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Review

Dietary supplementation of exogenous carbohydrase enzymes in fish nutrition: A review

Sergio Castillo, Delbert M. Gatlin III *

Department of Wildlife and Fisheries Sciences, Texas A&M University, College Station, TX 77843-2258, USA

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A B S T R A C T

A current priority in the aquaculture industry is the replacement of fishmeal with alternative feedstuffs, including plant-based protein ingredients, to ensure its sustainability. However, most plant-based feedstuffs have a wide variety of anti-nutritional factors, which may impair nutrient utilization, interfering with fish performance and health. The use of exogenous enzymes as feed additives to improve nutrient digestibility of plant-based feedstuffs has been researched extensively in poultry and swine. In aquaculture, the use of phytase to improve phosphorus utilization has emerged quite readily. However, the use of carbohydrase enzymes has not been as nearly as common in aquatic species, despite their promising effects in improving nutrient digestibility by hydrolyzing non-starch polysaccharides present in plant feedstuffs. Based on the information gathered in this review, supplementation of exogenous carbohydrases to plant-based fish diets should improve nutrient digestibility and reduce nutrient excretion. On the other hand, the effects of exogenous carbohydrases on fish performance are still unclear due to the difficulty in cross-study comparisons. Overall, based on the information gathered in this review, it is clear that research on exogenous carbohydrase supplementation in aquaculture nutrition is not extensive. According to promising results and opportunities found in other non-ruminant animals, and favorable effects found in aquaculture species studied to date, it may be significant to increase research on this subject because it could be a useful tool to improve and sustain commercial aquaculture.

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1. Introduction

In recent years one prominent area of research in aquaculture nutrition has focused on the replacement of fishmeal with plant-based protein ingredients to support the globally expanding aquaculture industry and to ensure its sustainability (Gatlin et al., 2007; NRC, 2011). However, most plant-based feedstuffs have a wide variety of anti-nutritional factors such as phytin, non-starch polysaccharides (NSP) and protease inhibitors, which may impair nutrient utilization, as well as impair fish performance and health (Francis et al., 2001; NRC, 2011).

Attempts to improve the digestibility of plant proteins have included the use of hydrothermal treatments such as extrusion, as well as fractionation of crops to reduce the content of anti-nutritional factors and increase their protein concentration. While these approaches have

* Corresponding author. Tel.: +1 979 847 9333.
E-mail address: d-gatlin@tamu.edu (D.M. Gatlin).

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been shown to improve protein and energy digestibility of numerous plant protein feedstuffs, the digestibility of many ingredients remains low because of a lack of the enzymes needed for breaking down the complex cell wall structure that encapsulates other nutrients (Glencross et al., 2012; NRC, 2011).

The application of exogenous enzymes as feed additives to improve nutrient digestibility of plant-based feedstuffs has been research extensively in poultry and swine, and is now broadly used throughout the world as a way to reduce the anti-nutritional effects of NSP and phytic acid, increasing the utilization of carbohydrates and phosphorus, respectively (Adeola and Cowieson, 2011). In aquaculture, the use of phytase to improve phosphorus utilization from plant feedstuffs has emerged quite rapidly (Cao et al., 2007; Cheng et al., 2004; Dalsgaard et al., 2009; Kumar et al., 2012). However, in the case of carbohydrase enzymes, their use in aquaculture feeds has not been as nearly as widespread, regardless of their positive effects on nutrient digestibility (Adeola and Cowieson, 2011).

Carbohydrases include all enzymes that catalyze a reduction in the molecular weight of polymeric carbohydrates, but more than 80% of the global carbohydrase market is accounted for by two dominant proteins, xylanase and glucanase. In addition, other commercially available carbohydrases include α-amylase, β-mannanase, α-galactosidase and pectinase. Practically all feed-relevant carbohydrases are in the same group of proteins, the hydrolase/glycosidase family, hydrolyzing carbohydrate polymers to generate decreased molecular weight oligo- or polysaccharides (Adeola and Cowieson, 2011).

Because the study of carbohydrase supplementation in aquaculture feeds is recent and scarce, this review is an attempt to compile most of the research completed to date in this regard, describing the specific effects of this group of enzymes on nutrient digestibility and fish performance, to encourage additional study in this subject and suggest opportunities for future research.

