Introduction, spread and establishment of the invasive clam *Corbicula* spp. in Switzerland

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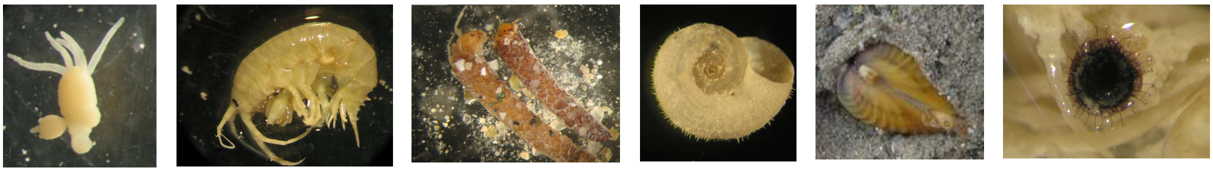

From left to right:
Hydra sp., *Dikerogammerus villosus*, *Athripsodes cinereus*, *Gyraulus albus*, *Corbicula fluminea*, statoblast of *Cristatella mucedo.* All animals were found in Lake Neuchâtel (photos: Stephanie Schmidlin and Pascal Stucki).

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Summary

Invasive species are of great concern in conservation biology, in economy and as well as in human health. River and lakes are vulnerable ecosystems and are prone to human-caused introductions of non-indigenous species. Research on the ecology of invasive species, their impact on native communities and the introduction pathways is needed to manage these invasive species and to prevent further introductions.

The present thesis concentrates on aquatic invasive invertebrate species and documents the spread of the Asian clam *Corbicula* spp. into Switzerland. In particular, we focused on *Corbicula fluminea* and examined its ecological preference, population structure and dispersal in the river Rhine. Furthermore, we analysed the clam's and other non-indigenous molluscs' possible impact on the native biodiversity in a sandy flat in Lake Neuchâtel.

A literature survey about the influence of invasive non-indigenous species on the biodiversity in the river Rhine documented great changes in river morphology, water quality and species composition during the last century. River engineering, pollution and the opening of canals connecting formerly separated river systems, allowed the invasion of many new species. Some of them reached extraordinary densities and hampered the development of native taxa. Many typically riverine species were replaced by large numbers of euryoecious and non-indigenous species. Competition for food and space, the hosting of parasites and intraguild predation were the main biological mechanisms underlying the alteration of the river community. Most studies on invasive species showed negative correlations between introduced invasive species and native biodiversity but experimental evidence is so far lacking.

The Asian clam *C. fluminea* has been introduced in the Lower Rhine with ballast water of cargo ships in the second half of the 1980ties and was first recorded in Basel, Switzerland, in 1995. There, the clam established a well structured population. It occurred initially in the internationally navigable section of the river Rhine and in the Canal de Huningue, which obtains water containing clam larvae from the river Rhine. Our field survey showed that the clam preferred slowly flowing, shallow water sites with fine-grained sediment, mainly sand. A substratum-choice experiment in the river Rhine confirmed the empirical evidence.

In spring 2011, there is still no evidence that the clam has colonized any tributaries of the Rhine in the region of Basel. However, in 2003, *C. fluminea* passed a weir and was found 22 km upstream of Basel where cargo shipping is absent. In the same year, records were made in Lake Constance and in Lake Neuchâtel and subsequently in other Swiss lowland lakes.

Today, their interconnecting rivers have not yet been colonized apart from some river sections near lake outlets and the river Aare between Aarau and its confluence with the river Rhine.

We present evidence for separate introductions of an identical haplotype of *C. fluminea* into five lakes in Switzerland based on mitochondrial DNA-sequences of the COI in specimens sampled. This indicates passive dispersal of the clam by human activities and/or waterfowl. All but one of the 72 genetically analysed individuals were assigned to a single haplotype of *C. fluminea*. A second haplotype belonging to the sister species *Corbicula fluminalis* was found only in the river Rhine near Basel. Recent records of specimens which were not genetically analysed all showed the shell morphology of *C. fluminea*, confirming the dominance of this clam in Swiss rivers and lakes. Passive dispersal by waterfowl, recreational boating and other human activities may facilitate the further spread of *C. fluminea* in Switzerland. However, the clam might be less successful in colonizing rivers with rapid current, which might be important refuges for native species.

We investigated a sandy flat in Lake Neuchâtel using SCUBA diving to assess the abundance of macroinvertebrate species, and to analyse the impact of non-indigenous mollusc species (*C. fluminea*, *Dreissena polymorpha*, *Potamopyrgus antipodarum* and *Lithoglyphus naticoides*) on the native macroinvertebrate community. The non-indigenous molluscs dominated the sand flat in numbers and influenced the composition and diversity of native macroinvertebrates, mostly by transforming the sandy substratum into a partly hard substratum habitat. Differences observed in community composition between shallow (< 3.5 m) and deep sites (≥ 5 m) resulted to a certain extent from the reduced abundance of *D. polymorpha* at shallow sites most probably due to depth-selective feeding of ducks. A shell decay study showed that the shells of *C. fluminea* and *D. polymorpha* persist for a longer period in the sediment than those of native molluscs. Therefore, shells of these non-indigenous molluscs have a long-lasting impact through modification of sandy habitat. Several native taxa benefit from such ecosystem engineering, but for other taxa with more specific habitat requirements it might be harmful.

In Lake Neuchâtel, high densities of *C. fluminea* negatively influenced the abundance of sand preferring native taxa. Negative impacts of *C. fluminea* in industrial facilities such as clogging of water pipes along the river Rhine are also known. Consequently, we recommend classifying *C. fluminea* as an invasive species in Switzerland and further monitoring and studying this clam.

General Introduction

After the loss of habitats, invasive species are recognised as the major threat for global biodiversity (Meffe and Carroll 1997). Particularly in freshwater habitats the load of invasive species is very high and among the leading threats to freshwater ecosystems and biodiversity (Sala 2000). At the same time only about a quarter of studies on biological invasion are dedicated to inland waters and most of them are situated in North America (Gherardi 2007). Scientific studies aim to understand invasion processes and may lead in the best case to the prevention of further introductions or to a sustainable management of the introduced invasive species. Complete eradication from a new site as in the case of the seaweed *Caulerpa taxifolia* in California was hardly ever possible in Europe (Anderson 2005, Genovesi 2005). Genovesi (2005) showed that in European inland waters only local eradication success was achieved from semiaquatic species (e. g. the nutria or *Myocastor coypus* in Britain; Baker 2006). However, so far no complete eradications of alien invertebrates and marine organisms have been recorded. In Genovesi's opinion, the lack of eradication attempts in Europe is "*probably due to the limited awareness of the public and the decision makers, the inadequacy of the legal framework, and the scarcity of resources*" (Genovesi 2005).

Based on the Convention on Biological Diversity (Article 8. In-situ Conservation, letter h; www.cbd.int) all countries who signed the convention should "*prevent the introduction of, control or eradicate those alien species which threaten ecosystems, habitats or species*". To work out a strategy on how to deal with invasive species, the commission of the European communities (2008) summarized the nature of the problem as follows:

"…"*Alien species" are species which are introduced outside their natural past or present distribution area and succeed in surviving and subsequently reproducing. "Invasive Alien Species" (IAS) are alien species whose introduction and/or spread threaten biological diversity. The Millennium Ecosystem Assessment revealed that IAS impact on all ecosystems. The problem of biological invasions is growing rapidly as a result of increased trade activities. Invasive species (IS) negatively affect biodiversity e.g. by competing with other organisms and changing habitat structure, being toxic, being a reservoir for parasites or a vector for pathogens, hybridising with related species or varieties, predating on native organisms, altering the local food web, e.g. invasive plants alter nutrient availability, disrupting pollination services, causing extinction of native species, being an ecosystem engineer by altering energy and nutrient flows, as well as physical factors in habitats and ecosystems. IS can cause congestion in waterways, damage to forestry, crops and buildings and damage in urban areas. The costs of preventing, controlling and/or eradicating IS and the environmental and economic damage are significant. The costs of control, although lower than the costs of continued damage by* *the invader, are often high. These costs could be avoided or minimised by decisions to prevent and stop introductions at an earlier stage*" (Commission of the European Communities, 2008).

This summary highlights the variety of severe impacts invasive species may have for the ecology and economy as a result of growing globalisation of trade markets. In Switzerland, the Federal Office for the Environment (FOEN 2008) treats invasive alien species within the Swiss Release Ordinance (SRO; German: Schweizerische Freilassungsverordung, FrSV). In Article 51 an environmental monitoring for invasive alien species and scientific investigations, whether a causal connection could exist between observed damage and the presence of the monitored organisms, are mandatory.

In the scientific literature the term "invasive species" is not consistently used. To overcome the confusion of the term, Colautti and MacIssac (2004) suggest focusing on an invasion framework which is process-based and includes operational terms such as "stages" with no proper meaning. If the term "invasive" is still required Colautti and MacIssac (2004) prefer to speak of individual populations instead of the entire species since a biological invasion is mostly a biogeographical phenomenon rather than a taxonomic one. In this dissertation the term "invasive" is used according to the commission of the European communities (2008) but references to single stages will also be made. Nentwig (2010) distinguished four main generalized process stages in biological invasions:

1) Introduction: Usually only a few individuals are introduced and they are not yet a threat to other organisms.

2) Establishment and adaptation: Population size is increasing and impact on native biodiversity is still low. This stage may last very short or take several decades, depending often on the life-history traits of an introduced species and habitat conditions at the new site.

3) Invasion: In an enlarging area the population size increases strongly. This leads to new dispersal events in so far not yet colonised sites. This is the stage of biological invasion. Pressure on native species increases and may lead to considerable impacts. Economical damage is likely.

4) Saturation: All suitable habitats in the new range are colonized and no further expansion is possible. Impact on native species is mostly serious, ecosystems may have changed and economical damage is costly.

Williamson's "Tens Rule" (Williamson 1996) suggests that 10% of introduced species into a new environment can establish and another 10% of those will spread (stage 2 and 3). But Jeschke and Strayer (2005) could show that for vertebrates and insects the probability of establishing and spreading lies around 50%, and for aquatic species it is even higher (e.g. fish:

55% establish and 60% spread). The major invasion vectors of aquatic non-indigenous species into Europe are shipping, aquaculture and stocking activities (Gollasch 2006). They underline three main qualities of the act of dispersal of non-indigenous species: The spread occurs with the help of men (1), over biogeographical barriers (2) and within relative short time periods (3). That means that neither the introduced taxa nor the native community had time for evolutionary adaptation to the new situation (Nentwig 2010).

Why is *Corbicula* spp. the focus of this work?

In Europe, *Corbicula* spp. was first recorded in France and Portugal in 1980 (Mouthon 1981), and in the Lower Rhine in the Netherlands in 1985 (Bij de Vaate and Greijdanus-Klaas 1990). In 1995, the clam was reported for the first time in the river Rhine near Basel in Switzerland (Rey et al. 2004). *Corbicula fluminea* and *Corbicula fluminalis,* well-known of having negative impact on indigenous species in other invaded parts of the world (Leff 1990, Strayer 1999), are perceived as potential threats to Swiss freshwater habitats and organisms. They are therefore under surveillance by the authorities and need monitoring and scientific research (Wittenberg 2005).

With this thesis I intend to broaden the knowledge about the invasion process of the genus *Corbicula* into Switzerland and to identify potential effects the clam might have on native biodiversity. My work may raise the awareness of invasive aquatic species and their ways of introduction and may serve to decision makers in the management of invasive aquatic species and conservation biology.

In the following part, I will present the main ecological features of the genus *Corbicula* as background information and then give details about the aims of the thesis.

The genus *Corbicula* (Corbiculidae familiy)

Occurrence

The genus *Corbicula* occurs naturally in Australia, Southeast Asia, India, Middle and Near East and as well as in Africa. In the Pleistocene, *Corbicula* was spread in Europe but shrunk to a rest population in the Kaukasus during the last glaciation (Illies 1978, Krolopp 1987, Meijer and Preece 2000). The global dispersal of *Corbicula* started in the early 20th century parallel to the Chinese emigration wave to North America. The first record was made in British Colombia and from then on, the clam’s spread over the world (Counts 1981). Thanks to the international trade, it reached far destinations in the ballast water of cargo ships and easily dispersed within European waterways (Gollasch 2006, Galil et al. 2007). Today, it is widespread in North and South America and in Europe (Lee et al. 2005; Europe: Renard et al. 2000, Pfenninger et al. 2002, Sousa et al. 2008).

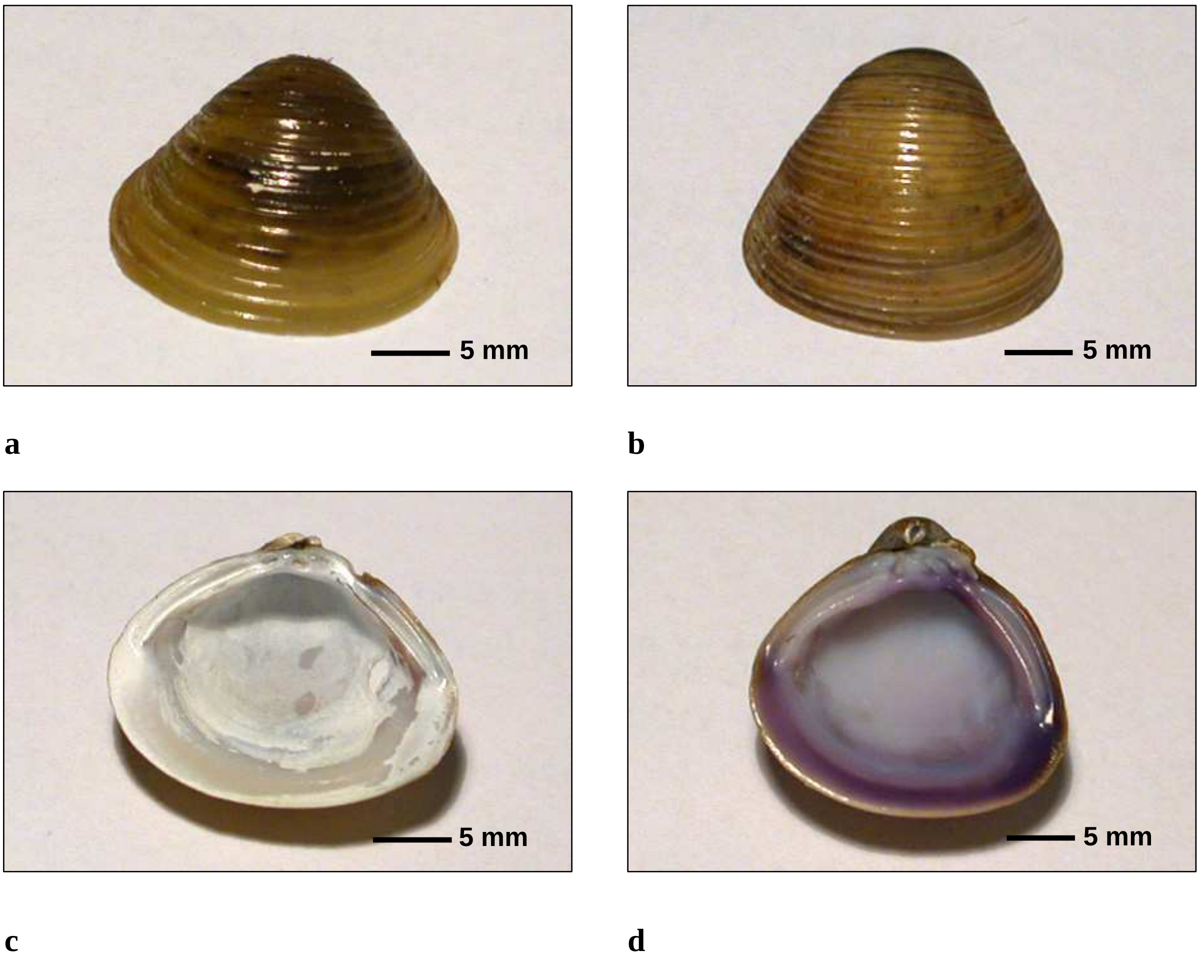

Figure 1 Presentation of the external view of *C. fluminea* (round form, 1a) and of *C. fluminalis* (saddle form, 1b) and the inner view of *C. fluminea* (1c) and of *C. fluminalis* (1d). Both specimens were collected in the river Rhine near Basel (photos: S. Schmidlin 2003).

Morphological taxonomy and evolutionary systematic

General uncertainties exist about the number of *Corbicula* species present in several Asiatic, American and European freshwater ecosystems, their taxonomy and their origin(s) (Renard et al. 2000, Siripattrawan et al. 2000, Pfenninger et al. 2002, Park and Kim 2003, Lee et al. 2005, Sousa 2007, Hedtke et al. 2008). Based on morphometric and genetic analyses two morphotypes were found in French and Dutch rivers (Renard et al. 2000). One belongs to the species *C. fluminea* (few wide, concentric ridges and a round shell form) and the other to *C. fluminalis* (many narrow, concentric ridges and a saddle-shaped shell form). A third species

Corbicula spec. was found but it was not possible to name the taxon. Pfenninger et al. (2002) confirmed the presence of mitochondrial haplotypes of *C. fluminea* and *Corbicula* spec. as defined by Renard et al. (2000) in the river Rhine, but they also highlighted the repeatedly observed mismatches in morphological and genetic species identification and therefore preferred referring to the *Corbicula* complex. Park and Kim (2003) examined the different *Corbicula* lineages within the native Asian range and classified *C. fluminalis* and *Corbicula* spec. sensu Renard et al. (2000) only as freshwater *Corbicula* without a specific nomenclature.

In general, in my thesis I will use the morphological terms *C. fluminea* for the round form and *C. fluminalis* for the saddle-shaped form (Figures 1a−d).

Ecological and life-history traits

Corbicula usually lives in well-oxygenated lotic and lentic systems in sediments of different composition (Belanger et al. 1985). Compared with other freshwater bivalve species the clam seems to be less tolerant to environmental fluctuations such as elevated temperature, hypoxia, emersion, low pH and low calcium concentration (Byrne and McMahon 1994, McMahon 1999, Johnson and McMahon 1998, Sousa et al. 2008). The clam filter- and pedal-feeds and allocates most of the assimilated energy to growth and reproduction (McMahon 1999, Hakenkamp et al. 2001).

In many invaded areas, studies about life-history traits exist (North-America: Aldridge and McMahon 1978; South-America: Cataldo and Boltovskoy 1998; Europe: Meister 1997, Rajagopal et al. 2000) and they all agree with the words of Füreder and Pöckel (2007): *"The relatively short lifespan, early maturity, high fecundity, bivoltine juvenile release patterns, high growth rates, small juvenile size, and the capacity for downstream dispersal of* C. fluminea *make it highly invasive and adapted for life in unstable lotic habitats subject to unpredictable catastrophic environmental disturbances."*

In summary, the invasion success and subsequent dispersal of the clam relies more on its high fecundity and short life-span (r-strategy) and its association with human activities than on its physiological tolerance (McMahon 2002, Sousa et al. 2008).

Aims of the thesis

The aims of my thesis were to follow up the spread of the invasive clam genus *Corbicula* into Switzerland, to examine its ecological preferences and its potential effects on native freshwater communities. To assess possible introduction pathways into Switzerland we combined first observations records with molecular data.

In **Chapter 1**, we examined the impact of invasive non-native species on the biodiversity in the river Rhine on behalf of a literature survey. We reviewed major changes in the biota of the river Rhine, focusing on mechanisms underlying changes in species abundance following the invasion of non-native species. Our emphasis was on benthic macroinvertebrates, such as *Corbicula*, but interactions with other animals were also considered. Additionally, we identified important gaps in knowledge and suggested areas for further research.

In **Chapter 2**, we examined the distribution of *Corbicula* along the bank of the river Rhine, in three tributaries and in the Canal de Huningue in the region of Basel (Switzerland, Germany and France) in 2003. Additionally, we carried out an experiment on substratum preferences and measured several abiotic variables and analysed them in relation to the clam's occurrence and abundance. Further, we followed up the population growth of *Corbicula* in the river Altrhein to assess seasonal changes in the size structure of this river population.

In **Chapter 3**, we expanded the area of the *Corbicula* survey from **Chapter 1** to whole Switzerland and analysed mitochondrial DNA-sequences of *Corbicula* clams sampled at different sites in Europe. Additionally, we discussed possible dispersal vectors and introduction pathways into the alpine country.

In **Chapter 4**, using SCUBA-diving we investigated the native macroinvertebrate community in relation to the densities of four alien mollusc species (*C. fluminea*, *Dreissena polymorpha*, *Potamopyrgus antipodarum* and *Lithoglyphus naticoides*) in a sandy flat of Lake Neuchâtel, Switzerland. A controlled shell decay study was performed to give insight in the persistence of native and alien mollusc shells and the possible implications for other macroinvertebrates.

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Chapter 1: Effects of Invasive Non-native Species on the Native Biodiversity in the River Rhine

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Introduction

Besides habitat degradation, the impacts of non-native invasive species are a major cause of extinction of native species (Groombridge 1992, Sala et al. 2000, Cox 2004). Invading species may interact with the native biota in a variety of ways, for example, by competition, predation, parasitism, disease and hybridization. Some non-native species may enter an ecosystem and remain at low densities for many years or disappear gradually whereas others might have a profound impact on the existing community by changing species abundance, food webs and energy fluxes. Linking invasion patterns with interspecific processes is often difficult but such information is crucial to predict the impacts of non-native species on the biodiversity of newly invaded locations (Moyle and Light 1996, Williamson 1996, 1999).

The Convention on Biodiversity exhorts the contracting parties to "*prevent the introduction, control or eradicate those alien species which threaten ecosystems, habitats or species*" (Glowka et al. 1994). To implement these directives, detailed knowledge on native biodiversity, and on potential interactions between invading non-native species and native species is required. Compared to the attention paid to extinctions in terrestrial habitats, much less focus has been given to species loss in freshwater ecosystems, and this despite several studies demonstrating a growing number of extinctions in freshwater animal species (fishes, molluscs, crayfishes; e.g. Kaufman 1992, Strayer 1999, Ricciardi and Rasmussen 1999).

This chapter examines the impact of invasive non-native species on the biodiversity in the river Rhine. The occurrence and spread of non-native species are relatively well documented in the Rhine (e.g. Tittizer et al. 2000, Geitler et al. 2002, Rey et al. 2004). Quantitative studies on changes in abundance of non-native species and on species composition of native communities complement these reports (e.g. Van den Brink et al. 1990,

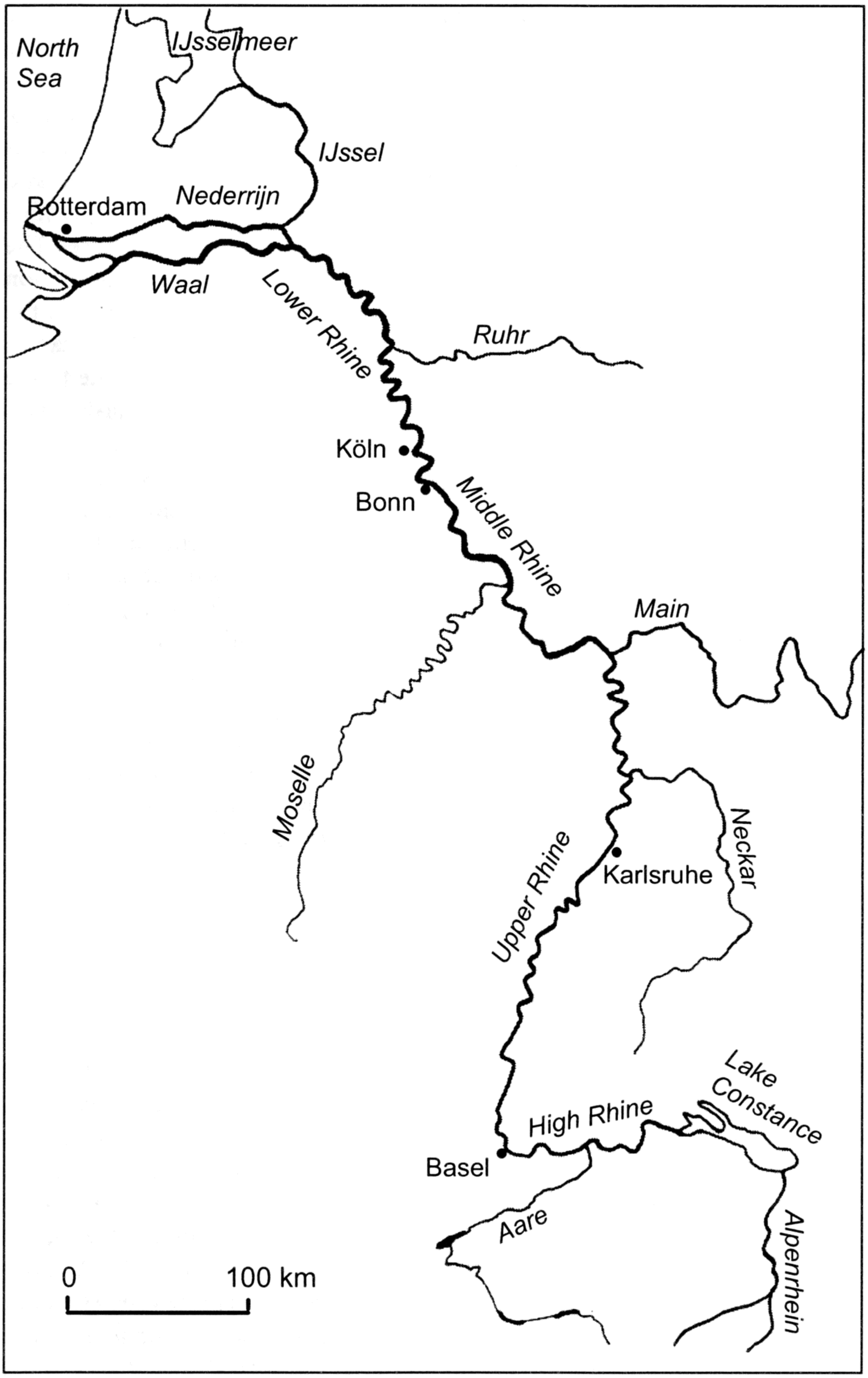

Figure 1.1 Map of the river Rhine, with most of the locations mentioned in the text.

mechanisms underlying changes in species abundance following the invasion of non-native species. Our emphasis is on benthic macroinvertebrates but interactions with other animals are also considered. Along the way, we identify important gaps in knowledge and suggest areas for further research.

