

## Diversity and distribution of freshwater molluscan fauna in reservoirs and headwater streams of the Kala Oya river basin in Sri Lanka

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Received: 29.04.2021    Revised: 15.06.2021    Accepted : 17.06.2021    Online: 15.09.2021

**Abstract** In this study, the variation of aquatic molluscan diversity concerning seasonal water level fluctuations (WLF) and sediment texture was investigated in some perennial irrigation reservoirs and the associated headwater streams in the Kala Oya river basin in Sri Lanka. Altogether 11,752 molluscan specimens belonging to 10 gastropod taxa (96.6%) and 2 bivalve taxa (3.4%) were identified. Of these, 11,282 specimens (96.0%) were from reservoir sampling sites and the remainder 470 (4.0%) was from the associated headwater streams. Of the gastropods, the individuals of the genus *Melanoides* showed the highest distribution index (DI) of 0.75 followed by *Bellamya* (DI = 0.63) and *Thiara* (DI = 0.60). The DI of the gastropod molluscs showed a significant positive relationship with their shell size ( $p < 0.05$ ). Although molluscan diversity and taxa richness were comparatively lower in headwater streams than in reservoir sampling sites, Viviparidae (*Bellamya*;  $0.06 \pm 0.03$ ), Bithyniidae (*Bithynia*;  $0.21 \pm 0.07$ ) and Thiaridae (*Thiara*;  $4.8 \pm 1.9$  and *Melanoides*;  $1.1 \pm 0.8$ ) showed higher relative abundance (expressed as individuals per  $\text{dm}^3$ ) in the headwater streams. The reservoir water level fluctuation showed a significant negative relationship with molluscan taxa richness ( $p < 0.05$ ), but not with the Shannon-Weaver diversity index ( $p = 0.073$ ). The distribution of molluscs was also found to be related to the sediment texture where the most abundant gastropod genera *Bellamia*, *Bithynia*, and *Thiara* were widely distributed in sandy substrates in reservoirs and associated streams in the Kala Oya river basin.

**Keywords:** freshwater molluscs, gastropod distribution, irrigation reservoirs, Thiaridae, Viviparidae, water level fluctuation

### INTRODUCTION

Molluscs are one of the most important biotic elements in aquatic ecosystems and contribute to ecosystem functioning by intensive biofiltration, bioturbation, decreasing bottom current velocity, increasing microhabitat complexity and heterogeneity, decomposing litter, and serving as a major food source for fishes and birds (Bódis et al. 2014; Vaughn et al. 2008; Padghane et al. 2017). Molluscan populations are responsible for any changes in aquatic environments and are therefore considered ecosystem engineers (Gutiérrez et al. 2003; Lathlean and McQuaid 2017; Yan et al. 2020). Being ecosystem engineers, they are directly

or indirectly involved in changing the physical state of the biotic/abiotic components and the other constituents in the habitat and hence contribute to the overall resource availability (Bódis et al. 2014). Molluscs also help increase the productivity of aquatic systems so that their abundance can be treated as an indirect measure of aquatic productivity (Waghmare and Kulkarni 2015; Padghane et al. 2017; Vaughn 2017). In the fields of bioindication and biomonitoring, freshwater gastropods and bivalves have been successfully used to obtain information on the quality of freshwater ecosystems and quantify the exposure, and to determine the effects of contaminants (Markert et al. 1999; Zuykov et al. 2013; Srivastava



and Singh 2020) owing to their large size, limited mobility, high abundance, and relative easiness to collect and identify (Oehlmann and Schulte-Oehlmann 2003; Ladeiro et al. 2014; Khan et al. 2019).

Freshwater molluscs are sensitive to natural disturbances such as floods, droughts, competition with invasive alien fauna, and habitat alteration (Bandara et al. 2021; Sousa et al. 2021), and seasonal water level fluctuation (WLF) in reservoirs (Kolding and van Zwieten 2012). All these disturbance events result in drastic changes in their diversity (Dudgeon et al. 2006; Régnier et al. 2009), and distribution patterns (Geist 2011; Buffagni 2021).

In Sri Lanka, the majority of the early studies on freshwater molluscs were carried out in the mountain streams of the central highlands, and focussed on their taxonomical aspects (e.g., Fernando 1969; Starmühlner 1974, 1984). There were subsequent attempts to investigate the ecology of molluscs relating to their diversity and distribution and to assess their importance in environmental monitoring programs. For example, Idroos and Manage (2012) studied the relationships of some molluscan genera with physicochemical parameters in stream habitat. Gamlath and Wijeyaratne (1997) highlighted the importance of some aquatic gastropod species as bioindicator organisms in a lotic water body. Also, another study conducted in the Negombo estuary indicated that some other molluscan taxa such as *Cerithidea* sp., *Dentalium* sp., Hydrobiid sp., *Terebralia palustris*, *Faunus ater*, and Thiarid sp. could be used as bioindicators in the assessment of wetland health (Dahanayaka and Wijeyaratne 2006). In addition, Wijeyaratne and Bellanthuduwa (2017) reported that the molluscan community showed significant spatial variations and that *Bithinia tentaculata* and *Pila globosa* could be used as possible bioindicators to detect water and sediment quality in an urban wetland ecosystem.

