Re-evaluation of essential amino acids in fish by a meta-analytical approach

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pelo júri, e só essas, foram efetuadas.

O Presidente do Júri,

Porto, ______/______/_________

MSC

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RESUMO

O presente trabalho consistiu numa avaliação meta-analítica da informação disponível nos estudos dose-resposta que visam estimar valores de requerimento dos aminoácidos essenciais na dieta de peixes produzidos em aquacultura. Esta avaliação envolveu um total de 177 tratamentos experimentais, distribuídos por 121 artigos publicados, que abrangem 45 espécies de peixes. O ganho de peso, o coeficiente térmico de crescimento e a retenção azotada.foram os critérios de resposta escolhidos para estimar os valores de requerimento. Para o tratamento estatístico dos dados recolhidos foi utilizado um de dois modelos: um modelo cinético de saturação com 4 parâmetros e uma regressão polinomial de segunda ordem. A análise efectuada revelou a existência de uma homogeneidade significativa na informação recolhida nos estudos dose-resposta, nomeadamente para a arginina, histidina, isoleucina, leucina, lisina, metionina, fenilalanina e triptofano. O modelo cinético de saturação com 4 parâmetros obteve um bom ajuste aos dados provenientes de estudos dose-resposta para a lisina, arginina, leucina, isoleucina e fenilalanina, considerando o ganho de peso como critério de resposta. Os valores de requerimento obtidos para a histidina, metionina e triptofano foram estimados por via de uma regressão polinomial de segunda ordem, na qual a curva descendente permite inferir que elevados níveis destes aminoácidos podem provocar uma redução do crescimento do peixe. A informação disponível nos estudos dose-resposta para a treonina e valina, incluídos nesta avaliação, não permitiu estimar qualquer valor de requerimento para os diferentes critérios de resposta considerados.

Palavras-chave: Estudos dose-resposta; aminoácidos essenciais; avaliação meta-analítica; valor das necessidades.

ABSTRACT

A meta-analytical evaluation of available data on dose-response to dietary essential amino acids (EAA) in fish from over 177 feeding trials reported in 121 published studies covering about 45 fish species was performed. Weight gain (WG), thermal growth coefficient (TGC) and nitrogen retention (NR) were selected as outcomes to evaluate the optimum requirement value for each EAA. A four parameter saturation kinetic model (SKM – 4 parameter) or a second order polynomial regression analysis (SOPR) were used to model the data sets. The present analysis showed that there exists considerable homogeneity of several data on EAA requirement of fish species included in this study, namely for arginine (Arg), histidine (His), isoleucine (Ile), leucine (Leu), lysine (Lys), methionine (Met), phenylalanine (Phe) and tryptophan (Trp). The SKM – 4 parameter model adjusted well to the compiled data from Lys, Arg, Leu, Ile and Phe dose-response studies, when WG was used as an outcome. Dietary requirement values estimated for His, Met and Trp were achieved through a quadratic model (SOPR), which means that high levels of these EAA in the diet are causing a growth reduction in fish. Available data on valine (Val) and threonine (Thr) from dose-response studies didn't allow the estimation of a requirement value for any of the response criteria used.

Keywords: Dose-response studies; EAA; meta-analytical evaluation; requirement value.

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ABBREVIATIONS

AA – Amino acid

Arg – Arginine

BCAA – Branched chain amino acid

BL – Broken-line regression

BW – Brackish water

CAA – Crystalline amino acid

CL – Crude lipid

CP – Crude protein

Cys - Cystine

EAA – Essential amino acid

FAO – Food and Agriculture Organization

FM – Fish meal

FW - Freshwater

His – Histidine

Ile - Isoleucine

Leu – Leucine

Met - Methionine

NR – Nitrogen retention

Phe - Phenylalanine

SKM – Saturation kinetic model

SOPR – Second order polynomial regression

SW - Seawater

TGC – Thermal growth coefficient

Thr - Threonine

Trp - Tryptophan

TSAA – Total sulfur amino acid

Tyr – Tyrosine

Val – Valine

WG – Weight gain

1 – Introduction

1.1 – Global aquaculture perspective

Over the years, world population has been growing as well as the demand for fishery products, which rapidly begun to be scarce to meet the need. For that reason, aquaculture production has developed, becoming a major global industry and an important source of income and food in many countries. The preference for healthier foods, contributed as well to an increment of fish farming industry (FAO, 2012; NRC, 2011).

For the last three decades (1980-2010), global aquaculture production increased almost 12 times, at an average annual rate of 8.8 percent, providing now about one half of the fish and shellfish that is directly consumed by humans. In the course of a half a century, aquaculture has expanded from being almost negligible to fully comparable with capture production with regard to feeding people in the world (Figure 1). It is expected that the aquaculture will continue to grow (FAO, 2012).

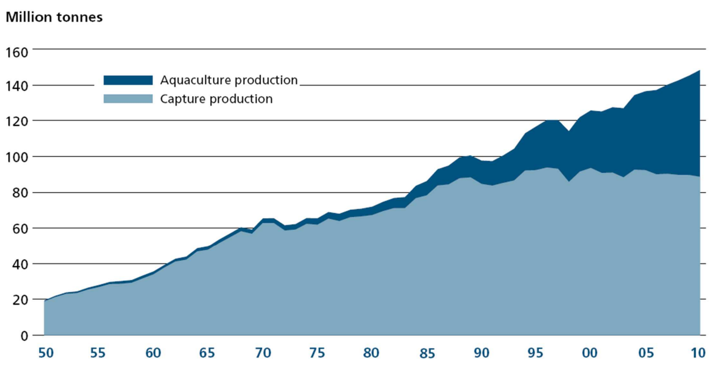

Figure 1. World capture fisheries and aquaculture production (Source: The State of World Fisheries and Aquaculture – Part 1 – World Review of Fisheries and Aquaculture, FAO, 2012)

Almost 600 aquatic species are raised in captivity worldwide (about 190 countries) for production in farming systems and facilities of varying input intensities and technological sophistication, using freshwater (FW), brackish water (BW) and seawater (SW). Fish farming dominates aquaculture production with FW fishes representing 56.4 percent (33.7 million tonnes), diadromous fishes about 6.0 percent (3.6 million tonnes) and SW fishes about 3.1 percent (1.8 million tonnes) of total production. Figure 2 summarizes the production volumes of the fish major categories.

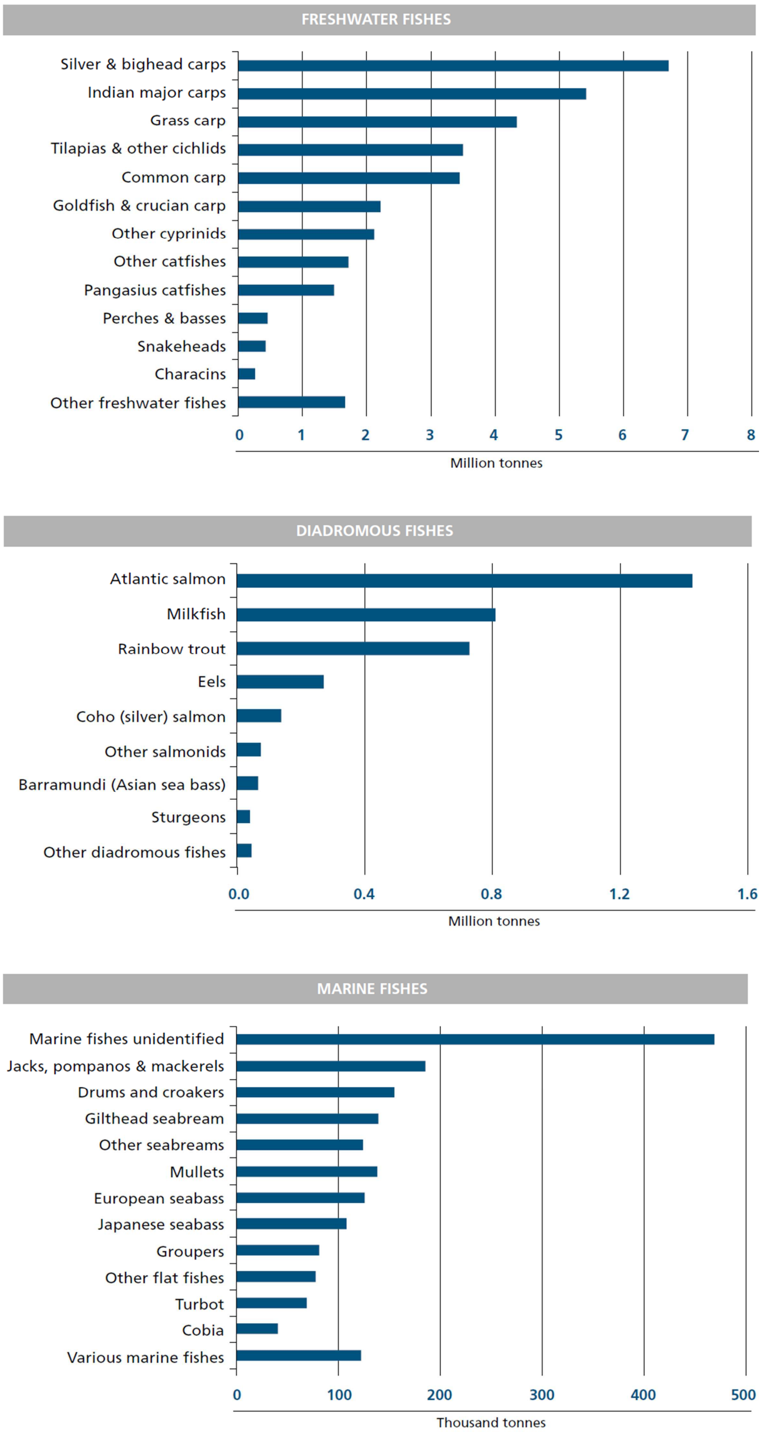

Figure 2. Production of major fish species or fish species group from aquaculture in 2010 (Source: The State of World Fisheries and Aquaculture – Part 1 – World Review of Fisheries and Aquaculture, FAO, 2012)

Asia accounted for 89 percent of world aquaculture production by volume in 2010, and this was dominated by the contribution of China, that remains the major producer, which accounted for more than 60 percent of world aquaculture production by volume in 2010 (about 36.7 million tonnes) (FAO, 2012).

1.2 – Feed costs in aquaculture

According to Food and Agriculture Organization (FAO) (2012), "aquaculture is the farming of aquatic organisms including fish, molluscs, crustaceans and aquatic plants. Farming involves some form of intervention in the rearing process in order to enhance production, such as regular stocking, feeding, protection from predators, etc." These interventions imply costs, mainly in intensive aquaculture production systems. In contrast to extensive and semi-intensive farming systems where the cultured species obtains almost all the nutrients they need from naturally available pond food organisms, fish maintained under intensive culture conditions are entirely dependent on the external provision of a nutritionally "complete" diet during their culture cycle (Ahmed and Khan, 2004b). It is estimated that almost 50 percent of global aquaculture production is from species that depend on feed inputs (NRC, 2011).

Considering that intensive aquaculture feed expenses generally account for 40-60% of the total production costs, its reduction constitutes a prime subject for research (Ahmed, 2012; NRC, 2011). Thus, development of nutritious, environmental friendly and cost-effective diets is of utmost importance to ensure the success and sustainability of a fish farming enterprise (Ahmed, 2009; Marcouli et al., 2006; NRC, 2011). The primary reason for the high cost of feed is the high percentage of crude protein (CP) (35-55 percent) that usually is provided by high-quality fish meal (FM) (Ahmed and Khan, 2004b; Luo et al., 2006). FM is very expensive which causes the demand for cheaper protein sources of known biological values (Drakeford and Pascoe, 2008; Gatlin et al., 2007; Yang et al., 2011). Furthermore, in recent years, the availability of FM has decreased and this situation is not expected to recover in the near future. As a result, feed manufacturers have become increasingly interested in reducing the dependence on traditional ingredients, particularly FM, for use in marine feeds (Drakeford and Pascoe, 2008; Gatlin et al., 2007). Thus, several attempts have been made in exploring the possibility of replacing FM with less expensive and worldwide available plant feedstuffs (Drakeford and Pascoe, 2008; Gatlin et al., 2007). Soybean meal and cereal grain are generally utilized to replace all or a portion of FM for low cost and economical diet formulation for fish (Gatlin et al., 2007). However, lower protein content (Kaushik and Hemre, 2010), dietary essential amino acids deficiencies/ unbalance (such as lysine and methionine) (He et al, 2013; Niu et al., 2013; Zhang et al., 2008), lower digestibility of the diet (mainly of the carbohydrates) (Tulli and Tibaldi, 2001) and endogenous anti-nutritional factors (Francis et al., 2001) was reported to be the major problems of using plant protein sources as the main dietary component, thus reducing fish growth and feed utilization. It is expected that development of low or non-FM based diets, capable of supporting adequate growth rates necessary for a profitable production of farmed fish, will require the combination of different plant ingredients and eventual supplementation with essential amino acids (EAA) to meet the required EAA profile of the fish (Kaushik and Hemre, 2010; NRC, 2011). Therefore, information on requirement of dietary protein and EAA of fish species is a pre-requisite for identifying alternative sources of protein in order to formulate more efficient and economical diets.

1.3 – Protein requirements in fish feeds

Protein, providing the body with energy and participating in the synthesis of hormones, antibodies, enzymes and tissues, plays an essential role in growth and development of fish and is considered one of the most important nutrient in fish feeds (Cao et al, 2012).

In the late 1950s, Halver and their collaborators were the first investigators to do some research about protein and amino acid requirements of fish, in Chinook salmon (*Oncorhynchus tshawytscha*). Since then, numerous studies with other fish species have been carried out, and the literature is predicted to continue to grow.

Dietary crude protein (CP) concept, based on the assumption that proteins contain 16% N (CP = N x 6.25), has been largely used by nutritionists and feed manufacturers over the years but recent research (Mariotti et al., 2008; Helland et al., 2010) found some failures in using a fixed conversion factor. Nitrogenous compounds in feeds do not only involve amino acids (AAs) but also include non-protein nitrogenous components. Since the requirement for protein is influenced by both components, it does not necessarily represent the animal's metabolic AAs requirements for growth. Hence, the sum of individual AAs in ingredients only seems to account about 80-90% (Mariotti et al, 2008) or even 70% (Helland et al, 2010) of the true protein content of certain protein-rich-ingredients, such as FM.

All dietary proteins sources are not identical in their nutritive value, as their AA profile and digestibility differs markedly (NRC, 1993). It is important to realize that protein requirement provides a simple basis for formulation of practical feeds, particularly when there's a lack of information about EAA requirements and optimal levels of lipid and carbohydrate as energy sources are not well defined for a given species. Considering the wide variety of feedstuffs that are used nowadays in the formulation of aquafeeds, actual estimates of protein requirements should be considered highly approximate (NRC, 2011).

Fish generally have considerably higher protein requirement (expressed in % of dietary protein content) than those of terrestrial homeothermic animals (Bowen, 1987; NRC, 2011). This is mainly due to differences in energy requirements between both groups of animals. The basal energy needs of fish are considered lower than those of homeothermic animals, due to aquatic mode of life, poikilothermy and ammoniotelism (Kaushik and Seiliez, 2010). Based on comparisons of protein efficiency ratios (PER) in a number of farmed animals, it becomes clear that fish and terrestrial animals differ only in relative protein concentration in the diet required for achieving maximum growth rate, as the protein requirements in absolute terms are similar (grams of protein intake per unit of weight or per unit of weight gain) (Bowen, 1987; Cowey and Luquet, 1983). As explain above, the differences in relative protein concentration in the diet are due to the lower energy requirement of fish (Bowen, 1987; Kaushik and Seiliez, 2010).

According to Oliva-Teles et al. (2011), carnivorous fish species have higher protein requirement than omnivorous species, which may either be related to natural feeding habits or to higher growth rate potential. Comparatively to salmonids, most carnivorous marine fish species have higher protein requirements and lower protein retention (as percentage of intake). The explanation for this difference is not well known yet, and it may be related either to nutritional specificities or to an inadequacy of diet formulation (Tibaldi and Kaushik, 2005).

Due to high cost of protein compared to that of other energy-yielding nutrients, such as carbohydrates and lipids, and also due to the ammonia excretion associated with the catabolism of excess amino acids, the use of protein as dietary energy source is considered undesirable (NRC, 2011). Because of this, some attempts has been made to reduce dietary amino acid catabolism, an effect commonly referred to as "protein-sparing". This process, in which the body uses energy from sources other than protein, is a strong argument for using digestible protein/digestible energy ratio (DP/DE) as a more rational way of expressing protein requirement than the traditional dietary "crude protein" requirement (percentage CP of diet) (NRC, 2011).

A decrease in DP/DE ratio attained either by reducing the dietary protein level or by increasing the energy level has been reported to be extremely efficient in improving protein (nitrogen) utilization and reducing nitrogenous loses (NRC, 2011). In general, increasing lipid content of the diet can help to reduce dietary protein (amino acid) catabolism, as protein sparing by dietary lipids has been described in a number of species. However, there is also evidence that lipid supplementation can have a limited impact on efficiency of protein utilization under certain conditions (Azevedo et al., 2004), or even a negative effect, caused by undesired levels of lipid deposition (Tibbetts et al., 2005), which may have long-term implications regarding nutritional value, organoleptic properties, transformation yield and storage time of fish carcass. Most fish species, particularly carnivorous fish, have a limited ability to utilize carbohydrates efficiently for energy purposes and high dietary levels of these compounds lead to prolonged post-prandial hyperglycemia (Enes et al., 2011).

Values reported in the literature suggest that protein requirements, as a proportion of the diet mass, decrease as fish increase in size (NRC, 2011). However, despite requiring lower dietary protein concentrations, larger fish frequently reveals lower nitrogen retention efficiency than do smaller fish and/or juvenile stages, thus optimum dietary DP/DE appears to be different according to growth stage (Azevedo et al., 2005; Dumas et al., 2007).

Generally, all feeding and growth functions increase as water temperature rises. However, up to now no convicting evidence exists to show that protein requirement or optimal DP/DE ratio is affected by water temperature or other abiotic factors (e.g., salinity), at least within a “normal” range of conditions (NRC, 2011).

1.4 – Amino acids requirements of fish

Beside their role as building blocks of protein, AAs also occupy a central position in cellular metabolism since almost all biochemical reactions are catalysed by enzymes composed of amino acid. AAs are crucial for carbohydrate and lipid metabolism, for the biosynthesis of structural molecules and various important compounds (ie. adrenalin, thyroxine, melanin, histamine, porphyrins, choline, folic acid and nicotinic acid, bile salts etc), and as a metabolic source of energy or fuel (Tacon, 1987; NRC, 2011).

Twenty primary AAs are used by cells in protein biosynthesis. For nutritional purposes, primary amino acids may be divided into two groups: EAA, and non-essential amino acids (NEAA). The AAs that cannot be synthesized natively by the animal’s body or at a rate sufficient to meet the physiological needs of the growing animal are referred to as EAAs. Thus, these EAAs must be supplied in the diet. In contrast, NEAAs are those AAs that can be synthesized in the animal’s body from precursors and consequently do not have to be supplied in a ready-made form in the diet (Tacon, 1987, NRC, 2011). The essentially of various AAs for fish has been determined either by feeding trials involving the successive deletion of each AA in the diet or by isotopic-labeling studies (Wilson, 1989).

From available data, it seems that all fish require the same 10 EAAs. These include arginine (Arg), histidine (His), isoleucine (Ile), leucine (Leu), lysine (Lys), methionine (Met), phenylalanine (Phe), threonine (Thr), tryptophane (Trp) and valine (Val). From a feed formulation viewpoint, it is important to know that tyrosine (Tyr) is synthesized from Phe (EAA) and cystine (Cys) is synthesized from Met (EAA). For that reason, these two AAs are named semiessential or conditionally essential. Therefore, the dietary requirement for these EAA is dependent on the dietary concentration of the corresponding Cys and Tyr precursors. These amino acids are frequently included in estimates of requirements (e.g. total sulfur amino acid requirement – TSAA) (NRC, 2011).

Along with EAAs, fish have a nonspecific requirement for a source of amino groups (also known as non-specific nitrogen) for the synthesis of NEAAs. Although the NEAAs are not dietary essential nutrients, they perform numerous important physiological functions at the cellular or metabolic level, being named dietary non-essential amino acids only because the body tissues are able to synthesize them on demand from available precursors (Tacon, 1987, NRC, 2011).

1.5 – Essential Amino Acids – Roles and Deficiency Signs

1.5.1 – Arginine

Arg has been reported to be one of the limiting amino acids in plant protein sources such as maize, sesame meal and zein (Abidi and Khan, 2009; Mai et al. 1994). Several studies have established that Arg is of utmost importance in the overall activity of the immune system of fish (Buentello et al., 2007; Lall, 2000), being of physiological relevance in diseased-animals and in stress situations in which there is a depletion of Arg level in the blood. Its function is not only being a building block for proteins but also plays an important role as a precursor of nitric oxide, an effector molecule in inflammatory and immunological tissue, and polyamines, which are required for DNA synthesis and cell proliferation and differentiation (Narita et al. 1995; Wan et al, 2006). Moreover, Arg also serves as a potent stimulant of insulin and growth hormone, possibly due to its roles in anabolic processes (Wan et al., 2006). According to Mommsen et al (2001), Arg is a much stronger insulinotropin than glucose in fishes, increasing the titers of insulin, IGF-1, growth hormone, glucagon and glucagon-like peptide-1.

1.5.2 – Histidine

His, an EAA found abundantly in hemoglobin, plays a key role in growth, tissue formation and repair, being also the direct precursor of histamine which arise from controlled and uncontrolled pathways and take part in allergic and inflammatory reactions. It is also an important source of carbon atoms in the synthesis of purines (Ahmed and Khan, 2005b; NRC; 2011). Moreover, His and related components (imidazoles) may play important biochemical roles, such as in osmoregulation process, muscle pH buffering and detoxification of reactive carbonyl species (Waagbo et al., 2010; Ahmed, 2013), as well as in the maintenance of myelin sheaths that act as protectors for nerve cells (Ahmed and Khan, 2005b). There is some evidence that His mitigates cataract development in Atlantic salmon smolts, but the exact mechanism behind this process is not completely understood (Waagbo et al., 2010).

1.5.3 – Lysine

Lys is the EAA found in the highest concentration in the carcass of many fish species and is also found in high concentration in ingredients such as FM and blood meal (Wilson and Cowey, 1985; NRC, 1993). However, in feeds formulated with high levels of plant protein ingredients, especially CG byproducts, such as maize gluten meal and wheat gluten, Lys is found in low concentrations (Gatlin et al., 2007; Kaushik and Seiliez, 2010). Consequently, Lys is commonly the first limiting amino acid in feeds, particularly those formulated with high levels of plant protein ingredients or with protein ingredients processed under harsh conditions (He et al., 2013; NRC, 2011).

