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EFFECTS OF FEEDING, STARVATION, AND REFEEDING ON THE FATTY ACID COMPOSITION OF CHANNEL CATFISH, *ICTALURUS PUNCTATUS*, TISSUES

JAMES H. TIDWELL,* CARL D. WEBSTER and JULIA A. CLARK
Community Research Service, Aquaculture Research Center, Kentucky State University, Frankfort, KY 40601, U.S.A. Tel.: (502) 227-6925

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Abstract—1. The effects of feeding, food deprivation (14 and 28 days) and refeeding (starved 14 then fed 14 days) on the fatty acid composition of white muscle, liver and brain of pond-raised channel catfish (*Ictalurus punctatus*) were investigated.

2. Levels of n-3 fatty acids were significantly higher ($P < 0.05$) in white muscle of fish starved 28 days (10.7%) than in fish fed throughout the study (8.0%), due primarily to an increase in 22:6(n-3) docosahexaenoic acid or DHA.

3. Significantly higher levels of 20:5(n-3) (eicosapentaenoic acid or EPA) were found in livers of fish starved 28 days ($P < 0.05$) compared to fish fed throughout the study.

4. Results suggest that the fatty acid compositions of channel catfish white muscle and liver are subject to only limited perturbation during periods of starvation and refeeding and that the brain is extremely well protected.

INTRODUCTION

Fatty acid composition is important to membrane structure. Alterations of the fatty acid composition of a tissue may affect the biochemical and physical properties of that tissue. A number of authors have shown that the fatty acid composition of many, if not all, fish species is a reflection of dietary lipid (Worthington and Lovell, 1973; Yingst and Stickney, 1979). Tidwell and Robinette (1990) demonstrated that fish size and age can also significantly influence fatty acid composition. Their data showed that when fish are well fed, 79% of the variation in unsaturated/saturated ratios of white muscle could be explained by fish age and size and that monenes were preferentially deposited. However, limited information is available on alterations in fatty acid composition during periods of reduced food availability or starvation.

Kiessling *et al.* (1989) found that when ration levels for rainbow trout (*Oncorhynchus mykiss*) were reduced, palmitoleic acid, 16:1(n-9) and oleic acid, 18:1(n-9) decreased and eicosapentaenoic acid or EPA, 20:5(n-3), and docosahexaenoic acid or DHA, 22:6(n-3), increased. Studies with carp, *Cyprinus carpio* (Murata and Higashi, 1980) and whitefish, *Coregonus muksun* (Soivio *et al.*, 1989) have also reported decreases in monounsaturated fatty acids and increases in polyunsaturated fatty acids (PUFA) levels after a period of starvation. Conservation of particular fatty acids during starvation may be an indicator of their relative importance to the respective tissue. If fish are refed, fatty acid composition may revert to pre-starvation levels or even overcompensate (Weatherly and Gill, 1981). In carp, a 20-day period of refeeding, after fish had been starved 66 days, resulted in an increase in monoenoic fatty acids and a concomitant decrease in DHA percentage (Murata and Higashi, 1980).

The purpose of this study was to evaluate effects of food deprivation for varying periods and refeeding on fatty acid composition of white muscle, liver and brain in channel catfish grown in ponds.

MATERIALS AND METHODS

Animals and experimental conditions

Channel catfish (mean individual weight 35 g) were randomly stocked into each of 12, 0.04-ha ponds and randomly assigned one of four feeding regimes for the period immediately preceding harvest: 1—continually fed (control); 2—fasted 14 days; 3—fasted 28 days; 4—fasted 14 days then refed 14 days. All fish were fed a commercially prepared floating diet (Purina Catfish Chow, 32% crude protein and 4% crude fat). There were three replicate ponds per treatment. Fish were fed twice daily (8:30 a.m. and 3:30 p.m.) and offered as much feed as they would consume in 20 min.

