Indian Journal of Marine Sciences
Vol. 3, December 1974, pp. 131-134

Energy Conversion in the Shrimp, *Metapenaeus monoceros* (Fabricius), Fed on Detritus

S. Z. QASIM
National Institute of Oceanography, Dona Paula, Caranzalem 403301
and
D C V. EASTERSON
Central Marine Fisheries Research Institute, Cochin 682018

Received 24 *June* 1974

Energy budget of *M. monoceros* was estimated using estuarine detritus as food. Rates of consumption, defaecation, assimilation, growth and metabolism in the juvenile shrimp increased with the size of the animal. Gross growth efficiency (P/C or K_1) and net growth efficiency (P/A or K_2) were highest in the size range 17-20 mm. Average gross and net efficiencies were 21·6 and 24·1% respectively. Food efficiency was inversely related to growth efficiency and the assimilation efficiency was of the order of 93%. A comparison of estimates of gross, net and assimilation efficiencies in various animals made by different authors showed that these differ over a wide range and the growth efficiency seems difficult to express by a common factor.

RATE of sedimentation and chemical characteristics (including caloric value) of organic detritus from a tropical estuary (Cochin backwater) have been discribed by Qasim and Sankaranarayanan[1]. They have observed that young specimens of the shrimp *Metapenaeus dobsoni* could survive on detritus pellets almost indefinitely. In the present communication quantitative data on energy conversion of the shrimp, *M. monoceros*, using detritus as food are presented.

Materials and Methods

Sea water, collected from Cochin backwater in carboys (80 l) was allowed to stand for about 72 hr. The settled detritus was removed by decantation and filtration. Weighed amounts of residues on the filters were offered as food to the shrimp. Wet weight-dry weight determinations were also carried out on detritus.

M. monoceros specimens collected from the backwater were acclimatized in the laboratory for about a week. Generally 1-2 days after the capture, the shrimps moulted. The acclimatized shrimps were then distributed in rectangular, flat and shallow plastic troughs with 7-8 l sea water. The height of water in these troughs did not exceed 8-9 cm. Each trough contained 2-10 shrimps depending on their size, and was covered with a nylon net tied with a rubber band. Every morning the faecal matter, which was in the form of strings, quite distinct from detritus, was collected with the help of a fine pipette and weighed. Each experiment was continued for 14 days, during which period none of the shrimps moulted. However, if the prawns were kept longer than 14 days, moulting did occur, suggesting that while they were feeding on detritus the intermoult period became longer than that on other foods such as mussel meat.

Prawns were weighed before and after the experiments. The remaining detritus (unconsumed) in the trough was recovered by filtration and weighed. Thus the entire ration of detritus was supplied in the beginning of the experiment and the shrimps were allowed to feed on detritus *ad libitum*.

Caloric values of detritus and faecal matter were determined using the method of Karzinkin and Tarkovskaya[2].

Results and Discussion

Life History and Feeding Behaviour of M. monoceros

The shrimp has been reported to breed in the sea (not estuaries) throughout the year. It has two periods of maximum breeding — June to August and October to December[3]. The early larval history of the shrimp is passed in inshore waters and at the late mysis stage, when about 3·0 mm in length, it enters estuarine areas and soon settles to the bottom. The size of *M. monoceros* caught from Cochin backwater ranges from 10 to 102 mm. In the estuary it grows at the rate of 6·7 mm/month. However, the largest specimens measuring 165 mm are caught from the sea[4]. George[5] has analysed 1213 stomachs of this shrimp and deduced that small sized specimens measuring 10-15 mm largely subsist on planktonic crustaceans, whereas the average sized specimens, below 50 mm in length, consume large quantities of detritus. In shrimps larger than 50 mm, detritus was found in small proportions and the food largely included animal matter.

Small shrimps (10-15 mm) when kept in experimental troughs or in an aquarium tank, immediately went to the bottom and from there made periodic excursions to the surface. Their swimming periodicity increased towards the evening, and in the dark, most of the shrimps kept on swimming at or near the surface. If *Artemia* nauplii were introduced into the trough, they were soon eaten by these shrimps. A greater activity cycle shown by the young shrimps towards the evening was probably to escape predation in the dark while hunting for planktonic food. Larger shrimps (20-30 mm) remained at the bottom, and, unless disturbed, seldom came up to the surface. If a layer of mud was present at the bottom, they immediately buried themselves in it and only the two antennules and their stalked-eyes could be seen moving about exploring the mud. When detritus was offered as food, they tried to bury themselves in it, but the quantity of detritus being small, they made dashing movements here and there and at the same time nibbled detrital particles. Still larger shrimps measuring 40-50 mm and above, when provided with sufficient mud, remain consistently at the bottom buried in the mud.

