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Research article

Inverting nutrient fluxes across the land-water interface – Exploring the potential of zebra mussel (*Dreissena polymorpha*) farming

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ABSTRACT

We studied the potential of zebra mussel farming for nutrient retention in a eutrophic lake. Duplicate experimental long-line cultivation units were deployed and mussel growth and nutrient retention were quantified after 28 months. Mussels grew well at shallow water depth (<3 m) and our 625 m^2 (lake area) experimental units produced 507 and 730 kg dry biomass, respectively, of which 94% were shells. These yields corresponded to an average retention of 92.7 ± 23.1 kg C, 6.1 ± 0.68 kg N, and 0.43 ± 0.04 kg P retention, or 742 kg C, 49 kg N, and 3.5 kg P for a full-size (0.5 ha) mussel farm. We estimate that concentrating the long-lines to a depth of 2.5 m would probably have doubled these yields, based on the differences in mussel growth among depths. We further estimate that a full-size cultivation unit (0.5 ha) thus could compensate for the annual total-P run-off from 23 ha, or the biologically available P from approximately 49 ha of agricultural soils. As traditional measures have proven insufficient, decision-makers need to facilitate novel approaches to mitigate the negative effects of cultural eutrophication. We envision that zebra mussel farming, within their invaded range, provides a promising approach to invert nutrient losses in lakes and coastal lagoons.

1. Introduction

Cultural eutrophication has long been, and still is, one of the major threats to surface water quality (EEA, 2018), resulting in severe algal blooms, deep water hypoxia/anoxia, and fish kills (Smith et al., 1999; Conley et al., 2009). Growing human populations and demands for increased food production continue to increase nutrient stress on ecosystems. Increased nutrient run-off due to agricultural land use and point source pollution is still contributing to the eutrophication of inland and coastal waters, despite efficient nutrient reductions in sewage treatment plants. In recent years, investments in urban blue-green infrastructure have been made to avoid stormwater events and nutrient run-off, while artificial wetlands have been constructed to trap nutrients in agricultural landscapes (Uusi-Kämppä et al., 2000; Mendes et al., 2018). Also, in-lake remediation practices such as biomanipulations (Shapiro and Wright, 1984; Hansson et al., 1998) and the aluminum treatment of surface sediments (e.g. Huser et al., 2016; Rydin et al., 2017) have been deployed to reduce phosphorus regeneration and re-occurring algal blooms, and ultimately to improve water quality. Although these measures contribute to decreases in external and internal nutrient loads, the long-term control or remediation of eutrophication has been precarious (Schindler 2012), calling for additional and innovative approaches.

In recent years marine mussel cultivation has shown a promising nature-based approach for the remediation of eutrophication, being unique by inverting the otherwise unidirectional transport of nutrients from land to water. In coastal environments the farming of blue mussels (*Mytilus edulis*) has successfully compensated for the nutrient discharge in coastal regions (Lindahl et al., 2005). Van der Schatte Olivier et al. (2018) estimated that cultivated bivalves globally remove 49 000 tons of nitrogen (N) and 6000 tons of phosphorus (P) per year from coastal marine areas, and approximated the economic value of this ecosystem service (primarily food production) to 1.20 billion USD. Beside for human consumption, harvested mussels have also been processed (Lindahl 2013) and used as a high-quality substitute for fish meal in feed for poultry farming (Jönsson et al., 2011) or as an organic fertilizer (Spångberg et al., 2013), resulting in the efficient shunting of nutrients back to the agricultural sector. Lindahl et al. (2005) argue that the benefits of mussel farming for society are apparent, while negative side effects for the environment are minor and fully acceptable.

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In freshwaters, the zebra mussel (*Dreissena polymorpha*) could be a suitable species for similar nutrient remediation measures (e.g. Schernewski et al., 2019). Similar to many marine mussel species, but contrary to most freshwater species, zebra mussels have free-living veliger larvae that, together with the species' wide environmental tolerance (Hallstan et al., 2010 and references therein), contribute to their high dispersal capacity and invasive behavior. Invasions by zebra mussels have dramatically altered the ecosystems of the Great Laurentian lakes (Nalepa et al., 1998; Mills et al., 2003), as mussels imply a top-down mechanism on pelagic primary production (Caraco et al., 2006) and strengthen the link between phytoplankton and benthic secondary production (Connelly et al., 2007). Zebra mussel invasions have also caused clogging problems in the water-intake systems of industrial and drinking-water plants, primarily in the USA (MacIsaac, 1996). In Europe, zebra mussels have since long dispersed to most of the large rivers and many lakes (Strayer 1991), as well as to coastal lagoons (Orlova et al., 2006), but the negative impacts of zebra mussel invasions have been less extensive in Europe than in North America. Instead, the establishment of zebra mussels, and subsequent retention of nutrients, has likely counteracted the effects of cultural eutrophication in many lakes and rivers and resulted in increased water clarity (Stoeckman and Garton 2011, Smit et al., 1993). Indeed, Dzialowski and Jessie (2009) showed that zebra mussels can greatly reduce algal biomass and mask eutrophication effects of nutrient pulses up to 150 mg P/L on algal biomass. Several studies have therefore addressed the potential use of zebra mussels in water quality remediation (e.g. Elliott et al., 2008; McLaughlan and Aldredge, 2013; Schernewski et al., 2019), while a single study has done small-scale tests (Friedland et al., 2019). These studies stress the potential of zebra mussel cultivation for the long-term improvement of water quality and the sustainable production of protein-rich feed within their invaded range, while also considering the potential ecological risks and benefits.

