

# Impact of invasive Asian clams, *Corbicula* spp., on a large river ecosystem

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## SUMMARY

1. Over the past few decades, Asiatic clams (*Corbicula* spp.) have spread spectacularly in several large European rivers. In the River Meuse, a transnational lowland river, a substantial chlorophyll *a* decline has been recorded since the mid-2000s, which seems to be related to the invasion by these exotic bivalves. This study aimed at verifying this hypothesis, using data on clam density from field surveys, water quality monitoring data and a simulation model.

2. *Corbicula* density was estimated at between 50 and 900 m<sup>-2</sup>, depending on the site. Assuming a maximum filtration rate per clam body mass of 0.086 m<sup>3</sup> g C<sup>-1</sup> day<sup>-1</sup> at 20 °C, derived from the literature, we ran simulations with a non-stationary model to estimate the impact of the bivalve on the river plankton and water quality.

3. In the stretches where the invasive clams were most abundant, we estimated a 70% loss of phytoplankton biomass, due to their filtration, and a 61% decline in annual primary production compared with a situation without clams. Model simulations also showed that zooplankton may have suffered as much as a 75% loss of biomass.

4. The simulations also point to substantial effects of *Corbicula* on the river oxygen budget and on nutrient cycling. We suggest that, in the heavily regulated sectors of the river, the loss of planktonic production due to these invasive filter-feeders negatively affects other suspension feeders and alters ecosystem processes and productivity.

**Keywords:** invasive molluscs, lowland river, modelling, plankton

## Introduction

Exotic benthic filter-feeders in rivers affect various ecosystem compartments and processes: they reduce the plankton (Cohen *et al.*, 1984; Caraco *et al.*, 1997; Welker & Walz, 1998; Jack & Thorp, 2000; Akopian *et al.*, 2001; Descy *et al.*, 2003), compete with native bivalves such as Unionidae (Strayer & Smith, 1996; Parker, Patterson & Neves, 1998; Vaughn & Spooner, 2006) and cause a decline in dissolved oxygen by reducing photosynthesis in the water column and increasing benthic oxygen consumption (Effler *et al.*, 1996; Garnier, Billen & Palfner, 1999; Hakenkamp & Palmer, 1999; Caraco *et al.*, 2000). A major effect at the ecosystem level is the transfer of

organic carbon from the water column to the river bed (see e.g. Bachmann & Usseglio-Polatera, 1999; Garnier *et al.*, 1999; Descy *et al.*, 2003; Caraco, Cole & Strayer, 2006).

Most studies have been devoted to the invasive mussels *Dreissena polymorpha* (and, to a lesser extent, *D. bugensis*) while comparatively few papers have addressed the effects of the basket clams *Corbicula* spp. The effect of *Corbicula* on phytoplankton biomass in the Potomac River was demonstrated in the early 1980s (Cohen *et al.*, 1984), however, and it is likely to be significant in other river systems colonised by these clams. They are particularly efficient invaders of river systems, reaching up to several thousand m<sup>-2</sup> in the Rio Parana, Argentina (Boltovskoy,

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Izaguirre & Correa, 1995) and up to 25 000 m<sup>-2</sup> in Lake Constance (Werner & Rothhaupt, 2007).

The genus *Corbicula*, mainly native to Asia, has the particularity of including diverse reproductive strategies (from free-swimming larvae to incubation of larvae in gills) (Glaubrecht, Fehér & Von Rintelen, 2006) and sexual dioecious species as well as hermaphrodites. Some or all *Corbicula* hermaphrodites reproduce through androgenesis, a rare form of asexual reproduction in which descendants are clones of their father (reviewed in Pigneur *et al.*, 2012). Interestingly, the invasive lineages found in America and Europe seem to be mainly androgenetic, and this reproductive mode could have contributed to the invasive success of the basket clams (Hedtkke *et al.*, 2008; Pigneur *et al.*, 2011, 2012). *Corbicula* clams are particularly known for their fast spread and, because they are benthic filter-feeders which can reduce phytoplankton density (Cohen *et al.*, 1984; Vaughn & Hakenkamp, 2001), compete with native species (Fuller & Imlay, 1976; Karatayev *et al.*, 2003) and damage industrial cooling systems (Isom, 1986). Although *Corbicula* is an important invasive bivalve group, the taxonomic status of the invasive lineages remains unresolved and it is still debated which species invaded America and Europe and what is their origin. Three main morphotypes have been recorded in European rivers, the forms R, S and Rlc, genetically characterised as three distinct genetic lineages, each exhibiting virtually no genetic polymorphism and thus being considered as a clonal lineage (Pigneur *et al.*, 2011). Both forms R and S were found sympatrically among others in the Meuse. Form S is usually identified as *C. fluminalis*. Form R, morphologically identified as *C. fluminea*, would belong to the lineage *C. leana* according to mitochondrial DNA (Pigneur *et al.*, 2011).

The effects of *Corbicula* on river ecosystems could be as large as those reported for the zebra mussels. Indeed, the filtering capacity of *Corbicula* is rather high: several studies, conducted mostly in the laboratory, have reported a wide range of individual filtration rates, between 16 and 745 mL h<sup>-1</sup> (e.g. Cohen *et al.*, 1984; Vohmann *et al.*, 2010). When measured over long periods of time and expressed per unit of clam body mass in carbon (C) units, *Corbicula* spp. filtration rate values appear to be in a lower range: 0.02–0.07 (Liu, Xie & Wu, 2009), 0.06–0.45 (Vohmann *et al.*, 2010), 0.02–0.03 (Hwang *et al.*, 2010) and 0.55 m<sup>3</sup> g C<sup>-1</sup> day<sup>-1</sup> (Cercio & Noel, 2010). Filtration rate may vary substantially, depending on temperature (Lauritsen, 1986), phytoplankton composition (Liu *et al.*, 2009), season (Hornbach *et al.*, 1984), food concentration and feeding

history (Hornbach *et al.*, 1984; Lauritsen, 1986; Vohmann *et al.*, 2010), density (as a result of refiltration by a clam bed; see Elliott, Aldridge & Moggridge, 2008) and clam reproductive cycle and condition (Viergutz, Linn & Weitere, 2012). *Corbicula* can also feed pedally, when buried in the sediment, thereby contributing significantly to benthic carbon cycling and to sediment oxygen consumption (up to 46% for a density of 1250 m<sup>-2</sup>; Hakenkamp & Palmer, 1999).

