



Fish-Oil Finishing Diets: A strategy to recover long-chain polyunsaturated fatty acids in Fish previously fed alternative dietary lipids

Baweja Sonu*

*Assistant Professor (Zoology) RIMT University, Mandi Gobindgarh, Punjab,
Email: drsbaweja@gmail.com

Manuscript details:

Received : 15.03.2018
Accepted : 21.04.2018
Published : 26.04.2018

Editor: Dr. Arvind Chavhan

Cite this article as:

Baweja Sonu (2018) Fish-Oil Finishing Diets: A strategy to recover long-chain polyunsaturated fatty acids in Fish previously fed alternative dietary lipids, *Int. J. of Life Sciences*, Volume 6(2): 466-472.

Copyright: © Author, This is an open access article under the terms of the Creative Commons Attribution-Non-Commercial - No Derives License, which permits use and distribution in any medium, provided the original work is properly cited, the use is non-commercial and no modifications or adaptations are made.

Available online on
<http://www.ijlsci.in>
ISSN: 2320-964X (Online)
ISSN: 2320-7817 (Print)

ABSTRACT

The global aquaculture industry is one of the fastest growing food production sectors, playing an important role in fulfilling the seafood demand of a growing human population. Marine fish oils have been widely used as the main lipid source in feeds for farmed fish being a good and only reliable source of n-3 highly unsaturated fatty acids (n-3 HUFAs). Although the fish oil production has remained static, the demand for fish oil is increasing over recent years. Thus the current trend is finding the suitable alternatives to fish oils in aquafeeds, without compromising overall growth performance and final nutritional quality of farmed fish. The terrestrial alternative lipids (vegetable oils and animal fats) are the poor sources of n-3 HUFAs. The flesh of farmed fish raised on feeds containing alternative lipids may contain limited amount of n-3 HUFAs. One way to reduce to the use of declining fish oil resources in aquafeeds and to improve the nutritional quality (in terms of n-3 HUFAs) of farmed fish fed on alternative lipids, may be to use finishing feeds containing fish oil before harvesting. This review attempts to compile all principal information available regarding the efficacy of finishing feeding strategy in aquaculture.

Keywords: Fish oil, Alternative lipids, Finishing feeds, n-3 HUFAs

INTRODUCTION

Since the late 1980s, with capture fishery production relatively static, aquaculture has been responsible for the impressive growth in the supply of fish for human consumption (SOFIA, 2016). During the last 25 years, aquaculture production grew by up to 8.5% annually (FAO, 2012) and currently covers roughly half the global demand for fish and fish products for human consumption. The rapidly increasing aquaculture industry has been fuelled by the subsequent use of manufactured aqua feeds. Conventionally, fish oil (FO) is one of the key biological sources of feeding components for aquaculture.

FO-enriched feeds used in aquaculture currently accounts for up to 87% of the global supply of FO as a lipid source (Tacon et. al., 2006). Thus, the challenge for fish nutritionists is to reduce the utilization of fish oil in aqua feed formulations with readily available and more economical terrestrial alternatives (Turchini et. al., 2009). In comparison with terrestrial alternatives (vegetable oils and animal fats), fish oils used in aquaculture feeds are highly enriched in beneficial omega-3 polyunsaturated fatty acids (n-3 PUFA). In particular, dietary long-chain (C20–22) LC-PUFA such as eicosapentaenoic (EPA; 20:5n-3), docosahexaenoic (DHA; 22:6n-3) and arachidonic (ARA; 20:4n-6) acids are required by fish to support somatic growth and survival (Harel et. al., 2001; Copeman et. al., 2002; Trenzado et. al., 2008), stress resistance (Bell et. al., 1998) and successful ontogeny (Mourete et. al., 1991; Villalta et. al., 2005; Benitez-Santana et. al., 2007). However, the terrestrial alternatives to fish oil are characterized by a wide range of fatty acid compositions and are notably lacking in meaningful concentration of LC-PUFA (Turchini et. al., 2010). Thus, the substitution of fish oil with any alternative source results in a reflection of the dietary fatty acid composition in fish flesh, a potentially undesirable trait from n-3 LC-PUFA consumption viewpoint (Rosenlund et. al., 2010).

As a consequence of this, there is an interest to combat fatty acid modification of farmed fish. The most common approach has been the potential implementation of a finishing period on a FO-based diet (wash-out or finishing diet) to modify the final fatty acid make-up of fish previously reared on diets containing alternative dietary lipids (Jobling, 2004; Turchini et. al., 2006). However, the initial concentration of fat in the tissue in question directly affects the time required for the fatty acid composition of a tissue to be influenced by a dietary change. The main results of this research are reported and discussed in the present review.

