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Not a Silent Invasion: The Reaction of European Naturalists to the Spread of Zebra Mussel (*Dreissena polymorpha*) in the 19th—Early 20th Century

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Abstract: The case of naturalization of the zebra mussel, *Dreissena polymorpha* (Pallas, 1771), in countries lying beyond its native Ponto–Caspian range is remarkable as one of the first instances when the scientific community as early as the mid-19th century was fully aware of the non-indigenous status of a particular species as well as of the need for the study and monitoring of this process. Based on a study of contemporary sources, I reconstruct the early response of European naturalists (including those who today would be called "citizen scientist") to the invasion of *Dreissena* and describe their attitudes to the problem, including the divergence in opinion about the origin and the means of dispersal of this bivalve species. An analysis of papers published in English, French, German, and Russian between 1774 and 1920 showed that the invasion of *D. polymorpha* was by no means "silent"; quite the opposite, it provoked an immediate reaction from naturalists. The scientific agenda for the study of the new invader was proposed in England as early as 1838.

Keywords: zebra mussel; dispersal; natural history; citizen science; invasion ecology; history of zoology

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1. Introduction

Dreissena polymorpha (Pallas, 1771), or the zebra mussel, or *Wandermuschel* (=wandering shell) in the German literature [1], represents an iconic example of a very fast and efficient invasion of a freshwater species to regions and ecosystems situated far beyond its native area. The invasion of *Dreissena* may result in drastic changes in the recipient ecosystems and communities and have a negative economic impact. This bivalve species (family Dreissenidae J.E. Gray, 1840) is notoriously known as an overly aggressive and successful invader; since the 1800s, it has gained a foothold in many countries of Western and Central Europe as well as in North America [2–4]. The zebra mussel spread is ongoing [5], and it continues to conquer new regions, like North European Russia [6] and West Siberia [7,8]. In the late 20th century, another species of the genus, *Dreissena bugensis* (Andrusov, 1897), or the quagga mussel, repeated the success of its congeneric, being found today in many regions outside its native range [4,9]. Only a small fraction of available review publications discussing the invasion ecology and ecological and economic impacts of invasive zebra mussel populations can be cited here [4,5,10–14]. Limanova [15,16] compiled an impressive list of publications devoted to various aspects of the systematics, morphology, and ecology of *D. polymorpha*. According to this bibliography, 1920 papers on these subjects were issued between 1774 and 1977; not being exhaustive, this compilation shows the increasing interest of naturalists in the wandering freshwater mussel and provides an opportunity to quantify this interest and illustrate it graphically (Figure 1). The most recent review shows that the body of literature data is increasing steadily: 1502 papers were published between 1989 and 2011 and another 1034 during the decade between 2012 and 2021 [4].

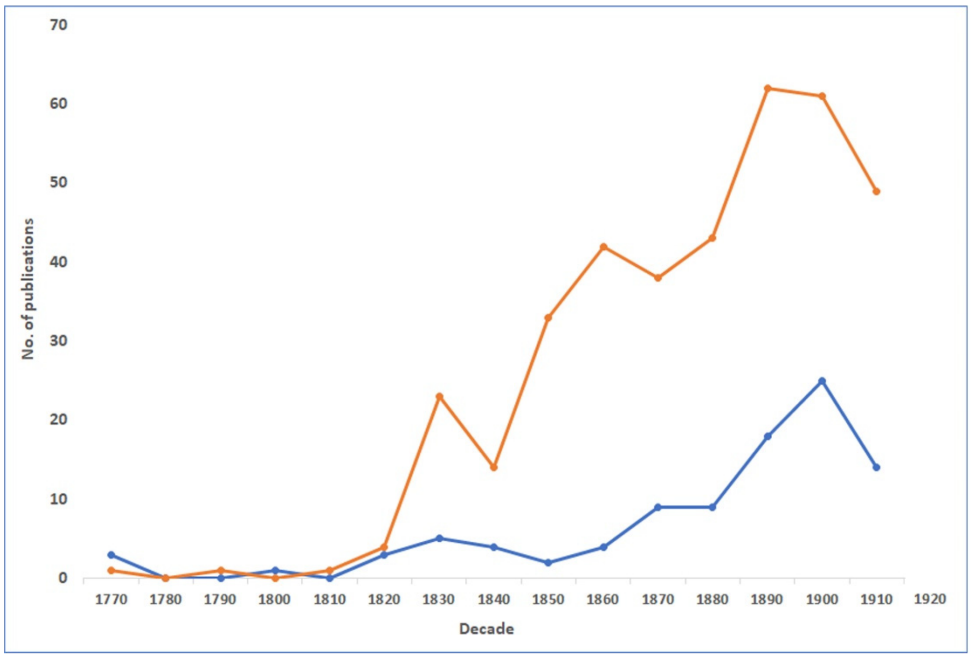

Figure 1. The increase in publications on *Dreissena polymorpha* published between 1770 and 1920 in Russia (blue line) and Western and Central Europe (orange line). Each point corresponds to the total number of publications per decade. The primary data were obtained from Limanova [15,16].

The native (historical) range of *D. polymorpha* lies in the Ponto–Caspian basin. In the Pleistocene, the zebra mussel was broadly distributed in Europe, but the cooling events of the Quaternary period dramatically reduced its distribution, and by the onset of the Anthropocene, this bivalve (more precisely, the nominative subspecies, *D. polymorpha polymorpha*) occupied a relatively small area, being confined to the lower courses of rivers emptying into the Black Sea (the Danube, Dnieper, and Volga rivers) [3]. The fast spread of *D. polymorpha* to many regions of Europe can, thus, be considered a return of an aboriginal species resurrecting its former range. In other words, the zebra mussel in Europe should not be treated (in many cases) as a "true" invader. The freshwater pearl mussels of the genus *Unio* Retzius, 1788 represent another example of this sort, actively restoring the lost part of their former range in Western Siberia [8]. The dispersal of *D. polymorpha* may be viewed as a part of a much broader process named 'The faunal Ponto-Caspianization' of European water systems [17]. The role of the Ponto–Caspian region as an important source of invasive species (as well as a target basin for numerous invasions from other areas) has repeatedly been discussed in the literature (see [17–21] and references therein).

