# Freshwater Biology

## Impact of the invasive Asian clam, Corbicula spp., on a large river ecosytem

**Impact of the invasive Asian clam, *Corbicula* spp., on a large river ecosytem**

Lise-Marie Pigneur[1*], Elodie Falisse[1], Kathleen Roland[1], Etienne Everbecq[2], Jean-François

Deliège[2], Joseph S. Smitz[3], Karine Van Doninck[1], Jean-Pierre Descy[1]

[1] Research Unit in Environmental and Evolutionary Biology, University of Namur, B-5000
Namur, Belgium

[2] Aquapole R&D Unit, University of Liège, B-4000 Liège, Belgium

[3] Centre Environnement, University of Liège, B-4000 Liège, Belgium

\* Corresponding author

E-mail: lise-marie.pigneur@unamur.be

Tel: +32 81724428

Fax: +32 81724362

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**Abstract**

During the past recent decades, Asiatic clams (*Corbicula* spp.) have spread spectacularly in several large European rivers. In the River Meuse, a transnational lowland river, an important 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 that hypothesis, using clam density data from field surveys, water quality monitoring data, and a simulation model. Estimated *Corbicula* densities were between 50 and 900 individuals $m^{-2}$, depending on the site. Using a maximum filtration rate per clam body mass of 0.086 $m^3$ g $C^{-1}$ $day^{-1}$ at 20°C derived from the literature, we ran simulations with a non-stationary model to estimate the impact of the exotic bivalve on the river plankton and water quality. In the stretches where the invasive clams developed best, comparison with a clam-free scenario allowed estimating a 70 % phytoplankton biomass loss due to their filtration, leading to a 61 % loss of annual primary productivity. Model simulations also showed that zooplankton may have suffered as much as 75 % loss in terms of biomass. The simulations also point to substantial effects of the invasive *Corbicula* on the river oxygen budget and on nutrient cycling. We expect that, in the heavily regulated sectors of the river, the loss of planktonic production due to the invasive filter-feeders will negatively affect other suspension feeders and alter ecosystem function and productivity.

**Key words**: invasive molluscs, lowland river, plankton, modelling

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**Introduction**

Effects of exotic benthic filter-feeders in rivers involve impact at various ecosystem compartments and processes: reduction of plankton (Cohen *et al*., 1984; Caraco *et al*., 1997; Welker & Walz, 1998; Jack & Thorp, 2000; Akopian *et al*., 2001; Descy *et al*., 2003), competition with native bivalves such as Unionids (Strayer & Smith, 1996; Parker *et al*., 1998; Vaughn & Spooner, 2006), decline of dissolved oxygen from reduction of photosynthesis in the water column coupled with increased benthic oxygen consumption (Effler *et al*., 1996; Hakenkamp & Palmer, 1999; Garnier *et al*., 1999; Caraco *et al*., 2000). A major effect at ecosystem level is transfer of organic carbon from the water column to the benthos (see e.g. Bachmann & Usseglio-Polatera, 1999; Garnier *et al*., 1999; Descy *et al*., 2003; Caraco, Cole & Strayer, 2006). Most studies, however, have been devoted to the invasive mussels *Dreissena polymorpha* (and, to a lesser extent, *D. bugensis*), and comparatively few papers have addressed the impacts of the basket clams *Corbicula* spp. Yet *Corbicula* impact on phytoplankton biomass was demonstrated in the Potomac River in the early 1980s (Cohen *et al*., 1984) and it is likely to be significant in river systems colonized by these clams. They are particularly efficient invaders in river systems, reaching up to several thousand m$^{-2}$ in the Rio Parana (Boltovskoy, Izaguirre & Correa, 1995) and up to 25000 m$^{-2}$ 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 *et al*., 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

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to be mainly androgenetic and this reproductive mode could have contributed to the invasive success of the basket clams (Hedtke *et al*., 2008; Pigneur *et al*., 2011; Pigneur *et al*., 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).

The impacts 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 laboratory conditions, have reported a wide range of individual filtration rates, between 16 and 745 ml h$^{-1}$ (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 rates appear to be in a smaller range: 0.02-0.07 (Liu *et al*., 2009), 0.06-0.45 (Vohmann *et al*., 2010), 0.02-0.03 (Hwang *et al*., 2010) and 0.55 m$^3$ g C$^{-1}$ day$^{-1}$ (Cerco & Noel, 2010). Filtration rates may vary substantially, depending on temperature (Lauritsen, 1986), phytoplankton composition (Liu *et al*., 2009), season (Hornbach *et al*., 1984), food concentration and clam feeding history (Hornbach et al., 1984; Lauritsen 1986; Vohmann *et al*., 2010), clam density (as a result of refiltration by a clam bed, see Elliott *et al*., 2008) and clam reproductive cycle and clam condition (Viergutz *et al*., 2012). *Corbicula* can also feed by pedal-feeding, 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 individuals m$^{-2}$; Hakenkamp & Palmer, 1999).

Assuming that data on bivalve densities and filtering rates are available, further steps are still necessary to demonstrate unambiguously their impact in the natural environment, particularly on phytoplankton in river systems. Indeed, phytoplankton abundance in rivers does vary depending on several factors controlling growth and biomass. Those have been

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reviewed by several authors, e.g. Reynolds & Descy (1996), who stressed the overwhelming importance of physical factors, i.e. discharge, light in the water column and temperature, interacting with changes in river morphology in a complex way, determining variable residence times during downstream transfer. Therefore, the best approach to understand the dynamics of potamoplankton and to assess the impact of filter-feeders is the use of mathematical models. For instance, Caraco *et al.*, (1997), using a box-flow model, demonstrated the influence of the invasive zebra mussels *Dreissena polymorpha* in the R. Hudson (USA), and Descy *et al.*, (2003) explored the effects of the same species on potamoplankton biomass and composition in a section of the R. Moselle (France, Luxembourg and Germany).

