Killer Shrimp (*Dikerogammarus villosus*) Ecological Risk Screening Summary

U.S. Fish & Wildlife Service, December 2020 Revised, December 2020 Web Version, 9/29/2021

Organism Type: Invertebrate Overall Risk Assessment Category: High



Photo: Grabowski M. Licensed under Creative Commons Attribution-Noncommercial-Share Alike 4.0. Available:

http://www.marinespecies.org/aphia.php?p=image&tid=148586&pic=74304. (December 2020).

1 Native Range and Status in the United States

Native Range

From Dettloff et al. (2020):

"Ponto-Caspian basin. Widely distributed in the lower reaches of the Danube River system in the region of Eastern Europe/Ukraine (Mordukhai-Boltowskoi 1969, Nesemann et al. 1995). Its original distribution was restricted to the lower Danube by the narrow valley of the Dunakanyar near the confluence of the Danube and Ipoly Rivers (Nesemann et al. 1995)."

Status in the United States

No records of Dikerogammarus villosus in trade or in the wild in the United States were found.

From Dettloff et al. (2020):

"Not established in North America"

Dikerogammarus villosus is listed as prohibited by State agencies in Michigan (Michigan Invasive Species 2020) and Wisconsin (Wisconsin Department of Natural Resources 2013).

Ohio lists *Dikerogammarus villosus* as an invasive species (ODNR 2020). "Under Ohio Administrative Code 1501:31-19-01, it shall be unlawful for any person to possess, import or sell live individuals of the species listed below. With the exception of White Perch, the species listed below must be headless, preserved in ethanol or formaldehyde, or eviscerated (internal organs removed)."

Means of Introductions in the United States

No records of *Dikerogammarus villosus* in the wild in the United States were found. The following section refers to potential means of introductions.

From Dettloff et al. (2020):

"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

This ERSS was previously published in September 2017. Revisions were completed to incorporate new information and conform to updated standards.

From Dettloff et al. (2020):

"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."

From CABI (2019):

"D. villosus can be confused with the two other congeners currently spreading in Europe, namely Dikerogammarus bispinosus and Dikerogammarus haemobaphes. Moreover, for a long time D. bispinosus has been considered a subspecies of D. villosus (e.g., Dedju 1967). However, besides certain morphological differences, these three species are isolated both genetically and reproductively (Müller et al., 2002)."

2 Biology and Ecology

Taxonomic Hierarchy and Taxonomic Standing

According to Horton et al. (2020), *Dikerogammarus villosus* (Sowinsky, 1894) is the current valid name for this species. It was originally described as *Gammarus marinus var. villosa* Sowinsky, 1894, which is still a synonymized name according to Horton et al. (2020).

From Horton et al. (2020):

"Biota > Animalia (Kingdom) > Arthropoda (Phylum) > Crustacea (Subphylum) > Multicrustacea (Superclass) > Malacostraca (Class) > Eumalacostraca (Subclass) > Peracarida (Superorder) > Amphipoda (Order) > Senticaudata (Suborder) > Gammarida (Infraorder) > Gammaridira (Parvorder) > Gammaroidea (Superfamily) > Gammaridae (Family) > *Dikerogammarus* (Genus) > *Dikerogammarus villosus* (Species)"

Size, Weight, and Age Range

From Dettloff et al. (2020):

"Size: Up to 30 mm (Nesemann et al. 1995). Males grow to be larger than females, and sexual maturity is reached at 6 mm in length (Devin et al. 2004)."

Environment

From Dettloff et al. (2020):

"*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 is able to tolerate [water] 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)."

Climate

No information on climate requirements was found for D. villosus.

Distribution Outside the United States

Native From Dettloff et al. (2020):

"Ponto-Caspian basin. Widely distributed in the lower reaches of the Danube River system in the region of Eastern Europe/Ukraine (Mordukhai-Boltowskoi 1969, Nesemann et al. 1995). Its original distribution was restricted to the lower Danube by the narrow valley of the Dunakanyar near the confluence of the Danube and Ipoly Rivers (Nesemann et al. 1995)."