In the laboratory, the larger shrimps ate practically all types of food offered to them and behaved like omnivores. When kept in a crowded condition, they attacked other shrimps and ate those which had freshly moulted including their carcasses, and behaved like carnivores. It is thus evident that shrimps are able to convert living, dead and decaying zooplankton, nekton, epiphyton, benthos and detritus into shrimp meat and form an interesting group of animals to study the energy conversion phenomenon.

Energy Conversion

Estimation of energy conversion by the shrimp from detritus was made by the following equation given by Crisp[6]:

$$C = P+R+G+U+F \qquad \ldots(1)$$

where C = intake of food or energy, P = energy utilized for growth, R = energy utilized as heat for metabolism, G = energy utilized for gonad activities, U = energy passed out of the body as urine or other soluble material, F = energy not absorbed and passed out as faeces. Since the biomass is expressed in units of mass, R and U are not directly applicable in the present case[6]. Similarly, G will not be applicable since the experiments were of short duration and the animals used were immature.

For other expressions the terminology of International Biological Programme given by Crisp[6] was followed. Thus:

Assimilation $A = C-F$ ...(2)

Gross growth efficiency or K_1 of Ivlev[7] $= P/C$ ...(3)

Net growth efficiency or K_2 of Ivlev[7] $= P/A$ ...(4)

Efficiency of assimilation $= A/C$ ...(5)

Food coefficient $= C/P$ ...(6)

Caloric contents of the shrimp, detritus and faecal material are given in Table 1. The values of detritus obtained in this investigation were slightly higher than those determined earlier from organic carbon and major metabolites[1].

The total amount of food consumed was determined by subtracting the weights of detritus at the beginning and end of each experiment. The food consumed, the faecal matter produced and the increase in weight of the shrimp were converted into energy units from the data given in Table 1. These are shown in Table 2. In the 1st experiment, small sized shrimps measuring 14-16 mm were used and in the next 4 experiments, progressively larger specimens were taken. As seen from Table 2, the average calories consumed and the faecal matter produced by the shrimps were related to the size of the animal. Similarly, the growth (P), assimilation (A) and metabolism (R) were directly proportional to the size of the shrimp, except in experiment 4, where the energy of growth showed a slight decline from that of the smaller specimens used in experiment 3 (Table 2).

Values of gross growth efficiency P/C or K_1 and net efficiency P/A or K_2 are also given in Table 2. Both P/C and P/A varied with the size of the animal; but maximum gross and net efficiencies of 35 and 36% respectively were obtained in experiments 2 and 3 in which the sizes of the shrimp ranged from 17-20 and 19-20 mm respectively. Average values of P/C and P/A, however, were about 21 and 24% respectively. It is interesting to note that in the present experiments, values of gross growth efficiency did not vary greatly from those of net

TABLE 1 — CALORIC VALUES OF SHRIMP (*M. monoceros*), DETRITUS AND FAECAL MATTER

Material	No. of estimations	Range cal/g dry wt	Mean cal/g dry wt
Entire shrimp	4	2899·4-3214·8	3065·76
Detritus	5	451·2-461·5	457·68
Faecal matter	2	56·7-60·8	58·74

TABLE 2 — ENERGY BALANCE SHEET OF *M. monoceros* AFTER 14 DAYS OF GROWTH WHEN FED ON ESTUARINE DETRITUS

Expt No.	No. of shrimps used	Size range (mm)	Consumption C (cal)	Faecal matter F (cal)	Assimilation A $C-F$ (cal)	Energy of growth P (cal)	Metabolism R $C-(P+F)$ (cal)	Gross growth efficiency or 'ecological efficiency' P/C or K_1 %	Net growth efficiency P/A or K_2 %	Food coefficient C/P	Assimilation efficiency A/C %
1	8	14-16	9·02	0·53	8·49	1·50	6·99	16·60	17·70	6·02	94·12
2	10	17-20	67·28	2·12	65·16	23·70	41·46	35·20	36·40	2·84	96·84
3	10	19-20	151·00	5·11	145·89	52·80	93·09	35·00	36·20	2·86	96·61
4	3	34-36	291·33	29·60	261·75	48·30	213·43	10·60	18·50	6·03	89·83
5	2	41-42	510·90	55·11	455·79	53·40	402·39	10·50	11·70	9·57	89·21
Average			205·91	18·49	187·41	35·94	151·47	21·60	24·10	5·46	93·32

growth efficiency. This is possibly because the food consumed was in a readily assimilable form and little loss of energy occurred through defaecation. The assimilation efficiency A/C ranged from 89 to 97% (Table 2).

