Ecosystem engineering by mussels supports biodiversity and water clarity in a heavily polluted lake in Dhaka, Bangladesh

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Abstract: Freshwater mussels (Unionida) are globally endangered but perform crucial ecosystem services in temperate ecosystems. Their status and role in tropical regions are poorly understood, resulting in a nearly complete lack of effort toward their conservation. Understanding mussel functions in developing countries is particularly important because costly interventions to restore habitat functionality are often infeasible. We investigated the role of mussels in the nearshore zone of Dhanmondi Lake, a narrow, polluted lake in central Dhaka, Bangladesh, during the dry season. Sampling at 50 sites 1 to 3 m from the shore revealed dense mussel populations, averaging 218 individuals (ind)/m^2 from 2 species (*Lamellidens marginalis* and *Parreysia caerulea*). Based on laboratory filtration rates and in-situ size-frequency distribution, we calculated that mussels filter the equivalent of the volume of the lake margins in 21 h. This filtration capacity appears to explain the lake's high water clarity (>2 m visibility during the dry season), despite copious nutrient availability for algal growth. Although it is heavily polluted, the nearshore zone of the lake has a diverse macroinvertebrate fauna, featuring up to 16 invertebrate families/0.25 m^2. Strong positive correlations among mussel density, macroinvertebrate richness, and diversity were revealed through 2-min kick-samples, and indicate that mussels act as *microhabitat engineers* that promote localized biodiversity. Loss of mussel communities could result in further loss of ecosystem services, which would be costly to replace through other means. Moreover, our data suggest that mussel abundance may be used to identify sites of high macroinvertebrate biodiversity in tropical freshwaters and, thus, help to focus management efforts in the most cost-effective way.

Key words: ecosystem services, Unionida, macrozoobenthos, eutrophication, filtration, tropical lake, ecological engineering, habitat restoration, functional ecology, population biology, habitat assessment, Bivalvia

Conservation of keystone species, i.e., those that have a disproportionate effect on survival and growth of other species, is crucial for maintaining organization and diversity of ecological communities (Paine 1969, Mills et al. 1993, Bond 1994). In temperate freshwater habitats, mussels of the order Unionida serve as keystone species whose loss can have far-reaching and complex consequences on the rest of the ecosystem. Moreover, freshwater mussels can serve as ecosystem engineers that make habitat more suitable for other organisms and as indicator species that can help in the assessment of the health of freshwater systems (Vaughn and Hakenkamp 2001, Gutiérrez et al. 2003, Salanki et al. 2003, Vaughn et al. 2008).

The unique standing of mussels in freshwater ecosystems is a result of their ability to affect multiple trophic levels and to provide an integral link between pelagic and benthic habitats (Nalepa et al. 1991, Vaughn and Hakenkamp 2001, Vaughn et al. 2008). They remove algae, bacteria, pollutants, nutrients, and organic compounds from the water via filter-feeding. In situations of high mussel densities, this activity can lead to biological oligotrophication, in which a decrease in nutrients and phytoplankton biomass can ultimately result in increased water clarity and greater macrophyte growth (Welker and Walz 1998, Vaughn and Hakenkamp 2001). Mussels also affect nutrient dynamics through excretion, biodeposition of pseudofeces, and bioturbation (Lewandowski and Stanczykowska 1975, McCall et al. 1979, Nalepa et al. 1991, Vaughn and Hakenkamp 2001, Howard and Cuffey 2006).

Freshwater mussels can affect patterns of distribution and abundance of other organisms. Mussels and their shells provide habitat and shelter for various aquatic organisms including Turbellaria, oligochaetes, caddisfly larvae, tardigrades, and mites (Strayer et al. 1994, Beckett et al.

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1996, Spooner and Vaughn 2006). They serve as a food source for predators, such as muskrats and fish (Tyrell and Hornbach 1998), and stabilize sediments from resuspension (Strayer et al. 1994). As a consequence, presence of mussels can promote benthic macroinvertebrate biomass and biodiversity, as shown by Howard and Cuffey (2006) and Aldridge et al. (2007) for temperate, fluvial ecosystems. In addition to effects at the macrohabitat level (e.g., mussels alter system-wide plankton dynamics), which have been revealed for various temperate waters (e.g., Spooner and Vaughn 2006), we would expect mussels to affect their ecosystem on a microhabitat scale (e.g., microhabitat engineering), but this prediction has never been tested.

Mussels also are counted among the most endangered groups of animals (Bogan 1993). Western countries are acknowledging that healthy mussel populations are vital for maintaining freshwater biodiversity and ecosystem functioning and are investing heavily in their protection. For example, over the past 15 y, the European Union has invested or budgeted >€60 million in 21 major LIFE (Financial Instrument for the Environment) projects that focus on the conservation of European freshwater mussel species (http://ec.europa.eu/environment/life/). However, the functions of mussels in temperate freshwaters are comparatively well understood, but we lack data on their roles in tropical ecosystems (Siddiqui et al. 2007, Bogan 2008). Many aquatic systems in the tropics—particularly in urban areas—are highly polluted and may not be suitable for mussels to survive (Ali et al. 1998, Kumar 2002, Douda 2010). Pollutants and climatic conditions may negatively or positively affect the filtering ability and ecosystem functioning of mussels that manage to survive (Englund and Heino 1996). Mobilizing the necessary political support to start efforts toward the protection of these vulnerable animals in the tropics is difficult without information on the value of mussels to tropical ecosystems and people (Allen et al. 2010). Identifying keystone taxa can help to identify sites of high biological diversity and value and to focus limited resources toward conservation of threatened ecosystems.

Mussels are attracting increased interest as a tool for habitat restoration, bioremediation, and biomonitoring because of their ability to alter structure and biodiversity of aquatic environments (Gutiérrez et al. 2003, Spooner and Vaughn 2006, Aldridge et al. 2007). The role of mussels in freshwater systems in developing countries may be especially important because resources for costly interventions to maintain or restore habitat functionality may be unavailable.