Lipid analysis

Three fish per pond were randomly sampled for fatty acid analysis of white muscle, liver and brain. Tissues were removed, immediately frozen in liquid nitrogen (−196°C) and stored (−40°C) until lipid extraction. Lipid extraction was according to Bligh and Dyer (1959). Fatty acid methyl esters were obtained according to the method of the AOAC (1984) and analysed using a Hewlett–Packard 5890 II gas chromatograph equipped with an Omegawax 320 30-m fused-silica capillary column (Supelco, Inc., Bellefonte, PA) and a flame-ionization detector. The carrier gas was helium. Oven temperature was programmed from 160 to 220°C at 2°C/min and then from 220 to 270°C at 10°C/min. Detector response was recorded and quantitated with an electronic integrator–recorder. An internal standard was added and fatty acid methyl esters were identified by comparison and

*To whom correspondence should be addressed.

Table 1. A comparison of the composition of some fatty acids (rel.%) in white muscle from channel catfish either fully fed (control), starved 14 days, starved 28 days, or starved 14 days then refed 14 days*

	Treatment				
Fatty acid	Control	Starved 14 days	Starved 28 days	Refed	Stocking†
14:0	0.98 ± 0.04	0.88 ± 0.06	0.89 ± 0.03	0.90 ± 0.01	1.10 ± 0.00
16:0	16.96 ± 0.15ab	17.57 ± 0.12a	16.24 ± 0.27c	16.84 ± 0.20bc	18.15 ± 0.07
16:1(n-7 or 9)	3.43 ± 0.17	3.29 ± 0.08	3.03 ± 0.13	3.25 ± 0.09	3.95 ± 0.49
18:0	5.95 ± 0.02	6.41 ± 0.12	6.28 ± 0.20	6.26 ± 0.31	5.50 ± 0.57
18:1(n-9)	33.27 ± 0.54	33.13 ± 1.67	32.26 ± 1.98	32.70 ± 0.83	38.40 ± 0.99
18:2	10.84 ± 0.23	11.18 ± 0.11	10.60 ± 0.50	10.89 ± 0.12	15.55 ± 1.34
18:3(n-3)	1.11 ± 0.10ab	0.95 ± 0.02b	1.31 ± 0.13a	1.06 ± 0.08ab	0.95 ± 0.21
20:1(n-9)	1.23 ± 0.13	1.17 ± 0.04	1.14 ± 0.04	1.20 ± 0.08	1.50 ± 0.14
20:2(n-6)	1.11 ± 0.02	1.17 ± 0.04	1.08 ± 0.05	1.14 ± 0.09	0.90 ± 0.14
20:3(n-6)	1.93 ± 0.05a	2.07 ± 0.10a	1.67 ± 0.06b	1.97 ± 0.07a	1.70 ± 0.28
20:4(n-6)	2.59 ± 0.20	2.52 ± 0.18	2.98 ± 0.40	3.82 ± 1.10	2.30 ± 0.71
20:5(n-3)	1.21 ± 0.21b	1.22 ± 0.05ab	1.70 ± 0.26a	1.49 ± 0.15ab	0.75 ± 0.07
22:5(n-6)	1.03 ± 0.06	1.06 ± 0.05	1.06 ± 0.10	1.18 ± 0.14	1.05 ± 0.35
22:5(n-3)	1.22 ± 0.02	1.18 ± 0.06	0.43 ± 0.12	1.28 ± 0.07	0.80 ± 0.14
22:6(n-3)	4.28 ± 0.79b	5.74 ± 0.34ab	6.14 ± 0.31a	5.73 ± 0.27ab	3.10 ± 0.42
Other	1.10 ± 0.02	0.97 ± 0.02	1.20 ± 0.04	1.19 ± 0.03	0.55 ± 0.08
Total	88.25 ± 0.44	90.49 ± 0.31	89.05 ± 0.63	90.91 ± 0.57	96.25 ± 0.31
Sat.	24.10 ± 0.08ab	25.04 ± 0.58a	23.72 ± 0.18b	24.23 ± 0.58ab	25.00 ± 0.71
Monene	38.19 ± 0.81	37.79 ± 0.68	36.68 ± 2.07	37.40 ± 1.14	43.85 ± 1.34
Diene	11.95 ± 0.22	12.35 ± 1.69	11.67 ± 0.55	12.03 ± 0.21	16.45 ± 1.20
Triene	3.38 ± 0.07	3.35 ± 0.09	3.30 ± 0.10	3.37 ± 0.06	2.65 ± 0.07
PUFA‡	25.96 ± 0.50	27.66 ± 0.12	28.66 ± 1.06	29.28 ± 1.94	27.40 ± 0.56
n-3	7.98 ± 0.58b	9.25 ± 0.72ab	10.73 ± 0.53a	9.72 ± 0.50ab	5.60 ± 0.28
n-6	17.99 ± 0.13	18.41 ± 0.45	17.92 ± 0.53	19.56 ± 1.45	21.80 ± 0.28
n-3/n-6	0.44 ± 0.03b	0.50 ± 0.02ab	0.60 ± 0.04a	0.50 ± 0.01ab	0.26 ± 0.01

