Aquaculture 544 (2021) 737083

Contents lists available at ScienceDirect

Aquaculture

journal homepage: www.elsevier.com/locate/aquaculture

Energy utilisation efficiencies of digested protein, fat and carbohydrates in striped catfish (*Pangasius hypophthalmus*) for whole body and fillet growth

L.T.T. Phan [a], J. Kals [d], K. Masagounder [b], J. Mas-Muñoz [c], J.W. Schrama [a,*]

[a] Aquaculture and Fisheries, Wageningen University and Research, Wageningen, The Netherlands
[b] Evonik Nutrition & Care GmbH, Hanau-Wolfgang, Germany
[c] De Heus Animal Nutrition B.V., The Netherlands
[d] Livestock Research, Wageningen University and Research, Wageningen, The Netherlands

ARTICLE INFO

Keywords:
Energy evaluation
Energy metabolism
Fillet growth
Bioenergetics
Net energy
Energy efficiency
Digestible macronutrients
Pangasius hypophthalmus

ABSTRACT

This study aimed to assess the effect of dietary macronutrient composition on the relationship between RE and DE intake (i.e., the maintenance energy requirements and the slope [kg_{DE}]); to quantify the energy utilisation efficiencies of digested protein, fat and carbohydrates for whole body growth as well as fillet growth in striped catfish (*Pangasius hypoththalmus*). To achieve these aims, a 63-day experiment was conducted on striped catfish (29.1 g). A total of 4 diets were studied at 2 feeding levels, low vs. high (12 vs. 22 $g.kg^{-0.8}.d^{-1}$, respectively), which resulted in a 4 × 2 factorial design. The four diets had contrasting inclusion levels of protein, fat and carbohydrates. Striped catfish digested part of the non-starch polysaccharides (33.6–71.0%) while starch is almost completely digested (> 94%). By conducting the regression between RE and DE intake over diets, the energy utilisation efficiency for striped catfish was estimated at 71% through the equation: RE = − 42 (se 9.2) + 0.71 (se 0.049) DE intake, (R^2 = 0.95). Dietary macronutrient composition did not affect the relationship between RE and DE intake. Multiple regression between RE as a function of digested protein, fat and carbohydrates intake (in $g.kg^{-0.8}.d^{-1}$) was also conducted to estimate the energy utilisation efficiency of digested protein, fat and carbohydrates. The estimated energy efficiencies of digested protein, fat and carbohydrates for energy retention at the whole fish level were 64%, 80% and 58%, respectively. The energetic values of dCP, dFat and dCarb for whole body growth differ from the energetic values for fillet production. For fillet growth, digested protein had a higher potential compared to digested fat and carbohydrates, however this needs to be used in a balanced ratio with digested fat and carbohydrates.

1. Introduction

Protein, fat and carbohydrates can provide the essential energy needs of fish for maintenance and growth. Protein is the key macronutrient for new tissue accretion. Dietary protein is preferred to be used for growth instead of providing energy, because protein is often costly. In addition, the use of protein for energy causes NH_4^+ excretion, which burdens the culture environment. Fat and carbohydrates are preferably used for energy supply, either directly for ATP production or indirectly in the form of fat storage for future energy needs, in order to spare protein. The success of culturing striped catfish depends on the efficient conversion of protein, fat and carbohydrates into growth. To achieve an efficient feed conversion, formulating balanced diets requires information on the amount of nutrients needed for maintenance and for growth. For many, especially newly cultured fish species, such nutritional information is often lacking. Striped catfish is one of the major fish species cultured worldwide (FAO, 2018). The annual production of striped catfish has strongly increased over the past two decades. Currently, the annual production of striped catfish was over 1.1 million tons globally (FishstatJ, 2020). Although striped catfish is already cultured at a large scale for some time, information regarding their nutritional requirements is still limited.

For many fish species, the optimal dietary energy content is calculated by using the factorial approach (Glencross et al., 2011; Glencross, 2008). In this approach the energy requirements for maintenance and for growth are calculated from an estimated relationship between the digestible energy intake (DE) and the retained energy (RE). This relationship (i.e., RE = intercept + slope x DE intake) is normally derived

* Corresponding author.
E-mail address: johan.schrama@wur.nl (J.W. Schrama).

https://doi.org/10.1016/j.aquaculture.2021.737083
Received 31 March 2021; Received in revised form 29 May 2021; Accepted 20 June 2021
Available online 24 June 2021

from experiments using only one diet given at various rations. As for instance was done for striped catfish (Glencross et al., 2011), European seabass (Lupatsch et al., 2010) and barramundi (Glencross, 2008). In this factorial approach of calculating the total DE requirements of a fish species, the slope of the linear relationship or the energy utilisation efficiency (kg_{DE}) is assumed to be constant and unaffected by the dietary composition. However, for various fish species it has been shown that the kg_{DE} is influenced by the dietary macronutrient composition; e.g. for barramundi (*Lates calcarifer*) (Glencross et al., 2017), carp (Phan et al., 2019) and Nile tilapia (*Oreochromis niloticus*) (Schrama et al., 2012). For striped catfish the information is insufficient to evaluate if the relationship between RE and DE is affected by the type of diet. In other words, it is unclear if the dietary macronutrient composition alters the energy requirements for maintenance and/or the energy utilisation efficiency (kg_{DE}) in striped catfish.

The impact of the dietary macronutrient composition on the relationship between DE and RE has been the reason in pig nutrition to move from an energy evaluation system on a DE basis towards a system on a net energy (NE) basis already more than fifty years ago (CVB, 1993; Noblet et al., 1994). In a NE approach, the DE is differentiated into digestible energy originated from protein, fat and carbohydrates with each having its own energy utilisation efficiency ($k_{g,NE}$). The advantage of a NE evaluation system is the ability to quantify and make a distinction between the energy utilisation efficiencies of digested protein ($k_{NE,dCP}$), fat ($k_{NE,dFat}$) and carbohydrates ($k_{NE,dCarb}$). In fish, the energy utilisation efficiency of digested protein, fat and carbohydrates have been quantified for tilapia and trout (Schrama et al., 2018), barramundi and carp (Phan et al., 2019), and snakehead (Phan et al., 2021). However, the energy utilisation efficiency of digested protein, fat and carbohydrates for striped catfish are still unknown.

Of the total global seafood production, fish fillets are the main part used for human consumption, while filleting waste e.g. liver, viscera, head, bone, skin and scales are commonly used as by-products for animal feed. Insights into the potential of digested macro nutrients to attribute to specifically the fillet growth and the growth of possible other defined body compartments (i.e., liver, viscera, and the rest fraction) might reduce the filleting waste. More importantly, it can attribute to the development of an alternative feed evaluation system considering the economic priority of the fish fillet. Currently, feed formulation has been mainly focused on getting the optimal macronutrient composition for the growth of fish at the whole body level. An alternative feed evaluation system, which would focus on the growth or the energy utilisation efficiency at the compartment level could be a tool to make feed formulations more tailor-made and efficient. However, such an approach of relating fillet growth to the intake of digested macronutrients on the compartment level has, to the best of our knowledge, not been attempted earlier for any fish species.

To fulfil the above described knowledge gaps for striped catfish, this study aims to: 1. assess the effect of dietary macronutrient composition on the relationship between RE and DE intake; 2. quantify the energy utilisation efficiencies of digested protein, fat and carbohydrates for whole body growth on striped catfish to be able to use a NE evaluation system for striped catfish; 3. quantify the energy potential of digested protein, fat and carbohydrates to contribute to fillet growth in contrast to the growth of the other defined body compartments.

2. Materials and methods

2.1. Experimental diets

A total of four diets were formulated with different dietary inclusion levels of crude protein (243–380 $g.kg^{-1}$), crude fat (44–236 $g.kg^{-1}$) and carbohydrates (352–601 $g.kg^{-1}$) using the triangle approach (Raubenheimer, 2011) to create a wide contrast between macronutrients (i.e., crude protein, fat and total carbohydrates) (Table 1). The variability in the dietary macronutrient composition was created by varying the inclusion level of cassava (a high starch ingredient) and soya oil (Table 1).

Table 1
Formulation and composition of four experimental diets fed to striped catfish.

