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Effect of feeding level on the digestibility of alternative protein-rich ingredients for African catfish (*Clarias gariepinus*)

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ABSTRACT

Apparent digestibility coefficients (ADC) of nutrients and individual amino acids (AA) for 13 feed ingredients as affected by feeding level were determined for African catfish, a species of economic importance in Africa. Results from two trials are reported. In each trial, ADC were determined using a reference diet and test diets with yttrium oxide as indicator. Juvenile African catfish (averaging 53.9 g, trial 1; 40.4 g, trial 2) were stocked in tanks connected to a common recirculation aquaculture system. Ingredients tested included hydrolysed feather meal (HFM), fishmeal (FM), insect meal (IM), soybean meal (SBM), sunflower meal (SFM), poultry meal (PM), corn dried distillers grains with solubles (CDDGS), faba beans (FB), lupine meal (LM), pea protein (PP), guar meal (GM), canola meal (CM) and yeast meal (YM). The effect of feeding level on ADC was determined by feeding fish restrictively (80% satiation) for 5 weeks and subsequently to apparent satiation for 2 weeks. Inclusion of yeast meal at 30% resulted in low palatability. ADC of nutrients were significantly affected by feeding level (except for fat and carbohydrate), but the effect was ingredient-dependent. African catfish was able to digest protein very effectively in almost all tested ingredients with ADC values ranging from 85.6 to 105.1% across feeding periods. Several ingredients tested, including animal protein ingredients and YM had similar high ADC for dry matter as FM. However, the ADC of AA differ among ingredients, indicating a need for digestible amino acid profile data. Methionine (Met) was the first limiting essential amino acid in HFM, FB, and LM with values ranging from 5–6 g/kg, expressed as digestible Met (dMet) per unit of digestible protein (DP), compared to FM (27 g dMet/kg DP). IM had comparable and sometimes higher overall digestible essential AA values compared to FM, except for methionine and lysine. For oilseeds and legumes, SBM tended to be the best quality AA source, as it had the highest digestible essential amino acid profile. These data provide information concerning nutrient and digestible AA values, which will allow a more efficient use of alternative ingredients in African catfish diets. Formulating diets based on the digestible AA in ingredients will aid precise feed formulation, thereby minimising economic losses and reducing the environmental footprint of aquaculture production.

1. Introduction

Due to the scarcity of fishmeal together with the increased production of aqua-feeds, numerous studies have been conducted on alternative ingredients in fish diets over the past decades. The vast majority of these studies have established the authenticity of fishmeal as the most suitable protein source for fish, due to its balanced amino acid (AA) profile, high digestibility and palatability (Che et al., 2017; Dam et al., 2019; Hardy, 2010). However, the global demand for fishmeal in aquaculture production has put a strain on the economic and environmental sustainability of this sector. Potential overfishing of marine fish species used for feed production conflicts with the demand for

Abbreviations: AA, Amino acid; dAADP, Dietary digestible amino acid content expressed per unit of digestible protein; ADC, Apparent digestibility coefficient; BW, Body weight; DM, Dry matter; EAA, Essential amino acids.

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sustainable aquaculture and therefore is drives the reduction of fishmeal usage (Couto et al., 2016; FAO, 2018; Naylor et al., 2009). For these reasons, there has been a growing need for more insight into the potential of alternative protein sources in aquafeed to enable the increasing demand for aqua-feeds (Kaushik et al., 2004; Taufek et al., 2016).

Several alternative novel ingredients (animal and plant origin) of nutritional and economic benefits are now being investigated for the total or partial replacement of fishmeal in fish diet (Basto et al., 2020; Che et al., 2017; Davies and Ezenwa, 2010; dos Santos Cardoso et al., 2020; Fagbenro, 1998; Glencross et al., 2020; Goda et al., 2007; Lee et al., 2020; Nazzaro et al., 2021; Toko et al., 2008; Tomas-Vidal et al., 2019; Wang et al., 2008). In spite of these promising alternatives, it is quite difficult to get an ingredient with a complete AA profile that is not limiting in at least one essential AA (Gomes et al., 1995). Moreover, plant proteins contain anti-nutritional factors (NRC, 2011), which can reduce the availability of AA (Cai and Burtle, 1996; Ghosh et al., 2019). Therefore, to achieve an optimum diet that contains all essential AA (EAA), mixtures of plant and animal protein ingredients are used in formulating aquafeeds (Tomas-Vidal et al., 2019). Investigating the digestibility values of these ingredients is an essential step in formulating balanced practical diets (Glencross, 2020; Gomes et al., 1995).

In terms of feed formulation, the quality of feed ingredient depends on their digestible amino acid profile, protein and energy (Fagbenro, 1996, 1998; Glencross, 2020; Henken et al., 1985a; Ovie and Eze, 2014). Since the larger part of feed formulation is based on the protein content, reliable data on the digestible AA content of these different ingredients for each species is considered a necessary prerequisite (Basto et al., 2020; Gomes et al., 1995; Wolfe et al., 2016). Data on AA digestibility of feed ingredients for African catfish (*Clarias gariepinus*) are relatively limited, compared to other cultured fish species, like rainbow trout (*Oncorhynchus mykiss*), Nile tilapia (*Oreochromis niloticus*) and Atlantic salmon (*Salmo salar*) (NRC, 2011). Currently in Africa, the culture of African catfish is growing steadily due to the increasing local demand and high market price value. Moreover, the species voracious eating behaviour, fast growth rate, and ability to survive in adverse environmental conditions (Fagbenro et al., 1999), makes it relatively easy to be farmed in the natural inland freshwater areas. Evaluating the nutritional values of novel and array of ingredients for this species will play an important role in establishing how efficient African catfish is able to accept, digest and utilize the feedstuffs used (Allan et al., 2000; Udo and Umoren, 2011). Such information will be useful to simulate the ideal amino acid profile in the diets of African catfish and the production of least-cost feed, one of the problem to be resolved in its development.

There is considerable controversy regarding the effect of feeding level on the apparent digestibility coefficient (ADC) of nutrients in fish. Only a few studies have addressed the potential impact of increasing feeding level on the ADC in fish species. These include, Nile tilapia, rainbow trout and African catfish, with most results being negatively correlated to ADC (Haidar et al., 2016; Henken et al., 1985b; Staessen et al., 2020). However, Cho and Kaushik (1990) came to a different conclusion in their study that ADC of nutrients were not affected by feeding level or feeding rate. Apart from Henken et al. (1985b) who determined the effect of feeding level on nutrient ADC in African catfish, no study so far has been carried out to have a better understanding of the relationship between feeding level and AA ADC in African catfish. Therefore, the present study was undertaken (1) to obtain values for nutrients and AA digestibility of selected ingredients of plant and animal origin, (2) to evaluate the effect of feeding level on ADC of ingredients, and (3) to provide data on digestible AA of ingredients that will allow a greater accuracy in feed formulation for African catfish.

2. Materials and methods

This experiment was approved by the Animal Welfare Body of Wageningen University, The Netherlands. All procedures applied to the animals were in line with the Dutch legislation (Act on Animal Experiments) and were classified as not being an animal experiment according to Dutch legislation. The experiment was carried out at the Aquaculture Research Facility of Wageningen University (The Netherlands). Because of a limited number of aquaria equipped with settling units for feces collection, the experiment was conducted in two trials: six test ingredients were tested in the first trial while seven ingredients were investigated in the second trial. Both trials were identical regarding the experimental set-up, housing and sampling procedure, only the initial weight was different and consequently also the stocking density.

2.1. Diet preparation

The ingredient composition of the test diets, the analysed nutrient composition of the ingredients and experimental diets are summarized in Tables 1, 2 and 3 respectively. A reference diet (control) was formulated by combining information on the recommended amino acid requirements of Nile tilapia, common carp (*Cyprinus carpio*) and channel catfish (*Ictalurus punctatus)* (NRC, 2011), since information on amino acid requirement of African catfish is relatively scarce. Test ingredients were sourced from a wide range of protein-rich ingredients of both animal and plant protein origin; hydrolysed feather meal (HFM), LT70 fishmeal (FM), insect meal (IM) from black soldier fly larvae (*Hermetia illucens*), soybean meal (SBM), sunflower meal (SFM), poultry meal (PM), corn dried distillers grains with solubles (CDDGS), faba beans (FB), lupine meal (LM), pea protein (PP), guar meal (GM), canola meal (CM) and single cell protein from brewer's yeast (*Saccharomyces cerevisiae*) (yeast meal, YM). The test diets are composed of 70% control diet with 30% test ingredient, except for HFM and GM, which were included at 15% in the mixture to prevent any negative effect that high inclusion levels may pose on digestibility. Yttrium oxide was added as inert marker for the determination of ADC. The diets were extruded floating pellets with sizes ranging from 3 to 3.5 mm, produced by Skretting ARC Norway using a twin-screw extruder (Wenger, Sabetha, KS, U.S.A). Diets were stored at 4 °C throughout the duration of the experiment.

