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Review Article

Recent advances in sturgeon nutrition

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ABSTRACT

Sturgeons are fish species of biological and economical importance, and most of them are endangered, vulnerable or rare because of their large size, late sexual maturity, long period between spawning, and longevity. These unique biological characteristics make them highly susceptible to overfishing, degradation of habitat and spawning ground, and contamination of water and sediments by pollutants. The objective of the current review is not to exhaustively include all studies on sturgeon nutrient requirements and utilizations conducted under laboratory conditions, but to critique some studies and update previous reviews. The goal is to provide a basis for recommendations for future research so that these important fish species can be managed and produced sustainably. Energy, protein, lipid carbohydrate, vitamin, and mineral requirements and utilizations were reviewed or critiqued. Future studies to develop suitable chemically defined diets to support good growth of sturgeon are urgently needed. Furthermore, future experiments should be designed systematically with more consideration on within and among studies and within and among different species of sturgeon. Finally, future experiments should be designed with a systematic approach with multiple doses (inputs) and multiple responses (outputs) at several levels of hierarchical organization in a biological system using traditional biochemical and modern molecular techniques and computer modeling with proper experimental design and methodology. This approach will provide a more realistic and holistic understanding of the mechanisms of nutrient requirements and utilizations, which will help us better manage wild sturgeon stocks and produce sturgeon more efficiently and sustainably under aquaculture conditions.

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1. Introduction

Sturgeons are species of biological (evolutional, geographical, morphological, anatomical, and physiological) and economical (ecological, recreational, and aquacultural) importance. These species belong to the phylum Chordata, superclass Osteichthyes, class Actinopterygii, order Acipenseriformes and family Acipenseridae. There are 27 species in the Acipenseridae family, but 4 species are extinct (Birstein, 1993). The 23 extant species are grouped into 4 genera with 2 species in *Huso,* 2 species in *Scaphirhynchus*, 3 species in *Pseudoscaphirhynchus* and 16 species in *Acipenser* (Scott and Crossman, 1973). These fishes evolved 250 million years ago in the Jurassic period and are considered genetically "living fossils" (Birstein, 1993; Billard and Lecointre, 2001). Furthermore, sturgeons maintain many primitive characteristics, such as a heterocercal caudal fin, a cartilaginous skeleton, a notochord in adults, and 5 rows of bony dermal plates (scutes) in the longitudinal body (Scott and Crossman, 1973). These fishes are also unique that they have a high capacity for hybridization, and in sympatric distribution nearly all species will hybridize (Billard and Lecointre, 2001). Sturgeons mainly live in temperate waters (from subtropical to sub-Arctic) of the Northern hemisphere; some grow and sexually mature in marine and brackish waters but migrate to freshwater to spawn, while others are land locked in freshwater for their entire life cycle (Billard and Lecointre, 2001).

Beluga sturgeon (*Huso huso*) in the Black, Caspian, and Azov Seas is the largest freshwater fish, which can reach a maximum weight of 1,000 kg, and shovelnose sturgeons (*P. kaufmanni, P. hermanni*, and *P. fedtschenkoi*) in the Aral Sea are the smallest sturgeons with a

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Table 1
Macronutrient requirements of different species of sturgeon.

Nutrients	Rainbow trout[1]	White sturgeon	Siberian sturgeon	Chinese sturgeon	Persian sturgeon	Beluga sturgeon	Stella sturgeon	Lake sturgeon	Adriatic sturgeon	Amur sturgeon	Russian sturgeon	Hybrid sturgeon
DP/DE, kcal/kg	4,200	NT	NT	NT	NT	NT	NT	NT	NT	NT	NT	NT
Protein, %	38	40[2]	42[3]	40–45[4]	40[5]	NT	NT	NT	NT	NT	NT	37[6]
Fatty acid, %												
18:3 (n-3)	0.7–1.0	R[7]	NT	NT	NT	NT	NT	NT	NT	NT	NT	NT
n-3 LC-PUFA	0.4–0.5	R[7]	NT	NT	NT	NT	NT	NT	NT	NT	NT	NT
18:2 (n-6)	1.0	R[7]	NT	NT	NT	NT	NT	NT	NT	NT	NT	NT
Cholesterol	NT	NT	NT	NT	NT	NT	NT	NT	NT	NT	NT	NT
Phospholipid	NT	NT	NT	NT	NT	NT	NT	NT	NT	NT	NT	NT

DP = digestible protein; DE = digestible energy; NT = not tested; R = required; LC-PUFA = long-chain polyunsaturated fatty acids.
[1] NRC, 2011 and listed as a reference.
[2] Moore et al. (1988).
[3] Médale et al. (1995).
[4] Xiao et al. (1999).
[5] Mohseri et al. (2007).
[6] Guo et al. (2012).
[7] Deng (1996).

maximum weight of 0.5 kg (Doroshov, 1985). These fishes usually have a subcylindrical body, an extended hard snout, and a ventral protrusible mouth with barbels (Billard and Lecointre, 2001). They are excellent bottom-feeders because they have very sensitive barbels on the underside of their snouts to detect bottom animals and their long and protruding mouth to suck up prey. The gastrointestinal tract of sturgeons is also very unique because their pyloric stomach walls are hypertrophied into a gizzard-like organ, the intestines of adult sturgeons have a functional ciliated epithelium, and their hindguts are modified into spiral valves (Buddington and Doroshov, 1986).

Over 80% of the existing sturgeon species are endangered, vulnerable, or on the brink of extinction (IUCN Red List, 2017) because of their late sexual maturity (3 to more than 20 years) and long period between spawning (2 to more than 5 years) in the wild (Birstein, 1993; Billard and Lecointre, 2001). Furthermore, their large size (3 to over 2,000 kg) and longevity (3 to over 100 years) make them very susceptible to overfishing, degradation of habitats and spawning grounds, and contamination of water and sediments by pollutants (Billard and Lecointre, 2001). Many species of sturgeon are currently being cultured for release to the wild to augment natural populations or are produced by aquaculture for human food consumption to relieve the fishing pressure on their wild stocks (Billard and Lecointre, 2001; Bronzi et al., 2011).

The objective of the current review is not to exhaustively include all studies on sturgeon nutrient requirements and utilizations conducted under laboratory conditions, but to critique some studies and to update previous reviews (Hung, 1988, 1991a,b; Médale et al., 1995; Hung and Deng, 2002; García-Gallego et al., 2009). Furthermore, despite considerable global interest in sturgeon aquaculture, there is still a paucity of information on sturgeon nutrient requirements and utilizations, and even on the general nutrition of sturgeons (Tables 1–4); this information is urgently needed for success in culturing these species of fish. The ultimate objective of this review is to encourage and to provide a basis and rationale for recommendations for future research so that these important fish species can be managed and produced sustainably.

2. Energy

To our knowledge, the only energetic studies that have determined the relationships among several components of the energy budget in sturgeons were conducted by Médale and Kaushik (1991), Médale et al. (1991), Cui et al. (1996), and more recently by Guo et al. (2012). Médale and Kaushik (1991) studied the energy utilization of 40-, 230-, and 1,500-g Siberian sturgeon (*Acipenser baerii*) using a trout feed with 50% crude protein, 11% fat, and 21.5 kJ/g dry diet. These authors found that feed intake decreased with size. Energy retention (ER) was higher in the 1,500-g sturgeon (55% as body lipid) than in the 40- and 230-g sturgeon, which retained energy mainly as body protein. Endogenous nitrogen loss was 60 mg/kg BW per day in sturgeon fasted for 4 weeks. As noted by the authors, a limitation of this study was the discrepancy between the comparative slaughter and the indirect calorimetric methods. A better indirect calorimetry similar to that used by Gisbert et al. (2001) should be used in future energetic studies of sturgeons with the comparative slaughter method.

Médale et al. (1991) studied the utilization of dietary non-protein energy in the Siberian sturgeon (initial body weight [IBW] = 49 g) using 2 dry diets (51% crude protein and 22 kJ/g dry diet) containing either 21.8% lipid and 9.9% crude starch or 12.5% lipid and 20% highly digestible starch. The sturgeon were fed 8 weeks of the 2 diets, and those fed the 21.8% lipid and 9.9% crude starch diet had lower specific growth rate (SGR), SGR = (ln FBW- ln IBW)/Days, where IBW and FBW were initial and final body weights, respectively, and feed efficiency (FE), FE[1] (%) = 100 × Wet weight gain/Weight dry feed fed, than those fed a diet with 12.5% lipid and 20% highly digestible carbohydrate. These authors reported that digestible energy was higher in the sturgeon fed the diet containing lower lipid and higher digestible carbohydrate. The increase in digestible energy resulted from an increase in body lipid in the sturgeon, while urinary and gill energy[2] were not different in sturgeon under the 2 dietary treatments. Fecal energy was higher in sturgeon fed the low-lipid and high-digestible carbohydrate diet. These results suggested that dietary lipid is a better energy source than carbohydrate to spare dietary protein in Siberian sturgeon. This study, however, used not only 2 diets with 2 levels of lipid but also 2 sources and 2 levels of carbohydrates; thus, the conclusions drawn tend to be very general. Future studies should be conducted using dose–response methods with a more graded level of a single source of dietary lipid, protein, and carbohydrate, similar to those used by Guo et al. (2012) so that a better cause-effect relationship can be established among the different energetic components in the sturgeon.