The River Rhine

With a length of 1,320 km and a catchment area of 185,000 km^2, the river Rhine is one of the largest rivers in central Europe (Van Urk 1984, Friedrich and Müller 1984). It originates in the Eastern Swiss Alps, flows north to form the frontier with Liechtenstein and Austria (Alpenrhein), and empties into Lake Constance (Figure 1.1). The Rhine (High Rhine) then re-emerges and flows west, mainly on the border between Switzerland and Germany. In Basel, it turns to the north and forms the southern part of the border between France and Germany (Upper Rhine) in a wide valley, before entering Germany exclusively (Middle Rhine). Here, the Rhine encounters some of its main tributaries (the Neckar, the Main and then the Moselle). Between Bingen and Bonn, the Rhine flows through the Rhine gorge, a formation created by erosion (this gorge is a UNESCO World Heritage Site since 2002). After passing the Ruhr area, the Rhine (Lower Rhine) turns west into The Netherlands. After crossing the border, it splits into three main distributaries, the Waal, the IJssel and the Nederrijn/Lek, before discharging into the North Sea.

The flow regime can be characterized as rain-fed/snow-fed, the highest water levels usually being attained in March−May and the lowest in August−November. The mean annual river discharge of the Rhine is 1,032 m^3/s in Basel and 2,260 m^3/s (range 800−12,000 m^3/s) at the Dutch border. This results in the minimum and maximum water levels differing by up to 8 m in The Netherlands (Van Geest et al. 2005).

The deterioration of the Rhine started in the Middle Ages, with the deforestation of large areas on the floodplains (Nienhuis and Leuven 1998). By the early 18th century, almost all beech and oak forests had been replaced by grassland. The river morphology became increasingly degraded because of straightening, reduction of channel networks to a single channel, and disconnection from the floodplain. In the 19th century, major river regulations in the Upper and Lower Rhine modified the river bed. For example, in the so-called Tulla-correction carried out between 1817 and 1874 and also in subsequent channelisations, the Upper Rhine north of Basel was transformed from a river system up to 6 km wide, with numerous branches, slow-flowing meanders, islands, and sand and gravel flats, into a 130-m-wide, fast-flowing petrified canal (Grand Canal d'Alsace). During channelisation, flood control dams were built, stone groynes were constructed to strengthen the channel, and some parts of the river bank were reinforced by stones.

Since Roman times, the Rhine has been a navigable waterway, carrying travellers and goods deep inland. As the river became more important as transport route, it was channelled even more to increase its discharge and maintain its depth. In modern times, cargo shipping on the Rhine is possible from Rotterdam (North Sea) to Rheinfelden, 20 km upstream of Basel. The importance of international shipping increased further with the construction of river-connecting canals. The Rhine-Main-Danube Canal connects the Rhine via the Danube with the Black Sea which, in turn, is connected by canals and rivers to the Caspian Sea (see Galil et al. 2007). Another navigation route to the Black Sea and Caspian Sea is the German Mittelland-Elbe-Vistula-Pripyat-Bug-Dnieper canal system.

Parallel to the channelisation, the floodplain of the Rhine has been extensively modified to extend agricultural and industrial areas and settlements. Nowadays, the Rhine is a completely man-manipulated river, more intensively used than ever before (Tittizer and Krebs 1996). Besides its function as transportation route, it provides water for communities and industry, is used to generate hydroelectric power, provides cooling water and a means of effluent transport, and is increasingly a focus for recreation. Despite profound alterations of river characteristics, the river still has a large (albeit not unlimited) self-cleaning capacity, and natural and semi-natural banks and areas of the floodplain, with abandoned meanders, brooks, sand and gravel pits, and remnants of riparian forest still harbour an extraordinarily high diversity of plants and animals, and are therefore of high conservation value (e.g. LfU 2000, Baur et al. 2002).

Native Biodiversity and Invasion History

Faunal diversity decreased dramatically in the river Rhine between 1900 and 1970 (Kinzelbach 1972, Van den Brink et al. 1990, Streit 1992). For example, species richness of selected groups of macroinvertebrates in the Dutch section of the Rhine declined from 83 species in 1900 to 43 species in 1940 and to 41 species in 1981/1987 (Van den Brink et al. 1990, Den Hartog et al. 1992). Omitting the non-native species arriving in the 20th century, however, the total number of species for 1940 would be 40, and only 27 for 1981/1987. Schöll (2002) presented a list of 21 typical riverine macroinvertebrate species (seven mayflies, 10 stoneflies and four caddis flies) occurring in the German part of the Rhine in 1900 − none were found in the river between 1960 and 2000. Most probably, these specialized benthic species went extinct in the river Rhine. However, the actual causes of extinction are unknown.

In the Rhine near Basel, the number of stonefly species declined from 13 to four between 1910 and 1990, and those of mayflies from 19 to 13 (Küry 1994).

The decline of the freshwater fauna in the river Rhine is linked to extensive habitat deterioration caused by channelisation and flow regulation by weirs, stream fragmentation, organic pollution from land-use activities, toxic contaminants from municipal and industrial sources, and interactions with an increasing number of non-native species (Streit 1992, Baur and Ringeis 2002, Van der Velde et al. 2002, Nehring 2003). Since the industrial revolution and the construction of sewage systems, domestic and industrial pollution have led to a gradual deterioration in water quality, and this from the second half of the 19th century to the end of the 1960s. Water quality was very poor during the period 1950−1970, with low oxygen levels, serious eutrophication, high chemical and organic pollution loads, salination caused by French potassium mines and mining water from brown coal mines in Germany, and thermal pollution (Rhine river water temperature has risen by approximately 2 °C above its natural value, Admiraal et al. 1993).

Faunal diversity in the river Rhine was lowest in the late 1960s, when levels of toxicants were highest and oxygen levels extremely low (Kinzelbach 1972, Streit 1992). During the period 1970−1986, waste water treatment plants were constructed along the river, resulting in improvements of water quality including an increase in oxygen levels and a reduction of some heavy metals and organic pesticides. Also, faunal diversity began to recover (Admiraal et al. 1993). Driven partly by the toxic spill following the Sandoz accident (see below), ministers from riparian countries decided in 1986 to establish the Rhine Action Programme. One of its aims is the restoration of the river ecosystem.

Haas et al. (2002) described three successional phases in the development of benthic communities in the German section of the Rhine, following the extreme toxic and organic contamination which the river has known in earlier times.

1. From 1970 to 1986, the aquatic community was species-poor and still in an early recovery. Because of the remaining organic pollution, only sewage-resistant taxa such as the leech *Erpobdella octoculata*, the isopod *Asellus aquaticus*, the snail *Radix ovata*, sponges, chironomids and oligochaetes occurred. The non-native zebra mussel *Dreissena polymorpha* started to colonise hard substrates. However, the major Sandoz industrial accident near Basel in 1986, when runoff from water used in firefighting carried nearly 30 t of toxic chemicals (insecticides, fungicides and herbicides) into the Rhine, caused serious damage to the flora and fauna over hundreds of kilometres, resetting the recovery process. In 1987, benthic faunal densities were still close to zero (Den Hartog et al. 1992). Yet, *D. polymorpha* was able to

quickly recolonise the Rhine following the Sandoz spill because of the immigration of pelagic larvae from unaffected sites.

2. In 1987 and 1988, the non-native amphipod *Corophium curvispinum* (=*Chelicorophium curvispinum*), and the Asiatic clams *Corbicula fluminea* and *C. fluminalis* invaded the Rhine. Already in 1989, the population density of *C. curvispinum* in the Middle and Lower Rhine was so high that the hard substrate of the channel bottom had been essentially completely overgrown due to the species' engineering activity. The *D. polymorpha* population collapsed because adult shells were rapidly overgrown by *C. curvispinum*, and their muddy tubes inhibited the development of new *D. polymorpha* patches − the planktonic larvae can settle only on hard surfaces (Van der Velde et al. 1994, Tittizer and Krebs 1996, Haas et al. 2002).

3. A new phase started with the invasion of the amphipod *Dikerogammarus villosus* in 1995. In 2000, maximum densities of 3,000 individuals /m2 were recorded. Since 1996, the population densities of *C. curvispinum* have decreased whereas *D. polymorpha* has recovered and again reached high densities. Subsequent to the appearance of *D. villosus*, two other amphipods, *Gammarus tigrinus* and *Echinogammarus ischnus*, have declined in the Upper Rhine; *G. tigrinus* finally disappeared in 1999. In 1997 and 1998, three new non-native invertebrates reached the river Rhine, originating from the Danube and the Ponto-Caspic region: the isopod *Jaera istri*, the turbellarian worm *Dendrocoelum romanodanubiale* and the polychaete *Hypania invalida* (Haas et al. 2002).

There is an accelerating colonisation rate of non-native macroinvertebrate species in the Rhine (Figure 1.2). The shape of the cumulative colonisation curve shows that 55% of the total number of colonisations were recorded after 1970. Thus, more than half of all colonisations in the 175-year record have been reported these last 35 years. The average rate of colonisation has increased from 0.15 new species established per year in the period 1831−1970 to 0.74 new species per year for the period 1971−2005. Considering exclusively the period 1991−2005, the current rate of colonisation averages 1.27 new species per year.

Similarly to macroinvertebrates, fish species composition in the river Rhine has altered in the past century. There is ample evidence that the river engineering works have had deleterious effects on the species number and abundance of fish (Lelek and Köhler 1989). Associated river modifications have led to the disappearance of specific spawning grounds, feeding biotopes and nursery areas, and to the obstruction of migration routes. The construction of fish passes at almost every weir along the main stream section seems to have been insufficient to prevent the decline of the migrating fish populations. Low oxygen

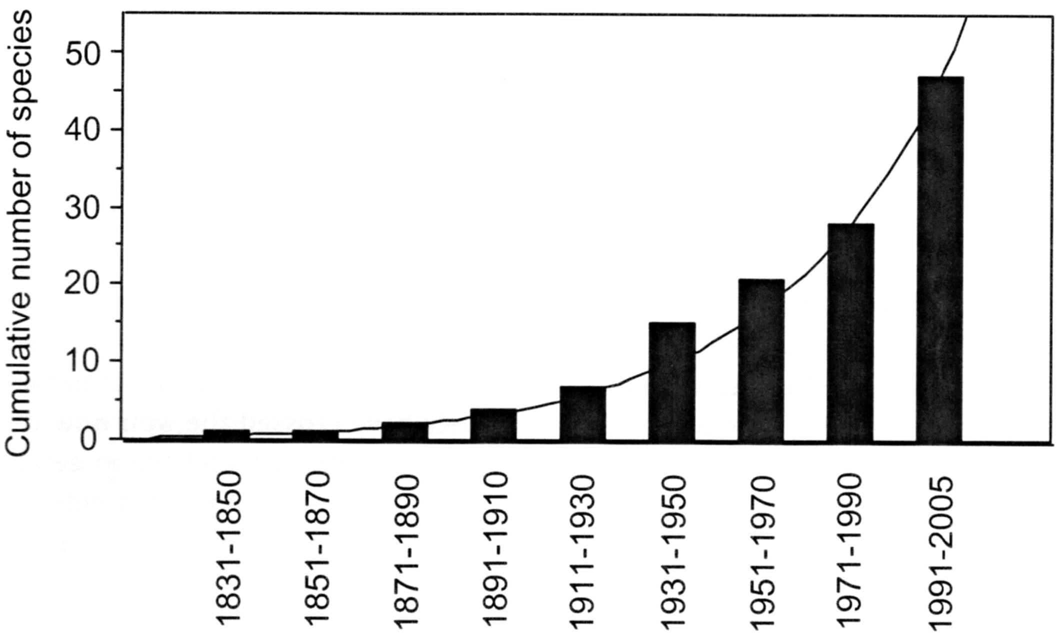

Figure 1.2 Increasing number of non-native macroinvertebrate species colonising the river Rhine. Cumulative data are shown for periods of 20 years (note: the *last bar* includes data for only 15 years). The exponential model was fitted by least-squares regression ($y=5.5936 \times 10^{-22} e^{0.0265t}$, $n=9$, $R^2=0.98$, t indicates the year). Data were obtained from Tittizer et al. (2000), Geitler et al. (2002) and Rey et al. (2004).

concentration and the massive discharge of toxic materials contributed substantially to this decline. Since the water quality of the Rhine began to improve in the 1970s, however, the fish community has been recovering (Cazemier 1988, Lelek and Köhler 1989).

Lelek (1996) presented a list of 27 non-native fish species for the German part of the Rhine. Eighteen of the 27 species (67%) were intentionally introduced by fishermen, another seven species (26%) having been inadvertently introduced by the aquarium trade. Interestingly, among the phytoplankton, an ecologically important group, no non-native species have yet been observed in the Rhine (Nehring 2005).

About one of two non-native aquatic species entering German rivers could spread over large areas, and about one of five non-native species have become invasive (Nehring 2003). In the Rhine delta in The Netherlands, the proportion of non-native species in the biodiversity of river channels and floodplain lakes ranges from 7−10% among macrophytes to 5−12% among macroinvertebrates and 17−19% among fish (Van den Brink et al. 1996). In the Middle and Upper Rhine, non-native species represent 10−15% of total species richness (Haas et al. 2002). Non-native species dominate in terms of total abundance and biomass, however, the values exceeding 80% (Tittizer et al. 2000, Haas et al. 2002).

Thus, species composition in the river Rhine has changed remarkably in the past four decades. Replacing characteristic riverine species, large numbers of euryoecious and non-native species, in particular macroinvertebrates and fish, have invaded this river system (e.g. Van den Brink et al. 1988, 1990). Some of the species entered the river via ports and estuaries, and then moved upstream whereas others moved downstream after entering via canals. Several of these species have penetrated into the larger, still-water expanses but others seem to be restricted to flowing water (Van der Velde et al. 2002). Cargo shipping appears to influence the velocity of spread in invasive species. For example, the clam *C. fluminea* spread approximately 150 km per year in the navigable part of the Rhine but only 2.4 km per year upstream of Basel, where cargo shipping is largely reduced (Schmidlin and Baur 2007). *Corbicula fluminea* may also be displaced by waterfowl, because juvenile clams use their mucous secretions to stick to ducks' feet.

Interestingly, the number of non-native species decreases significantly upstream of Rheinfelden where cargo shipping ends (Rey et al. 2004). However, the weir in Rheinfelden is not an absolute barrier for the spread of invading species. In fact, several non-native species have crossed the weir and are now spreading upstream (e.g. *D. polymorpha*, *C. fluminea*, and the annelids *Branchiura sowerbyi* and *Caspiobdella fadejewi*), some having even entered the tributary Aare (e.g. the gastropod *Potamopyrgus antipodarum* and the flatworm *Dugesia tigrina*; Rey et al. 2004).

Species Interactions and Mechanisms of Replacement

Amphipods

The amphipod *Corophium curvispinum*, originating from the Ponto-Caspic region, was first observed in the Middle and Lower Rhine in 1987 (Schöll 1990). A few years later, *C. curvispinum* was found to be by far the most numerous macroinvertebrate species in the Lower Rhine (Van den Brink et al. 1991). Its density increased up to 200,000 specimens /m^2 on groynes (Van den Brink et al. 1993). It has been claimed that *C. curvispinum* had filled an 'empty niche' because it was the first tubiculous amphipod to colonise the Rhine (Den Hartog et al. 1992). The animals produced extensive mats of dense silty tubes which covered all available hard surface. As a consequence, other epilithic invertebrates were negatively affected by this muddy layer. Significant declines in population densities were recorded for the amphipod *Gammarus tigrinus*, the zebra mussel *Dreissena polymorpha*, the gastropod *Potamopyrgus antipodarum*, the caddis fly *Hydropsyche contubernalis*, and several species of

Chironomidae (Van den Brink et al. 1993). The former three are non-native species whereas *H. contubernalis* is native. It has been suggested that these changes in abundance were at least partly the result of competition for food − *C. curvispinum, D. polymorpha* and *H. contubernalis* are all filter-feeders (Rajagopal et al. 1999). In fact, the exponential increase in the density of *C. curvispinum* during 1989−1991 coincided with a decrease in the concentrations of total organic carbon and total suspended matter in the Lower Rhine, which may be related to an increase in filtration capacity in the river. Stable isotope analysis showed very similar values for carbon and nitrogen sources in the stone-dwelling *C. curvispinum*, *D. polymorpha* and the sand-dwelling Asiatic clams *Corbicula fluminea* and *C. fluminalis*, indicating a common source of phytoplankton and particulate organic matter for these filter-feeding animals (Marguillier et al. 1998).

Besides competition for food, there might also have been competition for space among benthic macroinvertebrates. For example, specimens of *D. polymorpha* were observed to be completely overgrown by the tubes of *C. curvispinum*. Moreover, in building its muddy tubes, the amphipod modifies the substrate, thereby preventing the settlement of larvae of *D. polymorpha*. However, relatively little is known about the fundamental features of tube building activity and filtration rate in *C. curvispinum*.

The impact of the population explosion of *C. curvispinum* on the density of other macroinvertebrates has also resulted in a shift in the diet of the European eel *Anguilla anguilla*. In 1989, prior to the population explosion of *C. curvispinum*, *Gammarus tigrinus* and *Dreissena polymorpha* dominated the diet of the eel (Van der Velde et al. 1998). In 1994, however, *C. curvispinum* occurred in 80% of the eels sampled whereas *G. tigrinus* decreased in percentage occurrence from 32 to 4%. Similarly, *D. polymorpha* was eaten to a far lesser extent in 1994 than in 1989 (Van der Velde et al. 1998). The perch *Perca fluviatilis* showed a similar shift in diet (Kelleher et al. 1998).

The amphipods *C. curvispinum* and *Dikerogammarus villosus* and the isopod *Jaera istri* act as intermediate hosts for a variety of parasites of the eel. In the German part of the Rhine, nine metazoan species were found to infest eels (Sures et al. 1999). Among-site differences in eel parasite diversity was related to the presence and abundance of invading crustacean species (Sures and Streit 2001).

Since 1984, there has also been a significant increase in the distribution and abundance of the amphipod *Gammarus tigrinus*, which originated from North America. In many sections of the Rhine, *G. tigrinus* has displaced *Gammarus duebeni*, a native and originally widespread species in Western Europe (Tittizer et al. 2000). In the late 1990s, however, the abundance of

G. tigrinus declined sharply, coincidental with the invasion of the amphipod *Dikerogammarus villosus.* This species is native to the Ponto-Caspian region and has invaded Western Europe via the Main-Danube canal, appearing in the river Rhine at the German-Dutch border in 1994−1995 (Tittizer et al. 2000). *D. villosus* has wide environmental tolerances in terms of temperature and salinity, and thus is able to colonise various microhabitats.

Stable isotope analyses have shown that *D. villosus* is a predatory species whereas *G. duebeni* is a detrivorous/herbivorous amphipod. It was hypothesized that the rapid expansion of *D. villosus*, and its devastating impact on *G. duebeni* and related species may involve intraguild predation, rather than interspecific competition. In laboratory experiments, survival of female *G. duebeni* was lower when male *D. villosus* − rather than male *G. duebeni* − were present (Dick and Platvoet 2000). Similarly, *D. villosus* preyed upon *G. tigrinus*. *D. villosus* killed and consumed recently moulted and, less frequently, intermoult victims. Thus, the predatory impact of *D. villosus* is not restricted to the short (approximately 12 h) period of post-moult vulnerability, facilitating rapid eliminations of all stages of reproducing females (Dick and Platvoet 2000). No male *G. duebeni* was killed during the experiment, indicating that the larger males are more able to fend off any predatory attack, although this may not be the case at moult (Dick 1996). Compared to other freshwater amphipods, the large size of *D. villosus* might partly explain its successful predatory behaviour.

Gut content analyses showed that *D. villosus* preyed also on *C. curvispinum* in the wild, thereby interfering in the interspecific competition for space between the two filter-feeders *C. curvispinum* and *D. polymorpha*. In amphipods and many other arthropods, intraguild predation has been increasingly recognized as an important mechanism in structuring communities (e.g. Polis et al. 1989). In many cases, intraguild predation may override interspecific competition. In the present example, intraguild predation also appears to be the mechanism for the exclusion of both non-native and native species.

Molluscs

The zebra mussel *Dreissena polymorpha*, originating from the Caspian and Black Sea region, was first recorded in the Lower Rhine near Rotterdam in 1826. In the following decades, it expanded upstream and reached large densities (Kinzelbach 1972). However, water pollution in the mid-20th century, and subsequent competitive interactions with *C. curvispinum* strongly reduced *D. polymorpha* populations in the Rhine. Continuous improvement in water quality these past decades and reduced *C. curvispinum* densities have allowed the *D.*

polymorpha populations to recover; nowadays, they have again attained densities of up to 40,000 individuals /m^2.

The zebra mussel attaches to solid surfaces using adhesive byssal fibres, and possesses a planktonic larval (veliger) stage which can remain in the water column for several weeks before settlement. Native unionid mussels have a complex life cycle in which the larvae are obligate parasites of fish, with survivorship dependent on the availability of appropriate fish hosts and accessibility to favourable habitats. Adult unionid mussels live partially buried in the sediments of lakes and rivers, with their posterior shell exposed to the water column, providing a suitable surface for colonisation by *D. polymorpha*. Infestation by *D. polymorpha* is considered to impair the metabolic activity (feeding, respiration, excretion) and locomotion of unionid mussels, thereby depleting their energy reserves and effectively starving them to death (Haag et al. 1993). Moreover, data from North America demonstrate that *D. polymorpha* can also harm other suspension-feeding bivalves by depleting food resources (phytoplankton) through massive filtration (Caraco et al. 1997).

Dreissena polymorpha has virtually eliminated the native unionid fauna in many parts of the lower Great Lakes in North America (Ricciardi et al. 1998, Strayer 1999). In the Rhine, the decline of the highly specialized and endangered unionid mussels and other filter-feeding macroinvertebrates could also partly be due to competition with *D. polymorpha*. However, *D. polymorpha* is not harmful to all riverine species. In North America, the clam provides other benthic invertebrates with nourishment (in the form of faecal deposits) and shelter (interstitial spaces between clumped mussel shells), resulting in a local enhancement of abundance and diversity for these other species (Ricciardi 2005). Non-native deposit feeders may increase in abundance whereas native filter-feeders are out-competed by *D. polymorpha*. Among the invertebrates responding positively to zebra mussel colonisation are non-native oligochaetes, leeches, amphipods, gastropods, larval chironomids and aquatic weeds (Ricciardi et al. 1997, Karatayev et al. 2002). Thus, invading species may also have synergistic impacts which facilitate the establishment of other invaders.

The clams *Corbicula fluminea* and *C. fluminalis*, originating from Southeast Asia, were first recorded in the Lower Rhine in The Netherlands in 1985 (Bij de Vaate and Greijdanus-Klaas 1990). Six years later, the clams were found near Karlsruhe in the Upper Rhine and, in 1995, *C. fluminea* was reported near Basel in Switzerland (Rey et al. 2004). *C. fluminea* is restricted to the gravely-sandy river bottom because sticking structures are lacking. The clam reached densities of 1,800 individuals /m^2 in the Rhine (Haas et al. 2002). Den Hartog et al. (1992) suspected that the spill of toxic waste from the Sandoz accident in

1986, affecting the Rhine over hundreds of kilometres, contributed to the clams' success because most macroinvertebrates were killed and, as a consequence, their niches were unoccupied.

Several mechanisms by which *Corbicula* may affect native bivalves have been proposed (Strayer 1999). Dense populations of *Corbicula* may deplete concentrations of phytoplankton and other edible suspended particles, thereby 'starving out' native bivalves. Modest to dramatic declines in phytoplankton or seston have been recorded in habitats with high *Corbicula* density in North America (Leff et al. 1990, Phelps 1994). Dense populations of *Corbicula* may ingest large numbers of unionid sperm, glochidia and newly metamorphosed juveniles (Strayer 1999). Because *Corbicula* pedal feeds on edible particles in the sediments, it may deplete also this food resource, affecting some sphaeriids and juvenile unionids which use benthic organic matter as food. *Corbicula* actively disturbs the sediments, so dense populations may reduce habitat quality and space for native bivalves.

Several studies show that the impact of *C. fluminea* on native benthic species depends on both site and community characteristics (Leff et al. 1990, Strayer 1999). The clam severely affected native mollusc assemblages in some North American rivers but can coexist with other bivalves at other sites. Similar information on the impact of *Corbicula* on native macroinvertebrates in the river Rhine is not yet available.

Why are There so many Non-Native Species in the Rhine?

The number of non-native animal species colonising the river Rhine is still increasing (Figure 1.2). Furthermore, non-native plant species constitute a significant proportion of the vegetation of the river bank and floodplain (Schwabe and Kratochwil 1991). A variety of mutually non-exclusive hypotheses have been suggested to explain the success of invaders in the river Rhine: (1) vacant niches, (2) disturbances preventing strong interspecific competition, (3) the creation of new niches by invasive species, (4) ecosystem instability (invasional meltdown), (5) groups of co-adapted invaders, and (6) enemy-free space.

