

# Habitat segregation mediates predation by the benthic fish *Cottus gobio* on the exotic amphipod species *Gammarus roeseli*

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**Abstract** Predation is often considered as one of the most important biotic factor determining the success of exotic species. The freshwater amphipod *Gammarus roeseli* has widely colonized Western Europe, where it is frequently found in sympatry with the native species (*Gammarus pulex*). Previous laboratory experiments revealed that *G. roeseli* may have an advantage over *G. pulex* through differential predation by native fish (brown trout). Morphological anti-predator defences (spines) were found responsible for lower rates of predation on the invasive *G. roeseli*. Here, using both field surveys and laboratory experiments, we tested if a differential of predation exists with other fish predators naturally encountered by gammarids. The main predators present in our field site were nocturnal benthic feeders (mainly bullheads, *Cottus gobio*). Fish diet analysis showed that, compared to its global availability in the river, *G. roeseli* was less consumed than *G. pulex*. In the field, however, *G. roeseli* was found mainly in the aquatic vegetation whereas *G. pulex* was found in all habitat types. Laboratory experiments in microcosms revealed that *G. roeseli* was less prone to predation by *C. gobio* only when vegetation was present. Depending on the type of predator, the differential of predation could therefore be mediated by antipredator behaviour, and a better usage of refuges, rather than by morphological defences.

**Keywords** Anti-predator behaviour · Biological invasion · Predation

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## Introduction

Invasions of freshwater ecosystems by exotic organisms dramatically increased in the past decades and are now recognized as one of the most serious threats to biodiversity and community structure (Lodge 1993; Ricciardi and MacIsaac 2000). Understanding the underlying mechanisms of these invasions is a crucial step towards forecasting the outcomes of future invasions. Biological invasions also provide opportunities to study the ecological and evolutionary processes of interactions between species (Mooney and Cleland 2001; Sakai et al. 2001). New interspecific interactions emerging after a recent colonization by an invader may be important factors determining the success of the invasion (Wolfe 2002). Predation by native species is commonly emphasized as one of the most important biotic parameters determining the success or failure of exotic species. Establishment of a new species can be favoured when the impact of native predators is low, but the same invader might fail to establish if local predation rates are unsustainable (Robinson and Wellborn 1988; Reusch 1998; Sakai et al. 2001; Shea and Chesson 2002). Local predators may also drive community invasibility by altering the outcome of interactions between native and invasive species through enemy-mediated apparent competition, or enemy-mediated coexistence (Chañeton and Bonsall 2000; Shurin 2001; Çelik et al. 2002; González and Burkart 2004). Predator-prey interactions are influenced by a wide variety of factors. These include prey behaviour and morphology reducing the probability of predator encounter and/or capture (Abrams 2001; Holway and Suarez 1999). Interactions between predators and prey may also be modulated by the physical environment (Kinzler and Maier 2006). Habitat diversity usually provides refuges for prey and therefore reduces the risk of predation by lowering the

numbers of encounters with predators (Harrison et al. 2005; Kerfoot and Sih 1987).

Gammaridae species (Crustacea, Amphipoda) from different origins have colonized numerous new geographic areas over the last century (Jazdzewski 1980; Witt et al. 1997). Gammarids have a central position in the freshwater food web, as consumers (decay material feeders, omnivorous), but also as prey for invertebrate, fish and even bird predators (MacNeil et al. 1997). *Gammarus roeseli* (native from the balkan area, Karaman and Pinkster 1977) has colonized several Western European countries over the past century (Jazdzewski 1980). Recently, Bollache et al. (2006) showed experimentally that, compared to the smooth-bodied native species (*Gammarus pulex*), the presence of spines in *G. roeseli* reduces the predation by a native fish predator, the brown trout (*Salmo trutta*). However, this observation was not extended to other species of fish, and no data are currently available from the field on the differential of predation between gammarid species. In natural environments, gammarids have to face up different fish species, which may differ in their sensitivity to harmful stimuli. In addition, gammarids are known to select their micro-habitat according to various environmental factors (Meijering 1991; Henry and Danielopol 1999), including the presence of kairomones from predators (Starry et al. 1998; Baumgärtner et al. 2003). Their specific behaviour may therefore alter the differential of predation in nature, in addition to, or replacing, the morphological defences. For example, perception of benthic fish predation pressure alters *G. roeseli* distribution in sediments of different size (Baumgärtner et al. 2002, 2003). However, these observations were not connected directly with an evidence for a differential in predation rate.

