Aquatic Conservation: Marine and Freshwater Ecosystems

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Declines in Freshwater Mussels and Loss of Mussel–Invertebrate Interactions in the Subtropical Waterbodies of Dhaka, Bangladesh

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ABSTRACT

1. Freshwater mussels are a globally threatened taxon, but little is known about population trajectories for species outside Europe and North America. To contribute to understanding of mussel conservation status outside these regions, we surveyed mussel and other invertebrate populations in waterbodies across Dhaka, Bangladesh, to assess population trends and the role of mussels in structuring benthic communities.
2. We found that mussel populations in Dhanmondi Lake, our focal waterbody, have declined in density by approximately 90% between 2010 and 2023. *Lamellidens marginalis* declined by 90.8% from an average density of 47.9 ± SE 7.1 mussels $0.25\,\mathrm{m}^{-2}$ in 2010 to 4.4 ± SE 0.7 mussels $0.25\,\mathrm{m}^{-2}$ in 2023, while *Indonaia caerulea* declined by 89.4% from an average density of 6.6 ± SE 1.0 mussels $0.25\,\mathrm{m}^{-2}$ in 2010 to 0.7 ± SE 0.1 mussels $0.25\,\mathrm{m}^{-2}$ in 2023.
3. Previously detected associations between mussels and other invertebrate taxa, and between mussels and community composition, have been lost. Non-mussel invertebrates have also declined significantly, with an average decrease in abundance of 27%, alongside decreases in family richness and Shannon-Wiener diversity. These declines occurred despite apparent improvements in water quality.
4. Findings from other waterbodies across Dhaka also suggest the loss of mussel species including *L. marginalis*, *I. caerulea* and *Parreysia corrugata* from some locations, as well as the presence of the non-native mussel *Pilsbryoconcha exilis* at river sites.
5. Our results reflect a wider, global pattern of enigmatic declines in freshwater mussels and the possible loss of associated ecosystem functioning, which may be going unnoticed in less-studied areas including the subtropics.

1 | Introduction

Freshwater mussels (Unionida) are a globally threatened taxon (Lopes-Lima et al. 2018) yet play important roles in freshwater ecosystems. As filter feeders, mussels remove algae and organic matter as well as pollutants from the water column (Vaughn, Gido, and Spooner 2004; Strayer 2014), improving water clarity and quality (Atkinson et al. 2013). By depositing organic matter (faeces and pseudofaeces), mussels contribute to the translocation of nutrients from the water column to benthic sediments (Strayer 2014), which they can also aerate through burrowing (Boeker et al. 2016). As well as these metabolic and active processes, mussel shells provide habitat and shelter for other species (Vaughn and Spooner 2006; Ilarri et al. 2018).

As a result of these ecosystem engineering effects, mussel abundance and diversity can be positively correlated with invertebrate biodiversity (e.g., Vaughn and Spooner 2006; Aldridge, Fayle, and Jackson 2007; Ilarri et al. 2018; Simeone, Tagliaro, and Beasley 2021). Some mussel species have stronger effects on invertebrate communities than others (Spooner and Vaughn 2006; Ollard, Chowdhury, and Aldridge 2023), for example, due to differences in body size or habitat preferences, which means that mussel community composition as well as abundance is important. These associations can be linked to particular taxa or functional feeding groups (as described by Cummins 1973). For example, mussels can facilitate collectors, which feed on fine detritus, by providing food through biodeposition (Howard and Cuffey 2006), supporting taxa including Oligochaeta (Spooner and Vaughn 2006; Paul et al. 2009) and Chironomidae (Vaughn and Spooner 2006; Paul et al. 2009). Mussels can also provide a substrate for algae (Vaughn, Spooner, and Galbraith 2007), providing food for the scraper functional group (Simeone, Tagliaro, and Beasley 2021) including the snail families Lymnaeidae and Viviparidae (Aldridge, Fayle, and Jackson 2007).

Despite this importance in supporting other taxa, mussels are threatened and declining worldwide (Böhm et al. 2021), with 45% of assessed species categorised by the IUCN as extinct, threatened or near threatened (Lopes-Lima et al. 2018). Declines in mussel populations are characterised by extinctions in rare and range-restricted species as well as local extirpations and decreases in abundance of common, widespread species (Galbraith, Spooner, and Vaughn 2010; Vaughn 2010; Nakamura, Sousa, and Mesquita-Joanes 2023; Ollard and Aldridge 2023). Losses include gradual declines in density and recruitment as well as unexplained large-scale die-offs and mass mortality events (Haag 2019). These changes may have large cascading effects on invertebrate communities and on ecosystem functioning (Vaughn 2010; van Ee, Johnson, and Atkinson 2022; Hopper et al. 2023). Alongside this global decline in mussels, other freshwater invertebrates are also undergoing widespread declines (van Klink et al. 2020). Freshwater invertebrates are particularly vulnerable due to often high regional endemism, small home ranges and poor dispersal ability (Collier, Probert, and Jeffries 2016). Since mussel abundance appears to be positively associated with, and may actively increase, invertebrate abundance, it may also be predicted that the loss of mussels from ecosystems could further degrade invertebrate communities.

The drivers of decline in freshwater mussels as well as other invertebrates are varied and often enigmatic. Habitat degradation, including channel modification and dredging, reduces or disturbs benthic substrate available to mussels (Aldridge 2000; Sousa et al. 2021), while dam construction alters flow regimes and nutrient transfer (Vaughn and Taylor 1999) and obstructs the migration of host fish required by mussel larvae for development (Modesto et al. 2018). Pollutants, including pharmaceuticals (Gilroy et al. 2020), pesticides (Salerno et al. 2018), heavy metals (Cope et al. 2021) and emerging contaminants such as microplastics (Berglund et al. 2019), pose a particular threat to filter feeders since exposure and the potential for bioaccumulation is high. Climate change increases the frequency of drought events and the risk of heat stress and stranding (Galbraith, Spooner, and Vaughn 2010; Vaughn, Atkinson, and Julian 2015), as well as the frequency of extreme flow events which can dislodge mussels from the sediment (Sotola et al. 2021). Invasive species, including other bivalves, threaten mussels, such as through competition for food, settling space and access to larval hosts (Sousa, Pilotto, and Aldridge 2011; Strayer and Malcom 2018). Changes to host fish populations, including overharvesting and stocking with non-native species, also threaten mussel recruitment and dispersal (Modesto et al. 2018). Pathogens and parasites can also threaten mussels and lead to mass mortality events (Grizzle and Brunner 2009; Brian and Aldridge 2019; Richard et al. 2020). Many of these threats also apply to other invertebrates.

Tracking mussel population change over time can help to identify threats and highlight needs for intervention. Past datasets and long-term monitoring offer important resources to characterise population and species trajectories (Hopper et al. 2024), which are generally poorly understood in unionids (Lopes-Lima et al. 2021), particularly outside Europe and North America (Aldridge et al. 2023).

