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REVIEW

REVIEWS IN Aquaculture

Recent advances and future directions in practical diet formulation and adoption in tropical Palinurid lobster aquaculture

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Abstract

The spiny lobsters *Panulirus ornatus* and *Panulirus homarus* are important developing tropical aquaculture species, with high demand and limited supply. The established industry in Vietnam relies on wild-caught mixed seafood bycatch as feed, a practice linked to water quality degradation and potentially disease proliferation in lobster aquaculture, necessitating formulated feed development. The emerging Indonesian and Australian industries lack the crustacean and mollusc component of the seafood bycatch used in Vietnam, increasing the need for manufactured feeds. The development of such feeds is reliant on knowledge of nutrient requirements, ingredient quality, physical feed requirements, and the link between feeding behaviour and feeding methods. This review will elaborate on the development of these knowledge areas to date and outline the two main reference diet recipes that are available as the basis for future research. Research to date has focused on developing a feed recipe that will be consumed and supports adequate growth rather than steering commercial least-cost formulation practices. Future research is clearly needed to inform formulation, but equally an understanding of the disparate emerging lobster farming industries and their drivers for the adoption of formulated feeds is required to ensure that such research is applied. This will require engagement throughout the supply chain to ensure that research is implementable and to address farmer perception toward formulated feeds. Technical aspects of feed manufacture and scale-up of feed developments will be critical to the adoption of research results, while validation through semi-commercial benchmarks and demonstration farm models are expected to increase commercial uptake of developed feeds.

KEYWORDS
formulated feed, nutrient requirement, Panulirus ornatus, Panulirus homarus, spiny lobster, trash fish

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1 | INTRODUCTION

Spiny lobsters are among the world's most valuable seafood,[1,2] driven by strong demand and limited global supply.[3] Lobster farming relies heavily on wild-caught seafood as the major source of nutrition.[4–6] In Vietnam this includes fish, crabs, mussels and echinoderms, reflecting the natural food preferences of lobsters.[4,5,7–9] While this practice ensures that feeds are palatable and largely nutritionally complete, it has led to considerable water quality degradation that in turn can make the environment less suitable for lobster culture and lead to disease.[7,10,11] Water quality and access to appropriate and affordable feed have been identified as major perceived constraints to the lobster aquaculture industry[5] both of which lead the industry toward development and implementation of formulated feeds. With the expansion of the lobster industry in Vietnam and emerging industry in Indonesia, it is increasingly important to develop formulated feeds to ensure sustainable development [3116,11]. We, therefore, aim to critically evaluate and summarise available data on nutrient and feed requirements in the context of spiny lobster biology and industry development, identify barriers to implementation of formulated feeds, and suggest future research focus areas.

Spiny lobsters undergo significant changes in body form, feeding and digestive physiology through their lifecycle.[12] Phyllosoma larvae are specialised toward planktonic feeding and puerulus is a non-feeding life stage.[13–15] Since the majority of tropical lobster production grows out of wild-caught pueruli[3,5] this review will focus on post-puerulus juvenile to adult lobsters. Puerulus supply in Southeast Asia is made up of two species; *Panulirus ornatus and Panulirus homarus*, with the former dominating puerulus recruitment in Vietnam and the latter more common in Indonesia.[3] Recent commercial hatchery development in Australia has focused on *P. ornatus*. These two species will therefore be the main focus of this review, drawing information from research conducted on other spiny lobsters where it is relevant.

2 | SPECIES DIFFERENCES (PANULIRUS HOMARUS CF PANULIRUS ORNATUS)

P. homarus and P. ornatus are both farmed in Indonesia and Vietnam, while commercial production of *P. ornatus* has begun in Australia. There is nascent lobster aquaculture development using these same two species in the Philippines and India, although both lack government support and commercial investment (Jones et al., 2019). Until recently, *P. ornatus* comprised 90% of Vietnamese production and the remaining 10% attributable to *P. homarus*.[3] Puerulus capture in Indonesia is dominated by *P. homarus*[3] and the export of this species has provided the basis for recent increase of lobster aquaculture volumes in Vietnam, which is now comprised of approximately 1500 t of *P. ornatus* production and 2000 t of *P. homarus* (*pers.comm*. Dr Le Anh Tuan, Nha Trang University, 30 August 2020). Once growout is complete, these species are marketed differently, with the higher value *P. ornatus* exported to China, while *P. homarus* are marketed domestically within Vietnam. It appears that both species will feature prominently in the future of tropical lobster aquaculture, necessitating an understanding of their relative growth dynamics and feed requirements.

Reported growth for *P. homarus* is higher than for *P. ornatus* up to approximately 100 g after which *P. ornatus* grows faster.[16] This results in an overall faster growth rate for *P. ornatus* which is likely due to maturation of *P. homarus* at a smaller size. Both species appear to respond similarly to MOS supplementation,[17,18] suggesting that the importance of gut microflora control is common across lobster species. By comparison, these tropical species are much faster growing than the various well-known temperate species subject to significant fisheries (eg. *Jasus edwardsii*, *Panulirus cygnus*). The tropical species reach an acceptable market size in 1 to 2 years, while the temperate species require more than 4 years of growth.[19] Thus, the tropical species appear to be the best candidates for aquaculture development.