It has been argued that human alterations of habitat make a community vulnerable to invasions and that extreme natural disturbances facilitate the establishment of non-native species (Mack et al. 2000). Community vulnerability to invasions has been ascribed to a combination of several factors, such as the presence of vacant niches, habitat modification, and disturbance before and after invasion. Recent findings indicate that species-rich communities are less vulnerable to invasions (at least, in terrestrial habitats; Cox 2004).

Moreover, invasibility is known to increase if a community lacks certain species present under normal conditions (Kühn and Klotz 2007).

The invasional meltdown model (Hufbauer and Torchin 2007) predicts that ecosystems subjected to a chronically high frequency of species introduction will become progressively unstable and easier to invade, as each introduced species has the potential to facilitate subsequent invaders (Simberloff and Von Holle 1999). Invasional meltdown may occur through one of two processes: frequent disturbance through species introductions progressively lowers community resistance to invasion, and increased introductions lead to a higher frequency of potential facilitations and synergies between invaders (Ricciardi 2005). Highly active invasion corridors (in the present case, canals) may introduce numerous species from one and the same region (e.g. the Ponto-Caspic region), and thus may reunite groups of co-adapted species, either in simultaneous introductions (e.g. a host arriving with its parasites) or in successive introductions, thereby assembling contiguous links of a non-native food web.

If co-adaptation reduces the intensity of predation and parasitism, then positive interactions probably dominate invasion 'groups', and successive introductions of co-adapted species might result in a higher success of invaders than would introductions of unacquainted species (Ricciardi 2005). This could be an alternative to the enemy release hypothesis, which relates the success of an invader to the absence of its natural predators and parasites in the invaded region. Each of the examples presented above could be explained by at least one of these six hypotheses. However, experimental tests of these hypotheses are lacking for the Rhine.

Conclusions

The river Rhine is a good example for how a combination of different factors structure benthic communities. River modification deteriorated certain habitats but also created new habitats. Prolonged pollution changed the original communities and caused the loss of certain species, creating open niches for pollution-tolerant invaders. Major disturbances, such as the Sandoz accident in 1986, subsequently enabled the invasion of many new species which reached unprecedented densities. The Rhine-Main-Danube Canal, opened in 1992−1993, provided additional opportunities for the immigration of non-native species from the Ponto-Caspian region, some of them being co-adapted. After reduction of the pollution in the Rhine, recolonisation seemed to favour invaders, rather than native species. These invaders suppressed the development of populations of native species. At the present day, the number of invaders is still increasing.

For the development of appropriate conservation strategies for the river Rhine, detailed knowledge of the ecological consequences of invasive non-native species for the native biota is required. The present review shows that, in most cases, negative impacts of invasive species on native species have been deduced from correlative evidence. Evidently, there is an urgent need for experimental studies on interactions between invasive and native species. Numerous rare native species in the Rhine are threatened with extinction by the combined impacts of environmental degradation and species invasions (e.g. by *D. polymorpha*). From a conservation perspective, the habitat requirements, population dynamics and persistence of rare native species deserve increased attention. Restoration to pristine conditions is not feasible in the Rhine. However, several promising ecological restoration projects are of vital importance to preserve those facets of the originally unique biodiversity of the river Rhine and its floodplain still present today.

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Chapter 2: Distribution and substrate preferences of the invasive clam *Corbicula fluminea* in the river Rhine in the region of Basel (Switzerland, Germany, France)

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Abstract

The Asiatic clam *Corbicula fluminea* invaded the river Rhine in the Netherlands and Germany in the 1990s. It was first recorded in Switzerland (Basel) in 1995. We examined the distribution of the clam at 76 sites along the bank of the river Rhine, in three tributaries (Wiese, Birs, Ergolz) and in the Canal de Huningue in the region of Basel (Switzerland, Germany and France) in 2003. *C. fluminea* was found in the river Rhine and in the Canal de Huningue, which obtains water from the river Rhine. *C. fluminea* was recorded 22 km upstream of Basel, but not any further. This indicates a mean upstream spread of 2.4 km per year. It had not yet colonized any of the tributaries examined. The clam was most abundant on fine-grained substrates (sand) with slowly flowing, shallow water. This finding was confirmed by a substrate choice experiment in the river Rhine. Our results show that the spread of *C. fluminea* in the river Rhine does not stop where cargo shipping ends. Passive dispersal by waterfowl and recreational boating may facilitate further upstream spread. *C. fluminea* might be less successful in colonizing rivers with rapid current such as the mentioned tributaries. These are assumed to serve as refuges for native molluscs.

Key words: Asiatic clam, invasive species, range expansion, substrate choice

Introduction

The spread of invasive species is generally recognized as one of the major threats to biodiversity (Meffe and Carroll 1997). The effects of non-indigenous plants and animals on natural communities in rivers and lakes are well documented (Josefsson 1999, Westman and Savolainen 2001, Dönni and Freyhof 2002). For example, introduced mollusc species may reduce or even eliminate native mollusc fauna by competition (Byers 2000, Strzelec 2000, Cowie 2002, Maronas et al. 2003). In other cases, however, introduced molluscs coexist with native mollusc species (Pointier and David 2004).

The influence of the bivalve *Corbicula fluminea* (O. F. Müller, 1774) on indigenous species is inconsistent. It can coexist with other bivalves at some sites (Savannah River, South Carolina, Leff et al. 1990; Ohio River, Ohio, Miller and Payne 1998), but can also severely affect native mollusc assemblages at other places (*C. fluminea manilensis* Philippi, 1844, Altamaha River, Georgia, Gardner et al. 1976; sedimentation basin at a nuclear power plant, South Carolina, Boozer and Mirkes 1979; St. Johns River, Florida, Belanger et al. 1990).

C. fluminea, originating from Southeast Asia, began to expand in the 20th century. It is now widespread in rivers of North and South America as well as in Europe. In the river Rhine, *C. fluminea* was first recorded in the Netherlands in 1985 (Glöer and Meier-Brook 1998). Since the clam was found in the Lower Rhine, it has spread rapidly upstream most probably with cargo ships. Six years later, the species was found near Karlsruhe (Germany), 675 km upstream of Rotterdam, and in 1995 *C. fluminea* was first reported in Switzerland near Basel, 865 km from Rotterdam (Rey and Ortlepp 2002). Den Hartog et al. (1992) suspected that a spill of toxic waste (Sandoz accident) near Basel in 1986, affecting the whole river over hundreds of kilometres, contributed to the clams' success because most of the invertebrates were killed and, as a consequence, their niches were unoccupied. However, independent of this accident, molluscan diversity of the river Rhine declined strongly in the past 150 years because of huge river corrections, industrial pollution, organic sewage and other invading species (Kinzelbach 1972). Compared to the North American diversity of molluscs with 300 species of native unionid bivalves, the river Rhine appears to be species-poor with 22 bivalve and 33 gastropod species (including newly introduced species; IKRS 2002, Panama City Fish and Wildlife Service 2004).

In Europe, two *Corbicula* species are distinguished (*Corbicula fluminea* and *Corbicula fluminalis*, O. F. Müller, 1774). To date, it is yet unclear whether more *Corbicula* species occur in Europe. A recent morphometric analysis showed that two distinguishable morphotypes with few intermediates coexist in the river Rhine (Pfenninger et al. 2002). DNA-analysis resulted in three highly distinctive genotypes without intermediates. Interestingly, the morphological traits seem to be unreliable, since both morphotypes showed all genotypes. For that reason, Pfenninger et al. (2002) suggested to refer to the *Corbicula*-complex. In our study, 98.7% of the clams belonged to the morphotype of *C. fluminea*. It is therefore likely that we are dealing with only one species of *Corbicula*.

It was hypothesized that the spread of *C. fluminea* would stop in the river Rhine where cargo shipping ends (i.e. in Rheinfelden, 20 km upstream of Basel). We tested this hypothesis by examining the current distribution of *C. fluminea* in the river Rhine and its tributaries in the region of Basel. We also assessed seasonal changes in the size structure of a *C. fluminea* population in the Rhine. To test whether the substrate preference of *C. fluminea* observed in the river Rhine results from active choice, we conducted a controlled choice experiment in which three different types of substrates were offered to clams. Knowledge on the rate of spread and the substrate preference of invasive clams could be helpful in managing river structures to suppress spreading of the clam.

Material and Methods

Field survey

We examined the distribution of *C. fluminea* at 76 sites along the bank of the river Rhine (mean discharge: 1032 m^3/s), in three tributaries (Wiese, 11.3 m^3/s; Birs, 15.2 m^3/s; Ergolz, 1.9 m^3/s) and in the Canal de Huningue (12.0 m^3/s) in the region of Basel. Substrate of these tributaries was sampled qualitatively. Bottom samples were taken along the river at distances ranging from 200 m to 1 km in spring, summer and autumn 2003. Apart from the minimum distance of 200 m, sampling sites were chosen depending on accessibility. For the river Rhine, we focused on the bank in the city of Basel, the sections near tributary estuaries and the furthest upstream sites where *C. fluminea* was known to occur (near Rheinfelden in 2001; C. Oberer, pers. comm.).

At each sampling site ecological variables were recorded following Baur and Ringeis (2002): altitude (range 230–280 m a.s.l.), width of the river, water depth at the sampling site (mean of three measurements), and water current at the surface (classified into three groups and measured with the use of a table tennis ball (mean of five measurements): (0) standing water, (1) slow, ≤ 0.3 m/s, and (2) fast > 0.3 m/s). Additionally, the type of substrate (silt < 0.063 mm; sand: 0.063–2.0 mm; gravel: 2.1–63.0 mm; stones 63.1–200 mm; boulders and bedrock > 200 mm; DIN 4022), light exposure of the habitat (assigned to three classes: (1) shady, (2) lightly sun-exposed, and (3) sun-exposed), and the type of the habitat adjacent to the river was assessed. We also recorded the type of riverbank.

The presence of *C. fluminea* was recorded as follows: (0) absent, (1) empty shells present, and (2) living individuals (> 3 mm in shell length) present. Where living clams were found, their abundance was estimated according to Rey and Ortlepp (2002): I (1–9 individuals/m^2), II (10–20 ind./m^2), III (21–50 ind./m^2), IV (51–200 ind./m^2), V (201–500 ind./m^2), VI (501–1000 ind./m^2) and VII (> 1000 ind./m^2). For abundance estimates, substrate including clams from an area of 1 m^2 was sampled with a D-framed net.

We also examined the spatial distribution of *C. fluminea* in a cross-section through the river Altrhein (47° 38’ N, 7° 34’ E), a remnant of the former river Rhine (mean discharge 30 m^3/s), 4 km north of Basel. Bottom samples were taken along a transect of 150 m from the French to the German bank at depths ranging from 10 to 150 cm. Depth and type of substrate were recorded. The deepest part (37 m wide) could not be examined due to high water current.

To examine seasonal changes in the size structure of a *C. fluminea* population, clams were collected at intervals of approximately 6 weeks from spring to autumn 2003 (10 March, 21 April, 29 May, 10 July, 21 August, 2 October) at the same site in the river Altrhein. Samples were obtained as described above. To obtain juveniles, samples of 1 L bottom substrate were dried at 80° C for 24 hours, put through sieves with mesh sizes of 6.3, 2.0, 1.0 and 0.2 mm and later examined under a binocular microscope. Shell length and height of each clam were measured with a caliper to the nearest 0.1 mm. For clams < 4.0 mm, a binocular microscope with stage micrometre was used. Water temperature was recorded at each sampling occasion. Data on the water chemistry of the river Rhine were obtained from the station Weil am Rhein (Germany) near Basel (AUE 2003).

Substrate choice experiment

To examine the substrate preference of *C. fluminea*, we conducted a field experiment in the river Altrhein. The experimental design followed Belanger et al. (1985) and Olabarria et al. (2002). Four replicates with a total of 576 clams were run between July and October 2003. A replicate consisted of six plastic containers (30 cm in diameter, 15 cm deep), each of them subdivided with plastic walls into three sectors of equal size. Three containers were filled with three different types of substrate (T1–T3) for testing the clams’ preference and three containers were filled with the same type of substrate in all sectors to examine the distribution of individuals by chance (T4–T6; Figure 2.1). The following substrates were chosen: sand (A, 0.2–2 mm, obtained from the river Altrhein, organic matter content (OMC) = 3.7%), fine gravel with sand (B, 1–3 mm, from the river Rhine near Huningue, OMC = 1.6%), and gravel (C, 2–63 mm, from the river Rhine near Huningue, OMC = 3.8%). It was hypothesized that the animals will move to the sector containing the most preferred substrate. Before the experiment, the substrates were dried at 80° C for 24 h to remove benthic organisms. Plastic containers were positioned in the river Altrhein in such a way that the substrate surface was situated at a depth of 13–18 cm. Individuals of *C. fluminea* (> 12 mm in shell length) were collected at the experimental site immediately before the tests. For each container 24 clams were randomly assigned to three groups of eight individuals each. The 24 clams per container correspond to a density of 340 individuals /m^2. The clams of each group were labelled individually using a water resistant paint marker. The clams were placed group-wise on the line separating two sectors (Figure 2.1). The sector opposed to the current was referred to position I, the other sectors clockwise to position II and III (the current was parallel to the wall separating sector II and III). The same procedure was used for the three containers with a single substrate. An experimental trial lasted for 2 hours. After 1 h, 70–80% of the clams were already buried in the substrate, confirming the findings of Belanger et al. (1985).

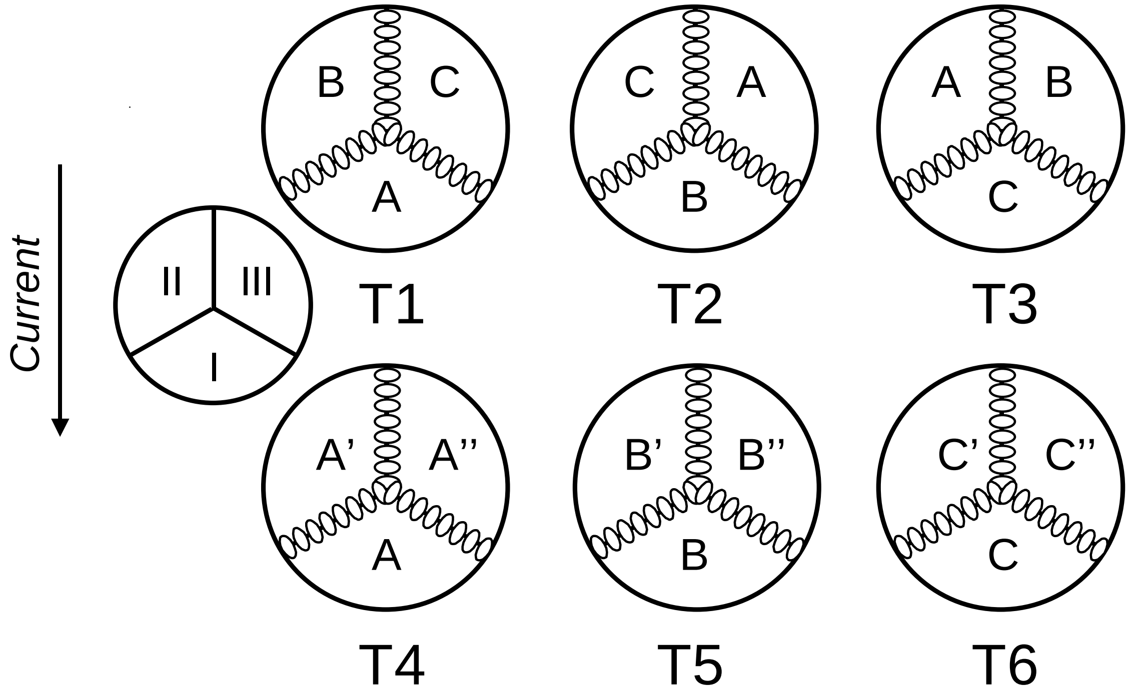

Figure 2.1 Experimental design with the treatments T1–T6 to test the substrate preference of *Corbicula fluminea*. Containers were subdivided into three sectors of equal size. Each sector contained a substrate: A refers to sand, B to fine gravel with sand, and C to gravel. Dots on the separating walls represent the clams' starting positions. The arrow indicates the water current.

At the end of each trial we recorded the position of each clam. Preliminary studies, in which clams were placed in the centre of each sector, revealed immediate vertical movements. Within a few minutes most clams started to investigate the environment with their feet. Once having moved to the preferred sector the clams began to bury.

Statistical analyses

Data analysis was performed using StatView (Version 5.0, Abacus Concepts, 1998). The frequency of occurrence of *C. fluminea* in relation to different substrate types and environmental variables was analysed using contingency tables. The effect of single environmental variables on the presence/absence of *C. fluminea* was examined using a logistic regression model. In the field experiment, deviations of the clams' substrate choice from a uniform distribution (no choice) were analysed using contingency tables.

Results

Field survey

Specimens of *C. fluminea* were exclusively found in the river Rhine, in the Canal de Huningue, and in streams connected with the Canal de Huningue (Figure 2.2). The Asiatic clam could not be found in any of the tributaries Wiese, Birs and Ergolz. Living specimens of *C. fluminea* were recorded at 22 of 76 investigated sites (28.9%), empty shells at a further 8 sites (10.5%). In the river Rhine, *C. fluminea* has spread 22 km upstream of Basel as indicated by two living individuals (both measuring 15 mm in shell length) and two empty shells. At other potentially suitable sites further upstream, *C. fluminea* was not recorded in 2003.

In the river Rhine, the local density of *C. fluminea* decreased towards the current edge of distribution. In the river Altrhein (7 km downstream of Basel), 200–600 clams/m^2 were recorded. In Basel, the density of *C. fluminea* varied from 5–200 individuals/m^2 and at localities situated upstream of Basel from 1–20 individuals/m^2. In the Canal de Huningue, densities of 10–50 individuals/m^2 were recorded.

The occurrence of *C. fluminea* was influenced by the type of substrate ($\chi^2 = 19.92$, $df = 4$, $P = 0.0005$). The clam was most frequently found on fine grained substrates such as silt (33.3%), sand (33.3%) and fine gravel (30.0%). Hard substrates such as bedrock and boulders were never occupied by the clam, except for juveniles of up to 3 mm shell length, which were

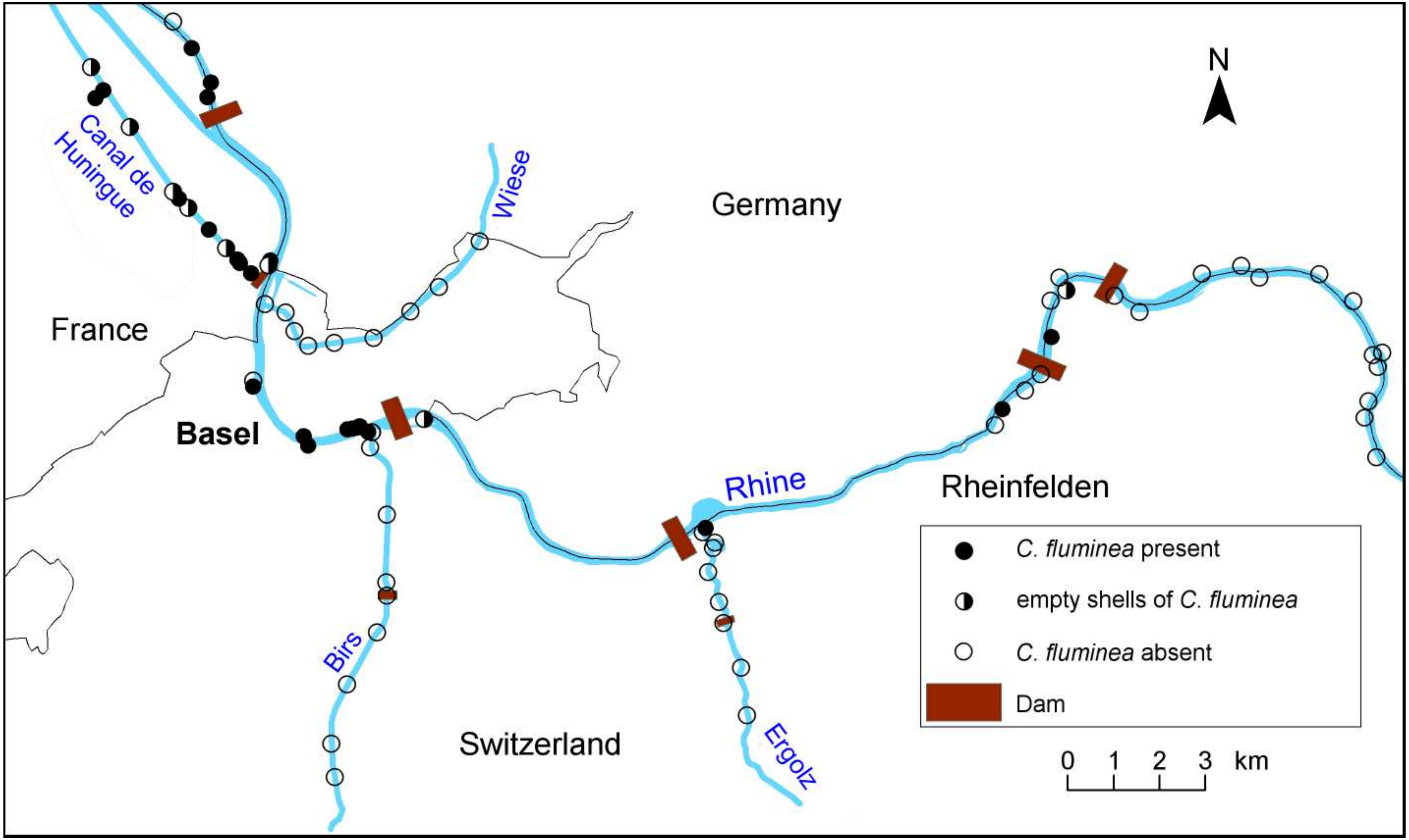

Figure 2.2 Distribution of *Corbicula fluminea* in the surroundings of Basel in 2003.

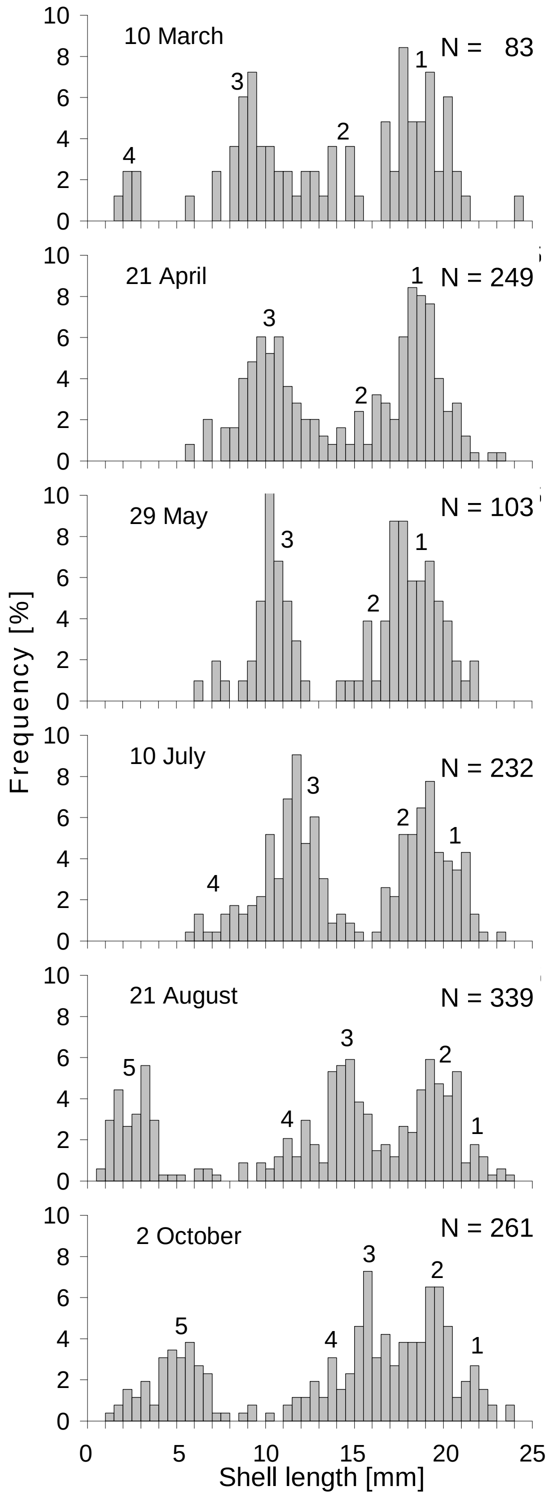

Figure 2.3 Seasonal changes in the size distribution of *Corbicula fluminea* in the river Altrhein near Basel between 10 March and 2 October 2003. The numbers 1–5 on the top of the bars indicate the possible cohorts; N refers to the numbers of clams measured, which were grouped in size classes of 0.5 mm.

attached to large stones and other adult clams. Water current also affected the occurrence of *C. fluminea* (χ^2 = 16.38, *df* = 3, *P* = 0.0009). Living clams were exclusively found in slowly running and standing waters. No effect of light exposure, vegetation of the bank, water depth at sampling site or river width of the site on the presence of *C. fluminea* was found (logistic regression, in each case $P > 0.2$).

The transect sampling across the river Altrhein revealed that *C. fluminea* was most abundant (up to 600 clams/m^2) on sandy substrates near the banks of the river. The abundance decreased with increasing water current towards the middle of the channel. No *C. fluminea* was found at places where the substrate consisted of stones.

The size distribution of *C. fluminea* in the river Altrhein indicated the presence of a well-established population (Figure 2.3). The size distribution recorded on 10 March 2003 showed four peaks which may refer to four cohorts (1–4). Cohort 1 with a median shell length of 19 mm was the oldest, followed by cohort 2 (peak at a shell length of 14 mm), cohort 3 (9 mm) and cohort 4 (2.2 mm). In April cohort 4 was only represented by empty valves and was therefore not considered in the size distribution. In August, a new cohort (5) appeared with a peak at a shell length of 4 mm.

