Review

Cultivation of zebra mussels (*Dreissena polymorpha*) within their invaded range to improve water quality in reservoirs

C. McLaughlan*, D.C. Aldridge

Aquatic Ecology Group, Department of Zoology, University of Cambridge, Downing Street, Cambridge CB2 3EJ, United Kingdom

**Abstract**

Algal and cyanobacterial blooms in reservoirs are driven by nutrient enrichment and may present economic and conservation challenges for water managers. Current approaches such as suppression of algal growth with barley straw, ferric dosing or manipulation of fish stocks have not yielded long term successes. A possibility that has sparked growing interest is the encouragement and cultivation of natural filter feeders, such as mussels, which remove suspended matter from the water and reduce nutrient levels through bio-deposition and assimilation.

This review focusses on the zebra mussel (*Dreissena polymorpha*) as a tool for enhancement of water quality in reservoirs. Native to the Ponto-Caspian region, this species has invaded many lakes and reservoirs across North America and Western Europe, where it occurs in very high densities. While purposeful introduction of a non-native species into new sites is socially unacceptable, we investigate the possible benefits of encouraging increased abundance of zebra mussels in sites where the species is already established.

We estimate that the annual nitrogen and phosphorus input into a large UK reservoir (Grafham Water) could be assimilated into zebra mussel biomass by encouraging settlement onto 3075 m and 1400 m of commercial mussel ropes, respectively. While zebra mussel cultivation has an incredible capacity to push eutrophic systems towards a clear water state, there are many risks associated with encouraging an invasive species, even within sites where it has already established. The zebra mussel is a prominent biofouler of native unionid mussels and raw water pipes, it changes the physical characteristics of the places it inhabits, in sites low in phosphorus it can be responsible for toxic cyanobacterial blooms, it alters nutrient cycling and community structure and it can have negative impacts on amenity value. Increased propagule pressure from elevated numbers of veliger larvae in the water column may increase the risk of spread to other locations. This may render some reservoir systems, such as dammed rivers which have outflows to downstream watercourses, unsuitable for cultivation. Such reservoirs are especially common in North America.

---

*Corresponding author. Tel.: +44 1223 336617; fax: +44 1223 336676.
E-mail addresses: cm645@cam.ac.uk, cgm500@googlemail.com (C. McLaughlan), da113@cam.ac.uk (D.C. Aldridge).

0043-1354/$ – see front matter © 2013 Elsevier Ltd. All rights reserved.
http://dx.doi.org/10.1016/j.watres.2013.04.043
We consider the practicalities of putting a zebra mussel cultivation system into place and identify gaps in knowledge. We conclude that zebra mussel cultivation offers an attractive tool for managing nutrient-enriched reservoirs, but that the benefits and costs must be balanced on a site-by-site basis.

1. Introduction

Nutrient enrichment of freshwaters, both within natural lakes and man-made impoundments such as reservoirs, is a serious ecological and economic problem worldwide (e.g. Smith et al., 1999). Driven in large part by the intensification of agriculture (Matson et al., 1997), elevated levels of nutrients (eutrophication), particularly phosphorus (P) (Schindler, 1977) and nitrogen (N), can cause seasonal blooms of algae and cyanobacteria (phytoplankton), which in reservoirs can cause difficulties for water purification and supply (Parsons and Jefferson, 2006), including the generation of taste and odour problems (Hayes and Greene, 1984). Changes in the productivity, biomass and species composition of phytoplankton can also lead to biodiversity loss and the degradation of these sites as places for recreational activities such as fishing and sailing. Furthermore, shifts in phytoplankton composition can favour species of bloom-forming cyanobacteria, many of which produce toxins (e.g. microcystins) that can lead to adverse effects for human health (Cooke and Kennedy, 2001).

Responses to the problem of eutrophication in reservoirs include precipitation of phosphorus with iron salts, sediment dredging, artificial mixing and manipulation of water levels (Brierley and Harper, 1999), with a general shift in recent years towards more ‘natural’ solutions, based on the principals of ‘biomanipulation’. Classical biomanipulation (Shapiro and Wright, 1984) involves reducing the abundance of planktivorous fish in a lake, in order to allow herbivorous zooplankton to increase and graze on excess algae. Other methods of restoration similarly attempt to tip the balance of the ‘alternate equilibria’ from a turbid, phytoplankton-dominated system towards a clear, macrophyte dominated state (Scheffer et al., 1993). Examples include suppression of algal growth with barley straw (Pretty et al., 2003; Garbett, 2005) and floating reedbeds (Garbett, 2005). It is well known that restoration of freshwater ecosystems is complicated and may require complimentary methods to be employed. As yet this has not been achieved satisfactorily for drinking water reservoirs, where a balance must be found between many stakeholder requirements, including recreation, conservation of biodiversity, and potable supply.

Providing innovative solutions to the problem of eutrophication in reservoirs presents challenges and opportunities for the water industry and researchers. One possibility, which has received growing interest from the water industry, is the use of natural filter feeders, such as bivalves, sponges and bryozoans, to improve water quality through their removal of suspended material from the water column. This concept has already received considerable attention in the context of lake restoration (Reeders and Bij de Vaate, 1990;
Soto and Mena, 1999), and enhancement of water quality in marine and estuarine environments (Lindahl et al., 2005; Stybel et al., 2009). At the centre of many of these studies is the use of invasive non-native filter feeders, which can reach very high abundances and thus drive marked ecosystem-level changes. In particular, the zebra mussel, Dreissena polymorpha, is well known for its huge filtering capacity, which has transformed water clarity in many ecosystems where it has become invasive (MacIsaac, 1996; Caraco et al., 1997; Strayer et al., 1999). Native to the Ponto-Caspian region of Eastern Europe, the zebra mussel spread across large parts of Western Europe during the 19th and 20th century and continues to increase in distribution and abundance (Aldridge et al., 2004). The species was first recorded in North America during the 1980s, and, along with its congener the quagga mussel (Dreissena rostriformis bugensis), has since established widely throughout the Great Lakes, the eastern United States (and especially the Mississippi drainage) and has now been discovered in a number of sites in the western United States (USGS, 2012).

