Kafkas Univ Vet Fak Derg
25 (5): 731-740, 2019
DOI: 10.9775/kvfd.2018.21341

Kafkas Universitesi Veteriner Fakultesi Dergisi
ISSN: 1300-6045 e-ISSN: 1309-2251
Journal Home-Page: http://vetdergikafkas.org
Online Submission: http://submit.vetdergikafkas.org

Review

Relationship Between Polyunsaturated Fatty Acids and Animal Production: A Review

Shiyun TANG [1] Shijin GUO [2] Jianjun WANG [1] Yumao WANG [1] Shijun FU [1] Zhiqiang SHEN [1,2]

[1] Shandong Binzhou Animal Science and Veterinary Academy, Animal Nutrition Branch, Shandong Binzhou, P. R. CHINA
[2] Shandong Lvdu Ante Animal Drug Co. Ltd, Research and Development Center, Shandong Binzhou, P. R. CHINA

Article ID: KVFD-2018-21341 Received: 13.11.2018 Accepted: 06.05.2019 Published Online: 08.05.2019

How to Cite This Article

Tang S, Guo S, Wang J, Wang Y, Fu S, Shen Z: Relationship between polyunsaturated fatty acids and animal production: A review. *Kafkas Univ Vet Fak Derg,* 25 (5): 731-740, 2019. DOI: 10.9775/kvfd.2018.21341

Abstract

Polyunsaturated fatty acids (PUFAs) play important roles in maintaining normal physiological conditions and, consequently, in animal health. Two PUFAs families, n-6 and n-3 fatty acids (FAs), are physiologically and metabolically distinct. The focus on PUFAs has been gradually extended from the apparent properties of growth performance, antioxidant ability and immune function to the mechanism of molecular regulation and mechanism such as regulating the expression of related genes and the anticancer action mechanism, which strengthen the understanding of the theoretical basis and application of animal husbandry in a range of animal species. The present review focuses on current knowledge related to the origin, biological function and practical application of PUFAs in animal production.

Keywords: *Polyunsaturated fatty acids Biological function Animal production Application*

Çoklu Doymamış Yağ Asitleri ve Hayvansal Üretim Arasındaki İlişki: Derleme

Öz

Çoklu doymamış yağ asitleri normal fizyolojik süreçlerin ve bunun sonucu olarak da hayvan sağlığının sağlanmasında önemli rol oynamaktadır. İki çoklu doymamış yağ asitleri ailesi olan n-6 ve n-3 yağ asitleri fizyolojik ve metabolik olarak önemlidir. Büyüme performansı, antioksidan kabiliyeti ve immun fonksiyonlarından moleküler regülasyon ve ilgili genlerin ekspresyonunun ve anti kanser mekanizmaları gibi mekanizmalardaki belirgin özellikleri nedeniyle çoklu doymamış yağ asitlerine ilgi artmıştır. Bu durum pek çok hayvan türünde yetiştiricilik konusunda teorik temellerin anlaşılmasına katkıda bulunmuştur. Bu derleme, çoklu doymamış yağ asitlerinin hayvansal üretimdeki yeri, biyolojik fonksiyonları ve pratik uygulamaları üzerine güncel bilgiye odaklanmıştır.

Anahtar sözcükler: *Çoklu doymamış yağ asitleri, Biyolojik fonksiyon, Hayvansal üretim, Uygulama*

INTRODUCTION

Feeding fat has nutritional and economic advantages to satisfy energy requirement and replace carbohydrates with inexpensive lipid sources. Fatty acids (FAs) are important ingredients and essential substances of fats and oils. Based on their chemical structure FA can be differentiated into three groups: saturated, monounsaturated and polyunsaturated fatty acids (PUFAs). The biological reactivity of FA is defined by the length of the carbon chain and by both the number and position of any double bonds present. While saturated fatty acids (SFAs) do not contain double bonds within the acyl chain, unsaturated fatty acids (UFAs) contain at least one double bond. When two or more double bonds are present, these UFAs are referred to as polyunsaturated fatty acids (PUFAs). Dietary imbalance of the n-6/n-3 PUFAs ratio can affect human health, especially with high n-6/n-3 PUFAs ratios [1].

FAs supplies have been demonstrated to alter immune cells function because FAs alter the composition of the cells' membrane phospholipids, which relates to the membrane lipid fluidity, signal transcription factors, and bioactive synthesis of lipid mediators [2]. Several studies have documented that PUFAs not only play an important role in maintaining structure and function of cell membrane, enhancing immune function, promoting growth and development, regulating lipid metabolism and related gene

İletişim (Correspondence)
+86-543-3403002; Fax: +86-543-3252652
fsj311@163.com

expression, but also reducing thrombosis, reducing the incidence of cardiovascular diseases as well as resisting cancer [3]. With the reduction of production cost and continuous pursuit of high quality animal product, the application of PUFAs in animal production has been a subject of great public attention and concern. The focus on PUFAs has been gradually extended from the apparent properties of growth performance, antioxidant ability and immune function to the mechanism of molecular regulation and mechanism such as regulating the expression of related genes and the anticancer action mechanism, which strengthen the understanding of the theoretical basis and application of animal husbandry in a range of animal species. This paper briefly described the origin, biological function and practical application of PUFAs in animal production.

SOURCES OF PUFAs

Polyunsaturated fatty acids are mainly found in all natural foods in varying amounts, but fatty foods contain the most. Generally speaking, vegetable oils are the most concentrated sources of PUFAs in the Western diet and include sunflower oil, safflower oil, corn oil, flax oil, sesame seed oil, pumpkin seed oil and canola (or rapeseed) oil. The exceptions include plants that grow in tropical climates, such as the oils extracted from chocolate and coconuts. These oils are highly saturated, and so are very stable and undoubtedly safe and beneficial.

Table 1 illustrated the members and typical sources of the n-6 and n-3 PUFA families. Linoleic acid (LA) is the parent FA of the n-6 family, which occurs in almost every dietary fat and attains major proportions in some common vegetable oils. Due to its wide distribution and abundance in many common dietary fats, many populations over-consume LA, and consequently the intake of n-3 FAs fatty acids is very often lower than ideal. γ-linolenic acid (18:3n-6 or GLA) is a trace constituent in some animal PLs and ruminant fats. It is more readily available from seed oils of evening primrose (8-10%), borage (20-25%) and blackcurrant (15-18%). Arachidonic acid (AA) is present in lean meat, especially in free-living animals, liver and egg lipids. It is rare in the plant kingdom, but it has been reported in marine algae and other aquatic plants.

Alpha-linolenic acid (ALA), the parent FA of the n-3 family, is primarily present in the plant kingdom. Among the common vegetable oils, it is readily available in canola (6-10%) and soybean (5-8%) oils. Marine fish such as mackerel, salmon, sardine, herring and smelt are excellent sources of eicosapentaenoic acid (EPA), docosapentaenoic acid (DPA) and docosahexaenoic acid (DHA). Fish oil (FO) containing 60% of EPA and DHA is usually sold as sources of these important n-3 PUFAs. Algal oils and single-cell oil sources of the long-chain PUFAs are now becoming available to provide EPA+DHA+AA. Furthermore, genetically modified oil sources are now being developed and will be widely available in the near future by the genetic manipulation of soy and other plants.