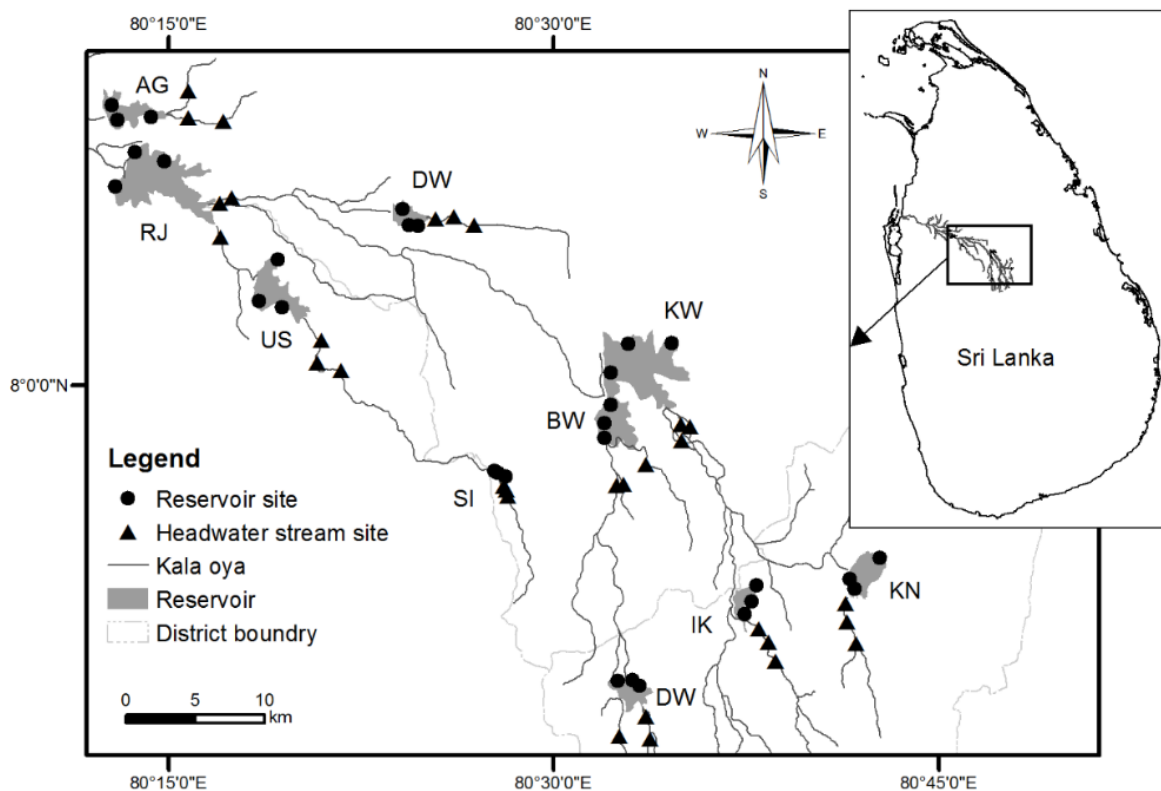
Being a tropical country with rich molluscan biodiversity, Sri Lanka is blessed with 103 river

basins and a large number of seasonal and perennial irrigation reservoirs that are associated with headwater streams. However, apart from the study carried out by Weliange et al. (2017), who investigated the patterns of diversity and structure of benthic macroinvertebrates along the temporal and longitudinal gradients in two lotic ecosystems in the wet and dry zones of Sri Lanka, there is a dearth of information relating to the distribution and variation of aquatic molluscan fauna in reservoirs and associated headwater streams of the country. In the present study, an attempt is made to investigate the distribution and diversity of molluscan taxa in selected irrigation reservoirs and associated headwater streams of the Kala Oya river basin in Sri Lanka with WLF in reservoirs and soil texture of the sediments. The results of this study would be useful to future conservation efforts in freshwater ecosystems in the country and could be integrated into monitoring their health status.

## MATERIALS AND METHODS

### *Study sites*

This study was conducted in the Kala Oya river basin, which is the second-largest river basin in Sri Lanka having many irrigation reservoirs constructed in the past. This river basin is in the North-Western part of the country, and its main catchment and sub-catchment areas extend from the central hill areas to the lowland region. For the present study, ten irrigation reservoirs, namely Angamuwa (AG), Balaluwewa (BW), Dewahuwa (DW), Ibbankatuwa (IK), Kandalama (KN), Katiyawa (KT), Kalawewa (KW), Rajanganaya (RJ), Siyambalangamuwa (SI) and Usgala-Siyambalangamuwa (US) and the associated headwater streams were selected to study the variation of WLF of these reservoirs and sediment texture on the taxa richness, diversity, and distribution of molluscan fauna inhabiting there (Figure 1).



**Fig 1** Selected sampling points in reservoirs (black dots) and in associated headwater streams (black triangles) in the Kala Oya river basin. Angamuwa (AG), Balaluwewa (BW), Dewahuwa (DW), Ibbankatuwa (IK), Kandalama (KN), Katiyawa (KT), Kalawewa (KW), Rajanganaya (RJ), Siyambalangamuwa (SI) and Usgala-Siyambalangamuwa (US).