While cultivation of invasive species offers considerable potential for reservoir management, it does not come without economic and ecological risks. Public perceptions differ considerably on the acceptability of such approaches across different geographies. For the water industry to embrace successfully the potential offered by cultivating filter feeders, it is necessary to balance these benefits against the risks. In this review we first assess the evidence for effective improvement of water quality by filter feeders, including worked examples of the changes that could be possible. We then look at some case studies of filter feeders being used as biofilters, to provide an overview of the ‘state of the art’. Next we consider suitable cultivation methods, identifying challenges and current research taking place. Finally we review the possible risks associated with the cultivation of non-native filter feeders in reservoir systems and discuss how these risks can be best managed.

2. Zebra mussels as ecosystem engineers

There is good reason to believe that freshwater filter feeders can contribute to improved water quality, and they are often considered to function as ‘keystone organisms’ or ‘ecosystem engineers’. Filter feeders are characterised by a system that processes large volumes of water (suspension feeders) or settled sediments (deposit feeders) in order to trap and concentrate food from their surroundings. Because filter feeding brings food to the animal, they are typically sedentary and often possess features that enable them to adhere securely to hard surfaces (e.g. the byssus threads of zebra mussels) or secure themselves into the benthos (e.g. the muscular foot of unionid mussels). Filter feeders can affect ecosystem processes in a number of ways. Mussels, the focal group of this review, can enhance water quality for other taxa through filtration of suspended particles, create habitat through biodeposition of faeces and pseudofaeces, mix and oxygenate sediments through bioturbation, and provide a colonisable substrate and refuge for other taxa and conspecifics (Spooner and Vaughn, 2006; Sousa et al., 2009; Fig. 1).

In a conservation context, the ideal situation when considering manipulation measures using mussels would be to facilitate native filter-feeders, such as unionid mussels. Aldridge et al. (2007) found higher macroinvertebrate diversity in UK rivers associated with higher abundance of native freshwater mussels. There is no doubt that native mussels can influence algal densities through their filtering activities; a single unionid has been shown to be capable of filtering up to 40 L of water per day (Tankersley and Dimock, 1993). However freshwater unionids are in decline worldwide (Bogan, 1993), and this coupled with their complex lifecycle of requiring fishes to serve as hosts to their larvae means large scale artificial cultivation and propagation would be necessary. This has been achieved in the lab, but it is acknowledged as a difficult and labour-intensive process (e.g. McIvor, 2004). Stybel et al. (2009) suggested that the duck mussel (Anodonta anatina) would be a suitable native biofilter in the Szczecin Lagoon, Germany, but acknowledged that at a natural density of only 1–2 individuals m⁻², they would have to be reared up in aquaculture basins to produce sufficient filtration capacity for manipulation of algal densities. Other native species such as bryozoans and sponges remove seston from reservoir water, but are relatively poorly studied. The sponge Spongilla lacustris can filter water at a rate of 7 L water h⁻¹ g⁻¹ dry weight and the bryozoan Plumatella...
fungosa 2.2 L water h\(^{-1}\) g\(^{-1}\) dry weight (Ostroumov, 2005). However, with these taxa typically forming only thin layers and being patchily distributed in most systems, their contribution to ecosystem engineering may be limited.

Conversely, the contribution of the non-native zebra mussel, *D. polymorpha*, to changes in water clarity is very well documented. With the species occurring in densities of up to 700,000 m\(^{-2}\) (*Pathy, 1994*) and dominating the benthic biomass of many invaded systems, zebra mussel invasions have often been linked to beneficial changes to reservoir water quality. With increasing interest from the water industry in the potential to harness them on a larger scale, zebra mussels will provide the prominent example of a biofilter in the context of this review.

### 2.1. Filtration effects of zebra mussels

Recent qualitative observations at reservoirs infested with *D. polymorpha* suggest that their extremely high filtering capacity could be harnessed within the framework of the alternate equilibria model, where previously bivalve molluscs have not been considered (Fig. 2). Zebra mussels can filter a wide range of suspended particles of greater than 0.7 \(\mu\)m from the water (Sprung and Rose, 1988). A percentage is assimilated (typically in the size range of 15–40 \(\mu\)m, Ten Winkel and Davids, 1982) and the rest deposited to the benthic zone as faeces and pseudofaeces. Large filtration capacity helps explain the extreme changes in water clarity and chlorophyll a levels seen after the arrival of *D. polymorpha*. Reeders and Bij de Vaate (1989) showed that the collective feeding of the zebra mussels in the Dutch lakes Ijsselmeer and Markermeer was enough to filter the volume of both lakes at least once or twice per month. In their meta-analysis of zebra mussel impacts, Higgins and Vander Zanden (2010) noted a mean decrease in chlorophyll levels of 47.3% \((n = 45)\) post-invasion, and an increase in secchi disk levels of 38.5% \((n = 46)\). One prominent example is the Hudson River, where Caraco et al. (1997) observed an 85% decline in phytoplankton in the two years following zebra mussel invasion. Reduction in phytoplankton levels often results in increased water clarity and thus more macrophytic plants, which in turn provides habitat and refugia for invertebrates and fish. For this reason, zebra mussels represent a potentially valuable tool in the manipulation of eutrophic freshwaters.