BIOLOGICAL FUNCTIONS OF PUFAs

Influence on Membrane Fluidity

Polyunsaturated fatty acids play an important role in the composition of all cell membranes where they maintain homeostasis for correct membrane protein function and influence membrane fluidity, thus regulating cell signaling processes, cellular functions and gene expression. The fluidity

Table 1. *Typical sources of n-6 and n-3 PUFAs*

Family	Common Name	Systematic Name	Abbreviation	Typical Sources
n-6 family	Linoleic acid	cis-9,cis-12-octadecadienoic	18:2n-6 (LA)	most vegetable oils
	γ-Linolenic acid	cis-6,cis-9,cis-12-octadecatrienoic acid	18:3n-6 (GLA)	evening primrose, borage and black currant seed oils
	Homo-γ-linolenic acid	cis-8,cis-11,cis-14-eicosatetrienoic acid	20:3n-6 (DGLA)	very minor component in animal tissues
	Arachidonic acid	cis-5,cis-8,cis-11,cis-14-eicosatetraenoic acid	20:4n-6 (AA)	animal fats, liver, egg lipids, fish
	Docosatetraenoic acid	cis-7,cis-10,cis-13,cis-16-docosapentaenoic acid	22:4n-6	very minor component in animal tissues
	Docosapentaenoic acid	cis-4,cis-7,cis-10,cis-13,cis-16-docosapentaenoic acid	22:5n-6	very minor component in animal tissues
n-3 family	α-Linolenic acid	cis-9,cis-12-cis-15-octadecatrienoic acid	18:3n-3 (ALA)	flaxseed oil, perilla oil, canola oil, soybean oil
	Stearidonic acid	cis-6,cis-9,cis-12,cis-15-octadecatetraenoic acid	18:4n-3 (SA)	fish oils, genetically enhanced soybean oil, blackcurrant seed oil, hemp oil
	Eicosapentaenoic acid	cis-5,cis-8,cis-11,cis-14,cis-17-eicosapentaenoic acid	20:5n-3 (EPA)	fish, especially oily fish (salmon, herring, anchovy, smelt and mackerel)
	Docosapentaenoic acid	cis-7,cis-10,cis-13,cis-16, cis-19-docosapentaenoic acid	22:5n-3 (n-3 DPA)	fish, especially oily fish (salmon, herring, anchovy, smelt and mackerel)
	Docosahexaenoic acid	cis-4,cis-7,cis-10,cis-13,cis-16,cis-19-docosapentaenoic acid	22:6n-3 (DHA)	fish, especially oily fish (salmon, herring, anchovy, smelt and mackerel)

of the membrane is dependent on the lipid composition of the membrane and among the significant components of cell membranes are the phospholipids. The types of FAs in the diet determine the types of FAs that are available to the composition of cell membranes. A phospholipid made from a saturated fat has a different structure and is less fluid than the one that incorporates an essential FA. PUFAs are important constituents of all cell membranes, which confer on membranes properties of fluidity, and thus determine and influence the behavior of membrane-bound enzymes and receptors [4]. PUFAs had an inhibitory effect on cell proliferation/viability and strongly increased tumor cell lipid peroxidation in a dose-dependent manner [5]. n-3 PUFAs supplementation can modify the membrane phospholipid fatty acid composition and modulate the second messenger signaling pathways in the adult cardiac myocytes. However, because the unsaturated double bonds of PUFAs are susceptible to the oxidation of free radicals, excessive intake of PUFAs can lead to the enhanced lipid peroxidation *in vivo* and reduce cell membrane fluidity. They are able to decrease the cholesterol level in the neuronal membrane, which would otherwise decrease membrane fluidity, which in turn would make it difficult for the cell to carry out its normal functions and increase the cell's susceptibility to injury and death. These consequences for cell function are not restricted to absolute levels of FAs alone; rather it appears that the relative amounts of n-3 PUFAs and n-6 PUFAs in the cell membranes are responsible for affecting cellular function. In addition, n-3 PUFAs had ameliorative effects on the oxidative tissue degeneration and inflammatory processes induced by CCl_4 treatment in rats [6].

Polyunsaturated fatty acids are important components of phospholipid in neuronal membranes, which play important roles in signal transduction of cellular surface. DHA accounts for 10% of the brain phospholipids, and it also has a high content in the central nervous system, mainly distributing in acetylcholine, amino phospholipids and serine glycerol [7]. DHA is instrumental in the function of brain cell membranes, which are important for the transmission of brain signals. By making cell membranes more fluid, n-3 PUFAs, especially DHA, improve communication between the brain cells and lack of n-3 PUFAs in the body can cause a communication breakdown in the brain. EPA and DHA could affect signal transduction in brain cells by activating peroxisomal proliferator-activated receptors (PPARs), inhibiting G-proteins and protein kinase C, as well as calcium, sodium, and potassium ion channels. In addition, DHA and EPA can affect the membrane structure of sperm cells, making the sperm membrane with good fluidity and participating in cell response mediated in protein, which could influence the production of lipid-mediated conductor, cell signal transduction as well as gene expression [8].

Lipid Metabolism

Polyunsaturated fatty acids, particularly those of the n-3 family, play essential roles in the maintenance of energy balance and glucose metabolism. n-3 PUFAs, in addition to affecting general properties of cells as membrane components, play a role in modulating the production of both lipid (eicosanoids) and protein (cytokines) mediators. The n-3 family of PUFAs appear to have the unique ability to enhance thermogenesis and thereby reduce the efficiency of body fat deposition. PUFAs exert their effects on lipid metabolism and thermogenesis by upregulating the transcription of the mitochondrial uncoupling protein-3, and inducing genes encoding proteins involved in fatty acid oxidation (e.g. carnitine palmitoyltransferase and acyl-CoA oxidase) while simultaneously down-regulating the transcription of genes encoding proteins involved in lipid synthesis (e.g. fatty acid synthase). n-3 PUFAs can inhibit the activity of fatty acid synthase (FAS), diacylglycerol acylase and hydroxymethyl glutarate coenzyme A reductase to promote the oxidative decomposition of fatty acids, thus depress the synthesis of triglyceride (TG) and reduce the content of low density lipoprotein (LDL) receptor in the liver to inhibit total cholesterol (TC) synthesis and absorption, finally reducing the level of TG and TC in the serum [9].

Lipid metabolism, inflammation, oxidative stress and endothelial function play important roles in the pathogenesis of cardiovascular disease (CVD), which may be affected by an imbalance in the n-6/n-3 PUFAs ratio [10]. Low n-6/n-3 PUFAs ratio (1:1 and 5:1) had a beneficial effect on cardiovascular risk factors by enhancing favorable lipid profiles, having anti-inflammatory and anti-oxidative stress effects, and improving endothelial function. In contrast, a high n-6/n-3 PUFAs ratio (20:1) had adverse effects.

Regulation of Gene Expression

Supplementation of PUFAs has become an important dietary strategy to reduce hepatic lipogenesis in rodents and humans by inducing the regulation of gene expression. PUFAs can affect gene expression through various mechanisms including, but not limited to, changes in membrane composition, intracellular calcium levels, and eicosanoid production. Furthermore, PUFAs and their various metabolites can act at the level of the nucleus, in conjunction with nuclear receptors and transcription factors, to affect the transcription of a variety of genes. Several of these transcription mediators have been identified and include the nuclear receptors peroxisome proliferator-activated receptor (PPAR), hepatocyte nuclear factor (HNF)-4α, and liver X receptor (LXR) and the transcription factors sterol-regulatory element binding protein (SREBP) and nuclear factor-κB (NFκB). Their interaction with PUFAs has been shown to be critical to the regulation of several key genes of lipid metabolism [11].

