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Polyunsaturated Fatty Acid Content of Wild and Farmed Tilapias in Thailand: Effect of Aquaculture Practices and Implications for Human Nutrition

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The total lipid content and fatty acid composition of the muscle tissue of tilapia (*Oreochromis niloticus*) and of hybrid red tilapia (*Oreochromis* sp.) from different culture systems and from the natural and artificial environment of Thailand were compared. Wild fish and fish reared under the most extensive conditions had a more favorable fatty acid profile for human consumption as they contained higher proportions of 18:3n-3, 20:5n-3, and 22:6n-3, higher n-3/n-6 PUFA ratios, and lower proportions of 18:2n-6. The muscle tissue of intensively cultured fish was characterized by increased fat deposition that was mainly saturated and monounsaturated fatty acids and 18:2n-6. It is undesirable for the consumer to reduce 20:5n-3 and 22:6n-3 in farmed tilapia and replace them with elevated 18:2n-6. It is recommended that the amount of 18:2n-6 in the feed of the intensively reared tilapia should be reduced by substituting vegetable oils rich in 18:2n-6 with oils rich in 18:1n-9 and/or 18:3n-3.

KEYWORDS: Fatty acids; PUFA; tilapia; *Oreochromis niloticus*; human nutrition; Thailand

INTRODUCTION

Polyunsaturated fatty acids (PUFA) are essential for normal growth, development, and reproduction in all vertebrates, including fish and humans (*1*, *2*). Because vertebrates are not able to synthesize n-3 or n-6 fatty acids (FA), these must be supplied in the diet. The C_{18} FA, 18:2n-6 and 18:3n-3, are therefore often referred to as essential fatty acids, but in those species that are unable convert them to the C_{20} and C_{22} PUFA, these longer chain derivatives are essential and must be supplied in the diet.

In fish, eicosapentaenoic acid (20:5n-3) and docosahexaenoic acid (22:6n-3) are found in high concentrations in the phosphoglycerides of cellular membranes, and 22:6n-3 is particularly abundant in the retina and brain, where it has a crucial role maintaining the structure and function of the excitable membranes of these tissues (*3*). Docosahexaenoic acid is also of key importance for the development and function of human neural tissues (*4*). Furthermore, 20:4n-6 and 20:5n-3 are precursors for the eicosanoids, a group of highly biologically active compounds, which have a wide range of physiological actions, for example, in blood clotting, the immune response, the inflammatory response, cardiovascular tone, renal function, neural function, and reproduction (*5*). The intake of n-3 PUFA, and specifically 20:5n-3 and 22:6n-3, which are found in high concentrations in fish and seafoods, is therefore considered to be beneficial against many health disorders (*6*). There is now compelling evidence from clinical and epidemiological research that increased consumption of long-chain PUFA of the n-3 series, such as 20:5n-3 and 22:6n-3, is efficient in the prevention or attenuation of many cardiovascular problems and inflammatory conditions (*7*).

Fish and marine mammals are by far the richest sources of long-chain n-3 PUFA in nature. At present, fish products comprise an important part of the human diet, and demand is expected to increase (*8*). Given static or declining wild fisheries (*8*), aquaculture has a significant role in ensuring fish supplies. Tilapia farming makes a large and growing contribution to global fish supplies, and Nile tilapia (*Oreochromis niloticus)* is now the ninth most important species produced in the world (*9*). Strains of red tilapia (*Oreochromis* sp.) are also gaining importance as a preferred tilapia for culture in Asia, including Thailand, because of their attractive color and increased marketability.

As farmed fish becomes a major contributor to world fish supplies, it is important to maintain the high lipid nutritional quality of the product and to continue to provide large amounts of the health-promoting n-3 PUFA for the consumer. Tilapia culture is highly diverse and consists of a broad spectrum of systems, practices, and operations. The aim of this study was to test the hypothesis that the PUFA content of farmed and wild tilapia in a major tilapia producer country, Thailand, would vary substantially according to management. Fish were sampled from

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Table 1. Summary of Groups of Fish Sampled during the Field Survey

group	species	culture system	sampling period	site	main pond, feed inputs
W 1	*O. niloticus* male	wild	June 2001	small reservoir, Ayuthaya province	natural food
W 2	*O. niloticus* mixed sex	wild	May 2001	Huai Nam Kum reservoir, Sri Sa Ket province	natural food
W 3	*O. niloticus* male	wild	June 2001	Bung Boraphet Swamp, Nakhon Sawan province	natural food
W 4	*O. niloticus* mixed sex	wild	June 2001	Mae Khlong River, Kanchanaburi province	natural food
EP	*O. niloticus* male	extensive catfish–tilapia polyculture	March 2001	Chachoengsao Province, Ban Pho district	off-farm pig manure daily
EM	*O. niloticus* male	extensive monoculture	August 2002	Bangkok, Lad Kra Bang district	grass from around pond bimonthly, drained wastewater from snakehead culture
SP 1	*O. niloticus* male	semi-intensive polyculture	March 2001	Nakhon Phatom province, Nakhon Chaisri district	chicken manure weekly, rice bran, brewery byproducts
SP 2	*O. niloticus* male	semi-intensive polyculture	March 2001	Nakhon Pathom province, Nakhon Chaisri district	chicken manure weekly, rice powder, whiskey byproducts
SP 3	*O. niloticus* male	semi-intensive polyculture	March 2001	Nakhon Pathom province, Bang Lane district	chicken or pig manure weekly, rice bran, domestic byproducts, blood meal, wastewater from prawn culture
SP 4	*O. niloticus* male	semi-intensive polyculture	August 2002	Bangkok, Lad Kra Bang district	chicken manure weekly, rice bran, blood meal, domestic byproducts
SP 5	*O. niloticus* male	semi-intensive shrimp–tilapia polyculture	May 2002	Pathumthani province, AIT ponds	commercial pellet (type A) and pond natural food
SP 6	*O. niloticus* male	semi-intensive polyculture	August 2002	Bangkok, Lad Kra Bang district	ami-ami[a] as fertilizer, chicken manure weekly, maize flour, mung bean meal, slaughter-house byproducts
SI 1	*O. niloticus* male	semi-intensive polyculture with poultry farming	March 2001	Nakhon Phatom province, Lam Look Bou district	chicken and duck wastes/manure daily, commercial pellet (type A) weekly
SI 2	*O. niloticus* male	semi-intensive monoculture with poultry farming	August 2002	Khon Kaen province, Muang district	chicken wastes/manure/spilled feed, commercial pellet (type C) daily
SI 3	*O. niloticus* male	semi-intensive polyculture with pig farming	August 2002	Khon Kaen province, Muang district	pig wastes/manure daily
SI 4	*O. niloticus* male	semi-intensive monoculture with pig farming	August 2002	Khon Kaen province, Ubon Ratana district	pig manure weekly, commercial pellet (type D) daily
SM 1	*O. niloticus* male	semi-intensive monoculture	March 2001	Nakhon Pathom province, Nakhon Chaisri district	chicken manure weekly, tofu, rice bran, beer slug, domestic byproducts
SM 2	*O. niloticus* male	semi-intensive monoculture	March 2001	Bangkok, Lad Kra Bang district	chicken manure weekly, rice bran, blood meal, domestic byproducts
SM 3	*O. niloticus* male	semi-intensive monoculture	March 2001	Nakhon Pathom province, Nakhon Chaisri district	chicken manure weekly, tofu, rice bran, beer slug, domestic byproducts
IN 1	*O. niloticus* male	intensive monoculture in river	May 2001	fish market, Si Sa Ket province	commercial pellet (type A)
IN 2	*O. niloticus* male	intensive monoculture in river	August 2002	Khon Kaen province, Ubon Ratana district	commercial pellet (type B)
IN 3	*O. niloticus* male	intensive monoculture in river	August 2002	Khon Kaen Province, Ubon Ratana District	commercial pellet (type B)
IR 1	red hybrid male	intensive monoculture in brackish water ponds	March 2001	Samut Songkhram province, Lard Yai district	commercial pellet (type A)
IR 2	red hybrid male	intensive monoculture in river	August 2002	Khon Kaen province, Ubon Ratana district	commercial pellet (type B)
IR 3	red hybrid male	intensive monoculture in river	May 2001	fish market, Si Sa Ket province	commercial pellet (type A)