3 | FEED INGESTION AND DIGESTION

Formulated feed development for lobsters is in its infancy, with considerable focus on physical form and appetite enhancement in order to achieve acceptable feed intake. Ingestion in crustaceans is a complex process, involving a combination of chemo-sensing and manipulative appendages in addition to mouthparts that combine to determine the objects that are ingested. Optimising feed intake, therefore, requires an understanding of the function of feeding appendages and mouthparts that lead to ingestion. Morphology of the mouthparts and foregut of members of the genera *Panulirus* and *Jasus* are highly similar[13] and so are combined for the purpose of this section. Juvenile and adult spiny lobster mouthparts function to create respiratory currents across the gills, primary feed trituration and to manipulate feed particles into the oesophagus.[8] Periopods appear to be the primary appendages for selecting feed to be passed to maxillipeds for primary feed size reduction and further manipulation.[13,14,20] Water currents formed by the three sets of maxillipeds may transport small particles toward the mouth opening while passing larger particles anteriorly to two sets of maxillae. Setae and spines on the maxillae are used to select and direct food into the mandibles, while discarding unwanted food particles anteriorly.[20] Mandibles are heavily calcified and contain molar and incisor processors that use shear forces for size reduction of large and calcified material as it is ingested, before further trituration in the gastric mill.[13] External size-reduction of food materials results in waste feed particles escaping the mouthparts or being rejected without ingestion, leading to inefficient feed intake and utilisation which may be reduced by appropriate formulated feed size and shape.[14,20]

The chitin-lined foregut (proventriculus) of post-puerulus lobsters is divided into anterior (cardiac) and posterior (pyloric) sections.[21,22] Ossicles in the anterior section make up the gastric mill which is responsible for particle size reduction after feed ingestion.[13,21] The cardiopyloric valve allows small particles to enter the posterior section of the foregut while those too large to pass through combine with enzymes from the midgut gland (hepatopancreas) and are reprocessed through the gastric mill.[21] A further screening step occurs upon exiting the posterior foregut, where a filter press ensures that only very fine particles and liquids enter the midgut gland for further digestion and absorption.[21] Particles that do not pass through the filter press are either passed to the mid-gut for defecation or mixed with those particles that were too large to pass through the cardiopyloric valve before again passing through the gastric mill.[21] This process dictates that feed particles must be able to be ground to a fine size before digestion. Fine grinding of feed raw materials has commonly been used for shrimp feeds for this reason, as evidenced by optimal growth of *Litopenaeus vannamei* when feed particle sizes average 124 μm prior to feed production.[23] Indigestible particles greater than 100 nm are excluded from the midgut gland (hepatopancreas) of *Penaeus monodon*,[24] indicating that improved growth associated with fine grinding is likely due to more rapid trituration and digestion rather than facilitating direct transfer of feed particles into the midgut gland.

Interestingly, reducing the particle size of fish meal below 500 μm failed to improve feed apparent digestibility for *J. edwardsii*[25] however it remains unknown whether fine grinding is required for optimal feed intake and growth in spiny lobsters. Feed intake of formulated feed by lobsters is considered to be limited by foregut capacity[26,27] which is likely influenced by the expansion of the feed after ingestion and the passage of feed out of the foregut. Extruded feeds typically expand considerably upon hydration and may therefore take up more physical space than pressed pellets, reducing the capacity for new feed ingestion. Considering the size-selective recycling of feed particles through the gastric mill, gut passage rate is likely related to the particle size of raw materials. Thus particle size and rate of digestion are likely important for optimising feed intake capacity and appetite revival between meals.[26] In this sense, rate of digestion is independent of apparent digestibility coefficient (ADC), since ADC and gut transit rate can be inversely correlated,[28] indicating that slower rates of gut transit facilitate more complete digestion. Alternatively, water-soluble ingredients such as hydrolysates and sodium caseinate are likely to facilitate rapid transfer of feed to the gastric gland, making them rapidly available for assimilation and growth and freeing up foregut space for further feed ingestion. This approach was pioneered with *J edwardsii*[29,30] in an attempt to make a low carbohydrate feed with large amounts of soluble protein from sodium caseinate. The application of this concept appears to have been limited for this species due to the importance of carbohydrate as an energy source and relatively low protein requirement, however, it features in recently published reference diets for the subtropical lobster *Sagmariasus verreauxi* and tropical slipper lobsters *Thenus australiensis* with almost 50% of the feed comprised of sodium caseinate.[31,32]

4 | NUTRITION AND NUTRIENT REQUIREMENTS

4.1 | Nutrition and size relationships

Little is known about differences in nutrient requirements in relation to lobster age or size. While many species of fish have decreasing protein requirement as a percentage of the feed as the fish increase in size[33–36] it appears that lobsters (*J. edwardsii*) have the opposite trend[37,38] although data is lacking for the Palinurid lobsters of particular interest for this review. As well as being unnecessarily expensive, excess protein leads to nitrogen waste, contributing to existing water quality issues with lobster aquaculture. Therefore, optimal nutrient levels, particularly for protein, need to be confirmed and elaborated for the future of sustainable economic aquafeeds for spiny lobsters.