Here we used field surveys and laboratory controlled microcosm experiments to examine the differential susceptibility to fish predation between two co-occurring amphipod species: the native *G. pulex* and the exotic *G. roeseli*. The objectives of this study were (i) to determine if predation rates differ between the two gammarids species in the field; (ii) to examine if the predators select gammarids species based on their morphology or their behaviour (distribution in habitat and usage of refuges).

## Materials and methods

### Study site

*G. pulex* and *G. roeseli* were collected from the river Ouche, in Dijon (eastern France), where the two species occur in sympatry. The river Ouche is a mid size river, with a width of 15 m and a depth of 40 cm where samples have been collected. The river bottom is covered

with sand, gravel, small stones and plants providing refuges for small benthic preys. Water flow remained constant over the sampling period. Fish predators present at the site were mainly *Cottus gobio* (bullhead), but other species like *Salmo trutta* (brown trout), *Noemacheilus barbatulus* (stone loach) and *Perca fluviatilis* (perch) can also be found (Conseil Supérieur de la Pêche, personal communication). The study site was categorized by three main habitat types based on vegetation and substrate characteristics.

### Proportion of *G. pulex* and *G. roeseli* in the river macrohabitats, in river drift and in fish diet

To determine the relative abundance of both *Gammarus* species in the benthos, 15 samples were taken in March 2002 using a Surber net sampler (31 × 33 cm, 0.1 m<sup>2</sup> aperture, and 500 µm mesh). Three samples were made in vegetation near the river edge, 6 in sand and fine gravels (diameter <1 cm), 6 in coarse gravel and stones (diameter >1 cm), these last categories of substrate being found in the middle of the river bed.

One week after benthos sampling, the relative abundance of *G. pulex* and *G. roeseli* in the drift was measured using three drift nets (50 × 50 cm, mesh size 500 µm) placed side by side in the middle of the river (water depth 35 cm, water temperature 7–8°C, dissolved oxygen 9.2–11.6 mg.l<sup>-1</sup> and conductivity 552–684 µS.cm<sup>-1</sup>, data from Rhône-Méditerranée-Corse Water Agency, <http://rdb.eaurmc.fr>). Nets fitted the river bottom closely, preventing animals from drifting underneath. The nets were emptied every hour during 24 hours, from noon on the first day to noon on the second day (two replicates, 10–11 March and 19–20 March). Every hour, samples were placed in separate tubes and preserved in 70% alcohol. In the laboratory, amphipods were sorted manually from the debris, identified to species using the keys proposed by Chevreux and Fage (1925) and counted. Data were analysed using a stepwise analysis (backward procedure) to simplify the model by removing non significant ( $P < 0.05$ ) effects and interactions.

To estimate the proportion of both *Gammarus* species in the fish diet, a total of 103 bullheads were sampled on a 500 m length river section by electric fishing the day following the second drift sample, between 0800 to 1000 h. Electric fishing was made and supervised by the Conseil Supérieur de la Pêche. In accordance with Guidelines for Electric Fishing Best Practice (Beaumont et al. 2002), the electric fishing equipment (Dream électronique “Héron”) was set to deliver a low voltage dc fields. This is because dc has good anodic galvanotaxis, induces tetanus only in the near vicinity of the electrode and has the lowest recorded rate of injury for any waveform type. Fish were immediately killed by decapitation and transferred to the laboratory, where they were dissected. Stomach contents were kept

separately and preserved in 70% alcohol. Electric-fishing occurred on a river section where densities of bullhead can reach 12 to 25 individuals per m<sup>2</sup> (Lagrue et al. 2007), a naturally common density (Andreasson 1971). Thus, removing such a number of fish is unlikely to affect the local fish density. Identifiable *Gammarus* (i.e. those not entirely digested and possessing characteristics allowing species identification, see Lagrue and Bollache 2006) found in fish stomachs were sorted and counted. Samples were preserved in 70% alcohol before gammarid identification. Observed numbers of *G. pulex* and *G. roeseli* in the different macro-habitats, drift and fish diet were compared using  $\chi^2$  goodness of fit tests, or Fisher exact test (2-tail) (Siegel and Castellan 1988).

