Final Report

Structure and dynamics of the filter feeding functional group of benthic macroinvertebrates: insights from trait measurements and laboratory experiments (NKFIH OTKA FK_19 132605)

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The results of the project were published in 5 research papers in international scientific journals (4 Q1, 1 D1), and presented at 7 international and 5 national conferences. A popular science paper partially related to the topic of the project was also published,

I had hoped that more of the papers could be published in D1 journals. In this regard, I comment that Biological Invasions used to be a D1 journal (in fact, one of my previous D1 papers was published there), and Current Zoology was ranked D1 at the time of the submission.

Overall, I consider the project as successful, since (1) it yielded important insights into the ecology of filter feeders. (2) I managed to place the results in an even broader context in most cases which made them more generally relevant. (3) It also supported my professional development as I gained experience in observational and experimental work with live animals. I am grateful for the support of NKFIH.

Results

Module 1. Morphometric analyses

1A. Intraspecific variability of filter mesh size in invasive Ponto-Caspian corophiids

I studied an extensive material of the three invasive Ponto-Caspian corophiids, revealing a considerable and complex variability in their filter mesh sizes [1]. The extent of variation was the highest in the most successful invader (*Chelicorophium curvispinum*); however, the contribution of intraspecific variability to invasion success was not evident. The among-individual variation within samples could be partitioned into components related to body size (ontogenetic niche shift/differences among cohorts) and gender (ecological sexual dimorphism) as well as a seemingly random component (individual specialization), varying widely in extent and relative contributions.. The filter mesh size 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 filter mesh size 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 overlap observed between *C. curvispinum* and *C. robustum* in some cases indicates that factors other than food particle size might also play a role in their coexistence. Overall, the

study highlighted that the complex variability in filter mesh size can be linked to several ecological drivers and the studied species appear to be suitable model organisms for identifying these.

Beyond the planned study on the three invasive Ponto-Caspian corophiids of the Danube basin, I also had the chance to examine the oligohaline species of the Balic Sea [2]. This was an interesting system since both native and invasive species were involved and habitat characteristics (salinity gradient, substrate types) offered additional opportunities for niche differentiation. The filter mesh size measurements revealed considerable differences among the three native species (*Apocorophium lacustre*, *Corophium multisetosum* and *C. volutator*), whereas the invasive *Chelicorophium curvispinum* showed strong overlap with *A. lacustre*. Nevertheless, the spatial separation by salinity and substrate types might decrease the intensity of competition for food. Our data for co-occurring populations also indicated that *A. lacustre* might be able to decrease its filter mesh size overlap with *C. curvispinum* by character displacement. On the other hand, the niche shift of *A. lacustre* might increase its overlap with *C. multisetosum*. In summary, the results could be presented as an interesting case study providing insight into the not-fully-explored multidimensional nature of niche differentiation and its implications for biological invasions.

1B. Overlaps in filter mesh size among different taxonomic groups of filter feeders, relationship with the particle size distribution of the suspended matter

I decided to skip this module due to the COVID-19 pandemic situation and focus on additional filter mesh size measurements (1A) and later in the project on experimental studies (2A) instead.

Module 2. Laboratory experiments

2A. Filtering capacity in the invasive Dikerogammarus *species*

To capitalize on synergies with Csaba Vad's OTKA project (FK_21 138215), I decided to study the filtering activity of the invasive Ponto-Caspian mysids instead that of the *Dikerogammarus* spp. This group was especially interesting in this regard as their filtering mechanism was debated in the literature due to the inherent difficulty of observing live specimens undisturbed. We tried to clarify the mechanism using *Limnomysis benedeni* [3]. Based on slow-motion video recordings of specimens resting on the wall of the aquarium, we were able to demonstrate that the filtration currents are generated synergistically by the maxillae, the thoracic exopods, and possibly also by the epipods of the first thoracopods and the oostegites in adult females. We could confirm the previously questioned existence of a forwardly directed ventral filtration current between the two rows of thoracopods; however, food particles can approach the mouth from a relatively wide angle. The rows of bristled setae on the proximal lobe of the maxillae can be regarded as the main filters present in most mysids. *L. benedeni* also bears accessory filtering setae on the basis of the second thoracopods indicating specialization for filter feeding. It is also likely that some even more specialized pelagic species with bristled setae on their thoracic endopods can use their 'feeding basket' for filtering. Clarifying the filtering mechanism represented a major contribution to our understanding of the functional morphology in mysids.

