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Effects of Unilateral Eyestalk Ablation on Moulting, Growth, Reproduction and Energy Budget of *Macrobrachium nobilii*

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Abstract

Unilateral eyestalk ablation in juvenile *Macrobrachium nobilii* advanced the onset of sexual maturity by 88 days. During a 330-day experiment, ablated prawns undertook nine moults as adults, carried seven clutches and produced an average of 5,935 eggs. Nonablated prawns undertook four moults as adults, carried three clutches and produced only 2,042 eggs. Ablated female prawns allocated more energy for egg production than did nonablated females (0.98 J egg^{-1} and 0.72 J egg^{-1}, respectively); this was accomplished by an improvement of food conversion efficiency in ablated females.

Introduction

Lack of spawners is the biggest constraint in the hatchery production of prawn seedlings (Muthu and Laxminarayana 1982). Hence priority in prawn culture research is given to investigations regarding the reproduction of prawns in captivity (Conte 1978). Artificial induction of spawning in penaeid shrimp has been carried out successfully by controlling environmental parameters such as photoperiod (Laubier-Bonichon and Laubier 1979), temperature, i.e., thermal stimulation (Lumare 1976) and by eyestalk ablation (Idyll 1971; Lumare 1979). The last mentioned method is the simplest. For over a decade, eyestalk ablation has been used to induce ovarian maturation and spawning in many captive penaeids such as *Penaeus monodon* and *P. merguiensis* (Alikunhi et al. 1975), *P. setiferus*

(Brown et al. 1980), *Penaeus semisulcatus* (Browdy and Samocha 1985) and lobsters, such as *Panulirus homarus* (Radhakrishnan and Vijayakumaran 1984 a, b). Hitherto, eyestalk ablation studies have been restricted to marine prawns and lobsters and were undertaken only with particular reference to vitellogenesis, ovulation and associated breeding activities (Lumare 1979; Emmerson 1980).

In reptantians, moulting and reproduction are antagonistic events. On the other hand, in natantians energy demanding processes like moulting and spawning are synergistic; the available energy has to be apportioned simultaneously for these events. Data on allocation of energy for somatic growth and reproduction of crustaceans are meagre (e.g., Pandian and Balasundaram 1982). Among *Macrobrachium* species, the effects of different diets (Manik 1976; Nelson et al. 1977; Boonyaratpalin and New 1982; Millikin et al. 1980), salinity (Smith et al. 1982) and water quality (Summer and Eversole 1978; Cripps and Nakamura 1979; Menasveta 1982) have been studied using intact *M. rosenbergii.*

It is known that ablation causes precocious moulting as well as enhancement of growth (Mauviot and Castell 1976) and egg production (Browdy and Samocha 1985). The question is: from which source the ablated prawns draw the extra energy required for these activities? No investigation regarding the quantification of energy income and investment by intact and ablated prawns has been undertaken. The present paper represents a contribution to this emerging area in a riverine, diedysic, iteroparous caridean prawn *Macrobrachium nobilii.*

M. nobilii is a riverine prawn occurring beneath boulders of the river-bed in groups of 2-7 individuals. It is distributed in southeastern India, New Caledonia, Gavataks and Tuamotu islands. It grows to a maximum size of 3-5 g.

Materials and Methods

Healthy individuals of *Macrobrachium nobilii* (Henderson and Mathai), collected from the river Cauvery at Grand reservoir (10^o 50"N: 76^o 43"E) during March 1984 were acclimatized (30 ± 1^{o}C) for a period of about 15 days. Over 30 freshly moulted individuals weighing 250 ± 50 mg were selected for the experiments; ten were treated as control; the others were ablated. Ablation was performed by severing the left eyestalk at the narrow proximal end in the region of the articulating membrane, using a pair of fine sterilized scissors

(Caillouet 1973). The wound was cauterized by placing a hot blunt needle over it. During the 330-day rearing experiment there was no mortality. Several intermoult prawns in both series were killed to determine the water and calorific contents at the commencement of the experiment; from these, calorific content of the experimental animals of each series was estimated separately.

