

Protein and Amino Acid Nutrition of Marine Fish Species

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Abstract

Intensive aquaculture of marine fish species has highly expanded during the last decades and has potential for further increase. An increased and consistent supply of high quality aquafeed will be required to sustain this production and to guaranty the production of protein of high biological value for humans. Protein is the most abundant and expensive dietary nutrient in aquafeeds and fish meal is still the major dietary protein source in marine aquafeeds. Given the zootechnical, environmental and economical importance of a well-balanced diet, fine-tuning of dietary protein and amino acid composition to closely meet fish requirements are therefore of utmost importance. This is of particular importance when it is considered the dietary replacement of fish meal by more sustainable and renewable protein sources, such as plant feedstuffs, which have amino acids unbalances, antinutritional factors, lower protein content and digestibility, and devoid or containing very low concentrations of some particular micronutrients, as taurine. Concomitantly, in fish the utilization of amino acids for energy purpose is considered high, and so optimization of amino acids/protein accretion has great importance and practical implications. Besides the nutritional proprieties of amino acids, emerging evidence shows that some of them have functional properties, regulating key metabolic pathways crucial to maintenance, growth, and immune responses, being of strong interest in fish production. The importance of gaining further knowledge regarding amino acid requirements, metabolism and utilization as functional ingredients in aquaculture fish species will be stressed.

Keywords: Amino acids; Aquaculture; Marine fish; Nutrition; Protein; Requirement

Introduction

Intensive aquaculture is a feed-based production system and, therefore, improved diet specification is needed to reduce cost and increase productivity while guarantying the production of high biological value protein for humans. To address this, critical information is required on protein requirement of the target species at different phases of life cycle. Indeed, protein is one of the most expensive dietary component and a major factor influencing fish growth performance, feed cost and nitrogen pollution, and thus of the productivity and environmental sustainability of farmed fish. A deficient supply of dietary protein leads to decreased growth and therefore economic production loss, but provided in excess of requirements, protein is catabolized and used for energy purposes, increasing the nitrogen load to the environment. The knowledge on species protein and essential amino acid (EAA) requirements and optimum dietary EAA profile is therefore of particular importance for the formulation of cost-effective diets aiming to maximize growth and protein retention while minimizing nitrogen excretion. This data is also a pre-requisite for the correct evaluation of alternative protein sources to fishmeal in order to reduce the actual dependency of aquafeed of this commodity. Apart from low digestible protein content of most plant feedstuffs, plant protein feedstuffs also have deficiencies in certain essential amino acids such as lysine, methionine and arginine and functional amino acids as taurine and hydroxyproline (Aksnes *et al.*, 2008; Zhang *et al.* 2013; Salze & Davis, 2015). Thus, dietary AA deficiencies/unbalance may occur when plant feedstuffs are used as the main dietary ingredients, thus reducing growth and feed utilization (Gatlin *et al.* 2007). It is likely that production of non-fishmeal diets, capable of supporting growth rates necessary for the economic production of farmed fish, will require the adoption of more modern formulation approaches, taking into account nutrient availability, especially in regard to EAA, and combining different plant feedstuffs and EAA supplementation to meet the required EAA for the species (Nunes *et al.* 2014).

Protein requirements

Fish species requires high dietary protein levels, 2-4 times higher than those of farm animals, although in absolute terms (protein per unit of weight gain) requirements are not higher than those of farm animals (Table 1; Bowen, 1987). The higher protein content of fish diets might be incorrectly attributed to the carnivorous feeding habits of fish; however, it is mostly due to the differences in energy requirements between fish and farm animals. Fish are heterothermic animals, and therefore do not spend much energy for maintenance. Energy requirements for maintenance is circa 10-20 times lower in fish than in farm animals, which homoeothermic animals, and therefore spend large amounts of energy to maintain body temperature (Cho and Kaushik, 1990). Moreover, fish also have low maintenance protein requirements, representing only 11 to 35% of the total protein needs (Cho and Kaushik, 1990; McGoogan and Gatlin, 1998; Lupatsch *et al.* 2001; 2003; Dias *et al.* 2003; Peres and Oliva-Teles, 2005; Ozório *et al.* 2009). Thus, dietary protein content in relation to the dietary energy density is higher in fish than in farm animals, this explaining their apparently high dietary protein requirements.

Table 1. Growth performance, diet and protein utilization efficiency of fish and terrestrial animals¹.

	Fish	Terrestrial animals
Specific growth rate	2.77	2.45
Dietary protein content (%)	40.3	20.0
Daily protein intake at maximum growth (mg Prot/g BW/day)	16.5	12.0
Protein retention (% protein intake)	31.0	29.0
Protein efficiency ratio	1.95	1.97
Feed conversion efficiency	0.78	0.26

¹Adapted from Bowen (1987); BW, body weight.

Dietary protein requirements of marine fish species have been investigated mostly based on conventional dose-response studies, yielding minimum protein required to attain maximum growth. Studies indicate that dietary protein requirement for maximum growth of marine fish range between 27% and 55% (Table 2). Lower dietary protein requirement is

usually recorded for omnivorous species, such as white seabream and two-banded seabream, than for carnivorous species. These differences in dietary protein requirements may be related either to differences between species in feeding habits or in growth potential (Oliva-Teles *et al.* 2011). Comparatively to salmonids, most carnivorous marine fish species apparently have higher protein requirements and use dietary protein less efficiently. Indeed, protein retention as percentage of intake ranges between 30-40% for salmonids and between 25-35% in marine carnivorous fish (Tibaldi & Kaushik, 2005; Lall and Anderson, 2005). This difference in protein efficiency may have a nutritional basis or may be due to inadequate diet formulation. This being the case, it is expectable that better knowledge of nutritional requirements of marine fish may improve protein utilization efficiency and consequently allow a reevaluation of dietary protein requirements (Tibaldi & Kaushik, 2005).

Dietary protein may be used for plastic or for energy purposes, depending on the overall dietary protein to energy ratio. Moreover, fish are well adapted to metabolize protein and they use it preferentially to lipids or carbohydrates as an energy source (Walton and Cowey, 1982). Thus, optimization of dietary digestible protein to digestible energy (DP:DE) ratio is of crucial importance in improving protein utilization as it will allow sparing protein from energy purposes and use it preferentially for protein synthesis (Cho and Kaushik, 1990). Indeed, DP:DE ratio is a more rational way of expressing protein requirements than dietary crude protein alone (NRC, 2011). For marine fish species, recommendation of optimum dietary DP:DE ratio range from 20 to 32 g DP/MJ DE, depending on species (NRC, 2011). On the other hand, for salmonids optimum dietary DP:DE ratio is 17-18 g DP/MJ DE (Hillestad and Johnsen, 1994; Hillestad *et al.* 1998). This huge difference between groups of fish may be related to the capacity of salmonids of using higher dietary lipid than marine fish (Peres & Oliva-Teles, 1999a; NRC, 2011).

An optimization of the DP:DE ratio, through the reduction of dietary protein level with or without the concomitant increase of the energy level, reduce the utilization of protein to meet energy requirements, reducing ammonia excretion and environmental impact of aquaculture (Cho, 2008; NRC, 2011). In seabass, for example, reduction of dietary protein level from 56 to 48% led to a significant reduction (about 26%) of the relative contribution of protein catabolism to energy expenditure and a reduction (about

28%) of ammonia excretion (Peres & Oliva-Teles, 2001). Similarly, for blackspotted croaker a reduction of 7.5% of dietary protein level reduced ammonia excretion in about 20% (Li *et al.*, 2016a) and for red drum a reduction of dietary protein from 45 to 35% reduced ammonia excretion in about 22% (Webb & Gatlin, 2003) and reduced the 6h post-prandial ammonia production in about 56% (Wu & Gatlin, 2014). For the majority of the fish species lipids have proven to be more efficient energy suppliers than carbohydrates (Enes *et al.* 2010). Protein sparing by dietary lipids has been shown to occur in most fish species (Cho, 2008). However, magnitude of protein-sparing effect of lipid supplementation seems to be dependent dietary protein level, being more pronounced for lower protein levels (Dias *et al.* 1998). Indeed, sea bass fed diets including a protein level that meets protein requirements (Peres & Oliva-Teles, 1999b) no improvement of growth or protein utilization was achieved by increasing dietary lipid level from 12 to 24% (Peres and Oliva-Teles, 1999b). Similarly, for other fish species, it has also been reported that the increase of lipid level of diets with an adequate protein level as no major effect of protein utilization (McGoogan & Gatlin, 1999; Ozório *et al.* 2006; Velázquez *et al.* 2006; Bonaldo *et al.* 2010; Sevgili *et al.* 2014). In Senegalese sole, it was also observed that temperature may affect the degree of protein sparing by non-protein energy (Guerreiro *et al.* 2014). Some species, such as the Senegalese sole, are even less tolerant and high dietary lipid levels negatively affect growth and protein utilization (Dias *et al.* 2004; Guerreiro *et al.* 2012). The main concern of increasing dietary lipid level is the increase of lipid deposition in the carcass, which may negatively affect the nutritional value, organoleptic properties, transformation yield and storage time of fish. In fish, particularly in carnivorous fish, dietary carbohydrates utilization is limited (Stone, 2003; Enes *et al.* 2009; 2011). High dietary levels of carbohydrates lead to prolonged post-prandial hyperglycemia and inefficient carbohydrate utilization (Enes *et al.* 2011). Heat treatment may be required to improve digestive utilization of carbohydrates and modern technologies have allowed to extend the dietary incorporation of carbohydrates in diets of some fish species, like seabass and seabream, up to 20-30% (Couto *et al.* 2008; Oliva-Teles *et al.* 2011).

Table 2. Protein requirement of several marine fish species.

Species		Weight range (g)	Protein requirement (%)	Protein range tested (%)	Diet energy (MJ/GE)	Diet protein sources	References
Black Seabream	<i>Sparus macrocephalus</i>	13-56	41	32-49	16	FM	Zhang <i>et al.</i> 2010
Blackspot seabream	<i>Pagellus bogaraveo</i>	23-62	40	20-60	20	FM, pea meal, SBM	Silva <i>et al.</i> 2006
Blackspotted croaker	<i>Nibea diacanthus</i>	61-200	48.8	36-52	15.7	FM	Li <i>et al.</i> 2016a
Common dentex	<i>Dentex dentex</i>	2.5-15	50	40-55	21-22	FM, BM, SBM	Espinós <i>et al.</i> 2003
		10-37	50	50-57	22	FM, albumin	Skalli <i>et al.</i> 2004
		90-262	43	39-51	22	FM	Skalli <i>et al.</i> 2004
		17-25	49	44-59	21	FM, BM, SBM	Tibaldi <i>et al.</i> 1996
European seabass	<i>Dicentrarchus labrax</i>	5.6-30	48	36-56	20	FM	Peres & Oliva-Teles, 1999
		37-57	50	30-50	19	FM	Hidalgo & Alliot, 1988
Humpback grouper	<i>Cromileptes altivelis</i>	180-320	53	41-53	18-21	FM, MM, WM, casein	Usman <i>et al.</i> 2005
Hybrid grouper	<i>Epinephelus fuscoguttatus</i> × <i>E. lanceolatus</i>	2.5-64	50	40-55	18.8-21.6	FM, WM, DGM	Rahimnejad <i>et al.</i> 2015
Gilthead seabream	<i>Sparus aurata</i>	3-21	40	10-60		Casein, CPSP, AA	Sabaut & Luquet, 1973
		10-64	45	40-55	22	FM	Santinha <i>et al.</i> 1996
		0.8-3.3	55	35-65	20	FM	Vergara <i>et al.</i> 1996a
		5.5-30	46	42-58	20-21	FM	Vergara <i>et al.</i> 1996b
Malabar grouper	<i>Epinephelus malabaricus</i>	17-81	55	44-60	19-23.4	FM, krill, WG, casein	Tuan & Williams, 2007
Red spotted grouper	<i>Epinephelus akaara</i>	8-36	51	32-62	21	FM, casein	Wang <i>et al.</i> 2016a

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Grouper	<i>Epinephelus coioides</i>	10-25	48	35-60	14	FM, casein	Luo <i>et al.</i> 2004
Japanese seabass	<i>Lateolabrax japonicas</i>	6.3-67.9	41	36-46	17.2	FM, SBM, BY, WM, SVM,	Ai <i>et al.</i> 2004

Table 2. (Continued).

