

## Bioenergetics of feeding and metabolic cost of living in freshwater Caridean prawns

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**Abstract.** The relative partitioning of food energy for processes like moulting, metabolism and growth of the freshwater prawns, *Macrobrachium lanchesteri* (Palaemonidae) and *Caridina weberi* (Atyidae) have been detailed through a bioenergetic scheme. The two species of prawns expend the same amount of food energy for the above processes. Conspecific population density inhibited growth by an overall increase in exuvial production, metabolism and faeces production. Moulting-growth relationship of *Macrobrachium lanchesteri* has been presented as a model for determining accurate measurements of moulting and growth of crustaceans.

**Keywords.** Caridean prawns; food energy; metabolic cost.

### 1. Introduction

Food energy partitioning has been widely studied in relation to the nutritional score of several animals (Hoar *et al* 1979; Slansky and Scriber 1985; Tytler and Calow 1985; Pandian and Vernberg 1987a, b). Prawns constitute an important aquatic resource for human exploitation and hence, the need for culture fishery of prawns is being stressed the worldover (Pillay 1979; Jhingran 1982). While data on absolute and relative growth in Crustaceans, including prawns, have been detailed by Hartnoll (1982), recent publications have also projected the value of deriving food energy partitioning schemes for Crustaceans (Vernberg 1987). Considerable work on the accelerating effect of eye-stalk ablation on the growth and reproduction of prawns and lobsters is also documented (Mauviot and Castell 1976; Ponnuchamy *et al* 1981; Quackenbush and Herrnkind 1981; Radhakrishnan and Vijayakumaran 1984a, b; Sindhu Kumari and Pandian 1987). Most of the work on freshwater prawns is however restricted to the riverine varieties and paucity of information on the quantification of growth in captivity of these species, leads to inconclusive analyses of their performance in the physiological energetics of food conversion.

The freshwater habitats in and around Bangalore harbour two varieties of prawns, the larger palaemonid *Macrobrachium lanchesteri* (de Man) and the smaller atyids, *Caridina nilotica* (de Man), *C. weberi* and *C. rajadhari* (Anantha Raman *et al* 1986). Earlier, considerable information on the effects of several abiotic and biotic factors on the food conversion and growth of *M. lanchesteri* and *C. weberi* has been reported. Based on these reports, an overview on the feeding energetics and metabolic cost of living of these carideans has been presented in this paper.

### 2. Material and methods

The details of *M. lanchesteri* and *C. weberi* collection from the local habitats of

Bangalore, methods of laboratory rearing, determination of moulting frequency, food intake, growth and conversion efficiency are detailed by Ponnuchamy *et al* (1983). Table 1 presents the information on the work on physiological energetics of food conversion in *M. lanchesteri* and *C. weberi* in relation to abiotic and biotic factors. The overall data from these works have been used to describe how the energy budget of Caridean prawns are affected by the abiotic and biotic factors.

### 3. Results and discussion

The food energy budget for a prawn may be represented as follows (see also figure 1):

$$C = L + \Delta G. \quad (1)$$

Where  $C$  = food energy consumed;  $L$  = Energy loss due to (i) Faeces and urine =  $Fu$ , (ii) exuviae =  $E$ , (iii) metabolism =  $M$  and  $G$  = increase or decrease in energy content of prawn.

Therefore

$$C = Fu + E + M + \Delta G. \quad (2)$$

Table 2 summarises the values of  $Fu$ ,  $E$ ,  $M$  and  $\Delta G$  calculated as percentages of  $C$  elaborated by *M. lanchesteri* reared under various experimental conditions. The best value of  $G$  was obtained for the prawn reared in an ideal population density. Conspecific density inhibits  $G$  by an overall increase in  $E$ ,  $M$  and  $Fu$ . Higher  $G$  was also obtained for prawns of smaller sizes and those fed on *Tubifex tubifex* worms. This confirms the size-related growth pattern of the prawn and that tubificid worms provide a good nutritional source for them. A comparatively higher  $G$  for a food ration level of 15% again confirms that this level of  $C$  is optimum for these prawns. Considerable inhibition of  $G$  was evident for large size prawns and for those reared in 6‰ salinity. It is also evident that  $G$  was lowered considerably at a ration level of 25%, indicating increased expenditure of energy for  $M$ . This is in conformity with the observations of Paloheimo and Dickie (1966a) for fishes. These authors pointed out that a decrease in the gross conversion efficiency of food is

