REPRODUCTION IN CAPTIVITY AND GROWTH OF Penaeus monodon, FABRICIUS IN POLYNESIA

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ABSTRACT

To develop shrimp farming in French Polynesia where no indigenous commercial species of penaeid prawn exists, the first step is to select the right species according to the following criteria: maturation and spawning in captivity, mass production of post-larvae, fast growth at semi-intensive density, acceptability of artificial diet, disease resistance and hardiness.

This paper presents the results on P. monodon, Fabricius, the largest Indo-Pacific species. Experiments have been conducted in the "Centre Océanologique du Pacifique" in Tahiti Island where the environmental conditions are: water temperature range 25-29 C, salinity 35 ppt, pH 8.2.

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Beginning with 9 females and 4 males from Fiji and New-Caledonia, kept in sand bottom 12 m^3 tanks, F1 generation was obtained in November 1975 and F2 generation in August 1976. Maturation is induced after one eye ablation by pinching the eyestalk. From May to July, 6 females from 45 to 130 g gave 18 spawnings which totalized 3.3 x 10^6 eggs, thus proving it is possible to sustain a commercial operation from captive reared animals. Mass mortalities which occurred during the larval rearing are now under control by use of antifungicides and antibiotics.

Protein and energy requirements were studied by means of purified and artificial diets. It has been found that a 40% protein content and 3.3 kcal/g diet gives the best growth performance. An artificial dry pellet has been developed and 25 g mean weight animals have been harvested after 7 months in earth rearing ponds at a density of 10 ind/m^2.

Among 6 penaeid species under experiment in Tahiti, P. monodon is the most promising for the South Pacific tropical area.

INTRODUCTION

Due to the high temperature which allows full production year round, the tropical area seems to be highly propitious for development of penaeid shrimp farming. Recent results in this field show different answers between the species as to their growth capacity in a given context, thus proving the interest for selection of the right species before beginning a commercial operation.

The choice is wide in French Polynesia where no local species of economic interest exists in the field. Numerous species were to be tested for criteria necessary to economic feasibility. Since temperature and salinity are constant year round, the following criteria have been retained:

- Reproduction in captivity: All the existing shrimp farms depend on the field catch of juveniles or females ready to spawn. For this reason, shrimp farming areas are restricted to traditional fishing grounds, production depends on natural spawning seasons and supply is a heavy economical load.

- Mass production of juveniles: In captivity the available number of females ready to spawn the same day will always be inferior to the possible catches in the sea. So larval rearing must be adapted to the number of available eggs and must give high survival.

- Fast growth in semi-intensive conditions on artificial food: The economic feasibility of a rearing is strongly correlated with the productivity by square meter and food cost. It seems necessary to

support minimum densities of 10 to 20 ind/m^2 and to produce shrimp between 15 and 30 g mean weight. With density above some ind/m^2, the natural productivity of the ponds is unable to support good growth. The use of fresh by-products is limited by the supplies, the storage and the induced pollution in ponds. The availability of artificial food is essential and those species which tolerate a low level of proteins will be the most interesting.

- Diseases resistance: In tropical area the water temperature in tanks and ponds is often above 28 C; this promotes growth of bacterial populations which can be pathogenic.

- Hardiness: The high temperatures also favor different stresses. Under conditions of semi-intensive or intensive rearing, it is often necessary to handle the shrimps, especially those around 1 g, where the density is decreased by transferring the juveniles to larger ponds; this is done for better utilization of the ponds and to fit the amount of food to an accurate count of shrimps. At harvest, it is also important that the animals have a desirable appearance.

The following paper presents the results obtained in the "Centre Océanologique du Pacifique" (COP) created by the "Centre National pour l'Exploitation des Océans" (CNEXO) in French Polynesia, after one year of experimentation on P. monodon as to its answers to the above criteria. This Indo Pacific species is particularly abundant in the Philippines, Taiwan and Indonesia where it is raised with Chanos chanos (Ling, 1972); post-larvae are traditionally caught in the field but hatcheries have been developed in the last years. Main data on that species are available from the works of Villaluz (1969), Liao (1973), Forster and Beard (1974) and the Seafdec maturation team (1976).

