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Original article

Comparison of nutritional quality and volatile flavor compounds among bighead carp from three aquaculture systems

Beijuan Hu [a,b], Jie Zhou [a], Huimin Qiu [a], Xinxin Lai [a], Jing Li [a], Di Wu [a,b], Junqing Sheng [a,b], Yijiang Hong [a,b,*]

[a] School of Life Science, Nanchang University, Nanchang 330031, China
[b] Jiangxi Province Key Laboratory of Aquatic Animal Resources and Utilization, Nanchang University, Nanchang 330031, China

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ABSTRACT

To explore the differences in the nutritional quality of the muscles of bighead carp from different environments and aquaculture systems, we investigated three types of water bodies typically used for aquaculture: A common culture pond (NC), a natural lake (PY), and a cold water reservoir (XHK). Parameters affecting quality were evaluated, including muscle microstructure, fatty acid profiles, amino acid profiles, and volatile compounds. Fish from the XHK reservoir had the smallest muscle fiber diameter and the highest muscle fiber density (25.3 fibers/0.01 mm^2), while muscle fiber density was lowest in fish from the NC pond (9.7 fibers/0.01 mm^2). The bighead carp from the XHK reservoir had a much wider variety of unsaturated fatty acids, as well as higher levels of total polyunsaturated fatty acids. Eicosapentaenoic acid (EPA), docosahexenoic acid (DHA), and arachidonic acid (AA) were all significantly more abundant in the XHK group, increases of 7.48%, 12.12%, and 17.49%, respectively ($P < 0.05$). The bighead carp from NC contained more "fishy" volatile flavor substances, as well as hydrocarbons with higher threshold values. Fish from XHK and NC had a greater umami intensity due to the presence of abundant volatiles with special aromas, including 1-Octene-3ol, DL-Menthol, and 2-ethyl-.

1. Introduction

The aquatic conditions of aquaculture systems impact various properties of farmed aquatic animals, including appearance and nutritional value (Valente et al., 2011). In China, freshwater aquaculture systems are dominated by ponds and reservoirs; lake and river aquaculture systems are less common (China, 2019). The dynamics of a given culture system are controlled both by abiotic natural factors and by human influences (Brönmark and Hansson, 2002). Characteristics of pond culture systems include large quantities of feeds and fertilizers, high stocking densities, sophisticated management techniques, and small water surfaces (Costa et al., 2014). Although pond aquaculture systems substantially increase fishery production and associated incomes (Wang et al., 2015a,b), the use of such systems intensifies environmental problems, including water eutrophication, high nitrogen and phosphorous loads, and algal blooms; Pond systems also increase the risk of catastrophic fish diseases (Costa et al., 2014; Mia, 2015). To address such concerns, sustainable ecological aquaculture models, such as culture-based fisheries (CBFs), are widely used. These systems do not require human intervention, as the fishery species consume natural food organisms, such as phytoplankton and zooplankton (Li and Xu, 1995). Under the CBF model, farm-produced seed fish are released into reservoirs or lakes and recaptured using fishing methods that depend on the trophic state of the water body (Jayasinghe et al., 2005). In most reservoirs and lakes characterized by large surface areas, rich natural bait communities have developed rapidly (Guo et al., 2012; Wang et al., 2015a,b).

Fish nutrition and flavor are affected by environmental conditions, including water and sediments, as well as food source, such as feed ingredients or plankton taxa (Josephson et al., 1991). However, it is unclear whether consumers will be satisfied with the nutritional value and flavor of fish raised under natural conditions in reservoirs and lakes. For example, previous studies have shown that Ictalurid catfish raised in ponds often acquire undesirable off-flavors prior to harvest (Tucker and Schrader, 2019). However, wild crabs, which inhabited rivers or lakes and consumed natural food, had greater umami intensity and nutritional quality than pond-

* Corresponding author.
E-mail address: yjhong2008@163.com (Y. Hong).

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reared crabs raised on formulated feed (Wang et al., 2016). Indeed, the nutritional value of aquaculture species differs depending on the environmental characters of the aquaculture system, including diet (Zhuang et al., 2016) and water temperature (Copeman et al., 2013). From a market perspective, flavor and quality are the primary standards for fish selection (Jorge et al., 2019). Textural characters, including muscle fibers and water-holding capacity, are also important factors affecting the perceived quality of the flesh (Wang et al., 2015a,b). In some countries, CBFs have effectively increased fishery production by utilizing natural aquatic environmental resources (Xie and Liu, 2014). The theories and practices associated with the successful extensive stocking of reservoirs and lakes, such as primary productivity, have become well developed (Jayasinghe et al., 2005; Guo et al., 2012), but comparisons of flavor and nutrition among pond, reservoir, and lake culture systems are scarce.

Bighead carp (*Arischthys nobilis*; family Cyprinidae) are widely distributed in Southeast Asia. Bighead carp are the seventh most intensively-cultured fish species (Fu et al., 2016). The increasing introduction and stocking of bighead carp in most reservoirs in China has not only increased fish production, but it has proved an effective bio-management strategy, as algal blooms have been prevented or eliminated (Guo et al., 2012). As a representative economically important freshwater fish, bighead carp provide abundant unsaturated fatty acids and protein (Upadhyaya et al., 2019). It is worth noting that ω-3 polyunsaturated fatty acids, especially EPA and DHA, play an important role in the prevention of diseases, such as cardiovascular disease (Hong et al., 2015).

