

REVIEW

REVIEWS IN Aquaculture

A strategic roadmap for carbohydrate utilization in crustaceans feed

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Abstract

Carbohydrates serve as essential macronutrients in aquaculture feeds, providing cost-efficiency and numerous advantages, including energy supply, pellet stability, reduced ammonia excretion, and support for exoskeleton synthesis in crustaceans. Despite their significance, research on carbohydrate nutrition in crustaceans has been relatively limited compared to finfish. This comprehensive review addresses this knowledge gap by presenting contemporary insights into carbohydrate utilization in commercially important crustacean species, encompassing shrimps, prawns, crabs, lobsters, and crayfishes. The review underscores the pivotal role of carbohydrates, identifies limiting factors, and outlines strategies for enhancing efficiency. Wheat and sorghum/milo emerge as particularly promising carbohydrate sources. Nevertheless, determining species-specific carbohydrate inclusion levels remains essential for further investigation. This review also emphasizes species-specific distinctions in carbohydrate utilization during starvation, influenced by factors such as age, moulting stage, and digestive capacity. Challenging the misconception that carbohydrates are superfluous for crustaceans is imperative. Additional research to advance comprehension of their utilization mechanisms is vital. Enhanced knowledge of carbohydrate utilization can pave the way for economically sustainable and environmentally friendly feeds in crustacean aquaculture. Furthermore, exploring exogenous enzyme potential, optimizing pre-treatment methodologies, and harnessing probiotics can further augment carbohydrate utilization. These advancements hold promise for bolstering the growth and sustainability of the crustacean industry, meeting the surging demand for seafood production while minimizing environmental impact.

KEYWORDS

carbohydrate nutrition, carbohydrate sources, carbohydrates utilization, crustaceans, protein-sparing

1 | INTRODUCTION

Crustacean farming is of significant importance due to its economic contributions, role in food security, environmental sustainability, conservation efforts, and technological advancements. By adopting responsible and sustainable practices, crustacean farming offers a dependable and eco-friendly seafood supply while bolstering local

communities and relieving strain on wild populations. The total marine capture production of crustaceans was 5.63 million tonnes (MT), whereas the marine and coastal aquaculture production was about 6.76 MT in 2020.¹ With a contribution of 4.48 MT from inland aquaculture (including lakes, ponds, and rivers), the total production of crustaceans in aquaculture reached approximately 11.24 MT. This accounts for nearly 67% of the overall crustacean production and

represents more than double the production level from a decade ago (5.7 MT in 2010), indicating a steady growth in crustacean aquaculture.¹ In this context, a nutritionally balanced feed in aquaculture is of the utmost importance for the growth of cultured species in specific environments.^{2,3} Nevertheless, feed cost in aquaculture production systems accounts for around 50%–70% of the total production cost, and the culture of crustaceans, especially shrimps, in the intensive farming system always accounts for a considerable input cost for feed.⁴ The protein-sparing effects of lipids and carbohydrates significantly reduce the feed cost, where carbohydrates are the least expensive energy-yielding nutrient for aquatic animals.^{2,5} However, aquatic animals cannot tolerate a very high level of dietary carbohydrate.⁵ Though there is no dietary requirement for carbohydrates in aquatic animals, its inclusion up to a tolerable limit with the sparing of protein for energy supply makes the aquaculture feed cost-effective and environment-friendly.^{6–8}

Onwards with energy supply, dietary carbohydrate plays other roles in crustaceans. Accordingly, glucose, in addition to energy supply, can act as the precursor of chitin synthesis, which influences moulting to improve crustaceans' growth.⁸ While the first investigations into crustacean carbohydrates were documented in 1877⁹ and 1879,¹⁰ research on this subject remains constrained. The scarcity of studies on direct glucose tolerance tests for crustaceans limits the proper understanding of physiological as well as metabolic responses. Various factors like the moulting stage, nutritional status, diurnal rhythm, and environmental conditions (temperature, salinity, etc.) influence the glucose uptake from the gastrointestinal tract and its subsequent metabolism.^{11,12} Moreover, the inherent changes in the haemolymph glucose level during different moulting cycles necessitate life-cycle and moulting-stage specific glucose tolerance tests for crustaceans. So, it is challenging to conclude glucose tolerant or intolerant behaviour of crustaceans. However, recent molecular approaches could help better understand carbohydrate utilization by crustaceans. There are very limited reviews on carbohydrate utilization in crustaceans where carbohydrate utilization in shrimps,⁶ use of energy reserves during starvation in crustaceans,⁷ and brief context on carbohydrate digestion, glucose transport, and endocrine regulation in crustaceans mainly shrimps⁸ have been discussed. The current review has aimed to discuss carbohydrate nutrition in terms of its physiological and metabolic importance, along with limitations of its utilization and probable strategies to improve its utilization to produce cost-effective feed for crustaceans. A variety of crustacean species comprising shrimps and prawns, crabs, lobsters, and crayfishes, including commercially important species, have been covered in this review.

2 | IMPORTANCE, SOURCES, AND LEVELS OF DIETARY CARBOHYDRATES

2.1 | Importance of carbohydrates in aquaculture feed for crustaceans

Protein and lipids are the macronutrients that are considered to optimize the feed due to their cost. The optimization of dietary protein

levels in crustaceans can be achieved by incorporating lipids and/or carbohydrates as non-protein energy sources. However, the inclusion of lipids is constrained by factors such as pellet stability, palatability, and digestibility, with the recommended maximum level of lipids in crustacean feed being below 12%.^{13,14} Hence, the inclusion of carbohydrates as non-protein energy source in the crustacean feed has got importance, and its dietary level can be maximized through strategic intervention like the use of gelatinized starch and supplementation of exogenous carbohydrates, and so forth. Furthermore, dietary carbohydrates play a crucial role as binding components, enhancing the water stability of pelleted feed.^{15,16} In the case of lobsters (*Jasus edwardsii*), it has been observed that increasing the amount of gelatinized maize starch in the feed improves feed intake over a 5-h period.¹⁷ This finding suggests that higher levels of carbohydrates support the stability of the feed in seawater for a longer duration, consequently reducing the leaching of attractants, and as a result, it promotes higher feed intake.¹⁷ The main importance of carbohydrates in crustacean nutrition has been mentioned in Figure 1.

2.2 | Sources and composition of carbohydrates used in crustacean nutrition

Plants generally contain two types of carbohydrates, that is, energy reserve polysaccharides and structural polysaccharides.¹⁸ The predominant constituent of energy reserve polysaccharides is starch. The structural polysaccharides are also known as non-starch polysaccharides (NSPs), which contain a significantly low amount of starch and are indigestible carbohydrates.¹⁸ Carbohydrates in animal feeds mostly come from cereals such as wheat, maize, rice, oat, rye, barley, triticale, sorghum, and roots such as cassava, potatoes, and so forth. (Table 1). Furthermore, plant-protein sources such as soybean, rapeseed, pea, groundnut, linseed, cottonseed, jatropha, and so forth, contribute significant carbohydrates to the feed. Biological (e.g., feeding habit, genotype, physical activity, etc.), dietary (e.g., composition, inclusion level, feeding strategies, processing, etc.), and environmental (e.g., temperature, salinity, photoperiod, etc.) factors influence dietary carbohydrate utilization.⁵ Optimization of these factors can improve the utilization of dietary carbohydrates in aquatic species.

Depending on the variety, the root sources of carbohydrates, potato, and cassava consist of over 80% starch based on dry matter (Table 1). Additionally, the starch from all these root sources (potato, sweet potato, and cassava) has a similar amount of amylose, averaging around 20%–25%. However, the starch granule size of potato (37.97–46.47 μm)¹⁹ is higher than that of other sources. It has been found that crustaceans utilize the larger granule of potato starch less efficiently.^{6,1} Among cereals, the starch content varies from 51% to 90% on a dry matter basis, with oats having the lowest and rice having the highest starch content (Table 1). However, an exception is oats bran, which can contain up to 48% starch. Moreover, considering the starch from the bran of cereals, it can reach up to 25%. Most cereals contain primarily two different types of starch granules: type A or large granules, and type B or smaller granules. However, the major contribution

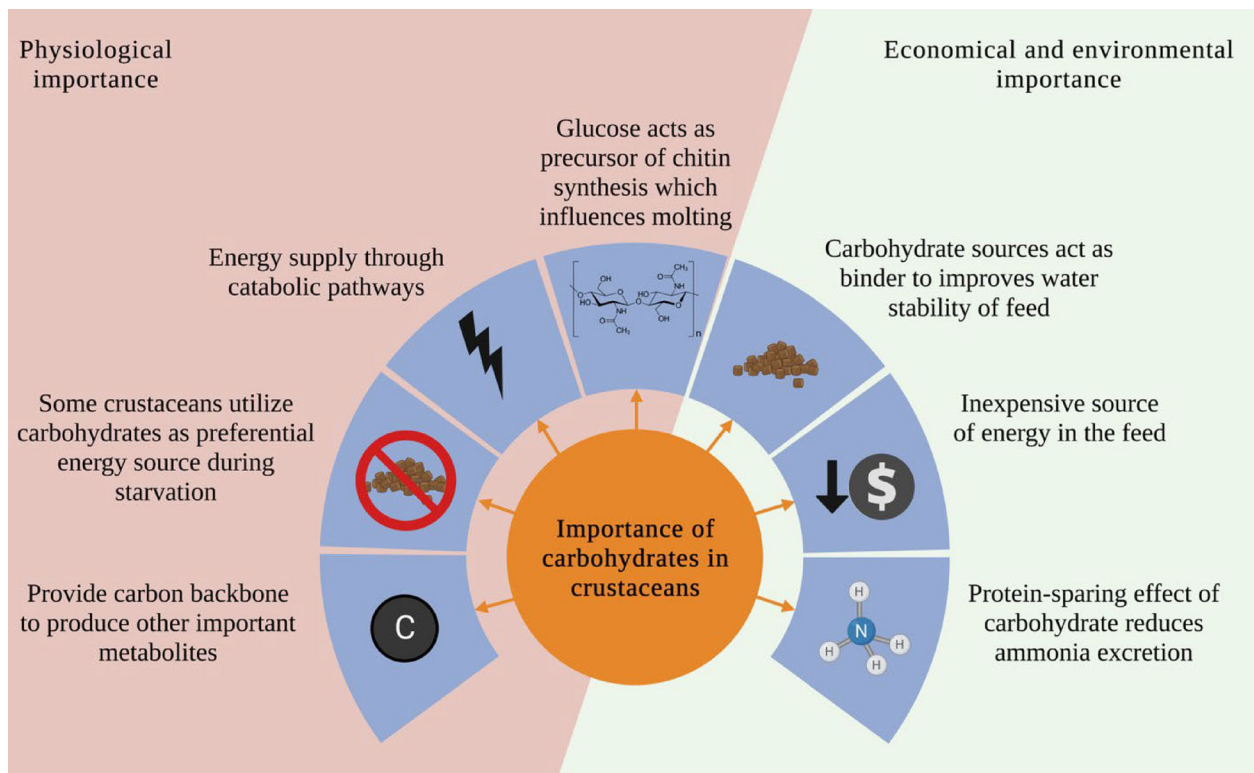


FIGURE 1 Major physiological, economical, and environmental importance of carbohydrates in crustaceans. Apart from providing energy, carbohydrates play an essential physiological role in crustaceans. For instance, glucose is a precursor for exoskeleton synthesis and provides a carbon backbone for other crucial metabolites. Additionally, carbohydrates act as binders to improve feed stability. They also have a protein-sparing effect and help reduce the overall cost of the feed.

(around 70%) comes from the large granules based on weight. Rye (62.5 μm) and triticale (50 μm) have larger starch granules compared to other sources, and this should be taken into account when preparing crustacean feed, similar to potato starch. Another important point to consider is the presence of NSPs, which are significantly higher in the bran of cereals compared to the grains (Table 1).

2.3 | Dietary levels of carbohydrate in crustacean feed

Generally, crustaceans utilize dietary polysaccharides more efficiently than oligo- or monosaccharides. The addition of glucose in the feed of the prawn beyond 10% caused marked growth inhibition.⁶² There are two main reasons that can explain the poor utilization of simple sugars by crustaceans.⁷ First, the absorptive site may become saturated with other nutrients such as amino acids, which hinder the assimilation process. As a consequence, the inability to effectively assimilate simple sugars leads to an accumulation of excess glucose in the system. In order to maintain a balance and prevent the hyperglycaemia, the excess glucose is excreted. Second, the rapid absorption of simple sugars leads to an increase in glucose levels in the haemolymph, which triggers the excretion of excess glucose to maintain proper glucose balance and homeostasis. Overall, in both situations, the excretion of

glucose occurs as a regulatory mechanism to ensure the proper balance and utilization of dietary glucose by crustaceans. However, the need for glucose excretion suggests a limitation in the efficient utilization of glucose as an energy source in these circumstances.^{6,63} Regardless, disaccharides such as sucrose can be utilized as well as polysaccharides and are even better than a potato or maize starch as reported in the case of black tiger shrimp.⁶³

The regulation of amylase expression in the spiny lobster *Panulirus argus* was found to be inadequate in response to dietary carbohydrate levels sourced from wheat flour, resulting in a significant disparity in amylase activity within the gut.⁶⁴ Furthermore, it was observed that a high dietary carbohydrate content downregulates the expression of the α -amylase gene in *P. argus*.⁶⁵ In contrast, an intriguing finding in *J. edwardsii* suggests an increase in the specific activity of α -amylase, which supports the utilization of stored carbohydrates as a preferred energy source during short-term food deprivation (24–72 h).¹⁷ This implies that *J. edwardsii* possesses a mechanism for efficiently utilizing stored carbohydrates when faced with limited food availability. However, carbohydrates such as starch could influence the growth without affecting the amylase activity as found in case of Pacific white shrimp larvae which showed reduced growth at 1% starch inclusion level in the feed but did not affect the amylase activity.⁶⁶ The carbohydrate utilization in crustaceans is a complex process and is not known clearly. For example, the addition of 0.52%

TABLE 1 Commonly used carbohydrate-rich ingredients in aquaculture feed.