[1] To maintain consistency in the review, some of the feed efficiency values were re-calculated from the feed: gain ratio or feed conversion efficiency from the original reports.
[2] Definitions of different energy components of fishes can be found in NRC (1981) and Chapter 4 of NRC (2011).

Table 2
Essential amino acid (EAA) requirements of sturgeon (dry matter basis).

EAA	Siberian sturgeon, mg/100 g BW per day	White sturgeon, g/100 g protein	Rainbow trout[1], g/100 g digestible protein	Siberian sturgeon fully vitellogenic oocytes, g/100 g amino acid	White sturgeon whole body tissue, g/100 g amino acid	White sturgeon egg, g/100 g amino acid
Arginine	2.8	4.8	4.0	6.0	7.6	5.3
Cysteine	–	0.2	–	0.7	0.5	1.2
Histidine	1.1	2.3	2.1	2.9	2.4	1.3
Isoleucine	2.1	3.0	2.9	5.0	4.6	5.0
Leucine	3.2	4.3	4.0	8.2	6.8	6.3
Lysine	6.3	5.4	6.3	8.2	8.2	9.3
Methionine	–	2.0	2.9[2]	2.7	3.2	3.5
Phenylalanine	1.5	3.0	1.8[3]	4.5	4.9	4.8
Threonine	2.2	3.3	2.9	4.4	5.0	5.3
Tryptophan	–	0.3	0.7	0.7	0.7	–
Tyrosine	–	2.3	–	3.7	3.5	4.7
Valine	2.3	3.3	3.2	5.7	5.0	6.2
Reference	Kaushik et al. (1991)	Ng and Hung (1995)	NRC, 2011 Chapter 18 Table 18-1	Gisbert et al. (2002)	Ng and Hung (1994)	Ng and Hung (1994)

[1] Essential amino acid requirements of rainbow trout is listed for comparison purpose, and the values are recalculated based on a 38% digestible protein.
[2] Methionine + Cysteine.
[3] Phenylalanine + Tyrosine.

Table 3
Vitamin requirements of different species of sturgeon.

Vitamins	Rainbow trout[1]	White sturgeon	Siberian sturgeon	Chinese sturgeon	Persian sturgeon	Beluga sturgeon	Stella sturgeon	Lake sturgeon	Adriatic sturgeon	Amur sturgeon	Russian sturgeon	Hybrid sturgeon
Water soluble, mg/kg												
Vitamin C	20	NT	R[2]	NT	NT	R[3]	200–400[4]	NRG[5]	NT	NT	NT	NT
Thiamin	1	NT	NT	NT	NT	NT	NT	NT	NT	NT	NT	NT
Riboflavin	4	NT	NT	NT	NT	NT	NT	NT	NT	NT	NT	NT
Vitamin B_6	3	NT	NT	NT	NT	NT	NT	NT	NT	NT	NT	NT
Pantothenic acid	20	NT	NT	NT	NT	NT	NT	NT	NT	NT	NT	NT
Niacin	10	NT	NT	NT	NT	NT	NT	NT	NT	NT	NT	NT
Biotin	0.15	NT	NT	NT	NT	NT	NT	NT	NT	NT	NT	NT
Vitamin B_{12}	R	NT	NT	NT	NT	NT	NT	NT	NT	NT	NT	NT
Folacin	1	NT	NT	NT	NT	NT	NT	NT	NT	NT	NT	NT
Choline	800	NT	NT	NT	NT	NT	NT	NT	NT	NT	NT	NT
Myoinositol	300	NT	NT	NT	NT	NT	NT	NT	NT	NT	NT	NT
Fat soluble												
Vitamin A, mg/kg	0.75	NT	NT	NT	NT	NT	NT	NT	NT	1,050 IU/kg diet[6]	NT	NT
Vitamin D, μg/kg	40	NT	NT	NT	NT	NT	NT	NT	NT	NT	NT	NT
Vitamin E, mg/kg	50	NT	NT	NT	NT	R[7]	NT	NT	NT	NT	NT	NT
Vitamin K, mg/kg	R	NT	NT	NT	NT	NT	NT	NT	NT	NT	NT	NT

NT = not tested; R = required; NRG = not required for growth.
[1] NRC, 2011 and listed as reference.
[2] Xie et al. (2006).
[3] Falahatkar et al. (2006).
[4] Desimira et al. (2013).
[5] Moreau et al. (1999a,b).
[6] Wen et al. (2008).
[7] Amlashi et al. (2011).

Cui et al. (1996) studied the effects of rations from starvation to maximum in the 2.4-g to 22.5-g white sturgeon (*Acipenser transmontanus*). These authors reported that, within each size, SGR increased linearly with increasing rations, and FE was the highest at the maximum ration. The specific growth rate decreased with increasing fish size at the maximum ration. Digestible energy ranged from 94.8% to 96.4% of intake energy, and urinary and gill energy decreased with increased ration size. At the maximum ration, an average 64.9% of the metabolizable energy was spent on metabolism and 35.1% on net energy for growth. This study, however, was limited by the use of live tubificid worms because of the unique feeding habit (continuous nibbling) of cultured white sturgeon (Cui et al., 1997) in laboratory settings. This approach made intake energy difficult to estimate accurately and made the manipulation of energy density and protein energy ratio impossible. Furthermore, as noted by the authors, the linear relationship between growth and ration in sturgeon fed tubificid worms is different from the curvilinear relation of growth and ration in sturgeon fed dry artificial feeds (Hung and Lutes, 1987). This difference further complicated the extrapolation and thus the usefulness of the energetic budget to sturgeon fed dry artificial feeds under practical conditions of aquaculture production. Future studies should be conducted using more water-stable dry feeds with different protein and lipid concentrations, such as those used by Hung et al. (1998).

Guo et al. (2012) studied the effects of dietary protein level on the energetic budget of the 25-g hybrid sturgeon (*A. baerii* × *Aeromonas gueldenstaedti*) using diets with 7 levels of protein. These authors reported that after the 8-week growth trial, the SGR increased when dietary protein increased from 25% to 40% and then decreased thereafter. Intake energy decreased with increasing dietary protein, but protein retention was inversely

Table 4
Mineral requirements in different species of sturgeon.

Item	Rainbow trout[1]	White sturgeon	Siberian sturgeon	Chinese sturgeon	Persian sturgeon	Beluga sturgeon	Stella sturgeon	Lake sturgeon	Adriatic sturgeon	Amur sturgeon	Russian sturgeon	Hybrid sturgeon
Macrominerals, %												
Calcium	NR	NT	NT	NT	NT	NT	NT	NT	NT	NT	NT	NT
Chlorine	NT	NT	NT	NT	NT	NT	NT	NT	NT	NT	NT	NT
Magnesium	0.05	NT	NT	NT	NT	NT	NT	NT	NT	NT	NT	NT
Phosphorous	0.7	NT	0.5–0.9[2]	NT	NT	NT	NT	NT	NT	NT	NT	NT
Potassium	NR	NT	NT	NT	NT	NT	NT	NT	NT	NT	NT	NT
Sodium	NR	NT	NT	NT	NT	NT	NT	NT	NT	NT	NT	NT
Microminerals, mg/kg												
Copper	3										7–8[3]	
Iodine	1.1	NT	NT	NT	NT	NT	NT	NT	NT	NT	NT	NT
Iron	NT	NT	NT	NT	NT	NT	NT	NT	NT	NT	NT	NT
Manganese	12	NT	NT	NT	NT	NT	NT	NT	NT	NT	NT	NT
Selenium	0.15	NT	NT	NT	NT	11.6–20.3[4]	NT	NT	NT	NT	NT	NT
Zine	1.5	NT	NT	NT	NT	NT	NT	NT	NT	NT	NT	NT

NR = not required under practical conditions; NT = not tested.
[1] NRC (2011).
[2] Xu et al. (2011).
[3] Wang et al. (2016).
[4] Arshad et al. (2011).

related to dietary protein. Urinary energy, on the other hand, showed a positive relationship with dietary protein. Urinary energy, as percentages of intake energy, increased with increasing dietary protein levels. These authors proposed an energy budget for the hybrid sturgeon as follows: 100 Intake energy = 35.08 Fecal energy + 4.53 Urinary energy + 34.1 Metabolizable energy + 26.23 Net energy for growth. These authors also suggested that economic and environmental impacts should be considered when using high-protein diets for sturgeon because energy is one of the most important nutrients for animals. There are, however, only 3 studies on sturgeon energetics; therefore, more studies are needed to provide a better understanding of the biological mechanisms of energy utilization in sturgeons.

3. Protein

3.1. Optimum dietary protein

Optimum dietary protein at 40.5% (Moore et al., 1988), 40% (Médale et al., 1995), 40% to 45% (Xiao et al., 1999), 40% (Mohseni et al., 2007), and 37% (Guo et al., 2012) has been reported for the maximal growth of white (145 g IBW), Siberian (20 to 40 g IBW), Chinese (*Acipenser sinensis*, 8 to 34 g IBW), Persian (*Acipenser persicus*, 137 g IBW) and hybrid (*A. baerii* × *A. gueldenstaedti*) (25 g IBW) sturgeons, respectively. It is unclear whether there is a true difference in protein requirements among the different sturgeon species or the difference in protein requirements are mainly resulted from the different methodologies used in the studies. The different methodologies included different initial body weights, sources of dietary protein, other dietary components, experimental conditions, and statistical methods used among the studies. The difference in protein requirements among these sturgeon species, however, is relatively small, which makes using 40% as an estimate of the protein requirement of a new species of sturgeon feasible until a more accurate requirement is determined by a dose–response growth trial.

