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Cover: Rufous-headed Hornbill *Rhabdotorrhinus waldeni* © Philip Godfrey C. Jakosalem.

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COMMUNICATION

Spatial and temporal variation in the diversity of malacofauna from Aripal stream of Kashmir Himalaya, India

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Abstract: This paper presents the spatial and temporal variation in the diversity of malacofauna in relation to the water chemistry of the Aripal stream of Kashmir Himalaya. A total of 12 species were reported which belong to four families, Lymnaeidae, Physidae, Planorbidae, and Bithyniidae from class Gastropoda, and two families, Cyrenidae and Pisidiidae from class Bivalvia. The family Planorbidae contributed 34% to the total annual molluscan population followed by Lymnaeidae (28%) and Bithyniidae (18%). During the collection, *Gyraulus* sp., *Planorbis* sp., and *Bithynia tentaculata* were prevalent at all sites, with predominance of *Bithynia tentaculata*. Species richness and abundance were observed maximum at site A3 (down-stream) and minimum at site A1 (up-stream) while in the case of temporal variation, species richness and abundance were maximum in summer and minimum in winter. Shannon-Wiener index, Simpson index, Margalef index, and Pielou evenness index were used to calculate the diversity, dominance, richness, and evenness of molluscan species, respectively. Physico-chemical parameters revealed a non-significant spatial variation (P >0.05) except pH, total hardness, and alkalinity while a significant temporal variation (P <0.05) was observed in the physico-chemical parameters except dissolved oxygen. A significant positive correlation was seen between the molluscan species and total hardness. In the present study, the stone mining, channel morphology of stream, habitat heterogeneity, and physico-chemical parameters were also found to promote the spatial and temporal diversity of malacofauna.

Keywords: Abundance, classification, distribution, freshwater ecosystems, macrobenthic invertebrates, molluscs, Pearson's correlation, physico-chemical parameters, richness.

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Author details: Zahoor Ahmad Mir—PhD Research Scholar, Department of Zoology, University of Kashmir is currently working in the Fish Biology and Limnology Research Laboratory of the Department and has a keen interest in the taxonomy and diversity of macrobenthic invertebrates along with the limnology of Kashmir Himalayan streams. Dr. Yahya Bakhtiyar—Assistant Professor, Department of Zoology, University of Kashmir is currently working in the Fish Biology and Limnology Research Laboratory of the Department and his focus of research is fish population dynamics, fish reproductive biology, zooplankton, macrobenthic invertebrates, biomonitoring, and limnology of the waterbodies of Jammu and Kashmir.

Author contributions: ZAM—field survey, data collection, identification, photography, statistical analysis, and manuscript preparation. YB—research supervision, drafting of research problem, and manuscript preparation.

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INTRODUCTION

Molluscs serve as sources of food for fishes, birds and mammals (Wosu 2003). Molluscs also act as intermediate hosts to helminth parasites that cause diseases such as schistosomiasis and fascioliasis in humans and livestock (Mostafa 2009; Alhassan 2020; Silva et al. 2020). Freshwater molluscs, being detritus feeders, play a significant role in improving water quality (Martin 1991; Reddy 1995). Freshwater bodies are inhabited by two classes of molluscs: Gastropoda and Bivalvia, with the Gastropoda forming the largest group (Lydeard et al. 2004). Both gastropods and bivalves are diverse in aquatic ecosystems such as lakes, ponds, wetlands, springs, streams, and rivers, which act as models for ecological studies (APHA 1998). Ecological parameters like temperature, nature of substratum, type of vegetation, and water chemistry play significant role in the occurrence, distribution, and density of freshwater molluscs (Bournard et al. 1987; Boulton & lake 1992; Linke et al. 1999). Temperature has a major impact on the seasonal distribution and abundance of freshwater molluscs (Biggs et al. 1990). Bottom substrate such as boulders, cobbles, pebbles, gravel, and sand provide a suitable habitat for the colonization and establishment of molluscs in streams (Hynes 1970; Habib & Yousuf 2012). Growth of vegetation such as macrophytes and periphyton along and within the stream increases the density, distribution, and diversity of molluscs (Nelson et al. 1990; Bilby & Ward 1991; Ghani et al. 2017). Water chemistry parameters (viz., pH, alkalinity, hardness) influence the abundance and richness of molluscs (Peeters & Gardeniers 1998). The spatial and temporal variation in both biotic and abiotic parameters change the adaptation strategies along with the composition, distribution, and diversity of mollusc communities (Rosillon 1987; Poff & Ward 1989). The freshwater molluscs are facing threats from various sources such as water pollution, habitat destruction through dams and channelization, and climate change (Peeters & Gardeniers 1998; Primack 2002). The studies on Indian Himalayan malacofauna is meager compared to other parts of India (Blanford & Godwin-Austen 1908; Rao 1993; Aravind et al. 2010; Sharma et al. 2010) and in Kashmir Himalaya, a well-documented work has been carried out on the diversity of benthic molluscan fauna (Qadri et al. 1981; Dhar et al. 1985; Pandit et al. 2002; Yousuf et al. 2006; Bhat & Pandit 2010; Habib & Yousuf 2014; Allaie et al. 2019). Despite the work carried out in the field of limnology, there is still a lack of knowledge and fragmentary information regarding habitat heterogeneity and changing riparian land use patterns along the hill streams. These aspects have a profound impact on the occurrence, abundance, and richness of benthic fauna and have been considered during the present study on the spatial and temporal variation in the diversity of malacofauna from the Aripal stream of Tral, Kashmir Himalaya.

