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REVIEWS IN Aquaculture

REVIEW

Essential amino acid requirements of fish and crustaceans, a meta-analysis

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Abstract

A meta-analysis of literature data on essential amino acid (EAA) requirements of fish and crustaceans was performed to re-estimate EAA requirements and provide ideal amino acid profiles. Large numbers of studies have been conducted on EAA requirements of fish and crustaceans over the past decades. However, estimated EAA requirements of different species showed a large variation due to differences in methodological approaches and regression models. An extensive search and inclusion of literature on EAA requirements were conducted following the Preferred Reporting Items for Systematic Reviews and Meta-Analyses guidelines in this study, resulting in a dataset of 358 studies covering 77 species. The relative percentage of maximum weight gain was used as the outcome to evaluate the 10 EAA requirements. Forest plots analysis was employed for heterogeneity analysis, study weight allocation and re-estimation of the requirements. Results showed that trophic level, water temperature and dietary EAA inclusion levels affected EAA requirements estimation. The meta-analysis suggested that the estimated 10 EAA requirements (expressed as % crude protein, CP) of the fish were: arginine (Arg) 5.0 (±0.14), histidine (His) 2.0 (±0.11), isoleucine (Ile) 3.3 (±0.16), leucine (Leu) 4.9 (±0.24), valine (Val) 3.8 (±0.11), lysine (Lys) 5.2 (±0.12), sulfur amino acids (Met + Cys) 3.5 (±0.18), total aromatic amino acids (Phe + Tyr) 6.2 (±0.12), threonine (Thr) 3.5 (±0.18) and tryptophan (Trp) 0.9 (±0.08). Estimated EAA requirements (expressed as % CP) of crustaceans were Arg 5.1 (±0.31), His 2.5 (±0.15), Ile 4.3 (±0.97), Leu 5.7 (±0.08), Val 4.3 (±0.30), Lys 4.9 (±0.28), Met + Cys 3.2 (±0.18), Phe + Tyr 5.1 (±0.65), Thr 3.8 (±0.04) and Trp 0.8 (±0.15).

Shujuan Xing and Xiaofang Liang contributed equally to this study.

KEYWORDS
essential amino acids, forest plot, heterogeneity analysis, ideal protein concept, systematic review, trophic level

1 | INTRODUCTION

In recent years, the state of food security and nutrition in the world has been undermined due to climate variability, conflicts, economic downturns and pandemic.[1] The reliable and stable supply of good quality protein- and energy-dense ingredients as feed ingredients with low environmental footprints is an essential requisite for the sustainable development of aquaculture. Reducing dietary protein levels while ensuring an ideal amino acid profile that meets the animals' requirements are effective means of optimizing production costs and minimizing nitrogen losses in farm animals.[2,3] It is widely recognized that aquatic animals do not specifically require proteins, but instead, they have a requirement for a well-balanced mixture of amino acids obtained from the diet.[4] Amino acids serve as substrates for protein synthesis and contribute to the growth of aquatic animals. Moreover, they play essential role in regulating feed intake, intermediary metabolism, cell signalling, immune response and the health of farmed animals,[2,5] including fish and crustaceans.[6] Amino acids are categorized into nutritionally essential (or indispensable) amino acids (EAAs or IAAs), conditionally essential amino acids and non-essential (or dispensable) amino acids (NEAAs or DAAs). In all studied fish and crustaceans, the same 10 EAA need to be supplied in their diets: arginine (Arg), histidine (His), isoleucine (Ile), leucine (Leu), valine (Val), lysine (Lys), methionine (Met), phenylalanine (Phe), threonine (Thr) and tryptophan (Trp). Given that any imbalance amino acids are likely to disrupt protein synthesis and turnover, leading to adverse consequences such as nitrogen loss into the environment. Therefore, determining the precise requirements and the limiting order of EAA is of utmost importance for the sustainable development of aquaculture. There are hundreds of fish and crustaceans reared in aquaculture, while only a few of them have had their nutritional requirement comprehensively studied.[7] Similar to other farmed animals, the formulation of feeds for fish or shrimp recognizes the concept of ideal protein, though studies in this area are limited to a few species.[8–15]

The whole body amino acid (AA) profile and the ratio of individual EAA to the sum of EAA (A/E ratios) have been used to develop early guidelines or rough estimation of the EAA requirement of fish.[9,16] It is also well reckoned that the EAA requirement profile would reflect that of the whole body or muscle EAA profiles.[8,15] The criterion for establishing the ideal EAA pattern in certain fish has involved observing a decrease in nitrogen gain after removing or reducing a specific EAA in their diets.[11,17] In addition, measurement of the oxidation of radio-labelled tracer EAA or other methods have been employed to determine the requirements for some EAA.[18–20] The majority of EAA requirement data has been obtained through conventional growth trial conducted over a specific time period. In these studies, a basal diet, either purified or practical formulated, is designed with a deficiency in the target EAA while assuming it satisfies all other known nutrient requirements of the animal, and graded levels of the tested EAA are then supplemented to several other test diets.[21–24] In the majority of studies, the most commonly measured response has been the whole-body weight gain, either complemented or not with other biomarkers of physiological or metabolic interest.[25]

Over the past decades, several attempts have been made to review existing data on EAA requirements of farmed fish and shrimp,[6,7,26–29] raising various issues and concerns. There is considerable variation not only among species but also even within species in the published experimentally determined recommendations. The observed variability in data from dose–response studies can be attributed to several factors related to the experimental conditions, including the quality and composition of the control or basal diet (which should be deficient in the EAA under consideration), the number of levels and range of EAA concentrations tested (ranging from deficiency to excess), environmental factors, the size of fish/shrimp and the duration of the trial. Moreover, analyses of data vary in terms of statistical tools, response criteria, mathematical models and the unit of expression of data (per g diet, per unit protein content etc.) from one study to another.[6,25–27,30]

As mentioned above, a substantial amount of data on EAA requirements of fish and crustaceans have been updated and summarized.[6,25,26] However, due to significant variations in data, literature data has been compiled and compared without further analysing EAA requirements. The determination of general EAA requirements was previously based on the EAA composition of whole fish. In recent decades, some attempts have been made to undertake analyses of EAA requirements by collecting original data from the literature, recalculating specific response variables and applying different mathematical models (e.g., broken-line, quadratic and saturation kinetics).[29,31,32] For example, in the work of Peres and Oliva-Teles,[32] they reviewed the EAA requirements of marine fish species and standardized the growth rate in each study to make growth performance comparable across studies. These standardized growth rates and amino acid inclusion levels were then re-fitted with the saturation kinetic model (SKM) to estimate the EAA requirement. In the aforementioned reviews, limitations also existed: (1) the potential inclusion of low-quality studies due to the lack of data filtering; (2) inconsistency in data homogeneity used for meta-analysis; (3) variations in weight gain among fish at different growth stages resulting from the absence of standardized animal weight gain; (4) a need for enhanced oversight regarding the weight contribution of each study to the final estimate; (5) exclusion of literature in other languages (with English abstracts); and (6) failure in re-estimating EAA requirement in a certain model (e.g., SKM). Statistical meta-analysis provides a method to integrate and standardize information, enabling meaningful comparisons. In animal science, meta-analysis has proven to be an efficient way to renew previously published data by creating novel empirical models, allowing progress in both understanding and prediction aspects.[33]

Given the above points, the objectives of the present meta-analysis are to (i) undertake a systematic analysis of existing data on EAA requirement in fish and crustaceans; (ii) examine the factors influencing the required dietary EAA levels; and (iii) provide insights into future research needs concerning EAA nutrition in fish and crustaceans.

2 | MATERIALS AND METHODS

2.1 | Literature searching and selection

AA requirements of fish and nutritional regulation of AA metabolism have been subject to several reviews,[25–27,29,32,34–36] and the latest one was by Mai et al.[6]

An extensive search of the EAA requirement literature was conducted using Scopus, Web of Science and China National Knowledge Infrastructure (CNKI) following the Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) guidelines. First, we submitted the search query to Scopus within the title, abstract and keywords to retrieve records. The search query included a combination of the following terms: (EAA W/1 requirement AND fish) OR (EAA W/1 requirement AND shrimp) OR (EAA W/1 requirement AND crab). Where EAA was replaced with the specific amino acid in the literature search of each amino acid. For example, (Lysine W/1 requirement AND fish) OR (Lysine W/1 requirement AND shrimp) OR (Lysine W/1 requirement AND crab) was used as the search query for Lys requirement literature. No language restriction was applied during the literature search in order to retrieve all potential studies. The specific retrieval process is provided in the Supplementary File 1. Records from Scopus, Web of Science and CNKI were 669, 1043 and 576, respectively. Thereafter, all the retrieved records were imported into Endnote software X9 to remove duplicate records ($n = 1510$). Irrelevant literature was removed by reading the title and abstract of each record. Finally, a total of 674 peer-reviewed publications spanning 58 years (1964–2022) were included in the preliminary dataset (Figure 1).

