PHYSIOLOGICAL AND BIOCHEMICAL STUDIES ON THE SPINY LOBSTER *PANULIRUS HOMARUS*

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of
Doctor of Philosophy

by

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DECLARATION

I hereby declare that this work has been originally carried out by me under the guidance and supervision of **DR. E. VIVEKANANDAN**, Scientist, Madras Research Centre of Central Marine Fisheries Research Institute, Madras - 600 105 and that this work has not been submitted elsewhere for any other degree.

Madras - 105
1-02-1989

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CERTIFICATE

This is to certify that this thesis entitled **'Physiological and biochemical studies on the spiny lobster Panulirus homarus'** submitted by Mr. E.V. Radhakrishnan, M.Sc., for the degree of Doctor of Philosophy in Zoology to the University of Madras, is based on the results of the experiments and investigations carried out independently by him under my guidance and supervision since April, 1983 till todate. The thesis or any part thereof has not previously formed the basis for the award of any degree, diploma, associateship or fellowship.

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Physiological and biochemical studies on the spiny lobster Panulirus homarus

1 INTRODUCTION

For more than 100 years, lobsters have been the subject of extensive research. Aiken (1980) estimated that more than 1000 research papers have probed the details of lobster biology during the current century. Interest in the fundamental and the applied biology of the lobsters has been growing steadily, not only because of the commercial importance of the group, but also because the lobsters are an excellent group for physiological and biochemical research. Economic, rather than practical scientific considerations have been tempered during the past 20 years, because the need has been for rapid empirical development of aquaculture system for the lobsters. Most of these studies, therefore, have concentrated on the physiological and biochemical processes that govern growth. Inspite of this, there are significant gaps in the study of the growth governing factors and the published information is incomplete, contradictory in many respects and biased on one or two species.

The growth process basically represents a balance between wear and deterioration on one hand and repair and regeneration on the other, a process that leads to increase in body size. For animals with exoskeleton, growth basically involves moulting. Moulting is a process which dominates the crustacean's life and hence, few aspects of crustacean

physiology are as important as moulting. Feeding, metabolism and reproduction are affected directly or indirectly by the periodic replacement of the integument and the underlying cycle of metabolite accumulation (Passano, 1960).

Drach (1939) recognised morphological, physiological and culticular changes associated with moulting in the crustaceans and divided the moult cycle into 4 basic periods, 5 major stages and several substages. This basic system was accepted with modifications for a variety of crustaceans including the lobsters. The morphological and biochemical changes occurring during moult cycle have been studied in detail in the homarid lobsters, especially in the American lobster, **Homarus americanus**. (for e.g., Donahue, 1954; Aiken, 1973; Gilgan and Zinck, 1975). During the moult cycle, pronounced biochemical changes have been observed to occur in **Homarus** (Heath and Barnes, 1970). In the palinurid lobsters, the moult cycle was classified in **Panulirus japonicus** (Schwabe et al., 1952), **P.homarus** (Berry, 1971) and **P. marginatus** (Lyle and Mac Donald, 1983) based on the original classification of Drach. However, information available on the biochemical changes accompanying moulting is meagre in the palinurid lobsters (Scheer and Scheer, 1951; Schwabe et al., 1952; Travis, 1955 a,b, 1957; Dall, 1977).

The moult cycle is believed to be regulated by the interaction of two hormonal factors; the Moult Inhibiting Hormone (MIH), from an eyestalk neurosecretory complex, called the X-organ (Bliss, 1951; Passano, 1951) and Moulting Hormone, from a non-neural endocrine gland called Y-organ (Gabe, 1953, 1954; Echalier, 1955, 1959). The relationship between eyestalk removal (removal of MIH) and accelerated moulting in decapods was established many years back (Abramovitz and Abramovitz, 1940; Smith, 1940; Scudamore, 1947; Bauchau, 1948; Passano, 1953). However, there have been occasional conflicting reports concerning effect of eyestalk removal on moulting in different species of lobsters (Sochasky, 1973). For instance, Donahue (1951, 1955) and Flint (1972) provided data showing that eyestalk removal delayed moulting in **H. americanus**. The information on the effect of eyestalk removal in the palinurid lobsters is also controversial. Travis (1951, 1954) and Dall (1977) reported that eyestalk ablation was ineffective in **P. argus** and **P. cygnus**. Aiken (1980) concluded that eyestalk ablation did not accelerate moulting in the palinurid lobsters. However, later studies by Quackenbush and Herrnkind (1981) and Radhakrishnan and Vijayakumaran (1982, 1984, 1987a) evidenced remarkable acceleration of moulting frequency in the eyestalk ablated **P. argus**, **P. homarus** and **P. ornatus**. Sochasky et.al (1973) pointed out that many

factors like sex, maturity, moult stage, food and social behaviour of the lobsters can affect the response of a lobster to eyestalk removal.

Any factor that affects the moulting process is bound to affect the growth process directly or indirectly. Food is one of the most important factors that influence moulting as well as growth. Attempts to define the role of food on moulting and growth were initiated only in the early '70s (Conklin, 1980), in response to the anticipated needs of commercial lobster aquaculture. Subsequently, it was evidenced in the homarid (Castell and Budson, 1974) and in the palinurid (Chittleborough, 1974) lobsters that food influenced the moulting frequency and growth rate. However, the observations made on the food consumed were rarely quantitative and there are few data on the chemical composition of the food (Marshall and Orr, 1955). Quantification of food and knowledge of chemical composition of the consumed food provide insight into identifying the optimum quantity of the specific food that promotes maximum growth of the lobsters.

Quantity of food consumption of a predator like the lobster is directly dependent upon the size of the available prey and the feeding strategy adopted by the predator to counter the prey. Depending upon the number, size and nature

of prey, the predator decides what and how to predate (Hughes, 1980). Hence, it is imperative to study the foraging strategy to quantify the minimum, optimum and maximum size of the prey that could be foraged by a predator. Most of the studies related to foraging strategy of the crustaceans are on the crabs (for e.g., Elner and Jamieson, 1979; Du Preez, 1984) and on the American lobster, **H. americanus** (Evans and Mann, 1977; Elner and Campbell, 1981; Elner, 1982), which possess strong chelae to crush the shells of the molluscan prey. The palinurid lobsters do not have powerful chelae but have to depend upon mandible for crushing the hard-shelled molluscs. Surprisingly, the hard-shelled molluscs form the most preferred natural food of the palinurid lobsters (Berry, 1971; Smale, 1978) and hence, the palinurids may have to adopt a definite strategy to break the shell of the molluscan prey. There is only limited information on the feeding strategy of the palinurid lobsters (**Jasus lalandii** : Pollock, 1979; Griffiths and Seiderer, 1980).

Most studies on moulting, food consumption and growth of the American lobster, **H. americanus** and its European counterpart, **H. gammarus** were conducted with an objective to provide clues for culture of these lobsters. However, any attempt on commercial culture of the homarid lobsters has not proved successful due to the following reasons : i) very

aggressive and cannibalistic behaviour when reared in groups; and ii) very slow growth in temperate conditions. The high mortality due to cannibalism and the prolonged culture exercise of nearly 8 years to attain commercial size (Hughes et.al., 1972) have led to the conclusion that culturing the homarid lobsters may not be possible for the present. Barring a few pilot scale operations, presently there are no commercially viable lobster farming operations anywhere in the world (Van Olst et.al., 1980). Contrary to the homarid lobsters, the spiny lobsters have several characteristics that make them attractive for commercial cultivation. (Radhakrishnan and Vijayakumaran, 1987b). Even under conditions of high density and crowding, there is little aggression and cannibalism (Chittleborough, 1974; Phillips et.al., 1977). The growth rate is also considerably fast under tropical conditions (Mohammed and George, 1968; Tamm, 1980). Radhakrishnan and Vijayakumaran (1982) established, for the first time, that the growth rate of the spiny lobster, **P. homarus** could be accelerated 3 to 7 times by bilateral eyestalk ablation, leading to attainment of harvestable size (200 g) from juvenile stage (50 g) in 3 months. Later, Silas et.al. (1984) also reported enormous weight increase in 3 other spiny lobsters, viz., **P. polyphagus, P. ornatus** and **P.versicolor** by bilateral eyestalk ablation. High expectations not withstanding, spiny

lobster culture is in its infancy and much basic research is still required.

Crucial to optimisation of growth is an understanding of the energetics where, the fate of food consumed is quantified in terms of caloric equivalents. The bioenergetics and growth of an organism can be defined through construction of an energy budget. The energy value of the food consumed (C) is lost through unassimilable material (faeces, F), nitrogenous waste products (U) and the energy demands of metabolism (R) and the net energy gain is channelled into growth (P) (Warren and Davis, 1967). In crustaceans, energy loss associated with moulting (E) is also considered. Studies on the energetics of the lobsters, however, have been restricted to one or two parameters of the energy budget. For instance, Van Olst et.al. (1976), Felix (1978), Bartley (1980), Bartley et.al. (1980) and Bordner and Conklin (1981) studied the food consumption and/or growth in **H. americanus**; Capuzzo and Lancaster (1979) studied the utilization of biochemical components of the food by **H.americanus** . Dall (1974) studied the indices of nutritional state in the western rock lobster, **P. longipes**. Winget (1969) and Kasim (1986) estimated the oxygen consumption of **P.interruptus** and **P. polyphagus**, respectively. Information available on the complete energy budget is meagre (Logan and Epifanio, 1978;

Zoutendyk, 1979). Estimation of all the major components of energetics is necessary not only for application in culture practices but also to fully understand the physiological status of the animal. Reviewing the crustacean energetics, Vernberg (1987) also stressed the need for estimating the complete energy budget.

In the present study on the spiny lobster, **P.homarus**, the bioenergetic components, viz., food consumption (C), egestion (F+U) and growth (P) of the lobster were determined; metabolism was the only component that was not determined, but was calculated. Earlier estimations on lobster metabolism were based on oxygen consumption of the animal for a short duration of a few hours (Winget, 1969; Kasim, 1986). Estimation of metabolism through long term experiment is considered advantageous than estimating oxygen consumption for a short duration. Kinne (1960) considered feeding rate and conversion efficiency estimates as better parameters for assessing metabolic rates and efficiencies, as they provide i) the less restricted maintenance conditions during feeding experiments, ii) the possibility of observing one and the same individual over a long period of time, iii) the possibility of measuring the effects of quantitative and qualitative feeding on metabolism (Paloheimo and Dickie, 1966a,b) and iv) the possibility of measuring the total

metabolism including the energy expended on part or total anaerobiosis.

The experiments conducted in the present study on **P.homarus** may be categorised into the following major heads : i) brief classification of different moult stages in a moult cycle with an objective to correlate changes in the biochemical constituents during the moult stages; ii) study on the feeding strategy of **P. homarus** by offering different size groups of the mussel, **Perna viridis** to different size classes of the lobster; iii) effects of isolation, eyestalk ablation and quality of food on the energetics and iv) effects of eyestalk ablation and quantity of food on the energetics of the lobster.

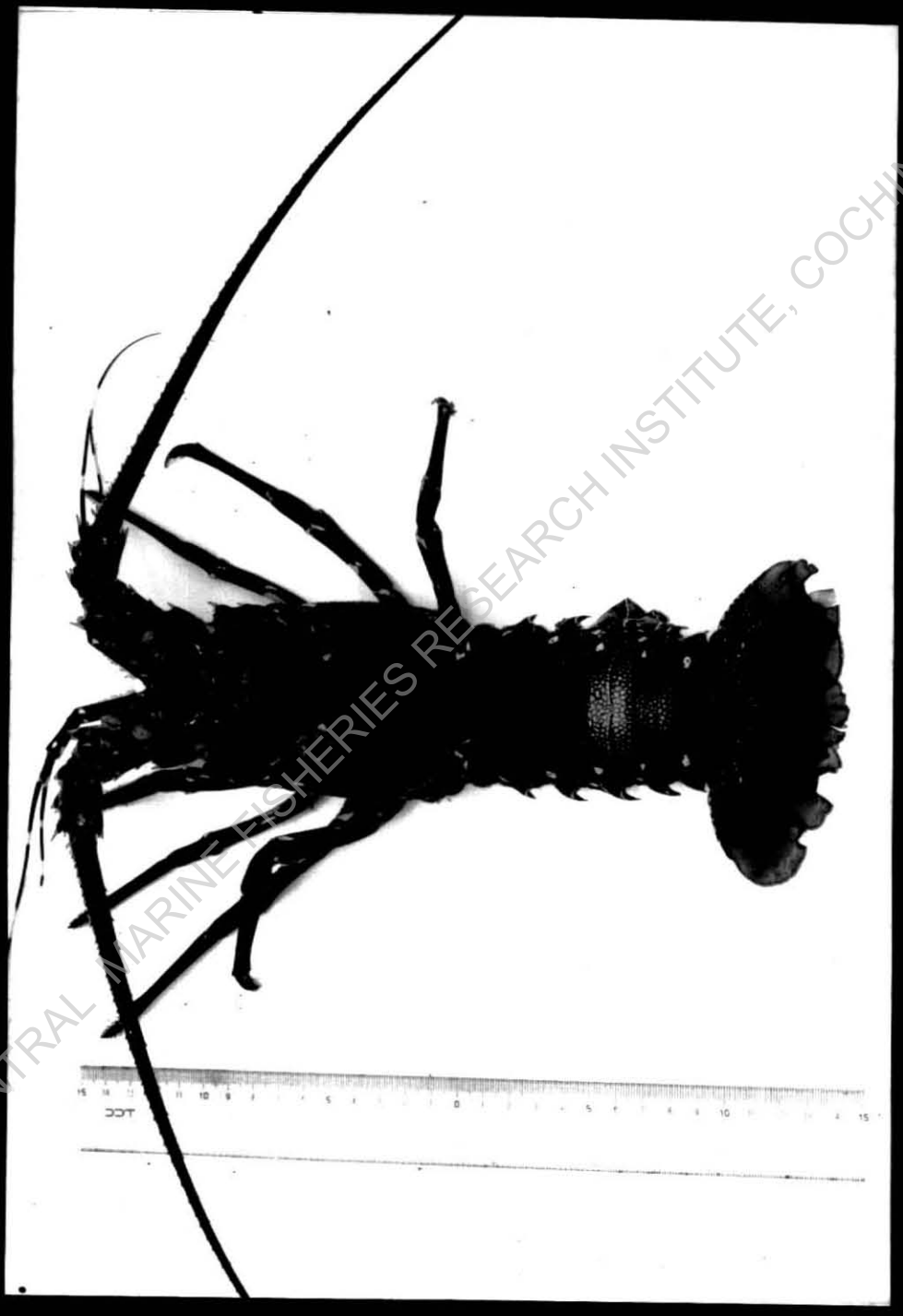
2. MATERIALS AND METHODS

The spiny lobster **P. homarus** (Plate 2.1) forms seasonal fishery off Kovalam, a fishing village, 25 km south of Madras. The lobsters were purchased from local fishermen and were maintained in the laboratory in fibreglass aquaria (200 x 100 x 40 cm) containing 800 litres of filtered seawater. The lobsters were fed with freshly opened clam, **Meretrix casta.** The aquarium water was replaced by fresh seawater every day. Aeration was provided by an air compressor. The animals were exposed to natural photoperiodicity prevalent in the laboratory. The salinity (Strickland and Parsons, 1965), pH and oxygen (modified Winkler method) in the aquaria were monitored fortnightly. The lobsters used for all the experiments in the present study were from this common rearing aquaria. The size of the lobsters and condition of each experiment are described in the respective chapters.

2.1 Measurement of length and weight

The carapace length (the distance along the dorsal midline from the transverse ridge between the supraorbital horns to the posterior extremity of the cephalothorax; Berry, 1971) of the lobster was measured to the nearest mm by using vernier caliper.

Plate 2.1. Dorsal view of the spiny lobster, **P.homarus**



All weighings on total weight, tail weight (whole abdomen) and meat weight (tail weight-tail exoskeleton weight) were made in a top pan balance to an accuracy of 0.1g.

2.2. Eyestalk ablation

Eyestalks of the test lobsters were ablated by removing both the eyestalks at the base using a 0.5 mm nylon thread. The nylon thread was placed around the base of the eyestalk in a loop and the eyestalk was cut by pulling both the ends of the thread. The wound was closed by keeping the finger pressed on it for a minute. To minimise the stress, one eyestalk was ablated on a day and the other was removed on the following day. At no instance the wound got infected. No mortality of lobsters occurred due to the ablation stress. Electric cauterizer was not used for ablating the eyestalks as the supraorbital horns obstructed the operation.

2.3 Estimation of water, ash and chitin contents

The water content of the whole lobster, abdominal muscle and the food was determined by drying the material in an hot air-oven at 90°C for 24 hr. The water content of the midgut gland (also called hepatopancreas or digestive gland) was determined by sacrificing the lobster in a deep freezer for 10 min; the midgut gland was dissected out and the wet weight was determined by weighing in a monopan electric

balance to an accuracy of 0.1 mg. A sample of the tissue was then dried in an hot air-oven at 90°C for 24 hr.

The ash content of the whole lobster and food was determined by burning the dry samples in a muffle furnace at 550-600°C for 8 hr. The ash content of the abdominal muscle and midgut gland was calculated by subtracting the total dry weight of lipid, carbohydrate and protein from the total dry weight of the respective tissue.

The chitin content of the whole lobster was calculated by subtracting the total dry weight of lipid, carbohydrate, protein and ash from the total dry weight of the lobster.

2.4 Biochemical estimations and calorimetry

Estimations on biochemical components, viz., lipid, carbohydrate and protein were made on the whole lobster, midgut gland, abdominal muscle and the food materials. For estimations, the whole lobster, midgut gland, muscle and the food were dried at 55°C for 4 days. Protein (Biuret method), carbohydrate (Phenol - Sulphuric acid method) and lipid (Chloroform-Methanol method) were estimated following Raymont et.al. (1964).

For estimation of calorific values, dried samples of the whole lobster, muscle, exuvia, faeces and food were

separately ground into fine powder and stored in a desiccator. Midgut gland was stored in the desiccator without grinding. The calorific estimations were made using a Parr semi-micro bomb calorimeter (No.1200). For every 10-12 estimations, the bomb was standardised using a pellet of benzoic acid. In a few estimations, especially the faeces, the sample was not completely oxidized due to adhering sand particles; the values obtained in these estimations were discarded.

2.5 Estimation of food utilization parameters

The scheme of energy balance followed in the present study is that of the IBP formula (Petrusewicz and Macfadyen, 1970) and is represented as,

$$C = (P + E) + R + F + U$$

where C is the food consumed, P, the growth, E, the exuvia, R, the material lost as heat due to metabolism, F, the faeces and U, the nitrogenous excretory products.

2.5.1 Estimation of C

In all the experiments on the effects of quality and quantity of food on food utilization, **P. homarus** was offered food at 1600 hours and the unconsumed food was removed at 0900 hours on the following morning, i.e. the lobster was

exposed to the food for 17 hr. The unconsumed food was siphoned carefully into a filter, washed with distilled water, dried at 90°C for 24 hr and weighed. To estimate the dry weight of the food consumed, a sample of food was dried every day; the dry weight of the unconsumed food was subtracted from the dry weight of food offered. Calorific equivalents of C were made by substituting the energy value (joules, J) of the food to the dry weight.

2.5.2 Estimation of F

The faeces of **P. homarus** is in the form of ribbon and settles easily at the bottom of the aquarium. The faeces was collected 2 days in a week by siphoning into a bolting silk filter, washed with distilled water, dried in an hot air-oven at 90°C for 24 hr and weighed in a monopan balance to an accuracy of 0.1 mg. The total faeces production by each lobster in an experiment was calculated by raising the faecal production on the days of faeces collection to the entire experimental duration.

2.5.3 Estimation of U

Ammonia forms more than 80% of the total nitrogenous excretory production in the lobsters (Pandian, 1975). Ammonia excreted by **P. homarus** was estimated at biweekly interval following Phenolhypochlorite method of Solorzano

(1969). For determining the quantity of ammonia excreted, the lobsters, immediately after feeding were transferred from the experimental aquaria to separate containers with fresh filtered seawater. The initial quantity of ammonia dissolved in water was estimated before transferring the lobsters. The ammonia content of the water was again estimated 12 and 24 hr after transfer of the animals. After 24 hr, the lobsters were released back to the experimental aquaria. From this, ammonia excreted during the 24 hr duration was determined. Estimations thus made at biweekly interval were subsequently raised to the entire experimental duration. The reason for estimating ammonia excretion by keeping the lobsters in separate containers was to avoid interference by the ammonia released by the food in the experimental aquaria and also to avoid the effect of aeration on ammonia. To estimate the energy excreted as ammonia, the energy equivalent of 20.5 J for 1 mg of ammonia (Brafield, 1985) was used.

2.5.4 Estimation of P

The term conversion has been used to refer growth, i.e. the P of the IBP terminology. Before commencement of the experiment, the test individuals were starved for 24 hr in order to empty the alimentary canal. Subsequently, wet (live) weight of the individuals was determined at the beginning of each experiment. To estimate the initial dry

weight of the test individuals, 'Sacrifice method' (Maynard and Loosli, 1962) was adopted. A group of at least 5 sample individuals of similar body weight and experimental state served as control to determine the initial water and energy contents. These sample individuals were sacrificed and dried in an hot air-oven at 55°C until weight constancy was attained. Water and energy contents of the control individuals represented those of the test individuals at the commencement of the experiment. The P was calculated by subtracting the dry weight/energy content of the individual at the commencement of the experiment from the final dry weight/energy content of the individual at the end of the experiment.

Since exuvia (E) forms part of converted energy in the crustaceans, the energy lost through exuvia is considered as part of conversion in the present study.

2.5.5 Estimation of R

As the C, F, U and P were estimated, metabolism (R = respiration) was calculated.

Rates of feeding, assimilation and conversion were calculated to the respective quantity (mg dry weight or Joules) of food consumed, assimilated and converted relating to live mid-weight (g) of the lobster per unit time (day).

Mid-weight is the mid-point between the initial and final weight of the lobster during the experiment. Efficiencies of assimilation and net conversion efficiency (K_2) were calculated in percentage relating Ae to C and P to Ae, respectively.

2.5.6 Calculation procedure related to food utilization

$$\text{Feeding rate} = \frac{\text{Food consumed (C)}}{\text{Mid-body weight of the lobster (g) X day}}$$

$$\text{Assimilation rate} = \frac{\text{Food assimilated (Ae)}^{*}}{\text{Mid-body weight of the lobster (g) X day}}$$

* estimated subtracting faeces (F) and urine (U) from food consumed (C), i.e. Ae = C - (F + U)

$$\text{Conversion rate} = \frac{\text{Food converted (P+E)}}{\text{Mid-body weight of the lobster (g) X day}}$$

Metabolic rate = Assimilation rate - Conversion rate

$$\text{Metabolic rate}^{**} \text{ (ml } O_2\text{/g/hr)} = \frac{\text{Metabolic rate (mg/g live mid-body wt/day)}}{20.098 \text{ X } 24}$$

** estimated considering 20.098 J as the oxycalorific

equivalent of 1 ml of O_2 consumed (Engelman, 1966).

$$\text{Assimilation efficiency} = \frac{\text{Food assimilated}}{\text{Food consumed}} \times 100$$

$$\text{Net conversion efficiency } K_2 = \frac{\text{Food converted}}{\text{Food assimilated}} \times 100$$

$$\text{Protein efficiency ratio (P E R)} = \frac{\text{Live weight gain(g)}}{\text{Dry weight(g) of protein consumed}}$$

2.6 Statistical analysis

All statistical tests such as mean, standard deviation, test of significance (student's 't' test), ANOVA, correlation coefficient and regression were made following Snedecor and Cochran (1967).

3. MOULT STAGES AND BIOCHEMICAL CHANGES DURING MOULT CYCLE

3.1 Introduction

Much of a lobster's life is spent either preparing for the ensuing moult or recovering from the preceding moult. The time between the moults may be divided into several stages that are identifiable morphologically and physiologically. Though a number of techniques have been described for determining the various stages of the moult cycle in crustaceans (Drach, 1939; Charniaux-Legrand, 1952; Skinner, 1958; Scheer, 1960; Kurup, 1964; Drach and Tchernigovtzeff, 1967; Nagabhushanam and Rao, 1967; Kamiguchi, 1968; Stevenson, 1968; Aiken, 1973; Reaka, 1975; Hopkins, 1977; Peebles, 1977; Vigh and Fingerman, 1985), the most convenient and reliable technique was proved to be microscopic observations on the setal development in pleopods or uropods. Using this method, Drach (1939) first classified the brachyuran moult cycle and later Drach and Tchernigovtzeff (1967) redefined and modified the scheme. However, due to non-existence of uniformity in the moulting pattern of different crustaceans, a general classification may not be possible. In many instances, crustacean workers have found it useful to modify the original criteria in order to stage accurately a particular species (Stevenson et.al., 1968). For the spiny lobster **P. homarus**, Berry (1971)

broadly divided the moult cycle into four macroscopically distinguishable stages by following the changes in the external characteristics of the integument. But a higher degree of resolution usually is afforded by observing diagnostic microscopic changes which are representative of a particular moult stage (Lyle and MacDonald, 1983). In the present study, an attempt has been made to precisely classify the moult cycle of **P. homarus** into distinct stages by i) microscopically observing the setal development in the pleopods and ii) by following the morphological changes in the external characters such as relative rigidity of the carapace and appearance of decalcified ecdysial line in the branchiostegite area.

Most studies on moult cycle and duration of each moult stage are on the American lobster, **H. americanus** (for e.g., Aiken, 1980). Though the pattern of moulting is unique in all species of lobsters, the intermoult duration and the proporation of time spent in each stage of moult cycle is variable. In **H.americanus**, for instance, the final preparation for ecdysis alone spans several weeks and the intermoult duration varies from 15-600 days depending upon the age and condition of the lobster (Mauchline, 1977). On the contrary, the information on the tropical palinurid lobsters is scanty and the available information suggests that the palinurids moult frequently and complete one moult

cycle in 36-107 days depending upon the age (Berry, 1971). As information on the duration of each moult stage is not available on the tropical palinurid lobsters, the time spent in each moult stage by the spiny lobster **P. homarus** was determined in the present study.

The morphological changes in the moult cycle is accompanied by biochemical changes in various tissues of lobsters (Schwabe et.al., 1952; Travis, 1955a,b; Dall, 1977). Generally, the major biochemical constituents viz., lipid, carbohydrate and protein are accumulated during intermoult and premoult stages for subsequent utilization during ecdysis (Drach, 1939; Waterman, 1960; Andrews, 1967; O'Connor and Gilbert, 1968; Spindler-Barth, 1976). There are contradictory views on the importance and contribution of each of the biochemical constituents for ecdysis. For instance, Scheer and Scheer (1951) and Scheer et.al. (1952) reported protein as the primary energy source in the palinurids **P.penicillatus** and **P. japonicus**, rather than carbohydrate and fat. However, many later workers on the homarid lobsters concluded lipid and glycogen as the major organic reserves for utilization during ecdysis (Passano, 1960; Vonk, 1960; Barclay et.al. 1983; Chang and O' Connor, 1983). Due to inadequate data on the palinurid lobsters, it is not clear whether the frequently moulting palinurids adopt differential criteria in

the utilization pattern of biochemical constitutents for ecdysis. In the present study, the changes in the major biochemical constituents, namely, lipid, carbohydrate and protein and changes in water and energy contents during different stages of the moult cycle in the midgut gland and the abdominal muscle of **P. homarus** have been determined to understand i) the accumulation and utilization of these organic reserves in different stages of the moult cycle and ii) the relative contribution of these biochemical constituents for ecdysis.

3.2 Materials and methods

3.2.1 Observations on moult cycle

Six **P. homarus** (carapace length : 45-50 mm) in intermoult stage, 3 in each sex were reared in 2 fibreglass aquaria (size : 90 x 60 cm; volume of water: 200 l) and fed on the freshly opened clam, **Meretrix casta** daily. Once a week, the distal half of a single pleopod of all the lobsters was excised, mounted in water on glass slides, covered with a cover-slip and examined with a compound microscope and transmitted light at 40 x. Totally 8 pleopods were available for examination in each lobster and this was sufficient for observation of one moult cycle. External characteristics such as shell hardness and morphological changes were recorded at 2 day interval during late premoult and early

postmoult. Ecdysis was recorded as and when it occurred. The classification suggested in this study is the basis for moult stage based estimations on biochemical constituents in the ensuing experiment.

3.2.2 Biochemical estimations

All biochemical estimations were carried out on freshly caught male lobsters (carapace length: 45-50 mm) from the sea off Kovalam, near Madras. In order to avoid any probable seasonal variation in the biochemical components, analyses were conducted on lobsters collected between February and April, when the lobster fishery was maximum at Kovalam. The lobsters for biochemical analyses were selected from 5 moult stages, namely, A - early postmoult; B - late postmoult; C - intermoult; D_0 - early premoult and D_4 - late premoult. Estimations on each moult stage were carried out on 4 lobsters. The quantitative estimations on water, ash, lipid, carbohydrate, protein and energy were made on dry tissues of the midgut gland and abdominal muscle following standard procedures mentioned in sections 2.3 and 2.4.

As the lobsters used for the estimations were collected from the wild, there was no uniformity in the size (CL: 45-50 mm) of the lobsters representing different moult stages. Renaud (1949), Ansell and Trevallion (1967) and Dare and Edward (1975) have pointed out the limitations of

presenting variations in biochemical components as percentage values and have stressed the importance of expressing the data in terms of absolute weight. In the present study, the values on all the components have been expressed as absolute values. For this expression, the weight of the individual component was calculated by considering the weight of the lobster in stage D_4 as 100 g. The change in weight of the lobster during each stage of the moult cycle was subsequently calculated by using the values reported by Vijayakumaran and Radhakrishnan (1987a), who followed the change in weight of **P.homarus** during each moult stage in the laboratory.

3.3 Results

3.3.1 Classification of moult cycle

P. homarus completed one moult cycle (from ecdysis to ecdysis) in 51.7 days. The morphological changes of developing setae in the pleopods and the time spent in each stage of the moult cycle are summarized in Table 3.1.

Stage A or early postmoult

Stage A commenced as soon as ecdysis was complete; entire body soft; pleopod setal lumen wide and filled with granular matrix; lasted for 21-22 hr.

Table 3.1 Classification of moult stage of P. homarus

Moult stage	Morphological changes	Time spent (days)	(%)
A (early post-moult)	Integument very soft; matrix in the pleopod setae full and extended upto the tip; inner wall of setae wavery	0.9	1.7
B (late post-moult)	Integument flexible; matrix full in the setae; inner wall of setae wavery	2.5	4.8
C (intermoult)	Hardening of carapace including branchiostegite area complete; pigments closely applied to base of pleopod setae; matrix tapered towards the centre of setae	21.0	40.6
D (premoult)			
D_o (early premoult)	Retraction of epidermis from the cuticle	18.0	34.9
D_1-D_3 (mid-premoult)	Development of new setae	7.0	13.6
D_4 (late premoult)	Appearance of longitudinal decalcified line in the branchiostegite area	2.3	4.4
E (ecdysis)	Final phase of moulting; lasted 3-4 minutes.	0.0	0.0

Stage B or late postmoult

The carapace almost hard, except the branchiostegite area; matrix full in the setae (Plates 3.1a and b); occupied 4.8% of each moult cycle.

Stage C or intermoult

The carapace completely hardened; dark green pigment in the pleopods closely applied to the base of the setae with clearly formed articulations (Plate 3.1c); matrix tapered towards the centre of the setae (Plate 3.1d); occupied 40.6% of the total duration of each moult cycle.

Stage D or premoult

This is the most important period in the entire moult cycle. Stage D has 5 substages and 10 subdivisions; but only 2 substages, the early premoult (stage D_0) and the late premoult (stage D_4) are described in the present study.

Separation of epidermis and cuticle between the bases of the apical part of the pleopodal setae (apolysis) was the first indication of stage D_0; a clear zone formed between the base of the old setae and the retracted epidermis at the end of stage D_0 (Plate 3.1e); the retracted epidermis completely free from the old cuticle. This stage occupied 34.9% of the total moult cycle duration and 66.0 % of the time spent in stage D.

Plate 3.1a. Stage B or late postmoult; pigment close to the border of the pleopod (magnification : 10 x 10 X)

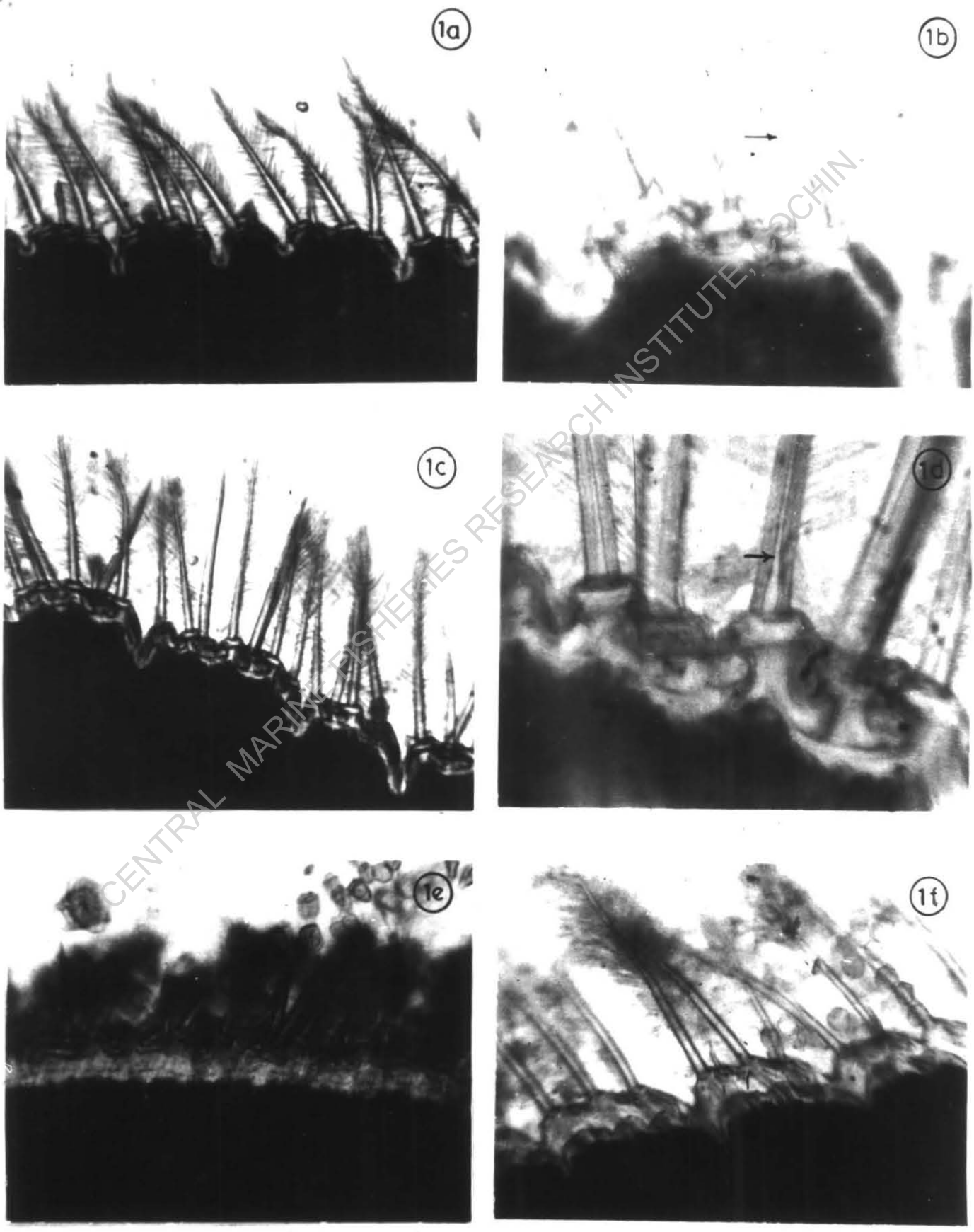
3.1b. Stage B; arrow indicates the matrix portion, which occupies almost the entire setal lumen (magnification : 10 x 45X)

3.1c. Stage C or intermoult; formation of articulation at the base of the setae (magnification : 10 x 10X)

3.1d. Stage C; arrow indicates centering of the matrix in the setal lumen (magnification : 10 x 45X) compared to Stage B (Plate 3.1b).

3.1e. Stage D_0 or early premoult; retraction of epidermis from the base of old setae (magnification : 10 x 10X)

3.1f. Stage D_4 or late premoult; formation of new setae with barbules (magnification : 10 x 10X)



Stage D_4 is the final stage of D; characterised by the appearance of new setae with barbules protruding into the clear zone between the old and the new cuticle in the pleopod (Plate 3.1f); a longitudinal decalcified line in the branchiostegite area of the carapace formed (Plate 3.2a,b). Water absorption started in late D_4 stage resulting in dorsal distention at the junction of the carapace and abdomen. The entire stage D occupied 52.9% of the total moult duration.

Stage E or ecdysis

During ecdysis, the animal pulled out of the old exoskeleton; completed the phase in 3-4 min.

3.3.2 Biochemical changes during moult cycle

The wet weight of the midgut gland ranged from 4.7 (Stages C and D_o) to 5.1 g (Stages A and B) (Table 3.2) and the difference between the minimum and maximum wet weights of the midgut gland was not statistically significant ($t = 1.2$; $P > 0.05$). The dry weight of the midgut gland ranged from 1.2 (Stages A and B) to 2.0 g (Stage D_o) and the difference is statistically different ($t = 5.7$; $P < 0.05$). The water content of the midgut gland reduced from 75.7 (Stage A) to 58.3% (Stage D_o) ($t = 25.2$; $P < 0.005$; significant) and subsequently increased to 63.1% in Stage D_4 ($t = 5.6$; $P < 0.005$; significant).

Plate 3.2a. Lateral view of carapace during stage D_4 or late premoult; arrow indicates formation of decalcified ecdysial line in the branchiostegite area

3.2b. Lateral view of carapace during stage C or intermoult showing absence of decalcified ecdysial line (for comparison with Plate 3.2a).

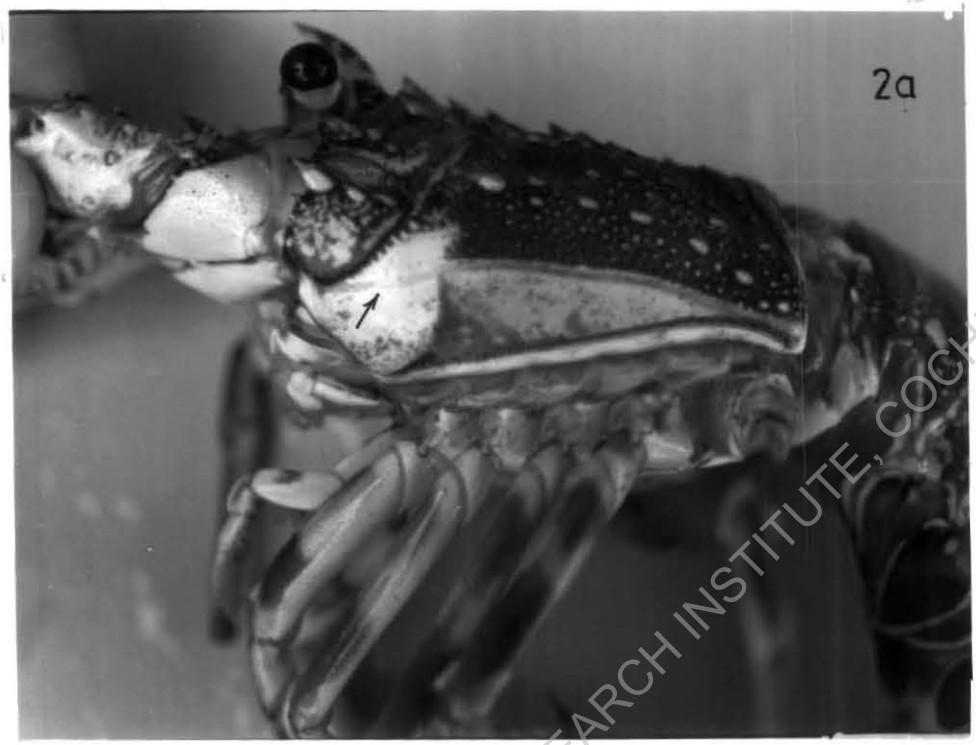


Table 3.2 Wet and dry weights, water and energy contents in midgut gland and muscle of P. homarus in different stages of the moult cycle; ± represents SD.

Parameter	Midgut gland					Muscle				
	A	B	C	D_o	D_4	A	B	C	D_o	D_4
Wet weight (g)	5.1 ± 0.6	5.1 ± 0.4	4.7 ± 0.1	4.7 ± 0.8	5.0 ± 0.8	28.4 ± 2.3	26.6 ± 1.4	25.9 ± 2.1	25.9 ± 0.6	28.5 ± 3.1
Dry weight (g)	1.2 ± 0.1	1.2 ± 0.1	1.8 ± 0.2	2.0 ± 0.1	1.8 ± 0.2	6.6 ± 0.2	6.4 ± 0,4	6.6 ± 0.8	7.1 ± 1.2	7.5 ± 0.8
Water (%)	75.7 ± 1.3	72.7 ± 2.4	62.0 ± 1.8	58.3 ± 1.6	63.1 ± 2.0	76.6 ± 2.3	75.8 ± 1.4	74.6 ± 2.1	72.4 ± 0.6	73.7 ± 3.1
Energy (KJ/g)	23.2 ± 0.5	23.2 ± 1.0	24.5 ± 1.2	23.6 ± 1.3	26.9 ± 1.0	22.6 ± 0.2	18.6 ± 0.3	21.0 ± 2.3	21.8 ± 1.0	20.5 ± 0.9

There was no appreciable change in the wet and dry weights and water content of the abdominal muscle during the moult stages (Table 3.2). The energy content of the muscle ranged from 18.6 to 22.6 KJ/g (mean: 20.9 KJ/g). Compared to the energy content of the midgut gland (mean: 24.3 KJ/g) which is a storage organ (Passano, 1960; Vonk, 1960; O'Connor and Gilbert, 1969), the energy content of the muscle was 14% lesser.

The percent composition of lipid, carbohydrate and protein during the moult stages A,B,C,D_o and D_4 were calculated separately for the midgut gland and muscle and presented in Fig. 3.1. The lipid content in the midgut gland ranged from 30.0 (Stage C) to 42.2 % (Stage D_4) of dry weight. Following utilization of lipid during ecdysis, the lipid content in Stage A decreased to 37.5 %. In the muscle, the percentage of lipid was not only lower (9.8 - 12.8%) than the midgut gland, but also did not exhibit marked fluctuation during the moult cycle; protein was the dominant constituent in the muscle (67.2 - 76.0 %).

To determine the total lipid, carbohydrate, protein and energy in the midgut gland or muscle, the quantity of the individual component/g dry weight was multiplied by the total dry weight of the midgut gland or muscle and expressed as the absolute value. The total lipid in the midgut gland increased

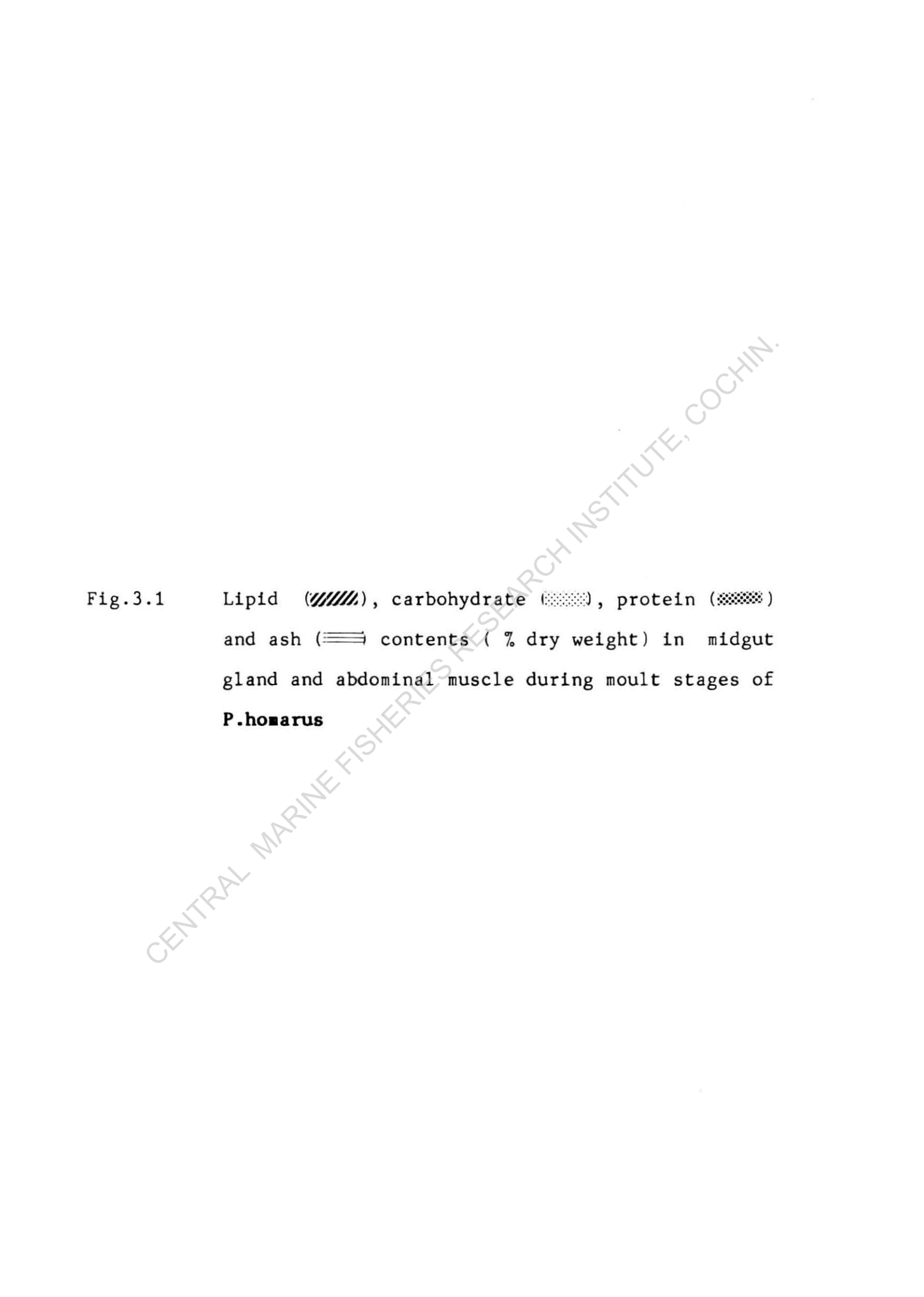
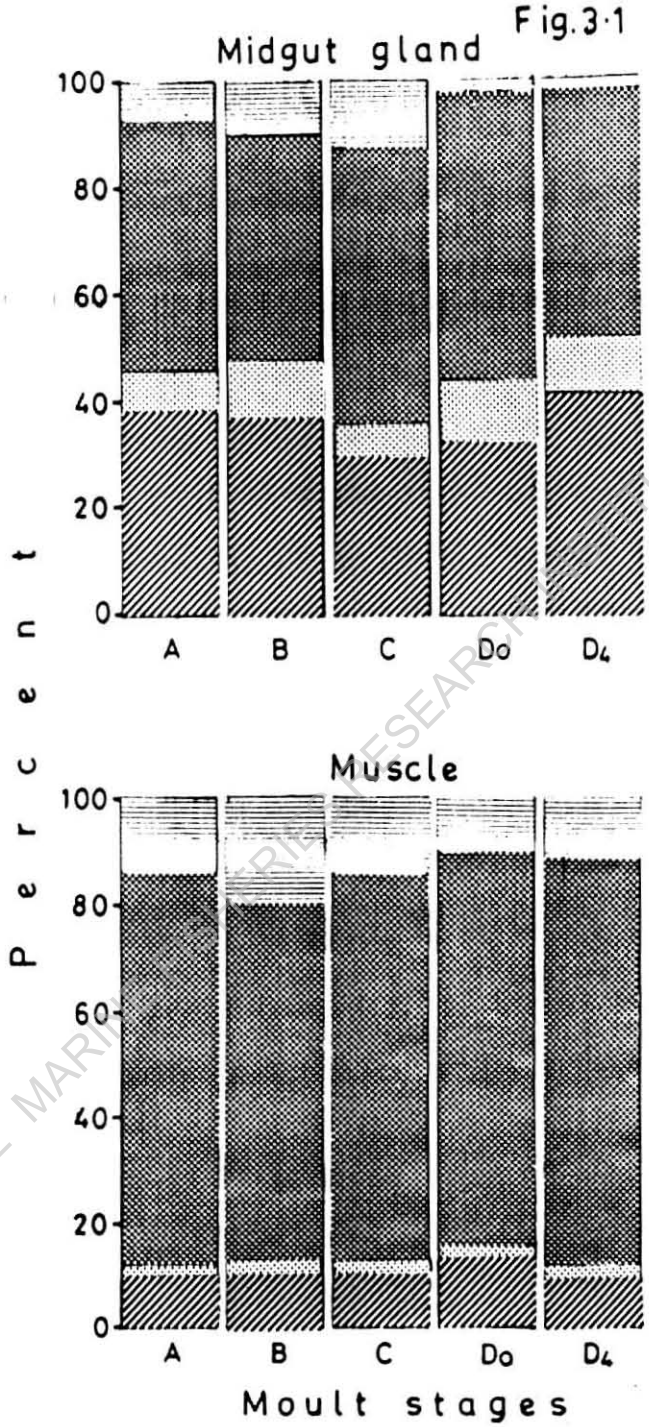


Fig.3.1 Lipid (▨), carbohydrate (▩), protein (▩) and ash (▤) contents (% dry weight) in midgut gland and abdominal muscle during moult stages of **P.homarus**

Fig.3·1



immediately after ecdysis from 450 to 760 mg dry weight in Stage D_4 (Fig. 3.2). In other words, the lipid content decreased from 760 mg prior to ecdysis to 450 mg immediately after ecdysis indicating utilization of 310 mg lipid during ecdysis. The lipid content in the muscle was very high in Stage D_o (910 mg) than all other stages, indicating accumulation of the lipid in the muscle till early premoult stage.

The total carbohydrate in the midgut gland increased sharply from 100 mg in Stage C to 250 mg in Stage D_o and subsequently decreased to 90 mg in Stage A (Fig. 3.3). The carbohydrate content of the muscle varied from 80 to 110 mg and did not show remarkable change between the moult stages.

The total protein in the midgut gland increased from Stage B (520 mg) to Stage D_o (1,005 mg) and subsequently decreased in Stages D_4 (830 mg) (Fig. 3.4). The protein content in the muscle was maximum in Stage D_4 (5,700 mg), i.e. just prior to moulting.

The total energy of the midgut gland increased after Stage A (30.4 KJ) upto Stage D_4 (49.5 KJ) (Fig. 3.5). In other words, the total energy decreased from 49.5 KJ (Stage D_4) to 30.4 KJ (Stage A), indicating utilization of 19.1 KJ of energy during ecdysis.