**Table 1.** Laboratory studies on the effects of abiotic and biotic factors on the food conversion in *M. lanchesteri* and *C. weberi*—data source.

Variables	<i>M. lanchesteri</i>	<i>C. weberi</i>	References
Population density (no/15 l water)	1, 2, 4, 8, 16 and 24	1, 2, 4, 8, 16 and 24	Ponnuchamy <i>et al</i> (1984a)
Body size (mm)	10–20, 21–30, 31–40, 41–45 and 46–50	10–15, 16–20 and 21–25	Ponnuchamy <i>et al</i> (1984b)
Quality of food	<i>Tubifex</i> worms, Fish muscle	<i>Tubifex</i> worms, Fish muscle	Ponnuchamy (1981)
Rational levels (% body weight)	0, 1, 3, 6, 12, 15, 20 and 25	0, 3, 6, 12, 24, 30, 35 and 40	Ponnuchamy <i>et al</i> (1983)
Salinity (‰ S)	FW, 2, 4, 6 and 8	FW, 3, 4, 6 and 8	Ponnuchamy (1981)
Light intensity (ft. c.)	6.2, 10.3 and 40.8	6.2, 10.3 and 40.8	Ponnuchamy <i>et al</i> (1981)

FW. Freshwater.

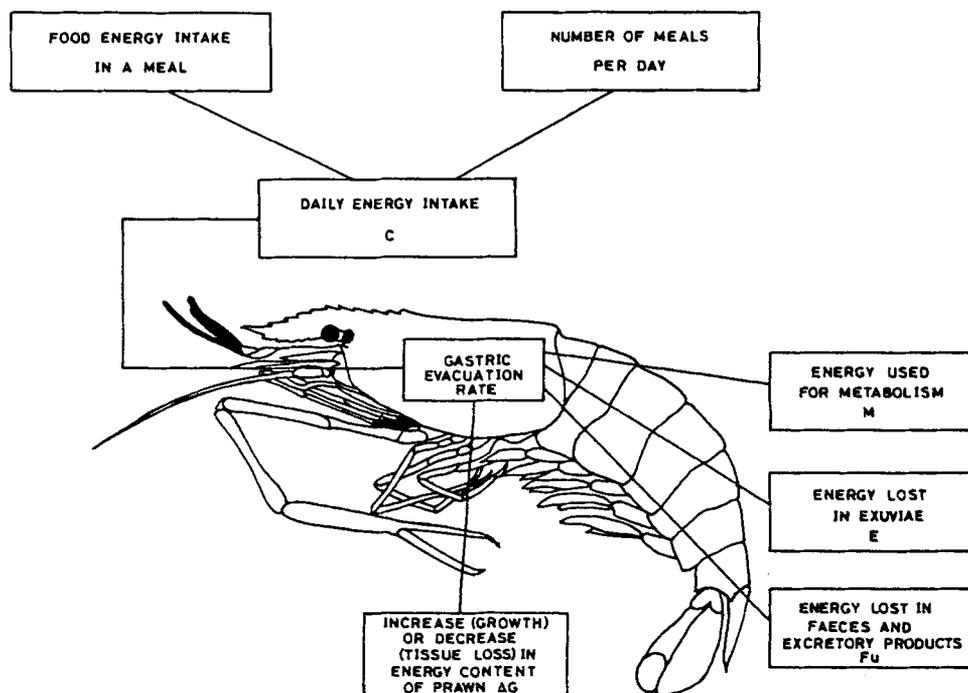


Figure 1. Schematic diagram of food energy partitioning in prawns.