Alternative dietary lipid sources

Marine fish oils have been widely used as the main lipid source in feeds for farmed fish because they have been a good source of the n-3 HUFAs. The demand for fish oils has increased over recent years although production has remained static, and the current trend is towards the complete or partial replacement of fish oils by alternative lipid sources such as vegetable oils and animal fats in feeds for farmed fish which are characterized by the wide fatty acid compositions (Table1). The common vegetable oils used as alternative

lipids in the feeds of farmed fish species include palm oil, soybean oil, canola oil, sunflower oil, cottonseed oil, groundnut oil, coconut oil, olive oil, corn oil, sesame oil, linseed oil etc, has been studied in many fish species such as rainbow trout (Trushenski et. al., 2011a; Masiha et. al., 2013, Twibell et. al., 2011; Guler and Yildiz, 2011; Brown et. al., 2010; Yildiz et. al., 2013), brown trout (Arslan et. al., 2012), cobia (Trushenski et. al., 2011b), pike perch (Kowalska et. al., 2010), *Huso huso* (Hosseini et. al., 2010), *Litopenaeus vannamei* (Gonzalez-Felix et. al., 2010), Caspian great sturgeon (Hassankiadeh et. al., 2013), African catfish (Bababola et. al., 2011), Japanese seabass (Xue et. al., 2006), etc. Most vegetable oils are rich in unsaturated 18C fatty acids viz. oleic acid (18:1n-9), linoleic acid (18:2 n-6), alpha-linolenic acid (18:3 n-3) but are poor sources of n-3 HUFAs, so the flesh of farmed fish given feeds containing high concentrations of vegetable oils may contain a limited amount of n-3 HUFAs. The terrestrial animal lipid sources used in the feeds of farmed fish are processing by-products, such as lard (rendered fat from pigs), poultry fat, goat fat, tallow (TAL from cattle and sheep), which has been studied in many fish species such as Brown trout (Turchini et. al., 2003), Japanese sea bass (Xue et. al., 2006), Grass carp (Zhen-Yu et. al., 2006), catfish (Bababola et. al., 2011), Rainbow trout (Liu et. al., 2004; Bayraktar and Bayir, 2012), common carp (Baweja and Babbar, 2015) etc. In general, animal fats contain high levels of SFA, ranging from 28.5% in poultry fat to 47.5% in beef TAL. Together with the high levels of MUFA, animal fats are good sources of dietary energy for fish. Although VO are completely lacking in n-3 HUFA, animal fats are reported to contain these fatty acids (Moretti & Corino, 2008). In particular, there are several studies in which the presence of eicosapentaenoic acid, 20:5 n-3 (EPA) and docosahexaenoic acid, 22:6 n-3 (DHA) in the lipid fraction of swine, bovine and poultry derived products have been reported. However, the n-3 HUFA content of animal fat is extremely limited, commonly reported only at trace level, and hence these lipid sources can be considered lacking in n-3 HUFA. In general, research reports that animal fats when incorporated at no more than 50% of the dietary lipid level have no negative effects on fish growth performance as long as the EFA requirements are met (Turchini et. al., 2003; Bureau & Gibson, 2004).

However, PUFA conversions are known to occur in a variety of freshwater fish species. In general, both desaturases and elongases are activated in fish fed a diet (vegetable oils or animal fats) containing 18-carbon

Table 1: Fatty acid composition (% total fatty acids) of fish oils, vegetable oils and animal fats used in aqua feed formulations

Oils/fats	SFA	MUFA	LA	ALA	EPA	DHA	n-6 PUFA	n-3 PUFA	n-3/n-6 ratio
Fish oils									
Anchovy oil	28.8	24.9	1.2	0.8	17.0	8.8	1.3	31.2	24.0
Capelin oil	20.0	61.7	1.7	0.4	4.6	3.0	1.8	12.2	6.8
Menhaden oil	30.5	24.8	1.3	0.3	11.0	9.1	1.5	25.1	16.7
Herring oil	20.0	56.4	1.1	0.6	8.4	4.9	1.4	17.8	12.7
Cod liver oil	19.4	46.0	1.4	0.6	11.2	12.6	3.0	27.0	9.0
Vegetable oils									
Crude palm oil	48.8	37.0	9.1	0.2	-	-	9.1	0.2	0.0
Soybean oil	14.2	23.2	51.0	6.8	-	-	51.0	6.8	0.1
Canola oil	4.6	62.3	20.2	12.0	-	-	20.2	12.0	0.6
Sunflower oil	10.4	19.5	65.7	-	-	-	65.7	0.0	0.0
Cottonseed oil	45.3	17.8	51.5	0.2	-	-	51.5	0.2	0.0
Groundnut oil	11.8	46.2	32.0	-	-	-	32.0	0.0	0.0
Corn oil	12.7	24.2	58.0	0.7	-	-	58.0	0.7	0.0
Linseed oil	9.4	20.2	12.7	53.3	-	-	12.7	53.3	4.2
Animal fats									
Pork lard	38.6	44.0	10.2	1.0	-	-	10.2	1.0	0.1
Poultry fat	28.5	43.1	19.5	1.0	-	-	19.5	1.0	0.0
Beef tallow	47.5	40.5	3.1	0.6	-	-	3.1	0.6	0.2

