

Combining data-driven methods and lab studies to analyse the ecology of *Dikerogammarus villosus*

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ABSTRACT

The spread of aquatic invasive species is a worldwide problem. In the aquatic environment, especially exotic Crustacea are affecting biodiversity. The amphipod *Dikerogammarus villosus* is such an exotic species in Flanders, which is rapidly spreading and probably has a serious impact on aquatic communities. The purpose of the present study was to make use of lab results, field data and modelling techniques to investigate the potential impact of this species on other macroinvertebrates. All types of prey that were used in predator–prey experiments (*Gammarus pulex*, *Gammarus tigrinus*, *Crangonyx pseudogracilis*, *Asellus aquaticus*, *Cloeon dipterum* and *Chironomus* species) were consumed by *D. villosus*, especially species that were less mobile such as the *Chironomus* species. The presence of gravel somewhat reduced predation by providing shelter to the prey. Substrate preference experiments indicated that *D. villosus* preferred a stony substrate. Using decisions trees to construct habitat suitability models based on field observations, it could be concluded that *D. villosus* is mainly found in habitats with an artificial bank structure, a high oxygen saturation and a low conductivity, which corresponds with canals with a good chemical water quality. Moreover, a synecological classification tree, based on the abundance of the taxa present in the macroinvertebrate communities, indicated that the presence of *D. villosus* negatively affected the presence of the indigenous *G. pulex*. When the laboratory experiments and the field observations are combined, it can be concluded that *D. villosus* can seriously affect macroinvertebrate communities in Flanders.

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1. Introduction

The introduction of exotic species has increased enormously during the past decades. Therefore, invasive species are considered as an important factor contributing to a change in the composition of local fauna and flora all around the world (Vitousek et al., 1996). The colonisation process is facilitated by transport routes created by man (i.e. canals) (Bij de Vaate et al., 2002), while ballast water from ships is considered to be one of the major sources of unintentional intercontinental introductions (Gollasch, 1996). One of these invasive species that is already widely distributed throughout Europe is *Dikerogammarus villosus* (Bollache et al., 2004). Due to its fast and successful spread (Vanden Bossche, 2002; Devin et al., 2003, 2005; Josens et al., 2005; Casellato et al., 2006; Pöckl, 2007), native biota in watercourses across Europe are affected by *D. villosus* through competition and predation (Devin et al., 2005; Josens et al., 2005). The dispersal of this species is mainly related to the hydrological regimes and the substrate type of the watercourse (Devin et al., 2003; Kley and Maier, 2005; Van Riel et al., 2006; 2007). The biological resistance may also play a role in the invasive behaviour of certain

species (Levine, 2000): sites with a low diversity have more vacant niches to be filled and can more easily be colonised. Other aspects that may substantially affect the dispersal of *D. villosus* are temperature, salinity (Brujls et al., 2001) and the availability of food (Devin et al., 2003). Moreover, *D. villosus* is an omnivore that predaes on other macroinvertebrates and also consumes detritus or even plant material (Mayer et al., 2008). Water plants can therefore act as a source of food, but also as a refuge, where prey can hide against predation by fish (Devin et al., 2003). Since 1997, *D. villosus* has been found in Flemish watercourses (Messiaen et al., in press). *D. villosus* was first observed in the Albertcanal, while nowadays it also occurs in other canals and other stagnant and running watercourses in Flanders. However, despite its ability to invade freshwater ecosystems very fast, *D. villosus* seems to have difficulties to invade certain watercourses in Flanders (Messiaen et al., in press).

Linking invasions with interspecific interactions is often difficult, but this information can be helpful in the prediction of the impact of invaders on the biodiversity of new host locations (Williamson, 1996; Holway and Suarez, 1999). Lab experiments have been proven useful to determine the impact of *D. villosus* on a microcosm scale (Dick and Platvoet, 2000; Dick et al., 2002). A problem with these experiments is how to translate these results to field situations. Therefore, it can be useful to make conclusions based on lab experiments combined with field observations and data-driven models.

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Several authors agree that models are becoming an essential tool for decision-making management of watercourses. Moreover, predictive modelling is a time and cost effective method to investigate the relation between the occurrence of a species and the biotic and abiotic habitat. However, knowledge about invasive species is mainly based on either laboratory experiments or field data analysed by common computational methods such as ordination techniques. Williamson (1996) claimed that invasive species are hard to predict, however, more sophisticated techniques such as artificial neural networks (Dedecker et al., 2004; D'heygere et al., 2006; Gabriels et al., 2007), decision trees (Breiman et al., 1984; Dakou et al., 2007) and Bayesian belief networks (Adriaenssens et al., 2004) have shown to have a high potential to model ecological data.