In this study, we compiled data of chlorophyll *a* in the R. Meuse over the past decade, and we conducted field surveys of *Corbicula* densities in this river wherever possible. We used published data on filtration rates, available environmental data and a modelling approach (Everbecq *et al.,* 2001; Descy *et al.,* 2011) to simulate the effects of clam filtration on the potamoplankton of the R. Meuse. The overall objective of the study was to quantify the impact of the invasive clams on potamoplankton and on key ecosystem variables and processes in a lowland river.

**Material and methods**

*Site description and data collection*

Despite its relatively short length (905 km), the Meuse is a transnational river that flows through several countries: France, Belgium and the Netherlands. The total catchment area is 34,548 km², 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")

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and the industrial centers of Wallonia and the southern Netherlands. It provides cooling water

for industries and power plants and receives thermal discharges. A major part of the land in

the watershed is used intensively for agriculture, which implies diffuse inputs of nutrients. In

the studied reach, located in Wallonia, the mean annual discharge was 107 $m^3$ $s^{-1}$ in 2005 at

Tailfer, located at km 518 from the source (Fig. 1). A comprehensive description of the R.

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 data base

established by the International Meuse Commission (IMC, http://www.meuse-maas.be) in the

framework of its water quality monitoring network.

*Estimates of* Corbicula *densities*

The history of the colonization 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 (see Fig. 1) and one additional site in the French part of

the river (Ham-sur-Meuse) was sampled in 2009. Metal frames of 900 cm² or 500 cm² were

placed randomly on the bottom and the living clams found in the substrate were counted, and

shell size was measured. Whenever possible, the densities were assessed in at least three

different substrate types to take into account the spatial heterogeneity linked to the substrate

preference of *Corbicula* (Schmidlin & Baur, 2007). During our sampling campaigns,

*Corbicula* clams were found in the R. Meuse up to Saint-Mihiel (Fig.1)

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*Modelling potamoplankton dynamics*

Simulations of phytoplankton were performed using the PEGASE model (Smitz *et al.,* 1997; Deliège *et al.,* 2009), developed for estimating river water quality, at the scale of a whole watershed. PEGASE (Planification Et Gestion de l'ASsainissement des Eaux) is an integrated "basin/river model" which enables to calculate in a deterministic way the water quality in a river network according to pollutant inputs. PEGASE comprises three submodels: (i) a hydrological and hydrodynamic sub-model, which calculates discharge and hydrodynamics, using daily discharge data from a few gauging stations; (ii) a thermal sub-model, 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 parameters 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 details in Everbecq *et al*., (2001) and in Descy *et al*., (2003, 2011), with applications to the rivers Meuse, Moselle and Loire (see Tables 1 and 2 for main equations and parameter values). The model simulates five functional categories of phytoplankton, in order to reproduce the "successions" usually observed in lowland rivers: (1) diatoms which form spring blooms (represented by *Stephanodiscus* spp.);

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(2) small centric diatoms developing in late spring and in summer (represented by *Cyclotella* spp.); (3) green algae and cryptophytes, with optimum development in summer; (4) grazing-resistant, filamentous diatoms (*Aulacoseira* spp.); (5) and small filamentous summer diatoms (*Skeletonema* spp.). Zooplankton is represented by two functional groups of rotifers, *Brachionus*-like and *Keratella*-like, with different growth, grazing and assimilation rates. The equations and parameters used to simulate plankton dynamics are presented in Tables 1 and 2, along with those used for simulating *Corbicula* impact. Owing to lack of data on clam population dynamics, we used reference clam biomasses for the different rivers stretches sampled in 2007 and 2009, varying between 1 g C m$^{-2}$ (i.e. ~20 adult clams m$^{-2}$) in the upper stretch located in the French sector of the R. Meuse, to the maximal densities observed around the French-Belgian border, at river km 486 (25 g C m$^{-2}$ i.e. ~450 adult clams m$^{-2}$). To render the variation of 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 observations of clam density in the R. Meuse from 1998 (see results section). 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). In order to compare the data, we expressed the filtration rate per unit of body mass (as C) per day (m$^3$ g C$^{-1}$ day$^{-1}$). Body mass could be derived from clam size by the following formula, established from measurements, on 80 individuals, of shell dimensions and of organic carbon (measured with a Carlo Erba CN analyser after drying the fleshy parts at 105°C for 24 h):

Clam body mass as g C = 0.0148. (H $^{2,2685}$)   with H = shell height in cm

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Based on this formula, we recalculated published values whenever shell dimensions were available, and took into account temperature effects assuming a $Q_{10}$ of 2. These calculations gave a maximum filtration rate of 0.086 $m^{-3}$ g $C^{-1}$ $d^{-1}$ at 20°C, and a dependence on temperature (Table 2). This value is very close to those of Liu *et al*., (2009) and of Viergutz *et al*., (2012), when recalculated using shell size.

As shown in Table 2, edibility coefficients took into account 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* was 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 in 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 $m^{-3}$or mg chl *a* $m^{-3}$ with a constant C:chl *a* ratio of 37) and of zooplankton (g C $m^{-3}$), as well as production and loss rates (sedimentation, mortality, respiration, grazing). For model output comparison 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://aquaphyc.environnement.wallonie.be).

## Results

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

From 2003, a decrease of phytoplankton has been observed in the R. Meuse at most sites of the French and Belgian sectors. The decline is even stronger since 2004-2005 (Fig. 3). A

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summary of the data on phytoplankton biomass and abiotic factors in the R. Meuse in 1996 and in 2010 is presented in Table 3. The year 1996, well before *Corbicula* reached significant density in the river, was chosen as a reference for comparison. Whereas most abiotic parameters remained stable, chlorophyll *a*, zooplankton abundance and the vertical light attenuation coefficient presented substantially lower values in 2010. This indicates that, as phytoplankton biomass decreased, water clarity increased. A slight decrease of soluble reactive phosphate (SRP) may have occurred in the Belgian Meuse, but it was not apparent in the data from upstream monitoring sites: for instance, in Ham-sur-Meuse, average SRP concentration has remained above 0.12 mg $L^{-1}$ in the period 2005-2010.