### Field sampling

Field sampling was carried out from August 2014 to April 2015 by visiting the sampling sites once in two-month intervals. As littoral zones are characterised by a high natural variability, which is increasingly threatened by multitude of anthropogenic disturbances including morphological alterations and can be regions of high biodiversity and productivity, serving as crucial habitat for macroinvertebrates (James et al. 1998; Porst et al. 2015), sampling sites were fixed in the littoral zones of the reservoirs. Three sampling sites from within each selected reservoir and three other sampling sites from along its associated headwater stream were randomly selected. At each sampling visit, three sediment samples were collected from the knee depth location in the marginal littoral zone from within each site in each reservoir and the associated headwater stream using a 6 cm diameter soil corer driven into the

sediment to a depth of 15 cm (volume 0.5 dm<sup>3</sup>) (IAEA 2003). Consequently, on each sampling occasion, there were 9 benthic samples from a reservoir and 9 samples from the headwater stream. As such, during the 5 sampling visits to the 10 reservoir sites, 450 sediment samples from the 10 reservoirs, and another 450 samples from the associated headwater streams were obtained for the present analysis.

Each sediment sample was wet sieved separately *in situ* through a 1 mm sieve (<https://archive.epa.gov/water/archive/web/html/ch07b.html>), and the mollusc specimens retained on the sieve mesh were collected, preserved in 10% formalin, and transported to the laboratory for further analysis. As mollusc specimens were preserved, 'sample transport time and storage' were irrelevant for maintaining the quality of samples.

In addition, during the sampling period, a sediment sample (volume 0.5 dm<sup>3</sup> each) was collected from each benthic sampling site in the

reservoir and its associated headwater stream, using the same soil corer driven into the sediment to a depth of 15 cm, to study the sediment texture. In total, there were 30 reservoir sediment samples and 30 headwater stream sediment samples.

#### *Laboratory analysis*

In the laboratory, the molluscan specimens in each sample were identified to the nearest possible taxonomic category using the identification keys by Fernando and Weerawardhane (2002) and Yule and Yong (2004), and the number of individuals belonging to each taxon was counted and the abundance was expressed as individuals per dm<sup>3</sup>. After counting, the shell length of each individual was measured to the nearest mm using a vernier caliper, and the mean shell size ( $\pm$ SD) of each genus was determined.

Also, each sediment sample was transferred separately to a 1-liter measuring cylinder, filled with water to its 1 L level, stirred well, and kept for about 24 hours to settle. After the suspension was fully settled, the total height of the sediment column and individual heights of different soil component layers (i.e., coarse sand, medium sand, fine sand, clay, and silt) were measured, and percentages of each soil component were calculated. Thereafter, the soil type of each sediment sample was determined by the online soil texture calculator available in Natural Resources Conservation Service Soils, United States Department of Agriculture ([https://www.nrcs.usda.gov/wps/portal/nrcs/detail/soils/survey/?cid=nrcs142p2\\_054167](https://www.nrcs.usda.gov/wps/portal/nrcs/detail/soils/survey/?cid=nrcs142p2_054167)).

Further, reservoir hydrological data (i.e., reservoir area/capacity data and daily water level data) were obtained from the respective regional irrigation offices and the Mahaweli Authority of Sri Lanka. Using the above hydrological data, the water level fluctuation for the study period (WLF) (i.e., the difference between the maximum and minimum water level) of each reservoir was calculated.

#### *Statistical analyses*

Shannon-Weaver diversity index ( $H'$ ) (Shannon and Weaver 1949), taxa richness (TR), and taxa distribution index (DI) of molluscs were determined separately for each reservoir and its associated headwater stream. Here, the molluscan DI was defined as the ratio between the number of sampling

points with a particular mollusc taxon and total sampling points (Pérez-Quintero 2007). Non-metric multidimensional scaling (NMDS) and subsequent analysis of similarity (ANOSIM) based on Bray-Curtis similarity (Clarke and Warwick 2001) were performed to determine the similarity of molluscan taxa densities among reservoir sites and headwater stream sites. Before analysis, molluscan abundance data were  $\ln(x + 1)$  transformed to reduce non-normality of data. Box plots of  $H'$  and TR were prepared separately for the reservoirs and associated headwater streams. Relative abundance of molluscan taxa in reservoirs and headwater streams were mapped by QGIS 3.0 software package (<https://qgis.org/en/site/forusers/download.html>) and indicated as column graphs. The effects of WLF on  $H'$  and TR were tested by linear regression techniques. Medians of densities of the different molluscan taxa in different soil types were compared by Kruskal-Wallis test, followed by Dunn's post-hoc test (with Bonferroni correction). Shannon-Weaver diversity indices and taxa richness were determined using the PAST 3.17 biostatistical software (Hammer et al. 2001; Hammer 2017). Both NMDS and ANOSIM were performed using the PRIMER 5 statistical software package while the regression analyses were performed using the MINITAB 17 software package at  $\alpha=0.05$ . Kruskal-Wallis test followed by Dunn-Bonferroni post-hoc analysis was conducted using Microsoft EXCEL 2013 with XLSTAT tool pack (<https://www.xlstat.com/en/download/xlstat>).

