

Killer Shrimp (*Dikerogammarus villosus*)

Ecological Risk Screening Summary

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Photo: S. Giesen, NOAA Great Lakes Environmental Research Laboratory

1 Native Range, and Status in the United States

Native Range

From CABI (2015):

“The amphipod is native to the lower reaches of the rivers discharging into the Black Sea and Caspian Sea (Dedju, 1967; Neseemann et al., 1995; Vaate et al., 2002).”

Status in the United States

From Dettloff et al. (2015):

“Not established in North America”

Means of Introductions in the United States

From Dettloff et al. (2015):

“Due to its high tolerance to varying levels of salinity, oxygen and temperature, *D. villosus* is considered a highly likely candidate for introduction to the Great Lakes through ballast water

transport from European ships ([Bruijs] et al. 2001, Dick and Platvoet 2001, Dick et al. 2002, Grigorovich et al. 2002, MacIsaac 1999, Mills et al. 1993, Ricciardi and Rasmussen 1998).”

Remarks

From Dettloff et al. (2015):

“*Dikerogammarus bispinosus* was originally described as a subspecies of *D. villosus* (Martynov 1925), but a more recent genetic study by Müller et al. (2002) demonstrated that these two taxa should be considered to be separate species.”

“*Obesogammarus aralensis*, listed by Grigorovich et al 2003 as having a high probability of invading the Great Lakes, is most likely a synonym for *Dikerogammarus villosus*.”

2 Biology and Ecology

Taxonomic Hierarchy and Taxonomic Standing

From CABI (2015):

“Domain: Eukaryota
Kingdom: Metazoa
Phylum: Arthropoda
Subphylum: Crustacea
Class: Malacostraca
Subclass: Eumalacostraca
Order: Amphipoda
Suborder: Gammaridea
Family: Gammaridae
Genus: *Dikerogammarus*
Species: *Dikerogammarus villosus*

Dikerogammarus villosus Sowinsky 1894 is a valid amphipod species.”

Size, Weight, and Age Range

From CABI (2015):

“The maximum reported body length is 30 mm.”

From Dettloff et al. (2015):

“Males grow to be larger than females (Devin et al. 2004).”

From Devin and Beisel (2006):

“The females are sexually mature at 6 mm in length, when they reach 4 to 8 weeks old. [...] Hatching length is about 1.8 mm.”

Environment

From Devin and Beisel (2006):

“Salinity (up to 12‰), and can occupy every substratum except sand. The species is only present in areas with low current velocity.”

Climate/Range

From Dettloff et al. (2015):

“This species is able to tolerate temperatures from 0-35°C, with an optimal temperature range of 5-15°C (Bruijs et al. 2001, Maazouzi et al. 2011, van der Velde et al. 2009, Wijnhoven et al. 2003). It naturally occurs at 17 ppt but can tolerate salinities ranging from 0 to 20 ppt (Bruijs et al. 2001, Grigorovich et al. 2003).”

Distribution Outside the United States

Native

From CABI (2015):

“The amphipod is native to the lower reaches of the rivers discharging into the Black Sea and Caspian Sea (Dedju, 1967; Neseemann et al., 1995; Vaate et al., 2002).”

Introduced

From CABI (2015):

“*D. villosus* is a recent invader of Central and Western Europe freshwater ecosystems.”

“Between 1920 and 1980, *D. villosus* invaded the entire lower and middle sections of the Danube River and in 1994 it was recorded in the lower Rhine River in the Netherlands for the first time (Vaate and Klink, 1995). Further spread of the species occurred through the southern migration corridor, including the Danube River (Black Sea basin) and the Rhine River (North Sea basin) hydrologically connected through the Main-Danube canal (Vaate et al., 2002). *D. villosus* has now been documented in all major rivers of Western Europe (reviewed in Neseemann et al., 1995; Vaate et al., 2002; Jazdzewski and Konopacka, 2002; Bollache et al., 2004). In 2003, this amphipod was found in the Bug River in Poland (Konopacka, 2004), indicating its migration through the central European invasion corridor (Dnieper > Vistula > Oder > Elbe > Rhine).”

“The species has now been found in the UK (BBC, 2010; 2011a, b).”

From Grabowski and Lowry (2016):

“DISTRIBUTION

Austria (origin: alien)

Belarus (origin: alien)

Belgium (origin: alien) [...]

Czechoslovakia (origin: alien)
France (origin: alien)
Germany (origin: alien)
Great Britain (origin: alien)
Hungary (origin: alien)
Italy (origin: alien) [...]
Netherlands (origin: alien)
Poland (origin: alien) [...]
Switzerland (origin: alien) [...]
Yugoslavia (origin: alien)”

Means of Introduction Outside the United States

From CABI (2015):

“Natural dispersal of *D. villosus* occurs by active migration (Nesemann et al., 1995; Vaate et al., 2002; Jazdzewski and Konopacka, 2002; Josens et al., 2005). The speed of active *D. villosus* upstream range extension may reach up to 40 km/year, or approximately 100 m/day (Josens et al., 2005).”

“Shipping has been identified as the primary vector for accidental introductions of *D. villosus* over large distances (e.g., Vaate et al., 2002; Jazdzewski and Konopacka, 2002; Dick, 2009).”

“Intentional introductions of *D. villosus*, though possible, have not been reported.”

From Devin and Beisel (2006):

“The most likely introduction vector is shipping (ballast water and hull fouling of vessels).”

