Review

Alien macroinvertebrates in Croatian freshwaters

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Abstract

Alien aquatic macroinvertebrates, especially invasive crustaceans and molluscs, have heavily impacted native species and ecosystem processes in freshwaters worldwide. Knowledge on alien species distribution is necessary to understand their dispersal dynamics and prevent future invasions, and to predict and reduce undesirable impacts. Literature data on alien macroinvertebrate species (AMS) in Croatia are sparse and a complete inventory of alien macroinvertebrates in Croatian freshwaters has never been conducted. The aim of this study was to present a database of AMS in Croatian freshwaters and to analyse their origin, pathways of introduction and distribution. The AMS database was built based on literature data and the authors' unpublished data, and included a total of 1,411 records from 689 sites across Croatia. In total, 29 AMS were recorded until 2019, belonging to five major taxonomic groups: subphylum Crustacea (16 species) and phyla Mollusca (7 spp.), Annelida (4 spp.), Cnidaria (1 sp.), and Platyhelminthes (1 sp.). The area of origin of most species is the European Ponto-Caspian region (19 spp., 66%), and the rest originate from North America (5 spp.), Asia (4 spp.) and New Zealand (1 sp.). The most important pathways of unintentional primary introductions were stowaway-shipping (20 spp., 69%) and contaminant-fish stocking (6 spp., 21%). All 29 AMS species were found in the Black Sea Basin (Danube Basin) and five of those were also recorded in the river catchments of the Adriatic Sea Basin. For most AMS, the Sava and Drava Rivers are the main river corridors for their westward spread from the Danube. Since studies of AMS dispersal mechanisms are lacking and only a few studies report the impacts of invasive AMS in Croatia, future studies should be focused on the dispersal dynamics and ecological impact of invasive macroinvertebrates in Croatian freshwaters.

Key words: database, distribution, non-indigenous, invasive species, inland waters, area of origin, pathway

Introduction

Freshwaters are highly threatened globally due to multiple pressures, with many new emerging threats and cumulative stressors that have deepened the freshwater biodiversity crisis (Reid et al. 2019). Habitat degradation, pollution and invasive species have been listed as the most important drivers of biodiversity change in freshwaters (Dudgeon et al. 2006), with invasive species as the least reversible driver of change in aquatic ecosystems (Strayer 2010; Havel et al. 2015). Range expansions of a high number of alien species across European freshwaters are synergistically facilitated by different human activities (Nunes et al. 2015). The most important pathways and vectors for alien macroinvertebrate species (AMS) are transport by ships (Minchin and Gollasch 2002; Gollasch 2007), construction of canals interconnecting previously isolated river basins (Bij de Vaate et al. 2002; Leuven et al. 2009), and intentional introductions (Arbačiauskas et al. 2010, 2011). Some AMS also spread by natural, unaided dispersal from the point of primary introduction (e.g. Hudina et al. 2009). In European freshwaters, approximately 200 alien invertebrates (Strayer 2010; Rabitsch et al. 2012; Nunes et al. 2015) and 76 alien fish species (Lehtonen 2002) have been recorded, and their introductions into freshwaters are continuously on the rise, both in the number of species and pathways of introduction (Nunes et al. 2015). Impacts of invasive macroinvertebrates range from the complete elimination of counterpart native species, by competition/predation and spread of disease, to alteration of native communities or ecosystem-level services (Laverty et al. 2015; Gallardo et al. 2016). However, although many studies have indicated the substantial environmental and socio-economic impacts of AMS (e.g. Crawford et al. 2006; Rewicz et al. 2014), there is still a lack of basic faunistic and distribution data for AMS in many European countries.

There are ten peer-reviewed country check-lists for all taxonomic groups of freshwater AMS in Europe. The numbers of species per country range from 15 species in Lithuania (Arbačiauskas et al. 2011) and 19 AMS in Belarus (Karatayev et al. 2008), to 64 AMS in Italy (Gherardi et al. 2008) and 70 AMS in Ukraine (Alexandrov et al. 2007). Other countries with a published check-list for AMS include Austria (46 spp., Moog et al. 2008), Belgium-Flanders (48 spp., Boets et al. 2016), France (44 spp., Devin et al. 2005), Germany (53 spp., Gollasch and Nehring 2006), Portugal (44 spp., Anastácio et al. 2019) and Spain (45 spp., García-Berthou et al. 2007). These studies showed that crustaceans and molluscs represent the majority of AMS, and that the most important areas of their origin are the European Ponto-Caspian region, North America and South/Southeast Asia. Although the number of AMS was reported to be less than 2% of the total number of countries' freshwater macroinvertebrates species (Devin et al. 2005; Karatayev et al. 2008; Gherardi et al. 2008; Moog et al. 2008), invasive AMS often represent a relatively high proportion of macroinvertebrate assemblages, especially in large rivers. For example, the main European inland waterways are highly biologically contaminated, because invasive AMS have dominated benthic macroinvertebrate assemblages either in terms of taxa richness or total abundance, or both (Arbačiauskas et al. 2008).

Many alien species from different taxonomic groups have been recorded in Croatian freshwaters: nine vascular plants (Nikolić et al. 2013; Mitić and Hruševar 2018), 32 fishes (19 established) (Piria et al. 2018; Ćaleta et al. 2019), three reptile species (Jelić and Jelić 2015) and two semiaquatic mammal species (Boršić et al. 2018). Out of the 66 invasive alien species of European Union concern (EC 2016, 2017, 2019), 23 species are present in Croatia, of which 11 (48%) are obligate aquatic species (Boršić et al. 2018, Mihinjač 2019). Distribution data on AMS in Croatian freshwaters have been focused on particular taxonomic groups, and only the distribution of alien crustaceans (Decapoda: Hudina et al. 2009, 2013, 2017; Maguire et al. 2011, 2018; Peracarida: Žganec 2009; Žganec et al. 2009, 2010, 2015, 2018) and a few molluscs (Lajtner and Crnčan 2011; Beran 2013, 2015; Beran et al. 2013) have been better studied. In a recent study that assessed the level of biocontamination of macroinvertebrate assemblages in four major Croatian rivers (Ćuk et al. 2019), 21 AMS were recorded, of which nine were widespread and abundant. However, a complete inventory of alien macroinvertebrates has not been conducted in Croatian freshwaters. Our ability to prevent or control future invasions and reduce undesirable impacts of invasive AMS in Croatia is hampered by limited knowledge of the identity and distribution of alien species in the region. Therefore, the objective of this study was to present an up-to-date checklist of AMS in Croatian freshwaters, and to analyse their origin, pathways of introduction and distribution patterns. To achieve these goals, all known records of AMS in Croatia from the literature and unpublished sampling campaigns of the authors until 2019 were collated into a Croatian alien macroinvertebrate species database.

Materials and methods

Study area

Croatia is located in Southeast Europe, on the eastern Adriatic Sea coast, with 56,594 km^2 land area and 31,067 km^2 maritime area. The southernmost part of the country (approx. 50%) lies within the Dinaric karst area (Dinaric Alps), and is composed predominantly of carbonate rock with a diverse geomorphology (9,000 caves and pits, ravines and karst valleys, sinking rivers) and a sparse surface river network. The northern part of the country has more diverse geology with a domination of silicate lithology and a dense river network formed after the desiccation of the Pannonian Sea (Čanjevac and Orešić 2020).

