Musselodling har stor potential som miljöåtgärd i Mälaren – Rapport från ett pilotprojekt i Ekoln

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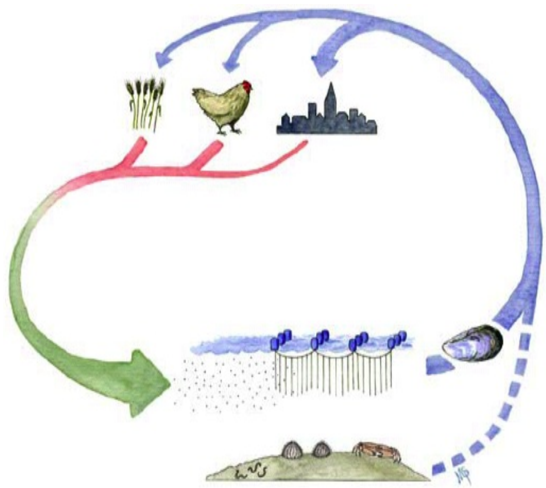
Bakgrund och syfte

Mälarens vattenvårdsförbund (MVF) har 2008 beslutat att under 2 år finansiera inköp och driften av en pilotanläggning för odling av vandrarmusslor (*Dreissena polymorpha*) i Ekoln, Mälaren. För detta har 360 kkr anslagits för 2009–2010. Projektet innebär en start för vidareutveckling och anpassning av ”Agro-Aqua kretsloppskonceptet”, som är utarbetat för havsmiljön (se Lindahl m.fl. 2005), till sjöar där arten förekommer. Konceptet går i korthet ut på att genom musselodling fånga in näring (främst kväve och fosfor) som läckt från landekosystemen (t.ex. från jordbruksmark och reningsverk) och föra tillbaka den till den agrara sektorn genom att låta musselkött ingå som en beståndsdel i hönsfoder (se figur 1).



Figur 1. Flödesschema som visar Agro-Aqua kretsloppskonceptet där musselodling kompenserar för närsaltsläckage från reningsverk och areella näringar till ytvatten. Genom användning som hönsfoder skapar Agro-Aqua kretsloppskonceptet ett återflöde av näring till den agrara sektorn. Efter Kollberg och Lindahl (2006).

Metoden

Under vårvintern 2009 har vi köpt in och installerat två pilotodlingar av s.k. longline typ för odling av vandrarmusslor i Ekoln. Odlingarna täcker en yta på 25 x 50 m och ligger i södra ändan av sjön, samt utanför Fredrikslunds gård. Varje enhet består av 4 km odlingsband som hänger mellan ca 0,3 och 2,5 m djup. Odlingarna kom på plats tidigt under juni 2009 (med hjälp av en inhyrd pråm med kran) och odlingsbanden koloniserades snabbt därefter av de frisimmande mussellarver i sjön. I bilagan finns några bilder som visar odlingsenheterna på plats i Ekoln.

Preliminära resultat fram till hösten 2011

Det mest tråkiga resultatet i detta projekt är att en av odlingsenheterna under augusti 2010 utsattes för omfattande sabotage. Någon hade skurit sönder diverse linor och enheten kom drivande i land i den norra delen av sjön. Den saboterade odlingsenheten fick ligga på land över vintern och sjösattes igen under våren 2010, d.v.s. innan musslornas parningstid och tiden då man kan förvänta att stora mängder mussellarver bottenfäller.

Under vintern 2009–2010 har vi också regelbundet tagit prov på ytsediment och sedimenterande material innanför och utanför odlingen insamlats för att kvantifiera effekter av musselodlingarna på näringshalten i bottensedimenten. Prover har tagits med ^{31}P-NMR för att kvantifiera olika former av fosfor. Ett antal prov på musslor från den saboterade odlingsenheten hade tagits innan sabotaget. Proven visade på stora antal med små musslor.

Den ena av musselodlingarna, den som har legat på plats utanför Fredrikslund i två år, skulle ha skördats under hösten 2011. Som följd av sjukskrivningar och bristande bemanning, vilket bl.a. resulterade i att ett "skördeverktyg" inte hunnits konstruera, har skörden dock skjutits upp till våren 2012. Den andra enheten ska skördas under hösten 2012. Vid skörd ska musslornas storlek och biomassa bestämmas, samt ska vi göra mätningar på CNP i musselkött och skal.

Som följd av sabotage och upprepade höga hyreskostnaden för en pråm med lyftkran, har kostnaden för iläggning och underhåll av odlingarna varit oproportionerligt hög. Anslagen från Mälarens vattenvårdsförbund har därför förbrukats i dagsläget, men institutionen kommer att finansiera skörd och analyser av musselkött, skal och sediment för att fullfölja pilotstudien enligt planerna.

Nytta för MVF

Hittills genomförda åtgärder mot eutrofieringen har fokuserat på att minska närsaltsläckage till sjöar och vattendrag och har varit föga framgångsrika (förutom utbyggnaden av reningsverken med fosforfällning i slutet på 1960-talet). Andra åtgärder som minimeringsfiske och behandling av ytsediment för att minska internbelastningen har genomförts med växlande framgång. Genom odling och skörd av vandrarmusslor i recipienten avlägsnas och återförs näring aktivt tillbaka till den agrara sektorn (t.ex. som hönsfoder). Detta nytänkande innebär således en förbättrad chans att få bukt med eutrofieringen och uppfyllandet av regionala och nationella miljömål.

