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Research Article

Life Cycle and Secondary Production of Four Species from Functional Feeding Groups in a Tropical Stream of South India

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This study focused on life strategies of species from functional feeding groups (FFGs) found in a tropical stream of the Sirumalai hills, South India. We examined the life cycle and secondary production of species of shredders (*Lepidostoma nuburagangai*), scrapers (*Baetis* sp.), collectors (*Choroterpes alagarensis*), and predators (*Neoperla biseriata*). In addition, we studied the assemblage structure of functional feeding groups. We found the collectors occupied the highest percentage, followed in turn by scrapers, predators, and shredders. The diversity of FFGs was higher at riffle areas and assemblage with stream substrates differing in each functional group. An asynchronous life cycle was observed for *Baetis*, *C. alagarensis*, and *N. biseriata*, while *L. nuburagangai* was found in four to five generations per year. We acquired data on secondary production of scraper species of *Baetis*, which reached the highest values among all investigated species. This observation stresses the importance of scrapers as playing a key role in converting coarse particulate organic matter to fine particulate organic matter with low or high abundances of shredder population and maintaining the food chain in tropical streams.

1. Introduction

Tropical forests cover 15–20% of the earth's land surface and about half of this is being converted to agricultural land and for other human purposes. More than 50% of the world's biodiversity is found in the tropical forests. Freshwater ecosystems are relatively more important than the terrestrial ecosystems because aquatic organisms are highly susceptible to climatic variation and anthropogenic impact [1]. The allochthonous organic substrate provides protection and habitat space and it has fundamental importance as a food source for aquatic macroinvertebrates [2]. Aquatic macroinvertebrates are classified into four major functional feeding groups (FFGs) based on the morphobehavioural mechanisms of food acquisition rather than taxonomic groups as follows: shredders, scrapers, collectors, and predators [3].

Feeding measures that contribute to fluvial trophic dynamics encompass FFGs and provide information on the balance of feeding strategies (food acquisition and morphology) in the benthic assemblage [4]. The major food sources utilized by macroinvertebrates are the epilithic layer that grows on the surfaces of substrates (consumed by scrapers), the coarse detritus of leaves falling from riparian vegetation (consumed by shredders), the fine detritus either deposited on the substrate or suspended in the water column (consumed by collector/filter-feeders), and live animals (consumed by predators) [3–5].

The knowledge of FFGs has been widely studied throughout the world and is central to the River Continuum Concept [6]. FFGs are also used in water quality assessment [4, 7], energy transfer studies [8, 9], and food chain modelling [10], but information is lacking on the life cycle and secondary production of FFGs in tropical regions, especially India. The threats faced due to tourism, grazing, hunting, poaching, agriculture, deforestation, and land use have resulted in a loss of aquatic biodiversity in India [11–13]. Therefore conservation of existing and functionally important species is an urgent need to preserve the aquatic biodiversity in India. In this study, we examined the life cycle pattern and secondary production of aquatic insect species from the four

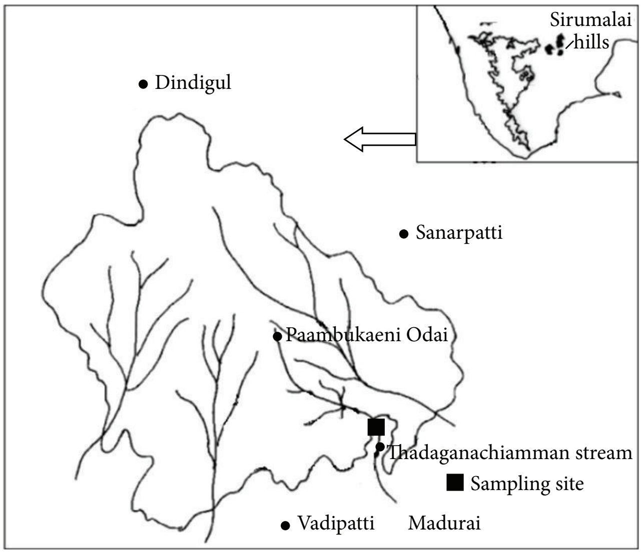


Figure 1: Study area—Siurmalai hills, southern India.

major functional feeding groups. In addition, we studied the assemblage structure of functional feeding groups in a tropical stream of South India.