3.2. Optimum protein-to-energy ratio

Protein energy ratios have been studied in hybrid (*A. baerii* × *A. gueldenstaedti*), Persian and pallid (*S. albus*) sturgeons by Guo et al. (2012), Molla and Amirkolaie (2011), Mohseni et al. (2013), and Kittel and Small (2014). Based on the SGR, Guo et al. (2012) reported an optimum protein-to-gross energy ratio of 40% for a 17.9 kJ/g diet in 25-g hybrid sturgeon fed isoenergetic diets with graded concentrations of protein (25% to 55% at a 5% increment with a mixture of fishmeal [FM] and soybean meal [SBM]). Mohseni et al. (2013) reported in the 103-g Persian sturgeon that significantly higher SGR was observed in sturgeon fed a 40% protein and 19 kJ/g diet than those fed diets containing 45% to 50% protein and 16 to 18 kJ/g diet, whereas no significant difference in FE was observed in sturgeon fed the different diets. Kittel and Small (2014) reported that 73.3-g pallid sturgeon fed diets with 32% to 53% crude protein and 14.7 to 18.1 kJ/g diet grew similarly, as long as the gross energy was more than 14.7 kJ/g diet. Although no significant difference was reported in this study, the sturgeon fed the 40% protein and 18.1 kJ/g diet showed the best weight gain. Amrkolaie et al. (2012) reported that, in the 15 to 250 g beluga sturgeon, the total energy requirement was 27.5 to 109.5 kJ/fish per day, and the total protein requirement was 0.60 to 2.05 g/fish per day, respectively, using a factorial approach. Due to the complexity, the different approaches used, and the different ways the results were expressed, it is difficult to compare this study with the other 3 studies (Guo et al., 2012; Mohseni et al., 2013; Kittel and Small, 2014). Furthermore, this study did not provide sufficient information to convert the energy and protein requirements of beluga sturgeon to the more commonly used units of kJ/g and % of protein in the diet, which the other 3 studies adopted. Due to the complexity and insufficient information in the Materials and Methods section, it is not clear whether the study of Amrkolaie et al. (2012) was conceptually correct. However, with a wide range of experimental methods (2012), the narrow range of optimum protein-to-energy ratios (40% protein to 18 to 19 kJ/g diet) in several species of sturgeon suggested that it is reasonable to use these values in designing experimental diets for a new species of sturgeon until the actual value is determined. The results of Molla and Amirkolaie (2011) are not reviewed here because of the incorrect identification of the experimental design (naming a 3 × 3 factorial design as a 2 × 2 factorial design) and questionable statistical analyses using n (replications) = 50 instead of the true replications of 3.

3.3. Essential amino acids

There is a paucity of information on the essential amino acid (EAA) requirements of sturgeons, and there have been no new requirement studies since our last review in 2002 (Hung and Deng, 2002). The only EAA requirements estimated were in Siberian and

white sturgeons by Kaushik et al. (1991) and Ng and Hung (1995), respectively (Table 2). Neither study used a conventional dose–response growth trial because it is expensive and difficult to conduct and, more importantly, it takes a long time to complete the requirements of all 10 or so EAA. Another difficulty of using conventional dose–response growth trials to determine the requirement for individual EAA is that no suitable crystalline amino acid mixture diet exists that can support adequate growth in white sturgeon. Ng et al. (1996) showed significantly lower growth and FE of white sturgeons fed a crystalline amino acid mixture diet than those fed a diet with intact protein of a similar amino acid composition.

Kaushik et al. (1991) and Ng and Hung (1995) used whole-body tissue patterns or A:E ratios (ratio of individual EAA to the sum of EAA × 100) to estimate the EAA requirements of Siberian and white sturgeons, respectively. This method was first introduced by Arai (1981), with subsequent studies showing high correlations between whole-body EAA patterns and EAA requirement patterns in several species of fish (Cowey and Luquet, 1983; Wilson and Poe, 1985). Other studies also used whole-body, muscle, and egg patterns of EAA as an index to formulate diets with an ideal amino acid pattern (Arai, 1981; Ketola, 1982; Cowey and Luquet, 1983). The EAA pattern of whole body and egg in white sturgeon (Ng and Hung, 1994) and fully vitellogenic oocytes of Siberian sturgeon (Gisbert et al., 2002) were given in Table 2 as a reference. Gisbert et al. (2002) used a fully vitellogenic oocyte amino acid profile to estimate the EAA requirement of Siberian sturgeon, and their values were comparable to those of whole-body and egg essential amino acid profiles of white sturgeon (Table 2). However, it is difficult to compare their values with those of Kaushik et al. (1991) and Ng and Hung (1995) because the units are different in all 3 studies (Table 2). Future studies should use a more standardized unit so that comparisons among studies with different sturgeon species are possible.

Kaushik et al. (1991) noted that whole-body tissue EAA patterns and A:E ratios should be used only in defining an ideal dietary EAA pattern until quantitative EAA requirements using conventional growth or biochemical and metabolic responses to graded levels of the concerned amino acid in the diet are determined for the new sturgeon species.

3.4. Alternative protein sources

Alternative protein sources have been studied in white (Stuart and Hung, 1989), Amur (*Acipenser schrenckii*, Xu et al., 2012), hybrid (*Aeromonas nacarii* × *Acipenser baeri*, Sicuro et al., 2012), shovelnose (*S. platorbynchus*, Kittel et al., 2014), and Siberian (Kaushik et al., 1994; Rónyai et al., 2002; Mazurkiewicz and Przybył, 2003; Zhu et al., 2011; Xue et al., 2012; Yun et al., 2014; Sicuro et al., 2012) sturgeons. Stuart and Hung (1989) compared the growth performances of white sturgeon fed 7 alternative proteins to those that were fed the control protein (casein: wheat gluten: spray-dried egg white, 62:30:8 by weight) diet in an 8-week study using the sturgeon purified diet formulation (Hung et al., 1987). These diets were isonitrogenous (38% crude protein) and isoenergetic. The alternative proteins were either protein concentrates with 90% or higher crude protein content (casein, gelatin, defatted zein, and soybean concentrate grade II); the herring meal was obtained from a commercial feed mill, the shrimp meal was prepared in the laboratory, and both the herring and shrimp meals were defatted. Percent body weight increase (%BWI), %BWI = 100 × (FBW − IBW)/IBW, where IBW and FBW were initial and final body weight, respectively, showed that white sturgeon (16 g IBW) fed the control, casein, and defatted shrimp meal diets had significantly higher %BWI than those fed diets with other proteins. Sturgeon fed the defatted herring meal diet had significantly higher %BWI than those fed the SBM diet, which was in turn higher than those fed the egg white diet. Sturgeon fed the gelatin and defatted zein diets had the lowest %BWI. The protein efficiency ratio (PER) of sturgeon fed these diets showed a very similar pattern to those of %BWI. The patterns of FE, however, were slightly different, with the highest in sturgeon fed the casein diet, followed by the control, defatted shrimp meal, defatted herring meal, soybean, and egg white diets; those fed the gelatin and zein diets had negative FE values. The authors noted that the unexpected lower %BWI and FE in sturgeon fed the defatted herring meal and the defatted shrimp meal was resulted from the defatting process, which might have decreased the quality of these proteins (Deng et al., 2005). Furthermore, the poor %BWI and FE of sturgeon fed the egg white diet did not result from the poor protein quality but was more strongly associated with other factors, such as the very hard pellets of the egg white diet, which might have affected the palatability of the diet, as suggested by Hung et al. (1987).

Xu et al. (2012) compared the %BWI of Amur sturgeon (26 g IBW) fed diets with 0, 25%, 50%, 62.5%, 75%, 87.5%, and 100% of FM replaced with soybean isolate (SBI, alkali-extracted, acid-precipitated at its isoelectric point) with a 40% crude protein diet formulation in an 8-week growth trial. These authors showed that the replacement of FM with 75% or higher SBI resulted in significantly lower %BWI, whereas the %BWI values were not different in sturgeon fed diets with as high as 62.5% of the FM replaced by SBI. Sturgeon fed diets with 63.5% of their FM replaced by SBI also had a significantly higher FE than those fed diets with higher replacement of FM by SBI. These authors concluded that, in a 40% crude protein diet, 58% of the FM can be replaced by SBI with no significant growth effect in Amur sturgeon, using the broken line method as stated by Zeitoun et al. (1976).

Sicuro et al. (2012) fed 365-g hybrid sturgeon (*A. nacarii* × *A. baeri*) for 60 days with 1 of 4 isonitrogenous and isoenergetic diets, which were abbreviated as the FM, CG55, CG55MP25 and CG45PM25 diets. The body weight of the sturgeon fed the CG55 diet with 55% corn gluten meal, 8% herring meal, and 10% merigel was not significantly different from those fed the FM diet with 54% herring meal, 3.5% corn gluten meal, and 18% merigel. The body weight of the sturgeon fed the CG55MP25 diet with 55% corn gluten meal, 25% pea meal, 2% herring meal, and 5% merigel was also not significantly different from those fed the CG45PM25 diet with 45% corn gluten meal, 25% pea meal, 6% herring meal, and 5% merigel. Sturgeon fed the latter 2 diets, however, had significantly lower body weight than those fed the former 2 diets. Sturgeon fed the CG55 diet had the highest FE, followed by those fed the FM diet, and those fed the CG55MP25 and the CG45PM25 had the lowest FE. These authors recommended that corn gluten meal, but not pea meal, be used to replace FM in the hybrid sturgeon diet.