4.2 | Protein and amino acid requirements

Growth of *P. ornatus* appears to increase linearly with increasing digestible protein in the feed[39] at least for feed containing up to 56% digestible protein (61% crude protein). This is consistent with *P. cygnus*, with the best growth and feed conversion coming from the highest protein, lowest fat feeds tested[40] but is not consistent with *J edwardsii* which appears to have clear dietary protein optimum at 29%–31% digestible protein (approx. 37% crude protein).[38] This indicates that generalising nutrient criteria across genre of spiny lobsters may be misleading.

Deriving appropriate nutrient requirements is predicated on removing non-target growth-limiting factors, which appears to have been the case with earlier attempts to quantify protein requirements for *P. ornatus*, indicating a lower requirement of 53% crude protein.[41] Meeting these high protein requirements effectively with appropriate raw materials will be important for the future development of feeds for *P. ornatus* and *P. homarus*. While lobsters are a particularly valuable aquaculture product, the high cost of protein-dense ingredients will necessitate cost–benefit analysis to understand the trade-off between growth and dietary protein levels in commercial feed development.

Amino acid requirements have not been a research priority for lobster nutrition studies, presumably due to the high levels of fish meal or other marine proteins typically used eg.[6,42,43] and the assumption that essential amino acid requirements will be met by the marine protein component. The closest guidance for essential amino acid requirements comes from prawn feeds where requirement values have been well studied and are similar across species.[44] If we assume that the higher protein requirement documented for *P. ornatus* also necessitates a proportionately high level of essential amino acids as a percentage of feed, we can hypothesise essential amino acids requirements for lobsters according to Table 1. While kuruma prawns have minimum protein requirement of 42% DM,[45] commercial examples contain similar protein levels to those required by *P. ornatus*.[41,43,47] These kuruma prawn diets appear to be among the highest performing feeds for *P. ornatus*,[41] however, appetite stimulation and growth rates appear to be superior when fresh mussels are the primary feed material,[43,48] consistent with findings with *J. edwardsii*.[49] Mussels and other reference seafood products like squid and fish all contain large amounts of protein on a dry matter basis (Table 1) which is likely a major contributor to the success of these proteins as feed for *P. ornatus*. While the minimum essential amino acid requirements for kuruma prawns appears to be consistently lower than mussel and other reference proteins, the amino acid pattern in relation to lysine level is consistent across the kuruma prawn requirement value and

TABLE 1 Hypothesised essential amino acids requirements for *P. ornatus* based on kuruma prawn amino acid requirements in relation to protein requirement and comparison to reference proteins

	Kuruma prawn requirements[44,45]	*P. ornatus* presumed requirements	Squid meal[44]	Fish meal (Anchovy)[44]	Blue Mussel[46]	Kuruma prawn requirements	Squid meal	Fish meal (Anchovy)	Blue Mussel	Kuruma prawn requirements	Squid meal	Fish meal (Anchovy)	Blue Mussel
	% feed	% feed	% DM	% DM	% DM	% CP	% CP	% CP	% CP	% Lys	% Lys	% Lys	% Lys
Protein	42	61[41]	76.5	65.4	59.6								
Arginine	1.6	2.3	5.8	3.7	4.0	3.8	7.6	5.6	6.7	84.2	84.2	96.5	72
Histidine	0.6	0.9	2.1	1.6	1.1	1.4	2.7	2.4	1.8	31.6	31.6	34.2	30.5
Isoleucine	1.3	1.9	4.0	3.1	2.6	3.1	5.2	4.7	4.4	68.4	68.4	66.4	59.9
Leucine	1.9	2.8	6.9	5.0	3.9	4.5	9.0	7.6	6.5	100	100	115.5	97.8
Lysine	1.9	2.8	6.0	5.1	4.3	4.5	7.8	7.8	7.2	100	100	100	100
Methionine	0.7	1.0	2.7	2.0	1.3	1.7	3.5	3.0	2.2	36.8	36.8	44.9	38.2
Phenylalanine	1.5	2.2	3.3	2.7	2.3	3.6	4.3	4.1	3.9	78.9	78.9	54.4	52.1
Threonine	1.3	1.9	3.4	2.8	2.7	3.1	4.5	4.3	4.5	68.4	68.4	57.1	55.2
Valine	1.4	2.0	4.0	3.5	2.8	3.3	5.2	5.4	4.7	73.7	73.7	65.9	68.7

Note: Presumed *P. ornatus* requirements are minimum criteria derived by adjusting kuruma prawn amino acid requirements by a factor of 1.42, in line with their differing protein requirements. Note that cysteine and tryptophan are excluded due to inconsistency of analysis and reporting.

the reference proteins (Table 1) and is likely to be a good reference for the development of our knowledge on essential amino acids requirements. The total amount of specific amino acids, as well as the ratio of essential to non-essential amino acids, may mediate the requirement values. Both squid and mussel proteins stand out in being particularly high in arginine as a % of protein compared to the equivalent value for fish meal, which may contribute to the success of mussels as a sole feed for spiny lobsters.