To our knowledge, this is the first study that tests the suitability and capacity of zebra mussel cultivation as an in-lake remediation measure that inverts the otherwise unidirectional flow of nutrients from land to inland waters. More specifically, we deployed two experimental long-line cultivation units in Lake Ekoln, a eutrophic lake where zebra mussels have been an integral part of the lake ecosystem since the early 20th century (Josefsson and Andersson 2001). We deployed these units during 2.5 years and studied biomass accumulation and retention of carbon (C), nitrogen (N), and phosphorus (P) by cultivated mussels at different depths. We then quantified the relative role of N and P retention by mussel cultivation in the nutrient budget of the lake, and compared with major nutrient loads to the lake. Lastly, we conjectured how (and where) zebra mussel cultures can supplement on-land remediation practices to mitigate cultural eutrophication of lakes and coastal lagoons and contribute to improved water quality and sustainable feed production.

2. Materials and methods

2.1. Study site

Lake Ekoln is the northernmost, relatively isolated basin of Lake Mälaren, Sweden's third largest lake. Lake Ekoln has a surface area of 29.8 km^2, a mean depth of 15.4 m, a maximum depth of 50 m, and a water renewal time of less than one year. Lake Ekoln has long been a recipient of point source pollution from the Uppsala sewage treatment plant (serving the city's approximately 200 000 inhabitants), as well as from diffuse sources originating from agricultural land use (c. 40% of total nutrient loads) and single households (also c. 40%) in the catchment. The lake is well buffered (alkalinity 2.2 meq/L, pH 7.6–8.0) and eutrophic (surface water Chl. a 6.0–8.6 μg/L), with mean annual total-N concentrations exceeding 1600 μg/L and mean annual total-P ranging 36–46 μg/L. The lake usually stratifies down to 6–8 m during summer. Phytoplankton communities are commonly dominated by diatoms in spring and by cyanobacteria (predominated by *Microcystis aeruginosa*) during calm summer conditions. Zebra mussels were unintentionally introduced to Lake Ekoln as early as the 1920s (Josefsson and Andersson 2001) and have developed high population densities (Goedkoop et al., 2011). From Lake Ekoln zebra mussels have dispersed south to other hard-water basins of north-eastern Lake Mälaren (down to Stockholm), while further dispersal is limited by the soft water of the central and western basins of Lake Mälaren and by the brackish water of the Baltic Sea (Hallstan et al., 2010).

2.2. Larval settlement rates

Settlement rates of veliger larvae were quantified prior to the launching of our cultivation units by deploying a submersed buoy with four horizontal arms to which horizontally placed non-glazed tiles (15 × 15 cm) were attached. This construction was placed at 2 m depth (i.e. well below maximum ice thickness) in mid-lake in early July, which is the time of spawning for zebra mussels, and retained in early spring the following year. Upon collection the tiles were transferred to vials containing 70% ethanol, and transported to the laboratory where larvae were counted, and shell length measured using a digital caliper.

2.3. Mussel cultivation

Two experimental cultivation units of long-line type (Scanfjord, surface area on the lake 12.5 × 50 m) were put in place in Lake Ekoln in mid-June, one in the southern end of the lake (59.732 N, 17.601 E) and the other off the eastern shores (59.749 N, 17.632 E). Sites were selected to (i) have good water exchange and a water depth of at least 10 m, (ii) not interfere with borders of natural reserves (that partly include the lake), and (iii) not hinder boat traffic and recreational fishery. Necessary permits were obtained from regional authorities and landowners. Each of the two units had 6000 m of long-lines (4.5-cm wide bands), corresponding to a total surface of 540 m^2 per unit. Unfortunately, the southern unit was sabotaged during the first summer: its anchor lines had been cut and the entire unit had drifted a few hundred meters until it hit the lake floor off the southern shore at a water depth of some 5 m. Shortly after the sabotage the unit was towed back to its original position and re-anchored with steel wiring.

