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The nutritional requirements of the Japanese shrimp *Penaeus japonicus*

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Abstract. — ***Penaeus japonicus*** *is probably the best known species among penaeids or even among shrimps. In juveniles, the protein requirement was best studied and Japanese shrimp appears as the most demanding penaeid species. Some discrepancies remain among estimations of the protein requirement. They may be related to several factors such as energy level of the diet, digestibility or biological value of protein or other nutritional factors. The essential amino acids are well known, however from a quantitative point of view the requirements in each of these amino acids remain to be determined. The fatty acid utilization and mainly the role of essential fatty acids was well studied :* ***Penaeus japonicus,*** *like most of the sea fish species, has a low ability to elongate and desaturate C18 highly unsaturated fatty acids. The essentiality of both cholesterol and phospholipids was well demonstrated and represents one of the most original features of penaeid nutrition. The feeding value of several carbohydrates was studied and phenomena such as the « diabetic » behavior of the shrimp, its low amylase activity, the beneficial effects of glucosamine, were pointed out. However much information on the actual capability of kuruma shrimp to use carbohydrates from practical sources are still lacking. Furthermore almost nothing is known on energy requirements or recommendations. Vitamin nutrition of* ***P. japonicus*** *was rather poorly studied, mainly from a quantitative point of view. Mineral nutrition retained little attention but several original traits were elucidated such as the detrimental effect of dietary iron, the rather high phosphorus requirement and the ability to use phosphorus from various sources which is very different from that of upper vertebrates. In summary much information on the requirements of* ***P. japonicus*** *juveniles is now available but often remains limited from a quantitative point of view. On the other hand, the nutritional requirements of larvae are much less known and breeder's ones are almost unknown.*

INTRODUCTION

Several reviews or bibliography were recently devoted to penaeid shrimp nutrition (New, 1976, 1980; Kanazawa, 1982; Guillaume, 1987). Among the different species of penaeids interesting aquaculturists, *Penaeus japonicus* was mostly studied. Since the first efficient mixed diets were used by Kanazawa et *al.* (1970), most nutritional requirements of juveniles studied, at least for macro ingredients. The nutrition of larvae is much more difficult to approach, but recent success in larval rearing with microbound diets or microcapsules have also information in this field. This review gives an overview of the known requirements of *P. japonicus* with emphasis on their quantitative estimations without giving details on mechanisms involved.

THE PROTEIN REQUIREMENT

Gross protein requirement

— Gross protein requirements of juveniles

Like most aquatic animals penaeid shrimps require a high protein level in their diet. In *P. japonicus* juveniles the optimal level was studied by Deshimaru and Shigeno (1972), Balacz *et al.* (1973), Deshimaru and Kuroki (1974a), and Deshimaru and Yone (1978b). From their results (Table 1) it is obvious requirement is at least 52 % of the diet when measured in small shrimp fed on casein-albumin diets, both for maximal growth and best feed efficiency. In these conditions levels of protein exceeding 60 % lead a clear depressing effect on growth. Nevertheless in a precious review, Deshimaru and Shigeno (1972), referring to a set of experiments, insisted on the improvement of feed efficiency obtained when crude protein content exceeded 60 %. Therefore the optimal level seems to be more elevated for best food to gain ratio than for growth.

As mentioned by Kanazawa (1982) this requirement is the strongest among all other penaeid species, a phenomenon that was often explained by nutritional habits. In fact this requirement should be related to specific growth rate and therefore to age or size as demonstrated in *P. stylirostris* by Colvin and Brand (1977) and in *Crangon crangon* by Regnault and Luquet (1974).

Table 1. Dietary protein requirement of *P. japonicus.*

Initial Weight	Source of protein	Optimal levelq	Author
—	Various	>60	Deshimaru and Shigeno 1972
—	Shrimp meal	>40	Balasz et *al.* 1973
0.6 g	Casein albumin	46	Deshimaru and Kuroki 1974a
0.8 g	Casein	52	Deshimaru and Yone 1978b
(Zoe)	Casein 5 +Carbohydrates 15	55 45-55	Teshima and Kanazawa 1984
(Zoe - mysis 2)	Casein 25 Hen egg protein	45 >50	Besbes 1987

— Gross protein requirements of larvae

For larvae (Table 1) two experiments carried out in this field have shown a lower requirement during the early stages, *ie in zoea* which is herbivorous. More precisely the work of Teshima and Kanazawa (1984) demonstrated the sparing effect of carbohydrates against protein. Results of Besbes (1987) indicate that a microbound diets containing 44 % protein even sustains faster growth than a diet containing 50 % of protein from casein and hen egg until mysis 3 stage.