*Colonization and distribution of* Corbicula *in the R. Meuse*

Between 1998 and 2005, the basket clam, *Corbicula spp.,* has expanded upstream in the R. Meuse, and has reached high abundance in different parts of the river. Fig. 4 presents a synthesis of the data, extracted from a study of benthic macroinvertebrates by Usseglio-Polatera & Beisel (2010), with the upstream limit of colonization of the river, and estimates of the clam densities 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, i.e. 20 – 880 clams $m^{-2}$ (Table 4), with maxima in a substratum composed of sand and gravels. 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, i.e. when the status of *Corbicula* invasion in the whole river was known; the data base on point and non-point inputs to the river network was updated for this year. Fig. 5 presents the calculated values of

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discharge and temperature for 2005 at Tailfer, i.e. in the most impacted stretch of the river, used as reference for most simulations. In order to assess the impact of *Corbicula*, two scenarios were used: one "with *Corbicula*", including clams at observed densities (see material and 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 mollusks achieved the greatest density. In those river sections, *Corbicula* filtration resulted in a marked decline of phytoplankton from late spring to the end of the growing season, representing a maximal total biomass loss up to 70 %. The model also allowed estimating that, without *Corbicula*, planktonic primary production would have amounted to 748 g C m$^{-2}$ over the whole year, whereas the simulations with *Corbicula* provided an annual estimate of 288 g C m$^{-2}$ for the most impacted sector. This would be a loss of ~61 % of phytoplankton production. The calculations also show an indirect impact of *Corbicula* on zooplankton through the decrease of phytoplankton biomass, resulting in a loss of zooplankton of about 75 % over the whole growing season in the river sector where *Corbicula* density was the highest (Fig. 7, top).

*Modelled impact on water quality*

Simulations also enabled us to approach 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, likely as a result from a reduced P uptake by phytoplankton, as shown by the good agreement between measured and simulated values in the scenario with *Corbicula* (Fig. 7, middle). The change in the light attenuation coefficient

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observed in the field measurements (Table 3) is reflected in the simulation with and without clams (Fig. 7, bottom). According to the model calculations, the chlorophyll *a* decline brought about by *Corbicula* resulted in a substantial decrease of the light attenuation coefficient, explaining the reported increase in water clarity. The effect on dissolved oxygen (DO) concentration in the river is shown in Fig. 8 for a site where clam density was highest. The model simulations were in good agreement with the measured values from a monitoring station (Fig. 8, top), with minimal measured and simulated values around 7 mg $L^{-1}$. Although the average difference of daily DO concentration between the scenarios with and without *Corbicula* remained relatively modest (~0.7 mg $L^{-1}$), maximal daily DO losses amounted to > 2 mg $L^{-1}$ in mid-summer. As shown by the annual budget of the different processes determining DO concentration (Fig. 8, bottom), total DO consumption from water column and benthos processes did not increase in the scenario with *Corbicula*, but it decreased. Rather, the loss of DO was the result of reduced photosynthesis from phytoplankton biomass losses. As for the direct contribution of *Corbicula* to benthic oxygen consumption, it was about 10 % on average in the most impacted sector, but it could reach up to 30 % at the end of summer, when clam biomass was highest (~35 g C $m^{-2}$) and when the temperature was still around 20°C.

**Discussion**

A strong decline of phytoplankton has been observed in the R. Meuse in the past decade (Fig. 3), although physical and chemical parameters have remained stable, except the water transparency, which is directly linked to the phytoplankton biomass. In addition, recent plankton surveys have provided evidence that zooplankton abundance has also substantially

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decreased, barely reaching maxima of 100 rotifers $L^{-1}$, to be 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 was shown by Descy *et al.*, (2009) from analysis of

water quality data for the period 1970-2005. A substantial decrease in suspended sediment

occurred in 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

1990-2000 decade. 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.*, 2009a). 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 occurs, generally, from March to October (Descy &

Gosselain, 1994; Gosselain, Descy & Everbecq, 1994). As for macronutrients, only SRP

shows a decreasing trend (Descy *et al.*, 2009b), but not to a level that could significantly limit

phytoplankton growth: whereas the half-saturation constant for phosphorus of the main

phytoplankton taxa present in the R. Meuse is ~10 μg $L^{-1}$ (Van Donk & Kilham, 1990), the

average SRP concentration near the Belgian-French border was ~150 μg $L^{-1}$ in the recent

years, with minimum concentrations still remaining above 30 μg $L^{-1}$ (http://www.meuse-

maas.be).

Therefore, as phytoplankton growth conditions have improved rather than degraded, we

hypothesized that the chlorophyll *a* decline in the R. Meuse may be explained by increased

losses. The zebra mussel (*Dreissena polymorpha*) has been present in the R. Meuse for more

than a century, but it does not seem to have impacted the ecosystem and its plankton to a

measurable extent, contrary to other lowland rivers (see introduction), likely because it never

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reached large population densities in the R. Meuse. By contrast, major changes have affected the river in the past decade since the invasion by the bivalves of the genus *Corbicula*. The clams progressed steadily upstream since the mid-1990s, first in the Dutch and Belgian sectors, then, from the mid-2000s, in the French sector of the river. 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* densities and filtration rates, and provided calculations of different variables with and without *Corbicula*, allowing an assessment of the changes brought about by the invaders in the river system.

First, they allowed to validate the hypothesis that, among the variables that control potamoplankton development, losses due to *Corbicula* filter-feeding were the most likely to be responsible for the observed decrease of chlorophyll *a* and of rotifer abundance. Similar dramatic effects of filter-feeders on river plankton were shown in other systems colonized by exotic bivalves (Cohen *et al*., 1984; Caraco *et al*., 1997; Jack and 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 maximal, phytoplankton biomass was reduced roughly by 70%, by reference to a 2005 scenario without the invading bivalves, but with no change in key environmental variables that control potamoplankton development (light, temperature, hydrology, nutrient inputs). This biomass reduction corresponded to a productivity loss of 460 g C m$^{-2}$ year$^{-1}$, representing 61.5 % of the calculated gross production. In the Belgian sector of the R. Meuse, this loss of production may have affected the whole food web, given that, due to a rather heavy river regulation and hydraulic management, the loss of planktonic productivity has not been compensated by increased benthic primary production by macrophytes which occurred in similar situations in

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other rivers (Caraco *et al.*, 2000; Strayer *et al.*, 2008). Nor was loss of chlorophyll *a* compensated by a proportional increase of 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.