Even assuming that data on bivalve densities and filtration rates are available, further steps are necessary to demonstrate unambiguously their effect in the natural environment, particularly on phytoplankton in rivers. Indeed, phytoplankton abundance in rivers does vary depending on several factors controlling growth and biomass. Those have been reviewed by several authors, for example Reynolds & Descy (1996), who stressed the overwhelming importance of physical factors, that is, discharge, light in the water column and temperature, interacting with changes in river morphology in a complex way and determining variable residence times during downstream transfer. Therefore, the best approach to understand the dynamics of potamoplankton, and to assess the effect of filter-feeders, is to use mathematical models. For instance, Caraco *et al.* (1997) used a box-flow model to demonstrate the influence of zebra mussels *Dreissena polymorpha* in the R. Hudson (USA), while Descy *et al.* (2003) explored their effects on potamoplankton biomass and composition in a section of the R. Moselle (France, Luxembourg and Germany). In this study, we aimed at evaluating the extent to which changes that have occurred in the River Meuse over the past decade might be attributable to the colonisation of the river by the exotic Asiatic clams, *Corbicula* spp. We expected a substantial impact of the invasive bivalves on potamoplankton biomass and production, as well as effects on the oxygen budget and on water clarity, as a result of the decline in chlorophyll *a*.

## Methods

### Site description and data collection

Despite its relatively short length (905 km), the Meuse is a transnational river that flows through France, Belgium and the Netherlands. The total catchment area is 34 548 km<sup>2</sup>, with nearly 9 million inhabitants. The river is regulated by weirs and locks that allow navigation between the ports of Rotterdam and Antwerp (through the 'Canal Albert') and the industrial centres of Wallonia and the southern Netherlands. It provides cooling water

for industry and power plants and receives thermal discharges. A major part of the land in the catchment is used intensively for agriculture, which implies diffuse inputs of nutrients. In the reach studied, in Wallonia, the mean annual discharge was  $107 \text{ m}^3 \text{ s}^{-1}$  in 2005 at Tailfer, located at km 518 from the source (Fig. 1). A comprehensive description of the Meuse basin, including long-term changes in water temperature, suspended matter, discharge and orthophosphate, can be found in Descy *et al.* (2009). Collection of data on chlorophyll *a*, nutrients and suspended matter was carried out over the period 1998–2010, from a database established by the International Meuse Commission (IMC, <http://www.meuse-maas.be>) in the framework of its water quality monitoring network.

#### Estimates of *Corbicula* density

The history of the colonisation of R. Meuse by *Corbicula* may be derived from the data published by Swinnen *et al.* (1998) and Vanden Bossche (2002). During the present study, we performed quantitative observations by sampling quadrats of the river bottom when the river

level was lowered for technical maintenance in September 2007. Seven sites distributed between Namur and the French border were investigated: Tailfer, Godinne, Houx, Dinant, Waulsort, Hastière and Heer-Agimont (Fig. 1) and one additional site in the French part of the river (Ham-sur-Meuse) was sampled in 2009. Metal frames of  $900 \text{ cm}^2$  or  $500 \text{ cm}^2$  were placed randomly on the bed, and the living clams found in the substratum were counted and shell length was measured. Whenever possible, density was assessed in at least three different substratum types to take account of spatial heterogeneity linked to the substratum preferences of *Corbicula* (Schmidlin & Baur, 2007). During our sampling campaigns, form R *Corbicula* clams were found in the R. Meuse up to Saint-Mihiel (Fig. 1). Form S has, to date, never been found upstream of Tihange (Fig. 1).

#### Modelling potamoplankton dynamics

Simulations of phytoplankton were performed using the PEGASE model (Smitz *et al.*, 1997; Delière *et al.*, 2009), developed for estimating river water quality, at the scale of a whole catchment. PEGASE (Planification Et Gestion