Possible dietary factors of variation - The role of essential and semi essential amino acids

The protein requirement depends on many nutritional factors such as lipids, carbohydrate content or energy level. But, with the exceptions mentioned above, the sparing effect of these nutrients has been little studied. The protein requirement is also very dependent on essential amino acids (EAA) content and balance. The well known qualitative requirement in EAA, related elsewhere, will not be commented on but the work of Deshimaru and Shigeno (1972), and Deshimaru (1982) on the balance of EAA deserves some attention since it led to the conclusion that short necked clam protein is the best protein fitting the requirements of *P. japonicus* or, in other words, the protein with best EAA profile. Calculating the sum of sulfured and aromatic amino acids, supposing they were semi essential as they are in vertebrates these data are proposed in table 2 in a form suitable for linear programming.

Table 2. Profile of essential and semi essential amino acids in the protein of short necked clam *(Ruditapes philippinarum)* after Deshimaru, 1981.

	Profile of EAA and SEAA in clam protein		Suggested level for P. japonicus
	% of protein	% of EAA + SEAA	% of diet
Methionine	3.02	5.98	1.57
Methionine + Cystine	3.28	6.49	1.70
Threonine	5.82	11.52	3.03
Valine	3.87	7.66	2.01
Isoleucine	7.11	14.06	3.70
Phenylalanine	3.78	7.36	1.96
Phenylalanine + Tyrosine	8.30	16.42	4.32
Lysine	7.50	14.84	3.90
Histidine	2.25	4.45	1.17
Arginine	7.98	15.79	4.15
Tryptophane	0.90	1.78	0.47

However it must be noticed that these recommendations do not correspond to individual amino acid requirements as used in the formulation of upper vertebrate diets by linear programming; the only supplementation in EAA were done in *P. japonicus* by Kitabayashi *et al.* (1971) (arginine and methionine) and by HEW and Cuzon (1982) (lysine and arginine). But these experiments did not bring estimations of the requirements in individual EAA or of SEAA; the very slow growth of kuruma shrimp when fed on regimes where protein was replaced by a mixture of amino acids (Deshimaru and Kuroki, 1975) is perhaps the main cause of this deficiency.

THE ENERGY REQUIREMENT, CARBOHYDRATES AND LIPIDS

Energy needs

Little data is available on energy metabolism in crustaceans (Capuzzo, 1982) except at the biochemical level where the energy yielding pathways were studied, mainly by Zandee (1966) in *Astacus* sp. But such studies are lacking in *P. japonicus*. Even the optimal protein/energy ratio level remains to be determined in this species. Theorically the energy value, either digestible or metabolizable, is difficult to calculate due to the lack of balance studies. However, the digestible energy level of efficient semi purified shrimp diets apparently ranges from 14 to 17 MJ DE kg-1. Nevertheless the energy value of classical diets is more difficult to calculate since the digestibility coefficients of nutrients remain unknown in most feedstuffs.

Carbohydrate supply

Carbohydrates are very efficient energy sources in most animals for standard metabolism, muscular energy expenditure, and other processes needing ATP. But, large terrestrial carbohydrates such as starch are not very digestible in marine animals because of lower amylase activities. On the other hand very available sugars such as glucose are too quickly absorbed and may induce hyperglycaemia. Such a phenomenon was demonstrated in *P. japonicus* by Abdel Rahman *et al.* (1979) who observed that 10 % glucose inhibited growth while polysaccharides (¿ starch, dextrin and glycogen) and mainly disaccharides (maltose and sucrose) sustained good performances. These results demonstrate the existence of « diabetic » phenomena in shrimp similar to those known in fish. They also suggest the importance of further studies on the digestibility of carbohydrates in vegetable feedstuffs and on their metabolic effects in shrimp.