Data compiled from National Research Council, 1993; Gunstone et al., 1994; Hertrampf and Piedad-Pascual, 2000
ALA, a-linolenic acid, 18:3 n-3; DHA, docosahexaenoic acid, 22:6 n-3; EPA, eicosapentaenoic acid, 20:5 n-3; LA, linoleic acid, 18:2 n-6; MUFA, monounsaturated fatty acids; PUFA, polyunsaturated fatty acids; SFA, saturated fatty acids.

fatty acids (18:3n-3, 18:2n-6) in comparison with fish fed a diet (fish oil) containing HUFA (Tocher et al., 2001; Leaver et al., 2008).

The first step in the fatty acid elongation and desaturation pathway is the production of stearidonic acid (18:4 n-3) from alpha-linolenic acid (18:3 n-3) catalyzed by the D6 desaturase enzyme. The product can then be successively elongated by fatty acid elongase and further desaturated by the D5 desaturase enzyme to EPA (20:5 n-3) (Sargent et al., 2002; Nakamura & Nara, 2004). The eventual production of DHA (22:6 n-3) requires the combination of two further elongations, a D6 desaturation and, finally, a chain-shortening reaction (Sprecher et al., 1995). The fatty acid desaturation and elongation pathway has been extensively studied in fish at both the molecular and enzymatic levels (Tocher et al., 2003, 2006; Bell et al., 2001; Hastings et al., 2004; Agaba et al., 2004; Zheng et al., 2004, 2005; Oxley et al., 2005). However, for many freshwater fish species, the conversion of C18 PUFA to long-chain PUFA seems to occur at a very slow rate (Tocher et al., 2006) because

of limiting delta-6 and delta-5 desaturation steps (Buzzi et al., 1997; Tocher et al., 2006; Vagner and Santigosa, 2011).

Finishing Feeding Strategy

The principal drawback of fish oil replacement is the resultant influence on fillet fatty acid composition (Sargent et al., 2002; Turchini et al., 2003; Seierstad et al., 2005). One way to boost the n-3 HUFA concentration of farmed fish could be to use 'finishing' feeds (wash-out diets) containing fish oil to modify the final fatty acid composition of fish previously reared on diets containing alternative lipid sources so that fatty acid composition of the fish flesh could thus be altered to meet the consumer expectation of a product that is rich in n-3 HUFAs (e.g. Jobling et al., 2002; Bell et al., 2003; Glencross et al., 2003; Robin et al., 2003). Although switching back to a FO-based finishing feed will restore tissue LC-PUFA levels (Lane et al., 2006; Turchini et al., 2006; Jobling et al., 2008; Benedito-Palos et al., 2009; Fountoulaki et al., 2009), the restoration rate and magnitude of fillet fatty acid profile vary with the

composition of the grow-out feed used. Such a finishing diet strategy has been suggested and developed for various fish species, including medium fatty fish species such as turbot (*Psetta maxima*) (Robin et. al., 2003), fatty fish such as Atlantic salmon (*Salmo salar*) (Jobling, 2003; 2004) and lean fish species such as Atlantic cod (*Gadus morhua*) (Jobling et. al., 2008) and Murray cod (*Maccullochella peelii peelii*) (Turchini et. al., 2006).

Bell et. al., 2003 suggested that Atlantic salmon can be raised on diets in which FO is replaced with different blends of vegetable oils and fish oil for the entire seawater culture phase, without apparent detriment to fish growth and health. However, for fish in which vegetable oil replaced >66% of the added dietary oil, considerable reductions of flesh concentrations of both 20:5(n-3) and 22:6(n-3) occurred. Returning fish previously fed 100% vegetable oils to a marine fish oil diet for a period before harvest allowed flesh (n-3) HUFA concentrations to be restored to 80% of values in fish fed FO throughout the seawater phase although 18:2(n-6) remained significantly higher. Restoration of the fatty acid composition of red seabream (*Pagrus auratus*) using a fish oil finishing diet after grow-out on plant oil based diets was reported by Glencross et. al., 2003. The results of this study, particularly the increases in LC-PUFA, supported the usefulness of a fish oil based finisher diet for fish raised predominantly on plant oil based diets. Izquierdo et. al., 2005 also suggested that it is possible to substitute up to 60% fish oil by vegetable oils in diets for gilthead seabream without affecting growth and feed utilization even for a long feeding period. Muscle DHA and ARA contents are reduced but recovered after 60 days of feeding a fish oil diet, whereas EPA muscle contents are not only reduced in a higher extent but are not recovered after 90 days of feeding fish oil. Whereas, Fountoulaki et. al., 2009, concluded that re-feeding gilthead sea bream previously fed vegetable oil based diets with a fish oil finishing diet for 120 days was not adequate for restoration of DHA, ARA and EPA. Baweja and Babbar, 2016 suggested that inducing a dietary shift from terrestrial oil (vegetable oil or animal fat) based feeds to fish oil based feeds supplied as finishing diet before harvesting strongly increases long chain PUFA concentration in common carp as compared to those fed only terrestrial oil based feeds throughout the rearing period. Similarly, Maraz et. al., 2012 and Schultz et. al., 2014 also suggested finishing feeding strategy for production of common carp with a required flesh FA composition for purposes

