Feeds development for post-larval spiny lobster: A review

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Abstract On-growing of spiny lobster from wild seed is a thriving aquaculture industry in SE Asia and most notably in Vietnam where production of the tropical lobster *Panulirus ornatus* is estimated at more than 2,000 tonnes per annum. Present culture relies on lobsters being fed fresh fishery by-catch. The dwindling supply of these feeds and their downstream environmental impact have increased the priority to develop sustainable and more ecofriendly pelleted feeds. Efforts to develop palatable and high performance pelleted dry feeds for spiny lobster grow-out is reviewed in this paper with particular emphasis on Australian research with temperate (*Jasus* spp.) and tropical (*P. ornatus*) species. This research has increased our understanding of the lobster's requirements for critical nutrients such as protein and total lipid and progressed the development of pelleted dry feeds for lobster grow-out.

Key words: rock lobster, nutrition, digestibility, protein, attractants

Spiny lobsters (Palinuridae) are one of the world's most valuable seafoods with high market appeal in Asia, Europe and America. Most capture lobster fisheries are either over-exploited and in decline or are being managed for their maximum sustainable yield (Phillips, 2000, 2005). Aquaculture appears to be the only long-term way of meeting market demand for spiny lobsters. Although laboratory-scale rearing of the larvae from egg to puerulus has been achieved for many species, including P. elephas, P. japonicus, P. longipes, Jasus lalandii, J. edwardsii and J. verreauxi (Kittaka, 2000; Matsuda and Yamakawa, 2000), commercially-viable hatchery production of spiny lobsters is still thought to be a long way off. Until successful hatchery technology is developed, the only practical way of increasing the volume of marketed lobster is to capture juveniles from the wild and on-grow them to market size, thereby circumventing the high natural mortality that otherwise would occur (Phillips et al., 2003). The tropical ornate lobster Panulirus ornatus is probably the best candidate for aquaculture as it has the shortest oceanic larval development phase of 4-6 months (Dennis et al., 2001) and the fastest

post-larval growth rate, capable of attaining a market size of 100-105 mm carapace length (~1 kg) within 18 months after settlement (Phillips *et al.*, 1992; Skewes *et al.*, 1997; Dennis *et al.*, 1997; Hambrey *et al.*, 2001).

The on-growing of *P. ornatus* is a flourishing industry in many parts of SE Asia and notably in Vietnam where the abundance of wild lobster juveniles has enabled lobster grow-out aquaculture to develop rapidly with 2,000 tonnes, worth US\$70-75 M, being harvested in 2001/02 (Thuy and Ngoc, 2004). In Vietnam, lobsters are fed exclusively on fresh fishery by-catch. However, the diminishing supply and increasing cost of by-catch, together with the downstream environmental impacts of this type of feeding, are strong incentives for the development of more eco-friendly pelleted lobster feeds.

Despite more than 30 years of research to develop a suitable compounded (artificial) feed for rearing juvenile spiny lobsters (see Conklin, 1980; Booth and Kittaka, 1994; Brown *et al.*, 1995), progress has been slow and our knowledge of their nutritional requirements is still sparse. However, progress in developing suitable pelleted dry feeds for spiny

lobster grow-out has gained considerable momentum in the past 5-10 years. This paper reviews this more recent research and identifies areas where further research is critically needed.

First principles of feeds development

Knowing what the animal prefers to eats in the wild is a useful guide when developing an artificial feed for the animal. Analysis of the contents of the foregut of postlarval spiny lobsters reveals a wide variety of molluscs (predominantly, bivalves gastropods and chitons), crustaceans (predominantly barnacles, crabs and other decapods), polychaete worms, echinoderms and occasional (incidental?) amounts of macroalgae (Joll and Phillips, 1986; Booth and Kittaka, 1994; Barkai et al., 1996; Mayfield et al., 2000; Goni et al., 2001). This diet selection characterizes them as opportunistic carnivores of predominantly benthic invertebrates. Thus they most likely have evolved to most efficiently utilize foods that are high in protein, low in lipid and moderate to high in starch since glycogen is the major energy store of molluscs and typically 14-24% of the ash-free dry matter (Dall et al., 1991; Lodeiros et al., 2001; Orban et al., 2002). Studies on the digestive enzymes of juvenile and adult spiny lobsters attest to their carnivorous feeding preference with high proteolytic (trypsin, chymotrypsin and carboxypeptidase A), moderate carbohydrase (α -amylase, β -glucosaminidase, laminarinase and cellobiase) and comparatively low lipase activities (Barkai et al., 1996; Johnston, 2003; Radford et al., 2005). Interestingly, amylase and laminarinase specific activities were reported to decrease as a function of lobster size, implying that carbohydrate might be a more important dietary constituent for juveniles than adult spiny lobsters (Johnston, 2003).