Species		Weight range (g)	Protein requirement (%)	Protein range tested (%)	Diet energy (MJ/GE)	Diet protein sources	References
Olive flounder	<i>Paralichthys olivaceus</i>	256-442	45	40-50	18	FM	Kim <i>et al.</i> 2010
		4.1	51	35-65	17	FM	Kim <i>et al.</i> 2005
		13	44	30-60		FM	Kim <i>et al.</i> 2005
		8.1-40	45	25-60	17	FM	Kim <i>et al.</i> 2004
Patagonian blennie	<i>Eleginops maclovinus</i>	41-74	35	9-44	20	FM, WM	Sá <i>et al.</i> 2015
Red drum	<i>Sciaenops ocellatus</i>	2	40	35-45	14.5	Red drum muscle	Serrano <i>et al.</i> 1992

Table 2. (Continued).

Red seabream	<i>Pagrus major</i>	1.6-6.8	52	27-52		FM, casein	Takeuchi <i>et al.</i> 1991
Rockfish	<i>Sebastes schlegeli</i>	3.2-12.4	50	45-55	17.5-19	FM, casein, SBM	Cho <i>et al.</i> 2015
Senegalese sole	<i>Solea senegalensis</i>	6.4-24	50	45-50	19	FM; CG, WG	Guerreiro <i>et al.</i> 2012

		12-32	53	40-60	24	FM; CG, WG	
Sharpnout seabream	<i>Diplodus puntazzo</i>	49-113	52	14-68	21	FM	Coutinho <i>et al.</i> 2012
Turbot	<i>Scophthalmus maximus</i>	90-160	50	39-57	15	FM	Lee <i>et al.</i> 2003
Two-banded seabream	<i>Diplodus vulgaris</i>	6-20	36	5-55	22	FM	Ozório <i>et al.</i> 2009
White seabream	<i>Diplodus sargus</i>	22-36	27	6-49	21	FM	Sá <i>et al.</i> 2008
Yellowtail	<i>Seriola quinqueradiata</i>	3.6-33.6	50	35-55	(15% lipids)	FM	Takeuchi <i>et al.</i> 1992
Yellowtail kingfish	<i>Seriola lalandi</i>	>200	46		12	Commercial diet	Booth <i>et al.</i> 2010
		200-1000	47		15	Commercial diet	Booth <i>et al.</i> 2010
		>1000	43		18	Commercial diet	Booth <i>et al.</i> 2010
Zebra seabream	<i>Diplodus cervinus</i>	7-20	44	6-54	20-21	FM, CPSP	Coutinho <i>et al.</i> 2016a

BM, blood meal; BY, beer yeast; CG, corn gluten; CPSP, soluble fish protein concentrate; FM, fish meal; MM, mysid meal; SVM, squid visceral meal SBM, soybean meal; WG, Wheat gluten; Wheat meal, WM.

EAA Requirements

Ten essential amino acid (EAA) must be provided by dietary ingredients as they cannot be synthesized by fish (arginine, histidine, isoleucine, leucine, lysine, methionine, phenylalanine, threonine, tryptophan and valine). Cysteine may be synthesized from methionine and tyrosine from phenylalanine, being considered semi-essential amino acids. Deficiency in only one of these AA will impair protein synthesis and depress fish growth (Wilson, 2002). Quantitative AA requirements for the 10 EAA were only determined for a few fish species (NRC, 2011).

For marine fish, quantitative requirements of some EAA was assessed by dose-response studies, based on animal growth or nitrogen retention responses to increasing dietary levels of the EAA under study (Table 3). Available data suggests some similarities but also a variation of EAA requirement among species. Part of this inter-species variation may be due to differences in methodological approaches, stressing the need for standardization methods (Dabrowski & Guderley, 2002). Several methodological issues have been raised including: the type and composition of the diet, which affect the capacity of fish to reach their maximum growth potential; the response criterion used to estimate requirements (growth, nitrogen retention, metabolic responses) and differences in the experimental design, statistical analysis and response modeling (Shearer, 2000; Bureau and Encarnaç o, 2006; Kaushik & Seiliez, 2010).

Table 3. Essential amino acids requirements (g/16g N) of some marine fish species estimated by dose-response studies.

	Arg	Lys	Met	Thr	Phe	Try	Tau	References
Asian seabass , <i>Lates calcarifer</i>	3.8	4.5	2.2					Murillo Gurrea <i>et al.</i> 2001; Coloso <i>et al.</i> 1999, 2004
Atlantic salmon , <i>Salmo salar</i>	4.1-5.1							Berge <i>et al.</i> 1997; Lall <i>et al.</i> 1994
Black sea bream , <i>Sparus macrocephalus</i>	7.7-8.1	8.6	4.5					Zhou <i>et al.</i> 2010a,b, 2011
Cobia , <i>Rachycentron canadum</i>	6.2	5.3	2.2-2.6					Zhou <i>et al.</i> 2006, 2007; Ren <i>et al.</i> 2014; Wang <i>et al.</i> 2016b
European seabass , <i>Dicentrarchus labrax</i>	3.9-4.6	4.82	0.9-2.7 (1.31)	2.3-2.6		0.5-0.7		Thebault <i>et al.</i> 1985; Tibaldi and Lanari, 1991; Tibaldi <i>et al.</i> 1993a,b,1994; Tibaldi and Tulli, 1999; Tulli <i>et al.</i> 2010
Gilthead seabream , <i>Sparus aurata</i>	<2.6	5.0	2.8 (4.0)			0.6		Luquet and Sabaut, 1974; Marcouli <i>et al.</i> 2006
Golden pompano , <i>Trachinotus ovatus</i>	6.3		2.5-3					Niu <i>et al.</i> 2013; Lin <i>et al.</i> 201
Grouper , <i>Epinephelus coioides</i>		5.6	2.73					Luo <i>et al.</i> , 2005, 2006
Japanese flounder , <i>Paralichthys olivaceus</i>	2.1	4.2-4.6	2.9	3.2				Forster and Ogata, 1998, Alam <i>et al.</i> 2000, 2002; 2003
Japanese seabass , <i>Lateolabrax japonicas</i>		5.8-6.1						Mai <i>et al.</i> 2006
Milkfish , <i>Chanos chanos</i>	5.3	4		4.5		0.6		Borlongan, 1991; Borlongan and Benitez, 1990; Coloso <i>et al.</i> 1992

Pacific threadfin , <i>Polydactylus sexfilis</i>	5.1				-		Deng <i>et al.</i> 2010
Red drum , <i>Sciaenops ocellatus</i>	4.2-5.0	4.4-5.7	3.0	2.3	1.69 (0.41 Tyr)	0.8	Brown <i>et al.</i> 1988; Moon and Gatlin, 1991; Craig and Gatling, 1992; Boren and Gatling, 1995; Barziza <i>et al.</i> 2000; Castillo <i>et al.</i> 2015; Pewitt <i>et al.</i> 2017
Red seabream , <i>Pagrus major</i>	4.7	3.6-4.4					Forster and Ogata, 1998; Rahimnejad and Lee., 2014
Rockfish , <i>Sebastes schlegeli</i>			2.8				Yan <i>et al.</i> 2007
Striped Bass , <i>Morone saxatilis</i>	4.1-4.4	4.3-4.9		2.45		0.6-0.7	Keembiyehetty <i>et al.</i> 1992; Griffin <i>et al.</i> 1994; Small, <i>et al.</i> 1999, 2000; Gaylord <i>et al.</i> 2005
Turbot , <i>Scophthalmus maximus</i>		5	2.6-3.3			0.9-1.9	Peres and Oliva-Teles, 2008; Qi <i>et al.</i> 2012; Ma <i>et al.</i> 2013; Klatt <i>et al.</i> 2016
Yellow croaker <i>Pseudosciaena crocea</i>		5.7-6.6	3.2-3.3				Mai <i>et al.</i> 2006; Zhang <i>et al.</i> 2008; Xie <i>et al.</i> 2012; Li <i>et al.</i> 2014
Yellow grouper <i>Epinephelus awoara</i>	6.5						Zhou <i>et al.</i> 2012
Yellowtail , <i>Seriola quinqueradiata</i>	3.4-3.8	4.1	3.3				Ruchimat <i>et al.</i> 1997a, b; Ruchimat <i>et al.</i> 1998

Special emphasis should be given to the composition of experimental diets (Nunes *et al.* 2014). In dose-response studies, purified or semi-purified diets are often used, in which protein bound-AA are replaced by crystalline-AA. In some studies, use of such diets was proven to be less effective in promoting fish growth than diets containing only intact protein (Cowey, 1995; Zarate and Lovell, 1997). This may be an issue, as it is important that fish fed the semi-purified diets perform as well as fish fed practical diets. Thus, for an unbiased evaluation of EAA requirement it is necessary to confirm that crystalline-AA are effectively utilized by the animals (Peres & Oliva-Teles, 2005). Maximum tolerable levels of crystalline-AA that do not impair growth performance or feed utilization efficiency may depend on fish species. For instance, in turbot a maximum of 19% of protein replacement by free AA was achieved without affecting growth performance (Peres & Oliva-Teles, 2005) but higher inclusion levels, around 30-55% of dietary protein, were reported as feasible for other species, such as gilthead seabream, red seabream, European seabass or Senegalese sole (Webb & Gatlin, 2003; Marcouli *et al.* 2005; Alam *et al.* 2005; Peres and Oliva-Teles, 2007; Perez-Jimenez *et al.* 2014).

Dietary EAA profile, EAA to non-EAA ratio and composition of the non-EAA fraction of the diets are also important issues, as it affects growth and protein utilization (Mambrini and Kaushik, 1995; Kaushik & Seiliez, 2010). The whole-body EAA profile is usually used as the most appropriate EAA profile for the ideal protein, however for marine species such as gilthead seabream, red seabream and European seabass, the fish meal EAA profile also provides satisfactory results (Marcouli *et al.* 2005; Alam *et al.* 2005; Peres & Oliva-Teles, 2007; Fig. 1). This is not unexpected, as fish meal is usually considered the most adequate protein source for fish and the EAA profile of fish species is not very different.