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

Interestingly, our simulations point to substantial effects of the invasive *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 of P inputs. Similarly, the modeling shows that the impact on the oxygen budget of the river is substantial, with a negative effect likely 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 *et al.*, 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 simulations, benthic consumption was lower in the scenario with *Corbicula*, as the flux of phytoplankton carbon to the sediment was reduced,

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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). Yet our estimates of *Corbicula* contribution to the sediment oxygen demand was, given the densities found in the R. Meuse, remarkably close to measured values in streambed sediments (Hakenkamp & Palmer, 1999).

Despite this study has improved the understanding on the impact of the invasive *Corbicula* in a lowland river, some obvious gaps remain. Further estimations of *Corbicula* densities in the R. Meuse are needed to follow the seasonal and interannual population dynamics, which may vary substantially. The dependence of *Corbicula* filtration rates 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 molluscs life cycle (e.g. Vohmann *et al*., 2010). Finally, the impacts at 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 ecosystem function and productivity issue as the invasive bivalves have the potential to alter food webs and biogeochemical processes.

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**Figures captions**

**Fig. 1** Location of the R. Meuse basin (left) and the sampling sites (right).

**Fig. 2** Variation of *Corbicula* biomass over time in the R. Meuse at Tailfer, as used for the model simulations.

**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.

**Fig. 4** Spatio-temporal distribution of *Corbicula* spp. (Bivalvia, Corbiculidae) in the Meuse River over the 1998-2005 period. Abundances per site are given in "number of individuals" per sampling campaign, applying a homogeneous field sampling protocol. This protocol included (i) Surber samples in three habitats of the littoral zone (fine sediment, coarse sediment and macrophytes), (ii) dredge samples of the profundal zone and (iii) artificial substrates (see Usseglio-Polatera and Beisel 2010 for further details).

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

**Fig. 6** Simulations of chlorophyll *a* concentration in the River Meuse in 2005 by the POTAMON model, from upstream to downstream. From top to bottom: at

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Remilly, km, 335; at Ham-sur-Meuse, km 460; at Tailfer, km 518.. Black line: calculated values, scenario with *Corbicula*; dashed line: calculated values, scenario without *Corbicula*; dots: measured chlorophyll *a*.

**Fig.7** Simulations of zooplankton biomass (top), soluble reactive phosphate (middle) and vertical light attenuation coefficient (bottom) in the River Meuse at Ham-sur-Meuse (km 460) in 2005 by the POTAMON model. Black line: calculated values, scenario with *Corbicula*; dashed line: calculated values, scenario without *Corbicula*.

**Fig. 8**. Simulated impact of *Corbicula* on dissolved oxygen (DO) in the R. Meuse, year 2005 at Ham-sur-Meuse (km 460). Top: calculated daily average DO concentration at Ham-sur-Meuse (black line) compared with data from continuous records (dotted line) at Hastière (km 481). Middle: difference in DO concentration due to *Corbicula*. Bottom: calculated annual fluxes of DO, due to different processes, and DO annual budget.

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Fig. 1 Location of the R. Meuse basin (left) and the sampling sites (right).
257x194mm (72 x 72 DPI)
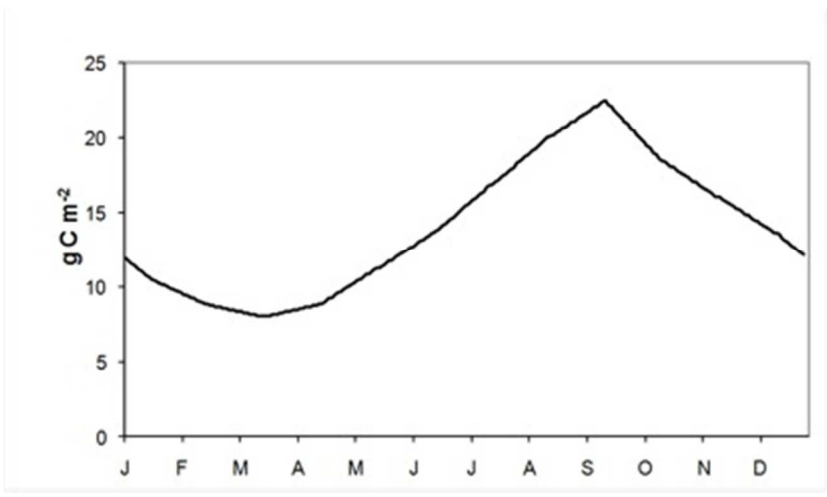
Fig. 2 Variation of Corbicula biomass over time in the R. Meuse at Tailfer, as used for the model simulations
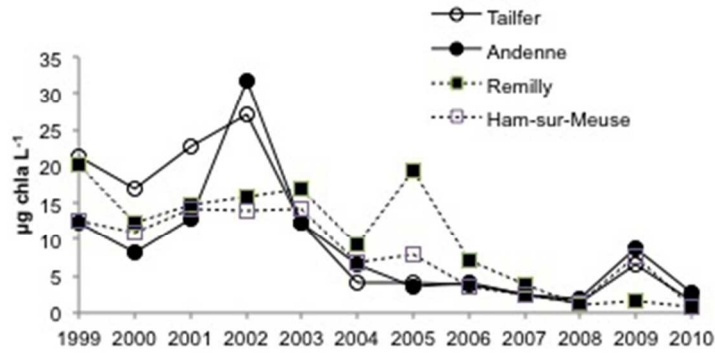145x85mm (72 x 72 DPI)