MATERIALS AND METHODS

Description of the study area

The present study has been carried out from the Aripal stream, located in the Tral town, between geographic coordinates 33.93°N and 75.10°E with an altitude of 1,662 m in the district Pulwama, Kashmir valley. The stream originates in the northern ridge of Greater Himalaya and forms one of the important tributaries of the Jhelum river in the district. The town is situated 11 km away from NH 44 Awantipora and nearly about 40 km from Srinagar city. The Aripal watershed covers an area of 380 km^2 in the sub-district and provides various ecosystem services such as a source of drinking water and irrigation for horticulture and agriculture purposes and also forms an opportunity for trout culture in the area. The stream forms an important reservoir of construction materials such as boulders, cobbles, pebbles, gravel, and sand, which boost the rural economy (Mir & Saleem 2016). During the survey, three sites were selected from the stream, on the basis of distance, altitudinal distribution, riparian land-use types, and stream heterogeneity. The sites were marked as site A1 at Aripal (up-stream), 34.01˚N & 75.04˚E, 1,902 m, site A2 at Chandrigam (mid-stream), 33.55˚N & 75.05˚E, 1,607 m, and site A3 at Kadelbal (down-stream), 33.53˚N & 75.02˚E, 1,583 m (Image 1). The geographical representation of the Aripal watershed along with sampling sites was created through Arc-GIS software (Figure 1).

Sampling, processing, and identification

Sampling was carried out on monthly basis from June 2018 to May 2019. The molluscan samples were collected by using standard bottom samplers (EU-WFD implemented) Surber net and D-net (HYDRO-BIOS) with 0.9 m^2 area and 0.5 mm mesh size (Rosenberg & Resh 1993; Barbour et al. 1999; Hayslip & Gretchen 2007). Wader and synthetic rubber gloves were used during wading in each sampling reach. A systematic method was followed to cover the different microhabitats in each sampling site (Peck et al. 2002). A standard operating

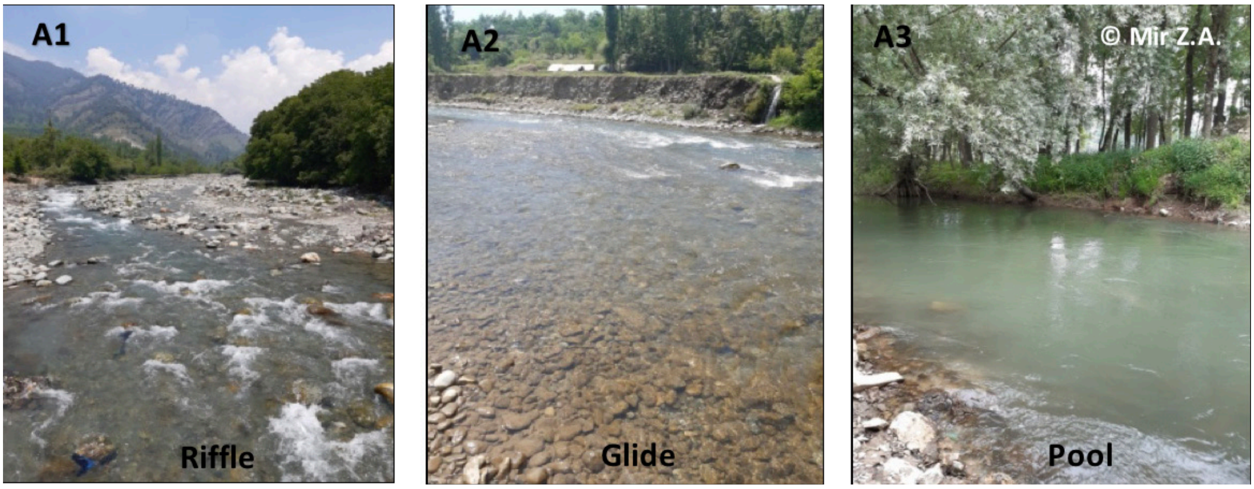

Image 1. Sample collection sites of Aripal stream with habitat heterogeneity. © Zahoor Ahmad Mir