Many protein sources experience some form of processing before being incorporated to feeds. During processing, proteins can be exposed to heat, both wet and dry heat and pressure or alkali. Moughan and Rutherfurd (1996) reported that when feedstuffs are subjected to these kind of conditions certain AAs can react with other compounds present in the food resulting in nutritionally unavailable compounds. Due to the reactive nature of its ε-amino group, Lys is particularly susceptible to this type of modification and can react with compounds, especially reducing sugars, which may be present in a feedstuff, resulting in production of Maillard reaction, and reducing its availability to the animal. Maillard compounds are not acid stable and during conventional AA analysis a proportion of these compounds revert back to Lys which leads to an overestimation (as much as 100%) of the amount of available Lys present in the feedstuff.

In addition to Lys being essential for protein synthesis, it works along with Met as a precursor of carnitine, which carries long chain fatty acids into the mitochondria for βoxidation of lipids (Bicudo et al, 2009; Walton et al, 1984b). Lys also affects collagen synthesis, because hydroxylysine with hydroxyproline, products of Lys and proline metabolism, are the main constituents of collagen (Bicudo et al, 2009; Sandell and Daniel, 1988).

1.5.4 - Methionine

Met is one of the first limiting EAA in plant feedstuffs for aquaculture species (Kaushik and Seiliez, 2010; Niu et al., 2013) and is required by terrestrial vertebrates, as well as fish, for normal growth and metabolic functions (Bae et al., 2011; Moon and Gatlin, 1991). In addition to its role as a precursor in protein synthesis, this sulfur-containing amino acid participates in other metabolic reactions, including the production of S-adenosylmethionine (SAM). SAM itself is involved in the synthesis of creatine, epinephrine, melatonin, and the polyamines spermine and spermidine, among several other substances (Brosnan and Brosnan, 2006b; NRC, 2011). Dietary Cys, a NEAA, has a Met sparing effect, as Cys is synthetized from Met. In the absence of dietary Cys, it can only be synthesized from Met so if Cys is present in the diet, part of Met may be spared from Cys synthesis. Thus, the requirement for TSAA can be met by either Met alone or the proper mixture of Met and Cys. In most animals, Cys can spare as much as 40-60% of the Met requirement. Therefore, it is important to consider the dietary Cys content to quantify the Met requirement of the cultured species for maximum growth and efficient feed utilization (Luo et al., 2005; Moon and Gatlin,1991; Niu et al, 2013).

1.5.5 - Phenyalanine

Phe is an aromatic amino acid and its requirement is influenced by the level of Tyr in the diet. Phe is precursor of Tyr, which in turn is a precursor of epinephrine and norepinephrine. Tyr is also a precursor of the thyroid hormones, triiodothyronine and thyroxine (Ahmed, 2009; Borlongan, 1992). Tyr is non-essential under conditions where ample Phe is taken up; however, if Phe is available in the diet at low or below minimal requirement levels, Tyr can become essential. Therefore, Phe requirement depends upon the amount of Tyr in the diet and the requirement varies with different fish species (NRC, 1993, 2011). There’s evidence that Phe is a precursor of many substances of biochemical importance other than protein, being preferentially used for the synthesis of other compounds of metabolic importance, such as hormones and neurotransmitters (Ahmed, 2009; Owen et al., 1999).

1.5.6 – Threonine

After Lys and Met, Thr is usually one of the most limiting amino acids in practical ingredients used for diet formulation (Ahmed et al., 2004) and revealed to be potentially marginal or limiting in practical diet formulations for sea bass, especially when plant protein sources such as maize or wheat gluten are used to replace substantial amounts of dietary FM protein (Tibaldi and Tulli, 1999). Thr stimulates the immune system and promotes thymus growth and activity, and also is essential for the formation of collagen and elastin. It plays an important role as a lipotropic agent, helping to prevent fat build-up in the liver (Ahmed, 2007). For being abundant in mucins, Thr is also useful for prevention of intestinal disorders and indigestion (Ahmed, 2007; NRC, 2011). Thus, the availability of Thr may limit intestinal mucin synthesis and therefore, reduce the gut barrier function, compromising mucus production mainly during stressful conditions (NRC, 2011). This emphasizes the importance of Thr for maintaining intestinal integrity, which is essential for regulating dietary amino acid supply to the whole body (Ahmed, 2007).

1.5.7 – Tryptophan

In addition to Lys, Met and Thr, Trp is one of the most limiting amino acids in plant proteins ingredients such as maize gluten meal, wheat germ meal, and soybean meal (Abidi and Khan, 2010b; Ahmed, 2012). It is an essential component of protein and plays an important role in the brain as a precursor of serotonin (5-HT), an important neurotransmitter (Abidi and Khan, 2010b, Hseu et al., 2003). Feeding high dietary levels of Trp increases the synthesis of serotonin which affects the behavioral response to stress, and reduces endogenously derived aggressiveness in different fish species (Winberg et al., 2001; Hoglund et al., 2007). Serotonin, in turn, can be converted to melatonin, a neural hormone thought to be related to the immune response and circadian rhythms in fish (Esteban et al., 2013; NRC, 2011).

Niacin, a water soluble vitamin, can also be synthesized from Trp (Coloso et al., 2004), although there is some evidence that Trp is an inefficient precursor of niacin in channel catfish (Ng et al., 1997). Trp is also needed for the synthesis of insulin like growth factor-1 (IGF-I) which is involved in the growth of fishes (Millward 1989; Dyer et al. 2004). Trp deficiency results in scoliosis, lordosis, eye cataracts, and increased liver and kidney levels of Ca, Mg, Na, and K (Walton et al. 1984a).

1.5.8 – Branched-Chain Amino Acids: Leucine, Isoleucine and Valine

A branched-chain amino acid (BCAA) is defined as an AA having aliphatic side-chains with a branch (a carbon atom bound to more than two other carbon atoms). The three proteinogenic BCAA are Leu, Ile and Val (NRC, 2011).

These three EAAs are primarily deposited in body protein, notably in skeletal muscles (Cowey and Walton, 1989). Val is also involved in the synthesis of the myelin (NRC, 2011). As hydrophobic AAs, they are largely found in the hydrophobic interior core of globular proteins where their interactions with other similar amino acids are very important for determining the three-dimensional shapes of these proteins and, therefore, their functions (Brosnan and Brosnan, 2006a). Thus, since BCAAs play a key role in the protein structure, most proteins have a relatively high proportion of these AAs, which represent a significant proportion of AAs consumed by animals (NCR, 2011). Leu is specific, among BCAAs, in its ability to stimulate insulin release from pancreatic β-cells and protein synthesis in muscle and adipose tissue through the target of rapamycin signaling pathway (Yang et al., 2008). It is also an important AA for the production of hemoglobin, and for the increment of growth hormone production (Abidi and Khan, 2007).

1.6 – Quantifying EAAs requirements

Fish, like other animals, do not have an absolute requirement for protein but require a well-balanced mixture of NEAA and EAAs (Wilson, 2002). It is also known that EAA deficiency may cause reduced growth and poor diet conversion (Wilson and Halver,1986). As a result, it is important to satisfy the EAA requirements of fish by formulating balanced feeds, especially nowadays, as it is of utmost importance reducing the actual dependency on fish meal in aquafeeds (NRC, 2011).

1.6.1 – Dose-response assays

The majority of the published dietary AA requirements have been established by conventional dose-response assays, based on animal growth or nitrogen retention in response to increasing dietary levels of the EAA under study (NRC, 2011; Shearer, 2000). In such studies, a basal diet, deficient in a single EAA but meeting all other known nutrient requirements of the animal, is supplemented with graded levels of the EAA under study (NRC, 2011). The experiment is usually conducted for a sufficient period of time (at least 8 to 12 weeks) to produce differences in the response variable (Cowey, 1992). The experimental animals are normally fed at rates approaching apparent satiation to ensure maximum growth, although in some cases, a restricted ration may be administrated (NRC, 2011).

Beyond dose-response studies, a number of other methods have also been applied in quantitative estimation of EAA requirements, but often as a complement to growth studies (Hauler and Carter, 2001b; NRC, 2011). These methodological approaches comprise amino acid oxidation studies that are based on tissue-free AA concentration (Kim et al., 1983; Mambrini and Kaushik, 1995), as well as measurement of serum and muscle AA levels (Bae et al, 2011; Wilson, 1989).

1.6.2 – EAA requirements in the context of feed formulation

Diets used in nutrition studies may be classified as purified, semi-purified or practical diets. Purified diets are those which contain only purified nitrogen sources (e.g. casein, gelatin, crystalline amino acids - CAA) and theoretically should provide the most precise dietary formulations. In semi-purified diets, the AA are primarily supplied by crystalline sources with a percentage of the protein supplied by practical feedstuffs (e.g. FM, maize gluten meal, soybean meal) used to increase palatability. Practical diets are those that contain only practical feedstuffs, representing a natural protein source (Griffin et al., 1992).

Since the inclusion of practical feedstuffs may decrease the precision of the formulation to ensure graded levels of the EAA under test, purified or semi-purified diets are often used in dose-response studies, in which part of protein bound-AA are replaced by EAA supplied in the free form (as a CAA). In these diets, CAA are supplemented to the basal diet to provide the AA pattern found in fish tissue protein, except for the tested EAA (NRC, 2011).

The use of CAA to meet EAA requirements in practical diets has proven quite useful due to the high cost of FM and concomitant increased utilization of more economical protein sources with lower biological value (unbalanced EAA profile) (Kaushik and Hemre, 2010; NRC, 2011). However, there is some controversy regarding the use of CAA to meet EAA requirements of fish, particularly due to concerns with fish acceptance of the dietary CAA (NRC, 2011). Several studies have shown that CAA were utilized as efficiently as those of intact protein origin in meeting EAA requirements of fish (Murai et al., 1987; Espe et al., 2006). In contrast, there is also evidence (Peres and Oliva-Teles, 2005; Zhou et al., 2007b) that CAA appear to be utilized with a lower efficiency than EAA supplied by intact protein. This occurrence may be due to the faster absorption of CAA in the gastrointestinal tract in relation to protein-bound AAs, resulting in temporary higher tissue or plasma free AA concentrations. These high free AA concentrations are thought to enhance the activities of amino acid-catabolizing enzymes leading to greater amino acid degradation and lower levels of protein synthesis (Murai et al., 1987; Cowey and Walton, 1988), which generally results in an overestimation of the requirement level (Cowey, 1994). Therefore, the use of techniques such as coating, encapsulation, or polymerization, in order to reduce the solubility and delay the absorption rate of CAA, have showed to improve the efficiency of CAA utilization in fish (Cho et al., 1992; Peres and Oliva-Teles, 2005; Zhou et al., 2007b). Despite the emergence of these techniques, NRC (2011) recommend a slightly higher “safety margin” when meeting a significant proportion of the requirement for an AA using CAA compared to using a highly digestible protein-bound AA sources. Most growth response assays, however, are based on deficient basal diet which is supplemented with graded levels of the deficient EAA supplied as a CAA.

1.6.3 – Statistical models used for estimating EAA requirements

The aim of a dose-response experiment is therefore to estimate a single value applicable to the whole population, taken into account the individual variation that exists within the population (Ajinomoto, 2012). Generally, to quantify dietary EAA requirements of fish, the dose-response data is examined using one or more statistical methods and the EAA requirement is estimated from the level that produces the maximum response (Shearer, 2000). According to Baker (1986), the choice of statistical method may have a crucial effect on the estimated value of the requirement. Ajinomoto (2012) reported two types of statistical models used in pigs and poultry dose-response assays, the linear model, which include both linear and quadratic functions, and the non-linear model, such as the linear-plateau (also known as broken line model - BL), curvilinear-plateau (or quadratic-plateau) or asymptotic model. However, this division seems not to be entirely consensual, as NRC (2011) describes BL as a linear model. Though, regardless of the different approaches, the BL model (Robbins et al., 1979) has reported to be the most widely used method of evaluating dose-response data in nutrient requirement studies in fish species (NRC, 2011, Shearer, 2000). Nevertheless, Encarnação et al. (2004) reported that use of the BL model resulted in an estimated dietary requirement for lysine (1.8% of diet) in rainbow trout that is lower than that derived from both the exponential and four-parameter saturation kinetic model (SKM 4-parameter) (2.3% of the diet). The latter requirement value agreed well with that reported by Rodehutscord et al. (1997) who used a similar dietary and data analysis model for the same specie. The comparative results of the previous studies suggest that the requirement value for rainbow trout (1.8% of diet), as proposed by NRC (1993) and derived from the use of the BL model, falls significantly below what is required to maximize weight gain (WG). The intercept of the two linear functions is clearly below the Lys level maximizing WG and therefore fails to accurately represent the response of the animal to increasing levels of this amino acid (NRC, 2011). These findings are in line with a re-evaluation of the data from previous studies proposed by Shearer (2000), using regression, that suggests that many published papers seriously underestimate the nutrient requirement in fish and refer the use of inappropriate statistical methods as the primary cause for the underestimation.

Despite the large number of studies conducted on the topic over the past 60 years, the EAA requirements of fish are still not well defined. Laboratory variance, with particular emphasis to composition of experimental diets used in dose-response experiments, has been claimed as a major issue affecting reliability of requirement estimates (Encarnação et al., 2004; Forster and Ogata, 1998; Hauler and Carter, 2001a, b; De Silva et al., 2000).

Systematic reviews usually comprise a detailed and comprehensive plan and search strategy defined at the outset, with the aim of reducing bias by identifying, evaluating, and synthesizing all relevant studies on a particular topic (Uman L., 2011). Often, systematic reviews include a meta-analysis component which involves using statistical models to synthesize the data collected from several studies into a single quantitative estimate (Petticrew and Roberts, 2006).

Thus, the aim of the present work is to re-evaluate available data on EAA requirements from several fish species through a quantitative systematic review in order to accurate the estimation of the optimum dietary level required, expressed in g/16 g N, for each EAA, based on different response criteria.

2 – Material and methods

2.1 – Selection of studies

Based on the number of studies available that provided viable values for inclusion in a quantitative systematic review, Arg, His, Ile, Leu, Lys, Met, Phe, Thr, Trp and Val were selected for evaluation. Weight gain (WG), thermal growth coefficient (TGC) and nitrogen retention (NR) were selected as outcomes to evaluate the requirement of each EAA. An extensive literature search was undertaken to identify studies in fish nutrition that satisfied the following criteria:

- Dose-response study;
- Presented outcomes of fish growth;
- The initial body weights (IBW) and weight gain (WG) of fish were either reported or could be calculated from the reported information;
- The experimental diets were formulated to be isonitrogenous and isoenergetic on a digestible basis;
- Trial duration was reported in the paper.

2.2 – Construction of database

Available data on EAA requirements of several SW, BW and FW fish species derive from studies that set the criteria described above, were collected. Data on different factors and response criteria were estimated and the corresponding estimate requirement values (expressed in dietary % and in g/16g N) were registered. These factors and response criteria include the following parameters:

- Fish species (common and scientific name);
- Initial body weight (g/fish);
- Water temperature (ºC);
- Salinity;
- Duration of feeding trial (days);
- Feeding regimen;
- Protein ingredients (intact protein sources);
- Dietary crude protein (%);
- Dietary crude lipid (%);
- Energy (KJ/g);
- EAA levels (% diet);

- EAA levels (g/16g N);
- TGC range;
- NR (%NI) range;
- Response variable;
- Statistical model.

A database was created with the foresaid information with the corresponding data from a total of over 177 feeding trials reported in 121 published articles covering about 45 fish species.

2.3 – Standardization of selected data

A meta-analytical evaluation can only be meaningful if the studies are comparable. Thus, the selected data were standardized to a common response unit of expression prior to re-evaluation. Data expressed in different units in different studies for a given criteria such as dietary CP, dietary crude lipid (CL) or energy, were normalized and expressed in terms of percentage on dry weight basis (CP and CL) and KJ/g wet weight (energy). EAA levels and EAA requirements were normalized and expressed either as percent of the diet or as percentage of crude protein (g/16 g N). As the initial sizes, growth rates and experimental conditions vary among studies, and to help the direct interstudy comparison of the growth data, response variables were calculated and then normalized by taking, for example, the maximum gain in mass in a given study as 100 and calculating the WG of the other groups in the study as a relative percentage to the maximum WG.

2.4 – Calculations

WG (%) = 100 x [(final body weight – initial body weight) / initial body weight)]

TGC = 1000 x [(final body weight $^{1/3}$ – initial body weight $^{1/3}$) / water temperature x days]

NR (% NI) = 100 x [(final body weight x final body nitrogen content) - (initial body weight x initial body nitrogen content)]/nitrogen intake

2.5 – Model selection

Two models, namely four parameter nutrient saturation kinetics model (SKM – 4 parameter) (Mercer et al., 1984) and second order polynomial regression (SOPR) analysis (a quadratic model) (Zeitoun et al., 1976) were selected as best suited for analyzing nutrient requirements by more accurately describe the complex physiological response of living organisms and for being continuous like the relation of growth to dose (Pack et al., 1995; Zeitoun et al., 1976). These models are similar in their ascending portions, but differ significantly as the EAA level exceeds the maximum response. The SKM 4-parameter model (Mercer et al., 1984) produces a sigmoid-shaped curve which reaches a plateau and the SOPR (Zeitoun et al., 1976), a symmetric parabola. Thus, whenever a level of EAA fed is high enough to produce a growth reduction, the SOPR analysis must be chosen instead of the SKM 4-parameter model (Shearer, 2000). For both models, the EAA level, expressed as % of crude protein, that produces a response of 95%Rmax is estimated as the requirement value.

In short, the mathematical formulas for the curves are as follows:

(1) Four-parameter nutrient saturation kinetics model (Mercer et al., 1984):

$$r = (b(K_{0.5})^n + R_{max}I^n) / (K_{0.5}{}^n + I^n)$$

where **r** is the physiological response, **I** is the dietary concentration, **b** is the intercept on the r axis, $\mathbf{R_{max}}$ is the maximum theoretical response, $\mathbf{K_{0.5}}$ is the concentration of I for ½ ($\mathbf{R_{max}}$ + b), and n is the apparent kinetic order.

(2) Second order polynomial regression (Zeitoun et al., 1976):

$$r = B_0 + B_1I + B_2I$$

where **r** is the physiological response, **I** is the dietary concentration, $\mathbf{B_0}$ is the intercept on the response (Y) axis, $\mathbf{B_1}$ and $\mathbf{B_2}$ are regression coefficients.

The two models were fitted using STATISTICA (version 11) by adopting the Gauss-Newton algorithm that finds the parameters that minimize the sum of squared differences between the values of the observed and predicted values of the dependent variable.

3 – Results and discussion

Tables 1 and 2 summarize data on EAA requirements, expressed as percentage of the dietary protein, of several SW and FW species used in this study. The requirements were estimated by dose-response studies and comprise requirements for growth and NR. The requirements for His, Ileu, Leu, Phe and Val were not considered in table 1 (SW fish species) because there is a lack of data for marine species. Given the research carried out up to now, at least seven species – channel catfish, Chinook salmon, common carp, mrigal carp, rohu carp, Nile tilapia and rainbow trout, present requirement values for the 10 EAA. The range of requirement' values for each EAA are discussed individually below.

Based on what was defined in the Material and Methods section (2.2), background information on the studies used in the re-evaluation of data on EAA requirements is presented in tables 3 – 12.

Figure 3 resumes the main statistical models used in the above mentioned studies (tables 3-12) for estimating the requirement EAA values and the relative percentage of each model.

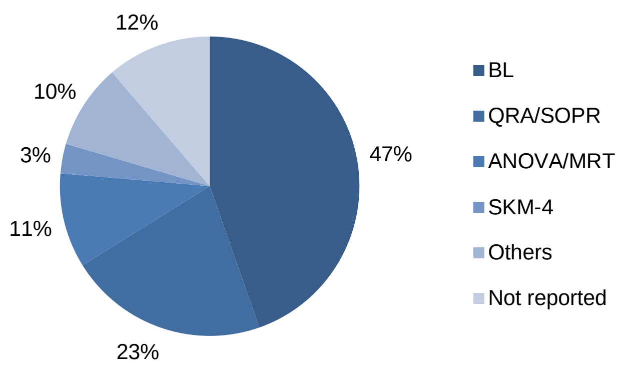

Figure 3. Statistical models used for estimating the requirement EAA values on dose-response studies.

Figures 4 – 6, 8 – 12, 14 – 23, 25 – 27 illustrate the response variables (% max) as a function of dietary protein level (g/16g N) for each EAA. Due to lack of data on available dose-response studies for NR, this response criterion was only determined for re-evaluation of Lys and Arg requirements (Figures 6 and 12). In this figures, the dietary EAA requirements is indicated by a triangle and by an arrow, corresponding to the EAA level at 95% of the maximum value established by the model.

Table 1. Essential amino acids requirements (g/16g N) of some marine fish species estimated by dose-response studies.

	Arg	Lys	Met	Thr	Try	References
Asian seabass *Lates calcarifer*	3.8	4.5	2.2	-	0.4	Murillo Gurrea et al., 2001; Coloso et al., 1999, 2004
Atlantic salmon *Salmo salar*	4.1-5.1	-	-	-	-	Berge et al., 1997; Lall et al., 1994
Black sea bream *Sparus macrocephalus*	7.7-8.1	8.6	4.5	-	-	Zhou et al., 2010a, b, 2011
Cobia *Rachycentron canadum*	-	5.3	2.6	-	-	Zhou et al., 2006, 2007
European seabass *Dicentrarchus labrax*	3.9	4.4	1.8-2.7	2.3-2.6	-	Tibaldi and Lanari, 1991; Tibaldi et al.,1994; Tibaldi and Tuli, 1999; Tulli et al., 2010
Gilthead seabream *Sparus aurata*	-	5.0	-	-	-	Marcouli et al., 2006
Golden pompano *Trachinotus ovatus*	-	-	2.5-3	-	-	Niu et al., 2013
Grouper *Epinephelus coioides*	-	5.6	2.73	-	-	Luo et al., 2005, 2006
Japanese flounder *Paralichthys olivaceus*	4.1-4.2	3.3-4.6	2.9-3	-	-	Alam et al., 2000, 2002; Forster and Ogata, 1998

Table 1. (Continued).