*Values are means ± SE for three replicate ponds. Three fish were analysed per pond, so treatment means represent analysis of nine individual fish. Means within a row having the same letter were not significantly different ($P > 0.05$).
†Stocking values are for comparative purposes and are not included in statistical analyses.
‡PUFA = polyunsaturated fatty acids.

their retention times with those of authentic standards (Supelco, Bellefonte, PA).

Statistical analysis

Data were analysed by analysis of variance (ANOVA) using the SAS ANOVA procedure (Statistical Analysis Systems, 1988). Duncan's multiple range test was used to determine where differences existed among means. Percentage data were transformed to arc sin values prior to analysis (Zar, 1984). Means are reported as untransformed data to facilitate comparison with related studies.

RESULTS

Saturated and unsaturated fatty acids

In fish fed throughout the study (controls), levels of saturated and unsaturated fatty acids were similar in the three tissues (white muscle, liver and brain). Fish starved for 28 days had significantly less ($P < 0.05$) saturated fatty acids in white muscle than fish starved for 14 days (Table 1). Livers from fish which had been starved and then refed had significantly lower ($P < 0.05$) levels of saturated fatty acids and higher percentages of monoenoic fatty acids than livers from fish starved for 14 days, but not different ($P > 0.05$) from controls or fish starved for 28 days. Diene levels were significantly lower in livers of fish starved 28 days than in fish starved 14 days.

Levels of n-3 fatty acids were significantly higher ($P < 0.05$) in the white muscle of fish starved 28 days than in control fish (10.7% and 8.0%, respectively). In the livers of fish starved 14 days, n-3 levels were significantly higher ($P < 0.05$) than control fish (Table 2). In livers of refed fish, n-3 levels were significantly lower than in fish starved 14 or 28 days ($P < 0.05$). The n-3/n-6 ratio was significantly increased by starvation (14 or 28 days) in white muscle and liver ($P < 0.05$). Refeeding caused n-3/n-6 ratios to return to control values. Starvation and refeeding caused no significant differences ($P > 0.05$) in the n-3/n-6 ratio of the brain (Table 3).

Individual fatty acids

Changes in concentrations of individual fatty acids in the white muscle were relatively small (Table 1). However, fish not fed for 28 days had significantly less 16:0 and 20:3(n-3) and significantly more docosahexaenoic acid (or DHA), 22:6(n-3) than fully fed control fish ($P < 0.05$).