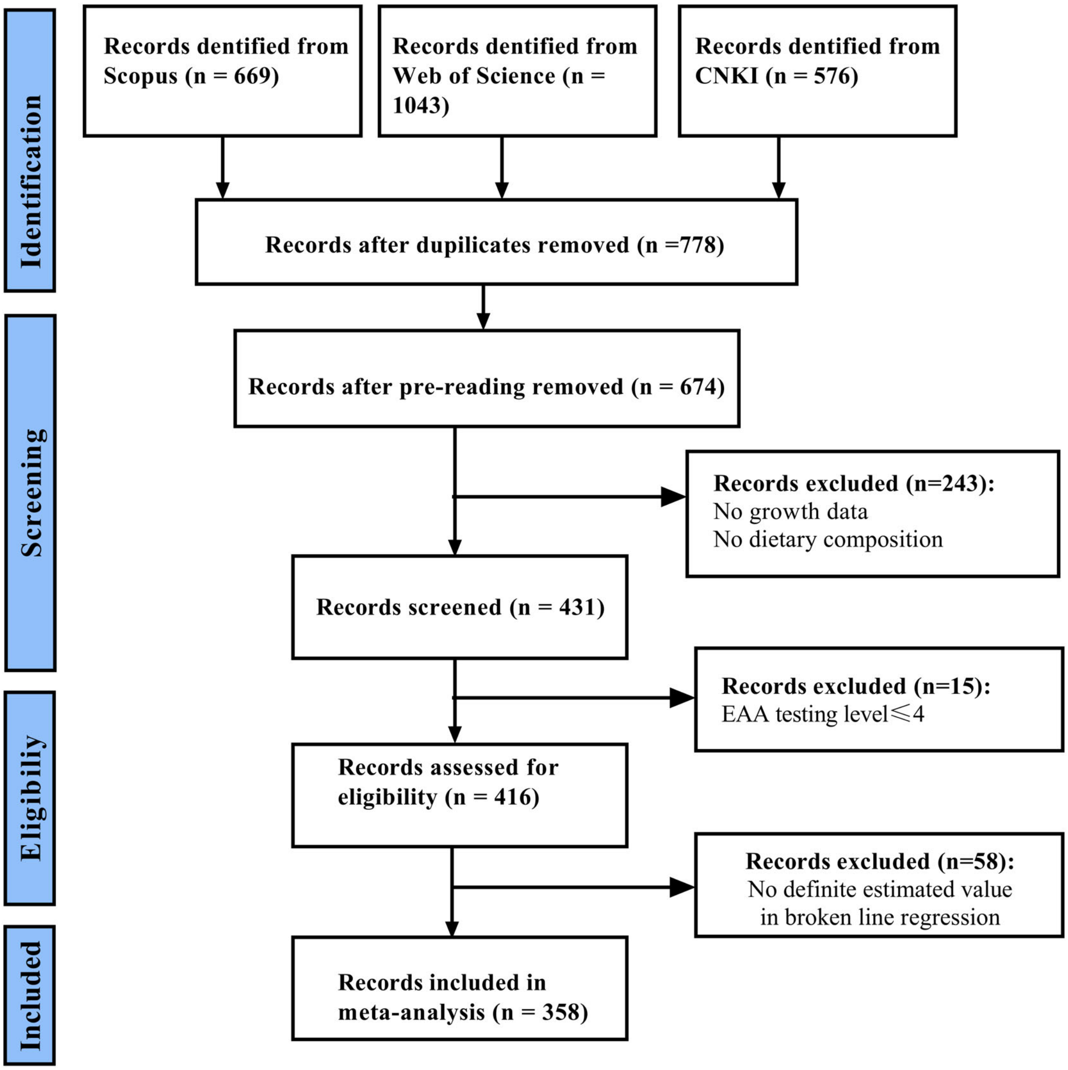

FIGURE 1 Flow chart of search results and details on selection criteria based on Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA).

TABLE 1 Studies considered eligible for meta-analysis of the requirement of each essential amino acid.

Species		Arg	His	Ile	Leu	Val	Lys	Met + Cys	Phe + Tyr	Thr	Trp	Total
Fish	Studies	53	19	22	26	21	62	46	19	33	19	
	Species	37	13	19	21	17	43	32	13	24	13	
Crustacean	Studies	6	2	3	3	3	5	5	3	4	4	
	Species	5	2	3	2	3	4	5	2	3	2	
Total studies		59	21	25	29	24	67	51	22	37	23	358
Total species		42	15	22	23	20	47	37	15	27	15	77

Abbreviations: Arg, arginine; His, histidine; Ile, isoleucine; Leu, leucine; Lys, lysine; Met + Cys, methionine + cystine; Phe + Tyr, phenylalanine + tyrosine; Thr, threonine; Trp, tryptophan; Val, valine.

Rigorous screening of the studies for further meta-analysis dataset was done according to the following criteria: (1) dose–response data can be calculated with sufficient information on initial and final fish body weight, duration and so on. (2) data on dietary EAA concentration (% CP) was present or can be calculated; and (3) the number of graded levels of dietary EAA was more than 4. The search results and selection procedures are presented in Figure 1. Studies ($n = 243$) lacking data on initial/final body weight or dietary EAA level (% CP) were excluded from the meta-analysis dataset. In addition, 15 studies with EAA testing gradients of less than 5 were removed from the dataset. After this screening process, 416 studies remained in the dataset, from which we extracted the following data: initial and final body weight, EAA gradient concentration (% CP), trial duration, water temperature, response criterion and mathematical model (Supplementary Files 1 and 2).

To ensure comparability and combination in the meta-analysis, eligible studies should share similarities. However, the studies we collected had different objectives, experimental designs, response criteria, analytical methodologies and so on. Therefore, the data from each study were subjected to the broken-line regression (BLR)[37] for further eligibility selection. Weight gain (WG) is the most common response criterion in the EAA requirement studies. However, the differences in fish size and trial duration among studies made it impractical to directly compare and combine WG values. Therefore, we normalized the WG to the percentage of maximum WG ($\%MaxG_n$) in each study using the Formula (1) to eliminate the impact of body weight on the re-estimation of EAA requirement.

$$\%MaxG_n = 100 \times \frac{\mathrm{WG}}{MaxWG} \tag{1}$$

where WG is the actual weight gain of each treatment in a specific study, *Max*WG is the maximum WG among all treatments in the study. Thereafter, the $\%MaxG_n$ and EAA concentrations (% CP) were subjected to the BLR to estimate the breakpoint (X_{bp}) value and standard error (SE). The studies with the definite estimated values of X_{bp} and SE were included in the dataset for the final meta-analysis.

BLR equation:

$$Y_1 = a_1 + b_1 \times X; Y \,\mathrm{at}\, X_{\mathrm{bp}} = a_1 + b_1 \times X_{\mathrm{bp}} \tag{2}$$

$$Y_2 = Y \,\mathrm{at}\, X_{\mathrm{bp}} + b_2 \times (X - X_{\mathrm{bp}}); Y = \mathrm{if}(X < X_{\mathrm{bp}}, Y_1, Y_2) \tag{3}$$

where Y is response criterion $\%MaxG_n$; X is dietary EAA concentration (% CP); a_1 is intercept on the y-axis for $X = 0$; b_1 is the slope of the first line; b_2 is the slope of the second line; X_{bp} is the breakpoint X value.

After the BLR screening, the dataset included 358 studies and covered 77 species of fish and crustaceans (Table 1).

2.2 | Forest plot analysis

2.2.1 | Effect size, variance and weighted effect size calculation

Following data selection, the literature included in the meta-analysis dataset underwent homogeneity analysis following the procedure described by Neyeloff et al.[38] The estimated EAA requirement value (X_{bp}) was used as the effect size (ES) since: (1) it is the most meaningful outcome of each study; (2) it allows for comparability across studies; (3) the variance (SE^2) and confidence intervals can be calculated.[39] Study weights in our meta-analysis were determined based on the precision of each study, since variations in study size (e.g., replicate number and animal number per replicate) were not significant between studies. Thus, the variance of the X_{bp} (SE^2) was used to weigh each study, and the individual study weight (w) was expressed as the inverse of variance:

$$w = \frac{1}{\mathrm{SE}^2} \tag{4}$$

with the definite effect size and the corresponding study weight, the individual weighted effect size ($\overline{X}_{\mathrm{bp}}$) was computed as:

$$\overline{X}_{\mathrm{bp}} = w \times \mathrm{ES} \tag{5}$$

2.2.2 | Heterogeneity analysis, fixed or random effects model selection

Heterogeneity analysis for each EAA was performed via Q statistics and I^2 statistics. The Q statistics assess heterogeneity among studies and I^2 statistics quantify this heterogeneity. The calculations followed equations below:

$$Q = \sum\left(w \times (ES)^2\right) - \frac{\left[\sum(w \times ES)\right]^2}{\sum w} \tag{6}$$

$$I^2 = 100 \times \frac{Q - df}{Q}. \tag{7}$$

In the present study, if the Q value was lower than the corresponding degree of freedom (df), the fixed effect model was applied; Otherwise, the random effect model was adopted.[38] The I^2 is expressed as the percentage of the total variability in a set of effect sizes due to true heterogeneity. As described by Deek et al.,[40] $I^2 \leq 40$ indicates homogeneity among studies. Therefore, if $I^2 \leq 40$, all studies in the tested dataset would be included in the meta-analysis; otherwise, further analysis of the heterogeneity source or removal of outliers from the dataset is needed.