Mussels were harvested after 861 days (south unit) and 862 days (north unit) of incubation in the lake. Long-lines were taken up by a hydraulic crane and mussels were removed with metal blades scraping both sides of the long-lines and collected in plastic containers. For each unit, seven subsamples of 0.5-m line stretches were collected in each of 10 half-meter depth intervals down to 5.0 m (i.e. 0–0.5 m, 0.5–1.0 m, etc. down to 5.0 m). These half-meter subsamples were immediately packed in pre-marked plastic bags, stored cool, and frozen (−20 °C) on the same day. These subsamples were used to estimate the accumulated mussel biomass for each depth interval and for testing for differences in biomass, C-, N-, and P-concentrations of mussels among depths and between units.

In the laboratory, mussels were removed from the frozen half-meter long-line subsamples. Particular care was taken to prevent mussels from thawing and losing liquid during handling. Length of individual mussels (largest shell length) from the northern unit were measured with a digital caliper and their soft tissue and shells separated with a scalpel. Mussels were then again stored at −20 °C individually (northern unit) or as a composite sample (southern unit). Pooled samples of three mussel size classes i.e. large (19–26 mm shell length), medium (13–19 mm) and small (≤13 mm) for the northern cultivation unit were analyzed for shell and soft tissue C and N using an elemental analyzer (Costech ECS 4010), as well as for P using molybdate reactive P after ignition of the sample at 550 °C (Murphy and Riley, 1962; Andersson, 1976). Individually frozen mussels from the northern unit were used to establish relationships between total fresh and dry biomass of mussels (i.e. shell and soft tissue), and between total dry biomass and soft-tissue dry biomass. Relationships were established by linear regression analysis for use in further

calculations:

relationship between total (shell plus soft tissue) dry and fresh biomass of individual mussels ($R^2 = 0.951$, n = 536),

$$\text{Total dry biomass} = 0.43 \times \text{total fresh biomass} \quad (1)$$

relationship between shell and soft tissue dry biomass of individual mussels ($R^2 = 0.886$, n = 195),

$$\text{Soft tissue dry biomass} = 0.06 \times \text{shell dry biomass} \quad (2)$$

relationship between total (shell plus soft tissue) dry biomass and soft tissue dry biomass of individual mussels ($R^2 = 0.899$, n = 195).

$$\text{Soft tissue dry biomass} = 0.06 \times \text{total dry biomass} \quad (3)$$

These relationships were combined with C, N, and P concentrations of mussels to calculate their total biomass (dry weight, used throughout), as well as C and nutrient retention by the cultivation units. Upscaling was done using the total surface of cultivation bands to obtain total yield (on 540 m^2 cultivation bands) which then was expressed as nutrient retention rates of cultivations per hectare of lake area and year.

2.4. Statistical analysis

We used one-way ANOVAs to test for effects of water depth intervals on, i) total (shell and soft tissue) mussel biomass, ii) soft tissue biomass and, iii) shell biomass on mussel cultivation bands in both northern and southern cultivation units. Moreover, one-way ANOVAs were run to analyze the effects of mussel size on i) N and P in soft tissue, ii) N in shell, iii) C:N in shell and soft tissue, and iv) differences in the relative abundances of mussels in different size classes (northern unit only). Tukey pairwise comparisons were made to check for size- and depth-specific differences among mussels. For both cultivation units, C and nutrient concentrations were compared between the depth intervals 0.5–1.0 m (surface) and 4.5–5.0 m (deepest interval) using independent *t*-tests. Biomass data for total (soft tissue plus shell), soft tissue and shell was log(x+1)-transformed to meet the assumption of normality. All statistical analyses were performed using IBM-SPSS Statistics for Macintosh, Version 22.0 (Armonk, NY: IBM Corp).

3. Results

3.1. Mussel growth

Larval settling rates on tiles were 3822 ± 292 ind/m^2 (mean ± standard error, used throughout) and showed two distinct size classes with shell size ranging 5–10 mm and ≤2 mm, respectively. These data also showed that mussels of the larger size class reached a mean size of 7.1 mm during their first warm season. Mussel larvae also settled readily on the long-lines during the first summer and grew well. At the time of harvest, peaks in total biomass (mussel shell plus soft tissue) of 175 ± 29 and 108 ± 20 g (dry biomass, used throughout) occurred at a depth of 0–0.5 m on mussel bands in the northern and southern units, respectively. Total mussel biomass (shell and soft tissue) declined rapidly to less than 100 g at depth intervals exceeding 2.0 m (Fig. 1A). The northern unit had slightly higher mean mussel biomass in depth intervals down to 2.0 m than the southern unit. One-way ANOVA showed significant effects of water depth on total biomass, soft tissue biomass, and shell biomass for both cultivation units (Table 1). The effects were largely due to higher mussel growth at shallower depth intervals. For example, in the northern unit, total mussel biomass at depth intervals down to 1.5 m was on average more than 20 times higher than that between 2.0 and 5.0 m depth ($p < 0.05$, Tukey's pairwise test) (Fig. 1A). There was no difference in total mussel biomass at depths intervals exceeding 2.0 m. Also in the southern unit, total mussel biomass at 0–0.5 m and 1.0–1.5 m depths was on average more than 25 times