The introduction of P. monodon in Polynesia has followed experiments on other species from New Caledonia (P. merguiensis, M. ensis), from the USA (P. aztecus) and from Japan (P. japonicus). Reproduction in captivity has been attained for all these species (Aquacop, 1975) but the growth on artificial food was low for P. merguiensis and M. ensis, and frequent diseases were encountered for P. aztecus and P. japonicus (Aquacop, 1977). Two other species, P. stylirostris and P. vannamei (recently introduced from Crystal River, Ralston Purina hatchery), are now under experiment.

MATERIAL AND METHODS

The first animals were imported from Fiji Islands and New-Caledonia; they were transported in oxygen-inflated plastic bags, each animals being first isolated in a semi-rigid plastic netting to prevent harmful activity. The environmental and rearing conditions are similar to those described for the reproduction in captivity of other species (Aquacop, 1975): salinity 35 to 35 ppt, water temperature 25

to 29 C, ph 8.15 to 8.35, sand coral bottom, reduction of natural light by shading cover cutting 60% of the light and artificial food.

Maturation is induced by pinching the eyestalk between the fingers to remove one eye; this is done on females from 35 to 100 grams. Females are observed every two days out of the tank or in the tank under the light of a waterproof torch which allows estimation of ovarian development: color, shape and texture; the females which seem ready to spawn are isolated in a 500-liter tank (Aquacop, 1975).

Larvae are reared in 500-liter tank following a technique adapted from Galveston Laboratory (Mock and Murphy, 1971) and which is routinely used at the COP. Table 1 gives the sequence, at 28 C, using a chlorinated water (1.5 ppm) which is dechlorinated by light and air bubbling prior to use. Salinity is 35 ppt. Unicellular algae are produced apart separately. Cylindrotheca are used fresh, and Tetraselmis (species isolated from local phytoplancton) fresh or frozen. Rotiferous (Brachionus plicatilis) are produced on Chlorella or Tetraselmis cultures.

As very little informations was available on the basic nutritional requirements of P. monodon the problem has been studied according to the following scheme: definition of protein needs by means of purified diets; formulation of different artificial diets with classical food ingredients to determine the optimum energy level and to compare different protein sources; then production, on an experimental scale, of a food for use in production tanks or ponds. Purified diets are prepared according to the technique described by Kanazawa (1974) and artificial diets are made using a moist pellet meal and a dryer for 12 hours at 45 C; water stability is from 10 to 24 hours. Circular fiber glass tanks have been used: 0.25 m^2 stocked with 15 animals of 1 g size for purified diets; 2 m^2 stocked with 50 animals of 2-3 g size for artificial diets. The water characteristics are temperature 27 C, salinity 35 ppt, pH 8.2. Food is given once a day at 15% of the biomass. Daily water change is around 10%. Different diets have been used (Table 2). Experiment A, determined protein level by means of purified diet made with casein vitamin free (duration 30 days). Experiment B, determined optimum energy level with isoprotein diets (duration 65 days). Experiment C, concerned protein level with artificial diets of similar energy levels (duration 60 days). Experiment D examines different protein sources, artificial diets with similar levels of protein and energy (duration 90 days).

Growth experiments in the field have been conducted in different rearing enclosures (Table 3): earth ponds, circular fiber glass tanks and floating cages. Water temperature, dissolved oxygen and pH are measured every day, their variations during the experiments being similar in the ponds (Figure 1). Daily renewal ratio of the water is between 10 to 30 % for the earth ponds. Worm-shaped pellets are given twice a day (formulae in Table 4); the amount is a percentage of the estimated biomass following the ratio given by Parker et al. (1974).

Adjustments are made by direct examination of the remaining pellets two or three hours after the distribution.