Despite the ecological importance of zebra mussel filtration, many predictions of their large-scale effects on ecosystems rely on extrapolations from rates obtained in laboratory experiments, not accounting for flow rates, elevated algal concentrations or the effect of re-filtration by colonies of mussels. The reported clearance rate (volume of water that is cleared of suspended particles per unit time) for *D. polymorpha* therefore varies widely within the literature. One of the most recent studies found some of the highest clearance rates to date; up to 574 ± 20 ml h\(^{-1}\) g\(^{-1}\) of wet tissue mass (Elliot et al., 2008). This study used large-scale industrial flumes trials at a water treatment works belonging to the UK water company, Thames Water. When additional algal cultures were dosed into the flumes, chlorophyll a removal increased approximately logarithmically with mussel density and there were no differences in the clearance of three different species of nuisance alga: Ankyra judayi, Pandorina morum and Cyclotella meneghinia.

### 2.2. Removal of pathogens

A key role in the treatment of potable water supplies is the removal of human waterborne pathogens. In recent years, it has become clear that many filter-feeding bivalve species can harbour environmentally-derived protozoan parasites as a result of concentrating them from the water column (Graczyk et al., 2003). Studies of zebra mussels collected adjacent to a wastewater discharge in the St. Lawrence River, Quebec, found an average of 440 oocysts of *Cryptosporidium parvum* in the haemolymph and soft tissue. It was calculated that over 24 h approximately 1.3 \(\times\) 10\(^7\) waterborne *C. parvum* oocysts could be removed by each square metre of mussel bed in the St. Lawrence River (Graczyk et al., 2001). Additional studies have shown zebra mussels to harbour *Giardia lamblia* and spores of *microsporidia* infectious to humans, including *E. intestinalis* and *Enteroctozena bienue* (Graczyk et al., 2004). While it is unclear whether filter feeders can serve to dramatically reduce pathogens within water supply reservoirs, it has been observed that counts of *C. parvum* oocysts are markedly lower at the draw-off points to the works than in the river abstraction points of some UK reservoirs supporting large zebra mussel populations (B. Holden, Anglian Water, pers. comm.).

### 2.3. Biodeposition effects

As well as their filtering activities, zebra mussels alter the benthic habitat by restructuring the substrate (Sousa et al., 2008).
deposition rates in a shallow lagoon from a background rate of non-sedimented algae and detritus bound in mucus and are periodically expelled by the inhalant siphon of the mussel (Stanczykowska et al., 1975). This results in organic enrichment of the sediment surrounding an aggregation of zebra mussels (Griffiths, 1993). This nutrient-rich habitat has been shown generally to enhance the macroinvertebrate abundance and biodiversity of the benthos (Ward and Ricciardi, 2007). The shelter and surface area provided by the mussels themselves are also an important factor in this phenomenon (Strayer et al., 1999). Bially and MacIsaac (2000) found that mussel-sediment habitat supported between 4.6 and 7 times more taxa than adjacent sediment that did not contain mussels. However the effects differ depending on particle size and taxonomic and functional groups. It is important to note that the small spatial scale of these types of studies could be misleading, if the increase in numbers of benthic invertebrates locally around zebra mussel beds is outweighed by declines in the entire lake or river (Strayer, 2006).

Daunys et al. (2006) found that zebra mussels increased deposition rates in a shallow lagoon from a background rate of 380 g m⁻² per year to 590 g m⁻² per year, which represented deposition of between 10 and 30% of the total particulate matter entering the lagoon. Mackie and Wright (1994) suspended zebra mussels in sediment traps with activated sewage sludge. Zebra mussel treatments showed significant reductions in turbidity, removal of up to 90% of phosphorus (P), mainly by biosedimentation, and reduced BOD (biochemical oxygen demand after 5 days at 20 °C), compared with controls, suggesting that zebra mussels could be a powerful tool in water treatment.

If zebra mussels were to be cultured to improve water quality in reservoirs, the pathway of nutrient removal from the water column through biodeposition should be taken into consideration. As well as improving water quality and biodiversity by reducing turbidity, zebra mussels could contribute to increased macroinvertebrate abundance and/or diversity in the benthic zone. However, as bound nutrients would remain in the sediment, measures such as occasional dredging may have to be considered alongside biofilter cultivation.

### 2.4. Nutrient uptake

A further major contribution that filter feeding communities, and especially zebra mussels, can make to nutrient removal from a reservoir is through the production of biomass. Zebra mussels sequester a large amount of N and P from the water column when they ingest seston, which would otherwise be available for phytoplankton productivity (Kuenzler, 1961; Stanczykowska, 1984). Zebra mussels can therefore play an important part in nutrient cycling within a water body, particularly when they occur in large numbers. In five lakes of the Jorka river watershed in Poland, a nutrient budget was calculated for the zebra mussels present, and showed amounts of N and P accumulated in their bodies was similar to the amounts stored in macrophytes. The importance of zebra mussels to nutrient cycles varied from lake to lake (Stanczykowska and Planter, 1985). Indeed, in Stanczykowska & Planter’s study, the effects zebra mussels have on nutrients within the water column is acknowledged in the literature as being complex and context dependent. Higgins and Vander Zanden (2010) carried out a meta-analysis and found that overall, there was no change in levels of total dissolved nitrogen in lakes between the pre and post-invasion period (n = 14). However, water clarity increased and turbidity was reduced in almost every case (with a mean 40% decrease in turbidity). Improved water clarity and reduced algal densities would be the ultimate goal of a water company with a eutrophic reservoir.

To quantify the role zebra mussels can play in nutrient sequestration, the amounts of N and P can be quantified in the tissues and shells of zebra mussels using laboratory techniques. Goedkoop et al. (2011) found concentrations of N and P in soft tissue averaged 100.9 ± 1.5 mg N g⁻¹ DW and 9.3 ± 0.2 mg P g⁻¹ DW. This information can be used to quantify the role zebra mussels could play in the nutrient budget of a eutrophic reservoir. For example, Goedkoop et al. (2011) calculated that the whole population of Lake Ekoln (Sweden) retained 1.2–1.8 ton P y⁻¹ (assuming a life span of 2–3 years). This amounted to 50–77% of the annual flux of P from the local sewage treatment plant to the lake. Other studies have quantified nutrient levels in shells, and these are much lower than for tissues; for example 0.45 mg g⁻¹ P in the Konin lakes of Poland (Krolak and Zdanowski, 2007). Jurkiewicz-Karnkowska (2005) quantified N in zebra mussel shells as 0.38 ± 0.05% N. Harvesting of zebra mussels may therefore offer an effective tool for nutrient removal from some waterbodies.