As for the fixed effect model, the effect summary ($\overline{es}$), the standard error ($SE_{\overline{es}}$) and the 95% confidence interval ($CI(\overline{es})$)were calculated according to the following formulae:

$$\overline{es} = \frac{\sum(w \times ES)}{\sum w} \tag{8}$$

$$SE_{\overline{es}} = \sqrt{\frac{1}{\sum W}} \tag{9}$$

$$CI(\overline{es}) = \overline{es} \pm 1.96 \times SE_{\overline{es}} \tag{10}$$

As for the random effect model, the weight of each study was adjusted with a constant (v). v value was calculated as follows:

$$v = \frac{[Q - df]}{\left(\sum w - \sum w^2 / \sum w\right)} \tag{11}$$

Then, the new weight of each study (w_v) was computed as follows:

$$w_v = \frac{1}{SE^2 + v} \tag{12}$$

Thereafter, we replaced w with w_v in Equations (6) and (7) and got the new Q_r and I_r^2 for the random effect model. Subsequently, the effect summary ($\overline{es}_v$), standard error ($SE_{\overline{es}_v}$) and the 95% confidence interval ($CI(\overline{es}_v)$) of the random effect model were computed following:

$$\overline{es}_v = \frac{\sum(w_v \times ES)}{\sum w_v} \tag{13}$$

$$SE_{\overline{es}_v} = \sqrt{\frac{1}{\sum w_v}} \tag{14}$$

$$CI(\overline{es}_v) = \overline{es}_v \pm 1.96 \times SE_{\overline{es}_v} \tag{15}$$

2.2.3 | Re-estimation of the EAA requirements

In our present study, the re-estimated EAA requirement for fish and crustaceans was determined by mathematically combining all the studies in the forest plots. The *x*-axis served as the scale for the effect size, with each row representing a study's effect size estimation presented as a bullet and a 95% confidence interval, except for the row labelled 'Mean'. In the forest plot, each bullet reflects the estimated EAA requirement for a study, and the size of the bullets represents the corresponding study's weight contribution to the meta-analytic result. A larger the bullet signifies a greater influence of that study on the weighted combined results. For each forest plot, the central diamond at the 'Mean' row indicates the weighted effect size of all the studies, representing the value of the re-estimated EAA requirement.

2.3 | The correlation analysis of experimental factors on EAA requirement

The studied factors included the trophic level of the fish species, water temperature and the average inclusion levels of dietary EAA (% CP). The EAA requirement re-estimate was obtained by fitting the BLR based on the raw data of dietary EAA inclusion levels (% CP) and $\%MaxG_n$ in each study. Before performing the correlation analysis, we standardized the estimated EAA requirement of individual studies using *z*-score transformation by IBM SPSS Statistics 25.

2.4 | Impact of fish trophic level on the EAA requirement analysis

To assess how the EAA requirement differs among fish trophic levels, studies in the meta-analysis datasets were categorized into three trophic level groups: (1) trophic level ≤3; (2) 3 < trophic level < 4; (3) trophic level ≥4. Subsequently, differences in each EAA requirement between trophic levels were compared and analysed. The trophic level of fish was sourced from FishBase (www.fishbase.se). The estimated EAA requirement value for each study was obtained using BLR model with dietary EAA inclusion levels (% CP) and $\%MaxG_n$ as independent and dependent variables, respectively.

2.5 | Overview of body weight distribution and corresponding EAA requirement in each study

To obtain fish body weight information involved in the study in the dataset, 10 scatter diagrams of body weight and the corresponding EAA requirement estimate were made. The abscissa axis was expressed as the fish's initial and final body weight (mean ± SD), the ordinate was the EAA concentration (% CP; mean ± SD), and the dots were the re-estimated requirement value from the BLR model.

2.6 | Ideal EAA patterns of fish and crustaceans

The re-estimated values of EAA requirement, based on the $\%MaxG_n$ and % CP for each study, were analysed using forest plots method described above, with fish species categorized by trophic level. The EAA requirement re-estimates were used to establish the ideal EAA patterns for fish and crustaceans. The ideal EAA profile was expressed as the proportion of each EAA relative to Lys (regard as 100).[7]

2.7 | Statistical analysis tools

Forest plots analysis was performed in Microsoft Excel 2019. One-way ANOVA was employed to compare EAA requirements among fish trophic levels, and *z*-score transformation was carried out in IBM SPSS Statistics 25. Figures were made using GraphPad Prism 8. Pearson correlation analysis between experimental factors and EAA requirement was conducted in OriginPro 2023b.

3 | RESULTS AND DISCUSSION

3.1 | Response criteria and model selection for meta-analysis

In fish and crustaceans, amino acids in the diet serve not only as the basic unit for protein synthesis[41] but also participate in various functions in the body, including serving as gustatory or olfactory feeding stimulants and catalysis of biological reactions (enzymes).[42–45] However, when it comes to the determination of the dietary requirement level for a specific EAA, such biochemical or metabolic response criteria are not fully explored, except in a few cases.[46–49]

In our dataset for meta-analysis, all studies recorded fish growth over varying durations during the experiment. Out of 358 studies, 349 studies used growth-related criteria, including WG, specific growth rate and thermal-unit growth coefficient, to estimate EAA requirements (Supplementary File 1). Therefore, WG was used as the response criterion in this meta-analysis. We calculated $\%MaxG_n$ based on each study's original initial and final body weight to eliminate the influence of different growth stages of fish on body WG. $\%MaxG_n$ was the new criteria for reassessing EAA requirement as it uses the same scale and has methodological consistency, and thus is comparable between studies.[36]

In the published studies on EAA requirements, the BLR and quadratic regression (QR) were the predominant mathematical models in our present dataset, constituting 43% and 45%, respectively. However, the choice between the models for nutrient requirement estimation remains controversial.[25,29,50–53] Some authors consider the QR model the most suitable for analysing transitions from a deficiency state to a balanced or toxic state.[54–56] Others argue that the BLR model is superior in presenting the theoretical essence of nutritional response essence, even though it is more challenging to fit than the simple polynomial.[57] In addition, the BLR model is preferred due to its sharp, rather than smooth transition observed when fish are fed diets with different doses of nutrients.[58–60] According to Pesti et al.,[57] the quadratic model is much more sensitive to the range of nutrient doses than the BLR model. They noted that adding extra EAA levels higher or lower than the "requirement" can impact the estimate of EAA requirement. In a comparative study by Elesho et al.[61] on the Met requirement estimation in African catfish using both models, adjusting the dietary Met inclusion level from 4–12 to 4–8 g/kg diet resulted in a reduced estimated value from 29.2 to 23.6 g/kg digestible protein (DP) when the QR model was adopted. However, the Met requirement estimated by the BLR model remined relatively stable, ranging from 19 to 18.4 g/kg DP.[61] In our meta-analysis dataset, the diverse experiment designs in each study led to varying nutrient concentration ranges. For instance, in the study of Arg requirement, the dietary Arg content ranged from 1.3%–5.6% crude protein (CP) in yellow perch diets,[62] and from 2.6% to 9.9% CP in grass carp diets.[63] Similarly, in the study on Lys requirement, the dietary Lys level varied from 2.4% to 10.8% CP in black-spotted croaker diets,[64] while it ranged from 2.2% to 5.4% CP in Asian seabass diets.[65] Therefore, the BLR model seems to be a more stable and consistent model for the estimation and comparison of studies than the QR model.

Nevertheless, we must recognize that the response of an animal to dietary increments of a limiting nutrient is not broken at one particular point. In addition to the two models mentioned above, a major development in the analyses of dose–response curve in nutrient requirement studies in animals was the introduction of the SKM by Mercer[66] in 1982. This four-parameter mathematical model is based on the concept that responses resulted from a series of enzymatically mediated steps, one of which is rate limiting and displays saturation kinetics. This model has also been applied in some later studies concerning amino acid requirements in fish or shrimp.[8,32,51,67] The original four-parameter model developed by Mercer has been refined to include potential adverse effects of excess nutrient supply or intake.[68] Salze et al.[29] compared four models (broken-line model, quadratic model, broken-quadratic model and saturation kinetic model) in 2017 and highlighted that the SKM requires careful experimental design, as it is sensitive to the number of experimental diets, which may result in a high possibility of obtaining an "outside" fit (where the estimate requirement falls outside the EAA range of the experimental diets). An "outside" fit should not be considered accurate. In addition, SKM is prone to failure in data convergence. Our preliminary analysis showed that the BLR model exhibited a better fit and was preferred over Mercer's SKM. Specifically, less than 50% (36%–48%) of studies could converge into SKM, while more than 72% (72%–94%) of studies successfully converged into BLR model. Therefore, in the present meta-analysis, the BLR was employed as it is considered a more plausible, feasible, stable and consistent choice for estimation and comparing studies compared to QR and SKM.