The early steps of an invasive process are of high interest since their study allows one to understand the pathways and mechanisms of migration and dispersal of the invading species, as well as patterns in the formation of their invasive ranges. There are two main approaches to this problem. One is based on a study of freshly collected specimens of non-indigenous species from various parts of their aboriginal and non-native ranges, which allows for the application of various molecular genetic and GIS techniques capable of reconstruction of the initial steps of dispersal and identifying the possible sources of invasion (e.g., [9,22–24]). Though this method of study may be extremely effective, in the case of the 'old' invaders, i.e., alien species that started their "conquest of the World" in the 17–19th centuries, an additional approach is applicable. I mean a study of the museum collections and old literary sources that may help to discover the "invisible" steps of invasions and document them more accurately than molecular research analyzing a set of recently collected individuals. Instances of this approach are rarer [25,26].

As it has been stated many times, biological invasions are a phenomenon having a profound social impact, since many non-indigenous animals and plants may be harmful or even dangerous to humans, their livestock, and crop plants, and can damage buildings and

urban infrastructure. The so-called "citizen science" is now one of the most effective tools to detect biological invasions and monitor them (see [27,28] and references therein). Not only professional scientists, but even amateur naturalists and mere laypeople, can contribute significantly to the field of invasion ecology. This raises a question about how well the people in recipient countries are (were) aware of the non-indigenous origin of a species, and in which way do (did) they respond to an assumed invasion. Are there other concerns, in addition to the purely scientific ones, that attract(ed) the attention of naturalists during the first (and often explosive) phases of an invasion? Answering these questions requires a better understanding of some important aspects of the human–wildlife interaction. In my earlier publication [25], I discussed the phases of the explosive invasion of the physid snail *Physella acuta* (Draparnaud, 1805) into the countries of Europe and Central Asia. According to historical documents, this process can be characterized as a "silent invasion" since the invasive origin of this snail was firmly established almost 200 years after its first scientific description in 1805.

In this paper, I study the first steps of the invasion of Europe by *Dreissena polymorpha*. Based on a plethora of contemporary sources, I try to understand how European naturalists, both professional and amateur, responded to this invasion and if they were fully aware of the non-aboriginal status of this bivalve and the possible pathways of their dispersal. To put it briefly, the main question of this paper is: was the zebra mussel invasion of Europe "silent" or not? A similar story was told by Griffiths et al. [29], who documented the response of governments and society to the zebra mussel invasion of the Laurentian Great Lakes. The studied period was 1988–1991, which is much closer to our times and, thus, the historical documents are much more abundant and detailed than those at my disposal.

2. Material and Methods

I obtained the primary data for my analysis from a large body of original papers published in four European languages (English, French, German, and Russian) between 1771 and 1920. These publications, devoted to various aspects of *Dreissena* studies, were analyzed from the point of view of their content, and all information contained in them concerning the zebra mussel invasion, occurrences, and possible paths of dispersal and introduction, was considered. The absence of such information in a historical document is sometimes also informative, and I did not omit such sources from the consideration. The upper time threshold (1920) was selected purely conventionally. The year 1920 is not marked by any important milestone in zebra mussel studies; this date merely roughly corresponds with the 150th anniversary of the discovery of *D. polymorpha* by P.-S. Pallas [29]. The first 150-year period of the studies of the zebra mussel witnessed the explosive invasion of this species into water systems of Western and Central Europe, and by the end of this period, *D. polymorpha* became firmly established in many regions of the continent [3].

3. Results

3.1. The Zebra Mussel Discovery and Its Pre-Anthropocene Range

Peter-Simon Pallas (1741–1811), a Russian naturalist of German origin, was the first zoologist to identify the zebra mussel as a distinct species and provide its scientific description. The place and date of this discovery are known with exhaustive exactness. During his long travel throughout "various provinces of the Russian Empire" (1768–1774) [30], Pallas explored the lower courses of the Volga and Ural River basins. Pallas found the specimens of a new species on 12 August 1769, in a small oxbow near the Budarin Forpost settlement—a small Cossack camp on the territory of the modern West Kazakhstan Region of the Republic of Kazakhstan [30] (p. 368). Shortly after that, Pallas found the same species near Kalenoi Forpost, another Cossack camp on the Ural River ([30], p. 375), and, finally, in the Caspian Sea near the Kamennyi (=Stony) Island between 26 and 31 August 1769 ([30], p. 435). Pallas described this new species under the name *Mytilus polymorphus*, classifying it thus as a member of the genus *Mytilus*, which includes chiefly marine and brackish-water bivalves. Only in 1835, a separate genus (*Dreissena*) was established for

this species by a Belgian zoologist Pierre-Joseph Van Bénéden (1809–1894), then working in Louvain [31]. The generic name is an eponym. The new genus was dedicated to J.H. Dreissens, a pharmacist in Mazeik Town (then in the Netherlands; nowadays it is Maaseik, Limbourg Province, Belgium), who collected a sample of specimens of this mussel in a local channel and gave it to Van Bénéden for study [31].

The fossil record of *D. polymorpha* is comparatively rich [3–5,31–33]. During the interglacial periods of the Pleistocene epoch, the zebra mussel could spread widely and was distributed much broader than in the early Holocene; its range occupied the entire basins of the Danube, Volga, Don, and Dnieper Rivers (Figure 2). However, this species was unable to penetrate other large river systems of Europe due to a lack of basin interconnections [3]. As a result of the last Quaternary glaciation (Würmian glacial stage), the range of *D. polymorpha* was significantly reduced. In the early Holocene, it covered the lower courses of the Volga, Don, Ural, and Danube River basins, from where mollusks began to slowly spread upstream, restoring their lost range. Already in the Middle Ages, river navigation could speed up this process [3].

