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Interaction of Ration and Unilateral Eyestalk Ablation on Energetics of Female *Macrobrachium nobilii**

S. SINDHU KUMARI
T.J. PANDIAN

School of Biological Sciences
Madurai Kamaraj University
Madurai 625 021
Tamilnadu, India

Abstract

Effects of different feeding levels on moulting, growth, reproduction, food utilization and energy partitioning were studied for 2-5 successive moulting periods in normal and unilaterally eyestalk-ablated female *Macrobrachium nobilii.* Diminishing rations entailed heavy mortality and extended the intermoult period, which was age- rather than weight-dependent and more influenced by ablation than ration. Growth was more a ration-dependent process. Rates of growth and metabolism were influenced by the interaction between ration and ablation. Conversion efficiency was influenced more by ration than ablation. Maximum numbers of eggs were produced by the ablated group receiving 80% of an ad libitum diet. Adults set priority for egg production and allocated a major fraction of the converted energy for it.

Introduction

Decapod crustaceans have been less investigated with regard to the bioenergetic parameters than other culture species (Vernberg 1987). Food availability is a critical environmental variable; a change in food supply may be reflected in moulting, growth and egg production. Eyestalk ablation is practiced to induce precocious moult and ovarian maturation, and to enhance growth; the effects of restricted ration on moulting, growth and egg production are described elsewhere (e.g., Sedgwick 1979; Ponnuchamy et al. 1983). However, such studies on

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*Dedicated to Professor O. Kinne on his 68th birthday (30 August 1923).

eyestalk-ablated prawns have not been undertaken so far. The objective of this paper is to examine the relative importance of food ration and ablation in causing precocious moulting, growth enhancement and fecundity.

Materials and Methods

Macrobrachium nobilii (Henderson and Mathai), collected from the River Cauvery at Grand Reservoir (10" 50" N: 76" 43" E), India, were acclimatized (30 ± 1 °C) for 15 days. Over 120 freshly moulted females, weighing 1 ± 0.05 g were selected for the experiment. About 60 prawns served as control (control series), which were divided into seven ration groups (100, 90, 80, 70, 60, 45 and 30% of *ad libitum* feeding; *ad libitum* refers to the quantum of food that a prawn consumes when food supply remains unrestricted), each consisting of at least six individuals. Another 60 prawns were unilaterally eyestalk ablated during intermoult stage and divided into seven ration groups corresponding to those in the control series. Each group was offered the selected ration of *Tubifex tubifex* daily for four hours, and the uneaten food was collected, dried at 80°C for 24 hours and weighed. For convenience, rations $> 60\%$ of *ad libitum,* were designated as higher and those $< 60\%$ as lower rations.

Ammonia excretion in all the test prawns was monitored for at least one complete moult cycle following the methods of Solorzano (1969). One mg of ammonia was considered equivalent to 24.7 J (Elliott 1976). The excretion values were expressed as the respective fractions of food consumed by the prawns. They were applied to the remaining moult cycles to estimate total ammonia excreted by the ablated or control series receiving different rations.

Eyestalk ablation, moult staging, exuvia collection and energy estimation were performed, as described by Sindhu Kumari and Pandian (1987). The bioenergetics components were estimated following the procedures described by Sindhu Kumari and Pandian (1987) for each moult period separately. The experiments and bioenergetics monitoring lasted for a maximum of 164 days involving 2-5 successive moult periods. Overall rates of consumption, assimilation, growth rate and metabolism were calculated by dividing the sum of products of the respective rates and duration for different moult cycles by the total number of days of the feeding period (see Sindhu Kumari and Pandian 1987).

Results

Intermoult Period

Diminishing ration extended the intermoult period in both control and ablated series (Table 1). The period was much prolonged in the starved individuals of both series. Whereas the starved groups moulted at the expense of reserves (see Table 2), those receiving lower (< 60%) rations extended the moult period to accumulate adequate reserves to meet the "moult cost" (Sindhu Kumari and Pandian 1987).

In general, the intermoult period was further prolonged at successive moults in all the tested prawns (Table 1). Extension of the period was a body-weight dependent factor in groups fed on higher ration. A significant positive correlation between midbody weight (mean of the sum of two successive intermoult body weights) and moult period was apparent in animals fed on higher rations (Fig. 1a). However, a negative one became apparent in groups fed lower rations (Fig. 1b). Evidently, the extension of the moult period at lower rations was to gather adequate "fuel" to meet the moult cost.