There is little information on the population biology of unionid mussels in Bangladesh, but research in 2010 showed that in Dhanmondi Lake in Dhaka, mussel densities were very high (>200 individuals m^{-2}), and mussel density was strongly positively correlated with invertebrate richness and diversity indices (Chowdhury, Zieritz, and Aldridge 2016). In addition, mussel density was positively associated with specific invertebrate families (Belostomatidae, Dytiscidae, Gerridae, Lymnaeidae, Planorbidae and Viviparidae) and functional feeding groups (predators and scrapers), and sites with higher mussel density showed greater similarity to one another in invertebrate community composition (Ollard, Chowdhury, and Aldridge 2023). However, mussel species identity was important; these patterns occurred for the large-bodied, higher density *Lamellidens marginalis* but not the smaller, less abundant *Indonaia caerulea* (previously *Parreysia caerulea*; Bolotov et al. 2022). *Lamellidens marginalis* and *Indonaia caerulea* are both listed as having conservation status of Least Concern by the IUCN Red List (Budha and Daniel 2010; Madhyastha, Budha, and Daniel 2010). Among other freshwater invertebrates, Rahman et al. (2022) found that significant declines in richness have occurred in Bangladesh in response to habitat degradation.

In the period since 2010, extensive works have taken place at Dhanmondi Lake to improve its aesthetic and amenity value, including removal of hanging toilets, which released sewage directly into the water as well as development of a secondary transfer station for the city waste management system. Ducks and tilapia fish have been stocked for the purpose of ecosystem improvement (Mithu 2021).

We revisited Dhanmondi Lake to resurvey mussel and invertebrate populations, 13 years after previous data on these populations were collected (Chowdhury, Zieritz, and Aldridge 2016; Ollard, Chowdhury, and Aldridge 2023). Since the lifespan of both species is up to approximately 10 years (Chowdhury, Zieritz, and Aldridge 2016), this sampling interval encompasses multiple generation times. Given the recent improvement works to the lake, we expected mussel populations in the lake to have remained stable or even increased. In addition, we hypothesised that less organic matter entering the lake may have led to decreased mussel size and slower growth rates, since this would result in lower food availability. We aimed to assess changes to mussel populations over the period, as well as to determine whether relationships between mussels and other invertebrates had remained constant over time. We also surveyed mussel populations at a further five lakes and two rivers around Dhaka, to build a broader picture of mussel distribution, community composition and habitats in the region.

2 | Methods

2.1 | Study Location

We conducted sampling in Dhanmondi Lake, Dhaka, Bangladesh (Table S1) from March to April 2023, repeating the methodology employed by Chowdhury, Zieritz, and Aldridge (2016) in January to March 2010. The lake is approximately 3 km long and 35–100 m wide. It has historically been heavily polluted, receiving sewage, industrial effluents and municipal and domestic waste water. Phosphate levels have been recorded in the hypereutrophic range (0.34–0.85 ppm, Hossain, Kabir, and Quraishi 2010). Further details of the site are described in Chowdhury, Zieritz, and Aldridge (2016).

We additionally sampled mussels at a further seven waterbodies in and around Dhaka from March to April 2023 to build a broader picture of freshwater mussel distribution. These were Boikali Lake, Ramna Lake, Mirpur Lake, Aftabnagar Lake, Hatir Jheel, the Turag River and the Buriganga River. All the sampling sites are in or close to densely populated urban areas. Areas of both Mirpur Lake and Aftabnagar Lake are used for aquaculture, and small-scale agriculture also occurs in the surrounding areas of these lakes. Both have wide, shallow margins with silty sediment. Hatir Jheel is a large lake surrounded by urban areas, with high levels of boat traffic. Boikali Lake and Ramna Lake are ornamental lakes situated in public parks. They have steeper, embanked margins. The Buriganga and Turag Rivers are large, very slow-flowing rivers flowing through both urban and cultivated areas, and have high levels of boat traffic. Coordinates for all sites are given in Table S1.

2.1.1 | Abiotic Variables

We measured the following abiotic variables for each waterbody: dissolved oxygen concentration (DO; mg L^{-1}), electrical conductivity (EC; μS cm^{-1}), pH, Secchi depth (cm), temperature (°C), chlorophyll a concentration (Chl a; μg L^{-1}), salinity (ppm), total dissolved solids (TDS; ppm) and nitrate and phosphate concentrations (mg L^{-1}). We measured Chl a concentration using a handheld fluorometer (Aquafluor Handheld Fluorometer, Turner Designs, Sunnyvale, CA, USA). We used handheld meters to measure pH, EC, TDS and temperature (Multiparameter Tester HI98130, Hanna Instruments Ltd, UK), salinity (SALscan20 Pocket Salinity Tester, SciQuip Ltd, UK) and DO (Dissolved Oxygen Meter PDO-519, Lutron Instruments, Taiwan). We collected water samples for nitrate and phosphate measurements and transported them to the laboratory of the Bangladesh Council of Scientific and Industrial Research (BCSIR) for analysis using American Public Health Association (APHA) standard methods 4110.B for nitrate and 4500/P.C for phosphate. We measured Chl a, DO, pH, EC, TDS, salinity, temperature and Secchi depth at 10 sites for each waterbody (these were a subset of the sites where mussels and macroinvertebrates were sampled). We collected water samples for nitrate and phosphate concentrations from three sites within each waterbody, except for Mirpur Lake where we only retrieved two samples (due to loss of the third sample). Abiotic conditions at each waterbody are reported in Appendix S1.

2.2 | Mussel and Invertebrate Sampling

Sampling sites were located 1–3 m from shore, at a depth of less than 2 m. Sites were separated by at least 50 m to avoid spatial autocorrelation. In Dhanmondi Lake, sampling sites were the same as those surveyed in 2010 (Chowdhury, Zieritz, and Aldridge 2016), with the exception of four sites that could no longer be accessed due to development, leaving a total of 46 sampling sites. At each of the other waterbodies, we surveyed 10 sites, again separated by a minimum of 50 m except for at Boikali Lake where the lake was too small to allow 10 sites using this approach, so a minimum of 20-m separation was used instead. Quadrat sampling for mussels, invertebrate kick samples and water sampling repeated the methods used by Chowdhury, Zieritz, and Aldridge (2016). No permits or approval of research ethics committees were required because all work was conducted with unregulated invertebrate species.

2.2.1 | Mussel Sampling

We conducted mussel sampling using a 0.25-m^2 quadrat placed on the lakebed or riverbed as closely as possible to the location used by Chowdhury, Zieritz, and Aldridge (2016), which we searched by hand to a depth of 10 cm until we had retrieved all mussels (no new mussels collected after 5 min of sampling). We recorded counts of mussel species and measured the length of each mussel along its longest axis using digital callipers, as well as the length of each external annual ring, again along its longest axis. We also measured the wet mass of each mussel using a portable balance. We roughly dried mussels for 10 s using a paper towel before weighing. We also recorded counts of shells of each species. We then returned all mussels to the water.

In addition, at waterbodies other than Dhanmondi Lake, where mussels were scarcer and the quadrat method therefore yielded less representative samples, we conducted a hand search of the sediment within an approximately 50-m radius of the sampling site, both in the water and on the bank. We used this qualitative approach to detect the presence of mussels and shells, but not as a quantitative method to measure density. Searches lasted for 10 min at every site except sites 4–10 in the Buriganga River, where mussel density was much higher and we considered that 5-min searches were sufficient. At Hatir Jheel, we conducted searches using a net rather than by hand sampling and only carried out these searches at three sites, since visual inspection suggested the presence of severe blue-green algae as well as inorganic contaminants, rendering hand-sampling too risky.