Liver concentrations of 16:0 and eicosapentaenoic acid (or EPA), 20:5(n-3) were significantly higher ($P < 0.05$) in fish starved 14 days than in control fish (Table 2). In livers of fish starved 14 or 28 days, EPA was significantly higher than in the livers of fish refed or fully fed throughout the study ($P < 0.05$). Livers of fish refed for 14 days had significantly lower levels of 16:0 than fish in other treatments ($P < 0.05$). Liver concentrations of 22:5(n-3) and DHA were significantly lower in refed fish than in fish starved 14 or 28 days ($P < 0.05$).

Differences in the concentration of individual fatty acids of the brain were extremely small (Table 3). Significant differences were largely due to extremely small within-treatment variations. In refed fish, levels of 16:0 in the brain were significantly higher than in fish starved for 14 or 28 days and 16:1(n-9) was significantly lower than in control fish or fish starved for 14 days ($P < 0.05$).

Table 2. A comparison of the composition of some fatty acids (rel.%) in liver from channel catfish either fully fed (control), starved 14 days, starved 28 days, or starved 14 days then refed 14 days*

	Treatment				
Fatty acid	Control	Starved 14 days	Starved 28 days	Refed	Stocking†
14:0	0.47 ± 0.03	0.53 ± 0.07	0.44 ± 0.05	0.49 ± 0.04	0.40 ± 0.00
16:0	15.66 ± 0.37b	16.90 ± 0.09a	15.96 ± 0.02ab	14.50 ± 0.53c	13.05 ± 0.92
16:1(n-7 or 9)	2.00 ± 0.19	1.80 ± 0.06	2.00 ± 0.26	2.07 ± 0.16	1.40 ± 0.00
18:0	9.73 ± 0.51	9.90 ± 0.38	9.54 ± 0.34	10.24 ± 0.48	12.00 ± 0.99
18:1(n-9)	33.75 ± 0.44ab	31.61 ± 0.56b	35.27 ± 0.35ab	36.55 ± 1.81a	28.75 ± 0.21
18:2	5.11 ± 0.10	5.62 ± 0.12	5.04 ± 0.24	5.02 ± 0.33	9.00 ± 0.00
18:3(n-3)	0.37 ± 0.04	0.39 ± 0.03	0.38 ± 0.06	0.32 ± 0.08	0.40 ± 0.00
20:1(n-9)	1.89 ± 0.08ab	1.44 ± 0.07b	1.49 ± 0.17b	2.19 ± 0.21a	1.25 ± 0.07
20:2(n-6)	0.98 ± 0.14	1.17 ± 0.03	0.93 ± 0.05	1.06 ± 0.09	1.20 ± 0.00
20:3(n-6)	2.65 ± 0.69	3.00 ± 0.06	2.45 ± 0.22	2.45 ± 0.52	4.40 ± 0.28
20:4(n-6)	5.39 ± 0.47	3.99 ± 0.99	4.29 ± 0.25	4.95 ± 0.45	8.55 ± 0.49
20:5(n-3)	1.09 ± 0.09b	1.57 ± 0.05a	1.84 ± 0.16a	0.93 ± 0.21b	0.75 ± 0.07
22:5(n-6)	2.23 ± 0.28a	2.02 ± 0.13ab	1.50 ± 0.08b	2.07 ± 0.23a	4.05 ± 0.49
22:5(n-3)	1.06 ± 0.07bc	1.36 ± 0.02ab	1.40 ± 0.12a	1.02 ± 0.13c	1.45 ± 0.07
22:6(n-3)	9.92 ± 0.79ab	11.30 ± 0.13a	10.84 ± 0.06a	8.79 ± 0.59b	8.65 ± 0.49
Other	1.15 ± 0.02	1.20 ± 0.02	1.19 ± 0.03	1.04 ± 0.02	0.90 ± 0.75
Total	93.48 ± 1.00	93.79 ± 0.54	94.56 ± 0.24	93.68 ± 0.71	96.20 ± 0.15
Sat.	26.16 ± 0.59ab	27.59 ± 0.58a	26.18 ± 0.25ab	25.50 ± 0.60b	25.70 ± 1.84
Monene	37.83 ± 1.50ab	35.00 ± 0.73b	38.90 ± 0.21ab	40.97 ± 1.89a	31.40 ± 0.14
Diene	6.09 ± 0.12ab	6.79 ± 0.53a	5.97 ± 0.25b	6.08 ± 0.33ab	10.20 ± 0.00
Triene	3.35 ± 0.67	3.75 ± 0.15	3.28 ± 0.22	3.00 ± 0.44	4.80 ± 0.28
PUFA‡	29.49 ± 1.89	31.21 ± 0.06	29.48 ± 0.42	27.21 ± 1.20	39.10 ± 0.99
n-3	12.54 ± 0.80bc	14.72 ± 1.24a	14.54 ± 0.28ab	11.05 ± 0.94c	11.25 ± 0.35
n-6	16.95 ± 1.12	16.49 ± 0.19	14.94 ± 0.44	16.17 ± 0.67	27.85 ± 0.64
n-3/n-6	0.74 ± 0.02b	0.89 ± 0.05a	0.98 ± 0.04a	0.68 ± 0.06b	0.40 ± 0.00

