Filter Feeding Potential of *Corbicula fluminea* in Lake Constance

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Abstract

Invasive species have led to changes in ecosystem structure, functions, and processes around the world. In aquatic systems, bivalves with their ability to filter feed can alter biogeochemical cycles and food web structures. The zebra mussel *Dreissena polymorpha* has got a lot of attention as it has caused large ecological and economical impacts in North America. Another less known but also very important freshwater invasive bivalve is the Asian clam *Corbicula fluminea*. This clam species has spread over North America in the last century and reached Europe in the 1980s. At the beginning of the 21st century, it was found isolated from other sightings at one spot in the eastern part of Lake Constance. From that point, it started to colonize the lake and has by now established itself well around the eastern end.

Daphnia spp. as the main zooplankton in Lake Constance is the basic food for planktivorous fish. Due to the regulations that reduced the pollution of the lake dramatically, fish stocks have declined in the last decades. Fishers have therefore asked to fertilize the lake with phosphate to increase the phytoplankton biomass and thus the one of the zooplankton. The goal of this thesis is to find out how much the total filtering potential of *C. fluminea* in Lake Constance would be if it spread around the whole lake and see whether that would mean that the clam would profit from more phytoplankton instead of the *Daphnia spp.*.

I estimated clam density at different depth levels at Lake Constance and calculated the filtered water volume using filtration rates from literature and a estimated potential area that the clams can colonize. I also looked at the depth distribution of the clams density and size and took sediment samples to correlate sediment properties with clam densities.

I estimated that the maximal mean filtration rate summed up over the whole lake is about 0.16 km^3 per day. This equals about 5 times the mean discharge of the Upper Lake of Lake Constance. With this rate the clams would effectively filter the volume of the whole lake in roughly a year, the water volume above the thermocline in about 64 days. As this is much higher than the estimated potential of *Daphnia spp.* (at least 2000 times as much) it is possible that the Asian clam will lessen the food availability for the zooplankton in Lake Constance. However, more data and dynamics would need to be included to make a profound statement on what that means for the management of the planktivorous fish food web in Lake Constance.

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1. Introduction

Ecosystem structures, functions, and processes around the world have been changing a lot in the last century. These changes are due to several factors, most of which are related to human actions. One of these factors is the spread of invasive species usually primarily introduced to a new region by humans. Besides affecting ecosystems, invasive species can have social impacts, for example in recreation or economy. Not all non-native species have large negative impacts, but invaded communities get altered on a broad and deep sliding scale by the introduction of every new species (Carlton 2002). In freshwater systems, invasion contributes to the loss of biodiversity. Collen et al. (2014) found that about 15 % of freshwater species are threatened by invasive ones.

1.1. Example of invasive bivalves

1.1.1. Dreissena species

Categorized within the top hundred most troublesome invaders is the zebra mussel *Dreissena polymorpha* (IUCN 2013), a mollusc from the Ponto-Caspian basin that has spread over Eurasia and North America causing a lot of change in freshwater ecosystems (Higgins und Vander Zanden 2010). Its close relative the quagga mussel *D. bugensis* has lately started to spread as well, adding to the impact by *D. polymorpha*. The zebra mussel in North America has not only altered ecosystems but caused large economic impacts. These come mostly from the fouling of water intakes at facilities for drinking water or power production and might be part of the reason why this mussel has attracted so much attention.

Ecological impacts The ecological impacts of these dreissenids, especially of *D. polymorpha*, can be widespread and in a lot of systems quite fundamental. Higgins und Vander Zanden (2010) have done a meta-analysis using published studies and long term monitoring data to evaluate the ecological impact of the two dreissenid mussels. As filter feeders, dreissenids caused a decline in suspended particulate matter and thus led to an increase in water clarity. This in turn impacted lakes' heat budget, nutrient regeneration, and deepening of the mixed layer as secondary effects of the dreissenid invasion.

Phytoplankton biomass decreased significantly in habitats that were invaded by these mussels. The decline correlated with the filtering capacity of the dreissenids, meaning the fraction of the water column they can filter in one day. Although this led to an increase in higher photosynthesis by biomass ratio, this was not enough to compensate for the huge loss in biomass and thus the total productivity of the pelagic autotrophs decreased substantially. Effects on zooplankton were significant for littoral and river habitats, where the invasion of dreissenids has led to a strong decline in its biomass. Not much data were available for pelagic systems and the decrease in zooplankton in these systems was not significant as the systems varied too much (Higgins und Vander Zanden 2010).

The loss in zooplanktonic biomass correlated moderately with the decrease in phytoplankton biomass. Dreissenids were associated with impacts on the pelagic–profundal energy pathway in which the energy fixed by phytoplankton gets transferred to zooplankton or profundal zooben-

thos. Biota that relied on this energy pathway were usually negatively impacted by the invasion of zebra and quagga mussels. However, there were also some positive effects especially for the inhabitants of benthic–littoral habitats. These were provided with resources that the mussels excreted in form of feces and pseudofeces as well as soluble nutrients. Thus, especially leaches, amphipods, and gastropods increased in abundance with the presence of dreissenid mussels (Higgins und Vander Zanden 2010).

All these impacts change a freshwater ecosystem dramatically which means that a lot of secondary impacts occur. For example, obligate planktivorous fish that cannot feed on the littoral biota lose a lot of their nutrition with zooplankton biomass decreasing. Therefore, their body conditions as well as reproduction and recruitment decline, changing population dynamics. Losers of the invasion by dreissenids were native benthic filter feeders as they lost their food base to the zebra and quagga mussels (Higgins und Vander Zanden 2010).

1.1.2. Corbicula fluminea

Another of the most important non-indigenous invasive species in aquatic ecosystems is *Corbicula fluminea* (Muller, 1774) the Asian clam (further in this text simply *Corbicula*) (McMahon 2002, Sousa et al. 2008a). This species shows a series of ecological and life history traits that makes it a really successful freshwater invader even though it shows poor physiological resistance and low physiological tolerances compared to native American species (McMahon 2000). Its long term tolerated temperature range goes from 2-36 °C, it is intolerant of even moderate hypoxia and and relatively sensitive to emergence out of water. However, *C. fluminea* is found from small streams to large lakes, as well as from all water bodies in sizes from ponds to large lakes. It can also inhabit canals, underground water piping, and industrial, potable water and power station raw water systems. While it prefers sand or fine gravel it can also be found on coarser or finer substratum and thrives in oligotrophic to eutrophic conditions. This species is a simultaneous hermaphrodite with an early maturity, usually high fecundity, twice-annual reproduction periods and short life spans. It can cross- and self-fertilize and therefore a new population can be founded by just one individual clam. With these traits it is made for a life in temporally unstable habitats with unpredictable, perturbation-induced faunal reductions as these traits allow this species to recover from catastrophic losses more rapidly than other bivalves. Furthermore, the clams can adapt these traits quickly to new environmental conditions if necessary, known as high ecophenotypic plasticity, which helps a lot in colonizing new habitats or living in a disturbed system. Another factor that contributes to the rapid spread of this species is the ability of its pediveliger and juveniles to stay suspended in turbulent water and therefore get hydrologically transported downstream. Upstream movement of juveniles can be mediated by fish, wading birds, and water fowl but has happened mostly due to anthropomorphic activities (McMahon 2000).

Spread around North America In the last century, *Corbicula* has spread from its native range in South-east Asia, Africa, and Australia throughout North America and from there to South America and Europe (reviewed in McMahon 2000). In 1924, empty shells were found in British Columbia (Counts 1981) while the first living clams were collected in 1938 in California (Burch 1944). The introduction of *C. fluminea* is attributed to Asian immigrants and has most likely happened in the early 1920s. However it is unclear whether this introduction happened intentionally or not. Most likely, anthropomorphic disturbances of aquatic systems led to the successful invasion of *C. fluminea* throughout North America as it made the habitats more habitable for the Asian clam while leading to declines in native mussel populations. It is

possible that all the Asian clams in North America derived from a single introduction as there is a lack of enzyme heterozygosity among the clams (McMahon 2000). It seems that only two long-distance dispersal events by humans contributed to the spread and that the majority of the spread of this species then happened by natural means from two to three major epicentres of artificial introduction (McMahon 1982, Counts 1986). As this species has colonized the eastern US drainage systems more rapid than *D. polymorpha* it might be the world's most invasive freshwater bivalve species.

Economic impacts However, even though this species' invasion has started before the one of the zebra mussels, far less studies have researched its impacts on the new locations. The spread of the Asian clam has led to a great economic impact especially for power stations by macro-fouling raw water. In comparison with the zebra mussel, it cannot attach to and therefore clog up the larger pipes but lodges in small diameter compounds such as heat exchangers and fouls the water in these compartments.

Ecological impacts There were not many studies done about the impacts on ecosystems that had good comparison values – meaning data about the conditions before the clams invaded. However, it seems that *C. fluminea* has been most successful in disturbed ecosystems while its impact on undisturbed ones was quite low, as for example it has only replaced native mussels in North America in the former cases but not in the latter (McMahon 2000). The filtration rate and the population density in a given water body determine the overall ecological impact of *Corbicula* as those are mostly associated with their filtering activity. Factors such as temperature regime, substrate type, food availability, oxygen concentration, and the water body morphometry influence the population density that this clam can reach locally (reviewed in Karatayev et al. 2005).

These clams can as well as the zebra mussels lead to a water clarification by their filtering abilities and therefore favour growth of rooted macrophytes, which leads to a shift in the primary production. By its ability to pedal feed, it can negatively impact borrowing detricores. However, it can also stimulate benthic productivity by increasing the pelagic-benthic coupling through deposition of organic matter on the bottom (Karatayev et al. 2005, Sousa et al. 2008a). Plant and animal species that live on hard substratum can profit from the *Corbicula* invasion as its shell provides a hard substratum on soft sediments when the clam settles there.

Corbicula has a lower wet total mass filtration rate per gram than zebra mussels (Karatayev et al. 2005) but the filtration rate is still considerably high (McMahon 2000) and it can filter large quantities of water in a short time period. With its large densities that it can reach, this clam is a major consumer of phytoplankton and can thus impact food webs of aquatic ecosystems by changing the phytoplankton community structure and limiting the seston availability for other filter feeding species especially zooplankton such as *Daphnia*. However, as this clam also extracts nitrogen to the water column phytoplankton growth might get stimulated (McMahon 2000).

The reduction of zooplankton can in turn lead to the reduction in biomass of planktivorous fish species and their predators which can well be part of game or commercial fish stocks. However, abundance of fish species that feed on bivalves might increase by the introduction of *Corbicula* while suppressing the establishment of high densities of the clam (Robinson und Wellborn 1988).

Spreading over Europe In Europe, *Corbicula fluminea* was first reported in south west France and in Portugal (Mouthon 1981) at the beginning of the 1980s. The clams have come from North America in the ballast water of ships. This is why they first colonized sea ports in the brackish water zone and spread out from there (Kinzelbach 1991). It is possible that the clams have spread over the mouth of Europe's rivers by shipment from one to the other. First colonization of the river Rhine by *C. fluminea* happened simultaneously at the Rheindelta and the Rheingau in 1987, from where it has spread upwards. It is likely that human mediated transport by ship has led to the spread over medium distances upstream, so that single individual clams or a couple of them could start a new population at one spot and then spread downstream by passive dispersal of juveniles and pediveligers. As the adult clams are very active and agile, they can move upstream over short distances by themselves, so can the larvae which are able to swim for a short time. In 1990, found densities increased and in 1991 mass occurrences were found at many spots mostly due to the low water level. In 1991, the most upstream finding was at Neuburg a.Rh. (at Rkm 354.0) but no mass occurrence was reported from there (Kinzelbach 1991). By 1996, the clams have almost reached Basel (Tittizer et al. 2000), while the first record in Switzerland dates back to 1997 (Turner et al. 1998).

Corbicula has been astonishingly successful in colonizing the Rhine river, which started immediately after the first introduction, while in other rivers it first stayed only at the mouth (Kinzelbach 1991). One factor might be that the Rhine is better navigable for shipping upstream, but this spread has also likely been favoured by the Schweizerhalle accident 1986 in Basel. This event led to a physical and chemical degradation of the river and as a consequence to mass mortality among many animal species in the Rhine, including predator species. For recolonization, the new *Corbicula* species had the same conditions as the native ones. As already mentioned, this clam is a good colonizer and had advantages in taking the opportunity, such as it was the case with the Rhine in the late 1980s (Denhartog et al. 1992).

