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Near-shore distribution of alien Ponto-Caspian amphipods in a European dam reservoir in relation to substratum type and occurrence of macroinvertebrate taxa

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Abstract – Knowledge of habitat requirements and interspecific interactions of invasive species helps predict their impact and spread. We determined the relationships within the invasive freshwater Ponto-Caspian amphipod assemblage, and their associations with macroinvertebrates in the near-shore zone of a central European lowland dam reservoir. We sampled five habitat types: bare sand at the water line, bare sand (0.2 m depth), bare sand (0.5 m depth), macrophyte-overgrown sand (1 m depth), stones (0.3 m depth) on four dates (October 2015–October 2016). *Pontogammarus robustoides* occurred in all habitats, *Dikerogammarus villosus* and *Echinogammarus ischnus* were limited to the stony bottom. Amphipod densities were positively associated with one another except *Dikerogammarus* juveniles, negatively correlated with adults. The occurrence of *D. villosus,* juvenile *Dikerogammarus* and *E. ischnus* was positively related to the presence of the shelter-forming bivalve *Dreissena polymorpha*. *Pontogammarus robustoides* was positively associated with sphaeriid clams and gastropods (shelters), as well as oligochaetes and chironomids (potential prey items). *Dikerogammarus villosus* and *E. ischnus* were positively related to chironomids and oligochaetes, respectively. Coexistence of various alien amphipods in the studied area, indicated by prevailing positive relationships in their assemblage, may be enabled by the abundance of shelters and rich food sources allowing habitat partitioning.

Keywords: Invasive species / substratum selection / interspecies interactions / macrozoobenthos

Résumé – Répartition des amphipodes exotiques Ponto-Caspiens sur le littoral d'un réservoir de barrage européen en fonction du type de substrat et de la présence de taxons de macro-invertébrés. La connaissance des besoins en matière d'habitat et des interactions interspécifiques des espèces envahissantes permet de prévoir leur impact et leur propagation. Nous avons déterminé les relations au sein de l'assemblage d'amphipodes d'eau douce envahissants Ponto-Caspiens, et leurs associations avec les macroinvertébrés dans la zone proche du rivage d'un réservoir de barrage de plaine d'Europe centrale. Nous avons échantillonné cinq types d'habitats : le sable nu du rivage, le sable nu (0.2 m de profondeur), le sable nu (0.5 m de profondeur), le sable recouvert de macrophytes (1 m de profondeur), les pierres (0.3 m de profondeur) à quatre dates (octobre 2015 à octobre 2016). *Pontogammarus robustoides* était présent dans tous les habitats, *Dikerogammarus villosus* et *Echinogammarus ischnus* étaient limités au fond rocheux. Les densités d'amphipodes étaient positivement associées les unes aux autres, à l'exception des juvéniles de *Dikerogammarus*, qui étaient négativement corrélées aux adultes. La présence de *D. villosus*, de *Dikerogammarus* juvéniles et *d'E. ischnus* était positivement liée à la présence du bivalve formant abri *Dreissena polymorpha*. *Pontogammarus robustoides* a été positivement associé aux sphaeriidés et aux gastéropodes (abris), ainsi qu'aux oligochètes et aux chironomes (proies potentielles). *Dikerogammarus villosus* et *E. ischnus* ont été positivement associés aux chironomes et aux oligochètes, respectivement. La coexistence de divers amphipodes exotiques dans la zone étudiée, indiquée par les relations positives

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prédominantes dans leur assemblage, peut être rendue possible par l'abondance des abris et la richesse des sources de nourriture permettant le cloisonnement de l'habitat.

Mots clés : Espèces envahissantes / sélection du substrat / interactions entre espèces / macrozoobenthos

1 Introduction

Invasive organisms constitute a considerable threat to global biodiversity (Simberloff, 2000; Simberloff *et al.*, 2013), freshwater habitats being one of the most susceptible to their impact (Dudgeon *et al.*, 2006; Ricciardi and MacIsaac, 2010). To be able to efficiently monitor, control and predict the spread and impact of invaders, we need to determine their habitat requirements and interactions with other biota, both native and alien. This requires both experimental studies determining causal relationships among observed phenomena and field surveys depicting real-world situations taking place in the wild.

Several species of Ponto-Caspian amphipod crustaceans (gammarids and corophiids) established their populations in benthic communities of European inland waters in the 20th century (Bij de Vaate *et al.*, 2002; Jażdżewski *et al.*, 2002). In invaded ecosystems, they prey upon (MacNeil *et al.*, 1997; Berezina and Panov, 2003; Devin *et al.*, 2003) and compete (Piscart *et al.*, 2011) with local benthic organisms, constitute a food source for fish (Grabowska and Grabowski, 2005; Kakareko *et al.*, 2005) and contribute to organic matter decomposition (MacNeil *et al.*, 2011). Therefore studies on factors affecting their distribution in the field are urgently needed.