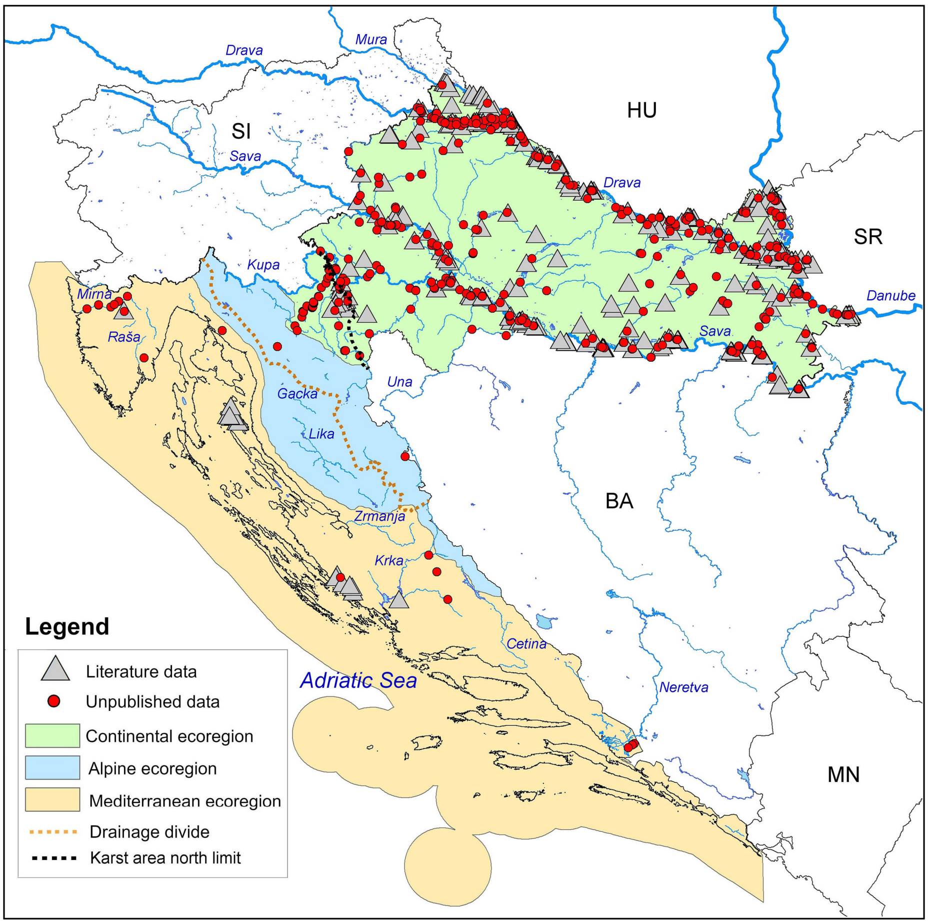

Figure 1. Map of all sites with records of alien macroinvertebrates in freshwaters of Croatia based on the literature or on the authors' unpublished data. The brown dotted line represents the divide between the Black Sea (Danube) and the Adriatic Sea basins, while the black dotted line indicates the approximate line between the Dinaric karst area (south of the line) and the continental, mostly non-karst area (north of the line).

There are three biogeographical regions in the territory of Croatia: Continental, Alpine and Mediterranean (Duplić et al. 2012; Figure 1). The continental biogeographical region, with its dominant silicate lithology, is bounded by the rivers Sava, Mura, Drava and Danube. It is the most populated area, and consists primarily of agricultural and urban areas intersected with forests (Magaš 2013). The remaining two biogeographical regions, Alpine and Mediterranean, lie in the karst area with a sparse river network. The Alpine biogeographical region contains a mountain belt and hills, and is dominated by forests. The Mediterranean biogeographical region covers the Eastern Adriatic coast and the islands, and is one of the most indented coasts on the Mediterranean (Duplančić Leder et al. 2004), marked by high biodiversity (Jelaska et al. 2010). Rivers of the Continental and most rivers of the Alpine biogeographical region (Dinaric karst area) belong to the Black Sea Basin (Danube drainage). These are the longest rivers in Croatia (Sava 518 km, Drava 323 km, Kupa 293 km and Danube 135 km). The rivers of the Adriatic Sea Basin are shorter and isolated, with direct connections (e.g. Zrmanja 69 km and Krka 73 km), or underground connections to the Adriatic Sea (e.g. sinking rivers Lika 78 km and Gacka 61 km) (Čanjevac and Orešić, 2020).

Data collection

All available existing literature about AMS distribution in Croatia until 2019 was collected by the authors based on their expertise. This resulted in a complete inventory and the creation of a database on AMS distribution in Croatian freshwaters. Only papers with geographic coordinates or the precise description of locations for AMS records that enabled records to be georeferenced were included into the database. In total, 60 literature sources with precise locations or coordinates for AMS in freshwaters of Croatia were discovered, ranging from one to a maximum of 14 literature sources per species (Table 1). In order to make the database more comprehensive, unpublished distribution data from the authors' sampling campaigns between 2000 and 2019 were also added into the database. The published literature data sources included 657 records of 29 species from 326 sites, while the unpublished data comprised 754 records of 21 species from 453 sites. These data were used to construct the Croatian alien macroinvertebrate species database, which contains a total of 1,411 records of AMS from 689 sites around Croatia. This includes data on the distribution of benthic macroinvertebrates and the freshwater jellyfish *Craspedacusta sowerbii* Lankester, 1880, that has both a benthic and planktonic stage, while the literature data on alien mosquitoes were excluded from the database since they inhabit small and intermittent water bodies not studied by the authors, and that require the use of different sampling methods.

The authors' unpublished records of AMS were obtained using different sampling methods in the period between 2000 and 2019 at 453 sites across Croatia, covering many different types of freshwater habitats (rivers, streams, lakes, reservoirs, gravel pits, etc.). Only sites with AMS present were included in the database. Sampling of benthic macroinvertebrates was conducted using a standard benthos hand net (25 × 25 cm, mesh size 500 μm), Ekman grab (15 × 15 cm) or dredge. Qualitative sampling, using a hand net during approximately 10 min, was conducted on all accessible microhabitats. Additionally, at many sites, five or ten replicate quantitative samples were collected from several dominant microhabitat types or multihabitat quantitative sampling was done following the AQEM protocol (AQEM 2002). Samples were fixed with 96% ethanol in the field. In the laboratory, macroinvertebrates were separated from the sediment and organic detritus, and stored in 70% ethanol for later identification. In some cases, visual inspection and snorkelling were performed to detect invasive mussels and clams on the bottom of the water body. Crayfish sampling was conducted using 5–10 baited LiNi traps per site, which were kept in the waterbody overnight (Westman et al. 1978). Crayfish were also caught by hand or snorkelling.

The final database compiled included not only data on the distribution of each species, but also data on species taxonomy, native range (origin), year

Table 1. List of the 29 alien macroinvertebrate species found to be present in freshwaters of Croatia with their taxonomic groups indicated, and presence/absence (1/0, respectively) in the Danube River, in two major river drainages, Sava and Drava (Danube tributaries), and in river catchments of the Adriatic Sea Basin (ASB). Area of origin, year of first record in Croatia, pathway of first introduction and literature sources are also shown for each species. (*species had disappeared from the Drava River).