Rónyai et al. (2002) showed that the 6-week SGR of 33-g Siberian sturgeon fed a diet with 13% FM, 14.7% meat meal, 15% precooked and extruded full-fat SBM, 53.3% wheat meal, and 2.5% yeast was significantly higher than those fed diets containing 13% FM, 38.4% full-fat soybean, 44.6% wheat meal, and 2.5% yeast or 14.7% meat meal, 38.4% full-fat SBM, 42.9% wheat meal, and 2.5% yeast. Supplementation of these diets with 1.12% L-lysine and 0.85% DL-methionine seemed to have no effect on SGR. However, there was no significant difference in the PER among sturgeon fed the 6 diets. This study suggested that a high level of substitution of animal protein with full-fat soybean meal would result in poorer growth of Siberian sturgeon.

Mazurkiewicz and Przybył (2003) determined the suitability of casein as an alternative protein in 6.8-g Siberian sturgeon in a 50-day growth trial using diets containing 50% crude protein with only 2 replications per dietary treatment. They found no significant

difference in SGR in sturgeon fed 1 of 3 diets (K7 containing 28% FM, 15.8% bloodmeal, and 7% sodium caseinate; K14 containing 21% FM, 15.3% bloodmeal, and 14% sodium caseinate; and K21 containing 14% FM, 14.8% bloodmeal, and 21% sodium caseinate). Their SGR, however, was significantly higher than those fed the remaining 3 diets (K28 containing 7% FM, 14.4% bloodmeal, and 28% sodium caseinate; K35 containing 13.9% bloodmeal and 35% sodium caseinate; and K0 containing only 35% FM and 16.3% sodium caseinate). On the other hand, FE and PER showed the same pattern, with the highest values observed in sturgeon fed the K0 diet, which was significantly higher than those fed the K7, K14, and K21 diets. Sturgeon fed the K28 and K35 diets had the lowest FE and PER values. These authors suggested that sodium caseinate can be used to replace part of the FM and bloodmeal (up to 21%) with no significant reduction in growth rate in Siberian sturgeon.

Kittel et al. (2014) investigated the sensitivity of 175-g shovelnose sturgeon to dietary soy using diets containing 0, 17%, 34%, and 51% SBM. These authors showed that SGR was not significantly different in those sturgeon fed diets with 0 to 34% SBM, but those fed the diet with 51% SBM had significantly lower SGR. There was also no difference in FE in sturgeon fed diets with 0 to 34% SBM; however, those fed the 51% SBM diet had significantly lower FE. As noted by these authors, the SGR and FE were low in shovelnose sturgeon fed all 4 diets compared to those in other species of sturgeon. Studies of Rónyai et al. (2002), Mazurkiewicz and Przybył (2003) and Kittel et al. (2014) were preliminary in nature because of various limitations, such as only 2 replications per treatment and too large an initial body weight of the sturgeon; thus, further studies are needed to confirm their results and recommendations.

Kaushik et al. (1994) fed 160-g (IBW) Siberian sturgeon 3 months of 1 of 2 isonitrogenous diets (45% crude protein and isoenergetic, crude protein/gross energy [P/E] = 21 g/MJ) with either vitamin-free casein, SBM, and casein mixture (1:1) or a closed formulation commercial diet containing 51% crude protein from fish meal with a P/E of 25 g/MJ. Sturgeon fed the casein or the casein and soybean mixture diets had higher final body weight, FE, and PER than those fed the commercial diet. Major limitations of the study were the lack of information on the formulation of the commercial diet, the different levels of native corn starch in the casein, and the casein-soybean mixture diet, and the use of only duplications per dietary treatment.

Zhu et al. (2011) fed 29-g Siberian sturgeon 8 weeks of diets with 44% to 49% crude protein using various levels of FM, animal protein blend (40% meat and bone meal, 40% poultry by-product meal, and 20% hydrolyzed feather meal) and spray-dried blood meal with and without crystalline amino acid supplementation. The percent body weight gain in sturgeon fed the diet with 50% of the FM replaced with the animal protein blend was not significantly different from those fed the diets without replacement of FM by animal protein blend. Furthermore, sturgeon fed the diet with 50% of FM replaced with the animal protein blend, but with lysine and threonine supplementation, had significantly higher %BWI than those sturgeon that were fed the diet without replacement of FM by the animal protein blend. On the other hand, FE was significantly higher only in the group fed the diet with 25% of FM replaced by the blend of animal proteins. These authors suggested that further studies are needed to explore the higher level of FM replacement by the animal protein blend with amino acid supplementation.

Xue et al. (2012) conducted an 8-week growth trial on 39-g Siberian sturgeon fed diets with 37% to 41% crude protein using different levels of FM and animal protein blend (40% poultry by-product meal, 35% meat and bone meal, 20% hydrolyzed feather meal and 5% spray-dried blood meal) as their major protein sources with or without amino acid supplementation. Body weight gain and SGR were not affected by the level of dietary FM or the level of replacement of FM by the animal protein blend. However, FE was significantly affected by the dietary protein level, but not by the level of FM replacement with the animal protein blend. These authors concluded that dietary protein could be reduced from 40% to 36% using their formulation without any significant reduction in %BWI. Furthermore, FM in their formulation can be totally replaced with the animal protein blend in the 36% or 40% crude protein diets without any significant reduction of %BWI in Siberian sturgeon.

Yun et al. (2014) fed 39-g Siberian sturgeon 8 weeks of diets with various levels of FM, plant protein blend (60% SBM and 40% wheat gluten meal), brewer's yeast, and squid meal with or without amino acid supplementation. They reported no significant reduction in SGR or FE when the dietary protein was reduced from 40% to 36%. Furthermore, there was no difference in SGR or FE in sturgeon fed diets with all the FM replaced with the plant protein blend with or without lysine, methionine, and threonine supplementation. The results from the above studies (Stuart and Hung, 1989; Rónyai et al., 2002; Mazurkiewicz and Przybył, 2003; Zhu et al., 2011; Sicuro et al., 2012; Xu et al., 2012; Xue et al., 2012; Kittel et al., 2014; Yun et al., 2014) suggested that protein blends or mixtures are better protein alternatives than a single source of protein for sturgeons. This outcome may have resulted from the complementary effects of different proteins to provide a more balanced essential amino acid profile than a single protein source.

Liu et al. (2009) determined the apparent digestibility coefficients (ADC) of FM, meat and bone meal, poultry by-product meal, hydrolyzed feather meal, fermented feather meal, solvent-extracted cottonseed meal, and SBM, which were 94.5%, 84.5%, 90.4%, 90.9%, 87.7%, 87.6%, and 91.8%, respectively, in 8.4-g Siberian sturgeon. These authors concluded that juvenile Siberian sturgeon could digest these animal and plant protein mixtures very effectively. They also found that the ADC of amino acids varied significantly within and among the different proteins. Therefore, they recommended that when formulating these proteins in sturgeon diets, the ADC of the amino acids should be considered in addition to the EAA requirement and the total EAA content of the proteins in the diets.

4. Lipid

4.1. Optimum dietary lipids

There has been only one study on the optimum dietary lipid requirement in sturgeon (Guo et al., 2011). Guo et al. (2011) fed 67-g hybrid sturgeon (*A. baerii* × *Acipenser gueldenstaedtii*) 10 weeks of 1 of 7 isonitrogenous (37% crude protein) diets with increasing levels (4% to 19%) of a fish oil and soybean oil mixture (50:50). Specific growth rate, but not FE was significantly affected by the levels of dietary lipids. Broken line analysis on SGR showed that dietary lipid requirement for maximum growth of juvenile hybrid sturgeon was at 11.1%. Increasing dietary lipid levels had no effect on whole-body protein level, but whole-body lipid increased significantly with increasing dietary lipid levels. Hybrid sturgeon fed the diet with the highest lipid (19%) also had the highest whole-body lipid content. These authors suggested that hybrid sturgeon had relatively high capacity to adapt to the high lipid diets. This suggestion is in agreement with Hung et al. (1998) who reported that no difference in SGR and FE in the 114-g white sturgeon fed diets with increasing capelin oil (18.2% to 29.4%) and decreasing FM (71% to 57.9% of Norse LT94) was found. White sturgeon fed the diet with the highest capelin oil (35.1%) and lowest FM (50.8%) showed significantly lower SGR and FE than those fed 18.2% to 29.4% capelin oil. Hung et al. (1998), however, could not suggest unequivocally of an optimum dietary lipid requirement for white sturgeon because dietary protein levels

were decreased concomitantly with increasing dietary lipids in the study. Amirkolaie et al. (2012) fed 61-g beluga sturgeon either a high-fat (30%) or low-fat (15%) diet at 100% or 60% satiation level for 3 months and they found no significant interaction between dietary lipid and feeding level on final body weight. Final body weight, however, were significantly affected by dietary lipid and feeding levels. On the other hand, there is no significant interaction between dietary lipid and feeding level in FE and FE was affected significantly only by feeding level. Definite conclusion, however, is difficult to draw from this study because only 2 levels of dietary lipids were used.