For calculating the relative age of prawns, the day of commencement of the experiment was considered as 0 day. The moult periods of a higher ration group (80% control and ablated) and a lower ration group (45% control and ablated) were plotted against relative age. Figs. 1c-d show that with advancing relative age, the moult period was extended, irrespective of the ration level in either series. This implies that the extension of the intermoult period is age-dependent rather than weight-dependent.

When subjected to analysis of variance, the data on the moult period of the first moult cycle of the control and ablated prawns revealed that: (i) ablation significantly reduced the intermoult period ($P < 0.0005$); (ii) ration also significantly influenced by intermoult period ($P < 0.005$); and (iii) the interaction between ration and ablation did not significantly affect the period ($P < 0.05$).

Growth

In the control and ablated series, higher rations supported positive growth, while the lower ones, negative growth (Table 2). The growth trends exhibited by the groups fed higher rations resembled that for the

Table 1. Intermoult period (day) of control and ablated *Macrobrachium nobilii* receiving different rations (% of *ad libitum*) for 2-5 successive moults. Each value represents the average performance of a minimum of six individuals. Values in parentheses indicate the total number of days to complete the respective number of moults.

Ration (%)		Control						Ablated					
		Number of moults						Number of moults					
		1	2	3	4	5	Mean	1	2	3	4	5	Mean
100	X	20	22	24	26	29(121)	24	18	20	21	23	25(107)	21
	±	2	3	2	3	3	3.5	2	3	2	3	2	2.7
90	X	24	25	27	29	30(135)	27	19	21	22	25	26(113)	23
	±	2	3	4	3	4	2.6	1	1	3	2	3	2.8
80	X	24	25	26	28	29(132)	26	18	21	22	24	25(110)	22
	±	3	3	3	2	2	2.1	3	2	3	3	2	2.7
70	X	26	26	28	29	31(140)	28	20	21	23	25	27(116)	23
	±	3	2	4	2	3	2.1	2	3	3	4	5	2.8
60	X	29	30	32	35	38(164)	33	25	27	28	29	30(139)	28
	±	4	3	5	3	3	3.7	3	3	4	3	4	1.9
45	X	35	38	41	43	+(157)	41	26	29	31	+	+(86)	29
	±	3	4	2	3		3.5	2	2	3			2.1
30	X	37	40	45	+	+(122)	41	29	31	+	+	+(66)	30
	±	5	3	5			3.3	2	3				2.6
0	X	56	+	+	+	+(56)	56	46	+	+	+	+(46)	46
	±	4					4.0	6					6.0

+Indicates the death of all test individuals.

Table 2. Mid body weight (mg) of control and ablated female *Macrobrachium nobilii* fed on different ration levels for 2-5 successive moults. Each value represents the average (mean ± SD) performance of a minimum of six individuals.

		Ration level (% of *ad libitum*)													
Moult number		100		90		80		70		60		45		30	
		Cont	Alb	Cont	Abl	Cont	Abl	Cont	Abl	Cont	Abl	Cont	Abl	Cont	Abl
1	X	1,070	1,077	1,058	1,091	1,047	1,086	1,061	1,080	1,060	1,067	998	986	979	970
	±	18	20	30	34	27	16	21	24	20	24	24	27	14	22
2	X	1,124	1,174	1,113	1,187	1,109	1,198	1,121	1,156	1,108	1,123	944	922	872	852
	±	16	19	23	27	22	24	21	17	18	18	12	14	16	13
3	X	1,166	1,258	1,161	1,265	1,162	1,298	1,172	1,229	1,152	1,177	878	837	727	+
	±	29	30	16	28	22	26	24	23	27	19	22	14		
4	X	1,204	1,333	1,203	1,341	1,207	1,389	1,212	1,296	1,192	1,231	799	+	+	+
	±	16	22	23	22	16	19	14	25	16	25	24			
5	X	1,276	1,400	1,275	1,419	1,270	1,471	1,265	1,356	1,239	1,285	+	+	+	+
	±	23	16	23	16	18	22	20	18	30	31				

+Indicates the death of all test animals.

