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BENEFITS OF PHOSPHOLIPIDS IN AQUAFEED DEVELOPMENT: A REVIEW

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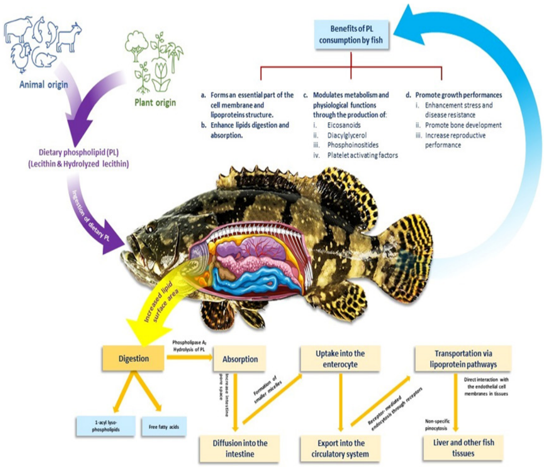
HIGHLIGHT

- The use of phospholipids in aquafeed is increasing and gaining wider consideration.
- Dietary phospholipids enhance digestion and absorption of other lipids in aquaculture species.
- Dietary phospholipids are vital for growth and good health of aquaculture stocks.
- Hydrolysed phospholipids are more efficient in aquatic feed utilisation and growth compared with normal phospholipids.

GRAPHICAL ABSTRACT



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ABSTRACT

Fish oil (FO) is the main source of lipids in aquafeed, but its use has become very unsustainable due to over-exploitation, scarcity and high cost. Plant oil has been proposed as an alternative to FO, but they are less digestible and not rich in fatty acids. In addition, larval and juvenile fish are unable to synthesise sufficient phospholipids (PLs) for their metabolic need. Hence, the necessity to supplement PLs in their diets. This review describes the application and beneficial impact of dietary PLs in aquafeed. PLs are an essential component of aquafeed as they supply energy for metabolic activities and enhance digestion and absorption of other dietary lipids. Plant-based PLs such as soy lecithin serve as an emulsifier that helps lipid catabolism by facilitating enzymatic hydrolysis in the fish's digestive system, besides improving nutrient absorption, growth and health. Studies on farm animals have confirmed the positive effects of PLs. Although the literature on aquafeed application is limited, to growth and health of farmed fish and crustaceans. The use of PLs in aquaculture is set to increase as both feed producers and farmers seek to maximise production through efficient feed utilisation and ensure sustainability in delivering quality fish to consumers.

Introduction

Lipids containing phosphorus are called phospholipids (PLs) (Tocher *et al.*, 2008) and they are amphiphilic; comprising a polar head and lipophilic tail, which has a constituent of two fatty acids, a glycerol or an amino-alcohol sphingosine backbone esterified at the "one" and "two" positions, and a phosphate group esterified at the "three" position. They all lead to the production of molecules such as ethanolamine, choline and inositol (Van Hoogevest & Wendel, 2014; Zhou & Rakariyatham, 2019) (Figure 1). PLs are natural components of cell membranes in all living organisms which contain emulsifying and antioxidant properties (Xie, 2019). There are two classes of PLs: Phosphoglycerides (where their alcohol is glycerol) and sphingolipids (where their alcohol is sphingosine) (El-Bacha & Torres, 2016). The most important and abundant of these PLs discovered in fish is phosphatidylcholine. Each phospholipid class is likely to have different effects on different fish species due to their unique roles (Kanazawa, 1993). The degree of unsaturation, differences in polar head group characteristics, and fatty alkyl-chain length are all factors affecting the structural variations of PLs from different sources (Sun *et al.*, 2018).

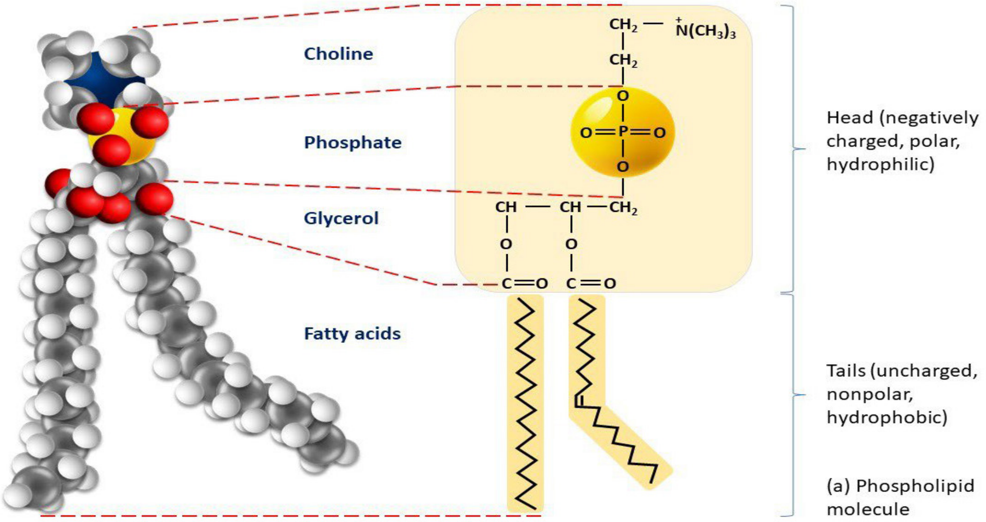

Figure 1: Microstructural figure of a phospholipid molecule comprising a hydrophilic head that contains choline or phosphate with glycerol that forms a phosphatidylcholine and hydrophobic tails. This image was adapted from Bruning (2009)