2.2. Fish and housing conditions

Juvenile African catfish (*Clarias gariepinus*) of mixed sex were obtained from a commercial brood stock farm (Fleuren & Nooijen BV, Nederweert, The Netherlands) 2 weeks prior to the start of the experiment and were reared at the Wageningen University experimental facilities (Carus Aquatic Research Facility, Wageningen, The Netherlands). For the first trial, 630 fish with an average weight of 53.9 g were randomly allocated among 21 experimental tanks (30 fish per tank). For the second trial, 840 fish weighing on average 40.4 g were randomly assigned among 24 experimental tanks (35 fish per tank). Each tank was equipped with air stones and swirl separators

Table 1
Ingredients composition of reference diet.

Ingredient (%)	Reference diet
Wheat	20.5
Maize	19.9
Wheat gluten	12.0
Fishmeal	12.0
Soy protein concentrate	12.0
Pea protein	12.0
Soya oil	3.00
Fish oil	3.00
DL-Methionine	0.80
L-Lysine	0.80
Monocalciumphosphate	3.00
Yttrium premix	0.15
Vitamin & mineral premix	0.44
Calcium carbonate	0.36

Table 2
Analysed nutrient and amino acids composition of test ingredients[1].

Nutrient (g/kg DM)	Test ingredients												
	FM	IM	PM	HFM	SBM	PP	FB	LM	GM	CM	SFM	CDDGS	YM
Dry Matter	918	949	950	959	875	895	874	910	917	914	913	876	935
Ash	170	92	125	18	72	60	37	39	54	66	77	55	86
Crude protein	751	613	691	913	553	564	325	413	601	371	453	320	450
Fat	97	131	138	77	27	41	22	74	93	94	34	156	23
Starch	12	24	7	10	18	69	361	22	8	13	23	10	80
NSP[2]	−30[4]	140	39	−18[4]	330	267	255	452	245	456	413	338	361
Total carbohydrate[3]	−18[4]	164	46	−8[4]	348	336	615	474	253	469	436	348	441
Energy (kJ/g DM)	21.1	23.2	23.0	24.8	27.2	20.5	18.9	20.6	21.9	21.4	19.8	23.5	19.2
Phosphorus	24.7	8.5	18.9	2.4	7.0	9.4	4.7	7.2	7.9	10.8	13.6	9.9	10.7
Calcium	36.8	25.5	25.0	3.6	3.5	1.7	0.8	1.6	2.1	8.0	5.2	0.4	4.3
Magnesium	2.7	3.4	1.5	0.4	3.5	2.6	0.8	2.3	4.1	5.1	6.3	4.2	1.8
Essential AA (g/kg DM)													
Arginine	42.6	31.9	46.2	60.8	40.9	42.9	25.5	42.2	82.1	21.5	34.3	13.4	20.6
Histidine	14.8	18.1	15.9	5.9	14.3	12.9	7.3	10.9	16.5	10.0	11.1	8.7	9.5
Isoleucine	28.1	27.5	25.7	42.6	24.4	20.7	10.8	15.2	17.7	14.1	17.7	11.0	17.1
Leucine	50.6	45.1	49.8	73.3	42.8	36.2	19.9	26.1	33.0	25.5	28.9	35.5	27.1
Lysine	55.9	41.2	40.5	16.3	33.6	36.7	16.9	18.4	25.0	20.2	19.1	9.2	25.7
Methionine	20.0	13.3	13.1	4.5	7.2	4.6	1.9	2.4	6.3	7.1	9.8	6.0	6.2
Phenylalanine	29.2	27.0	29.2	43.1	30.3	22.9	11.2	15.0	24.4	14.8	20.3	14.6	18.1
Threonine	28.5	25.3	27.7	41.1	20.3	18.5	9.2	13.5	17.0	16.4	15.9	12.0	18.3
Valine	31.1	37.5	32.4	60.8	24.5	21.7	11.5	14.6	19.9	17.8	19.9	14.7	20.4
Non-essential AA (g/kg DM)													
Alanine	44.9	39.1	46.7	42.7	23.7	21.8	11.1	13.4	21.4	16.3	19.6	23.5	25.4
Aspartic acid	69.2	66.0	58.2	61.6	68.2	56.7	29.9	38.7	60.5	27.6	42.7	21.5	38.5
Glutamic acid	100	63.5	91.1	96.9	106	78.6	45.8	80.4	125	61.2	85.2	56.6	69.4
Cystine	6.7	4.9	7.4	29.7	7.2	6.3	3.0	4.4	7.7	8.7	6.5	5.4	5.5
Glycine	46.6	32.5	64.3	68.8	22.8	20.7	11.1	16.3	29.2	18.5	24.0	13.2	18.6
Proline	28.1	35.6	45.0	100	27.6	22.1	11.9	15.8	20.4	23.4	19.4	27.1	28.0
Serine	29.1	25.8	29.5	104	27.6	24.8	13.1	18.4	27.4	16.0	18.8	15.4	21.3
Tyrosine	14.9	39.7	19.3	19.1	16.2	14.5	7.9	12.4	18.5	10.1	9.9	11.0	11.2
SAA (g/kg DM)	640	574	642	871	537	462	248	358	552	329	403	299	381

[1] AA, amino acid; SAA, sum of amino acid; DM, dry matter; HFM, hydrolysed feather meal; FM, LT70 fish meal; SBM, soybean meal; IM, insect meal from black soldier fly larvae (*Hermetia illucens*); SFM, sunflower meal; YM, yeast meal (*Saccharomyces cerevisiae*); GM, guar meal; LM, lupine meal; DDGS, dried distillers grain of corn; CM, canola meal; PP, pea protein; FB, faba beans; PM, poultry meal.

[2] NSP, non-starch polysaccharides were calculated as total carbohydrates – starch.

[3] Total carbohydrate was calculated as dry matter – crude protein – crude fat – ash content.

[4] The negative values for NSP and carbohydrates is most likely due to an overestimation of the calculation of crude protein as 6.25 times the measured N content. For FM and HFM, the Jones factor is lower than 6.25.

(AquaOptima AS, column height 44 cm; diameter 24.5 cm) for the collection of feces and spilled pellets. The tanks were connected to a common recirculating water system equipped with a sump, a drum filter (Hydrotech 500®, Hydrotech Engineering, Italy) and a trickling filter for maintaining water quality parameters within a set range. The total water volume of the RAS system was 5 m^3 and water loss due to evaporation was continuously compensated by the addition of well water. Water quality parameters were monitored regularly and set at optimal levels for African catfish. Temperature, conductivity and pH were measured using digital probes (temperature: Testo 110, Testo B.V., Almere, The Netherlands; conductivity: WTW LF318 and pH: WTW pH 340, WTW Wissenschaftlich-Technische Werkstätten GmbH, Weilheim, Germany). Merck tests (Merck KGaA, Darmstadt, Germany) were used for measuring ammonium (Aquamerck 1.11118.0001), nitrite (Aquamerck 1.0825.0001) and nitrate (Mercoquant 1.10020). Measured water quality parameters during trial 1 were as follows (mean ± SD): water temperature 27.3 ± 0.98 °C; pH, 7.3 ± 0.38; ammonium, 0.32 ± 0.24 mg/L; nitrite, 0.25 ± 0.14 mg/L; nitrate, 430 ± 66 mg/L and conductivity, 3802 ± 378 μS; and for trial 2 (mean ± SD): water temperature 27.9 ± 0.31 °C; pH, 7.4 ± 0.44; ammonium, 0.78 ± 0.59 mg/L; nitrite, 0.32 ± 0.34 mg/L; nitrate, 250 ± 0.0 mg/L and conductivity, 3257 ± 743 μS. Photoperiod was kept at 12 h light: 12 h dark.