Thus, we used gas chromatography-mass spectrometry (GC–MS) to compare flesh quality (e.g., muscle fiber structure), nutrition (e.g., fat content, protein content, fatty acid profile, and amino acid profile), and flavor among carp raised in three typical aquaculture systems: A cold-water reservoir (XHK), a natural lake (PY), and a common culture pond (NC). Our aim was to clarify the differences in nutritional value and flavor among bighead carp raised in the three aquaculture systems. Our results will provide preliminary data about freshwater culture systems.

2. Materials and methods

2.1. Study areas

The alpine cold-water reservoir (XHK) lies between 42° 15′–43°N and 11° 30′–12° 15′W (Fig. 1). It is 420 m above sea level, with an area of 90 ha. The nutrition at this site is poor. The natural lake (Poyang Lake, PY) lies between 42° 15′–43°N and 11° 30′–12° 15′W (Fig. 1). The average annual average temperature in this lake is 17 °C (Duan et al., 2016). The common culture pond (NC) lies between 42° 15′–43°N and 11° 30′–12° 15′W (Fig. 1). The surface area of the pond is about 1.32 acres, and the water is a nutrient rich.

2.2. Material and sample preparation

We captured a total of 45 healthy adult bighead carp (*Hypophthalmichthys nobilis*) from Xiahuikeng reservoir, Poyang Lake, and Nancheng pond. Carp were maintained in PVC tanks, supplied with a continuous flow of aerated well water at 21 °C. Muscle samples were obtained from the dorsal body (above the lateral line). Muscle samples were homogenized for use in subsequent experiments.

2.3. Microstructure

The muscles of three bighead carp from different sources were cut transversely into 0.5 × 0.5 cm blocks and fixed in formalin for 24 h. Fixed blocks were embedded in paraffin, sectioned, and stained with hematoxylin and eosin (Guo et al., 2009). The long and short diameters of 100 muscle cells from each sample were measured under an optical microscope; The cross-sectional areas of the muscle cells and the connective tissues per 0.01 mm^2 were also measured (Ayala et al., 2005; Taylor et al., 2002). Tissue images were observed and photographed using an Olympus BX41 biomicroscope with a digital camera.

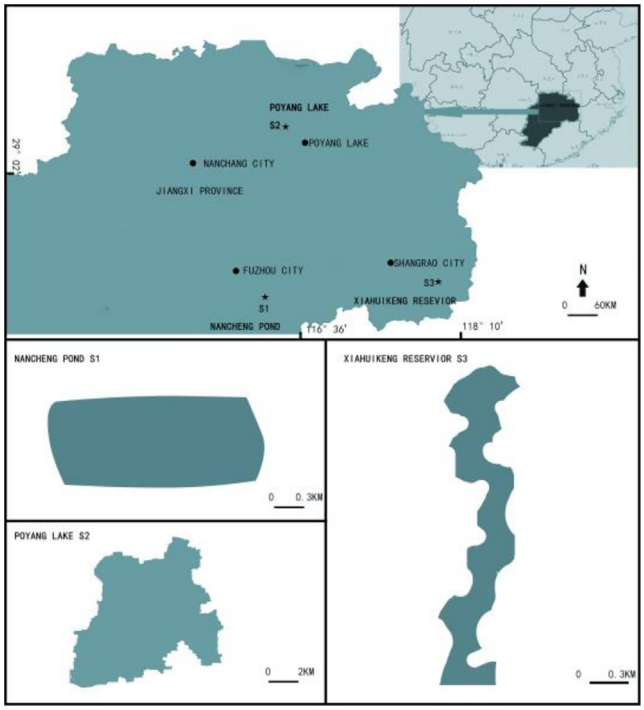

Fig. 1. Locations of the three research areas, and the sampling points within each area.

2.4. Basic nutrition

Gross chemical composition was analyzed following the methods of the Association of Official Analytical Chemists (AOAC) (Cunniff, 1995), with some modifications. Briefly, the moisture content was obtained by measuring the weight lost after mixed wet samples were dried in a drying oven at 105 ± 2 °C overnight. Crude fat and crude protein contents were determined using the methods of the AOAC, with modifications (Cunniff, 1995). Ash content was obtained after the incineration of moisture-free dry samples in a muffle furnace at 600 °C for 6 h.

2.5. Fatty acid analysis

All of the analyses were conducted according to methods described by the AOAC (Pang et al., 1995). Acidic hydrolysis was used for fatty acid extraction (Rozema et al., 2008). Pyrogallic acid was added to minimize fatty acid oxidative degradation. Ether was used for fatty acid extraction, followed by methylation to fatty acid methyl esters (FAMEs) using boron trifluoride and methanol. Capillary gas chromatography was used for FAME quantification, using triglyceride (triundecanoin) (C11: 0) as an internal standard. Samples were analyzed using a gas–liquid chromatograph (model 7890A; Agilent Technologies) equipped with a 7683B series injector. The carrier gas was helium, at a flow rate of 0.75 mL/min. After separation at 100 °C for 4 min, the temperature was increased to 240 °C at 3 °C/min for 15 min. Detector and injector temperatures

were 285 and 225 °C, respectively. Retention times were compared to the standards of the AOAC to determine peaks. Individual fatty acid levels were combined to determine total fat acids, and they were expressed as their triglyceride equivalents.