2. Materials and Methods

2.1. Study Area. The present study was carried out in a tropical stream (Thadaganachiamman stream) of South India between June 2007 and May 2008. The Thadaganachiamman stream of the Sirumalai hills is in the Eastern half of the Dindigul District. The Sirumalai hills form a minor range in the Deccan plain (latitude: 10°, 08′, 12″N, longitude: 78°, 01′, 08″E, and elevation: 375 m) of the Western Ghats and is a hilly region whose elevation ranges from 250 to 800 m.a.s.l. This perennial stream is situated about 32 km from Madurai city (Figure 1). The rainfall is between 156 and 195 cm ann^{-1}, unevenly distributed through the year with the highest rainfall received during the north-east monsoon (November) and south-west monsoon (June–August). Along the banks of the stream are thick stands of trees and shrubs whose leaves are the stream's principal source of organic detritus. Dominant riparian tree species are *Pongamia pinnata* (common name: Pongam or Indian Beech tree), *Syzygium cuminii* (Jamun), and *Commiphora caudata* (Hill Mango). The prominent herbs on the banks of the stream are *Cyperus bulbosus*, *Cyperus dubius, Fimbristlis schoenoides*, *Cyanotis cristata*, and *Commelina clavata*.

2.2. Sampling Methods. Month-wise sampling was done at study site of Thadaganachiamman stream. The physicochemical parameters and a stream profile were measured by Dinakaran and Anbalagan [14] and APHA [15]. In the study area, three 50 × 50 cm benthic samples were taken at random locations from riffle and pool. The sampling depth of riffle and pool of the stream ranged from 10 to 15 cm and 50–80 cm, respectively. Samples were collected in riffles, using 180 μm mesh kick-nets and 500 μm mesh dip nets used for pool sampling. Adult insects were sampled by sweep netting in the vegetation of stream corridor to confirm species identifications and determine emergence periods. A light trap was also used to collect adults. Soon after collection, the specimens were preserved in 70% ethanol.

2.3. Laboratory Analysis. All collected specimens were identified and classified based on their feeding pattern and morphological characters according to Dudgeon [5]. Further, the gut of specimens from each functional taxon was dissected out and the presence of taxa in the gut was observed under a stereoscopic dissection microscope to confirm the trophic category of four major functional feeding groups. The body length and head width of the four functional taxa were measured using an ocular micrometer in a stereoscopic dissecting microscope. Body lengths were converted to body mass for secondary-productivity calculations using dry mass length equations given in Benke et al. [16]. Individuals from all sites were combined to provide a large enough sample for production analysis. Further, secondary productivity was calculated using the size frequency method for all species and the instantaneous growth rate method for species where cohorts could be reliably separated [17].

2.4. Data Analysis. The distributional difference of aquatic insects between riffle and pool was estimated by one-way ANOVA. Size-frequency histograms based on body length and head width of four functional taxa were plotted using the software package, PAST version 2.08, and graphs were edited with Photoshop software. To test the relationship between body length and head width of taxa, linear regression was used. In this analysis, data was log transformed and estimated by the generalized linear regression model. The relationship of population density, biomass, and production of the four species was tested with two nonparametric tests of Kruskall-Wallis and Friedman test by using the software package, PAST version 2.08.