The presence of high concentrations of n-3 PUFAs, or shifts in n-6/n-3 ratios may modulate the expression of genes known to be critical to inflammatory processes [12]. The majority of studies examining PUFAs and gene expression

have been carried out in isolated cell systems and a few animal studies. Curtis et al.[13] had shown that α-linolenic acid (LNA, 18:3, n-3), EPA, or DHA reduce the expression of genes for TNFα and IL-1β in bovine chondrocytes. DHA played different regulating roles in lipid metabolism in different tissues to reduce body fat mass through regulating lipogenesis and lipolysis genes. In adipose tissue, DHA increased the expression of lipogenesis and lipolysis genes. In liver lipogenesis genes were decreased, but lipolysis genes were increased by DHA [14]. Similarly, mice fed FO had decreased mRNA levels for numerous inflammatory cytokines including IL-1β, IL-6, and TNFα in kidney, spleen, and peritoneal macrophages [15]. Feeding 6% α-LA-enriched camelina meal to lactating dairy cows reduced expression of IL-1β, IL-8, and TNF-α in peripheral blood mononuclear cells [16].

Immune Function

The beneficial effects of PUFAs are of obvious therapeutic interest, they are believed to be preventive in various chronic diseases, including rheumatoid arthritis, coronary heart disease, and stroke, and certain types of cancer, including breast, prostate, and colorectal cancers. Preclinical studies in cell culture and rodent models show that the EPA and DHA acids are immunomodulatory and can influence both innate and adaptive immunity [17]. EPA and DHA are usually used in the treatment of inflammatory diseases such as rheumatoid arthritis, psoriasis and ulcerative colitis. In the eye, deficiency of DHA is associated with abnormalities in the visual system, including retinitis pigmentosa, peroxisomal disorders and compromised growth and development in infants [18]. Dietary PUFAs can modulate the immune system to improve growth performance and health. Research showed that milk replacer containing FO weakened acute phase responses and the effect was linear in response as the FO FA replacement increased from 5 to 10% [19].

Various n-3 PUFAs have been reported to exert beneficial effects, such as protection against liver diseases, regulation of cholesterol, and reduction of blood pressure, which prevents cardiovascular diseases (CVDs) [20]. n-3 PUFAs can modify B-cell activation, antigen presentation to helper T cells, antibody production, surface expression of select molecules, development in bone marrow, and the relative percentage or frequency of B cells in specific tissues [21-23]. In addition, n-3 PUFAs can also exert immunomodulatory effects on lymphocytes by targeting plasma membrane molecular organization [24]. Several studies have indicated that n-3 PUFAs exert anti-inflammatory effects by regulating the expression of peroxisome proliferator activated receptors (PPARs) and nuclear factor kappa B (NF-κB) [25-27]. The inflammatory response is triggered by activation of NF-κB, which induces the expression of pro-inflammatory cytokines, adhesion molecules, chemokines, growth factors, and inducible enzymes, such as cyclooxygenase 2 (COX-2) and nitric oxide synthase (NOS) [28].

APPLICATION OF PUFAs IN ANIMAL PRODUCTION

Application in Poultry Diets

Previous studies in broiler chickens have shown different relationships between the fatty acid contents of diets and tissues, especially for breast and thigh meat [29,30]. Comparable levels of n-3 PUFAs in the meat can be achieved by only feeding the flaxseed oil diet in the last 3-4 weeks of the growth period [31]. The growth performance of broilers fed on n-3 PUFA-enriched diets (linseed oil) was not different from those fed on a control diet [32]. Dietary incorporation of linseed oil and pig lard during starter, grower and finisher phases can enrich broiler chickens meat with n-3 PUFAs [33].

Eggs enriched with n-3 PUFAs can be used to increase the n-3 PUFAs content of the human diet. In recent decades, the consumption of chicken meat has steadily increased and many studies have focused on the use of dietary modifications to improve the quality of the poultry egg and meat. More specifically, enhancing the functional value of poultry egg and meat through dietary intervention appears to be the most justified, safe, and efficient method [34]. The most efficient way of promoting the functional value of meat was to feed chickens a diet containing FO and rapeseed (10 g/L and 60 g/L diet, respectively) for the last three weeks before slaughter [35]. Such a dietary intervention not only increased the share of long-chain PUFAs and decreased the PUFAs n-6/n-3 ratio of meat lipids, but also increased the content of EPA and DHA in the edible parts of the carcass. López-Ferrer et al.[36] assessed the effect of a diet supplemented with FO on the FAs composition and quality of broiler meat. The results showed that high FO concentrations decreased the saturated and monoenoic FAs contents in the thigh samples. The amount of PUFAs (mainly as EPA, DPA and DHA) increased when FO added in the diets and the levels of total n-6 PUFAs resulted in slight changes, mostly in LA. The total egg yolk n-3 PUFAs was increased from 135.4 mg/egg to 344.5 mg/egg after 18-day feeding with the diet containing 15% Lin-PRO (flaxseed:pea = 1:1; wt/wt) [37]. For EPA and DHA, but not for LA, the diet effect was more distinct in the extensor carpi radialis compared to *longissimus* thoracis and *biceps femoris* [38]. The emulsified fat powder can improve serum SOD and GSH-Px the activity and decrease the content of MDA, improving the antioxidant performance of laying hens [39,40]. The effectiveness of the canola oil on the some metabolites ostriches was evaluated and indicated that glucose and total protein levels increased significantly, whereas total immunoglobulins insulin, albumin, ALT and AST did not change [41]. The main immune organs in poultry are the thymus, spleen, and bursa of *Fabricius*. During an immune response, mature lymphocytes and other immune cells interact with antigens in these tissues. Wang et al.[42] observed that feeding laying chickens diets rich in

n-3 PUFAs promoted the growth of the thymus, spleen, and bursa up to 4 weeks of age. However, from the age of 4 weeks onward, immune tissue weights began to decline, and the bursa degenerated between 4 and 8 week of age. Dietary n-3 PUFAs could decrease phagocytosis and lymphocyte proliferation in broiler chickens, highlighting the need for the poultry industry to consider the health status of poultry when poultry meat is being enriched with FO [43]. An increased ratio of membrane n-6 to n-3 is involved in the pathogenesis of depression and n-3 supplementation has shown positive effects in clinical trials [44]. Typical formulated broiler diets are deficient in n-3 PUFAs due to widening n-6/n-3 PUFAs ratio which could greatly affect performance, immune system of birds and meat quality. Ibrahim et al.[45] evaluated the effect of modifying dietary n-6 and n-3 PUFAs ratio from plant and animal oil sources on performance, behavior, cytokine mRNA expression, antioxidative status and meat FAs profile of broiler chickens. The results indicated that narrowing n-6/n-3 ratio through the addition of FO or LO improved growth performance and immune response of broilers and resulted in healthy chicken meat, enriched with long chain n-3 PUFAs.