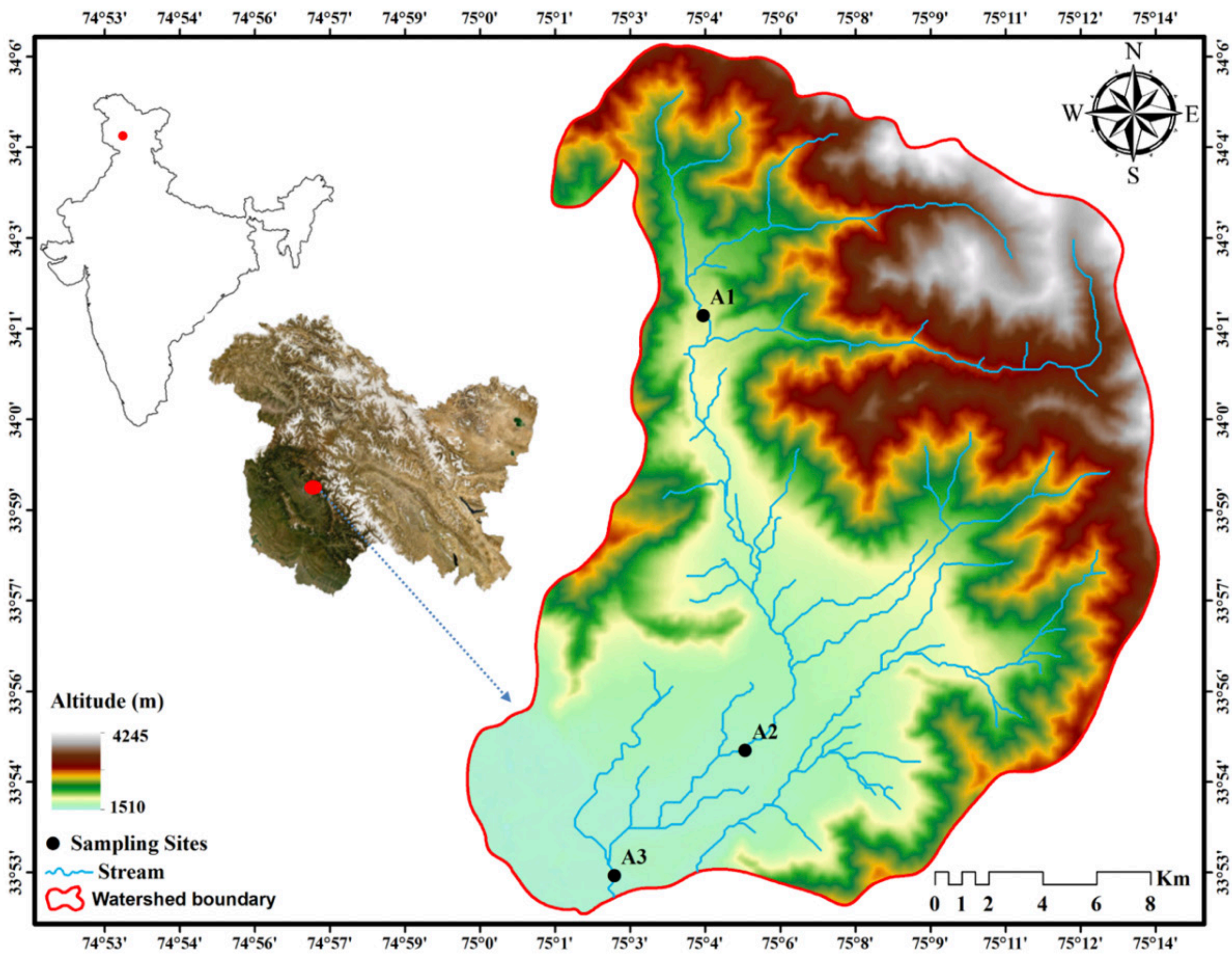

Figure 1. Geographical representation of sampling sites of Aripal stream, Tral, Kashmir Himalaya.

method in benthic macroinvertebrate sampling, developed by Moultan et al. (2000) and Carter & Resh (2001) was followed for filtration, sieving, removing, and sorting of molluscs and extraneous material from the sample. During processing, samples were fixed with 4% formalin and preserved with 70% ethanol. The identification was done with the help of dissecting stereo zoom microscope (Magnus MS 24) with Magcam DC 10 camera following taxonomic keys (Edmondson 1959; Rao 1989; Ramakrishna & Dey 2007).

Physico-chemical parameters

The physico-chemical parameters of water, viz., dissolved oxygen (DO), alkalinity (Alk), total hardness (TH), air temperature (AT), water temperature (WT), pH, electrical conductivity (EC), and total dissolved solids (TDS) were measured by following standard methods (APHA 1998).

Statistical analysis

Statistical analysis of data was performed by using MS excel 2016, SPSS 20, and Past 4 software. Shannon-Wiener index (1949), Simpson dominance index (1949), Margalef index (1958) and Pielou evenness index (1966) were used to calculate the diversity, dominance, richness, and evenness of molluscan species with the use of Past 4 software. Spatial and temporal data of physico-chemical parameters were subjected for one-way ANOVA followed by Duncan's multiple range test and the relationship with molluscan species was determined through two-tailed Pearson's correlation with the help of SPSS 20 software.

RESULTS

Molluscan diversity

During the present study, 1,509 individuals were collected from three different sites of the Aripal stream throughout the year. A total of 12 species were reported from six families and two classes. Gastropoda represented 10 species that belong to four families, Lymnaeidae, Physidae, Planorbidae, and Bithyniidae while the class Bivalvia was represented by two species belonging to two families, Cyrenidae and Pisidiidae (Table 1). The identified Gastropoda were *Radix auricularia*, *Lymnaea stagnalis*, *Pseudosuccinea columella*, *Racesina luteola*, *Physella acuta*, *Segmentina* sp., *Indoplanorbis exustus*, *Gyraulus* sp., *Planorbis* sp., and *Bithynia tentaculata.* The Bivalvia species were *Corbicula cashmirienses* and *Pisidium casertanum* (Table 1; Image 2). During the collection, *Gyraulus* sp., *Planorbis* sp., and *Bithynia tentaculata* were present at all the sites, while *Physella acuta* was observed only at site A2 (mid-stream) and *Lymnaea stagnalis, Segmentina* sp. *and Indoplanorbis exustus* were present only at site A3 (down-stream). *Radix auricularia, Pseudosuccinea columella*, *Racesina luteola*, *Corbicula cashmirienses* and *Pisidium casertanum* were reported from site A2 and site A3 of the stream (Table 2).

The class Gastropoda and Bivalvia contributed 82% and 18% to the total annual molluscan population (Figure 2). The family Planorbidae contributed 34% followed by Lymnaeidae (28%), Bithyniidae (18%), Cyrenidae (11%), Pisidiidae (7%), and Physidae (2%) to the total annual molluscan population (Figure 3). The species *Bithynia tentaculata* contributed 18% followed by *Gyraulus* sp. (16%), *Pseudosuccinea columella* (12%), *Radix auricularia* (10%), *Corbicula cashmiriensis* (10%), *Planorbis* sp. (8%), *Indoplanorbis exustus* (7%), *Pisidium casertanum* (7%), *Lymnaea stagnalis* (4%), *Racesina luteola* (3%), *Segmentina* sp. (3%), and *Physella acuta* (2%) to the total annual molluscan population (Figure 4).