Introduced From Dettloff et al. (2020):

"Dikerogammarus villosus was collected beyond its native range in the Austrian waters of the Danube for the first time in 1989 (Nesemann et al. 1995). By 1992, this species was abundant in several sampled sites of the Bavarian Danube. It has since spread along the main Danube canal, entering the Main River in 1994 and successfully invading the Rhine River, where it was sampled in the Netherlands, in 1995 (Bij de Vaate and Klink 1995, Van der Velde et al. 2000). As of 1996, this species has been observed in almost all large rivers of Western Europe, as well as in the Baltic Sea basin (Bij de Vaate et al. 2002, Bollache et al. 2004). More recent observations in the Bug River (Konopacka 2004) and the Vistula River (Bacela et al. 2008), as well as reports from the U.K. (BBC 2011), demonstrate its continuing expansion."

From Casellato et al. (2007):

"From its original Ponto-Caspian area, it had invaded central and western Europe [...] through the southern corridor connecting the Danube with the Rhine and the central corridor connecting the Dnieper with the Vistula, Oder, and Elbe basins (Bij de Vaate et al. 2002)."

According to CABI (2020), *Dikerogammarus villosus* has been reported as introduced and naturally reproducing in the following countries (year of introduction and original source material given after country name):

- Austria (1992; Nesemann et al. (1995))
- Belarus (2000-2005; Mastitsky and Makarevich (2007))
- Belgium (1998; Josens et al. (2005))
- Czech Republic (2003; Berezina and Duriš (2008))
- France (1997; Devin et al. (2001))
- Germany (1992; Bollache et al. (2004); Casellato et al. (2007))
- Hungary (1926; [Bij de] Vaate et al. (2002))
- Italy (2006; Casellato et al. (2006))
- Netherlands (1995; [Bij de] Vaate and Klink (1995))
- Poland (2001; Jazdzewski and Konopacka (2002))
- Slovakia (1999; Sporka (1999))
- Switzerland (2002; Lods-Crozet and Reymond (2006))
- Ukraine (1940s-1950s; Lubyanov (1957))

Means of Introduction Outside the United States

From GBIF Secretariat (2020):

"in Belgian part of the North Sea: Ships: accidental as attached or free-living fouling organisms [...] accidental with ballast water, sea water systems, live wells or other deck basins"

"in Czech Republic (Nation) : Secondary natural dispersal from alien source population. "Using the canals joining the different river systems, the species has reached the River Odra. There it quickly spread [natural dispersal] both up- and downstream [...]"

From CABI (2019):

"Natural dispersal of *D. villosus* occurs by active migration (Nesemann et al., 1995; [Bij de] 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., [Bij de] Vaate et al., 2002; Jazdzewski and Konopacka, 2002; Dick, 2009)."

"Intentional introductions of D. villosus, though possible, have not been reported."

Short Description

From Dettloff et al. (2020):

"*Dikerogammarus villosus* has a laterally compressed, curled, semi-transparent body consisting of a head (cephalon), thorax (pereon), and abdomen. Its head contains one pair of eyes, mouthparts (gnathopods) with relatively large and powerful mandibles, and two pairs of antennae. Its pereon consists of seven segments, each with a pair of walking legs (pereopods)— the first four pairs extending downward and forward and the last three pairs extending downward and backward. In females, extra branches that serve as space to shelter eggs are present on the walking legs. Its abdomen consists of six segments divided into two three-segment parts: pleosome (anterior) with brush-like limbs known as pleopods, and urosome (posterior) with shorter, immobile rod-like limbs called uropods. This species' body coloration can range from transparent and striped to a uniform dark pigmented color; however, the most frequent coloration pattern is a light spot or stripe on each segment against a dark background (Devin et al. 2001, Nesemann et al. 1995). Newly released young resemble adults but are microscopic in size.

This species can be distinguished from other *Dikerogammarus* species by the high, conical protuberances on its urosomes. In larger males (> 16mm), these bumps are tipped with three to five spines. Moreover, the second antennae have a sparsely haired peduncle and a flagellum with dense 'brush-like' tufts of setae (MacNeil et al. 2010)."

Biology

From Dettloff et al. (2020):

"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 [sic] 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 to 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)."

From CABI (2019):

"D. villosus is a dioecious species."