All animals were individually reared in 14 l aquaria. The physico-chemical properties of the water were: temperature 30°C; dissolved oxygen 6 mg l^{-1}; dissolved carbon dioxide 2.86 mg l^{-1}' pH 7.7; conductivity 425 μ Mhos om^{-1}; total hardness 236; alkalinity total (in terms of $CaCO_3$) 200 mg l^{-1}; alkalinity (Phenolphthalein) 30 mg l^{-1}; chlorides 15.2 mg l^{-1}; fluorides 0.004 mg l^{-1}; nitrites 0.04 mg l^{-1}; phosphates 0.013 mg l^{-1} and silicates 4.0 mg l^{-1}.

Ammonia was estimated in water samples collected from each aquarium, following the method of Solorzano (1969). One mg of ammonia was considered equal to 5.9 cal or 24.7 J (Elliott 1976).

The prawns were fed once a day for four hours (1000 to 1400 hours) on the tubificid worm *Tubifex tubifex*. *Tubifex* was selected as food for the following reasons: (i) *M. nobilii* responds more readily to live prey; (ii) the thread-like body of *T. tubifex* suits the feeding behaviour (manipulating process) of prawns, as the worms, which often form balls, can easily and quickly be picked up by the chelate legs and conveyed to the mouth; (iii) there is no wastage of food due to leaching and hence there is no fouling of the medium; (iv) high protein content of *Tubifex* (60%) makes it a promising feed for prawn culture (Boonyaratpalin and New 1982); (v) *Tubifex* can be cultured easily using organic wastes and water and may serve as a more economical feed than synthetic diets (Marian and Pandian 1984).

Intact strings of feces were collected at 0900 hours every day and dried at 80°C. The entire aquarium water was changed at 0930 hours every day.

Following the methods of Freeman and Bartell (1975), individuals were closely observed for the exact time of moult. Each exuvium was dried for six hours in hot air oven (80 ± 1°C) and weighed in a balance sensitive to 0.1 mg.

The onset of sexual maturity was recognized by the development of oostegites and ovigerous hairs on the pleopods as well as the appearance of pale green ovaries which could easily be observed through the transparent carapace. In males the second pair of chelate legs became elongated and more profusely covered with setae. Following sexual maturity, eggs were spawned immediately after the completion of ecdysis; the latter was designated as the berried moult to distinguish it from neuter moults which were not followed by spawning (Pandian and Balasundaram 1982).

Caloric contents of prawns, food, feces, exuvium and eggs were determined in a semi-microbomb calorimeter (Parr Instruments, USA) following the procedure described in the instruction manual for bomb calorimetry. Food consumption, egestion and production were estimated in terms of dry weight and then converted into energy units considering the energy density (J mg^{-1}) of the respective sample.

The IBP formula (Petrusewicz and MacFadyen 1970) was used to express the scheme of energy balance, i.e., $C = F + U + R + P$, where C is the food energy consumed, F the feces egested, U the nitrogenous energy excreted, R the energy expended on metabolism and P the growth (conversion). Food energy consumed was measured as the difference between the energy content of food offered and that of the uneaten food. The quantity of absorbed food energy (A) was estimated by subtracting F from C. Likewise the quantity of assimilated food energy (As) was estimated by subtracting U from A. Food energy converted into body substance (net somatic growth) was estimated as the difference between the energy content of an individual during successive moults. Mean of the sum of two successive intermoult body weights was considered as the mid body weight. Total growth (C = growth = conversion) of female prawns was the sum of the energy expended on net somatic growth, exuvia and egg production, whereas that of male prawns was the sum of net somatic growth and exuvia production. The proportion of food energy absorbed and the proportion of absorbed energy converted into body structure were considered as absorption and conversion efficiency, respectively.

$$\text{Absorption efficiency (\%)} = \frac{\text{energy absorbed}}{\text{energy consumed}} \times 100$$

$$\text{Conversion efficiency (\%)} = \frac{\text{energy converted}}{\text{energy absorbed}} \times 100$$

Results

Growth and moulting frequency

In general, eyestalk ablation resulted in acceleration of growth; the growth acceleration was observed on either sex throughout the

330-day experiment (Fig. 1). Within either series growth in males followed an exponential trend, while that of females was sigmoidal. The ablated and control males reached 2.1 g and 1.1 g, respectively, while the ablated and control females attained 1.25 and 0.8 g, respectively. Hence, unilateral eyestalk ablation and the choice of males for monosex culture of *Macrobrachium* are recommended.