This paper aimed to assess the most important variables which determine the habitat suitability of *D. villosus* using decision trees. Moreover, a synecological decision tree was developed to assess the impact of *D. villosus* on macroinvertebrate communities. In addition, predator–prey and substrate preference experiments were conducted in the laboratory to get more insight in the behaviour of *D. villosus*. In this way, models based on field observations can be used in combination with lab experiments to make useful predictions about the effect of the invasive species *D. villosus* on native macroinvertebrate communities.

2. Materials and methods

2.1. Lab experiments

Test organisms were collected with a handnet or artificial substrate from different watercourses in Flanders as described by De Pauw and Vanhooren (1983) and De Pauw et al. (1994). The predator–prey experiments were conducted in glass aquaria of 20×20×20 cm filled with 5 L of carbon filtered water. There was a constant light–dark cycle of 10 h light and 14 h dark, similar to the natural conditions for that period (February–March). Temperature was held constant at 20±1 °C and there was a constant aeration. Prey were brought into the aquaria 1 h before the predator was released, so prey were able to settle. In a multiple prey experiment, five individuals of the predator *D. villosus* were released in the aquaria containing four individuals of five different prey (*Asellus aquaticus*, *Crangonyx pseudogracilis*, *Gammarus pulex*, *Cloeon dipterum* and *Chironomus* species) (predator–prey ratio of 1/4). Individual predator–prey experiments with *A. aquaticus*, *C. pseudogracilis*, *G. pulex*, *G. tigrinus* and *C. dipterum* as prey were also conducted to study the interaction between prey and predator in the absence of other macroinvertebrates. In these experiments, five individuals of one prey species were put together with five individuals of *D. villosus* (predator–prey ratio of 1/1). All experiments lasted 24 h after which the survival of the macroinvertebrates was checked. To check the influence of the substrate on the predation, all experiments were conducted three times: once on gravel, once on sand and once without substrate. All predator–prey experiments were replicated five times.

The substrate preference was tested in glass aquaria of 30×21.5×23 cm (L×W×H) filled with 10 L of carbon filtered water. The environmental conditions were similar to those applied in the predator–prey experiments. The preference for three substrates (sand, gravel and leaf surrogate) was tested and checked after 24 h. Each aquarium was provided with three cups (400 mL) filled with substrate and one control cup without substrate. The cups were placed randomly in the aquarium. Leaf surrogate instead of natural leaf material was used to avoid a bias that could arise because leaf not only can provide shelter, but also can be used as a food source. To determine the substrate preference of the invasive *D. villosus* and the native *G. pulex*, 10 individuals of one species were released in an aquarium. To assess if substrate preference changed if prey and predator occurred together, an additional experiment was conducted, where 10 individuals of both species were put together in one

aquarium. The substrate preference was checked after 24 h. All substrate preference experiments were replicated five times.

The difference in survival between the species exposed on different substrates was checked for the multiple prey experiment with a two-way ANOVA followed by a post-hoc Tukey-test. Survival was the dependent variable whereas substrate and species were independent variables. The difference in survival on different substrates for the single prey experiments and the substrate preference were tested with Kruskal–Wallis ANOVA followed by post-hoc multiple comparisons (Conover, 1980). The shift in substrate preference was tested by means of a repeated measures ANOVA. All statistical analyses were performed using Statistica 7.0 (Statsoft, Inc., 2004).

2.2. Modelling field data

The dataset is based on the samples collected by the Flemish Environment Agency, which monitors a large number of sampling points scattered over the different stagnant and running freshwater systems in Flanders. Macro-crustaceans were sampled in six canals (Albertcanal, canal Bocholt–Herentals, canal Dessel–Schoten, canal Dessel–Kwaadmechelen, Zuid–Willemsvaart, canal Briegden–Neerharen), one natural river (Kleine Nete) and one semi-natural watercourse (Postelvaartje) and were identified at species level. Environmental variables, hydro-morphological characteristics and data of other macroinvertebrates were available. Depending on the depth of the watercourses, macroinvertebrates were sampled by handnet or artificial substrates: the samples from the canals were gathered with artificial substrates, the samples from Kleine Nete and Postelvaartje were collected by handnet.