An understanding of what attracts an animal to its food is also helpful when developing an artificial diet. A lot is known about chemoreception in marine decapods (see Lee and Myers, 1997; Grasso and Basil, 2002), and feeding preferences of spiny lobsters are also becoming better understood (Derby, 2000; Derby *et al.*, 2001; Grasso and Basil, 2002). Like homarid lobsters, spiny lobsters

have a well developed antennular chemosensory system for locating food, finding shelter and social interactions with other lobsters. Characteristically, feed attractants for crustaceans are low molecular weight, water and ethanol soluble, and amphoteric or basic compounds that are likely to be released from potential prey items. Thus to ensure an artificial feed will be perceived by the lobster as suitable food, it should leach a steady plume of attractants rich in free amino acids, especially taurine, glycine, arginine, glutamic acid and alanine, and other low molecular weight organic compounds such as organic acids, nucleotides and nucleosides, betaine or small peptides (Lee and Myers, 1997).

Since shrimp and lobsters show similar behavioural responses to chemical cues (Daniel et al., 2001), it is not surprising that commercial shrimp pellets have been tested to see if lobsters would eat and grow well on them. In Australian work with juvenile P. ornatus, P. cygnus and J. edwardsii, formulated shrimp pelleted feeds were readily eaten by the lobsters but their growth and survival were generally much poorer than those fed mussel flesh (Crear et al., 2000, 2002; Glencross et al., 2001; Smith et al., 2003). These observations suggest that the shrimp pellets were either nutritionally inadequate for, or not sufficiently attractive to, the lobsters. The latter appeared to be the most likely explanation as lobsters would cease feeding on the shrimp pellets within a 1-2 h of being offered whereas the attractiveness of mussel flesh persisted for 10 or more h.

Development of pelleted dry feed

General approach

The method used to develop an artificial feed for any newly husbanded animal typically follows one of two pathways: an iterative process based on diluting the animal's natural food with increasing amounts of less-natural constituents or a more structured process whereby the animal's requirements for key nutrients are defined and the ability of alternative feed ingredients to supply these nutrients is determined. Sometimes these two approaches may become blurred, especially in the early stages of artificial feed development when natural food

items are often used to improve the acceptance of compounded diets being used for nutritional requirement studies. This certainly has been the case with spiny lobsters where mussel flesh or other prey items have commonly been included in formulations to improve the acceptance of the pelleted feed (Crear *et al.*, 2000, 2002; Glencross *et al.*, 2001; Smith *et al.*, 2003; Perera *et al.*, 2005). This approach has enabled the nutritive value of potential feed ingredients to be determined and the lobster's requirements for critical nutrients to be further defined.

Nutritive value of feed ingredients

In considering the usefulness of a feed ingredient as a source of nutrients for assimilation by the animal, the likelihood of growth inhibitors or contaminating toxins being present must be considered. A thorough critique of this aspect is beyond the scope of this review. For an account of naturally occurring growth inhibitors and toxic contaminants, readers are referred to reviews by Hardy (1999), Francis et al. (2001), Hendricks (2002) and Burgos-Hernandez et al. (2005). Poor storage or handling of the ingredient can also diminish its value since bacterial contamination and/or oxidative decomposition during or after production can destroy critical nutrients or produce toxins such as biogenic amines (Aksnes and Mundheim, 1997; Opstvedt et al., 2000; Shakila et al., 2003). However, from a pure nutritional perspective, nutritive value of an ingredient is typically first assessed by measuring its apparent digestibility. Sadly, very little information is available on the apparent

Table 1. Apparent digestibility (mean \pm SE) of ingredients of potential use in artificial grow-out feeds for spiny lobsters