"D. villosus has been repeatedly observed to have strong affinity to aggregations of the mollusc Dreissena polymorpha, which can be explained by long co-evolution of these two species in their native Ponto-Caspian basin (reviewed in Casellato et al., 2006). In the absence of Dreissena, however, D. villosus often acts as a monodominant species in invaded macroinvertebrate communities due to its voracious predatory behaviour. 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). As a result, D. villosus has become one of the key secondary consumers occupying high trophic levels comparable to fish (Van Riel et al., 2006)."

"Being a large-bodied and numerous invertebrate species, *D. villosus* is readily consumed by fish. In the introduced range, *D. villosus* has been field-documented as a food item of the European eel *Anguilla anguilla*, Eurasian perch *Perca fluviatilis*, and burbot *Lota lota* (Eckmann et al., 2008)."

Human Uses

From CABI (2019):

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

Diseases

No records of OIE-reportable diseases (OIE 2020) were found for *Dikerogammarus villosus*.

From CABI (2019):

"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. (2020):

"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)."

3 Impacts of Introductions

From CABI (2019):

"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, [2011])."

"*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). However, *D. villosus* is also an omnivorous species able to act as an effective filter-feeder on microalgae (Platvoet et al., 2006)."

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* 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 gnatopods. 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."

From Dettloff et al. (2020):

"Moreover, *D. villosus* has been observed to kill or injure potential prey without consuming it (Dick et al. 2002)."

The following section refers to potential, not documented impacts of introductions.

From Dick et al. (2002):

"With many other invaders from the Ponto–Caspian established in the Great Lakes, this new invader may become part of a larger "invasional meltdown" (see Ricciardi and Rasmussen 1998; Simberloff and Von Holle 1999; Ricciardi 2001), particularly since zebra mussel (*Dreissena polymorpha*) beds, by providing substrate, may facilitate this large amphipod (see Stewart et al. 1998; Bially and MacIsaac 2000)."

From Casellato et al. (2007):

"Experts on aquatic ecology predict that *D. villosus* will soon invade Great Britain and the North American Great Lakes, where the zebra mussel had already settled, a circumstance which seems to favour the arrival of compatriots (Ricciardi et al. 1997, Ricciardi and Rasmussen 1998, Ricciardi 2001)."

From Bruijs et al. (2001):

"[...] *D. villosus* is an euryhaline, eurythermic species, [...] *D. villosus* may be able to survive (incomplete) ballast water exchange and subsequently be dispersed over large distances by means of ballast water and to develop large populations in temperate areas on a global scale."

4 History of Invasiveness

Dikerogammarus villosus has a long history of accidental introduction through shipping transport and natural dispersion through canals. This species readily established after many introductions in European waters. *D. villosus* can tolerate a broad range of environmental conditions. Peer-reviewed studies demonstrate that *D. villosus* has caused changes in zooplankton and macroinvertebrate communities where introduced. Experimental studies demonstrate it may affect nutrient conditions in freshwater systems due to its leaf-shredding activities, and that it may predate on native fish eggs where introduced. Negative impacts of introduction have been shown in peer-reviewed literature for this species. *Dikerogammarus villosus* is listed as prohibited by State agencies in Michigan, Ohio, and Wisconsin. The history of invasiveness is classified as High.

5 Global Distribution



Figure 1. Known global distribution of *Dikerogammarus villosus*. Locations are in the United Kingdom, France, Belgium, Germany, Netherlands, Poland, Hungary, Romania, Turkey, and Ukraine. Map from GBIF Secretariat (2020). Because the climate matching analysis (section 7) is not valid for marine waters, no marine occurrences were used in the climate matching analysis.

Additional source locations in Czech Republic, Poland, Slovakia, and Austria provided by Rewicz et al. (2015) will be added during the climate match.

6 Distribution Within the United States

No records of Dikerogammarus villosus in the wild in the United States were found.