To ensure best performances and feed utilization, an adequate amount of non-EAA should be provided in the diets, as EAA are not always efficiently used as non-specific nitrogen source for synthesis of non-EAA. In fact, diets with low levels of non-EAA are used less efficiently than diets with adequate EAA to non-EAA ratios in chickens, pigs and fish (Mambrini and Kaushik, 1994; Schuhmacher *et al.* 1995; Abboudi *et al.* 2009). For instance, the most adequate dietary EAA to non-EAA ratio for seabass was estimated to be 0.55-0.60 (Peres & Oliva-Teles, 2006; Fig. 1), which is similar to the ratios established for

salmonids and terrestrial animals (Green *et al.* 2002; Gomez-Requeni *et al.* 2003). Another important issue when using diets with protein-bound and crystalline-AA is to assure that the absorption of crystalline-AA is synchronized with that of protein bound-AA, for guaranteeing that all AA are present in the body AA-pool simultaneously (Fournier *et al.* 2002; Peres & Oliva-Teles, 2005, 2006, 2007). Otherwise, an unbalanced AA availability may occur at physiological and metabolic levels. Thus, it may be required to consider pre-coating crystalline-AA with agar or gelatin to delay their absorption. Besides, coating crystalline-AA also reduces leaching of crystalline-AA during diet exposure to water, and avoids problems related to the acidic diet in stomachless fish.

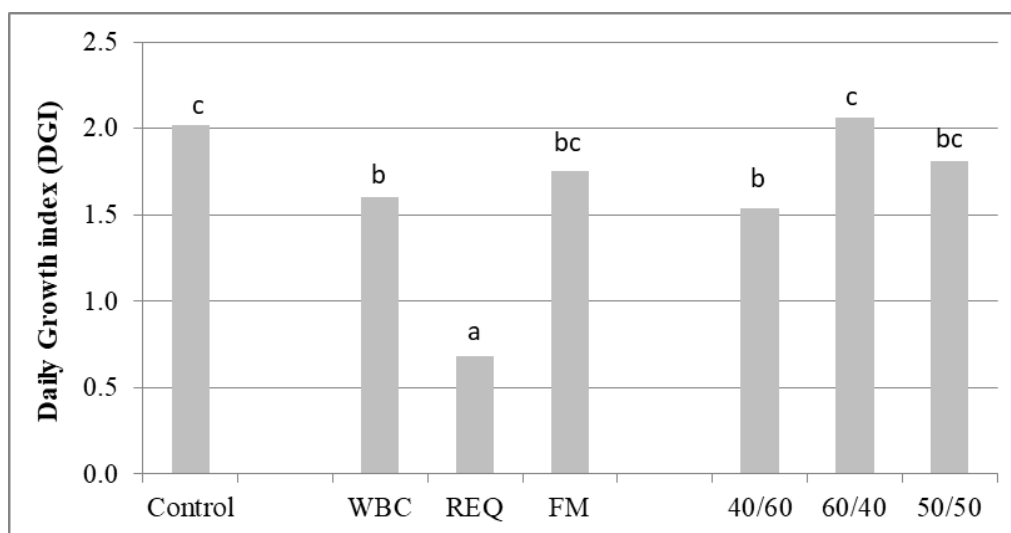


Fig 1. Comparison of European seabass performance fed a control diet (containing only intact protein) and test diets (containing free-AA replacing 60% of intact protein nitrogen of control diet) with different EAA profile and EAA/non-EAA ratio. WBC: whole body EAA profile; REQ: ideal protein EAA profile; FM: fish meal EAA profile) (Data from Peres & Oliva-Teles, 2006; 2007).

Despite the variability of EAA requirements among species, some similar pattern is also evident (Table 3). Hauler and Carter (2001) compiled available data on lysine requirement of fish species and concluded that in spite of the high variance of lysine requirements, requirements per unit of body mass gain was relatively stable, being estimated to be 18.5 g lysine for kg of whole-body weight. Kaushik and Seiliez (2010)

using a meta-analysis of the available data on lysine and methionine requirement in salmonids were able to draw similar dose-response patterns independent of species.

For marine fish species, meta-analysis of available data on lysine, methionine and arginine requirement for marine fish is presented in Fig 2, 3 and 4. For the other EAA, due to the limited number study, such approach was not possible. The four-parameter saturation kinetic model (Mercer *et al.* 1984) was used to analyze dose-response data. Experimental condition, growth rate and initial body weight greatly differ among studies, and therefore it was necessary to standardize the response criterion relatively to the maximum weight gain or maximum thermal growth coefficient within each study. This standardization is necessary for a direct interstudy comparison of growth data, due to differences in fish size, trail duration and magnitude of somatic growth in absolute terms. For lysine, methionine and arginine a compilation of 17, 11 and 16 studies, respectively, was used (see table 4, 5 and 6, respectively for references). Despite the scarcity of studies on EAA requirements for marine fish, data used for this meta-analysis fitted relatively well with the model used. Based on this meta-analysis, dietary lysine, methionine and arginine requirement to meet 95% of maximum weight gain of fish were estimated to be: 4.90 and 5.42 (g/16g N) for lysine (Fig. 2); 2.41 and 2.74 (g/16g N) for methionine (Fig. 3) and 4.54 and 4.73 (g/16g N) for arginine (Fig. 4).

The meta-analysis values obtained for lysine and methionine requirements fit well with the individual dose-response requirements evaluation (ranging from 3.3 to 56.5 and from 2.3 to 4.5 g/16g N for lysine and methionine, respectively; Table 4 and 5). Arginine requirement estimated by the meta-analysis was also within the values obtained based on dose-response studies (ranging from 3.8 to 8.1 g/16g N; Table 6), but although high, the R value explaining the fitness of arginine data was lower than that obtained for the other two amino acids. This discrepancy may be related to the range of values used in the dose-response studies used for fitting the meta-analysis models. Thus, more data is required for a better adjustment of the model and to have more confidence on the results (Fig 5).

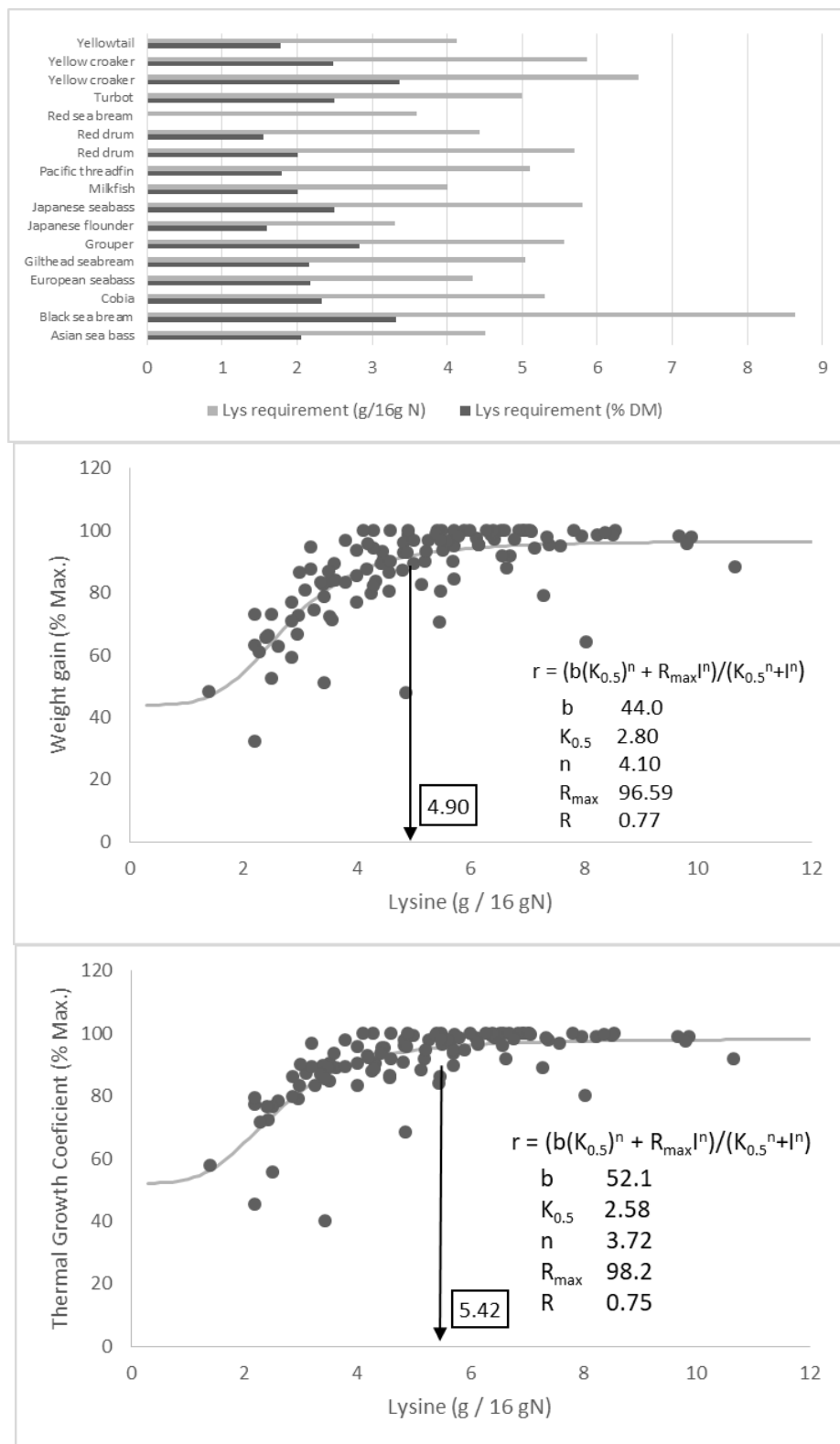
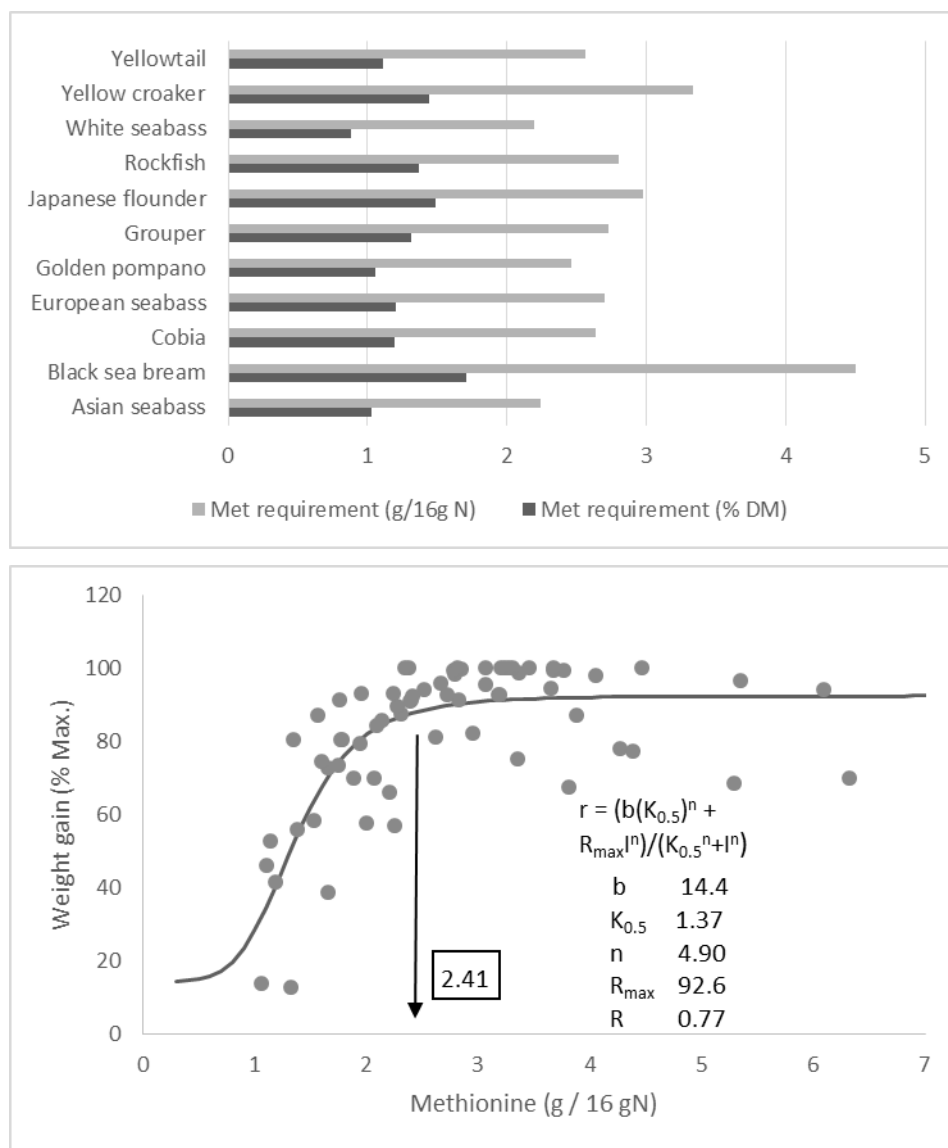


Fig 2. Analysis of literature data on lysine requirements of marine fish species (references in Table 4).