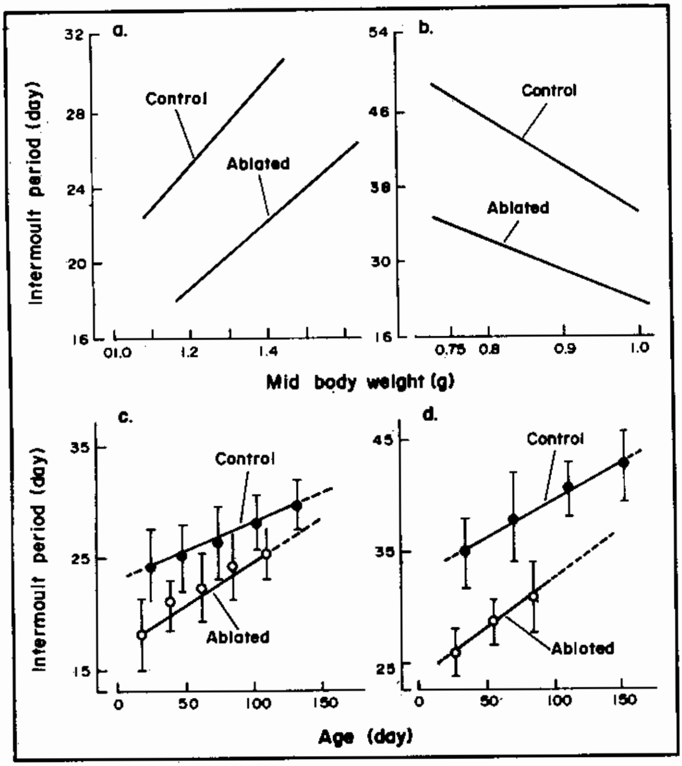

Fig. 1. Intermoult period as functions of midbody weight (for 1a and b) and age (1c and d) in control and ablated *Macrobrachium nobilii* receiving higher (80% of *ad libitum*) and lower (45% of *ad libitum*) sub-maximum ration. Regression equations: for 80% ration groups, control: - 1.0335 + 23.67 X, r 0.984; ablated: - 0.9188 + 17.79 X, r 0.989; and for 45% ration groups, control: 75.65 - 40.20 X, r - 0.988; ablated: 58.90 - 33.03 X, r - 0.981.

group fed *ad libitum*. All groups receiving 70-100% ration in the control series attained almost equal maximum size of 1.27 g; but in the ablated series, the group feeding 80% ration attained a maximum size of 1.47 g. Analysis of variance test was applied to the data on midbody weight attained during successive instars. The data obtained for positive growth by the control and ablated prawns fed on the higher rations were analyzed separately. The effect of instar number (= age) on midbody weight was significant in both the control ($P < 0.0005$) and ablated prawns ($P < 0.0005$). But its magnitude was more predominant on the control (F value = 595) than that of ablated (F value = 118). Ration also significantly influenced the midbody weight of both control ($P < 0.05$) and ablated ($P < 0.0005$) prawns. Comparison of the F values of the

Table 3. Moult increment (% of live body weight) during successive moults in control and ablated female *Macrobrachium nobilii* fed on different ration levels for 2-5 successive moults.

Moult number		Ration level (% of *ad libitum*)													
		100		90		80		70		60		45		30	
		Cont	Alb	Cont	Abl	Cont	Abl	Cont	Abl	Cont	Abl	Cont	Abl	Cont	Abl
1	X	*6.4	10.2	*5.9	10.4	*6.3	11.1	*6.0	*7.7	5.0	*5.8	-4.5	-6.4	-10.3	-10.7
	±	0.36	0.61	0.38	0.54	0.34	0.64	0.43	0.55	0.43	0.47	-0.31	-0.45	-0.56	-0.60
2	X	3.8	8.0	5.0	7.3	5.6	9.6	5.3	6.4	4.0	4.7	-6.0	-7.5	-12.3	-13.8
	±	0.25	0.58	0.30	0.48	0.28	0.47	0.40	0.50	0.40	0.39	-0.38	-0.49	-0.76	-0.65
3	X	3.7	6.4	3.7	5.9	4.5	7.2	3.8	6.0	3.9	4.9	-8.1	-11.1	-20.2	
	±	0.28	0.48	0.29	0.36	0.25	0.40	0.37	0.44	0.35	0.30	-0.39	-0.50	-0.85	
4	X	2.9	5.65	3.55	6.15	3.7	6.85	3.0	4.9	3.1	4.3	-10.0			
	±	0.20	0.36	0.25	0.32	0.20	0.38	0.31	0.32	0.29	0.33	-0.48			
5	X	*7.5	*4.6	*8.3	*5.5	*6.7	*5.0	*5.7	*4.5	*4.8	*4.45				
	±	0.43	0.30	0.60	0.28	0.35	0.31	0.42	0.31	0.39	0.30				