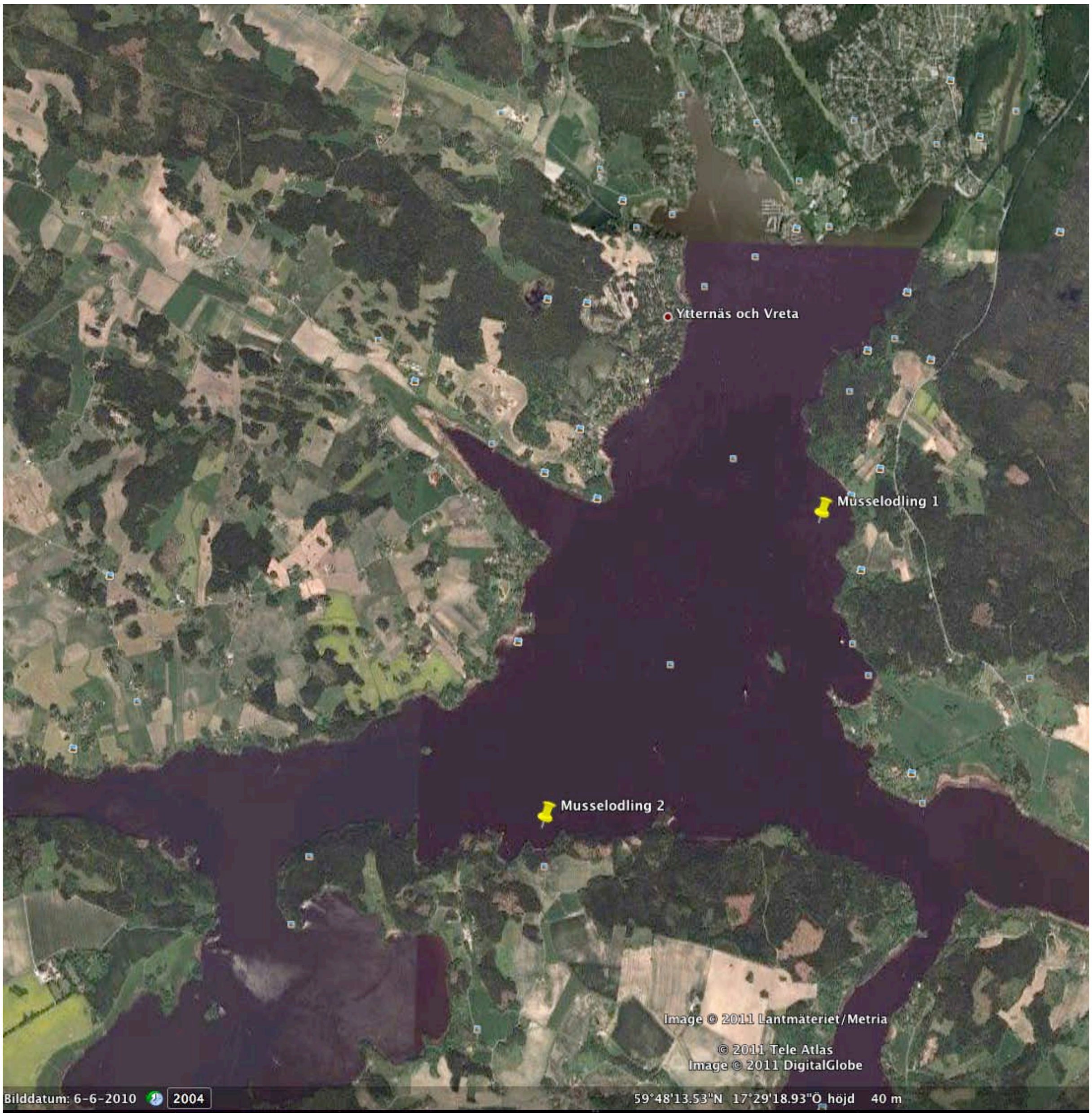
När skördat biomassa och näringskvaliteten av musselkött och skal har bestämts kan man göra bräkningar som visar hur mycket näring i form av N och P som kan avlägsna årligen per m^2 musselodling i Mälaren. Man får med andra ord inblick i potentialen av denna åtgärd för miljöförbättringar. Om åtgärden visar sig vara en effektiv och kostnadsmässigt acceptabel näringsfälla, som dessutom producerar en värdefull proteinkälla för värphöns och slaktkyckling, kan musselodling lanseras i större skala, t.ex. genom att bönder med fiskerätt parkerar ett antal odlingsenheter på sina vatten.

Till denna rapport bifogas också en vetenskaplig artikel. Artikeln är baserat på data från Ekoln, framtagen i ett tidigare, av Naturvårdsverket finansierad inventeringsprojekt, men belyser musslornas populationstätheter och näringshalter, samt deras roll i ekosystemet Ekoln. Vi tror att även den artikeln kan vara av intresse för MVF.

Tidplan för återstående aktiviteter

Projektet har ursprungligen planerats att pågå i två år, 2009–2010. I den ursprungliga projektplanen fanns dock redan en reservation för en förlängning under 2011. Som följd av ovan nämnda problem har projektet försenats med ytterligare ett år och skörd av musslor och mätningar av deras storlek och CNP kommer att göras under 2012. **Eftersom kontraktstiden har gått ut och ackumulerade kostnader inom projektet med 575 kkr vida överskrider de 360 kkr som beviljades av MVF, vill SLU rekvirera återstående 90 kkr enligt rådande avtal innan utgången på 2011.** SLU vill gärna diskutera med MVF om vidare finansiering av ett nytt projekt som behövs för skörd och analys av musslor under 2012.

Bilaga 1: Bilder från musselodlingarna.



Placering av de två musselodlingenheterna på Ekoln.

