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The Possible Failed Pre-Linnaean Introduction in the Mediterranean Sea: An Archival Case Study of the Brown Mussel *Perna perna*

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Abstract: Most species arriving from a donor to a recipient area do not succeed in establishing long-lasting self-sustaining populations. However, successful introductions are far better documented than those that failed, especially those occurring before or near the advent of the Linnaean binomial nomenclature. We report here an introduction from the mid-18th century (possibly in 1750 or 1751) of an exotic mussel transported as fouling on ship hulls from the western coast of Morocco (Atlantic Ocean) to the port of Marseilles (Mediterranean Sea). The exotic mussel, which survived several years, has been identified as probably being the brown mussel, *Perna perna*, a species with warm-water affinities, which much later became invasive in several areas of the world ocean. The documents of the 18th and early 19th century, which mentioned the event, held 'the curious' and 'amateurs', who harvested the mussels, responsible for its extirpation. More realistically, it is hypothesised that the mussel population did not survive the return of severe cold weather conditions, after a few relatively mild decades, in the context of the Little Ice Age (LIA). These conclusions were deduced from historical data and are therefore open to discussion.

Keywords: failed introduction; fouling on ship hulls; Little Ice Age; Mediterranean Sea; mollusc; *Perna perna*

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1. Introduction

Biological invasions are among the most worrying environmental issues of the 21st century (e.g., [1–6]). Invasive species are aliens (Non-Indigenous Species—NIS) whose populations have overcome a number of barriers such as survival, reproduction (the establishment of a self-sustaining population) and dispersal [3,7–14].

The number of NIS has been steadily increasing since World War II in most coastal areas worldwide. In some areas, a speeding-up has been observed, resulting in four worldwide hotspots of introduction in marine systems: the Mediterranean Sea, San Francisco Bay, the northeast coast of the USA, and the Sea of Japan [9,15–20]. The Mediterranean Sea, which has for millennia been a trading hub at the confluence of commercial routes from three continents, is by far the sea most severely hit by biological invasions. A recent and probably underestimated update counted almost 1 000 NIS, and their number has nearly doubled every 20 years since the beginning of the 20th century [7,19,21–30].

The global increase in NIS numbers and introduction rates recorded since the Industrial Revolution, and especially over the 20th century, is the direct consequence of the exponential and ongoing development of trading exchanges through maritime traffic. In the marine realm, this increase is closely related to the increasing frequency and speed of

ships (biofouling on hulls) combined with the increasing capacity for transporting larger volumes of seawater through ballast water systems [1]. Nowadays, biological invasions are a significant aspect of global change and a constant threat to biodiversity [31]. Historically, Elton's book [32] represents a cornerstone in the systematic inventorying and study of biological invasions and the subsequent exponential rise in scientific interest since. However, the transport of NIS by means of human activities began well before the Linnaean Era. The Linnaean Era corresponds to the advent of the binomial nomenclature, conventionally dated from 1753 in Botany and 1 January 1758 in zoology, respectively [33,34]. Several millennia ago, early farmers, during their migrations from northwestern Anatolia and Greece to western and central Europe, transported with them cultivated plants and cattle (e.g., wheat, goats, sheep), along with their associated flora and fauna [35,36]. The Polynesian rat *Rattus exulans* Peale, 1848, originating in Southeast Asia, was also transported accidentally or deliberately by Polynesian migrants to the islands they settled, from around 3000 BP [37–39]. In the marine realm, since at least the 15th century, wooden vessels, with fouling on their hulls, boring species in their hulls, and rock ballast within the ship's hold, contributed strongly to the introduction of species from one sea to another, such as the Japanese oyster *Magallana gigas* (Thunberg, 1793) (*Crassostrea gigas* (Thunberg, 1793)) to southern Europe [40]. Similarly, the Atlantic clam *Mya arenaria* Linnaeus, 1758, was probably brought to Europe from North America by Vikings [40,41]. A number of species, nowadays more or less cosmopolitan, could be native in a part of their range, as yet undetermined, and introduced elsewhere; Carlton [40,42] gave the name 'cryptogenic species' to these taxa which, in a given area, are not demonstrably native or introduced. Many putatively cryptogenic species could have been introduced during the early centuries of the European transoceanic voyages and circumnavigations, and, therefore, before the Linnaean Era.