2.3. Experimental procedures and sampling

At the start of each trail, total biomass and number of fish per tank were recorded. The diets within the two trials were studied with 3 replicates per treatment over a period of 4 weeks of restricted feeding followed by 3 weeks of satiation feeding. During the last 2 weeks of the restricted as well as the satiation feeding period, feces were collected. During the 49-day experimental period, fish were fed twice daily (in the mornings and afternoons). For the restricted feeding period, the aim was to provide an equal amount of feed across diets. Therefore, the feeding level was fixed at 17.6 $g/kg^{0.8}/d$ (about 80% of satiation) based on the mean weight of fish at the start of the restricted feeding period. The calculated daily feed ration per tank was set based on an expected growth using a FCR of 1 for all diets. Daily feed portions was divided into two equal parts and hand-fed twice a day at 9:00 and 15:30 h. During the first three days, the feeding level was gradually increased from 20% to 100% of the calculated ration to allow habituation to the diets. During the satiation period, fish were hand-fed twice daily at 9:00 and 15:30 h until voluntary feed ingestion stopped, with a maximum of 1 h per feeding. Mortality was checked twice a day, 30 min prior to feeding and dead fish were removed immediately. In case of mortality during the restricted feeding period, daily feeding rations were adjusted to the number of fish in the respective tank. Before feeding, a set of bottles was connected to the swirl separators in order to collect spilled pellets. Spilled and uneaten pellets was counted or weighed per tank 15 min after feeding was finished.

Feces were collected overnight (17.00 h – 7.30 h) during the last two weeks of the restricted and satiation period, using detachable collection bottles (250 mL) connected to the settling tanks. The fecal collection

Table 3
Analysed nutrient and amino acids composition of test diets[1].

	Trial 1							Trial 2							
	CON 1	FM	IM	HFM	SBM	YM	SFM	CON 2	PM	PP	FB	LM	GM	CM	CDDGS
Inclusion level (%)															
Test ingredient	–	30	30	15	30	30	30	–	30	30	30	30	15	30	30
Reference diet	100	70	70	85	70	70	70	100	70	70	70	70	85	70	70
Nutrient (g/kg DM)															
Dry Matter	889	897	907	898	886	888	899	893	896	899	889	893	897	900	892
Ash	75	100	78	63	72	77	74	76	84	69	65	64	71	72	68
Crude protein	419	514	482	498	461	426	423	411	490	454	372	412	434	401	385
Fat	112	115	116	96	87	89	88	113	119	92	90	102	109	111	128
Starch	275	202	204	247	212	234	209	282	202	215	310	216	245	215	217
NSP[2]	113	67	114	85	162	171	197	118	105	170	164	205	141	201	203
Total carbohydrate[3]	394	271	324	342	381	408	414	400	306	385	474	421	386	416	419
Energy (kJ/g DM)	21.3	21.2	21.8	21.8	20.9	20.5	20.7	21.0	21.5	21.0	20.7	21.0	21.2	21.3	21.7
Phosphorus	14.3	17.2	12.7	11.9	11.7	13.2	14.2	14.8	15.7	13.4	12.5	12.5	13.7	13.9	13.3
Calcium	13.5	19.9	16.7	11.3	10.2	10.7	10.9	13.7	16.4	10.3	10.2	10.0	12.0	11.7	9.8
Magnesium	2.0	2.2	2.4	1.7	2.4	2.0	3.3	2.3	2.0	2.5	2.0	2.3	2.5	3.0	2.8
Essential AA (g/kg DM)															
Arginine	23.5	29.7	27.4	29.5	28.6	23.0	26.9	22.8	28.9	29.6	25.3	29.1	30.2	22.5	21.0
Histidine	9.8	12.3	12.7	9.1	11.2	9.9	10.1	9.4	10.6	10.6	9.1	9.7	9.9	9.3	8.9
Isoleucine	16.4	20.6	20.4	21.0	19.2	16.9	16.8	15.3	17.7	17.4	14.9	15.3	15.4	15.0	14.0
Leucine	30.2	37.1	35.2	37.1	34.2	29.4	29.5	28.9	33.7	31.9	27.8	28.2	28.8	27.8	29.8
Lysine	27.6	36.3	31.8	25.6	29.3	26.7	24.7	27.2	30.0	30.6	25.6	24.9	26.4	24.8	22.0
Methionine	14.9	16.5	14.6	13.6	12.9	12.3	13.3	15.0	13.8	12.0	11.2	11.4	13.4	12.4	12.1
Phenylalanine	18.8	21.1	20.4	22.6	21.5	19.1	19.1	18.0	20.5	20.8	17.8	17.7	19.0	17.7	17.8
Threonine	13.9	19.0	18.0	18.3	16.2	15.4	14.6	13.5	16.9	15.3	13.0	13.7	13.6	14.1	12.8
Valine	17.7	22.4	24.8	25.4	20.0	18.9	18.5	16.7	20.7	19.2	16.5	16.1	16.7	17.2	16.1
Non-essential AA (g/kg DM)															
Alanine	17.8	26.0	24.4	21.7	19.8	20.1	18.2	17.4	24.6	19.1	16.5	16.4	17.8	17.0	18.7
Aspartic acid	33.3	44.6	43.2	37.9	43.0	34.9	35.7	32.5	39.0	40.9	33.9	34.9	35.5	31.1	29.4
Glutamic acid	88.4	93.3	83.7	90.5	93.3	83.2	87.0	86.1	84.1	86.3	77.6	84.5	89.2	77.9	77.0
Cystine	5.9	6.4	6.1	9.7	6.3	5.8	6.2	5.6	5.6	5.9	4.9	5.1	5.7	6.3	5.4
Glycine	17.8	26.4	22.7	26.0	19.4	18.1	19.6	17.5	28.7	19.0	16.6	17.3	18.8	17.5	16.2
Proline	28.0	29.4	32.0	39.6	28.5	28.7	25.8	28.1	31.3	27.0	24.4	24.5	26.9	26.4	26.2
Serine	18.8	23.1	22.7	32.1	22.1	19.9	19.1	18.5	21.1	20.9	18.0	18.7	19.2	17.8	17.6
Tyrosine	3.5	4.8	16.0	6.0	6.1	7.2	6.2	10.7	12.9	13.0	11.1	11.4	11.9	10.9	11.1
SAA (g/kg DM)	386	469	456	466	432	389	391	383	440	419	364	379	398	366	356

[1] AA, amino acid; SAA, sum of amino acid; DM, dry matter; CON, control; HFM, hydrolysed feather meal; FM, fishmeal; SBM, soybean meal; IM, insect meal; SFM, sunflower meal; YM, yeast meal; GM, guar Meal; LM, lupine Meal; DDGS, dried distillers grain of corn; CM, canola Meal; PP, pea protein; FB, faba Beans; PM, poultry Meal.

[2] NSP, non-starch polysaccharides were calculated as total carbohydrates – starch.

[3] Total carbohydrate was calculated as dry matter – crude protein – crude fat – ash content.

bottles were submerged in ice-filled styrofoam boxes to reduce microbial degradation. Feces were pooled per tank and stored at −20 °C for further analysis. At both end of the restricted and satiation period, fish were starved for 24 h and batch weighed per tank for final weight.

2.4. Analytical methods

The fecal samples were freeze-dried (Scanvac FD8 Coolsafe Advanced, LaboGene A/S, Denmark), then manually pulverized through a 1 mm screen sieve. Feed pellets and ingredients were grinded by a grinding machine (Retsch ZM 200). Proximate composition of ingredients, feed, fish and feces were assessed (in triplicate) according to ISO-standard analysis for determination of dry matter (ISO 6496, 1983), crude ash (ISO 5984, 1978), crude protein (ISO 5983, 1979); crude protein = Kjeldahl- N × 6.25), crude fat (ISO 6492, 1999) and starch (ISO 6493: 2000). Energy content was measured bomb calorimetric by direct combustion (IKA® werke, C7000; IKA analysentechnik, Weitershem, Germany). Yttrium, phosphorus, calcium and magnesium in feed and feces were determined from the ash by using inducted coupled plasma mass spectrometry according to the standard NEN 15510 (ICP-MS, 2007). Amino acids (excluding tryptophan) were analysed by Skretting ARC, Norway, using an automatic amino acid analyzer (Biochrom 30+, Biochrom Ltd., Cambridge, UK) and the methods described in the COMMISSION REGULATION (EC) No 152/2009 (Council, 2009). Diet, ingredient and fecal starch contents (incl. sugars) were determined via an enzymatic digestion as described by Goelema et al. (1998), excluding the ethanol washing step and was analysed by Nutricontrol (Veghel, The Netherlands). By excluding the ethanol step, sugars with less than 10 glucose units are included in the starch fraction and thereby gave a better calculation of the non-starch polysaccharide (NSP) content.