Several Ponto-Caspian amphipods (*Dikerogammarus villosus* (Sowinski, 1894), *Dikerogammarus haemobaphes* (Eichwald, 1841), *Echinogammarus ischnus* (Stebbing, 1899), *Chelicorophium curvispinum* (G.O. Sars, 1895)) are associated with hard substrata, such as stones, coarse gravel and solid artificial objects (Muskó, 1993; Dermott *et al.*, 1998; Devin *et al.*, 2003; Van Overdijk *et al.*, 2003; Kobak *et al.*, 2015; Borza *et al.*, 2017a). Other species, such as *Pontogammarus robustoides* (G.O. Sars, 1894), commonly occur on sandy bottoms (Gruszka, 1999; Jażdżewski *et al.*, 2002; Żytkowicz *et al.*, 2008). Macrophytes and colonies of the Ponto-Caspian zebra mussel (*Dreissena polymorpha* (Pallas, 1771)) also create living places for amphipods, increasing habitat complexity, offering anti-predation protection and food (Gosselin and Chia, 1995; Stewart *et al.*, 1998a; González and Burkart, 2004; Rewicz *et al.*, 2014), as well as attachment sites for corophiids (Van den Brink *et al.*, 1993; Lucy *et al.*, 2004). Food resources for omnivorous gammarids include detritus (Bącela-Spychalska and Van der Velde, 2013; Richter *et al.*, 2018), macroinvertebrates (mainly chironomid larvae and oligochaetes) (Bącela-Spychalska and Van der Velde, 2013; Rewicz *et al.*, 2014), periphyton covering hard surfaces and macrophytes (Berezina, 2007b), as well as mussel faeces and pseudofaeces (Karatayev *et al.*, 2002; González and Burkart, 2004). The proportion of macroinvertebrates increases in the diet of adult and large gammarids (Berezina, 2007a).

Interspecific interactions among amphipods can be quite complicated: they can live together in diverse habitats (Piscart *et al.*, 2010; Borza *et al.*, 2017b), allowing spatial segregation of species (Kley and Maier, 2005; Żytkowicz *et al.*, 2008). Alternatively, a stronger competitor can displace weaker ones to other habitats (Kley and Maier, 2003; Grabowski *et al.*, 2007; Kobak *et al.*, 2016). Intra-guild predation (Dick *et al.*, 1999; MacNeil, 2019) and cannibalism of adults preying upon juveniles (MacNeil *et al.*, 1999) may also affect the amphipod distribution (Devin *et al.*, 2003; Jermacz *et al.*, 2015a; Kobak *et al.*, 2015).

Selected relationships of the Ponto-Caspian amphipods with the above-mentioned environmental variables have already been examined in experimental studies (Platvoet *et al.*, 2009; Van Riel *et al.*, 2009; Bącela-Spychalska and Van Der Velde, 2013; Jermacz *et al.*, 2015a; Kobak *et al.*, 2015; MacNeil, 2019). Nevertheless, it is not always clear how these factors interact with one another in the wild to shape the actual distribution of alien species. For example, some authors highlight the positive effect of *D. polymorpha* beds on *Dikerogammarus* spp. (Devin *et al.*, 2003; Kobak and Żytkowicz, 2007; Kobak *et al.*, 2009; Boets *et al.*, 2010), while laboratory studies found the opposite (Gergs and Rothhaupt, 2008; Kobak *et al.*, 2015). Similarly, laboratory experiments show that amphipods include Chironomidae and Oligochaeta in their diet (Bącela-Spychalska and Van der Velde, 2013; Richter *et al.*, 2018), but conflicting evidence also exists (Koester *et al.*, 2016), and it is not known whether amphipods are spatially associated with these taxa in the field.

We intended to check whether and to what extent the relationships found in earlier laboratory experiments (Kley *et al.*, 2009; Platvoet *et al.*, 2009; Van Riel *et al.*, 2009; Boets *et al.*, 2010; Czarnecka *et al.*, 2010; Jermacz *et al.*, 2015a, 2015b; Kobak *et al.*, 2015, 2016, 2017; MacNeil, 2019) occur in real field conditions. We tested relationships of invasive Ponto-Caspian amphipod taxa with one another, as well as between them and other macroinvertebrates, in diverse habitats of a dam reservoir on a large European river. Such relationships have not been commonly tested so far, especially for the species used in our study and in anthropogenic water bodies, often constituting alien species hot spots (Bij de Vaate *et al.*, 2002; Żytkowicz *et al.*, 2008). We hypothesized that: (1) Amphipods associated with hard surfaces (*D. villosus*, *D. haemobaphes, E. ischnus*, *Ch. curvispinum*) would be positively associated with *D. polymorpha* colonies (Devin *et al.*, 2003; Van Overdijk *et al.*, 2003; González and Burkart, 2004; Kobak and Żytkowicz, 2007) and other hard-shelled molluscs, particularly at locations without *D. polymorpha*. (2) *Pontogammarus robustoides* would be less selective with regard to substratum type, inhabiting diverse habitats (Żytkowicz *et al.*, 2008; Czarnecka *et al.*, 2009; Jermacz *et al.*, 2015a). (3) Adult *D. villosus*, being the strongest competitor in the assemblage (Kley and Maier, 2003; Van Riel *et al.*, 2006), would be negatively related to the density of other amphipods and smaller conspecifics (Dick and Platvoet, 2000; Rewicz *et al.*, 2014; Jermacz *et al.*, 2015b; Kobak *et al.*, 2016). (4) The density of amphipods may be positively correlated with that of Chironomidae larvae and Oligochaeta if these organisms constitute suitable food sources for them (Bącela-Spychalska and Van der Velde, 2013). Some laboratory studies