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ORIGINAL PAPER

Retention of N and P by zebra mussels (*Dreissena polymorpha* Pallas) and its quantitative role in the nutrient budget of eutrophic Lake Ekoln, Sweden

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Abstract We quantified cover, population densities, size distribution and biomass of zebra mussels along 7 transects in eutrophic Lake Ekoln (Sweden). We also analyzed the elemental (C, N, P) composition of zebra mussel soft tissue and computed their retention rates of N and P their quantitative role in the lake's nutrient budget. We hypothesized that zebra mussels play an important role in the nutrient budget of the lake and speculate that the successive harvesting of cultured mussels could contribute to the lake's rate of recovery from cultural eutrophication. At depths exceeding 5 m, mussels covered consistently less than 5% or were absent. Similarly, mean densities were 3,158 $\pm$ 2,143 ind m^{-2} between 2 and 4 m, but rapidly declined at larger depths. Calculated clearance rates averaged 19.4 $\pm$ 2.3 km^3 y^{-1}, implying the entire lake is filtered every 8–10 days. Concentrations of N and P in mussel soft tissue averaged 100.9 $\pm$ 1.5 mg N g^{-1} DW and 9.3 $\pm$ 0.2 mg P g^{-1} DW. The lake population was estimated to 22.2 $\pm$ 2.6 $\times$ 10^{10} mussels, corresponding to a standing stock biomass of 362 $\pm$ 42 ton DW, or conservative estimates of 36.6 $\pm$ 4.3 ton N and 3.4 $\pm$ 0.4 ton P. Assuming a life span of 2–3 years gives a retention estimate of 1.2–1.8 ton P y^{-1} by mussels, corresponding to 50–77% of the annual P influx from Uppsala sewage treatment plant to the lake. Similarly, annual N-retention by zebra mussels makes up 13–20 ton N y^{-1}, largely equaling the annual N-deposition from atmospheric sources on the lake's surface. These retention rates correspond to only a few percent of the annual P-load from agricultural sources, but we argue that the quantitative role of zebra mussels in nutrient budgets is much larger if these budgets are adjusted for the bias introduced by coarse estimates of N and P pools that include a large share of refractory P.

Keywords Elemental composition · Population densities · Filter-feeding · Remediation · Eutrophication · Zebra mussel

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Introduction

The zebra mussel (*Dreissena polymorpha*) is a successful invader with large ecological (MacIsaac 1996; Karatayev et al. 1997; Simon and Townsend 2003; Caraco et al. 2006) and economic consequences (Khalanski 1997; Pimentel et al. 2000; Connely et al. 2007) in European and North American inland waters. The wide limits of environmental tolerance of zebra mussels result from a genetic polymorphism (see Orlova 2002), the production of large amounts of motile juvenile stages, and their ability to filter a wide size range of sestonic particles (Bastviken et al. 1998; Naddafi et al. 2007). These traits all likely contribute to their invasion success. Dense populations of zebra mussels affect food web structure and ecosystem function (e.g. Nalepa et al. 1998; Mills et al. 2003) by selectively and efficiently feeding on phytoplankton (Bastviken et al. 1998; Naddafi et al. 2007). This feeding behavior results in large reductions in the biomass of phytoplankton and microzooplankton subsequently increasing water clarity, changing phytoplankton community structure (MacIsaac 1996; Karatayev et al. 1997; Vanderploeg et al. 2001) and seston stoichiometry (Naddafi et al. 2008), and causing a shift in energy flow from pelagic to benthic pathways (Gergs et al. 2009). The establishment of zebra mussels and subsequent retention of nutrients has likely counteracted the effects of cultural eutrophication in many inland waters, although few studies have quantified this (Mellina et al. 1995, Effler and Siegfried 1998, Caraco et al. 2006). Indeed, Dzialowski and Jessie (2009) recently showed that zebra mussels can greatly reduce algal biomass and negate or mask the increasing effects of nutrient pulses up to 150 mg P l^{-1} on algal biomass. Several studies have therefore addressed the potential use of zebra mussels in water quality remediation (e.g. Reeders and Bij de Vaate 1990; Orlova et al. 2004; Elliott et al. 2008) or sewage sludge treatment (Mackie and Wright 1994).

Despite the critical role of zebra mussels in many aquatic ecosystems, no studies have addressed how zebra mussels affect nutrient budgets of lakes through retaining N and P in their tissue and shells. In this study we quantified relative cover, population densities, size distribution, biomass, as well as elemental (CNP) concentrations of zebra mussels in eutrophic Lake Ekoln and compute their role in the lake's nutrient budget. We speculate that the successive harvesting of cultured mussels can contribute to increase the lake's rate of recovery from cultural eutrophication. Our analysis of zebra mussel filtration rates and impact on lake nutrient dynamics contributes to our understanding of their effects on communities and ecosystem function.

Materials and methods

Study site and invasion history

Lake Ekoln (UTM 646170.3, 6624729) is the northernmost basin of Lake Mälaren, the third largest lake of Sweden. Lake Ekoln is a relatively large (surface area 29.8 km^2), eutrophic lake (total phosphorus 37 ± 5.6 μg P l^{-1}, total-N 1678 ± 149 μg N l^{-1}, annual means for 2000–2008 obtained from monitoring databases at our department), with a mean depth of 15.4 m, a maximum depth of 50 m, a volume of 0.458 km^3, a water renewal time of less than 1 year, and a (95%)-phosphorus equilibration time (i.e. 95% of the time to reach a new equilibrium between a new level of input and in-lake concentration) of 1 year (Wilander and Persson 2001). Detailed information on the morphometry of the lake is provided by Håkanson (1977). Soil types in the catchment are dominated by postglacial clay and moraine soils and land use consists of 30% agriculture and 62% forestry, while residential areas, largely dominated by the town of Uppsala just north of the lake, constitute some 2% of the catchment. Overall population in the catchment is close to 200,000 inhabitants, but some 80% of these live in Uppsala. Lake Ekoln has long been a recipient for point source pollution from the Uppsala sewage treatment plant, as well as for catchment's diffuse sources originating from agricultural activity (roughly 40%) and single households (also roughly 40%) (Larsson 2005). The Rivers Fyrisån and Örsundaån are the major inflows into Lake Ekoln.

Zebra mussels were introduced to Lake Ekoln in the 1920s, likely by ballast water from commercial shipping (Arwidsson 1926; Josefsson and Andersson 2001). Despite this early invasion and development of relatively large population densities in shallow areas (e.g. on rocky shores), no negative effects have been reported. The current distribution of the zebra mussel in Sweden is limited to the eastern basins of Lake Mälaren (including Lake Ekoln), Lake Hjälmaren and a number of other lakes in eastern central Sweden where calcareous soils dominate (Hallstan et al. 2010). This is likely due to the predominantly acidic bedrock, and, subsequently low-alkalinity waters, on the Scandinavian peninsula. The zebra mussel population in Lake Ekoln is among the species' northernmost global distribution.