Fig.3.2. Change in total lipid (mg dry weight) in midgut gland and abdominal muscle during moult stages of **P.homarus**

Fig.3·2

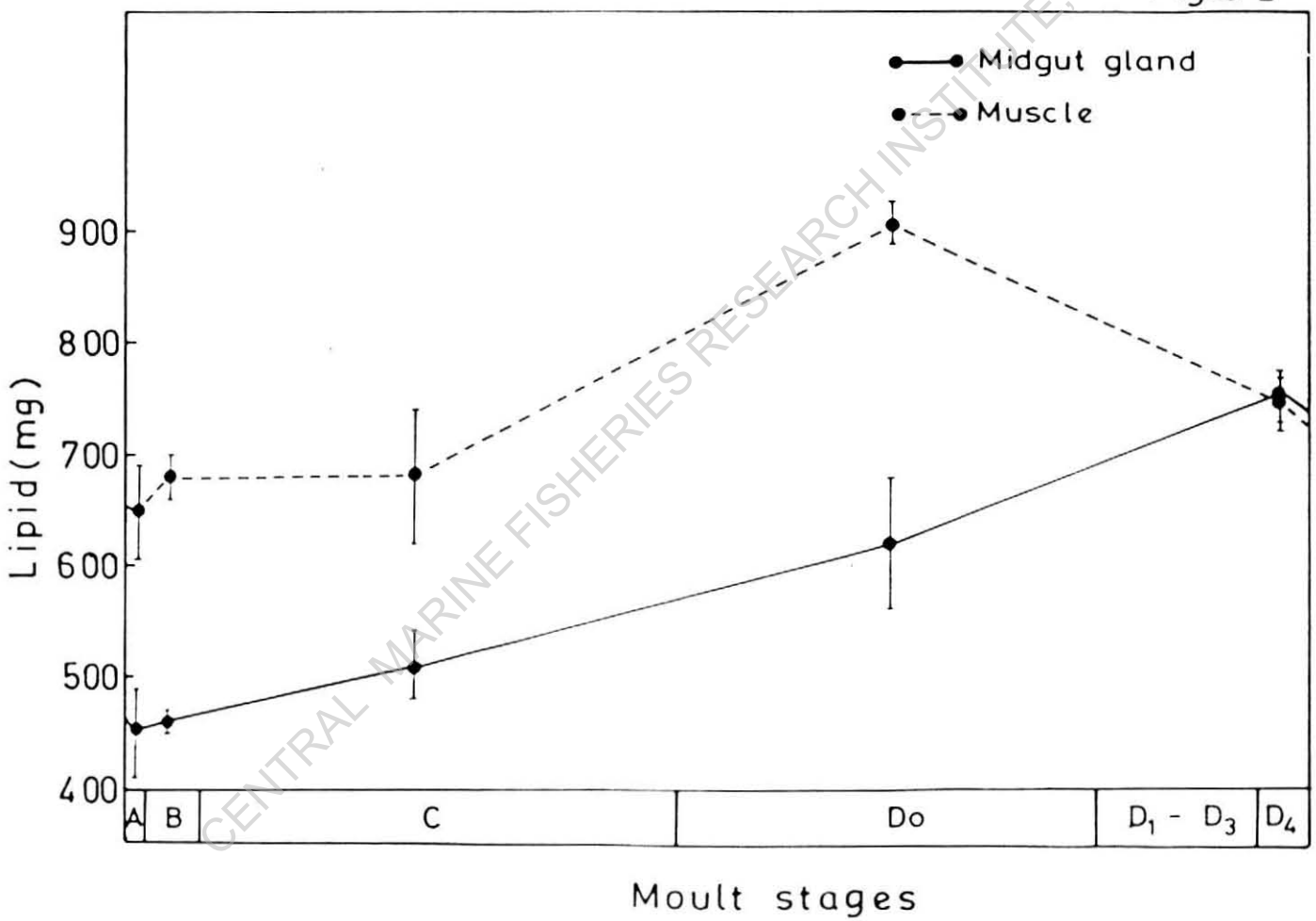


Fig.3.3. Change in total protein (mg dry weight) in midgut gland and abdominal muscle during moult stages of **P.homarus**

Fig.3·3

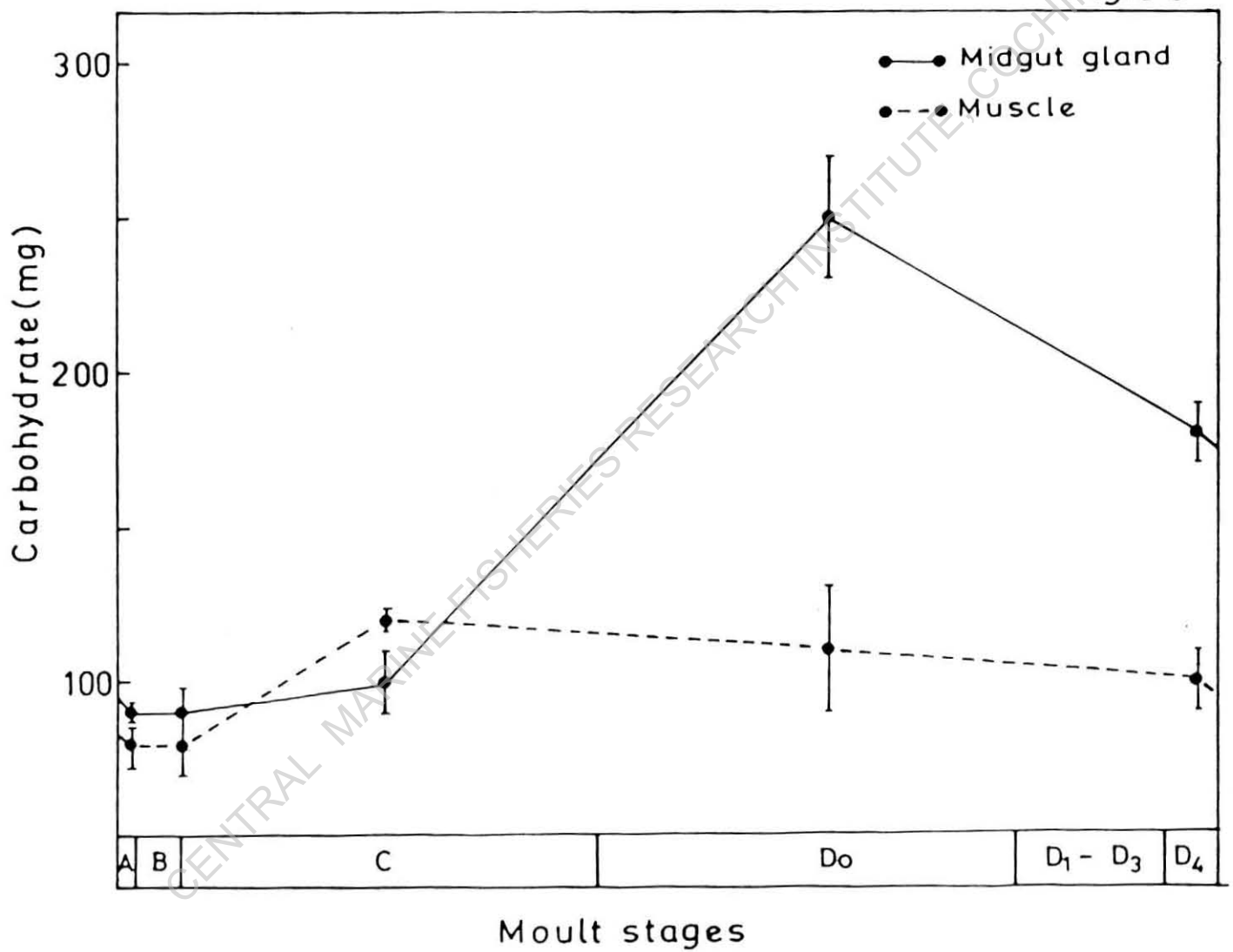


Fig.3.4. Change in total protein (mg dry weight) in midgut gland and abdominal muscle during moult stages of **P.homarus**

Fig. 3·4

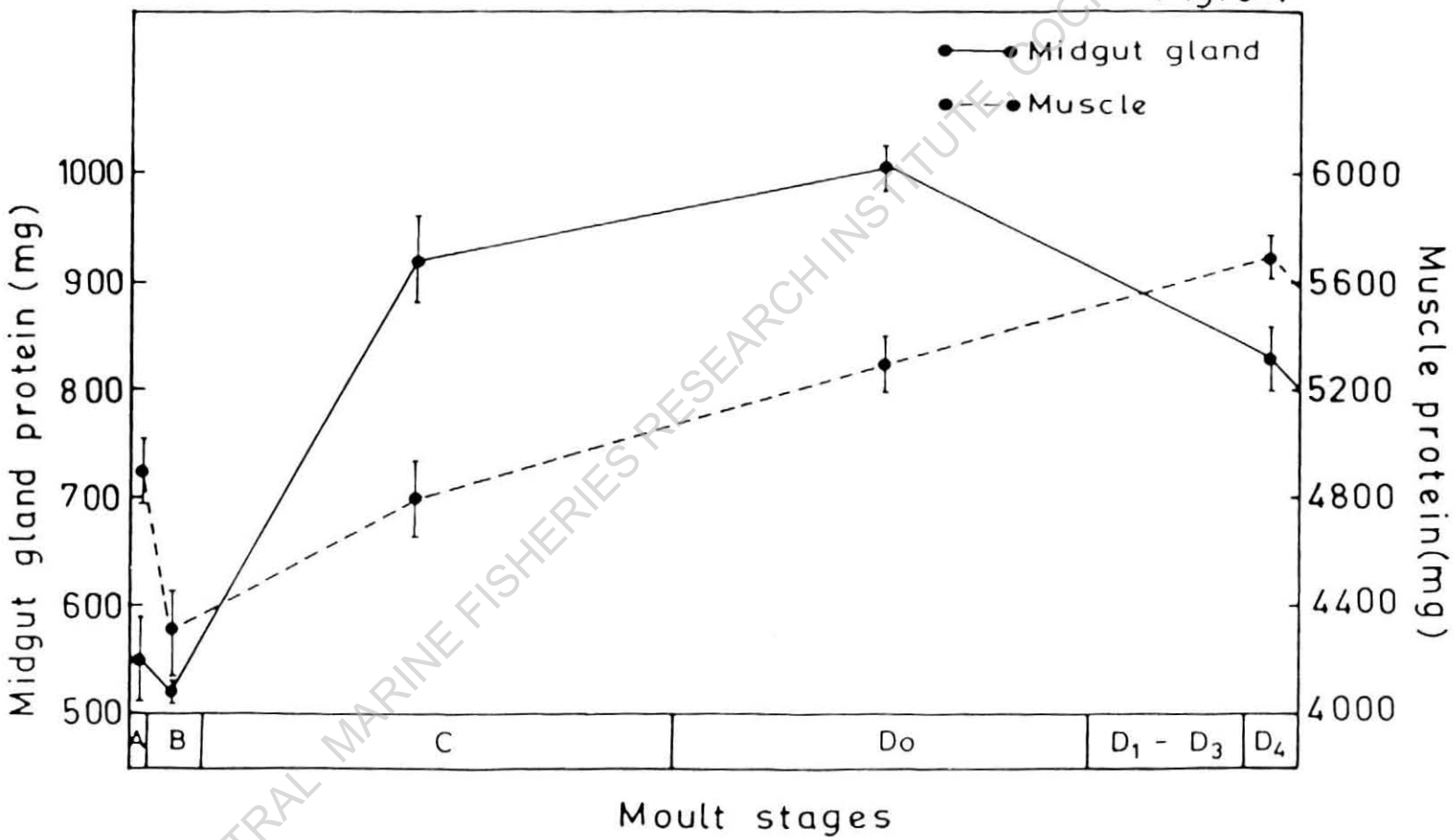
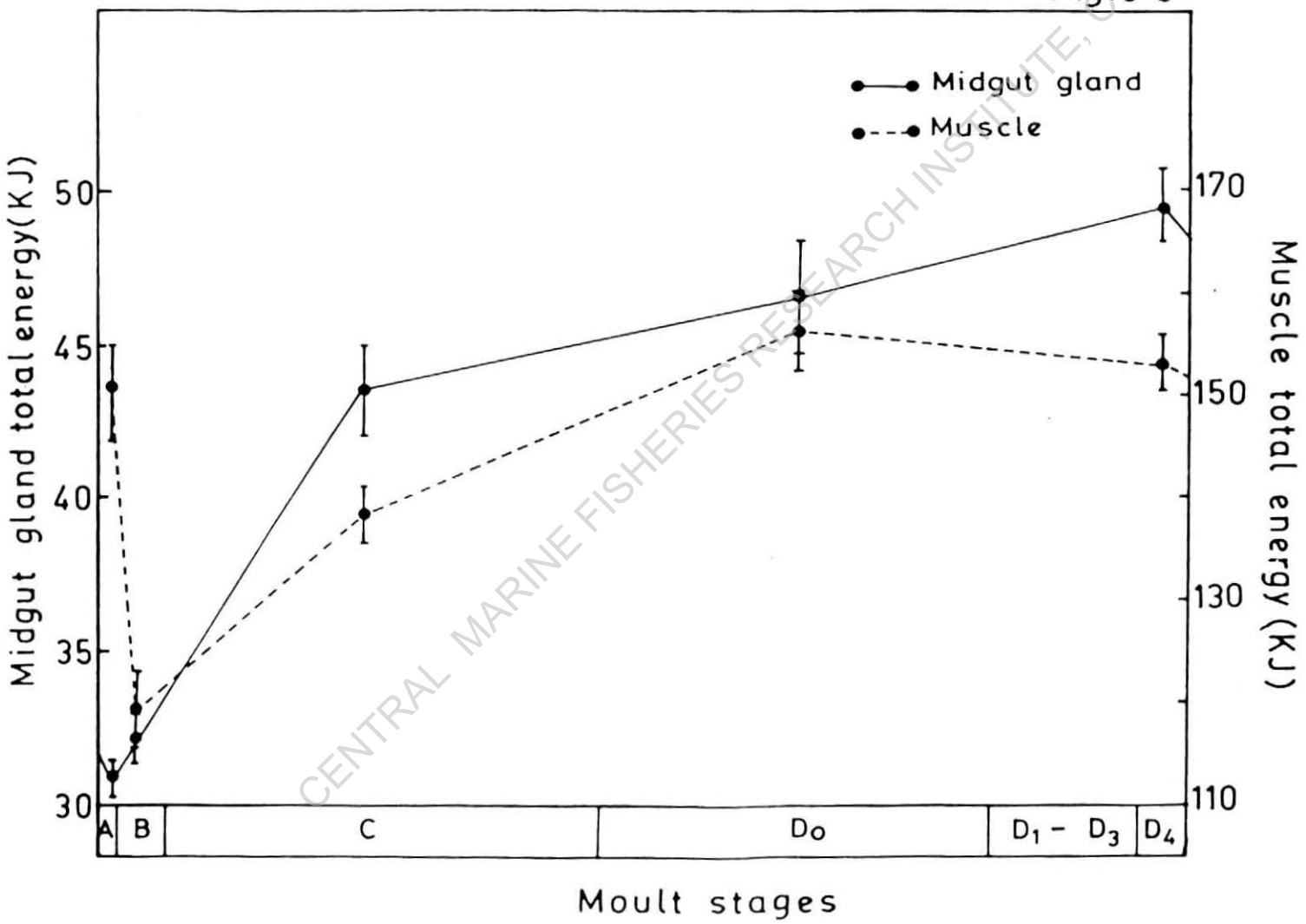


Fig.3.5. Change in total energy in midgut gland and abdominal muscle during moult stages of **P.homarus**

Fig. 3·5



The determination of duration of each moult stage and the biochemical/energy changes that occur during each moult stage has enabled estimation of rate of accumulation / utilization of the biochemical components/energy per day. After moulting, the lobster started accumulating the organic constituents and energy in the midgut gland and the muscle. This is clearly evident in the Stages B-D_0, when most of the constituents were accumulated in both the tissues. For instance, lipid, carbohydrate and protein were accumulated at the rate of 20.0, 4.0 and 10.5 mg/day during the B-C moult stage in the midgut gland (Table 3.3). However, during the D_4-A stage, i.e. during ecdysis, all the components were utilized in both the tissues. Whereas lipid was utilized at the maximum rate (134.8 mg/day) in the midgut gland, muscle contributed maximum protein (347.8 mg/day). Immediately after moulting, i.e. A-B stage, the protein decreased at the rate of 33.3 and 666.7 mg/day in the midgut gland and in the muscle, respectively. As the lobster does not feed during the A-B stage, it is understandable that large quantum of muscle protein was utilized during this stage (Table 3.3).

3.4 Discussion

Though the general scheme of classification of moult cycle was basically developed by Drach (1939) and Drach and Tchernigovtzeff (1967), there are many deviations in the

Table 3.3 Rate of change of lipid, carbohydrate, protein and energy in different moult stages in the midgut gland and muscle of P. homarus

Moult stage	Duration (day)	Midgut gland				Muscle			
		Lipid (mg/day)	Carbohydrate (mg/day)	Protein (mg/day)	Energy (KJ/day)	Lipid (mg/day)	Carbohydrate (mg/day)	Protein (mg/day)	Energy (KJ/day)
A - B	0.9	+ 11.1	0.0	- 33.3	+ 2.0	+ 33.3	0.0	- 666.7	- 33.9
B - C	2.5	+ 20.0	+ 4.0	+ 10.5	+ 4.6	0.0	+ 16.0	+ 200.0	+ 7.5
C - D_o	21.0	+ 5.2	+ 7.1	+ 7.2	+ 0.1	+ 11.0	- 0.5	+ 23.8	+ 0.8
D_o - D_4	18.0	+ 7.8	- 3.9	- 12.2	+ 0.2	- 8.9	- 0.6	+ 22.2	- 0.2
D_4 - A	2.3	- 134.8	- 39.1	- 121.7	- 8.3	- 43.5	- 8.7	- 347.8	- 1.3

classification of different groups of crustaceans. Schwabe et.al. (1952) attempted the classification of the Hawaiian spiny lobster **P. marginatus** using histological changes in the integument. Lyle and Mac Donald (1983) classified the moult cycle of the same species using exclusively the setogenic changes in the pleopods. Though the scheme developed by Lyle and Mac Donald (1983) could be adopted for classifying the moult stages of the spiny lobster, **P.homarus**, few deviations were followed in the present study. Division of early postmoult into stages A and B is difficult following the setal changes alone as there was no definite morphological difference in the setae between these two stages. Hence, these stages were classified using the relative rigidity of the carapace. Shell hardness and colour, though are unreliable indicators of moult stage, at times, are the only criteria that can conveniently be used (Aiken, 1980). The retraction of the matrix towards the centre of the setae is a useful character to place the lobster in intermoult stage (Stage C). In many natantians and macrurans, presence of internal cones formed by the retraction of the setal matrix is the most distinguishable feature of their entry in stage C (Stevenson, 1985). The centering of the matrix in **P. homarus** may be considered as equivalent to the formation of cone in other crustaceans.

Retraction of the epidermis from the cuticle at the base of the setae in the pleopods and uropods (apolysis) is one of the criteria for classifying stage D_o (Jenkin and Hinton, 1966). Further classification of the premoult stage using morphological changes in the newly developing setae is difficult due to strong pigmentation of the pleopod of **P.homarus** (Plate 3.1f). Lyle and MacDonald (1983) also expressed this difficulty in staging **P. marginatus.** However, the morphological changes in the tips of the new setae, which are projecting into the retracted transparent zone has been used for classifying Stages D_1, D_2 and D_3 in **P. marginatus.** In **P. homarus**, as in **P. marginatus**, separation of D_3 and D_4 based on setal changes is rather difficult. However, formation of the decalcified line in the branchiostegite area of **P. homarus** is a clear indication of entry of the lobster into Stage D_4. Under normal circumstances, the lobster moults within 48 hr after appearance of this character. Considering these factors, it may be concluded that the moult cycle in the palinurid lobster may be precisely classified by both external characteristics of the carapace and microscopic observation of setogenic changes in the pleopod; restriction to any one of these observations may lead to inaccurate classification of the moult cycle.

The moult cycle of **P. homarus** differs from the homarid lobsters at least in 2 aspects. Firstly, the intermoult duration was considerably shorter in **P. homarus** than in **H. americanus.** In the present study, **P. homarus** (CL :45-50 mm) completed one moult cycle in 51.7 days. A larger **P. homarus** might require longer duration for completion of a moult as it is known that the intermoult duration increases with increasing size of the lobster (Mauchline, 1977). Nevertheless, the intermoult duration of **H. americanus** is far longer. Aiken (1980) reported that the premoult of **H. americanus** may span for 3-6 months depending upon the size of the lobster and the final preparation for ecdysis may extend over days or even weeks; the ecdysis itself requires 15-20 minutes. Being a tropical animal, **P.homarus** not only could complete a moult in a shorter period, but also is in an advantageous position of completing the critical process of ecdysis in 3-4 min. Ability to complete this vulnerable phase rapidly and to recover full mobility immediately may be necessary for survival, since **P. homarus**, being gregarious, apparently does not moult in seclusion like the homarid lobsters (Dall, 1977). Secondly, the partitioning of the total moult duration between each moult stage is different between **H.americanus** and **P. homarus.** Whereas **P.homarus** spent 40.6 and 52.9% of the total moult cycle in stage C and D,

respectively (Table 3.1), **H.americanus** partitioned longer duration (52.6 % of the total moult cycle) in Stage C than in Stage D (44.0 %) (Aiken, 1980). However, duration of time spent in Stage D, especially in Stage D_o was flexible in **H.americanus**, as the homarid lobsters are known to remain in D_o stage for extended periods (anecdysis) depending upon the environmental conditions (Aiken, 1973). **P. homarus** does not undergo such a phenomenon.

The quantification of water, lipid, carbohydrate, protein and energy during every moult stage has revealed a few improtant aspects in the moulting physiology of the spiny lobster, **P. homarus.** The water content in the midgut gland decreased from Stage A (75.7%) to Stage D_o (58.3 %) and thereafter increased from late D_4 stage through ecdysis upto Stage A (Table 3.2). Dall and Smith (1978) have reported that water is ingested as well as absorbed during late premoult and redistributed within the body. Due to increased hydrostatic pressure, the carapace lifts clear of the decalcified ecdysial sutures above the bases of the legs, and thoracoabdominal membrane bulges outward at the juncture of the elevated carapace and the abdomen (Aiken, 1980). Hence, accumulation of water during late premoult is obligatory for the successful ecdysis of the lobster. In **P.homarus**, variation in water content was more pronounced in the midgut gland than in the muscle especially between Stages D_4 and A

and this observation is in agreement with the view that midgut gland is the major site of water absorption from the gut during ecdysis (Dall and Smith, 1978; Vijayakumaran and Radhakrishnan, 1987).

Contrary to water, the lipid was accumulated in the midgut gland from Stage A to D_4 (late premoult) (Fig. 3.2) and carbohydrate (Fig. 3.3) and protein (Fig. 3.4) were accumulated from Stage A to D_o (early premoult). In other words, carbohydrate and protein were utilized from the early premoult stage, whereas lipid was reserved exclusively for the ecdysis. Due to cessation of feeding, in the premoult stage, the decapods have the capacity to store ingested lipids (Chang and O'Connor, 1983). In **P. homarus**, lipid in the midgut gland was higher by 140 mg dry weight (an increase of 22.6 %) in stage D_o-D_4 than in the early stage, whereas protein and carhobydrate were lesser by 220 and 70 mg, respectively (Table 3.4). Such proecdysial increase in the midgut gland lipid was reported in **Cancer pagurus** (Paul and Sharpe, 1919; Renaud, 1949), **P. argus** (Travis, 1955a), **Gecarcinus lateralis** (O'Connor and Gilbert, 1968) **Orconectes virilis** (O'Connor and Gilbert, 1969), **Pachygrapsus marmoratus** (Lautier and Lagarrigue, 1976) and **Penaeus indicus** (Read and Caulton, 1980).

Table 3.4 Biochemical changes during stages D_0 - D_4 and D_4 - A in the midgut gland of P. homarus; the estimations were made by comparing with the respective earlier stages.

Biochemial components	D_o - D_4		D_4 - A	
	Change in dry weight (mg)	Percent	Change in dry weight (mg)	Percent
Lipid	+ 140.0	+ 22.6	- 310.0	- 40.8
Carbohydrate	- 70.0	- 28.0	- 90.0	- 50.0
Protein	- 220.0	- 21.0	- 280.0	- 33.7
Energy (KJ.	+ 3.0	+ 6.5	- 19.1	- 38.6

During ecdysis (Stages D_4-A), 310, 90 and 280 mg lipid, carbohydrate and protein were utilized, respectively. The proecdysial increase of lipid in the midgut gland is probably due to fatty acid synthesis and a fall immediately after ecdysis is due to attenuation of the lipid synthetic capacity and also to increased rate of transfer of lipid from the midgut gland to the haemolymph (Chang and O'Connor, 1983). The carbohydrate content also decreased considerably (by 50 % in the midgut gland) during ecdysis (Table 3.4). Though the smallest of the three biochemical components of the midgut gland, carbohydrate is known to play a major role in the form of glycogen during ecdysis in many crustaceans (Schwabe et.al., 1952; Passano, 1960; Vonk, 1960, Parvathy, 1971; Diwan and Usha, 1985). Carbohydrate is utilized as a precursor in chitin synthesis and also as an energy source in cuticular synthesis (Renaud, 1949; Schwabe et.al., 1952; Vonk 1960; Meenakshi and Scheer, 1961; Hornung and Stevenson, 1971). Compared to the reduction in lipid and carbohydrate, the reduction in protein in the midgut gland during ecdysis was lesser (33.7 %). However, the protein utilization commenced from early premoult stage and a total of 500 mg of protein was utilized from early premoult stage to ecdysis (Table 3.4). Following ecdysis, the protein content in the midgut gland and muscle further decreased upto Stage B as the freshly moulted lobster (Stage A) does not feed. The feeding

and accumulation of protein in the midgut gland commenced from Stage B. Read and Caulton (1980) reported initiation of protein synthesis in Stage B in the prawn, **Penaeus indicus**, i.e. as soon as the exoskeleton hardened and the animal started feeding.

Similar to protein, the total energy of the midgut gland and the muscle decreased during the non-feeding stage (Stage A) (Fig.3.5). During ecdysis, 19.1 KJ of energy was lost, which was contributed by all the biochemical constituents. Considering the energy equivalents for lipid, carbohydrate and protein as 39.4, 17.6 and 22.2 KJ/g, respectively (Schmidt-Nielsen, 1975), the contribution of each of the biochemical component towards ecdysis was calculated by using the reduction in weight of lipid (310 mg), carbohydrate (90 mg) and protein (280 mg) in the midgut gland during ecdysis (Table 3.4). The energy equivalents thus calculated for the utilized portion of lipid, carbohydrate and protein were 12.2, 1.6 and 6.2 KJ, respectively. Though the total calculated contribution (20.0 KJ) of the 3 biochemical constituents marginally exceeds the actual energy utilized (19.1 KJ) during ecdysis, it may be concluded that the lipid contributes the maximum energy (61%) for ecdysis in **P. homarus** and the contributions of protein (31 %) and carbohydrate (8 %) are far lesser than that of lipid.

4 PREDATOR - PREY RELATIONSHIP

4.1 Introduction

Most predatory crustaceans like the crabs **Scylla serrata** (Hill, 1976), **Carcinus maenas** (Walne and Dean, 1972; Elner and Hughes, 1978), **Portunus puber** (Ebling et.al., 1964), **Ovalipes punctatus** (Du Preez, 1984) as well as the American lobster, **H. americanus** (Ennis, 1973; Elner and Jamieson, 1979) prey mainly upon hard-shelled molluscs. The spiny lobsters like **P. homarus** (Berry, 1971; Smale, 1978), **P. argus** (Davis, 1977), **Jasus lalandii** (Heydorn, 1969; Newman and Pollock, 1974; Pollock, 1979, Griffiths and Seiderer, 1980) and **J. lalandei** (Fielder, 1965) are also known to prey upon the shelled molluscs. The crabs and homarid lobsters crack the molluscan shell by employing 'master chela' or 'crusher claw'. The palinurid lobsters are clawless and they use a far less powerful organ, viz., mandible, to crush the molluscan shell. With the available less powerful crushing organ, the palinurid lobsters have to probably adopt a definite feeding strategy to predate the hard-shelled molluscs.

Theories on optimal foraging have repeatedly demonstrated the influence of prey characteristics on the capacity and efficiency of the predator (Hughes, 1980). One of the most important prey characteristics which determines

the predatory efficiency is the size of the prey. The size of the prey assumes importance especially for the predators like the spiny lobster, **P. homarus,** which has to crush shells of different thickness when predating different size groups of molluscs. The shell girth (thickness) of the molluscan prey increases with increasing size, thereby posing considerable problem to the lobster. Surprisingly, there is very limited information on the predatory strategy of the spiny lobsters on different prey size (Pollock, 1979; Griffiths and Seiderer, 1980). Griffiths and Seiderer (1980) reported that the maximum size of the mussel that could be broken by the temperate rock lobster, **J. lalandii** increased with increasing size of the lobster; they also concluded that the rock lobster preferred small mussels, as small shells can be rapidly cracked. There is no study so far either on the 'critical size' (maximum shell size/girth that the lobster can break) (Griffiths and Seiderer, 1980) or on the preferred/optimum prey size of any of the tropical lobsters. To understand the behaviour and strategy of predation, and to determine the critical and optimal prey size for different size classes of the spiny lobster **P. homarus,** a series of 3 experiments were conducted by offering them different size groups of the green mussel, **P. viridis.**

Preliminary analysis of the gut of **P. homarus** captured from the wild revealed that the mussel forms the natural food of the lobster. Frequently, lobsters with empty stomach were also observed. It appears that the lobsters often face food scarcity. It is not known whether short term starvation affects the predatory capacity of the lobster. To assess the capacity of the starved lobster, another experiment was conducted by exposing **P. homarus** to short term starvation and subsequently offering different size groups of the mussel, **P. viridis.**

4.2 Materials and methods

The spiny lobster, **P. homarus** caught off Kovalam (Madras), was maintained in the laboratory in closed culture systems and fed on the meat of the clam, **Meretrix casta.** Healthy lobsters from this reserve were used for the experiments on predator - prey relationship. For all the experiments, only male lobsters in intermoult stage (Stage C) were used.

The experiments were conducted by individually rearing the lobsters in plastic rectangular aquaria of uniform size (61 x 40.5 cm; volume: 62 l). About 75 % of the sea water in each aquarium was replaced with fresh filtered sea water daily in the morning with minimum disturbance to the lobster. Except the experiment on

starvation, all the lobsters were acclimatised to the aquarium conditions. The lobsters were exposed to natural photoperiodicity prevalent in the laboratory. The water temperature was 26.5 ± 1.5°C and the salinity was 35 ± 0.6 ‰ during the experimental period. The aquaria were aerated by compressed air; the dissolved oxygen content was 4.0±0.2 ml/l.

For the experiments, the green mussel **P. viridis** was offered as prey to the lobster without removing the shell. The mussels collected from the intertidal bed in the vicinity of Madras were maintained in the laboratory for 3-4 days. Before exposing to the lobster, the byssal threads of the mussels were removed. The experimental lobsters were allowed to feed from 4 pm to 9 am, i.e. for 17 hr. The number of mussels consumed were noted at 9 am.

The shell length (SL) and the shell girth (SG, measured at a distance of 3 mm from the distal margin of the shell) of the mussel were measured by using vernier caliper to an accuracy of 0.01 mm. The wet and dry weights of the lobster and the mussel (after removing the shell) were determined to 0.1 mg accuracy using a monopan electric balance. The dry weight was determined after drying the mussel meat in hot air-oven at 90°C for 24 hr. The percent dry matter (26 ± 2.2 %) did not differ significantly between different size groups of the mussel and hence, the mean value

of 26 % (without shell) was used for converting wet weight of the mussel to the respective dry weight. The dry weight was further converted to energy values by using the mean energy content of the shell-free mussel (17.634 KJ/g), determined by using semi-micro bomb calorimeter.

A series of 4 experiments on different size classes of the lobster were conducted to understand i) the critical prey size; ii) the preferred prey size; iii) the optimum prey size; and iv) the effect of starvation on predation. The size of the predator and the prey used in the experiments are given in the respective sections.

4.3 Results

4.3.1 Feeding behaviour

The paired mandibles of **P. homarus** is a strong calcified structure, suited to crack hard shells of molluscs and crustaceans (Plate 4.1a). The dentition of the right mandible is different from that of the left (Plate 4.1b). The occluding surface of the left mandible has one prominent tubercle, which forms the upper lobe; the lower lobe has ridges and cavities. The right mandible has an upper tubercle and two smaller tubercles which fit into the cavities of the left mandible. The movements of the mandible is controlled by mandibular muscles. The two spines in front

Plate 4.1a. Paired mandible (dorsal view) of **P.homarus**

4.1b. Dentition of left and right mandibles

are fused together. The mandibular flagellum is at the joint where the spine joins the dorsal body of the mandibles (Plate 4.1a).

Whenever the shelled prey, **P. viridis** was offered to **P. homarus**, the following sequential feeding behaviour was observed: i) immediately after the food was offered, the antennular flagellum of the lobster flickered intensively and the lobster started moving towards the prey with well spread-out legs; ii) after detecting the prey by using the dactyls of the walking legs the prey was grabbed with first 3 pairs of walking legs and maxillipeds and iii) the maxillipeds and the walking legs guided the mussel to the proper position (vertical to the mandible) so as to crush the shell with the mandibles; iv) the distal flat shell margin was first trimmed by the mandibles and subsequently crushed exposing the mantle. Examination of the crushed shells showed that the flat anterior margin of the mussel was crushed in most cases (Plate 4.2a) and in some instances, the anterio-lateral portion was also crushed (Plate 4.2b); v) after inserting the sharp dactyls of the first 2 pairs of walking legs between the shells, the lobster started prising the shells apart; vi) the prised shells were further crushed and the meat was scooped and guided towards the mouth.

4.2a. Crushed shell remains of the mussel.

4.2b. Anteriolateral portion of the shells crushed by the lobster in a few instances

P. homarus predated mostly during night. However, starved lobsters were found to feed during day time also. The predation was affected during ecdysis. In preliminary experiments exposing mussel (with shell) and clam (without shell) to lobster (48 mm CL) in different moult stages (D_o-C), it was observed that **P. homarus** was unable to crush the shell of the mussel after entering Stage D_2 but continued to feed on soft clam meat till it entered Stage D_4. From Stage D_4 to Stage B (duration: 5 days), the lobster did not feed. Feeding on soft clam meat resumed 24 hr after ecdysis (Stage B). However, the lobster could crush shells of the mussel only 6 - 10 days after ecdysis (Stage C). Hence, the 4 experiments on predator - prey relationship were conducted on lobsters in intermoult stage (Stage C) so as to avoid the effect of moult stage on predation.

4.3.2 Critical prey size

The size of the lobster and mussel used in this experiment are given in Table 4.1. To determine the critical shell size which the lobster of different size groups can crush, each lobster was offered 5 mussels of the smallest size group on the first day. If atleast one mussel was consumed fully (mussels which were attempted but not consumed by the lobster were not considered), 5 mussels of the next larger size group were offered on the next day. The

Table 4.1 Carapace length (CL) and weight of the lobster and shell length (SL) of the mussel used in the experiment to determine critical prey size; each length value represents the mean of 5 mm size group

Sr. No.	Size of lobster CL (mm)	Wt(g)	N	Size of mussel SL (mm)
1	23.0	11.5	3	18,23,28
2	28.0	21.4	3	18.23,28,33
3	33.0	35.5	3	18,23,28,33,38
4	38.0	52.5	3	18,23,28,33,38,43
5	43.0	74.1	3	18.23.28,33,38,43,48
6	48.0	100.0	3	18,23,28,33,38,43,48,53,
7	53.0	134.9	3	18.23.28,33,38,43,48,53,58

experiment was discontinued when the lobster of each size class was unable to feed a particular size group after exposure for 5 days. The largest prey consumed by the lobster was considered to be the critical prey size (see also Griffiths and Seiderer, 1980).

The critical shell length of the mussel increased linearly with the size of the lobster (Fig. 4.1). Pollock (1979) also reported that small rock lobster **J. lalandii** (CL: 7.2 cm) could not break mussels larger than 60 mm SL, whereas larger lobsters (CL: 12.2 cm) could break mussels upto 89 mm SL.

To determine the critical size of prey in terms of body weight, the length (carapace length in mm (x) and weight (total weight in g) (y) relationship of the lobster as well as the length (shell length in mm) (x) and weight (total weight with shell in g) (y) relationship of the mussel were determined as follows:

lobster : $\log y = -3.0 + 2.98 \log x$

$r = 0.9997$

mussel : $\log y = -3.6 + 2.72 \log x$

$r = 0.9913$

By employing these equations, a positive linear relationship was established between the weight of the lobster and the critical weight of the mussel (Fig. 4.2). It could be

Fig.4.1. Relationship between size of lobster (carapace length) and critical breakable size of mussel (shell length)

Fig.4·1

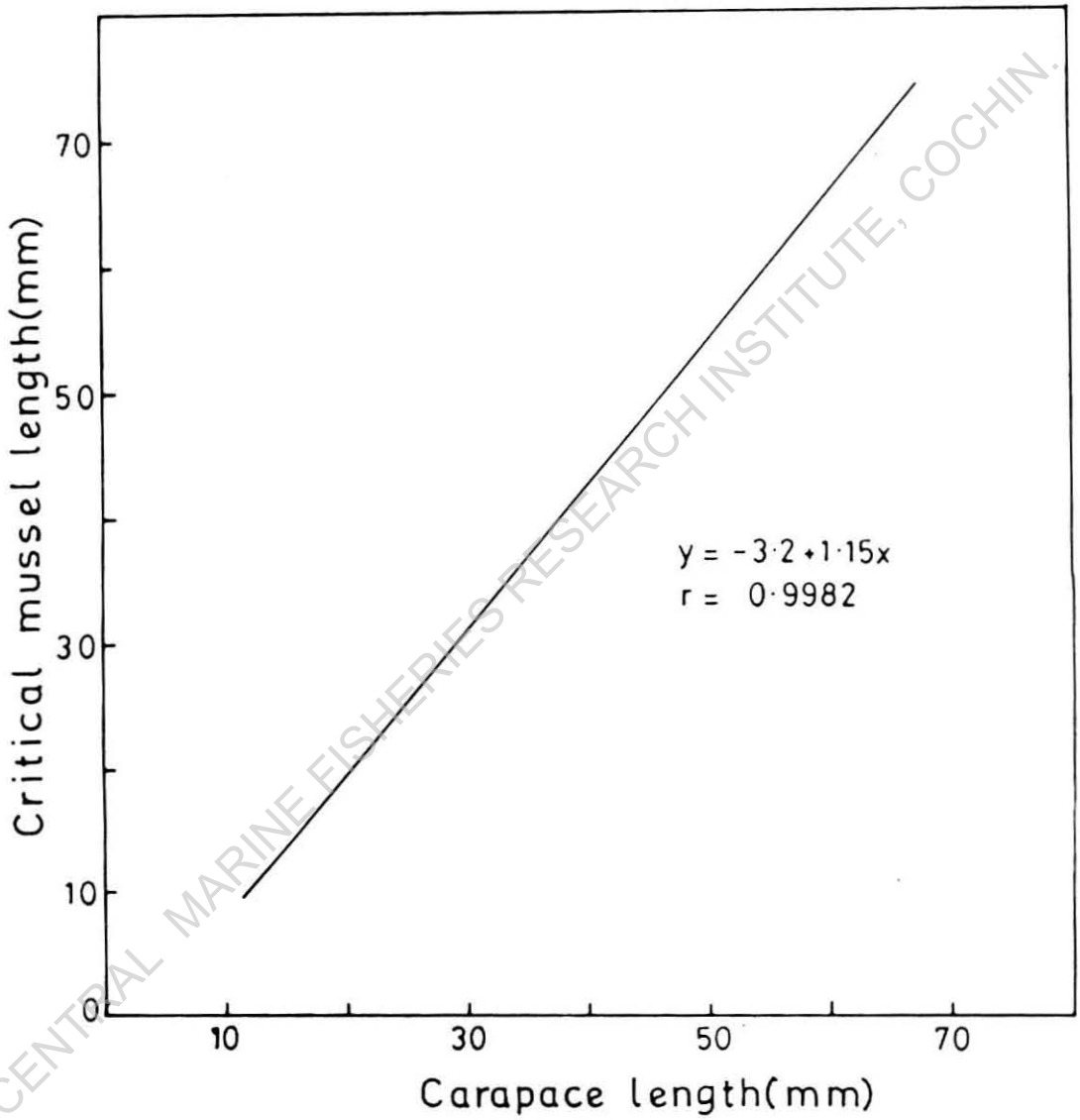
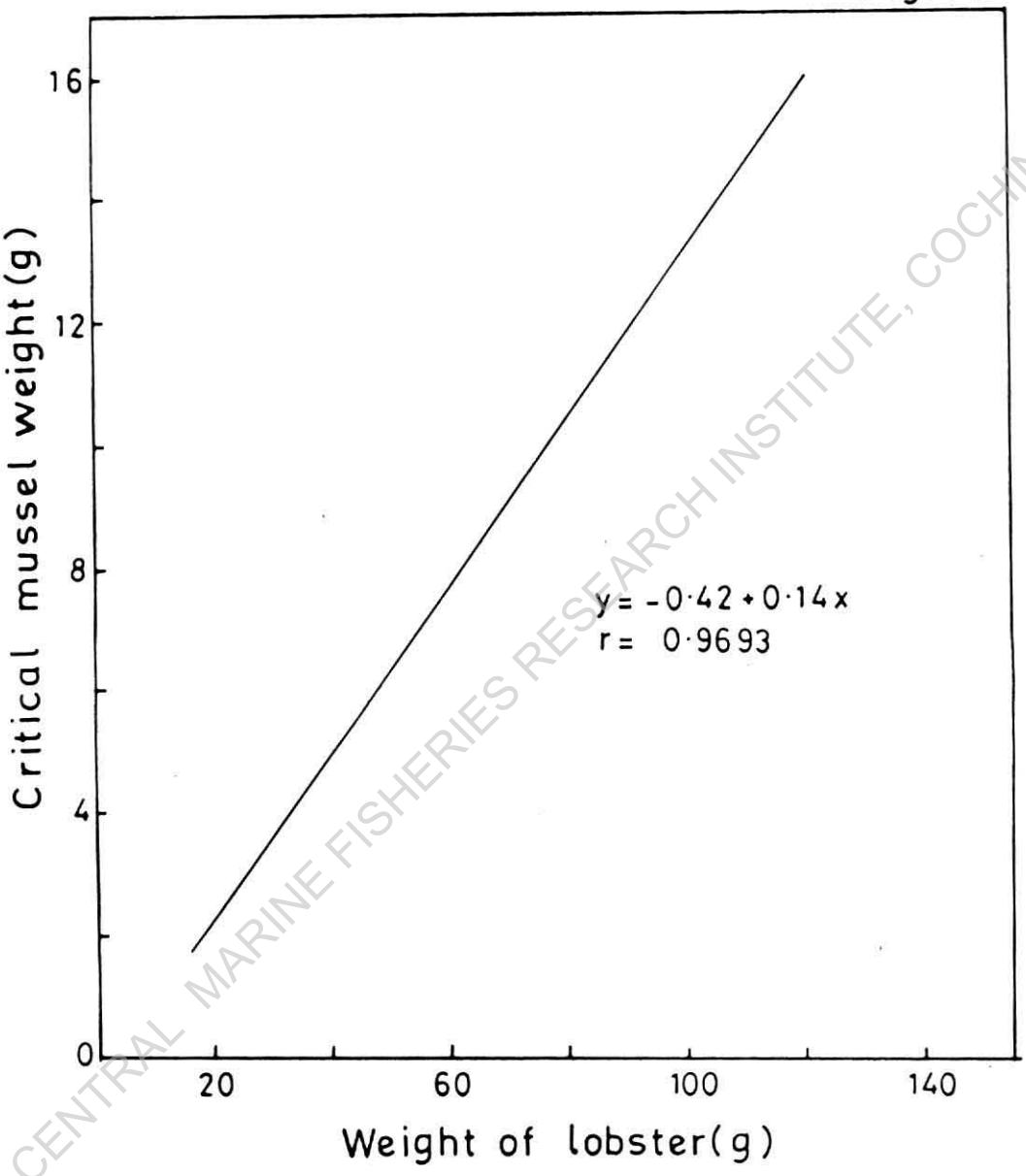


Fig.4.2. Relationship between size of lobster (live weight) and critical breakable size of mussel (live weight)

Fig.4·2



calculated from the figure that the lobster can handle mussel equivalent to 13 % of its body weight.

However, comparison of weight of the lobster with the weight of the mussel may not be appropriate to determine the predatory capacity of the lobster. The predatory capacity of the lobster may not be directly controlled by the weight of the prey, atleast when the prey is a hard-shelled mollusc like the mussel. The predatory capacity is directly controlled by the thickness (girth) of the mussel shell and capacity of the crushing organ (mandible) to break the shell. With increasing size of the mussel, the shell girth increased linearly (Fig. 4.3). The length of the mandible also increased linearly with increasing size of the lobster (Fig. 4.4). Since the size of the lobster was directly correlated with mandible length and critical size of the mussel, there was a direct correlation between mandible length and the shell girth it can crush. From Figure 4.5, it is evident that mandible of 10 mm length can break a shell of 2.6 mm girth. In other words, the mandible has the capacity to break the shell girth which is about 26 % of its length.

The shell girth of the mussel increased from the distal margin to the umbonal end. For instance, the shell girth of a mussel (25 mm SL) was 1.5 mm at a distance of 3 mm from the shell margin. The shell girth increased to 3.1 and

Fig.4.3. Relationship between shell length and shell girth of the mussel; shell girth was measured 3 mm from shell margin

Fig.4·3

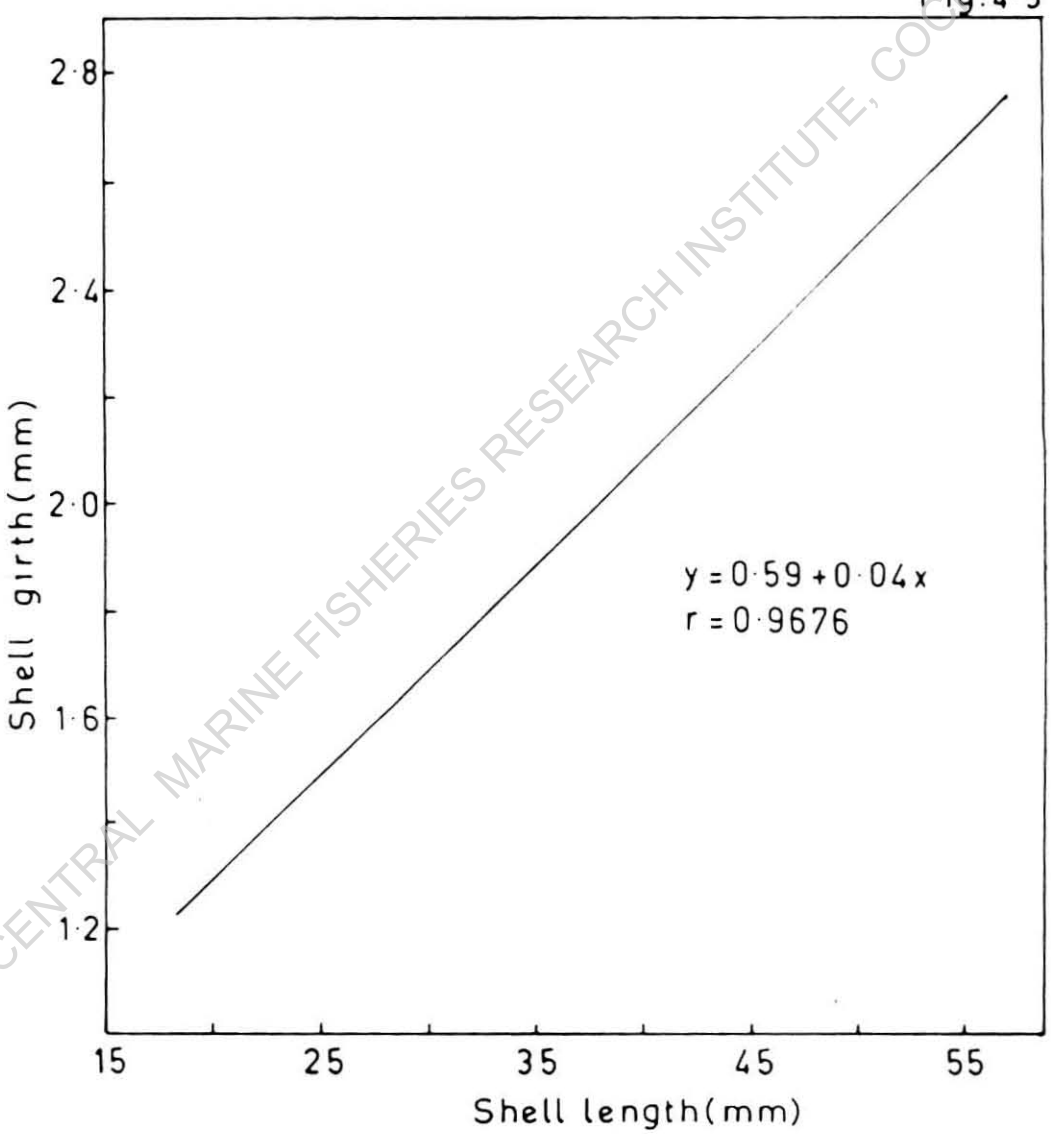


Fig.4.4. Relationship between size of lobster (carapace length) and mandible length

Fig.4·4

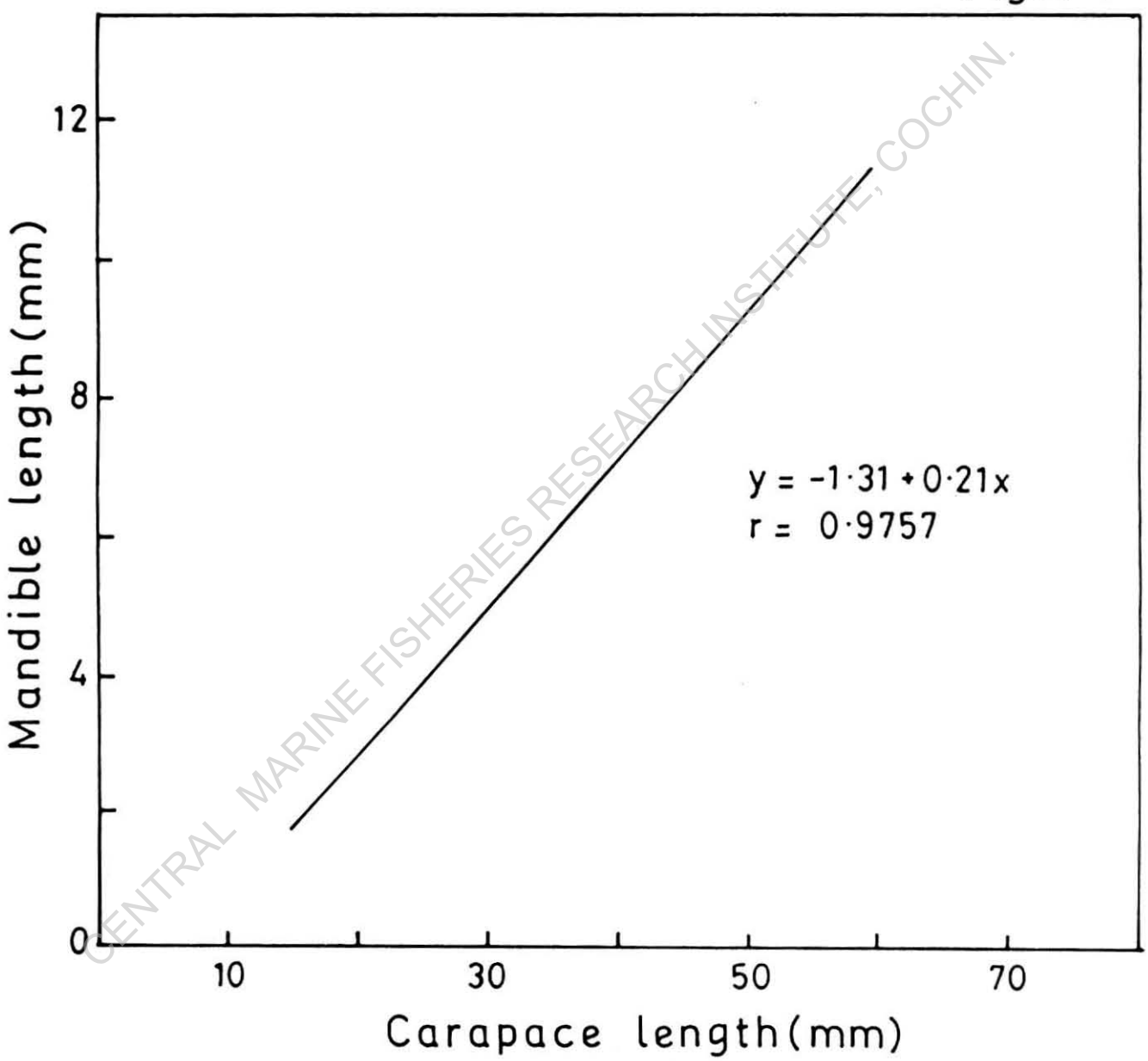
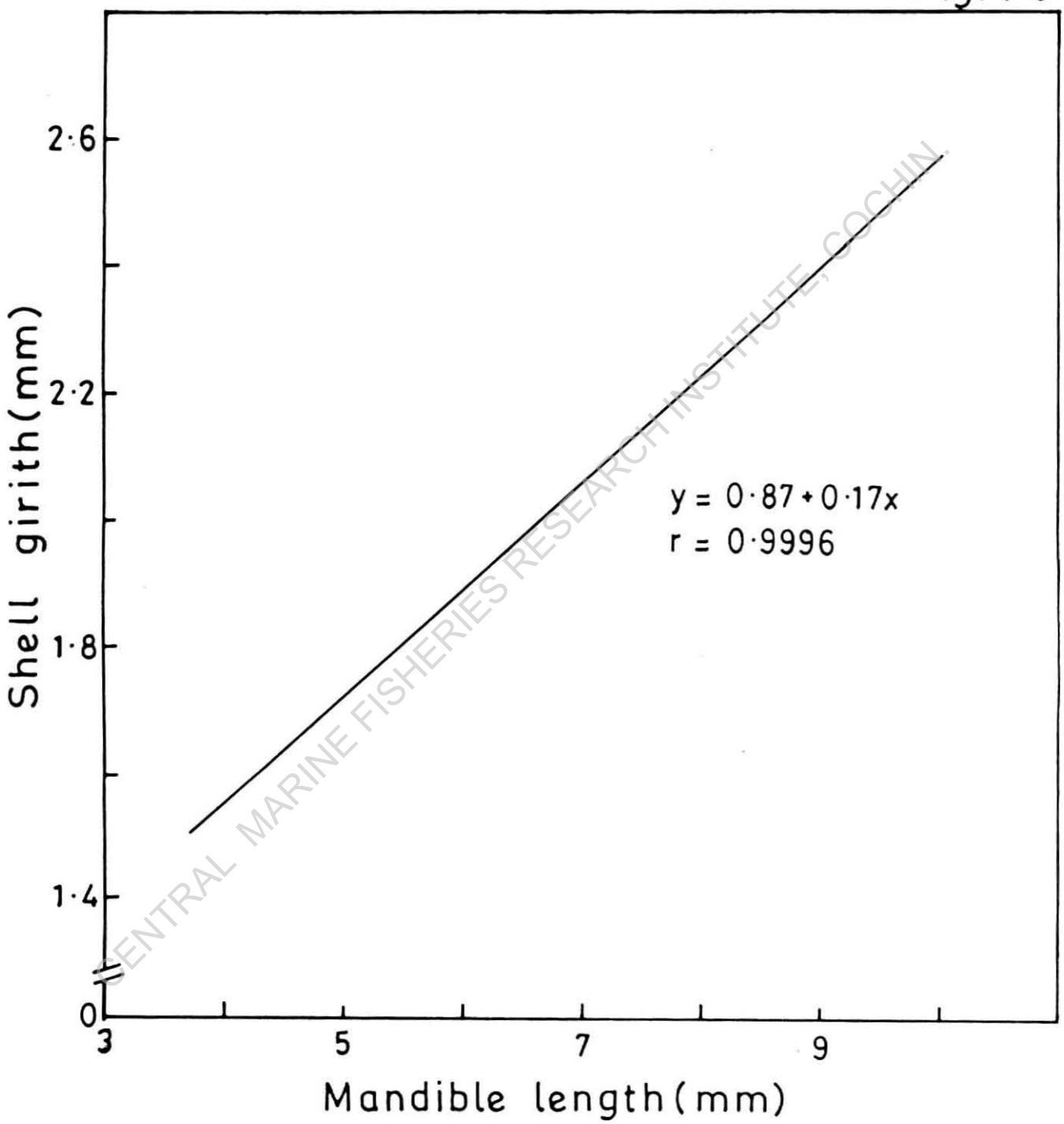


Fig.4.5. Relationship between mandible length of lobster and breakable mussel shell girth

Fig. 4·5



7.9 mm at 5 mm and half way from the distal margin, respectively. The shell girth of a larger mussel (55 mm SL) was 2.7, 4.7 and 15.4 mm at 3, 5 mm and half way from the distal margin, respectively. The lobster trimmed the shell from the distal margin upto a distance to which it can break the shell and when the shell girth exceeded 26 % of the mandible length, the lobster restricted the trimming and scooped the meat of the shell. However, if the prey was too small for the predator, it crushed the entire shell and sorted out the meat. Hence, it may be concluded that the mandible length of the lobster decides i) the critical size of the prey which the lobster could handle and ii) the distance from the distal margin of the shell upto which the shell has to be trimmed, thereby determining the effort which the lobster has to spend in crushing the shell.

4.3.3 Preferred prey size

To determine the size of the prey that was preferred by the lobster, 7 size classes of **P. homarus** were exposed to different size groups of mussel (5 numbers in each size group) simultaneously and consecutively for 3 days (Table 4.2). The number of mussels predated in each size group was replaced by an equal number of the same size group of mussels every day in order to maintain equal number of all size groups of prey.

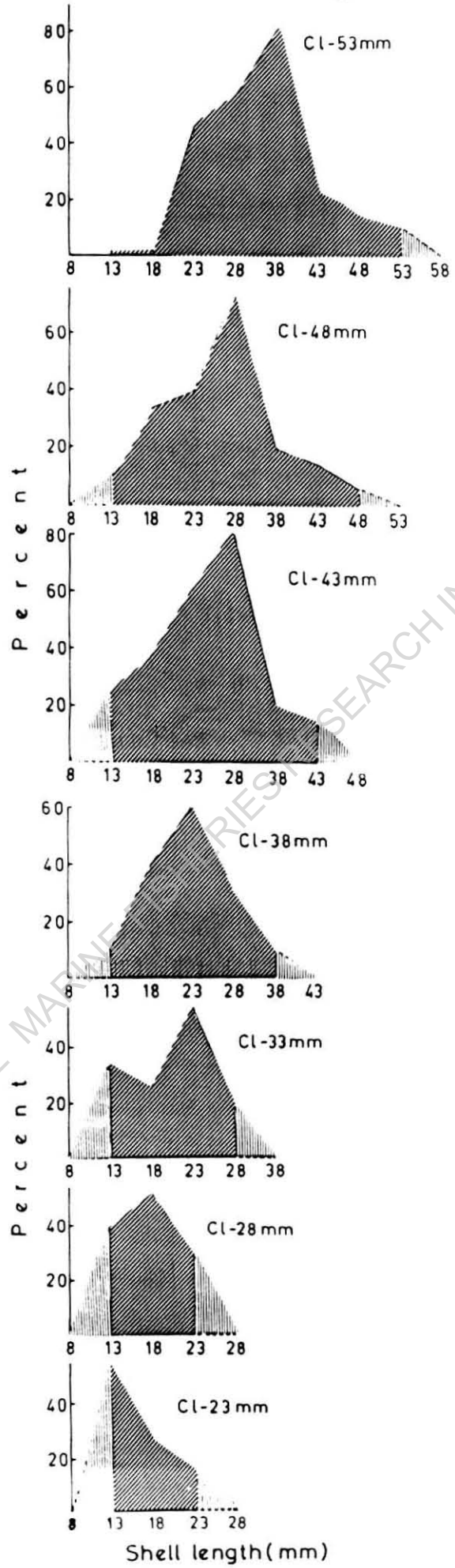
Table 4.2 Carapace length (CL) of the lobster and shell length (SL) of the mussel used in the experiment to determine preferred prey size; each length value represents the mean of 5 mm length group

Sr.No.	CL (mm)	N	SL (mm)
1	23	3	13,18,23
2	28	3	13,18,23
3	33	3	13,18,23,28
4	38	3	13,18,23,28,38
5	43	3	13,18,23,28,38,43
6	48	3	13,18,23,28,38,43,48
7	53	3	13,18,23,28,38,43,48,53

The size of prey preferred by the lobster increased with the size of the lobster. For instance, a 23 mm CL lobster predated mussels ranging from 13-23 mm SL. However, it preferred to predate on 13 mm SL mussel and 57 % of the total predation was on this size group (Fig. 4.6). A comparatively larger lobster of 53 mm CL predated mussels ranging from 23-53 mm SL with maximum predation on 38 mm SL (35 % of total predation). In the previous experiment (4.3.2), a positive linear relationship was established between the size of the lobster and the critical size of the prey; the critical size of the prey was 13 % body weight of the lobster. By substituting the weight equivalent to the carapace length of the lobster and preferred shell length of the mussel determined in this experiment, it is evident that the preferred size group not only increased with increasing size of the lobster, but also increased in terms of percent body weight of the predator. For instance, the preferred prey size (18 mm SL) of 28 mm CL lobster was 3 % of its body weight, whereas the preferred prey size (38 mm SL) of 53 mm CL lobster was 4 % of its body weight. It appears that the larger lobster prefers to predate on larger mussels so as to acquire maximum food and also to spend lesser effort by breaking the shells of few large mussels than by breaking the shells of many smaller mussels.

Fig.4.6. Percent of different size groups (shell length) of mussel predated by 7 size classes (CL:carapace length) of lobster; the unoffered size groups are represented as (|||||||||)

Fig. 4·6



The efficiency of the predator decreased sharply when the predator was exposed to prey larger than the preferred size. For instance, about 80 % of total predation of the 53 mm CL lobster was on the preferred prey size (38 mm SL) and lesser than the preferred prey size and only 20 % was on size larger than the preferred size (Fig. 4.6).

4.3.4 Optimum prey size

To determine whether the preferred prey size is the optimum size (in terms of energy acquisition of the lobster, an experiment was conducted by exposing different size groups of mussels to 3 size classes of lobster (Table 4.3).

In this experiment, each lobster was offered 15 mussels of the respective smallest size group for 17 hr (1600 - 0900 hr). The number of mussels consumed was noted and the next larger size group of mussels was offered on the next feeding day. The experiment was continued till all the size groups of mussels mentioned in Table 4.3 were offered. The number of mussels consumed by each size class of lobster decreased with increasing mussel SL. For instance, the smallest tested lobster (38 mm CL) predated 6.7 mussels/day of 23 mm SL and only 1.0 mussel/day of 38 mm SL (see also Fig. 4.6). Correspondingly, the energy acquired by the 38 mm CL lobster also decreased from 23.0 KJ/day (23 mm SL) to 12.4 KJ/day (38 mm SL) (Fig.4.7). Hence, the preferred size is

Table 4.3 Carapace length (CL) of the lobster and shell length (SL) of the mussel used in the experiment to determine optimum prey size; each length value represents the mean of 5 mm length group

Sr.No.	CL (mm)	N	SL (mm)					
			1	2	3	4	5	6
1	38	3	23	28	33	38		
2	48	3	28	33	38	43	48	
3	58	3	33	38	43	48	53	58

Table 4.4 Carapace length (CL) of the lobster and shell length (SL) of the mussel used in the experiment; each length value represents the mean of 5 mm length group

Sr.No.	CL (mm)	SL (mm)	Expt. duration (days)
1	38	18,23,28	4
2	48	28,33,38	4
3	58	38,43,48	4

Fig.4.9 Number of different size groups (shell length) of mussels and energy consumed by 3 size classes (Cl : carapace length) of lobster after 7 days of starvation; the values are mean of 4 feeding days.