7 Climate Matching

Summary of Climate Matching Analysis

The climate match for *Dikerogammarus villosus* was generally high for the contiguous United States with small areas of low climate match. The areas with highest match were in the Great Lakes basin, upper Midwest, and in small patches along the Rocky Mountains. Low match was found throughout Florida and the Gulf Coast, as well as in parts of the desert Southwest and Pacific Northwest. The overall Climate 6 score (Sanders et al. 2018; 16 climate variables; Euclidean distance) was 0.178, high (scores of 0.103 and greater are classified as high). The following States had medium individual Climate 6 scores: California, Connecticut, Idaho, Kentucky, North Carolina, Nebraska, New Hampshire, New Jersey, Nevada, Oregon, Rhode Island, South Dakota, Tennessee, and Washington. The following States had low individual Climate 6 scores: Alabama, Arkansas, Delaware, Florida, Georgia, Kansas, Louisiana, Maine, Minnesota, Mississippi, North Dakota, Oklahoma, South Carolina, and Texas. All other States had high individual Climate 6 score.

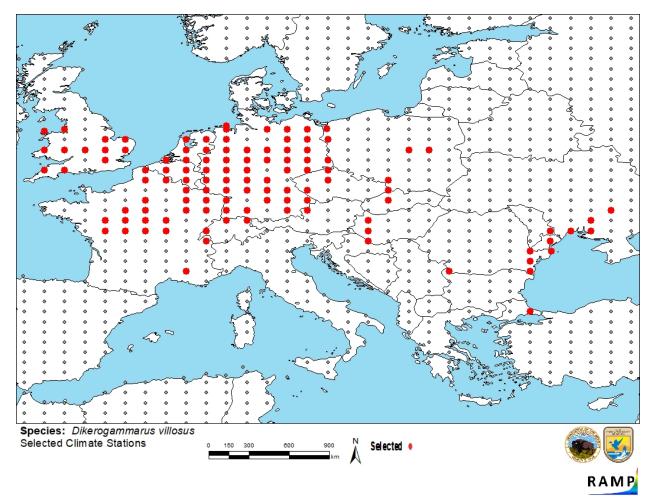


Figure 2. RAMP (Sanders et al. 2018) source map showing weather stations in Europe selected as source locations (red: United Kingdom, France, Belgium, Germany, Netherlands, Poland, Czech Republic, Slovakia, Austria, Hungary, Romania, Turkey, and Ukraine) and non-source locations (gray) for *Dikerogammarus villosus* climate matching. Source locations from GBIF Secretariat (2020) and Rewicz et al. (2015). Selected source locations are within 100 km of one or more species occurrences, and do not necessarily represent the locations of occurrences themselves.

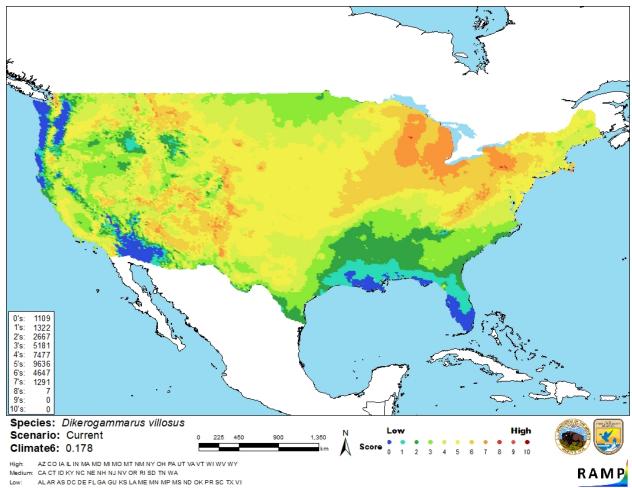


Figure 3. Map of RAMP (Sanders et al. 2018) climate matches for *Dikerogammarus villosus* in the contiguous United States based on source locations reported by GBIF Secretariat (2020) and Rewicz et al. (2015). Counts of climate match scores are tabulated on the left. 0/Blue = Lowest match, 10/Red = Highest match.

The High, Medium, and Low Climate match Categories are based on the following table:

Climate 6:	Overall
(Count of target points with climate scores 6-10)/	Climate Match
(Count of all target points)	Category
0.000≤X≤0.005	Low
0.005 <x<0.103< td=""><td>Medium</td></x<0.103<>	Medium
≥0.103	High

8 Certainty of Assessment

The certainty of assessment is High. There is quality information available about the biology and ecology of *Dikerogammarus villosus*. Records of introduction were found. Information on impacts and history of invasiveness were from peer-reviewed sources.