Field sampling

Mussels populations were sampled along 7 transects (identified by GPS), running perpendicular from the shoreline down to 10 m, by SCUBA-diving. These transects were Djupviken (648049.3, 6629140), Wik (638374.9, 6624588), Vreta (645677.1, 6627553), Skarholmen (647374.8, 6630273), Hässle (644390.1, 6625496), Flässjan (647494.7, 6626108), and Norsholmen (645841.8, 6624349). These transects covered all shores and substratum types in the lake, i.e. rocks, cobbles, gravel, sand, or clay. Along these transects, a 0.5 × 0.5 m frame was placed on the lake floor at each depth-meter between 10 and 1 m (n = 3) and the cover of mussels within this frame was estimated using a four-degree scale: 0 = mussels were missing, 1 = cover <5%, 2: cover 5–50%, 3: cover >50%. These cover classes were later transformed to relative cover using the mid percentage of a class, i.e. 0, 2.5, 27.5 and 75%, assuming that these values represent a mean cover for each class. Bottom substrata of sampled areas were classified and photographs, marked with transect number, depth, and replicate number, were taken from each of the sampled surfaces to verify cover estimates. Field work was done in October 2006, i.e. after the mussels' reproduction season and after the sedimentation of the autumn diatom bloom when visibility in the lake had increased.

We collected mussels at depths of 2 and 4 m from a 0.25 × 0.25 m subframe (n = 3), mounted within the larger 0.5 × 0.5 m frame. Mussels were then transferred to net bags, brought to the surface, and transported to the laboratory in ambient lake water. Mussel collection was restricted to 2 and 4 m depths, as harvesting mussels from all depths would have been too risky for our divers.

Laboratory processing and analysis

After sample collection, zebra mussels were frozen in the laboratory for later quantification of population density, size (shell length), dry weight and elemental concentrations. Shell length (longest length) was measured using a caliper equipped with a digital display (±0.01 mm) and a subsample of 22–35 mussels for 6 of the sites were freeze-dried to constant weight for quantification of individual dry weight (soft tissue only) and elemental analysis. Unfortunately, samples from Wik were lost due to thawing and excluded from elemental analyses. Samples of dry mass soft tissue were analyzed for C and N using a CHN analyzer (LECO CHN-932, Carlo–Erba Strumentazione) and for P, as phosphate, after hot hydrolysis with potassium persulphate according to Grasshoff et al. (1983). A power relationship ($R^2 = 0.54$, $P < 0.0001$, n = 177) was established to convert shell lengths (length, as mm) to tissue dry weight (DW, as mg):

$$\log_{10}(\mathrm{DW}) = -1.1569 + 1.9060 \times \log_{10}(\mathrm{length}) - 4.9457 \times (\log_{10}(\mathrm{length}) - 1.2741)^2.$$

For estimating the total *Dreissena* population in the lake, population densities at 3 m were assumed to equal those at 2 m, while population densities at 1 m were assumed to equal those at 4 m. These assumptions were justified by the similar mussel cover found for these depths (see Fig. 1). Mussel densities at 5, 6, 7, 8, 9, and 10 m were calculated by multiplying the proportion between the mean cover for a specific depth and the mean cover at 2 m depth (59.2%) with the quantified mean population densities at 4 m depth (=1,490 ind m^{-2}). This extrapolation may overestimate the mussel standing stock biomass, as mussels at greater depths tend to be smaller. However, visual inspection of the photographs of our sampling plots did not support that mussels were smaller at greater depths in Lake Ekoln. Total population density

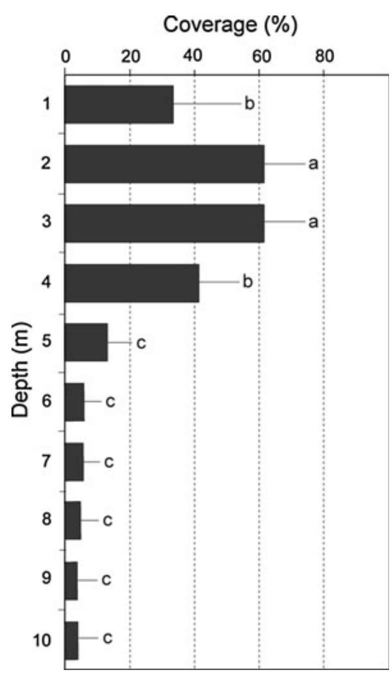

Fig. 1 Overall mean zebra mussel cover (±standard deviation, n = 6) among depth transects in Lake Ekoln

estimates (ind m^{-2}) within each depth stratum were then converted to standing stock biomass (mg DW m^{-2}) using the overall mean individual biomass (mg DW ind^{-1}) for all sites. The standard error of population size estimates also gave us a measure of error for these calculations. Standing stock biomass estimates (mg DW m^{-2}), for the sampling sites along the 7 transects, were then used to calculate depth-stratified mean population biomass. In the next step these depth-stratified mean population biomass estimates were extrapolated to the whole lake using hypsographic data (Håkanson 1977). Information on the hypsographic curve of the lake provides information on the bottom area in each depth stratum. These calculations resulted in an estimate of the whole-lake standing stock biomass of zebra mussels and the associated error.

Data on mussel size and elemental concentrations were ^{10}log-transformed prior to statistical analysis to meet the criterion for homogeneity of variance. ANOVAs were used to test for site and depth effects on mussel size and for differences in elemental concentrations among sites, while Tukey–Kramer HSD-tests were run for pairwise comparisons. Paired *t*-tests were used to test for differences in mussel densities between depths, while linear regressions were used to evaluate relationships between mussel size and soft tissue elemental concentrations. Statistics were run using JMP 7.0.2 for MacIntosh (SAS-Institute) with α set at 0.05. Data are presented as means ± standard error, unless else is stated. Mussel biomass and concentrations of CNP are expressed as mg per gram of dry weight.