of special nutritional needs. Yildiz et. al., 2017 documented recovery of fatty acid (n-3 HUFA) in rainbow trout initially fed vegetable oils was slow and requires more than 12 weeks of re-feeding with FO diet for complete restoration. Suomela et. al., 2017 examined that after receiving a vegetable oil-rich diet, restorative fish oil-rich feeding in the last stages of growth in European whitefish is nutritionally justified in order to balance nutritional gain for consumers with sustainable use of finite marine oils. Various studies have suggested that fish are unable to accumulate excessive amounts of SFA or MUFA. However, they seem to be able to accumulate significantly higher amounts of C18 PUFA which considerably affects the overall fatty acid composition (Torstensen et. al., 2004; Turchini et. al., 2003, 2006; Mourente et. al., 2005; Francis et. al., 2006). On the other hand, the general C18 PUFA elongase and desaturase capability in fish, even if stimulated by the use of vegetable oils, seems ineffective in compensating the exhausted HUFA intake in fish fed alternative lipid sources (Tocher et. al., 2003; Zheng et. al., 2004; Stubhaug et. al., 2005; Turchini et. al., 2006). Thus the use of alternative vegetable lipid sources characterized by a high content of SFA, i.e. palm oil, or MUFA, i.e. olive oil, or a blend of these oils is preferential in comparison with vegetable oils rich in C18 PUFA such as sunflower and linseed oils. The efficacy of a finishing period with a FO-based diet after a grow-out period during which fish have been fed with diets containing alternative lipid sources has been largely tested in Atlantic salmon (Bell et. al., 2003, 2004; Torstensen et. al., 2004), in temperate marine fish species (i.e. gilthead seabream, European sea bass and red seabream) (Glencross et. al., 2003; Izquierdo et. al., 2005; Montero et. al., 2005) and in warm water, fresh water species such as Murray cod and sunshine bass (Lane et. al., 2006; Turchini et. al., 2006, 2007). In all instances, the fatty acid make-up of fish can return to within the normal variability of fish continuously fed a FO-based diet after a period of several weeks. Consequently, fish fed diets with lower concentrations of dietary C18 PUFA will be able to restore the original fatty acid composition of the fish fillets more effectively (Turchini et. al., 2007). Thus, the results so far have been promising and adoption of finishing feed strategy for commercial applications has been proposed.

CONCLUSION

The review studied so far suggest that by using a mixed feeding strategy, the farmed fish can be started on feeds

containing high concentrations of alternative lipids low in n-3 HUFAs and then given 'finishing feeds' containing high concentrations of marine fish oils high in n-3 HUFAs, improve the final fatty acid make-up of fish previously fed with alternative lipid sources. Thus, restoration of an optimal fatty acid profile with a finishing diet following an alternative lipid grow-out diet, expected to result in a more rational utilization of aquaculture's still highly dependent limited resource of fish oils.

Conflicts of interest: The authors stated that no conflicts of interest.