RESULTS

Spawning and Larval Rearing

Five females and 3 males (40 to 100 g) were imported from Fiji Islands in July 1975, 2 females from New-Caledonia in December and 2 females and 1 female from Fiji in February 1976. The animals were well accustomed to rearing captivity conditions. They molted regularly every three weeks and were immediately impregnated prior to any ovarian development. After 4 months, the animals did not show any maturation signs so one eye was pinched on a 105 g female; the behavior of this shrimp was not modified and an ovarian development appeared 7 days later; its size increased and its color changed from white to dark green; the appearance of a granular texture was the sign of imminent spawning. The first one occurred 12 days after enucleation at 08.00 and gave 280,000 eggs, all viable. Two other females handled in the same way spawned 21 days later (380,000 viable eggs) but after one molt had occurred. The next month the same three animals were maturing again but only one spawning has been recorded while the other shrimp regressed their ovaries. This regression phenomenon was observed two months, then spawnings occurred again. During this period no maturation was visible on control animals. Later, in three months 6 females between 45 and 130 g gave a total of 3.3×10^6 eggs through 18 spawnings (average 180,000/spawning). Some females have been seen to mature again 5 days after a spawning. In July a new stock of adults was constituted with the biggest issues of the first spawning, 70 females between 50 and 80 g were epedonculated and the F2 generation was obtained one week later. During the coldest months, August and September, few maturations were observed; they started again in October.

Number of eggs is related to the weight of the female; 75,000 eggs for females of 45 g to 300,000 eggs for females of 140 g. Viability of the eggs is quite variable; some spawnings are totally or partially unfecundated. A low fecundation rate is often correlated with a high percentage of abnormal nauplii (distorted setae) which die when they molt in zoea I. Larval rearing points out the same problems encountered with the other species (Aquacop, 1977): a bacterial disease which is now controlled by Erythromycin used every two days from zoea I to P1 (1.0 ppm), and a fungus disease (Lagenidium and Sirolpidium) which is controlled by Treflan delivered by a continuous drop flow to kill the propagation forms. Production of 100 PL/liter with 80% survival from nauplii stages have been obtained in 500-liter tank. From M1 to P1, larvae are fed on frozen Tetraselmis and fresh rotiferous nauplii Artemia are given only 3 days from P1 to P4 before stocking in ponds. Half a million of P1 was produced.

Feeding Experiments (Figure 2)

Experiment A: The best growth performances with 40% casein and 18% starch content are 166% average weight increase and 80% survival rate. Experiment B: With 43% protein content in artificial diet the best performances were given by the 3.3 Kcal/g diet: 161% average weight increase and 78% survival rate. Experiment C: The 40% protein optimum level was confirmed with artificial diets of equal energy level: 159% of average weight increase (diet 2). Experiment D: The best growth performance was observed with diet 4 containing 25% alkan yeast (150% average weight increase and 84% survival rate) followed by diet 3 containing Spirulina (132% and 80%), and diet 1 containing white fish meal (134% and 64%).

Growth Experiments (Figure 3)

Semi-intensive Conditions: During the experiment 1 a deterioration of the bottom of the pond, due to an overfeeding combined with a nonadequate diet, might be responsible for the slow growth observed in March and April. The transfer of 8,000 animals in a clean pond (experiment 2) was followed immediately by good growth, 3 to 25 g in 133 days. The decrease in density (end of experiment 1, 04-8 to 05-26) was not sufficient to enhance the growth of the remaining animals, which started again only when they were transfered to another pond (experiment 3). Females were growing faster than males, especially in low density conditions. Harvesting was done by emptying the pond; shrimp did not burrow and went down with the water. Experiments 7 and 8 have been done to estimate the possibility of nursing. In 2 months average weight of 0.8 g was obtained from P4 post-larvae at density from 20 to 55/m^2: survival was total. The animals were harvested at the outlet pipe in plastic bags of 2 mm mesh and stocked immediately in the growing ponds, no mortality occurring during this handlings.

Intensive Conditions on Models: In a 12 m^3 outdoor tank without substrate and with strong aeration a good growth was obtained with 50 ind/m^2: 1 to 6.2 g in 49 days (experiment 5). In comparison a tank of equal capacity with clear water and sand bottom gave only a growth of 1 to 2.8 g in the same period; however, the density was higher 78 ind/m^2 (experiment 4).