### Microcosm experiment

The aim of this experiment was to control for possible bias in predation risk between *G. roeseli* and *G. pulex* as previously observed with the brown trout (Bollache et al. 2006), and to test whether habitat complexity influenced the predation pattern. Fish used in the laboratory experiments were also bullheads captured at the same site in October 2005. Only adult bullhead were selected for the experiments; total length ranging from 8 to 10 cm. Fish were acclimatized to laboratory conditions for 3 weeks prior to experiments in aerated tanks filled with tap water and under a constant light:dark cycle of 12:12 hours. During that period, fish were fed with gammarids randomly sampled in the study site. Microcosm experiments were performed in aquaria (40×21×25 cm) filled with a mix of 50% bullhead tank water and 50% tap water, and a washed river sand substrate. Water maintained at a temperature of 14°C and oxygenated through a water pump generating a continuous water flow in the aquaria. Four treatment were used: (1) A control group without predator, the two gammarid species and a sandy substrate, (2) a “simple habitat” group, similar to the control group, but where a bullhead was added, (3) a “complex habitat” group, where the habitat was supplemented with a piece of air brick (21.5×5×5 cm) sunk into the sand, in which both gammarids and bullheads could find refuge (a rough mimicry of field habitat with large gravels), (4) a “vegetation” group with the same complex habitat as previously described, plus a branch of vegetation (*Elodea canadensis* taken for the field site) sunk into the sand and long enough to reach the water surface (a rough mimicry of field habitat with stones and vegetation). Ten replicates per group were used.

Predators were placed into the aquaria 48 hours prior to the beginning of the experiment (MacNeil et al. 1999). Using a plastic sheet, bullheads were isolated in an area representing a third of the aquaria 15 min before gammarids

introduction. Twenty individuals of the two prey species, *G. pulex* and *G. roeseli*, were introduced in the other part of the aquaria. This density of prey (480 individuals.m<sup>-2</sup>) is close to the natural density of gammarids in our field study site. After the 15 min of acclimatization allowing gammarids to spread into the microcosm, the plastic sheet was removed to offer prey items to the fish predator. Forty eight hours later, the bullhead and all the surviving gammarids were removed and counted. This time was adjusted to prevent a too great proportion of prey being eaten by predators. Bullheads were later released, within a maximum time of one week, on their fishing site. The differential of predation between the two prey types was analysed in a paired design by Wilcoxon signed-ranks-test (Siegel and Castellan 1988). To avoid the confounding effect of prey size (Bollache et al. 2006), only male amphipods of similar size were used (mean total length=15.2 ± 0.05 for *G. pulex* and 15.5 ± 0.07 for *G. roeseli*). Measurements were taken prior to experiments (see Bollache et al. (2000) for methods).

### Results

#### Field study: proportion of *G. pulex* and *G. roeseli* in the macro-habitats, drift and in fish diet

In the river, the distribution of *Gammarus* species was significantly different across macro-habitats ( $\chi^2_2 = 235.2$ ,  $P < 0.0001$ , Table 1). *G. pulex* was equally abundant in all type of substrates, while *G. roeseli* was clearly more frequent in the vegetation. Overall, the ratio of *G. roeseli*:*G. pulex* was 1:3 (Table 1).

Number of drifting amphipods varied according to date of sampling, species and light/dark period (Backward elimination procedure, Global model  $F_{4,95}=16.44$ ,  $p < 0.0001$ ). More amphipods drifted during the second day

**Table 1** Number of individuals of *G. pulex* and *G. roeseli* sampled in the river Ouche (different macro-habitats), in the drift and in fish stomachs

Items recorded	<i>G. pulex</i>	<i>G. roeseli</i>
<i>Macro-habitats</i>		
Vegetation	304 (30.31%)	248 (74.03%)
Fine gravel and sand	170 (16.95%)	59 (17.61%)
Coarse gravel and stones	529 (52.74%)	28 (8.36%)
Total macro-habitats	1003 (100%)	335 (100%)
<i>Drift</i>		
Day drift	98 (43.17%)	9 (6.57%)
Night drift	129 (56.83%)	128 (93.43%)
Total drift	227 (100%)	137 (100%)
<i>Fish</i>		
<i>Cottus gobio</i> (n=103)	151	34

than during the first one (date effect,  $F_{1,95}=18.60$ ,  $P<0.0001$ ) but we found no difference in the proportion of individuals of each species, and in the proportion of individuals drifting during the day or the night period, between the two dates (interactions between date\*species and date\*light/dark were non significant and removed from the model). Amphipod numbers in day drift (light period) was low, increased markedly about one hour after sunset and decreased after dawn ( $F_{1,95}=27.37$ ,  $P<0.0001$ ). Overall, *G. pulex* was by far the most abundant in the drift ( $F_{1,95}=9.68$ ,  $P=0.0025$ ). In addition, the interaction between species and drift period (light/dark) was statistically significant ( $F_{2,94}=10.12$ ,  $p=0.002$ ; Table 1). Compared to the ratio of *G. roeseli*:*G. pulex* observed in the overall benthos sample, *G. roeseli* was significantly under-represented in day drift ( $\chi^2_1=16.17$ ,  $P<0.0001$ ) and over-represented in night drift ( $\chi^2_1=64.19$ ,  $P<0.0001$ ). Overall, the ratio of *G. roeseli*: *G. pulex* in the global drift was 1:1.8.

