

Competition for shelter sites: Testing a possible mechanism for gammarid species displacements



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Abstract

Invasions of alien gammarid species have led to reduced abundance of many native gammarid species and earlier gammarid invaders. Intra-guild predation (IGP) has been suggested as the main mechanism causing such species displacements. This study elucidates a mechanism for species displacement that is based on competition for shelter, viz. species excluding each other from a shelter place. Preferences of *Dikerogammarus villosus* and *Gammarus roeselii* for shelter space were studied in laboratory experiments. In contrast with night conditions both species showed a strong preference for shelter sites under daytime conditions so that all experiments were carried out under permanent light conditions. Single individuals of *D. villosus* sheltered more than those of *G. roeselii*. Intraspecific competition experiments with different size classes and sexes showed that in contrast with *D. villosus*, the size class had a significant effect on the mean sheltering proportion of individuals of *G. roeselii*. When both species were brought together in a basin with a shelter site to test interspecific competition, individuals of *G. roeselii* were actively pushed out of their shelters within 24 h, while *D. villosus* showed no change in shelter. This led to a significantly increased predation risk for *G. roeselii*, which was confirmed in an experiment in which a benthic fish was added. IGP only manifested itself after 48 h, indicating that competition for shelter preceded IGP. When shelter opportunities are in short supply, shelter exclusion may be one of the initial mechanisms for gammarid species displacements.

Zusammenfassung

Invasionen von neobiotischen Gammariden haben zu einer Reduzierung der Artenvielfalt von einheimischen und früher eingewanderten Gammariden geführt. Bisher wurde Gildeninterne Prädation (intra-guild predation, IGP) als Hauptursache für diese Artenverschiebung genannt. Diese Studie beschreibt einen anderen Mechanismus für Artenverschiebung, der auf Konkurrenz um Lebensräume basiert, wobei verschiedene Arten einander an der Nutzung von Unterschlüpfen hindern. In Laborexperimenten wurden die Präferenzen für Unterschlüpfen von *Dikerogammarus villosus* und *Gammarus roeselii* untersucht. Beide Arten bevorzugten Unterschlüpfen bei Tagesbedingungen, weswegen alle Experimente unter Dauerlichtverhältnissen durchgeführt

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wurden. Einzelne *D. villosus*-Individuen suchten mehr Schutz als *G. roeselii*-Individuen. Intraspezifische Konkurrenzexperimente mit verschiedenen Größenklassen und Geschlechtern zeigten, dass, im Gegensatz zu *D. villosus*, die Größenklasse einen signifikanten Einfluss auf den durchschnittlichen Anteil der *G. roeselii*-Individuen, die Schutz suchten, hatte. Um die Konkurrenz zwischen verschiedenen Arten zu testen wurden beide Arten zusammen in einem Becken gehalten. *G. roeselii*-Individuen wurden innerhalb von 24 Stunden aktiv aus ihren Unterschlüpfen verscheucht, während *D. villosus* keine Unterschiede zeigte. Dies führte zu einem signifikant erhöhten Prädationsrisiko für *G. roeselii*, welches in einem Experiment unter Anwesenheit einer benthische Fischart bestätigt wurde. Gildeninterne Prädation (IGP) trat erst nach 48 Stunden auf, was darauf hinweist, dass der Wettbewerb um Unterschlüpfte vor IGP stattfindet. Wenn nur wenige Unterschlüpfte vorhanden sind, kann die Verdrängung aus diesen Schutzorten einer der Mechanismen für Artenverschiebungen bei Gammariden sein.

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Introduction

Various gammarids are omnivorous invaders of freshwater ecosystems (MacNeil, Dick, & Elwood 1997; Felten, Tixier, Guerold, De Billy, & Dangles 2008; Platvoet, Van der Velde, Dick, & Li 2009b) impacting macro-invertebrate communities at high population density (Kelly, Bailey, MacNeil, Dick, & McDonald 2006; Van Riel et al. 2006; Noordhuis, Van Schie, & Jaarsma 2009). Invasions by alien gammarids lead to competition with native and earlier established alien species, which can result in habitat shifts, niche reduction or even exclusion and displacement of the competitively weaker species (Leuven et al. 2009; Platvoet, Dick, MacNeil, Van Riel, & Van der Velde, 2009a; Van der Velde et al. 2009; Van Riel, Van der Velde, & Bij de Vaate, 2009). Gammarid species can be arranged from highly to less predatory (Platvoet et al. 2009a; Stoffels et al. 2011; Bacela-Spychalska & Van der Velde, 2013; Dodd et al. 2014) with the Ponto-Caspian invader *Dikerogammarus villosus* being the most predaceous compared with native and earlier invasive gammarid species. This species is a threat to freshwater ecosystems owing to its predatory behaviour (Dick & Platvoet 2000; Van Riel et al. 2006; Platvoet et al. 2009b).

Based on laboratory experiments Intra-guild predation (IGP) is considered to be the main mechanism underlying gammarid species displacement processes (Dick, Montgomery, & Elwood 1993; Dick & Platvoet 1996, 2000; MacNeil, Bigsby, Dick, Hatcher, & Dunn 2003; Kinzler & Maier 2003; Dick 2008). To reduce predation risks, prey can try to escape from a predator and search for a shelter site. Shelter sites are a valuable resource and serve as protection, breeding or resting sites and in the case of predators also as a hiding place to ambush their prey. Availability of shelter sites has profound effects on IGP (Hacker & Steneck 1990; Garvey, Stein, & Thomas 1994; Kley & Maier 2005; MacNeil, Platvoet, & Dick 2008; Platvoet et al. 2009a). Furthermore, to avoid predation gammarids use shelter sites during the daytime and leave them at night, when the risk of predation by day active fish is reduced (Elliott, 2005; Lagrue et al. 2011; Van Riel, Van der Velde, & Bij de Vaate 2011). Devin, Piscart, Beisel, and Moreteau (2003) demonstrated

that shelters appear to be size-dependent for *D. villosus* as a relationship exists between substratum particle size and the length of individuals and a partial segregation was observed according to length of the gammarids. *D. villosus* dominates the stone environment of regulated rivers, lakes and canals for shipping and avoids sand and leaf litter while *Gammarus roeselii* hardly differentiates between substrates. In the presence of *D. villosus*, *G. roeselii* coexisted by occurring in submerged vegetation in a Rhine tributary (Kley & Maier 2005) and was displaced on hard substrates in Lake Constance (Hesselschwerdt, Necker, & Wantzen 2008). The preference for and domination of *D. villosus* in the stony littoral resulted in displacement of other gammarid species that needed to find alternative shelters such as sand, clay, leaf litter or vegetation when present. In this way a zonation of gammarid species can develop by which the species coexist in the same waterbody through habitat segregation (Hesselschwerdt et al. 2008; Platvoet et al. 2009a).

We studied the sheltering of *D. villosus* and *G. roeselii* per species and in interspecific competition experiments to find out if there are shelter differences and/or competition for shelter during the daytime, which may lead to replacement of one species by the other. The hypothesis was tested by a series of laboratory experiments with both species to find out, (a) if single individuals of these species show shelter behaviour when a shelter site is offered without interaction with other individuals, (b) if different sexes and size classes of each species show differences in sheltering behaviour when a number of individuals are introduced together in a microcosm (possible interactions between size classes and sexes), (c) if there is intra- or interspecific competition for shelter when the numbers introduced are varied, (d) if there is competitive exclusion in the presence or absence of a fish predator.

Materials and methods

Animal collection and handling

G. roeselii, was collected during the period May–September in 2008 in the Schipbeek brook

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