In all cohorts, the growth rate was highest between May and October (Table 2.1), most probably favoured by an increased water temperature (10 March: 7 °C; 21 April: 12 °C; 29 May: 15 °C; 10 July: 22 °C; 21 August: 24 °C; 02 October: 17 °C) and food availability in that period. However, the abundance of plant nutrients in 2003 did not differ from the 10-year mean value (Table 2.2).

Substrate choice experiment

In the substrate choice tests, clams did not bury in equal frequencies in sectors with different substrates (T1–T3; χ^2 = 14.68, *df* = 1, *P* = 0.0006; Table 2.3). The clams moved most frequently into sectors containing sand (41.7%) and less frequently into sectors containing fine gravel with sand (35.0%) or gravel only (23.3%). Thus, *C. fluminea* showed a preference for fine substrates. The position of the different substrate types in relation to the water current did not influence the preference of the clams (χ^2= 2.81, *df* = 1, *P* = 0.25). In containers with a single substrate (T4–T6), clams buried in equal frequencies in all sectors (χ^2 = 0.53, *df* = 1, *P* = 0.77). Water current slightly influenced the clams' choice of the sector in containers with a single substrate (T4–T6; χ^2= 6.79, *df* = 1, *P* = 0.034; Table 2.3). Most clams showed a positive rheotaxis. However, the effect of the substrate type was much stronger than the effect of the water current (randomised positions of substrate types in T1–T3).

Table 2.1 Mean shell length (SL; mm) and growth rate (Δ SL; mm/ 30 days) of each cohort in the river Altrhein in 2003. The age and the year of spawning were estimated (a = first spawning; b = second spawning) based on the shell length in October 2003.

Date		Cohort				
		1	2	3	4	5
10 March	SL	19.0	13.75	8.5	2.25	
	Δ SL	*0.36*	*1.25*	*0.54*	-	
21 April	SL	19.5	15.5	9.25	-	
	Δ SL	*0.00*	*0.79*	*0.00*	-	
29 May	SL	19.5	16.5	9.25	-	
	Δ SL	*1.07*	*1.07*	*1.96*	*1.41**	
10 July	SL	21.0	17.0	12.0	8.0	
	Δ SL	*0.71*	*1.43*	*2.50*	*2.32*	
21 August	SL	22.0	19.0	15.5	11.25	4.0
	Δ SL	*0.18*	*0.18*	*0.71*	*1.25*	*1.25*
2 October	SL	22.25	19.25	16.5	13.0	5.75
10 March – 2 Oct.	absolute SL growth	3.25	5.5	8.0	10.75	1.75
	Δ SL	*0.47*	*0.80*	*1.17*	*1.57*	
Age; year of spawning		3+; 2000	2+; 2001	1+; 2002a	1-; 2002b	1-; 2003

* from March to July

Table 2.2 Water chemistry data of the river Rhine at the station Weil am Rhein (Germany). Mean values and ranges were determined from fortnightly analyses. DOC: Dissolved Organic Carbon; SM: Suspended Matter (AUE 2003, IKRS 2005).

Parameters	2003		1995-2004	
	Mean	Range	Mean	Range
Oxygen (mg/l)	10.11	7.6–13.3	10.65	7.6–13.8
pH*	8.00	7.55–8.41	8.14	7.9–8.4
Temperature (°C)	14.0	3.5–26.7	12.6	3.8–25.3
Conductivity (µS/cm)	363.0	287.8–442.4	355.6	290.0–445
Discharge (m^3/s)	804.4	375–2125	1099.2	457–3216
DOC (mg/l)	2.18	1.57–3.52	2.07	1.1–3.8
SM (mg/l)	6.8	1.4–19.6	15.9	1–834.3
NH_4^+ (mg/l)	0.069	0.0338–0.113	0.071	0.02–0.226
NO_3^- (mg/l)	1.33	0.918–1.893	1.48	0.92–2.29
PO_4^{3-} (mg/l)	0.043	0.020–0.126	0.045	0.01–0.141

*data not available from the years 1999−2002

Table 2.3 Results of the substrate choice experiment. Figures indicate the number of *Corbicula fluminea* that chose a particular substrate type. Data of four replicates are pooled. Treatments are explained in Figure 2.1.

Treatment	Substrate		
	Sand (A)	Fine gravel with sand (B)	Gravel (C)
T1	31	37	25
T2	44	31	21
T3	43	31	20
T4	32/34/30[a]	-	-
T5	-	35/26/34[a]	-
T6	-	-	34/35/27[a]

[a] Corresponds to the number of clams found in the sectors X/X'/X'' in Figure 2.1.

Discussion

C. fluminea arrived in Basel (Switzerland) in 1995 (Rey and Ortlepp 2002). In 1997, *C. fluminea* was found near Augst, 11 km upstream of Basel, and in 2001 near Rheinfelden, 20 km upstream of Basel (C. Oberer, unpubl. data). In our survey, *C. fluminea* was recorded 2 km upstream of Rheinfelden in 2003, indicating a mean upstream spread of 2.4 km per year in the last 9 years. Compared with the annual dispersal distance since the clam entered the river Rhine in 1985, this is a low rate of spread (Glöer and Meier-Brook 1998). It is commonly assumed that the clam was introduced and spread by ballast water of cargo ships (Morton 1986) and that the larvae colonize downstream habitats by the water currents independently of shipping. Since cargo ships in the region of Basel rarely need ballast water, the clams must have other means of dispersal. We found one-year old *C. fluminea* upstream of the barrage of Rheinfelden where no cargo shipping occurs. From Rheinfelden upstream to the outlet of Lake Constance, *C. fluminea* does not yet occur (personal communication from three fishery inspectors: T. Stucki, K. Balsiger, J. Walter 2003). However, new occurrences of *C. fluminea* were reported from Lake Constance in August 2003 (Werner and Mörtl 2004) and from Lake Neuchâtel in November 2003 (Rey, unpublished data), and most recently, in Lake Morat in July 2005 (Fasel 2005). These new occurrences may result from independent non-intentional introductions.

In a protected area of the Savannah River (South Carolina), waterfowl has been suggested to displace *C. fluminea* at least 1.2 km per year (Voelz et al. 1998). Juvenile *C. fluminea* use their mucous secretions (Prezant and Chalermwat 1984, Dubois 1995, Schmidlin 2004) to stick to ducks' feet and to fishes (Brancotte and Vincent 2002), and thus might be transported over large physical barriers such as dams of hydro-electrical power plants. Adult clams can also attach to macrophytes by valve closure or getting stuck between the filaments/threads of algae (*Elodea* sp., *Cladophora* sp.), when the plants were pulled out of the water (H. Durrer, pers. comm.; Schmidlin 2004). Accidental transportation of *C. fluminea*, sticking on macrophytes (e.g. by recreational boating) may further contribute to its spread.

C. fluminea is used as fish bait by fishermen (Cazzaniga and Perez 1999, Brancotte and Vincent 2002) and sold as aquarium or pond accessory in pet shops and garden centres (Werner and Mörtl 2004). When cleaning an aquarium, the clam might be released into streams or lakes, as has been done with the gastropods *Physella* cf. *acuta* and *Planorbella* spp. (Horsak et al. 2004). It is assumed that both non-intentional and deliberate introduction of *C. fluminea* are important factors increasing the spread of this species.

Of the ecological variables examined only substrate type and water current affected the occurrence of *C. fluminea*. However, because substrate type (grain size) is correlated with water current (Dudgeon 1982), *C. fluminea* was most frequently found at sites with fine sediments and slow water current. Several hypotheses may explain the occurrence of *C. fluminea*. First, water current is an important factor in determining successful colonisation because it also determines food supply. The downstream increase of phytoplankton depends on flow duration, generation time of phytoplankton and increasing nutrient concentration (Yang et al. 1997). The outlet of Lake Constance and the numerous reservoirs adjacent to dams may provide sufficient phytoplankton for *C. fluminea* and other organisms living in the Rhine. In the turbulent tributaries examined, the productivity of seston, foremost micro-algae, could be limited and therefore not allow *C. fluminea* to reproduce, even though the clam is able to pedal-feed (Hakenkamp and Palmer 1999, Rajagopal et al. 2000, Mouthon 2001a,b).

Another hypothesis relates to the changing amount of water: Invasive clams may be sensitive to fluctuations in water height and current (periodic sediment turnover and transportation, falling dry; Rey et al. 2004). However, variation in water height and current are less pronounced in the river Rhine than in the tributaries examined. Furthermore, low water temperature has been suggested to limit the spread of *C. fluminea* (Schöll 2000). In the rivers examined in the present study, the water temperature of the tributaries Birs and Ergolz is not lower than that of the river Rhine.

Size distribution

In the population examined in the river Altrhein, we recorded slightly different size distributions compared with those found in the Upper Rhine near Mainz (Meister 1997). The Altrhein population most probably contained 2- to 3-year-old clams in October 2003, while 4- to 5-year-old individuals were found near Mainz. Growth conditions in the Altrhein may be more similar to those of the river Saone in France (Mouthon 2001a). Saone populations are characterised by a single annual reproduction period starting in May or June and ending in September or October. In our study, the spawning period most probably occurred in June and July because the first juveniles were recorded in August (cohort 5).

Substrate choice experiment

The results of our substrate choice experiment confirmed field observations and experimental evidence of Belanger et al. (1985), who found that *C. fluminea* prefers fine substrates, which contain more organic material (= potential food) than coarse ones (Dudgeon 1982). It could be expected that the clam moves to the substrate which provides the most food. In our experiment gravel contained most the organic matter in the form of hard layers consisting of fine sediments. However, in this form organic matter is only separable at high temperatures (700 °C) and therefore cannot be used by *C. fluminea*.

Our choice experiment also showed that the direction of water current can influence clam behaviour in homogeneous substrates (containers T4–T6). A positive rheotaxic behaviour allows the clams to move upstream without hitchhiking. However, since the majority of adult clams are buried in the substrate, the effect of current direction might be small. Molluscan upstream movements are frequently explained by search for food or space, compensation of drift, avoidance of predation and by hydrodynamic and biomechanical effects (Huryn and Denny 1997).

Effects on other species

C. fluminea could become a threat to other organisms, if it uses the same resources as other species. The most important resources to the clam are space and food. The favoured spatial resource, different types of fine substrate, is also used by unionids. Four species of unionids are known to occur in the region of Basel (Glöer and Meier-Brook 1998). In 2000, only empty shells of the clams *Unio pictorum* (Linnaeus, 1758) and *Unio tumidus* (Philipsson, 1788) were found (Rey and Ortlepp 2002). *C. fluminea* may compete with filter-feeders (other bivalves) and also with benthic consumers of organic matter.

Indeed, a preliminary study indicated that the molluscan assemblage experienced profound changes in the river Rhine near Basel between 1994 and 2003 (Schmidlin 2004). In 1994, *C. fluminea* did not yet occur at the two sites examined in Basel (Baur and Ringeis 2002). Nine years later, however, *C. fluminea* was together with the gastropod *Ancylus fluviatilis* (O. F. Müller, 1774) the most abundant mollusc at both sites and gastropod diversity has decreased. This decrease in species richness could partly be a result of competition with *C. fluminea* for space and food (Schmidlin 2004). The recent invasion of other species such as the polychaet *Hypania invalida* (Grube, 1860) and the amphipods *Chelicorophium curvispinum* (Sars, 1895) and *Dikerogammarus villosus* (Sovinsky, 1874) put additional pressure on native communities (Rey and Ortlepp 2002). However, experimental studies are needed to determine the impact of *C. fluminea* on native molluscan assemblages.

Conclusions

Our data show that the current distribution of *C. fluminea* in the river Rhine does not stop where cargo shipping ends. But the expansion of the clam is slow in comparison to the former spread in the river Rhine. Natural upstream movements of bivalves are hardly known. However, passive dispersal by waterfowl and recreational boating may facilitate further upstream spread of *C. fluminea* in the river Rhine. The substrate choice experiment showed that *C. fluminea* prefers fine grained sediments. *C. fluminea* seems to be less successful in colonizing rivers with rapid current such as the examined tributaries, in which the preferred substrate is less abundant. These tributaries may serve as refuges for native molluscs. Our study documents the initial phase of the invasion of *C. fluminea* in Switzerland. Most probably, this invasive species will further expand and colonize other rivers and lakes.

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Chapter 3: Separate introductions but lack of genetic variability in the invasive clam *Corbicula* spp. in Swiss lakes

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Abstract

This study documents the spread of the invasive clam *Corbicula* spp. in Switzerland since its first record in the River Rhine in 1995. Clams were newly recorded in several Swiss lowland lakes whose interconnecting rivers have not yet been colonized. We present evidence for separate introductions of an identical haplotype of *Corbicula fluminea* into five lakes in Switzerland in the years 2003–2010 based on the mitochondrial DNA-sequence of the COI in specimens sampled. This suggests passive dispersal of the clam by human activities and/or waterfowl. All but one of the 72 genetically analysed individuals were assigned to a single haplotype FW5 and to the species name *C. fluminea.* Recent records of specimens, which were not genetically analysed, displayed all the shell morphology of *C. fluminea,* confirming the dominance of this clam in Swiss rivers and lakes.

Key words: alien species, DNA sequencing, COI, invasive species, range expansion, *Corbicula*, Switzerland

Introduction

The basket clam *Corbicula fluminea* (Müller, 1774) originating from South-East Asia, was first recorded in Europe in the estuaries of the Dordogne (France) and the Tagus (Portugal) in 1980 (Mouthon 1981), and in the Lower Rhine in The Netherlands in 1985 (Bij de Vaate and Greijdanus-Klaas 1990). In 1991, *C. fluminea* was found near Karlsruhe in the Upper Rhine and, in 1995, the clam was reported near Basel in Switzerland (Rey et al. 2004). It is assumed that transportation by cargo ships is responsible for the rapid spread in the River Rhine

(Tittizer 1997, Leuven et al. 2009). Upstream of Basel, where cargo shipping stops, the spread of this invasive clam has been less rapid (Schmidlin and Baur 2007). Early in 2006, *C. fluminea* was only found in the River Rhine from Basel to the confluence of the River Aare (Table 3.1). At that time, no individuals of *C. fluminea* were found in other rivers connecting the lowland and pre-alpine lakes. However, isolated occurrences of the clam were reported from sites in Swiss lakes and the Austrian part of Lake Constance, indicating independent introductions (P. Stucki pers. communication; Werner and Mörtl 2004).

The rapid spread and persistence of *C. fluminea* throughout Europe, North and South America is related to its high growth rate, early onset of maturity, high fecundity, variety of reproductive strategies (Komaru et al. 1998, Hedke et al. 2008) and its ability to tolerate a wide range of environmental conditions (Mattice and Dye 1976, McMahon, 1983, 2002, Müller and Baur 2011). In the River Rhine, *C. fluminea* reaches densities of up to 10,000 individuals per m^2 (Mürle et al. 2008). *C. fluminea* clogs water intake pipes, electric power plant cooling systems and sewage treatment plants, causing enormous damage (Pimentel et al. 2007). In the U.S.A., costs associated with this clam are estimated to be more than US$ 1 billion per year (OTA 1993). As a dominant species of the macrozoobenthos, *C. fluminea* is involved in sequestering a large proportion of the carbon available for benthic production and consequently altering the ecosystem functioning (Sousa et al. 2008). The invasive clam decreases the abundance of benthic flagellates, bacteria and diatoms and affects other organisms by bioturbation of sediments (Hakenkamp et al. 2001). Valves of dead *C. fluminea*, however, can increase the surface area and substrate diversity of sandy bottoms resulting in an increase of benthic invertebrates (Werner and Rothhaupt 2007, Schmidlin et al. 2011).

Corbicula fluminalis (Müller, 1774), another basket clam with similar shell morphology, was also introduced to Europe in the past decades (Alf 1992, Bachmann and Usseglio-Polatera 1999). According to the description of the two species, *C. fluminea* has a round shell, whereas *C. fluminalis* has a more saddle-shaped shell (see also Marescaux et al. 2010). Based on morphological analyses, Renard et al. (2000) stated that the two species can be distinguished based on the shape of the shell. In contrast, Pfenninger et al. (2002) showed that the distinction of these species is problematic because an intermediate morphotype occurs. Moreover, examining mitochondrial and nuclear DNA, Pfenninger et al. (2002) and others (Lee et al. 2005, Hedke et al. 2008) found that the two species are not reciprocally monophyletic. These findings suggest that the so far widely used species names (*C. fluminea* and *C. fluminalis*) represent two distinct species with interspecific gene flow or, alternatively, they are a result of an incorrect systematic separation of a single species. A recent paper

Table 3.1 A. Locations of *Corbicula* spp. sampling sites, and number of individuals used for the COI analysis, assigned species, forms and haplotypes (in format: species-form-haplotype), year of sampling and year of first record at the locality. **B.** Locations of new records of the species *Corbicula fluminea* in Switzerland.

No **A**	Location	Country	Latitude N°	Longitude E°	Year of sampling	Number of individuals genetically analysed	Assignment	Collector	First record	Reference of first record
1	River Rhine, harbour of Basel	Switzerland	47.589	7.591	2008	1	1 *C. fluminea*-R-FW5	D. Küry	1995	a
2	River Rhine, harbour of Birsfelden	Switzerland	47.561	7.632	2008	2	1 *C. fluminea*-R-FW5 1 *C. fluminalis*-S-FW17	D. Küry	1995	a
3	River Rhine, Augst	Switzerland	47.539	7.714	2006	6	6 *C. fluminea*-R-FW5	S. Schmidlin	2003	b
4	Rigole, Petite Camargue Alsacienne, St. Louis-la-Chaussée	France	47.625	7.534	2006	5	5 *C. fluminea*-R-FW5	S. Schmidlin	1999	c
5	Altrhein, remnant of former River Rhine, Märkt	Germany	47.624	7.572	2006	6	6 *C. fluminea*-R-FW5	S. Schmidlin	1994	d
6	Lake Rotsee near Luzern	Switzerland	47.064	8.304	2008	6	6 *C. fluminea*-R-FW5	P. Steinmann	2006	e
7	Lake Murten near Sugiez	Switzerland	46.955	7.119	2008	6	6 *C. fluminea*-R-FW5	S. Schmidlin	2005	f
8	Lake Neuchâtel near Portalban	Switzerland	46.924	6.952	2006	6	6 *C. fluminea*-R-FW5	S. Schmidlin	2003	g
9	Lake Geneva near Morges	Switzerland	46.503	6.494	2010	6	6 *C. fluminea*-R-FW5	B. Lods-Crozet	2008	h
10	River Saône near Lyon	France	45.797	4.830	2006	6	6 *C. fluminea*-R-FW5	J. Mouthon	1994	i
11	Lake Constance, Rohrspitz	Austria	47.500	9.683	2006	6	6 *C. fluminea*-R-FW5	S. Werner	2003	j
12	River Donau, Schiffmühle Orth near Vienna	Austria	48.123	16.709	2008	4	4 *C. fluminea*-R-FW5	A. Heusler	1999	k
13	River Oder near Frankfurt a. d. Oder	Germany	52.347	14.557	2008	6	6 *C. fluminea*-R-FW5	O. Müller	2007	l
14	River Elbe near Dresden	Germany	51.071	13.700	2008	6	6 *C. fluminea*-R-FW5	K. Schniebs	1998	m

Table 3.1 continued

B	New records in Switzerland	Country	Latitude N°	Longitude E°	Assignment	Collector	First record	Reference of first record
15	Lake Constance near Münsterlingen	Switzerland	47.634	9.246	*C. fluminea*-R	ANEBO	2009	n
16	River Ron, outlet of Lake Rotsee	Switzerland	47.077	8.329	*C. fluminea*-R	H. Vicentini	2006	o
17	River Suhre, outlet of Lake Sempach	Switzerland	47.162	8.121	*C. fluminea*-R	H. Vicentini	2007	o
18	Lake Zürich	Switzerland	47.270	8.634	*C. fluminea*-R	L. De Ventura	2010	p
19	Lake Biel near le Londeron	Switzerland	47.053	7.074	*C. fluminea*-R	P. Stucki	2006	g
20	River Aare, Döttingen	Switzerland	47.568	8.254	*C. fluminea*-R	P. Steinmann	2006	e
21	River Aare, Brugg	Switzerland	47.485	8.214	*C. fluminea*-R	P. Steinmann	2010	e
22	Canal Aare near Aarau power station	Switzerland	47.394	8.029	*C. fluminea*-R	W. Hess	2009	q
23	River Reuss near Hünenberg	Switzerland	47.154	8.400	*C. fluminea*-R	P. Steinmann	2010	e
24	Lake Geneva, Bouveret	Switzerland	46.389	6.859	*C. fluminea*-R	B. Lods-Crozet	2008	h
25	Spittelmattbach near Basel	Switzerland	47.576	7.624	*C. fluminea*-R	D. Küry	2008	r
26	River Aare, Oftringen	Switzerland	47.320	7.898	*C. fluminea*-R	M. Karsai and A. Lanker	2011	this study
27	River Aare, Wynau	Switzerland	47.263	7.806	*C. fluminea*-R	A. Kirchhofer	2011	s
28	River Rhine, near Rietheim	Switzerland	47.614	8.260	*C. fluminea*-R	B. Baur	2011	this study

a: Rey et al. (1997); b: Rey et al. (2004); c: Mosimann (2000); d: Schöll (1995); e: P. Steinmann, pers. comm. f: Fasel (2005); g: P. Stucki, pers. comm.; h: B. Lods-Crozet, pers. comm.; i: Mouthon (1994); j: Werner and Mörtel (2004); k: Fischer and Schultz (1999) (Austria); l: Müller et al. (2007); m: Schöll (1998); n: ANEBO (2011);o: H. Vicentini, pers. comm.; p: L. De Ventura, pers. comm.; q: W. Hess (2009); r: D. Küry, pers. comm.; s: A. Kirchhofer, pers. comm.

suggests that the genus *Corbicula* could be considered as a polymorphic species complex (Pigneur et al. 2011). However, Pigneur et al. (2011) did not suggest any change in the taxonomical nomenclature (e.g. synonymi-zation).

According to the rules of taxonomy the actual species names (*C. fluminea* and *C. fluminalis*) are consequently still valid.

Here we present new data on the spread of *Corbicula* in Switzerland. We examined the mitochondrial DNA-sequence of the cytochrome oxidase subunit I (COI) in each specimen sampled in recently colonized lakes in Switzerland and several European rivers. To facilitate comparisons with previous and future genetic studies and to contribute to the needed revision of *Corbicula*, we present the taxonomic species name together with a form and a haplotype code following Pigneur et al. (2011). Thus, *C. fluminea* /form R/haplotype FW5 denotes individual(s) assigned to the species *C. fluminea* (i.e. taxonomical description) to a round (R) form (possible categories are: R: round, S: saddle and Rlc: round light coloured, see Pigneur et al. 2011) and to a mitochondrial haplotype FW5 (see Pigneur et al. 2011).

Methods

First, we compiled the information on the recent range expansion of *Corbicula* in Switzerland between 1995 and 2011 using the following sources: own field observations, personal communications from several researchers and data from unpublished reports.

For the genetic analysis, *Corbicula* samples were obtained from five lakes (four in Switzerland and one from the Austrian part of Lake Constance) and six rivers in Central Europe between 2006 and 2010 (Figure 3.1, Table 3.1). Clams were preserved in 70% ethanol and kept at 5 °C until analysis. Total DNA was extracted from foot muscle tissue using the Qiagen DNeasy Blood and Tissue Kit (Qiagen, Hombrechtikon, CH). A 659-bp fragment of the mitochondrial cytochrome oxidase subunit I (COI) was amplified for 72 specimens using the standard universal primers (see Folmer 1994). Samples were amplified for 40 cycles following the protocol of Pfenninger et al. (2002) after initial incubation at 94 °C for 3 min. Sequencing was outsourced to ecogenics GmbH (Zürich-Schlieren, CH; http://www.ecogenics.ch), which uses Applied Biosystems 3100 automated sequencer. Both strands (forward and reverse) were sequenced for all samples. To avoid contaminations between samples, PCR reactions were run at different periods and negative controls were added in each reaction group. Base pairs were checked manually and aligned using CodonCode Aligner version 3.7.1.1 (CodonCode Corporation, Dedham, US). Haplotypes obtained were compared with published COI sequences of *Corbicula* available on GenBank.