*Values are means ± SE for three replicate ponds. Three fish were analysed per pond, so treatment means represent analysis of nine individual fish. Means within a row having the same letter were not significantly different ($P > 0.05$).
†Stocking values are for comparative purposes and are not included in statistical analyses.
‡PUFA = polyunsaturated fatty acids.

Table 3. A comparison of the composition of some fatty acids (rel.%) in brain tissue from channel catfish either fully fed (control), starved 14 days, starved 28 days, or starved 14 days then refed 14 days*

	Treatment				
Fatty acid	Control	Starved 14 days	Starved 28 days	Refed	Stocking†
14:0	0.67 ± 0.01	0.65 ± 0.02	0.63 ± 0.03	0.67 ± 0.03	0.85 ± 0.07
16:0	17.96 ± 0.03ab	17.77 ± 0.07b	17.75 ± 0.07b	18.39 ± 0.31a	19.15 ± 0.07
16:1(n-7 or 9)	3.13 ± 0.01a	3.10 ± 0.06a	2.88 ± 0.02ab	2.82 ± 0.13b	3.40 ± 0.14
18:0	10.00 ± 0.06	9.94 ± 0.12	10.16 ± 0.22	10.33 ± 0.40	10.07 ± 0.03
18:1(n-9)	30.24 ± 0.32	29.96 ± 0.40	29.83 ± 0.13	30.16 ± 0.81	30.80 ± 0.14
18:2	2.49 ± 0.07	2.25 ± 0.09	2.27 ± 0.13	2.66 ± 0.16	5.85 ± 0.07
18:3(n-3)	0.33 ± 0.03a	0.21 ± 0.01b	0.26 ± 0.03b	0.30 ± 0.04ab	0.40 ± 0.00
20:1(n-9)	1.28 ± 0.02ab	1.27 ± 0.01ab	1.24 ± 0.00b	1.29 ± 0.01a	1.15 ± 0.14
20:2(n-6)	0.33 ± 0.01b	0.34 ± 0.01ab	0.37 ± 0.01a	0.35 ± 0.01ab	0.65 ± 0.07
20:3(n-6)	1.08 ± 0.05	1.14 ± 0.02	1.14 ± 0.06	1.09 ± 0.04	1.80 ± 0.00
20:4(n-6)	2.71 ± 0.09	2.78 ± 0.04	2.71 ± 0.06	2.69 ± 0.13	4.30 ± 0.00
20:5(n-3)	0.26 ± 0.01	0.23 ± 0.01	0.26 ± 0.03	0.25 ± 0.01	0.25 ± 0.07
22:5(n-6)	0.61 ± 0.01	0.63 ± 0.01	0.60 ± 0.01	0.66 ± 0.04	0.85 ± 0.07
22:5(n-3)	0.51 ± 0.01	0.50 ± 0.00	0.57 ± 0.04	0.48 ± 0.05	0.70 ± 0.00
22:6(n-3)	12.83 ± 0.25	12.75 ± 0.31	12.95 ± 0.65	12.96 ± 0.65	15.05 ± 0.78
24:1	2.13 ± 0.02	2.36 ± 0.08	2.36 ± 0.07	2.01 ± 0.14	1.50 ± 0.00
Other	1.12 ± 0.02	1.18 ± 0.01	1.34 ± 0.10	1.61 ± 0.03	1.15 ± 0.04
Total	87.66 ± 0.27	87.02 ± 0.68	87.03 ± 0.37	88.36 ± 0.52	97.97 ± 0.82
Sat.	28.87 ± 0.06	28.67 ± 0.03	29.03 ± 0.61	29.84 ± 0.63	30.62 ± 0.04
Monene	37.35 ± 0.32	37.24 ± 0.35	36.89 ± 0.20	36.76 ± 1.12	37.20 ± 0.14
Diene	2.82 ± 0.08ab	2.59 ± 0.09b	2.64 ± 0.12ab	3.01 ± 0.17a	6.50 ± 0.00
Triene	1.41 ± 0.01	1.35 ± 0.03	1.40 ± 0.03	1.39 ± 0.03	2.20 ± 0.00
PUFA‡	21.44 ± 0.39	21.11 ± 0.29	21.19 ± 0.21	21.76 ± 0.71	30.15 ± 0.78
n-3	13.93 ± 0.22	13.68 ± 0.33	13.85 ± 0.28	13.99 ± 0.67	16.40 ± 0.85
n-6	7.52 ± 0.19ab	7.43 ± 0.04ab	7.38 ± 0.06b	7.77 ± 0.05a	13.75 ± 0.07
n-3/n-6	1.86 ± 0.03	1.84 ± 0.06	1.90 ± 0.06	1.80 ± 0.08	1.19 ± 0.07

