.10.2009        | 47°40'49.3"N 19°07'33.6"E   | C-S             | 25 (13/12/0) 2.5–5.4  |
| 13         | Iza/Szöny             | Middle Danube| 24.08.2013        | 47°44'38.4"N 18°12'20.5"E   | C-R-S           | 23 (17/6/0) 2.8–5.1 25 (16/8/1) 2.8-2.8 |
| 14         | Szob                  | Middle Danube| 25.08.2013        | 47°48'53.6"N 18°51'50.6"E   | C-R-S           | 24 (12/10/2) 1.9–5.2 |
| 15         | Baja                  | Middle Danube| 29.08.2013        | 46°12'04.1"N 18°55'30.7"E   | C-R-S           | 24 (12/12/0) 2.2–5.1 24 (13/11/0) 3.3–6.6 |
| 16         | Novi Sad              | Middle Danube| 03.09.2013        | 45°15'41.8"N 19°53’13.7”E  | C-R-S           | 24 (13/11/0) 2.1–5  |
| 17         | Geisling power plant  | Upper Danube| 14.08.2013        | 48°58'26.0"N 12°21'44.0"E   | C-R-S           | 24 (14/10/0) 2.3–5.6  |
| 18         | Geisling power plant  | Upper Danube| 14.08.2013        | 48°58'44.9"N 12°19’56.9’E  | C-R-S           | 24 (14/10/0) 3.1–7.6 24 (18/6/0) 2.5–5  |
| 19         | Banatska Palanka/Bazias| Middle Danube| 08.09.2013       | 44°48'18.3"N 21°23’23.7”E  | C-R-S           | 24 (12/12/0) 2–4.8 24 (13/11/0) 3.1–6.7 24 (20/3/1) 1.7–4.6 |
| 20         | River Jantra mouth    | Lower Danube | 16.09.2013        | 43°40'26.9"N 25°37’10.0”E  | C-S             | 20 (10/9/1) 1.8–4.5  |
| 21         | Chiciu/Silistra       | Lower Danube | 19.09.2013        | 44°07’03.3”N 27°14’04.4”E  | C-R-S           | 24 (13/10/1) 2–5.3 27 (15/10/2) 2.1-7.7 |

(Continued)
Table 1 (continued)