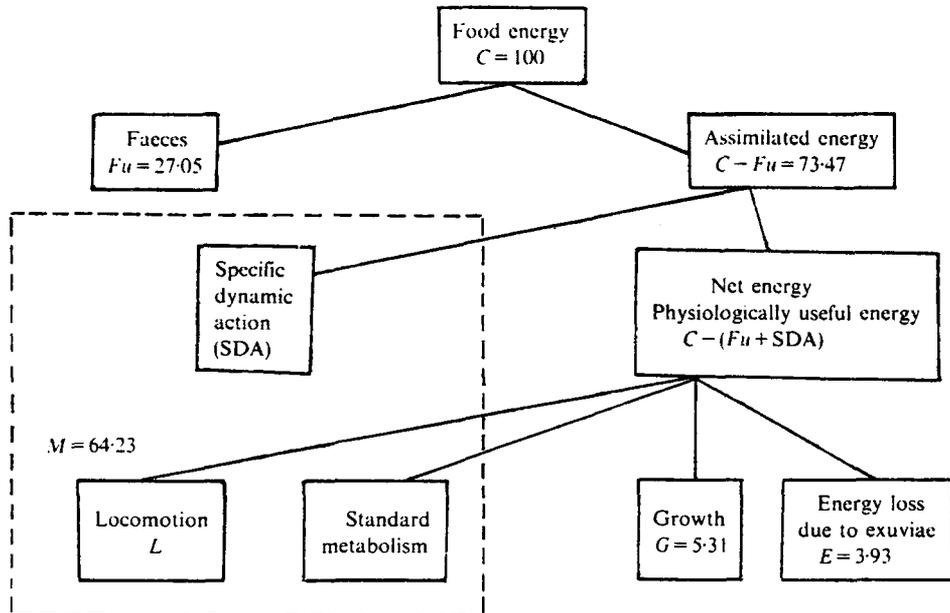
Table 2. Influence of various biotic and abiotic factors on the bioenergetics of feeding of *M. lanchesteri*.

Parameters	mg dry food energy consumed <i>C</i>	Energy conversion as % of <i>C</i>			
		Faeces <i>F</i>	Exuviae <i>E</i>	Metabolism <i>M</i>	Gain <i>G</i>
Population density (4/15 l water)	601.92	41.87	6.60	41.42	10.42
Size					
(10-20 mm)	256.91	27.77	2.32	60.23	9.57
(46-50 mm)	557.17	12.41	1.99	84.76	0.84
Quality of food					
<i>Tubifex</i> worms	539.61	29.53	4.18	61.08	9.38
Fish muscle	307.44	34.29	5.45	56.36	3.89
Ration level					
15%	523.62	39.72	2.48	49.33	8.47
25%	512.99	35.32	2.52	64.48	3.37
Salinity					
6‰	633.98	32.27	3.61	61.27	2.85
Light intensity					
6.2 ft. c.	669.30	14.46	1.37	80.14	4.32
40.8 ft. c.	822.67	14.76	2.13	78.12	4.99
	Mean ± SD	28.24 ± 12.54	3.27 ± 1.68	63.69 ± 13.81	5.81 ± 3.35

dependent on ration size, a relation which could be ascribed to increased metabolic demands associated with increased food processing. During the present study, large size, salinity and increased ration level/day appear to retard the growth of *M. lanchesteri*.

The data on  $F_u$ ,  $E$ ,  $M$  and  $G$  as percentages of  $C$  elaborated by *C. weberi* are indicated in table 3. The best value of  $G$  was obtained for smaller prawns reared on *Tubifex* worms confirming the size-related growth pattern of the prawns. The next higher value of  $G$  was observed for those reared on fish muscle, indicating the suitability of the food to elaborate the feeding pattern typical of caridinids (Fryer 1960). The  $G$  was also comparatively high for the prawns reared on tubificids, 2‰  $S$  and light intensity of 10.2 ft.c. Thus, large size, lower rations and higher salinity appear to retard growth of *C. weberi*.