Our goal was to assess the role, function, and importance of freshwater mussels to Dhanmondi Lake, a highly impacted lake in central Dhaka, Bangladesh. Specific objectives were to: 1) estimate the density, size-frequency distribution, and diversity of mussels in the nearshore zone of Lake Dhanmondi; 2) correlate mussel abundance with macroinvertebrate indices; and 3) estimate the filtration capacity of existing mussel populations.

METHODS

Study area and sites

We studied Dhanmondi Lake (lat 23°45.07′N, long 90°22.65′E) in central Dhaka (Fig. 1) from January to March 2010 during the dry season. We collected additional environmental data during the wet season from July to August 2010. This narrow, man-made lake was originally a navigational channel connected to the surrounding river system. The lake is ~3 km long, 35 to 100 m wide, 176,000 m^2 in area, 440,000 m^3 in volume, and on average, 2.5 m deep (Japan International Cooperation Agency 1987, Hossain et al. 2009, Khan and Rahman 2010). One box culvert near the residential area Sukrabad represents the only outlet of the lake, through which excess floodwater passes (Khan and Rahman 2010). Substrate type is clay with patches of silt and woody debris. Aquatic vegetation consists of macrophytes, such as *Eichhornia crassipes* (Mart) Solms, *Pistia stratiotes* Linnaeus, 1753, and *Telanthera philoxeroides* (Mart.) Moq., 1849 (Parveen et al. 1995). The lake features a number of fish species including Silver Carp (*Hypophthalmichthys molitrix* (Valenciennes, 1844)), Catla (*Catla catla* (Hamilton, 1822)), Rohu (*Labeo rohita* Hamilton, 1822), Pangas Catfish (*Pangasius pangasius* (Hamilton, 1822)), Nile Tilapia (*Oreochromis niloticus* (Linnaeus, 1758)), and Grass Carp (*Ctenopharyngodon idella* (Valenciennes, 1844)) (GWC, unpublished data).

Dhanmondi Lake is vital in maintaining the only drainage system of Dhanmondi and adjacent areas. Pollution sources are numerous and include sewage from hanging toilets of a floating population around the lake, municipal waste water, and effluents and garbage from adjacent industries, tanneries, hospitals, pathology centers, restaurants, and homes (Fig. 1). As a result, reported P concentrations range from 0.34 to 0.85 mg PO_4^{3-}/L or 110 to 277 µg P/L (Hossain et al. 2010), rendering Dhanmondi a hypereutrophic lake (Carlson 1977). In 2009, the lake's water was acidic and O_2-depleted, with localized pH values as low as 5.8, and biochemical O_2 demand (BOD) 7 to 9 mg/L (Razzak et al. 2012). Dhanmondi Lake is furthermore heavily contaminated, with Mn, Cu, Zn, Pb, and cyanide concentrations that exceed the recommended limits for drinking water, irrigation, and aquaculture (Hossain et al. 2010, Mokaddes et al. 2013). In 2001, coliforms exceeded the Environmental Quality Standards for recreation purposes (Department of Environment 2001).

Environmental parameters

We randomly selected 50 sites in the shallow, nearshore zone of the lake (1–3 m from the shore, where depth

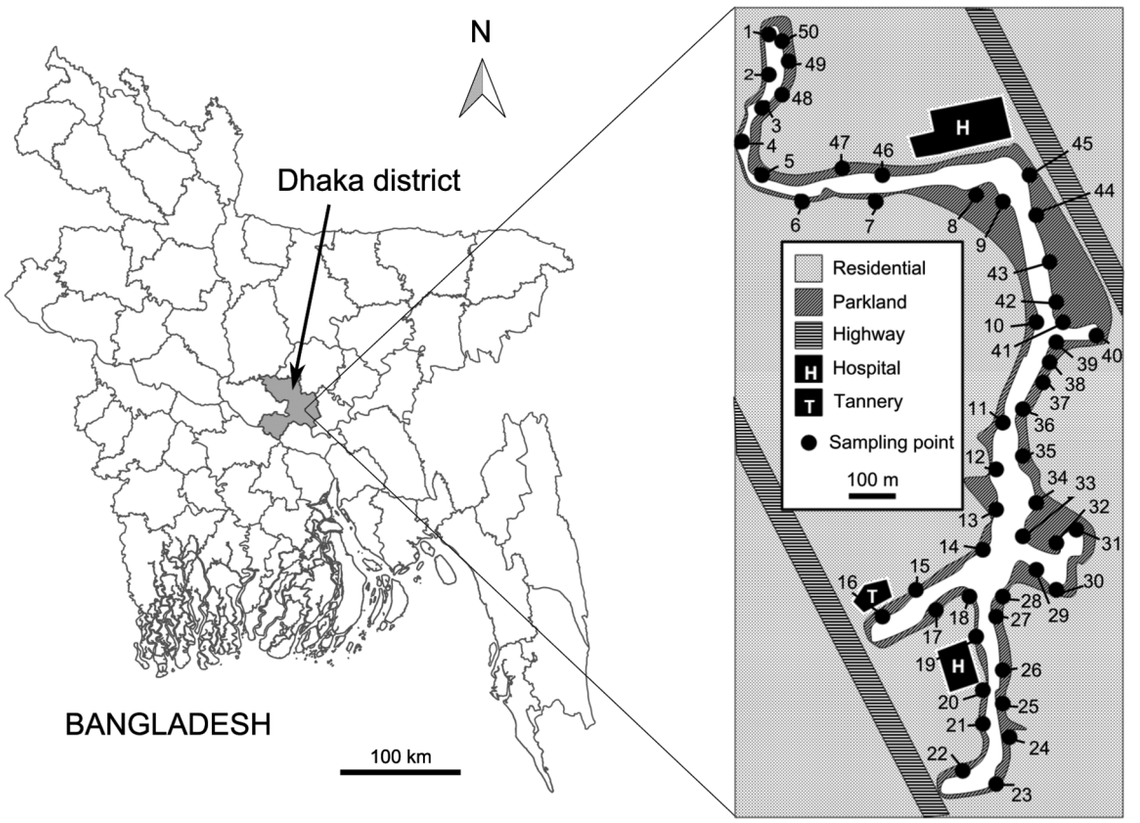

Figure 1. Locations of the 50 study sites in Dhanmondi Lake. One 0.5- × 0.5-m quadrat was sampled for mussels at each site during January to March 2010.