Compared to *G. roeseli*:*G. pulex* ratios in the benthos sample and in the drift, *G. roeseli* was significantly under-represented in the bullhead diet (Fisher exact test, 2-tailed,  $P<0.0001$  and  $P<0.0001$  respectively).

A more realistic comparison of fish diet vs. gammarid availability, according to fish feeding habit, was possible as *C. gobio* is a nocturnal and benthic predator, living among river gravels (Andreasson 1971; Fisher 2004). Its diet was therefore compared to the night drift composition and river bottom (both fine gravels and coarse gravels macro-habitat were pooled). *G. roeseli* was again significantly under-represented in *C. gobio* diet compared to the night drift sample (Fisher exact test, 2-tailed,  $P < 0.0001$ ), but over-represented compared to the river bottom (Fisher exact test, 2-tailed,  $P < 0.0001$ ) (Table 1). *G. roeseli* was more abundant in river vegetation than in fish diet (Fisher exact test, 2-tailed,  $P < 0.0001$ ; Table 1).

Ten stone loach (*Noemacheilus barbatulus*), a fish predator that occupies the same niche as *C. gobio*, were captured during electric fishing. Although anecdotic, it is worth noting that data obtained from these fish tend to support those obtained when using *C. gobio*. *N. barbatulus* ate the same proportion of *G. pulex* ( $N = 10$ ) and *G. roeseli* ( $N = 0$ ) as *C. gobio* (Fisher exact test, 2-tailed,  $P = 0.21$ ) and *G. roeseli* was less present in *N. barbatulus* diet compared to night drift (Fisher exact test, 2-tailed,  $P = 0.002$ ), whereas no difference in abundance was observed compared to river bottom (Fisher exact test, 2-tailed,  $P = 0.61$ ). Moreover, *G. roeseli* was again more abundant in river vegetation than in the stone loach diet (Fisher exact test, 2-tailed,  $P = 0.003$ ).

#### Microcosm experiment

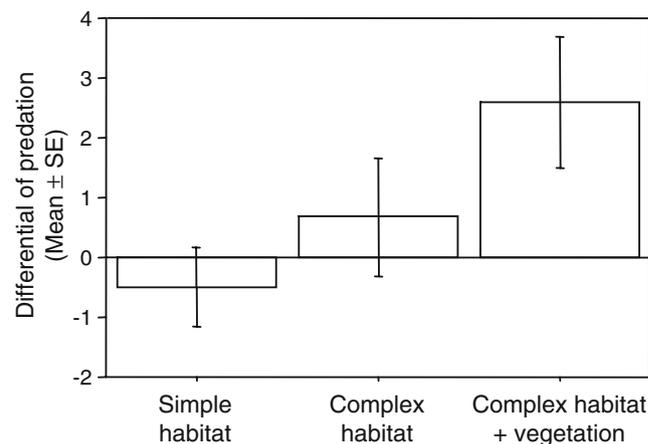
No difference in mortality was detected between *G. roeseli* and *G. pulex* in control groups (Wilcoxon matched-pairs

signed-ranks test:  $Z=0$ ,  $N=10$ ,  $P=1.00$ ). In both “simple habitat” and “complex habitat” microcosm experiments, bullheads preyed equally on *G. roeseli* and *G. pulex* (Wilcoxon matched-pairs signed-ranks test  $Z=0.63$ ,  $N=10$ ,  $P=0.53$  for simple habitat, and  $Z=1.00$ ,  $N=10$ ,  $P=0.31$  for complex habitat; Fig. 1). However, in complex habitats with vegetation, *G. roeseli* was significantly less likely to be consumed than *G. pulex*, (Wilcoxon matched-pairs signed-ranks test  $Z=2.07$ ,  $N=10$ ,  $P=0.04$ ) (Fig. 1). The presence of vegetation seems to reduce the predation pressure on the invasive species relative to the native species.

#### Discussion

Our study showed a selective predation by fish between the two *Gammarus* species, both in the field and in one type of microcosm experiment. These results indicate that bullhead preyed selectively on *G. pulex* relative to *G. roeseli* when vegetation was present. Therefore, selective predation was not based on relative prey abundance or difference in prey morphology, but more likely depend on the differential utilization of habitats by the two prey species. Gonzalez and Burkart (2004) found some similar results, although only in laboratory experiments, in another invasion context.

