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# The Braveheart amphipod: A review of responses of invasive *Dikerogammarus villosus* to predation signals

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Predator pressure is a fundamental force driving changes at all levels of the community structure. It may protect native ecosystems from alien species. Therefore, resistance to diverse predators resulting from a universal anti-predator strategy seems crucial for invasion success. We present a comprehensive review of the responses of an invasive amphipod *Dikerogammarus villosus* to sympatric and allopatric predator signals. We summarize diverse aspects of the gammarid anti-predator strategy, including predator identification, morphological and behavioral adaptations, effectiveness of shelter use and resistance to indirect predator effects. The response of *D. villosus* is independent of predator species (including totally allopatric taxa), which assures the high flexibility of its predator recognition system. It has harder exoskeleton and better capability of utilizing shelters compared to other gammarids, resulting in relatively high resistance to predators. Therefore, it can use predator kairomones as indirect food signals (sharing the diet with the predator) and follow the predator scent. This resistance may allow *D. villosus* to reduce the costs of its physiological responses to predators and sustain growth in their presence. This might facilitate the invasion success by increasing its competitive advantage.

1 **The Braveheart amphipod: a review of responses of invasive *Dikerogammarus villosus* to**  
2 **predation signals**

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## 9 Abstract

10 Predator pressure is a fundamental force driving changes at all levels of the community structure.  
11 It may protect native ecosystems from alien species. Therefore, resistance to diverse predators  
12 resulting from a universal anti-predator strategy seems crucial for invasion success. We present a  
13 comprehensive review of the responses of an invasive amphipod *Dikerogammarus villosus* to  
14 sympatric and allopatric predator signals. We summarize diverse aspects of the gammarid anti-  
15 predator strategy, including predator identification, morphological and behavioral adaptations,  
16 effectiveness of shelter use and resistance to indirect predator effects. The response of *D. villosus*  
17 is independent of predator species (including totally allopatric taxa), which assures the high  
18 flexibility of its predator recognition system. It has harder exoskeleton and better capability of  
19 utilizing shelters compared to other gammarids, resulting in relatively high resistance to  
20 predators. Therefore, it can use predator kairomones as indirect food signals (sharing the diet  
21 with the predator) and follow the predator scent. This resistance may allow *D. villosus* to reduce  
22 the costs of its physiological responses to predators and sustain growth in their presence. This  
23 might facilitate the invasion success by increasing its competitive advantage.

24

25 **Key words:** predator consumptive and non-consumptive effects, anti-predator strategy, invasive  
26 species, prey-predator interaction, kairomones,

27

28

## 29 Introduction

30 *Dikerogammarus villosus* (Sovinsky, 1894) is a gammarid of Ponto-Caspian origin,  
31 commonly regarded as one of the most invasive freshwater species in the world (DAISIE, 2009).  
32 In its native region, it lives in the lower courses of large rivers of the Black, Azov and Caspian  
33 Sea basins, and well as in limans formed at their outlets (Rewicz et al., 2014). It has spread in  
34 central and western Europe using the southern migration corridor sensu Bij de Vaate et al.  
35 (2002), through the Danube and Rhine rivers (Bij de Vaate et al., 2002), as well as the central  
36 corridor (through the Dnieper, Bug, Vistula and Elbe rivers) (Grabowski et al., 2007; Mastitsky  
37 & Makarevich, 2007). At present, it occupies the widest novel range (most of Europe, excluding  
38 Iberian and Scandinavian Peninsulas, but including Great Britain) and reaches the highest  
39 abundances in invaded areas within the group of several invasive Ponto-Caspian gammarid  
40 species (Rewicz et al., 2014).

41 In novel areas, *D. villosus* exerts a strong impact on local biota through several  
42 mechanisms. Firstly, it is an omnivore with the tendency to food of animal origin, efficiently  
43 preying on many invertebrate species (Krisp & Maier, 2005), including the intra-guild predation  
44 on local amphipod species (Dick & Platvoet, 2000; MacNeil & Platvoet, 2005; Kinzler et al.,  
45 2009). In general, *D. villosus* strongly prefers animal food over plants (Bacela-Spychalska & van  
46 der Velde, 2013) and grows better on it (Gergs & Rothhaupt, 2008a), but the recent studies have  
47 revealed that under certain conditions it can act as a typical herbivore, consuming mainly plant  
48 food (Hellmann et al., 2015; Koester, Bayer & Gergs, 2016; Richter et al., 2017). This points to  
49 its high plasticity and ability to use various available food resources (Mayer, Maas & Waloszek,  
50 2012), depending on local circumstances. Moreover, it efficiently competes with other  
51 gammarids, both native and other aliens, for food, shelters and optimum habitats (Dick, Platvoet

52 & Kelly, 2002; Hesselschwerdt, Necker & Wantzen, 2008; Jermacz et al., 2015a). These  
53 mechanisms are responsible for the reduction in the occupied ranges and abundances of native  
54 species, outcompeting them to less suitable habitats, sometimes even leading to local  
55 displacement (Dick, Platvoet & Kelly, 2002; Muskó et al., 2007; Hesselschwerdt, Necker &  
56 Wantzen, 2008; Platvoet et al., 2009). Furthermore, *D. villosus* can exert some more subtle  
57 effects on ecosystem functioning. For instance, being a less efficient shredder than other  
58 amphipods, displaced by its appearance, *D. villosus* may negatively affect food webs by reducing  
59 the numbers of organisms relying on shredded organic material (MacNeil et al., 2011). On the  
60 other hand, *D. villosus* does not respond to predation risk by reduction in feeding (Jermacz and  
61 Kobak 2017), therefore it can be still capable of shredding organic material when other  
62 amphipods suffer non-consumptive costs of predator pressure (Abjörnsson et al., 2000; Jermacz  
63 & Kobak, 2017; Richter et al., 2017).

