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REVIEW

REVIEWS IN Aquaculture

Mineral nutrition in penaeid shrimp

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Abstract

This review summarises the current knowledge of mineral nutrition for penaeid shrimp. It investigates how the aquatic environment and the lifecycle of shrimp affect requirements and the role that minerals play in shrimp health. Methods of supplying minerals via either water or to feed, and novel ways of supplementing minerals within feed, are discussed. The requirements for individual minerals are summarised with recommendations for minimum levels of dietary inclusion for semi-intensive and intensive commercial shrimp culture presented where data permits. Estimates of dietary requirement remain broad for most minerals for the main shrimp production species (*Penaeus vannamei*, *Penaeus monodon* and *Penaeus japonicus*), with some essential minerals remaining unstudied (Table 2 in Section 5.10). Mineral nutrition will become more important as intensification and diversification of production systems provide new challenges to shrimp aquaculture.

KEYWORDS

micronutrients, mineral deficiency, moult, shrimp nutrition, trace elements, water supplementation

1 | INTRODUCTION

The mineral requirements of shrimp have not been a research priority. Early studies concluded that shrimp grown under extensive systems generally do not require mineral supplementation[1] and were instead able to rely on substrate, minerals dissolved in water and any provided feed.[2] However, intensification is changing the scenario and supplementation is now required. Production is being increasingly optimised, leading to markedly faster growth, higher stocking densities and biomass, and shorter production cycles. With this increased intensification a review of the mineral requirements of cultured shrimp becomes a priority.

Minerals can be classified as essential, conditionally essential or non-essential. Determining the essentiality of a mineral is a critical first step before assessing its requirement in an animal. As defined by Frieden[3]: 'an element is considered essential when a deficient intake produces an impairment of function and when restoration of physiological levels of the element prevents or relieves the deficiency'. Minerals which are deemed essential need to be provided in appropriate amounts and in a form that is biologically available.

1.1 | The aqueous environment

The mineral requirements of aquatic animals are dependent on the environment in which they live. Many marine decapods are osmotic conformers, whereby the concentration of salts is comparable to the surrounding environment, with only limited enhancement or depletion of specific ions.[4,5] In contrast, species living in freshwater and many estuarine species maintain haemolymph ion concentrations above that of the surrounding waters (hyperosmoregulation). In these situations, species are constantly absorbing unwanted water through osmosis and losing scarce small ions through passive diffusion.[5]

Penaeid shrimp are typically euryhaline in that they can tolerate large ranges of salinity. For example, *Penaeus monodon* can hyperosmoregulate when in low salinity water and become hypoosmotic as salinity increases.[6] This enables *P. monodon* to have comparable growth or survival when grown over a range of 10–35 ppt.[7,8] Similarly, *Penaeus vannamei* and *Penaeus brasiliensis* have been shown to have no difference in survival or weight gain when reared in salinities as low as 4 ppt up to 32 ppt[9,10] and 15 or 25 ppt,[11] respectively.

Minerals in water can be an important source for the animal, with absorption through the integument, gills and the gut.[12] Dissolved minerals are the most bioavailable, with those present as particulates having negligible bioavailability.[13] However, the term 'dissolved' is more of an operational one to describe the chemical speciation of water but may not be an accurate indicator of the bioavailability. Instead, water chemistry significantly affects the availability of minerals to an organism, including the osmo-potential of individual ions, as well as hardness, pH, specific gravity and total alkalinity.

When rearing marine species, the ideal composition of minerals in water is usually that which matches the environment in which they naturally inhabit. Typical characteristics of seawater are salinities of 34.5 ppt, density of specific gravity of 1.027 kg/L at 25°C, pH of 8.1, total alkalinity of 116 mg/L and total hardness is 6570 mg/L as $CaCO_3$ for salinity at 34.5 ppt, as reported by Boyd.[14] Proportions of individual ions in seawater will vary depending on geographical location but in general, Na^+ and Cl^- are the predominate ions constituting 85.7% of salinity; followed by Mg^{2+} and sulphate, 11.2% of salinity; Ca^{2+}, 2.3%; K^+, 2.3%.[14,15] Meanwhile, the other major ions only comprise 0.8% of total salinity including carbonate, bromine, strontium, boric acid, fluorine and silica. The composition of trace minerals in marine seawater is highly variable but often requires highly sensitive analytical equipment for measurement due to their very low concentration. Although all elements in the periodic table can be found in seawater, those of known relevance for prawn nutrition include Co, Cu, Fe, Mn, Se and Zn.[16] Elements which may also be required as ultra-trace minerals, such as Mo, V and Si are also present.

1.2 | Requirements for larvae

Mineral requirements vary with an organism's age and stage of development. Larval crustacea have larger surface area to body size ratios. However, the degree to which mineralisation of the exoskeleton occurs in each life stage varies, making assumptions regarding absolute mineral requirements challenging. For example, in the shrimp *Penaeus paulensis* a steady increase in ash occurs from the early nauplius stage (9% ash) until the second protozoeal stage (25% ash), but declines in the mysis and early post-larval (from 20% to 12% ash) periods.[17] Spider crabs have higher ash in the zoea (30% ash) which then declined in the megalopa (15%).[18] In slipper lobsters, ash content declined from the first larval stage (39.1%) to the post-larval stage (15.3%).[19] However, after the first moult as a juvenile, the exoskeleton undergoes mineralisation where ash content is at its highest concentration (50.8%). This increase in ash was predominately associated with increased concentrations of Ca. Together these observations indicate that changes can occur in the mineral requirements of each stage of crustacean development.

Research into the mineral requirements of larval crustaceans remains scarce despite these observations. Preliminary investigations into the effect of mineral concentrations in water show that larval quality of *Macrobrachium rosenbergii* can be improved by balancing water concentrations of Ca:Mg (240:300 ppm).[20] The influence of dietary minerals on larval quality is unclear. This in part reflects the industry practise of using live feeds, that is, *Artemia* and algae, to deliver nutrients without direct control of mineral content. Where larval diets are produced, they are tailored towards ease of production and feeding, rather than to reflect the variety and content of natural feeds.[21] Understanding the mineral composition of *Artemia* and algae may be insightful; however, it is unclear as to the proportion of minerals which are assimilated from ingested algae/*Artemia* by larvae.

1.3 | Moulting

The moult cycle of penaeid shrimp comprises four major phases: (i) moult (reduced feeding and active ecdysis), (ii) post-moult (reduced feeding and exoskeleton soft to firm but yielding to pressure), (iii) intermoult (feeding and exoskeleton hard) and (iv) pre-moult (not feeding and exoskeleton has chitinous pigmented cuticular layer where carapace will readily separate with pressure).[22] Growth is achieved in a stepwise fashion, whereby moulting or ecdysis occurs, followed by the rapid intake of water to enlarge the new cuticle before hardening and remineralisation occur.

The amount of mineral that shrimp lose through moulting remains poorly defined. The exoskeleton is comprised of an organic matrix with various mineral salts, of which Ca carbonate, Ca phosphate, Mg carbonate and silicon dioxide predominate.[23,24] To conserve minerals, shrimp actively reabsorb minerals from the old exoskeleton during the pre-moult stage by endogenously secreting chitinase into the old exoskeleton to breakdown the organic matrix. As the nutrients are released from the old exoskeleton, they enter the shrimp's haemolymph, which acts as the major store for minerals, as well as for other nutrients such as amino acids and carotenoids.[24] It is estimated that 38% of nutrients from the old exoskeleton can be recovered based on breakdown from chitinase.[25] This absorption process is reflected in the concentrations of cations Mg, Na, K, and Ca in the haemolymph which are highest at moulting, then drop as they are used to mineralise the new exoskeleton. Concentrations then remain stable during the intermolt period. This pattern has been observed in several decapods including the pink shrimp *Penaeus duorarum*,[22] Indian shrimp *Penaeus indicus*,[26] *Panulirus argus*[27] and *Homarus vulgaris*[28] and is likely common to all species within the group.

The time before moulting is characterised by an increase in the animals total osmolarity, increased haemolymph volume and inflation of the new exoskeleton. Concentrations of both Na and K in the haemolymph increase.[22] Following the moult, the new exoskeleton is at first poorly mineralised and permeable to both salt and water, which leads to osmotic changes in the haemolymph. These changes are temporary as the mineralisation of the new exoskeleton enables the shrimp to exert greater control over osmotic fluxes.[25]

Crustacea eat their moults to further recycle minerals and other nutrients. Numerous species have been observed to feed on their moults.[29–32] *P. monodon* and *P. vannamei* routinely ingest all their moult except for the hardest component, the carapace (pers. obs. by H. Truong, CSIRO and H. Duong, Viet-Uc). While ingestion of moults appears common, it is unknown how well minerals are digested and absorbed in the gut and are thus able to be used again by the animal.