2.2.2 | Invertebrate Sampling

We sampled invertebrates at every second site in Dhanmondi Lake (25 sites total). We measured counts at each site using

2-min kick-samples within a 3-m radius of the quadrat, using a square-framed net with frame width 25 cm and mesh size 250 µm. We identified all invertebrates to family level, except planarians that we identified only to class. We also categorised invertebrates into functional feeding groups (predator, scraper, shredder or collector-gatherer) following the system proposed by Cummins (1973), using classifications reported in the literature for tropical freshwater invertebrates. Functional group assignments and references are reported in Appendix S2. We carried out invertebrate sampling at Dhanmondi Lake only.

2.3 | Data Analysis

We conducted all analyses in R v4.2.2 using standard statistical tests in base R.

We assessed changes in mussel and invertebrate density, abundance and diversity (richness and Shannon-Wiener index) between Dhanmondi Lake sites in 2010 and 2023 using paired *t*-tests. We calculated family-level richness as the total number of families (excluding mussels) found at each site. Family-level Shannon-Wiener diversity for each site was calculated using the package *vegan* v2.6-4 (Oksanen et al. 2022).

In addition, we assessed correlations between changes in mussels and in invertebrates by subtracting the count in 2010 from that in 2023, such that negative results indicated a decline at the site and positive values an increase at the site. We then tested correlations using Spearman's rank tests.

We tested associations between mussel density and invertebrate abundance, richness and Shannon diversity using linear regressions of invertebrate metrics against mussel density. We tested associations between mussel density and specific invertebrate families and functional feeding groups using negative binomial regressions using the function *glm.nb* from the package *MASS* v7.3-58.1 (Venables and Ripley 2002) and the package *car* v3.1-1 (Fox and Weisberg 2019). We also tested changes in counts of invertebrates between the two sampling years using negative binomial regression.

We also used RDA to analyse the relationships between environmental variables, mussel occurrence and invertebrate community composition across the 2 years in Dhanmondi Lake, using the function *rda* from the package *vegan*. We used Hellinger-transformed species count data as the response matrix, including only sites from Dhanmondi Lake in 2010 and 2023 for which environmental data were also collected ($n = 30$ sites). We used mussel density of both species separately, pH, EC, DO, Chl a and Secchi depth as predictors. We tested the RDA model using the function *anova.cca* from the *vegan* package.

To analyse the effect of physicochemical variables on mussel occurrence across waterbodies, we tested mussel presence/absence at sites using mixed effects logistic regression with waterbody as a random effect, using the function *glmer* from the package *lme4* v1.1-31 (Bates et al. 2015). We only included sites in these analyses for which both abiotic variables and mussels were sampled. Mussels were coded as present at a site if at least one live individual was found. We tested the effect of abiotic variables on mussel length using mixed effects linear regression with both site and waterbody as random effects, using the function *lmer* from the package *lme4*. For nitrate and phosphate concentration only, we used simple linear regression rather than mixed effects regression since nutrient concentration was measured only once at each site, leading to perfect correlation between site and concentration; additionally, since there were few sites with data for both nutrient concentration and mussel lengths, and therefore few or a single site(s) per waterbody, there was further strong correlation between waterbody and concentration. Therefore, we did not include random effects in these regressions. To test temperature, we first detrended data due to the effect of time of day on measured water temperature. We did this by fitting a linear regression to temperature against time of day across all sites. We then took residuals for each site.

We also conducted principal component analysis (PCA) using abiotic variables (salinity, EC, TDS, Chl a, DO, pH, time-adjusted temperature and Secchi depth). We then extracted PC1 and PC2. We used mixed effects logistic and linear regressions to test the effect of these PCs on mussel presence versus absence and length, respectively. We conducted PERMANOVA to test clustering according to waterbody, using the function *adonis2* from the package *vegan*.

3 | Results

3.1 | Mussel Declines

Across sites in Dhanmondi Lake, mussels of both species present in the lake declined significantly (Figure 1). *Lamellidens marginalis* declined by 90.8% from an average density of 47.9 ± SE 7.1 mussels $0.25\,m^{-2}$ in 2010 to 4.4 ± SE 0.7 mussels $0.25\,m^{-2}$ in 2023 (paired *t*-test: $t_{(45)} = 10.95$, $p < 0.001$). *Indonaia caerulea* declined

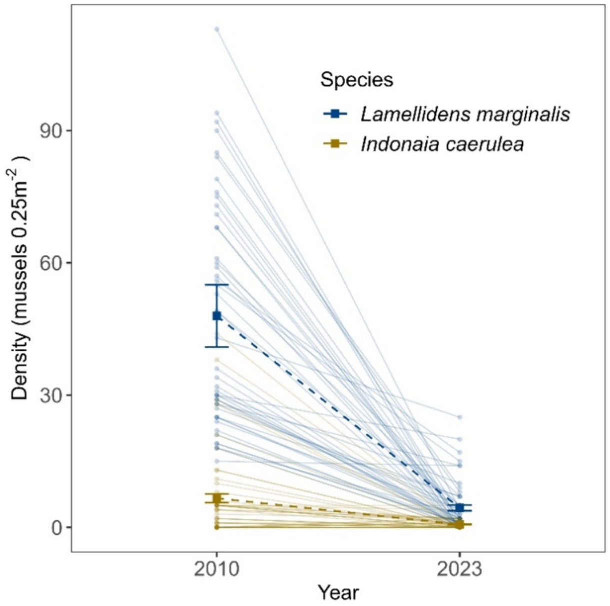

FIGURE 1 | Changes in density of mussel species between 2010 and 2023 at 46 sites in Dhanmondi Lake for *Lamellidens marginalis* and *Indonaia caerulea*. Bold points with standard error bars and dashed lines represent waterbody-wide averages for each species, while values for individual sites are lighter with unbroken lines.

by 89.4% from an average density of 6.6 ± SE 1.0 mussels 0.25 m^{-2} in 2010 to 0.7 ± SE 0.1 mussels 0.25 m^{-2} in 2023 (paired *t*-test: $t_{(45)} = 3.88$, $p < 0.001$).

The average length of live *L. marginalis* was significantly different between 2010 and 2023, and lengths of live mussels from both years also differed significantly from shells collected in 2023 ($F_{(2,2585)} = 16.11$, $p < 0.001$); all pairwise comparisons were significant ($p < 0.01$ for all cases). Lengths of *L. marginalis* were lowest for live mussels in 2023 (59.7 ± SE 0.9 mm), followed by live mussels in 2010 (64.6 ± SE 0.3 mm) and highest for shells collected in 2023 (69.7 ± SE 1.4 mm). Length for *I. caerulea* also differed significantly according to sample type ($F_{(2,365)} = 4.239$, $p = 0.0151$), although the only significant pairwise comparison was for live and shell samples in 2023 ($p = 0.014$). Lengths of *I. caerulea* followed the same ranking as for *L. marginalis*, being lowest for live mussels in 2023 (34.1 ± SE 1.6 mm), followed by live mussels in 2010 (37.1 ± SE 0.4 mm) and shells in 2023 (39.8 ± SE 1.4 mm).