## RESULTS

In total, 11,752 mollusc specimens belonging 12 genera underclass Gastropoda [ $n = 11,348$  (96.6%)] and Bivalvia [ $n = 404$  (3.4%)] were recorded during the study period. There were 10 gastropods genera namely *Bellamya*, *Bithynia*, *Thiara*, *Melanoides*, *Indoplanorbis*, *Gyraulus*, *Planorbis*, *Lymnaea*, *Planorbella*, and *Pila* while the bivalve genera were *Polymesoda* and *Lamellidens*. Of the gastropod molluscs, *Bellamya* (29.09%), *Bithynia* (29.06%), *Thiara* (20.92%), and *Melanoides* (10.64%) were the most abundant in the study area. The maximum distribution index (DI) of 0.75 was registered for the genus of *Melanoides* followed by *Bellamya* (DI = 0.63) and *Thiara* (DI = 0.60). Of the molluscs recorded 11,282 (96%) were from reservoir sampling sites, and the remainder 470 (4%) were

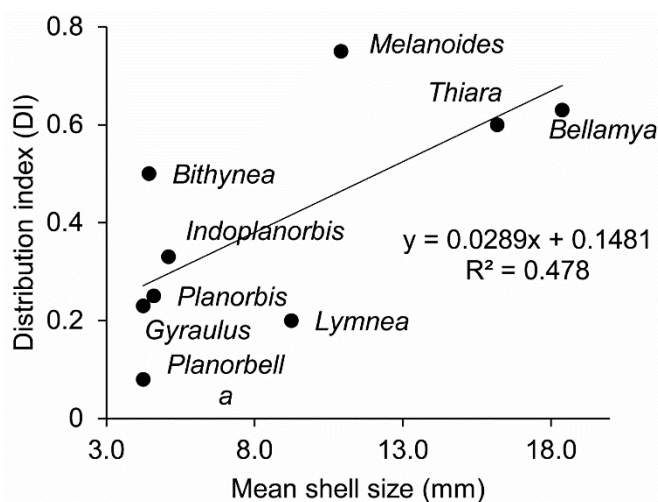
from headwater streams sampling sites. The lowest DI values of 0.20, 0.10, and 0.08 were recorded for the genera *Lymnaea*, *Pila* and *Planorbella* respectively (Table 1).

**Table 1** Mean shell size ( $\pm$  SD), distribution index, and the number of individuals of molluscan taxa recorded in the present study.

Class	Family	Genus	n	%	Mean shell size (mm)	Distribution Index (DI)
Gastropoda	Vivaparidae	<i>Bellamya</i>	3419	29.09	18.4 $\pm$ 0.08	0.63
	Paludetrinidae	<i>Bithynia</i>	3415	29.06	4.4 $\pm$ 0.01	0.50
	Thiaridae	<i>Thiara</i>	2458	20.92	16.2 $\pm$ 0.09	0.60
	Thiaridae	<i>Melanoides</i>	1250	10.64	10.9 $\pm$ 0.10	0.75
	Planorbidae	<i>Indoplanorbis</i>	313	2.66	5.1 $\pm$ 0.09	0.33
	Planorbidae	<i>Gyraulus</i>	203	1.73	4.3 $\pm$ 0.03	0.23
	Planorbidae	<i>Planorbis</i>	200	1.70	4.6 $\pm$ 0.10	0.25
	Lymnaeidae	<i>Lymnaea</i>	50	0.43	9.3 $\pm$ 0.24	0.20
	Planorbidae	<i>Planorbella</i>	22	0.19	4.3 $\pm$ 0.05	0.08
	Pilidae	<i>Pila</i>	18	0.15	40.0 $\pm$ 0.31	0.10
Bivalvia	Corbiculidae	<i>Polymesoda</i>	254	2.16	30.9 $\pm$ 0.21	0.23
	Unionidae	<i>Lamellidens</i>	150	1.28	51.5 $\pm$ 0.29	0.40

The mean shell sizes of gastropod mollusc genera ranged from 4.3 mm (*Gyraulus* and *Planorbella*) to 18.4 mm (*Bellamya*), and these shell sizes were positively correlated with their corresponding distribution indices (DI) ( $r = 0.69$ ;  $p$

$< 0.05$ ; Figure 2) except the genus *Pila*, which had the largest mean shell size of 40 mm. This observation indicates that the gastropod genera with larger shell sizes exhibited a greater DI.



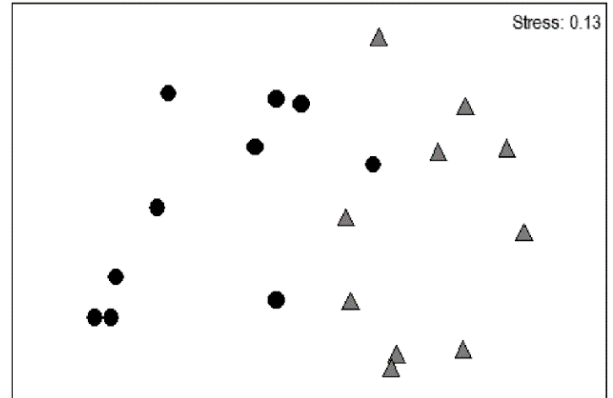
**Fig 2** The effect of shell size on the distribution of gastropod molluscs in the Kala Oya river basin. Note: Distribution of *Pila* (exceptionally large gastropod showing outlier) and bivalve molluscs are not included in the figure.