Eyestalk ablation also accelerated moulting frequency in both sexes. Ablated prawns moulted up to 20 times while controls moulted up to 17 times. Thus, the overall intermoult periods of the ablated and control prawns were 16.0 ± 2.5 and 19.2 ± 1.5 days, respectively. Whereas ablation significantly ($P < 0.05$) reduced the intermoult

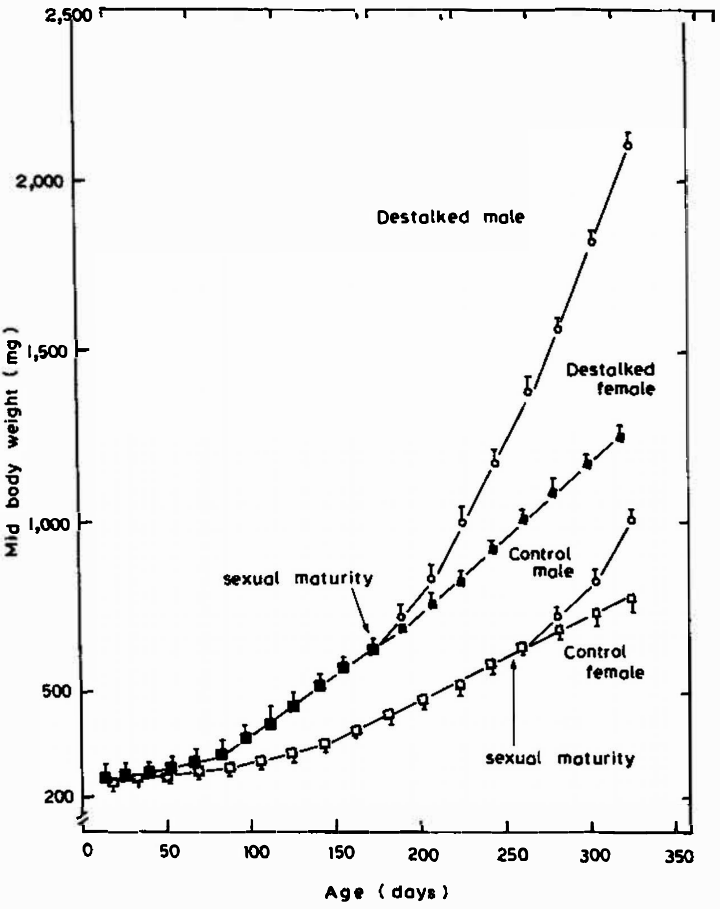

Fig. 1. Growth trends observed for the control and ablated *Macrobrachium nobilii*. Moulting days are indicated by interrupting points. Bars on the data points indicate standard deviation.

period, the difference between intermoult periods observed among the males (control 19.30 ± 1.6, ablated 16.25 ± 2.7 days) and females (control 19.7 ± 1.4, ablated 16.0 ± 2.3 days) of either series was not statistically significant ($P > 0.05$).

Typical of a crustacean, the intermoult period of *M. nobilii* increased from about 17 days in the first few moults to about 22 days during the 17th moult of control prawns (Fig. 2). In the ablated series, the duration increased from 13 days to 21 days during the corresponding moults. This phenomenon suggests that the remaining