In earlier laboratory experiments on the feeding of zooplankton, the values of P/C were found to be more variable than those of P/A. Thus, when pre-adult *Daphnia* were fed on different concentrations of *Chlamydomonas*, P/C ranged from 4-13%, whereas P/A varied within a narrow range 55-59%[8]. The energy of egestion F in *Daphnia*, calculated by difference, was found to be very high (about 80%). Slobodkin[9], using the term ecological efficiency for gross growth efficiency or K_1, found that in *Daphnia* ecological efficiency ranged from 4-13%. In the crab *Menippe mercenaria*, P/A and P/C did not differ widely[10], these were high (71 and 68% respectively) while the assimilation efficiency was 96%.

Table 2 also gives the food coefficient of *M. monoceros*. The food coefficient was inversely related to both gross and net efficiencies, i.e. when P/C and P/A values were high, C/P values were low and vice versa.

Thus the energy budget of the shrimp would be as follows:

Average energy of estuarine detritus = 458 cal/g dry wt
Energy of growth P = 35·93 cal or 18%
Energy in faecal matter F = 18·49 cal or 9%
Respiration and excretion of soluble matter (determined by difference) $R+U$ = 151·47 cal or 73%
Average water content of shrimp = 82·77%
Therefore, 100 cal of detrital energy consumed = 0·047 g of live prawn

[Because 458 cal = 1 g of detritus; therefore, 100 cal = 0·22 g of detritus. Since average growth efficiency = 21·6% (Table 1), 100 cal of detritus consumed = 0·047 g of prawn.]

Earlier studies on marine food chains are largely restricted to phytoplankton → zooplankton, algae → demersal animals, zooplankton → fish relationships; and in no investigation so far such an important constituent as detritus has been studied as a source of energy either to pelagic or demersal animals[11]. While discussing the food chain in Cochin backwater earlier, a generalized pathway has been given in which the importance of detritus in the estuarine food chain has been emphasized[12-14]. Both phytoplankton and zooplankton pass through decomposition stages in the environment and in certain situations their contribution, in what is collectively termed as detritus, may be quite considerable[1]. It has been estimated that in the upper layer of the sea, dead cells very often constitute 8% of the living cells and in deeper layers the dead cells could increase to 80%[15]. Similarly, the animal part of detritus is 10% of the living materials. The rate of detritus consumption in the epiplankton is 20% and in the bathyplankton 45% of the standing stock of living organism[15]. A descriptive account giving the importance of detritus as food of even the most carnivorous species has been given by Darnell[16]. It is therefore evident that detritus, consisting of plant and animal matter, organic

TABLE 3 — PERCENTAGE VALUE OF GROSS GROWTH EFFICIENCY (P/C OR K_1), NET GROWTH EFFICIENCY (P/A OR K_2) AND ASSIMILATION EFFICIENCY (A/C) IN SOME ANIMALS AS DETERMINED BY DIFFERENT AUTHORS