*Neuter moult (no egg production). Others were berried moults (eggs were produced) except the moults undertaken by 45 and 30% ration-fed control and ablated groups.

control (4.18) and ablated (14.47) groups revealed that the effect of ration on the latter was 3.5 times greater than on the former. Growth was more a ration-dependent than an ablation-dependent process.

Increase in size, which occurs between successive instars, is termed the moult increment and is expressed as percentage of live weight. The following may be inferred (Table 3): (i) the moult increment diminished during successive instars except during the fifth one; (ii) higher rations (> 60%) ensured a minimum of 2-4% moult increment; and (iii) lower rations caused lower increments or even negative growth; groups receiving lower rations tolerated a maximum of 20% weight loss to ensure successful moults; hence the tolerance for survival through a moult is about 20% weight loss.

Food Use

While food energy consumed by a prawn decreased with diminishing ration, the decrease was not proportional to the reduction in ration. For instance, controls receiving 30% ration managed to consume 47% (4.99 kJ; *ad libitum,* 10.68 kJ) and the ablated prawns receiving the corresponding ration consumed 39% (4.04 kJ; *ad libitum,* 10.3 kJ) of that in prawns receiving 100% ration (Table 4). Obviously, the groups fed lower rations partially compensated for the decreased ration by eating more as a result of the extended intermoult period.

Maximum growth was exhibited by the groups receiving 80% ration (control 1.15 kJ moult^{-1}; ablated 2.08 kJ moult^{-1}) in either series. The data on food consumption and each of the growth components like somatic growth, exuvia production and egg output were subjected to regression analysis to learn how ration influenced these components. Somatic growth (r = control 0.8516; ablated 0.783) was significantly correlated with food consumption. For a unit increase in food consumption, energy allocated for somatic growth or egg production was higher in the ablated prawns (0.12, 0.178 kJ, respectively) than in the control (0.100, 0.10 kJ). But the exuvia production was not correlated with food consumption, as was obvious from the negative values of parameter b in the regressions (control - 0.0044; ablated - 0.0065) and smaller r values (control 0.458; ablated 0.565). Briefly, the ration influenced somatic growth and egg production through ablation, while it hardly affected exuvia production. Energy expended on metabolism by the groups receiving the higher and lower rations was 81 and 92% of consumption, respectively. The controls incurred a greater energy loss on metabolism than the ablated prawns.

Table 4. Overall energy budget of control and eyestalk-ablated female *Macrobrachium nobilii* (1 ±0.05 g) fed on different ration levels for 2-5 successive moults. All values are given in kJ per prawn per moult and efficiency in %.

Parameter number	Ration level (% of *ad libitum*)													
	100		90		80		70		60		45		30	
	Cont	Alb	Cont	Abl	Cont	Abl	Cont	Abl	Cont	Abl	Cont	Abl	Cont	Abl
Consumption	10.68	10.30	10.64	9.78	9.44	8.43	8.51	7.81	8.79	8.00	7.69	5.0	4.99	4.04
Feces + urine	0.99	0.94	0.89	0.72	0.70	0.63	0.55	0.43	0.48	0.44	0.35	0.27	0.24	0.19
Assimilation	9.69	9.36	9.75	9.06	8.73	7.80	7.96	7.38	8.31	7.56	7.34	5.63	4.75	3.85
Metabolism	8.56	7.80	8.63	7.53	7.58	5.72	6.98	5.90	7.48	6.68	7.11	5.44	4.60	3.74
Growth (conversion)	1.13	1.56	1.12	1.52	1.15	2.08	0.98	1.48	0.83	0.88	0.23	0.19	0.15	0.11
a. Somatic growth	0.23	0.34	0.24	0.33	0.24	0.38	0.19	0.24	0.15	0.16	-0.17	-0.23	-0.27	-0.31
b. Exuvium	0.40	0.39	0.39	0.39	0.38	0.37	0.36	0.35	0.40	0.38	0.40	0.42	0.42	0.42
c. Egg	0.50	0.83	0.49	0.80	0.53	1.33	0.43	0.89	0.28	0.34	-	-	-	-
Assimilation efficiency	90.73	90.87	91.64	92.64	92.58	92.53	93.54	94.49	94.54	94.50	94.45	95.42	95.19	95.29
Conversion efficiency	11.66	16.67	11.49	16.78	13.27	26.67	12.31	20.06	9.99	11.64	3.13	3.37	3.16	2.86