Fig. 4·8

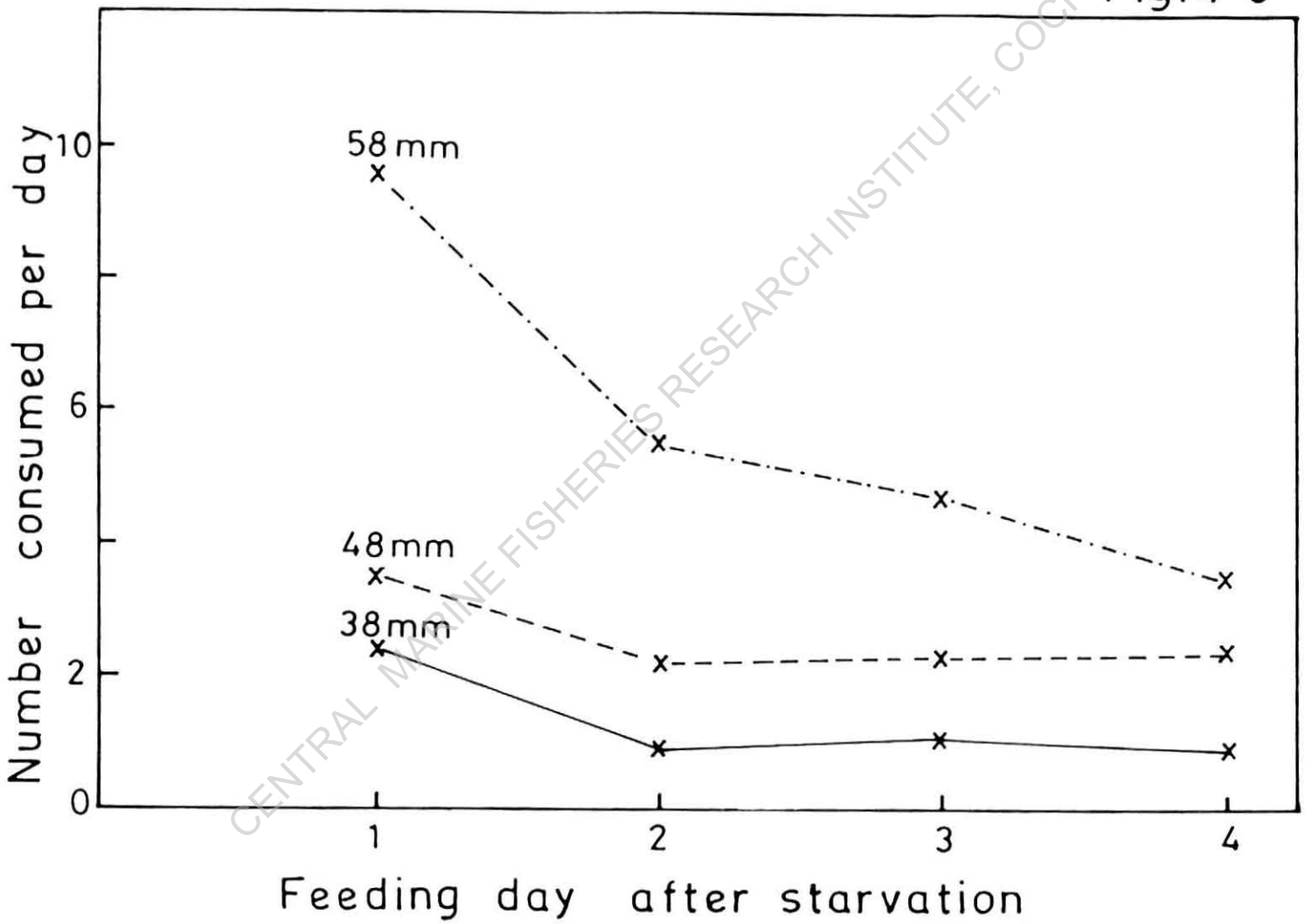


Fig.4.8. Number of mussels consumed by 3 size classes (carapace length : 38,48 and 58 mm) of lobster after 7 days of starvation; the values on different size groups of mussel are pooled

consumed by the predator was recorded every day; the number of mussels consumed every day was replaced by an equal number of same size group of prey so that the number of mussels of each size group was constant.

After 7 days of starvation, different size classes of lobster consumed maximum number of mussels on the I feeding day than the subsequent 3 feeding days. This trend was more conspicuous in the largest tested size class of lobster (58 mm CL), which predated 9.5 mussels on the I day of feeding and only 3.5 mussels on the IV day of feeding (Fig. 4.8).

The number of prey consumed on the 4 feeding days was pooled and the equivalent energy values are presented in Fig. 4.9. The result suggests that the lobster was able to predate all the available size groups of the mussel after 7 days of starvation. The starved and refed lobsters exhibited marginal difference in predatory efficiency compared to normally feeding lobsters (Section 4.3.4). For instance, the 58 mm CL lobster acquired maximum energy (36.7 KJ/day) by predating 43 mm SL mussel compared to a regularly feeding 58mm CL lobster, whose optimum prey size was 48 mm SL (Fig.4.7).

the optimum size for the small lobsters. However, the optimum prey size was not the preferred prey size in all size classes of lobster. For instance, the preferred prey size groups were 28 and 33 mm SL for 48 and 58 mm CL lobsters, respectively; the optimum prey size (in terms of energy acquisition) for these size classes were 33 and 48 mm SL (Fig. 4.7). Hence, the larger lobsters acquired maximum energy by predating larger prey than the preferred size group.

It is deduced from this experiment that i) the smaller lobster (< 43 mm CL) acquires maximum energy by predating the preferred size group; and ii) the larger predator (> 43 mm CL) acquires maximum energy if exposed to prey larger than the preferred size; and hence, iii) the preferred prey size is not the optimum prey size for all the size classes of the lobster.

4.3.5 Effect of starvation on predation

To determine the effect of starvation on predation of the lobster, 3 size classes of **P. homarus** were starved for 7 days and each size class was subsequently offered 3 size groups of mussel simultaneously for 4 days (Table 4.4). Each lobster was offered 5 numbers of each size group of mussel. In other words, each lobster was offered 15 mussels representing 3 size groups. The size and number of mussels

Fig. 4·7

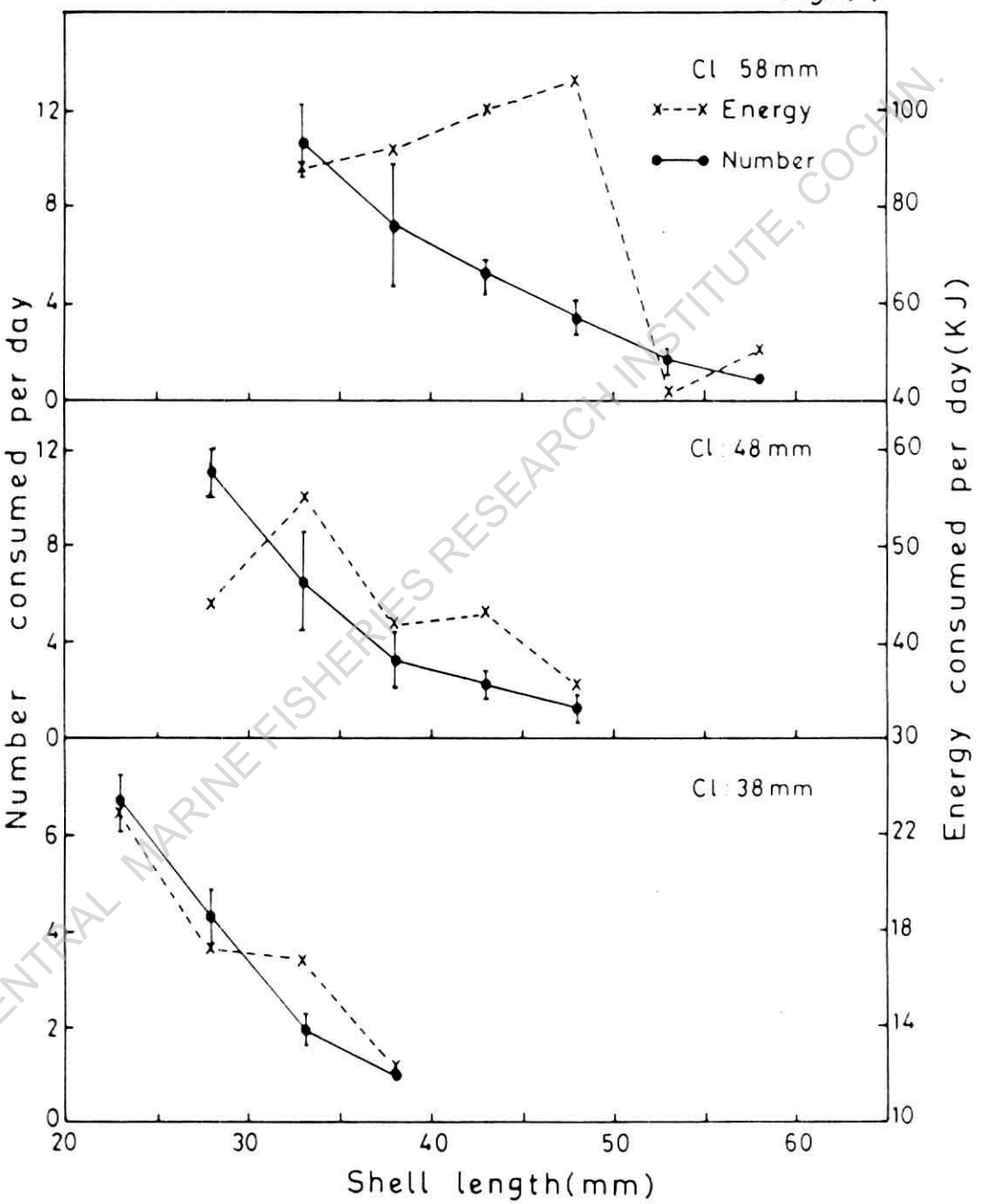
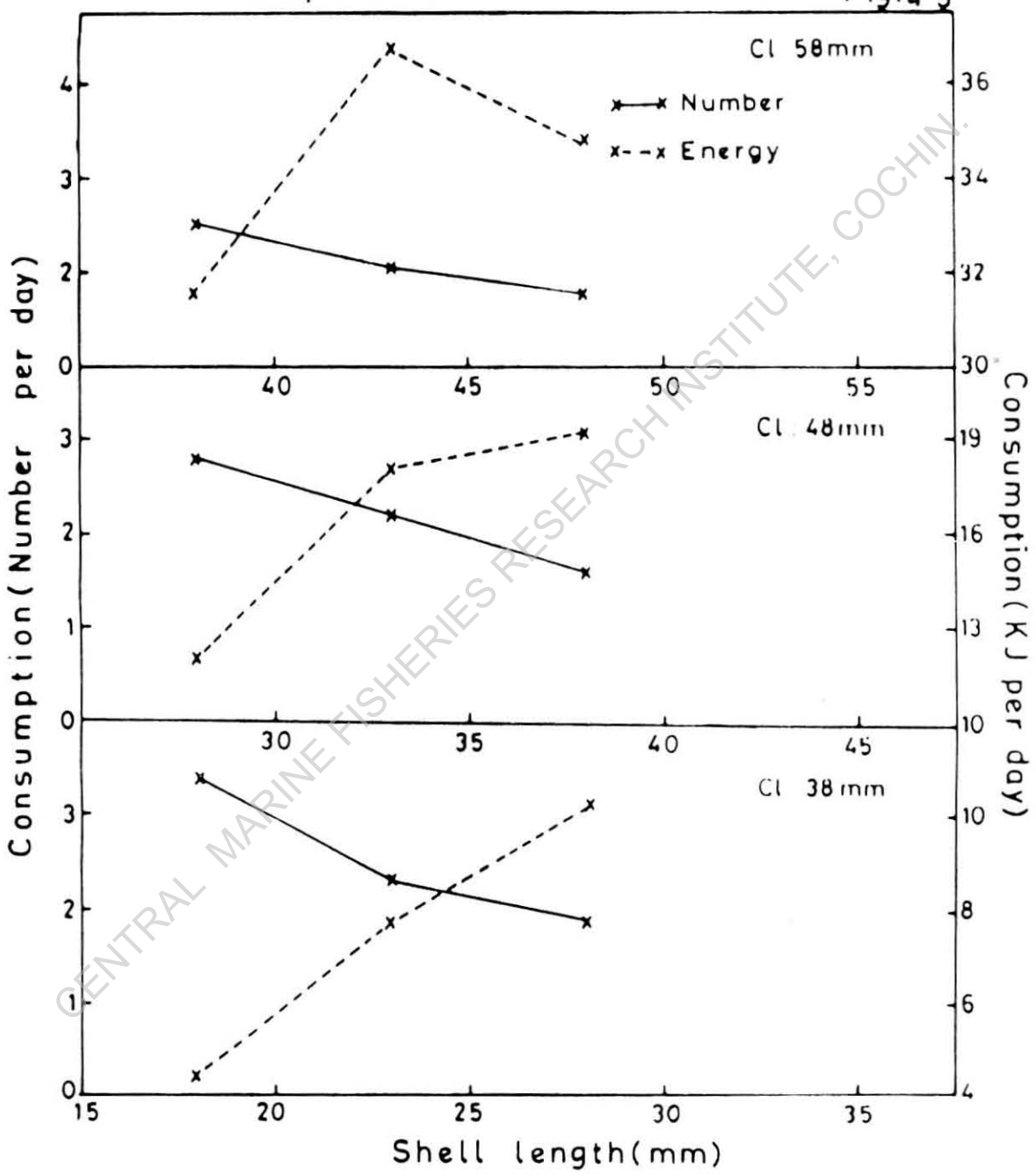


Fig.4.7. Number of different size groups (shell length) of mussels and energy consumed by 3 size classes (Cl: : carapace length) of lobster.

Fig.4.9



4.4 Discussion

The results obtained in the first 3 experiments have revealed a strong positive correlation (with very high 'r' values) between the size of the predator and the critical, preferred and optimum size of the prey (Table 4.5; see also Fig. 4.1 and 4.2). As mandible length of the lobster directly determined the critical, preferred and optimum shell girth of the mussel that could be broken (Fig. 4.10) and as mandible length was positively correlated with the size of the lobster (Fig. 4.4), the critical, preferred and optimum sizes of the prey were positively correlated with the size of the predator in terms of length (Fig. 4.11) as well as weight (Fig. 4.12). The different size classes of lobster had the capacity to predate prey which was 13 % of its body weight; however, the lobster preferred prey which was 3-4 % of its weight.

The shell girth of the mussel played an important role in determining the predatory efficiency of the lobster. If the size of the prey was large, the lobster could crush the shell girth which was 26 % (from the shell margin) of the mandible length (see Fig. 4.5). If the prey was smaller and within the handling capacity, the lobster trimmed about 3 mm of the mussel shell from the shell margin irrespective of the size of the mussel. As the shell girth at 3 mm site

Table 4.5 Values of least square estimates in the relationship between size of the lobster (x) and critical, preferred and optimum size of the mussel (y)

Prey size	a	b	r
i. carapace length (mm) vs shell length (mm)			
Critical size	- 3.20	1.15	0.9982
Preferred size	- 5.07	0.79	0.9710
Optimum size	- 11.72	0.98	0.9813
ii. lobster weight (g) vs mussel weight (g)			
Critical size	- 0.42	0.14	0.9693
Preferred size	- 0.21	0.03	0.9440
Optimum size	- 1.11	0.05	0.9830
iii. mandible length (mm) vs shell girth (mm)			
Critical size	0.87	0.17	0.9996
Preferred size	0.66	0.13	0.9722
Optimum size	0.47	0.16	0.9779

Fig.4.10. Relationship between mandible length of lobster and critical, preferred and optimum length of mussel shell broken.

Fig. 4·10

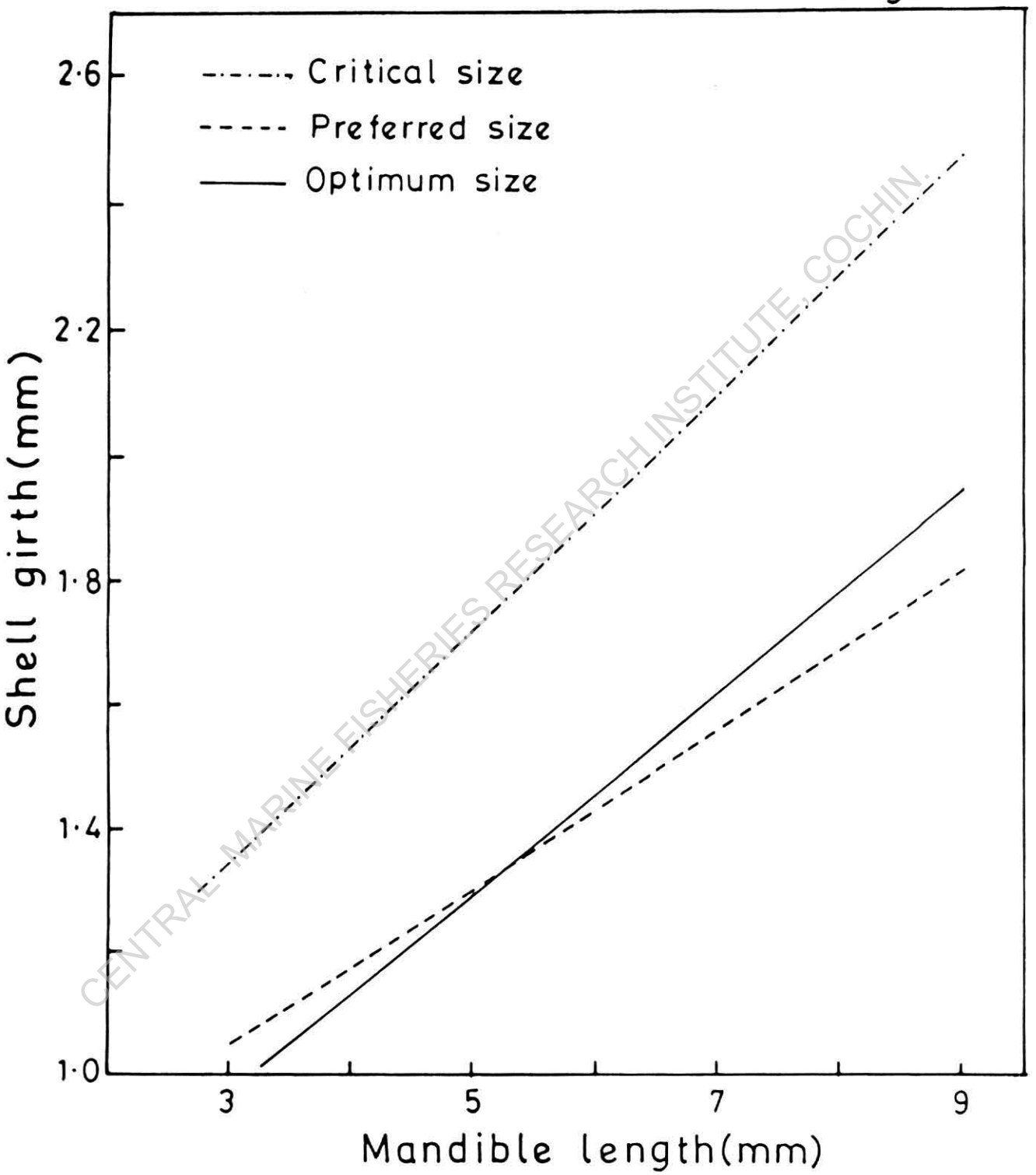


Fig.4.11. Relationship between carapace length of lobster and critical, preferred and optimum length of mussel shell broken.

Fig. 4·11

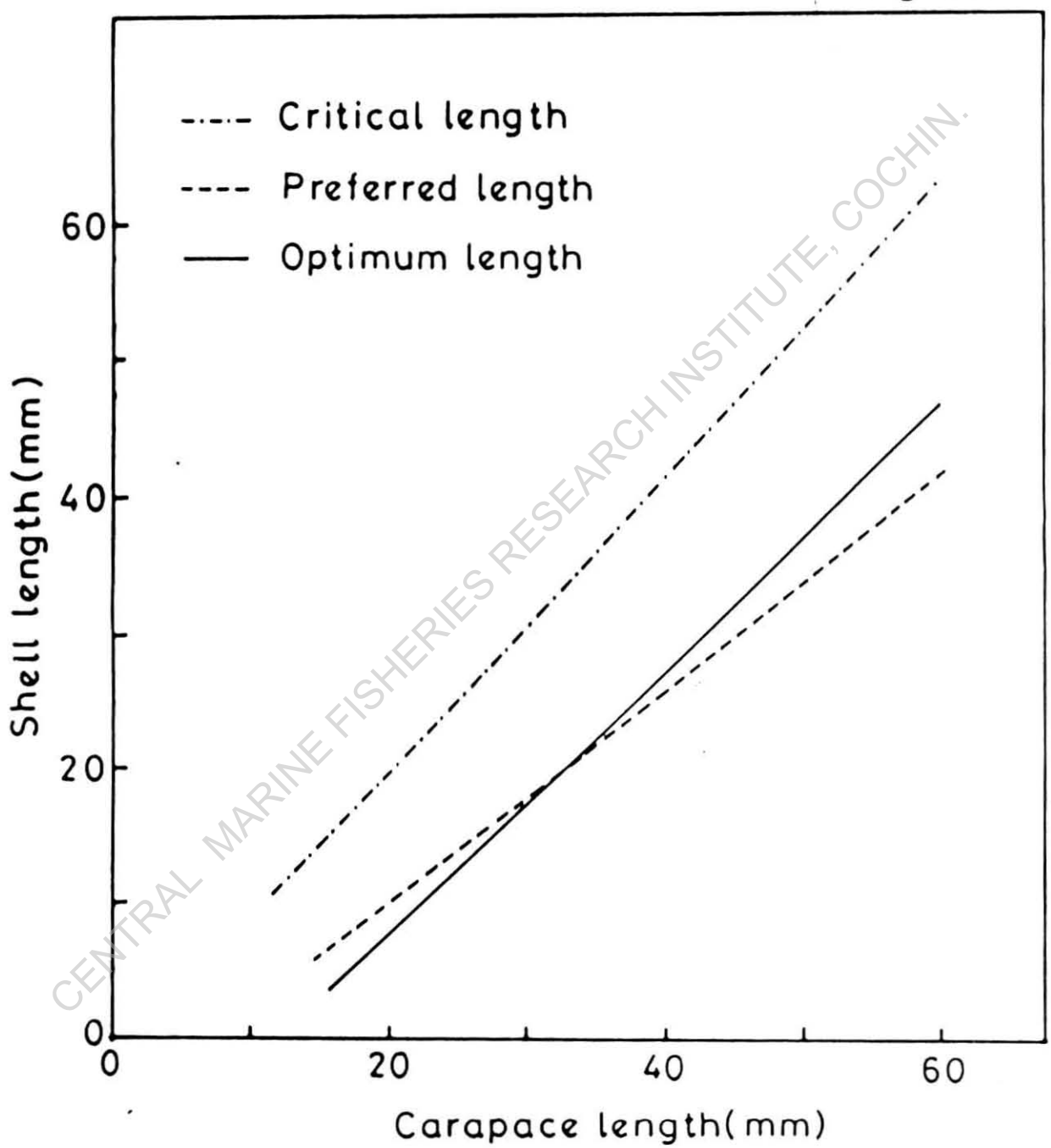
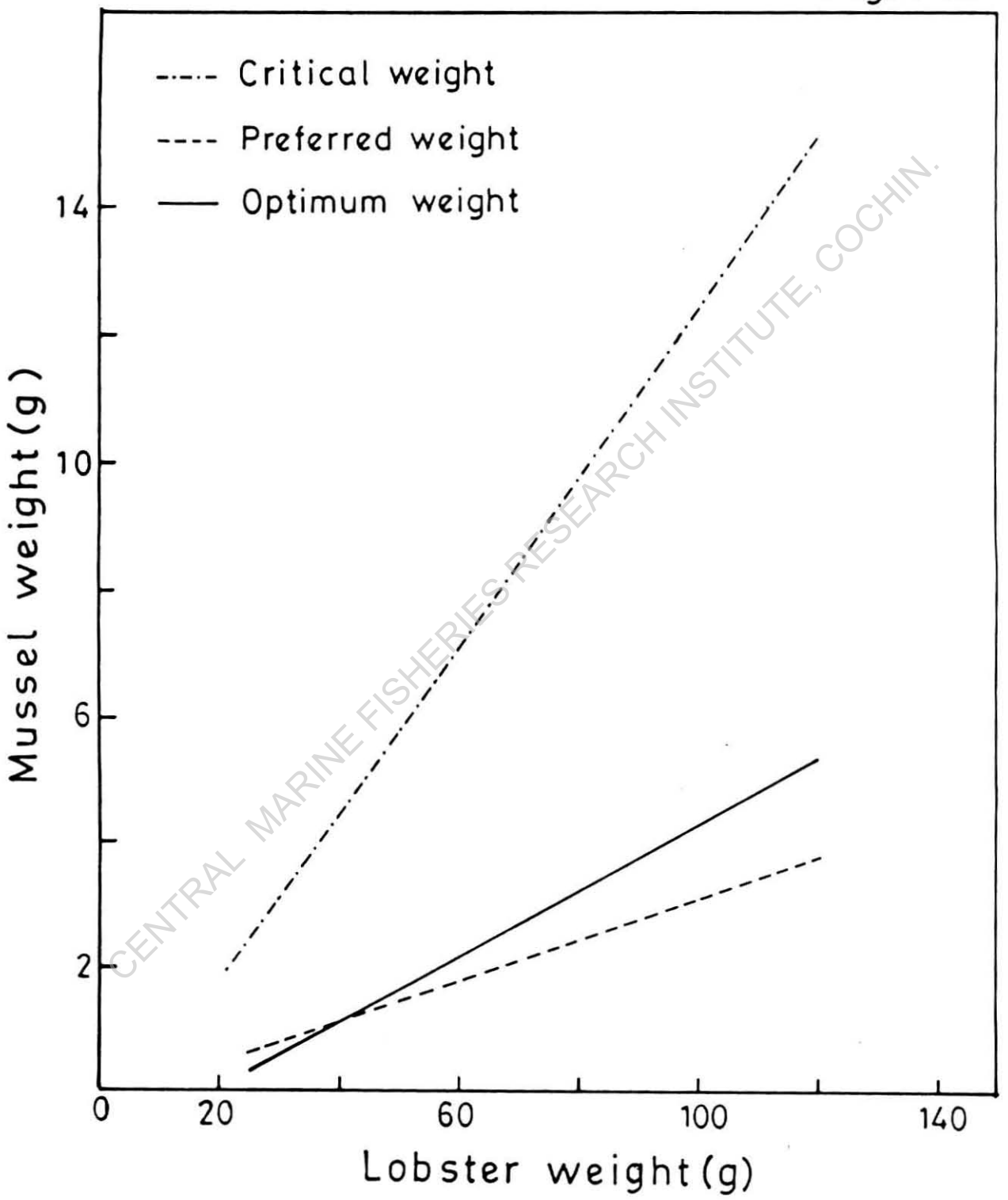


Fig.4.12. Relationship between live weight of lobster and critical, preferred and optimum live weight of mussel predated.

Fig.4·12



increased with increasing size of the mussel (Fig. 4.3), the lobster which was offered different size groups of mussel had to crush shells of different shell girth. For instance, a 38 mm CL lobster (mandible length: 7.5 mm) had to crush shell girth of 1.46, 1.65 and 1.95 mm when predating 23, 28 and 38 mm SL mussel, respectively; however, the reward of energy did not increase by crushing larger shells and the lobster acquired 24.0, 18.2 and 12.1 KJ/day, respectively (Fig. 4.7). Hence, a 38 mm CL lobster acquired maximum energy by crushing shell girth of 1.46 mm (23 mm SL) and the 23 mm SL was the preferred size group of mussel for the lobster (Fig. 4.6). Hence, the lobster broke shell girth (1.46 mm, which was about 20 % of the mandible length) optimum to its breaking power and succeeded to acquire maximum energy. The lobster could not crush a very strong shell and at the same time crushing smaller mussels with very thin shell girth may prove to be no advantage because the acquisition of energy may not compensate the energy spent on crushing the prey. Hence, the lobster of different size classes preferred to crush the optimum shell girth in order to obtain maximum energy.

This kind of foraging strategy appears to be obligatory for the lobsters, as it does not possess powerful chelae like the crabs and the homarid lobsters. Crabs like **Ovalipes punctatus** (Du Preez, 1984), **Carcinus maenas** (Elner and Hughes, 1978), **Cancer iroratus** and the American lobster,

H. americanus (Elner, 1982) possess crusher chela and are not only capable of crushing very thick shelled molluscs but also are capable of prising open any large sized shells. Du Preez (1984) concluded that since the swimming crab, **O. punctatus** had a variety of bivalve opening techniques that varied with prey size and shell strength, it has no upper prey size limit. As the lobster does not posses similar morphological advantage, it is forced to adopt predatory strategy to suit the main predatory organ, viz., the mandible.

Starving the lobster for 7 days did not appreciably reduce the predatory efficiency. Starvation forms part of the life of the lobster. It was observed during the present study that the normal lobster starved for 5 days from Stage D_4 to Stage B during every moult cycle (Chapter 3). During this period, the lobster did not feed even on soft molluscan meat removed from the shell. Hence, during every moult cycle lasting 45-55 days (45 - 50 mm CL lobster), the lobster did not feed for about 5 days, i.e. about 10 % of every moult cycle, it starved. Hence, starvation for a short duration of 7 days did not appreciably affect the predatory efficiency of the lobster. Perhaps, longer duration of starvation may result in predating smaller size groups of prey than the optimum size.

5 EFFECT OF FOOD QUALITY ON FOOD UTILIZATION

5.1 Introduction

A number of biotic and abiotic factors are known to influence food intake, growth and metabolism of an animal. It is imperative to identify these factors and study their effects on food utilization parameters so as to provide optimum rearing conditions, especially to the culturable organisms like the lobster. Food quality has been identified as one of the important factors that influences growth process in animals (Brown, 1957; Ford, 1977; Sedgwick, 1979a). Study on the effects of food quality on food utilization would provide valuable clues on the nature of food that could be recommended for achieving maximum growth rate. Though potential for culture of lobsters is vast, there is only limited attempt to identify the food that provides maximum growth rate. The available studies have concentrated on the effects of formulated feed with varying lipid, carbohydrate and protein contents on the growth of the lobsters, especially in the American lobster, **H. americanus** (Castell, et.al., 1976, 1977; Mauviot and Castell, 1976; Capuzzo and Lancaster, 1979). These studies have repeatedly demonstrated that pellet instability results in unrecoverable loss of the diet, leading to deterioration in water quality. Furthermore, pellet diet is not readily accepted by most of

the spiny lobsters (personal observation). The spiny lobsters have the tendency to tear and eat the food material with the help of the mandible and hence, pellet is not suited for their feeding behaviour. The unsuitability of the pellet feed calls for studies on the effect of natural food on the food utilization of the spiny lobsters.

The lobsters feed selectively under natural conditions. Berry (1971) observed that the diet of the spiny lobster, **P.homarus** consists mostly of mussels.Chittleborough (1974) reported that the rock lobster, **P.longipes cygnus**, although accepts a wide range of animals as food, prefers molluscs to fish. Phillips et.al. (1980) also reported that the lobsters are selective of the food they eat, despite reputation as scavengers or omnivores. The proportion of food items in the stomach of the lobsters is reported to be different from the relative abundance of the food items in the habitat. For instance, the proportion of the crabs in the diet of **H. americanus** was much higher than the relative density in the field (Weiss, 1970; Ennis, 1973). Evans and Mann (1977) reported selective feeding behaviour of **H.americanus** in the laboratory too. They estimated that the lobster predating on crabs gained 15 times more energy and 4 times more protein than the lobster consuming sea urchin. Despite these clues available on the selective

feeding of the lobsters in the natural as well as laboratory conditions, there is no detailed investigation on the effect of different natural food on food utilization of the lobsters. In the present work, the effects of 4 different food, viz., mussel, clam and fish and combination of these three food on rates and efficiencies of feeding, assimilation and conversion have been studied in the spiny lobster, **P.homarus.**

There are number of publications on the effects of eyestalk ablation on moulting frequency, food intake and growth of the lobsters (Mauviot and Castell, 1976; Castell et.al., 1977; Vijayakumaran and Radhakrishnan, 1984; Radhakrishnan and Vijayakumaran, 1987a). Removal of eyestalk and consequently the elimination of Moult Inhibiting Hormone, has been established to result in accelerated moulting frequency and thereby in enhanced growth rate (see also Aiken, 1980). However, later studies on the spiny lobsters, **P. homarus** (Radhakrishnan and Vijayakumaran, 1984, 1987a), **P. ornatus, P. polyphagus** and **P.versicolor** (Silas et.al., 1984) have conclusively shown that eyestalk ablation accelerates moulting frequency as well as growth rate. There is no study so far on the effects of interaction of eyestalk ablation and food quality on food utilization of the lobsters.

The lobsters adopt definite pattern of social behaviour (Aiken and Waddy, 1977; Ford, 1977). The American lobster, **H. amaericanus**, for instance, is solitary in living and when reared in groups, it becomes cannibalistic; the physiological status of the animal is also affected, resulting in delayed moulting (Cobb, 1968, 1970; Cobb and Tamm, 1974). In contrast, most spiny lobsters are gregarious. Chittleborough (1975) reported that the spiny lobster **P.longipes cygnus** grew less rapidly when reared individually than when held in groups. However, Radhakrishnan and Devarajan (1986) observed no significant difference in the growth rate of the isolated and group-reared **P.polyphagus.** In the present study, the effects of isolation and group-rearing on food utilization of the gregarious **P.homarus** have been investigated.

Hence, the 3 factors, viz., food quality, eyestalk ablation and isolation were selected for the study on food utilization of the spiny lobster **P.homarus.** The interaction of the 3 factors on food utilization was investigated by designing the following 4 experiments: i) food utilization of isolated, normal lobster receiving different food, ii) food utilization of isolated, bilaterally eyestalk ablated lobster receiving different food, iii) food utilization of group-reared, normal lobster receiving different food and

iv) food utilization of group-reared, bilaterally eyestalk ablated lobster receiving different food.

5.2 Materials and methods

The size of the selected lobsters and the experimental conditions are presented in Table 5.1. In the two experiments on the isolated lobsters, each lobster was reared in individual aquarium; in the two experiments on group-rearing, 4 lobsters were reared in each aquarium. Each test group receiving different food in all the experiments was maintained in quadruple or in triplicate. In all the experiments, equal number of males and females were used.

Each experiment was divided into 4 groups, each group receiving one of the following 4 food: i) the green mussel, **Perna viridis**, ii) the backwater clam, **Meretrix casta**, iii) the clupeid fish and iv) combination of the three food. Among the selected food, the mussel formed the preferred food of the lobster; the clam is a backwater inhabitant and hence, is not available for the marine lobster; the clupeid fish, though co-inhibits and is available to the lobster, **P.homarus** is incapable of predating fast moving fish. Hence, the latter two food items do not form the natural food of the lobster.

Table 5.1 Experimental condition in the study on effect of food quality on food utilization of P. homarus

Expt. No.	Condition of lobster	No.of lobster	Initial size CL(mm)	Initial size Wt(g)	Size of aquarium (cm)	Volume of water (l)	Temp. (°C)	Sal. (‰)	O_2 Content (ml/l)	Duration (day)
1.	Isolated, normal	1 lobster x 4 food (quadruple)	44.6 ± 1.4	92.4 ± 8.4	61 x 40.5	61.8	24.8 ± 0.6	35.2 ± 0.8	4.2 ± 0.2	100
2.	Isolated, ablated	1 lobster x 4 food (quadruple)	46.6 ± 1.7	100.9 ± 8.4	61 x 40.5	61.8	24.8 ± 2.0	35.2 ± 0.6	4.5 ± 0.7	100
3.	Group-reared, normal	4 lobster x 4 food (triplicate)	47.4 ± 1.8	105.4 ± 14.1	90 x 60	216.0	26.4 ± 2.4	34.8 ± 0.8	4.2 ± 0.4	83
4.	Group-reared, ablated	4 lobster x 4 food (triplicate)	51.1 ± 2.6	119.9 ± 17.4	90 x 60	216.0	26.2 ± 2.2	35.5 ± 0.6	4.0 ± 0.8	118

The green mussel cultured in the lagoon near the laboratory (Sreenivasan et.al., 1988), was brought to the laboratory once in 3 days and was maintained in the laboratory. The backwater clam was collected daily from the Kovalam backwaters. Before feeding the experimental lobsters, the shells of the mussel and the clam were removed and only the animal tissue was offered. The clupeid was collected from the fishermen and stored in deep freezer; the required quantity was thawed every day, cut into small pieces after removing the scales, gut and gonad and fed to the lobsters. The group receiving mixed food was offered equal proportion of the three food.

All the experimental lobsters were fed **ad libitum.** The **ad libitum** quantity for each food was arrived at by feeding the lobsters on excess quantity of food on the first 3 days of the experiment; the quantity was revised after every moult. Food was weighed to the nearest 1 mg in a top pan balance and fed daily at 4 pm and the unconsumed food was removed at 9 am on the following day (feeding duration: 17 hr). Faeces was collected two days in a week and the total faeces egested was estimated as mentioned in Chapter 2.5.2.

The procedures on eyestalk ablation, estimation of biochemical and energy values and the methods followed for determining the food utilization parameters are described in Chapter 2.

5.3 Results

The water, ash, lipid, carbohydrate, protein and energy contents of mussel, clam, fish and mixed food are presented in Table 5.2. The major differences among the different food were: i) The ash content was 50 % higher in the fish (12.6 %) than in the mussel (8.4 %); ii) the lipid content was marginally lower in the clam (7.0 %) than in all other food; iii) the protein content was 40% higher in the fish (74.8 %) than in the clam (53.5 %); iv) carbohydrate content was extremely high in the clam (29.3 %)) than in the fish (1.1 %); Lakshmanan and Nambisan (1980) also reported high carbohydrate content (27.4 %) in the clam, **M. casta** from Cochin backwaters; and v) energy content differed marginally between the food and the minimum (mussel: 17.6 KJ/g) and maximum (fish: 20.5 KJ/g) values were significantly different ($t = 3.5$; $P < 0.05$). The values for each component in the mixed food were the respective average of all the 3 food.

Table. 5.2 Biochemical composition of food offered to P.homarus

Parameters	Mussel	Clam	Fish	Mixed food*
Water (%)	76.3 ± 2.1	76.3 ± 2.9	77.5 ± 3.1	76.7 ± 0.6
Ash (%)	8.4 ± 0.1	9.3 ± 0.2	12.6 ± 1.9	10.1 ± 1.8
Lipid (%)	9.9 ± 1.9	7.0 ± 1.2	9.1 ± 2.0	8.7 ± 1.2
Protein (%)	69.3 ± 4.6	53.5 ± 3.5	74.8 ± 4.8	65.9 ± 9.0
Carbohydrate (%)	7.3 ± 1.8	29.3 ± 1.4	1.1 ± 0.1	12.6 ± 12.0
Protein: Carbohydrate	9.5	1.8	68.0	5.2
Energy (KJ/g)	17.6 ± 0.4	18.8 ± 1.2	20.5 ± 2.5	19.0 ± 1.0

* Mean value of the other 3 food

5.3.1 Effect of food quality on food utilization of isolated, normal lobster

Feeding rate

The group receiving mixed food exhibited the highest feeding rate (371.3 J/g live body weight/day) and the groups receiving mussel (243.2 J/g/day) and fish (245.2 J/g/day) consumed far lesser (Table 5.3); the highest and the lowest values were significantly different (mixed food vs mussel: $t = 10.0$; $P < 0.05$). It is evident from this experiment that the isolated, normal **P. homarus** has the capacity to increase the feeding rate by 52.7 % depending upon the type of food. In the group which exhibited the maximum feeding rate (i.e. mixed food), it was observed that the lobster preferred to feed on the soft bodied clam and mussel; fish was consumed in very limited quantity. Though the 3 food were offered in equal proportion to the group receiving mixed food, the consumption of clam, mussel and fish formed 42, 39 and 19 % of the total food consumed, respectively. However, the lobster did not exhaust the most preferred food, viz., clam and unfed remains of all the 3 food were observed every day.

Assimilation

P. homarus exhibited uniformly high assimilation efficiency (mean: 98 %) in all the experimental groups. Consequently, assimilation rate fluctuated in correspondence to the feeding rate.

Table 5.3 Effect of different food on food utilization paratmeters of isolated, normal P.homarus; rates are expressed as J/g live lobster/day; efficiencies as %; each value represents average of 4 lobsters; ± represents S.D.

Parameters	Mussel	Clam	Fish	Mixed
Feeding rate	243.2 ± 19.1	281.9 ± 17.2	245.2 ± 12.3	371.3 ± 23.2
Assimilation rate	237.8 ± 19.2	276.4 ± 17.4	241.5 ± 12.4	363.1 ± 23.3
Conversion rate				
E*	6.9 ± 1.4	7.0 ± 0.4	6.6 ± 0.2	7.4 ± 1.1
P**	14.2 ± 1.2	15.6 ± 1.0	17.5 ± 1.5	20.8 ± 1.8
E + P	21.1 ± 1.5	22.6 ± 2.0	24.2 ± 2.1	28.2 ± 1.8
Metabolic rate	216.8 ± 18.4	253.8 ± 16.2	217.3 ± 11.2	334.9 ± 22.2
(ml O_2/g/hr)	0.45 ± 0.02	0.53 ± 0.03	0.45 ± 0.04	0.69 ± 0.05
Assimilation efficiency	97.9 ± 1.4	97.8 ± 0.8	98.5 ± 0.2	97.8 ± 0.5
Conversion efficiency (K_2)				
WE'	8.8 ± 1.3	8.5 ± 0.6	10.1 ± 0.5	7.8 ± 0.2
WOE"	5.9 ± 0.4	5.8 ± 0.2	7.2 ± 0.3	5.7 ± 0.4

* Exuvia; ** Growth
' with exuvia; " without exuvia

Conversion

The conversion rate (including exuvia) was maximum (28.2 J/g/day) in the group receiving mixed food (Table 5.3). The remarkable difference in the feeding rate between the groups resulted in significant difference in the conversion rate. For instance, the 52.7 % difference in the feeding rate between the groups receiving mussel and mixed food resulted in about 30 % higher conversion rate in the group receiving mixed food than the group receiving mussel. However, the group receiving fish, which fed at a low rate, exhibited comparatively high conversion rate (24.2 J/g/day) than the groups receiving mussel and clam. The comparatively higher conversion rate in the group feeding on fish was possible due to the highest conversion efficiency (K_2 = 10.1 %) exhibited by this group. After excluding the energy lost as exuvia, the K_2 remained the highest in the group receiving fish (7.2 %) and the value was significantly higher ($t = 6.8$; $P < 0.05$) than the group receiving mixed food (5.7 %), which exhibited the maximum feeding and conversion rates.

In the present study, exuvia is included as a form of converted energy, as it is part of growth. The experimental groups lost 26.2 to 34.2 % of converted energy as exuvia (Table 5.4). Exuvia is an energy dilute tissue; the mean

Table 5.4 Percent of conversion lost as exuvia in P. homarus; the estimations were made based on dry weight and energy

Condition of lobster	Mussel		Clam		Fish		Mixed	
	Dry wt.	Energy	Dry wt.	Energy	Dry wt.	Energy	Dry wt.	Energy
Isolated, normal	70.4	34.2	58.1	31.0	58.4	27.3	50.0	26.2
Isolated, ablated	31.1	11.4	71.4	40.3	70.0	39.5	62.9	23.2
Group-reared, normal	44.8	20.0	56.5	27.8	70.6	41.0	55.3	26.6
Group-reared, ablated	45.5	19.6	51.4	19.9	57.9	28.5	48.0	21.2

energy content of exuvia of normal lobster was 4.257 KJ/g, as against the mean energy content of 14.125 KJ/g of the lobster. Hence, the lobster discarded a low quantum of energy (mean: 29.7 % of converted energy) as exuvia and a major portion of the converted energy (70.3 %) was utilized for actual body growth. In terms of dry weight, however, the exuvia formed a major component of conversion; the dry weight of exuvia of the lobster receiving different food ranged from 50.0 to 70.4 % of the converted dry matter (mean: 59.2 %) (Table 5.4).

Metabolic rate

The metabolic rate fluctuated in correspondence with the feeding rate. For instance, the highest (mixed food: 334.9 J/g/day or 0.69 ml O_2/g/hr) and the lowest (mussel: 216.8 J/g/day or 0.45 ml O_2/g/hr) metabolic rates were exhibited by the groups which exhibited the highest and the lowest feeding rates (Table 5.3). The 52.7 % difference in the feeding rate between the groups receiving mixed food and mussel resulted in almost equal percentage of difference in the metabolic rate also. In other words, almost equal percentage of consumed food energy (88.6 - 90.2 %; mean: 89.5 %) was spent on metabolism by the groups receiving different food.

Intermoult duration

P. homarus moulted twice during the experimental period. At the commencement of the experiment, all the lobsters were in intermoult stage (stage C) and the first moult was completed in 27.4 to 39.0 days (mean: 33.4 ± 4.3 days). The intermoult duration between the first and the second moult was 47.0 to 50.5 days (mean: 49.1 ± 1.3 days) (Table 5.5). The intermoult duration among the test individuals receiving different food was not statistically significant.

5.3.2 Effect of food quality on food utilization of isolated, ablated lobster

Feeding rate

The isolated, ablated lobster receiving mixed food exhibited the highest feeding rate (688.2 J/g/day) and the group receiving fish exhibited the lowest feeding rate (260.2 J/g/day) (Table 5.6); these values were significantly different ($t = 25.4$: $P < 0.05$). Thus, the isolated, ablated lobster increased the feeding rate by more than 2.5 times depending upon the nature of food. Similar to the normal individual, the ablated lobster not only consumed the mixed food with the highest rate, but also preferred to consume more clam (42 %) and mussel (38 %) than fish (20 %) in the mixed food.

Table 5.5 Intermoult duration (days) of P. homarus; ± represents SD

Food	Isolated		Group-reared			
	Normal	Ablated	Normal	Ablated		
	I-II moult	I-II moult	I-II moult	I-II moult	II-III moult	III-IV moult
Mussel	49.4 ± 4.5	37.0 ± 3.0	50.4 ± 1.5	31.8 ± 3.5	32.5 ± 2.5	32.0 ± 0.8
Clam	49.5 ± 3.5	35.2 ± 4.0	52.0 ± 1.0	28.6 ± 3.1	33.9 ± 3.7	37.0 ± 4.2
Fish	50.5 ± 6.5	31.5 ± 3.5	*	37.3 ± 1.8	38.3 ± 1.8	33.0 ± 2.6
Mixed	47.0 ± 6.3	32.5 ± 3.5	51.0 ± 2.0	28.9 ± 0.8	30.9 ± 0.8	30.1 ± 3.2
Mean	**49.1** ± 1.3	**34.1** ± 2.2	**51.1** ± 0.7	**31.7** ± 3.5	**33.9** ± 2.8	**33.0** ± 2.5

* Moulted once after 53 days from commencement of experiment; did not moult thereafter till completion of experiment.

Table 5.6 Effect of different food on food utilization parameters of isolated, ablated P. homarus; rates are expressed as J/g live lobster/day and efficiencies as %; each value represents average of 4 lobsters; ± represents S.D.

Parameters	Mussel	Clam	Fish	Mixed
Feeding rate	368.0 ± 4.2	598.4 ± 20.7	260.2 ± 9.2	688.2 ± 16.0
Assimilation rate	358.8 ± 4.3	588.9 ± 20.9	252.6 ± 9.3	680.0 ± 16.1
Conversion rate				
E*	4.3 ± 0.6	9.3 ± 0.4	10.9 ± 1.2	16.6 ± 0.2
P**	33.4 ± 1.8	13.8 ± 1.2	14.8 ± 1.0	56.6 ± 4.5
E + P	37.7 ± 1.7	23.1 ± 1.8	27.6 ± 3.0	73.2 ± 4.2
Metabolic rate	322.1 ± 3.1	565.9 ± 19.6	225.0 ± 8.4	618.7 ± 15.2
(ml O_2/g/hr)	0.67 ± 0.06	1.17 ± 0.04	0.47 ± 0.08	1.30 ± 0.02
Assimilation efficiency	97.6 ± 0.8	98.4 ± 0.3	97.1 ± 0.4	98.8 ± 0.2
Conversion efficiency (K_2)				
WE'	10.5 ± 0.5	4.0 ± 0.3	11.0 ± 0.8	10.8 ± 0.6
WOE"	9.3 ± 0.5	2.4 ± 0.3	6.8 ± 0.8	8.3 ± 0.6

* Exuvia; ** Growth

' with exuvia: "without exuvia

Assimilation

The assimilation rate ranged from 252.6 J/g/day (fish-fed) to 680.0 J/g/day (mixed food-fed). The assimilation efficiency was high (mean: 97 %) in all the 4 groups.

Conversion

As a result of the highest feeding rate, the conversion rate (including exuvia) was maximum in the ablated lobster fed on mixed food (73.2 J/g/day) (Table 5.6). However, the conversion rate of the group fed on mussel (37.7 J/g/day) was about 63 % higher than the group fed on clam (23.1 J/g/day), though the feeding rate of the mussel-fed lobster was 62% lower than that fed on clam. Similarly, the conversion rate of the fish-fed lobster was marginally higher (27.6 J/g/day) compared to the clam-fed group though the feeding rate of the group receiving fish was only about 40 % of the feeding rate of the group receiving clam.

The low conversion rate of the group receiving clam was due to the lowest net conversion efficiency. Whereas the conversion efficiency was almost equal in the groups receiving mussel, fish and mixed food (mean K_2 with exuvia: 10.8 %), the K_2 of the group receiving clam was considerably lower (4.0 %). Though the normal lobster converted the clam

almost with equal efficiency as that of the other food (Table 5.3), the ablated lobster was not able to convert the carbohydrate rich clam with high efficiency.

The energy lost as exuvia ranged from 11.4 (mussel-fed lobster) to 40.3 % (clam-fed lobster) of the converted energy. In terms of dry weight, 31.1 % (mussel-fed) to 71.4 % (clam-fed) of converted dry matter was lost as exuvia (Table 5.4).

Metabolic rate

As in the previous experiment, the metabolic rate was a function of the feeding rate in the ablated lobster too. The highest (mixed food-fed: 1.30 ml O_2/g/hr) and the lowest (fish-fed: 0.47 ml O_2/g/hr) metabolic rates were in the groups which exhibited the maximum and minimum feeding rates (Table 5.6). The percentage of consumed food energy spent on metabolism was almost equal among the groups receiving different food (89 - 91 %).

Intermoult duration

Like the normal lobsters, the ablated lobsters also moulted twice during the experimental period. However, all the ablated lobsters were in late premoult stage at the end of the experiment; continuation of the experiment for a few more days would have resulted in the third moult. The

lobsters were ablated during intermoult stage (stage C). The ablated lobsters did not exhibit significant acceleration in moulting initially compared to the normal lobsters and the intermoult duration of the normal and ablated lobsters to complete the first moult was not statistically significant ($t = 0.8$; $P > 0.05$). However, the intermoult duration between the I and the II moult was significantly lesser ($t = 8.1$; $P < 0.05$) in the ablated lobsters (mean: 34.1 days) than that of the normal lobsters (mean: 49.1 days) (Table 5.5).

5.3.3 Effect of food quality on food utilization of group-reared, normal lobster

Feeding rate

The normal lobster reared in group and fed on mixed food exhibited the highest feeding rate (191.1 J/g/day) and the group receiving fish exhibited the lowest feeding rate (116.5 J/g/day) (Table 5.7); the highest and the lowest feeding rates were significantly different ($t = 12.9$; $P < 0.05$).

Assimilation

As in the previous experiments, the assimilation efficiency was uniformly high (mean: 97.8 %) in all the

Table 5.7 **Effect of different food on food utilization parameters of group-reared, normal P.homarus; rates are expressed as J/g live lobster/day and efficiencies as %; each value represents average of 3 groups of lobsters;** ± represents S.D

Parameters	Mussel	Clam	Fish	Mixed
Feeding rate	161.8 ± 12.2	160.9 ± 6.4	116.5 ± 9.2	191.1 ± 4.8
Assimilation rate	157.4 ± 12.3	157.9 ± 6.5	113.9 ± 9.3	187.5 ± 4.9
Conversion rate				
E*	5.4 ± 0.3	8.4 ± 0.4	5.0 ± 0.2	8.8 ± 0.5
P**	21.7 ± 1.6	14.2 ± 0.4	7.2 ± 0.6	24.3 ± 0.1
E + P	27.0 ± 1.3	19.5 ± 0.1	12.2 ± 0.6	33.1 ± 0.3
Metabolic rate	130.4 ± 11.4	138.4 ± 6.0	101.7 ± 8.3	134.4 ± 4.7
(ml O_2/g/hr)	0.27 ± 0.01	0.27 ± 0.02	0.21 ± 0.02	0.32 ± 0.01
Assimilation efficiency	97.4 ± 0.8	98.1 ± 0.4	97.8 ± 0.5	97.9 ± 0.6
Conversion efficiency (K_2)				
WE'	17.2 ± 0.2	12.4 ± 0.1	10.7 ± 0.1	17.7 ± 0.1
WOE"	13.8 ± 0.1	9.0 ± 0.1	6.3 ± 0.6	13.0 ± 0.1

* Exuvia; ** Growth
' with exuvia; " without exuvia

groups resulting in positive relationship between feeding rate and assimilation rate.

Conversion

The conversion rate (including exuvia) was maximum in the group receiving mixed food (33.1 J/g/day) and minimum in the group fed on fish (12.2 J/gday); the highest and the lowest conversion rates were in the respective groups which exhibited the maximum and minimum feeding rates. However, the conversion rate of the group receiving clam was considerably lower either including (19.5 J/g/day) or excluding (14.2 J/g/day) exuvia than that of the group receiving mussel (27.0 or 21.7 J/g/day) eventhough the feeding rates of these groups were almost equal (mean: 161.4 J/g/day) (Table 5.7).

The high conversion rate exhibited by the group receiving mixed food was possible due to the highest feeding rate and conversion efficiency (K_2 = 17.7 %). The K_2 of the group receiving mussel was also equally high, resulting in high conversion rate compared to the groups receiving clam and fish.

The percent of energy lost as exuvia formed 20.0 (mussel-fed) to 41.0 % (fish-fed) of the total converted energy. In terms of dry weight, the exuvial weight ranged

from 44.8 to 70.6 % of the total converted dry matter (Table 5.4).

Metabolic rate

The metabolic rate ranged from 0.21 (fish-fed) to 0.32 (mixed food-fed) ml O_2/g/hr. In other words, the 70 % higher feeding rate in the group receiving mixed food resulted in 50 % higher metabolic rate than the group receiving fish.

Intermoult duration

The intermoult duration ranged from 50.4 to 52.0 days and the mean intermoult duration of the normal, group-reared **P. homarus** receiving different food was 51.1 days (Table 5.5).

5.3.4 Effect of food quality on food utilization of group-reared, ablated lobster

Feeding rate

Contrary to the previous 3 experiments in which the group receiving mixed food exhibited the maximum feeding rate, in the experiment on the group-reared, ablated lobster, the group fed on clam exhibited the maximum feeding rate (282.2 J/g/day); the feeding rate of the group receiving mixed food was lesser (248.5 J/g/day) and these values were

significantly different ($t = 3.87$; $P < 0.05$). The feeding rate was the lowest in the group fed on fish (140.2 J/g/day). Hence, the feeding rate of the group fed on clam was about 2 times higher than that of the group which was offered fish (Table 5.8).

Assimilation

The assimilation rate ranged from 136.2 (fish-fed) to 278.6 (clam-fed) J/g/day. The assimilation efficiency, like the earlier experiments, was uniformly high in all the groups and ranged from 97.2 to 98.6 %.

Conversion

The maximum conversion rate was not exhibited by the group which consumed the maximum food (clam-fed). The conversion rate (including exuvia) was maximum in the group fed on mixed food (44.8 J/g/day) (Table 5.8). Though the feeding rate of the group receiving mixed food was significantly lower, the converison rate was significantly higher ($t = 4.5$; $P < 0.05$) than that of the group which received clam. Similar to the normal, group-reared lobster, the conversion rate of the ablated, group-reared lobster, which was fed on fish was far lower than that of the other groups either including (17.2 J/g/day) or excluding

Table 5.8 Effect of different food on food utilization parameters of group-reared, ablated P.homarus; rates are expressed as J/g live lobster/day and efficiencies as %; each value represents average of 3 groups of lobsters; ± represents S.D

Parameters	Mussel	Clam	Fish	Mixed
Feeding rate	194.8 ± 6.4	282.3 ± 26.3	140.2 ± 11.2	248.5 ± 11.3
Assimilation rate	189.4 ± 6.5	278.6 ± 26.4	136.2 ± 11.3	243.6 ± 11.4
Conversion rate				
E*	8.1 ± 0.4	7.7 ± 0.6	4.9 ± 0.2	9.5 ± 1.0
P**	33.3 ± 0.5	30.9 ± 3.3	12.4 ± 1.3	35.4 ± 3.0
E + P	41.3 ± 0.9	38.6 ± 2.8	17.2 ± 1.5	44.8 ± 2.6
Metabolic rate	148.2 ± 6.2	240.1 ± 25.4	119.0 ± 11.0	198.5 ± 10.4
(ml O_2/g/hr)	0.31 ± 0.3	0.50 ± 0.02	0.25 ± 0.01	0.42 ± 0.02
Assimilation efficiency	97.6 ± 0.6	98.6 ± 0.2	97.2 ± 0.6	98.0 ± 0.8
Conversion efficiency (K_2)				
WE'	21.9 ± 1.9	13.8 ± 1.2	12.2 ± 0.8	18.5 ± 1.4
WOE"	17.6 ± 1.4	11.0 ± 1.1	8.7 ± 0.6	14.5 ± 0.9

* Exuvia; ** Growth
' with exuvia; " without exuvia

(12.4 J/g/day) exuvia; the low conversion rate was probably due to low feeding rate.

Whereas the highest feeding and conversion rates were in the groups fed on clam and mixed food, respectively, the highest conversion efficiency (K_2: 21.9%) was in the group fed on mussel.

The ablated, group-reared lobster lost energy equivalent to 4.9 (fish-fed) to 9.5 (mixed food-fed) J/g/day in the form of exuvia. In terms of energy consumed or converted, the lobster receiving different food lost, on an average, 3.6 or 22.3 % of energy, respectively. In terms of dry weight, the mean loss was 50.7 % of the total converted dry matter.

Metabolic rate

The metabolic rate of the group fed on clam (0.50 ml O_2/g/hr) was 2 times higher than that of the group fed on fish (0.25 ml O_2/g/hr). However, both the groups expended equal percentage (85 %) of the consumed energy towards metabolism.