	Species /Taxonomic group	Danube River	Sava drain.	Drava drain.	ASB catch.	Origin	Year of first rec.	Pathway of first introd.	References
	PLATYHELMINTHES (1)								
	TURBELLARIA								
1	*Dendrocoelum romanodanubiale* (Codreanu, 1949)	0	0	1	0	Ponto-Caspian	2015	stowaway	57
	CNIDARIA (1)								
	HYDROZOA								
2	*Craspedacusta sowerbii* Lankester, 1880	0	1	1	1	East Asia	1993	unaided	7; 16; 20; 53; 54; 55; 56
	ANNELIDA (4)								
	OLIGOCHAETA (2)								
3	*Branchiura sowerbyi* Beddard, 1892	0	1	1	0	South Asia	1956	contaminant	2; 3; 5; 19; 57
4	*Potamothrix moldaviensis* Vejdovský & Mrazek, 1902	1	0	1	0	Ponto-Caspian	2015	stowaway	57
	POLYCHAETA (1)								
5	*Hypania invalida* (Grube, 1860)	1	0	1	0	Ponto-Caspian	2001	stowaway	12; 14; 57
	HIRUDINEA (1)								
6	*Caspiobdella fadejewi* (Epshtein, 1961)	0	1	0	0	Ponto-Caspian	2015	contaminant	57
	MOLLUSCA (7)								
	GASTROPODA (3)								
7	*Ferrissia fragilis* (Tryon, 1863)	0	1	0	0	North America	2008	contaminant	40; 41
8	*Physella acuta* (Draparnaud, 1805)	1	1	1	1	North America	1838	contaminant	1; 40; 41; 48; 49; 57
9	*Potamopyrgus antipodarum* (Gray, 1843)	0	0	1	1	New Zealand	2007	unaided	57
	BIVALVIA (4)								
10	*Corbicula fluminea* (O.F. Müller, 1774)	1	1	1	1	East Asia	2001	contaminant	13; 43; 44; 57
11	*Dreissena bugensis* (Andrusov, 1897)	1	0	1	0	Ponto-Caspian	2013	stowaway	57
12	*Dreissena polymorpha* (Pallas, 1771)	1	1	1	0	Ponto-Caspian	1990	contaminant	6; 7; 8; 9; 10; 12; 20; 25; 26; 33; 39; 42; 44; 57
13	*Sinanodonta woodiana* (Lea, 1834)	1	1	1	1	East Asia	2001	contaminant	11; 12; 30; 41; 44; 50; 57
	CRUSTACEA (16)								
	AMPHIPODA (8)								
14	*Chelicorophium curvispinum* (G.O. Sars, 1895)	1	1	1	0	Ponto-Caspian	1968/69	stowaway	4; 12; 18; 23; 24; 27; 28; 32; 44; 45; 51; 57
15	*Chelicorophium sowinskyi* (Martynov, 1924)	0	1	1	0	Ponto-Caspian	1968/69	stowaway	51; 57
16	*Chelicorophium robustum* (G.O. Sars, 1895)	1	0	0	0	Ponto-Caspian	2013	stowaway	4; 28; 32; 45; 57
17	*Dikerogammarus villosus* (Sowinsky, 1894)	1	1	1	0	Ponto-Caspian	2001	stowaway	12; 22; 23; 51; 57
18	*Dikerogammarus haemobaphes* (Eichwald, 1841)	1	1	0	0*	Ponto-Caspian	1968/69	stowaway	4; 12; 18; 22; 23; 32; 34; 45; 57
19	*Dikerogammarus bispinosus* Martynov, 1925	1	0	0	0	Ponto-Caspian	2001	stowaway	12; 18; 22; 23; 24; 32; 44; 45; 51; 57; 59
20	*Echinogammarus ischnus* (Stebbing, 1899)	1	0	1	0	Ponto-Caspian	2015	stowaway	51; 57; 59
21	*Obesogammarus obesus* (G.O. Sars, 1896)	1	0	0	0	Ponto-Caspian	2001	stowaway	12; 18; 22; 23; 51; 57
	ISOPODA (1)								
22	*Jaera istri* Veuille, 1979	1	1	1	0	Ponto-Caspian	1968/69	stowaway	4; 12; 18; 44; 45; 51; 57
	MYSIDACEA (4)								
23	*Hemimysis anomala* G.O. Sars, 1907	1	0	0	0	Ponto-Caspian	2005	contaminant	18; 21
24	*Katamysis warpachowskyi* G.O. Sars, 1893	1	0	0	0	Ponto-Caspian	2005	contaminant	21; 51
25	*Limnomysis benedeni* (Czerniavsky, 1882)	1	1	1	0	Ponto-Caspian	2004	contaminant	17; 18; 21; 45; 51; 57
26	*Paramysis lacustris* (Czerniavsky, 1882)	1	0	0	0	Ponto-Caspian	2001	contaminant	12; 60

Table 1. (continued).

	DECAPODA (3)								
27	*Faxonius limosus* (Rafinesque, 1817)	1	0	1	0	North America	2003	unaided	15; 29; 38; 58
28	*Pacifastacus leniusculus* (Dana, 1852)	0	1	1	0	North America	2008	unaided	29; 31; 35; 36; 37; 38; 46; 52; 58
29	*Procambarus virginalis* Lyko, 2017	0	0	1	0	North America	2013	release	47; 58
	TOTAL	20	15	20	5	5 donor regions	1838–2015	4 pathways	No. ref per spp.: avg = 4.9, min = 1, max = 14

References (ordered by year of record): 1 – Cantraine (1838), 2 – Devidé (1956), 3 – Matoničkin (1957), 4 – Matoničkin et al. (1975), 5 – Kerovec et al. (2016), 6 – Mišetić et al. (1991), 7 – Kranjčev (1993), 8 – Lajtner et al. (2004), 9 – Lajtner et al. (2008), 10 – Lajtner (2012), 11 – Paunović et al. (2006), 12 – Paunović et al. (2007b), 13 – Paunović et al. (2007a), 14 – Zorić et al. (2011), 15 – Maguire and Klobučar (2003), 16 – Stanković (2007), 17 – Bogut et al. (2007), 18 – Božić (2007), 19 – Kerovec and Kerovec (2014), 20 – Stanković and Ternjej (2010), 21 – Wittman (2007), 22 – Žganec (2009), 23 – Žganec et al. (2009), 24 – Czirok et al. (2008), 25 – Erben et al. (2009), 26 – Ivanek (2012), 27 – Borza et al. (2010), 28 – Borza (2011), 29 – Hudina et al. (2009), 30 – Lajtner and Crnčan (2011), 31 – Maguire et al. (2008), 32 – Horvai et al. (2012), 33 – Stević et al. (2013), 34 – Žganec et al. (2010), 35 – Hudina et al. (2011b), 36 – Hudina et al. (2012), 37 – Hudina et al. (2011a), 38 – Maguire et al. (2011), 39 – Šarić (2011), 40 – Srkoč (2015), 41 – Beran (2013), 42 – Beran et al. (2013), 43 – Dekić (2013), 44 – Pekez (2013), 45 – Žganec et al. (2018), 46 – Hudina et al. (2013), 47 – Samardžić et al. (2014), 48 – Zrinščak (2014), 49 – Beran (2015), 50 – Bielen et al. (2016), 51 – Borza et al. (2015), 52 – Hudina et al. (2017), 53 – Matoničkin Kepčija et al. (2015), 54 – Matoničkin Kepčija et al. (2016), 55 – Rašan et al. (2015), 56 – Sever (2015), 57 – Ćuk et al. (2019), 58 – Maguire et al. (2018), 59 – Žganec et al. (2015), 60 – Borza et al. (2019)

of first record and pathway of introduction. These additional data were assembled based both on primary literature in scientific journals (e.g. Hudina et al. 2009; Boets et al. 2016) and in web-based searches in invasive species databases (both global – Global Invasive Species Database (GISD) and regional – Europe: European Alien Species Information Network (EASIN) and Delivering Alien Invasive Species Inventories for Europe (DAISIE)).