3. Results

The physicochemical parameters of the study area are given in Table 1. In total, 19 species belonging to 15 families and 8 orders of aquatic insects were collected from both riffle and pool areas of the stream. The collected specimens were classified based on their feeding pattern into shredders, scrapers, collectors, and predators. Among functional feeding groups of this stream, the collectors occupied the highest percentage (52%), followed by scrapers (18%), predators (16%), and shredders (14%). FFGs diversity was significantly (F = 2.3, P = 0.001) related to riffle than the pool area revealed by one-way ANOVA. The shredders and scrapers were primarily associated with leaf litter at pool, while collectors and predators were predominant in riffles where they were found in the substrates of bedrock, boulders, pebbles, leaf litter, and woody debris (Table 2). The monsoonal effects altered the distribution of aquatic insects, with the high diversity and

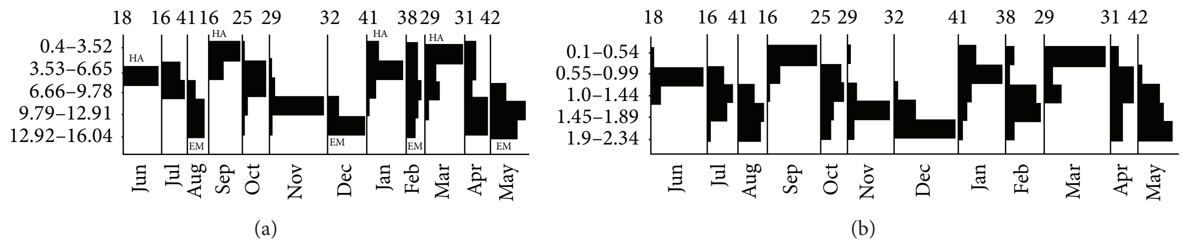


Figure 2: Size frequency distribution of *L. nuburagangai*, (a) body length (mm), and (b) head width (mm) (HA—hatching; EM—emergence).

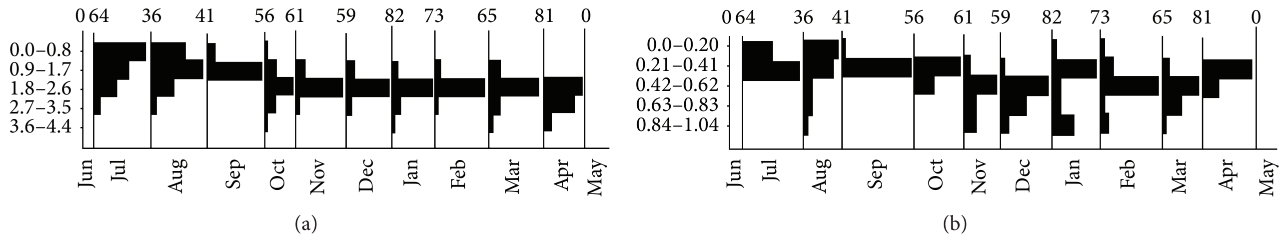


Figure 3: Size frequency distribution of (a) body length (mm) and (b) head width (mm) of *Baetis* sp.

Table 1: The physicochemical parameters (mean ± SE) of a Thadaganachiamman stream in the Sirumalai hills of Southern India.

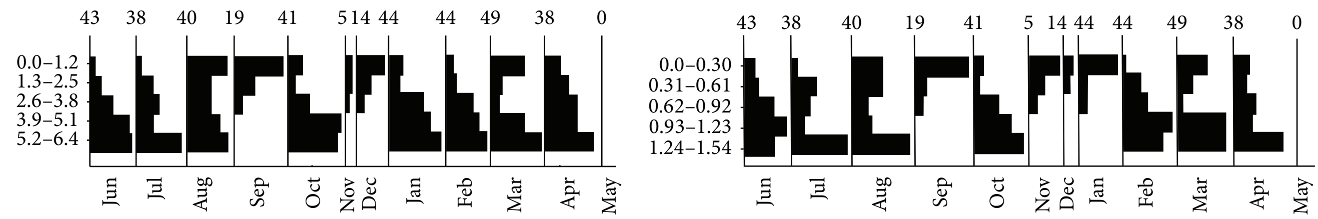
Parameter	Riffle	Pool
Air temperature (°C)	28.5 ± 1.2	28.5 ± 1.2
Water temperature (°C)	24.0 ± 1.3	25 ± 1.1
Dissolved oxygen (mgL^{-1})	13.0 ± 0.6	11.5 ± 0.8
pH	6.5 ± 0.01	6.5 ± 0.01
Conductivity (μmhos/cm)	0.2 ± 0.002	0.2 ± 0.002
Stream width (m)	1.0 ± 0.3	—
Stream depth (cm)	14.0 ± 1.5	60.0 ± 4.3
Current velocity (cm/sec)	0.4 ± 0.06	0.6 ± 0.04
Bedrock (%)	30.0 ± 2.3	—
Boulders (%)	25.0 ± 2.8	—
Pebbles (%)	27.0 ± 1.9	—
Gravels (%)	10.0 ± 2.1	—
Sand (%)	4.0 ± 0.5	20.0 ± 1.4
Silt (%)	3.0 ± 0.2	5.4 ± 0.4
Leaf litter (%)	30.0 ± 3.1	50.0 ± 8.2
Woody debris/twigs (%)	10.0 ± 1.5	20 ± 4.4
Canopy cover (%)	60.0 ± 5.2	60.0 ± 5.2
Riparian cover (%)	80.0 ± 5.2	80.0 ± 5.2