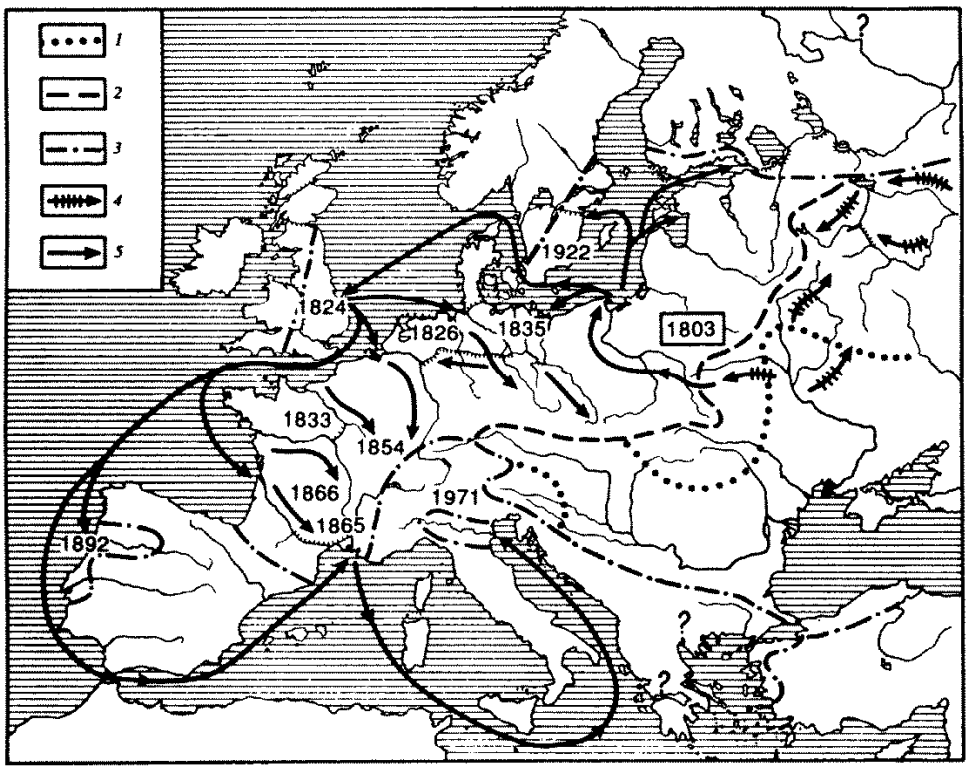

Figure 2. A map illustrating the process of *D. polymorpha* dispersal through Europe in the 19–20th centuries. 1—The Early Holocene distribution; 2—the range of *D. polymorpha* by the start of the Anthropocene; 3—the range of *D. polymorpha* in the early 1990s; 4—routes of dispersal prior to 1803; and 5—routes of dispersal after 1803. The numbers correspond to the dates of the first finds of the zebra mussels in various countries. Modified from Starobogatov and Andreeva [3].

The turning point in the history of the *D. polymorpha* invasion is associated with the construction of canals that connected the Volga and Dnieper basins with the basins of rivers flowing into the Baltic Sea. The first constructions of this sort dated back to the Peter the Great epoch in Russia. According to Andrusov [31], the Vyshevolotsk channel system, opened in 1709, could serve as the first corridor of the invasion of *D. polymorpha* into Central Europe. It connected the Volga basin with the Baltic Sea basin through the Lake Ladoga and the Neva River. This point of view was questioned by many authors, who proposed another corridor—the Oginsk Channel, opened in 1803 [2,3,34]. It connected the Dnieper basin with the Neman River system. The arguments against the Vyshevolotsk channel

system as the "window to Europe" for the zebra mussel included the relatively low water temperature in the Neva River, which this mussel probably cannot sustain, and the full absence of records of *D. polymorpha* in the Baltic Sea basin prior to the 1820s [3]. Indeed, the first record of this species in the vicinities of St. Petersburg (the Neva River basin) was published only in 1883 [2].

The first scientific records of the zebra mussel outside its native range date back to the mid-1820s, when it was found in England (in 1824) [35] and in the former East Prussia (in 1825) [36]. Subsequently, this bivalve was registered in many European countries, and at the end of the 19th, its invasive range already covered some parts of the Iberian Peninsula (see Figure 2).

3.2. The European Naturalists' Response to the D. polymorpha Invasion–England

The bibliography of *D. polymorpha* studies in Europe shows that prior to the 1830s, the number of publications on this species remained very low. The decade starting in 1830 witnessed a sharp increase in naturalists' interest in this mussel (see Figure 1), which can be surely related to the first findings of the zebra mussel in some parts of Europe. By around 1830, this species had become a subject of close attention for zoologists in Britain, Belgium, Germany, and several other countries.

The United Kingdom is a country in which one of the earliest findings of the invasive mussel was made (Table 1). The exact date of its penetration into the British Isles remains unknown, but one can assume that it happened 5–10 years before 1825, when the first scientific publication on this subject appeared [35]. Its author, James De Carle Sowerby (1787–1871), is a well-known paleontologist, who described, among others, many species of fossil Mollusca. According to his report, *D. polymorpha* were living in abundance in commercial docks on the Thames, in Rotherhithe (nowadays, it is a district of London), where a local gentleman used them as bait for perch [35]. Sowerby correctly identified this as *Mytilus polymorphus* (though he ascribed the authorship of this name to Gmelin, not to Pallas) living in Russia and the Danube River basin; however, he did not state that this bivalve is non-indigenous to the British Isles. He remarked only that "the British specimens are much larger and finer than any foreign ones I have seen". The latter remark shows that specimens of *Dreissena* from continental Europe were accessible for a British naturalist, either from a public museum or a private collection.

Table 1. The dates of the first records of *Dreissena polymorpha* in various countries of Western and Central Europe (1800–1920s). Compiled after several sources [2–5,26,31].

Year (Decade)	Country (Basin)	Year (Decade)	Country (Basin)
Around 1790	Hungary	1840 or 1843	Denmark
The late 1800s	Poland	1855	The Seine River, France
1824	England	1856	The Loire River, France
1825	East Prussia	Near 1861	South Germany (Bavaria)
1826	The Netherlands	1865	The Rhone River, France
1827 or 1828	Central Germany (near Berlin)	1866	The Garonne River, France
1833 or 1834	Belgium	1892	Portugal **
1833 or 1834	Scotland	1896	The Severnaya Dvina River basin (the upper course), Russia
1835	Northern Germany (the lower Elbe basin)	1890s	The Czech Republic
1838	France, the Nord Departement *	1922	Southern Sweden

* This information is given by Andrusov [31] and Starobogatov and Andreeva [4] only. Prié [26] does not mention this record. ** Andrusov [31] gives another date of the infiltration of *D. polymorpha* to Portugal—1880.