The diversity was observed highest at site A3 (2.25) and lowest at site A1 (1.04), dominance was recorded highest at site A1 (0.37) and lowest at site A3 (0.12), species richness was observed highest at site A3 (1.47) while lowest at site A1 (0.41) and evenness was recorded highest at sites A1 & A3 (0.94) while lowest at site A2 (0.78) (Figure 5).

In the temporal variation of malacofauna, the diversity was observed highest in summer season (2.33) while lowest in winter season (2.06), dominance was recorded maximum in winter season (0.14) while minimum in summer season (0.11), species richness was observed maximum in summer season (1.74) while minimum in winter season (1.45) and evenness was recorded maximum in spring season (0.89) while minimum in summer season (0.86) (Figure 6).

Physico-chemical parameters

During the study, a total of eight physico-chemical parameters were recorded. The air temperature (AT) ranged from 4–25 ˚C with a mean value of 16.3±7.5 ˚C, water temperature (WT) ranged from 7.67–19 ˚C with mean value of 13.2±3.7 ˚C, dissolved oxygen (DO) ranged from 8.13–14.33 mg/L with mean value of 11.1±1.8 mg/L, pH ranged from 7.33–8.47 with mean value of 7.8±0.4, electrical conductivity (EC) ranged from 126.67–368.67 µs cm^{-1} with mean value of 256.3±84.4 µs cm^{-1}, total dissolved solids (TDS) ranged from 62–184.33 mg/L with mean value of 121.6±42.1 mg/L, total hardness

Table 1. The systematic list of malacofauna from Aripal stream.

Phylum	Class	Order	Family	Genus/Species
Mollusca	Gastropoda	Basommatophora	Lymnaeidae	*Radix auricularia*
				Lymnaea stagnalis
				Pseudosuccinea columella
				Racesina luteola
			Physidae	*Physella acuta*
			Planorbidae	*Segmentina* sp.
				Indoplanorbis exustus
				Gyraulus sp.
				Planorbis sp.
		Mesogastropoda	Bithyniidae	*Bithynia tentaculata*
	Bivalvia	Veneroida	Cyrenidae	*Corbicula cashmiriensis*
			Pisidiidae	*Pisidium casertanum*