	Arg	Lys	Met	Thr	Try	References
Japanese seabass *Lateolabrax japonicas*	-	5.8-6.1	-	-	-	Mai et al., 2006
Milkfish *Chanos chanos*	5.3	4	-	4.5	0.6	Borlongan, 1991; Borlongan and Benitez, 1990; Coloso et al., 1992
Pacific threadfin *Polydactylus sexfilis*	-	5.1	-	-	-	Deng et al., 2010
Red drum *Sciaenops ocellatus*	4.2-5.0	4.4-5.7	-	2.3	-	Brown et al., 1988; Craig and Gatling, 1992; Boren and Gatling, 1995; Barziza et al., 2000
Red seabream *Pagrus major*	-	3.6-4.4	-	-	-	Forster and Ogata, 1998
Rockfish *Sebastes schlegeli*	-	-	2.8	-	-	Yan et al., 2007
Turbot *Scophthalmus maximus*	-	5	-	-	-	Peres and Oliva-Teles, 2008
Yellow croaker *Pseudosciaena crocea*	-	5.7-6.6	3.2-3.3	-	-	Mai et al., 2006; Xie et al., 2012; Zhang et al., 2008;
Yellow grouper *Epinephelus awoara*	6.5	-	-	-	-	Zhou et al., 2012b
Yellowtail *Seriola quinqueradiata*	3.5	4.1	2.56	-	-	Ruchimat et al.,1997a, b; Ruchimat et al.,1998

Table 2. Essential amino acids requirements (g/16g N) of some freshwater fish species estimated by dose-response studies.

	Arg	His	Isol	Leu	Lys	Met	Phen	Thr	Try	Val	References
African catfish *Clarias gariepinus*	4.5	1	-	-	5.7	3.2	-	-	1.1	-	Fagbenro et al., 1998, 1999a, b; Fagbenro and Nwanna, 1999; Khan and Abidi, 2009
Arctic charr *Salvelinus alpinus*	-	-	-	-	-	1.8	-	-	-	-	Simmons et al., 1999
Atlantic salmon *Salmo salar*	-	-	-	-	-	-	-	2.7	-	-	Bodin et al, 2008
Channel catfish *Ictalurus punctatus*	3.3-4.3	1.5	2.6	3.5	5.0-5.1	2.3-3.4	2.1	2.2	0.5	3	Buentello and Galtin, 2000; Cai and Burtle, 1996; Harding et al., 1977, Robinson et al., 1980a, b, 1981; Wilson et al., 1977, 1978, 1980
Chinook salmon *Oncorhynchus tshawytacha*	6	1.8	2.4	3.9	5	1.5	4.4	2.3	0.5	3.2	Chance et al., 1964; DeLong et al, 1962; Halver, 1965 (abstract); Halver et al, 1958, 1959 (abstract); Klein and Halver, 1970
Chum salmon *Oncorhynchus keta*	-	1.6	-	-	4.8	-	-	3	0.7	-	Akiyama et al., 1985a, b
Coho salmon *Oncorhynchus kisutch*	4.9-5.8	1.8	-	-	-	-	-	-	-	-	Klein and Halver, 1970; Luzzana et al., 1998
Common carp *Cyprinus carpio*	4.3	2.1	2.5	3.3	5.7	2.1-3.1	3.4-6.5	3.9	0.8	3.6	Nose, 1979; Schwartz et al., 1998
Freshwater catfish *Mystus nemurus*	-	-	-	-	3.5	-	-	-	-	-	Tantikitti and Chimsung, 2001
Grass carp *Ctenopharyngodon idella*	-	-	-	-	5.9	-	-	-	-	-	Wang et al., 2005

Table 2. (Continued).

	Arg	His	Isol	Leu	Lys	Met	Phen	Thr	Try	Val	References
Hybrid clarias *Clarias gariepinus x C. macrocephalus*	4.5-5	-	-	-	-	-	-	-	-	-	Singh and Khan, 2007
Hybrid striped bass *Morone chrysops x M. saxatilis*	4.1-4.4	-	-	-	4	2.5	-	2.6	0.6-0.7	-	Gaylord et al., 2005; Griffin et al., 1992, 1994; Keembiyehetty and Galtin, 1992, 1993, 1997
Indian catfish *Heteropneustes fossilis*	5.1-5.7	1.4	-	-	-	-	-	3.2	0.8	-	Ahmed, 2007, 2012, 2013; Khan and Abidi, 2011
Jian carp *Cyprinus carpio var. Jian*	-	-	-	-	5.9	-	-	-	-	-	Zhou et al., 2008
Jundia *Rhamdia quelen*	-	-	-	-	4.5-5.1	-	-	-	-	-	Montes-Girão and Fracalossi, 2006
Lake trout *Salvelinus namaycush*	-	-	1.5-2.1	2.7-3.7	-	-	-	-	-	1.8-2.2	Hughes and Rumsey, 1983
Largemouth bass *Micropterus salmoides*	4.2	-	-	-	-	-	-	-	-	-	Zhou et al., 2012a
Mrigal carp *Cirrhinus mrigala*	4.6	2.1	3.2	3.9	5.8	3	3.3	4.2-4.5	0.95	3.8	Ahmed, 2004, 2009; Ahmed and Khan, 2004a, b, 2005a,b, 2006 ; Ahmed et al, 2003; Benakappa and Varghese, 2002; Khan and Ahmed, 2005
Nile tilapia *Oreochromis niloticus*	4.2	1.7	3.1	3.4	5.1	1.8-2.7	3.8	3.8	1	2.8	Nguyen and Davis, 2009; Santiago and Lovell, 1988
Pacu *Piaractus mesopotamicus*	-	-	-	-	4.4-5.9	-	-	-	-	-	Abimorad et al., 2010; Bicudo et al., 2009

Table 2. (Continued).

	Arg	His	Isol	Leu	Lys	Met	Phen	Thr	Try	Val	References
Rainbow trout *Oncorhynchus mykiss*	3.4-4	1.7	4.15	4	3.7-8.1	2.4	2	2.6-3	0.5-0.6	4	Bodin et al, 2008; Kim, 1993; Kim et al., 1992; Rodehutscord et al, 1995a, b, 1997; Walton et al., 1984a, b, 1986
Rohu carp *Labeo rohita*	3-5.8	2-2.3	3.8-4	3.8-3.9	4.5-4.8	2.6	2.9-3.1	3.8-4.2	0.9-1.1	3.8-4	Abidi and Khan, 2004a,b, 2007, 2008, 2009, 2010a, b, 2011; Khan and Abidi, 2007a, b, 2009,2011; Murthy and Varghese, 1995, 1997
Silver perch *Bidyanus bidyanus*	6.8	-	-	-	6	-	5.7	-	-	-	Ngamsnae et al., 1999; Yang et al., 2011
Striped bass *Morone saxatilis*	-	-	-	-	4.9	-	-	2.45	-	-	Small and Soares, 1999, 2000
Tilapia *Sarotherodon mossambicus*	4.0	-	-	-	4.1	1.3	-	-	-	-	Jackson and Capper, 1982
Yellow catfish *Pelteobagrus fulvidraco*	-	-	-	-	8.3	-	-	-	-	-	Cao et al., 2012
Yellow perch *Perca flavescens*	4.3-4.9	-	-	-	-	-	-	-	-	-	Twibell and Brown, 1997

3.1 – Lysine

WG was used as the response variable for estimating Lys requirements in 65% of the studies used in fish. This is in line with a previous re-evaluation of fish Lys requirements made by Hauler and Carter (2001b) that reported WG as the most frequently chosen response variable for evaluating Lys requirements in fish.

More than half of dose-response studies considered used the BL as statistical model (53%). However, a SKM-4 parameter model (Mercer et al, 1984) adjust well to the compiled data and was used to reevaluate requirements in this study, since it has been suggested to be one of the most appropriate statistical models to describe amino acid requirement responses (Mercer et al., 1989; Shearer, 2000). Based on this model, dietary Lys level meeting 95% of the Lys requirement for maximum WG was estimated to be 5.9 g/16g N (Figure 4). The same model was used to plot TGC (% max) and NR (% max) against dietary Lys level (g/16g N) (Figures 5 and 6), and the Lys requirement was estimated to be 6.5 g/16g N and 5.3 g/16g N for TGC (% max) and NR (% max), respectively. Data used for this Lys requirement re-evaluation fitted well with the SKM-4 parameter model, giving a correlation coefficient value of 0.8 for all response variables.

The Lys requirement values obtained with the present meta-analytical approach was within the individual dose-response Lys requirements estimated in the different studies, and that ranged from 3.3 to 8.6 g/16g N (Tables 1 to 3). However, when the collected data was submitted to a box-plot evaluation (Figure 7), the Lys requirement values for black seabream (Zhou et al., 2010a), rainbow trout (Rodehutscord et al., 1997) and yellow catfish (Cao et al., 2012), are considered outliers, and the range become narrow (3.3 to 6.55 g/16g N). Nevertheless, it is important to notice that the Lys requirements of SW fish and FW carnivorous fish are generally higher that of omnivorous and herbivorous fish species (Zhou et al., 2007a). This fact may clarify the high Lys requirement value of rainbow trout and yellow catfish but does not explain the black seabream Lys requirement value. When the mentioned articles were excluded from the present re-evaluation, slight or no difference occurred on estimation of requirement values. Based on SKM-4 parameter model, dietary Lys level meeting 95% of the Lys requirement for maximum WG was estimated to be 6.0 g/16g N. When TGC (% max) and NR (% max) were plotted against dietary Lys level (g/16g N), the Lys requirement was estimated to be 6.5 g/16g N and 5.4 g/16g N, respectively.

Table 3. Data collected from dose-response lysine (Lys) requirement studies.

Fish species		Initial body weight (g/fish)	Water temperature (ºC)	Salinity	Trial duration (days)	Feeding Regimen	Protein ingredients	Diet crude protein (%)	Diet crude lipid (%)	Energy (kJ/g)	References
Common name	Scientific name										
African catfish	*Clarias gariepinus*	15.4	28	FW	70	Satiation	Casein, gelatin	40	-	12	Fagbenro et al., 1998
Asian sea bass	*Lates calcarifer*	13.1	27	SW	84	Fixed ration	Peruvian FM, zein, SM	45.5	10	-	Murillo Gurrea et al., 2001
Black sea bream	*Sparus macrocephalus*	9.13	28	SW	56	Satiation	FM, SPC, gelatin	38	15	15.7 (DE)	Zhou et al., 2010a
Channel catfish	*Ictalurus punctatus*	200	26.7	FW	49	Fixed ration	Casein, gelatin	24	-	12	Wilson et al., 1977
Channel catfish	*Ictalurus punctatus*	200	26.7	FW	56	Fixed ration	Casein, gelatin	30	-	14.4	Robinson et al., 1980a
Chum salmon	*Oncorhynchus keta*	1.35	15	SW	28	Satiation	Casein	40	-	-	Akiyama et al., 1985a
Cobia	*Rachycentron canadum*	1.25	28.5	SW	56	Satiation	FM, WGI	44	16	-	Zhou et al., 2007a
Common carp	*Cyprinus carpio*	1.54	25	FW	42	Satiation	-	38.5	-	-	Nose, 1979
European seabass	*Dicentrarchus labrax*	0.85	25.5	SW	70	Fixed ration	MG, HM, gelatin	50	14	17.5 (DE)	Tibaldi and Lanari, 1991
Freshwater catfish	*Mystus nemurus*	8	26	FW	90	Satiation	FM, gelatin	35	11	17	Tantikitti and Chimsung, 2001
Gilthead seabream	*Sparus aurata*	3.5	24	SW	42	Satiation	LT-FM	43	13.5	-	Marcouli et al., 2006
Grass carp	*Ctenopharyngodon idella*	3.15	28.7	FW	90	Fixed ration	WGl, casein, gelatin	38	5	14.0 (DE)	Wang et al., 2005
Grouper	*Epinephelus coioides*	15.84	29	SW	56	Satiation	FM, SPC	48	10	-	Luo et al., 2006
Hybrid striped bass	*Morone chrysops x M. saxatilis*	8	24.5	BW	63	Fixed ration	Red drum muscle	35	-	-	Keembiyehetty and Galtin, 1992
Hybrid striped bass	*Morone chrysops x M. saxatilis*	11	28	FW	56	Fixed ration	Casein, gelatin	35	-	-	Griffin et al., 1992
Japanese flounder	*Paralichthys olivaceus*	3	19.5	SW	63	Satiation	Zein, FM, gelatin	47	11	-	Forster and Ogata, 1998
Japanese seabass	*Lateolabrax japonicus*	5.5	28.5	SW	70	Satiation	FM, SBM, zein, WM	43	12	-	Mai et al., 2006
Jian carp	*Cyprinus carpio var. Jian*	7.89	21	FW	80	Satiation	FM, RGM	32	5	-	Zhou et al., 2008
Jundia	*Rhamdia quelen*	1.4	30.5	FW	119	Satiation	Casein, gelatin	33	5	14.6	Montes-Girão and Fracalossi, 2006
Milkfish	*Chanos chanos*	5.92	29	SW	84	Fixed ration	White FM, zein	50	-	-	Borlongan and Benitez, 1990
Mrigal carp	*Cirrhinus mrigala*	0.63	26.5	FW	56	Satiation	Casein, gelatin	40	-	17.9 (GE)	Ahmed and Khan, 2004b
Nile tilapia	*Oreochromis niloticus*	0.041	27	FW	56	Satiation	Casein, gelatin	28	-	10.5 (DE)	Santiago and Lovell, 1988
Pacific threadfin	*Polydactylus sexfilis*	3	25	SW	56	Satiation	Pacific threadfin muscle	35	11.5	19.1 (GE)	Deng et al., 2010
Pacu	*Piaractus mesopotamicus*	4.3	30.3	FW	74	Satiation	Casein, gelatin	32	5	17.6	Bicudo et al., 2009
Pacu	*Piaractus mesopotamicus*	8.66	29.6	FW	90	Satiation	FM, SBM, MG	28	7.8	18.4 (GE)	Abimorad et al., 2010

Table 3. (Continued).

Fish species		Lys levels (% diet)	Lys levels (g/16gN)	Termal growth coefficient	Nitrogen retention (%NI)	Lys requeriment (% diet)	Lys requirement (g/16gN)	Response variable	Statistical Model	References
Common name	Scientific name									
African catfish	*Clarias gariepinus*	1.6-2.60	4-6.5	0.53-0.64	-	2.29	5.73	WG	BL	Fagbenro et al., 1998
Asian sea bass	*Lates calcarifer*	1.0-2.5	2.17-5.43	1.56-1.97	-	2.06	4.5	WG, survival, FER	BL	Murillo Gurrea et al., 2001
Black sea bream	*Sparus macrocephalus*	2.08-4.05	5.5-10.7	0.7-0.81	28-34	3.32	8.64	SGR	SOPR	Zhou et al., 2010a
Channel catfish	*Ictalurus punctatus*	0.75-1.65	3.1-8.3	0.83-1.63	-	1.2	5.1	WG, SFLC	MRT	Wilson et al., 1977
Channel catfish	*Ictalurus punctatus*	0.7-2	2.3-6.7	0.46-1.53	-	1.5	5	WG	MRT	Robinson et al., 1980a
Chum salmon	*Oncorhynchus keta*	0.38-4	1.0-10.0	0.37-1.01	-	1.93	4.82	WG	MRT	Akiyama et al., 1985a
Cobia	*Rachycentron canadum*	1.15-3.25	2.6-7.4	0.90-1.13	-	2.33	5.3	SGR	BL	Zhou et al., 2007a
Common carp	*Cyprinus carpio*	0.0-2.4	0-6.2	- 0.02-0.32	-	2.2	5.7	SGR	Not reported	Nose, 1979
European seabass	*Dicentrarchus labrax*	1.20-2.45	2.4-4.9	0.36-0.47	14.9-26.1	2.17 / 2.22	4.34 / 4.44	WG / GPR	BL	Tibaldi and Lanari, 1991
Freshwater catfish	*Mystus nemurus*	0.7-3.1	2-8.86	0.22-0.43	18.8-27.2	1.2145	3.47	SGR	SKM-4 parameter	Tantikitti and Chimsung, 2001
Gilthead seabream	*Sparus aurata*	1.56-3.43	3.63-7.97	0.84-0.95	34.4-39.9	2.16	5.04	DPD	SKM-4 parameter	Marcouli et al., 2006
Grass carp	*Ctenopharyngodon idella*	0.69-3.08	2-8.86	0.23-0.35	11.6-21.5	2.24	5.89	WG, FE	SOPR	Wang et al., 2005
Grouper	*Epinephelus coioides*	1.92-3.95	4-8.2	0.65-0.91	24-30	2.83	5.56	WG	BL	Luo et al., 2006
Hybrid striped bass	*Morone chrysops x M. saxatilis*	1.14 - 2.37	3.3-6.8	0.9-1.1	-	1.41	4.03	WG, FE	BL	Keembiyehetty and Galtin, 1992
Hybrid striped bass	*Morone chrysops x M. saxatilis*	0.8-2.2	2.3-6.3	0.71-0.99	-	1.4	4	WG, FE	BL	Griffin et al., 1992
Japanese flounder	*Paralichthys olivaceus*	1.03-3.1	2.2-6.6	0.40-0.88	8.2-20.5	1.6 / 2.0 / 2.2	3.3 / 4.2 / 4.6	SGR / FE / NR	BL	Forster and Ogata, 1998
Japanese seabass	*Lateolabrax japonicus*	1.28-4.25	3-9.9	0.83-1.00	-	2.49 / 2.61 / 2.6	5.8 / 6.07 / 6.05	SGR / FER / PER	BL	Mai et al., 2006
Jian carp	*Cyprinus carpio var. Jian*	0.7-2.21	2.2-6.9	0.31-0.79	9.4-33.3	1.92	5.9	WG	BL	Zhou et al., 2008
Jundia	*Rhamdia quelen*	0.99-2.15	3-6.5	0.28-0.37	19.9-49.6	1.485 / 1.683	4.5 / 5.1	WG	BL / SOPR	Montes-Girão and Fracalossi, 2006
Milkfish	*Chanos chanos*	0.7-2.7	1.4-5.4	0.2-0.35	-	2	4	WG	SOPR	Borlongan and Benitez, 1990
Mrigal carp	*Cirrhinus mrigala*	1.5-2.75	3.8-6.9	0.21-0.36	13.51-27.36	2.3	5.75	WG, FCR, PER	SOPR	Ahmed and Khan, 2004b
Nile tilapia	*Oreochromis niloticus*	1.1-1.9	3.9-6.8	0.43-0.51	-	1.43	5.12	WG	BL	Santiago and Lovell, 1988
Pacific threadfin	*Polydactylus sexfilis*	1.26-2.91	3.6-8.31	1.11-1.18	34.6-40.3	1.79	5.1	SGR	BL	Deng et al., 2010
Pacu	*Piaractus mesopotamicus*	0.9-1.96	2.8-6.1	0.63-0.73	20.5-40.5	1.4-1.5	4.4-4.7	WG, FE, NR	SOPR	Bicudo et al., 2009
Pacu	*Piaractus mesopotamicus*	0.68-1.96	2.4-7	0.49-0.72	27.9-32.7	1.64	5.86	WG	BL	Abimorad et al., 2010

Table 3. (Continued).

Fish species		Initial body weight (g/fish)	Water temperature (ºC)	Salinity	Trial duration (days)	Feeding Regimen	Protein ingredients	Diet crude protein (%)	Diet crude lipid (%)	Energy (kJ/g)	References
Common name	Scientific name										
Rainbow trout	*Oncorhynchus mykiss*	51	15,7	FW	55	Satiation	WGl	34	27.9	20.1 (DE)	Rodehutscord et al., 1997[1]
Rainbow trout	*Oncorhynchus mykiss*	13,7	15	FW	42	Satiation	Casein, gelatin	35	-	15	Kim et al., 1992
Rainbow trout	*Salmo gairdneri*	5	15	FW	84	Satiation	Cod white muscle	45	-	16.9 (DE)	Walton et al., 1984b
Red drum	*Sciaenops ocellatus*	2,7	28	BW	56	Fixed ration	PM, ShM	35	-	-	Brown et al., 1988
Red drum	*Sciaenops ocellatus*	6-7 / 1-2	-	SW	56	Fixed ration	Freeze-dried red drum muscle / zein, red drum muscle	35	-	-	Craig and Gatlin, 1992
Red sea bream	*Pagrus major*	1,7	22,5	SW	56	Satiation	Zein, FM, gelatin	48	14	-	Forster and Ogata, 1998
Rohu carp	*Labeo rohita*	0,66	26	FW	84	Satiation	Casein, gelatin	40	-	17.9	Abidi and Khan, 2010a
Silver perch	*Bidyanus bidyanus*	4,7	27	FW	70	Satiation	WGl, MG, FM, SM, zein	38.7	10.7	-	Yang et al., 2011
Striped bass	*Morone saxatilis*	1,5 / 6	23	FW	56 / 70	Fixed ration	FM, MG	42	-	13.4 (DE)	Small and Soares, 2000
Tilapia	*Sarotherodon mossambicus*	1,7	25	FW	42	Fixed ration	White FM, SBM, groundnut	40	-	12.6 (DE)	Jackson and Capper, 1982
Turbot	*Scophthalmus maximus*	18,1	18	SW	56	Satiation	MG, FM, SFPC	50	15	18.5 (DE)	Peres and Oliva-Teles, 2008
Yellow catfish	*Pelteobagrus fulvidraco*	1,48	28	FW	56	Satiation	FM, SPC	40.5	6.5	18	Cao et al., 2012
Yellow croaker	*Pseudosciaena crocea*	0,0027	23	SW	30	Satiation	LT-FM, LT-KM, SM, hydrolysed FM, MG	51	18.5	22.3	Xie et al., 2012
Yellow croaker	*Pseudosciaena crocea*	1,23	28,5	SW	70	Satiation	FM, MG, SBM, WM	43	12	-	Zhang et al., 2008
Yellowtail	*Seriola quinqueradiata*	68,2	25,8	SW	40	Satiation	Brown FM, MG, WGl	43.1	15.9	15.5 (DE)	Ruchimat et al., 1997a

Table 3. (Continued).