D. villosus was observed for the first time in 1997 in a stretch of 130 km in the Albertcanal. In 1997 and 1998, about 250 km of other canals were also invaded (Messiaen et al., in press). Therefore, if *D. villosus* could maintain its high dispersal rate, other canals such as the canal Dessel–Schoten, the natural river Kleine Nete and the semi-natural river Postelvaartje, could easily be invaded by 1999. However, if *D. villosus* could not penetrate into certain systems, this may only indicate that certain hydro-morphological, biotic or physical–chemical characteristics of the watercourses are influencing its invasion. In total, 232 presence or absence data were available with information on the hydro-morphological characteristics, physical–chemical and biotic variables. Information about the community composition and the presence or absence of other taxa were available. Individuals belonging to the Crustacea were identified to species level, while other taxa were identified to family or genus level. In 145 samples, *D. villosus* was absent, while in 87 other samples the species was present.

The independent variables consisted of physical–chemical, structural measurements (some of which are continuous and others discrete) and the abundance of other taxa, while the output variable was the presence or absence of *D. villosus*. For the construction of the decision trees, the machine learning package WEKA-J 48 algorithm (Witten and Frank, 2005) was used. This algorithm is used to construct pruned C4.5 classification trees tested at four pruning confidence factors (PCF): 0.5, 0.25, 0.1 and 0.01. Trees are constructed using the so-called 'Top–Down Induction of Decision Trees' (Quinlan, 1986), whereby a pruning factor can be used to avoid that too detailed trees are trained. The PCF has an effect on the error rate estimate in each node. The difference between error estimate of a parent node and its splits decreases when the PCF increases and vice versa. Optimal pruning is an important mechanism as it improves the transparency of the induced trees by reducing their size, as well as enhances their classification accuracy by eliminating errors that are present due to noise in the data (Goethals, 2005). Also binary splits were used for the development of the decision trees to reduce their complexity.

The trees were evaluated based on two performance measures: the percentage of Correctly Classified Instances (CCI) and the Cohen's kappa

statistic (K). Both are based on the true positive (TP), false positive (FP), false negative (FN) and true negative (TN) cases predicted by each model (Fielding and Bell, 1997). The CCI is calculated as:

$$CCI = \frac{TP + TN}{TP + FP + FN + TN} \times 100$$

The Cohen's kappa statistic is calculated as:

$$K = \left((TP + TN) - \left(\frac{(TP + FN)(TP + FP) + (FP + TN)(FN + TN)}{n} \right) \right) \div \left(n - \left(\frac{(TP + FN)(TP + FP) + (FP + TN)(FN + TN)}{n} \right) \right)$$

Gabriels et al. (2007) assess the K values as follows: 0–0.2 poor; 0.2–0.4 fair; 0.4–0.6 moderate; 0.6–0.8 substantial and 0.8–1.0 excellent. In general, a model with a CCI of at least 70% and K higher than 0.4 is considered as good (Goethals, 2005). The model training was based on different training and validation methods. Threefold, tenfold, 50-fold and 100-fold cross-validations were applied to search for optimal model performance (Goethals et al., 2007).

3. Results

3.1. Lab experiments

The multiple prey experiment showed that there was a strong predation on all macroinvertebrates in the presence of *D. villosus* (Fig. 1), while the survival of *D. villosus* was 100%. Especially midge larvae (*Chironomus* species), mayflies (*C. dipterum*) and waterlice (*A. aquaticus*) were strongly predated. The highest survival was usually found with gravel as substrate, except for *G. pulex* which had the highest survival with sand substrate. There was a significant difference in survival of the different prey ($p < 0.001$) and a significant difference in survival when using different substrates ($p = 0.040$). Also the interaction substrate*species was significant ($p = 0.031$). A post-hoc Tukey-test indicated a significant difference for the combination no substrate-stone ($p = 0.033$), but no significant difference for the combination no substrate-sand ($p = 0.64$) and sand-stone ($p = 0.23$).

