

Mya arenaria – an ancient invader of the North Sea coast

Matthias Strasser

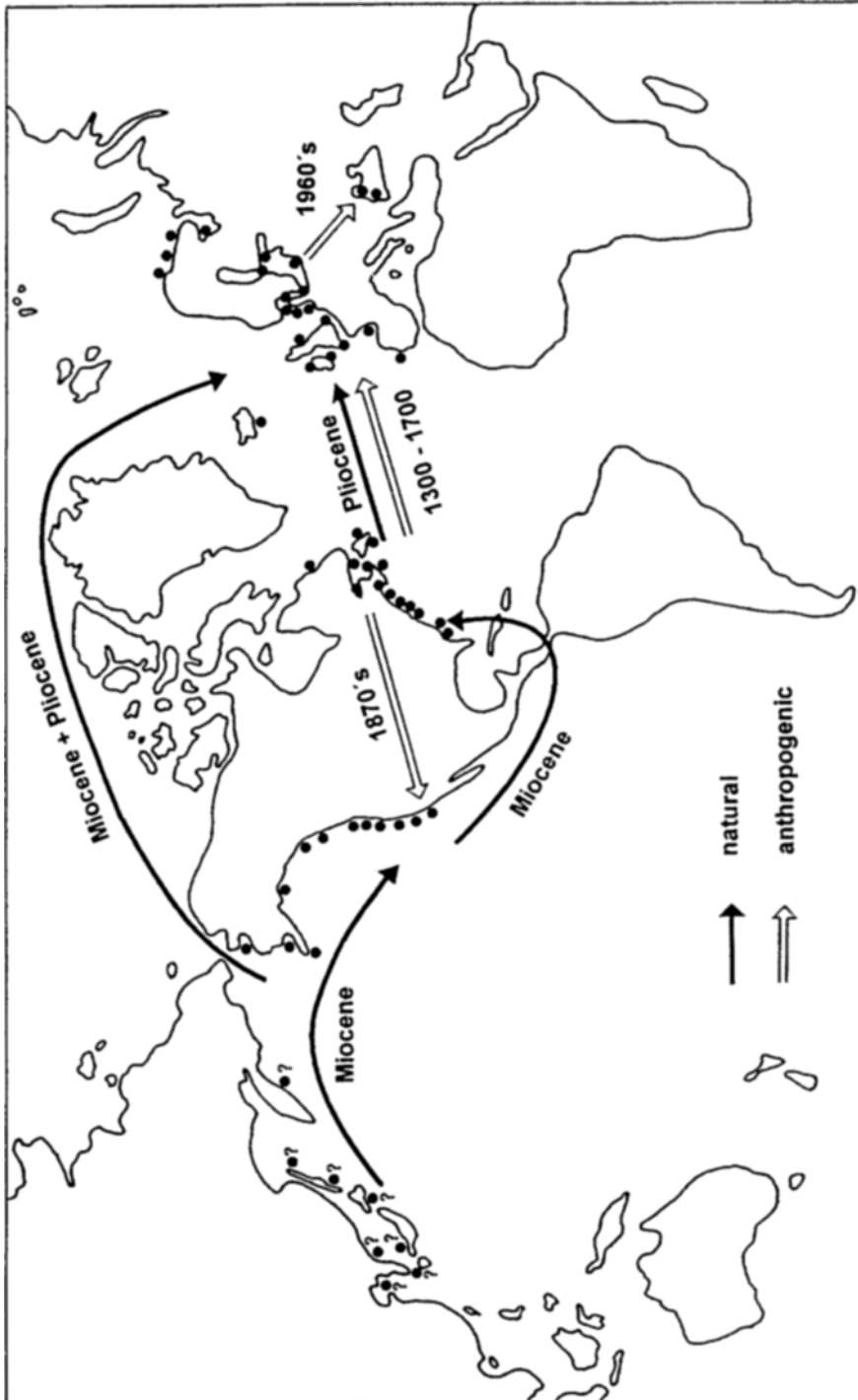
*Alfred-Wegener-Institut für Polar- und Meeresforschung, Wattenmeerstation Sylt,
D-25992 List, Germany*