Fish species		Lys levels (% diet)	Lys levels (g/16gN)	Termal growth coefficient	Nitrogen retention (%NI)	Lys requeriment (% diet)	Lys requirement (g/16gN)	Response variable	Statistical Model	References
Common name	Scientific name									
Rainbow trout	*Oncorhynchus mykiss*	0.45-5.8	-	-	-	2.77	8.14	PD	EF	Rodehutscord et al., 1997[1]
Rainbow trout	*Oncorhynchus mykiss*	0.72-1.6	2.1-4.6	1.19-1.98	21.40-46.7	1.3	3.71	WG	ANOVA	Kim et al., 1992
Rainbow trout	*Salmo gairdneri*	1.04-2.6	2.3-5.8	1.04-1.6	-	1.9	4.2	WG	MRT	Walton et al., 1984b
Red drum	*Sciaenops ocellatus*	1.2-2.4	3.4-6.9	0.18-0.44	-	2	5.7	SFLC	MRT	Brown et al., 1988
Red drum	*Sciaenops ocellatus*	1.0-2.5	2.9-7.1	1.49-2.14 (DGI)	-	1.55	4.43	WG, FE	BL	Craig and Gatlin, 1992
Red sea bream	*Pagrus major*	1.23-3.16	2.5-6.7	0.65-0.97	27.4-37.9	1.7 / 2.1 / 2.1	3.6 / 4.3 / 4.4	SGR / FE / NR	BL	Forster and Ogata, 1998
Rohu carp	*Labeo rohita*	1.2-2.2	3-5.5	0.1-0.34	8.0-38.0	1.8-1.91	4.5-4.8	WG, FCR, PER, PRE	BL / SOPR	Abidi and Khan, 2010a
Silver perch	*Bidyanus bidyanus*	0.9-2.7	2.5-7.2	0.27-0.54	15-30	2.32	5.96	WG	SOPR	Yang et al., 2011
Striped bass	*Morone saxatilis*	0.92-2.1 / 1.48-3.09	3.5-7.4	0.25-0.32	24.5-34	2.1	4.9	WG, SGR, FCR, ANU	BL	Small and Soares, 2000
Tilapia	*Sarotherodon mossambicus*	1.42-2.44	3.6-6.1	0.38-0.56	25.3-35	1.62	4.05	WG	MRT	Jackson and Capper, 1982
Turbot	*Scophthalmus maximus*	1.19-3.11	2.5-6.4	0.45-0.58	20.4-30	2.5	5	WG	SKM-4 parameter	Peres and Oliva-Teles, 2008
Yellow catfish	*Pelteobagrus fulvidraco*	1.73-4.19	4.3-10.3	0.57-0.73	-	3.31	8.32	SGR	BL	Cao et al., 2012
Yellow croaker	*Pseudosciaena crocea*	2.48-4.1	4.9-8	0.26-0.38	32.5-51.1	3.37 / 3.34	6.55 / 6.49	SGR / survival	SOPR	Xie et al., 2012
Yellow croaker	*Pseudosciaena crocea*	1.27-4.22	3.0-9.8	0.48-0.61	-	2.48 / 2.45 / 2.43	5.77 / 5.7 / 5.65	SGR / FER / PER	BL	Zhang et al., 2008
Yellowtail	*Seriola quinqueradiata*	1.05-3.05	2.4-7.1	0.80-0.95	15.6-22.6	1.78	4.13	WG, FE	BL	Ruchimat et al., 1997a

FW, freshwater; SW, seawater; BW, brackish water; FM, fish meal; SM, squid meal; SPC, soy-bean protein concentrate; WGl, wheat gluten; MG, maize gluten; HM, herring meal; SBM, soy-bean meal; RGM, rice gluten meal; PM, peanut meal; ShM, shrimp meal; SFPC, soluble fish protein concentrate; DE, digestible energy; GE, gross energy; DGI, daily growth index; WG, weight gain; FER, feed efficiency ratio; SGR, specific growth rate; SFLC, serum free lysine concentration; GPR, gross protein retention; DPD, daily protein deposition; FE, feed efficiency; NR, nitrogen retention; PER, protein efficiency ratio; FCR, feed conversion ratio; SGR, specific growth rate; PD, protein deposition; PRE, protein retention efficiency; ANU, apparent nitrogen utilization; BL, broken line regression; SOPR, second order polynomial regression; MRT, Duncan's multiple-rang test; SKM, saturation kinetic model; EF, exponential function; ANOVA, analysis of variance.

[1] this article does not have the information required for statistical treatment

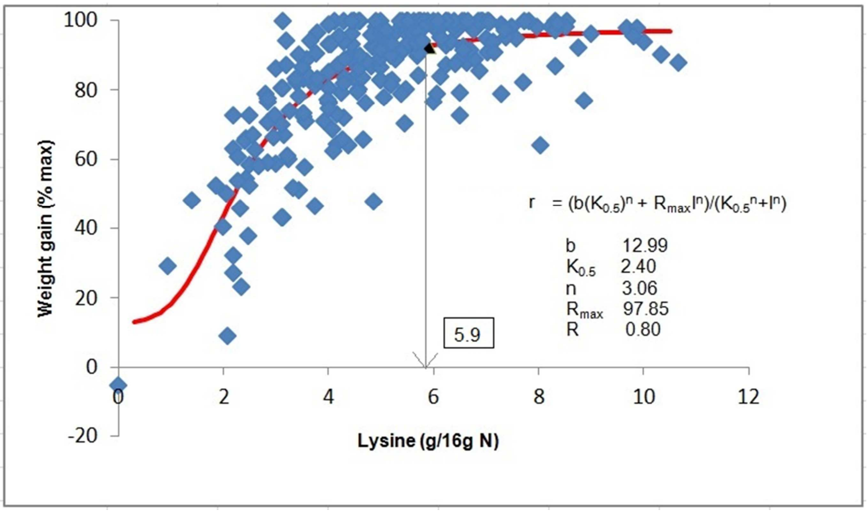

Figure 4. Weight gain (% max) as a function of dietary lysine level (g/16 g N).

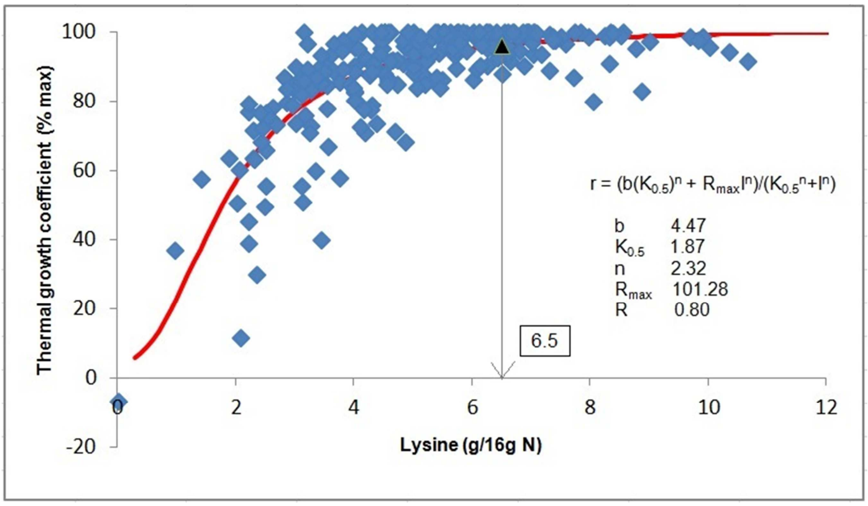

Figure 5. Thermal growth coefficient (% max) as a function of dietary lysine level (g/16 g N).

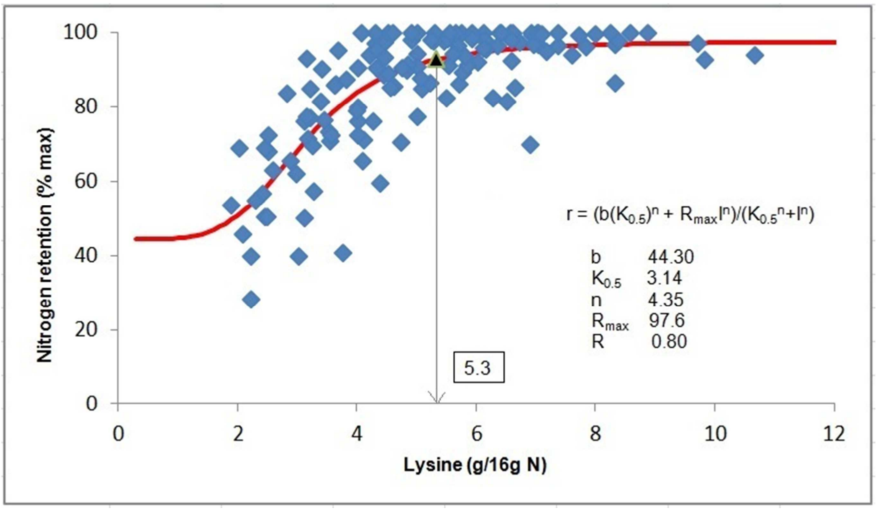

Figure 6. Nitrogen retention (% max) as a function of dietary lysine level (g/16 g N).

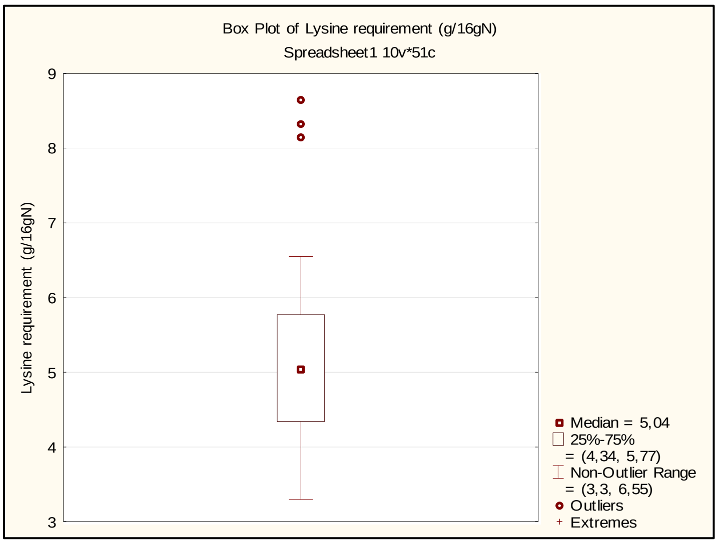

Figure 7. *Box plot* of dose-response lysine requirement studies.

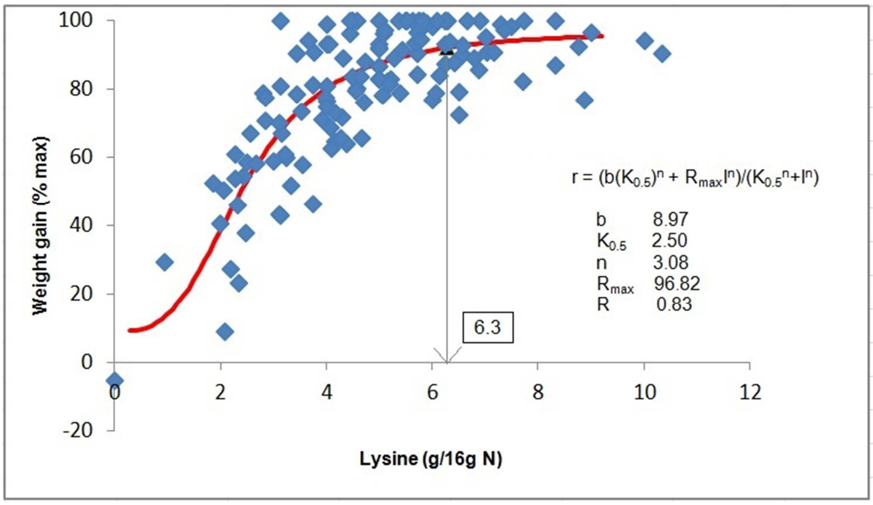

Figure 8. Weight gain (% max) as a function of dietary lysine level (g/16 g N), for freshwater species.

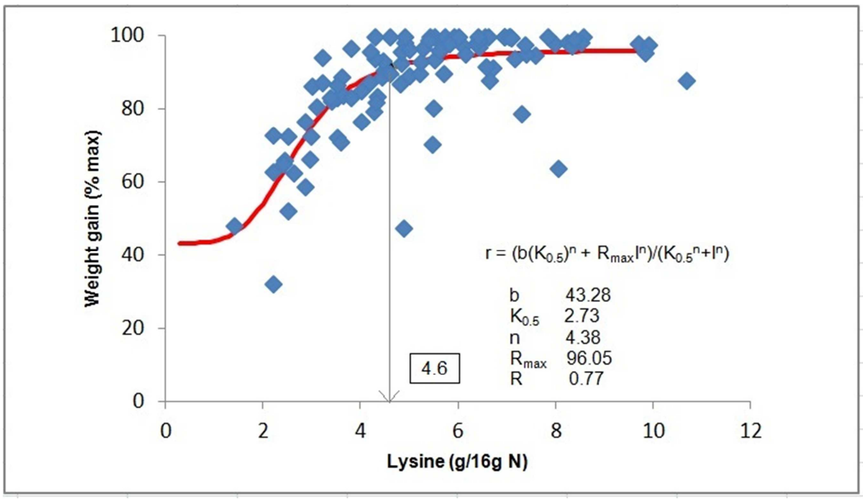

Figure 9. Weight gain (% max) as a function of dietary lysine level (g/16 g N), for seawater species.

Meta-analysis of Lys requirements of FW and SW seem to indicate that there are differences among fish species of the two habitats. While the optimum dietary Lys requirement of FW fish species was about 6.3 g/16g N (Figure 8) that of SW fish was estimated to be 4.6 g/16g N (Figure 9). However, it is important to notice that available data to estimate requirements was smaller for SW species than for FW species, and this may influence the evaluation.

According to literature, the wide variation observed in the Lys requirements among fish species (Table 3) may be related to differences in the following parameters: (1) the dietary protein sources, the reference amino acid pattern and the dietary energy in the diets (Forster and Ogata, 1998; Simmons et al., 1999; De Silva et al., 2000); (2) fish size and age, feeding regime, feed allowance, diet formulation and rearing conditions (Kim et al., 1992; Encarnação et al., 2004); (3) species (strains), availability of amino acid and amino acid sources (Akiyama et al.,1997; Forster and Ogata, 1998; De Silva et al., 2000); (4) response variable and statistical model used to estimate the requirement value (Rodehutscord et al., 1997).

3.2 – Arginine

Similarly to Lys, BL was the model most used for analyzing data collected from Arg dose-response studies (about 67% of the experiments) (Table 4). Despite that, a continuous approach has been reported to better reflect the physiological response of fish (Shearer, 2000). Thus, a SKM-4 parameter regression analysis (Mercer et al, 1984) was applied to predict the response to the dietary Arg level. On adjusting this model to WG and TGC, the optimum Arg level was estimated to be 7% and 5.8% of dietary protein, respectively (Figures 10, 11). The lower requirement value found for TGC can in part be explained by the correction related to thermic differences among studies that caused a reduction in data dispersion and consequently provided a higher correlation coefficient value (R = 0.83) (Figures 10, 11). When NR was plotted against dietary Arg concentrations, the requirement was estimated at 5.6 g/16g N (Figure 12), a value much close to that obtained with TGC as growth parameter estimation. However, as can be seen in table 4, not all studies have information on this response variable and for this reason only 16 studies were included for regression.

Table 4. Data collected from dose-response arginine (Arg) requirement studies.

Fish species		Initial body weight (g/fish)	Water temperature (ºC)	Salinity	Trial duration (days)	Feeding Regimen	Protein ingredients	Diet crude protein (%)	Diet crude lipid (%)	Energy (kJ/g)	References
Common name	**Scientific name**										
African catfish	*Clarias gariepinus*	16.6	28	FW	70	Satiation	Casein, gelatin	40	-	12	Fagbenro et al., 1999a
Asian sea bass	*Lates calcarifer*	2.6	29	SW	84	Fixed ration	Peruvian FM, zein, SM	48.5	10.3	-	Murillo Gurrea et al., 2001
Atlantic salmon	*Salmo salar*	111	15	SW	98	Satiation	Casein, MG	40	-	-	Lall et al., 1994
Atlantic salmon	*Salmo salar*	383	6.5	SW	126	Satiation	Zein, FM, MG	42	-	14.7	Berge et al., 1997
Black seabream	*Sparus macrocephalus*	10.5	28	SW	56	Satiation	FM, SPC	38	14.2	15.5	Zhou et al., 2010b
Channel catfish	*Ictalurus punctatus*	6.7	27	FW	56	Fixed ration	Casein, gelatin	24	-	11.5	Robinson et al., 1981
Channel catfish	*Ictalurus punctatus*	11.4	27	FW	56	Satiation	Casein, gelatin	24	-	-	Buentello and Galtin, 2000
Chinook salmon	*Oncorhynchus tshawytacha*	3.5	10	FW	70	-	Casein, gelatin	40	-	-	Klein and Halver, 1970
Coho salmon	*Oncorhynchus kisutch*	0.9	15	FW	56	Satiation	WGl, casein, gelatin	45.2	-	-	Luzzana et al., 1998
Coho salmon	*Oncorhynchus kisutch*	0.9	15	FW	56	Fixed ration	WGl, casein, gelatin	45.2	-	-	Luzzana et al., 1998
Coho salmon	*Oncorhynchus kisutch*	2.9	10	FW	70	-	Casein, gelatin	40	-	-	Klein and Halver, 1970
Common carp	*Cyprinus carpio*	0.57	25	FW	42	Satiation	-	38.5	-	-	Nose, 1979
European seabass	*Dicentrarchus labrax*	2.1	25	BW	63	Fixed ration	MG, HM	46	12	-	Tibaldi et al., 1994
Hybrid clarias	*C. gariepinus x C. macrocephalus*	6.5	26	FW	28	Fixed ration	Casein, gelatin	40	-	17.9	Singh and Khan, 2007
Hybrid striped bass	*M. chrysops x M. saxatilis*	3.1	28	FW	98	Fixed ration	Casein, gelatin	35	-	-	Griffin et al., 1994
Hybrid striped bass	*M. chrysops x M. saxatilis*	7.1	28	FW	70	Fixed ration	Casein, gelatin	35	-	-	Griffin et al., 1994
Indian catifish	*Heteropneustes fossilis*	5.1	-	FW	84	Satiation	Casein, gelatin	40	-	18	Khan and Abidi, 2011
Japanese flounder	*Paralichthys olivaceus*	1.9	21	SW	40	Fixed ration	Casein, gelatin	50	9.8	-	Alam et al., 2002
Largemouth bass	*Micropterus salmoides*	25.0	28	FW	56	Satiation	FM, ShM, MG, casein, SPC, WGl	45.9	12.2	21.5	Zhou et al., 2012a
Milkfish	*Chanos chanos*	0.7	29	SW	84	Satiation	Casein, gelatin	40	-	-	Borlongan, 1991
Mrigal carp	*Cirrhinus mrigala*	0.6	27	FW	56	Fixed ration	Casein, gelatin	40	-	17.9	Ahmed and Khan, 2004a
Nile tilapia	*Oreochromis niloticus*	0.02	27	FW	56	Satiation	Casein, gelatin	28	-	-	Santiago and Lovell, 1988

Table 4. (Continued).

Fish species		Arg levels (% diet)	Arg levels (g/16gN)	Termal growth coefficient	Nitrogen retention (%NI)	Arg requeriment (% diet)	Arg requirement (g/16gN)	Response variable	Statistical Model	References
Common name	**Scientific name**									
African catfish	*Clarias gariepinus*	1.4-2.4	3.5-6	0.56-0.62	-	1.8	4.5	WG	BL	Fagbenro et al., 1999a
Asian sea bass	*Lates calcarifer*	0.73-3.73	1.59-8.11	0.39-0.56	-	1.8	3.8	WG, survival, FER	BL	Murillo Gurrea et al., 2001
Atlantic salmon	*Salmo salar*	1.1-3.2	2.8-8	1.18-1.4	35-42	1.6	4.1	WG, FE, NR	BL	Lall et al., 1994
Atlantic salmon	*Salmo salar*	1.13-2.86	2.7-6.6	0.98-1.22	0.43-0.68	2.12-2.16	5.0-5.1	WG, NR	LM	Berge et al., 1997
Black seabream	*Sparus macrocephalus*	1.85-3.46	4.9-9.1	0.83-0.97	36-44	2.79 / 3.1	7.74 / 8.1	SGR / PER	BL / SOPR	Zhou et al., 2010b
Channel catfish	*Ictalurus punctatus*	0.2-1.6	0.8-6.7	0.05-0.38	-	1.0	4.3	WG	BL	Robinson et al., 1981
Channel catfish	*Ictalurus punctatus*	0.5-2.0	2.1-8.3	0.24-0.49	16-35	0.8-0.9	3.3-3.8	WG, FE	BL	Buentello and Galtin, 2000
Chinook salmon	*Oncorhynchus tshawytacha*	1.6-3.6	4.0-9.0	0.68-0.92	-	2.4	6.0	WG	LSR	Klein and Halver, 1970
Coho salmon	*Oncorhynchus kisutch*	1.58-3.84	3.5-8.5	0.83-0.93	23-28	2.2	4.9	WG	BL	Luzzana et al., 1998
Coho salmon	*Oncorhynchus kisutch*	1.58-3.84	3.5-8.6	0.72-0.80	29-33	2.5	5.5	WG	BL	Luzzana et al., 1998
Coho salmon	*Oncorhynchus kisutch*	1.2-3.6	3.0-9.0	0.58-1	-	2.3	5.8	WG	LSR	Klein and Halver, 1970
Common carp	*Cyprinus carpio*	0-2.89	0-7.5	0.04 - 0.47	-	1.66	4.3	SGR	Not reported	Nose, 1979
European seabass	*Dicentrarchus labrax*	1.8	2.2-6.2	0.53-0.63	17-22	1.8	3.9	WG	BL / SKM-4 parameter	Tibaldi et al., 1994
Hybrid clarias	*C. gariepinus x C. macrocephalus*	1.8	2.5-5.6	1.21-2.21	-	1.78 / 2	4.45 / 5	WG / FCR	SOPR	Singh and Khan, 2007
Hybrid striped bass	*M. chrysops x M. saxatilis*	1-2.4	2.9-6.9	0.45-0.51	-	1.53	4.37	FE	BL	Griffin et al., 1994
Hybrid striped bass	*M. chrysops x M. saxatilis*	0.6-2	1.7-5.7	0.45-0.62	-	1.55 / 1.45	4.43 / 4.14	WG / FE	BL	Griffin et al., 1994
Indian catifish	*Heteropneustes fossilis*	2.04-2.26	3.8-6.3	0.89-2.31 (DGI)	15-42	2.04-2.26	5.1-5.65	AWG, FCR, PRE, ERE	BL / EF	Khan and Abidi, 2011
Japanese flounder	*Paralichthys olivaceus*	2.0	2.5-6.5	0.46-0.92	19-48	2.04 / 2.1	4.08 / 4.2	WG / FCE	BL	Alam et al., 2002
Largemouth bass	*Micropterus salmoides*	1.9	3.7-6.6	0.64-0.75	42-50	1.9	4.2	WG	BL	Zhou et al., 2012a
Milkfish	*Chanos chanos*	2.1	3.65-6.25	0.13-0.24	-	2.1	5.3	WG	BL	Borlongan, 1991
Mrigal carp	*Cirrhinus mrigala*	1.8	2.5-5.6	0.19-0.35	-	1.8	4.6	WG, FCR, PER	SOPR	Ahmed and Khan, 2004a
Nile tilapia	*Oreochromis niloticus*	1.2	2.1-6.4	0.47-0.51	-	1.2	4.2	WG	BL	Santiago and Lovell, 1988

Table 4. (Continued).