The survival of the predator *D. villosus* in the single prey experiments was at least 96%. In the single prey experiments (Fig. 2), there was a

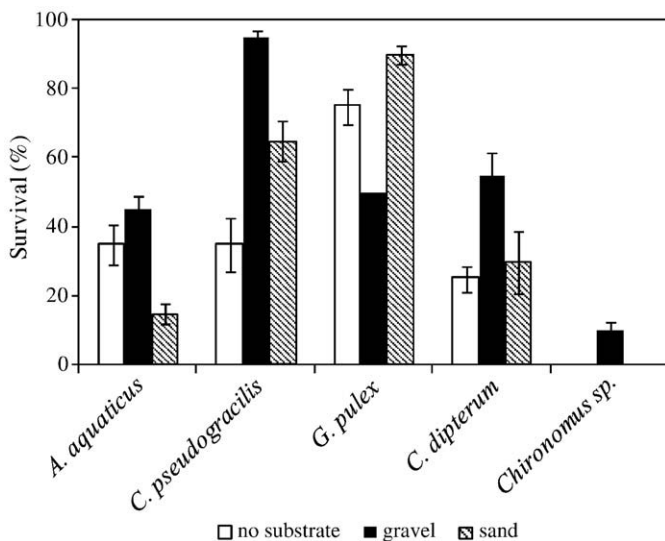


Fig. 1. Survival of the prey (*Asellus aquaticus*, *Crangonyx pseudogracilis*, *Gammarus pulex*, *Cloeon dipterum*, *Chironomus* species) after 24 h exposure to the predator *Dikerogammarus villosus* in the multiple prey experiments when exposed without substrate, on gravel and on sand.

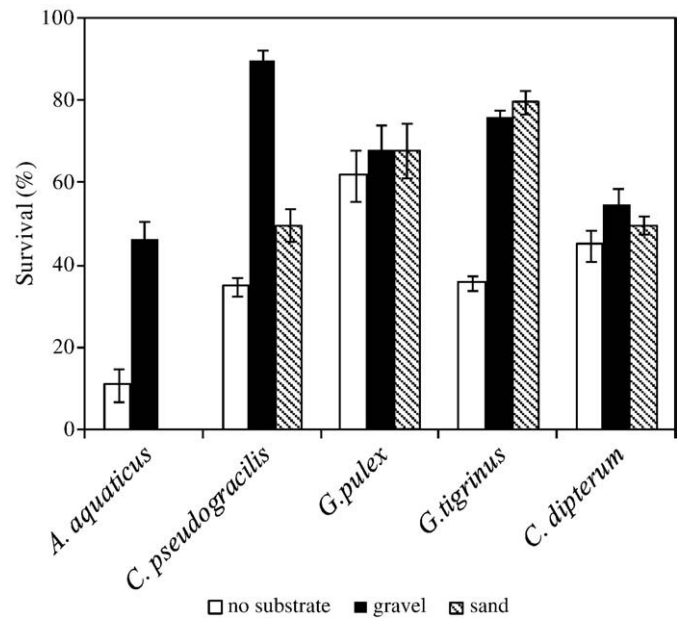


Fig. 2. Survival of the prey (*Asellus aquaticus*, *Crangonyx pseudogracilis*, *Gammarus pulex*, *G. tigrinus* and *Cloeon dipterum*) after 24 h exposure to the predator *Dikerogammarus villosus* in the single prey experiments when exposed without substrate, on gravel and on sand.

significant difference in the survival of *A. aquaticus* ($p < 0.001$), *C. pseudogracilis* ($p = 0.025$) and *G. tigrinus* ($p = 0.002$) when different substrates were used. There was no significant difference in survival on different substrates for *G. pulex* ($p = 0.97$) and *C. dipterum* ($p = 0.94$). As in the multiple prey experiment, survival was again highest on gravel in the single species experiments. Results of the multiple comparison tests are given in Table 1. Due to the difference in predator–prey ratio between the multiple and single prey experiment, it was not possible to compare the survival rate of the macroinvertebrates between these experiments.

The single species substrate preference experiments (Table 2) showed that *D. villosus* has a clear preference for gravel ($p = 0.034$): after 24 h, $63.3 \pm 5.7\%$ of the individuals were found between the gravel. *G. pulex* had no clear preference for a particular substrate ($p = 0.11$) and most of the individuals ($70 \pm 26.5\%$) were present in the water column after 24 h. When both species were exposed together, there was a significant shift in substrate preference of *G. pulex* ($p = 0.003$) and *D. villosus* ($p = 0.006$): more individuals of *D. villosus* and less individuals of *G. pulex* were present in the gravel.

3.2. Field observations

Based on the field observations (Fig. 3), it could be concluded that *D. villosus* was mainly present in watercourses with a relatively low Multimetric Macroinvertebrate Index Flanders (MMIF; Gabriels et al., in press) (index for the assessment of water quality in Flanders according to the European Water Framework Directive) and thus a poor to moderate biological water quality and a low macroinvertebrate

Table 1

Post-hoc multiple comparisons (p -values) of the survival on the different substrates during the single prey experiments (*Asellus aquaticus*, *Crangonyx pseudogracilis*, *Gammarus tigrinus*).