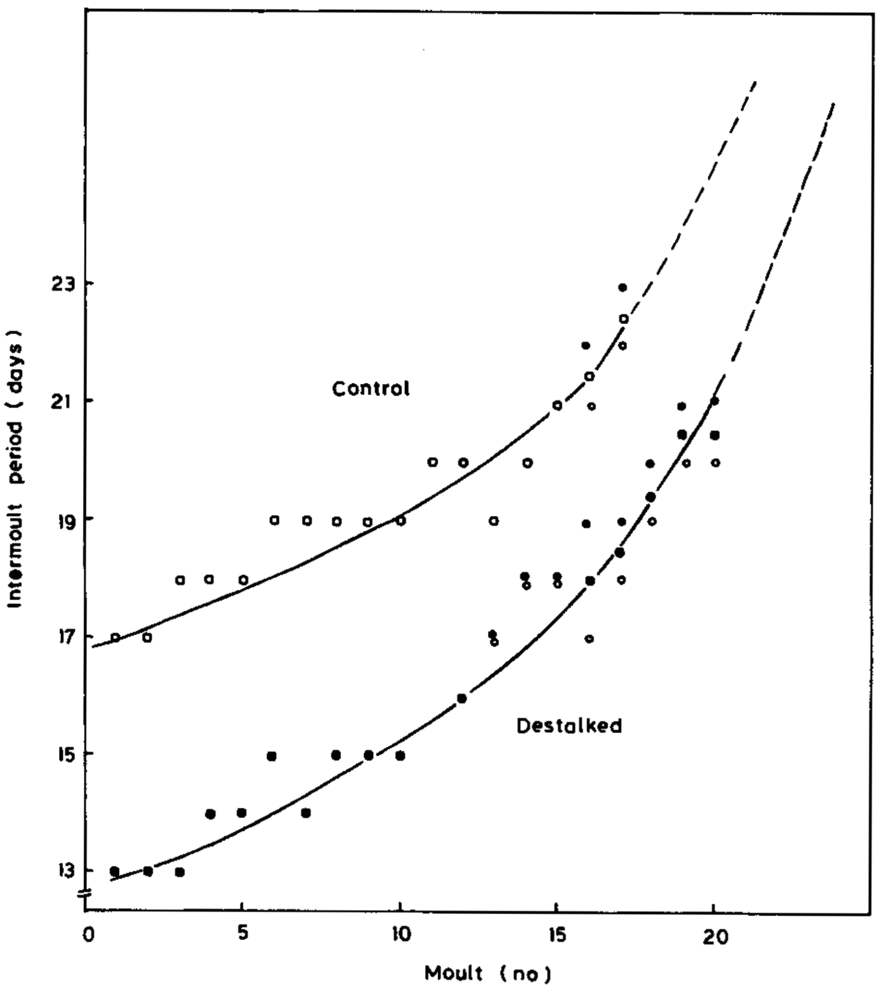

Fig. 2. Intermoult period as function of successive moults in control (open circles) and ablated (closed squares) *Macrobrachium nobilii*.