Ingredient	Dry matter	Crude protein	Total lipid	Gross energy	Ref			
	Apparent digestibility coefficient (%)							
Marine protein sources								
NZ blue mussel meal		97.6 ± 0.1			1			
NZ green-lipped mussel meal	76.4 ± 3.0	88.8 ± 1.98	63.7 ± 6.04	83.3 ± 2.45	2			
Shrimp head meal		77.2 ± 19.1			1			
Crustacean meal (Lango)	53.2 ± 3.0	85.2 1.98	53.4 ± 6.04	72.0 ± 2.45	2			
Fish meal (67% CP)		62.5 ± 1.4			1			
Fish meal (67% CP)	67.4 ± 3.0	84.2 1.98	78.1 ± 6.04	80.7 ± 2.45	2			
Squid meal		7.3 ± 2.3			1			
Krill meal	68.5 ± 3.0	88.6 ± 1.98	64.4 ± 6.04	77.5 ± 2.45	2			
Terrestrial protein sources								
Lupin flour		100.1 ± 6.0			1			
Wheat gluten		90.1 ± 9.7			1			
Soybean meal		60.5 ± 19.0			1			
Pea meal		52.0 ± 8.7			1			
Canola meal		38.3 ± 13.7			1			

Measured in *J. edwardsii* (Ward *et al.*, 2003a)

²Measured in *P. ornatus* (Unpublished data: S.J. Irvin and K.C. Williams, CSIRO Marine & Atmospheric Research)

digestibility of feed ingredients for spiny lobster and this is an area where further work is needed. Table 1 provides data on the apparent digestibility of some feed ingredients that have been used in feeds development research for spiny lobsters. As for penaeid shrimp (Smith et al., 2001) and mud crab (Catacutan et al., 2003), spiny lobsters digest the protein of animal and some plant meals with high efficiency. Particularly interesting is the high apparent digestibility of lupin and wheat gluten protein, a finding that is similar to that observed for fish and other crustaceans (Smith et al., 2001). However, the apparent digestibility of the protein in commercial squid meal measured in J. edwardsii was unexpectedly low (7 %) and suggests that excessive heating and protein denaturation during the manufacturing process may have been the cause. Whether or not that result is typical of processed squid meal or an aberrant batch of the product is unknown. Clearly, more work needs to be done to measure the digestibility of feed ingredients that have potential to be used in artificial feeds for spiny lobsters. With P. ornatus, difficulties in collecting a representative sample of faeces have been overcome by using a novel balloon method, which prevents voided faeces coming in contact with the water (Irvin and Tabrett, 2005).

State of nutritional knowledge pre-2000

Several reviews on the nutritional requirements of spiny lobsters have been published (Conklin, 1980; Kanazawa, 1994). However, the paucity of work with spiny lobsters meant that information gathered on the clawed homarid lobsters was heavily relied upon for these reviews. Kanazawa and Koshio (1994) and Teshima (1997) compared the essential lipid nutrition of the Japanese spiny lobster P. japonicus with that of homarid lobster and penaeid shrimp and concluded that essential fatty acid, phospholipid and sterol requirements of these crustaceans are all very similar. However, it must be stated that less than a handful of studies were relied upon in reviewing the essential lipid requirements of spiny lobsters. The intent of this paper is not to present a comprehensive review of spiny lobster nutrition but rather to update our knowledge on this subject by examining more recent research and how this

is being used to develop high performance pelleted feeds for grow-out of spiny lobsters.

State of protein and lipid knowledge post-2000

A coordinated Australian growth study examined the dietary protein and total lipid requirements of very small (<4 g initial weight) P. cygnus, P. ornatus and J. edwardsii lobsters (Glencross et al., 2001; Smith et al., 2003; Ward et al., 2003). Six pelleted dry feeds containing incremented amounts of crude protein (from 35 to 60% dry matter) at each of two levels of total lipid (6 and 10%, dry matter) were prepared centrally and distributed to the collaborating laboratories. An additional diet of either fresh blue mussel, Mytilus edulis or a kuruma (Penaeus japonicus) shrimp feed was included in the experimental array as a reference. In each of the experiments, lobster survival was good (>75%) and growth improved curvilinearly with increasing dietary protein content but the response depended on both the lipid content of the feed and the species of lobster. With P. cygnus, the best growth occurred with feeds containing 55% crude protein (DM) and was better for the lowthan the high-lipid feeds (Glencross et al., 2001). With P. ornatus, the best growth occurred at calculated dietary protein asymptotes of 47 and 53% (DM) for the 6 and 10% lipid feeds, respectively; at the higher protein levels, lobster growth was better for the high- compared to the low-lipid feeds (Smith et al., 2003). With J. edwardsii, dietary lipid level had no significant effect on the response to protein with growth being best at calculated dietary digestible protein asymptotes of 33-35%, dry matter (equivalent to 42-47% crude protein, dry matter) (Ward et al., 2003b). Eight pelleted feeds containing serially incremented protein (from 35 to 60%, dry matter) at a constant total lipid content of 9% dry matter were examined in another study with larger J. edwardsii (initial weight of \sim 70 g) (Crear et al., 2001). As with small lobsters, growth rate of the larger lobsters improved curvilinearly with increasing dietary protein but the response flattened out only when the dry matter crude protein content of the feed was greater than 50%. In all four studies, the reference feed (mussel flesh or kuruma shrimp pellets) resulted in significantly better growth, often