Intermoult duration

The group-reared, ablated lobster moulted frequently than the normal lobster and completed 4 moults during the

experimental duration of 118 days. The mean intermoult duration of the groups receiving mussel, clam, fish and mixed food were 32.1, 33.2, 36.2 and 30.0 days, respectively (see Table 5.5). The mean intermoult duration of the group-reared, ablated lobster receiving different food (32.9 days) was about 35 % lesser than that of the group-reared, normal lobster (51.1 days).

5.3.5 Energy budget

The energy partitioned by **P. homarus** towards processes related to body functions and body structures was calculated as percentage of energy consumed by the lobster in each experiment. The energy allotted to each of the energetic components, namely, production (growth+exuvia), metabolism and egestion (faeces+urine) is plotted in Figure 5.1 and 5.2. The lobster in all the 4 experiments expended considerable quantum of consumed energy (80.0 to 96.5 %) towards metabolism. Whereas the energy spent on egestion was almost equal in all the lobsters, the group-reared lobsters allotted nearly 2 times more energy for production than the isolated lobster; the isolated, ablated **P. homarus** receiving different food, allotted, on an average, 8.5 % of the consumed energy for growth and the group-reared, ablated, lobster converted on an average, 16.0 % of the consumed energy towards production. In all the 4 experiments, the

Fig. 5.1 Energy allotted for egestion (), metabolism ( ), production () and exuvia () by isolated, normal and isolated, ablated **P. homarus**

Fig. 5·1

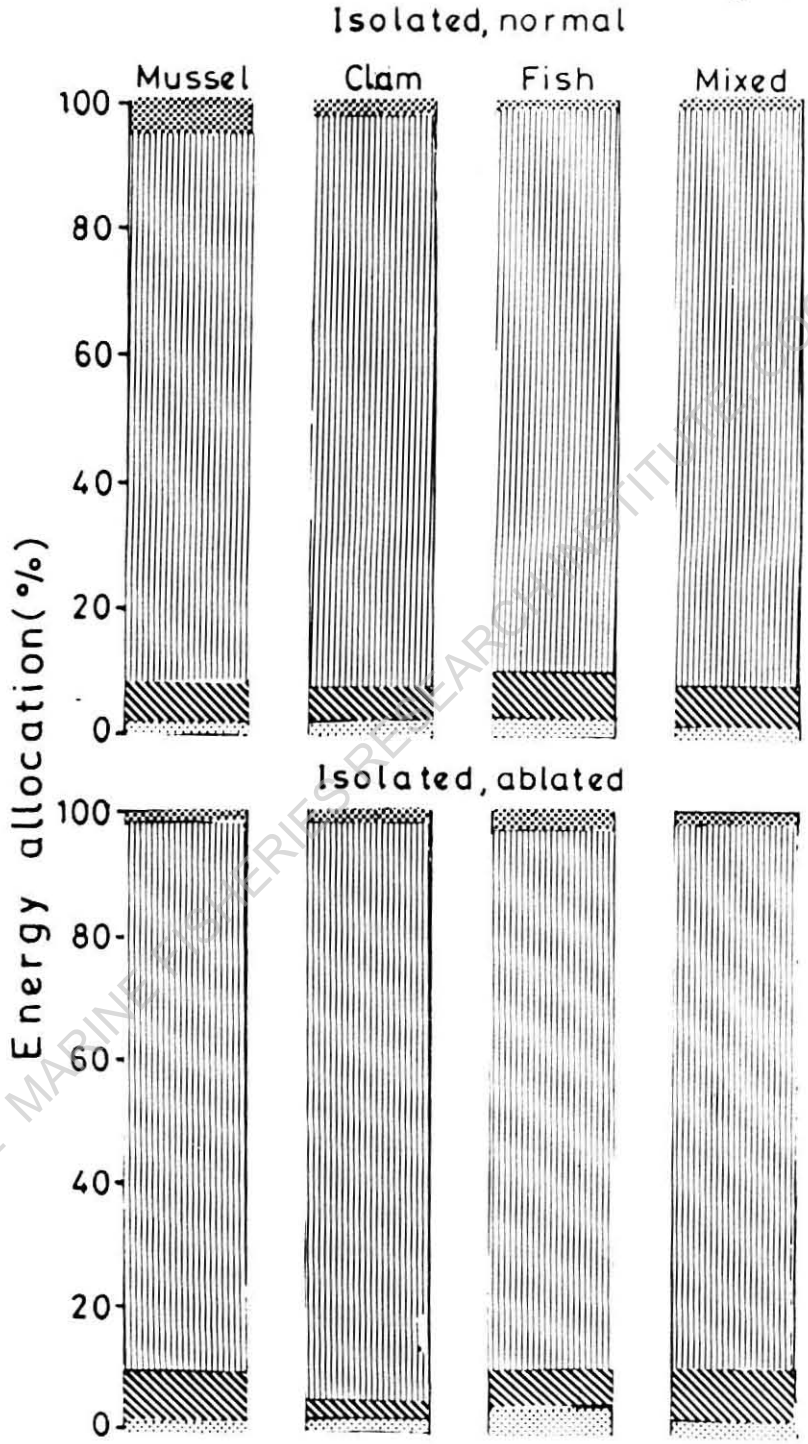
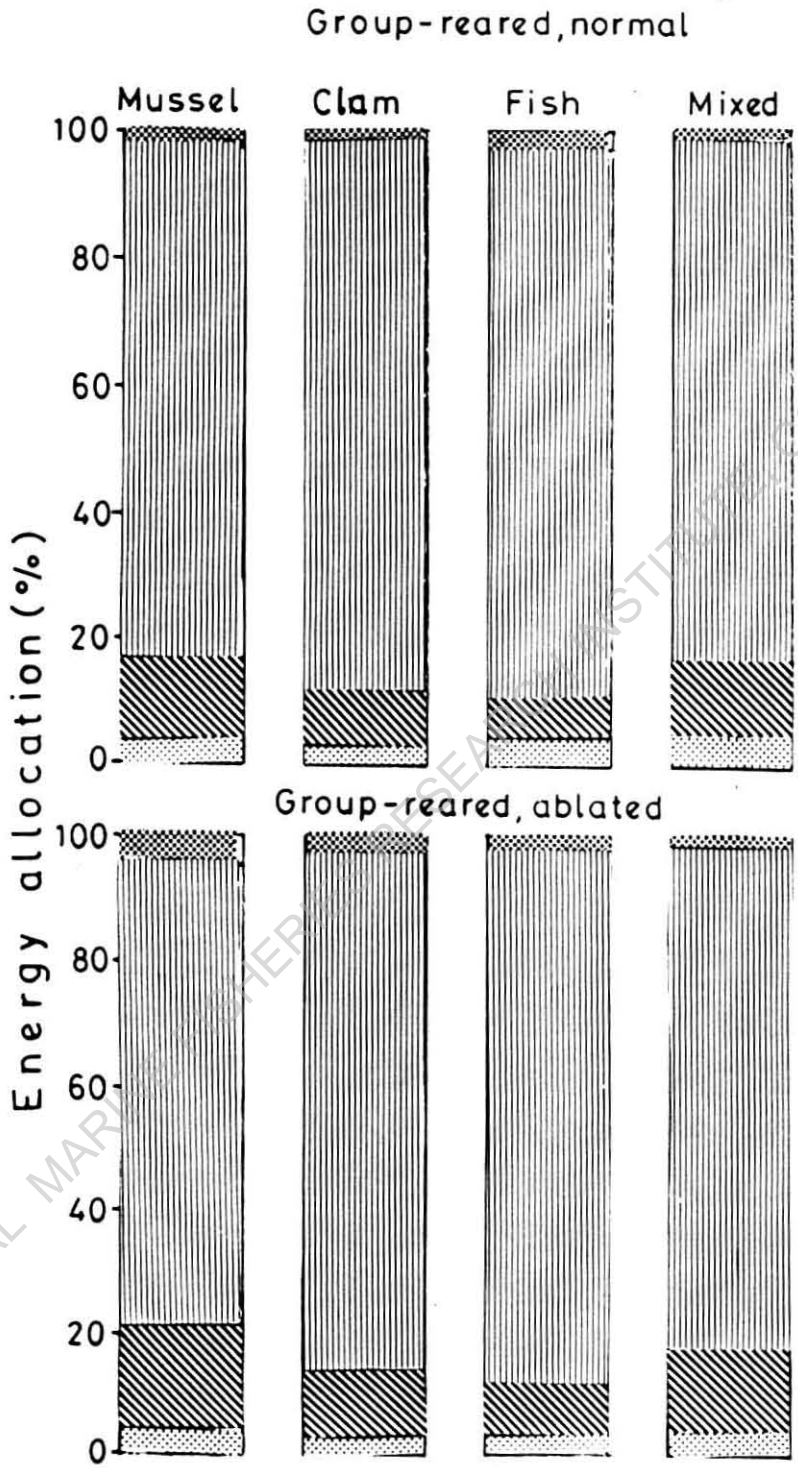


Fig. 5.2 Energy allotted for egestion (), metabolism ( ), production () and exuvia () by group-reared, normal and group-reared, ablated **P. homarus**

Fig.5·2



energy allotted for production was lesser in the groups receiving clam and fish than the groups receiving mussel and mixed food.

To understand the effect of eyestalk ablation on energy partition, the percent of energy allotted by the lobsters receiving different food were pooled. The energy allotted for the different bioenergetic components was almost equal among the normal and ablated lobsters. For instance, the isolated, normal lobster allotted 2.5, 6.0 and 89.5 % of the consumed energy towards exuvia, growth and metabolism, respectively; the corresponding values for the isolated, ablated lobster were 2.4, 6.4 and 89.2 % (Table 5.9). However, the partition of energy differed between the isolated and the group-reared lobsters. The isolated lobster, on an average, allotted 89.3 % towards metabolism, which is higher than the energy allotted by the group-reared lobster (82.4 %). The allocation of reduced quantum of energy towards metabolism enabled the group-reared lobster to divert more energy (11.5 %) towards growth than the isolated lobster (6.2 %). The group-reared lobster allotted (3.7 %) about 50 % more energy towards another form of growth, i.e. for exuvial production than the ablated lobster (2.5 %).

Table 5.9 Energy budget of P. homarus; the values were calculated as percent of respective food energy consumed (C); for calculation, the values obtained in the respective experiment on different food were pooled

Condition of lobster	C	P	E	R	F+U
Isolated, normal	100	6.0	2.5	89.5	2.0
Isolated, ablated	100	6.4	2.4	89.2	2.0
Mean	**100**	**6.2**	**2.5**	**89.3**	**2.0**
Group-reared, normal	100	10.3	3.9	83.6	2.2
Group-reared, ablated	100	12.7	3.5	81.1	2.7
Mean	**100**	**11.5**	**3.7**	**82.4**	**2.5**

5.3.6 Live weight increase

As **P.homarus** is a commercially important species, aquaculturists may be interested to know the growth of the lobster and the tail and meat weight of the lobster. The live weight increase of the lobster in the 4 experiments was plotted against time in a scatter diagram. The weight of the lobster increased linearly with time. Mohammed and George (1968) reported asymptotic growth curve for **P.homarus** for the entire life span of 10 years. In the present study, the experiments were conducted for 83-118 days, which is a short duration, considering the longevity of **P. homarus**. Any small segment in the growth curve (restricted to short duration) is linear against time, provided the animal has not entered the asymptotic growth phase. The experimental **P. homarus** were in pre-adult stage and hence, linear growth could be expected in a short duration. The linear growth, determined by least square estimate, is plotted in Figure 5.3 and 5.4 and the a, b and r values are given tn Table 5.10. In all the 4 experiments, the live weight increase of the groups receiving clam or fish was lesser than the groups receiving mussel or mixed food. For instance, the isolated, ablated lobster receiving clam or fish increased the live weight from 96 to 169 g or 156 g, respectively in 83 days; the group receiving mussel increased the live weight from 105 to 238 g and the group receiving mixed food from 90 to 245 g in 83 days. The

Fig. 5.3 Regression lines on increase in live weight of isolated, normal and isolated, ablated **P. homarus** during the experimental duration

Fig. 5·3

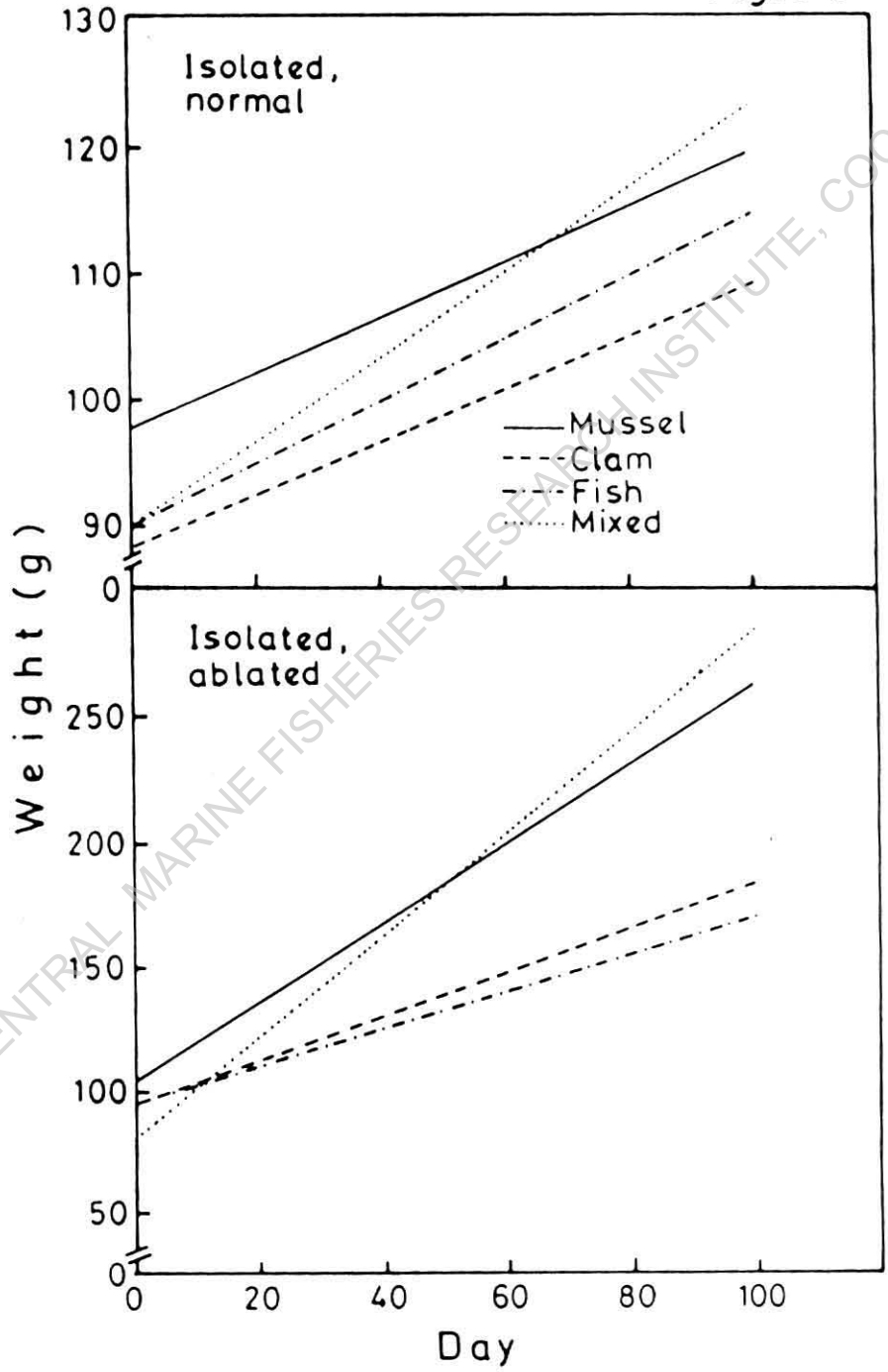


Fig. 5.4 Regression lines on increase in live weight of group-reared, normal and group-reared, ablated **P. homarus** during the experimental duration

Fig.5·4

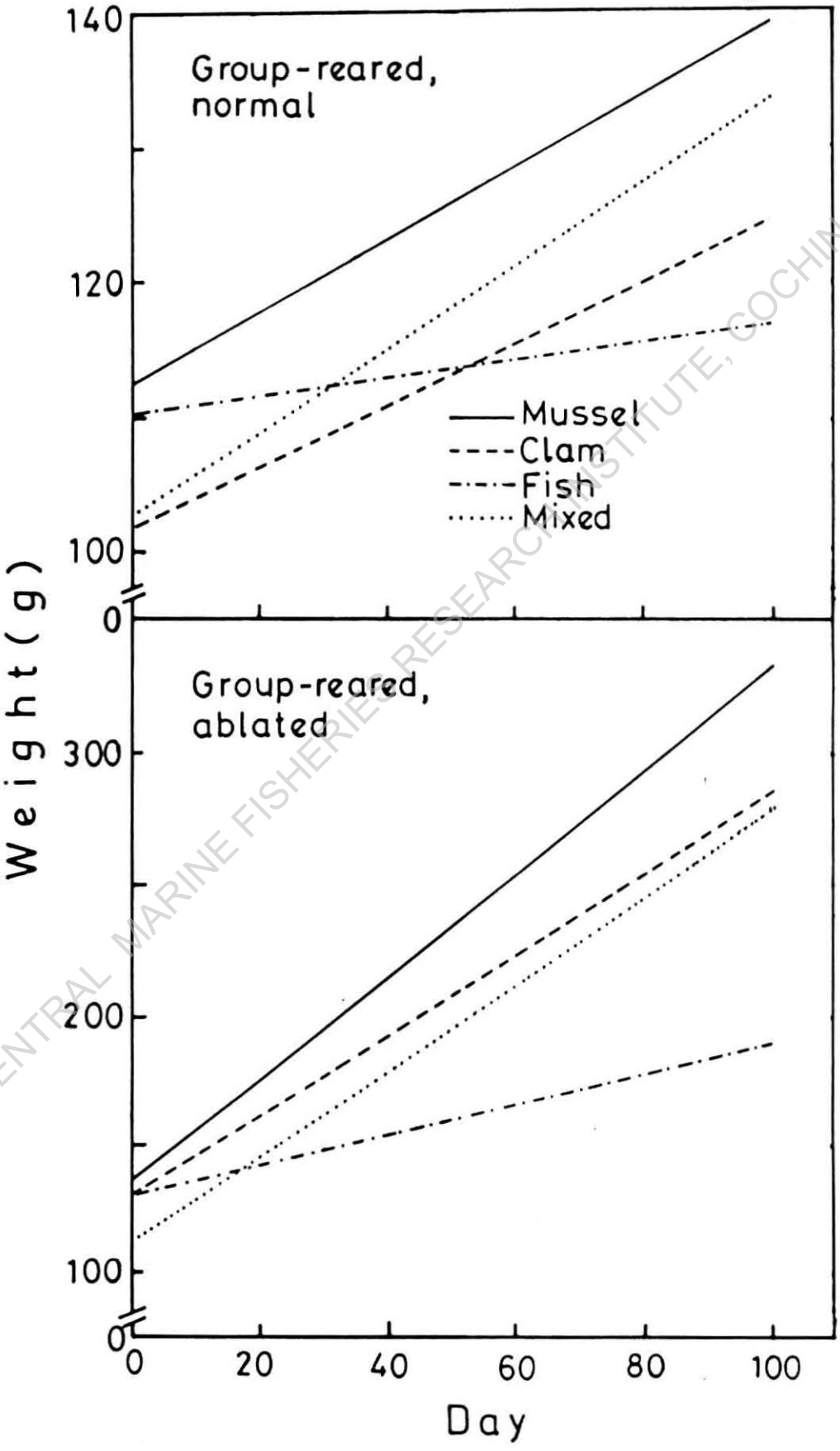


Table 5.10 Values of a, b and r in the least square estimate of live weight (g) (y) on time (day) (x) in P.homarus receiving different food

Condition of lobster		Mussel	Clam	Fish	Mixed
Isolated, normal	a.	98.0	88.0	90.3	90.0
	b.	0.21	0.21	0.24	0.33
	r.	0.986	0.993	0.990	0.972
Isolated, ablated	a.	104.0	94.0	97.5	82.0
	b.	1.62	0.90	0.71	2.05
	r.	0.979	0.992	0.982	0.966
Group-reared normal	a	112.3	101.4	110.0	102.8
	b.	0.27	0.23	0.07	0.31
	r.	0.901	0.989	0.998	0.976
Group-reared, ablated	a.	137.8	132.8	130.1	111.8
	b.	1.93	1.53	0.62	1.67
	r.	0.999	0.994	0.988	0.933

'b' value, i.e., the slope of the regression, represents the growth. The 'b' values were lower (0.07 - 0.33) in all the normal lobsters and were remarkably higher (0.62 - 2.05) in all the ablated lobsters. Hence, under the experimental conditions, the ablated lobsters exhibited faster growth in terms of live body weight than the normal lobsters. Considering the live weight gain (mean r = 1.44) (Table 5.10) and the energy partitioning (12.7 % of the consumed energy; Table 5.9), group-rearing and bilateral eyestalk ablation appear to be better suited for maximum growth.

The percentage of wet tail weight and the wet meat weight (meat in the tail) in the total live body weight of the lobster was estimated in the group-reared, normal and ablated lobsters at the end of the experiment. The mean percentage of tail (34.6 % of total body weight) and meat (25.6 % of total body weight) were higher in the normal lobsters than the ablated individuals (tail: 28.9 %; meat: 23.0%) (Table 5.11). Though the percentage of tail or meat weight was lesser in the ablated lobsters, the total wet weight of tail or meat was considerably higher in the ablated lobsters. For instance, the total live weight of the normal (group-reared) lobster receiving mixed food increased from 103.0 to 127.5 g in 80 days, whereas the total live weight of the ablated lobster increased from 112.5 to 240.0 g in 80

Table 5.11 Percent of tail and meat in the total live body weight of normal and ablated lobsters reared in group

Food	Tail weight (%)		Meat weight (%)	
	Normal	Ablated	Normal	Ablated
Initial	32.7 ± 2.0	32.7 ± 2.0	25.8 ± 2.7	25.8 ± 2.7
Final				
Mussel	35.3 ± 1.2	28.0 ± 2.2	26.7 ± 1.7	22.3 ± 1.3
Clam	32.7 ± 1.4	27.4 ± 2.4	25.6 ± 1.4	20.6 ± 2.5
Fish	34.9 ± 1.3	30.7 ± 1.9	25.4 ± 1.4	25.1 ± 1.1
Mixed	35.3 ± 1.4	29.4 ± 2.1	24.5 ± 0.7	23.9 ± 2.3
Mean	**34.6 ± 1.1**	**28.9 ± 1.3**	**25.6 ± 0.8**	**23.0 ± 1.7**

days (Fig. 5.4). In other words, the ablated lobster receiving mixed food increased the live body weight by nearly 2 times than the normal lobster in equal duration of time. Considering the respective tail and meat weight percentage of the normal and ablated lobsters (Table 5.11), the total wet tail (69 g) or meat (55 g) weight of the ablated lobster receiving mixed food was 55 - 70 % higher than the tail (44 g) or meat (33 g) weight of the normal lobster after 80 days of rearing. Hence, the net gain of rearing the ablated lobster may be remarkably higher than rearing the normal lobster.

5.3.7 Water, ash and biochemical contents of the lobster

The water content of the normal lobster receiving different food was equal at the end of the experiment (mean: 64.1 $\pm$ 1.5 %); the water content of the midgut gland (mean: 60.4 $\pm$ 3.5 %) or the muscle (mean: 71.3 $\pm$ 0.4%) also did not differ much (Table 5.12). However, the water content of the ablated lobster receiving clam (77.5 %) was statistically higher than that of the group receiving fish (65.7 %) ($t = 12.7$; $P < 0.05$). The water content of the ablated lobster (70.7 %) was higher than the water content of the normal lobster (64.1 %); the water content of the midgut gland or muscle was also higher in the ablated lobster.

Table 5.12 Hepatic index and water content of normal and ablated P.homarus receiving different food; the estimations were on group-reared lobster

Food	Normal				Ablated			
	Hepatic Index*	Water content (%)			Hepatic Index*	Water content (%)		
		Whole	Midgut gland	Muscle		Whole	Midgut gland	Muscle
Initial	5.4 ± 0.4	69.9 ± 2.1	65.6 ± 3.7	74.9 ± 1.3	5.4 ± 0.4	69.9 ± 2.1	65.6 ± 3.7	74.9 ± 1.3
Final								
Mussel	4.2 ± 0.4	61.5 ± 1.8	63.5 ± 2.1	71.3 ± 2.4	3.6 ± 0.2	71.5 ± 2.1	69.9 ± 2.9	74.4 ± 2.6
Clam	4.9 ± 0.2	65.0 ± 1.2	62.6 ± 3.7	71.7 ± 1.1	2.3 ± 0.1	77.5 ± 2.2	77.3 ± 0.7	79.0 ± 1.1
Fish	4.9 ± 0.5	64.8 ± 0.8	61.1 ± 2.8	71.6 ± 0.8	3.9 ± 0.4	65.7 ± 1.2	59.2 ± 2.2	77.3 ± 1.2
Mixed	4.7 ± 0.3	65.0 ± 2.0	54.5 ± 1.5	70.7 ± 1.6	4.0 ± 0.2	68.1 ± 2.5	68.9 ± 3.0	76.2 ± 1.7
Mean	**4.7 ± 0.3**	**64.1 ± 1.5**	**60.4 ± 3.5**	**71.3 ± 0.4**	**3.5 ± 0.7**	**70.7 ± 4.4**	**68.8 ± 6.4**	**76.7 ± 1.7**

* Hepatic index : $\frac{\text{Wet weight of midgut gland (g)}}{\text{Wet weight of lobster (g)}}$

The ash content of the different food ranged from 8.4 to 12.6 % (Table 5.2). The difference in the ash content among the food did not result in statistically different ash content between the lobsters (Table 5.13 and 5.14). The mean ash content of the normal (32.0 %) and ablated (31.3 %) lobsters was also almost equal (mean: 31.7 %). The ash content of **P. homarus** is comparable to that of **H. americanus** fed different diets (30.0 to 37.8 %; Capuzzo and Lancaster, 1979).

The chitin content of the normal lobster ranged from 12.2 (mussel-fed) to 19.4% (fish-fed) (mean: 15.0 %) and that of the ablated lobster from 13.9 (mussel-fed) to 19.9 % (clam-fed) (mean: 17.3 %). The chitin content of normal **H.americanus** receiving different pellet diet ranged from 10.3 to 15.1 % (Capuzzo and Lancaster, 1979).

To understand the effect of different food on the biochemical contents of the normal and eyestalk ablated lobsters, the lipid, carbohydrate and protein contents in the abdominal muscle and in the entire lobster were estimated at the completion of the experiments on group-reared lobsters. At the commencement of the experiment, the lipid, carbohydrate and protein contents of the lobster were 7.1, 3.5 and 36.5 %, respectively. At the end of the experiments, the lipid content of the normal and ablated lobsters

Table 5.13 Percent composition of biochemical, ash and chitin contents in the whole body and abdominal muscle of group-reared, normal P. homarus receiving different food; calculations were based on dry weight

Components	Mussel	Clam	Fish	Mixed
Lipid				
Whole	16.0 ± 1.6	14.7 ± 0.8	19.3 ± 1.2	19.3 ± 1.8
Muscle	15.0 ± 1.5	14.3 ± 1.0	13.1 ± 0.8	14.9 ± 0.7
Carbohydrate				
Whole	1.8 ± 0.1	2.0 ± 0.1	1.2 ± 0.1	1.6 ± 0.1
Muscle	1.9 ± 0.6	3.7 ± 0.2	1.7 ± 0.2	3.8 ± 0.3
Protein				
Whole	40.8 ± 3.7	35.7 ± 2.2	24.6 ± 0.9	35.8 ± 3.3
Muscle	73.1 ± 3.7	72.7 ± 1.5	78.5 ± 1.6	70.0 ± 1.8
Ash				
Whole	30.2 ± 2.4	31.5 ± 1.6	35.5 ± 2.8	30.9 ± 1.2
Chitin*				
Whole	12.2	16.1	19.4	12.4

* Chitin (%) : 100 - (Percentage of protein + carbohydrate + lipid + ash)

Table 5.14 **Percent composition of biochemical, ash and chitin contents in the whole body and abdominal muscle of group-reared, ablated P. homarus receiving different food; calculations were based on dry weight**

Components	Mussel	Clam	Fish	Mixed
Lipid				
Whole	19.4 ± 1.3	12.4 ± 0.3	16.8 ± 1.2	17.7 ± 1.1
Muscle	7.8 ± 0.6	5.3 ± 0.4	6.2 ± 0.4	7.9 ± 0.2
Carbohydrate				
Whole	1.6 ± 0.1	1.8 ± 0.02	1.0 ± 0.1	3.6 ± 0.6
Muscle	2.3 ± 0.2	1.5 ± 0.1	4.4 ± 0.1	3.6 ± 0.2
Protein				
Whole	35.0 ± 2.5	33.8 ± 1.3	30.4 ± 2.5	33.1 ± 2.2
Muscle	74.2 ± 2.6	64.7 ± 3.0	67.6 ± 3.2	79.7 ± 2.4
Ash				
Whole	30.1 ± 2.3	32.1 ± 1.1	32.9 ± 3.3	31.2 ± 1.0
Chitin*				
Whole	13.9	19.9	18.9	16.5

* Chitin (%) : 100 - (Percentage of protein + carbohydrate + lipid + ash)

receiving different food changed in correspondence to the lipid content of the food. The lipid content of the clam, for instance, was lower (7.0 %) compared to that of mussel (9.9 %) or fish (9.1 %) (Table 5.2). Consequently, the lipid content of the lobsters receiving clam was lower (normal: 14.7%; ablated: 12.4 %) than that of the group receiving mussel (normal: 16.0 %; ablated: 19.4 %) or fish (normal: 19.3 %; ablated : 16.8 %) (Table 5.13 and 5.14). The lipid content in the muscle of the ablated lobster was remarkably lower than that of the normal lobster; for instance, the mean lipid content in the muscle of the ablated lobsters receiving different food was only 6.8 %, whereas the mean lipid content of the normal lobster was 14.4 %. It appears that the lipid requirement of the ablated lobster may be higher, resulting in utilization of the available lipid.

The carbohydrate content was remarkably high in the clam (29.3 %) than the mussel (7.3 %) and the fish (1.1 %). The lobsters fed on clam exhibited higher carbohydrate content than most other groups. However, the percentage of carbohydrate in the muscle of the clam-fed group was either marginally higher or lower than the other groups.

Protein is an essential component of crustacean food for tissue growth and maintenance. Protein may also be catabolised as a source of energy by the crustaceans (Cowey

and Sergent, 1972). Utilization of protein is affected by the nature of the dietary protein source, the level of protein intake and the ability of an organism to utilize other dietary components as source of energy (Capuzzo, 1982). The protein content of the normal lobster receiving high protein food, viz., fish (74.8 %), was the lowest (24.6 %) than that of all the other groups (35.7 to 40.8 %). Hence, Protein Efficiency Ratio, (PER = Live weight gain (g)/Dry weight of protein consumed (g)) of normal as well as ablated **P. homarus** was negatively correlated with protein content of the food (Fig. 5.5) with the following equations:

Normal : Protein content of food (x) Vs PER (y)

$y = 1.153 - 0.012\ x$

$r = 0.803$

Ablated : Protein content of food (x) Vs PER (y)

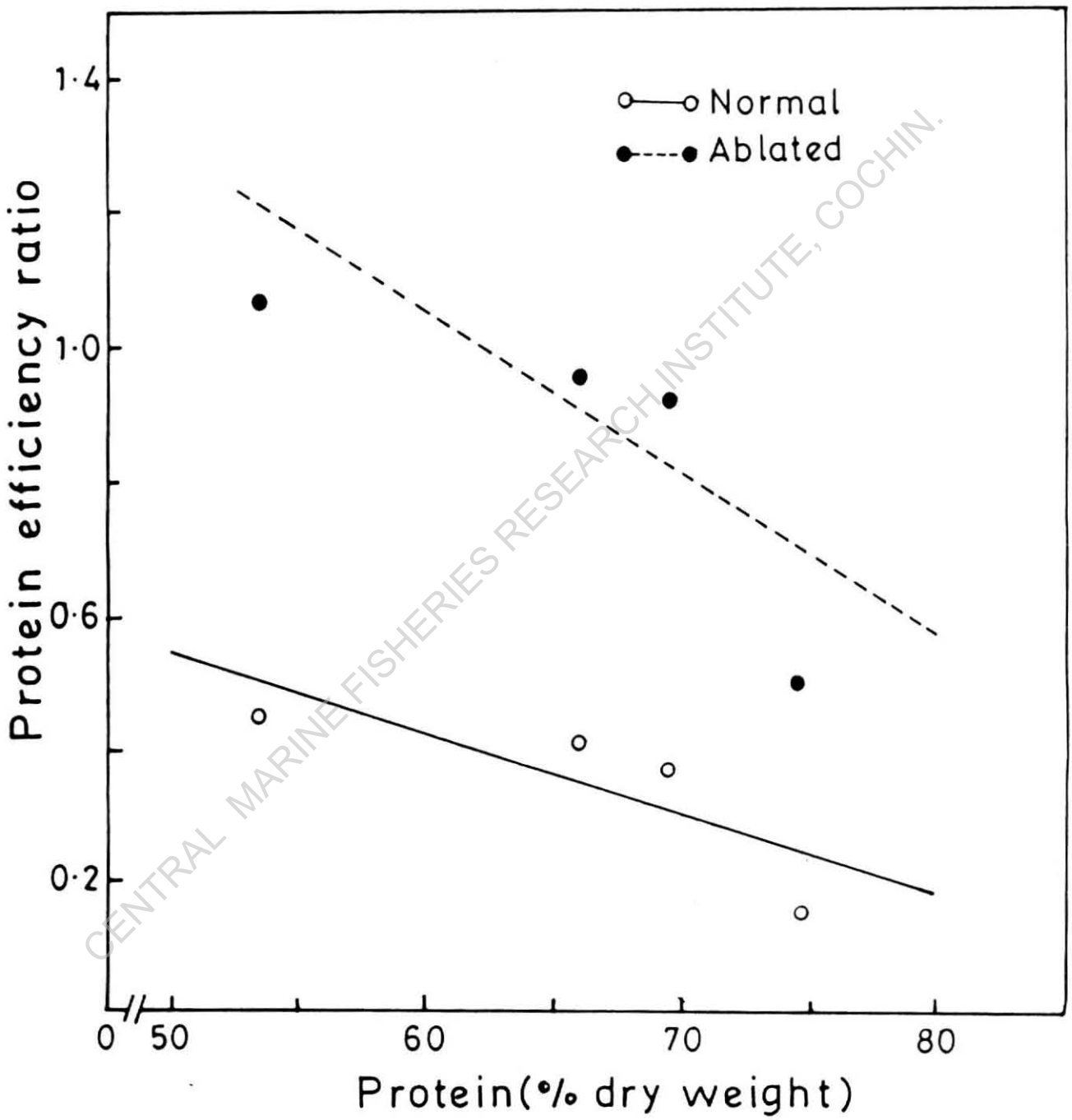
$y = 2.344 - 0.022\ x$

$r = 0.823$

In the American lobster **H.americanus** (Capuzzo and Lancaster, 1979) and in the prawns (Colvin, 1976; Sedgwick, 1979a; Millikin et.al., 1980) also, values of the PER were negatively correlated to the dietary protein levels. In **H.americanus**, the PER decreased from 2.7 (protein content of food: 16.7 %) to 0.9 (protein content: 51.0 %).

Fig. 5.5 Regression lines between protein content of food and Protein Efficiency Ratio (PER) in normal and ablated **P. homarus**

Fig.5·5



5.4 Discussion

The 4 experiments on the effect of i) different food, ii) eyestalk ablation and iii) isolation on the food utilization have revealed a few important aspects on the physiological energetics of the spiny lobster, **P.homarus.** For determining the individual effect of the 3 factors on the food utilization, the experiment on the group-reared, normal lobster may be considered as control, since **P.homarus** is gregarious in nature. Hence, i) the changes in the food utilization pattern of the group-reared, normal lobster is solely due to the effect of different food; ii) the difference between the food utilization pattern of the group-reared, normal lobster (control) receiving a particular food and the food utilization of the group-reared, ablated lobster receiving the same food is solely due to the effect of eyestalk ablation; iii) the difference between the food utilization pattern of the group-reared, normal lobster (control) receiving a particular food and the food utilization of the isolated, normal lobster receiving the same food is solely due to isolation; and iv) the changes within the experiment on the isolated, ablated lobster is the interaction of all the 3 factors.

5.4.1 Effect on feeding rate

The test of ANOVA on the feeding rates of **P. homarus** receiving different food revealed that the quality of food significantly affected the feeding rate in all the 4 experiments ($P < 0.001$) (Table 5.15). The feeding rates of the groups receiving mussel, clam, fish and mixed food were 161.8, 160.9, 116.5 and 191.1 J/g/day, respectively in the control experiment on the group-reared, normal lobster (Table 5.7). The 60 % higher feeding rate of the group receiving mixed food than the feeding rate of the group receiving fish was due to the preference of the molluscan diet by the lobster. The natural food of **P. homarus** consists primarily of molluscs, like the green mussel. Though the lobster do not encounter the backwater clam, **P.homarus** readily accepted the clam meat when offered. Perhaps, the soft nature of the molluscan meat would have induced the lobster to prefer the molluscs. The group receiving mixed food also preferred to feed on the clam followed by the mussel. The lobster fed on fish exhibited the lowest feeding rate and in the group receiving mixed food too, the fish was the least preferred. Fish does not form the natural food of many crustaceans. Chittleborough (1974) reported that the spiny lobster, **P. longipes cygnus** preferred to feed on molluscs than fish. The prawn, **Metapenaeus monoceros** also exhibited the lowest feeding rate when fed on

Table 5.15 Analysis of variance on the feeding rate of P.homarus consuming different food

Condition of lobster	Source of variation	SS	df	MS	F	P
Isolated,	Between food	32363.8	3	10787.9	21.29	<0.001
normal	Residual	4054.7	8	506.8		
	Total	36418.5	11			
Isolated	Between food	354733.9	3	118244.6	401.10	<0.001
ablated	Residual	2358.0	8	294.8		
	Total	357091.9	11			
Group-reared,	Between food	8519.9	3	2840.0	25.52	<0.001
normal	Residual	890.7	8	111.3		
	Total	9410.6	11			
Group-reared,	Between food	34892.7	3	11630.9	31.49	<0.001
ablated	Residual	2954.4	8	369.3		
	Total	37847.1	11			

trash fish compared to **Artemia** and pellet diet (Royan et.al., 1976). The fact that **P.homarus** receiving mixed food exhibited the maximum feeding rate suggests that the animal prefers to be exposed to different food materials, enabling selective feeding on the preferred food, supplemented with other food in limited quantity.

Isolating **P.homarus** resulted in considerable increase in the feeding rate. The feeding rate of the isolated, normal lobster was higher by 50-110% (mean: 80%) than the group-reared, normal lobster. The separation of a single individual from the gregarious habitat might have induced physiological stress on the animal, leading to higher metabolic rate. The metabolic rates of **P.homarus** in the 4 experiments of the present study supports this conclusion. The mean metabolic rate (0.53 ml O_2/g/hr) of the isolated (normal) individuals was about 2 times higher than the mean metabolic rate of the group-reared (normal) individuals (0.27 ml O_2/g/hr). The enhanced metabolic rate of the isolated individuals would have resulted in higher feeding rate.

Comparison of the feeding rates of the group-reared normal and ablated lobsters revealed that the feeding rate of the ablated lobsters consuming different food was 20-75 % (mean: 40 %) higher than the normal lobsters. Hence, bilateral eyestalk ablation induced 40 % higher feeding rate

in **P.homarus.** Vijayakumaran and Radhakrishnan (1984) and Radhakrishnan and Vijayakumaran (1987a) also reported that eyestalk ablation resulted in 50-75 % higher food consumption in **P. homarus** and **P.ornatus.** Similar results were obtained in the American lobster, **H. americanus** (Castell et.al., 1977). However, the information available on the effect of eyestalk ablation in the prawns is contradictory. Whereas Ponnuchamy et.al. (1981) reported no marked difference in the feeding rate of normal and ablated freshwater prawn, **Macrobrachium lanchesteri,** Pandian and Sindhukumari (1985) reported that unilateral eyestalk ablation induced hyperphagia. The latter authors suggested that eyestalk ablation releases the crustacean from the regulation of growth inhibiting hormone and increases the quantity of growth excitatory hormone in the blood and hence, the animal is induced to consume more food.

The appetite of eyestalkless crustaceans may also be stimulated by the hyperglycemic hormone (HGH), which is present in the eyestalk. It has been reported that eyestalk ablation results in hypoglycemia in several crustaceans (Dean and Vernberg, 1965; Johnston and Fisher, 1968; Rangnekar and Madhyastha, 1971). Scheer and Scheer (1951) analysed the blood sugar level in the spiny lobsters, **P.japonicus** and **P.penicillatus** and reported that the blood sugar ranged from

22.6 to 23.5 mg/100 ml in the normal lobster and from 12.0 to 14.0 mg/100 ml in the ablated lobster. A number of investigators have correlated reduced blood sugar level in the crustaceans to higher food intake (Kleinholz and Little 1949; see also Chang and O'Connor, 1983; Fingerman, 1987). It appears that eyestalk ablation leads to hyperphagia due to the following reasons: i) increase in the quantity of growth excitatory hormone in the blood and thereby higher food consumption; and / or ii) the removal of hyperglycemic hormone leading to hypoglycemia and thereby hyperphagia.

The process of locating the food was not hampered by eyestalk removal since the lobsters generally do not make effective use of the eyes for locating the food. As the lobster is a nocturnal feeder, it probably makes use of the sensory receptors situated on the antennules, dactyls of the walking legs and the mouth parts for locating the food (Ache, 1977).

5.4.2 Effect on assimilation

The assimilation efficiency of **P. homarus** was uniformly high (97.1-98.8 %), leading to high assimilation rate in all experiments. The estimations on rate and efficiency of assimilation might be marginally an overestimate in the present study. In all the experiments, the faeces was siphoned out 24 hr after the food was

offered. It is possible that a small fraction of the faeces would have dissolved during the 24 hr period due to agitation of water caused by the aerator and the lobster. Furthermore, ammonia excretion was considered to form the entire nitrogenous excretion of **P. homarus** in the present study. Parry (1960) and Pandian (1975) reported that urea, aminoacids, purines and uric acid also form the nitrogenous excretion of marine crustaceans, though in very limited quantity. In **P. homarus**, ammonia excretion itself was meagre (mean: 1.79 mg/g/hr). Though the percentage of other nitrogenous excretory products would have been negligible, the unestimated nitrogenous excretion and the dissolved faeces would have resulted in marginal overestimation of assimilation efficiency. Nevertheless, high assimilation efficiency is not uncommon in carnivorous crustaceans (Dall and Moriarty, 1983). The assimilation efficiency of the prawns, **Palaemon serratus, Pandalus platyceros** (Forster and Gabbot, 1971), **Penaeus setiferus, P. aztecus** (Condrey et.al, 1972) and **Metapenaeus bennettae** (Moriarty, 1977) ranged from 97-98 %.

5.4.3 Effect on intermoult duration

The difference in the intermoult duration was pronounced between the normal and ablated lobsters and the other factors like isolation and food quality did not

appreciably influence the intermoult duration. For instance, the intermoult duration of the isolated (49.1 days) and the group-reared (51.1 days) normal lobster was almost equal (Table 5.5). Similarly, the intermoult duration of the group-reared, normal individual receiving different food ranged from 50.4 to 52.0 days (mean: 51.1 ± 0.7 days); the low coefficient of variation (1.4 %) suggests that the difference in intermoult duration among the lobsters receiving different food was not significantly different.

Eyestalk ablation resulted in shortening of intermoult duration. The mean intermoult duration of the ablated lobster (group-reared) was 32.9 days and that of the normal (group-reared) lobster was 51.1 days (Table 5.5). The effect of eyestalk ablation on the intermoult duration/moulting frequency has been studied in detail in several crustaceans (Abramovitz and Abramovitz; 1940; Smith, 1940; Scudamore, 1947; Bauchau, 1948; Passano, 1961; Rao et.al., 1973; Mauviot and Castell, 1976; Castell et.al., 1977; Aiken, 1980; Quackenbush and Herrnkind, 1981; Radhakrishnan and Vijayakumaran, 1984, 1987a). Most of the authors have reported that eyestalk removal accelerates moulting. There are also occasional conflicting reports that eyestalk removal delays moulting (Donahue, 1951, 1955; Donahue and Flinp, 1972). Based on the reports of Travis

(1951, 1954), Dall (1977) and Dall and Barclay (1977) on **P. argus** and **P. cygnus,** Aiken (1980) concluded that eyestalk ablation does not accelerate moulting in the palinurid lobsters. Reviewing the available information on the effect of eyestalk ablation on moulting, Sochasky et.al. (1973) concluded that the eyestalk removal shortens the intermoult duration and the contradictory results reported by few authors may be due to difference in methodology or reproductive interference in the animal (see also Fingerman and Fingerman, 1976). Later studies have conclusively indicated acceleration of moulting due to removal of eyestalk and the presence of Moult Inhibiting Hormone (MIH) in the eyestalk of the palinurid lobsters. Quackenbush and Herrnkind (1981) evidenced that **P. argus** responds to eyestalk ablation by accelerating the moulting cycle. Radhakrishnan and Vijayakumaran (1984) also evidenced pronounced acceleration of moulting frequency in the eyestalk ablated **P.homarus** (early juveniles to adults) irrespective of the reproductive status of the animal. Attempts on isolation and partial characterization of the MIH from the eyestalks (Rao, 1965; Quackenbush and Herrnkind, 1983; Chang, 1985; See also Fingerman, 1987) also confirmed the presence of MIH in the sinus glands of the eyestalks of the homarid and palinurid lobsters.

5.4.4 Effect on conversion

In addition to accelerating the moulting frequency, eyestalk ablation accelerated the rate and efficiency of conversion. The mean conversion efficiency (K_2) of the group-reared, ablated lobster (13.0 %) was higher than the K_2 of the normal lobster (10.5 %). To ascertain the effect of eyestalk ablation on conversion, earlier data published on other lobsters and prawns were recalculated and presented in Table 5.16. For the purpose of comparison, the growth of the group-reared **P. homarus** in the present study was also recalculated as Food Conversion Ratio (FCR = Food consumed (dry weight)/Live weight gain (g)). The FCR of **P. homarus**, the other lobsters and prawns suggest that the ablated crustaceans are capable of converting the consumed food more efficiently than the normal individuals.

Due to higher feeding rate, accelerated moulting and higher conversion efficiency, the conversion rate was higher in the ablated lobster. Whereas the mean conversion rate (without exuvia) of the normal lobster (group-reared) was 16.9 J/g/day, that of the ablated lobster (group-reared) was 28.0 J/g/day, i.e. the ablated lobster exhibited about 65 % higher conversion rate than the normal lobster. Working on the effect of eyestalk ablation on weight gain in the crab, **Eriocheir sinensis**, Koch (1952) reported that increase in

Table 5.16 Food conversion ratio (FCR) of normal, unilaterally (U.A) and bilaterally eyestalk ablated (B.A) lobsters and prawns

Species	Temp (°C)	Food	Condition	FCR*	Reference
Panulirus homarus	23-29	Mussel	Normal	3.9	Present study
			B.A	1.4	
		Clam	Normal	4.0	
			B.A	1.8	
		Fish	Normal	8.3	
			B.A	2.7	
		Mixed	Normal	2.4	
			B.A	1.6	
Panulirus homarus	26-30	Clam	Normal	4.1	Vijayakumaran & Radhakrishnan, 1984
			B.A	2.0	
Panulirus ornatus	23-28	Mussel	Normal	4.7	Radhakrishnan & Vijayakumaran, 1987
			B.A	1.0	
Homarus americanus	15	Pellet	Normal	45.1	Castell et .al., 1977
			B.A	5.2	
Macrobrachium lanchesteri	Tropical	Tubifex	Normal	19.2	Ponnuchamy et. al., 1981
			B.A	5.2	
Macrobrachium nobilii	Tropical	-	Normal	9.5	Pandian & Sindhukumari, 1985
			U.A	6.5	

* FCR : $\frac{\text{Food consumed (dry weight)}}{\text{Live weight gain}}$

weight was simply the result of absorption of excess water. Based on the total nitrogen in normal and ablated crabs before and after moulting, he suggested that eyestalk ablation resulted in increased volume but not in real tissue synthesis. In the present study too, the water content of the ablated lobster (mean: 70.7 %) was higher than that of the normal lobster (mean: 64.1 %) in all the experiments (Table 5.12). However, the total dry weight and the total energy of the ablated lobster were higher than those of the normal lobster at the end of all the experiments. For instance, the dry weight of the (group-reared) normal and ablated lobsters were 45 and 72 g, respectively on the 80th day of the experiment (initial dry weight: 38 g). Hence, the present experiments confirm that new tissue synthesis is accelerated in the ablated **P. homarus**. After 83 or 118 days of accelerated weight gain, the ablated lobster had protein content almost equal to the normal lobster. The only significant difference in composition was the lower level of lipid deposition in the abdominal muscle of the ablated lobster (Tables 5.13 and 5.14). Mauviot and Castell (1976) also reported accelerated rate of protein deposition and tissue synthesis and lower level of lipid deposition in the muscle and hepatopancreas of the ablated **H. americanus**.

Another important change induced by eyestalk ablation was shrinkage of midgut gland. The mean hepatic index of the

normal lobster receiving different food was 4.7 whereas the mean hepatic index of the ablated lobster was only 3.5 (Table 5.12). The shrinkage of midgut gland was pronounced in the ablated lobsters receiving clam. Whereas the hepatic index of the normal lobster receiving clam was 4.9, that of the ablated lobster was only 2.3. Since the clam had higher carbohydrate content, an instant source of energy, and lower protein and lipid content, the ablated lobster could not store the organic reserves. The shrinkage of the midgut gland in the ablated lobster suggests that the accumulation of organic reserves in the midgut gland and the subsequent liberation may be governed by eyestalk hormone. Yamamoto (1960), Fingerman et.al. (1967) and Nagabhushanam and Diwan (1974) reported that eyestalk ablation results in depletion of reserves and degeneration of the midgut gland in crayfish and crab.

Similar to the effect of eyestalk ablation on growth, the different food that were offered to the lobster considerably influenced the conversion rate. The conversion rates (without exuvia) of the group-reared, normal lobster receiving mussel, clam, fish and mixed food were 21.7, 14.2, 7.2 and 24.3 J/g/day, respectively (Table 5.7). The conversion rate of the lobster feeding on mixed food was nearly 3.5 times higher than that of the lobster feeding on

fish. Though the feeding rates of the groups receiving mussel (161.8 J/g/day) and clam (160.9 J/g/day) were almost equal, the conversion rate was far lower in the clam-fed group. The difference in the conversion rate of the experimental groups may be due to the difference in the biochemical composition of the food. The protein and carbohydrate contents of the food ranged from 53.5 (clam) to 74.8 % (fish) and 1.1 (fish) to 29.3 % (clam), respectively. The difference in protein and carbohydrate contents between the food changed the protein-carbohydrate ratio. The fish had the highest protein-carbohydrate ratio (68.0) and the clam had the lowest ratio (1.8) (Table 5.2). The two extremes in the protein-carbohydrate ratio might have resulted in low conversion rate in the groups receiving clam and fish.

Optimum protein level in the food is essential for maximum tissue growth. Low dietary protein content (30 %) may result in inadequate protein to maintain optimum growth rate (Clifford and Brick, 1979; Millikin et.al., 1980). Excess protein (> 75 %) in the food also results in slow growth of many crustanceans (Andrews et.al., 1972; Venkataramiah et.al., 1975; Royan et.al., 1976; see also New, 1976). The decrease in Protein Efficiency Ratio (PER) with increasing food protein content in **P.homarus** suggests that very high protein content in the food may not be

optimally utilized by **P. homarus.** The high PER at low dietary protein levels is attributed to the protein sparing effect of non-protein dietary energy sources (Capuzzo, 1982). In the present study, the protein content of different food was high (53.5 to 74.8 %). Though the biochemical content of the food was not manipulated as in the pellet diet, the present study suggests that protein content of 65-70 % or protein-carbohydrate ratio of 5-10 as in the mixed food and mussel may be suited for achieving the maximum rate and efficiency of conversion in **P. homarus.**

Isolated rearing did not result in higher conversion rate despite 80 % higher feeding rate of the isolated individuals. The mean conversion rate (without exuvia) of the isolated, normal lobster was almost equal to that of the group-reared lobster (16.9 J/g/day).

5.4.5 Effect on exuvial production

The exuvia formed a considerable quantum of the converted food. Under the present experimental conditions, the lobster lost 11.4 to 41.0 % of the converted energy as exuvia (mean: 27.3 %). In terms of dry weight, the percentage of exuvia formed 31.1 to 71.4 % of the converted dry matter (mean: 56.4 %) (Table 5.4). The percentage loss through exuvia is comparable with that of prawns and crabs.

The crab, **Menippe mercenaria** lost 22.7 % of the converted energy as exuvia (Mootz and Epifanio, 1974). The freshwater prawn, **Macrobrachium lanchesteri** lost 58.9 % of the converted dry matter as exuvia (Ponnuchamy et.al., 1981). In the present study, the exuvial production was influenced by all the 3 tested factors. The exuvia formed 20.0 % of the converted energy in the (group-reared, normal) lobster feeding on mussel and 41.0 % in the lobster feeding on fish (Table 5.4). Similarly the rate of exuvial production also differed between the lobsters receiving different food. For instance, the lobster receiving mixed food and fish produced exuvia equivalent to 8.8 and 5.0 J/g/day (Table 5.7). It appears that the exuvial production is affected not only by the type of food but also is influenced by the feeding rate. The high feeding rate (mixed food: 191.1 J/g/day) resulted in higher rate of exuvial production (8.8 J/g/day).

However, the response of exuvial production to eyestalk ablation differed from this trend. Though the feeding rate was higher in the ablated lobster, the higher feeding rate did not result in higher percent of converted energy loss as exuvia. For instance, the ablated lobster (group-reared), on average, lost lesser percentage of converted food as exuvia compared to the normal lobster in terms of dry weight (normal: 56.8 %; ablated: 50.6 %) as well as energy (normal: 28.9 % ; ablated: 22.3 %). The ablated

lobster was able to reduce the loss of dry matter and energy through exuvia by increasing the water content and reducing the energy content of the exuvia. The water content in the exuvia of the ablated (65.7%) lobster was significantly higher than that of the normal lobster (56.7 %) ($t = 12.3$; $P < 0.05$); the exuvial protein and energy contents of the ablated lobster (protein: 8.3 %; energy: 3.47 KJ/g) was lesser than those of the normal lobster (protein: 11.4 %; energy: 4.53 KJ/g) (Table 5.17). The lesser energy and protein content in the exuvia of the ablated lobster may be due to the following reasons: i) The ablated lobster utilized the available protein (Fig. 5.5) and converted the assimilated energy (Tables 5.7 and 5.8) more efficiently than the normal lobster. The higher quantity of the utilized food resource was used for actual body growth, thereby minimising the protein and energy loss through exuvia. ii) The crustaceans are known to extensively resorb minerals from the old exoskeleton during late premoult stage (Stage D_3) (Passano, 1960). As the ablated lobster moulted frequently than the normal individual, the resorption from the exoskeleton would have been higher, resulting in lesser exuvial protein and energy contents in the exuvia.

However, compared to many other crustaceans, the mean protein and energy contents of the exuvia of the normal and

Table 5.17 Water (%), ash and protein (% dry weight) and energy content (KJ/g) of exuvia of normal and ablated P.homarus reared in group

Parameter	Normal	Ablated
Water	56.7 ± 1.6	65.7 ± 1.5
Ash	63.0 ± 1.2	64.8 ± 0.8
Protein	11.4 ± 1.2	8.3 ± 0.8
Energy	4.53 ± 0.1	3.47 ± 0.2

ablated **P.homarus** were higher. For instance, Du Preez (1983) estimated the energy content of the exuvia of the swimming crab, **Ovalipes punctatus** (normal) as 2.94 KJ/g. The energy and total organic content of the exuvia of normal **P. homarus** were 4.53 KJ/g and 36 %. Hence, the nutritive value of the lobster exuvia is higher than many crustaceans. This may be the reason for the lobsters receiving inadequate food consuming the exuvia of other lobsters (personal observation).

5.4.6 Effect on metabolic rate

The metabolic rate, which was the major component of the energy budget of **P. homarus** (Fig. 5.1 and 5.2), was affected by the 3 experimental factors. The mean metabolic rate of the isolated, normal lobster (0.53 ml O_2/g/hr) was nearly 2 times higher than the mean metabolic rate of the group-reared (normal) lobster (0.27 ml O_2/g/hr). As **P.homarus** is gregarious in behaviour, isolated rearing probably induced higher metabolic rate, resulting in 80 % higher feeding rate (see also section 5.4.1). The quality of food also induced 50 % variation in the metabolic rate in the control (group-reared, normal) experiment (see Table 5.7).

Eyestalk ablation accelerated the metabolic rate. The mean metabolic rate of the ablated (group-reared) lobster (0.37 ml O_2/g/hr) was nearly 50 % higher than the mean

metabolic rate of the normal (group-reared) lobster (0.27 ml O_2/g/hr). Eyestalk ablation in the crustaceans appears to lead to a series of interconnected hormonal processes regulating the metabolism. The exact nature and mode of action of hormones in regulating the metabolism is not properly understood. The X-organ-sinus gland complex is believed to play a major role in the regulation of metabolism of decapods (Bliss, 1951; Passano, 1960; Kleinholz, 1975; Lockwood, 1968; Keller et.al., 1985). The removal of MIH (due to ablation), which inhibits the secretion of Y-organ, may be responsible for regulating the metabolic rate (Chang, et.al., 1985). Chang and O'Connor (1983) suggested that the hyperglycemic hormone (HCH) of the eyestalk, which indirectly is responsible for hyperphagia, is also the hormone involved in metabolic regulation. As eyestalk ablation acts upon a number of metabolic parameters, it is difficult to precisely determine the hormonal factor(s) responsible for regulating the metabolic rate.