2.5. Calculation

Daily weight gain (g/d) was calculated as the differences between the average initial (W_i) and final (W_f) body weight of fish divided by the duration of the experiment (t). Feed conversion ratio (FCR; g/g) on dry matter (DM) basis was calculated as (feed intake × dry matter content of the feed)/(final weight of fish – initial weight of fish). Feed intake (FI; % BW/d) was calculated as FI/t/Wg × 100%, where FI is feed intake (g), t is the number of days, and Wg is the geometric mean BW (g) of each feeding period, respectively. The Wg was calculated as e (($\ln W_t + \ln W_0$)/2), where W_0 and W_t are the initial and final BW (g) for each feeding period, respectively. Specific growth rate (SGR; %/d) was calculated as ($\mathrm{LnW_f} - \mathrm{LnW_i} \times 100$)/t, where t is the duration of the experiment in days (d). Fish survival (%) was calculated as number of fish at the beginning of the experiment divided by the number fish at the end of the experiment x 100.

The ADC of AA and macronutrients of diets were calculated according to the following formula described by Cheng and Hardy (2002) using yttrium oxide as inert marker, ADC (%) = 100 × [1 − (Yttrium concentration in the feed × concentration nutrient in feces)/(Yttrium concentration in the feces × concentration nutrient in feed)]. The dry matter ADC of the diets was calculated as, ADC (%) = 100 × [1 − (Yttrium concentration in the feed /Yttrium concentration in the feces)]. The ADC of dietary component in the test ingredient were calculated using the following equation as described by Teuling et al. (2017); $ADC_{test\ ingredient} = ADC_{test\ diet} + (ADC_{test\ diet} - ADC_{reference\ diet})$ x (0.7 x $Nutrient_{reference\ diet}$/0.3 x $Nutrient_{test\ ingredient}$) x 100%, where $ADC_{test\ diet}$ and $ADC_{reference\ diet}$ are the apparent digestibility coefficient (%) of the dietary component in the test diet and the reference diet, respectively. $Nutrient_{reference\ diet}$ and $Nutrient_{test\ ingredient}$ are the nutrient contents (g/kg DM) or the gross energy (kJ/g) in the reference diet and test ingredient, respectively. The concentrations of yttrium and nutrients were expressed on DM basis. Total carbohydrate was calculated as dry matter minus crude protein minus crude fat minus ash content. The NSP fraction was calculated as total carbohydrates minus starch.

2.6. Statistical analysis

Tanks (trial 1 $n = 21$; trial 2 $n = 24$) were considered as experimental units. Due to differences in the start weight, performance data were subjected to a one-way analysis of variance (ANOVA) within trials. Furthermore, performance data were separately analysed per feeding period because the variance differed between the feeding periods (e.g., feeding level). Combined data regarding digestibility during restricted and satiation feeding were analysed using GLM procedure of repeated measurement to test the effect of feeding period (restricted vs. satiation feeding), ingredient and their interaction. The effect of ingredient was tested against the between tank variation. The level of significance adopted was 5%. Tukey's multiple range test was performed when finding significant interactions between factors. All data analysis were carried out using statistical analysis systems (SAS Institute) statistical software package version 9.1.

3. Results

The same reference diet was used in trial 1 and 2, however, the trails were conducted at different times using different batches of African catfish of the same origin. Differences between the respective ADC of the reference diet were examined using a one-way ANOVA to check if there was a trail effect. Result showed no significant difference in nutrients and AA ADC ($P > 0.05$) of the reference diets between trials.

Performance parameters are presented in Supplementary Table A. Fish were fed the same ration during the restricted period, therefore, feed intake did not differ ($P > 0.05$; Table 4). In both trials at the start of the restricted feeding period, fish promptly accepted all the experimental diets with the exception of YM. YM feeds were rejected in the first two days, after which fish slowly adapted to this diet. This was reflected by an increase in feed intake over time. During satiation feeding, feed intake in trail 1 and 2 was respectively, 2.89 and 3.66% BW/d averaged over all diets. Within trial 1, satiation feed intake differed among diets ($P < 0.01$; Table 4). In this trial, the lowest satiation feed intake (2.63% BW/d) was observed in fish fed the YM diet, whereas, SBM diet had the highest intake of 3.11% BW/d, while all other test diets (FM, IM, HFM and SFM) had similar satiation feed intakes as the control diet. The ranking in feed intake expressed in g/d was slightly different. Feed intake expressed in g/d was highest for FM and IM and lowest for YM (Table 4). The ingredients tested in trial 2 (PM, PP, FB, LM, GM, CM and CDDGS) did not induce difference in satiation feed intake, both on g/d as well as % BW/d basis ($P > 0.05$; Table 4).

The ADC of macro-nutrients, energy and minerals of experimental diets are presented in Supplementary table B, because this study mainly focused on the ADC of ingredients. Ingredient ADC values of nutrients,

Table 4
Effect of dietary ingredient on feed intake of African catfish during restricted feeding and satiation feeding[1].

Parameters		Trial 1									Trial 2								
	FL	CON1	FM	IM	HFM	SBM	YM	SFM	SEM	*P*-value[2]	CON2	PM	PP	FB	LM	GM	CM	CDDGS	SEM	*P*-value[2]
FI (g/d)	R	2.10	2.10	2.10	2.10	2.10	2.09	2.08	–	–	1.74	1.74	1.74	1.74	1.74	1.64	1.74	1.74	–	–
	S	5.23^{bc}	6.04^{c}	5.81^{c}	4.76^{ab}	5.45^{bc}	4.19^{a}	4.57^{ab}	0.21	***	5.50	5.42	5.50	5.87	5.50	5.01	5.28	5.10	0.21	NS
RFI (%/BW/d)	R	2.74	2.60	2.60	2.72	2.75	2.78	2.76	–	–	3.00	2.89	3.00	2.97	3.02	2.84	3.03	3.17	–	–
	S	2.99^{ab}	3.03^{ab}	2.95^{ab}	2.79^{ab}	3.11^{b}	2.63^{a}	2.76^{ab}	0.08	**	3.65	3.41	3.61	3.91	3.74	3.46	3.66	3.81	0.11	#

^{abc}Values in the same row within a trail lacking common superscripts are statistically different ($P < 0.05$) according to Tukeys' multiple comparison test.

[1] FI, feed intake; RFI, relative feed intake; CON, control; HFM, hydrolysed feather meal; FM, fish meal; SBM, soybean meal; IM, insect meal; SFM, sunflower meal; YM, yeast meal; GM, guar meal; LM, lupine meal; CDDGS, corn dried distillers grain; CM, canola meal; PP, pea protein; FB, faba beans; PM, poultry meal; SEM, standard error of mean; FL: feeding level (R or S); R, restricted feeding; S, satiation feeding.

[2] NS, not significant $P > 0.1$; # $P < 0.10$; **$P < 0.01$; ***$P < 0.001$. Feed intake was not analysed during restricted period because feeding level was fixed.

which are placed in between brackets in Tables 5 and 6, were excluded from the statistical analysis. This is because of the low contribution of these ingredients to the experimental diets (less than 8% of the total nutrient content in the test diet originating from the test ingredient), which amplifies the measurements errors in the calculated ingredient ADC values. This implication can lead to estimated ingredient ADC values <0% and also >100%, which occurred for the nutrient ADC of some ingredients (Table 5). Except for fat and energy, feeding level had a significant effect on all macro-nutrients digestibilities. Feeding level influenced nutrients digestibility at a different degree, with the most significant response found in NSP digestibility ($P < 0.001$), followed by DM, ash and starch ($P < 0.01$). The least impact was observed in protein and energy ($P < 0.05$) digestibility. Furthermore, an interaction effect was found between feeding level and dietary treatments on fat, NSP and starch digestibility. Feeding levels showed a contrasting trend on nutrient ADC among ingredients. For some ingredients (e.g., FM, IM and LM), protein digestibility increased with increased feeding level while others (e.g. PM and PP) decreased with feeding level.