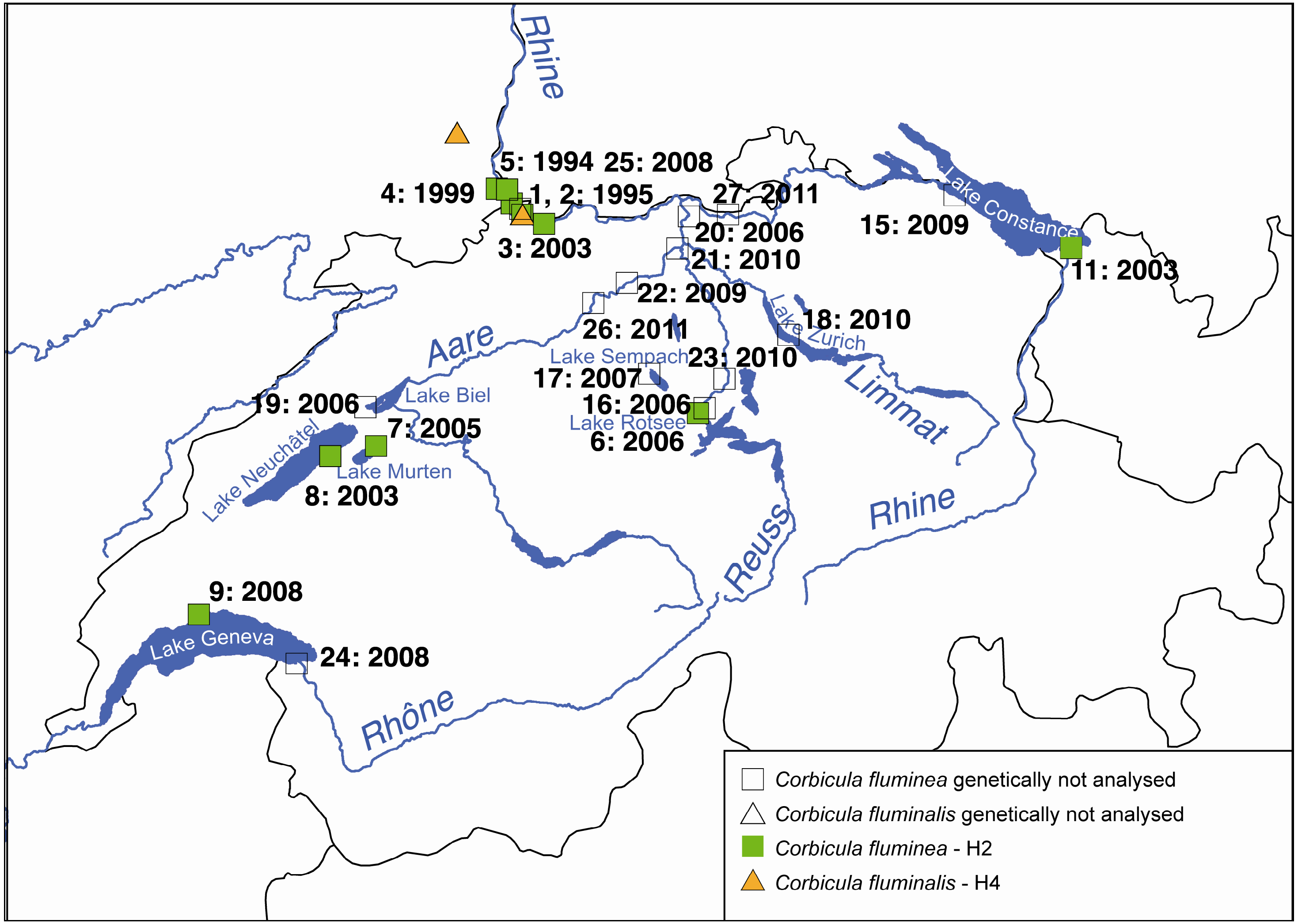

Figure 3.1 Records of *Corbicula* spp. in Switzerland. Green squares refer to the haplotype FW5, the orange triangle to the haplotype FW17. In this study each individual with FW5 haplotype was assigned to the form R and to the species name *C. fluminea* and each individual with FW17 to the form S and to the species name *C. fluminalis*. Empty squares refer to individuals of *C. fluminea* form R which were not genetically analysed.

Results

The compiled new records demonstrated the further spread of *Corbicula fluminea*/form R in Switzerland since 1995 (Table 3.1, Figure 3.1). In the River Aare, *C. fluminea*/form R was found near Wynau, Oftringen, Brugg and Aarau, in the River Reuss near Hünenberg, in the River Suhre near Oberkirch at the outlet of Lake Sempach, in the River Ron near the outlet of the Lake Rotsee, in a side brook of the River Wiese near Basel and in the River Rhine from Basel to Rietheim, a few kilometres upstream of the confluence with the River Aare. Furthermore, the clam was also detected in Lakes Constance (2003), Neuchâtel (2003), Murten (2005), Rotsee (2006), and Biel (2006), Lake Geneva (2008) and Lake Zürich (2010; Table 3.1B, Figure 3.1). However, large sections of the interconnecting rivers are not yet invaded by the clam. In the lakes, all records were made close to harbours or canals (Lakes Neuchâtel, Murten, Rotsee, Geneva and Constance). In contrast, one specimen of *C. fluminalis*/form S was exclusively found in the region of Basel in the River Rhine.

Seventy-one of the 72 individuals that were genetically analysed share the FW5 haplotype (following Pigneur et al. 2011) and could be taxonomically assigned to *C. fluminea* and morphologically to the form R (Table 3.1A). Thus, 71 *C. fluminea* specimens sampled in Lakes Constance, Neuchâtel, Murten, Rotsee, Geneva and in the Rivers Rigole, Saône, Oder, Elbe, Danube and the Rhine (Basel, Birsfelden and Augst) belong to the group *C. fluminea*/form R/haplotype FW5. One of the two individuals collected in the River Rhine near Birsfelden had a saddle-shaped shell and was assigned to *C. fluminalis*/form S/haplotype FW17 (Table 3.1A, Figure 3.2). Thus, individuals with a distinct shell form and discrete haplotype coexist at this locality.

Discussion

The present study illustrates the most recent spread of *Corbicula* in Switzerland. Clams were newly recorded in several lowland lakes whose interconnecting rivers are not yet colonized. This suggests passive dispersal of the invasive clam by human activities or animal vectors and independent introductions. The transport of pleasure boats from lakes to lakes and from rivers to lakes is the most probable pathway for the introduction of *Corbicula* into the lakes examined. For example, Lake Rotsee is well-known for its international rowing regatta (e.g. the World Championship in 2001). The transport of rowing boats from regatta to regatta increases the probability of introducing *Corbicula* to other water bodies. Recreational boating

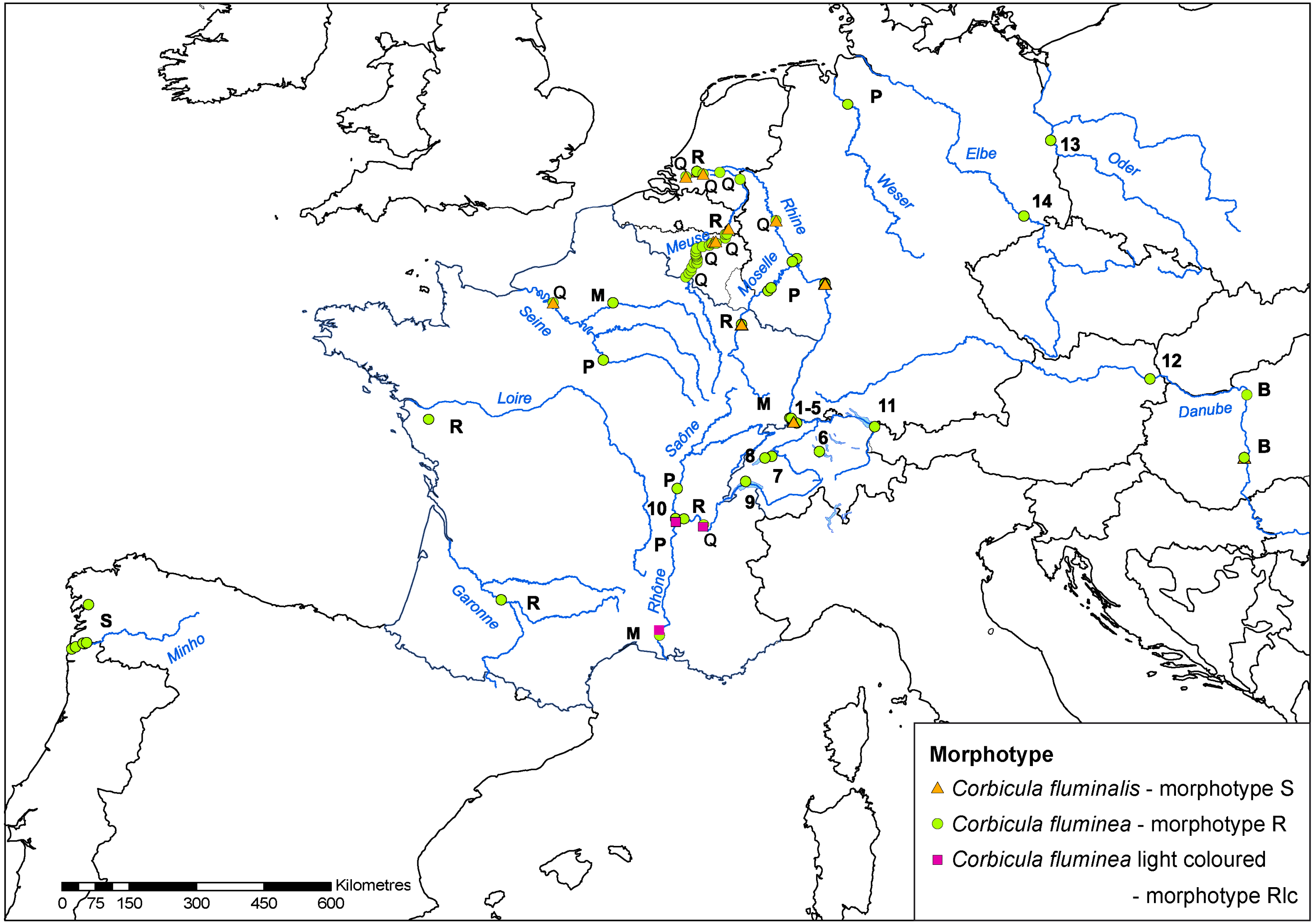

Figure 3.2 Distribution of *Corbicula* with known haplotypes in Europe (not all sites are shown). Capitals refer to the authors: R: Renard et al. (2000), P: Pfenninger et al. (2002), S: Sousa et al. (2007) B: sequences published by Bódis in Genbank in 2010, M: Marescaux et al. (2010) and combined data from GenBank. Figures (1-14) indicate the sampling sites of the present study (see also Table 1A). Coordinates of additional sampling sites are listed in the Appendix 1.

is generally assumed to contribute to the dispersal of alien species (Burgin and Hardiman 2011).

Passive transport of *Corbicula* by waterfowl is another possible pathway for distant transportation of clams. Lowland lakes in Switzerland serve as resting and feeding places for over-wintering water birds (Keller and Burkhard 2010). During the winter season waterfowl frequently cross Switzerland from Northeast (Lake Constance) to Southwest (Lake Geneva), providing opportunities for passive transportation. A similar range expansion of *Corbicula* has been recorded in lakes in the United States (Thompson and Sparks 1977). There, the spread of the invasive clam was related to the migration corridors of waterfowl. Passive dispersal on bird feet or in feathers seems to be likely due to sticky mucous secretions of juvenile clams, which facilitate attachment (Voelz et al. 1998, Brancotte and Vincent 2002).

The lack of genetic diversity found in *Corbicula* spp. in Switzerland is not unexpected. Other studies reported similar low levels of genetic diversity. For instance, Siripattrawan et al. (2000) recorded a single haplotype in *Corbicula* samples from Michigan and North Carolina, which was genetically distinct from the single haplotype found in specimens collected in Utah and New Mexico.

Introduced *Corbicula* populations from temperate, subtropical, and tropical localities in North and South America were also dominated by the same haplotype, demonstrating its wide geographical range (Lee et al. 2005, Hedke et al. 2008). This most widespread lineage is the same both in Europe and America. In Europe, this haplotype occurs from the Iberian Peninsula to the Black Sea (Rhine: Pfenninger et al. 2002; Danube: GenBank sequences provided by Bódis et al. 2011; Loire: Renard et al. 2000; Minho: Sousa et al. 2007). Introductions from a single locality and/or post-colonisation from other introduced populations could partly explain the low genetic diversity found in Europe and North and South America. However, this haplotype is also one of the most common haplotypes in the clam’s native range (haplotype FW5; Park and Kim 2003). Introduced individuals of *Corbicula* may reproduce by androgenesis, a relatively rare mode of asexual reproduction (Komaru et al. 1998, Hedtke et al. 2008). This form of reproduction reduces the genetic diversity. However, asexual reproduction is a common means to become invasive despite low genetic diversity (Roman and Darling 2007).

In our study, the only site with a co-existence of two haplotypes (FW5 and FW17) was in the River Rhine near Birsfelden where international cargo shipping is possible. Haplotypes other than FW5 have been recorded at much lower frequency in Europe (Pfenninger et al. 2002). Thus, competitive interactions among different haplotypes should be considered.

Darrigran (1991) suggested that clams identified as *Corbicula fluminea*/form R/haplotype FW5 have some competitive advantage over other *Corbicula* species with FW17 haplotype. In the La Plata region of South America, haplotype FW17 has been replaced almost completely by the dominant haplotype FW5 (Darrigran 1991, Lee et al. 2005). Considering the high abundance and wide distribution of haplotype FW5 in Europe and the clam's tolerance to low temperatures (Müller and Baur 2011), it is not surprising to find this haplotype in the newly colonized lakes in Switzerland.

Mitochondrial haplotypes can be unambiguously identified. In our study, haplotypes corresponded to species and forms (*C. fluminea*/ form R/haplotype FW5, *C. fluminalis*/form S/haplotype FW17). However, the species status remains uncertain. Specimens collected by Pfenninger et al. (2002) and the sample analysed in this study in the River Rhine harbouring the haplotype FW17 belong to the same lineage as the haplotype IV from the river Rhône analysed by Renard et al. (2000). Interestingly, these individuals with haplotype IV had the round shell form of *C. fluminea* (*C. fluminea*/form R/haplotype FW17, see also Pigneur et al. 2011). Several other studies showed mismatches between operational taxonomic units (OTUs) and operational genetic units (OGUs, Renard et al. 2000, Siripattrawan et al. 2000, Pfenninger et al. 2002, Glaubrecht and Korniushin 2003, Park and Kim 2003), possibly due to androgenesis. Based on findings in freshwater populations of *Corbicula*, Lee et al. (2005) concluded that any systematic interpretation relying exclusively on mitochondrial lineages could be misleading due to discrepancies between mitochondrial and nuclear markers. This highlights the need to analyse both morphological and genetic (mitochondrial and nuclear) variation in future studies.

There is an increasing interest in incorporating genetic analyses into biomonitoring programs (DeWalt 2011). Any discrepancy between OTU- and OGU-based analyses (Pilgrim et al. 2011) requires a detailed consideration of the correspondence between taxonomic and genetic units. In this case, we advocate a parallel assignment of individuals to both an OTU and an OGU until the taxonomic nomenclature incorporates recent evidence of genetic analyses.

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Appendix 1

Appendix 1 Locations of *Corbicula* spp. records in Europe. Coordinates were extracted either from the references or they were added according to the localities mentioned in the literature. Localities were ordered following the authors: R: Renard et al. (2000), P: Pfenninger et al. (2002), S: Sousa et al. (2007), M: Marescaux et al. (2010), B: Bódis et al. (2011), Q: Pigneur et al. (2011). *Indicates mismatch between species and haplotype. Remark: Pigneur et al. (2011) did not assign individuals to a species.

Location	Country	Latitude N °	Longitude E °	Species	Morphotype	Haplotype	Author
Loire, Nantes	France	47.02	-1.50	*C. fluminea*	R	I	R
Loire, Nantes	France	47.02	-1.50	*C. fluminea*	R	II	R
Garonne, Golfech	France	44.12	0.83	*C. fluminea*	R	I	R
Rhône, Jonage	France	45.80	5.03	*C. fluminea**	Rlc	IV	R
Moselle, Argancy	France	49.20	6.20	*C. fluminea*	R	I	R
Moselle, Argancy	France	49.20	6.20	*C. fluminalis*	S	V	R
Meuse, km 252	Netherlands	50.84	5.71	*C. fluminalis*	S	V	R
Rhine, Dordecht	Netherlands	51.78	4.75	*C. fluminalis*	S	V	R
Rhine, Dordecht	Netherlands	51.78	4.75	*C. fluminea*	R	I	R
Oise	France	49.41	2.81	*C. fluminea*	R		M
Seine	France	-	-	*C. fluminalis*	S		M
Gard	France	43.86	4.61	*C. fluminea* *C. fluminea* - light coloured	R, Rlc		M
Danube, near Paks	Hungary	46.58	18.87	*C. fluminalis*	S	ZF80	B
Danube, near Paks	Hungary	46.58	18.86	*C. fluminea*	R	Hap97	B
Danube, near Göd	Hungary	47.68	18.86	*C. fluminea*	R	Hap98	B
Weser km 360, Bremer Weserwehr Canal	Germany	53.05	8.88	*C. fluminea*	R	H2	P
Weser km 360, Bremer Weserwehr Canal	Germany	53.05	8.88	*C. fluminea*	R	H2	P

Appendix 1 continued

Location	Country	Latitude N °	Longitude E °	Species	Morphotype	Haplotype	Author
Moselle km 141, Wintrich	Germany	49.86	6.93	*C. fluminea*	R	H2	P
Moselle km 21, Lehmen	Germany	50.32	7.47	*C. fluminea*	R	H2	P
Moselle km 2, Koblenz	Germany	50.37	7.58	*C. fluminea*	R	H2	P
Moselle km 166, Detzem	Germany	49.80	6.85	*C. fluminea*	R	H2	P
Rhine km 492 RHA, Ginsheim	Germany	49.97	8.35	*C. fluminea*	R	H2	P
Rhine km 492 RHA, Ginsheim	Germany	49.97	8.35	*C. fluminea*	R	H2	P
Rhine km 492 RHA, Ginsheim	Germany	49.97	8.35	*C. fluminea*	R	H2	P
Rhine km 493, Ginsheim?	Germany	49.96	8.35	*C. fluminea*	R	H2	P
Weser km 360, Bremer Weserwehr Canal	Germany	53.05	8.88	*C. fluminea*	R	H24	P
Moselle km 21, Lehmen	Germany	50.32	7.47	*C. fluminea*	R	H12	P
Moselle km 166, Detzem	Germany	49.80	6.85	*C. fluminea*	R	H11	P
Saône near Mâcon	France	46.32	4.82	*C. fluminea*	R	H29	P
Saône near Mâcon	France	46.32	4.82	*C. fluminea*	R	H28	P
Moselle km 141, Wintrich	Germany	49.86	6.93	*C. fluminea*	R	H14	P
Moselle km 141, Wintrich	Germany	49.86	6.93	*C. fluminea*		H10	P
Moselle km 141, Wintrich	Germany	49.86	6.93	*C. fluminea*	R	H13	P
Saône near Mâcon	France	46.32	4.82	*C. fluminea*	R	H27	P
Seine near Fontainebleau	France	48.41	2.71	*C. fluminea*	R	H31	P
Rhône near Lyon	France	45.74	4.83	*C. fluminea* - light coloured	Rlc	H25	P
Rhine km 492 RHA, Ginsheim	Germany	49.97	8.35	*C. fluminalis*	S	H4	P
Rhine km 492 RHA, Ginsheim	Germany	49.97	8.35	*C. fluminalis*	S	H9	P
Rhine km 493, Ginsheim	Germany	49.96	8.35	*C. fluminalis*	S	H5	P
Rhine km 493, Ginsheim	Germany	49.96	8.35	*C. fluminalis*	S	H1	P
Rhône near Lyon	France	45.74	4.83	*C. fluminea* - light coloured	Rlc	H26	P
Rhône near Lyon	France	45.74	4.83	*C. fluminea* - light coloured	Rlc	H8	P
Rhine km 492 RHA, Ginsheim	Germany	49.97	8.35	*C. fluminalis*	S	H6	P

Appendix 1 continued

Location	Country	Latitude N °	Longitude E °	Species	Morphotype	Haplotype	Author
Rhine km 493, Ginsheim	Germany	49.96	8.35	*C. fluminalis*	S	H3	P
Minho, O Carrascal	Portugal	41.91	-8.82	*C. fluminea*	R	Sousa4	S
Minho, O Carrascal	Portugal	41.91	-8.82	*C. fluminea*	R	Sousa1	S
Minho, Cerveira	Portugal	41.96	-8.75	*C. fluminea*	R	Sousa4	S
Minho, Cerveira	Portugal	41.96	-8.75	*C. fluminea*	R	Sousa2	S
Minho, Valença	Portugal	42.05	-8.56	*C. fluminea*	R	Sousa4	S
Minho, Valença	Portugal	42.05	-8.56	*C. fluminea*	R	Sousa3	S
Minho, Caldelas de Tui	Portugal	42.05	-8.60	*C. fluminea*	R	Sousa4	S
Minho, Caldelas de Tui	Portugal	42.05	-8.60	*C. fluminea*	R	Sousa3	S
Minho, Eirado	Portugal	42.08	-8.52	*C. fluminea*	R	Sousa4	S
Minho, Eirado	Portugal	42.08	-8.52	*C. fluminea*	R	Sousa2	S
Lima, Geraz	Portugal	42.73	-8.68	*C. fluminea*	R	Sousa4	S
Meuse, Revin	France	49.94	4.64		R	FW5	Q
Meuse, Vireux-Molhain	France	50.09	4.72		R	FW5	Q
Meuse, Chooz	France	50.10	4.81		R	FW5	Q
Meuse, Heer-Agimont	Belgium	50.17	4.82		R	FW5	Q
Meuse, Hastière	Belgium	50.22	4.82		R	FW5	Q
Meuse, Waulsort	Belgium	50.20	4.87		R	FW5	Q
Meuse, Dinant	Belgium	50.26	4.91		R	FW5	Q
Meuse, Houx	Belgium	50.30	4.90		R	FW5	Q
Meuse, Godinne	Belgium	50.35	4.87		R	FW5	Q
Meuse, Rivière	Belgium	50.36	4.87		R	FW5	Q
Meuse, Talifer	Belgium	50.39	4.88		R	FW5	Q
Meuse, Beez	Belgium	50.47	4.91		R	FW5	Q
Meuse, Sclayn	Belgium	50.49	5.03		R	FW5	Q
Meuse, Huy	Belgium	50.52	5.23		R	FW5	Q
Meuse, Tihange	Belgium	50.53	5.26		R	FW5	Q
					S	FW17	
Meuse, Amay	Belgium	50.55	5.31		R	FW5	Q
					S	FW17	

Appendix 1 continued

Location	Country	Latitude N °	Longitude E °	Species	Morphotype	Haplotype	Author
Meuse, Liège-Monsin	Belgium	50.67	5.64		R	FW5	Q
Meuse, Hermalle-sous-Argenteuy	Belgium	50.71	5.68		R	FW5	Q
Meuse, Lixhe	Belgium	50.76	5.68		R	FW5	Q
Meuse, Cuijk	Netherland	51.73	5.88		R	FW5	Q
Meuse, Alem	Netherland	51.79	5.35		R	FW5	Q
Rhine-Meuse delta, Moerdijk	Netherland	51.68	4.60		R	FW5	Q
					S	FW17	
Rhine-Meuse delta, “Midden”	Netherland	51.76	4.21		R	FW5	Q
					S	FW17	
Seine, Posés	France	49.31	1.23		R	FW5	Q
					S	FW17	
Rhine, Köln	Germany	50.94	6.96		R	FW5	Q
					S	FW17	
Rhône, Creys	France	45.73	5.49		R	FW5	Q
					Rlc	FW4	

Chapter 4: Alien molluscs affect the composition and diversity of native macroinvertebrates in a sandy flat of Lake Neuchâtel, Switzerland

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Abstract

The spread of alien molluscs is a serious threat to native biodiversity in fresh waters. Alien freshwater molluscs may deplete the resources of native species and alter the physical structure of the habitat through their shell mass. These changes might have both positive and negative effects on native community members. We investigated the native macroinvertebrate community in relation to the densities of four alien mollusc species (*Corbicula fluminea*, *Dreissena polymorpha*, *Potamopyrgus antipodarum* and *Lithoglyphus naticoides*) in a sandy flat of Lake Neuchâtel, Switzerland. The habitat examined was dominated by these alien mollusc species. The abundance of the alien molluscs did not directly impact the native community assembly. However, *C. fluminea* and *D. polymorpha* influenced the composition and diversity of native macroinvertebrates by transforming the sandy substratum into a partly hard substratum habitat. Substantial differences in community composition between shallow (<3.5 m) and (≥5 m) deep sites were recorded. At shallow sites, the abundance of *D. polymorpha* was significantly reduced as a result of depth-selective feeding of ducks. A controlled shell decay study revealed that shells of alien molluscs (*C. fluminea*, *D. polymorpha*) persist for a longer period in the sediment than those of native molluscs. Consequently, shells of alien molluscs have a long-lasting impact by modifying the sandy habitat. This form of ecosystem engineering favours the occurrence of several native taxa, but is disadvantageous for other taxa with specific habitat requirements, and thus can be regarded as an indirect impact of competition.

Key words: alien species, lake littoral, macroinvertebrates, *Corbicula fluminea*, *Dreissena polymorpha*, ecosystem engineer, SCUBA-diving

Introduction

Invasive species often reduce the local biodiversity and probably will influence the global biodiversity in the future (Sala et al. 2000, Nentwig 2007). Interactions between invasive and native species, including competition, predation and transmission of diseases and parasites can change natural communities (Mooney et al. 2005). Invasive species may also function as ecosystem engineers by altering abiotic and/or biotic factors of habitats or by creating novel habitats, and thereby facilitating native species (Jones et al. 1997, Gutierrez et al. 2003).

Freshwaters are experiencing declines in biodiversity far greater than those in the most affected terrestrial ecosystems (Dudgeon et al. 2006). Besides of pollution, destruction or degradation of habitat and flow modification, the invasion of non-native species is a major threat to native freshwater biodiversity (Strayer 1999). One of the most important groups of freshwater invaders includes molluscs that suspension-feed on phytoplankton and seston, graze on periphyton, or browse on vascular plants (Strayer 2010). Furthermore, invasive molluscs may act as ecological engineers by creating large amounts of shells (Gutierrez et al. 2003, Sousa et al. 2009). This shell material can persist for a long time after the molluscs die, providing habitat for other organisms, especially in soft sediments (Strayer and Malcom 2007), and playing an important part in cycling of CO_2 and Ca^{2+} (e.g. Green 1980, Chauvaud et al. 2003).

In the past decades, European inland waters have been increasingly affected by the colonisation of non-native molluscs, causing significant changes in aquatic communities (Strzelec 2000, Mörtl and Rothhaupt 2003, Baur and Schmidlin 2007, Gergs and Rothhaupt 2008, Sousa et al. 2008a). For example, the invasion of the zebra mussel, *Dreissena polymorpha* (Pallas, 1771*)*, influenced the abundance of sediment bacteria, caused both benthic algal blooms and declines in native unionid mussel and fish populations as well as changes in physical and chemical attributes that define the habitat for all resident species (Higgins and Vander Zanden 2010).