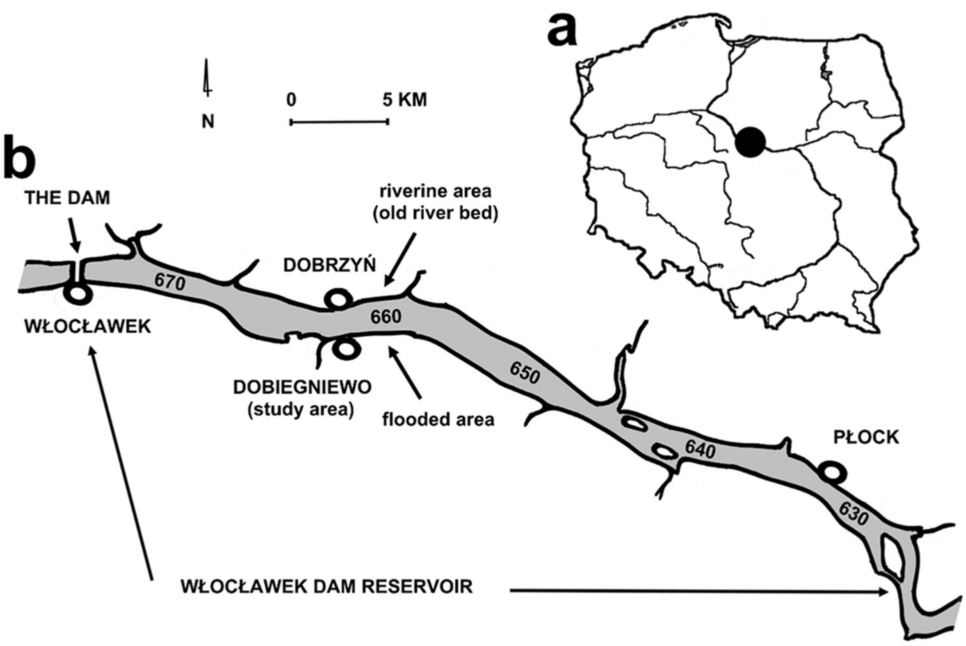

Fig. 1. Study area. (a) Location of the Włocławek Dam Reservoir in Poland. (b) Study sites.

suggest that omnivorous amphipods may be attracted to chironomids (Gergs and Rothhaupt, 2008), though others do not confirm such observations (Czarnecka *et al.*, 2010). Alternatively, as the growing body of evidence shows that Ponto-Caspian amphipods are more herbivorous than previously believed (Koester *et al.*, 2016, 2018), the densities of these taxa may be independent of one another.

2 Methods

2.1 Study area and sample collection

The Włocławek Dam Reservoir (Fig. 1a) was created in 1970 on the lower Vistula River (Poland). This is a large (area: 75 km^2; capacity: 400 million m^3), shallow (average depth: 5.5 m; maximum depth: 15 m) and eutrophic reservoir with a high length: width ratio, regular shape and very short retention time (4–5 days) (Giziński *et al.*, 1989). During the study, the maximum amplitude of the water level was 67 cm (data from the Polish Water Management "Polish Waters", Regional Water Management Board in Warsaw, Suppl. material 1). The bottom fauna (including sensitive species) are able to survive long periods of air exposure (LT50 over 8 days at a water content of 7.1%) provided that the substratum is humid (Poznańska-Kakareko *et al.*, 2017). That 8-day threshold was exceeded only once during our study period (10 days in January 2016), but the fauna had enough time for recovery (Leigh *et al.*, 2016; Vander Vorste *et al.*, 2016) before our next sampling.

We collected samples along the left bank of the middle part of the reservoir (52°37′03″N 19°19′37″E) in a flooded area (Fig. 1b) with a gentle bottom slope. We took samples from five types of typical near shore bottom habitats in the area: (1) bare sand at the water line; (2) bare sand at a depth of 0.2 m; (3) bare sand at a depth of 0.5 m; (4) sandy bottom overgrown by macrophytes; (5) stony substratum (Tab. 1). We collected samples on four dates: 14 October 2015; 2 April 2016; 5 July 2016; 18 October 2016. On each date, we sampled three sites randomly selected in each habitat type, at least 5 m apart (12 separate samples from each habitat altogether). On each date, we established the positions of sampling sites in the two shallowest habitat types (1–2) to keep a constant depth depending on the fluctuating position of the water line. We defined the positions of sampling sites in the other habitat types (3–5) by the presence of specific habitat features. Due to the differences in bottom types among the habitats as well as in size, abundance and mobility among various taxa, we used three different sampling methods (Tab. 1). At the sandy bottom, we collected sediment-dwelling macroinvertebrates (except amphipods) using a core sampler with a catching area of 22 cm^2, penetrating sediments to a depth of 29 cm (3 subsamples per sample). We sieved the collected sediments through a 0.5 mm sieve. We collected amphipods from the sandy bottom (quantitatively (Everall *et al.*, 2017; Tubić *et al.*, 2017)) using a 30-cm wide Surber net (1 mm sieve). One sample included sediments collected by dragging the net 30 cm along the bottom to sweep the surface layer of sediments, which resulted in a catching area of 900 cm^2. One sample from the stone habitat was a single irregular piece of concrete (mean diameter: 14 cm, SD = 5.2). We carefully removed stones from the water and gently scraped and rinsed out all organisms (including amphipods) onto the sieve from their upper surface. As the stones were buried in sand, only their upper surface was available to settling fauna. All these methods allowed us to take quantitative samples, that is, to collect all macroinvertebrate individuals from a given bottom area, thus their results can be considered as comparable among habitats for each taxon. We preserved the fauna in 4% formaldehyde. We estimated the projected areas of photographed top stone surfaces available for the fauna using ImageJ software (http://rsb.info.nih.gov/ij). We calculated densities of all organisms per 1 m^2. In the laboratory, we identified the fauna to species or genus (as far as possible) according to Piechocki and Wawrzyniak-Wydrowska (2016) for Mollusca, Wiederholm (1983) for Chironomidae larvae, Kasprzak (1981) and Timm (2009) for Oligochaeta, Konopacka (2004) for Amphipoda. Trichoptera, Ceratopogonidae and Nematoda (only single specimens found) were not identified to a lower taxonomic level.

2.2 Statistical analysis

Due to the highly right-skewed distributions of amphipod densities (skewness ranging from 2.6 to 5.0), to compare amphipod densities among various substrata and seasons, we conducted 2-way Generalized Linear Models (GLM) (gamma distribution, log link function) with sampling date and habitat type as factors. Dependent variables in these analyses were densities (with each data point modified as X+1 to avoid zero values, not handled by the gamma distribution) of identified amphipod taxa: *P. robustoides*, *E. ischnus* and *D. villosus*, as well as juvenile *Dikerogammarus* spp. (where the species identity was impossible to determine). Nevertheless, due to the very low occurrence of *D. haemobaphes* adults (just 2 individuals in the entire study, see Results section), it is likely that most of the juvenile *Dikerogammarus* spp. were in fact *D. villosus*. Due to the low occurrence of *D. haemobaphes*, as well as of *Ch. curvispinum*, we excluded them from the analysis. We further analysed significant effects in the models with pairwise contrasts as post-hoc tests.