Animal	Food	P/C or K_1 %	P/A or K_2 %	A/C %	Authors
CRUSTACEA					
Balanus balanoides	Nauplius larva	35·9*	—	—	Crisp[23]
Calanus finmarchicus	*Skeletonema costatum*	34·0	—	61·7	Corner *et al.*[24]
C. helgolandicus	Seston	—	—	74-91	Corner[25]
Daphnia pulex	*Chlamydomonas*	4·0-13·0	55·0-59·0	—	Richman[8]
D. pulex	do	4·0-13·0	—	—	Slobodkin[9]
Elminius modestus	Nauplii	37·3*	—	—	Crisp[23]
Euphausia pacifica	*Artemia* nauplii	9·0	30·0	80·0	Lasker[26]
Manippe mercenaria	Fish	68·0	71·0	96·0	Sushchenya and Clare[10]
Metapenaeus monoceros	Estuarine detritus	21·6	24·1	93·3	Present authors
Mysis relicta	*Daphnia pulex*	—	—	85·0	Lasenby and Langford[27]
Orchestia bottae	Decaying sea weed	8·0-30·0	30·0-60·0	—	Sushchenya[28]
Palaemonetes pugio	Faecal pellets of *P. pugio*	—	—	82·0	Johannes and Satomi[21]
ANNELIDA					
Tubifex tubifex	Mud	—	62·0	50·0	Ivlev[29]
MOLLUSCA					
Aplysia punctata	Algae	—	15-73	45-73	Carefoot[30]
Nerita tessellata	do	3·0	12	40·0	Hughes[22]
N. versicolor	do	5·0	13·0	39·0	do
N. peloronta	do	4·0-7·0	5·0, 8·0	41·0, 43·0	do
Tegula funebralis	do	16·5	23·5	70·3	Paine[31]
FISHES					
Alburnus alburnus	Cyclops	12·1	16·4	79·9*	Ivlev[32]
Megalops cyprinoides	*Metapenaus monoceros*	22·2-44·2	—	86·4-97·7	Pandian[33]
Ophiocephalus striatus	do	18·5-43·7	—	86·6-93·3	do
Pleuronectes platessa	*Mytilus edulis*	14·3-26·1	—	—	Colman[34]

*Calculated by present authors.

aggregates, bacteria and fungi, is ingested at almost all trophic levels of the marine food chains.

Although laboratory data on gross growth efficiency or ecological efficiency of many animals are now available, a comparative study of the growth efficiency has seldom been made to arrive at a realistic figure of the transformation of energy from food. Welch[17], using the energy values obtained by earlier workers, found that the range in gross growth efficiency (K_1) was from 15 to 35% and net growth efficiency ranged from 20 to 90%. He deduced a negative correlation between K_2 and assimilation efficiency and a non-linear relationship between K_1 and assimilation efficiency. He postulated that carnivores have relatively high assimilation efficiency and low K_2 values, whereas herbivores and detritus feeders have low assimilation efficiency and high K_2 values. Ricker[18] has, however, indicated that environmental conditions such as temperature, dissolved oxygen and food supply seem to affect the assimilation efficiency. Slobodkin[19] concluded that ecological efficiency is of the order of 5 to 20%. Engleman[20], from both laboratory and field data on arthropod → macrofauna energetics, concluded that ecological efficiency ranges from 8 to 30%.

Table 3 gives the values of P/C, P/A and A/C in some animals for which data are available. In Crustacea, the reported P/C values ranges from 4 to 68%, the P/A values from 24 to 71% and A/C values from 62 to 96%. In all those crustaceans, where assimilation efficiency is high, the net growth efficiency is close to gross efficiency. It is interesting to note that the shrimp, *Palaemonetes pugio*, when fed on its own faecal pellets, gave an assimilation efficiency of 82%[21].

Published information on the energetics of annelids is very scarce. However, the worm *Tubifex tubifex* when fed on mud, gave a net growth efficiency of 62% and assimilation efficiency of 50% (Table 3). In molluscs, both P/C and P/A values were found to be low — 3 to 16·5% and 5 to 23·5% respectively (Table 3). Their assimilation efficiency was also low and had a range 39 to 70%. The difference in the energy budget of *Nerita peloronta* was found to be associated with the change in habitat[22]. In fishes, the range in P/C values was from 12 to 44%, with A/C values varying within a limited range (80 to 98%; Table 3).

With such a wide variation in the estimates of efficiencies of different animals, it is doubtful to conclude that either gross or net growth efficiency would have any constancy and that any reasonable estimate of efficiency based on averages would have a wide acceptance. There seems little justification to assume that any one value would be preferred by different animals living under widely different ecological conditions.

In *M. monoceros*, the estimates of gross, net and assimilation efficiencies fall within the accepted limits (Table 3). However, it would be interesting to know if the deduction made here that 100 cal of food (detritus) consumed gives rise to about 0·05 g of live prawn, would remain valid when the shrimp is fed on different types of food. We expect that a change in the diet would be associated with a change in the assimilation efficiency. This would alter the values of F, which in turn would affect the values of P/C. However, the nature of food supply would probably not alter the gross growth efficiency considerably, and therefore, it would probably fall within a range fairly close to that of detritus.

Acknowledgement

The authors thank Prof. D. J. Crisp, F.R.S., for the stimulating discussion one of them (S.Z.Q.) has had with him on energy measurements and Dr (Miss) Sumitra Vijayaraghavan for her considerable assistance in this work.