Populations with high densities of the Asian clam *Corbicula fluminea* (O. F. Müller, 1774) caused modest to dramatic declines in phytoplankton and seston (Leff et al. 1990, Phelps 1994). Strayer (1999) assumed that large numbers of unionid sperm, glochidia, and newly metamorphosed juveniles might be ingested in dense populations of *C. fluminea*. In contrast to the zebra mussel, *C. fluminea* actively disturbs the sediment by pedal feeding. Thus, high densities of *C. fluminea* may reduce both habitat quality and food supply for native macroinvertebrates (Hakenkamp and Palmer 1999). On the other hand, a short-term field experiment in the Lake Constance demonstrated that valves of *C. fluminea* enhanced the density of the mayfly *Caenis* spp. on soft substrate and that living clams hindered juvenile *C. fluminea* with a chemical cue from settling in close proximity to reduce intraspecific competition (Werner and Rothhaupt 2007, 2008). Furthermore, a laboratory experiment showed that valves of *C. fluminea* increased the abundance of benthic invertebrates in poorly structured sediment (Werner and Rothhaupt 2008). However, there are still huge gaps in our understanding of how *C. fluminea* impacts native benthic invertebrate communities in natural freshwater bodies.

Corbicula fluminea is nowadays one of the most abundant mollusc species in many European lowland lakes and rivers, often co-occurring with other alien species and interacting with the native community (Schmidlin and Baur 2007, Sousa et al. 2008b, Werner and Rothhaupt 2008, Müller and Baur 2011). The clam colonized lake Neuchâtel, Switzerland, in 2003 (P. Stucki, personal communication). In this lake three other alien molluscs occur: *D. polymorpha* (first recorded in 1976; Pedroli 1978), and the snails *Potamopyrgus antipodarum* (J. E. Gray, 1843; first recorded in 1978; Crozet et al. 1980) and *Lithoglyphus naticoides* (C. Pfeiffer, 1828; first recorded in 1998; CSCF 2010).

We examined the native benthic macroinvertebrate community in relation to the densities of these four alien molluscs in a sand flat of the littoral zone of Lake Neuchâtel with the assumption that alien molluscs influence native communities. We also conducted a field experiment to assess the decay rate of empty shells of different mollusc species. In particular, we addressed the following questions:

1) How frequently and in which density do the alien molluscs *C. fluminea*, *D. polymorpha*, *P. antipodarum* and *L. naticoides* occur in the sandy flat in Lake Neuchâtel?
2) Do alien species influence the community assembly of native benthic macroinvertebrates?
3) Do the four alien molluscs act as ecosystem engineers by providing shells with a low decaying rate as additional hard substratum and thus facilitates other macroinvertebrate taxa?

Material and Methods

Study area

Lake Neuchâtel (surface area: 217.9 km², mean depth: 64.2 m) is a pre-alpine, calcareous, mesotrophic lake situated at the foot of the Jura Mountains in Western Switzerland. Its drainage area covers approximately 2,670 km^2. The littoral zone covers 26.5% of the area of Lake Neuchâtel and sand flats constitute a significant part of this zone (Sollberger 1974). Both the field survey and the shell decay assessment were conducted in a shallow sandy section of the littoral zone at the south-eastern shore of Lake Neuchâtel near the port of Portalban (46.922 N, 6.949 E). The study area measured about 600 m x 500 m and is situated in close proximity of a bird and wetland reserve of national importance.

Field survey

Using SCUBA-diving, benthic macroinvertebrates were collected from the sandy substratum in an area of about 0.3 km^2 on five occasions. On each occasion, 10-14 sampling sites, arranged at distances of 30-50 m along 600-m long transect lines running perpendicular to the shore line, were considered. The survey was conducted on the following dates: 20 May 2007 (2 transects, each with 12 sampling sites), 21 October 2007 (2 transects each with 10 sampling sites), 24 May 2008 (1 transect with 14 sampling sites), 18 October 2008 (1 transect with 14 sampling sites), and 16 May 2009 (1 transect with 13 sampling sites). For each of the 85 sampling sites, we measured shore distance, water depth, cover of submerged vegetation (a semiquantitative estimate), type of sediment and organic matter of the sediment and determined the geographical coordinates using GPS (Garmin Geko 201). However, because of the strong inter-correlation of environmental variables (shore distance and water depth) and of the low variation in the remaining variables we used only water depth in the data-analyses. The water depth ranged from 0.73 to 22.14 m (N=85).

At each of the 85 sites, macroinvertebrates were collected using a circular metallic frame (radius: 11 cm, 7 cm high). The frame was pressed by hand into the sandy substratum and the topmost 5 cm of the bottom material was transferred into a bag with a mesh size of 2.0 mm using a small shovel. Three of these subsamples were collected at each sampling site. Macroinvertebrates were labelled, preserved in 75% ethanol and then returned to the laboratory for examination.

Macroinvertebrates were later identified to the lowest taxonomic level possible using the keys of Schwab (1995), Grabow (2000), and Tachet et al. (2006) for various invertebrate groups, Glöer and Meier-Brook (1998) and Glöer (2002) for Mollusca, Neubert and Nesemann (1999) for Hirudinae, Lechthaler and Stockinger (2005) for Trichoptera and Studemann et al. (1992) for Ephemeroptera.

Assessment of shell decay rate

We measured the relative decay rate of shells [(initial shell weight – final shell weight) / initial shell weight] over 1 year in five mollusc species co-existing in Lake Neuchâtel: two native gastropods (*Bithynia tentaculata* [Linnaeus, 1758], *Valvata piscinalis* [O. F. Müller, 1774]), one alien gastropod (*P. antipodarum*) and two alien bivalves (*C. fluminea*, *D. polymorpha*). We used shells from living animals sampled in the field survey near Portalban. The animals were killed in 75% ethanol. The soft bodies were removed from the shells and the shells were air-dried. We constructed water-resistant “litter” bags measuring 8 cm x 9 cm using window screening with a mesh size of 2.0 mm. We placed either 7 shells of *B. tentaculata* (mean shell height: 9.2 mm), 7 shells of *V. piscinalis* (4.1 mm), 10 shells of *P. antipodarum* (4.2 mm), 10 valves of *C. fluminea* (mean valve length: 18.0 mm) or 10 valves of *D. polymorpha* (15.4 mm) in single bags. The total weight of shells or valves in each bag was measured to the nearest 0.01 mg before the bag was sealed. For each species 20 bags were used (in total 100 bags). Bags were fixed with a rope and metallic sticks on the sandy substratum (> 30 cm apart from each other) at water depths of 1 m (20 bags), 6 m (40 bags) and 8 m (40 bags). We placed bags into the field on 24 May 2008 and retrieved them on 16 May 2009. We carefully removed the shells from the bags and cleaned them. Air-dried shells were reweighed. In total, we recovered 89 of the 100 bags initially exposed.

The water of Lake Neuchâtel was supersaturated with $CaCO_3$ in 2007-2009 (total hardness $CaCO_3$: 2.78−144 mg l^{-1}; Ca^{2+}: 2.0−56.2 mg l^{-1}; pH: 8.0−8.5; SCPE Neuchâtel, Service de la protection de l'environnement; www.les3lacs.ch 2007-2009).

Statistical analyses

Macroinvertebrates from the three subsamples at each sampling site were pooled resulting in 85 samples for data analyses. Raw data (number of individuals recorded for each species) from each sample were used in all analyses. Altogether 23,342 individuals were assigned to a species or a higher taxonomic group. On all five sampling occasions molluscs were the most abundant group (74.8 – 88.5% of the individuals collected, grand mean = 82.4%). We therefore examined seasonal differences (May versus October) in the abundance of molluscs and the remaining macroinvertebrate taxa. Because the proportion of molluscs and that of the remaining taxa did not show any significant differences between the samples collected in May and October (χ^2 = 2.47, *df* = 1, *P* = 0.12), we pooled the samples from different sampling seasons for community analyses. The frequency distribution of sampling sites in relation to water depth was bimodal. Consequently, based on water depth, sampling sites were assigned to two groups: shallow sites with a depth <3.5 m [N = 71 sites (83.5%), mean depth 1.90 m, range 0.73 – 3.34] and deep sites with a depth ≥5 m [N = 14 sites (16.5%), mean depth 8.94 m, range 5.00 – 22.14 m].

Analysis of similarities (ANOSIM; Clarke 1993) was used to test community-based separation of samples collected at shallow and deep sites. ANOSIM is a non-parametric multivariate analysis that compares the mean of the ranked similarities within and between water depth groups based on R values. R ranges from -1 to +1. An R value of 1 indicates that the most similar sites belong to the same depth group. R=0 indicates that sites with high and low similarities occur in equal frequencies in both depth groups, whereas an R value of -1 shows that the most similar sites belong to different depth groups. ANOSIM was run using the Bray-Curtis dissimilarity index (Podani 2000) with 999 permutations.

Indicator species analysis (INDVAL; Dufrene and Legendre 1997) was run to identify characteristic taxa of shallow and deep sites, respectively. Analysis of variance using distance matrices (called ADONIS in R), referred to also as "permutation MANOVA", "nonparametric MANOVA" (Anderson 2001, McArdle and Anderson 2001) or "multivariate regression analysis of distance matrices" (Zapala and Schork 2006), was used to test how alien mollusc taxa influence community similarity of native taxa [for further details see Zapala and Schork (2006) or Oksanen et al. (2009)]. For the distance matrices, we used the Bray-Curtis dissimilarity index with 999 permutations.

Generalized linear models (GLM) with Poisson distribution were used to test how the four most abundant alien taxa (see result: *D. polymorpha*, *C. fluminea*, *P. antipodarum* and *L. naticoides*) influence the numbers of native taxa, native individuals, protected taxa, protected individuals, taxa with sand preference, individuals with sand preference, native taxa with hard bottom preference and native individuals with hard bottom preference. The application of Poisson distribution was necessary because of the many zeros in the response variables. The abundances of the four alien taxa were log(x+1) transformed to decrease the impact of extreme values. Overdispersion was tested following Wetherill and Brown (1991). If abundance data were not overdispersed then the final model was selected based on Akaike's Information Criterion (AIC). If data structure showed overdispersion, we fitted quasipoisson models and model selection was performed manually. We used each alien mollusc species as an independent variable in model building. To get reliable mathematical models, we ran GLMs for variables with data from at least 10 species occurrences. In cases with fewer occurrences, the impact of alien molluscs on native protected species and sand preferring taxa at deep sites was not tested.

To take into account size differences among alien mollusc species and potential effects of empty mollusc shells on the native community, we expressed the abundance of the four alien molluscs in the GLMs in four different ways: A) numbers of living individuals, B) shell weight of living individuals, C) shell weight of living and empty (dead) individuals, and D) shell weight of empty (dead) individuals.

To estimate the shell mass at each sampling site, we used the mean shell weight of each species measured in the shell decay study (see below), multiplied by the corresponding numbers of individuals per m^2. *L. naticoides* was not considered in the shell decay study. We therefore calculated its shell weight following the protocol used in the shell decay study.

The relative shell decay rate was calculated based on the pre- and post-experimental weight of shells in each bag. To compare shell decay rates, a nested linear model was fitted to the data with the relative shell decay rate as response variable and with type of origin (native vs. alien) and taxon (*B. tentaculata, V. piscinalis, C. fluminea, D. polymorpha* and *P. antipodarum*, nested with the type of origin) as categorical predictors next to water depth and individual shell weight as continuous predictors. We started with the full model and simplified it based on AIC. For all analyses, we used the R statistical computing environment (R Development Core Team 2009). ANOSIM and analysis of variance using distance matrices (= ADONIS) were calculated using the *vegan* package (Oksanen et al. 2009), for testing overdispersion the *qcc* package (Scrucca 2004), and for INDVAL (Dufrene and Legendre 1997) the *labdsv* package was used (Roberts 2010).

Null models are frequently used to elucidate assembly rules or a set of mechanisms (e.g. competition) that lead to non-random patterns in multi-species assemblages (Gotelli and Graves 1996, Ulrich 2004). Null models are adequate tools for detecting biotic interactions based on distributional data of taxa. However, these models are based on the assumptions that there are no differences among habitat characteristics, no influence of the biogeographical and evolutionary history of the samples, and that only biotic interactions and chance variation are responsible for the community patterns observed (Gotelli and Graves 1996, Ulrich 2004). In the present study, most of these requirements were fulfilled because sampling was restricted to a relatively homogenous (sandy) habitat limited in space (0.3 km^2) and time (sampling period < 2 years). Tests of null models were originally developed for presence/absence data in studying species communities (Gotelli 2000). Recent advances allow an examination of null models for data sets with species abundances (Ulrich and Gotelli 2010). We used the standardised number of "abundance checkerboard" (CA_{ST}) to identify possible competitive interactions between native taxa. CA_{ST} represents an abundance analogy of "checkerboard" distributions (Diamond 1975), a distribution pattern where species pairs never co-occur together (Ulrich and Gotelli 2007). CA_{ST} varies between 0 (indicates no competition) and 1 (indicates strong competition). To test whether a calculated CA_{ST} value comes from a chance event or reflects real competition, we compared the calculated CA_{ST} values with a null distribution using IT null model algorithm (Ulrich and Gotelli 2010) based on 100 random assemblages. The IT algorithm reassigns all individuals randomly to matrix cells with probabilities proportional to the totals of observed row and column abundances until total abundances are reached for each row and column. The IT algorithm shows a low Type I error rate compared to other algorithms (Ulrich and Gotelli 2010).

First, we run our null models for both shallow and deep sites separately. To elucidate the possible impact of the four alien species (*C. fluminea*, *D. polymorpha*, *L. naticoides* and *P. antipodarum*) within depth level, sampling sites were further divided into two groups: (1) sampling sites with low abundance of alien species (abundance of the alien species was less than the median of their total abundance at the depth level), and (2) sampling sites with high abundance of alien species (abundance of alien species was equal to or larger than the median of their total abundance). We compared the raw abundance checkerboard values and their relative positions compared to the generated null distributions. Null models were run using CoOccurrence software (Ulrich 2006).

Results

Taxa richness and abundance

We found 45 taxa among the 17,929 individuals collected at shallow sites and 36 taxa among the 5,413 individuals at deep sites (Table 4.1). The alien bivalve *C. fluminea* was the only species occurring at all shallow (71) and deep (14) sampling sites. Further taxa with high frequencies of occurrence were *Pisidium* sp. (shallow sites: 95.8%; deep sites: 85.7%), *D. polymorpha* (93.0%; 100%), Oligochaeta (93.0%; 92.9%) and *P. antipodarum* (91.6%;

Table 4.1 Frequency of occurrence of the identified macroinvertebrate taxa (number of sites), mean density (± standard error**)** and maximum density of individuals in shallow (<3.5 m) and deep (≥5 m) littoral sites near Portalban in Lake Neuchâtel. The origin (native or alien) and protection status are also indicated

Group	Taxon	Shallow sites (<3.5 m; N = 71)			Deep sites (≥5 m; N = 14)			Type of origin[1]	Protection status[2]
		Frequency of occurrence (%)	Mean density ind./m^2 (± se)	Maximum density ind./m^2	Frequency of occurrence (%)	Mean density ind./m^2 (± se)	Maximum density ind./m^2		
PORIFERA	*Spongilla lacustris***	32 (45.1)	na	na	0 (0.0)	0.0 (0.0)	0.0	N	n
HYDROZOA	*Hydra viridissima*	7 (9.9)	10.0 (5.5)	343.2	5 (35.7)	42.1 (15.5)	528.0	N	n
TURBELLARIA	Turbellaria indet.**	1 (1.4)	0.1 (0.1)	8.8	2 (14.3)	18.2 (7.3)	246.4	N	n
	Dugesia sp. (cf. *D. tigrina*)**	0 (0.0)	0.0 (0.0)	0.0	2 (14.3)	3.1 (1.1)	35.2	A	n
OLIGOCHAETA	Oligochaeta spp.	66 (93.0)	215.2 (25.3)	968.0	13 (92.9)	226.9 (30.5)	941.6	N	n
	Branchiura sowerbyi	11 (15.5)	1.9 (0.5)	17.6	1 (7.1)	0.6 (0.3)	8.8	A	n
HIRUDINAE	*Erpobdella* sp.**	23 (32.4)	12.2 (2.8)	123.2	6 (42.9)	8.8 (1.6)	52.8	N	n
	*Alboglossiphonia heteroclita***	7 (9.9)	3.2 (1.6)	105.6	6 (42.9)	8.2 (1.4)	35.2	N	n
	*Glossiphonia complanata***	2 (2.8)	0.3 (0.2)	8.8	4 (28.6)	5.7 (1.4)	44.0	N	n
	Helobdella stagnalis	29 (40.9)	11.8 (2.6)	96.8	9 (64.3)	17.6 (2.6)	88.0	N	n
GASTROPODA	*Bithynia tentaculata***	37 (52.1)	25.5 (7.9)	554.4	10 (71.4)	30.2 (4.4)	149.6	N	n
	Lithoglyphus naticoides	44 (62.0)	19.0 (3.6)	184.8	7 (50.0)	13.8 (2.2)	52.8	A	n
	Potamopyrgus antipodarum	65 (91.6)	470.0 (74.5)	3264.8	11 (78.6)	257.1 (28.0)	748.0	A	n
	Valvata piscinalis	3 (4.2)	1.5 (1.0)	70.4	7 (50.0)	17.6 (2.7)	79.2	N	n
	Radix auricularia	2 (2.8)	0.3 (0.2)	8.8	0 (0.0)	0.0 (0.0)	0.0	N	n
	Radix balthica	3 (4.2)	0.6 (0.3)	17.6	3 (21.4)	1.9 (0.4)	8.8	N	n
	Lymnea stagnalis	1 (1.4)	0.1 (0.1)	8.8	0 (0.0)	0.0 (0.0)	0.0	N	n
	Gyraulus albus	4 (5.6)	3.4 (2.6)	193.6	7 (50.0)	15.7 (3.4)	114.4	N	n
	Gyraulus crista	1 (1.4)	0.1 (0.1)	8.8	3 (21.4)	3.1 (0.8)	26.4	N	3
	Planorbis carinatus	2 (2.8)	0.5 (0.4)	26.4	0 (0.0)	0.0 (0.0)	0.0	N	3
BIVALVIA	*Sphaerium corneum*	0 (0.0)	0.0 (0.0)	0.0	1 (7.1)	0.6 (0.3)	8.8	N	n
	Pisidium spp.	68 (95.8)	232.8 (31.0)	1460.8	12 (85.7)	143.9 (18.3)	413.6	N	n
	*Corbicula fluminea**	71 (100.0)	515.6 (65.9)	3599.2	14 (100.0)	404.8 (76.3)	2657.6	A	n

Table 4.1 continued

	*Dreissena polymorpha***	66 (93.0)	586.0 (99.7)	5368.0	14 (100.0)	1963.0 (192.4)	5473.6	A	n
BRYOZOA	*Cristatella mucedo*	2 (2.8)	0.3 (0.16)	8.8	5 (35.7)	52.2 (14.0)	396.0	N	n
CRUSTACEA	*Dikerogammarus villosus***	16 (22.5)	2.4 (0.5)	17.6	5 (35.7)	11.9 (2.2)	61.6	A	n
	*Gammarus pulex***	1 (1.4)	0.1 (0.1)	8.8	2 (14.3)	1.3 (0.4)	8.8	N	n
	Asellus aquaticus	0 (0.0)	0.0 (0.0)	0.0	6 (42.9)	34.6 (8.9)	299.2	N	n
COLEOPTERA	*Donacia* sp.	4 (5.6)	1.2 (0.8)	61.6	0 (0.0)	0.0 (0.0)	0.0	N	n
DIPTERA	Chironominae**	50 (70.4)	44.0 (7.7)	308.0	12 (85.7)	65.4 (6.4)	184.8	N	n
	Orthocladiinae**	8 (11.3)	1.0 (0.3)	8.8	0 (0.0)	0.0 (0.0)	0.0	N	n
	Tanypodinae	3 (4.2)	0.5 (0.3)	17.6	6 (42.9)	6.9 (1.5)	52.8	N	n
	Ceratopogonidae	8 (11.3)	1.5 (0.6)	35.2	2 (14.3)	2.5 (0.7)	17.6	N	n
EPHEMEROPTERA	*Centroptilum luteolum*	2 (2.8)	0.3 (0.2)	8.8	0 (0.0)	0.0 (0.0)	0.0	N	4
	Cloeon dipterum	1 (1.4)	0.1 (0.1)	8.8	0 (0.0)	0.0 (0.0)	0.0	N	n
	Caenis macrura	9 (12.7)	3.8 (1.9)	140.8	1 (7.1)	1.3 (0.5)	17.6	N	n
	Caenis horaria	12 (16.9)	6.8 (3.9)	290.4	3 (21.4)	2.5 (0.6)	17.6	N	n
	Caenis luctuosa	7 (9.9)	2.6 (1.3)	96.8	1 (7.1)	0.6 (0.3)	8.8	N	n
	*Ephemera vulgata**	2 (2.8)	0.3 (0.2)	8.8	0 (0.0)	0.0 (0.0)	0.0	N	3
	*Ephemera lineata**	15 (21.1)	5.1 (1.7)	114.4	1 (7.1)	0.6 (0.3)	8.8	N	1
	*Ephemera danica**	13 (18.3)	4.1 (1.3)	61.6	0 (0.0)	0.0 (0.0)	0.0	N	4
LEPIDOPTERA	*Acentria ephemerella*	4 (5.6)	0.7 (0.4)	17.6	0 (0.0)	0.0 (0.0)	0.0	N	n
ODONATA	*Ischnura* sp.	1 (1.4)	0.1 (0.1)	8.8	0 (0.0)	0.0 (0.0)	0.0	N	n
TRICHOPTERA	*Athripsodes cinereus*	48 (67.6)	22.8 (3.1)	140.8	7 (50.0)	21.4 (4.1)	132.0	N	n
	Ceraclea dissimilis	0 (0.0)	0.0 (0.0)	0.0	2 (14.3)	1.3 (0.4)	8.8	N	n
	Mystacides azureus	13 (18.3)	2.6 (0.8)	52.8	3 (21.4)	10.1 (2.7)	88.0	N	n
	Oecetis lacustris	14 (19.7)	2.5 (0.6)	26.4	1 (7.1)	2.5 (1.0)	35.2	N	n
	*Molanna albicans**	17 (23.9)	5.5 (1.4)	52.8	3 (21.4)	4.4 (1.3)	44.0	N	n
	Agraylea multipunctata	1 (1.4)	0.1 (0.1)	8.8	0 (0.0)	0.0 (0.0)	0.0	N	n

na: not assessed; *High preference for sandy microhabitats (Tachet et al. 2006); **High preference for hard microhabitats (Tachet et al. 2006).

[1] Type of origin: N: native, A: alien

[2] Duelli (1994): n: not on the red list, 1 = prone to extinction (=endangered based on IUCN categorisation); 3 = endangered (=vulnerable based on IUCN categorisation) and 4 = potentially endangered (=rare based on IUCN categorisation)

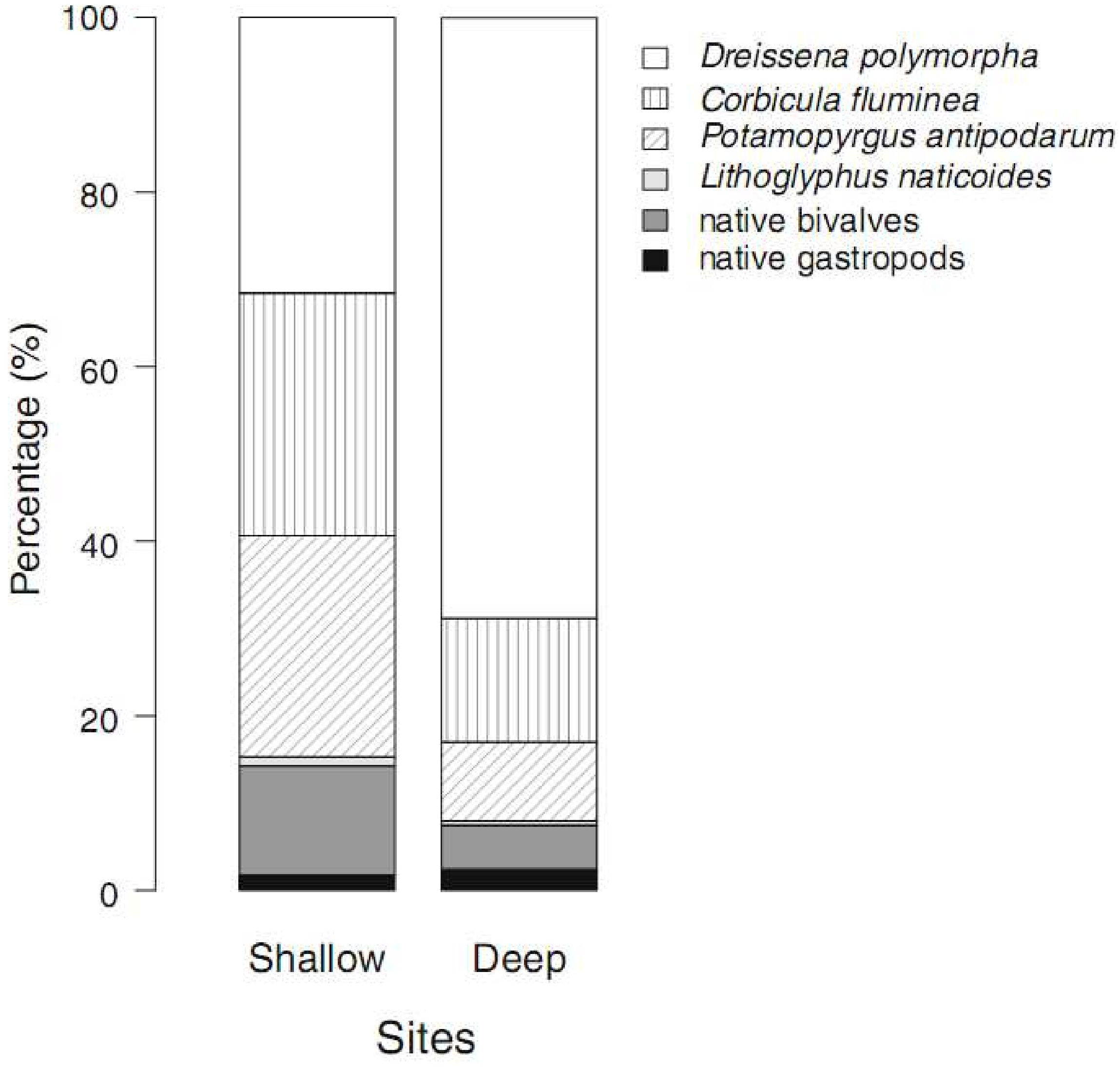

Figure 4.1 Relative distribution of mollusc individuals (%) among alien and native taxonomic groups at shallow (<3.5 m, N= 14,969) and deep (≥ 5 m, N= 4,437) sites in Lake Neuchâtel.