There is extensive literature dealing with ancient (i.e., pre-Linnaean) introductions. Understandably, it is the species that have succeeded in becoming established long-term that have been the subject of investigations. Yet, at every moment and throughout the world's oceans, the flow of propagules, juveniles, and adults of candidate species transported by man is vast. The overwhelming majority of them will, however, not be able to overcome the barriers (filters) that prevent their establishment [8,11,21,43]. It is well known that history only remembers the winners. Very little is known about these failed introductions, including when during the invasion process they became unsuccessful and why, although such information would be crucial to understanding, mitigating, and even eradicating NIS [44]. Here, we report on the basis of three little-known local archives from the 18th and 19th centuries the arrival of an unidentified mussel, the 'yellow mussel from Saphy', in the port of Marseilles (Provence, France) in around 1750, its installation, and then its extirpation. On the basis of the short description provided, the maritime links and ports of call at that time, the archives of the port of Marseilles, and climate data, an attempt has been made to determine the species and to formulate hypotheses regarding the plausible causes of its failure to become permanently established. Obviously, in the absence of the recorded specimens, our hypotheses deduced from historical literature are still open to discussion.

2. Material and Methods

Three historical sources provide evidence of the presence in Marseilles, France, in the middle of the 18th century, of populations of a likely non-native mussel species [45–47].

Villet (1775: 115 [45]), in the catalogue of his natural history cabinet, wrote: 'Nr 2121—Superb and large mussel, yellow in colour, pearly inside, of the exotic species at Marseilles, where it had been transported from Saphy, and produced different shades from the mussels of Barbary; it is no longer present at Marseilles' (Translated from French by the authors of the present article: '*N° 2121 Superbe & grande Moule, jaune, nacrée en dedans, de l'espèce exotique à* Marseille, *où elle avoit été transportée* de Saphy, *& avoit produit des nuances différentes des moules de Barbarie; il n'y en a plus à Marseille*'. The spelling of the French at the

time has not been replaced by the current spelling). The species is further mentioned by Villet (1775: 118 [45]) as 'Nr 2178—Yellow mussel of Saphy' (Translated from the French: '*N° 2178 Moule jaune de Saphy*'). Antoine Villet was a Marseilles merchant who owned one of the richest natural history collections in Provence, especially with regard to marine species [48].

Darluc (1786:178 [46]) wrote: 'The following species are exotic: they have been taken from the keel of the vessels which have come to Marseilles; thrown over the rocks of the citadels, they multiplied for several years. The curious almost destroyed the species (. . .). The same quite yellow. This mussel came from Saphi' (Translated from the French: '*Les espèces suivantes sont exotiques: elles ont été prises sur la quille des bâtiments venus à Marseille; jettés sur les rochers des citadelles, elles ont multiplié pendant quelques années. Les curieux en ont presque détruit l'espèce* (. . .). *La même toute jaune. Cette moule nous est venue de Saphi*').