The proportion of respective PUFAs in the chicken partly depends on diet and an increase in the proportion of n-3 PUFAs in the diet has been shown to improve fertility. Diet supplementation with linseed oil has capability to make the suitable changes in the lipid contents of sperm as well as the improvement in live percentage of sperms [46]. Blesbois et al.[47] measured the effects of dietary n-3 PUFAs supplementation on the reproductive capacity of adult male turkeys in industrial flocks. The FO diet very effectively increased the percentage of n-3 PUFAs (22:5n-3 and 22:6n-3) in spermatozoa and correspondingly decreased the percentage of n-6 PUFAs (20:4-6 and 22:4n-6). These changes did not affect the spermatozoa content of n-9 PUFAs, particularly of 22:3n-9 which is abundant in turkey spermatozoa (9-12% of the total FAs). The supplementation was effective in the middle as at the end of the reproductive period. The reproductive capacity of males was modified by the diet and the positive effect of the n-3 supplemented diet increased with age (increase in hatching rates of nearly 2 points at 48-58 weeks for males fed FO diet). These results indicated that n-3 PUFAs enrichment of the turkey diet induced changes in spermatozoa PUFAs, with an overall positive effect on the reproductive capacity of adult males, especially during the decreasing phase of the annual reproductive period.

Application in Swine Diets

Sow Nutrition: Addition of fat to the diets of sows during late gestation and (or) lactation can increase milk production and fat content of colostrum and milk. The maternal dietary fat during the perinatal period affected the type and quantity of the FAs in milk, which was one of the most important pathways to afford nutrition for neonates [48]. For sows, PUFAs can not only influence the composition of FAs in sows, but also affect the composition of FAs in the body tissues of piglets through the composition of FAs in colostrum and milk, which can provide plenty of FAs and energy supply for piglets with the aims to improve the survival rate and growth of piglets as well as the reproductive performance of sows. Supplementation of the maternal diet with FO or linseed oil increased the level of n-3 PUFAs of the piglets in a tissue-specific manner. The response of Δ6-desaturase and Δ5-desaturase protein expression in female piglets to the dietary manipulation was also tissue-specific, suggesting that the increase in n-3 PUFAs content in the progeny was related, at least partially, to the activation of Δ6-desaturase and Δ5-desaturase expression [49].

The administration of different oils to sows during lactation can alter the FAs composition of the offspring piglets at weaning, although the type of FAs was not consistent [50]. The percentage of solids in milk was greater for sows fed the tallow diet, due to an increase in the fat and ash content. Compared with percentages of FAs in milk of sows fed the control diet, the percentages of C10:0, C14:0, C16:0, C16:1, and C18:3 FAs were lower and the percentages of C18:0 and C18:1 FAs were higher in milk of sows fed tallow diets. Litter weaning weight was greater for pigs from sows fed tallow diets than for pigs from control sows. Pigs from tallow-fed sows had greater carcass fat weight and fat percentages and lower water and protein percentages. The diet containing 8% corn oil starting seven days before farrowing until weaning significantly increased the contents of serum-lipid-related indexes in the sows [51]. Although the triglyceride content did not change, the C18:2n-6 content was higher in the colostrum and in the *longissimus thoracis* muscle of offspring pigs at both investigated stages. The total n-6 content and the ratio of n-6 to n-3 generally increased. These results demonstrated that maternal dietary fat during lactation affected the FAs' composition of the *longissimus thoracis* muscle of progeny at weaning and had persistent effects in later life.

Growing-Finishing Pigs Nutrition: Fatty acids' composition in the pig body is related to their composition in the diet. The deposition of n-3 PUFAs in the body depended on the source of fat in the diet and the increase of n-3 PUFAs intake increased their deposition in the pig body. Sobol et al.[52] reported that loin and shoulder of pigs (with high intramuscular fat content) fed a diet enriched with the mixture of linseed, rapeseed, and FO meet the European Union recommendations for human nutrition for products considered as either PUFAs n-3 sources or products with high PUFAs n-3 content. Alvarez-Rodriguez et al.[53] found out that total n-3 PUFAs content (mainly α-linolenic acid, ALA) was greater in organic than in conventional pork, probably due to ALA content from dietary vegetable oils. The source of n-3 PUFAs and dietary n-6/n-3 ratios allow for the favourable manipulation of the fatty acid composition

of pork, indicating that fatty acids composition in the pig body was related to their composition in the diet and the deposition of n-3 PUFAs in the body depended on the source of fat in the diet. However, increasing ALA and EPA + DHA intake enhances their deposition in the body, their net DE decreases [54].

Boar Nutrition

Pig spermatozoa contains a significant amount of DHA. Intake of different types and sources of PUFA has been shown to change the fatty acid composition of animal sperm and affect sperm quality [55]. FO (rich in n-3 PUFAs) has been shown to alter sperm structure and penetration resistance, and to increase sperm number and antioxidant capacity [56]. In addition, semen quality was significantly affected by the dietary n-6/n-3 PUFAs ratio. It has previously been reported that diets with a n-6/n-3 FA ratio of 1.6:1 could increase the proportion of intact acrosome of the boar's spermatozoa. Oils that are rich in n-3 PUFAs also significantly increased sperm density and sperm number [57]. Lin et al.[58] determined the effects of different dietary n-6/n-3 ratios on the reproductive performance of breeding boars and found that proper n-6/n-3 PUFAs ratio in the diet of breeding boars enhanced the development of testis and accessory sex gland function, and improved sperm quality, which may be related to favorable hormone metabolism and antioxidant capacity.

Application in Ruminant Diets

Reproductive Performance: Different types of fats have been utilized in an attempt to improve reproductive function in ruminant animals. FAs derived from plants and oil seeds have exerted a major impact on reproductive performance, some of the most common sources include sunflower, linseed, cottonseed, rapeseed and soybean. Animal fat (tallow) and calcium salts of SFAs may escape in a significant percentage rumen hydrogenation to be incorporated into adipose tissue and milk. Fish by-products contain a high proportion of PUFAs and pass without being altered in the rumen exerting no effects on rumen fermentation. There is strong evidence linking consumption of diets high in n-3 PUFAs with reduced circulating peripheral inflammatory markers such as PGF2α. Supplementation of n-3 PUFA enriched diet improves the pregnancy rate in the cow and buffalo [59], which is explained by a reduction in the uterine PGF2α secretion and/or decrease in the sensitivity of the CL to PGF2α during critical stage of embryonic development, preventing the onset of luteolysis and facilitating the establishment of pregnancy. Inflammatory eicosanoids including PGF2α, in particular, can significantly affect reproduction outcomes such as the onset of oestrus, embryo survival and parturition. Supplementation of EPA and DHA rich FO for about 10 weeks around the time of mating improved the number of POF and ovulation rate. The twinning and kidding were also enhanced in FO supplemented goats possibly by lowering the E2 and PGFM concentration during the window of pregnancy recognition [60].

Polyunsaturated fatty acids are critical nutrients which play an important role in maintaining the physical properties of the sperm membrane fluidity. In general, PUFAs are major component of the sperm cell membranes and thus the major mechanism that PUFAs can affect the sperm quality is associated with membrane physiological characteristics. Te incorporation of PUFAs into diet is able to cause alteration of fatty acid profile of sperm plasma membrane and results in improved sperm quality. Dietary supplementation with PUFAs can alter fluidity/permeability of sperm membrane and enhance reproductive performance in male ruminants thought improving testis development, spermatogenesis, motility and viability of sperm before and post freezing [61]. There have been a lot of studies carried out in various ruminants species reports have been published *(Table 2)*.