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.
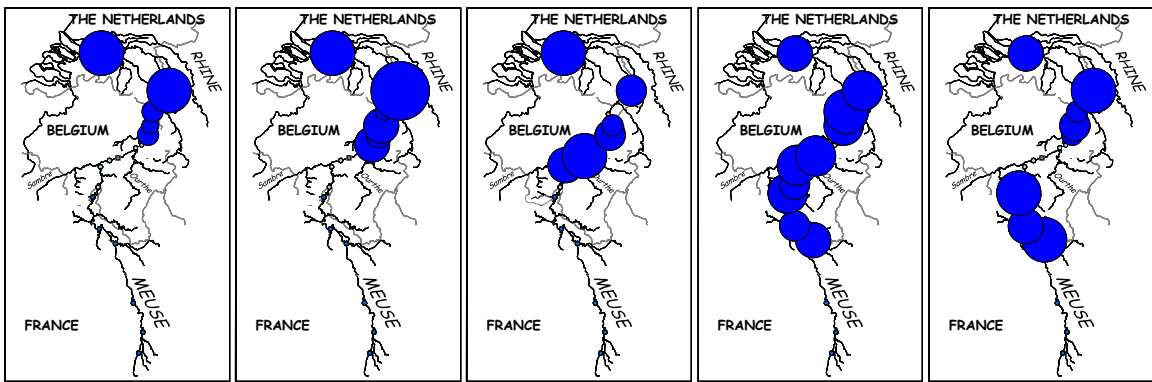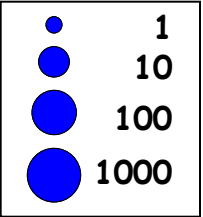137x71mm (72 x 72 DPI)

Fig. 5 Simulations by the PEGASE model of discharge and temperature in the River Meuse at Tailfer in 2005.
159x91mm (72 x 72 DPI)