Table 5. Overall rates ($J \cdot g^{-1}$ midbody weight day^{-1}) of consumption, assimilation, growth and metabolism of control and eyestalk-ablated female *Macrobrachium nobilii* (1 ± 0.05 g) fed on different ration levels for 2-5 successive moults.

	Ration level (% of *ad libitum*)													
	100		90		80		70		60		45		30	
Parameters	Cont	Abl	Cont	Abl	Cont	Abl	Cont	Abl	Cont	Abl	Cont	Abl	Cont	Abl
Consumption	366	371	333	332	303	288	257	272	227	242	218	228	146	148
Assimilation	331	340	305	307	281	267	240	257	215	228	207	216	139	142
Growth	291	280	270	253	243	196	210	208	193	201	201	209	135	138
Metabolism	40	60	35	54	38	71	30	49	22	27	6	7	4	4
Somatic growth	8	13	8	12	8	14	6	8	4	5	-5	-9	-8	-12
Exuvia production	14	14	12	13	12	13	11	12	10	12	11	16	12	16
Egg production	18	22	15	2	18	44	13	29	8	10	-	-	-	-

Rates of consumption, assimilation, growth and metabolism are summarized in Table 5. Analysis of variance test (Table 6) showed that ablation significantly influenced the growth rate, but not consumption or metabolic rate. However, all the rates were influenced by ration. While there was an interaction between ration and ablation in the growth and metabolic rates, no such effect was observed in the consumption rate.

Table 6. Summary of analysis of variance for the data on consumption rate (Cr), growth rate (Pr) and metabolic rate (Mr) as functions of ration and ablation.

Source	Parameter	SS	d.f.	M.S.	F value	P
Total	Cr	568,547	83	-	-	-
	Pr	52,907	83	-	-	-
	Mr	259,781	83	-	-	-
Between treatment	Cr	4,032	1	4,032	3.972	> 0.05
	Pr	11,476	1	11,476	835.22	< 0.0005*
	Mr	946	1	946	2.150	> 0.05
Between ration	Cr	491,399	6	81,899.83	80.691	< 0.0005*
	Pr	29,675	6	4,946	359.96	< 0.0005*
	Mr	211,711	6	35,285	80.193	< 0.0005*
Interaction	Cr	2,067	6	344.50	0.330	> 0.05
	Pr	10,794	6	1,799	130.93	< 0.0005*
	Mr	16,313	6	2,719	6.179	< 0.0005*
Error	Cr	71,049	70	1,014.98	-	-
	Pr	962	70	13.74	-	-
	Mr	30,811	70	440	-	-

The daily pattern of ammonia excretion studies conducted for a complete moult cycle showed that ammonia excretion was cyclical (Fig. 2). A remarkable feature in the pattern of ammonia excretion is the post-moult increase, probably due to protein breakdown. Irrespective of the changes in ration level, the general pattern of ammonia excretion did not change both in the control and ablated prawns. Prawns receiving 45% ration extended the intermoult period, especially the premoult stage. Compared to the intermoult stage, there was significant increase in ammonia excretion during premoult ('t' values: 100% ration-fed control 3.94, ablated 3.65; 45% ration-fed control 5.85, ablated 10.08, $P < 0.0005$) and postmoult (45% ration-fed control 9.53, ablated 9.53; 45% ration-fed control 6.98, ablated 8.23, $P < 0.0005$) stages. Between the