The average partitioning of food energy for  $F_u$ ,  $E$ ,  $M$  and  $G$  of *M. lanchesteri* and *C. weberi* under various biotic and abiotic factors are presented in figure 2 (see also tables 2 and 3). In spite of the differences in their finite body size, taxonomic position, food and niche selection (as indicated in table 4), the two natantians apportioned nearly same amount of food energy ( $C$ ) for  $F_u$ ,  $E$ ,  $M$  and  $G$ . This again suggests that the two species may not be too diverse in their systematic positions. The average values of food energy partitions for *M. lanchesteri* and *C. weberi* are as follows:

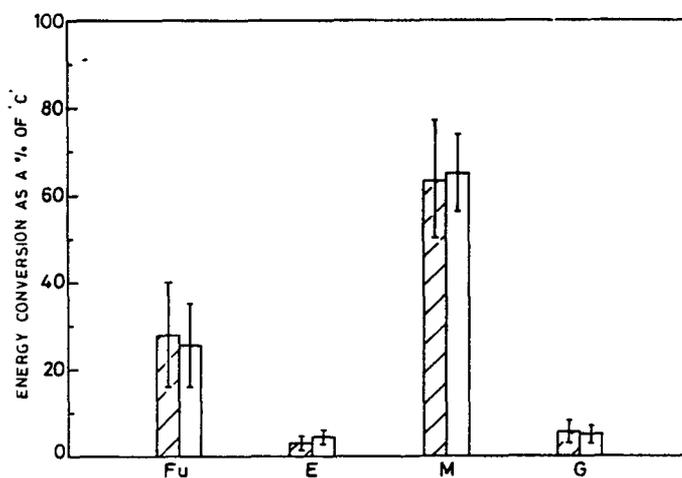


Considerably higher energy expenditure (65%) on metabolism is comparable to the value of 75% reported for other aquatic thermoconformers (Brett 1970). While the  $E$  of *M. lanchesteri* was lower than  $G$ , the  $E$  and  $G$  of *C. weberi* were equal (see also figure 2). This suggests that moulting is more frequent in *C. weberi* and that the per moult weight (%) is also higher as compared to that in *M. lanchesteri*.

The energy budgets of these two species are not comparable to that reported for

**Table 3.** Influence of various biotic and abiotic factors on the bioenergetics of feeding of *C. weberi*.

Parameters	mg dry food energy consumed <i>C</i>	Energy conversion as % of <i>C</i>			
		Faeces <i>F</i>	Exuviae <i>E</i>	Metabolism <i>M</i>	Gain <i>G</i>
Population density (8/15 l water)	274.65	34.01	3.78	58.79	3.41
Size					
(10–15 mm)	185.91	19.08	5.98	64.93	10.01
(21–25 mm)	306.62	16.43	5.58	74.41	3.58
Quality of food					
<i>Tubifex</i> worms	283.11	31.87	3.61	59.07	5.52
Fish muscle	513.73	21.33	2.77	69.83	6.06
Ration level					
12%	143.17	38.85	7.26	51.90	1.99
40%	368.49	33.13	4.69	57.99	4.19
Salinity					
2‰	283.03	33.30	5.19	55.70	5.81
4‰	292.65	36.88	4.56	56.05	2.51
Light intensity					
6.2 ft. c.	429.59	12.32	2.15	81.50	4.53
10.3 ft. c.	283.60	7.02	5.11	82.42	5.45
	Mean ± SD	25.86 ± 10.96	4.60 ± 1.47	64.77 ± 9.97	4.82 ± 2.04



**Figure 2.** Food energy (*C*) partitioning values for faeces (*Fu*), exuviae (*E*), metabolism (*M*) and growth (*G*) of *M. lancesteri* (▨) and *C. weberi* (□).

the marine prawn *Metapenaeus dobsoni* (Thomas 1978: consumption (100%) = assimilation (80.18%) + faeces (19.82%); assimilation = growth (38.79%) + moult (0.60%) + metabolism (40.79%)). Markedly higher *G* was reported for *M. dobsoni* as compared to that of *M. lancesteri* or *C. weberi*. Further, lower *E* was observed for

Table 4.