| Sample no. | Site          | Water body | Date          | Geographic coordinates | Species present | Studied materials | C. curvispinum | C. robustum | C. sowinskyi |
|------------|---------------|------------|---------------|-------------------------|-----------------|-------------------|----------------|-------------|-------------|
| 22**       | Sf. Gheorghinei| Lower Danube | 25.09.2013    | 45°09′34.3″N 28°54′32.2″E | C-R-S           | 13 (6/7/0)        | 2.5–4.7          | 10 (7/3/0)   | 2.2–6.9      |
| 23         | Tiszasziget   | River Tisza | 14.07.2019    | 46°11′07.9″N 20°06′16.8″E | C-R-S           | 24 (12/12/0)      | 2.3–5.5          | 24 (14/10/0) | 2.6–8.2      |
| 24         | Nagymaros     | Middle Danube | 17.07.1917   | 47°47′17.2″N 18°57′39.4″E | S               | 10 (6/4/0)        | 2.2–3.9          |             |             |
| 25         | Budapest      | Middle Danube | 30.09.1932   | 47°29′21.7″N 19°07′05.7″E | S               | 10 (6/4/0)        | 2.3–5.5          |             |             |
| 26         | Vác           | Middle Danube | 30.09.1930   | 47°47′05.6″N 19°07′00.9″E | S               | 5 (4/1/0)         | 3.1–4.3          |             |             |
| 27         | Szeged        | River Tisza  | 9-10.1943     | 46°15′00.3″N 20°09′16.6″E | S               | 25 (11/10/4)      | 1.3–4.1          |             |             |
| 28         | Rajka         | Middle Danube | 28.05.2003   | 47°59′25.0″N 17°14′17.4″E | C-S             | 21 (13/7/1)       | 1.5–6.3          |             |             |
| 29         | Ossenberg     | River Rhein  | 28.05.2013    | 51°35′08.0″N 6°35′55.1″E | C-R-S           | 2 (1/1/0)         | 2.8–5.6          | 24 (11/11/2) | 2.7–9        |
| 30         | Rastatt       | River Rhein  | 8.2011        | 48°53′15.8″N 8°08′12.6″E | C-R-S           | 22 (13/9/0)       | 2.8–4.8          | 6 (4/2/0)   | 3.7–7.5      |
| 31         | Kratecko      | River Sava   | 10.09.2016    | 45°23′57.6″N 16°37′22.0″E | C-S             | 24 (13/11/0)      | 2–4.7            |             |             |
| 32         | Tiszfured     | River Tisza  | 03.08.2019    | 47°38′25.4″N 20°43′37.7″E | C-S             | 24 (12/12/0)      | 2.1–4.1          |             |             |
| 33         | Kiskőre       | River Tisza  | 14.05.2013    | 47°28′42.1″N 20°30′49.5″E | C-S             | 19 (9/10/0)       | 4.3–6.2          |             |             |
| 34         | Kiskőre       | River Tisza  | 31.07.2013    | 47°28′42.1″N 20°30′49.5″E | C-S             | 25 (13/12/0)      | 2.8–5.8          |             |             |
| 35         | Kiskőre       | River Tisza  | 30.04.2014    | 47°28′42.1″N 20°30′49.5″E | C-S             | 10 (6/4/0)        | 4.6–6            |             |             |
| 36         | Kiskőre       | River Tisza  | 30.06.2014    | 47°28′42.1″N 20°30′49.5″E | C-S             | 11 (7/4/0)        | 2.9–5.2          |             |             |
| 37         | Kiskőre       | River Tisza  | 30.08.2017    | 47°28′42.1″N 20°30′49.5″E | C-S             | 23 (11/12/0)      | 2.1–4.8          |             |             |
| 38         | Rózinowo      | River Vistula | 29.04.2016   | 52°43′21.8″N 18°59′11.1″E | C               | 14 (9/5/0)        | 2.9–5.6          |             |             |
| 39         | Rózinowo      | River Vistula | 04.11.2016   | 52°43′21.8″N 18°59′11.1″E | C               | 10 (3/5/2)        | 2–3.4            |             |             |
| 40         | Szolnok       | River Zaghyva | 12.07.2016   | 47°10′24.5″N 20°12′09.4″E | C-S             | 24 (15/9/0)       | 2.2–5.2          |             |             |

Notes:
Species codes: C. curvispinum, R. robustum, S. sowinskyi. Numbers refer to all individuals (females/males/juveniles) and min-max. body length.
* Included in Borza, Arbačiauskas & Zettler (2021).
** Included in Borza et al. (2018).
Geographic coordinates are approximate in most cases.

This procedure was repeated 10 times per specimen, each measurement performed on different setae. The full dataset is available under DOI: 10.6084/m9.figshare.12826535.
Statistical analysis

The statistical analysis of the data was performed in R 3.6.3 (R Core Team, 2020). Two specimens (1 C. curvispinum, 1 C. sowinskyi) considered as outliers were excluded from the analysis (Fig. S1). In line with aim 1 (‘Range of intraspecific variation’), violin plots (‘vioplot’ package; Adler & Kelly, 2019) were used to visualize the overall range and distribution of individual FMS means per species. To allow the comparison among the species represented with different sample sizes, the individual-based rarefaction curves of the FMS ranges were generated using basic R functions.