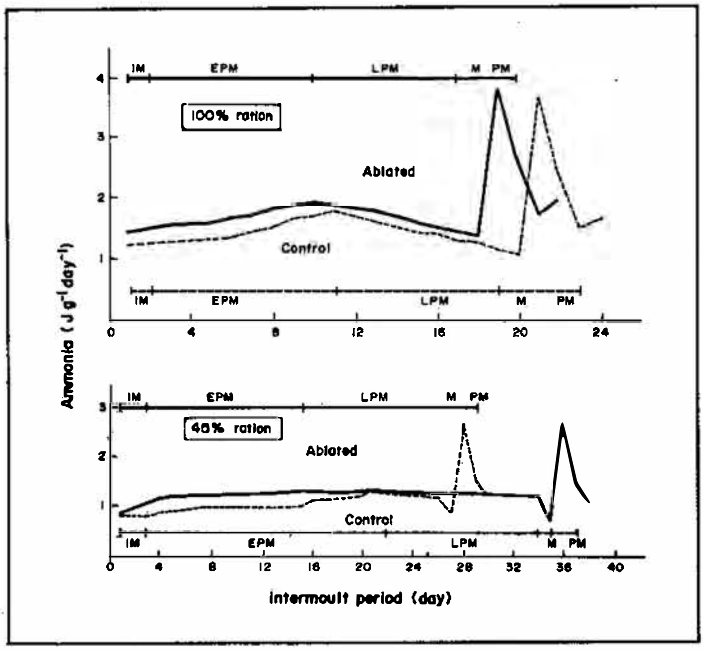

Fig. 2. Daily pattern of ammonia excretion during a complete moult cycle by control (---) and ablated (–) *Macrobrachium nobilii* fed on 100 (upper panel) or 45% (lower panel) ration. Vertical bars indicate standard deviation. IM = intermoult; EPM = early premoult; LPM = late premoult; M = moult; PM = post moult.

control and ablated series, ammonia excretion by the latter was significantly higher during intermoult ('t' value = 2.72 for 100% ration-fed group and 2.71 for 45% ration-fed group, $P < 0.05$) and premoult stages ('t' value = 9.68 for 100% ration-fed group and 7.95 for 45% ration-fed group, $P < 0.0005$). However, the difference observed during the postmoult stage was not statistically significant.

Geometric derivations (Thomson 1941) of the somatic growth rate as a function of ration in the control and ablated series showed 51, 80 and 100% as the maintenance, optimum and maximum rations, respectively (Fig. 3). The maintenance and optimum rations were 187 and 189 for the control, and 293 and 297 J g^{-1} day^{-1} for the ablated prawns, respectively.

Conversion efficiency of the control group receiving > 60% ration ranged between 10 and 13%, whereas in the ablated series the range was remarkably higher, i.e., 11-27% (Table 4); the 80% ration-fed ablated group showed a two-fold increase over its counterpart control. The increase in the other ablated groups was not so pronounced.

When subjected to analysis of variance, the data on conversion efficiency of the second intermoult period showed that the efficiency of

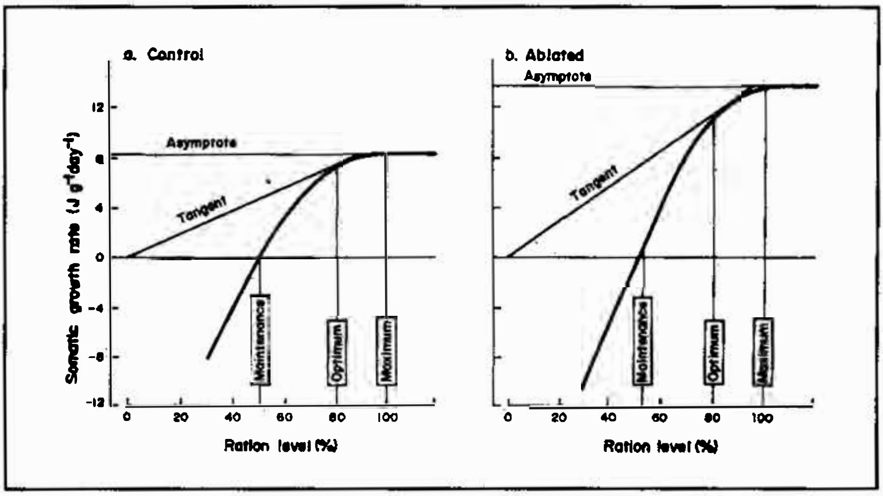

Fig. 3. Geometrical derivations of maintenance, optimum and maximum ration for (a) control and (b) ablated *Macrobrachium nobilii.*

conversion was influenced by the independent action of ablation ($P < 0.0005$), ration ($P < 0.0005$) as well as by their interaction ($P < 0.0005$). However, the magnitude of the effect of ration (F value = 99) was higher than that of ablation (F value = 44) or the interaction between ration and ablation (F value = 5).