The mean metabolic rate of the normal (group-reared) **P. homarus** (0.27 ml O_2/g/hr) is higher than the values reported for **H. americanus** (Capuzzo and Lancaster, 1979) and many other temperate crustaceans (Wolvekamp and Waterman, 1960). However, the oxygen consumption of tropical crustaceans are uniformly higher than their temperate counter

parts. For instance, the oxygen consumption of the macruran, **Cambarellus shufeldtii** ranged from 0.34 to 0.65 ml O_2/g/hr at 29°C (Fingerman, 1955). Wolvekamp and Waterman (1960) have tabulated the oxygen consumption rate of a number of crustaceans. From this table, it is evident that oxygen consumption ranging form 0.4 to 1.2 ml O_2/g/hr is not uncommon for tropical crustaceans. In the present study, the metabolic rate (0.47 - 1.30 ml O_2/g/hr) estimated in the experiment on the isolated, ablated lobster was much higher than that of the lobsters of the other experiments. The reason for very high metabolic rate in this particular experiment, may be due to the interaction of the 3 factors, viz., isolation, ablation and different food on the food utilization pattern of the lobster. The feeding rates of the isolated, ablated **P. homarus** was several times higher than any other experimental group; the conversion efficiency was lower than any other group; the conversion rate did not follow any uniform pattern comparable to the other groups. Hence, the interaction of the 3 factors adversely affected the food utilization of the isolated, ablated lobster, resulting in elevated metabolic level.

6 EFFECT OF FOOD QUANTITY ON FOOD UTILIZATION

6.1 Introduction

In natural conditions, the animals encounter different concentration of food materials and often face low concentration, leading to reduced food consumption or near starvation. The effect of reduced food consumption on the food utilization has been well studied in fishes (for e.g., Gerking, 1955, 1971; Pandian, 1967; Brett et. al., 1969; Pandian and Raghuraman, 1972; Vivekanandan, 1976). These studies have revealed that feeding rate influences the rates and efficiencies of assimilation, conversion and metabolism. Studies on the effect of feeding rate on growth has helped the fishery biologists to suggest valuable clues on the optimum ration required for maximum growth rate of fishes in culture farms. Similar exhaustive studies on the ration-induced changes are not available in the lobsters. However, available information indicate that the growth process is influenced by the quantity of food consumed. Low ration influenced both moulting frequency and size increment per moult in the American lobster, **H. americanus** (Stewart and Squires, 1968). Later study on **H. americanus** by Bartley et.al., (1980) revealed that rate and efficiency of conversion are also remarkably influenced by change in ration level. The studies on **H. americanus** provide information only

on moulting frequency, growth and conversion efficiency without mentioning about assimilation and metabolic rate at different feeding levels. Study on the effect of ration on the food utilization is lacking in palinurid lobsters. Limited information on **P. longipes cygnus** (Chittleborough, 1975) indicates that the first effect of a mild shortage of food is a reduction in frequency of moulting and under more severe condition of food shortage or starvation, moulting frequency further decreases and size increment per moult is also reduced,

Studies on the physiological processes underlying growth have commonly agreed that there exists a basic maintenance metabolic requirement which must be satisfied by food energy intake before energy is available for other uses (Paloheimo and Dickie, 1966a). Hence, one requires basic knowledge on the metabolic demands of maintenance. Furthermore, it is a prerequisite to identify the optimum and maximum feeding rates of culturable species. Though the optimum and maximum feeding rates have been quantified in a few culturable prawns (Katre and Reddy, 1976; Sumitra Vijayaraghavan et . al., 1982; Sedgewick, 1979 b; Ponnuchamy et . al., 1981), there is no attempt to quantify these important ration levels in the lobsters. In the present study, the spiny lobster **P.homarus** was exposed to different rations ranging from starvation to **ad libitum** feeding not

only to quantify maintenance, optimum and maximum rations but also to understand the effect of ration on survival, moulting, growth, assimilation and metabolism.

In the previous experiments on the effect of food quality on the food utilization of **P. homarus**, it was evidenced that eyestalk ablation induced hyperphagia, resulting in higher rates of feeding, conversion and metabolism. It is not known whether the ablated lobster receiving reduced ration i) could maintain higher rates of conversion and metabolism than the normal lobster and ii) whether the maintenance, optimum and maximum rations of the ablated lobster will be different from those of the normal individual. In the present study, two experiments were conducted on the effect of different ration levels on the food utilization of normal and eyestalk ablated **P. homarus.**

6.2 Materials and methods

Healthy individuals of **P. homarus** (carapace length: 48.8 $\pm$ 2.4 mm; live weight: 104.0 $\pm$ 13.7 g) in intermoult stage were selected from the common reserve in the laboratory. Equal number of males and females were used. The selected lobsters were divided equally for the two experiments; The first 24 lobsters served as normal

individuals for the first experiment; the other 24 lobsters were ablated for the second experiment. Each experiment was divided into 6 groups of 4 individuals each; six rations (0, 10, 25, 50, 75 and 100 % of maximum feeding rate) were selected and each group was offered one of the 6 rations. To determine the maximum feeding rate (100 % ration), a preliminary experiment was conducted by individually feeding 3 normal and 3 eyestalk ablated lobsters **ad libitum** for 5 days on fresh mussel meat and the maximum food consumed was estimated. The quantity of food to be offered for different rations was calculated based on the maximum food consumed by the normal and ablated lobsters. The quantity of food was revised after every moult.

The experimental lobsters were acclimatised to the laboratory conditions and feeding schedules for 7 days before commencement of the experiment. For the experiment, the lobsters were reared individually in aquaria of equal size (size: 61 x 40.5 cm; vol: 61.8 l). Fresh mussel **(Perna viridis)** meat was offered as food for the lobsters. The food was weighed to an accuracy of 0.1 mg in a monopan electric balance. Food was offered at 4 pm every day and the unconsumed food, if any, was removed on the following day at 9 am. The aquarium water was completely changed every day. All the aquaria were aerated continuously on all the days of the experiment. Ammonia was estimated at bi-weekly

intervals. Exuvia, when produced, was weighed and the dry weight was determined. The live weight of the experimental lobsters was determined 10 days after each moult. The duration of each experiment was 100 days.

The mean water temperature during the experiment was 26.0 ± 2°C, the salinity was 34.0 ± 1 ‰ and the dissolved oxygen concentration was 4.4 ± 0.8 ml/l. The experiments were conducted in natural photoperiodicity prevalent in the laboratory. The methods of collection of faeces and unconsumed food and procedure followed to estimate food utilization parameters are described in Chapter 2.

6.3 Results

6.3.1 Effect of food quantity on food utilization of normal lobster

Survival

The starved normal lobster survived for 68.7 ± 2.0 days. All the starved lobsters died in intermoult stage. The other groups receiving different ration survived for the entire experimental duration of 100 days.

Feeding rate

The normal **P. homarus** fed **ad libitum** consumed 12.5 mg dry food/g live lobster/day (Table 6.1) or 220.1 J/g live

Table 6.1 **Effect of ration on food utilization parameters of normal P.homarus; the rates are expressed as mg dry weight/g live lobster/day and efficiencies as %;** ± represents SD.

Parameters	Ration (%)					
	0	10	25	50	75	100
Feeding rate	-	1.5 ± 0.1	3.3 ± 0.3	5.0 ± 0.4	9.7 ± 0.3	12.5 ± 1.2
Assimilation rate	-	1.4 ± 0.2	3.3 ± 0.3	4.8 ± 0.4	9.4 ± 0.3	12.0 ± 1.0
Conversion rate						
E	-	-	1.4 ± 0.2	1.3 ± 0.1	2.2 ± 0.1	2.6 ± 1.2
P	- 1.6 ± 0.01	- 1.5 ± 0.02	0.3 ± 0.06	0.3 ± 0.02	0.9 ± 0.06	0.8 ± 0.04
E + P	- 1.6 ± 0.01	- 1.5 ± 0.02	1.1 ± 0.10	1.6 ± 0.02	3.1 ± 0.02	3.4 ± 0.03
Metabolic rate	1.6 ± 0.01	2.9 ± 0.20	2.2 ± 0.10	3.2 ± 0.20	6.3 ± 0.40	8.6 ± 0.60
Assimilation efficiency	-	97.9 ± 0.9	98.2 ± 0.3	97.0 ± 0.4	96.7 ± 0.4	96.4 ± 0.3
Conversion efficiency(K_2)						
WE	-	-	33.8 ± 3.10	34.4 ± 2.6	33.0 ± 2.5	28.9 ± 2.8
WOE	-	-	-	6.8 ± 0.4	8.8 ± 0.5	6.6 ± 0.3

lobster/day (Table 6.2). All the groups receiving lower rations consumed the entire quantity of food offered except during moulting.

Though the lower rations fixed were 10, 25, 50 and 75 % of maximum feeding rate, the actual quantity of food offered/consumed by the lobster deviated from the target ration due to the following reasons : i) The water content of the food ranged from 74-78 % during the experimental duration of 100 days. The day-to-day difference in water content influenced the dry weight and the energy equivalent of the food offered/consumed: ii) The group receiving **ad libitum** food moulted more frequently and exhibited faster growth than the other groups. After initial fixation of the quantity of food to be offered to 10, 25, 50 and 75 % ration groups, the quantity was revised after every moult. For example, the group receiving **ad libitum** food consumed 12.7 mg dry food/g/day (100 % ration) from the commencement of the experiment to the first moult; after the first moult, the lobster increased the feeding rate to 16.2 mg/g/day. The ration for the group receiving 10 % of maximum food consumption was fixed based on the feeding rate of 12.7 mg/g/day prior to the first moult and subsequently revised to 10 % of 16.2 mg/g/day on the day the 100 % group commenced feeding after the second moult. As the group receiving 10 % ration did not moult and increase the body weight on that

Table 6.2 Effect of ration on food utilization parameters of normal P.homarus; the rates are expressed as J/g live lobster/day and efficiencies as %; ± represents SD.

Parameters	Ration (%)					
	0	10	25	50	75	100
Feeding rate	-	25.5 ± 2.7	58.9 ± 3.6	87.8 ± 4.6	171.0 ± 5.9	220.1 ± 19.4
Assimilation rate	-	25.3 ± 2.7	58.6 ± 3.6	86.8 ± 4.6	168.3 ± 5.8	215.7 ± 18.3
Conversion rate						
E	-	-	5.9 ± 0.6	5.6 ± 0.4	9.6 ± 0.8	11.2 ± 1.0
P	- 14.3 ± 0.7	- 13.9 ± 1.2	- 3.0 ± 0.2	4.3 ± 0.4	11.2 ± 1.1	11.5 ± 1.8
E+P	- 14.3 ± 0.7	- 13.9 ± 1.2	2.9 ± 0.3	9.9 ± 0.8	20.8 ± 1.8	22.7 ± 1.6
Metabolic rate	14.3 ± 0.7	13.9 ± 1.2	55.7 ± 2.8	76.9 ± 3.6	147.6 ± 13.6	193.0 ± 15.8
ml O_2/g/hr	0.03 ± 0.010	0.08 ± 0.004	0.12 ± 0.008	0.16 ± 0.010	0.31 ± 0.020	0.40 ± 0.020
Assimilation efficiency	-	99.4 ± 0.2	98.9 ± 0.8	98.6 ± 0.8	98.4 ± 0.6	98.0 ± 0.5
Conversion efficiency(K_2)						
WE	-	-	5.0 ± 0.5	11.4 ± 1.0	12.5 ± 1.1	10.6 ± 0.5
WOE	-	-	-	4.9 ± 0.2	6.5 ± 0.4	5.2 ± 0.3

day, the ration offered was higher than the target ration of 10 %. As a result of this, the group receiving 10 % ration consumed 1.5 mg/g/day during the experiment (Table 6.1), whereas it should have consumed only 1.25 mg/g/day. Deviation from the target ration was observed in 25, 50 and 75 % rations too. Nevertheless, for the sake of uniformity and convenience, the rations have been identified as 10, 25, 50 and 75 %.

Assimilation

The assimilation rate increased with increasing ration in terms of dry weight as well as energy. The assimilation efficiency was uniformly high in all the rations and averaged to 97.2 % on dry weight basis and 98.8 % on energy basis.

Conversion

The starved lobster lost 1.6 mg dry weight/g/day or 14.3 J/g/day. At the commencement of the experiment, the mean dry weight and mean energy of a single lobster was 27.9 g and 398 KJ, respectively; at the time of death, the dry weight and energy reduced to 16.0 g and 146 KJ, respectively, i.e. the starved lobster lost 42.7 % dry weight or 63.3 % energy during the survival period of 68.7 days.

The group receiving 10 % ration lost 1.5 mg dry weight/g/day or 13.9 J/g/day during the experimental period of 100 days. The lobsters receiving 25 % ration and above exhibited conversion rate (including exuvia) and the conversion rate increased with increasing ration. For instance, the conversion rate increased from 2.9 J/g/day in the group receiving 25 % ration to 22.7 J/g/day in the group receiving 100 % ration (Table 6.2). However, the difference in the conversion rate between the groups receiving 75 and 100 % ration was not statistically significant ($t = 2.07$; $P > 0.05$).

The net energy conversion efficiency (including exuvia) was the lowest (5.0 %) in the 25 % ration level and was higher in the 50,75 and 100 % ration levels (10.6-12.5%). The efficiency of convering the assimilated dry matter was higher (28.9-34.4 %) than converting the energy. This was possible because the exuvia formed an average of 76.1 % of total converted dry matter in the 50, 75 and 100 % rations and only 50.7 % of the total converted energy in the same rations. By excluding the exuvia, the conversion efficiency was only marginally higher (6.6 - 8.8 %) in terms of dry weight compared to the efficiency (4.9 - 6.5 %) based on energy.

Intermoult duration

The starved group and the group receiving 10 % ration did not moult during the respective survival period. The group receiving 25 % ration moulted once and the other 3 groups receiving higher rations moulted twice. There was pronounced effect of ration on intermoult duration. For instance, the group receiving 50 % ration moulted in 72 days and the group receiving 100 % moulted in 43 days (Table 6.3). At the commencement of the experiment, all the test individuals were in intermoult stage (stage C) and hence, the intermoult duration upto the first moult need not be considered.

Metabolic rate

The metabolic rate increased with increasing ration and the metabolic rate of the group receiving 100 % ration (0.40 ml O_2/g/hr) was 13.3 times higher than that of the starved lobster (0.03 ml O_2/g/hr) (Table 6.2).

6.3.2 Effect of food quantity on food utilization of ablated lobster

Survival

The ablated lobster succumbed to starvation/low ration earlier than the normal lobster. The ablated group

Table 6.3 Survival and intermoult duration (days) of P.homarus receiving different ration

Ration (%)	Normal			Ablated			
	Survival duration	Intermoult duration upto I moult	I-II	Survival duration	Intermoult duration upto I moult	I-II	II-III
0	68.7 ± 15.0	*	-	53.0 ± 2.0	21.5 ± 2.5	**	-
10	100.0#	*	-	84.5 ± 2.5	19.7 ± 2.5	44.0 ± 8.0	**
25	100.0#	66.5 ± 6.5	-	100.0# ±	24.5 ± 1.6	33.7 ± 2.8	35.0 ± 3.0
50	100.0#	20.0 ± 2.5	72.0 ± 4.0	100.0#	23.7 ± 3.1	33.7 ± 4.9	36.0 ± 4.0
75	100.0#	19.5 ± 2.6	65.0 ± 3.6	100.0#	28.0 ± 0.0	26.0 ± 1.0	30.0 ± 3.0
100	100.0#	18.0 ± 1.6	43.0 ± 4.1	83.0 ± 19.3	25.0 ± 2.2	26.5 ± 2.5	31.0 ± 2.5

* did not moult till death

** died prior to II or III moult

survived for the entire experiment

receiving 0 and 10 % ration survived for 53.0 and 84.5 days, respectively (Table 6.3). The groups receiving 25,50 and 75 % ration survived the entire experimental duration of 100 days. Of the 4 individuals receiving 100 % ration, 2 individuals died between 53 and 80 days of the experiment, resulting in mean survival of 83.0 days. Survival of the lobster receiving **ad libitum** food was apparently affected by decomposition of unconsumed food which fouled the water. Since the quantum of **ad libitum** food offered to the ablated lobster was more than that of the normal lobster, water spoilage was more pronounced in the experiment on the ablated lobster than in the experiment on the normal lobster. Though the aquarium water was changed every day and the water was aerated on all the days of the experiment, the survival duration of the ablated lobsters receiving **ad libitum** food was lesser. Bartley et al. (1980) also reported that excess ration presented to **H. americanus** just prior to moulting was not consumed by the lobster, leading to water spoilage and depletion of dissolved oxygen and finally resulting in mortality.

Feeding rate

The group receiving **ad libitum** food consumed 17.6 mg dry food/g live lobster/day (Table 6.4) or 309.5 J/g/day (Table 6.5). Similar to the experiment on the normal

Table 6.4 Effect of ration on food utilization parameters of ablated P.homarus; the rates are expressed as mg dry weight/g live lobster/day and efficiencies as %; ± represents SD.

Parameters	Ration (%)					
	0	10	25	50	75	100
Feeding rate	-	2.5 ± 0.01	5.4 ± 0.2	9.1 ± 0.6	13.1 ± 0.6	17.6 ± 1.5
Assimilation rate	-	2.5 ± 2.7	5.3 ± 3.6	8.5 ± 4.6	12.4 ± 5.8	16.2 ± 18.3
Conversion rate						
E	2.6 ± 0.0	2.6 ± 0.1	2.6 ± 0.1	3.1 ± 0.2	2.9 ± 0.1	3.9 ± 0.1
P	- 3.3 ± 0.2	- 1.1 ± 0.1	0.2 ± 0.1	0.4 ± 0.02	1.4 ± 0.01	1.2 ± 0.12
E+P	-0.7 ± 0.03	1.5 ± 0.01	2.8 ± 0.01	3.5 ± 0.02	4.3 ± 0.04	5.1 ± 0.04
Metabolic rate	0.68 ± 0.08	0.98 ± 0.7	2.50 ± 0.7	5.00 ± 0.4	8.20 ± 0.6	11.10 ± 1.0
Assimilation efficiency	-	99.0 ± 0.1	97.6 ± 0.0	93.9 ± 1.4	95.0 ± 2.0	92.0 ± 0.8
Conversion efficiency(K_2)						
WE	-	60.0 ± 0.8	51.6 ± 2.6	41.7 ± 2.3	34.2 ± 1.4	30.7 ± 3.1
WOE	-	-	0.3 ± 0.02	5.1 ± 0.2	11.3 ± 0.8	7.4 ± 0.6

Table 6.5 Effect of ration on food utilization parameters of ablated P.homarus; the rates are expressed as J/g live lobster/day and efficiencies as %; ± represents SD

Parameters	Ration (%)					
	0	10	25	50	75	100
Feeding rate	-	49.4 ± 2.6	95.4 ± 3.9	160.1 ± 19.0	230.9 ± 8.6	309.5 ± 17.9
Assimilation rate	-	49.0 ± 2.6	93.7 ± 3.8	153.6 ± 8.3	222.9 ± 10.3	291.3 ± 14.2
Conversion rate						
E	11.6 ± 1.0	11.6 ± 0.8	11.9 ± 1.8	12.4 ± 1.2	13.1 ± 1.3	15.4 ± 1.2
P	- 20.9 ± 1.7	- 15.9 ± 1.2	1.8 ± 0.9	5.5 ± 0.5	22.6 ± 1.3	16.0 ± 1.8
E+P	- 9.3 ± 0.2	- 4.3 ± 0.3	13.7 ± 1.2	17.9 ± 1.5	35.7 ± 3.2	31.4 ± 2.4
Metabolic rate	9.3 ± 0.2	53.3 ± 1.5	80.2 ± 4.0	127.5 ± 9.2	187.2 ± 16.7	260.0 ± 19.4
ml O_2/g/hr	0.02 ± 0.001	0.11 ± 0.001	0.17 ± 0.020	0.27 ± 0.020	0.39 ± 0.020	0.54 ± 0.040
Assimilation efficiency		99.2 ± 0.4	98.2 ± 1.0	95.9 ± 1.2	96.5 ± 2.0	94.1 ± 2.0
Conversion efficiency(K_2)						
WE	-	-	14.5 ± 1.3	11.6 ± 4.4	16.0 ± 1.2	10.8 ± 0.5
WOE	-	-	1.9 ± 0.06	3.4 ± 0.8	9.8 ± 0.5	5.2 ± 0.3

lobster, the feeding rate of the ablated lobster receiving 10, 25, 50 and 75 % ration levels deviated from the target ration. For instance, the group receiving 10 % ration should have consumed 1.8 mg/g/day but due to reasons mentioned in section 6.3.1, the feeding rate was 2.5 mg/g/day.

The maximum feeding rate (100 % ration) of the ablated lobster (309.5 J/g/day) was about 40 % higher than that of the normal lobster (220.1 J/g/day). Hence, the quantum of food received/consumed by the ablated lobster at 10, 25, 50 and 75 % ration was comparatively higher than the feeding rate of the corresponding group of the normal lobster.

Assimilation

The assimilation efficiency was very high in all the feeding levels. However, the efficiency decreased with increasing ration on dry weight as well as energy basis. For instance, assimilation efficiency was 99.0 % at 10 % ration and was 92.0 % at 100 % ration (Table 6.4; these two values were statistically significant; $t = 5.9$; $P < 0.05$). This inverse relationship was not observed in the normal lobster, which assimilated the different quantity of food with almost equal efficiency (Tables 6.1 and 6.2).

Conversion

The starved lobster lost 0.7 mg dry weight/g/day or 9.3 J/g/day. Compared to the starved normal lobster (14.3 J/g/day), the ablated lobster lost lesser energy on starvation. However, unlike the starved normal lobster which did not moult, the starved ablated lobster moulted once during survival and inclusion of the exuvial energy as part of growth has reduced the energy loss of the starved ablated lobster. By excluding the exuvia, it was calculated that the starved ablated lobster lost 20.9 J/g/day, which was about 46 % higher than the energy lost by the starved normal lobster (14.3 J/g/day). At the commencement of the experiment, the mean energy of a single lobster was 519 KJ; after 53 days (at the time of death), the total energy of the starved ablated lobster reduced to 167.6 KJ, i.e. an energy los of 67.7 %, which is almost equal to the energy loss of the starved normal lobster (63.3 %).

The ablated group receiving 10 % ration lost 4.3 J/g/day compared to 13.9 J/g/day by the normal lobster. Here too, the ablated lobster moulted once unlike the normal lobster, which failed to moult. The ablated lobster receiving 25% ration and above exhibited conversion rate and the conversion rate increased from 2.8 (25 %) to 5.1 mg/g/day (100 %) with increasing ration (Table 6.4). In terms of

energy, the conversion rate of the group receiving 75 or 100% ration (mean: 33.6 J/g/day) was about 2 times higher than that of the groups receiving 25 or 50 % ration (mean: 15.8 J/g/day).

Similar to the results obtained from the experiment on the normal lobster, the net conversion efficiency was higher on the basis of dry weight (30.7 - 60.0 %) than on energy basis (10.8 - 16.0 %) due to the low energy content of the exuvia. The efficiency, calculated by excluding exuvia, was maximum in the group receiving 75% ration in terms of dry weight (11.3 %) as well as energy (9.8 %). The conversion efficiency of the group receiving 75 % ration was statistically higher than that of the group receiving 100 % ration in terms of dry matter ($t = 3.1$; $P < 0.05$) as well as energy ($t = 12.1$; $P < 0.05$).

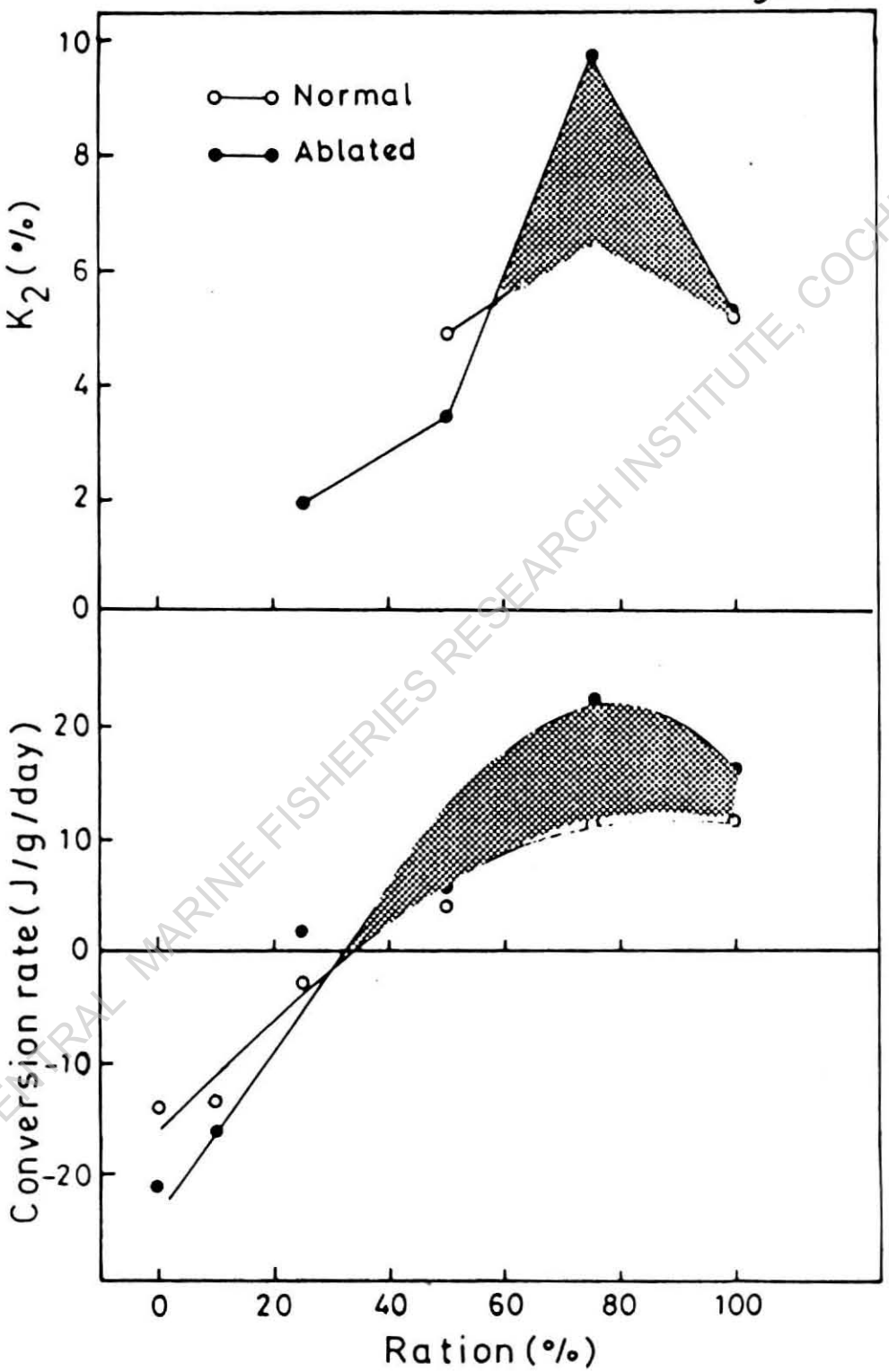
Comparison of the conversion rate curves of the normal and ablated lobsters revealed that ration higher than 35 % resulted in higher conversion rate in the ablated lobster than the normal lobster. For instance, the normal and ablated lobsters feeding at an equal ration (75 %) exhibited conversion rates of 11.5 and 22.0 J/g/day, respectively. Though the difference in conversion rate between the normal and the ablated lobster reduced as the ration approached the maximum, it is clear that the ablated

lobster exhibited higher conversion rate than the normal lobster above 35 % ration. Working on the effect of eyestalk ablation on the growth of different sizes of **P. homarus,** Vijayakumaran and Radhakrishnan (1984) also reported that the conversion rate of the ablated lobster (2.9 mg/g/day) was higher by nearly 2.5 times than that of the normal lobster (1.2 mg/g/day) at a given feeding rate of 10 mg/g/day.

The ablated lobster was able to exhibit higher conversion rate than the normal lobster due to higher conversion efficiency in ration above 50 % level (Fig. 6.1). It appears that the ablated lobster is capable of enhancing the conversion efficiency to meet the high energy requirement of accelerated tissue synthesis consequent upon greater volume increase after moulting. However, at lower rations, the conversion efficiency of the ablated lobster was lower than the normal lobster. Unlike the normal lobster, the ablated lobster receiving lower ration expended part of the consumed energy towards moulting, resulting in lower conversion efficiency. By including exuvia, the conversion efficiency of the normal and ablated lobster was almost equal (K_2: 11.5 %) at 50 % ration (Tables 6.2 and 6.5).

Fig. 6.1 Effect of ration on conversion rate and energy conversion efficiency (K_2; excluding exuvia) of normal and ablated **P. homarus**. (▒▒▒) area indicate increase in conversion due to eyestalk ablation.

Fig. 6·1



Intermoult duration

The starved lobster moulted once and the group receiving 10 % ration moulted twice during the survival period of 53.0 and 84.5 days, respectively; the other 4 groups receiving higher ration moulted 3 times during the experimental duration of 100 days (Table 6.3). The intermoult duration of the groups receiving higher rations of 75 and 100 % (mean intermoult duration: 28.4 days) was shorter than that of the groups receiving 25 and 50 % ration (mean intermoult duration: 34.6 days). Compared to the normal lobster, there were two differences in the intermoult duration of the ablated lobster, i) the intermoult duration of the ablated lobster was much shorter at any given ration level. For instance, at 100 % ration, the ablated lobster moulted in 26.5 - 31.0 (mean: 28.8) days, whereas the normal lobster moulted in 43.0 days; ii) the effect of ration on the intermoult duration was more pronounced in the normal lobster than the ablated lobster. For instance, the intermoult duration of the normal lobster receiving 100 % ration (43.0 days) was shorter by about 40 % than the intermoult duration of the group receiving 50 % ration (72.0 days); the mean intermoult duration I - III moult) of the ablated group receiving 100 % ration (28.8 days) shortened by only 17 % than the intermoult duration of the group receiving 50 % ration (34.9 days).

Metabolic rate

The metabolic rate of the starved ablated lobster was 9.3 J/g/day (0.02 ml O_2/g/hr); the metabolic rate of the group receiving 100 % ration was about 27 times higher (260.0 J/g/day or 0.54 ml O_2/g/hr) than the starved lobster. Compared to the starved normal lobster (0.03 ml O_2/g/hr), the starved ablated lobster spent lesser on metabolism. However, the ablated lobster expended more energy on metabolism than the normal lobster in all the other ration levels (Tables 6.2 and 6.5).

The metabolic rate of the normal and ablated lobsters increased linearly with increasing ration (Fig. 6.2) with the following equations:

Normal : $y = 0.027 + 0.0036\ x$

$r = 0.986$

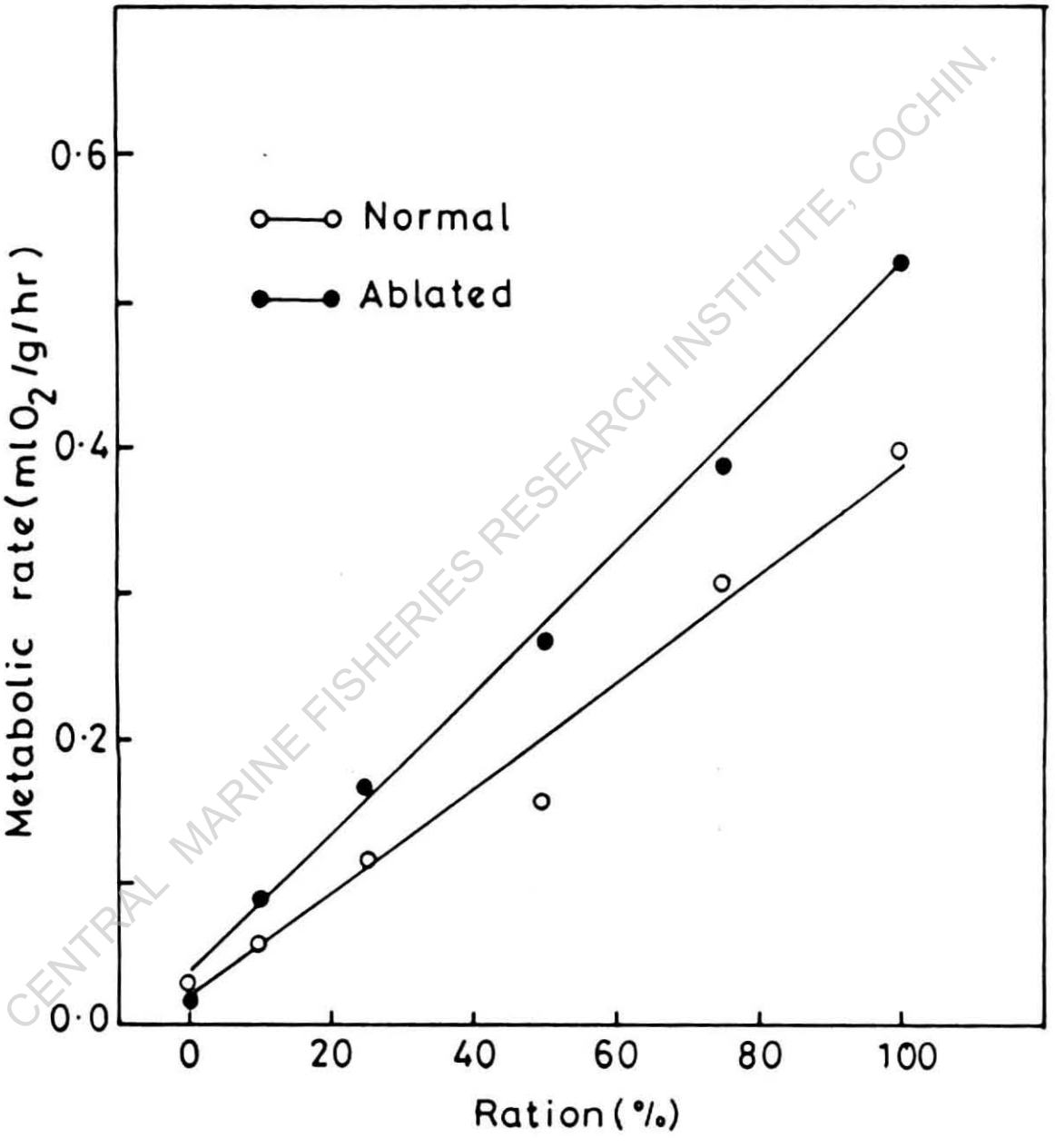
Ablated : $y = 0.038 + 0.0049\ x$

$r = 0.996$

The difference in the metabolic rate between the normal and ablated lobster increased with increasing ration. For instance, the metabolic rate of the ablated lobster (0.11 ml O_2/g/hr) was about 25 % higher than that of the normal lobster (0.08 ml O_2/g/hr) at 10 % ration. At 100 % ration, the metabolic rate of the ablated lobster (0.54 ml O_2/g/hr)

Fig. 6.2 Effect of ration on metabolic rate of normal and ablated **P.homarus**

Fig. 6·2



was 35 % higher than that of the normal lobster (0.40 ml O_2/g/hr).

6.3.3 Water, ash and energy contents of normal and ablated lobsters

At the commencement of the experiment, the water, ash and energy contents of **P. homarus** were 67.5 % , 31.0 % and 13.4 KJ/g, respectively. To determine the effect of ration on water, ash and energy contents of the normal and eyestalk ablated lobsters, estimations were made at the completion of the experiment. The water, ash and energy contents of the normal lobster were linearly related to the ration (Fig. 6.3) with the following equations :

Water : $y = 77.68 - 0.124\ x$

$r = - 0.919$

Ash : $y = 37.4 - 0.06\ x$

$r = - 0.893$

Energy : $y = 9.06 + 0.060\ x$

$r = 0.934$

The water, ash and energy contents of the ablated lobster also followed a similar trend (Fig. 6.4) with the following equations:

Water : $y = 84.3 - 0.110\ x$

$r = - 0.951$

Fig. 6.3 Effects of ration on water, ash and energy contents of the normal **P. hoeuarus**

Fig. 6·3

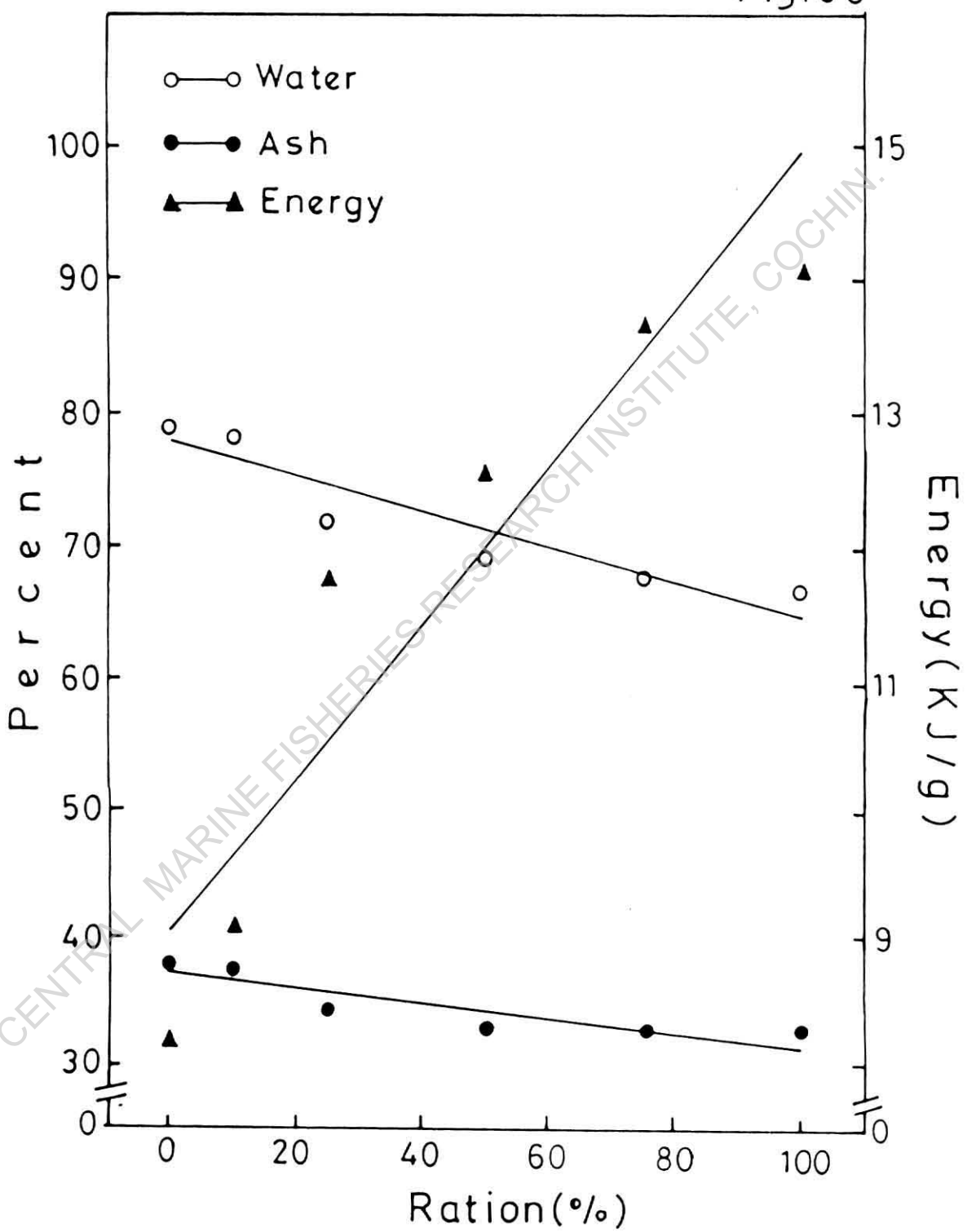
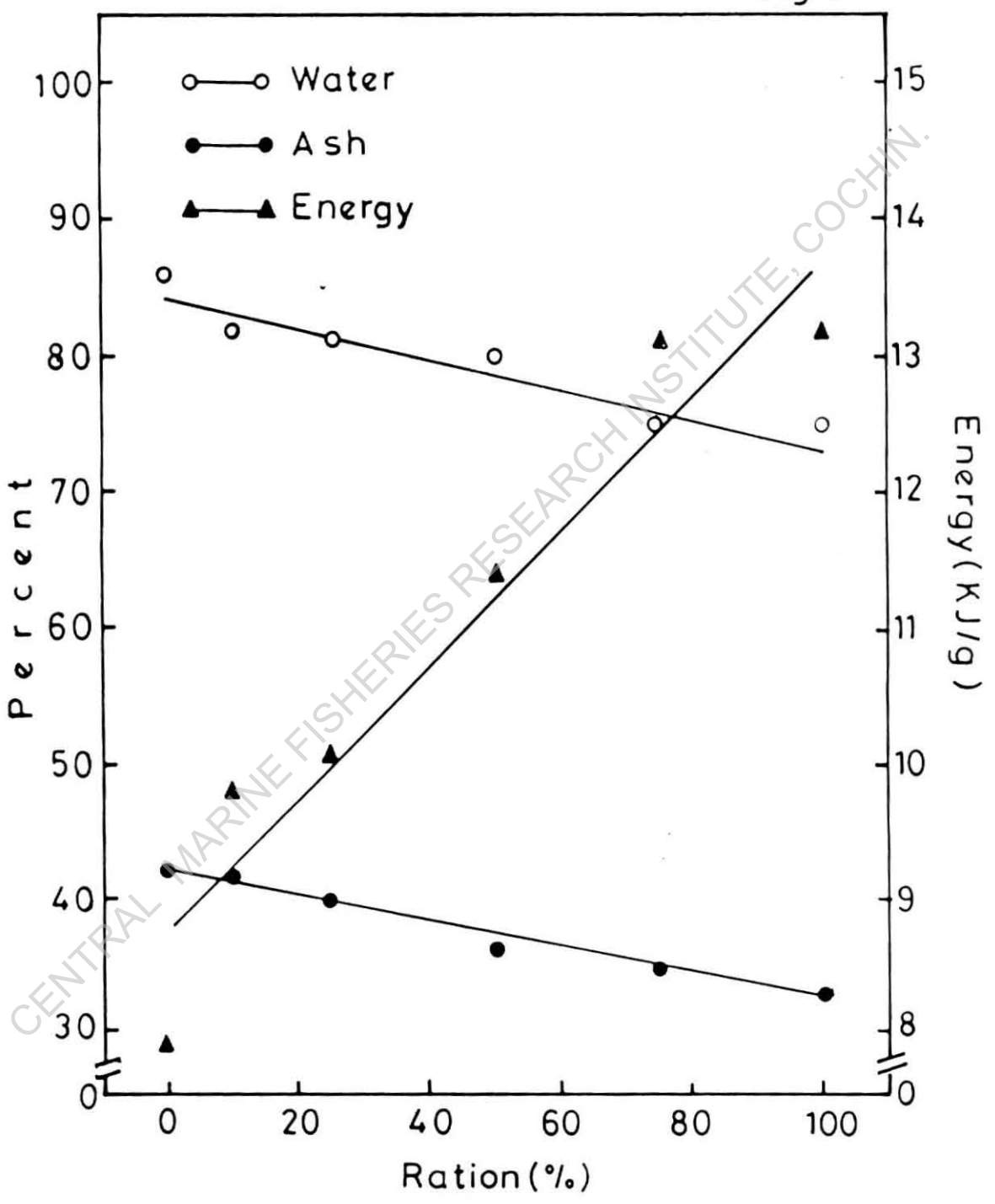


Fig. 6.4 Effects of ration on water, ash and energy contents of the ablated **P. homarus**

Fig. 6·4



Ash : $y = 41.9 - 0.090 x$

$r = - 0.984$

Energy : $y = 8.7 + 0.050 x$

$r = 0.959$

In all the rations, the water and ash contents were higher and the energy content was lower in the ablated lobster than the normal lobster.

6.3.4 Energy budget

To quantify partition of the consumed energy towards different processes related to body functions and body structures, the energy allocated for growth, metabolism and egestion was calculated as percentage of energy consumed. The energy allocated for metabolism (mean: 82.2 %) and for growth (mean: 5.1 %) by the ablated lobster was marginally lesser than the energy allocated for metabolism (mean:87.2 %) and for growth (mean:5.5 %) by the normal lobster (Table 6.6). As these differences are not statistically significant, it may be concluded that allocation of the consumed energy for the different energy parameters is almost equal in the normal and ablated lobsters (see also chapter 5.3.5).

6.4 Discussion

The study on the effect of interaction of starvation or very low ration (10 % of maximum feeding rate) and

Table 6.6 Energy budget of normal and ablated P.homarus receiving different ration; the values were calculated as percent of respective food energy consumed (C)

Ration (%)	C	Normal				Ablated			
		P	E	R	F+U	P	E	R	F+U
10	100	0	0	99.2	0.8	0	0	99.2	0.8
25	100	0	0	95.5	0.5	1.9	12.5	84.1	1.8
50	100	4.9	6.4	87.6	1.1	3.4	7.7	79.6	4.1
75	100	6.5	5.6	86.3	1.6	9.8	5.7	81.1	3.5
100	100	5.2	5.1	87.7	2.0	5.2	5.0	84.0	5.9
Mean	**100**	**5.5**	**5.7**	**87.2**	**1.6**	**5.2**	**5.1**	**82.2**	**3.8**

bilateral eyestalk ablation has revealed the following 3 major interlinked responses of **P. homarus**: i) the ablated starved lobster survived for only 53.0 days, which is lesser than the survival duration (68.7 days) of the normal starved lobster; ii) whether normal or ablated, the starved lobster withstood total energy loss of about 65 % from the body and further loss resulted in death. As the ablated lobster lost 65 % of the total energy quicker (in 53.0 days) than the normal lobster (in 68.7 days), the ablated lobster succumbed earlier than the normal lobster. In other words, the ablated lobster lost higher rate of energy (20.9 J/g/day; Table 6.5) than the normal lobster (14.3 J/g/day; Table 6.2); iii) the higher rate of energy loss and the resultant shorter survival duration were due to moulting by the ablated lobster even under starvation/very low ration. Whereas the normal starved lobster did not moult and thereby conserved energy, the ablated starved lobster moulted once (the lobster receiving 10 % ration moulted twice) and expended energy on processes related to moulting, resulting in shorter survival duration. It appears that the ablated lobster, irrespective of food availability, is forced to moult due to removal of Moult Inhibiting Hormone (MIH) from the eyestalk. Under starvation, the ablated lobster probably utilises stored energy from the midgut gland towards moulting.

It has been reported that the normal prawns, **Palaemon lamarrei** (Katre and Reddy, 1976), **Macrobrachium lanchesteri** (Ponnuchamy et al., 1981) and **Metapenaeus monoceros** (Sumitra Vijayaraghavan et al., 1982) moulted under starvation. These studies suggest moulting in the normal crustaceans as a metabolic necessity, occurring at the expense of stored organic reserves irrespective of food availability. In the present study, the normal lobster moulted if it was forced to starve from the premoult stage (stage D) but the lobster failed to moult if the starvation commenced from the intermoult stage (stage C). Hence, it may be concluded that moulting is dependent on the nutritional and physiological status of the normal lobster, whereas moulting is a necessity for the ablated lobster, irrespective of the nutritional status. This is further confirmed from the fact that the intermoult duration of the normal lobster was very high at 50 (72.0 days) or 75 % (65.0 days) rations than the 100 % (43.0 days) ration, whereas the intermoult duration of the ablated lobster did not vary much among these ration levels (26.0 - 36.0 days) (Table 6.3).

The maximum feeding rate of the noraml (220.1 J/g/day) and ablated (309.5 J/g/day) **P. homarus** in this experiment was marginally lower than the maximum feeding rate of the normal (243.2 J/g/day) and ablated (368.0 J/g/day) lobster receiving mussel in the experiment on food quality.

Nevertheless, the 40 - 50 % higher feeding rate of the ablated lobster than the normal lobster confirms that bilateral eyestalk ablation induces hyperphagia in the spiny lobster, **P. homarus** (see also Chapter 5.4.1).

To understand the effect of feeding rate on the conversion rate of normal (Fig. 6.5) and ablated (Fig. 6.6) lobsters, the conversion rate was plotted against the respective feeding rate. Whereas the curve of the normal lobster was asymptotic, that of the ablated lobster decreased beyond certain feeding rate. In the absence of a generally suitable transformation, a smooth curve was fitted. The objective of this plot was to identify the following parameters: i) the maintenance feeding rate, i.e. the feeding rate that just maintains the lobster without any weight change; ii) the optimum feeding rate, i.e. the rate that provides the greatest growth for the least intake (most efficient); and iii) the maximum feeding rate, i.e. the feeding rate that just provides the maximum growth rate (see also Pandian, 1967; Brett et al., 1969; Katre, and Reddy 1976, 1977; Vivekanandan, 1976; Sumitra Vijayaraghavan et al., 1982). The above mentioned parameters may be derived geometrically (Thomson, 1941). The feeding rate in which the curve passes through the intercept is the maintenance feeding rate. The optimum feeding rate is determined by drawing a

tangent to the curve from the origin, and the maximum feeding rate is the asymptotic level. The maintenance, optimum and maximum feeding rates thus determined for the normal **P. homarus** were 67.5, 135.0 and 210.0 J/g/day, respectively (Fig. 6.5); the corresponding values for the ablated lobster were 95.0, 187.5 and 250.0 J/g/day (Fig.6.6). The maximum feeding rates thus estimated to provide the maximum growth rates of the normal and ablated lobsters were lower than the observed maximum feeding rates of the normal (220.1 J/gday) and ablated (309.5 J/g/day) lobsters. Sumitra Vijayaraghavan et. al. (1982) also reported that the maximum feeding rate determined from geometric derivation was lower than the observed maximum feeding rate of the prawn, **Metapenaeus monoceros.** Brett et. al. (1969) opined that the parameter most difficult to determine accurately was the maximum feeding rate, involving the asymptote and maximum growth rate, the values for which were subject to greater variablility than most of the other rates. Nevertheless, the values obtained in the present study revealed that the maximum feeding rate that provided the maximum growth rate was higher in the ablated lobster (250.0 J/g/day) than that of the normal lobster (210.0 J/g/day).

Similar to the maximum feeding rate, the optimum and maintenance feeding rates were higher in the ablated lobster

Fig. 6.5 Geometric derivation of various parameters of conversion rate (= growth) with accompanying feeding rate in the normal **P. homarus**

Fig.6·5

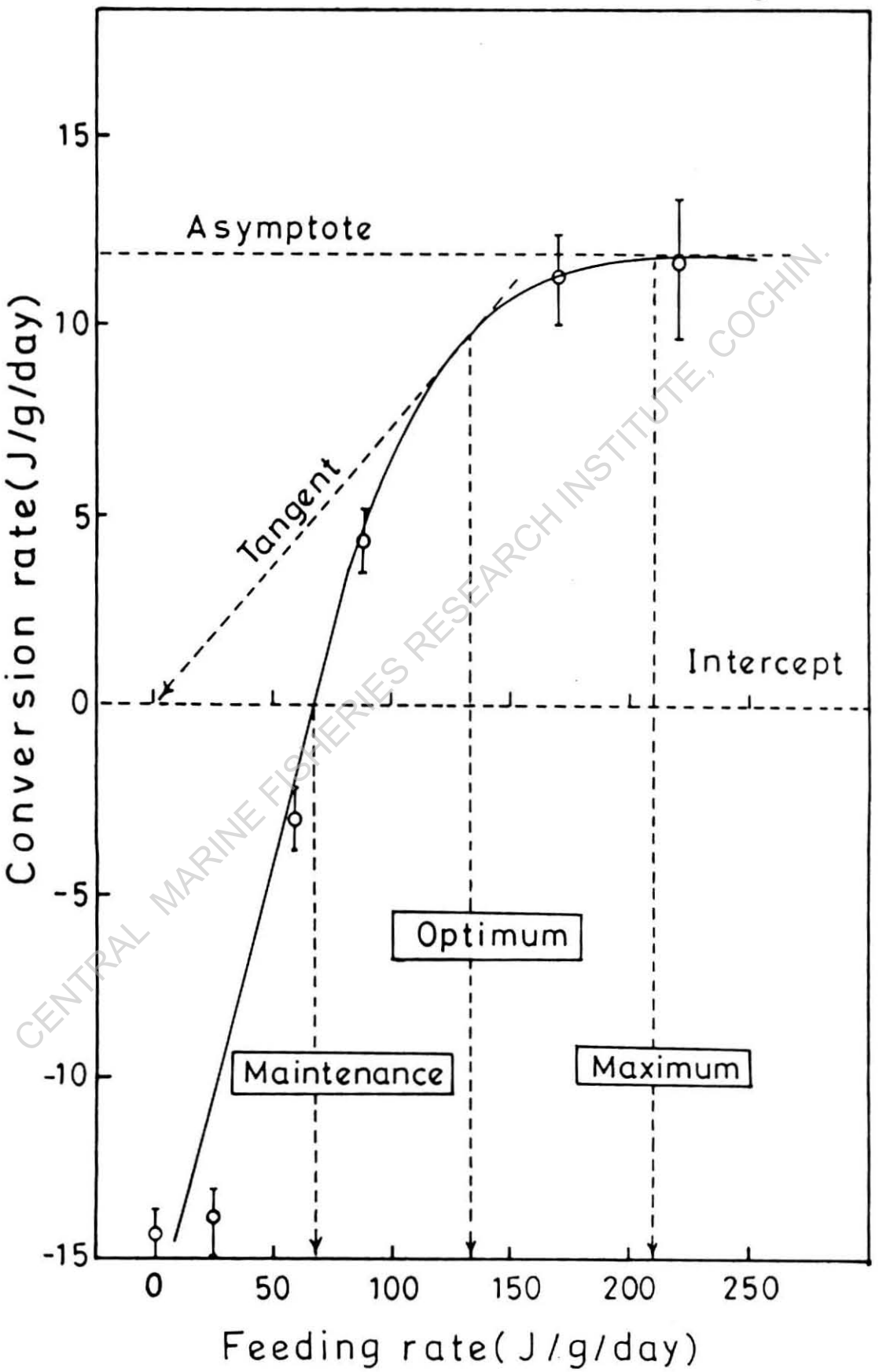
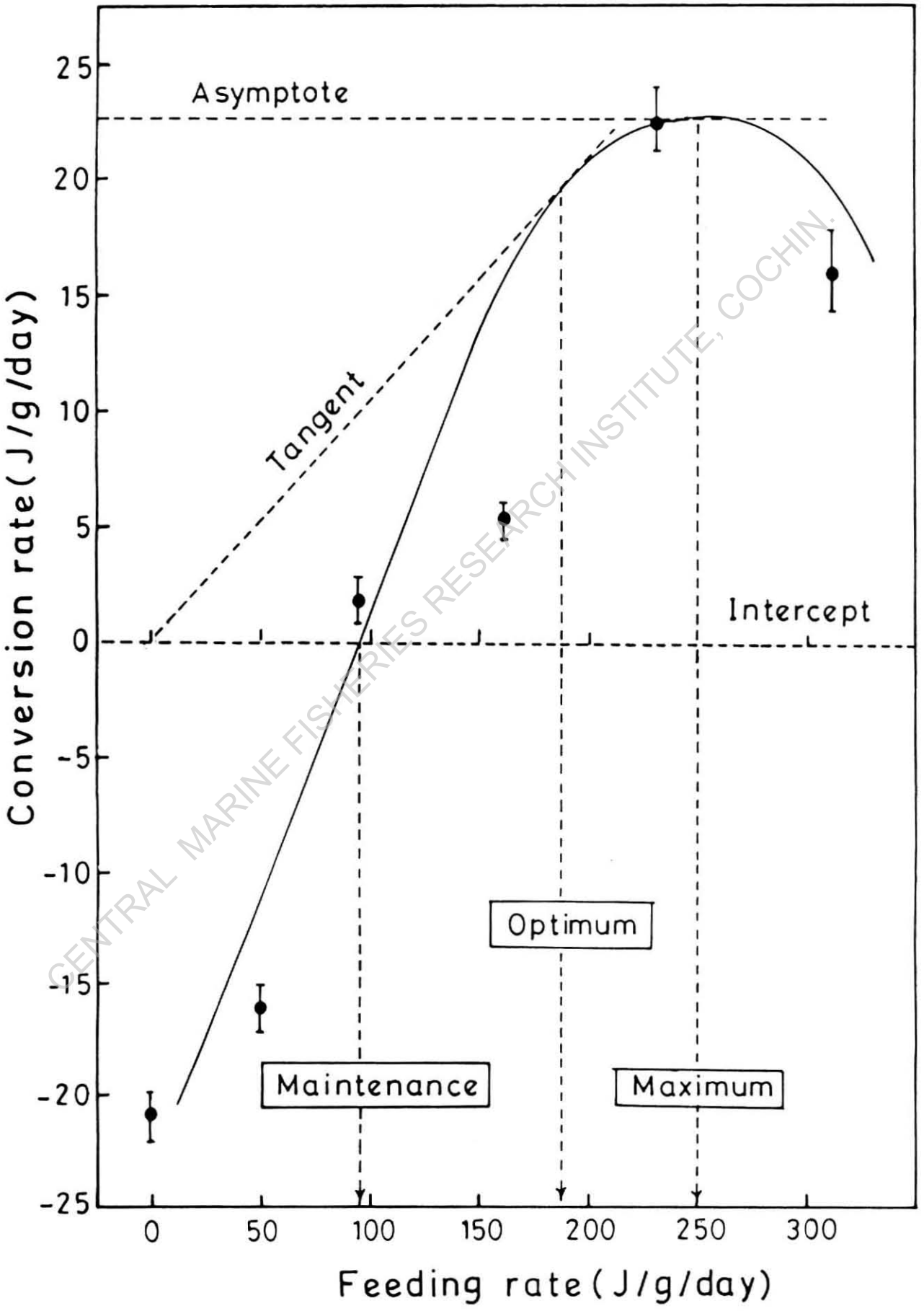


Fig. 6.6 Geometric derivation of various parameters of conversion rate (= growth) with accompanying feeding rate in the ablated **P. homarus**.

