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Effect of Detritus Quality on Energy Allocation in Chironomids

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Abstract: Bioenergitics of *Kiefferulus barbitarsis* and *Tanypus bilobatus* was studied by providing different nutrient sources (mixed algal powder, *Chlorella*, vegetable waste, sheep manure and silt) to the larvae. *K. barbitarsis* ingested vegetable waste at the rate of 2359 J/g/day and realized a production rate of 187 $J.g^{-1}day^{-1}$. Production rate of *K. barbitarsis* (546 $J.g^{-1}day^{-1}$) and *T. bilobatus* (200 $J.g^{-1}day^{-1}$) reared in mixed algal powder was significantly higher than those reared in silt medium (*K. barbitarsis*: 114 $J.g^{-1}day^{-1}$; *T. bilobatus*: 98 $J.g^{-1}day^{-1}$). Assimilation efficiency of *K. barbitarsis* (57.3 or 60.3%) and *T. bilobatus* (62.0 or 56.3%) reared in mixed algal powder or *Chlorella* was higher than that of the larvae reared on other media. LSD test showed that the mean assimilation efficiency of the larvae varied significantly with the nutrient source. The larvae reared in the mixed algal powder and *Chlorella* displayed high net production efficiency (*K. barbitarsis* 59.8 of 66.4 %; *T. bilobatus*: 36.5 and 48.0%). *K. barbitarsis* and *T. bilobatus* pupae in the mixed algal powder, *Chlorella*, sheep manure, vegetable waste or silt medium expended 835.1, 876.5, 915.5, 845.3 or 881.5 $J.g^{-1}.day^{-1}$ and 675.8; 741.3, 928.8, 880.3 or 777.1 $J.g^{-1}day^{-1}$ respectively on metabolism during the metamorphic period and metamorphosed with an efficiency ranging from 59.8 to 76.1% and 60.8 to 71.8% in *K. barbitarsis* and *T. bilobatus* respectively.

Key words: Energy allocation · Chironomus · *K. barbitarsis* · *T. bilobatus* · Chlorella

INTRODUCTION

Bioenergetics proves a powerful tool to assess the impact of environmental factors on the physiology of organisms [1]. Reviews on feeding and transformation of food in insects [2-5] indicate the selective predominance of studies on herbivorous insects and the paucity of information on carnivores, detritivores and sanguivores. The dearth of information on detritivores is apparently less due to the problems encountered in the estimation of one or the other of the bioenergetics components [6]. In their natural habit, chironomid larvae are exposed to a wide range of food material, which differ not only in their nutrient content, but also in particle size. Besides environmental factors such as temperature, dissolved oxygen and pollutants, food quality and particle size may considerably influence the rate and efficiencies of detritus ingestion and utilization [7, 8]. The present study was undertaken to provide energy budgets for two species of chironomids *K. barbitarsis* and *T. bilobatus* using different nutrient sources.

MATERIALS AND METHODS

To assess the influence of nutrient source on growth and energy partitioning of *K. barbitarsis* and *T. bilobatus*, 400 to 500 freshly hatched larvae were reared in 10*l* cap. plastic trays containing 5*l* water under laboratory condition. To begin with, these larvae were reared on 2 to 20 g substrates (Nutrient) like mixed algal powder (*Chara fragilis* 30%, *Hydrilla verticillata* 30%, *Wolffia arrhiza* 30% and *Lemna monia* 10%), sheep manure (Aerobically fermented and dried), vegetable wastes (fermented and dried, vegetables such as cabbage, brinjal and cauliflower leaves at equal proportion), silt from native pond at 2g intervals or *Chlorella* cells (12.0×10^6 to 18.0×10^6 cells/ml) as nutrient source. From

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this, the optimum nutrient concentration for maximizing growth was determined. Accordingly for *K. barbitarsis* larva 12.0 g.3l^{-1} mixed algal powder, 12.0 g.3l^{-1} sheep manure, 14.0 g.3l^{-1} vegetable waste, 16.0g.3l^{-1} silt and 18.0 x 10^6 cells of *Chlorella* ml^{-1} were found to be optimum level. Likewise for *T. bilobatus*, the optimum level of nutrient sources which favoured the growth of *T. bilobatus* were 10.0.3l^{-1} mixed algal powder, 10.0g.3l^{-1} sheep manure, 12.0 g.3l^{-1} vegetable wastes, 16.0 g.3l^{-1} silt and 18.0 x 10^6 cells ml^{-1} *Chlorella* cells.