	P	C	F	M
	"Protein"	"Protein" +Carb	"Protein" +Fat	"Protein" +Carb+Fat
Diet composition (g.100 g^{-1}, as-is)				
Cassava	0.0	34.3	0.0	30.0
Soy bean oil	0.0	0.0	17.9	12.5
Fishmeal	15.7	10.3	12.8	9.0
Rapeseed meal	7.0	4.6	5.7	4.0
Soybean meal	17.4	11.4	14.3	10.0
Feather meal	7.0	4.6	5.7	4.0
Methionine	0.5	0.3	0.4	0.3
Lysine	0.7	0.5	0.6	0.4
Tryptophan	0.2	0.1	0.1	0.1
Wheat	12.2	8.0	10.0	7.0
Rice bran full fat	17.4	11.4	14.3	10.0
Wheat flour	13.9	9.1	11.4	8.0
Mono calcium phosphate	4.2	2.8	3.5	2.4
Premix[#]	4.0	2.6	3.3	2.3
Chemical composition (g.kg^{-1}, DM)				
DM	961	949	950	953
Crude protein	380	260	300	243
Total fat	62	44	236	165
Total carbohydrates	430	601	352	505
Starch	209	375	187	334
NSP	221	226	164	171
Crude ash	132	99	117	91
Yttrium	0.35	0.23	0.28	0.19
Gross energy (kJ.g^{-1}, DM)	18.3	17.9	21.8	20.7
CP/GE	20.8	14.5	13.8	11.7
DP/GE at low feeding level	21.9	14.4	14.3	11.6
DP/DE at high feeding level	22.1	14.4	14.8	11.7

P, diet with a high protein content; C, the P diet supplemented with starch; F, the P diet supplemented with fat; M, the P diet supplemented with fat and starch; Carb, Carbohydrates; DM, dry matter; CP, crude protein, GE, gross energy, DP, digestible protein; DE, digestible energy; [#]De Heus Animal nutrition B.V. closed premix formula for vitamins and trace minerals to meet the requirements of fresh water fish (NRC, 2011).

The high protein diet (P-diet) was formulated by using protein sources like fish meal, soybean meal and rapeseed meal. This P-diet was mixed with cassava (30%) to create high starch diet (C-diet), with soya oil (12.5%) to create a high fat diet (F-diet), or with both cassava and soya oil to create a diet high in fat and starch (M-diet). All diets were studied at 2 feeding levels, low vs. high, which resulted in a 4 × 2 factorial design with a total of 8 treatments. This design aimed to create large contrasts between the digestible macronutrient intake among the 4 different diets to be able to conduct the multiple regression analysis of energy retention (i.e., growth response) as a function of digestible protein (dCp), digestible fat (dFat) and digestible carbohydrates intake (dCarb). Due to this large range in macronutrients, diets were formulated to have a constant ratio between protein and premix content. Diets were formulated using the protein requirements averaged over freshwater teleost fish (NRC, 2011).

Diets were produced by De Heus (Vinh Long, Vietnam). All ingredients except soy oil in the F- and M-diet and premix were hammer-milled through a 0.9 mm screen at 1470 rpm and mixed in a 60-L batch mixer for 240 s. Prior to extrusion, these mixtures were conditioned for 10 s at a temperature between 85 and 100 °C. Diets were extruded on a twin-screw extruder with a capacity of 150 kg/h using a 2 mm die at 95–110 °C. This produced 3 mm floating pellets, which were dried at 95 °C for 10 min. Thereafter pellets of the F- and M-diet were vacuum coated with soy oil. After coating, pellets were cooled at 30–33 °C for 10 min. Pellets were screened through a 2 mm mesh-sized basket to remove fines before feeding to fish.

2.2. Fish handling

The study (project number: 2018.W-0021.001) was evaluated by the Ethical Committee of Animal Experiments of Wageningen University, The Netherlands and carried out at the research and development centre of De Heus (Vinh Long, Vietnam) in compliance with Vietnamese law.

A total of 2980 striped catfish (*P. hypothalamus)*, with a mean body weight of 29.1 g (SE 0.05) were obtained from Vinh Long, Viet Nam. The experiment lasted 63 day. At the start of the experiment, groups of 120 fish were batch-weighed and randomly assigned to one of the twenty four tanks, giving 3 replicates for each of the 8 treatments (2 feeding levels x 4 diets). At the end of the experiment, fish in each tank were batch-weighed and counted to calculate the average final body weight. The growth performance was calculated based on the difference between the average initial and average final body weight of the fish. The experiment was conducted using 500-L tanks, integrated in a RAS system. The water flow per tank was 30 L/min. The measured water quality parameters during the experiment for temperature, oxygen, pH, conductivity, NH_4-N, NO_2-N and NO_3-N were 28.6 ± 0.49 °C, 5.0 ± 1.04 mg/L, 7.2 ± 0.22, 2.8 ± 0.59 mS/m, <0.5 mg/L, <0.5 mg/L, and < 50 mg/L, respectively.

Striped catfish were hand-fed twice a day from 09:00 to 10:00 h and from 16:00 to 17:00 h. Fish were fed restrictively one of two feeding levels based on metabolic body weight. The planned feeding levels were 12 vs. 22 $g.kg^{-0.8}.d^{-1}$. The daily feed amount was calculated based on the mean initial body increased with the expected growth which was derived from the realized feed intake and using an assumed FCR of 1.1. The first 2 weeks of the experiment were planned to gradually to increase the feed intake from 10% to 100% of the planned feeding level. However, the first week after the start of the experiment the response of the fish was minimal. Therefore the adaptation period was extended to 3 weeks. The last two weeks of the experiment, fish fed Diet M were not able to finish all feed due to the rainy weather. Therefore the feeding level at all treatments were reduced.

2.3. Sampling

At the start of the experiment, 100 fish from the initial population were euthanized by an overdose of Aqui-S (Aqui-S New Zealand Ltd., Lower Hutt, New Zealand). Of these, 50 were used for the analysis of the initial whole body composition and the other for initial composition of body compartments. At the end of the trial, forty fish from each tank were euthanized similarly to determine the final whole body composition ($n = 20$) as well as final composition of body compartments ($n = 20$). To prepare for the chemical analyses of the final composition of body compartments, whole fish were dissected and separated into four compartments: 1) liver without bile bladder, 2) viscera, which including bile bladder, pancreas, stomach, intestine and gonad glands, 3) fillet, and 4) the rest fraction, which comprised of head, bones, skin and air bladder. Compartment samples were pooled per tank (being the experimental unit) and stored at ⁻20 °C.

2.4. Chemical analysis

After sampling the fish and fish compartments were pooled per tank (experimental unit) and stored at −20 °C. Sample preparation and chemical analysis for protein, fat, energy, dry matter, ash and phosphorus were executed as described by Saravanan et al. (2012). Starch was analysed as described in Maas et al. (2019). In feed and faeces, carbohydrates ($g.kg^{-1}$) on a dry matter basis was calculated by deducting protein, fat and ash from 1000. The total amount of NSP ($g.kg^{-1}$) was calculated by deducting starch from carbohydrates.

2.5. Nutrient digestibility estimates

Yttrium oxide was used as a marker (Table 1). Protein, fat, starch, dry matter and ash were analysed in feed and faeces. Feed was sampled every week to have a representative sample of the feed given to fish. Each tank was connected to a separate settling unit to collect faeces. Each settling unit was equipped with an ice-cooled glass bottle at the bottom to prevent bacterial degradation of the faecal nutrients during collection. Faeces settled overnight were collected daily prior to the morning feeding from week 4 to week 9 of the experiment. The procedure of faeces collection was identical as described by Meriac et al. (2014).

The apparent nutrient digestibility coefficients ($ADC_{nutrient}$) of the diets were calculated using the following equation:

$$ADC_{nutrient} = \left(1 - \left(marker_{diet}/marker_{faeces}\right) \times \left(Nutrient_{faeces}/Nutrient_{diet}\right)\right) \times 100\%,$$

where $marker_{diet}$ and $marker_{faeces}$ is the yttrium concentration of the diet and faeces, and the $Nutrient_{diet}$ and $Nutrient_{faeces}$ are the dry matter (DM), protein, fat, carbohydrates or energy content of the diet and faeces, respectively.

2.6. Nutrient balance calculations

Feed intake was the average of the daily feed intake. The average daily feed intake was calculated using the daily consumed amount of feed (in g) per tank divided by the number of fish per tank. To standardise for differences in body weight and digestible macronutrient intake, nitrogen and energy balance parameters were expressed per unit of mean metabolic body weight. Metabolic body weight was calculated as $BW^{0.8}$ with BW expressed in kg. The mean metabolic body weight was calculated as the average of the initial and final metabolic body weight. The calculation of the energy and nitrogen balances were based on those described by Saravanan et al. (2012). The intake of each macronutrient on a gross basis was determined by multiplying the averaged feed intake for each treatment by the macronutrient content in the diet. The digestible macronutrient intake was determined by multiplying the gross nutrient intake with the diet-specific apparent digestibility coefficient (ADC) for each macronutrient. The energy and nutrient retention rates were determined from the gain of energy, protein, fat and carbohydrates, calculated by the difference between the initial and the final whole-body macronutrient composition. The branchial and urinary N losses (BUN) were calculated using the difference between digestible N, N intake and N retention. The branchial and urinary energy (BUE) was estimated by multiplying BUN by 24.85, which is the energy content (in kJ) of 1 g excreted nitrogen with the assumption that NH_3-N is the only form of N excreted (Bureau et al., 2003). The metabolisable energy intake was determined by the difference between the digestible energy intake and the BUE. The heat production was measured by deducting the ME from the RE.