Short Description

From CABI (2015):

“The species demonstrates conspicuous pigmentation polymorphisms, with striped, spotted and uniform morphs. This polymorphism is not related to the moult cycle or the life cycle, and may rather serve as a mechanism allowing *D. villosus* to minimize the probability of being detected by predators on different substrata (Müller et al., 2002; Devin et al., 2004). The other prominent morphological features of the species include: large and powerful mandibles making *D. villosus* an effective predator (Mayer et al., 2008); long densely situated setae on the flagellum but not on other parts of antenna II; dorsal tubercles on urosome segments I and II with 3-5 spines (Eggers and Martens, 2001). Juvenile individuals resemble adults, but are much smaller in size.”

Biology

From Dettloff et al. (2015):

“*Dikerogammarus villosus* inhabits fresh/brackish water, lakes, rivers, and canals in areas with low current velocity (Devin and Beisel 2006). It can adapt to a wide variety of substrates as well

as a wide range of temperature, salinity, and oxygen levels. This species attaches itself to fastened banks, sheet-pile walls, and surface algae mats and can inhabit any substrate except sand (Crosier and [Molloy] 2006, Devin and Beisel 2006). It can also anchor itself within deep rock pools and under porous stones (Nesemann et al. 1995). In the lower Rhine, this species reaches its highest densities on hard substrates, primarily boulders, rocks, and pebbles within 3 meters of the shoreline (Kelleher et al. 1998, Platvoet et al. 2009). Different size classes of individuals tend to separate spatially, with the smallest individuals typically found on roots or macrophytes and larger individuals found in cobble (Mayer et al. 2008). In river sections of high habitat complexity, *D. villosus* is able to coexist with other species of gammarids (Kley and Maier 2005).”

“*Dikerogammarus villosus* is a omnivorous predator of many macroinvertebrates, including other gammarids, and is also able to collect detritus and to filter out suspended algae (Mayer et al. 2008). It exhibits a cannibalistic nature by occasionally eating conspecific newborns and weak adults (Devin and Beisel 2006, Dick and Platvoet 2000, Dick et al. 2002, Mordukhai-Boltovskoi 1949, Platvoet et al. 2009). Moreover, *D. villosus* has been observed to kill or injure potential prey without consuming it (Dick et al. 2002).”

“This amphipod is reproductive year round in its native range (Devin et al. 2004, Mordukhai-Boltovskoi 1949). Mean fecundity is around 30 eggs per female; however, females can lay up to 194 eggs clutch, giving this species the highest fecundity of the European gammarids (Devin et al. 2004, Kley and Maier 2003, 2006, Pöckl 2007). In winter, when water temperatures drop to between 5.5 and 10.5°C, females exhibit a growth rate between 2.2 and 2.9 mm/month, while males show a slower growth rate of about 1.3 to 1.6 mm/month. With warmer spring water temperatures of 14.5-22°C, there is no significant difference in growth rate between the two sexes, and *D. villosus* is able to grow 2.6 mm in two weeks (Devin et al. 2004). Based on these observed growth rates, *D. villosus* may reach sexual maturity in as little as one month in 20°C waters (Devin et al. 2004). Well-established populations exhibit a female-biased sex ratio, with females making up about 60% of a mature population (Devin et al. 2004). Possible reasons for this skewed ratio include males’ larger body size, which makes them more prone to fish predation, and the presence of feminizing bacteria (Devin et al. 2004).”

Human Uses

From CABI (2015):

“*D. villosus* does not have any economic value or provide any social benefit. It is not used in environmental services.”

Diseases

From CABI (2015):

“Studies on parasites of *D. villosus* are very scarce. In its native range, this amphipod has been reported to host two microsporidian species (Ovcharenko and Wita, 1996; Wattier et al., 2007), three trematode species (Chernogorenko et al., 1978; Sudarikov et al., 200[2]), and an epibiont ciliate (Fernandez-Leborans, 2001). In its introduced range, *D. villosus* has been documented to

host only microsporidian parasites (Wattier et al., 2007). There is no published information on the role parasites play in the population dynamics of *D. villosus*.”

Threat to Humans

From Dettloff et al. (2015):

“There is little or no evidence to support that *Dikerogammarus villosus* has the potential for significant socioeconomic impacts if introduced to the Great Lakes.”

“The socio-economic impact of this species on invaded areas of Western Europe is largely unknown. However, the ability of this species to consume eggs or juvenile stages of small fish creates a potential concern for fishery populations (Devin and Beisel 2006).”

From Devin and Beisel (2006):

“Health and Social Impact Unknown.”

3 Impacts of Introductions

From CABI (2015):

“Large body size, extremely voracious predatory behaviour, high fecundity and wide environmental tolerance make this amphipod a very successful invader of European waters. Invasion of *D. villosus* often results in significant local reduction or even extinction of native amphipods and other macroinvertebrates on which it preys (reviewed in Haas et al., 2002; Grabowski et al., 2007). *D. villosus* is included on the list of the 100 most invasive exotic species of Europe (Devin and Beisel, 2009), and has been deemed the worst non-native invader of England and Wales's waterways by the Environment Agency (BBC, 2011b).”