Growth Performance: Ponnampalam et al.[71] investigated the effect of diets containing n-3 PUFAs on muscle long-chain n-3 FAs content in lambs fed low and medium-quality roughage diets. Fish meal (80 g DM) can increased the muscle long-chain n-3 PUFAs content and decreased the ratio of n-6/n-3 in lamb meat. Feeding soy meal (75g DM modestly increased both the long-chain n-3 and n-6 PUFAs content of meat, resulting in no difference in the n-6/n-3 ratio of meat. The protected canola seed (6% DM) diet did not have a major effect on muscle n-3 FA but resulted in an increase in n-6 and the n-6/n-3 ratio of meat. Demirel et al.[72] reported that the lambs supplemented with FO plus linseed oil had greater concentrations of C14:0 in the polar lipid fraction of lamb musculus semimembranosus than lambs supplemented with a Ca salt of palm oil, but this was not the case for the neutral lipid fraction. Kim et al.[73] determined the effect of modifying the n-6:n-3 PUFAs ratio in a concentrate-based diet on feed intake, apparent nutrient digestibility, plasma hormones, and long chain FA composition of the ruminal contents, liver, and muscle of lambs. The results indicated that increasing the n-3 PUFAs in the diet with select oil sources decreased the n-6 to n-3 ratio in ruminal digesta, liver, and fore-shank muscle of growing lambs fed high concentrate diets. This change would likely improve the suitability of lamb meat as a healthful food.

Lactation: Ruminal biohydrogenation, combined with mammary lipogenic and Δ-9 desaturation pathways, considerably modifies the profile of dietary FA and thus milk composition [74]. Ruminal biohydrogenation of dietary unsaturated FAs are relatively constant, whereas secretion of these in milk is more variable absorbed. Dietary lipids are extensively hydrogenated by rumen micro-organisms, and the extent of this biohydrogenation is a major determinant of long-chain fatty acid profiles of animal products (milk, meat). Numerous studies demonstrated that marine oil supplementation could affect rumen lipid metabolism by altering the activity of specific ruminal bacteria involved in

Table 2. *Effect of dietary PUFAs enriched fat sources on semen quality*

Reference	Species	Fat Source	Percent Inclusion	Effect
Samadian et al.[62]	Ram	Fish oil	3%	Increased the proportion of DHA in sperm fatty acid composition, improved sperm concentration and motility
Esmaeili et al.[57]	Ram	Palm oil, sunflower oil, fish oil	35 g/d	Improved prefreezing semen characteristics after thawing, 35 days after the removal of fatty acid source, the percentage of C22:6 was highest in the fish oil treated group
Fair et al.[63]	Ram	Protected fish oil	2%	Increased semen concentration but no effect on other semen quality parameters including semen volume, wave motion, and progressive linear motion
Radmanesh et al.[64]	Ram	Calcium salts of soybean oil	4%	Improved the volume of semen and total sperm count in ejaculate
Dolatpanah et al.[65]	Goat	Fish oil and Vit. E	2.5% and 0.3g/kg DM	Improved testes development enhanced the quality and quantity of goat semen
Adeel et al.[66]	Buffalo	Sunflower oil, sunflower seed	1%	Improved the quality of sperm including motility and hypo-osmotic swelling of post-thawed sperm
Santos et al.[67]	Buffalo	Palm kernel cake	1%	Improvement of sperm quality, with higher sperm motility and higher levels of spermatozoa with plasma membrane integrity
Brinsko et al.[68]	Stallion	Commercially available nutriceutical formulated	250 g	Improved the motion characteristics of cool-stored stallion semen and the freezability of semen
Moallem et al.[69]	Bull	Flaxseed oil, fish oil	450 g/d (84.2 g/d C18:3 n-3)	Changed in the characteristics of both fresh and frozen-thawed semen, increased motility and progressive motility of sperm
Khoshvaght et al.[70]	Bull	Fish oil	1.2% DM	Improved fresh and post-thaw semen quality in Holstein bulls via alteration of sperm fatty acid composition

bio-hydrogenation and isomerization of dietary PUFAs [75]. With greater interest in increasing the n-3 PUFAs content of human diets, interest has also developed to increase these FAs in animal products. FO can modify ruminal or systemic functions, stimulating increased conversion of linoleic acid into transvaccenic and conjugated linoleic acids [76]. Supplementing the diet of partially grazing cows with FO and sunflower oil increased the milk cis-9, trans-11 CLA content, and that increase remained relatively constant after one week of oil supplementation [77]. Zhao et al.[78] investigated the relationship of FAs composition with specific bacteria involved in hydrogenation of 18-carbon UFA in response to dietary oil sources. These results demonstrated that unprotected FO and sunflower oil affected ruminal fermentation and produced series of bio-hydrogenation intermediates. Alterations in ruminal bio-hydrogenation were associated with changes in the abundance of *B. proteoclasticus*, but *B. proteoclasticus* was not the dominant bacterium in producing C18:0.

CONCLUSIONS AND FUTURE PROSPECTS

Polyunsaturated fatty acids are critical nutrients for normal growth and development and play an important role in the composition of all cell membranes where they maintain homeostasis for correct membrane protein function and influence membrane fluidity, thus regulating cell signaling processes, cellular functions and gene expression. Dietary supplementation with PUFAs can alter fluidity/permeability of sperm membrane and enhance reproductive performance in ruminants thought improving testis development, spermatogenesis, motility and viability of sperm before and post freezing. More important, n-3 PUFAs can significantly affect circulating peripheral inflammatory markers such as PGF2α as well as a number of hormones and cytokines and these peripheral markers can have a significant effect on reproduction outcomes. In addition, the structure of fat tissue of monogastric animals (pigs, poultry) is very similar to the fat structure of the feedstuffs on which the animals are fed, which means that source and type of fat in an animal feed can greatly influence the composition of fatty tissue and deposits in the resultant carcasses. Since PUFAs give rise to a variety of biologically active compounds which all have important roles in pathological and physiological processes, a proper understanding is needed regarding the contribution these active compounds have on the coinciding increases in inflammatory diseases seen with the disruption of the balance in the ratio of n-6 to n-3 PUFAs. So, it is necessary to conduct further researches to make clear about the effect of optimum n-6 to n-3 PUFAs ratio on various animals and their different stages, thereby contribute to modifying their diets in practice and achieve maximum effect on reproduction.

Disclosure Statement

No potential conflict of interest was reported by the authors.

Acknowledgments

This study was partly funded by the Innovation Program of Modern Agricultural Industry System of Shandong (SDAIT-21-15) and Agricultural Scientific and Technological Innovation Project of Shandong Academy of Agricultural Sciences (No. CXGC2017B02).

REFERENCES

1. Ibrahim D, El-Sayed R, Khater SI, Said EN, El-Mandrawy SAM: Changing dietary n-6:n-3 ratio using different oil sources affects performance, behavior, cytokines mRNA expression and meat fatty acid profile of broiler chickens. *Anim Nutr,* 4, 44-51, 2018. DOI: 10.1016/j.aninu.2017.08.003

2. Calder PC: Marine omega-3 fatty acids and inflammatory processes: effects, mechanisms and clinical relevance. *BBA-Mol Cell Biol L,* 1851 (4): 469-484, 2015. DOI: 10.1016/j.bbalip.2014.08.010

3. Patterson E, Wall R, Fitzgerald GF, Ross RP, Stanton C: Health implications of high dietary omega-6 polyunsaturated fatty acids. *J Nutr Metab*, 2012 (2): 539426, 2012. DOI: 10.1155/2012/539426

4. Das UN: Essential fatty acids: Biochemistry, physiology and pathology. *Biotechnol J,* 1 (4): 420-439, 2006. DOI: 10.1002/biot.200600012

5. Nano JL, Nobili C, Girard-Pipau F, Rampal P: Effects of fatty acids on the growth of Caco-2 cells. *Prostaglandins Leukot Essent Fatty Acids,* 69 (4): 207-215, 2003. DOI: 10.1016/S0952-3278(03)00083-8