In line with aim 2 (‘Components of intraspecific variation’), the within-individual variation of FMS was modelled per species with linear mixed-effect models (‘nlme’ package; Pinheiro et al., 2020), including individual FMS means, body length, and sex as fixed factors, and samples as a random factor (intercept). The marginal $R^2$ (fixed effects) and conditional $R^2$ (fixed and random effects) of the models (Nakagawa & Schielzeth, 2013) was calculated using the ‘sem.model.fits’ function (‘piecewiseSEM’ package; Lefcheck, 2016).

To reveal the components of among-individual variation, linear mixed-effect models were used for samples containing more than 18 specimens of a species without juveniles and a male/female sex ratio higher than 2/3 ($N = 22$ for C. curvispinum, $N = 6$ for C. robustum, and $N = 8$ for C. sowinskyi). The selection of the optimal models was based on the protocol proposed by (Zuur et al., 2009). Individuals were considered as a random effect (intercept) in all cases. The optimal variance structures were selected in models including all considered fixed effects. The set of potential variance covariates and functions was based on the results of the modelling of within-individual variation. The variance structure with the lowest Akaike Information Criterion (AIC) was considered as optimal, if the likelihood-ratio test with the second best model was significant. Otherwise, the simpler (fewer degrees of freedom) model was selected. Body length (first or second order

Figure 2 The filtering setae of C. curvispinum (4.2 mm, male). One of the original photographs used for the measurements. The black line illustrates the unit of measurement.
polynomial) and sexes were considered as fixed effects with or without interaction, implying eight potential combinations. The selection of the optimal combination of fixed effects was based on the likelihood-ratio test (stepwise elimination of non-significant effects starting with the most complex model) using models fitted with the maximum likelihood (‘ML’) method. The optimal models were refitted with the restricted maximum likelihood (‘REML’) method for the estimation of parameters and variance components.

To characterize the component of among-individual variation not explainable by the body length and sex effects (i.e., random effect), models with the most complex fixed formula (2nd order polynomial of body length in interaction with sex) without variance covariates were fitted per samples and species. The relative share of variance components (fixed, random, and residual) was visualized in two-dimensional scatterplots.

In line with aim 3 (‘Drivers of intraspecific variation’), the effect of variables potentially accounting for the variation among samples was tested in mixed-effect models. The simultaneous analysis of all available explanatory variables was not feasible due to the heterogeneity of the material. The effect of species combinations could only be tested in *C. curvispinum* and *C. sowinskyi*, since *C. robustum* co-occurred with the other two species in all samples. In these models, mean-centered FMS data were used as the dependent variable, the presence/absence of congeneric competitors was included as the fixed effect, the random effect comprised three nested levels: (1) water body (as in Table 1), (2) sample and body length, and (3) individual (body length was included as a random slope while the other terms as random intercepts), whereas individual FMS means and body length were used as variance covariates (power function). The FMS differences between species combinations were estimated by Tukey contrasts using the ‘multcomp’ package (Hothorn, Bretz & Westfall, 2008).

The potential effect of habitat types could be tested based on a rough categorization (stagnant vs. flowing waters) only in *C. curvispinum*, since only this species occurred in stagnant waters (in the Baltic Sea and Lake Balaton; samples 1–7). However, habitat types could not be analyzed jointly with species combinations due to the large overlap in the two factors (only samples 38–39 from the River Vistula represented allopatric occurrences of the species in a river). Therefore, the habitat effect was tested separately in a similar model as species combinations (Tukey contrasts were not necessary in this case since two types were considered only), and the potential roles of the two effects are discussed.

Temporal differences in FMS could be tested directly in samples taken at different times at the same site. Within-year changes (samples 33–34, 35–36, and 38–39 for *C. curvispinum*, and 33-34 for *C. sowinskyi*) were analyzed in mixed-effect models featuring sample IDs, sex, body length, and all their interactions as fixed effects, individual IDs as a random effect, and individual FMS means and body length as variance covariates (power function). The optimal combination of fixed effects was determined based on likelihood-ratio tests in ‘ML’ models, and the parameters were estimated in the optimal model refitted with ‘REML’. Among-year differences were tested with a similar approach.
in samples 33-37 for *C. curvispinum*, in this case including years as a fixed effect instead of sample IDs.