Source type	Ingredient	Ingredient form	Total carbohydrate content (% dry matter) ^a	Starch (% dry matter)	Starch granule size (µm)	Starch composition		Total non-starch polysaccharide (% dry matter)	Annual production in 2021 (million tonnes) ^b	References	
						Amylose (%)	Amylopectin (%)				
Roots	Potato	Tuber	81.4	60–80	37.97–46.47	20–30	70–80	6	376.1 (E)	19–21	
	Sweet potato	Tuber	89.8	46.8–73.6	8.4–15.6	15–29	71–85	8.8	88.9 (E)	22–24	
	Cassava	Tuber (fresh) Starch	93.8	85–90	9.5–13.6	18–24	76–82	4.3	314.8 (E)	25–27	
Cereals	Wheat	Whole grain	83.9	60–75	2–11 (B-granule); 23–28 (A-granule; 70%–80% by weight)	25	75	11.9	770.9	28,29	
		Screenings	78.0								
		Germ meal	56.1								
		Bran	73.2	15–25				37.4		28,30	
		Distillers grain	55.3								
		Starch									
	Maize (corn)	Whole grain		84.3	75	15	25	75	9.7	1210.2 (E)	28,31,32
		Bran		77.7	9–23				37.6		33,34
		Germ meal		66.0	6–21						34
		Gluten feed		68.9	15						35
		Gluten meal		27.8	20						35
		Starch									
	Rice	Whole grain		83.7	90	3–9	0–33	67–100	0.6–2.0	787.3	36,37
		Bran		65.1	10–55	2–8	6	94	30.8		38,39
	Oats	Whole grain		80.0	51–65	60 (20–150)	19–34	66–81	23.2	22.6	28,40
Bran			69.6	38–48						41	
Rye	Whole grain		86.3	72.8	31 (A-type: 62.5, 85%; B-type: 9.3)	30	70	14.7	13.2	33,42	
	Bran		75.6	13–28				42.2		33,43	
Barley	Whole grain		82.4	51–61	Large: 20 (79%); Medium: 7.5 (11%); Small: 2.3 (10%)	25	75	18.7	145.6	28,44,45	
Triticale	Whole grain		84.7	63–66	A-type: 10–50 (>70%); B-type: 2–10 (<30%)	19–24	76–81	13.1	14.9	33,46	
Sorghum	Whole grain		83.7	70	5–25	24	76	5.4	61.4	33,47	

TABLE 1 (Continued)

Source type	Ingredient	Ingredient form	Total carbohydrate content (% dry matter) ^b	Starch (% dry matter)	Starch granule size (µm)	Starch composition		Total non-starch polysaccharide (% dry matter)	Annual production in 2021 (million tonnes) ^c	References
						Amylose (%)	Amylopectin (%)			
Other sources ^a	Soybean	Whole seed	33.3	11–12	0.7–4	12–16	84–88	21.7	371.7 (E)	28,48
		Meal	37.6					21		33
Rape or colza seed	Whole seed	Whole seed	28.8						71.3	28,49
	Meal	Meal	46.9	0.2–2.5				22		28,50
Peas (green)	Whole seed	Whole seed	71.4	47.02	5–20	54.4	45.6	18	20.5	
		Starch								
Groundnuts (excluding shelled)	Decorticated seed	Decorticated seed	19.9						53.9	51
	Meal	Meal	34.7	12.5						
Linseed (flaxseed)	Whole seed	Whole seed	31.9					16.5	3.3 (E)	52
	Whole seed	Whole seed	54.1	12.2–16.6				25.7	–	28,53
Sunflower	Whole seed	Whole seed	32.0					31.5	58.2	28
	Whole seed	Whole seed	64.7	51.1	6.1–28.1	30	70	17.1	1.7 (E)	54–56
Broad beans and horse beans (green)	Whole seed	Whole seed								
	Whole seed	Whole seed	52.0	4–10				40.5	1.4	28,57
Lupins	Whole seed	Whole seed	24.8	0.6–1.6					0.5 (E)	58
	Meal	Meal	47.4							
Coconuts (in shell)	Copra meal (kernel)	Copra meal (kernel)	66.7					52	63.7 (E)	59
	Kernel meal	Kernel meal	19.6	9.4–11.2				13.6	–	28,60

^aThese other sources are not primarily used as carbohydrate source.

^bData source: Feedipedia (www.feedipedia.org); total carbohydrate = 100 – (crude protein + ether extract + ash); digestible fraction = starch + total sugar.

^cData source: FAOSTAT (www.fao.org/faostat); 'E' indicates estimated production value.

glucosamine to the feed enhanced the growth of the kuruma prawn (*Marsupenaeus japonicus*), whereas the opposite result was found when chitin was added.⁶⁷ However, supplementation of 10% natural chitin, which is equivalent to 44% shrimp head meal or 5% purified chitin enhanced the growth of giant freshwater prawn (*Macrobrachium rosenbergii*) post-larvae.⁶⁸

In spite of the numerous reviews conducted on the nutritional requirements of different crustaceans,^{69–76} carbohydrates have been given little importance. The conclusions drawn from these reviews are as follows: (i) carbohydrates are considered less important as a macro-nutrient in crustacean nutrition, (ii) carbohydrates primarily play a crucial role in protein-sparing, and (iii) they serve as a less expensive source of energy for formulating feed. The authors explained the effect of various carbohydrate levels in the feed of different crustacean species even though, a concrete conclusion did not come in terms of optimum requirements. However, the lack of research on the carbohydrate requirement or 'the maximum inclusion level' of carbohydrates using an isonitrogenous and isolipidic diet limits the clear conclusion about carbohydrate requirement in crustaceans. There is a scarcity of scientific literature pertaining to the maximum inclusion level or optimum level of carbohydrate for various crustacean species using approximately isonitrogenous and isolipidic experimental diets. A meticulous examination of the available studies yielded a limited number of research sources (Table 2) that have reported findings on this specific aspect. However, it is essential to clarify that in requirement studies, the term 'carbohydrate' primarily refers to the requirement or maximum inclusion level of a specific carbohydrate source in the crustacean feed. Therefore, it may be more appropriate to consider the maximum dietary inclusion level up to the tolerable limit of crustaceans as a cost-effective energy source, rather than using the term 'carbohydrate requirement'. In Table 2, we have provided the maximum inclusion levels of tested carbohydrate sources in the feeds of various crustacean species under specified conditions.

Interestingly, the Indian prawn (*Penaeus indicus*) can utilize as much as 40% of purified starch in the feed without compromising growth and survival.⁸⁰ The studies showed that the corn starch can be incorporated into the feeds of Pacific white shrimp, oriental river prawn (*Macrobrachium nipponense*), red swamp crayfish (*Procambarus clarkii*) at levels of 20%, 15%, and 20.3%, respectively.^{77,81,87} The maximum permissible level of bread flour as source of carbohydrates in the feed of *Penaeus monodon* was found to be 35%.⁷⁹ Cassava meal can be incorporated up to 10% in the feed of green mud crab (*Scylla paramamosain*) without any negative effect.⁸⁸

The inclusion level of carbohydrates varies with the source. Regardless of the carbohydrate source, tolerable dietary carbohydrate inclusion level for crustaceans ranges from 20% to 30%.⁸ Ultimately, it would be inappropriate to generalize these values for all crustacean species. Studies on carbohydrate digestibility can provide secondary information about these aspects. The freshwater-dwelling European crayfish, *Astacus astacus* juveniles when fed with feeds containing graded levels of protein (22%, 31%, or 40%), lipid (5.5%–16%), and carbohydrate (9.2%–25.8%) for 394 days, exhibited a high survival rate at 31% protein along with moderately high carbohydrate (16.6%)

and a low lipid content (7%).⁸⁹ Further, in comparison to the younger juveniles, the older animals showed better responses to higher dietary lipid and carbohydrate levels.⁸⁹ In Caribbean spiny lobster feed, the inclusion level of carbohydrate is limited to 20% due to the slow uptake of glucose from haemolymph when fed with a 35% carbohydrate feed.⁶⁴ Also, the inclusion level of carbohydrates can vary with pre-processing, source, and nature of the carbohydrates used to prepare feed for crustaceans.

3 | CARBOHYDRATE DIGESTIBILITY IN CRUSTACEANS

Digestibility, defined as the organism's ability to break down consumed food material, plays a crucial role in the overall utilization of carbohydrates in crustaceans. A thorough understanding of carbohydrate digestibility is essential for several reasons. First, it allows us to assess the efficiency with which crustaceans can extract energy from different carbohydrate sources, enabling us to formulate feeds that meet their nutritional requirements more accurately. Second, studying carbohydrate digestibility in crustaceans helps identify the factors that influence digestion, both inherent to the organism itself and originating from the carbohydrate source. This knowledge is instrumental in developing strategies to enhance carbohydrate utilization and optimize feed formulations for improved growth and performance. Additionally, considering the processing effect on carbohydrate digestibility is vital. Processing techniques applied to carbohydrate sources can impact their digestibility in crustaceans, influencing their overall nutritional value. To provide a comprehensive overview, Table 3 summarizes the dry matter, carbohydrate, and energy digestibility of various carbohydrate sources studied in commercially important crustacean species. Commonly studied carbohydrate sources include maize or corn, wheat, rice, and sorghum or milo, with variations in their pure or processed forms such as native or gelatinized starch. Understanding the digestibility of carbohydrates in crustaceans not only contributes to their nutritional management but also plays a significant role in developing sustainable and cost-effective feeding practices for crustacean production.

Among the various sources of carbohydrates, wheat flour as starch source with higher apparent digestibility as compared to other sources¹⁰² is preferentially used in crustacean feed to enhance the growth performance of Pacific white shrimp (*Penaeus vannamei*),¹⁰⁹ European lobster (*Homarus gammarus*),¹¹⁰ spiny rock lobsters (*Jasus edwardsii*),¹¹¹ and Caribbean spiny lobster (*Panulirus argus*).^{65,102} Black tiger shrimp (*Penaeus monodon*) juvenile is reported to utilize dietary sucrose or dextrin better than other carbohydrates.¹¹² Typically, the digestibility of starch is decided by its amylose and amylopectin content. Starch that is rich in amylose has poor digestibility than those rich in amylopectin and accordingly, corn starch with 76%–99% amylopectin has good digestibility in shrimps.⁶ So, starch with high amylopectin content can be used efficiently as a source of energy in the crustacean feed.

The structure of the starch in terms of granule size can also affect its utilization. In comparison to maize starch (10–20 µm)¹¹³ or wheat

TABLE 2 Permissible dietary inclusion levels of tested carbohydrate (CHO) sources for different crustacean species under specified conditions.

Species	CHO source	Dietary composition ^b				Trial days	Rearing condition ^e	Optimum CHO level	Conclusion based on ^f	References			
		CHO levels ^a	CP%	EE%	CF%						GE	MP ^c	IBW ^d (g)
Shrimps and prawns													
Pacific white shrimp (<i>Penaeus vannamei</i>)	Corn starch	10–35 (6)	37.6–37.8	5.3–5.5	5.2–30.2	-	P	1.0	56	BW (6–8 ppt), 26.7°C	20	WG%, feed intake, FCR dilution, and survival%	77
	Wheat starch	14–30 (4)	26.8–38.2	8.6–8.9	-	-	P	0.3	56	LS (3 ppt), 27–30°C	19	WG%, survival%, and hepatopancreas histology	78
Black tiger prawn (<i>P. monodon</i>)	Bread flour	5–35 (4)	38.7–40.5	9.5–11.9	3.2–16.1	-	E	0.1	56	SW (32–33 ppt), 27–29°C	35	WG%, SGR, FCR, and survival%	79
	Corn starch	20–30 (3)	30–40	8.1–8.7	4.6–5.2	-	P	0.5	56	SW (32–34 ppt), 27–29°C	30	WG, FCR, and survival (based on protein-sparing effect)	63
Indian prawn (<i>P. indicus</i>)	Purified starch	10–40 (4)	33.3–37.6	6.0	15–45	19.0–20.2	E	0.1	30	SW (16 ppt), 26–27°C	40	WG%, FCR, survival%, and % increase in length	80
Oriental river prawn (<i>Macrobrachium nipponense</i>)	Corn starch	5–35 (6)	38.0–38.7	7.3–7.6	2.1–32.2	10.6–15.4	P	0.1	56	FW, 25–29°C	15	WG%, SGR, and survival%	81
Crabs													
Green mud crab (<i>Scylla paramamosain</i>)	Cassava meal	0–30 (4)	41.7–42.8	7.6–7.9	8.2–34.1	-	P	0.3	56	SW	10	WG%, FCR, PER, and survival %	82
Chinese mitten crab (<i>Eriocheir sinensis</i>)	Wheat starch	12–32 (5)	35.3–35.8	5.2–5.4	6.1–27.0	13.3–16.7	P	11	63	FW, 24–26°C	22–27	Growth, anti-oxidant capacities, and innate immunity	83
Gazami crab (<i>Portunus trituberculatus</i>)	Corn starch	0–30 (6)	42.2–42.9	7.9–8.1	1.1–30.6	13.6–18.8	E	7.9	56	SW (22.5–25.5 ppt), 27–30.5°C	8.78–9.84	WG%	84
Lobsters and crayfishes													
Spiny rock lobster (<i>Scyllarus edwardsii</i>)	Pre-gelatinized starch	15.7–50.5 (4)	31.3–32.5	2.9–18.7	-	14.0–15.6	E	5.1	84	SW (33–36 ppt), 17.9°C	27	WG (carbohydrate to lipid ration is 2:1)	85
Australian red claw crayfish (<i>Cherax quadricarinatus</i>)	NFE (major dextrin)	16.1–43.0 (dextrin, 0–27.2) (5)	30.9–32.0	4–12.0	4.4–24.5	16.9–17.9	P	1.5	56	FW, 28.7°C	29.01 (dextrin, 13.07)	WG% and FCR (carbohydrate to lipid ratio 3.6:1)	86
Red swamp crayfish (<i>Procambarus clarkii</i>)	Corn starch	5–35 (7)	34.9–36.0	6.2–6.8	-	17.3–18.2	E	0.4	56	FW, 19°C	20.3	WG%, SGR, FCR, feeding rate, body composition, hepatopancreas histology haemolymph glucose	87

^aMinimum–maximum levels of CHO used in feeds; numbers of feeds are indicated in bracket.