To check the relationships between particular amphipod taxa and other organisms, as well as their habitat associations, we conducted a Correspondence Analysis (CA) with log-transformed densities of the most common groups of macrozoobenthos (*i.e.* Chironomidae, Oligochaeta, Gastropoda, *D. polymorpha*, Sphaeriidae) and amphipods: *P. robustoides*, *E. ischnus* and *D. villosus*, as well as juvenile *Dikerogammarus* spp. For macrozoobenthos, we combined lower taxonomic units (species and genera) to reduce the number of variables. We assumed that omnivorous amphipods would be unlikely to discriminate between particular species as potential food sources. As in the first run of this analysis the stony habitat appeared to distinctly depart from the others, we conducted a second CA, excluding samples collected from stones, to further evaluate more subtle relationships in the remaining habitats, potentially obscured by the strong distinctness of the stony habitat.

We analysed relationships among amphipods and other organisms using GLMs (gamma distribution with log-link function due to the highly right-skewed distribution of the data) with the density of a particular amphipod group (modified as X+1, see above) as a response variable, sampling date as a categorical factor (to control for its effect), and densities of the above mentioned groups of macrozoobenthos and other amphipods as continuous covariates. We conducted separate GLMs for each habitat type (in which a given amphipod group occurred), using sets of taxa occurring in particular habitats. This approach allowed us to check for interspecific relationships independent of their potential preferences for or avoidances of specific habitat types (*i.e.* within each habitat). Assuming that juveniles are unlikely to affect adults, we did not use their densities as explanatory variables in the analyses of adult individuals, only the other way round.

GLMs were conducted with SPSS 26.0 (IBM inc.) and CAs with Vegan 2.5–3 package for R (Oksanen *et al.*, 2018).

Table 1. Characteristics of study habitats.

Characteristics / Habitats	Sandy water line	Sand 0.2 m	Sand 0.5 m	Macrophytes	Stones
Substratum	Sandy bottom at the water line, partially submerged	Sandy bottom without vegetation	Sandy bottom without vegetation	Sandy bottom with dense submerged vegetation, mostly *Potamogeton perfoliatus*, *P. lucens*, *Myriophyllum spicatum*, *Ceratophyllum demersum*, *Nuphar lutea*	Single stone (irregular pieces of concrete – parts of worn-out bank reinforcement placed on the sandy bottom)
Depth	At the water line, 0.0 m	0.2 m	0.5 m	0.7–1.0 m	0.3 m
Distance from the shore	0 m	1 m	5 m	15 m	1 m
Macrofauna/amphipod sampling (subsamples making a single sample)	3 × core sampler/1 × Surber net	3 × core sampler/1 × Surber net	3 × core sampler/1 × Surber net	3 × core sampler/1 × Surber net	1 stone with a known area (macrofauna and amphipods together)