2.7. Retained energy in body compartments

The retained energy in each compartment was determined from the gain of energy, calculated by the difference between the initial and the final compartment energy composition. The retained energy in each compartment was also expressed per unit of metabolic body weight.

2.8. Statistics

Data was analysed by using the statistical analysis systems (SAS Institute) statistical software package version 9.1. Two-way ANOVA was used to investigate the effect of diet, feeding level and their interaction on the apparent digestibility coefficients, growth performance, nitrogen and energy balance data.

Linear regression between RE (in $kJ.kg^{-0.8}.d^{-1}$) and DE intake (in $g.kg^{-0.8}.d^{-1}$) was applied to quantify the energy utilisation efficiency (k_{gDE}) of each diet using the model:

$$RE_i = \mu + \beta \times DE_i + e_i \quad (1)$$

where μ is the intercept, β is the energy utilisation efficiency; e_i is error term and $i = 1, \ldots, n$ with $n = 6$ per diet. The difference in the slopes of the regression lines between the different diets was tested using a general linear model with RE as dependent variable, DE as covariate and diet as a fixed factor. If the interaction effect diet x DE is significant ($P < 0.05$), the slopes are different across diets.

Multiple regression of retained energy (RE) (in $kJ.kg^{-0.8}.d^{-1}$) as a function of dCP, dFat and dCarb (in $g.kg^{-0.8}.d^{-1}$) was applied to estimate the energy utilisation efficiency of each digestible macronutrient using the model:

$$RE_i = \mu + \beta_1 \times dCP_i + \beta_2 \times dFat_i + \beta_3 \times dCarb_i + e_i \quad (2)$$

where μ is the intercept, being an estimate for fasting heat production (FHP); β_1, β_2, β_3 the energy utilisation efficiency of dCP ($k_{NE;dCP}$), dFat ($k_{NE;dFat}$) and dCarb ($k_{NE;dCarb}$), respectively; e_i is the error term and i = 1, …, 24. The linearity and curve-linearity were checked in the relationship of RE with dCP, dFat and dCarb. The similar procedure of multiple regression of RE (in $kJ.kg^{-0.8}.d^{-1}$) was applied for each body compartment. Significance was set at $P < 0.05$.

3. Results

Striped catfish had a daily weight gain ranging from 5.9 to 12.6 g. $kg^{-0.8}.d^{-1}$ for the low vs. high feeding level, respectively (Table 2). At the end of the experiment, the final body weight almost doubled at the low feeding level and quadrupled at the high feeding level. Final body weight was affected by feeding level, diet and the interaction between the two ($P < 0.01$; Table 2).

The ADCs of the macronutrients are given in Table 3. There was an interaction effect between diet type and feeding level for the ADC of protein ($P < 0.05$), while there was a tendency of an interaction effect between diet type and feeding level for the ADCs of energy, fat and carbohydrates. A higher feeding level lowered the ADCs of most nutrients ($P < 0.05$), except starch. Feeding level, starch and fat supplementation affected the digestibility of the non-starch polysaccharides (NSP) in striped catfish ($P < 0.01$). Starch supplementation increased the ADC of NSP from 51% to 62%, averaged over the low starch diets (diet P and F) and the high starch diets (diet C and M) ($P < 0.01$), while fat supplementation decreased the ADC of NSP from 61% to 50% averaged over the fish fed the low fat diets (diet P and C) and the fish fed the high fat diets (diet F and M) ($P < 0.01$) (Fig. 1). Increasing the feeding level decreased the ADC of NSP from 62% at the low feeding level to 49% at the high feeding level averaged over diets ($P < 0.01$). Increasing the dietary starch inclusion level increased the ADC of starch from 96% to 99% averaged over the fish fed the low starch diets and the fish fed the high starch diets ($P = 0.03$) (Fig. 1).

Data on the initial and final body composition of striped catfish are presented in Supplementary Table S1. At the start of the experiment, the body fat content of striped catfish was 50 $g.kg^{-1}$ (on a wet weight basis) and at the end on averaged 119 $g.kg^{-1}$, ranging from 61 to 171 $g.kg^{-1}$. The final body fat content was affected by diet and feeding level ($P < 0.05$). This was also reflected in the energy retention (RE) as fat (Table 4), being affected by feeding level and by diet ($P < 0.001$). Averaged over all treatments, RE as fat was 58 $kJ.kg^{-0.8}.d^{-1}$ and RE as protein was 31 $kJ.kg^{-0.8}.d^{-1}$ (Table 4). On energy basis, the ratios between fat and protein gain was unaffected by feeding level ($P > 0.1$), but differed between diets ($P < 0.001$; Table 4). Dietary supplementation of starch as well as fat increased the proportion of RE retained as fat compared to RE as protein (Table 4). The final body protein content was neither affected by diet nor by feeding level ($P > 0.05$), but the protein efficiency (i.e., retained N as percentage of digested N) was influenced by diet and feeding level ($P < 0.01$; Table 4). Dietary supplementation of fat and starch increased protein efficiency. At the high feeding level, protein efficiency was 42% at diet P, 50% at diet C, 53% at diet F and 56% at diet M. The complete N balances of striped catfish is presented in Supplementary S2.

The first research aim was to assess the effect of diet composition (i.e., macro-nutrient content) on the relationship between RE and DE intake for striped catfish. The estimated linear relationships between RE and DE for each diet are given in Fig. 2. For striped catfish, the slopes of the relationships or k_{gDE} values were not affected by dietary composition ($P > 0.05$). Because the slopes or the k_{gDE} values were similar between diets, all data were pooled to generate a general relationship between RE and DE

Table 2
Growth performance of striped catfish, ($n = 3$), fed 4 different diets at 2 feeding levels (FL) for 63 days.

	P	C	F	M			*P* values	
FL	"Protein"	"Protein" +Carb	"Protein" +Fat	"Protein" +Carb+Fat	SEM	Diet	FL	Diet x FL
Final BW (g)								
Low	72^{c}	59^{d}	69^{cd}	63^{cd}	2.4	<0.001	<0.001	0.004
High	127^{a}	101^{b}	130^{a}	108^{b}				
Feed intake ($g.d^{-1}$)								
Low	0.8	0.8	0.7	0.7	—*	—*	—*	—*
High	1.7	1.6	1.7	1.6				
Feed intake ($g.kg^{-0.8}.d^{-1}$)								
Low	8.4	9.2	8.5	8.9	—*	—*	—*	—*
High	13.6	14.6	13.3	14.2				
Daily weight gain ($g.kg^{-0.0.8}.d^{-1}$)								
Low	7.4	5.9	7.2	6.4	0.19	<0.001	<0.001	0.154
High	12.3	10.4	12.6	11.0				
FCR								
Low	1.13^{z}	1.57^{x}	1.17^{z}	1.40^{y}	0.030	<0.001	<0.001	0.208
High	1.10^{Z}	1.40^{X}	1.06^{Z}	1.29^{Y}				
Survival (%)								
Low	100.0	99.7	100.0	100.0	0.14	0.585	0.995	0.299
High	100.0	100.0	99.7	100.0				

P, diet with a high protein content; C, the P diet supplemented with starch; F, the P diet supplemented with fat; M, the P diet supplemented with fat and starch; Carb, carbohydrates; FL, feeding level; *P* values for effects of diet, feeding level or the interaction, respectively; BW, body weight; *No statistical analysis was conducted on feed intake because feed intake was controlled at 2 feeding levels; FCR, feed conversion rate.

^{abcde} For parameters with a significant interaction effect between diet and feeding level, means lacking a common superscript differ ($P < 0.05$).

^{xyz} & ^{XYZ} For parameters with a significant effect of diet, diets with a lacking a common letter in the superscript differ ($P < 0.05$) and for parameters with a significant feeding level effect, means having a different case letter in the superscript differ between feeding level ($P < 0.05$).

Table 3
Apparent digestibility coefficient (ADC) (%) of dietary nutrients in striped catfish ($n = 3$) fed 4 diets at 2 feeding levels (FL) for 63 days.