“*D. villosus* has been nicknamed the “killer shrimp” for its extremely aggressive behaviour towards native invertebrate species. Due to its large body size and well developed mouthparts, *D. villosus* is an effective predator, which kills or simply bites off much more prey than it can consume (Dick et al., 2002). In all the European aquatic systems where it has become established, *D. villosus* has largely replaced both indigenous and exotic amphipod species (Kelleher et al., 1999; Dick and Platvoet, 2000; Whitfield, 2000; Dick et al., 2002; Kley and Maier, 2003; Bollache et al., 2004; MacNeil and Platvoet, 2005; Lods-Crozet and Reymond, 2006). In addition, it readily consumes fish eggs (Casselato et al., 2007) and even attacks fish larvae (Schmidt and Josens, 2004). Due to its predatory activities, *D. villosus* significantly changes natural food webs of invaded ecosystems and occupies high trophic levels comparable to fish (Van Riel et al., 2006).”

“In a number of European waterbodies, it has been observed to outcompete both native and exotic amphipods (e.g., Kelleher et al., 1999; Dick and Platvoet, 2000; Kley and Maier, 2003; Lods-Crozet and Reymond, 2006).”

“In addition, due to its broad tolerance to salinity and temperature, *D. villosus* may survive in ballast waters of cargo ships and thus become globally dispersed in temperate areas (Bruijs et al., 2001). The examples of the most likely regions to be invaded by *D. villosus* in the near future include the Great Britain (Dick, 2009) and North America (Ricciardi and Rasmussen, 1998).”

From Dick et al. (2002):

“*Dikerogammarus villosus* predatory behaviour included shredding of prey and infliction of "bite" injuries on multiple victims. *Dikerogammarus villosus* killed significantly greater numbers of macroinvertebrates than did the native *Gammarus duebeni*, which is currently being replaced by *D. villosus*. This invader thus appears to impact on freshwater ecosystems through its exceptional predatory capabilities.”

From Truhlar et al. (2014):

“The alien amphipod *Dikerogammarus villosus* is spreading rapidly through Europe where it has displaced native gammarids including *Gammarus pulex*. The resultant change in shredder communities has considerable implications for the dynamics of resource availability within invaded systems. [...] The leaf (*Salix alba*) shredding efficiency, defined as the leaf mass consumed over the 4-day experiment per amphipod-day, was measured for *D. villosus* and *G. pulex* under extreme temperature and conductivity conditions, in single species and mixed species aquaria. [...] At high temperatures (25°C), *D. villosus* shredded significantly more leaves than size-matched *G. pulex*. An inspection of daily leaf disc consumption found that the two species showed significantly different leaf consumption patterns, with *D. villosus* consuming more leaves earlier in the experiment. These results suggest that *D. villosus* invasion could lead to ecosystem-level changes in leaf processing, such as greater leaf processing earlier in autumn and at higher temperatures, which could alter nutrient dynamics and community assemblages within invaded systems.”

From Casellato et al. (2007):

“Our experiments show that whitefish eggs are most highly appreciated by *D. villosus*, together with chironomid larvae, at least in a laboratory mesocosm. [...] Our laboratory experiments demonstrate that this species is able to break egg shells, using its mandibles and gnathopods. Fish production in Lake Garda, and possibly of other European lakes invaded by this species (Bollache 2004), could be seriously threatened if *D. villosus* populations continue to increase.”

The following search was used to identify literature on impacts of introduction:

https://scholar.google.com/scholar?hl=en&q=%22dikerogammarus+villosus%22+impacts&btnG=&as_sdt=1%2C24&as_sdtp=

4 Global Distribution

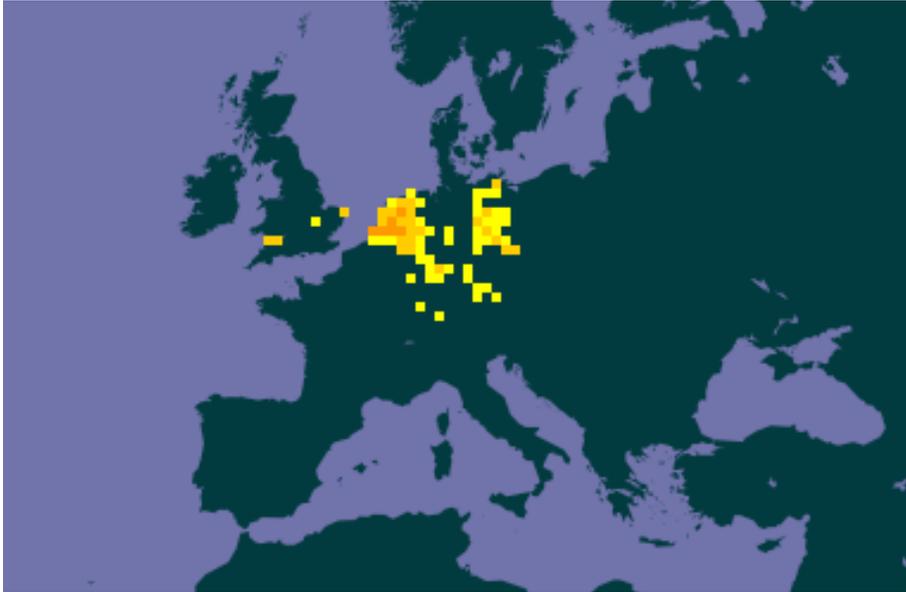


Figure 1. Map of known global distribution of *Dikerogammarus villosus*. Map from GBIF (2013).

