Biological Invasions

The invasions of the Chinese mitten crab and the Zebra mussel in Europe and North America

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Section 1: Introduction

From about 225 million years ago, through Mesozoic and Cenozoic, the earth's landmass Pangea broke apart into continents (Simpson, 1983). These continents started to drift across the surface of the planet, and in Tertiary times barriers arose between the biological communities on them. Becoming separated from each other by the seas and oceans, being divided themselves into smaller fractions with the appearance of mountain chains and deserts, these biological communities each evolved in their own, specific direction. Thus, countless bigger and smaller enclaves known as Wallace Realms (Elton, 1958) originated, each with a specific community of unique animals and plants.

Some species evolved dispersal techniques to overcome the barriers that separated the enclaves, especially birds. Many of them are known to migrate across the world, taking with them microscopic forms of life: many protozoa, rotifers and waterfleas, not to mention seeds of plants are often world-wide in distribution. But a great many other plants and animals have never had the opportunity of ranging over the whole world. They were confined to their own region for long enough to change profoundly and adapt to the conditions specific for this region. Three other processes increase the complexity of the distribution patterns as we see them now. The first is that groups that were formerly very widespread have retreated and may be found, say, only in one continent or island or lake (Elton, 1958). The second is that after the long periods of isolation in Tertiary times that created the Wallace realms there was some remingling of faunas (see Vermeij, 1991) before the third process started: the appearance of man as the great dispenser of all kinds of life forms all around the entire world.

Taking with him cattle and agricultural plants, mankind deliberately transferred many species across the geographic barriers to dispersal. However, most of the species were transferred accidentally, mainly with ships. Many alien species have been introduced into ecosystems (especially coastal and estuarine) everywhere on earth. A great number of them associated with the business of oyster culture: this is the greatest agency of all that spreads marine animals to new quarters of the world (Elton, 1958). But also the digging of canals and the accidental transport on ships has caused big changes in the distribution of species (Elton, 1958; Vermeij, 1991). Even today, geographic barriers to dispersal and gene flow are readily breached by ballast water transport (Carlton and Geller, 1993). Carlton and Geller (1993) estimated that on any one day 3000 species may be in motion around the world in the ballast water of ocean going vessels (Carlton, 1996a).

Islands and estuarine/freshwater systems have been disturbed profoundly by the introduction of new species (Cohen and Carlton, 1995; Simberloff, 1995). Especially estuarine/freshwater systems are furthermore altered by changes in the nutrient balance caused by human activities (Essink, 1998; Raffaelli, 1999). There is ample literature about estuarine/freshwater systems. Some of them have been monitored for extended periods of time (e.g. Cohen and Carlton, 1998; Essink, 1998; Nicholls, 1997; Raffaelli, 1999), making it possible to assess the influence of invasions together with other (often long-term) changes in the system, placing the effects of each in the proper perspective (e.g. Nicholls, 1997).

The examples of successful invaders of the estuarine/freshwater systems are numerous. For example, in one single system, the San Francisco Bay delta and estuary, 234 exotic species have become established (Cohen and Carlton, 1998). The consequences of invasions can be disastrous (e.g. Travis, 1993). In this report I present case studies on the invasion of estuarine/freshwater ecosystems in North America and Europe by two animals: The Chinese mitten crab (*Eriocheir sinensis*) and the zebra mussel (*Dreissena polymorpha*). Furthermore I will discuss factors influencing these and other invasion events, and the state of Dutch estuarine/freshwater ecosystems as far as invasions are concerned.

Section 2: The Chinese mitten crab, *Eriocheir sinensis*

Figure 1. The chinese mitten crab, *Eriocheir sinensis*. This picture was downloaded from http://www2.delta.dfg.ca.gov/mittencrab/pictures.html.

Section 2.1: Biology of the mitten crab

The Chinese mitten crab (Fig. 1) owes its name to its hairy claws. It is a catadromous species, meaning it grows and develops in freshwater, but must migrate to marine areas for reproduction and larval development (Gollasch, 1997; Kamps, 1937). After the first stages of larval development, the young crabs migrate back to fresh water, as described by Adema (1991). At low tides, when the net flow in the river/estuary is towards the sea, they cling to the bottom of the river/estuary. At rising tides when the net current is the other way they leave the bottom and flow with the currents up the river (Adema, 1991; Kamps, 1937). This way they can travel up to 3 km per day (Adema, 1991). The young crabs grow extremely rapidly: in the first year they moult 10 times (including larval stage) and at these first moultings their size increases by 22.5 % (Adema, 1991; Kamps, 1937). It has been reported that young crabs grew by 100% in only two weeks (Adema, 1991). After 1-3 years they reach an average width of 70 mm. At a width of 28-40 mm the crabs are sexually mature, but only at a width of 50 mm will most of the animals migrate back to the sea to reproduce (Adema, 1991; Kamps, 1937; Panning, 1952). After reproduction the adults die, and the lifecycle is complete (Fig. 2).

The mitten crab is known for its tendency to migrate: In Europe, it was reported up to 750 km upstream the river Elbe (Adema, 1991; Kamps, 1937) and in its native habitat, living crabs were found even 1400 km upstream the river Yang-tse-Kiang (Gollasch, 1997).

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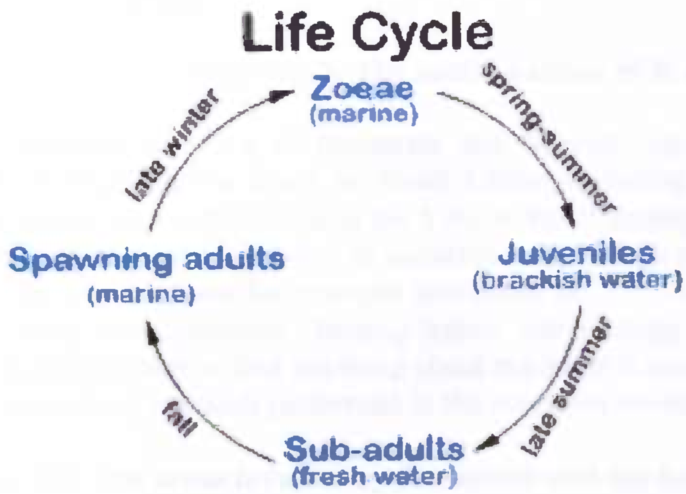

Figure 2. Lifecycle of the chinese mitten crab, showing where the several developmental stages occur. The sub-adults will stay in freshwater for 1-3 years. This picture was downloaded from http://www2.delta.dfg.ca.gov/mittencrab/life_hist.html.

It is a truly omnivorous crab, known to exploit a wide range of food types (Verweij, 1978). Analysis of stomach contents however has revealed that it feeds mainly on plant material (Halat and Resh, 1996).

For hiding (especially when moulting) and to avoid desiccation, *E. sinensis* excavates small burrows in water banks mostly about 10 cm below the water surface or, in tidal areas, in between high tide and low tide water levels (Fig. 3). These burrows have a width of 2-12 cm and a depth of 20-80 cm (Adema, 1991; Kamps, 1937).