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Fig. 6 Simulations of chlorophyll a concentration in the River Meuse in 2005 by the POTAMON model, from upstream to downstream. From top to bottom: at Remilly, km, 335; at Ham-sur-Meuse, km 460; at Tailfer, km 518.. Black line: calculated values, scenario with Corbicula; dashed line: calculated values, scenario without Corbicula; dots: measured chlorophyll a.
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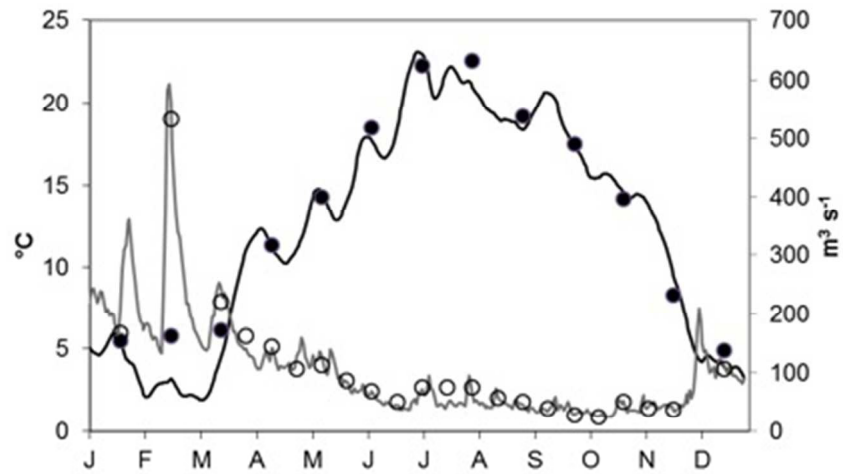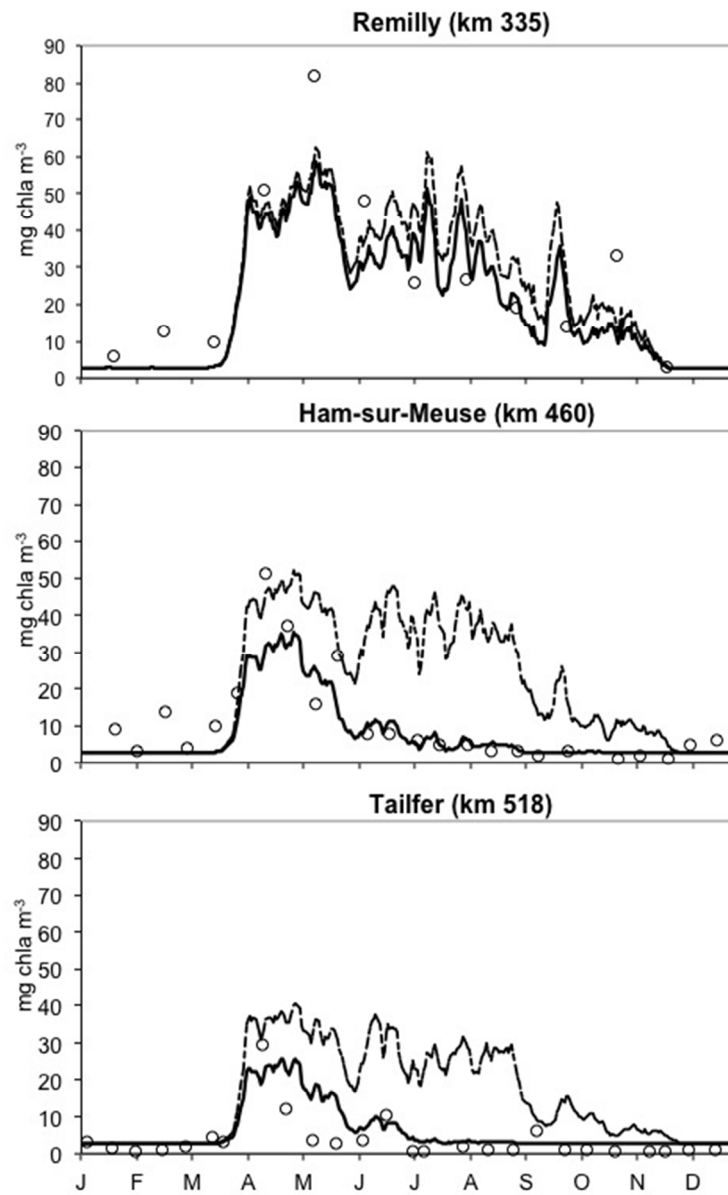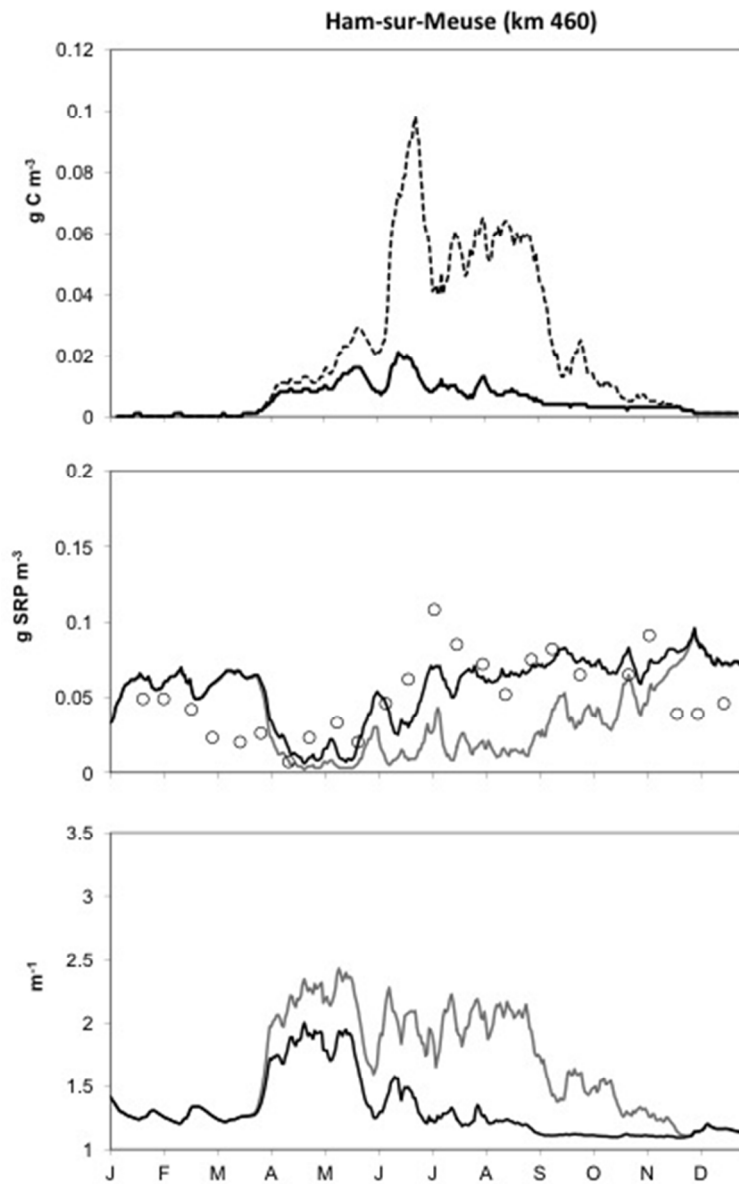53
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Fig.7 Simulations of zooplankton biomass (top), soluble reactive phosphate (middle) and vertical light attenuation coefficient (bottom) in the River Meuse at Ham-sur-Meuse (km 460) in 2005 by the POTAMON model. Black line: calculated values, scenario with Corbicula; dashed line: calculated values, scenario without Corbicula.
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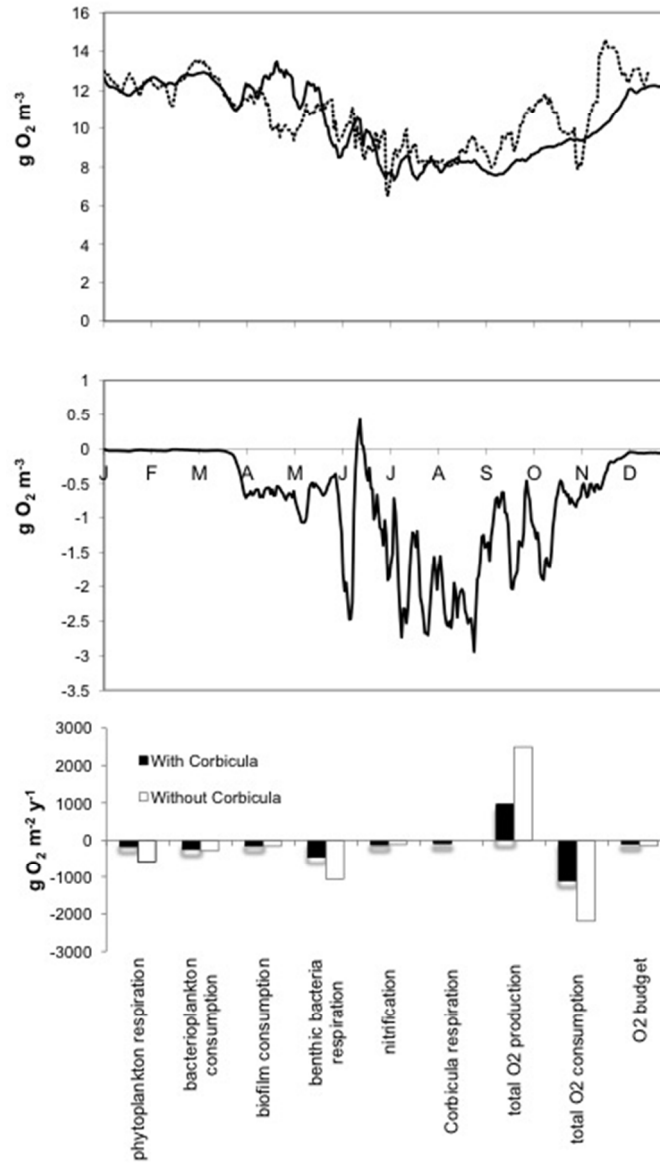
Fig. 8. Simulated impact of Corbicula on dissolved oxygen (DO) in the R. Meuse, year 2005 at Ham-sur-Meuse (km 460). Top: calculated daily average DO concentration at Ham-sur-Meuse (black line) compared with data from continuous records (dotted line) at Hastière (km 481). Middle: difference in DO concentration due to Corbicula. Bottom: calculated annual fluxes of DO, due to different processes, and DO annual budget.
145x257mm (72 x 72 DPI)