	No substrate–stone	Stone–sand	Sand–no substrate
<i>Asellus aquaticus</i>	0.019	<0.001	0.90
<i>Crangonyx pseudogracilis</i>	0.049	0.13	1.00
<i>Gammarus tigrinus</i>	0.049	1.00	0.02

Table 2

Average substrate preference (\pm standard deviation) for *Dikerogammarus villosus* and *Gammarus pulex* after 24 h, when exposed separately and together.

	Separately		Together	
	<i>D. villosus</i>	<i>G. pulex</i>	<i>D. villosus</i>	<i>G. pulex</i>
Sand (%)	0.0	0.0	0.0	0.0
Water (%)	30.0 \pm 17.3	70.0 \pm 26.5	16.7 \pm 15.3	63.3 \pm 25.2
Leaf surrogate (%)	6.7 \pm 11.5	13.3 \pm 5.8	13.3 \pm 5.8	23.3 \pm 20.8
Gravel (%)	63.3 \pm 5.7	16.7 \pm 20.8	70.0 \pm 10.0	6.7 \pm 5.7

diversity. *D. villosus* was mostly found in alkaline waters with a high oxygen saturation and a low conductivity, thus with a good chemical water quality (Fig. 3). The species also preferred a low percentage of sand, a low stream velocity and a reinforced or artificial bank structure and was never present in rivers with a natural bank structure and a high stream velocity (Fig. 3).

A synecological analysis of *D. villosus*, based on the abundances of 27 taxa present in the macroinvertebrate communities, resulted in a classification tree (Fig. 4). 82% of the instances were correctly classified