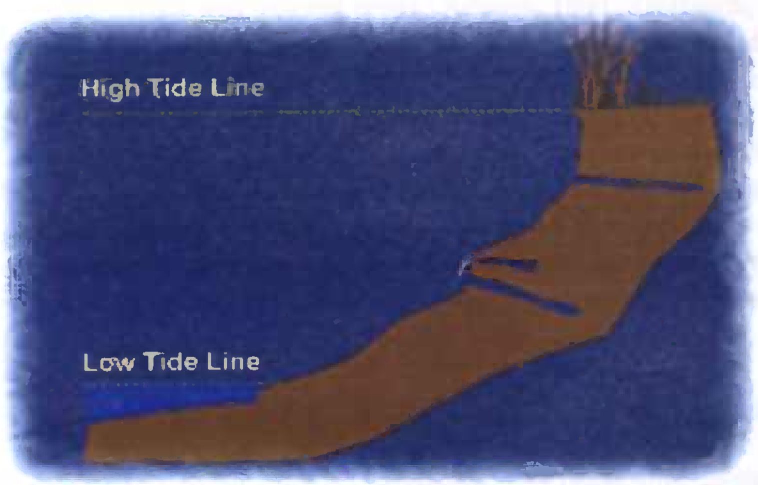

Figure 3. Schematic drawing of burrows of *E. sinensis*, excavated between high tide and low tide waterlevels. This picture was downloaded from http://www2.delta.dfg.ca.gov/mittencrab/life_hist.html.

Little is known about natural enemies of the Chinese mitten crab in its native habitat. Adema (1991) supposed that in Europe, the younger crabs are probably eaten by predatory fish, but the adult crabs don't seem to have natural enemies (Adema, 1991; Panning, 1952). In North America, white sturgeon, striped bass, bullfrogs, loons and egrets have been reported to pray upon them. Furthermore other predatory fishes, including largemouth bass, and large sunfishes, river otters, racoons and other wading birds are presumed to consume mitten crabs (California dept. of Fish and Game, Internet). However, no research has been done on this topic, so no information about the impact of this presumed predation on the vast populations of *E. sinensis* is available.

Section 2.2: The native habitat of *E. sinensis*

E. sinensis is native to temperate and tropical regions of China. It occurs from Vladivostock (Russian Far East) to South China, including Japan and Taiwan (Gollasch, 1997), the centre of occurrence being the Yellow Sea (Panning, 1952). Panning (1952) reports that *E. sinensis* occurs en masse in its homeland: the annual catch of the special mitten crab-fishery in the Liao-ho river for example accounted for 3.7 – 6.8 million animals. Most of the literature about its occurrence, feeding habits and ecology in its homeland is written in Chinese, making it hard to find anything about the niche it occupies originally. However there is a lot to learn from research performed in the countries invaded by this animal.

Section 2.3: The areas invaded by *E. sinensis* and the history of the invasion events

In 1912, the Chinese mitten crab was reported for the first time in Europe: a specimen was caught by a fisherman in the Aller river, a side river of the Weser in the northern part of Germany (Kamps, 1937; Panning, 1952). However, the Chinese mitten crab must have been present a few years before this date, probably introduced from China by ballast water transport (Kamps, 1937; Panning, 1952). By 1925, the amount of mitten crabs caught by fishermen was too big to describe every catch separately, and the first females with eggs were reported. By 1928, the crab had become very abundant in the Elbe, a river near by the Weser. In 1929, *E. sinensis* was reported in Holland for the first time (Adema, 1991). By 1935, it occurred throughout Holland and had become a nuisance at various places (Adema, 1991; Kamps, 1937). This and the further spread in Europe probably happened by active migration via rivers, canals and coastal areas (Adema, 1991; Gollasch, 1997). Today, the crab occurs all over Europe, including Finland, Sweden, Russia, Poland, Germany, Denmark, Holland, Belgium, France, Portugal (Cabral and Costa, 1999) and Great Britain (Adema, 1991; Attrill and Thomas, 1996).

Outside of Europe, *E. sinensis* was reported in the 1950s on Hawaii (Gollasch, 1997). Since the 1960s the species has also been reported in North America: a Chinese mitten crab was found in the Detroit river 1965, and in 1973 a specimen was caught in Lake Erie (Adema, 1991; Nepszy and Leach, 1973). It was reported in the Mississippi delta in 1987 (Adema, 1991) and one of the most recent invasions is taking place in the San Francisco Bay estuary, since 1993.

Section 2.4: The consequences of the invasions by *E. sinensis*

Section 2.4.1: Economic damage

Fishermen experience major economic troubles with the mitten crab: it is known to damage fishing nets, and the fish in it (Adema, 1991; Kamps, 1937; Panning, 1952). Also, the crabs cause a major loss of time to the fishermen as they become entangled in the nets. Indeed, shrimp trawlers from recently invaded San Francisco Bay report substantial damage: the massive amount of crabs damages the shrimp, and it is time-consuming to remove them from the nets (California Dept. of Fish and Game, Internet).

Also, mitten crabs are a nuisance to anglers, eating almost any bait used (California dept. of Fish and Game, Internet; Kamps, 1937; The author's own experience). Occurring in large quantities, the crabs can reduce the catch.

E. sinensis is known to be a secondary host for the oriental lung fluke (*Paragonimis westermanni*), thus being a potential threat to public health (Adema, 1991; California dept. of Fish and Game, internet; Cohen and Carlton, 1997; Resh, 1997).

Also, it can damage agriculture by eating rice-shoots (California Dept. of Fish and Game, internet; Cohen and Carlton, 1997).

Furthermore, the burrows excavated by mitten crabs can have a negative effect on water bank stability and increase bank erosion (Fig. 5), especially when occurring en masse (Fig. 6).

Figure 5. Increased bank erosion caused by the burrowing activities of mitten crabs. This picture was downloaded from http://www2.delta.dfg.ca.gov/mittencrab/pictures2.html.

Figure 6. Mass occurrence of burrows excavated by *E. sinensis*. This picture was downloaded from http://www2.delta.dfg.ca.gov/mittencrab/pictures2.html.

Thus damage can be caused to riverbanks, coast protection and harbour installations (Gollasch, 1997; Halat and Resh, 1996; Panning, 1952).

Occasionally, Chinese mitten crabs cause inconvenience in settled areas, when they encounter obstacles on the way to their breeding grounds and en masse leave the water. In some cases streets were reported flooded with crabs, which climbed into houses and scared local people.

Section 2.4.2: Ecological impact

The influence of *E. sinensis* on the communities it invaded is not exactly clear. Being an omnivore, it uses a food source that is rarely limiting in aquatic systems (Moyle and Light, 1996a). So, little food competition with native animals is to be expected. Other negative interactions with native animals have not been described either. In North America, it is presumed to compete with the red swamp crayfish (*Procambarus clarkii*) and reduce abundance and growth rates of the signal crayfish (*Pacifastacus leniusculus*) in San Francisco Bay (California dept. of Fish and Game, internet; Resh, 1997). This interaction remains to be investigated, and is still subject to debate.