64       The invasion success of *D. villosus* is regarded to result from several traits of its biology,  
65 including its fast growth rate, high fecundity, tolerance to wide ranges of abiotic factors, in  
66 particular raised salinity, as well as high plasticity and omnivory (Grabowski et al., 2007).  
67 Another trait contributing to its spread is the ability to adhere to various hard substrata and  
68 materials, including boat hulls and diving equipment (Bacela-Spychalska et al., 2013). Although  
69 it is not well adapted to air exposures (Poznańska et al., 2013), under suitable conditions, e.g.  
70 hidden in a zebra mussel colony, it can survive several days (Martens & Grabow, 2008),  
71 sufficient for successful transport to another water body.

72       Yet another important trait which can potentially affect the invasive potential of species is  
73 an effective strategy of energy saving (Becker et al., 2016) observed also under predation risk  
74 (Jermacz, Dzierżyńska-Białończyk & Kobak, 2017; Jermacz & Kobak, 2017). In recent years,

75 we have conducted a series of experimental studies on the reactions of *D. villosus* to predation  
76 cues and their potential implications to its functioning and invasiveness. In this review, we  
77 provide a synthesis of our research on these topics accompanied by the results of other authors  
78 on the biology of *D. villosus* and related amphipod species.

79

## 80 **Survey Methodology**

81 To obtain a comprehensive set of literature reports on interactions between predators and  
82 amphipod prey, we have conducted a literature survey in the Scopus database, using the  
83 following keywords: *Dikerogammarus villosus* or gammarid or amphipod combined with: an  
84 anti-predator response or predator impact or anti-predator behavior or predator defense or  
85 predator kairomone or predation risk or prey response.

86

## 87 **Prey-predator relationships in the context of biological invasions**

88 Predation is one of the most powerful forces in the nature, affecting the evolution of prey  
89 and predator species and modifying interactions among organisms (Mowles, Rundle & Cotton,  
90 2011; Turner & Peacor, 2012). On one hand, predators kill and consume prey individuals,  
91 removing them from the population and creating selective pressure, which results in so called  
92 “consumptive effects” of a predator (Werner & Peacor, 2003). On the other hand, prey species  
93 respond to the presence of predators by various forms of constitutive (permanent) and induced  
94 defenses, stimulated by the presence of a danger. These defense mechanisms include behavioral  
95 (de Meester et al., 1999; Gliwicz, 2005), morphological (Pettersson, Nilsson & Brönmark, 2000;  
96 Dzialowski et al., 2003; James & McClintock, 2017), physiological (Slos & Stoks, 2008; Glazier  
97 et al., 2011) and life-history related (Ślusarczyk, Dawidowicz & Rygielska, 2005) changes

98 aiming at reducing the probability and/or efficiency of a predator attack. Defense responses are  
99 displayed by a wide range of taxa, from protozoans (Wiąckowski, Fyda & Ciećko, 2004) through  
100 virtually all invertebrate taxa (Koperski, 1997; Lass & Spaak, 2003; Thoms et al., 2007; Kobak,  
101 Kakareko & Poznańska, 2010) to vertebrates (Gliwicz, 2005). Anti-predation mechanisms can be  
102 impressively efficient, leading to the long-term starvation of predators despite the high  
103 abundance of prey individuals (Gliwicz, 1986). Nevertheless, they are also quite costly,  
104 consuming energy utilized for the construction of defensive structures and compromising the  
105 habitat quality and/or food abundance, which finally leads to the decrease in growth rate and  
106 reproduction (Gliwicz, 1994, 2005; de Meester et al., 1999; Clinchy, Sheriff & Zanette, 2013).  
107 These energetic expenses are called “non-consumptive effects” of predator presence (Werner &  
108 Peacor, 2003) and sometimes generate losses comparable to those caused by consumptive  
109 predator effects (Preisser, Bolnick & Benard, 2005; Creel & Christianson, 2008). Therefore, the  
110 ability to adequately recognize the danger imposed by predators, depending on their feeding  
111 mode (Wudkevich et al., 1997; Wooster, 1998; Åbjörnsson et al., 2000), present condition (e.g.  
112 satiation level) (Åbjörnsson et al., 1997), abundance (Pennuto & Keppler, 2008) and size  
113 (Kobak, Kakareko & Poznańska, 2010) is crucial to the avoid unnecessary (leading to energy  
114 wasting) or maladaptive (increasing the probability of death) responses.

115 Biological invasions add a new and interesting aspect to predator-prey interactions. In old  
116 systems, coevolving together for a long time, both sides are well adjusted to each other. The  
117 responses of prey species can be fine-tuned to specific predators (Wudkevich et al., 1997;  
118 Weber, 2003; Boeing, Ramcharan & Riessen, 2006), but also predator preying modes allow them  
119 to feed efficiently on available victims (Gliwicz, 2005). However, alien species, just transported  
120 to their novel locations, face completely new, unknown communities, containing new predators



121 and new prey. On one hand, these local consumers may be unfamiliar with alien prey organisms  
122 and unable to forage on them efficiently, which can be an advantage of the newcomers (Meijer et  
123 al., 2016). On the other hand, alien species are also not adapted to their new, potential predators  
124 which may prevent them from employing efficient anti-predation mechanisms and lead to an  
125 evolutionary trap: inefficient or even maladaptive responses or the lack of reactions to a danger  
126 (Salo et al., 2007; Zuharah & Lester, 2010).