ABSTRACT: *Mya arenaria* currently occupies a wide geographical range in the northern hemisphere, on both coasts of the Atlantic as well as on the Pacific east coast. Some authors claim it also occurs on the Pacific west coast. The species originated in the Pacific during the Miocene and was already present on both Atlantic coasts in the Pliocene. However, it died out on the east coasts of the Pacific and the Atlantic during glaciation of the Pleistocene. With the aid of man it was reintroduced to the North Sea some 400–700 years ago and to the East Pacific last century. In the 1960s it was also introduced to the Black Sea. *M. arenaria* invaded new habitats by different modes: (1) natural range expansion (2) intentional as plantings, (3) unintentional as a ballast species and (4) unintentional as a byproduct of oyster transplants. Properties that may favor its wide range of distribution and invading success are: high fecundity; planktonic dispersal stages and life stages that lend itself to unintentional transport by humans; a broad spectrum of habitat and food preference; tolerance of a wide range of environmental conditions such as salinity and temperature; longevity, and perhaps relatively large size.

INTRODUCTION

The soft sediment bivalve *Mya arenaria* is unique because it is by far the earliest introduced species to the North Sea shore that scientists are aware of (Reise et al., 1999). *Mya* is presently widely distributed at least over both northern coasts of the Atlantic as well as over the North Pacific east coast. However, it not only occurs over a wide geographical range, but also often plays a dominating role in local benthic communities. In European waters *Mya* was found to be the species with the highest biomass in a study on the south-west coast of England (Warwick & Price, 1975). It is also one of the three most important producers of benthic biomass and calcimass in the Wadden Sea (Beukema, 1982, 1992) and among the dominating species on the west coast of Sweden (Evans & Tallmark, 1977) and in the Baltic Sea (Brey, 1991; Powilleit et al., 1995). During the last few centuries the clam was such a typical component in the Baltic Sea that the last stage of the Baltic development has been called the *Mya* Sea (Hessland, 1946). After its introduction in the 1960s, it became a mass element in the Romanian part of the Black Sea (Gomoiu, 1981).

On the Atlantic coast of North America it is reported as a dominating species in Nova Scotia (Emerson et al., 1988) and from many estuaries in New England (Newell & Hidu, 1986). In Canada and the United States it is or was an important commercial fish-



ery (Amaratunga & Misra, 1989; Hidu & Newell, 1989). On the Pacific coast it was usually dominating the benthic community after dry periods in a study in San Francisco Bay (Nichols et al., 1990).

In this paper I will trace the invasion history of *M. arenaria* and explore the reasons that may be responsible for its successful invasion. I will use a terminology after Carlton (1989), where a biological invasion means the arrival, establishment and subsequent diffusion of a species in a community in which it did not previously exist. Mechanisms of invasions can be divided into dispersal by human activity (introduction) and natural dispersal (range expansion).

PRESENT DISTRIBUTION OF *M. ARENARIA*

Mya arenaria currently occurs at least on both coasts of the North Atlantic as well as on the North Pacific east coast. No records are known from the southern hemisphere. As the geographical range of *M. arenaria* could reveal valuable information about spreading rates and properties such as temperature and salinity requirements, an attempt is made to describe the present distribution (Fig. 1). However, it is difficult to describe the exact worldwide range since statements of some authors contradict each other. Most problems are caused by different opinions about the assignment of specimens to either *M. arenaria*, *M. truncata* or *M. japonica*. For example, some authors claim the existence of *M. arenaria* on the Pacific west coast (Laursen, 1966; Bernard, 1979; Goshima, 1982), while others argue that records from the West Pacific are misidentifications of *M. japonica* (MacNeil, 1965; Strauch, 1972). Therefore, a question-mark is added to the West Pacific records of *M. arenaria* in Fig. 1.

According to Laursen (1966) all records for *M. arenaria* he checked from within Arctic regions actually belonged to *M. truncata* f. *ovata*. These old records are not included in Fig. 1, but new records from Arctic regions should also be treated with caution. However, even a conservative geographical range, considering only references from undisputed areas, demonstrates the widespread present occurrence of *M. arenaria*.