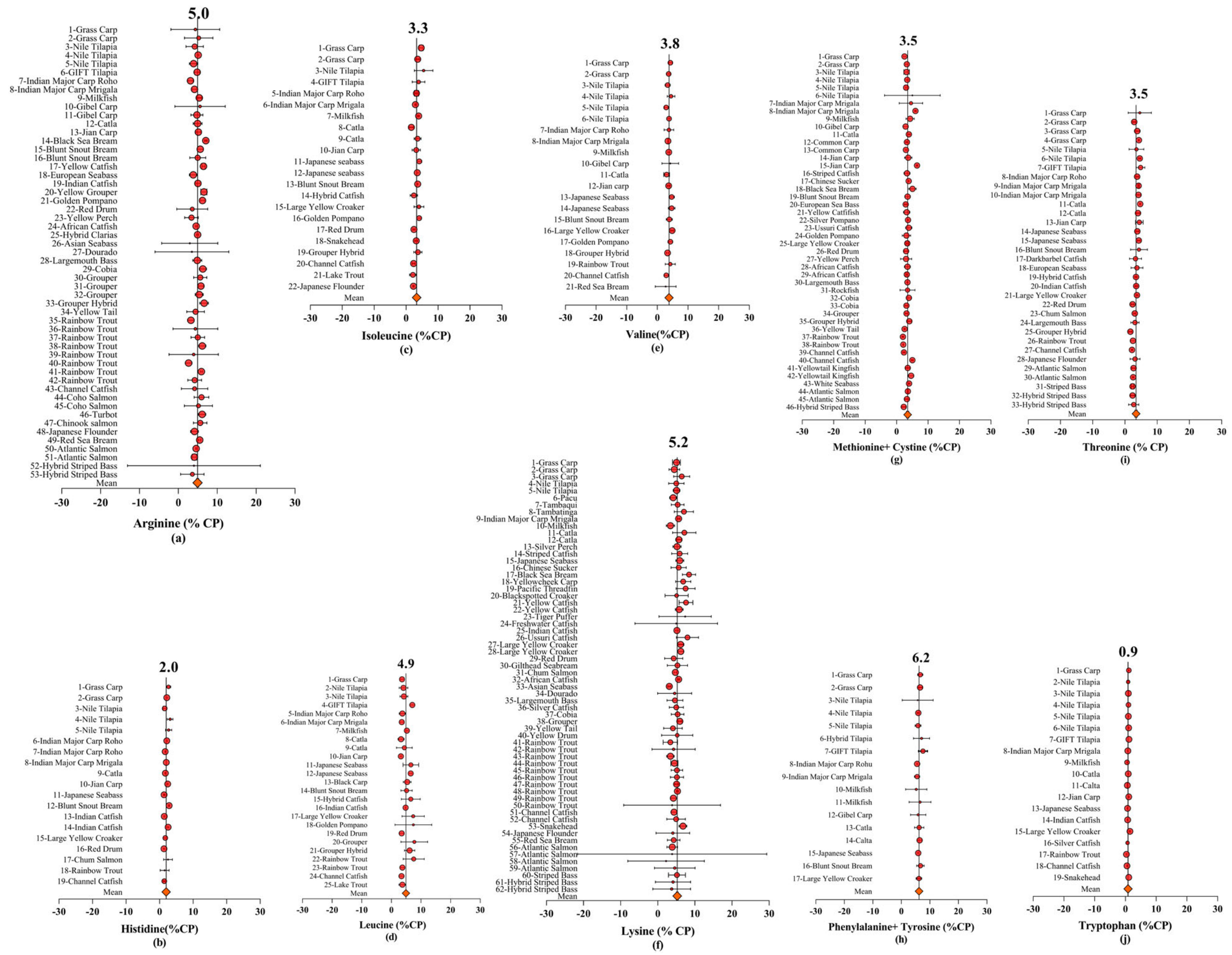

FIGURE 2 Forest plot presentation of meta-analytic estimates on the minimal levels of 10 EAA in different fish species: (a) arginine, (b) histidine, (c) isoleucine, (d) leucine, (e) valine, (f) lysine, (g) methionine + cystine, (h) phenylalanine + tyrosine, (i) threonine, (j) tryptophan. Each bullet reflects the estimated EAA requirement for a study. The size of the bullet represents the corresponding study's weight contribution to the meta-analytic result. In each forest plot, the central diamond at the "Mean" row indicates the weighted effect size, representing the value of the re-estimated EAA requirement. The re-estimate requirement value was depicted on the top of each figure. EAA, essential amino acid.

3.2 | Forest plot analysis

3.2.1 | Heterogeneity analysis

Q statistics and I^2 statistics from the heterogeneity of variance test, based on the fixed and random model, are presented in Supplementary File 3 along with forest plots of the results (Figures 2 and 3). The result of heterogeneity analysis indicated the use of the random effect model for analysing all sub-datasets of the 10 EAA in all fish species studies. Most EAA sub-datasets showed Q >df and I^2 <40%, except for Leu and Phe + Tyr, with I_r^2 values of 65.8% and 51.0%, respectively (Supplementary File 4). The study estimating the Leu requirement of Indian major carp[69] introduced considerable heterogeneity to the Leu dataset. This possibly due to the narrow and low Leu addition level (3.38%–5.08% CP) in this study. Thus, this study was excluded from the analysis, resulting in an I_r^2 of 38%. In the Phe + Tyr dataset, heterogeneity was observed due to two trials on channel catfish.[70] This heterogeneity might be attributed to two factors. First, channel catfish, with a higher trophic level (4.3), may have specific requirements compared to other fish species in the Phe + Tyr dataset (trophic level ≤3.7). Second, the lower estimation could be related to poor growth performance of fish or narrow dietary Phe + Tyr levels (3.33%–5.83% CP) studied. Thus, these two studies were excluded from the forest plots, resulting in a reduced I_r^2 to 30.5% (Supplementary File 4).

For crustaceans, where Q <df in the Leu and Thr datasets indicate little variance in effect sizes, the fixed effect model was applied. For the remaining EAA datasets, the random model was adopted (Supplementary File 5). In the Trp dataset, heterogeneity was noted due to a study on Pacific white shrimp.[71] The higher Trp requirement in this study could be related to higher Trp addition levels and the smaller range of growth differences between treatments compared to

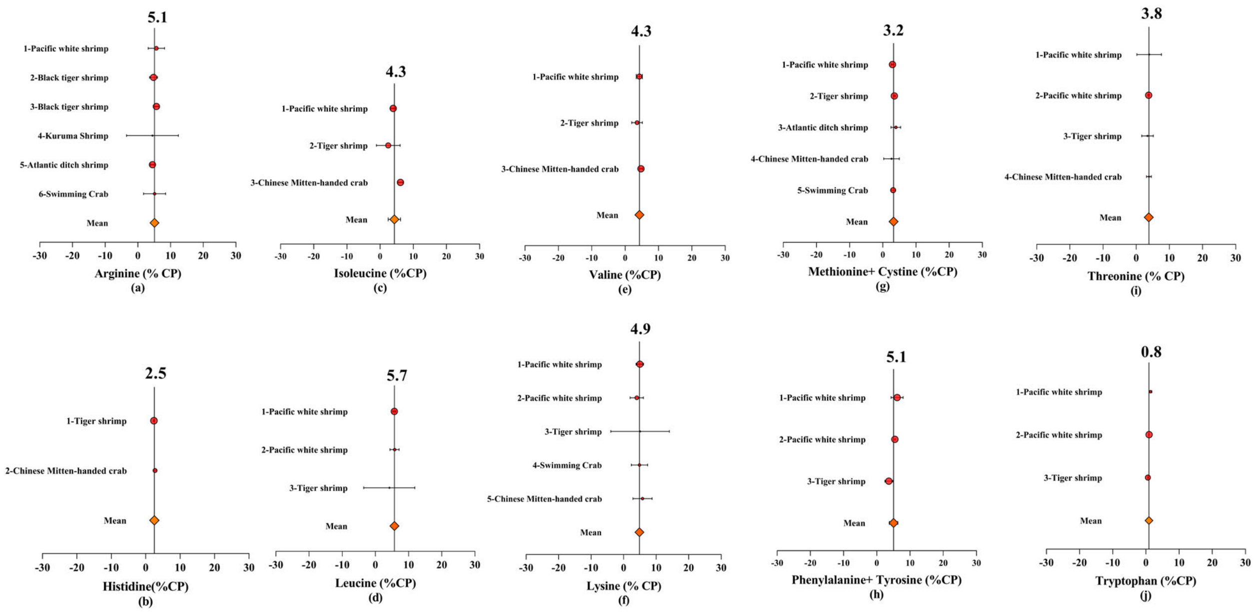

FIGURE 3 Forest plot presentation of meta-analytic estimates on the minimal levels of 10 EAA for crustaceans: (a) arginine, (b) histidine, (c) isoleucine, (d) leucine, (e) valine, (f) lysine, (g) methionine + cystine, (h) phenylalanine + tyrosine, (i) threonine, (j) tryptophan. Each bullet reflects the estimated EAA requirement for a study. The size of the bullet represents the corresponding study's weight contribution to the meta-analytic result. In each forest plot, the central diamond at the 'Mean' row indicates the weighted effect size, representing the value of the re-estimated EAA requirement. The re-estimate requirement value was depicted on the top of each figure. EAA, essential amino acid.

other studies on Pacific white shrimp.[72,73] Excluding this study from the dataset reduces I_r^2 to 7.8%.