[a] A commercial byproduct of the monosodium glutamate industry (cassava processing), which was added to ponds to stimulate plankton blooms. Monosodium glutamate is a cooking powder in crystal form produced usually from cassava.

a number of aquaculture systems ranging from extensive rural ponds with virtually no inputs to highly intensive systems where the nutrition of fish is exclusively dependent on commercial formulated diets.

MATERIALS AND METHODS

Chemicals. Chloroform, methanol, isohexane, and diethyl ether were of HPLC grade from Fisher (Loughborough, Leicestershire, U.K.). Concentrated sulfuric acid (Aristar grade) and Merck silica gel 60 thin-layer chromatography (TLC) plates (no. 5721) and high-performance TLC (HPTLC) plates (no. 5633) were obtained from VWR (Lutterworth, Leicestershire, U.K.). All other chemicals were obtained from Sigma (Poole, Dorset, U.K.).

Fish Sampling. A total of 25 sampling sites from 10 provinces in Thailand were visited during March−June 2001 and August 2002 (**Table 1**). Sampling sites included fish farms, natural water bodies, and fish markets from which eight fish were sampled from each. The culture system of the farms ranged from extensive with minimum pond and feed inputs to highly intensive, where fish were feeding only on a commercial formulated diet (**Table 2**) at high feeding rates and frequencies. Information about the culture systems and management practices was obtained during informal discussions with farmers.

Fish sampling at the farms was carried out at a number of ponds whenever that was possible, using a seine net (5 mm mesh size). Fish from the wild were caught by local fishermen using fishing rods or nets and were obtained alive. Fish purchased from the markets were alive, and the vendor, for example, the commercial company that cultured the fish, verified their origin (trademark). The fish were killed by a blow to the head, individually placed in airtight polyethylene bags, and immersed in abundant crushed ice until transported to the laboratory within a couple of hours of sampling. A portion of muscle (about 2.5 × 3 cm) was removed from the dorsal muscle tissue of each fish, skin and bones were removed, and the flesh was placed in an airtight

Table 2. FA Composition (Percent of Total FA) of the Commercial Diets Given to the Various Farmed Tilapia (Values Represent Means of Three ± SD)[a]

	type A: IN1, IR1, IR3, SP5, SI1	type B: IN2, IN3, IR2	type C: S12	type D: S14
16:0	19.69 ± 0.95	24.91 ± 1.15	25.99 ± 1.41	24.25 ± 1.28
18:0	5.11 ± 0.33	6.78 ± 0.41	3.87 ± 0.17	6.04 ± 0.35
16:1n-7	5.88 ± 0.22	5.06 ± 0.21	3.38 ± 0.16	3.01 ± 0.16
18:1n-9	14.86 ± 0.87	17.36 ± 0.95	20.02 ± 0.91	18.06 ± 0.85
18:1n-7	2.53 ± 0.04	2.42 ± 0.06	1.07 ± 0.04	1.98 ± 0.11
18:2n-6	13.22 ± 0.68	14.18 ± 0.83	30.07 ± 1.97	17.89 ± 1.01
20:4n-6	1.29 ± 0.05	1.25 ± 0.07	0.16 ± 0.02	1.05 ± 0.08
18:3n-3	1.34 ± 0.12	1.39 ± 0.09	2.03 ± 0.11	1.32 ± 0.10
20:5n-3	11.48 ± 0.50	5.21 ± 0.33	2.23 ± 0.23	4.89 ± 0.31
22:6n-3	10.94 ± 1.38	9.50 ± 1.11	4.34 ± 0.88	10.14 ± 1.21
total SFA	30.14 ± 0.98	37.04 ± 1.23	33.24 ± 1.47	35.08 ± 1.35
total MUFA	25.11 ± 0.97	27.06 ± 1.02	25.70 ± 0.99	26.19 ± 0.82
total PUFA	43.63 ± 1.83	34.54 ± 1.17	40.99 ± 2.01	32.74 ± 1.62
total DMA	1.12 ± 0.10	1.36 ± 0.11	nd	nd
total n-6 PUFA	15.83 ± 0.80	16.85 ± 0.95	30.78 ± 1.98	20.07 ± 1.28
total n-3 PUFA	27.80 ± 1.57	17.68 ± 1.20	10.21 ± 0.95	18.67 ± 1.31
(n-3)/(n-6)	1.76 ± 0.10	1.05 ± 0.07	0.33 ± 0.04	0.93 ± 0.10

[a] Total SFA included 14:0, 15:0, 16:0, 18:0, 20:0, and 22:0. Total MUFA included 16:1n-9, 16:1n-7, 18:1n-9, 18:1n-7; 20:1 isomers, 22:1 isomers, and 24:1n-9. Total n-6 PUFA included 18:2n-6, 18:3n-6, 20:2n-6, 20:3n-6, 20:4n-6, 22:4n-6, and 22:5n-6. Total n-3 PUFA included 18:3n-3, 18:4n-3, 20:3n-3, 20:4n-3, 20:5n-3, 22:5n-3, and 22:6n-3. nd, not detected percentages (<0.1%).

polyethylene bag and immediately stored at −20 °C. Samples were transported back to the United Kingdom in dry ice.