Chitin being a polymer of glucosamine the addition of this aminated sugar was tested by Kitabayashi *et al.* (1971) who observed a beneficial effect of the supplementation. The authors even determined the optimal dietary level of glucosamine (0.53 %) and noticed that chitin had a growth depressing effect. Unfortunately studies of Deshimaru and Kuroki (1974b) failed to corroborate the essentiality, or semi-essentiality, of glucosamine in *P. japonicus*, perhaps because of differences in diet composition.

Chitinase and cellulase activities were found in the digestive tract of some crustacea; however practical implications of such activities, if occuring in *P. japonicus*, remain to be studied.

In conclusion carbohydrates sustaining good growth in semi- purified diets for *P. japonicus* are known, but fewer quantitative informations are available. In larvae (as mentioned in the previous paragraph) diets may contain as much as 35 % carbohydrates; in juveniles the optimal level seems to be close to 15-20 %, but acccording to Maugle *et al.* (1983), this level could be brought to almost 30 % without marked growth depressing effects with the addition of amylase; such an addition, needing microencapsulation would lead to a sparing of protein amounting to 30 % of the supply.

Lipidic nutrition

— *Gross lipid optimal level*

The need for total lipid is devoid of scientific meaning, especially when energy level carbohydrate and protein contents are not stated precisely. Nevertheless several experiments have shown that growth performances tend to decrease when the dietary lipid content exceeds 10 %. Provided essential nutrients are in sufficient amount, very good performances are registered with 6 to 8 % of total lipid.

— *Requirements for essential fatty acids*

The qualitative needs of crustaceans for EFA were reviewed by several authors including Castell (1981) and Galois (1987); since the very demonstravive experiments of Kanazawa et *al.* (1979b,c), and Jones *et al.*, (1979). *P. japonicus* is known to be unable of synthezing 18 :2 n-6, 18 :3 n-3, 20 :5 n-3 (EPA) and 22 :6 n-3 (DHA), which can be considered as « essential » (broad meaning); the relative efficiency of several fatty acids in promoting growth or decreasing mortality was also tested both in juveniles (Kanazawa *et al.*, 1979a) and larvae (Jones *et al.*, 1979). From these data it is well demonstrated that long chain highly unsaturated fatty acids (Hufa) give best results and are the main requirement in essential fatty acids (EFA); linolenic acid which is bioconverted in.EPA and DHA at a too slow rate is less efficient; if supplied without EPA or DHA, even at a high percentage, it remains markedly insufficient for maximal growth promotion.

The role of linoleic acid and other fatty acids of the n-6 series is less clear : it is less efficient than linolenic and n-3 Hufa and in normal condition 20 : 4 n-6 is at a rather low percentage in shrimp lipids. But Deshimaru et *al.* (1979) demonstrated that a mixture of vegetable and marine oil was more efficient in growth promotion than pure marine oils. Therefore the n-6 family may be required, though at a much lower level than n-3 for the synthesis of some prostaglandines deriving from 20 : 3 n-6 or 20 : 4 n-6. Unfortunately almost nothing is known in this field. Furthermore little data is available on the possible antagonistic effect of excess of n-6 Hufa on elongation desaturation of n-3 Hufa.

— *Requirement for phospholipids*

The requirement for phospholipids, in opposition to that of EFA, is very specific of crustaceans. It was noticed by Kanazawa *et al.* (1979d) when studying the high nutritive value of *Tapes* lipids. Its nature, its importance and its quantitative values were further studied by Teshima and Kanazawa (1980), Teshima *et al.* (1986), etc.. The higher efficiency of phospholipids containing choline or inositol (phosphatidylcholine and phosphatidyl-inositol) rich in HUFA was demonstrated as well as their role in the transportation of cholesterol and other lipids (Teshima and Kanazawa, 1980; Teshima *et al.*, 1986b).