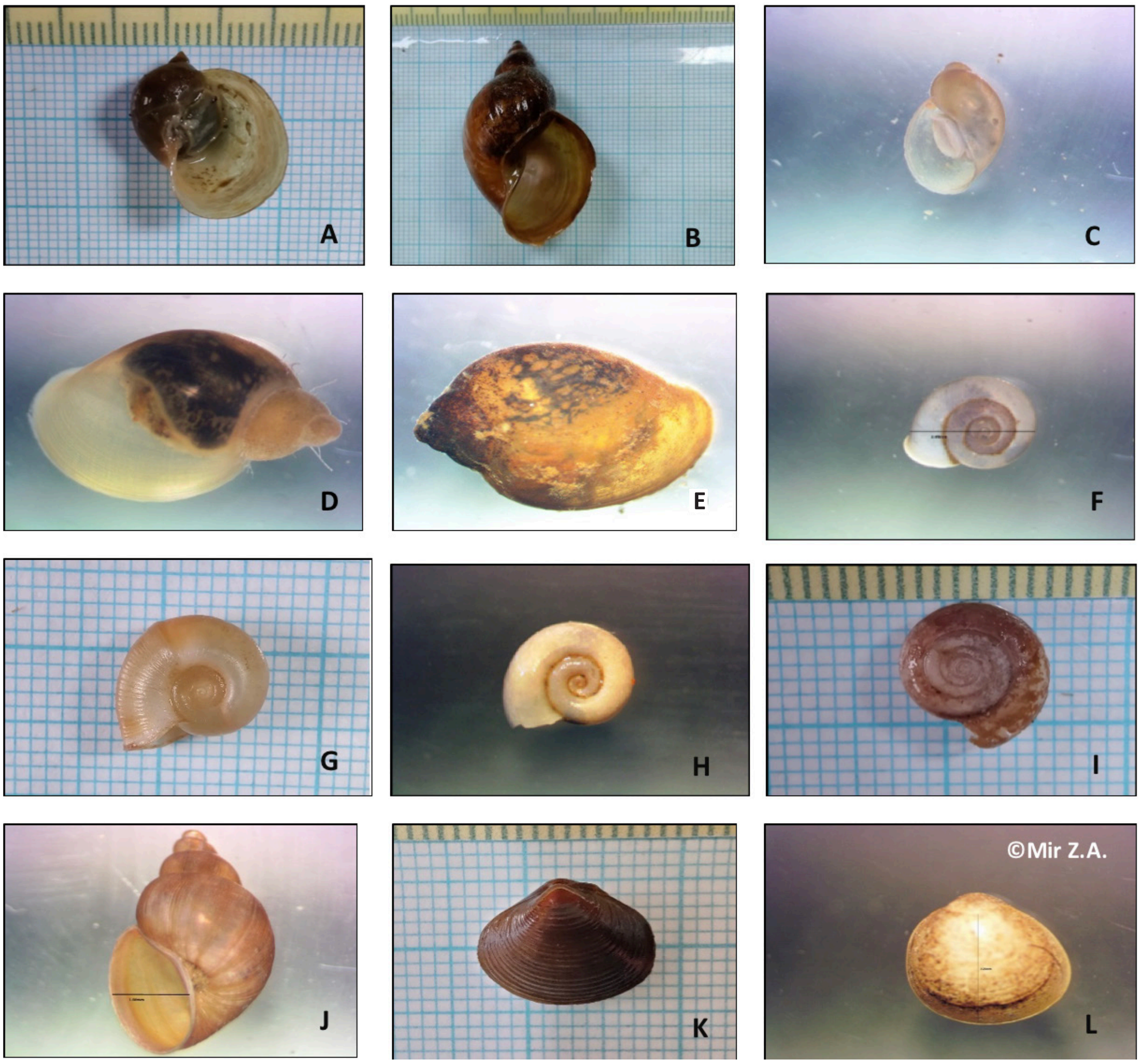

Image 2. Collected and identified molluscan species from Aripal stream: A—*Radix auricularia* | B—*Lymnaea stagnalis* | C—*Pseudosuccinea columella* | D—*Racesina luteola* | E—*Physella acuta* | F—*Segmentina* sp. | G—*Indoplanorbis exustus* | H—*Gyraulus* sp. | I—*Planorbis* sp. | J—*Bithynia tentaculata* | K—*Corbicula cashmirienses* | L—*Pisidium casertanum*. © Zahoor Ahmad Mir

Table 2. Species composition of malacofauna at different sites of Aripal stream.

	Genus/Species	Site A1	Site A2	Site A3
1	*Radix auricularia*	-	+	+
2	*Lymnaea stagnalis*	-	-	+
3	*Pseudosuccinea columella*	-	+	+
4	*Racesina luteola*	-	+	+
5	*Physella acuta*	-	+	-
6	*Segmentina* sp.	-	-	+
7	*Indoplanorbis exustus*	-	-	+
8	*Gyraulus* sp.	+	+	+
9	*Planorbis* sp.	+	+	+
10	*Bithynia tentaculata*	+	+	+
11	*Corbicula cashmiriensis*	-	+	+
12	*Pisidium casertanum*	-	+	+

(+) presence; (-) absence

Table 3. Range and mean values of physico-chemical parameters from Aripal stream.

	Parameters	Min	Max	Mean±SD
1	AT (°C)	4	25	16.3±7.5
2	WT (°C)	7.7	19	13.2±3.7
3	DO (mg/L)	8.1	14.3	11.1±1.8
4	pH	7.3	8.5	7.8±0.4
5	EC (µs cm^{-1})	126.7	368.7	256.3±84.4
6	TDS (mg/L)	62	184.3	121.6±42.1
7	TH (mg/L)	35.7	161.7	94.8±32.9
8	Alk (mg/L)	61.3	137	94.2±21.5

Min—minimum | Max—maximum | SD—standard deviation.

(TH) ranged from 35.7–161.67 mg/L with mean value of 94.8±32.9 mg/L and alkalinity (Alk) ranged from 61.33–137 mg/L with mean value of 94.2±21.5 mg/L (Table 3).

The descriptive analysis in the physicochemical parameters of the Aripal stream on spatial and seasonal scale is presented in the Table 4 & 5, respectively.

A relationship between the molluscan species and physico-chemical parameters of the Aripal stream showed a significantly positive correlation with the total hardness. The *Radix auricularia*, *Racesina luteola*, *Gyraulus* sp., *Planorbis* sp., and *Corbicula cashmirienses* revealed a very significant positive correlation (P <0.01) with total hardness while the *Lymnaea stagnalis*, *Pseudosuccinea columella*, *Segmentina* sp., *Indoplanorbis exustus*, and *Pisidium casertanum* revealed a significant positive correlation (P <0.05) with total hardness. Besides the *Pseudosuccinea columella*

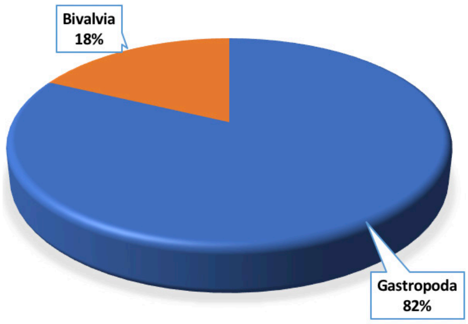

Figure 2. The annual percent contribution of Gastropoda and Bivalvia to the total molluscan population.

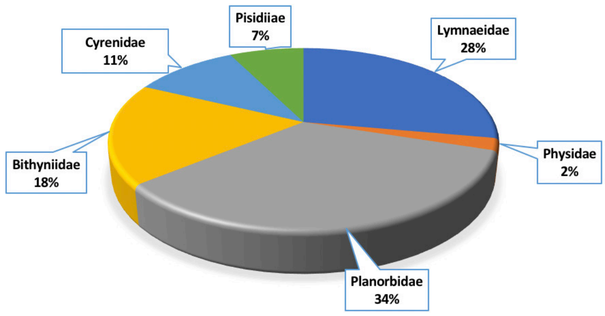

Figure 3. The annual percent contribution of different families to the total molluscan population.

and *Pisidium casertanum* showed a significant positive correlation (P <0.05) with water temperature and pH. The *Planorbis* sp. showed a very significant positive correlation (P <0.01) with air temperature and water temperature. The *Bithynia tentaculata* revealed a very significant positive correlation (P <0.01) with air temperature and water temperature while a negative significant correlation (P <0.05) with alkalinity (Table 6).

DISCUSSION

The ecology of a place and the seasons of a year play an important role in the distribution and abundance of organisms. During the present study, the distribution and abundance of freshwater molluscs were monitored in the Aripal stream of Kashmir Himalaya, where 12 species were reported which belong to six families and two classes. Out of 12 species, 10 species belong to class Gastropoda, and the remaining two species belong to class Bivalvia. The family Planorbidae showed a high contribution to the total molluscs at all the selected sites of the stream, followed by the Lymnaeidae and Bithynidae. Sharma et al. (2010) observed similar results regarding the diversity and distribution of

Table 4. Spatial variation in the physico-chemical parameters from Aripal stream.