	FL	P	C	F	M			*P* values	
		"Protein"	"Protein" +Carb	"Protein" +Fat	"Protein" +Carb+Fat	SEM	Diet	FL	Diet x FL
Dry matter	Low	77.7^{z}	83.4^{xy}	79.6^{yz}	84.6^{x}	0.64	<0.001	<0.001	0.053
	High	71.5^{Z}	79.5^{XY}	75.6^{YZ}	82.4^{X}				
Energy	Low	85.9^{x}	88.2^{xy}	88.1^{xy}	90.2^{x}	0.67	<0.001	<0.001	0.055
	High	80.1^{X}	84.8^{XY}	85.1^{XY}	88.5^{X}				
Protein	Low	90.6^{a}	87.9^{abc}	91.2^{a}	89.3^{a}	0.75	<0.001	<0.001	0.010
	High	85.2^{bc}	84.5^{c}	91.2^{a}	88.3^{ab}				
Fat	Low	88.2^{y}	88.0^{y}	94.6^{x}	95.6^{x}	0.73	<0.001	0.002	0.069
	High	84.0^{Y}	87.0^{Y}	92.4^{X}	95.5^{X}				
Carbohydrates	Low	78.9^{y}	88.5^{x}	75.7^{y}	87.0^{x}	0.76	<0.001	<0.001	0.081
	High	72.5^{Y}	84.4^{X}	68.6^{Y}	83.6^{X}				
Starch	Low	95.5	99.0	95.1	99.3	1.77	0.101	0.460	0.506
	High	94.7	99.1	99.3	99.4				
NSP	Low	63.1^{xy}	71.0^{x}	53.1^{y}	62.6^{x}	2.88	<0.001	<0.001	0.359
	High	51.5^{XY}	60.0^{X}	33.6^{Y}	52.6^{X}				
Ash	Low	31.7^{c}	39.0^{a}	31.1^{c}	39.0^{a}	0.99	<0.001	<0.001	0.034
	High	23.7^{d}	34.0^{bc}	23.5^{d}	36.8^{ab}				
Phosphorus	Low	32.2^{y}	40.9^{x}	34.4^{y}	42.9^{x}	1.19	<0.001	<0.001	0.067
	High	25.8^{Y}	34.5^{X}	23.9^{Y}	39.4^{X}				

P, diet with a high protein content; C, the P diet supplemented with starch; F, the P diet supplemented with fat; M, the P diet supplemented with fat and starch; Carb, carbohydrates; DM, dry matter; NSP, non-starch polysaccharides.
^{abcde} For parameters with a significant interaction effect between diet and feeding level, means lacking a common superscript differ ($P < 0.05$).
$^{xyz\ \&\ XYZ}$ For parameters with a significant effect of diet, diets with a lacking a common letter in the superscript differ ($P < 0.05$) and for parameters with a significant feeding level effect, means having a different case letter in the superscript differ between feeding level ($P < 0.05$).

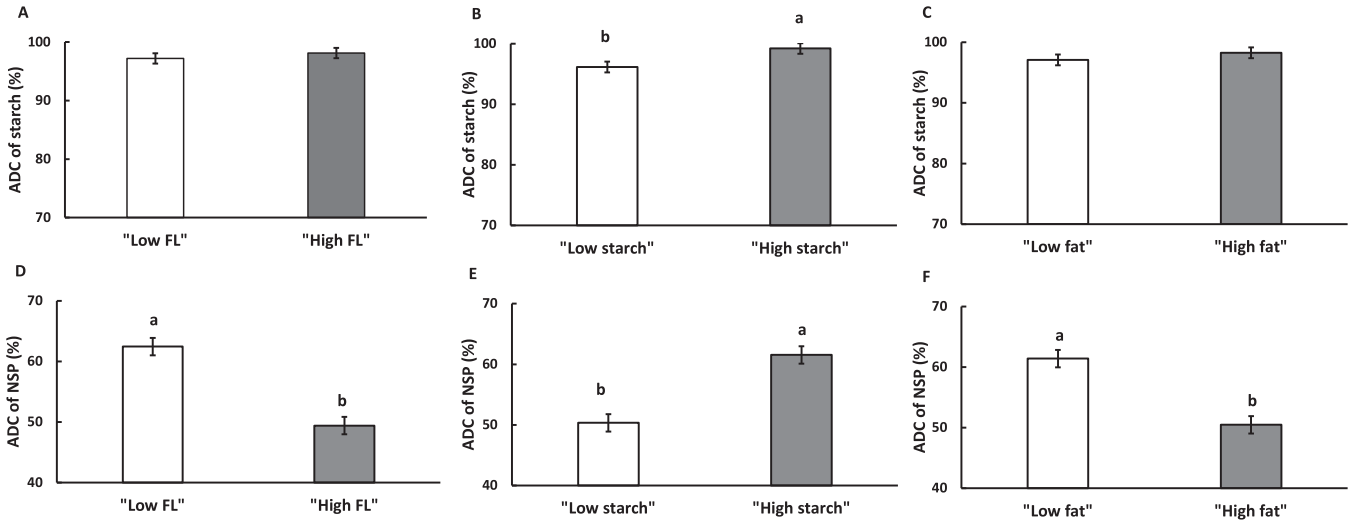

Fig. 1. The effect of feeding level (FL), starch supplementation and fat supplementation on the apparent digestibility (ADC) of starch (Panel A, B, C) and on ADC of non-starch polysaccharides (NSP) (Panel D, E, F) in striped catfish. These main effects were analysed by three-way ANOVA (2 starch levels x 2 fat levels x 2 feeding levels). Values of "Low FL" and "High FL" are means values over all diets (panel A & D). Values of "Low starch" is the mean of Diet-P and Diet-F across both FL and "High starch" is the mean of Diet-C and Diet-M across both FL (Panel B & E). Values of "Low fat" is the mean of Diet-P and Diet-C across both FL and "High fat" is the mean of Diet-F and Diet-M across both FL (Panel B & E). Bars within panels having a different letter are different ($P < 0.05$).

intake over diets. By conducting the regression between RE and DE intake over diets, the energy utilisation efficiency for striped catfish was estimated at 71% through the equation: RE = − 42 (se 9.2) + 0.71 (se 0.049) DE intake, ($R^2 = 0.95$). From this equation the energy requirements for maintenance were estimated at 50 $kJ.kg^{-0.8}.d^{-1}$.

The second aim was to quantify the energy utilisation efficiencies of digested protein, fat and carbohydrates for growth (i.e., estimating the NE equation for striped catfish). Therefore multiple linear regression between RE (in $kJ.kg^{-0.8}.d^{-1}$) and dCP, dFat and dCarb (in $g.kg^{-0.8}.d^{-1}$) was conducted and resulted in following estimated relationship with an R^2 of 0.95:

$$RE = -33.7\ (se\ 7.93) + 15.1\ (se\ 2.24)\ dCP + 31.5\ (se\ 2.04)\ dFat + 9.9\ (se\ 1.14)\ dCarb \quad (3)$$

Table 4
Energy balance (kJ.kg$^{-0.8}$.d^{-1}) of striped catfish, (n = 3), fed 4 different diets at 2 feeding levels (FL) for 63 days.

	FL	P	C	F	M				
		"Protein"	"Protein"	"Protein"	"Protein"			*P* values	
			+Carb	+Fat	+Carb+Fat	SEM	Diet	FL	Diet x FL
GE	Low	147	157	175	175	3.1	<0.001	<0.001	0.118
	High	239	248	275	279				
DE	Low	127^{f}	139^{ef}	154de	158^{d}	3.2	<0.001	<0.001	0.008
	High	191^{c}	210^{b}	234^{a}	247^{a}				
BUE	Low	7	5	5	4	0.3	<0.001	<0.001	0.058
	High	10	6	6	5				
ME	Low	120^{f}	134^{ef}	149de	154^{d}	3.2	<0.001	<0.001	0.006
	High	182^{c}	204^{b}	228^{a}	242^{a}				
HP	Low	74	85	72	76	5.1	0.025	<0.001	0.137
	High	88	102	91	113				
RE	Low	46	49	77	78	3.9	<0.001	<0.001	0.468
	High	93	102	137	129				
RE as protein	Low	26	18	25	21	2.1	<0.001	<0.001	0.548
	High	42	36	44	38				
RE as fat	Low	20^{y}	30^{xy}	52^{x}	57^{x}	3.7	<0.001	<0.001	0.548
	High	51^{Y}	66^{XY}	93^{X}	90^{X}				
RE as fat: RE as protein	Low	0.8^{z}	1.7^{y}	2.1^{xy}	2.8^{x}	0.18	<0.001	0.577	0.256
	High	1.2^{z}	1.9^{y}	2.2^{xy}	2.4^{x}				
Protein efficiency*	Low	39^{z}	39^{y}	48^{y}	48^{x}	3.1	0.009	0.007	0.637
	High	42^{z}	50^{y}	53^{y}	56^{x}				

P, diet with a high protein content; C, the P diet supplemented with starch; F, the P diet supplemented with fat; M, the P diet supplemented with fat and starch; Carb, carbohydrates; GE, gross energy; DE, digestible energy; BUE, branchial urinary energy; ME, metabolisable energy, HP, heat production RE, retained energy. *Protein efficiency is retained protein divided by digestible protein intake (%).
^{abcde} For parameters with a significant interaction effect between diet and feeding level, means lacking a common superscript differ ($P < 0.05$).
$^{xyz\ \&\ XYZ}$ For parameters with a significant effect of diet, diets with a lacking a common letter in the superscript differ ($P < 0.05$) and for parameters with a significant feeding level effect, means having a different case letter in the superscript differ between feeding level ($P < 0.05$).