twice as good, as the best experimental feed. These results suggest that different spiny lobster species have different dietary protein and lipid requirements and thus may require feeds specifically tailored for each species. However, as the growth of the lobsters on the pelleted experimental feeds was poor, it is questionable whether these results truly were a reliable measure of the animals' dietary protein and lipid requirements

Improving the acceptance of pelleted dry feeds

A common observation in all of the above studies was that lobsters would readily eat the pelleted experimental feed when first given but would then be ignored after being immersed in the water for 1-2 hours. This contrasted with the response to mussel flesh where lobsters continued to feed after it was in the water for 10 or more hours. This observation prompted experiments to examine why the attractiveness of pelleted feed diminished after such a short time of immersion. Working with juvenile J. edwardsii, Tolomei et al. (2003) measured the excitatory capacity and the attractability of shrimp pellets and mussel flesh after these had been immersed in water for periods of up to 8 h. They also examined the chemoattraction of different concentrations of glycine, taurine and betaine. The lobster's attraction to shrimp pellets and mussel flesh declined with increasing immersion time. However, feeding shrimp pellets that had been soaked for periods of 0.5, 2, 4 or 8 h did not affect the growth, feed conversion or survival of the lobsters during a 12-week growth trial. The greatest feeding behavioural response (antennule flicking) of the lobsters occurred with glycine at concentrations of 10^{-4} to 10^{-6} mol/L while the concentration of taurine had to be increased to 10⁻² mol/L to get a similar high behavioural response; the response to betaine remained low at all concentrations over the range 10^{-8} to 10^{-2} mol/L.

A quite different response was observed with juvenile *P. ornatus* (Williams *et al.*, 2005). They sought to characterize feeding cues by quantitating the nitrogenous compounds leaching from mussel flesh or pelleted dry feeds following immersion in water over a period of 7.5 h and correlating the leachate with the preference of the lobsters to the

same soaked or non-soaked feeds. Homogenates of natural prey items, either polychaete, shrimp, mussel or squid, were included in the pelleted feed so that the chemical signatures of the leachates would be different. The lobster's feeding preference was most positively correlated with the amount of soluble protein, glycine and taurine that leached from the feeds. However, lobsters showed a much higher preference for mussel flesh than for the pelleted dry feeds even when 5-h soaked mussel was compared with non-soaked pelleted feed. These results suggested that increasing feeding frequency and including protein hydrolysates and other free amino acid-rich ingredients in the dietary formulation might be practical ways for prolonging the attractiveness of pelleted artificial feeds. Floreto et al. (2001) used krill hydrolysate to enhance the acceptance of soybean-based feeds for the American lobster, Homarus americanus, and found that soybean could provide almost 90% of the dietary protein with no adverse effects on growth relative to feeding mussels.