5 Distribution Within the United States

From Dettloff et al. (2015):

“Not established in North America”

6 Climate Matching

Summary of Climate Matching Analysis

The climate match (Sanders et al. 2014; 16 climate variables; Euclidean Distance) was high around the Great Lakes and in scattered locations across the Rocky Mountain states and Desert Southwest. Low match occurred over much of the southern and central portions of the United States and along all ocean coastlines. Climate 6 match indicated that the contiguous U.S. has a high climate match. The range for a high climate match is 0.103 and greater; Climate 6 match of *Dikerogammarus villosus* is 0.154.

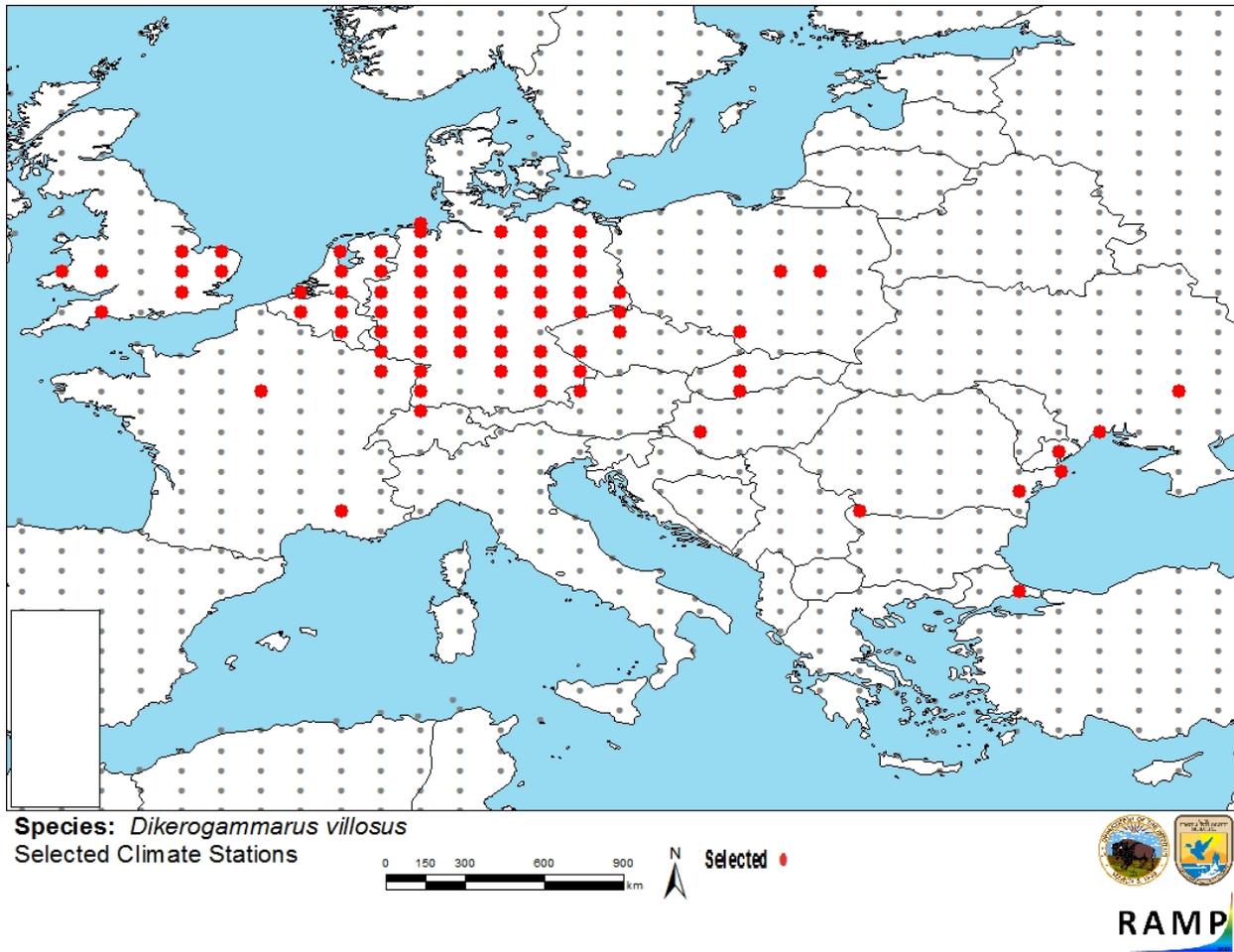


Figure 2. RAMP (Sanders et al. 2014) source map showing weather stations selected as source locations (red) and non-source locations (gray) for *Dikerogammarus villosus* climate matching. Source locations from GBIF (2013) and Rewicz et al. (2015).