Lake Constance then was reached quite quickly but isolated from other spots where the clams have been spotted. Werner und Moertl (2004) reported a first finding of *C. fluminea* from a sandy patch between the old and the new mouth of the Rhine river in Austria. First they only found fresh shells, but at a second sighting they also spotted living individuals which made them sample that spot quantitatively. The largest clam they found was 17 mm, which indicates that this species has not been at that spot for long. As there were also no findings nearby, they concluded that this species was found shortly after its introduction to Lake Constance. Most likely it reached it by the selling of pet stores or garden centres, as it cannot be transported via hulk over land.

1.2. C. fluminea in Lake Constance

Lake Constance is a pre-alpine, oligotrophic lake that has been invaded by several species in the last decades. One of them is *D. polymorpha* which is present since the 1960s. It is one of the most successful and abundant invasive macroinvertebrates in this lake and thus has led to certain changes in the ecosystem especially in the structure of the benthic community (Gergs und Rothhaupt 2015). Since the beginning of the 21st century, *C. fluminea* is part of those invasive species and has reached very high local densities. In such places, up to 90 % of the littoral community biomass can be constituted by these clams (Werner und Rothhaupt 2007). Low water temperatures and especially a severe low water event in the winter of 2005/06 led to a mass mortality of these clams in Lake Constance. As only about 1 % of the whole *Corbicula* community survived that winter, its spread around Lake Constance was slowed (Werner und

Rothhaupt 2008b). However, as we have seen, this species is really good at colonizing so its spread has not been stopped by this event and thus it could only be a matter of time until it has colonized Lake Constance completely.

With the desired decline in phosphate pollution in Lake Constance in the last decades it is now on a level that does not support fish densities as high as before. This is problematic for the professional fishers at Lake Constance which therefore argue for fertilizing the lake with small amounts of phosphate. As this nutrient limits phytoplankton growth, fertilization should lead to higher phytoplankton biomass thus more food for zooplankton on which planktivorous fish nourish themselves (Armbruster 2013, Tagblatt 2014). The most important filter feeders of the zooplankton community in Lake Constance are members of the *Daphnia* species, which dominate mostly due to their biomass (Pintocoelho 1991a). The question is whether, in the unlikely case that the phosphate fertilization would be approved, fish stocks would really grow as there is now an additional filter feeder in the system that might just be the only one profiting: *Corbicula fluminea*.

Research in other aquatic systems has shown that this clam species can have large impacts on phytoplankton abundance and therefore compete for food with zooplankton. For example, Cohen et al. (1984) could contribute the depression of phytoplankton in the Potomac River to the invasion of *Corbicula*. Local reduction in seston concentrations around Asian clam populations were found in streams by Leff et al. (1990). However, this did not seem to impact the native clams in that system. In another river system, the average density of *C. fluminea* (350 m^{-2}) was found to be able to clear the water column above the area (average 5.25 m) in 1-1.6 days during the summer (Lauritsen 1986). In hypereutrophic lake water, the Asian clam reduced chlorophyll *a* concentration by more than 60 % over seven days. Despite the excretion of nitrogen by the clams, the phytoplankton biomass declined. The community also shifted to a dominance by copepods (Beaver et al. 1991). In a blackwater river however, the filtering impacts of *C. fluminea* were relatively low and its influence on the trophic dynamics of the river therefore quite small, even though the clams constituted much of the benthic biomass. Most likely, these low impacts can be contributed to the stressful environment the river displayed for the clams (Stites et al. 1995).

If conditions in Lake Constance are favourable for the clam, and that seems to be the case, its filtering activity might be an important contributor to phytoplankton removal. By now, it has not spread over the whole lake with high densities but what if it does? The goal of this thesis was to evaluate the potential of the filter feeding by *C. fluminea* in the case that it spreads around the whole lake by building a simple mathematical model. To build such a model, data on filtration rates and potential clam densities are required (Pigneur et al. 2014). Furthermore, a number for the area that the clams can potentially colonize is needed. Total filtration then is the sum of the products of potential clam density, average filtration rate, and the colonizable area (Cahoon und Owen 1996).

I also used the opportunity to examine the samples for abundance of other benthic invertebrate groups and the grain sizes distribution in the sediments of the sampling spots. These results were then correlated with the *Corbicula* densities.

2. Material and Methods

2.1. Filtration rate

The filtration rate is the amount of water that filtering species can filter over a certain time period. The idea was to conduct an experiment to determine a rate for the *Corbicula* clams from Lake Constance, using a video camera to get a film of a clam filtering water including a coloured droplet. By getting the velocity of the droplet while it is being sucked in by the clam and the diameter of the clams siphon I would have calculated how much water flows through the siphon. I discarded this idea quickly as it would not have been really accurate and would not include real feeding activity.

Literature research showed that many factors are influencing the filtration rate of this clam species, so one had to design the experiment to determine this rate carefully. This is also one of the reasons why the values for *Corbicula* filtration rates vary so much from one study to the next. Physical environmental conditions such as temperature (Lim et al. 2005) and seasonal changes (Viergutz et al. 2012) lead to variation in filtration rates. Also, the biological environment such as food concentration (Lauritsen 1986, Lim et al. 2005, Way et al. 1990) and phytoplankton composition (Buttner und Heidinger 1981) have an impact on the amount of water the clams filter. Food concentration and filtration rate correlate negatively, as the clams can adjust physiologically to get to an optimal phytoplankton removal (Way et al. 1990). Buttner und Heidinger (1981) found that *Corbicula* selects its food by size, shape, specific gravity, and quality. This means that, depending on the assemblage of the phytoplankton, filtration rates vary among habitats. In the experiments of Way et al. (1990), they found that the highest filtration rates were measured when particles of the size range present in the natural habitat of the clams were used. Using cultured algae for an experiment in the lab to determine filtration rate can overestimate real rates for natural seston (Doering und Oviatt 1986). Cahoon und Owen (1996) showed that experiments using only one type of algae led to higher filtration rates than when measured with natural algae assemblages. Furthermore, the feeding history of clams as well as their reproductive cycle and density can influence filtration rates (reviewed in Pigneur et al. 2014). Consequently, individual filtration rates had varied widely between clams in laboratory experiments.

Researches have not used a standardized method for their filtration rate experiments which makes it hard to compare their results (Karatayev et al. 2005). This also means that one cannot just use the method as everyone else did but design ones own experiment with reference to what has been done before. I realized that designing and conducting an experiment to measure filtration rates for Lake Constance conditions well, was beyond the scope of a bachelor thesis, considering the other questions that need answering. Thus I decided to use filtration rates from different papers for my calculation. These should give us a good first estimate of what to expect.

Values from literature (see Table 2.1) These values for filtration rates were chosen by several characteristics. Cahoon und Owen (1996) used raw lake water for their filtration rate experiments, which means that the clams fed on natural phytoplankton. Diluted 'f/2' medium was

Table 2.1.: Filtration rates (FR) from the literature that were used for the model calculations.

Reference	Used FR	Unit	Used size	Conversion
Cahoon und Owen (1996)	1.12	$\mathrm{l\ ind^{-1}\ day^{-1}}$	None	None
Atkinson et al. (2011)	164.38	$\mathrm{ml\ mg(wtw)^{-1}\ h^{-1}}$	Weight	wet tissue weight (wtw) = 0.34110 · (whole wet weight) + 0.1646 (Atkinson 2008, p. 117)
Pigneur et al. (2014)	0.086	$\mathrm{m^{-3}\ g(C)^{-1}\ day^{-1}}$	Height	Clam body mass as $\mathrm{g(C) = 0.0148 \cdot H^{2.2685}}$

added to stimulate the phytoplankton growth. Clams, taken from the lake and kept in aerated tanks for a couple of days, were used in only one experiment each. In water volumes of 3-10 L, one to four *Corbicula* were placed in separated vessels having some sand on the ground. Phytoplankton was measured indirectly as chlorophyll *a*. Cahoon und Owen (1996) calculated their filtration rates for each vessel and time interval, accounting for phytoplankton growth using control vessels and then dividing it by number of clams to get individual filtration rates.

The number from Atkinson et al. (2011) I selected because they used filtered stream water which means that the clams were also feeding on natural plankton assemblages. Their experimental set-up was individual clams in aerated tanks and they measured for different time periods. They used flow cytometry to enumerate suspended particles, a more precise method than direct counts (Atkinson et al. 2011) which is another reason why this paper was chosen. With the concentration measurements from the flow cytometry they calculated specific clearance rates according to Coughlan (1969). I used the clearance rate they calculated for organic material during the periods of net filtration for my calculations.

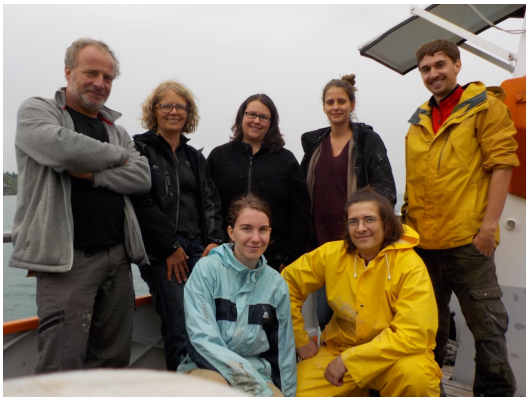
The last filtration rate I took from Pigneur et al. (2014). The authors of that paper recalculated published filtration rates by putting them into a single unit and accounting for temperature effects. This way they were able to compare the published data and find a maximum filtration rate at a temperature of 20 °C which they used for their simulation of the impact of *Corbicula spp.* on the Meuse ecosystem.

In comparison, while Cahoon und Owen (1996) calculated mean filtration rated per individual clam, Atkinson et al. (2011) and Pigneur et al. (2014) calculated relative rates based on the size of the clams, which is probably more helpful if transferring to another study region, where the mean clam size might be different.

2.2. Area and density

First I planned to calculate the colonizable area by comparing sediment data of Lake Constance with sediment preferences of *C. fluminea*. However, the only available data on sediments of this lake gave average grain size of the sand and the silt fraction, but not more details. This data then indicated that most of the lakes sediment mean grain size is in the sand fraction and just few parts of the lake might be too silty for the Asian clam. There is no literature on sediment preferences of the clam for specific mean grain sizes, thus it would have been highly inaccurate to make an assumption only based on the available data about which areas might

(a) Van Veen bottom sampler



(b) The sampling team of trip 2

Figure 2.1.: Equipment of our boat trips

get colonized. Furthermore, the sediment data only reached a depth of 8 m, but *Corbicula* also lives deeper in the lake. Therefore, I decided to use another approach for including the area in my calculations; by getting density estimates for different depth levels to account for spatial difference at least in one variable. I also decided to take sediment samples and analyse them to probably find a link between clam densities and grain size distribution.

2.3. Collecting samples at Lake Constance

Samples of *Corbicula* were collected on two boat and one snorkelling trip covering three transects in the eastern part of Lake Constance. As I was interested in the depth dependent *C. fluminea* densities, samples during the boat trips were taken at three to four water depths, always around 6 m, 10 m, and 15 m and if a *C. fluminea* was found at 15 m samples at 20 m were taken. A Van Veen bottom sampler (see Figure 2.1a) was used on both trips, unfortunately one got lost during the second trip and we needed to switch to a lighter one. This sample taking method has been used by others to get *Corbicula* densities for example by Sousa et al. (2008b).

On the first trip, four of us went on a small motor boat from Langenargen eastward. Samples were taken on the lake in front of Nonnenhorn (DE), measuring depth with a hand echo sounder and manoeuvred the grab sampler on a rope by hand. Pulled up samples were put into sieve beakers (mesh size 250 μm) and sieved by shaking the beakers half submerged in the lake. I stored the sieved samples in zip locked bags and labelled them with location, sample number and sample depth, respectively. Five samples of benthic invertebrates were taken each at 6 m and 10 m water depth. As no clam was visible in the samples at 15 m we only took three at that depth and did not go deeper. At each depth a sediment sample was additionally taken, meaning the whole sample we pulled up was transferred into tuber boxes without sieving them first to process them fully in the lab for determining the sediment composition.

On the second trip, we went with the Kormoran ship of LUBW (Landesanstalt für Umwelt, Messungen und Naturschutz Baden-Württemberg) where an electronic winch was available to manoeuvre the grab sampler. On two transects, one in front of Rohrspitz and the other one close by Lindau, five samples of benthic invertebrates were taken at each of the four depths. Those samples were also processed with a sieve not only by hand but also with a water jet. Again, sediment samples were taken from each depth at each of the two transects.