averaged ~1 m and was ≤2 m; Fig. 1). Sites were 50 to 60 m apart. We measured 6 environmental variables at each of the 50 sites during the wet and dry seasons in 2010 for a detailed assessment of the current trophic status and physicochemical characteristics of the lake. We measured water temperature once with a digital thermometer. We made ≥3 measurements of chlorophyll *a* (chl *a*) concentration/site with a fluorometer (Aquafluor Handheld Fluorometer, Turner Designs, Sunnyvale, California). Concentration of dissolved O_2 (DO), pH, and conductivity were measured using handheld DO (DO_2 Meter 9200®; Jenway, Stone, UK), pH (ecoTestr pH2; Oakton Instruments, Vernon Hills, Illinois), and conductivity (ECTestr 11+ Eutech Instruments; Oakton Instruments) meters. From each site, we collected 3 random sediment cores to a depth of 10 to 15 cm for subsequent determination of organic content in the laboratory by organic mass-loss on ignition (Downing and Rath 1988). We homogenized samples with a spatula, dried them for 24 h at 70°C to constant mass, and weighed them. We ignited the dry samples in a muffle furnace for 4 h at 500°C, allowed them to cool to room temperature in a desiccator, and weighed them. At sites 1 to 20, we recorded Secchi depth, total P (HACH Lange test kit; HACH Corporation, Loveland, Colorado), total N (HACH Lange test kit), and Ca (HACH Lange test kit) (Fig. 1).

Mussel sampling and collection of population parameters

We assessed freshwater mussel diversity, population densities, and size-frequency distributions at each of the 50 sites within one 0.5- × 0.5-m quadrat that was randomly placed 1 to 3 m from the bank (i.e., the 1–3 m nearshore zone; n = 50 samples). The quadrat was subdivided into 4 sectors, each of which was searched systematically by hand for mussels down to ~10 cm sediment depth until no new mussel had been collected for 1 min. Quadrats typically were searched for a total of ~10 min. We identified mussels to species following Siddiqui et al. (2007) and counted them. We measured their shell length (SL) with vernier calipers following Aldridge (1999). For growth estimations, we measured SL at each continuous ring around the entire shell (= annulus) from 20 randomly selected specimens of each species following Aldridge (1999). We took each specimen from a different quadrat, thereby encompassing the entire lake margin. We used a random number generator to randomly select the

20 quadrats from the original 50 sampled. From each of the 20 quadrats, we chose a single mussel by applying a random-number generator to the lined-up mussels. Where the specimen selected had no clear annuli or had evident damage to the shell, we chose an adjacent specimen instead. Mussels were returned to the lake at the point of collection.

Macroinvertebrate sampling

To investigate diversity and abundances of other macroinvertebrates and their association with mussels, we collected a 2-min kick-sample with a standard square-framed net (frame width: 25 cm, mesh size: 250 μm) within a 3-m radius of the mussel quadrat at each of the 50 sites. We sampled all available habitats in proportion to their occurrence following the protocol of Furse et al. (1981). All taxa were identified to family level.

Filtration rate of individual mussels

To assess the importance of mussels as biofilters in the lake, we measured filtration rates in the laboratory in January 2010. The filtration rate of a mussel is defined as the volume of water that passes through the mussel's gills per unit time and can be approximated as clearance rates, i.e., the decrease in the concentration of chl *a* as phytoplankton is filtered out of the water (Coughlan 1969, Riisgård 2001, McIvor 2004). We transported 20 randomly selected specimens of each of the 2 mussel species (*P. caerulea* and *L. marginalis*) to the laboratory in lake water at ~20°C (approximate lake temperature at time of collection) where we measured chl *a* clearance rates. We allowed mussels to acclimatize to room conditions and temperature of 21°C for ~4 h. We placed each mussel individually in a randomly selected beaker with 0.5 L of algae-rich water collected from Ramna Lake (lat 23°44′16″N, long 90°24′00″E), which had a chl *a* concentration of 49.13 ± 12.42 μg/L and similar levels of organic and inorganic pollution as Dhanmondi Lake (Razzak et al. 2012, Mokaddes et al. 2013). Three control beakers held no mussels. We measured chl *a* concentration at the start of the experiment and in each beaker after 1 h with a fluorometer (Aquafluor Handheld Fluorometer). Care was taken not to touch or otherwise disturb the mussels. Shells showed no signs of periphyton growth.

Data analysis

We calculated trophic state indices (TSI) based on chl *a* concentration, total P concentrations, and Secchi depth (Carlson 1977). We calculated population growth curves, Walford plots, and von Bertalanffy equation coefficients as described in detail by Aldridge (1999) and Zieritz and Aldridge (2009). We estimated macroinvertebrate diversity at each of the 50 sites with Simpson's index as

$$D = 1 - \sum n(n-1)/N(N-1), \qquad \text{(Eq. 1)}$$

where n = the total number of individuals of a particular species, and N = the total number of individuals of all species (Simpson 1949). D varies from 1 to 0, with 1 representing infinite diversity and 0 representing no diversity.