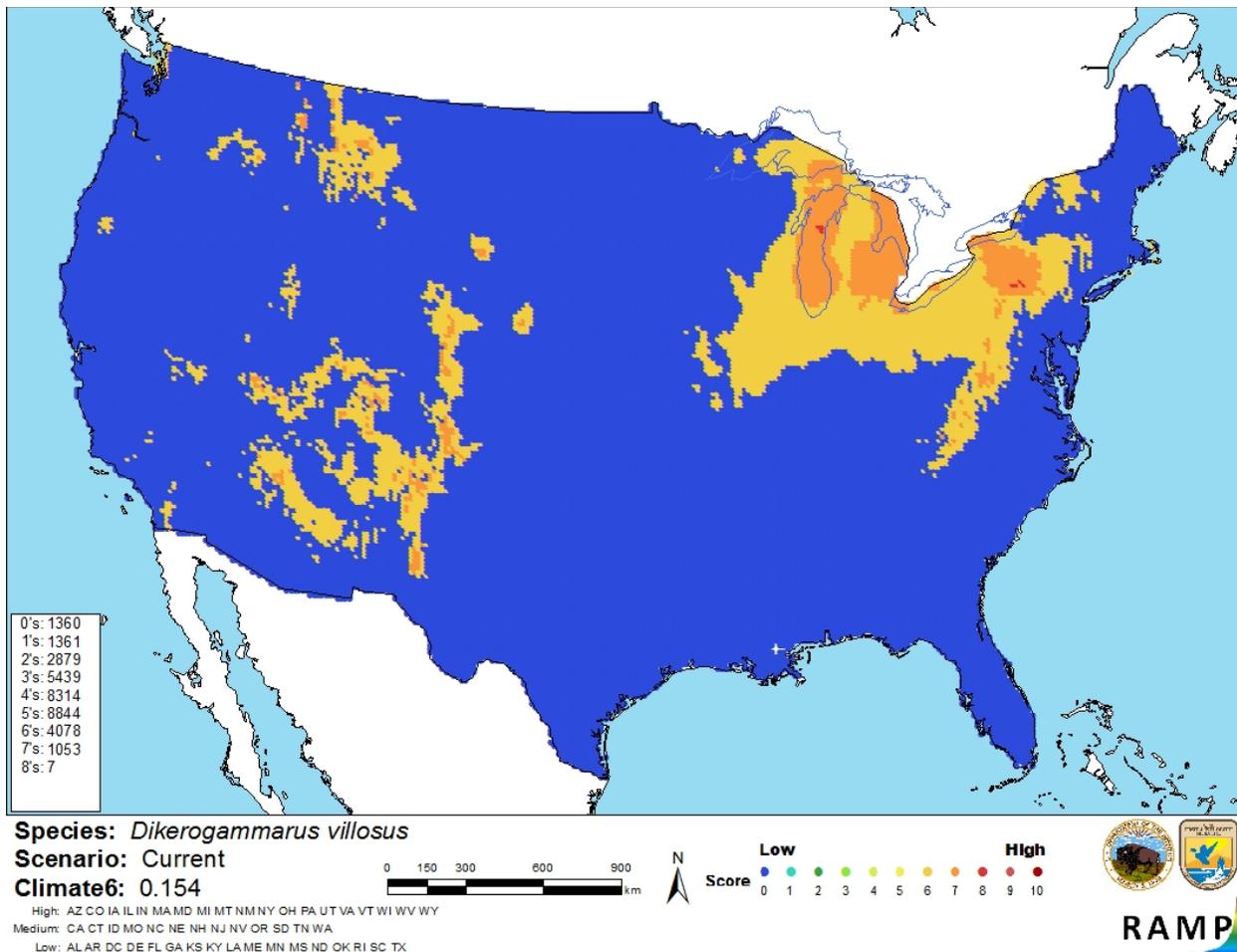


Figure 3. Map of RAMP (Sanders et al. 2014) climate matches for *Dikerogammarus villosus* in the contiguous United States based on source locations reported by GBIF (2013) and Rewicz et al. (2015). 0= Lowest match, 10=Highest match. Counts of climate match scores are tabulated on the left.

The “High”, “Medium”, and “Low” climate match categories are based on the following table:

Climate 6: Proportion of (Sum of Climate Scores 6-10) / (Sum of total Climate Scores)	Climate Match Category
$0.000 \leq X \leq 0.005$	Low
$0.005 < X < 0.103$	Medium
≥ 0.103	High

7 Certainty of Assessment

The biology and ecology of *D. villosus* are well-known. Negative impacts from introductions and spread of this species are adequately documented in the scientific literature. No further information is needed to evaluate the negative impacts the species is having where introduced. Certainty of this assessment is high.

8 Risk Assessment

Summary of Risk to the Contiguous United States

D. villosus is establishing and causing adverse impacts outside its native range, and is continuing to spread to new locations. Native to rivers draining into the Black and Caspian Seas, *D. villosus* is now found in almost all major Western European rivers and in the United Kingdom. The species can tolerate a wide range of environments, although zebra mussels (*Dreissena polymorpha*) may facilitate its establishment by creating particularly favorable conditions. *D. villosus* is highly fecund and can breed year-round if water temperatures are warm enough. Impacts of *D. villosus* include alteration of food webs and decline or extirpation of populations of native macroinvertebrates and fish. The species exhibits a high climate match to the contiguous United States, particularly around the Great Lakes where established zebra mussels could aid *D. villosus* spread. Overall risk for this species is high.

Assessment Elements

- **History of Invasiveness (Sec. 3): High**
- **Climate Match (Sec. 6): High**
- **Certainty of Assessment (Sec. 7): High**
- **Remarks/Important additional information: Host of several parasites**
- **Overall Risk Assessment Category: High**

9 References

Note: The following references were accessed for this ERSS. References cited within quoted text but not accessed are included below in Section 10.

CABI. 2015. *Dikerogammarus villosus* (Killer Shrimp) [original text by S. Mastitsky]. Invasive Species Compendium. CAB International, Wallingford, United Kingdom. Available: <http://www.cabi.org/isc/datasheet/108309>. (May 2015).

Cassellato, S., A. Visentin, and G. La Piana. 2007. The predatory impact of *Dikerogammarus villosus* on fish. Pages 495-506 in *Biological invaders in inland waters: profiles, distribution, and threats*. Springer, Dordrecht, The Netherlands.