4.2. Essential fatty acids

Essential fatty acid (EFA) requirement of 8-g white sturgeon was determined by Deng (1996) in a 16-week growth trial. The sturgeon were fed 1 of 8 purified diets that contained 12% tripalmitin, 11% tripalmitin + 1% tristearin, 11% tripalmitin + 1% triolein, 11% tripalmitin + 1% trilinolein, 11.5% tripalmitin + 0.5% trilinolein, 11% tripalmitin + 1% highly unsaturated fatty acids, 12% deodorized menhaden oil, and 12% control oil (corn oil: cod liver oil: lard, 1:1:1 by weight). Sturgeon fed the control oil diet had significantly higher SGR and FE than those fed the menhaden oil diet, which in turn was higher than those fed the remaining 6 diets. Body lipid concentration and hepatosomatic index were significantly higher in fish fed the menhaden and control oil diets than those fed the remaining diets. Lipid concentrations in liver were more responsive to dietary lipids than those in muscle lipid. Fatty acid compositions in the tissue reflected the dietary fatty acid profiles.

The fatty acid compositions of the tissue indicated that white sturgeon could desaturate and elongate 18:2 (n-6) and 18:3 (n-3). The level of 20:3 (n-9) was undetectable in fish fed diets with both (n-3) and (n-6) fatty acids, but higher in fish fed the diets deficient in n-3 or n-6 fatty acids. These results suggest that white sturgeon requires both (n-3) and (n-6) fatty acids. These authors also suggested that the ratios of 20:3 (n-9) to 20:4 (n-6) and 20:3 (n-9) to 22:6 (n-3) in the liver phospholipid can be used as indices of EFA deficiency in juvenile white sturgeon. Limitation of this study, however, is that it is not clear whether the poor growth and abnormal ratios of 20:3 (n-9) to 20:4 (n-6) and 20:3 (n-9) to 22:6 (n-3) in the liver phospholipid of sturgeon was resulted from EFA deficiency or the possible low digestibility of the synthetic triacylglycerols, such as tripalmitin, tristearin, triolein, and trilinolein, when compared to that of the natural triacylglycerols, such as the menhaden and control oil (corn oil: cod liver oil: lard, 1:1:1 by weight). Digestibility coefficient of the above synthetic triacylglycerols should be determined to eliminate the possibility of their poor digestibility as a confounding factor in the above study. Furthermore, a chemically defined diet using other synthetic triacylglycerols with similar digestibility to the fish oil should be developed so that qualitative and quantitative EFA requirement can be determined unequivocally.

4.3. Optimum dietary protein-to-lipid ratios

Optimum dietary protein-to-lipid ratio was studied in Persian sturgeon by Mohseni et al. (2007) and Hassani et al. (2011). Mohseni et al. (2007) fed 139-g Persian sturgeon 21 weeks of 1 of 8 diets containing either 40% or 45% of protein and 10%, 15%, 20%, or 25% lipid. Levels of dietary protein and interaction between levels of dietary protein and lipid had no significant effect on SGR of sturgeon fed these diets. However, SGR was significantly affected by the levels of dietary lipid. Protein efficiency ratio, on the other hand, was affected by the levels dietary protein, but not by levels of dietary lipid, and the interaction between protein and lipid levels was also not affected. Furthermore, levels of dietary protein, lipid, and interaction between protein and lipid levels had no effects on FE. These authors based on SGR concluded that the optimum diet protein-to-energy ratio was 40% and 18 to 20 mg/kJ, respectively. Persian sturgeon juvenile fed the diet with 40% crude protein and 25% lipid had the best overall growth performances.

Hassani et al. (2011) fed Persian sturgeon fingerlings (10 g IBW) 140 days with 1 of 12 diets in a 4 × 3 factorial experiment and the 12 diets contained either 40%, 45%, or 50% crude protein and 18.5, 19.8, 21.1, or 22.4 MJ/kg diet. Dietary lipid and nitrogen free extract in these diets also varied from 8% to 26% and 7% to 30%, respectively. Specific growth rate was not significantly affected by the dietary protein, energy, and interaction between protein and energy levels, but PER was significantly affected by dietary protein, energy, and their interaction. Feed efficiency was affected only by dietary energy level, but not by dietary protein or the protein and energy interaction. These authors concluded that diets containing 40% protein and 20.1% to 25.9% lipid with a P/E of 17.86 g/MJ can meet the dietary requirement without adverse effect on the Persian sturgeon fingerlings. The major limitation of this study is that the formulations of the experimental diets were not provided. The optimum protein-to-lipid ratios for other species of fish, however, have not been mentioned in all the NRC Nutrient Requirement in fishes (NRC, 1973; 1977; 1983; 1993; 2011) because it is not based on a sound biological concept. Therefore, usefulness of this ratio in the above studies is highly questionable.

4.4. Alternative lipid sources

Xu et al. (1993) fed 35-g white sturgeon 9 weeks of purified diets containing 15% of either control (corn oil: cod liver oil: lard 1:1:1), corn oil, cod liver oil, lard, linseed oil, soybean oil, safflower oil, or canola oil, and they found no significant difference in %BWI, FE, or whole-body proximate composition among the dietary treatments. Xu et al. (1996) also reported that white sturgeon could desaturate and elongate linoleic acid (18:2 n-6) and linolenic acid (18:3 n-3). The lack of growth difference in sturgeon fed the above diets may have resulted from the relatively large size (35 g IBW) and short period (9 weeks) of the growth trial as well as the absence of a depletion period. The lack of growth difference in this study may also have resulted from the very low EFA requirement and, more importantly, from the fact that all these natural oils/fats may contain a sufficient amount of EFA to prevent EFA deficiency, such as poor growth and FE in a 9-week feeding trial. Future studies should use smaller fish, longer feeding periods, and a depuration/acclimation period of 2 to 3 weeks before the beginning of the feeding trial.

Gawlicka et al. (2002) fed 3-day post-hatched white sturgeon larvae diets with 17%, 25%, 33%, and 42% lipid for 24 days. The diet with 17% lipid was commercially available with a closed formulation; thus, the composition of ingredients was unavailable. The other 3 diets contained 2% soy lecithin (SL) and 2% cod liver oil (CLO), 8% SL and 6% CLO, and 14% SL and 10% CLO. Sturgeon larvae fed the diet with 17% lipid had significantly higher SGR than those fed the diets with 25% and 42% lipid, but they were not different from those fed the diet with 33% lipid. Ebrahimnezhadarabi et al. (2011) fed 720-g juvenile beluga sturgeon 8 to 9 weeks of isonitrogenous and isoenergetic diets with 5% fish oil, but 6%, 4%, 2%, and 0 of soybean oil and 0, 2%, 4%, and 6% phospholipids, respectively. These authors reported that there were no significant differences in serum triacylglycerol and cholesterol levels or liver alanine aminotransferase, aspartate aminotransferase, and lipase activities. No growth performance data were reported in this study. Both the studies of Gawlicka et al. (2002) and Ebrahimnezhadarabi et al. (2011) were very preliminary in nature, and more studies are needed to ascertain the feasibility of using either soy lecithin or

phospholipids as an alternative lipid source in the sturgeon diets. Hung and Lutes (1988) fed white sturgeon (11 to 34 g IBW) 6 weeks of 4 isonitrogenous and isoenergetic diets in a 2 × 2 factorial design to determine whether lecithin or choline was essential in the sturgeon diet. The diets were supplemented with either 0 or 8% refined soy lecithin and 0 or 0.8% choline chloride. Sturgeon fed the 2 diets with both supplementations or only choline chloride had significantly higher %BWI than those fed the diet with only 8.0% soy lecithin, which in turn was higher than those fed the diet without both supplementations. The feed efficiency of sturgeon fed the diet without both supplementations was significantly lower than those fed the other 3 diets, but there were no significant differences in FE in those fed the remaining 3 diets. These results suggested that there is no requirement for lecithin, but there is a requirement for choline in sturgeon. Furthermore, refined soy lecithin can be used to replace some of the oil mix in the white sturgeon diet as an alternative source of dietary lipid.

Alternative dietary lipids to replace fish oil have also been studied in Russian and beluga sturgeons by Şener et al. (2006), Hosseina et al. (2010), Fackjouri et al. (2011), and Hassankiadeh et al. (2013). Şener et al. (2006) divided 144-g (IBW) Russian sturgeon into 4 groups for approximately 10 weeks: the control group diet contained 10% fish oil; the group 1 diet contained 5% fish oil, 2.5% corn oil (CO), and 2.5% sunflower oil (SFO); the group 2 diet contained 10% CO; and the group 3 diet contained 10% SFO. They found no difference in SGR, but the sturgeon in group 3 had significantly lower FE. They concluded that, among the vegetable oils, SFO had a better growth effect than corn oil for Russian sturgeon. There are several problems with this study, which may limit the usefulness of their results to improve the understanding of lipid nutrition in the sturgeon. These problems include the low SGR and FE, which may have resulted from the low water temperature (16 °C). More importantly, the experimental design may have introduced some major confounding factors because the protein sources and levels in the 4 diets (25% to 40% FM, 0.5% to 33% SBM, 7% to 14.5% sunflower meal, 7.5% to 20.5% corn meal) and carbohydrate concentrations (0 to 13% wheat meal) varied with various sources and concentration of the dietary oils.