To assess variation in water quality, we used presence–absence data of macroinvertebrate families to calculate Biological Monitoring Working Party (BMWP) scores for each site. We used modified indicator scores for each family taken from the work of De Zwart and Trivedi (1995) on Indian fresh waters. We excluded mussels from BMWP scoring.

We calculated clearance rate, i.e., decrease in chl *a* concentration (C) filtered out over time t, for each mussel as

$$m = M([\ln C_0 - \ln C_1]/t) - A, \qquad \text{(Eq. 2)}$$

where M is the volume of suspension (0.5 L/beaker) and A is the background rate at which particles settle out of suspension (measured in control beakers with no mussels present). We used a general linear model (GLM) in R (version 3.1; R Project for Statistical Computing, Vienna, Austria) fitting clearance rate as the response variable, species as a factor with 2 levels, mussel length as a covariate, and the interaction factor to test whether clearance rate differed between species or was influenced by mussel size.

We used the size-frequency distribution and density data for the 2 species to calculate population filtration rates (FRp) with an approach similar to that used by McIvor (2004) as follows: 1) We calculated the length-specific filtration rate for each mussel length and species present in the population based on regression equations for length–clearance rate distributions, 2) multiplied them by the number of mussels of that species and length, and summed the values to yield group filtration rates for the 2 species (for the number of individuals in the size-frequency distribution sample). 3) We divided these group filtration rates by the number of individuals, to give a mean individual filtration rate for the 2 populations, 4) which we then multiplied by the estimated number of each species, which was calculated as mean density/m^2 obtained from quadrat sampling multiplied by 12,500 m^2 (the area of the lake's 1-to-3-m nearshore zone measured in Google Earth®) to give population filtration rates for the nearshore zone. 5) We multiplied these values by 0.9 to account for the fact that 10% of mussels at any one time are likely to be resting (i.e., they have their valves closed) (Englund and Heino 1996). Considering that current evidence suggests similar filtration activity of mussels during day and night (Haag 2012 and references therein), we assumed that mussels filtered 24 h/d. We calculated the time taken ($t_{0.5}$) for the mussels to reduce the concentration of filterable particu-

Table 1. Means (± SD) and ranges for 10 environmental variables measured at 20 or 50 sites (Fig. 1) across Dhanmondi Lake during the dry (January to March 2010) and wet (July to August 2010) seasons. Trophic class was assigned according to Carlson (1977). n.a. = not applicable.

Environmental variable	Dry season	Wet season	Trophic class	Sites
pH	7.4 ± 0.3 (6.9–8.0)	7.5 ± 0.3 (6.9–8.0)	n.a.	1–50
Conductivity (μS/cm)	296 ± 22 (255–324)	175 ± 9 (145–189)	n.a.	1–50
Dissolved O_2 (mg/L)	4.3 ± 0.4 (3.7–5.2)	6.9 ± 1.3 (4.6–9.0)	n.a.	1–50
Organic content of sediment (%)	4.49 ± 1.34 (2.39–10.13)	4.85 ± 1.48 (2.84–10.84)	n.a.	1–50
Water temperature (°C)	20.7 ± 0.8 (19.4–22.5)	29.8 ± 1.3 (27.3–32.4)	n.a.	1–50
Chlorophyll *a* (μg/L)	9.76 ± 2.24 (7.18–14.40)	16.98 ± 4.77 (3.44–24.69)	meso- to eutrophic	1–50
Secchi depth (cm)	174 ± 36 (110–240)	121 ± 10 (110–140)	meso- to eutrophic	1–20
Total P (mg/L)	0.30 ± 0.11 (0.17–0.55)	0.13 ± 0.04 (0.05–0.20)	eu- to hypereutrophic	1–20
Total N (mg/L)	5.7 ± 1.9 (2.0–11.0)	2.3 ± 1.1 (1.0–5.0)	n.a.	1–20
Ca (mg/L)	73 ± 4 (60–78)	47 ± 8 (33–68)	n.a.	1–20

late matter in a given water volume (V_C) to ½ its original value as

$$t_{0.5} = (-\ln[0.5]V_C)\mathrm{FR_P}, \qquad \text{(Eq. 3)}$$

assuming no increase in concentration from algal growth and that all particles are filtered by mussels (McIvor 2004).

RESULTS

Environmental parameters

Water temperature was on average ~9°C warmer during the wet than the dry season (Table 1). Total P and N concentrations (at sites 1–20) were high and indicated a eutrophic to hypereutrophic state (Table 1). However, Secchi depth values (measured at sites 1–20 and averaging 1.7 and 1.2 m during the dry and the wet season, respectively) and chl *a* concentrations (measured at all sites and averaging 9.76 and 16.98 μg/L during the dry and the wet season, respectively) indicated a meso- to eutrophic status. Conductivity values (measured at all sites) were moderate throughout the year but higher during the dry than the wet season (Table 1). O_2 saturation (measured at all sites) ranged from 41 to 58% during the dry season and 60 to 118% during the wet season (based on minimum and maximum absolute O_2 values and average temperatures during the dry and the wet season, respectively). pH (measured at all sites) was neutral to slightly alkaline throughout the year.

Diversity and abundance of Unionida

Two species of mussels were found in the nearshore zone of Dhanmondi Lake. *Lamellidens marginalis* (Lamarck, 1819) was present at all 50 sites, whereas *Parreysia caerulea* (Lea, 1831) was found at 35 sites. Average mussel density was 218 individuals (ind)/m^2 (range 40–452 ind/m^2) in the 1-to-3-m nearshore zone of the lake, of which 186 ind/m^2 (20–452 ind/m^2) were *L. marginalis* and 32 ind/m^2 (0–176 ind/m^2) were *P. caerulea*. In total, 320 *P. caerulea* and 2359 *L. marginalis* specimens were found. Sampling was confined to the zone within 1 to 3 m of shore, but inspection of mussels from bridges in the central lake indicated that mussels were distributed throughout the lake bed.