Re-examination of protein requirements

To test the value of including krill meals in feed formulations for spiny lobsters, an experiment was carried out with juvenile P. ornatus to re-examine dietary protein requirements (Smith et al., 2005). Freeze-dried krill hydrolysate and freeze dried krill meal were used at a constant inclusion rate of 8 and 30%, respectively, and the protein content of the feed serially increased by adding incremental amounts of fish meal at the expense of starch to produce five isolipidic feeds that varied from 34 to 61% crude protein dry matter (31 to 56% digestible crude protein dry matter). An additional diet of thawed green-lipped mussel, Perna canaliculus, was included in the treatment array as a reference. The formulation and determined chemical composition of these feeds are detailed in Table 2. During the 8-week experiment, growth rate of the lobsters fed the pelleted feed four-times daily continued to increase with increasing dietary crude protein content, with no suggestion of the response plateauing even at the highest level examined (61%, dry matter; 56% digestible, dry matter) (Fig. 1). Thus, juvenile *P. ornatus*, require high dietary

Table 2.	Formulation and key chemical composition* of feeds used in re-e	valuating				
the dietary protein requirement of juvenile <i>P. ornatus</i> (Smith <i>et al.</i> , 2005)						

Attribute	Feed label							
	33CP	40CP	47CP	54CP	61CP	Mussel		
-	Formulation (% as used)							
Fish meal	0	9.0	18.0	27.0	36.0			
Starch	27.1	20.4	13.6	6.8	0			
Fish oil	4.4	3.3	2.2	1.1	0			
Diatomaceous earth	5.6	4.4	3.3	2.2	1.1			
Wheat flour	14.0	14.0	14.0	14.0	14.0			
Krill meal	30.0	30.0	30.0	30.0	30.0			
Krill hydrolysate	8.0	8.0	8.0	8.0	8.0			
Other ¹	10.9	10.9	10.9	10.9	10.9			
	Composition (dry matter basis)							
Crude protein	33.8	40.4	46.6	53.6	61.2	57.4		
Dig. CP	31.0	36.8	41.9	48.9	56.3	nd		
Lipid	13.0	13.7	13.8	12.8	12.8	11.5		
Gross energy (kJ/g)	19.6	19.6	20.2	20.5	20.8	19.6		
Digest. energy (kJ/g)	17.9	18.2	18.4	18.7	19.0	nd		

See Smith *et al.* (2005) for more information on the other ingredients and the chemical composition of the feeds

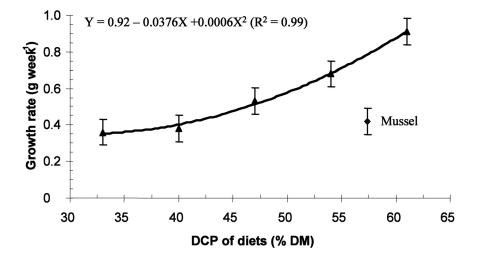


Fig. 1. Relationship between the digestible crude protein (DCP) content of the feed (on a dry matter basis) (X) and growth rate of P. ornatus lobsters fed pelleted feeds for the 0-8 week period of the growth response experiment (Y). The growth rate of lobsters fed thawed green-lip mussel is shown at its corresponding crude protein content (dry matter basis). Error bars are \pm SEM.

protein specifications (viz, >60% crude protein, dry matter; >56% digestible crude protein, dry matter) to achieve high growth rates on pelleted feeds.

Adequacy of mussel flesh as sole feed

Interestingly, lobsters fed the thawed mussel in the experiment of Smith et al. (2005) grew well for the first four weeks but thereafter the growth rate of the lobsters progressively declined and deaths, mainly at times of moulting, increased. Survival of lobsters fed thawed mussel was only 41% compared to 73-84% for lobsters fed pelleted feeds. Moreover, mussel-fed lobsters became increasingly pale in colour, and those that died were invariably very pale or pink-tinged. Junio-Menez and Ruinata (1996) also found thawed green mussel, Perna virdis, to be an inadequate sole feed for juvenile P. ornatus with only 6% of lobsters surviving the 4-month experiment. In a New Zealand study with juvenile J. edwardsii, fresh blue (Mytilus galloprovincialis) or green-lipped (P. canaliculus) mussel resulted in significantly better growth and survival than feeding 3-day aged mussels or frozen mussel (James and Tong, 1997). These studies collectively indicate that freezing may have deleteriously altered the nutritional quality of the mussel, perhaps reducing vitamin potency or altering the bioavailability of some critical micronutrient. The paleness of the lobsters fed the mussel in the study of Smith et al. (2005) suggested a sub-optimal intake of astaxanthin.