Parameters	<i>M. lanchesteri</i>	<i>C. weberi</i>
Family	Palaemonidae	Atyidae
Finite body size (mg)	8,050	400
Feeding habit	Carnivore or omnivore	Detritivore or omnivore
Niche	Bottom regions	Marginal zones

*M. dobsoni* as compared to the two natantians studied presently. Perhaps, the formulated diets offered to *M. dobsoni* yield better growth in that species as compared to the natural foods offered to *M. lanchesteri* and *C. weberi*. Interestingly, all the 3 species of natantians studied so far appear to expend more or less similar amounts of energy on  $F_u$  which is the second major process of energy loss next to metabolism.

In crustaceans, the growth rate is determined by two processes (i) the increase in size at each moulting and (ii) the frequency with which moults occur (Hepper 1967). Since *M. lanchesteri* and *C. weberi* expend comparable amounts of energy for  $F_u$ ,  $E$ ,  $M$  and  $G$ , the former larger species was selected as a model to determine the frequency of moulting. Mauchline (1976) has commented that growth factors (i.e. per moult increments in carapace length) are not constant in many crustaceans, but rather, decrease at successive moults. Hepper (1967) reported that, in lobster, the period between moults increased with age and therefore although the increments would be same at each moult, they would occur less frequently. However, the earlier workers measured the growth indirectly by taking the carapace lengths of the exuviae. Hence, the exact growth may not be correctly represented. Working on the brachyuran, *Gecarcinus lateralis* (Skinner 1966) idealized the sketch of the changes in total biomass as the animal progressed from one intermoult to the next. The author stated that  $G$  is conservative and a day or so after ecdysis the animal eats the old exoskeleton. In the next intermoult stage, the weight of the animal is greater than its previous intermoult weight, but somewhat less than the maximal weight reached in the premoult period.

Observation on moult-growth relationship of *M. lanchesteri* are presented in figure 3. The amount of food intake/prawn/day decreased with advance in the weight of the prawns and successive moults. While there were no apparent differences in the food consumption ( $C$ ), conversion ( $Ce^i - Ce^{iv}$ ), exuvial loss ( $E^i - E^{iv}$ ) and intermoult durations at successive moults the growth/or yield ( $Y^i - Y^{iv}$ ) was slightly sigmoid. Figure 3 conforms to the general observations of Skinner (1966), but a lack of quantified data on food intake, growth and exuvial loss in *Gecarcinus* do not permit a discussion presently.

The relationship between feeding rate, rates of assimilation, metabolism and yield are considered to be important parameters in the culture of aquatic animals (see also Winberg 1960; Paloheimo and Dickie 1965, 1966a, b; Bagenal 1978). Figures 4 and 5 represent these relationships for *M. lanchesteri* and *C. weberi* respectively. In either species, the rates of assimilation and metabolism increased with increases in the feeding rate. Nelson and Knight (1978) working on the juvenile *M. rosenbergii* indicated an apparent increase in the rate of metabolism following ingestion of food. Paloheimo and Dickie (1966a), using an indirect method of assessing total