Growth and population structure

Information obtained from growth curves (Fig. 2, Table 2) and size-frequency distributions (Fig. 3A, B) revealed that shells of each age-class were found for both

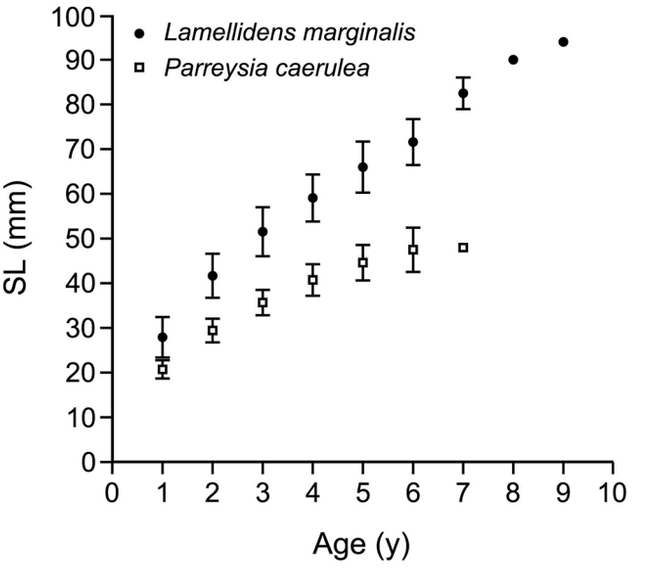

Figure 2. Mean (±1 SE) shell length (SL)/y of age of *Parreysia caerulea* (n = 20) and *Lamellidens marginalis* (n = 20) from Dhanmondi Lake during January to March 2010.

Table 2. Growth parameters for *Lamellidens marginalis* and *Parreysia caerulea* at Dhanmondi Lake. k = growth constant (rate at which SL_∞ is achieved); SL_∞ = asymptotic shell length (calculated from Walford equation); SL_{max} = observed maximum shell length in the field; Age_{max} = maximum age. Absolute growth rates (in bold) are given by slope of Walford equation.

Species	Walford equation	k	SL_∞ (mm)	SL_{max} (mm)	Age_{max}
Lamellidens marginalis	y = **0.891**x + 14.962	0.12	137	94	10
Parreysia caerulea	y = **0.725**x + 14.587	0.32	53	48	8

mussel species. For *L. marginalis*, the lack of growth rings in 2 specimens with shell lengths of 22 and 24 mm, respectively, indicated that they were born in the year of sampling, i.e., in 2010. We found no *P. caerulea* from 2010 but a relatively high number of 2009-born juveniles (characterized by ~19–24 mm in length; Figs 2, 3A, B). The multimodal distributions of abundances across size classes in *P. caerulea* and *L. marginalis* suggest that recruitment is irregular (Fig. 3A, B).

Association with macroinvertebrate fauna

In total, we found 3032 specimens of macroinvertebrates other than mussels in kick-samples. These specimens belonged to 16 families and 3 phyla (Arthropoda, Mollusca, and Annelida; Table 3). Chironomid Diptera (20% relative abundance) and viviparid Gastropoda (17%) were the dominant families, followed by belostomatid Hemiptera (11%). Simpson's diversity index calculated from macroinvertebrate (except Unionida) abundance data ranged from 0.46 to 0.94/site, with an average value of 0.79 ± 0.13.

Mussel density was strongly and positively correlated with macroinvertebrate taxon richness (r_s = 0.715, n = 50, $p < 0.001$), Simpson's diversity index (r_s = 0.451, n = 50, $p < 0.001$), and BMWP scores (r_s = 0.689, n = 50, $p < 0.001$) of the sites (Fig. 4A–C). These associations were particularly strong at densities >40 mussels/0.25 m^2 (~3.7 on the log[mussel density]-scale; Fig. 4A–C). The number of other macroinvertebrate taxa also differed between sites with 1 vs 2 mussel species (t = 11.19, df = 46, $p < 0.001$). Sites with both *P. caerulea* and *L. marginalis* had fewer macroinvertebrate taxa (8 families on average) than those where *P. caerulea* was absent (14 families on average).

Clearance rates and filtration capacity

Three of 40 mussels did not open during the filtration experiment and were not included in subsequent analyses. The average clearance rate per mussel in the laboratory was 247 mL/h, and some of the larger mussels cleared almost 900 mL/h (Fig. 5). Clearance rates increased with SL, but neither this relationship nor clearance rates differed significantly between the 2 species