A third, much later document mentions this species and the event (de Villeneuve 1821: 782–783 [47]): 'A vessel which arrived from Safi, on the coast of Barbary, about the middle of the last century, had brought on its keel a kind of mussel close to *Mytilus afer*. This mussel had multiplied considerably in the Gulf of Marseilles, when an 'amateur', named Mr Rougon, had them harvested and destroyed all these mussels, after keeping enough for his exchanges. This species has been extirpated; there are only a few specimens preserved in several cabinets [of natural history], notably that of Mr de Gouffé. This shell, examined with attention, appeared to us different from *Mytilus afer*, and we have included it in the catalogue under the name of *Mytilus safi*. It is marked with concentric green and yellow zones. Its size and shape are those of *Mytilus edulis*. It is not flattened on the hinge like *Mytilus galloprovincialis*' (Translated from the French: '*Un vaisseau arrivé de Safi, sur la côte de Barbarie, vers le milieu du siècle dernier, avait apporté sur sa quille une espèce de moule voisine du* Mytilus afer. *Cette moule avait multiplié considérablement dans le golfe de Marseille, lorsqu'un amateur, nommé M. Rougon, fit pêcher et détruire toutes ces moules, après en avoir réservé suffisamment pour ses échanges. Cette espèce a été anéantie; il n'en existe que quelques exemplaires dans plusieurs cabinets, notamment chez M. de Gouffé. Cette coquille, examinée avec attention, nous a paru différente du* Mytilus afer, *et nous l'avons insérée dans le catalogue sous le nom de* Mytilus safi. *Elle est marquée de zones concentriques vertes et jaunes. Sa grosseur et sa forme sont celles de* Mytilus edulis. *Elle n'est pas aplatie sur la charnière comme le* Myt. galloprovincialis').

We examined the collections of the Muséum d'Histoire Naturelle de Marseille, the Muséum d'Histoire Naturelle d'Aix-en-Provence, the Musée Requien of Avignon, France, and the Musée Océanographique of Monaco, which may have housed the private collections bequeathed by the heirs of the owners of the above-mentioned natural history cabinets. We also consulted the archives of the Chambre de Commerce de Marseille, where information concerning the arrival and departure of vessels in the port of Marseilles, and their port of call, is archived [49].

The proxy for climate at the time of the possible introduction event was the number of months (per 5-year period) when the Rhone River was totally or partially ice-bound at Arles (Provence), near its mouth (a few dozen kilometres west of Marseilles) [50,51].

3. Results and Discussion

Where did the 'yellow mussel' arrive from? Villet [45], Darluc [46], and de Villeneuve [47] indicated Safi (also spelled Saphy and Saphi). Safi (*Asfa* in Arabic) is a port on the Atlantic coast of Morocco (32°17′ N, 9°14′ W). It is one of the oldest seaports of the African northwestern Atlantic, perhaps corresponding to the ancient Carcunticus founded by the Carthaginians, several centuries BCE (Pliny the Elder in [52]). The city was under Portuguese rule from 1488 to 1541. Subsequently, it played an important role in Morocco as one of the safest and most easily usable ports in the country, as related by Bidé de Maurville, a French captive in Morocco [53], and Louis de Chénier, consul of the French court in Morocco in 1767 [54]. The study of the archives of the Chambre de Commerce de Marseille [49] failed to identify vessels arriving from Safi between 1740 and 1749. In

contrast with, e.g., Smyrna (now Izmir; Turkey) and Tunis (Tunisia), Safi has always been a port of call of very minor importance for Marseilles' trade [55]. During the year 1750, at least two vessels, arriving from Safi, actually anchored in the port of Marseilles. These two vessels were the *Saint-François de Paul* under Captain Christophe Zanzanie and another ship of unknown name under Captain Megy, arriving on 31 May 31 and 29 December 29, respectively [49]. From 1751 to 1755, 18 vessels from Safi port arrived in Marseilles, the peak being in 1752, with seven ships. While the cargo manifests of these vessels specify their register tonnage (50 to 150 register tons, a customary unit at the time but since superseded) and the contents of their cargo (wax, copper, Arabic gum, raw wool, and even ostrich feathers), they obviously do not say anything about the species that putatively populated their hulls.