abundance found during postmonsoonal period ($F = 1.14$, $P = 0.001$).

Dominant species were selected from each functional feeding group of shredder, scraper, collector, and predator for studying life cycle pattern and secondary production. *Lepidostoma nuburagangai* Dinakaran et al. [18] as a shredder, *Baetis* sp. as a scraper, *Choroterpes alagarensis* Dinakaran et al. [19] as a collector, and *N. biseriata* Zwick et al. [20] as a predator were taken for this study. The gut analysis of these four functional species was done to confirm the respective trophic category. The fragments of leaf and wood in the gut of *L. nuburagangai*, large amounts of diatoms, periphytons, and plant detritus in the gut of *Baetis*, periphytons, diatoms, and fine detritus in the gut of *C. alagarensis* and animal materials in the gut of *N. biseriata* were observed (Table 3).

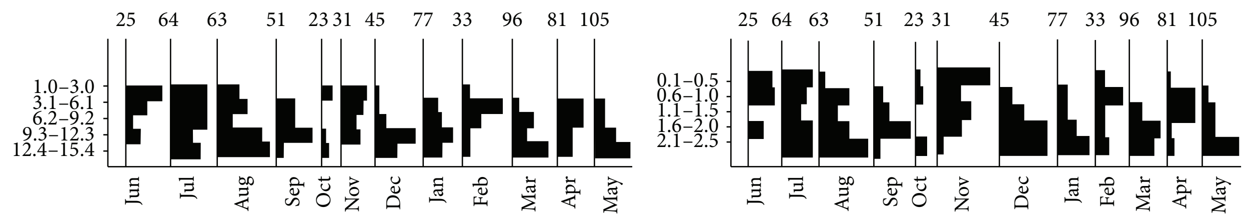
Size frequency histograms for body length and head capsule width of *L. nuburagangai* revealed four separate cohorts: the first cohort hatched from eggs in June, with rapid growth followed by adult emergence in August; a second cohort hatched from eggs in September and grew for 4 months and adults emerged in December; the third cohort hatched from eggs in January and grew for 1-2 months and adults emerged in February; the fourth cohort hatched from eggs in March and grew for 1-2 months and adults emerged in April and May (Figure 2). The cohorts of *Baetis* and *C. alagarensis* showed asynchronous nymph development with continuous emergence except during the summer (Figures 3 and 4). *N. biseriata* showed four generations that could be easily separated throughout the autumn, winter, spring, and summer, but the major emergence took place in early summer (March and April), with the new generation appearing in the samples in July. Adults of *N. biseriata* were found between May and August and December and January (Figure 5).