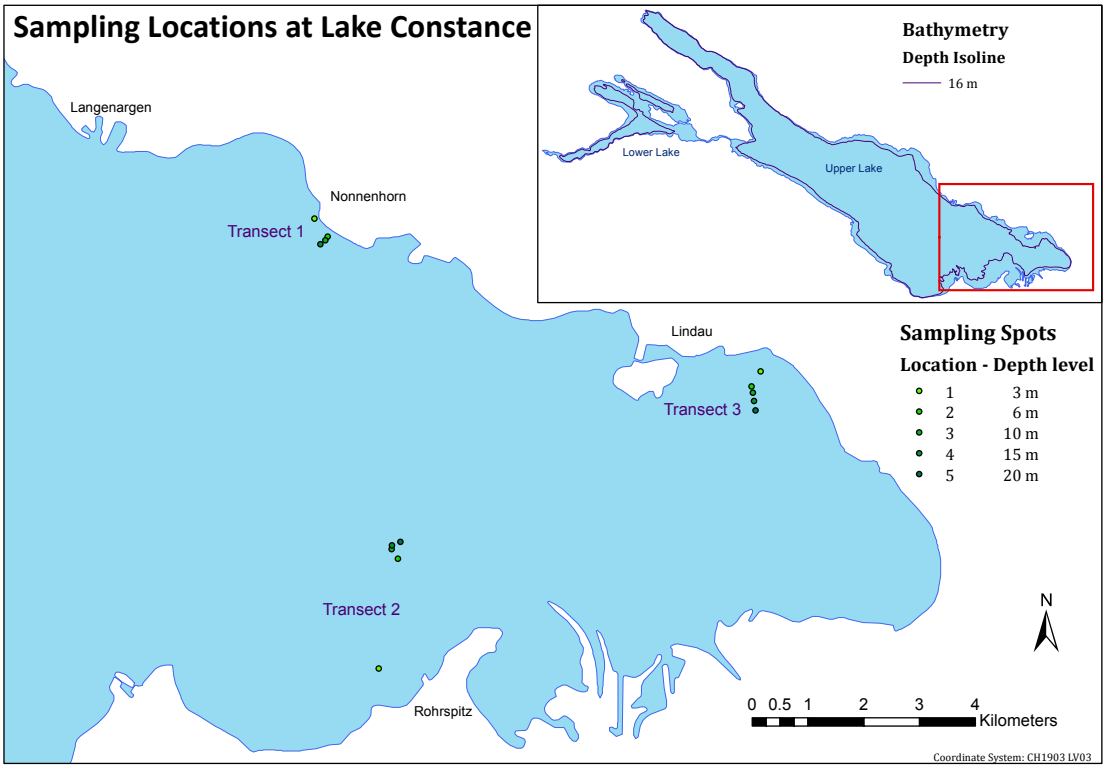
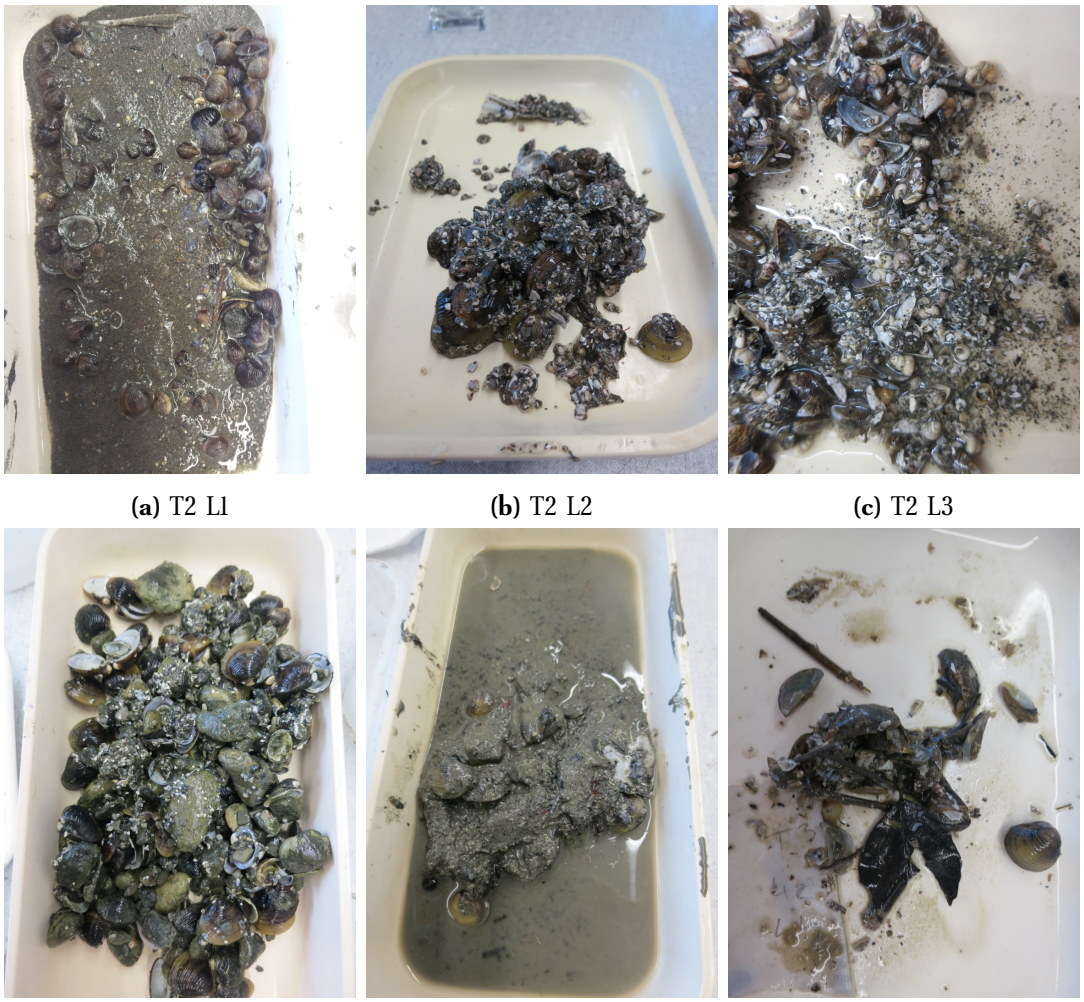


Figure 2.2.: Approximate sampling spots for the three transects that were covered on the sampling trips. The isoline in the small map shows approximately until which distance from the lake shore and therefore in which area *Corbicula* was found at reasonable densities.

To get density estimates for shallow water we had to go snorkelling as the Van Veen bottom grab sampler did not work above a water depth of 2 m. Three spots were selected for getting the samples as close by the transects as was accessible. Water depth was estimated at each spot. They lay between 1 m and 3 m depth depending on the accessibility of the site. The transects in front of Rohrspitz and Lindau were so shallow at the beginning that getting out to higher depth would have meant walking out too far. We used a metal frame of about the same area size as the grab sampler which was put down on the lake ground. The sediment that was within that frame was showeled by hand into a net with mesh size of 250 μm until about 10 cm of sediment depth. The content left in the net was then transferred under water into zip-loc bags. At each transect, a sediment sample was also collected in a tuber box. Water levels of the lake were different on the different days we sampled.

The map in Figure 2.2 shows the sampling area with the approximate locations of the sampling spots, as well as the labelling of the transects. I ended up having data from three transects and 4-5 depth levels. The first transect was in front of Nonnenhorn (Germany), the second close to the Rohrspitz (Austria), and the third near Lindau (Germany). Depth levels were labelled with the numbers one to five, where one being the 3 m depth level and 5 the 20 m depth level. These labels are further referred to as "location".



(a) T2 L1 **(b)** T2 L2 **(c)** T2 L3

(d) T3 L1 **(e)** T3 L2 **(f)** T3 L4

Figure 2.3.: Samples that were sieved on boat from different transects (T) and locations (L) before they were analysed for benthic invertebrates

2.4. Processing samples in the lab

All samples were held in a 4 °C room until further processing. I then put each sample on a tray and looked it through for *C. fluminea, Dreissena* mussels, and any other living organism that could be found by eye. Figure 2.3 shows a range of how different the samples that were taken looked after they were filtered with the 250 μm net. *Dreissena* and other benthic invertebrates were identified and counted. I used the count of animals to see whether there was a correlation between numbers of *Corbicula* and any other found species group using the statistical software R (see B.2).

I counted *C. fluminea* clams for each sample and with a digital caliper (resolution 0.1 mm, accuracy: $\pm$0.2 mm) measured height, length, and width of each clam. I also weighed them with a balance (d = 0.01 g) to get the whole wet weight including the shell. The clams were either eaten or disposed of afterwards.

(a) Set up for the wet sieving of the sediments

(b) The unsieved sediments from transects 2 and 3 (upper and lower row, respectively)for the locations 2-5 (left to right)

Figure 2.4.: Processing of the sediments of the locations 2-5

2.5. Processing sediments

As I had a lot of sediment per sample for the depth 6 m, 10 m, 15 m, and 20 m, I was able to try several methods of processing them. First I dried part of them at 60 °C for 30 hours, weighed them afterwards and then burned them for 300 min at 450 °C. This way, the organic matter got burned and I took the weight again. Unfortunately, the sediments were so clayey that the material stuck so much together that it was not possible to sieve them afterwards, which meant that this method is not an option for those sediments. It was also not possible to make them wet again, to do the sieving that way.

The next trial was with a tower of sieves on a sieving shaker using the wet samples and some additional water. As the sieves were not tight enough, the water did run off in the gaps taking light sediment along.

The last try was with a wet sieving equipment, where it was possible to have water running through at small amounts (see Figure 2.4a). After two rounds with too large sub sample sizes I tried to process, I found an amount that worked. Unfortunately, it was not that much and due to a limited amount of time I could only process one sub sample per location. The sieving tower consisted of eight sieves with the mesh sizes of 8 mm, 4 mm, 2 mm, 1 mm, 0.5 mm, 250 μm, 125 μm, and 63 μm. Depending on the sub sample, the sieving process took 10-25 min during which the sediment tower was always being shaken but water was not always flowing, as with to much water it still drained between the sieves. The run off water at the bottom of the tower, which contained the finest sediment fraction, was collected in buckets, one per sub sample. After the sieving, the material captured by each sieve was carefully transferred to a porcelain bowl, noting the sieve mesh size. For the transfer, I used a brush and water. It was still not that simple to make sure that everything got into the bowl, and especially for the 2 mm, 1 mm, and 0.5 mm sieve there might have been some losses. Those bowls were then left to dry for five days before they were put into an oven at 105 °C. The buckets with the run off water were left standing in the sun for five days to let the sediment set as well as some of the water evaporate. Unfortunately, putting them in full sun light did not stimulate evaporation much, so that there was still a lot of water left after those five days. As it was not possible to put the buckets into the oven I took out as much water as possible using a beaker and a

pipette. Except for the samples from 20 m depth, the sediment has well settled so that little of it got lost with the water. For the samples 2-5 and 3-5 some got inevitably lost with the water but due to limited time I could not wait longer until processing them further. After taking out the water I transferred the sediments with the leftover water to porcelain or aluminium bowls and put them into the oven at 105 °C as well. All samples were left in the oven for 28 h, then weighed and transferred into the burner for 5 h at 450 °C. Afterwards, they were weighed again to measure the organic matter content.

The sediments from the shallower waters were fortunately less clayey so that it was possible to sieve them dry. This means, I dried them for about 2 days at 60 °C, and then after weighing transferred them into the burner, where they burned at 450 °C for 5 h. After that all the organic matter was burned and after weighing them again I started sieving them. I used the same sieve mesh sizes as above plus two more (16 mm and 31.5 mm) as there were some larger pebbles visible by eye. The sieve tower was shaken by a sediment shaker for about 20 min after which each sediment fraction got weighed.

For each sampling spot I got the amount of sediment that was in each range of grain sizes plus one value for organic matter. This data was then tested for any correlation with the mean *Corbicula* densities using the statistical software R (see B.3).

2.6. Statistics and calculations

Statistical analysis on the *C. fluminea* data was performed with the statistical software R. I did ANOVA tests for the density data (meaning number of clams per sample) as well as for the measured size indicators that where used to calculate individual filtration rates (see B.4).

To calculate filtration rates of *C. fluminea* at Lake Constance in the event that they spread across the whole lake (Ober- and Untersee) I needed to calculate areas per depthlevel, density estimates per depth level and mean filtration rates per depth level per clam. For the area I got data from Rosi Sieber from Eawag who used a TIN model on GIS data for Lake Constance. I then added up several depths for the area of each of the depth levels (see Table 3.1). Deeper areas were not used as *C. fluminea* will most likely not colonize there (see B.6).