Results

Mussel cover exceeded 40% between 2 and 4 m, but declined with increasing depth (Fig. 1). At depths exceeding 5 m mussels covered consistently less than 5% or were absent, except at Norsholmen where cover still was between 5 and 50% at 10 m. Also at 1 m depth, mussel cover was lower than between 2 and 4 m. At Norsholmen large amounts of dead shells were also found at depths exceeding 4 m. At Norsholmen and Hässle the lake floor consisted of a stony substratum down to 4 and 8 m, respectively. Along the other transects sand/clay sediments dominated, with single stones occurring in the littoral zone. Overall mean mussel densities were 3,479 ± 924 at 2 m and 1,489 ± 500 ind m^{-2} at 4 m, but the difference was not significant (paired *t* test, $P = 0.073$). At Vreta, mussel density at 4 m depth was only 21 ± 14 ind m^{-2} and conspicuously lower than at the other sites. Mean size of mussels differed among sites ($P < 0.0001$), but was similar between 2 and 4 m (Table 1). Size frequencies plots of mussel size for the other sites showed bimodal patterns with a primary peak below 10 mm, representing the young-of-the-year mussels, and a secondary peak representing adult mussels with shell lengths exceeding 16 mm (Fig. 2). A particularly high frequency of small individuals was observed at Vreta, where 43% of the mussels was smaller than 10 mm. Conversely, at Wik, only 2.6% of the mussels were smaller than 10 mm. When size was converted to biomass, individual biomass was highest at Wik and lowest at Vreta, 24.36 ± 0.44 and 8.23 ± 0.53 mg ind^{-1}, respectively (Fig. 2). Overall mean individual biomass was 16.31 ± 1.90 mg ind^{-1}.

Phosphorus and nitrogen concentrations in soft tissue showed marked among-site variation, but did not differ with depth (Table 1). Tissue P-concentrations peaked at Hässle with 10.48 ± 0.28 mg P g^{-1} and ranged from 8.52 ± 0.14 to 9.36 ± 0.44 mg P g^{-1} for the other sites (Fig. 3a). Overall mean tissue P-concentration was 9.36 ± 0.28 mg P g^{-1} for the 6 transects. Tissue N-concentrations were lowest at the mid-lake site Flässjan with 95.35 ± 1.73 mg N g^{-1}, but between 4% (Vreta) and 10% (Skarholmen) higher at the other sites (Fig. 3b). Overall mean tissue N-concentration was 100.94 ± 1.51 mg N g^{-1}. Also tissue C-concentrations were lower at Flässjan than at the other sites (Fig. 3c), and showed an overall mean of 494.16 ± 2.99 mg C g^{-1}. Tissue concentrations of P and C were independent of size, but tissue N-concentrations showed a positive relationship with size ($R^2 = 0.177$, $P < 0.0001$, $n = 178$) (data not shown).

The whole-lake population was estimated to $22.2 \pm 2.6 \times 10^{10}$ mussels. Extrapolating individual biomass to whole-lake standing stock biomass estimates, using depth-stratified densities, resulted in 362 ± 42 tons DW (Table 2). Scaling-up the mean concentrations of phosphorus and nitrogen in mussels resulted in estimated pools of 3.4 ± 0.4 tons P and 36.6 ± 4.3 tons N associated with the zebra mussel population. Also 174.3 ± 20.3 tons C was fixed in zebra mussel soft tissue.

Table 1 Two-way ANOVA results for site- and depth-dependent differences in mussel size and concentrations of phosphorus (P), nitrogen (N), and carbon (C) in soft tissue

Factor	Size			P			N			C		
	df	F	*P*	*df*	F	*P*	*df*	F	*P*	*df*	F	*P*
Site	6	71.292	<0.0001	5	4.159	0.0014	5	6.209	<0.0001	1	9.847	<0.0001
Depth	1	0.219	0.6398	1	0.085	0.7708	1	0.649	0.4215	5	15.011	0.0002
Site × depth	6	12.838	<0.0001	5	1.022	0.4062	5	2.412	0.0384	1	4.337	0.001