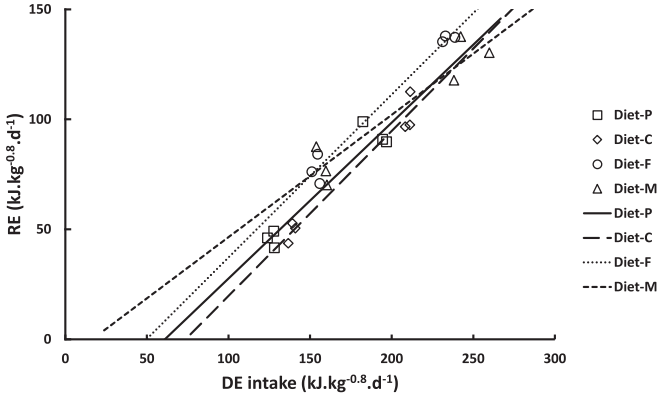

Fig. 2. Relationship between retained energy (RE) and digestible energy intake (DE) for striped catfish fed one of four experimental diets: P, diet with a high protein content; C, the P diet supplemented with starch; F, the P diet supplemented with fat; M, the P diet supplemented with fat and starch (□ Diet P: RE = −43 (SE 16.5) + 0.71 (SE 0.102) DE (R^2 = 0.92), ◇ Diet C: RE = −55 (SE 13.0) + 0.75 (SE 0.073) DE (R^2 = 0.96), ○ Diet F: RE = −37 (SE 10.9) + 0.74 (SE 0.055) DE (R^2 = 0.98), Δ Diet M: RE = −9 (SE 19.5) + 0.56 (SE 0.094) DE (R^2 = 0.90)) on striped catfish. Digestible energy demand for maintenance is 61, 74, 50 and 17 kJ.kg$^{-0.8}$.d^{-1} for diet P, C, F and M, respectively.

By dividing the coefficients of dCP, dFat and dCarb of 15.1, 31.5, 9.9 kJ.g^{-1}, respectively in Eq. 3 by the energetic value of these macronutrients (23.6 kJ.g^{-1}, 39.5 kJ.g^{-1} and 17.2 kJ.g^{-1} for CP, fat and carbohydrates, respectively), the energy utilisation efficiency of dCP, dFat and dCarb ($k_{NE;dCP}$, $k_{NE;dFat}$, and $k_{NE;dCarb}$) were determined as 64%, 80% and 58% for striped catfish, respectively. The intake of dCP, dFat and dCab were all linearly related to RE (i.e., no polynomial effect was present, $P > 0.05$).

The third aim was to quantify the energy utilisation efficiencies of digested protein, fat and carbohydrates for growth of the different body compartments. Therefore, RE in four different body compartments (fillet, liver, viscera and rest fraction) were measured at all treatments (Table 5). By summation of the energy retention of these four body compartments an alternative total energy retention ($RE_{\sum comp}$) was calculated. The estimated values of $RE_{\sum comp}$ and also treatment effects on this parameter (Table 5), match very well with that of RE measured by homogenizing whole fish (Table 4). Also the estimated relationship between RE and dCP, dFat and dCarb using both types of RE gave similar equations (Eq. 3 versus Eq. 4; Table 6).

The estimated relationships between RE and digestible nutrient

Table 5
The net energy equations of the four different compartments, their sum and the whole body of striped catfish.

	Equation	R^2	
Whole body homogenised	NE = RE + 33.7 = 15.1 dCP + 31.5 dFat +9.9 dCarb	0.95	(3)
Whole body Σ compartments	NE = RE + 25.0 = 14.1 dCP + 29.7 dFat +9.4 dCarb	0.95	(4)
Liver	NE = RE + 0.1 = 0.2 dCP + 0.1 dFat +0.2 dCarb	0.84	(5)
Viscera	NE = RE + 4.2 = 0.1 dCP + 6.6 dFat +2.0 dCarb	0.65	(6)
Fillet	NE = RE + 14.4 = 5.9 dCP + 5.9 dFat +2.5 dCarb	0.85	(7)
Rest fraction	NE = RE + 6.2 = 7.9 dCP + 17.1 dFat +4.8 dCarb	0.89	(8)

NE, net energy; RE, retained energy; dCP, digestible protein; dFat, digestible fat; dCarb, digestible carbohydrates (comprising of starch, sugars and non-starch polysacchrides)
In the estimated equation of the present study, NE is expressed in kJ.kg$^{-0.8}$.d^{-1} and digestible nutrient intakes (dCP, dFat and dCarb) in g.kg$^{-0.8}$.d^{-1}.
Whole body homogenised, the equation was created with RE calculated based on the whole body energy composition data. Whole body Σ compartments, the equation was created with RE calculated based on the sum of RE in the four defined compartments.

Table 6
Retained energy (kJ.kg$^{-0.8}$.d^{-1}) in compartments of striped catfish, ($n = 3$), fed 4 different diets at 2 feeding levels (FL) for 63 days.

	FL	P	C	F	M			*P* values	
		"Protein"	"Protein" +Carb	"Protein" +Fat	"Protein" +Carb+Fat	SEM	Diet	FL	Diet x FL
Liver RE	Low	0.7	1.0	0.8	1.1	0.08	0.013	<0.001	0.411
	High	1.4	1.6	1.4	1.5				
Viscera RE	Low	4^{y}	6^{xy}	13^{xy}	14^{x}	2.8	0.004	0.004	0.951
	High	10^{Y}	13^{XY}	18^{XY}	22^{X}				
Fillet RE	Low	12	11	14	12	2.0	0.076	<0.001	0.465
	High	25	23	30	31				
Rest RE	Low	34	38	50	54	3.6	<0.001	<0.001	0.425
	High	62	58	82	81				
RE total	Low	50	56	77	81	3.8	<0.001	<0.001	0.215
	High	98	96	132	135				

P, diet with a high protein content; C, the P diet supplemented with starch; F, the P diet supplemented with fat; M, the P diet supplemented with fat and starch; Carb, carbohydrates; RE, retained energy; RE total, the total of RE in compartments (RE total = Liver RE + viscera RE+ fillet RE + the rest fraction RE).
^{xyz} & ^{XYZ} For parameters with a significant effect of diet, diets with a lacking a common letter in the superscript differ ($P < 0.05$) and for parameters with a significant feeding level effect, means having a different case letter in the superscript differ between feeding level ($P < 0.05$).

intake for each of the four compartment are given in Table 6. The ratio between the regression coefficients of dCP, dFat and dCarb varied between the different compartments. In the viscera the major contribution to RE came from dFat and dCarb, while the energetic contribution of dCP was minor to viscera gain (Eq. 6; Table 6). In contrast, fillet energy gain was strongly derived from dCP and less from dFat and dCarb compared to other compartments (Eq. 7; Table 6). In fillet, the energy utilisation efficiency of dCP (5.9/23.6 × 100) was 25% and higher than the energy utilisation efficiency of dFat and dCarb with values of 14.9% and 14.5%, respectively which were similar.

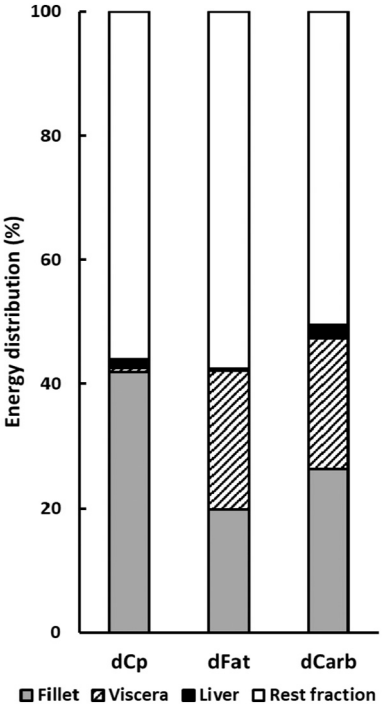

Fig. 3. Energy distribution of digested protein (dCP), digested fat (dFat) and digested carbohydrates (dCarb) over different body compartments (liver, viscera, fillet and the rest fraction) in striped catfish. Distribution of digested protein (dCP) in liver, viscera, fillet and the rest fraction was calculated by dividing the coefficients of dCP in in liver (Eq. 5, Table 6), viscera (Eq. 6, Table 6), fillet (Eq. 7, Table 6) and the rest fraction (Eq. 8, Table 6) by the coefficients of dCP in Eq. 4 (Table 6). Similarly, energy distribution of digested fat (dFat) and digested carbohydrates (dCarb) in different body compartments (Eq. 5, 6, 7, 8, Table 6) were calculated by dividing the coefficients of dFat and dCarb in compartments by the coefficients of dFat and dCarb in Eq. 4, Table 6, respectively.