In the same year, however, the invasive nature of the zebra mussel in the UK was acknowledged by another British zoologist, John Edward Gray (1800–1875), a prominent student of Mollusca. In his paper devoted to the classification of some bivalve genera, Gray mentioned this species under the name *Mytilus*? *volgensis* and added that "it most likely has been introduced with timber from the Volga" [37]. More importantly, Gray tried to understand how the animal could have reached the British Isles and suggested that the zebra mussel may sustain for a relatively lengthy period out of water. The naturalist claimed that he kept an individual of *Dreissena* "for three weeks, when it was still healthy" [37]. This was, perhaps, one of the earliest instances of an experimental approach to the problem of biological invasions, attempted purposely and with a full understanding of its significance.

The subsequent British literature on *D. polymorpha* can be roughly divided into two parts. The first part includes a number of relatively short research notes documenting new or remarkable observations of the zebra mussel in different regions of that country (e.g., [38–40]). Some of these notes were rather concise, sometimes not lengthier than 8–10 lines, in which the circumstances of the findings were described with relevant details. A typical (and unabridged) example of such a record note is given below:

"Some eight years ago, while angling in an old milldam at Toton, Notts, with my brother, he pulled up on his hook a specimen of *Dreissena polymorpha*, adhering to a stone. The dam is supplied by the Erewash, a small shallow stream which joins the Trent nearly a mile from the place, that river being the nearest navigable water. I afterwards found numbers of these Mollusks adhering to the stones underneath the waterfall of a pond at Lentou, near Nottingham, to which they must have gone up a very small brook fully a mile from a canal; in which, however, though I have frequently searched, I have never found them—George Wolley; 9, Cambridge Street, Liverpool, February 23rd, 1846" [38].

It is not always clear in such laconic reports if their authors were aware of the invasive origin of the discussed species and if they realized the need for precise documentation of such findings, which would help to trace the spread of *D. polymorpha* through the country. Most probably, the authors wished to inform their peers of the record of a new and interesting species and did not intend to contribute to a better understanding of the invasion process. However, some of them seemed to pay close attention to the new naturalizing species and were deeply impressed by the pace and efficacy of its spread. Thus, as early as 1836, the Reverend Berkeley stated that the zebra mussel "is now found in almost every part of Europe, in inland seas, marshes, canals, tanks, and running streams" ([39], p. 573). Even a fast examination of Figure 2 and Table 1 will show how exaggerated this statement was. In 1836, the "wandering" mussel was found only in a few localities beyond its original range.

The lists of species of a local malacofauna, where the zebra mussel was included (e.g., [41,42]), must be also classified as belonging to the first category.

Amateur naturalists were very numerous in Great Britain at that time, and most of them were educated men, including physicians, engineers, officers, and (rather commonly) churchmen and gentlemen of independent means [43]. Many of them now would be called "citizen scientists". However, the vast majority of these naturalists did not produce voluminous monographs on mollusks or other groups of animals, and their literary production often was represented by such research notes and 'letters to editor'. The scientific interests of such men were very broad. For example, in 1846, George Wolley published in the same journal two more notes, entitled "Anecdote of the stoat's preying upon bats" and "Exotic spiders imported in dye-woods" (the latter one demonstrates Wolley's attention to the introduced species of animals).

These publications, however, served to accumulate primary data and as the empirical material for generalizations made by more "advanced" amateurs or by professed scientists affiliated with universities or museums (the number of the latter was rather low due to the deficiency of teaching and researcher positions). Roebuck [44] published, at the very end of the studied period (in 1921), a paper in which these scattered distributional records of the 19th–early 20th century were reviewed and summarized.

The second group in the British literary source is formed by comprehensive works, in which the whole aquatic malacofauna of the country was reviewed. Some of these publications were high-standard taxonomic monographs aimed at professional zoologists (e.g., [45–47]), and others were popular guidelines for amateurs, less abundantly illustrated and much more accessible, both in terms of price and content (e.g., [48–50]). Generally, such publications provided a more or less detailed description of the shell and, sometimes, the internal morphology of *Dreissena*, and gave an outline of its current distribution in the country. However, the questions of invasion ecology and dispersal mechanisms of the species were rarely addressed in detail by their authors. As for dispersal, most authors repeated the hypotheses discussed in the works of Gray, Strickland, and other authorities who wrote about *D. polymorpha* in England. In most cases, the non-indigenous status of this mollusk in England was fully realized, and, for instance, Forbes and Hanley ([45], p. 167) called it "a species of ancient origin, and one of the members of the old Aralo-Caspian fauna". The most peculiar approach to the problem of *Dreissena* in the UK can be found in a monograph on the "*British conchology*" by Jeffreys (see Section 3.3).

Hugh Strickland (1811–1853), a prominent English naturalist of that time, authored one of the first special publications on the colonization of Britain by the zebra mussel. He fully realized the theoretical importance of the study of this invasion both for zoology and geology. Strickland documented a very fast (about two to three years) colonization of the Avon River at Evesham, in Worcestershire, by *D. polymorpha* and concluded that for a geologist, for instance, the study of this invasion may help to understand "the distribution of organic remains, and the sudden appearance and disappearance of particular species in a given stratum" ([51], p. 361). The transport of timber was, according to the author, the main means of dispersal of the zebra mussel within England. Strickland also mentioned that some people intentionally *planted* the bivalve into novel places, such as around Bristol. Strickland even went as far as to formulate an agenda for *Dreissena* studies in Great Britain. He expressed this in such words: "It appears desirable to record <. . .> [the finds of *Dreissena*], because it may interest some of our field-naturalists to watch the gradual spread of this species over the kingdom. Its propagation is so astonishingly rapid, that it will probably become, in a few years, one of our commonest British shells" ([51], p. 363). This prophecy proved true very soon [52]. In 1845, i.e., only 20 years after the publications of Sowerby and Gray, Brown stated that the invading mussel was so firmly naturalized in Britain that it "may fairly been considered a British shell" ([53], p. 98).