2.6. Amino acid analysis

All of the analyses were performed according to the methods of the AOAC (Pang et al., 1995; Rozema et al., 2008; Zielinski et al., 2017). We performed acid hydrolysis using hydrochloric acid (HCl, 6 N) for 24 h at 110 °C. Hydrolyzed samples were oxidized with performic acid at 0–5 °C overnight. Acid hydrolysis with HCl was repeated, and followed by alkaline hydrolysis for 22 h with 4.2 N NaOH at 110 °C. Following hydrolysis, we quantified amino acid profiles with a Beckman amino acid analyzer (model 6300; Beckman Coulter), using step gradients of sodium citrate buffers with the cation-exchange post-column ninhydrin derivation method.

2.7. Volatile compounds analysis

Volatile compounds were analyzed as described by Zhang et al. (2016), with modifications. The volatile compounds were isolated using the headspace solid-phase microextraction (HS-SPME) method. Carboxen/polydimethylsiloxane (CAR/PDMS; Supelco) fiber was used for volatile compound absorption. GC–MS analysis was performed on a 7890 gas chromatograph ion trap connected to a 5975 mass spectrometer (PE, Palo Alto). The effluent from the capillary column was splitless. We used a DB-35 capillary column (30 m long × 0.25 mm internal diameter × 0.25 μm film thickness, Agilent Technologies), and the carrier gas was helium (99.999% purity) at a flow rate of 1.0 mL/min. The oven temperature was increased from 40 °C to 100 °C at 5 °C/min, then again to 150 °C at 7 °C/min, and finally to 230 °C at 5 °C/min. The oven temperature was maintained at 230 °C for 5 min. The MS conditions were as follows: Detector interface temperature, 230 °C; Ion source temperature, 150 °C; And electron multiplier voltage, 400 V. The GC/MS-detected mass spectra of the volatile components in the samples were then compared with the mass spectrum patterns available in the National Institute of Standard and Technology (NIST) library version 0.5a (Arlorio, 2014).

2.8. Statistical analysis

All samples were analyzed independently at least three times. All of the data are presented as the means ± standard deviations (SD) of each group of samples (n = 3), except the volatile compound results. Statistically significant differences were identified using one-way analyses of variance (ANOVAs), with Fisher's LSD post hoc tests, using the SPSS statistical package (v.22, IBM, NY, USA).

3. Results

3.1. Microstructure

The microstructures of the bighead carp muscles differed visibly among the three groups (Fig. 2). In all of the bighead carp, irrespective of source, the arrangements of the muscle tissues were somewhat regular. Striations arose from alternating protein-dense A-bands and less dense I-bands within the myofibril. Morphologically, samples from XHK exhibited loosely-arranged muscle cells with very regularly aligned striations, and obvious muscle bundle separation (Fig. 1-a). Muscle cells were thin, and there was abundant connective tissue among muscle cells (Fig. 1-d). The muscle bundles in the samples from Poyang Lake (PY) were not obviously separated (Fig. 1-b), but connective tissue among muscle cells remained abundant (Fig. 1-e). The muscle bundles in the samples from NC were the most clearly separated (Fig. 1-c). Compared with the muscle cells of the fish from the XHK reservoir (XHK) and from PY, the muscle cells of the fish from Nancheng Pond (NC) were larger, and there was little connective tissue among muscle cells.

Using an image analyzer, which measured muscle cells per 0.01 mm^2, we found that the NC samples had the fewest muscle cells per unit area (9.7 fibers), followed by PY (13.1 fibers), and XHK (25.3 fibers); There were significant differences in cells per unit area among the three groups ($p < 0.05$; Table 1). The long and short diameters of the muscle cells, as well as the areas of connective tissue with respect to muscle cells, were also analyzed statistically. We found that the short diameters of the muscle cells in the NC samples were significantly greater than those of the other two groups ($p < 0.05$). However, the long diameters of the muscle cells did not differ significantly between the NC and PY samples ($p > 0.05$). The short diameters of the muscle cells were lowest in the XHK samples (13.54 μm), followed by the PL samples (18.14 μm) and the NC samples (23.94 μm); these short diameters differed significantly among the three groups ($p < 0.05$). Connective tissue was least abundant in the NC samples (12.29%), followed by the XHK samples (36.44%) and the PY samples (38.50%). This suggested that bighead carp from XHK and PY generally had more collagen in their muscles.

3.2. Basic nutrition

The proximate compositions of all studied samples were relatively varied (Fig. 3). The relative proportions of crude protein and crude fat were highest in the samples from PY. The XHK samples had 14.9% crude protein content, whereas crude protein content in the NC and PY samples was 18.1% and 18.2%, respectively. All of the samples were found to be rich sources of protein. Crude fat content was significantly greater in the PY group ($p < 0.05$), a twofold increase over the NC and XHK groups. Moisture content was significantly greater in the XHK group ($p < 0.05$). Ash content did not differ significantly among groups.

3.3. Fatty acid profiles of bighead carp

Across the bighead carp from three different sources, we detected a total of 15 fatty acids, including five saturated fatty acids (SFAs), three monounsaturated fatty acid (MUFAs), and seven polyunsaturated fatty acid (PUFAs; Table 2). There were no significant differences in SFAs among groups ($p > 0.05$), but the bighead carp from XHK had slightly higher levels of SFAs (30.53%) than the bighead carp from the other two sites. The bighead carp from NC and PY contained approximately the same levels of SFAs (26.88% and 26.44%, respectively). The most abundant SFA was palmitic acid (16: 0), accounting for more than half of all SFAs. Stearic acid (18: 0), which was slightly less abundant than palmitic acid (16: 0), was the second most abundant SFA. Notably, the levels of all SFAs except palmitic acid were lowest in the XHK group.