What is the 'yellow mussel'? We were unsuccessful in finding the specimens, even a few of them, mentioned by Villet [45], Darluc [46], and de Villeneuve [47], in the collections of the museums of natural history of the region (France and Monaco). This is not surprising, as the collections of the cabinets of the natural history of Marseilles were seized during the French Revolution when they belonged to 'counter-revolutionaries' (French National Convention period, 1792 to 1795), and then dispersed (French Directory period, 1795 to 1799) [56]. However, the origin of the vessels (the Atlantic coast of Morocco) and the description of the specimens of 'yellow mussel' provide a basis for referring it to a species under the modern taxonomy. Four species of mussel are native to Atlantic Morocco: the bearded horse mussel *Modiolus barbatus* (Linnaeus, 1758), the Adriatic horse mussel *Modiolus adriaticus* (Lamarck, 1819), the blue mussel *Mytilus edulis* Linnaeus, 1758, and the brown mussel *Perna perna* (Linnaeus, 1758), also known as the African mussel [57]. The first two earlier taxa are much smaller than the latter ones and different in shape and colour, so they are unlikely to correspond to the 'yellow mussel'. *Mytilus edulis* was well known to Darluc [46] and de Villeneuve [47], who specifically ruled out the possibility that the 'yellow mussel' could correspond to it. In addition, despite an extreme variability in shape and colour, *M. edulis* is never yellowish [58]. *Mytilus edulis* and the Mediterranean mussel *M. galloprovincialis* Lamarck, 1819, belong to a complex of closely related taxa of mussels, the *Mytilus edulis* complex [59]. Finally, *Perna perna* seems to be the best candidate to match the 'yellow mussel'. Unfortunately, the main taxonomic characteristic of the species (i.e., the divided posterior retractor mussel scar), was not noticed by de Villeneuve [47]. Most *P. perna* specimens are brown in colour, but yellowish and greenish and even green shells are not uncommon [58,60–63]. It is worth noting that de Villeneuve [47] pointed out that the 'yellow mussel' was close to *Mytilus afer* Gmelin, 1791, a taxon nowadays regarded as a heterotypic synonym of *P. perna* [64]. The name used by de Villeneuve [47], *Mytilus safi*, is a nomen nudum that was never used subsequently. Although one should remain cautious regarding the identification of a species solely on the basis of ancient writings, almost three centuries later (thus corresponding to a pre-Linnaean event), it appears very likely that the 'yellow mussel from Safi' could be identified as *P. perna*.

What about *Perna perna*? This large mussel is up to 15 cm in length [57,58,62,65]. It mainly thrives attached to rocks in the shallow infralittoral zone, but can be found down to 100 m in depth; in contrast with *Mytilus edulis* and *M. galloprovincialis*, it does not colonise the lower midlittoral zone [57,60,62]. Densities of up to 27,000 small individuals have been recorded [66]. Its native distribution ranges from the Iberian Peninsula to Senegal and from Angola to South Africa (eastern Atlantic); it is also known from southeastern Africa (Indian Ocean) and the southwestern Mediterranean Sea [57,62,67–71]. *Perna perna* has been introduced to South America, in the context of at least two introduction events, from northwestern and southwestern Africa, respectively [68]. It has also been introduced in the Gulf of Mexico via fouling on boat hulls and/or ballast waters [66,67,72,73]. In contrast, *P. perna* is threatened by invasive mussels, such as the Mediterranean *Mytilus galloprovincialis*, in areas where it is native, such as South Africa [74]. In addition, it is resistant to disturbances by human activities, including contamination, and can outcompete native *Mytilus* species [75,76]. *Perna perna*, although not a tropical species, is a species with

warm water affinities; it therefore benefits from the current global warming and has been spreading eastwards to Tunisia in the southern Mediterranean Sea and northwards in the western Atlantic Ocean [60,61,68].