REFERENCES

- Agaba M, Tocher DR, Dickson C, Dick JR and Teale AJ (2004) A zebrafish cDNA encoding a multifunctional enzyme involved in the elongation of polyunsaturated, monounsaturated and saturated fatty acids. *Marine Biotechnology* 6: 251-261.
- Arslan M, Sirkecioglu N, Bayir A, Arslan H and Aras M (2012) The influence of substitution of dietary fish oil with different vegetable oils on performance and fatty acid composition of brown trout, *Salmo trutta*. *Turk. J. Fish. Aquatic Sci.* 12: 575-583.
- Bababola TO, Apata DF, Omotosho JS and Adebayo MA (2011) Differential effects of dietary lipids on growth performance, digestibility, fatty acid composition and histology of African catfish (*Heterobranchus longifilis*) fingerlings. *Food Nutr. Sci.* 2, 11-21.
- Baweja S and Babbar BK (2015) Growth performance and tissue fatty acid composition of *Cyprinus carpio* (Linn.) reared on feeds containing animal fats as fish oil replacement. *The Bioscan* 10: 655-660.
- Baweja S and Babbar BK (2016) Restoration of fatty acid composition of common carp *Cyprinus carpio* (Linnaeus, 1758) fed terrestrial oil based diets using fish oil finishing diet. *Indian Journal of Fisheries* 63: 49-56.
- Bayraktar K and Bayir A (2012) The effect of the replacement of fish oil with animal Fats on the growth performance, survival and fatty acid profile of rainbow trout juveniles, *Oncorhynchus mykiss*. *Turk. J. Fish. Aquat. Sc.* 12: 661-666.
- Bell JG, Henderson RJ, Tocher DR and Sargent JR (2004) Replacement of dietary fish oil with increasing levels of linseed oil: modification of flesh fatty acid compositions in Atlantic salmon (*Salmo salar*) using a fish oil finishing diet. *Lipids* 39:223-32.
- Bell JG, McEvoy J, Tocher DR, McGhee F, Campbell PJ and Sargent JR (2001) Replacement of fish oil with rapeseed oil in diets of Atlantic salmon (*Salmo salar*) affects tissue lipid composition and hepatocyte fatty acid metabolism. *J. Nutr.* 131:1535-43.
- Bell JG, Tocher DR, Farnsdale BM and Sargent JR (1998) Growth, mortality, tissue histopathology and fatty acid compositions, eicosanoid production and response to stress, in juvenile turbot fed diets rich in [γ]-linolenic acid in combination with eicosapentaenoic
- Bell JG, Tocher DR, Henderson RJ, Dick JR and Crampton VO (2003) Altered fatty acid compositions in Atlantic salmon (*Salmo salar*) fed diets containing linseed and rapeseed oils can be partially restored by a subsequent fish oil finishing diet. *The Journal of Nutrition* 133: 2793-2801.
- Benedito-Palos L, Navarro JC, Bermejo-Nogales A, Saera-Vila A, Kaushik S and Perez-Sanchez J (2009) The time course of fish oil wash-out follows a simple dilution model in gilthead sea bream (*Sparus aurata* L.) fed graded levels of vegetable oils. *Aquaculture* 288: 98-105.
- Benitez-Santana T, Masuda R, Carrillo EJ, Ganuza E, Valencia A, Hernandez-Cruz CM and Izquierdo MS (2007) Dietary n-3 HUFA deficiency induces a reduced visual response in gilthead seabream *Sparus aurata* larvae. *Aquaculture* 264: 408-417.
- Brown TD, Francis DS and Turchini DM (2010) Can Dietary Lipid Source Circadian Alternation Improve omega-3 Deposition in Rainbow Trout? *Aquaculture* 300: 148-155.
- Bureau D and Gibson J (2004) Animal fats as aquaculture feed ingredients: nutritive value, product quality and safety. *Aquafeed International* 7: 32-37.
- Copeman LA, Parrish CC, Brown JA and Harel M (2002) Effects of docosahexaenoic, eicosapentaenoic, and arachidonic acids on the early growth, survival, lipid composition and pigmentation of yellowtail flounder (*Limanda ferruginea*): a live food enrichment experiment. *Aquaculture* 210: 285-304.
- FAO (Food and Agriculture Organization of the United Nations) (2012) State of World Aquaculture 2006. FAO Fisheries Technical Paper No. 500. FAO Fisheries Department; Food and Agriculture Organization of the United Nations, Rome. FAO Fisheries Department, Food and Agriculture Organization of the United Nations, Rome.
- Fountoulaki E, Vasilaki A, Hurtado R, Grigorakis K, Karacostas I, Zengas I, Rigos G, Kotzamanis Y, Venou B, and Alexis MN (2009) Fish oil substitution by vegetable oils in commercial diets for gilthead sea bream (*Sparus aurata* L.): effects on growth performance, flesh quality, and fillet fatty acid profile; recovery of fatty acid profiles by a fish oil finishing diet under fluctuating water temperatures. *Aquaculture* 289:317-326.
- Francis DS, Turchini GM, Jones PL and De Silva SS (2006) Effects of dietary oil source on growth and fillet fatty acid composition of Murray cod, *Maccullochella peelii*. *Aquaculture* 253: 547-56.
- Glencross BD, Hawkins WE and Curnow JG (2003) Restoration of the fatty acid composition of red seabream (*Pagrus auratus*) using a fish oil finishing diet after grow-out on plant oil based diets. *Aquacult Nutr* 9: 409-418.
- Gonzalez-Felix ML, Silva FSD, Davis DA, Samocha TM, Morris TC, Wilkenfeld JS and Perez-Velazquez M (2010) Replacement of fish oil in plant based diets for Pacific white shrimp (*Litopenaeus vannamei*). *Aquaculture* 309: 152-158.
- Guler M and Yildiz M (2011) Effects of dietary fish oil replacement by cottonseed oil on growth performance and fatty acid composition of rainbow trout (*Oncorhynchus mykiss*). *Turk. J. Vet. Anim. Sci.* 35: 157-67.
- Gunstone FD, Harwood JL and Padley FB (1994) *The Lipid Handbook*. The University Press, Cambridge.
- Harel M, Gavasso S, Leshin J, Gubernatis A and Place AR (2001) The effect of tissue docosahexaenoic and arachidonic acids levels on hypersaline tolerance and leucocyte composition