127 Recognition of a predator may be based on variable stimuli, including chemical, visual  
128 and/or mechanical cues. In the aquatic environment, due to its relative darkness and high density  
129 of the medium, chemical recognition is regarded as the most important (Wisenden et al., 2009;  
130 Jermacz, Dzierżyńska-Białończyk & Kobak, 2017). Prey organisms can potentially recognize  
131 three sources of chemical predation cues: alarm cues produced by wounded conspecifics  
132 (Czarnołęski et al., 2010; Kobak & Ryńska, 2014; Jermacz, Dzierżyńska-Białończyk & Kobak,  
133 2017), scents of consumed conspecifics included in predator faeces (Ślusarczyk & Rygielska,  
134 2004; Jermacz, Dzierżyńska-Białończyk & Kobak, 2017) or other exudates and/or direct  
135 predator metabolites, independent of their diet (Kobak, Kakareko & Poznańska, 2010; Jermacz,  
136 Dzierżyńska-Białończyk & Kobak, 2017). The first two options can be potentially utilized by  
137 alien organisms to detect unknown predators. Moreover, alien organisms can recognize predators  
138 taxonomically related to those living in their native range (Sih et al., 2010) or use learning to  
139 associate new predator scents with the perceived danger cues (Chivers, Wisenden & Smith,  
140 1996; Wisenden, Chivers & Smith, 1997; Martin, 2014). The latter approach is commonly  
141 exhibited by fish (Korpi & Wisenden, 2001), whereas in invertebrates predator recognition is  
142 often innate, displayed also by naïve individuals (Dalesman, Rundle & Cotton, 2007; Ueshima &  
143 Yusa, 2015).

144

145 **Predator recognition by *Dikerogammarus villosus***

146 For a perfect invasive species, the mechanism of predator detection should be universal,  
147 enabling the recognition and subsequent response to a novel predator without a common  
148 evolutionary history. As a consequence of an improper identification of a predator signal, prey  
149 species are exposed to higher predation due to the lack of responses or maladaptive responses  
150 (Åbjörnsson, Hansson & Brönmark, 2004; Banks & Dickman, 2007). Such a scenario was  
151 presented by Pennuto and Keppler (2008) who demonstrated that a native *Gammarus fasciatus* is  
152 able to avoid a narrower range of potential predators than an invasive *Echinogammarus ischnus*.  
153 Moreover, ineffective recognition of danger could result in costly defense reactions when the  
154 predation risk is low (Lima & Dill, 1990; Dunn, Dick & Hatcher, 2008) as was experimentally  
155 shown for *Gammarus minus* responding to a predatory fish *Luxilus chrysocephalus* (Wooster,  
156 1998). Therefore, appropriate predation risk assessment is crucial for an adequate response and  
157 optimization of energy expenditure.

158 Laboratory experiments demonstrated the ability of *D. villosus* to recognize diverse fish  
159 predators, including bottom dwellers: the racer goby *Babka gymnotrachelus* (Jermacz,  
160 Dzierżyńska-Białończyk & Kobak, 2017), European bullhead *Cottus gobio* (Sornom et al., 2012)  
161 and spiny-cheek crayfish *Orconectes limosus* (Hesselschwerdt et al., 2009), as well as fish  
162 swimming in the water column: the Eurasian perch *Perca fluviatilis*, Amur sleeper *Perccottus*  
163 *glenii* (own unpublished observations) and red-bellied piranha *Pygocentrus nattereri* (Jermacz,  
164 Dzierżyńska-Białończyk & Kobak, 2017). Among these species, the goby, bullhead and perch  
165 have co-occurred with the gammarid in its home range, the Amur sleeper and crayfish were met  
166 several dozen years ago in its novel areas, whereas the piranha originates from another continent

167 and had no previous contact with *D. villosus*. Above-mentioned studies indicate a universal  
168 method of predator recognition exhibited by *D. villosus*, effective with regard to both native and  
169 novel predatory species. A situation when potential naïve prey recognizes and responds to a  
170 novel predator can be explained by several mechanisms. For example, conspecifics can be  
171 present in the predator diet, providing information about predation risk (Chivers & Smith, 1998),  
172 as it was demonstrated for another invasive gammarid *Pontogammarus robustoides* (Jermacz,  
173 Dzierżyńska-Białończyk & Kobak, 2017). Moreover, the novel predator can be closely related to  
174 some native predators (Ferrari et al., 2007; Sih et al., 2010) and therefore release similar signals.

175 The avoidance reactions of *D. villosus* were studied by Jermacz et al. (2017b) in a flow-  
176 through Y-maze allowing gammarids to select an arm with or without the scent of predators fed  
177 on different diets. This study indicated that the avoidance of predators was induced in the  
178 presence of kairomones emitted by hungry predators (starving for 3 days), including totally  
179 allopatric, tropical *P. nattereri* (Jermacz, Dzierżyńska-Białończyk & Kobak, 2017). The  
180 avoidance response of *D. villosus* to hungry American spiny-cheek crayfish was also noted by  
181 Hesselschwerdt et al. (2009). Thus, the predator identification system of *D. villosus* seems to be  
182 independent of the presence of conspecifics in the predator's diet. Nevertheless, it should be  
183 noted that *D. villosus* did also recognize the predator diet and used it as an additional source of  
184 information about the predator status and current level of predation risk, though its responses to  
185 satiated predators did not include avoidance (see the chapter "Positive response of *D. villosus* to  
186 the predation cue" below) (Jermacz, Dzierżyńska-Białończyk & Kobak, 2017). Avoidance of a  
187 hungry predator, which is most determined to obtain food, and modifications of the responses to  
188 satiated predators suggest that *D. villosus* is capable of effective risk assessment and flexible  
189 responses, adjusted to the current situation. A similar relationship between the level of predator

190 satiation and prey response was observed in the case of a water beetle *Acilius sulcatus*,  
191 responding only to hungry perch, but not to satiated fish (Åbjörnsson et al., 1997).

192 The versatility of the predator detection mechanism of *D. villosus* could be related to the fact  
193 that active components of kairomones emitted by unrelated predators are often very similar (von  
194 Elert & Pohnert, 2000). Therefore prey can react to diverse predators, including those which  
195 evolved in isolated ecosystems. In temperate European water bodies, fish usually have broad diet  
196 ranges and most of them feed on invertebrate food at least at particular life stages (Wootton,  
197 1990; Gerking, 1994). Thus, a general response to hungry fish of particular size seems beneficial  
198 under such conditions. *Dikerogammarus villosus* is an invasive species characterized by a high  
199 dispersal rate. During the dispersal, the probability of meeting a novel predator is high, therefore  
200 species exhibiting universal defense mechanisms and/or the capability of quick adaptations are  
201 more likely to be successful invaders.