A special aspect of the zebra mussel invasion of the UK (and other urbanized European countries) was its rapid infiltration into the water supplies of London and other cities. In Manchester, thriving colonies of *D. polymorpha* were detected by around 1850. Dyson reported his observations on these mussels living in the pipes that supplied the city from the nearby waterworks; the mussels were also highly abundant in the reservoir that served as the source of water [54]. In the London water supplies, *D. polymorpha* was also recorded around 1850. Woodward reported that the mollusks were "noticed in the iron-pipes of London, incrusted with a ferruginous deposit" ([55], p. 267). Tate [52] explained the astonishing quantities of *Dreissena* in water pipes due to their avoidance of light, which was thought to be characteristic of this mollusk. The harmful effects of the alien bivalve were completely realized in other countries of Europe by the end of the 19th century and further stimulated the studies of the biology and ecology of this species [56,57] (Figure 3).

Figure 3. A photograph, taken in 1912, showing a mass of *Dreissena* individuals removed from an unfiltered water main at Hampton-on-Thames, England. From Kirkpatrick [56].

3.3. The 19th–Early 20th Century Discussion of the Dispersal Mechanism(s) of D. polymorpha in Europe

The first English publications on *D. polymorpha* colonizing that country opened a long discussion concerning the ways and routes of the zebra mussel dispersal outside its native range. This debate lasted more than a century and is only briefly summarized here. Table 2 provides a concise overview of the diverging hypotheses proposed in the 19th–early 20th century. Another source of data on the debate is the monograph on the dispersal of mollusks ("shells") written by Harry Wallis Kew (1868–1948) in the late 19th century ([58], pp. 210–221). It should be noted that almost no author of the studied period insisted that there was only one mechanism of dispersal of *Dreissena*; usually, two or more possible (and not mutually exclusive) explanations were proposed. Certain naturalists even tried to conduct experiments with the mussel, attempting to determine how long it can survive out of water [37] or how quickly a juvenile completes its development to anchor itself to the substratum [51]. It seems that the possibility of dispersal of the veligers, i.e., pelagic (swimming) larvae of *Dreissena*, was not considered for most of the 19th century. The first detailed description of the veliger of *D. polymorpha* was published by Eugene Korschelt (1858–1946), a German embryologist, in 1891 [59,60]. Immediately after that publication, Kew highlighted the exceptional potential of the veligers as the means of *Dreissena* dispersal [58].

Seventy years of observations made by numerous naturalists in Great Britain led Kew, in 1893, to the conclusion that the zebra mussel "is perhaps better fitted for dissemination by man and subsequent establishment than any other fresh-water shell; tenacity of life, unusually rapid propagation, the faculty of becoming attached by a strong byssus to extraneous substances, and the power of adapting itself to strange and altogether artificial surroundings have combined to make it one of the most successful molluscan colonists in the world" ([58], pp. 219–220).

Whereas most authors acknowledged the non-indigenous status of the zebra mussel in Western and Central Europe, there was an opposition to this widespread view, represented by two prominent malacologists, the British John Gwyn Jeffreys (1809–1885) and the Danish Otto Andreas Lowson Mörch (1828–1878). Both men remained unconvinced that the first findings of *D. polymorpha* in England in 1824 marked its recent arrival to the country. In their opinion, "the silence of [the 18th century] writers" cannot be seen as ultimate proof: many widespread species of European freshwater mollusks were described scientifically long

after Linnaeus, and the new discoveries of the early 19th century showed that some species of aquatic mollusks could be overlooked by naturalists for decades. In other words, the zebra mussel could be a rare member of native European fauna, surviving in refugia, from which it started to spread since the onset of the Industrial Revolution and the Napoleonic wars [46,61,62]. Using some obscure descriptions published around 1780, Mörch [61] argued that *Dreissena* might have been distributed in the interior of Germany prior to this year and that these mussels inhabited the rivers of the Rhine basin. The upper courses of the Rhine, in Mörch's opinion, were the source of zebra mussel colonies found in the Netherlands around 1826 [61].

Table 2. The divergence of opinion among researchers on the origin and means of dispersal of *Dreissena polymorpha* in Western and Central Europe.

Hypothesis	Dispersal Mechanisms	Source
1. *Dreissena* is a native mollusk of Western and Central Europe, overlooked by earlier naturalists [46,61,62] or—for the time being—it survived in some refugia [2,63], from which it started to disperse in recent times (with the help of humans or naturally).	1a. Natural drift with floating pieces of timber, "down one of the European rivers, and across the German Ocean"	[51]
	1b. Natural dispersal via artificial canals	[2,3,51,52,57]
	1c. Native, originally rather rare, species, which began to spread in historical time with, for instance, 'pontoon-trains of the army of Napoleon'	[61,62]
	1d. Natural dispersal of free-swimming larvae (veligers)	[58,63,64]
	1e. Natural dispersal via large and motile aquatic animals (zoochory)	[31] *
2. *Dreissena* in Western and Central Europe is an alien species, which can disperse either naturally or with the assistance of humans. The latter mechanism is, perhaps, most efficient.	2a. On the bottoms of marine ships	[2,31,58]
	2b. Commerce (export and transport of timber on ships and rafts, both among and within countries)	[2,37,39,49,52,58]
	2c. With river boats and/or in fishing nets transported from one drainage basin to another	[2,57,65]
	2d. Intentional introduction (for unknown reasons)	[51]

* Though Andrusov [31] mentioned zoochory as a means of *Dreissena* dispersal (referring to Kobelt), he thought this mechanism of spread was of negligible importance.