Energy Partitioning

For a better understanding of the impact of ration on the energy partitioning process, the cumulative data on growth (P) was divided into (i) net somatic growth, (ii) exuvia, and (iii) egg production. At lower rations (45 and 30%), the prawns strived for sustenance at the expense of their body weight; they underwent weight loss which was higher in the 30% group than in the 45% group (Table 2). Ablated prawns suffered a greater loss of body weight at lower rations. Eyestalk ablation may prove fatal if feeding is restricted.

Control as well as ablated prawns (except the 80% ration-fed group) allocated comparatively less energy for somatic growth than for exuvia or egg production. The ablated prawns receiving higher rations allocated 1.5, 1.4, 1.6, 1.3 and 1.1 times more energy for somatic growth than the respective controls.

An almost equal quantum of energy (≈ 0.39 kJ) was expended on exuvia production by groups fed higher rations. Energy expended on exuvia production was higher (≈ 0.42 kJ) at the lower than the higher rations.

The ablated prawns allocated more energy for egg production (Table 7). For example, energy allocated for net somatic growth, exuvia production and egg production by the control group receiving 80% ration was 21, 33 and 46%, respectively; their ablated counterparts allocated 18, 18 and 64%, respectively. At lower rations there was no egg production, as all the available energy was channelled for the synthesis of exoskeleton. Prawns receiving 45% ration showed initial signs of ovarian development which later regressed.

At any higher ration and moult, clutch size of the ablated series was greater than that of its counterparts in the control series (Table 8). Such an enhanced reproductive output can boost the hatchery production of prawn seedlings. Barring the 60% ration group, all groups in the ablated series undertook berried moults more frequently. Prawns fed 80% ration produced eggs consistently at all the five successive moults under observation. In all the groups fed sub-maximum ration, egg production progressively increased during successive moults. Analysis of variance of the data on egg production during the third moult revealed that the independent effects of ablation ($P < 0.0005$) and ration ($P < 0.0005$), as well as their interaction ($P < 0.0005$), significantly influenced the process.

Table 7. Energy partitioning (as % of total growth) for somatic growth, exuvia production and egg production in control and eyestalk-ablated female *Macrobrachium nobilii*.

	Ration level (% of *ad libitum*)									
	100		90		80		70		60	
Parameter	Cont	Abl	Cont	Abl	Cont	Abl	Cont	Abl	Cont	Abl
Somatic growth	20.4	21.8	21.4	21.7	20.9	18.3	19.4	16.2	18.1	18.2
Exuvia production	35.4	25.0	34.8	25.7	33.0	17.8	36.7	23.7	48.2	43.2
Egg production	44.2	53.2	43.8	52.6	46.1	63.9	43.9	60.1	33.7	38.6

Discussion

Diminishing rations resulted in the extension of the intermoult period of *M. nobilii*. *Panulirus longipes* exhibits similar behavior under diminishing rations (Chittleborough 1975), as does *Carcinus maenas* (Klein Breteler 1975) and *Palaemon lamarrei* (Katre and Reddy 1976).

In *M. nobilii*, percentage growth increment decreased with increasing body weight. Though not universal, this feature has been recorded for many crustaceans, e.g., *M. rosenbergii* (Rajyalakshmi 1964), *Palaemon serratus* (Forster 1970), *Penaeus japonicus* (Choe 1971). These prawns are characterized by indeterminate growth, and size limitation is the result of diminishing moult increment with increasing size. Severe food shortage also reduced the increment in *P. longipes* (Chittleborough 1975). Ration affected the maximum weight attained by *M. nobilii*. It is not clear whether the depression in growth rate is brought about by diminishing the moult increment (Knowlton 1974), extending the intermoult period (Chittleborough 1975) or both.

The ammonia excretion rate was higher in the ablated prawns. Similar results were reported by Ananthakrishnan et al. (1981) for *M. lanchesteria*, in which the increased ammonia output was reported to be related to the removal of the eyestalk neuroendocrine system, which may be elaborating the principle(s) responsible for the regulation of ammonia excretion (Regnault 1979).