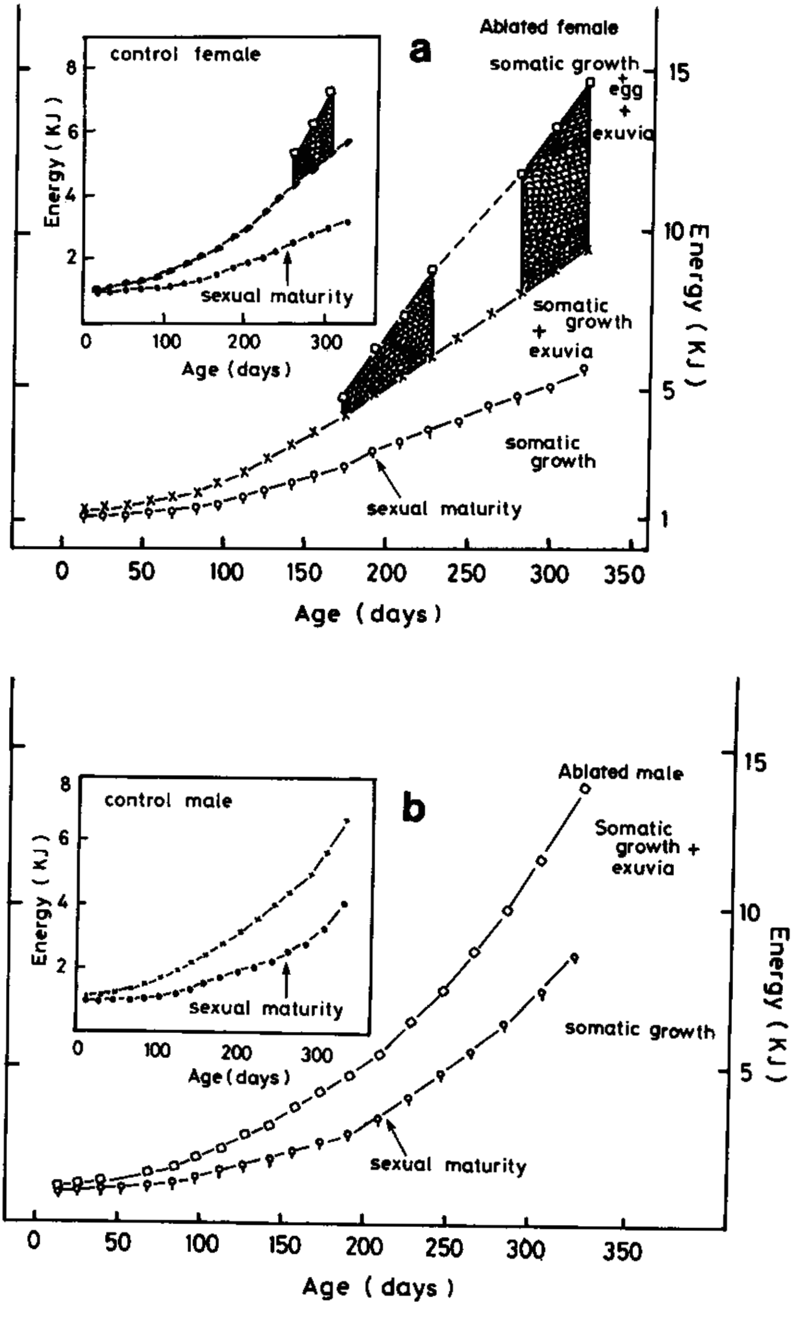

Fig. 3. Total and net somatic growth trends observed for female (Panel a) and male (Panel b) ablated *Macrobrachium nobilii*. Windows in the respective panels indicate the trends observed for control female and male *M. nobilii*.

eyestalk in ablated prawns may have been gradually compensating for the lost eyestalk.

Eyestalk ablation accelerated not only growth and moulting frequency but also the onset of sexual maturity. Sex became distinguishable in controls at the 14th moult on the 261st day of the experiment (Fig. 1). Of four adult moults undertaken by the female, three were berried. In the ablated series, sex became distinguishable at the 12th moult on the 173rd day, or 88 days earlier than the controls. Of nine adult moults undertaken by the series, seven were berried.

Food utilization

To acquire the extra energy for more frequent moulting and egg output ablated prawns may become hyperphagic and/or more efficient food converters. Table 1 shows that ablated *M. nobilii* adopted both strategies. In the control series, either sex consumed ≈ 54 kJ and assimilated ≈ 48.9 kJ of food. In the ablated series, male prawns consumed 83 kJ whereas the female prawns consumed 60 kJ. Conversion efficiency of control male and female *M. nobilii* was 11.5 and 13% while that of ablated prawn was 16 and 24%, respectively.

The difference in conversion efficiency between male and female prawns was due to the extra energy required for egg production (1.5 kJ in control and 5.3 kJ in ablated females, respectively).

The magnitude of hyperphagia and efficiency responses significantly ($P < 0.05$) differed between the sexes in the ablated series (Table 1). The ablated males consumed 1.5 times more (83 kJ) food and converted the food 1.4 times more efficiently (16%) than control males. Ablated females doubled their conversion efficiency (24%) but hyperphagia was not as pronounced (1.1 times more than the control) as in ablated males.