Predator-prey interactions depend on both predator and prey characteristics, but also on the structure of the environment. In order to minimize their risk of predation, invertebrate prey have developed many adaptations, including antipredator behaviours or chemical and morphological defences (Kerfoot and Sih 1987; Tollrian and Harvell 1999). For example, in several species of freshwater gammarids, reduced swimming activity, better use of



**Fig. 1** Differential of predation between different prey species (number of *G. pulex* eaten – number of *G. roeseli* eaten).  $N=10$  replicates (10 different bullheads), with 20 preys of each species provided per fish (see text)

shelters provided by the habitat, and morphological structures such as dorsal spines or carbonate deposit have been reported to offer protection against vertebrate predators (Andersson et al. 1986; Holomuzki and Hoyle 1990; Friberg et al. 1994; Ruff and Maier 2000; Bollache et al. 2006). In our study, lower predation rates on *G. roeseli* suggest that the two species differ in their ability to avoid predation by *C. gobio*. Differential predation between *G. roeseli* and *G. pulex* mediated by the presence of protective spines, as previously observed with trout predator (Bollache et al. 2006), might not be the only factor responsible for this pattern. *G. roeseli* found in Burgundy rivers are likely to encounter predators and habitats similar to those in its native area (Bollache L., pers. observation). Habitat structure and diversity seem to have a more important role in the differential of predation between invasive and native amphipods (Kinzler and Maier 2006). The habitat use shown by the two species, with *G. pulex* frequently found on the bottom of the river among gravel and stones whilst *G. roeseli* is more localized in aquatic vegetation, could then explain this differential of predation. In a chalk stream, *G. pulex* was shown to seasonally switch its habitat preference to avoid direct contact with its bullhead predator; bullheads displaying the opposite habitat switch (Harrison et al. 2005). However, the river investigated in this study has very different conditions of temperature, flow and water clarity to those of chalk streams and bullhead distribution is unlikely to show seasonal variations. Gammarids are consumed by a wide variety of fish (Dahl 1998): benthic (bullheads, loach) and drift feeders (or water-column predators, brown trout, perch) that feed primarily on prey drifting in the water column. Benthic predators were nevertheless more abundant in our study site than the drift predators. Differential predation between two prey species may be the result of passive and/or active anti-predator prey characteristics such as behaviour or morphology. For example, in Irish rivers, the invasive amphipod *Gammarus tigrinus* drift less than the native species *Gammarus duebeni celticus* and could therefore diminish its predation rate by drift feeders and ducks (MacNeil et al. 2003). Similarly, the usage of vegetation as preferred habitat by *G. roeseli* should be an efficient way to escape benthic predators like bullhead, while decrease activity and drift during the night, combined with the presence of anti-predator spines studies could be adaptive against predation by drift feeders (Edmunds 1974). This was in part confirmed by our results: *G. roeseli* was over-represented in *C. gobio* diet compared to the river bottom, but not compared to the vegetation. This means that, when leaving the shelter of vegetation, *G. roeseli* increased its predation risk. Intraguild predation has also been hypothesized as a primary mechanism leading to the elimination of the native amphipod *G. duebeni* by the predatory *G. pulex* (Dick et al.

1999). No such pattern was observed between *G. pulex* and *G. roeseli* in our system.

Spines of *G. roeseli* were inefficient to prevent predation by bullhead even though they previously proved to be an efficient defence against trout predators (Bollache et al. 2006). While trouts tend to chew their prey before ingestion (Bollache et al. 2006), therefore exposing themselves to the amphipod spines, bullheads have the particularity to suck up their prey (Keith and Allardi 2001), ingesting them head-first. In this case, the dorsal spines of *G. roeseli*, which have an antero-posterior orientation, are probably harmless to the predator (see Bollache et al. 2006 for picture). In addition, the observed difference of predator sensitivity to *G. roeseli* spines could be due to their degree of co-evolution with the prey. The trouts used previously in laboratory experiments were naïve to *G. roeseli* (Bollache et al. 2006), while bullheads used in the present study were natural predators of *G. roeseli*, taken from the field.

Predictions about the impact of natural predators on the success of invaders require a clear and complete understanding of all mechanisms driving predator–prey interactions. However, empirical evidences of “natural enemy escape opportunities” remain scarce (Byers 2002, Hazlett et al. 2003). Whether *G. roeseli* anti-predator behaviour has evolved in response to its establishment in new this area or was originally present still need to be elucidated, but such rapid adaptations have already been documented among invasive species (Phillips and Shine 2006). Further studies are needed to investigate the temporal stability of habitat segregation in *G. roeseli* and its efficiency as an anti-predator strategy, but we can propose that the strategies selected by this invasive species to avoid predation appear to be multi-factorial.

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