The experiment conducted in the floating cages has been biased. The shrimp were harmed by prior handling. The growth was thus poor but the survival was high and the behavior of the animals was satisfactory: the grass-like plastic bottom of the cage made the pellet available for the shrimp as feces and small particules passed through the canvas. In these conditions fouling is not important and it seems possible to keep the cages in position for 4 months without problems.

During this set of experiments no disease with mass mortality occurred. The animals seemed very hardy; attacks were noticed only on

shrimp in tanks where conditions were poor or after too much handling; black eroded parts appeared on the carapace and tip of appendages showed necrosis. Terramycin incorporated into the food (1 ppt) stopped this disease which did not seem epizootic.

The behavior of P. monodon is different from the other species; they burrow superficially in earth or sand bottom, deeper in muddy bottom; they tend to aggregate and are generally very quiet, resting on the bottom. They also like to cling to substrates: algae in ponds or vertical net in the floating cages. When they are seen swimming around the pond it is often a sign of underfeeding. No cannibalism has been noticed.

DISCUSSION

The first consistent results on the maturation and reproduction of penaeid prawns in captivity are quite recent. Shokita (1970) obtained spawning of P. latisulcatus maintained in aquarium. Idyll (1971) and Caillouet (1973) induced the maturation of P. duorarum by a double eyestalk ablation but no spawning occurred. Liao (1973) noticed maturation of P. penicillatus and P. monodon in captivity but the eggs were not fecundated. Since 1973, Aquacop (1975) has obtained in captivity numerous spawnings and multiple generations of P. merguiensis (F6) and P. aztecus (F3) and some spawnings of P. japonicus (F2) and M. ensis; the maturation of P. aztecus has to be induced by pinching one eyestalk. Moore et al. (1974) obtained viable eggs from P. californiensis which have matured in captivity. Arnstein and Beard (1975), after unilateral eyestalk ablation, induced the maturation of P. orientalis, P. monodon and P. occidentalis but the eggs were not fecundated. Hanson et al. (in press) reviewing the works on this problem, concluded the time was near when the penaeid rearing could be routinely done from captive reared animals. Seafdec team (1976) has recently obtained results on P. monodon by unilateral eyestalk ablation. Caubere et al. (1976) obtained maturations and some spawnings of P. japonicus by variations of the photo and thermoperiod. Laubier-Bonichon (1976), using the same species and monitoring the same factors obtained numerous spawnings which always gave viable eggs year round.

The role of the neurosecretory cells of the eyestalk glands of decapods and their specific action on the molt and the maturation cycles are not well known (Farges, 1975). But the main result of the unilateral eyestalk ablation is to obtain maturation while females with their two eyes in the same environmental conditions never mature. The validity of this technique is confirmed by the results on P. aztecus and also on P. stylirostris and P. vannamei (Hanson et al., 1976; data from Galveston laboratory and Ralston Purina Company). However, this ablation may induce earlier maturation compared with natural conditions: at the COP, on P. vannamei the maturation of

females between 20 and 40 g is observed only after eyestalk ablation while this maturation occurs naturally for females over 40 g.

On P. monodon, the maturation is always attained but it happens that the ovulation process does not go untill spawning. This might be correlated with the handling of females. On the other species of penaeid the ovarian development can be seen through the carapace by examination in the tanks; the carapace of P. monodon is dark and it is necessary to handle the animals. This is often followed by a regression of the ovaries if the handling takes place more than 48 hours before spawning; the handling does not seem to disturb the maturation in the last two days. The multiple spawnings of one female in a short period of time lead to the conclusion that it is possible to support a commercial operation using only a small number of females kept in captivity. Actually, the fecundation process and its direct consequence, the viability of the eggs, is not satisfactory; a high number of totally or partially unfertilized spawnings has been observed in the last experiments. It is too early to arrive at an explanation, but the size of the males may be indicative; they are smaller (30 to 40 g) than those of the first trials (70 to 90 g). By extrapolation of the preceding data and by assuming a fecundation rate of 50% and a 60% survival from nauplii to post-larvae it seems possible to produce as many as 25.10^6 PL/year with a 12 m^2 tank stocked with 3 large females per m^2 with a 1/1 sex ratio. Getting one generation in 9 months also opens the way to genetic selection.