For the density estimates I first calculated the number of clams per m^2 for each of the samples, taking into account the effective area of the different sampling devices. I then calculated the mean density per depth level based on all samples. These five numbers I used further on as the mean densities (number of clams per m^2). I also calculated the standard deviation for each depth level which I then used to get high and low density estimates as follows: $\mathrm{mean} \pm \mathrm{sd}$. If the low density estimate was negative, I set the number to 0 as negative densities do not make sense (see B.1).

For each depth level I calculated mean filtration rates based on the numbers I got from the references (see B.5). Again, I first calculated the filtration rate for each clam using whichever size indicator that the corresponding reference used. From those numbers I then took the mean for each depth level, which means of course that for some depth levels the mean is based on much more clams than for others (for the number of clams see Table 3.1). These five numbers per reference were then used for further calculations.

To get the estimate of how much water *C. fluminea* could filter through if they spread all over Lake Constance I combined all these numbers as shown in Equations (2.1) & (2.2).

$$\mathrm{FR}(\mathrm{dl}) = \mathrm{Area}(\mathrm{dl}) \cdot \mathrm{density}(\mathrm{dl}) \cdot \mathrm{meanfiltrationrate}(\mathrm{dl}) \tag{2.1}$$

$$\mathrm{FR}_{\mathrm{total}} = \mathrm{FR}(2) + \mathrm{FR}(6) + \mathrm{FR}(10) + \mathrm{FR}(15) + \mathrm{FR}(20) \tag{2.2}$$

FR(dl) means "total filtration rate per depth level" where "dl" indicates the depth level. This was done for low, high, and mean density estimates. Those numbers where then compared with the mean discharge of Lake Constance as well as with its volume (see B.7).

Furthermore, I also calculated the amount of wet biomass (tissue without shell) that would result from clams spreading all over Lake Constance (see B.8). For that I used the linear regression from Atkinson (2008) to calculate wet tissue mass for each clam from the total wet mass. From that I got the mean wet biomass for each depth level, which then were used to calculate the estimate for whole Lake Constance the same way as shown in Equations 2.1 and 2.2 just with "mean biomass" instead of "mean filtration rate". I only did this for mean density estimates.

3. Results

3.1. Correlation between numbers of C. fluminea and other groups of benthic invertebrates

For most groups of benthic invertebrates there was no correlation between their numbers found and *Corbicula* density. For Oligochaeta and snails though, the tests showed highly significant positive correlation, but as it was really hard to find all snails that were alive it is unlikely that the result for this species group is useful. Correlation between *C. fluminea* numbers and numbers of other bivalves excepting *Dreissena* was highly significant and quite strong. This might indicate that the more other bivalves are found at one spot the higher the likelihood of finding *Corbicula* clams at the same spot. This is most likely not due to a direct causation, but indicates a location preference of bivalves in general and low interspecies competition. As finding all these other benthic invertebrate was not a priority when looking through the sample it was not done very carefully. So chances that a lot were not seen are quite high implying that a more careful survey would need to be conducted for investigating this.

3.2. Correlation between C. fluminea densities and sediment grain size distribution

All Pearson correlations between *C. fluminea* densities and sediment grain size were positive except the one for the fraction of 0-63 μm, where the correlation was -0.62 ($p < 0.05$). Highly significant correlations were found for grain size classes 125 μm, 500 μm, 1 mm, and 2 mm. While the correlation with 4 mm was still significant, the *Corbicula* density did not show significant correlation with the amount of sediment in the classes with the larger grain sizes as well as those of 63 μm and 250 μm. The correlation coefficient r was highest for 500 μm (0.89), closely followed by 125 μm (0.86), then 1 mm and 2 mm (both 0.76) and lowest for 4 mm (0.62). There was also a significant ($p=0.02$) positive correlation between density and the amount of organic matter ($r=0.61$).

Another way of looking at the data is adding the amount in the sieving size fractions together into gravel (2 mm - 31.5 mm), sand (63 μm - 1 mm) and silt (<63 μm) and then testing them for correlation. Pearson results show a highly significant strong positive correlation between the amount of sand and *Corbicula* densities ($r=0.81$), while the one with the gravel fraction is positive but not significant ($r=0.40$, $p=0.16$). Results for the silt fraction are the same as for the sieving size fraction 0-63 μm, meaning significantly negative, as I have not further separated this sediment part.

3.3. Densities of C. fluminea in Lake Constance

Table 3.1 shows the mean densities that I calculated based on my sampling. Densities were significantly influenced by transect ($p=0.008$) and location ($p = 2.2 \cdot 10^{-16}$), while also the interaction between transect and location was highly significant ($p=0.0007$). This means that I could have gotten significant results with less samples. Significant differences between locations

Table 3.1.: The second column shows the binning borders for the area of each depth level; The table further displays the number of clams found per depthlevel (n), how many samples I had per depthlevel (number in brackets show how many samples contained no clam) and density calculations per depthlevel

				Density [clams/m^2]		
Depthlevel	Area from depths...	n	# of samples	low	mean	high
3 m	0-4 m	517	15(0)	291	534	778
6 m	5-8 m	163	15(0)	110	191	272
10 m	9-12 m	124	15(0)	91	152	213
15 m	13-17 m	20	13(7)	0	28	69
20 m	18-22 m	1	10(9)	0	2	8.4

make sense as one would expect that there is a difference in mean densities between the different depth levels. Correlation tests showed that there is a significant negative correlation between mean densities and depth, meaning that densities decrease with increasing depth. That there are significant density differences between transects is acceptable as I expect that the local environment of Lake Constance does not favour *Corbicula* populations everywhere on the same magnitude. To get a representative density estimate for the whole lake I think these differences between the transects actually help to get a number that might be close to a mean for the whole lake.

The LUBW has done some sampling shortly before we did using a dredge which they pulled over the lake ground at different water depths for about 100 m. Then they counted the clams they collected with this methods. Their numbers are much lower (1.07 for 5 m, 0.68 for 10 m) than mine, which most likely means that the dredge does not collect sediment as deep as the Van Veen sampler or hands did.

3.4. Filtration rates of C. fluminea for Lake Constance

The results of my filtration rate estimates for Lake Constance are shown in Table 3.2. In the text, the numbers in the parentheses are the range I got when calculating the values with low and high density respectively. While calculations based on Atkinson et al. (2011) and Pigneur et al. (2014) are quite close, the numbers from Cahoon und Owen (1996) are much lower and only about one third of the others. Looking at the numbers from the more recent authors, *Corbicula* would filter through the whole Lake Constance in roughly 300 days (200-550 days) if they spread throughout the whole lake with abundance similar to what they reach at the eastern end. As not the whole volume contains phytoplankton, it is actually more interesting how fast they filter through the volume that is above the thermocline where the food is and where also the *Daphnia* live. Lake Constance is a warm monomictic lake. Therefore it gets mixed through only once in the year (during winter) while it is stratified over the summer months. Typical thermocline displacements are 5-10 m. I set the thermocline at a depth of 22 m, as that was the deepest layer where I let *Corbicula* live as well in my model. This depth level seems to be in the range of the big temperature gradient shown in summer temperature profiles for Lake Constance in Lorke (2007, Figure 2d) and IGKB (2014, Figure 3.1.2c). The clams would filter through roughly 1.5 % (0.85-2.25 %) of the water volume above the thermocline per day. This means they would clear that water (ignoring new input) in about 64 days (44-116 days). If comparing the volume that the clams can filter with the one of the water columns above

Table 3.2.: Calculated filtration rates based on my model per reference filtration rate for low, mean and high density estimates; Total filtration rates (TFR) in km^3/day; Percentage that the clams can filter per day of the total volume of Lake Constance (% LCV) and of the volume above the thermocline at 22 m (% VT) of the whole lake and just of the littoral water column (% VTL) as well as the percentage of the filtration rate compared with the mean discharge of Lake Constance Upper Lake (% MD)

	Cahoon			Atkinson			Pigneur		
	low	mean	high	low	mean	high	low	mean	high
TFR	0.025	0.047	0.068	0.089	0.162	0.236	0.087	0.158	0.229
% LCV	0.053	0.097	0.142	0.186	0.339	0.494	0.18	0.329	0.478
% VT	0.247	0.455	0.666	0.870	1.586	2.309	0.844	1.537	2.237
% VTL	1.586	2.919	4.274	5.586	10.179	14.622	5.416	9.867	14.363
% MD	79	145	213	278	506	737	269	491	714

the area they live, meaning the littoral part of the lake, it is about 10 % (5.5-14.5 %) per day. Therefore, the littoral water would be cleared within 10 (7-18) days if the lake water did not mix or move at all. But as there is a steady flow through Lake Constance with water coming from several rivers, the Rhine being the largest, and leaving through the Rhine at the western end, one cannot say that they have the potential to clear the lake. Probably more reasonable is the comparison with the mean discharge of 372 m s^{-1} (AFU SG). The calculated filtration volumes are about 5 (2.7-7.2) times as much as the mean discharge. This means that the clams filter much more water per day than the amount flowing through the lake. As mentioned before, for the total filtration rate based on Cahoon und Owen (1996) all these numbers would be smaller or larger in the case of amount of days by a factor of 3.

4. Discussion

4.1. C. fluminea and other benthic invertebrates

As this part of the sampling processing was not done very carefully, my results are not very helpful in really determining the effect, that the abundance of *C. fluminea* has on other benthic invertebrates. My correlation results suggest that these Asiatic clams must not have a negative effect on other invertebrates but might even make the environment more favourable for some. Hakenkamp et al. (2001) found that there was no impact of *C. fluminea* abundance on the meiofauna in their field experiment. Werner und Rothhaupt (2008a) have actually done experiments in Lake Constance to determine the abundance of ten macro invertebrate taxa in dependence on different *Corbicula* presences. The different taxa responded differently; some negative, others positive. However, fed clams were mostly preferred over starved clams and many species especially liked having clam shells on the ground as that provided them with more structural diversity.

There was no significant correlation between *Corbicula* and *Dreissena polymorpha*. However, in a lot of sediments I looked through, the zebra mussels I found were attached to living clams or their shells. This supports the thesis that *Corbicula* can alter the sediment surface by providing hard substrate on sandy sediments and thus increasing the habitat range for species that are limited to hard substrates such as *D. polymorpha* (Werner und Rothhaupt 2007). This could therefore lead to an indirect impact caused by higher abundance of zebra mussels which might be worth investigating in a further study.

4.2. Influence of sediment grain size distribution on C. fluminea density

The negative correlation between *Corbicula* abundance and the amount of sediment in the silt fraction goes along with the literature, which has also reported that these clams showed low densities on silt (Karatayev et al. 2003, 2005). Several studies found that *Corbicula* densities were highest on sandy substrates (Leff et al. 1990; reviewed in Karatayev et al. 2005; Schmidlin und Baur 2007), which does not invalidate my correlation results, as they were significantly positive for most of the grain size classes within the sand fraction as well as for the sand fraction all together. Belanger et al. (1985) found in a laboratory experiment that *Corbicula* prefers finer sand to coarse sand. This is somewhat reproduced by my results where correlation is higher for two of the finer sand grain sizes compared to the 1 mm, but I would not conclude that just from my results, as there was no correlation between density and the 63 μm as well as the 250 μm fraction. Schmidlin und Baur (2007) also found that the clams preferred finer sand to coarse one. As density in my results also correlated significantly positively with the 2 mm and 4 mm grain size classes, it seems that the presence of gravel does not have an adverse effect. As weight was the unit for the amount, it could definitely be that in the sediment samples where the finer gravel section was high in weight a lot of sand was also present, which then led to the high clam densities. The positive correlation that I found between *C. fluminea* abundance and the amount of organic matter in the sediment has been reported before in literature (Belanger et al. 1985, Schmidlin und Baur 2007). This is probably due to the ability of these clams to also pedal feed, which means that enriched sediments provide further food for

them (Vaughn und Hakenkamp 2001). Grain size clearly decreased with depth and so did the numbers of *Corbicula*. It is likely that this decrease in clam numbers is at least partially due to the change in grain size.

The littoral sediments of Lake Constance have a mean grain size range from coarse silt to coarse sand (Schmieder et al. 2004), where mainly fine-grained sediments were found at the north-eastern exposed shore, while the south-western part contained mostly coarse-grained sediments. Combining this information with that from the sediment preference of the clams, Lake Constances littoral part seems to be a good habitat for *C. fluminea*, as at least the main grain sizes are mostly in a range that the clams prefer.