Parameters	Site A1	Site A2	Site A3
AT (°C)	15.4±6.5^{a}	16.5±8^{a}	16.8±8.1^{a}
WT (°C)	12.4±2.8^{a}	14.2±4.7^{a}	13.1±3.5^{a}
DO (mg/L)	10.7±1.2^{a}	11.6±2.1^{a}	10.8±2.2^{a}
pH	7.6±0.3^{b}	7.9±0.4^{a}	7.9±0.3^{a}
EC (µs cm^{-1})	226±90.3^{a}	258.9±80.7^{a}	283.9±82.2^{a}
TDS (mg/L)	108.4±44.8^{a}	122.8±39.8^{a}	133.8±41.5^{a}
TH (mg/L)	78.3±32.8^{b}	94.6±29^{ab}	111.5±36.9^{a}
Alk (mg/L)	80.9±20.1^{b}	92.1±19.4^{ab}	109.5±25^{a}

Parameter sharing the same superscript among the sites are nonsignificant (*P* >0.05); one-way ANOVA applied followed by Duncan's multiple range test.

Table 5. Seasonal variation in the physico-chemical parameters from Aripal stream.

Parameters	Summer	Autumn	Winter	Spring
AT (°C)	24.1±1.3^{a}	17.4±5^{b}	6.7±2.5^{c}	16.9±5.4^{b}
WT (°C)	17.4±2.9^{a}	12.8±3.3^{b}	9.7±1.5^{c}	13±2.2^{b}
DO (mg/L)	10.2±2.1^{a}	11.1±1.9^{a}	11.7±1.8^{a}	11.2±1.6^{a}
pH	7.7±0.3^{b}	8±0.6^{a}	7.6±0.2^{b}	7.9±0.1^{ab}
EC (µs cm^{-1})	183.8±68.5^{b}	315.7±55.6^{a}	335.1±32^{a}	190.6±38.2^{b}
TDS (mg/L)	87.7±31.6^{b}	156.8±30^{a}	150.1±24.8^{a}	92±26.4^{b}
TH (mg/L)	108.1±51.1^{a}	90±19.1^{ab}	71.8±24.4^{b}	109.3±26.6^{a}
Alk (mg/L)	78±17.7^{b}	87.6±17.7^{b}	120.1±25.9^{a}	91±12.1^{b}

Parameter sharing the same superscript among the seasons are nonsignificant (*P* >0.05); one way ANOVA applied followed by Duncan's multiple range test.

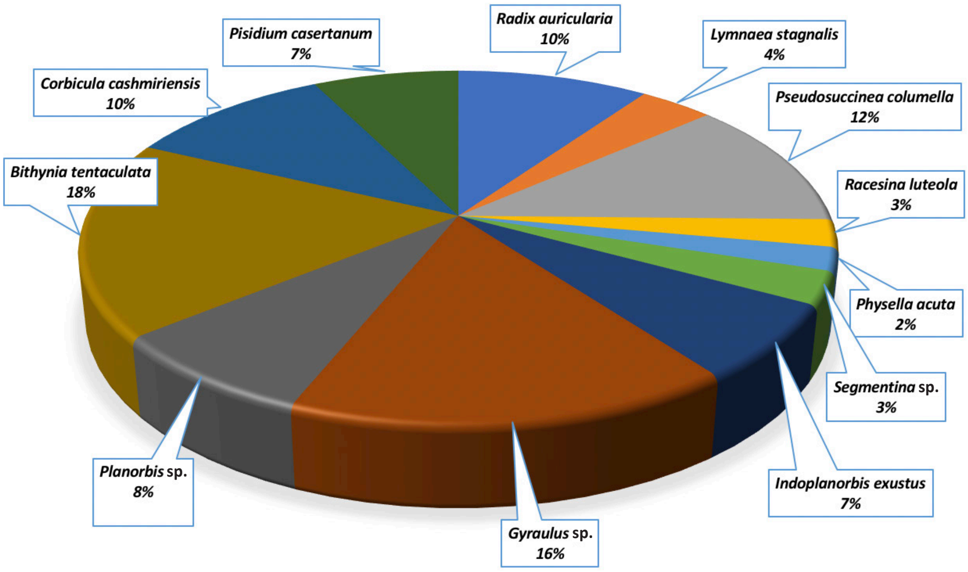

Figure 4. The annual percent contribution of different species to the total molluscan population.

Table 6. Correlation between the molluscan species and physico-chemical parameters from Aripal stream.

Malacofauna	AT	WT	DO	pH	EC	TDS	TH	Alk
Radix auricularia	0.48	0.5	-0.28	0.4	-0.06	-0.06	0.82**	0.15
Lymnaea stagnalis	0.16	0.06	-0.28	0.29	0.08	0.09	0.68*	0.39
Pseudosuccinea columella	0.48	0.61*	0.01	0.60*	0.01	0.02	0.65*	0.14
Racesina luteola	0.55	0.56	-0.20	0.46	-0.10	-0.05	0.81**	-0.01
Physella acuta	0.13	0.23	0.51	0.43	0.07	0.13	0.06	-0.19
Segmentina sp.	0.20	0.13	-0.32	0.16	0.18	0.14	0.62*	0.38
Indoplanorbis exustus	0.31	0.20	-0.37	0.24	0.11	0.10	0.68*	0.28
Gyraulus sp.	0.42	0.33	-0.38	0.24	-0.06	-0.07	0.78**	0.18
Planorbis sp.	0.72**	0.74**	-0.33	0.43	-0.26	-0.24	0.79**	-0.18
Bithynia tentaculata	0.90**	0.95**	-0.38	0.24	-0.57	-0.50	0.50	-0.70*
Corbicula cashmiriensis	0.23	0.29	-0.02	0.50	0.12	0.11	0.73**	0.43
Pisidium casertanum	0.46	0.61*	0.03	0.61*	-0.11	-0.08	0.67*	0.07

'*' significant correlation at *P* <0.05; '**' highly significant correlation at *P* <0.01; two-tailed Pearson's coefficient of correlation (r) applied.