Levels of MUFAs and PUFAs differed significantly among carp from different sources ($p < 0.05$). We found that PUFAs were more abundant than MUFAs and UFAs. PUFA levels were highest in the XHK group (41.27%) and the PY group (30.38%), and lowest in the NC group (26.39%). Together, eicosapentaenoic acid (EPA, C20: 5n3) and docosahexaenoic acid (DHA, C22: 6n3) were over twice as abundant in the XHK group as compared to the NC group; this difference was significant ($p < 0.05$). Levels of EPA plus DHA in the PY group were intermediate between these two extremes. Arachidonic acid (AA, C20: 4) was most abundant in group XHK (17.49%), and much less abundant in fish from the NC and PY groups (5.45% and 2.97%, respectively). MUFA levels ranged from

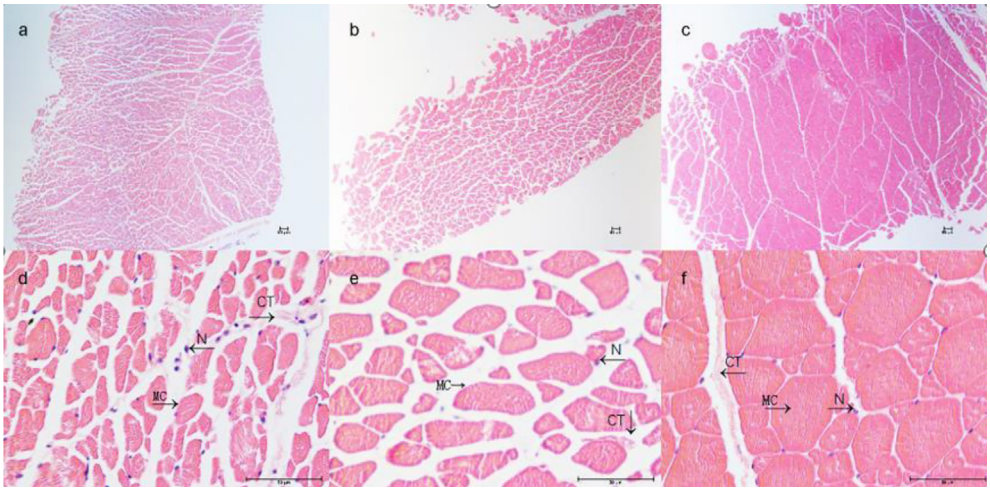

Fig. 2. Transections of muscle tissues of bighead carp from three sources. a: XHK × 40; b: PY × 40; c: NC×40; d: XHK × 400; e: PY × 400; f: NC × 400. (XHK = Xiahuikeng Reservoir; PY = Poyang Lake; NC = Nancheng Pond; MC: muscle cell; CT: Connective tissue; N: Cell nucleus).

Table 1
Muscle cells of bighead carp from three sources.

	XHK	PY	NC
Muscle Cell Density (cells/0.01 mm$^{2)}$	25.3 ± 1.30^{a}	13.1 ± 0.96^{b}	9.70 ± 1.08^{c}
LD (μm)	18.31 ± 0.66^{b}	14.65 ± 1.95^{a}	36.43 ± 1.69^{a}
SD (μm)	13.54 ± 0.47^{c}	18.14 ± 0.78^{b}	23.94 ± 1.13^{a}
Myocyte Area (%)	63.56 ± 2.34^{b}	61.50 ± 1.86^{b}	87.71 ± 1.09^{a}
Connective Tissue (%)	36.44 ± 2.34	38.50 ± 1.86	12.29 ± 1.09
Ratio (M/C)	1.85 ± 0.18^{b}	1.66 ± 0.15^{b}	7.84 ± 0.91^{a}

Note: Values within the same row not sharing a common superscript letter are significantly different ($p < 0.05$); LD = long diameters of cells; SD = short diameters of cells; M = Myocyte area; C = Connective tissue.

13.87% in the bighead carp from XHK to 27.75% in the bighead carp from NC (Table 3). In general, the bighead carp from XHK were lower in SFAs and richer in PUFAs, such as EPA, DHA, and AA.

3.4. Amino acid profiles of the bighead carp

Results are presented as mean ± SD (n = 3). Values within the same row not sharing a common superscript letter are significantly different ($P < 0.05$); EAA = essential amino-acid, NEAA = non-essential amino acid, HEAA = semi-essential amino acid, DAA = delicious amino acid.

Across the bighead carp from three different sources, 17 amino acids were detected, including seven essential amino acids [EAAs; threonine (Thr), valine (Val), methionine (Met), phenylalanine (Phe), isoleucine (Ile), leucine (Leu), and Lysine (Lys)], two semi-essential amino acids [HEAAs; histidine (His) and arginine (Arg)], and eight non-essential amino acids [NEAAs; aspartic acid (Asp), glutamic acid (Glu), serine (Ser), glycine (Gly), alanine (Ala), tyrosine (Tyr), cysteine (Cys), and proline (Pro)]. Similar levels of TAAs, EAAs, and NEAAs were measured in the bighead carp from NC and PY; levels of TAAs, EAAs, and NEAAs were significantly higher in the bighead carp from NC and PY as compared to those from XHK ($P < 0.05$). There were no significant differences in HEAA levels among the bighead carp from the three sources. Glu was most abundant amino acid across all of the investigated fish in the XHK, PY, and NC groups, with levels of 2.40 g/100 g, 2.93 g/100 g, and 2.94 g/100 g, respectively. Asp was another abundant amino acid. Compared with the bighead carp from XHK, the