^bDietary composition indicates crude protein (CP), ether extract (EE), crude fibre (CF), and gross energy (GE, in MJ kg⁻¹).

^cMethod of processing (MP), that is, pelleting (P) or extrusion (E).

^dIBW, initial body weight.

^eSalinity (FW, freshwater; SW, sea water; LS, low salinity) and temperature.

^fWG, weight gain; SGR, specific growth rate; FCR, feed conversion ratio; PER, protein efficiency ratio.

TABLE 3 The apparent digestibility coefficient (ADC) of dry matter, carbohydrates and energy in relation to different types and levels of carbohydrates (CHO) fed to crustacean species.

Species	IBW ^a (g)	Trial days	Rearing conditions ^b	Faecal collection method	CHO source	Types	IL ^c (%)	ADC (%)		
								DM ^d	CHO	Energy
Shrimps and prawns Pacific white shrimp (<i>Penaeus vannamei</i>)	8.8	5 (3 days conditioning – 2 days collection)	SW (30 ppt), 28–30°C	Siphoning	Wheat starch	Native	30	50.6	71.3	90
					Whole wheat (soft white: 40% hard kernel, 60% soft kernel)	Native		52.5	67.7	
					Nutribinder® (primarily sorghum)	Gelatinized		56.9	69.4	
					Grain sorghum	Native		38.4	57.9	
					Steam cracked corn	Steamed		23.3	40.2	
					Wheat	Pre-extrusion	30	82.1	87.0	91
	13	6 (3 days conditioning – 3 days collection)	SW (30 ppt), 26.4°C	Siphoning		Dry-extrusion		66.5	81.3	
						Wet-extrusion		66.7	77.1	
					Corn flour	Pre-extrusion		70.6	78.4	
						Dry-extrusion		73.1	82.8	
						Wet-extrusion		50.7	65.9	
					Rice flour	Pre-extrusion		85.6	94.4	
Black tiger shrimp (<i>P. monodon</i>)	1.0	56	BW (6–8 ppt), 26.7°C	Siphoning		Native	10	49.8		77
							15	54.6		
							20	59.1		
							25	61.6		
							30	68.1		
							35	69.0		
	30–40	7th–21st			Bread flour	Gelatinized	5	75.7		79
							15	82		
							25	82.7		
							35	86.9		
							35	66.5	80.9	92
							65.2	78.1		

TABLE 3 (Continued)

Species	IBW ^a (g)	Trial days	Rearing conditions ^b	Faecal collection method	CHO source	Types	IL ^c (%)	ADC (%)		References	
								DM ^d	CHO		
					Second-grade clear wheat flour			68.0	83.6		
	0.6	56	SW (32–34 ppt), 27–29°C	Siphoning	Glucose Dextrin	Native	20–30	60.8–66.0 67.6–70.9		63	
	1.9	74	SW (29–30 ppt), 24–26.5°C	Siphoning	Starch Wheat starch Sucrose	Extruded	20	66.8–72.7	92	82	61
	3.0	7	SW	Siphoning	Potato starch Maize starch Dextrin			76 75 71	90 78 86	81 80 78	
	10	7	SW	Dissection	Pregelged starch Wheat flour Wheat flour	Pre-gelatinized Native Native	30	37.9 63.3 76.6	76.7 68.8 93.3	46.4 68.2	93 94
				Faeces collection onto a screen				80.1	102.6		
				Siphoning, then centrifuged and decanted				57.5	103		
				Dissection	Wheat starch	Pre-gelatinized		57.8	82.6		
				Faeces collection onto a screen				82.8	86.5		
				Siphoning, then centrifuged and decanted				69.9	88.6		
Giant freshwater prawn (<i>Macrobrachium rosenbergii</i>)	40–50	135 (10 days conditioning – 3 days faecal collection)	FW, 26.9°C	Siphoning	Corn Milo Wheat Barley	Native	35			79.1 78.4 76.8 78.4	95
Crabs											
Giant mud crab (<i>Scylla serrata</i>)	148.3	7	SW (32 ppt)	Siphoning	Copra meal Wheat flour Rice bran	Extruded	30	89.4 90.6			96
	95.7		SW (26 ppt), 28.75°C	Tweezers were used for faecal collection	Wheat flour Alpha cellulose	Native	30	89.2 93.2			97
								70	79.9	77.4	

(Continues)

TABLE 3 (Continued)

Species	IBW ^a (g)	Trial days	Rearing conditions ^b	Faecal collection method ^b	CHO source	Types	IL ^c (%)	ADC (%)		References
								DM ^d	CHO	
Chinese mitten crab (<i>Eriocheir sinensis</i>)	50	35	FW, 25.6–26.8°C	(Modified Catacutan et al., 2003) ⁹⁶ Immediate pipetting (a Pasteur pipet) was used for faeces collection (Goytortua-Bores et al., 2006) ⁹⁸	Rice bran	Native	30	74.9	80.8	99
Lobsters and crayfishes										
Spiny rock lobster (<i>Jasus edwardsii</i>)	115.4	21 days conditioning before faecal collection	SW, 18°C	As per Irvin and Williams (2007) and Irvin and Tabrett (2005)	Dextrin Carboxymethyl cellulose Wheat starch Maize starch Potato starch Pre-gelatinized maize starch	Native	35	79.0 76.4 73.2 62.1 68.0 71.1	99.4 91.2 59.1 59.7 83.7	100
Caribbean spiny lobster (<i>Panulirus argus</i>)	90–150	30	SW (36 ppt), 26°C	As per Irvin and Tabrett (2005) ¹⁰¹ and modified by Simon (2009) ¹⁰⁰	Wheat flour Maize starch Rice starch	Native	40.9 30 30	46.4 38.7 47.8	90.7 60.1 81.4	102
Red swamp crayfish (<i>Procambarus clarkii</i>)	30	8		Faecal collection chambers described by Brown et al. (1986) ¹⁰³	Wheat shorts Cooked corn	Native Extruded	30	82 85	87 90	104
Australian red claw crayfish (<i>Cherax quadricarinatus</i>)	3.6	30	FW, 27°C	Siphoning	Textured wheat	Native	15	87.5	91.7	105
	94.5	7	FW, 27°C	Siphoning	Sorghum Canola meal Lupin meal	Native	30	94.4 79.3 82.7	92.3 86.9 90.0	106
	10		FW, 27°C	A special Pasteur pipette with a siphon was used to collect the faeces from each aquarium 4 h after feeding, as recommended by Jones and De Silva (1997) ¹⁰⁷	Textured wheat meal Sorghum meal	Native	15	90.8 90.9		108

^aIBW, initial body weight.^bSalinity (FW, freshwater; BW, brackishwater; SW, sea water) and temperature.^cL, inclusion levels.^dDM, dry matter.

starch (<20 μm),¹¹⁴ larger granule potato starch (20–100 μm)¹¹³ is found to be utilized less efficiently by crustaceans.⁶¹ Nonetheless, appropriate processing methods such as cracking, cooking, gelatinization, and so forth modify the structure of the dietary carbohydrate to make it more digestible and bioavailable in the aquatic species.¹¹⁵ Accordingly, the extruded wheat flours at dietary inclusion level of 30% is reported to be more digestible (apparent digestibility coefficient, ADC 70%) than its native counterpart (ADC 60.6%) in giant mud crab (*Scylla serrata*).^{96,97} Ultimately, there was no difference in digestibility between native and pre-cooked dietary starch in shrimp.⁶ Generally, the utilization of wheat as a source of starch was found to be more promising than other sources. In the case of spiny rock lobster, the digestibility of wheat starch (91%) was observed to be higher than that of maize starch (59%)¹⁰⁰ and due to its higher digestibility wheat starch is preferentially used in crustacean experimental diet as carbohydrate source.¹⁰⁹ Similarly, in *J. edwardsii*, native wheat was found to be more digestible among different raw plant starches.^{100,111,116,117}

In black tiger shrimp, the ADCs of dry matter and carbohydrate of feeds containing wheat starch, sucrose and maize starch were reported to be higher than the feeds containing potato starch or dextrin as a carbohydrate source.⁶¹ The same was true for Pacific white shrimp, where the ADC of dry matter of both wheat starch and whole wheat was higher than maize.⁹⁰ These results indicate more efficient digestion of wheat as a carbohydrate source than maize. In another study on Pacific white shrimp demonstrated that the ADCs of dry matter and energy of pre- and wet-extruded wheat were much higher than maize with same processing conditions.⁹¹ Yet, dry-extruded maize had a higher ADC than the dry-extruded wheat.⁹¹ These indicate that the processing methods could influence the ADC of dry matter and energy of various carbohydrate sources differently in the same crustacean species. Additionally, among various carbohydrate sources (wheat, maize flour, rice flour, and sorghum), the highest dry matter (85.6%) and energy (94.4%) ADCs were recorded in the feed containing unextruded rice flour.⁹¹ Higher dry matter and carbohydrate ADCs for wheat flour (native) than maize starch were found in Caribbean spiny lobster.¹⁰²

In contrary to what we discussed about the carbohydrate digestibility of maize and wheat, in case of Pacific white shrimp and Caribbean spiny lobster, the different trends of ADCs of dry matter and energy of maize and wheat were reported in prawn, crabs, and lobsters. The ADC of energy of native corn (maize; 79.1%) was higher than native wheat (76.8%) in giant freshwater prawn.⁹⁵ Similarly, higher ADC of dry matter of extruded corn meal than extruded wheat flour was reported in giant mud crab.⁹⁶ Moreover, in the case of red swamp crayfish, ADC of dry matter and energy of extruded corn was respectively lower and higher than native wheat shorts which consists of leftover particles of bran, germ and flour produced during the milling process.¹⁰⁴ These observations indicate the species-specific differences of dry matter and energy digestibility of different carbohydrate sources. The dry matter digestibility of extruded wheat flour (70%) was higher than that of native wheat flour (60.6%) when added at 30% in feed of giant mud crab.^{96,97} When feeding black tiger shrimp

with extruded wheat, maize, or potato starch at a 20% inclusion level, it has been observed that the size of the starch granules can affect the ADC of carbohydrates.⁶¹ Accordingly, potato starch with a larger granule size (20–100 μm)¹¹³ had lower ADC of carbohydrate⁶¹ compared to maize (10–20 μm)¹¹³ or wheat (<20 μm)¹¹⁴ starch, significantly low carbohydrate ADC was recorded than maize or wheat starch.

Besides, the different inclusion levels of the same carbohydrate source may affect its digestibility in different species. Graded levels of gelatinized starch of bread flour (5%, 15%, 25%, and 35%) in the feed of black tiger shrimp showed increasing ADC of dry matter with increasing inclusion level.⁷⁹ Similar trend was also found in case of Pacific white shrimp when fed with increasing levels of native corn starch (10%, 15%, 20%, 25%, 30%, and 35%) with higher ADC of dry matter in the group fed feed with 35% native corn starch.⁷⁷ However, it is important to note that in both the studies, cellulose was used as filler and the inclusion level of cellulose decreased with the increasing dietary bread flour or corn starch. The higher level of cellulose in the feeds with lower bread flour or corn starch could reduce dry matter digestibility.⁷⁷

In the crustacean feed, sorghum or milo as carbohydrate source could be equivalent or better than wheat flour. The ADCs of carbohydrate and energy of native sorghum meal (milo) were similar to native textured wheat and native wheat in Australian red claw crayfish¹⁰⁸ and giant freshwater prawn,⁹⁵ respectively. Moreover, the higher ADCs of dry matter and carbohydrate of native sorghum than native textured wheat was reported in Australian red claw crayfish when fed at a 15% inclusion level.¹⁰⁵ In Pacific white shrimp, the ADCs of dry matter and energy were similar for wet extruded dietary milo or sorghum compared to wheat processed under similar conditions.⁹¹ Interestingly, when it came to dry extruded milo, it exhibited higher ADCs of dry matter and energy than dry extruded wheat in this particular shrimp species.⁹¹ On the other hand, sorghum without extrusion (pre-extrusion) showed lower ADCs of dry matter and energy compared to wheat of similar conditions in this species.⁹¹ Similarly, native grain sorghum was reported to have significantly lower ADCs of dry matter and energy than native wheat starch when fed to Pacific white shrimp at a 30% inclusion level.⁹⁰ These observations suggest that the proper processing (preferably dry-extrusion) of sorghum prior to use in the feeds of different crustacean species can enhance its utilization.