Moulting requires energy and involves a net loss of protein, lipid, carbohydrate and minerals.[31] These costs can be substantial. For example, *P. vannamei* required a minimal of 0.36% of its consumed energy for moulting during the trial period and this energy demand increased with higher moulting frequencies.[33] In the zooplankton (*Daphnia*), the demand for Ca and P during moulting constrained the accumulation of carbon.[34] A significant expenditure of energy is particularly important during the post-moult phase in order to effectively synthesis and remineralise the new exoskeleton.[25]

Imbalances of minerals in either water or diet can elicit problems in mineral deposition or withdrawal of the exoskeleton. For water, the composition of the exoskeleton is influenced by the availability of minerals. For example, *Penaeus latisulcatus* had low mineral content in their exoskeletons after being grown in inland saline water that was deficient in K. Supplementation of the water with K, led to improvements in the mineralisation of the exoskeleton to the point where animals reached levels equivalent to those reared in seawater (30 ppt salinity).[35] Mineral deficiencies and imbalances in water and formulated diets can result in moult-related diseases, such as soft-shelling and mortality.[36]

1.4 | Requirements for broodstock

Changes in mineral composition occur with reproductive development. In *P. vannamei*, ovary maturation led to decreases in Cu in muscle and increases in Mn in the hepatopancreas.[37] Similarly, depletion of both Ca and Mg occurred from both muscle and hepatopancreas in hatchery-exhausted *P. vannamei* (hatchery cycle of 100–120 days) for both sexes, compared to levels in newly caught wild animals. In contrast, concentrations of trace elements (Zn, Cu, Fe and Mn) in muscle became higher during this process.[38] These changes may reflect metabolic adjustments for reproduction or alternatively transfer of minerals to the gonads. Shrimp deficient in minerals are likely to have reduced fecundity, with observations of altered composition and quality of the eggs.[39] Together, these findings highlight the need for research into the role that minerals play in broodstock and hatchery management.

2 | ROLES OF MINERALS ON IMMUNE RESPONSE

In humans and domestic animals, the roles of minerals in immunity is established. For example, minerals play important roles in oxidative reactions, antioxidant capacity, cell proliferation and function, antimicrobial activity, inflammation and in adaptive immune responses.[40] Deficiency of some minerals is known to adversely impact the immune system, to predispose the host to pathogen infection and lead to greater risk of developing disease.[40] In shrimp, however, the effect of mineral deficiency on immunity and disease is not well studied and thus poorly understood. Like in other aquatic animals, this lack of knowledge in shrimp is complicated by the multiple sources of minerals to the host (diet and environment), the effect of these sources and interaction with other minerals and nutrients.[41]

Under experimental conditions, diseases associated with mineral deficiencies or imbalances have been observed. The current authors have observed occurrences of cramp tail syndrome, wherein the tail muscle contracts after handling, and pigment deficiency syndrome, an abnormal colouration of the exoskeleton of shrimp which were fed mineral imbalanced diets, including varying concentrations of 12 minerals in purified diets[42] and varying concentrations of Ca, P, Mg, Se, Mn and Zn in practical diets (pers. obs. H. Truong from unpublished experiment; Figure 1). These conditions are common nutritional diseases linked with mineral imbalances.[43] A common disease expressed in crustaceans as a result of mineral deficiency is soft shelling.[36] It causes abnormal appearance of soft or papery-thin shells. The inclusion of dietary Ca and P were shown to reverse the expression of soft shelling in *P. monodon*.[36] Diets which contained a Ca:P ratio of 1 produced a 3-fold increase in weight gain (62% vs. 18%) and 89% recovery in soft-shelling compared to diets without supplemental Ca or P. It was important to observe the higher Ca and P concentrations in the hepatopancreas and depressed concentrations in the exoskeleton of soft-shelled shrimp. Soft-shelled shrimp fed Ca and P deficient diets had lower survival and weight gain compared to those fed supplemented diets. Deficiencies of minerals that are important for shell formation can be linked to clinical signs or diseases related to moulting where shrimp will show (i) difficulty to moult, (ii) once moulted, difficulty to reharden exoskeleton thus having soft shells which can then lead to (iii) carapace lesions and further bacterial infections.[43]

Dietary supplementation of some minerals can improve the immune performance of shrimp. Cu, for example, plays a vital role in many proteins and enzymes found in shrimp including being the core component of hemocyanin which is analogous to haemoglobin and its oxygen carrying element iron found in vertebrates. Hemocyanin also functions as an important protein in invertebrate immunity.[44] Additionally, Cu is a co-factor of other important immune enzymes including tyrosinase, Cu–Zn superoxide dismutase and ferroxidase among others. The role of Cu in shrimp immune function was observed by increased total hemocyte counts and super oxide production when

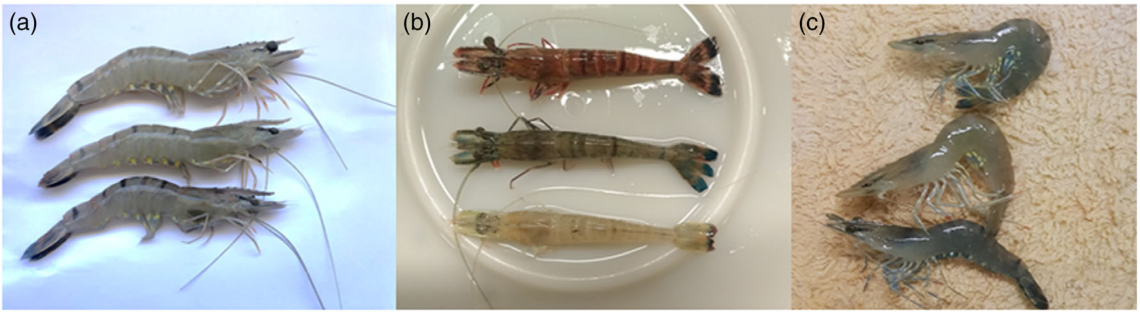

FIGURE 1 Effects of dietary mineral imbalance on gross shrimp morphology. Images are (a) healthy shrimp fed practical fishmeal-based diets in an experiment system compared to shrimp showing mineral-related diseases; (b) pigment deficiency syndrome when fed mineral-imbalanced, semi-purified diets as part of Truong et al.[42] (varying concentrations of 12 minerals in purified diets); and (c) cramp tail syndrome when fed varying dietary concentrations of Ca, P, Mg, Se, Mn and Zn in practical fishmeal-based diets (unpublished data, Truong et al.)

included in *P. monodon* diets in the form of CuCl and at levels between 10 and 30 mg/kg.[45] The effect on immune parameters also corresponded with increased growth rates at the same doses while higher doses of CuCl supplementation were associated with no increase in immune function and decline in growth rate. A commercial organic Cu additive also increased several immune parameters in the hemolymph and hepatopancreas including superoxide dismutase (hepatopancreas only), alkaline phosphatase, acid phosphatase, lyzosyme (hepatopancreas only) and phenoloxidase (hemolymph only) in *P. vannamei*.[46] Similar findings were also observed in Chinese mitten crabs, where $CuSO_4$ supplementation increased immune responses and improved resistance to *Aeromonas*.[47] The requirement of added Cu to shrimp diets appears to increase innate immunity activity which likely reflects its pivotal role in several immune molecules. However, toxic effects of Cu have been shown when there is excessive use or over exposure to Cu such as through its use in pond management as an effective algicide.[48,49]

There is growing evidence of immunological functions of other trace minerals demonstrated in shrimp. For example, Se proteins are important in redox reactions, antioxidant activity and immune cell growth and function. Expression of the genes for selenoprotein H/M/W1 have been detected in penaeid shrimp tissues.[50] Shrimp that were fed a diet supplemented with 0.3 ppm organic Se observed improved growth and survival and had lower infection severity in survivors following challenge with Taura Syndrome Virus, compared to those fed the non-supplemented basal diet or supplemented with 0.3 ppm inorganic Se.[51] Mn also plays an important role in antioxidant capacity of crustaceans as the enzyme Mn superoxide dismutase combats cellular oxidative stress.[52,53] Zn supports shrimp immune function by playing a role in protein production relating to hemocyte production counts, phagocytotic activity and growth of tissue[54] and is similar to the role of Zn in other animals.[55]

The prophylactic use of minerals to improve immunity and disease resistance in shrimp is scarce, and more research is needed to understand the relationship between mineral availability from both the environment and diet and their effect on disease predisposition or prevention.

3 | METHODS OF MEASURING MINERAL REQUIREMENTS

Mineral requirements can be measured in several ways. One approach is to measure mineral content of tissues as a proxy for essentiality. A second method uses formulation trials to assess the effects of differing levels of inclusion on shrimp growth and physiology. Third, biochemical pathways can be investigated to gauge mineral requirements.

Numerous studies in shrimp examine mineral content of tissues to determine mineral requirements and essentiality as outlined in Table 1. These studies indicate that the exoskeleton can store Ca, P and K and the hepatopancreas, Cu and Zn from dietary sources. Incorporation of minerals into specific functional tissues provides evidence that the dietary supply of these minerals is required beyond levels in seawater.