Why did the introduction fail? The 'yellow mussel' was immediately perceived as exotic, and its introduction vector was identified as the fouling on the hulls of vessels arriving in the port of Marseilles [45–47]. Darluc [46] mentions that the mussels were thrown on the rocks below the citadels. Before leaving a port for a new voyage, the hull was sometimes cleaned (careening) of the largest fouling organisms, whose presence would slow down the boat. This ship maintenance, still practised nowadays, though less frequently because of the use of antifouling paints, was in use in the 18th century. That was also the case in the port of Marseilles, as illustrated in a painting by Vernet (Figure 1), where the citadels can be identified as Fort-Saint-Jean and Fort-Saint-Nicolas. These still-standing forts, which frame the entrance of the port, were erected by the king of France, Louis XIV 'the Sun King', between 1660 and 1664, not to protect the city from enemy fleets but to subdue the rebellious spirit of its inhabitants who, after almost 21 centuries of independence (an independence which was, according to historians, relative and open to discussion), had recently been incorporated into the Kingdom of France [77] (Figure 2).

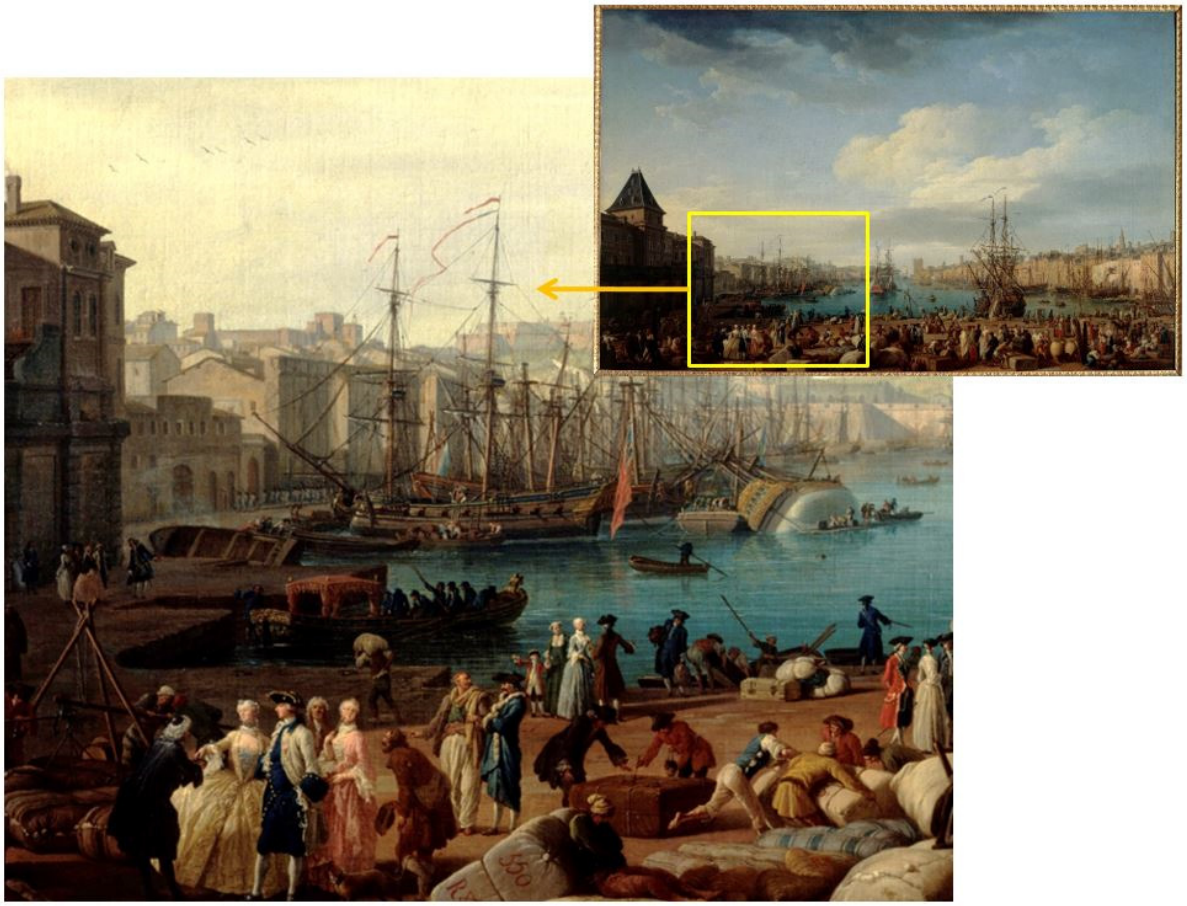

Figure 1. Top right, view of the port of Marseilles, seen from the Pavillon de l'Horloge du Parc within the port ('L'intérieur du port de Marseille, vu du pavillon de l'horloge du Parc'), painting by Claude-Joseph Vernet, 1754, conserved in the Musée National de la Marine in Paris (France). Below left, a detail showing, on the right, a vessel careened to allow workers, onboard small boats, to scrape the fouling from the hull. Reprinted with permission from the Musée National de la Marine (Agence Photographique de la Réunion des Musées Nationaux, Paris, France).

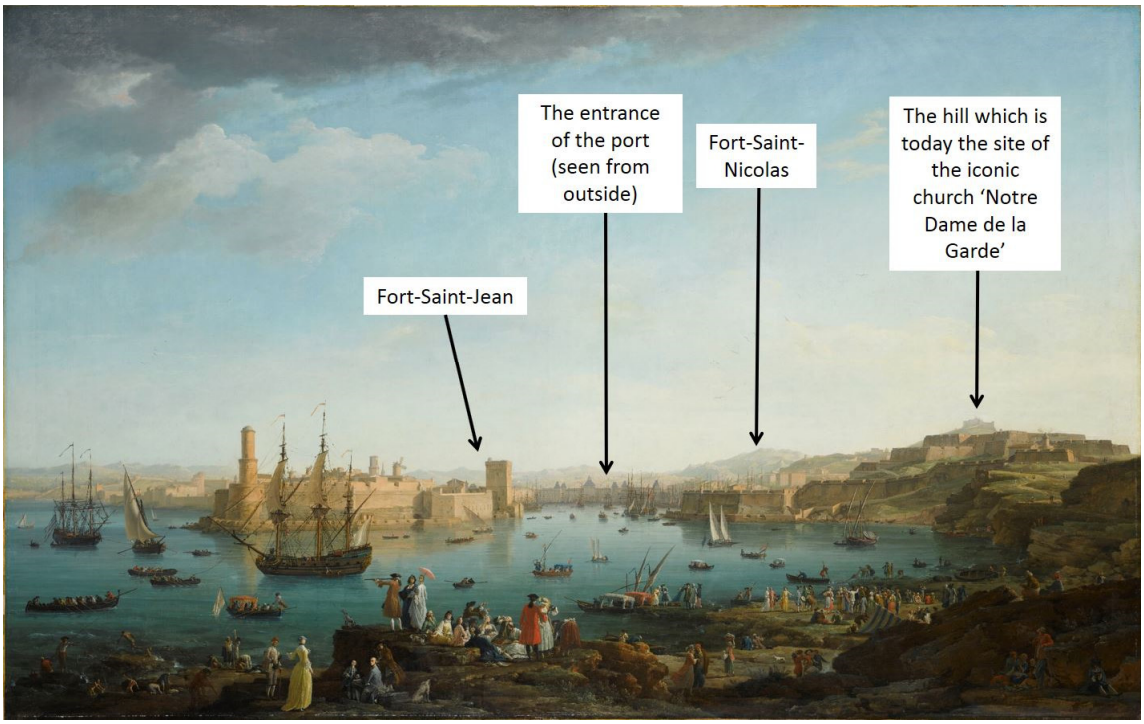

Figure 2. The port of Marseilles in 1754, near the time of the arrival of the 'yellow mussel'. The entrance is seen from outside, from the hill named 'Tête de More'. Painting by Claude-Joseph Vernet, conserved in the Louvre Museum in Paris (France). Reprinted with permission from the Musée du Louvre (Agence Photographique de la Réunion des Musées Nationaux, Paris, France).