The pathway is the part of the introduction process that results in the alien species relocation to a place outside its native range (Hulme et al. 2008) and includes both the vector that carries an organism and the route (geographic path) along which it travels (Carlton and Ruiz 2005). For our database, six categories of pathways, defined by Hulme et al. (2008), were used: five pathways of primary introduction (*release, escape, contaminant, stowaway,* and *corridor*), and an additional category, *unaided*, which describes the natural spread of a species after its initial introduction into an area outside its native range. Since the exact pathway of primary introduction is not known in most cases of AMS in Croatia, species were assigned to the most likely primary introduction pathway based on the literature (Arbačiauskas et al. 2011; Nunes et al. 2015; Boets et al. 2016) or on a database search. An assessment of uncertainty for each pathway assignment, as recommended by Essl et al. (2015), was performed using the best expert judgment.

Spatial data analysis

Spatial analysis was conducted to examine the number of species present per UTM square grid 10 × 10 km using Quantum GIS version 3.8.1. Water

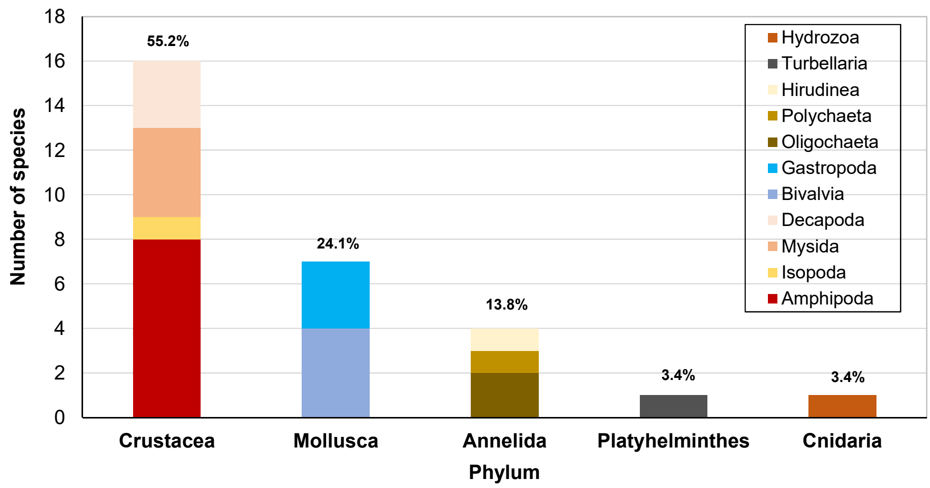

Figure 2. Number of alien macroinvertebrate species in Croatian freshwaters belonging to four phyla (Mollusca, Annelida, Platyhelminthes, Cnidaria) and the subphylum Crustacea. The percentage representation of each of those five groups is given above the bars.

body types inhabited by AMS, and the number and distribution of species in the Adriatic and Black Sea Basins and major river catchments within, were also analysed.

Results

In total, 29 alien macroinvertebrate species were recorded in Croatian freshwaters (Table 1) belonging to four different phyla (Annelida, Cnidaria, Mollusca, Platyhelminthes) and the subphylum Crustacea (phylum Arthropoda). Because the records of the polychaete *Manayunkia speciosa* Leidy, 1859 (Pekez 2013) and the bryozoan *Pectinatella magnifica* (Leidy, 1851) (Franjević et al. 2015) found in the literature are questionable, these species were not included in the database. The majority of species found (16) are crustaceans belonging to four different orders, with most species (8) from the order Amphipoda (Figure 2). There are seven species of molluscs (4 Bivalvia, 3 Gastropoda), four annelids (2 Oligochaeta, 1 Polychaeta, 1 Hirudinea), one flatworm (Platyhelminthes, Turbellaria) and one hydromedusa (Cnidaria, Hydrozoa).

Most species (19 spp., 66%) originate from the European Ponto-Caspian region and the ten non-European species are from North America (5 spp.), Asia (4 spp.) and New Zealand (1 sp.) (Figure 3). Most crustaceans are from the Ponto-Caspian region, except three North American crayfish species (Table 1). Molluscs found in Croatia have the most diverse origin: two bivalves, *Dreissena bugensis* (Andrusov, 1897) and *Dreissena polymorpha* (Pallas, 1771), originate from the Ponto-Caspian region; two bivalves, *Corbicula fluminea* (O.F. Müller, 1774) and *Sinanodonta woodiana* (Lea, 1834), originate from East Asia; two snails, *Ferrissia fragilis* (Tryon, 1863) and *Physella acuta* (Draparnaud, 1805), are from North America, and one snail, *Potamopyrgus antipodarum* (Gray, 1843), originates from New Zealand. The flatworm *Dendrocoelum romanodanubiale* (Codreanu, 1949)

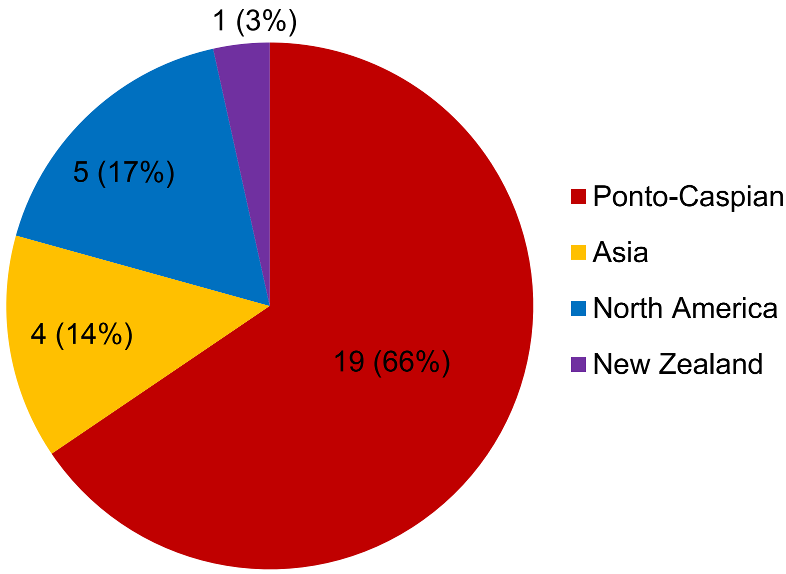

Figure 3. Area of origin (native range) of the 29 alien macroinvertebrate species recorded in Croatia and the respective number of species and percentage.