In the first half of the 20th century, this hypothesis was accepted by Zhadin (1896–1974) ([63], p. 70). This Russian author believed that *Dreissena* survived the Pleistocene glacial epochs in refugia situated in North Germany, from where it began its spread to England and other countries of Western Europe. In addition, Zhadin criticized the version that *Dreissena* arrived in England with timber export from Russia. He noted that the lower courses of the Volga and Don River basins, where the Holocene range of the zebra mussel was situated, are almost avoid of forests, and export timber was yielded in the territories of Russia, located much north, where *D. polymorpha* was absent. Equally, Zhadin disputed an old idea that the zebra mussel could arrive in England attached to the bottoms of marine ships ([66], pp. 302–303). In his opinion, this hypothesis was untenable since *Dreissena* is hardly able to sustain long travel through saline waters, like the waters of the North Sea. However, Zhadin did not reject the key role of canals and other inter-drainage connections, which serve as corridors for zebra mussel dispersal.

The belief that *D. polymorpha* in Western and Central Europe may be a relic of some ancient epochs is not without support today. In 2011, Buynevich et al. [67] reported the finds of shells of *Dreissena* on the southern Baltic Sea coast in deposits formed between 800 and 1200 AD. The authors proposed the "early arrival scenario", according to which the zebra mussel might have infiltrated the Baltic region more than 1000 years ago through poorly drained waterways. Medieval river navigation, including Viking river voyages from Constantinople to the Baltic Sea via the Dnieper River and the Black Sea, is seen as a human-

mediated way of *Dreissena* dispersal. Some data supporting this hypothesis can be found in an earlier paper by Deksbakh [2], who described a find of numerous subfossil shells of the zebra mussel in Belarus. There were other possibilities for the transport of the mussel to Western Europe between 1200 and 1800 [67]. The existence of the Pleistocene refugia situated in Central and Eastern Europe cannot be ruled out either. In a series of recent studies, the application of molecular methods helped to identify such refugia for some species of pearl mussels (Unionidae), another family of freshwater Bivalvia [8,66,68,69].

3.4. The European Naturalists' Response to the D. polymorpha Invasion–French Literature

According to the recent review by Prié [26], the first arrival of *D. polymorpha* in France must be dated as 1852. However, some older authors, for example, Locard [70] and Fischer [71], gave an earlier date, 1838, when this species was found in the Nord Department (see also Andrusov [31] and Starobogatov and Andreeva [3]). The exact date of the invasion remains, thus, disputable. Von Martens [72] believed that the zebra mussel used at least two invasion corridors to reach France. The first one was the Rhine River (upstream of the Netherlands) and the second was formed by the Sambre–Oise canal system situated at the Belgian–French border. Some modern authors (e.g., [3]) believe that the source of the *Dreissena* invasion of France could be the London port, where the species became naturalized 15–20 years earlier (see above). By the end of the 19th century, the zebra mussel was common throughout the country and mentioned by numerous local naturalists [70]. Fischer estimated that it took the species about 30 years to become naturalized throughout almost all of France [71].

The French literature on *Dreissena* prior to 1920 was represented by essentially the same genres as the English literature: (1) short record notes, documenting the first findings of the mussel in particular regions of France; (2) checklists of local malacofauna; and (3) comprehensive monographs aimed at the detailed description of freshwater mollusk species, including *D. polymorpha*. The data provided in the publications of the two first categories served as primary data for analytic studies of the distribution of the species (e.g., [70,73]). In 1864, P. Fischer stated that the spread of the zebra mussel "in the waters of Central and Western Europe is one of the most curious facts in the geographical distribution of mollusks. Every day we witness new invasions of this mollusk, the successive stages of which can be carefully noted. When we encounter it in a certain [new] locality, it swarms there in such a way that its presence at a previous time could not have been passed over in silence" ([73], p. 309). This conclusion coincides with those made by Fischer's counterparts in England (see above).

The authors of large monographic works on French malacofauna placed the zebra mussel in their volumes, but they either totally avoided discussion of its non-aboriginal origin in the country and the possible mechanisms of its dispersal [74,75] or touched these subjects only in passing [76]. For instance, Dupuy, having presented a lengthy description of the species' morphology and the overview of its current distribution in France, added only that "the mussel was carried on the hulls of Volga boats to the Baltic Sea, and from the Baltic to England and in the rivers of Holland, Belgium, and France" ([76], p. 661). A paper by Gassies [77] is a good example of a publication documenting the arrival of *D. polymorpha* in a new locality in France (Agen). Many short notes of this kind were scattered throughout French scientific journals, primarily in *Journal de Conchyliologie*, which served as an important disseminator of such information. That by Gassies was unusual in the respect that the writer accompanied his record with a detailed overview of the previous taxonomic work on this mollusk and a lengthy discussion of the mechanisms of its invasion (adding, although, nothing new to the hypotheses of the preceding writers). Gassies, who believed that marine and river navigation was the main vector of *Dreissena* dispersal, attempted to imagine how the process of its naturalization began. In his own words, "the boats, as they approach the quays or other boats, create a sort of friction which is enough to cause a certain number of *Dreissena* to be released, which, as they soon lay their eggs, reproduce rapidly, especially considering the slow currents in the canals, where the locks keep the

water in a state of stagnation which allows the animals to multiply extremely" ([77], p. 23). Based on a presumed close affinity between freshwater zebra mussels and marine (edible) mussels, Gassies wondered if *Dreissena* is suitable as human food, and, seemingly, planned to make some experiments to confirm this: "We do not yet know whether experiments have been carried out to assess their edible qualities. We will wait until our specimens have reached a suitable size before subjecting them to the same culinary preparations as those used for *Mytilus edulis*. Perhaps we will also try the condiments used in certain areas of the Agenais region to prepare *Anodonta* and *Unio*, without claiming to be introducing a new treat to the gourmet table" ([77], p. 23). I do not know if the author was able to put this plan into practice, though Gassies reported he managed to establish a colony of *Dreissena* in aquaria and, thus, he could conduct such a culinary experiment. His work contained a description of other observations, made in aquaria in order to study the movement and larval morphology of the zebra mussel ([77], pp. 24–25).