Linear regression equations indicated that the body length and head width of all four species were significantly correlated (Figure 6). The population density, biomass, and production of the four functional taxa were significantly related as shown by one-way ANOVA, Friedman test and Kruskal-Wallis test. The total annual secondary production of *Baetis* reached the highest values (514 mg m^{-2} y^{-1}) among all investigated species. The high production of these taxa was observed during July, January, and April, which reflects higher densities occurring in these months, whereas lower production was observed between October and December. The ratio of productivity to biomass (P/B ratio) indicated four to five cohort productions in *L. nuburagangai* and eight to



(a) (b)

Figure 4: Size frequency distribution of (a) body length (mm) and (b) head width (mm) of *C. alagarensis*.



(a) (b)

Figure 5: Size frequency distribution of (a) body length (mm) and (b) head width (mm) of *N. biseriata*.

nine cohort productions in *Baetis* sp. and *C. alagarensis* sp. and *N. biseriata* (Table 4).

4. Discussion

According to the River Continuum Concept [6], middle order streams were dominated by collectors, scrapers, predators, and shredders. Similarly, third order stream of the present study area had the highest percentage of collectors. This may be due to the enormous FPOM concentration available in the study sites. The highest aquatic insect diversity was observed in riffle areas due to the rich variety of substrates available in this habitat that provides habitat heterogeneity for the colonization of aquatic insects in streams. Similar results were found in other streams of South India [11]. In this study the highest diversity and abundance of aquatic insects were observed during postmonsoonal periods. The low insect abundance and diversity during monsoon are probably due to heavy water flow or flood. Leaf litter in the pool had its highest abundance of shredder and scraper species. The high insect abundance in pools during postmonsoon and low insect abundance in depositional areas (pools) during the dry season (March) are likely due to the fluctuation of physical and chemical parameters [21, 22]. Habitat heterogeneity is an important factor influencing macroinvertebrates distribution in streams [23]. Similar results were found in the streams of India [24].

Most permanent streams in the temperate zone have both autumn-winter and spring-summer growth periods while shredder species had two generations per year [25]. *L. nuburagangai* had four to five generations per year. In temperate forest streams, leaf fall occurs mainly in the autumn [26], whereas, in tropical streams, year-round leaf litter input [27], which may favour the additional generations for shredders. This finding contrasts with the study of Yule et al. [28], they reported the lack of insect shredder hosts and other shredding consumers, including fishes, shrimps, crabs, and prosobranch snails in tropical streams. The shredder *L. nuburagangai* occupies a key role in the energy and nutrient transfer from terrestrial to stream ecosystems. However, the fact that all life stages of *L. nuburagangai* are present at any given time maximizes exploitation of the continuous allochthonous input in tropical streams and facilitates population turnover. The *P*/*B* ratio of *L. nuburagangai* cohort was 4.8 or 5 a ratio indicating higher growth rates [29]. Bright [30] who reviewed the present knowledge of secondary production in inland waters concluded that yearly P/B ratios depend primarily on voltinism. Yule et al. [28] has pointed out that the dependence of the benthos on allochthonous material results from the highest biomass occurring in winter and early spring in temperate streams. This appears also to be true for the shredder of *L. nuburagangai* as their biomass was high during early spring (April-May).

Baetis species have been found elsewhere to be abundant in macrophytes and roots of marginal vegetation in riffles and pools [31]. Likewise, the South Indian *Baetis* was abundant in macrophytes and ubiquitous in pools and riffles. *Baetis* is associated with macrophytes because they support periphytic algae, which is food for the nymphs. The importance of autochthonous foods for macroinvertebrate production in forest streams was unexpected, but this has been reported elsewhere. Fujitani [32] showed that benthic algae were an important component in the diet of mayfly larvae in a Japanese stream. *Baetis* exhibited asynchronous development with most size classes present throughout the year in these South Indian streams. The same pattern was observed in tropical streams of Hong Kong [33] with similar annual production, but lower than the Australian stream [34], while higher than a Neotropical Costa Rica stream [35].