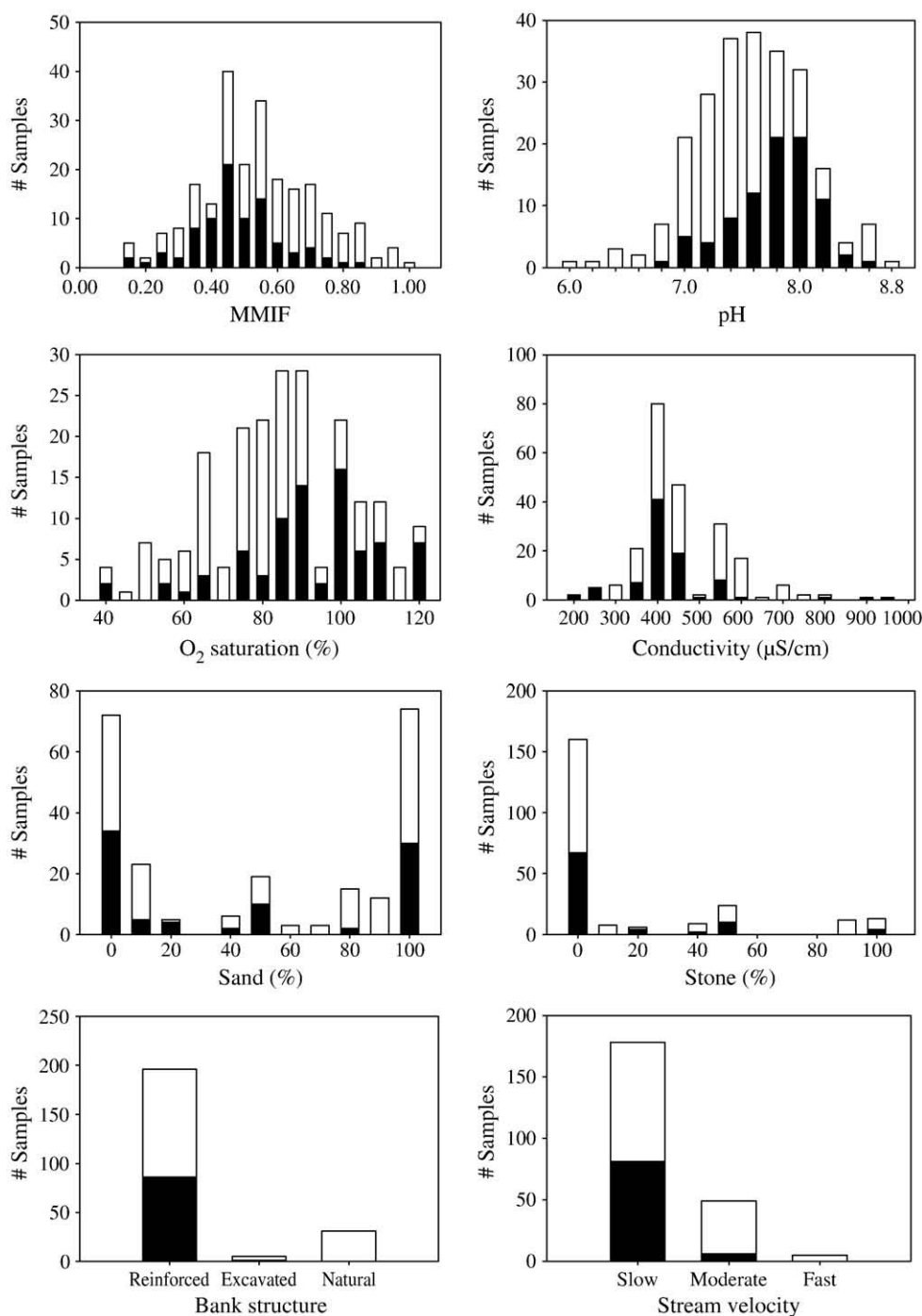


Fig. 3. Presence (black) or absence (white) of *Dikerogammarus villosus* in the field samples in function of the Multimetric Macroinvertebrate Index Flanders, pH, oxygen saturation, conductivity, sand content, stone content, bank structure and stream velocity.

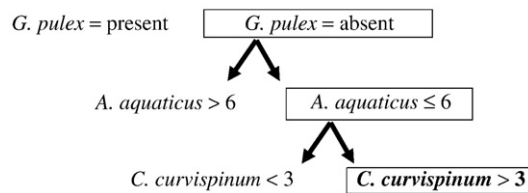


Fig. 4. Synecological analysis by means of a classification tree for *Dikerogammarus villosus* (PCF=0.01) based on the abundance of *Gammarus pulex*, *Asellus aquaticus* and *Chelicorophium curvispinum* (standard text = absence of *D. villosus*, bold text = presence of *D. villosus*).

with a $K=0.6$. Three taxa (*G. pulex*, *A. aquaticus* and *Chelicorophium curvispinum*), all belonging to the Crustacea, were important to determine the presence of *D. villosus*. The exotic *D. villosus* was present when the indigenous *G. pulex* was absent, when *A. aquaticus* was only present in very low numbers and when the invasive amphipod *C. curvispinum* occurred.

3.3. Habitat suitability model

The minima, maxima and averages of each variable are listed in Table 3. Only 11 (width, flow velocity, bank structure, bed-rock, stone, sand, water plants, algae, oxygen saturation and conductivity) of the 17 available variables, were included for the development of the decision tree. The six variables that were excluded, did not contribute to the optimisation of the decision tree.

Different pruning factors and validation methods were used to obtain an optimal tree. For a PCF of 0.01, a tree with four leaves was constructed (Fig. 5). For this tree, 77% of the instances were correctly classified and $K=0.5$. The most important variables determining the presence or absence of *D. villosus* were bank structure, oxygen saturation and conductivity. The model showed that *D. villosus* preferred rivers with artificial banks, a high oxygen saturation and a low conductivity.

A general overview of the results obtained by making use of different methods is given in Table 4. The results clearly indicate that the combined information on the presence of *D. villosus* is determined by lab studies, field data and classification trees.

4. Discussion

4.1. Impact on macroinvertebrate communities

Results of the predator–prey experiments showed a similar predatory behaviour of *D. villosus* compared to the results of previous

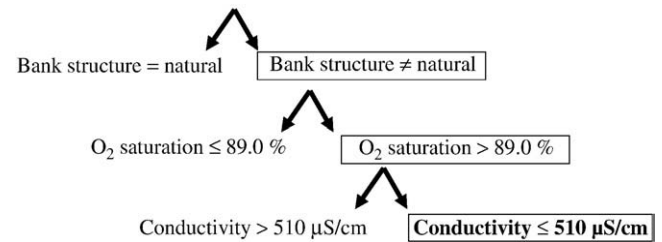


Fig. 5. Decision tree for habitat suitability for *Dikerogammarus villosus* (PCF=0.01) (standard text = absence of *D. villosus*, bold text = presence of *D. villosus*).