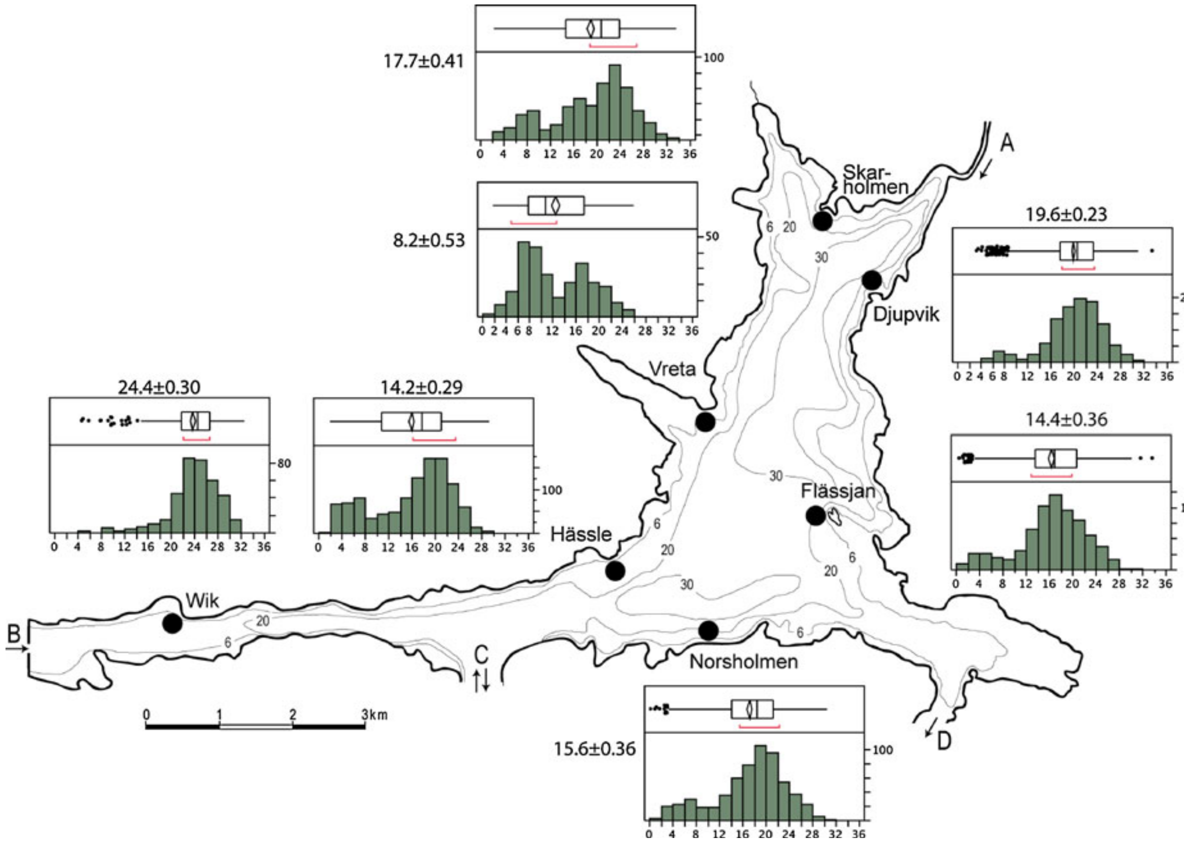

Fig. 2 Map of Lake Ekoln showing frequency distribution plots for zebra mussel size (shell length as mm, along x-axis, number along the y-axis). *Box plots* show means, medians, and 25- and 75-percentiles, while *whiskers* show 10- and 90-percentiles. Also sampling locations (*black dots*), depth isoplets (6, 20 and 30 m), major inlets (*A*- River Fyrisån, *B*- River Örsundaån), the Gorran strait (*C*) and the outlet into Skofjärden (*D*) are shown

Discussion

Our results show that 3.4 ± 0.4 tons P and 36.6 ± 4.3 tons N were associated with the zebra mussel population, indicating an efficient nutrient retention by zebra mussels in Lake Ekoln. These numbers should be seen as conservative estimates as they (1) are based on soft tissue biomass only, thus neglecting N and P concentrations in shells, (2) disregard population losses through predation and (3) do not account for shell banks as nutrient sinks. Assuming that P and N associated with shells is 6.8% of that in soft tissue (Królak and Zdanowski 2007) would further increase the P and N pool of zebra mussels by 0.23 tons P and 2.5 tons N. The P-pool in zebra mussel biomass thereby exceeds the annual discharge of P from the Uppsala sewage treatment plant, which amounts 2.2 ± 0.1 tons P y^{-1} (data for 2005–2007) (Fig. 4).

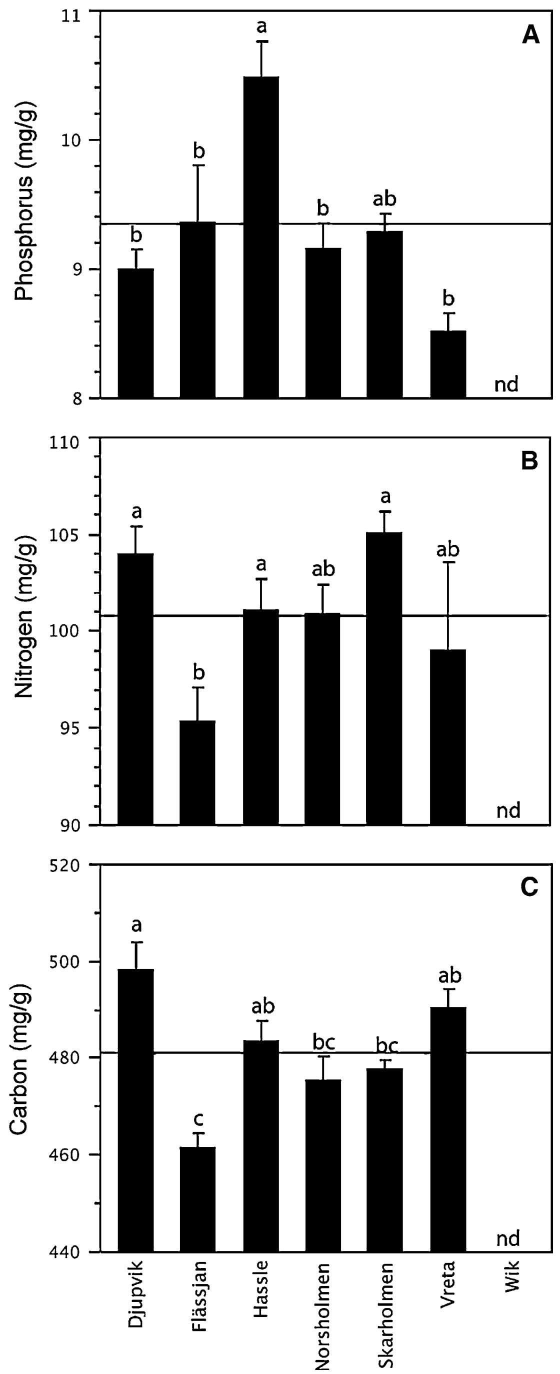

Fig. 3 Phosphorus (**a**), nitrogen (**b**), and carbon (**c**) concentrations (means ± 1 standard error) per gram dry weight of zebra mussel soft tissue for different sampling sites in Lake Ekoln. *Letter codes* denote significant differences between sites (Tukey HSD tests, $P < 0.05$), i.e. sites that do not have letters in common are significantly different. *nd* not determined. Note that different depths (2 and 4 m) were pooled as no effect of depth was found (see text). *Grey lines* give the overall mean

A similar comparison for N shows that zebra mussel-N is some 15% of the amount of N released from the sewage plant, mainly due to low N-retention in the plant (some 50%). Assuming that zebra mussels longevity is 2–3 years (Chase and Baily 1999) implies that P-retention by mussels corresponds to 1.2–1.8 ton P y^{-1}, or 50–77% of the annual P influx from sewage. Similarly, annual N-retention by zebra mussels makes up 13–20 ton N y^{-1}, or 5–8% of the annual sewage-related N-load. However, N-retention by mussels amounts 80–120% of the annual N-deposition from atmospheric sources on the lake's surface (5 kg N ha^{-1} y^{-1}, Swedish Environmental Protection Agency, http://www.naturvardsverket.se/sv/Tillstandet-i-miljon/Overgodning/Kvavenedfall/). These numbers show that zebra mussels play an important role in the nutrient dynamics of Lake Ekoln.