No substantial changes in the estuarine communities have been linked to the presence of *E. sinensis* in Europe, suggesting a rather small ecological impact of this species to the areas infested. However, it has to be considered that no studies using long-term data sets have been done on this topic. Such studies will be performed in time, when information on changes in recently invaded estuaries, which have been monitored for extended periods of time, becomes available. Within this framework, much is to be expected from studies on the effects of the recent invasion in the San Francisco Bay estuary.

Section 2.5: Attempts to control *E. sinensis* in the invaded areas

Because of the economic damage it causes, extensive research has been done to find a way to eradicate *E. sinensis* from the areas infested. In the 1930s, when the Chinese mitten crab started to become a nuisance in Europe, governmental committees were established to find an effective way to combat the invader. Many mechanical and chemical ways have been tested (e.g. Kamps, 1937; Panning, 1952), but none seemed to have a significant effect on the vast populations of mitten crabs. Even DDT did not affect the crabs and after several years the committees were cancelled (Adema, 1991; Kamps, 1937). It was hoped that populations would stabilise at acceptable levels after initial mass occurrence (Adema, 1991).

Unfortunately, this hope has not come true. The Chinese mitten crab still commonly occurs throughout Europe, regularly en masse, still being a nuisance to fishermen and water authorities (Adema, 1991; de Vroome, pers. comm.). To the author's best knowledge, no reports on biological control of this animal exist. In the early days of the committees, this method was not yet so well known. In the meantime, biological control has been successfully applied against various pest organisms, so it might be useful to carefully examine the possibilities for application of this method on *E. sinensis*.

Section 3: The zebra mussel, *Dreissena polymorpha.*

Figure 7. The zebra mussel *Dreissena polymorpha.* This picture was downloaded from http://www.wes.army.mil/el/zebra/lhiabiog.html#musat.

Section 3.1: Biology of the zebra mussel

The zebra mussel (Fig. 7) gets its name from the striped pattern of its shell. However, the pattern is highly variable to where there are no stripes, only dark or light coloured shells: hence its Latin name "*polymorpha*" (Fig. 8).

Figure 8. Some phenotypes of the zebra mussel. This picture was downloaded from http://www.wes.army.mil/el/zebra/lhiabiog.html.

Zebra mussels are dioecious and live in freshwater, where they can reach a length of 5 cm. At a shell length of 10 mm the animals are sexually mature. When water temperatures reach 11-12 °C, females release eggs, and males release sperm into the water. The eggs are fertilised externally, and hatch into free swimming veliger larvae. The veliger feeds and grows in the plankton for about 10-14 days (Boelman et al., 1997) to up to a month (USGS, internet) before it settles to a substratum, gradually metamorphosing into a shelled juvenile (Fig. 9).

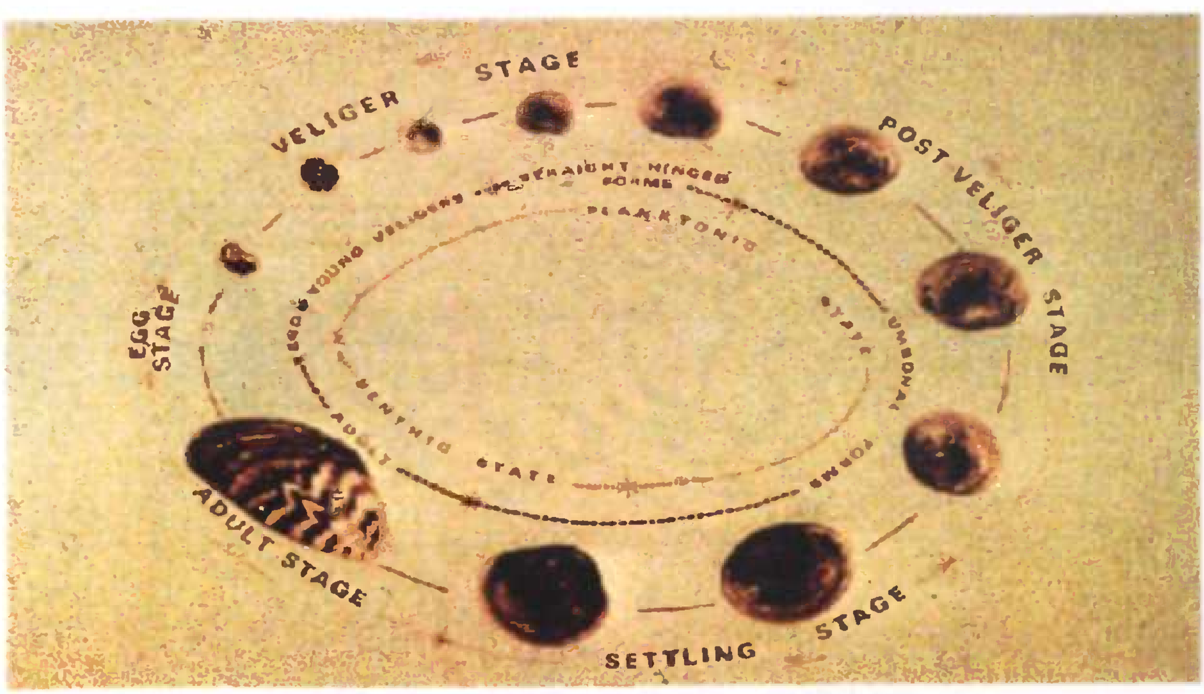

Figure 9. Lifecycle of *Dreissena polymorpha*. This picture was downloaded from http://www.science.wayne.edu/~jram/zmussel.htm#slide21.

Juveniles and adult zebra mussels attach to solid substrates, using threads formed from the byssus (Fig. 7), an organ originating near the foot (USGS, internet). They can quickly colonise new areas/surfaces and rapidly achieve high densities (Boelman et al., 1997). Zebra mussels are notorious for their tendency to foul solid substrates: densities of 700.000 individuals/square meter have been reported (USGS, internet). *D. polymorpha* can remain attached to the same substrate for life, or, if conditions become unsuitable, release from its byssal threads. Once detached, individuals can be carried around passively by water currents or move actively using their foot, reattaching to another solid substrate when suitable conditions are found.

Zebra mussels are filter feeders, feeding mainly on algae (USGS, internet). A single individual can filter up to 8.5 litres of water per day, filtering out particles up to less than 1 µm (Boelman et al., 1997; Sprung and Rose, 1988). To construct their shell, zebra mussels need calcium at a minimal concentration of 10 mg/l (Boelman et al., 1997).

Linear growth rate can range from 1.0 to 1.6 cm per year. The maximum annual production reported for a zebra mussel population is 29.8 g of dry tissue/sq. meter/year, the highest recorded for freshwater or marine bivalves (Boelman et al., 1997).

Zebra mussels are eaten by a variety of fish and waterfowl (e.g. MacIsaac, 1994; Molloy et al., 1997; Thorp et al., 1998). Especially diving ducks have specialised on predation of these mussels (e.g. de Leeuw, 1997).