202

### 203 **Anti-predator defense mechanisms of *Dikerogammarus villosus***

#### 204 ***Site selection and shelter occupancy***

205 For a benthic organism, one of the most important elements of the anti-predator strategy is  
206 related to the optimal substratum choice. In general, prey survival rate increases with the level of  
207 substratum complexity and heterogeneity (Crowder & Cooper, 1982; Holomuzki & Hoyle, 1988;  
208 Czarnecka, 2016). Therefore, the distribution of benthic invertebrates depends on the bottom  
209 character (Czarnecka et al., 2009; Jermacz et al., 2015b) and their efficiency of using available  
210 substrata as shelters (Holomuzki & Hoyle, 1988; Kobak, Jermacz & Płachocki, 2014; Kobak et  
211 al., 2016).

212 Compared to other gammarids, *Dikerogammarus villosus* is regarded as a sit-and-wait  
213 animal, spending most of its time in a shelter (Kinzler & Maier, 2006; Kley et al., 2009; Platvoet  
214 et al., 2009; Beggel et al., 2016). Laboratory experiments have demonstrated that it prefers the  
215 substratum consisting of large gravel or stones (>6 cm in diameter), which provides them with  
216 suitable protection and enough empty space to move (Kobak, Jermacz & Dzierżyńska-  
217 Białończyk, 2015). Perhaps due to its low activity (Beggel et al., 2016), changes in shelter  
218 occupancy in the presence of predators observed in various studies are ambiguous. In the  
219 presence of benthivorous fish (European bullhead), *D. villosus* was observed to reduce its  
220 presence in the open field (i.e. outside shelters) and activity considerably, from ca. 55% under  
221 control conditions to only 20% of the total experimental time (Sornom et al., 2012). However, in  
222 other studies, the reduction in the open field occupancy in the presence of predatory gobies was  
223 only slight, though significant (Jermacz et al., 2015a; Jermacz & Kobak 2017), or no response  
224 was observed at all (Beggel et al., 2016; Jermacz et al., 2017). These discrepancies might have  
225 resulted from the varying quality of shelters that could be occupied always or only in the  
226 presence of danger, as well as from the location of food. Sornom et al. (2012) found that in the  
227 presence of predators *D. villosus* decreased its activity and stayed more often in the shelters  
228 made of holes in the solid substratum, whereas the mesh shelters were always occupied  
229 irrespective of the predator presence (>80% of the total time). In the studies by Jermacz et al.  
230 (2015a) and Jermacz & Kobak (2017) gammarids spent more than 95% of the total experimental  
231 time in gravel substratum under control conditions, which allowed for only a small, though still  
232 significant change in response to predators. Also Jermacz et al. (2017a) and Beggel et al. (2016)  
233 found that gammarids spent most of their time in gravel shelters even in the absence of predators.  
234 Jermacz & Kobak (2017) observed gammarids to limit their occupation of the open space in the

235 presence of predators when food was present in the direct vicinity of their shelters, whereas they  
236 kept exploring the unsheltered area in search for distant food sources. Thus, the presence of food  
237 can increase gammarid activity, which in turn can be reduced by the predation cue when the food  
238 is available at a short distance.

239 *Dikerogammarus villosus* often occurs on hard and complex substrata, difficult to access by  
240 predators. Stone substratum was found to offer it more protection against fish predation  
241 compared to *Gammarus fossarum*, *G. pulex* and *G. roeselii*, but this advantage disappeared on  
242 sand (Kinzler & Maier, 2006). In the wild, *D. villosus* was often found associated with zebra  
243 mussel (*Dreissena polymorpha*) colonies (Devin et al., 2003; Boets et al., 2010). Kobak et al.  
244 (2014) demonstrated that living dreissenids provided *D. villosus* with the most effective shelter  
245 against fish predators (the racer goby and Amur sleeper), compared to stones, macrophytes and  
246 shell litter. It should be noted that this shelter was also useful against a species without a  
247 common evolutionary history and exhibiting a different feeding strategy than the sympatric  
248 gobies (the Amur sleeper). This study demonstrated the positive effect of dreissenids on prey  
249 survival only in the case of *D. villosus*, but not for other invasive (*P. robustoides*) and native  
250 (*Gammarus fossarum*) species. However, in contrast to our studies, Beekey et al. (2004) showed  
251 that also native prey, including amphipods, experiences lower predation pressure in dreissenid  
252 beds.

253 Dreissenid beds can offer more effective protection to less active species, such as *D. villosus*  
254 (Kobak, Rachalewski & Bączela-Spychalska, 2016), spending most time in the shelter (Beggel et  
255 al., 2016; Jermacz & Kobak, 2017). This indicates that the presence of gregarious bivalves may  
256 promote the establishment of *D. villosus*. Dreissenid colonies, in contrast to other substratum  
257 types, form aggregations of objects bound with one another by byssal threads, hard to penetrate

258 by fish (Kobak, Kakareko & Poznańska, 2010) which, in association with the high attachment  
259 ability of *D. villosus* compared to other gammarids (Bacela-Spychalska, 2016) may make a  
260 mussel bed a perfect shelter for this species. Moreover, the hard substratum which supplies not  
261 only shelter and clinging possibility, but also food resources, such as a colony of *D. polymorpha*,  
262 seems to be an optimal habitat for the invasive gammarids and may allow them to limit their  
263 exploration activity (Jermacz & Kobak, 2017). Mussels provide both effective anti-predator  
264 protection (Beekey, McCabe & Marsden, 2004; McCabe et al., 2006; Kobak, Jermacz &  
265 Płachocki, 2014) and valuable food resources, such as organic-rich pseudofaeces and  
266 macroinvertebrate prey of increased abundance (Gergs & Rothhaupt, 2008b; Kobak et al., 2016).