2. Non-starch polysaccharides and mechanisms of action of carbohydrase enzymes: nutritional implications

The main function of exogenous supplementation of carbohydrases is to hydrolyze complex NSP present in plant feedstuffs that non-ruminant animals are incapable of hydrolyzing with their endogenous pool of digestive enzymes. In fish, the presence of digestive enzymes that specifically hydrolyze the β-glycosidic bonds of NSP seems to be very low or nonexistent (Krogdahl et al., 2005; NRC, 2011). Some of these NSP are present as part of the cell wall, thus shielding substrates from contact with the digestive enzymes, or as part of cell content where their presence may interfere with digestion and absorption due to their chemical nature (Bach-Knudsen, 1997; Nitrayová et al., 2009). The classification of NSP found in commonly used plant feedstuffs for aquaculture feeds is presented in Table 1.

In addition to NSP hydrolysis, one of the most important benefits of carbohydrase supplementation is the reduction in NSP-induced digesta viscosity. Exogenous carbohydrases have been reported to facilitate a decrease in the degree of polymerization of feed, reducing its viscosity and liberating carbohydrate oligomers, therefore improving nutrient utilization (Vahjen et al., 2007).

Carbohydrase supplementation increases digestibility of energy-yielding nutrients, such as starch and fat, because NSP reduce the capacity for nutrient absorption by reducing enzyme accessibility to substrates (Adeola and Bedford, 2004). The improvement in fat digestibility is especially noteworthy because NSP are known to increase hydrolysis of bile salts and hence reduce fat utilization (Vahjen et al., 2007). In addition, it is possible that carbohydrases act to improve nitrogen and amino acid utilization as well, by increasing the access to protein for digestive proteases (Tahir et al., 2008). Lastly, it seems that carbohydrases improve energy utilization by shifting absorption of energy-yielding nutrients to the proximal intestine. The shift in nutrient utilization to the more proximal intestine would decrease host–microbe competition for nutrients and ensure availability of nutrients where absorption efficiency is greatest (Adeola and Cowieson, 2011).

As with other nutrients, carbohydrase enzymes are also involved in improving availability of minerals in diets to the target organism. This may be explained by the relationship between phytic acid and NSP in plants. In cereal grains and legumes, most of the phosphorus is bound in phytic acid. Consequently, when carbohydrases hydrolyze their substrates, phytin phosphorus and other minerals may be exposed to digestive enzymes as well as liberated for absorption. Therefore, the increase in mineral availability as a result of carbohydrase supplementation is an indirect response to the carbohydrases' effect (Adeola and Cowieson, 2011).

Furthermore, carbohydrase supplementation has been shown to increase gut health in animals fed high-NSP diets. NSP-induced increases in digesta viscosity encourage slower diffusion rates, accumulation of particulate matter for microbial adhesion, and greater flow of solids rather than liquid. These factors encourage slower shedding of microorganisms and increased proliferation of harmful bacteria (Vahjen et al., 1998). Therefore, by reducing digesta viscosity, carbohydrase supplementation reverses these negative effects. Moreover, by increasing the proportion of lactic and organic acids (Kiarie et al., 2007), reducing ammonia production (Kiarie et al., 2007), and increasing volatile fatty acid concentration (Hübener et al., 2002), indicative of hydrolytic fragmentation of NSP, carbohydrases may promote and support growth of beneficial bacteria, thereby improving gut and overall health of the animal (Adeola and Cowieson, 2011).

3. Carbohydrase enzyme supplementation in aquaculture nutrition

The study of the effects of exogenous carbohydrase enzyme supplementation on aquaculture species has increased in recent years as summarized in Table 2. Nonetheless, for aquaculture nutrition this topic is still relatively new and research to date is insufficient.

Carter et al. (1994) were pioneers in the supplementation of exogenous enzymes in fish diets containing plant-based feedstuffs. By supplementing a soybean meal-based diet (33% by weight) for Atlantic

Table 1
Classification of non-starch polysaccharides found in commonly used plant feedstuffs for aquaculture feeds.
Adapted from Sinha et al. (2011).

Category	Monomeric residue	Linkage	Plant feedstuffs
Cellulose	Glucose	β-(1 → 4)	Cereals (barley, corn, wheat) and legumes (soybean, cottonseed, rapeseed/canola, lupin)
Non-cellulosic polymers			
Arabinoxylans	Arabinose and xylose	β-(1 → 4)-linked xylose units	Cereals (barley, corn, wheat, oat, sorghum)
Mixed-linked β-glucans	Glucose	β-(1 → 3) and β-(1 → 4)	Barley and oat
Pectic polysaccharides			
Arabinans	Arabinose	α-(1 → 5)	Cereal co-products
Galactans	Galactose	β-(1 → 4)	Lupin, soybean
Arabinogalactans (type I)	Arabinose and galactose	β-(1 → 4)	Grain legumes (soybean, lupin)
Arabinogalactans (type II)	Arabinose and galactose	β-(1 → 3,6)	Canola/rapeseed cotyledon