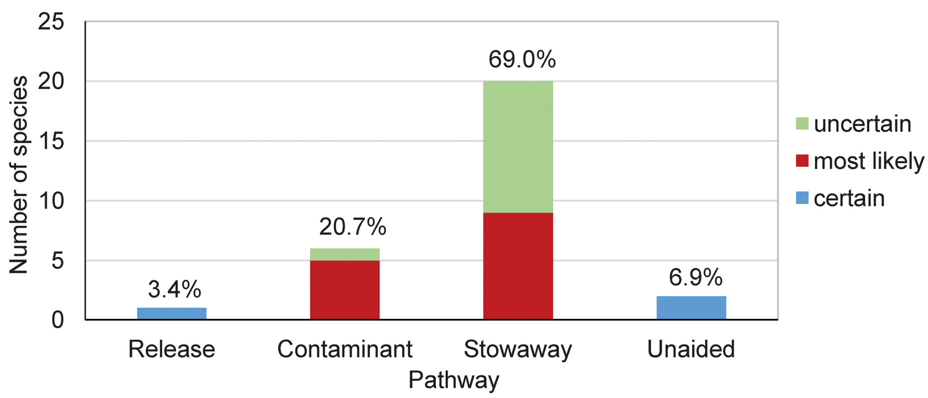

Figure 4. Pathways of alien macroinvertebrate species primary introduction into Croatian freshwaters with three levels of uncertainty established for each species (percentages of the total number of AMS recorded are shown above bars).

originates from the Ponto-Caspian region and the freshwater jellyfish *Craspedacusta sowerbii* Lankester, 1880 originates from East Asia.

Of the six pathways defined by Hulme at al. (2008), stowaway (20 spp. or 69%) and contaminant (6 spp. or 21%) were the most likely pathways of primary introduction for most species into Croatian freshwaters (Figure 4). Transport by attachment on the hull of ships navigating the Danube, Sava and Lower Drava, was likely the main vector for species primarily introduced by the stowaway pathway. The most AMS primarily introduced by the contaminant pathway were likely introduced into the waters of continental Croatia as contaminants of fish stocking/aquaculture (e.g. free-swimming larvae of *Dreissena* or *Corbicula*, or parasitic glochidia of *Sinanodonta* on introduced fish). Only one species, the invasive crayfish *Procambarus virginalis* Lyko, 2017, was primarily introduced by illegal release into the Šoderica gravel-pit lake near the Drava River (Koprivnica)

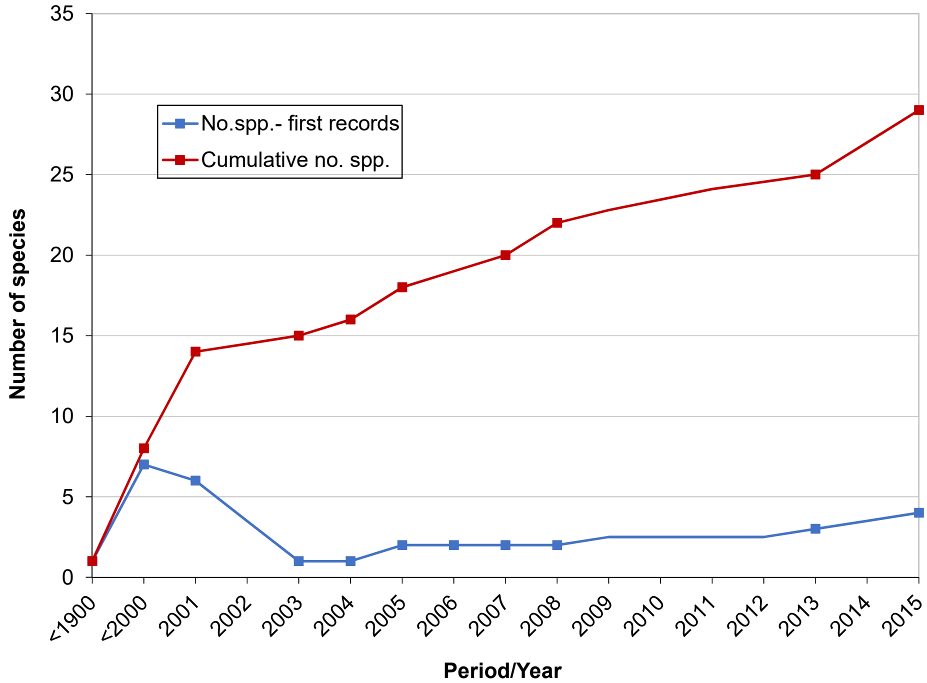

Figure 5. Number of new alien macroinvertebrate species (blue line) and cumulative number of species (red line) recorded between 1838 and 2015 in Croatian freshwaters.

(Samardžić et al. 2014), while two other invasive crayfish species, *Pacifastacus leniusculus* (Dana, 1852) and *Faxonius limosus* (Rafinesque, 1817), entered Croatian waters unaided from neighbouring countries by downstream dispersal through the Mura and Danube Rivers, respectively (Hudina et al. 2009). The signal crayfish *P. leniusculus* was also secondarily introduced into the lower course of the karst Korana River, where it was illegally released in 2011 (near Karlovac) (Hudina et al. 2013).

The first AMS detected in freshwaters of Croatia, the snail *P. acuta*, was recorded in Dalmatia in 1838 (Cantraine 1838), i.e. in the Mediterranean biogeographical region (Table 1). The first species recorded in the 20th century was *B. sowerbyi*, which was found in the pond of the Botanical Garden in the capital city of Zagreb (Devidé 1956). After that, three alien crustacean taxa (*Chelicorophium* sp., *Dikerogammarus haemobaphes* (Eichwald, 1841) and *Jaera istri* Veuille, 1979) were recorded in the middle part of the Sava River by Matoničkin et al. (1975). Later, the zebra mussel, *D. polymorpha*, was recorded in the Dubrava reservoir on the Drava River in 1990 (Mišetić et al. 1991) and the freshwater jellyfish, *C. sowerbii*, in a gravel pit near the Drava River in 1993 (Kranjčev 1993). Altogether, only eight AMS were recorded before 2000. The most pronounced peaks of new AMS records in Croatia, four and six records, were in 1968 and 2001, respectively (Figure 5). This was due to a comprehensive study of macroinvertebrates along the Sava River in 1970 (Matoničkin et al. 1975), and to another study of the Croatian section of the Danube River during the 1st Joint Danube Survey (JDS1) published in 2007 (Paunović et al. 2007b). In the period from 2002 to 2015, the majority of new species was recorded in 2015, with

