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The importance of essential fatty acids and their ratios in aquafeeds to enhance salmonid production, welfare, and human health

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Long chain polyunsaturated fatty acids (LC-PUFA), namely those from omega-3 (n-3) and omega-6 (n-6) families, are paramount for both fish and human nutrition. Some of these biomolecules cannot be synthesized *de novo* and must be acquired through the diet, being termed dietary essential fatty acids (EFA). Fish requirements for EFA have traditionally been met through the incorporation of fish oil (FO) in the formulation of aquafeeds. However, with limited supply of FO the aquaculture industry is searching for additional sustainable sources of LC-PUFA. This has significantly shifted the type of ingredients used in aquafeed formulation, namely vegetable oils (VO) deficient in long-chain omega-3, often resulting in imbalanced levels and ratios of fatty acid classes. Such imbalances can negatively affect fish performance and welfare, as well as the levels of health promoting omega-3 LC-PUFA present in fish fillets. Given the relevance that salmonid aquaculture plays in global fish production (principally Atlantic salmon, *Salmo salar*), as well as its growing role as a source of dietary health promoting omega-3 LC-PUFA for humans, the present review summarizes the scientific knowledge available to date on the dietary requirements for LC-PUFA by salmonids and humans. We discuss the implications of using imbalanced aquafeed formulations upon fish performance and welfare, as well as the subsequent consequences for human nutrition, along with current efforts to replace FO by alternative ingredients such as algal oil (AO) that can safeguard high-quality salmonid products for human consumption.

KEYWORDS

Atlantic salmon, LC-PUFA, human nutrition, omega-3, omega-6, trout

1 Introduction

Aquaculture is among the most promising industries to address human malnutrition and diet-related diseases (Naylor et al., 2021). Seafood is an important source of vital nutrients, such as structural and functional lipids rich in omega-3 (*n*-3) fatty acids (FA), some of which are vital for human health (Tocher, 2015; Oliver et al., 2020). For all species, some of these FA are termed essential fatty acids (EFA) as they cannot be synthesized *de novo* and must be acquired through diet (Calder, 2020; Sharma and Mandal, 2020; Troesch et al., 2020). Among EFA, LC-PUFA act as regulators of metabolism and immune function, being key for disease prevention (see reviews by Tocher (2003); Glencross (2009); Oliver et al. (2020)). More specifically, omega-3 LC-PUFA participate in metabolic pathways in the resolving phase of inflammation and return to homeostasis, whereas omega-6 LC-PUFA participate in metabolic pathways associated with the formation of pro-inflammatory molecules (Calder, 2013; Ortega-Gómez et al., 2013; Hundal et al., 2022; Huyben et al., 2023).

Fish are acknowledged as important sources of dietary EFA for humans (Tocher, 2015; Oliver et al., 2020). Oily fish, particularly salmonids, are a versatile and popular seafood and regarded as one of the best sources of omega-3 PUFA for humans (Nichols et al., 2014; FAO, 2020). Salmonids, namely Atlantic salmon *Salmo salar*, are undeniably one of the pillars of marine fish aquaculture and the most important aquaculture commodity traded in value since 2013 (FAO, 2022). Salmonids have a limited ability to produce omega-3 long chain PUFA (omega-3 LC-PUFA) from their precursor alpha-linolenic acid, ALA; 18:3*n*-3 (Bell et al., 1997; Tocher et al., 2019). Whilst the levels of these LC-PUFA required to sustain good fish growth are relatively low (Ruyter et al., 1999; Menoyo et al., 2007), the dietary requirements to maintain suitable fish health are somewhat higher (Bou et al., 2017; Lutfi et al., 2022); so too are the levels needed to maintain fish as good sources of LC-PUFA for humans (Nichols et al., 2014; Tocher et al., 2019). Consequently, aquafeeds must incorporate suitable and balanced levels of LC-PUFA to support fish growth and health, as well as requirements for deposition in their muscle for human food requirements (Glencross et al., 2023).