The inability of *M. nobilii* receiving 45 and 30% *ad libitum* to produce eggs (Table 8), implies that ovarian development requires more than 45% ration. Nutritional status was shown to affect significantly gonadal development and fecundity of *P. monodon* (Primavera et al. 1979).

The primary question posed in this study was: what effect does the restriction of feeding have on the partitioning of energy for somatic growth, exuvia production and egg production. Both control and ablated prawns tended to invest more energy on egg production, as indicated by the scope for egg production, but the scope for egg production is greater in the latter (Fig. 4). Accelerated rate of egg production was also observed in the *ad libitum*-fed ablated *P. semisulcatus* (Browdy and Samocha 1985) and *M. nobilii* (Sindhu Kumari and Pandian 1987). Perhaps eyestalk ablation triggers greater lipid synthesis, which is necessary for a faster rate of gonadal maturation. Millamena and Catacutan (1990) showed that ablation led to increased lipid deposition in the hepatopancreas and ovary until full maturity of *P. monodon*.

Table 8. Fecundity (eggs per clutch) of control and eyestalk-ablated female *Macrobrachium nobilii* fed on different ration levels for 2-5 successive moults.

Moult number	Ration level (% of *ad libitum*)													
	100		90		80		70		60		45		30	
	Cont	Alb	Cont	Abl	Cont	Abl	Cont	Abl	Cont	Abl	Cont	Abl	Cont	Abl
1	-	690±50	-	710±	-	870±40	-	-	-	-	-	-	-	-
2	962±36	1,124±64	898±36	948±40	1,039±66	1,212±40	840±46	964±53	604·50	630±48	-	-	-	-
3	1,164±66	1,340±36	1,124±52	1,389±48	1,216±76	1,496±40	1,010±50	1,194±60	685·35	742±38	-	-	-	-
4	1,328±46	1,528±70	1,340±39	1,528±68	1,480±78	1,826±80	1,216±68	1,408±70	744·45	860±54	-	-	-	-
5	-	-	-	-	-	2,096±84	-	1,628±80	-	-	-	-	-	-

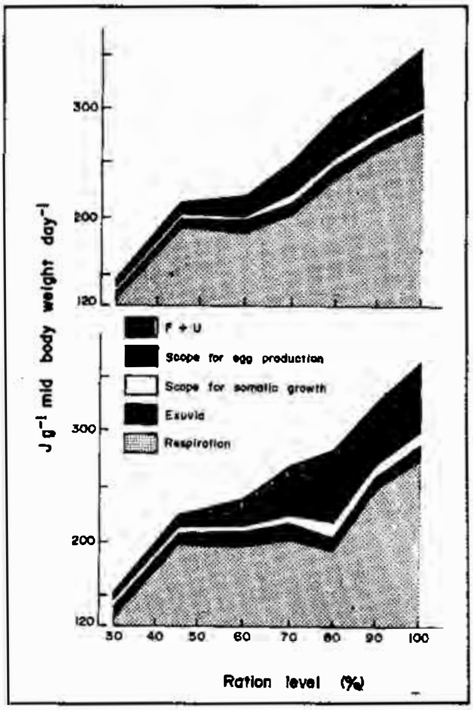

Fig. 4. Quantitative partitioning of the energy intake in (a) control and (b) ablated *Macrobrachium nobilii*.

Expenditure on maintenance was 51% of the maximum consumption (Cr max) in the control and ablated *M. nobilii*. Jones and Momot (1983) reported that *Orconectes virilis* used three times as much energy for maintenance as for growth. Ponnuchamy et al. (1983) reported that 43 and 24% of the Cr max (Cr max = the maximum quantum of food eaten by a prawn) as Cr maint (Cr maint = the ration at which the prawn incurs no positive or negative growth) for *M. lanchesteri* and *C. weberi*, respectively. However, they did not indicate the reproductive status of the experimental animals. Perhaps the ovigerous/spawning prawns require more energy for maintenance.

The optimum ration can be characterized as that which provides for the greatest growth for the least food intake resulting in a maximum growth efficiency. Katre and Reddy (1976) and Ponnuchamy et al. (1983) fixed the optimum ration for *P. lamarrei* and *M. lanchesteri* as 162 and 236 mg$\cdot$g^{-1}$\cdot$day^{-1}, respectively. This represents 79 and 71% of their respective maximum consumption. These and the present data suggest that the optimum ration for freshwater species is between 70 and 80% of *ad libitum*.

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