Annual inflow of P from the rivers Fyrisån and Örsundaån, extracted from regional monitoring databases at our department, is 24.5 ± 2.7 and 34.2 ± 2.7 tons P y^{-1}, respectively. These external P-loads by far exceed the retention by zebra mussels. However, the major share of the annual P-load typically comes with the spring flood and high-flow events in fall and winter when the rivers carry high sediment (clay) loads. P associated with fine particles (< 16 μm) strongly dominates the refractory and authigenic P fractions in suspended matter that was not available for algal growth (Huijun et al. 2010). This conjecture suggests that a large share of the annual P-load to Lake Ekoln is not available for biological production. If instead the annual mean biomass of phytoplankton of 6.4 ± 1.5 μg Chl *a* l^{-1} (seasonal mean chlorophyll *a* concentrations for 0–8 m in Lake Ekoln), representing biologically active P, is converted to units of P (using a C/chlorophyll conversion factor of 47 (Riemann et al. 1989) and applying C:P = 106 and N:P = 16, i.e. the Redfield ratio) calculations show that on average 3.7 ± 0.8 tons P and 58.6 ± 13.4 tons N are associated with phytoplankton biomass. These numbers imply that nutrient turnover of P and N by zebra mussels is 32–50% and 22–33%, respectively, of that associated with phytoplankton (assuming that mussels grow to adult size in 2 or 3 years, see above). However, due to the relatively short water renewal time of Lake Ekoln (less than 1 year), a large share of phytoplankton biomass will also be flushed out from the lake. Conversely, the sessile mussels with their

Table 2 Mussel densities, biomass (means ± 1 standard error) and tissue concentrations of phosphorus (P), nitrogen (N), and carbon (C) for different depth intervals

Depth interval (m)	Area (km^2)	Density (ind m^{-2})	Biomass (tons dw)	P (tons)	N (tons	C (tons)
0–1	1.82	1490 ± 707	44.4 ± 5.2	0.41	4.47	21.33
1–2	2.43	3479 ± 1307	138.1 ± 16.1	1.28	13.93	66.42
2–3	2.43	3479 ± 1307	138.1 ± 16.1	1.28	13.93	66.42
3–4	0.767	1490 ± 707	18.6 ± 2.2	0.17	1.88	8.96
4–5	0.767	631 ± 72	7.9 ± 0.9	0.07	0.79	3.80
5–6	0.767	281 ± 32	3.5 ± 0.4	0.03	0.35	1.69
6–7	0.825	246 ± 30	3.3 ± 0.4	0.03	0.33	1.59
7–8	0.825	228 ± 29	3.1 ± 0.4	0.03	0.31	1.48
8–9	0.825	210 ± 23	2.8 ± 0.3	0.03	0.29	1.36
9–10	0.825	193 ± 22	2.6 ± 0.3	0.02	0.26	1.25
Sum	12.29	–	362.3 ± 42.2	3.37	36.55	174.29

Depth-specific areas were obtained from Håkanson (1977) and hypsographic data for Lake Ekoln. Biomass calculations were made using a mean individual mussel biomass of 16.31 ± 1.90 mg ind^{-1} and linear interpolation. See text for further explanation

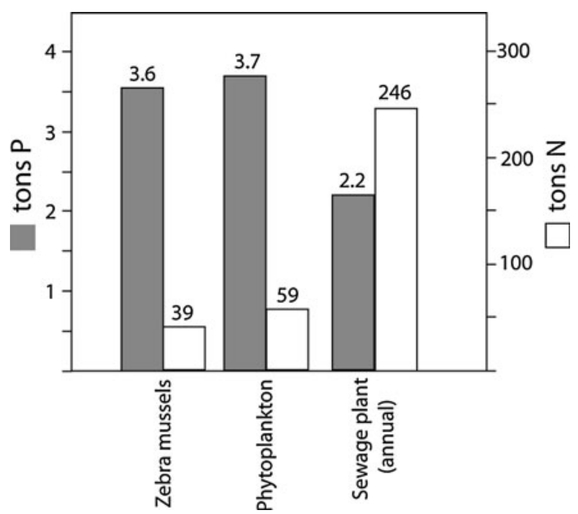

Fig. 4 Phosphorus (*grey*) and nitrogen (*white*) contents of the Lake Ekoln zebra mussel population in relation to annual effluents from the Uppsala sewage treatment plant and annual mean phytoplankton biomass

longer life span contribute to an efficient nutrient retention in the lake.

Using the mean monthly clearance rates of zebra mussels in Naddafi et al. (2007), determined at in situ temperature and using phytoplankton of a nearby meso-eutrophic lake, and assuming that the clearance rate for March (not measured) equals that for November and that the clearance rates for December–February (not measured) equals zero, provides an overall annual mean clearance rate of 6.1 ml mg^{-1} DW h^{-1}. Applying this clearance rate to the Lake Ekoln's zebra mussel population results in a clearance rate of 19.4 ± 2.3 km^3 y^{-1}, implying that the entire lake is turned over every 8–10 days. Naddafi's et al. (2007) overall mean clearance rate is in the lower range of that found by Bastviken et al. (1998), who reported clearance rates of 24–63 ml $mussel^{-1}$ h^{-1} for slightly smaller zebra mussels at 16–20°C. Clearance rate estimates, however, are based on short-term measurements and zebra mussels feed intermittently, rather than continuously (e.g. Walz 1978). Assuming that zebra mussels spend 50% of their time feeding would still mean that the entire volume of the lake is filtered in 16–20 days. Although these calculations have their limitations, they further illustrate the huge impact of zebra mussels on this lake.