### 3. Case studies of biofilters for improved water quality

Observational studies on the effects of large bivalve populations on water clarity have prompted authors to conduct manipulative experiments. These have examined the potential of encouraging/cultivating bivalves as biofilters, both in freshwaters and the marine environment.

#### 3.1. Early use of zebra mussels as biofilters

As algal control agents, zebra mussels have been hailed as a more stable option than encouraging zooplankton, whose populations are prone to fluctuate (Harper and Ferguson, 1982). Almost thirty years ago, the practical applications of zebra mussels in eutrophication control were examined in a canal in Poland (Piesik, 1983). A net barrier was placed in one of the channels of the River Oder and the one year old population of zebra mussels that settled there was subsequently studied. Mass settlement, with densities of up to 448,970 indiv. m⁻² of net area was observed, and these mussels succeeded in removing dissolved nutrients from the water.

In The Netherlands, there has also been interest in biological manipulation to improve water quality of shallow lakes using zebra mussels since the 1980s. Richter (1986) gave
preliminary results of a study in Lake Tjeukemeer, which suggested zebra mussels could be an effective tool for reducing algal densities in Dutch lakes, given appropriate hard substrate on which to proliferate. However this study was within small lake enclosures, and there was only one main type of alga present: Oscillatoria agardhii. Reenders and Bij de Vaate (1990) reviewed the potential for zebra mussels to play a role in water quality management, taking in situ measurements of filtration rates. They found that population density of mussels only needed to be 675 m$^{-2}$ in Lake Wolderwijd (a lake with a mean depth of 1.5 m and a surface area of 2600 ha) in order to compensate for algal growth. They emphasised the important role zebra mussels could play in reducing the P load through biodeposition from the water column to the sediment, as faeces and pseudofaeces. Whilst increased biodeposition of P this does not result in permanent removal, Reenders and Bij de Vaate (1990) argued that P was, at least, taken out of the water column. One potential problem that must be considered, however, if a large amount of N & P were to be deposited to the sediment, is that the resultant microbial respiration rates could result in reduced oxygen in the sediments (Newell, 2004). This could lead to inhibition of coupled nitrification—denitrification, release of P back into the water column and toxic H$_2$S gas could build up. This situation is unlikely to occur unless densities of mussels are very high, and any cultivation should take this into account. Antsulevich (1994), using the example of the Neva Bay in the Gulf of Finland, addressed the problem of how zebra mussel cultivation would work in practice. He proposed the construction of artificial reefs (large metal frames) which could be periodically removed and cleaned of encrusting organisms. If biofilters were to be used for improving water quality, a system allowing easy, permanent removal of the filter feeder biomass would ensure removal of N and P from the system in the long term. Much more recently, Stybel et al. (2009) identified the opportunities of using zebra mussels in the Szczecin Lagoon in Germany. They attempted to make a more business-like case for the 'aquaculture' of zebra mussels, and also touched on the question of disposal or commercial sale of harvested mussels.

3.2. Use of biofilters in marine systems

The importance of bivalves as filter feeders in the marine environment is well known (e.g. see Dame et al., 1984; Dame, 1993). In their review paper, Prins et al. (1998) acknowledge that the processing of large amounts of particulate matter by bivalves, and resulting changes in nutrients available for phytoplankton can be seen on an estuarine scale. Perhaps the most comprehensive assessment of the applied use of filter feeders for environmental improvement, coupled with the potential for commercial production of bivalve biomass, comes from Lindahl et al. (2005). This review described the possibility of cultivating the blue mussel, Mytilus edulis, for bioremediation of eutrophic coastal areas in Sweden, and modelled the expected changes in nutrient levels that could realistically be achieved. They also proposed an interesting solution to the funding of such mussel farms (presuming that the trade in the mussels alone would not provide enough capital). This was a ‘nutrient trading scheme’, where the polluters (e.g. wastewater treatment facilities) must pay for the cost of mitigating the amount of nutrient release their business causes. Of course it is not realistic to expect the biological manipulation of reservoirs to be paid for by nutrient emitters, and often N and P are from diffuse sources which are very difficult to trace (Pretty et al., 2003). However, this does highlight the need to take cost into consideration in the design, and to consider the possible end-uses of any harvested material. The 'Agro-Aqua' recycling system set out by Lindahl et al. (2005) summarises how mussels can be cultivated to assimilate nutrients (in this case from the marine environment), and then be recycled to the land upon harvesting, and used for chicken feed, fertiliser or human consumption. This ensures permanent removal of N and P from the system. Blue mussels were converted to a meal suitable for incorporation into chicken feed and fed to both laying and broiler hens in Sweden. Chickens were found to prefer mussel to conventional fodder, and no adverse effects on production values such as egg quality were reported (Lindahl et al., 2005; Jönsson, 2009). A pilot study using blue mussels (shells and flesh) as a fertiliser for grain cultivation found a 25–50% increase in crop growth compared to non-fertilised land (Lindahl and Kollberg, 2008) This meant mussels were just as effective as manure as a fertilising agent.

4. Cultivation systems

Lindahl et al. (2005) sourced their blue mussels from commercial marine long-line cultivation systems. If the presumption is made that freshwater filter feeders such as zebra mussels could make a significant difference to reservoir water quality, one of the biggest questions that remains is how best to encourage their growth in the most cost-effective way, using cultivation that is both practical to install and which is amenable to harvesting, should this be required. Aesthetics is also a key consideration, especially in reservoirs that are also used for recreational purposes.