Devin, S., and J. N. Beisel. 2006. *Dikerogammarus villosus*. Delivering Alien Species Inventories for Europe (DAISIE). Available: http://www.europe-aliens.org/pdf/Dikerogammarus_villosus.pdf. (September 2016).

Dettloff K., G. Núñez, E. Baker, and A. J. Fusaro. 2015. *Dikerogammarus villosus*. USGS Nonindigenous Aquatic Species Database, Gainesville, Florida, and NOAA Great Lakes Aquatic Nonindigenous Species Information System, Ann Arbor, Michigan. Available: <http://nas.er.usgs.gov/queries/greatlakes/FactSheet.aspx?SpeciesID=3&Potential=Y&Type=2&HUCNumber=>>. (June 2015).

- Dick, J. T. A., D. Platvoet, and D. W. Kelly. 2002. Predatory impact of the freshwater invader *Dikerogammarus villosus* (Crustacea: Amphipoda). *Canadian Journal of Fisheries and Aquatic Sciences* 59(6):1078-1084.
- GBIF (Global Biodiversity Information Facility). 2013. GBIF Backbone Taxonomy: *Dikerogammarus villosus* (Sowinsky, 1894). Global Biodiversity Information Facility, Copenhagen. Available: <http://www.gbif.org/species/4315705>. (September 2014).
- Grabowski, M., and J. Lowry. 2016. *Dikerogammarus villosus*. In: T. Horton, J. Lowry, C. De Broyer, D. Bellan-Santini, C. O. Coleman, M. Daneliya, J.-C. Dauvin, C. Fišer, R. Gasca, M. Grabowski, J. M. Guerra-García, E. Hendrycks, J. Holsinger, L. Hughes, D. Jaume, K. Jazdzewski, J. Just, R. M. Kamal'tynov, Y.-H. Kim, R. King, T. Krapp-Schickel, S. LeCroy, A.-N. Lörz, A. R. Senna, C. Serejo, B. Sket, A. H. Tandberg, J. Thomas, M. Thurston, W. Vader, R. Väinölä, R. Vonk, K. White, and W. Zeidler. World Amphipoda database. World Register of Marine Species. Available: <http://www.marinespecies.org/aphia.php?p=taxdetails&id=148586>. (September 2016).
- Rewicz, T., R. Wattier, M. Grabowski, T. Rigaud, and K. Baćela-Spychalska. 2015. Out of the Black Sea: phylogeography of the invasive killer shrimp *Dikerogammarus villosus* across Europe. *PLoS ONE* 10(2):e0118121.
- Sanders, S., C. Castiglione, and M. Hoff. 2014. Risk Assessment Mapping Program: RAMP. US Fish and Wildlife Service.
- Truhlar, A. M., J. A. Dodd, and D. C. Aldridge. 2014. Differential leaf-litter processing by native (*Gammarus pulex*) and invasive (*Dikerogammarus villosus*) freshwater crustaceans under environmental extremes. *Aquatic Conservation: Marine and Freshwater Ecosystems* 24(1):56-65.

10 References Quoted But Not Accessed

Note: The following references are cited within quoted text within this ERSS, but were not accessed for its preparation. They are included here to provide the reader with more information.

- BBC. 2010. Alien 'killer' shrimp found in UK. BBC News. Available: <http://www.bbc.co.uk/news/science-environment-11246642>.
- BBC. 2011a. Hunt widens for 'killer shrimp' in Wales. BBC News. Available: <http://www.bbc.co.uk/news/uk-wales-south-west-wales-12625147>.
- BBC. 2011b. 'Killer' shrimp is the worst alien invader of Britain's waterways which officials say are costing billions of pounds to tackle. BBC News. Available: <http://www.bbc.co.uk/news/uk-14428585>.
- Bollache, L. 2004. *Dikerogammarus villosus* (Crustacea: Amphipoda): another invasive species in Lake Geneva. *Revue Suisse de Zoologie* 111:309-313.

- Bollache, L., S. Devin, R. Wattier, M. Chovet, J.-N. Beisel, J. C. Moreteau, and T. Rigaud. 2004. Rapid range extension of the Ponto-Caspian amphipod *Dikerogammarus villosus* in France: potential consequences. *Archiv für Hydrobiologie* 160:57-66.
- Bruijs, M. C. M., B. Kelleher, G. van der Velde, and A. bij de Vaate. 2001. Oxygen consumption, temperature and salinity tolerance of the invasive amphipod *Dikerogammarus villosus*: indicators of further dispersal via ballast water transport. *Archiv für Hydrobiologie* 152(4):633-646.
- Chernogorenko, M. I., T. I. Komarova, and D. P. Kurandina. 1978. The life-cycle of the trematode *Plagioporus skrjabini* Kowal, 1951 (Allocreadiata, Opecoelidae). *Parazitologiya* 12(6):479-486.
- Crosier, D., and D. P. Molloy. 2006. Killer shrimp - *Dikerogammarus villosus*. New York State Museum, New York.
- Dedju, I. I. 1967. Amphipods and mysids of the basins of rivers Dniester and Prut. Nauka Press, Moscow.
- Devin, S., and J.-N. Beisel. 2006. *Dikerogammarus villosus*. Delivering Invasive Alien Species Inventories for Europe (DAISIE). Available: http://www.europe-alien.org/pdf/Dikerogammarus_villosus.pdf.
- Devin, S., and J.-N. Beisel. 2009. *Dikerogammarus villosus* (Sowinsky), killer shrimp (Gammaridae, Crustacea). In *Handbook of alien species in Europe*. Springer Series in Invasion Ecology 3.
- Devin S., C. Piscart, J.-N. Beisel, and J. C. Moreteau. 2003. Ecological traits of the amphipod invader *Dikerogammarus villosus* on a mesohabitat scale. *Archiv für Hydrobiologie* 158:43-56.
- Devin, S., C. Piscart, J.-N. Beisel, and J.-C. Moreteau. 2004. Life history traits of the invader *Dikerogammarus villosus* (Crustacea: Amphipoda) in the Moselle River, France. *International Review of Hydrobiology* 89:21-34.
- Dick, J. T. A. 2009. *Dikerogammarus villosus*, the amphipod. Invasive Alien Species in Northern Ireland. National Museums Northern Ireland, Cultra, Holywood, County Down, Northern Ireland. Available: <http://www.habitas.org.uk/invasive/species.asp?item=50005>.
- Dick, J. T. A., and D. Platvoet. 2000. Invading predatory crustacean *Dikerogammarus villosus* eliminates both native and exotic species. *Proceedings of the Royal Society of London Series B* 267(1447):977-983.
- Dick, J. T. A., and D. Platvoet. 2001. Predicting future aquatic invaders; the case of *Dikerogammarus villosus*. *Aquatic Nuisance Species* 4:25-27.