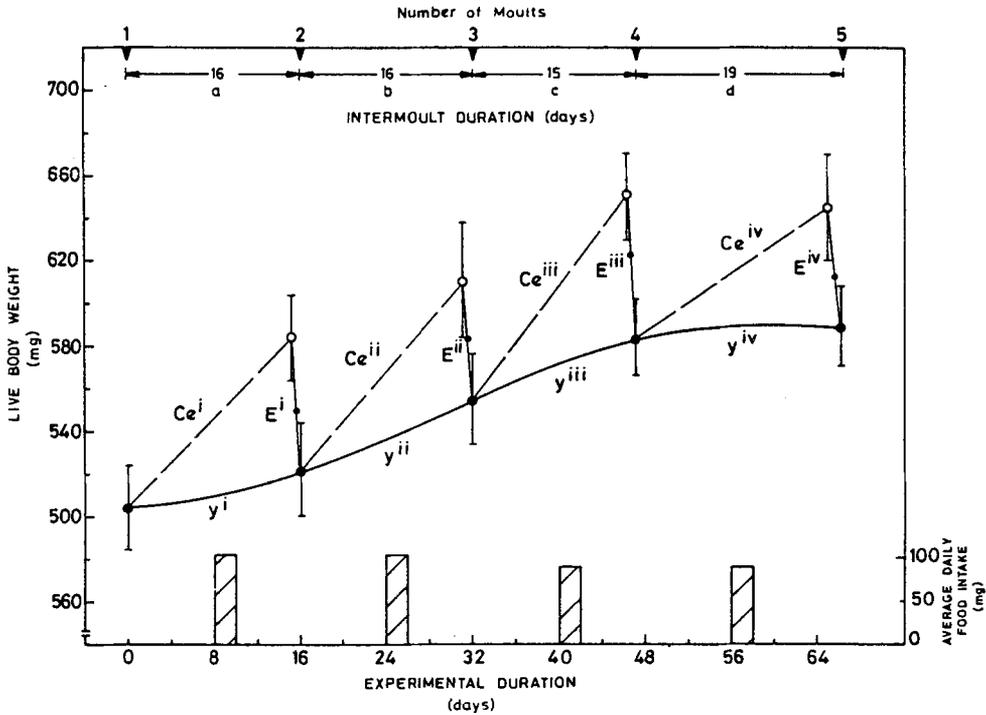


Figure 3. Changes in live body weight of *M. lanchesteri* in relation to moulting.

$Ce^i - Ce^{iv}$  = Total tissue conversion during the 4 intermoult (a, b, c and d).

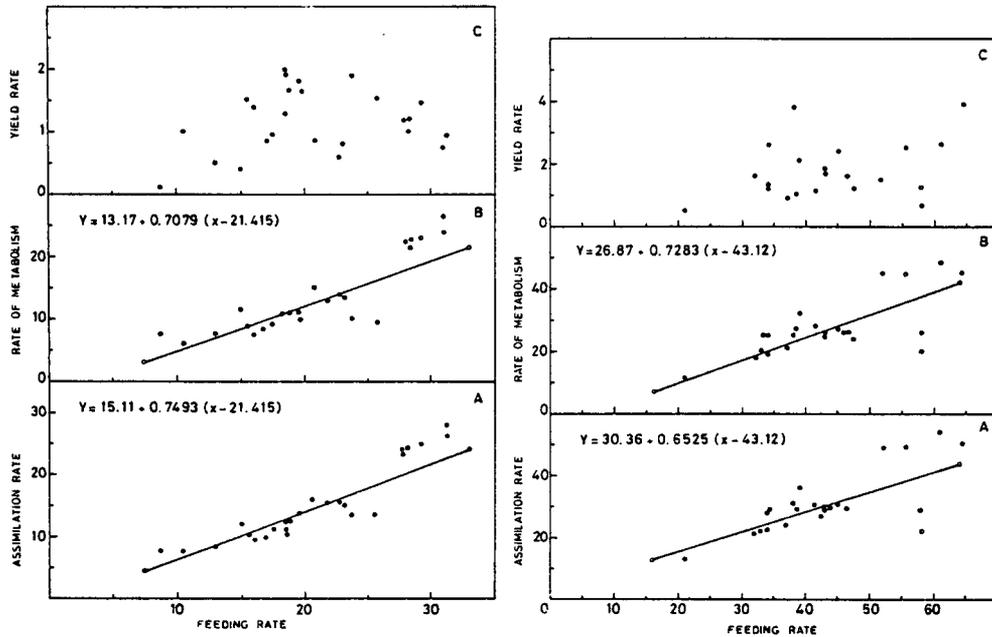
$E^i - E^{iv}$  = Tissue loss due to exuviae (2, 3, 4 and 5).