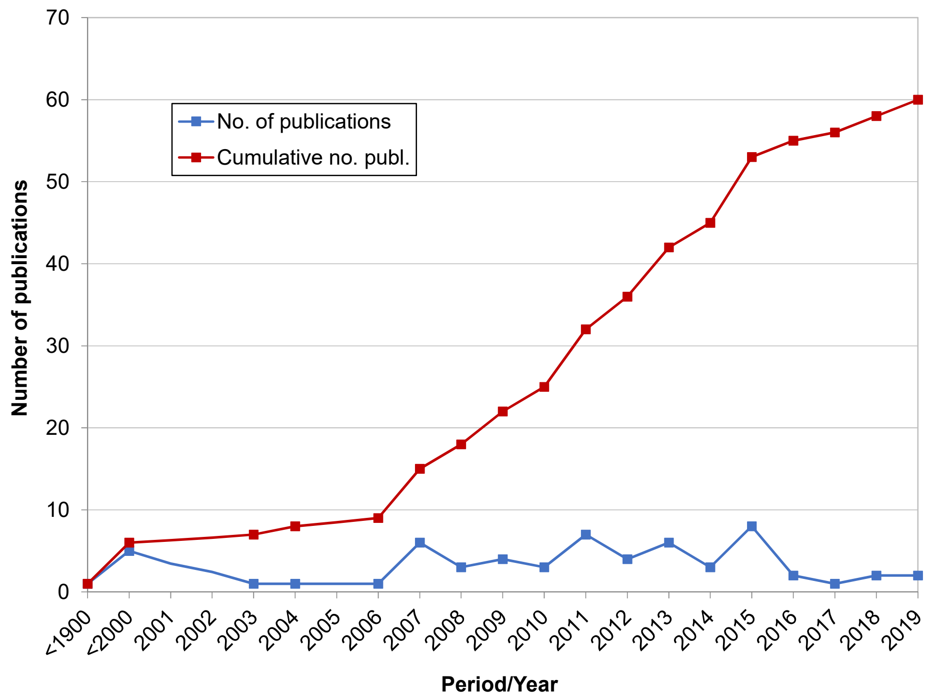

Figure 6. Number of publications related to AMS in Croatia between 1838 and 2019.

no new records in seven of those years and a low average number of new recorded species per year (1.1) (Figure 5). The time analysis of the publications with records of AMS showed that, prior to 2000, there was little research interest in the study of freshwater AMS in Croatia, since only six citations from that period were found. From 2003 to 2019, there were one to eight publications per year, with the maximum number (8) in 2015. The cumulative number of publications increased fast from 2007 to 2015, but subsequently the number of new publications per year declined (Figure 6).

The 29 AMS were recorded from a total of 14 different water body or habitat types (six lotic and eight lentic habitats). The majority of records in the database were from lotic habitats (1,300 or 92.1%) and a few (111 or 7.9%) from lentic habitats. The most lotic records were from large rivers (Danube – 248 records, Sava – 321, Drava – 413 and Mura – 17), while most records from lentic habitats (78.4%) were from artificial water bodies (reservoirs, artificial lakes, gravel pits and fishponds).

All 29 AMS species were found in the Black Sea Basin (BSB) and five of those were also recorded in the Adriatic Sea Basin (ASB). Table 1 shows the distribution of species in the Sava and Drava River drainages and in the course of the Danube River (not the whole drainage): 20 AMS were recorded in the course of Danube River and in the Drava drainage, with fewer species (15) in the Sava drainage. In most ASB river catchments, only one AMS was recorded. The highest number (three AMS) was recorded in the Mirna catchment (*C. fluminea*, *P. acuta*, *P. antipodarum*), while two AMS were recorded in the catchments of the Dubračina (Tribalj reservoir: *C. fluminea*, *S. woodiana*) and Krka River (*C. sowerbii*, *P. acuta*). Interestingly, only empty shells of two bivalves, *D. polymorpha* and *S. woodiana*, were

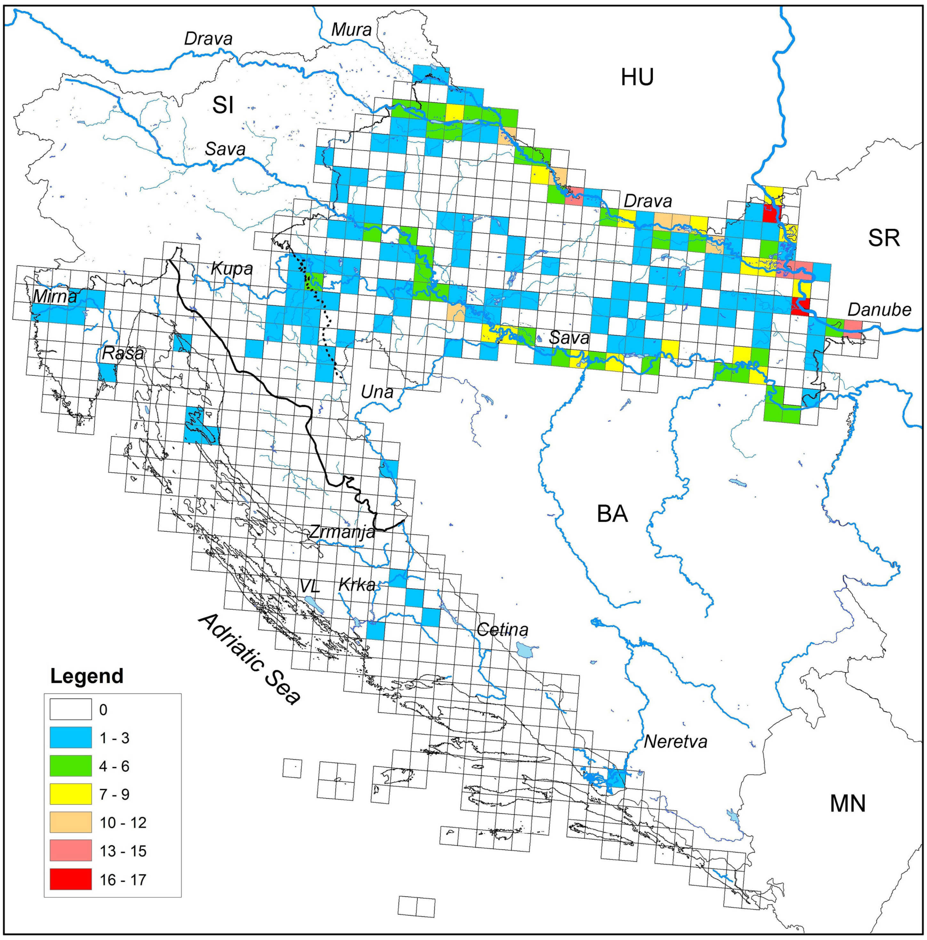

Figure 7. Map of Croatia with 10×10 km square grid and the number of alien macroinvertebrate species per square (ranging from blue referring to 1–3 species, to red referring to 16–17 species). White squares indicate either no AMS recorded or no sampling data available (VL – Vrana Lake in Dalmatia).

found in the Vransko Lake near Biograd (ASB) (Beran et al. 2013), despite numerous sampling campaigns on this lake from 2011 to 2019. The most widespread and likely invasive macroinvertebrate species in Croatian freshwaters are the bivalves *C. fluminea*, *D. polymorpha* and *S. woodiana*, the snail *P. acuta*, the amphipods *D. villosus* and *C. curvispinum*, the isopod *J. istri* and the decapods *P. leniusculus* and *F. limosus*. All these species were recorded in the BSB and, for the majority of them, the Sava and Drava Rivers represent the corridors of westward spread from the Danube. In the rivers of the ASB, three out of those nine widespread and potentially invasive species were found: *P. acuta*, *C. fluminea* and *S. woodiana*.