4.3 | Energetics: fat, carbohydrates and protein as energy sources

Crustaceans generally do not grow well on feeds containing more than 10% lipid[50] and lobsters fed 'trash' fish also appear to perform better on lower lipid fish species.[4] Homarid lobsters have a preference for carbohydrate over lipid energy[51] although it is not clear if this represents positive aspects of dietary carbohydrates, or an aversion to diets with excessive lipids, consistent with other farmed crustaceans. *P. cygnus* likewise grow better on feeds with 6% fat compared to 10% fat, with the difference coming from fish oil.[40] Data concerning optimum lipid content for *P. ornatus* is limited, however, they appear to grow better at 10% lipid rather than lower levels, and they appear to be better able to take advantage of higher protein feeds at this dietary lipid level.[41] As described above, this study was inconclusive due to the commercial karuma shrimp feed supporting much higher growth than any of the experimental feeds. Nonetheless, this commercial feed contained 12.2% lipid and therefore indicates that there may be an optimal level of lipid above 10% in feeds for *P. ornatus*, which critically needs to be elucidated for appropriate feed formulation.

Limited information is available on carbohydrate source on growth characteristics of lobsters. Carboxymethylcellulose (CMC) is digestible for *J. edwardsii* and carbohydrate sources differ with their postprandial residence time, indicating differences in the speed of digestion or glucose utilisation.[30] Carbohydrate source may also impact intermolt period, which will be reflected in growth rates.[52] Carbohydrates are likely to be a major component of lobster feeds in order to effectively maintain water stability, necessitating an understanding of growth impacts and dose-optimisation of carbohydrate sources for lobster feeds. Alternatively, less conventional feeds relying on protein binding, with or without transglutaminase to facilitate binding, may better facilitate elevated protein content through eliminating the carbohydrate binder.

4.4 | Lipids: fatty acids, cholesterol and phospholipid requirements

Little is known about the fatty acids requirements of spiny lobsters. Omega-3 fatty acids are generally considered to be essential for crustaceans, as are the specific highly unsaturated omega-3 fatty acids eicosapentaenoic acid (EPA; 20:5n-3) and docosahexaenoic acid (DHA; 22:6n-3).[44] Williams[1] reported on previously unpublished data that suggested a requirement for EPA + DHA of 1.8% of the feed for *P. ornatus* which remains our sole guidance on likely fatty acids requirements for Palinurid lobsters.

Cholesterol is one of the key differences between the nutrient requirements of fish and crustaceans.[44] While fish can synthesise sufficient cholesterol to meet their needs, crustaceans require certain levels in their feeds in order to meet their cholesterol requirements for steroid hormone synthesis, conjugation of bile salts and regulation of cell membrane fluidity.[44] Irvin, Williams, Barclay and Tabrett[42] studied the cholesterol requirement for *P. ornatus*, arriving at an interim recommendation of 4 g/kg. While this study was designed to define requirements of *P. ornatus* for cholesterol, size-selective mortality in this trial likely affected results and only the feed with the highest dose differed from the others. Further research has indicated that 3 g/kg cholesterol supplementation supported greater growth and survival than higher levels[53] although lower supplementation levels were not investigated. Further refinement of cholesterol requirements and the need for supplementation will be important for more economical development of lobster feeds in the future, and to avoid negative effects of over-supplementation.

Phospholipids are required in order to transport lipid-soluble nutrients, including cholesterol, within the hemolymph.[54] The dietary essentiality of cholesterol and its dependence on phospholipids for transport has caused researchers to study the dietary requirements for these two nutrients in concert. It appears that spiny lobsters and slipper lobsters are able to synthesise phospholipids sufficiently to negate any essential nutritional requirement[55,56] however the interrelationship between these nutrient groups has been insufficiently explored since both of these studies supplemented dietary cholesterol in all feeds.

4.5 | Ingredient quality

A major focus of spiny lobster feed development to date has been to support sufficient feed intake and growth, which has generally fallen short of that provided by feeding fresh mussels.[48,57–60] Lobsters appear to be very sensitive to certain tastants or other feed quality traits that are lost on freezing, with poorer growth results reported when using frozen mussels as food compared to fresh ones.[39,61,62]

Heating raw materials during the drying process can reduce their nutritive value or palatability, as demonstrated for European lobsters.[63] This may go some way to explaining the large differences in raw material digestibility values determined for different protein raw materials for *J. edwardsii*[64] with reported values between 7% and 97% protein digestibility for different raw materials. This variability is particularly pronounced for squid protein, which is hypothesised to be due to temperature-induced protein aggregation during processing,[65] however, species-specific and methodological differences between studies is difficult to rule out as causes of variation.

Different fish meal types also affected the growth and potentially survival of *P. homarus*[66] which may be due to freshness, heating processes or other, yet to be defined, quality criteria. Developing raw material quality criteria will be important for the production of formulated lobster feeds of consistently high quality.

Storage conditions and processing freshness impact the quality of raw materials in aquafeeds, typically measured by total volatile nitrogen (TVN) and biogenic amines in the raw material.[67–69] Quantification of the impact of these quality parameters in 'trash' fish and raw materials for formulated feed will be critical for the future development of lobster feed formulations.