4.1. Zebra mussel habitat requirements

Although zebra mussel growth rates and abundance are limited by factors such as flow rate, food availability and temperature, (Mackie and Claudi, 2010) their growth habit means that without a hard substrate of some kind, they are unable to settle and proliferate in the first place. As with many bivalves, they must attach by their byssus threads to solid substrate, and consequently are found typically on submerged vegetation, shells of other mussels, stones and hard man-made structures such as piling, dam walls and marginal impoundments (Smit et al., 1993). The sensitivity of zebra mussel veliger larvae to ultraviolet radiation means that settlement typically occurs at depths >30 cm, but can be shallower in shaded areas (Claudi and Mackie, 1994). Over the course of time after establishment, the shells of dead zebra mussels form a substrate on which others can settle, enabling establishment into benthos that was previously soft and uninhabitable. Three factors which can negatively affect settlement are silt and detritus, competition with other organisms such as sessile macroalgae and predators, and fluctuations in
water levels (Smit et al., 1993). Kilgour and Mackie (1993) found when comparing different types of substrate for settlement that zebra mussels preferred to be on the inside of tubes than the outside: suggesting they favour a sheltered environment and/or that providing this shelter reduces predation by birds and fish. Many authors stress the importance of providing substrate for mussels when considering their use as biofilters (Richter, 1986; Reeders and Bij de Vaate, 1992; Lindahl et al., 2005; Stybel et al., 2009). There are several different ways to fulfil this habitat requirement.

4.2. Types of cultivation system

There are many ways of farming mussels. In marine systems, a long-line approach is typically used that was developed in Sweden in the early 1980s (Ackefors and Haamer, 1987). The mussels are grown on vertical 6 m suspenders attached to horizontal lines. Natural settlement is allowed, although in many countries mussel larvae are introduced to the line. On the Swedish West coast, this type of line can produce 40 kg blue mussels m⁻² year⁻¹, with this amount of mussels filtering the phytoplankton biomass produced by around 25 m² of sea surface in this year (Lindahl et al., 2005).

An alternative approach is to propagate on horizontal fishing nets, fixed at 2.5 m depth (Stybel et al., 2009). Fenske (2005) found an average 6400 zebra mussels m⁻² on experimental horizontal nets in the Szczecin Lagoon, which at a mass of 1 g after 2 years growth would give a yield of 6.4 kg m⁻²; substantially less than that of blue mussels. If zebra mussels were to be harvested as a nutrient removal tool, they may need to be harvested during months when they are of the highest condition (i.e. April–May; Costa et al., 2008). Harvesting at around 24 months would help avoid the risk of dropping off the ropes and losses from predation (Stybel et al., 2009). Another suggestion, from Antsulevich (1994) was artificial reef modules which sit on the sediment and have removable metal frames for harvesting. These may be less readily harvested than commercially available ‘Smartfarms’, which offer an off-the-shelf system that includes mechanical harvesting equipment. Vertical mussel farms utilise the body of water efficiently, and Smartfarms are also more stable than long lines (Walter and De Leeuw, 2007). However the costs are high when considering using these systems in small reservoirs, when zebra mussels are currently a product with no commercial value. Smartfarms cost approximately 38,000 Euro per hectare (based on 2009 prices, Stybel et al., 2009), and once set up also require labour costs for husbandry. If a full economic costing for this type of operation were to be carried out, every stage from the launching of equipment to the eventual harvesting (including labour costs and maintenance of equipment) would need to be considered. It is also recognised that harvesting the mussel biomass would not be appropriate in every case, and each reservoir would need to be considered individually. Indeed, simply encouraging resident zebra mussel biomass to serve as a sink for N and P within a reservoir, and for their biodeposition effects to direct nutrients towards the benthos, may provide substantial improvement to water clarity.

A recent study (Paalvast et al., 2012) described a simple but effective way of increasing biodiversity on hard substrate, by testing structures with hanging ropes of different materials and lengths within the Port of Rotterdam. The aim was generally to improve biodiversity in the port, not to target a specific species for cultivation, but nonetheless they saw settlement on their floating ‘Pontoon’ structures dominated by the blue mussel, M. edulis, after a few months. They saw biomass decrease by 50% from the edge to the centre of a pontoon, demonstrating the importance of sufficient flow of seston. Optimal density of mussels was seen at 4–8 ropes m⁻². Studies in UK freshwaters suggest that specialist spat ropes with a complex structure can produce very high densities of zebra mussels (C. Mclaughlan, unpublished data: Fig. 3). These ropes are cheap and can be attached to many different structures, either around the edges of a reservoir or to custom made floating rigs.

One such attachment structure which would allow placement of mussels at various points around a reservoir and which would also be aesthetically pleasing is a floating artificial reedbed. Ropes for mussel growth could be placed around such a construction. Reedbeds are a method of bioremediation

![Fig. 3](image-url)
being trialled for the treatment of nutrient-enriched reservoirs by several UK water companies (Garbett, 2005; A. Wallen, Thames Water, pers. comm.). The principal behind any ‘constructed wetland’ is to provide filtration and sedimentation capacity and habitat amongst the roots for zooplankton communities (Jing et al., 2001; Garbett, 2005). This action, combined with the filtration capacity of zebra mussels, could provide a dual ‘living filter’. The shelter provided by the structure could also be conducive to maximal zebra mussel growth. A trial of this type of rig is currently underway in a UK reservoir.