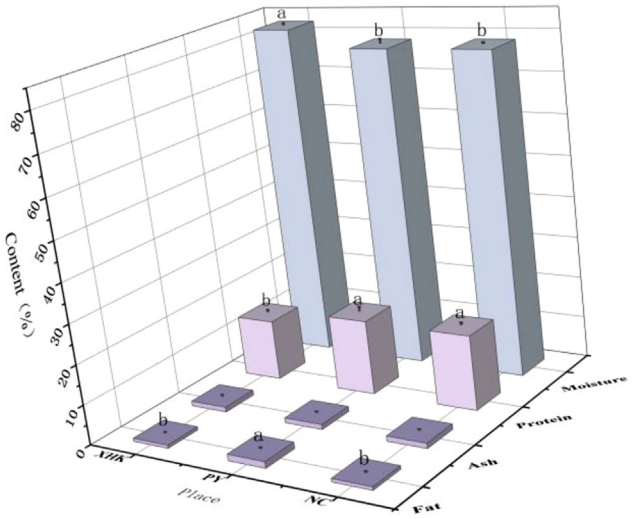

Fig. 3. Basic nutritional values of bighead carp from three sources, Note: Different superscript letters within the same row correspond to significant differences ($p < 0.05$), while the same superscript letters within the same row indicate that the values are not significantly different ($p > 0.05$).

bighead carp from NC and PY had significantly higher levels of Asp ($P < 0.05$). Bighead carp from NC and PY had approximately the same levels of delicious amino acids (DAAs): 4.88 g/100 g and 4.99 g/100 g, respectively. The relative abundances of individual DAAs in the muscle tissues were similar among the investigated bighead carp from NC and PY.

3.5. Volatile compounds in the bighead carp

Using the NIST mass spectrometry database, we analyzed the composition and relative levels of the main volatile flavor substances (Table 4). The levels of volatile compounds in the muscles differed among experimental groups. In total, we detected 42 compounds across the bighead carp from XHK, PY, and NC, including seven alcohols (six, five, and one, respectively), nine aldehydes (six, five, and five, respectively), three ketones (two, one, and

Table 2
Fatty acid compositions of bighead carp from three sources.

	Content%		
	XHK	PY	NC
(12:0)	0.54 ± 0.02^{c}	2.96 ± 0.38^{b}	4.96 ± 0.34^{a}
(14:0)	0.43 ± 0.03^{b}	0.83 ± 0.05^{a}	1.10 ± 0.18^{a}
(16:0)	15.59 ± 0.83^{b}	17.41 ± 2.03^{a}	15.65 ± 1.11^{b}
(18:0)	13.7 ± 0.43^{a}	4.75 ± 0.36^{b}	4.77 ± 0.58^{b}
(20:0)	0.27 ± 0.01^{b}	0.29 ± 0.01^{b}	0.39 ± 0.04^{a}
(16:1)	2.27 ± 0.15^{b}	5.22 ± 0.15 b	10.62 ± 2.32 a
(18:1)	11.21 ± 0.58^{b}	18.74 ± 0.87^{a}	16.36 ± 1.49^{a}
(20:1)	0.39 ± 0.02^{c}	1.13 ± 0.01^{a}	0.77 ± 0.01^{b}
(18:2)	1.98 ± 0.01^{b}	3.16 ± 0.31^{b}	5.38 ± 0.65^{a}
(18:3)	1.46 ± 0.07^{b}	4.65 ± 0.17^{a}	5.68 ± 0.65^{a}
(20:2)	0.41 ± 0.03^{a}	0.26 ± 0.02^{b}	0.30 ± 0.01^{b}
(20:3)	0.31 ± 0.02	0.37 ± 0.03	0.36 ± 0.09
(20:4)	17.49 ± 1.09^{a}	2.97 ± 0.1 c	5.45 ± 0.52 b
(20:5)	7.48 ± 0.65^{a}	6.64 ± 0.38 a	4.88 ± 0.01 b
(22:6)	12.12 ± 1.34^{a}	12.32 ± 1.33 a	4.33 ± 0.22 b
EPA+DHA	19.61 ± 1.48^{a}	18.96 ± 1.48 a	9.22 ± 0.22 b
Total SFA	30.53 ± 0.92	26.24 ± 2.33	26.88 ± 0.9
Total MUFA	13.87 ± 0.49^{b}	25.09 ± 0.91^{a}	27.75 ± 2.59^{a}
Total PUFA	41.27 ± 1.21^{a}	30.38 ± 1.43^{b}	26.39 ± 0.81^{b}

Notes: Results are presented as mean ± SD (n = 3). Values within the same row not sharing a common superscript letter are significantly different ($p < 0.05$); SFA = saturated fatty acids, MUFA = monounsaturated fatty acids, PUFA = polyunsaturated fatty acids.

Table 3
Amino acid compositions of bighead carp from three sources.