The NMDS ordination of 10 reservoirs and their associated headwater streams indicated that there

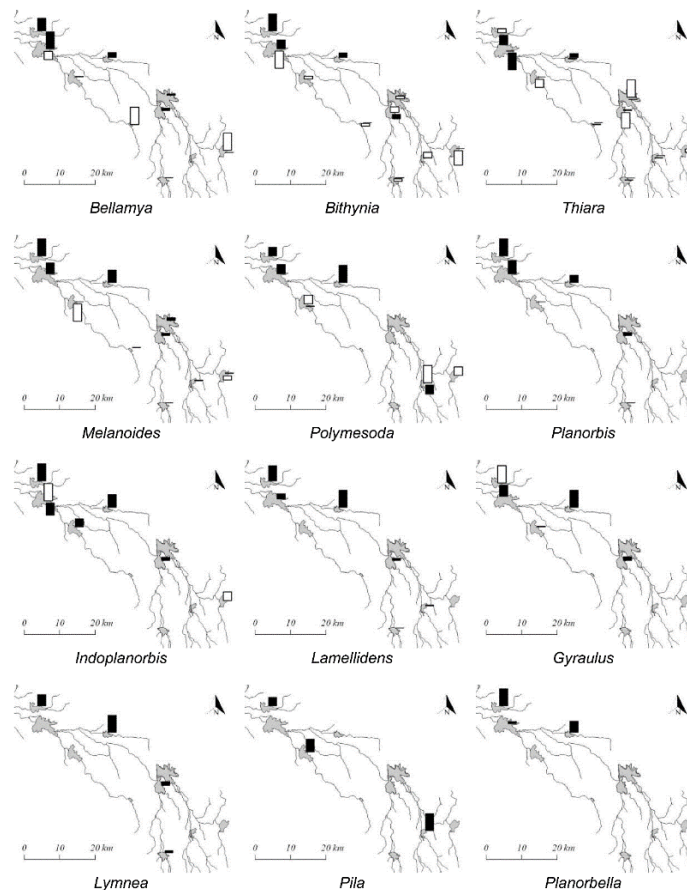
was a clear separation of two clusters representing headwater streams and reservoirs respectively

(Figure 3), and these two clusters were significantly different from each other (Global R = 0.514,  $p < 0.05$ , one-way ANOSIM).

From the maps of relative abundance of molluscan genera, expressed as individuals per  $\text{dm}^3$  (Figure 4), it is evident that *Planorbis*, *Lamellidens*, *Pila*, *Lymnaea*, and *Planorbella* were not present in the headwater streams but the reservoirs. The genera that belonged to the families Viviparidae (*Bellamya*;  $0.06 \pm 0.03$ ), Bithyniidae (*Bithynia*;  $0.21 \pm 0.07$ ) and Thiaridae (*Thiara*;  $4.8 \pm 1.9$  and *Melanoides*;  $1.1 \pm 0.8$ ) showed higher densities and distributions in the headwater streams (Figure 4). *Bithynia*, *Polymesoda*, and *Indoplanorbis* were the other molluscan genera present in headwater streams of some reservoirs.



**Fig 3** NMDS plot showing the group separation of mollusc density between reservoir sites (●) and headwater stream sites (▲).

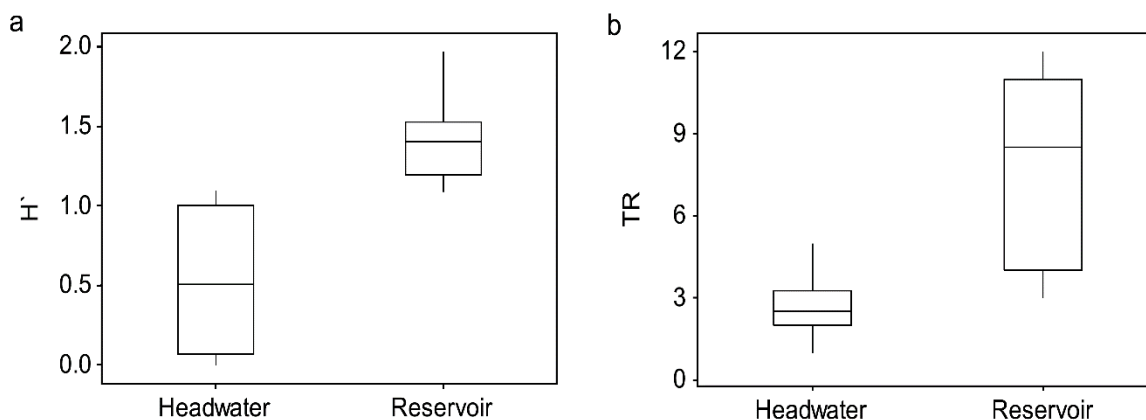


**Fig 4** Distribution and relative abundance (individuals per  $\text{dm}^3$ ) of molluscan genera in the study reservoirs and associated headwater streams of the Kala Oya river basin. The height of each bar represents the relative abundance (■ - reservoir, □ - headwater stream).