For further evaluation study, *K. barbitarsis* and *T. bilobatus* larvae were reared in the nutrient sources at the respective assessed optimum level in triplicate separately. During the culture period, water quality parameters such as dissolved oxygen, pH, CO_2, ammonia and BOD were analyzed daily by following the method of APHA [9] and were at uniform level in all the culture medium. The water level on the culture medium was also maintained at constant by adding water equivalent to that of daily water evaporation. At three days time intervals, the growth of the larvae in each medium was monitored by doing sub samples. Then the weight of the larvae was measured with least disturbance and was immediately returned to the respective culture medium.

The scheme of energy budget followed in the present study is the IBP formula of Petrusewicz and Mac Fadyen [10] usually represented as:

$$C = F + P + U + R \quad (1)$$

Where, C is the food energy consumed, F the faeces egested, P the growth, U the nitrogenous excretion and R the energy expended on metabolism. The procedure described by Muthukrishnan and Palavesam [6] considering the gut clearance time, gut content weight of the larvae and the energy input into the medium through the egesta was followed for the estimation of food consumption and egestion. Food energy absorbed (A) by the larva was calculated by subtracting the energy equivalent of the faeces (F) egested from that of the food consumed (C).

$$A = C\text{-}F \quad (2)$$

Food energy assimilated (As) was calculated as the difference between the energy equivalent of the urine excreted (U) and food absorbed (A).

$$As = A\text{-}U \quad (3)$$

Production was calculated considering the initial and the final energy content of the larva. Energy allocated to secretion of materials for construction of the tube was negligible and could not be estimated precisely. Therefore, it was not considered for the estimation of production. Energy expended on metabolism by the larva was calculated considering the oxygen consumption rate of the larva and the oxygen-energy quotient (1 ml O_2 = 20.5 J) applied for other detritus feeders (e.g. *Chironomus plumosus*: [11]; *Pteronarcys scotti*: [12]).

Metabolism (R) was also calculated as the differences between assimilation (As) and production (P).

$$R = As\text{-}P \quad (4)$$

Ammonia excreted by the larvae was estimated daily following the phenol-hypochlorite method of Solorzano [13]. Considering the ammonia-energy equivalent (1 mg NH_3 = 16.86J) reported by Brafield and Solomon [14], ammonia excretion in terms of J was calculated.

Rates of consumption, assimilation, production and metabolism and excretion were calculated as described in Muthukrishnan and Pandian [5]. Efficiencies of assimilation (Ase), gross and net production were calculated by relating A to C, P to C and C and A respectively and expressed in percentage.

Energy budget for the nine-feeding pharate pupal and adult stages were calculated following the method recommended by Muthukrishnan and Pandian [15]. Considering the mid-body weight and duration, metabolic rate for the pharate pupal and adult stage was calculated. Metamorphic efficiency was calculated as percentage of pupal energy transferred to adult. Egg production efficiency was calculated in percentage relating the energy expended on egg production to energy content of freshly emerged adult [16].

The biochemical constituents such as nitrogen and energy in the nutrient source, larvae, pupal and adults were estimated following by using Microkjeldhal apparatus and Parr 1421 Semi-Microbomb Calorimeter (Parr Instrument, Moline, USA), respectively. The results obtained in the present study were subjected to appropriate statistical analysis following the methods described by Zar [17].

RESULTS

K. barbitarsis and *T. bilobatus* larva consumed 26.57 and 24.73J *Chlorella* in a span of 12 and 16 days. Extension of larval duration from 12 to 15 days by