Forest plots effectively summarize the individual study results and their weights to the combined effect in a systematic review.[74] In our present study, the studies included in each EAA re-estimation dataset exhibited low heterogeneity (I_r^2 <40%) (Supplementary File 3). The SE of the breakpoint (X_{bp}) in the BLR model measures the accuracy of a specific experiment. A large SE in a study suggests lower accuracy in estimating using the BLR model, resulting in a smaller weight in the final weighted combination effect. Some datasets for each EAA showed large SEs. For instance, in the Arg dataset, the large SE in the study by Griffin et al.[75] on hybrid striped bass might be related to the relatively low R^2 (0.54) of the fitted BLR model as well as a poor survival rate. Consequently, the re-estimated Arg requirement value in hybrid striped bass is 4.0% CP, with the smallest contribution to the combined effect size (weight of 0.14%; Figure 2a). Similarly, the very low R^2 (0.22) of the study by Espe et al.[76] on Atlantic salmon in the Lys dataset was the possible cause of the large SE (Figure 2f).

TABLE 2 Re-estimation value of essential amino acid requirement based on forest plots analysis (mean ± SE).

	Fish	Crustacean
Arg	5.0 ± 0.14	5.1 ± 0.31
His	2.0 ± 0.11	2.5 ± 0.15
Ile	3.3 ± 0.16	4.3 ± 0.97
Leu	4.9 ± 0.24	5.7 ± 0.08
Val	3.8 ± 0.11	4.3 ± 0.30
Lys	5.2 ± 0.12	4.9 ± 0.28
Met + Cys	3.5 ± 0.18	3.2 ± 0.18
Phe + Tyr	6.2 ± 0.12	5.1 ± 0.65
Thr	3.5 ± 0.18	3.8 ± 0.04
Trp	0.9 ± 0.08	0.8 ± 0.15

Note: Data are expressed as % crude protein.
Abbreviations: Arg, arginine; His, histidine; Ile, isoleucine; Leu, leucine; Lys, lysine; Met + Cys, methionine + cystine; Phe + Tyr, phenylalanine + tyrosine; Thr, threonine; Trp, tryptophan; Val, valine.

3.2.2 | Re-estimation of the requirements for all the 10 EAA

The results of the re-estimated requirements for Arg, His, Ile, Leu, Val, Lys, Met + Cys, Phe + Tyr, Thr and Trp by meta-analysis are summarized in Table 2, with detailed original data available in Supplementary File 1. In animals, tyrosine (Tyr) and cystine (Cys) can be synthesized from Phe and Met, respectively. Therefore, the dietary requirement for these EAA depend on the dietary concentration of the corresponding precursors. These two amino acids are included in estimates of EAA requirement and expressed as Met + Cys and Phe + Tyr. For fish species, the estimation of the Phe + Tyr requirement excluded high trophic-level fish species, as the two trials on channel catfish introduced significant heterogeneity to the dataset.[70] Therefore, the Phe + Tyr requirement were re-estimated for fish species

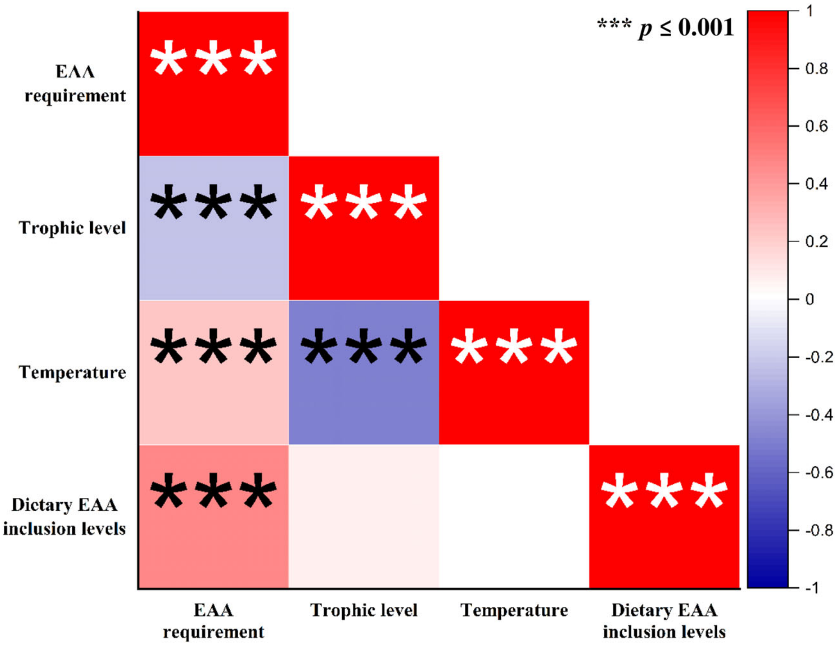

FIGURE 4 The correlation analysis between influencing factors (trophic level, water temperature and dietary EAA inclusion levels) and the EAA requirements of fish. Dietary EAA inclusion level is expressed as % CP. CP, crude protein; EAA, essential amino acid.

with a trophic level no higher than 3.7. For channel catfish (trophic level 4.2), the requirement value was estimated as 4.6% CP. In the case of crustaceans, though there are only two trials (Tiger shrimp and Chinese mitten-handed crab) in the His re-estimation dataset, their differences in His requirement are small (2.4% and 2.7% CP, respectively) and the combined re-estimated value is 2.51% CP. The number of studies in the other EAA datasets for crustaceans is no less than 3.

Dos Santos[31] re-estimated 45 fish species using Mercer's SKM and QR models. The estimated values (% CP) were as follows: Arg 7.0%, His 2.1%, Ile 2.5%, Leu 4.1%, Lys 5.9%, Met 3.2%, Phe 4.6%, Trp 0.9%. However, re-estimations for Val and Thr were not available. Peres and Oliva Teles[32] adopted Mercer's SKM to re-estimate three EAA in marine fish. The estimated values (% CP) were Arg 4.54%, Lys 4.9% and Met 2.41%. The differences between the previous and present results can be attributed to the meta-analysing methods discussed earlier.

This meta-analysis standardized the body WG in each study by % $MaxG_n$, and the estimated EAA requirement is expressed as dietary protein concentration (% CP). These standardizations help reduce the impact of variations in initial body weight and dietary protein content among different studies on the re-estimated value.[32] Therefore, the re-estimated EAA requirement is applicable to all growth stages of cultured animals.