The mineral composition of an organ or tissue can be related to its function, thus mineral concentration in tissues can indicate the mineral-nutrition status.[56] For example, shrimp exoskeletons are the most mineral dense tissue. As discussed earlier, moulting can confound the mineral concentration of exoskeletons, but this can be avoided by sampling animals in the intermoult phase. Exoskeleton concentrations of macro-minerals such as Ca and P are useful where a depletion in the exoskeleton is associated with mineral deficiencies such as soft-shelling.[36]

The hepatopancreas of shrimp is used to store selected minerals and could be a proxy of mineral nutrition.[56] For example, in *P. vannamei* concentrations of Mg increase in a linear fashion with levels in the water. The shrimp actively enrich Mg so that levels within the hepatopancreas are much higher than the surrounding water.[57] However, this effect was not observed for K. Further understanding of the dynamics of how shrimp use the hepatopancreas to store minerals is required to be able to use this organ as a measure of confidence.

Formulation trials involve the addition of graded levels of the mineral (usually in an inorganic form) to a purified or semi-purified diet and measuring the physiological response of the animals. Mineral essentiality can also be investigated by incorporating a mineral at a single

TABLE 1 Concentration of minerals in shrimp tissues following feeding on either a basal diet or diet supplemented with the respective mineral (mineral-added)

	Whole body			Exoskeleton			Hepatopancreas			
Tissue	Basal	Mineral-added[a]	Species/ Reference	Basal	Mineral-added	Reference	Basal	Mineral-added	Reference	Muscle composition (based on seafood database[183])
Ash (%)	13.2	12.6	M[42]	41.1	43.5	V[58,64]	8.0	8.1	V[64]	1.6
Ca (g/kg)	9.4	9.2	J,[60] M[42]	88.2	94.1	V,[63,64] M[36]	24.1	21.6	M,[36] V[58,64]	1.0
P (g/kg)	2.2	2.3	M,[42,62] J[60]	26.4	30.1	V,[63,64] M[36]	8.5	6.8	J,[60] M,[36] V[64]	2.4
Na (g/kg)	2.8	3.1	M[42]	10.2	1.3	V[58]	–	–	–	2.5
K (g/kg)	3.6	3.6	M[42,184]	1.1	1.2	V[58]	–	–	–	2.3
Mg (g/kg)	1.6	1.0	J,[60] M[42]	4.1	4.3	V[63,67]	12.8	12.3	J,[60] V[58,67]	0.4
Cu (mg/kg)	36.6	72.4	M[42,45]	32.4	47.2	V[5858]	30.1	170.0	V[61]	5.5
Mn (mg/kg)	1.3	5.5	M[42]	26.3	19.7	V[58,63]	–	–	–	
Se (mg/kg)	0.7	1.2	M[42]	–	–	–	–	–	–	0.4
Zn (mg/kg)	20.1	19.2	V,[66] M[42]	61.9	44.1	V[63]	52.3	98.7	M,[66] V[5858]	15.8

Note: Values are averages of reported values in *P. vannamei* (V), *P. japonicus* (J) and/or *P. monodon* (M) studies. Levels of minerals in 'mineral-added' diets varied. Refer to Table S10. for detailed dataset. Ref, cited reference. '–', information not available.

[a]Based on the level which produced the largest change in tissue composition of ash or mineral compared to the basal diet.

level and examine the effects of varying other minerals. Essentiality studies of this kind are useful as they account for the requirement of a mineral in the presence and absence of other dietary minerals.[42,58–60] Mineral essentiality can be assessed in screening designs, for example, a Plackett–Burman design such as the one employed in Truong,[42] as they reduce the noise from mineral interactions by assessing a mathematically proofed combination of factors. These designs enable assessment of a large array of minerals at the same time to determine if each is essential. The design enables requirements of a single mineral to be quantified, while enabling interaction with other minerals to be measured. Further optimisation is required following a screening design to determine the requirement level of the essential mineral.

Stunting due to mineral deficiencies has been observed using experimental diets using ingredients with negligible mineral content. Experiments using semi- or purified diets with casein as the predominant protein source, have observed negative effects on growth due to deficiencies in Cu,[42,61] P,[59,62–64] K,[59] Mg,[42,60] Se,[42,65] Mn[42] and Zn.[66] In controlled conditions, the effects of mineral deficiencies can be clearly elucidated, and can guide the identification of mineral-associated retardation during commercial culture.

Assessment of biological pathways involved in mineral utilisation can provide a direct measure of mineral requirements. This can involve measuring the activity of enzymes and the expression of genes in tissues.[46,67,68] However, one caveat of this approach is that measuring enzyme activity or gene expression at its maximum may not reflect optimal conditions in a growing animal.[16,69] Despite this limitation, this method is useful in elucidating key biological pathways involving minerals and the environments in which these pathways are activated.

Tests that assay specific biological pathways of mineral utilisation are limited for shrimp, but are fast developing, mainly for *P. vannamei*.[70–72] Development of a genome-scale metabolic network for *P. vannamei* allows study of metabolic systems and can be used to simulate the need and utilisation of nutrients. Using such models, the transport and exchange reactions of minerals has been assessed to determine the species' requirements. The models quantify requirements for Zn, Mg and Cu that are in agreement with published literature (requirements of 0.0059% Zn, 0.12% Mg and 0.0034% Cu), while requirements of Ca, P, K and Mn differed.[71] Caution must be taken when extrapolating these models as their interpretation and accuracy is dependent on the quality and comprehensiveness of the genome-scale metabolic networks. Similar models for other shrimp are required but are currently restricted by the lack of genomic data. For shrimp, certain biological pathways are not well established, and significant effort is required in this space before these technologies can be used to assess mineral status on growth and immunity.

4 | METHODS OF MINERAL SUPPLEMENTATION

Minerals can be provided to shrimp either via the water in which they live or via food. In this section, we provide consideration of these two pathways and strategies for their combined management in shrimp systems.

4.1 | Supplementation of minerals via water

The amount and composition of minerals dissolved in the water in which animals inhabit has a great bearing on the physiology of shrimp. At its broadest, the amount of minerals present can be measured by salinity, which gives an indication of the overall osmotic stresses an animal may face. However, hardness and alkalinity are also important for shrimp production.[73]

Hardness measures the concentration of divalent cations (such as Ca, Mg and strontium), expressed as parts per million Ca carbonate (ppm $CaCO_3$) or mg/L. Alkalinity measures the concentration of bases and is similarly expressed as ppm $CaCO_3$ or mg/L. Alkalinity, hardness and pH are interrelated, but their differences determine their management practices. For example, the addition of limestone will contribute to both an increase in hardness and alkalinity while the use of Na bicarbonate ($NaHCO_3$) will contribute to alkalinity but not hardness. Low hardness is a reliable indicator that Ca water concentration is low, however high hardness does not necessarily reflect a high Ca concentration as Mg and other divalent cations contribute to water hardness. These intricacies are important to understand for the management of water mineral profiles.

Producers can adjust the water in production facilities to improve water chemistry. In open ponds, salinity can drop in wet seasons, through rainfall and freshwater run off, and by dilution of estuarine source waters. Some production systems use ground water of low salinity or freshwater. In each situation, producers may adjust salinity levels accordingly through the addition of seawater or salts. Hardness, alkalinity and pH can be adjusted through the addition of mineral salts. Key ionic minerals such as Ca sulphate (gypsum), K chloride (potash), K sulphate, Mg sulphate and Na chloride may be specifically added to correct for deficiencies in water chemistry.[74] This desire to correct for water chemistry is more fundamental to production than considerations of specific mineral requirements.[2,75]

The addition of certain minerals to water can have a high impact on production. For example, in low salinity environments, it has been repeatedly shown that both Mg and K are required to maintain growth.[57,76–81] For example, in water of 4 ppt salinity, increasing K^+ levels from 5 to 40 mg/L linearly improved post-larval survival and weight of *P. vannamei* while Mg^{2+} levels above 10 mg/L (up to 160 mg/L) were associated with better survival.[57] Furthermore in these environments, maintenance of Na:K at a ratio of 27.6 and Mg:Ca at a ratio of 3.4 was found to be most effective in maintaining growth in *P. vannamei*.[82] The importance of having the correct water mineral composition, even in high salinity water (30 ppt), was demonstrated by Zhu et al.[83] who showed that dietary K could not substitute availability in water. In that study, final weight of *P. vannamei* was reduced by 37%, specific growth rate by 26%, protein efficiency by 25% and feed conversion efficiency by 27.5% when K levels in water were reduced from 332 to 101 mgL^{-1}. These losses in production could not be addressed by additional dietary supplementation of K. In large systems using low-salinity water it may be more cost effective and practical to add specific salts to the system, rather than trying to bring all salts to a level that is comparable to a marine environment. By understanding the importance of specific minerals to water chemistry and for shrimp physiology, farmers can be selective in how they adjust salinity in their production systems.

4.2 | Dietary supplementation

4.2.1 | Sources of minerals for dietary supplementation

Nutritionists use inorganic minerals such as mono-calcium phosphate (MCP), magnesium phosphate (MgP) and mono-sodium phosphate (MSP) and mineral premixes to supplement the endogenous mineral content of ingredients to create a diet that meets the mineral requirements for shrimp. This strategy usually provides the macro minerals and the better-known trace minerals.

Most mineral premixes contain predominately inorganic salts, due to the low cost and availability of these forms. Thus, mixes typically contain Ca and P, as Ca chloride, carbonate or phosphate, cobalt (as cobalt chloride or sulphate), Cu (as Cu sulphate or chloride), Fe (as iron sulphate), K (as K iodide, phosphate or chloride), Mg (as Mg sulphate) and Na (as Na phosphate or chloride).