Dietary PLs may be derived from natural sources (plants and animals) or synthetic sources. Natural PLs are preferred in the formulation of diets because they are sustainable, environmentally friendly and cheap (Van Hoogevest & Wendel, 2014). Fish like herring, anchovies, salmon, krill, mackerel and sardines are rich in PLs, comprising highly polyunsaturated fatty acids (PUFA) like eicosapentaenoic acid (EPA) and docosahexaenoic acid (DHA), which are both easily digested (Khan *et al.*, 2018a; Sun *et al.*, 2018). Soybean oil, corn oil, linseed oil, rapeseed oil and palm oil are some examples of plant-based phospholipid sources, which serve as potential alternatives to aquatic sources in fish feed production (Rana *et al.*, 2009; Gunstone, 2011). Plant-based meals are a great alternative to marine-sourced meals, but they contain a lesser proportion of PLs (Sargent *et al.*, 2002). It has been shown that the effects of marine PLs are more potent than plants in fish meals (Jaxion-Harm, 2021). For instance, gilthead seabream (*Sparus aurata*) larvae will experience better growth when fed with marine PLs than soy lecithin (Saleh *et al.*, 2015). However, despite the superior effects of marine PLs, its scarcity and unsustainability due to the impacts of climate change pose a great concern on its utilisation.

Dietary PLs play key roles in (i) minimising the leaching of water-soluble nutrients from feed, thereby improving diet quality (Coutteau *et al.*, 1997); (ii) helping to improve the emulsification of dietary lipids and aid their absorption in the gut (Koven *et al.*, 1993); (iii) providing nutrients such as essential fatty acids (EFAs) for energy and phosphorus for growth, reproduction, bone formation and synthesis of nucleic acid; and, (iv) carrying of fat-soluble vitamins and carotenoid pigments that play an important role in maintaining normal growth and health of aquaculture stocks (Tocher, 1995; Bell & Koppe 2010). PLs form the outer layer of lipoproteins responsible for transporting the absorbed fatty acids from the intestines to the bloodstream, and throughout the body (Chapman *et al.*, 1978; Jaxion-Harm, 2021).

The lack of PLs in fish feed can cause aquaculture fish stocks to suffer impaired lipid transportation from the intestines or liver to other tissues, which results in steatosis (Caballero *et al.*, 2004; Morais *et al.*, 2006). Therefore, the inclusion of PLs in fish diet is an important step (Tocher *et al.*, 2008). Depending on lipid content, feed formulation and analytical methods used, PLs may account for between 5% and 25% of the total lipid in standard commercial fish feed (Johnson & Barnett, 2003). The larvae of marine fish species require a higher content of PLs in their feed. For example, the Japanese flounder (*Paralichthys olivaceus*) needs a 7% PLs content in its feed, whereas the red bream (*Pagrus major*) and knife jaw (*Oplegnathus fasciatus*) need 5% to 7%. In comparison, the larvae of the freshwater species *Cyprinus carpio* need 2% PLs only in its feed, while *Plecoglossus altivelus* needs 3% to 5% (Torcher *et al.*, 2008). The requirement for PLs in adult fish has not been well established (Olsen *et al.*,1999), probably due to their ability to synthesise PLs from dietary precursors, and are unlikely to benefit from supplementation (La, 1990). Many studies have demonstrated that PLs may be supplemented in the diet of marine and freshwater fish species at a level of 2% to 4% to improve their growth (Tocher *et al.*, 2008; Saleh *et al.*, 2013).

Based on the literature, PLs are crucial for aquatic animal growth, but their effect is species- and stage-specific. To our best knowledge, there is limited literature to summarise this information. Therefore, this review aims to improve our understanding of how PLs enhance growth performance in aquaculture. This review also describes the effects of PLs on specific fish species and their research gaps.

Common Phospholipids (PLs) in Aquafeed

PLs in aquafeed predominantly comprise lecithin and hydrated lecithin, which can either be of animal or plant origin. The mechanism of uptake, breakdown and utilisation of these PLs by cultured fish stocks is similar to mammals (Tocher, 2003) (Figure 2), and the resultant enriched fish with high EPA and DHA for human consumption (Figure 3). For example, studies have shown that PLs are the most efficient way to provide sea bass (Dicentrarchus labrax) with dietary EPA and DHA (Gisbert *et al*., 2005). Fish are more likely to divert short and medium-chain fatty acids for energy, while long-chain unsaturated fatty acids (UFA), such as EPA and DHA, are selectively reserved in their body (Khan *et al*., 2018; Campos *et al*., 2019).