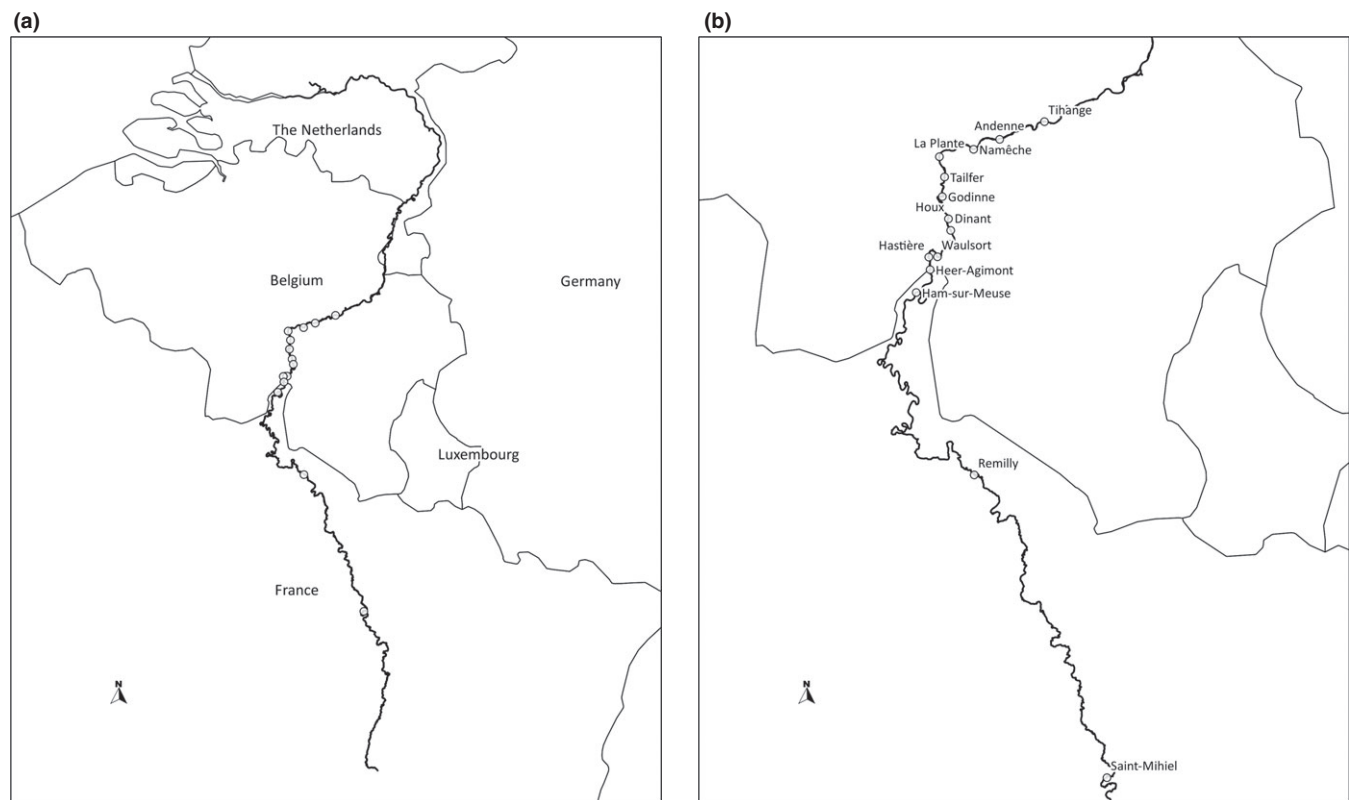


Fig. 1 Location of the R. Meuse basin (a) and the sampling sites (b).

de l'Assainissement des Eaux) is an integrated 'basin/river model' which enables deterministic calculation of the water quality in a river network according to pollutant inputs. PEGASE comprises three submodels: (i) a hydrological and hydrodynamic submodel, which calculates discharge and hydrodynamics, using daily discharge data from a few gauging stations; (ii) a thermal submodel, which calculates water temperature from daily data at several sites, taking into account thermal releases from power plants; and (iii) a water quality submodel, including ecological and biological processes within the aquatic ecosystem, as well as point and non-point sources of organic matter and macronutrients, in different forms (dissolved and particulate, readily bioavailable or slowly degradable). In the present application, the model operated in non-stationary mode, computing hydrology, temperature and water quality variables from source to mouth of the river, using data on river morphology and water level regulation by navigation dams, and measurements of incident light (data from the Belgian Royal Meteorological Institute), discharge and temperature as forcing variables.

The POTAMON model, running within PEGASE, was used for simulating phytoplankton concentrations. This model has been described in detail by Everbecq *et al.* (2001) and by Descy *et al.* (2003, 2011), with application to the rivers Meuse, Moselle and Loire. The model parametrisation was the same as in Descy *et al.* (2011), with clam density adapted for the River Meuse in 2005, and with an updated clam filtration rate. Owing to the lack of data on clam population dynamics, we used reference clam biomasses for the different river stretches sampled in 2007 and 2009, varying from 1 g C m<sup>-2</sup> (i.e. c. 20 adult clams m<sup>-2</sup>) to 25 g C m<sup>-2</sup> (i.e. c. 450 adult clams m<sup>-2</sup>). To capture variations in clam biomass over the year, monthly coefficients were applied, varying from 0.5 in winter to 1.4 in late summer. This seasonal pattern was inferred from the studies by Bachmann (2000). An example of simulated variation of clam biomass at Tailfer, our main study site, is presented at Fig. 2. Despite the obvious uncertainties associated with these estimates of clam biomass, the values used in the simulations were well within the range of estimates of clam density observed in the Meuse in 1998 (see Results). Owing to the availability of various data, the year 2005 was chosen for the model simulations.

The filtration rate of *Corbicula* used for the simulations was derived from a review of published filtration rates (see Introduction). To compare the data, we expressed the filtration rate per unit of body mass (as C) per day (m<sup>3</sup> g C<sup>-1</sup> day<sup>-1</sup>). Body mass could be derived from

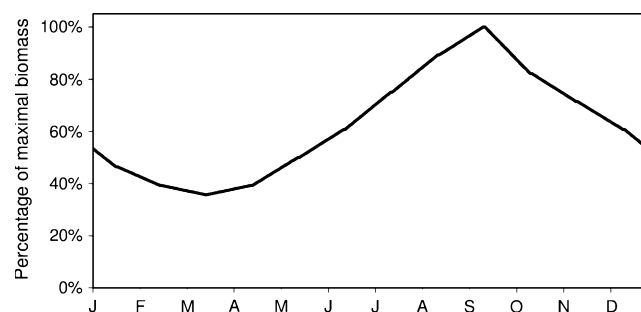


Fig. 2 Seasonal variation of *Corbicula* relative biomass (expressed as % of maximum biomass) in the R. Meuse, as used for the model simulations.

clam size by the following formula, established from measurements, on 80 individuals, of shell dimensions (height) and of organic carbon (measured with a Carlo Erba CN analyser after drying the fleshy parts at 105°C for 24 h):

$$\text{Clam body mass as g C} = 0.0148 \cdot (H^{2.2685}), \quad (1)$$

where H is shell height in cm.