The health benefits of omega-3 LC-PUFA and the need to diversify the source of ingredients displaying high levels of these EFA to be incorporated in aquafeeds is widely accepted (Tocher, 2015). Given the global importance of salmonid aquaculture, this review aims to 1) briefly summarize the scientific knowledge available on salmonid requirements for dietary EFA; 2) document the implications that the use of imbalanced aquafeed formulations can have on human nutrition; and 3) examine the potential alternative EFA sources to FO that can be considered, targeting the production of high-quality salmonid products. An emphasis is given on how optimizing the omega-3 nutritional parameters of aquafeeds can improve fish performance and welfare, while safeguarding those qualities that consumers rely on these seafoods to supply.

2 LC-PUFA importance for fish

2.1 Metabolism and role of LC-PUFA in fish

In general, freshwater fish species can synthesize LC-PUFA from precursors, whilst marine fish have a more limited capacity to do so (Ishikawa et al., 2019; Twining et al., 2021). Salmonids are diadromous and move from freshwater to marine environments or vice versa, being able to convert ALA into omega-3 LC-PUFA, such as eicosapentaenoic acid (EPA; 20:5*n*-3) and docosahexaenoic acid (DHA; 22:6*n*-3), as well as linoleic acid (LA, 18:2*n*-6) into arachidonic acid (ARA; 20:4*n*-6). Thus, ALA and LA are key precursors of other EFA (Punia et al., 2019). Unlike most marine fish to which EPA, DHA, and ARA are considered essential because their rate of biosynthesis is either non-existent, or low and insufficient to meet physiological demands (Glencross, 2009; Castro et al., 2016), salmonids have a relatively higher ability to produce EPA and DHA from ALA (Bell et al., 1997; Tocher et al., 2019). Despite some *de novo* synthesis, the levels of omega-3 and omega-6 LC-PUFA resulting from these pathways are not high enough to meet the nutritional requirements of fish when challenged (Agaba et al., 2005; Leaver et al., 2008; Castro et al., 2012; Sprague et al., 2019); and to meet the nutritional needs of human consumers (Sanden et al., 2011; Nichols et al., 2014; Tocher et al., 2019).

In fish, LC-PUFA play key roles in cell membranes and cellular synthesis, ionic regulation and pigmentation (Tocher, 1995; Sargent et al., 2003; Tocher, 2003; Glencross, 2009; Lutfi et al., 2022). They are also required for the proper development and function of the neural system (Innis, 2007; Litz et al., 2017), having an important role in reproduction (Tocher, 2003; Glencross, 2009) and the protective intestinal barrier function (Huyben et al., 2020; Løvmo et al., 2021). LC-PUFA also control metabolic functions (e.g., being chemical messengers or effectors of secondary messengers), endocrine pathways (e.g., acting as hormone precursors), and are key for immune functions (Glencross, 2009; Huyben et al., 2023).

2.2 Dietary requirements of LC-PUFA for salmonids

Farmed fish must be provided suitable levels of dietary LC-PUFA to meet their physiological demands, welfare, and produce high-quality fillets rich in omega-3 LC-PUFA. The dietary requirements of LC-PUFA for salmonids are summarized in Supplementary Table 1. These requirements vary among species, environmental conditions, stressors, and age, and are also influenced by the absolute and relative values of these fatty acids in the total dietary lipid. For instance, omega-3 LC-PUFA requirements range from 10 to 25 g/kg of aquafeed depending on species, fish age and farming conditions (Tocher et al., 2000; Glencross, 2009; Glencross et al., 2014; Bou et al., 2017; Huyben et al., 2021; Lutfi et al., 2022).

Requirements for LC-PUFA are typically higher during the early life stages to sustain the high level of demands required during early development of the neural and visual system in the fish (Tocher, 2010). Notably, EPA and DHA are especially important for the growth and development of fry, parr, and smolt, with DHA playing a pivotal role in neural growth and development (Innis, 2007; Litz et al., 2017). When salmonids undergo smoltification and transition from life in freshwater to seawater, their FA profile changes as a pre-adaptive response to this new environment. More specifically, there is a peak in omega-3 LC-PUFA biosynthesis, with FA profiles displaying higher levels of LC-PUFA, namely EPA and DHA (Tocher et al., 2000; Bendiksen et al., 2003). These shifts affect cellular processes involved in adaptation to seawater, such as ionic regulation and synthesis of prostaglandins (Spector and Yorek, 1985; Mustafa and Srivastava, 1989).