Lipid Extraction and Fatty Acid Analysis. The total lipid from wet muscle tissue and from diets was extracted and measured gravimetrically according to the method of Folch et al. (*10*). Wet muscle samples and diets were homogenized in chloroform/methanol (C/M 2:1, v/v) using an Ultra-Turrax tissue disrupter (Fisher Scientific, Loughborough, U.K.). The homogenates were filtered, and a Folch extract was prepared. Samples were kept on ice under nitrogen between procedures and lipid extracts stored in C/M (2:1, v/v) at a final concentration of 10 mg of lipid/mL at −20 °C under nitrogen. Solvents contained 0.05% (w/v) butylated hydroxytoluene (BHT) as an antioxidant.

Lipid class analysis was performed using double-development high-performance thin-layer chromatography (HPTLC) as described by Olsen and Henderson (*11*). Samples were chromatographed in methyl acetate/propan-2-ol/chloroform/methanol/0.25% (w/v) KCl (25:25:25:10:9, v/v) to separate phospholipid classes and in isohexane/diethyl ether/glacial acetic acid (80:20:2, v/v) to separate neutral lipids and cholesterol. Lipid classes were visualized by spraying with 3% cupric acetate (w/v) in 8% phosphoric acid (v/v) and charred at 160 °C for 15 min. Lipid classes were quantified by scanning densitometry (370 nm) using a CAMAG TLC scanner 3 (version Firmware 1.14.16), and scanned images were recorded automatically in a computer using a special software (winCATS Planar Chromatography Manager, version 1.2.0).

Fatty acid methyl esters (FAME) were prepared by acid-catalyzed transesterification of 1 mg of total lipid with 0.1 mg of heptadecanoic acid (Sigma Chemical Co., St. Louis, MO) as internal standard using 2 mL of 1% (v/v) sulfuric acid in methanol and 1 mL of toluene under nitrogen at 50 °C for 16 h. Crude FAME were purified by TLC in isohexane/diethyl ether/acetic acid (90:10:1, v/v) and visualized by spraying lightly the edge of the plate with 1% (w/v) iodine in $CHCl_3$. FAME were scraped from the plate and eluted with isohexane/diethyl ether (1:1, v/v). Purified FAME were redissolved in isohexane containing 0.05% BHT and stored under nitrogen at −20 °C prior to gas−liquid chromatography (GLC).

Fatty acid methyl esters were separated and quantified by GLC (Fisons 8000 series, Thermo-Finnegan, Hemel Hempstead, U.K.) using a CP Wax 52CB fused silica capillary column (30 m × 0.32 mm i.d.) (Chrompak, London, U.K.). Hydrogen was used as carrier gas at a flow rate of 2.5 mL/min, and temperature programming was from 50 to 150 °C at 40 °C/min and from 150 to 225 °C at a rate of 2 °C/min, and the final temperature of 225 °C was maintained for 5 min. Individual methyl esters were identified by comparison to known standards and by reference to published data (*12*). Peak areas of fatty acids were quantified with reference to the peak area of 17:0 internal standard and computed automatically by a computing integrator (Chromcard for Windows, ThermoQuest, Milan, Italy).

Statistical Analysis. Data from individual fish were treated as independent samples. A nonparametric statistical analysis was used because for each variable tested at least one group of samples had an asymmetric distribution (non-normality), and when the groups were normally distributed, they had unequal variances (heteroscedasticity). The heteroscedasticity and non-normality could not be corrected using data transformation. The data were subjected to Kruskal−Wallis one-way analysis of variance by ranks, and the significance of the Kruskal−Wallis test was assessed by the SPSS statistical package (version 10.0.1) for Windows (SPSS Inc., Chicago, IL) and was rejected at an α level of 0.05. The values given for the total lipid content, lipid classes, and fatty acids of fish represent the medians of eight fish ± interquartile range (IQR). Values that do not share the same letter in the tables are significantly different.

RESULTS AND DISCUSSION

Total Lipid and FA Contents of Muscle Tissue from Farmed and Wild Tilapias. The mean total lipid (TL) contents of the muscle tissue from the different groups of fish ranged from 5.59 to 21.84 mg/g of wet weight of tissue (**Table 3**). These values are generally low but within the range of values reported in the literature for Nile tilapia (*O. niloticus*) (*13*) and for red tilapia hybrid (*Oreochromis* sp.) (*14*). The TL contents of all three intensively raised Nile tilapia groups (IN1, IN2, and IN3) and the three intensive raised red tilapia groups (IR1, IR2, and IR3) were similar and in general higher than those of the wild, extensively and semi-intensively cultured groups of fish (**Table 3**). Higher fat content in cultured fish reared on commercial diets is a general phenomenon observed for a variety of species, both freshwater and seawater (see, e.g., refs *15* and *16*).

Table 3. Total Lipid (TL) Content of the Muscle Tissue of the Wild and Cultured Groups of Fish[a]

fish group	wt range (g)	TL (mg/g of tissue)
W1	258.3–2428.5	5.82 ± 2.02 ab
W2	16.6–63.9	6.09 ± 0.45 ab
W3	98.0–246.6	6.96 ± 2.37 abc
W4	91.8–268.2	8.71 ± 4.87 abcde
EP	10.8–80.2	5.73 ± 1.55 a
EM	115.2–186.2	6.30 ± 2.55 abc
SP1	65.1–120.3	5.59 ± 1.22 a
SP2	50.7–120.4	6.23 ± 1.10 ab
SP3	78.6–305.0	6.30 ± 1.60 ab
SP4	196.9–318.5	8.98 ± 1.25 abcde
SP5	105.5–236.2	9.34 ± 3.40 abcde
SP6	177.4–244.9	9.60 ± 4.77 abcde
SI1	226.3–406.9	7.24 ± 2.77 abcd
SI2	150.3–352.6	8.28 ± 4.40 abcde
SI3	26.8–48.8	8.60 ± 0.90 abcde
SI4	283.2–532.4	8.88 ± 6.45 abcde
SM1	249.4–356.7	5.88 ± 2.75 a
SM2	146.8–358.5	7.10 ± 2.02 abc
SM3	194.6–283.5	10.09 ± 2.92 abcde
IN1	414.7–588.2	11.83 ± 5.05 bcde
IN2	599.7–935.8	17.38 ± 10.77 de
IN3	298.3–621.9	21.84 ± 18.50 e
IR1	530.2–756.4	12.63 ± 4.35 cde
IR2	666.9–985.2	15.57 ± 6.60 cde
IR3	337.9–466.2	18.01 ± 20.72 de

[a] Values represent medians ± IQR (interquartile range, $n = 8$). Values in the same column that do not share the same letter are significantly different at $P < 0.05$.