Another French naturalist of the late 19th century deserves special consideration here. It is Arnould Locard (1841–1804), perhaps the only author of the studied period, attempting to put the discussion of invasive *Dreissena* in Europe in an evolutionary context. In 1893, Locard published a lengthy monographic article aimed at a taxonomic revision of the European dreisseniid bivalves [70]. He stressed that the zebra mussel demonstrates huge conchological variability in diverse areas of its invasive range. In the opinion of Locard, this variability means that the "primitive type" of *Dreissena* (i.e., that found by Pallas in the Volga and Ural rivers), after its infiltration to other basins of Europe, underwent dramatic phenotypic changes induced by the new living conditions. As Locard explained, "given such diversity in the appearance of the habitat, we will not be surprised to see that the primitive type, thus passing from one environment to another, did not always remain absolutely identical to itself. This resulted in considerable polymorphism, which is clearly evident when we compare series of Dreissensies of various origin. If certain colonies still preserve exactly the characteristics of the primitive type, others, on the contrary, present forms absolutely different from this normal type; and these are not simply individual modifications, because it is easy to see that these new beings group together according to their shape, just as easily as the first ones, that they are continually similar to each other, even in very distant colonies, and finally that they reproduce still similar to themselves" ([70], p. 122). Locard did not hesitate to hypothesize that the naturalists were observing the gradual formation of new species of *Dreissena* in diverse parts of Europe. As for his views on the essence of the species, Locard was an extreme nominalist in this regard. He belonged to the so-called "New school" of malacology (see [78,79] for details), and, together with other members of this school, believed that the terms "species" and "variety" are utterly arbitrary and that zoologists use them only for the sake of convenient classification. While most other malacologists of the epoch would treat these divergent forms of *D. polymorpha* merely as intraspecific variations, Locard described them as full species and gave them binomial names. In his monograph, he recognized as many as 31 distinct species of *Dreissena* in Europe and Asia Minor [70], and these species were in many cases not allopatric (or vicariant) entities, equal to the "local races" of other systematists. Locard believed that several such "minor" species can live in sympatry. For example, in a sample taken from the Elbe River near Hamburg, he could distinguish no less than four "species" [*Dreissena fluviatilis* (=*D. polymorpha*), *D. servaini*, *D. sulcata*, and *D. westerlundi*], and nine species were found by him in Paris' city water supplies (*D. fluviatilis*, *D. curta*, *D. tumida*, *D. arnouldi*, *D. occidentalis*, *D. belgrandi*, *D. recta*, *D. lutetiana*, and *D. paradoxa*). The mechanism(s) of the formation of these sympatric species were unclear to Locard (at least, he did not explain them in any way). Perhaps he held the Lamarckian idea about the direct influence of the environment on speciation, but Locard cited neither Lamarck nor Neolamarckist biologists [70]. On the other hand, he acknowledged that a change in conchological traits is not an obligate outcome of an invasion of a new locality. The "primitive type" of *Dreissena* remained unchanged in many regions of Europe, and

shells collected from many invasive populations were indistinguishable from the zebra mussel of the Volga River [70].

Subsequent authors did not follow the classification proposed by Locard. Neither Andrusov, in 1897 [31] (pp. 341–344), nor Skorikov, in 1903 [80], agreed to accept the numerous species erected by the French malacologist. Skorikov treated them as intraspecific morphs. Today, most of these species are considered junior synonyms of *D. polymorpha*; and only a small fraction of species described by Locard from Asia Minor are accepted as valid [81].

Locard, however, discussed not only the classification of *Dreissena*. He mentioned that the competitive abilities of the zebra mussel exceed those of the native species of the genera *Anodonta* and *Unio* (both belonging to the freshwater family Unionidae) and, therefore, can potentially drive them from their habitats. Discussing the colonization of urban water supplies by *D. polymorpha*, Locard emphasized that these mussels can play a positive role: being filter feeders, the mussels can serve to purify water. It would be useful if people could control the zebra mussel population by keeping its numbers at a moderate level [70]. These remarks show that the author fully realized the ecological and economic consequences of the invasion.

I wish to add to this paragraph that *D. polymorpha* quickly became a popular subject of anatomical and embryological studies in the French-speaking zoological community. Van Beneden, a Belgian zoologist and the author of the generic name *Dreissena*, published detailed accounts on the external and internal morphology of the zebra mussel [82,83], which were later regarded as a classical morphological work on this subject. By the end of the 19th century, *D. polymorpha* was, probably, one of the best studied species of freshwater mollusks in this relation. Only a small fraction of original studies, published in various languages and devoted to the anatomy, physiology, and embryonic development of this mussel can be mentioned here [59,60,84–86].

3.5. The European Naturalists' Response to the D. polymorpha Invasion–German Literature

The bibliography compiled by Limanova [15,16] shows that German-speaking authors were the most prolific researchers of *Dreissena* in Europe; the number of their publications on this species exceeds the number of publications authored by English and French naturalists by roughly 1.5 times combined. On the other hand, the response of German zoologists to the zebra mussel invasion followed the pattern described above, as exemplified by English and French authors. The topics and genres represented in the German scientific literature were much the same as in other countries, which allows me to avoid a detailed review of the German publications, presenting instead a rather cursory summary of the most remarkable observations and opinions.

The earliest date of registration of *D. polymorpha* in the territory of modern Germany was, in the 19th century, a matter of debate. Though most researchers believed that the mussel was introduced to this area in the first third of the century, Mörch [61,62] attempted to prove that an obscure German conchologist (Sander, a gymnasium teacher in Carlsruhe) described this species as early as 1780. Martens [72] strongly criticized Mörch's opinion, arguing that the Danish zoologist misunderstood the report by the 18th-century author. After all, according to Martens, Mörch seemed to underrate the enthusiasm and zeal of German *Muschelsammler* (shell collectors), who hardly could overlook this peculiar species had it been really living in the country around 1780. Stein ([87], p. 106) witnessed that, near 1800, shells of *Dreissena* were imported from Austria to Prussia, and the collectors paid up to five silver groschen for such rare specimens (most probably, these shells were brought from the lower Danube basin).