78.6%). ANOSIM analysis confirmed the separate handling of shallow and deep sites, because the communities at either depth were distinct (R = 0.175, P = 0.012). Analysis with only native taxa showed a similar separation by depth (R = 0.162, P = 0.042).

Indicator species analysis identified *Spongilla lacustris* (Linnaeus, 1758) as the single indicator species for shallow sites (indicator value [IV]= 0.45, P = 0.006), whereas deep sites were characterised by 14 indicator taxa. The alien bivalve *D. polymorpha* had the highest indicator value (IV = 0.77, P = 0.007) at deep sites, followed by *V. piscinalis* (IV = 0.46, P = 0.001), *Asellus aquaticus* (Linnaeus, 1758; IV = 0.43, P = 0.001) and *Gyraulus albus* (O. F. Müller, 1774; IV = 0.41, P = 0.001).

The abundances of mollusc individuals in relation to all individuals sampled were almost identical at shallow and deep sites (83.5% vs. 83.8%). However, the composition of gastropods and bivalves was different: gastropod individuals accounted for 28.1% of all molluscs at shallow sites, but only for 11.9% at deep sites ($\chi^2 = 494.2$, $df = 1$, $P < 0.001$). This difference was mainly a result of depth-dependent differences in the abundance of *P. antipodarum, D. polymorpha, C. fluminea* and *Pisidum* sp. (Figure 4.1). Among native gastropods, only *B. tentaculata* reached more than 1% of the total mollusc abundance (shallow sites: 1.4%, deep sites: 1.1%). The percentage of alien mollusc individuals was larger at deep sites (92.5%) than at the shallow sites (85.7%, $\chi^2 = 144.6$, $df = 1$, $P < 0.001$).

The overall density of all macrobenthic taxa averaged 2,222 individuals /m^2 at shallow sites and 3,402 individuals /m^2 at deep sites. Bivalves contributed 1,334 and gastropods 521 individuals /m^2 at shallow sites. At deep sites bivalves showed an even higher abundance (2,512 ind./m^2; gastropods: 339 ind./m^2).

The bivalve *D. polymorpha* showed the highest density of individuals of the taxa collected. The median density of *D. polymorpha* was higher at deep sites than at shallow sites (290 ind./m^2 vs. 1,835 ind./m^2, two-sided two-sample Wilcoxon-test: W = 793.5, $P < 0.001$). The maximum density of *D. polymorpha*, however, did not differ between shallow and deep sites (5,368 vs. 5,474 ind./m^2). Similarly, the median density of *C. fluminea, P. antipodarum* and *L. naticoides* did not differ between shallow and deep sites (*C. fluminea*: 352 vs. 189 ind./m^2: W = 654, $P = 0.064$; *P. antipodarum*: 150 vs. 194 ind./m^2: W = 536.5, $P = 0.644$; *L. naticoides*: 8.8 vs. 0.5, W = 550, $P = 0.518$).

Six species found at shallow sites are on the red list of Switzerland (*Gyraulus crista* [Linnaeus, 1758], *Planorbis carinatus* [O. F. Müller, 1774], *Centroptilum luteolum* [Müller, 1776], *Ephemera vulgata* [Linnaeus, 1758], *Ephemera lineata* [Eaton, 1870] and *Ephemera danica* [Müller, 1764]; Duelli 1994). Only two of them were found at deep sites (*G. crista, E. lineata*; Table 4.1).

Impact of alien molluscs on community structure

Six of the taxa recorded at the shallow sites were alien (*Branchiura sowerbyi* [Beddard, 1892], *L. naticoides, P. antipodarum, C. fluminea, D. polymorpha* and *Dikerogammarus villosus* [Sowinsky, 1894]). In addition to these six species a further alien species (*Dugesia tigrina* [Girard, 1850]) was found at deep sites.

Table 4.2 Summary of the analyses of variance using distance matrices testing the effect of alien taxa on the native community similarity (ADONIS). Significant results are in bold.

Alien taxa	Shallow sites						Deep sites					
	Df	SS	MS	F	R^2	*P*	Df	SS	MS	F	R^2	*P*
Lithoglyphus naticoides	1	0.94	0.94	5.26	0.064	**0.001**	1	0.53	0.53	3.08	0.168	**0.012**
Potamopyrgus antipodarum	1	0.40	0.40	2.25	0.027	**0.031**	1	0.31	0.31	1.80	0.099	0.086
Corbicula fluminea	1	0.90	0.90	4.98	0.060	**0.001**	1	0.11	0.11	0.62	0.034	0.724
Dreissena polymorpha	1	0.73	0.73	4.05	0.049	**0.002**	1	0.66	0.66	3.80	0.208	**0.006**
Residuals	66	11.85	0.18		0.800		9	1.56	0.17		0.492	
Total	70	14.82			1		13	3.18			1	

Table 4.3 Minimal adequate models showing the influence of the alien *D. polymorpha*, *C. fluminea*, *P. antipodarum*, and *L. naticoides* on the numbers of native taxa, native individuals, protected taxa, protected individuals, taxa with sand preference, individuals with sand preference, native taxa with hard bottom preference and native individuals with hard bottom preference. The abundance of alien molluscs was expressed in four different ways (indicated by capitals): A) number of living individuals, B) shell weight of living individuals, C) shell weight of living and dead individuals (empty shells) and, D) shell weight of dead individuals (empty shells). Effect size (Estimate), standard error (se) and significance value (*P*) are presented for approach A (significant effects are in bold). For the approaches B-D symbols indicate significant positive (+), negative (−) or non-significant (NS) effects. At deep sites GLMs were not run for protected and sand preferring taxa because these groups consisted of less than 10 individuals (see materials and methods). Dependent variables which did not enter the model are not listed.

Dependent variable	Factor	Shallow sites						Deep sites					
		A			B	C	D	A			B	C	D
		Estimate	se	*P*				Estimate	se	*P*			
N. of native taxa	*Corbicula fluminea*	**0.100**	**0.040**	**0.015**	+	+	+						
	Dreissena polymorpha	**0.211**	**0.026**	**<0.001**	+	+		**0.250**	**0.077**	**0.001**	+	NS	NS
	Potamopyrgus antipodarum											NS	+
	Lithoglyphus naticoides					−							
N. of native individuals	*Corbicula fluminea*	**0.345**	**0.086**	**<0.001**	+	+	+						
	Dreissena polymorpha	**0.288**	**0.059**	**<0.001**	+	+		**0.411**	**0.645**	**0.003**	+	+	
N. of protected taxa[2]	*Corbicula fluminea*	-0.274	0.181	0.130	NS	NS		na					
	Dreissena polymorpha	**0.253**	**0.114**	**0.027**	NS	+		na					
	Lithoglyphus naticoides				NS			na					
N. of protected individuals[2]	*Corbicula fluminea*	**-1.074**	**0.287**	**<0.001**	−	−		na					
	Dreissena polymorpha	**0.277**	**0.138**	**<0.001**	+	+		na					
	Potamopyrgus antipodarum	**0.405**	**0.153**	**0.010**				na					
	Lithoglyphus naticoides				+			na					
N. of taxa with sand preferrence[1]	*Dreissena polymorpha*	0.191	0.108	0.076	+	NS		na					
	Potamopyrgus antipodarum						+	na					
	Lithoglyphus naticoides	**0.405**	**0.177**	**0.022**	+	+		na					
N. of individuals with sand preferrence[1]	*Corbicula fluminea*	**-0.632**	**0.130**	**<0.001**	−	−		na					
	Dreissena polymorpha	**0.278**	**0.079**	**<0.001**	+	+		na					
	Potamopyrgus antipodarum	**0.311**	**0.087**	**<0.001**	+			na					
	Lithoglyphus naticoides	**0.439**	**0.130**	**<0.001**	+	+		na					
N. of native taxa with hard bottom preference[3]	*Corbicula fluminea*	**0.145**	**0.058**	**0.016**	+	+	+						
	Dreissena polymorpha	**0.188**	**0.038**	**<0.001**	+	+		**0.386**	**0.156**	**0.013**	+	+	
	Potamopyrgus antipodarum												+
N. of native ind. with hard bottom preference[3]	*Corbicula fluminea*	**0.531**	**0.126**	**<0.001**	+	+	+						
	Dreissena polymorpha	**0.474**	**0.081**	**<0.001**	+	+							
	Potamopyrgus antipodarum					−	−						
	Lithoglyphus naticoides	**-0.456**	**0.179**	**0.013**	−								

[1] Sand preference following Tachet et al. (2006), taxa with a preference value of 5 were considered.

[2] Protected taxa following Duelli (1994).

[3] Hard bottom preference following Tachet et al. (2006), taxa with preference values of 4 and 5 were considered.

Analysis of variance using distance matrices (ADONIS) revealed that the changes in the abundance of the four alien species explain 20.0% of the variation of the native community at shallow sites and 50.8% of that at deep sites. At shallow sites, *C. fluminea* and *L. naticoides* were the best explanatory variables, whereas at deep sites the abundance of *D. polymorpha* and *L. naticoides* explained most (Table 4.2).

GLMs identifying the effects of alien molluscs indicated that their number had a positive impact on most of the response variables at shallow sites (Table 4.3). Exceptions were a negative influence of *L. naticoides* on the number of native individuals with hard bottom preference at shallow sites, and of *C. fluminea* on the numbers of invertebrate individuals with sand preference and on the number of protected individuals. Similar results were obtained at shallow sites when the abundance of the few alien species was expressed by the weight of living animals (approach B; Table 4.3). Considering shell weight of both living and dead animals as independent factor, GLMs revealed similar but less pronounced effects at shallow sites, but *L. naticoides* had a negative impact on the numbers of native taxa and *P. potamopyrgus* negatively influenced the number of individuals with hard bottom preference (approach C, Table 4.3). Using the weight of empty shells as predictor variable (approach D), *C. fluminea* kept the positive influence on most native groups but lost the negative influence on the native protected and sand preferring individuals while empty shells of *P. antipodarum* enhanced the number of native taxa with sand preference.

Most remarkably is the positive influence of *D. polymorpha* on the number of native invertebrate individuals, and on both the numbers of native taxa and taxa with hard bottom preference at deep sites in the first three approaches. In the fourth model (approach D), only *P. antipodarum* had a positive impact on both the number of native individuals and the number of hard bottom preferring taxa (Table 4.3).

Considering the null model of random patterns of species assemblage, CA_{ST} values of 0.015 were obtained for shallow sites and 0.035 for deep sites. At shallow sites, the expected values were 0.015 (lower and the upper limits of the 95% confidence intervals of the null assemblages were 0.014 and 0.017) and 0.021 (0.015 and 0.026) for deep sites. This indicates that the impact of competition structuring the benthic macroinvertebrate community is moderate and differs among depths. The comparison with the null distributions showed that the macroinvertebrate community at shallow sites was randomly organised, whereas the community at deep sites may be partly structured by competitive interactions. High abundance of each alien species increased only moderately the competition in the community as indicated by the standardised number of abundance checkerboard (Figure 4.2).

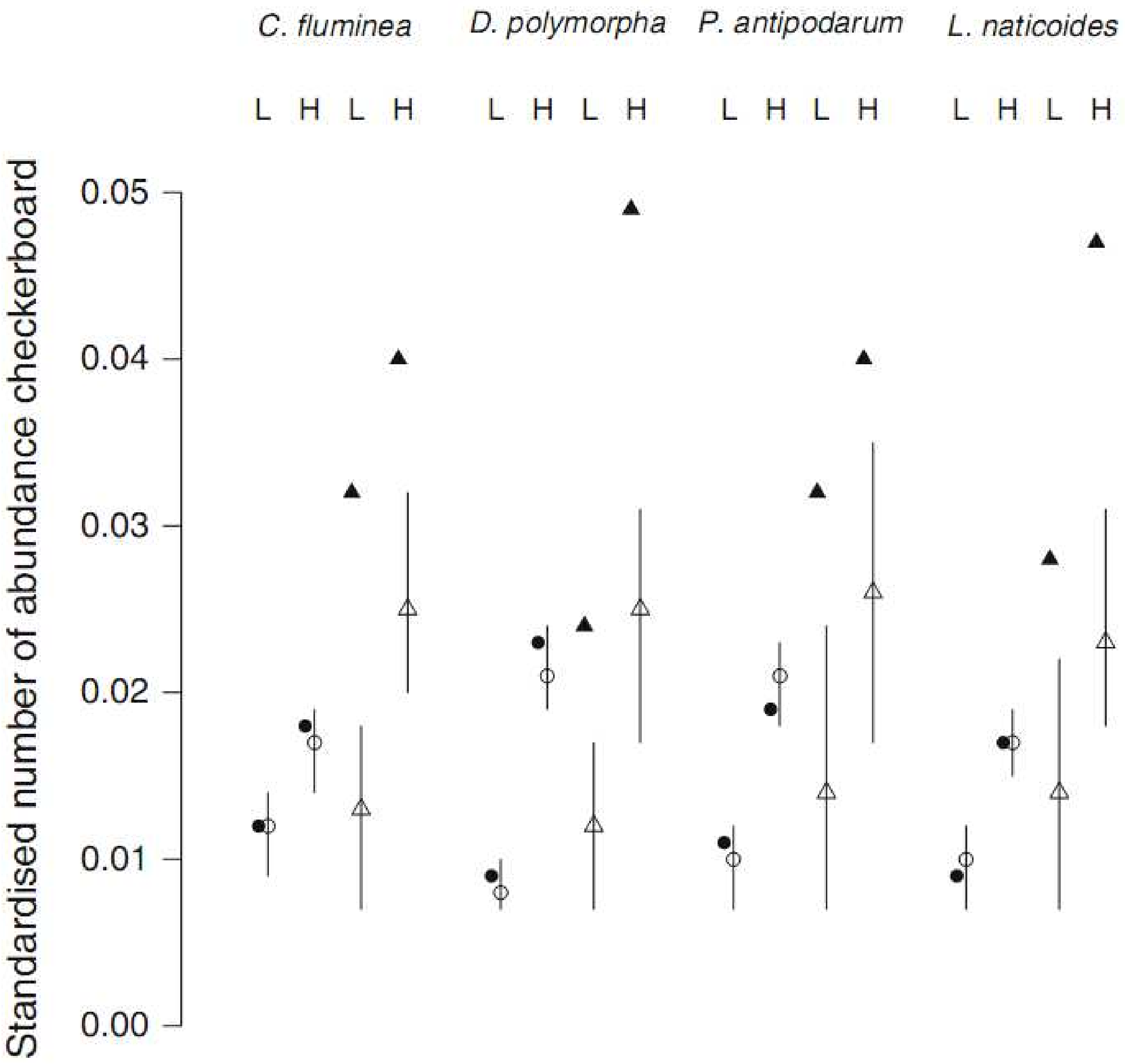

Figure 4.2 The impact of low (L) and high (H) abundance of four alien species (*C. fluminea, D. polymorpha, P. antipodarum* and *L. naticoides*) at shallow (circles) and deep (triangles) sites on the standardised number of abundance checkerboard (full symbols) and its comparison with random species assemblages (open symbols show expected mean values and whiskers the 95% confidence intervals). Standardised number of abundance checkerboard reflects the strength of competition within the community structure.

Total shell mass and shell decay rates

The total shell mass of living and dead individuals of the six most abundant mollusc species amounted to 700.9 g/m^2 at shallow sites and 1,275.0 g/m^2 at deep sites in Lake Neuchâtel (Table 4.4). The four alien species (*C. fluminea, D. polymorpha*, *P. antipodarum*, *L. naticoides*) contributed to 98% and 97% of the total shell mass at shallow and deep sites, respectively. Considering single species, *C. fluminea* contributed to 69% and 37% of the total shell mass at shallow and deep sites. The corresponding figures for *D. polymorpha* were 27% and 59%. The shells of these two invasive clams constituted more than 95% of the organic hard substrate on the sandy bottom of the lake and thus changed the habitat characteristics for benthic organisms.

Table 4.4 Total shell mass (in g/m^2) of living and dead individuals of four alien and two native mollusc species at shallow (depth <3.5 m) and deep (depth 5.0 m – 22.4 m) sites in Lake Neuchâtel.

Species		Shallow sites			Deep sites		
		living	empty	living + empty	living	empty	living + empty
Corbicula fluminea$^+$	Cf	314.5	165.8	480.3	246.9	221.6	468.5
Dreissena polymorpha$^+$	Dp	137.1	53.9	191.0	459.3	289.2	748.5
Potamopyrgus antipodarum$^+$	Pa	2.2	14.2	16.4	1.2	20.0	21.2
Bithynia tentaculata	Bt	0.4	8.6	9.0	0.5	4.8	5.3
Valvata piscinalis	Vp	0.0	2.2	2.3	0.4	29.2	29.5
Lithoglyphus naticoides$^+$	Ln	1.3	0.6	1.9	0.9	1.1	2.0

$^+$ alien species

Table 4.5 Summary of the minimal adequate model of the effects of origin (native vs. alien) and shell weight on the decay rate of mollusc shells.

Factor	Estimate	SE	t-value	*P*
Intercept	21.267	2.164	9.830	<0.001
Origin (alien)	-9.659	3.353	-2.881	0.005
Weight	-14.151	7.767	-1.822	0.071

Considering the shell decay study, model selection removed the factors taxon (within origin) and water depth, and left the factors origin (native or alien) and shell weight in the minimal adequate model (Table 4.5). The analysis revealed that shells of the studied alien species have a significantly slower relative decay rate than those of native species (mean loss in 1 year: *C. fluminea* 2.3%, *D. polymorpha* 10.0%, *P. antipodarum* 10.9%, *B. tentaculata* 20.0%, and *V. piscinalis* 21.9%; Table 4.5, Figure 4.3) and that shell weight has a marginally negative effect on the relative decay rate (Table 4.5, Figure 4.4). Thus, the bigger and heavier alien molluscs *C. fluminea* and *D. polymorpha* lost less shell material within one year than smaller native molluscs (Figure 4.4).

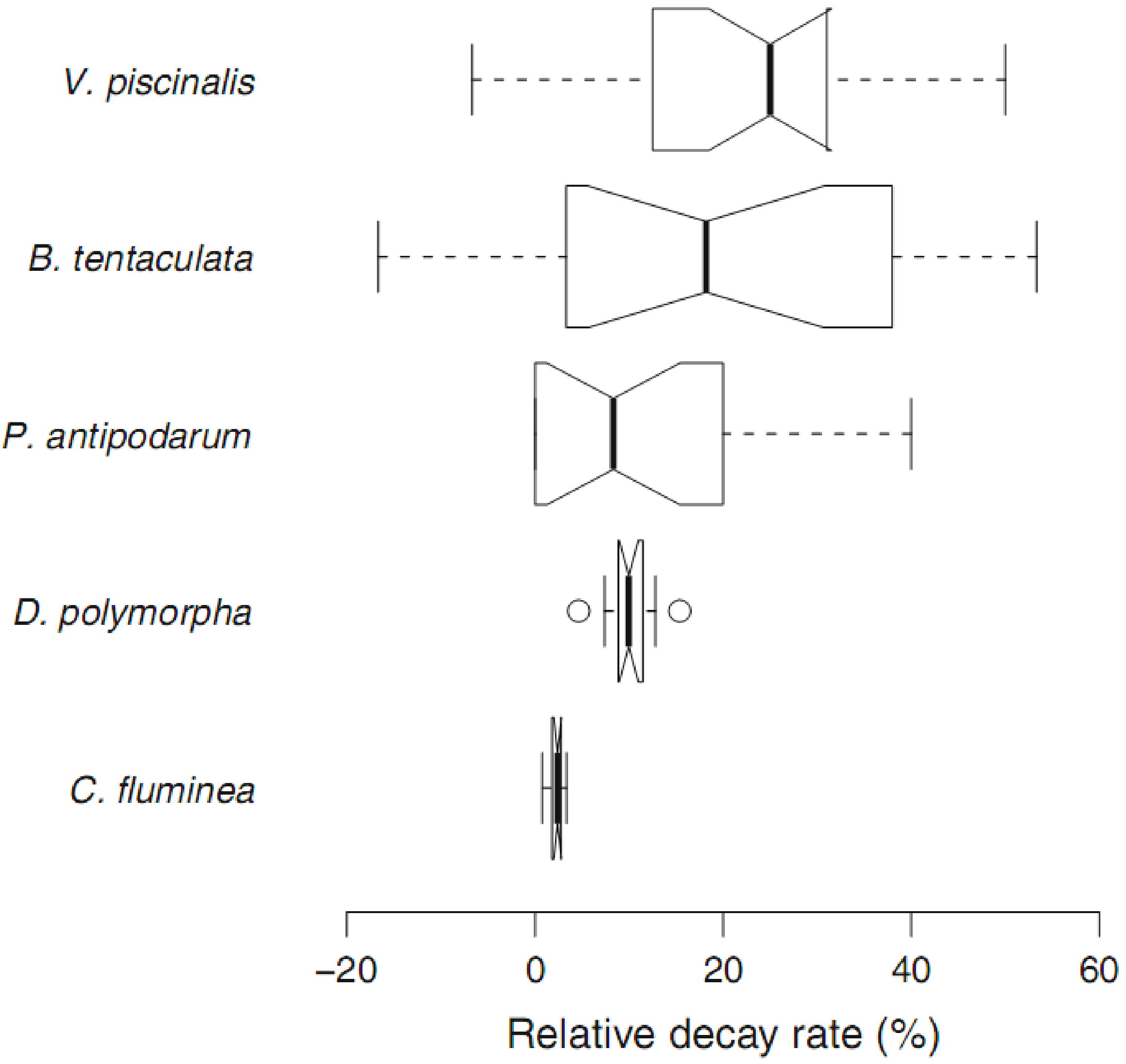

Figure 4.3 Relative decay rate of shell material of three alien (*C. fluminea, D. polymorpha, P. potamopyrgus*) and two native (*B. tentaculata, V. piscinalis*) molluscs in Lake Neuchâtel.

Discussion

The present study shows that the benthic macroinvertebrate community in a sandy flat of the littoral zone of Lake Neuchâtel is dominated by a few alien mollusc species (*C. fluminea, D. polymorpha, P. antipodarum*). Our analyses suggest that the composition and diversity of native macroinvertebrates are influenced by the abundances of alien molluscs which transform sandy substratum into a partly hard substratum habitat. However, patterns strongly depend on the water depth at the sampling sites. Null-model analysis testing the impact of alien molluscs on community assembly suggests that shallow sites are randomly organised,

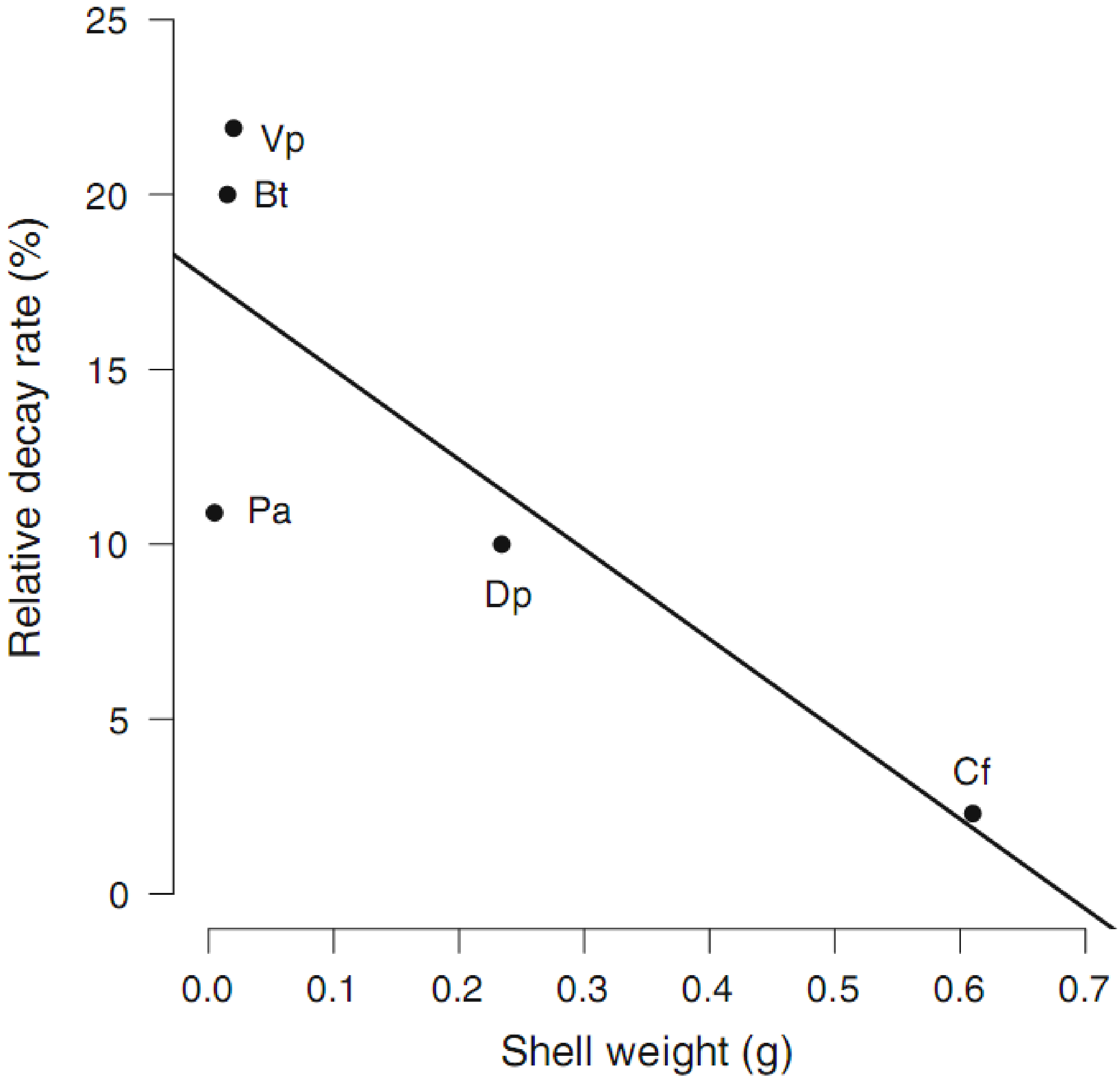

Figure 4.4 Relative decay rate of shell material in five species of freshwater molluscs, averaged over all retrieved bags, as a function of mean shell weight of each species (r^2= 0.70, n= 5, P = 0.077) in Lake Neuchâtel. Bt, *B. tentaculata*; Cf, *C. fluminea*; Dp, *D. polymorpha*; Pa, *P. antipodarum*; Vp, *V. piscinalis*. Full species names are given in Table 4.4.

whereas deep sites are influenced by competitive interactions among native community members. Our shell study also shows that valves and shells of the studied alien species persist for a longer period in the sediment than those of native species, and consequently have a longer-lasting impact through habitat modification than those of native mollusc species. These findings indicate that alien mollusc species have a profound impact on native macroinvertebrates by changing habitat characteristics of the sandy bottom.