In line with aim 4 ("Consequences on niche differentiation"), interspecific differences were characterized based on the FMS range overlaps in co-occurring populations.
RESULTS

Range of intraspecific variation

Individual FMS means ranged in the studied material between 2.34 and 8.28 μm in *C. curvispinum*, between 2.51 and 5.97 μm in *C. robustum*, and between 1.08 and 3.23 μm in *C. sowinskyi* (Fig. 3A). The individual-based rarefaction curves indicated that the differences in FMS ranges among the three species were largely independent of sample sizes (Fig. 3B).

Components of intraspecific variation

In all three species, the ln-transformed within-individual variation of FMS showed linear positive dependence on the ln-transformed individual mean of FMS and linear negative dependence on the ln-transformed body length, whereas sexes did not have a significant effect (Table 2). The random effect increased the $R^2$ of the models only moderately, indicating little differences in the within-individual variation of FMS among samples (Table 2).

The optimal models per samples and species included various combinations of fixed effects and variance covariates (Table 3, Table S1–S3, Fig. S2), indicating that the sources of among-individual variation of FMS were variable among populations. Seven out of the eight possible combinations of fixed effects was observed with the exception of non-linear body length effect without sex effect (row 3 in Table 3). The lack of both body length and sex effects (row 1 in Table 3) was relatively common in *C. curvispinum* and *C. sowinskyi*; however, it was not observed in *C. robustum*. The sex effect occurred almost always coupled with a certain type of body length effect (with or without interaction; rows 5–8 in Table 3) with only one exception in *C. robustum*. Non-linear body length effect (rows 6 and 8 in Table 3) was observed in *C. curvispinum* and *C. robustum* but not in *C. sowinskyi*.

The models featuring all fixed effects (allowing the comparison of the fixed, random, and residual components of among-individual variation within samples) revealed that random variance among individuals exceeded the component explained by all considered fixed factors in the majority of samples in *C. curvispinum* (16 out of 22), but not in *C. robustum* (3 out of 6) or *C. sowinskyi* (3 out of 8; Fig. 4A, Table S4). The random component also exceeded residual (i.e., within-individual) variance in most cases in all three species (20 out of 22 in *C. curvispinum*, 5 out of 6 in *C. robustum*, and 6 out of 8 in

| Species                              | Intercept Estimate (SE) | FMS mean (ln) Estimate (SE) | Body length (ln) Estimate (SE) | Marginal $R^2$ | Conditional $R^2$ |
|--------------------------------------|-------------------------|-----------------------------|-------------------------------|---------------|------------------|
| *C. curvispinum* (df = 697)          | −6.29 (0.18)            | 3.21 (0.14)                 | −0.52 (0.10)                  | 0.54          | 0.57             |
| *C. robustum* (df = 190)             | −5.53 (0.43)            | 3.98 (0.37)                 | −1.42 (0.18)                  | 0.40          | 0.43             |
| *C. sowinskyi* (df = 287)            | −5.20 (0.19)            | 3.53 (0.30)                 | −1.04 (0.19)                  | 0.37          | 0.41             |

Table 2 Parameter estimates (fixed effects) and explained variance proportions of the mixed-effect models of within-individual variation. All $p < 0.0001$. 

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The variance explained by the fixed effects exceeded residual variance in 13 out of 22, 6 out of 6, and 5 out of 8 cases in *C. curvispinum*, *C. robustum*, and *C. sowinskyi*, respectively (Fig. 4C, Table S4).