Darluc [46] accused 'the curious' of having made the 'yellow mussel' disappear. De Villeneuve [47] was more specific: he named the amateur naturalist, Mr Rougon, who collected the specimens necessary for his exchange of 'curiosities' and destroyed the remainder. The truth of this explanation is debatable. We can speculate that Mr Rougon and others were happy to harvest as much as possible of such a new, exotic, and proliferative species for his pleasure as a shell collector, for food, or even for the ship owners, all of which might have contributed in part to its disappearance. However, the reproductive and dispersal ability of mussels, in suitable habitats, is so high that human-induced extirpation might appear quite unlikely. *Perna perna* is an *r* strategist, producing thousands of spats per square metre [78], which accounts for its invasive status outside of its native range [66,72].

Can we consider that pollution, near the entrance to the port of Marseilles, was involved in the brown mussel's extirpation? Ports in the past were heavily polluted, sometimes more than modern ports (see e.g., [79]). However, *P. perna* is very resistant to several classes of pollutants; it accumulates them and exhibits non-lethal physiological alterations and, for these reasons, can be used as an efficient pollution bioindicator [80,81]. Like other species of mussels and sea urchins, it can even be favoured by organic pollution [82,83]. In addition, a municipal decree from the early 1700s prohibits industrial discharges in the port of Marseilles.

More realistically, we can think that *P. perna*, a relatively thermophilic species, was not adapted to the cold waters of the Gulf of Lions, of which Marseilles is in the easternmost part [84,85]. This was especially the case in the middle of the Little Ice Age (LIA), conventionally defined as a period extending from at least the 16th to the 19th centuries [86–89]. During the LIA, the Rhone River, at the time the second largest river of the Mediterranean watershed after the Nile River with regard to its annual discharge rate and located ~50 km west of Marseilles, was often partially or totally ice-bound in winter (while it has been frozen over only once since the 1940s; Table 1). However, the period of 1720–1750 was relatively mild in the area, as evidenced by the low number of freezing episodes of the

Rhone River [50]. Thereafter, a peak of frost occurred in the 1750s and 1760s (Table 1), heralding one of the coldest phases of the LIA in Europe, the Dalton minimum [88,90,91]. We can therefore hypothesise that this local mild episode may have allowed the establishment of the 'yellow mussel', before or around 1750, and then the subsequent cooling peak, which started in the 1750s, may have destroyed the population of mussels, rather than its harvesting by an amateur collector of exotic shells.

Table 1. Number of months (per 5-year period) when the Rhone River was totally or partially ice-bound at Arles (Provence), near its mouth (a few dozen kilometres west of Marseilles). Data from Pichard [50] and Pichard and Roucaute [51]. The database actually extends from 1302 to 1999 and 2002 CE, respectively.

Period (Calendar Years CE)	Totally Frozen over (Number of Days) (Pichard and Roucaute [51])	Totally or Partially Frozen over (Number of Months) (Pichard [50])
(. . .)	(. . .)	(. . .)
1723–1727	0	2
1728–1732	20	2
1733–1737	0	0
1738–1742	0	0
1743–1747	0	1
1748–1752	10	1
1753–1757	~104	9
1758–1762	19	2
1763–1767	~67	7
(. . .)	(. . .)	(. . .)
1943–1947	0	0
1948–1952	0	0
1953–1957	~31	1
1958–1962	0	0
1963–1967	~8	0
1968–1972	0	0
1973–1977	0	0
1978–1982	0	0
1983–1987	0	0
1988–1992	0	0
1993–1997	0	0
1998–2002	0	-

What is the likely date of the 'yellow mussel of Safi' event? The exact date of the event is not specified. De Villeneuve [47] simply states that it was in the middle of the 18th century. However, a 'window of opportunity' can be delimited. The period 1740–1750, relatively mild, is favourable; but the archives do not mention ships arriving from Safi except in 1750 [49]. From 1751, ships arrived regularly from Safi, the peak being in 1752. From 1753 until the end of the century, the extreme cold of the LIA (Table 1) made the establishment and survival of *Perna perna* very unlikely. The winter of 1753–1754 was the coldest, with the Rhone River being totally frozen over for more than two months [51]. As the mussel is said to have survived for several years, its likely date of arrival is 1750 or 1751, and its likely date of extirpation is 1753, or a few years later.