Dietary requirements for omega-3 LC-PUFA also change with farming conditions and the health status of fish. Compared to controlled laboratory systems, fish held in cage farming environments experience seasonal shifts in salinity, temperature, and incidence of pathogens. As an example, while n-3 LC-PUFA requirements for post-smolt Atlantic salmon (~185-550 g) range between 5-8% of the total pool of FA in the laboratory (Glencross et al., 2014; Bou et al., 2017; Huyben et al., 2021), under cage farming conditions these needs may exceed 10% (Lutfi et al., 2022). Indeed, lipid metabolism and the composition of cellular membranes are modified to endure changes in seawater temperature, with lower temperatures promoting higher levels of EPA and DHA (Norambuena et al., 2016; Rosenlund et al., 2016).

2.3 Implications of LC-PUFA deficiencies and imbalanced ratios in fish

Inadequate levels of LC-PUFA in the diet of salmonids can affect fish performance, particularly feed conversion, negatively impacting growth and survival (Ruyter, 2000; Berge et al., 2009; Glencross et al., 2015; Selvam et al., 2021). Some studies also report an increased sensitivity to stressful conditions (Bell et al., 1991; Thompson et al., 1996; Huyben et al., 2023) and a decreased resistance to pathogens (Martinez-Rubio et al., 2012). Stress and pathogens are common under fish-farming conditions, being responsible for mass mortalities that cause major economic losses. Therefore, it is desirable to preventively enhance fish resistance to these challenging conditions. For instance, by adjusting LC-PUFA levels in aquafeeds it is possible to reduce the impacts of heart and skeletal muscle inflammation associated with Atlantic salmon reovirus infection, one of the most prevalent inflammatory diseases in salmon farms (Martinez-Rubio et al., 2012). More recently, high levels of LC-PUFA have also been linked with higher resistance to chronic stress (Huyben et al., 2023).

Meeting an optimal ratio between LC-PUFA omega-6 and omega-3 FA is paramount, as it modulates metabolic and immune functions (Patterson et al., 2012; Huyben et al., 2020). In Atlantic salmon, this ratio is substantially affected when provided only with the short-chain PUFA (Sprague et al., 2019). Notably, when fed a diet devoid of any LC-PUFA but including a 3:1 ratio of ALA : LA, the salmon parr endogenously synthesize their own omega-3 LC-PUFA at a ratio of 27:1 against omega-6 LC-PUFA. Even with a 1:3 ratio of ALA : LA the fish synthesize omega-3 LC-PUFA at a ratio of about 3:1. Hundal et al. (2021) suggested that increasing the dietary n-6/n-3 FA ratio in salmon feeds can affect the way they respond to stressors in an aquaculture setting, possibly affecting the fish robustness. Other studies have suggested that EPA levels ideally should be higher than those of ARA and DHA, due to its role in the anti-inflammatory response and as an antagonizing agent of ARA-derived pro-inflammatory mediators (Martinez-Rubio et al., 2012). Consequently, the EPA : DHA ratio should also be considered and ideally maintained at 1.5:1, as insufficient EPA levels negatively affects the anti-inflammatory response (Martinez-Rubio et al., 2012). However, maintaining this optimal ratio in commercial farms is a challenge, as the abundance of EPA in LC-PUFA sources is limited, and therefore few LC-PUFA sources have such an ideal ratio of EPA : DHA. Furthermore, research on the effect of an imbalanced omega-3:omega-6 ratio on Atlantic salmon health and performance are somewhat contradictory; whilst some studies show no effects, or even negative results, others report no adverse impact of higher dietary levels of omega-6 LC-PUFA on fish growth and survival (Grisdale-Helland et al., 2002; Menoyo et al., 2007; Sissener et al., 2016). These discrepancies, however, might arise from differences in the trial design or nutritional history of the animals (e.g. lipid reserves), among other study parameters.

The FA composition of fish lipids is predominantly influenced by diet (Sargent et al., 1999; Glencross et al., 2014; Xu et al., 2020; Glencross et al., 2023). Changes in the final product are well known to impact its nutritional quality for consumers; it has also been observed to result in suboptimal pigmentation (Lutfi et al., 2022) and poorer processing (smoking) qualities, features that lead to processor and retailer rejection (Johansen and Jobling, 1998; Tocher et al., 2003).