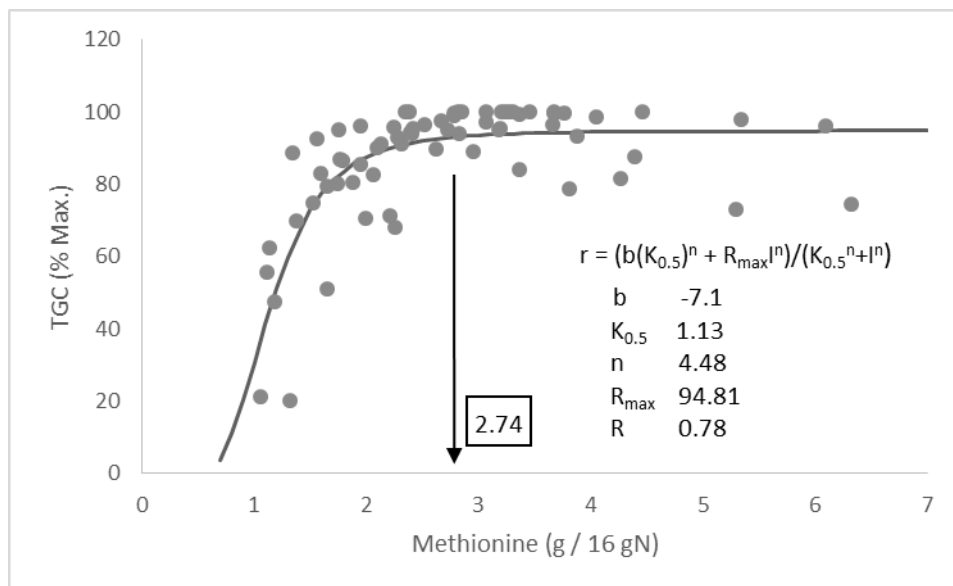


Fig 3. Analysis of literature data on methionine requirements of marine fish species (references in Table 5).

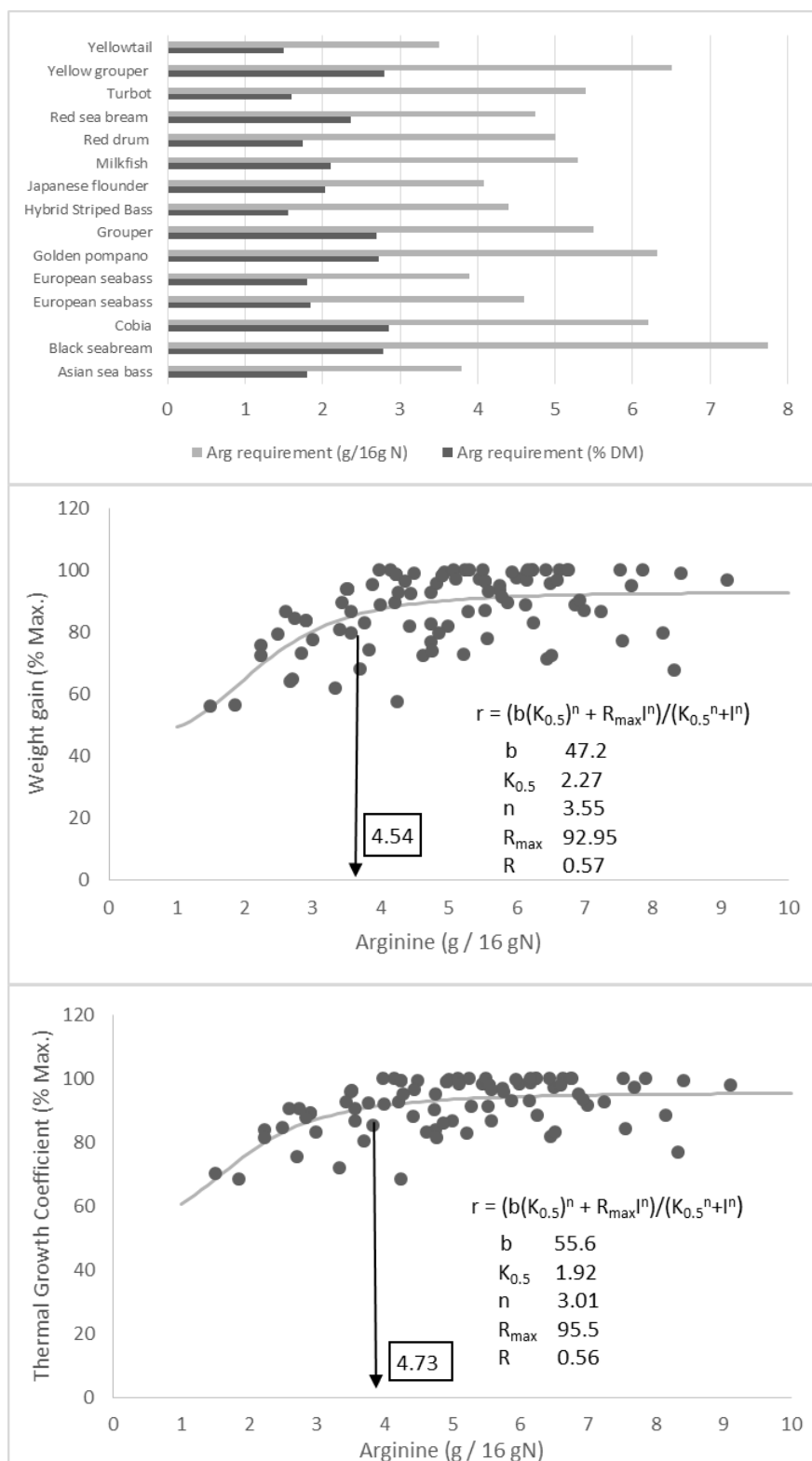


Fig 4. Analysis of literature data on arginine requirements of marine fish species (references in Table 6).

Peres, H. and Oliva, A. 2017. Protein and amino acid nutrition of marine fish species. En: Cruz-Suárez, L.E., Ricque-Marie, D., Tapia-Salazar, M., Nieto-López, M.G., Villarreal-Cavazos, D. A., Gamboa-Delgado, J., López Acuña, L.M. y Galaviz-Espinoza, M. (Eds), Investigación y Desarrollo en Nutrición Acuicola Universidad Autónoma de Nuevo León, San Nicolás de los Garza, Nuevo León, México, pp. 438-492. ISBN 978-607-27-0822-8.

Table 4. Data collected from dose-response lysine (Lys) requirement studies.

Common name	Scientific name	Initial body weight (g/fish)	Water temperature (°C)	Trial duration (days)	Feeding Regimen	Protein ingredients	Diet crude protein (%)	Diet crude lipid (%)	Energy (kJ/g)	References
Asian sea bass	<i>Lates calcarifer</i>	13.1	27	84	FR	FM, zein, SM	45.5	10	-	Murillo-Gurrea <i>et al.</i> 2001
Black sea bream	<i>Sparus macrocephalus</i>	9.1	28	56	Satiation	FM, SPC, Gel	38	15	15.7(DE)	Zhou <i>et al.</i> 2010b
Cobia	<i>Rachycentron canadum</i>	1.25	28.5	56	Satiation	FM, WG	44	16	-	Zhou <i>et al.</i> 2007b
European seabass	<i>Dicentrarchus labrax</i>	0.85	25.5	70	FR	MG, HM, Gel	50	14	17.5(DE)	Tibaldi & Lanari, 1991
Gilthead seabream	<i>Sparus aurata</i>	3.5	24	42	Satiation	LT-FM	43	13.5	-	Marcouli <i>et al.</i> 2006
Grouper	<i>Epinephelus coioides</i>	15.8	29	56	Satiation	FM, SPC	48	10	-	Luo <i>et al.</i> 2006
Hybrid striped bass	<i>(Morone chrysops × saxatilis)</i>	8	24.5	63	FR	Red drum muscle,	48	10	15	Keembiyehetty and Gatlin, 1992
Hybrid striped bass	<i>(Morone chrysops × saxatilis)</i>	11	28	56	FR	Casein, Gel	35			Griffin <i>et al.</i> 1992
Japanese flounder	<i>Paralichthys olivaceus</i>	3	19.5	63	Satiation	Zein, FM, Gel	47	11	-	Forster & Ogata, 1998
Japanese seabass	<i>Lateolabrax japonicus</i>	5.5	28.5	70	Satiation	FM, SBM, zein, WM	43	12	-	Mai <i>et al.</i> 2006
Milkfish	<i>Chanos chanos</i>	5.92	29	84	FR	FM, zein	50	-	-	Borlongan & Benitez, 1990
Pacific threadfin	<i>Polydactylus sexfilis</i>	3	25	56	Satiation	Pa. threadfin muscle	35	11.5	19.1(GE)	Deng <i>et al.</i> 2010
Red drum	<i>Sciaenops ocellatus</i>	2.7	28	56	FR	PM, ShM	35	-	-	Brown <i>et al.</i> 1988

Red drum	<i>Sciaenops ocellatus</i>	6-7/1-2	-	56	FR	Red drum muscle	35	-	-	Craig and Gatlin, 1992
Red sea bream	<i>Pagrus major</i>	1.7	22.5	56	Satiation	Zein, FM, Gel	48	14	-	Forster & Ogata, 1998
Turbot	<i>Scophthalmus maximus</i>	18.1	18	56	Satiation	MG, FM, SFPC	50	15	18.5(DE)	Peres & Oliva-Teles, 2008
Yellow croaker	<i>Pseudosciaena crocea</i>	0.03	23	30	Satiation	FM, KM, SM, MG	51	18.5	22.3	Xie <i>et al.</i> 2012
Yellow croaker	<i>Pseudosciaena crocea</i>	1.23	28.5	70	Satiation	FM, SBM, CGM, WM	43	12	-	Zhang <i>et al.</i> 2008
Yellowtail	<i>Seriola quinqueradiata</i>	68.2	25.8	40	Satiation	FM, MG, WG	43.1	15.9	15.5(DE)	Ruchimat <i>et al.</i> 1997a

Table 4. (Continued).