With knowledge on the filtering mechanism, we could focus on comparing the filtering capacity of the four the invasive Ponto-Caspian mysid species [4]. First, I made measurements

on their filter areas and filter mesh sizes to have a morphological reference. We found relatively small but consistent differences in the primary filter area among the species, indicating that morphological constraints due to the enclosed position of the setae might limit the possibility for differentiation. The primary filter mesh sizes were small in all four species (0.69–2.73 μm) with moderate but consistent intraspecific differences, suggesting that the benefit of being able to capture small particles might outweigh the pressure for differentiation. The experimental quantification of the clearance rates was harder than I expected. Initial trials with the climate chamber and fluorecence-based measurements of algae concentration (AquaPen) did not yield reliable results in the beginning. However, the application of water baths and flow-cytometer-based measurements in cooperation with Varsha Rani and Csaba Vad finally lead to success. The observed clearance rates were in accordance with the morphological characteristics of the species, highlighting that auxiliary filters (present in *L. benedeni*) are needed to increase filtering capacity considerably. Our study confirmed that food particle size can contribute to the niche differentiation of facultative filter feeders, but also indicated that they can tolerate a higher overlap than obligate ones. The observed differences were related to the habitat preferences and predatory potentials of the species, suggesting that complementarity among the different niche axes might further facilitate their coexistence.

As a follow-up on the filtering study and building on the experience of Katalin Patonai, we tried to determine the overall trophic positions of the four invasive Ponto-Caspian mysid species by stable isotope analysis. We combined this with the comparative analysis of their functional responses conducted by Anna Bessenyei (MSc thesis supervised by me). The combination of these two methods yielded congruent results which made the conclusions more robust and made the study relevant to a broader readership [5]. The order of the species based on the attack rate parameters of the functional response models matched with their mean δ15N values, indicating a correspondence between their predatory potentials and trophic positions in their invaded habitat. *Hemimysis anomala* had the highest attack rate on zooplankton presumably due to its higher degree of specialization linked to its pelagic lifestyle. Contrary to our expectations, the largest species, *Paramysis lacustris*, had an intermediate predatory efficiency and trophic position, similar to those of *L. benedeni* but higher than those of the smallest species, *Katamysis warpachowskyi*. Nevertheless, all of the four species exhibited a considerable predatory potential, suggesting that any of them can contribute significantly to their combined predatory impact depending on their densities. The congruence between the results of the two methods shows that the species can realize their different predatory potentials in their invaded environment, indicating favorable conditions (i.e., food availability and spatial heterogeneity) which allowed dietary differentiation. We recommend the combined use of functional responses and stable isotope analysis, which might allow robust conclusions to be drawn on the trophic ecology of the species and also provide further insights into the studied ecosystem.

2B. Phenotypic plasticity in the filter mesh size of corophiids

Preliminary trials at keeping corophiids alive in laboratory conditions were not successful. Since the mysid filter feeding experiment also faced initial difficulties causing delay, I decided to skip this module and focus on mysids.

Publications

Research papers

[1] Borza, P (2021): Intraspecific variability in the filter mesh size of suspension feeding organisms: the case of invasive Ponto-Caspian corophiids (Crustacea: Amphipoda). PeerJ 9: e11245. DOI: 10.7717/peerj.11245
https://peerj.com/articles/11245.pdf

[2] Borza, P., Arbačiauskas, K., Zettler, M.L. (2021): Multidimensional niche differentiation might buffer invasion impacts: the case of oligohaline corophiids (Crustacea: Amphipoda) in the Baltic Sea. Biological Invasions 23(6):1891-1900. DOI: 10.1007/s10530-021-02479-7
https://link.springer.com/article/10.1007/s10530-021-02479-7

[3] Borza, P., Duleba, M., Egri, Á. (2023): Filter feeding in the mysid crustacean *Limnomysis benedeni*: Evidence of the maxillary pump and the ventral filtration current. Zoologischer Anzeiger 302: 260-265. DOI: 10.1016/j.jcz.2023.01.002
https://www.sciencedirect.com/science/article/pii/S0044523123000025