Protein requirements for that species seem to be around 40% the same as for P. aztecus (Venkataramiah et al., 1975); they are higher than for P. vannamei or P. stylirostris (25 to 30%) but less than for P. japonicus or P. merguiensis (Aquacop, 1976). Many sources of protein can be used, either vegetal or animal, to produce artificial diets and the choice will be based on the avaibility and cost of the raw materials locally. Lee (1970) studying digestion and absorption in P. monodon with various sources of protein, concluded the effect was irrespective of the animal or vegetal origin. The optimization of a low level protein pellet is always easier than that of a high one. From the above experiments the main date are 40% protein and 3.3 Kcal/g of energy.

The physical and chemical conditions recorded during growth experiments in ponds are encountered in most of the South Pacific Islands. It seems necessary to have a pumping device to prevent the rise of temperature above 33 C during the hot months and to allow evacuation of rainfall water by surface outlet during the rainy season. Most of the previous recorded experiments on P. monodon concerned wild-caught fry and very low stocking density in ponds mixed with milk-fish. Villaluz (after Shigueno, 1975) thinks 500 kg/ha/yr can be produced under non feeding conditions and some other data give a production as high as 2.8 T/ha/yr in 4 months in high productivity milk fish nursery ponds, proving that P. monodon can grow well on a mainly vegetable diet; but in number of others experiments the survival rate was poor. This species is omnivorous and under laboratory conditions can eat any kind of food (Villaluz, 1969). In

Polynesia where the primary productivity is very low and where no fertilization has been used to enhance it, theoretical growth has been computed from the available data, and the two curves showing optimum and medium growth are presented in Figure 4. It appears possible to produce 25 g animals from 0.5 g juveniles in 140 days in semi-intensive conditions and to produce 6 T/ha/yr. From the preliminary results of the model in intensive conditions and from the data of Beard (1972), a goal of 20 T/ha/yr could be reached. The growth potentiality difference between males and females suggests that a suitable selection could improve the results.

In Polynesia many lagoons are available and the floating cage technique could be highly interesting; it will need a suitable food but the cost of land and pumping will be nil.

P. monodon also appears to be a speciesthat will grow to 30 g without a large increase in the food conversion ratio. This is particularly important to the market for frozen shrimp-tails.

CONCLUSION

The responses of P. monodon to the many criteria used in selecting the right species for rearing in tropical environments are highly positive.

- Maturation and reproduction in captivity occur throughout the year with temperature above 25 C; one generation is reached in 9 months; multiple spawnings and number of eggs will soon allow to sustain commercial operation from captive reared animals.

- Intensive breeding techniques allow production of 100 PL/liter if bacteria and fungi are controlled.

- Growth in semi-intensive conditions is high and average weight reaches 25 g in 6 months.

- Intensive cultivation in suitable tanks or floating cages seems possible as the species is not cannibalistic and accustomed to crowding.

- Artificial food with a mean level of protein (40%) and low gross energy level (3.3 Kcal/g) is readily accepted.

- No epidemic disease has been yet encountered and P. monodon is very tolerant to handling.

This work has been conducted comparatively with six others species: P. aztecus, P. japonicus, P. merguiensis, M. ensis for 3 years; P. vannamei and P. stylirostris more recently. Actually P. monodon gives the best promise.

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Table 1. - P. monodon larval rearing sequence at 28°C

Day	Stage	Tank (liters)	Food species	Food density/cc	Water change	Treatment	Larval density (liter)
0	eggs	500					
1	ω -N	50					
2	N	500				T	100-150
3	N, Z_1	500	Cylindrotheca	8×10^4	NO		
4	Z_1	500	Cylindrotheca	10×10^4	NO	ET	
5	Z_1, Z_2	500	Cylindrotheca	15×10^4	NO	T	
6	Z_2, Z_3	500	Tetraselmis	10^4	NO	ET	
7	Z_3, M_1	500	Tetraselmis	4×10^4	Total	T	
8	M_1, M_2	500	Tetraselmis Rotiferous	2×10^4 10	1/2	T	
9	M_2, M_3	500	Tetraselmis Rotiferous	2×10^4 10	3/4	T	
10	M_3, P_1	500	Tetraselmis Rotiferous	2×10^4 10	3/4	T	80-100
11	P_2	500	Artemia	5	3/4	T	
12	P_3	500	Artemia	5	3/4	T	
13	P_4	500	Artemia	5	3/4	T	
14	PL stocked in nursing ponds.						