Fig. 6·6



than in the normal lobster . The maintenance feeding rate (= maintenance metabolic rate) of the ablated lobster (95.0 J/g/day) was higher by nearly 50 % than the normal lobster (65.5 J/g/day). The accelerated maintenance metabolic level of the ablated lobster suggests that removal of eyestalk hormones primarily enhances the metabolic rate of **P. homarus.** It may be concluded that the primary effect of eyestalk ablation on maintenance metabolism, coupled with induced hyperphagia (as discussed in Chapter 5.4.1) enhances the feeding rate of the ablated lobster.

The enhanced feeding rate and the accelerated moulting frequency, in turn resulted in higher conversion rate of the ablated lobster (Fig. 6.1). As in the previous experiments on food quality, the water content of the ablated **P. homarus** was higher than the normal lobster in all the rations. For instance, the water content of the normal lobster was 67 % and that of the ablated lobster was 75 % at 100 % ration (Fig. 6.3 and 6.4). Though the water content of the ablated lobster was higher than that of the normal individual, the total dry weight and the total energy of the ablated lobster was higher than the normal lobster at any ration (see also Chapter 5.4.4). Hence, the two experiments on ration confirm the conclusion of the previous 4 experiments on food quality that accelerated growth in the ablated lobster is not due to higher water content alone and

Fig. 6.7 Effect of feeding rate on scopes for conversion (growth + exuvia), metabolism (maintenance + Specific Dynamic Action and activitity) and egestion (faeces + urine) in the normal **P. homarus**

Fig. 6·7

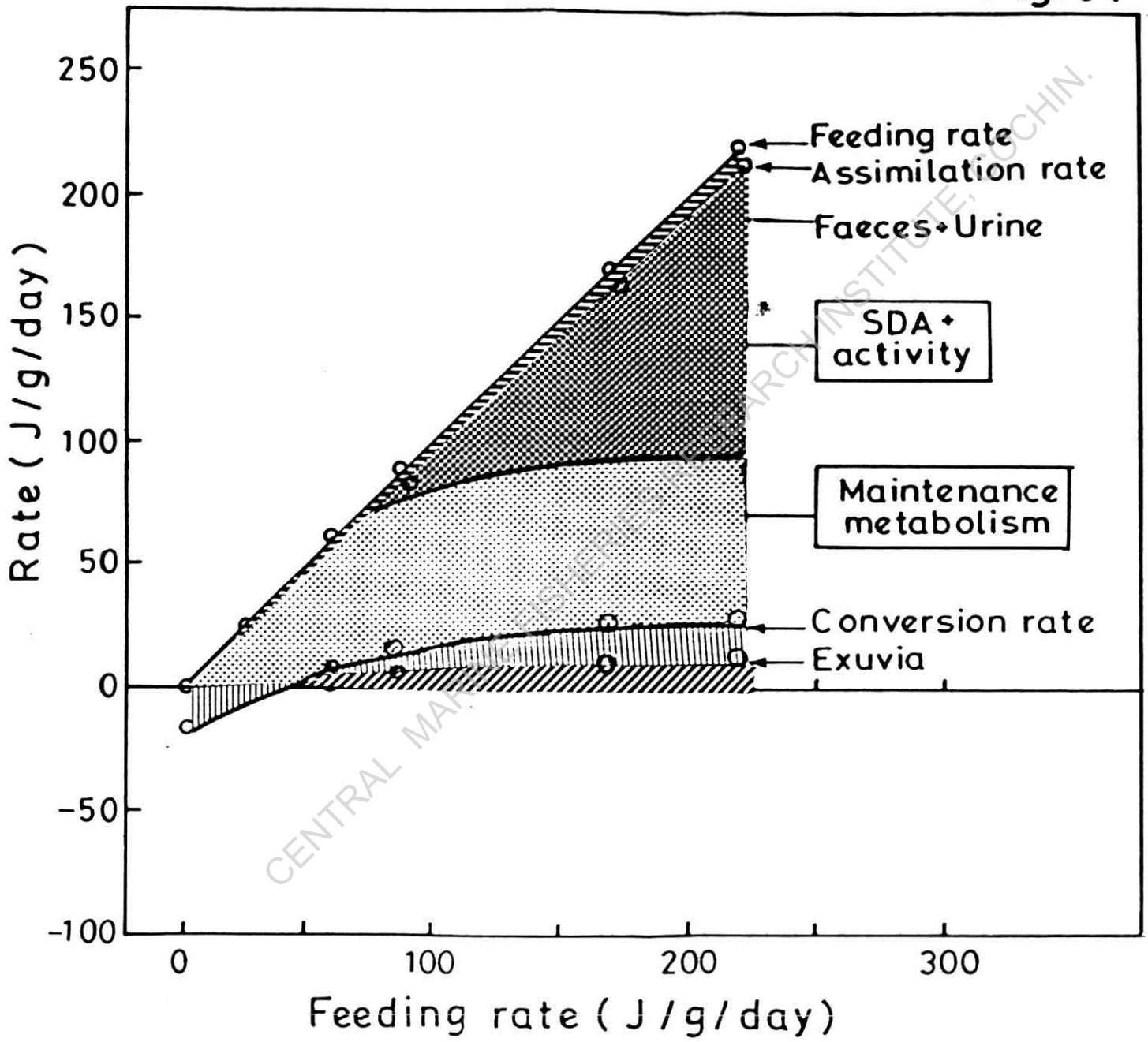
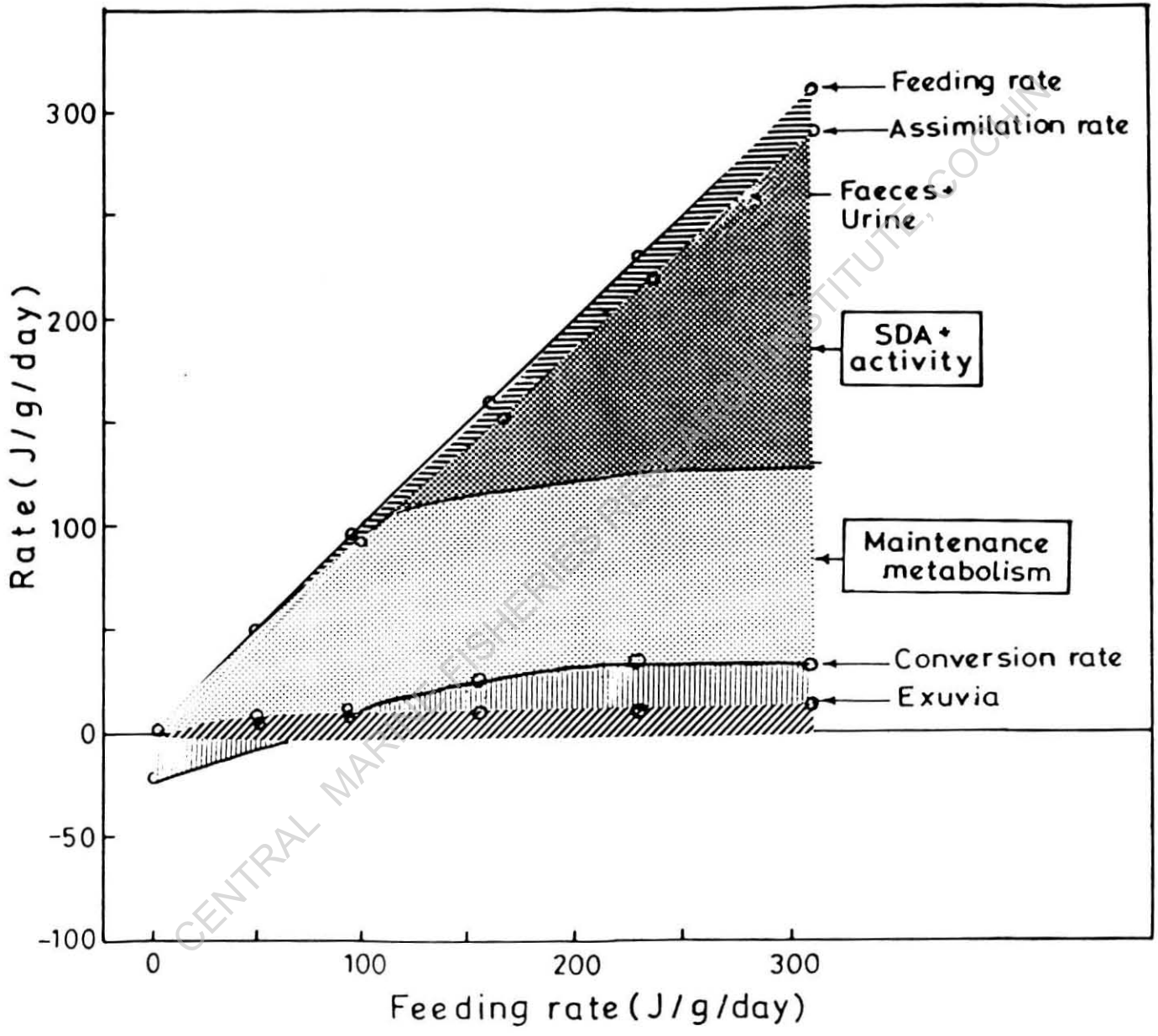


Fig. 6.8 Effects of feeding rate on scopes for conversion (growth + exuvia), metabolism (maintenance + Specific Dynamic Action and activity) and egestion (faeces + urine) in the ablated **P. homarus**

Fig. 6·8



The increase in SDA was more pronounced beyond the optimum feeding rate. For instance, the SDA of the ablated lobster was 52.5 J/g/day (28 % of feeding rate) at the optimum feeding rate (187.5 J/g/day); the SDA increased to 165.0 J/g/day (53 % feeding rate) at the maximum feeding rate (309.5 J/g/day). At the maximum feeding rate, the ablated lobster expended more energy on SDA (165.0 J/g/day) than the normal lobster (125.5 J/g/day). The higher SDA of the ablated lobster would have been due to higher quantity of food consumed (40%) and the consequent mechanical trituration processes. However, the percentage of consumed energy spent on the SDA (55 % of maximum feeding rate) was almost equally high in both the normal and ablated lobsters receiving **ad libitum** feeding.

7 CONCLUSION

The experiments conducted on the spiny lobster, **P. homarus** have produced evidences that number of factors induce complex but definite changes in the physiological and biochemical processes of the animal. Firstly, moulting inflicts a number of biochemical changes within the animal. To satisfy the physiological requirements of the animal prior to, during or after ecdysis, quantitative changes occur in water, lipid, carbohydrate, protein and energy contents of different tissues. For instance, as accumulation of water during late premoult is obligatory for successful ecdysis, water is absorbed from late D_4 stage onwards through ecdysis upto stage A. The energy yielding biochemical components, namely, lipid, carbohydrate and protein, which are accumulated in the midgut gland and muscle during intermoult stages, are utilised prior to and during ecdysis. During ecdysis, 310, 90 and 280 mg of lipid, carbohydrate and protein are utilised respectively; lipid contributes the maximum energy (61 %) for ecdysis and the contributions of protein (31 %) and carbohydrate (8 %) are far lesser than lipid. Hence, similar to the homarid lobsters (Passano, 1960; Vonk, 1960; Chang and O'Connor, 1983), lipid is the major organic material that is utilized for ecdysis of the palinurid lobster, **P. homarus**.

Secondly, the external factors also play major role in the quantitative changes of the biochemical components and in the moulting frequency of the animal. For instance, the biochemical constitution of the food consumed is reflected as the biochemical constituent of the animal. However, inverse relationship between the biochemical content of the food and the animal is also possible as in protein utilization efficiency.

Contrary to the conclusion of Aiken (1980), the moulting frequency of the palinurid lobster is accelerated by bilateral eyestalk ablation. In the present study, the ablated **P. homarus** moulted, on an average, in 33.0 days, whereas the normal lobster moulted, on an average, in 51.1 days (Table 5.5). Hence, the present study and the earlier publications of Quackenbush and Herrnkind (1981), Radhakrishnan and Vijayakumaran (1984) and Silas et. al. (1984) have conclusively shown that eyestalk ablation results in accelerated moulting in the palinurid lobsters. This conclusion supports the evidence of the presence of MIH, which was partially characterized by Quackenbush and Herrnkind (1983) in **P. argus.**

The quantity of food consumed is another major factor that determines the moulting frequency. The normal lobster receiving 0 and 10 % ration failed to moult; the intermoult

duration reduced from 72 days in 50 % ration to 43 days in 100 % ration. The moulting frequency of the lobster receiving 100 % ration of different quality of food was almost equal. Hence, it appears that 75 to 100 % ration is obligatory for optimum moulting frequency irrespective of the type of food the lobster consumes.

Hence, the water, energy and biochemical changes that occur during moult cycle and the intermoult duration/moulting frequency may be considered as indices of the physiological status of the lobster. A consideration of the moulting physiology must include both the sequential morphological events which make up the moult cycle and the biochemical changes that occur during the cycle, for neither is explicable without the other.

As the spiny lobsters do not prefer pellet diet, aquaculturists may have to depend upon natural food till a stable and acceptable pellet diet is formulated exclusively for the spiny lobsters. Being the most preferred natural prey, the green mussel may be probable choice as food for the lobster. The experiments on prey-predator relationship have revealed the feeding strategy of **P.homarus** when offered live mussel prey. The mandibles of the lobster could not crush large mussel with very strong shell; crushing very small mussel may not be advantageous for the lobster because of

lesser acquisition of energy per mussel. Hence, different size classes of **P. homarus** prefer to predate on the respective size group of mussel, from which maximum energy could be derived. As the mandible length of the lobster directly determines the critical and optimum shell girth of the mussel that could be broken and as the mandible length is directly proportional to the size of the lobster, the critical and optimum size of the prey are dependent on the size of the lobster. **P. homarus** could predate mussel upto 13% of its own body weight and the optimum prey size is 3-4% of the lobster's body weight. By predating the optimum prey size, the lobster acquires the maximum energy. For instance, a 48 mm CL lobster acquired 55.5 KJ/day by predating the optimum size (33 mm SL) mussel. The energy acquired by predating smaller (28 mm SL) or larger (48 mm SL) mussel was 43.3 or 35.4 KJ/day, respectively.

Starvation for shorter duration of 7 days does not appreciably affect the predatory efficiency of **P. homarus**, as starvation forms part of the life of the lobster. The lobster (carapace length: 45.50 mm) passes through 5 day non-feeding period prior to, during and after every moult. However, prolonged starvation results in inability of the animal to moult, leading to death in 68.7 days. The ablated lobster on starvation, survives for only 53.0 days. Whether

normal or ablated, the starved lobster withstands total energy loss of 65 % from the body and any further loss results in death.

The factors tested in the present study, viz., isolation, eyestalk ablation and quality and quantity of food considerably influcenced the pattern of food utilization in **P. homarus.** The individual effects of isolation, ablation and food quality on food utilization are summarized in Table 7.1. Based on the effects of these factors, the following conclusions are drawn : i) **P. homarus** reared in isolation exhibits about 80 % higher feeding rate (mean feeding rates of isolated (normal) and group-reared (normal) lobsters were 285.4 and 157.6 J/g/day, respectively). The 80 % higher food intake is expended on metabolism (mean metabolic rates of isolated and group-reared lobsters were 0.53 and 0.27 ml O_2/g/hr, respectively), resulting in 40 % lesser conversion efficiency. As 80 % higher feeding rate does not result in higher conversion rate, isolated rearing of **P.homarus** is not advisable. However, the optimum density to achieve maximum growth of **P. homarus** in culture system has to be studied; ii) eyestalk ablation induces series of interlinked physiological processes, resulting in remarkable changes in food utilization pattern. The ablated lobster exhibits 40 % higher feeding rate and 50 % higher metabolic rate than the normal lobster. Nevertheless, accelerated

Table 7.1 Effects of isolation, eyestalk ablation and food quality on the important physiological parameters of P. homarus ; the units of expression of different parameters are mentioned in earlier chapters

Parameter	Isolation*	Ablation**	Difference among food***
Intermoult duration	No difference	35 % shorter	No difference
Feeding rate	80 % higher	40 % higher	60 % difference
Conversion rate	No difference	65 % higher	3.5 times difference
K_2	40 % lesser	25 % higher	120 % difference
Live weight gain	-	2 times higher	120 % difference
Meat weight		65 % higher	No difference
Energy for growth	70 % lesser	Marginally higher	-
Protein utilization	-	2 times higher	Inverse relationship
Protein and lipid deposition in muscle	-	lesser lipid in muscle	-
Hepatic index	-	25 % lesser	Lesser in clam-fed
Energy loss through exuvia	No difference	10 % lesser	2 times difference
Metabolic rate	2 times higher	50 % higher	50 % difference

* Comparison between group-reared, normal (control) and isolated, normal lobster.

** Comparison between group-reared, normal (control) and group-reared, ablated lobster

*** Difference among different food in the group-reared, normal (control) lobster

moulting frequency, higher rate (65%) and efficiency (25%) of conversion and 2 times higher protein utilization efficiency are the advantages of eyestalk ablation. As the eyestalk ablation results in acceleration of synthesis of new tissue, it is advantageous to culture **P. homarus** after bilateral eyestalk ablation. For instance, a pre-adult ablated lobster (stocking size: 100 g live weight; food: mussel) attains 331 g in 100 days; a normal lobster attains only 139 g in the same period (Fig. 5.4). The meat weight that could be realised from the ablated and normal lobster is 74g (considering 22.3 % tail weight) and 37 g (26.7 % meat weight) (Table 5.11), respectively. Hence, 2 times higher net gain could be achieved by eyestalk ablation. However, it may be mentioned here that the ablated lobster has to be offered about 40 % more food than the normal lobster, which may increase the cost of food. But the net gain of increase in meat weight of the ablated lobster may offset the increase in cost of food; iii) the quality of food has pronounced effect on the feeding rate of **P. homarus.** The lobster consumes more mussel or clam than fish. As offering mixed food and mussel results in maximum rate and efficiency of conversion respectively, it is suggested that **P. homarus** may be offered mussel-dominant mixed food for obtaining the maximum rate and efficiency of conversion. It may be

mentioned here that the green mussel is easily available in Madras coast and at present it does not have consumer demand.

The effect of food quantity on food utilization has revealed that **ad libitum** feeding may not result in maximum rate and efficiency of conversion due to excess energy expenditure on SDA. To achieve maximum growth rate of **P. hoamrus** in aquaculture practices, it is suggested that the lobster may be reared after bilateral eyestalk ablation and offered food equivalent to 75% of maximum feeding rate due to the following results obtained in the experiment on quantity of food: i) the conversion rate was higher in all the ablated groups than the corresponding normal groups receiving different rations ; ii) among the ablated groups, the group receiving 75 % ration converted the food faster and more efficiently than the other groups; iii) maintenance, optimum and maximum feeding rates of the ablated **P. homarus** were 95.0, 187.5 and 250.0 J/g/day, respectively; the optimum feeding rate formed 75 % of the maximum feeding rate; and iv) excess feeding may result in a) water spoilage, b) mortality, c) expenditure of more energy on SDA and d) higher feed cost.

The major problems of culturing the temperate lobsters like the American lobster, **H. americanus** are i) the cannibalistic nature and ii) slow growth. The present study

on the tropical spiny lobster, **P. homarus** revealed that both these problems could be overcome i) due to the gregarious nature of **P. homarus** and ii) by accelerating the growth by manipulating the important factors that determine the growth rate of the lobster. Furthermore, the ability of **P. homarus** to assimilate the consumed food with very high efficiency, is also an advantage. **P. homarus** receiving different food assimilated with very high efficiency (above 95 %). The low expenditure of energy on egestion of faeces and nitrogenous excretory wastes even when offered high protein diets like the mussel (protein content: 69.3 %) or fish (protein content: 74.8 %), is an advantage from the aquaculture point of view.

In the present study, group-rearing, bilateral eyestalk abaltion, mussel dominant mixed food and 75 % of maximum feeding rate have been identified as the optimum conditions for achieving maximum rate and efficiency of conversion of **P. homarus.** However none of the experimental conditions in the present study provided the optimum condition for achieving the maximum rate and efficiency of conversion. For instance, the experiments on quality of food were conducted by offering food **ad libitum** and the experiments on quantity of food were conducted on isolated lobster. Nevertheless, by substituting the result obtained

in the experiment on ration (food: mussel) to the group-reared, ablated lobster receiving mussel, the maximum achievable rate and efficiency of conversion could be calculated. The optimum feeding rate (75 % of maximum feeding rate) thus calculated would be 146.1 J/g/day for the group-reared, ablated lobster (maximum feeding rate: 194.8 J/g/day). As the K_2 of the isolated lobster receiving 75 % ration (9.8 %) was about 90 % higher than the lobster receiving 100 % ration (5.2 %) (Table 6.5 %), it may be presumed that the group-reared lobster also would have exhibited 90 % higher conversion efficiency (33.4 %) if it had received 75 % ration instead of 100 % ration (K_2 at 100 % ration: 17.6 %; Table 5.8). Applying assimilation efficiency of 97.6 % and K_2 of 33.4 % to the feeding rate of 146.1 J/g/day, the conversion rate would be 47.6 J/g/day (instead of 33.3 J/g/day). In terms of increase in live body weight, a pre-adult, group-reared, ablated lobster (live body weight: 100 g) receiving 75 % ration would reach 463 g in 100 days instead of 331 g (as the lobster receiving 100 % ration). Considering 22.3 % meat weight, meat weight of 103 g could be realised instead of 74 g. Hence, by providing the optimum conditions, viz., group-rearing, bilateral eyestalk ablation, mussel food (or mussel-dominant mixed food) and 75 % ration, considerably higher net gain (in the form of higher meat weight) could be achieved.

Despite the several characteristics that make the spiny lobster attractive for commercial cultivation, unsuccessful attempts in rearing the phyllosoma larvae to puerulus stage have inhibited development of commercial lobster farms. However, until reliable techniques for culturing phyllosoma larvae are developed, large number of juveniles which are caught at present along with commercial size lobsters could be collected and reared in culture farms by employing optimum conditions.

8. SUMMARY

1. The moult cycle of the spiny lobster, **P. homarus** was classified into 5 stages, viz., stage A (early postmoult), stage B (late postmoult), stage C (intermoult), stage D (premoult) and stage E (ecdysis). The morphological changes in each stage are briefly described.

2. The biochemical changes in the midgut gland and abdominal muscle were quantified in different stages of moult cycle. The water content in the midgut gland decreased from 75.7 % in stage A to 58.3 % in stage D_o and thereafter increase upto stage A. Contrary to water, the lipid was accumulated in the midgut gland from stage A (30.0 % of dry weight) to stage D (42.2 %) and carbohydrate and protein were accumulated from stage A to stage D_o. During ecdysis, 310, 90 and 218 mg of lipid, carbohydrate and protein, respectively were utilized from the midgut gland.

3. The water content in the abdominal muscle decreased from 76.6 % in stage A to 72.4 % in stage D_o and thereafter increased upto stage A. In the muscle, the percentage of lipid was not only lower (9.8 - 12.8 %) than the midgut gland but also did not exhibit marked fluctuation

during the moult cycle. Protein was the dominant constituent of the muscle (67.2 - 76.0 %).

4. The feeding strategy of **P. homarus** was studied by exposing different size groups of live mussels to different size classes of lobster (size of lobster : 23-53 mm carapace length; size of mussel: 18-58 mm shell length). The critical, preferred and optimum size of the mussel that could be predated by the lobster were positively correlated with the size of the predator. The different size class of lobster predated prey upto 13 % of its own body weight. The optimum prey size (from which the lobster acquired the maximum energy) was 3-4% of the size of the predator. Starvation for 7 days did not appreciably reduce the predatory efficiency of the lobster.

5. To understand the effects of isolation, bilateral eyestalk ablation and food quality on food utilization of **P. homarus**, 4 experiments were conducted by selecting mussel, clam, fish and a combination of the 3 food as 4 feeding groups. The protein content was 40 % higher in fish (74.8 %) than the clam (53.5 %) and carbohydrate content was extremely high (29.3 %) in the clam than the fish (1.1 %).

6. In the experiment on the isolated, normal lobster, the maximum feeding rate (371.3 J/g/day) was exhibited by the group receiving mixed food; the groups receiving mussel (243.2 J/g/day) and fish (245.2 J/g/day) consumed far lesser. Assimilation efficiency was very high (mean: 98 %) in all the groups. The conversion rate (20.8 J/g/day) and efficiency (K_2: 7.2 %) were maximum in the groups receiving mixed food and fish, respectively. The highest metabolic rate (0.69 ml O_2/g/hr) was exhibited by the group receiving mixed food.

7. The maximum feeding rate (688.2 J/g/day) of the isolated, eyestalk ablated lobster was exhibited by the group receiving mixed food; the group receiving fish exhibited the lowest feeding rate (260.2 J/g/day). The conversion rate was maximum (56.6 J/g/day) in the group receiving mixed food followed by the mussel-fed group (33.4 J/g/day); the maximum K_2 was also in these two groups. The highest metabolic rate (1.3 ml O_2/g/hr) was exhibited by the group receiving mixed food.

8. The group-reared, normal lobster receiving mixed food exhibited the highest feeding rate (191.1 J/g/day), followed by the mussel-fed group (161.8 J/g/day). The maximum conversion rate and conversion efficiency

(mussel: 13.8 %; mixed food: 13.0 %) were exhibited by the same groups. The metabolic rate ranged from 0.21 (fish-fed) to 0.31 (mixed food-fed) ml O_2/g/hr.

9. In the experiment on the group-reared, ablated lobster, the maximum feeding rate was exhibited by the group receiving clam (282.2 J/g/day). The conversion rate was maximum in the mixed food-fed (35.4 J/g/day) followed by the mussel-fed group (33.4 J/g/day). The conversion efficiency was maximum in the group receiving mussel (K_2: 17.2%). The metabolic rate ranged from 0.25 (fish-fed) to 0.50 (clam-fed) ml O_2/g/hr.

10. The lobster in the 4 experiments lost 11.4 - 40.3 % of the converted energy or 31.1 - 71.4 % of the converted dry matter as exuvia. The intermoult duration of the normal lobster (mean: 51.0 days) was more than that of the ablated lobster (32.0 days).

11. Estimation of energy budget of **P. homarus** receiving different food in the 4 experiments revealed that the lobster expended considerable quantum of the consumed energy (80.0 - 94.5 %) on metabolism. The energy spent on egestion was almost equal in all the 4 experiments and the energy allotted for exuvial production was marginally higher in the group-reared lobster than the isolated lobster. The group-reared lobster allotted

nearly 2 times more energy for growth than the isolated lobster.

12. The live weight increase of the ablated lobster was considerably higher than the normal lobster during the experimental period. The live weight increase of the group receiving mussel or mixed food was higher than that of the group receiving clam or fish.

13. The mean percentage of tail (34 % of total body weight) and meat weight (26 % of total body weight) were higher in the normal lobster than those of the ablated individual (tail: 28 %; meat: 23 %). There was not much difference in the percentage of tail or meat weight in the groups receiving different food.

14. The mean water content of the ablated lobster (%) was higher than the mean water content of the normal lobster (64.1 %). The mean ash contents of the normal (32.0 %) and the ablated (31.3 %) lobster were almost equal. The mean chitin contents of the normal and ablated lobsters were 15.0 and 12.3 %, respectively.

15. The lipid content in the muscle of the ablated lobster was remarkably less (mean: 6.8 %) than that of the normal lobster (mean: 19.1 %). The protein content of the muscle ranged from 70.0 - 78.5 % and 64.7 - 79.7 %

in the normal and ablated lobsters, respectively. The Protein Efficiency Ratio (PER) was higher in the ablated lobster than the normal lobster; the PER of normal and ablated lobster was negatively correlated with the protein content of the food.

16. The effects of ration (0, 10, 25, 50, 75 and 100 % of maximum feeding rate) on survival and food utilization of normal and ablated **P. homarus** were studied. The starved, normal lobster survived for 68.7 days. The starved lobster lost 14.3 J/g/day and the group receiving 10 % ration lost 13.9 J/g/day. The normal lobster receiving **ad libitum** food consumed 220.1 J/g/day. The assimilation efficiency was uniformly high (98.8 %) in all the rations. The conversion rate increased with increasing feeding rate and was 11.5 J/g/day at 100 % ration. The conversion efficiency (K_2) was maximum at 75 % ration (6.5 %). The metabolic rate of the group receiving 100 % ration (0.40 ml O_2/g/hr) was 13.5 times higher than that of the starved lobster (0.03 ml O_2/g/hr).

17. The ablated lobster receiving 0 and 10 % ration survived for 53.0 and 84.5 days, respectively. The starved lobster lost 9.3 J/g/day and the group receiving 10 % ration lost 4.3 J/g/day. The ablated group receiving

ad libitum food consumed 309.5 J/g/day. The assimilation efficiency was very high in all the rations. The group receiving 75 or 100 % ration (mean: 33.6 J/g/day) converted the consumed food energy by about 2 times faster than the group receiving 25 or 50 % ration (mean: 15.8 J/g/day). The maximum conversion efficiency (K_2: 9.8 %) was exhibited by the group receiving 75 % ration. The metabolic rate of the group receiving 100 % ration (0.54 ml O_2/g/hr) was about 27 times higher than that of the starved lobster (0.02 ml O_2/g/hr).

18. Whereas the normal, starved lobster and the normal lobster receiving 10 % ration did not moult, all the ablated lobsters moulted. The percentage of converted energy lost as exuvia was higher in the ablated lobster (starved: 11.6 %; 100 % ration: 15.4 %) than the normal lobster (25 % ration: 5.9 %; 100 % ration: 11.2 %). The intermoult duration of the normal lobster receiving 50 % ration (72 days) was higher than that of the normal lobster receiving 100 % ration (43 days). The itnermoult duration of the ablated lobster receiving 25-100 % ration was almost equal (mean: 33.0 days).

19. Water and ash contents of the normal and ablated lobsters were negatively correlated and the energy

content was positively correlated with increasing ration.

20. Geometric derivation of conversion rate revealed that the maintenance, optimum and maximum feeding rates of the normal **P. homarus** were 67.5, 133.0 and 210.0 J/g/day, respectively; the corresponding values for the ablated lobster were 95.0, 187.5 and 250.0 J/g/day.

21. Construction of energy budget on the lobster receiving different rations revealed that the energy allocated for metabolism (mean: 82.2 %) and for growth (mean: 5.1 %) by the ablated lobster was marginally lesser than the energy allocated for metabolism (mean: 87.2 %) and for growth (mean: 5.5 %) by the normal lobster.

22. For aquaculture, group-rearing, bilateral eyestalk ablation, mussel dominant mixed food and 75 % of maximum feeding rate are recommended as the optimum conditions for achieving the maximum rate and efficiency of conversion in the spiny lobster, **P. homarus.**

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10 APPENDIX

List of publications on lobsters by E.V. Radhakrishnan

1. **Radhakrishnan, E.V. 1977.** Breeding of laboratory reared spiny lobster **Panulirus homarus** (Linnaeus) under controlled conditions. **Indian J. Fish.** 24, 269-270.

2. **Radhakrishnan, E.V.** and Vijayakumaran, M. 1982. Unprecedented growth induced in spiny lobsters. **Mar. Fish. Infor. Serv. T & E. Ser.,** 43, 6-8.

3. **Radhakrishnan, E.V** and Vijayakumaran, M. 1984. Effect of eyestalk ablation in the spiny lobster **Panulirus homarus** (Linnaeus). 1. On moulting and growth. **Indian J. Fish.** 31, 130-147.

4. Vijayakumaran, M. and **Radhakrishnan, E.V.** 1984. Effect of eyestalk ablation in the spiny lobster **Panulirus homarus** (linnaeus). 2. On food intake and conversion. **Indian J. Fish.** 31, 148-155.

5. **Radhakrishnan, E.V** and Vijayakumaran, M. 1984. Effect of eyestalk ablation in the spiny lobster **Panulirus homarus** (Linnaeus). 3. On gonadal maturity. **Indian J. Fish.** 31, 209-216.

6. Silas, E.G., **Radhakrishnan, E.V** and Vijayakumaran, M. 1984. Eyestalk ablation - New idea boosts growth of Indian spiny lobster. **Fish Farming International** 2, 10-11.

7. **Radhakrishnan, E.V.** and Devarajan, K. 1986. Growth of the spiny lobster **Panulirus polyphagus** (Herbst) reared in the laboratory. **Proc. Symp. Coastal Aquaculture** , 1164-1170.

8. **Radhakrishnan, E.V.** and Vijayakumaran, M. 1986. Observations on the feeding and moulting of laboratory reared phyllosoma larvae of the spiny lobster **Panulirus homarus** (Linnaeus) under different light regimes. **Proc. Symp. Coastal Aquaculture** 4, 1261-1266.

9. Vijayakumaran, M. and **Radhakrishnan, E.V.** 1986. Effects of food density on feeding and moulting of phyllosoma larvae of the spiny lobster **Panulirus homarus** (Linnaeus). **Proc. Symp. Coastal Aquaculture** 4, 1281-1285.

10. **Radhakrishnan, E.V.** and Vijayakumaran, M. 1987. Hormonal control of growth and reproduction in the spiny lobster, **Panulirus ornatus. Symp. Physiol. Crust.** Aurangabad (Abstract No.26).

11. Vijayakumaran, M. and **Radhakrishnan, E.V.** 1987. Water uptake at ecdysis and variation of water content in haemolymph and tissues in the moult cycle of the spiny lobster **Panulirus homarus. Symp. Physiol. Crust.** Aurangabad (Abstract No.11).

12. **Radhakrishnan, E.V.** and Vijayakumaran, M. 1987. Potential of spiny lobster culture - an assessment. **CMFRI Special Publication No.40** (Abstract No. 70).

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BREEDING OF LABORATORY REARED SPINY LOBSTER *PANULIRUS HOMARUS* (LINNAEUS) UNDER CONTROLLED CONDITIONS

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ABSTRACT

Juveniles of the spiny lobster, *Panulirus homarus* reared in the laboratory attained sexual maturity under controlled conditions. They successfully mated and spawned in captivity for the first time in India. The carapace length of the two females at the first sexual maturity and berried condition were 57.8 mm and 57.9 mm. The approximate incubation period of the berry was found to be 15 days.

Observations on the biology and breeding characteristics of *Panulirus homarus* in the fishery of the southwest coast of India and of the South African coast were made by George (1967) and Berry (1970, 1971) respectively. Berry (1971) reported that female *P. homarus* bred repetitively up to four breeding cycles in an year. The breeding of the laboratory reared *P. homarus* is reported here for the first time in India. Chittleborough (1974) successfully reared the western rock lobster from puerulus stage to maturity and spawned them in captivity under controlled conditions

In the field laboratory of the Central Marine Fisheries Research Institute at Kovalam near Madras, *P. homarus* were grown in groups provided with sufficient shelter. Groups of juveniles of the species with a mean carapace length of 35 mm were stocked in large tanks of 10,000 litres capacity during January 1977. The lobsters were fed *ad libitum* daily at 7 p.m. with mussels (*Mytilus* sp.), clams (*Katylesia* sp.) or fishes (*Thrissocles* sp.). The holding tanks were cleaned and filled with fresh seawater every fortnight. The temperature of the water in the tank varied between 26.1°C and 29.8°C. The carapace length (measured along the mid dorsal line from the ridge behind the eyes to the posterior margin of the carapace), total length (measured from the anterior ridge of the carapace to the tip of the telson), total bodyweight and maturity conditions were recorded during water change in the tanks. During the course of observation on 25-3-1978 two berried females of (a) carapace length 57.8 mm, total weight 185 g; and (b) carapace length 57.9 mm and total weight 204 g were noticed in berried condition in the tanks. The berry of the former specimen was in an advanced stage of development and that of the latter with orange coloured eggs. The lobsters were transferred to a breeding tank filled

with fresh filetered sea water and fed daily with estuarine clams, *Katylesia* sp. in excess. The lobster with advanced-stage eggs, on examination showed the developing embryos with eyes, and the eggs hatched out into phyllosoma larvae on the night of 3-4-1978. The berry of the other lobster did not undergo further development and completely shed the eggs after a few days. The freshly hatched out phyllosoma larvae were carefully transferred to another tank containing fresh filtered sea water and fed with newly hatched *Artemia* nauplii. These larvae were reared for 15 days when they developed into the second phyllosoma stage. Thereafter, the larvae perished due to heavy ciliate attack.

The experiment indicated that the laboratory reared juvenile *P. homarus* attained maturity at carapace length of about 57.9 mm. The tar-spot indicating the mated condition of the female, with eggs in advanced stage of incubation was observed on 4-3-1978. Since the berried condition was not observed on 19-3-1978 when regular fort-nightly observation of the lobsters were made, it is apparent that the fertilization and transfer of eggs have occurred in between 19-3-1978 and 25-3-1978. It is therefore deduced that the approximate incubation period of the eggs in the pleopods could be a maximum of 15 days. Berry (1970) reported an incubation period of 30 days for *P. homarus* off east coast of Southern Africa. Chittleborough (1976) has reported an inverse relationship between incubation period of eggs (19-68 days) and water temperature in *P. longipes cygnus*. In the lobster with orange coloured eggs the tar-spot was not observed. It is probable that these eggs were infertile eggs and were shed by the animal subsequently.

The author is grateful to Dr. E. G. Silas, Director, Central Marine Fisheries Research Institute, for encouragement and to Shri T. Tholasilingam, Officer-in-charge, Madras Research Centre of Central Marine Fisheries Research Institute, for his guidance and help. Thanks are also due to the staff of the Field Centre of CMFRI, Kovalam for their co-operation during the experiment.

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UNPRECEDENTED GROWTH INDUCED IN SPINY LOBSTERS

E.V.Radhakrishnan and M.Vijayakumaran

Introduction

With the ever increasing demand, the lobster fishing grounds all over the world are being heavily exploited and this is also true in Indian lobster fishery. Attempts for growing lobsters in captivity in order to augment the production have met with only partial success. Apart from other problems their slow growth rate is one of the main constraints. Investigations have been carried out at the Field Laboratory of the Central Marine Fisheries Research Institute at Kovalam, Madras since 1976 to rear the spiny lobster *Panulirus homarus*, which contributes to a major portion of the lobster fishery in southern parts of India. Early juveniles of this species have been consistently reared in the laboratory to marketable sizes in a period of sixteen to eighteen months. However, it was felt that it may not be economically feasible to carryout large scale culture of lobsters unless the rearing period is brought down considerably. The only way to accomplish this is by accelerating the growth rate of lobsters and this has been the major concern of the CMFRI Laboratory at Kovalam, resulting in several experimental studies.

It has been well established that the X-organ sinus gland complex in the eyestalk of crustaceans plays a major role in the control of moulting and growth in them. Experiments in ablation of eyestalks and thereby removal of the gland complex was not found to be useful in the acceleration of moulting in *P. cygnus* in Australia and *P. argus* in America, leading to the conclusion that Moult Inhibiting Factor (MIH factor) may not be present in the eyestalk of palinurid lobsters. However, encouraging results have been obtained for the first time in accelerating moulting frequency and weight gain in the spiny lobster *P. homarus* consequent to the present experiments in removal of eyestalks.

Early juveniles, maturing and mature *P. homarus* ranging from 20 to 250 g in body weight were used in this study. The technique used was bilateral removal of eyestalks by ligation. Lobsters were reared in groups and equal number of males and females were used in all the treatments. Salinity of the seawater used varied between 32 and 35‰ and the water temperature ranged from 22 to 33.8° C. In the experiments the lobsters were fed *ad libitum* on the clam *Meretrix casta* twice daily. In one of the experiments mussel meat and chopped fishes were given once daily initially and clam meat twice daily later.

Moulting frequency

The results prove that eyestalk removal accelerated frequency of moulting in *P. homarus*, indicating the presence of an MIH factor in the eyestalk. Whereas the control lobsters moulted 4 times in 140 days reaching 70 g, the ablated lobsters moulted 7 times to reach the marketable size of 200 g in the same period. Intermoult period increased with the size in both ablated and control lobsters, but the increase in ablated ones was considerably lower than that of the control.

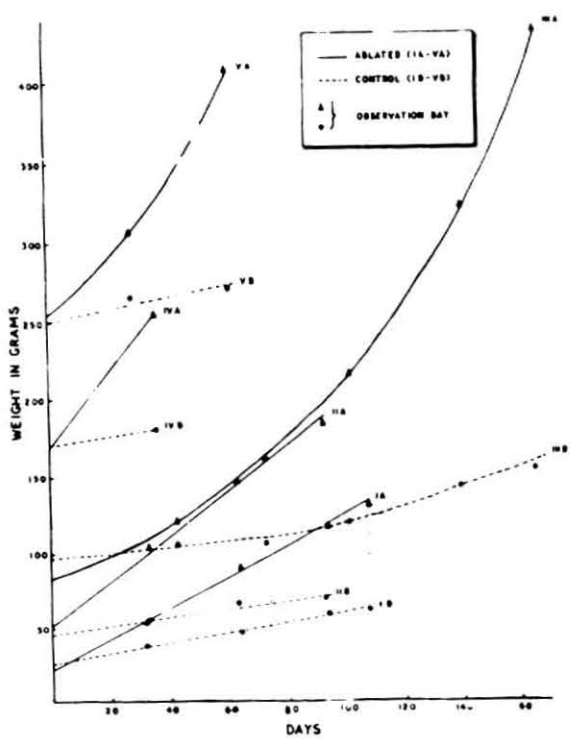

Fig. 1. Increase in weight in eye ablated and control spiny lobsters *P.homarus* in different experiments.

Weight gain

The weight gain in ablated and control lobsters from experiments I to V is shown in Figure 1. Growth of lobsters is a manifestation of moul-

Table 1. *Growth of ablated and control lobsters Panulirus homarus*

Expt. No.		Description	No. of lobsters	INITIAL		FINAL		Total No. of days	Increase in weight/day (g) (Average)	% increase/day
				CL (mm)	Wt. (g)	CL (mm)	Wt. (g)			
I	A	ABLATED	14	27.0	20.4	53.1	131.0	108	1.02	5.0
	B	CONTROL	14	28.7	24.8	39.7	62.3		0.35	1.4
II	A	ABLATED	6 × 3 (18 Nos)	36.5	49.7	59.7	184.3	93	1.45	2.9
	B	CONTROL	6 × 2 (12 Nos)	35.8	46.8	41.9	71.3		0.26	0.55
III	A	ABLATED	10	44.7	84.5	77.4	432.0	165	2.1	2.48
	B	CONTROL	10	47.3	98.6	56.2	155.7		0.35	0.35
IV	A	ABLATED	4	56.2	169.0	65.3	255.0	36	2.38	1.46
	B	CONTROL	4	58.2	169.2	59.2	181.0		0.33	0.19
V	A	ABLATED	6	66.1	256.5	77.8	408.0	61	2.5	0.97
	B	CONTROL	6	66.0	250.3	67.4	272.5		0.36	0.14
VI	A	ABLATED	5	41.2	69.4	53.0	141.0	63	1.14	1.64
	B	CONTROL	5	39.9	66.0	44.2	83.4		0.28	0.42

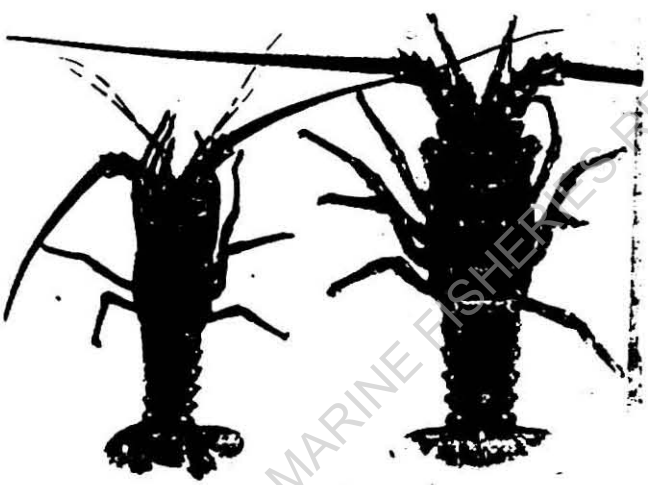

Fig. 2. Growth difference in eye ablated (right) and control (left) spiny lobsters.

ting and size and weight increase at moult. Eyestalk ablation in *P. homarus* accelerated both these factors and enhanced growth rate obtained is the cumulative effect of these two. Three to sevenfold increase in weight was obtained in ablated lobsters compared to the control (Fig. 2). Weight increase per day is proportional to the size of the lobsters. Ablated juveniles recorded an average increase of 1.02 g/day while the increase was only 0.35 g/day in the control. Weight increase per day gradually increased with size and the maximum of 2.5 g/day was obtained in maturing and mature lobsters (Table 1). Eventhough relative increase in growth, expressed in terms of percentage weight gain per day, was more in early juveniles, absolute increase in bodyweight was higher in bigger lobsters. Maximum weight gain of 4.6 g/day was obtained in an ablated mature lobster weighing 256 g.

Food conversion

Accelerated growth is achieved by increased food consumption and assimilation and by better conversion efficiency. The experiments show that in *P.homarus*, at *ad libitum* level of feeding, food consumption of ablated lobsters was twice that of the control animals, recording two to three fold increase in food conversion efficiency. Even when equal quantities of food wire given to both the groups in Expt.VI the ablated ones recorded four fold increase in weight compared to control. This would indicate that increased food intake in ablated individuals only may be supplementing the individuals only may be supplementing the accelerated growth rate caused mainly by hormonal imbalance.

Tail weight

The proportion of tail weight to body weight of ablated and control lobsters weighing 200 g and above shows that there is no significant difference in this relationship between the experimental and control animals. The percentage dry matter in the flesh also showed similar trend indicating that ablation do not alter this relationship.

General remarks

Apparantly there is a Moult Inhibiting Hormone Factor in the eyestalk of spiny lobsters, which on removal accelerate the growth significantly. Further experiments are in progress to

map out the gland so that manipulation of the hormone produced by the gland may accelerate the growth rate without impairing the vision of the lobsters. This basic discovery opens up further avenues for advanced research in lobster endocrinology.

From the present results it is clear that it would be possible to grow marketable size lobsters from juvenile stage in 5 to 6 months and to double the size in another 3 or 4 months. Such phenomenal growth would throw open great possibilities of developing genetically fast growing strains of lobsters and more than all make *P. homarus* a very suitable candidate species for culture.

We are thankful to Dr. E. G. Silas, Director, CMFRI for constant encouragement and guidance.

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EFFECT OF EYESTALK ABLATION IN SPINY LOBSTER *PANULIRUS HOMARUS* (LINNAEUS): 1. ON MOULTING AND GROWTH

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EFFECT OF EYESTALK ABLATION IN SPINY LOBSTER *PANULIRUS HOMARUS* (LINNAEUS): 1. ON MOULTING AND GROWTH

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ABSTRACT

Bilateral eyestalk ablation accelerated moulting frequency and weight gain in juvenile, maturing and mature *Panulirus homarus*, irrespective of their reproductive status. Three- to seven-fold increase in weight gain was obtained on eyestalk ablation. Ablation also did not incapacitate the lobsters in locating food, nor did it interfere with regeneration of autotomised limbs. The study indicates the presence in *P. homarus* of the Moult Inhibiting Hormone (MIH) and the Gonad Inhibiting Hormone (GIF) factors in the eyestalk.

INTRODUCTION

It has been reported that the eyestalk ablation accelerated moulting and weight gain in the American lobster *Homarus americanus* (Sochasky et al 1973, Rao et al 1973, Aiken and Waddy 1975, Mauviot and Castell 1976), but there are very few reports on the effect of eyestalk ablation in palinurid lobsters. Travis (1954) could not induce moulting in *Panulirus argus* by eyestalk ablation and concluded that there is no moult-inhibiting substance in the eyestalk. Dall (1977) also did not get any positive response to eyestalk ablation in *P. cygnus*. He therefore suggested that, in palinurid lobsters, the moult inhibiting hormone (MIH) is either secreted by neurosecretory cells situated elsewhere or, if secreted by cells within the eyestalk, not secreted in significant quantities. Subsequent experiments, with injected crustecdysone (Dall and Barclay 1977), certainly indicated lack of interference from MIH. Based on these observations, Aiken (1980) concluded that eyestalk ablation apparently does not accelerate moulting in palinurid lobsters. However, very recently, Quackenbush and Herrnkind (1981) reported increased gonadal development and accelerated moult cycle in eyestalk ablated *P. argus*.

The present report deals with the moulting and weight gain obtained as a result of eyestalk ablation in the palinurid lobster, *Panulirus homarus*. at the Field laboratory of Central Marine Fisheries Research Institute, at Kovalam, Madras.

MATERIAL AND METHODS

Juvenile, maturing and mature *P. homarus* were collected by hand-picking from the surf-ridden areas and by operating bottom-set gill net in nearshore waters of Kovalam. The experimental lobsters were acclimatised to laboratory conditions, and were fed on a diet of clam meat (of *Meretrix casta*). The experiments were conducted in rectangular fibreglass tanks (90 cm x 60 cm x 60 cm) as well as in 1.2 m-diameter polyethylene-lined tanks. Salinity of the seawater, used as medium, varied between 32 and 35‰ and the water temperature between 22 to 33.8°C. A total of eight experiments were carried out.

EXPERIMENTS

Experiments I-V

The objective of the experiments I-V was to study the effect of eyestalk ablation on feeding, growth, moulting, survival and gonad development of different sizes of *P. homarus*. Healthy lobsters ranging from 24.0 mm carapace length (CL) and 14 g weight to 71.7 mm CL and 297 g weight were used. The eyestalks were ablated at the base with a cauterizer. To minimise stress on the lobster, one of the eyestalks was ablated at first, and the other on the subsequent day. The lobsters were released back to the rearing system immediately after ablation.

Equal number of males and females were used in all the experiments except the sixth, where three females and two males were used. Lobsters were fed *ad libitum* on clam, *Meretrix casta*, twice daily. In experiment III, however, the green mussel *Perna viridis* and chopped trash fish were given, once daily for the first two months and, afterward, clam alone as in other experiments. Weighed quantity of food was given everyday in the evening and the remains were taken out and weighed next morning. After the removal of the leftover, three-fourth of the water in the rearing tank was replaced by fresh filtered seawater. After three hours food was offered again and, further three hours later, the feed-remains were taken out and water changed completely. The carapace length, total length and weight of the lobsters were measured every month. The maturity condition was also noted at the time of measurement. Majority of the lobsters moulted at night, and, when it occurred, moulting was recorded and the carapace length and weight of exuvia were noted. For interpretation of moulting and growth, group-averages were taken.

Experiment VI

In this experiment, equal quantity of food, at *ad libitum* feeding level, was given to both ablated and control groups once every evening, to find out whether the growth acceleration of ablated lobsters was solely due to increased consumption or due to physiological changes caused by ablation or to a combination of both. Water was changed completely once every morning. All other

conditions were similar to those mentioned in the previous experiments. One of the lobsters from this experiment was reared for 249 days and the moult cycle followed up to seven moults. After two moults, the lobster was fed *ad libitium* once daily.

Experiment VII

This experiment was to study whether maximum growth in ablated lobsters could be obtained by feeding *ad libitum* only once a day. All other conditions were similar to the previous experiments.

Experiment VIII

The effect of starvation on ablated lobsters was studied in this experiment. In order to prevent cannibalism, the experimental lobsters were reared individually in rectangular plastic tanks (60 cm x 30 cm x 30 cm). Water was changed completely once a day with fresh filtered seawater.

At the end of each experiment the lobsters were dissected and the hepatopancreas, gonads and muscle were removed, weighed and dried to a constant weight at 60° in an hot-air oven. Tail weight and meat weight of all the lobsters were also noted. Tail weight, meat weight and hepatopancreas weight of lobsters of experiments I-V were grouped into 10 mm-carapace-length intervals, and the mean values are presented.

REMARKS

Moulting frequency

Eyestalk ablation accelerated moulting frequency in all size groups, resulting in shortened intermoult period. Intermoult period increased with increasing size in both ablated and control lobsters. When ablated lobsters moulted five times in 108 days (Expt. I) control lobsters moulted only thrice in the same period. The same trend was noticed in all the experiments (Table 1). The moulting frequency and weight gain of an ablated lobster reared for 249 days (from Expt. VI) is shown in Table 2. Initially, the intermoult period showed a steady increase with size, but the period between V and VI moult was considerably lesser. The lobster died while moulting for the 7th time after ablation. The moulting frequencies of starved, ablated lobsters were higher than those of control lobsters (Table 3).

Weight gain

Compared to the normal ones, the ablated lobsters exhibited three to seven-fold increase in weight gain. (Fig. 1-4). In experiment I, the ablated juveniles recorded an average increase of 1.02 g|day, while the increase was only 0.35 g|day in the control. Weight gain in ablated lobsters increased with size and a maximum of 2.5 g|day (Expt. IV and V) was obtained in maturing

TABLE 1. *Average intermoult period* (± S.D) *for ablated and control* P. homarus (A: ablated; C: Control).

Expt. No.	Duration (days)	No. of animals		Initial weight (g)	Intermoult period (days)					No. of moults
					Up to I moult	I-II	II-III	III-IV	IV-V	
I	108	14	A	20.4±5.1	7.2±4.1	12.5±1.1	15.5±2.8	22.1±3.7	34.2±8.0	5
		14	C	24.8±4.1	22.1±11.4	30.8±5.0	39.9±4.3	—	—	3
II	93	18	A	49.7±6.0	10.0±4.4	15.9±3.5	20.8±2.4	27.6±2.9	—	4
		12	C	46.8±7.3	15.9±10.5	33.8±7.9	40.3±5.2	—	—	3*
III	165	10	A	84.5±1.9	12.3±6.4	27.1±2.5	32.8±9.0	37.3±3.3	36.8±0.5	5
		10	C	98.6±13.4	43.0±12.2	50.0±7.3	60.0±5.6	—	—	3
IV	36	4	A	169.0±24.8	17.3±7.6	—	—	—	—	1
		4	C	169.2±27.6	23.0±17.8	—	—	—	—	1**
V	61	6	A	256.5±22.2	14.8±10.7	30.8±3.6	—	—	—	2
		6	C	250.3±30.0	13.2±7.8	51.3±18.6	—	—	—	2***
VI	63	5	A	69.4±7.4	13.2±8.9	31.4±4.0	—	—	—	2
		5	C	66.0±4.7	33.4±17.8	—	—	—	—	1
VII	42	6	A	72.6±9.1	8.0±4.9	23.0±9.9	—	—	—	2
		6	C	72.2±10.0	28.7±14.6	—	—	—	—	1

* Did not complete the third moult
** Did not complete the first moult
*** Did not complete the second moult

TABLE 2. *Moulting frequency and weight gain in an ablated lobster reared for 249 days.*

Number of moults	Carapace length (mm)	Weight (g)	Increase in weight (g)	Percentage increase in weight	Intermoult period (days)
Initial	42.1	79	—	—	—
I	48.5	117	38	38.1	23
II	55.2	164	47	40.1	22
III	60.7	214	50	30.5	37
IV	65.8	270	56	26.2	42
V	73.0	377	107	39.6	43
VI	81.8	534	157	41.6	37
VII	Died while moulting				49

and mature lobsters (Table 4). In Expt. VI, in which equal quantity of food was provided for both ablated and control, weight gain was 1.14 g|day in the ablated lobsters and 0.28 g|day in the control. In Expt. VII, wherein the lobsters were fed *ad libitum* only once a day, the increase in weight was respectively 1.22 g|day and 0.21 g|day in the ablated and control groups. A maximum weight increase of 165 g in a single moult (V moult of the animal after ablation) was recorded in a lobster weighing 300 g in Expt. III, the intermoult period being 37 days.

Average percent weight gain per moult in ablated lobsters varied from 23 to 55. In control lobsters the weight gain declined from an average of 43%

TABLE 3. *Effect of starvation on moulting and survival in ablated and control* P. homarus (CL: Carapace length).

Treatment	Sex	Initial		Final		Survival (Days)	Moulting frequency (Days)	
		CL (mm)	Weight (g)	CL (mm)	Weight (g)		I Moult	II Moult
Ablated	Male	54.4	145	56.6	160	40	12	—
	Female	53.2	142	57.0	202*	56	7	40
Control	Male	58.2	190	58.8	176	76	15	—
	Female	63.2	225	63.2	225	85	—	—

* Weight increase was due to mere accumulation of water

in early juveniles (25 g size) to 5.4% in adults (250 g size). The ablated lobsters did not show such a decreasing trend with size in percent weight gain at moult. In ablated lobsters, increase in weight at the first moult depended on the

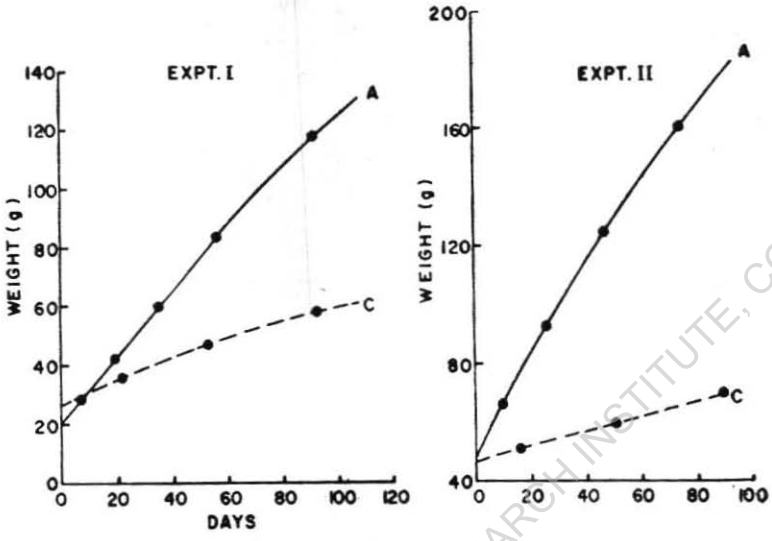

FIG. 1. Weight gain in eyestalk-ablated and control *P. homarus* in experiments I and II.

time taken for the moult after ablation or, more precisely, the moult stage at which ablation was carried out. For example, while the weight gain was 33% in lobsters moulted 10 days after ablation, it was 45.2% in those which completed the first moult after 16 days.