Across Dhaka, we found live mussels at six of the eight sampled waterbodies (Figure 2), with no live mussels found at either Ramna Lake or Hatir Jheel, although large numbers of shells were present embedded in bank sediments at Ramna Lake. Across the waterbodies, we found three species of live unionid mussels: the native *Lamellidens marginalis* and *Indonaia caerulea* and the introduced *Pilsbryoconcha exilis*. *Lamellidens marginalis* was present in Dhanmondi Lake, Aftabnagar Lake, Mirpur Lake, Boikali Lake and the Turag River. We found *P. exilis* in both the Turag and Buriganga Rivers, where it dominated mussel communities, making up 100% of live sampled individuals in the Buriganga River and an average of 85.0% ± SE 6.9% of samples in the Turag River. We found *I. caerulea* only in Dhanmondi Lake, with one shell also found at Aftabnagar Lake. In addition, we found large numbers of the invasive venerid mussel *Corbicula fluminea* at the Turag and Buriganga River sites, and shells of *Parreysia corrugata* at the Buriganga River and Boikali Lake.

3.2 | Invertebrate Declines

Invertebrates (excluding mussels) also declined across sites, decreasing significantly across all tested metrics (family richness, Shannon-Wiener diversity and total abundance) from 2010 to 2023 (Figure 3). Number of families decreased from 9.3 ± SE 0.8 families per sample in 2010 to 6.2 ± SE 0.4 in 2023 (paired *t*-test: $t_{(24)} = 3.23$, $p = 0.004$). Shannon-Wiener diversity decreased

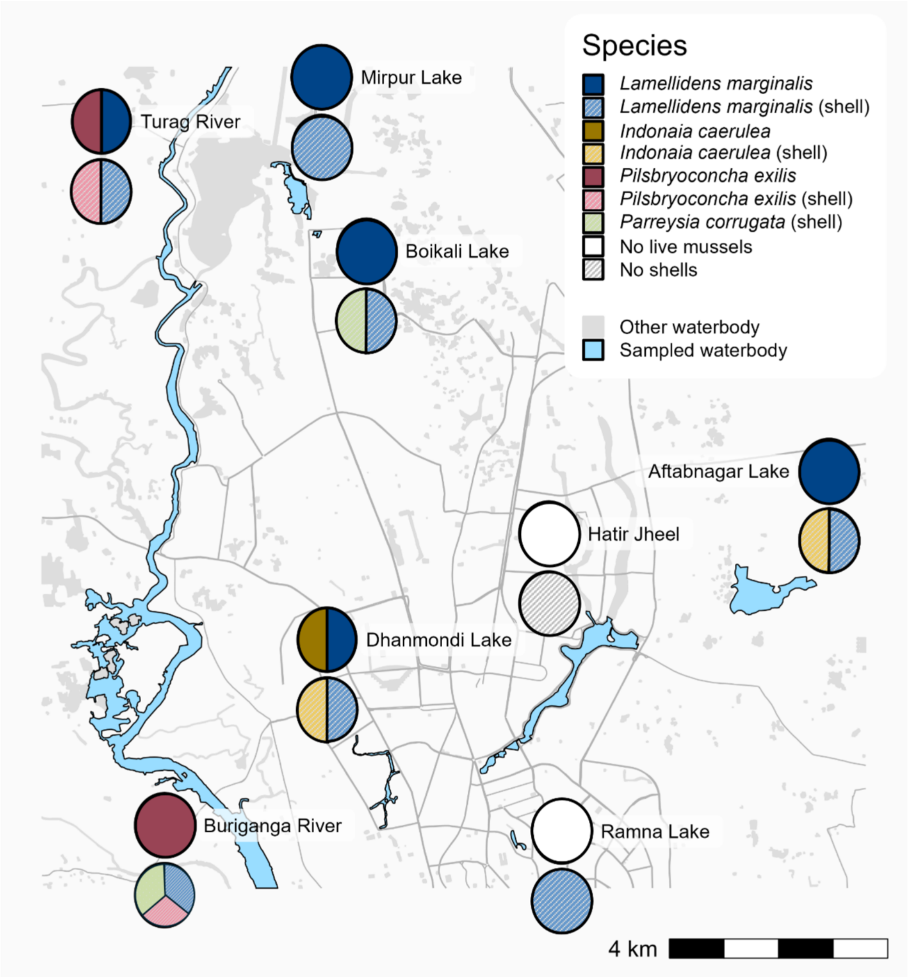

FIGURE 2 | Map of Dhaka area showing location of sampled waterbodies. Circles show the species composition of live mussels (top) and shells (bottom) found at each waterbody in 2023, aggregated across sampling sites. Note that circles show presence/absence rather than proportional species composition. Map data from OpenStreetMap.

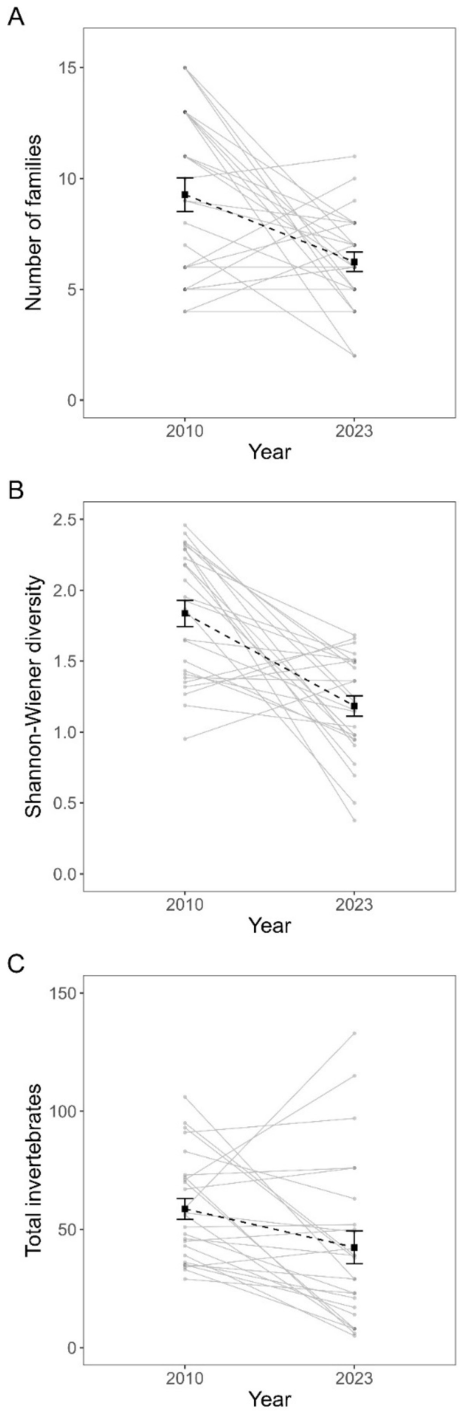

FIGURE 3 | Change in (A) invertebrate family richness, (B) Shannon-Wiener diversity and (C) total abundance across sites in Dhanmondi Lake from 2010 to 2023. All values exclude mussels. Bold points with standard error bars and dashed lines represent waterbody-wide averages, while values for individual sites are grey with unbroken lines.

from 1.84 ± 0.09 in 2010 to 1.18 ± SE 0.07 in 2023 (paired *t*-test: $t_{(24)} = 4.94$, $p < 0.001$). Total invertebrate abundance decreased from 58.7 ± SE 4.4 individuals per sample in 2010 to 42.4 ± SE 6.9 in 2023 (paired *t*-test: $t_{(24)} = 2.38$, $p = 0.025$).