- Eggers, T. O., and A. Martens. 2001. [Identification key to the freshwater amphipods (Crustacea) of Germany]. Bestimmungsschlüssel der Süßwasser-Amphipoda (Crustacea) Deutschlands. *Lauterbornia* 42:1-68.
- Fernandez-Leborans, G. 2001. A review of the species of protozoan epibionts on crustaceans. III. Chonotrich ciliates. *Crustaceana* 74(6):581-607.
- Grabowski, M., K. Jazdzewski, and A. Konopacka. 2007. Alien Crustacea in Polish waters - Amphipoda. *Aquatic Invasions* 2:25-38.
- Grigorovich, I. A., R. I. Colautti, E. L. Mills, K. Holeck, A. G. Ballert, and H. J. MacIsaac. 2003. Ballast-mediated animal introductions in the Laurentian Great Lakes: retrospective and prospective analyses. *Canadian Journal of Fisheries Aquatic Sciences* 60:740-756.
- Grigorovich, I.A., H. J. MacIsaac, N. V. Shadrin, and E. L. Mills. 2002. Patterns and mechanisms of aquatic invertebrate introductions in the Ponto-Caspian region. *Canadian Journal of Fisheries Aquatic Sciences* 59:1189-1208.
- Haas, G., M. Brunke, and B. Strei. 2002. Fast turnover in dominance of exotic species in the Rhine River determines biodiversity and ecosystem function: an affair between amphipods and mussels. Pages 426-432 in E. Leppakoski, S. Gollasch, and S. Olenin, editors. *Invasive aquatic species of Europe: distribution, impacts and management*. Kluwer Academic Publishers, Dordrecht, The Netherlands.
- Jazdzewski, K., and A. Konopacka. 2002. Invasive Ponto-Caspian species in waters of the Vistula and Oder basins and the southern Baltic Sea. Pages 384-398 in E. Leppakoski, S. Gollasch, and S. Olenin, editors. *Invasive aquatic species of Europe: distribution, impacts and management*. Kluwer Academic Publishers, Dordrecht, The Netherlands.
- Josens, G., A. bij de Vaate, P. Usseglio-Polatera, R. Cammaerts, F. Cherot, F. Grisez, P. Verboonen, and J. P. vanden Bossche. 2005. Native and exotic Amphipoda and other Peracarida in the River Meuse: new assemblages emerge from a fast changing fauna. *Hydrobiologia* 542:203-220.
- Kelleher, B., P. J. M. Bergers, F. W. B. Van den Brink, F. W. B. Giller, G. van der Velde, and A. bij de Vaate. 1998. Effects of exotic amphipod invasions on fish diet in the Lower Rhine. *Archiv für Hydrobiologie* 143:363-382.
- Kelleher, B., G. van der Velde, P. S. Giller, and A. bij de Vaate. 1999. Dominant role of exotic mass invaders in the diet of important fish species of the River Lower Rhine, The Netherlands. *Crustacean Issues* 12:35-46.
- Kley, A., and G. Maier. 2003. Life history characteristics of the invasive freshwater gammarids *Dikergammarus villosus* and *Echinogammarus ischnus* in the river Main and the Main-Donau canal. *Archiv für Hydrobiologie* 156(4):457-469.