Generally, ADC values for nutrients in ingredients tested were high, especially for ingredients of animal origin. DM digestibility of all ingredients differed significantly ($P < 0.01$). For ingredients of animal origin, DM digestibility values exceeding 74% were recorded for FM, PM, IM, and HFM while values for legumes and oilseeds were above 60.4%. Fat in animal ingredients (95.1%) was better digested than that of vegetable ingredients (88.4%). In the same way, energy ADC was averagely 91.3% for animal protein ingredients and 81.7% for plant protein ingredients. The highest crude protein digestibility (105.1%) was recorded in GM, followed by SBM (96.5%) while the lowest values were found in IM and CDDGS (85.6% and 86.5%, respectively). FM displayed moderate value for crude protein ADC (averaged over both periods, 94.2%). Overall, ADC values for GM were exceptionally high (beyond 100%) for most of the nutrients analysed.

Apparent AA digestibility coefficients of the test ingredients are presented in Table 6. No significant differences in ADC for AA were observed between both feeding periods except for methionine and glutamic acid. The digestible essential AA content of each ingredient, expressed per unit of digestible protein (dAA/DP) are visualized in Fig. 1-3 and digestible non-essential AA content in Supplementary fig. A-C. Overall, the ordering of ingredients from highest to lowest dAA/DP content varied strongly between the different amino acids. The dAA/DP content of Met in test ingredients of animal origin was highest for FM (27 g dMet/kg DP) and lowest for HFM (5 g dMet/kg DP). Also, all tested legumes had a low digestible Met content, which ranged from 5 to 14 g dMet/kg DP. IM and PM had a similar dAA/DP content of Met (20 and 19 g dMet/kg DP, respectively) though lower than FM (Fig. 1). Except for HFM, the dAA/DP content of histidine in all ingredients was larger than that of FM (20 g dHis/kg DP). HFM had a histidine content of only 6 g dHis/DP (Fig. 1). All legumes had a lower dAA/DP content of threonine compared to FM. IM, HFM and CM had a higher dAA/DP content of threonine compared to FM. All other ingredients had a comparable digestible threonine content as FM (Fig. 1). All ingredients had a lower dAA/CP content of lysine than that of FM (76 g dLys/kg DP), though the digestible lysine content of IM was only slightly lower. HFM had the lowest digestible lysine content (17 g dLys/kg DP) (Fig. 2). Regarding the digestible arginine content, only CDDGS and YM had a value lower than FM. All other ingredients had an equal or higher dAA/DP content of arginine compared to FM (59 g dArg/kg DP). GM had a very high digestible arginine content, being 131 g Arg/kg DP (Fig. 2). Regarding the digestible phenylalanine and isoleucine content, only some ingredients were below the content in FM (Fig. 3). Excluding SBM, the tested legumes had a lower digestible valine content compared to FM (Fig. 3). Considering all essential AA of tested ingredients, IM was the closest to FM regarding its dAA/DP profile.

4. Discussion

Digestibility and palatability are fundamental measurements used in evaluating the nutrient availability and quality of feed ingredients for specific species and thus for formulating balanced diets. This research assessed the digestibility and satiation feed intake of 13 ingredients in African catfish, in which the protein contents were sourced from animal, plant, or single-cell protein origin.

Palatability is an important factor which determines the value and quality of an ingredient (Glencross, 2020). In trial 1, YM showed to have a lower palatability for African catfish compared to other ingredients based on the measured satiation feed intake (Table 4). Similarly, Solomon et al. (2017) observed reduced feed intakes in African catfish fed a yeast containing diet. The lower palatability of the YM diet was also observed during the first week of restricted feeding period, which was intended as an adaptation period to the experimental diets. During this adaptation period, all diets were well accepted by the fish, except for YM diet, which resulted in a longer feeding time for this diet. Fish fed the YM diet swallowed the pellets but often expelled them back into the water afterwards. A similar behaviour was observed in sunshine bass (*Morone chrysops* × *M. saxatilis*) fed yeast containing diets (Gause and Trushenski, 2011). The lower palatability of YM may be related to a bitter taste, which can be present in fermented yeast products (In et al., 2005; Shotipruk et al., 2005). In trail 1, FM and IM resulted in the highest feed intake (in g/d) in African catfish. This is well in line with literature that FM (NRC, 2011) and insect meals (Makkar et al., 2014; Ng et al., 2001) are highly palatable for fish. Fish fed HFM and SFM diets had a lower satiation feed intake (in g/d) than FM and IM diets, but no expulsion after ingestion as seen with YM occurred during the adaptation period. Plant ingredients contains anti-nutritional substances that may affect palatability and reduce feed intake (Gatlin et al., 2007; Nazzaro et al., 2021; Teles et al., 2020). However, in the current study, diets were extruded and consequently heat liable anti-nutritional factors would have most likely be neutralized. This may explain the absence of difference in satiation feed intake between ingredients in trial 2. The impact of extrusion might also be involved in the observed high satiation feed intake at the SBM diet.

In the current study, the effect of feeding level on nutrient ADC was quite variable among feed ingredients (Table 5). A significant interaction effect between the ADC of ingredients and feeding level was observed for the digestibility of fat, NSP and carbohydrate. The differences in ADC between restricted and satiation feeding could be due to variability in the satiation feed intake between the test diets (i.e., ingredients). However, the change in ADC between both periods was not correlated with the realized satiation feeding level (data not shown). At satiation feeding level, the DM digestibility decreased for SFM, FB and LP but for all other ingredients, digestibility increased with increased feeding level. This is in contrast to what has been reported previously, as ADC appeared to decrease at high feeding level (Haidar et al., 2016; Henken et al., 1985b). The higher transit of dietary material through the gastrointestinal tract with a high feeding level (satiation) was suggested as an explanation, as it may reduce the ability of the fish to digest/absorb the diet (Henken et al., 1985b). The negative effect of increased feeding level on the ADC of most legumes and oilseeds may be due to the high fibre content in these ingredients (Table 2) (Haidar et al., 2016; Staessen et al., 2020). This may also explain the interaction between feeding level and the ADC of NSP and carbohydrate in this study. Haidar et al. (2016) observed that diets with high amounts of NSP tend to be less well digested, especially at high feeding level. The explanation would be that NSP can hold high amounts of water and form gum-like masses in the intestine of fish, which may increase viscosity and reduce digestive enzyme activity (Francis et al., 2001). The differences between ingredients regarding the influence of feeding level (restricted vs. satiation) on ADC in the current study might be also due to differences between the ingredients in water absorption capacity and viscosity. This may lead to altered gastric transit time, thereby affecting the

Table 5
Apparent digestibility coefficient (ADC) of nutrients in ingredients fed to African catfish during the experimental period[1].

ADC (%)	Test ingredients														Pooled SEM	*P*-value[2]		
	FL	FM	IM	PM	HFM	SBM	PP	FB	LM	GM	CM	SFM	CDDGS	YM		I	FL	FL*I
Dry matter	R	83.7	76.5	87.2	74.0	73.3	80.0	82.1	77.5	106.2	73.3	66.9	64.8	78.3	3.69	***	**	#
	S	95.3	89.3	89.9	93.4	77.3	80.8	80.3	74.6	111.1	75.8	60.4	72.2	87.2				
Ash	R	44.7	50.3	69.4	(−182.0)[4]	11.7	63.3	65.3	47.2	169.5	46.8	26.3	91.7	71.0	10.9	***	**	NS
	S	63.0	71.7	56.6	(−55.2)	54.3	59.7	75.8	83.4	166.1	72.0	44.4	124.3	83.5				
Crude protein	R	93.1	85.6	90.4	87.1	92.2	93.8	87.6	93.9	105.1	89.8	92.4	86.9	87.2	1.16	***	*	#
	S	95.4	90.1	89.2	91.5	96.5	92.7	87.3	94.8	103.1	89.9	92.5	86.5	87.8				
Fat	R	98.6	95.0	99.1	69.2	77.1	91.0	85.5	95.9	93.0	95.2	86.1	90.9	(84.1)	2.97	***	#	***
	S	103.1	100.5	98.7	96.9	89.7	88.6	84.2	95.2	91.1	97.0	67.6	90.6	(99.2)				
Starch	R	–[5]	–[5]	–[5]	–[5]	(101.6)	103.5	98.4	(105.3)	(112.7)	(113.4)	(98.2)	(83.4)	99.5	1.04	***	**	**
	S	–[5]	–[5]	–[5]	–[5]	(111.0)	112.8	95.4	(118.4)	(403.5)	(191.7)	(120.8)	(114.2)	103.9				
NSP	R	–[5]	28.4	–[5]	–[5]	39.7	41.0	29.8	50.6	119.7	49.2	37.2	31.8	51.9	8.61	***	***	***
	S	–[5]	71.0	–[5]	–[5]	36.1	57.3	55.1	42.6	123.3	47.1	21.0	46.8	72.9				
Total Carbohydrate	R	–[5]	51.5	–[5]	–[5]	52.4	58.5	77.9	60.7	111.4	56.4	44.7	36.2	69.1	7.23	***	#	NS
	S	–[5]	89.1	–[5]	–[5]	49.4	64.2	77.9	52.6	131.6	59.6	30.2	46.0	86.9				
Energy	R	93.4	81.5	91.3	83.8	82.0	83.8	84.2	81.4	104.3	78.0	71.7	68.2	78.4	2.93	***	*	NS
	S	101.1	91.6	93.4	94.7	82.7	84.6	82.5	79.0	108.0	79.9	63.2	73.6	87.6				
Calcium[3]	R	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	S	36.9	67.7	62.1	(49.3)	−16.8	(71.0)	(263.5)	(186.8)	(751.8)	70.9	29.2	(2296.0)	124.5	26.2	#	–	–
Phosphorous[3]	R	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	S	59.6	58.7	65.2	(37.0)	34.4	60.1	59.2	61.1	89.4	59.6	49.9	116.0	120.7	5.05	***	–	–
Magnesium[3]	R	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	S	89.7	85.1	79.5	(71.0)	58.3	65.2	34.4	64.8	94.9	67.7	51.4	98.9	105.3	4.71	***	–	–