3 LC-PUFA importance for humans

3.1 Dietary requirements for LC-PUFA by humans

Based on scientific evidence available, multiple organizations (e.g., the World Health Organization, the European Food Safety Authority, or the American Heart Association) promote the regular intake of omega-3 LC-PUFA, with recommended doses of up to 250 – 500 mg/day (EFSA Panel on Dietetic Products Nutrition, 2010). Oily fishes, such as salmon, are considered one of the best dietary sources of EPA and DHA (Henriques et al., 2014; Nichols et al., 2014). However, the FA profile of salmon is modulated by the aquafeeds provided during grow-out. Due to changes in aquafeed formulations, the content of EPA and DHA present in salmon fillets halved between 2004 and 2015 (Sprague et al., 2016). This shift has resulted in the need to increase the number of salmon servings to meet human dietary requirements. More specifically, international guidelines recommend consumers to now eat at least 2 servings per week of these oily fishes to meet requirements for omega-3 LC-PUFA (EFSA Panel on Dietetic Products, Nutrition, and Allergies (NDA), 2014; Norwegian Scientific Committee for Food and Environment (VKM), 2022).

3.2 Benefits of adequate LC-PUFA intake in humans

There is growing scientific evidence highlighting the importance of LC-PUFA for humans (see reviews by Saini and Keum (2018) and Oliver et al. (2020)). The effects of LC-PUFA on human health and nutrition have been recognized since the 1970s, with the first studies evidencing the benefits of omega-3 LC-PUFA in mortality associated with cardiovascular disease (CVD) (Jump et al., 2012; Endo and Arita, 2016). Since then, the effectiveness of omega-3 LC-PUFA against CVD has further been confirmed (Bucher et al., 2002; Delgado-Lista et al., 2012). Omega-3 LC-PUFA also seem to play a role against age-related cognitive impairments, such as dementia or Alzheimer's disease (Gogus and Smith, 2010; Dangour et al., 2012). Other conditions that may be regulated by LC-PUFA include eczema, diabetes, allergy, asthma, thrombosis, macular degeneration, and some types of cancer (Gogus and Smith, 2010; Oliver et al., 2020). Benefits have also been reported when fighting inflammatory diseases, such as rheumatoid arthritis, Crohn's disease, and ulcerative colitis (Cabré et al., 2012; Miles and Calder, 2012). These health promoting features are attributed to the mechanism of action of these fatty acids on inflammatory pathways and their regulatory role in the immune system. More specifically, eicosanoids derived from ARA (e.g., prostaglandins and leukotrienes) drive inflammatory responses, whereas eicosanoids derived from EPA produce an anti-inflammatory response that antagonizes ARA-derived eicosanoids (Calder, 2007; Calder et al., 2009).

The optimal omega-6:omega-3 ratio for humans is yet to be fully understood, but it is suggested to range between 2.5-5:1 (Gogus and Smith, 2010). Current average diet of Western populations displays a much higher ratio, ranging approximately 10-25:1 (Molendi-Coste et al., 2011; Tocher et al., 2019). This ratio is distant from that of ancestral populations, which ranged at 1-4:1 (Tocher et al., 2019; Oliver et al., 2020).

Reducing the dietary intake of omega-6 PUFA may be difficult to achieve in some regions. For example, these are key nutrients in Mediterranean diets rich in olive oil, which is also rich in omega-9 but relatively poor in omega-3 (Calder et al., 2009). Consequently, increasing the intake of omega-3 LC-PUFA appears as a more feasible approach to attain a more balanced proportion between these two FA families (Tocher, 2015). This can be achieved by increasing the intake of EPA and DHA through an enhanced consumption of fish and other seafood with high levels of these fatty acids.

4 Aquafeeds as sources of LC-PUFA for aquaculture products

4.1 Traditional sources of LC-PUFA for aquafeeds

Traditionally, LC-PUFA requirements in farmed fish have been met using FO, as it features a relatively high content of omega-3 LC-PUFA and a balanced FA profile to support fish performance, welfare, and secure a high-quality final product for human consumption. However, the use of FO in aquafeeds is constrained because supply cannot keep up with demand (Delgado-Lista et al., 2012; Tocher, 2015).