Dietary carotenoid and astaxanthin

Carotenoids are an expensive (about US\$3,000/kg of active astaxanthin) and critical component of crustacean feeds but little is known of the carotenoid requirements of tropical spiny lobsters. Most animals are unable to synthetise carotenoids *de novo* and thus are dependent on an exogenous dietary supply to meet their requirements (Meyers and Latscha, 1997). In crustacean and fish, astaxanthin is the predominant carotenoid. It is stored as free astaxanthin or as astaxanthin esters where the astaxanthin molecule is attached to a fatty acid. Astaxanthin has many functions in crustaceans. It has been demonstrated to be important in reproductive performance (Pangantihon-Kuhlmann *et al.*, 1998; Perez-Velazquez *et al.*, 2003) and in

larval and post-larval development (Petit *et al.*, 1997; Pan *et al.*, 2001). It also appears to have an important role as an antioxidant and to be involved in immunocompetence and stress tolerance (Meyers and Latscha 1997; Linan-Cabello *et al.*, 2002; Chien *et al.*, 2003). In crustaceans, astaxanthin is not readily synthesised from other ingested carotenoids, with β -carotene having the highest bio-conversion efficiency of about 50% (Meyers and Latscha 1997).

Crear et al. (2002) evaluated six commercial shrimp pelleted feeds and fresh blue mussel, M. edulis as feeds for juvenile J. edwardsii. Three of the shrimp feeds were formulated for the kuruma shrimp, P. japonicus and the other three for the black tiger shrimp, Penaeus monodon. These feeds were fed to slight excess for 134 days and measurements made of growth performance, carapace colour and body composition of the lobsters. Lobsters grew significantly better on the mussel than on the shrimp pelleted feeds but other productivity traits did not differ greatly between the various feeds. However at the conclusion of the experiment, carapace colour of the lobsters differed markedly between the feeds, with colour scores being markedly higher for the three kuruma shrimp feeds (4.2-5), lowest for the black tiger shrimp feeds (1.4-1.8) and intermediate for the mussel (4). Highly significant curvilinear and linear relationships were found between dietary carotenoid content and the lobster's carapace colour and tissue carotenoid content, respectively. These authors concluded that lobsters need a dietary carotenoid level of around 115 mg/kg to ensure a carapace colouration score of >4, equivalent to that of wild-caught juvenile J. edwardsii.

The poor growth, low survival and pale exoskeleton colouration of juvenile *P. ornatus* fed frozen green-lipped mussel in the work of Smith *et al.* (2005) prompted a further study to examine the dietary astaxanthin requirement of this species (Barclay *et al.*, 2006). They carried out a 12-week experiment with juvenile *P. ornatus* fed either pelleted feeds supplemented with astaxanthin (providing total dietary carotenoid contents of 30, 60, 90 or 120 mg/kg) or one of two frozen mussel reference feeds-blue, *M. edulis*, or green-lipped, *P. canaliculus*, mussels. The pelleted feeds were based

on the formulation of the best feed in the earlier study (Feed 61CP; Table 2) except that astaxanthin was incrementally added to produce the desired dietary astaxanthin specifications. Neither growth rate nor survival showed a dose response to dietary astaxanthin but lobsters fed the two mussel feeds consistently grew more slowly and survival tended

to be lower, especially during the last 4-weeks of the experiment (Fig. 2A). Exoskeleton colour increased directly as the dietary carotenoid content of the pelleted feeds increased but the colour of lobsters fed the mussel was only poorly related to the carotenoid content of the mussel (Fig. 2B). Similarly, whole body total carotenoid content of the

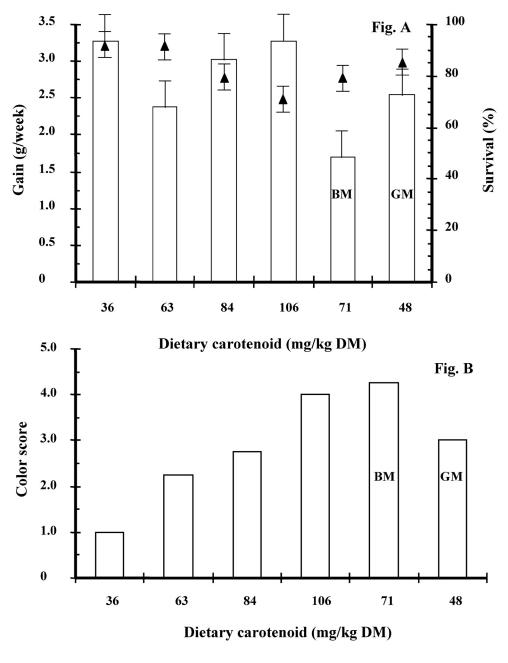


Fig. 2. Effects of dietary carotenoid on growth (bars) and survival (\blacktriangle) (Fig. A) and on exoskeleton color score (Fig. B) of juvenile *P. ornatus* fed either pelleted feeds providing incremental supplements of free astaxanthin or frozen blue, *M. edulis* (BM) or frozen green-lipped, *P. canaliculus*, (GM) mussel. Error bars are \pm SEM (n = 4).