Section 3.2: The native habitat of *D. polymorpha*

The zebra mussel is believed to have originated in the northern Euxinian Basin, the contemporary Black Sea, at the end of the Pleistocene era (Kinzelbach, 1992). In 1769, Pallas was the first to describe populations of this species, from the Caspian sea and Ural River (Boelman et al., 1997; USGS, internet).

Figure 10. The distribution of *D. polymorpha* in Europe. Grey areas and black spots indicate the presence of zebra mussels. This picture was taken from Kinzelbach, 1992.

Section 3.3: The areas invaded by *D. polymorpha* and the history of the invasion events

The historical expansion of *D. polymorpha* started in the 19th and 20th century, from the rivers to the north of the Black Sea, mainly from the Dnieper system (Kinzelbach, 1992). Since the end of the 18th century, it has invaded the neighbouring river systems along newly completed ship canals, often using the ships themselves as vectors. Thus, scattered across Europe, many small communities were established, mainly in harbours. From there, it rapidly occupied the northern part of central and western Europe (Fig. 10).

Since 1985, D. polymorpha has invaded the Great Lakes in North America, and is rapidly expanding on that continent (Fig. 11).

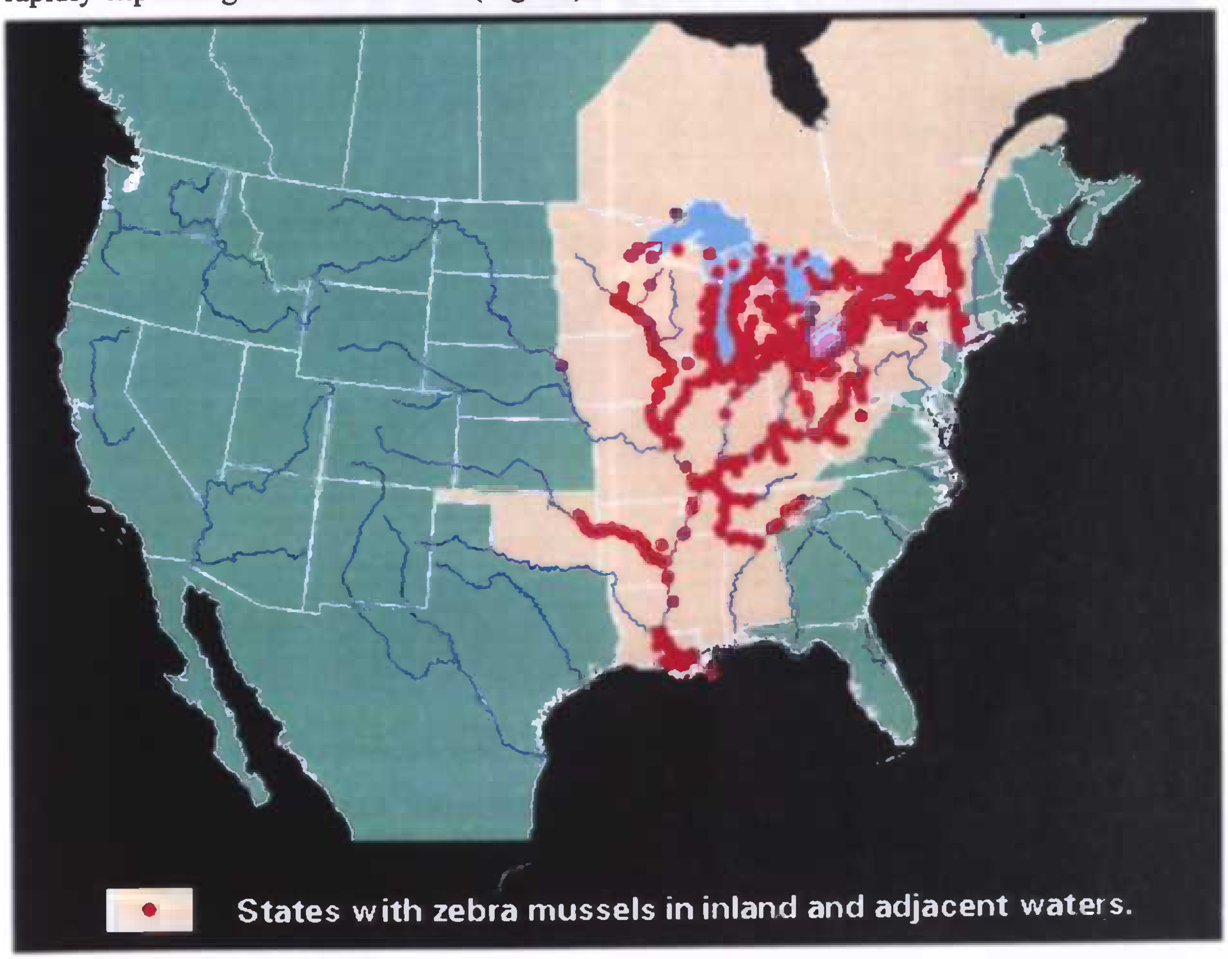

Figure 11. Distribution of the zebra mussel in North-America, by august 1999. This picture was downloaded from http://nas.er.usgs.gov/zebra.mussel/.

Section 3.4: The consequences of invasions by zebra mussels

Section 3.4.1: Economic damage

D. polymorpha causes problems in industrial and domestic water supplies. With its byssal threads it can attach to plastic, concrete, wood, fibreglass, iron surfaces, and surfaces covered with conventional paints (Boelman et al., 1997). Attached en masse, it can render inoperable mitre gates on locks, fire prevention systems that rely on pumping up water from rivers or lakes, reservoir release structures, navigation dams and buoys, pumping stations, other water intake structures, dredges, and commercial and recreational vessels.

Water intake pipes are clogged (Fig. 13) and navigational buoys have been reported to sink due to the weight of attached zebra mussels (USGS, internet). No structure in the water is safe from these macrofoulers (Fig. 12). When a thick layer of zebra mussels covers a surface, it can cause anoxia and pH reduction, exacerbating corrosion rates. Maintenance costs then increase dramatically.