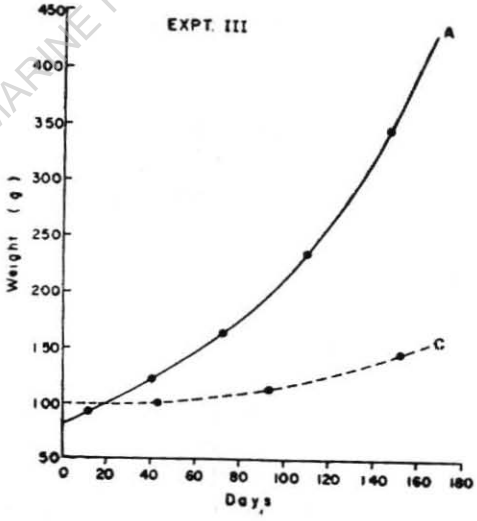

FIG. 2. Weight gain in eyestalk-ablated and control *P. homarus* in experiment III.

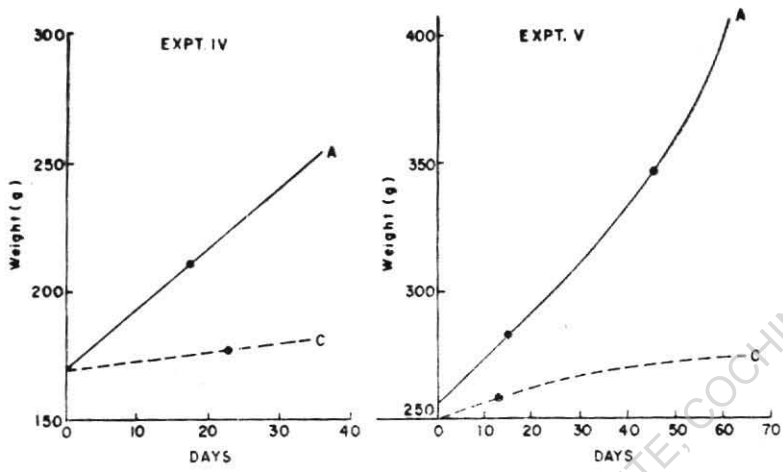

FIG. 3. Weight gain in eyestalk-ablated and control *P. homarus* in experiments IV and V.

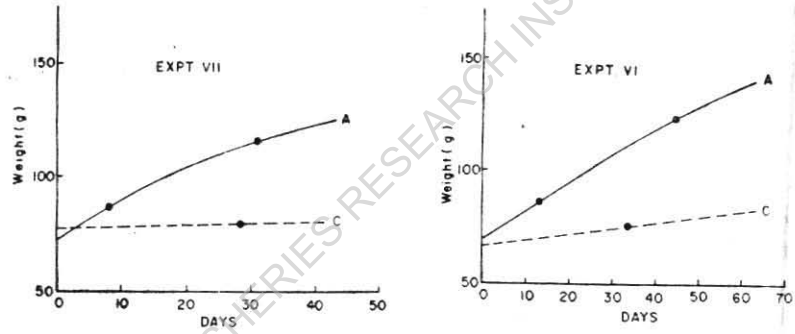

FIG. 4. Weight gain in eyestalk-ablated and control *P. homarus* in experiment VI and VII.

Increase in carapace length

The increase in carapace length of ablated and control lobsters 1 to V are given in Fig. 5. In the control group increase in carapace length per day gradually decreased with size. However, in ablated lobsters no such trend was observed and the carapace length increased by 0.2 to 0.25 mm|day in all the size groups (Table 4).

The increase in carapace length and percent increase at each moult in experiments I-III are presented in Table 5. Percent increase in carapace length at moult did not show any definite decreasing trend with size in ablated lobsters as did weight gain. In control, however, the percent increase in carapace length decreased with size. An increase of 9.9% in the III moult of the control groups in experiment III may have been due to the low temperature during December-January period (23-25°C) and consequent prolonged inter-moult period. This effect of temperature was also seen in the weight increase.

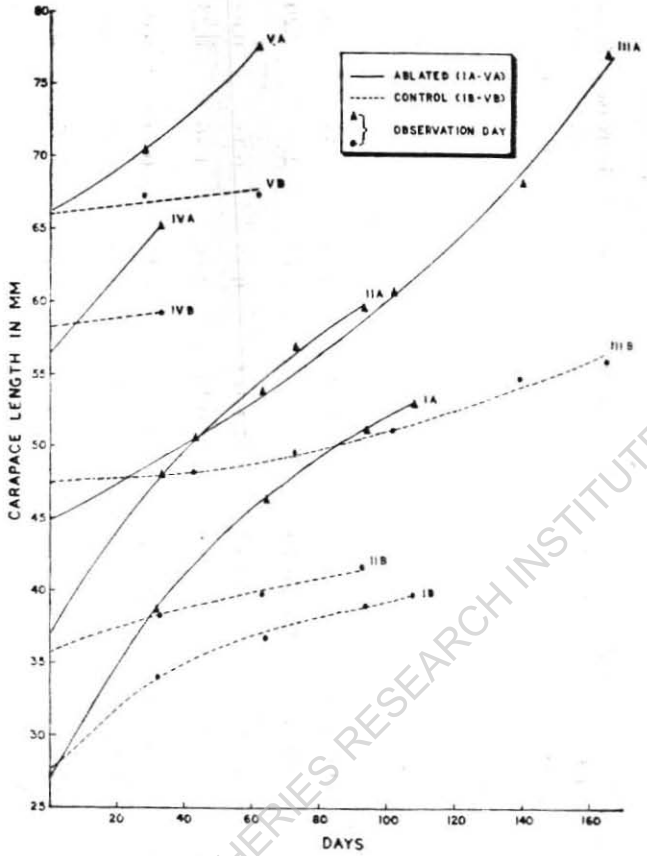

FIG. 5. Increase in carapace length in eyestalk-ablated and control *P. homarus* in experiments I-V.

Difference in growth between sexes

The total percent increase in carapace length and weight gain of male and female ablated lobsters and the control ones are given in Table 6, from which it is seen that, in the control, the males grew faster than the females. But in the ablated no such differential trend could be observed.

Effect on hepatopancreas

The percent of hepatopancreas in total body weight (hepatic index) and the percent dry matter in ablated and control lobsters are shown in Table 7. The hepatopancreas in ablated lobsters lost the normal colouration and looked like flimsy bags. While hepatic index in ablated lobsters was only 1% less than that in control lobsters, the average dry weight of the hepatopancreas of the former was about 14% less than that of control group in almost all size groups.

Tail weight and meat weight

Table 8 shows the tail weight, meat weight and the percent dry matter in the meat of ablated and control lobsters at the conclusion of the experiments.

TABLE 4. *Growth of ablated and control* P. homarus (S.D. in brackets) (A: ablated; C: Control).

Expt. No. date of start & duration (days)	Treatment	No. of lobsters	Initial CL (mm)	Initial Weight (g)	Final CL (mm)	Final Weight (g)	Increase in wt. (total) g|days	Increase in wt.| day (g)	% increase in wt.| day	Increase in CL| day (mm)
I	A	14	27.0(2.3)	20.4(5.1)	53.1(2.8)	132.0(22.6)	110.6|108	1.02	5.00	0.24
29-3-82 (108)	C	14	28.7(2.0)	24.8(4.2)	39.7(3.2)	62.3(14.0)	37.5|108	0.35	1.40	0.09
II	A	18	36.5(1.6)	49.7(6.0)	59.7(4.2)	184.3(37.0)	134.6|93	1.45	2.90	0.25
23-4-82 (93)	C	12	35.8(2.1)	46.8(7.3)	41.9(3.6)	71.3(16.0)	24.5|93	0.26	0.55	0.07
III	A	10	44.7(3.0)	84.5(1.9)	77.4(3.1)	432.0(61.1)	347.5|165	2.10	2.48	2.20
1-9-81 (165)	C	10	47.3(2.4)	98.6(13.4)	56.2(2.4)	155.7(19.2)	57.1|165	0.35	0.35	0.05
IV	A	4	56.2(6.0)	169.0(24.8)	65.3(3.3)	255.0(25.9)	86.0|36	2.48	1.46	0.25
15-3-82 (36)	C	4	58.2(2.9)	169.2(27.6)	59.2(2.9)	181.0(28.3)	11.7|36	0.33	0.19	0.03
V	A	6	66.1(3.1)	256.5(22.2)	77.8(0.8)	408.0(10.6)	151.5|61	2.50	0.97	0.20
3-4-82 (61)	C	6	66.0(3.5)	250.3(30.0)	67.4(4.0)	272.5(33.7)	22.2|61	0.36	0.14	0.02
VI	A	5	41.2(0.6)	69.4(7.3)	53.0(1.5)	141.0(16.7)	71.6|63	1.14	1.64	0.20
19-5-82 (63)	C	5	41.7(2.1)	66.0(4.7)	44.2(1.6)	83.4(7.9)	17.4|63	0.28	0.42	0.07
VII	A	6	42.3(1.7)	72.6(9.1)	50.7(3.3)	123.8(19.4)	51.2|42	1.22	1.68	0.20
24-6-82 (42)	C	6	42.3(2.0)	72.2(10.0)	43.9(2.3)	81.0(11.8)	8.9|42	0.21	0.29	0.04

TABLE 5. *Increase (Inc.) in carapace length (CL) and percent increase at moult of ablated (A) and control (C) P. homarus.*

Expt. No.	Treatment	Initial CL (mm)	Moult I		II		III		IV		V	
			Inc. (mm)	%	Inc. (mm)	%	Inc. (mm)	%	Inc. (mm)	%	Inc. (mm)	%
I	A	27.0±2.3	3.4	11.8	5.0	16.9	5.6	16.2	5.0	12.5	5.9	13.1
	C	28.7±2.0	2.5	9.3	4.2	13.1	2.6	7.2				
II	A	36.5±1.6	4.1	11.2	5.2	12.8	5.3	11.6	5.7	11.1		
	C	35.8±2.1	1.3	3.6	2.2	5.9	2.0	5.1				
III	A	44.7±3.0	1.7	3.8	3.6	7.8	5.0	10.0	7.1	12.9	8.9	14.3
	C	47.3±2.4	1.0	2.1	2.2	4.6	5.0	9.9				
IV	A	56.2±6.0	4.8	8.5								
	C	58.2±2.9	0.7	1.2								
V	A	66.1±3.1	2.2	3.3	5.5	8.0						
	C	66.0±3.5	0.4	0.6								

TABLE 6. *Percentage increase in carapace length and weight in males and females of ablated* (A) *and control* (C) P. homarus.

Expt. No.	Treatment	Duration of Expt.(days)	% increase in CL		% increase in weight	
			Male	Female	Male	Female
I	A	108	103.8	89.8	600.0	486.4
	C		41.1	35.9	165.0	139.0
II	A	93	63.4	65.0	264.0	277.8
	C		19.4	14.3	60.6	43.4
III	A	165	—	74.0	—	423.0
	C		24.5	13.9	73.8	44.4
IV	A	36	17.6	13.0	51.7	41.3
	C		1.2	1.5	6.6	7.2
V	A	61	14.9	10.5	53.4	63.2
	C		1.7	2.3	11.0	6.4
VI	A	63	28.7	27.8	96.8	99.1
	C		8.0	4.0	35.8	19.9
VII	A	42	13.2	27.2	45.6	101.9
	C		5.5	2.1	14.8	7.6

The tail weight and meat weight in ablated lobsters were 1 to 2.7% less than those in normal lobsters. The percent dry matter also showed about 2% reduction in ablated lobsters. However, the total edible meat in eyestalk-ablated lobsters was far more than that usually obtained in normal lobsters. The tail weight of males was always lower than that of the females in both ablated and control lobsters; this difference being greater in ablated ones (4-5%).

Morphological and behavioural changes

Normally, *P. homarus* loses its natural colour (greenish blue) after the first moult in captivity. The pale lobsters, however, regained their natural colour one moult after eyestalk ablation. Later, this colour gradually faded after each moult and, in some cases, 'albino' lobsters were noticed after three or four moults. Some of the pale lobsters, including the 'albinos', regained their pigmentation again. Further experiments with different diets (unpublished) showed that the food plays a major role in the colouration of lobsters: lobsters fed with green mussels (*P. viridis*) maintained the natural colour in both ablated and control lobsters, while those fed with clams (*M. casta*) lost the colouration gradually.

Eyestalk ablation did not interfere with the regeneration of autotomised limbs in *P. homarus*. Regeneration of limbs lost in the intermoult stage was seen

TABLE 7. *The hepatic index and percent dry matter in hepotopancreas of ablated and control* P. homarus.

ABLATED				CONTROL			
Carapace length (mm)	Weight (g)	Hepatic index	Per cent dry matter	Carapace length (mm)	Weight (g)	Hepatic index	Per cent dry matter
46-55.9	96-165	3.2±1.08	22.3±7.2	46-55.9	104-135	5.4±2.30	34.4±3.7
(51.8)	(130.7)			(51.6)	(120.0)		
56-65.9	153-297	2.8±0.74	22.2±8.3	56-65.9	176-315	3.4±1.20	39.2±7.7
(60.7)	(220.2)			(63.5)	(237.8)		
66-75.9	244-304	2.8±0.42	23.9±3.6	*66-75.0	270-380	3.3±0.97	37.0±11.6
(68.6)	(267.6)			(66.9)	(315.5)		
76-85.9	400-500	2.4±0.50	26.0±7.2	*76-85.9	376-470	1.9±0.70	24.7±4.8
(79.7)	(456.8)			(77.2)	(423.0)		

* The values for larger size groups of control specimens are taken from other rearing experiments which are treated similarly.

TABLE 8. *Percent tail weight, meat weight and dry matter in meat of ablated and control* P. homarus

ABLATED					CONTROL				
Carapace length (mm)	Weight (g)	Tail weight (%)	Meat (%) weight	Per cent matter dry	Carapace length (mm)	Weight (g)	Tail weight (%)	Meat weight (%)	Per cent dry matter
45-55.9	96-165	30.0±3.1	23.5±3.35	22.3±2.9	46-55.9	104-135	32.7±2.0	25.8±2.7	25.1±1.3
(51).8	(130.7)				(50.2)	(120.0)			
56-65.9	153-297	28.0±4.6	26.4%3.15	22.1±4.3	56-65.9	176-315	34.2±1.5	28.5±1.3	26.0±2.5
(60.7)	(220.2)				(63.5)	(237.8)			
66-75.9	244-304	32.3±1.8	26.0±1.50	22.6±1.7	*66-75.9	270-380	32.3±4.5	28.0±2.4	24.4±2.3
(68.6)	(267.6)				(69.9)	(315.5)			
76-85.9	400-500	31.7±2.9	26.0±2.50	22.5±3.2	*76-85.9	376-470	32.9±1.0	26.6±3.2	21.0±3.0
(79.7)	(456.8)				(77.2)	(423.0)			

* The values for larger size groups of control specimens are taken from other rearing experiments which are treated similarly.

in the first moult after ablation, but this was seen to be postponed to the next moult if autotomy happened in late-premoult. In ablated lobsters, the armature on the carapace became sharper and the walking legs stouter and, when handled, they were more aggressive than the normal ones.

In 90% of the ablated lobsters, after second or third moult, an antennule-like outgrowth developed at the site of the ablated eye, which may be either single, or bifid or trifid. With each subsequent moult this structure also increased in size. But in a very few cases (10%) such structure was not developd even after 5 moults.

The survival of ablated lobsters in the experiments was on an average 70% (43-100%) while that of the control was 97% (70-100%). The highest mortality of ablated lobsters was recorded in early juveniles (Expt. I). Death of both ablated and control lobsters was generally during moulting, or immediately after it. It was also observed that, when there was oxygen depletion due to power failure or to non-functioning of aerators, the ablated lobsters became more susceptible than the controls. Hence, the greater mortality occurred in the ablated lobsters may more probably be due to sudden fluctuations in the experimental conditions than due to any stress caused by ablation.

Discussion

Negative response of two palinurid lobsters, the tropical *P. argus* (Travis 1951, 1954) and the sub-tropical *P. cygnus* (Dall 1977), to bilateral eyestalk ablation has led to the speculation that, in palinurids, MIH is secreted by cells other than those in the eyestalk or, if it is secreted in in the eyestalk, the quantity is so insufficient as to affect moulting. Sochasky (1973) attributed Travis' failure in inducing precocious moulting in *P. argus* to gonadotropic interference, as the lobsters used by her were prepubertal or mature. Quackenbush and Herrnkind (1981) reported acceleration of gonad development in *P. argus* when ablated in spring and summer, but they did not find any significant difference in body weight or carapace length in ablated lobsters ten weeks after ablation. In their experiments, 41.6% of the ablated, mature females moulted in 48.5 $\pm$ 12.4 days, whereas 39% of the controls completed the first moult in 81.0 $\pm$ 10.7 days. In the rest of the ablated females (58.4%), which did not moult during the course of the experiment, the gonad index was high compared to that of the moulted (ablated) ones as well as of the intact controls. This led them to infer that eyestalk ablation accelerated moult cycle and gonad development in *P. argus*, but not simultaneously.

The present results of bilateral eyestalk ablation in *P. homarus* show that the acceleration of moulting frequency and gonad development is pronounced in all size groups (14-g early juveniles to 297-g adults) irrespective of the reproductive status and seasons, indicating the presence of Moult Inhibiting Hormone (MIH) and Gonad Inhibiting Hormone (GIH) in the syestalk.

In *P. homarus*, we have not considered the time taken to complete the first moult after ablation for interpreting moult acceleration, since this period is dependent on the moult stage at which ablation is performed. It is not known whether Quackenbush and Herrnkind (1981) had used lobsters in the same moult stage for ablation. It is possible that the 41.6% that moulted earlier were in the premoult stage at the time of ablation, and the rest, which did not moult, were in early intermoult stage, which makes it rather difficult to conclude whether ablation accelerated moulting frequency or not. However, the shorter duration taken for the first moult by ablated *P. argus* may be indicative of the possible presence of MIH factors in their eyestalks. This is further substantiated by isolation and partial characterization of MIH and GIH in *P. argus* (Quakenbush and Herrnkind 1983).

The accelerated growth in ablated lobsters is due to increased moulting frequency and higher percent weight gain at each moult. While faster moulting was attributed to the removal of MIH factors from the eyestalk, higher percent weight gain at moult was presumed to be due to elimination of hormone that regulates water uptake during ecdysis (Carlisle 1955), as eyestalkless lobsters became abnormally large after several moults. Koch (1952) ascribed the abnormal size increase to increased water uptake and not to tissue synthesis. In *P. homarus*, the large size attained by ablated lobsters is not due to mere accumulation of water, as was evident from the dry matter present in the meat (Table 8). However, the slightly lower percent dry matter observed in the ablated lobster meat may be due to cumulative addition of a small percentage of water retained in the tissue at each moult cycle, as ablated lobsters enter into next premoult faster, thereby all the water absorbed during ecdysis may not have been completely replaced by tissues. Mauviot and Castell (1976) also found lower percent of dry matter in the dorsal muscle of ablated *Homarus americanus* compared to intact control.

Eyestalk ablation did not incapacitate the lobsters in detecting food probably because of their well-developed chemoreceptive system (Ache and Macmillan 1980). For *P. homarus*, which inhabits the rocky coastal areas and is normally actively feeding at dusk, visual sighting may be of secondary importance for locating food. In both ablated and normal lobsters the general behavioural pattern for detecting the food was found to be the same: once the walking legs came into contact with the food, in a quick movement the object was grabbed. Antennular activity was also found to be increased on the introduction of the food.

The eyestalk factors probably regulate the storage and mobilization of organic reserves utilized for moulting and reproduction. Eyestalk ablation resulted in low hepatic index and percent dry weight of hepatopancreas, which may be indicative of the utilization of this reserve in tissue synthesis. Depletion of hepatopancreatic reserves due to eyestalk ablation was reported in *H. americanus* (Aiken

1980), as well as in crabs (Adiyodi 1969, Yamamoto 1960). A detailed study is, however, required to pinpoint the exact role of eyestalk factors in controlling hepatopancreatic metabolism.

The significance of the development of an antennule-like outgrowth in the place of the ablated eye is not fully understood. Development of such outgrowth in naturally blind (wild) *P. japonicus* was reported by Yosii (1931). Herbst (1896) had observed that the eyestalk regenerates when it is amputated at a region distal to the optic ganglia, whereas, when amputated at a level proximal to the ganglia, it produces an antenna. This he had explained as a specific morphogenetic effect of the optic ganglia on the development of the eye. However, subsequent experiment did not support this hypothesis.

The results of our study shows that further research is required to establish the hormonal role in moulting and growth in palinurid lobsters. As in many other decapods, reproduction and somatic growth are antagonistic in normal *P. homarus* and, since ablation accelerated the moult cycle and gonadal development simultaneously, this antagonistic relationship seems to be altered by bilateral eyestalk ablation. The acceleration of the moulting cycle and the higher percent weight gain at moult, irrespective of the reproductive status, lead us to believe that, under eyestalk ablation, in *P. homarus*, as in other decapods like *Eriocheir sinensis* and *Pachygrapsus marmoratus*, the relative emphasis is on somatic growth rather than on gonadal growth. The presence of MIH, as indicated here, in tropical palinurids, which are exposed to minimal seasonal environmental fluctuations; contradicts the view of Aiken (1980) that MIH exists primarily to regulate seasonal moulting and, therefore, it may not be significant in lobsters, to which this is not a requirement.

Whether MIH and GIH in *P. homarus* represent a single hormone with diverse functions or are they distinct hormones with different target tissues can only be concluded from characterisation of these hormones. However, the instances of synchronous occurrence of moulting and gonadal growth presently observed suggest the possibility that the hormonal mechanisms involved in moulting and reproduction are the same or, if they are different, they act synergistically in ablated lobsters.

In our trials with the controls, the duration taken by *P. homarus* for attaining about 200 g from an initial 25 g is about 16 months. The present study, therefore, indicates the possibility of growing *P. homarus* from 25 g to 200 g in about five months and to double that size in another two to three months more through eyestalk ablation and proper feed schedules. However, the necessity to maintain optimum environmental conditions needs to be emphasised as oxygen depletion in the culture conditions was a major cause for mortality in ablated lobsters especially during and just after moulting. It may be that the high oxygen requirement of ablated lobsters is due to the high feeding and metabolic rate.

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EFFECT OF EYESTALK ABLATION IN THE SPINY LOBSTER *PANULIRUS HOMARUS* (LINNAEUS): 2. ON FOOD INTAKE AND CONVERSION

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EFFECT OF EYESTALK ABLATION IN THE SPINY LOBSTER *PANULIRUS HOMARUS* (LINNAEUS): 2. ON FOOD INTAKE AND CONVERSION

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ABSTRACT

Eyestalk ablation induced hyperphagia and increased food consumption by 50 to 75% in *Panulirus homarus*. Feeding rate decreased with increase in size, in both ablated and control lobsters. In ablated lobsters the conversion efficiency was maximum at low feeding rate. The percent loss of converted food as exuvia was an average of 43.2% in ablated and 64.0% in control lobsters.

INTRODUCTION

Bilateral eyestalk ablation enhances moulting frequency and weight gain in the spiny lobster *Panulirus homarus* (Radhakrishnan and Vijayakumaran 1982, 1983, and Silas 1983). The accelerated moulting frequency is attributed to the removal of Moult Inhibiting Hormone (MIH) factors as a result of the eyestalk ablation. The influence of increased food intake and conversion leading to higher weight gain in ablated *P. homarus* has been studied. A report on the effect of eyestalk ablation on increased food consumption, conversion ratio and accelerated growth rate in the American lobster, *Homarus americanus* is available (Castell et al 1976), but no such study has been carried out so far on palinurid lobsters.

MATERIAL AND METHODS

P. homarus, ranging in carapace length from 24.3 mm and in weight 14 g (juveniles) to 71. 7 mm and 297 g (adults), were used in this study. In experiments I to V clam meat (of *Meretrix casta*) was fed *ad libitum* twice daily, in the morning (1100-1400 hrs) and in the evening (1700-0800 hrs). In experiment VI, equal quantity (equivalent to the *ad libitum* quantity fed to the control) was fed to the ablated and control lobsters in the evening. In experiment VII, lobsters were fed *ad libitum* food once a day (evening). (For further details refer Radhakrishnan and Vijayakumaran 1983.) The temperature in the culture system ranged from 26 to 33.8°C.

Feeding rate, conversion rate, gross conversion efficiency and conversion factor, in terms of wet/dry weight food to live weight animal, were calculated using the following equations Pandian and Vivekanandan 1976):

$$\text{Feeding rate} = \frac{\text{food consumed (wet/dry) (mg)}}{\text{gram live body weight x number of days}}$$

$$\text{Conversion rate} = \frac{\text{live weight gain (mg)}}{\text{gram live body weight x number of days}}$$

(Gram live body weight mentioned above is the mid point of initial and final weights.)

$$\text{Gross conversion efficiency (\%)} = \frac{\text{live weight gain x 100}}{\text{food consumed (wet/dry)}}$$

$$\text{Conversion factor} = \frac{\text{food consumed (wet/dry)}}{\text{live weight gain}}$$

RESULTS

Eyestalk ablation induced hyperphagia and increased food consumption by 50-96.5%. Feeding rate, conversion rate, conversion efficiency and conversion factor, calculated in terms of wet weight of food consumed to live weight gain and dry weight of food to live weight gain, are presented in Tables 1 and 2 respectively. Food consumption decreased with increase in size in both ablated and control lobsters, the decrease being only 33% in ablated and 46% in the controls. Gross food conversion efficiency (excluding weight of exuvia), in terms of dry weight of food, decreased in control lobsters from 38.4% in juveniles to 13.3% in mature ones. When exuvia weight was also included in the calculations, the same figures ranged from 78% in juveniles to 58% in mature adults. No such definite trend was noticed in ablated lobsters. Food offered remaining equal in control and ablated lobsters, as in experiment VI, the feeding rate of ablated individuals was much less (36.2 mg/g live body weight/day) compared to the controls (46.7 mg). This was due to the fact that average weight (mid point of initial and final weights) of ablated individuals was much higher (105.2 g) than the controls (75.7 g), resutling from the faster growth rate in ablated lobsters. Food conversion efficiency in this experiment, however, was more than double in ablated lobsters (112.5% without exuvia and 172.0% including exuvia) compared to that of the controls (29.8% without exuvia and 76.0% including exuvia). The lowest food conversion factor (0.9 and 0.6 without and with exuvia, respectively) also was rcorded in this experiment for ablated lobsters (Table 2). In experiment VII, where food was offered *ad libitum* once daily, food consumption of ablated lobsters was almost twice that of the controls and food conversion efficiency more than double (without exuvia weight). This conversion efficiency compares well with those obtained in experiments I-V where food was offered *ad libitum* twice daily.

TABLE 1. *Feeding rate, conversion rate, conversion efficiency and conversion factor, on the basis of wet weight of feed to live weight of the eyestalk-ablated (A) and control (C)* P. homarus.

Expt. No. & duration (days)	No. of animals	Treatment	Feeding schedule	Weight (g) Initial and Final	Feeding rates (mg)	Conversion rate (mg) excluding wt. of exuvia	Conversion rate (mg) including wt. of exuvia	Conversion efficiency (%) excluding wt. of exuvia	Conversion efficiency (%) including wt. of exuvia	Conversion factor excluding wt. of exuvia	Conversion factor including wt. of exuvia
I (108)	14	A	*a.l.*	204-131.0 (75.7)*	117.30	13.53	24.10	11.5	20.5	8.7	4.9
	14	C	t.d.	24.8-62.5 (43.7)	79.62	7.95	16.20	10.0	20.3	10.0	4.9
II (98)	18	A	*a.l.*	49.7-184.3 (117.0)	94.61	12.37	22.90	13.1	24.2	7.6	4.1
	12	C	t.d.	48.8-71.3 (59.1)	72.3	4.60	11.80	6.4	16.3	15.6	6.1
III**											
IV (36)	4	A	*a.l.*	169.0-255.0 (212.0)	73.85	11.27	21.80	15.3	29.5	6.5	3.4
	4	C	t.d.	169.3-181.0 (175.2)	41.92	1.86	6.80	4.4	16.2	22.7	6.2
V (61)	6	A	*a.l.*	256.0-408.0 (332.0)	71.54	7.43	13.90	10.4	19.4	9.6	5.2
	6	C	t.d.	250.3-272.5 (261.4)	40.38	1.39	6.10	3.4	15.1	29.4	6.6
VI (63)	5	A	e.	69.4-141.0 (105.2)	36.92	10.80	16.60	29.3	45.0	3.4	2.2
	5	C	o.d.	66.0-83.4 (74.7)	47.69	3.70	9.40	7.8	19.7	12.8	5.1
VII (42)	6	A	*a.l.*	72.6-123.8 (98.2)	87.69	12.41	20.70	14.2	23.6	7.0	4.2
	6	C	o.d.	72.2-80.8 (76.5)	44.62	2.77	7.20	6.2	16.1	16.1	6.2

* Values in parenthesis show the mid point of initial and final weights

** Not included for feed conversion studies since different diets were given initially to the group

a.l. = *ad libitum;* t.d. = twice daily; o.d. = once daily; e = equal quantity.

TABLE 2. *Feeding rate, conversion rate, conversion efficiency and conversion factor, on the basis of dry weight of feed to live weight of the animal, in eyestalk ablated (A) and control (C)* P. homarus.

Expt. No. & duration (days)	No. of animals	Treatment	Feeding schedule	Weight (g) Initial and Final	Feeding rates (mg)	Conversion rate (mg) excluding wt. of exuvia	Conversion rate (mg) including wt. of exuvia	Conversion efficiency (%) excluding wt. of exuvia	Conversion efficiency (%) including wt. of exuvia	Conversion factor excluding wt. of exuvia	Conversion factor including wt. of exuvia
I (108)	14	A	*a.l.*	20.4-131.0 (75.7)*	30.5	13.53	24.10	44.4	79.0	2.3	1.3
	14	C	t.d.	24.8-62.5 (43.7)	20.7	7.95	16.20	38.4	78.0	2.6	1.3
II (93)	18	A	*a.l.*	49.7-184.3 (117.0)	24.6	12.37	22.90	50.3	93.0	2.0	1.1
	12	C	t.d.	48.8-71.3 (59.1)	18.8	4.60	11.80	24.5	63.0	4.1	1.6
III**											
IV (36)	4	A	*a.l.*	169.0-255.0 (212.0)	19.2	11.27	21.80	58.7	114.0	1.7	0.9
	4	C	t.d.	169.3-181.0 (175.2)	10.9	1.90	6.80	17.0	63.0	5.9	1.6
V (61)	6	A	*a.l.*	256.0-408.0 (332.5)	18.6	7.40	13.90	40.0	75.0	2.5	1.4
	6	C	t.d.	250.3-272.5 (261.4)	10.5	1.40	6.10	13.3	58.0	7.5	1.9
VI (53)	5	A	e.	69.4-141.0 (105.2)	9.6	10.80	16.60	112.5	172.0	0.9	0.6
	5	C	o.d.	66.0-83.4 (74.7)	12.4	3.70	9.40	29.8	76.0	3.4	1.3
VII (42)	6	A	*a.l.*	72.6-123.8 (98.2)	22.8	12.40	20.70	54.5	91.0	1.8	1.1
	6	C	o.d.	72.2-80.8 (76.5)	11.6	2.80	7.20	23.9	62.0	14.2	1.6

* Values in parenthesis show the mid point of initial and final weights
** Not included for feed conversion studies since different diets were given initially to the group
a.l. = *ad libitum;* t.d. = twice daily; o.d. = once daily; e = equal quantity.

In *P. homarus*, both ablated and control, an average of 25% live body weight is lost as exuvia at each moult. But the percentage of converted food lost as exuvia was significantly lower in ablated lobsters (Table 3). For example, a 100 g control lobster moults to 115 g, losing 25 g as exuvia in the process. The total increase in body weight, then, is 40 g, out of which 25 g is lost in the form of exuvia. In ablated lobsters of the same size the total increase was about 70 g but the loss as exuvia was only 25 g as in the case of the control lobsters. In the former 62.5% of the converted food was lost as exuvia while the loss was only 35% in ablated lobsters.

TABLE 3. *Moult weight and its percentage in total weight increase in ablated and control* P. homarus.

Expt. No. and Duration (Days)	Treatment	Total weight increase (g)	Moult weight (g)	Moult weight in total weight increase (%)
I	Ablated	196.7	86.2	43.8
(108)	Control	76.2	38.7	50.8
II	Ablated	248.8	114.2	45.9
(93)	Control	64.6	39.9	60.8
IV	Ablated	166.7	80.7	48.4
(36)	Control	43.0	31.3	72.8
V	Ablated	282.1	131.4	46.6
(61)	Control	97.5	75.3	77.2
VI	Ablated	109.7	38.1	34.7
(63)	Control	44.3	26.9	60.7
VII	Ablated	85.2	34.0	39.9
(42)	Control	23.1	14.2	61.5

DISCUSSION

In *P. homarus*, the large size attained by ablated lobsters does not appear to be due to mere accumulation of water but to subsequent tissue synthesis which replaces the water absorbed during ecdysis. Since the ablated lobster enters into the next premoult faster, the metabolism has to be geared up to meet the accelerated tissue build-up. The increased weight gain in ablated lobster has resulted from higher consumption, higher conversion efficiency and lower percent loss of converted food as exuvia. In early juveniles the difference in conversion efficiency between ablated and controls was negligible (6% excluding exuvia weight and 1% including exuvia weight) and the three fold increase in weight of ablated lobsters is due to the other two factors stated above. The conversion efficiency for control lobsters compares favourably with that obtained (36%) in *Panulirus*

interruptus (Bartley et. al., 1980).The conversion efficiency recorded in Experiment VI was more than twice the average value obtained in Experiments I to V, eventhough the food consumed was less than half the quantity. The increased conversion efficiency was to meet high metabolic requirements of ablated lobsters. The quantity of food given in this experiment, however, was insufficient and this resulted in cannibalistic tendency. The conversion efficiency and weight gain recorded in Experiments VII, where food was given *ad libitum* once daily, were comparable to those of the other experiments where food was offered twice; which may be due to the marginal difference in feeding rate between the two groups (Table 2). In both the cases the ablated lobsters did not show cannibalistic behaviour, indicating that food given *ad libitum* once daily is sufficient to prevent cannibalism. Since no appreciable difference in growth was obtained when food was given *ad libitum* once or twice daily, the feeding can be restricted to *ad libitum* once a day. The conversion factor 0.9 to 2.5 (excluding exuvia weight) recorded in these experiments in ablated *P. homarus* is higher than that reported (4.96-5.50) for eyestalk-ablated *H. americanus* reared in elevated temperature (15°C) and fed *ad libitum* on moist diet preparations (Castell et al 1976).

The relationship of feeding rate to conversion rate and to conversion efficiency (on dry weight of food to live weight of lobster) irrespective of feeding schedule and size of the lobster is shown in Figure 1 A & B. There was no significant difference in conversion efficiency in relation to feeding rate in normal lobsters, since they were fed *ad libitum* in all the experiments. But, in ablated lobsters, conversion efficiency was highest at lowest feeding rate and this decreased with increasing feeding rate. This indicates that ablated lobsters are capable of enhancing conversion efficiency to meet high requirement of tissue synthesis consequent to the greater volume increase at moult. Food conversion rate is lowest at low feeding rate and increases with increasing feeding rate in both ablated and control lobsters. However, at a particular feeding rate the conversion rate is higher in ablated lobsters than the controls. The striped portion in the figure indicates the quantum of difference in conversion rate that can be attributed to the effect of ablation.

Eventhough the growth rate of both ablated and control lobsters decreased with size, the effect of eyestalk ablation on bigger lobsters is more pronounced than on smaller ones. In ablated early juvenile lobsters the weight increase was only three times that of the controls, while the increase was seven times in adult lobsters. This difference may be due to the following reasons:

1. The food consumption was only about 50% more than that of the controls in ablated early juveniles, while it was over 75% in adults.
2. The conversion efficiency (including weight of exuvia) was almost the same in ablated juveniles and controls, while it was more than 30% (with exuvia) of the control in ablated adults..

3. The difference in percent loss of converted food as exuvia between ablated and control juveniles was only 7%, whereas it was about 30% in adults.

It is observed here that, at low feeding rate (1% dry food/g live body weight as in Experiment VI), the ablated *P. homarus* converted food to tissue more efficiently, although the growth rate was about 30% less compared to the

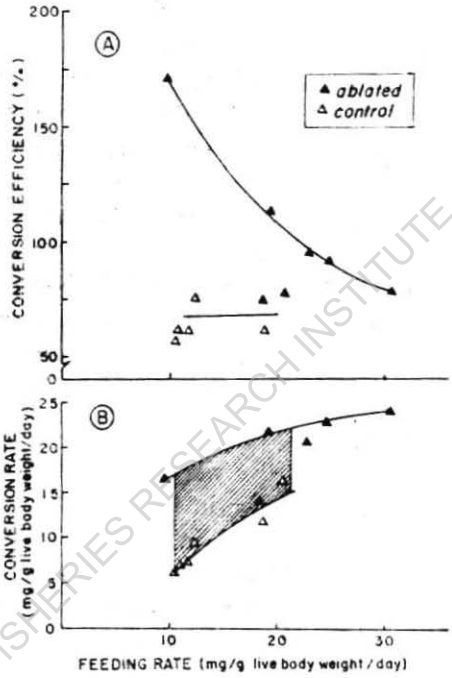

FIG. 1. Conversion efficiency (A) and conversion rate (B) in relation to feeding rate in eyestalk-ablated and control *P. homarus*. Shaded position indicates the quantum of difference in conversion rate induced by ablation.

groups fed once or twice *ad libitum* (2.3-2.5% dry food/g live body weight) of more or less similar size, as in Experiments II and III. Since all the controls in these experiments were fed *ad libitum* levels, no such relationship could be worked out for them. This observation is in agreement with the view of Paloheimo and Dickie (1966) that at low feeding levels poikilothermic organisms convert food to tissue more efficiently but with reduced growth rate and at higher feeding levels increased growth rates are obtained at the expense of lower conversion efficiency. The optimum feeding level necessary to obtain maximum conversion efficiency and growth rate is yet to be worked out for eyestalk-ablated *P. homarus*. Conversion efficiency of 44 to 112.5% (without exuvia) recorded in ablated *P. homarus* exceeds the approximate limit of 50% conversion efficiency suggested by Sedgewick (1979) for economically viable penaeid prawn culture. This study reveals the possibility that maximum weight gain can be obtained in ablated lobsters by optimising feed, which will also reduce the production costs

of the culture system. The high conversion, and the substantial weight increase of lobsters in shorter duration opens up scope for economically feasible lobster culture, using juveniles which do not fetch reasonable price in the market. Culture of mature lobsters may still be profitable since the absolute weight increase is higher in this group as shown in the present experiments.

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EFFECT OF EYESTALK ABLATION IN THE SPINY LOBSTER *PANULIRUS HOMARUS* (LINNAEUS): 3. ON GONADAL MATURITY

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ABSTRACT

Eye ablation induced accelerated gonadal growth in males and females, indicating gonad inhibiting principles in the eyestalk. Eyestalk removal resulted in 'pink haemolymph' in maturing and mature females and also inhibited the development of secondary sexual characters in them. The normal antagonistic relationship of moulting and reproduction was changed to one of synergism in ablated lobsters. Ablation of eyestalks initiates relatively strong moulting tendency than reproduction in *P. homarus*.

INTRODUCTION

Bilateral eyestalk ablation has been reported to accelerate gonad development as well as moult cycle in many crustaceans including shrimp (Panouse 1943; Demeusy 1965; Fingerman and Fingerman 1976; Rangneker and Deshmukh 1968; Aiken and Waddy 1976; Mauviot and Castell 1976; Quackenbush and Herrnkind 1981; and Nagabushanam and Kulkarni 1982). It has been suggested that the gonadal development in decapods is controlled by inhibiting hormone (GIH) factors produced by X-organ sinus gland complex in the eyestalk which in turn is assumed to control the synthesis of gonad stimulating substances (GSH) that probably originate in the brain and thoracic ganglion. Reviewing the literature on decapod reproductive endocrinology, Adiyodi and Adiyodi (1970) postulated the presence and inter-relationship of six hormones in controlling moulting and reproduction in decapod crustaceans. The role of eyestalk hormones on gonadal development in palinurid lobsters has been recently studied by Quackenbush and Herrnkind (1981 and 1983). The present paper reports on the effect of bilateral eyestalk ablation on gonadal development of juvenile, maturing and mature lobster *Panulirus homarus*.

MATERIAL AND METHODS

Gonad condition of ablated and control juvenile, maturing and mature *Panulirus homarus* was observed in Experiments I-V, where food was given *ad libitum* twice daily (for details refer Radhakrishnan and Vijayakumaran 1984).

The maturity stage and weight of the gonads of lobsters that died during the course of the experiments were also recorded. The wet and dry weight of the gonads of lobsters in these experiments were grouped and presented in 10-mm-carapace-length intervals. The gonad condition of starved control and ablated lobsters (Radhakrishnan and Vijayakumaran 1984) were also examined. One more experiment on the effect of eyestalk ablation on gonadal maturity of maturing *P. homarus* was conducted in November, the beginning of the breeding season of *P. homarus* at Kovalam. Twenty maturing lobsters with an average carapace length of 52.4 mm and weight 127.9 g were divided into two groups, each group containing five males and females. Both eyestalks of one of the groups were ablated. Both the groups were fed with equal quantity of clam meat (of *Meretrix casta*) once a day. The experiment had to be discontinued after 16 days, since all the ablated lobsters died due to asphyxiation. The carapace length, weight, gonad weight and maturity stage of all the control and ablated lobsters were recorded.

The ovary stage and morphological criteria for development stages of ovary have been classified following Berry (1971). Gonad index (GI) was calculated by the formula

$$\frac{\text{Gonad wet weight}}{\text{Weight of the lobster}} \times 100$$

Appearance of secondary sexual chracters in females and the reproductive behaviour of males and females of both ablated and control groups were observed.

RESULTS

Gonadal development in males

Eyestalk ablation is noticed to result in significant size and weight increase in vasa deferentia of juvenile, maturing and mature males. However, development of androgenic gland and spermiogenesis was not examined in this study. The gonad index of ablated males in all the experiments was higher than that of control animals. In ablated males gonad index increased with increase in size, whereas in control lobsters it showed increase up to 75.9 mm carapace length and thereafter decrease (Table 1). Percent dry matter in gonads also showed increase with size in both ablated and control lobsters, the value being higher in ablated lobsters, which indicates real tissue synthesis. Hypersecretion of matrix was observed in the swollen vas deferens of ablated males.

Gonadal development in females

Ablation accelerated ovary development in juvenile, maturing and mature *P. homarus*. The gonad index of ablated and control females are shown in Table 2. In juvenile lobsters (Expt. I and II) ovary reached only stage II (pink, light

TABLE 1. *Gonad index and per cent dry matter in gonad of male (ablated and control)* **P. homarus.**

ABLATED					CONTROL				
Carapace length (mm)	No. of lobsters	Weight (g)	Gonad index	Per cent dry matter in gonad	Carapace length (mm)	No. of lobsters	Weight (g)	Gonad index	Per cent dry matter in gonad
46-55.9 (51.3)	6	96-149 (124.0)	1.7 ± 0.4	33.1 ± 3.6	46-55.9 (49.0)	4	104-116 (108.0)	0.7 ± 0.1	32.6 ± 2.0
56.65.9 (59.7)	8	153.240 (182.3)	2.6 ± 0.6	37.1 ± 3.8	56-65.9 (63.3)	8	180-285 (236.3)	0.9 ± 0.4	36.9 ± 4.2
66-75.9 (68.6)	9	244-304 (266.6)	3.7 ± 1.7	41.7 ± 1.3	*66-75.9 (70.8)	6	270-345 (313.1)	1.6 ± 0.5	40.1 ± 2.7
76-85.9 (78.2)	3	395-429 (408.0)	4.63 ± 0.3	45.9 ± 1.7	*76-85.9 (77.7)	4	350-415 (375.8)	1.31 ± 0.2	40.2 ± 2.2

* Values for larger size groups of control specimens are taken from other rearing experiments which are treated similarly.

TABLE 2. *Gonad index and per cent dry matter in gonad of female (ablated and control)* P. homarus.

ABLATED					CONTROL				
Carapace length (mm)	No. of lobsters	Weight (g)	Gonad index	Per cent dry matter	Carapace length (mm)	No. of lobsters	Weight (g)	Gonad index	Per cent dry matter
46-55.9 (51.8)	5	110-165 (131.5)	1.1±0.6	27.6±7.2	46-55.9 (49.9)	7	89.5-141 (116.5)	0.25±0.1	26.8±2.2
56-65.9 (61.0)	7	159-297 (224.6)	1.0±0.7	37.2±5.9	56-65.9 (63.5)	9	224-262 (237.0)	0.6±0.3	26.9±4.6
66-75.9 (69.9)	8	239-470 (326.0)	1.8±0.8	36.5±1.0	*66-75.9 (71.2)	6	350-410 (373.0)	0.95±0.4	26.4±5.8
76-85.9 (80.2)	4	404-500 (471.0)	1.0±0.5	32.0±9.5	*76-85.9 (76.8)	3	420-520 (470.0)	0.7±0.2	29.1±6.2

* Values for larger size groups of control specimens are taken from other rearing experiments which are treated similarly.

orange) after 108 days and 96 days respectively, whereas in control lobsters the ovary was in stage I (white, flattened). In maturing and mature lobsters (Expts. III, IV and V) the ovary was in stage IV (bright coral red) in ablated ones and in stage II in controls at the end of the experiments, which lasted 36 to 65 days.

The ovaries of maturing females, which were ablated in November, were also found to be in stage IV after 16 days when they all died apparently due to asphyxiation. Ovaries of the control lobsters in this experiment remained in stage II itself. The average gonad index of two females which moulted during this period was 1.2. The three which did not moult, however, had a higher gonadal index of 1.5 (average), which is 25% higher than that of the moulted ones. The gonad index of the controls was an average of 0.4. Ablation of maturing and mature lobsters in most part of the year accelerated the development of the ovary significantly. However, ablation of maturing and mature lobsters in reproductive season yielded a higher GI of 1.5 to 2.6 compared to that obtained in post-breeding season, 0.8-1.5, though both attained stage IV.

The ovary of a starved ablated lobster also advanced to stage IV after 47 days, in which time it had completed two moults. The first moult was seven days after ablation and the lobster oviposited and subsequently shed the unfertilized ova before the second moult.

In many of the maturing and mature ablated females "pink haemolymph" was found before the first moult when the period taken to moult was over ten days and between first and second moults in those which moulted within ten days of ablation.

Development of secondary sexual characters

The secondary sexual characters such as decalcified 'window' on the sternal plate and the ovigerous setae on pleopods did not appear in female lobsters ablated in immature stage and reached the size at which normally these characters appear. Normally, in laboratory-reared *P. homarus*, these characters appear at the onset of sexual maturity (55 mm CL) (Radhakrishnan, 1977).

Reproductive behaviour

Abnormal reproductive behaviour was noticed in ablated males; even those males with less than 45 mm carapace length forcefully deposited spermatophoric mass on the sternal plate of other ablated males and immature females. Normally male lobsters of above 55 mm carapace length was found to mate with females but not with other males, even though in another species of spiny lobster, *P. ornatus*, collected from wild, one instance of spermatophoric-mass deposition on a male measuring 60 mm carapace length was noticed by us at Madras.

Discussion

Accelerated gonad development in both males and females of *P. homarus* by bilateral eyestalk ablation indicates the presence of Gonad Inhibiting Hormone (GIH) factors in the eyestalk. Ablation in juveniles brought the ovary only to previtellogenic stage, which is in agreement with the view of Adiyodi and Adiyodi (1970) that the ovary needs to reach a particular stage before they respond to the declining titre of the GIH. Quackenbush and Herrnkind (1981) also had reported that in *P. argus* ovaries of the females below 70 mm carapace length did not become vitellogenic after bilateral eyestalk ablation.

In maturing and mature *P. homarus*, the ovary readily responded to the removal of eyestalk, which is evident from the high gonad index, a function of reproductive activity of marine invertebrates (Bennet and Giese 1955, and advanced development of ovary. Quackenbush and Herrnkind (1981) reported that the gonad index of ablated and non-moulted *P. argus* females was about three times that of the moulted ones and opined that in *P. argus* eyestalk ablation accelerated either moulting or reproduction but not simultaneously. In *P. homarus*, however, the 25% difference in gonadal index of moulted and non-moulted ablated females was due to the higher weight gain in moulted ones, indicating that ablation accelerated both moulting and gonadal development. However, as reported earlier (Radhakrishnan and Vijayakumaran 1983), in ablated *P. homarus* the relative emphasis is on moulting and somatic growth rather than on gonadal growth. This view is further supported by our subsequent observation of ablated *P. homarus* moulting with fertilized eggs and even with "naupliosomae' on their pleopods (unpublished). These lobsters have mated and oviposited after eyestalk ablation.

The cause of the "pink haemolymph" in ablated lobsters is not clearly understood. According to Adiyodi (1968) the Female Specific Protein (FSP) accumulates in the haemolymph prior to the onset of vitellogenesis. Whether this is due to lack of FSP uptake by ovary or to resorption from the ovary is not known. Aiken (1980) noticed pale green haemolymph in mature female *Homarus americanus* and suggested that either of these events would produce the colouration of the haemolymph. Further studies on transport of vitellogenin from the hepatopancreas through the blood is required to establish the appearance of "pink haemolymph" in *P. homarus*.

The non-development of secondary sexual characters such as decalcified 'windows' on the sternal plate and ovigerous setae on the pleopods in eyestalk-ablated females show the regulatory role of GIH in controlling the development of these characters. Adiyodi and Adiyodi (1970), citing similar results in *Carcinus maenus* and *Pachygrapsus marmoratus*, had also suggested that probably GIH allows time for the development of brooding characters inasmuch as it restrains the rate of vitellogenesis in the ovary.

The effect of eyestalk ablation is more pronounced in the male gonads and the difference in gonad index between control and ablated is higher in males than females (Tables 1 and 2). It will be interesting to find out to what extent the higher gonad development induced by eyestalk ablation is responsible for the lower percent of tail weight in males (Radhakrishnan and Vijayakumaran 1983).

The observation that ablated males of even less than 45 mm carapace length deposists spermatophoric mass on other lobsters irrespective of the sex, and even on lobsters in advanced moulting stage (D4), shows that their reproductive activity is accelerated. Besides, they develop an urge to deposit the spermatophoric mass. This indescriminate deposition of spermatophoric mass may be due to the high pressure developed in the vas deference from hypersecretion of matrix. If the resulting spermatophoric mass is deposited on a reproductively active ablated female this can lead to fertilization, oviposition and release of phyllosoma larvae, provided the lobster does not moult before the hatching of the larvae. To what extent the antagonistic relationship of moulting and reproduction in normal *P. homarus* is altered by eyestalk ablation is not clear and it necessitates further studies on isolation and characterization of hormones controlling, moulting, growth and reproduction.

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Eyestalk ablation

NEW IDEA BOOSTS GROWTH OF INDIAN SPINY LOBSTER

A SPECTACULAR three to tenfold increase in weight over the normal has been achieved by eyestalk ablation in four species of spiny lobsters (*Panulirus homarus, P. ornatus, P. polyphagus* and *P. versicolor*) at the Central Marine Fisheries Research Institute (CMFRI). This increase in weight is obtained within 21 to 33 moulting weeks.

Six species of spiny lobsters known from the Indian seas have an internal as well as an external market. The fall in production from about 3000 metric tons in 1975 to 1153 tons in 1983 has been a matter of great concern. This decline in stocks is also accompanied by a decrease in the size in the catch in coastal lobster grounds.

Spiny lobsters have protracted larval life extending over several months. At the CMFRI, while experiments on nutrition and growth of the phyllosoma larvae of *P. homarus* and other species are underway, research on inducing growth and maturation, and on reproductive physiology and endocrinology were initiated in 1979 following the encouraging results on the growth of baby lobsters from puerulus stage, to mature adults in barely two years. Controlled group rearing of lobsters (early juveniles of 50 g size) feeding with mussel and clams showed that 200 g *P. homarus* and *P. polyphagus*, and 300 g *P. ornatus* could be obtained in 12 months.

Encouraged by this success, we tried eyestalk ablation on early juveniles and mature animals for growth trends and inducement of maturity. The results have been astounding.

Eyestalk ablation in all these four species clearly showed that:

- There is no mortality due to trauma.
- Feeding activity is not handicapped.
- Regeneration of autotomised appendages are not affected.

Bilateral eyestalk ablation accelerated moulting frequency and substantial weight gain, irrespective of the size or reproductive status of the animal, in all the four species tried.

Juveniles

Juveniles of *P. homarus* have been grown from about 85 g to 432 g in 23 weeks by bilateral eyestalk ablation while the controls showed an increase of hardly 57 g during this period (Fig. 1). Still more remarkable is the case of *P. ornatus* where an animal ablated at 132 g reached 1613 g in 33 weeks, while the unablated control gained only 161 g (Fig. 2). Further, two *P. ornatus* with a mean weight of 1513 g when ablated attained 2725 g total weight in 21 weeks — an increment of 1212 g as against 51 g in the controls.

Weight increase was in "quantum jumps" in lobsters and as such the effect of eyestalk ablation in relation to weight gain was more in mature lobsters. As high as 165 g increase in a single moult — 5th moult after ablation with intermoult period of 37 days — was recorded in a 300 g *P. homarus*. In mature *P. ornatus*, a weight increase of over 400 g per moult in about 40 days has been recorded.

Group culture experiments

P. homarus

1 In an experiment involving 14 early juvenile *P. homarus* (mean weight 20.4 g) the average growth increment in ablated lobsters was 111.6 g in 15 weeks, the corresponding growth control being 37.5 g. The ablated lobsters moulted five times during this period and the control only three times.

2 In repetitive trials of 13 weeks with *P. homarus* (40-55 g) varying from 12-18 numbers, the weight increment was 135 g in ablated and only 25 g in control lobsters. While the ablated lobsters moulted four times, all the controls did not complete the third moult.

3 In mature *P. homarus* (230-297 g) varying from 4 to 6 numbers, within nine weeks the ablated lobsters moulted twice and increased their weight by 161 g while all the controls could not complete the second moult and the weight increase was as low as 22 g.

P. polyphagus

In a group of mature *P. polyphagus* (mean weight 195 g) fed with mussel meat, the mean weight increase in ablated lobsters was 348 g, whereas in the control lobsters the mean increase was only 67 g in 22 weeks. The ablated lobsters moulted five times and the control three times.

P. versicolor

In *P. versicolor* (400-500 g) in a period of 19 weeks, the ablated lobster gained an average weight of 493 g while no weight increase was noticed in the control. The ablated one moulted three times and the control only once.

P. ornatus

1 In 19 weeks a group of three eyestalk ablated *P. ornatus* moulted four times and increased their mean weight from 164 g to 715.0 g (an increase of 550.5 g) where as the weight increase in the control which moulted twice was only 65.4 g.

2 The mean weight of four ablated *P. ornatus* increased by 482.5 g (575.5-1068.0) in 12 weeks, while in the controls the weight increase was only 85.0 g. Ablated lobsters moulted three times and the control only once.

Increased consumption and conversion efficiency and lower per cent loss of converted food as exuvia were responsible for the significant weight gain in ablated lobsters. The conversion ratio was two in ablated and five in the control *P. homarus* in terms of dry weight of food to live weight of the animals. The conversion ratio is further reduced to 0.6 to 1.3 in ablated lobsters and 1.2 to 1.9 in controls when weight of exuvia, which is part of the converted food, is included in the calculation.

In ablated lobsters only an average of 45.2 per cent of the converted food was lost as exuvia, while in the controls this loss was 64 per cent. This should be of interest to the prospective lobster culturist, since a major portion of the food supplied to ablated lobsters is converted into edible meat.

Food

We have also noted that when food supply is restricted to the extent of half the *ad libitum* quantity, the ablated *P. homarus* could double the conversion efficiency to catch up with the high metabolic rate. Here again, the weight increase was four to five times that of the controls which were fed *ad libitum*. However, with restriction in feed, a cannibalistic tendency appeared in ablated lobsters.

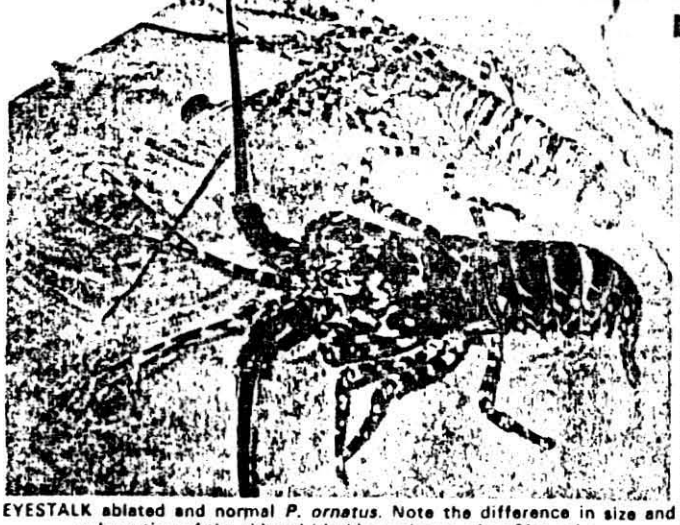
Food plays a major role in maintaining the coloration of spiny lobsters. Ablated lobsters fed on mussels retained the natural colour or the coloration was more intense, while those fed on clam and trash fish became pale and even albinos. Normal lobsters also become slightly paler in captivity.

Ablated lobsters feed at any time of the day, unlike the normal ones which generally feed during night. This feeding behaviour will be advantageous in a culture system. Further, ablated lobsters do not require shelters, thereby reducing the operational cost.

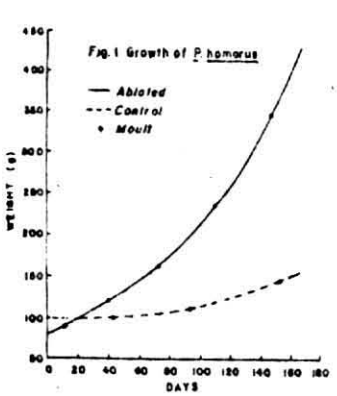
In addition to enhancing moulting frequency and weight gain, eyestalk ablation resulted in accelerated gonad development in *P. homarus*. Ablated lobsters could mate and oviposit viable eggs.