studies (Dick and Platvoet, 2000; Dick et al., 2002; Krisp and Maier, 2005). Not only native species, but also the exotic species *G. tigrinus* and *C. pseudogracilis* originating from North America were predated. In this way, *D. villosus* can not only have an influence on native fauna, but also on exotic species, as was already observed in the river Rhine and the river Meuse (Jensen et al., 2005; Van Riel et al., 2006). In the presence of *D. villosus*, a general decline in macroinvertebrate diversity and abundance in natural systems was observed (Van der Velde et al., 2000; Van Riel et al., 2003; Devin et al., 2005). Gammaridae used to be classified as shredders feeding with dead organic matter and leaves (Gayte and Fontvieille, 1997), where intraguild predation was seen as an exception. More recent research based on the analysis of the gut content (Platvoet et al., 2005) and numerous lab experiments (Dick et al., 2002; Kelly et al., 2002; Van Riel et al., 2003; Krisp and Maier, 2005) showed that Gammaridae are actually omnivores consuming many different types of food, where intraguild predation is more common than expected. This was also supported by our results, where *D. villosus* predated other gammarids sharing the same niche. Despite its predatory behaviour, *D. villosus* should not be seen as a carnivore: studies conducted by Platvoet et al. (2005), Maazouzi et al. (2007) and Mayer et al. (2008) showed that *D. villosus* is an omnivorous species able to eat plant as well as animal material. This diverse food spectrum probably contributed to the successful spread of this species.

The synecological classification tree revealed that the indigenous *G. pulex* and the exotic *D. villosus* did not occur together, which could be an indication of interspecific competition between both species. The interspecific interaction is most likely due to a combination of predation and competition for the same niche. The absence of *A. aquaticus* when *D. villosus* is present, is probably also due to predation. However, the absence of *D. villosus* at high abundances of *A. aquaticus* could also partly be explained by the preference of *D. villosus* for a good chemical water quality. *A. aquaticus* is a pollution tolerant species, which can also be present in high numbers when the chemical water quality is poor. The last species that was related to the presence of *D. villosus*, was *C. curvispinum*. *C. curvispinum* is a Ponto-Caspian species that established in high numbers and probably eased the invasion by *D. villosus*. Devin et al. (2003) described an association between small individuals of *D. villosus* and *C. curvispinum*, which co-evolved over a long period as they originate from the same area. However, they could not clearly define their relationship as one of competition, predation or commensalism. Nevertheless, this association fits the invasional meltdown theory (Simberloff and Von Holle, 1999), which states that positive interactions between species originating from the same area increase the probability of a successful establishment.

4.2. Substrate preference

The substrate preference experiment pointed out that *D. villosus* preferred gravel substrate, as was also found in previous lab studies (Van Riel et al., 2003; MacNeil and Platvoet, 2005; Kley and Maier, 2006; Van Riel et al., 2007). Studies conducted in the Moselle river

Table 3
Minima, maxima and averages as well as classes of the considered variables.

Variable	Minimum	Maximum	Average
Width (m)	2	125	36
Depth (cm)	20	400	95
Bed-rock (%)	0	100	25
Stones (%)	0	100	20
Sand (%)	0	100	48
Loam (%)	0	25	0.6
Sludge (%)	0	100	6
Conductivity (μS/cm)	247	1870	472
Oxygen saturation (%)	33	195	91
pH	6.9	8.7	7.7
T (°C)	7.0	26.5	18.1
Multimetric Macroinvertebrate Index Flanders	0.15	0.95	0.54
Water plants	Present–Absent		
Littoral plants	Present–Absent		
Algae	Present–Absent		
Flow velocity	Slow–Moderate–Fast		
Bank structure	Reinforced–Excavated–Natural		
<i>Dikerogammarus villosus</i>	Present (n = 87)–Absent (n = 145)		

Table 4Overview of the results obtained on the ecology of *Dikergammarus villosus* based on different methods.

Lab experiments		Field data	Classification trees
Chemical water quality		Present in rivers with high oxygen saturation, low conductivity, high pH	Present in rivers with high oxygen saturation, low conductivity Absent when <i>Asellus aquaticus</i> (pollution tolerant) is abundant
Physical habitat	Preference for gravel, absent on sand	Prefers rivers with reinforced bank structure, avoids sand substrate	Present in rivers with a non-natural bank structure <i>Gammarus pulex</i> absent due to habitat competition
Community	Influence on substrate choice of <i>Gammarus pulex</i> Predation on all prey	Causes a decrease in relative presence of <i>Gammarus pulex</i> and <i>Gammarus tigrinus</i> Present in watercourses with poor to moderate biological water quality	<i>Gammarus pulex</i> and <i>Asellus aquaticus</i> absent due to predation Co-occurrence with <i>Chelicorophium curvispinum</i>