5. A theoretical scenario

To illustrate the potential contribution of zebra mussels to the nutrient budget of a reservoir we will use Grafham Water Reservoir (Cambridgeshire, UK; 52°18′12.76″N, 0°19′15.32″E) as a representative example. Grafham draws water from the River Great Ouse, a lowland river within an agricultural catchment and with large inputs of treated domestic effluents. The reservoir has a residence time of 212 days and a volume of 55,494 ML. Therefore in a year we estimate that 95,544 ML water enters this reservoir. The mean TN (total nitrogen) and TP (total phosphorus) for Grafham during 2009 was 7.72 and 2.29 mg/L respectively (Peter Barratt, Anglian Water, pers. comm.). This represents an annual TN of 738 kg and TP of 28 kg.

Zebra mussel growth rates can be very fast. For example, monitoring plates deployed at Ardleigh Reservoir (Suffolk, UK) in July 2006 and resurveyed in January 2007 were fouled by zebra mussels attaining a maximum length of 15 mm and a density of up to 40,000 m⁻² (D. Aldridge, unpublished data). A full 12 month’s growth in UK lowland reservoirs results in a mean length of approximately 20 mm (B. Holden, Anglian Water, pers. comm.). Growth rates and potential biomass varies at different depths and zebra mussels will not typically settle at locations of <1 m depth due to the harmful effects of UV (Claudi and Mackie, 1994). In this example we will assume growth on attachment structures placed at a depth of 1–4 m, mean length of 20 mm and mean density of 20,000 m⁻². We will assume the total N and P content of mussels to be that reported by Goedkoop et al. (2011) of 100.9 ± 1.5 mg N g⁻¹ DW and 9.3 ± 0.2 mg P g⁻¹ DW. The dry mass of a 20 mm zebra mussel can be estimated at 0.02 g (Kryger and Riisgard, 1988).

If a mussel farm was installed, with vertical ropes 3 m long and fouling on all sides, assuming these ropes were spaced 1 m apart on the horizontal supporting rope, 1 m linear length and fouling on all sides, assuming these ropes were spaced 1 m apart on the horizontal supporting rope, 1 m linear length could yield 3 × 2 × 20,000 × 0.02 × 100.9 = 2,421,60 mg TN = 0.24 kg TN; and 3 × 2 × 20,000 × 0.02 × 9.4 = 22,560 mg TP = 0.02 kg TP. Therefore, to strip the entire annual budget of N from the water at Grafham would require a farm of 3075 m linear length and to strip the P would require a length of 1400 m.

While the calculations provided are indicative for the potential role that zebra mussel cultivation could have on N and P budgets in a reservoir, they come with some caveats. First, they assume equal mussel growth and densities across all surfaces and second, they assume even mixing of water. A ‘Smartfarm’ rig would be quite an expensive option, although it would be long-lasting and potentially incur lower harvesting costs in the long term. The same growth could also be achieved using a simple long line system of ropes hanging vertically in the water. The pros and cons of these two types of system would have to be weighed up on a case-by-case basis. For example, in a very large reservoir, where cultivation and harvesting were expected to be carried out over many years, a Smartfarm may be more suitable. These more sturdy structures could also be moved around reservoirs according to need, and to prevent the creation of anoxic conditions in the sediment (Newell, 2004). Several smaller rigs placed around a reservoir to maximise water flow past the mussels, and minimise aesthetic concerns may be an effective option.

6. Risks

While the full scale deployment of a biofilter cultivation system in reservoirs has considerable theoretical appeal, it is also pertinent to consider any potential risks and how these might be mitigated.

6.1. Public perception

The public perception of encouraging species which are known to be ecological and economic pests, such as zebra mussels, may need to be managed. Where cultivation of zebra mussels has been encouraged in other European countries (e.g. The Netherlands, Germany) there have been no reported public concerns. It is important to emphasise (to both scientists and the public) that we would not advocate the introduction of zebra mussels for water quality management, but rather propose that we consider embracing their positive attributes in systems where they are already established.

6.2. Biofouling

Zebra mussels are known to be prolific biofoulers (Clarke, 1952; Claudi and Mackie, 1994; Elliott et al., 2001; Higgins and Vander Zanden, 2010), and it is estimated that the UK water industry spends >£0.5 m per year removing zebra mussel biomass from fouled works (Oreska and Aldridge, 2011). Consequently, much research is focused on eradication from their invaded range and especially within drinking water and power plants (e.g. Aldridge et al., 2006). By encouraging the growth of zebra mussels within a potable supply reservoir it is necessary to consider whether this would increase the level of fouling within the raw water supply to the works. To a large extent, this depends on what proportion of the total zebra mussel biomass within the reservoir is associated with the rigs. It is likely that in most reservoirs the rigs would only generate a small source of mussel veliger larvae because mussels will be widespread across the reservoir bed on dam walls, pontoons, and other hard structures. There is some uncertainty within the literature as to whether increased propague pressure even correlates to fouling of structures. Kovalak et al. (1993) visited 10 power plants located around Lake Huron and Lake Erie in the US, and found the greatest amount of fouling at relatively low lake mussel densities. They attributed this to differences in water flow and the
effects of crowding and reduced food supply within the pipes. Horvath and Lamberti (1999) recorded the survival of zebra mussel veligers and found that they are highly susceptible to damage by physical forces (e.g. shear) and therefore, mortality in turbulent streams such as those in pipeline intakes could be more important in limiting population density than propague pressure. It is logical to assume that pipes and other structures within a water works will have a carrying capacity for zebra mussels (i.e. space for attachment and amount of available food flowing past in the water), irrespective of the available veligers from the reservoir.