267 When shelters are limited (e.g. on sandy unvegetated nearshore bottoms in the wild), *D.*  
268 *villosus* exhibits an avoidance response to the predator cue, as shown by Hesselschwerdt et al.  
269 (2009) and Jermacz et al. (2017b) in a Y-maze. This response was observed in the presence of  
270 hungry predators (starving for 3 days), likely to pose the highest danger to their potential prey.  
271 Thus, in the absence of suitable shelters and presence of a direct danger, a temporary increase in  
272 activity and active avoidance seems to be an optimum response. In natural conditions, such a  
273 response is likely to result in leaving the predator area or finding the nearest shelter, after which  
274 the activity is reduced as the predation risk decreases.

275

### 276 ***Aggregation forming***

277 Shelter choice depends not only on the substratum quality but also the presence or absence of  
278 conspecifics and heterospecific gammarids (Jermacz et al., 2015a, 2017). Laboratory  
279 experiments showed that *D. villosus* preferred shelters occupied by conspecifics over empty  
280 shelters and conspecifics located apart from shelters (Jermacz et al., 2017). Moreover, *D. villosus*

281 exhibited a preference for shelters inhabited by conspecifics over those occupied by  
282 heterospecific gammarids (*P. robustoides*), thus forming single-species aggregations (Jermacz et  
283 al., 2017). Nevertheless, in the presence of predators, the selectivity of gammarids was reduced  
284 and they grouped alike with conspecifics and heterospecifics. The choice of the substratum  
285 already inhabited by other prey individuals is an example of aggregation behavior combined with  
286 the benefits of sheltered conditions. The main advantage of the aggregation strategy is reduction  
287 of the individual risk of predation (Hamilton, 1971). On the other hand, the weakness of this  
288 strategy is the facilitation of detection by a predator, especially by species using vision for prey  
289 detection (Ioannou & Krause, 2008). However, when gammarids are aggregated under sheltered  
290 conditions, their detection seems to be difficult, especially in a situation of good color matching  
291 with their shelter, as in the case of *D. villosus* and *D. polymorpha*.

292 Notwithstanding the protective role of gammarid aggregations against predators, *D. villosus*  
293 did not increase the intensity of its grouping in shelters in the presence of predators (Sornom et  
294 al., 2012; Jermacz et al., 2017), in contrast to its relatives, e.g. *Pontogammarus robustoides*  
295 (Jermacz et al., 2017). However, also in contrast to other gammarid species, *D. villosus* exposed  
296 to predation cues formed conspecific aggregations in open places, in the absence of shelters  
297 (Jermacz et al., 2017). The effectiveness of such a response as a protection against predators was  
298 demonstrated under laboratory conditions: fish (the racer goby) avoided aggregated prey and  
299 consumed it less efficiently than singletons (Jermacz et al., 2017). This may be a consequence of  
300 the aforementioned clinging abilities of *D. villosus* (Bacela-Spychalska, 2016) and/or the  
301 hardness of its exoskeleton (Błońska et al., 2015), which are greater than those of other  
302 gammarids and increase predator handling costs, thus contributing to the resistance of such  
303 aggregations against predators. On the other hand, the easiest prey for predators were single



304 inactive individuals (Jermacz et al., 2017), indicating that this state should be avoided by  
305 gammarids seeking protection against predation.

306

### 307 ***Depth selection***

308 For an aquatic organism, the choice of an appropriate habitat is also related to water depth.  
309 Fish predation pressure at shallow nearshore locations can be significantly lower than at deeper  
310 sites (Gliwicz, Słoń & Szynkarczyk, 2006; Perez et al., 2009). The experiment conducted in a 1  
311 m deep tank with a depth gradient demonstrated that *D. villosus* in the presence of the racer goby  
312 relocated from the deepest zone, occupied preferentially under safe conditions, to the shallower  
313 bottom. Moreover, it also climbed upwards along the vertical tank walls and attached near the  
314 water surface (Kobak et al., 2017). Gobies are bottom-dwelling predators, rarely swimming  
315 freely in the water column, therefore the escape to the water column seems to be an effective  
316 response against them. Our experimental results are reflected in field observation made in Lake  
317 Balaton occupied by Ponto-Caspian Gobiidae (Ferincz et al., 2016), where *D. villosus* occurs  
318 mainly on the stones near the water surface (Muskó et al., 2007).

319

### 320 ***External factors affecting gammarid responses to predators***

321 The responses of *D. villosus* to predator cues are modified by environmental pollution. The  
322 gammarids exposed to the solution of 500 µg of cadmium per liter of water were observed to  
323 hide less often and be more active than the control individuals. Moreover, they no longer  
324 changed their behavior in response to the presence of predators (Sornom et al., 2012).

325 Yet another potential factor that can potentially affect prey responses to predators is the  
326 presence of parasites. *Dikerogammarus villosus* in European waters is parasitized by a

327 microsporidian *Cucumispora dikerogammari* (Bacela-Spychalska et al., 2012). This parasite was  
328 found to affect the behavior of its host, making it more active, but also decreasing its predation  
329 efficiency (Bacela-Spychalska, Rigaud & Wattier, 2014). This could potentially expose  
330 parasitized individuals to predator attacks and reduce their defense capabilities, though at present  
331 no evidence exists for that and further studies are needed on this topic.

332 Finally, it should be noted that not all responses of *D. villosus* to predators can be considered  
333 as anti-predator defenses (Tab. 1). The predator diet can strongly modify the behavior of  
334 gammarids and switch their responses from a typical avoidance to even preference for predator  
335 scents. See the chapter “Positive response of *D. villosus* to the predation cue” below for the  
336 details.

337

### 338 ***Dikerogammarus villosus* as prey**

339 Prey selection is a universal process, in which predators must choose among prey that  
340 differ in density and defense strategy. To optimize their fitness, predators should select those  
341 prey species whose abundance is high and hunting cost is low (Emlen, 1966). Many variables  
342 can influence prey choice. Some of them are related to prey characteristics such as prey defense  
343 mechanisms, including behavioral (Andersson et al., 1986), morphological (Bollache et al.,  
344 2006), physiological adaptations (Clinchy, Sheriff & Zanette, 2013) or to environmental factors,  
345 such as habitat structure, food and temperature (Crowder & Cooper, 1982). As a consequence of  
346 effective anti-predator defenses of prey, the predator pressure is lower than could be expected  
347 from the size of a prey population. Effective predation also depends on predator hunting strategy  
348 and its flexibility (Grabowska et al., 2009).