- Kley, A., and G. Maier. 2005. An example of niche partitioning between *Dikerogammarus villosus* and other invasive and native gammarids: a field study. *Journal of Limnology* 64:85-88.
- Kley, A., and G. Maier. 2006. Reproductive characteristics of invasive gammarids in the Rhine-Main-Danube catchment, South Germany. *Limnologica* 36:79-90.
- Konopacka, A. 2004. Invasive amphipods (Crustacea, Amphipoda) in Polish waters. *Przeład Zoologiczny XLVIII*:141-162.
- Lods-Crozet, B., and O. Reymond. 2006. Bathymetric expansion of an invasive gammarid (*Dikerogammarus villosus*, Crustacea, Amphipoda) in Lake Léman. *Journal of Limnology* 65:141-144.
- Maazouzi, C., C. Piscart, F. Legier, and F. Hervant. 2011. Ecophysiological responses to temperature of the “killer shrimp” *Dikerogammarus villosus*: is the invader really stronger than the native *Gammarus pulex*? *Comparative Biochemistry and Physiology - Part A: Molecular & Integrative Physiology* 159:268-274.
- MacIsaac, H. J. 1999. Biological invasions in Lake Erie: past, present and future. Pages 305-322 in M. Munawar, T. Edsall and I.F. Munawar, editors. *The state of Lake Erie (SOLE) - past, present and future - a tribute to Drs. Joe Leach and Henry Regier*. Backhuys Publishers, Netherlands.
- MacNeil, C., and D. Platvoet. 2005. The predatory impact of the freshwater invader *Dikerogammarus villosus* on native *Gammarus pulex* (Crustacea: Amphipoda); influences of differential microdistribution and food resources. *Journal of Zoology* 267:31-38.
- Martynov, A. V. 1925. Études sur les Crustacés de mer du bassin du bas Don et leur distribution éthologique. *Ezhegodnik Zoologicheskago Muzeya Imperatorskoi Akademii Nauk* 25:1-115.
- Mayer, G., G. Maier, A. Maas, and D. Waloszek. 2008. Mouthparts of the Ponto-Caspian invader *Dikerogammarus villosus* (Amphipoda: Pontogammaridae). *Journal of Crustacean Biology* 28:1-15.
- Mills, E. L., J. H. Leach, J. T. Carlton, and C. L. Secor. 1993. Exotic species in the Great Lakes: a history of biotic crises and anthropogenic introductions. *Journal of Great Lakes Research* 19:1-54.
- Müller, J. C., S. Schramm, and A. Seitz. 2002. Genetic and morphological differentiation of *Dikerogammarus* invaders and their invasion history in Central Europe. *Freshwater Biology* 47:2039-2048.

- Nesemann, H., M. Pöcki, and K. J. Wittmann. 1995. Distribution of epigean Malacostraca in the middle and upper Danube (Hungary, Austria, Germany). *Miscellanea Zoologica Hungarica* 10:49-68.
- Ovcharenko, N. A., and I. Wita. 1996. New data on microsporidium *Nosema dikerogammari*. *Parazitologiya* 30:333-335.
- Platvoet, D., J. T. A. Dick, C. MacNeil, M. van Reil, and G. van der Velde. 2009. Invader-invader interactions in relation to environmental heterogeneity leads to zonation of two invasive amphipods, *Dikerogammarus villosus* (Sowinsky) and *Gammarus tigrinus* Sexton: amphipod pilot species project (AMPIS) report 6. *Biological Invasions* 11:2085-2093.
- Pöckl, M. 2007. Strategies of a successful new invader in European fresh waters: fecundity and reproductive potential of the Ponto-Caspian amphipod *Dikerogammarus villosus* in the Austrian Danube, compared with the indigenous *Gammarus fossarum* and *G. roeseli*. *Freshwater Biology* 52:50-63.
- Ricciardi, A., and J. B. Rasmussen. 1998. Predicting the identity and impact of future biological invaders: a priority for aquatic resource management. *Canadian Journal of Fisheries and Aquatic Sciences* 55(7):1759-1765.
- Schmidt, O., and G. Josens. 2004. Preliminary study of the scars borne by Gammaridae (Amphipoda, Crustacea). *Belgian Journal of Zoology* 134:75-78.
- Sudarikov, V. E., A. A. Shigin, Y. V. Kurochkin, V. V. Lomakin, R. P. Stenko, and N. I. Yurlova. 2002. *Matacercariae of trematodes - parasites of the freshwater molluscs of the Central Russia*. Nauka Press, Moscow.
- Vaate, A. bij de, K. Jazdzewski, H. A. M. Ketelaars, S. Gollash, and G. van der Velde. 2002. Geographical patterns in range extension of Ponto-Caspian macroinvertebrate species in Europe. *Canadian Journal of Fisheries and Aquatic Sciences* 59:1159-1174.
- Vaate, A. bij de, and A. G. Klink. 1995. *Dikerogammarus villosus* Sowinsky (Crustacea: Gammaridae), a new immigrant in the Dutch part of the Lower Rhine. *Lauterbornia* 20:51-54.
- Van der Velde, G., R. S. E. W. Leuven, D. Platvoet, K. Bacela, M. A. J. Huijbregts, H. W. M. Hendriks, and D. Kruijt. 2009. Environmental and morphological factors influencing predatory behaviour by invasive non-indigenous gammaridean species. *Biological Invasions* 11:2043-2054.
- Van Riel, M. C., G. van der Velde, S. Rajagopal, S. Marguillier, F. Dehairs, and A. bij de Vaate. 2006. Trophic relationships in the Rhine food web during invasion and after establishment of the Ponto-Caspian invader *Dikerogammarus villosus*. *Hydrobiologia* 565:39-58.

- Wattier, R. A., E. R. Haine, J. Beguet, G. Martin, L. Bollache, I. B. Muskó, D. Platvoet, and T. Rigaud. 2007. No genetic bottleneck or associated microparasite loss in invasive populations of a freshwater amphipod. *Oikos* 116(11):1941-1953.
- Whitfield, J. 2000. Shrimp eat shrimp. *Proceedings of the Royal Society of London Series B* 267:977-983.
- Wijnhoven, S., M. C. van Riel, and G. van der Velde. 2003. Exotic and indigenous freshwater gammarid species: physiological tolerance to water temperature in relation to ionic content of the water. *Aquatic Ecology* 37:151-158.