6. Karaman M, Özen H, Dağ S, Atakişi O, Çığşar G, Kaya O: Ameliorative effect of omega-3 in carbon tetrachloride toxicity. *Kafkas Univ Vet Fak Derg*, 23, 77-85, 2017. DOI: 10.9775/kvfd.2016.15862

7. Sarkadi-Nagy E, Wijendran V, Diau GY, Chao AC, Hsieh AT, Turpeinen A, Lawrence P, Nathanielsz PW, Brenna JT: Formula feeding potentiates docosahexaenoic and arachidonic acid biosynthesis in term and preterm baboon neonates. *J Lipid Res*, 45 (1): 71-80, 2004. DOI: 10.1194/jlr.M300106-JLR200

8. Calder PC, Yaqoob P: Understanding omega-3 polyunsaturated fatty acids. *Postgrad Med,* 121 (6): 148-157, 2009. DOI:10.3810/pgm.2009.11.2083

9. Moreno C, Macías A, Prieto A, de la Cruz A, González T, Valenzuela C: Effects of n-3 polyunsaturated fatty acids on cardiac ion channels. *Front Physiol,* 3 (3): 245, 2012. DOI: 10.3389/fphys.2012.00245

10. Yang LG, Song ZX, Yin H, Wang YY, Shu GF, Lu HX, Wang SK, Sun GJ: Low n-6/n-3 PUFA ratio improves lipid metabolism, inflammation, oxidative stress and endothelial function in rats using plant oils as n-3 fatty acid source. *Lipids*, 51 (1): 49-59, 2016. DOI: 10.1007/s11745-015-4091-z

11. Sampath H, Ntambi JM: Polyunsaturated fatty acid regulation of genes of lipid metabolism. *Annu Rev Nutr,* 25, 317-340, 2005. DOI: 10.1146/annurev.nutr.25.051804.101917

12. Weaver KL, Ivester P, Seeds M, Douglas Case L, Arm JP, Chilton FH: Effect of Dietary fatty acids on inflammatory gene expression in healthy humans. *J Biol Chem*, 284 (23): 15400-15407, 2009. DOI: 10.1074/jbc.M109.004861

13. Curtis CL, Hughes CE, Flannery CR, Little CB, Harwood JL, Caterson B: *n-3* fatty acids specifically modulate catabolic factors involved in articular cartilage degradation. *J Biol Chem,* 275 (2): 721-724, 2000. DOI: 10.1074/jbc.275.2.721

14. Sun C, Wei ZW, Li Y: DHA regulates lipogenesis and lipolysis genes in mice adipose and liver. *Mol Biol Rep,* 38, 731-737, 2011. DOI: 10.1007/s11033-010-0160-9

15. Calder PC: Dietary modification of inflammation with lipids. *Proc Nutr Soc,* 61 (3): 345-358, 2002. DOI: 10.1079/PNS2002166

16. Rezamand P, Hatch BP, Carnahan KG, McGuire MA: Effect of α-linolenic acid-enriched diets on gene expression of key inflammatory mediators in immune and milk cells obtained from Holstein dairy cows. *J Dairy Res,* 83 (1): 20-27, 2016. DOI: 10.1017/S0022029915000709

17. Miyata J, Arita M: Role of omega-3 fatty acids and their metabolites in asthma and allergic diseases. *Allergol Int,* 64 (1): 27-34, 2015. DOI: 10.1016/j.alit.2014.08.003

18. Sangiovanni JP, Chew EY: The role of omega-3 long-chain polyunsaturated fatty acids in health and disease of the retina. *Prog Retin Eye Res,* 24 (1): 87-138, 2005. DOI: 10.1016/j.preteyeres.2004.06.002

19. Ballou MA, Cruz GD, Pitroff W, Keisler DH, DePeters EJ: Modifying the acute phase response of Jersey calves by supplementing milk replacer with omega-3 fatty acids from fish oil. *J Dairy Sci,* 91 (9): 3478-3487, 2008. DOI: 10.3168/jds.2008-1016

20. Kromhout D, Yasuda S, Geleijnse JM, Shimokawa H: Fish oil and omega-3 fatty acids in cardiovascular disease: Do they really work? *Eur Heart J,* 33 (4): 436-443, 2012. DOI: 10.1093/eurheartj/ehr362

21. Teague H, Harris M, Fenton J, Lallemand P, Shewchuk B, Shaikh SR: Eicosapentaenoic and docosahexaenoic acid ethyl esters differentially enhance B-cell activity in murine obesity. *J Lipid Res,* 55 (7): 1420-1433, 2014. DOI: 10.1194/jlr.M049809

22. Gurzell EA, Teague H, Duriancik D, Clinthorne J, Harris M, Shaikh SR, Fenton JI: Marine fish oils are not equivalent with respect to B-cell membrane organization and activation. *J Nutr Biochem,* 26 (4): 369-377, 2015. DOI: 10.1016/j.jnutbio.2014.11.005

23. Rockett BD, Melton M, Harris M, Bridges LC, Shaikh SR: Fish oil disrupts MHC class II lateral organization on the B-cell side of the immunological synapse independent of B-T cell adhesion. *J Nutr Biochem,* 24 (11): 1810-1816, 2013. DOI: 10.1016/j.jnutbio.2013.02.013

24. Shaikh SR, Jolly CA, Chapkin RS: n-3 Polyunsaturated fatty acids exert immunomodulatory effects on lymphocytes by targeting plasma membrane molecular organization. *Mol Aspects Med,* 33 (1): 46-54, 2012. DOI: 10.1016/j.mam.2011.10.002

25. Jump DB: n-3 polyunsaturated fatty acid regulation of hepatic gene transcription. *Curr Opin Lipidol,* 19 (3): 242-247, 2008. DOI: 10.1097/MOL.0b013e3282ffaf6a

26. Kota BP, Huang TH, Roufogalis BD: An overview on biological mechanisms of PPARs. *Pharmacol Res,* 51 (2): 85-94, 2005. DOI: 10.1016/j.phrs.2004.07.012

27. Lefebvre P, Chinetti G, Fruchart JC, Staels B: Sorting out the roles of PPAR alpha in energy metabolism and vascular horneostasis. *J Clin Invest,* 16, 571-580, 2006. DOI: 10.1172/JCI27989

28. Hanada T, Yoshimura A: Regulation of cytokine signaling and inflammation. *Cytokine Growth Factor Rev,* 13 (4-5): 413-421, 2002. DOI: 10.1016/S1359-6101(02)00026-6

29. Abdulla NR, Loh TC, Akit H, Sazili AQ, Foo HL, Mohamad R, Abdul Rahim R, Ebrahimi M, Sabow AB: Fatty acid profile, cholesterol and oxidative status in broiler chicken breast muscle fed different dietary oil sources and calcium levels. *S Afr J Anim Sci,* 45 (2): 153-163, 2015. DOI: 10.4314/sajas.v45i2.6

30. Kanakri K, Carragher J, Hughes R, Muhlhausler B, Gibson R: The effect of different dietary fats on the fatty acid composition of several tissues in broiler chickens. *Eur J Lipid Sci Technol,* 120 (1): 1700237, 2018. DOI: 10.1002/ejlt.201700237

31. Kanakri K, Carragher J, Hughes R, Muhlhausler B, Gibson R: A reduced cost strategy for enriching chicken meat with omega-3 long chain polyunsaturated fatty acids using dietary flaxseed oil. *Br Poult Sci,* 58, 283-289, 2017. DOI: 10.1080/00071668.2017.1293798