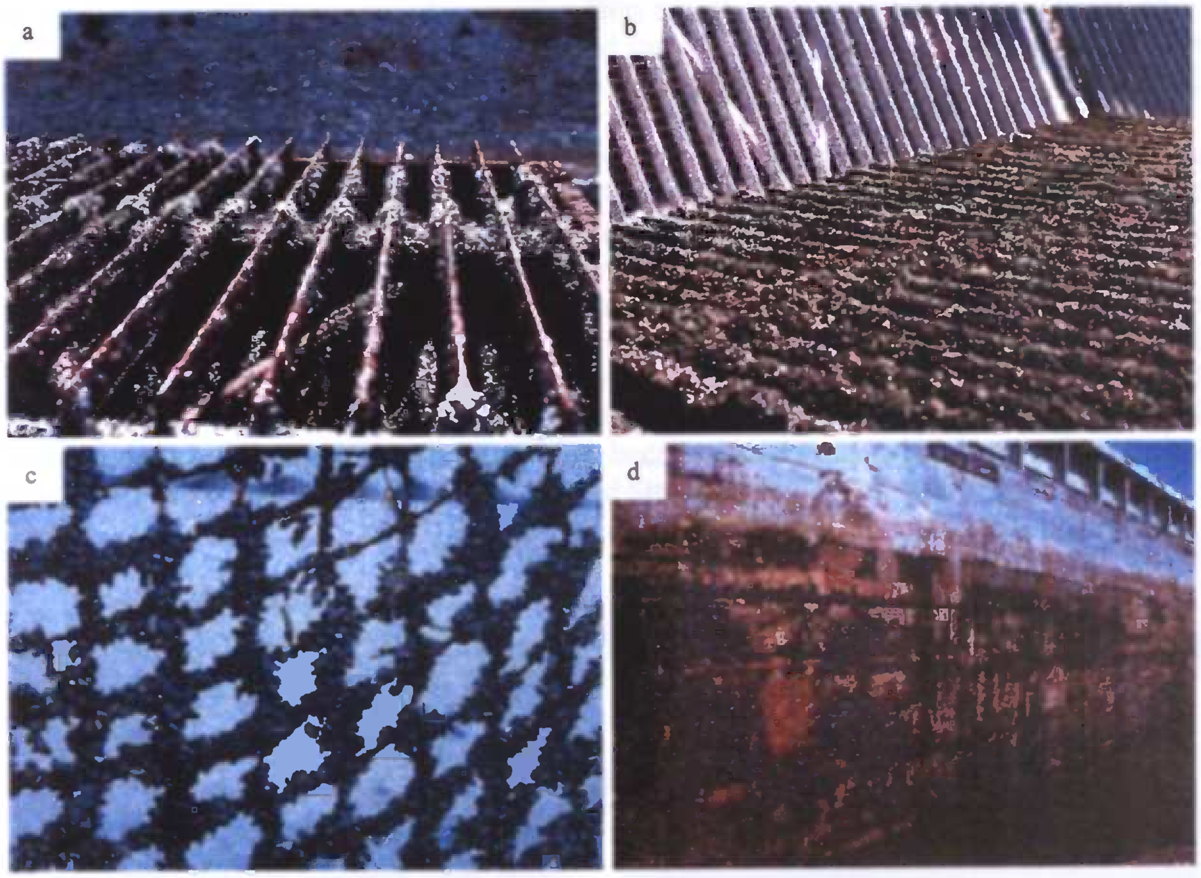

Figure 12. Zebra mussels fouling grids (a, b), a fishing net (c), and a commercial vessel (d). This picture was downloaded from http://www.wes.army.mil/el/zebra/impactsg.html.

Although the effect on fish populations seems to be minimal according to early studies (USGS, internet; e.g. Pace et al., 1998), zebra mussels are feared to affect populations of commercial fish species via changes in the foodweb. Altogether, it has been estimated that *D. polymorpha* could cause 5 billion dollars in damage in the United States alone by the year 2000 (Boelman et al., 1997).

Figure 13. A water intake pipe blocked by zebra mussels. This picture was downloaded from http://www.wes.army.mil/el/zebra/impactsg.html.

Section 3.4.2: Ecological impact

The ecological impact of *D. polymorpha* can be called dramatic. Zebra mussels have been reported to cause major alterations in the systems they invaded. Occurring in dense populations they are known to substantially affect macro-ecological parameters. Dissolved oxygen levels decrease (Effler et al., 1998), and carbon stocks change in constitution because microbial communities of waters infested with this mussel change dramatically (Findlay et al., 1998).

The impact of the mussels as filterers of the water column have been stressed by Reeders et al. (1989) and Reeders and Bij de Vaate (1990), stating that the entire water body of Ijsselmeer, a lake in the Netherlands infested with zebra mussels, is filtered once or twice each month and that the mussels might be able to affect algal biomass.

Native unionid clams in infested waters show a sharp decline in number, fitness and recruitment (Nichols and Amberg, 1999; Schloesser and Nalepa, 1994; Strayer and Smith, 1996), which is assigned to fouling (Fig. 14) and competition for food (Strayer and Smith, 1996). Entire communities of unionids may disappear from waters infested by zebra mussels within 5 years, and some unionids might even become extinct due to zebra mussels (Ricciardi et al., 1995; Schloesser et al., 1996; Strayer and Smith, 1996; USGS, internet).

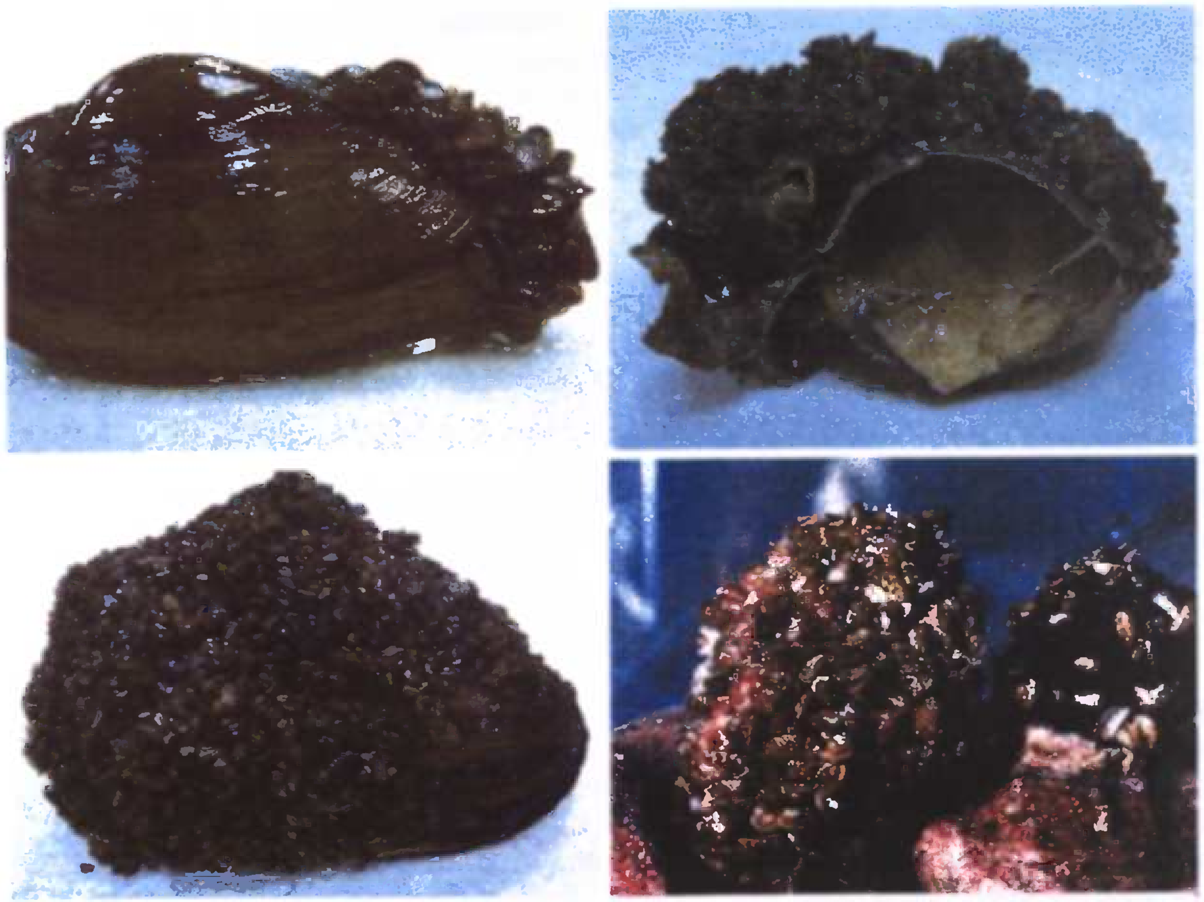

Figure 14. Unionid clams fouled with zebra mussels. These pictures were downloaded from http://www.wes.army.mil/el/zebra/impactsg.html#othorg.