**Table 1**. Variables and processes of the plankton submodel

| | description | units | equation |
|---|---|---|---|
| **Phytoplankton** | | | |
| $phy_j$ | phytoplankton concentration | mgC L$^{-1}$ | |
| Tpphy | production rate | s$^{-1}$ | Kopt (T) . min (Red_P, Red_N, Red_Si) . f(I) |
| Kopt (T) | light saturated rate of photosynthesis | mgC mgC$^{-1}$ s$^{-1}$ | Kopt (Topt) . e$^{(-(T-Topt)^2 / dtek^2)}$ |
| T | temperature | °C | |
| Nut | nutrient concentration | mg L$^{-1}$ N,P,Si | |
| Red_Nut | limitation factor (growth) | - | (Q-Qmin) / (Qopt-Qmin) |
| Red_Nut_Up | limitation factor (uptake) | - | Nut/(Nut + KNut) |
| Q | nutrient quota | mgNut mg C$^{-1}$ | |
| Qmin | minimum nutrient quota | mgNut mg C$^{-1}$ | |
| Qopt | optimum nutrient quota | mgNut mg C$^{-1}$ | |
| f(I) | light limitation factor | - | $$\frac{2}{H}\int_0^H \frac{I(z,t)/(2.Ik)}{\left[1+(I(z,t)/(2.Ik))^2\right]}dz$$ $$= \frac{2}{ke.H}\left[arctg\frac{I_0(t)}{2Ik} - arctg\frac{I_0(t)e^{-ke.H}}{2Ik}\right]$$ |
| I(z,t) | available light | µE m$^{-2}$ s$^{-1}$ | $I_0(t)$ . e$^{-ke \cdot z}$ |
| $I_0(t)$ | incident light energy | µE m$^{-2}$ s$^{-1}$ | |
| Ik | light saturation constant | µE m$^{-2}$ s$^{-1}$ | $b_0$. I/($b_1$ + I) |
| ke | extinction coefficient | m$^{-1}$ | $$k_1 + \sum_j k_{2j}\ phy_j + k_3\ POC$$ |
| $k_1, k_2, k_3$ | extinction coefficient parameters | | |
| POC | particulate organic carbon | mgC L$^{-1}$ | |
| Tmphy | mortality rate | s$^{-1}$ | $tmphy_{20}$ . qmphy e$^{[(T-20)/10]}$ |
| Trphy | respiration rate | s$^{-1}$ | $trphy_{20}$ . qrphy e$^{[(T-20)/10]}$ |
| Tsphy | sedimentation rate | s$^{-1}$ | vsphy/H |
| Graz | grazing rate | s$^{-1}$ | tfzoo . tfzoophy . zoo |
| tfzoophy | edilibility coefficient by zooplankton | | |
| tfcrbphy | edilibility coefficient by *Corbicula* | | |
| **Zooplankton** | | | |
| $zoo_i$ | zooplankton concentration | mgC L$^{-1}$ | |
| $tfzoo_m$ | maximum filtration rate | L mgC$^{-1}$ d$^{-1}$ | $tfzoo_{m20}$ qgzoo e$^{[(T-20)/10]}$ |
| tfzoo | filtration rate | L mgC$^{-1}$ d$^{-1}$ | $tfzoo_m$   if  phyG ≤ Cphyzoo <br> $tfzoo_m$ . Cphyzoo/phyG  if  phyG > Cphyzoo |
| phyG | grazable phytoplankton | mgC L$^{-1}$ | $$\sum_j tfzoophy_j \cdot phy_j$$ |
| trzoo | respiration rate | s$^{-1}$ | $trzoo_{20}$ . qrzoo e$^{[(T-20)/10]}$ |
| tmzoo | mortality rate | s$^{-1}$ | $tmzoo_{20}$ . qmzoo e$^{[(T-20)/10]}$ |
| **Benthic filters** | | | |
| Corbi | *Corbicula* concentration | mgC m$^{-2}$ | |
| $Tfiltcrb_m$ | maximum filtration rate | L mgC$^{-1}$ d$^{-1}$ | $Tfiltcrb_{m20}$ (Topt) . e$^{(-(T-Topt)^2 / dtek^2)}$ |
| Tfiltcrb | filtration rate | L mgC$^{-1}$ d$^{-1}$ | $Tfiltcrb_m$. Kphycrb / (phytotcrb + Kphycrb) |
| phytotcrb | edible phytoplankton | mgC L$^{-1}$ | $$\sum_j tfcrbphy_j \cdot phy_j$$ |
| Kphycrb | saturation constant | mgC L$^{-1}$ | |