The digestibility of complex carbohydrates or polysaccharides is found to be higher than the less complex ones and monosaccharides. Accordingly, black tiger shrimp fed feeds with different levels (20%, 25%, and 30%) of glucose, dextrin and starch showed higher ADC of dry matter for the starch-containing feeds.⁶³ Significantly lower ADCs of dry matter, carbohydrate and energy for dextrin were found in black tiger shrimp compared to wheat, potato or maize starch.⁶¹ Nonetheless, dietary disaccharides such as sucrose at a 20% inclusion level had ADCs similar to polysaccharides and even better than a potato or maize starch in black tiger shrimp⁶¹ probably due to the presence of different glucosidases in this species.

In addition to different physical and processing factors, the inherent biological factor like species specificity is one of the important

factors which can affect the digestibility of different sources of carbohydrates. For example, the ADCs of dry matter and energy of native wheat flour were found to be higher in Pacific white shrimp than in *Scylla serrata* when fed with a 30% inclusion level.^{91,97} Therewith, at a 30% dietary inclusion level, the ADC of dry matter of extruded corn was higher in giant mud crab (93.2%) than the red swamp crayfish (85%).^{96,104} Though there are many reports on ADCs of different carbohydrate sources as listed in Table 3, more research are needed to explore new carbohydrate sources for commercially important crustacean species in a more systematic way.

4 | CARBOHYDRATE UTILIZATION IN CRUSTACEANS

4.1 | Brief context of digestion, absorption, and metabolism

Studies on different digestive enzymes of crustaceans were started several years ago.⁹ Naturally, crustaceans mostly depend on animal prey (e.g., molluscs, other crustaceans, small invertebrates, etc.) to fulfil their need for essential amino acids and polyunsaturated fatty acids for ensuring growth and reproduction.¹¹⁸ Hence, crustaceans need various digestive enzymes to digest wide range of food items. Moreover, the paradigm shifts in the use of fishmeal alternatives in aquafeed resulted in high proportionate or absolute use of plant-sourced proteins. In recent years, the inclusion of carbohydrates and lipids have been increased considerably in the crustacean feed to explore it is protein-sparing effect. This has led to higher proportion of carbohydrates in the aquafeed, which may not be favourable to be utilized by fish and crustaceans. The presence of wide variety of digestive enzymes has been reported in crustacean species which includes peptidases (both endo and exopeptidases), amylase, lipase, esterases along with chitinase, cellulase and hemicellulase to digest insoluble carbohydrates like chitin, cellulose, and hemicellulose.^{119–121} Besides, Kooiman¹²² reported a wide range of carbohydrases such as α -galactosidase, saccharase, cellobiase, lactase (low), α -xylosidase, maltase, isomaltase, β -1,3-glucanase, cellulase, mannase, and chitinase in crayfish, *Astacus*. Interestingly, *Astacus* is a carnivore species rather than an omnivore,¹²³ which possesses all carbohydrate-digesting enzymes including digestive enzymes for insoluble carbohydrates. However, the digestion of different complex algal polysaccharides^{124,125} is poor in crustaceans.^{126,127} The quantitative analysis of digestive enzymes in giant freshwater prawns revealed that digestive enzymes are not the limiting factor for poor nutrient utilization but rather the ability to absorb the nutrients.¹²⁸

Digestion is influenced by anatomy and mechanical functions of the digestive system, production level of enzymes, and dietary composition both in vertebrates and invertebrates.¹¹⁰ Different types of dietary carbohydrates are digested by a wide variety of enzymes (α -amylase, cellulase, chitinase, laminarinase, xylanase, α - and β -glucosidase, α - and β -galactosidase, β -mannosidase, α -xylosidase, cellobiase, chitobiase, mannanase, 1,3-glucanase, sucrase, saccharase, maltase,

and isomaltase) present in different commercially important crustaceans. Generally, the digestion of the carbohydrate is done by two groups of carbohydrate-digesting enzymes such as glucidases and glucosidases which act on 'polysaccharides' and 'oligo and disaccharides', respectively to produce simple sugars for absorption. The final product of carbohydrate digestion depends on the substrate type like disaccharides (e.g., sucrose, lactose, maltose, etc.), oligosaccharides (e.g., raffinose, stachyose, etc.), homoglycans (e.g., starch, cellulose, inulin, etc.) and heteroglycans (e.g., hyaluronic acid, chondroitin-4-sulfate, etc.).

The activity of carbohydrate-digesting enzymes, such as α -amylase, is highly regulated by the type of carbohydrate present in the feed. For instance, α -amylase activity was observed to be significantly higher in *J. edwardsii* lobsters fed with mussel flesh, which contains approximately 21.5% glycogen on a dry weight basis, compared to those on formulated feeds. However, the activity of this enzyme was found to decrease with increasing levels of dietary pre-gelatinized maize starch (7%–27%), indicating the superior nutritional value of mussel glycogen compared to other carbohydrate sources.^{100,116} Nonetheless, no significant effect on α -glucosidase activity in this lobster species was found when comparing fresh mussel flesh and formulated feeds.¹¹⁶ The specific activity of α -amylase in Atlantic white shrimp (*Penaeus setiferus*) showed an inverse relationship with the carbohydrate concentration in the feed, with lower specific activity observed at higher carbohydrate concentrations (0%, 11.6%, and 22.6%).¹²⁹ This finding suggests that dietary protein acts as an inducer, influencing the activity of α -amylase in the shrimp.¹²⁹ These results highlight the importance of considering the protein-to-carbohydrate ratio in formulated feeds for optimal enzyme activity and nutrient utilization in Atlantic white shrimp.

Unlike fish where the digested nutrients are absorbed across the brush border membrane of the enterocytes lining in the post-gastric alimentary tract and then enter into the circulatory system through the basolateral membrane,¹³⁰ absorption of digested nutrients in crustaceans mainly occurs in the hepatopancreas through specialized cells. The importance of hepatopancreas for nutrient absorption along with its morphology and physiology in crustaceans has been reported long ago.^{131,132} Among the different cells present in the hepatopancreas, the R-cells are known to perform the absorptive function and are also involved in the storage of glycogen and lipids which act as the major source of energy during starvation.¹³² Besides hepatopancreas, the midgut also helps in nutrient absorption and acts as a secondary absorptive organ in crustaceans; for example, glucose absorption takes place in midgut at a very low rate.¹¹ Generally, complete digestion of polysaccharides produces monosaccharides which can be absorbed by the R-cells (German, Restzellen, reserve cell) of the brush border in the hepatopancreas and then transported into the haemolymph. The transportation of monosaccharides, mainly glucose is done with the help of carrier proteins present in the plasma membrane known as glucose transporters.¹³³ These transporter proteins can be classified into two categories: (a) Na^+ -dependent glucose transporters consist of Sodium-glucose transport (SGLT) proteins, and (b) Na^+ -independent facilitative glucose transporters consist of Glucose

transporter (GLUT) family.^{134–136} The SGLT proteins transport glucose against a concentration gradient with the help of Na⁺K⁺ATPase pump¹³⁷ whereas, the GLUT proteins transport glucose through facilitated passive diffusion into the haemolymph. The GLUT protein can be expressed in any cell related to carbohydrate metabolism, unlike SGLT which is expressed in certain cells.¹³⁸ Very little knowledge is available about SGLT in crustaceans and most sequence studies have done on GLUT family.

The existence of different important metabolic pathways (e.g., glycolysis, gluconeogenesis, Krebs cycle, pentose-phosphate pathway, chitin synthesis, glycogenesis and glycogenolysis, etc.) in different crustacean species has been hypothesized in many reports and provided a basic understanding of these key metabolic pathways in crustaceans.^{139–145} Recent advances in a molecular study (especially sequencing) ultimately confirms all these metabolic pathways in crustaceans which can be found on the NCBI website.

4.2 | Carbohydrate as energy source during starvation

There are many reports which suggest that crustaceans utilize their energy reserves in different ways based on the period of starvation (short- or long-term), species, gender, moulting stage, nutritional status (types of energy reserves), and so forth. In this section, the major focus has been given to the role of carbohydrates during starvation in crustaceans. Besides being a precursor of chitin synthesis, glycogen, the stored form of carbohydrate plays an important role to serve as an energy source during starvation.⁷ The majority of glycogen is stored in the hepatopancreas.^{146,147} In the case of the southwestern Atlantic crab (*Neohelice granulata*, previously known as *Chasmagnathus granulata*), approximately 1% of the total hepatopancreatic mass is reported to consist of glycogen.¹⁴⁸ A general remark on the energy harnessing during starvation regarding crustaceans suggests more preferential utilization of lipid reserves or body proteins than carbohydrates to meet the energy requirement.⁷ Although there are substantial reports on this concept of 'preferential use of lipids or proteins than carbohydrates',^{7,149–156} generalization of this concept for all the crustaceans may not be appropriate (Table 4). For instance, Chinese white shrimp (*Fenneropenaeus chinensis*) showed a shift from utilizing pure protein during starvation to equal utilization of protein and lipid or a lipid-carbohydrate mixture during later satiation feeding.¹⁶⁷ The share of carbohydrate in energy production during starvation may be lesser than lipids or proteins in some crustaceans. After 84 days of starvation and then 21 days of re-feeding to California spot prawn (*Pandalus platyceros*) resulted only about 6.3% of total metabolized reserves contributed from carbohydrates, whereas lipid and protein respectively contributed 73.1% and 20.6% of the total metabolized reserves during this time.¹⁶⁸ In starving crabs, the preferential use of protein over carbohydrate becomes more dominant in case of eyestalk crabs which may be due to more conversion of protein into carbohydrate during starvation in eyestalk crabs.^{152,169,170}

Long-term starvation (80 days) study showed increase in glycogen content in muscle and hepatopancreas of maroon stone crab (*Menippe rumphii*) up to the 15th and 20th day of starvation, respectively, whereas the lipid content of both tissues decreased constantly.¹⁶¹ This finding concluded that the lipids could be preferentially used as an energy source during the initial days of fasting and after 3 weeks, the lipid and glycogen were utilized synergistically to meet the energy demand during fasting.¹⁶¹ While, during short-term starvation, freshwater crustacean species like giant freshwater prawns preferentially used carbohydrates as an energy source at initial phase and shifted towards synergistic use of lipids and carbohydrates for energy at later phase.¹⁶⁰ Both protein and carbohydrate contents in the hepatopancreas of Northern crayfish (*Faxonius virilis*, previously known as *Orconectes virilis*) were found to be reduced significantly during 2 weeks of fasting and decreased in an identical proportion in the first week of fasting.¹⁶⁴ During the short-term starvation period of 5 days, Pacific white shrimp of intermolt stage exhibited a significantly rapid decrease in plasma and hepatopancreatic glucose levels along with a decrease in hepatopancreatic glycogen content.¹⁵⁹ The hepatopancreatic acylglycerides decreased during later times; however, no change in plasma or hepatopancreatic protein content was found during these 5 days of fasting.¹⁵⁹ A study conducted on spiny lobsters (*J. edwardsii*) demonstrated that the inclusion of gelatinized maize starch at levels up to 47% had a positive impact on dry matter intake. However, it was observed that haemolymph glucose regulation during feeding was inadequate, and glucose was not efficiently utilized as an energy source.¹⁷ Instead, glucose was stored as glycogen, which proved to be a valuable energy reserve during short-term food deprivation. Additionally, the specific activity of α -amylase increased, while the total protease activity decreased during periods of short-term starvation.¹⁷ These findings indicate that digestible carbohydrates have a beneficial effect on feeding behaviour in spiny lobsters and may play a crucial role in maintaining nutritional conditions during short-term periods of food scarcity.

On the other hand, long-term starvation of 80 days leads to a significant reduction in the glycogen and lipid contents of the body with lowered moult number, specific growth rate and hepatosomatic index in Australian red claw crayfish (*Cherax quadricarinatus*) (6.27 g), whereas starvation for 50 days and then 30 days of re-feeding exhibited recovery of these parameters.¹⁶⁵ Similarly, Australian red claw crayfish juveniles (1 g body weight) showed decrease in body glycogen content along with decrease in lipid content during 50 days of long-term starvation.¹⁶⁶ In the case of Namib river crab (*Potamonautes warreni*; also known as South African Mooi River crab), prolonged starvation of 6 weeks resulted from a reduction of D-glucose concentration in haemolymph by 400% with more than 55% reduction in haemocyanin level.¹⁶³

The utilization of specific energy reserves may also be affected by the previous nutritional history. For example, previously high protein-fed *N. granulata* (southwestern Atlantic crab) showed a decrease in the synthesis of glucose from ¹⁴C-alanine resulting declined haemolymph glucose level on third day of fasting.¹⁶² It maintained the haemolymph glucose level as well as hepatopancreatic glycogen content

TABLE 4 Preferential utilization of carbohydrates as energy source during starvation in crustaceans.