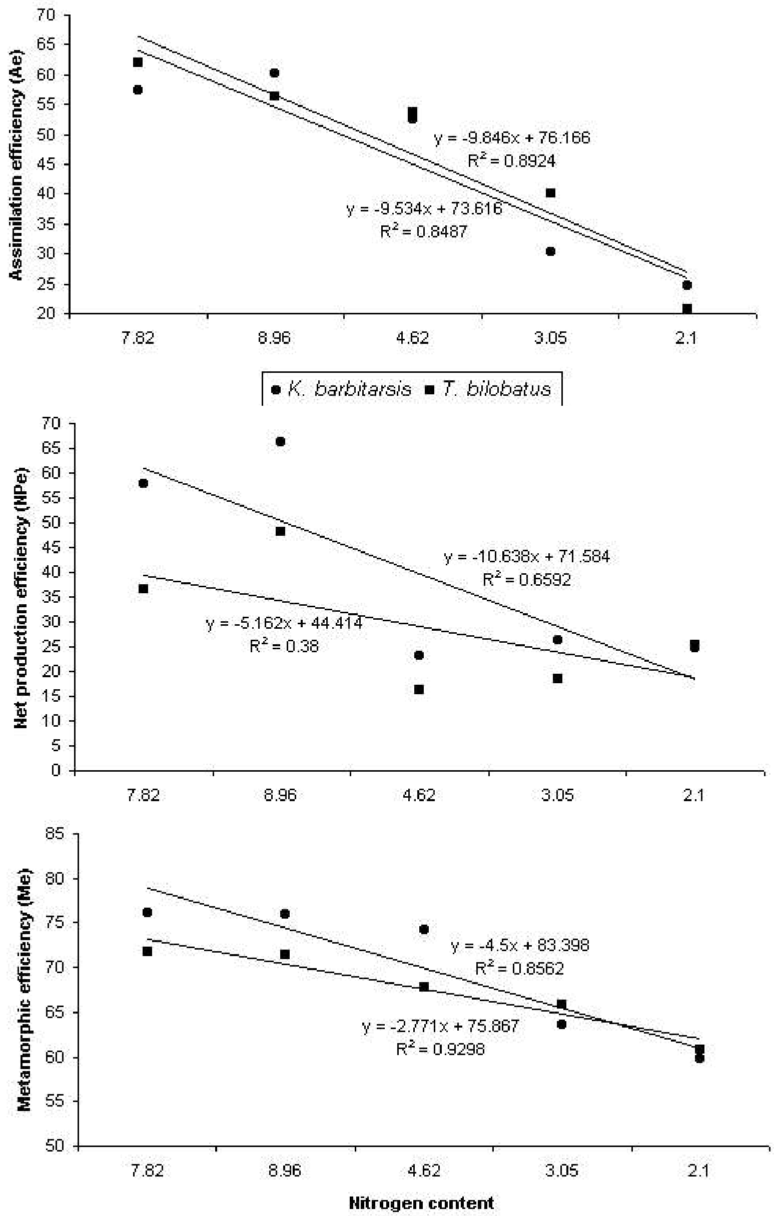

Fig. 1: Correlation co-efficient for the relationship between nitrogen content of the nutrient source and assimilation efficiency, Net production efficiency and metamorphic efficiency of K. barbitarsis and T. bilobatus larvae

K. barbitarsis and 16 to 18 days by *T. bilobatus* fed on sheep manure resulted in increase of consumption to 76.6 and 61.1 J, respectively (Tables 1 and 2). Feeding rate of the larvae reared in mixed algal powder medium was also significantly less than that reared on sheep manure and vegetable waste. Two way analysis of variance showed that the variance in consumption rate due to food quality is statistically more significant ($F_{0.05}$ at Df 4/9 = 4.55; P <0.05) than that between species ($F_{0.05}$ at 1/9 = 0.94; P >0.05).

K. barbitarsis and *T. bilobatus* larva fed on mixed algal powder, egested 17.1 and 9.7 J of faeces in a span of about 12 and 16 days. Larva fed on sheep manure or vegetable waste egested 2 or 4 times more faeces than that fed on mixed algal powder. Larvae reared on silt medium egested the maximum quantity of faeces.

Energy assimilated by the larvae fed on the chosen nutrient sources ranged from 16.0±1.0 to 40.2±0.8J for *K. barbitarsis* and 12.2±0.8 to 32.9±2.5 for *T. bilobatus*. The ingested food assimilated at the rate of 386.9 to

Table 1: Bioenergetics of *K. baribitaris* larva as a function of food quality. Each value (X±SD) represents the average performance of 3 replicates each containing not less than 250 larvae