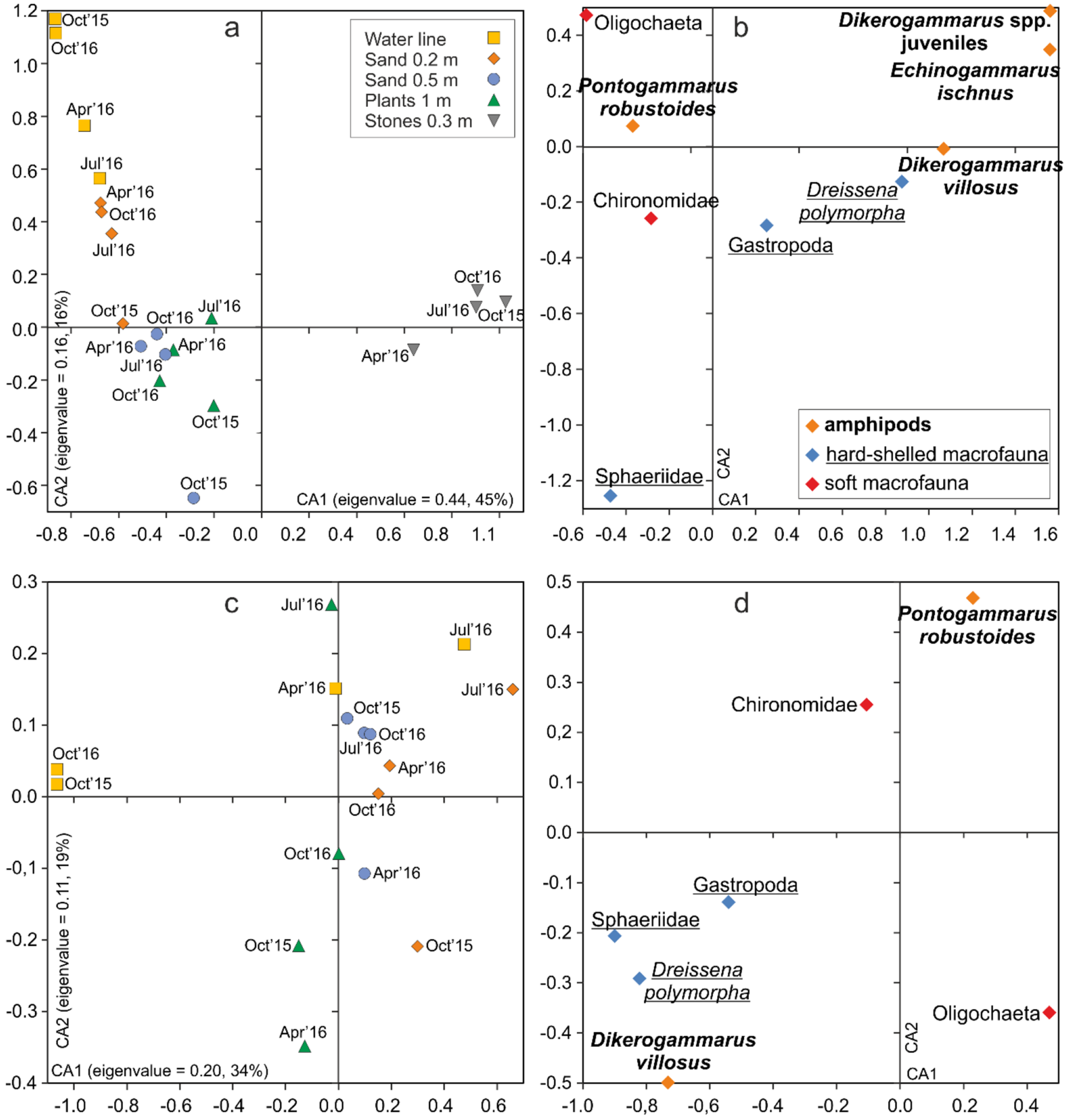

Fig. 2. Correspondence analysis ordination of macroinvertebrate taxa (including amphipods) and sites belonging to different habitat types. The analysis was based on samples from all the habitats (a and b) or excluding stone sites (c and d).

3 Results

3.1 Macroinvertebrate distribution (including amphipods) in particular habitats

The highest total macroinvertebrate density, averaged across all the sampling dates (20 247 ind m^{-2}) was found on the stony bottom (Suppl. material 2) whereas the lowest density was found at the water line (461 ind m^{-2}) (Suppl. material 2).

The Correspondence Analysis (Fig. 2) showed a high differentiation of the stony habitat from the remaining samples along the first CA axis (Fig. 2a). The stones were mainly occupied by *D. villosus*, juvenile *Dikerogammarus* spp., *E. ischnus*, *D. polymorpha* (12 000 ind m^{-2}, over 60% of the total macroinvertebrate density in this habitat, Suppl. material 2) and gastropods (Fig. 2b). The soft bottom samples were dominated by *P. robustoides*, chironomids, oligochaetes and sphaeriid clams.

The second CA axis discriminated the shallower sandy sites from deeper locations (Figs. 2a and 2b). The water line habitat was inhabited only by Oligochaeta (89% of the total density) and Amphipoda (*P. robustoides*) (10%) (Suppl. material 2). The sandy bottom at a depth of 0.2 m was inhabited by Chironomidae larvae (43%), Oligochaeta (34%) and Amphipoda (*P. robustoides*) (23%). The greatest density and richness of chironomids, Oligochaeta and Bivalvia (except *D. polymorpha*, reaching the highest density on stones) was found on the deeper sandy bottom (depth of 0.5 and 1 m with macrophytes) (Suppl. material 2).

The CA analysis carried out on sandy substrata only (Figs. 2c and 2d) revealed associations between *D. villosus* and hard-shelled taxa (*D. polymorpha*, gastropods and sphaeriids), as well as between *P. robustoides* and Chironomidae, Oligochaeta.

3.2 Amphipod distribution in particular habitats and seasons

Pontogammarus robustoides was present in all habitats and on all dates (Fig. 3a; Suppl. material 2), though at different densities, as shown by a significant habitat type × sampling date interaction (Tab. 2a). Significant differences in its density among habitats occurred on both autumn dates (Fig. 3a; Suppl. material 3a). Its density was lower at the water line than elsewhere and, in October'16, higher on stones than in the other habitats (Fig. 3a; Suppl. material 2, 3a).

The density of *D. villosus* (Fig. 3b; Suppl. material 2) depended on a significant interaction between habitat type and sampling date (Tab. 2b). On all the dates, its density was higher on the stony bottom than among macrophytes (Fig. 3b; Suppl. material 3a), whereas it was absent from the other habitats. Its density in October'15 was higher than on the other dates (Fig. 3b; Suppl. material 3b).

Dikerogammarus juveniles, *E. ischnus*, *D. haemobaphes* and *Ch. curvispinum* occurred almost exclusively on the stony bottom (Fig. 3b; Suppl. material 2). This resulted in a