Based on this formula, we recalculated published values whenever shell dimensions were available in the publications and took into account temperature effects assuming a Q<sub>10</sub> of 2. These calculations gave a maximum filtration rate of 0.086 m<sup>-3</sup> g C<sup>-1</sup> day<sup>-1</sup> at 20 °C, which is very close to the estimates of Liu *et al.* (2009) and of Viergutz *et al.* (2012), when recalculated using shell size.

Edibility coefficients took into account the preference of *Corbicula* for small phytoplankton, whereas filamentous diatoms were considered less edible, as suggested by direct observations of phytoplankton samples (data not shown). As *Corbicula* has been reported to feed mostly on small seston (Hwang *et al.*, 2004), no direct predation on zooplankton was considered in the model.

The output of the model consisted of daily values, at different river sites, of water quality variables and of each plankton category. These results were the concentrations of phytoplankton (in g C m<sup>-3</sup> or mg chl *a* m<sup>-3</sup> with a constant C:chl *a* ratio of 37) and of zooplankton (g C m<sup>-3</sup>), as well as production and loss rates (sedimentation, mortality, respiration, grazing). For comparing model outputs with calculated values, we used water quality and chlorophyll *a* data available from the IMC monitoring network, from S.I.E.R.M. (Système d'Information sur l'Eau Rhin-Meuse; <http://rhin-meuse.eaufrance.fr/>), from Vivaqua (<http://www.vivaqua.be>) and from SPW (Service Public de Wallonie; <http://aqua-phyc.environnement.wallonie.be>).



## Results

### Observed changes in chlorophyll *a* and water quality variables

From 2003, a decrease in phytoplankton has been observed in the R. Meuse at most sites in the French and Belgian sectors. The decline has been even stronger since 2004–2005 (Fig. 3). A summary of the data on phytoplankton biomass and abiotic factors in the R. Meuse in 1996 and 2010 is presented in Table 1. The year 1996, well before *Corbicula* reached significant density in the river, was chosen as a reference for comparison. Whereas most abiotic parameters remained in the same range, chlorophyll *a*, zooplankton abundance and the vertical light attenuation coefficient presented substantially lower values in 2010. This suggests that as phytoplankton biomass decreased, water clarity increased. A slight decrease in soluble reactive phosphate (SRP) may have occurred in the Belgian Meuse, but it was not apparent in the data from upstream monitoring sites: for

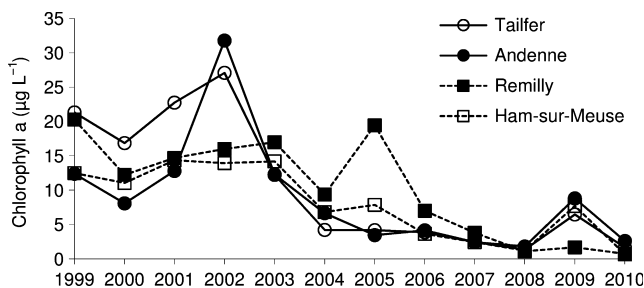


Fig. 3 Mean annual concentration of chlorophyll *a* in the River Meuse, at four sites, in France (Remilly, km 335 and Ham-sur-Meuse, km 460) and in Belgium (Tailfer, km 518 and Andenne, km 548); see locations in Fig. 1. Sources: S.I.E.R.M, Vivaqua and SPW.

**Table 1** Comparison of data from the R. Meuse in 1996 (site: Tailfer) and 2010 (sites: Tailfer and La Plante). Most data cover the March – November period. Substantial changes are in bold

	Tailfer (1996)	Tailfer/La Plante (2010)
Temperature (°C)	4–22.1	9.2–25.21
pH	7.5–8.5	7.57–8.62
Extinction coefficient ( $\text{m}^{-1}$ )	<b>1.02–3.74</b>	<b>0.70–1.74</b>
Discharge ( $\text{m}^3\text{s}^{-1}$ )	24–607	25.8–948
$\text{PO}_4^{3-}$ ( $\text{mg P L}^{-1}$ )	<b>0.007–0.189</b>	<b>0.005–0.078</b>
$\text{NO}_3^-$ ( $\text{mg N L}^{-1}$ )	0.77–4.34	1.94–2.86
$\text{NH}_4^+$ ( $\text{mg N L}^{-1}$ )	0.01–0.26	0.015–0.107
Chlorophyll <i>a</i> ( $\mu\text{g L}^{-1}$ )	<b>17.5–164.2</b>	<b>0.5–4.34</b>
Zooplankton ( $\text{ind L}^{-1}$ )	<b>0–2000</b>	<b>0–80</b>

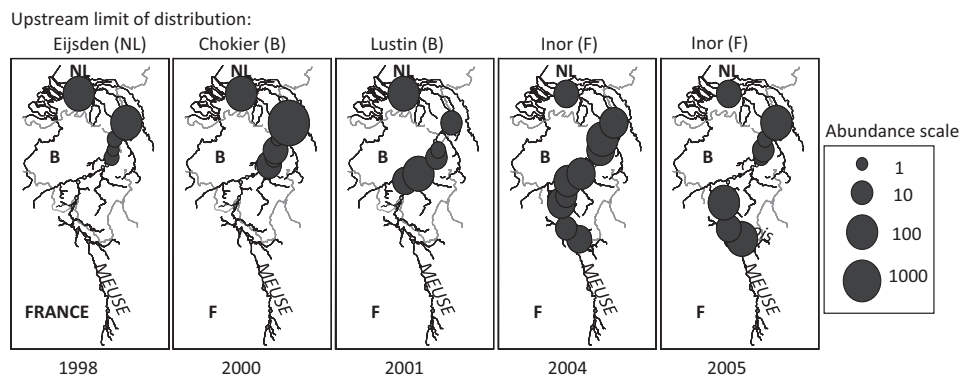
instance, in Ham-sur-Meuse, average SRP concentration has remained above  $0.12 \text{ mg L}^{-1}$  in the period 2005–2010.