Shannon-Weaver diversity ( $H'$ ) and taxa richness (TR), compared using boxplots (Figure 5), indicated both diversity indices were comparatively lower along the headwater streams than those within

the reservoirs. In the box plots, the maximum (upper-quartiles) of headwater streams are lower than the minimum (lower-quartile) of the reservoirs

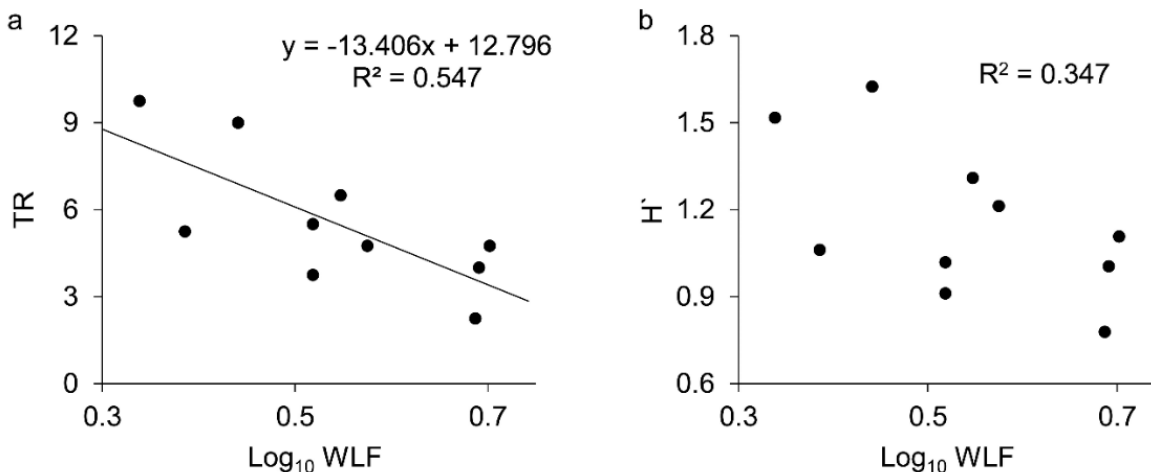
(Figure 5). This indicates that the reservoirs have more favourable habitats for molluscan fauna than in the headwater streams.



**Fig 5** Box plots of (a) Shannon-Weaver diversity index ( $H'$ ) and (b) taxa richness (TR) of molluscan genera in headwater streams and reservoirs. Horizontal bars in the boxes are median values, lower and upper margins of boxes are 25% and 75% percentiles respectively, and whiskers are upper and lower limits of ranges.

Taxa richness (TR) of molluscan genera had significant negative linear relationship with the  $\log_{10}$  WLF [ $r = -0.73$ ,  $p < 0.05$ ; Figure 6(a)]. Although Shannon-Weaver diversity index ( $H'$ ) of

molluscs also showed a negative relationship with  $\log_{10}$  WLF, the relationship was not significant at 0.05 probability level ( $r = -0.58$ ,  $p > 0.05$ ) [Figure 6(b)].



**Fig 6** Relationship between (a) taxa richness (TR) versus log water level fluctuation in reservoirs ( $\log_{10}$  WLF) and (b) Shannon-Weaver diversity index ( $H'$ ) versus  $\log_{10}$  WLF.

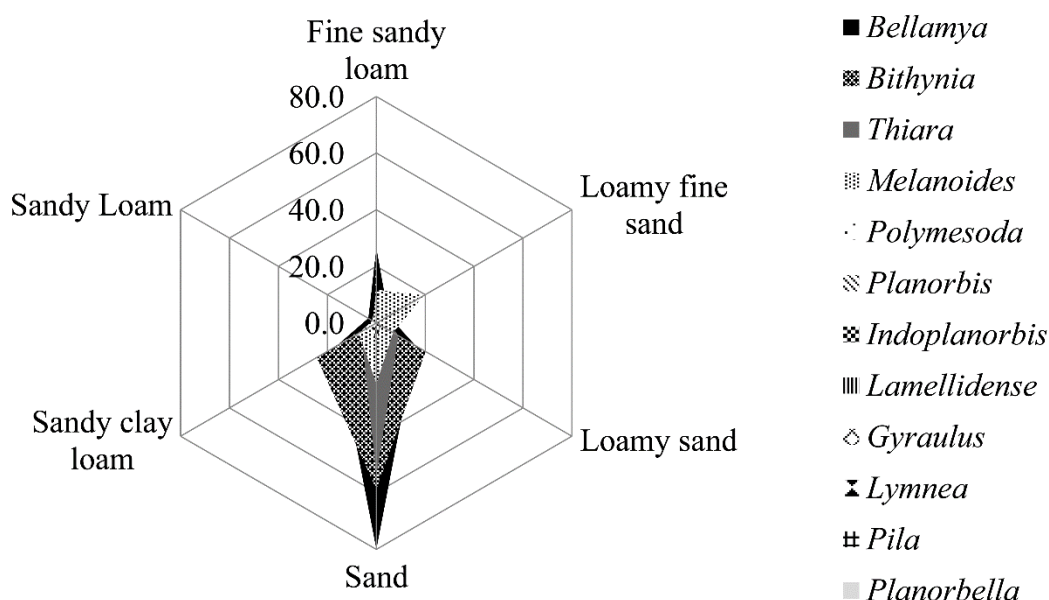
The results of the Kruskal-Wallis test showed that the median values of molluscan genera abundance in different soil types in the sampling

sites were significantly different ( $H = 37.87$ ,  $df = 5$ ,  $p < 0.05$ ). Significantly higher molluscan densities were recorded in the sandy bottoms than in all the