References

1. Qasim, S. Z. & Sankaranarayanan, V. N., *Mar. Biol.*, **15** (1972), 193.
2. Karzinkin, G. S. & Tarkovskaya, O. I., in *Techniques for the investigation of fish physiology*, edited by E. N. Pavlovskii (Israel Programme for Scientific Translation), 1964, 122.
3. George, M. J., *Indian J. Fish.*, **9** (1962), 110.
4. Mohammed, K. H. & Rao, P. V., *J. mar. biol. Ass. India*, **13** (1972), 149.
5. George, M. J., *Indian J. Fish.*, (1974), (in press).
6. Crisp, D. J., in *Methods for the study of marine benthos*, edited by N. A. Holme & A. D. McIntyre (Blackwell Scientific Publication, Oxford & Edinburgh), 1971, 207.
7. Ivlev, V. S., *Usp. soverm. Biol.*, **19** (1945), 98 (in Russian). Translated by W. E. Ricker, *J. Fish. Res. Bd Can.*, **23** (1966), 1727.
8. Richman, S., *Ecol. Monogr.*, **28** (1958), 273.
9. Slobodkin, L. B., *Ecology*, **40** (1959), 243.
10. Sushchenya, L. M. & Claro, R., in *Issledovaniya Tsentral no-Amerikan shikh Morei*, No. 1, pp. 217-30 [Kiev: Naukova Dumka Press (in Russian)], *Fish. Res. Bd Can.*, Translation No. 931, 1966, 1.
11. Mann, K. H., in *Advances in ecological research*, Vol. 6, edited by J. B. Cragg (Academic Press, London & New York), 1966, 1.
12. Qasim, S. Z., in *Marine food chains*, edited by J. H. Steele (Oliver & Boyd, Edinburgh), 1970, 45.
13. Qasim, S. Z., *Indian J. Fish.*, **19** (1972), 11.
14. Wyatt, T. & Qasim, S. Z., *Limnol. Oceanogr.*, **18** (1973), 301.
15. Patipa, T. S., Pavlova, E. V. & Mironov, G. N., in *Marine food chains*, edited by J. H. Steele (Oliver & Boyd, Edinburgh), 1970, 142.
16. Darnell, R. M., *Ecology*, **42** (1961), 553.
17. Welch, H. E., *Ecology*, **49** (1968), 755.
18. Ricker, W. E., *Ecol. Monogr.*, **16** (1946), 373.
19. Slobodkin, L. B., in *Advances in ecological research*, Vol. 1, edited by J. B. Cragg (Academic Press, London & New York), 1962, 69.
20. Engleman, M. D., *Ecol. Monogr.*, **31** (1961), 221.
21. Johannes, R. E. & Satomi, M., *Limnol. Oceanogr.*, **11** (1966), 191.
22. Hughes, R. N., *Mar. Biol.*, **11** (1971), 12.
23. Crisp, D. J., in *Grazing in terrestrial and marine environments*, edited by D. J. Crisp (Blackwell Scientific Publications, Oxford), 1964, 251.
24. Corner, E. D. S., Cowey, C. B. & Marshall, S. M., *J. mar. biol. Ass. UK*, **47** (1969), 254.
25. Corner, E. D. S., *J. mar. biol. Ass. UK*, **41** (1961), 5.
26. Lasker, R., *J. Fish. Res. Bd Can.*, **23** (1966), 1291.
27. Lasenby, D. C., Langford, R. R., *Limnol. Oceanogr.*, **18** (1973), 280.
28. Sushchenya, L. M., in *Structure and dynamics of aquatic communities and populations*, pp. 120-35 [Acad. Nauk. Ukr. S.S.R. Institute of Biology of Southern Seas (in Russian)]; *Fish. Res. Bd Can.*, Translation No. 978, 1967, 1.
29. Ivlev, V. S., *Int. Rev. ges. Hydrobiol. u. Hydrogr.*, **38** (1939), 449.
30. Carefoot, T. H., *J. mar. biol. Ass. UK*, **47** (1967), 565.
31. Paine, R. T., *Limnol. Oceanogr.*, **16** (1971), 86.
32. Ivlev, V. S., *Bull. Math. Biophys.*, **22** (1960), 371.
33. Pandian, T. J., *Mar. Biol.*, **1** (1967), 16.
34. Colman, J. A., *J. mar. biol. Ass. UK*, **50** (1970), 113.