On the European coast the northernmost records of *M. arenaria* are given from northern Norway and Murman in the Barents Sea (Galkin, 1998). It is also reported from the White Sea (Maksimovich, 1978) and from the coast of Iceland (Óskarsson, 1961). However, it needs to be stressed that earlier reports of *M. arenaria* from Iceland were later assigned to *M. truncata* f. *ovata* (Laursen, 1966). According to Stokland (1985) *M. arenaria* is present along the entire Norwegian coast, but no collection sites are

◀ Fig. 1. Assumed natural and anthropogenic invasion pathways of *Mya arenaria* and present distribution. Further explanations in the text. Distribution is based on records given in Amanieu, 1969; Appeldoorn, 1983; Bacon et al., 1998; Bernard, 1979; Beukema, 1982; Bourget, 1983; Carl & Guiguet, 1957; Carlton, 1979, 1989; Feder & Paul, 1974; Foster, 1946; Galkin, 1998; Gomoiu, 1981; Goshima, 1982; Guimarães & Galhano, 1988; Hanna, 1966; Himmelman & Hamel, 1993; Lassig, 1965; MacDonald & Thomas, 1980; Maksimovich, 1978; McLusky & Elliott, 1981; Miac et al., 1997; Minchin & Sheehan, 1995; Muus, 1967; Newell, 1964; Nichols, 1985; Óskarsson, 1961; Porter, 1974; Powilleit et al., 1995; Rasmussen & Heard, 1995; Reise, 1985; Savchuk, 1976; Stewart & Bamford, 1976; Theroux & Wigley, 1983; Valera & Céidigh, 1964; Warwick & Price, 1975; Winther & Gray, 1985; Zaklan & Ydenberg, 1997

cited. In the Baltic Sea *M. arenaria* is found up to the Gulf of Bothnia and the Gulf of Finland (Lassig, 1965). The clam is present in the entire Wadden Sea and on the coast of Great Britain. The southern limit on the Atlantic east coast appears to be Portugal (Guimarães & Galhano, 1988). In addition *M. arenaria* exists on the Romanian (Gomoiu, 1981) and the former Russian coast (Savchuk, 1976) of the Black Sea. Statements about its occurrence in the Mediterranean Sea were not considered in Fig. 1 because either no collection site was cited (Ziegelmeier, 1957) or the cited reference could not be found in the literature list (Bernard, 1979).

The northernmost records on the Atlantic west coast are from Labrador (Foster, 1946). *M. arenaria* is also reported from the northern Gulf of St. Lawrence (Himmelman & Hamel, 1993) and Newfoundland (Bacon et al., 1998). Most references come from the area between Nova Scotia, Canada and Maryland, USA (e.g. Appeldoorn, 1983; Theroux & Wigley, 1983). The southernmost record is from Georgia (Rasmussen & Heard, 1995). A statement about *M. arenaria* in Florida (Theroux & Wigley, 1983) is disregarded because no reference to specimens or collection site are given.

On the Pacific east coast *M. arenaria* occurs from North Sound and Bristol Bay in Alaska (Bernard, 1979) down to Monterey Bay, California (MacNeil, 1965; Bernard, 1979). Reports from San Diego (Hanna, 1966) are considered to be false by Carlton (1979), who extensively reviewed records of *Mya* on the Pacific east coast.

If identifications of *M. arenaria* from the Pacific west coast are correct it ranges from the coast of Kamchatka in the north down to southern Japan and the Gulf of Chihli, China (Bernard, 1979).