By dividing the coefficients of dCP in liver (0.2), viscera (0.1), fillet (5.9) and the rest fraction (7.9) by the total of these values, the energy distribution of digested protein intake in liver, viscera, fillet and the rest fraction was determined (Fig. 3). The majority of the energy from the digested protein was allocated to the fillet (42%). The energy distribution values of digested fat and carbohydrates in fillet were 20% and 26%, respectively (Fig. 3).

4. Discussion

Carbohydrates is an important energy source for non-carnivorous fish species like tilapia, carp and catfish. In this study on striped catfish, between 15.2% to 42.3% of the total DE intake originated from digested starch, depending on the dietary composition. This large contribution of starch to DE is partly due to the high digestibility of starch observed for striped catfish in this study. The digestibility of starch was larger than 95% (Table 3), which is comparable to the ADC values reported for starch in rainbow trout (Burel et al., 2000), common carp (Phan et al., 2019), African catfish (Leenhouwers et al., 2006) and Nile tilapia (Amirkolaie et al., 2006). The current ADC values of starch for striped catfish are higher than the values reported for barramundi (88%) (Glencross et al., 2017) and turbot (82%) (Burel et al., 2000). The variability in starch digestibility between studies might relate to differences in the degree of gelatinization of the starch. Gelatinization of (native) starch has been proven to enhance its digestibility in a wide range of fish species, especially in carnivorous fish (Krogdahl et al., 2005; Peres and Oliva-Teles, 2002). But also for non-carnivorous fish (i.e., tilapia), extruded feeds generally have a higher starch digestibility compared to steam pelleted feeds (Maas et al., 2020). In the current study the striped catfish diets were produced by extrusion and therefore the starch present in the diets was most likely well gelatinized, which contributed to the high ADC of starch. In various fish species (often carnivores) the digestibility of starch decreases at increasing starch inclusion levels; e.g. in barramundi (Glencross et al., 2012; Glencross et al., 2017), snakehead (Phan et al., 2021) and rainbow trout (Meriac et al., 2014). Opposite to this, striped catfish in the current study showed an increased ADC of starch when cassava was included into the diets. Even at a starch inclusion level of 375 g.kg^{-1} DM, the digestion of starch was not hampered in striped catfish. These findings indicate that striped catfish is well able to digest starch. Therefore, starch can be an important source providing DE in practical diets for striped catfish.

It is often suggested that NSP have no nutritional value for fish, because they are not digested and or fermented in the fish intestine. However, the current study on striped catfish shows that between 4.7 and 17.8% of total the DE originated from digested NSP. The lowest ADC

of NSP in the current study was 33.6% and indicated that NSP are digested/fermented in striped catfish. Similarly, positive ADCs for NSP have been reported for Nile tilapia (Maas et al., 2019) and African catfish (Leenhouwers et al., 2007). Comparable to Nile tilapia (Maas et al., 2020), there was a large variability in the ADC of NSP between treatments in the current study. In Nile tilapia, the ADC of NSP depends on the type of NSP, with soluble NSP being better digestible than in-soluble NSP and pectins better than cellulose (Maas et al., 2019). The (high) digestibility of NSP in striped catfish and tilapia can be due to the activity of exogenous enzymes and or fermentation in the intestine. Depending on the type of NSP, NSP are digested by enzymes like xylanase, β-glucanase, β-mananase and or (enzymes from) bacteria in the intestine (Romano et al., 2018). In the present study, fish fed the low feeding level had a higher ADC of NSP than fish fed the high feeding level. This indicates that the digestibility of NSP is dependent on feeding level, i.e. the amount of NSP intake, which was also found in Nile tilapia (Haidar et al., 2016). The more NSP being consumed, the lower its ADC. Hydrolysis or fermentation of NSP takes time and requires interaction between NSP and enzymes and or bacteria. A higher NSP intake possibly increased the throughput and consequently decreased the time for the NSP and the bacteria or enzymes to interact. Additionally, fat supplementation in the current study decreased the ADC of NSP, possibly by hampering a proper contact between NSP, enzymes as well as bacteria. An adverse effect of fat on the abundance of the microbial population by disrupting their membrane integrity, impairing the uptake of nutrients, and inhibiting energy production results in cell death with the surfactant properties of fat (Desbois and Smith, 2010). The present study demonstrates that NSP are not inert for striped catfish. In other words, NSP can be digested and contribute to the digested energy. However, understanding the factors affecting the ADC's of NSP's in striped catfish, like NSP intake as well as dietary fat content requires further assessment.

Feed evaluation systems are often based on digestible nutrients, i.e. the DE approach. These evaluation systems assume that the ADC values of ingredients are additive when formulating diets. In the current study, diet type significantly affected the ADC of protein. Diluting the high protein diet with cassava starch and oil, which do not contain protein, changed the ADC of protein. This indicates that the ADC of protein is not additive as it is dependent on the ingredients included in the diet. This compiles with earlier findings for barramundi (Glencross et al., 2017) and snakehead (Phan et al., 2021). This indicates that the assumption of the additivity of ingredients in the current feed evaluation systems is not always valid. Another assumption in feed evaluations systems based on digestible nutrients is that the ADC values of diets or dietary macronutrients are independent of the context, e.g. being not affected by feeding level, salinity or temperature. In the present study, the interaction between feeding level and diets affected the protein ADC and tended to affect ADC of energy, carbohydrates and fat. Such an interaction effect was also found in carp (Phan et al., 2019) and snakehead (Phan et al., 2021). This suggests that the feeding level should be considered in digestibility trials, which are used to obtain data for practical diet formulation. The effect of feeding level and its interaction with diet on ADC of macronutrient implies that the nutritional value of an ingredient and/or diet is dependent on the feeding level. The practical implication of this is, that digestibility trails, which are done to determine the ADC of ingredients for formulating balance diets, should be done at feeding levels that are equal/representative for the practical conditions during the commercial culture of fish.

Averaged over the four diets, the digestible energy demand for maintenance for striped catfish was determined at 50 $kJ.kg^{-0.8}.d^{-1}$. This value is comparable to the value found for striped catfish of 40 $kJ.kg^{-0.8}.d^{-1}$ by Glencross et al. (2011) and other fish species like: rainbow trout (*Oncorhynchus mykiss)* (38 $kJ.kg^{-0.8}.d^{-1}$) (Glencross, 2009), barramundi (*Lates calcarifer*) (43 $kJ.kg^{-0.8}.d^{-1}$) (Glencross, 2006; Glencross, 2008), European sea bass (*Dicentrarchus labrax*) (45 $kJ.kg^{-0.8}.d^{-1}$) and gilthead seabream (*Sparus auratus*) (48 $kJ.kg^{-0.8}.d^{-1}$) (Glencross, 2008; Glencross and Bermudes, 2012; Lupatsch et al., 2003; Williams et al., 2006; Williams et al., 2003). It is also comparable to the minimal values reported for Nile tilapia (Meyer-Burgdorff et al., 1989), but the current value in striped catfish is only half of the maximal value found for Nile tilapia (110 $kJ.kg^{-0.8}.d^{-1}$) (Haidar et al., 2016). This example of Nile tilapia, shows that a wide range in the digestible energy demand for maintenance (53–110 $kJ.kg^{-0.8}.d^{-1}$) can exist within the same species (Haidar et al., 2016; Schrama et al., 2012). Within a species, factors like stocking density (Lupatsch et al., 2010), temperature (Glencross and Bermudes, 2010) or body size (Glencross, 2008) can affect the energy demand for maintenance. Differences in maintenance requirements between species may also be species-related (i.e., feeding habit, living habitat). Yet, irrespective of the type of energy evaluations system used, variation in the digestible energy for maintenance needs to be considered in the determination of the optimal dietary energy content of the diet.

When combining the data of all diets tested in this study, the estimated energy utilisation efficiency for striped catfish was 71%. This value is higher than the k_{gDE} value of 51% for striped catfish estimated by Glencross et al. (2011). However, the energy utilisation efficiency in the current study is in line with the range of $k_{g,DE}$ values estimated of 55 to 79% for barramundi, (Glencross, 2006; Glencross, 2008); 49 to 66% for common carp (Phan et al., 2019); 62 to 74% for rainbow trout (Glencross, 2009) and 64 to 82% for European seabass (Lupatsch et al., 2001; Lupatsch et al., 2003; Lupatsch et al., 2010; Peres and Oliva-Teles, 2005).

It was expected on forehand that the striped catfish used in the present study would have a lower energy utilisation efficiency than those used by Glencross et al. (2011), as the fish in this study were smaller than the fish used by Glencross et al. (2011). Generally, within a species, smaller fish show a lower energy utilisation efficiency than larger fish (Glencross, 2008). This contradiction could be because the body size factor in the present study was less influential than the nutrient composition of the experimental diets. In fact, the inclusion level of dietary fat is higher in the present study than in the study of Glencross et al. (2011). The energy utilisation efficiencies of the high fat diets were higher than the ones of the low fat diets (Glencross et al., 2017; Phan et al., 2019). This suggests that diet composition might have played a role in the differences of the energy utilisation efficiency found for striped catfish between the present study and the study of Glencross et al. (2011).