	Content g/100 g		
	XHK	PY	NC
Thr	0.66 ± 0.05^{B}	0.86 ± 0.05^{A}	0.84 ± 0.03^{Ab}
Val	0.80 ± 0.03	1.08 ± 0.13	1.04 ± 0.05
Met	0.44 ± 0.05^{B}	0.57 ± 0^{A}	0.57 ± 0.03^{Ab}
Ile	0.69 ± 0.03^{B}	0.92 ± 0.02^{A}	0.92 ± 0.02^{A}
Leu	1.23 ± 0.1^{B}	1.56 ± 0.01^{A}	1.55 ± 0.06^{A}
Phe	0.56 ± 0.03^{B}	0.74 ± 0^{A}	0.71 ± 0.02^{A}
Lys	1.20 ± 0.15^{B}	1.69 ± 0.07^{A}	1.7 ± 0.05^{A}
Asp	1.51 ± 0.05^{B}	1.97 ± 0.14^{A}	1.94 ± 0.03^{A}
Glu	2.40 ± 0.18	2.93 ± 0.11	2.94 ± 0.16
Ser	0.60 ± 0.01^{B}	0.76 ± 0.01^{A}	0.75 ± 0.05^{A}
Gly	0.72 ± 0.02^{B}	0.87 ± 0.02^{A}	0.83 ± 0.04^{Ab}
Pro	0.50 ± 0.07	0.63 ± 0.04	0.63 ± 0.04
Ala	0.83 ± 0.05	1.07 ± 0.11	1.07 ± 0.12
Cys	0.09 ± 0^{B}	0.12 ± 0^{A}	0.12 ± 0^{A}
Tyr	0.34 ± 0.01^{B}	0.51 ± 0.01^{A}	0.56 ± 0.03 A
His	0.26 ± 0^{C}	0.49 ± 0.04^{A}	0.37 ± 0.01^{B}
Arg	0.98 ± 0.07	1.22 ± 0.05	1.24 ± 0.22
Total EAA	5.60 ± 0.24^{B}	7.44 ± 0.13^{A}	7.36 ± 0.1^{A}
Total NEAA	7.01 ± 0.11^{B}	8.88 ± 0.05^{A}	8.85 ± 0.16^{A}
Total HEAA	1.25 ± 0.07	1.71 ± 0.08	1.61 ± 0.22
Total AA	13.87±0.4^{B}	18.04±0.22^{A}	17.83±0.17^{A}
DAA	3.91±0.14^{B}	4.9±0.14^{A}	4.88±0.13^{A}

one, respectively), five alkanes (two, three, and two, respectively), eight alkenes (four, three, and five, respectively), four aromatics (one, two, and two, respectively), two acids (zero, two, and zero, respectively), and four other compounds. We identified four volatile compounds (1-Octen-3-ol, octanal, nonanal, and 3-Octadecene) as characteristic of the bighead carp because these compounds were identified in all of the bighead carp, irrespective of source. The highest levels of alcohols (20.565%) were detected in XHK; alcohols were twice as abundant in bighead carp from XHK as compared to those from NC. The highest levels of 1-Octene-3-ol were identified in XHK samples (11.013%), followed by PY samples (6.175%) and NC samples (6.042%). DL-Menthol was detected in the PY group only, and 1-hexanol, 2-ethyl- was detected in the XHK group only. 1-Nonanol and 1-Octanol were two common alcohols detected in the samples from XHK and PY, and these compounds were absent in NC. Tetradecanal (C14) accounted for a large proportion of the total alcohols in NC. Ketone levels were highest in samples from XHK (1.778%), followed by samples from PY (1.441%), and samples from NC (0.342%). We detected 2-Nonanone in NC samples, 2-Undecanone in PY samples, and 2-Undecanone and 2-Octanone in XHK samples. Across all of the volatile compounds, hydrocarbons were the most abundant. Alkane levels were highest in the NC samples (48.551%), followed by PY samples (26.466%) and XHK samples (16.001%). Only two acids were detected across all samples, and only in samples from PY.

4. Discussion

In this study, the flesh quality and flavor of bighead carp from three typical types of aquaculture systems were evaluated. Differences among the studied groups were noticeable. Our results revealed that samples from XHK and PY had higher muscle densities, PUFA levels, and umami intensities. In contrast, fish in the NC group had a higher protein content and harder muscles. We initially predicted that fish cultured in high-density tropical ponds would be low in UFAs, high in protein, and have tender muscles, whilst fish raised under natural conditions would have high levels of UFAs and a pleasant aroma. Our results were partially consistent with our predictions. Several studies have investigated the impacts of environmental conditions on qualities such as fatty acid composition, flavor quality, and basic nutrition (Hong et al., 2015; Kong et al., 2012). Major differences in nutrition content were associated with various environmental variables, including habitat (Cengiz et al., 2010), dietary sources (Shao et al., 2014), water temperature (Bjørnevik et al., 2003), and water surface area (Rincón et al., 2016).

A previous study indicated that water bodies with larger surface areas might stimulate hypertrophy in the muscle fibers of gilthead sea bream (Valente et al., 2011). In addition, muscle cellularity was shown to differ considerably based on abiotic factors, such as exercise training (Johnston and Moon, 1980). Exercise training allows fish to quickly recruit muscle cells, leading to short-term cell proliferation (Rincón et al., 2016). PY lake is the largest freshwater lake in China (Duan et al., 2016), and XHK reservoir has a large surface area (90 ha). One possible explanation for the smaller muscle cell diameter and higher muscle cell density observed in the XHK and PY groups is that aquaculture systems with larger surface areas provide a greater space for fish movement and exercise, leading to intense cell proliferation in the fish from the XHK reservoir and PY lake. In a similar study of meat quality in Atlantic salmon, fish reared in standard cages had lower proportions of hypertrophied white muscle fibers, because these fish were reared in smaller spaces (Totland et al., 1987).