Several other larger aquatic animals are suffering from fouling by zebra mussels (Fig. 15 and 16).

Figure 15. A crayfish fouled by zebra mussels. This picture was downloaded from http://www.wes.army.mil/el/zebra/impactsg.html.

Figure 16. A turtle fouled by zebra mussels. This picture was dwonloaded from http://www.wes.army.mil/el/zebra/impactsg.html.

In waters infested with *D. polymorpha*, phytoplankton and microzooplankton biomass concentrations decrease (Caraco et al, 1997; Pace et al., 1998). Because of that, planktivorous fish might decrease in number, although early studies indicate this effect seems to be slight (Pace et al., 1998). The concomitant increase in water clarity (Fahnenstiel et al., 1995), might cause increases in macrophyte populations. Macrophyte beds provide cover and act as nurseries for some species of fish. Via these mechanisms, the zebra mussel could affect fish populations and distributions (USGS, internet).

Also, the distribution pattern of other larger animals is affected. Changes in behaviour, distribution and number of diving ducks, which are known to feed on *D. polymorpha*, have been reported in infested areas in the US and Europe (Halloway, 1996; de Leeuw, 1997; Wormington and Leach, 1992).

Thus, the early concerns that *D. polymorpha* will disrupt the lower food web in areas newly infested, with effects reverberating up the food chain (Roberts, 1990) seem to have become reality.

Section 3.5: Attempts to control *D. polymorpha* in infested areas

Because of the immense economic and ecological damage, extensive research has been done to control *D. polymorpha*. Virtually all control methods have been tested, including physical, chemical and biological control.

Section 3.5.1: Physical and chemical control

Most physical and chemical control methods described are meant for preventive and reactive treatment of facilities exposed to untreated water, and cannot be used to control zebra mussels in the environment. Preventive control methods include repellent construction materials, antifouling coatings, chemical use, and thermal treatment. Reactive control methods are mostly crude physical procedures such as mechanical cleaning, high-pressure water jetting, carbon dioxide pellet blasting, freezing, and desiccation. These methods are described in detail by Boelman et al. (1997).

Section 3.5.2: Biological control

Three groups of organisms have potential to control Dreissena populations in the environment: selectively toxic microbes, natural enemies (i.e. predators and parasites, see Molloy et al., 1997) and deadly competitors. In Europe *Dreissena* population dynamics, densities and biomass are very similar to those encountered in the recently invaded American waters (Molloy, 1998), having the profound economic and ecological effects discussed in this report. "Natural" enemies have had a century to adapt to the presence of this mussel in Europe. Still, they are unable to suppress *Dreissena* populations to levels below ecological or economic impact thresholds. Therefore, "natural" enemies from invaded areas do not seem to be suitable for control of *D. polymorpha* (Molloy, 1998; e.g. MacIsaac, 1994; Thorp et al, 1998).

One deadly competitor was reported by Van der Velde et al. (1994) (see also Bij de Vaate and Greijdanus-Klaas, 1992). In the Netherlands, *Dreissena* populations have declined due to the invasion of the amphipod *Corophium curvispinum*, which also originated in the Ponto-Caspian area. In the lower parts of the Dutch River Rhine, *C. curvispinum* seems to outcompete *D. polymorpha* for food and substrate for attachment. It has been suggested to import this species into North America for the control of Dreissena populations (van der Velde et al., 1994). However, since *C. curvispinum* itself could cause ecological damage just as bad or even worse than the damage caused by *D. polymorpha* (Drent, pers comm.), this seems to be no option.

More is to be expected from selectively toxic microbes. These are naturally occurring microbes that happen to produce a specific compound selectively toxic to a certain species, in this case the zebra mussel. Although in nature maybe too rare to have a significant effect, if applied in artificially high densities these microbes are the most promising candidates for biological *Dreissena* management. At least one suitable bacterial strain has been identified, and will be commercially available soon (Molloy, 1998).

Section 4: Factors influencing the success of invasions

Put simply, a community is invasible when an introduced species (an invader) is able to increase when rare (Crawley, 1987). This does not imply that the invader necessarily becomes dominant, outcompetes native species, or causes fundamental changes in the invaded communities. On the contrary, most of the successful invaders remain present at low numbers, quietly integrated in the invaded community (Moyle and Light, 1996a; 1996b). However, as described in the case studies above *E. sinensis* and especially *D. polymorpha* did not integrate quietly. Not only did they manage to invade and establish themselves in several communities, they also had a significant impact on the communities they invaded. In the next sections I will discuss the traits that made our invaders so successful, and factors influencing the invasibility of communities.

Section 4.1: Traits making our invaders successful

Chinese mitten crabs as well as zebra mussels are both examples of very successful invaders. Both have invaded and continue to invade ecosystems around the world, and have managed to establish themselves on almost all continents. What traits enabled these animals to become so successful? First of all, both species have a broad tolerance to climatological conditions, and abiotic parameters like salinity, pH, pollution and low oxygen content (Adema, 1991; Effler et al, 1998; Gollasch, 1997; Johnson and Padilla, 1996).

Once dispersed (by man), a number of traits enabled them to establish and become abundant rapidly. First, they occupy an empty niche. Before *E. sinensis* arrived, no freshwater brachyuran crab occurred in brackish and freshwater zones of the European and North American estuaries (Gollasch, 1997; Wolff, 1999). And before *D. polymorpha* arrived, there was no freshwater mussel that could attach to solid substrates (Johnson and Carlton, 1996). Solid substrates were abundantly provided by man with the construction of stone groins and other artificial stabilising agents, bridge abutments, dams etc. in freshwater (e.g. Bij de Vaate et al., 1992; Den Hartog and van der Velde, 1987).

Second and third, both species have a high rate of recruitment and are not restricted by predation. Of enemies, *E. sinensis* has few or none (Adema, 1991), and one female can produce 200.000 to 900.000 eggs in her life (Adema, 1991). For *D. polymorpha* many natural enemies have been documented (e.g. Molloy et al., 1997), but the high recruitment rate typical of *Dreissena* populations inherently makes them very difficult for natural enemies to control (Molloy, 1998). One single *Dreissena* female can produce up to one million eggs per spawning season (USGS, internet).