9 Risk Assessment

Summary of Risk to the Contiguous United States

The Killer Shrimp (*Dikerogammarus villosus*) is a small freshwater and brackish amphipod native to the Ponto-Caspian basin of Europe. The species can tolerate a wide range of environments, and can breed year-round if water temperatures are warm enough. *Dikerogammarus villosus* is listed as prohibited by State agencies in Michigan (Michigan Invasive Species 2020) and Wisconsin (Wisconsin Department of Natural Resources 2013). The history of invasiveness is classified as High. *D. villosus* has spread to new waterways through accidental shipping transport and natural dispersion through canal systems. Zebra mussels (*Dreissena polymorpha*) may facilitate its establishment by creating particularly favorable conditions. Peer-reviewed literature has demonstrated the species has a negative impact on zooplankton and macroinvertebrate communities in newly established areas. Experimental studies demonstrate the species may adversely affect native fish populations and water quality once established in new areas. The overall climate match was High, particularly around the Great Lakes where established zebra mussels could aid *D. villosus* spread. The certainty of assessment is High. The overall risk assessment category is High.

Assessment Elements

- History of Invasiveness (Sec. 4): High
- Overall Climate Match Category (Sec. 7): High
- Certainty of Assessment (Sec. 8): High
- Remarks/Important additional information: No additional remarks.
- Overall Risk Assessment Category: High

10 Literature Cited

Note: The following references were accessed for this ERSS. References cited within quoted text but not accessed are included below in Section 11.

- Bruijs MCM, Kelleher B, van der Velde G, bij de Vaate A. 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.
- [CABI] CAB International. 2019. Dikerogammarus villosus (Killer shrimp) [original text by Mastitsky S]. CABI Invasive Species Compendium. Wallingford, United Kingdom: CAB International. Available: https://www.cabi.org/isc/datasheet/108309 (December 2020).
- Cassellato S, Visentin A, La Piana G. 2007. The predatory impact of *Dikerogammarus villosus* on fish. Pages 495–506 in Biological invaders in inland waters: profiles, distribution, and threats. Dordrecht, The Netherlands: Springer.

Dettloff K, Núñez G, Baker E, Fusaro AJ. 2020. Dikerogammarus villosus (Sowinsky, 1894).
Gainesville, Florida: U.S. Geological Survey, Nonindigenous Aquatic Species Database, and Ann Arbor, Michigan: NOAA Great Lakes Aquatic Nonindigenous Species Information System. Available: https://nas.er.usgs.gov/queries/greatlakes/FactSheet.aspx?SpeciesID=3&Potential=Y&Ty pe=2&HUCNumber (December 2020).

- Dick JTA, Platvoet D, Kelly DW. 2002. Predatory impact of the freshwater invader *Dikerogammarus villosus* (Crustacea: Amphipoda). Canadian Journal of Fisheries and Aquatic Sciences 59(6):1078–1084.
- GBIF Secretariat. 2020. GBIF backbone taxonomy: *Dikerogammarus villosus* (Sowinsky, 1894). Copenhagen: Global Biodiversity Information Facility. Available: https://www.gbif.org/species/4315705 (December 2020).
- Horton T, Lowry J, De Broyer C, Bellan-Santini D, Coleman CO, Corbari L, Costello MJ, Daneliya M, Dauvin J-C, Fišer C, Gasca R, Grabowski M, Guerra-García JM, Hendrycks E, Hughes L, Jaume D, Jazdzewski K, Kim Y-H, King R, Krapp-Schickel T, LeCroy S, Lörz A-N, Mamos T, Senna AR, Serejo C, Sket B, Souza-Filho JF, Tandberg AH, Thomas JD, Thurston M, Vader W, Väinölä R, Vonk R, White K, Zeidler W. 2020. World Amphipoda database. *Dikerogammarus villosus* (Sowinsky, 1894). Accessed through: World Register of Marine Species. Available: http://www.marinespecies.org/aphia.php?p=taxdetails&id=148586 (December 2020).
- Michigan Invasive Species. 2020. Killer shrimp (*Dikerogammarus villosus*). Available: https://www.michigan.gov/invasives/0,5664,7-324-68002_73847-368450--,00.html (December 2020).
- [OIE] World Organisation for Animal Health. 2020. OIE-listed diseases, infections and infestations in force in 2020. Available: http://www.oie.int/animal-health-in-the-world/oie-listed-diseases-2020/ (December 2020).
- [ODNR] Ohio Department of Natural Resources. 2020. Ohio's injurious aquatic invasive species. Publication 5490 R0120.
- Rewicz T, Wattier R, Grabowski M, Rigaud T, Bącela-Spychalska K. 2015. Out of the Black Sea: phylogeography of the invasive killer shrimp *Dikerogammarus villosus* across Europe. PLoS ONE 10(2):e0118121.
- Sanders S, Castiglione C, Hoff M. 2018. Risk Assessment Mapping Program: RAMP. Version 3.1. U.S. Fish and Wildlife Service.
- Truhlar AM, Dodd JA, Aldridge DC. 2014. Differential leaf-litter processing by native (Gammarus pulex) and invasive (Dikerogammarus villosus) freshwater crustaceans under environmental extremes. Aquatic Conservation: Marine and Freshwater Ecosystems 24:56–65.