Common name	Scientific name	Lys levels (% diet)	Lys levels (g/16gN)	TGC	Nitrogen retention (%NI)	Lys requirem. (% DM)	Lys requirem. (g/16g N)	Response variable	Statistical Model	References
Asian sea bass	<i>Lates calcarifer</i>	1.0-2.5	2.17-5.43	1.56-1.97		2.06	4.5	WG/FER	BL	Murillo Gurrea <i>et al.</i> 2001
Black sea bream	<i>Sparus macrocephalus</i>	2.08-4.05	5.5-10.7	0.7-0.81	28-34	3.32	8.64	SGR	SOPR	Zhou <i>et al.</i> 2010b
Cobia	<i>Rachycentron canadum</i>	1.15-3.25	2.6-7.4	0.90-1.13		2.33	5.3	SGR	BL	Zhou <i>et al.</i> 2007
European seabass	<i>Dicentrarchus labrax</i>	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 & Lanari, 1991
Gilthead seabream	<i>Sparus aurata</i>	1.56-3.43	3.63-7.97	0.84-0.95	34.4-39.9	2.16	5.04	DPD	SKM	Marcouli <i>et al.</i> 2006
Grouper	<i>Epinephelus coioides</i>	1.92-3.95	4-8.2	0.65-0.91	24-30	2.83	5.56	WG	BL	Luo <i>et al.</i> 2006
Japanese flounder	<i>Paralichthys olivaceus</i>	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	<i>Lateolabrax japonicus</i>	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 <i>et al.</i> 2006
Milkfish	<i>Chanos chanos</i>	0.7-2.7	1.4-5.4	0.2-0.35		2	4	WG	SOPR	Borlongan & Benitez, 1990
Pacific threadfin	<i>Polydactylus sexfilis</i>	1.26-2.91	3.6-8.31	1.11-1.18	34.6-40.3	1.79	5.1	SGR	BL	Deng <i>et al.</i> 2010
Red drum	<i>Sciaenops ocellatus</i>	1.2-2.4	3.4-6.9	0.18-0.44		2	5.7	SFLC	MRT	Brown <i>et al.</i> 1988
Red drum	<i>Sciaenops ocellatus</i>	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	<i>Pagrus major</i>	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 & Ogata, 1998
Turbot	<i>Scophthalmus</i>	1.19-3.11	2.5-6.4	0.45-0.58	20.4-30	2.5	5.0	WG	SKM	Peres & Oliva-Teles,

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	<i>maximus</i>									2008
Yellow croaker	<i>Pseudosciaena</i>	2.48-4.10	4.86-8.03	0.25-0.36		3.37-3-34	6.55-6.49	SGR/survival	SOPR	Xie <i>et al.</i> 2012
	<i>crocea</i>									
Yellow croaker	<i>Pseudosciaena</i>	1.27-4.22	2.95-9.81	0.48-0.61		2.48/2.45/2.43	5.87/5.70/5.65	SGR/FE/PER	BL	Zhang <i>et al.</i> 2008
	<i>crocea</i>									
Yellowtail	<i>Seriola</i>	1.05-3.05	2.4-7.1	0.80-0.95	15.6-22.6	1.78	4.13	WG, FE	BL	Ruchimat <i>et al.</i> 1997a
	<i>quinqueradiata</i>									

ANOVA, analysis of variance; ANU, apparent nitrogen utilization; BL, broken line regression; DE, digestible energy; DGI, daily growth index; DPD, daily protein deposition; EF, exponential function; FCR, feed conversion ratio; FE, feed efficiency; FER, feed efficiency ratio; FM, fish meal; FR: Fixed ration; GE, gross energy; Gel, gelatin; GPR, gross protein retention; HM, herring meal; MG, maize gluten; MRT, Duncan's multiple-rang test; NR, nitrogen retention; PD, protein deposition; PER, protein efficiency ratio; PM, peanut meal; PRE, protein retention efficiency; RGM, rice gluten meal; SBM, soy-bean meal; SFLC, serum free lysine concentration; SFPC, soluble fish protein concentrate; SGR, specific growth rate; SGR, specific growth rate; ShM, shrimp meal; SKM-4, saturation kinetic model-4 parameter; SM, squid meal; SOPR, second order polynomial regression; SPC, soy-bean protein concentrate; TGC: thermal growth coefficient WG, weight gain; WG, wheat gluten.

Table 5. Data collected from dose-response methionine (Met) requirement studies.

Common name	Scientific name	Initial body weight (g/fish)	Water temperature (°C)	Trial duration (days)	Feeding Regimen	Protein ingredients	Diet crude protein (%)	Diet crude lipid (%)	Energy (kJ/g)	References
Asian seabass	<i>Lates calcarifer</i>	2.59	26	84	FR	FM, SM, SBM	46	10.5	16	Coloso <i>et al.</i> 1999
Black sea bream	<i>Sparus macrocephalus</i>	14.21	28	56	Satiation	FM, SPC	38.5	15	15.7	Zhou <i>et al.</i> 2011
Cobia	<i>Rachycentron canadum</i>	11.61	29	56	Satiation	Brown FM, WG	44	16		Zhou <i>et al.</i> 2006
European seabass	<i>Dicentrarchus labrax</i>	13.4	23	84	Satiation	FPC, WG, Gel, SPC, SBM	44	14.5	19 (GE)	Tulli <i>et al.</i> 2010
Golden pompano	<i>Trachinotus ovatus</i>	12.4	29.5	56	Satiation	FM, MG, SBM, PM, SPC	43	13		Niu <i>et al.</i> 2013
Grouper	<i>Epinephelus coioides</i>	13.25	29.25	56	Satiation	FM, SPC	48	9.8	14.3 (DE)	Luo <i>et al.</i> 2005
Japanese flounder	<i>Paralichthys olivaceus</i>	2.8	21.6	40	FR	Casein, Gel	50	9.6		Alam <i>et al.</i> 2000
Rockfish	<i>Sebastes schlegeli</i>	43.61	19.5	65	Satiation	FM	48.7	10.4	18.9	Yan <i>et al.</i> 2007
White seabass	<i>Atractoscion nobilis</i>	5.6	18	57	FR	FM, SBM; SPC, CGM, WM	40	10		Salze <i>et al.</i> 2017
Yellow croaker	<i>Pseudosciaena crocea</i>	1.23	28.5	70	Satiation	FM, SBM, WM	43	12		Mai <i>et al.</i> 2006
Yellowtail	<i>Seriola quinqueradiata</i>	23.3	24.8	30	Satiation	FM, SPC, WG, Gel	43	17	16.3 (DE)	Ruchimat <i>et al.</i> 1997b

Table 5. (Continued).

Common name	Scientific name	Met levels (% diet)	Met levels (g/16gN)	Cys level (% diet)	TGC	Nitrogen retention (%NI)	Met requirement (% DM)	Met requirement (g/16g N)	Response variable	Statistical Model	References
Asian seabass	<i>Lates calcarifer</i>	0.62-1.08	1.35-2.35	0.31	0.69-0.77		1.03	2.24	WG	BL	Coloso <i>et al.</i> 1999
Black sea bream	<i>Sparus macrocephalus</i>	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 <i>et al.</i> 2011
Cobia	<i>Rachycentron canadum</i>	0.61-1.68	1.4-3.8	0.67	0.92-1.32		1.19	2.64	SGR	QRA	Zhou <i>et al.</i> 2006
European seabass	<i>Dicentrarchus labrax</i>	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 <i>et al.</i> , 2010
Golden pompano	<i>Trachinotus ovatus</i>	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 <i>et al.</i> 2013
Grouper	<i>Epinephelus coioides</i>	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 <i>et al.</i> 2005
Japanese flounder	<i>Paralichthys olivaceus</i>	0.53-2.03	1.06-4.06	0.06	0.22-1.05	7.3-25.8	1.49 / 1.44	2.98 / 2.88	WG / FE	BL	Alam <i>et al.</i> 2000
Rockfish	<i>Sebastes schlegeli</i>	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 <i>et al.</i> 2007
White seabass	<i>Atractoscion nobilis</i>	0.64-1.28	1.6-3.2	0.51	1.11-1.35		0.88-1.21	2.22-3.00	TGC	SKM/ BQM	Salze <i>et al.</i> 2017
Yellow croaker	<i>Pseudosciaena crocea</i>	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 <i>et al.</i> 2006
Yellowtail	<i>Seriola quinqueradiata</i>	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 <i>et al.</i> 1997b

ANOVA, analysis of variance; ANU, apparent nitrogen utilization; BL, broken line regression; BQM, broken quadratic model; DE, digestible energy; DGI, daily growth index; DPD, daily protein deposition; EF, exponential function; FCR, feed conversion ratio; FE, feed efficiency; FER, feed efficiency ratio; FM, fish meal; FR: Fixed ration; GE, gross energy; Gel, gelatin; GPR, gross protein retention; HM, herring meal; MG, maize gluten; MRT, Duncan's multiple-rang test; NR, nitrogen retention; PD, protein deposition; PER, protein efficiency ratio; PM, peanut meal; PRE, protein retention efficiency; RGM, rice gluten meal; SBM, soy-bean meal; SFLC, serum free lysine concentration; SFPC, soluble fish protein concentrate; SGR, specific growth rate; SGR, specific growth rate; ShM, shrimp meal; SKM-4, saturation kinetic model-4 parameter; SM, squid meal; SOPR, second order polynomial regression; SPC, soy-bean protein concentrate; TGC: thermal growth coefficient WG, weight gain; WG, wheat gluten.

Table 6. Data collected from dose-response arginine (Arg) requirement studies.

Common name	Scientific name	Initial body weight (g/fish)	Water temperature (°C)	Trial duration (days)	Feeding Regimen	Protein ingredients	Diet crude protein (%)	Diet crude lipid (%)	Energy (kJ/g)	References
Asian sea bass	<i>Lates calcarifer</i>	2.6	29	85	FR	FM, zein, SM	48.5	10.3		Murillo-Gurrea <i>et al.</i> 2001
Black seabream	<i>Sparus macrocephalus</i>	10.5	28	56	Satiation	FM, SPC	38	14.2	15.5	Zhou <i>et al.</i> 2010c
Cobia	<i>Rachycentron canadum</i>	3.4	30.5	63	Satiation	FM, CGM	46	14		Ren <i>et al.</i> 2014
European seabass	<i>Dicentrarchus labrax</i>	0.8	26	60	Satiation	HM, CGM	40	12.6		Tibaldi <i>et al.</i> 1993
European seabass	<i>Dicentrarchus labrax</i>	2.1	25	63	FR	MG, HM	46	12		Tibaldi <i>et al.</i> 1994
Golden pompano	<i>Trachinotus ovatus</i>	18.8	25	56	Satiation	FM, CGM, RSM, PNM	43	12.5		Lin <i>et al.</i> 2015
Grouper	<i>Epinephelus coioides</i>	16	26.5	56	Satiation	FM, SPC	48	11	17.3	Luo <i>et al.</i> 2007
Hybrid Striped Bass	<i>M.saxatilis x M.chrysops</i>	7.2	28	70	Satiation	Casein, Gel	35	6	19.2	Griffin <i>et al.</i> 1994
Hybrid Striped Bass	<i>M.saxatilis x .chrysops</i>	3.1								Griffin <i>et al.</i> 1994
Japanese flounder	<i>Paralichthys olivaceus</i>	1.9	21	40	FR	Casein, Gel	50	9.8		Alam <i>et al.</i> 2002
Milkfish	<i>Chanos chanos</i>	0.7	29	84	Satiation	Casein, Gel	40			Borlongan, 1991
Red drum	<i>Sciaenops ocellatus</i>	3.8	29	49	FR	Red drum muscle	35		13.4	Barziza <i>et al.</i> 2000
Red sea bream	<i>Pagrus major</i>	13.3		63	Satiation	FM, SPC	50	15		Rahimnejad & Lee, 2014
Turbot	<i>Psetta maxima</i>	7.4	17	84	Satiation	FM, FPC, CGM	56	18	24	Fournier <i>et al.</i> 2003
Yellow grouper	<i>Epinephelus awoara</i>	4.2	28	56	Satiation	FM, SBM	43	10		Zhou <i>et al.</i> 2012b
Yellowtail	<i>Seriola quinqueradiata</i>	32.0		28	Satiation	Casein, FM	42		15.3	Ruchimat <i>et al.</i> 1998

Table 6. (Continued).