Hosseini et al. (2010) compared the final body weight, weight gain, and FE of 206-g beluga sturgeon fed diets with 50.5% FM and 5.4% of either fish oil, soybean oil, or canola oil. They found no significant differences in the growth performances of sturgeon maintained on the 3 dietary treatments for 120 days. The fatty acid compositions of muscle in the sturgeon were significantly different, reflecting the marked difference in the 3 dietary oils. These authors concluded that beluga sturgeon can use soybean oil and canola oil equally well as fish oil. They noted, however, that the lack of a well-balanced fatty acid composition of the 2 plant oils may limit their total replacement of the fish oil in the beluga sturgeon diet. They suggested that other aspects, such as liver fatty acid composition, histological effect, and other sizes and ages of beluga sturgeon, should be considered in future experiments. Similar to Xu et al. (1993), the beluga sturgeon used in this study were too large (206 g IBW), and 120 days may not have been long enough to deplete all the endogenous EFA in the beluga sturgeon. A longer study with smaller sturgeon and a short period of feeding a fat-free diet to deplete the endogenous EFA in the sturgeon is highly desirable in future studies. This approach would unequivocally prove that the long-term replacement of dietary fish oil with plant oils would not result in poor growth performance in beluga sturgeon as a result of EFA deficiency.

Fackjouri et al. (2011) fed 215-g IBW beluga sturgeon 6 weeks 1 of 5 diets containing different levels of fish oil and soybean oil (SBO): the control diet had no fish oil or SBO, the low-SBO diet had only 5.4% SBO, the high-SBO diet had 17.4% SBO, low-fish oil diet had 5.4% fish oil, and high-fish oil diet had 17.4% fish oil. These authors reported that SGR of sturgeon fed the high-fish oil diet was significantly higher than those fed the control and the low-SBO diets, but they were not different from those fed the high-SBO and low-fish oil diets. Feed efficiency was lowest in sturgeon fed the control diet, which was significantly lower than those fed the diets with high SBO and high fish oil. Furthermore, the feed efficiency of the sturgeon fed the control diet was not different from those fed either the low-SBO or low-fish-oil diets. The low SGR (0.7–1.2) and low FE may have resulted from the low water temperature (15 °C) and short duration of the growth trial (6 weeks). As noted by the authors, future studies should be conducted with higher water temperature and a longer duration.

Hassankiadeh et al. (2013) fed 27-g Caspian great sturgeon (*H. huso*) 60 days of 1 of 5 diets: the control diet contained 10% fish oil (kilka fish oil); diet A contained 5% fish oil, 2.5% SFO, and 2.5% SBO; diet B contained 5% fish oil, 2.5% SFO, and 2.5% canola oil (CAO); diet C contained 5% fish oil, 2.5% SBO, and 2.5% CAO; and diet D contained 3.3% SFO, 3.3% SBO, and 3.3% CAO. There were no significant differences in SGR or FE among sturgeon fed the 5 diets, and the authors concluded that it was feasible to substitute fish oil with a mixture of vegetable oils in the diets of farmed juvenile great sturgeon without any negative effects on growth performance. The FE, however, was low (67% to 68%) in this study compared with that of Xu et al. (1993). The low FE might have resulted from the low lipid content of the diets (10%) and the high feeding rate (5% to 6% BW/d by hand 3 times per day) used in the study, which may limit the usefulness of their conclusion and recommendation in the great sturgeon diets.

5. Carbohydrate

5.1. Optimum dietary carbohydrate

Fynn-Aikins et al. (1992) fed 45-g white sturgeon 8 weeks of 1 of 6 diets with 0 to 35% of D-glucose in 7% increments using the purified diet formulation of Hung et al. (1987). They found that sturgeon fed the diet with no D-glucose had significantly lower %BWI and ER than those fed diets with 21% or higher D-glucose. Feed efficiency was significantly lower in those sturgeons fed the diet with no D-glucose than those fed diets with 21% and 27% D-glucose. These results suggested that some D-glucose (14% to 35%) in the diet is beneficial to the growth of sturgeon. Furthermore, unlike the dietary crystalline amino acid mixture, which supports inferior growth compared to natural protein with a similar amino acid composition, the highly available D-glucose would support growth comparable to that of those fed similar amount of a complex carbohydrate, the dextrin diet (Hung et al., 1987, 1989). This claim is also supported by the increased lipogenic enzyme activities (glucose-6-phosphate dehydrogenase, 6-phosphogluconate dehydrogenase, isocitrate dehydrogenase, and malic enzyme) with increasing dietary D-glucose from 0 to 35%. This conclusion is further supported by Fynn-Aikins et al. (1993), who found no adverse effect on white sturgeon fed a diet with 35% D-glucose for 8 weeks compared to those fed a diet with 20% dextrin and 10% cellulose based on growth performances, clearance of sulfobromophthalein, and the liver:plasma ratio of alanine aminotransferase and aspartate aminotransferase.

5.2. Carbohydrate source and digestibility

Kaushik et al. (1989) fed 90-g and 150-g Siberian sturgeon 12 weeks of 1 of 5 diets containing different carbohydrate sources (38% of crude starch, gelatinized starch, extruded starch, or 46% of extruded corn) and a commercial diet with a closed formulation.

These authors reported that sturgeon did not use complex carbohydrates such as crude starch well. However, those fed diets with extruded starch, gelatinized starch, and extruded corn had significantly higher final body weight than those fed the commercial diet, which had a higher final body weight than those fed the crude starch diet. They concluded that diets with high levels of highly digestible carbohydrates adversely affected liver size, morphology, and function in the Siberian sturgeon. The limitations of this study again included only duplications per dietary treatment and a lack of information on the formulation of the diet.

Hung et al. (1989) fed 25-g white sturgeon 8 weeks of 1 of 8 purified diets containing either 27% of maltose, glucose, raw corn starch, dextrin, sucrose, lactose, fructose, or cellulose. In general, % BWI and FE in sturgeon decreased in the same order as above, but ER showed a more distinct difference, with the highest values in sturgeon fed the glucose or maltose diets, followed by those fed the raw corn starch, dextrin, or sucrose diets; the sturgeon fed the lactose, fructose, or cellulose diets had the lowest ER values. Lipogenic enzyme activities also showed a decreasing pattern similar to those mentioned above. The poor growth performance of sturgeon fed the lactose and sucrose diets resulted from the low lactase and sucrase activities in the small and large intestinal brush border membrane vesicle preparation, respectively. One of the reasons for the poor utilization of lactose, sucrose and fructose was their poor digestibility. Indeed, ADC values were 57% for sucrose, 53% for fructose, and 36% for lactose, which were similar to those of raw corn starch (32%), whereas they were 99.9% for maltose, 99.8% for galactose, 99.4% for glucose, and 75% for dextrin (Herold et al., 1995). Furthermore, white sturgeon seemed to be intolerant to lactose, sucrose, and fructose because Hung et al. (1990) showed that sturgeon fed these diets had significantly lower hepatosomatic indices and liver glycogen contents than those fed glucose, maltose, or dextrin diets. Furthermore, sturgeon fed the glucose, maltose, dextrin, and raw corn starch diets had normal livers histologically, but those fed the lactose, sucrose, and fructose diets showed moderate condensation of hepatocyte cytoplasm and a decreased number of glycogen-containing intracytoplasmic vacuoles. The distal intestine of sturgeon fed the lactose, sucrose, and fructose diets also contained a significantly higher amount of luminal water. The cytoplasm in the mucosal epithelial cells of the distal intestine was occupied by a few large, irregular, non-glycogen-containing vacuoles. The increased amount of luminal water in the distal intestine of sturgeon fed the sucrose, lactose, or fructose diets was similar to that observed in the large intestines of higher vertebrates with diarrhea secondary to disaccharide intolerance.

5.3. Carbohydrate utilization

The poor utilization of some carbohydrates by white sturgeon may have resulted from their intolerance to highly digestible carbohydrates, similar to diabetes mellitus in humans, due to their inability to regulate absorbed glucose. Hung (1991c) used a traditional oral challenge test to explore whether, similar to other cavernous fish, white sturgeons also have this type of carbohydrate intolerance, which is typically characterized by a long duration of high plasma glucose concentration after being fed high levels of highly digestible carbohydrates. White sturgeon was orally administered 167 mg/100 g body weight of glucose, galactose, fructose, maltose, sucrose, lactose, dextrin, raw corn starch, or cellulose in gelatin capsules. Sturgeon orally administered glucose indeed showed peak plasma glucose of 19 mmol/L, and the high concentration persisted from 2 to 24 h after the oral administration of glucose. The amplitude and duration of the high plasma glucose concentrations were much higher than those observed previously in common carp (Furuichi and Yone, 1981), channel catfish (Wilson and Poe, 1987), and hybrid tilapia (Lin et al., 1995). It was suspected that the handling stress of oral administration and subsequent capturing and blood sampling had a confounding effect by increasing the release of cortisol in the blood, which in turn increased the blood glucose as a secondary response to the stress.