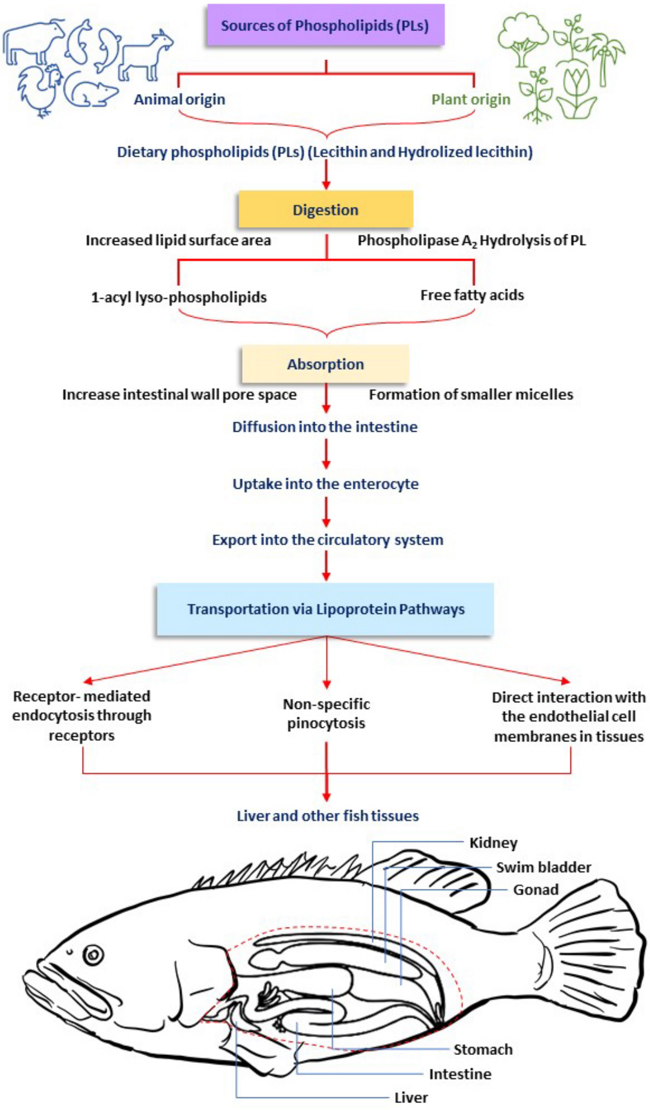

Figure 2: Source and utilisation of dietary phospholipids in fish

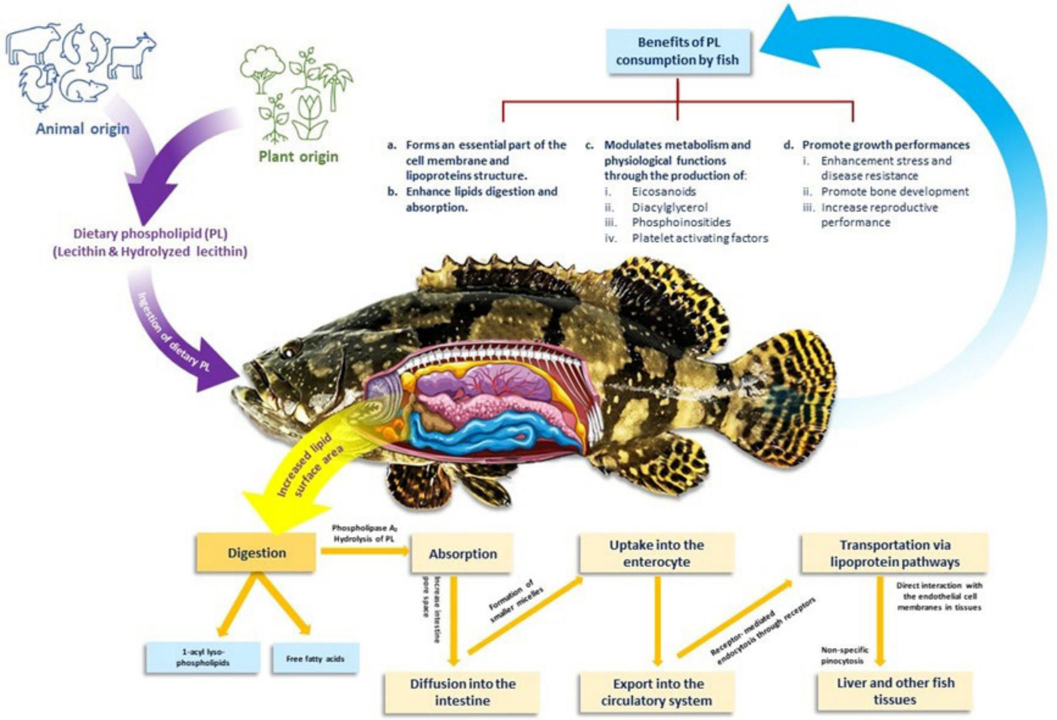

Figure 3: Role of dietary phospholipids and effects on cultured fish

Effects of Dietary PLs

Figure 4 (a) shows a heightened interest in phospholipid use in aquaculture dietary research between 2020 and 2023, with a 19% study contribution compared with between 1979 and 1985, which showed a 4% contribution. Furthermore, due to new discoveries on the significant impacts of PLs on fish dietary needs, studies have covered about 66 aquaculture species (fish, crustaceans and mollusks) across 25 countries [Figure 4 (b)], of which China (27%) emerged as the lead contributor, followed by Japan (12%), Iran (10%), USA (9%) and Belgium (7%). Among the species investigated, shrimp (22%) was given the highest attention, followed by crabs (11%), sea bream (11%) and trout (5%). A total of 74% of research involved marine species, while freshwater and estuary species were at 24% and 2%, respectively [Figure 4 (c)]. This focus on marine species was probably due to the established fact that the larvae of marine fish species required higher PLs compared with freshwater species.

The impact of dietary PLs on a range of fish biometric, physiological and biochemical parameters and responses has also been investigated. They include growth, survival, biochemical composition, lipid, fatty acid and amino acid metabolism, antioxidant capacity, digestive enzyme activities, histology, stress resistance, gene expression, serum biochemistry, reproductive performance, intestinal microbiota, immune capacity, digestibility, bone development and cholesterol mobilisation (Table 1).