	Nutrient source				
Parameters	Mixed algal powder	Chlorella	Sheep manure	Vegetable waste	Silt from pond
Larval duration (Days)	12	12	15	15	22
Consumption (J)	45.65±2.54	26.57±1.47	76.57±1.10	104.0±4.94	101.26±3.70
Faeces (J)	17.14±0.88	8.81±0.16	33.74±1.50	69.99±2.63	73.93±5.30
Absorption (J)	28.55±1.70	17.8±1.40	42.8±0.31	34.4±2.6	27.33±1.70
Excretion (J)	2.38±0.13	1.73±0.12	2.67±0.17	2.8±0.14	2.40±0.20
Assimilation (J)	26.17±1.50	16.02±1.00	40.17±0.80	31.60±1.20	24.93±1.30
Production (J)	13.98±0.59	10.63±0.21	9.34±0.27	8.27±0.25	6.17±0.30
Metabolism (J)*	12.19±1.00	5.38±1.73	30.81±0.78	23.34±2.47	18.76±1.10
Metabolism (J)* *	14.23±0.40	8.05±0.35	22.23±1.20	20.17±1.25	16.63±1.20
Consumption rate (J/g/day)	1782.9±98.91[a]	641.71±35.52[b]	1611.67±11.27[c]	2359.33±111.74[d]	1878.60±69.50[e]
Absorption rate (J/g/day)	1115.08±78.72	428.75±34.12	902.38±6.74	777.47±58.22	507.11±30.00
Excretion rate (J/g/day)	92.82±4.99	41.87±3.01	56.44±3.60	63.03±3.14	45.15±3.20
Assimilation rate (J/g/day)	1022.12±65.60	386.90±32.60	845.51±16.00	716.87±20.20	468.15±24.30
Production rate (J/g/day)	545.82±23.00	256.85±4.96	197.67±5.75	186.82±5.60	114.41±6.10
Metabolic rate1 (J/g/day)*	476.09±37.50[a]	203.32±41.90[b]	652.56±15.68[c]	527.61±55.72[d]	354.36±20.80[e]
Metabolic rate2 (J/g/day)**	555.43±15.61	304.23±13.22	470.48±25.40	455.82±28.25	308.60±21.90
Assimilation efficiency (%)	57.32±0.40[a]	60.30±1.70[b]	52.46±1.30[c]	30.38±1.07[d]	24.61±2.00[e]
Pe1 (%)	30.65±0.60[a]	40.00±1.80[b]	12.22±0.20[c]	7.95±0.14[d]	6.13±0.50[e]
Pe2 (%)	57.84±1.20[a]	66.35±6.10[b]	23.25±0.80[c]	26.17±1.06[d]	24.74±1.90[e]

* calculated as (A-P + U); **-Estimated respirometrically

Values in rows superscript with different alphabets are statistically significant (P<0.05)

Table 2: Bioenergetics of *T. bilobatus* larva as a function of food quality. Each value (X±SD) represents the average performance of 3 replicates each containing not less than 250 larvae

	Nutrient source				
Parameters	Mixed algal powder	Chlorella	Sheep manure	Vegetable waste	Silt from pond
Larval duration (Days)	16	16	18	18	22
Consumption (J)	29.04±1.82	24.73±1.83	61.11±2.52	47.78±1.26	58.53±3.80
Faeces (J)	9.74±0.13	9.32±0.81	26.59±2.09	27.41±0.79	44.93±3.50
Absorption (J)	19.28±1.76	15.40±1.03	34.52±0.43	20.37±0.49	13.56±0.80
Excretion (J)	1.27±0.02	1.47±0.10	1.67±0.40	1.20±0.00	1.37±0.10
Assimilation (J)	18.01±0.80	13.93±0.60	32.85±2.50	19.17±1.60	12.20±0.80
Production (J)	6.57±0.20	6.68±0.14	5.34±0.58	3.55±0.18	3.10±0.10
Metabolism (J)*	11.45±1.56	7.15±1.00	27.77±2.00	15.61±0.56	9.07±0.90
Metabolism (J)* *	8.56±0.60	7.16±0.50	12.19±0.80	11.37±0.80	11.50±0.90
Consumption rate (J/g/day)	885.46±55.39[a]	718.90±53.23[b]	1997.06±82.04[c]	1769.75±46.70[d]	1786.10±66.00[e]
Absorption rate (J/g/day)	587.84±53.75	447.86±29.91	1128.10±14.15	846.90±93.85	425.29±25.80
Excretion rate (J/g/day)	38.82±0.62	42.90±2.78	54.56±0.81	44.56±0.17	42.85±1.50
Assimilation rate (J/g/day)	549.14±5.60	404.94±4.20	1073.53±40.50	710.05±7.80	382.44±26.00
Production rate (J/g/day)	200.40±5.99	194.19±4.16	174.62±19.64	130.80±7.00	98.20±3.90
Metabolic rate1 (J/g/day)*	382.43±3.74[a]	207.93±29.21[b]	907.41±12.03[c]	578.15±20.52[d]	284.22±26.90[e]
Metabolic rate2 (J/g/day)**	263.72±18.29	208.14±14.53	398.37±26.14	421.11±29.63	363.63±23.50
Assimilation efficiency (%)	62.02±2.00[a]	56.34±0.60[b]	53.76±0.50[c]	40.12±0.30[d]	20.90±1.60[e]
Pe1 (%)	22.62±1.00[a]	27.01±0.74[b]	8.73±0.80[c]	7.43±0.40[d]	5.37±0.60[e]
Pe2 (%)	36.48±0.80[a]	47.98±0.60[b]	16.26±0.40[c]	18.52±0.50[d]	25.40±2.10[e]