**Drivers of intraspecific variation**

The mixed-effect model including species combinations as an explanatory variable indicated that the FMS of *C. curvispinum* was significantly smaller in allopatry (mean ± SE: 3.41 ± 0.25 µm at 3.75 mm body length; Fig. 5A, Table 4) than in the presence of *C. sowinskyi* only (4.31 ± 0.19 µm). However, the presence of *C. robustum* did not increase the FMS of *C. curvispinum* any further (3.99 ± 0.20 µm). The presence or absence of congeneric competitors did not have a significant effect on the FMS of *C. sowinskyi* (1.84 ± 0.10 µm alone, 2.01 ± 0.08 µm in the presence of *C. curvispinum* only, and 1.96 ± 0.09 µm in the presence of both other species at 3.55 mm body length; Fig. 5B, Table 4).

The model involving habitat types estimated a similar FMS difference in *C. curvispinum* between stagnant and flowing waters as between the species combinations (alone vs. with *C. sowinskyi*; Table 4).

The modeling of temporal differences revealed that within-year changes in the FMS of *C. curvispinum* in the River Tisza (Kisköre) could be explained by sex and body length effects (Table 4, Fig. S3). By contrast, a significant temporal effect was detected in *C. sowinskyi* at the same site in the year 2013 (Table 4, Fig. S4). Similarly, the seasonal difference as well as the body length effect was significant in *C. curvispinum* in the River Vistula (Table 4, Fig. S5).

The modeling of all five samples from Kisköre revealed that the sex and body length effects were similar in all three years (i.e., the interactions were not significant), making the estimation of among-year differences straightforward. The FMS of *C. curvispinum* did not change significantly between 2013–2014; however, the decrease by 2017 was significant compared to both previous years (Table 4, Fig. S3).
Figure 4 Variance components in the mixed-effect models of FMS by samples and species (all fixed effects included). (A) Fixed vs. random. (B) Residual vs. random. (B) Residual vs. fixed. White circles: C. curvispinum, grey squares: C. robustum, black triangles: C. sowinskyi. Dashed lines indicate slope = 1.
Consequences on niche differentiation

The FMS ranges of *C. curvispinum* and *C. robustum* overlapped considerably in all samples where they were both present (mean ± SD: 1.88 ± 0.48 µm, N = 9; Fig. 6). By contrast, the FMS ranges of *C. curvispinum* as well as *C. robustum* never overlapped with that of *C. sowinskyi* (−0.67 ± 0.30 µm, N = 10 between *C. curvispinum* and *C. sowinskyi*; −0.37 ± 0.08 µm, N = 4 between *C. robustum* and *C. sowinskyi*; Fig. 6).

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**Figure 5** FMS as a function of the presence/absence of congeneric competitors. (A) *C. curvispinum*. (B) *C. sowinskyi*. CC, *C. curvispinum*; CR, *C. robustum*; CS, *C. sowinskyi*. 0, absent; 1, present.

Full-size [ DOI: 10.7717/peerj.11245/fig-5 ]
DISCUSSION

Range of intraspecific variation

The analysis revealed that FMS in corophiids shows considerable and complex variability; however, the extent of the variation might be different per species. Among the three studied Chelicorophium sp., the FMS of the most successful invader—C. curvispinum—varied within the broadest range, indicating that the trait is more flexible in this species than in the other two. Although the data do not prove that the other two species would not be able to shift their FMS beyond the observed limits under certain circumstances, the rarefaction indicates that the difference is not a mere sampling artefact. This was also supported by the fact that the FMS of C. curvispinum was highly variable even locally in some of the samples. The relationship between trait plasticity and invasion success is equivocal; a meta-analysis on plants concluded that invasive species are on average not more plastic than their native or non-invasive counterparts (Palacio-López & Gianoli, 2011). The higher invasion success of C. curvispinum compared to the other two species is attributable mainly to the fact that it was the only species that could expand its range in the central invasion corridor (Bij de Vaate et al., 2002) which might have several different explanations. Being able to adjust the FMS within a broad range appears to be an inherently advantageous skill; however, how much this might have contributed to the invasion success of the species is hard to tell. Nevertheless, it would also be interesting to compare the three invasive Ponto-Caspian species with the non-invasive ones in this regard.