Although the dietary macronutrient composition tended to result in small numerically differences in the energy utilisation efficiency ($k_{g,DE}$), the dietary macronutrient composition did not significantly affected the relationship between RE and DE intake. This finding is in contradiction with the results found for carp (Phan et al., 2019), barramundi (Glencross et al., 2017), tilapia (Schrama et al., 2012), rainbow trout (Rodehutscord and Pfeffer, 1999; Schrama et al., 2018) and snakehead (Phan et al., 2021), where dietary macronutrients composition affected $k_{g,DE}$. The absence of a diet effect on the energy utilisation efficiency for striped catfish in the current study may be because the contrast in the dietary composition between treatments is not large enough to create a significant effect. However, the contrast applied in the current study was similar to those in earlier studies. Another reason for the absence of an effect of dietary macronutrient composition on $k_{g,DE}$ might be that in striped catfish the energy utilisation efficiencies of digested protein, fat and carbohydrates (64%, 80% and 58%) are relatively similar compared to other fish species.

The estimated energy utilisation efficiency of digested protein ($k_{NE;dCP}$) for striped catfish was 15.1 $kJ.g^{-1}$. The value of $k_{NE;dCP}$ estimated for striped catfish is in the range of the estimates of $k_{NE;dCP}$ for carp 11.2 $kJ.g^{-1}$ (Phan et al., 2019), tilapia 11.5 $kJ.g^{-1}$ (Schrama et al., 2018), snakehead 12.5 $kJ.g^{-1}$ (Phan et al., 2021), barramundi 15.2 $kJ.g^{-1}$ (Phan et al., 2019) and trout 15.1 $kJ.g^{-1}$ (Schrama et al., 2018) (Fig. 3). In addition, the digestible protein retention efficiency (DPE), or the retained protein as percentage of digestible protein for striped catfish was 56% (Table 4) and is comparable to the values found for Nile tilapia

(53%) (Haidar et al., 2018) and snakehead (54%) (Phan et al., 2021).

The energy utilisation efficiency of digestible fat ($k_{NE;dFat}$) for striped catfish was 31.5 kJ.g^{-1} and is comparable to the $k_{NE;dFat}$ values found for carp (34.1 kJ.g^{-1}), tilapia (35.8 kJ.g^{-1}) and snakehead (31.0 kJ.g^{-1}) based on linear relationships (Phan et al., 2019; Schrama et al., 2018). This similarity indicates that the ability to utilise digested fat for growth is comparable between the species mentioned.

The estimated energy utilisation efficiency of dCarb ($k_{NE;dCarb}$) for striped catfish was 9.9 kJ.g^{-1}. This reflects that 58% of the digested carbohydrates were retained as energy in the body, which implies that striped catfish can metabolise dCarb. The $k_{NE;dCarb}$ value for striped catfish is comparable to the value found for tilapia (Schrama et al., 2018), common carp (Phan et al., 2019; Schrama et al., 2018) and rainbow trout (Schrama et al., 2018), but much higher than the value found for barramundi (18%) (Phan et al., 2019) and snakehead (5%) (Phan et al., 2021) (Fig. 3). In addition, the linearity in the NE and dCarb relationship in the current study indicates that striped catfish can deal with high intake levels of dCarb. This indicates that digested carbohydrates can be absorbed, liberated to ATP for daily activities or converted to adipose tissue through lipogenesis in an efficient way.

The present study found similarities in the energy utilisation efficiencies of digested protein, fat and carbohydrates between striped catfish, tilapia, trout (Schrama et al., 2018) and common carp (Phan et al., 2019), but it was different for barramundi (Phan et al., 2019) and snakehead (Phan et al., 2021). However, within a species, it is unknown whether environmental conditions, i.e., temperature, salinity, dissolved oxygen can affect the energy utilisation efficiencies of digested protein, fat and carbohydrates. Furthermore, it can be hypothesised that with age of the fish, these utilisation efficiencies alter due to changes in the ratio between protein and fat deposition. These topics require further assessment.

Currently, NE equations developed for fish feed are based on the whole body level. The potential to use a NE equation for fillet growth has as far as we know not yet been investigated. The advantage of a NE equation for fillet growth is to predict the energy potential of digested protein, fat and carbohydrates of a diet formulation for fillet growth specifically. In the present study, the energy potential of digested protein for fillet growth is 42% and twice the amount of that for digested fat (20%) and 1.6 times the amount for carbohydrates (26%) (Fig. 3). Because digested protein is the most valuable macronutrient for fillet energy gain, the optimal dietary protein to energy ratio may be determined at a higher level in the diet tailor-made for fillet growth compared to the optimal dietary protein to energy ratio for growth based on whole body level.

As stated above the energy potential of digested carbohydrates for fillet growth is only 6% higher than that of digested fat for sparing protein in fillet (Fig. 3). However, this still implies that for fillet production, carbohydrates is a better energy source than fat. Yet, when using carbohydrates as an energy source this can also increase the amount of faecal waste depending on the type of carbohydrates used (starch vs. NSP). The ADC of starch is higher than that of NSP (Maas et al., 2020). Formulating practical diets with only protein is not feasible because carbohydrates is required to provide energy and necessary for the matrix of the pellet. Fat can also provide energy and is required for the essential fatty acids and fat soluble vitamins. If protein is used as a main energy source, this will increase the total ammonium nitrate (TAN) excretion and hamper the environment. A formulation with only protein is likely not economically viable making the inclusion of carbohydrates or fat as an energy source an economic necessity.

5. Conclusions

Starch is almost completely digested by striped catfish and non-starch polysaccharides are partly digested. The dietary macronutrient composition did not affect the energy utilisation efficiency in striped catfish. This might be due the relative small differences in the energy utilisation efficiencies of dCP, dFat and dCarb, which were 64%, 80% and 58%, respectively, in striped catfish. Digested starch was utilized efficiently in stripe catfish. The energetic values of dCP, dFat and dCarb for whole body growth differ from the energetic values for fillet production. For fillet growth, digested protein has a higher potential compared to digested fat and carbohydrates, however this needs to be used in a balanced ratio with digested fat and carbohydrates.

Funding information

This research project was funded by the combined financial input of TKI Topsector: Agri & Food (project number: AF-16174; The Netherlands), De Heus Animal Nutrition B.V. (The Netherlands) and Evonik operations GmbH (Germany). Furthermore De Heus contributed in kind by making their research facility available in Vinh Long (Vietnam) to perform the current experiment.

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.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.aquaculture.2021.737083.

References

Amirkolaie, A.K., Verreth, J.A.J., Schrama, J.W., 2006. Effect of gelatinization degree and inclusion level of dietary starch on the characteristics of digesta and faeces in Nile tilapia (*Oreochromis niloticus* (L.)). Aquaculture 260 (1), 194–205. https://doi.org/10.1016/j.aquaculture.2006.06.039.

Bureau, D.P., Kaushik, S.J., Cho, C.Y., 2003. Bioenergetics. In: Fish Nutrition (Third Edition). Elsevier, pp. 1–59.

Burel, C., Boujard, T., Tulli, F., Kaushik, S.J., 2000. Digestibility of extruded peas, extruded lupin, and rapeseed meal in rainbow trout (*Oncorhynchus mykiss*) and turbot (*Psetta maxima*). Aquaculture 188 (3), 285–298. https://doi.org/10.1016/S0044-8486(00)00337-9.

CVB, 1993. Centraal Veevoederbureau Veevoedertabel (Animal Feedstuffs Table). Lelystad.

Desbois, A.P., Smith, V.J., 2010. Antibacterial free fatty acids: activities, mechanisms of action and biotechnological potential. Appl. Microbiol. Biotechnol. 85 (6), 1629–1642.

FAO, 2018. Global Aquaculture Production. United Nations Fisheries and Aquaculture Department.

FishstatJ, F., 2020. FishStatJ-Software for Fishery and Aquaculture Statistical Time Series. *FAO Fisheries Division [online], Rome. Updated, 22*.

Glencross, B.D., 2006. Nutritional management of barramundi, *Lates calcarifer* - a review. Aquac. Nutr. 12, 291–309.

Glencross, B.D., 2008. A factorial growth and feed utilization model for barramundi, *Lates calcarifer* based on Australian production conditions. Aquac. Nutr. 14 (4), 360–373.

Glencross, B.D., 2009. Reduced water oxygen levels affect maximal feed intake, but not protein or energy utilization efficiency of rainbow trout (*Oncorhynchus mykiss*). Aquac. Nutr. 15 (1), 1–8.