3.3 | Factors influencing data on EAA requirement

3.3.1 | Dietary EAA inclusion level

The correlation analysis of factors influencing EAA requirement in fish, including trophic level, temperature and dietary EAA inclusion levels, is depicted in Figure 4. There is a significant positive correlation between EAA requirement and dietary EAA inclusion level when both parameters are expressed as a percentage of dietary protein. This correlation is expected, given that each study was fitted to determine the optimal requirement within the experimental design. For example, a higher Arg requirement (7.1% CP) was observed in black sea bream with a dietary Arg inclusion level of 4.8%–9.1% CP,[77] while lower Arg inclusion levels (1.3%–5.6% CP and 1.3%–4.4% CP) resulted in lower Arg requirement estimates for yellow perch (3.4% CP)[59] and Indian major carp (3.1% CP).[78] The effect of EAA inclusion level on EAA requirement may be associated with the protein or EAA sources in the formula. In the black sea bream study, a practical diet comprising fish meal and soybean protein concentrate was used, with Arg content in the basal diet of 1.85% diet (4.83% CP). However, the studies on yellow perch and Indian major carp employed purified diets, with Arg content in the basal diet at 0.44% diet (1.33% CP) and 0.47% diet (1.25% CP), respectively. The elevated Arg inclusion in the experiment diet was created by adding more crystalline amino acid (CAA) mixtures, while inappropriate inclusion in the feeds, inefficient utilization of the CAAs and the higher digestibility of purified diet may lead to an overestimate of EAA requirement.[32,79] On the other hand, achieving substantial WG during the growth trial enhances the precision of the estimates.[29] Nevertheless, in some studies, the range of amino acid inclusion levels did not result in large differences in fish growth. One example is, in the study of Lys requirement for blackspotted croaker (*Protonibea diacanthus*), fish were fed experimental diets with gradient Lys levels from 2.4% to 10.7% CP for 8 weeks. The results showed that the %$MaxG_n$ as between 89% and 100% across treatments, which is too narrow to generate a precise estimate value.[64] Similar problems

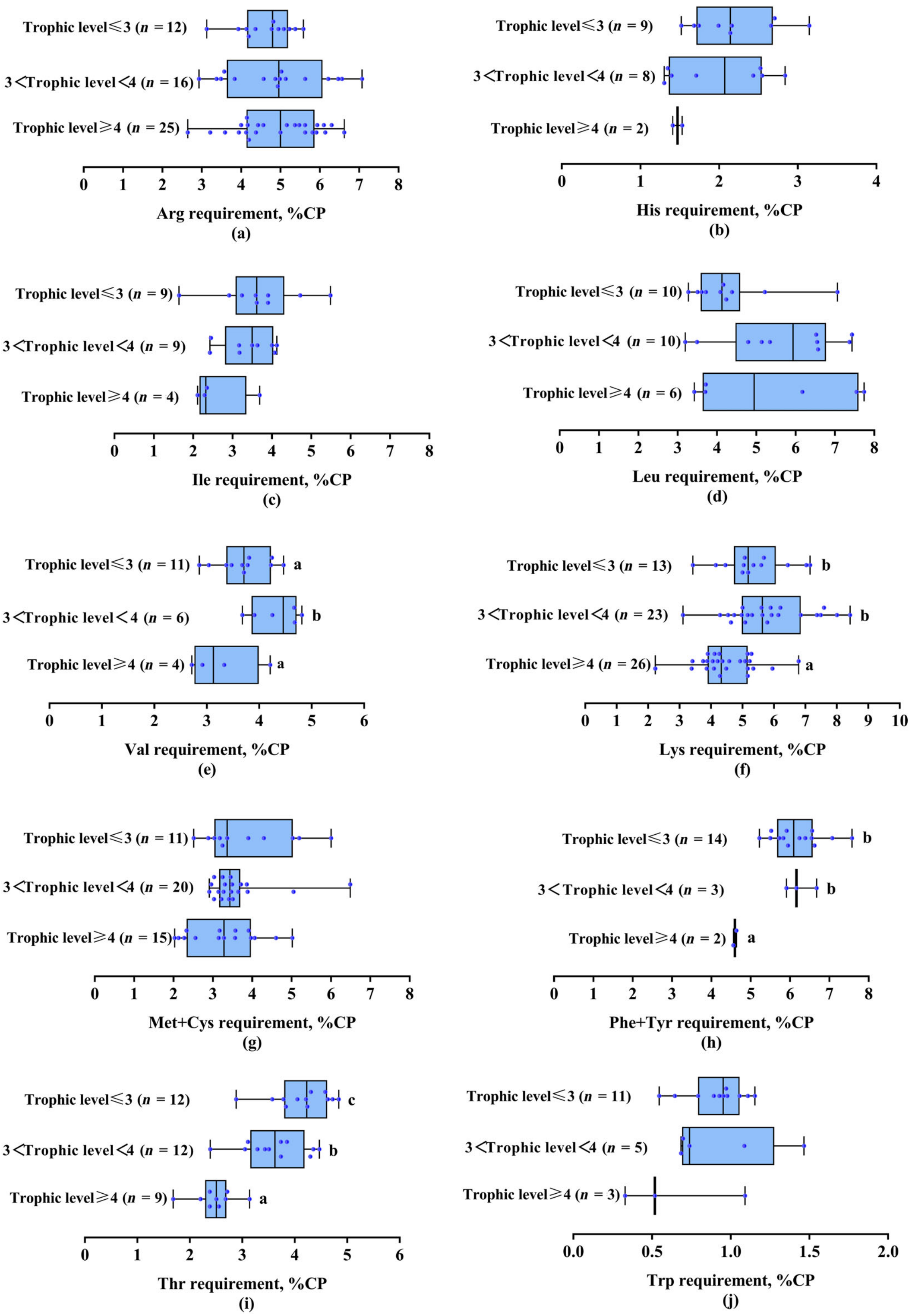

FIGURE 5 Impact of trophic level of fish on the essential amino acid requirements. (a) Arginine (Arg), (b) histidine (His), (c) isoleucine (Ile), (d) leucine (Leu), (e) valine (Val), (f) lysine (Lys), (g) methionine + cystine (Met + Cys), (h) phenylalanine + tyrosine, (i) threonine, (j) tryptophan. *n*, number of studies.

have been observed in other studies, including the study of Met + Cys requirement in yellowtail kingfish[80]; the study of Leu requirement in grouper[81]; the study of Arg requirement in hybrid striped bass and Nile tilapia[75,82,83]; the study of Ile requirement in Lake trout.[84]

In addition, the antagonistic effects among AAs could impact EAA requirement.[6] For instance, the well-known antagonistic interactions include branched-chain amino acids (Leu, Ile and Val) antagonism and Lys–Arg antagonism, where an excess of one (or two) of these EAA increase the requirement for the others.[6,85–87] However, there is currently limited research on the antagonistic effects of AAs on their requirements, and further investigation is needed in the future.

3.3.2 | Trophic level

EAA requirement (% CP) exhibited a negative correlation with fish trophic level, primarily influenced by Lys, Val, Phe + Tyr and Thr requirements (% CP) (Figure 4 and 5). Specifically, fish with high trophic levels (≥4) have significantly lower Lys, Thr and Phe + Tyr requirements (% CP) than those with lower trophic levels. Moreover, the Val requirement for fish with 3 < trophic level <4 was higher than that for fish with either lower or higher trophic levels (Figure 5). The relatively low EAA requirement in high trophic level species (Salmonidae) may be due to their efficient protein retention compared to omnivorous and herbivorous species, resulting in reduced amino acids utilization as an energy source.[7]

3.3.3 | Temperature

A significant positive correlation between EAA requirement and temperature was observed (Figure 4). This is consistent with data for high trophic-level fish species (*Salmonidae*), which demonstrated lower requirements for certain EAA (Lys, Val, Phe + Tyr, Thr) compared to low trophic-level fish species (Figure 5). As poikilotherms, the metabolic rates and energy expenditures of fish and shrimp are influenced by water temperature.[88,89] The fasting heat production values of fish are 5- to 20-fold lower than those of homeothermic terrestrial vertebrates when standardized for weight differences.[88] Therefore, the lower metabolic rate in cold-water fish (mainly *Salmonidae*) may be a possible reason for the lower EAA requirement than others. The potent influence of water temperature on metabolic rate and energy expenditure affects nutrient requirements and growth performance in poikilothermic vertebrates including fish.[88,90,91] One major issue to recognise is that with increasing temperature, there is also an increase in voluntary feed intake overall, without necessarily involving variations in the relative proportions of EAA. In addition, the rise in oxidation and absorption of amino acids at high temperatures may also increase amino acid requirements. DeLong et al.[92] suggested increased amino acid oxidation in chinook salmon at higher water temperature, and Conceição et al.[93] documented that high water temperatures led to increased absorption and depletion rates of amino acids, along with elevated retention efficiency of yolk nutrients in African catfish (*Clarias gariepinus*).

3.3.4 | Feeding strategies

Excess or lack of EAA in the feed may affect feed intake in animals, including fish.[2,94–96] In studies focusing on EAA requirement, researchers used either satiety feeding strategies or restricted feeding strategies. For satiety feeding, an excess or deficiency of EAA in the feed can significantly affect palatability and feed intake,[55,97–99] thereby affecting fish growth. Body WG is a crucial parameter in estimating EAA requirement, and growth differences resulting from varying feed intake can affect the estimated EAA requirement value.[100] In the study by Alam et al.,[98] which investigated the Met requirement of Japanese flounder using experiment diets with Met levels between 1.06% and 4.06% CP. Results showed that low Met inclusion (≤2.26% CP) significantly reduced feed intake. This decreased feed intake affected the growth performance, introducing a variable in the Met requirement estimation. Similar effects were observed in Met requirement studies of yellow catfish and grass carp, where both low- and high-dietary Met inclusion negatively affected feed intake.[55,99] Moreover, Hauler et al.[97] fed Atlantic salmon for 76 days using experimental feeds with 11 different Lys levels (2.26%–5.33% CP) and performed both restricted and satiety feeding strategies. The results showed that compared to restricted feeding, satiety feeding increased feed intake and final weight, but decreased nutrient digestibility (dry matter, protein and energy). In such cases, variations in growth arise not just from different levels of EAA in the feed but also from the intake of unequal nutrients amount, ultimately affecting the estimation value. Restricted feeding can minimize differences in feed intake between treatments.[26,61,65,100,101] According to Chiu et al.,[100] trout fed with satiety and restricted feeding strategies showed different estimates of Arg requirement (3.5% CP vs. 4.2% CP). Nevertheless, when requirements were calculated based on the daily amount of Arginine consumed, the values were similar between the two feeding methods (7.6 mg vs. 7.5 mg).