Fish species		Initial body weight (g/fish)	Water temperature (ºC)	Salinity	Trial duration (days)	Feeding Regimen	Protein ingredients	Diet crude protein (%)	Diet crude lipid (%)	Energy (kJ/g)	References
Common name	**Scientific name**										
Rainbow trout	*Oncorhynchus mykiss*	7.0	10	FW	84	Fixed ration	White FM, zein, gelatin	45	-	-	Walton et al., 1986
Rainbow trout	*Oncorhynchus mykiss*	12.6	15	FW	42	Satiation	Casein, gelatin	35	-	-	Kim et al., 1992
Rainbow trout	*Oncorhynchus mykiss*	47.0	17	FW	51	Satiation	WGl	34	27.8	20.1 (DE)	Rodehutscord et al., 1995b[1]
Red drum	*Sciaenops ocellatus*	3.8	29	SW	49	Fixed ration	Red drum muscle	35	-	13.4	Barziza et al., 2000
Rohu carp	*Labeo rohita*	0.6	28	FW	56	Satiation	Casein, gelatin	40	-	17.9	Abidi and Khan, 2009
Rohu carp	*Labeo rohita*	1.7	27	FW	60	Satiation	Casein, gelatin	40	-	-	Murthy and Varghese, 1995
Silver perch	*Bidyanus bidyanus*	0.4	19	FW	84	Satiation	Casein, gelatin	40	15.5	20.5	Ngamsnae et al., 1999
Tilapia	*Sarotherodon mossambicus*	1.7	25	FW	49	Fixed ration	Groundnut, soya, FM	40	-	-	Jackson and Capper, 1982
Yellow grouper	*Epinephelus awoara*	4.2	28	SW	56	Satiation	FM, SBM	43	10	-	Zhou et al., 2012b
Yellow perch	*Perca flavescens*	11.0	22	FW	56	Satiation	Casein, gelatin	33	-	-	Twibell and Brown, 1997
Yellowtail	*Seriola quinqueradiata*	32.0	-	SW	28	Satiation	Casein, Brown FM	42	-	15.3	Ruchimat et al., 1998

Table 4. (Continued).

Fish species		Arg levels (% diet)	Arg levels (g/16gN)	Termal growth coefficient	Nitrogen retention (%NI)	Arg requeriment (% diet)	Arg requirement (g/16gN)	Response variable	Statistical Model	References
Common name	**Scientific name**									
Rainbow trout	*Oncorhynchus mykiss*	1.6-1.8	1.8-6.2	0.83-1.40	-	1.6-1.8	3.6-4	WG	BL	Walton et al., 1986
Rainbow trout	*Oncorhynchus mykiss*	1.4	1.3-7.1	1.06-1.84	23-38	1.4	4.0	WG	BL	Kim et al., 1992
Rainbow trout	*Oncorhynchus mykiss*	0.15-1.65	-	-	-	1.2	3.4	PD	EF	Rodehutscord et al., 1995b[1]
Red drum	*Sciaenops ocellatus*	1.8	1.9-7.9	0.57-0.84	22-29	1.75 / 1.44 / 1.48	5 / 4.11 / 4.23	WG / FE / PER	BL	Barziza et al., 2000
Rohu carp	*Labeo rohita*	1.22-1.39	1.3-4.4	0.13-0.4	14-37	1.22-1.39	3.05-3.47	WG, SGR, FCR, PER, PRE, ERE	BL	Abidi and Khan, 2009
Rohu carp	*Labeo rohita*	2.3	3.65-6.25	0.16-0.29	-	2.3	5.8	WG	BL	Murthy and Varghese, 1995
Silver perch	*Bidyanus bidyanus*	2.7	5.3-7.3	0.17-0.22	33-48	2.7	6.8	WG	BL	Ngamsnae et al., 1999
Tilapia	*Sarotherodon mossambicus*	1.6	4-8.0	0.43-0.5	29-34	1.6	4.0	WG	MRT	Jackson and Capper, 1982
Yellow grouper	*Epinephelus awoara*	2.8	4.7-7.6	0.63-0.73	20-23	2.8	6.5	SGR, WG	QRA	Zhou et al., 2012b
Yellow perch	*Perca flavescens*	1.6	1.3-5.6	0.11-0.67	-	1.61 / 1.41	4.87 / 4.27	WG / FE	QRA	Twibell and Brown, 1997
Yellowtail	*Seriola quinqueradiata*	1.5	3.4-5.8	5.44-6.36 (DGI)	21-27	1.5	3.5	WG	MRT	Ruchimat et al., 1998

FW, freshwater; SW, seawater; BW, brackish water; FM, fish meal; SM, squid meal; MG, maize gluten; SPC, soy-bean protein concentrate; WGl, wheat gluten; HM, herring meal; ShM, shrimp meal; SBM, soy-bean meal; DE, digestible energy; DGI, daily growth index; WG, weight gain; FER, feed efficiency ratio; SGR, specific growth rate; SFLC, serum free lysine concentration; GPR, gross protein retention; DPD, daily protein deposition; FE, feed efficiency; NR, nitrogen retention; PER, protein efficiency ratio; FCR, feed conversion ratio; PD, protein deposition; PRE, protein retention efficiency; ANU, apparent nitrogen utilization; BL, broken line regression; LM, linear model; SOPR, second order polynomial regression; LSR, least squares regression; MRT, Duncan's multiple-rang test; SKM, saturation kinetic model; EF, exponential function; QRA, quadratic regression.

[1] this article does not have the information required for statistical treatment

Table 5. Data collected from dose-response leucine (Leu) requirement studies.

Fish species		Initial body weight (g/fish)	Water temperature (ºC)	Salinity	Trial duration (days)	Feeding Regimen	Protein ingredients	Diet crude protein (%)	Diet crude lipid (%)	Energy (kJ/g)	References
Common name	**Scientific name**										
Channel catfish	*Ictalurus punctatus*	7,14	26,7	FW	56	Fixed ration	Casein, gelatin	24	-	11.5	Wilson et al., 1980
Chinook Salmon	*Oncorhynchus tshawytacha*	2,47	10	SW	56	Fixed ration	Casein, gelatin	41	-	14.8	Chance et al., 1964
Common carp	*Cyprinus carpio*	0,55	25	FW	42	Satiation	-	38.5	-	-	Nose, 1979
Common carp	*Cyprinus carpio*	4,32	26	FW	43	Satiation	-	38.5	-	-	Nose, 1979
Lake trout	*Salvelinus namaycush*	3,18	8,3	FW	84	-	AM, BM, CM	35	-	16.2	Hughes and Rumsey, 1983
Mrigal carp	*Cirrhinus mrigala*	0,64	28	FW	56	Fixed ration	Casein, gelatin	40	-	17.9 (GE)	Ahmed and Khan, 2006
Nile Tilapia	*Oreochromis niloticus*	0,057	27	FW	56	Satiation	Casein, gelatin	28	-	10.5 (DE)	Santiago and Lovell, 1988
Rainbow trout	*Oncorhynchus mykiss*	49	15,7	FW	53	Satiation	WGl	34	27.5	20.1 (DE)	Rodehutscord et al., 1997[1]
Rohu carp	*Labeo rohita*	0,4	26,75	FW	56	Satiation	Casein, gelatin	40	-	17.8	Abidi and Khan, 2007

Table 5. (Continued).

Fish species		Leu levels (% diet)	Leu levels (g/16gN)	ILe level (% diet)	Termal growth coefficient	Nitrogen retention (%NI)	Leu requeriment (% diet)	Leu requirement (g/16gN)	Response variable	Statistical Model	References
Common name	**Scientific name**										
Channel catfish	*Ictalurus punctatus*	0.6-2	2.5-8.3	-	0.38-0.54	-	0.84	3.5	WG	BL	Wilson et al., 1980
Chinook Salmon	*Oncorhynchus tshawytacha*	1-3.1	2.4-7.6	-	0.21-0.68	-	1.6	3.9	WG	Not reported	Chance et al., 1964
Common carp	*Cyprinus carpio*	0.0-2.5	0-6.5	0.95	- 0.01 a 0.49	-	1.27	3.3	SGR	Not reported	Nose, 1979
Common carp	*Cyprinus carpio*	0.0-5	0-13	2.86	- 0.02 a 0.37	-	1.27	3.3	SGR	Not reported	Nose, 1979
Lake trout	*Salvelinus namaycush*	0.96-2.24	2.7-6.4	0.9	1.06-1.25	-	1.3-1.7	2.74-3.66	WG	MRT	Hughes and Rumsey, 1983
Mrigal carp	*Cirrhinus mrigala*	0.75-2	1.9-5	-	0.16-0.32	13.56-33.86	1.54	3.85	WG, FCR, PER	SOPR	Ahmed and Khan, 2006
Nile Tilapia	*Oreochromis niloticus*	0.6-1.2	2.1-4.3	-	0.45-0.52	-	0.95	3.39	WG	BL	Santiago and Lovell, 1988
Rainbow trout	*Oncorhynchus mykiss*	1-4.2	-	-	-	-	1.36	4	PD	EF	Rodehutscord et al., 1997[1]
Rohu carp	*Labeo rohita*	0.75-2.0	1.9-5	-	0.19-0.39	-	1.5-1.57	3.75-3.92	WG, FCR, PER, BPD	SOPR	Abidi and Khan, 2007

FW, freshwater; SW, seawater; AM, anchovy meal; BM, blood meal; CM, cottonseed meal; WGl, wheat gluten; DE, digestible energy; GE, gross energy; WG, weight gain; SGR, specific growth rate; FCR, feed conversion ratio; PER, protein efficiency ratio; PD, protein deposition; BPD, body protein deposition; BL, broken line regression; MRT, Duncan's multiple-rang test; SOPR, second order polynomial regression; EF, exponential function.

[1] this article does not have the information required for statistical treatment

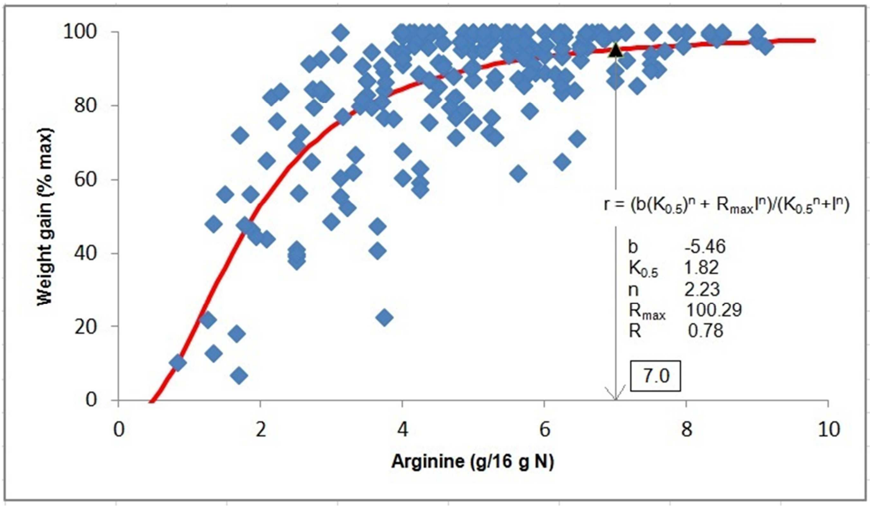

Figure 10. Weight gain (% max) as a function of dietary arginine level (g/16 g N).

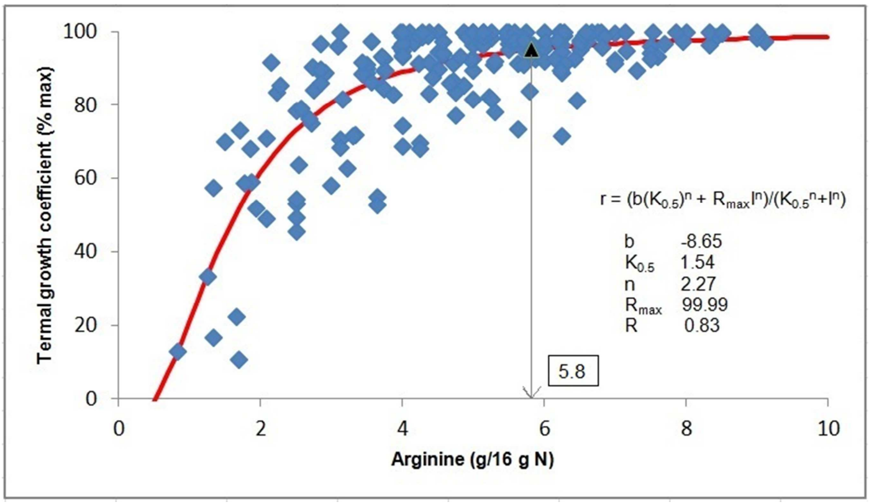

Figure 11. Thermal growth coefficient (% max) as a function of dietary arginine level (g/16 g N).

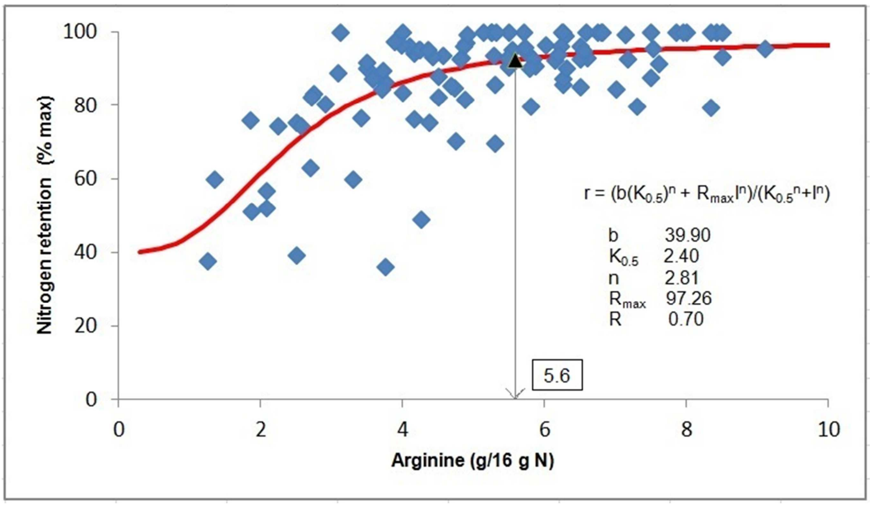

Figure 12. Nitrogen retention (% max) as a function of dietary arginine level (g/16 g N).

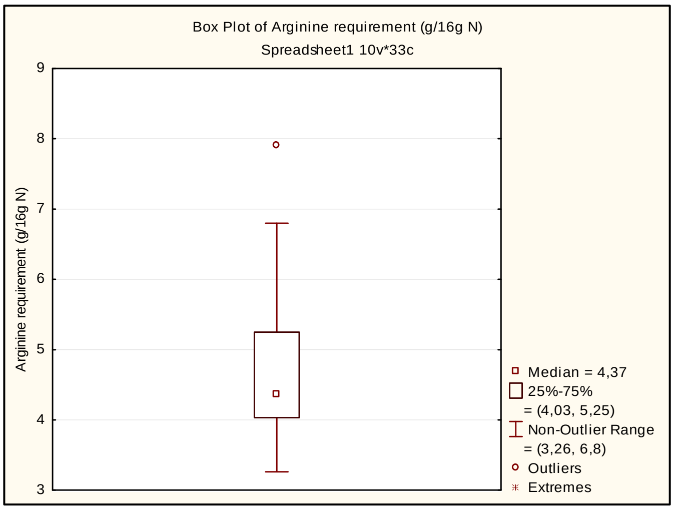

Figure 13. *Box plot* of dose-response arginine requirement studies.

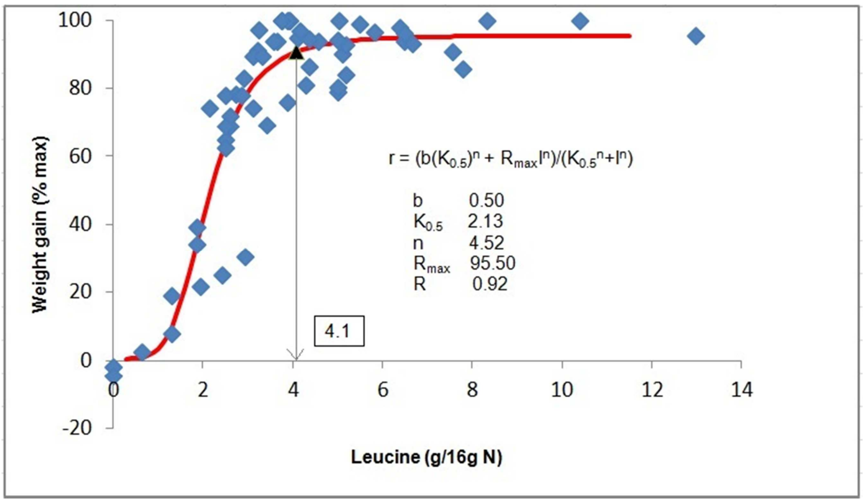

Figure 14. Weight gain (% max) as a function of dietary leucine level (g/16 g N).

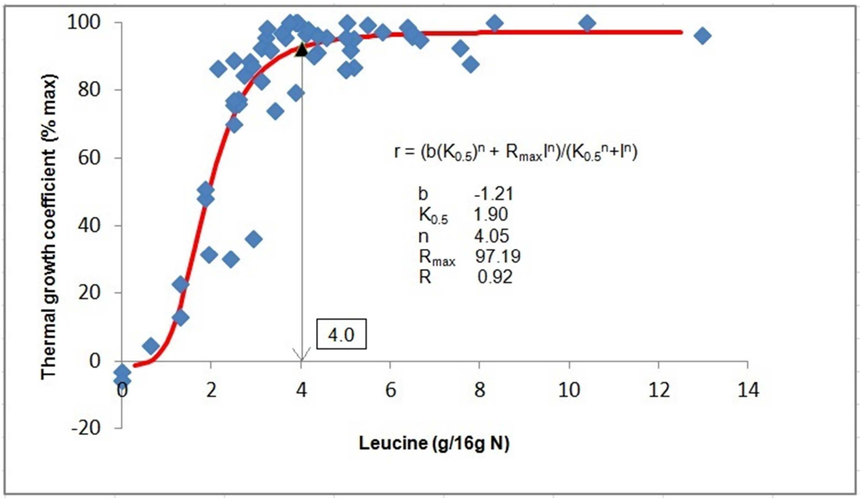

Figure 15. Thermal growth coefficient (% max) as a function of dietary leucine level (g/16 g N).

As found in Lys, the statistical re-evaluation requirement values obtained for Arg fitted well with the individual dose-response requirements estimation, which range from 3.3 to 8.1 g/16g N (Tables 1, 2 and 4). However, when the collected data was submitted to a box-plot analysis (Figure 13), the Arg requirement value estimated for black seabream (Zhou et al., 2010b) was detected as outlier and removing it from the analysis, the range of determined values become narrow (3.3 to 6.8 g/16g N). However, a re-evaluation of Arg requirement by removing this data set, considering WG as response criterion, revealed no difference on Arg requirement value (7.0 g/16g N), that remained slightly higher than values obtained based on the latter range (3.3 to 6.8 g/16g N).

In addition to laboratory variances, this high variation of Arg requirements among species can in part be explained by the role of Arg in several metabolic pathways, such as precursor of polyamine and nitric oxide (Narita et al., 1995, Wan et al., 2006), and also by the variable capacity of each species for urea production (Anderson, 2001).

3.3 – Branched-Chain Amino Acids

Apart from the factors previously mentioned in 3.1 and 3.2 that may explain the wide variation found in the requirements for EAA among fish species, another important factor that can affect the specific requirements of Leu, Ile and Val is the composition of the test diets in terms of the presence or absence of other BCAA (Ahmed and Khan, 2006). The data of tables 5 and 6 shows the Leu and Ile requirements estimation on the presence of a certain amount (in many studies the value is not reported) of Ile and Leu, respectively. Thus, the wide variability of BCAA values will certainly hamper the standardization process required for a re-evaluation, compromising the accuracy of dietary requirement estimation of the other BCAA under study.

3.3.1 – Leucine

Despite the scarcity of dose-response studies for estimating the optimum dietary Leu requirement for fish, data used in the present re-evaluation fitted well with the SKM-4 parameter model (Mercer et al., 1984). Based on dose-response curve, dietary Leu required to meet 95% of maximum WG was estimated to be 4.1 g/16g N (Figure 14). Likewise, when dietary Leu levels were regressed against TGC, using the same model, a similar requirement value (4.0 g/16g N) was obtained (Figure 15).

These values are at the upper limit of the individual dose-response requirements estimation (ranging from 3.2 to 4 g/16g N) (Tables 2, 5) and a possible explanation for that was the present choice for using the SKM-4 parameter model (Mercer et al, 1984) instead of a non-continuous regression analysis which has been reported to underestimate the EAA requirements (Fuller and Garthwaite, 1993; Hauler and Carter, 2001b).

3.3.2 – Isoleucine

The relationship between WG and dietary Ile levels was best expressed by the SKM-4 parameter model (Mercer et al, 1984), and the Ile requirement in the growth response curve was estimated at 2.5% of dietary protein (Figure 16). However, when dietary Ile levels were plotted against TGC, the same statistical model could not be set, probably due to scarcity of available data on dose-response studies for this EAA.

The estimated Ile requirement value was in the range of the individual dose-response requirements estimation (from 1.8 to 4.2 g/16g N) (Tables 2, 6).

3.3.3 – Valine

None of the statistical models used fitted well with available data. The SKM-4 parameter model (Mercer et al, 1984) could not be set and the SOPR analysis presented a low correlation coefficient value (R = 0,5). This fact may be due to the heterogeneity of data (Figure 17) and to the reduced number of dose-response studies available for estimate the optimum dietary Val requirement (Tables 2, 7).

3.4 – Phenylalanine

A SKM-4 parameter (Mercer et al., 1984) regression analysis of WG and TGC against dietary Phe concentrations estimated a requirement value of 4.6 and 4.1 g/16g N, respectively (Figure 18, 19). Once the requirement of this aromatic EAA is influenced by the Tyr level in the diet, experiments in which the Tyr value was not reported (Ngamsnae et al.,1999) or was equal to zero (absence) (Nose, 1979), were not included in statistical analysis. Data collected from Santiago and Lovell (1988) was also excluded due to inconsistency of results and high disease related-mortalities in two aquaria reported by the authors.

Table 6. Data collected from dose-response isoleucine (Ile) requirement studies.