4.6 | Minerals

Minerals requirements of spiny lobsters have not been studied to date, with the presumption that requirements are satisfied by the culture water and feed without the necessity for supplementation.[1] Calcium, copper, phosphorous, potassium, magnesium, selenium and zinc are all required by crustaceans,[70] however it is unclear to what extent they need to be supplemented in practical feeds. Loss of minerals through ecdysis may impart a periodic necessity for supplementation and therefore some level of all of these minerals is recommended in practical feeds.[54,71]

Phosphorous and calcium play important structural and functional roles in crustaceans and their requirements are interrelated.[70] Phosphorous is typically in poor supply from good quality seawater whereas calcium is abundant and able to be absorbed from the water.[44,70] While calcium is not required in the feed for marine crustaceans, it is generally present in raw materials, which can inhibit phosphorous availability[70] leading to recommendations of calcium: phosphorus ratios less than 2:1 and in some cases, less than 0.5:1.[70] Phosphorous requirement values for crustaceans range from 1% to 2% of the feed[44] which leaves a broad range of potential minimum requirement values for phosphorous and maximum requirement values for calcium.

4.7 | Vitamins

Vitamins are required for optimal growth, metabolic function and survival.[44] Lobsters are no exception,[54] although their requirements have yet to be quantified. Requirements for all vitamins have been quantified for shrimp species[44] and lobsters are hypothesised to have similar requirements.[54] Vitamin supplementation is required for optimum growth and FCR of lobsters given feed containing predominantly wild fish, fish meal and wheat[4] which would imply that wild fish are, or can be, insufficient in vitamins for optimum production. While many vitamin requirements are relatively conserved between crustacean species, those for vitamin C, choline and inositol vary widely between species.[44,72] For other vitamins, it may be most prudent to follow requirements for kuruma prawns (*Marsupenaeus japonicus*) for preference and then for tiger prawns where kuruma prawn data is missing until further knowledge is generated for lobsters (Table 2).

Inositol is a low molecular weight sugar molecule that forms phospholipids (phosphatidylinositol)[44] and functions as an osmolyte.[73] Inositol-containing phospholipids can be cleaved into Inositol 1,4,5-triphosphate which is involved in control of critical cellular processes[44] and thus has vitamin-like properties. Of particular interest for lobster feeds is that Inositol 1,4,5-triphosphate mediates olfaction[74–76] and may therefore activate feeding responses in lobsters. Controlled release of inositol should therefore be studied in relation to sustained feeding behaviour on pelleted feeds.

TABLE 2 Vitamin requirements for kuruma and tiger prawns adapted from Reference 44

	Kuruma Prawn	Tiger Prawn
Fat-soluble vitamins		
A	-	2.5
D	-	100
E	-	90
K	-	35
Water-soluble vitamins		
Thiamin	60–120	14
Riboflavin	80	23
B6	120	72–89
Pantothenic acid	-	100
Niacin	400	7.2
Biotin	-	2
B12	-	0.2
Folacin	-	2
Choline	600	6200
Inositol	2000	3000
Vitamin C	50–100	50–100

4.8 | Astaxanthin and other carotenoids

Astaxanthin accumulation in lobster tissues indicates a potential antioxidant and health function of this carotenoid[61] which may increase resistance to stressors as has been shown for penaeid shrimp.[77,78] Astaxanthin is required at 50 ppm for optimal carapace color[61] although the benefits of higher supplementation levels remain unclear. Supplementation of 70 mg/kg gave better growth and feed conversion than lower levels[53] contrasting with previous results that indicated no difference in growth rates with astaxanthin supplementation up to 81 mg/kg in feeds for *P. ornatus*.[61] Further research found that a feed containing 800 mg/kg astaxanthin provided 55% higher growth than a feed containing 100 mg/kg.[66] Anecdotal evidence further suggests that 100 mg/kg of carotenoids reduces oxidative stress in the clawed lobster *Homarus gammarus*, increasing growth and survival.[79] Future research should elucidate whether this effect is consistent and whether it is specific to astaxanthin or whether it can be replaced by more cost-effective antioxidants.

4.9 | Nutrition and health

Manipulation of gut microflora appears to be important for optimisation of growth and health of spiny lobsters. Mannanoligosaccharide

(MOS) supplementation can support gut health, microbial community and growth rates of both *P. ornatus* and *P. homarus*.[17,80] *P. ornatus* responded to MOS supplementation to a feed of frozen fish and prawns with 10-fold higher abundance of aerobic bacteria, accompanied by more than 50% improvement in weight gain and improved survival, particularly after *Vibrio* challenge.[80] While MOS increased growth and intestinal health consistently for both species, both studies used particularly small lobsters, with a final weight of 2.9 and 4 g for *P. ornatus* and *P. homarus*, respectively. It appears that the optimal inclusion level of MOS decreases with lobster size[17] so validation for larger lobsters may be worthwhile for efficacy and cost optimisation. Probiotics have been investigated for *P. ornatus*, largely focused on bacterial disease resistance rather than growth effects.[81,82] While probiotics appear effective in *Vibrio* control, their implementation in feeds can be problematic due to their thermal sensitivity, limiting their use to cold-pressed pellets or post-processing applications. In light of the efficacy of MOS it is important to optimise methods of manipulating gut microflora for optimal growth and health benefits. For example, salts of organic acids have proven effective in controlling *Vibrio* in shrimp feeds[83,84] with sodium propionate increasing feed intake, growth and digestibility of phosphorous and energy.[83]