* calculated as (A-P + U); **-Estimated respirometrically

Values in rows superscript with different alphabets are statistically significant (P<0.05)

Table 3: Energy budget for the non-feeding pharate pupal and adult stages of *K. barbitaris* fed on chosen nutrient source. Each value (X±SD) represents the average performance of 5 observation

	Nutrient source				
Parameters	Mixed algal powder	Chlorella	Sheep manure	Vegetable waste	Silt from pond
Terminal larva (J/larva)	13.30±0.23	12.62±0.25	11.20±0.16	10.36±0.23	8.00±0.18
Pupa (J/pupa)	8.85±0.38	8.20±0.20	6.87±0.20	5.89±0.14	4.44±0.15
Pharate pupal duration (day)	1.00±0.00	1.00±0.00	1.00±0.00	1.00±0.00	1.00±0.00
Metabolism (J)	4.45±0.18	4.42±0.12	4.34±0.06	4.48±0.11	3.56±0.12
Pharate pupal metabolic rate (J/g/day)	835.06±48.86	876.45±21.92	915.54±27.75	845.26±161.38	881.52±33.06
Pupal case (J)	0.54±0.02	0.52±0.02	0.47±0.01	0.44±0.02	0.42±0.01
Adult (J)	6.73±0.23	6.22±0.14	5.10±0.14	3.74±0.08	2.66±0.11
Pharate adult duration (day)	1.00±0.00	1.00±0.00	1.00±0.00	1.00±0.00	1.00±0.00
Metabolism (J)	2.12±0.18	1.98±0.08	1.77±0.07	2.15±0.07	1.79±0.05
Pharate adult metabolic rate (J/g/day)	560.00±39.27	561.25±18.63	545.11±11.84	684.78±41.56	686.66±15.90
Metamorphic metabolic rate (J/g/day)	697.53±49.50	718.85±58.35	730.33±48.50	747.02±40.50	784.09±48.0
Metamorphic efficiency (%)	76.06±1.23	75.91±0.70	63.53±0.59	63.53±0.59	59.75±0.77

Note: Values in the rows superscript with different alphabets are statistically significant (P<0.05; LSD Test)

Table 4: Energy budget for the non-feeding pharate pupal and adult stages of *T. bilobatus* fed on chosen nutrient source. Each value (X±SD) represents the average performance of 5 observation

	Nutrient source				
Parameters	Mixed algal powder	Chlorella	Sheep manure	Vegetable waste	Silt from pond
Terminal larva (J/larva)	7.25±0.15	6.49±0.13	5.57±0.21	4.98±0.08	3.66±0.14
Pupa (J/pupa)	5.05±0.10	4.33±0.14	3.26±0.06	2.89±0.03	2.19±0.07
Pharate pupal duration (day)	1.00±0.00	1.00±0.00	1.00±0.00	1.00±0.00	1.00±0.00
Metabolism (J)	2.21±0.08	2.16±0.04	2.28±0.14	2.09±0.04	1.47±0.08
Pharate pupal metabolic rate (J/g/day)	675.77±15.56	741.30±25.49	928.82±31.25	880.31±6.11	777.07±16.32
Pupal case (J)	0.54±0.01	0.49±0.01	0.49±0.02	0.41±0.02	0.38±0.00
Adult (J)	3.66±0.12	3.09±0.11	2.23±0.05	1.91±0.01	1.34±0.06
Pharate adult duration (day)	1.00±0.00	1.00±0.00	1.00±0.00	1.00±0.00	1.00±0.00
Metabolism (J)	0.85±0.10	1.24±0.03	1.06±0.04	0.99±0.03	0.85±0.01
Pharate adult metabolic rate (J/g/day)	363.58±47.20	596.18±9.08	624.70±15.68	594.14±10.92	582.88±13.59
Metamorphic metabolic rate (J/g/day)	519.68±20.80	668.74±26.80	676.80±32.00	737.25±48.50	679.98±36.60
Metamorphic efficiency (%)	71.84±3.17	71.45±0.37	67.81±0.76	65.92±0.50	60.75±0.93