N : nauplius Z : zoe M : mysis P : post-larva T : treflan E : erytromycin

Table 2. - Diets used to develop formula food for P. monodon (values expressed in terms of percentage of total diet)

Exp	Ingredients	Diets 1	2	3	4	5	6	Common part of the diets
A	Casein	30	30	40	40	55	55	Codliver oil : 7 - Agar agar : 3 - Chitin : 0.8 -
	Glucose	-	18	-	18	-	18	Na citrate : 0.3 - Na succinate : 0.3 -
	Starch	18	-	18	-	18	-	Ca lactate, $CaCO_3$, $CaHPO_4$: 10 - Cholesterol : 0.5 -
	Cellulose	25	25	15	15	-	-	Vitamin mix : 5
	Protein %	30	30	40	40	55	55	
B	Wheat meal	-	20	14	18			Fish meal : 35 - Soya meal : 10 - Corn, distiller dried grains : 7 - Leucaena meal : 3 - Dried whey : 4 - Gluten : 7 - Yearts : 4 - Ca lactate, $CaCO_3$, $CaHPO_4$: 2 - Vitamin mix : 4
	Cod liver oil	2	4	10	6			
	Cellulose	22	-	-	-			
	Kcal/g	2.6	3.3	3.6	3.1			
C	Fish meal	9	12.5	18				Soya meal : 15 - Brewer's yeart : 10 - Ca lactate, $CaHPO_4$, $CaCO_3$: 4 - Vitamin mix : 4
	Shrimp meal	10	12	15				
	Cereal mix	39.5	36	30				
	Cod liver oil	8.5	6.5	4				
	Protein %	35	40	45				
D	Fish meal	25						Shrimp meal : 8 - S.F.P.C. : 5 - Blood meal : 8 - Milk : 6 - Rice : 8 - Cassata : 5 - Seed meals : 16 - Cod liver oil : 5 - Ca lactate, $CaHPO_4$, $CaCO_3$: 6 - Vitamin mix : 5 - Guaramate : 3
	Meat meal		25					
	Spirulina			25				
	Alkan Yeast				25			
	idem + methionin					25		
	Limiting factor	V*	M*	L*	M*	L*		

(*) - M : methionin - V : Valin - L : lysin - S.F.P.C. : Soluble Fish Protein Concentrate

Table 3. - Diets used in growth experiments 1 to 8

Ingredients	Exp 1 to 6	Exp 7 - 8
Shrimp meal	8	22
Blood meal	11	9
Meat meal	21.5	-
Gluten, wheat	10	14
Rice	6	-
Peanut oil-cake	17	-
Soya oil-cake	-	10
S.F.P.C. 80	6	5
Cod liver oil	4	4
Mineral mix	3	5.5
Vitamin mix	5	4
Methionin	0.5	-
F.P.C.	-	15
Spirulina	-	7.5
Brewer's yeast	-	5