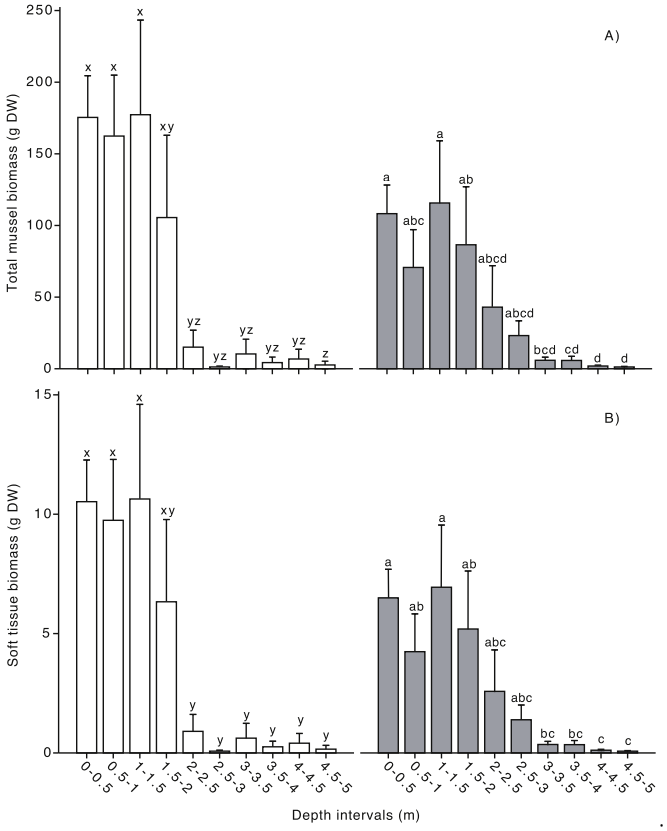

Fig. 1. Total mussel biomass (soft tissue and shell, mean ± SE, as g DW) (A), as well as soft tissue biomass (mean ± SE, as g DW) (B) for different depth intervals of the northern (white bars) and the southern (grey bars) cultivation units. Bars that have no letters in common indicate significant differences ($p < 0.05$) by Tukey's pairwise comparisons.

higher than at 3.0–5.0 m. Mean total biomass for both units was consistently less than 10.3 mg/g at depth intervals exceeding 3.0 m. Mussel soft tissue biomass followed a similar pattern (Fig. 1B), with substantially higher values at shallower depth intervals (<2.0 m) than at deeper intervals in the northern unit ($p < 0.05$). In the southern unit the decline in mussel and soft tissue biomass at ≥ 2 m depth was less dramatic and showed more of a gradual decline between 2.0 and 3.5 m. Among all depth intervals of the northern unit, intermediate-sized mussels (13–19 mm) made up 48 ± 7.8% of total abundance and was higher than that of both small (35 ± 7.7%) and large (16 ± 4.79%) mussels. We found no effect of mussel size on shell N-concentrations, on C:N ratio of shells, and on P-concentrations in soft tissue (Table 1).

3.2. Nutrient and carbon retention by mussels

P-concentrations of mussel soft tissue ranged 8.05–8.73 g/kg and was similar among size classes in the northern unit, while the mixed size class sample for the southern unit showed slightly higher soft tissue P-concentrations (Tables 1 and 2). P-concentrations of shells were only analyzed for a mixed-size mussel sample and similar for both cultivation units. Interestingly, shell P, but not soft tissue P (*t*-tests, $p > 0.180$), varied strongly with depth and were 40% (southern unit) and 148% (northern) higher for mussels in the 0.5–1.0 m depth interval than those at 4.5–5.0 m depth (*t*-tests, $p < 0.039$). Hence, the overall mean of 8.31 ± 0.19 and 10.85 ± 0.31 gP/kg (Table 2) were used in further calculations of P-retention by mussel soft tissue in the northern and southern units, respectively.

N-concentrations of soft tissue were highest for small mussels (<13 mm) with 104.58 ± 0.79 g/kg, and then declined by 5% and 11% ($p <$

Table 1
One-way ANOVA results for effects of depth (depth intervals) on mussel dry biomass for the northern (North) and southern (South) cultivation units and of mussel size on C, N, and P tissue concentrations for the northern unit (per unit of dry weight). Note that no tests were run between the two units, as the southern unit had been sabotaged at an early stage (see text for details). nd denotes "not determined".