From a formal point of view phospholipids should be classified among the semi essential dietary components, at least in juveniles, since their biosynthesis from fatty acids, glycerol choline and inositol is possible, though very slow. But in larvae the essentiality of phospholipids is much more pronounced since Kanazawa *et al.* (1985) observed a complete and early mortality in larvae fed on microbound diets well fortified in linoleic, linolenic and n-3 HUFA, as well as in cholesterol but devoid of phospholipids. The addition of soybean phosphatidylcholine had a very marked action on both survival and growth.

The values given in table 3 show that the recommendations appear higher in larvae than in juveniles.

Table 3. Suggestions for dietary levels of essential lipids for *P. japonicus* juveniles and larvae.

Juveniles	n-3 + n-6 Essential fatty acids	0.5-1	Kanazawa et *al.* 1979a
	Phospholipids	1	Kanazawa et *al.* 1979d
	Cholesterol	0.2	Shudo et *al.* 1971
		0.5	Kanazawa et *al.* 1971
		2.1	Deshimaru and Kuroki 1974b
Larvae	(n-3- Hufa acids (EPA + DHA)	1	Kanazawa et *al.* 1985
	Phospholipids	3.5-6	Kanazawa et *al.* 1985
	Cholesterol	1	Teshima et *al.* 1983

The essentiality of cholesterol, apparently specific of all arthropods, is well known both in juveniles (Teshima and Kanazawa, 1971; Teshima, 1982) and larvae (Teshima *et al.*, 1983). Nevertheless this precursor of sex or moulting hormones and vitamin D, which has also a structural function in membranes can be obtained by bioconversion of many sterols from plant origin, mainly from ergosterol, stigmasterol and i sitosterol, both in juveniles and larvae (Teshima, 1982; Teshima *et al.*, 1983).

The values indicated in table 3 correspond to best estimations of the requirements of juveniles and larvae.

— *Interrelationship between essential lipids*

The efficiency of lecithin in juveniles depends, among other factors, on their content in EFA. Therefore the requirement for phospholipids is qualitatively bound to that of HUFA. More striking is the transportation of cholesterol depending on phospholipids present in the haemolymph, there is an inverse relationship between the « needs » in both nutrients;

this interrelationship was demonstrated in *P. vannamei* juveniles by Clarck and Lawrence (1988). A similar very clear interaction was revealed by Kanazawa *et al.* (1985) in their study on EFA and phospholipids of larvae : if the diet contained 6 % soybean phosphatidylcholine (PC) growth and survival were almost identical with 0.5 and 1 % n-3 Hufa, while with 3.5 % of PC 0.5 % of n-3 Hufa already appeared insufficient.

VITAMIN NUTRITION

No complete study on qualitative requirements for vitamin was published for *P. japonicus* as far as WE. know. But a distinction must first be made between the A and B groups : in the former group vitamins A and D do not appear strictly essential since they can be derived from carotenoids and cholesterol respectively. The capacity of bioconversion of several carotenoids into vitamin A appears broad in upper crustacea and many authors use i caroten instead of vitamin A with very good results. The ability of shrimp to derive vitamin D from sterols probably exists though little is known on the role of this vitamin in crustacea and, *a fortiori*, on the quantitative needs of penaeids (Fisher, 1960). Vitamin E was the first vitamin which was demonstrated to be essential in crustacea; it plays a very important role in reproduction, its deficiency inducing male sterility in *P. indicus* as shown in our laboratory (Cahu and Fachfach, 1989), but no data are available for *P. japonicus*. As far as we known vitamin K is perhaps not required by crustaceans, where it even could lead a detrimental effect (Fisher, 1960).

Table 4. Vitamin requirements of juvenile *Penaeus japonicus*.

Vitamin	Requirement (mg %)			
	Kanazawa et al. 1976	Guary et al. 1976	Deshimaru and Kuroki 1979	Civera 1989
Ascorbic acid	—	1000-2000	300	—
Choline	60	—	Dispensable	—
Inositol	200	—	400	>400
Thiamine	—	—	6-12	—
Pyrodoxine	—	—	12	—

In the B group

A. the essentiality of riboflavin, pantothenic acid, nicotinic acid, biotin, folic acid and vitamin B12 remains to be demonstrated,

B. it is likely since these vitamins were found to be required in most insects studied

C. paraaminobenzoic acid essentiality is doubtful if we refer to insects (House, 1974). The requirements for other water soluble vitamins are shown in table 4.