Lipid Class Composition. The lipid class composition was variable among the 25 groups of wild and farmed tilapia (**Table 4**). Amounts of total neutral lipids ranged from 2.1 to 17.3 mg/g of wet weight of tissue, whereas those of total polar lipids ranged from 2.8 to 5.9 mg/g of wet weight of tissue. Triacylglycerols (TAG) and cholesterol were the major neutral lipid classes (**Table 4**). Phosphatidylcholine (PC) and phosphatidylethanolamine (PE) were the major polar lipid classes, in general agreement with other studies that have been conducted with tilapia (*14*, *17*) and other freshwater fish species (*13*). Across the spectrum of intensity, the increased TL in the muscle tissue of fish was due to an increase mainly in TAG and to a lesser extent in other lipid classes (**Table 4**). The polar lipid content, especially in muscle tissue, is considered to be stable, and only the depot fat triacylglycerols vary (*13*).

Fatty Acid Composition of Muscle Total Lipid. The intensively cultured groups of Nile and red tilapias contained increased amounts of total saturated fatty acids (SFA), total monounsaturated fatty acids (MUFA), and total PUFA on a per gram tissue basis compared to the wild and less intensively cultured fish (**Table 5**). This was particularly marked in the IN1, IN2, IN3, and IR3 groups. However, whereas PUFA was the dominant category of fatty acids in the majority of the wild and nonintensively cultured fish, it was the smallest fraction of FA in the intensively cultured Nile and red tilapia groups (**Table 5**).

Table 4. Lipid Class Composition (as Milligrams per Gram of Tissue) of the Wild and Cultured Groups of Fish[a]

group	PC	PE	PS	PI	TAG	cholesterol	total polar	total neutral
W1	1.73 ± 0.17 abc	0.87 ± 0.13 a	0.16 ± 0.03 a	0.24 ± 0.02 ab	1.46 ± 2.50 abcd	0.96 ± 0.18 ab	3.26 ± 0.37 a	2.81 ± 2.32 abc
W2	2.06 ± 0.19 abcd	1.02 ± 0.19 abc	0.27 ± 0.06 abc	0.28 ± 0.05 abcd	0.45 ± 1.02 a	1.00 ± 0.20 ab	4.11 ± 0.50 abcd	2.12 ± 0.69 a
W3	2.00 ± 0.53 abcd	1.14 ± 0.27 abcd	0.27 ± 0.07 abc	0.34 ± 0.11 abcd	1.41 ± 1.27 abc	0.93 ± 0.28 a	4.06 ± 1.06 abcd	2.80 ± 1.34 ab
W4	2.14 ± 0.36 abcd	1.13 ± 0.27 abcd	0.23 ± 0.04 abc	0.36 ± 0.07 bcd	2.71 ± 3.71 abcdef	1.31 ± 0.31 bcd	4.16 ± 0.77 abcd	4.66 ± 4.17 abcde
EP	1.76 ± 0.29 ab	0.95 ± 0.36 abc	0.13 ± 0.06 a	0.17 ± 0.12 a	0.64 ± 0.29 ab	1.15 ± 0.19 abcd	3.45 ± 0.58 a	2.28 ± 0.89 ab
EM	1.98 ± 0.24 abcd	0.89 ± 0.16 ab	0.22 ± 0.04 abc	0.31 ± 0.05 abcd	1.52 ± 2.24 abcdef	1.00 ± 0.31 abc	3.69 ± 0.55 abcd	2.82 ± 2.43 abcd
SP1	1.78 ± 0.48 abcd	0.89 ± 0.22 ab	0.23 ± 0.07 abc	0.27 ± 0.09 abcd	0.49 ± 0.11 a	1.02 ± 0.12 abc	3.61 ± 0.98 abc	2.09 ± 0.29 a
SP2	1.64 ± 0.27 a	0.90 ± 0.11 a	0.19 ± 0.08 abc	0.21 ± 0.09 ab	0.80 ± 0.78 ab	1.04 ± 0.21 abcd	3.25 ± 0.66 a	2.91 ± 0.61 abc
SP3	2.03 ± 0.44 abcd	0.94 ± 0.16 abc	0.24 ± 0.02 abc	0.28 ± 0.06 abc	1.28 ± 1.16 abc	0.87 ± 0.18 a	3.84 ± 0.67 abcd	2.63 ± 1.10 ab
SP4	2.46 ± 0.48 bcd	1.24 ± 0.15 abcd	0.19 ± 0.14 ab	0.29 ± 0.06 abcd	2.64 ± 1.29 abcdef	1.26 ± 0.18 abcd	4.48 ± 0.69 abcd	4.31 ± 0.83 abcde
SP5	2.20 ± 0.52 abcd	1.32 ± 0.28 bcd	0.25 ± 0.05 abc	0.43 ± 0.11 cd	3.55 ± 3.50 bcdef	1.25 ± 0.41 bcd	4.36 ± 0.83 abcd	5.17 ± 3.60 abcde
SP6	2.09 ± 0.54 abcd	0.96 ± 0.22 abc	0.19 ± 0.05 ab	0.30 ± 0.07 abcd	4.76 ± 3.73 bcdef	1.10 ± 0.28 abcd	3.77 ± 0.83 abcd	5.94 ± 3.70 bcde
SI1	1.81 ± 0.95 abcd	0.87 ± 0.32 ab	0.29 ± 0.14 abc	0.31 ± 0.26 abcd	1.74 ± 1.60 abcde	0.93 ± 0.22 a	3.56 ± 1.85 abcd	3.50 ± 2.31 abcd
SI2	2.27 ± 0.67 abcd	1.01 ± 0.30 abcd	0.24 ± 0.07 abc	0.37 ± 0.14 bcd	2.54 ± 3.28 abcdef	1.20 ± 0.42 bcd	4.13 ± 1.21 abcd	4.05 ± 3.75 abcde
SI3	2.24 ± 0.20 abcd	1.34 ± 0.10 cd	0.32 ± 0.02 c	0.44 ± 0.04 cd	2.13 ± 0.82 abcdef	1.10 ± 0.05 abcd	4.83 ± 0.19 cd	3.76 ± 0.90 abcde
SI4	2.39 ± 0.65 cd	0.98 ± 0.38 abcd	0.23 ± 0.07 abc	0.36 ± 0.18 abcd	3.50 ± 4.71 bcdef	1.11 ± 0.38 abcd	4.10 ± 1.31 abcd	4.85 ± 5.16 bcde
SM1	1.42 ± 0.84 a	0.74 ± 0.39 a	0.20 ± 0.13 ab	0.19 ± 0.12 a	1.77 ± 1.34 abcd	0.87 ± 0.54 ab	2.80 ± 1.66 a	3.03 ± 0.87 abc
SM2	1.72 ± 0.15 ab	0.95 ± 0.10 abc	0.24 ± 0.03 abc	0.26 ± 0.04 ab	1.97 ± 1.03 abcde	0.96 ± 0.08 ab	3.46 ± 0.40 ab	3.57 ± 1.39 abcd
SM3	1.97 ± 0.43 abcd	1.08 ± 0.14 abcd	0.31 ± 0.09 bc	0.29 ± 0.08 abcd	3.76 ± 3.11 abcdef	1.17 ± 0.28 abcd	4.19 ± 0.89 abcd	5.99 ± 2.09 bcde
IN1	1.81 ± 0.69 abcd	0.94 ± 0.51 abc	0.17 ± 0.07 a	0.28 ± 0.08 abcd	6.34 ± 4.20 cdef	0.96 ± 0.35 abc	3.61 ± 1.41 abcd	8.89 ± 4.35 cde
IN2	2.97 ± 1.74 d	1.70 ± 0.67 d	0.29 ± 0.08 bc	0.48 ± 0.08 d	8.03 ± 7.81 def	2.44 ± 0.89 d	5.90 ± 2.90 d	11.37 ± 8.17 de
IN3	2.48 ± 1.32 d	1.23 ± 0.32 abcd	0.27 ± 0.13 abc	0.31 ± 0.21 abcd	15.32 ± 15.26 f	1.56 ± 0.83 cd	4.60 ± 2.39 bcd	17.31 ± 16.20 e
IR1	2.50 ± 0.35 cd	1.06 ± 0.17 abcd	0.24 ± 0.07 abc	0.36 ± 0.08 abcd	6.09 ± 4.42 cdef	1.07 ± 0.23 abcde	4.68 ± 0.63 bcd	7.75 ± 4.56 cde
IR2	3.07 ± 0.95 d	1.35 ± 0.35 bcd	0.19 ± 0.03 a	0.35 ± 0.11 abcd	8.30 ± 3.99 cdef	1.55 ± 0.55 bcd	5.24 ± 1.57 bcd	10.16 ± 4.87 cde
IR3	2.20 ± 0.85 abcd	1.11 ± 0.53 abcd	0.21 ± 0.01abc	0.31 ± 0.08 abcd	11.31 ± 17.48 ef	1.18 ± 0.93 abcd	4.26 ± 1.25 abcd	13.33 ± 18.96 de