[1] Presented values are means ($n = 3$) per diet/ingredient within each experiment. HFM, hydrolysed feather meal; FM, fish meal; SBM, soybean meal; IM, insect meal; SFM, sunflower meal; YM, yeast meal; GM, guar meal; LM, lupine meal; CDDGS, corn dried distillers grain; CM, canola meal; PP, pea protein; FB, faba beans; PM, poultry meal; SEM, standard error of mean; I, ingredients; FL, feeding level; IxFL, interaction between ingredients and feeding level; R, restricted feeding; S, satiation feeding; NSP, non-starch polysaccharide.

[2] NS, not significant $P > 0.1$; # $P < 0.10$; *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.

[3] Chemical analysis was not performed for calcium, phosphorus and magnesium during for restricted period due to insufficient fecal materials.

[4] The values in the brackets were excluded from statistical analysis because the contribution of the nutrient originating from the ingredient was less than 8% of the nutrient content in the test diet.

[5] ADC values were not calculated for FM, IM, PM and HFM because these ingredient do not contain these nutrients.

Table 6
Apparent digestibility coefficient (ADC) of amino acids in ingredients fed to African catfish during the experimental period[1].

ADC (%)	Test ingredients														Pooled SEM	*P*-value[2]		
	FL	FM	IM	PM	HFM	SBM	PP	FB	LM	GM	CM	SFM	CDDGS	YM		I	FL	FL*I
Essential AA																		
Arginine	R	96.4	95.9	92.9	93.1	97.5	97.1	94.7	98.6	100.6	95.7	97.9	93.6	90.3	0.69	***	NS	NS
	S	98.0	97.9	93.8	95.1	99.6	95.7	94.2	98.3	100.9	95.1	98.6	92.6	90.8				
Histidine	R	94.8	91.9	88.8	77.4	96.5	95.5	89.7	95.2	101.8	93.0	97.0	88.2	85.2	1.29	***	#	**
	S	97.3	91.7	89.4	89.3	98.1	93.4	89.7	94.2	102.5	92.6	95.1	89.0	86.3				
Isoleucine	R	94.1	93.2	87.9	91.8	95.5	94.0	89.4	95.7	104.5	90.0	95.8	86.7	85.5	1.36	***	NS	NS
	S	95.3	95.4	87.6	92.0	99.3	90.2	90.1	93.4	105.4	89.9	96.0	85.5	85.6				
Leucine	R	95.4	93.1	89.3	91.0	94.8	95.0	91.5	96.2	102.1	91.3	94.3	90.6	87.9	1.11	***	NS	NS
	S	96.5	96.1	89.1	92.5	98.6	91.5	91.3	94.3	104.4	91.4	94.5	89.6	87.8				
Lysine	R	96.2	95.9	91.2	78.1	96.4	97.3	91.4	96.3	104.4	93.0	96.2	84.7	87.7	1.26	***	NS	**
	S	97.5	96.7	91.8	91.0	98.3	95.7	92.2	94.4	102.1	91.4	95.5	83.9	89.2				
Methionine	R	95.1	96.0	92.7	(79.7)	98.0	95.1	(80.0)	(90.6)	(104.6)	95.9	97.7	94.5	84.5	0.88	***	*	***
	S	95.7	96.7	92.0	(88.8)	100.4	86.3	(79.0)	(89.8)	(104.9)	95.0	98.0	90.8	85.4				
Phenylalanine	R	93.4	95.6	90.4	91.9	95.4	95.6	91.7	96.1	102.5	93.4	95.0	92.0	89.3	1.18	***	NS	NS
	S	94.5	97.7	89.7	93.4	98.3	91.8	89.4	93.3	104.0	91.0	94.9	89.3	89.7				
Threonine	R	95.0	93.3	88.5	87.6	93.3	93.9	89.0	95.0	104.8	89.3	94.5	85.6	79.8	1.23	***	NS	NS
	S	96.1	95.2	88.7	89.5	98.1	90.0	88.9	93.4	104.3	88.9	93.8	85.2	81.0				
Valine	R	94.1	93.8	87.9	91.4	93.4	93.1	90.3	94.0	103.0	90.6	94.1	87.3	85.4	1.40	***	NS	NS
	S	95.7	95.1	88.0	91.7	98.3	88.9	89.3	91.2	105.3	90.1	94.8	85.3	86.0				

ADC (%)	Test ingredients														Pooled SEM	*P*-value[2]		
	FL	FM	IM	PM	HFM	SBM	PP	FB	LM	GM	CM	SFM	CDDGS	YM		I	FL	FL*I
Non-essential AA																		
Alanine	R	95.5	93.5	91.8	88.6	92.7	93.7	87.8	94.4	104.5	93.2	94.2	91.3	87.0	1.32	***	NS	NS
	S	96.2	95.2	91.7	90.9	98.4	89.0	88.9	93.0	105.0	92.3	95.4	90.5	87.2				
Aspartic acid	R	92.1	93.8	85.0	87.5	97.9	96.5	92.3	96.4	103.5	94.4	98.1	88.2	82.9	1.06	***	NS	NS
	S	94.7	95.5	88.9	91.0	99.2	94.4	92.9	95.0	102.9	94.4	96.6	87.9	83.3				
Glutamic acid	R	95.9	93.8	91.3	90.3	98.1	97.6	93.1	98.1	101.5	96.4	98.4	93.5	90.1	0.71	***	*	*
	S	97.8	96.3	92.6	94.8	99.3	96.3	93.2	97.7	101.5	96.3	97.6	93.4	90.7				
Cystine	R	86.1	82.0	73.4	88.0	96.4	81.1	74.4	91.7	104.0	89.6	96.2	83.6	70.0	2.41	***	#	NS
	S	92.2	86.8	76.6	88.6	99.0	76.0	77.6	90.1	109.6	92.1	92.8	86.5	72.7				
Glycine	R	94.5	89.0	91.9	91.8	91.4	92.6	86.2	94.9	102.9	91.7	93.6	86.9	83.4	1.41	***	NS	NS
	S	96.1	91.2	93.4	92.6	96.6	88.8	87.4	93.5	103.4	91.7	93.9	87.4	84.3				
Proline	R	95.0	93.7	92.3	92.9	95.2	92.6	86.2	96.3	104.7	90.4	95.0	91.9	88.7	1.20	***	NS	NS
	S	97.2	95.3	92.3	94.2	98.1	89.4	87.1	94.6	106.4	90.8	94.3	92.0	88.9				
Serine	R	94.3	92.9	88.2	93.4	95.7	94.2	92.2	95.7	102.7	90.7	96.2	89.9	79.0	1.00	***	NS	NS
	S	96.6	94.9	89.5	93.6	98.6	91.2	91.3	94.6	103.5	91.2	95.0	89.6	81.4				
Tyrosine	R	84.7	99.5	90.0	98.1	98.1	98.6	96.1	97.0	97.2	95.7	99.2	92.1	88.1	1.41	***	NS	*
	S	85.2	100.5	92.7	89.9	98.1	96.4	94.0	94.9	102.0	93.0	99.2	91.9	91.4				
SAA	R	94.6	94.0	90.0	90.9	96.1	95.5	91.1	96.5	102.3	93.1	96.4	90.4	86.2	1.02	***	NS	NS
	S	96.3	95.8	90.9	93.0	98.7	92.8	91.1	95.3	102.9	92.7	96.0	89.8	87.0				

[1] HFM, hydrolysed feather meal; FM, fish meal; SBM, soybean meal; IM, insect meal; SFM, sunflower meal; YM, yeast meal; GM, guar meal; LM, lupine meal; CDDGS, corn dried distillers grain; CM, canola meal; PP, pea protein; FB, faba beans; PM, poultry meal; SEM, standard error of mean; I, ingredients; FL, feeding level; IxFL, interaction between ingredients and feeding level; R, restricted feeding; S, satiation feeding.
[2] NS, not significant $P > 0.1$; # $P < 0.10$; *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.