Table 5: Assimilation efficiency and net production efficiency of some aquatic insects

Species	Food	Methods followed	Ae (%)	Pe2 (%)	Reference
Ephemeropters					
Hexagenia limbata	Natural sediment	Gravimetric method (Gut loading and gut clearance time)	8-36	88	Zimmerman and Wissing [23]
Tricorythodius minutus	Diatom	”	49	-	McCullough *et al.* [29]
Odonata					
Pyrrhosoma nymphula	Daphnia	Gravimetric method (Gut loading and Gut clearance time)”	85	51	Lawton [18]
	Chironomus	”	84		
	Cloenon	”	91		
	Asellus	”	77		
Brachythemis contaminata	*Artemia salina*	”	89	48.1	Pandian and Mathavan [19]
Orthetrum Sabina	*A. salina*	”	90		Mathavan [20]
Lestes sponsa	Tubificids	”			
	Daphnia	”	45	85	Fischer [30]

Table 5: Continues

Plecoptera					
Arconeuria californica	Blackfly and Caddisfly larva	”	75-85	Heiman and Knight [21]	
Pteronarcys scotti	Leaf (Preleached leaf, free of midrib) and detritus	”	11-16	34.2	McDiffett [12]
Hemiptera					
Sphaerodema annulatus	Culex larva	Gravimetric method (Gut loading and gut characteristics)	93-97		Venkatesan and Rao [31]
Hedriodiscus truquii	Natural plant materials	”	64.2	56	Stockoner [32]
Simulius austeni	Diatoms	Radio tracer method (^{14}C)	27.8-59.4		Ladle and Hansford [33]
Simulium sp.	Diatoms	Ash ratio method	56		McCullough [29]
S. ornatum	Blue green algae	Radio tracer method (^{14}C)	36		Ladle and Hansford [33]
S. ornatum	Desmid	”	68		Schroder [34]
Simulium sp.	Natural detritus	Growth and Respiration	17-1.9		Wooton [22]
Chironomus plumosus	Natural detritus	Radio tracer method (^{14}C)	2-14	69-84	Johannsson [11]
K. barbitarsis	Chlorella	Gravimetric method	60.3	66.4	Present study
	Mixed algal powder	(Gut loading and Gut characteristics and Gut content and faeces egested)	57.3	57.8	Present study
	Sheep manure	”	52.5	23.3	Present study
	Vegetable waste	”	30.4	26.2	Present study
	Silt	”	24.6	24.7	Present study
T. bilobatus	Chlorella	”	56.3	47.9	Present study
	Mixed algal powder	”	60.0	36.6	Present study
	Sheep manure	”	53.7	16.2	Present study
	Vegetable waste	”	40.1	18.5	Present study
	Silt	”	20.9	25.4	Present study

1022.1 $J.g^{-1}.\ day^{-1}$ or 382.4 to 1073.5 $J.g^{-1}.\ day^{-1}$ by *K. barbitarsis* or *T. bilobatus* larva (Tables 1 and 2). The larvae fed on *Chlorella* and mixed algal powder assimilated the food with greater efficiency than those fed on the other tested nutrients. LSD test showed that in both species, the variation in mean assimilation efficiency of the larvae reared on the tested nutrient source was statistically significant. The nitrogen content of the nutrient source tested in the present study ranged from 2.10-8.96%. A highly significant positive correlation coefficient for the relationship was obtained between nitrogen content and assimilation efficiency of both *K. barbitarsis* and *T. bilobatus* ($Y=21.0 + 4.7 X$; $r^2 = 0.91$) (Fig. 1).