Unfortunately, I could not include the sediment data of Lake Constance into my model as the available data was not detailed enough and also did only cover depths down to 8 m. This might be a further step, which of course would include the time intensive sampling and processing of sediments to get a good data set on the grain size distributions of the lake sediments in the upper 20 m or so. If that data was available, maybe one could use my findings on the correlation between detailed grain size fractions and clam density to build a dispersal model of *C. fluminea* in Lake Constance based on sediment availability.

4.3. Density and filtration rate

While I found that *C. fluminea* is most abundant at the 3 m depth level, the biggest individuals were found at 6 m. The average size of the clams from 10 m depth was also larger than the one from 3 m. Figure 4.1 shows the size distribution over the five depth levels for all transects combined. The overall trend is also evident at the individual transect level (see Figure A.1). The smaller size of the clams in the shallow water might be explained by still being in range of hunting water fowls or man-made disturbances.

Comparing my density estimate to numbers found at other places they don't seem to be that large. Pigneur et al. (2014) have found densities from 20-880 individuals per square meter which includes my range but even my highest estimate is only a sixth of what Werner und Rothhaupt (2007) mentioned as local densities. This clam has shown before that it reaches very high densities at the beginning of colonizing an area but then declining to a lower probably more stable abundance (Phelps 1994). Maybe that is what has happened in Lake Constance as well and therefore could explain the lower density numbers from my samples.

The much lower numbers of filtration rates for Cahoon und Owen (1996) might be an effect of having rates per individual clam but not taking into account the sizes of the clams. As the sizes varied significantly with depth, mean filtration rates from Atkinson et al. (2011) and Pigneur et al. (2014) changed with depth and accounted for these variances, while the one from Cahoon und Owen (1996) stayed the same, being mostly lower than the first two, which led to these much lower total rates.

As mentioned before, I think the filtration rates relative to clam size are more useful to use for a site which is not the primarily studied one, as they can better account for differences in mean clam size that might occur. On the other hand, Cahoon und Owen (1996) measured over longer time periods, reaching up to eight days, which might be more representative of what really happens in a lake than rates measured only over 3 h as in Atkinson et al. (2011).

This large discrepancy shows that to predict more accurate numbers for filtration rates, it would be useful to do an experiment with conditions close to Lake Constance's with local clams and then use those numbers in the model.

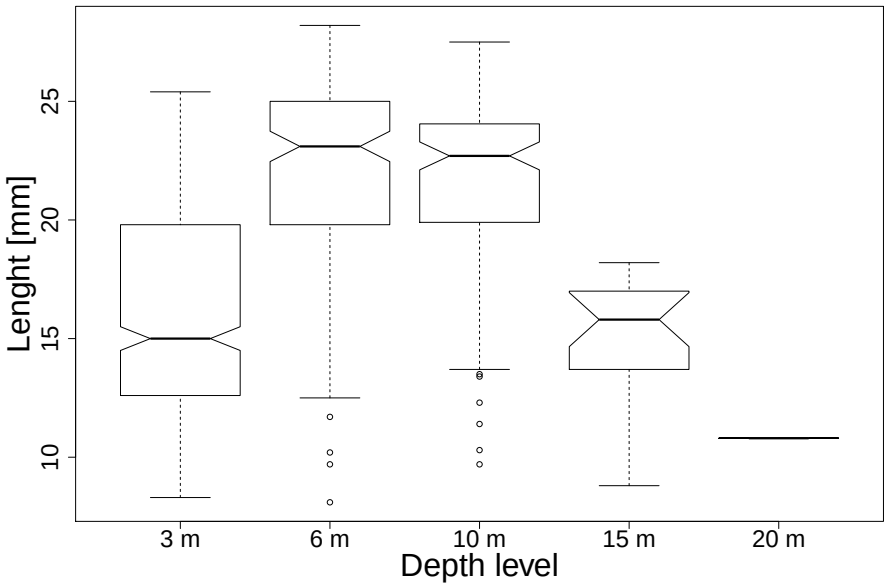


Figure 4.1.: Distribution of shell length of the clams over the depth levels for all three transects combines.

4.4. The impact of Corbicula fluminea on Lake Constance

It has been shown that *C. fluminea* can have a negative effect on phytoplankton abundance when occurring at high biomass (Cohen et al. 1984, Phelps 1994). Based on my samples, *Corbicula* might reach a total of 41'000 tonnes of clam wet tissue weight in Lake Constance. This is a lot compared to the approximately 1070 tonnes of fish stocks that were caught in 2011 at Lake Constance (IBKF 2011). Therefore, I would conclude that the reachable biomass for the Asian clam is quite high and thus an impact on the phytoplankton abundance of Lake Constance is likely. On the other hand, bivalves are more likely to control food resources when the water volume is comparably small to the clam biomass and the hydrological residence time is long (Vaughn und Hakenkamp 2001). This is not the case for Lake Constance, which means that the influence of *Corbicula* on the phytoplankton abundance might not be too great.

The calculated total filtration rate numbers based on the filtration rate values from Atkinson et al. (2011) and Pigneur et al. (2014) can be used as maximal total filtration rates, the one based on Cahoon und Owen (1996) is a more conservative one. As the question was whether the clams would profit from the additional phosphate more than *Daphnia spp.*, a comparison of filtration rates between these organisms would be helpful. Using a mean filtration rate derived from values for individual *Daphnia* from Pintocoelho (1991b) and density measurements in Lake Constance for August 2015 (done for the IGKB) I calculated a total filtration rate of *Daphnia spp.* in Lake Constance. As this was just roughly done, I assumed that this zooplankton species lived with the same density in all the water volume above the thermocline. The numbers I got were 11'326 m^3 per day if the *Daphnia* lived in the whole lake (pelagic and littoral) and 1'764 m^3 per day if only in the volume in the littoral part of the lake. These numbers are nowhere near the filtration potential of the clams spread throughout the whole lake (lowest potential: 25'346'536 m^3 per day). Therefore, even though the numbers for the *Daphnia* are only roughly calculated it is clear that the clams would be the dominant filter feeders and would take much more of the phytoplankton out of the lake than the zooplankton does.

This goes along with the results from controlled experiments in two Korean lakes, which showed that the large zooplankton affected the phytoplankton biomass much less than the *Corbicula* clams. *Corbicula* was also shown to be much more efficient than *Daphnia* in terms of the C-flux to biomass ratio, which allowed them to clear large volumes of water of algae in a short time (Hwang et al. 2004). Grazing impacts by zooplankton in the Potomac river have also been estimated to be one magnitude less than the pressure on phytoplankton by *C. fluminea* (Cohen et al. 1984). It is thus likely, that phosphate fertilizing in Lake Constance would not help much in improving food conditions for planktivorous fish but more likely support the Asian clam in establishing in Lake Constance. However, if the clams mostly filter the water from the littoral water column and the *Daphnia* live and feed from the pelagic part, competition might be low. In that case and without strong water currents, if the fertilizers would be applied in the middle of the large lake, it could be that the zooplankton profit and therefore enhance the food amount available for the planktivorous fish. Important for this competition is thus in addition to the filtration rate the filtering reach of the clams, which live at the bottom of the lake, and the water flows within the lake. The water around *Corbicula* colonies is most likely poor in phytoplankton as this area acts as food sink. However, water further away might still be a food source where grazing is lower than phytoplankton production (Lopez et al. 2006). If *Daphnia* lives near to those areas or the water flux is big enough to bring the phytoplankton close to them they might get enough food to have a good growth rate. Consequently, spatial distribution of the zooplankton and phytoplankton is important and should be included in a more detailed analysis of the state of the grazing competition in Lake Constance. Furthermore, as the time scale of phytoplankton generation lies within days, modelling the currents in Lake Constance would help in evaluating how local the phytoplankton blooms would be.

As several physical factors are influencing phytoplankton abundance which in turn has an effect on the filtering activity of *Corbicula*, simulations with mathematical models can be a good approach for estimating the impact of the clams on the seston availability (Pigneur et al. 2014). Using that approach, these authors included phytoplankton dynamics, clam densities, and clam filtration rate into their model and ran simulations for the river Meuse. Losses of about 70 % of phytoplankton biomass were simulated for stretches with the highest clam densities. The annual primary production declined by 61 % and the zooplankton community lost up to 75 % of their biomass (Pigneur et al. 2014). To get a more detailed estimate, they suggest looking for example at seasonal clam population dynamics and influences on the filtration rate of the clams. Furthermore, also impacts on the whole ecosystem level of river Meuse should be looked at to find out whether the clams have the potential to alter processes and functions such as food web dynamics (Pigneur et al. 2014).

Based on my calculations, it is definitely possible that *C. fluminea* does have a significant impact on phytoplankton in Lake Constance and therefore, further studies should look at it more precisely to determine the influence that this ecosystem engineer has on the food chain from phytoplankton over zooplankton to planktivorous fish. A simulation model as done by Pigneur et al. (2014) would help in further estimating the impact of *C. fluminea* on phytoplankton availability for *Dapnia spp.* It would also be good to include seasonal and inter-annual population dynamics of the clams, phytoplankton, and *Daphnia spp.* to get more helpful predictions. As mentioned before, as it is a really large lake, spatial distributions might also matter and should not be neglected. These data could be crucial in determining management strategies for enhancing fish biomass at Lake Constance.

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A. Additional Figure

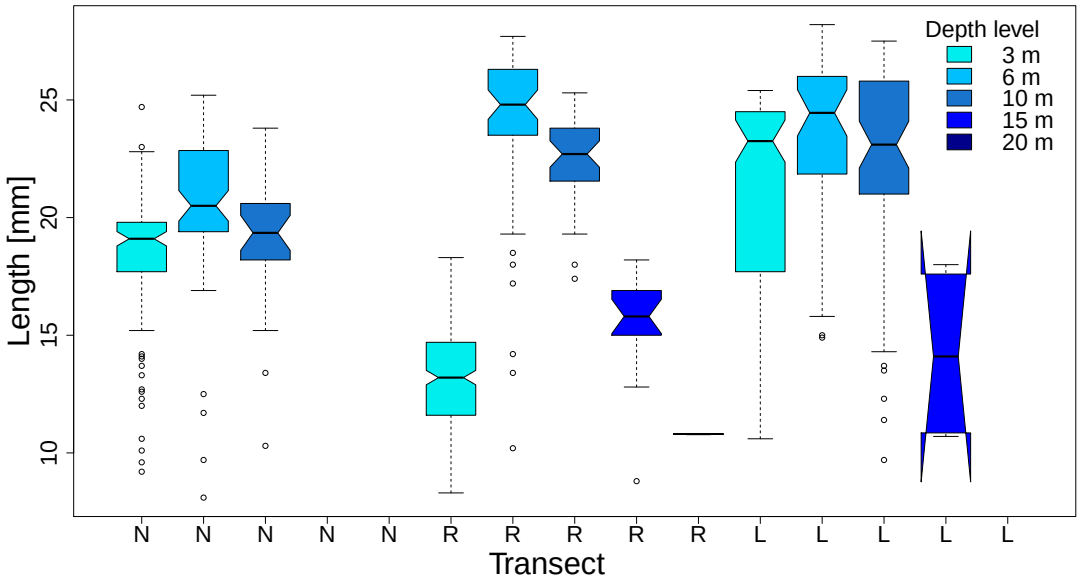

Figure A.1.: Distribution of shell length of the clams for each combination of depth level and transect (N: Nonnenhorn, R: Rohrspitz, L: Lindau)