Fish species		Initial body weight (g/fish)	Water temperature (ºC)	Salinity	Trial duration (days)	Feeding Regimen	Protein ingredients	Diet crude protein (%)	Diet crude lipid (%)	Energy (kJ/g)	References
Common name	**Scientific name**										
Channel catfish	*Ictalurus punctatus*	7,14	26,7	FW	56	Fixed ration	Casein, gelatin	24	-	11,5	Wilson et al., 1980
Chinook salmon	*Oncorhynchus tshawytacha*	0,98	10	SW	56	Fixed ration	Casein, gelatin	41	-	14,8	Chance et al., 1964
Common carp	*Cyprinus carpio*	3,5	25	FW	42	Satiation	-	38,5	-	-	Nose, 1979
Lake trout	*Salvelinus namaycush*	3,18	8,3	FW	84	-	AM, BM, CM	35	-	16,2	Hughes and Rumsey, 1983
Mrigal carp	*Cirrhinus mrigala*	0,61	28	FW	56	Fixed ration	Casein, gelatin	40	-	17,9 (GE)	Ahmed and Khan, 2006
Nile tilapia	*Oreochromis niloticus*	0,087	27	FW	56	Satiation	Casein, gelatin	28	-	10,5 (DE)	Santiago and Lovell, 1988
Rainbow trout	*Oncorhynchus mykiss*	47	16	FW	59	Satiation	WGl	33	28	20,1 (DE)	Rodehutscord et al., 1997[1]
Rohu carp	*Labeo rohita*	0,4	26,75	FW	56	Satiation	Casein, gelatin	40	-	17,9	Khan and Abidi, 2007

Table 6. (Continued).

Fish species		Ile levels (% diet)	Ile levels (g/16gN)	Leu level (% diet)	Termal growth coefficient	Nitrogen retention (%NI)	Ile requeriment (% diet)	Ile requirement (g/16gN)	Response variable	Statistical Model	References
Common name	**Scientific name**										
Channel catfish	*Ictalurus punctatus*	0,3-1,3	1,3-5,4	-	0,15-0,56	-	0,62	2,58	WG	BL	Wilson et al., 1980
Chinook salmon	*Oncorhynchus tshawytacha*	0,5-2,0	1,2-4,9	3,68	0,38-0,8	-	1	2,44	WG	Not reported	Chance et al., 1964
Common carp	*Cyprinus carpio*	0-4,29	0-11,1	4,27	-0,02- 042	-	0,96	2,5	SGR	Not reported	Nose, 1979
Lake trout	*Salvelinus namaycush*	0,54-1,26	1,5-3,6	1,6	1,17-1,25	-	0,7-0,9	1,54-2,06	WG	MRT	Hughes and Rumsey, 1983
Mrigal carp	*Cirrhinus mrigala*	0,5-1,75	1,3-4,4	-	0,16-0,33	13,26-33,78	1,26	3,15	WG, FCR, PER	SOPR	Ahmed and Khan, 2006
Nile tilapia	*Oreochromis niloticus*	0,4-1,1	1,4-3,9	-	0,44-0,51	-	0,87	3,11	WG	BL	Santiago and Lovell, 1988
Rainbow trout	*Oncorhynchus mykiss*	0,5-1,53	-	-	-	-	1,37	4,15	PD	EF	Rodehutscord et al., 1997[1]
Rohu carp	*Labeo rohita*	0,75-2,0	1,9-5	-	0,31-0,43	-	1,52-1,59	3,8-4	WG, FCR, PER, SGR, PPV	SOPR	Khan and Abidi, 2007

FW, freshwater; SW, seawater; AM, anchovy meal; BM, blood meal; CM, cottonseed meal; WGl, wheat gluten; DE, digestible energy; GE, gross energy; WG, weight gain; SGR, specific growth rate; FCR, feed conversion ratio; PER, protein efficiency ratio; SGR, specific growth rate; PD, protein deposition; PPV, protein predictive value; BL, broken line regression; MRT, Duncan's multiple-rang test; SOPR, second order polynomial regression; EF, exponential function.

[1] this article does not have the information required for statistical treatment.

Table 7. Data collected from dose-response valine (Val) requirement studies.

Fish species		Initial body weight (g/fish)	Water temperature (ºC)	Salinity	Trial duration (days)	Feeding Regimen	Protein ingredients	Diet crude protein (%)	Diet crude lipid (%)	Energy (kJ/g)	References
Common name	**Scientific name**										
Channel catfish	*Ictalurus punctatus*	11,76	26,7	FW	56	Fixed ration	Casein, gelatin	24	-	11,5	Wilson et al., 1980
Chinook salmon	*Oncorhynchus tshawytacha*	0,67	10	SW	56	Fixed ration	Casein, gelatin	41	-	-	Chance et al., 1964
Common carp	*Cyprinus carpio*	1,48	25	FW	42	Satiation	-	38,5	-	-	Nose, 1979
Lake trout	*Salvelinus namaycush*	7,04	8,3	FW	84	-	AM, BM, CM	35	-	16,2	Hughes and Rumsey, 1983
Mrigal carp	*Cirrhinus mrigala*	0,62	28	FW	56	Fixed ration	Casein, gelatin	40	-	17,9 (GE)	Ahmed and Khan, 2006
Nile tilapia	*Oreochromis niloticus*	0,05	27	FW	56	Satiation	Casein, gelatin	28	-	10,5 (DE)	Santiago and Lovell, 1988
Rainbow trout	*Oncorhynchus mykiss*	49	15,7	FW	53	Satiation	WGl	34	28	20,1 (DE)	Rodehutscord et al., 1997[1]
Rohu carp	*Labeo rohita*	0,16	26	FW	42	Fixed ration	Casein, gelatin	40	-	17,9	Abidi and Khan , 2004b

Table 7. (Continued).

Fish species		Val levels (% diet)	Val levels (g/16gN)	Termal growth coefficient	Nitrogen retention (%NI)	Val requeriment (% diet)	Val requirement (g/16gN)	Response variable	Statistical Model	References
Common name	**Scientific name**									
Channel catfish	*Ictalurus punctatus*	0,4-1,6	1,7-6,7	0,29-0,62	-	0,71	2,96	WG	BL	Wilson et al., 1980
Chinook salmon	*Oncorhynchus tshawytacha*	0,65-1,9	1,6-4,6	0,71-0,9	-	1,3	3,17	WG	Not reported	Chance et al., 1964
Common carp	*Cyprinus carpio*	0,5-1,5	1,3-3,9	-0,04-0,29	-	1,39	3,6	SGR	Not reported	Nose, 1979
Lake trout	*Salvelinus namaycush*	0,78-1,82	0,9-2,2	1,09-1,15	-	0,62-0,78	1,77-2,23	WG, SFVC	MRT	Hughes and Rumsey, 1983
Mrigal carp	*Cirrhinus mrigala*	0,75-2	1,9-5	0,17-0,33	13,91-34,48	1,5	3,75	WG, FCR, PER	SOPR	Ahmed and Khan, 2006
Nile tilapia	*Oreochromis niloticus*	0,0-1,5	0,0-3,9	-0,04-0,29	-	0,78	2,8	WG	BL	Santiago and Lovell, 1988
Rainbow trout	*Oncorhynchus mykiss*	0,62-3,42	-	-	-	1,36	4	PD	EF	Rodehutscord et al., 1997[1]
Rohu carp	*Labeo rohita*	0,75-2	1,9-5	0,12-0,19	8,63-27,03	1,63 / 1,5 / 1,5	4 / 3,75 / 3,75	WG / FCR / PD	SOPR	Abidi and Khan , 2004b

FW, freshwater; SW, seawater; AM, anchovy meal; BM, blood meal; CM, cottonseed meal; WGl, wheat gluten; GE, gross energy; DE, digestible energy; WG, weight gain; SGR, specific growth rate; SFVC, serum free valine concentration; FCR, feed conversion ratio; PER, protein efficiency ratio; PD, protein deposition; BL, broken line regression; MRT, Duncan's multiple-range test; SORP, second order polynomial regression; EF, exponential function.

[1] this article does not have the information required for statistical treatment.

Table 8. Data collected from dose-response phenylalanine (Phe) requirement studies.

Fish species		Initial body weight (g/fish)	Water temperature (ºC)	Salinity	Trial duration (days)	Feeding Regimen	Protein ingredients	Diet crude protein (%)	Diet crude lipid (%)	Energy (kJ/g)	References
Common name	Scientific name										
Channel catfish	*Ictalurus punctatus*	200	26,7	FW	56	Fixed ration	Casein, gelatin	24	-	9,6	Robinson et al., 1980b
Chinook salmon	*Oncorhynchus tshawytacha*	2,6	10	SW	56	Fixed ration	Casein, gelatin	41	-	14,8	Chance et al., 1964
Common carp	*Cyprinus carpio*	1,54	25	FW	42	Satiation	-	38,5	-	-	Nose, 1979
Common carp	*Cyprinus carpio*	1,5	25	FW	42	Satiation	-	38,5	-	-	Nose, 1979
Common carp	*Cyprinus carpio*	1,52	25	FW	28	Satiation	-	38,5	-	-	Nose, 1979
Mrigal carp	*Cirrhinus mrigala*	0,57	26,2	FW	56	Fixed ration	Casein, gelatin	40	-	17,9	Ahmed, 2009
Nile tilapia	*Oreochromis niloticus*	0,013	27	FW	56	Satiation	Casein, gelatin	28	-	10,5 (DE)	Santiago and Lovell, 1988
Rainbow trout	*Oncorhynchus mykiss*	13	15	FW	42	Satiation	Casein, gelatin	35	-	16	Kim, 1993
Rohu carp	*Labeo rohita*	0,18	26,75	FW	56	Satiation	Casein, gelatin	40	-	17,9	Khan and Abidi, 2007
Silver perch	*Bidyanus bidyanus*	10	19	FW	84	Satiation	Casein, gelatin	41	15,5	20,5	Ngamsnae et al., 1999

Table 8. (Continued).

Fish species		Phe levels (% diet)	Phe levels (g/16gN)	Tyr level (% diet)	Termal growth coefficient	Nitrogen retention (%NI)	Phe requeriment (% diet)	Phe requirement (g/16gN)	Response variable	Statistical Model	References
Common name	Scientific name										
Channel catfish	*Ictalurus punctatus*	0,2-0,8	0,8-3,3	0,6	0,52-1,39	-	0,5	2,1	WG, FE	BL	Robinson et al., 1980b
Chinook salmon	*Oncorhynchus tshawytacha*	0,96-3,5	2,3-8,5	0,4	0,48-0,65	-	1,7	4,4	WG	Not reported	Chance et al., 1964
Common carp	*Cyprinus carpio*	0,0-2,75	0,0-7,1	0	-0,07-0,27	-	2,5	6,5	SGR	Not reported	Nose, 1979
Common carp	*Cyprinus carpio*	0,25-2	0,6-5,2	2,86	-0,04-0,41	-	1,3	3,4	SGR	Not reported	Nose, 1979
Common carp	*Cyprinus carpio*	0,0-2	0,0-5,2	1	-0,04-0,36	-	1,3	3,4	SGR	Not reported	Nose, 1979
Mrigal carp	*Cirrhinus mrigala*	0,5-1,75	1,3-4,4	1	0,16-0,32	14,9-34,24	1,3	3,25	WG, FCR, PER	SOPR	Ahmed, 2009
Nile tilapia	*Oreochromis niloticus*	0,6-1,8	2,1-6,4	0,5	0,41-0,51	-	1,05	3,75	WG	BL	Santiago and Lovell, 1988
Rainbow trout	*Oncorhynchus mykiss*	0,26-1,75	0,7-5	1,33	0,63-1,57	12,7-36,7	0,7	2	WG	BL	Kim, 1993
Rohu carp	*Labeo rohita*	0,4-1,65	1-4,1	1	0.37-0,51	14,29-33,61	1,16-1,22	2,9-3,05	SGR, FCR, PER, BPD	SOPR	Khan and Abidi, 2007
Silver perch	*Bidyanus bidyanus*	0,0-0,8	0-2	-	0,55-0,69	26,1-30,6	2,26	5,7	WG	BL	Ngamsnae et al., 1999

FW, freshwater; SW, seawater; DE, digestible energy; WG, weight gain; FE, feed efficiency; SGR, specific growth rate; PER, protein efficiency ratio; FCR, feed conversion ratio; BPD, body protein deposition; BL, broken line regression; SOPR, second order polynomial regression.

Table 9. Data collected from dose-response histidine (His) requirement studies.

Fish species		Initial body weight (g/fish)	Water temperature (ºC)	Salinity	Trial duration (days)	Feeding Regimen	Protein ingredients	Diet crude protein (%)	Diet crude lipid (%)	Energy (kJ/g)	References
Common name	**Scientific name**										
African catfish	*Clarias gariepinus*	0.22	27.5	FW	84	Satiation	Casein, gelatin	40	-	17.9	Khan and Abidi, 2009
Channel catfish	*Ictalurus punctatus*	6.67	26.7	FW	56	Fixed ration	Casein, gelatin	24	-	11.5	Wilson et al., 1980
Chinook salmon	*Oncorhynchus tshawytacha*	3	10	SW	70	Fixed ration	Casein, gelatin	40	-	-	Klein and Halver, 1970
Chum salmon	*Oncorhynchus keta*	1.35	15	SW	28	Satiation	Casein	40	-	-	Akiyama et al., 1985a
Coho salmon	*Oncorhynchus kisutch*	3.17	10	SW	70	Fixed ration	Casein, gelatin	40	-	-	Klein and Halver, 1970
Common carp	*Cyprinus carpio*	1.7	25	FW	42	Satiation	-	38.5	-	-	Nose, 1979
Indian catfish	*Heteropneustes fossilis*	4.65	24.5	FW	56	Fixed ration	Casein, gelatin	40	-	17.9	Ahmed, 2013
Mrigal carp	*Cirrhinus mrigala*	0.61	26.5-28.5	FW	56	Fixed ration	Casein, gelatin	40	-	17.9	Ahmed and Khan, 2005b
Nile Tilapia	*Oreochromis niloticus*	0.075	27	FW	56	Satiation	Casein, gelatin	28	-	10.5 (DE)	Santiago and Lovell, 1988
Rainbow trout	*Oncorhynchus mykiss*	40	17	FW	53	Satiation	WGl	34	28.4	20.1 (DE)	Rodehutscord et al., 1997[1]
Rohu carp	*Labeo rohita*	0.4	26-27.5	FW	42	Fixed ration	Casein, gelatin	40	-	17.9	Abidi and Khan, 2004a
Rohu carp	*Labeo rohita*	1.8	26-28.5	FW	60	Satiation	Casein, gelatin	40	-	-	Murthy and Varghese, 1995

Table 9. (Continued).

Fish species		His levels (% diet)	His levels (g/16gN)	Thermal growth coefficient	Nitrogen retention (%NI)	His requeriment (% diet)	His requirement (g/16gN)	Response variable	Statistical Model	References
Common name	**Scientific name**									
African catfish	*Clarias gariepinus*	0.25-0.5	0.6-1.3	0.13-0.35	8.38-34	0.4 / 0.4-0.42	1 / 1-1.05	WG, FCR, PER, PRE, ERE	BL / SOPR	Khan and Abidi, 2009
Channel catfish	*Ictalurus punctatus*	0.1-0.8	0.4-3.3	0.11-0.62	-	0.37	1.54	WG	BL	Wilson et al., 1980
Chinook salmon	*Oncorhynchus tshawytacha*	0.7-1.3	1.8-3.3	0.94-0.99	-	0.7	1.75	WG	LSR	Klein and Halver, 1970
Chum salmon	*Oncorhynchus keta*	0.13-1.92	0.33-4.8	0.45-0.92	-	0.7	1.6	WG	MRT	Akiyama et al., 1985a
Coho salmon	*Oncorhynchus kisutch*	0.5-1.3	1.3-3.3	0.81-0.93	-	0.7	1.8	WG	LSR	Klein and Halver, 1970
Common carp	*Cyprinus carpio*	0.0-1	0.0-2.6	0.07-0.37	-	0.8	2.1	SGR	Not reported	Nose, 1979
Indian catfish	*Heteropneustes fossilis*	0.25-0.75	0.6-1.9	0.29-0.69	13.26-33.78	0.54	1.35	WG, FE	SOPR	Ahmed, 2013
Mrigal carp	*Cirrhinus mrigala*	0.25-1.5	0.6-3.9	0.18-0.32	-	0.85	2.13	FCR, PER	SOPR	Ahmed and Khan, 2005b
Nile Tilapia	*Oreochromis niloticus*	0.2-0.8	0.7-2.9	0.39-0.45	-	0.48	1.72	WG	BL	Santiago and Lovell, 1988
Rainbow trout	*Oncorhynchus mykiss*	0.26-1.35	-	-	-	0.58	1.7	PD	EF	Rodehutscord et al., 1997[1]
Rohu carp	*Labeo rohita*	0.25-1.5	0.6-3.8	0.14-0.25	-	0.82	2.05	WG, FCR	SOPR	Abidi and Khan, 2004a
Rohu carp	*Labeo rohita*	0.32-1.3	0.8-3.3	0.16-0.34	-	0.9	2.25	WG	BL	Murthy and Varghese, 1995

FW, freshwater; SW, seawater; WGl, wheat gluten; DE, digestible energy; WG, weight gain; FCR, feed conversion ratio; PER, protein efficiency ratio; PRE, protein retention efficiency; ERE, energy retention efficiency; SGR, specific growth rate; FE, feed efficiency; PD, protein deposition; BL, broken line regression; SOPR, second order polynomial regression; LSR, least square regression; MRT, Duncan's multiple-rang test; EF, exponential function.

[1] this article does not have the information required for statistical treatment.

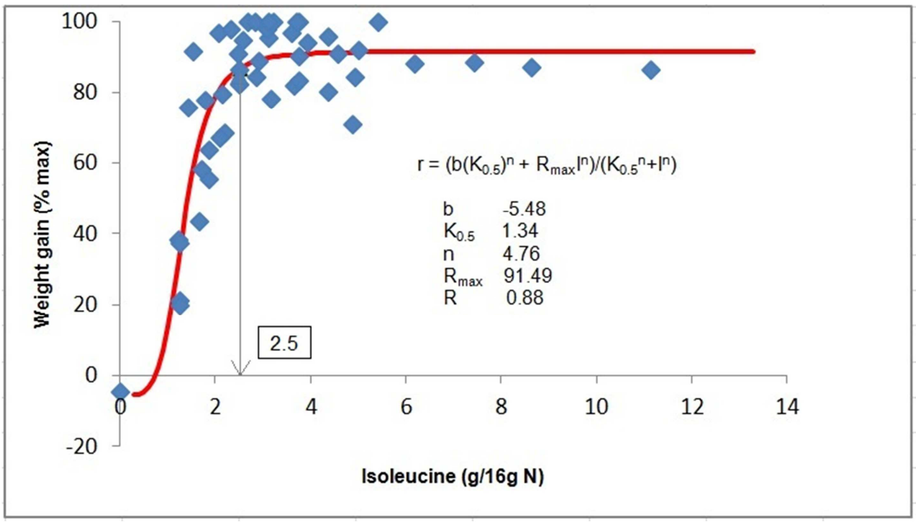

Figure 16. Weight gain (% max) as a function of dietary isoleucine level (g/16 g N).

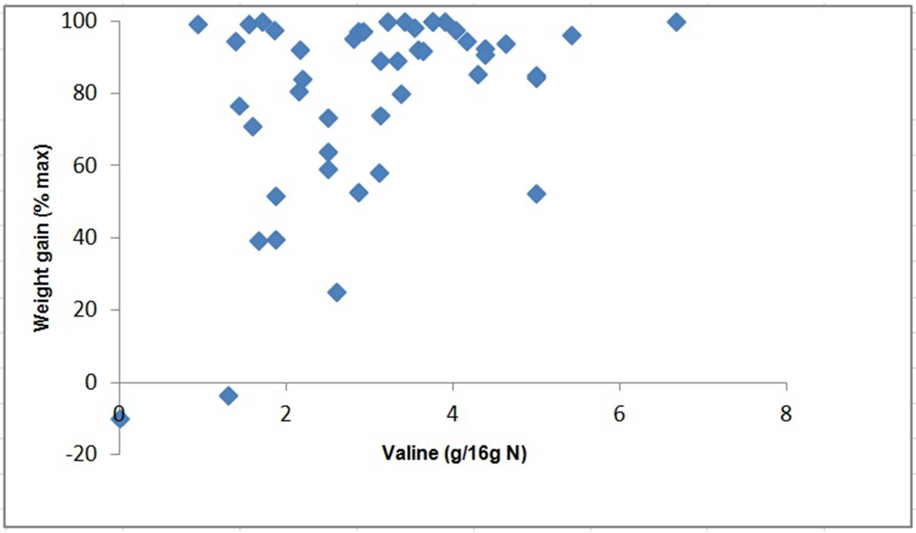

Figure 17. Weight gain (% max) as a function of dietary valine level (g/16 g N).

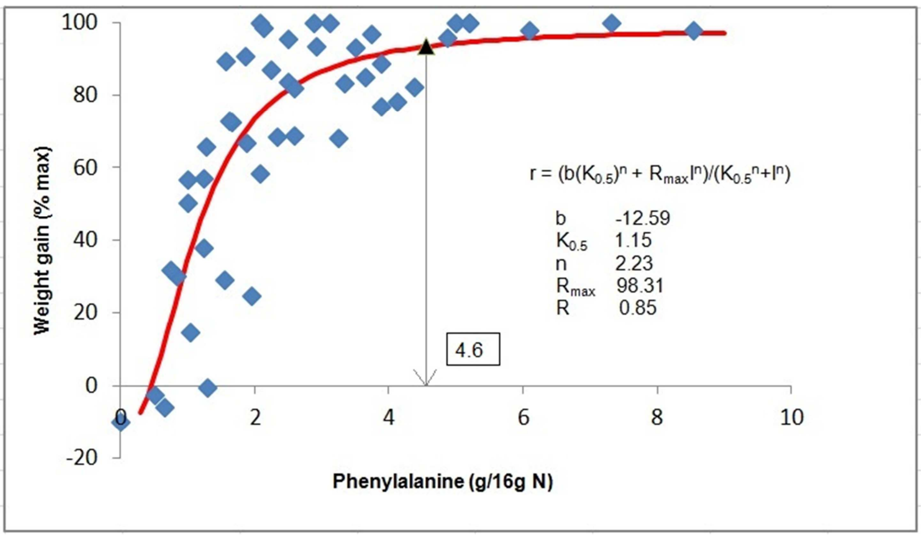

Figure 18. Weight gain (% max) as a function of dietary phenylalanine level (g/16 g N).