The distribution pattern of AMS in Croatia and the numbers of species per 10×10 km UTM square, categorised in seven classes, are shown in Figure 7. The highest numbers of AMS per UTM square were recorded along the Danube River, followed by sections along the Drava and Sava Rivers. From the total of 827 10 × 10 km UTM squares of the country, 179 of those (21.6%) showed positive records, i.e. with at least one AMS recorded. Since the database did not include all studied sites, i.e. sites without records of AMS, white squares (648 or 78.4%) represent both areas without positive records and areas for which data on freshwater benthic macroinvertebrates were not available. Of the 179 squares with positive records, most had 1–3 AMS (118 squares, 65.9%), followed by those with 4–6 AMS (33 squares, 18.4%), 7–9 AMS (16 squares, 8.9%), 10–12 AMS (6 squares, 3.4%), 13–15 AMS (4 squares, 2.2%) and 16–17 AMS (2 squares, 1.1%).

Discussion

This study provides the first comprehensive survey of AMS in Croatian freshwaters, with a total of 29 recorded species, most of which crustaceans and molluscs. For most of these species, the European Ponto-Caspian region was the donor area. When compared to similar studies of AMS in other European countries, the number of AMS in Croatia lies between the lower values of 15 AMS in Lithuania (Arbačiauskas et al. 2011) and 19 species in Belarus (Karatayev et al. 2008), and higher AMS richness in eight other countries (Austria – 46 species, Belgium-Flanders – 48 spp., France – 44 spp., Germany – 53 spp., Italy – 64 spp., Portugal – 44 spp., Spain – 45 spp. and Ukraine – 70 spp.).

It is well known that freshwater alien species are a highly non-random subset of freshwater biota, with vertebrates, molluscs and crustaceans being over-represented, while insects are under-represented (Karatayev et al. 2008; Strayer 2010). This is also observed among AMS in Croatia, where they were dominated by crustaceans and molluscs. However, insects usually dominate among native species richness (e.g. Moog et al. 2008), and the majority of the 126,000 freshwater animal species are insects (Balian et al. 2008). There are many reasons for the under-representation of insects among freshwater alien species (Strayer 2010; Fenoglio et al. 2016), and one additional reason could be the lower insect species richness in hypopotamal (brackish water) reaches of tributary rivers, oligohaline and coastal waters of the Black Sea and Caspian Lake, where the Ponto-Caspian AMS originated from (Moog et al. 2008).

The dominance of AMS originating from the European Ponto-Caspian region in Croatia is similar to some other European countries (Austria: Moog et al. 2008; Belarus: Karatayev et al. 2008, Serbian section of the Danube: Paunović et al. 2007b, 2015). In Austria and Croatia, as well as in the Serbian section of the Danube, the dominance of AMS originating from the Ponto-Caspian region is because the Danube River presents the southern European corridor for the western spread of these species (Bij de Vaate et al. 2002), from where they have entered into major tributaries. In Belarus, the dominance of Ponto-Caspian species among AMS is due to their spread through the central invasion corridor (Karatayev et al. 2008). On the other hand, in some countries on the coast of the Atlantic Ocean, like Belgium-Flanders (Boets et al. 2016), Germany (Gollasch and Nehring 2006), Portugal (Anastácio et al. 2019) or whole Iberian Peninsula (Muñoz-Mas and García-Berthou 2020), with better trade connections to

North America, AMS are mostly of North American origin. Therefore, country's geographic position and major trade connections, as well as historic and present inland shipping along major corridors, largely determined origin of AMS in European countries. Croatian freshwaters belong to the Black Sea and Adriatic Sea Basins, with the drainage divide lying in the Dinaric karst area (Figure 1). Thus, the majority of Croatian freshwaters within the Danube drainage (major rivers Sava and Drava) are connected to the southern migration corridor (Bij de Vaate et al. 2002), which relatively recently (after 1992) became the most important corridor for the spread of Ponto-Caspian species to western Europe (Leuven et al. 2009). In Croatia, the Danube is likely the source of most AMS found in the Sava and Drava drainages. Only three Ponto-Caspian species (*Dendrocoelum romanodanubiale*, *Caspiobdella fadejewi* (Epshtein, 1961) and *Chelicorophium sowinskyi* (Martynov, 1924)) and one South Asian species (*Branchiura sowerbyi*) were not found in the Croatian section of the Danube. However, those four species were found in other sections of the middle to lower Danube (Paunović et al. 2015) and were also likely introduced to the Sava or Drava, or both, from the Danube. Thus, the Sava and Drava Rivers most likely represent the main corridors for the westward spread of most AMS in Croatia.

The lower number of AMS in the Sava drainage than in the Drava drainage was surprising, as more species could be expected in the Sava due to the longer navigational reach and more intensive shipping traffic. The main difference between the Sava and Drava in Croatia is the fact that the lowest part and mouth of the Sava (rkm 0–207) are in Serbia, while the Drava reach in Croatia stretches from the mouth to rkm 323. Also, they have different importance regarding river ship traffic in Croatia: the Sava is navigable to the mouth of the Kupa River at rkm 583 for larger ships and to rkm 653 for smaller ships, while the Drava is navigable to rkm 82 for larger ships and rkm 199 for smaller ships (Ministry of Sea Traffic and Infrastructure 2020). Similar differences in AMS numbers between Sava and Drava were established in a previous study (Ćuk et al. 2019), which showed higher biocontamination of macroinvertebrate assemblages along the main course of the Drava River. Analysis of the AMS numbers per UTM 10 × 10 km squares also showed that there were more squares with higher numbers of AMS along the Drava River. This result is likely the consequence of the closer distance of this river within Croatian borders to the Danube. Accordingly, some species have not yet succeeded invading the Sava River in Croatia. For example, two crustaceans, the amphipod *Echinogammarus ischnus* (Stebbing, 1899) and the crayfish *F. limosus* (Rafinesque, 1817), present in the Lower Sava in Serbia (Žganec et al. 2018; Lucić et al. 2015), have not yet spread into the Croatian section of the Sava River. However, these two species were found in the Croatian section of the Drava (Žganec et al. 2015; Maguire et al. 2018). Also, it can be assumed that the most recent invader, *D. bugensis,* established a population in the Lower Drava due to the proximity to the Danube and intense river traffic in this region. Similar physical-chemical conditions in the Drava River and the Danube River, and different conditions in the Sava River (Ćuk et al. 2019), could also be responsible for the more successful establishment of alien species in the Drava River. In addition, reservoirs are likely the main reason why the bivalve *D. polymorpha* (abundant in the Drava River, but very rare in the Sava River) and the snail *P. antipodarum* (found in abundant populations only in the Drava River) are characteristic species for the main course of the Drava River, especially near the three large reservoirs (Ćuk et al. 2019).