Reared in the nutrient source like *Chlorella*, sheep manure, vegetable waste or silt medium, *K. barbitarsis* and *T. bilobatus* converted 6.6, 9.3, 8.3 or 6.2 J and 6.7, 5.3, 3.6 or 3.1 J into larval tissues respectively (Table 1 and 2). Gross and net production efficiencies of the larva were highest for those feeding *Chlorella* and mixed algal powder. LSD test showed that the variation in mean gross and net production efficiencies of the larvae reared on the chosen nutrient media were statistically significant ($P < 0.05$). Therefore, with less amount of *Chlorella* or mixed algal powder, it is possible to produce more chironomid larvae. Based on production rate also, the above conclusion holds good. For instance, production rate of *K. barbitarsis* larva ingesting *Chlorella* or mixed algal powder was as high as 545.82 or 256.85 $J.g^{-1}day^{-1}$ compared with 197.67, 186.82 or 114.41 $J.g^{-1}day^{-1}$ of that feeding sheep manure, vegetable waste or silt medium (Table.1). Comparison of assimilation efficiency with the net production efficiency of *K. barbitarsis* and *T. bilobatus* pointed out a linear relationship between them (Table 1 and 2). Both the efficiencies increased with the nitrogen content of the nutrient source. The correlation coefficient obtained for the relationship between nitrogen content of the nutrient sources and net production efficiency of both *K. barbitarsis* and *T. bilobatus* was statistically more significant ($Y = 7.0 + 5.1 X$; $r^2 = 0.83$) (Fig.1)

The estimated metabolic rate was low (304.2 $J.g^{-1}day^{-1}$ in *K. barbitarsis* and 208.14 $J.g^{-1}day^{-1}$ in *T. bilobatus*) for the larvae fed on *Chlorella*. Feeding mixed algal powder, sheep manure or vegetable waste increased the metabolic rate of the larvae. However, in both the species, the indirect estimate of metabolic rate (as the difference between As and P) of the larvae fed on sheep manure or vegetable waste was higher than the corresponding respirometric estimates. Two-way analysis of variance showed that the variance in metabolic rate due to food quality or species were highly significant ($F_{0.05}$ at Df 1/9 and Df 4/9 = 2.34 and 1.69; P<0.05 to 0.01). In both the species, ammonia excretion rate was less for the larvae feeding mixed algal powder and *Chlorella* than that of those reared on other nutrient sources (Tables 1 and 2).

Pupal energetic data are provided in Tables 3 and 4. Use of mixed algal powder enabled the larva to realize maximum growth (13.30 J of *K. barbitarsis* and 7.25J of *T. bilobatus*); sheep manure; vegetable waste and silt significantly decreased the energy content of the terminal larva. Energy expended on pupal case ranged from 0.38 to 0.54 J for the larvae reared on different nutrient media (Tables 3 and 4). During the pupal period, *K. barbitarsis* or *T. bilobatus* expended 3.56 to 4.45 or 1.47 to 6.68 J on metabolism at the rate of 835.06 to 915.5 or 675.8 to 928.8 $J.g^{-1}day^{-1}$ respectively. The rate was lowest for the larva feeding mixed algal powder. On the basis of metamorphic efficiency also, mixed algal powder appears to be a suitable nutrient medium for the culture of *K. barbitarsis* or *T. bilobatus* larva. The efficiency was about 61% for the larva feeding sheep manure, vegetable waste or silt medium and 71.6% for those feeding mixed algal powder or *Chlorella* (Tables 3 and 4). Higher metamorphic efficiency affords emergence of larger adults with higher fecundity. Most of the factors which influence net conversion efficiency and also influence metamorphic efficiency. In the present study, metamorphic efficiency of both *K. barbitarsis* and *T. bilobatus* correlated significantly with the nitrogen content of the food ingested ($Y = 59.1 + 1.8x$; $r^2 = 0.86$) (Fig.1). Apparently, with increasing nitrogen content of food, food ingested by *K. barbitarsis* and *T. bilobatus* increased resulting in a better conversion of food into larval tissues as well as larval reserves into adult tissues.