Species	Period of starvation	Response during starvation	Reference
Kuruma shrimp (<i>Marsupenaeus japonicus</i>)	28 days	After a week of starvation, hepatopancreas glycogen level declined sharply from 3.6 mg/g to 0.4 mg/g and remained similar for 21 days and then slightly increased to 1 mg/g on 28 days observation. Overall, the starved shrimps consumed primarily carbohydrates, then lipids for energy and proteins were utilized significantly only during the final week of starvation.	157
Ghost shrimp (<i>Palaemonetes argentinus</i>)	15 days	The branchial ectoparasite (<i>Probopyrus ringueleti</i>) affected ghost shrimp preferentially utilized carbohydrate reserves as energy source during starvation; whereas, shrimps without branchial ectoparasite infestation preferentially utilized lipids for energy and preserved their carbohydrate reserves during fasting period.	158
Pacific white shrimp (<i>Penaeus vannamei</i>)	5 days	Short-term starved intermolt shrimps used carbohydrate (haemolymph glucose and hepatopancreatic glycogen) as preferential energy source.	159
Giant freshwater prawn (<i>Macrobrachium rosenbergii</i>)	8 days	During first 4 days, major oxidative substrate was carbohydrate which accounted 74%, whereas, lipids and protein contributed 18% and 8% of the total oxidative substrate, respectively. After 8 days, carbohydrate remained major contributor (51%) of total oxidative substrate and lipids and protein contributed 34% and 15%, respectively.	160
Maroon stone crab (<i>Menippe rumphii</i>)	80 days	Initially, lipids were used as energy source. After 3 weeks, a combination of lipids and glycogen were used. After 2 months, the glycogen content of muscle and hepatopancreas and lipid content of muscle had decreased to its minimum and most of lipid reserves from hepatopancreas were utilized. At this stage, decrease in protein content of both muscles and hepatopancreas was noticed.	161
Southwestern Atlantic crab (<i>Neohelice granulata</i>)	21 days	Crabs previously fed with high carbohydrate feeds preferentially used carbohydrates during first 6 days of fasting and the production of glucose from ¹⁴ C-alanine was increased after 15 days of fasting.	162
Spiny rock lobster (<i>Jasus edwardsii</i>)	3 days	Lobsters utilized stored glycogen as a source of energy during short-term food deprivation irrespective of carbohydrate levels in the feeds while soluble protein content remained unchanged.	17
Namib river crab (<i>Potamonautes warreni</i>)	42 days	D-glucose concentration in haemolymph was depleted by 400% with more than 55% reduction in haemocyanin level.	163
Northern crayfish (<i>Faxonius virilis</i>)	14 days	Carbohydrate and protein were depleted in abdomen from 4.5 to 1.5 µg/mg and 69 to 53 µg/mg, respectively. In case of hepatopancreas, carbohydrate, and protein were depleted from 18 to 11.3 µg/mg and 70 to 40 µg/mg, respectively.	164
Australian red claw crayfish (<i>Cherax quadricarinatus</i>)	80 days	Long-term starvation resulted in lower levels of lipids, and glycogen along with lower number of moults and specific growth rate. However, there were no changes in the soluble protein levels.	165
	50 days	Crayfish juveniles (1 g) showed decrease in body glycogen content along with decrease in lipid content during long-term starvation.	166

even after 15 days of fasting and only after 21 days of fasting, the haemolymph glucose and hepatopancreatic glycogen content were decreased probably due to reduced gluconeogenic capacity.¹⁶² Whereas, in the same experiment, the previously high carbohydrate-fed southwestern Atlantic crab used hepatopancreatic glycogen as preferential energy source during first 6 days of fasting and the raising haemolymph glucose and hepatopancreatic glycogen content were found after 15 days of fasting probably due to increased gluconeogenic capacity.¹⁶² These results suggest that the same species could have a differential preference to energy sources during normal feeding and fasting periods based on previous nutritional history.

Besides the above-mentioned factors, the mobilization of energy reserve may also be affected due to stress or pathogenic attack. The branchial ectoparasite (*Probopyrus ringueleti*) affected ghost shrimp (*Palaemonetes argentinus*) preferentially used carbohydrate reserves during 15 days of starvation, whereas the control group (without any branchial ectoparasite infestation) preferentially utilized lipids for energy and preserved their carbohydrate reserves during 15 days of fasting.¹⁵⁸

4.3 | Specific dynamic action and dietary carbohydrate

The specific dynamic action (SDA) is a metabolic response characterized by an increase in energy expenditure following the ingestion and digestion of food. Over the past century, numerous hypotheses have been proposed to explain the physiological processes underlying SDA, categorized as (a) pre-absorptive processes involving meal heating, gut peristalsis, enzyme secretion, protein catabolism, acid secretion, intestinal remodelling, and blood pH regulation; (b) absorptive processes related to intestinal absorption, nutrient transport, and hormone-induced postprandial metabolism; and (c) post-absorptive processes including protein synthesis, ketogenesis, amino acid deamination and oxidation, glycogen and urea production, renal excretion, and growth-related costs.¹⁷¹ We highly recommend that readers refer to the review by McCue¹⁷¹ for a comprehensive and detailed explanation of the physiological phenomena of SDA.

While extensive research has been conducted on SDA in various organisms, including crustaceans, the influence of dietary carbohydrates on this physiological process remains relatively understudied. Despite the limited number of studies specifically investigating the relationship between SDA and dietary carbohydrate in crustaceans, these investigations have provided valuable insights into the metabolic response of crustaceans to different dietary compositions. In this section, we will explore the current understanding of SDA in crustaceans with a particular focus on the role of dietary carbohydrate and its potential effects on energy expenditure and metabolic pathways.

A study on the protein-sparing action of dietary carbohydrates on American lobster, *Homarus americanus* found that increasing dietary carbohydrate levels (22.85%, 27.47%, and 31.27%) with decreasing protein levels (23.30%, 19.97%, and 16.65%) did not show a correlation with SDA.¹⁷² However, similar SDA values (17.1%–17.6%) were

observed among these three groups of lobsters, suggesting that the relationship between SDA and dietary factors is more complex than a simple linear association between carbohydrate intake and increased metabolism.¹⁷² Another study on supplementation of dietary fibre (α -cellulose: 0%, 5%, 10%, and 15%) in *M. rosenbergii* feeds showed that feeds containing cellulose (5%–15%) led to higher SDA coefficients (37% to 386%) after 6 h of feeding compared to cellulose-free feed.¹⁷³ Feeds with 5%–15% cellulose were assimilated more efficiently than cellulose-free feeds, suggesting a positive influence of cellulose on SDA.¹⁷³ The influence that the cellulose in the feed has on the SDA is also dependent on the way the prawns metabolize the cellulose. For example, *M. rosenbergii* has been shown to metabolize cellulose by fermentation and produces volatile fatty acids (VFAs)¹⁷⁴ which may contribute to SDA during metabolism.

An interesting study by Radford¹⁷⁵ provides important insight on the effect of feeding time and different carbohydrate sources on SDA of juvenile *J. edwardsii*. Lobsters that were fed in the morning exhibited a significantly lower SDA compared to lobsters fed at night indicating lobsters fed in the morning experienced lower energy loss during digestion.¹⁷⁵ So, feeding juvenile *J. edwardsii* in the morning could allow them to optimize the energy content of their meals, potentially leading to increased growth. Furthermore, *J. edwardsii* fed glucose resulted in a lower SDA compared to glycogen, sucrose, and maltose indicates that glucose is less efficiently utilized in terms of post-absorptive metabolism.^{117,175} Although lobsters could digest all the general carbohydrates but require more energy for the digestion and metabolism of glycogen and sucrose.¹⁷⁵ Additionally, lobsters fed agar had a significantly higher haemolymph glucose concentration than unfed lobsters, while alginate and carrageenans had similar responses to unfed lobsters.¹⁷⁵ These findings indicate that the SDA can be used as a technique to assess carbohydrate digestion in juvenile *J. edwardsii*.¹⁷⁶

These studies suggest that the relationship between SDA and dietary factors is not straightforward and involves complex interactions. Further investigation is needed to understand the underlying mechanisms and optimize the utilization of dietary carbohydrates in crustaceans.

5 | FACTORS AFFECTING CARBOHYDRATE UTILIZATION IN CRUSTACEANS

Utilization of carbohydrates by aquatic animals is found to be poor and the same is true for crustaceans. There are many factors regulating the utilization of this inexpensive energy source. These factors are more or less similar to factors limiting carbohydrate utilization in finfish.⁵

5.1 | Species-specific response

The ability of carbohydrate utilization varied among the crustacean species. This variation may be due to diversity in the digestive

enzymes, metabolic utilization, preferential energy source, genetic variation, and so forth. For example, lobsters poorly digest carbohydrates compared to shrimps,¹¹ which leads to an argument for the preferential use of protein as an energy source by lobsters rather than carbohydrates.

Typically, giant freshwater prawn has a relatively high activity of α -amylase than other crustaceans followed by Pacific white shrimp and Indian prawn.^{128,177,178} The variation in digestive enzyme activity ultimately affects the capacity of carbohydrate utilization in different crustacean species. Species-specific cellulase activity can also be seen in the crustaceans like giant freshwater prawns fed with dietary crude fibre up to 10%.¹⁷⁹ The giant freshwater prawn exhibits enhanced growth through an increase in gastric emptying time, which aids in nutrient absorption.¹⁷⁹ In contrast, Australian red claw crayfish, despite having cellulase, did not show any growth improvement when fed with α -cellulose.¹⁸⁰ Moreover, a dietary α -cellulose content exceeding 12% negatively impacts their survival, growth, and feed conversion efficiency.¹⁸⁰

5.2 | The trophic level of crustaceans

Commercially important crustaceans play various roles within aquatic ecosystems and occupy different trophic levels based on their feeding habits. The trophic level of a crustacean is a critical factor that influences its dietary composition and the utilization of carbohydrates. Additionally, it is important to note that crustaceans can change their trophic level as they develop. Larval size determines their position in planktonic food webs, and many species undergo trophic level shifts during ontogenetic development.¹⁸¹ Shrimp, such as *P. vannamei*, are classified as secondary consumers and feed on detritus, algae, and small invertebrates. They occupy a trophic level higher than primary consumers like zooplankton. Crabs, like *Callinectes sapidus*, exhibit a range of feeding habits. Some crabs are scavengers, consuming decaying organic matter and detritus, while others are predators that prey on small fish, molluscs, or other crustaceans. Although there are limited studies on how trophic level affects carbohydrate utilization, comparing the digestibility of carbohydrates can provide some general insights. For instance, the ADCs of dry matter and energy were higher in Pacific white shrimp than in *S. serrata* when fed a feed with a 30% inclusion level.^{91,97} Lobsters, such as the Caribbean spiny lobster, are carnivorous predators found at higher trophic levels. They feed on a variety of prey, including fish, crabs, molluscs, and other crustaceans, placing them as tertiary consumers. In the feed of Caribbean spiny lobsters, the inclusion level of carbohydrates is limited to 20% due to the slow uptake of glucose from the haemolymph when fed a feed containing 35% carbohydrates.⁶⁴ Freshwater-dwelling European crayfish juveniles exhibited a high survival rate when fed a feed with 31% protein, along with moderately high carbohydrate content (16.6%) and low lipid content (7%) as mentioned previously.⁸⁹ Furthermore, older crayfish individuals showed a better response to higher dietary lipid and carbohydrate levels compared to younger juveniles.⁸⁹ Crayfish can occupy different trophic levels depending on their specific

feed and habitat. Considering the trophic level is crucial for maximizing dietary carbohydrate utilization in crustaceans. Understanding how the trophic level influences their feeding behaviour and dietary requirements helps in formulating appropriate feeds that provide optimal carbohydrate sources. By taking trophic level into account, researchers and aquaculture farmers can enhance the utilization of dietary carbohydrates and promote sustainable and efficient production practices in the crustacean industry.

5.3 | Effects of age and moulting stages

The utilization of carbohydrates may be positively or negatively affected with the age. The amylase activity of flower crab (*Portunus pelagicus*) was reported to be increased with age¹⁸² and this finding suggests the more activity of amylase thereby relatively more utilization of carbohydrates in the later life stages of crustaceans. Additionally, the high carbohydrate feed increases the energy reserves in the adult *Parastacus brasiliensis* (a freshwater crayfish) that supports reproduction by providing excess energy required during this physiological stage.¹⁸³

Besides the life stages, the utilization and energy reserves of carbohydrates are also affected by moulting stages.^{143,145} The increased level of carbohydrates is required during pre-moulting stage to act as a precursor of chitin synthesis.¹⁸⁴ Moreover, the specific effects of 'eyestalk factors' which are currently known as crustacean hyperglycaemic hormone (CHH) on the blood sugar and hepatopancreatic glycogen storage varies with different moulting stages.^{185,186} Additionally, the occurrence of pentose-phosphate pathway is found to be high during intermolt stage (primarily stage C) and reduced in pre-moult stage^{6,144,187,188} and this finding suggests the metabolic changes during moulting stages and thereby variation in carbohydrate utilization.

5.4 | Digestibility

As mentioned earlier (Section 3), the digestibility of carbohydrates in crustaceans can be influenced by various inherent factors, as reported in the case of fish studies.^{5,18,189,190} These factors can originate from the source itself or within the organism. Additionally, the processing effects should not be overlooked. Among the different carbohydrate sources studied in various crustacean species, maize or corn, wheat, rice, and sorghum or milo, in their pure or processed form as native or gelatinized starch, have been commonly examined. Research indicates that wheat as a carbohydrate source exhibits more efficient digestion than maize in species such as black tiger shrimp⁶¹ and Pacific white shrimp.^{90,91} Similarly, Caribbean spiny lobster showed higher dry matter and carbohydrate apparent digestibility coefficients (ADCs) for wheat flour (native) compared to maize starch.¹⁰² However, in Pacific white shrimp, dry-extruded maize had a higher ADC than dry-extruded wheat,⁹¹ suggesting that processing methods can influence the ADC of dry matter and energy from different carbohydrate

sources within the same crustacean species. On the contrary, the ADC of energy for native corn (maize) (79.1%) was higher than that for native wheat (76.8%) in the case of giant freshwater prawns.⁹⁵ Likewise, the ADC of dry matter for extruded corn meal was higher than that for extruded wheat flour in giant mud crab.⁹⁶ These findings highlight the impact of processing techniques and source variations on the ADC of dry matter and energy from different carbohydrate sources among crustacean species. In general, understanding the digestibility of carbohydrates is crucial for regulating carbohydrate utilization in crustaceans. Factors such as source origin, inherent characteristics, and processing methods can significantly influence the digestibility and subsequent utilization of carbohydrates. Researchers have observed variations in digestibility coefficients among different carbohydrate sources in various crustacean species. These findings emphasize the importance of considering processing effects and source variations when formulating feeds for crustaceans to optimize their carbohydrate utilization and overall nutritional efficiency.