[a] Values represent medians ± IQR ($n = 8$). Values in the same column that do not share the same letter are significantly different at $P < 0.05$. Total polar lipids include phosphatidylcholine, phosphatidylethanolamine, phosphatidylserine, phosphatidylinositol, lysophosphatidylcholine, sphingomyelin, and phosphatidylglycerol/cardiolipin. Total neutral lipids include triacylglycerols, cholesterol, sterol esters, and free fatty acids.

Table 5. Amounts of Total SFA, Total MUFA, and Total PUFA (as Milligrams per Gram of Wet Weight of Tissue) Found in the Wild and Cultured Groups of Fish[a]

group	saturated	monounsaturated	polyunsaturated	ΣFA
W1	1.06 ± 0.82 ab	0.52 ± 0.57 ab	1.39 ± 0.52 abc	3.00 ± 1.95 ab
W2	1.07 ± 0.27 ab	0.44 ± 0.10 a	1.49 ± 0.25 ab	3.05 ± 0.62 ab
W3	1.48 ± 0.57 abcd	1.04 ± 0.60 abcde	1.66 ± 0.55 abcd	4.40 ± 1.67 abcd
W4	2.12 ± 1.65 abcd	1.36 ± 1.35 abcde	1.89 ± 0.75 abcd	5.45 ± 3.82 abcd
EP	0.84 ± 0.17 a	0.29 ± 0.08 a	1.41 ± 0.47 a	2.58 ± 0.72 a
EM	1.23± 0.57 abc	0.56 ± 0.37 abc	1.49 ± 0.57 abcd	3.30 ± 1.45 abcd
SP1	1.02 ± 0.17 ab	0.49 ± 0.15 ab	1.40 ± 0.17 a	3.05 ± 0.50 ab
SP2	0.99 ± 0.37 ab	0.55 ± 0.30 ab	1.53 ± 0.20 ab	3.05 ± 0.77 ab
SP3	1.47 ± 0.72 abcd	0.58 ± 0.32 ab	1.95 ± 0.72 abcd	4.05 ± 1.72 abcd
SP4	1.73 ± 0.25 abcd	1.43 ± 0.42 bcde	1.98 ± 0.25 abcd	5.20 ± 0.85 abcd
SP5	2.12 ± 1.60 bcd	1.87 ± 1.65 bcde	1.82 ± 0.50 abcd	5.65 ± 3.37 bcd
SP6	2.08 ± 1.15 abcd	1.13 ± 0.97 abcde	2.51 ± 1.02 bcd	5.95 ± 3.15 abcd
SI1	1.78 ± 1.12 abcd	0.89 ± 0.70 abcde	1.80 ± 1.32 abcd	4.40 ± 2.87 abcd
SI2	1.65 ± 0.35 abcd	1.32 ± 0.77 abcde	1.75 ± 0.27 abcd	4.80 ± 1.12 abcd
SI3	1.54± 0.30 abcd	1.20 ± 0.15 abcde	1.98 ± 0.27 abcd	4.75 ± 0.37 abcd
SI4	1.85 ± 1.82 abcd	1.34 ± 1.82 bcde	1.86 ± 1.30 abcd	5.05 ± 4.85 abcd
SM1	1.42 ± 0.70 abc	0.81 ± 0.42 abcd	1.69 ± 0.82 abcd	4.10 ± 1.85 abc
SM2	1.40 ± 1.20 abcd	1.08 ± 1.12 abcde	1.63 ± 0.25 abcd	4.20 ± 2.60 abcd
SM3	2.24 ± 0.75 bcd	1.72 ± 1.00 bcde	2.62 ± 0.45 cd	6.70 ± 1.80 bcd
IN1	3.63 ± 1.77 cd	3.62 ± 2.15 de	2.66 ± 1.20 cd	10.20 ± 5.05 cd
IN2	3.71 ± 0.89 cd	4.09 ± 3.00 e	2.76 ± 1.42 d	10.60 ± 6.92 d
IN3	5.10 ± 4.92 cd	6.28 ± 5.50 e	3.40 ± 2.02 d	15.05 ± 12.25 d
IR1	3.35 ± 2.15 cd	3.15 ± 2.75 cde	2.94 ± 1.15 d	9.60 ± 6.05 cd
IR2	4.17 ± 1.87 cd	4.54 ± 2.15 de	3.04 ± 1.20 cd	12.10 ± 5.20 cd
IR3	4.90 ± 3.30 d	5.56 ± 4.15 e	3.12 ± 1.60 d	13.60 ± 9.12 d

[a] Values represent medians ± IQR for $n = 8$. Values in the same column that do not share the same letter are significantly different at $P < 0.05$. The total fatty acid content (ΣFA) represents the sum of saturated, monounsaturated, and polyunsaturated fatty acids as well as the sum of dimethyl acetals; saturated fatty acids include 14:0, 16:0, 18:0, 20:0 and 22:0; monounsaturated fatty acids include 16:1n-9, 16:1n-7, 18:1n-9, 18:1n-7, 20:1n-11, 20:1n-9, 20:1n-7, 22:1n-11, 22:1n-9, and 24:1n-9; polyunsaturated fatty acids include 18:2n-6, 18:3n-6, 20:2n-6, 20:3n-6, 20:4n-6, 22:4n-6, 22:5n-6, 18:3n-3, 18:4n-3, 20:3n-3, 20:4n-3, 20:5n-3, 22:4n-3, 22:5n-3, and 22:6n-3.