- in striped bass (*Morone saxatilis*) larvae. *Fish Physiology and Biochemistry* 24: 113–123.
- Hassankiadeh MN, Khara H, Sadati MAY and Parandavar H (2013) Effects of dietary fish oil substitution with mixed vegetable oils on growth and fillet fatty acid composition of juvenile Caspian great sturgeon (*Huso huso*). *Aquacult. Int.* 21: 143–55.
- Hastings N, Agaba MK, Tocher DR, Zheng X, Dickson CA and Dick JR (2004) Molecular cloning and functional characterization of fatty acyl desaturase and elongase cDNAs involved in the production of eicosapentaenoic and docosahexaenoic acids from alpha-linolenic acid in Atlantic salmon (*Salmo salar*). *Marine Biotechnology* 6: 463–474.
- Hertrampf JW and Piedad-Pascual F (2000) *Handbook on Ingredients for Aquaculture Feeds*. Kluwer Academic Publishers, Dordrecht.
- Hosseini SV, Abedian-Kenari A, Rezaei M, Nazari MR, Feas X and Rabbani M (2010) Influence of the in vivo addition of alpha-tocopheryl acetate with three lipid sources on the lipid oxidation and fatty acid composition of Beluga sturgeon, *Huso huso*, during frozen storage. *Food Chem.* 118: 341–48.
- Izquierdo MS, Robaina L, Caballero MJ, Rosenlund G and Gines R (2005) Alterations in fillet fatty acid profile and flesh quality in gilthead seabream (*Sparus aurata*) fed vegetable oils for a long term period. Recovery of fatty acid profiles by fish oil feeding. *Aquaculture* 250: 431–444.
- Jobling M (2003) Do changes in Atlantic salmon, *Salmo salar* L., fillet fatty acids following a dietary switch represent wash-out or dilution? Test of a dilution model and its application *Aquaculture Research* 34: 1215–1221.
- Jobling M (2004) Are modifications in tissue fatty acid profiles following a change in diet the result of dilution? Test of a simple dilution model. *Aquaculture* 232: 551–562.
- Jobling M, Larsen AV, Andreassen B and Olsen RE (2002) Adiposity and growth of post-smolt Atlantic salmon *Salmo salar* L. *Aquaculture* 33: 533–541.
- Jobling M, Leknes O, Saether BS and Bendiksen EA (2008) Lipid and fatty acid dynamics in Atlantic cod, *Gadus morhua*, tissues: Influence of dietary lipid concentrations and feed oil sources. *Aquaculture* 281: 87–94.
- Kowalska A, Zakes Z, Jankowska B and Siwicki A (2010) Impact of diets with vegetable oils on the growth, histological structure of internal organs, biochemical blood parameters, and proximate composition of pikeperch, *Sander lucioperca* (L.). *Aquaculture* 301: 69–77.
- Lane RL, Trushenski JT and Kohler CC (2006) Modification of fillet composition and evidence of differential fatty acid turnover in sunshine bass *Morone chrysops* x *M. saxatilis* following change in dietary lipid source. *Lipids* 41: 1029–1038.
- Leaver M, Villeneuve L, Obach A, Jensen L, Bron J, Tocher D and Taggart J (2008) Functional genomics reveals increases in cholesterol biosynthetic genes and highly unsaturated fatty acid biosynthesis after dietary substitution of fish oil with vegetable oils in Atlantic salmon (*Salmo salar*). *BMC Genomics* 9: 299.
- Liu KKM, Barrows FT, Hardy RW and Dong FM (2004) Body composition, growth performance, and product quality of rainbow trout (*Oncorhynchus mykiss*) fed diets containing poultry fat, soybean/corn lecithin, or menhaden oil. *Aquaculture* 238: 309–328.