Some mineral premixes also contain trace minerals in other forms, such as hydroxychlorides and chelated minerals. This is because there is increasing evidence that these forms of supplementation can be more effective. Thus, trace minerals can be provided as either Mn sulphate or as organic Mn glycine, Se as either Na selenite or as organic Se-methionine or enriched yeast and Zn as either Zn sulphate or organic Zn lysine/methionine/glycine.[54,84–96] Despite this, some trace minerals are typically not included and so there is potential for these to be lacking in diets.

Hydroxychloride trace minerals are engineered crystalline structures that have tight covalent bonds, making them less soluble or reactive than sulphates. The single hydroxyl group (OH^-) prevents oxidation or connection with other metal components. The availability of hydroxychloride minerals is not well understood in penaeid shrimp. However, in one study supplementation with Cu hydroxychloride led to equivalent increases of the element as using Cu sulphate in the carapace, hepatopancreas and whole body of *P. vannamei*.[97]

Nanotechnology involves the prescription of minerals with particle sizes ranging from 1 to 100 nm. Nanoparticles have been applied to aquaculture to improve absorption and retention and to reduce the risk of toxicity. For example, administration of Se as nanoparticles has been demonstrated to be effective for multiple fish species.[98] Furthermore, its use is more effective than traditional Se forms like Se selenite[99–101] and Se-methionine,[100,101] in terms of growth and health indices. Recent reports have considered nano-minerals in shrimp. Ghaffarizedah et al.[102] determined the ideal inclusion rate of nano-Se was 0.38 mg/kg based on weight gain. Depressed growth and elevated oxidative stress were observed above these levels, indicating that toxicity can still occur with nano-forms of Se in shrimp.

Mineral chelation, most often with amino acid ligands, improves the bioavailability of minerals compared to inorganic salts. Numerous studies have demonstrated this in shrimp.[54,68,96,103,104] The structure of the molecule allows for the bonded mineral to be carried into the mucosal cell as an intact chelate.[105] This minimises the formulation of insoluble complexes with other nutrients. However, if the metal-chelate separates and becomes ionic before it is absorbed through the mucosal wall, then the benefits of the chelated mineral are lost and are subject to the same limiting factors as minerals in feedstuffs or as inorganics.

Amino acid-chelates have a protein-sparing effect, as observed in mammalian species[105] and more recently in shrimp.[68] In these studies, increased weight gain and/or protein utilisation were observed when the mineral was provided as an amino acid-chelate, compared to the same level of inclusion as an inorganic salt. For the shrimp study, chelates increased weight gain by 25.7% and increased the concentration of protein in the post-prandial haemolymph by 5.6% (4.65 vs. 4.40 g dl^{-1}) when compared to shrimp fed equivalent levels of inorganic minerals (5 g/kg).[68] The mechanism of how chelates improve protein utilisation remains unknown. However, it may be caused by the activation of proteinases as well as enzymes involved in anabolism.

Mineral-enriched yeasts provide a bioactive source of elements. However, the high cost and relatively low concentration of minerals in the product compared to other forms, has restricted use to human nutrition rather than for animal feed.

Some ingredients used to make aquafeeds are good sources of minerals. These include fishmeal, poultry meal, meat by-products, microbial biomass or algal meal, which each provide a diverse and generally bioavailable source of minerals. These ingredients have the additional benefit of contributing unknown growth factors and can improve diet attraction and palatability.

Specific studies have investigated the effects of using microbial biomass and algal meals, which are of interest to aquaculture nutritionists as ingredients that can potentially wholly or partially replace fish-based products. Microbial biomass was able to sustain growth and survival when used to replace fishmeal and oil in diets for *P. monodon*.[106] Microbial biomass also increased the whole-body composition of ash and protein suggesting a better assimilation of minerals and protein compared to the high fishmeal diets. Similarly, inclusions of a microalgae meal increased the dietary mineral concentration of Cu, Fe, Mn and Zn compared to the fishmeal control which resulted in significantly higher growth rates and higher shrimp concentration of Mn in *P. vannamei*.[107]

4.2.2 | Interaction in diet matrix

A diversity of mineral-nutrient interactions can occur in the diet matrix which can lead to so-called secondary mineral deficiencies.[108] The effect of these interactions depends on a myriad of factors such as concentration of specific minerals (especially the ratio of Ca to P, see Section 5.3), composition and processing of the diet and ingredients, age and species of the animal, and environmental factors. Although these interactive effects have been readily identified in other species, evidence is scarce for shrimp although they are likely to occur.

Dietary protein can affect mineral utilisation and vice versa. In carp, addition of cobalt was shown to have a protein-sparing effect based on increased growth, protein efficiency and incorporation of labelled-leucine into muscle.[109] In terrestrial species, protein provided as casein increased the Cu content of liver in lambs by 43% compared to protein from soy-flour,[108] while diet supplementation of L-cysteine at 0.4% reduced copper absorption in chicks.[110] It is likely that substances of high chelating and reducing potential like free amino acids can bind copper and form complexes that are poorly absorbed. Interactions with other nutrients include vitamins, antibiotics, antioxidants, complex-forming substances, alkaloids and glucosides.

The occurrence of negative interactions can be reduced by using stable forms of minerals and other nutrients (vitamins, antioxidants). Mineral chelates have shown improved mineral availability. Encapsulation of nutrients using chelating agents such as EDTA, chitosan, carboxymethyl cellulose, and so forth to prevent nutrient leaching in aquafeed diets has been considered.[111–113] Although this technique improves diet stability and is likely to minimise nutrient interactions, the effect on nutrient utilisation by the animal have been contradictory. The advantages of encapsulating minerals on mineral metabolism need further study.

5 | DIETARY REQUIREMENTS OF INDIVIDUAL MINERALS

This section reviews the current understanding of dietary requirements for individual minerals in shrimp. Ranges from published articles from crustacea and from individual penaeid shrimp species are presented (Figures 2–4). In addition, values for both fresh and saltwater fish are also illustrated in the same graphs for comparison.[16]

Mineral requirement studies for crustacea were selected based on the following criteria: (i) an inorganic mineral source was supplemented to a basal diet; (ii) growth, survival or mineral composition of tissue were assessed; and (iii) a recommendation on mineral essentiality or requirement in penaeid species was provided. Based on available literature, we focused on Ca, P, Ca:P ratios, K, Mg, Cu, Fe, Mn, Se and Zn.[16] Details of the studies specific to shrimp are listed in Tables S1–S9 and include details of the species studied, initial weight, feeding duration, diet type, dietary protein source, mineral source, minimum and maximum mineral inclusion, water exchange, water salinity and other parameters on which the mineral essentiality or requirements were assessed.

5.1 | Calcium

Calcium (Ca) is typically the most abundant mineral within animals. It is a major constituent of structural components and is required for muscle contractions, nerve function and coagulation. Its importance means that it is the most researched mineral in the nutrition of terrestrial livestock, with requirement values known for most production breeds and life stages.[114,115]

Ca supplementation is usually not required for marine fish, as it can usually be obtained from the water. Furthermore, Ca deficiency has been difficult to establish in fish species cultured in low salinity