Among invertebrate families that were found in both sampling years, five of the 10 families showed significant declines in abundance using negative binomial regression (Table S3): Naididae declined by 72.3%, Chironomidae declined by 92.4%, Belostomatidae declined by 99.7%, Lymnaeidae declined by 84.5% and Baetidae declined by 99.4%. In addition, six families present in 2010 were not found in 2023 samples (all losses were statistically significant), while 16 families were detected in 2023 but not 2010. Of these, only the increase for Libellulidae was statistically significant (Table S3).

When invertebrates were assigned to functional feeding groups (FFGs), three of the four FFGs showed significant declines in abundance using negative binomial regression. Collectors declined by 89.2%, from 19.59 ± 1.66 individuals per sample in 2010 to 2.11 ± 0.45 individuals per sample in 2023 ($\chi^2_{(1)} = 131.674$, Holm-adjusted $p < 0.001$). Predators declined by 93%, from 20.07 ± 2.15 individuals per sample in 2010 to 1.41 ± 0.27 individuals per sample in 2023 ($\chi^2_{(1)} = 148.616$, Holm-adjusted $p < 0.001$). Shredders declined by 92.9%, from 0.91 ± 0.50 individuals per sample in 2010 to 0.07 ± 0.04 individuals per sample in 2023 ($\chi^2_{(1)} = 9.114$, Holm-adjusted $p = 0.006$). There was no significant change in the abundance of scrapers, with 20.98 ± 2.95 individuals per sample in 2010 and 19.46 ± 4.60 individuals per sample in 2023 ($\chi^2_{(1)} = 0.057$, Holm-adjusted $p = 0.811$).

3.3 | Mussel–Invertebrate Associations

The change in mussel density at sites in Dhanmondi Lake was significantly positively correlated with change in invertebrate biodiversity, both as family richness (Spearman's rank test: $S = 1214.1$, $\rho = 0.533$, $p = 0.006$) and Shannon-Wiener diversity (Spearman's rank test: $S = 1288.5$, $\rho = 0.504$, $p = 0.010$), so that sites showing a greater decline in mussel density also showed a greater decline in invertebrate biodiversity (Figure 4). However, there was no significant correlation between change in mussel density and change in total invertebrate abundance (Spearman's rank test: $S = 1700.1$, $\rho = 0.346$, $p = 0.090$, NS).

There was no significant correlation between mussel density at each site in 2023 and any metrics of invertebrate diversity or abundance (family richness: $F_{(1,48)} = 1.589$, $p = 0.214$; Shannon-Wiener diversity: $F_{(1,48)} = 1.162$, $p = 0.287$; total abundance: $F_{(1,48)} = 0.0846$, $p = 0.772$). There was also no significant association in 2023 between mussel density and abundance of any individual invertebrate family or functional feeding group ($p > 0.05$ for negative binomial regressions in all cases).

3.4 | Abiotic Conditions

In Dhanmondi Lake, we found significant increases between 2010 and 2023 for DO ($t_{(9)} = -4.71$, Holm-adjusted $p = 0.003$), EC ($t_{(10)} = -4.19$, Holm-adjusted $p = 0.004$) and Secchi depth ($t_{(11)} = -10.52$, Holm-adjusted $p < 0.001$). pH decreased significantly ($t_{(17)} = 4.21$, Holm-adjusted $p = 0.002$). Chl a showed no significant change ($t_{(14)} = -1.45$, Holm-adjusted $p = 0.169$, NS) (Figure 5).

Redundancy analysis (Figure 5) showed that invertebrate community composition across the 2 years (2010 and 2023) at sites

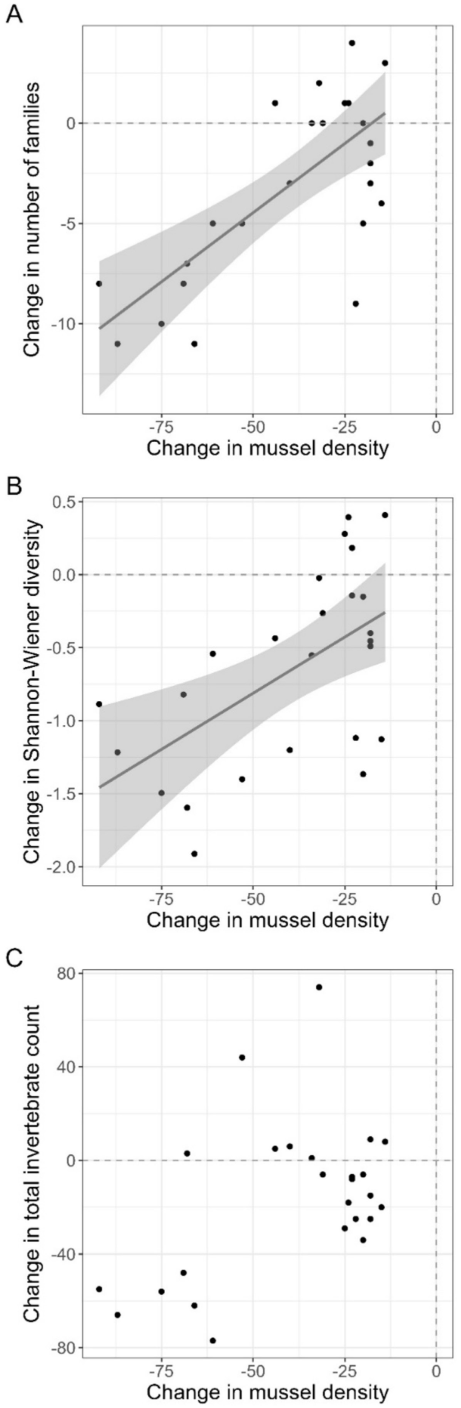

FIGURE 4 | Associations between the change in mussel density between 2010 and 2023 and changes in (A) family richness, (B) Shannon-Wiener diversity and (C) total invertebrate abundance at sites in Dhanmondi Lake. Negative values represent declines while positive values represent increases. Dashed lines indicate axes of zero change. Linear regressions are plotted for panels A and B, for which associations were statistically significant.

in Dhanmondi Lake was significantly affected by both mussel density and environmental predictors (adjusted $R^2=0.205$, $F_{(7,22)}=2.07$, $p=0.001$). The first two constrained axes (RDA1 and RDA2) explained a combined 73.0% of the variation in community composition across sites. Density of *L. marginalis* ($F_{(1)}=4.06$, $p=0.001$) and *I. caerulea* ($F_{(1)}=2.15$, $p=0.032$), chlorophyll a ($F_{(1)}=2.05$, $p=0.044$) and pH ($F_{(1)}=2.88$, $p=0.06$) were all significant predictors of variation in community composition.

Using mixed effects logistic regression to model mussel presence/absence against individual abiotic variables for *L. marginalis*, no variables significantly improved prediction compared to a model including only waterbody as a random effect ($p>0.05$ when comparing full model and reduced model for all variables). Variables tested were time-adjusted temperature, pH, EC, TDS, salinity, DO, Secchi depth and Chl a concentration. Other mussel species did not occur at a sufficient number of different waterbodies to test in this way. Using logistic regression, there was also no significant effect of either nitrate or phosphate concentration on mussel presence versus absence, although no mussels of any species were found at the sites with the highest nitrate and phosphate concentrations (sites in Mirpur Lake and Hatir Jheel).