Wisconsin Department of Natural Resources. 2013. Regulated Invasive aquatic invertebrates except crayfish. Available:

https://dnr.wi.gov/topic/invasives/speciesnr40list.asp?filterby=category&filterval=aquatic %20invertebrates%20except%20crayfish&addfilter=classification (December 2020).

11 Literature Cited in Quoted Material

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.

- Bially A, MacIsaac HJ. 2000. Fouling mussels (*Dreissena* spp.) colonize soft sediments in Lake Erie and facilitate benthic invertebrates. Freshwater Biology 43:85–97.
- BBC. 2011. '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.
- Berezina NA, Duriš Z. 2008. First record of the invasive species *Dikerogammarus villosus* (Crustacea: Amphipoda) in the Vltava River (Czech Republic). Aquatic Invasions 3(4):455–460.
- Bij de Vaate A, Jazdzewski K, Ketelaars HAM, Gollash S, van der Velde G. 2002. Geographical patterns in range extension of Ponto-Caspian macroinvertebrate species in Europe. Canadian Journal of Fisheries and Aquatic Sciences 59:1159–1174.
- Bij de Vaate A, Klink AG. 1995. *Dikerogammarus villosus* Sowinsky (Crustacea: Gammaridae), a new immigrant in the Dutch part of the Lower Rhine. Lauterbornia 20:51–54.
- Bollache L. 2004. *Dikerogammarus villosus* (Crustacea: Amphipoda): another invasive species in Lake Geneva. Revue Suisse de Zoologie 111:309–313.
- Bollache L, Devin S, Wattier R, Chovet M, Beisel J-N, Moreteau JC, Rigaud T. 2004. Rapid range extension of the Ponto-Caspian amphipod *Dikerogammarus villosus* in France: potential consequences. Archiv für Hydrobiologie 160:57–66.
- Casellato S, Piana G la, Latella L, Ruffo S. 2006. *Dikerogammarus villosus* (Sowinsky, 1894) (Crustacea, Amphipoda, Gammaridae) for the first time in Italy. Italian Journal of Zoology 73:97–104.
- Chernogorenko MI, Komarova TI, Kurandina DP. 1978. The life-cycle of the trematode *Plagioporus skrjabini* Kowal, 1951 (Allocreadiata, Opecoelidae). Parazitologiya 12(6):479–486.
- Crosier D, Molloy DP. 2006. Killer shrimp *Dikerogammarus villosus*. New York: New York State Museum.