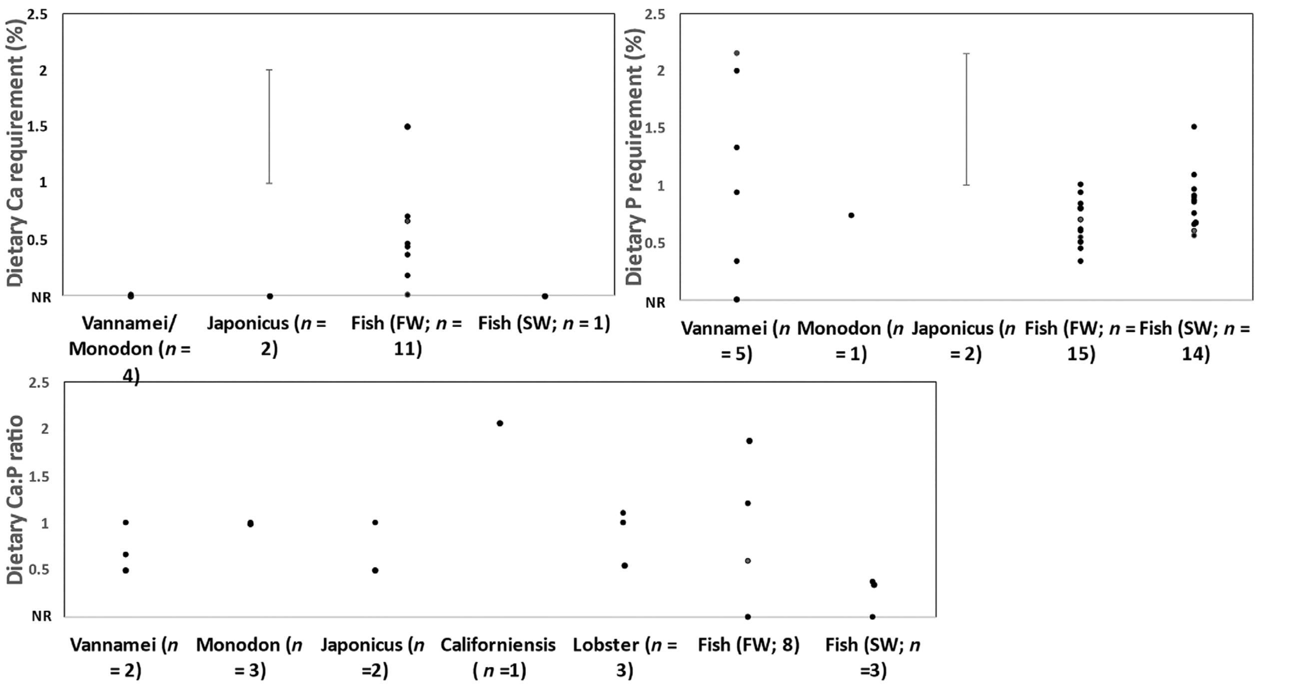

FIGURE 2 Dietary requirements of calcium (Ca), phosphorus (P) and Ca:P ratios for fresh and saltwater fish,[16] *Homarus americanus* (American Lobster)[60,138,185] and different species of penaeid shrimp. Values on the *x*-axis ($x = 0$) indicate that the mineral is not required, or for Ca:P there is no relationship (NR). $N =$ indicates the number of studies referenced. Points indicate the value(s) that was recommended. Whiskers indicate the range that was recommended. Details of the shrimp studies are listed in Tables S1–S3

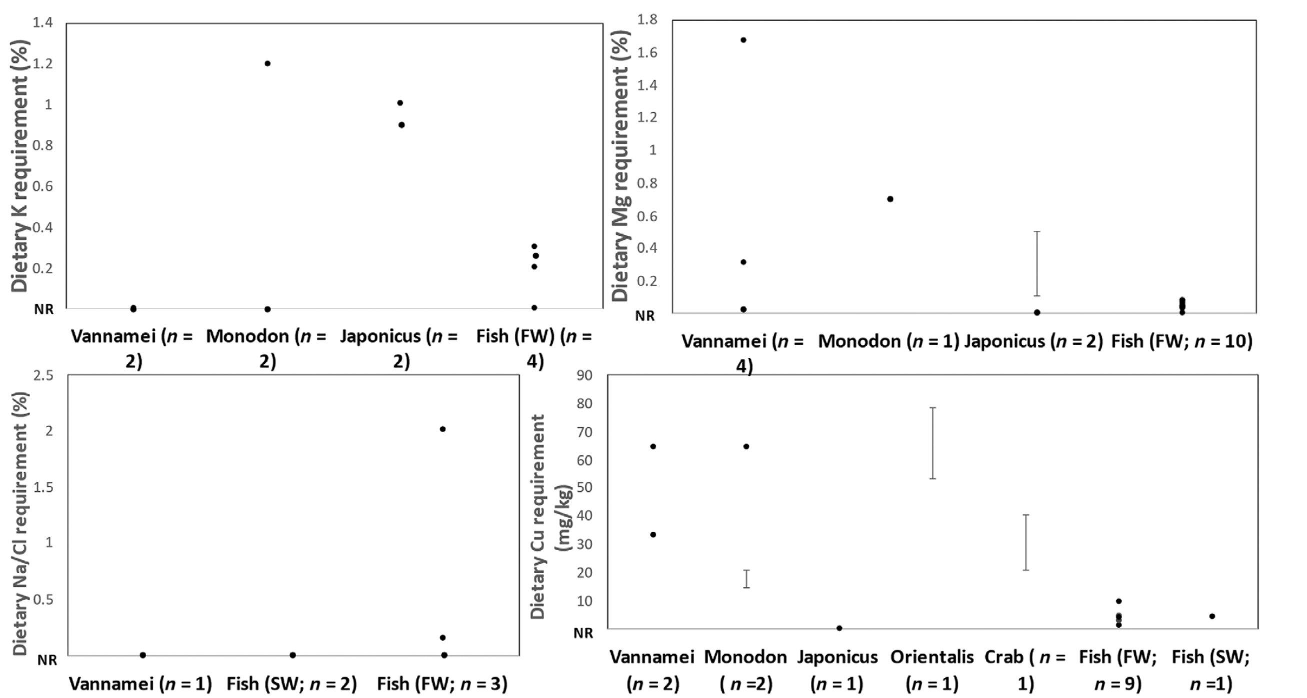

FIGURE 3 Dietary requirements of potassium (K), magnesium (Mg), sodium (Na)/chloride (Cl) and copper (Cu) for fresh and saltwater fish,[16] Chinese Mitten Crab *Eriocheir sinensis*[47] and different species of penaeid shrimp. Values on the *x*-axis ($x = 0$) indicate that the mineral is not required (NR). $N =$ indicates the number of studies referenced. Points indicate the value(s) that was recommended. Whiskers indicate the range that was recommended. Details of the shrimp studies are listed in Tables S4–S7

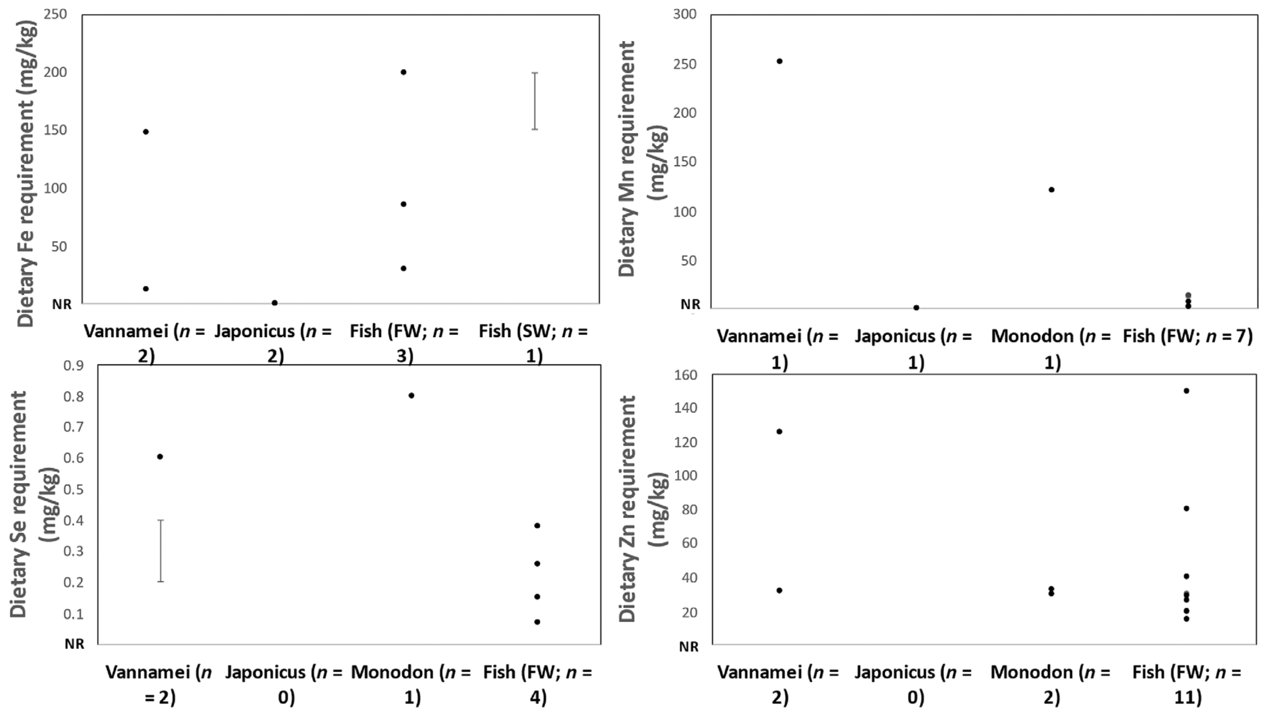

FIGURE 4 Dietary requirements of iron (Fe), manganese (Mn), selenium (Se) and zinc (Zn) for fresh and saltwater fish[16] and different species of penaeid shrimp. Values on the *x*-axis ($x = 0$) indicate that the mineral is not required (NR). $N =$ indicates the number of studies referenced. Points indicate the value(s) that was recommended. Whiskers indicate the range that was recommended. Details of the shrimp studies are listed in Tables S8 and S9

environments. Some freshwater fish do however require supplementation. For example, the blue tilapia *Oreochromis aureus*[116,117] and hybrid tilapia *Oreochromis niloticus* x *O. aureus*, require dietary supplementation of 0.17%–0.7%.[16,118] Measures of hardness and alkalinity of water are important parameters that affect availability of Ca, and these can be more significant than salinity per se.[119] Fish can directly absorb Ca from the water and its presence in the ideal range will improve the retention of other salts like Na and K resorbed from fish blood.