A higher fraction of MUFA in intensively farmed fish compared to their wild counterparts has also been reported for other fish species including Atlantic salmon (*Salmo salar*) (*18*) and turbot (*Scophthalmus maximus*) (*19*). This was largely due to the increased presence of 18:1n-9 in tissues of farmed fish, which is consistent with our findings (23.2−29.5% of ΣFA, data not shown). The commercial feeds were not particularly rich in MUFA (**Table 2**), although 18:1n-9 predominates, and in fact the percentages of dietary MUFA were lower than the tissue percentages in these groups of fish. Saturated and monounsaturated FA are the main products of fatty acid synthesis de novo in fish (*20*), and it appears that FA arising from de novo synthesis may also be incorporated into tissue storage lipids. However, differential oxidation and deposition of dietary fatty acids could also account for this observation. In an in vivo study using ^{14}C-labeled fatty acids, Olsen et al. (*17*) found that a significant de novo synthesis of SFA and MUFA occurred in tilapia (*O. niloticus*) even when fish were fed diets containing 9% of crude lipid with substantial amounts of n-3 highly unsaturated fatty acids (HUFA).

The amounts of SFA that were incorporated in the muscle tissues of tilapia increased with increasing feed inputs (**Table 5**) but comprised a similar proportion of the muscle ΣFA among the different groups of tilapias. It may be that the amounts of SFA in the muscle lipids of tilapia are regulated within a narrow physiological range, as has been suggested for other fish species (*21*).

There were marked differences among the various wild and cultured tilapias with regard to the individual PUFA (**Table 6**). The largest difference was in the content of 18:2n-6, with fish from the intensively cultured groups characterized by greatly increased amounts of 18:2n-6 compared with wild fish (**Table 6**). The increased amounts of 18:2n-6 originated from the high inclusion of grains and/or plant seed oils in the commercial diets (**Table 2**) and are a common feature in cultured fish (see, e.g. refs *18* and *19*). Increased amounts of 18:2n-6 were also found in the semi-intensive monoculture fish as well as in the lipids of the SP1, SI2, and SI4 groups of tilapias (**Table 6**). This is probably attributed to their feeding on supplements that were rich in this FA such as soybean meal, rice bran, and domestic

Table 6. Major PUFA in the Muscle Tissues of Wild and Cultured Fish (Milligrams per 100 g of Wet Weight of Tissue)[a]

group	18:2n-6	18:3n-3	20:4n-6	20:5n-3	22:6n-3
W1	23.4 ± 8.8 abcde	19.2 ± 14.2 de	16.9 ± 5.9 abcdef	4.2 ± 2.9 ab	37.1 ± 13.3 a
W2	6.6 ± 0.9a	4.8 ± 1.6 ab	27.2 ± 8.7 f	10.0 ± 2.3 bcde	48.0 ± 13.4 abc
W3	34.7 ± 12.0 a	15.8 ± 6.8 bcde	22.6 ± 10.7 abcdef	4.7 ± 1.7 abc	43.5 ± 8.6 ab
W4	11.8 ± 7.0 ab	8.7 ± 7.8 abcde	21.6 ± 2.5 cdef	17.7 ± 4.1 e	67.6 ± 17.0 abc
EP	6.8 ± 3.9a	3.4 ± 0.7a	25.0 ± 12.0 def	11.3 ± 3.8 de	43.9 ± 9.0 ab
EM	19.4 ± 9.3 abc	10.7 ± 13.5 bcde	20.2 ± 2.2 bcdef	9.3 ± 3.0 bcde	53.7 ± 29.1 abc
SP1	32.0 ± 7.2 abcdef	3.0 ± 0.8 a	22.4 ± 3.4 def	4.8 ± 1.9 abcd	41.8 ± 8.1 ab
SP2	30.3 ± 19.8 abcde	6.8 ± 2.1 abcd	18.4 ± 2.4 abcdef	8.6 ± 2.9 bcde	40.8 ± 6.5 a
AP3	11.0 ± 6.0 abc	8.2 ± 7.3 abcde	21.5 ± 8.5 abcdef	10.2 ± 4.2 bcde	73.1 ± 22.8 abc
SP4	50.0 ± 6.5 bcdef	5.3 ± 3.3 abc	12.6 ± 3.6 ab	5.2 ± 0.7 abcd	90.0 ± 9.3 c
SP5	40.6 ± 21.8 abcdef	16.3 ± 18.0 cde	16.6 ± 4.8 abcdef	4.4 ± 0.6 ab	43.5 ± 11.2 ab
SP6	40.2 ± 33.3 abcdef	31.8 ± 21.7 e	21.1± 4.7 cdef	9.0 ± 1.5 bcde	59.9 ± 10.1 abc
SI1	26.5 ± 13.5 abcd	17.9 ± 24.8 bcde	19.1 ± 11.2 abcdef	9.8 ± 6.0 bcde	53.4 ± 34.7 abc
SI2	58.3 ± 20.8 bcdef	6.5 ± 2.7 abcd	18.3 ± 3.7 abcdef	4.9 ± 0.7 abcd	52.8 ± 10.2 abc
SI3	39.9 ± 8.9 abcdef	12.7 ± 5.1 bcde	19.1 ± 3.0 abcdef	5.0 ± 1.2 abcd	73.4 ± 8.8 abc
SI4	51.4 ± 57.6 cdef	5.2 ± 9.3 abcd	12.6 ± 4.3 a	3.9 ± 2.6 ab	82.6 ± 36.4 bc
SM1	48.8 ± 29.0 abcdef	8.1 ± 3.7 abcd	19.5 ± 16.1 abcdef	6.1 ± 2.1 abcde	39.3 ± 21.3 a
SM2	55.7 ± 41.4 abcdef	10.6 ± 4.7 abcde	14.4 ± 7.2 abcd	3.1 ± 1.7 a	37.3 ± 16.6 a
SM3	89.8 ± 19.3 def	11.3 ± 3.2 bcde	25.3 ± 6.9 ef	5.8 ± 0.9 abcde	56.8 ± 10.2 abc
IN1	92.7 ± 44.0 ef	6.1 ± 4.0 abcd	16.1 ± 6.5 abcdef	10.3 ± 5.4 cde	85.9 ± 40.0 c
IN2	92.5± 61.6 ef	10.3 ± 4.9 abcde	18.2 ± 5.8 abcdef	3.7 ± 1.3 a	102.8 ± 41.5 c
IN3	129.6 ± 108.0 f	15.0 ± 6.7 bcde	16.2 ± 3.7 abcde	4.5 ± 3.9 abcd	96.5 ± 42.6 c
IR1	100.4 ± 194.9 ef	7.9 ± 6.2 abcde	14.9 ± 4.9 abc	10.8 ± 3.6 cde	93.5 ± 29.6 c
IR2	112.7 ± 61.8ef	11.5 ± 7.0 abcde	17.2 ± 4.2 abcdef	4.9 ± 2.3 abcd	96.0 ± 21.6 c
IR3	112.7 ± 75.6 ef	8.5 ± 6.8 abcde	12.4 ± 4.4 abc	10.8 ± 9.7 bcde	102.5 ± 32.6 c