- Dedju II. 1967. Amphipods and mysids of the basins of rivers Dniester and Prut. Moscow: Nauka Press.
- Devin S, Beisel JN, Bachmann V, Moreteau JC. 2001. *Dikerogammarus villosus* (Amphipoda: Gammaridae): another invasive species newly established in the Moselle River and French hydrosystems. Annals of Limnology 37: 21–27.
- Devin S, Beisel JN. 2006. *Dikerogammarus villosus*. Delivering Invasive Alien Species Inventories for Europe. Available: http://www.europealiens.org/pdf/Dikerogammarus_villosus.pdf.
- Devin S, Beisel JN. 2009. *Dikerogammarus villosus* (Sowinsky), killer shrimp (Gammaridae, Crustacea). In Handbook of alien species in Europe. Springer Series in Invasion Ecology 3.
- Devin S, Piscart C, Beisel J-N, Moreteau JC. 2003. Ecological traits of the amphipod invader *Dikerogammarus villosus* on a mesohabitat scale. Archiv für Hydrobiologie 158:43–56.
- Devin S, Piscart C, Beisel J-N, Moreteau JC. 2004. Life history traits of the invader *Dikerogammarus villosus* (Crustacea: Amphipoda) in the Moselle River, France. International Review of Hydrobiology 89:21–34.
- Dick JTA. 2009. *Dikerogammarus villosus*, the amphipod. Invasive Alien Species in Northern Ireland. Cultra, Holywood, County Down, Northern Ireland: National Museums Northern Ireland. Available: http://www.habitas.org.uk/invasive/species.asp?item=50005.
- Dick JTA, Platvoet D. 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 JTA, Platvoet D. 2001. Predicting future aquatic invaders, the case of *Dikerogammarus villosus*. Aquatic Nuisance Species 4:25–27.
- Fernandez-Leborans, G. 2001. A review of the species of protozoan epibionts on crustaceans. III. Chonotrich ciliates. Crustaceana 74(6):581–607.
- Grabowski M, Jazdzewski K, Konopacka A. 2007. Alien Crustacea in Polish waters -Amphipoda. Aquatic Invasions 2:25–38.
- Grigorovich IA, Colautti RI, Mills EL, Holeck K, Ballert AG, MacIsaac HJ. 2003. Ballastmediated animal introductions in the Laurentian Great Lakes: retrospective and prospective analyses. Canadian Journal of Fisheries Aquatic Sciences 60:740–756.

- Grigorovich IA, MacIsaac HJ, Shadrin NV, Mills EL. 2002. Patterns and mechanisms of aquatic invertebrate introductions in the Ponto-Caspian region. Canadian Journal of Fisheries Aquatic Sciences 59:1189–1208.
- Haas G, Brunke M, Strei B. 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 Leppakoski E, Gollasch S, Olenin S, editors. Invasive aquatic species of Europe: distribution, impacts and management. Dordrecht, The Netherlands: Kluwer Academic Publishers.
- Jazdzewski K, Konopacka A. 2002. Invasive Ponto-Caspian species in waters of the Vistula and Oder basins and the southern Baltic Sea. Pages 384–398 in Leppakoski E, Gollasch S, Olenin S, editors. Invasive aquatic species of Europe: distribution, impacts and management. Dordrecht, The Netherlands: Kluwer Academic Publishers.
- Josens G, bij de Vaate A, Usseglio-Polatera P, Cammaerts R, Cherot F, Grisez F, Verboonen P, vanden Bossche JP. 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, Bergers PJM, Van den Brink FWB, Giller FWB, van der Velde G, bij de Vaate A. 1998. Effects of exotic amphipod invasions on fish diet in the Lower Rhine. Archiv für Hydrobiologie 143:363–382.
- Kelleher B, van der Velde G, Giller PS, bij de Vaate A. 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, Maier G. 2003. Life history characteristics of the invasive freshwater gammarids *Dikerogammarus villosus* and *Echinogammarus ischnus* in the river Main and the Main-Donau canal. Archiv für Hydrobiologie 156(4):457–469.
- Kley A, Maier G. 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, Maier G. 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. Przeglad Zoologiczny XLVIII:141–162.
- Lods-Crozet B, Reymond O. 2006. Bathymetric expansion of an invasive gammarid (*Dikerogammarus villosus*, Crustacea, Amphipoda) in Lake Léman. Journal of Limnology 65:141–144.