Annual P-sedimentation is estimated to 11–16 ton P y^{-1} (range 2000–2008), which was calculated by multiplying a calibrated sedimentation constant of 0.94 y^{-1} with the lake volume and mean water concentration (H. Olsson, unpublished data, but see also Ahlgren et al. 1988). This sedimentation estimate includes the 1.8 tons annually incorporated by zebra mussels, representing some 11–16% of sedimentation. This number should also be considered an underestimate as retention in mussel biomass, and increased rates of biodeposition caused by mussels, contributes to increased energy and nutrient fluxes from pelagic to benthic habitats (Gergs et al. 2009). For example, Gergs et al. (2009) found biodeposition rates of 0.025–0.10 mg $mussel^{-1}$ day^{-1} and a linear relationship between seston concentrations and biodeposition by zebra mussels. Our estimate of zebra mussel retention represents the biologically most active pool of 'sedimenting' P. We argue that nutrient budgets in lakes with dense populations of zebra mussels (or other species) should focus more on the relative shares of N and P that are actively turned over by the mussels and less on nutrient forms that are largely bio-unavailable, e.g. through P-fractionation (e.g. Hieltjes and Lijklema 1980; Goedkoop and Pettersson 2000). Such 'bio-adapted' nutrient budgets would reduce the bias introduced by coarse estimates of N and P pools that include refractory P (Huijun et al. 2010) and provide a better tool for detecting effects of measures that aim at reducing lake eutrophication.

The Swedish zebra mussel populations, with their distributions at the 59° northern latitude are among the northernmost populations worldwide (Strayer 1991). At these high latitudes constraints on reproduction may occur, as zebra mussels need a spawning temperature of 12°C (Sprung 1993). Our data show that zebra mussels can establish dense populations at these high latitudes. Also, recruitment on artificial substrata (i.e. tiles) deployed in the epilimnion of Lake Ekoln and downstream basins have shown annual recruitment rates averaged 17022 ± 650 ind m^{-2} (U. Grandin, unpublished data). These recruitment studies also showed that young-of-the-year zebra mussels reach a shell length of 7.1 ± 1.7 mm (maximum 13 mm) during their first summer. The second peak in our size-frequency plots is around 20 mm, likely representing 1.5–2 year old individuals. This conclusion is supported by the finding of Chase and Baily (1999), who reported zebra mussel ages of 2–4 years, based on size frequencies. These results provide evidence of a thriving population, and suggests high growth rates even at these high latitudes.

The analysis of zebra mussel impact on in-lake nutrient dynamics contributes to our understanding of their effects on ecosystem function, but also suggests a possible way of removing nutrients from the lake by systematic culturing and harvesting. Lindahl et al. (2005) launched the concept of Aqua-Agro recycling for blue mussels *Mytilus edulis*. This concept describes how nutrients from agricultural and other sources are trapped by mussel cultures in uncontaminated coastal areas and recycled to the agricultural sector by using mussels as an important, sustainable source of proteins in poultry farming. The Aqua-Agro concept thus efficiently traps nutrients, supplies a sustainable feed resource, and contributes to increased water quality. Also zebra mussels have a high potential in water quality remediation practices (e.g. Reeders and Bij de Vaate 1990; Orlova et al. 2004; Elliott et al. 2008), but the accumulation of metals (Berny et al. 2003) or organic pollutants (Berny et al. 2003, Bruner et al. 1994) in mussel tissue, due to the filtration of contaminated particles, has been identified as a major set back for this approach. However, the accumulation of pollutants in mussels is strongly site-dependent. In Lake Ekoln Cd and Pb concentrations in mussels (n = 8) were 0.080 ± 0.032 mg Cd kg^{-1} WW and 0.117 ± 0.075 mg Pb kg^{-1} WW (recalculated assuming DW/WW = 10%), which is well below the maximum level of for human food stuff of and 1.0 mg Cd kg^{-1} WW and 1.5 mg Pb kg^{-1} WW (European Commission 2006). Also, these mussel samples (n = 2) did not contain detectable concentrations of a suite of modern pesticides, DDT, Lindane and beta-HCH (W. Goedkoop, unpublished data). Therefore, the culturing and harvesting of zebra mussels in relatively unpolluted eutrophied lakes, using the long-lines technique used in the culturing of marine mussels, could have a great potential to contribute to improved water quality. Conservative calculations, based on soft tissue only and assuming mussel densities of 8,000 ind m^{-2}), indicate that a single culture unit of long-line type (15 × 60 m, offering 1,440 m^2 of substratum) could fix some 1,2 kg P y^{-1} and 13 kg N y^{-1} or 13 kg P ha^{-1} y^{-1} and 143 kg N ha^{-1} y^{-1}. The recycling of nutrients from mussel farming units to the agricultural sector not only implies a reflux of nutrients across the land–water interface, but also that the amount of 'new' nutrients needed in animal husbandry can be reduced, thus potentially reducing its contribution as a diffuse source of nutrients in surface waters. Obviously, sites for such farming activities should be selected with care to avoid the further dispersal and/or establishment of zebra mussels and to minimize the accumulation of contaminants.

In conclusion, our conservative calculations showed that the annual retention by zebra mussels in Lake Ekoln largely equaled atmospheric N-deposition on the lake's surface or made up 50–77% of the annual P influx from Uppsala sewage treatment plant to the lake. These numbers indicate huge ecosystem effects and show that zebra mussels play a quantitatively important role in the nutrient budget of this lake, particularly so if these budgets are corrected for the large share of P (i.e. clay-particle associated) that is not unavailable for biological production. The efficient trapping of nutrients by zebra mussel filtration provides an ecosystem service that can be used to increase water quality and contribute with an important source of proteins in poultry and/or fish farming. Economic analysis has shown that marginal cleaning costs of nutrients in mussel cultures are lower than traditional abatement measures (Gren et al. 2009), further pinpointing their potential. Possibly, mussel farming could become an integral part of farms adjacent to lakes where zebra mussels already are established and is in line with current European policies towards increased aquaculture activities for food production.

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