### Colonisation and distribution of *Corbicula* in the R. Meuse

Between 1998 and 2005, *Corbicula* spp., expanded upstream in the R. Meuse and became abundant in different parts of the river. Figure 4 presents a synthesis of the data, extracted from a study of benthic macroinvertebrates by Usseglio-Polatera & Beisel (2010), with the upstream limit of colonisation of the river and estimates of the clam density in the sampled sites. The densities recorded in that study were in the same range as those we observed from our sampling campaigns in 2007 and 2009, that is,  $20\text{--}880 \text{ m}^{-2}$  (Table 2), with maxima in a substratum composed of sand and gravel. The highest densities were recorded in 2009 in Ham-sur-Meuse, close to the France-Belgium border.

### Modelled impact on plankton biomass and production

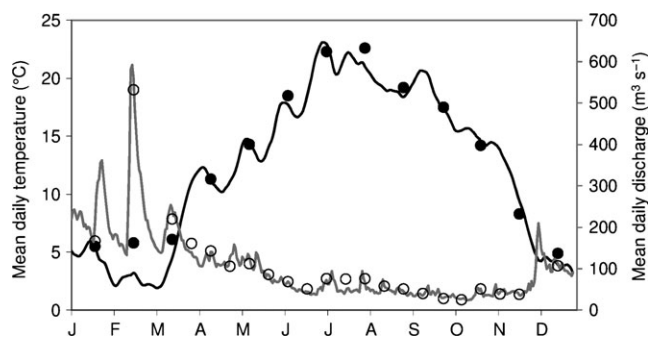
The simulations presented here (Figs 5–8) were run for the year 2005, that is, when the status of *Corbicula* invasion in the whole river was known; the database on point and non-point inputs to the river network was updated for this year. Tailfer, located in the most impacted stretch of the river, has been used as reference for most simulations. To assess the impact of *Corbicula*, two scenarios were used: one ‘with *Corbicula*’, including clams at observed densities (see Methods) and a second, ‘without *Corbicula*’, where the clam density was set to zero. Calculated chlorophyll *a* concentration can be compared with the measured values at several sites located in the French and Belgian stretches of the R. Meuse (Fig. 6). The simulations without clams allow assessment of the effect on phytoplankton biomass in the different river sections: not surprisingly, the impact was greatest where the molluscs achieved the greatest density. In those river sections, *Corbicula* filtration resulted in a marked decline in phytoplankton from late spring to the end of the growing season, representing a maximal total biomass loss of up to 70%. The model also gave an estimate that, without *Corbicula*, planktonic primary production would have amounted to  $748 \text{ g C m}^{-2}$  over the whole year, whereas simulations with *Corbicula* suggested values of  $288 \text{ g C m}^{-2}$  for the most impacted sector, a loss of *c.* 61% of phytoplankton production. The calculations also show an indirect impact of *Corbicula* on zooplankton via the decrease in phytoplankton biomass, resulting in a loss of zooplankton of about 75% over the



**Fig. 4** Spatiotemporal distribution of *Corbicula* spp. (Bivalvia, Corbiculidae) in the Meuse over the period 1998–2005 (modified, from Usseglio-Polatera & Beisel, 2010). Abundance per site is given as 'number of individuals' per sampling campaign, applying a homogeneous field sampling protocol (see Usseglio-Polatera & Beisel, 2010 for detailed protocol).

**Table 2** Sampling locations in the R. Meuse and clam density range (minimum and maximum) estimated in 2007 (except Ham-sur-Meuse; 2009). Nos.  $m^{-2}$  = number of live clams per square metre. (\* only one substratum sampled)

Sites	Estimated densities
Ham-sur-Meuse	180–880 $m^{-2}$
Heer-Agimont	52 $m^{-2}$ (*)
Hastière	200–300 $m^{-2}$
Waulsort	22–467 $m^{-2}$
Dinant	67–300 $m^{-2}$
Houx	411–556 $m^{-2}$
Godinne	78–544 $m^{-2}$