ORIGIN OF *M. ARENARIA* AND ITS INVASION HISTORY

Since shells of mollusks are preserved in the fossil record, it was possible to study the evolution and migration of *M. arenaria* in geological time. It is believed to have originated in the Pacific during the Miocene (22.5–5.0 10^6 years ago) as a successor of *M. fujiei* (MacNeil, 1965; Strauch, 1972). The oldest records of *M. arenaria* were in late Miocene formations on the Pacific west coast in Japan and roughly from the same time on the Pacific east coast in California (Strauch, 1972). No proof exists on which side of the Pacific the clam evolved, but both MacNeil (1965) and Strauch (1972) suspect it was in Japan. Later, but still in the Miocene, it first appeared in Atlantic waters in the Yorktown Formation of Virginia (MacNeil, 1965; Strauch, 1972). While MacNeil (1965) and Bernard (1979) believe *M. arenaria* reached Virginia by way of the Arctic (Fig. 1), Strauch (1972) suggests a Central American passage because the Bering Strait did not open until the Pliocene (5.0–1.6 10^6 years ago). According to Strauch (1972) *M. arenaria* made its first appearance in Europe in the late Pliocene. He assumes that it reached Europe by crossing the Atlantic. However, Vermeij (1989) considers *M. arenaria* to have invaded from the Pacific to the Atlantic as part of the Trans-Arctic Interchange via the Bering Strait. Some authors believe that *M. arenaria* survived glaciation in the Pleistocene only on the Atlantic west coast and that all populations on the entire Pacific coast and on the Atlantic east coast died out (MacNeil, 1965; Strauch, 1972). However, according to Bernard (1979) *M. arenaria* also survived the Pleistocene on the Pacific west coast in Japan. It is believed that after the Pleistocene the invasion history of *M. are-*

naria was substantially influenced by human activity. Probably between the thirteenth and seventeenth century it invaded the European coast for the second time. According to Hessland (1946) *M. arenaria* reinvaded Europe during the sixteenth or seventeenth century. He argued that the clam could not have crossed the Atlantic without the aid of man. Instead, travellers might have brought specimens either intentionally as food or bait or unwittingly together with oysters or in the bilge water of ships. Recently, Petersen et al. (1992) dated shell material from Denmark to the thirteenth century and suggested that *Mya* could have been transferred to Europe by the Vikings.

It also reinvaded the Pacific east coast through human activity. It was probably first introduced as a byproduct of oyster transplants from the Atlantic side to San Francisco Bay prior to 1874 (Stearns, 1881; Hanna, 1966). On the Pacific east coast it was later also intentionally planted as a commercial fishery (Hanna, 1966; Carlton, 1989).

The most recent introduction occurred in the Black Sea around 1960. Adult specimens were first discovered close to Odessa and Ilichesk, the largest ports in the Black Sea, in 1966 (Savchuk, 1976). It was probably transported there as a ballast species by oil tankers from the Baltic Sea (Leppäkoski, 1994). It is important to note that in a survey in German ports adult specimens were found in the sediment of ballast water tanks and as a fouling organism on the hull of a ship (Gollasch, 1996). Although *Mya* was initially introduced since the thirteenth century to the east Atlantic, east Pacific and the Black Sea by man, it needs to be pointed out that there was also a substantial natural range expansion (especially in Europe) leading to the present distribution (Fig. 1).

CHARACTERISTICS OF *MYA ARENARIA*

Several characteristics of species have been suggested as predictors of successful invaders (e.g. Lodge, 1993; Williamson, 1996, and references therein), some of which are overlapping or even contradicting (Lodge, 1993). Some of the most widely cit-

Table 1. Characteristics of *Mya arenaria* that may be relevant to its invading success on the North Sea shore. Further explanations in the text

Characteristics	<i>M. arenaria</i>
Previous success as an invader	Yes
Abundant and widespread in native range	Yes
High invasion pressure	?
Large and long-lived	Yes
Life cycle with dispersal stage	Yes
Potential to form a resting stage	No
<i>r</i> -selected, high fecundity, short generation time, high growth rate	(Yes)
Broad spectrum of habitat and food preference	Yes
Preference for disturbed habitats	No
Tolerant of wide range of physical conditions	Yes
Lack of parasites and disease	Yes/?
Lack of predators	No
High genetic variability	?
Occupying a previously empty niche	(No)

ed characteristics are summarized for *Mya* in Table 1 and will be discussed in the following.

Previous success outside the North Sea

The characteristic of previous success as an invader holds true because prior to its arrival in Europe (1) during the Pliocene and (2) some 400–700 years ago, *Mya* successfully invaded the Atlantic west coast during the Miocene (Fig. 1). Abundance and widespreadness in its native range is also fulfilled, if the Atlantic west coast – with perhaps the only surviving populations after the Ice Age – is regarded as the native range and the distribution there was similar 400–700 years ago to how it is today. The characteristic of high invasion pressure is based on the assumption that invading success is positively correlated with the number of individuals introduced (Williamson, 1996).