[a] Values represent medians ± IQR for $n = 8$. Values in the same column that do not share the same letter are significantly different at $P < 0.05$.

byproducts and probably to a high 18:2n-6 content in their pond natural food stimulated by the input of these supplements. There was no trend in the amounts of 18:3n-3 present across the spectrum of intensity, and consequently the 18:2n-6 to 18:3n-3 ratio differed widely between groups of fish. In wild fish (W1−W4) the ratio varied from 1.3 to 2.2, whereas in intensively reared fish (IN1−3 and IR1−3) it was 8.9−14.7 with scattered values across the whole range for the remaining groups (data not shown). This ratio is important in considering the relative rates of desaturation and elongation of 18:2n-6 and 18:3n-3 to their long-chain derivatives because they compete for the desaturase and elongase enzymes (*13*).

The amounts of 22:6n-3 were slightly increased in the intensively reared fish compared to the wild, extensive, and semi-intensive groups, whereas amounts of 20:4n-6 and 20:5n-3 remained fairly constant across groups (**Table 6**). It is very well established that dietary FA intake is the major determinant of tissue fatty acid composition in fish (see, e.g. ref *22*). Tilapias are omnivorous and highly opportunistic feeders, and their diet may consist of a wide range of prey items such as plant material, detritus, zooplankton, macrophytes, insect larvae, and fish eggs (*23*). The PUFA profile of the wild and less intensively reared fish therefore reflects the availability of these PUFA in the different environments.

When the results are expressed as FA concentration (% ΣFA), a rather different pattern emerges (**Table 7**). The muscle lipids of wild and nonintensively cultured fish were characterized, in general, by higher proportions of C_{20} and C_{22} PUFA and, specifically, of 22:6n-3, 20:5n-3, and 20:4n-6 than those found in the intensively cultured tilapia (**Table 7**). The intensively cultured Nile and red tilapia contained significantly lower percentages of 22:6n-3 (7.0−10.0% of ΣFA) than those of most wild and nonintensively cultured fish, whereas decreased percentages of this FA were also found in the semi-intensive monoculture groups (SM group) (8.1−9.0% of ΣFA). The lipids of the intensively cultured fish contained decreased percentages of 20:5n-3 (0.3−1.0% of ΣFA) also (**Table 7**). Overall, 20:5n-3 was present in low concentrations in the muscle lipids of all tilapia (0.3−4.3% of ΣFA), including the intensively cultured tilapia, which had received substantial amounts of 20:5n-3 from their commercial diets (**Table 2**), with fish from the extensive polyculture (EP) containing the highest proportions (4.3% of ΣFA) in their tissues. Thus, wild fish contained amounts of 22:6n-3 4−9 times higher than their content of 20:5n-3 (**Table 6**), whereas some intensively cultured fish had much higher amounts of 22:6n-3 than 20:5n-3 despite a dietary ratio of 22:6n-3 to 20:5n-3 of about 1−2 (**Table 2**). Such markedly higher proportions of 22:6n-3 than 20:5n-3 are not common in fish oils (*2*). Selective catabolism of 20:5n-3 (β-oxidation) relative to 22:6n-3 probably accounts for this (*2*).

The muscle lipids of wild-caught tilapia were also characterized by high concentrations of 20:4n-6 (**Table 6**). Similar or even higher proportions of this FA were also found in the extensively cultured tilapia (EP and EM) and in some semi-intensively cultured groups that had been reared on low feed inputs (SP1, SP2, and SP3) (**Table 7**). In general, tropical fish from the wild, of both freshwater and marine origin, are known to include considerable amounts of 20:4n-6 in their lipids (*24*). In contrast, the % ΣFA of 20:4n-6 in the muscle lipids of the intensively cultured tilapia was ≈4−8-fold lower than that found in the wild and extensively cultured fish (**Table 7**). A higher concentration of 20:4n-6 in the muscle tissue of wild compared to farmed fish has also been reported for all fish species studied so far, both freshwater and marine (see, e.g. ref *15*).

Up to now, the importance of 20:4n-6 in the formulation of commercial diets has been overlooked as research has focused on the n-3 PUFA requirements of fish (*25*, *26*). Dietary 20:4n-6 has been shown to improve the growth and survival of several fish species, including tilapia (*31*). More research is required to investigate the role of 20:4n-6 and the optimum levels of 20:4n-6, 20:5n-3, and 22:6n-3 in the nutrition, immune function, and reproductive performance of farmed fish in general (*26*). Current commercial diets for this species in Thailand may not contain an appropriate level of 20:4n-6.

Modern industrialized societies are characterized by an increase in energy intake, saturated fat, and n-6 PUFA and a

Table 7. Major Fatty Acids (Percent of ΣFA Identified) in the Muscle Lipids of the Wild and Cultured Fish[a]