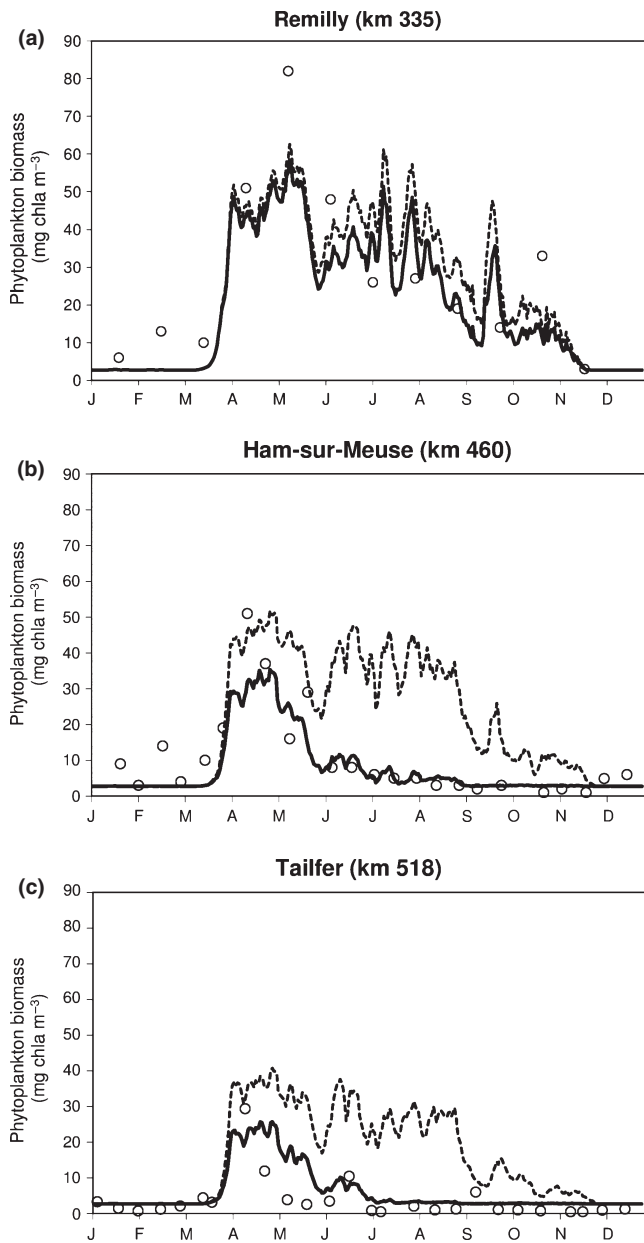
**Fig. 5** Simulations by the PEGASE model of mean daily discharge and temperature in the River Meuse at Tailfer in 2005.

whole growing season in the river sector where *Corbicula* density was the highest (Fig. 7a).

#### Modelled impact on water quality

Simulations also enabled us to assess the clam impact on some key physical and chemical parameters and on the oxygen budget in the river (Figs 7 & 8). Dissolved phosphorus concentration (SRP) has increased, probably as a

result of the reduced uptake of P by phytoplankton, as shown by the good agreement between measured and simulated values in the scenario with *Corbicula* (Fig. 7b). The change in the light attenuation coefficient observed in the field measurements (Table 2) is reflected in the simulation with and without clams (Fig. 7c). According to the model calculations, the chlorophyll *a* decline brought about by *Corbicula* resulted in a substantial decrease in the light attenuation coefficient, explaining the reported increase in water clarity. Model simulations of dissolved oxygen (DO) concentration in the river where clam density was highest were in good agreement with the measured values from a monitoring station (Fig. 8a), with minimal measured and simulated values around 7 mg  $L^{-1}$ . Although the mean difference of daily DO concentration between the scenarios with and without *Corbicula* remained relatively modest (c. 0.7 mg  $L^{-1}$ ), maximal daily DO losses amounted to >2 mg  $L^{-1}$  in mid-summer. As shown by the calculation of the different processes determining DO concentration in summer conditions (Fig. 8c), total DO consumption from water column and benthic processes did not increase in the scenario with *Corbicula*, but decreased. Rather, the loss of DO was the result of reduced photosynthesis by the depleted phytoplankton. In such conditions (Fig. 8c), from being autotrophic in a clam-free scenario ( $P/R = 1.15$ ), the river became heterotrophic in the scenario with clams in the most affected sector ( $P/R = 0.58$ ), with respiration by benthic bacteria and clam respiration being the major DO consumption terms. As for the direct contribution of *Corbicula* to benthic oxygen consumption, it was about 10% on average in the most affected sector, but could reach up to 30% by the end of summer, when clam biomass was highest (c. 35 g C  $m^{-2}$ ) and when the temperature was still around 20 °C. On an annual basis, the DO

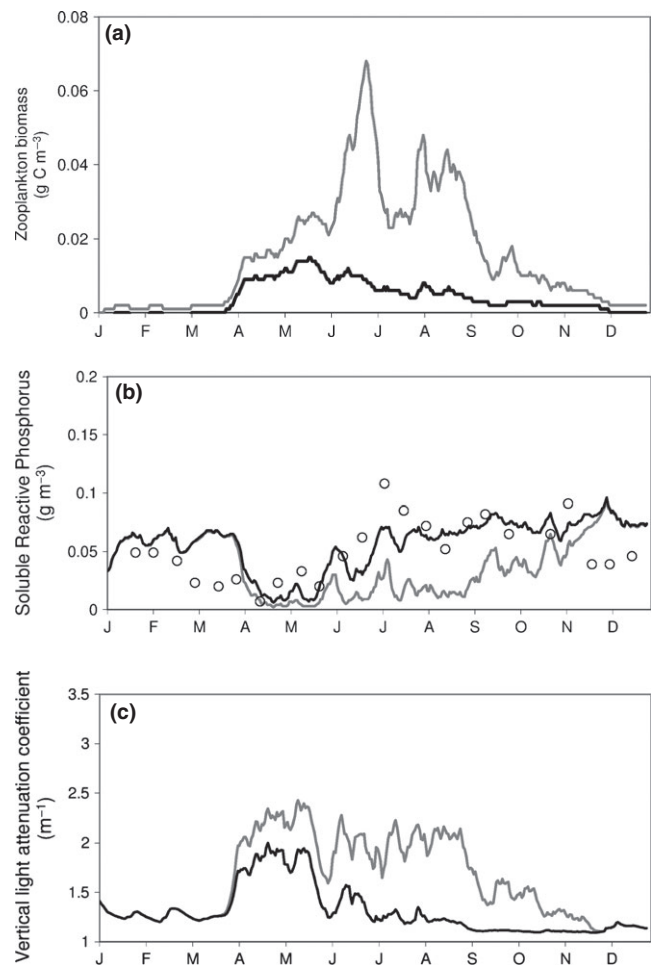


**Fig. 6** Simulations of chlorophyll *a* concentration in the River Meuse in 2005 by the POTAMON model, from upstream to downstream. (a) Remilly, km, 335; (b) Ham-sur-Meuse, km 460; (c) Tailfer, km 518. Black line: modelled values, scenario with *Corbicula*; dashed line: modelled values, scenario without *Corbicula*; dots: measured chlorophyll *a*.

budget was still negative in the scenario with clams (Fig. 8b), whereas it was positive in the clam-free scenario.