Muscle fiber diameter and density are the factors that primarily influence the textural characteristics of the flesh (Johnston et al., 2000). Ayala el al. reported that muscle fiber diameter was negatively correlated with fish hardness (Ayala et al., 2005). Apart from muscle fiber diameter and density, the taste of fish meat is related to its collagen content of the connective tissue in fish muscle (Rincón et al., 2016). Increased connective tissue in the muscle improves the ability of the muscle to retain moisture and to prevent juice loss (Lin, 2010). Collagen content in fish muscle might be partially related to a decrease in cathepsin activity (Jiang et al., 2016a,b). It is possible that our results revealed potential mechanisms underlying flesh quality that are driven by the type of aquaculture system. The NC group had only 12.29% connective tissue, while the XHK and PY groups had 36.44% and 38.50% connective tissue, respectively. The results suggested that the bighead

Table 4
Volatile compounds in the bighead carp from three sources.

	Compounds	Content (%)		
		XHK	PY	NC
Alcohols				
	1-Octen-3-Ol	11.013	6.175	6.042
	1-Heptanol	1.167	1.702	_
	1-Nonanol	1.499	0.966	_
	1-Octanol	3.729	3.951	_
	Dl-Menthol	_	0.557	_
	1-Hexanol, 2-Ethyl-	2.253	_	_
	2-Octen-1-Ol, (E)-	0.904	_	_
	Total	20.565	13.351	6.042
Aldehydes				
	Butanal, 2-Ethyl	2.380	_	2.816
	Octanal	2.955	3.760	1.156
	Nonanal	6.481	9.751	2.237
	Tetradecanal	_	1.500	8.142
	Pentadecanal-	1.144	_	_
	Hexadecanal	_	_	0.370
	Decanal	0.836	0.612	_
	Benzaldehyde, 3-Ethyl-	_	0.683	_
	Pentanal, 3-(Hydroxymethyl)-4, 4-Dimethyl-	2.177	_	_
	Total	15.973	16.306	14.721
ketones				
	2-Nonanone	_	_	0.342
	2-Undecanone	1.066	1.411	_
	2-Octanone	0.712	_	_
	Total	1.778	1.411	0.342
Hydrocarbons (Alkanes, Alkanes, Alkenes, Aromatics)				
Alkanes	Heptadecane	_	23.842	48.080
	Hexadecane	0.597	_	0.471
	Pentadecane	_	1.734	_
	Undecane	_	0.890	_
	Heneicosane	15.407	_	_
	Total	16.004	26.466	48.551
Alkenes	3-Tetradecene, (Z)-	0.896	_	0.704
	3-Octadecene, (E)-	3.255	1.026	2.268
	(-)-Alpha-Cedrene	7.891	_	1.417
	1H-3a, 7-Methanoazulene, Octahydro-3, 8, 8-Trimethyl-6-Methylene-, (3R, 3as, 7S, 8as)-	0.698	_	_
	Di-Epi-. Alpha. -Cedrene	_	_	0.920
	Cyclohexene, 3-(1, 5-Dimethyl-4-Hexenyl)-6-Methylene-, [S-(R*, S*)]-	_	_	0.424
	Naphthalene, 1, 2, 3, 5, 6, 7, 8, 8a-Octahydro-1, 8a-Dimethyl-7-(1-Methyletheny	_	1.729	_
	1, 6, 10-Dodecatriene, 7, 11-Dimethyl-3-Methylene-, (E)-	_	0.670	_
	Total	12.74	3.425	5.733
aromatics	Naphthalene, 2-Methyl-	_	8.327	1.482
	Naphthalene, 1, 6-Dimethyl-4-(1-Methylethyl)-	3.874	_	1.259
	Benzene, Pentamethyl-	_	1.112	_
	Naphthalene	_	1.586	_
	Total	3.874	11.025	2.741
Acids	Butyric Acid, 2, 2-Dimethyl-, Vinyl Ester	_	1.536	_
	N-Hexadecanoic Acid	_	0.496	_
	Total	0	2.032	0
Other compounds	Decamethylcylopentasiloxane	_	_	3.068
	1, 3, 6-Octatriene, 3, 7-Dimethyl-, (Z)-	_	_	0.721
	Phenol, 2-Methoxy-3-(2-Propenyl)-	_	_	18.45
	Cyclotrisiloxane, Hexamethyl-	2.097	_	_
	Total	2.097	0	22.239

carp from PY lake and XHK reservoir had tender meat, which is preferred by customers.

Fish trigger several adaptive mechanisms, such as tighter muscle tissues, when exposed to lower temperatures (Chen et al., 2018). Similarly, the XHK reservoir is located at a high altitude and has low temperatures, while the low annual average temperature at PY lake is 17 °C (Duan et al., 2016). Temperature may be factor explaining the tenderness of the muscles in the XHK and NC groups. The relative concentrations of unsaturated fatty acids increase at lower temperatures, in order to maintain cell fluidity (Laurel et al., 2012). Consistent with this, we found that PUFAs were the most abundant fatty acids; PUFA levels the XHK were higher than those recorded in previous studies (Kaneniwa et al., 2000). This finding was consistent with our predictions. In fish, the activity of fatty acid desaturase, which is involved in the biosynthesis of functionally-active highly unsaturated fatty acids (i.e., EPA, DHA, and AA) from C_{18} PUFAs, is also modulated by water temperature (Tocher et al., 2004). Moreover, temperature and fatty acid composition directly or indirectly affect the composition of volatile compounds (Josephson et al., 1985).