Glencross, B.D., Bermudes, M., 2010. Effect of high water temperatures on the utilisation efficiencies of energy and protein by juvenile barramundi, *Lates calcarifer*. Fish. Aquac. J. 14, 1–11.

Glencross, B.D., Bermudes, M., 2012. Adapting bioenergetic factorial modelling to understand the implications of heat stress on barramundi (*Lates calcarifer*) growth, feed utilisation and optimal protein and energy requirements–potential strategies for dealing with climate change? Aquac. Nutr. 18 (4), 411–422.

Glencross, B., Hien, T., Phuong, N., Cam Tu, T., 2011. A factorial approach to defining the energy and protein requirements of Tra catfish, *Pangasianodon hypothalamus*. Aquac. Nutr. 17 (2).

Glencross, B., Blyth, D., Tabrett, S., Bourne, N., Irvin, S., Anderson, M., Smullen, R., 2012. An assessment of cereal grains and other starch sources in diets for barramundi (*Lates calcarifer*)–implications for nutritional and functional qualities of extruded feeds. Aquac. Nutr. 18 (4), 388–399.

Glencross, B.D., Blyth, D., Bourne, N., Cheers, S., Irvin, S., Wade, N.M., 2017. An analysis of partial efficiencies of energy utilisation of different macronutrients by barramundi (*Lates calcarifer*) shows that starch restricts protein utilisation in carnivorous fish. Br. J. Nutr. 117 (4), 500–510. https://doi.org/10.1017/s0007114517000307.

Haidar, M.N., Petie, M., Heinsbroek, L.T., Verreth, J.A., Schrama, J.W., 2016. The effect of type of carbohydrate (starch vs. nonstarch polysaccharides) on nutrients

digestibility, energy retention and maintenance requirements in Nile tilapia. Aquaculture 463, 241–247.
Haidar, M.N., Bleeker, S., Heinsbroek, L.T.N., Schrama, J.W., 2018. Effect of constant digestible protein intake and varying digestible energy levels on energy and protein utilization in Nile tilapia. Aquaculture 489, 28–35. https://doi.org/10.1016/j.aquaculture.2017.12.035.
Krogdahl, Å., Hemre, G.I., Mommsen, T., 2005. Carbohydrates in fish nutrition: digestion and absorption in postlarval stages. Aquac. Nutr. 11 (2), 103–122.
Leenhouwers, J., Adjei-Boateng, D., Verreth, J., Schrama, J., 2006. Digesta viscosity, nutrient digestibility and organ weights in African catfish (*Clarias gariepinus*) fed diets supplemented with different levels of a soluble non-starch polysaccharide. Aquac. Nutr. 12 (2), 111–116.
Leenhouwers, J.I., ter Veld, M., Verreth, J.A., Schrama, J.W., 2007. Digesta characteristiscs and performance of African catfish (*Clarias gariepinus*) fed cereal grains that differ in viscosity. Aquaculture 264 (1–4), 330–341.
Lupatsch, I., Kissil, G.W., Sklan, D., 2001. Optimization of feeding regimes for European sea bass *Dicentrarchus labrax*: a factorial approach. Aquaculture 202 (3), 289–302. https://doi.org/10.1016/S0044-8486(01)00779-7.
Lupatsch, I., Kissil, G.W., Sklan, D., 2003. Comparison of energy and protein efficiency among three fish species gilthead sea bream (*Sparus aurata*), European sea bass (*Dicentrarchus labrax*) and white grouper (*Epinephelus aeneus*): energy expenditure for protein and lipid deposition. Aquaculture 225 (1), 175–189. https://doi.org/10.1016/S0044-8486(03)00288-6.
Lupatsch, I., Santos, G.A., Schrama, J.W., Verreth, J.A.J., 2010. Effect of stocking density and feeding level on energy expenditure and stress responsiveness in European sea bass *Dicentrarchus labrax*. Aquaculture 298 (3), 245–250. https://doi.org/10.1016/j.aquaculture.2009.11.007.
Maas, R.M., Verdegem, M.C., Schrama, J.W., 2019. Effect of non-starch polysaccharide composition and enzyme supplementation on growth performance and nutrient digestibility in Nile tilapia (*Oreochromis niloticus*). Aquac. Nutr. 25 (3), 622–632.
Maas, R.M., Verdegem, M.C., Wiegertjes, G.F., Schrama, J.W., 2020. Carbohydrate utilisation by tilapia: a meta-analytical approach. Rev. Aquac. 12 (3), 1851–1866.
Meriac, A., Eding, E.H., Schrama, J., Kamstra, A., Verreth, J.A., 2014. Dietary carbohydrate composition can change waste production and biofilter load in recirculating aquaculture systems. Aquaculture 420, 254–261.
Meyer-Burgdorff, K.-H., Osman, M., Günther, K., 1989. Energy metabolism in *Oreochromis niloticus*. Aquaculture 79 (1–4), 283–291.
Noblet, J., Fortune, H., Shi, X.S., Dubois, S., 1994. Prediction of net energy value of feeds for growing pigs. J. Anim. Sci. 72 (2), 344–354. https://doi.org/10.2527/1994.722344x.
NRC, 2011. Nutrient Requirements of Fish and Shrimp. National Academies Press.
Peres, H., Oliva-Teles, A., 2002. Utilization of raw and gelatinized starch by European sea bass (*Dicentrarchus labrax*) juveniles. Aquaculture *205* (3), 287–299. https://doi.org/10.1016/S0044-8486(01)00682-2.
Peres, H., Oliva-Teles, A., 2005. Protein and energy metabolism of European seabass (*Dicentrarchus labrax*) juveniles and estimation of maintenance requirements. Fish Physiol. Biochem. 31 (1), 23–31.
Phan, L.T.T., Groot, R., Konnert, G.D.P., Masagounder, K., Figueiredo-Silva, A.C., Glencross, B.D., Schrama, J.W., 2019. Differences in energy utilisation efficiencies of digestible macronutrients in common carp (*Cyprinus carpio*) and barramundi (*Lates calcarifer*). Aquaculture 511, 734238. https://doi.org/10.1016/j.aquaculture.2019.734238.
Phan, L.T.T., Masagounder, K., Mas-Muñoz, J., Schrama, J.W., 2021. Differences in energy utilization efficiency of digested protein, fat and carbohydrates in snakehead (Channa striata). Aquaculture 532, 736066. https://doi.org/10.1016/j.aquaculture.2020.736066.
Raubenheimer, D., 2011. Toward a quantitative nutritional ecology: the right-angled mixture triangle. Ecol. Monogr. 81 (3), 407–427.
Rodehutscord, M., Pfeffer, E., 1999. Maintenance requirement for digestible energy and efficiency of utilisation of digestible energy for retention in rainbow trout, *Oncorhynchus mykiss*. Aquaculture *179* (1), 95–107. https://doi.org/10.1016/S0044-8486(99)00155-6.
Romano, N., Kanmani, N., Ebrahimi, M., Chong, C.M., Teh, J.C., Hoseinifar, S.H., Kumar, V., 2018. Combination of dietary pre-gelatinized starch and isomaltooligosaccharides improved pellet characteristics, subsequent feeding efficiencies and physiological status in African catfish, Clarias gariepinus, juveniles. Aquaculture *484*, 293–302. https://doi.org/10.1016/j.aquaculture.2017.09.022.
Saravanan, S., Schrama, J.W., Figueiredo-Silva, A.C., Kaushik, S.J., Verreth, J.A., Geurden, I., 2012. Constraints on energy intake in fish: the link between diet composition, energy metabolism, and energy intake in rainbow trout. PLoS One 7 (4) e34743.
Schrama, J.W., Saravanan, S., Geurden, I., Heinsbroek, L., Kaushik, S., Verreth, J., 2012. Dietary nutrient composition affects digestible energy utilisation for growth: a study on Nile tilapia (*Oreochromis niloticus*) and a literature comparison across fish species. Br. J. Nutr. 108 (2), 277–289.
Schrama, J.W., Haidar, M.N., Geurden, I., Heinsbroek, L.T.N., Kaushik, S.J., 2018. Energy efficiency of digestible protein, fat and carbohydrate utilisation for growth in rainbow trout and Nile tilapia. Br. J. Nutr. 119 (7), 782–791. https://doi.org/10.1017/S0007114518000259.
Williams, K.C., Barlow, C.G., Rodgers, L., Hockings, I., Agcopra, C., Ruscoe, I., 2003. Asian seabass *Lates calcarifer* perform well when fed pelleted diets high in protein and lipid. Aquaculture 225 (1), 191–206.
Williams, K.C., Barlow, C.G., Rodgers, L., Agcopra, C., 2006. Dietary composition manipulation to enhance the performance of juvenile barramundi (*Lates calcarifer* Bloch) reared in cool water. Aquac. Res. 37 (9), 914–927.