Components of intraspecific variation

The within-individual variation of FMS was primarily determined by the individual mean of the trait. Since variable mesh sizes within a net are not adaptive (Crittenden, 1981),
this might indicate that the reliability of the morphogenesis decreases as the distances between the bristles increase, which in the end might determine the upper limit of FMS within the group. The within-individual variability of FMS also decreased slightly with body size which might indicate selection during the ontogenesis where individuals with lower variability have a higher chance of attaining large body size. Developmental instability often reflects environmental stress (De Anna, Bonisoli-Alquati & Mousseau, 2013); however, since the within-individual variation of FMS showed little differences among samples, such a relationship seems to be unlikely, at least within the stress gradient represented by the studied samples.

The analysis revealed that the among-individual variation of FMS within populations could be partitioned into body size and sex-related as well as seemingly random components, the absolute extent and relative contribution of which varied within wide limits. The rather heterogeneous material of this explorative study did not allow variance components to be used as dependent variables; nevertheless, they might be indicative of important ecological phenomena and so are worthy of further investigation.

The body length dependency of FMS has been observed previously in corophiids as well as in other crustacean taxa (Brendelberger & Geller, 1985; Suh & Choi, 1998). This pattern most likely reflects an ontogenetic niche shift induced by intraspecific competition (Nakazawa, 2015); however, differences among cohorts cannot be excluded either.
especially if the relationship is not linear as in some of the samples in the present study. Borza, Arbačiauskas & Zettler (2021) found that the effect was missing in Corophium multisetosum Stock, 1952 in the Baltic Sea and the present results showed that the extent of body size dependency can vary within species, as well. The strength of the relationship might depend on the intensity of intraspecific competition modulated by the abundance and/or size distribution of food particles.

Borza et al. (2018) supposed that the slight intersexual differences observed the Lower Danube in the three invasive Ponto-Caspian Chelicorophium species might be related to the high overall dimorphism in the group affecting the body size measurement, so the phenomenon is ecologically not relevant. However, in the light of the present results showing that sex-related differences vary among samples, it seems more likely that they indeed have a relevant biological background. Sexual dimorphism in niche-related traits can evolve as a result of the interplay between sexual selection and ecological character displacement (De Lisle, 2019). Remarkably, the sex effect was accompanied by body length dependency in almost all samples, indicating that it might also be related to the intensity of intraspecific competition. However, the degree of sexual dimorphism as well as its interaction with body size was variable among the samples exhibiting body length dependency in FMS, implying that the two effects are not regulated completely in the same way.

The unexplained component of among-individual variation can be interpreted as individual specialization, usually driven by intra- and interspecific competition, ecological opportunity, and predation (Bolnick et al., 2003; Araújo, Bolnick & Layman, 2011; Dall et al., 2012). Given that corophiids are sedentary animals, a potential determinant in the present case might be the micro-scale position of individuals, influencing their food supply through the density and species composition of their neighbors; i.e., the strength of intra- and interspecific competition (Tilman, 1994). Since the literature on individual specialization is based predominantly on behavioral traits or food composition, studying the morphological variability of filtering structures in corophiids might provide important contributions to our general understanding of the phenomenon.

**Drivers of intraspecific variation**

The analysis revealed an apparent pattern in the FMS of C. curvispinum in relation to species combinations, namely that the species had consistently dense filters when occurring alone, while it had on averages sparser but highly variable filters in the presence of C. sowinskyi (irrespective of the presence of C. robustum). Nevertheless, since two out of the three waters with allopatric occurrence were stagnant (Baltic Sea, Lake Balaton), and the FMS values of the species third, riverine site (River Vistula) did not represent an outlier compared to the sympatric samples, habitat types (stagnant vs. flowing) could explain the pattern with similar probability.