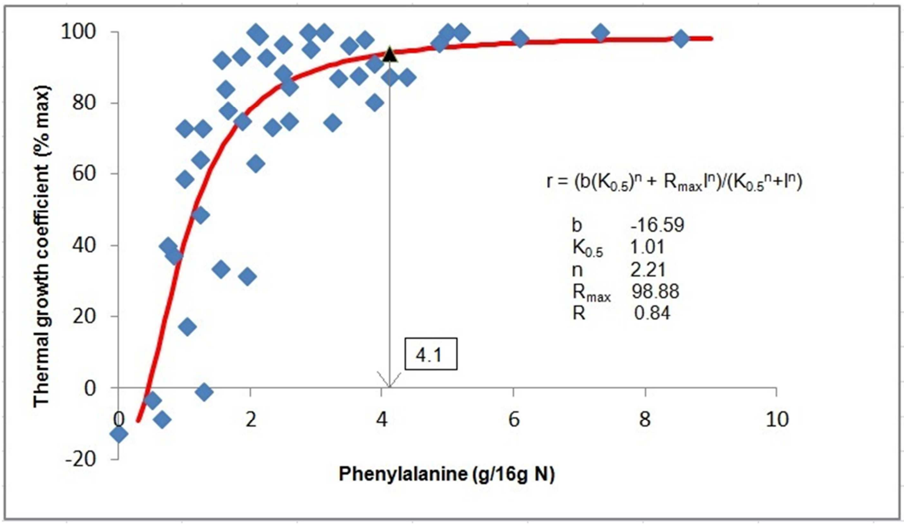

Figure 19. Thermal growth coefficient (% max) as a function of dietary phenylalanine level (g/16 g N).

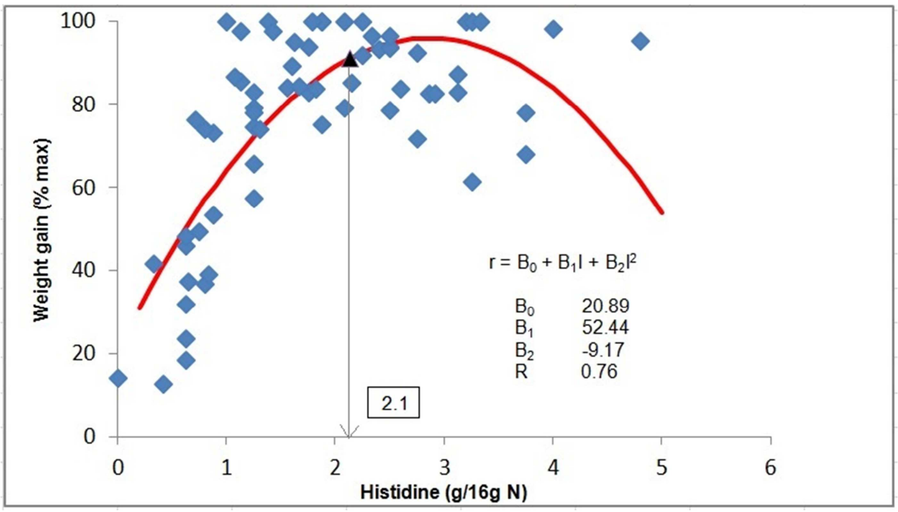

Figure 20. Weight gain (% max) as a function of dietary histidine level (g/16 g N).

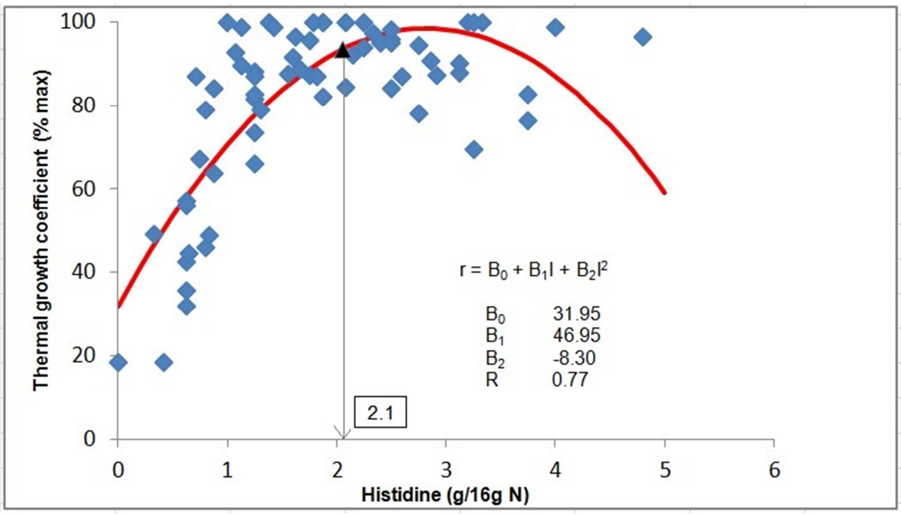

Figure 21. Thermal growth coefficient (% max) as a function of dietary histidine level (g/16 g N).

The estimated Phe requirement values were in the range of the individual dose-response requirements estimation (from 2 to 6.5 g/16g N) (Tables 2, 8). One likely reason for this wide spectrum of requirement values among studies may be the presence or absence of Tyr in the test diet and, if present, its amount.

3.5 – Histidine

Of the two statistical models used in the present re-evaluation, the SOPR (Zeitoun et al., 1976) was the one that better reflected the response of fish to dietary His levels (Figure 20). Based on this model, dietary His level meeting 95% of the His requirement for maximum WG was estimated to be 2.1 g/16g N (Figure 20). This value is in agreement with the obtained from TGG (2.1 g/16g N) (Figure 21).

A symmetrical curve in the context of fish EAA requirement studies means that higher levels of the dietary EAA under study are causing growth depression of fish, presumably due to a toxic effect. According to Murthy and Varghese (1995), growth of rohu decreased when the His dietary level exceeded the optimum requirement concentration. The authors attributed the reported decrease to use of energy in nitrogenous excretion, because excess amino acid is deaminated and excreted in the form of ammonia (Walton, 1985).

The estimated His requirement values were in the range of the individual dose-response requirements estimation (from 1 to 2.25 g/16g N) (Tables 2, 9).

3.6 – Methionine

Several dose-response studies have shown that the presence of the nonessential amino acid Cys in the diet represents a “sparing effect” by reducing the amount of dietary Met required for maximum growth (Fagbenro et al., 1999b). Therefore, it is important to consider the dietary Cys content to quantify the Met requirement of the cultured species for maximum growth and efficient feed utilization (Luo et al., 2005).

The values of dietary Cys content included in the diets used in the evaluation of Met requirement for several fish species are shown in table 10. However, available collected data is not enough to estimate the dietary Met requirements taking in consideration the presence or absence of Cys in the diet. For that reason, the present re-evaluation considered the overall set of data. Thus, the relationship between WG and dietary Met levels (g/16g N) was best expressed by the SOPR model and the Met requirement in the growth response curve was estimated at 3.2% of dietary protein

(Figure 22). Similar trend was also observed for TGC: based on 95% of the maximum TGC, a level of 3.1% of dietary protein is required for Met (Figure 23).

The symmetric curve achieved by the SOPR may be attributed to TSAA toxicity and amino acid catabolism. According to literature, an excess amount of TSAA caused depressive effect such as reduction in growth and feed efficiency in mrigal carp (Ahmed et al., 2003) and also was reported to cause fish stress (Walton, 1985), leading to extra energy expenditure toward deamination and excretion of the same.

The estimated Met requirement values fitted well with the individual dose-response requirements, which range from 1.3 to 4.5 g/16g N (Tables 1, 2 and 10). However, when the collected data was submitted to a box-plot evaluation (Figure 24), the Met requirement value estimated for black seabream (Zhou et al., 2011) was considered an outlier, and removing it from the analysis the range become narrow (1.3 to 3.4 g/16g N). When the mentioned article was excluded from the present re-evaluation, only a slight difference occurred on estimation of requirement values. Based on SOPR, dietary Met level meeting 95% of the Met requirement was estimated to be 3.1 g/16g N for maximum WG and 3.0 g/16g N for maximum TGC, respectively.

One likely reason for this wide spectrum of requirement values among studies may be the presence or absence of Cys in the test diet and, if it is present, its amount.

3.7 – Tryptophan

A SORP (Zeitoun et al, 1976) analysis of WG and TGC against dietary Trp concentrations estimated a requirement value of 0.9 and 0.8 g/16g N, respectively (Figures 25, 26).

Such as His and Met, the reversed U-shaped dose-response curve may be attributed to Trp toxicity and amino acid catabolism. Murthy and Varghese (1997) reported that excessive levels of Trp may have led to an accumulation and oxidation of Trp to ketones and to the production of toxic metabolites that adversely affected growth of rohu. According to Walton (1985), another possible reason for poor growth of fish species fed a diet with an excessive level of Trp may be related to use of energy for nitrogenous excretion, since excess Trp was probably deaminated and excreted in the form of ammonia.

The estimated Trp requirement values were in the range of the individual dose-response requirements estimation (from 0.41 to 1.13 g/16g N) (Tables 2, 11).

Table 10. Data collected from dose-response methionine (Met) requirement studies.

Fish species		Initial body weight (g/fish)	Water temperature (ºC)	Salinity	Trial duration (days)	Feeding Regimen	Protein ingredients	Diet crude protein (%)	Diet crude lipid (%)	Energy (kJ/g)	References
Common name	**Scientific name**										
African catfish	*Clarias gariepinus*	18.7	28	FW	70	Satiation	Casein, gelatin	40	-	12.6	Fagbenro et al., 1999b
Arctic charr	*Salvelinus alpinus*	20.5	12	FW	112	Satiation	Gelatine, MG, HM, SBM	40	17	17.5 (DE)	Simmons et al., 1999
Asian seabass	*Lates calcarifer*	2.59	26	BW	84	Fixed ration	Peruvian FM, SM, SBM	46	10.5	16	Coloso et al., 1999
Black sea bream	*Sparus macrocephalus*	14.21	28	SW	56	Satiation	FM, SPC	38.5	15	15.7	Zhou et al., 2011
Channel catfish	*Ictalurus punctatus*	14	25	FW	42	Fixed ration	Menhaden FM, SBM	27.7	-	18.45	Cai, Y and Burtle, 1996
Channel catfish	*Ictalurus punctatus*	202	27	FW	42	Fixed ration	Casein, gelatin	24	-	11.5	Harding et al., 1977
Cobia	*Rachycentron canadum*	11.61	29	SW	56	Satiation	Brown FM, WGI	44	16	-	Zhou et al., 2006
Common carp	*Cyprinus carpio*	569	23	FW	85	Fixed ration	Gelatin, peas, SPC	40.2	6.9	16.9	Schwartz et al., 1998
Common carp	*Cyprinus carpio*	2.4	25	FW	42	Satiation	-	38.5	-	-	Nose, 1979
Common carp	*Cyprinus carpio*	2.4	26	FW	43	Satiation	-	39.5	-	-	Nose, 1979
European seabass	*Dicentrarchus labrax*	13.4	23	SW	84	Satiation	FPC, WGl, gelatine, SPC, enzyme-treated soyabean	44	14.5	19 (GE)	Tulli et al., 2010
Golden pompano	*Trachinotus ovatus*	12.4	29.5	SW	56	Satiation	FM, MG, SBM, PM, SPC	43	13	-	Niu et al., 2013
Grouper	*Epinephelus coioides*	13.25	29.25	SW	56	Satiation	FM, SPC	48	9.8	14.3 (DE)	Luo et al., 2005
Hybrid striped bass	*Morone chrysops x M. saxatilis*	8.6	24	FW	56	Fixed ration	Lyophilized red drum muscle	35	-	13.6 (DE)	Keembiyehetty and Gatlin, 1993
Japanese flounder	*Paralichthys olivaceus*	2.8	21.6	SW	40	Fixed ration	Casein, gelatin	50	9.6	-	Alam et al., 2000
Mrigal carp	*Cirrhinus mrigala*	0.45	27	FW	42	Fixed ration	Casein, gelatin	40	-	17.9 (GE)	Ahmed et al., 2003
Nile Tilapia	*Oreochromis niloticus*	0.062	27	FW	56	Satiation	Casein, gelatin	28	-	-	Santiago and Lovell, 1988
Nile Tilapia	*Oreochromis niloticus*	5.62	28.3	FW	56	Fixed ration	CM, SBM, gelatin	28	5	17.3	Nguyen and Davis, 2009
Rainbow trout	*Oncorhynchus mykiss*	51	16.8	FW	49	Satiation	WGl	34	27.7	20.1 (DE)	Rodehutscord et al., 1995a[1]
Rockfish	*Sebastes schlegeli*	43.61	19.5	SW	65	Satiation	FM	48.7	10.4	18.9	Yan et al., 2007
Rohu carp	*Labeo rohita*	0.66	26.5	FW	84	Satiation	Casein, gelatin	38	-	17.9 (GE)	Abidi and Khan, 2011
Tilapia	*Sarotherodon mossambicus*	1.7	25	FW	49	Fixed ration	Groundnut, SBM, FM	40	-	-	Jackson and Capper, 1982
Yellow croaker	*Pseudosciaena crocea*	1.23	28.5	SW	70	Satiation	FM, SBM, WM	43	12	-	Mai et al., 2006
Yellowtail	*Seriola quinqueradiata*	23.3	24.8	SW	30	Satiation	Brown FM, SPC, WGl, gelatin	43	17	16.3 (DE)	Ruchimat et al., 1997b

Table 10. (Continued)

Fish species		Met levels (% diet)	Met levels (g/16gN)	Cys level (% diet)	Termal growth coefficient	Nitrogen retention (%NI)	Met requeriment (% diet)	Met requirement (g/16gN)	Response variable	Statistical Model	References
Common name	Scientific name										
African catfish	*Clarias gariepinus*	0.8-1.6	2.0-4.0	0	0.62-0.69	-	1.28	3.2	WG	BL	Fagbenro et al., 1999b
Arctic charr	*Salvelinus alpinus*	0.36-0.96	0.9-2.4	1	0.41-1.46	-	0.7	1.76	WG	QRA	Simmons et al., 1999
Asian seabass	*Lates calcarifer*	0.62-1.08	1.35-2.35	0.31	0.69-0.77	-	1.03	2.24	WG	BL	Coloso et al., 1999
Black sea bream	*Sparus macrocephalus*	0.75-2.35	1.9-6.1	0.31	0.84-0.98	30-43	1.71 / 1.72	4.5	SGR / PPV	SOPR	Zhou et al., 2011
Channel catfish	*Ictalurus punctatus*	0.35-1.55	0.8-3.7	0.4	0.62-0.78	-	0.94	3.41	WG, SGR, FE, PR, PER, ANPU	QRA	Cai and Burtle, 1996
Channel catfish	*Ictalurus punctatus*	0.25-1.25	1-7.3	0	0.99-1.75	-	0.56	2.34	WG	LR	Harding et al., 1977
Cobia	*Rachycentron canadum*	0.61-1.68	1.4-3.8	0.67	0.92-1.32	-	1.19	2.64	SGR	QRA	Zhou et al., 2006
Common carp	*Cyprinus carpio*	0.49-1.34	1.2-3.3	0.42	0.47-1.03	-	0.9	2.13	WG, PD	BL	Schwartz et al., 1998
Common carp	*Cyprinus carpio*	0-2	0-5.2	0	- 0.04-0.24	-	1.19	3.1	SGR	Not reported	Nose, 1979
Common carp	*Cyprinus carpio*	0-1.2	0-1.2	2	- 0.04-0.22	-	0.8	2.1	SGR	Not reported	Nose, 1979
European seabass	*Dicentrarchus labrax*	0.49-1.62	1.1-3.7	0.4	0.32-0.58	15.69-27.52	1.2/0.8	2.7/1.8	WG / PD	BL	Tulli et al., 2010
Golden pompano	*Trachinotus ovatus*	0.86-1.45	2-3.4	0.2	0.86-1.2	15.7-24.1	1.06-1.27	2.46-2.95	WG, NRE	BL	Niu et al., 2013
Grouper	*Epinephelus coioides*	0.55-1.81	1.1-3.8	0.26	0.47-0.76	16.3-31.6	1.31	2.73	WG	BL	Luo et al., 2005
Hybrid striped bass	*Morone chrysops x M. saxatilis*	0.6-1	1.7-2.9	0.13	0.6-1.15	-	0.87/0.86	2.49	WG/FE	BL	Keembiyehetty and Gatlin, 1993
Japanese flounder	*Paralichthys olivaceus*	0.53-2.03	1.06-4.06	0.06	0.22-1.05	7.28-25.77	1.49 / 1.44	2.98 / 2.88	WG / FE	BL	Alam et al., 2000
Mrigal carp	*Cirrhinus mrigala*	0.5-2	1.3-5	1	0.13-0.25	-	1.2	3	WG, FCR	SOPR	Ahmed et al., 2003
Nile tilapia	*Oreochromis niloticus*	0.15-1.35	0.5-4.8	0.15	0.41-0.46	-	0.75	2.68	WG	BL	Santiago and Lovell, 1988
Nile tilapia	*Oreochromis niloticus*	0.33-0.57	1.2-2	0.45	0.9-1.12	-	0.49	1.75	WG	BL	Nguyen and Davis, 2009
Rainbow trout	*Oncorhynchus mykiss*	0.2-1.1	-	Variable	-	-	0.8	2.4	PD	EF	Rodehutscord et al., 1995a[1]
Rockfish	*Sebastes schlegeli*	0.58-3.08	1.2-6.3	0.12	0.34-0.72	18.1-30.8	1.37	2.8	SGR	ANOVA	Yan et al., 2007
Rohu carp	*Labeo rohita*	0.4-1.4	1.1-3.7	0.04	0.12-0.45	-	1	2.6	WG, FCR, PRE, ERE	BL, SOPR	Abidi and Khan, 2011
Tilapia	*Sarotherodon mossambicus*	0.53-0.86	1.3-2.2	0.74	0.41-0.55	28.3-37.1	0.53	1.325	WG	MRT	Jackson and Capper, 1982
Yellow croaker	*Pseudosciaena crocea*	0.66-1.89	1.5-4.4	0.29	0.61-0.81	-	1.44 / 1.39	3.34 / 3.22	SGR / FCE	SOPR	Mai et al., 2006
Yellowtail	*Seriola quinqueradiata*	0.57-1.58	1.3-3.7	0.31	0.52-2.59	4.2-40.8	1.11	2.56	WG, FE	BL	Ruchimat et al., 1997b

FW, freshwater; SW, seawater; BW, brackish water; FM, fish meal; SM, squid meal; MG, maize gluten; HM, herring meal; SBM, soy-bean meal; SPC, soy-bean protein concentrate; WGl, wheat gluten; FPC, fish protein concentrate; PM, peanut meal; WM, wheat meal; CM, cottonseed meal; DE, digestible energy; GE, gross energy; NR, nitrogen retention; WG, weight gain; SGR, specific growth rate; FE, feed efficiency; PRE, protein retention efficiency; FCR, feed conversion ratio; PER, protein efficiency ratio; PD, protein deposition; PPV, protein predictive value; ANPU, apparent net protein utilization; NRE, nitrogen retention efficiency; FCE, feed conversion efficiency; PR, protein retention; BL, broken line regression; QRA, quadratic regression analysis; SOPR, second order polynomial regression; LR, linear regression; ANOVA, analysis of variance; MRT, Duncan's multiple-rang test.

[1] this article does not have the information required for statistical treatment

Table 11. Data collected from dose-response tryptophan (Trp) requirement studies.

Fish species		Initial body weight (g/fish)	Water temperature (ºC)	Salinity	Trial duration (days)	Feeding Regimen	Protein ingredients	Diet crude protein (%)	Diet crude lipid (%)	Energy (kJ/g)	References
Common name	**Scientific name**										
African catfish	*Clarias gariepinus*	11.5	28	FW	70	Satiation	Casein, gelatin	40	-	12	Fagbenro and Nwanna, 1999
Asian seabass	*Lates calcarifer*	5.3	26	SW	84	Fixed ration	FM, gelatin, SM	52	9.76	-	Coloso et al., 2004
Channel catfish	*Ictalurus punctatus*	200	26.7	FW	56	Fixed ration	Casein, gelatin	24	-	9.6	Wilson et al., 1978
Chum salmon	*Oncorhynchus keta*	1.1	-	FW	28	-	Casein	40	-	-	Akiyama et al., 1985b
Common carp	*Cyprinus carpio*	1.8	*25*	FW	42	Satiation	-	38.5	-	-	Nose, 1979
Hybrid striped bass	*Morone chrysops x M. saxatilis*	42.4	26	FW	49	Fixed ration	Menhaden FM	35	10	15.07	Gaylord et al., 2005[a]
Indian catfish	*Heteropneustes fossilis*	4.44	22.75	FW	56	Fixed ration	Casein, gelatin	40	-	17.9	Ahmed, 2012
Milkfish	*Chanos chanos*	7.7	28	SW	84	Fixed ration	FM, gelatin	49	-	17	Coloso et al., 1992
Mrigal carp	*Cirrhinus mrigala*	0.62	28	FW	56	Fixed ration	Casein, gelatin	40	-	17.9 (GE)	Ahmed and Khan, 2005a
Nile Tilapia	*Oreochromis niloticus*	0.056	27	FW	56	Satiation	Casein, gelatin	28	-	-	Santiago and Lovell, 1988
Rainbow trout	*Oncorhynchus mykiss*	14	15	BW	84	Fixed ration	White FM, gelatin	55	-	18.3	Walton et al., 1984a
Rainbow trout	*Oncorhynchus mykiss*	50	15.5	FW	64	Satiation	WGl	33	27.6	20.1 (DE)	Rodehutscord et al., 1997[1]
Rohu carp	*Labeo rohita*	1.5	28	FW	56	Satiation	Casein, gelatin	40	-	-	Murthy and Varghese 1997
Rohu carp	*Labeo rohita*	0.37	25.75	FW	84	Satiation	Casein, gelatin	40	-	17.9	Abidi and Khan, 2010b

Table 11. (Continued)

Fish species		Trp levels (% diet)	Trp levels (g/16gN)	Termal growth coefficient	Nitrogen retention (%NI)	Trp requeriment (% diet)	Trp requirement (g/16gN)	Response variable	Statistical Model	References
Common name	**Scientific name**									
African catfish	*Clarias gariepinus*	0.12-0.52	0.3-1.3	0.52-0.58	-	0.43	1.1	WG	BL	Fagbenro and Nwanna, 1999
Asian seabass	*Lates calcarifer*	0.11-0.61	0.24-1.36	0.36-0.71	-	0.21	0.41	WG	BL	Coloso et al., 2004
Channel catfish	*Ictalurus punctatus*	0.05-0.34	0.2-1.7	0.21-0.93	-	0.12	0.5	WG	BL	Wilson et al., 1978
Chum salmon	*Oncorhynchus keta*	0.05-0.56	0.13-1.4	0.38-1.42 (DGI)	-	0.29	0.73	WG	MRT	Akiyama et al., 1985b
Common carp	*Cyprinus carpio*	0-0.5	0-1.3	- 0.04-0.41	-	0.3	0.8	SGR	Not reported	Nose, 1979
Hybrid striped bass	*Morone chrysops x M. saxatilis*	0.1-1.4	-	-	-	0.21-0.25	0.6-0.7	WG, FE, PRE, PTC, PIGF-1	SKM-4, 5 parameter	Gaylord et al., 2005[1]
Indian catfish	*Heteropneustes fossilis*	0.04-0.54	0.1-1.4	0.28-0.68	13.26-30.91	0.32	0.8	WG, FCR, PER, PD	SOPR	Ahmed, 2012
Milkfish	*Chanos chanos*	0.09-0.61	0.2-1.2	0.03-0.33	-	0.31	0.63	WG, FER	MRT	Coloso et al., 1992
Mrigal carp	*Cirrhinus mrigala*	0.06-0.56	0.2-1.5	0.11-0.30	-	0.38	0.95	WG, FE	SOPR	Ahmed and Khan, 2005a
Nile Tilapia	*Oreochromis niloticus*	0.05-0.45	0.2-1.6	0.43-0.49	-	0.28	1	WG	BL	Santiago and Lovell, 1988
Rainbow trout	*Oncorhynchus mykiss*	0.08-0.6	0.1-1.1	0.21-1.07	-	0.25	0.45	WG	MRT	Walton et al., 1984a
Rainbow trout	*Oncorhynchus mykiss*	0.13-0.56	-	-	-	0.2	0.58	PD	EF	Rodehutscord et al., 1997[1]
Rohu carp	*Labeo rohita*	0.06-0.55	0.15-1.38	0.2-0.34	-	0.452	1.13	WG	BL	Murthy and Varghese 1997
Rohu carp	*Labeo rohita*	0.2-0.45	0.5-1.1	0.09-0.29	0.11-0.36	0.36-0.38	0.90-0.95	WG, FCR, PER, PPV	SOPR	Abidi and Khan, 2010b

FW, freshwater; SW, seawater; BW, brackish water; FM, fish meal; SM, squid meal; WGl, wheat gluten; DGI, daily growth index; WG, weight gain; SGR, specific growth rate; FE, feed efficiency; PRE, protein retention efficiency; PTC, plasma tryptophan concentration; PIGF-1, plasma insulin-like growth factor; FCR, feed conversion ratio; PER, protein efficiency ratio; PD, protein deposition; FER, feed efficiency ratio; PPV, protein predictive value.; DE, digestible energy; GE, gross energy; BL, broken line regression; MRT, Duncan's multiple-rang test; SKM, saturation kinetic model; SOPR, second order polynomial regression; EF, exponential function;

[1] this article does not have the information required for statistical treatment

Table 12. Data collected from dose-response threonine (Thr) requirement studies.