*Values are means ± SE for three replicate ponds. Three fish were analysed per pond, so treatment means represent analysis of nine individual fish. Means within a row having the same letter were not significantly different ($P > 0.05$).
†Stocking values are for comparative purposes and are not included in statistical analyses.
‡PUFA = polyunsaturated fatty acids.

DISCUSSION

The ratio of n-3/n-6 fatty acids of white muscle and liver increased in starved fish. Most changes in n-3 levels and n-3/n-6 ratios of liver and white muscle were due to increases in DHA. Increases in DHA in the muscle of starved carp have been reported (Murata and Higashi, 1980; Takeuchi and Watanabe, 1982). In starved rainbow trout, DHA increased in the body and liver (Takeuchi and Watanabe, 1982; Kiessling *et al.*, 1989). Conservation of DHA may be due to its greater importance as an essential component of biological membranes. Membrane lipids are largely composed of phospholipids (Oritz and Gomez-Fernandez, 1987) and lipids from white muscle are known to be predominately phospholipids (Cai and Curtis, 1990).

The importance of PUFA in neural tissues has been demonstrated (Martinez, 1989). In this study, fatty acid levels in the brain were found to be similar among all treatments, indicating that fish may maintain brain fatty acid relationships at narrowly defined levels. This is in agreement with Bourre *et al.* (1989) who reported that in mice, the development of a deficiency of PUFA in the brain may require feeding n-3 deficient diets for several generations. Only during extremely adverse conditions do organisms modify the fatty acid composition of the brain (Martinez, 1989).

Although statistically significant treatment differences were identified in all tissues, the actual magnitude of changes were small. Yu *et al.* (1977) suggested that a mechanism exists in fish that regulates fatty acid composition. A biochemical strategy to maintain body composition during periods of starvation may be an adaptation to seasonal periods of fasting that many fish experience as part of their natural life cycle (Weatherly and Gill, 1981).

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