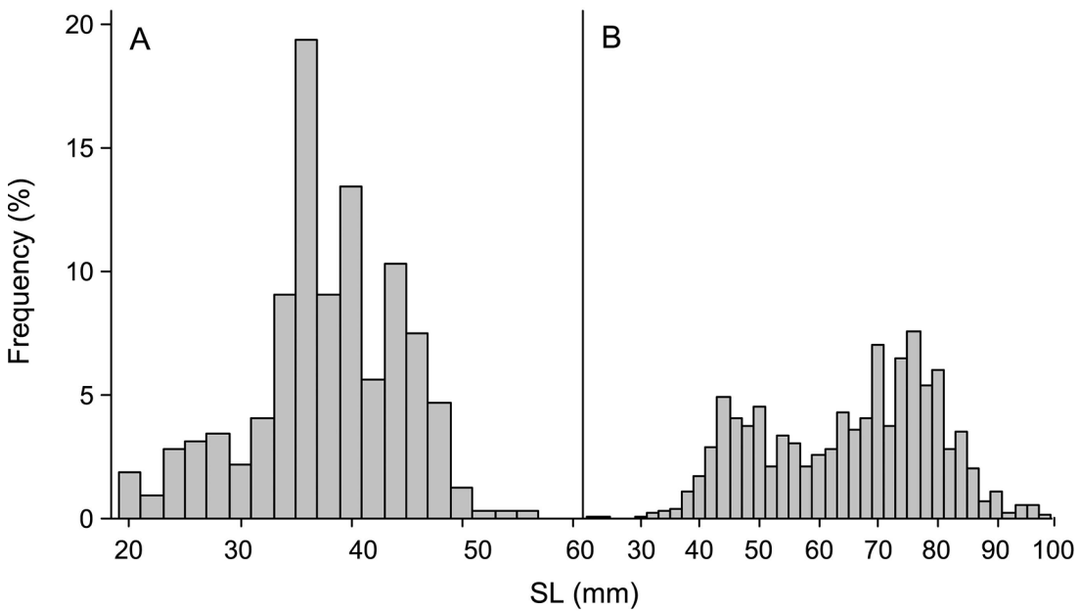

Figure 3. Size-frequency distribution of *Parreysia caerulea* (n = 320) (A) and *Lamellidens marginalis* (n = 2359) (B) shell length (SL) at Dhanmondi Lake during January to March 2010.

Table 3. Mean (± SD) and range of specimens/macroinvertebrate family and site collected by 2-min kick-sampling at 50 sites in Dhanmondi Lake.

Higher taxonomy	Family	Mean ± SD (range)
Phylum Mollusca	Bithyniidae	2 ± 3 (0–13)
Class Gastropoda	Pleuroceridae	1 ± 2 (0–7)
	Thiaridae	2 ± 7 (0–50)
	Viviparidae	10 ± 15 (0–103)
	Lymnaeidae	1 ± 2 (0–6)
	Planorbidae	4 ± 4 (0–17)
Phylum Annelida		
Class Clitellata	Naididae	3 ± 4 (0–13)
Phylum Arthropoda	Palaemonidae	5 ± 7 (0–35)
Order Decapoda	Potamidae	1 ± 3 (0–21)
Order Coleoptera	Dytiscidae	4 ± 5 (0–21)
Order Ephemeroptera	Baetidae	4 ± 5 (0–17)
Order Hemiptera	Belostomatidae	7 ± 5 (0–21)
	Gerridae	3 ± 3 (0–13)
	Mesoveliidae	1 ± 1 (0–5)
Order Diptera	Chironomidae	12 ± 10 (0–45)
Order Odonata	Coenagrionidae	1 ± 1 (0–5)

(general linear model, response variable = m, covariate = SL: $F_{1,35}$ = 8.35, p = 0.007; factor = species: p = 0.438; interaction factor: p = 0.774; r^2 = 0.19; Fig. 5). The regression equation describing the relationship between m and SL was calculated for both species combined and was $m = 2.1812SL^{1.1481}$. Based on this regression equation and size-frequency distributions for the 2 species recorded in the lake (Fig. 3A, B), the average in situ filtration rate for a mussel in Dhanmondi Lake was estimated to be 138 mL/h for *P. caerulea* and 262 mL/h for *L. marginalis*.

Given average in situ filtration rates and mussel densities (32 *P. caerulea* and 186 *L. marginalis*/m^2), freshwater mussels in the nearshore zone of the lake filter 54 L h^{-1} m^{-2}. Considering that ~10% of mussels are not filtering at any given time, and that the 1-to-3-m nearshore zone of Dhanmondi Lake was estimated to cover an area of 12,500 m^2, freshwater mussels in this part of the lake filter a collective volume of 607,500 L/h. *Lamellidens marginalis* provides ~92% and *P. caerulea* provides ~8% of the filtering power. Assuming an average depth of 1 m within the 1-to-3-m nearshore zone, the mussels would take ~21 h to filter the equivalent water volume (i.e., 12,500 m^3) and 14 h to filter out ½ the particulate matter of this zone.

DISCUSSION

Dhanmondi Lake and its biota are exposed to severe anthropogenic pollution (Hossain et al. 2010, Razzak et al. 2012, Mokaddes et al. 2013). Despite high levels of organic and inorganic pollutants, the water of the lake is surprisingly clear and biodiversity is remarkably high. Our results indicate that this water quality is in large part because of the presence of and functions served by dense populations of freshwater mussels. *Lamellidens marginalis* is the major contributor in this respect, whereas *P. caerulea* plays a comparatively minor role.

A mussel-rich lake in central Dhaka

Lamellidens marginalis and *P. caerulea* are 2 of the most common and widespread mussels of Indo-Burma (Subba Rao 1989, Nesemann et al. 2007, Ramakrishna and