Nowadays, numerous freshwater habitats are dominated by alien taxa (Ricciardi and MacIsaac 2000, Tittizer et al. 2000, Wirth et al. 2010), and in many cases by alien molluscs

(Karatayev et al. 2003, Lewin and Smolinski 2006, Sylvestre et al. 2007, Nalepa et al. 2010). Similarly, Lake Neuchâtel has recently been invaded by the alien molluscs *D. polymorpha*, *C. fluminea*, *P. antipodarum* and *L. naticoides*. We found substantial differences in the composition of benthic macroinvertebrates between shallow (< 3.5 m) and deep (≥ 5 m) sites of a sandy flat. The depth-related difference in the density of alien species was most pronounced in *D. polymorpha*, which could be the result of the water-depth depending feeding behaviour of diving ducks (Werner et al. 2005, Keller and Burkhardt 2010). Diving ducks have to manage their feeding costs and energy budget (de Leeuw et al. 1999). Consequently, they prey first upon the easily reachable mussels (*D. polymorpha*) at shallow sites before they exploit deeper sites. This foraging pattern fits our observations that the density of *D. polymorpha* was lower at shallow than at deep sites and that mainly small (1 year-old and younger) *D. polymorpha* individuals occurred at shallow sites, whereas at deep sites several years old individuals dominated. Similarly, the zebra mussel showed a decline in abundance of 95% at shallow sites (1 and 3 m) in Lake Constance following the feeding of ducks over one winter (Werner et al. 2005). Interestingly, duck do not feed on *C. fluminea*, which has thicker valves than *D. polymorpha* and lives buried in the upper layer of sand (Schmidlin and Baur 2007).

Several studies suggest that alien species generally have a negative impact on native communities (Strayer 1999, 2010, Rahel 2002, Arndt et al. 2009). However, Botts et al. (1996) demonstrated in a field experiment that *Dreissena* species can change the physical structure of sandy habitats which in turn may lead to increased densities of native species. Similarly, short-time experiments showed that several native macroinvertebrate taxa may benefit from the presence of *C. fluminea* in sandy habitats (Werner and Rothhaupt 2007, 2008). Sousa et al. (2009) reviewed the eco-engineering effects of alien bivalves, including *C. fluminea* and *D. polymorpha*. Both bivalves cause a decrease in turbidity and increase light penetration in the water column because of filter feeding. The increase in light and visibility may enhance macrophyte growth. Interstices between clams and mussels provide refuge from predators to other invertebrates and shells can be colonized by algae, freshwater sponges, gastropods, amphipods and other invertebrates. Moreover, alien mussels might provide additional sources by biodeposition (Mitchell et al. 1996, Mörtl and Rothhaupt 2003). Our results are in agreement with the above mentioned studies showing that alien molluscs might have both positive and negative effects on native communities. We should note, however, that the biological explanation of the negative impact of *L. naticoides* (revealed by GLMs) is rather challenging because the species was present only in low density.

The results of ADONIS support both views: alien mollusc species influence the structure of the native macroinvertebrate community in a sandy flat of the littoral zone of Lake Neuchâtel. The relationships between the abundance of the four alien mollusc species and native community variables suggest a positive effect on the native community structure. Thus, habitat transformation by increasing the amount of hard substratum in the sand flat might be advantageous for several native taxa, but it might be disadvantageous for other taxa adapted to the conditions of sandy habitat. Indeed, *C. fluminea* was found to have a negative impact on the number of individuals with sand preference and on the number of protected species. This negative effect of a species on other species through habitat modification (i.e. ecosystem engineering) can be regarded as way of indirect competition (Gonzalez et al. 2008). The differential impact of *C. fluminea* and *D. polymorpha* can be explained by their different habitat use (burrowing vs. surface dwelling; e.g. Schmidlin and Baur 2007, Higgins and Vander Zanden 2010). Our findings support the use of trait-based analyses in invasion ecology (Townsend and Hildrew 1994, Statzner et al. 2008, Ordonez et al. 2010) and its applications in conservation issues because most sand-preferring native taxa are threatened in Switzerland (Table 4.1).

Alien species can transform a competitively structured native community into a randomly organised one (Sanders et al. 2002). Our null-model analysis showed that native benthic macroinvertebrate communities were structured randomly at shallow sites. At deeper sites, however, competition was important in structuring the community. At both depths, these patterns were not influenced by any of the alien mollusc species examined. Consequently, water depth per se has a stronger effect on the native community assembly than the four alien species. We assume that this difference between shallow and deep sites comes from the difference in the abundance of *D. polymorpha* caused by duck feeding (see above). However, stochastic and demographic processes might also influence the abundance of analysed taxa (Gotelli and McCabe 2002).

The relative shell decay rates (2.3% − 21.9% of the initial shell mass per year) recorded in the present study are similar to the values measured in other molluscs in the U.S.A. (Strayer and Malcolm 2007). We found that the relative shell decay rate of alien mollusc species is slower than that of native ones. This means that the shells of alien species persist for a longer period in and on the sediment, and consequently, have a long-lasting impact on the community structure through modification of the habitat.

It is important to note that some factors may restrict the generalisation of our conclusions. First, our samples deal with the topmost 5 cm of the sediment only.

Consequently, the patterns observed might be different by applying other sampling techniques paying more attention to animals living deeper in the sediment (Waringer 1987). Second, we used bags with a mesh size of 2 mm for handling samples. In other studies sampling devices with a mesh size of 1.2 mm or even smaller have been applied (Carter and Resh 2001). Consequently, the size distribution of macroinvertebrates sampled in our study might be biased slightly towards taxa with larger bodies.

Conclusions

In summary, our study showed that a sandy flat of the littoral zone of the Lake Neuchâtel is seriously invaded by alien mollusc species. The observed patterns suggest that the existence of these mollusc species (*D. polymorpha, C. fluminea, P. antipodarum* and *L. naticoides*) and their empty shells transform the sandy habitat into a more structured habitat with some hard substratum. This effect favours the occurrence and abundance of several native taxa, but it is disadvantageous for a limited number of taxa with specific habitat requirements. The present study is to our knowledge one of the first which demonstrates depth-dependent impacts of alien species on the native community of a freshwater lake. These findings call the attention to the careful examination of the impact of alien ecosystem engineers to native communities, because negatively impacted taxa might have a high conservation value.

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General Discussion

Freshwater ecosystems are very vulnerable to invasive species. Once an introduced species got established in a lake or river it is hardly possible to remove it again from the new environment (Genovesi 2005). Therefore, knowledge about the invasive organism and its introduction pathway(s) is important to prevent further introductions and to manage existing invasions. This thesis provides information about the spread of the invasive clam *Corbicula* in Switzerland, its preferred ecological niche, and on potential effects on native communities in a river and in a lake. Basic knowledge on the genetic composition (haplotypes) of *Corbicula* individuals and on their assumed introduction pathways is also presented.

Chapter 1 shows on how a combination of different factors structures the benthic community of the river Rhine. River modifications and prolonged pollution changed the original communities and caused the loss of certain species, creating open niches for pollution-tolerant non-indigenous species. Major disturbances enabled the invasion of many new species which reached unprecedented densities. Through the Rhine-Main-Danube Canal, opened in 1992−1993, many non-indigenous species from the Ponto-Caspian region entered the river Rhine system. Some of them were co-adapted and lead to facilitated establishment of other introduced species (Simberloff and Von Holle 1999, Sures et al. 1999). After reduction of the pollution in the Rhine, invaders re-colonised faster and more numerously empty niches than native species. These invaders suppressed the development of populations of native species. Replacing characteristic riverine species by large numbers of euryoecious and non-indigenous species, in particular macroinvertebrates and fish, has remarkably changed the species composition in the river Rhine (e.g. Van den Brink et al. 1988, 1990). The main biological mechanisms favouring these changes are competition for food and space (e.g. *Corbicula*), hosting of parasites (amphipods and isopods) and intraguild predation (*Dikerogammerus villosus*). At the present day, the number of invaders is still increasing.

The first chapter also shows that in most cases negative impacts of invasive species on native species have been deduced from correlative evidence. Evidently, there is an urgent need for experimental studies on interactions between invasive and native species. From a conservation perspective, ecological studies on rare native species should be intensified. Ecological restoration projects are crucial to preserve those facets of the originally unique biodiversity of the river Rhine and its floodplain which is still present today.

Chapter 2 documents the initial phase of the invasion of *C. fluminea* in Switzerland. The distribution of *C. fluminea* in the Swiss part of the river Rhine in 2003 was restricted to the first 22 km upstream of Basel and to a canal and streams fed with water from the river Rhine. This indicated a low mean upstream spread of 2.4 km per year since the clam reached Switzerland in 1995. It had not yet colonized any of the tributaries examined. Densities varied from 1 to 600 individuals per m^2 and decreased towards the edge of the upstream occurrence. The size distribution of *C. fluminea* in the river Altrhein indicated the presence of a well-established population with 2- to 3-year-old clams. In all cohorts, the growth rate was highest between May and October favoured by the increased water temperature and the availability of phytoplankton in that period. The clam was most abundant on fine-grained substrates (sand) with slowly flowing, shallow water. We confirmed this finding by a substrate choice experiment in the river Rhine. Although most clams showed a positive rheotaxis (movement against the current) in this experiment, we assume that active upstream dispersal is less important for the clam's spread. Additionally, our results showed that *C. fluminea* reached sites in the river Rhine where cargo shipping does not occur. To pass obstacles such as weirs, passive dispersal by waterfowl and recreational boating are more likely and may facilitate further upstream spread. *C. fluminea* might be less successful in colonizing rivers with rapid current. These are assumed to serve as refuges for native molluscs and need therefore to be preserved in a dynamic state.

The results of **Chapter 3** support the assumptions made in **Chapter 2**: Individuals of *C. fluminea* were most recently recorded in several lowland lakes whose interconnecting rivers have not yet been colonized. This makes passive dispersal of the invasive clam by human activities or animal vectors highly probable. Specially, recreational boating stays in the focus of introduction vectors as most of the new clam occurrences were found near harbours with many boats (Burgin and Hardiman 2011). The closely related species *C. fluminalis* was only observed in the region of Basel in the river Rhine, where it co-occurrs with *C. fluminea*.

Mitochondrial DNA-sequences from *Corbicula* samples collected in Swiss and other European rivers and lakes revealed that all but one of 72 examined individuals harboured a single haplotype of *C. fluminea*. Therefore an assignment to the original population in Europe was not feasible and other molecular techniques are required (e.g. microsatellites) to detect the source population of the introduced individuals. Nevertheless, due to the geographical proximity, the river Rhine near Basel served most probably as source for all subsequent introductions of *C. fluminea* into Swiss rivers and lakes. The detected main haplotype dominates both the native range in Asia and introduced populations in North- and South-America (Park and Kim 2003, Lee et al. 2005). In the river Rhine in Germany and in French rivers, other haplotypes occur which could have been separately introduced as well (Renard et al. 2000, Pfenninger et al. 2002, Marescaux et al. 2010). Either these haplotypes have not been introduced into Switzerland because of their low abundance and consequently low probability to be passively transported, or alternatively, if they have been introduced they could not sufficiently establish and vanished again. *C. fluminalis* has a lower reproductive output and a narrower physiological niche (e.g. salt concentration; Meister 1997) than *C. fluminea* what could explain the absence of its sister species in the rest of Switzerland. However, in lake Garda in northern Italy, both species co-exist (Ciutti and Cappelletti 2009). Recent records of clam individuals in Switzerland showed all the shell morphology of *C. fluminea*, confirming the dominance of this clam species in Swiss rivers and lakes.

Chapter 4 deals with the ecological impact of non-indigenous molluscs on the native benthic invertebrate community in Lake Neuchâtel. We found that our study site, a sandy flat, was dominated by three of the four co-existing non-indigenous mollusc species (*C. fluminea*, *D. polymorpha* and *P. antipodarum*). They influenced the composition and diversity of native macroinvertebrates by transforming the sandy substratum into a partly hard substratum habitat. We recorded substantial differences in community composition between shallow (< 3.5 m) and deep sites (≥ 5 m). We assume that these differences are, at least partly, a result of the reduced abundance of *D. polymorpha* at shallow sites due to depth-selective feeding of ducks. Null-model analysis testing the impact of alien molluscs on community assembly suggests that shallow sites are randomly organised, whereas deep sites are influenced by competitive interactions. However, the results of the GLMs showed that the non-indigenous mollusc have an overall positive effect on the numbers of native taxa, native individuals, protected individuals, taxa with sand preference, individuals with sand preference, native taxa with hard bottom preference and native individuals with hard bottom preference, both at shallow and deep sites. This was correct for all applied model approaches, when non-indigenous species abundance was expressed as the abundance of living non-indigenous mollusc individuals (1), as shell weight of living individuals (2), as shell weight of living and empty shells or (3), as shell weight of empty shells only (4). Thus, the observed statistical influences point rather to structural (shell) effects than to biotic interactions between the molluscs and other organisms. An exception to the rule is the clam *C. fluminea* which showed significant negative impacts on numbers of protected and sand preferring individuals in upper water depths. Members to both groups, among others, are the sand-burrowing mayflies *Ephemera* spp. In this particular case, interspecific interaction with *C. fluminea* and biotic impacts, such as bioturbation, biodeposition, and nutrient reallocation, seem to play a more important role than the structuring effect by shells. In the context of conservation biology, this outcome is alarming. On the other hand, taxa with a hard bottom preference were enhanced by *C. fluminea* in all approaches at shallow sites, what shows the significance of dead clams that lie on the sediment surface providing physical habitats and interstitial refuges (Werner and Rothhaupt 2007).

Our shell decay study showed that valves and shells of non-indigenous species persist for a longer period in the sediment than those of native species. As a result, they have a longer-lasting impact through habitat modification than those of native mollusc species. This form of ecosystem engineering favours the occurrence of several native taxa which seek for hiding places and colonisation space but might also be disadvantageous for other taxa with specific habitat requirements. Our findings call attention to a careful examination of the impact of non-indigenous species to native communities, because negatively affected taxa might have high conservation value.

The spread of *Corbicula* spp. from a process-based point of view

The process-based view of the spread of *Corbicula* spp. in Switzerland (Colautti and MacIssac 2004, Nentwig 2011, see general introduction) allows in the following section an evaluation of the invasiveness of the two *Corbicula* species. Spreading up to the border of Switzerland until 1995, *Corbicula* spp. certainly fulfilled the first two criteria of the dispersal of non-indigenous species: They colonized new freshwater habitats with the help of men, crossing biogeographical barriers (by cargo shipping, man-made waterways, recreational boating, aquarium trade and fishery), but once in the novel geographical region, the spread of *Corbicula* spp. depended also on natural transport mechanisms such as transfer by waterfowl and larval drift. The third criterion, spreading in relative short time scale, is true as well. As in **Chapter 1** and **2** described, *Corbicula* spp. colonised the navigable trade routes of the river Rhine quickly: *C. fluminea* and *C. fluminalis* were first recorded in the Lower Rhine in The Netherlands in 1985 (Bij de Vaate and Greijdanus-Klaas 1990). Both species reached soon high abundance of 1,800 individuals per m^2 (Haas et. al. 2002) and ten years later in 1995 and 865 km far from the first observation sites, both clams were reported near Basel in Switzerland (Rey et al. 2004). The upstream colonisation up to the confluence of the High Rhine and the river Aare (about 54 km from Basel) needed another ten years (see **Chapter 3**) and was only achieved by *C. fluminea*. The river High Rhine served most probably as primary source of origin for all following introductions into Switzerland because all genetically examined animals from Swiss population showed the same haplotype (H2) as the main haplotype present in the river Rhine (Pfenninger et al. 2002; **Chapter 3**).

Introduced lake populations reached in Lake Constance maximum densities of 3,520 individuals > 5 mm per m^2 within four to six years (Werner and Rothhaupt 2007) and in the same time and in a comparable habitat (sandy littoral) similar figures were recorded in lake Neuchâtel (3,599 individuals per m^2; **Chapter 4**). In Lake Neuchâtel, three years after the first observation of the clam, the distribution of *C. fluminea* was patchy and density was low. But already one year later in 2007, i.e. four years after the first record, the clam was wide spread on the sandy flat and reached high density and frequency. The invasive clam had a negative impact on the numbers of protected and sand preferring native taxa. Thus, stage 3 of the invasion process (invasion), took place in a few years only and adaptive behavioural or even evolutionary reactions to the clam were hardly possible for most of the biota in the lake. Furthermore, since in both lake sites similar maximal densities were observed, stage 4 (saturation) may have already occurred locally (Werner and Rothhaupt 2007, Nentwig 2010, **Chapter 4**).

The two *C. fluminea* populations detected in Lake Geneva in 2008 (Morges and Bouveret) show so far low densities, but they are expected to increase (B. Lods-Crozet, pers. comm.).

The sister species *C. fluminalis* reached locally a well established state (state 2, Nentwig 2010) with more than 200 individuals per m^2 (Schweizerhalle near Basel, Mürle et al. 2008) but shows low abundance in the rest of the so far introduced section. Any observations or evidence of having negative impact on native organisms are lacking, what does, however, not exclude minor impacts. Nevertheless, by the time being (2011) *C. fluminalis* in Switzerland cannot be considered as invasive, in contrast to *C. fluminea*.

Outlook

This thesis documented the spread of the Asian clam *Corbicula* spp. into Switzerland in the absence of highly interconnected waterways as they are common in other neighbouring European countries (e.g. France and Germany). The clam's ecological preferences, its population structure and its impact on the native freshwater community were studied. Furthermore, the present thesis illustrates the occurrence and abundance of aquatic invasive macrozoobenthic species in the river Rhine and in the lake Neuchâtel, focusing in particular on non-indigenous molluscs.

Following the Article 51 in the Swiss Release Ordinance, we monitored *C. fluminea*, known to be invasive in other regions (Strayer 1999), and studied possible connections existing between observed damage and the presence of the monitored organisms (**Chapter 2**,

4). We demonstrated the harm to the rare and endangered mayflies *Ephemera* spp. population caused by high densities of *C. fluminea*. However, the underlining mechanisms in this species interaction are not known and because of the low number of mayflies an experimental approach is less likely accomplished. Doing research with native mollusc appears more realistic. Though, the absence of living unionid mussels at the study sites in the river Rhine (**Chapter 2**) and in Lake Neuchâtel (**Chapter 4**) is alarming. Fortunately, in other parts of the sandy littoral in lake Neuchâtel, where *C. fluminea* was not observed yet or is only present in low densities, unionid mussels are still abundant (B. Lods-Crozet, pers. comm.) and could maybe be used for experimental research in the future (as asked for in **Chapter 1**) and repopulate the former sites in Lake Neuchâtel.

Even if the damaging effect of *C. fluminea* on native organism has a causal proof in Switzerland, eradication of the species without harming the native freshwater community will not be possible and there would be no guarantee for future re-introductions (**Chapter 3**, Genovesi 2005). Therefore, prevention of man-made introductions and preservation of dynamic river structures are the most realistic measurements we can take to protect the biodiversity of Swiss river and lakes.

What kind of ecological, economical and health consequences can we expect when *C. fluminea* is further spreading in all principle low land water bodies of Switzerland? Ecological consequences include the change in composition and abundance of freshwater invertebrate taxa and the modification of habitat structures (as already discussed). *C. fluminea* will contribute to a biological homogenisation of Swiss waterbodies (Rahel 2007). In which extent this changes affect higher and/or lower trophic levels (e.g. fish, birds, zooplankton, phytoplankton) or ecosystem services (water quality) may serve as future research questions. Apart from the direct effects of *C. fluminea* on benthic macroinvertebrates, there is only anecdotic evidence of water birds (S. Werner, pers. comm.), crayfish and muskrats (own observation) consuming the clam occasionally.

Due to its tolerance to low water temperatures (Müller and Baur 2011) the clam will surely continue to spread in Switzerland in lowland regions and with continued global warming the effect of moderate winter will further promote the invasion success of *C. fluminea* (Weitere et al. 2009). This development will be unintentionally enhanced in even higher situated river regions by the increasing number of hydro-electrical power plants (BAFU 2011), providing suitable habitat in their reservoirs.

Economically, *C. fluminea* has caused so far “affordable” damage for affected industries. The employees of the water quality observation station adjacent to the river Rhine in Basel, spend a few working days a year with the cleaning of small water pipes clogged with the clam (R. Dolf, pers. comm.). Another industrial facility in Switzerland, depending on cooling water from the river Rhine, had the same problem but at a larger scale. With the gained knowledge about the population structure in the river Rhine (**Chapter 2**) yearly maintenance cost could be set a limit to about CHF 50,000 (Schmidlin 2007). In the United States, an often quoted value of over US$ 120 billion is spent annually on control and prevention measures of invasive species (Pimentel et al. 2000). For instance, the Watershed Management Plan for Otsego Lake, a central New York glacial lake, provides for prevention of non-indigenous invasive species a stringent boat inspection and washing program. These measurement expenses average US$ 30,000 per year, much of which has been covered by collecting a launch fee. After implementation of the inspections, only one boat was refused access, and less than 1% required washing before allowed access. However, zebra mussels (*Dreissena polymorpha*) and water chestnut (*Trapa natans*) have since been found in the lake. The program continues to be supported because other non-indigenous invasive species may have been prevented or may be prevented in the future (Horvath 2008). A similar approach in Switzerland seems not feasible. However, information campaigns among certain groups, like boat owners or managers of pet shops were taken into consideration by some cantonal authorities working on water protection issues (e.g. canton Basel-City, canton Vaud) after being informed about the results of this thesis.

Usually, *C. fluminea* is not associated to health issues in Switzerland as this is the case in other non-indigenous species (e.g. the plant *Ambrosia artemisiifolia*; Ambrosia 2011). Nevertheless, there is evidence for health concerns caused by the clam in Europe. In northeast Portugal human consumption of freshwater clams and mussels is common. Melo et al. (2006) showed that over a third of *C. fluminea* specimens examined were carrying oocysts of *Cryptosporidium* (a protozoan parasite which affects the intestines of mammals and leads typically to an acute short-term infection). Consumption of the clam might therefore cause a human cryptosporidiosis outbreak. In addition, man could become accidental host when clams carry parasites (e.g. *Aspidogaster conchicola*, a holarctic trematode; Lucius and Loos-Frank 2008). Filter-feeding clams accumulate as well non-biological substances such as metals and compounds of certain pesticides (Basack et al. 1997). However, it is not a recent Swiss tradition to consume clams and therefore no health hazard should be expected. Independent from the presence of the clam, all mentioned sources of human disease (but the internal parasites) may be found in open water and thus threaten the drinking water supply. Melo et al. (2006) recommended *C. fluminea* therefore as a bioindicator for those substances and to integrate the clam in a water quality alert system. The results of another study (Faust et al. 2009) indicated that *C. fluminea* (and other filter-feeding molluscs) can remove and reduce the infectivity of avian influenza (AI) viruses in water. As many of the lakes in Switzerland invaded by *C. fluminea* are feeding and resting places of migratory birds that might carry the AI virus, the role of the clam in fighting the disease might become important.

To sum up, in Switzerland, the expected economical and so far not existent health consequences of *C. fluminea* are of minor concern, but although the proven ecological impacts are restricted to few organisms, cascading effects are not to be ruled out and the clam needs to stay under further surveillance.

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Curriculum Vitae

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2004 – 2006	University of Applied Sciences Northwestern Switzerland. School for Teacher education. Teaching-diploma for higher education in biology and geography.
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Conference contribution

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Working Experience

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