Life history traits

Mya is considered a relatively large and long-lived bivalve although there are regional differences. Calculated growth curves for different geographic areas in Europe and North America showed maximum sizes between some 60 and 100 mm (Brousseau, 1979; Winther & Gray, 1985). Very large individuals are reported to exceed 140 mm (Coe & Turner, 1938; Linke, 1939; Kühl, 1951). A large body size may allow high numbers of eggs which perhaps favor a wide range of distribution. A lifespan of 10–12 years is considered normal on the Atlantic east coast (Brousseau, 1978a) with a maximum of 28 years reported from the Bay of Fundy (MacDonald & Thomas, 1980).

Mya has a life cycle with dispersal stages (planktotrophic larvae and juveniles) but, like all mollusks, no potential to form a resting stage. Transport by humans is possible at any life stage (see above). Depending on the geographic area, spawning takes place once or twice annually, usually starting in spring (see Brousseau, 1987, for a review). In European waters the majority of larvae usually appear in May/June (e.g. Günther, 1992; personal observations), although they may be found as late as October (Jørgensen, 1946). A single annual spawning event has been suggested for the Wadden Sea (Günther, 1992), the west coast of Sweden (Möller & Rosenberg, 1983), the east coast of Denmark (Munch-Petersen, 1973), and the Black Sea (Began, 1979). Two reproductive periods have been reported from Oslofjord (Winther & Gray, 1985) and the south coast of England (Warwick & Price, 1975). The larval stage usually lasts for about 2–3 weeks (Thorson, 1946; Medcof, 1950). In laboratory studies the larval phase lasted between 10 and 35 days (Loosanoff & Davies, 1963), suggesting that *Mya* is capable of delaying settlement if conditions are not optimal. Larval growth, survival, and length of larval stage were dependent on salinity, temperature and food (Stickney, 1964). The majority of larvae do not metamorphose until a size of 200 μm is reached (Jørgensen, 1946; Loosanoff & Davies, 1963; Stickney, 1964). The new settlers live in the upper 2 cm of the substrate as long as they are < 10 mm (Blundon & Kennedy, 1982; Zwarts & Wanink, 1989) and may anchor themselves in the sediment with byssus threads (Smidt, 1951; Kühl, 1955). With advancing growth longer siphons are developed which enable *Mya* to bury deeper into the sediment, increasing their chances of escaping predation (Zwarts & Wanink, 1989; Zaklan & Ydenberg, 1997). In the Wadden Sea the majority of clams

>50 mm are found in the sediment at a depth of between 15 and 20 cm (Zwarts & Wanink, 1989) but at a maximum depth of 40 cm (Kühl, 1981). While large clams establish a permanent burrow (Linke, 1939; Medcof, 1950; Hidu & Newell, 1989), small clams are still prone to different mechanisms of dispersal. After settlement and metamorphosis *Mya* is subject to postlarval dispersal through passive resuspension into the water column (Roegner et al., 1995) and active byssus drifting (Armonies, 1994), although the latter mode does not seem to be quantitatively important (Armonies, 1998). Drifting clams in the water column did not exceed 2 mm shell length (Möller, 1986; Armonies, 1992). It has been shown that dispersal by bedload sediment transport can result in translocation of large quantities of juveniles up to 15 mm shell length (Emerson & Grant, 1991) which may contribute to intertidal zonation on exposed shores (Matthiessen, 1960 a). A passive subtidal transport of clams of up to 25 mm was suggested for the Baltic Sea (Kube, 1996) and occasionally shells up to 40 mm long were caught in intertidal bedload traps (Emerson & Grant, 1991).