PCA of abiotic variables across sites and waterbodies showed distinct and statistically significant clustering of sites according to waterbody (PERMANOVA with 999 permutations: pseudo-$F_{(7,72)}=137.22$, $R^2=0.930$, $p=0.001$; Figure 6). PC1 explained 52.7% of variance between sites, and PC2 explained a further 21.7%. However, neither PC1 nor PC2 significantly improved prediction of *L. marginalis* presence versus absence when tested in mixed effects models. Presence versus absence of mussels (*L. marginalis* and *P. exilis*) across sites and abiotic conditions is shown in Figure 6.

4 | Discussion

We found that in Dhanmondi Lake, mussel populations of both *Lamellidens marginalis* and *Indonaia caerulea* have fallen in density by approximately tenfold between 2010 and 2023; *L. marginalis* has also decreased in average body size. In addition, across Dhaka mussel species appear to have become rare or been lost from lakes and rivers, with shells but no live individuals of species found at multiple waterbodies, although it is possible that live individuals of the species were present but not detected. At the same time, populations of other macroinvertebrates have also declined in Dhanmondi Lake, linked to falling mussel densities, and associations between mussels and invertebrates have been lost. Possible drivers for these declines include contamination by heavy metals, pesticides and other pollutants; effects of invasive species, including invasive mussels; and fish stocking for aquaculture, as well as other impacts of anthropogenic disturbance including physical habitat alteration. These factors are likely to have synergistic effects on mussels and other invertebrates.

In addition to this decline in mussel density, mussels in 2023 also showed size differences compared to 2010. For both *L. marginalis* and *I. caerulea*, live mussels measured in 2023 were smaller than shells (which are assumed to be older due to the long persistence time of mussel shells in waterbodies); for *L. marginalis*, they were also smaller than live mussels measured in 2010. The short lifespan (often <10 years) of these species means that such rapid changes are possible over the 13-year sampling interval. Growth in mussels is highly

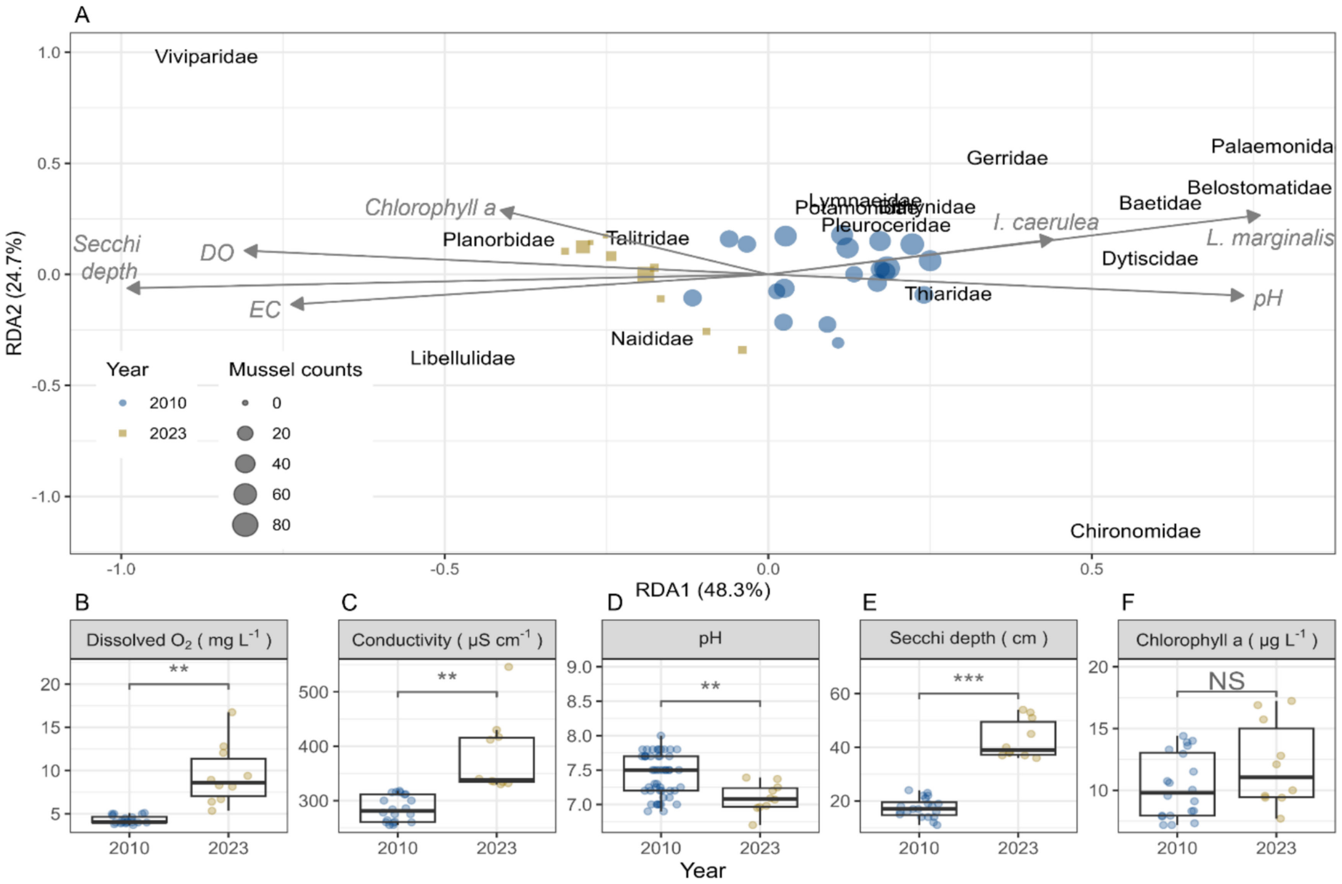

FIGURE 5 | (A) RDA plot showing community composition at sites from 2010 (blue circles) and 2023 (yellow squares) and its relationship with environmental variables and mussel density. The size of each point is proportional to the total number of mussels of both species (individuals $0.25\,\mathrm{m}^{-2}$) at the site. To avoid overcrowding, only families contributing more than 0.05 to overall variation have bene plotted; other families can be assumed to fall close to the centre of the plot. (B–E) Changes in abiotic variables DO, EC, pH, Secchi depth and Chl a concentration in Dhanmondi Lake between 2010 and 2023. For 2010, $n = 50$ for all variables except Secchi depth where $n = 20$. For 2023, $n = 10$ for all variables. $^*p < 0.05$; $^{**}p < 0.01$; $^{***}p < 0.001$; NS, not significant.

plastic within species and populations (Haag and Rypel 2011). Decreases in size may reflect a reduction in food availability (Arter 1989; Versteegh et al. 2010), potentially as a result of decreased organic matter input; growth can also be restricted by other stressors such as turbidity and temperature (Luck and Ackerman 2022). It is also possible that smaller average size could also reflect younger average age and therefore higher recruitment (or shorter lifespan, if fewer mussels live long enough to grow to larger size). However, comparison of growth patterns showed that for both *L. marginalis* and *I. caerulea*, average size was shorter at every age (Figure S1), suggesting that this was not the case here and that the size differences we found were not caused by differences in age structure.