$Y^i - Y^{iv}$  = Actual tissue yield during the 4 intermoult (a, b, c and d).

▨ = Average daily food intake during the 4 intermoult (a, b, c and d).

metabolism, demonstrated that *ad libitum* feeding required an energy expenditure of 6–8 times that for maintenance feeding in fishes. The relationship between the rates of feeding and yield was found to decrease on either side of the optimum feeding level for *M. lanchesteri* (figure 4). However, no such pattern was observed in *C. weberi* and the yield rate did not show any relationship with the feeding rate (figure 5). Under varied experimental conditions, *M. lanchesteri* regulates its yield rate despite increases in feeding rates. In spite of no apparent increases in  $G$  with increases in feeding rates of the *Poecilia reticulata*, regulation of  $B (= G)$  has also been reported to occur under varied experimental conditions (Krishnamurthy *et al* 1984). From this, it is evident that *M. lanchesteri* would successfully colonize the freshwater habitats and elaborate considerable  $G$ .

The capacity of *M. lanchesteri* to regulate  $G$  under various conditions may be the cause for its reported wide distribution in the freshwater habitats (see also Anantha Raman *et al* 1986). Though the size of *M. lanchesteri* is relatively smaller than *M. rosenbergii*, since it spends the entire life in freshwater, it might prove to be more suitable for culture in inland lentic habitats than the latter species.



Figures 4 and 5. Scattergrams of rates of assimilation (A), metabolism (B) and yield (C) in relation to the feeding rate of (4) *M. lanchesteri* and (5) *C. weberi*. The points represent the average values obtained for prawns reared under various biotic and abiotic factors.

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### References

- Anantha Raman K V, Ravichandra Reddy S and Katre Shakuntala 1986 Distribution and abundance of prawns in the freshwater habitats of Bangalore, South India; *Proc. Indian Acad. Sci. (Anim. Sci.)* **95** 77-87
- Bagenal T 1978 *Methods for assessment of fish production in freshwaters* (Oxford: Blackwell Scientific Publications)
- Brett J R 1970 Fish—the energy cost of living; in *Marine aquaculture* (ed. W J McNeil (Oregon: Oregon State University Press) pp 37-52
- Fryer G 1960 The feeding mechanism of some atyid prawns of the genus *Caridina*; *Trans. R. Soc. Edinburgh* **64** 217-244
- Hartnoll R G 1982 Growth; in *Biol. Crustacea* **2** 111-196
- Hepper B T 1967 On the growth at moulting of lobsters (*Homarus vulgaris*) in Cornwall and Yorkshire; *J. Mar. Biol. Assoc. U. K.* **47** 629-643
- Hoar W S, Randall D J and Brett J R 1979 Fish physiology; *Bioenergetics Growth* **8** 786
- Jhingran V G 1982 *Fish and fisheries of India* 2nd edition (Delhi: Hindustan Publication Corpn.)
- Krishnamurthy C, Purushothama M N, Narasimha Rao C H, Katre Shakuntala and Ravichandra Reddy S 1984 Efficiency of food conversion in the guppy *Poecilia reticulata* in relation to sex determination; *Pol. Archw. Hydrobiol.* **31** 403-416