The competitor-effect seems plausible, since the two species show marked differences in FMS indicating niche differentiation by food particle size; therefore, the shift of C. curvispinum towards larger FMS in the presence of C. sowinskyi could be interpreted as ecological character displacement (Dayan & Simberloff, 2005). Nevertheless, some of the
sympatric samples show that the coexistence of the two species is possible even with FMS in *C. curvispinum* as small as in the River Vistula. Also, parallel changes could not be observed in *C. sowinskyi*; however, this might potentially be attributable to the asymmetric nature of the interaction; i.e., smaller mesh sizes can capture large particles but not vice versa, implying that the intensity of competition is stronger on the species with the coarser mesh.

Current velocity has been demonstrated to regulate FMS in hydropsychid caddisflies (*Loudon & Alstad, 1992*); however, its direct effect in the present case seems unlikely. Corophiids are active filterers, creating currents inside their tubes by the beating of their pleopods; therefore, they do not depend on the ambient currents. In the end, competitors and currents both can influence the abundance and size distribution of food particles; therefore, they can be expected to have an indirect effect on FMS. However; disentangling their roles would require more detailed data on the suspended matter.

The inconsistent results on temporal changes might have a similar explanation. The size distribution of suspended particles might shift variably in time, resulting in different pressures for FMS adaptation. Nevertheless, the fact that significant FMS shifts have been observed in some cases at a time interval of only ~2.5 months provides some insight into the mechanism of the adaptation. Although this interval is commensurate with the generation time of corophiids (*Muskó, 1992*) allowing changes to occur even in genetically determined traits by natural selection, such a consistent shift between two generations indicates the dominant role of phenotypic plasticity.

**Consequences on niche differentiation**

Information on the intraspecific variation of FMS put the interactions among the species into a new perspective (*Borza et al., 2018*). The fact that the FMS ranges of *C. curvispinum* and *C. sowinskyi* never overlapped in co-occurrence despite the considerable intraspecific differences among sites confirmed that their interaction can be seen as a clear case of niche differentiation by food particle size. The consistent differences between the FMS ranges of *C. robustum* and *C. sowinskyi* suggest that their interaction is similar to the one between *C. curvispinum* and *C. sowinskyi*, although somewhat less flexible. However, the strong overlaps and in some cases the almost complete absence of differentiation between *C. curvispinum* and *C. robustum* calls the role of food particle size as the most important niche axis allowing their coexistence into question. Although the potential for differentiation by FMS might increase the stability of their coexistence (*Ashby et al., 2017*), other factors—possibly related to body size differences (*Borza et al., 2018*)—can be assumed to play a decisive role, as well.

**CONCLUSIONS**

In summary, the study revealed a considerable extent of intraspecific variation in the FMS of invasive Ponto-Caspian corophiids which might potentially be reflected in the food web positions of the species. The identified components of variation were themselves variable among populations, indicating that intra- and interspecific competition can modulate the FMS in complex ways. The results also contributed to our understanding of
the niche differentiation among the species; however, the heterogeneity of the material allowed only a limited insight into the drivers and mechanisms of variability, warranting further studies with more strictly controlled field parameters and experimental approaches.

Although there might be idiosyncrasies among groups of suspension feeders differing in filtering mechanisms, habitat use, and life history; intraspecific variability in FMS can be expected to be widespread and potentially be of community-level importance in keystone species. Identifying the drivers and mechanisms of the variability might lead to a better understanding of the functioning of aquatic ecosystems as well as a better ability at assessing and predicting the impacts of anthropogenic disturbances. The studied species—especially the most flexible *C. curvispinum*—appear to be suitable model organisms to this end.

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**Competing Interests**

The authors declare that they have no competing interests.

**Author Contributions**

- Péter Borza conceived and designed the experiments, performed the experiments, analyzed the data, prepared figures and/or tables, authored or reviewed drafts of the paper, and approved the final draft.
Data Availability
The following information was supplied regarding data availability:

The full dataset is available under DOI: 10.6084/m9.figshare.12826535.

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