## Discussion

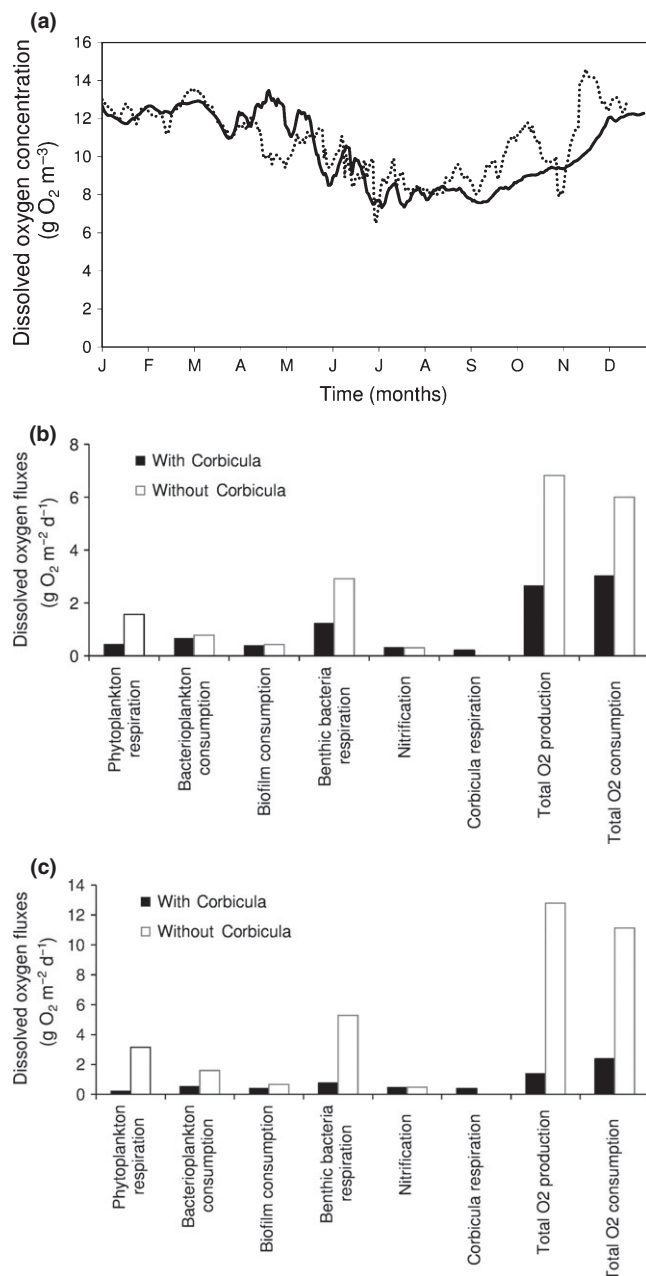
A strong decline in phytoplankton has been observed in the R. Meuse in the past decade (Fig. 3), although physi-



**Fig. 7** Simulations of (a) zooplankton biomass, (b) soluble reactive phosphorus and (c) vertical light attenuation coefficient (bottom) in the River Meuse at Ham-sur-Meuse (km 460) in 2005 by the POTAMON model. Black line: modelled values, scenario with *Corbicula*; grey line: modelled values, scenario without *Corbicula*. Dots: measured SRP.

cal and chemical parameters have remained stable (except for water transparency, which is directly linked to the phytoplankton biomass). In addition, recent plankton surveys have provided evidence that zooplankton abundance has also substantially decreased, barely reaching maxima of 100 rotifers  $L^{-1}$ , compared with numbers in the 1000s  $L^{-1}$  in the 1990s (Viroux, 2000).

Increased water transparency may also have resulted from a decrease in suspended matter concentration: indeed, a diminishing trend in the latter was shown by Descy *et al.* (2009) from the analysis of water quality data for the period 1970–2005. A substantial decrease in suspended sediment occurred at the beginning of the 1990s and may explain, through greater light availability in the water column, the high chlorophyll *a* concentrations recorded in the R. Meuse in the decade 1990–2000.



**Fig. 8** Simulated impact of *Corbicula* on dissolved oxygen (DO) in the R. Meuse, year 2005: (a) modelled daily mean DO concentration (black line) at Ham-sur-Meuse (km 460) compared with data from continuous records (dotted line) at Hastière (km 481), (b) modelled mean daily DO fluxes for the year 2005, (c) modelled DO fluxes for a typical summer day.

By contrast, the phytoplankton decline observed in the river since the mid-2000s is rather unexpected with regard to this long-term trend. Among the other physical factors influencing phytoplankton growth and development, temperature has shown a slight increasing trend (Descy *et al.*, 2009). Discharge has also exhibited an increasing trend related to more extreme flood events

(Tu *et al.*, 2005). It is unlikely that these changes affected phytoplankton growth, which generally occurs from March to October (Descy & Gosselain, 1994; Gosselain, Descy & Everbecq, 1994). As for macronutrients, only SRP showed a decrease (Descy *et al.*, 2009), but not to a value that could limit phytoplankton growth: whereas the half-saturation constant for phosphorus of the main phytoplankton taxa present in the R. Meuse is *c.* 10 µg L<sup>-1</sup> (Van Donk & Kilham, 1990), the average SRP concentration near the Belgian-French border has been *c.* 150 µg L<sup>-1</sup> in recent years, with even the minimum concentration remaining above 30 µg L<sup>-1</sup> (<http://www.meuse-maas.be>).