For crustaceans, Ca supplementation in the diet is typically not required as they can usually source requirements from the water. Ca is an important mineral in crustaceans, present at high levels within the body, predominately as Ca carbonate in the exoskeleton (∼30% in shrimp[120]) but also as the most abundant cation as Ca^{2+} (4.75 mmol/g in exoskeleton, 16.3 mmol/L in haemolymph).[121] In the crabs *Sesarma rectum* (Randall, 1840) and *Neohelice granulata* (Dana, 1851), the addition of dietary Ca (Ca chloride) was shown to effect concentrations of the mineral in haemolymph, but no dietary requirement was extrapolated.[122] Dietary Ca may be required during reproduction, as levels are depleted in both muscle and hepatopancreas of hatchery-exhausted shrimp.[38] However, studies in penaeid shrimp using growth trials and tissue composition report no dietary Ca requirement for *P. vannamei* and *P. monodon*[58,62–64] (Figure 2). Indeed, excessive dietary Ca (as chloride, carbonate or phosphate salts) were found to inhibit growth. While dietary Ca supplementation is not required, the relation between dietary Ca and P is important and this is discussed further in Section 5.3.

5.2 | Phosphorus

Phosphorus (P) occurs in organisms as phospholipids, ATP/ADP and creatine phosphate energy molecules, nucleic acids and buffers (e.g., phosphates).[123] In addition, P, along with Ca, is a major component of the skeletal system in vertebrates and in the exoskeleton of crustacea.

Fish have a requirement for P that is typically higher than that for terrestrial livestock. Water is a poor source of P and so fish have evolved to conserve this element.[119] P is predominately lost through excretion in the urine and thus losses are potentially greater for freshwater species due to the large volume of urine produced.[119] Despite this, levels of dietary supplementation for both fresh and saltwater species (Figure 2) are similar. Freshwater catfish (*Ictalurus punctatus*) had the lowest value (0.33%)[124] increasing to 0.60% in freshwater reared Atlantic salmon (*Salmo salar*)[125] and further to 0.91% in saltwater yellow croaker (*Pseudosciaena crocea*).[126] Deficiencies have been observed in fish fed raw ingredients like poultry protein concentrate with no additional P supplementation.[127]

In crustaceans, P requirements are poorly defined. Requirement values ranged between 0.34% and 2.2% in *P. vannamei* (Figure 2). Only one study showed that supplementation of inorganic P (as Na phosphate) was ineffective in inducing a weight gain response or change in carapace or hepatopancreas concentrations,[63] however this lack of effect may be a result of only one level of P (1.7%) being assessed. P requirements were highest for post-larvae, 2.09%–2.20%, when considered in practical diets containing 53% fishmeal.[128]

Recommendations for other species are 0.74% for *P. monodon*[62] and 1.0% to 2.11% for *Penaeus japonicus*.[59,60,129]

P varies in its availability, both among ingredients and for each species. In plant-based ingredients, most P is in the form of phytate which is highly insoluble. However, availability can be improved for plant-based ingredients by adding the enzyme phytase, which releases phosphorus from the inositol ring. In fishmeal, P can be present as di- and tri-Ca phosphates which are also insoluble to digestion. Generally, however, animal meals are higher sources and have higher availability of P compared to plant-based meals. Fishmeal contains a range of 1.75%–6.0% P, poultry by-product meal contains 0.6%–5.3% P, while solvent-extracted soybean meal contains 0.65%–0.72%.[130] Replacement of fishmeal with animal and plant proteins can reduce the P content of diets and has been associated with reduced weight gain.[131]

Values of available P for different feed ingredients have been established for terrestrial and some fish species. However, this is not generally the case for shrimp. Available P of inorganic sources have been determined for *P. vannamei* where Na phosphate (68.2% P apparent digestibility) and K phosphate monobasic (68.1% P apparent digestibility)[132] and mono-Ca phosphate (71.5% P apparent digestibility), and monoammonium phosphate (114% P apparent digestibility)[133] were shown to have the highest availability of P compared to other inorganic sources. Available P data remains absent for other ingredients, and this represents a challenge when formulating diets for penaeid shrimp.

5.3 | Ca:P ratios

The ratio of Ca to P in diets is important as the two minerals interact. For terrestrial livestock, supply of either element as either limiting or excessive will impact absorption of both. P availability often places an upper limit on Ca absorption. Conversely, excessive Ca can adversely affect the utilisation of P, likely due to the formation of insoluble complexes in the gut lumen which reduces the absorption of P.[134] Thus, ensuring the ratio of these two elements is balanced is important for shrimp nutrition.

Fish do not appear to be bound to strict Ca:P ratios as is seen in terrestrial livestock. Many fish species reared in both fresh and seawater observed no relationship between Ca and P,[16] with a few exceptions being *Chrysophrys major* requiring a Ca:P of 0.34:0.68 in seawater[135] and catfish *I. punctatus* requiring 1.5:0.8 in freshwater.[136]

For crustaceans, dietary Ca:P is considered important, as it has been implied in affecting weight gain, and in the prevention of structural deformities such as soft shelling. It is recommended that Ca:P be maintained at a ratio of 1:1 or less in *P. vannamei*, *P. monodon* and *P. japonicus* (Figure 4). Peñaflorida[62] suggested that Ca levels should not exceed P levels in diets for *P. monodon*. In *Penaeus californiensis*, higher ratios of 2.06:1–2.24:1 were recommended, although low ratios were not investigated.[137] Similarly, lobsters also reported an ideal Ca:P of 1:1 or lower where superior growth and carapace length was achieved compared to higher ratios.[138] These findings indicate an importance of balancing diets for Ca:P for crustaceans. However, achieving this balance is complicated since shrimp can obtain Ca from the rearing environment. Nevertheless, the goal would be to ensure that dietary Ca levels are similar to P where a ratio of 1:1 or less is ideal as to avoid the negative effect of Ca on P availability.

The concentration of Ca in water will affect Ca:P. Ca:P ratios of whole shrimp are slightly greater than 4:1 and remains consistent whether shrimp are fed a basal or a mineral-supplemented diet (Table 1). The amount of Ca in the body is much greater than the dietary requirement and highlights the ability for shrimp to readily obtain Ca from seawater. For this reason, production systems using water with limited dissolved Ca may require supplementation. Increasing concentrations of Ca in water have been shown to positively correlate with shrimp survival and production. However, this relationship may be confounded by other parameters which were also correlated with Ca hardness such as alkalinity.[139]

5.4 | Potassium

Pottasium (K) acts together with Mg, Na and Cl, as electrolytes in the body for regulation of intracellular osmotic pressure and acid–base balance. K is also required for the metabolism of protein, glycogen and glucose.

In fish, requirements for K are typically met through dietary intake without supplementation. Requirements vary between species where it was required at 0.2%–0.3% for hybrid channel catfish *Ictalurus punctatus* × *I. furcatus*[140] and channel catfish[141] reared in freshwater and not required for red sea bream *Pagrus major* reared in saltwater[142] or channel catfish reared in freshwater and fed practical diets.[143] From these four studies, it does suggest that seawater and practical diets are sufficient sources of K for fish. However, the ratio of ions in water is important and an imbalance, such as hypo- or hyper-osmotic environments will impair an organism's ability to osmoregulate. Dietary K sources can reduce osmotic stresses on an animal in these situations.[144]

In shrimp, K is the next most abundant mineral after Ca (Table 1) and there has been significant research towards understanding requirements for this mineral. Requirements for dietary K of 1.2% (as K chloride) and 0.9%–1.0% (as K phosphate and K carbonate or K chloride) were observed for *P. monodon* and *P. japonicus*, respectively (Figure 3).

While dietary supplementation is important and animals do use this source, the availability of K in water is also critical. Dietary supplementation cannot compensate for K-deficient water.[83] For example, in *P. vannamei*, the inclusion of K in diets (as KCl) was not as effective as supplementation of K in water. In that study, supplementation of K to 50 ppm in seawater improved biomass and weight gain.[76] K requirements are also dependent on the levels of other nutrients, especially to other minerals (Na, Cl and Mg) and amino acids (arginine).[76,78,103]

5.5 | Magnesium

Magnesium (Mg) has diverse functions, acting as a catalyst for a wide array of enzymes vital for the metabolism of carbohydrates, lipids, nucleic acids and proteins. Mg is also required in osmoregulation, cell membrane integrity and modulating neuromuscular transmission.

Mg deficiencies are well documented in fish.[119] For most species, uptake from water can only provide a portion of requirements and so dietary sources are needed.[16] Notable exceptions are freshwater tilapia *Oreochvomis mossambicus* reared in freshwater,[145] and the red sea bream reared in seawater.[146]

For shrimp, most Mg is found in the exoskeleton (Table 1[25]). Dietary requirements for the mineral vary widely from dispensable up to 0.35% for *P. vannamei* (Figure 3). Mg requirement in *P. japonicus* remains unclear as only two studies have investigated Mg addition with conflicting results. Deshimaru and Yone[59] showed that removal of dietary Mg produced no effect on weight gain, while in another study the addition of Mg at 0.01% and 0.05% improved weight gain.[60] This discrepancy may be due to variability in the availability of Mg in rearing water. For example, adding Mg to water to 130 ppm has been shown to improve survival of *P. vannamei*.[76] The importance of dietary Mg has only recently been assessed in *P. monodon* where an inclusion of 0.7% Mg (as Mg oxide) was shown to improve feed efficiency and increase Mg body composition.[42] Mg is considered a requirement for reproduction as levels are reduced in the muscles and hepatopancreas in hatchery-exhausted shrimp[38] and an increase in Mg occurs in the ovaries during maturation.[37] Fishmeal can be a poor source of Mg (0.05%–0.3%) compared to other ingredients (e.g., soybean meal contains 0.2%–0.4% Mg)[16] and so practical diets with a high proportion of fishmeal can potentially be deficient for shrimp.