Although an ablated male appears to invest nearly 1.5 times (≈ 64 kJ) more energy on metabolism, than an ablated female, almost similar quantum of energy was invested on total growth, i.e., about 12 kJ by males and 13 kJ by females. Consequent to the increased frequency of moulting in the ablated series, prawns of either sex invested about 4 kJ on exuvia. An ablated female spawned eggs equivalent to 5.3 kJ and hence could allocate only about 4 kJ on net somatic growth, whereas the males allocated 7.6 kJ for the same. Since both the rate and efficiency of growth were significantly

Table 1. Energy budget of control (♂ and ♀) and ablated (♂ and ♀) *Macrobrachium nobilii* during the experimental period of 330 days. All values are given in kJ/prawn and efficiency in %.

Parameter	Control ♂	Control ♀	Ablated ♂	Ablated ♀
Consumption	54.7 ± 1.5	53.5 ± 1.0	83.0 ± 1.5	60.2 ± 1.3
Faeces	5.0 ± 0.3	4.9 ± 0.2	6.7 ± 0.9	4.8 ± 0.8
Absorption	49.7 ± 0.9	48.6 ± 1.2	76.3 ± 1.0	55.4 ± 0.6
Excretion	0.30 ± 0.05	0.29 ± 0.04	0.54 ± 0.05	0.4 ± 0.03
Assimilation	49.4 ± 1.0	48.3 ± 0.9	75.8 ± 1.0	55.0 ± 0.8
Metabolism	43.7 ± 0.8	42.0 ± 0.6	63.5 ± 1.0	41.6 ± 0.8
Growth	5.7 ± 0.28	6.3 ± 0.3	12.3 ± 0.3	13.4 ± 0.2
(a) Somatic growth	3.1 ± 0.1	+2.2 ± 0.1	7.6 ± 0.3	+4.2 ± 0.2
(b) Exuvium	2.6 ± 0.1	2.6 ± 0.2	4.7 ± 0.2	3.9 ± 0.1
(c) Egg	—	++1.5 ± 0.08	—	++5.3 ± 0.2
Absorption efficiency	91.0 ± 1.0	91.0 ± 1.0	92.0 ± 2.0	92.0 ± 1.0
Conversion efficiency	+++11.5 ± 3.0	13.0 ± 3.0	+++16.0 ± 3.0	24.0 ± 4.0

+Somatic growth : Control ♀ vs Ablated ♀ ($P < 0.0005$)
++Egg production : Control ♀ vs Ablated ♀ ($P < 0.0005$)
+++Conversion efficiency : Control ♂ vs Ablated ♂ ($P < 0.05$)

enhanced, unilateral ablation may save considerable time and feed cost of production of *Macrobrachium*.

Energy partitioning

For convenience, energy stored in the body is considered here as net somatic growth. Cumulative growth, i.e., the energy loss as exuvia at successive moults together with the net somatic growth is referred here as total somatic growth. Total growth in successive instars is the sum of somatic growth and reproductive output. Fig. 3 presents the trends obtained for the total growth of ablated and unablated female and male prawns. Energy accumulated during growth of control or destalked females is the same as that of the respective males. Hence, rearing males for meat production and females for egg production is almost equally advantageous.

Table 2 presents quantitative data obtained on energy allocated for somatic and reproductive growth, from which the following inferences are possible: (i) as the mid body weight during successive adult moults increases energy invested on growth and reproduction per intermoult period increases in both ablated and unablated prawns; (ii) considering only the first three adult intermoult periods when the mid body weight was more or less equal, ablated prawns invested significantly ($P < 0.05$) more energy both on growth (0.8 kJ) and egg production (2.0 kJ) than the controls (growth 0.6 kJ; reproduction 1.5 kJ). Thus independent of body weight eyestalk ablation promotes greater energy investment on growth and reproduction; (iii) investment on egg production per instar during successive adult intermoult periods was 2 to 3 times greater than that on net somatic growth in both ablated and nonablated prawns; for instance, during the third intermoult period, controls expended 190 J on net somatic growth and 520 J on egg production while the ablated prawns averaged 290 J and 702 J, respectively; (iv) during the experimental period ablated individuals undertook more (9) adult moults than the controls (4). Consequently, ablated adults were able to invest approximately 3.5 times more energy on somatic growth and egg production.