- Maraz J, Zajic T and Pickova J (2012) Culture of common carp (*Cyprinus carpio*) with defined flesh quality for prevention of cardiovascular diseases using finishing feeding strategy. *Neuroendocrinol. Lett.* 33: 60–67.
- Masiha A, Ebrahimi E, Soofiani N M and Kadivar M (2013) Effect of Dietary Vegetable Oils on the Growth Performance and Fatty Acid Composition of Fingerlings of Rainbow Trout, *Oncorhynchus mykiss*. *Food Sci. Technol.* 1: 21–29.
- Montero D, Robaina L, Caballero R and Izquierdo MS (2005) Growth, feed utilization and flesh quality of European sea bass (*Dicentrarchus labrax*) fed diets containing vegetable oils: a time-course study on the effect of a re-feeding period with a 100% fish oil diet. *Aquaculture* 248: 121–134.
- Moretti VM and Corino C (2008) Omega-3 and trans fatty acids. In: Nolle LML, Toldra F (eds) *Handbook of Processed Meats and Poultry Analysis*, CRC Press, Crystal Bay, pp: 233–271.
- Mourente G, Dick JR, Bell JG and Tocher DR (2005) Effect of partial substitution of dietary fish oil by vegetable oils on desaturation and β -oxidation of [1-¹⁴C]18:3n-3 (LNA) and [1-¹⁴C] 20:5n-3 (EPA) in hepatocytes and enterocytes of European sea bass (*Dicentrarchus labrax* L.). *Aquaculture* 248: 173–186.
- Mourente G, Tocher DR and Sargent JR (1991) Specific accumulation of docosahexaenoic acid (22-6n-3) in brain lipids during development of juvenile turbot *Scophthalmus maximus* L. *Lipids* 26, 871–877.
- Nakamura MT and Nara TY (2004) Structure, function, and dietary regulation of delta-6, delta-5, and delta-9 desaturases. *Annual Review of Nutrition* 24: 345–376.
- National Research Council (1993) *Nutrient Requirements of Fish*. National Research Council, National Academy Press, Washington.
- Oxley A, Torstensen BE, Rustan AC and Olsen RE (2005) Enzyme activities of intestinal triacylglycerol and phosphatidylcholine biosynthesis in Atlantic salmon (*Salmo salar* L.). *Comparative Biochemistry and Physiology B* 141: 77–87.
- Robin JH, Regost C, Arzel J and Kaushik SJ (2003) Fatty acid profile of fish following a change in dietary fatty acid source: model of fatty acid composition with a dilution hypothesis. *Aquaculture* 225: 283–293.
- Rosenlund G, Corraze G, Izquierdo M and Torstensen BE (2010) The effects of fish oil replacement on nutritional and organoleptic qualities of farmed fish. In: Turchini GM, Ng WK, Tocher DR (Eds.), *Fish Oil Replacement and Alternative Lipid Sources in Aquaculture Feeds*. CRC Press, Taylor & Francis group, Boca Raton, FL, USA, pp: 487–522.
- Sargent JR, Tocher DR and Bell JG (2002) The lipids. In: Halver JE, Hardy RW, editors. *Fish nutrition*, 3rd ed. San Diego: Academic Press, pp: 181–257.
- Schultz S, Koussoroplis AM, Changizi-Magrhoor Z, Watzke J and Kainz M (2014) Fish oil-based finishing diets strongly increase long-chain polyunsaturated fatty acid concentrations in farm-raised common carp (*Cyprinus carpio* L.). *Aquac. Res.*: 1–11.
- Seierstad SL, Poppe TT, Koppang EO, Svindland A, Rosenlund G and Froyland L (2005) Influence of dietary lipid composition on cardiac pathology in farmed Atlantic salmon, *Salmo salar*. *Journal of Fish Diseases* 28: 677–690.