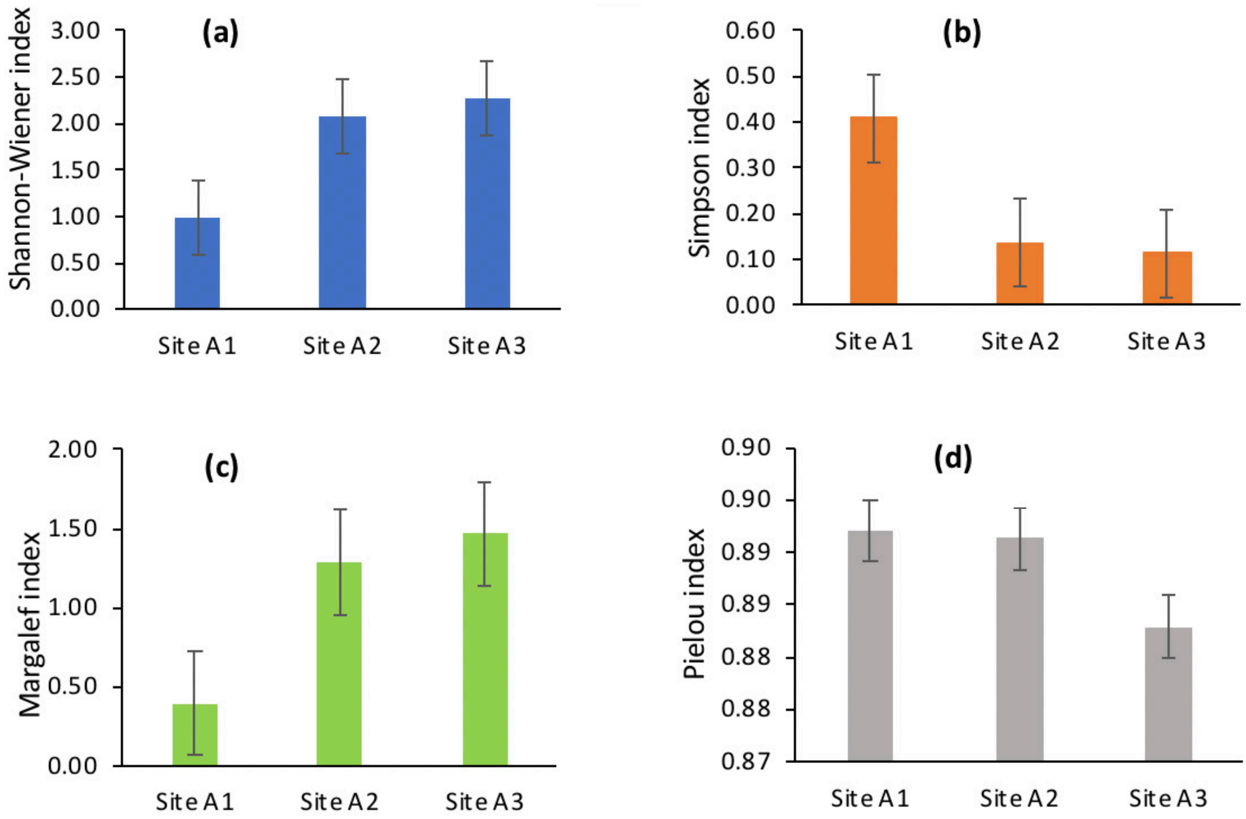

Figure 5. Spatial variation in the diversity of malacofauna from Aripal stream.

Gastropoda. Hora et al. (1955) observed the prevalence of *Gyraulus* sp., *Indoplanorbis exustus*, and *Valvata* sp. in the Kashmir valley. However, in our case, *Gyraulus* sp., *Planorbis* sp., and *Bithynia tentaculata* were recorded from all the sites which may be attributed to the availability of food and shelter in the form of leaf litter, aquatic macrophytes, periphyton, and organic-rich bottom sediments of different sites. The high prevalence of *Bithynia tentaculata* in the stream may be due to the better capability of utilizing the organic matter available in the bottom substrate. The presence of *Lymnaea stagnalis*, *Segmentina* sp., and *Indoplanorbis exustus* with the increase in electrical conductivity and total dissolved solids at site A3 may act as bioindicator of pollution. Wagh et al. (2019) noticed similar results with respect to freshwater molluscs in the Amravati district of Maharashtra, India. The selected sites along the stream face various types of disturbances. The site A1 is disturbed due to stone mining, floods, and land-use changes, site A2 is disturbed mainly from washing clothes and domestic sewage and site A3 receives the agricultural runoff from surrounding agricultural land. The presence of few species at site A1 (up-stream) may be the key cause of stone mining, occasionally torrential flow during floods, and change in land-use patterns which may cause habitat instability and result negative impacts upon the molluscan fauna. However, the species number increased abruptly towards the downstream which may be attributed to the reduction in the stream slope, low velocity, stability of bottom substrate, the inflow of nutrients from surrounding agricultural land, and sedimentation of fine organic matter. Further high diversity, richness, and evenness were observed at site A3 (down-stream) and low values at site A1 (up-stream). The high diversity, richness, and evenness in the downstream may reflect the stability of bottom substrate due to downward serpentine flow, formation of pool-rich stretches, and presence of different microhabitats by the introduction of woody debris and growth of periphyton and submerged macrophytes. The findings are validated by Strzelec & Krolczyk (2004) who reported that sandy bottom, vegetation, and organic sedimentation are the most suitable substrate for rich molluscan fauna. The richness of the molluscan species at site A2 and site A3 may also be attributed to the combined effect of higher values of alkalinity, pH, total hardness, and total dissolved solids. During the present study, majority of molluscan species showed a significant positive