DISCUSSION

In the present study, *K. barbitarsis* larva ingested the silt at a faster rate (1878.6 $J.g^{-1}$ day^{-1}) and assimilated the food with an efficiency of 24.6%. On the other hand, reared on *Chlorella* it ingested at a comparatively lower rate (641.7 $J.g^{-1}day^{-1}$) and assimilated the food with 60.3% efficiency. Assimilated efficiencies of *K. barbitarsis* and *T. bilobatus* are less than those of carnivorous odonate nymphs such as *Pyrrhosoma nymphula* (77-85% [18]), *Btrachythemis contaminata* and *Orthetrum sabina* (89 % [19, 20]) and the stone fly nymph *Acroneuria californica* (80% [21]). However, in the present study, the range of efficiencies displayed by *K. barbitarsis* (24.6-60.3%) and *T. bilobatus* (20.9 to 56.3%) is higher than that of other aquatic detririvorous insects such as *Chironomus plumosus* (2-14% [11]), *Pteronarcs scotti* (11-16% [12]) *Simulin* sp. (1.7-1.9% [22, 23]) (Table 5). Most of the low efficiency values reported in Table 5 pertain to the detritivores fed on natural sediment, unlike *K. barbitarsis* and *T. bilobatus* fed on *Chlorella*, mixed algal powder, sheep manure and vegetable waste. Therefore, it may be concluded that food quality and food retention time in the gut determine the assimilation efficiency. In a series of publications, Pandian and Marian [24, 25] reported a significant linear relation between nitrogen content of the food and assimilation / absorption efficiency of aquatic animals.

The interest of most insect physiologists has centered on sustaining the presence or absence of specific nitrogenous excretory materials in insects. Unfortunately, most of them have failed to quantify the nitrogenous excretory products and energy loss due to excretion [5]. The data provided by Staddon [26] for the larvae of the neuropteran *Sialis lutaria* and Staddon [27] for the odonante nymph *Awshna cyanea* pointed out that ammonia comprised over 80% of the total faecal nitrogen. Therefore, due consideration must be given to the energy loss due to ammonia excretion by *K. barbitarsis* and *T. bilobatus* larva reared on a wide range of nutrient sources. The rate ranged from 45-93 $J.g^{-1}day^{-1}$ for *K. barbitarsis* and 39 to 55 J. $g^{-1}day^{-1}$ for *T. bilobatus*. The reason for such wide differences in the excretion rate is not clearly understood. However, it may be pointed out that the nature of the nutrient which provides the nitrogen (such as plant protein, animal protein and animal excreta) to the larvae may partly account for such differences in the excretion rate. Further studies are required in this aspect.

The net production efficiencies of *K. barbitarsis* and *T. bilobatus* obtained in the present study are less than those of other aquatic detritivores like *C. plumosus* (69-84% [11]) and *H. limbata* (88% [23]). One of the key factors that determine net production efficiency is the rate of expenditure of energy on metabolism. The respirometric estimates of metabolic rate of *K. barbitarsis* ranged from 208 to 421 $J.g^{-1}$ day^{-1}, when the larvae were maintained at 27°C. On the other hand *H. limbata* and *C. plumosus* were maintained at 15°C. Understandably, higher temperature (27°C) at which *K. barbitarsis* and *T. bilobatus* were reared in the present study is responsible for the greater drain of energy on metabolism resulting in decreased net production efficiency. Food quality is another important factor, which can influence net production efficiency. . The quality of the nutrients (such as animal protein, plant protein and animal excreta) may also account for such differences in the net production efficiency. The efficiency is high when chemical compositions of the food and the consumer's tissue are more or less similar [28].

The life span of the adult and reproductive success of the holometabolous insects, especially those which do not feed more as adults is determined by the efficiency with which the larval reserves are converted into adult tissues. This efficiency, called metamorphic efficiency, depends on a host of factors like the duration of metamorphic period, size of the terminal larva, the rate at which energy is expended on maintenance metabolism and temperature [5]. Most of the factors which influence net conversion efficiency (such as food quality and available) also influence metamorphic efficiency. In the present study, metamorphic efficiency of *K. barbitarsis* and *T. bilobatus* correlated significantly with the nitrogen content of the food ingested ($Y = 59.1 + 1.8x$; $r^2 = 0.86$). Apparently, with increasing nitrogen content of food, food ingested by *K. barbitarsis* and *T. bilobatus* increased resulting in a better conversion of food into larval tissues as well as larval tissues into adult tissues.

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