[4] Borza, P., Rani, V., Vad, C.F (2024): Niche differentiation among facultative filter feeders: Insights from invasive Ponto-Caspian mysids. Current Zoology 70: 513–521. DOI: 10.1093/cz/zoad030
https://academic.oup.com/cz/article/70/4/513/7224221

[5] Patonai, K., Bessenyei, A., Vad, C.F., Borza, P. (2024): Functional responses correspond to stable isotope-based trophic positions among four invasive Ponto-Caspian mysid species (Crustacea, Mysida). Neobiota 93: 187-201. DOI: 10.3897/neobiota.93.121346
https://neobiota.pensoft.net/article/121346

International conference presentations

Borza, P.. Intra- and interspecific variation of filter mesh size in corophiids (Crustacea: Amphipoda). 35th Congress of the International Society of Limnology (SIL), 22-27.08.2021, Gwangju, Korea. Poster (online)

Patonai, K., Borza, P. Using stable isotope analysis for the detection of niche differentiation among four invasive Ponto-Caspian mysid species. GLEON Virtual All Hands' Meeting, 13-17.02.2023. Poster (online)

Borza, P., Rani, V., Vad, C.F. 2023.The role of filter feeding in the niche differentiation among coexisting invasive Ponto-Caspian mysids (Crustacea: Mysida). Symposium for European Freshwater Sciences (SEFS). 18-23.06. 2023, Newcastle, UK. Oral presentation.

Patonai, K., Vad, C.F., Borza, P. 2023. What makes an invader successful? Niche differentiation of four invasive mysid species. 4th International Conference on Community Ecology, 20-22.09.2023. Trieste, Italy. Oral presentation.

Patonai, K., Bessenyei, A., Vad, Cs., Borza, P., Combining field and laboratory methods for robust assessment of the trophic ecology of four co-occurring invasive Mysid species.

Association for the Sciences of Limnology and Oceanography (ASLO), 2-7.06.2024, Madison, Wisconsin, USA. Oral presentation.

Borza, P. Insights into the trophic ecology of invasive Ponto-Caspian mysids (Crustacea: Mysida). 4th CESAMIR - Central European Symposium for Aquatic Macroinvertebrate Research, 07-12.07.2024, Stará Lesná, Slovakia. Oral presentation.

Patonai, K., Bessenyei, A., Vad, Cs., Borza, P., Combining field and laboratory methods for robust assessment of the trophic ecology of four co-occurring invasive Mysid species. . 49th Annal Congress of SQÉBC (Société Québecoise pour l'Étude Biologique du Comportement), Nov 15-17, 2024, Montréal, Canada. Oral presentation.

National conference presentations

Borza, P., Betekintés a tegzesrákok (Crustacea: Amphipoda: Corophiidae) ökológiai kölcsönhatásaiba szűrőkészülékük résméretének vizsgálatán keresztül. XV. Makroszkopikus Vízi Gerinctelenek (MaViGe) konferencia, 2021.11.18-19., Agárd. Szóbeli előadás.

Borza P., Duleba M., Egri Á. A hasadtlábú rákok (Crustacea : Mysida) szűrési mechanizmusa. LXIII. Hidrobiológus Napok, 2022.10.05-07., Tihany. Szóbeli előadás.

Borza P. Fajon belüli és fajok közötti változékonyság tegzesrákok (Crustacea: Amphipoda: Corophiidae) szűrőkészülékének résméretében. LXII. Hidrobiológus Napok, 2021.10.06-08., Tihany. Szóbeli előadás.

Borza, P., Rani, V., Vad, C.F. A szűrő táplálkozás szerepe a ponto-kaszpikus inváziós hasadtlábú rákok (Crustacea: Mysida) niche-elkülönülésében. XVI. Makroszkopikus Vízi Gerinctelenek (MaViGe) konferencia, 2023.04.13-14., Tihany. Szóbeli előadás.

Patonai, K., Borza, P. Inváziós hasadtlábú rákok (Mysida) trofikus szerepének felmérése stabil izotóp elemzéssel hazai édesvizekben. ÚNKP Záró Konferencia, 2023.08.31., Budapest. Szóbeli előadás.

Popular science article

Borza, P. (2024): Hasadtlábú rákok – Vizeink kecses jövevényei. Élet és Tudomány 79(42): 1325-1327.
https://eletestudomany.hu/hasadtlabu-rakok-vizeink-kecses-jovevenyei/