other bottom types. The soil type of fine sandy loam had the second-highest molluscan density followed by substrates with sandy clay loam and loamy sand soil types (Figure 7). Dunn's post-hoc test (with Bonferroni correction) indicated that among the total of 6 soil types, mollusc density in fine sandy loam showed a significant difference between all the other soil types except sand. The genera density in loamy fine sands was significantly different only with the sand bottoms, and that in loamy sand bottoms showed significant difference with the sand bottoms and sandy loam bottoms. Also, the genera

density in sand bottoms had significant differences from those in sandy clay loams and sandy loam. There were significant differences in genera density between sandy clay loam bottoms and sandy loam bottoms (Table 2). *Bellamyia*, *Bithynia*, and *Thiara* were the prominent inhabitants in the sandy substrates. *Bithynia* was also found in bottom habitats with sandy clay loam and loamy sand. *Melanoides* was the widely distributed genus in all substrate types and was the most distributed molluscan genus in the Kala Oya river basin.



**Fig 7** Mean densities of molluscan taxa in different soil types. Y-axis shows the percentages of the soil types.

**Table 2** Probability levels of Dunn's post-hoc test (with Bonferroni correction) of comparison of densities of molluscan genera in different sediment soil types.

	Fine sandy loam	Loamy fine sand	Loamy sand	Sand	Sandy clay loam
Loamy fine sand	<b>0.013</b>				
Loamy sand	<b>0.000</b>	<i>0.458</i>			
Sand	<i>0.604</i>	<b>0.026</b>	<b>0.002</b>		
Sandy clay loam	<b>0.010</b>	<i>0.377</i>	<i>0.723</i>	<b>0.028</b>	
Sandy Loam	<b>&lt; 0.0001</b>	<i>0.545</i>	<b>0.014</b>	<b>&lt; 0.0001</b>	<b>0.019</b>

Bold values: Significant at least at  $p < 0.05$  probability level; Non-bold, italic values: Not significant ( $p > 0.05$ )



## DISCUSSION

This study investigated the distribution and diversity of molluscan fauna in some reservoirs and associated headwater streams in the Kala Oya river basin, Sri Lanka their sediment texture and water level fluctuations (WLF) in the reservoirs. Results revealed that the molluscs dominated in reservoirs (96.0%) than in the associated headwater streams (4.0%). Further, the gastropod molluscs were more abundant in reservoirs as well as in headwater streams (96.6%) than the bivalve molluscs (3.4%). Results also revealed that the molluscan diversity and their taxa richness were high in reservoirs with less variation in WLF.

Although molluscs are a marine group of animals, many genera of the two major molluscan classes, Gastropoda and Bivalvia, have expanded their distribution to various inland freshwater habitats such as reservoirs and streams (Purchon 1968; Kappes and Haase 2012; Wanninger and Wollesen 2019). The gastropod and bivalve molluscs were present in both the irrigation reservoirs and the associated headwater streams investigated in the present study. It was interesting to note that gastropods exhibited a wider distribution than the bivalves in both these habitats in the Kala Oya river basin. For example, the abundance of some gastropod genera such as *Bellamyia*, *Bithynia*, *Thiara*, and *Melanoides* were found to be much higher in headwater streams than in the reservoir habitats. Similar observations were made by Du et al. (2011) in a eutrophic lake in China where some endemic gastropod species continued to occur in the associated springs and upstream rivers, although they disappeared in the lake body. This might be due to the reason that stream habitats are more conducive than reservoir habitats because they were important refuges for some gastropod genera.

The shell size of the gastropods also plays a major role in this wide distribution. Data analysis revealed that the distribution index (DI) of gastropods showed a significantly positive relationship with their shell size. This indicates that large-shelled gastropods can distribute widely in reservoirs as well as in the associated streams and increase their abundance in these habitats than the small-shelled gastropods (Table 1). Of the ten gastropod genera recorded in this study, the gastropod genera with the highest % abundance

were *Bellamyia*, *Bithynia*, *Thiara*, and *Melanoides*. It is interesting to note that these four genera also had the highest recorded DI values. [e.g., *Bellamyia* (DI = 0.63), *Bithynia* (DI = 0.5), *Thiara* (DI = 0.60), and *Melanoides* (DI = 0.75)]. However, the gastropod genus *Pila*, having the largest shell size of 40 mm, was an exception. This genus represented an outlier with a very low DI of 0.01 (Table 1). The species of this genus are reported to occur in freshwater shallow bottom habitats that are rich with decaying organic substances (Wijeyaratne and Bellanthuduwa 2017). Hence the low DI registered for *Pila* in the current study might be due to the reason that it was confined into the littoral zone of reservoirs that contains a substantial amount of organic substances compared to the littoral zone in associated headwater streams that are continuously subjected to be washed away by the rapid water flow.