B. Code Listings

Listing B.1: Calculation of the densities of *C. fluminea*

```
## Bachelorarbeit: Corbicula fluminea im Bodensee
## Berechnen der Durschnittlichen Corbicula-Dichten pro Wassertiege
## Daten aus Excel-Spreadsheet im csv Format von Organismsgroups_
    LakeConstanceSamples
## Madleina Gerecke, August 2015

###Windows Directory und Datensatz
# setwd("D:/Bachelorarbeit/Berechnungen")
# Organismsgroups_LakeConstanceSamples <- read.csv("D:/Bachelorarbeit/
    Feldarbeit/Organismen/Organismsgroups_LakeConstanceSamples.csv", sep
    =",")

### Ubuntu Directory und Datensatz
setwd("/media/madleina/ETH/Bachelorarbeit/Berechnungen")
Organismsgroups_LakeConstanceSamples <- read.csv("/media/madleina/ETH/
    Bachelorarbeit/Feldarbeit/Organismen/Organismsgroups_
    LakeConstanceSamples.csv")

n <- ncol(Organismsgroups_LakeConstanceSamples)
m <- nrow(Organismsgroups_LakeConstanceSamples)


####Kuerzen des Datensatzes auf Corbicula Daten
CD <- Organismsgroups_LakeConstanceSamples[-1,-7:-n]
m = m-1

#########noch reihen mit unnuetzen Daten rausnehmen
#if (CD$Transekt=0) omit


nperm2 <- matrix(nrow=m, ncol =1)  ## generiert leere Matrix...
CD <- cbind(CD, nperm2) ## ...die dann an CD angefuegt wird, um gefuellt
    zu werden


####Calculate Density per m2
for (i in 1:m){
  CD[i,6] <- as.double(CD[i,6])
  if (CD[i,5]=="La")
    CD[i,7] = CD[i,6]/(0.22*0.25) ##Groesse des Greifers La
  if (CD[i,5]=="Lh")
    CD[i,7] = CD[i,6]/(0.237*0.21) ## Groesse des Greifers Lh
  if (CD[i,5]=="F")
    CD[i,7] = CD[i,6]/(0.248*0.26) ## Groesse des Metallrahmens
}

### Exportieren der Dichte Daten pro Sample
write.csv(CD, file="Corbicula_Densities.csv", row.names = FALSE)
```

```
#### getdensity for each depthlevel into one matrix
density <- matrix(nrow=5, ncol=3)
for (i in 1:5){
  ## mean
  density[i,1]=mean(CD$nperm2[CD$Location==i], na.rm = TRUE)
  ##low
  density[i,2]=max(mean(CD$nperm2[CD$Location==i], na.rm = TRUE) - sd(CD$
      nperm2[CD$Location==i], na.rm = TRUE),0)
  ##high
  density[i,3]=mean(CD$nperm2[CD$Location==i], na.rm = TRUE) + sd(CD$
      nperm2[CD$Location==i], na.rm = TRUE)
}



#### Name column and rows and export Data
colnames(density) <- c("mean", "low", "high")
rownames(density) <- c("3 m", "6 m", "10 m", "15 m", "20 m") #Zeilen
    benennen
write.csv(density, file = "Density.csv") #exportieren


#### Calculate numbers found per depthlevel
n1 <- sum(CD$Corbicula[CD$Location==1])
n2 <- sum(CD$Corbicula[CD$Location==2])
n3 <- sum(CD$Corbicula[CD$Location==3])
n4 <- sum(CD$Corbicula[CD$Location==4])
n5 <- sum(CD$Corbicula[CD$Location==5])


### Calculate how many samples per depthlevel
s1 <- sum(CD$Location==1 & !CD$Greifer=="LH")
s2<- sum(CD$Location==2 & !CD$Greifer=="LH")
s3 <- sum(CD$Location==3 & !CD$Greifer=="LH")
s4 <- sum(CD$Location==4 & !CD$Greifer=="LH")
s5 <- sum(CD$Location==5 & !CD$Greifer=="LH")

s1a <- sum(CD$Location==1 & !CD$Greifer=="LH" & CD$Corbicula==0)
s2a<- sum(CD$Location==2 & !CD$Greifer=="LH" & CD$Corbicula==0)
s3a <- sum(CD$Location==3 & !CD$Greifer=="LH" & CD$Corbicula==0)
s4a <- sum(CD$Location==4 & !CD$Greifer=="LH" & CD$Corbicula==0)
s5a <- sum(CD$Location==5 & !CD$Greifer=="LH" & CD$Corbicula==0)
```

Listing B.2: Calculation of the correlation between *C. fluminea* densities and other numbers of other benthic invertebrates as well as depth of the lake

```
## Bachelorarbeit: Corbicula fluminea im Bodensee
## Testen der Korrelation zwischen allen Organismengruppen-Anzahl
## Testen der Korrelation zwischen Corbicula-Anzahl und Wassertiefe
## Daten aus Excel-Spreadsheet im csv Format von Organismsgroup_
    LakeConstance_Samples
## Madleina Gerecke, August 2015

#Organismsgroups_LakeConstanceSamples <- read.csv("F:/Bachelorarbeit/
    Feldarbeit/Organismen/Organismsgroups_LakeConstanceSamples.csv", sep
    =";")
```

```
#f?r Ubuntu
Organismsgroups_LakeConstanceSamples <- read.csv("/media/madleina/ETH/
    Bachelorarbeit/Feldarbeit/Organismen/Organismsgroups_
    LakeConstanceSamples.csv")
n <- ncol(Organismsgroups_LakeConstanceSamples)
m <- nrow(Organismsgroups_LakeConstanceSamples)


## Organismen Korrelationen
### Matrix mit nur noch Organismen (ohne Corbicula) Spalten
Korrelation <- Organismsgroups_LakeConstanceSamples[-1:-5]  ##
    Korrelation is Data Frame


### Korrelationen pr?fen zwischen allen Organismengruppen
library(Hmisc)
spearman <- rcorr(as.matrix(Korrelation), type="spearman") # Korrelation
    gemäss Spearman
pearson <- rcorr(as.matrix(Korrelation), type="pearson") # Korrelation
    gemäss Pearson

###Get Data into Matrix form
rs <- spearman$r
ns <- spearman$n
Ps <- spearman$P

rp <- pearson$r
np <- pearson$n
Pp <- pearson$P


#### Reusltate für Corbicula in Matrix speichern
Corbicula <- matrix(nrow = 6, ncol = 14)
Corbicula <- rs
c <- nrow(Corbicula)
Corbicula <- Corbicula[-7:-c,]
Corbicula[2,] <- ns[1,]
Corbicula[3,] <- Ps[1,]
Corbicula[4,] <- rp[1,]
Corbicula[5,] <- np[1,]
Corbicula[6,] <- Pp[1,]
rownames(Corbicula) <- c("Spearman␣r", "Spearman␣n", "Spearman␣P", "
    Pearson␣r", "Pearson␣n", "Pearson␣P")

### Exportieren der Daten
setwd("/media/madleina/ETH/Bachelorarbeit/Berechnungen/Correlation_
    Results") #Ubuntu
#Windows
write.csv(Corbicula, file = "Corr_Corbicula_Organisms_Results.csv")



### Wassertiefe Korrelation
Tiefe <- matrix(nrow=m, ncol=2)
Tiefe[,2] <- Organismsgroups_LakeConstanceSamples[[6]]
Tiefe[,1] <- Organismsgroups_LakeConstanceSamples[[3]]
```

```
wassertiefe_s <- rcorr(Tiefe, type="spearman")
wassertiefe_p <- rcorr(Tiefe, type="pearson")
plot(Tiefe)

Wassertiefe <- matrix(nrow=3, ncol =2)
Wassertiefe[1,1] <- wassertiefe_s$r[1,2]
Wassertiefe[1,2] <- wassertiefe_p$r[1,2]
Wassertiefe[2,1] <- wassertiefe_s$n[1,2]
Wassertiefe[2,2] <- wassertiefe_p$n[1,2]
Wassertiefe[3,1] <- wassertiefe_s$P[1,2]
Wassertiefe[3,2] <- wassertiefe_p$P[1,2]
colnames(Wassertiefe) <- c("Spearman", "Pearson")
rownames(Wassertiefe) <- c("r", "n", "P")

#### Resultate exportieren
write.csv(Wassertiefe, file="Correlation_Depth_Corbicula.csv")
```

Listing B.3: Calculation of the correlation between *C. fluminea* densities and sediment grain fractions

```
## Bachelorarbeit: Corbicula fluminea im Bodensee
## Berechnen der Sedimentdaten und Korrelation mit Dichten pro Location
## Daten aus Excel-Spreadsheet im csv Format von Organismsgroups_
    LakeConstanceSamples
## Madleina Gerecke, August 2015


####Setzen von Working Directory und Importieren der Datensaetze für
    Sediment
  ### if problem in reading csv check which seperater was used
###Windows
#### In Ubuntu
setwd("/media/madleina/ETH/Bachelorarbeit/Feldarbeit/Sediment")

Wet <- read.csv("/media/madleina/ETH/Bachelorarbeit/Feldarbeit/Sediment/
    Wetsieving.csv", sep=",")
Dry <- read.csv("/media/madleina/ETH/Bachelorarbeit/Feldarbeit/Sediment/
    Drysieving.csv", sep=";")

sediment <- matrix(0, nrow= 14, ncol=16)
colnames(sediment) = c("Transect", "Location", "Depth", "OM", "31.5mm", "
    16mm", "8mm", "4mm", "2mm", "1mm", "500mum", "250mum", "125mum", "63
    mum", "0", "Corbicula␣Density")
wet <- Wet[,-5:-7]
nw = nrow(wet)
ns = nw/10

### transfer wet sieving data into sediment matrix
for (i in 1:ns){
  ## variables for help to get correct rows
  j = (i-1)*10+1
  k = i*10
  l = i*10-2
  h = i*10-1
  ## filling sediment matrix
  sediment[i,1] <- wet$Transect[j]
  sediment[i,2] <- wet$Location[j]
  sediment[i,3] <- wet$Depthlevel[j]
```

```
  sediment[i,4] <- sum(wet$OM.g.[j:k], na.rm = TRUE)
  sediment[i,7:14] <- wet$Class.weight[j:l]
  sediment[i,15] = wet$Class.weight[h]+wet$Class.weight[k]
}


## transfer dry sieving data into sediment matrix
dry <- Dry[,-3:-5]
for (i in 1:3){
  s = 11+i
  sediment[s,1] <- dry$Transect[i]
  sediment[s,2] <- dry$Location[i]
  sediment[s,3] = 2
  sediment[s,4] <- dry$OM[i]
  for (e in 5:14){
    d = e-1
    if (dry[i,d]!=0){
      sediment[s,e] = dry[i,d]-78.44 ## abzug des leergewichts
    }
  }
  sediment[s,15] = dry[i,14]-245.34
}

### Exportieren
write.csv(sediment, file="sediment.csv", row.names = FALSE)

#### Importieren der Dichtedaten -> Dafür Density.R zuerst laufen lassen
Corbicula_Densities <- read.csv("/media/madleina/ETH/Bachelorarbeit/
    Berechnungen/Corbicula_Densities.csv", stringsAsFactors=FALSE)
Dichte <- Corbicula_Densities[-3:-6]

#### Berechnen der Corbicula Dichten pro Location
Corb_Den <- matrix(nrow=14, ncol=1)
Corb_Den[1] = mean(Dichte$nperm2[1:5], na.rm = TRUE)
Corb_Den[2] = mean(Dichte[6:10,3], na.rm = TRUE)
Corb_Den[3] = mean(Dichte[11:13,3], na.rm=TRUE)
Corb_Den[4] = mean(Dichte[15:20,3], na.rm=TRUE)
Corb_Den[5] = mean(Dichte[22:26,3], na.rm=TRUE)
Corb_Den[6] = mean(Dichte[27:31,3], na.rm=TRUE)
Corb_Den[7] = mean(Dichte[32:36,3], na.rm=TRUE)
Corb_Den[8] = mean(Dichte[37:41,3], na.rm=TRUE)
Corb_Den[9] = mean(Dichte[42:46,3], na.rm=TRUE)
Corb_Den[10] = mean(Dichte[47:51,3], na.rm=TRUE)
Corb_Den[11] = mean(Dichte[52:56,3], na.rm=TRUE)
Corb_Den[12] = mean(Dichte[57:61,3], na.rm=TRUE)
Corb_Den[13] = mean(Dichte[62:66,3], na.rm=TRUE)
Corb_Den[14] = mean(Dichte[67:71,3], na.rm=TRUE)

library(Hmisc)
spearman <- rcorr(Corb_Den, sediment[,4:15], type = "spearman")
pearson <- rcorr(Corb_Den, sediment[,4:15], type="pearson")

rs <- spearman$r
ns <- spearman$n
Ps <- spearman$P

rp <- pearson$r
```

```
np <- pearson$n
Pp <- pearson$P


#### Resultate von Korrelationsanalyse in Matrix speichern
Sed_Corb <- matrix(nrow = 6, ncol = 14)
Sed_Corb <- rs
c <- nrow(Sed_Corb)
Sed_Corb <- Sed_Corb[-7:-c,]
Sed_Corb[2,] <- ns[1,]
Sed_Corb[3,] <- Ps[1,]
Sed_Corb[4,] <- rp[1,]
Sed_Corb[5,] <- np[1,]
Sed_Corb[6,] <- Pp[1,]
rownames(Sed_Corb) <- c("Spearman r", "Spearman n", "Spearman P", "
    Pearson r", "Pearson n", "Pearson P")
Sed_Corb <- Sed_Corb[,-1]


### Korrelationsresultate exportieren (Vorsicht: Spaltennamen werden um
    eins nach links verschoben)
write.csv(Sed_Corb, file = "Correlation_Sed_Corb_Results.csv")


### Correlation between Density and amount in grain fraction
n <- nrow(sediment)
sed <- matrix(ncol = 6, nrow=n)
sed[,1:3] <- sediment[,1:3]
for (i in 1:n){
  sed[i,4] <- sum(sediment[i,5:9])
  sed[i,5] <- sum(sediment[i,10:14])
  sed[i,6] <- sediment[i,15]
 }
colnames(sed) <- c("Transect", "Location", "Depthlevel", "gravel", "sand"
    , "silt")

par(mfrow=c(1,3))
plot(sed[,4],Corb_Den)
plot(sed[,5],Corb_Den)
plot(sed[,6],Corb_Den)

sp <- rcorr(Corb_Den, sed[,4:6], type = "spearman"); sp
pe <- rcorr(Corb_Den, sed[,4:6], type = "pearson"); pe
particles <- matrix(nrow = 4, ncol=3)
for (i in 1:3){
  particles[1,i] <- sp$r[1,(i+1)]
  particles[2,i] <- sp$P[1,(i+1)]
  particles[3,i] <- pe$r[1,(i+1)]
  particles[4,i] <- pe$P[1,(i+1)]
}

colnames(particles) <- c("gravel", "sand", "silt")
rownames(particles) <- c("spearman_r", "spearman_p", "pearson_r", "
    pearson_p")
write.csv(particles, file="Corr_Corb_Particlesize.csv")
```