3.3.5 | Diet types and protein sources

As mentioned earlier, the quality and composition of the control or basal diet should be sufficiently deficient in the target EAA under consideration. This implies appropriate choice of protein sources which are chemically well defined. Nguyen and Davis[60] indicated that purified diets led to a lower Met requirement estimate compared to practical diets due to the high-nutrient digestibility in purified diets. Accordingly, in rainbow trout, Kim et al.[102] estimated a Lys requirement of 3.7% CP using a purified diet, while Lee et al.[103] reported a Lys requirement of 5.1% CP using a practical diet. In addition, the Arg requirement of Nile tilapia using purified and practical diets was estimated as 4.2% CP and 5.1% CP, respectively, based on the $\%MaxG_n$ re-estimation.[82,83] Peres and Oliva-Teles[32] and Zhou et al.[79] suggested that CAAs added in purified diets appear to be utilized less efficiently than EAA of intact protein source. This inefficient CAAs utilization could lead to an overestimation of requirements. CAAs might be absorbed more rapidly and/or earlier in the gastrointestinal tract than protein/peptide-bound AAs.[36,104,105] This faster and/or earlier absorption may result in a greater proportion of the CAAs being catabolized and not used for protein biosynthesis.[104,106] However, several studies indicated that CAAs can be as efficiently utilized as those from

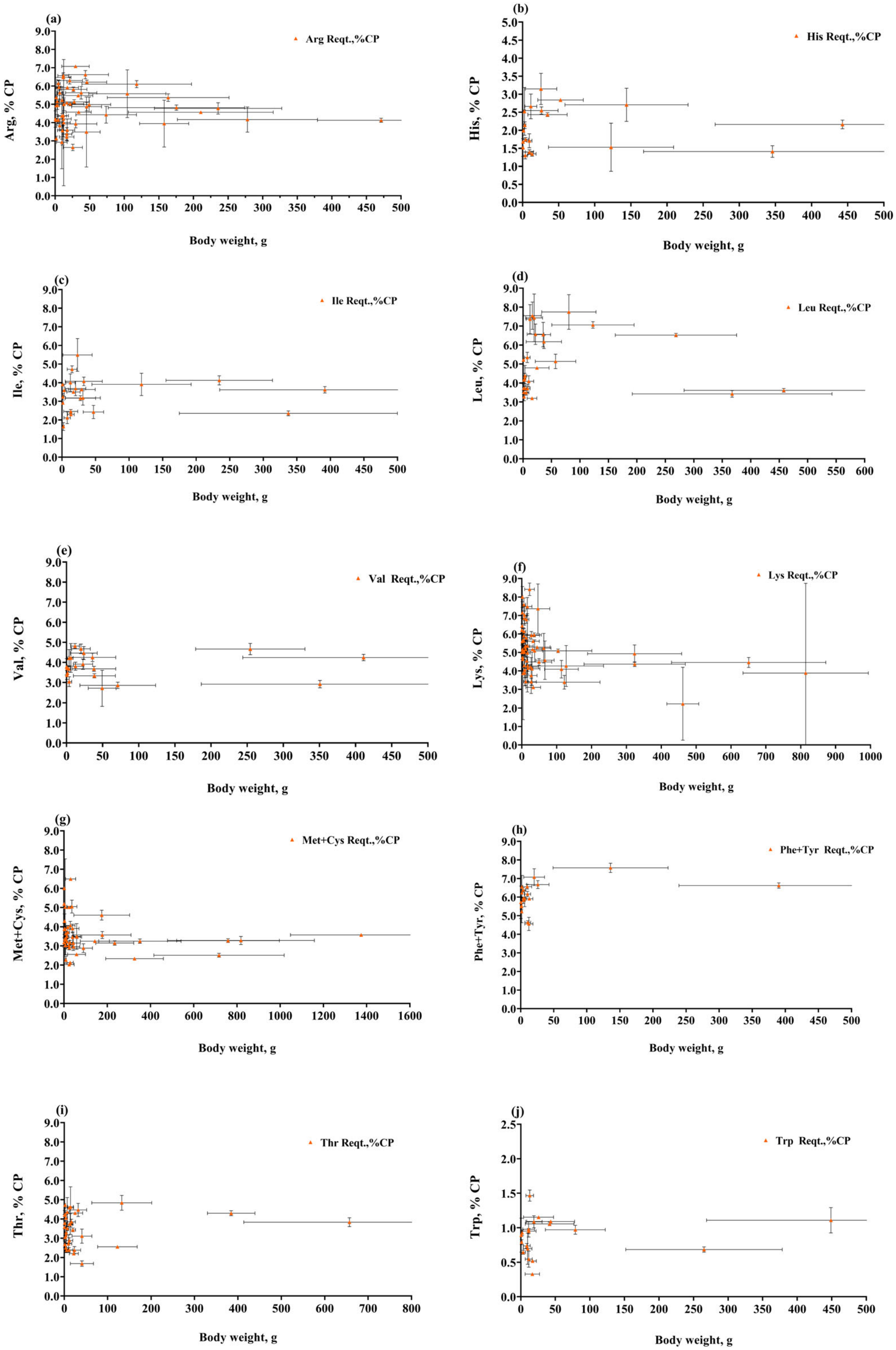

FIGURE 6 Distribution of fish body size (mean ± SD) and essential amino acid concentration (% of crude protein [% CP]; mean ± SD) tested in different studies in the dataset. (a) Arginine (Arg), (b) histidine (His), (c) isoleucine (Ile), (d) leucine (Leu), (e) valine (Val), (f) lysine (Lys), (g) methionine + cystine (Met + Cys), (h) phenylalanine + tyrosine (Phe + Tyr), (i) threonine (Thr), (j) tryptophan (Trp).

intact protein sources to meet fish EAA requirements.[107–110] Some studies have provided convincing evidence of improved metabolic utilization of CAAs when fed more frequently daily.[106,111] To address the issues of faster CAA absorption and leaching, techniques such as encapsulation, precoating and polymerization are employed to reduce the solubility and absorption rate. It is advisable to improve the assimilation of CAAs by fish and crustaceans, especially considering their slow feeding habits, by using effective feed binders, attractants and by increasing the daily feeding frequency at the farm level.[6]

Expressing estimates on a digestible basis will reduce variability and ensure precise comparison of values among species.[7] However, in most studies on EAA requirement estimation, digestible protein or digestible AA was not considered. Just a few studies have suggested estimating EAA requirements based on digestible level.[49,61,112,113] Recommendations for future research on EAA requirement should