6 | FEED PROCESSING STRATEGIES TO IMPROVE CARBOHYDRATE UTILIZATION IN CRUSTACEANS

The utilization of carbohydrate has limitations in all aquatic organisms. Many authors reviewed and provided different strategies to improve the carbohydrate utilization in finfish.^{5,18,73} The use of carbohydrate-rich feed is not only beneficial in economic point of view, but also for environmental aspects. Addition of more carbohydrate in a growing feed would be helpful for production of less-polluting feed for crustaceans.

6.1 | Dehulling of raw ingredients

The seeds of plant-based ingredients typically have an outer covering called the seed coat, also known as the hull contains a significant amount of various antinutritional factors (ANFs) and fibre which affect their optimum utilization in aquafeed. Therefore, dehulling of the plant-based carbohydrate-rich ingredients can improve their utilization in crustacean feed. Dehulling can remove most of the ANFs and consequently improve the overall digestibility of different plant-based ingredients.¹⁹¹ The digestibility of dehulled plant-based protein like lupin showed an improved digestibility when fed to black tiger shrimp.¹⁹² The approach can be adopted for carbohydrates sources.

6.2 | Thermal treatment during feed preparation

Thermal treatments such as cooking and steaming increase the bio-availability of nutrients and enhance their digestibility. Apart from bioavailability of the nutrients, stable feed pellet is a must for crustacean species for their slow feeding behaviour. Application of thermal treatment gelatinizes the starch which enhances durability and water

stability of feed pellets.¹⁹³ The native potato starch (ADC 72%) and corn starch (ADC 85%) are less digestible than pre-cooked potato (ADC 93%) and corn (ADC 94%) starch, respectively in shrimps.⁶ However, the increasing inclusion level of gelatinized maize starch from 15% to 55% on dry weight reduced starch digestibility from 92% to 79% in spiny rock lobsters.¹⁰⁰ In this aspect, ingredient-specific treatment would be a better approach for preparation of crustacean feed. The changes in the dry matter, as well as energy digestibility of different carbohydrate sources subjected to different extrusion processes (no extrusion, dry extrusion and wet extrusion) in the feed of Pacific white shrimp⁹¹ proves the ingredient-specific efficacy of extrusion process for improving carbohydrate digestibility in crustaceans.

7 | FARMING STRATEGIES TO IMPROVE CARBOHYDRATE UTILIZATION IN CRUSTACEANS

7.1 | Ambient temperature

Temperature plays an important role in the regulation of the carbohydrate metabolism in crustaceans.¹⁹⁴ At lower temperature, feed consumption, nutrient absorption, and metabolic utilization were found to be lower in red swamp and southern white river crayfish (*Procambarus zonangulus*) and increasing temperature in the culture system could increase feed intake and carbohydrate utilization in these crustacean species.¹⁹⁵ While crustaceans tolerate a relatively broad temperature range, cultivating them at their optimal temperature could significantly enhance growth and feed intake, improving feed utilization. This is exemplified by the green rock lobster (*Sagmariasus verreauxi*), which displayed 100% survivability between 14.5°C and 25.0°C.¹⁹⁶ Notably, the species recorded its highest specific growth rate and feed consumption at 21.5°C.¹⁹⁶ The intrinsic optimum temperature range for 'cold-water' and 'temperate and tropical' crustacean species was found to be 6.91–9.06°C and 19.68–27.00°C, respectively.¹⁹⁷ Temperature slightly above the higher optimum level may improve the carbohydrate utilization in the crustacean probably through enhancing the metabolic activities. A similar approach can be seen in the case of finfish species like rohu (*Labeo rohita*).¹⁹⁸ At ambient temperature (26°C), the performance of non-gelatinized starch was not as good as that of gelatinized starch. However, when the groups fed with non-gelatinized starch were exposed to higher temperature (32°C) for a week, rohu exhibited improved growth and feed utilization, surpassing the performance of those fed with gelatinized starch.¹⁹⁸

7.2 | Water salinity

Growth of crustaceans depends on a combination of dietary protein and carbohydrate and ambient salinity in culture system as found in Pacific white shrimp.¹⁹⁹ To promote better growth, it is advantageous to maintain an optimal salinity level in the culture system, as this reduces the energy required for osmoregulation. Pacific white shrimp

reared in low salinity (3 ppt) exhibited maximum growth when fed with 20% dietary carbohydrate.²⁰⁰ The use of 15%–20% of dietary carbohydrate reduced stress of Pacific white shrimp reared in low saline condition.²⁰⁰ Additionally, the optimum dietary carbohydrate level for maximizing the specific growth rate of Pacific white shrimp at salinity levels of 1, 2, 4, 8, and 16 ppt was found to be 29.9, 27.6, 26.9, 26.3, and 22.3%, respectively,²⁰¹ thus dietary carbohydrate level is important for successful culture of this species, particularly at low salinities.⁷⁸ Dietary carbohydrate along with protein play an important role in Pacific white shrimp at acute salinity-mediated stress conditions by regulating the expression of carbohydrate metabolic enzymes¹³⁸ and also glucose receptors (GLUT1) in different tissues.²⁰² Therefore, the role of carbohydrates as stress mitigators in low salinity conditions is significant. In such conditions, elevated glucose levels serve as osmolytes,²⁰³ helping maintain haemolymph osmolality and providing the necessary energy to cope with adverse circumstances. Therefore, when culturing crustaceans in relatively low saline water, incorporating a higher amount of dietary carbohydrates can contribute to improved species performance.

8 | FEED FORMULATION AND FEEDING STRATEGIES TO IMPROVE CARBOHYDRATE UTILIZATION IN CRUSTACEANS

8.1 | Tailoring dietary fibre for different species

When it comes to selecting the type of fibre for a crustacean feed, it is important to consider the specific nutritional needs and digestive physiology of the crustacean species in question. While soluble and insoluble fibre are both valuable components of a balanced feed, the optimal type of fibre may vary depending on the species. In general, crustaceans can benefit from a combination of soluble and insoluble fibre sources in their feed. Soluble fibres, such as pectin and gums, have the ability to form a gel-like substance when mixed with water, which can help slow down the release of glucose during digestion. The tolerable limit of dietary crude fibre may vary among various species but a lower inclusion level is always recommended for improving the efficiency of carbohydrate utilization. Accordingly, the increasing level of dietary α -cellulose resulted in reduced ADC of dry matter and protein in giant freshwater prawns.¹⁷⁴ However, due to the presence of endogenous cellulases, a high ADC of dietary α -cellulose (about 80%) was reported in giant freshwater prawn.¹⁷⁴ Similar observations were reported in the case of spiny lobster (*J. edwardsii*), which showed around 94% ADC for carboxymethyl cellulose.¹⁰⁰ Nevertheless, increasing dietary cellulose resulted in increasing specific dynamic action (SDA) with increased energy requirement in giant freshwater prawn.¹⁷³ On the other hand, the dietary fibre such as cellulose is associated with a delay in gastric transit time which helps in efficient digestion and absorption of dietary protein.²⁰⁴ Unlike penaeid shrimp, freshwater prawn can utilize as high as 30% of dietary fibre²⁰⁵ due to the presence of endogenous cellulase enzyme.¹⁷⁴ Therefore, it could be advantageous to include dietary crude fibre within acceptable limits, as this can yield

several beneficial effects. These effects include facilitating a gradual release of glucose from dietary carbohydrates, optimizing gastric transit time to enhance nutrient digestion and absorption, and serving as an energy source for select crustacean species.

8.2 | Use of feed additives

8.2.1 | Exogenous enzymes

Exogenous enzyme supplementation to reduce or eliminate the detrimental effect of antinutritional factors (ANFs) present in the high plant-based feed is one of the common practice in aquafeed production.²⁰⁶ Supplementation of exogenous enzymes is found to be promising for larval nutrition with improved carbohydrate utilization even at later life stages of crustaceans.²⁰⁷ Supplementation of exogenous β -glucosidases in the shrimp feed was found to improve the bioavailability of sugars from apparently indigestible carbohydrates like cellulose and chitin,²⁰⁸ thus may aid in production of low-cost shrimp feed. Although, the live feed provides exogenous sources of enzymes during larval development, but the amount may not be sufficient to show a significant effect on nutrient utilization. For example, *Artemia* as live feed contributed very little amount of exogenous enzyme than required in Atlantic white shrimp (*P. setiferus*) larvae.²⁰⁹ Furthermore, the carnivores' ability to produce a sufficient quantity of carbohydrases solely from natural food sources is believed to be restricted.²¹⁰ The lack of existing literature on this aspect limits further discussion.

Phytase, another commercially important exogenous enzyme, plays a crucial role in mitigating the negative effects of phytic acid and enhancing the utilization of plant-based ingredients. Phytic acid, also known as phytate, is a storage form of phosphorous (P) that is bound to inositol within the fibre of raw whole cereal grains, oilseeds, and nuts.²¹¹ Phytase enzymes are widely distributed among various life forms, with microorganisms being the most promising source, followed by plants. Major sources of microbial phytases include filamentous fungi like *Aspergillus ficuum*, *Mucor piriformis*, and *Cladosporium* species.²¹² Supplementation of phytase (500 FTU) in a soybean-based feed not only reduced the nitrogen and phosphorus burden on the culture system but also significantly altered the fatty acid composition of *P. monodon* tissue.²⁰⁶ Likewise, the dietary supplementation of microbial phytase in freshwater prawn feeds has been found to enhance the utilization of plant-derived feed ingredients.²¹³

In addition to exogenous β -glucosidases and phytases, the inclusion of other exogenous enzymes such as xylanase, cellulase, and more can be beneficial in improving the utilization of carbohydrate-rich plant-based feeds in crustaceans. Along with improving the utilization of carbohydrates in crustaceans, this will reduce the feed cost and create a more efficient feed.

8.2.2 | Dietary supplementation of biogenic amines

There are variations in the effect of different biogenic amines on the carbohydrate metabolism in crustacean. Generally, serotonin,

dopamine, octopamine, norepinephrine, and epinephrine have hyperglycemic effect in crustaceans.²¹⁴ Serotonin and enkephalins exhibit negative effect on CHH release, whereas dopamine shows a positive effect on the release of CHH in the haemolymph of crustaceans.²¹⁵ During cold shock, hyperglycaemia is induced not only by CHH but also by the release of various biogenic amines such as serotonin, dopamine, and epinephrine. These amines potentially cause hyperglycaemia by stimulating the release of norepinephrine and/or octopamine.²¹⁶ Furthermore, serotonin (5-HT) plays a pivotal role in optimizing the utilization of glucose in the haemolymph²¹⁷ by activating phosphofructokinase in the hepatopancreas, thereby initiating the glycolysis process. Administration of serotonin in decapod southwestern Atlantic crab and Spiny-cheek crayfish (*Faxonius limosus*, previously known as *Orconectes limosus*) resulted in hyperglycaemia in haemolymph mediated through enhancing CHH release from the sinus gland in both submerged and air-exposed condition.²¹⁸ Whereas, serotonin-induced hyperglycaemia in both intact and eyestalk-ablated Indian prawns suggesting its effect does not depend on CHH release.²¹⁹ On the other hand, when serotonin was administered along with dopamine, it induced hyperglycaemia specifically in eyestalk-intact specimens of monsoon river prawn (*Macrobrachium malcolmsonii*)²²⁰ and giant freshwater prawn.²²¹ This hyperglycemic effect was observed through the reduction of total carbohydrate and glycogen content, as well as the enhancement of phosphorylase activity in the hepatopancreas. These findings suggest that the hyperglycaemia induced by serotonin and dopamine administration is mediated by CHH.

Another important biogenic amine dopamine helps crustaceans in adapting to environmental stressors²²² and induces hypo- or hyperglycaemia depending on the species. For example, dopamine induces hyperglycaemia in black tiger shrimp,²²³ Pacific white shrimp,²²⁴ and European green crab (*Carcinus maenas*),²²⁵ but induces hypoglycaemia through inhibiting CHH release in red swamp crayfish,²²⁶ Danube crayfish (*Astacus leptodactylus*) and mantis shrimp (*Squilla mantis*).²²⁷

Melatonin administration reduced total carbohydrate and glycogen, and increased phosphorylase activity in the hepatopancreas of both intact and eyestalk-ablated freshwater field crab (*Oziotelphusa senex senex*) which suggests that 5-HT-induced hyperglycaemia in this species is not mediated by CHH.²²⁸ Similar results were also reported in the case of the Chinese mitten crab (*Eriocheir sinensis*) including a reduction of total carbohydrate and glycogen, and increased phosphorylase activity in muscle.²²⁹ A study on tyramine showed that giant freshwater prawns fed with feeds containing 1 and 10 mg/kg tyramine stimulated aerobic glycolysis initially (after 3 days of feeding) and then induced anaerobic glycolysis (after 7 days of feeding) to maintain homeostasis.^{230,231}

Based on the above results from different crustacean species of different biogenic amines in the crustacean feed may give a promising effect on better utilization of glucose. Specifically, biogenic amines which can induce hyperglycaemia independent of CHH release could be helpful to maintain homeostasis and energy supply from stored carbohydrates in crustaceans during eyestalk ablation which is a common practice for induction of maturation and spawning.²³² General glucose homeostasis, mode of action of crustacean hyperglycemic

hormone (CHH) and how other hormones and biogenic amines regulate glucose homeostasis in crustaceans has been illustrated in Figure 2.