(France) indicated that *D. villosus* was present on different types of substrates (Devin et al., 2003), however, there was a difference in preference based on the age and size of the species. Juveniles were more often present between roots and macrophytes whereas adults had a preference for boulders and stones. In the present study, the native *G. pulex* had no clear substrate preference. These results partially match with the results of MacNeil and Platvoet (2005), who found that *G. pulex* was seldom present between gravel and stones. When *G. pulex* was found between gravel, as a protection against predators, there was a difference in preference for gravel between small and large individuals of *G. pulex*. Elliott (2005) discovered that there was a day–night cycle. During day-time, small individuals had a preference for gravel whereas large individuals preferred larger stones. During the night, there was no clear substrate preference and most of the individuals swam in the water column. When *D. villosus* and *G. pulex* occurred together, we found less individuals of *G. pulex* on the gravel substrate. Also Van Riel et al. (2007) found that, although predation on *G. pulex* by *D. villosus* was rare, *G. pulex* was excluded from the preferred habitat and therefore more present in the water column. In this way, *G. pulex* can be more vulnerable to predation by fish.

4.3. Habitat suitability

The developed habitat suitability model indicated that watercourses with an artificial bank structure consisting of stones and concrete, a high oxygen saturation and a low conductivity were preferred by *D. villosus*. Also in other studies, it was indicated that *D. villosus* prefers stony substrates (Devin et al., 2003; Van Riel et al., 2006). Until 2006, *D. villosus* was not found in fast flowing rivers in the study area, as was also observed in the river Meuse (Josens et al., 2005). In other parts of Europe, *D. villosus* seemed to be excluded from smaller rivers (Bij de Vaate et al., 2002) and dispersal mainly took place through canals. *D. villosus* can thus invade artificial watercourses, however, the water quality regarding oxygen content and conductivity has to be good. The species avoided watercourses with a good biological water quality, which possibly means that natural systems with a high diversity of macroinvertebrates are more resistant to invasions than watercourses with a low diversity. Nevertheless, according to Bollache et al. (2004), it is possible that in the near future, whole drainages of natural and semi-natural rivers, can be invaded by this species. Therefore, continuous monitoring of invasive species remains necessary.

Values higher than 70% for CCI and 0.4 for *K* indicated that the presence of *D. villosus* based on physical and chemical characteristics was well predicted by the developed classification tree. However, in the present study, only a part of Flanders was investigated and especially samples from artificial watercourses were studied. These

sampling locations were selected based on the knowledge that many exotic species occurred in this region, which could possibly cause problems. If more samples of all types of watercourses were used, a more robust tree could have been constructed. In addition, the different invasion stages as described by Kolar and Lodge (2001) and Colautti and MacIsaac (2004) were not considered here since only presence or absence data were used. However, the results of the present paper indicate that classification trees are easy to handle and are able to model the habitat suitability of invasive species. Furthermore, the reliability of the models could be improved by the application of prevalence adjusted optimisation and the combination of data-driven and knowledge based models (Mouton et al., 2009). The combination of lab results, field data and models can be used to take measures against the further spread of exotic species because by combining these approaches, more valuable information can be integrated. In this way, combining these different approaches can be useful to support decision-making in water management. The establishment of exotic species often involves an ecological degradation, which is not reflected in the assessment indices. Therefore, it is appropriate to make use of other techniques to assess the impact on native communities. A next step could be the combination of decision trees with dynamic models such as cellular automata or in-stream migration models (Dedecker et al., 2006).

5. Conclusion

The invasive species *D. villosus* showed a predatory behaviour towards native and exotic macroinvertebrates. Besides its predatory behaviour, a lot of other elements like the high tolerance, the broad spectrum of food sources and the high reproductive output contribute to the success of this species. The presence of *D. villosus* is related with the bank structure, flow velocity and chemical water quality. As has also been stated in other studies, *D. villosus* invades artificial watercourses such as canals more easily because of their low flow velocity and hard substrate. Artificial connections between rivers and the global transport via ballast water help the further dispersal of this species. Natural systems might serve as a barrier against invasions, however, once established, they are becoming a part of the ecosystem and are difficult to exterminate. This paper showed that lab experiments in combination with models based on field observations gave valuable information regarding the ecology of a species. This kind of combined lab and field data complemented with models can serve as a useful tool to support decision-making in water management.

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