Factor	Variable	Unit	TSS	MSS	df	F	Sign.
Depth (m)	Total biomass (g)	North	62.22	5.00	9, 52	11.52	***
		South	32.51	2.44	9, 50	8.48	***
	Soft tissue biomass (g)	North	15.31	1.19	9, 52	10.57	***
		South	8.77	0.62	9, 50	7.16	***
	Shell biomass (g)	North	60.80	4.89	9, 52	11.54	***
		South	31.96	2.40	9, 50	8.51	***
Mussel size (mm)	Soft tissue P (g kg^{-1})	North	4.81	0.94	2, 9	1.27	ns
		South	nd	nd	nd	nd	
	Soft tissue N (g kg^{-1})	North	300,01	126.83	2, 11	23.61	***
		South	nd	nd	nd	nd	
	Shell N (g kg^{-1})	North	1.51	0.24	2, 11	1.17	ns
		South	nd	nd	nd	nd	
	Soft tissue C:N	North	0.38	0.15	2, 11	18.54	***
		South	nd	nd	nd	nd	
	Shell C:N	North	223.94	41	2, 11	1.60	ns
		South	nd	nd	nd	nd	

*** denotes $p < 0.001$, **$p < 0.01$, *$p < 0.05$, **and** ns **"**not significant.

Table 2
Concentrations of C, N, and P (mean ± SE, as g/kg DW) in mussel soft tissue and shells for different mussel size classes (northern unit, except shell-P) and for pooled mussel samples (southern unit). *nd denotes "not determined.*

Tissue	Size class (mm)	Unit	C	N	P
Soft tissue	≤13	North	467.16 ± 1.44	104.58 ± 0.79	8.15 ± 0.45
	13–19	North	461.60 ± 4.85	99.56 ± 1.30	8.73 ± 0.16
	19–26	North	454.57 ± 3.98	94.12 ± 0.91	8.05 ± 0.29
	9–26	South	476.50 ± 9.60	114.33 ± 6.18	10.85 ± 0.31
Shell	≤13	North	130.86 ± 0.37	3.22 ± 0.12	nd
	13–19	North	128.92 ± 1.70	3.24 ± 0.12	nd
	19–26	North	130.40 ± 0.26	2.92 ± 0.11	nd
	9–26	North	nd	nd	0.12 ± 0.02
	9–26	South	129.93 ± 3.75	4.53 ± 0.61	0.13 ± 0.01

0.05), respectively for intermediate- (13–19 mm) and large-sized (20–26 mm) mussels (Tables 1 and 2). We found no effect of mussel size on shell-N in the northern unit. The mixed-size class sample from the southern unit also had higher N-concentrations in both soft tissue and shells than those from the northern unit, likely due to a large share of smaller mussels. N-concentrations shells and soft tissue in the northern unit, as well as that of shells from the southern unit were not affected by depth (*t*-tests, $p \geq 0.060$). Soft tissue samples from the southern unit, however were 9% richer in N at 4.5–5.0 m than at 0.5–1.0 m depth (*t*-test, $p = 0.019$). The overall mean of 3.14 ± 0.09 (northern) and 4.53 ± 0.61 (southern) gN/kg were used in further calculations of N-retention by shells (Table 2). Similar to the effect on soft tissue N-concentrations, mussel size also affected the C:N ratio (by weight) of soft tissue (Table 1), averaging 4.50 for the smallest, 4.63 for the intermediate, and 4.83 for the largest size class (data not shown). No effect of mussel size on shell C:N was found.

Soft tissue C did not differ between mussels from shallow (0.5–1.0 m) and deep (4.5–5.0 m) depth intervals in both cultivation units, while C-concentrations of shells were slightly (1.2%) higher in the shallow depth interval only in the northern unit (*t*-test, $p = 0.017$). The overall mean of 461.6 ± 2.4 (northern) and 477.0 ± 9.6 gC/kg (southern) were used in further calculations of soft tissue C-retention.

Upscaling by combining harvested biomass and mussel C, N, and P concentrations showed that the total sequestered N and P by our experimental cultivation units corresponded to 5.6–6.5 kg N and 0.40–0.46 kg P during 28 months (Table 3), or 38.4–44.8 kgN/ha.y and 2.7–4.2 kgP/ha.y. The cultivation units also were a large sink for carbon, fixing 76–109 kg C over the 28 months (Table 3), of which the vast majority (some 75%) was in shells, which also made up 94% of harvested biomass. Overall, shells corresponded to 74 ± 0.1% of C, 35 ± 0,3% of N, and 16 ± 0.1% of P sequestered by mussels, respectively.