Two other species that have contributed to these differences in the alien macroinvertebrate species richness between Sava and Drava are *P. leniusculus*, spread into the Drava River unaided by downstream dispersal from the tributary Mura, and *P. virginalis,* which was deliberately introduced into a gravel pit next to the Drava River. The rare alien species *Potamothrix moldaviensis* Vejdovský & Mrazek, 1902 was also found only in the Drava River. Furthermore, the number of AMS in the Drava River has likely decreased from 21 to 20, since the invasive amphipod *D. haemobaphes*, previously found in the Drava (Žganec et al. 2009; Horvai et al. 2012), could not be found in the area after 2011, despite intensive sampling (Ćuk et al. 2019; Žganec *unpublished*). The most probable reason for its disappearance is the arrival of *D. villosus* that is known as an aggressive invader (Rewicz et al. 2014) that could outcompete *D. haemobaphes* (see Žganec et al. 2018). Therefore, although the major rivers Sava and Drava act as the main corridors for the westward spread of AMS from the Danube, the observed pattern of AMS distribution between these two major river basins is in contrast with ship traffic intensity. This is likely due to a combination of different abiotic and biotic factors: the presence of three large reservoirs along the Drava, proximity of the Croatian Drava reach to the Danube, similar substrate and physical-chemical parameters between the Drava and the Danube, and the outcomes of interactions between ecologically similar invasive species.

The lack of deliberate introductions and the isolation of Croatian rivers and lakes in the Adriatic Sea Basin are the probable reason for small number of AMS in these waters. There is also evidence that some highly invasive species, such as *D. polymorpha*, have succeeded in establishing only a short-lived population in the large, shallow Vrana Lake near Biograd in Dalmatia (Beran et al. 2013). Its disappearance from this lake is rather due to the effects of high summer temperatures (> 30 °C) than due to increased salinity during dry years with low water level and inflow of sea water (Rubinić and Katalinić 2014). Massive mortality of *D. polymorpha* occurs when water temperatures above 25 °C last for long periods of time (White et al. 2015). Over the past 10 years, such temperatures often occurred in the Vrana Lake (Žganec *unpublished*) and were likely responsible for the disappearance of *D. polymorpha*. Only empty shells of another invasive species, *Sinanodonta woodiana*, were found on the shore of the same lake. It is presumed that live individuals of this species, transported from continental parts of Croatia, were used as fishing bait, and *S. woodiana* did not establish a population because it cannot survive the brackish water (oligohaline-mesohaline) conditions in the lake (Beran et al. 2013).

The majority of AMS primary introductions to Croatia were unintentional, with stowaway and contaminant as the most probable pathways of primary introduction. Only two invasive crayfish, *P. virginalis* (primary introduction) and *P. leniusculus* (secondary introduction), were released intentionally (Hudina et al. 2013; Samardžić et al. 2014). On the other hand, release was the primary pathway for most of the alien freshwater fishes (Piria et al. 2018; Ćaleta et al. 2019), since they were primarily introduced intentionally, mostly via aquaculture. Studies by Piria et al. (2018) and Ćaleta et al. (2019) showed that only nine out of 32 recorded alien freshwater fish species were introduced unintentionally. The situation with the five alien aquatic vertebrates (three reptiles and two mammals) is similar; three alien turtles were intentionally released (Jelić and Jelić 2015), while the introduction pathway of coypu (*Myocastor coypus* (Molina, 1782)) and muskrat (*Ondatra zibethicus* (Linnaeus, 1766)) was secondary unaided dispersal from neighbouring countries (Boršić et al. 2018).

Benthic macroinvertebrates represent one of five biological quality elements for the ecological status assessment of surface waters required by the Water Framework Directive. Moreover, they are also the most commonly used element (Birk et al. 2012). Although AMS dominate along most of the large rivers in Europe (Arbačiauskas et al. 2008), there is no consensus about how to treat AMS, i.e. to include or exclude them from the standard monitoring protocol of river ecological status (Orendt et al. 2010). In the previous study by Ćuk et al. (2019), the authors concluded that, in many situations, inclusion of AMS into calculations of biological indices used for the assessment of the ecological status of major rivers in Croatia could provide unreliable results, implying that such indices should undergo revision regarding the presence of AMS. More importantly, it was concluded that there is a lack of knowledge about AMS sensitivity to pollution and other stressors, such as altered hydromorphology, and little is known about their suitability as bioindicators. Therefore, more studies regarding those issues are urgently needed.

Currently there are 29 AMS in Croatian freshwaters, of which 18 species are widespread and can be considered potentially invasive. However, since sampling in lentic habitats was less represented, it is possible that some alien species that prefer lentic habitats (e.g. three mysids) are much more widespread. Thus, future studies of AMS in Croatia focusing on lentic water bodies could increase numbers of invasive AMS in Croatia. Most widespread AMS have been spreading to the west (while *P. leniusculus* has spread to the east) along Croatian major large rivers, the Sava and Drava, tributaries of the Danube River. Although many of these AMS have already spread from the Danube to the Sava and Drava Rivers, some have just started to spread there: the amphipod *E. ischnus* (Žganec et al. 2015) and the bivalve *D. bugensis* (Andrusov, 1897) (Lajtner *unpublished*) have invaded the Lower Drava during this decade. In addition, the amphipod *D. villosus* recently invaded the Croatian section of the Sava River (Žganec et al. 2018). All these cases indicate that other AMS (e.g. the amphipod *Chelicorophium robustum*) could be expected to spread from the Danube to the Drava and Sava, while some are expected to spread downstream from neighbouring countries (e.g. the crayfish *F. limosus* from the Slovenian section of the Drava, Govedič 2017). It can also be expected that some invasive AMS will spread even further by entering into medium sized tributaries and lentic water bodies in the Sava and Drava Basins.

Very little is known about the impact of invasive macroinvertebrate species in Croatia – only few studies have reported the impacts of invasive crayfish on native species (Hudina et al. 2011b, 2017) or of the invasive *Dikerogammarus* amphipods on native peracarid crustaceans (Žganec et al. 2018). Furthermore, studies of dispersal mechanisms of invasive AMS are completely lacking in Croatia. Therefore, in order to prevent future invasions or predict and reduce the undesirable impacts of AMS, future studies should be focused on the dispersal dynamics and ecological impact of invasive aquatic macroinvertebrates in Croatia. Also, a very important issue to consider is the potential spread of invasive species from the Danube Basin to the Adriatic Sea Basin, which harbours many endemic species (e.g. Žganec et al. 2016) that could be threatened by invaders. Unfortunately, the national legislation on alien and invasive species (Official Gazette 2018, 2019) considers only three decapod crustaceans included on the national "black list" (*F. limosus*, *P. leniusculus*, *P. virginalis*), which is currently the same as the list of invasive alien species of Union concern (EC 2016, 2017, 2019). All other invasive AMS are not covered by any regulations, even though some of them (e.g., *D. polymorpha*, *D. bugensis*, *C. fluminea*, *P. antipodarum*, *D. villosus*, *D. haemobaphes*, *E. ischnus*) could present substantial threat to freshwater biodiversity, especially in rivers draining to the Adriatic Sea. Therefore, these species should be considered for inclusion in the national "black list", while future monitoring of benthic macroinvertebrates should include protocols that would ensure early warning and rapid response in case of their detection in the rivers of the Adriatic Sea Basin. Finally, further spread of AMS in Croatian freshwaters could likely be reduced by raising awareness of people living next to large rivers (especially anglers and boat owners), while "check, clean and dry" protocols (GB Non-native species secretariat, 2020) should urgently be included in national regulations.

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