Fourth, both species are able to spread rapidly once introduced in a region. As mentioned, *E. sinensis* is known for its tendency to migrate 100s of kilometres. Moreover, the planktonic marine larval phase can be carried along coastal areas by sea-currents, infesting new estuaries (Adema, 1991). The rapid spread in Europe throughout the 20th century illustrates the effectiveness of these traits. For *D. polymorpha* the planktonic larval stage is also of great advantage: the veligers are carried to new areas by water currents. The adult stage of *D. polymorpha* can also be dispersed by water currents, while attached to drifting substrates (e.g. Johnson and Padilla, 1996). The planktonic developmental phases have also enabled the mitten crab and the zebra mussel to embark on ships, in ballast water tanks (see section 1; section 4.3).

Finally, they are not restricted by competition with native species. *E. sinensis* does not seem to have any serious competitors, as stated in section 2.4.2. *D. polymorpha*, as a filterfeeder depending on phytoplankton for food, is a superior competitor for this resource. It simply outcompetes native filterfeeders and pelagic planktivores (e.g. Johnson and Carlton, 1996; Strayer and Smith, 1996). The only species able to outcompete *D. polymorpha* is another invader, originating from the same area as *D. polymorpha* itself (see section 3.5.2). It would be fascinating to study the interactions between these two species in their native habitat where they appear able to coexist indefinitely.

Section 4.2: Factors making communities susceptible to invasion

What factors make a community invasible? Although in principle all communities are invasible (Crawley, 1987), there do seem to be differences in the degree of invasibility. Some communities seem to be more invasible than others. Here I will discuss the factors that are thought to determine the degree of invasibility of a community.

Biotic as well as abiotic factors influence invasibility. The invader must cope with the native biological community, and with the abiotic circumstances. Much research has been done on these topics, and in some cases it has been found that biotic factors only play a minor role (e.g. Moyle and Light, 1996a; 1996b). However, other studies suggest a more significant role for biotic factors: especially biological diversity is presumed to influence invasibility.

It is commonly believed that diverse communities better resist invasion by exotic species than do simple communities. The reason for this is the idea that more diverse assemblages more fully utilise available resources, thus leaving little resource space for individuals of new species. This mechanism follows from the species-packing or diffuse

competition models of MacArthur (1970), and is an extension of the empty niche concept in invasion biology (Crawley, 1987), as reviewed by Levine and D'Antonio (1999). Indeed, the success of invasion of estuarine/freshwater systems by *E. sinensis* and *D. polymorpha* has been ascribed to the presence of empty niches (section 4.1) and the fact that these systems were profoundly disturbed (by man), rendering native communities small, impoverished and thus susceptible to invasion (e.g. Carlton and Geller, 1993; Cohen and Carlton, 1998).

However, the evidence for this link between diversity and invasibility is weak. First, confusion of two distinct features, susceptibility to invasion itself (the actual invasibility) and vulnerability to impact of invasion are often confused. Small communities often seem more susceptible to invasions then their more diverse counterparts, because the impact of invasions on smaller communities is generally more serious (Levine and D'Antonio, 1999; Moyle and Light, 1996b). Moreover, theoretical community studies on the effect of diversity on invasibility often yield mixed results, and species facilitating settlement of invaders, so called "invasion promoters", can occur more frequent in diverse communities, as reviewed by Levine and D'Antonio (1999).

With exotic species and resident species showing the same responses to the environment, the effects of diversity on invasibility are likely to be swamped by factors covarying with diversity at broader spatial scales. Thus, the factors influencing diversity might have a bigger effect on invasibility than diversity itself. More specific research and development of comprehensive regional data sets are needed to evaluate the mechanisms underlying this effect (Cohen and Carlton, 1998; Levine and D'Antonio, 1999).

Section 4.3: The role of mankind in present invasion events

As described by Vermeij (1991) interchange between biotas, in which barriers to dispersal are breached and formed is a natural process, has been going on for millions of years. Indeed, the idea that community structure and constitution are dynamic rather than static, takes more and more hold among ecologists. However, it is undisputed that in the human-dominated biosphere, the natural barriers to dispersal are being breached on an unprecedented scale.

Mankind played a major role in the dispersal of *D. polymorpha* and *E. sinensis*. Both species owe their worldwide distribution largely to ballast water transport, a means by which thousands of species are in motion around the world every day (Adema, 1991; Carlton, 1996a; Carlton and Geller, 1993; Gollasch, 1997).

As described in sections 2.3 and 3.3, the rate of local spread of our two invaders is highly increased by the digging of canals (USGS, internet; Kinzelbach, 1992) and transport on for example recreational boats (Johnson and Padilla, 1996). Especially for *D. polymorpha* the potential human mediated dispersal mechanisms are almost limitless (Carlton, 1993; Johnson and Carlton, 1996).

Next to active and passive transport of specimens, mankind specifically enhances conditions for invaders. The solid substrates in freshwaters created by man, from which *D. polymorpha* profited as mentioned in section 4.1, are examples of this.

Finally, mankind influences and changes ecosystems by for example altering nutrient-balances, as mentioned in sections 1 and 4.2. Although ecologists have not agreed yet on the mechanisms, it is clear that these changes also affect invasibility.

Section 5: High impact vs. low impact invasions

As mentioned in section 4, not all invasions have the same impact. Most of the invasions documented did not result in fundamental changes in the invaded systems, so-called low impact invasions. However, sometimes, as in the case of the zebra mussel, invasions do lead to radical changes. These high impact invasions typically result in major shifts in community structure and constitution. Often native species decline in number, and can eventually become extinct.

Now, for half a century ecologists have been trying to understand what it is that makes some invasions so damaging and other invasions unsuccessful or negligible. As mentioned, a link between high impact and low native diversity has often been suggested (Levine and D'Antonio, 1999; Moyle and Light, 1996b). Furthermore, Moyle and Light (1996b) stated that at least concerning fish-invasions predatory invaders are more likely to cause extinctions among native species than invading detritivores or herbivores. However, contemporary literature is largely devoid of general statements concerning the difference between high-impact and low-impact invasions.

Indeed, despite the increase in the number of quantitative and theoretical studies in the last decade aimed at the challenge of making invasion ecology a predictive science, records on the ecology of invasions still tend to be anecdotal. Predictions and general statements are scarce, and the predictions and statements being made are not especially impressive. Perhaps the most striking feature of reports on invasive ecology continues to be the absence of manipulative experiments in the tradition of modern community ecology.

Section 6: Invasions in the Dutch estuaries and freshwater systems.

The majority of the Dutch estuaries and freshwaters have been profoundly disturbed by man. Several exotic species have established, mostly due to the removal of barriers that obstructed their extension and the creation of new habitats, all caused by human activity (e.g. Den Hartog and Van der Velde, 1987). Most of the invaders established themselves in new man-made habitats and heavily disturbed habitats, but were unsuccessful in penetrating well-established, stable, aquatic communities (Den Hartog and Van der Velde, 1987).