5.6 | Sodium and chlorine

These minerals are both essential elements. Together they form common salt, which is the cheapest, most palatable and freely used mineral supplement in terrestrial animals and humans.[114] Sodium (Na) and chlorine (Cl) are often considered with K for their essential roles in acid:base balance and osmoregulation. However, unlike K, dietary requirements for Na and Cl are difficult to demonstrate in fish and crustaceans.[16] These minerals are typically abundant in marine water and feedstuffs, and thus metabolic deficiencies have rarely been observed.

In fish, the addition of Na and Cl to diets has been effective when rearing in freshwater. Dietary NaCl requirements in euryhaline Red Drum (*Sciaenops ocellatus*) were demonstrated when reared in fresh water where 2%–0% in diets resulted in increased growth.[147] No growth improvement was observed in brackish water (6% salinity) or seawater (35% salinity). Similar improvements in growth and feed conversion efficiency were reported for European sea bass (*Dicentrarchus labrax*)[148] and Asian sea bass (*Lates calcarifer*)[149] in freshwater with the addition of NaCl to the diet at 3% and 4%, respectively.

In shrimp, little research has been conducted on Na and Cl requirements. Dietary supplementation with NaCl at 1% and 2% did not improve weight gain of *P. vannamei* when reared in 4% salinity water.[103]

While an effect of Na and Cl in diets has not been shown, it is important to acknowledge that NaCl is the most used osmolyte added to water.[150,151]

5.7 | Copper

Copper (Cu) is essential for the activation of a myriad of enzymes relating to reproduction, bone development, growth, connective-tissue development and pigmentation of skin appendages.

In fish, dietary supplementation of Cu is required in all species assessed and ranges from 1.5 to 10 mg/kg.[16,152] Interactions between Cu and other minerals is evident. In fish, interactions between Cu and Se were reported where the inclusion of dietary Cu had an inverse relationship with Se accumulation in the liver of Atlantic salmon.[153]

In crustaceans, Cu is a trace mineral that plays a significant function as it is the elemental oxygen-carrier in haemolymph, known as hemocyanin. Hemocyanin constitutes 40% of Cu stores in shrimp.[16] Thus, shrimp and other crustaceans have a relatively high requirement for Cu compared to other taxa (Figure 3). Dietary Cu (as Cu sulphate) is required for Chinese mitten crab where the optimal Cu range of 20.8–40.3 mg/kg regulates growth and immune response.[47] Requirements for Cu have been observed in four shrimp species (*P. vannamei*,[58,61] *P. monodon*,[42,45] *Penaeus orientalis*,[154] *Penaeus chinensis*[155]) but not for *P. japonicus* where removal of Cu from a mineral premix produced no effect on weight gain.[60] A requirement of 32–34 mg/kg was reported in *P. vannamei* based on a regression model assessing graded inclusion levels of Cu (as Cu sulphate) and weight gain.[61] Similarly, a model of weight gain and feed efficiency in *P. monodon* indicated an optimal dietary Cu requirement (as copper chloride) of 15–21 mg/kg.[45] *P. orientalis* indicated the highest dietary requirement of 53 mg/kg (as Cu sulphate), with 78 mg/kg to achieve optimal growth, however, 53 mg/kg was likely enough based on diminishing Cu concentrations in the hepatopancreas in diets with more than 53 mg/kg Cu.[154] The positive effect of Cu supplementation on crustacean growth demonstrates that Cu requirements cannot be met by seawater and thus require dietary sources. However, Cu absorption in diets is usually poor due to antagonists in feed such as phytate with which Cu will readily form insoluble complexes.[85]

Although dietary Cu deficiencies are well documented, so too are toxicity effects due to excessive Cu.[16] Elevation of Cu in diets (>50 mg/kg) or in water (0.9 mg/L) produces toxic effects leading to impaired growth in shrimp.[45,156]

5.8 | Iron, manganese, selenium and zinc

Few trace minerals have been nutritionally assessed across shrimp species. Here, we focus on iron (Fe), manganese (Mn), selenium (Se) and zinc (Zn; Figure 4) as these have received the most research and have demonstrated functional roles in crustaceans.

Fe is needed for the normal function of many enzyme systems (cytochromes, catalases and peroxidases). Vertebrates use Fe as the main element in respiratory processes being the oxygen carrier in red blood cells, haemoglobin and myoglobin. Fe is more available in animal-based ingredients than in those derived from plants. In animals, most Fe is present as heme which is readily digested. In contrast, in plants, availability is reduced by the presence of phytate which leads to the formation of insoluble ferric phosphate.

For fish, dietary Fe requirements have been demonstrated for all fish species assessed, including channel catfish, common carp *Cyprinus carpio*, red sea bream and hybrid red tilapia with requirements ranging from 30 to 199 mg/kg.[157–160] Feed is the major source of Fe for fish as it is present in very low concentrations in water.[16]

For crustaceans, Fe is considered an essential element. It predominately occurs in the hepatopancreas and is known to be actively transported and metabolised in the haemolymph of crabs.[161,162] However, despite its role, dietary supplementation is usually not required beyond levels found in feed ingredients. Fe concentration of the basal diet (12 mg/kg) was thought to be satisfactory in *P. vannamei*[163] while the inclusion of Fe above 7 mg/kg had a toxic effect in *P. japonicus*.[60] Removal of Fe from a mineral premix reduced hepatopancreas concentrations in *P. vannamei* but had no effect on weight gain.[53] Similarly, in *P. japonicus* the removal of Fe from a premix did not influence weight gain.[59] Fe requirements have not been assessed in *P. monodon*.

There may be a requirement for supplementary Fe during breeding. The element appears to be used during the maturation of ovaries in *P. vannamei* where increased Fe concentrations were observed in mature ovaries (cortical stage),[37] while hatchery exhausted females showed reduced Fe concentrations in the hepatopancreas compared to wild-caught shrimp.[38] Similarly, females have higher concentrations of Fe than males.[164]

The nutrition of Mn, Se and Zn will be discussed together. Mn functions as an activator, component and cofactor of several enzyme systems, particularly those in the citric acid cycle. Se is essential in the enzyme glutathione peroxidase and functions with vitamin E to protect against oxidative damage of cells tissues and membranes. In mammals, dietary Se is required in very low quantities, and is readily absorbed regardless of source.[115] However, Se inadequacy can cause weakened or abnormal muscle and vascular membranes. Zn is an essential component of many metalloenzymes and a cofactor in many enzymes systems. Zn is mainly involved with the metabolism of lipid, protein and carbohydrate. Requirements for Zn may be higher when plant-based ingredients are used due to the presence of phytase which reduces the availability of the element.

In fish, dietary supplementation of Mn, Se and Zn is required in all species.[16,152] Fish cannot obtain enough of these elements from seawater as the concentrations are too low (i.e., Mn 2.0 $\mu g\ L^{-1}$, Se 4.0 $\mu g\ L^{-1}$ and Zn 10 $\mu g\ L^{-1}$).[15] Average dietary requirements across species are 8.7 mg/kg Mn, 0.21 mg/kg Se and 37.7 mg/kg Zn. Due to their many roles in nutrient metabolism, deficiencies of these minerals will impair growth and cause skeletal abnormalities and embryo mortalities.[119] Additionally, Mn, Se and Zn all have roles in immune response and disease resistance. In fish, supplementation with Se and Zn resulted in improved immuno-competence and oxidative status in rainbow trout *Orconchinhus mykiss*[165] and Mn and Se supplementation increased resistance to bacterial kidney disease in the sockeye salmon *Orcorhynchus nerka*.[166]

In crustaceans, Mn, Se and Zn are all considered essential. Dietary requirements for Mn, Se and Zn have been investigated in *P. vannamei* and *P. monodon*, while only data for Mn was available for *P. japonicus* (Figure 4). For *P. vannamei*, removal of Mn, Se and Zn from a mineral premix led to lower concentrations of the respective mineral in the hepatopancreas.[58] However, the premix used in this experiment had concentrations of Mn (251.6 mg/kg) that were much higher than that required for other species. For Se, graded inclusions (as Na selenite) showed that optimised weight gain was achieved with 0.2–0.4 mg/kg.[65] Providing adequate levels of Se is paramount, as low amounts of dietary Se (0.13 mg/kg) led to reduced growth and hepatopancreas antioxidant capacity. However, at levels above 0.81 mg/kg, growth was improved but signs of toxicity on hepatopancreas were reported.[167] For Zn, inclusion at 15 mg/kg (as Zn carbonate) is recommended based on concentrations in the hepatopancreas.[168] Zn has also been shown to be required for ovary development in broodstock.[37] Two studies have investigated Mn, Se and Zn requirements for *P. monodon*. The first identified requirement of each mineral based on single concentrations of each mineral.[42] In the second study, seven concentrations of Zn were assessed to identify that supplementation at 35 mg/kg in diets (as Zn sulphate) improved growth, whole body Zn composition and non-specific immune response in animals reared in lower salinity water (19–21 ppt).[66] For *P. japonicus*, Mn requirements were not confirmed as its removal from a mineral premix in the diet did not affect growth.[60]

5.9 | Other trace minerals

Only the nine minerals discussed in the preceding sections of this review have documented requirements for penaeid shrimp. Additional minerals may in time be shown to be essential but will require focused research to understand their role.