Lecithin

Lecithin is a glycerol phospholipid sourced from animals, plants or microbes, with varying amounts of sphingosyl PLs, glycolipids, triglycerides and fatty acids. There are over 40 varying formulations of lecithin, ranging from naturally sourced oil extracts to synthetic and purified ones (Wendel, 2014). Lecithin from soybean constitutes the most abundant source of oil-seed (Van Nieuwenhuyzen, 2015). As a

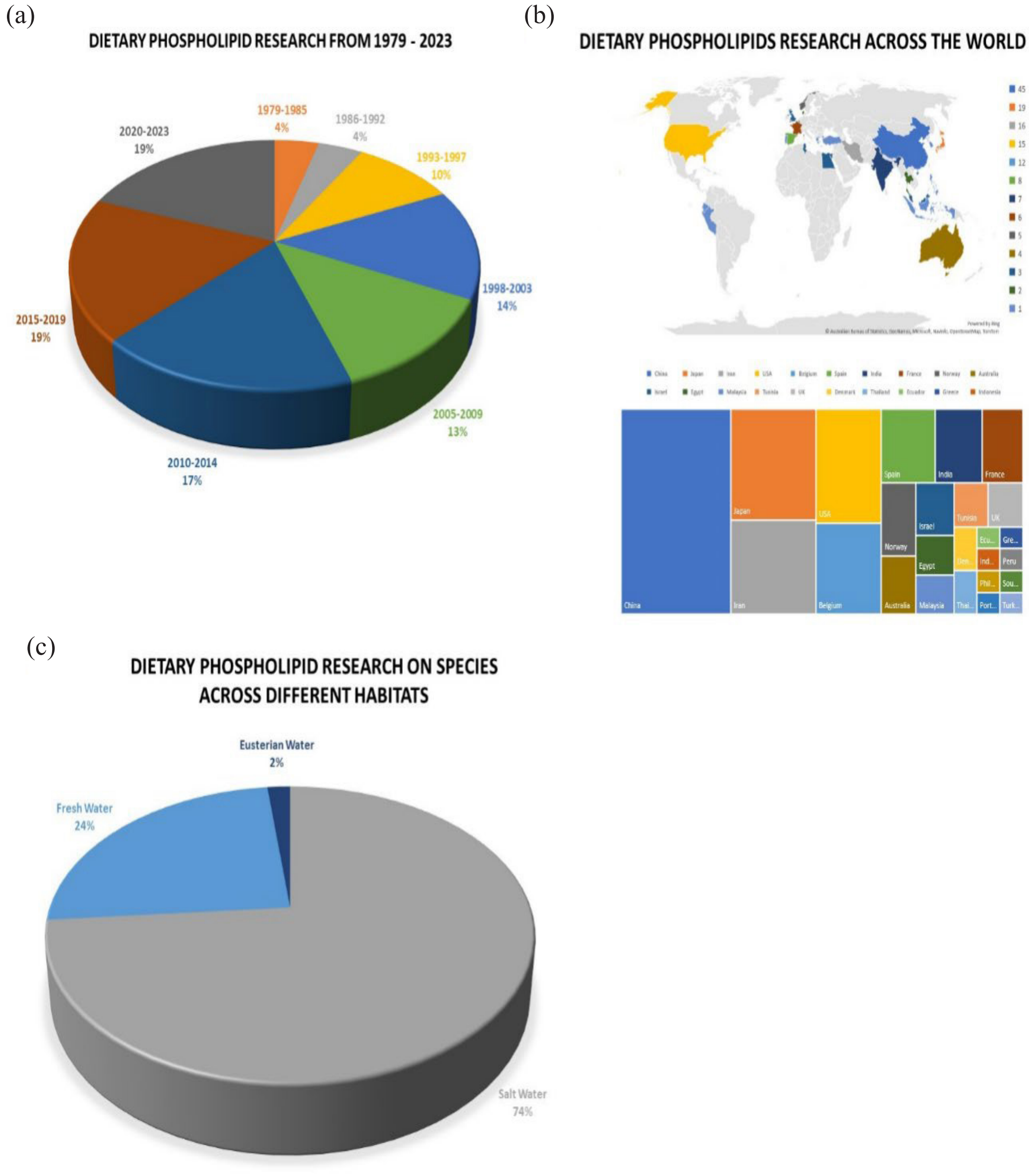

Figure 4: (a) Percentage of aquaculture dietary studies focusing on PLs between 1979 and 2023; (b) top contributing countries in aquaculture dietary studies focusing on PLs; and (c) type of aquaculture species used in PLs diet studies

Table 1: Effects of dietary phospholipid on aquaculture species according to life stage and culture duration

Species	Life Stage	Percentage and Purity of PLs (%)	Culture Duration	Effects of PLs on Aquaculture Species	References
Turbot (*Scophthalmus maximus*)	Juvenile	0.1-0.25% (-5%)	56 days	Enhanced growth and decreased lipid deposition	Xu *et al*., 2022
Turbot (*Scophthalmus maximus*)	Juvenile	0.1-0.55% (-20%)	56 days	Enhanced lipid metabolism and lipid utilisation coefficient	Li *et al*., 2019
Shrimp (*Penaeus monodon)*	Post-larvae		42 days	Enhanced growth, high carcass fatty acid composition	Khan *et al*., 2018a
Rainbow trout (*Oncorhynchus mykiss*)	Juvenile	0.9%	56 days	Enhanced digestibility, growth performance	Adhami *et al*., 2021a
Rainbow trout (*Oncorhynchus mykiss*)	Juvenile	0.2%	56 days	Enhanced growth, serum biochemical parameters and immune-related gene expression	Taghavizadeh *et al*., 2020
Hybrid tilapia (*Oreochromis aureus* ♂× *Oreochromis niloticus* ♀)	Juvenile	0.0125-0.025%	8 weeks	Improved growth and nutrient utilisation	Li *et al*., 2010a
Channel catfish (*Ictalurus punctatus*)	Juvenile	0.025% (25%)	10 weeks	Enhanced feed utilisation, antioxidative capacity and body composition	Liu *et al*., 2020
Crusian carp (*Carassais auratus gibelio*)	Juvenile	0.05-0.1%	67 days	Enhanced growth performance, lower FCR, cholesterol liver, muscle lipid	Li *et al*., 2010b