As well as fouling hard structures, zebra mussels are well known biofoulers of native species of mussel (unionids). Zebra mussels attach directly to native mussels, competing for food, reducing body condition and causing the underlying unionids to sink into the mud (Baker and Hornbach, 1997; Sousa et al., 2011). In the US, whole populations of unionids were extirpated from Lakes Erie and St. Clair within 2–3 years of the zebra mussel invasion (Schloesser et al., 1996). This is a serious ecological impact of zebra mussels, especially as unionids are in decline worldwide (Bogan, 1993). It is, however, unlikely that encouragement of zebra mussels in a reservoir would be viewed as a threat to the conservation of unionid mussels. In Europe, the unionid species of conservation importance (e.g. *Margaritifera margaritifera*, *Pseudanodonta complanata*, *Unio crassus*) are not associated with reservoir habitats (Killeen et al., 2004). Unionid species of greatest conservation concern in North America are also typically riverine, and Bogan (1993) cites the damming of rivers as the main event in their decline, as it resulted in the local loss of the mussels’ specific host fish. In addition, if zebra mussels are already present in the reservoir, the impacts of zebra mussel fouling on unionids may not be worsened by the encouragement of more zebra mussels on artificial substrates. Of greater concern might be the possible effect of increasing zebra mussel propague pressure where rivers downstream of the reservoir do still contain important unionid populations. This risk would need to be assessed on a site-by-site basis.

6.3. The risk of increasing propague pressure

The invasive success of zebra mussels is partly attributed to the large number of veliger larvae produced (up to 1 million per individual per year; Maclsaac et al., 1992) which can remain in the water column for up to 33 days before settling (Stanczykowska, 1977). Their spread can be facilitated both by natural processes (e.g. downstream in rivers or attached to other animals) and through human-mediated transport, such as within ballast water, recreational boats and by fishermen (Strayer, 2009).

While we do not advocate the intentional introduction of zebra mussels to new localities for cultivation, if a larger population is encouraged this increases the number of veligers that can be generated. We must therefore consider the possibility that this extra propague pressure could increase the chance of establishment in nearby waterbodies where they were not previously present.

In considering the risk of increased propague pressure, it is important to consider the type of reservoir where cultivation would be taking place. For example, many reservoirs in the UK are man-made impoundments, which draw water in from a river system, but which may not have any outflow. The risk of spreading zebra mussels would therefore be small compared with the American Great Lakes, where the many interconnected waterways make rapid colonisation possible (Johnson and Carlton, 1996). Reservoirs within dammed rivers may serve as a major source of veligers to downstream sites and may be unsuitable for encouragement of zebra mussels. Reservoirs that are subject to high levels of recreational activities such as boating and angling are likely to have security measures that would negate the additional risk posed by an increase in veliger abundance. Both of these situations are likely to arise when considering reservoirs in the USA, as dammed river reservoirs predominate, particularly in the southern and south-western part of the country. In the USA, the spread of zebra mussels from their original discovery in the Great Lakes can often be tracked along navigable rivers where recreational boating takes place (Johnson and Carlton, 1996). These factors may make many USA reservoirs less suitable for zebra mussel cultivation than those commonly found in Europe. However the key to this issue is to consider each reservoir on a case-by-case basis and conduct an assessment of the risk.

6.4. Changes in phytoplankton composition

With their large filtering capacity and wide dietary preferences, it is no surprise that zebra mussels can drive a change in phytoplankton biomass and community composition upon entering a system (MacIsaac, 1996). Selective removal of algae and rejection of cyanobacteria from the water is one route by which mussel presence could enhance the abundance of toxic cyanobacteria, such as *Microcystis aeruginosa*. Zebra mussels have been shown to graze and ingest toxic strains of cyanobacteria; both single celled and as colonies (Dionisio Pires and Van Donk, 2002; Dionisio Pires et al., 2005a,b). There is some disagreement in the literature about whether cyanobacteria is preferentially rejected at the feeding stage and/or as pseudofaeces. Vanderploeg et al. (2001) showed rejection of colonial groups of *M. aeruginosa* and preferential ingestion of green algae. However Dionisio Pires and Van Donk (2002) reported the opposite for single celled cyanobacteria species. Dionisio Pires et al. (2005a) went further and looked at both colony-forming and filamentous cyanobacteria, and again concluded that zebra mussels are capable of both grazing and ingesting these two forms and may thus reduce the abundance of harmful cyanobacteria in reservoir systems.

Real life examples of zebra mussel invasion have been associated with markedly different changes in cyanobacterial abundance. In Lake IJsselmeer in The Netherlands, cyanobacteria were more common in areas of the lake with low zebra mussel density, and the mussels are actively used as a tool for removal of cyanobacterial blooms (Dionisio Pires et al., 2005b). Conversely, in the US zebra mussels have generally been blamed for strengthening the dominance of cyanobacteria upon invasion, for example in Lake Erie, Lake Huron and Saginaw Bay (Vanderploeg et al., 2001). The Hudson River, however, showed a 778-fold decrease in cyanobacterial density post-zebra mussel invasion (Smith et al., 1998). Subsequent years saw recovery of cyanobacteria, but high biomass
tended to be explained not by the presence and filtering activities of zebra mussels, but by water temperature (Fernald et al., 2007).

A cause for the difference in response of cyanobacteria to zebra mussel invasions has been attributed to not only to temperature, but also light intensity and nutrient ratios (Vanderploeg et al., 2001). Zebra mussels are known to excrete high amounts of phosphate, therefore creating a low N:P ratio (Bykova et al., 2006). Cyanobacteria can then thrive in this environment as they can store more nitrogen than other phytoplankton (Wojtal-Frankiewicz et al., 2010). Lakes that are poor in P seem therefore to be more vulnerable to the effects of zebra mussels on driving cyanobacterial change. Raikow et al. (2004) gave a critical level of 25 μg P L⁻¹, below which zebra mussels would positively influence cyanobacteria. Lake IJssemeer has concentrations between 50 and 100 μg P L⁻¹ (Dionisio Pires et al., 2005a), which may explain why in this instance zebra mussels tend to lead to reduced cyanobacteria and algae through their filtration activity. The baseline N:P ratios could therefore be a critical factor in deciding whether or not it would be appropriate to initiate a cultivation programme in a given reservoir.