32. Kanakri K, Muhlhausler B, Carragher J, Gibson R, Barekatain R, Dekoning C, Drake K, Hughes R: Relationship between the fatty acid composition of uropygial gland secretion and blood of meat chickens receiving different dietary fats. *Anim Prod Sci,* 58 (5): 828-833, 2016. DOI: 10.1071/AN16268

33. Milanković B, Ćirić J, Krstić M, Starčević M, Baltić B, Šefer D, Đorđević V, Popović M, Marković R: Effect of dietary fatty acid pattern on growth performance, carcass characteristics, fatty acid profile, and serum biochemistry parameters in broiler chickens. *Kafkas Univ Vet Fak Derg*, 25 (4): 507-516, 2019. DOI: 10.9775/kvfd.2018.21205

34. Zhang W, Xiao S, Samaraweera H, Lee EJ, Ahn DU: Improving functional value of meat products. *Meat Sci,* 86 (1): 15-31, 2010. DOI: 10.1016/j.meatsci.2010.04.018

35. Konieczka P, Czauderna M, Smulikowska S: The enrichment of chicken meat with omega-3 fatty acids by dietary fish oil or its mixture with rapeseed or flaxseed-effect of feeding duration. *Anim Feed Sci Technol,* 223 (1): 42-52, 2017. DOI: 10.1016/j.anifeedsci.2016.10.023

36. López-Ferrer S, Baucells MD, Barroeta AC, Grashorn MA: n-3 enrichment of chicken meat. 1. Use of very long-chain fatty acids in chicken diets and their influence on meat quality: Fish oil. *Poult Sci,* 80 (6): 741-752, 2001.

37. Nain S, Renema RA, Korver DR, Zuidhof MJ: Characterization of the n-3 polyunsaturated fatty acid enrichment in laying hens fed an extruded flax enrichment source. *Poult Sci,* 91 (7): 1720-1732, 2012. DOI: 10.3382/ps.2011-02048

38. Wolf C, Ulbrich SE, Kreuzer M, Berard J, Giller K: Differential partitioning of rumen-protected n-3 and n-6 fatty acids into muscles with different metabolism. *Meat Sci*, 137 (3): 106-113, 2018. DOI: 10.1016/j.meatsci.2017.11.007

39. Fu SJ, Guo SJ, Shen ZQ, Zhang ZM: Effect of emulsified fat powder on the laying performance, egg quality, serum biochemical parameters and antioxidant activity. *J Chem Pharm Res*, 8 (7): 176-181, 2016.

40. Fu SJ, Guo SJ, Shen ZQ: Effects of polyunsaturated fatty acids on immune response of avian. *J Chem Pharm Res*, 9 (4): 334-337, 2017.

41. Motlagh MK: Effect ofomega-3 resource on glucose and total protein in ostriches. *Kafkas Univ Vet Fak Derg*, 21, 225-228, 2015. DOI: 10.9775/kvfd.2014.12083

42. Wang YW, Field CJ, Sim JS: Dietary polyunsaturated fatty acids alter lymphocyte subset proportion and proliferation, serum immunoglobulin G concentration, and immune tissue development in chicks. *Poult Sci,* 79 (12): 1741-1748, 2000. DOI: 10.1093/ps/79.12.1741

43. Al-Khalifa H, Givens DI, Rymer C, Yaqoob P: Effect of n-3 fatty acids on immune function in broiler chickens. *Poult Sci,* 91 (1): 74-88, 2012. DOI: 10.3382/ps.2011-01693

44. SøborgHusted K, Bouzinova EV: The importance of n-6/n-3 fatty acids ratio in the major depressive disorder. *Medicina*, 52 (3): 139-147, 2016. DOI: 10.1016/j.medici.2016.05.003

45. Ibrahim D, El-Sayed R, Khater SI, Said EN, El-Mandrawy SAM: Changing dietary n-6:n-3 ratio using different oil sources affects performance, behavior, cytokines mRNA expression and meat fatty acid profile of broiler chickens. *Anim Nutr,* 4 (1): 44-51, 2018. DOI: 10.1016/j.aninu.2017.08.003

46. Pena FJ, Macias GB, Samper JC, Aparicio IM, Tapia JA, Ortega FC: Dissecting the molecular damage to stallion spermatozoa: The way to improve current cryopreservation protocols? *Theriogenology,* 76 (7): 1177-1186, 2011. DOI: 10.1016/j.theriogenology.2011.06.023

47. Blesbois E, Douard V, Germain M, Boniface P, Pellet F: Effects of n-3 polyunsaturated dietary supplementation on the reproductive capacity of male turkeys. *Theriogenology,* 61 (2): 537-549, 2004. DOI: 10.1016/S0093-691X(03)00207-3

48. Innis SM: Metabolic programming of long-term outcomes due to fatty acid nutrition in early life. *Matern Child Nutr,* 7 (S2): 112-123, 2011. DOI: 10.1111/j.1740-8709.2011.00318.x

49. Missotten J, De Smet S, Raes K, Doran O: Effect of supplementation of the maternal diet with fish oil or linseed oil on fatty-acid composition and expression of Δ5- and Δ6-desaturase in tissues of female piglets. *Animal,* 3 (8): 1196-1204, 2009. DOI: 10.1017/S1751731109004455

50. Vicente JG, Isabel B, Cordero G, Lopez-Bote CJ: Fatty acid profile of the sow diet alters fat metabolism and fatty acid composition in weanling pigs. *Anim Feed Sci Technol,* 181 (1-4): 45-53, 2013. DOI: 10.1016/j.anifeedsci.2013.02.002

51. Ci L, Sun HL, Huang YP, Guo J, Albrecht E, Zhao RQ, Yang XJ: Maternal dietary fat affects the LT muscle fatty acid composition of progeny at weaning and finishing stages in pigs. *Meat Sci,* 96 (3): 1141-1146, 2014. DOI: 10.1016/j.meatsci.2013.10.033

52. Sobol M, Raj S, Skiba G: Effect of fat content in primal cuts of pigs fed diet enriched in n-3 polyunsaturated fatty acids on health-promoting properties of pork. *J Anim Feed Sci,* 25 (1): 20-28, 2016. DOI: 10.22358/jafs/65583/2016

53. Alvarez-Rodriguez J, Villalba D, Cubilo D, Babot D, Tor M: Organic practices and gender are effective strategies to provide healthy pork loin. *J Integ Agr,* 15 (3): 608-617, 2016. DOI: 10.1016/S2095-3119(15)61172-8

54. Sobol M, Skiba G, Raj S: Effect of n-3 polyunsaturated fatty acid intake on its deposition in the body of growing-finishing pigs. *Anim Feed Sci Technol,* 208, 107-118, 2015. DOI: 10.1016/j.anifeedsci.2015.06.027

55. Waterhouse KE, Hofmo PO, Tverdal A, Miller RR: Within and between breed differences in freezing tolerance and plasma membrane fatty acid composition of boar sperm. *Reproduction,* 131 (5): 887-894, 2006. DOI: 10.1530/rep.1.01049

56. Estienne MJ, Harper AF, Crawford RJ: Dietary supplementation with a source of omega-3 fatty acids increases sperm number and the duration of ejaculation in boars. *Theriogenology,* 70 (1): 70-76, 2008. DOI: 10.1016/j.theriogenology.2008.02.007