Shrimp (*Penaeus japonicus*)	Post-larvae	1.5% (95%)	40 days	Provide stable growth	Kontara *et al*., 1998
Nile tilapia (*Oreochromis niloticus*)	Adult	0.45 g/kg	60 days	Improved feed digestion and absorption, growth performance and innate immune response	El-Sayed *et al*., 2021
Sea urchins (*Lytechinus variegatus*	Juvenile	1.0-6.4%	12 weeks	Enhanced total weight gain	Gibbs *et al*., 2009
Hybrid grouper (*E. fuscoguttatus* ♀× *E. lanceolatus* ♂)	Larvae	1.87-7.25%	23 days	Increased specific growth rate and activity of antioxidant enzymes (CAT, SOD and T-AOC)	Huang *et al*., 2021
Stellate sturgeon (*Acipenser stellatus*)	Juvenile	0.3-3.9%	75 days	Promoted growth, digestive enzymes activity (pepsin, trypsin, chymotrypsin, bile salt-activated lipase and α-amylase) and reduced hepatic lipid deposition	Jafari *et al*., 2021
Gilthead sea bream (*Sparus aurata L.*)	Juvenile	1%	70 days	Increased growth, feed intake and protein utilisation efficiency and liver status	Kokou *et al*., 2021
Turbot (*Scophthalmus maximus*)	Juvenile	0.1-0.5% (98%)	8 weeks	Regulated intestinal mucosal barrier and enhanced intestinal microbiota	Li *et al*., 2022
Largemouth bass (*Micropterus salmoides*)	Juvenile	1 g/kg	64 days	Increased intestinal digestive enzyme activity and liver metabolism. It also regulated the diversity of the species' intestinal flora	Lu *et al*., 2022

Shrimp (*Litopenaeus vannamei*)	Post-larvae	20-80 g/kg	27 days	Increased weight gain and specific growth rate	Niu *et al*., 2011
Amberjack (*Seriola dumerili*)	Juvenile	14-54 g/kg	30 days	Enhanced feed intake and growth performance	Uyan *et al*., 2009
Largemouth bass (*Micropterus salmoides*)	Juvenile	5.34-9.11%	30 days	No significant impact on growth, but significantly reduced liver, muscle and whole-body lipid deposition	Wang *et al*., 2022
Large yellow croaker (*Larmichthys crocea*)	Larvae	57.2-85.1 g/kg	30 days	Enhanced growth, survival, digestive enzymes and stress tolerance	Zhao *et al*., 2013

phospholipid source, lecithin has the ability to improve stress resistance, growth performance and survival in cultured marine and freshwater fish species, as well as crustaceans (Jamali *et al.*, 2019). Several studies have reported the benefits of dietary lecithin at varying rates of inclusion in aquafeeds. They include the Nile tilapia (*Oreochromis niloticus*) (0.3, 0.6 and 0.9 g/kg of diet) (El-Sayed *et al.*, 2021), sea urchins (*Lytechinus variegatus*) (1, 2.5, 4, 5.2, 6.4, 7.6, and 8.8%) (Gibbs *et al.*, 2009), hybrid grouper (*E. fuscoguttatus*♀× *E. lanceolatus*♂) (1.87, 3.61, 5.53, 7.25 and 9.69%) (Huang *et al.*, 2021), stellate sturgeon (*Acipenser stellatus*) (0.3, 0.9, 1.6, 2.7, 3.9, 5.3 and 5.4%) (Jafari *et al.*, 2021), gilthead sea bream (*Sparus aurata L.*) (0.53, 1 and 2%) (Kokou *et al.*, 2021), shrimp (*Litopenaeus vannamei*) (0, 10, 20, 40 and 80 g/kg of diet) (Niu *et al.*, 2011), amberjack (*Seriola dumerili*) (14, 37 and 54 g/kg of diet) (Uyan *et al.*, 2009), largemouth bass (*Micropterus salmoides*) (1.49, 3.21, 5.34, 7.20 and 9.11%) (Wang *et al.*, 2022), and large yellow croaker (*Larmichthys crocea*) (26.0, 38.5, 57.2, 69.5 and 85.1 g/kg of diet) (Zhao *et al.*, 2013).

Hydrolysed Lecithin

The elimination of a fatty acid by phospholipase in lecithin hydrolysis produces an end-product known as hydrolysed lecithin (HL), which is more hydrophilic and easily absorbed by aquaculture stocks (Joshi, 2010; Li *et al.*, 2019). Although enzymes in fish can convert PLs into HL, they are unable to naturally synthesise sufficient PLs, hence, the need to supplement HL in their diets for growth promotion (Adhami *et al.*, 2021 a). HL molecules have very solid surface-active properties due to the two distinctly different hydrophilic and lipophilic areas. The emulsifying ability of HL on dietary lipids is about five times higher than other PLs in general (Zhang, 2007), and this may partly explain their effects on lipid metabolism (Li *et al.*, 2019).