Trace minerals and their requirement in nutrition and role in physiology remains an area of interest across humans and animals. Research into the role of trace minerals remains difficult due to the minute concentrations required and limits to the accuracy of analytical methods. For these reasons, the essentiality of these minerals can be difficult to determine.

For terrestrial species, there is certainty over the essentiality of trace minerals boron, cobalt, Cu, iodine, Fe, Mn, molybdenum, silicon, Se and Zn.[115] Vanadium may also be essential.[169]

Boron has proven essentiality in many species including humans, mice, poultry and fish where it plays a regulatory role in metabolism of minerals in bone.[170] Essentiality assessment of boron in shrimp provided preliminary evidence for its dietary requirement.[42]

For fish, information on requirements and biochemical roles of trace minerals remains limited.[13,171] It is likely that both fish and crustaceans will require minerals known to be required by terrestrial animals. However, the presence of trace minerals in the aquatic environment makes it difficult to characterise deficiencies of these minerals. Furthermore, the inclusion of mineral-rich ingredients such as fishmeal in diets will likely meet requirements.

In crustaceans, few dietary supplementation studies involving trace metals have occurred. Over 75 trace minerals can be detected in shrimp, however, the role of these elements remains unclear.[42] Chromium has been shown to influence glucose homeostasis where expressions of genes involved in insulin signalling pathways and glucose metabolism were down-regulated in *P. vannamei* when fed chromium-supplemented diets.[172] Chromium may also be important for the cross-linking of chitosan in crustacean shells.[119,173] Cobalt is found in cobalamin (Vitamin B-12) and supplementation of this vitamin improved growth in *P. monodon*.[174,175] Furthermore, cobalt may be involved in the electronic synapses in the brain of crustaceans.[176,177] Like these examples, many other trace minerals are involved in metabolic processes and need to be investigated in penaeid shrimp. Requirements for trace minerals with low requirements are likely to be met by common feedstuffs used in aquafeed. However, this should not prevent further research as mineral deficiencies may present as industry moves away from fishmeal-based diets and for operations in mineral-deficient waters.

5.10 | Summary of requirements

Table 2 summarises the recommended dietary levels of minerals for the three most important penaeid shrimp species in aquaculture, *P. vannamei*, *P. monodon* and *P. japonicus*, based on the information discussed in this review. The information presented in the table can provide a guide for aquaculture nutritionists to formulate diets. It will also guide future research to fill gaps in our knowledge of penaeid nutrition.

TABLE 2 Summary table of recommended dietary levels for minerals of various penaeid species

Mineral	Species: *Penaeus vannamei*	*Penaeus monodon*	*Penaeus japonicus*
Macro-minerals (%)			
Ca	NR	NR	NR
P	1–2	0.74	1–2
Ca:P ratio	≥1	≥1	≥1
K	NR	≥1	0.9
Mg	0.26–0.35	R	0.1–0.5
Micro-minerals (mg/kg)			
Cu	32–34	15–21	NR
Fe	R	Not tested	NR
Mn	R	R	NR
Se	0.2–0.6	R	Not tested
Zn	32	32–34	Not tested

Abbreviations: NR, not required; R, required but no value available.

6 | INTENSIFICATION AND MINERAL NUTRITION

Production systems can be faced with stresses that increase the likelihood of mineral deficiencies. It is the intensification of production that is likely to bring the most challenges. Intensification leads to high stocking densities and biomass, as well as faster growth and associated higher frequency of moulting. For example, stocking densities influenced the trace mineral concentration of hepatopancreas and macro-mineral concentrations of the exoskeleton and muscle of brown *P. californiensis*.[178] These changes were attributed to the differences in ingested mineral content from feed and sediment and may relate to increased feeding competition in higher stocking densities of >8 shrimp compared to four per m^2.

In commercial conditions, Boyd[179] compared production systems between Thailand and Vietnam, including the application of minerals. In Thailand, production of 1 m.t. of *P. vannamei* required 0.58 ha land and 5400 m^3 water, whereas in Vietnam, requirements were 1.76 ha land and 15,100 m^3 water.[179] In both, minerals were added to ponds to maintain suitable water chemistry. In Thailand, which had higher shrimp intensification, half of the 39 farms assessed applied minerals consisting of various combinations of Ca chloride, Ca sulphate, Mg chloride, Mg sulphate, K chloride, K sulphate, Na chloride and Na carbonate to ponds. This compares to farms in Vietnam, which had comparably less intensive shrimp production, where only six out of 54 farms assessed used a mineral mix (containing Ca, Mg and K salts). This study alludes to the higher need for mineral supplementation in intensive systems.

Biofloc systems are characterised by having low water exchange which contrasts markedly with traditional clear or green water systems. The emphasis of biofloc systems is to maintain water quality by managing microbes with the production system rather than by water exchange. Reduced water exchange, however, means that close attention must be given to maintaining water chemistry including the provision of minerals. This typically involves the routine application of minerals to maintain the biofloc and to remediate water chemistry.[180]

Oral delivery methods of minerals through diets and natural feed provide an important source of minerals in this system. Mineral water profile (e.g., K:Mg:Ca ratios) need to be routinely monitored and managed, particularly during periods of low salinity or high biomasses, where it is likely supplementation is required to correct mineral low levels or imbalances. Presence of microbial aggregates (bioflocs) and other natural feed sources will likely impact the mineral availability in the system. However, studies on mineral supplementation and shrimp requirements in such systems have been limited partly due to the difficulty of managing mineral inputs and the interacting effect on mineral utilisation. The study conducted by Castille and Lawrence[181] may provide some key directions. The authors assessed the dietary deletion of constituents from compounded feeds in *P. vannamei* stocked in ponds where shrimp were allowed access to natural foods developing in their environment. Interestingly, the removal of the mineral premix had a negative effect on growth of juvenile shrimp stocked at higher densities (450 g/m^2), however this result was not observed when smaller shrimp were stocked at lower densities (247 g/m^2). The results confirm that natural feeds and rearing water can satisfy requirements for minerals however mineral deficiencies are more prone to occur when stocking densities vastly exceed the natural food supply of the pond, like in super-intensive conditions.

Intensive shrimp production systems with minimal water-exchange such as biofloc result in the depletion of some minerals and the accumulation of others in water over time. For example, in one study, an increase in K^+ and Mg^{2+} and decrease in Sr^{2+}, Br^- and Cl^- occurred when shrimp were reared over a period of 49 days using biofloc water that had been cultured for 62 days previously. In this study, there was no water exchange over the entire period and the shrimp were reared at very high densities of 457 shrimp/m^3.[182] Some water exchange may be required in these systems (within or between production cycles) to ameliorate chemical imbalances including minerals.

7 | CONCLUSIONS

This review has identified a lack of information for the requirements for important trace minerals such as Fe, Mn, Se and Zn, as well as other trace minerals shown to be important in fish and terrestrial species, but currently not studied in shrimp. Even in the case of the macro-mineral Mg, requirements for *P. monodon* are yet to be confirmed. Greater knowledge is needed for mineral requirements at different life stages, including critical stages of moulting. Few studies have considered the potential effect of ontogeny on mineral requirements, despite the observed changes in ash and mineral composition between life stages and the known roles these elements play during development and maturation.

The development of functional genomics, proteomics and metabolomic approaches offers new avenues to investigate the biochemical pathways that require minerals. Although this requires significant initial investment, it will result in a more rapid and direct method for determining mineral requirements, especially for the many overlooked trace elements where it may not be possible or economic using other methods.

Novel advanced technologies in mineral chelates and encapsulation have significant potential to improve delivery and absorption of these nutrients, potentially in a stage-specific or targeted manner. All these factors must consider the potential influence of the diet matrix, including interactive effects between minerals and other dietary ingredients. The establishment of these areas will allow shrimp nutrition to progress into the space of precision feeding, as practiced by more mature animal production industries and enable shrimp production to successfully intensify further.

AUTHOR CONTRIBUTIONS

Truong HH: Conceptualization; investigation; writing – original draft; methodology; visualization; data curation; resources. **Hines BM:** Writing – original draft; supervision; visualization. **Emerenciano MG:** Writing – original draft; conceptualization; investigation; resources. **Blyth D:** Resources; methodology; funding acquisition; conceptualization. **Berry S:** Writing – original draft; conceptualization; investigation; resources. **Noble TH:** Conceptualization; investigation; writing – original draft; methodology; resources. **Bourne NA:** Methodology; resources; investigation. **Wade N:** Supervision; resources; conceptualization. **Rombenso AN:** Conceptualization; investigation; writing – original draft; visualization; supervision; resources. **Simon CJ:** Conceptualization; investigation; writing – original draft; methodology; visualization; resources; supervision.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study will be made available by the authors upon request.

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Additional supporting information can be found online in the Supporting Information section at the end of this article.

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