Listing B.4: Statistical analysis of the used data

```
#20150920 analysis of density and size of corbicula
# data collected by madleina gerecke for her bsc thesis
# data structure: 3 sites
#                 5 depths
#                 5 quantitative grab or grid samples per site

### For Ubuntu
setwd("/media/madleina/ETH/Bachelorarbeit/Statistik")



library(lmerTest)

library(ggplot2)



d <- read.csv("Densities_Jukka.csv") # read the data
h <- read.csv("Height_Jukka.csv") # read the data

l.tmp <- read.csv("Length.csv")
w.tmp <- read.csv("Weight.csv")

head(d) # are all OK?
head(h) # are all OK?


### Modify data for length and weight
n = nrow(l.tmp)
l.tmp$ID_sam[1] <- 1
l.tmp$cond[1] <- 0
w.tmp$ID_sam[1] <- 1
w.tmp$cond[1] <- 0
for (i in 2:n){
    l.tmp$ID_sam[i] <- ifelse(l.tmp$Sample[i-1] == l.tmp$Sample[i],l.tmp$
        ID_sam[i-1], l.tmp$ID_sam[i-1]+1)
    l.tmp$cond[i] <- ifelse(l.tmp$Sample[i-1] == l.tmp$Sample[i], 0, 1)
    w.tmp$ID_sam[i] <- ifelse(w.tmp$Sample[i-1] == w.tmp$Sample[i],w.tmp$
        ID_sam[i-1], w.tmp$ID_sam[i-1]+1)
    w.tmp$cond[i] <- ifelse(w.tmp$Sample[i-1] == w.tmp$Sample[i], 0, 1)
}

## Are they okay?
head(l.tmp)
head(w.tmp)

### Get one wrong value correct
l.tmp$Lenght..mm. <- ifelse(l.tmp$Lenght..mm. > 40, l.tmp$Lenght..mm./10,
    l.tmp$Lenght..mm.)
w.tmp$Weight..g. <- ifelse(w.tmp$Weight..g. > 10, w.tmp$Weight..g./10, w.
    tmp$Weight..g.)

l <- l.tmp
w <- w.tmp
```

```
d$tr <- as.factor(d$tran) # converting to factor.
d$lo <- as.factor(d$loc) # converting to factor.
d$ID <- as.factor(d$ID_sam) # converting to factor.
l$tr <- as.factor(l$Transekt) # converting to factor.
l$lo <- as.factor(l$Location) # converting to factor.
l$ID <- as.factor(l$ID_sam) # converting to factor.
w$tr <- as.factor(w$Transekt) # converting to factor.
w$lo <- as.factor(w$Location) # converting to factor.
w$ID <- as.factor(w$ID_sam) # converting to factor.
h$tr <- as.factor(h$tran) # converting to factor.
h$lo <- as.factor(h$loc) # converting to factor.
h$ID <- as.factor(h$ID_sam) # converting to factor.

head(d) # are all OK?
head(h) # are all OK?
head(l)
head(w)

str(d)
str(h)
str(l)
str(w)

options(scipen=99)   #switches off exponential notation


hist(d$dens)  # checking the distribution, expecting that assumptions for
    anova violated

hist(log(d$dens+20)) # possible correction


# define the models, density

d0 <- lm(dens ~  tr*lo,  data=d) # fixed effects model, 2-way anova

d1 <- lm(log(dens+20) ~  tr*lo,  data=d) # fixed effects model, 2-way
   anova

plot(d0)  #checking residuals, looks like some issues

plot(d1)  #looks better

anova(d0)

anova(d1) #both give qualitatively same interpretation


boxplot(dens ~  lo*tr,  data=d, notch=TRUE)
boxplot(dens ~ lo, data=d)


# analysis of size differences, sample as nested random factor
```

```
## Height

hist(h$height) # histogram looks pretty good


h0 <- lm(height ~  tr*lo + ID, data=h) # treating sample (ID) as fixed
    factor

h1 <- lmer(height ~  tr + lo + (1|ID), data=h) # random intercept, sample
     as random group


#seems like the program has issues with estimating tr*lo term because
    there are some empty combinations (no data), too bad, but SPSS will do
     it.

boxplot(height ~  lo*tr + ID,  data=h, notch=TRUE)

boxplot(height ~  lo*tr,  data=h, notch=TRUE) # looks like for each
    transect largest mean individual size is at intermediate depth,
    interesting

boxplot(height ~  lo,  data=h, notch=TRUE) # becomes very clear when
    looked at like this


#testing this by setting the transect as random effect and depth as a
    fixed factor

h2 <- lmer(height ~  lo + (1|ID), data=h) # random intercept, sample as
    random group, including variation among transects

anova(h2) #test for fixed effect, location

rand(h2) #test for random effect, sample ID

plot(lsmeans(h2, test.effs=NULL)) # these are the model predicted means
    for each depth, looks very nice


### for lenght

hist(l$Lenght..mm.) # histogram looks okay


l0 <- lm(Lenght..mm. ~  tr*lo + ID, data=l) # treating sample (ID) as
    fixed factor

l1 <- lmer(Lenght..mm. ~  tr + lo + (1|ID), data=l) # random intercept,
    sample as random group
```

```
#seems like the program has issues with estimating tr*lo term because
    there are some empty combinations (no data), too bad, but SPSS will do
     it.

boxplot(Lenght..mm. ~ lo*tr + ID, data=l, notch=TRUE)

boxplot(Lenght..mm. ~ lo*tr, data=l, notch=TRUE) # looks like for each
    transect largest mean individual size is at intermediate depth,
    interesting

boxplot(Lenght..mm. ~ lo, data=l, notch=TRUE) # becomes very clear when
     looked at like this



#testing this by setting the transect as random effect and depth as a
    fixed factor

l2 <- lmer(Lenght..mm. ~ lo + (1|ID), data=l) # random intercept, sample
     as random group, including variation among transects

anova(l2) #test for fixed effect, location

rand(l2) #test for random effect, sample ID

plot(lsmeans(l2, test.effs=NULL)) # these are the model predicted means
    for each depth, looks very nice


### for weight

hist(w$Weight..g.) # histogram looks not so great
hist(log(w$Weight..g.)) #not better



w0 <- lm(Weight..g. ~ tr*lo + ID, data=w) # treating sample (ID) as
    fixed factor

w1 <- lmer(Weight..g. ~ tr + lo + (1|ID), data=w) # random intercept,
    sample as random group



#seems like the program has issues with estimating tr*lo term because
    there are some empty combinations (no data), too bad, but SPSS will do
     it.

boxplot(Weight..g. ~ lo*tr + ID, data=w, notch=TRUE)

boxplot(Weight..g. ~ lo*tr, data=w, notch=TRUE) # looks like for each
    transect largest mean individual size is at intermediate depth,
    interesting

boxplot(Weight..g. ~ lo, data=w, notch=TRUE) # becomes very clear when
    looked at like this
```

```
#testing this by setting the transect as random effect and depth as a
    fixed factor

w2 <- lmer(Weight..g. ~  lo + (1|ID), data=w) # random intercept, sample
    as random group, including variation among transects

anova(w2) #test for fixed effect, location

rand(w2) #test for random effect, sample ID

plot(lsmeans(w2, test.effs=NULL)) # these are the model predicted means
    for each depth, looks very nice
```

Listing B.5: Calculation of the filtration rates per reference and depthlevel

```
## Bachelorarbeit: Corbicula fluminea im Bodensee
## Berechnen der Filtrierraten
## Daten aus Excel-Spreadsheet im csv Format von Corbicula_
    LakeConstanceSamples
## Madleina Gerecke, August 2015


### Directory is folder where everything will be combined
### For Windows
# setwd("D:/Bachelorarbeit/Berechnungen")
# Data <- read.csv("D:/Bachelorarbeit/Feldarbeit/Corbicula/Corbicula_
    LakeConstanceSamples.csv", sep=",")

### For Ubuntu
setwd("/media/madleina/ETH/Bachelorarbeit/Berechnungen")
Data <- read.csv("/media/madleina/ETH/Bachelorarbeit/Feldarbeit/Corbicula
    /Corbicula_LakeConstanceSamples.csv", sep=",")

m <- nrow(Data)


#### Filtrierrate nach Atkinson
Atkinson <- matrix(nrow=m, ncol = 10)
Atkinson <- Data[2:3]
Atkinson[,3] = 0.3411*Data$Weight..g. + 0.1646 # Calculating wet tissue
    weight (g)
Atkinson[,4] = 164.38*Atkinson[,3] # Calculatin FR per clam(ml h^-1)
Atkinson[,5] = Atkinson[,4]*24 # FR per day
Atkinson[,6] = Atkinson[,5]*0.000001 # convert to m3 (FR day^-1)
colnames(Atkinson) = c("Location", "Depthlevel", "Wet␣tissue␣weight", "FR
    ␣(ml/h)", "FR(ml/day)", "FR(m3/day)")

#### Filtrierrate nach Pigneur
Pigneur <- matrix(nrow=m, ncol=10)
Pigneur <- Data[2:3]
Pigneur[,3] = 0.0148*(Data$Height..mm./10)^(2.2685) # Calculating Clam
    body mass (g)
Pigneur[,4] = 0.086*Pigneur[,3] # Calculating Filtration rate per clam (
    m3 day^-1)
```

```
colnames(Pigneur) = c("Location","Depthlevel", "Clam body mass", "FR per
    clam")


#### Filtrierrate nach Cahoon
Cahoon <- matrix(nrow = 1, ncol=2)
Cahoon[1] <- 1.12 ## liter per clam per day
Cahoon[2] <- Cahoon[1]/1000 ## m^3 per clam per day



x <-Data[2:3]
y <- x$Location[x$Depthlevel..m.==15]

#### mean Filtration rate per depth level
FR <- matrix(nrow=5,ncol=3)
for (i in 1:5){
  FR[i,1] = mean(Atkinson[Atkinson$Location==i,6], na.rm=TRUE)
  FR[i,2] = mean(Pigneur[Pigneur$Location==i,4], na.rm=TRUE)
  FR[i,3] = Cahoon[2]
}

rownames(FR) <- c("3 m","6 m", "10 m", "15 m", "20 m")
colnames(FR) = c("Atkinson", "Pigneur", "Cahoon")

### export FR-Matrix to csv-file for further usage
write.csv( FR, file="Filtrationrates.csv")
```