3.3. Economic analysis

The total investment costs for our experimental cultivation units were 59 300 € (Table 4), of which the costs for mounting and deployment, i.e. 24 200 €, were unexpectedly high as this was a labor-intensive process that also included the rental of a towing boat and divers. Once in place, however, the cultivation units can be used multiple times/years, resulting in annual investment costs of 7680 €. Operational costs were strongly dominated by labor-intensive harvest, which to a large extent was done manually. The average cost for harvesting the mussels was 7350 €/y over the two years. Note that this analysis only includes costs and not income from mussel meat (and shells), nor any societal refund for delivered ecosystem services.

4. Discussion

Table 3
Biomass and yield of C, N, and P (as kg) by whole mussels, shell, and soft tissue (as kg dry biomass) for the northern (North) and southern (South) cultivation units after 28 months of growth in Lake Ekoln.

Variable	Unit	Whole mussels	Shells	Soft tissue
Biomass (kg)	North	730	686	43.8
	South	507	477	30.4
C (kg)	North	109.1	81.8	27.3
	South	76.4	56.8	19.6
N (kg)	North	6.5	1.9	4.6
	South	5.6	2.0	3.6
P (kg)	North	0.46	0.09	0.37
	South	0.40	0.06	0.34

Our northern and southern experimental cultivation units produced 507 and 730 kg dry weight mussel biomass, respectively, of which 94% consisted of shell biomass. These biomass numbers correspond to production rates of 19 and 27 ton/ha.y (fresh weight), which seem low compared to the 270 ton/ha.y (fresh weight) of blue mussel yield that Lindahl et al. (2005) reported for an optimal high-salinity site at the Swedish west coast, but in the same range as the 12–40 ton/ha.y for blue mussel cultures in brackish water locations in the Baltic proper (Hedberg et al., 2018, their Table 1). Mussel yield in our small (12.5 × 50 m) experimental units corresponded to an average retention of 92.7 ± 23.1 kg C, 6.1 ± 0.68 kg N, and 0.43 ± 0.04 kg P during the 28 months that they were in place. These numbers correspond to 742 kg C, 49 kg N, and

Table 4
Economic analysis of zebra mussel cultivation, split into investment costs and operational costs in Euros.

Category	Specification	Costs (€)	Annual costs (€)
Investments costs	Purchase 2 cultivation units	25 800	
	Mounting & deployment, incl. salaries	24 200	
	Consumables	4000	
	Transport (truck rent)	700	
	Rent of boat + crane	1300	
	Other salaries	3300	
	Total	59 300	7 680[a]
Operational costs	Rent of boat with crane	4000	
	Harvest, incl. salaries	14 700	
	Mussel transport and preparation	1200	
	Total	19 900	9 950[b]
Overall total costs		79 200	17 630

[a] Annual investment cost = total investment cost*r/(1-(1 + r)$^{-T}$ where r = 0.05 (discount rate) and T = 10 technical life length plus operational costs.
[b] Cost per year calculated by dividing cost by 2 (i.e. two years from start to harvest).

3.5 kg P for a full-size (i.e. 25 × 200 m, or 0.5 ha of lake surface) mussel farm, or 3465 kg C/ha.y, 229 kgN/ha.y, and 16.4 kgP/ha.y (by lake surface area). This N-retention is in the same range as the 30–390 kgN/ha.y reported for floating wetlands by Choudhury et al. (2019). Concentrating the long-lines to a maximum depth of 2.5 m (instead of 6 m) could likely have doubled our yields, based on the differences in growth rate (and biomass accumulation) between shallow and deep depth intervals (Fig. 1). Taking this into account, an optimized, full-size zebra mussel cultivation unit could likely compensate for the annual P run-off from 23 ha of agricultural soils, assuming a net area-specific run-off of 0.29 kg P/ha.y (SMHI, 2020). Refining this calculation by assuming that 46% of total P in agricultural run-off is non-clay-associated, biologically available in the rivers entering Lake Ekoln (Persson 2001) implies that a full-size cultivation unit of 0.5 ha could compensate for the annual leakage of biologically available P from some 49 ha of agricultural soils in the catchment.

Mass balance calculations also show that a full-size zebra mussel cultivation unit (0.5 ha lake surface) could compensate for 6% of the bioavailable P (BAP) of the sewage treatment plant annual emissions (Fig. 2), using the annual sewage total-P discharge of 1700 kg and assuming bioavailable-P is 34% of total-P (Li and Brett 2015). Comparisons of nutrient pools and sources stress the predominant role of the lake's estimated mussel population of 10^7 mussels (Goedkoop et al., 2011) for the nutrient cycling of Lake Ekoln (Fig. 2). This large mussel population filters a water volume equivalent to the entire lake every 8–10 days (Goedkoop et al., 2011), thereby functioning as an efficient biofilter and contributing to the efficient biodeposition of phytoplankton. Considering that our mussel farm populations were very small compared to the *in situ* population, we could not expect any positive effects on water quality of our cultivation units. As at least 15% of mussel P is associated with shells, the accumulating spent shell deposits may also be a significant long-term sink for P due to high resistance to erosion of the aragonite mineral of the shells (Pathy and Mackie 1993). Strayer and Malcolm (2007) conclude that zebra mussels are capable of producing large amounts of spent shells (>10 kg dry mass m^{-2}) in standing and/or hard waters where shell production rates by far exceed decay rates, further enhancing P withdrawal. Although several studies have shown that dense zebra mussel populations can play a key role in the N and P retention of lakes (e.g. Goedkoop et al., 2011; Pennuto et al., 2012), the long-term C, N, *and* P-sink provided by spent shells likely is an overlooked ecosystem service provided by zebra mussels.