group	18:2n-6	18:3n-3	20:4n-6	20:5n-3	22:6n-3
W1	7.9 ± 0.8 abcde	6.2 ± 2.4 a	5.4 ± 2.1 ab	1.3 ± 0.2 abcdef	10.4 ± 7.0 abcde
W2	2.1 ± 0.3 a	1.6 ± 0.5 abcdef	7.8 ± 2.7 a	3.1 ± 0.6 ab	15.3 ± 2.0 abc
W3	7.4 ± 2.3 abcde	3.3 ± 0.8 ab	4.6 ± 1.7abcd	1.1 ± 0.3 bcdef	10.5 ± 2.0 abcde
W4	2.2 ± 0.5 ab	1.6 ± 0.4 abcdef	4.1 ± 2.5 abcde	3.1 ± 1.9 ab	12.5 ± 5.8 abcde
EP	2.8 ± 1.2 ab	1.3 ± 0.3 bcdef	9.4 ± 2.0 a	4.3 ± 0.7 a	16.4 ± 1.6 ab
EM	5.5 ± 0.7 abc	3.2 ± 1.2 ab	6.1 ± 2.1ab	2.5 ± 0.7 abc	14.7 ± 4.6 abc
SP1	10.2 ± 1.0 de	1.0 ± 0.2 cdef	7.8 ± 1.0 a	1.6 ± 0.5 abcd	14.2 ± 1.8 abcd
SP2	9.0 ± 4.0 abcde	2.1 ± 0.3 abcde	5.5 ± 2.2 abcd	2.7 ± 1.6 abc	12.9 ± 3.0 abcde
SP3	2.8 ± 0.5 ab	2.2 ± 0.8 abcde	5.0 ± 1.0 abc	2.5 ± 0.3 abc	16.8 ± 3.7a
SP4	9.6 ± 0.8 cde	1.0 ± 0.3 cdef	2.5 ± 0.6 bcdef	1.0 ± 0.3 cdef	17.4 ± 3.1ab
SP5	6.5 ± 0.8 abc	2.6 ± 1.1abcd	2.8 ± 2.1 bcdef	0.7 ± 0.6 def	7.6 ± 4.6 de
SP6	7.2 ± 3.4 abcd	5.7 ± 1.4 a	3.7 ± 1.2 abcdef	1.6 ± 0.8 abcde	10.1 ± 4.2 abcde
SI1	5.3 ± 2.9 abc	4.2 ± 2.3 ab	3.9 ± 2.3 abcde	2.2 ± 0.8 abcd	11.2 ± 4.6 abcde
SI2	11.6 ± 1.9 de	1.3 ± 0.2 bcdef	3.6 ± 1.7 abcdef	1.0 ± 0.4 bcdef	10.9 ± 5.1 abcde
SI3	8.2 ± 1.3 abcde	2.7 ± 0.8 abcd	4.0 ± 0.5 abcdef	1.1 ± 0.2 bcdef	15.0 ± 2.1 abc
SI4	10.7 ± 1.9 de	1.1 ± 0.4 bcdef	2.1 ± 1.3 bcdef	0.7 ± 0.2 def	15.8 ± 5.2 abc
SM1	10.9 ± 4.1 cde	2.1 ± 0.9 abcde	4.5 ± 3.8 abcd	1.4 ± 0.9 abcde	9.0 ± 4.1 bcde
SM2	11.5 ± 5.3 de	2.0 ± 0.7 abcde	3.0 ± 2.3 abcdef	0.6 ± 0.5 def	8.1 ± 5.7 cde
SM3	13.6 ± 2.4 e	1.7 ± 0.4 abcdef	3.5 ± 2.1 abcdef	0.9 ± 0.3 cdef	8.3 ± 3.2 cde
IN1	8.8 ± 1.5 bcde	0.6 ± 0.1 f	1.7 ± 0.9 cdef	1.0 ± 0.3 abcdef	9.1 ± 2.7 cde
IN2	8.7 ± 0.7 abcde	0.8 ± 0.2 ef	1.6 ± 0.5 def	0.3 ± 0.1 f	8.8 ± 2.9 cde
IN3	8.9 ± 0.5 abcde	1.0 ± 0.3 def	1.1 ± 2.4 ef	0.3 ± 0.3 ef	7.0 ± 2.7 e
IR1	10.2 ± 1.7 de	0.9 ± 0.2 ef	1.6 ± 0.5 def	1.1 ± 0.3 abcdef	10.0 ± 3.4 bcde
IR2	10.1 ± 1.1 cde	0.9 ± 0.3 ef	1.5 ± 0.7 bcdef	0.4 ± 0.1 ef	8.1 ± 1.4 cde
IR3	8.1 ± 0.6 abcde	0.6 ± 0.1 f	0.9 ± 0.5 f	0.8 ± 0.1 def	7.1 ± 3.1 e

[a] Values represent medians ± IQR for $n = 8$. Values in the same column that do not share the same letter are significantly different at $P < 0.05$.

decrease in the intake of n-3 PUFA, due to changes in food production and technology over the past century (*28*). It is estimated that the present so-called "western" diet is providing a n-6/n-3 PUFA ratio of around 15−25:1 compared to a value of about 1−2:1 that is considered to be optimum (*28*). These changes in dietary fat patterns have been linked with the occurrence of many health disorders common in the western/industrialized world such as coronary heart disease and various types of cancer (*1*, *29*). Overproduction of eicosanoids derived from 20:4n-6 leads to enhanced ischemic and inflammatory tendencies, thereby being a major risk factor in many pathological conditions (*30*). These types of disorders, once considered a problem primarily of the western world, are rapidly becoming a public health problem in many parts of Asia (*29*, *31*). Excess dietary linoleic acid has been linked to many chronic diseases of the elderly in Japan (*29*).

Because the input of n-6 PUFA is often excessive and the n-6/n-3 PUFA ratio imbalanced in humans, it is recommended that the intake of n-3 PUFA, and particularly 20:5n-3 and 22:6n-3, in our diet be increased (*28*, *29*, *32*). Consuming fish is the only realistic way of increasing the intake of 20:5n-3 and 22:6n-3 for the great majority of the world's population. It is therefore essential that in the drive to increase aquaculture production the quality of the product for the human consumer is not compromised. Substitution of fish meal and fish oil with meals and oils of vegetable origin will substantially alter flesh FA composition if the correct balance is not achieved (*8*). Excessive deposition of 18:2n-6 is undesirable because it will reduce any conversion of 18:3n-3 to 20:5n-3 and 22:6n-3 and will unbalance the production of eicosanoids toward the proinflammatory n-6 series prostaglandins in both the fish and the human consumer. The work of Lands et al. (*5*) showed the most effective way to modulate proinflammatory eicosanoids was to decrease dietary 18:2n-6 and increase n-3 PUFA. The oil from linseed (flax) grown in temperate regions is a rich source of 18:3n-3, but as yet no equivalent seed plant has been found in the tropics. However, it is now established in humans that dietary 22:6n-3 is ≈10 fold more effective than dietary 18:3n-3 in raising tissue 22:6n-3 concentrations due to the low rate of conversion of 18:3n-3 to 22:6n-3 (*33*).

In this study tilapia reared in different aquaculture systems with varied nutrient inputs had widely different FA compositions. The fish with the highest proportion of long-chain PUFA and the highest n-3 to n-6 ratios, therefore being the most favorable for the human consumer, came from the wild or most extensively farmed systems. Fish from the most intensively farmed systems had higher contents of SFA, MUFA, and 18:2n-6, leading to lower n-3 to n-6 ratios. It is therefore recommended that vegetable meals and oils containing lower amounts of 18:2n-6 and more 18:3n-3 should be used in commercial feeds if the favorable flesh lipid composition of wild fish is to be replicated.

ABBREVIATIONS USED

FA, fatty acid; MUFA, monounsaturated fatty acids; PUFA, polyunsaturated fatty acids; SFA, saturated fatty acids; PC, phosphatidylcholine; PE, phosphatidylethanolamine; PS, phosphatidylserine; PI, phosphatidylinositol; TAG, triacylglycerols, IQR, interquartile range.

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