8.3 | Microbial approach

Although there is no permanent gut microbial community in crustacean species, the most common gut microflora in decapods is *Vibrio* sp., *Moraxella* sp. and *Flavobacterium* sp.²³³ The gut microflora in crustaceans is less diverse than that of cultured fish.²³³ Dietary supplementation of short-chain fructo-oligosaccharides improved the immunity of Pacific white shrimp through improving the beneficial gut microbial community; however, most of these microbes were found to be unculturable species.²³⁴ Similarly, supplementation of galacto-oligosaccharides and resistant starch improved the gut microbiota and short-chain fatty acids production in green mud crab.²³⁵ Additionally, 16S rRNA gene sequencing showed variation in the gut microbial diversity in Norway lobster (*Nephrops norvegicus*) under different feeding regimes (frozen mussel fed, dry formulated pellet fed or starvation).²³⁶ These reports indicate that the gut microbial population of crustaceans can be modified through dietary interventions.

Besides, an interesting report on the effect of dietary carbohydrates on gut microbiota of Pacific white shrimp showed that complex carbohydrates were not a good source of energy for this species when reared in low saline water due to an increase in opportunistic pathogenic bacteria in the gut.²³⁷ However, only corn starch was used as complex carbohydrate in this research and other sources of carbohydrates were sucrose and glucose. So, general statement based on a single complex carbohydrate may not be appropriate. Although Proteobacteria was abundant in the gut of all carbohydrate-fed groups, the group fed with corn starch exhibited a decrease in Actinobacteria and an increase in Firmicutes in Pacific white shrimp.²³⁷ Besides dietary interventions, the gut microbial community can vary during development stages as found in ornate spiny lobster (*Panulirus ornatus*).²³⁸ Yet, throughout the developmental stages (6–7 days post-emergence [dpe], 52 dpe, and 13 months post-emergence [mpe]), phyla Tenericutes and Proteobacteria were the most abundant community in the gut.²³⁸ Supplementation of feed probiotic generally improves the microbial diversity in the gut of both fish and crustaceans.²³⁹ The factors and different strategies to improve the gut microbial composition of Pacific white shrimp have been reviewed recently which showed the use of probiotic in the crustacean feed may play a remarkable role in improving the overall dry matter digestibility.²⁴⁰ Based on these findings, it can be concluded that supplementation of feed-specific probiotic, prebiotic, or both as symbiotic probably can improve the carbohydrate utilization by crustacean.

8.4 | Feeding strategies

Feeding strategies concerning the culture system, life stage of the species and type of feed should be adopted for efficient production of

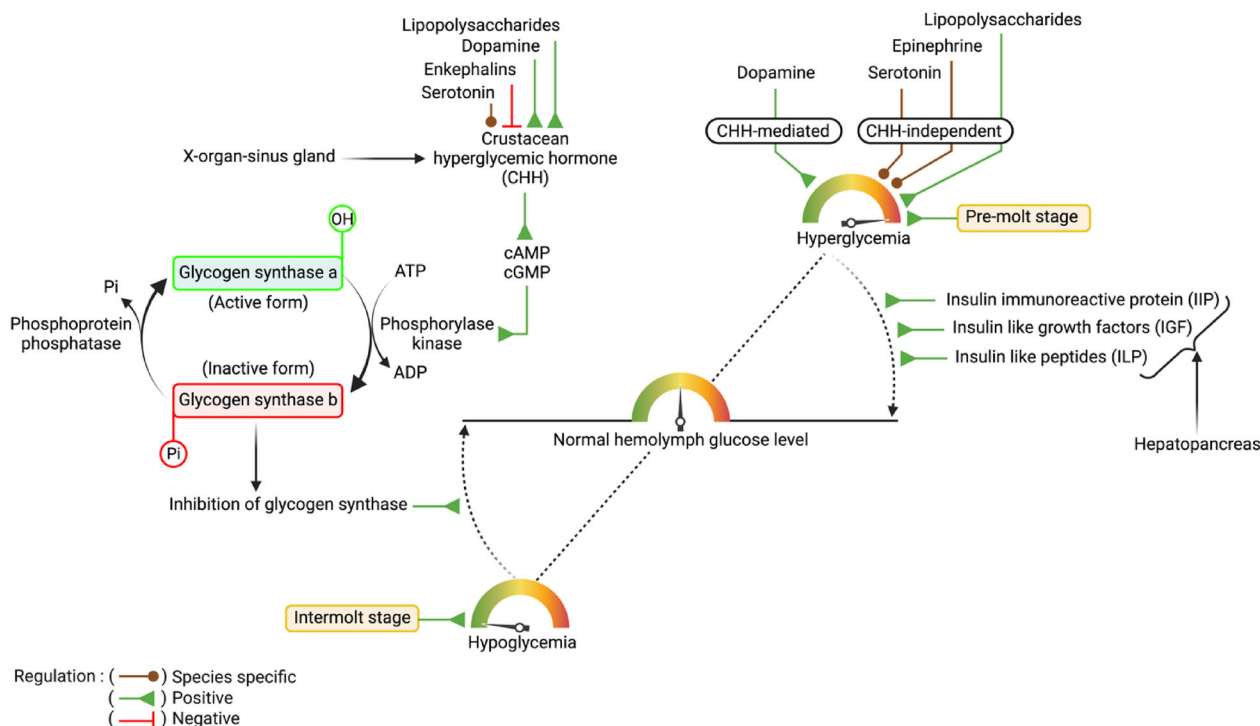


FIGURE 2 Glucose homeostasis and mode of action of crustacean hyperglycemic hormone (CHH) in crustaceans. Hyperglycaemia in crustaceans is mediated through two pathways. First, the CHH-mediated pathway, where dopamine supports hyperglycaemia, and secondly, the CHH-independent pathways, where hormones like serotonin and epinephrine show species-specific regulation and lipopolysaccharides enhance hyperglycaemia. Hyperglycaemia is also encountered during the pre-molt stage. Biogenic amines such as insulin immunoreactive protein (IIP), insulin-like growth factors (IGF), and insulin-like peptides (IIP) secreted from the hepatopancreas help maintain normal haemolymph glucose levels during hyperglycemic conditions. Conversely, hypoglycemic conditions naturally occur during the intermolt stage. Different biogenic amines regulate cyclic AMP and GMP synthesis, which in turn inhibits glycogen synthesis during hypoglycaemia to support normal glucose levels in the haemolymph.

crustacean.⁷¹ Similarly, different feeding strategies can be adopted to improve the utilization of carbohydrates by the crustacean. Increasing feeding frequency of 38% carbohydrate-containing feed up to four times a day was found to increase carbohydrate digestibility with improved growth in Pacific white shrimp.²⁴¹ As we know, crustaceans are sluggish feeders, and hence, the feeding frequency should be increased to enhance the feed intake with some exception like temperate lobsters. Increased feeding frequency can result in slow rise of glucose in the haemolymph to facilitate better metabolic utilization. On the other hand, less frequent feeding for high carbohydrate feed may lead to hyperglycaemia and poor metabolic utilization of carbohydrates.

8.4.1 | Protein-sparing effect of dietary carbohydrates

The protein-sparing effect of carbohydrates in the crustacean feed has already been discussed in the previous section under nutritional requirement for various crustacean species. Regardless, it is worth noting that variation in the carbohydrate levels in feeds used in protein requirement studies can provide secondary data to get

information about carbohydrate level at the optimum protein levels which shows optimum performance in terms of growth, survival, and physio-metabolic responses. Optimization of dietary protein level using non-protein energy sources can be done through the incorporation of lipid and/or carbohydrate. However, as mentioned earlier, the negative impact of lipids on pellet stability and palatability restricts their inclusion levels in feed. Therefore, to maximize carbohydrate inclusion, it is beneficial to implement certain approaches such as starch gelatinization and the use of exogenous enzymes. These approaches play a significant role in enhancing the utilization of carbohydrates in feeds. Moreover, carbohydrates can serve as valuable binding components, enabling the production of water-stable and highly palatable feeds.^{15,16} In a recently published review on carbohydrate utilization in finfish,⁵ the authors relied on data from few protein requirement studies to determine the optimal or maximum permissible limit of carbohydrates. However, considering the carbohydrate level directly corresponding to the optimum protein level as the 'optimum' or 'maximum permissible' level for carbohydrates may not be highly reliable. For that reason, we have extracted data from the protein requirement studies to know the total carbohydrate level (TC%) as well as nitrogen-free extract level (NFE%) to calculate the ratio of crude protein to total carbohydrate (CP:TC) and crude protein to

TABLE 5 Inferring dietary carbohydrate (CHO) level from crude protein (CP) requirement studies of crustaceans.

Species	IBW ^a (g)	Rearing condition ^b	Protein levels (%)	Dietary lipid (%)	Dietary Energy (MJkg ⁻¹)	Optimum CP (%)	CHO sources	CHO levels ^c (%)	TC ^d (%)	CP:TC	NFE ^e (%)	CP:NFE	References
Shrimps and prawns													
Pacific white shrimp (<i>Penaeus vannamei</i>)	6.2	SW (35 ppt), 25°C	31, 35, 39, 43, 47	4.7–5.2		43	Wheat flour	47.2, 39.6, 31.9, 24.6, 19.5	46.2	0.9			242
	1.6	SW (35 ppt), 28°C	5, 15, 40	10	16	40	Native wheat flour	60.91, 49.54, 19	41	1.0	19	2.1	243
	1.3	SW (31.61 ppt), 26.6°C	25, 30, 35, 40, 45	8.6–9.4	16.2–16.9	33.4	Wheat flour	10 (5)	41.5	0.8			244
							Corn starch	2 (5)					
							Dextrin	298, 24.6, 19.3, 13.9, 8.6					
	6.5	Biofloc in SW (32 ppt), 26°C	20, 25, 30, 35	8.0–8.1	15.8–16.5	25	Wheat meal	58.5, 50, 41.5, 33	53.2	0.5			245
	0.3	Low saline (2 ppt), 27.5°C	25, 30, 35, 40, 45	7.8–8.0	19.1–19.8	33.5–34.4	Wheat flour	20 (5)	48.2	0.7			246
	0.7	SW (30 ppt), 28°C	25, 30, 35, 40, 45, 50	8.1–8.3		34.5	Corn starch	37.4, 31.5, 25.7, 19.8, 13.9	50.9	0.7			247
	4.8					35.6	Wheat flour	34.5 (6)		0.7			
	10.5					32.2	Starch	30, 25, 20, 15, 10, 5		0.6			
	4.0	ISW (15 ppt), 31.3–31.9°C	20, 25, 30, 35, 40, 45, 50	8.2–8.4	18.1–19.2	39.3–39.8	Starch	39.8, 34.8, 29.8, 24.8, 19.8, 14.8, 9.5	43.6	0.9	40.6	1.0	248
Black tiger shrimp (<i>P. monodon</i>)	0.002	SW (35 ppt and between 12th to 15th day, the salinity was reduced to 15 ppt), 26°C	25, 35, 45, 55	9.8–10.2	10.5–16.3	35	Dextrin	15, 14, 13, 12, 11, 10, 9			29.2	1.2	249
	3.1	Outdoor tanks with SW (32.4 ppt), 26.6–29.4°C	30, 35, 40	11.8–12.3	19.6–20.7	30–35	Corn starch	40, 30, 20, 10					
							Cellulose	1.3, 2.8, 4.3, 11.3, 22.8, 35.3					
							Alginate	15 (7)					
Giant freshwater prawn (<i>Macrobrachium rosenbergii</i>)	0.2	FW, 28.5°C	23, 32, 40, 49	10.5–11.6		40	Wheat flour	35.9, 32.4, 28.7	40.6	0.7			250
	0.2	FW, 28.5°C	23, 32, 40, 49	10.5–11.6		40	Starch (pre-cooked)	38.7, 29.3, 19.7, 12.2	39.8	1.0			251
	0.2–1.2	FW, 28.5°C	34.6, 26.5, 24.5, 18.4, 12.5	0.6–2.0	15.3–19.8	25–35	Cellulose	5 (4)	24.9	1.0			252
			18.4, 19.9, 23.6, 24.4, 27.3	1.1–1.5	14.2–17.9	24.4–27.3	Potato starch	34, 36.5, 39, 41.5, 44	25.3	1.0			
							Cellulose	20, 15, 10, 5, 0					
Crabs													
Chesapeake blue crab (<i>Callinectes sapidus</i>)	1.2–1.3	SW (25 ppt), 23°C	23, 37, 49	10.4–11.3		37	Starch	29.1, 16.3, 4.4	56.7	0.7			253
Chinese mitten crab (<i>Eriocheir sinensis</i>)	1.1	FW, 27.8°C	29.78, 34.09, 38.98, 44.19, 48.65, 54.77	7.0–10.6	14.5–14.9	39.0–42.5	Corn starch	37, 30, 22.5, 15, 8, 1	40.7	1.0	33.3	1.2	254
	3.6	FW, 27.5°C	25, 30, 35, 40	4.4–6.6	16.2–16.4	35	Wheat middlings	38, 29.5, 21, 13.5	53.6	0.7			255
							Rice bran	17, 12, 7, 2					

(Continues)

TABLE 5 (Continued)