The fact that, for some sites and species, we found only shells, rather than live mussels, suggests that these species have become rare at these sites or may have been locally extirpated. There is little other information available on mussel distributions in the area. However, *Lamellidens corrianus*, *Lamellidens jenkinsianus*, *Parreysia corrugata* and the non-native *Novaculina gangetica* have been reported from the Turag river (Mandal and Ahmed 2014; Baki, Hossain, and Bhouiyan 2016) and *L. jenkinsianus* from the Buriganga River (Baki, Hossain, and Bhouiyan 2016) in addition to the species we recorded. If these species were still present at the sites in 2023, they are likely to have been rare.

Other invertebrate taxa in Dhanmondi Lake also declined, and invertebrate family-level richness, total abundance and Shannon-Wiener diversity all decreased. Among individual invertebrate families, those that decreased in abundance generally did so by a large amount (70%–> 99%). Of the commonly occurring taxa, snail families (Viviparidae, Planorbidae, Bithyniidae and Thiaridae) were the only ones to remain approximately stable over the period (although Lymnaeidae did decline significantly). Additionally, three out of four functional feeding groups showed significant declines (all > 85%)—collectors, predators and shredders (although shredders contained only two rare families so results should be treated cautiously), demonstrating the community-wide nature of declines. Only scrapers did not decline, largely due to the stability of Viviparidae counts, which contributed a large proportion of counts of this group.

The loss of mussels and other invertebrates at sites in Dhanmondi Lake were linked: Sites that lost more mussels also lost more invertebrate diversity (family richness and Shannon-Wiener diversity). Supporting this, redundancy

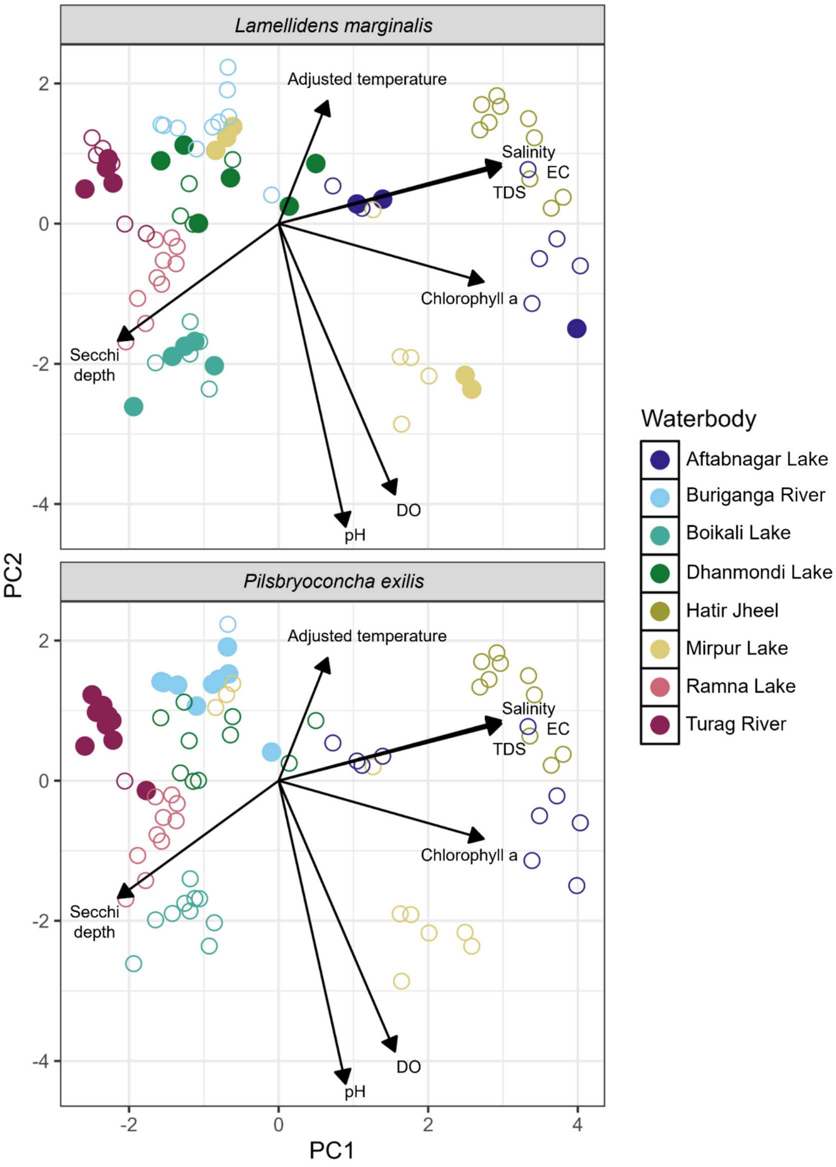

FIGURE 6 | PCA of abiotic variables measured across sites and waterbodies, showing mussel species presence versus absence for *Lamellidens marginalis* (top) and *Pilsbryoconcha exilis* (bottom). Points represent individual sampling sites and are coloured according to the waterbody in which they are located; both plots show identical PCA results. Open circles are sites where no live individuals of the species were found, while closed circles are sites where at least one live individual of the species was found. *L. marginalis* and *P. exilis* co-occurred only at the Turag River. Presence versus absence data for *Indonaia caerulea* is not plotted, since it was found only at four sites where abiotic variables were also measured, all within Dhanmondi Lake. Aftabnagar Lake = al, Buriganga River = Bg, Boikali Lake = bk, Dhanmondi Lake = dl, Hatir Jheel = hj, Mirpur Lake = ml, Ramna Lake = rl, Turag River = tr.

analysis showed that differences in invertebrate communities were driven by mussel density as well as by environmental factors, specifically chlorophyll *a* concentration and pH. The influence of mussel density on invertebrate community composition may reflect a loss of interspecific interactions resulting from the ecological engineering effects of mussels. Alternatively, sites that lost more mussels and other invertebrates may have undergone greater ecological degradation, such as physical disturbance or contamination (although we did not detect any differences in measured water quality parameters), causing decreases in both mussel density and invertebrate diversity. However, there was no association between loss of mussels and change in overall invertebrate abundance, mainly due to the fact that there were very high numbers of snails (mostly Viviparidae, but also Planorbidae, Bithyniidae and Thiaridae) at some sites, including sites with large decreases in mussels, which outweighed decreases in other, less abundant taxa.

In 2010, mussel density (for *L. marginalis* but not *I. caerulea*) in Dhanmondi Lake was strongly positively correlated with invertebrate biodiversity (Chowdhury, Zieritz, and Aldridge 2016; Ollard, Chowdhury, and Aldridge 2023), as well as with specific invertebrate families and functional feeding groups (Ollard, Chowdhury, and Aldridge 2023). However, this relationship appears to have broken down—mussels are no longer associated with invertebrate diversity or abundance, or with any specific families or functional feeding groups. It is possible that if mussels were facilitating other taxa, mussel densities are now too low to have any significant effects.