Studies on the use of HL and levels of inclusion in aquafeed are few, and those available have focused on channel catfish (*Ictalurus punctatus*) (0, 125, 250, 375 and 500 mg/kg) (Liu *et al.*, 2020), rainbow trout (*Oncorhynchus mykiss*) (0, 3, 6 and 9 g/kg of diet; 1, 2, and 3 g/kg of diet) (Taghavizadeh *et al.*, 2020; Adhami *et al.*, 2021a), hybrid tilapia (*O. aureus* ♂ × *O. niloticus* ♀) (Li *et al.*, 2010), crucian carp (*Carassius auratus gibelio*) (0.1%) (Li *et al.*, 2010b), turbot (*Scophthalmus Maximus*) (0, 1000, 2500, 4000, 5500 mg/kg of diet; 0.1, 0.25, and 0.5%) (Li *et al.*, 2019; Xu *et al.*, 2022), common carp (*Cyprinus carpio Var. Jian*) (Wang *et al.*, 2009), tiger prawns (*Penaeus monodon*) (Khan *et al.*, 2018a; 2018b) and kuruma prawns (*Penaeus japonicus Bate*) (1.5%) (Kontara *et al.*, 1998).

Emulsification of Lipids

The emulsification of lipids and formation of micelles exposes more lipid molecules for contact with lipase (Adhami *et al.*, 2021a). Emulsifiers increase the surface area of lipids and promote the translation of fatty acids to form micelles, a step that is very important to improve lipid digestion and absorption (Kim *et al.*, 2018). Some properties of phospholipid emulsion include the formation of tiny droplets when the molecules are homogenised at high pressure, which may lack stability in pH values lower than 3 at high ionic strength and also likely to disintegrate at elevated temperatures (McClements & Gumus, 2016).

The micelle size is one of the most important factors determining the absorption of lipids and lipophilic substances. For example, the absorption of cholesterol by HL micelles, which are smaller in size, is 15 times greater than that of lecithin micelles which have larger size (Reynier *et al.*, 1985). The micelles produced will ultimately increase the bioavailability of nutrients (Li *et al.*, 2019; Liu *et al.*, 2020).

Studies have shown that other PLs like HL that may act as emulsifiers have greater efficiency in improving the utilisation of dietary lipids in livestock (Hosseini *et al.*, 2018; Mohammadigheisar *et al.*, 2018). As HL has higher emulsifying abilities than lecithin (Liu *et al.*, 2020; Taghavizadeh *et al.*, 2020), the micelles formed by HL are smaller and more stable than those of other PLs and bile salt (Adams, 1996). For instance, HL has been reported to have a critical micelle concentration (CMC) of 0.02 to 0.2 mmL^{-1}, which is 20 to 200 times more potent than bile (CMC = 4 mmL^{-1}) and lecithin (CMC = 0.3 to 2 mmL^{-1}) (Longmuir, 2002). Li *et al.* (2019) showed that HL was an emulsifier with five times higher capacity than lecithin, facilitating the breakdown of fats and the formation of micelles with fatty acids.

On the other hand, an increase in surface area between nutrients and intestinal villi will improve feed conversion and growth. Taghavizadeh *et al.* (2020) reported that 2 g/kg dietary HL increase the villi height to 442.87 ± 8.89 µm in *O. mykiss* compared with 336.62 ± 0.63 µm in the control group. The same result was recorded in the broiler with jejunum villi height of HL fed groups, which at 1,072.95 µm, was greater than that of the positive 847.56 µm and negative 917.28 µm controls (Boontiam *et al.*, 2017). Another experiment showed that the jejunum villi height of broilers fed with HL was 1034.7 µm compared with those fed with a high-energy diet (848.3 µm) and low-energy diet (918.3 µm) (Hosseini *et al.*, 2018). In *I. punctatus*, no significant differences in villi height and muscular layer thickness were found across all treatments (Liu *et al.*, 2019). Adult Nile tilapias (*O. niloticus)* fed with 0.3 g of lecithin per kg of feed resulted in a higher midgut villi length (637.83 ± 23.9 µm) than that recorded in the control group (428.80 ± 38.8 µm) (El-Sayed *et al.*, 2021). Hence, it can be deduced that the increased villi height observed in the aforementioned fish species enhances their feed conversion and growth performance upon being fed dietary PLs. A common trend observed in previous studies was a linear increase of villi height with an increased level of dietary PLs up to the optimum, but after a decline effect was reported. Therefore, it is necessary to keep to the optimum inclusion range when formulating species-specific diets.

Digestibility and Absorption of Nutrients

When the water-in-oil emulsion is stabilised, it allows the formation of micelles by fatty acids, thereby improving lipid metabolism, nutrient digestibility, and growth performance of the animals (Zampiga *et al.*, 2016; Zhao *et al.*, 2017). Efficient digestion and absorption only occur when consumed lipids are emulsified and integrated into micelles within intestinal digestion (Maldonado-Valderrama *et al.*, 2011). Based on an enzyme activity assay after PLs ingestion, the digestive ability and absorption performance in fish have improved (Perez-Casanova *et al.*, 2006; Liu *et al.*, 2020). When the activity of digestive enzymes involved in the digestion of various substances in diets was increased, this indicated an improvement in the fish's ability to extract nutrients from the diet (Furné *et al.*, 2005). Li *et al.* (2019) reported that juvenile turbots (*S. maximus*) fed with dietary HL had a significant increase in enzyme activity leading to efficient lipid utilisation.