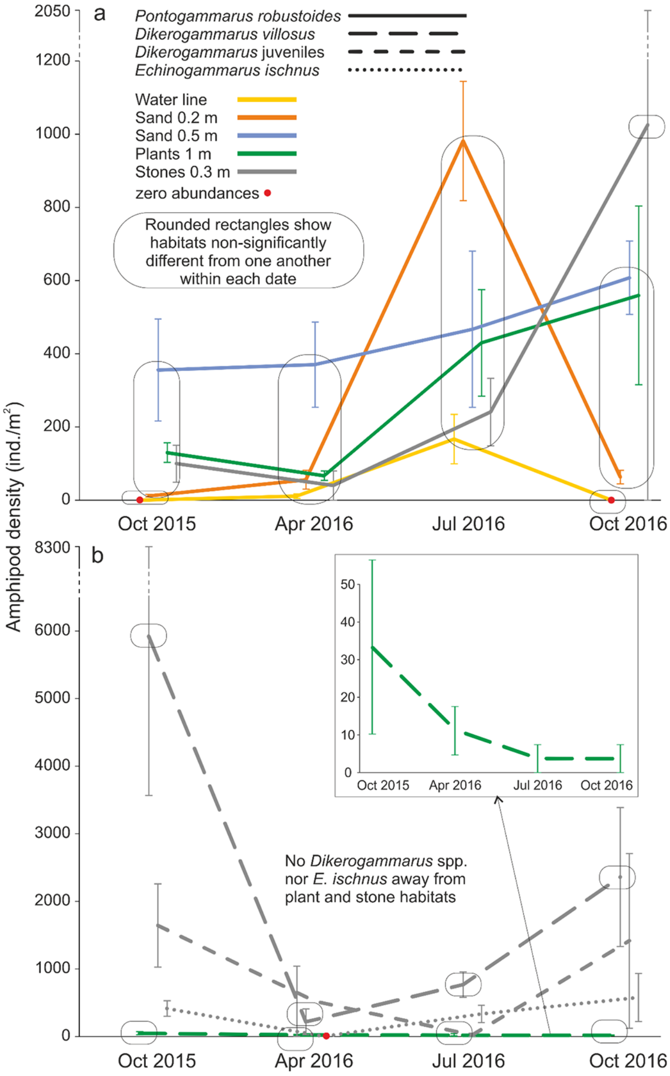

Fig. 3. Mean densities (±SE) of amphipod species/groups in various habitats on particular dates. (a) Density (ind m^{-2}) of *Pontogammarus robustoides* (b) Density (ind m^{-2}) of *Dikerogammarus villosus*, *Dikerogammarus* spp. juv. and *Echinogammarus ischnus*.

Table 2. Two-way Generalized Linear Models (Gamma distribution, log link function) to test the effect of sampling date and habitat type on the density of amphipods.

Species/group	Effect	df	$\chi 2$	*P*
(a) *Pontogammarus robustoides*	Sampling date (D)	3	327.2	<0.001*
	Habitat type (H)	4	67.9	<0.001*
	D × H	12	929.8	<0.001*
(b) *Dikerogammarus villosus*	Sampling date (D)	3	13.8	0.003*
	Habitat type (H)	4	894.4	<0.001*
	D × H	12	37.9	<0.001*
(c) *Dikerogammarus* juveniles	Sampling date (D)	3	4.5	0.215
	Habitat type (H)	4	178.3	0.001*
	D × H	12	17.9	0.119
(d) *Echinogammarus ischnus*	Sampling date (D)	3	79.5	<0.001*
	Habitat type (H)	4	948.3	<0.001*
	D × H	12	317.8	<0.001*

*Asterisks indicate statistically significant effects.

significant habitat type effect for *Dikerogammarus* juveniles (Tab. 2c). *E. ischnus* was absent in April'16, which caused a significant habitat type × sampling date interaction (Tab. 2d). *D. haemobaphes* and *Ch. curvispinum* were not formally analysed due to their very low density.

3.3 Relationships between amphipods and macroinvertebrate taxa

The density of *P. robustoides* was positively related to the occurrence of hard-shelled taxa: sphaeriid clams among macrophytes and Gastropoda on stones (Tab. 3a; Suppl. material 4). It was also positively associated with the presence of chironomids (macrophytes and stones) and oligochaetes (macrophytes). On the other hand, *P. robustoides* was negatively associated with *D. polymorpha* on plants (Tab. 3a; Suppl. material 4). Moreover, its density was positively associated with the occurrence of other amphipods: *D. villosus* and *E. ischnus* on stones (Tab. 3a; Suppl. material 4).

The occurrence of *D. villosus* was positively correlated to the presence of *D. polymorpha* and Chironomidae and negatively associated with oligochaetes on stones (Tab. 3b; Suppl. material 4). Moreover, it was positively related to the occurrence of other amphipods: *E. ischnus* and *P. robustoides* (Tab. 3b; Suppl. material 4). The occurrence of *Dikerogammarus* juveniles was positively associated with *D. polymorpha* and *E. ischnus* and negatively related to adult *D. villosus* (Tab. 3c; Suppl. material 4). The density of *E. ischnus* was positively related to that of *D. polymorpha*, Oligochaeta, *D. villosus* and *P. robustoides* and negatively associated with Gastropoda (Tab. 3d; Suppl. material 4).

4 Discussion

4.1 Associations of amphipods with hard substrata (stones, molluscs)

All the amphipods studied except *P. robustoides* were strongly associated with stony substrata. This confirms earlier experimental and field observations on *D. villosus* (Van Riel *et al.*, 2009; Kobak *et al.*, 2015; Borza *et al.*, 2017a), *D. haemobaphes* (Muskó, 1993; Wawrzyniak-Wydrowska and Gruszka, 2005; Muskó *et al.*, 2007) and *E. ischnus* (Dermott *et al.*, 1998). It should be noted that all stones in our study area were fouled by the zebra mussel, definitely modifying the conditions for the bottom fauna. Thus, amphipods in our study had no other option for the hard substratum but to have some contact with mussel colonies, as all the available stones were overgrown by mussels to a variable extent. However, we found positive relationships between these taxa in the analyses conducted separately for each habitat type, that is, irrespective of animal preferences for particular habitats. Thus, amphipod densities were higher on stones more densely overgrown by mussels. This habitat forming bivalve provides benthic organisms with shelters and food sources (Karatayev *et al.*, 1997), but also reduces oxygen resources (Effler *et al.*, 1996) and increases the amount of waste products (Gergs and Rothhaupt, 2008). The positive relationship between amphipods and mussels in our study confirms laboratory and field observations of *D. villosus* (Devin *et al.*, 2003; Boets *et al.*, 2010), *D. haemobaphes* (Kobak and Żytkowicz, 2007; Kobak *et al.*, 2009) and *E. ischnus* (Stewart *et al.*, 1998b; Van Overdijk *et al.*, 2003; González and Burkart, 2004). Several non-amphipod taxa also increase their densities and/or exhibit preferences for mussel colonies, including mayflies (DeVanna *et al.*, 2011), gastropods (Stewart *et al.*, 1999), chironomids (Wolnomiejski, 1970) and turbellarians (Stewart *et al.*, 1998a; 1998b). Nevertheless, laboratory experiments have shown a more complex picture of amphipod-mussel interactions, indicating the lack of preferences or even active avoidance of mussels by *D. villosus* (Gergs and Rothhaupt, 2008; Kobak *et al.*, 2015). This was attributed to the increased ammonium content and/or reduced oxygen concentration in a colony (Gergs and Rothhaupt, 2008; Kobak *et al.*, 2015). Our results show that the benefits of living in a mussel colony prevailed over disadvantages in the field. Probably, attributes of the dam reservoir, such as good oxygenation (Poznańska *et al.*, 2009, 2010) and fast water exchange (Giziński *et al.*, 1989) reduced negative effects of a mussel bed. This suggests that amphipods can make fine adjustments of their habitat selection depending on multiple environmental factors and select zebra mussel colonies only when the local environmental conditions permit.