4.10 | Attractants

Decapods contain chemoreceptors on appendages, including walking legs and antennae, used to discriminate food from other particles.[85,86] In homarid lobsters these sensors are particularly sensitive to mussel extracts, but are also stimulated by a range of small nitrogenous compounds such as L-glutamate, hydroxyproline, ammonium chloride, L-aspartate, L-arginine, glycine, glutathione, betaine and taurine, in order of diminishing importance.[85,86] These nitrogenous compounds can be incorporated into lobster feeds in the form of fresh seafood, krill meal, fish hydrolysates or in refined forms of compounds such as amino acids or betaine, in order to increase feed intake.[6,43,48]

Taurine and glycine are the main water-soluble components from mussel flesh likely to contribute to feed chemoreception by lobsters.[43] Both compounds leach from the feed over time and are hypothesised to contribute to the extended feeding response documented for mussels compared to pelleted feeds, which are only consumed over a 2–3 h period[43,87] after which the attractant properties of the pellets are lost or the foregut capacity of lobsters limits further ingestion.[27]

Krill products have been seen as particularly important to ensure high uptake of feed and allow the formation of a dry feed for subadult lobsters without the need for fresh seafood components[48,88] however smaller lobsters (1 g) appear to respond much more strongly to fresh seafood products.[66] It is unclear whether this represents an ontogenetic shift in feeding preference or differences between raw materials used or experimental design. It is clear that more research is required into drivers of appetite and feed intake in spiny lobsters.

A common way to increase attractiveness of protein sources has been to hydrolyse the proteins, solubilising the protein and increasing the number of binding sites between amino acids and lobster chemoreceptors. Krill hydrolysates effectively improve growth of *P. ornatus*[88] although the authors have also identified that this product adds considerable cost to the feed and it is desirable to explore alternatives. Further research has identified that a variety of fish and crustacean hydrolysates can increase feed intake over a two-week period, however, it has yet to be established whether this translates into faster growth.[6] Defining criteria for hydrolysates or other appetite stimulants that consistently improve growth will be important for optimising growth rates and cost-effectiveness of commercial development of lobster feeds.

5 | PHYSICAL PROPERTIES OF FEED

Optimising the size and shape of feed is likely to minimise the need for external trituration, thereby reducing waste. Lobsters manipulate and break up pellets before ingestion and the degree to which this is necessary depends on the pellet size in relation to the lobster size. *J. edwardsii* progressively improve in feeding efficiency as they grow, with larger lobsters producing less waste, particularly for larger pellets.[20] Noodle-shaped pellets lead to superior growth of *P. ornatus* compared to disk-shaped pellets, however, those fed trash fish grew significantly better than any of the formulated foods, suggesting that other factors influenced growth to a larger degree than pellet shape.[89]

J. edwardsii feed more efficiently on 5 mm pellets in 35–45 mm carapace length (CL) size class, and 7 mm in 60–70 mm CL size class,[20] however, this study used square-cut pellets of equal length to diameter and it is unclear whether this result is consistent with noodle-shaped pellets. Cox, Jeffs and Davis[14] suggest that the less robust mouthparts of early juvenile (10–15 mm CL) *Panulirus argus* may be more suited to elongated, soft, pulpy feeds in the 1–2 mm range, while also suggesting that feed size and shape are not as important for larger lobsters. It is likely that fracturing of feed in its manipulation and trituration leads to considerable feed lost.[14,20]

Another factor impacting the physical properties of feed is moisture content and it has been recommended that feed for spiny lobsters contains at least 15% moisture.[66] This may reflect the effect of heat damage during drying on nutritional quality or creating textural differences, either of which could affect feed intake and/or growth. A better understanding of the reasons for this result is important, since it is challenging to store feed with greater than 10% moisture due to fungal and mould spoilage. Approaches to solve these challenges have either included mould-inhibitors or necessitate fresh manufacture of the feed prior use, cold storage or freezing. While freezing is convenient on a research-scale[48,58,90] it makes storage expensive and difficult, especially in locations where electricity is not available in close proximity to farms. Alternatively, 0.5%–1% glycerol inclusion can help maintain high moisture content of extruded feed.[91] Glycerol reduces available moisture (water activity) for mould formation[92] and may be useful for the development of a formulation of extruded feeds for small lobsters (<8 g) where moisture and texture appear to be important (Table 3,[90,93]). Mould formation in moist feeds can be further inhibited by organic acids and their salts, particularly propionic,

TABLE 3 Recommended pellet diameter, hardness and length for *P. ornatus*[93]

Lobster weight	Soft/Hard	Length
2 g	Soft	10–15 mm
50–60 g	Hard	10–20 mm
>100 g	Hard	10–35 mm

benzoic, sorbic, acetic acids and combinations thereof.[94] The combination of humectants such as glycerol and organic acids may therefore yield an appropriate shelf-stable moist feeds for lobster juveniles.