Supply limitations of LC-PUFA in aquaculture were first addressed by using different VO. Whilst these oils can support fish growth, they display high levels of omega-6 PUFA and are devoid of omega-3 LC-PUFA (Tocher, 2003; Glencross, 2009). The dietary replacement of FO by VO also dilutes omega-3 content and modifies the FA profile and lipid content of fish (Bell et al., 1997; Bou et al., 2017; Hundal et al., 2022; Glencross et al., 2023). Often advocated as more sustainable ingredients for aquafeeds than FO, the production of VO also creates environmental impacts due to intensive agricultural practices impacting land use, freshwater use and biodiversity for example, which cannot be overlooked (Shepherd and Little, 2014).

4.2 Alternative sources of LC-PUFA for aquafeeds

To fill the gap between demand and supply of omega-3 LC-PUFA, the aquaculture industry has focused on the potential use of unexploited fisheries, such as krill, calanoid copepods, and mesopelagic fish (Tocher, 2015; Tocher et al., 2019). Whilst these are potentially good omega-3 sources, the harvesting of these organisms comes with technological challenges, high costs, and environmental concerns (Herbert-Read et al., 2022). Another alternative could be through the valorization of by-products resulting from fish processing industries. Indeed, by-product resources already comprise close to 50% of all fish oil produced in 2020 and 30% of all fishmeal (Glencross and Bachis, 2021).

The production of genetically modified (GM) oilseed products has also been advocated as a solution for supplying omega-3 LC-PUFA. It can be easily scalable by using the infrastructures already available to produce VO and its use in salmon diets does not negatively affect fish growth or health (Tocher et al., 2019; Napier and Betancor, 2022; Ruyter et al., 2022; Davis and Devine, 2023). GM yeast strains have also been developed for the same purpose, but these are still unlikely to produce sufficient volumes at affordable prices to meet current demands (Hatlen et al., 2012; Tocher et al., 2019),. Moreover, given the overall negative perception that GM products still have in some countries, the use of aquafeeds formulated using GM oilseed products remains less likely to be accepted by some consumers (Desaint and Varbanova, 2013; Lucht, 2015).

Of all alternatives currently being evaluated, algal oil (AO) derived from heterotrophic organisms - classified as such due the very close molecular phylogenetic relationship to microalgae and absence of a clear definition- appears to hold the greatest potential to fill the gap between demand and supply for affordable omega-3 LC-PUFA (Tocher et al., 2019; Santigosa et al., 2020; Tibbets et al., 2020; Santigosa et al., 2021). Lipid levels vary among algal species and growth conditions, but marine microalgae generally present higher concentrations of LC-PUFA, particularly EPA and DHA (Li-Beisson et al., 2019). While the development of efficient and cost-effective large-scale microalgal photoautotrophic cultivation systems is yet to be achieved (Oliver et al., 2020), heterotrophic production by fermentation under controlled conditions is already well established and can attain higher production yields (Vigani et al., 2015; Lowrey et al., 2016). Moreover, heterotrophic production delivers a higher level of lipid (Ríos et al., 2018) at lower production costs (Muller-Feuga, 2013).

Overall, it is expected that novel sources of omega-3 LC-PUFA will become available in greater volume and at a cost that enables their greater use in aquafeed to restore EPA and DHA levels and to safeguard the performance, health and welfare of farmed fish as well as delivering high quality seafood products for human consumption (Turchini et al., 2022).

5 Guidelines for future research

Current commercial aquafeed formulations for salmonids are generally designed to meet the minimum requirements of EPA and DHA (Lutfi et al., 2022). However, although these low levels can support fish growth, there have been numerous incidences where levels this low have negatively impacted fish health and welfare, robustness, and nutritional value of the final product. It is therefore critical to re-evaluate the benefits of increasing EPA and DHA levels in salmonid diets, restoring nutritional qualities back to those levels seen before FO became a limiting ingredient. Additionally, requirements for LC-PUFA need to be further considered under non-ideal farming conditions, such as higher thermal regimes, hypoxia and/or infections (Huyben et al., 2021; Huyben et al., 2023).

Author contributions

IC, BG and ES equally contributed to the design of the project and to the writing and commenting of the manuscript. All authors contributed to the article and approved the submitted version.

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Conflict of interest

Author IC was employed by company Veramaris V.O.F.

The remaining authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

Supplementary material

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