Failed vs. successful introductions. The number of exotic species arriving from a donor region to a putative recipient area, whether as propagules, juveniles, or adult individuals, is high, and the number of individuals is huge. Many taxa that can be found in introduction vectors such as ballast waters and on ship hulls have not actually been found in the recipient area (e.g., [1,92–99]). Such observations have allowed Williamson and Fitter [100] to theorize the 'tens rule', which establishes that an average of 10% of taxa cross each barrier of the introduction process, from, e.g., non-established to established, then from established to invasive. Though not universal, the tens rule fits well, in particular, with the case of the Mediterranean NIS macrophytes [3].

In the Mediterranean Sea, a total of 573 to 986 exotic species have been listed, depending upon the authors [27,30,101,102], but almost 25% of them (208 NIS) were only reported once or twice and are therefore considered casual [30]. The absence of the reporting of such casual species can be due to either an artefact due to the scarcity of taxonomic experts and unequal attention to species' introduction or an unsuccessful attempt of the taxon to establish a self-sustaining population [44]. Failed introductions can, however, be very informative and contribute to research on (successful) biological invasions. In many cases, they may constitute challenges to the main explanatory mechanisms such as abiotic and biotic resistance, propagule pressure, or genetic constraints [44]. Well-documented cases of the temporary but eventually unsuccessful establishment of exotic species are abundant for trees and terrestrial vertebrates but remain scarce for herbaceous plants and arthropods [44] and are very uncommon in the marine realm. A rare example can be found in a strain of the green macroalga *Caulerpa taxifolia* (Vahl) C. Agardh, known as the Mediterranean Australian Aquarium Strain (MAAS) [103,104]. This strain, which corresponds to the successful invasive strain in the Mediterranean Sea, was unintentionally released from a public aquarium in the Sea of Japan [105] in the spring of 1992 and 1993; it established four colonies, less than 1 m in diameter, which disappeared in the succeeding winters, probably because of low winter water temperatures [105,106]. Another example is that of the large brown alga *Saccorhiza polyschides* in the Mediterranean, which, despite a number of attempts, never succeeded in colonising the Mediterranean, with the exception of Sicily [107]. The present case of *Perna perna*, a contemporary worldwide successful NIS, but a failed one in the Mediterranean three centuries ago, constitutes a singular example of a failed introduction because of the scarcity of such cases in the marine realm and, more broadly, because of its reported antiquity. It demonstrates that failed introductions can help us to better understand the relative importance of some factors determining invasions.

4. Conclusions

Exotic species successful in establishing long-lasting, self-sustaining populations are understandably better known than those that failed. Yet, propagules, juveniles, and adult individuals of candidate species arriving through introduction vectors to recipient areas, (through, e.g., ballast waters, fouling on ship hulls, and oyster and mussel culture) but failing to naturalize are a thousand or million-fold more numerous than the successful ones. The 'yellow mussel of Safi', which we identify as *Perna perna*, offers a valuable and ancient case study of a failed biological invasion. This species with warm-water affinities arrived in the port of Marseilles, France, on a ship hull, around the core of the Little Ice Age (LIA; 18th century); after a careening and hull-cleaning operation, it was thrown on the rocks at the entrance of the port and established a self-sustaining population. The arrival probably occurred during a relatively mild episode of the LIA. The authors who described the temporary presence of the 'yellow mussel' (actually more brown than yellow), then its disappearance, blamed the 'curious' and 'amateurs' who harvested it for its extirpation. More realistically, its survival and short-lasting establishment took advantage of two relatively mild decades, and its extirpation resulted from the return of the severe cold weather conditions that characterised the Little Ice Age.

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