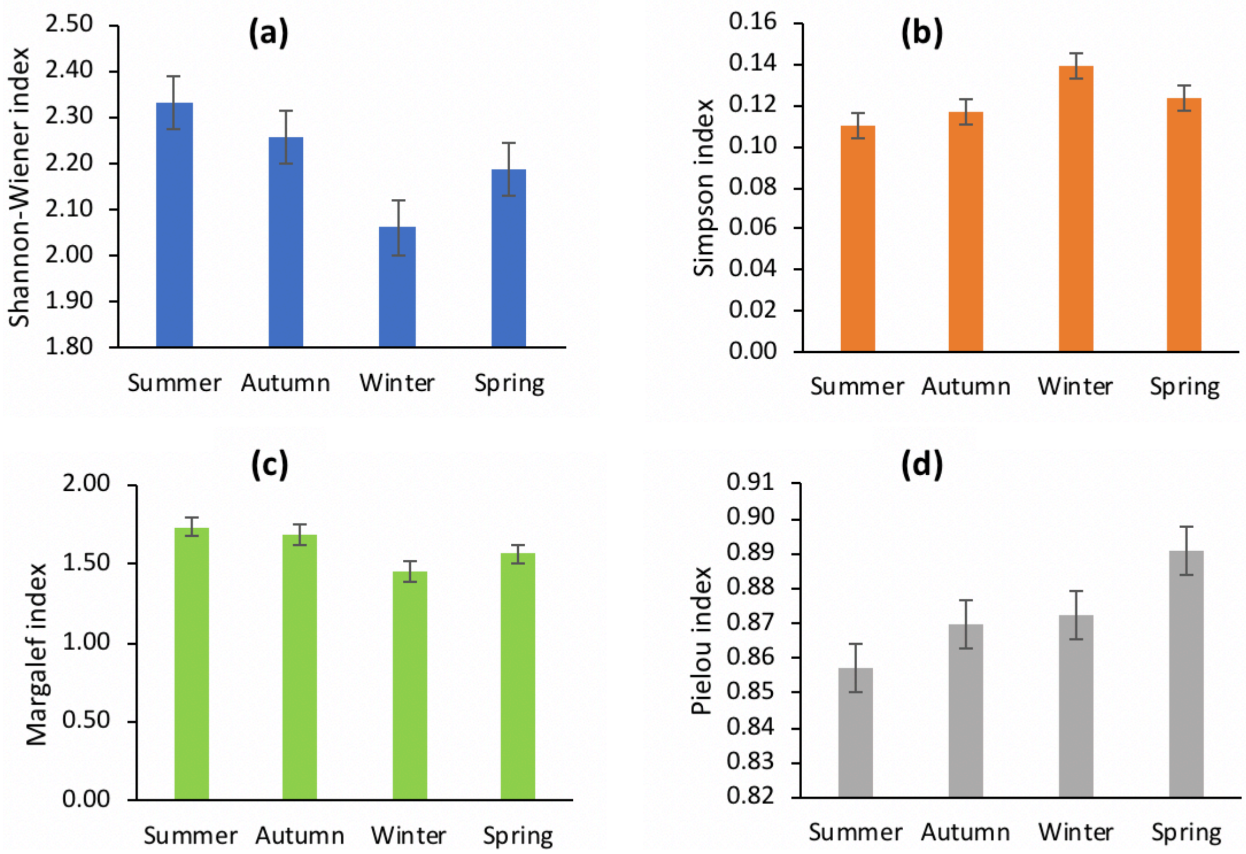

Figure 6. Temporal variation in the diversity of malacofauna from Aripal stream.

correlation with physico-chemical parameters. Many workers have reported a positive correlation between these parameters and mollusca (Malhotra et al. 1996). The dissolved oxygen showed spatially and temporally non-significant variation in the stream and also revealed a non-significant correlation with molluscan species. A similar trend was observed in earlier studies (Sharma 1986). In the temporal variation of mollusca, the species diversity and richness were observed maximum in the summer season while minimum in the winter season. This may be related to the two important parameters, viz., temperature and organic matter. The increase in the temperature during the summer season may activate the decomposition of organic matter suspended in the bottom substrate and may accelerate its conversion into inorganic nutrients. This process may promote the growth and structure of periphyton and macrophytes which form the suitable substrate for malacofauna. The statement is related to the findings of various other authors as well (Dutta & Malhotra 1986; Malhotra et al. 1996; Bath et al. 1999). The present study presents the spatial and temporal diversity patterns of malacofauna in the Aripal stream of Kashmir Himalaya. Mollusca as one of the components of macrobenthic invertebrates play role in the regulation of suspended organic matter within the bottom substrate of streams. The study emphasizes the need for the conservation of streams and their role in shaping the occurrence, distribution, abundance, and richness of malacofauna. Streams as freshwater ecosystems provide habitat for diverse flora and fauna and thus form an important model for ecological studies.

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