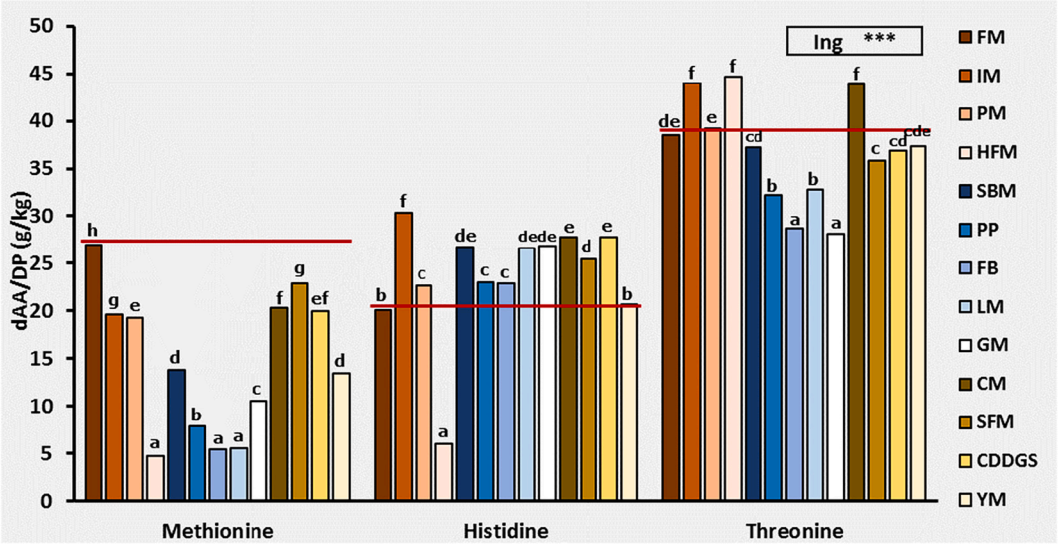

Fig. 1. Digestible methionine, histidine and threonine expressed per digestible protein (dAA/DP) of various ingredients fed to African catfish. Red line showing fish meal dAA/DP compared to other ingredients. Ing, ingredients; HFM, hydrolysed feather meal; FM, fish meal; SBM, soybean meal; IM, insect meal; SFM, sunflower meal; YM, yeast meal; GM, guar meal; LM, lupine meal; CDDGS, corn dried distillers grain; CM, canola meal; PP, pea protein; FB, faba beans; PM, poultry meal. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

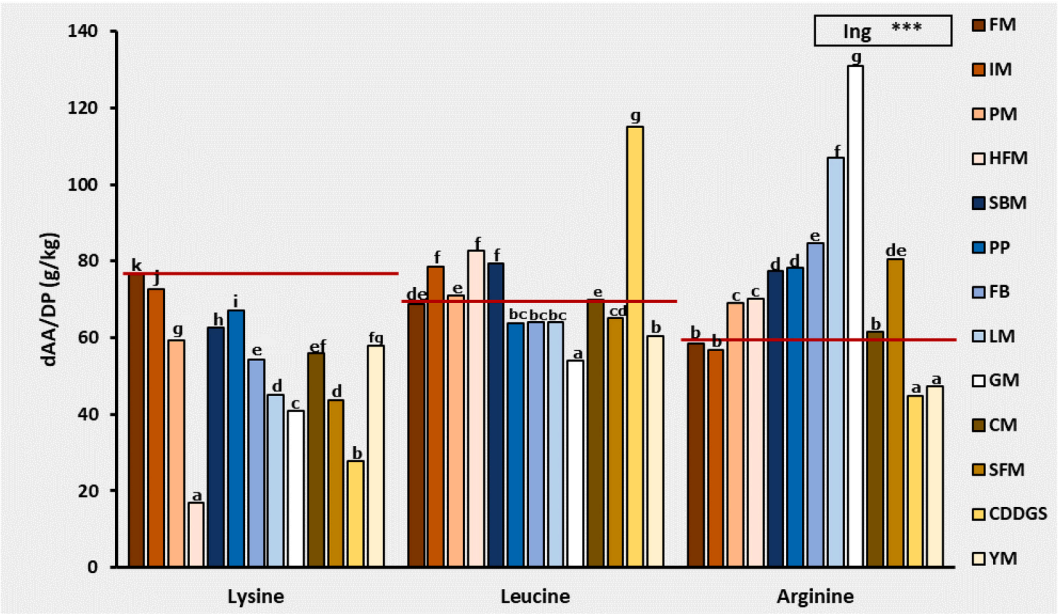

Fig. 2. Digestible lysine, leucine and arginine expressed per digestible protein (dAA/DP) of various ingredients fed to African catfish. Red line showing fish meal dAA/DP compared to other ingredients. Ing, ingredients; HFM, hydrolysed feather meal; FM, fish meal; SBM, soybean meal; IM, insect meal; SFM, sunflower meal; YM, yeast meal; GM, guar meal; LM, lupine meal; CDDGS, corn dried distillers grain; CM, canola meal; PP, pea protein; FB, faba beans; PM, poultry meal. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

effectiveness of enzymes. In contrast, Storebakken and Austreng (1987) found no significant difference in digestibility when feeding level was increased in rainbow trout. In another study, Cho and Kaushik (1990) demonstrated that neither feeding frequency nor feeding level affected the ADC of dry matter, crude protein, lipid and gross energy in rainbow trout. Differences in outcome is an indication that the effect of feeding level on nutrient ADC could be dependent on species, methodologies applied and ingredients used in diet formulation (Imtiaz, 2018). Findings from the present study suggest that the effect of feeding level on crude protein digestibility is dependent on the ingredient.

As expected, our results showed a consistent trend for a higher DM and CP digestibility among ingredients of animal origin and a lower DM and CP digestibility for several plant ingredients in African catfish. This result is in line with the observation reported for rainbow trout and yellowtails (both *Seriola lalandi* and *Seriola dumerili*) fed various feed ingredients (Dam et al., 2019; Lee et al., 2020; Tomas-Vidal et al., 2019). Generally, a low DM digestibility indicates the presence of a high quantity of indigestible substances or anti-nutritional factors in the feedstuffs (Dam et al., 2019; Lee et al., 2020; Li et al., 2013). Compared to animal protein ingredients, a lower ADC for plant protein ingredients has been reported in literature. This has generally been attributed to the negative effect of a high fibre content (Che et al., 2017; Lee et al., 2020; Luo and Tan, 2008; Zhou and Yue, 2012). On the other hand, Allan et al. (2000) reported a 99% nitrogen digestibility for wheat (which contains