349 Under experimental conditions, *D. villosus*, exhibited higher survival than other  
350 gammarids, including both native and invasive species, in the presence of diverse predators, such

351 as the sympatric Ponto-Caspian gobies or the allopatric European bullhead and Amur sleeper  
352 (Kobak et al., 2014; Błońska et al., 2015; Błońska et al., 2016). The lower consumption of *D.*  
353 *villosus* compared to *Gammarus roeselii* by the turbot (*Lota lota*) was also observed by Kley et  
354 al. (2009). A similar result was shown by Błońska et al. (2015), who demonstrated that the racer  
355 goby always consumed preferentially native *G. fossarum* over *D. villosus* even if the gammarids  
356 were immobilized and unable to defend themselves. However, the goby did not exhibit any  
357 selectivity towards the waterborne chemical signals of native and invasive amphipods in a Y-  
358 maze (Błońska et al., 2015). On the other hand, Błońska et al. (2016) demonstrated that  
359 immobilized *D. villosus* and native *G. fossarum* were equally selected by other goby species (the  
360 round goby *Neogobius melanostomus* and the tubenose goby *Proterorhinus semilunaris*) and the  
361 European bullhead, whereas mobile *D. villosus* specimens were avoided, irrespective of the  
362 presence or absence of shelters. This indicates that the effective anti-predator responses of *D.*  
363 *villosus* determined its survival under the pressure of these predator species (Błońska et al.,  
364 2016). The coarse and complex substratum (gravel, stones and zebra mussel colonies) also  
365 improved the survival of *D. villosus* compared to fine substrata and other gammarid species  
366 (Kinzler & Maier, 2006; Kobak, Jermacz & Płachocki, 2014). These results suggest that the  
367 mechanisms of the resistance of *D. villosus* to different predators may vary depending on their  
368 hunting mode, size and/or other traits.

369         The effectiveness of goby predation on *D. villosus* was described in detail by Jermacz et  
370 al. (2017a). They demonstrated that under particular conditions, for example when gammarids  
371 were active or aggregated, the percentage of successful gobiid attacks was lower than 25%. The  
372 predation efficiency exceeded 50% only in the case of single inactive gammarid individuals.  
373 Moreover, even when a fish already had a gammarid in its mouth, the prey was still able to

374 escape without any visible damage. Such a low effectiveness of predation forces predatory  
375 species to multiply their effort to achieve the desired satiation level or choose alternative prey  
376 species if available. Necessity of feeding on prey generating high handling costs is unfavorable  
377 for the predator condition. For example, under laboratory conditions Błońska et al. (2015)  
378 demonstrated that gobiids fed with native *G. fossarum* or chironomid larvae grew significantly  
379 better than individuals forced to feed on *D. villosus*. In fact, the latter group of fish exhibited a  
380 weight loss after a 4-week exposure.

381         These observations confirm that *D. villosus* is a comparatively poor food item for its  
382 potential predators, and is likely to be avoided in the presence of alternative prey species, which  
383 can make it relatively safe in the natural environment. Generally, amphipods are considered as  
384 one of the most important elements of the diet of many fish species (MacNeil, Dick & Elwood,  
385 1999), however experimental results (Kobak, Jermacz & Płachocki, 2014; Błońska et al., 2015,  
386 2016) demonstrated that the role of *D. villosus* as food for the fish community could be  
387 significantly different than that of its native counterparts, often replaced by the alien species  
388 (Dick & Platvoet, 2000; Dick, Platvoet & Kelly, 2002; Beggel et al., 2016).

389

### 390 **Positive response of *Dikerogammarus villosus* to the predation cue**

391         In general, a chemical signal indicating predator presence induces a defense response  
392 responsible for the reduction of predation risk. However, in the case of omnivorous species,  
393 capable of feeding on predator faeces or their dead bodies, or partly sharing their diet, a  
394 predation signal not always indicates only a danger and, as a consequence, not always induces a  
395 defense response. Such a unique situation takes place in the case of *Dikerogammarus villosus*.  
396 As mentioned earlier, *D. villosus* actively avoided the scent of hungry predators in a Y-maze

397 (Jermacz, Dzierżyńska-Białończyk & Kobak, 2017). However, it did not exhibit an avoidance  
398 reaction to the predation cues emitted by predators fed with chironomids or other gammarids  
399 (including conspecifics). On the contrary, it showed an active preference, moving towards such a  
400 scent in a Y-maze (Jermacz, Dzierżyńska-Białończyk & Kobak, 2017). A similar response was  
401 induced by the presence of alarm cues released by crushed conspecifics and other gammarid  
402 species. This reaction suggests that this omnivorous and cannibalistic species is able to use the  
403 predation signal as a source of information about the location of a feeding ground. As shown in  
404 the above sections of this review, *D. villosus* is characterized by an effective defense strategy  
405 (Kobak, Jermacz & Płachocki, 2014; Błońska et al., 2015, 2016; Jermacz et al., 2017), therefore  
406 being relatively safe in the presence of predators, especially when alternative prey items are  
407 available in the vicinity (Jermacz et al., 2015a; Błońska et al., 2016). In such a situation, *D.*  
408 *villosus* may follow a predator to feed on its faeces or sense wounded invertebrates being its  
409 potential prey. A similar trade-off between the predator avoidance and foraging was observed in  
410 the case of *Gammarus pulex*, which in the presence of food did not respond to the predation  
411 signal, contrary to the situation when it was exposed only to predator kairomones (Szokoli et al.,  
412 2015).