6 | FEEDING BEHAVIOUR

It appears that feeding *P. argus* and *J. edwardsii* to excess, once daily, is a superior method than the same ration spread between two daily meals.[26,95] However, this may be species-specific, with *P. ornatus* and *Panulirus versicolor* both reported to grow better when fed multiple meals per day.[41,96] It has also been proposed that feeding at or just after dusk is preferable to feeding at other times for both *P. argus* and *J. edwardsii*.[95,97] Feeding behaviour changes with the developmental stage, with increasing daylight feeding activity as lobsters progress from instar two to instar four (ie from the second to fourth juvenile stage).[87] Competitive interactions facilitated through communal rearing are thought to be important to stimulate feeding behaviour, resulting in superior growth when lobsters are reared communally rather than individually.[48,87] Feeding methods and rates are therefore likely to be size-specific and relate to the social environment, indicating that they are best studied under commercial or semi-commercial densities. This is evidenced by the success of co-feeding *P. ornatus* with trash fish and commercial feed on a 1:1 basis under research conditions, but the failure of lobsters to eat the commercial feed under commercial validation conditions.[90] Typical practice in Vietnamese commercial seacage lobster farming is to feed fresh trash fish once per day in the evening (Le Anh Tuan, pers. comm. Jan 2022). The efficacy of more than one feed per day under commercial conditions has not been investigated.

7 | REFERENCE FEEDS

Feeds for lobster research to date have developed in two clearly different directions, but with the common focus of forming a matrix that supports sufficient feed intake. The more traditional method of feed development has started with a fish meal base and a starch binder, aided by a synthetic ethylene/vinyl acetate copolymer pelleting agent to improve pellet binding (Aquabind[98]) and produced as a semi-moist pellet Table 4.[6] Mixed fresh seafood has been included for palatability, however, it was recently identified that krill meal is more effective in supporting growth and survival of *P. ornatus*.[48] An alternative approach has been put forward for slipper lobsters and the temperate

TABLE 4 Reference feed 1[48]

Ingredient	Inclusion (g.100 g^{-1} diet)
Fishmeal	61
Krill meal	10
Wheat flour	6
Wheat gluten	6
MOS (mannan oligosaccharide)	0.5
Fish oil	1.6
Carpohyll pink	1
Cholesterol	0.2
Lecithin	1
Mineral premix	0.6
Vitamin premix	1.1
Stay C	0.4
Binder (aquabind)	1
Water	9.6
Analysis:	
Dry matter (DM g.100 g^{-1})	82.3
Crude protein (g.100 g^{-1} DM)	64.3
Total lipid (g.100 g-1 DM)	12.2
Ash (g.100 g-1 DM)	13.9

spiny lobsters *Sagmariasus verreauxi*[31,32] and *J. edwardsii*[29,30] that is based on sodium caseinate, presumably for its highly concentrated water-soluble protein, and bound with transglutaminase to form protein cross-linkages rather than relying on starch for binding (Table 5). The combination of transglutaminase and sodium caseinate is used extensively in food technology to recombine meat products and alter textural properties of protein-bound food,[99,100] and its application to lobster feeds allows more space for the high protein requirement. Protein content and palatability are delivered through green shell mussel (GSM) meal and betaine, while lipid is increased through krill oil, which combines with lecithin to deliver 1.39% of the feed as phospholipid. While the importance of phospholipid has been tested in these feeds, it is very difficult to interpret their importance due to the exceedingly low growth rate in this experiment, amounting to only 4.5% body weight gain over a period of 50–55 days.[31] Both reference diets include 1% Carophyll Pink 8%, equating to 800 ppm astaxanthin and 1% lecithin. They differ slightly in their cholesterol inclusion, indicating the need to optimise cholesterol further. Both reference feeds have identified the need for high levels of protein and moderate lipid. While both of these feeds are appropriate references for future development and incorporate various aspects of knowledge gained to date, they both contain ingredients that are not commonly seen in commercial formulations, or at least not at the same inclusion level, due to the cost of the ingredients. Implementation and adoption of feed formulations for lobsters are likely to require significant cost-optimization before their commercialisation is possible. While these reference feeds both currently support inferior growth compared to fresh mussels,[48,56] their potential for implementation appears promising in

TABLE 5 Reference feed 2[31,32]

Ingredient	Inclusion (g.100 g^{-1} diet)
Sodium caseinate	48.5
Defatted GSM meal	23.9
Krill oil	14.3
Lecithin	1
Cholesterol powder	0.5
Carophyll pink	1
Choline chloride	1
Vitamin C	0.5
Betaine	1
Vitamin premix	1.3
Mineral premix	1.3
Transglutaminase	5.7
Analysis	
Dry matter (DM g.100 g^{-1})	65
Crude protein (g.100 g^{-1} DM)	62.2
Total lipid (g.100 g^{-1} DM)	15.9
Ash (g.100 g^{-1} DM)	7.4

areas where fresh seafood bycatch is not readily available. Both feeds represent the product of the research that has gone into lobster growout feed development to date and provide a basis for further development.