Common name	Scientific name	Arg levels (% diet)	Arg levels (g/16gN)	Thermal growth coefficient	Nitrogen retention (%NI)	Arg requirement (% DM)	Arg requirement (g/16gN)	Response variable	Statistical Model	Reference
Asian sea bass	<i>Lates calcarifer</i>	0.73-3.73	1.59-8.11	0.39-0.56		1.8	3.8	WG/FER	BL	Murillo Gurrea <i>et al.</i> 2001
Black seabream	<i>Sparus macrocephalus</i>	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 <i>et al.</i> 2010b
Cobia	<i>Rachycentron canadum</i>	1.76-3.75	3.8-8.2	0.90-1.06		2.85	6.2	WG	SOPR	Ren <i>et al.</i> 2014
European seabass	<i>Dicentrarchus labrax</i>	1.07-2.70	2.68-5.19	0.53-0.69		1.85	4.6	WG	BL	Tibaldi <i>et al.</i> 1993
European seabass	<i>Dicentrarchus labrax</i>	1.8	2.2-6.2	0.53-0.63	17-22	1.8	3.9	WG	BL/SKM	Tibaldi <i>et al.</i> 1994
Golden pompano	<i>Trachinotus ovatus</i>	2.05-3.58	4.8-8.3	1-1.23		2.73	6.32	WG	QRA	Lin <i>et al.</i> 2015
Grouper	<i>Epinephelus coioides</i>	1.78-3.31	3.7-6.9	0.97-0.96		2.7	5.5	WG	BL	Luo <i>et al.</i> 2007
Hybrid	<i>M.saxatilis x</i>	1-2.4	2.5-6.0	0.39-0.47		1.55	4.4	WG	BL	Griffin <i>et al.</i> 1994
Striped Bass	<i>M.chrysops</i>									
Japanese flounder	<i>Paralichthys olivaceus</i>	2.0	2.5-6.5	0.46-0.92	19-48	2.04/2.1	4.08 / 4.2	WG/FCE	BL	Alam <i>et al.</i> 2002
Milkfish	<i>Chanos chanos</i>	2.1	3.65-6.25	0.13-0.24		2.1	5.3	WG	BL	Borlongan, 1991
Red drum	<i>Sciaenops ocellatus</i>	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 <i>et al.</i> 2000
Red sea bream	<i>Pagrus major</i>	1.42-3.08	2.8-6.2	0.85-0.97		2.37	4.74	WG	BL	Rahimnejad & Lee, 2014
Turbot	<i>Psetta maxima</i>					1.6-3	3-5.4	WG	ANOVA	Fournier <i>et al.</i> 2003
Yellow grouper	<i>Epinephelus awoara</i>	2.8	4.7-7.6	0.63-0.73	20-23	2.8	6.5	SGR, WG	QRA	Zhou <i>et al.</i> 2012b
Yellowtail	<i>Seriola quinqueradiata</i>	1.5	3.4-5.8	5.44-6.36 (DGI)	21-27	1.5	3.5	WG	MRT	Ruchimat <i>et al.</i> 1998

ANOVA, analysis of variance; ANU, apparent nitrogen utilization; BL, broken line regression; DE, digestible energy; DGI, daily growth index; DPD, daily protein deposition; EF, exponential function; FCR, feed conversion ratio; FE, feed efficiency; FER, feed efficiency ratio; FM, fish meal; FR: Fixed ration; GE, gross energy; Gel, gelatin; GPR, gross protein retention; HM, herring meal; MG, maize gluten; MRT, Duncan's multiple-rang test; NR, nitrogen retention; PD, protein deposition; PER, protein efficiency ratio; PM, peanut meal; PNM: peanut meal; PRE, protein retention efficiency; RSM, Rapeseed meal, RGM, rice gluten meal; SBM, soy-bean meal; SFLC, serum free lysine concentration; SFPC, soluble fish protein concentrate; SGR, specific growth rate; SGR, specific growth rate; ShM, shrimp meal; SKM-4, saturation kinetic model-4 parameter; SM, squid meal; SOPR, second order polynomial regression; SPC, soy-bean protein concentrate; WG, weight gain; WG, wheat gluten.

Ideal Protein

The concept of ideal protein is that for a species, in a given physiological stage, there is an optimum dietary EAA profile that meets maintenance and production needs and maximizes nitrogen retention (Boisen, 2003). A protein with this optimum EAA profile is considered an “ideal protein”. In this ideal protein, each EAA can be computed as a proportion of the total EAA amount ($A/E \text{ ratios} = \text{EAA content} / \text{total EAA content including cysteine and tyrosine}$). Thus, quantitative requirements of all EAA can be estimated based on the A/E ratio, provided that the requirement of a single EAA is known. The EAA requirements of all other EAA is then expressed as a proportion of the reference EAA according to the relative proportion of each one in the optimum EAA profile.

Estimation of the EAA requirements based on the ideal protein concept is as a highly versatile approach that is being used extensively in pigs (Boisen, 2003) and poultry (Baker, 2003). This approach provides reliable and fast information of the EAA requirements, and is more economical than the classical dose-response method, and allows that modifications in requirements for all EAA related to animal age/size, physiological or environmental conditions can be easily estimated by evaluating changes in the requirement of a single amino acid. For consistent results with this approach it is required that reliable information on the optimum EAA profile for the animal is obtained and that the requirement of the EAA used as reference is accurately established (Boisen, 2003).

Lysine has been used as the reference AA in almost studies using the ideal protein approach, because it this AA is used mostly for protein accretion; it lacks metabolic interactions with other AA; its requirements is usually the highest among EAA; and it is generally the first limiting AA in practical diets, thus being the most susceptible to affect efficiency of protein utilization and ultimately growth (Ball *et al.* 2007). Due to lysine’s role as reference EAA, its requirement should be defined as precisely as possible to avoid biases in the estimation of the other EAA requirements based on the ideal protein approach.

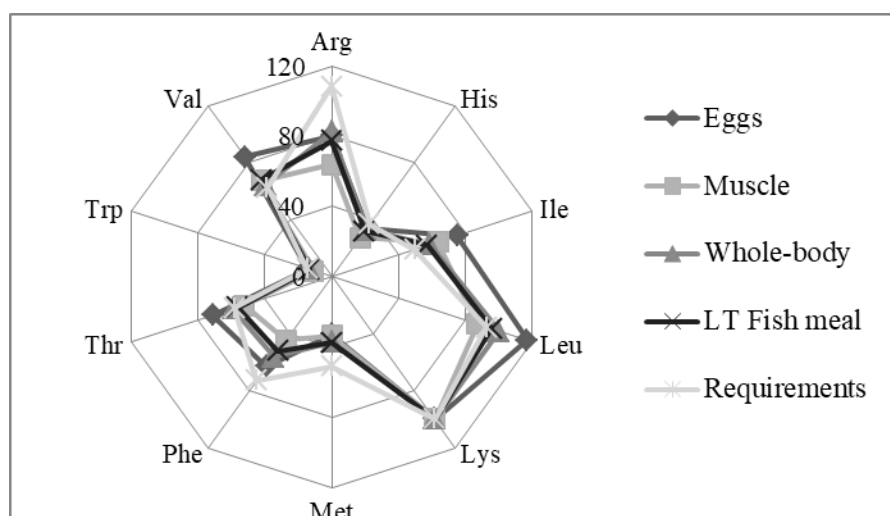


Fig 5. Comparison of EAA profile, expressed relatively to lysine (=100), of fish eggs, muscle and whole-body of different species, LT fish meal and requirement of gilthead seabream (data from Mambrini and Kaushik, 1995; Peres & Oliva-Teles, 2009).

Different EAA profiles have been used as indicative of the optimum dietary EAA profile, such as whole fish egg, whole fish larvae, fish muscle or whole fish carcass (Mambrini and Kaushik, 1995; Fig. 3). Among them, whole-body tissue composition seems to best fit the dietary EAA requirements profile and therefore it is generally used for establishing the optimum EAA profile. This, although whole-body AA reflecting better the EAA required for protein accretion and not taking into account the maintenance AA requirements (Peres and Oliva-Teles, 2009). Nevertheless, maintenance AA requirements usually represents a small fraction of total EAA requirements (Fournier *et al.* 2001; Lall 2005).

The whole-body EAA composition of selected marine fish species is presented in table 7. Mambrini and Kaushik (1995), using a factorial analysis, compared the EAA data available in the literature. These authors observed that although proteins from different tissues have different EAA profiles, the EAA profile of a given tissue seems to converge among species and was not affected by factors such as temperature, feeding rate or fish size. The authors also concluded that the whole-body EAA profile best reflected the optimum EAA profile of a reference protein. Further studies with marine species also suggest that the whole-fish EAA pattern best correlates

with EAA requirements, although it is not completely satisfactory for some fish (Rollin *et al.* 2003; Alam *et al.*, 2005; Luo *et al.* 2008; Peres & Oliva-Teles, 2009). For seabass and Japanese flounder, it was observed that the EAA profile of fish meal reflected better the EAA requirement pattern than the whole-body EAA profile (Alam *et al.* 2002; Peres & Oliva-Teles, 2007; Figure 5). However, for gilthead seabream, Peres and Oliva-Teles (2009) observed that the EAA profile determined by the deletion method correlates tightly to the whole-body EAA composition of seabream.

Table 7. Amino acid composition (g/ 16 g N) of whole-body tissue of some marine fish species¹.