Intestinal enzyme activities of protease, trypsin, lipase and amylase in adult Nile tilapia (*O. niloticus*) fed with dietary lecithin (0.3 g/kg diet) have shown significantly enhanced with an increase of dietary lecithin levels, but declined at inclusion levels of 0.6 and 0.9 g/kg. Maximum enzyme activity was reported at approximately 0.44 to 0.46 g/kg for tilapia (El-Sayed *et al.*, 2021). The liver and intestinal activities of protease and lipase in *M. salmoides* fed dietary HL (1 g/kg) were reported to be significantly higher (Lu *et al.*, 2022). Whereas an increase of dietary marine phospholipid and soybean lecithin in the diet of *S. aurata* larvae resulted in enhanced assimilation of polyunsaturated fatty acids, n-3 highly unsaturated fatty acids (predominantly 20:5n-3) and n-6 fatty acids (predominantly 18:2n-6) (Saleh *et al.*, 2015). Dietary soybean lecithin levels at 0.9 to 3.9% for juvenile stellate sturgeon (*A. stellatus*) enhanced the activities of gastric pepsin and pancreatic trypsin, chymotrypsin, bile salt-activated lipase and a-amylase enzymes (Jafari *et al.*, 2021). The inclusion of dietary PLs in low-FM diets for juvenile *S. aurata* enhanced feed utilisation (86 to 87.5%) (Kokou *et al.*, 2021).

This growth and feeding improvement were associated with high gastric and intestinal lipase, sodium-potassium adenosine triphosphatase

(Na^+/K^+-ATPase) and alkaline phosphatase (AKP) activities (Liu *et al.*, 2020). An increasing trend in lipase activities after adding PLs to dietary fat powder has also been reported in channel catfish *I. punctatus* (Adhami *et al.*, 2021a). In the crucian carp (*Carassais auratus gibelio*), groups fed 0.1% HL had a significantly higher apparent digestibility coefficient (ADC) of nutrients (Li *et al.*, 2010b). Supplementation of fat powder as an alternative lipid source in the diet of *O. mykiss* resulted in a reduction in body fat and fat digestibility by 60.01 ± 1.33%, but ingestion of 9 g/kg HL increased digestibility to 65.46 ± 0.93%. This indicated the ability of *O. mykiss* to digest fat powder and minimise its effects using HL (Adhami *et al.*, 2021a). Another study reported that dietary HL significantly increased ADC of fatty acids in *P. monodon* compared with those fed with dietary lecithin (Khan *et al.*, 2018b). The use of HL in the diet of *P. monodon* might be considered relevant due to the short gut passage time through improved digestibility and transport of fatty acids in plant-based diets (Khan *et al.*, 2018a).

In addition, improved efficiency of micelle formation by HL was reported to improve digestibility in broilers (Melegy *et al.*, 2010; Bingkun *et al.*, 2011). Compared with a soy-lecithin diet, HL diet achieved better absorption of lipids and fat-soluble substances in the gut of *P. monodon* (Khan *et al.*, 2018a). Improvement in lipid digestion has been observed in fish fed *S. salar* diets containing soybean lecithin (Craig & Gatlin, 1997; Kasper & Brown, 2003). Their studies found PLs in the gastrointestinal mucosa, with reduced non-polar lipid droplets while playing the role of lipid emulsifier, thereby improving digestion and absorption of dietary fatty acids (Jamali *et al.*, 2019). Therefore, the optimal dietary PL inclusion in aquafeed will vary from species to species and hence, the need to tailor the formulation to meet each species' requirement.

Application of PLs in Aquaculture Species

Literature has well documented the significant improvements in the growth performance of freshwater and marine aquaculture species with the inclusion of PLs in their diet (Tocher *et al.*, 2008). PLs-fed stocks have been observed to have enhanced nutrient absorption, effective transportation of fat-soluble vitamins and well-regulated hormones, eicosanoids and vitamin D synthesis (Liu *et al.*, 2020).

For example, the study on South American catfish (*Pseudoplatystoma fasciatum surubim*) juveniles fed with four semi-purified diets (casein–gelatin diet, linseed and olive oil, cod liver oil and soybean lecithin) for eight weeks found that those fed with soybean lecithin (1512 ± 502 g) experienced a significant growth improvement compared with other diets (Arslan *et al.*, 2008). The specific growth rate for *O. niloticus* fed with lecithin 0.3g/kg feed (1.71 ± 0.11% per day) was significantly higher than the control fish (1.26 ± 0.03% per day) (El-Sayed *et al.*, 2021). Juvenile *S. parus aurata* fed with dietary PLs from krill and soy lecithin at three different levels of inclusion (0.53%, 1.0% and 2.0%) demonstrated a significantly enhanced final weight gain improvement in krill (49.6 ± 1.7 g) and soy lecithin (49.5 ± 1.7 g) at a higher level supplement (Kokou *et al.*, 2021). For juvenile Stellate sturgeon (*A. stellatus*), the inclusion of 3.9% soy lecithin could increase the growth performance (Jafari *et al.*, 2021). Whereas for hybrid grouper larvae (*Epinephelus fuscoguttatus* × *E. lanceolatus*), a 9.1% of phospholipid inclusion in their diet could improve weight gain and specific growth rate (Huang *et al.*, 2021).