8 | ADOPTION OF FORMULATED FEED

Feed for lobsters cultured in Indonesia is entirely 'trash' fish,[16] generally consisting of just one or two species of small fish, predominantly sardines. In the locations where lobster farming is established, such as Lombok, there is very limited availability and low diversity of lowvalue seafoods that might be used as lobster feed. This in contrast to Vietnam where multiple fisheries, using a wide variety of gear, generate significant production of a wide diversity of seafood species including fish, crustaceans and molluscs. The smallest of these have limited human food value and are set aside for lobster farming. They are fresh (daily landings), nutritionally diverse and relatively inexpensive (≤$US1.00 per kg) and therefore provide effective nutrition for lobsters. Indonesia appears not to have an equivalent resource, and this has driven strong interest in development of manufactured feeds. In Australia there is limited history and culture of using trash fish for aquaculture growout and it is an unlikely development due to cost, environmental and biosecurity concerns.

8.1 | Constraints to adoption of formulated feeds

Petersen and Phuong[101] found that Vietnamese farmers perceive that lobsters do not adapt easily to manufactured diets (pellets), and that manufactured diets are generally more expensive and lead to slower growth rates than traditional diets. This perception is not based on experience, as manufactured pellets for lobster have not been available. It appears that feed companies have been reluctant to embrace production of lobster feed due to the small volumes that might be involved, as well as the perception of poorer performance. Economic analysis[5] however suggests a lobster feed would fetch a higher price and have a higher FCR than those used in traditional aquaculture (shrimp and fish), and therefore profitability may be strong even with smaller volumes. Despite this, there has been no push from Vietnamese lobster farmers to access a manufactured diet. The fledgling industry in Vietnam suffered a significant impact from a typhoon in 2017 that reduced production by 50%, and in turn reduced demand for the fresh seafood feed. Lower demand resulted in reduced cost of these feed sources, which may have lessened interest from aquafeed companies to produce a lobster feed.

8.2 | Strategies to enhance adoption of formulated feed

Because Indonesia has limited access to the equivalent variety of small seafood species that Vietnam utilises for lobster feed, the impetus for uptake of manufactured feeds is much stronger. The Indonesian government has an expectation that lobster aquaculture will transition to a manufactured feed, although they have not specified a requirement to do so in the new regulations concerning lobster aquaculture.[102] The Directorate General Aquaculture proposes to establish demonstration farms using manufactured feeds to explicitly reveal the advantages of such feeds in terms of both economics and condition of the lobsters produced. As Indonesian lobster aquaculture is in its infancy, it is hoped that it will develop with an established practice of using manufactured feeds, to maximise sustainability and avoid environmental and disease issues that, in Vietnam, have been linked to the use of fresh seafood. Indonesia, therefore, appears to be the most likely market to implement formulated feeds and the benchmark reference should be sardines rather than fresh mussels. If a formulated feed competes favourably with sardines on a cost-of-production basis, we anticipate that it will be well accepted by the market.

9 | POTENTIAL FOR IMPLEMENTATION OF FORMULATED FEEDS

Between 2010 and 2019 research and development interventions to promote lobster aquaculture in Indonesia[6] focussed on smallholders in impoverished coastal communities with limited opportunities other than fishing. This research revealed that the individuals and families involved were risk averse and unwilling to farm lobsters over extended periods to achieve marketable size.[103] Their preference was to sell the lobster seed they caught directly for cash, or on-grow the lobsters for only a short period and to a relatively small harvest size, which was uneconomic. Farmer's husbandry knowledge and financial capacity were very limited, resulting in the application of very poor nutrition to the lobsters they cultured. Although those operators on-growing lobsters expressed positive sentiment to accessing manufactured feeds, if and when they became available,[104,105] their entire business model was not sustainable and most operations failed. Subsequent consideration by researchers and government surmised that developmental interventions should focus on small and medium enterprises that were already involved in aquaculture. These existing businesses, with proven capacity in aquaculture, would more likely succeed in farming lobsters and have the financial capacity to apply best practice, including adoption of manufactured diets. Further, such operators are more likely to pro-actively advocate existing aquaculture feed suppliers and manufacturers to provide a lobster feed. From a business development perspective, manufacture of lobster feeds and adoption of them by lobster farmers in Indonesia is more likely with a market development strategy that focuses on SMEs and business profitability. Conversely, aquafeed manufacturers may invest with greater confidence when SMEs are the driving force of industry development.

10 | CONCLUSION

The development of lobster aquaculture across Vietnam, Indonesia and Australia is providing an increasing motivation for the development of commercial tropical lobster feeds. Competition with 'trash' fish and mixed fresh seafood feeds in Southeast Asia necessitates a cost-effective solution that also provides comparable growth. This is likely to be developed over a concerted effort to unravel feed requirements in several areas, including nutrient requirements, raw material quality and value, physical aspects of feed, feeding methods, appetite and health. Each of these aspects is important for the future development of commercially relevant feeds, which should be undertaken in consultation with the feed industry to ensure commercial relevance and implementation. Co-feeding commercial feeds and fresh ingredients show promise in its ability to spread the limited resource of trash fish and other by-catch further, however, it must be applied to commercial feeding conditions for implementation success.

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AUTHOR CONTRIBUTIONS

Leo Nankervis: Conceptualization; funding acquisition; investigation; methodology; project administration; writing – original draft; writing – review and editing. **Clive Jones:** Conceptualization; investigation; methodology; validation; writing – original draft; writing – review and editing.

DATA AVAILABILITY STATEMENT

Data available on request from the authors.

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