413

#### 414 **Costs of the anti-predator responses of *Dikerogammarus villosus***

415       Anti-predatory defenses of prey organisms usually result in considerable energetic costs  
416 of the development of additional structures, selection of suboptimal habitats and/or decreased  
417 feeding due to the higher vigilance focused on predator detection. The impact of the presence of  
418 predators on the feeding of *D. villosus* was checked by Jermacz & Kobak (2017). The  
419 gammarids considerably limited their feeding in the presence of predators (by 95 and 74%

420 depending on the location of food, placed in the direct vicinity of shelters or away from them,  
421 respectively). Surprisingly, this response was even stronger than that of the related species *P.*  
422 *robustoides* (77 and 33%, respectively), though the latter seems to be more susceptible to  
423 predation pressure. On the other hand, no decrease in feeding was observed when single  
424 gammarids did not have to search for their food, having it available directly in their shelters. This  
425 shows that the aforementioned limitation of feeding in the open field resulted from the limited  
426 activity of gammarids (when food was located close to the shelter) or their increased vigilance in  
427 the open field (when food was distant from the shelter and no reduction in the search time was  
428 observed).

429         Nevertheless, the most important result of the cited study was the demonstration that the  
430 growth rate of *D. villosus* supplied with food in their shelters (over a period of 2 weeks) was  
431 unaffected by the presence of predators. This confirms its relatively high resistance to the non-  
432 consumptive predator effects and shows it may thrive in a good physiological condition under  
433 predatory pressure. On the other hand, *P. robustoides* under the same conditions significantly  
434 reduced its growth rate by ca. 60% when exposed to predation cues (Jermacz & Kobak, 2017).  
435 Probably, the latter species needs more energy to sustain its anti-predation defenses and/or its  
436 generally higher activity, shown in another study (Kobak, Rachalewski & Bączela-Spychalska,  
437 2016). Reduction in growth under predation risk was also observed in the case of an amphipod  
438 *Hyaella azteca* as its morphological adaptations resulted in lower predator pressure (James &  
439 McClintock, 2017).

440         Resistance of *D. villosus* to predator non-consumptive effects was also confirmed by  
441 Richter et al. (2017), who did not observe any disturbance of gammarid feeding behavior under  
442 the pressure of a benthivorous fish, the European bullhead (*Cottus gobio*). In contrast, the

443 reduction in consumption in the presence of *Cottus gobio* kairomones was noted for another  
444 gammarid species - *Gammarus pulex* (Abjörnsson et al., 2000). According to Lagrue et al.  
445 (2015), armored detritivore prey did not respond numerically to the presence of predators in  
446 contrast to non-armored species. As it was mentioned, *D. villosus* is more armored than other  
447 gammarids (Błońska et al., 2015). In consequence of trade-offs between behavioral and  
448 morphological defenses, the cost of the anti-predator responses of *D. villosus* seems to be less  
449 pronounced than that of other gammarids.

450

#### 451 **Ecological significance of the anti-predator strategy of *Dikerogammarus villosus***

452 We have shown that *D. villosus* is capable of flexible predator recognition (Jermacz,  
453 Dzierżyńska-Białończyk & Kobak, 2017) allowing it to respond to both novel and known  
454 dangers. It seems unlikely that it may benefit from the naïvety of local predators in central and  
455 western Europe, as they are used to prey on native gammarids (MacNeil, Elwood & Dick, 1999)  
456 and not very selective with regard to their benthic food, consuming also large quantities of alien  
457 amphipods (Rezsú & Specziár, 2006; Eckmann et al., 2008). Moreover, predators of Ponto-  
458 Caspian origin, sympatric to the gammarids, such as several species of gobiid fish, also have  
459 invaded the same regions and co-occur with *D. villosus* in most of its current range, including it  
460 in their diet (Grabowska & Grabowski, 2005; Borza, Eros & Oertel, 2009; Brandner et al., 2013).  
461 Therefore, its ability to easily recognize potential dangers may be one of the traits facilitating its  
462 establishment in invaded areas.

463 The efficient defense mechanisms of *D. villosus* make this species relatively resistant to  
464 predation (Kobak, Jermacz & Płachocki, 2014; Jermacz et al., 2017), which may help it in its  
465 competition with other gammarids (Jermacz et al., 2015a; Beggel et al., 2016). Other, less

466 resistant and more often preyed species are preferentially removed from the environment by  
467 predators and must spend more energy and time on anti-predator vigilance, whereas *D. villosus*,  
468 as the least preferred potential food, may thrive in the presence of predators with no negative  
469 effect on its growth (Jermacz & Kobak, 2017). Moreover, its aggressive behavior may force  
470 competing gammarid species to less suitable habitats (Platvoet et al., 2009; Jermacz et al., 2015a)  
471 or make them swim more often in the water column, which further exposes them to fish  
472 predation (Jermacz et al., 2015a; Beggel et al., 2016). This is likely to be yet another, in addition  
473 to direct intra-guild predation and competition, factor making *D. villosus* an efficient competitor  
474 displacing other species from the areas in which it appears. That is why other gammarids often  
475 avoid the presence of *D. villosus*, increasing their migrations to new areas and switching to  
476 different habitats (Dick, Platvoet & Kelly, 2002; Hesselschwerdt, Necker & Wantzen, 2008;  
477 Platvoet et al., 2009; Jermacz et al., 2015a; Kobak, Rachalewski & Bączela-Spychalska, 2016).  
478 The negative impact of *D. villosus* on competing gammarids is highest on coarse substrata  
479 (gravel and stones) (Kinzler & Maier, 2006) and is likely to be augmented by the presence of  
480 zebra mussel colonies (Kobak et al., 2014), offering it a competitive advantage over its relatives.

481         Nevertheless, the nature of interactions between *D. villosus* and its related species is by far  
482 more complex. The presence of predators does have an impact on *D. villosus* behavior (Jermacz,  
483 Dzierżyńska-Białończyk & Kobak, 2017; Kobak et al., 2017; Jermacz et al., 2017) and may tame  
484 its interspecific aggression, allowing the competing species to stay in its presence. Jermacz et al.  
485 (2015a) have demonstrated that another gammarid *P. robustoides* is easily displaced from  
486 habitats preferred by both species in a safe environment, but the presence of predatory fish  
487 changes the situation, allowing *P. robustoides* to stay in the area co-occupied by *D. villosus*. It is  
488 difficult to distinguish whether this is due to the reduction of *D. villosus* aggression or the higher



489 substratum affinity of *P. robustoides* in the presence of predators (selecting the vicinity of the  
490 stronger competitor as the lesser evil), or both. Nevertheless, individuals of both species can take  
491 advantage of staying in a group and reduce the probability of a successful predator attack  
492 (Jermacz et al., 2017). This result also shows how important it is to consider the effect of  
493 predators when studying competitive interactions between species: in a predator-free situation,  
494 which is very unlikely in the wild, the consequences of competition may be easily overestimated.