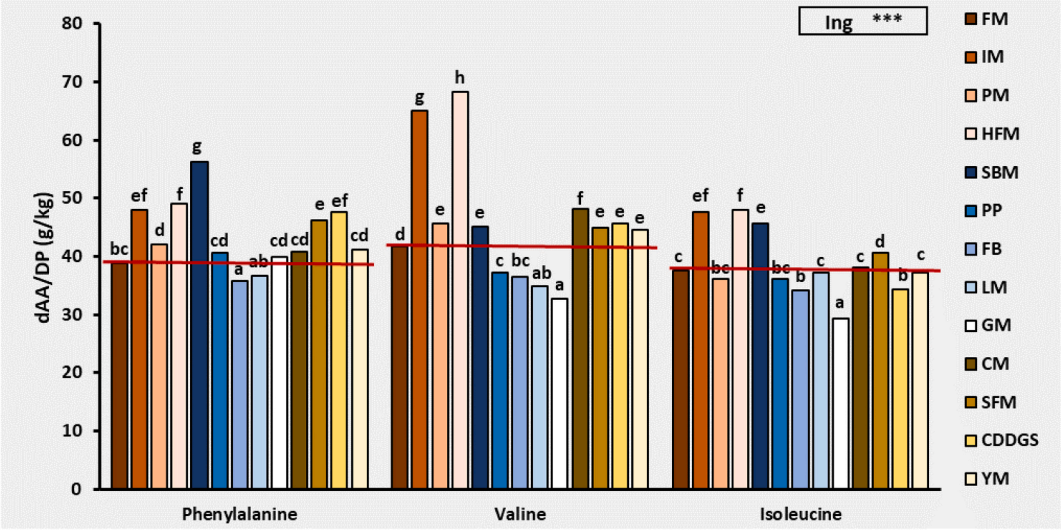

Fig. 3. Digestible phenylalanine, valine, isoleucine expressed per digestible protein (dAA/DP) of various ingredients fed to African catfish. Red line showing fish meal dAA/DP compared to other ingredients. Ing, ingredients; HFM, hydrolysed feather meal; FM, fish meal; SBM, soybean meal; IM, insect meal; SFM, sunflower meal; YM, yeast meal; GM, guar meal; LM, lupine meal; CDDGS, corn dried distillers grain; CM, canola meal; PP, pea protein; FB, faba beans; PM, poultry meal. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

15% protein, 80% carbohydrate) in the diet of silver perch (*Bidyanus bidyanus*). This is probably due to the omnivorous nature of this species (similar to African catfish). In evolution, both species may have developed mechanisms to digest and metabolize plant materials. These same mechanisms may explain why African catfish recorded high NSP digestibility in this study. Furthermore, for some ingredients (Table 5), ADC values are close to, or even above 100%, similar to what has been found in literature (Allan et al., 2000; Basto et al., 2020; Mo et al., 2019). In the current study, feces egested into water was collected by settling units. The ADC > 100% might be an indication for the occurrence of leaching. Determination of ADC by feces collection from water can lead to an overestimation compared to stripping of feces (e.g., Storebakken et al., 1998). Furthermore, the ADC > 100% for some ingredients, might be explained by the low nutrient contribution (less than 8%) from these ingredients to the experimental diet, thereby leading to higher uptake of this nutrient from the reference diet constituents to meet the species requirement (Basto et al., 2020). Another alternative explanation might be the presence of enzymes in some ingredients and or other factors that improve the ADC of the basal part in the test diets.

In the current study, differences in AA digestibility values confirm the notion that the protein quality varies widely among the different ingredients. Among the animal protein ingredients used in this study, HFM had the lowest AA digestibility, whereas IM had a digestibility similar to FM. The high overall AA ADC values recorded for fish fed IM makes it a potential substitute for FM. However, fish fed IM recorded the lowest protein ADC during the restricted feeding period. This low protein digestibility could be linked to the presence of chitin in the insect exoskeleton. Decreased nutrient digestibility due to the presence of chitin in insect meal has been reported in Nile tilapia, turbot (*Psetta maxima*) and Atlantic salmon (Fontes et al., 2019; Karlsen et al., 2017; Kröckel et al., 2012). It is interesting to note that even though IM showed a lower protein digestibility, it resulted in a similar growth performance as FM. In contrast, YM (considered to be a promising novel ingredient) resulted in the lowest AA digestibility and growth. Similar observations were reported in several studies especially when using a high inclusion level of YM (Al-Hafedh and Alam, 2013; Manoppo and Kolopita, 2016; Ovie and Eze, 2014; Pongpet et al., 2016). In light of the consistently low feed intake, low digestibility and poor growth of fish fed YM in this and previous studies, it would appear prudent to limit the amount of YM in the diets of African catfish until better understanding of the reasons for the low digestibility are elucidated. However, the inclusion of yeast in feeds for other species was found to potentially improve the feed efficiency and enhance the immune responses (Eryalçin et al., 2017; Ortuño et al., 2002; Siwicki et al., 1994; Torrecillas et al., 2014). Regarding oilseeds and legumes, SBM had relatively high protein and AA digestibility in African catfish and may be a useful alternative to FM in aquafeeds. Protein ADC of soybean meal varies between species and falls within the range of 76–98% (Tomas-Vidal et al., 2019). The present study confirms that the ADC for SBM in African catfish falls towards the higher end of this range (94.4%).

The protein quality of an ingredient is mainly determined by its AA profile and their digestibility. Therefore, AA digestibility data for common feedstuffs is of paramount importance (Anderson et al., 1992; Glencross, 2020). In the current study, we calculated the digestible AA (expressed per unit of digestible protein [DP]) (Figs. 1–3), in order to ascertain the potential values of various ingredients. Values for all ingredients were compared with the values obtained for digestible AA in FM. This is because FM has always been the preferred choice for protein source in aquafeeds due to its high nutrient and AA content (Hardy, 2010). Similar to most other studies (Che et al., 2017; Dam et al., 2019; Tomas-Vidal et al., 2019), a high digestible AA profile was recorded for FM in this study. However, FM was slightly lower in cysteine, serine and tyrosine compared to the other studied ingredients. Among the ingredients of animal origin, IM had comparable digestible AA values as FM indicating its potential for partial replacement of FM in an African catfish diet. A similar high amount in digestible EAA was reported for juvenile European sea bass (*Dicentrarchus labrax*) when fed insect larva (Basto et al., 2020). Similar to the result of Taufek et al. (2016) for African catfish fed cricket meal, leucine was the most abundant EAA in IM used in the current study. Except for methionine, histidine, and lysine, HFM had higher digestible essential AA content compared to FM. Regarding the studied plant ingredients, SBM showed a high potential for FM replacement as it recorded a comparable essential amino acid profile. This has also been reported for other fish species, such as pacu (*Piaractus mesopotamicus*) (Abimorad et al., 2008), channel catfish (Lim et al., 1998) and Nile tilapia (Furuya et al., 2001). With the exception of arginine, phenylalanine and histidine, the digestible EAA profile of other legumes was inferior to that of FM. This is consistent with the study on Atlantic salmon, where plant protein sources showed a lower lysine, methionine, threonine, and tryptophan content than fishmeal (Anderson et al., 1992). This implies that, for optimal utilization of these ingredients in diets, supplementation of cystalline amino acids is required

to compensate for the amino acids deficiencies. Methionine from yeast was the first limiting amino acid for pacu (Abimorad et al., 2008). In the current study, digestible methionine was moderately high in the yeast meal. This is in line with the findings of (Gaylord et al., 2004) on hybrid striped bass in which high availability values for methionine in brewer's yeast was recorded. Basto et al. (2020) suggested that the calculated sum of individual AA (SAA) should be regarded as the protein content of an ingredient (true protein). This is because analysed protein contains some other nitrogenous compounds that may contribute to the overall nitrogen estimate. In the current study, IM and SBM displayed the highest values for digestible SAA while PP, FB and YM had the lowest values. Conversely, European sea bass had higher sum of EAA for FM compared to other ingredients tested (Basto et al., 2020). This variation may be due to the fact that different species have different capacity to digest and utilize nutrients in raw materials, due to differences in their natural trophic feeding habits (i.e., herbivore, omnivore or carnivore) (Dam et al., 2019).

The digestible methionine requirement of African catfish was determined as 18.7 g dMet/kg DP (Elesho et al., 2021). In this study, the digestible methionine values for FM, IM, PM, CM, SFM, and CDDGS met and surpassed the digestible methionine requirement for African catfish with values ranging from 19 to 27 g dMet/kg DP. Combination of two or more of these ingredients may be sufficient for balanced feed formulation for African catfish. However, due to the lack of reliable data of other AA requirement for this species, we could not further compare the digestible values of other AA with their requirements. More in general, the high amount of digestible EAA in IM makes this ingredient particularly valuable for African catfish since besides its high AA profile, it also improved the growth of African catfish. However, the negative effect of the chitin content on protein digestibility must be carefully evaluated.

In conclusion, the macro-nutrient digestibility in African catfish (*Clarias gariepinus*) is affected by feeding level, but this effect of feeding level is dependent on the type of ingredient. A decline in digestibility with feeding level is present for ingredients with high carbohydrate content. Results indicated that the amino acids digestibility of various ingredients tested in African catfish varies considerably. Therefore, the study provides data of more precise information concerning nutrient and amino acid digestibility in this species. This will allow fish meal substitutions in practical feed based on digestible amino acids in alternative ingredients.

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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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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.aquaculture.2021.737108.

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