The life history of the diocious *M. arenaria* is characterized by high fecundity that increases with increasing female size, by repeated reproduction, and high larval and juvenile mortality that levels off close to the age of first reproduction (Brousseau, 1978 a; Brousseau & Baglivo, 1988; Malinowski & Whitlatch, 1988). Fecundity values for *Mya* for a single spawning season on the Atlantic west coast varied between 120 000 eggs (60-mm clam; Brousseau, 1978 b), 3 million eggs (63-mm clam; Belding, 1930, cited in Brousseau, 1978 b) and 1–5 million eggs (unknown size; Stickney, 1964). A high intrinsic rate of natural increase (r_{max}) of 4.74 was calculated for a population in Massachusetts (Brousseau, 1978 a).

The characteristic of short generation time and high growth rate does not universally hold true. Commito (1982) suggested that *Mya* delays reproduction to its fourth year in favor of rapid early growth to reach a depth refuge. First reproduction usually occurs at a size of about 20–50 mm, which corresponds to an age of 1–4 depending on growth conditions (Porter, 1974; Brousseau, 1978 a; Sadykhova, 1979; Commito, 1982; Rosenblum & Niesen, 1985; Winther & Gray, 1985; Brousseau & Baglivo, 1988). In most areas growth of *Mya* is fastest in its first years and decreases with age (e.g. Munch-Petersen, 1973; Brousseau, 1979; Appeldoorn, 1981; Miac et al., 1997). However, linear growth has also been reported (Feder & Paul, 1974; Warwick & Price 1975; Kube et al., 1996). Growth rates can vary considerably between areas (see Brousseau & Baglivo, 1987, for a review). For example, it took 6–7 years for *Mya* to reach a size of 51 mm in a study in Alaska (Feder & Paul, 1974) while it took only 1.5 years in Connecticut (Brousseau & Baglivo, 1987). Several factors have been mentioned to affect growth of *Mya*, such as sediment type (Swan, 1952; Newell & Hidu, 1982), salinity (Essink & Bos, 1985), exposure time (Wanink & Zwarts, 1993), disturbance (Emerson, 1990), latitude (Appeldoorn, 1983), and pollution (Appeldoorn, 1981).

Habitat, food and environmental tolerance

Mya has a broad spectrum of habitat and food preference. It is found most abundantly in intertidal and shallow subtidal areas (Lassig, 1965; Rasmussen, 1973; Newell & Hidu, 1986; Powilleit et al., 1995), but it can also reach subtidal depths of up to 192 m

(Theroux & Wigley, 1983). It is found in soft sea bottoms ranging from hard, stony sand to pure mud (Rasmussen, 1973). Although it may be more abundant in some substrates than in others, the type of soil seems to have little influence on the presence or absence of *Mya* (Turner, 1950; Muus, 1967; Theroux & Wigley, 1983). Apparently, the only requirements are substrates loose enough for *Mya* to dig in and yet stable enough to prevent their burrows from being destroyed too frequently (Medcof, 1950). The broad geographical range shows that *Mya* has no preference for disturbed habitats. For example, in Europe it invaded pristine habitats (North Sea 400–700 years ago) as well as eutrophicated parts of the Black Sea.

Mya feeds by filtering seawater (Newell & Hidu, 1986). However, fine particles from the surrounding bottom layer are also sucked in (Rasmussen, 1973), so that the stomach content is a combination of material mostly collected from the water column and a small amount from the sediment surface (Kamermans, 1994). Since the stomach content resembled the algal composition in the water column *Mya* did not seem to discriminate between food items. The diet, therefore, consisted of a variety of flagellates, blue-green algae, pelagic and benthic diatoms, and chlorococcales (Kamermans, 1994). In addition *Mya* is capable of absorbing dissolved organic material (Stewart & Bamford, 1976). In laboratory studies *Mya* larvae grew on several species of unicellular algae (Stickney, 1964).

Mya tolerates a wide range of salinities and temperatures and has high resistance to the presence of H_2S and to O_2 deficiency. The clam is a euryhaline osmoconforming bivalve (Beres & Pierce, 1981). In the Baltic Sea salinity gradually decreases in a northward direction. This gradient serves as a natural experiment to determine the lower salinity tolerance of *Mya*. The lowest mean salinity at which it exists in the Gulf of Bothnia is 4.5–5.0 psu (Lassig, 1965). Similar levels of 4 psu (Matthiessen, 1960 b) and 5 psu (Newell & Hidu, 1986) have been reported from the Atlantic west coast. The upper salinity limit must be > 35 psu since *Mya* persists in areas where these salinities are reached (Castagna & Chanley, 1973; Brousseau, 1978 a). Optimum salinity for rearing larvae in the laboratory was from about 16 to 32 psu (the highest value tested) (Stickney, 1964).