Ascorbic acid plays a very important role in practise because of its lack in most dry feedstuffs and it is very unstable during feed processing and storage. Because of these characteristics recommendations probably correspond to strong overestimations of the actual requirements (or to safety margins).

MINERAL NUTRITION

Most fields of mineral nutrition have still been less studied than vitamin nutrition in sea shrimp since seawater is the supplier of most required inorganic elements except phosphorus.

For this reason, the requirement for phosphorus, as well as for calcium, retained the attention of several authors, but their results show a great discrepancy (Table 5). The causes of such a discrepancy may be numerous but we have to mention the very clear results of Cheng (1986), and Civera and Guillaume (1989) indicating that the availability of P was very variable among different salts. One reason of such a variability, i.e. the absence of acidic pH in the « stomach », appears as previously underestimated. If very available sources of P are chosen, the actual requirement of *P. japonicus* for this element is probably below 1 % of the diet. On the other hand the optimal Ca/P ratio seems to be very difficult to determine since very good growth can be obtained without dietary Ca, this element being easily extracted from seawater (Deshimaru and Yone, 1978a).

Table 5. Calcium and phosphorus requirement of *Penaeus japonicus* and suggested Ca/P ratio.

Requirements			Sources		Authors
Ca	P	Ca/P	Ca	P	
1.24	1.04	1:1	$CaHPO_4.2H_2O$ $CaCO_3$	$CaHPO_4.2H_2O$	Kitabayashi et al 1971
0	2	—	$CaCO_3$	$NaH_2PO_4.2H_2O$	Deshimaru and Yone, 1978a
—	—	2:1	$CaCO_3$	$CaHPO_4$	Cuzon 1982
1-2	1-2	1:1	Several	Na_2HPO_4 NaH_2PO_4	Kanazawa et al 1984
0	1.5	—	Several	Na_2HPO_4	Cheng and Guillaume 1984
—	0.56	—	$CaCO_3$	Na_2HPO_4 phytate.	Civera and Guillaume

The usefulness of other minerals in dietary supplies is poorly known; iron can have a negative effect (KANAZAWA *et al.*, 1984) while other micro elements seem to be supplied in sufficient amount by seawater. In semi purified diets improvements of performances were obtained with the supplementation in potassium and magnesium; the optimal levels being of 0.9 and 0.3 for these elements respectively according to Kanazawa (1984). However, most trace elements as well are extracted directly from seawater and do not need to be added to the usual diet.

MISCELLANEOUS COMPONENTS

Very little is known on the role of fiber for *P. japonicus.* This component has received limited attention in other shrimp also, but beneficial effects of fiber were registered both for *Macrobrachium rosenbergii* and *P. aztecus.*

Concerning carotenoids that are added either pure or through concentrated sources in practical diets, little information is available (Otazu Abrill and Ceccaldi, 1984) despite of considerable economic importance of these compounds ubiquously found in crustaceans.

The existence of possible « growth factors » will be discussed elsewhere, but it may be recalled that nucleic acids are sometimes added to semi purified diets as growth promoters.

CONCLUSION

During the past two decades an impressive amount of knowledge was gathered in the field of *P.japonicus* nutrition, most of the work being done by the Japanese technicians. Of course many facets have not yet been studied, but the essentiality of nutrients known to be so in vertebrates was verified (except for some vitamins and minerals) and for the most important nutrients requirements have been estimated, while nothing was known 20 years ago. Some very original nutritional features were discovered such as phospholipid requirement and role in different steps of lipid metabolism. The very high value of the protein requirement in *P. japonicus* was also underlined and has led to the conclusion that this species was the most demanding penaeid. More recent exploration of larval needs have also been very successfull.

Unfortunately almost nothing is known in breeder nutrition : as far as we know it is still impossible to obtain good spawning in *P. japonicus* without using natural food. On the other hand for accurate least cost formulation of juvenile foods most estimations of the requirements should be submitted to further studies. New (1976) stated that « perhaps the most urgent task is the determination of quantitative amino acids requirements ». We think this statement remains valid; but more information is also needed in the field of energy requirements which correspond to the most expensive part of diets.

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