Notably, to date no UK reservoir has seen marked increases in cyanobacteria which can be attributed to the arrival and establishment of zebra mussels (M. Chipp, Thames Water; B. Holden, Anglian Water; pers. comm.). Data available for two UK reservoirs (Pitsford in Northamptonshire and Arbleigh in Essex) show mean P values between May and September 2011 of 51 and 60 μg P L⁻¹ respectively (A. Bossmith, Anglian Water; pers. comm.), which is well above the critical level described by Raikow et al. (2004). It therefore seems that zebra mussel enhancement in UK reservoirs is unlikely to result in elevated cyanobacterial problems.

The large filtration capacity of bivalve molluscs means that they often bioaccumulate toxins which can biomagnify up the food chain. In North American lakes with high heavy metal loadings molluscivorous birds that feed on zebra mussels have experienced reduced reproductive success due to metal poisoning (Maclsaac, 1996). Potable water supplies will not contain heavy metal concentrations of concern and fortunately zebra mussels are able to detoxify cyanotoxins. Pflugmacher et al. (1998) found the existence of a microcystin-LR glutathione conjugate inside zebra mussels. It appeared to be the first step in the detoxification process of cyanobacterial toxins after ingestion. Dionisio Pires et al. (2004) could not find this conjugate in mussels fed M. aeruginosa. However, they did notice that after assimilation levels of microcystin decreased rapidly and after three weeks only very low amounts were detectable. Zebra mussels have become important food for molluscivorous birds that feed on zebra mussels before they can cause harm to wildfowl.

6.5. Managing harvested mussel biomass

The relatively small and irregular supply of zebra mussel material may make the identification of a dependable market difficult. A more consistent supply is likely if the technique is rolled out to a wider range of sites, and if several water companies take the idea on board. Large quantities of zebra mussels are dealt with already by water companies when they remove fouling mussels from pipes and tanks, therefore disposal routes already exist. The predominant disposal route is to landfill (M. Chipp, Thames Water, pers. comm.) but more beneficial uses are being considered. One attractive route of disposal would be via existing on-site digesters. An important issue that may restrict the use of harvested material could be concentrations of heavy metals, as zebra mussels accumulate toxins from their surrounding environment (Sordyl and Gerken, 2002), and this could prevent use in, for example, poultry feed. Reenders and Bij de Vaate (1992) noted bioaccumulation of toxicants, especially organic pollutants and petroleum hydrocarbons in zebra mussel shell, tissue, and pseudofaeces in Lake Volkerak-Zoommeer, The Netherlands. However the pollutant level of reservoirs is likely to be low. Doherty et al. (1993) tested zebra mussels from two locations on Lake Erie for leachable contaminants and the mussels would not be classified as hazardous waste under US or Canadian law. Kreis et al. (1994) came to similar conclusions.

7. Conclusions

It is proposed in this paper that zebra mussels could provide part of a solution for some eutrophic reservoirs, simply by being encouraged to increase in biomass where they already occur, and harvesting at suitable intervals to remove nutrients permanently. What emerges from this review is that the risks and benefits need to be carefully considered and assessed on a site-by-site basis in order for this method to be used successfully and responsibly. Any decision to encourage mussels should be taken after discussion and appraisal with the relevant authorities, which may vary on a regional, national and international basis, depending on the perceived risks of the encouragement of an invasive species. For example, whole regions of the USA may be unsuitable for this cultivation system because dammed reservoirs are predominant, whereas in other localities the decision may depend upon the nitrogen and phosphorus ratios of a particular site and an assessment of the potential for mussel-driven cyanobacterial blooms. The risks of this species can be great, but the benefits to a potable water supply reservoir of having increased water clarity may be considerable. Moreover, in alga-dominated systems zebra mussels could provide ecological improvements by pushing the system towards a clear water state. As zebra mussels would not be released into completely new environments, water companies would likely already be familiar with the risks as a result of the first ‘natural’ invasion.

Our review identifies a number of knowledge gaps whose consideration may improve our ability to make informed decisions on the utility of zebra mussel enhancement. Many case studies exist for the use of mussels as biofilters, although they are largely pilot studies, and few examples of freshwater bivalves being used on a large scale to improve water quality have been published in the last ten years. There is also a lack of studies into designs for effective cultivation rigs (although see Lindahl and Kollberg, 2008; Paalvast et al., 2012). Further research is required beyond the pilot study level to understand the true potential of zebra mussel cultivation for
reservoir management. There remain knowledge gaps that preclude us from making reliable predictions about an enhanced zebra mussel community might alter the ecology of a particular reservoir. Despite the many studies, few generalities exist on the ecosystem-level effects of zebra mussels.

A factor that may encourage greater interest in cultivation of zebra mussels in reservoirs is the identification of an economically attractive disposal route. A significant gap in our knowledge relates to the possible end use of zebra mussel material which would be removed should zebra mussels be harvested regularly from these reservoirs. The existing default option is landfill, and such disposal carries costs. However, there are some solutions which have the potential to make mussel disposal cost-neutral or even revenue-generating, as well as offering environmental benefits. The first of these is their use as the protein component of poultry diets. This has been tried, with much success, with blue mussels; *M. edulis* (Lindahl and Kollberg, 2008; Jönsson et al., 2011). The second option is to use mussels as a plant fertiliser. Again this has been trialled with blue mussels, and farmers reported improved soil structure, pH and crop growth (Lindahl et al., 2005). Full scale field trials are needed to better understand the potential benefits offered to reservoir management from zebra mussel cultivation.

Fortunately, if problems were to arise following a large-scale cultivation programme, rigs used for biological manipulation could easily be removed from reservoirs, and conditions would be expected to quickly return to baseline levels. Biological manipulation using non-native filter feeders is not suggested as an alternative to reducing nutrient inputs into freshwaters, but it offers considerable promise to be used alongside existing methodologies where the non-natives already exist, and is an attractive alternative to the use of harmful chemicals and other ineffective and expensive options.

---

**REFERENCES**