On the other hand, *P. robustoides* was not related to *D. polymorpha* aggregations on stones and even negatively associated with this mollusc among macrophytes, confirming earlier laboratory observations (Kobak and Żytkowicz, 2007). However, we observed positive associations of *P. robustoides* with other hard-shelled taxa: gastropods (on stones) and sphaeriid clams (among macrophytes). The multivariate analysis suggested that *D. villosus* was also positively associated with other hard-shelled taxa on the soft bottom (Fig. 2d), where *D. polymorpha* was less common. This emphasizes the affinity of the studied amphipods to organisms increasing substratum complexity and providing solid objects (potential shelters) on the soft bottom.

4.2 Associations of amphipods with soft substrata (sand, macrophytes)

Juvenile *D. villosus* (Devin *et al.*, 2003; Kobak *et al.*, 2015) and adult *E. ischnus* (González and Burkart, 2004; Żytkowicz *et al.*, 2008) have previously been observed on macrophytes, but in our study they were either absent or rare in this habitat. Perhaps, *P. robustoides* was capable of outcompeting other taxa on these substrata, in contrast to the stony habitat, where numerous shelters allowed all the species to co-occur. *Pontogammarus robustoides* successfully defended shelters against *D. villosus* when it was introduced earlier to the environment (Kobak *et al.*, 2016), supporting this speculation. Nevertheless, the effect of various substratum types on the outcome of interference interactions between amphipod taxa is still to be checked in future experimental studies.

Pontogammarus robustoides is the least selective with regard to the substrata (Kobak and Żytkowicz, 2007; Żytkowicz *et al.*, 2008) and the most explorative of Ponto-Caspian amphipods (Kobak *et al.*, 2016). Accordingly, in our study, it was the only species reaching high densities in sandy habitats. This is consistent with earlier field observations of its occurrence in shallow sandy areas (Gruszka, 1999; Jażdżewski *et al.*, 2002; Żytkowicz *et al.*, 2008). The affinity of

Table 3. Generalized Linear Models (Gamma distribution, log link function) to test the relationships among particular amphipod groups and other macroinvertebrate taxa.

Amphipod	Habitat	Covariate	$\chi 2$	*P*	*B*
(a) *Pontogammarus robustoides*	Sand 0.2 m	Chir	3.1	0.079	
		Oli	0.4	0.534	
	Sand 0.5 m	Gastr	1.4	0.229	
		Dp	0.5	0.479	
		Sph	0.0	0.877	
		Chir	0.6	0.422	
		Oli	0.0	0.878	
	Plants	Dv	2.0	0.156	
		Gastr	0.1	0.714	
		Dp	5.9	0.015	−0.001
		Sph	62.2	<0.001	0.003
		Chir	40.4	<0.001	0.0001
		Oli	9.7	0.002	0.0001
	Stones	Dv	4.2	0.040	0.001
		Ei	9.6	0.002	0.005
		Gastr	6.3	0.012	0.00002
		Dp	2.9	0.089	
		Chir	57.2	<0.001	0.002
		Oli	0.1	0.796	
(b) *Dikerogammarus villosus*	Plants	Pr	0.7	0.401	
		Gastr	2.3	0.134	
		Dp	0.7	0.392	
		Sph	1.0	0.327	
		Chir	1.0	0.311	
		Oli	0.6	0.425	
	Stones	Pr	16.0	<0.001	0.002
		Ei	3.7	0.043	0.002
		Gastr	0.2	0.686	
		Dp	93.6	<0.001	0.0003
		Chir	20.0	<0.001	0.001
		Oli	15.8	<0.001	−0.004
(c) *Dikerogammarus* juveniles	Stones	Pr	0.6	0.427	
		Dv	11.1	0.001	−1.95
		Ei	9.0	0.003	3.23
		Gastr	2.7	0.099	
		Dp	7.1	0.008	0.6
		Chir	2.2	0.143	
		Oli	1.6	0.203	
(d) *Echinogammarus ischnus*	Stones	Pr	6.6	0.010	0.003
		Dv	7.9	0.005	0.003
		Gastr	5.7	0.017	−0.0005
		Dp	6.4	0.012	0.001
		Chir	1.9	0.165	
		Oli	7.1	0.008	0.031

Competitors/predators: Pr, *Pontogammarus robustoides*; Dv, *Dikerogammarus villosus*; Djuv, *Dikerogammarus* juveniles; Ei, *Echinogammarus ischnus.* Shelter providers: Gastr, Gastropoda; Dp, *Dreissena polymorpha*; Sph, Sphaeriidae; Chir, Chironomidae; Oli, Oligochaeta.
The models were conducted separately for each habitat type and included one of the amphipod groups as a response variable, sampling date (not shown) as a categorical factor and all other taxa present in a given habitat as covariates. Positive and negative values of regression parameters (B) shown for significant effects indicate positive and negative relationships (respectively).