Depth distributions of cultivated mussels were similar to that of the *in situ* population (Goedkoop et al., 2011) which reflects that growth conditions are near-optimal in the relatively warm, phototrophic zone, and less optimal in the deeper, colder waters with temporal hypoxia. Our zebra mussel cultivations only constituted a fraction of the entire lake population (e.g. Fig. 2), and phytoplankton assemblage composition and algal blooms are still regulated primarily by lake-intrinsic factors (e.g. internal P-loading, in-lake zebra mussel population). Potential local negative effects of settling feces and pseudofeces can likely be overcome by placing farm units in large lakes and coastal lagoons with relatively short water renewal times (i.e. 1–2 years) and strong hydrodynamics. In the long run the repeated removal of N and P through

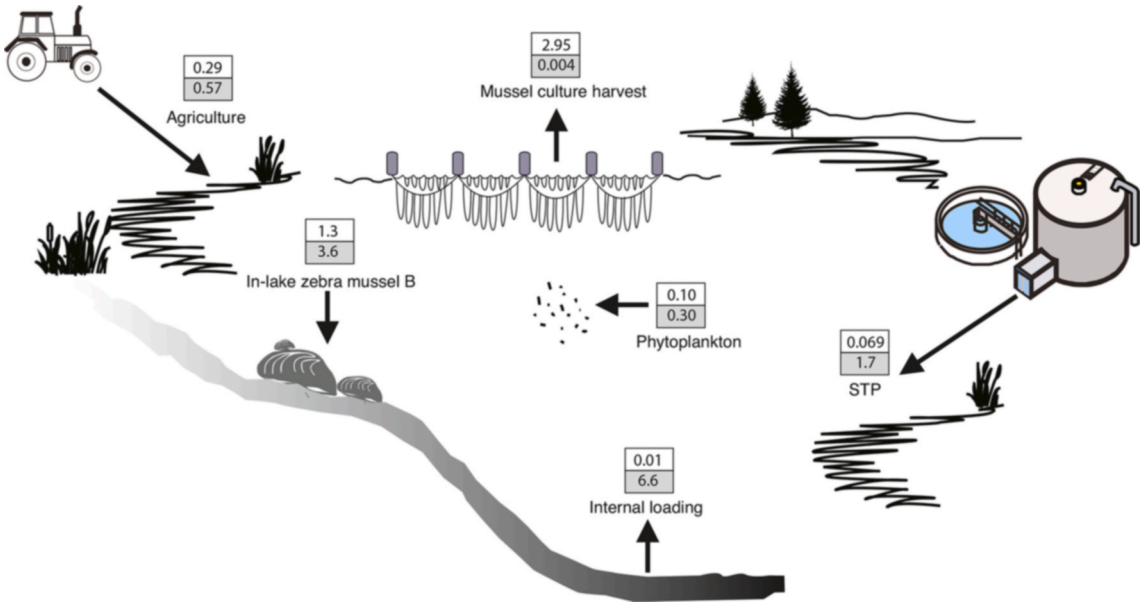

Fig. 2. Schematic overview showing mean values of major phosphorus fluxes to Lake Ekoln as kg/ha.y (white boxes) and as tons/y (grey boxes) originating from agricultural land use, the Uppsala Sewage Treatment Plant (STP), internal loading, as well as of the in-lake zebra mussel and phytoplankton populations and a full-size mussel cultivation unit (25 × 200 m). Note that calculation for P from the STP are expressed per area of urban land use in the catchment, that the internal loading estimate includes the assumption that this originates from the bottom area below 25 m (= 1000 ha according to the hypsographic curve for Lake Ekoln), while the retention in the in-lake zebra mussel is based on a distribution down to 10 m and the calculations by Goedkoop et al. (2011) with the addition of shell biomass using the mean values for Table 2.

zebra mussel yields, in concert with other remediation measures, should gradually contribute to increased water clarity and improved deep water oxygen conditions, and ultimately also remediate internal P-loading.