Species	IBW ^a (g)	Rearing condition ^b	Protein levels (%)	Dietary lipid (%)	Dietary Energy (MJ kg ⁻¹)	Optimum CP (%)	CHO sources	CHO levels ^c (%)	TC ^d (%)	CP:TC	NFE ^e (%)	CP:NFE	References
Giant mud crab (<i>Scylla serrata</i>)	11.2	SW (32 ppt), 26.4°C	32, 40, 48	6	14.7–18.7	32	Bread flour	13.5, 11.8, 10	51	0.7	31	1.1	256
				12			Cellulose	25.9, 16.2, 6.5					
							Bread flour	13.5, 11.8, 10	56.9	0.6	28.2	1.2	
							Cellulose	19.9, 10.2, 0.5					
	0.3	SW (28 ppt), 27°C	15, 20, 25, 30, 40, 45, 50, 55	7.5–8.0	16.8–17.1	46.9–47.0	Wheat flour	8 (8)	63.7	0.7	24.7	1.9	257
							Dextrin	51.8, 47, 4, 33, 26, 19.2, 12.3, 4.8, 0					
Gazami crab (<i>Portunus trituberculatus</i>)	2.5	SW (26–28 ppt), 26–28°C	31.6, 36.5, 41.7, 45.6, 50.2, 55.8	7.9–8.3	17.3	51.5	Dextrin	41.1, 34.2, 27.3, 20.5, 13.5, 6.7	70.1	0.7			258
	3.8	SW (26–28 ppt), 26.5–33.4°C	35, 43, 51	5	19.0–20.7	51	Dextrin	12.0 (3)	66.9	0.8			259
							Cellulose	28.4, 18.2, 8					
Lobsters and crayfish													
Spiny rock lobsters (<i>Isos edwardsii</i>)	3.6	SW (35 ppt), 18°C	25.4, 29.4, 33.1, 37.4, 43.4, 44.9	5	12.6–13.9	29.4	Pre-gelatinized maize starch	33.9, 27.3, 20.9, 14.5, 8.2, 1.8	27.3	1.1			260
			23.9, 28.9, 31.3, 36, 42.7, 49.9	9	13.2–15.1	31.3		32.4, 26.2, 20, 13.7, 7.5, 1	20	1.6			
American lobster (<i>Homarus americanus</i>)	300–500	SW, 20°C	0, 20, 40, 60	10		40	Corn starch	65, 45, 25, 5	40	1	25	1.6	261
							Cellulose	15 (4)					
Western rock lobster (<i>Panulirus cygnus</i>)	0.3–0.5	SW (35 ppt), 21.9°C	25.6, 31.9, 37.9, 41.2, 44.6, 49.3	5	16.6–17.8	49.3	Pre-gelatinized maize starch	30, 21.3, 20.9, 15.5, 11.6, 5	5	9.9			262
			32.8–50.6	9	18.6–19.3	50.6		26.8–5.2	5.2	9.7			
Australian red claw crayfish (<i>Cherax quadricarinatus</i>)	1.1	FW, 27°C	20, 25, 31, 37, 43, 49, 55	7.7–10.8	18.7–21.5	34.2	Sorghum meal	64.6, 56.1, 47.3, 37.8, 27.9, 17.9, 9	56.9	0.6	50.9	0.7	263
							Wheat meal	3 (7)					
Red swamp crayfish (<i>Procambarus clarkii</i>)	2.5	FW, 27–33°C	24, 27, 30	4	18.3–19.4	27	Wheat middlings	49.5, 44.8, 40.2	51.3	0.5	44.7	0.6	264
							α-Starch	4 (3)					
							Wheat middlings	39.8, 35.1, 30.4	49.4	0.6	43.1	0.6	
							α-Starch	4 (3)					

^aIBW, initial body weight.

^bSalinity (FW, freshwater; BW, brackishwater; SW, sea water; ISW, inland saline water) and temperature.

^cNumber of feeds is indicated in bracket.

^dTC, total carbohydrate of feeds.

^eNFE, nitrogen-free extract of feeds.

nitrogen-free extract (CP:NFE; Table 5). The main sources of carbohydrates used in the protein requirement studies has been also listed in the Table 5. Except for giant freshwater prawn,²⁵³ the ratio of CP to TC are found to be below one. The ratio below one suggests that at optimum level of dietary protein, the inclusion level of total carbohydrate is higher than the crude protein. However, the ratio of CP to NFE is found to be as high as 2.11 in case of Pacific white shrimp when fed with 40% CP as optimum protein level.²⁴³ Whereas, the ratio of CP to NFE was lower than one in the feed of Australian red claw crayfish²⁶³ and red swamp crayfish²⁶⁴ when fed with optimum dietary CP. It is important to note that the ratio depends on the optimum dietary crude protein level and the total carbohydrate and nitrogen-free extract can be taken as a reference level to use in the feeds of crustaceans when fed with optimum dietary crude protein.

9 | NUTRITIONAL PROGRAMMING AND GENETIC SELECTION

9.1 | Nutritional programming

Though nutritional programming has not yet been popular or studied in crustacean research but there are few reports on this aspect and provide promising results. Feed restriction during early development of Pacific white shrimp was found to modify the expression of metabolism-related genes.²⁶⁵ Both 40%²⁶⁶ and 70%²⁶⁵ feed restriction in this species during protozoa and post-larval stage resulted in higher expression of mRNAs related to enzymes coding for glycolysis and ATP synthesis as long-term effects, respectively. Additionally, the protozoa substage 1 and post-larval stage were suggested to have high molecular plasticity and ideal stage for early stimulation for nutritional programming in Pacific white shrimp.²⁶⁷ Nevertheless, complete feed restriction (starvation) resulted in an increase in the abundance of opportunistic pathogens, leading to detrimental effects on health.²⁶⁸ While these recent findings suggest the potential for nutritional programming to enhance the ability of crustacean species to utilize dietary carbohydrates during the growing stages, further research is needed to fully implement this technique.

9.2 | The development of genetically improved species

Production of genetically improved varieties of shrimps become a key priority in the shrimp industry to produce pathogen-free domesticated shrimps.²⁶⁹ In this regard, production of specific pathogen-free (SPF) shrimp stock and subsequently the terms like specific pathogen resistant (SPR) shrimp, specific pathogen tolerant (SPT) shrimp and even 'all pathogen exposed' (APE) shrimp gained popularity in the shrimp industry.^{270,271} Besides these disease-resistant shrimp brood stock production, a recent report suggests that the female reproductive traits like number of eggs per spawn (NE), number of nauplii per spawn (NN) and spawn frequency over 30 days (SF) can be improved

through genetic selection in Pacific white shrimp.²⁷² Based on these reports, it can be suggested that production of improved variety of different crustacean species with high carbohydrate utilization capacity without affecting the growth will be possible near future. Production of high carbohydrate-tolerant crustacean species will not only reduce the production cost through the protein sparing-effect of carbohydrate, but also improve water quality in intensive crustacean farming systems.

10 | SUMMARY AND FUTURE PERSPECTIVES

The role of carbohydrates in crustacean feed production is important but requires careful consideration to avoid negative effects on crustacean health. The inclusion level of carbohydrates should be based on factors such as source, nature, and processing to optimize utilization. Wheat and sorghum/milo have shown to be beneficial carbohydrate sources.⁸ However, determining the maximum permissible limit of carbohydrates for crustaceans, irrespective of the source, requires further investigation to provide species-specific recommendations. Additionally, the utilization of carbohydrates as an energy source during starvation varies among crustacean species and is influenced by factors such as age, moulting stage, and digestive capacity.

To advance our understanding of carbohydrate utilization in crustaceans and enhance the profitability of crustacean aquaculture, several critical research directions should be pursued. Although various strategies to improve carbohydrate utilization have been discussed above in Sections 6–8 based on scientific literature and briefly illustrated in Figure 3, the field remains relatively unexplored. The primary objective should be to bridge the knowledge gap in carbohydrate nutrition in crustaceans and make crustacean aquaculture more profitable. To achieve this, studies on the digestibility of different carbohydrate sources and forms should be expanded, focusing on isonitrogenous, isolipidic, and hetero-energetic diets. Additionally, there is a need to develop methodologies to track the utilization and fate of dietary-derived glucose. Utilizing source-specific pre-treatment methods, such as cooking, extrusion, gelatinization, and enzyme hydrolysis, can enhance ingredient performance, reducing the need for unnecessary high-cost treatments.^{193,211} Similarly, nutritional programming should be emphasized to develop carbohydrate-tolerant crustacean species, with attention given to identifying the optimal developmental window during early life and providing appropriate dietary stimuli.²⁶⁷

Furthermore, exploring high carbohydrate-tolerant genotypes in commercially important crustacean species and establishing selection and breeding programs, similar to those used in the shrimp industry, can contribute to enhancing carbohydrate utilization and improving profitability.^{269–271} Adoption of successful approaches, such as the production of SPF, SPR, SPT, and all-female producing (APE) shrimp stocks, can facilitate the achievement of high carbohydrate tolerance in crustaceans.^{237–239} Supplementing exogenous enzymes and biogenic amines in crustacean nutrition is another avenue to enhance

Strategies to improve carbohydrate utilization in crustaceans

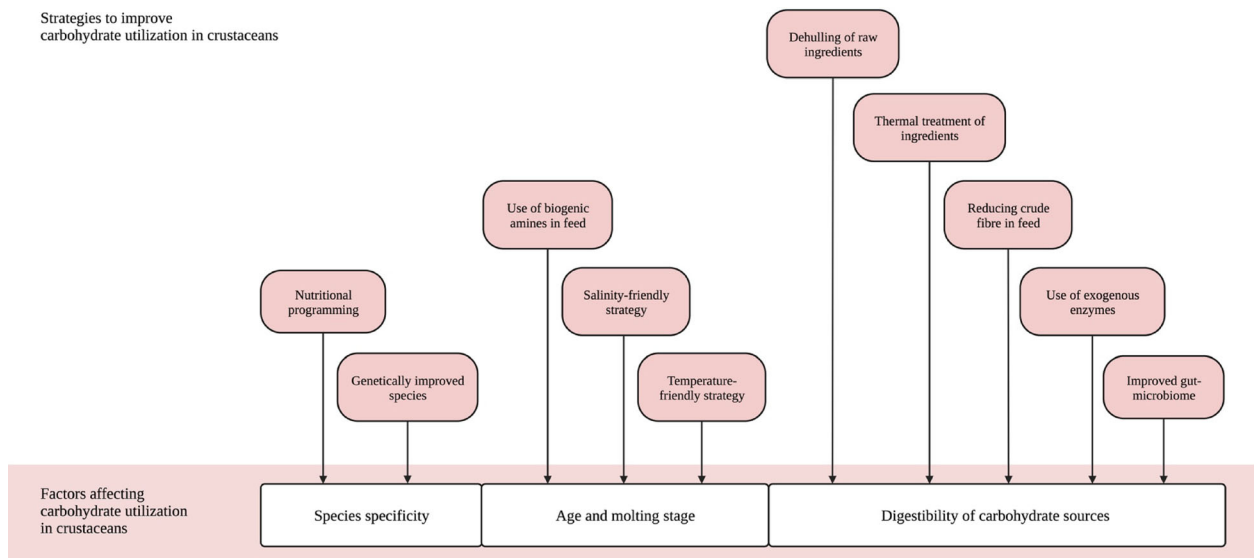


FIGURE 3 Major factors affecting carbohydrate utilization in crustaceans and strategies to improve its utilization. Enhancing carbohydrate utilization in crustaceans can involve nutritional programming and the selection of genetically improved, high-carbohydrate-tolerant species. Crustaceans can utilize a more significant amount of dietary carbohydrates when cultured at slightly higher temperatures than their optimal growth temperature and under lower salinity conditions. Dietary supplementation with biogenic amines could enhance carbohydrate utilization, particularly concerning moulting. Strategies such as dehulling, thermal treatment of ingredients, use of exogenous enzymes, and reducing crude fibre in the feed can enhance the digestibility of various carbohydrate sources. Furthermore, exploring targeted probiotics and manipulating the gut microbiome presents a promising strategy for improving carbohydrate utilization in diverse crustacean species.

carbohydrate utilization.⁵ Biogenic amines like melatonin, serotonin, and dopamine play vital roles in carbohydrate mobilization and metabolism, while exogenous enzymes such as β -glucanases, phytase, xylanase, and cellulase improve the utilization of carbohydrate-rich feeds.⁵ However, careful consideration of factors such as enzyme source, combination, dosage, properties, and delivery systems is essential for practical application.⁵ Additionally, research on the natural gut microbiomes of different crustacean species and their relationship with the host organism is crucial for targeted probiotic development.^{234–238} Probiotic application in aquaculture aims to promote beneficial microbial growth while suppressing pathogenic microorganisms in the gut.²³⁹ Advancements in metagenomics have facilitated the understanding of probiotic functionality.²³⁹ Additionally, probiotic research should go beyond natural gut microbiomes and attempt to improve carbohydrate utilization through gut microbiome modulation.

In conclusion, dispelling the misconception that carbohydrates are unnecessary for crustaceans and conducting further research to understand carbohydrate utilization mechanisms are essential steps toward advancing crustacean aquaculture. These efforts have the potential to make the industry more profitable and sustainable, benefiting both producers and consumers.

AUTHOR CONTRIBUTIONS

Vikas Kumar: Conceptualization; writing – review and editing; supervision. **Krishna Pada Singha:** Conceptualization; methodology; validation; investigation; writing – original draft; data curation; resources; visualization; formal analysis; writing – review and editing; funding

acquisition. **Narottam Prasad Sahu:** Writing – review and editing; supervision. **Parimal Sardar:** Writing – review and editing; supervision. **N. Shamna:** Writing – review and editing; supervision.

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CONFLICT OF INTEREST STATEMENT

The authors declare no competing or financial conflicts of interest.

DATA AVAILABILITY STATEMENT

All the supporting data and information are available within the manuscript.

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