P. robustoides to sandy habitats is aided by its adaptations to burrow in sediments (Poznańska *et al.*, 2013). In earlier field studies, it also reached high densities on macrophytes (Żytkowicz *et al.*, 2008; Czarnecka *et al.*, 2009). On the other hand, it preferred large-grained substrata (coarse gravel) in the laboratory (Jermacz *et al.*, 2015a), which may explain its occurrence and occasional high density on stones in our study.

4.3 Relationships within the amphipod assemblage

Amphipod taxa were mostly positively associated with one another within particular habitats. *D. villosus* was found as an effective intra-guild predator exterminating other amphipods, both native and alien (Dick and Platvoet, 2000; Krisp and Maier, 2005). Nevertheless, the opposite evidence exists, showing that the impact of *D. villosus* on amphipods is limited (Piscart *et al.*, 2010; Koester and Gergs, 2014). Our results seem to support the latter observation due to the limited number of negative relationships of *D. villosus* with other amphipods. Nevertheless, the drastic reduction in the density of *D. haemobaphes*, previously dominating in the studied area (Żytkowicz *et al.*, 2008), coincided with the arrival of *D. villosus* (ca. 2009, personal observation). Replacements between these two species were also observed at other locations (Kley and Maier, 2003).

Nevertheless, *D. villosus* had no negative effect on *E. ischnus*. They were able to share a common living space, being positively correlated with each other. Earlier, *E. ischnus* had been limited to offshore locations of the studied area (Żytkowicz and Kobak, 2008), whereas now has spread to near-shore sites. Similarly, Hellmann *et al.* (2017) and Koester *et al.* (2018) found positive correlations between *D. villosus* and *E. ischnus*. This phenomenon could be attributed to habitat complexity (MacNeil *et al.*, 2008; Piscart *et al.*, 2010) or variability of flow conditions (Borza *et al.*, 2017b) allowing spatial segregation. Perhaps, small *E. ischnus* utilizes smaller interstices among substratum particles, inaccessible for larger species (Borza *et al.*, 2018). Besides, the presence of *D. villosus* might reduce the pressure of other species on *E. ischnus*, allowing it to expand its occurrence. Such non-consumptive negative effects of *D. villosus* on large amphipods (increased mobility, migration and displacement) were observed by Van Riel *et al.* (2007), Jermacz *et al.* (2015b) and Kobak *et al.* (2016).

We observed positive relationships between amphipod species previously found as negatively associated: *P. robustoides* vs. *D. villosus* (Jermacz *et al.*, 2015b; Kobak *et al.*, 2016) and *P. robustoides* vs. *E. ischnus* (Żytkowicz and Kobak, 2008). The coexistence between *D. villosus* and *P. robustoides* may be facilitated by the presence of a top predator (fish) inhibiting their agonistic interactions (Jermacz *et al.*, 2015b). Benthivorous fish are common in the study area (Kakareko and Żbikowski, 2006), supporting this hypothesis. Another factor facilitating the amphipod coexistence in our study could be high food availability: high density of macroinvertebrates (Poznańska *et al.*, 2009, 2010), rich periphyton and detritus in mussel beds. This can reduce the predatory pressure of larger amphipods on their smaller relatives.

The only negative interaction within the amphipod assemblage in our study took place between *D. villosus* and *Dikerogammarus* juveniles. The latter (probably mostly *D. villosus*) were previously found to avoid adults in the field (Devin *et al.*, 2003) and laboratory (Kobak *et al.*, 2015). Although, in contrast to the findings by Devin *et al.* (2003), juveniles did not switch to other substrata, we observed a separation within the stony habitat. This mechanism is likely to help them avoid cannibalism of adults and limit intraspecific competition.

The high number of positive associations within the amphipod assemblage in our study may contribute to the local invasional meltdown effect (Simberloff and Von Holle, 1999). However, the confirmation of this phenomenon needs further studies involving other parts of the local invasive community.

4.4 Associations of amphipods with chironomids and oligochaetes

Adult amphipods were generally positively associated with chironomids and oligochaetes in macrophytes and stony habitats (Suppl. material 4). This might follow from preferences of both groups for the same habitats, or preferences of amphipods for other organisms as suitable food sources. The associations were observed separately for each habitat type, which partly excludes the former mechanism. Nevertheless, it is still possible that animals selected particular patches within each habitat (*i.e.* specific stones or plant patches). Ponto-Caspian gammarids were observed to prefer food of animal origin (Dick *et al.*, 2002; Krisp and Maier, 2005; Gergs and Rothhaupt, 2008; Maier *et al.*, 2011; Bącela-Spychalska and Van der Velde, 2013), suggesting the latter mechanism, although opposite evidence, pointing to the herbivorous nature of alien gammarids, also exists (Koester *et al.*, 2016, 2018). Nevertheless, they seem to be able to intake animal food at least under specific conditions. Furthermore, non-predatory *Dikerogammarus* juveniles were not associated with chironomids and oligochaetes in our study. It should be noted that relationships between adult amphipods and chironomids and oligochaetes occurred in structured habitats (plants, stones), where mobility is likely to be reduced due to the abundance of shelters, increasing the affinity to food-rich locations.

4.5 Summary

In a eutrophic, riverine, lowland dam reservoir, we observed multiple positive links existing within the studied amphipod assemblage as well as between its members and other benthic organisms. Thus, we demonstrated that in the presence of diversified, well sheltered habitats and abundant food resources, negative relationships among amphipods may be reduced, enabling the existence of a rich multispecies assemblage.

Conflict of interest

All authors declare that no conflict of interest exists.

Supplementary Material

Supplementary Material 1–4.

The Supplementary Material is available at https://www.kmae-journal.org/10.1051/kmae/2021005/olm.

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