S.F.P.C. 80 : Soluble Fish Protein Concentrate 80 %

F.P.C. : Fish Protein Concentrate

TAble 4. - Growth experiments on P. monodon

Exp	Rearing system	Stocked					Harvested					Duration	Survival %	Food conversion
		Date	Nb	M.W. (g)	Bm (g)	d	Date	Nb	M.W. (g)	Bm (g)	d			
1	720 m2 earth pond	01.01	23,713	0.01	-	33	04.10 05.26	10,460 12,200	2.9 5.3	30.3 64.0	31 17	100 146	96	4.1
2	728 m2 earth pond	04.08	8,000	2.9	23.2	10.9	08.17	7,200	25	180.0	9.9	133	90	3.0
3	680 m2 earth pond	05.26	12,200	5.3	64	17.9	08.11	9,700	18.1	175.6	14.3	75	80	4.1
4	12 m2 tank sand-bottom	02.16	940	1	0.9	78.3	05.07 06.14	200 734	5.4 9.3	1.1 6.8	78.3 61.1	81 118	99	-
5	12 m2 tank no substrate	02.16	600	1	0.6	50	05.07	415	7.6	3.1	34.6	81	69	-
6	floating cage 2 x 2 x 2	08.06	577	14.7	8.4	144	09.06	492	15.8	7.7	123	30	85	-
7	728 m2 earth pond	07.22	15,000	0.003	-	20.6	09.22	15,800	0.9	14.2	21.7	60	100	1.1
8	720 m2 earth pond	09.01	40,000	0.003	-	55	11.03	40,000	0.8	32	55	62	100	

M.W. : mean weight - Bm : Biamass - d : density

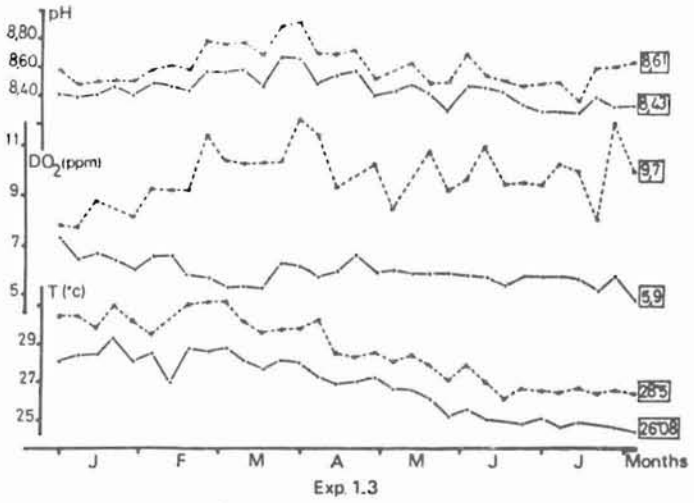

Fig 1 Changes in Temperature, Dissolved Oxygen and pH in ponds

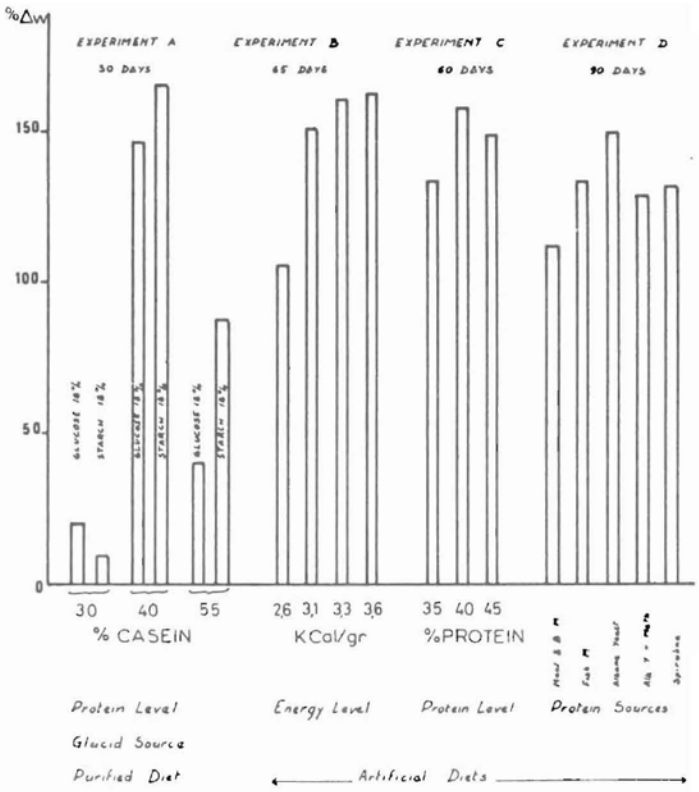

Fig 2 Growth performances by means of purified and artificial Diets on P. MONODON