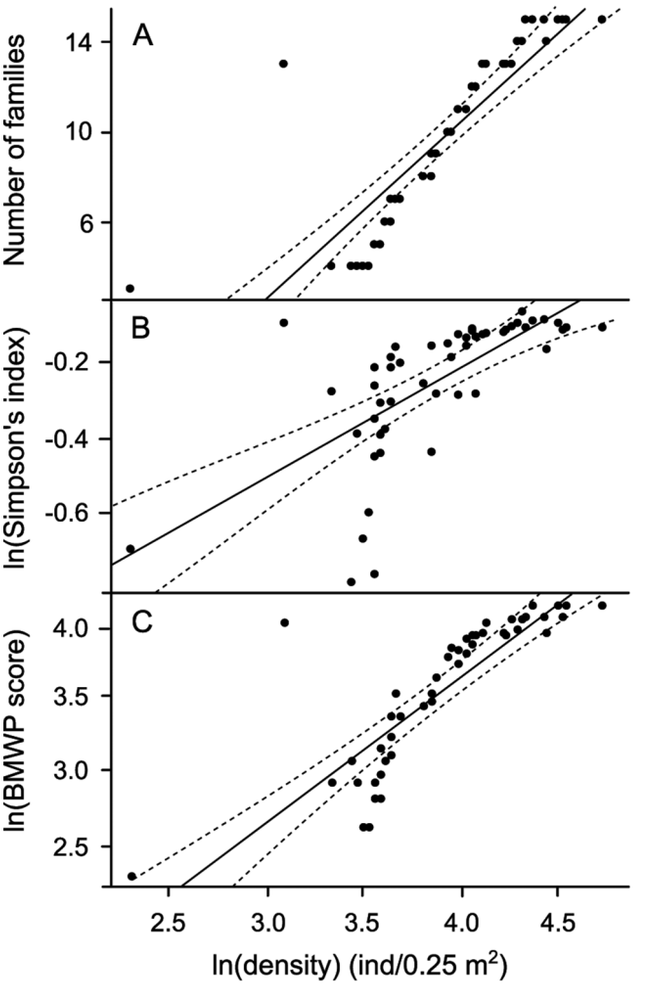

Figure 4. Relationships between freshwater mussel density and macroinvertebrate taxon richness (r_s = 0.715, n = 50, p < 0.001) (A), diversity (measured as Simpson index) (r_s = 0.451, n = 50, p < 0.001) (B), and water quality index (measured as Biological Monitoring Working Party [BMWP] score) (r_s = 0.689, n = 50, p < 0.001) (C) at 50 sites in Dhanmondi Lake during January to March 2010. Regression lines and 95% confidence intervals are represented by solid and dashed lines, respectively. Ind = individuals.

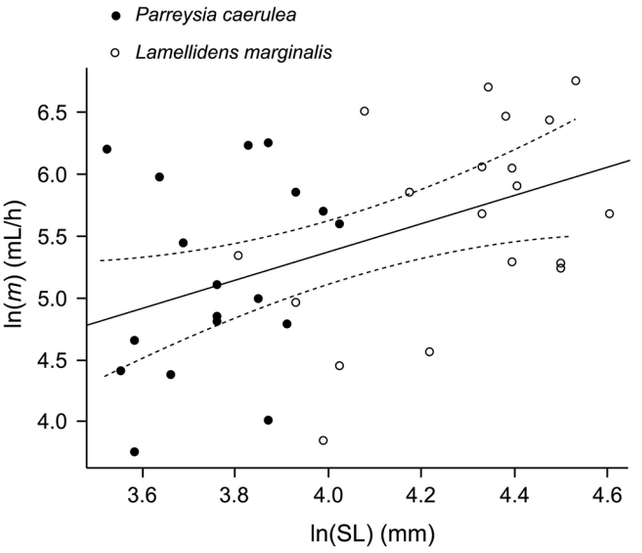

Figure 5. Relationship between shell length (SL) and clearance rate (m) in *Parreysia caerulea* and *Lamellidens marginalis* from Dhanmondi Lake during January to March 2010. Regression line (regression equation: $m = 2.1812SL^{1.1481}$) and 95% confidence intervals relate to the whole data set (i.e., both species combined).

Dey 2007). The conservation status of both species is currently assessed as of "Least Concern" (IUCN 2013), but our study shows that their populations can provide crucial ecosystem functions, rendering their protection imperative to ecosystems and people. In spite of severe organic and inorganic pollution (Hossain et al. 2010, Razzak et al. 2012, Mokaddes et al. 2013), both species form dense populations in Dhanmondi Lake. The observed average mussel density of >200 ind/m^2 at Dhanmondi Lake's nearshore zone exceeds mussel densities recorded from other areas of the world, where they rarely reach >20 ind/m^2 (e.g., Downing and Downing 1992, Zieritz et al. 2014). In the vast literature on freshwater mussels of North America and Europe, we are aware of only 1 published record in which density is >100 ind/m^2 (Haag 2012). In contrast, despite the scarcity of data on southern and eastern Asia, population densities >100 ind/m^2 have been recorded relatively frequently in this region (e.g., 118 ind/m^2 *Unio biwae* Kobelt, 1879 in Lake Biwa [Mori 1976]; 125 ind/m^2 *Parreysia* spp. and 84 ind/m^2 *Lamellidens* spp. in India [Kumar 2002]). Presence of comparatively dense mussel populations in subtropical freshwater systems is likely to be connected to high nutrient availability, light intensity, and temperature, resulting in higher productivity, metabolic rates, and food availability for mussels in subtropical than in temperate regions (Melack 1976, Reynolds 2006, Zieritz and Aldridge 2009).

The small number and absence of very young *L. marginalis* and *P. caerulea*, respectively, in our sample is probably a result of inefficient sampling. A greater number of small, juvenile specimens might have been captured by removing and sieving the sediment (Haag 2012).

Mussels as biofilters

The fact that comparatively high mussel population densities are achieved in a polluted, urban freshwater habitat, such as Dhanmondi Lake, is of particular significance when considering that the ecological processes performed by mussels are linearly related to biomass (Strayer et al. 1999, Vaughn et al. 2004). As a result, the effects of mussels on nutrient translocation and cycling increase with mussel abundance and biomass (Vaughn and Hakenkamp 2001). In Dhanmondi Lake's nearshore zone, where mussels are estimated to filter the water volume in 21 h, the intensive, steady removal of phytoplankton and other particles from the water column crucially affects the lake's ecosystem. In particular, it reduces phytoplankton biomass (as chl *a* concentration) and dramatically improves water clarity, as indicated by moderate algal biomass and high water transparency despite abundant N and P availability for algal growth. In other words, mussel filtration has altered this zone of the lake from a hypereutrophic/eutrophic state (as indicated by total P concentrations) to a eutrophic/mesotrophic state (as indicated by chl *a* concentrations and Secchi depth).