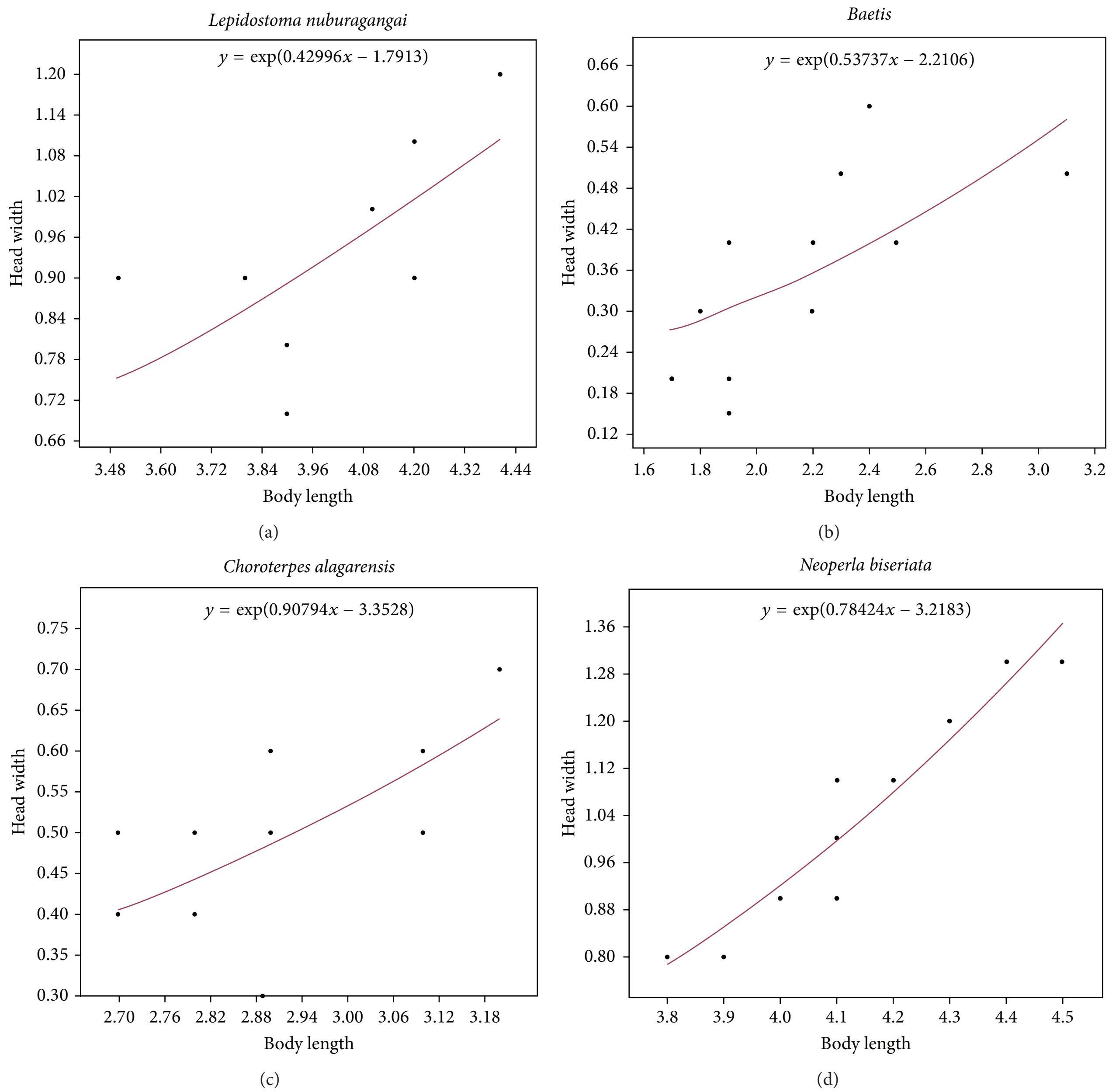


FIGURE 6: Linear regression model for head width and body length of four functional taxa.

TABLE 2: Density (individuals/m^2) of functional feeding groups in the stream substrates.