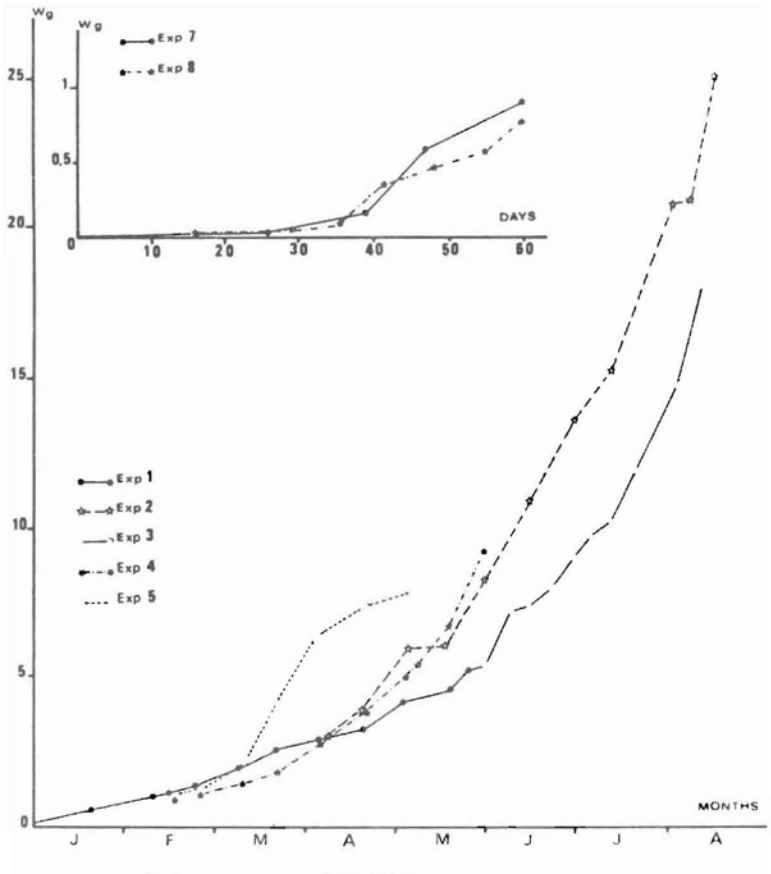

Fig 3 Growth curves of P. MONODON

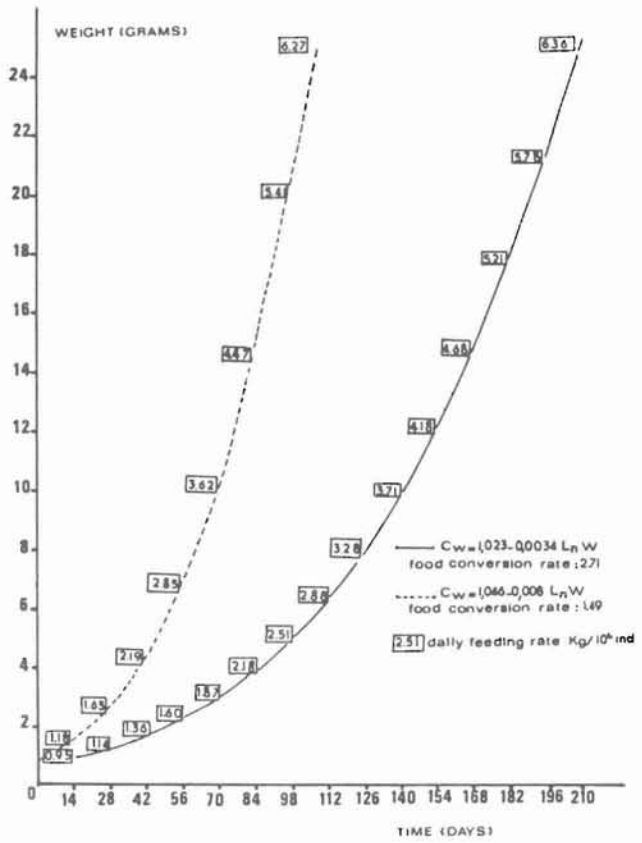

Fig 4 Theorical growth curves of P. Monodon