Under natural conditions *Mya* tolerates water temperatures down to $-2^\circ C$ in Alaska (Feder & Paul, 1974). It also persists in the St. Lawrence Estuary where freezing air temperatures may occur from October to May (Bourget, 1983). In the Wadden Sea it remained undamaged after the severe winter of 1995/1996 with more than 60 days of ice coverage on the tidal flats (personal observations). Mortality was likewise not enhanced after the severe 1978/1979 winter (Beukema, 1979). However, exceptionally severe winters are also known to have caused substantial mortality (e.g. Smidt, 1944; Rasmussen, 1973). Several reasons favor a critical upper temperature of about $28^\circ C$: (1) when this temperature was exceeded in Chesapeake Bay, large scale mortality of *Mya* often took place (Pfitzenmeyer, 1972); (2) highest temperatures at sites in Georgia where *Mya* was found (southernmost record on Atlantic west coast) are just below $28^\circ C$ (Rasmussen & Heard, 1995); (3) all larvae were dead after rearing for 14 days at $28^\circ C$ (Stickney, 1964).

The distribution of bivalve species is closely associated with their geographical thermal tolerance limits (Wilson, 1990). It appears that the southern distribution of *Mya* is restricted by an absolute limit of $28^\circ C$ for both adults and larvae. It has been sug-

gested that the distribution to the north is restricted by a critical spawning temperature of 10–12 °C (Nelson, 1928 cited in Brousseau, 1978 b) and of 12–15 °C needed for development of the veliger stage (Laursen, 1966). The existence of such a threshold is supported by laboratory studies. Optimal temperature for rearing *Mya* larvae was between about 17 °C and 23 °C, while high mortality and poor development were observed at 8 °C and lower (Stickney, 1964). Slow growth between 12 and 15 °C was reported by Loosanoff & Davies (1963). However, a critical spawning temperature of 10 °C is contradicted by a spawning peak of *Mya* at 4–6 °C in Massachusetts (Brousseau, 1978 b). Also, 10 °C is rarely reached in Labrador (northernmost record on Atlantic west coast) (Laursen, 1966). Brousseau (1978 b) suggested that the temperature at which maturation of the gonads occurs is more critical than the actual spawning temperature. Clearly, this issue needs further investigation.

Low oxygen concentrations and the presence of hydrogen sulfide can be tolerated for several days to weeks. At 10 °C a mortality of 50% (LD₅₀) was observed after 21 days in oxygen-deficient seawater of 0.15 ml O₂ l⁻¹, and after 17 days in the presence of H₂S (Theede et al., 1969). At O₂ concentrations of 0.5–1.0 ml l⁻¹ (8–15% saturation, 10–11 °C) 54 and 8% of the clams survived for 43 and 32 days respectively (Rosenberg et al., 1991).

The high tolerance of environmental factors is reflected in two statements made by Hidu & Newell (1989) about clam culture: “*Mya* larvae are among the most hardy that we have reared; one has to work overtime with incompetence to destroy a brood.” and “If *Mya* are hardy as larvae they are even more hardy as juveniles.”

Parasites, disease and predators

Several diseases and parasites are known to occur in *Mya* on the Atlantic west coast (Gibbons & Blogoslawski, 1989; Hidu & Newell, 1989, and references therein). *Mya* may be heavily affected by two types of cancer called disseminated neoplasia and germinomas (Landsberg, 1996). Clams categorized into high-severity neoplasia suffered mortalities of up to 78% in *Mya* in New England (Brousseau & Baglivo, 1991). On the Atlantic east coast no parasites have been found in *Mya* from the German Wadden Sea (Lauckner, personal communication). To my knowledge the occurrence of neoplasia has not been investigated in Western Europe.