57. Esmaeili V, Shahverdi AH, Alizadeh AR, Alipour H, Chehrazi M: Saturated, omega-6 and omega-3 dietary fatty acid effects on the characteristics of fresh, frozen-thawed semen and blood parameters in rams. *Andrologia,* 46 (1): 42-49, 2014. DOI: 10.1111/and.12040

58. Lin Y, Cheng X, Mao J, Wu D, Ren B, Xu SY, Fang ZF, Che LQ, Wu CM, Li J: Effects of different dietary n-6/n-3 polyunsaturated fatty acid ratios on boar reproduction. *Lipids Health Dis,* 15: 31, 2016. DOI:10.1186/s12944-016-0193-8

59. Nazir G, Ghuman SP, Singh J, Honparkhe M, Ahuja CS, Dhaliwal GS, Sangha MK, Saijpaul S, Agarwal SK: Improvement of conception rate in postpartum flaxseed supplemented buffalo with Ovsynch+CIDR protocol. *Anim Reprod Sci,* 137 (1-2): 15-22, 2013. DOI: 10.1016/j.anireprosci.2012.11.012

60. Mahla AS, Chaudhari RK, Verma AK, Singh AK, Singh SK, Singh G, Sarkar M, Dutta N, Kumar H, Krishnaswamy N: Effect of dietary supplementation of omega-3 polyunsaturated fatty acid (PUFA) rich fish oil on reproductive performance of the goat *(Capra hircus). Theriogenology,* 99, 79-89, 2017. DOI: 10.1016/j.theriogenology.2017.05.023

61. Tran LV, Malla BA, Kumar S, Tyagi AK: Polyunsaturated fatty acids in male ruminant reproduction-A review. *Asian-Australas J Anim Sci,* 30 (5): 622-637, 2017. DOI: 10.5713/ajas.15.1034

62. Samadian F, Towhidi A, Rezayazdi K, Bahreini M: Effects of dietary n-3 fatty acids on characteristics and lipid composition of ovine sperm. *Animal,* 4 (2): 2017-2022, 2010. DOI: 10.1017/S1751731110001308

63. Fair S, Doyle DN, Diskin MG, Hennessy AA, Kenny DA: The effect of dietary n-3 polyunsaturated fatty acids supplementation of rams on semen quality and subsequent quality of liquid stored semen. *Teriogenology,* 81, 210-219, 2014. DOI: 10.1016/j.theriogenology.2013.09.002

64. Radmanesh A, Kuhi HD, Riaci A: Relationship of dietary fat sources with semen characteristics, blood plasma metabolites and scrotal circumference in mature rams. *Iranian J Appl Anim Sci,* 5, 623-628, 2015.

65. Dolatpanah MB, Towhidi A, Farshad A, Rashidi A, Rezayazdi A: Effects of dietary fish oil on semen quality of goats. *Asian-Australas J Anim Sci,* 21, 29-34, 2008. DOI: 10.5713/ajas.2008.70035

66. Adeel M, Ijaz A, Aleem M, Rehman H, Yousaf MS, Jabbar MA: Improvement of liquid and frozen-thawed semen quality of Nili-Ravi buffalo bulls *(Bubalus bubalis)* through supplementation of fat. *Teriogenology,* 71 (8): 1220-1225, 2009. DOI: 10.1016/j.theriogenology.2009.01.008

67. Santos AX, Kahwage PR, Faturi C, Neto QT, Junior JBLL, Joele MRSP, Garcia AR: Feed supplementation with palm kernel cake-based concentrate increases the quality of water buffalo semen. *Anim Reprod,* 11 (2): 85-95, 2014.

68. Brinsko SP, Varner DD, Love CC, Blanchard TL, Day BC, Wilson ME: Effect of feeding a DHA-enriched nutriceutical on the quality of fresh, cooled and frozen stallion semen. *Theriogenology,* 63 (5): 1519-1527, 2005. DOI: 10.1016/j.theriogenology.2004.07.010

69. Moallem U, Neta N, Zeron Y, Zachut M, Roth Z: Dietary α-linolenic acid from flaxseed oil or eicosapentaenoic and docosahexaenoic acids from fsh oil differentially alter fatty acid composition and characteristics of fresh and frozen-thawed bull semen. *Teriogenology,* 83(7): 1110-1120, 2015. DOI: 10.1016/j.theriogenology.2014.12.008

70. Khoshvaght A, Towhidi A, Zare-Shahneh A, Noruozi M, Zhandi M, Dadashpour Davachi N, Karimi R: Dietary n-3 PUFAs improve fresh and post-thaw semen quality in Holstein bulls via alteration of sperm fatty acid composition. *Theriogenology,* 85 (5): 807-812, 2016. DOI: 10.1016/j.theriogenology.2015.10.023

71. Ponnampalam EN, Sinclairt AJ, Egan AR, Blakeley SJ, Leury BJ: Effect of diets containing n-3 fatty acids on muscle long-chain n-3 fatty acid content in lambs fed low- and medium-quality roughage diets. *J Anim Sci,* 79 (3): 698-706, 2001. DOI: 10.2527/2001.793698x

72. Demirel G, Wachira AM, Sinclair LA, Wilkinson RG, Wood JD, Enser M: Effects of dietary n-3 polyunsaturated fatty acids, breed and dietary vitamin E on the fatty acids of lamb muscle, liver and adipose tissue. *Br J Nutr,* 91 (4): 551-565, 2004. DOI: 10.1079/BJN20031079

73. Kim SC, Adesogan AT, Badinga L, Staples CR: Effects of dietary n-6:n-3 fatty acid ratio on feed intake, digestibility, and fatty acid profiles of the ruminal contents, liver, and muscle of growing lambs. *J Anim Sci,* 85 (3): 706-716, 2007. DOI: 10.2527/jas.2006-289

74. Chilliard Y, Glasser F, Ferlay A, Bernard L, Rouel J, Doreau M: Diet, rumen biohydrogenation and nutritional quality of cow and goat milk fat. *Eur J Lipid Sci Technol,* 109 (8): 828-855, 2007. DOI: 10.1002/ejlt.200700080

75. Huws SA, Lee MRF, Muetzel SM, Scott MB, Wallace RJ, Scollan ND: Forage type and fish oil cause shifts in rumen bacterial diversity. *FEMS Microbiol Ecol,* 73 (2): 396-702, 2010. DOI: 10.1111/j.1574-6941.2010.00892.x

76. Whitlock LA, Schingoethe DJ, Hippen AR, Kalscheur KF, Baer RJ, Ramaswamy N, Kasperson KM: Fish oil and extruded soybeans fed in combination increase conjugated linoleic acids in milk of dairy cows more than when fed separately. *J Dairy Sci,* 85 (1): 234-243, 2002. DOI: 10.3168/jds.S0022-0302(02)74072-1

77. AbuGhazaleh AA, Holmes LD: Diet supplementation with fish oil and sunflower oil to increase conjugated linoleic acid levels in milk fat of partially grazing dairy cows. *J Dairy Sci,* 90 (6): 2897-2904, 2007. DOI: 10.3168/jds.2006-684

78. Zhao TZ, Ma Y, Qu YH, Luo HL, Liu K, Zuo ZY, Lu XN: Effect of dietary oil sources on fatty acid composition of ruminal digesta and populations of specific bacteria involved in hydrogenation of 18-carbon unsaturated fatty acid in finishing lambs. *Small Ruminant Res,* 144, 126-134, 2016. DOI: 10.1016/j.smallrumres.2016.06.012