Deng et al. (2000) developed a combined technique of stomach intubation, dorsal aorta cannulation, and urinary catheterization in white sturgeon that allowed the quantitative delivery of a known compound, repeated sampling of blood, and continuous collection of urine samples from individual sturgeon with minimum stress. Deng et al. (2001) used the combined technique and found a lower peak plasma glucose concentration of 10 mmol/L, but a similar duration of 24 h until it returned to the basal level of 3 to 4 mmol/L. Gisbert et al. (2003) used the combined technique and compartmental modeling to study glycemic responses in white sturgeon after the oral administration of graded doses of D-glucose at 0, 250, 750, 1,000, 1,250, and 1,500 mg/kg body weight. The model of plasma glucose kinetics indicated that the rate constant for glucose absorption from the digestive tract into the bloodstream was significantly reduced, indicating that glucose absorption into the circulation was non-linear related to the dose and became saturated at higher dosages. In contrast, the glucose clearance rate increased with increasing plasma glucose concentrations, but the rate of gluconeogenesis appeared to decrease only slightly. This small reduction in gluconeogenesis may contribute to the prolonged high plasma glucose concentration in sturgeon after a glucose load. The modeling effort added a new dimension and better understanding of carbohydrate utilization in sturgeon. Future studies should employ modern molecular techniques, such as genomics, proteomics, and metabolomics, in addition to traditional assessments of growth performance and biochemical responses. Indeed, Gong et al. (2015) used a real-time quantitative polymerase chain reaction method (RT-qPCR) to measure gluconeogenesis enzyme mRNAs in Siberian sturgeon larvae that were first fed a high-glucose diet (57% glucose and 21.5% protein, which was supplied by the 35% FM) from first feeding to yolk absorption 8 to 12 days post-hatch (dph). The larvae were then fed a high-carbohydrate (35% dextrin and 21.5% protein, which was supplied by 46.5% FM) or a carbohydrate-free (67.7%, which was supplied 85.5% FM) diet from 14 to 140 dph, and the mRNA expression levels and activities of gluconeogenesis enzymes were measured at 13, 30, and 140 dph. Feeding the high-glucose diet at 8 to 12 dph depressed SGR at 13, 30, and 140 dph, and it inhibited the mRNA expression of fructose-1,6-bisphosphatase at 30 dph and increased the mRNA expression of phosphoenolpyruvate carboxykinase cytosolic forms and glucose-6-phosphatase (*G6Pase*) while inhibiting the activities of *G6Pase* at 140 dph in sturgeon fed the carbohydrate-free diet. These authors concluded that the gluconeogenesis pathway of sturgeon was affected by the dietary carbohydrate content at both the transcriptional and post-transcriptional levels. Feeding the high-glucose and low-protein diet from 8 to 13 dph in Siberian sturgeon affected their gluconeogenesis regulation later in life.

The effect of the Maillard reaction[3] on the 8-week growth performance in 25 to 27 g white sturgeon was studied by Deng et al. (2005). These authors used 3 min of 80 °C microwave moist heating followed by 1 h of 70 °C drying to prepare 5 experimental diets:

[3] The Maillard reaction can occur in animal feeds between reducing sugars and the amino group of amino acids, especially lysine, in the protein during moist heat treatment and storage. The loss of nutritional quality caused by the Maillard reaction is attributed to the destruction of essential amino acids, decreased digestibility, and eventually the production of antinutritional and toxic components. Products of the Maillard reaction are resistant to the digestive enzymes of animals, thus reducing the quality of dietary protein.

a control diet with 4% D-glucose, 2 diets with either 15% or 30% hydrolyzed potato starch (HPS), and 2 diets with 15% or 30% of D-glucose. The feeding rate varied from 1.7% to 3.2% BW/d, such that all treatment groups were fed the same amount of dietary protein and lipid. Sturgeon fed the control and 15% HPS diets had the highest SGR, followed by those fed the diet with 30% HPS; those fed the diet with 30% D-glucose had the lowest growth rate. Other growth performance indexes, such as protein and energy retention and whole-body lipid and muscle glycogen contents showed the same pattern with the sturgeon fed the 15% or 30% D-glucose diets. The low growth performance in sturgeon fed the 15% or 30% D-glucose diets was due to the Maillard reaction between the carbonyl group of the D-glucose, which is a reducing sugar, and the nucleophilic amino groups of the amino acids, especially the essential and usually the second most limiting amino acid, lysine, during the moist heating of the 2 diets. This conclusion was supported by the significantly lower lysine and glucose and the lower plasma lysine concentrations in the sturgeons fed the 2 D-glucose diets than in the sturgeons fed the control diet.

Mohseni et al. (2011) fed beluga sturgeon (892 g IBW) 112 days of 16 diets containing different protein, lipid, and carbohydrate concentrations in a 4 × 4 factorial design experiment to determine the optimum dietary carbohydrate:lipid ratio (C:L) to spare protein. These diets were formulated to contain 4 C:L ratios (0.8, 1.1, 1.4, and 1.7) and 4 protein concentrations (35%, 40%, 45%, and 50%). The feed efficiency and PER of sturgeon were significantly affected by the dietary protein and the interactions among dietary proteins, and C:L ratios on the SGR were also significantly affected. Sturgeon fed the diet with 35% protein and C:L ratio of 1.4 had better SGR than those fish fed the diets with a protein%: C:L ratio of 40%:0.6, 50%:0.8, or 50%:1.7. The authors concluded that beluga sturgeon could effectively utilize both lipid and carbohydrate as an energy source when the C:L ratio ranged from 0.8 to 1.7. Sturgeon fed the diet with 35% protein and C:L of 1.4 showed the best protein-sparing effect. Therefore, the efficiency of protein utilization by beluga sturgeon is dependent on the dietary carbohydrate concentrations. The optimum diet should contain 36% protein, 16.3% lipid, and 23.7% carbohydrate with a C:L ratio of 1.4, and a protein-to-energy ratio of 20.6 mg protein and 16.9 MJ/kg diet when beluga sturgeon is fed 1.5% BW/d.

Not only dietary composition but also feeding strategy will affect the growth performance of sturgeon. Lin et al. (1997) fed 9-g white sturgeon 8 weeks of 2 diets containing either 30% glucose or raw corn starch by either continuous feeding or 2 meals per day. Significantly higher SGR, FE, PER, body lipid content, and liver lipogenic enzyme activities were observed in white sturgeon under the continuous feeding program than in those that were fed 2 meals per day, regardless of dietary carbohydrate sources. Specific growth rate, FE, and PER, however, were significantly higher in sturgeon fed the raw corn starch diet than the glucose diet, regardless of the feeding strategy.

6. Vitamins and minerals

There is still a paucity of information on the vitamin and mineral requirements of sturgeons since the last review by Hung and Deng (2002). Those authors reviewed previous studies on the choline requirement of white sturgeon (Hung, 1989); vitamin C requirement of Siberian, lake, and hybrid sturgeons (Moreau et al., 1996, 1999a,b, Papp et al., 1995, 1999); vitamin C and vitamin E interaction of Adriatic, *Acipenser naccarii*, sturgeon (Agradi et al., 1993); and selenium requirement of white sturgeon (Silas S.O. Hung, unpublished data).

More recent vitamin C requirement studies were conducted in beluga, Siberian, and stellate (*Acipenser stellatus*) sturgeons by Falahatkar et al. (2006), Xie et al. (2006) and Desimira et al. (2013), respectively. Falahatkar et al. (2006) fed 5-month-old beluga sturgeon (38 g IBW) 1 of 6 diets containing either 0, 100, 200, 400, 800, or 1,600 mg ascorbic acid (ASA)/kg diet and found that final body weight, %BWI, plasma hemoglobin level, and carcass lipid and ash contents were significantly affected by the dietary concentration of ASA, but no external symptoms of scurvy were observed, even in fish fed the diet without ASA supplementation. There were, however, no discernible patterns in the final body weight, %BWI, plasma hemoglobin level, or carcass lipid and ash contents in the study. Desimira et al. (2013) fed 155-g stellate sturgeon 30 days of diets containing 0, 200, 400 or 800 mg ASA/kg diet and found significantly higher SGR, FE, and PER in sturgeon fed the diets with 200 and 400 mg ASA/kg diet than those fed the diets with either 0 or 800 mg ASA/kg diet. Limitations of the above 2 studies are a lack of information on the diet formulation, and insufficient information on the materials and methods. More importantly a more robust statistical analysis and suitable model, such as those of Hua (2013) and Lee et al. (2014, 2016), should be used to provide a more definite dietary ASA requirement of the 2 sturgeon species.

Xie et al. (2006) fed Siberian sturgeon (76 g IBW) 2 weeks of diets supplemented with 0 or 500 mg ASA/kg diet and then injected them with a sham or *Aeromonas hydrophila* lipopolysaccharide solution. The goal was to mimic infection and to determine the effect of dietary ASA on their immune responses 2 to 8 days after the injection. Specific growth rate and FE after 2 weeks of feeding the 2 diets and the injection were not affected by the dietary ASA or the injection treatments. Those sturgeon fed the diet without ASA supplementation, however, had significantly lower lysozyme concentrations than the 3 other treatment groups. These authors concluded that dietary ASA enhanced the immune response upon exposure to a simulated bacterial infection in Siberian sturgeon. Furthermore, endogenous ASA may be insufficient to achieve the optimal or maximum immune response in Siberian sturgeon.