Therefore, as phytoplankton growth conditions have improved rather than degraded, we hypothesised that the chlorophyll *a* decline in the R. Meuse could be explained by increased losses. The zebra mussel (*Dreissena polymorpha*) has been presented in the R. Meuse for more than a century, but does not seem to have affected the ecosystem and its plankton to a measurable extent, contrary to other lowland rivers (see Introduction), probably because it has never reached high population densities. By contrast, major changes have affected the Meuse in the past decade since the *Corbicula* invasion. The clams progressed steadily upstream since the mid-1990s, being found first in the Dutch and Belgian sectors and then, from the mid-2000s, in the French sector. In this study, we combined density estimates of *Corbicula* in the field and simulations with a deterministic basin model to quantify the impact of these invasive filter-feeders on the potamoplankton and on the ecosystem. The simulations used conservative estimates of *Corbicula* density and filtration rate, and provided calculations of different variables with and without *Corbicula*, allowing an assessment of the changes likely to have been brought about by the invader.

First, they allowed us to test the hypothesis that, among the variables that control potamoplankton development, losses due to *Corbicula* filter-feeding were the most probably to be responsible for the observed decrease in chlorophyll *a* and of rotifer abundance. Similar dramatic effects of filter-feeders on river plankton have been shown in other systems colonised by exotic bivalves (Cohen *et al.*, 1984; Caraco *et al.*, 1997; Jack & Thorp, 2000; Descy *et al.*, 2003) but the impact of *Corbicula* in rivers has been rarely quantified, owing to the complexity of the environmental controls on potamoplankton (Caraco *et al.*, 2006). Here, we were able to estimate that, in the stretches where clam density was highest, phytoplankton biomass was reduced roughly by 70%, compared with a 2005 scenario without the invader, but without change in key environmental variables



that control the potamoplankton development (light, temperature, hydrology, nutrients). This reduction in biomass corresponded to a loss in productivity of  $460 \text{ g C m}^{-2} \text{ year}^{-1}$ , representing 61.5% of the calculated gross production. In the Belgian sector of the R. Meuse, this loss of production could have affected the whole food web. Indeed, due to strict river regulation and hydraulic management, the river has been heavily modified into a deep channel with stone and concrete walls that have reduced the littoral zone (Micha & Borlée, 1989). The loss of planktonic productivity has thus not been compensated for by increased benthic primary production by macrophytes and periphyton which occurred in similar situations in other rivers (Caraco *et al.*, 2000; Strayer *et al.*, 2008). Nor was loss of chlorophyll *a* compensated for by a proportional increase in photosynthesis, as a result of an improvement of water transparency. Therefore, we expect a loss of productivity at all consumer levels, from native filter-feeders to fish.

The effect of *Corbicula* on the phytoplankton showed substantial seasonal variation, with a lesser effect in spring than in summer and autumn, stemming from the combination of several factors. The clam population size is lower in spring than in summer, feeding activity is low at low temperature and the discharge is higher in spring (and hence water residence time is short). As the flow rate decreases in summer, the current slows and the bivalves can filter a greater fraction of the water: this illustrates again that, beside filtration by invasive bivalves, discharge is a major factor regulating biological activities and the fate of plankton biomass in rivers (Strayer *et al.*, 2008).

Interestingly, our simulations point to substantial effects of *Corbicula* on water quality and nutrient cycles. For instance, SRP concentration in the R. Meuse was greatly increased in the presence of the clams, from an indirect effect on phytoplankton P uptake: if the phytoplankton had not been consumed, dissolved phosphorus concentration in the R. Meuse would have been lower, as a result of measures for reduction in P inputs. Similarly, the modelling showed that the impact on the oxygen budget of the river is substantial, with a negative effect probably to occur in summer. The calculated DO fluxes point to decreased photosynthesis as the major culprit, rather than to increased benthic consumption. This contrasts with findings from other studies, in which high densities of zebra mussels resulted in large benthic oxygen consumption (e.g. Bachmann & Usseglio-Polatera, 1999; Caraco *et al.*, 2000; Garnier *et al.*, 2000; Descy *et al.*, 2003) due to mussel respiration and increased degradation of organic carbon on bottom sediments. In our sim-

ulations, benthic consumption was lower in the scenario with *Corbicula*, as the flux of phytoplankton carbon to the sediment was reduced, resulting in lower benthic bacteria consumption. However, the model does not take into account the contribution of *Corbicula* buried in the sediment, which could be significant, as they affect, by pedal-feeding, organic matter cycling within the sediment (Hakenkamp & Palmer, 1999). However, our estimates of *Corbicula* contribution to the sediment oxygen demand were, given the densities found in the R. Meuse, remarkably close to measured values in streambed sediments (Hakenkamp & Palmer, 1999).

Although this study has improved our understanding on the impact of the invasive *Corbicula* in a lowland river, some obvious gaps remain. Further estimations of *Corbicula* density in the R. Meuse are needed to follow the seasonal and interannual population dynamics, which may vary substantially. The dependence of *Corbicula* filtration rate on different factors should also be studied in more detail, in particular phytoplankton concentration and algal type and size, as well as seasonal variations related to the mollusc life cycle (e.g. Vohmann *et al.*, 2010). Finally, the effects at the consumer level, resulting from possible competition for planktonic resources with other filter-feeders, require attention: there is, on the one hand, a biodiversity issue involving the native bivalves and other invertebrates (see for instance Thorp & Casper, 2002) but also an issue of ecosystem processes and productivity as the invasive bivalves have the potential to alter food webs and biogeochemical cycling.

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