Similarly, phospholipid inclusion also improves serum biochemical parameters, and immune-related gene expression for juvenile amberjacks (*Seriola dumerili*) (Uyan *et al.*, 2009), juvenile largemouth seabass (*M. salmoides*) (Lu *et al.*, 2022; Wang *et al.*, 2022), sea bream larvae (*S. auratus*) (Seiliez *et al.*, 2006), Atlantic salmon (*Salmo salar*) (Jaxion-Harm, 2021), yellow croakers (*Larmichthys crocea*) (Zhao *et al.*, 2013), rainbow trout (*O. mykiss*) (Taghavizadeh *et al.*, 2020; Adhami *et al.*, 2021b), crucian carps (*Carassais auratus gibelio*) (Li *et al.*, 2010b), hybrid tilapia (*O.*

aureus ♂× *O. niloticus* ♀) (Li *et al.*, 2010a) and turbots (*Scophthalmus maximus*) (Li *et al.*, 2019; Xu *et al.*, 2022). In addition, supplementation of soy lecithin at an optimal level of 3.56 g/100 g in the diet of early juvenile milkfish (*Chanos chanos*) also improved their survival, growth and carcass composition (Coutteau, *et al.*, 1997; Balito-Liboon *et al.*, 2018).

The positive impact is not only reported in teleost, but also in invertebrates like the Pacific white shrimp (*Litopeneaus vannamei*) (Hu *et al.*, 2011; Niu *et al.*, 2011b). Even, juvenile sea urchins (*Lytechinus variegatus*) fed with a 6% phospholipid diet were found to have improved gonadal maturation and fecundity (Gibbs *et al.*, 2009). Tiger prawns (*P. monodon*) fed with PLs not only showed improved growth and survival, but also increased muscle essential fatty-acid composition, especially EPA and DHA (Khan *et al.,* 2018a). Other shrimp species such as kuruma shrimp (*Penaeus japonicus*) fed with PLs were found to undergo frequent larvae metamorphoses and development at 1.40% to 1.45% per day (Kontara *et al.*, 1998; Khan *et al.*, 2018b). The use of 10 g/kg soy lecithin promoted a five-fold increment in growth (Li *et al.*, 2014) and 60% improvement in feed conversion ratio (Hou *et al.*, 2016) in blue swimming crab (*P. trituberculatus*), but excessive levels have been reported to impair physiological processes related to growth and tissue composition (Coutteau, *et al.*, 1997; Balito-Liboon *et al.*, 2018).

Correlating all the data proves that the inclusion of PLs in aquafeed can significantly enhance the growth of aquaculture stocks. Nevertheless, others showed that higher inclusion levels might either result in no effect or retardation of growth performance (Coutteau, *et al.*, 1997; Balito-Liboon *et al.*, 2018). Hence, it is paramount to ensure that the application of dietary PLs in aquafeed is designed to meets the optimum inclusion levels for a specific species, besides considering the purity of the PLs into consideration.

Health Improvement

Fatty acids and other lipids may affect the health of fish stocks in many ways; including, but not limited to their effects on growth, reproduction, behaviour, vision, osmoregulation, membrane fluidity for thermal adaptation and immune response (Arts & Kohler 2009). Dietary PLs and unsaturated fatty acids increases the permeability and fluidity of cell membranes resulting in improved immunity (Balfry & Higgs, 2001). As reported in previously studies, juvenile gilt-head seabream (*Sparus aurata*) fed with PLs in low-fish meal diet were able to undergo better growth and improved liver steatosis (Kokou *et al.*, 2021). A total antioxidant capacity colourimetric (T-AOC) assay reportedly detected a significant increase in antioxidant activities, such as superoxide dismutase (SOD) and catalase (CAT), in larval hybrid grouper (*Epinephelus fuscoguttatus* × *E. lanceolatus*) (Huang *et al.*, 2021). Activities of CAT and SOD in juvenile stellate sturgeon (*A. stellatus*) fed with soy lecithin also increased linearly in proportion with the lecithin quantity, while fat accumulation in the liver was minimised (Jafari *et al.*, 2021).

High dietary PLs inclusion at 69.5-85.1 g/kg may help enhance the stress tolerance of *L. crocea* larvae (Weirich & Reigh, 2001; Zhao *et al.*, 2013;) and improve its gut microbiota (Honjoh *et al.*, 1967; Li *et al.*, 2022). In *O. mykiss*, stocks fed with 2 g/kg dietary HL showed an increase of non-specific (lysozyme, C3 and C4) and specific immunoglobulin (IgM) reactions (Taghavizadeh *et al.*, 2020). Lysozyme is commonly used as a critical indicator of innate immune function in fish (Adel *et al.*, 2017; Xiao *et al.*, 2019). In addition, respiratory burst activity, phagocytic activity and phenol-oxidase levels were significantly enhanced in tilapia (*O. niloticus*) (El-Sayed *et al.*, 2021).

The influence of HL on lipid deposition has been reported in channel catfish (Liu *et al.*, 2020), rainbow trout (Taghavizadeh *et al.*, 2020; Adhami *et al.*, 2021a), and turbot (Xu *et al.*, 2022). The fish stocks had lower cholesterol and lipid levels compared with controls, besides improved immunity and hepatic antioxidant capacity (Liu *et al.*, 2020; Xu *et al.*, 2022). These are indicated by their aspartate transaminase (AST), alanine aminotransferase (ALT) and alkaline phosphatase (ALP) levels (Mu *et al.*, 2018; Zhang *et al.*, 2019), as well as total SOD and CAT activities (Mirghaed *et al.*, 2019; Liu *et al.*, 2020).

Conclusion

PLs is a very essential in the diet of aquaculture species. The application of PLs in aquafeed will not only improve growth performance and health status but also promote the profitability and sustainability of the entire aquaculture industry. There is a need for subsequent research to determine the specific amount of PLS needed to ensure optimal growth for each commercial species.

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Conflict of Interest

All authors declare that they have no conflicts of interest.

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