495 Moreover, as the reduction in the feeding rate of *D. villosus* in the presence of predators  
496 was observed by Jermacz & Kobak (2017), it is likely that the predatory impact of this gammarid  
497 on the local community can also be lower than expected on the basis of experiments conducted  
498 in fishless conditions.

499 Unexpectedly, given the high consumption of *D. villosus* commonly observed in the field  
500 (Kelleher et al., 1998; Grabowska & Grabowski, 2005; Eckmann et al., 2008; Borza, Eros &  
501 Oertel, 2009; Brandner et al., 2013; Czarnecka, Pilotto & Pusch, 2014), it was experimentally  
502 demonstrated that its dominance may in fact decrease the quality of food conditions for fish due  
503 to the higher difficulty of capturing and handling, as well as its weaker nutritional value leading  
504 to the poor growth on the diet based on this species, compared to the diets consisting of native  
505 gammarids or chironomid larvae (Błońska et al., 2015). Thus, although fish feed on *D. villosus* in  
506 the areas invaded by this species, it seems they would have thriven much better if this invasion  
507 had not occur and other gammarid species (usually displaced by the invader) had been available  
508 as alternative food (Błońska et al., 2015).

509

510 **Conclusion**

511 We have shown *Dikerogammarus villosus* as a species with efficient anti-predation  
512 mechanisms (both behavioral modifications and constitutive traits), relatively safe from  
513 predators and bearing lower costs of their non-consumptive effects (as indicated by its growth  
514 unaffected by the presence of fish), compared to related taxa. It can recognize sympatric and  
515 novel fish predators independent of their diet, though its precise responses are fine-tuned on the  
516 basis of food consumed by a predator, and can range from avoidance to preference. Sometimes  
517 *D. villosus* can be even attracted to a predator scent, probably utilizing their presence to locate  
518 potential food sources. Defense mechanisms of this species include activity reduction,  
519 aggregation and migration. In general, single immobile individuals outside the shelter are the  
520 most susceptible to predation. Therefore, threatened individuals try: (1) to stay in the shelter, at  
521 best co-occupied by other specimens; (2) if this is not possible, to move in search for a shelter;  
522 (3) if shelters are difficult to find, to aggregate with conspecifics, used as a substitute shelter; (4)  
523 if conspecifics are also difficult to locate (e.g. at a low density), to relocate to safer areas, e.g.  
524 away from the predator scent or to the shallower bottom. These traits are likely to give it a strong  
525 advantage in the competition with similar species, both natives and other invaders, and  
526 contribute to its invasive potential. Moreover, we have demonstrated a strong importance of  
527 predator effects on interactions among gammarid species involving *D. villosus*, which cannot be  
528 neglected in future studies on this topic. It is likely that under predatory pressure the competitive  
529 impact of *D. villosus* on other gammarids as well as its predation on zoobenthos organisms are  
530 reduced, altering its impact on local communities.

531

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535

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**Table 1** (on next page)

Anti-predation mechanisms of *Dikerogammarus villosus* and other changes induced by the presence of predators

- 1 Table 1. Anti-predation mechanisms of *Dikerogammarus villosus* and other changes induced by
- 2 the presence of predators

Trait	Comments	References
Constitutive traits (not changing in the presence of predators, but potentially protective)		
Staying inactive in the shelter	The species is less active than other gammarids	(Kley et al., 2009; Beggel et al., 2016; Kobak, Rachalewski & Bącela-Spychalska, 2016)
Aggregation in shelters	No increase in the presence of predators, but can contribute to the anti-predator protection	(Sornom et al., 2012; Jermacz et al., 2017)
Hard exoskeleton	Compared to other gammarids	(Błońska et al., 2015)
High clinging ability	Potentially may facilitate forming aggregations resistant to predators	(Bacela-Spychalska, 2016)
Changes induced by predators		
Increase in shelter occupancy time	Ambiguous results:	
	Shown in hole shelters, not shown in mesh shelters	(Sornom et al., 2012)
	Shown in the vicinity of food, not shown when food was distant	(Jermacz & Kobak, 2017)
	Weak but significant effect	(Jermacz et al., 2015a)
Utilization of coarse substrata (stones or zebra mussel colonies) as shelters	More efficient compared to other gammarid species	(Kinzler & Maier, 2006; Kobak, Jermacz & Płachocki, 2014)
Active defence	Better survival than that of <i>G. fossarum</i> in the presence of fish and without shelters	(Błońska et al., 2016)
Activity reduction	Shown in the presence of hole shelters, but not with mesh shelters	(Sornom et al., 2012)
Active avoidance	The scents of hungry predators	(Hesselschwerdt et al.,

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	(crayfish and fish), starving for 3 days, in a Y maze	2009; Jermacz, Dzierżyńska-Białończyk & Kobak, 2017)
Active preference	The scents of predators fed with conspecifics, other gammarids or chironomid larvae in a Y maze	(Jermacz, Dzierżyńska-Białończyk & Kobak, 2017)
Selection of shallower depth	In a 1-m depth gradient, in the presence of a benthic predator	(Kobak et al., 2017)
Aggregation in the open field		(Jermacz et al., 2017)
Reduction in selectivity towards conspecifics	Gammarids stop preferring conspecifics and form groups independent of species	(Jermacz et al., 2017)
Reduced consumption of food	Shown when food had to be searched for, not shown when food was present directly in the shelter	(Jermacz & Kobak, 2017)

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