Amino acid	Gilthead Seabream	European Seabass	White seabream	Turbot	Senegalese Sole
Arginine	8.7	8.4	8.6	7.6	6.8
Lysine	7.3	7.6	7.6	6.7	7.3
Histidine	2.8	2.4	2.4	2.3	2.6
Isoleucine	4.1	4.1	3.8	3.6	3.8
Leucine	7.0	7.2	7.2	6.4	7.1
Valine	4.4	4.6	4.2	4.1	4.6
Methionine	2.7	2.6	2.7	2.5	2.7
Phenylalanine	4.4	4.5	4.1	3.2	4.1
Threonine	4.2	4.3	4.1	4.3	4.1
Tyrosine	3.9	3.9	3	3.2	3.1
Aspartic Acid	9.0	9.5	7.9	6.8	10.1
Glutamic Acid	14.1	15.6	13.8	11.8	14.1
Serine	4.5	4.7	4.6	4.8	4.6
Glycine	7.4	7.1	9	9.3	8.2
Alanine	6.3	6.4	6.5	6.4	6.5
Proline	5.1	4.9	4.9	4.9	5.3
Reference	Kaushik, 1998	Kaushik, 1998	Unpublished data	Peres & Oliva- Teles, 2009	Silva, 2009

The optimum EAA profile may also be determined by the deletion method. This method was initially outlined by Wang and Fuller (1989) and is based on the concept that each EAA is

¹ Peres, H. and Oliva, A. 2017. Protein and amino acid nutrition of marine fish species. En: Cruz-Suárez, L.E., Ricque-Marie, D., Tapia-Salazar, M., Nieto-López, M.G., Villarreal-Cavazos, D. A., Gamboa-Delgado, J., López Acuña, L.M. y Galaviz-Espinoza, M. (Eds), Investigación y Desarrollo en Nutrición Acuicola Universidad Autónoma de Nuevo León, San Nicolás de los Garza, Nuevo León, México, pp. 438-492. ISBN 978-607-27-0822-8.

equally limiting to protein accretion, i.e. body protein accretion rate is directly related to single limiting-EAA and the reduction of a non-limiting EAA has no effect on nitrogen gain. Therefore, changes in nitrogen gain due to partial removal of one EAA in a diet otherwise balanced in its EAA profile will give an estimation of the requirement of that single EAA. The application of this method to all EAA will involve the formulation of a control diet, with a balanced EAA profile, and ten test diets identical to the control diet but replacing about 40-50% of a single EAA by a mixture of non-EAA while maintaining all diet isonitrogenous. The proportional reduction on nitrogen retention of each test diet relatively to the control diet is used to quantify the quantity of each EAA from the control diet that can be removed without affecting N retention (Fig. 6). This approach is largely used in pigs (NRC, 1998), but in fish it was only applied to salmonids (Green & Hardy, 2002; Rollin *et al.* 2003), silvery-black porgy (*Sparidentex hasta*), tilapia (Diogenes *et al.* 2016) and to gilthead seabream (Peres & Oliva-Teles, 2009) (Fig. 7).

Comparison of the EAA profiles obtained by the application of the amino acid deletion method denotes only small differences among fish species. The highest difference is on the arginine requirement, which is higher in gilthead seabream than in salmonids. Similarly, higher arginine requirement per g of nitrogen accretion was also estimated for marine fish species (1.04-1.11 g; gilthead seabream, European seabass and turbot) than for rainbow trout (0.86 g) (Fournier *et al.* 2002).

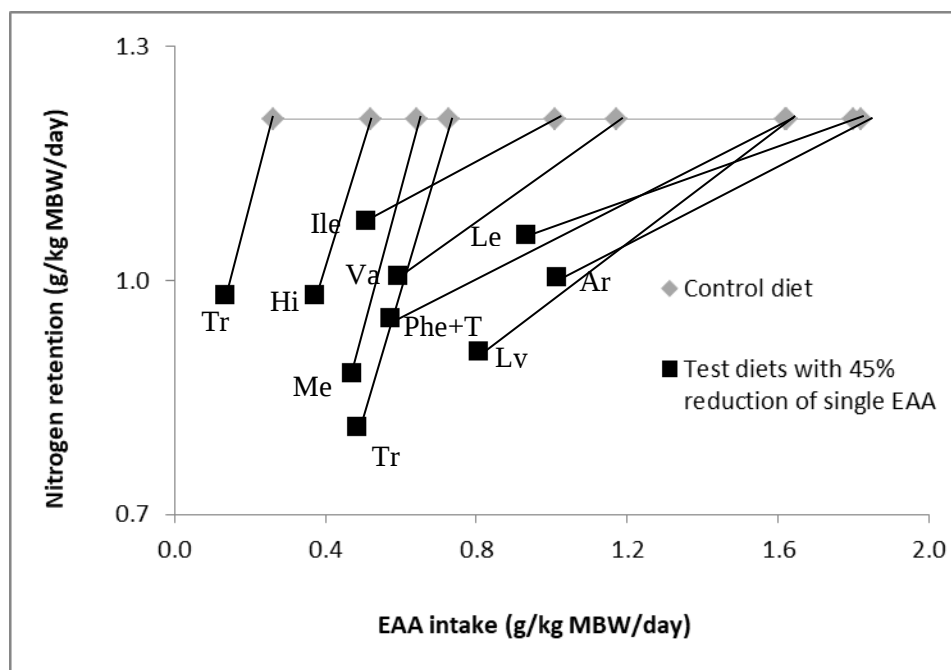


Fig 6. Application of amino acid deletion method: effect of deleting 45% of each EAA from the control diet on nitrogen retention of gilthead seabream (Peres & Oliva-Teles, 2009).

The EAA requirement estimated for different marine fish species using different approaches is summarized in table 8. As it can be seen, for gilthead seabream the EAA requirements estimated by the deletion method or by the whole-body composition are very consistent, except for Phe+Tyr. In fast growing animals.

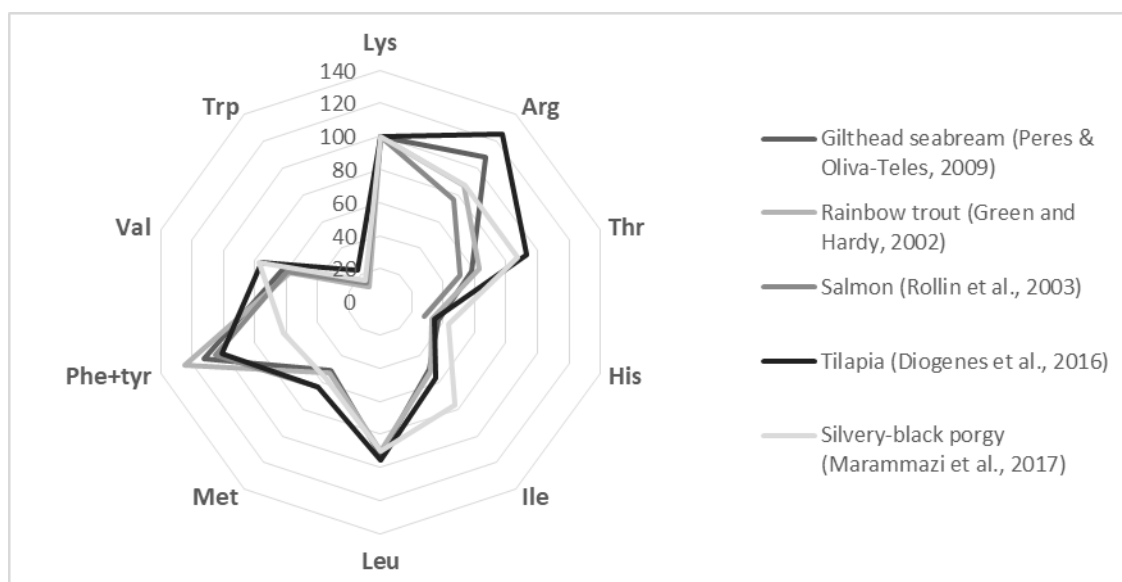


Fig 7. Comparison of the optimum EAA profile, determined by the deletion method, for gilthead seabream, rainbow trout and salmon (data presented relatively to lysine level =100).

Daily accretion of a specific EAA in the whole-body of fed fish has also been used to experimentally determine the EAA requirements. This approach was applied to tilapia, carp, white and Siberian sturgeon (Ogino, 1980; Jauncey *et al.* 1983; Kaushik *et al.* 1991; Ng & Hung, 1995). Although, this method usually provides a good estimate of the optimum dietary EAA profile, its application to estimate AA requirement for growth is questionable. EAA requirement values obtained by this method are usually lower than values obtained by dose-response studies. This is because this method ignores the maintenance requirements and the net efficiency of nitrogen retention that represents only 30 to 40% of the dietary nitrogen.

Given the scarcity of published information on EAA requirement for marine fish species, the application of the ideal protein approach seems a good strategy as it is a fast and practical way to estimate the dietary EAA pattern and to optimize dietary protein level. This information will be highly beneficial for the development of innovative low-cost and low-environmental impact diets by minimizing excess dietary protein level and nitrogen excretion. This information is also critical for a correct formulation of diets based on alternative protein sources to fish meal.

Table 8. Estimation of essential amino acid requirement for selected marine fish species.

Species	Gilthead seabream (<i>Sparus aurata</i>)	Gilthead seabream (<i>Sparus aurata</i>)	Red seabream (<i>Pagrus major</i>)	Common dentex (<i>Dentex dentex</i>)	European seabass (<i>Dicentrarchus labrax</i>)	Turbot (<i>Scophthalmus maximus</i>)	Striped bass (<i>Morone saxatilis</i>)
Method	Whole-body composition	EAA deletion	Whole-body composition	EAA increment	Whole-body composition	Whole-body composition	Whole-body composition
Arg	5.4	5.6	3.5	3.7	4.6	4.8	3.9
His	1.7	1.9	1.4	1.3	1.6	1.5	1.7
Ile	2.6	2.6	2.2	2.5	2.6	2.6	2.5
Leu	4.5	4.8	4.2	4.1	4.3	4.6	5.3
Lys	5.0	5.0	4.4	4.7	4.8	5.0	6.1
Met+Cys	2.4	2.6	2.2	2.2	2.3	2.7	2.8
Phe+Tyr	2.9	5.8	4.1	4.1	2.	5.3	4.7
Thr	2.8	3.0	1.8	2.4	2.7	2.9	3.1
Trp	0.6	0.8	0.6	0.5	0.6	0.6	0.8
Val	3.0	3.2	2.5	2.8	2.9	2.9	2.8
Reference	Kaushik, 1998	Peres & Oliva-Teles, 2009	Forster & Ogata, 1998	Kaushik & Tibaldi, 1998	Kaushik, 1998	Kaushik, 1998	Small & Soares, 1998

Amino acids as functional ingredients

The major fate of AA is towards protein synthesis, a minor proportion being used for different physiological functions but emerging evidence shows that some AA have growth and health promoting proprieties beyond their basic function on body (Wu, 2010a). These AA are known as functional AA, regulating key metabolic pathways that are crucial for maintenance, growth, reproduction and immune responses (Li *et al.* 2007; Wu, 2010a; Andersen *et al.* 2016). Dietary modulation of health, stress, and immune response by AA has already been confirmed in humans and terrestrial animals through dietary supplementation with functional AA at levels above the requirement for growth (Li *et al.* 2007). This approach is particularly interesting as the use of antibiotics and chemotherapeutic treatments in aquaculture is now highly regulated and restricted. Although little is known for fish, recent studies showed that arginine, glutamine, taurine, methionine, tryptophan, proline, and hydroxyproline may have functional proprieties in promoting growth, development and health in fish (Li *et al.* 2007; Andersen *et al.* 2016).