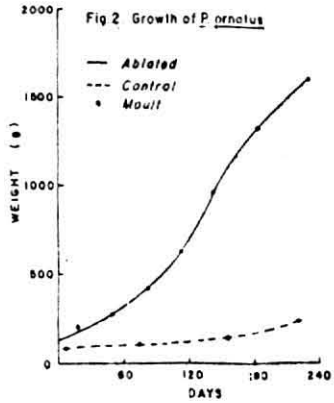
Hormones

The neurosecretory cells of the X organ-sinus gland complex in the eyestalk of crustaceans are known to produce hormones that regulate various physiological processes such as moulting, osmoregulation, metabolism and growth. Failure to induce accelerated moulting in eyestalk ablated American spiny lobster *P. argus* and the Australian *P. cygnus* led to the belief that eyestalks of spiny lobsters do not contain moult inhibiting hormone (MIH). However, the experiments of Quackenbush and Herrnkind (*Comp. Biochem. & Physiol.*, 69A (1981) 525-527) indicate that eyestalk ablation in *P. argus* accelerates moult cycle and



EYESTALK ablated and normal *P. ornatus*. Note the difference in size and colouration of the ablated (dark) specimen after 21 weeks.





Dr. E. G. Silas (right) with his colleagues E. V. Radhakrishnan and M. Vijayakumaran, holding an ablated "giant" *P. ornatus*. E. V. Radhakrishnan with an ablated *P. versicolor* that had added 500 g in 19 weeks.

gonad development but not weight gain.

Our study has shown that eyestalk ablation accelerates both moulting frequency and weight gain in all the four species tried so far, indicating the presence of MIH in the eyestalk of palinurids.

Certain outgrowths resembling antennules develop in place of the eye in ablated lobsters. Whether these outgrowths are sensory in nature and have any adaptive significance is not yet well understood.

CENTRES

Consumption is mainly of lobster tails and to prospective farmers tail weight of the lobster is important. The tail weight is about 33 per cent of the total weight in normal *P. homarus* of all sizes while it is around 30.5 per cent in ablated ones. But this slight reduction in per cent tail weight in ablated lobsters is not considered significant since the total weight increase is enormously high in them compared to the controls.

In the diversified fishing programmes in the artisanal sector at many centres in India, undersized (50-150 g) lobsters are caught in sizeable numbers which do not fetch a market price. Until the hatchery programme can be developed to breed and obtain puerulus stage, we may have to depend on rearing of baby lobsters to marketable size, if spiny lobster culture is to be taken up.

Early juveniles of more than one species may be caught which could be utilised for culture. Group rearing with proper feed schedules has shown that *P. homarus*, *P. polyphagus* and *P. ornatus* could be cultured together. The problem would be the chance production of inter-specific hybrids.

It is also possible that the lobsters of different sizes can be cultured together and the commercial size harvested whenever the demand is more and maximum price for unit weight can be obtained.

by E. G. Silas, E. V. Radhakrishnan and M. Vijayakumaran, Central Marine Fisheries Research Institute, Cochin.

Ranching might preserve turtles...

SCIENTISTS at the Central Marine Fisheries Research Institute (CMFRI) have successfully hatched eggs collected from nests made by female turtles in laboratories. Over the past three years more than 40,000 emerging hatchlings have been released by CMFRI into the sea. According to Dr. E. G. Silas, Director of the Institute, a programme for tagging turtles to determine their migratory, feeding and breeding habits is also in progress.

The project aims at enabling the Indian government to evolve a suitable policy for the conservation and management of sea turtles, already considered endangered as a species and included in the first schedule of the Indian Wildlife Protection Act. None of the five identified species are endemic and may undertake long migratory routes to feeding and breeding grounds.

Dr. Silas hopes that before long the Institute's researchers will be able to discover the reasons for the long sojourn of young turtles, their feeding and breeding habits and return to the nesting beaches. This would help formulate a programme of proper conservation and management of sea turtles.

While mariculture may not be economically viable because of the complicated life habits of sea turtles and lack of knowledge about vital aspects of their biology, husbandry may be a possible alternative. But this would be in the future when scientists are able to manipulate and control the environment, nutritional requirements, growth, reproduction and nesting cycles.

"We feel the option for us is stepping up recovery programmes to sea-ranching ones when methodologies and experience are gained in the proper incubation and release of hatchlings," said Dr. Silas.

Conservation methods like protecting nesting beaches from human interference and non-human predators, managing inshore ecosystems aimed at a higher rate of survival, and better recruitment of juveniles and adults should greatly enhance such programmes. Therefore, in the immediate future, ranching has a greater potential than mariculture of turtles.

Of the five Indian species, the Olive Ridley stands out as far as numbers are concerned, though commercial products obtained from it may not be of the quality obtainable from the green turtle or hawksbill.

Between 300,000 and 400,000 sea turtles nest on the beaches in the east coast state of Orissa in January-February. On an average, they lay about 30 million eggs in these months in clutches of 100 each. Allowing for predation by non-humans, destruction of earlier nests by subsequent nesting turtles and hatchling predation on beaches, only 25 per cent of the young survive to the point of moving into the sea.

Assuming one per cent of the hatchlings reach adulthood, at first maturity, which normally takes seven years, this would amount to 75,000 adult turtles in Orissa. If the annual estimate of recruitment is of this order, with females at 70 per cent, and with no animal remigration, saturation point is likely to be reached on the Orissa beaches.

Chinese raise output

DRAWING on their own and foreign experience, Chinese fish farmers have been introducing new technology which has increased production up to 20 times that from conventional ponds. Much of the development work was done by Wu Zhida, an engineer in Changzhou City.

Most of the hundreds of thousands of tons of carp and other fish farmed in China is raised in traditional earthen ponds. The new methods include use of pumps to circulate the water and thus increase oxygen content, scientific feeding.

Test in Taige township over five years yielded 10 to 12.5 tons of grass carp and bream from a one-tenth hectare pond. Results are reported to have been even better in Guizhou province where the weather is warmer.

The methods are said to save 80 per cent of the area and 60 per cent of the investment needed for the same production from traditional ponds. Further funds have been set aside in Guizhou for 12 more high-yielding ponds.

GROWTH OF THE SPINY LOBSTER *PANULIRUS POLYPHAGUS* (HERBST) REARED IN THE LABORATORY

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GROWTH OF THE SPINY LOBSTER *PANULIRUS POLYPHAGUS* (HERBST) REARED IN THE LABORATORY

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ABSTRACT

Growth of *Panulirus polyphagus* from the puerulus stage was studied in the laboratory for twenty eight months on a diet of *Meretrix casta* and *Perna viridis*. The lobsters were kept either in isolation or in groups of three per tank at laboratory temperature ranging between 21.4° and 29.5°C. The survival was higher (70%) in those reared in groups, however, the growth rate was not depressed in individuals held in isolation.

Carapace length positively correlated with total weight in both sexes of the tested individuals. In captivity the male grew faster than the female. For male the increase in carapace length on an average was 3.3 mm for each moult while it was only 2.6 mm for the female. But there was slight difference in intermoult duration between the sexes. The annual growth rate was 34 mm in carapace length for male and 28 mm for female during the first year and 20 mm for male and 20.5 mm for female during the second year. The female attained maturity at an average carapace length of 48 mm. Temperature affected growth ; the intermoult duration was prolonged at low water temperature.

INTRODUCTION

PALINURID LOBSTERS which is a highly priced commodity, forms a meagre fishery in India (CMFRI, 1979). But the occurrence of puerulii has been reported periodically in both east and west coasts of India (Rao and Kathirvel, 1971 ; Girijavallabhan and Devarajan (1972) ; Dutt and Ravindranath, 1975). Tholasilingam (1976) reported abundance of three different species of puerulii off Kovalam. It is possible to culture lobsters from the puerulii available in nature to adult sizes. Chittleborough (1974) and Phillips *et al.* (1977) reared a group of *Panulirus longipes cygnus* from puerulus to adult under subtropical conditions. Fielder (1964) studied the moulting and growth in temperate lobster *Jasus lalandei*. In India, Deshmukh (1966) studied the early metamorphosis of *Panulirus polyphagus*. Thomas (1972) reported the growth of *Panulirus homarus* in captivity and Kathirvel (1973) observed regeneration of a lost antenna with depressed growth in *P. polyphagus*. However, little is known on the growth pattern of tropical palinurid lobsters. The growth of the commercially important palinurid lobster *P. polyphagus* from puerulus to adult stage is reported for the first time in India.

The authors are grateful to Dr. E. G. Silas, Director, Central Marine Fisheries Research Institute for encouragement and Shri T. Tholasilingam for providing facilities and guidance. They are also thankful to Dr. E. Vivekanandan for helping in the preparation of the manuscript. Thanks are also due to the staff of Kovalam Field Centre of CMFRI for their help in carrying out the work.

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Material and Methods

In early May 1977, fifteen puerulus larvae of the spiny lobster *Panulirus polyphagus* measuring an average of 8.5 mm in carapace length were collected off Kovalam from Mangalore tiles suspended from a floating raft. They were brought to the field laboratory at Kovalam and acclimatized in three plastic tanks with a floor area of 0.16 sq.m. Five puerulii were held in each tank and were fed *ad libitum* on flesh of freshly opened clams *Meretrix casta* collected daily from Kovalam backwaters and green mussel *Perna viridis*. The lobsters seem to prefer mussel to clams. During the first nine months only monthly increase in carapace length and weight of lobsters were recorded.

After nine months, nine healthy individuals were selected and divided into two series. The first series consisted of six animals divided into two groups of three juveniles each and the second series with three animals placed in individual aquarium. Each fibreglass aquarium holding the animals had a floor area of 50×45 cm with 250 litres of filtered sea water. The animals were provided with hollow tiles for shelter.

The water in the aquarium was replaced twice a week by fresh filtered sea water. Salinity of the water in the aquarium varied from 32.5‰ to 36.2‰ and that of temperature from 21.4°-29.5°C. The water was aerated continuously. The aquarium tanks received 16 hr illumination.

The juvenile lobsters were fed on *Meretrix casta*. Food was supplied daily at dusk and the uneaten food was removed on the following morning. Preliminary observations revealed that the animals did not feed during day time. The tanks were cleaned once a week with least disturbance to the lobsters.

Growth measurements of individual lobsters were taken five days after each moult when the exoskeleton had sufficiently hardened. The size was recorded by measuring the carapace length (CL) to 0.1 mm accuracy along the mid-dorsal line from the ridge behind the eyes (between the rostral horns) to the posterior margin of the carapace. This was used as the standard length (Berry, 1971) in the present study. Live bodyweight of the animals was measured after removing free water as described by Chittleborough (1975).

In crustaceans increase in length and weight occur at and just following moulting. So the two interacting components involved in the growth processes are (*a*) moult increment (increase in size per moult), (*b*) intermoult duration (duration of the intermoult period). Here growth is mainly referred to as increase in carapace length and weight and growth rate as growth with time.

Results and Discussion

Growth of male and female P. polyphagus

When collected from the sea, the transparent puerulus larvae of *P. polyphagus* had a mean carapace length of 8.5 mm and weighed an average of 260 mg. The larvae did not feed till they completed the first moult. Within 2-4 days of their capture, about 80% of the larvae moulted to the post-larval phase.

As only the monthly averages of carapace length and weight were recorded during the first nine months of growth, the intermoult duration and moult increment for the period could not be studied. Fig. 1 presents the growth of male and female lobsters reared in groups for a period of 840 days from the time of capture. The males exhibited faster growth rate than the females resulting in larger size in unit time. The estimated average annual increment in carapace length was 34 mm in males and 28 mm in females during the first year and 20 mm and 20.5 mm in carapace

length for males and females respectively in the second year. The differential growth between sexes has been reported by earlier workers for both wild and laboratory reared palinurid lobsters. Mohammed and George (1968) observed higher growth rate in males than in females of *P. homarus* from mark-recovery studies. Thomas (1972) also estimated an average annual increase in carapace length of 30 mm in males and 17 mm in females of *P. homarus*. But Chittleborough (1974) and Phillips *et al.* (1977) found no difference in the growth rate of males and females of *P. longipes cygnus*. It is interesting to note from Fig. 1 that the growth curve of the female

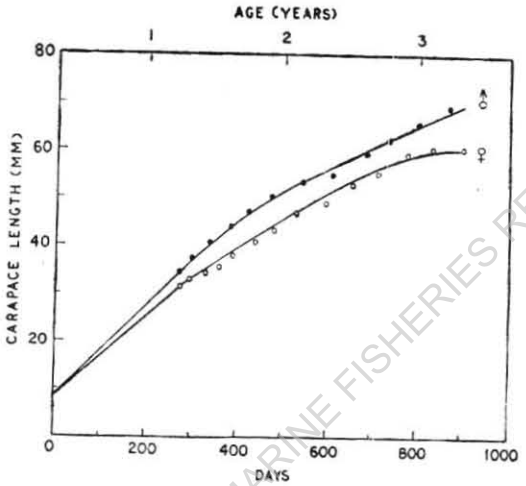

Fig. 1. *Panulirus polyphagus:* Mean increase in carapace length (mm) of males and females reared in groups during 840 days ; each point represents the average of about 3 individuals.

tapers off at about 42 mm CL, whereas it is not the case with males. This is apparently due to deceleration of growth rate in females which becomes evident at the time of attainment of sexual maturity (Berry, 1971). The females of *P. polyphagus* attained sexual maturity at an average carapace length of 48 mm when the lobsters were 2.2 years old. Philipps *et al.* (1977) estimated the age of *P. longipes cygnus* as 2.3 years old when the lobsters reached 40-42 mm CL. The difference in age between *P. polyphagus* and *P. longipes cygnus* was not due to the faster growth rate of *P. polyphagus*, but the estimated difference in age of settling puerulus larvae. Chittleborough and Thomas (1969) reported the age of newly settled puerulus larvae of *P. longipes cygnus* as 0.8 years whereas the age of puerulus of *P. polyphagus* was estimated as 0.4 years using the same method. The CL of female *P. polyphagus* in the present study reach asymptotic level when it was three years old during which period the male was still in its upward growth phase (Fig. 1). The differential growth rate may have some far reaching implications as it has been shown that the preponderance of one sex in the population is because of the sexual difference in growth (Qasim, 1966).

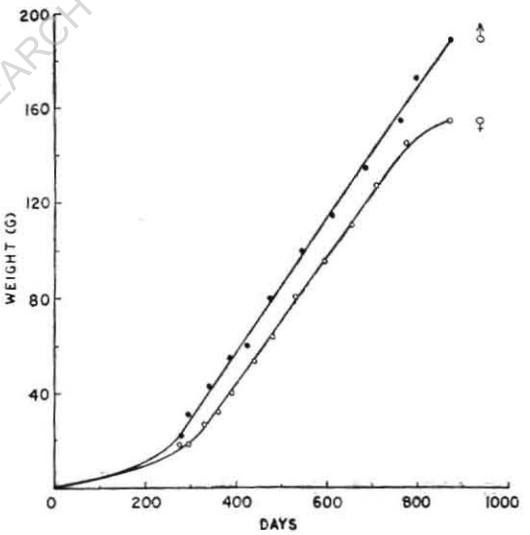

Fig. 2. *Panulirus polyphagus :* Mean increase in weight (g) of males and females reared in groups ; each point represents the average of about 3 individuals.

The estimated average annual increase in weight was 47.24 g in males and 33.74 g in females during first year and 117.76 g in males and 111.26 g in females for the second year (Fig. 2). The percentage increase in weight of *P. polyphagus* at moults ranged from 8.8 to 44%. The percentage increase in weight at

a moult decreased with increasing size of the lobsters. Travis (1954) and Fielder (1964) made similar observations for *P. argus* and *J. lalandei* respectively.

Fig. 3 shows the length-weight relationship in males and females. Weight is a function of length and is expressed by the equation $W = CL^n$, where W is the weight, L is the carapace length and C and n are constants. The mean CL and weight of the experimental males and females plotted graphically resulted in an exponential curve. The regression of log bodyweight (W in gram) on log carapace length was

Male $\log W = 3.14 \log L - 3.45$

Female $\log W = 3.71 \log L - 4.3$

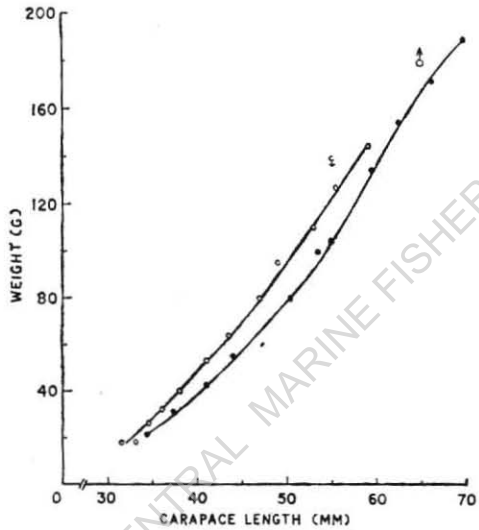

Fig. 3. *Panulirus polyphagus :* Relationship between carapace length (mm) and weight (g) of males and females; each point represents the average of about 3 individuals.

To understand the growth processes in lobsters, intermoult duration and moult increment were studied. The intermoult duration increased with age in both sexes (Fig. 4 a) and in males it was slightly longer than in females (52 and 45.5 days respectively). Though the females moulted 12 times and the males only 11 times in 800 days, females could attain only 60 mm CL, whereas the males attained 65 mm during the same period. Hence, the lobsters were not able to exhibit faster growth by shortening the intermoult duration. The increase in carapace length at moult (moult increment) was plotted against the number of moults (Fig. 4 b). Eventhough there was considerable variations in moult increment among individuals, as also noticed by Phillips *et al.* (1977), the mean moult increment in CL was higher for males (3.3 mm) than for females (2.6 mm). There was a gradual increase in the moult increment at successive moults in females for the first four moults, which thereafter fluctuated considerably. In males the moult increment in CL did not fluctuate much during successive moults ; but the increment was clearly higher than the female except in the VI moult (Fig. 4 b). Hence the larger size acquired by the male at unit time was due to a higher moult increment in carapace length than shortened intermoult duration. The differential growth rate may also be due to deceleration of growth rate in females after attainment of sexual maturity resulting in an increasing divergence of the growth curves of males and females with increase in size (Berry, 1971). Morgan (1977) also found that in wild adult *P. longipes cygnus*, moult increment depressed with increasing size with adult males having a higher moult increment than females of the same size. Chittleborough (1976) observed that moult increment of males of the same species increased from ages 3+ to 5+ years, while those of the females did not very significantly between these age groups, and the moult increment of females was significantly below that of males.

The effect of temperature on frequency of moulting in palinurid lobsters has been studied in detail by earlier workers (Travis, 1954 ; Serfling and Ford, 1975 ; Phillips *et al.*, 1977). The prolonged intermoult duration in lobsters

reared in groups in this experiment coincided with the fall in water temperature (Fig. 4 a, 4 c).

juveniles (upto an average of 30 mm CL) of *P. polyphagus* were observed to be gregarious and preferred to hide under shelter during day

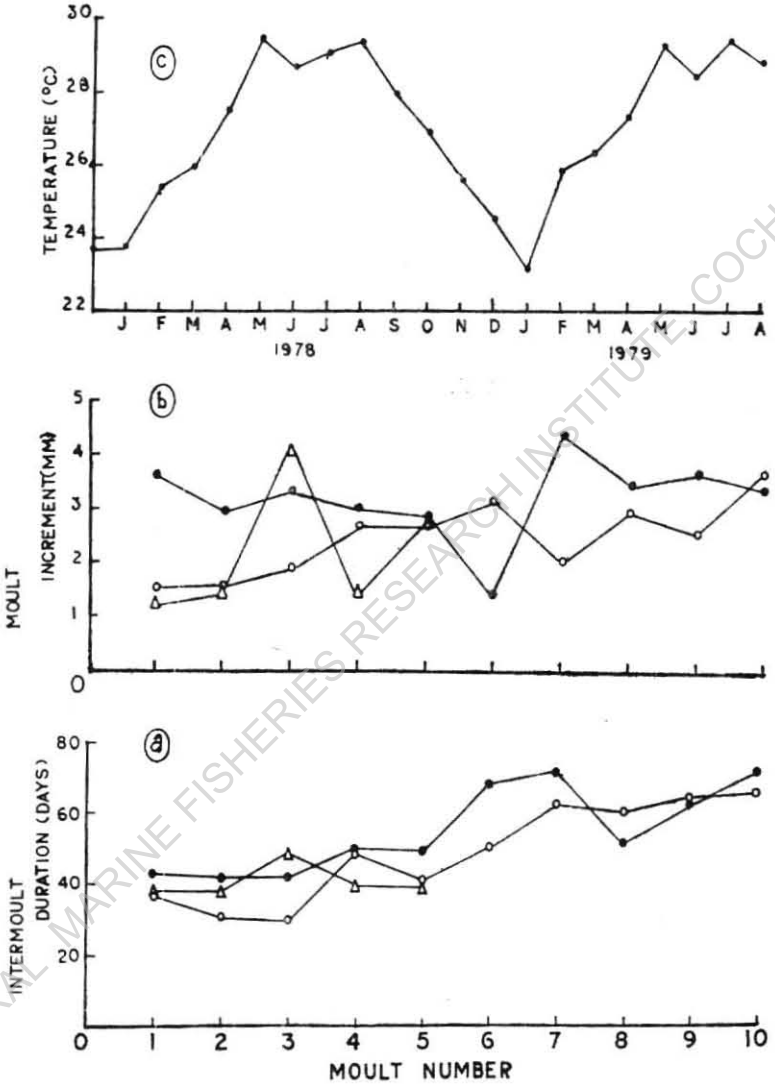

Fig. 4. *Panulirus polyphagus* : a. Mean intermoult duration against number of moults of male (●) and female (○) reared in groups of three. (△) represents the mean intermoult duration of three isolated individuals ; b. Mean moult increment in carapace length against number of moults of male (●) and female (○) reared in groups of three. (△) represents the mean moult increment in CL of isolated individuals and c. Monthly mean water temperature in the laboratory during 1978 and 1979.

Effect of social pressure on growth

Social pressures influence moulting and growth in crustaceans as this is presumably a reflection of their gregarious or solitary behaviour in nature (Aiken, 1977). The early

time. The isolated individuals confined to the shelter during the commencement of the experiment ; later they were foraging the bottom of the aquarium as they were acclimatized. *P. polyphagus* did not show significant

difference in growth rate when reared in isolation or in groups (Fig. 5). The intermoult duration (Fig. 4 a) and moult increment (Fig. 4 b) were almost similar in both the series, but the isolated individuals did not survive beyond the sixth moult (*i.e.* after 525 days). Phillips *et al.* (1977) also found no significant difference in the growth of isolated and grouped individuals of *P. longipes cygnus* until they were 3 years old and Chittleborough (1975) reported depressed growth rate in isolation for the same species which were more than 3 years old.

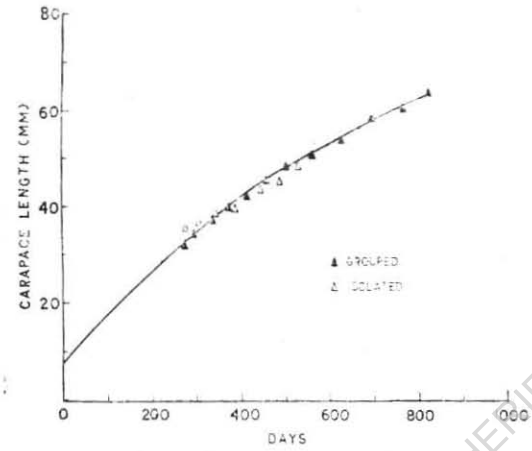

Fig. 5. *Panuliurs polyphagus :* Mean increase in carapace length (mm) of grouped (▲) and isolated (△) individuals ; each point of grouped series represents the average of about 6 individuals and that of isolated series 3 individuals.

Feeding behaviour during moulting

The animals stopped feeding 2-3 days before ecdysis ; moulting took place mostly during night. The moulting pattern was similar to other palinurid lobsters (Travis, 1954). After moulting the animals were inactive and were hiding under shelter. Feeding commenced 2-3 days after ecdysis. The peak consumption of food was 5-6 days after moulting, which gradually reduced as the next moult was nearing.

Mortality

Mortality in the aquarium was about 30% in those reared in groups during the experimental period of 840 days whereas all the animals in isolation died within 525 days. The mortality was mainly during moulting when the carapace or walking legs were entangled in the old exoskeleton and the animals were unable to free themselves. Moulting abnormalities were also noticed in early juveniles. The antennae and the head folded back interfering with the normal feeding of the animals. The lobsters below 25 cm CL autotomised limbs on handling, but it is uncommon in larger numbers of the species.

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OBSERVATIONS ON THE FEEDING AND MOULTING OF LABORATORY REARED PHYLLOSOMA LARVAE OF THE SPINY LOBSTER *PANULIRUS HOMARUS* (LINNAEUS) UNDER DIFFERENT LIGHT REGIMES

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ABSTRACT

Phyllosoma larvae of the spiny lobster *Panulirus homarus* hatched under laboratory conditions were fed on 1-2 day old *Artemia salina* nauplii. The feeding intensity and moulting frequency of the larvae were studied. When fed with one day old *Artemia* nauplii, the phyllosoma larvae consumed at an average rate of 15.1 ± 0.94 nauplii/day and moulted five times in 31.2 days to reach the IV phyllosoma stage. But those fed with two day old nauplii consumed 19.3 ± 1.6 nauplii/day and required 34 days to complete the fifth moult under similar environmental conditions.

Studies on the effect of light on the feeding and moulting of phyllosoma larvae indicated that consumption of *Artemia* nauplii was significantly higher in natural day-light periodicity, (15.1 ± 0.94 nauplii/day) than in 24 hr darkness (11.1 ± 0.57 nauplii/day) and 24 hr light (12.2 ± 0.45 nauplii/day). The reduced food consumption in the groups exposed to 24 hr dark and 24 hr light was reflected in the moulting frequency also. The phyllosoma completed the fifth moult in 31.2 days under natural day-light periodicity, while it required 37 days under 24 hr darkness and 35.5 days under 24 hr light.

INTRODUCTION

PHYLLOSOMA LARVAE of *Panulirus homarus* are positively phototactic and swim towards natural and artificial sources of light. Segal (1970) summarised the effect of varying photoperiods on marine invertebrates. But information on the effects of photoperiodism on feeding in crustacean larvae is limited (Templeman, 1936; Huntsman, 1923).

Since the phyllosoma larvae are selective feeders, nutritionally rich and suitable sized prey should be identified and supplied to ensure maximum survival and growth rates. This view has been stressed by earlier workers also (Saisho, 1966; Dexter, 1972; Wickins, 1972). Though early larval stages of *Panulirus inflatus* (Johnson and Knight, 1966) and *Panulirus longipes* (Saisho and Nakahara, 1960) were successfully fed on *Artemia* nauplii, the food consumption and growth in relation to size and nutritive aspects of the prey was not properly understood. The present study is on the effect of different photoperiods on feeding, moulting frequency and survival of phyllosoma larvae of *Panulirus homarus* and the larval feeding on two different sizes of *Artemia salina* nauplii.

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preparation of the manuscript. Thanks are also due to the staff of Kovalam Field Centre of Central Marine Fisheries Research Institute for their help in carrying out the work.

Material and Methods

An ovigerous female of *Panulirus homarus* (Linnaeus) released phyllosoma larvae in the field laboratory at Kovalam during February, 1979. The larvae were transferred to plastic tanks of 45 l capacity with fresh filtered sea water and fed freshly hatched *Artemia salina* nauplii. On the second day after hatching, the healthy larvae were divided into four series, each series having five groups of three larvae each. Two of the four series were exposed to natural day-night cycle (approximately 12 hr L : 12 hr D). Of the other two series, one was exposed to 24 hr darkness. The containers with the larvae were kept in a black wooden box and were exposed to light for 10 minutes everyday while changing the water and feeding. The fourth series of larvae were exposed to 24 hr light by using 40W flourescent lamp fixed 4 feet above the containers.

The larvae were reared in transparent plastic containers (150 ml capacity) with 100 ml of filtered (using 1μ filter) fresh seawater. The salinity of the water ranged from 32 to 34.5‰ and the temperature in rearing containers varied from 25.4 to 30.0°C with a mean of 28.1°C. The water was changed daily.

Of the two series exposed to natural day-night cycle, one was fed on freshly hatched *Artemia salina* nauplii and the other with second day *Artemia* nauplii. The groups exposed to 24 hr L and 24 hr D were fed on freshly hatched nauplii. In each container 125 nauplii were released daily at 1000 hrs after removing the unfed nauplii supplied on the previous day.

The containers were checked daily for exuviae and dead larvae, and the condition of each larva and the date of moulting was recorded. Since the length of the living larvae could not be measured accurately after each moult, the moulting frequency was considered as an index of growth. The experiment was conducted for 40 days.

Results and Discussion

The phyllosoma larvae exhibited a higher feeding activity almost alternating with a lower feeding on the subsequent day in all the tested photoperiods (Fig. 1, 2). Average daily consumption of fresh and second day *Artemia* nauplii increased with age of the larvae under natural day-night conditions. Feeding rate increased from 9 nauplii/day on the first day of the experiment to a peak of 31 nauplii on 27th day when fed with freshly hatched nauplii and the consumption increased from 8 nauplii/day to a maximum of 33 nauplii on the 15th day in larvae fed with second day nauplii (Fig. 1a, b). The consumption gradually decreased thereafter to 10 nauplii/day in the former group and 13.2 nauplii/day in the latter at the end of the experiment. The average consumption was higher in groups fed with second day *Artemia* nauplii (19.3 ± 1.16) than those fed with fresh nauplii (15.1 ± 0.94). The larvae fed with second day nauplii consumed a total of 656 nauplii to complete the fifth moult and those fed with freshly hatched nauplii consumed only 471 nauplii to complete the same number of moults. Though the consumption was higher, the phyllosoma required 34.0 days to complete the fifth moult when fed with second day nauplii, whereas, they required only 31.2 days to moult five times in the series fed with fresh nauplii (Table 1). Phyllosoma larvae fed with second day nauplii consumed 39% more food than those fed with fresh nauplii. In other words, the phyllosoma larvae increased its stomach capacity

to 1.4 times and that the larvae fed to satisfy its energy demand rather than to fill its stomach to the maximum capacity (Rozin and Meyer, 1961). Vivekanandan *et al.* (1976) also found that the freshwater murrel *Ophiocephalus striatus* consumed 33% more *Tilapia* muscle than goat liver to satisfy its energy demand as the goat liver contains 20% more energy than *Tilapia* muscle.

The size and activity of the prey also affected feeding in phyllosoma larvae. It is evident from the food consumption that the larvae preferred actively swimming large sized second day nauplii (0.85 mm) than slow moving freshly hatched nauplii (0.56 mm). Though the swimming activity of the phyllosoma larvae was not measured, visual observation showed that the second day nauplii swims faster than freshly

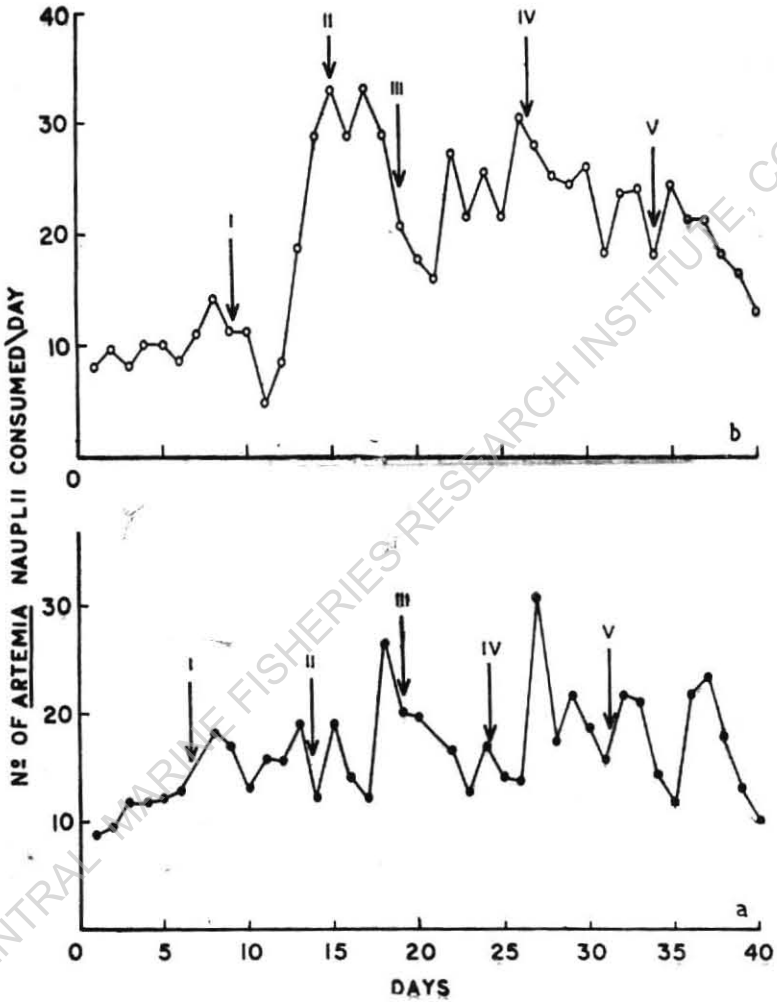

FIG. 1. Daily feeding pattern of phyllosoma larvae of *Panulirus homarus* in natural day-night periodicity : a. fed with freshly hatched *Artemia salina* nauplii and b. fed with second day *Artemia* nauplii. The arrows and numbers indicate the day of moulting and moult numbers of the larvae.

hatched nauplii. The higher energy expenditure by the phyllosoma larvae to catch the actively swimming prey resulted in delayed moulting and growth.

The effect of 24 hr darkness and light on feeding and moulting are shown in Fig. 2a and b. The daily consumption of nauplii did not fluctuate much in both the series. However, the consumption gradually reduced at the end of the experiment. The observed reduction in consumption in later stages of reared larvae of *P. homarus* can probably be attributed at least in part to either a qualitative deficiency in the diet of *Artemia* nauplii or to the inability of the phyllosoma larvae to capture sufficient quantities, or both (Robertson, 1968 ; Vijayakumaran and Radhakrishnan, 1980). The food consumption was significantly low in both 24 hr D (11.1 ± 0.57 nauplii/day ; students 't' = 6.45 ; p = <0.01 and 24 hr L (12.2 ± 0.45 nauplii/day; 't' = 4.9; p = <0.01) when compared to natural day-night periodicity (15.1 ± 0.94 nauplii/day). Those exposed to 24 hr D consumed a total of 410 nauplii to complete the fifth moult in 37.0 days and those in 24 hr L fed 435 nauplii to complete the same number of moults in 35.5 days (Table 1). It may be recalled that the larvae reared under natural day-night conditions consumed 417 nauplii and moulted five times in 31.2 days. The " continuous light "

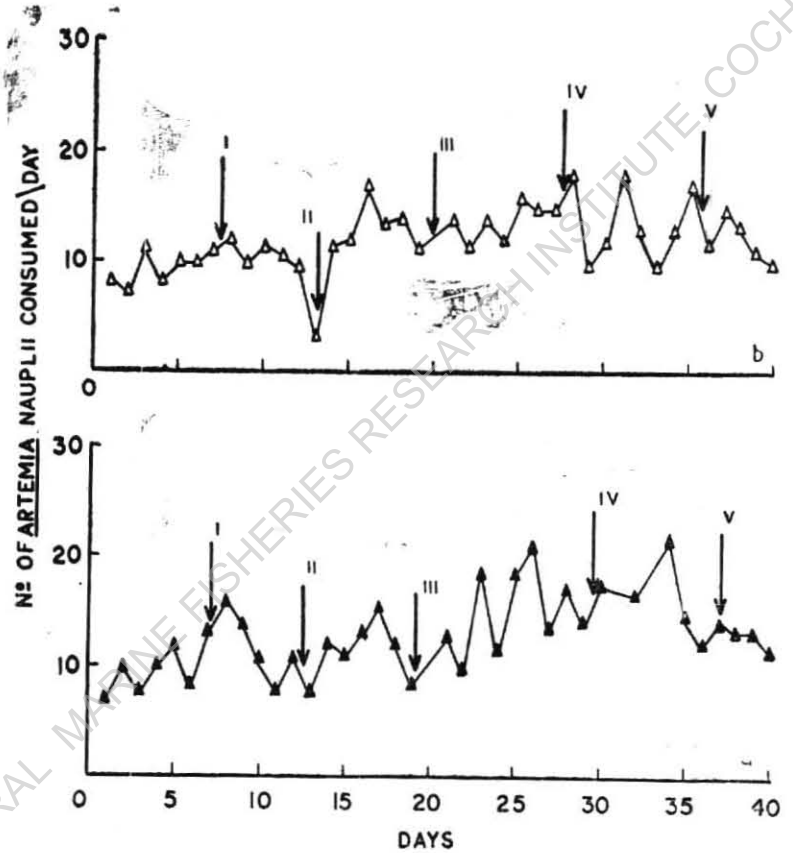

FIG. 2. Daily feeding pattern of phyllosoma larvae of *Panulirus homarus* fed with freshly hatched *Artemia salina* nauplii : a. in 24 hr. darkness and b. in 24 hr light. The arrows and numbers indicate the day of moulting and moult numbers of the larvae.

TABLE 1. *Effect of different photoperiods and size of prey on moulting frequency of phyllosoma larvae of* Panulirus homarus

	Natural Day-night Cycle I day nauplii*	Natural Day-night cycle II day nauplii*	24 hr darkness I day nauplii*	24 hr light I day nauplii*
Total days to moult 1	6.6±0.58 (6.0—7.0 days)	9.3±0.49 (9.5—10.0 days)	7.2±0.26 (7.0—7.5 days)	7.4±0.25 (7.0—7.5 days)
Total days to moult 2	13.6±1.2 (12.5—15.0 days)	15.0±0.65 (14.5—16.0 days)	12.5±0.25 (12.0—13.0 days)	13.3±0.64 (12.5—14.0 days)
Total days to moult 3	19.2±2.4 (17.5—22.0 days)	20.0±0.65 (19.5—21.0 days)	19.1±1.3 (17.5—21.0 days)	19.9±0.79 (19.9—20.5 days)
Total days to moult 4	25.1±4.2 (22.5—30.0 days)	26.7±1.2 (26.0—28.5 days)	29.4±1.8 (7.0—31.5 days)	27.6±0.63 (27.0—28.5 days)
Total days to moult 5	31.2±5.2 (27.0—37.0 days)	34.0±0.1. (33.0—35.0 days)	37.0±2.2 (34.0—39.5 days)	35.5±1.1 (34.0—36.5 days)

* Each average figure is based on about 15 individuals.

and "continuous darkness" would have affected the normal feeding activity of the phyllosoma larvae, resulting in slow growth. Chittleborough (1975) reported depressed growth in juvenile *P. longipes cygnus* under conditions of continuous darkness. Aiken and Waddy (1976) also reported increased moulting frequency and moult increment in *Homarus americanus* larvae when exposed to long photoperiods. But Bliss and Boyer (1964) observed faster growth in the crab *Gecarcinus lateralis* reared in constant darkness. From the present

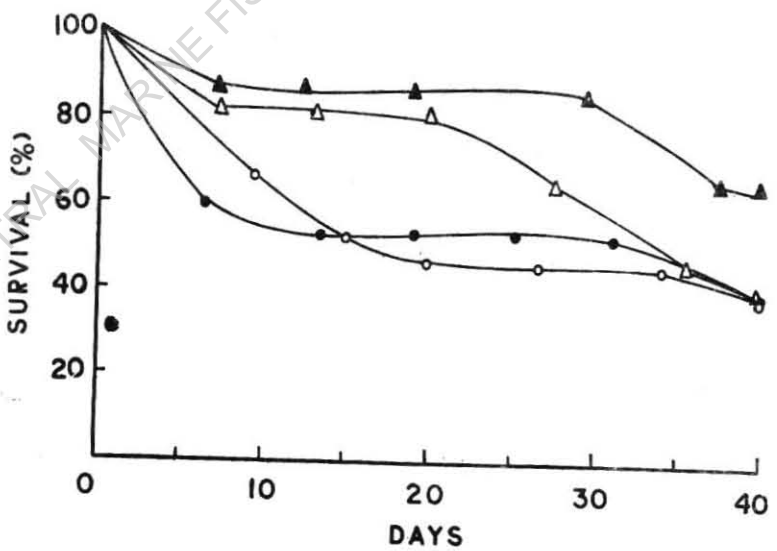

FIG. 3. Percentage survival of phyllosoma larvae of *Panulirus homarus* in natural day-night periodicity fed with freshly hatched nauplii (●), second day nauplii (O) and 24 hr darkness (▲) and 24 hr light (△) fed with freshly hatched nauplii.

study it appears that the tested photoperiods have altered the feeding rate first and in turn influenced the moulting frequency. It is clear from the observations that the moulting frequency was accelerated when the larvae consumed more nutritively rich food. Vivekanandan (1977) also concluded from his studies on *O. striatus* that environmental factors first altered feeding rate which in turn influenced metabolism and growth of fishes. The direct effect of darkness and light on growth through neuro-endocrine pathways is not known in phyllosoma larvae of *P. homarus*.

The percentage survival of phyllosoma larvae in the tested photoperiods during the experimental period is shown (Fig. 3). Though the growth rate was slow in 24 hr D, the maximum survival of the larvae (65%) was obtained in this photoperiod. The survival was low in all the other light regimes (40%). Templeman (1936) also reported higher survival rate of *H. americanus* larvae in complete darkness. At the end of the first moult of phyllosoma larvae, the lowest survival was in those reared in natural day-night periodicity fed with freshly hatched nauplii and the maximum in 24 hr D. In 24 hr L the highest mortality of larvae occurred during the fourth moult. The mortality of the larvae was caused by ciliate attack and change in feeding behaviour of the larvae. The late stage phyllosoma larvae seem to have difficulty in catching *Artemia* nauplii. A wide variety of protozoans attacked the phyllosoma larvae interfering in the swimming and feeding activity.

The positive phototactic behaviour of the phyllosoma larvae may be an advantage in feeding if an equally photopositive prey could be provided. Since long and short photoperiods does not have an accelerating effect on growth, alternating periods of light and dark and nutritionally rich food may be favourable for rearing phyllosoma larvae.

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Proc. Symp. Coastal Aquaculture, 1986, **4** : 1281-1285

EFFECTS OF FOOD DENSITY ON FEEDING AND MOULTING OF PHYLLOSOMA LARVAE OF THE SPINY LOBSTER *PANULIRUS HOMARUS* (LINNAEUS)

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ABSTRACT

Feeding response of the laboratory reared second stage phyllosoma larvae of the spiny lobster *Panulirus homarus* was studied individually on a diet of newly hatched *Artemia salina* nauplii. The density of food affected feeding and moulting under experimental conditions. With increase in density of *Artemia* nauplii from 1 to 100/60 ml, consumption also increased from an average of 0.5 to 27.8 nauplii/day. Percentage consumption increased from 50 when offered 1 nauplius/60 ml to 80 at a ration of 5 nauplii and thereafter decreased gradually to 27.8 at a density of 100 nauplii/60 ml.

Density showed positive correlation (p 0.05) with the number of nauplii consumed. The second stage phyllosoma required 30 days to complete third moult at a food density of 5 nauplii/60 ml and only 17 days at a density of 60 to 100/60 ml. Since there was no appreciable difference in moulting frequency of individuals offered more than 60 nauplii, maximum growth of phyllosoma may be obtained at a food density of 60 nauplli/60 ml.

INTRODUCTION

ESTIMATION of optimum feeding level is an important factor in controlled culture of larval stages of many fish and shellfish. Optimum rations help to prevent cannibalism by underfeeding, fouling of water by overfeeding and to avoid wastage of larval foods which are generally expensive. Studies on optimum food requirement of phyllosoma larvae of palinurid lobsters are limited (Inoe, 1965 ; Saisho, 1966) and no such study is reported for Indian lobsters.

All attempts to rear the larvae of palinurids in the laboratory from hatching to puerulus have been unsuccessful due to lack of suitable feeds to meet the changing nutritional requirements. However early larval stages are successfully fed on *Artemia* nauplii (Inoe, 1965 ; Jhonson and Knight, 1968 ; Dexter, 1972). Live or freshly killed chaetognaths, fish larvae, ctenophores and hydromedusae also proved to be excellent food sources (Mitchel, 1971). But the difficulty in obtaining sufficient numbers percludes these as food sources in lengthy laboratory studies (Dexter, 1972). Hence nauplii of *Artemia* remains as one of the best feeds for early larval stages of palinurid larvae.

The present study is intended to estimate the effects of density of *Artemia salina* nauplii on feeding and moulting frequency of phyllosoma larvae of the Indian spiny lobster *Panulirus homarus*.

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this study. We are also grateful to Dr. E. Vivekanandan, Madras Research Centre of CMFRI for help rendered in the preparation of the manuscript.

Material and Methods

Laboratory hatched phyllosoma larvae of the spiny lobster *Panulirus homarus* were fed on live *Artemia salina* nauplii from the second day after hatching. Majority of the larvae moulted into II stage after eight days. To determine optimum density of *Artemia* nauplii required as food daily, it was necessary to hold the larvae individually and culture them at a series of feeding levels. Experiments were conducted in the field laboratory of the Central Marine Fisheries Research Institute, Kovalam, Tamil Nadu, India.

Healthy II stage larvae were selected and reared individually in transparent plastic containers (capacity 125 ml) containing 60 ml of sea water. They were divided into nine groups, each containing four larvae and were fed on freshly hatched *Artemia salina* nauplii in the following rations : 1, 5, 10, 20, 40, 60, 80 and 100 per day. One of the groups was maintained without feeding to study the effect of starvation.

Artemia nauplii were counted and fed to the respective groups daily in the morning after changing water. Sea water used in the study was filtered through 1μ cartridge filters. Before changing water unfed nauplii of the previous day were removed and counted. Moulting of the larvae was recorded whenever it occurred. The moults were removed and preserved in 5% formalin.

The experiment was conducted in ambient water temperature which ranged from 25.4°C to 30°C with an average of 28.1°C. Salinity of the sea water used varied between 32‰ and 34.5‰. Larvae were kept under natural day light condition which prevailed in the laboratory. The study lasted for 37 days and at the end developmental stages attained by the larvae were recorded.

Results and Discussion

The number of nauplii consumed by the larvae increased from an average of 0.5 in the group given 1 nauplius to 27.8 in that offered 100 nauplii per day (Fig. 1), showing a positive correlation with density of food ($r = 0.959$, p 0.05). It is also evident from Fig. 1 that the larvae are capable of consuming more than 27.8 nauplii, if they are offered more than 100 nauplii per day.

Efficiency of consumption, measured as percentage of available food consumed, was greatest at lower feeding levels (Fig. 1). The reason is that at lower feeding levels the food supply was insufficient to meet the nutritional requirement of the larvae. Percentage of food consumed decreased gradually from 80 to 27.8 between daily rations of 5 and 100 nauplii. But at the lowest density of 1 nauplii/60 ml per day the percentage consumption was only 50, since the larvae became progressively weaker and were unable to catch the prey on its own effort.

Size increase over time (moulting frequency) and size increase per moult are considered as indices of growth in many crustaceans. In *Carcinus* and some other crustaceans nutrition influences size increase over time by controlling moulting frequency and not size increase per moult (Aiken, 1977). In his study size increase per moult could not be measured as it would result in harming the larvae. Preserved moults also could not be measured accurately and hence moulting frequency is considered as growth.

Under starvation and at the lowest ration of 1 nauplius per day the larvae did not moult at all and survived only for 14 and 17 days

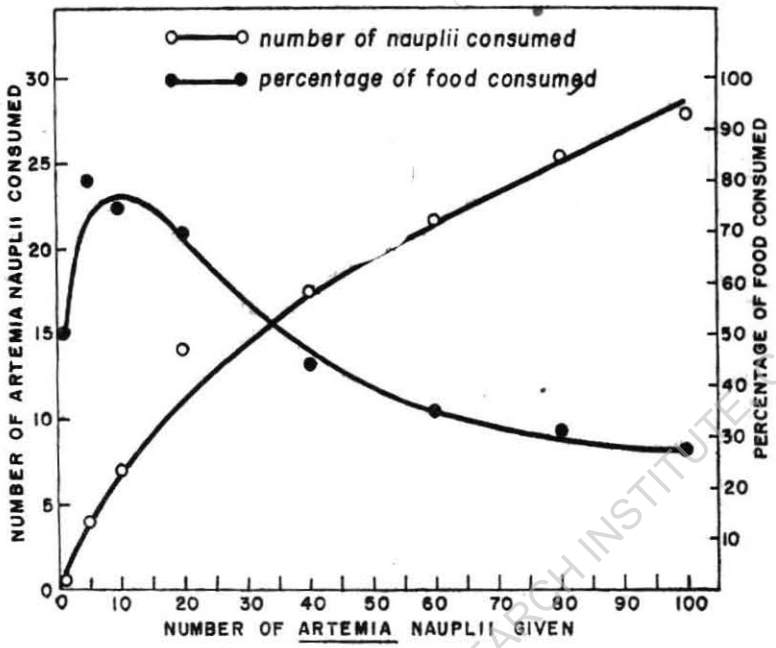

FIG. 1. Number of *Artemia salina* nauplii consumed and percentage consumption in relation to density of nauplii by the phyllosoma larvae of *Panulirus homarus*.

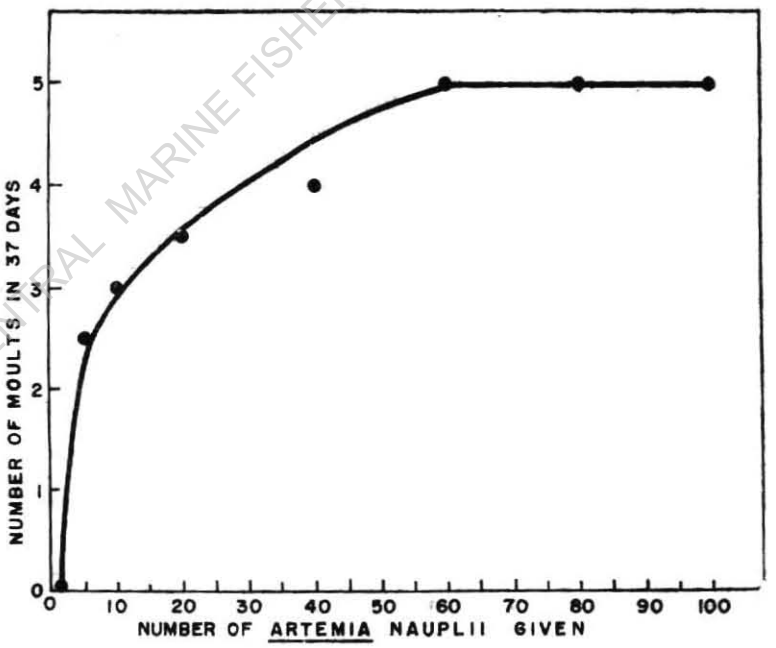

FIG. 2. Moulting frequency of phyllosoma larvae of *Panulirus homarus* in relation to density of food (*Artemia salina* nauplii).

respectively. Starvation and shortage of food resulting in reduced moulting frequency was reported in larvae of the American lobster *Homarus americanus* also by Carlberg and Van Olst (1976). Moulting frequency in *P. homarus* larvae increased from an average of 2.5 when 5 *Artemia* nauplii were offered daily to 5 at a ration of 60 nauplii (Fig. 2) indicating that food availability influences moulting frequency. The same phenomenon has been observed in the phyllosoma larvae of *Panulirus japonicus* by Saisho (1966). He was able to shorten the intermoult period of the first three stages of the phyllosoma of *P. japonicus* by increasing brine shrimp nauplii from 3-5 to 30-40 per ml. Increase in food density from 60 nauplii to 100 eventhough resulted in more consumption did not increase moulting frequency in *P. homarus* larvae. Maximum consumption, therefore, does not indicate maximum growth in phyllosoma larvae of *P. homarus*.

Inoe (1965) suggested that the phyllosoma larvae of *P. japonicus* can be cultured by maintaining 4 brine shrimp nauplii per ml of water, but size of the food should be altered with stage of phyllosoma. Our study indicates that a density of 1 freshly hatched *Artemia salina* nauplius per ml of water is optimum for culturing phyllosoma larvae of *P. homarus* individually since maximum moulting frequency could be attained at a ration of 60 nauplii/60ml of water per day in our experiment. Under this ration the larvae consumed at an average 21.6 nauplii per day. By offering 1.25 freshly hatched *Artemia salina* nauplii per ml to phyllosoma larvae cultured in groups of three, Radhakrishnan and Vijayakumaran (1986) obtained growth rates comparable to the maximum reported here. In their study the larvae consumed only 15.1 ± 0.94 nauplii per day to give this growth rate, indicating that when cultured in groups the larvae consume less and give maximum growth rate.

Total number of moults, the number of days required for each moult and the developmental stage attained by the larvae at the end of the experiment are presented in Table 1. With increase in ration from 5 to 60 nauplii per day

TABLE 1. *Total number of moults, number of days required for each moult and the developmental stage attained after 37 days by II stage phyllosoma larvae* Panulirus homarus *under varying ration of* Artemia salina *nauplii (The larvae took 8 days to reach II stage after one moult)*

Moult	Number of days taken under different ration of nauplii								
	0/day	1/day	5/day	10/day	20/day	40/day	60/day	80/day	100/day
I	—	—	8.5	7	7	6	6	6	6.5
II	—	—	13.5	8	5.5	7	5	5	5.5
III	—	—	8	15	8.5	5	6	6	6
IV	—	—	—	—	12	10	9	8	8.5
V	—	—	—	—	—	—	7	8	7.5
Stage attained after 37 days, by the larvae	Died after 14 days	Died after 17 days	IIIc	IIIc	III c & IV a	IV b	V a	V a	V a

intermoult period decreased from 8.5 to 6 days between the first and second moults; from 13.5 to 5 days between the second and third moults; from 15 to 6 days between third and fourth moults and from 12 to 8 days between fourth and fifth moults. The reduction in intermoult period with increase in density of food suggests that moulting is controlled by the nutritional status of the larvae. Individuals receiving lower rations were only in III c stage or in IV a stage at the end of the experiment (37th day), whereas those receiving higher rations reached V a stage (Table 1). It is observed that at food densities of more than 40 nauplii/60 ml III stage larvae reached IV stage after only two moults, skipping an intermediary moult. At densities lower to this, the larvae required three moults from III to IV stage. Density of food therefore is correlated with speedy development by skipping some of the stages. This finding is supported by the observations of other workers also. Carlberg and Van Olst (1976) opined that in palinurids increased number of larval stages can result from lack of food essential for growth. Robertson (1968) is of the view that other things being equal a well fed larva will be further advanced in the next stage than a poorly fed one.

The study was concluded after 37 days since larvae started dying. Slight reduction in feeding was observed towards the end of the experiment. Many workers (Robertson, 1968; Dexter, 1972) have attributed the reduction in feeding in late larval stages of palinurids to changing nutritional requirements of the larvae. Rearing of palinurid larvae can be carried out with success only if we are able to find out suitable feeds for different larval stages.

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ABSTRACTS

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WATER UPTAKE AT ECDYSIS AND VARIATION OF WATER CONTENT IN HAEMOLYMPH AND TISSUES IN THE MOULT CYCLE OF THE SPINY LOBSTER, PANULIRUS HOMARUS (LINNAEUS)

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Water uptake at ecdysis in the spiny lobster Panulirus homarus has been studied by following the weight of lobsters at periodic intervals. Lobsters undergoing ecdysis ingested an average 19.5% water and an additional 9.1% within the first three hours after ecdysis. Water content in the haemolymph is minimum at D_1 stage and increased dramatically soon after moulting (Stage A). Then it declined steadily till D_1 stage. The amount of water is highest in B stage and lowest in D_0 stage in muscle and gonad. In hepatopancreas the water content shows little variation in the late premoult and early postmoult (D_3 - A) but increases steadily through B stage and reaches maximum in C_1 stage. Hormonal control of water balance in P. homarus is also discussed.

HORMONAL CONTROL OF GROWTH AND REPRODUCTION IN THE SPINY LOBSTER., PANULIRUS ORNATUS (FABRICIUS)

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Effect of bilateral eyestalk ablation on moulting, weight gain and gonadal maturity is described in three size groups of the spiny lobster Panulirus ornatus. Eyestalk ablated lobsters moulted frequently and attained more than ten-fold increase in weight when compared to normal ones. Ablated lobsters gained a mean increase in weight of 45.2% at each moult whereas the normallobsters attained only an average of 13.1% per moult. Inter moult period increased with size in both ablated and control lobsters. Faster growth in ablated lobsters is obtained through accelerated moulting frequency and phenomenal weight increase at each moult.

Eyestalk ablation accelerated gonadal development in maturing and mature individuals. Ablated lobsters mated and ovipcsited like normal ones. P. ornatus as in P. homarus showed stronger moulting tendency than reproduction when ablated. The increased moulting frequency and gonadal maturity indicates probably the presence of Moult Inhibiting (MIH) and Gonad

Inhibiting (GIH). Hormones in the eyestalk of Panulirus ornatus. The interrelationship of MIH and GIH and their role in controlling growth and reproduction is discussed. The weight gain in ablated P. ornatus and P. homarus is compared and the prospects of aquaculture outlined.

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ABSTRACTS

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70. POTENTIAL OF SPINY LOBSTER CULTURE — AN ASSESSMENT

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Fluctuating catches and increasing demand in both internal and international markets for lobster tails necessitate augmentation of production through proper management strategies and possible aquaculture practices. The technical feasibility of economically viable aquaculture of a few species of spiny lobsters is under investigation at the Field Laboratory, Kovalam, Madras. Since production of postlarval lobsters through captive breeding and rearing under controlled conditions is not possible, any serious attempt to cultivate spiny lobsters should begin with rearing the juveniles which are caught in large numbers along with the commercial size lobsters.

It has been shown that commercial size (200 g) lobsters can be grown in less than half the time that is required in nature by proper feeding schedules and environmental management. A further reduction in this growing period has been achieved by inducing accelerated growth by eyestalk ablation. Enhancement of growth in ablated lobsters up to twenty times the normal rate indicates possibilities of rearing lobsters in shorter duration. The present status and the problems which need further attention for developing commercially feasible lobster culture are discussed based on these investigations.