Fish species		Initial body weight (g/fish)	Water temperature (ºC)	Salinity	Trial duration (days)	Feeding Regimen	Protein ingredients	Diet crude protein (%)	Diet crude lipid (%)	Energy (kJ/g)	References
Common name	**Scientific name**										
Atlantic salmon	*Salmo salar*	0.8	14.7	FW	36	Satiation	WGl, CM, gelatin	40	25.1	22.4	Bodin et al., 2008
Channel catfish	*Ictalurus punctatus*	200	26.7	FW	56	Fixed ration	Casein, gelatin	24	-	9.6	Wilson et al., 1978
Chinook salmon	*Oncorhynchus tshawytacha*	5.9	15	FW	70	Fixed ration	Casein, gelatin	40	-	-	DeLong, D. et al., 1961
Chinook salmon	*Oncorhynchus tshawytacha*	1.25	15	FW	70	Fixed ration	Casein, gelatin	40	-	-	DeLong, D. et al., 1961
Chinook salmon	*Oncorhynchus tshawytacha*	3	8	FW	70	Fixed ration	Casein, gelatin	40	-	-	DeLong, D. et al., 1961
Chum salmon	*Oncorhynchus tshawytacha*	1.35	15	FW	28	Satiation	Casein	40	-	-	Akiyama et al., 1985a
Common carp	*Cyprinus carpio*	1.9	25	FW	42	Satiation	-	38.5	-	-	Nose, 1979
European seabass	*Dicentrarchus labrax*	7.5	21.1	SW	65	Satiation	MG, HM, gelatin	48.6	14.1	20.8	Tibaldi and Tulli, 1999.
Hybrid striped bass	*Morone chrysops X M. saxatilis*	9.8	26.5	FW	56	Fixed ration	Red drum muscle	35	-	-	Keembiyehetty and Galtin, 1997
Indian catfish	*Heteropneustes fossilis*	3.6	28.25	FW	56	Fixed ration	Casein, gelatin	40	-	17.9	Ahmed, 2007
Milkfish	*Chanos chanos*	1.29	29	SW	70	Satiation	Casein, gelatin	40	-	-	Borlongan, 1991
Mrigal carp	*Cirrhinus Mrigala*	1.07	28.3	*FW*	56	Fixed ration	Casein, gelatin	40	-	-	Benakappa and Varghese, 2002
Mrigal carp	*Cirrhinus Mrigala*	0.52	26.75	FW	56	Fixed ration	Casein, gelatin	40	-	17.9	Ahmed et al., 2004
Nile Tilapia	*Oreochromis niloticus*	0.054	27	FW	56	Satiation	Casein, gelatin	28	-	-	Santiago and Lovell, 1988
Rainbow trout	*Oncorhynchus mykiss*	47	17	FW	51	Satiation	WGl	34	27.8	20.1	Rodehutscord et al., 1995b[1]
Rainbow trout	*Oncorhynchus mykiss*	1.8	14.7	FW	24	Satiation	WGl, CM, gelatin	40	25.1	22.4	Bodin et al., 2008
Red drum	*Sciaenops ocellatus*	2.8	27	SW	56	Fixed ration	Lyophilized red drum muscle	35	-	13.4	Boren and Galtin, 1995
Rohu carp	*Labeo rohita*	0.58	27	FW	56	Satiation	Casein, gelatin	40	-	17.9	Abidi and Khan, 2008
Striped bass	*Morone saxatilis*	2.7	23	FW	70	Fixed ration	Menhaden FM, MGl	42	-	13.4	Small and Soares, 1999

Table 12. (Continued)

Fish species		Thr levels (% diet)	Thr levels (g/16gN)	Termal growth coefficient	Nitrogen retention (%NI)	Thr requeriment (%diet)	Thr requirement (g/16gN)	Response variable	Statistical Model	References
Common name	**Scientific name**									
Atlantic salmon	*Salmo salar*	0.5-2.176	1.3-5.5	0.21-0.78	10.6-40.17	1.066	2.665	WG, PG, TA	BL	Bodin et al., 2008
Channel catfish	*Ictalurus punctatus*	0.3-1.25	1.3-5.2	0.77-2.10	-	0.53	2.21	WG, SFTC	BL	Wilson et al., 1978
Chinook salmon	*Oncorhynchus tshawytacha*	0.4-1.81	1-4.5	-0.03-0.31	-	0.9	2.25	WG	Not reported	DeLong, D. et al., 1961
Chinook salmon	*Oncorhynchus tshawytacha*	0.6-1.8	1.5-4.5	0.36-0.46	-	0.9	2.25	WG	Not reported	DeLong, D. et al., 1961
Chinook salmon	*Oncorhynchus tshawytacha*	0.6-1.1	1.5-2.8	0.56-0.75	-	0.9	2.25	WG	Not reported	DeLong, D. et al., 1961
Chum salmon	*Oncorhynchus tshawytacha*	0.24-2.8	0.59-7	0.3-0.96	-	1.2	3	WG	MRT	Akiyama et al., 1985a
Common carp	*Cyprinus carpio*	0-2	0-5.2	- 0.08-0.4	-	1.5	3.9	SGR	Not reported	Nose, 1979
European seabass	*Dicentrarchus labrax*	0.76-2.46	1.6-5.1	0.51-0.59	19.5-24.5	1.12-1.26	2.3-2.6	WG	BL, SOPR, SKM-4 parameter	Tibaldi and Tulli, 1999.
Hybrid striped bass	*Morone chrysops X M. saxatilis*	0.49-1.25	1.4-3.6	0.93-1.24	-	0.9	2.6	WG, FE, PER	BL	Keembiyehetty and Galtin, 1997
Indian catfish	*Heteropneustes fossilis*	0.50-1.75	1.3-4.4	0.22-0.51	13.75-35.28	1.27	3.17	WG, FCR, PER, BPD	SOPR	Ahmed, 2007
Milkfish	*Chanos chanos*	1.13-2.2	2.84-5.5	0.18-0.36	-	1.8	4.5	WG	BL	Borlongan, 1991
Mrigal carp	*Cirrhinus Mrigala*	1-2.1	2.5-5.3	0.08-0.31	-	1.66	4.15	WG, SGR	BL	Benakappa and Varghese, 2002
Mrigal carp	*Cirrhinus Mrigala*	1-2.25	2.5-5.6	0.17-0.32	-	1.8	4.5	WG, FCR, PER	SOPR	Ahmed et al., 2004
Nile Tilapia	*Oreochromis niloticus*	0.2-1.6	0.7-5.7	0.38-0.49	-	1.05	3.75	WG	BL	Santiago and Lovell, 1988
Rainbow trout	*Oncorhynchus mykiss*	0.14-1.69	-	-	-	1.04	3.03	PD	EF	Rodehutscord et al., 1995b[1]
Rainbow trout	*Oncorhynchus mykiss*	0.5-2.175	1.3-5.4	0.75-1.84	22.3-43.45	1.058	2.645	WG, PG, TA	BL	Bodin et al., 2008
Red drum	*Sciaenops ocellatus*	0.49-1.25	1.4-3.6	0.46-0.94	16.0-32.5	0.8	2.28	WG, FE, PCE, PER, SFTC	BL	Boren and Galtin, 1995
Rohu carp	*Labeo rohita*	0.75-2.0	1.9-5	0.15-0.33	-	1.51-1.70	3.77-4.2	WG, FCR, PER, PPV	SOPR	Abidi and Khan, 2008
Striped bass	*Morone saxatilis*	0.61-1.4	1.5-3.3	0.01-0.02	21.5-30.4	1.03	2.45	WG, SGR, FCR, ANU	LSR	Small and Soares, 1999

FW, freshwater; SW, seawater; WGl, wheat gluten; CM, cod meal; MG, maize gluten; HM, herring meal; MGl, maize gluten; WG, weight gain; PG, protein gain; TA, threonine accretion; SFTC, serum free threonine concentration; SGR, specific growth rate; FE, feed efficiency; PER, protein efficiency ratio; FCR, feed conversion ratio; BPD, body protein deposition; PD, protein deposition; PPV, protein predictive value; PCE, protein conversion efficiency; ANU, apparent nitrogen utilization; BL, broken line regression; MRT, Duncan's multiple-rang test; SOPR, second order polynomial regression; SKM, saturation kinetic model; EF, exponential function; LSR, least square regression.

[1] this article does not have the information required for statistical treatment

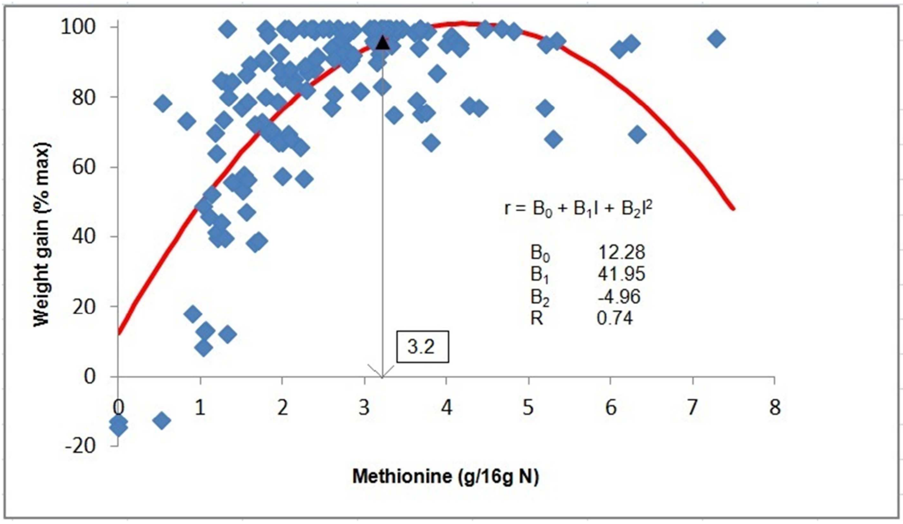

Figure 22. Weight gain (% max) as a function of dietary methionine level (g/16 g N).

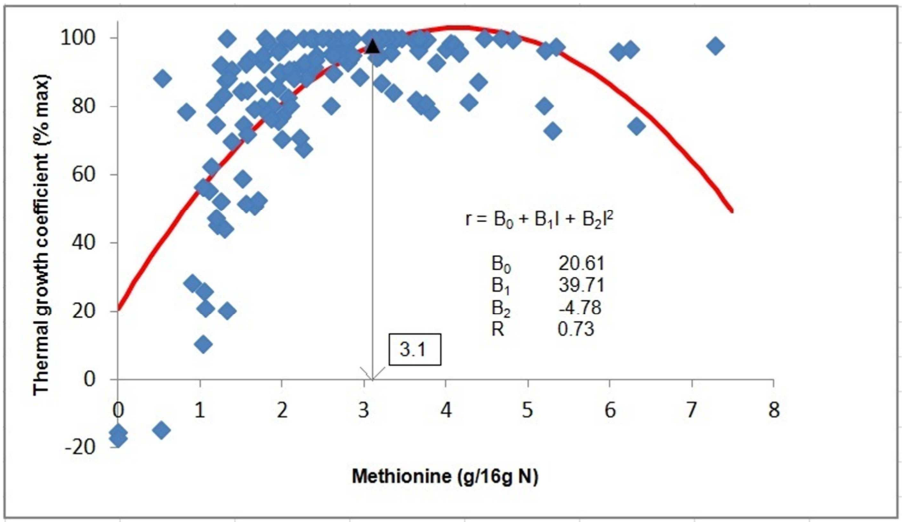

Figure 23. Thermal growth coefficient (% max) as a function of dietary methionine level (g/16 g N).

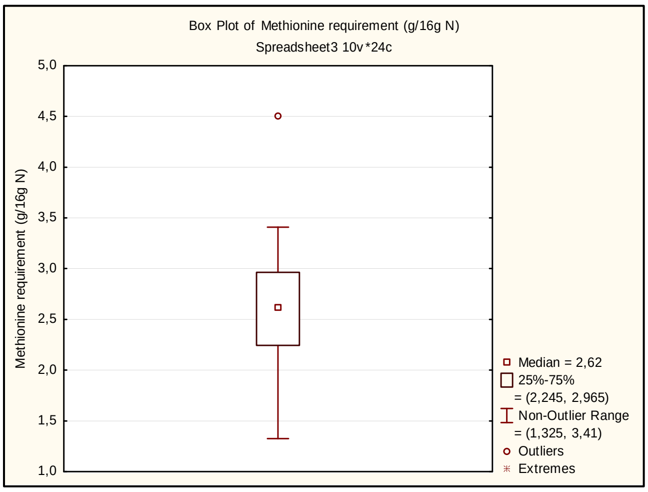

Figure 24. *Box plot* of dose-response methionine requirement studies.

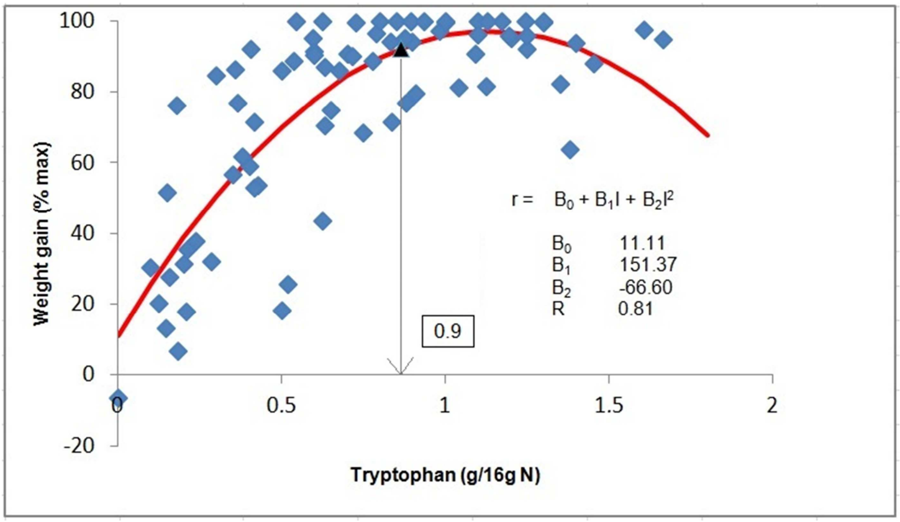

Figure 25. Weight gain (% max) as a function of dietary tryptophan level (g/16 g N).

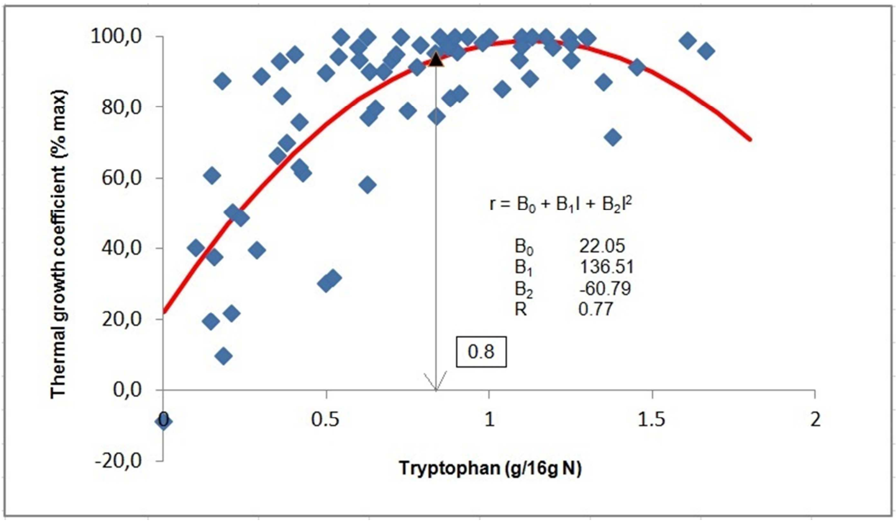

Figure 26. Thermal growth coefficient (% max) as a function of dietary tryptophan level (g/16 g N).

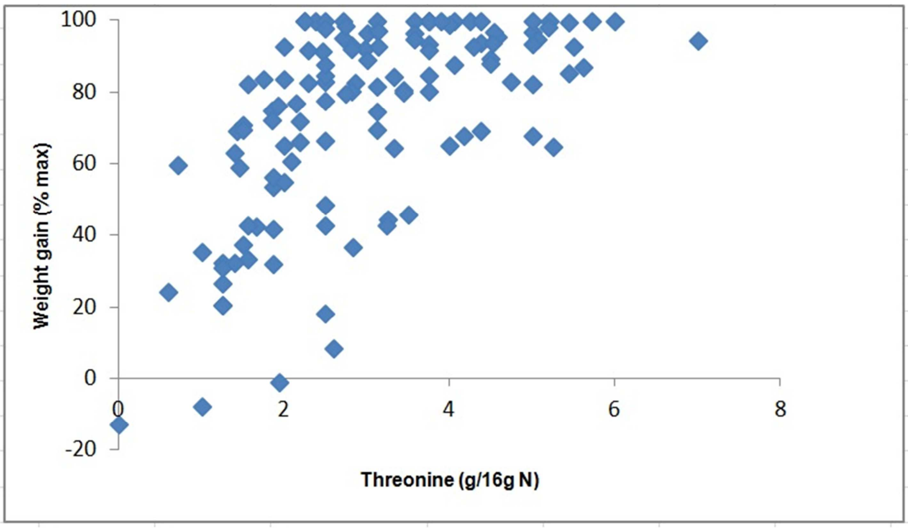

Figure 27. Weight gain (% max) as a function of dietary threonine level (g/16 g N).

3.8 – Threonine

On subjecting the WG (% max) as a function of dietary Thr levels (g/16g N) to SKM-4 parameter (Mercer et al, 1984) regression analysis, the correlation coefficient value was about 0.69. A poor quadratic relationship (R = 0.68) was also found between the same variables. This fact may be due to the heterogeneity of data (Figure 27). In fact, several authors have stated a toxic effect (Borlongan, 1991; Ahmed et al., 2004; Ahmed, 2007) and stress caused by excess Thr in the diet, leading to extra energy expenditure towards deamination and excretion (Walton 1985). Tibaldi and Tulli (1999) reported the wide variation in dietary Thr requirements and the different apparent sensitivities of the fish species to disproportionate levels of dietary Thr. Keembiyehetty and Galtin (1997) suggested that Thr requirements could possibly change to a limited extent according to the amino acid composition of test diets, like has been reported in other animals.

4 – Conclusion and future studies

Determining the EAA requirements of cultured fishes is of great importance due to the significant effects of these nutrients on muscle deposition, feed cost and nitrogen pollution. Therefore, it was a subject of concern for the last few decades, and a number of dose-response studies have been published so far. Nevertheless, this is the first study that aimed to re-evaluate several fish requirements for all EAA through a quantitative systematic point of view.

From the present analysis, it can be concluded that there exists considerable homogeneity of data on the EAA requirement of fish species included in this study, with exception of two EAA (Val and Thr). Table 13 summarizes the optimum requirement value for each EAA estimated in this study, considering different response criteria.

	Arg	His	Ile	Leu	Lys	Met	Phe	Thr	Trp	Val
WG	7.0	2.1	2.5	4.1	5.9	3.2	4.6	-	0.9	-
TGC	5.8	2.1	-	4.0	6.5	3.1	4.1	-	0.8	-
NR	5.6	-	-	-	5.3	-	-	-	-	-

Table 13. Optimum requirement values for each EAA studied (g/16 g N), considering different response criteria.

Despite the homogeneity of data, we also detected the existence of some methodological failures in a number of studies, which certainly contributed to a minor accuracy on the estimation of the dietary EAA requirement value. These methodological shortcomings include the failure to include EAA levels high enough to produce a maximum response and failure to space EAA input levels closely enough to adequately model the dose-response relationship. Some authors avoided these problems, conducting a second experiment, based on the results of a first experiment, in which another set of diets were used with the addition of smaller increments of the EAA under study to the basal diet, in order to provide a more accurate dietary EAA requirement value.

Among the response criteria available, only a few studies considered nitrogen retention (NR) as an outcome to estimate the EAA requirement value. However, there is some evidence that protein deposition may be considered as the most meaningful, accurate and sensitive outcome because weight gain (WG) is not the result of protein retention only, but also involves fat deposition. Thus, future research should be aware of this evidence in order to improve the quality of this sort of studies.

Another concern is the appropriate choice of the analytical method to evaluate the optimum dietary EAA requirement value. Analysis of variance (ANOVA), for example, is considered inappropriate to estimate nutrient requirements from dose-response data, as EAA levels are treated as discrete rather than continuous and for that reason the optimum nutrient level is quantified as a range between two input levels. Despite being widely used in dose-response studies, broken-line regression (BL) is usually described as underestimate the requirement value. Thereby, we suggest the use of curvilinear models to analyze the data from dose-response studies.

5 – References

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