lobsters increased linearly with increasing dietary carotenoid for the pelleted feeds but the relationship was less clear for the mussel-fed lobsters (Fig. 3A). However, most of the carotenoid in the mussel was not astaxanthin, but other pigments most likely originating from the microalgae that had been consumed. When whole body astaxanthin content of the lobsters was examined in relation to the

free astaxanthin content of the feed, an excellent curvilinear relationship was seen for all feeds (Fig. 3B). Although the range of dietary astaxanthin examined in the experiment did not affect lobster productivity, it did markedly affect exoskeleton colour and tissue astaxanthin content, which could have important implications on the animal's immunocompetence and on the market acceptance of

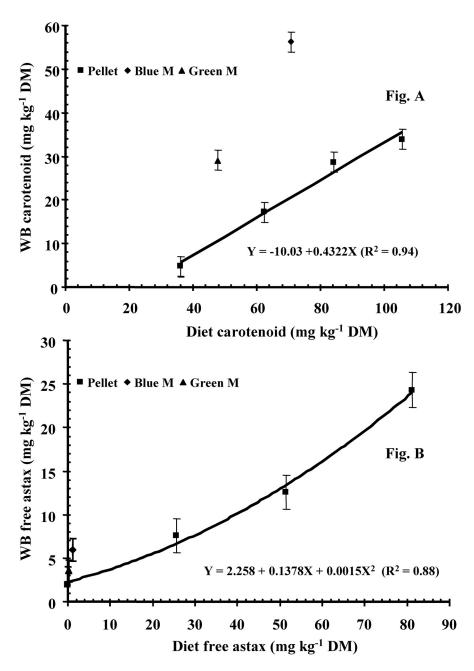


Fig. 3. Effects of dietary carotenoid content and whole body (WB) carotenoid content (Fig. A) and dietary free astaxanthin (astax) content and free astax content (Fig. B). Error bars are \pm SEM (n = 4).

the cultured lobster. Moreover, the study confirmed the findings of the earlier study (Smith *et al.*, 2005) that frozen mussels are not a suitable sole feed for P. ornatus

Neither the study of Crear *et al.* (2002) nor that of Barclay *et al.* (2006) were able to demonstrate an improved productivity response to dietary carotenoid, and thus could not define a true requirement. However, both studies showed dietary carotenoid supply had a clear and marked effect on lobster colouration, a feature that has considerable impact on the marketing and the priced paid for the lobster. If for this reason alone, a total dietary carotenoid specification of at least 100 mg/kg, and an astaxanthin equivalent of not less than 70 mg/kg, is recommended.

Future research perspectives

Much progress has been made in the past five years or so to better define the nutritional requirements of post-larval spiny lobsters and to develop suitable compounded pelleted dry feeds. This research has shown that the tropical P. ornatus grows best when provided with feeds that are high in digestible protein (>56 % dry matter) and with 10-11 % total lipid dry matter. More temperate species such as P. cygnus and J. edwardsii appear not to need as high a dietary protein or lipid specification as P. ornatus but this conclusion needs further validation. Very little recent research has been done to quantify the lobster's requirements for essential lipids, especially sterol, phospholipid and essential fatty acids, and this will assume greater importance when terrestrial feed ingredients are used to replace marine sources in cheaper dietary formulations. A compounded artificial feed that is well accepted by Panulirus and Jasus lobsters and which produces good growth and survival has been developed. However, this formulation presently requires high inclusion rates of krill products, which are expensive. The task ahead for researchers will be to develop less expensive feed formulations that lobsters readily accept and grow well on. This will require more information on the apparent digestibility and acceptability of alternative and cheaper feed ingredients, most likely of terrestrial rather than marine origin, and further definition of the lobster's requirements for critically important nutrients and energy.

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