For *D. polymorpha*, most of the Dutch waters are too shallow (1-2 meters deep) for the maintenance of stable, well developed populations, which require a depth of more than 2 metres (Van der Velde et al., 1994; Bij de Vaate, 1991). In the great rivers and several lakes depths of >2 meters occur, the biggest being Lake IJsselmeer. The economic damage caused by zebra mussels in the Netherlands is small because the invasion of this species started two centuries ago, which is before the industrial revolution. Engineers involved in construction of water supply systems using surface water were able to adapt these structures to unexpected problems with this fouling animal in a very early stage (Van der Velde et al., 1994). Over the years then, engineers in The Netherlands have gained considerable experience in handling this mussel species (Van der Velde et al., 1994). Nowadays, the zebra mussel is being used as a biomonitor species because of its sensitivity to various kinds of pollution and the fact that it accumulates various toxic substances (Van der Velde et al., 1994). Dutch scientists have even tried to use *Dreissena* for the clearance of hypertrophic waters, in order to restore submerged macrophyte vegetation and to obtain a well developed population of clear-water-associated pike (*Essox lucius*), while reducing that of bream (*Abramis brama*) and the commercially valuable pike-perch (*Stizostedion lucioperna*). A review of these and other positive applications of *Dreissena* for water management is given by Smit et al. (1994).

E. sinensis has established itself throughout the Netherlands and occurs in almost all freshwaters (Fig. 17).

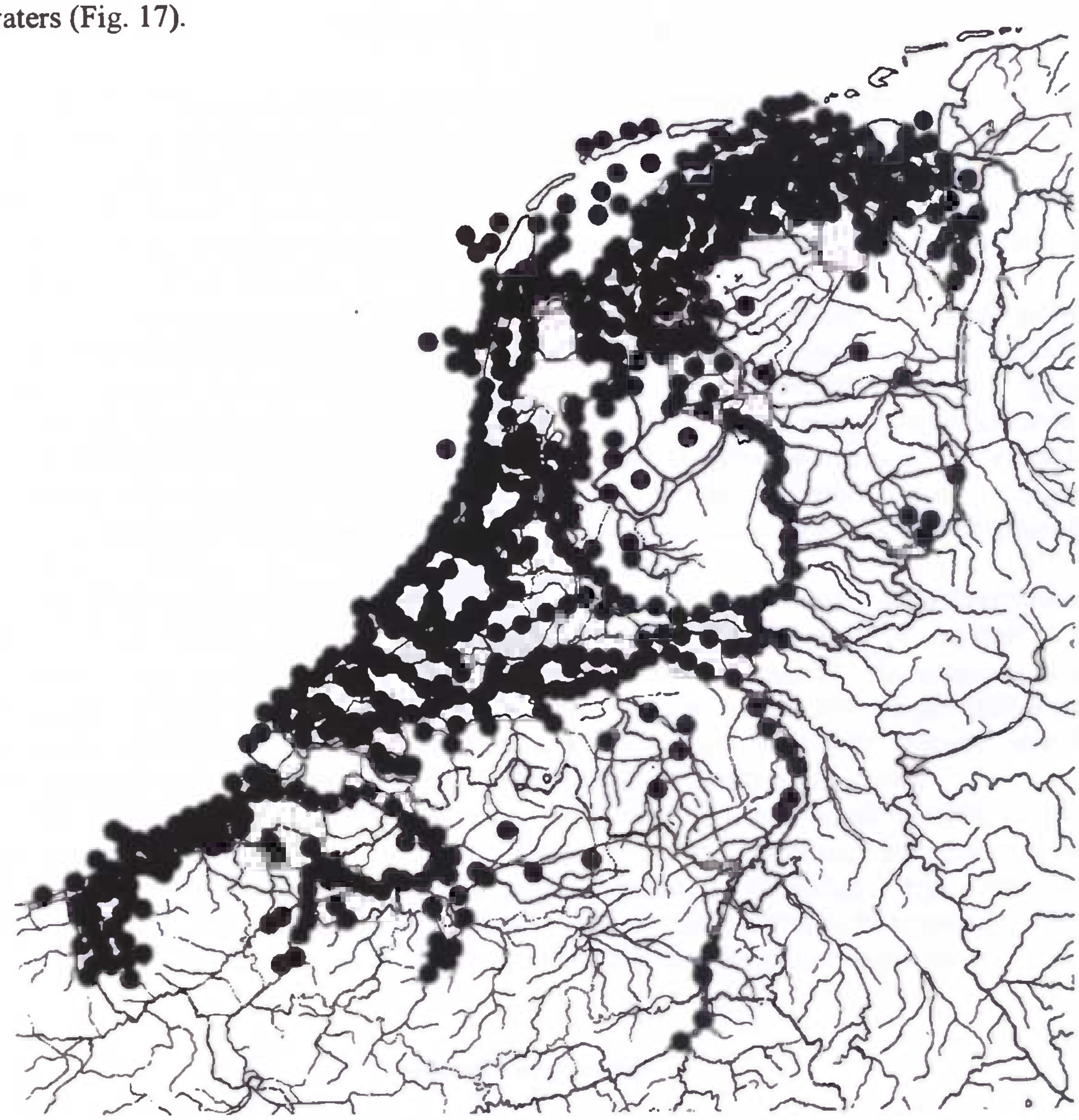

Figure 17. Distribution map of *E. sinensis* in the Netherlands. This picture was taken from Adema, 1991.

Next to our two invaders, the Dutch brackish and freshwaters have been successfully invaded by about 26 invertebrates, 13 species of fish and 9 species of plants (Den Hartog and Van der Velde, 1987; but see Reise et al., 1999). According to Den Hartog and Van der Velde (1987) this number is surprisingly small, and native species populations are only in a few cases considerably affected. However, as mentioned before, no comprehensive long-term datasets are available to assess the impact of the various invasions. The future development of such datasets will be of vital importance for our understanding of the never ending process of invasions and their impacts.

Section 7: Conclusions.

In the two case studies presented in this report the successful invasions of E. sinensis and D. polymorpha into European and North American waters are described. In contrast to D. polymorpha, invasions by E. sinensis do not seem to have a very big ecological impact. However, both species have managed to establish large populations in estuaries and freshwater systems on both continents and cause considerable economic damage. Methods for control have not been found yet.

In their success, a great number of factors play a role, among which are several properties of the organisms themselves but also properties of the communities they invaded. The most important role of all was played by man, who dispersed these two species worldwide and also changed and disturbed native communities, rendering them vulnerable to invasion by these two and many other species. How this disturbance of native communities, their diversity and invasibility are correlated is still the subject of debate among ecologists. Moreover, literature is largely devoid of general statements concerning factors determining the impact of invasions.

E. sinensis and D. polymorpha are well established in the Dutch estuaries/freshwaters. Generally, E. sinensis is still regarded as a nuisance species. This is in contrast to D. polymorpha, whose positive qualities are more and more emphasised. An example is the application for improvement of water quality. In general, the Dutch estuaries and freshwaters did not suffer notably from these or other invasions. However, long-term datasets, vital for accurate assessments of damages caused by invasions are absent from literature.

The build-up of such comprehensive long-term datasets, together with a more experimental approach in field-research and a focus on factors controlling native communities are of vital importance for our understanding of invasions in today's and tomorrow's ecosystems. Hopefully, this understanding will in time enable ecologists to accurately predict future invasions and their impacts, and prevent damaging invasions from happening.

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