- SOFIA (2016) The State of World Fisheries and Aquaculture [online] Available from: <http://www.fao.org/documents/card/en/c/2c8bcf47-2214-4aeb-95b0-62ddef8a982a>
- Sprecher H, Luthria DL, Mohammed BS and Baykousheva SP (1995) Reevaluation of the pathways for the biosynthesis of polyunsaturated fatty acids. *The Journal of Lipid Research* 36: 2471–2477.
- Stubhaug I, Frøyland L and Torstensen BE (2005) β -oxidation capacity of red and white muscle and liver in Atlantic salmon (*Salmo salar* L.) – effects of increasing dietary rapeseed oil and olive oil to replace capelin oil. *Lipids* 40: 39–47.
- Suomela JP, Tarvainen M, Kallio H and Airaksinen S (2017) Fish Oil Finishing Diet Maintains Optimal n-3 Long-Chain Fatty Acid Content in European Whitefish (*Coregonus lavaretus*). *Lipids* 52(10):849-855.
- Tacon AGJ, Hasan MR and Subasinghe RP (2006) Use of fishery resources as feed inputs to aquaculture development: trends and policy implications. *FAO Fisheries Circular No.* 1018.
- Tocher DR (2003) Metabolism and functions of lipids and fatty acids in teleost fish. *Reviews in Fisheries Science* 11: 107–184.
- Tocher DR, Bell JG, MacGlaughlin P, McGhee F and Dick JR (2001) Hepatocyte fatty acid desaturation and polyunsaturated fatty acid composition of liver in salmonids: effects of dietary vegetable oil. *Comparative Biochemistry and Physiology B* 130: 257–270.
- Tocher DR, Zheng X, Schlechtriem C, Hastings N, Dick JR and Teale AJ (2006) Highly unsaturated fatty acid synthesis in marine fish: cloning, functional characterization, and nutritional regulation of fatty acyl delta 6 desaturase of Atlantic cod (*Gadus morhua* L.). *Lipids* 41: 1003–1016.
- Torstensen BE and Stubhaug I (2004) Beta-oxidation of 18:3n-3 in Atlantic salmon (*Salmo salar* L.) hepatocytes treated with different fatty acids. *Lipids* 39: 1–8.
- Trenzado CE, Morales AE and de la Higuera M (2008) Physiological changes in rainbow trout held under crowded conditions and fed diets with different levels of vitamins E and C and highly unsaturated fatty acids (HUFA). *Aquaculture* 277: 293–302.
- Trushenski JT, Blaufuss P, Mulligan B and Laporte J (2011a) Growth performance and tissue fatty acid composition of rainbow trout reared on feeds containing fish oil or equal blends of fish oil and traditional or novel alternative lipids. *N. Am. J. Aquacult.* 73: 194–203.
- Trushenski JT, Gause B and Lewis HA (2011b) Selective fatty acid metabolism, not the sequence of dietary fish oil intake, prevails in fillet fatty acid profile change in sunshine bass. *N. Am. J. Aquacult.* 73: 204–211.
- Turchini G M, Torstensen B E and Ng W (2009) Fish oil replacement in finfish nutrition. *Reviews in Aquaculture* 1: 10–57.
- Turchini GM, Mentasti T, Froyland L, Orban E, Caprin F, Moretti VM and Valfre F (2003) Effects of alternative dietary lipid sources on performance, tissue chemical composition, mitochondrial fatty acid oxidation capabilities and sensory characteristics in brown trout (*Salmo trutta* L.). *Aquaculture* 225: 251–267.
- Turchini GM, Francis DS and De Silva SS (2006) Modification of tissue fatty acid composition in Murray cod (*Maccullochella peelii peelii*, Mitchell) resulting from a shift from vegetable
- Turchini GM, Francis DS and De Silva SS (2007) Finishing diets stimulate compensatory growth: results of a study on Murray cod, *Maccullochella peelii peelii*. *Aquaculture Nutrition*
- Turchini GM, Ng WK and Tocher DR (2010) *Fish Oil Replacement and Alternative Lipid Sources in Aquaculture Feeds*. CRC Press, Taylor and Francis Group, Boca Raton, FL, USA. 551 pp.
- Twibell R G, Gannam A L, Ostrand S L, Holmes J S A and Poole J B (2011) Altered growth rates, carcass fatty acid concentrations, and tissue histology in first-feeding steelhead fed a fish-meal- and fish-oil-free diet. *N. Am. J. Aquacult.* 73(0): 230-238.
- Vagner M and Santigosa E (2011) Characterization and modulation of gene expression and enzymatic activity of delta-6 desaturase in teleosts: a review. *Aquaculture* 315: 131–143.
- Villalta M, Estevez A, Bransden MP and Bell JG (2005) The effect of graded concentrations of dietary DHA on growth, survival and tissue fatty acid profile of Senegal sole (*Solea senegalensis*) larvae during the *Artemia* feeding period. *Aquaculture* 249, 353–365.
- Xue M, Luo L, Wu X, Ren Z, Gao P, Yu Y and Pearl G (2006) Effects of six alternative lipid sources on growth and tissue fatty acid composition in Japanese sea bass (*Lateolabrax japonicus*). *Aquaculture* 260: 206–214.
- Yildiz M, Erolodogan OT, Engin K, Gulcubuk A and Baltaci MA (2013) Effects of dietary cottonseed and/or canola oil inclusion on the growth performance, FA composition and organ histology of the juvenile rainbow trout, *Oncorhynchus mykiss*. *Turk. J. Fish. Aquat. Sci.* 13: 453–464.
- Yildiz M, ErolodoganTO, Ofori-Mensah S, Engin K and Baltaki MA (2017) The effects of fish oil replacement by vegetable oils on growth performance and fatty acid profile of rainbow trout: Re-feeding with fish oil finishing diet improved the fatty acid composition. *Aquaculture* (accepted article) DOI: 10.1016/j.aquaculture.2017.12.030
- Zheng X, Seiliez I, Hastings N, Tocher DR, Panserat S and Dickson CA (2004) Characterization and comparison of fatty acyl D6 desaturase cDNAs from freshwater and marine teleost fish species. *Comparative Biochemistry and Physiology B* 139: 269–279.
- Zheng X, Torstensen BE, Tocher DR, Dick JR, Henderson RJ and Bell JG (2005) Environmental and dietary influences on highly unsaturated fatty acid biosynthesis and expression of fatty acyl desaturase and elongase genes in liver of Atlantic salmon (*Salmo salar*). *BBA-Mol Cell Biol L* 1734: 13–24
- Zhen-Yu D, Pierre C, Wen-Hui Z, Pascal D, Li-Xia T and Yong-Jian L (2006) Biochemical alterations and body lipid composition in the herbivorous grass carp (*Ctenopharyngodon idella*) fed high-fat diets. *Brit. J. Nutr.* 95: 905–15.