- Mauviot J C and Castell J D 1976 Moults and growth enhancing effects of bilateral eyestalk ablation on juvenile and adult American lobsters (*Homarus americanus*); *J. Fish. Res. Board Can.* **33** 1922-1929
- Nelson S G and Knight A W 1978 Ecological energetics and its application to the evaluation of diets for aquatic species, with special regard to the giant Malaysian prawn, *Macrobrachium rosenbergii*; *World Maricult. Soc.* **8** 779-785
- Paloheimo J E and Dickie L M 1965 Food and growth of fishes I. A growth curve derived from experimental data; *J. Fish. Res. Board Can.* **22** 521-542
- Paloheimo J E and Dickie L M 1966a Food and growth of fishes II. Effects of food and temperature on the relation between metabolism and body weight; *J. Fish. Res. Board Can.* **23** 869-908
- Paloheimo J E and Dickie L M 1966b Food and growth of fishes III: Relations among food, body size and growth efficiency; *J. Fish. Res. Board Can.* **23** 1209-1248
- Pandian T J and Vernberg F M 1987a *Animal energetics. Protozoa through insecta* Vol. 1 (California: Academic Press) pp 511
- Pandian T J and Vernberg F M 1987b *Animal energetics. Bivalvia through reptilia* Vol. 2 (California: Academic Press) pp 619
- Pillay T V R 1979 The state of aquaculture; in *Advances in Aquaculture*; (eds.) T V R Pillay A Dill Wm (England: Fishing News Books Ltd.) pp 1-10
- Ponnuchamy R 1981 *Studies on the bioenergetics of feeding and behaviour of a few freshwater prawns*, Ph.D. thesis, Bangalore University, Bangalore
- Ponnuchamy R, Ravichandra Reddy S and Shakuntala K 1981 Effects of eyestalk ablation on growth and food conversion efficiency of the freshwater prawn *Macrobrachium lancesteri* (de Man); *Hydrobiologia* **77** 77-80
- Ponnuchamy R, Ravichandra Reddy S and Katre Shakuntala 1983 Effects of different ration levels on survival, moulting and food conversion in two freshwater prawns; *Proc. Indian Acad. Sci. (Anim. Sci.)* **92** 147-157
- Ponnuchamy R, Ravichandra Reddy S and Katre Shakuntala 1984a Comparative studies on the effects of population density on moult production and food conversion in two freshwater prawns; *Proc. Indian Acad. Sci. (Anim. Sci.)* **93** 517-525
- Ponnuchamy R, Ravichandra Reddy S and Katre Shakuntala 1984b Moults production and food conversion in two freshwater prawns in relation to body size; *J. Indian Inst. Sci.* **65** 109-114
- Quackenbush L S and Herrnkind W F 1981 Regulation of moult and gonadal development in the spiny lobster *Panulirus argus* (Crustacea: Palinuridae): effect of eyestalk ablation; *Comp. Biochem. Physiol.* **A69** 523-527
- Radhakrishnan E V and Vijayakumaran M 1984a Effect of eyestalk ablation in the spiny lobster *Panulirus homarus* 1: On moulting and growth; *Indian J. Fish.* **31** 130-147
- Radhakrishnan E V and Vijayakumaran M 1984b Effect of eyestalk ablation in the spiny lobster *Panulirus homarus* (Linnaeus) 3: On gonadal maturity; *Indian J. Fish.* **31** 209-216
- Sindhu Kumari S and Pandian T J 1987 Effects of unilateral eyestalk ablation on moulting, growth, reproduction and energy budget of *Macrobrachium nobili*; *Asian Fish. Sci.* **1** 1-17
- Skinner D M 1966 Breakdown and reformation of somatic muscle during the moult cycle of the land crab *Gecarcinus lateralis*; *J. Exp. Zool.* **163** 115-124
- Slansky F Jr and Scriber J M 1985 Food consumption and utilization; in *Comprehensive insect physiology, biochemistry and pharmacology* G A Kerkuit and L I Gibbert (eds) (Oxford: Pergamon Press) pp 87-164
- Thomas M M 1978 Artificial feed; in *Breeding and rearing of marine prawns*; CMFRI special publication No. 3 pp 89-91
- Tytler P and Calow P 1985 *Fish energetics, new perspectives* (London, Sydney: Crom Helm)
- Vernberg F M 1987 Crustacea; in *Animal energetics* (eds) T J Pandian and F M Vernberg (California: Academic Press) pp 302-373
- Winberg G G 1960 Rate of metabolism and food requirements of fishes; *Fish. Res. Board Can. Trans. Ser.* **194** 202