Data presented in Table 3 confirm the inferences drawn from Table 2. The ablated females of comparable body weight not only produced more eggs per clutch but also individually heavier eggs. On average, an ablated female produced 5,935 eggs, each containing 0.89 J in comparison to 2,042 eggs (0.7 J egg^{-1}) produced by controls.

Table 2. Energy allocation for somatic growth, exuvia production and egg production (J/moult) in control and ablated *Macrobrachium nobilii* after sexual maturity. Each value represents the average performance of not less than five animals.

Mid body weight during successive intermoult period (mg)		Total growth		Somatic growth		Exuvia production		Egg production	
Control	Ablated	Control	Ablated	Control	Ablated	Control	Ablated	Control	Ablated
*642 ± 20	*639 ± 30	920 ± 30	1,083 ± 28	235 ± 18	223 ± 20	217 ± 16	210 ± 18	468 ± 18	650 ± 20
*696 ± 24	*699 ± 35	949 ± 25	1,174 ± 24	219 ± 17	268 ± 18	236 ± 18	230 ± 21	494 ± 20	676 ± 36
*743 ± 20	*764 ± 44	953 ± 32	1,235 ± 30	190 ± 20	290 ± 27	243 ± 19	243 ± 27	520 ± 24	702 ± 28
●788 ± 26	*830 ± 33	456 ± 29	1,271 ± 40	182 ± 15	295 ± 16	274 ± 18	261 ± 16	—	715 ± 40
	●920 ± 35	—	689 ± 35	—	402 ± 24	—	287 ± 11	—	—
	●1,015 ± 40	—	731 ± 26	—	425 ± 19	—	306 ± 12	—	—
	*1,095 ± 38	—	1,482 ± 31	—	357 ± 21	—	319 ± 13	—	806 ± 29
	*1,170 ± 27	—	1,495 ± 33	—	335 ± 20	—	325 ± 10	—	835 ± 28
	*1,250 ± 39	—	1,563 ± 34	—	358 ± 23	—	330 ± 12	—	875 ± 23
	Total	3,278	10,723	826	2,953	970	2,511	1,482	5,259
Mean/instar	$\overline{X}$	820	1,191	207	328	243	279	494	751
	±	242	316	25	65	24	45	21	87

* Berried moult ● Neuter moult

Table 3. Egg production and egg size of control and ablated *Macrobrachium nobilii* reared for a period of 330 days.

Moult no. and mid body wt. (mg) after sexual maturity Control	 Ablated	Eggs (No./clutch) Control	 Ablated	Dry wt. of eggs (mg/clutch) Control	 Ablated	Energy content of an egg (J) Control	 Ablated
*642 ± 20	*639 ± 30	648 ± 16	750 ± 20	18 ± 6	25.4 ± 6	0.72 ± 0.008	0.88 ± 0.008
*696 ± 24	*699 ± 35	684 ± 24	768 ± 18	19 ± 5	26.0 ± 7	0.72 ± 0.009	0.88 ± 0.009
*743 ± 20	*764 ± 44	710 ± 22	789 ± 22	20 ± 7	27.0 ± 8	0.73 ± 0.009	0.89 ± 0.009
•788 ± 26	*830 ± 33	—	803 ± 20	—	27.5 ± 8	—	0.89 ± 0.008
	•920 ± 35	—	—	—	—	—	—
	•1,015 ± 40	—	—	—	—	—	—
	*1,095 ± 38	—	905 ± 24	—	30.9 ± 6	—	0.89 ± 0.001
	*1,170 ± 27	—	938 ± 27	—	32.1 ± 4	—	0.89 ± 0.005
	*1,250 ± 39	—	982 ± 20	—	33.6 ± 5	—	0.89 ± 0.004
	Total	2,042	5,935	57	202.5		
	Mean/instar $\overline{X}$	681	**848	19	***28.9	0.72 ± 0.004**	0.89 ± 0.003
	±	25	92	0.82	3.2		