Both the Shannon-Weaver diversity index ( $H'$ ) and taxa richness (TR) of molluscs were higher in reservoirs than in headwater streams in the Kala Oya river basin. Here, TR in reservoirs exhibited a wide range but a wide range of  $H'$  occurred in the stream habitats. Furthermore, the WLF in reservoirs had a significant negative influence on TR of molluscan fauna, and to a certain degree on the  $H'$ . These results indicate that at the low and intermediate levels of environmental perturbation in terms of WLF in reservoirs, a higher diversity of molluscan genera is favoured. Weerakoon et al. (2021) reported that in the same study reservoirs of the present study, five reservoirs (US, AG, KT, RJ, and KN) showed low WLFs than the remaining reservoirs (DW, SI, KW, BW, and IK). Also, when zero WLF was assumed in the stream habitats, where low  $H'$  and TR were registered, it appeared that at the low levels of environmental perturbation, headwater stream habitats would also register greater diversity indices of molluscan taxa. Pérez-Quintero (2011) has also shown that in the watercourses of two Mediterranean acid mine drainage-impacted river basins of the southern Iberian Peninsula, species richness of molluscs was influenced by environmental gradients related to habitat heterogeneity and environmental variability. In the reservoir habitats of the present study, seasonal WLFs mainly due to the release of water for irrigation, cause littoral zone exposure. As such WLF in irrigation reservoirs, which is essentially an anthropogenic perturbation can be considered as a

major determinant of molluscan diversity and taxa richness in the littoral zone. Therefore, the reservoirs and associated headwater streams in the Kala Oya river basin, perhaps, conform to the intermediate disturbance hypothesis (Connell 1978).

Molluscan distributions are strongly associated with the habitat substrate structure (Harman 1972; Brönmark 1985; Čejka 2011; Glöer and Grego 2015). The bottom sediment structure in the marginal zones of irrigation reservoirs of the present study is bound to change due to WLF. During the elevated water level, marginal zones with sandy soil are inundated, while bottom sediments of reservoirs during low water level are predominantly characterized by fine sandy loam texture. It was evident in this study that higher densities of several molluscan genera occurred in sandy bottom substrates, followed by substrates with fine sandy loam and those with sandy clay loam and loamy sand soil types. Sandy bottoms are known to be supreme habitats for freshwater molluscs as their feeding grounds (Schmidlin et al. 2012; Beran 2020). As the texture of bottom sediments is influenced by WLF, it can be postulated that reservoir WLF has a prominent influence on the diversity and distribution of molluscan genera both directly through littoral exposure and indirectly through sediment characteristics.

Rich molluscan densities in the aquatic habitats provide prime ecosystem services by converting fine particulate matter into energy in the aquatic food webs (Strayer 2014; Vaughn 2017). Moreover, these molluscan species structure phytoplankton communities, which greatly influence biological productivity (Mo et al. 2017). Zhu et al. (2013) have shown that the presence of gastropods resulted in a significant change in physicochemical properties of water and phytoplankton communities. Predatory birds are known to play an important role in governing the population densities of the molluscs in the marginal habitats of freshwater bodies (Silva et al. 2008; Padghane et al. 2017). According to the personal observations of the first author of this paper, herons and egrets were the abundant bird predators in the study sites. Hence, the molluscan distribution and diversity in freshwater ecosystems play an important role in facilitating the food links and nutrient dynamics. As some benthic macroinvertebrates, including mollusks, are known to be excellent bioindicators (Oehlmann and

Schulte-Oehlmann 2003; Idroos and Manage 2012), the findings of the present study would be useful to future conservation efforts in freshwater ecosystems and for monitoring their health status.

## CONCLUSION

Freshwater molluscs are sensitive to natural disturbances such as floods, droughts, competition with invasive alien fauna and habitat alteration, and seasonal water level fluctuation (WLF) in reservoirs. All these disturbance events result in drastic changes in their diversity and distribution patterns. From the present study carried out in 10 reservoirs and associated headwater streams in the Kala Oya river basin, Sri Lanka, it was found that the molluscs dominated in reservoirs (96.0%) than in the associated headwater streams (4.0%). Further, the gastropod molluscs were more abundant in reservoirs as well as in headwater streams (96.6%) than the bivalve molluscs (3.4%). This study also revealed that the molluscan diversity, as well as the taxa richness, were high in reservoirs where there were no profound variations of WLFs, and that gastropods exhibited a wider distribution than the bivalves in both habitats. Further, it was found that large-shelled gastropods distributed widely in reservoirs as well as in the associated streams with high abundance than the small-shelled gastropods. This study also showed that at the low and intermediate levels of environmental perturbation in terms of WLF in reservoirs, a higher diversity of molluscan genera was favoured. Seasonal WLF in reservoirs is mainly due to the release of water for irrigation, which causes littoral zone exposure, and as such, this anthropogenic perturbation can be considered as a major determinant of molluscan diversity and taxa richness in the littoral zone. It was also evident from this study that densities of several molluscan genera were influenced by bottom sediment characteristics, signifying sandy bottom substrates were more favourable for occurring higher densities of several molluscan genera. As the texture of bottom sediments is influenced by WLF, it can be postulated that reservoir WLF has a prominent influence on the diversity and distribution of molluscan genera both directly through littoral exposure and indirectly through sediment characteristics. Due to the ability of molluscan fauna for structuring phytoplankton communities, their role in aquatic food webs, and

their importance as bioindicators, the investigation of distribution and diversity of freshwater molluscs would be useful to future conservation efforts in freshwater ecosystems and for monitoring their health status.

## ACKNOWLEDGEMENTS

Financial support for this study was from the University of Kelaniya, and Knowledge Enhancement and Institutional Development Fund of University Grants Commission, Sri Lanka.

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