Our economic analysis was strongly predominated by labor-intensive work associated with the deployment of cultivation units and the harvesting of mussels (Table 4). In total these costs were 38900 €, or 49% of the total costs of the venture. We should stress that our experimental cultivation units were not designed for good economic return, nor optimizing mussel yield, but primarily to provide pioneering results for the production of mussels in a freshwater environment. Calculated costs should therefore be seen as overestimates. Much of the work was done by staff (including expensive consultants) that lacked experience of this infrastructure and type of work. Also, the long-lines technique required extensive manual labor, as weights and hooks needed to be attached. Due to these high initial costs and labor costs, the cost estimates for harvesting N and P exceeded 1600 and 23 000 €/kg, respectively. These high costs should, of course, be seen as crude overestimates and by far exceed the costs of 15–63 €/kgN and 225–900 €/kgP for blue mussel cultures in the Baltic proper reported by Gren et al. (2009). Once in place the cultivation units can be used multiple times or years, resulting in annual maintenance costs of 7680 € or less. Costs for harvest can be cut dramatically if modern, hydraulic brush-systems, operated from a vessel, can be used. This would, however, require the use of nets instead of long-lines for mussel cultivation. Costs can be further cut when water owners that invest in mussel farming get investment help, and get paid for the ecosystem services they provide (e.g. inverting nutrient fluxes from land to water and improving water quality) and the sustainable feed they produce (e.g. for poultry or fish farming) which is valued to 1.8 €/kg mussel meal (Filipelli et al., 2020). Additionally, more advanced technical solutions and larger cultivations units can contribute to further trim the costs, while an income for produced mussel meat and any refund for the delivered ecosystem service will also improve the venture's economy.

Obviously, further spread of zebra mussels should be prevented and farming is an option only within their invaded range (McLaughlan and Aldredge, 2013). Also, selected sites for farming should align with current legislation (e.g. boating routes, distance from land), have approval from land owners, and avoid popular boating and fishing sites. The invaded range of zebra mussels has for a very long time covered large parts of the European continent (Strayer 1991), including many coastal lagoons (Werner et al., 2012). In recent years compensatory mussel farming of blue mussels has been successful in coastal waters (e.g. Lindahl et al., 2005; Petersen et al., 2014). However, the farming of blue mussels in the brackish Baltic Sea (salinity 7–8‰) is not an efficient measure against eutrophication, as blue mussels grow slowly in brackish waters (Stadmark and Conley 2011; Minnhagen 2017). Zebra mussels are present in high abundances in many of the coastal lagoons of the Baltic Sea (Werner et al., 2012) and could therefore provide a sound farming alternative to blue mussels. Zebra mussel farms near the mouths of major tributaries, may provide a better option to trap nutrients in brackish water coastal lagoons. Zebra mussels have been a predominant species in these ecosystems for many years and are confined to coastal waters by the higher salinity of the offshore sea. Our study shows that zebra mussels can easily be cultivated and efficiently trap biologically available nutrients due to their high growth rates. We therefore see zebra mussel farming as a promising, powerful, and innovative in-lake/lagoon-internal measure that efficiently traps highly bioavailable nutrients and provides the capacity to reduce net-nutrient losses (cf. Lindahl et al., 2005).

5. Conclusion

As Schernewski et al. (2019) point out, traditional measures to reduce external nutrient loads to inland and coastal waters seem insufficient to achieve good water quality. Land-based measures to trap P in the catchment (e.g. wetland restorations and artificial wetland constructions) primarily will reduce the runoff to rivers and lakes of particle-associated P with low bioavailability. The strength of mussel farming lies in its removal of biologically highly available P and its capacity (1) to produce negative emissions by inverting the unidirectional flux of limiting nutrients from land to water and contribute to improved water quality, while simultaneously (2) producing a sustainable feed resource for poultry and/or fish farming. Our study shows that zebra mussels can play a role in reducing emissions near the source of pollution, i.e. in lakes and coastal lagoons of brackish water seas. If zebra mussel farming is to be applied on larger scales, however, the infrastructure to easily harvest and process mussels should be in place. In addition, land and water owners (farmers) who invest in mussel farming should receive economic compensation not only for the high-protein feed they produce, but also for the ecosystem service they provide by inverting the flux of nutrients from land to water. Decision-makers need to facilitate these novel approaches in order to ultimately mitigate the negative effects of cultural eutrophication and not allow history to keep repeating itself.

Credit author statement

Willem Goedkoop has developed the idea for the study, applied for the funding, has been involved in the planning performance of the study and sample/data analysis, and has taken the lead in writing, Maidul I Choudhury has been involved in data analysis, statistics, the production of figures and illustrations, and the writing, Danny CP Lau has done CNP analysis of mussel tissues, data compilation, and has contributed to the writing, Ulf Grandin has been involved in the funding application, the planning of the study, as well as data evaluation and writing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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