Without further data, it is difficult to pinpoint specific causes of these severe declines. A range of possible stressors may have contributed, and it is likely that multiple stressors, possibly interacting synergistically, may be responsible. For waterbodies across Dhaka, mussels were found across a wide range of environmental conditions, showing broad environmental tolerance. Comparison with 2010 suggests Dhanmondi Lake has improved in quality with much higher dissolved oxygen and greater Secchi depth in 2023. This is supported by local reports that the lake has become cleaner, with less untreated waste entering the water. However, we did find a significant decrease in pH, which could be linked to mussel and invertebrate declines (Wang et al. 2008; Taskinen et al. 2011). The cause of this decrease in pH is unclear. In 2023, pH in Dhanmondi Lake averaged 7.1, which may be around the lower tolerance threshold for *L. marginalis* (Natarjan and Susithira 2015).

Conductivity in Dhanmondi Lake increased significantly between 2010 and 2023, which could reflect higher levels of contaminants and can also harm mussel populations (Wang et al. 2017; Sanchez Gonzalez et al. 2021). Conductivity was very high at Hatir Jheel, probably reflecting high levels of contamination; Hatir Jheel also had much higher phosphate loading than other waterbodies, and together, these may explain the absence of mussels from the waterbody. Both nitrate and phosphate loading were also relatively high at Mirpur Lake, and within the lake, no mussels were present at the sites where nutrient loading was highest.

Heavy metal contamination, which has been associated with decreased mussel density (Cope et al. 2021), has also been reported for Dhanmondi Lake (Qureshi 2010; Uddin et al. 2023), the Buriganga River (Bhuiyan et al. 2014) and the Turag River (Banu et al. 2013). Heavy metal accumulation of Ni, Pb, Zn and Mn has been reported in *L. marginalis* from Dhanmondi Lake (Salam and Rokonujjaman 2016) and of Cr, Cd, Cu and Pb for *L. marginalis* in the Buriganga River (Saha et al. 2023). Both lethal and sublethal responses to heavy metals have been reported for *L. marginalis*, including valve closure (Yasmeen and Pathan 2021), lower growth (Hossain et al. 2023a) and increased mortality (Hossain et al. 2023a).

Pesticide contamination is also common across waterbodies in Bangladesh (Khatun et al. 2008; Hasan, Shahriar, and Jim 2019; Parvin, Haque, and Tareq 2022) and can also elicit both lethal and sublethal responses in *L. marginalis* (Moorthy et al. 1983; Kumar et al. 2012a, 2012b; Hossain et al. 2023b). Additionally, chemical treatment of waterbodies prior to and during fish aquaculture is common in Bangladesh. This can include dosing with pesticides, lime, salt or potash to suppress aquatic invertebrates (Salma et al. 2022), which are perceived to interact antagonistically with stocked fish. Dhanmondi Lake has reportedly been treated with lime, salt and potassium-based fertiliser (Md. Selim, pers. comm.), and treatment may also have occurred at other sampled waterbodies, particularly those with aquaculture activity (Mirpur Lake and Aftabnagar Lake).

Fish stocking also presents a possible threat to mussels in Dhaka lakes used for aquaculture. Dhanmondi Lake is regularly stocked with fish for aquaculture and angling, with 1.5 t of fingerlings reared and harvested every three months (Md. Selim, pers. comm.). Stocked species include *Labeo rohita*, *Catla catla*, *Labeo calbasu*, *Hypopthalmichthyes molitrix*, *Hypopthalmichthyes nobilis*, *Labeo gonius*, *Cirrhinus mrigala*, *Cirrhinus reba*, *Oreochromis mossambicus*, *Oreochromis niloticus*, *Channa punctata*, *Channa striatus*, *Channa marulius*, *Puntius sophore* and *Puntius sarana*.

Fish, especially if captive-bred, can be hosts for particular life stages of parasites such as trematodes, which can go on to infect mussels (Brian and Aldridge 2019). Additionally, stocking waterbodies with fish that are poor hosts for mussel larvae dilutes the pool of suitable hosts and could result in declines of host fish populations through competition or other antagonism (Douda et al. 2013). *L. marginalis* is a host generalist which can successfully use multiple fish species as hosts. However, the suitability of different host species varies. Among the species known to be stocked in Dhanmondi Lake, *Labeo rohita* and *Catla catla* may be poorer hosts compared to other species (Janakiram 2003; Sku et al. 2021, 2023). Therefore, the relative stocking abundances of these species may affect recruitment success in mussels. There is little information in the literature on suitable hosts for *I. caerulea* or the other mussel species found during our surveys. Fish can also interact with population densities of other invertebrates, including directly through predation (Jones and Sayer 2003) and indirectly through habitat alteration (Zambrano, Scheffer, and Martínez-Ramos 2001).

The invasive unionid *Pilsbryoconcha exilis* and the invasive venerid mussel *Corbicula fluminea* were abundant at riverine sites. They may have contributed to possible species losses at the Buriganga River. Elsewhere, *C. fluminea* has been implicated in mussel declines and lower mussel growth, which may be due to competition for food (Haag et al. 2021) and space, while large die-offs cause ammonia toxicity. Invasive unionid mussels can also show strong niche overlap and competition with native species (Geist et al. 2023). While *P. exilis* was only found at river sites in this study, it is commonly found in lakes and ponds elsewhere in Bangladesh and may be expected to spread more widely.

The results in Dhaka mirror declines of similar magnitude reported from mussel populations elsewhere (McDowell and Sousa 2019; Nakamura, Sousa, and Mesquita-Joanes 2023; Ollard and Aldridge 2023; Szlauer-Łukaszewska et al. 2024). There is a lack of information on mussel populations and trajectories outside Europe and North America (Aldridge et al. 2023), including for Southeast Asia (Zieritz et al. 2018). While nondirectional fluctuations in mussel communities can take place (Hopper et al. 2024), it is unlikely that the magnitude of declines we observed in Dhanmondi Lake fall within the mussel communities' normal range of variation. The declines we report in other invertebrates also reflect wider trends. This is the case both in Bangladesh, where Rahman et al. (2022) found a decrease in invertebrate richness associated with habitat degradation and globally (van Klink et al. 2020).

Our results show enigmatic declines in mussels as well as other freshwater taxa, involving both the possible loss of rarer species from locations as well as the decrease in abundance of common species. These declines can occur even when water quality is apparently improving. Such serious decreases in abundance are likely to have cascading effects on trophic webs and ecosystem functioning, with the loss of important interspecific interactions. This study should be regarded as an initial step towards developing a more comprehensive understanding of population trends in freshwater ecosystems in this region. Further surveys at future time points to extend the information reported here on population and ecosystem trajectories would enable a better understanding of these declines and their drivers and impacts. A combination of information about intact, non-degraded ecosystems to provide a baseline and regular surveying to match population trends to their possible drivers will be needed to enable effective, targeted conservation and restoration.

Author Contributions

Isobel Ollard: conceptualisation, methodology, formal analysis, investigation, writing – original draft, writing – review and editing, visualisation, project administration. **David C. Aldridge:** conceptualisation, methodology, writing – review and editing, supervision. **Fatima Jannat:** investigation, writing – review and editing. **Gawsia W. Chowdhury:** conceptualisation, methodology, investigation, resources, data curation, writing – review and editing, supervision, project administration.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Data are available through the Apollo Digital Repository at 10.17863/CAM.108485.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.