* Berried moult
• Neuter moult

** $P < 0.01$ Statistically significant
*** $P < 0.001$ Statistically highly significant

Discussion

The present study documents for the first time: (i) the events of moulting and growth as well as maturation and spawning of control and unilaterally eyestalk - ablated *Macrobrachium nobilii* reared for a long term (330 days) from sexually immature to adult; (ii) quantification of the energy income and expenditure of unablated and ablated *M. nobilii.*

Both control and ablated prawns became sexually mature at ≈ 600 mg in weight, i.e., sexual maturation is size-dependent rather than age-dependent in *M. nobilii.* Similar observations have been reported for *Panulirus argus* (70 mm carapace length; Quackenbush and Herrnkind 1981) and for *Penaeus monodon* (32 g weight; Poernomo and Hamami 1983). These observations suggest that the attainment of a critical minimum size or accumulation of a definite quantum of energy is associated with the onset of sexual maturity.

In *M. nobilii* somatic growth in males was comparatively higher than that of females in either series. Studies conducted on *Homarus americanus* (Ennis 1972) and *Cancer pagurus* (Bennett 1974) point out that moult increments (increase in size which occurs between one instar and the next) were smaller in females than in males. This is because reproduction is likely to require a large proportion of the available resources in females (Hartnoll 1982). In other words, reproduction is the dominant energy demanding process in adult females.

The increase in number of clutches and eggs per clutch in ablated *M. nobilii* is in accordance with the results obtained for other decapods as well. Wear and Santiago (1976) and Santiago (1977) obtained an average of 202,000 eggs by unilateral eyestalk ablation of *P. monodon.* In an identical experiment by AQUACOP (1977) an average of 180,000 eggs were obtained. Deterioration in spawn quality was reported for *P. indicus* (Emmerson 1980) and for *P. monodon* (Beard and Wickins 1980; Emmerson 1983). Browdy and Samocha (1985) described that unilateral eyestalk ablation of *P. semisulcatus* did not affect the spawn quality; they also pointed out that the declining quality of eggs demonstrated by other authors may not be a direct result of eyestalk ablation but rather an indirect effect of a worsening in condition of animals over time; the imbalance in the hormonal control of the maturation cycle due to inducement might have also caused the production of poor quality eggs.

In *M. nobilii* reared from the juvenile stage, early onset of sexual maturity and declining levels of the moult inhibiting hormone (MIH) and gonad inhibiting hormone (GIH) (Kulkarni and Nagabhushanam 1980) might have produced conducive conditions for the actions of the moulting hormone (MH) and gonad stimulating hormone (produced elsewhere). Moreover, as suggested by Anilkumar and Adiyodi (1985), if the eyestalk is the source of an oviposition-inducing hormone (OIH), unilaterally eyestalk-ablated prawns with an eyestalk intact would not suffer total loss of this hormone as opposed to the case in bilaterally eyestalk-ablated individuals.

Ablated female *M. nobilii* consumed 1.1 times more food than the control females. However, food conversion efficiency by the former was about twice ($P < 0.05$) that in the latter. Ponnuchamy et al. (1981) reported 7.5, 11 and 25% conversion efficiency, respectively, for control, unilaterally and bilaterally eyestalk-ablated *Macrobrachium lanchesteri.* Radhakrishnan and Vijayakumaran (1984a) observed that food consumption of ablated lobsters *(Panulirus homarus)* was almost twice that of controls and food conversion efficiency more than double. Though energy was invested for net somatic growth (control 25%, ablated 28%) and egg production (control 45%, ablated 49%) the emphasis was on the latter.

Despite the small size of *M. nobilii,* culture of this species can be encouraged because of its high value, simplicity of culture and contribution to rural nutrition. Like the widely cultured *M. rosenbergii, M. nobilii* possesses a number of desirable qualities to be recommended as a culture species. These include the ability to mature and reproduce in captivity, high growth and survival rates and consumer acceptability. However, the difference in growth between sexes demands monosex culture of these species to avoid size hierarchy. Also stocking density, diet, effects of environmental parameters, etc. need to be determined. Hybridization of *M. nobilii* with other desirable species may be a promising endeavor.

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