Clearance (filtration) rates of Dhanmondi Lake mussels are comparable to those reported for various other Asian, North American, and European species (Alimov 1969, Bruin and Davids 1970, Lewandowski and Stanczykowska 1975, McIvor 2004, Kim et al. 2011). However, Kryger and Riisgård (1988) reported filtration rates of same-sized *Anodonta* and *Unio* spp. exceeding those reported here by ~4×. At least part of this discrepancy is probably attributable to the fact that these authors measured filtration rates on undisturbed, buried mussels. Such an experimental setup was not feasible in our study, so clearance rates were estimated on specimens that lay on 1 valve. Given these comparatively unnatural experimental conditions, actual filtration rates of *P. caerulea* and *L. marginalis* may be considerably higher than reported here. Underestimation of filtration rates in our study is particularly likely when considering that higher temperatures present during the wet season would be expected to lead to higher filtration rates because of increased metabolic rates (Vanderploeg et al. 1995). Further underestimation of filtration rates, in particular for larger *L. marginalis* specimens, may have been caused by the fact that large mussels cleared almost 900 mL in a 500-mL water sample during the 1-h experiment. This situation indicates that food concentration in the container was very low at the end of the hour, which may have caused mussels to slow their filtration rate. Nevertheless, stress caused by pollution also might slow filtration of mussels at Dhan-

mondi Lake, and our results might be a true reflection of filtration activity in the lake.

Mussels as ecosystem engineers

In the nearshore zone of the lake, mussel density was very strongly positively correlated with macroinvertebrate richness and diversity and BMWP scores. Moreover, generally speaking, macroinvertebrate diversity was high at most sites when considering the various sources of pollution to which Dhanmondi Lake is subjected. Therefore, our results indicate that freshwater mussels can enhance biodiversity at the ecosystem level, as previously shown by, e.g., Aldridge et al. (2007), and on a microhabitat scale. Mussels appear to act as "microhabitat engineers".

Thanks to considerable research on the functional ecology of mussels in North American freshwaters, the mechanisms behind these patterns can at least be hypothesized. Mussels directly enhance habitat structure and complexity for other organisms because their shells serve as large, hard substrate (Vaughn and Hakenkamp 2001). Thus, an increase in mussel density may be expected to result in an increase in habitat structure for an increasing number of different organisms. Mussels also enhance habitat quality indirectly for a range of benthic organisms. Their filtering activity leads to decreased phytoplankton abundances and increased water clarity, which in turn, suppresses algal blooms and O_2 depletion and enhances benthic photosynthesis and O_2 levels (Tankersley and Dimock 1993, Lampert and Sommer 2007). Their burrowing activity mixes and aerates the substrate (Vaughn and Hakenkamp 2001, Gutiérrez et al. 2003). Thus, an increase in mussel density may be expected to increase O_2 availability and improve other habitat conditions, which would render the site suitable for a wider range of organisms including relatively sensitive ones, such as filter-feeding mayfly larvae (Connolly et al. 2004).

Mussels as bioindicators

The fact that mussel densities explained ~70% of the variation in macroinvertebrate taxon richness and water-quality index scores in the nearshore zone of Dhanmondi Lake could find application in a cost-effective and quick method to assess the status of tropical freshwater ecosystems. Macroinvertebrate taxon richness and water quality could be approximated by determination of freshwater mussel densities, which would require no taxonomic knowledge and could be carried out rapidly and entirely in the field (Aldridge et al. 2007). As such, this approach would circumvent the time-consuming and costly process of traditional biological water-quality assessment, which involves identification of macroinvertebrate diversity and abundance (Reynoldson 1984, Chatzinikolaou et al. 2006) and requires reliable identification keys, expert knowledge, and equipment to identify specimens, all of which tools are difficult if not impossible to obtain in developing countries. The new method proposed herein would be particularly useful to select sites of conservation priority and in making rapid comparisons among sites within or among water bodies. However, more studies across a diversity of lotic and lentic water bodies, including sampling at low mussel densities and in deep water, should be performed to test the generality of the patterns we observed at Dhanmondi Lake. Also, although our data clearly indicate that the presence of mussels improved conditions within Dhanmondi Lake, conditions in the lake are far from ideal as a result of ongoing pollution and nutrient enrichment. In fact, the lake may support such high densities of mussels *because* it is in poor enough condition to provide abundant food.

Conclusions

Bangladesh's freshwater habitats and the diverse fauna and flora they support are under threat from pollution, sedimentation, dam developments, and various other anthropogenic factors (Dudgeon et al. 2006, Allen et al. 2010). Water of Dhanmondi and other, similar lakes is being contaminated because of increased human activities including construction works and tourism (Hossain et al. 2010). In the coming decades, human-induced pressure will become even more intense given the increasing human population and economic growth in the region (United Nations 2004). In addition, climate change is likely to become a major threat for freshwater biodiversity in developing countries (Gopal et al. 2010, Woodward et al. 2010). Our study shows that mussels are pivotal in maintaining the functioning of a freshwater ecosystem in the center of Dhaka that is directly used by people. Mussels support biodiversity, provide high-quality habitat conditions in Dhanmondi Lake and clear water to thousands of people inhabiting the surrounding area. If this and other, similar mussel communities were to be lost, maintaining the systems' functionality would require high financial and other human inputs. Many Western countries have acknowledged the importance of freshwater mussels for some time and are investing heavily in protecting endangered species, such as the Freshwater Pearl Mussel *Margaritifera margaritifera* Linnaeus, 1758. We hope that our study will serve as an important piece of evidence for promoting the conservation of freshwater mussel populations in developing nations.

In addition, we have demonstrated the potential value of using mussels in monitoring freshwater systems. Comparison of mussel densities over spatial scales can help identify sites of conservation priority, especially in regions where taxonomic knowledge of invertebrates is comparatively poor and localized. Besides their use as bioindicators, native mussels should be considered a powerful tool

in the management and restoration of polluted bodies of fresh water.

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