Listing B.6: Calculation of the area and volumes needed

```
## Bachelorarbeit: Corbicula fluminea im Bodensee
## Berechnen der Fl?chen pro Tiefenlevel
## Daten aus Excel-Spreadsheet im csv Format von Bodensee_Aug2015_2 von
    Rosi Sieber
## Madleina Gerecke, August 2015


#### For Windows
# setwd("D:/Bachelorarbeit/Berechnungen")
# ## Get Rosi's Dataset
# Bodensee_Aug2015_2 <- read.csv("D:/Bachelorarbeit/Bodensee/Bathmetry/
    Bodensee_Aug2015_2.csv", sep=";")

#### For Ubuntu
setwd("/media/madleina/ETH/Bachelorarbeit/Berechnungen")
Bodensee_Aug2015_2 <- read.csv("/media/madleina/ETH/Bachelorarbeit/
    Bodensee/Bathmetry/Bodensee_Aug2015_2.csv", sep=";")

m <- nrow(Bodensee_Aug2015_2)
aperlevel <- rep(0,m)
Bodensee_Area <- cbind(Bodensee_Aug2015_2,aperlevel)

## cut it to needed depth (0-23 m)
Obersee <- Bodensee_Area[-25:-m,]
Untersee <- Bodensee_Area[253:276,]

### Calculate Area per depthlevel
```

```
for (i in 1:23){
  Obersee[i,5] = Obersee[i,3]-Obersee[(i+1),3]
  Untersee[i,5] = Untersee[i,3] - Untersee[(i+1),3]
}


#### Add depths that go into same depthlevel from Ober- und Untersee
Area <- matrix(nrow=5, ncol=2)
  Area[1,1] = sum(Obersee$aperlevel[1:5])+sum(Untersee$aperlevel[1:5])
  Area[2,1] = sum(Obersee$aperlevel[6:9])+sum(Untersee$aperlevel[6:9])
  Area[3,1] = sum(Obersee$aperlevel[10:13])+sum(Untersee$aperlevel
      [10:13])
  Area[4,1] = sum(Obersee$aperlevel[14:18])+sum(Untersee$aperlevel
      [14:18])
  Area[5,1] = sum(Obersee$aperlevel[19:23])+sum(Untersee$aperlevel
      [19:23])

### Calculate Volume above each Depthlevel
  Area[1,2] = sum(Bodensee_Area$Area[Bodensee_Area$Depth<=4])
  Area[2,2] = sum(Bodensee_Area$Area[Bodensee_Area$Depth<=8])
  Area[3,2] = sum(Bodensee_Area$Area[Bodensee_Area$Depth<=12])
  Area[4,2] = sum(Bodensee_Area$Area[Bodensee_Area$Depth<=17])
  Area[5,2] = sum(Bodensee_Area$Area[Bodensee_Area$Depth<=22])

rownames(Area) <- c("3 m", "6 m", "10 m", "15 m", "20 m")
colnames(Area) <- c("Area/Depthlevel","VolumeaboveDL")

write.csv(Area, file="Area.csv")


### Calculate on littoral volume for area above thermocline
Vp <- sum(Bodensee_Area$Area[Bodensee_Area$Depth==23]) * 22 ## pelagic
    volume
Vol_lit <- Area[5,2] - Vp

write.csv(Vol_lit, file="Volumenlitoral.csv")
```

Listing B.7: Calculation of the total filtration rate

```
## Bachelorarbeit: Corbicula fluminea im Bodensee
## Berechnen der Filtriermengen
## Daten aus den Excel-SpreadsheetArea, Density und Filtrationrates
## Madleina Gerecke, August 2015

### First run the following R-Skripts: Filtrierraten.R, Density.R, Area.R

# ### For Windows
# #### Working directory setzen
# setwd("F:/Bachelorarbeit/Berechnungen")
# ### Importieren der drei Datensets
# Area <- read.csv("F:/Bachelorarbeit/Berechnungen/Area.csv", sep=";",
    dec=",")
# Filtrationrates <- read.csv("F:/Bachelorarbeit/Berechnungen/
    Filtrationrates.csv", sep=";", dec=",")
# Density <- read.csv("F:/Bachelorarbeit/Berechnungen/Density.csv", sep
    =";", dec=",")
```

```
#### For Ubuntu
setwd("/media/madleina/ETH/Bachelorarbeit/Berechnungen")
Filtrationrates <- read.csv("/media/madleina/ETH/Bachelorarbeit/
    Berechnungen/Filtrationrates.csv")
Density <- read.csv("/media/madleina/ETH/Bachelorarbeit/Berechnungen/
    Density.csv")
Area <- read.csv("/media/madleina/ETH/Bachelorarbeit/Berechnungen/Area.
    csv")
Vol_lit <- read.csv("Volumenlitoral.csv")


### Berechnen der Filtriermengen pro Zeiteinheit
### Einheit m^3/day
Filtration <- matrix(nrow=24, ncol=3) ###Matrix daf?r erstellen
for (i in 1:3){
  ## Berechnen der Filtriermenge pro Tiefenlevel und f?r jede Referenz
  Filtration[1,i] = Area$Area.Depthlevel[1]*Density$mean[1]*
      Filtrationrates[1,1+i]
  Filtration[2,i] = Area$Area.Depthlevel[2]*Density$mean[2]*
      Filtrationrates[2,1+i]
  Filtration[3,i] = Area$Area.Depthlevel[3]*Density$mean[3]*
      Filtrationrates[3,1+i]
  Filtration[4,i] = Area$Area.Depthlevel[4]*Density$mean[4]*
      Filtrationrates[4,1+i]
  Filtration[5,i] = Area$Area.Depthlevel[5]*Density$mean[5]*
      Filtrationrates[5,1+i]
  ### Total der Filtriermengen pro Referenz bilden (m^3/day)
  Filtration[6,i] = sum(Filtration[1:5,i], na.rm = TRUE)
  ### Einheit ändern
  Filtration[7,i] = Filtration[6,i]*10^(-9)
  Filtration[8,i] = Filtration[7,i]/48*100 ### volume lake Constance: 48
      km^3
  Filtration[9,i] = Filtration[6,i]/24/60/60
  Filtration[10,i] = Filtration[9,i]/372*100 ### mean discharge from http
      ://www.umwelt.sg.ch/home/Themen/wasser/seen/bodensee.html
  x1=0
  y1=0
  for (j in 1:5){
    x  = Area$Area.Depthlevel[j]*Density$low[j]*Filtrationrates[j,1+i]
    x1 = x + x1
    y = Area$Area.Depthlevel[j]*Density$high[j]*Filtrationrates[j,1+i]
    y1 = y+y1
  }
  Filtration[11,i] = x1
  Filtration[12,i] = Filtration[6,i] - Filtration[11,i]
  Filtration[13,i] = Filtration[11,i]*10^(-9)/48*100
  Filtration[14,i] = Filtration[11,i]/24/60/60/372*100
  Filtration[15,i] = y1
  Filtration[16,i] = Filtration[6,i] - Filtration[12,i]
  Filtration[17,i] = Filtration[15,i]*10^(-9)/48*100
  Filtration[18,i] = Filtration[15,i]/24/60/60/372*100

  Filtration[19,i] = Filtration[6,i]/Area$VolumeaboveDL[5]*100 ###
      Compared to Volume above Thermocline (here 22m)
  Filtration[20,i] = Filtration[11,i]/Area$VolumeaboveDL[5]*100 ###
      Compared to Volume above Thermocline (here 22m)
  Filtration[21,i] = Filtration[15,i]/Area$VolumeaboveDL[5]*100 ###
```

```
      Compared to Volume above Thermocline (here 22m)

  Filtration[22,i] = Filtration[6,i]/Vol_lit$x*100 ### Compared to Volume
      above litoral Thermocline (here 22m)
  Filtration[23,i] = Filtration[11,i]/Vol_lit$x*100 ### Compared to
     Volume above litoral Thermocline (here 22m)
  Filtration[24,i] = Filtration[15,i]/Vol_lit$x*100 ### Compared to
     Volume above litoral Thermocline (here 22m)


}

rownames(Filtration) <- c("3 m", "6 m", "10 m", "15 m", "20 m", "mean(m^3/
    day)",
                          "mean(km^3/day)", "%LakeCVolume", "m^3/sec", "%
                              mittlererAbflussObersee",
                          "low(m^3/day)", "mean-low", "%VolumeLC", "%
                              meanDischarge","high(m^3/day",
                          "mean-high", "%VolumeLC", "%meanDischarge",
                          "%meanVolTher", "%lowVolTher", "%highVolTher",
                          "%meanVolLit", "%lowVollit", "%highVOllit")
colnames(Filtration) = c("Atkinson", "Pigneur", "Cahoon")


### export Filtration to csv-file
write.csv( Filtration , file="Filtration.csv", row.names = TRUE)
```

Listing B.8: Calculation of total wet body mass

```
## Bachelorarbeit: Corbicula fluminea im Bodensee
## Berechnen der Filtrierraten
## Daten aus Excel-Spreadsheet im csv Format von Corbicula_
    LakeConstanceSamples
## Madleina Gerecke, August 2015


### Directory is folder where everything will be combined
### For Windows
# setwd("F:/Bachelorarbeit/Berechnungen")
# Data <- read.csv("F:/Bachelorarbeit/Feldarbeit/Corbicula/Corbicula_
    LakeConstanceSamples.csv", sep=";")

### For Ubuntu
setwd("/media/madleina/ETH/Bachelorarbeit/Berechnungen")
Data <- read.csv("/media/madleina/ETH/Bachelorarbeit/Feldarbeit/Corbicula
    /Corbicula_LakeConstanceSamples.csv", sep=",")

m <- nrow(Data)

#### Calculating Wet tissue weight with formula from Atkinson
Atkinson1 <- matrix(nrow=m, ncol = 4)
Atkinson1 <- Data[2:3]
Atkinson1[,3] = Data$Weight..g.
Atkinson1[,4] = 0.3411*Data$Weight..g. + 0.1646
colnames(Atkinson1) = c("Location","Depthlevel", "Wet whole weight","Wet
    tissue weight")
```

```
####get mean "wet tissue weight" per depthlevel per clam
bodymass.tmp <- c()
par(mfrow = c(1, 5))
for (i in 1:5){
  bodymass.tmp[i] = mean(Atkinson1[Atkinson1$Location==i,4], na.rm = TRUE
      )
  hist(Atkinson1[Atkinson1$Location==i,4])
  }

summary(Atkinson1[Atkinson1$Location==1,4])
summary(Atkinson1[Atkinson1$Location==2,4])
summary(Atkinson1[Atkinson1$Location==3,4])
summary(Atkinson1[Atkinson1$Location==4,4])
summary(Atkinson1[Atkinson1$Location==5,4])


### Get Area and Density Data
Area <- read.csv("Area.csv") # Unit: m^2
Density <- read.csv("Density.csv")


### Calculate total body mass of Corbicula if spreading throughout Lake
    Constance
### = mean wet tissue weight per depthlevel * Area per depthlevel *
    Density per Depthlevel
bodymass <- matrix(nrow=7, ncol = 1)
for (i in 1: 5){
  bodymass[i] = bodymass.tmp[i]*Area$Area.Depthlevel[i]*Density$mean[i]
}
bodymass[6] = sum(bodymass[1:5])
bodymass[7] = bodymass[6]/1000

colnames(bodymass) <- c("wet␣tissue␣weight")
rownames(bodymass) <-c("3m", "6m", "10m", "15m", "20m", "Total␣(g)", "
    Total(kg)")

write.csv(bodymass, file = "Bodymass.csv", row.names = TRUE)
```

Listing B.9: Calculation of the filtration rate of *Daphnia spp.*

```
## Bachelorarbeit: Corbicula fluminea im Bodensee
## Berechnen der Filtriermengen von Daphnien
## Daten von LUBW und paper pinto-Coelho 1991 (art_12a.pdf), table 1
## Madleina Gerecke, Dezember 2015

#### For Ubuntu
setwd("/media/madleina/ETH/Bachelorarbeit/Berechnungen")

frdsppml = mean(12.9,16.2,8.2,12.9) ### Filtrationrate: mean of the four
    values given for the two different Daphnia species
                                    ### in ml per ind per day
frdsppm3 = frdsppml/1000/1000 ### Filtration rate in m3 per ind per day

dendspp_l = 8.55561/100000   ### individuals per liter
dendspp_m3 = dendspp_l *1000 ### individuals per cubic meter

VolumeLC <- read.csv("Area.csv")
```

```
VolumeLitoral <- read.csv("Volumenlitoral.csv")


### Daphnia in Lake Constance with whole volume above Thermocline
dendsppLCT = dendspp_m3 * Area$VolumeaboveDL[5]

### Daphnia in Lake Constance with litoral volume above Thermocline
dendsppLCL = dendspp_m3 * VolumeLitoral$x


### Calculating total Filtration for Daphnia spp in LC
FiltrationrateDaphnia <- c(2)
FiltrationrateDaphnia[1] <- frdsppm3 * dendsppLCT
FiltrationrateDaphnia[2] <- frdsppm3 * dendsppLCL
FiltrationrateDaphnia
```

C. Declaration of originality

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