The vitamin A requirement and its interaction with oxidized lipid had been studied in Amur and Siberian sturgeons by Wen et al. (2008) and Fontagné et al. (2006). Wen et al. (2008) fed 12-g Amur sturgeon 8 weeks of diets containing 10, 258, 510, 1,050, 2,020, 4,100, or 8,300 IU/kg diet. They found that %BWI, FE, and the hepatosomatic index (HSI) increased with increasing dietary vitamin A; these values reached a peak at 1,050 IU/kg diet. Amur sturgeon fed the diet with only 10 IU vitamin A/kg diet showed poor appetite and activity and significantly lower %BWI, FE, HSI, and condition factor. Broken-line regression analyses of weight gain and liver vitamin A concentrations showed that juvenile Amur sturgeon require a minimum of 923 IU vitamin A/kg diet for maximum growth and 1,981 IU vitamin A/kg diet for maximum liver storage. Fontagné et al. (2006) fed Siberian sturgeon larvae (30 mg IBW) 4 weeks of diets containing 0, 4% or 8% of an auto-oxidized capelin oil and 22,500 or 772,500 IU vitamin A as retinyl acetate per kilogram diet. They concluded that Siberian larvae fed a diet with oxidized capelin oil were subjected to increased oxidative stress, which may have resulted in poor growth, low survival rate, and higher deformity. The antioxidant defense enzymes (superoxide dismutase, catalase and selenium dependent glutathione peroxidase) of larval Siberian sturgeon did not appear to respond strongly to dietary oxidized oil. Furthermore, a high concentration of dietary vitamin A would provide Siberian sturgeon larvae partial relief from the adverse effects of dietary oxidized oil.

The vitamin E requirement of beluga sturgeon has been studied by Amlashi et al. (2011), who fed young-of-the-year beluga sturgeon (50 g IBW) diets supplemented with 0, 25, 50, 100, 200 or 400 mg vitamin E (DL-all-rac-α-tocopherol acetate)/kg diet for 8 weeks. These authors showed that juvenile beluga sturgeon fed a

diet without vitamin E supplementation had a significantly poorer SGR, FE, and PER than those fed diets with vitamin supplementation. They concluded that vitamin E supplementation had no effect on body composition, hematological parameters (hematocrit, total leukocyte count, and % lymphocytes, neutrophils, eosinophils and monocytes), osmotic erythrocyte fragility, plasma glucose and cortisol concentration, or lysozyme activity in the beluga sturgeon. These authors suggested that some vitamin E supplementation in the beluga sturgeon diet is needed to prevent any adverse growth effects.

Mineral (selenium [Se]), phosphorus, and copper [Cu]) requirements were studied by Arshad et al. (2011), Xu et al. (2011), and Jin et al. (2012) and Wang et al. (2016) in beluga, Siberian, hybrid (*H. huso* × *A. schrenckii*), and Russian sturgeons, respectively. Arshad et al. (2011) fed juvenile beluga sturgeon (3.5 g IBW) 8 weeks of purified diets with 1.26, 2.44, 3.01, 5.37, 11.56, and 20.26 mg Se/kg diet. They found that sturgeon fed diets with 1.26 and 2.44 mg Se/kg diet had significantly lower SGR than those fed diets with higher Se contents, and only sturgeon fed the 1.26 mg Se/kg diet had significantly lower FE than those fed diets with higher Se concentration. These authors recommended that the dietary requirement of Se by juvenile beluga sturgeon is between 11.56 and 20.26 mg Se/kg diet when Se supplementation is in the form of L-selenomethionine. A more precise Se requirement can be established using a more appropriate model and robust statistical method, such as those used by Hua (2013) and Lee et al. (2014, 2016) instead the one-way ANOVA used in the current study.

Xu et al. (2011) fed Siberian sturgeon (15 g IBW) 8 weeks of diets containing 0.12%, 0.20%, 0.29%, 0.39%, 0.48%, 0.60%, 0.69%, 0.80%, 0.99%, 1.19%, or 1.38% of phosphorus supplied as monobasic sodium phosphate (NaH_2PO_4). They found that SGR and FE were significantly affected by the dietary phosphorus concentrations. Based on the broken-line model analyses of %BWI and whole-body phosphorus concentrations, these authors suggested that the phosphorus requirement of juvenile Siberian sturgeon is between 0.50% and 0.87%. These authors also reported that whole-body crude lipid, ash content, and calcium concentrations in the whole-body, scute, and vertebrate and plasma calcium and phosphorus contents as well as ALP activity were significantly affected by the dietary phosphorus contents. These significant results most likely resulted from the use of improper statistical analyses because the sampling of 4 fish in a tank was considered a true replicate, which resulted in 12 replicates per treatment, although only 3 replicate tanks were used in the experiment. Jin et al. (2012) is not reviewed here because of improper experiment set up. Initial total length and initial body weight of the young hybrid sturgeon were significantly different even before feeding the experimental diets. The percent weight gain although significantly affected by dietary phosphorus contents is very small (−1.7% to 10.9%) making their recommendation highly questionable. Finally, the authors did not provide the biological rationale why dietary phosphorus content would affect the "antioxidant defense system and eradicate the free radicals, in order to reduce the antioxidant damage" and thus their recommendation of 0.63% to 1.15% dietary phosphorus content to reduce the antioxidant damage is also highly questionable.

Wang et al. (2016) formulated 7 semi-purified diets containing 0, 1, 2, 4, 6, 8, and 16 mg Cu/kg diet supplemented with copper sulfate ($CuSO_4 \cdot 5H_2O$). These diets contained 0.3, 1.5, 2.4, 4.4, 6.2, 8.3, and 16.1 mg Cu/kg diet, as determined with an inductively coupled plasma-atomic emission spectrophotometer. These authors reported significant differences in %BWI, FE, and whole-body and liver Cu concentrations in juvenile Russian sturgeon (11.8 g IBW) fed these diets for 8 weeks. They reported that Cu–Zn superoxide dismutase (Cu–Zn SOD) activity, total antioxidant capacity, and malondialdehyde concentrations in the liver as well as ceruloplasmin activity in the serum of the sturgeon were also significantly affected by the dietary Cu concentrations. A broken-line regression analysis of % BWI, whole-body Cu concentration, and liver Cu–Zn SOD activity indicated a requirement of 7 to 8 mg Cu/kg diet for juvenile Russian sturgeon fed the semi-purified diets.

7. Future research

A few of the studies reviewed above were based on questionable concepts or methodology, and their usefulness is highly questionable. Readers are highly encouraged to consult Gropp and Tacon (1994) and NRC (2011) to ensure that any experiment they have designed is based on sound biological concepts and commonly acceptable methodology. Important factors that need to be considered in the experimental design or methodology include fish size, water temperature, density of fish in each replicate, formulation and manufacturing of experimental diets, minimum number of replications, minimum number of fish per replicate, duration of the experiment, statistical analysis, etc.

The development of a suitable chemically defined diet using amino acids, fatty acids, glucose, and all the other essential nutrients in pure chemical forms to support good growth of sturgeons is urgently needed. Manipulating individual essential nutrients in this diet in traditional dose–response growth or biochemical trials will provide us with better information and unequivocal results on the qualitative and quantitative requirements for all the essential nutrients in the sturgeon diets. This information will provide us with a better understanding of the biochemical processes in sturgeons as a living organism, and more importantly, it will provide us with one of the most important basic metrics still missing for least-cost formulations. Furthermore, this information will definitely help sturgeon farmers improve their profitability because feed cost is usually more than 50% of the operating cost of a fish farm.

Future studies should also use the more modern "omic" techniques, such as proteomics, metabolomics, and lipomics, in addition to traditional single dose–response growth or biochemical methods, so that a more holistic picture will emerge to provide a better understanding of the nutrient requirements and utilizations by sturgeons. Future experiments should be designed systematically with more consideration within and among studies as well as within and among different species of sturgeon, such as those reported by Vaz et al. (2015). These goals can be achieved by applying different modeling techniques (Shear, 2000; Thornley and France, 2007; France and Kebreab, 2008; Dumas et al., 2007; 2010) to integrate data within and among studies to gain more holistic knowledge of different species of sturgeon. Finally, future experiments should be designed with a systematic approach with multiple doses (inputs) and multiple responses (outputs) at several levels of organization of hierarchy in a biological system (Thornley and France, 2007; France and Kebreab, 2008) using traditional biochemical and modern molecular biology techniques, and computer modeling. For example, the multiple doses (inputs) can include different nutrients and their concentrations in the diets, feeding rates, water temperatures and oxygen levels, stocking density, and photoperiods, and the responses (outputs) can include modern molecular biology measurements, such as genomic, proteomic, and metabolomic measurements, in addition to traditional growth performance and biochemical measurements. These types of experiments will no doubt generate massive amounts of data at different organizational levels of biological hierarchy, i.e., gene, protein, cell, tissue/organ, whole sturgeon, and group of sturgeon. These data are best handled by computer modeling to establish relationships among the different biological levels of organizations or aggregates. Fortunately, software for modeling, such as R (R Core Team, Vienna, Austria, 2015) is continually becoming much more

user friendly, and powerful computers are becoming less expensive and much more readily available. Furthermore, this type of research is complex; collaboration among fish biologists, ecologists, nutritionists, genomicists, proteomicists, metabolomicists, and computer modelers is highly desirable. This approach will provide a better, more realistic, and holistic understanding of the mechanisms of nutrient utilization and growth, which will ultimately help us better manage wild sturgeon stocks and produce sturgeon under aquaculture conditions more efficiently and sustainably.

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