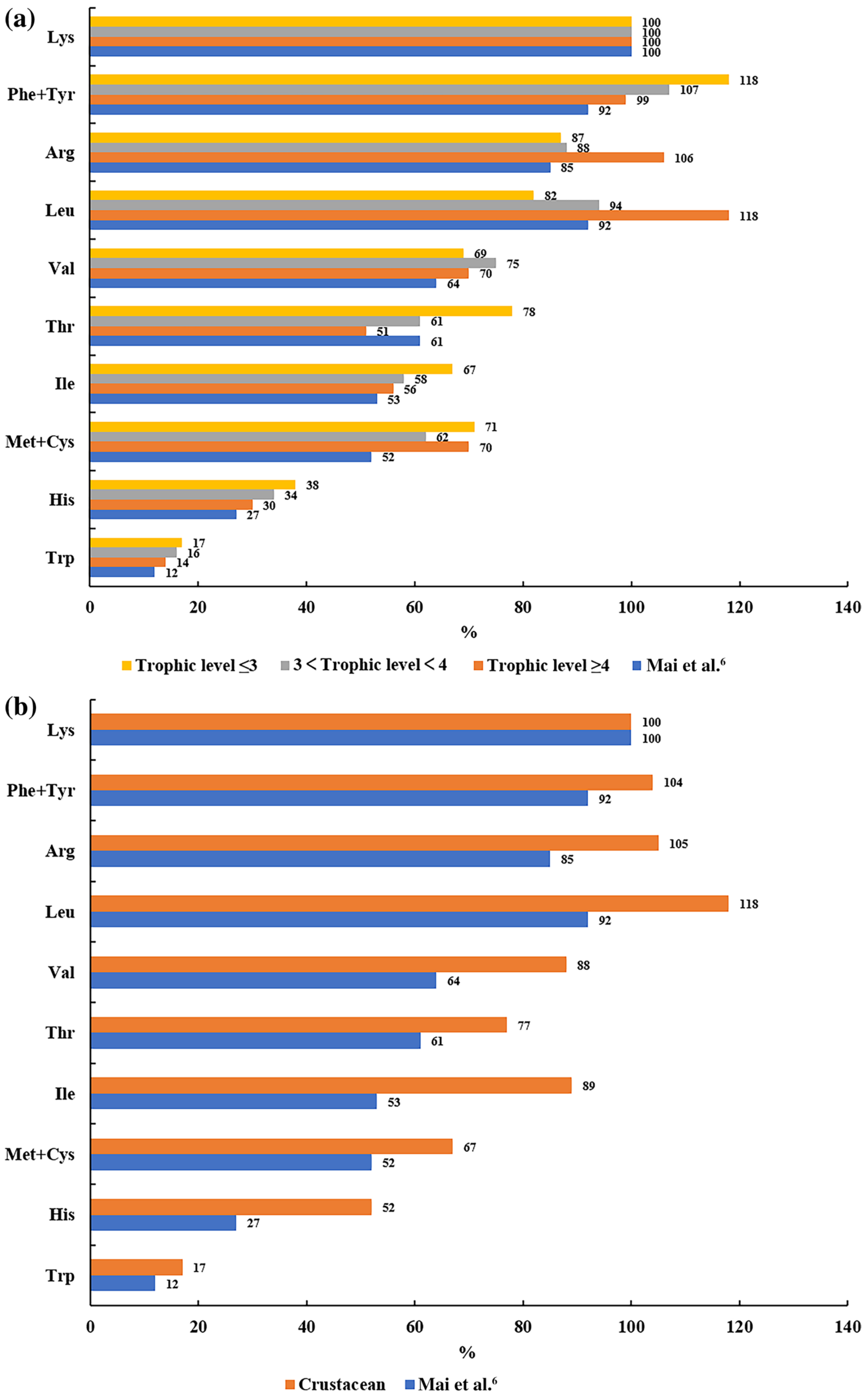

FIGURE 7 Ideal essential amino acid patterns of fish from different trophic level and crustaceans; for comparison, data from Mai et al.[6] is also provided. (a) Fish, (b) Crustaceans. Arg, arginine; Leu, leucine; Lys, lysine; Phe + Tyr, phenylalanine + tyrosine; Thr, threonine; Val, valine; Ile, isoleucine; Met + Cys, methionine + cystine; His, histidine; Trp, tryptophan.

emphasize obtaining more accurate estimates based on the use of digestible proteins.

3.3.6 | Body weight

Suggestions have been made that body weight of fish may influence protein and EAA requirement.[6,7,29,53] Such changes in EAA requirement of fish at different life stages could be related to potential differences in the efficiency of dietary protein utilization.[114–116] In this meta-analysis, the influence of body weight on EAA requirement was eliminated by standardizing WG and expressing it as dietary protein concentration (% CP). Therefore, no clear relationship between body weight and EAA requirement could be observed from the scatter charts (Figure 6). In line with this, Oliva-Teles et al.[117] performed a meta-analysis of dietary protein requirement in fish and did not observe a significant effect of body weight and dietary protein requirements. We must recognize that nearly all studies on EAA requirement have been undertaken with juvenile animals. Within our dataset, only 10% of studies using fish body weight ≥100 g: Arg, 5/53; His, 2/19; Ile, 3/22; Leu, 3/26; Val, 3/21; Lys, 5/62; Met+Cys, 7/46; Phe + Tyr, 1/19; Thr, 2/33; Trp, 2/19.

3.4 | Ideal protein concept and low-protein diet formulation for sustainable aquaculture

A lower dietary protein level can be achieved by including high-quality protein sources and by supplying the limiting AAs. This is an effective strategy to reduce dietary protein cost and nitrogen excretion by animals.[3,118] The concept of ‘ideal protein’ is defined as the EAA profile that precisely meets the requirement of the animal without any amino acid imbalance.[6] The application of the ideal EAA profile is crucial in formulating low-protein diet to optimize protein utilization efficiency and minimize nitrogen wastes in the environment. Previous studies have focused only on a limited number of EAA, such as Lys, Met and Arg. We used the re-estimated 10 EAA requirement values from this meta-analysis to establish the ideal EAA patterns. In Figure 7a,b, the ideal EAA profiles for fish and crustaceans, estimated by the meta-analysis of data from 355 studies in fish and 37 in crustaceans, are illustrated as the ratio of the nine EAA to Lys. In addition, a few studies have estimated the optimal EAA/NEAA ratio in the diets,[8,10] with recommended ratios of 1.0, 1.1 and 1.33 for European seabass, gilthead sea bream and rainbow trout, respectively.[10,119,120] Moreover, based on the muscle protein-bound AA profiles from 11 different species, Mclean et al.[15] revealed the EAA/NEAA (IAA/DAA) ratio to be in a very close range between 0.98 to 1.03.

3.5 | Practical implications

Considering the limited availability and price volatility of high-quality fish meals from capture fisheries, it is now well recognized that relying on fish meals as the major protein source in feeds for farmed fish and shrimp is not a sustainable practice.[1] Regarding the use of plant protein sources as alternatives to fish meal, there are still challenges, including issues with the amino acid profiles and the presence of anti-nutritional factors, like phytic acid, trypsin inhibitor, glycinin, β-conglycinin, gossypol and others. The trend over the years shows a decreasing reliance on fish meal for aquafeeds development.[121–123] This has also led to questions on the over dependence of aquaculture on terrestrial agricultural sources as protein sources for fish feed.[124–128] Such needed diversification of protein sources for the large number of cultured aquatic species depends on at least three factors: (1) the amino acid profile, protein bioavailability and amino acid sources; (2) the quantity and balance of amino acids; and (3) optimal dietary protein (amino acids) to digestible energy (DE) ratios.

Minimizing the contribution of dietary proteins/amino acids to meet the energy demands of farmed fish has been an issue dealt with seriously over the past decades. Energy metabolism in animals is closely related to the efficiency of amino acid utilization for protein synthesis. The utilization efficiency of dietary energy for whole-body growth, protein or fat deposition, can vary significantly depend on the levels and types of dietary macronutrients (carbohydrates, proteins and fats) in land animals[128] as well as in fish.[88] Expression of data on EAA requirement per unit DE in fish, compared to that of a typical terrestrial carnivore like kitten, shows that fish generally have high EAA needs per unit DE. Given that net energy (NE) systems are increasingly applied in farm animals, including fish, it might also be worth expressing data on EAA requirement as digestible AA per unit NE. As seen in Figure 6, the body weight range of fish used in the majority of EAA requirements studies corresponds to young, fast-growing animals, where the maintenance component can be small compared to larger animals. Currently, there is limited information available on the EAA requirement for maintenance, which is restricted to a small number of species.[51,85,129–131] The large size range of aquatic animals throughout their life cycle (from a few mg to kg) involves body proteins turnover, amino acid losses from skin, exuviation (shrimp), endogenous loss from the gut and synthesis of non-protein nitrogenous substances besides branchial/urinary losses. There is indeed a need to quantify the relative contribution of EAA requirement for maintenance.

4 | CONCLUSIONS

A meta-analysis was conducted, incorporating dose–response studies on the dietary EAA requirement of fish and crustaceans from over 358 studies covering 77 species. The analysis also investigated variations in EAA requirement among different trophic levels. Water temperature and trophic level are important factors affecting the EAA requirement of fish. Water temperature shows a positive correlation with EAA requirements for fish, while trophic level exhibits a negative correlation. The range of EAA additions in the experimental diets affects the estimation of EAA requirement, emphasizing the importance of an appropriate range and gradient of EAA addition for accurate estimations. In addition, the current research predominantly focuses on juvenile fish (90%), indicating a need for increasing emphasis on large-size fish in the future studies. Recommendation for future research include a focus on exploring the relationship between animal energy metabolism and the efficiency of amino acid utilization, as well as the use of amino acids for maintenance and growth allocation based on low-protein diet formulation.

AUTHOR CONTRIBUTIONS

Min Xue: Project administration; supervision; writing – review and editing; writing – original draft. **Shujuan Xing:** Methodology; data curation; writing – original draft; writing – review and editing. **Xiaofang Liang:** Data curation; writing – original draft; writing – review and editing. **Xiaoran Zhang:** Data curation. **Aires Oliva-Teles:** Writing – review and editing. **Helena Peres:** Writing – review and editing; methodology. **Min Li:** Data curation. **Hao Wang:** Data curation. **Kangsen Mai:** Writing – review and editing. **Sadasivam J. Kaushik:** Writing – review and editing; conceptualization; methodology.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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