Arginine and glutamine are the best prototypes of functional AA, being able to modulate immune function, cellular redox state and gastrointestinal integrity and, consequently, health status (Li *et al.* 2009; Oehme *et al.* 2010, Andersen *et al.* 2016). Arginine has important regulatory functions in nutrient metabolism and immune response, being of physiological relevance in diseased-animals and in stress situations in which there is a depletion of arginine level in the blood. Moreover, plasma free arginine levels decrease in fish under stressful conditions compared to non-stressed fish (Aragão *et al.* 2008, Costas *et al.* 2008). In fresh water fish, arginine has been reported to be a key-factor of important processes as the production of the pivotal precursor of polyamine synthesis, which enhances fish growth (Li *et al.* 2009; Cheng *et al.* 2012; Andersen *et al.* 2013; Pohlenz *et al.* 2014; Yue *et al.* 2015), the production of nitric oxide which increases immune response and diseases resistance during stress (Buentello & Gatlin, 1999; 2001; Buentello *et al.*

2007; Pohlenz *et al.* 2012a; 2014; Yue *et al.* 2015), and cellular signaling (Bronte and Zanovello, 2005; Holen *et al.*, 2014). Also in fresh water fish species, arginine is known as a more potent insulintropic metabolite than glucose, increasing the titers of insulin, IGF-1, growth hormone, glucagon and glucagon-like peptide-1 (Mommensen *et al.* 2001; Pohlenz, *et al.* 2013; Andersen *et al.* 2014). In marine fish species, dietary arginine supplementation beyond requirements for protein synthesis was shown to promote growth (Cheng *et al.* 2011) and eliciting positive changes to several components of the innate immune system (Tafalla & Novoa, 2000; Cheng *et al.* 2011; Costas *et al.* 2011; Han *et al.* 2013), oxidative status and intestinal maturation in seabass (Peres *et al.* 1997) and reduced cortisol levels in stress fish (Costas *et al.* 2013). Contrarily, recently it was observed that in gilthead seabream, arginine supplementation has no effect of growth and feed utilization (Coutinho *et al.* 2016b; Oliva-Teles *et al.* 2017), intestinal nutrient absorption capacity, amino acid metabolism and oxidative stress (Coutinho *et al.* 2016b). Also, for golden pompano, it was observed that a surplus of arginine, beyond the requirement level, lead to a reduction of growth performance and protein utilization efficiency (Lin *et al.* 2015). Excessive arginine levels may generate antagonism with lysine, impairing the lysine absorption (Berge *et al.* 1999; Kaushik *et al.* 1988), or may increase ureagenesis (Kaushik & Fauconneau, 1984; Oliva-Teles *et al.* 2017).

Glutamine is considered a pivotal amino acid, regulating several metabolic pathways, including stress and immune responses (Li *et al.* 2009, Andersen *et al.* 2016; 46, 29, 65, 63). Glutamine is utilized as a source of energy for nucleotide synthesis by all rapidly proliferating cells, including enterocytes and lymphocytes. Further, glutamine is known to stimulate muscle protein synthesis in mammals, improve gastrointestinal tract maturation and health. Being the precursor of glutathione, glutamine is also important to protect cells from oxidative stress (Li *et al.* 2007). In human and domestic animals, the benefits of dietary supplementation with glutamine are well documented and include benefits on growth, feed conversion, immune function, cellular antioxidant status and maintenance of

gastrointestinal functions and integrity (Wu *et al.* 2010b). Although little work in this area has been conducted so far in fish, there are recent evidences that open the possibility to extend these benefits to fish production. Studies with tilapia, Jian carp and hybrid striped bass confirmed that diet supplementation with glutamine significantly increased growth, intestinal function and structure (Yan & Qiu-Zhou, 2006; Lin & Xiau, 2006; Silva *et al.* 2010; Cheng *et al.* 2012; Jiang *et al.* 2015; Hu *et al.* 2015). Moreover, it has been observed that glutamine supplementation increased macrophage production of superoxide anion, neutrophil oxidative radical and lysozyme activity (Cheng *et al.* 2011; 2012) and has a protective effect against the oxidative stress in intestinal epithelial cells and hypoxia stress (Chen *et al.* 2009; Liu *et al.* 2015). It was also confirmed that dietary supplementation with arginine plus glutamine significantly increased feeding rate and growth during the first autumn (Oehme, *et al.* 2010). *In vitro* studies also showed that glutamine promoted fish enterocytes growth (Jiang *et al.* 2009) and increased non-specific T and B cell proliferation (Pohlenz *et al.* 2012b). Recently, it was observed that growth and feed utilization of gilthead sea bream juveniles was not affected by the dietary glutamine supplementation (Caballero-Solares *et al.* 2015; Coutinho *et al.* 2016), but it increased protein retention (Caballero-Solares *et al.* 2015), and modulated hepatic and intestinal antioxidant responses (Coutinho *et al.* 2016c).

Beyond their roles as substrates for protein synthesis, methionine and cysteine are involved in numerous roles in metabolism, being methyl donor for several methylation reactions, including DNA, and precursors of important molecules, such as glutathione and taurine, which are essential compounds in defense mechanisms against oxidative stress (Metayer *et al.* 2008; Andersen *et al.* 2016; Coutinho *et al.* 2017). In juvenile hybrid striped bass, it was observed that methionine deficiency in diet might exhaust reservoirs of non-enzymatic antioxidant defenses such as ascorbic acid, vitamin E or glutathione, and increase liver lipid oxidation. Oxidation of methionine residues also acts as scavenger of reactive oxygen species (Weissbach *et al.* 2005; Métayer *et al.* 2008; Feng *et al.* 2011).

Together, these negative repercussions may result in oxidative stress (Li *et al.* 2009; Andersen *et al.* 2016). Under stress situations it was reported a decrease of plasma free methionine, suggesting an increased use of this AA, probably related to the increased demand for glutathione and taurine (Aragão *et al.* 2008; Costas *et al.* 2010). However, in gilthead bream dietary methionine supplementation above the requirement level was not required to maintain normal hepatic glutathione levels (Perez-Jimenez *et al.* 2012). In European seabass it was showed to modulate the oxidative stress response but did not affect growth performance (Coutinho *et al.* 2017).

Taurine and hydroxyproline are non-protein AA that are abundant in fishmeal but not in plant protein sources. Taurine is considered a conditionally EAA, specially for marine fish species fed low-fishmeal based diets, and is involved in important biological functions, such as fat digestion, bile salt conjugation, antioxidant defense, osmoregulation, as well as development of visual, neural and muscular systems (Li *et al.* 2009; El-Sayed, 2014; Salze *et al.* 2015). Capacity to biosynthesize taurine depends on fish species, and for some carnivorous species supplementation of low-fish meal diets with taurine is required to maximize growth (Goto *et al.* 2001, 2003; Park *et al.* 2002; Matsunari *et al.* 2005, 2008; Takagi *et al.* 2010; Jirsa *et al.* 2014; Wu *et al.* 2015; Lopez *et al.* 2015; Al-Feky *et al.* 2016; Li *et al.* 2016b). Taurine-deficient diets are also known to impaired liver function (El-Sayed, 2014; Salze *et al.*, 2015), inducing green liver symptom is carnivorous fish species such as red seabream, yellowtail and Japanese flounder (Takagi *et al.* 2006, 2008, 2011; Goto *et al.* 2001). The role of taurine on lipid digestion and formation of bile salts is well documented (Salze & Davis, 2015). In fish, bile acids conjugations occur mainly with taurine; conjugated bile acid are actively absorbed distal intestine, thus maintaining adequate concentrations in most of the intestine (Salze & Davis, 2015). Low taurine level may impair conjugation of bile acids and so lipid digestion. Evidence shows that taurine supplementation increases bile salt content (Kim *et al.* 2007, 2015; Nguyen, *et al.* 2015),

although it appears to be independent from dietary lipid levels (Kim *et al.* 2008; Salze *et al.* 2015).

Increased evidences have also highlight the role of taurine as an antioxidant (El-Sayed, 2014; Salze *et al.* 2015). Taurine depletion may induce oxidative and inflammatory stress (El-Sayed, 2014; Salze *et al.* 2015). Taurine antioxidative action may be associated to its capacity to act as a non-specific scavenger of reactive oxygen species, to modulate the production of reactive oxygen species or to improve the antioxidant enzyme activity (Divakaran, 2006; Aydogdu *et al.*, 2007; Banuelos-Vargas *et al.* 2014; Feidantsis *et al.* 2014; Han *et al.* 2014). Dietary taurine supplementation reduced lipid peroxidation (Zhang *et al.* 2004; Aydogdu *et al.* 2007; Chang *et al.* 2011; Sevgiler *et al.* 2012; Hammes *et al.* 2012; Banuelos-Vargas *et al.* 2014). Taurine has also been reported to have some health benefits, including alleviation of metal toxicity (Gurer *et al.* 2001; Sevgiler *et al.* 2011; Hammes *et al.*, 2012) and resistance against hyperammonemia (Li *et al.* 2016).

Tryptophan is the only amino acid that can be converted into serotonin, the precursor of melatonin, having several important biological functions such as appetite regulation, immune response and health maintenance (Andersen *et al.* 2016). Some studies with animals, including fish, indicate that tryptophan is a rate limiting factor for serotonin synthesis, inducing a dose-dependent response (Johnston *et al.*, 1990; Herrero *et al.*, 2007). Consequently, and although the rate limiting step for melatonin synthesis is modulated by the enzymes AANAT and HIOMT, these reactions are dependent on substrate concentration and therefore, tryptophan also acts as limiting factor for melatonin production (Huether *et al.* 1992). Supplementing dietary tryptophan reduced aggressive behavior in different fish species (Winberg *et al.* 2001; Hodlund *et al.* 2005; Clotfelter *et al.* 2007). Tryptophan, through its precursors, serotonin and melatonin, is known to act as a free radical scavenger, playing key roles on cell redox balance by promoting the activity of antioxidative enzymes, which was also observed in fish species (Wen *et al.* 2014; Ciji *et al.* 2015). Recently for Senegalese sole it has shown that tryptophan has immunomodulatory

properties after a bacterial challenge (Azeredo *et al.* 2016), while the opposite was observed for seabass (Machado *et al.* 2015). In carp, it was observed that an appropriate dietary tryptophan level improves grass carp growth, intestinal immune response, barrier function and antioxidant status, and regulated the mRNA levels of related signal molecules, whereas as higher levels of tryptophan severely reduced growth (Wen *et al.* 2014). Dietary fortification with tryptophan also modulates growth and immuno-metabolic status of *Labeo rohita* juveniles exposed to nitrite (Ciji *et al.* 2015).

Proline and hydroxyproline are also considered conditionally EAA for some fish in both early life and adult stages, also having functional properties related to antioxidant and immune responses (Wu *et al.* 2011). Hydroxyproline is produced by post-hydroxylation of proline after protein synthesis. Dietary supplementation of low-fishmeal diets with hydroxyproline improved growth and collagen formation (Aksnes *et al.* 2008). However, for turbot, hydroxyproline supplementation of plant-based diets had no effect on growth, but increased tissues Hyp and muscle total collagen concentration (Zhang *et al.* 2013).

Conclusions

Diet formulation based on an adequate protein content and optimum EAA profile is a key factor to improve efficiency of AA utilization for protein accretion, therefore reducing nitrogen excretion. However, information on protein requirement and particularly on the requirements of the 10 classically considered EAA is limited for the majority of marine fish species with interest for aquaculture. This lack of information is of practical relevance when considering replacement of fishmeal by plant protein as main dietary protein sources, due to the potential unbalance of EAA that may occur.

Up to now, studies on EAA requirements of marine fish have been focused on a limited number of EAA, namely lysine, methionine and arginine, which are EAA that may be the first limiting in the most commonly, used feed ingredients. Recently, and as consequence of the use of plant feedstuffs as main dietary protein sources, particular attention has been given to taurine requirements. Estimation of EAA requirement based on the ideal protein concept is a highly versatile approach, allowing the estimation of the requirement of all EAA based on the determination of the requirement of just one EAA and the ideal protein EAA profile. Due to the high diversification of new marine species with interest for aquaculture, the ideal protein approach may be used as the first approach to provide fast and relatively inexpensive information of the EAA requirements.

The major proportion of AA is used for protein synthesis; a minor proportion being used for different metabolic purposes. Related to this, emerging evidence shows that some AA when incorporated at the diets at a level above requirements may have functional properties, regulating key metabolic pathways crucial for maintenance, growth, reproduction, oxidative status and immune responses of the animals. Further studies are needed to elucidate the AA induced changes and their potential application as modulators of growth and well-being of fish.

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