- Lubyanov IP. 1957. On the bioecological characteristics of benthic fauna of the middle Dnieper in relation to hydrologic works in Proceedings of the Thematic and Problem Workshops of the Zoological Institute. Issue VII, Problems of Hydrobiology of Inland Waters. Leningrad-Moscow: Academy of Sciences of the USSR 181–187.
- Maazouzi C, Piscart C, Legier F, Hervant F. 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 HJ. 1999. Biological invasions in Lake Erie: past, present and future. Pages 305–322 in Munawar M, Edsall T, Munawar IF, editors. The state of Lake Erie (SOLE) past, present and future a tribute to Drs. Joe Leach and Henry Regier. Netherlands: Backhuys Publishers.
- MacNeil C, Platvoet D. 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.
- MacNeil C, Platvoet D, Dick JTA, Fielding N, Constable A, Hall N, Aldridge D, Renals T, Diamond M. 2010. The Ponto-Caspian 'killer shrimp', *Dikerogammarus villosus* (Sowinsky, 1894), invades the British Isles. Aquatic Invasions 5(4):441–445.
- Mastitsky SE, Makarevich OA. 2007. Distribution and abundance of Ponto-Caspian amphipods in the Belarusian section of the Dnieper River. Aquatic Invasions 2:39–44.
- Mayer G, Maier G, Maas A, Waloszek D. 2008. Mouthparts of the Ponto-Caspian invader *Dikerogammarus villosus* (Amphipoda: Pontogammaridae). Journal of Crustacean Biology 28:1–15.
- Mills EL, Leach JH, Carlton JT, Secor CL. 1993. Exotic species in the Great Lakes: a history of biotic crises and anthropogenic introductions. Journal of Great Lakes Research 19:1–54.
- Mordukhai-Boltovskoi FD. 1949. Life cycle of some Caspian gammarids. Doklady Akademii Nauk SSSR 46:997–999.

Mordukhai-Boltowskoi. 1969. [Source material did not give full citation for this reference.]

- Müller JC, Schramm S, Seitz A. 2002. Genetic and morphological differentiation of *Dikerogammarus* invaders and their invasion history in Central Europe. Freshwater Biology 47:2039–2048.
- Nesemann H, Pöcki M, Wittmann KJ. 1995. Distribution of epigean Malacostraca in the middle and upper Danube (Hungary, Austria, Germany). Miscellanea Zoologica Hungarica 10:49–68.

- Ovcharenko NA, Wita I. 1996. New data on microsporidium *Nosema dikerogammari*. Parasitologiya 30:333–335.
- Platvoet D, Dick JTA, MacNeil C, van Reil M, van der Velde G. 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. 2001. Facilitative interactions among aquatic invaders: is an "invasional meltdown" occurring in the Great Lakes? Canadian Journal of Fisheries and Aquatic Sciences 58:2513–2525.
- Ricciardi A, Rasmussen JB. 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.
- Ricciardi A, Whoriskey FG, Rasmussen JB. 1997. The role of the zebra mussel (*Dreissena polymorpha*) in structuring macroinvertebrate communities on hard substrata. Canadian Journal of Fisheries and Aquatic Sciences 54:2596–2608.
- Schmidt O, Josens G. 2004. Preliminary study of the scars borne by Gammaridae (Amphipoda, Crustacea). Belgian Journal of Zoology 134:75–78.
- Simberloff D, Von Holle B. 1999. Positive interactions of nonindigenous species: invasional meltdown? Biological Invasions 1:21–32.
- Sporka F. 1999. First record of *Dikerogammarus villosus* (Amphipoda, Gammaridae) and *Jaera istri* (Isopoda, Asselota) from the Slovak-Hungarian part of the Danube river. Biologia 54(5):538.
- Stewart TW, Miner JG, Lowe RL. 1998. Macroinvertebrate communities on hard substrates in western Lake Erie: structuring effects of *Dreissena*. Journal of Great Lakes Research 24:868–879.
- Sudarikov VE, Shigin AA, Kurochkin YV, Lomakin VV, Stenko RP, Yurlova NI. 2002. Matacercariae of trematodes – parasites of the freshwater molluscs of the Central Russia. Moscow: Nauka Press.

- Van der Velde G, Leuven RSEW, Platvoet D, Bacela K, Huijbregts MAJ, Hendriks HWM, Kruijt D. 2009. Environmental and morphological factors influencing predatory behaviour by invasive non-indigenous gammaridean species. Biological Invasions 11:2043–2054.
- Van Riel MC, van der Velde G, Rajagopal S, Marguillier S, Dehairs F, Vaate A bij de. 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 RA, Haine ER, Beguet J, Martin G, Bollache L, Muskó IB, Platvoet D, Rigaud T. 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, van Riel MC, van der Velde G. 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.