Habitat	Substrate	Functional feeding groups (mean ± SE)			
		L. nuburagangai	*Baetis*	*C. alagarensis*	*N. biseriata*
Riffle	Bedrock	0	6 ± 0.9	5 ± 0.4	0
	Boulders	18 ± 1.1	12 ± 1.4	39 ± 1.1	36 ± 0.5
	Pebbles/gravels	0	1 ± 0.5	12 ± 2.3	15 ± 0.5
	Leaf litter	12 ± 2.9	25 ± 3.1	34 ± 1.3	39 ± 1.5
	Woody debris	13 ± 2.2	2 ± 0.4	5 ± 1.2	8 ± 1.1
Pool	Leaf litter	38 ± 1.6	48 ± 2.3	4 ± 0.4	0
	Woody debris	18 ± 2.1	5 ± 0.9	0	0

Table 3: The gut contents of functional feeding groups (mean ± SE).

Taxa	Functional group	Gut contents (%)				Number of specimens examined
		Plant detritus	FPOM	Diatoms	Animal detritus	
L. nuburagangai	Shredder	28 ± 0	0	0	0	25
Baetis sp.	Scraper	34 ± 5.8	0	51 ± 8.5	0	32
C. alagarensis	Collector	0	85 ± 11.5	9 ± 1.9	0	25
N. biseriata	Predator	0	0	0	14 ± 1.4	28

Table 4: Secondary production estimates (mean ± SE) for the four functional taxa using the size frequency method.

Taxa	Density (no. m^{-2} $year^{-1}$)	Biomass (mg m^{-2} $year^{-1}$)	Production (mg m^{-2} $year^{-1}$)	P/B
L. nuburagangai	720 ± 21	306 ± 11	1484 ± 21	4.8
Baetis sp.	1252 ± 28	514 ± 19	4264 ± 23	8.3
C. alagarensis	585 ± 13	185 ± 9	1555 ± 15	8.4
N. biseriata	231 ± 9	97 ± 5	864 ± 11	8.9
F test	3.649 ($P = 0.111$)			
Friedman test	0.5294 ($P = 0.004$)			
Kruskal-Wallis test	0.3371 ($P = 0.017$)			

Size frequency diagrams and P/B ratio revealed that *C. alagarensis* had asynchronous development with year-round emergence. Water temperature could be one factor affecting this pattern, because it also influenced the growth of *C. alagarensis* during winter and summer. The thermal equilibrium hypothesis [36, 37] predicts that each species has an optimum temperature that allows maximum reproductive success and population stability.

N. biseriata was multivoltine and their major emergence was in early summer. A similar life cycle pattern has been reported in tropical streams of northern Florida [38] and an Appalachian stream in Pennsylvania [39]. Hilsenhoff et al. [40] reported that stoneflies were very common in a Wisconsin stream, with an emergence period from early April to early May. Giberson and Garnett [41] recorded emergence in May in a stream in northern New Brunswick. *N. biseriata* nymphs in this study stream have shorter life cycles and higher survivorship and reach their terminal nymphal biomass more rapidly than *N. clymene* [38] suggesting the factors involved are higher stream temperatures and/or nutrient concentration in study stream.

This result reflects the fact that leaf litter in a tropical stream serves as food for macroinvertebrates [2] and predicts the production of functional feeding groups especially shredders [3]. This study found evidence that fallen leaves from streamside vegetation enter the stream in all months, while a substantial portion of leaf input occurs during January and June and thus supported high densities of FFGs in Kallar stream of southern India [42]. Similarly, the fast growth of shredders during January and June and asynchronous development of other FFGs (scrapers, collectors, and predators) occurred throughout the year in the present study. Among the four investigated species of FFGs, the secondary production of scraper species (*Baetis*) had the highest values (514 mg m^{-2} y^{-1}), which indicates that scraper plays a key role in converting allochthonous organic matter to fine particulate organic matter when low or high abundances of shredders occurs, thus maintaining the food chain in this tropical stream.

Conflict of Interests

The authors declare that there is no conflict of interests regarding the publication of this paper.

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