Martens himself dated the first arrival of this mussel in Germany to 1828 [72]. (Wiegmann [88] gave a slightly earlier date—1827). In his opinion, in the Baltic countries *D. polymorpha* was also a recent invader, not being presented there in the 18th century. According to Martens' detailed account, the mussel suddenly appeared in several regions of Germany between 1828 and 1835, which "caused a stir among naturalists themselves, but

they calmed down again when they were convinced that von Bär had already found it in a freshwater bay and that it was not even a new species, but the old *Mytilus polymorphus* Pall." ([72], p. 52). Karl von Baer [36] noted that the mussel was living in the desalinated bays of the Baltic Sea and in the lower courses of the rivers where it reached vast numbers. However, this biologist seemingly did not recognize *Dreissena* as an invader in East Prussia. Between 1837 and 1838, Wiegmann [88] clearly indicated its non-indigenous origin in Germany and guessed that the zebra mussel might have arrived there either from Poland or directly from East Prussia. Another vector of *Dreissena* dispersal discussed by this author was river navigation from the west. Wiegmann cited a communication by Professor Kilian of Manheim, who witnessed that, in 1835, *Dreissena* was found in high abundance on the keel of a ship that arrived at Manheim from Rotterdam ([88], p. 343). As it was stated many times, *Dreissena* is virtually unable to migrate upstream without the help of human vehicles (or zoochory) (e.g., [80]), and its passive dispersal from the Lower Rhine basin to Germany was improbable.

The large abundance of *D. polymorpha* in East Prussia, reported by von Baer in 1825 [36], may indicate that this species might have arrived there much earlier than the year of its first finding, which corresponds to the hypotheses of subsequent researchers [2,67].

The period of 1827(8)–1835 coincided with a marked increase in the number of publications on *Dreissena* in Europe, which took place in the 1830s (see Figure 1). The explanation for this sudden growth is that by the late 1830s, the new mussel was detected in several European states (the UK, the Netherlands, France, Belgium, Germany, Poland, and the Baltic countries) and raised a vivid interest in the scientific communities of these countries (see above). However, by 1865, when Martens' account [72] was published, the zebra mussel managed to occupy only a part of Germany; it was unknown in Bavaria and Swabia as well as in Switzerland. The first record of this species from the German part of the Danube basin (in Regensburg) is dated 1868 [89]. (According to Jaeckel [90], the first find of *D. polymorpha* in Bamberg in Bavaria was made around 1861). Clessin assumed that the source of this introduction was the Rhine Basin, not the Lower Danube. *Dreissena* used a canal connecting the Rhine and Main rivers and reached Regensburg through the Main-Danube canal [89]. In Austro-Hungary, this bivalve remained very rare and locally distributed even in the late 1880s [91–93]. For instance, *Dreissena* was unknown in the Danube River between Vilshoven in Bavaria and Budapest; Lampert [93] explained the findings of the mussel in the latter city by its transport with ships from the lower courses of the Danube, not by its passive dispersal downstream from the territory of Germany. Lampert stressed the fact that shells of *Dreissena* are known from the Pleistocene deposits of Northern Germany. Thus, this species is not truly "alien" to the country; it merely restores its lost range in Central Europe ([93], pp. 80–81).

It seems that the ecological peculiarities of *D. polymorpha*, especially its biotic interactions with other organisms of the biocoenoses, were a subject that German naturalists were a little more interested in than their colleagues in the UK, France, and Russia. The German literature of the discussed period is filled with such observations, directly relating to the invasion ecology of the zebra mussel, including its movement and mechanisms of migration. Numerous observational notes of this kind appeared in popular German scientific periodicals such as *Aus der Heimat* (From the Homeland), *Der Zoologische Garten* (The Zoo), *Blätter für Aquarien- und Terrarien-Kunde* (A Leaflet of Aquarium and Terrarium Science), etc. Struck [94,95] observed that *D. polymorpha* may use the bodies of motile animals (river crayfish) as a substratum for their settlement; this can represent a means for the zoochoric dispersal of the mollusk. The same author published a brief list of freshwater fish feeding on *Dreissena* in Germany [95]. The interactions between the zebra mussel and the native species of large unionid mussels were also a subject of observation and illustration (Figure 4). Frenzel [96] determined the suite of aquatic organisms associated with colonies of *Dreissena*; it includes larvae of various insects, the water louse, and gammarids as well as leeches and diatom algae (Bacillariaceae).

Figure 4. An *Anodonta* shell with attached individuals of *D. polymorpha*. A drawing that was published in the scientific popular leaflet *Aus der Heimat* in 1864 [97].

The same author described the slow movement of the juvenile mollusks by ejecting water from the outlet siphon and the simultaneous closure of the shell valves with a sharp contraction of the closing muscles. Alternatively, the mussel may use its foot to move. Frenzel also observed the migration of small colonies of *Dreissena* with the onset of winter from shallow areas to deeper places of a waterbody [96]. This also happens in cases where the substrate on which the zebra mussel colony is located (e.g., a submerged stone) is displaced or turned upside down, and the mollusks tend to return to their original position [96]. It turned out that adult mollusks are able to break off their byssal thread and move along the substrate in search of a new attachment site. The observations made by Frenzel were confirmed by other authors who worked in the next century [98,99].

Germany became, perhaps, the first European country where the disappearance of *Dreissena* from once-inhabited rivers due to water pollution was observed. In 1897, Friedel (quoted after [57]) showed this happened in the Spree River, where the zebra mussel had been living since the 1850s.

4. Conclusions

It is safe to argue that the zebra mussel invasion of Western and Central Europe became one of the earliest cases of a biological invasion that attracted an immediate response from professional scientists and citizen naturalists. Starting from its registration around 1824 in England [35,37] and in East Prussia in 1825 [36], this mollusk used to be a subject of studies of various sorts, ranging from short distribution notes to detailed accounts of its morphology and embryonic development. The turn of the 19th–20th centuries was marked by the appearance of a few generalizing publications on *Dreissena polymorpha* and related taxa [31,100]. The invasive nature of *D. polymorpha* in Central and Western Europe was fully realized, and there was a scientific discussion of the probable ways of its transport from the East. Lampert ([93], p. 80) wrote that the fact of such a rapid spread of a species that came from the East throughout Europe is surprising and has no analogs in history except for the rapid spread of the brown (Norway) rat (*Rattus norvegicus*) in the 18–19th centuries. So, it was by no means a "silent invasion", and the "wandering mussel" did not go unnoticed in all countries where it reached, especially because its effect on hydro-technical constructions became evident as early as the mid-19th century.

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