A host of predators have been reported to feed on *Mya*, including filter-feeding organisms (larval predators), crustaceans, gastropods, horseshoe crabs, starfish, nemertea, polychaetes, birds, fish, racoons and man (see Gibbons & Blogoslawski, 1989, for a review). On European flats negative adult-larval interactions have been found on the Swedish west coast (Möller, 1986; André & Rosenberg, 1991), but this factor did not seem to play an important role in the large-scale distribution pattern in the Wadden Sea (Strasser et al., 1999). The most important predators on juvenile *Mya* are the green crab *Carcinus maenas* (Jensen & Jensen, 1985), shrimp *Crangon crangon* (Möller & Rosenberg, 1983), plaice *Pleuronectes platessa* and flounder *Platichthys flesus* (De Vlas, 1979). Heavy predation pressure on larger clams may be exerted by oystercatchers *Haematopus ostralegus* and curlews *Numenius arquata* (Zwarts & Wanink, 1989). In the Baltic Sea *Mya* is the main prey for wintering sea ducks (Kube, 1996).

It is generally believed that predation is one of the most important factors counterbalancing the high reproductive output and thereby controlling population dynamics of *Mya* (e.g. Jensen & Jensen, 1985; Newell & Hidu, 1986; Günther, 1992; Strasser et al., 1999).

Genetics

Surprisingly little is known about the genetic variability in *Mya*. The only genetic studies I am aware of showed relatively low variation between two populations in Maine and Maryland (Morgan et al., 1978) and among *Mya* along the New England coast (Caporale et al., 1997). Future studies on genetic variability promise to be especially useful for *Mya* because they could contribute to settling uncertainties about its species status in the Arctic and on the Pacific west coast. In addition, they could confirm or reject the hypothesized invasion pathways (Fig. 1).

Occupation of an empty niche and interaction with recipient communities

After its reinvasion of the North Sea *Mya* occupied a vacant niche only in so far as no other intertidal bivalve lives that deep in the sediment. In the Wadden Sea other common infaunal bivalves live near the surface (*Cerastoderma edule*) or at average depths above 11 cm (*Macoma balthica*, *Scrobicularia plana*) (Zwarts & Wanink, 1989). Another deep burrowing bivalve (*Ensis americanus*) invaded the Wadden Sea in 1978, but it is primarily a subtidal species (Armonies & Reise, 1999). Regarding other factors, *Mya* shows high niche overlap with other common bivalves. For instance, they all rely on the same food source (Kamermans, 1994), most of them spawn roughly at the same time (personal observations), and the early stages are heavily preyed upon by the same set of predators (Reise, 1985).

No information is available on the effects of *Mya* on the North Sea community immediately after its reinvasion several hundred years ago. Today no negative effects on other species have been observed (Reise et al., 1999). In contrast, *Mya* became a mass element in the Black Sea after its introduction in the 1960s, prevailing over all native bivalves (Gomoiu, 1981). An example of competitive exclusion in the Black Sea was the replacement of populations of the bivalve *Corbula mediterranea* (Leppäkoski, 1994). During recent years the abundance of *Mya* in the Black Sea has decreased due to algal blooms and anoxia (Leppäkoski, 1994). In San Francisco Bay it was apparently itself outcompeted by another invader, the Asian clam *Potamocorbula amurensis* (Nichols et al., 1990).

CONCLUSIONS

Mya arenaria possesses several properties that are regarded as advantageous for the invasion of new areas: it successfully invaded new areas in the past and it is relatively abundant and widely distributed where it is native. It is large, long-lived and can occupy a broad range of habitat types. It has high fecundity, high tolerance against a wide spectrum of coastal environmental conditions and subsists on a wide variety of

foods. Finally, it has planktonic dispersal and life stages that lend it to transport by humans. The ability of the juveniles to attach themselves to firm substrates with byssus threads might be especially important for unintentional introductions to new habitats. Genetic studies could help to overcome speculations (1) about the exact geographical range of *M. arenaria* by clearly separating it from *M. japonica* and *M. truncata* and (2) about the assumed invasion pathways in geological and historical time.

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