**Table 2**. Parameters of the plankton submodel. All rates were temperature-adjusted considering a $Q_{10}$ of 2.0

|  |  | units | *Stephanodiscus hantzschii* | Small centric diatoms | Green algae | Large centric diatoms | *Skeletonema* |
|---|---|---|---|---|---|---|---|
| **Phytoplankton** |  |  |  |  |  |  |  |
| Kopt (at Topt) | light saturated rate of photosynthesis | mg C mg C$^{-1}$ d$^{-1}$ | 5.00 | 5.25 | 5.40 | 3.30 | 4.25 |
| Topt | optimal temperature for photosynthesis | °C | 11 | 17 | 21 | 25 | 26 |
| dtek | determines the shape of the Kopt : T curve | °C | 8 | 9 | 14 | 12 | 12 |
| b0 | parameter of the Ik equation | µE m$^{-2}$ s$^{-1}$ | 100 | 140 | 200 | 60 | 175 |
| b1 | parameter of the Ik equation | µE m$^{-2}$ s$^{-1}$ | 0 | 0 | 0 | 0 | 0 |
| k2 | specific extinction coefficient | m²mgC$^{-1}$ | 0.60 | 0.50 | 0.50 | 1.00 | 0.75 |
| KPO4 | half saturation constant for P-limited assimilation | mg P L$^{-1}$ | 0.01 | 0.01 | 0.02 | 0.01 | 0.01 |
| KN | half saturation constant for N-limited assimilation | mg N L$^{-1}$ | 0.10 | 0.10 | 0.10 | 0.10 | 0.10 |
| KSiO2 | half saturation constant for Si-limited assimilation | mg SiO2 L$^{-1}$ | 0.03 | 0.06 | 0.00 | 0.10 | 0.04 |
| Qopt PO4 | optimal quota for Phosphorus | mg P mg C$^{-1}$ | 0.03 | 0.02 | 0.02 | 0.02 | 0.02 |
| Qopt N | optimal quota for Nitrogen | mg N mg C$^{-1}$ | 0.15 | 0.15 | 0.15 | 0.15 | 0.15 |
| Qopt SiO2 | optimal quota for Silica | mg SiO$_2$ mg C$^{-1}$ | 1.20 | 1.20 | 0.00 | 1.80 | 0.60 |
| tmphy20 | mortality rate (at 20°C) | d$^{-1}$ | 0.17 | 0.15 | 0.16 | 0.10 | 0.14 |
| trphy20 | respiration rate (at 20°C) | d$^{-1}$ | 0.17 | 0.15 | 0.16 | 0.10 | 0.14 |
| vsphy | sedimentation velocity | m d$^{-1}$ | 1.50 | 1.25 | 0.80 | 1.50 | 1.00 |
| tfzoo1phy | edibility coefficient by *Brachionus*-like |  | 0.95 | 0.85 | 0.75 | 0.10 | 0.25 |
| tfzoo2phy | edibility coefficient by *Keratella*-like |  | 0.75 | 0.75 | 1.00 | 0.01 | 0.35 |
| tfcrbphy | edibility coefficient by *Corbicula* |  | 1.00 | 1.00 | 1.00 | 0.50 | 0.50 |
| **Zooplankton** |  |  |  |  |  |  |  |
| tfzoo1m20 | maximum filtration rate for *Brachionus*-like (at 20°C) | L mg C$^{-1}$ d$^{-1}$ | 1.60 |  |  |  |  |
| tfzoo2m20 | maximum filtration rate for *Keratella*-like (at 20°C) | L mg C$^{-1}$ d$^{-1}$ | 1.20 |  |  |  |  |
| cphyzoo1 | ILL for *Brachionus*-like | mg C L$^{-1}$ | 2.0 |  |  |  |  |
| cphyzoo2 | ILL for *Keratella*-like | mg C L$^{-1}$ | 1.5 |  |  |  |  |
| yzoo1 | growth yield for *Brachionus*-like |  | 0.15 | 0.15 | 0.12 | 0.10 | 0.15 |
| yzoo2 | growth yield for *Keratella*-like |  | 0.15 | 0.15 | 0.15 | 0.15 | 0.15 |
| tmzoo120 | mortality rate (at 20°C) of *Brachionus*-like | d$^{-1}$ | 0.13 |  |  |  |  |
| tmzoo220 | mortality rate of *Keratella*-like (at 20°C) | d$^{-1}$ | 0.11 |  |  |  |  |
| trzoo120 | respiration rate of *Brachionus*-like (at 20°C) | d$^{-1}$ | 0.13 |  |  |  |  |
| trzoo220 | respiration rate of *Keratella*-like (at 20°C) | d$^{-1}$ | 0.11 |  |  |  |  |
| tfcrbzoo1 | edibility coefficient of *Brachionus*-like by *Corbicula* |  | 0.70 |  |  |  |  |

| | | | |
|---|---|---|---|
| tfcrbzoo2 | edibility coefficient of *Keratella*-like by *Corbicula* | | 0.50 |

**Benthic filter-feeders**

| | | | |
|---|---|---|---|
| tfiltm20 | maximum filtration rate (at topt°C) | L mg C$^{-1}$ d$^{-1}$ | 0.086 |
| Toptfilt | optimal temperature for filtration | °C | 25 |
| dtfilt | determines the shape of the Tfilt : T curve | °C | 15 |
| kphydr | Saturation constant for mussels filtration | mg C L$^{-1}$ | 20 |
| ycorb | growth yield for *Corbicula* | | 0.25 |
| trcorb20 | respiration rate of *Corbicula* (at 20°C) | d$^{-1}$ | 0.01 |

**Table 3** Comparison of data (minimum – maximum) 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 |
| **Light attenuation coefficient ($m^{-1}$)** | **1.02- 3.74** | **0.70 – 1.74** |
| Discharge ($m^3\ s^{-1}$) | 24 - 607 | 25.8 – 948 |
| SRP (mg P $L^{-1}$) | 0.007 – 0.189 | 0.005 – 0.078 |
| $NO_3^-$ (mg N $L^{-1}$) | 0.77- 4. 34 | 1.94 – 2.86 |
| $NH_4^+$ (mg N $L^{-1}$) | 0.01 – 0.26 | 0.015 – 0.107 |
| **Chlorophyll *a* ($\mu g\ L^{-1}$)** | **17.5 – 164.2** | **0.5 – 4.34** |
| **Zooplankton (ind $L^{-1}$)** | **0 - 2000** | **0 - 80** |

**Table 4** Sampling locations in the R. Meuse and clam density range (minimum and maximum) estimated in 2007 (except Ham-sur-Meuse; 2009). Ind/m² = number of live clams per square meter. (* only one substrate sampled).

| Sites | Estimated densities |
|---|---|
| **Ham-sur-Meuse** | 180-880 ind/m² |
| **Heer-Agimont** | 52 ind/m² (*) |
| **Hastière** | 200-300 ind/m² |
| **Waulsort** | 22-467 ind/m² |
| **Dinant** | 67-300 ind/m² |
| **Houx** | 411-556 ind/m² |
| **Godinne** | 78-544 ind/m² |