Under certain conditions, volatile compounds are converted from autoxidation of proteins, amino acids, and lipids (Song et al., 2018). Based on previous studies, differences in the formation of volatiles among aquaculture system were probably due to differences in the activity levels of peroxidase and lipoxygenase under certain environmental conditions (Burnette et al., 1979; German et al., 1985). In most cases, unfavorable odors and tastes are due to the presence of geosmin or 2-methyl *iso*-borneol, which

are produced by cyanobacteria and actinomycetes in certain aquaculture ponds (Tucker and Schrader, 2019; Tucker, 2000). The high-density NC pond had several of these problems. Notably, 1-Heptanol, 1-Nonanol, and 1-Octanol were common alcohols in the XHK and PY groups, but these compounds were not detected in the NC group. Octanal and nonanal were detected in all of the studied samples, but levels of these compounds were higher in the XHK and PY groups. Importantly, 1-Octene-3ol lends a heavy, plant-like aroma to fish flesh (Josephson et al., 1983), while nonanal is characterized by strong aromas of green grass (Zhuang et al., 2016), and melon (Josephson et al., 1985). DL-Menthol, which was detected in the PY group, has a cool mint aroma, and 1-Hexanol, 2-ethyl-, which was detected in the XHK group, has a mild oil and rose flavor (Liao, 2008). However, the long-chain aldehydes of C13 contribute little to food flavor (Josephson et al., 1985). Tetradecanal (C14) accounted for a large proportion identified in the NC group. This may partially explain the poor taste of the bighead carp from NC. Consistent with this, Wang et al. concluded that wild crabs living under natural conditions had a stronger umami intensity than cultured crabs fed formulated food (Wang et al., 2016).

As filter-feeders, bighead carp feed on plankton and organic debris (Fu et al., 2016). The bighead carp in the XHK reservoir obtained all of their nutrients, including proteins and fatty acids, from plankton and organic debris in the water body. Plant protein sources often cause animals to remain unsatiated for long periods (Alami-Durante, et al., 2010). We suspected that the fish in the XHK reservoir usually remain unsatiated due to the intake of large amounts of plant protein. Previous studies have shown that decreases in muscle fiber diameter induced by starvation were correlated with a significant upregulation in the expression of lysosomal cathepsin D (Alami-Durante, et al., 2010; Cleveland et al., 2009).

Plankton composition is also affected by environmental factors, such as dissolved oxygen, nitrogen, phosphorus, and temperature (Melek et al., 2011; Ren et al., 2011). Previous studies have shown that plankton are the main source of n-3 PUFAs, such as EPA and DHA, for fish (Hong et al., 2015), while AA is regarded as a biomarker of allochthonous (terrestrial) organic matter (Gladyshev et al., 2015). Fish in the XHK group had the highest levels of the PUFAs EPA and DHA. Notably, fish in the XHK group also had highest average level of AA (C20: 4): 17.49%. AA levels in fish from the other sites were only 5.45% and 2.97%. EPA and DHA are viewed as useful lipids, because they decrease the risk of atherosclerosis (Wang et al., 2019).

The fatty acid and protein composition of fish flesh reflect the diet of the fish (Valente et al., 2011). Bighead carp in the NC pond consumed artificial feed, which is rich in protein. Thus, it was unsurprising that protein and EAA levels were higher in the NC group, while PUFA levels were higher in the XHK group. Similarly, Li et al. found that bighead carp, which have low trophic levels because they mainly feed on plankton, had the highest levels of total PUFAs (Li et al., 2011). In contrast, Valente et al. (2011) found that fish reared under extensive systems on natural foods had the highest protein levels.

Because pond culture systems are often characterized by high densities, aquatic animals in these systems may produce stress responses (Zhao et al., 2019). The higher concentrations of EAAs in the NC group may be due to the higher demand for energy production and functional protein synthesis, as these processes are related to stress responses and fatty acid transport. In addition, higher levels of non-EAAs (NEAAs) may be necessary for gluconeogenesis in organisms subjected to stressful rearing conditions (Zhao et al., 2019). Jiang et al. (2016a,b) found that muscle protein synthesis was regulated by the mammalian target of rapamycin (mTOR)/S6 kinase (S6K) signaling pathway in grass carp in response to different concentrations of tryptophan in the environment. We hypothesize that fish in different aquaculture system underwent metabolic changes related to nutrition composition, and that these metabolic changes were influenced by environmental factors. Importantly, EPA, DHA, and AA can be enzymatically converted to aldehyde- and alcohol-type volatile aroma compounds in finfish and oysters [51]. It should be noted that our fatty acids analysis identified considerable amounts of ω-3 fatty acids in the XHK group, even thoughα-linolenic and γ-linolenic acids were not detected separately.

There were significant differences in the nutritional quality and volatile flavor profiles among bighead carp from environmentally-distinct aquaculture systems. Microscopic analysis of the muscle revealed that the bighead carp from the XHK group had the highest muscle fiber density and the smallest muscle fiber diameter, indicating that the flesh was fine and tender. The fish in the NC group had tighter muscles, and the fish in the PY group were intermediate. We demonstrated that the proportions of crude protein and crude fat were higher in the PY and NC groups. Although a much wider variety of PUFAs was detected in the XHK group, and certain PUFAs (e.g., EPA, DHA, and AA) were significantly more abundant in this group, the overall levels of protein and crude fat were lower. If the sum of EPA content plus DHA content reflects the nutritive value of fish for humans, bighead carp from the XHK reservoir had the highest nutritive value. In addition, bighead carp from the XHK and PY groups have pleasant, plant-like aromas. In this study, we analyzed the nutritional values and flavors of fish from various aquaculture environments, and discussed the possible factors causing the observed differences, such as diet, temperature, and water surface area. It is likely that it will be increasingly important to develop aquaculture systems with minimal environmental impact, as well as strict quality assurance programs. However, the potential relationship between the culture system and the quality of the meat requires further investigation.

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Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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