



Nutritional requirement of two Amazonian aquacultured fish species, *Colossoma macropomum* (Cuvier, 1816) and *Piaractus brachypomus* (Cuvier, 1818): a mini review

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Summary

This short review will focus on the nutritional requirement of tambaqui (*Colossoma macropomum*) and pirapitinga (*Piaractus brachypomus*), two important aquacultured neotropical fishes for Latin American countries. Demonstrated is that despite the large number of studies on protein requirement for *C. macropomum*, most are inadequate. The principal difficulties with the various published papers are described. Using the nutritional ecology of the fish, some recommendations are presented to identify future research needs in the area. A focus on determining the nutrient requirement for *P. brachypomus* is featured since there are few studies regarding this species, as well as a focus on the differences in feeding plasticity with *C. macropomum*. Market and farming constraints and the nutritional ecology of these species in Latin America with special emphasis on Brazil, are also described.

Introduction

The Serrasalminae family is an economically and socially important group of freshwater fishes for most Latin American countries, mainly those in the Amazon region. Among this diverse group, tambaqui (*Colossoma macropomum*) and pirapitinga (*Piaractus brachypomus*) have been highlighted as important fish species because of their high growth rates as well as easy adaptability to intensive culture systems.

C. macropomum is the second most produced species in Brazilian aquaculture, mainly because of its high growth rate and low production costs compared to other farmed fish species. Although their natural habitat is the Amazon and Orinoco river basins, this species can be found in several other Latin American countries such as Bolivia, Peru, Colombia, Venezuela, Cuba, Dominican Republic, Honduras, Jamaica, and Panama. In most Latin American countries, *C. macropomum* is the main protein source in low-income communities, especially for the North region of Brazil. Some Brazilian government programs are trying to disseminate *C. macropomum* farming in low-income communities as a means to increase food security.

Despite the importance of *C. macropomum* for Latin American countries, especially in Brazil, very limited information is available on the nutrient requirements for this

species. This information is of utmost importance, since the future of tambaqui farming may depend upon the production of more efficient and species-specific diets to reduce production costs and help to establish an aquaculture production based on environmental sustainability.

Another economically important species is pirapitinga (*Piaractus brachypomus*), commonly known as red pacu or red cachama in some regions of Brazil and Latin American countries. This species belongs to the Characiformes order and Characidae family. These species were recently classified as a subfamily of Characidae, called Serrasalminae (Nascimento et al., 2010). Similar to *C. macropomum*, the original habitat of *P. brachypomus* is the Amazon and Orinoco river basins. Wild specimens can reach up to 20 kg live weight (Alcántara et al., 1990). However, this species can now be found in natural lakes of India, probably having been introduced in Bangladesh (Barua and Chakraborty, 2011), as well as also found in some research institutes in the USA. *P. brachypomus* has been commercially farmed in several Latin and Central America countries, with emphasis on Colombia and Brazil in which they are the second and seventh most-produced species in aquaculture systems, respectively (Vásquez-Torres and Arias-Castellanos, 2012; MPA, 2013). In Brazil, *P. brachypomus* farms are located in the mid-eastern and northern regions where they have been used in interspecific crosses with *C. macropomum* (MPA, 2013). The great potential of this species for intensive farming is due to its resistance to handling, rusticity, quality of flesh and high spawning success by hormonally-induced reproduction; however, their slower growth rates compared to *C. macropomum*, the presence of intramuscular Y-shaped bones in the fillet, lack of technology to improve final product quality and the paucity of information on their nutrient requirements make *P. brachypomus* farming very artisanal, considering their great economic potential.

Based on the importance of these species in Latin America aquaculture, our goal was to give a perspective to researchers from Latin America and other countries regarding the information and recent findings in our and other research groups on the nutrient requirements of these species. Despite a previous lack of studies, we used all available data; a critical evaluation was made based on standard nutrition principles and on the assumption that the dietary intake of a wild fish

fulfills its nutrient requirement, which is then reflected in the organ nutrient status (Hamre et al., 2013).

Colossoma macropomum

Protein and amino acids

Although the importance of protein/amino acid nutrition for fish farming is well known, the quantitative protein requirement for *C. macropomum* has rarely been studied. Actually, the number of papers published on the effect of dietary protein levels on growth and feed efficiency of *C. macropomum* is far higher compared to those of the other nutrients (Table 1). However, there are broad discrepancies on protein recommendations among the studies. Summarizing the data in Table 1 into three different life stages, the protein requirements varied up to 71, 33 and 60% for *C. macropomum* weighing from 1 to 50 g, 50 to 100 g, and 100 to 250 g, respectively. These are great variations for fish within the same life stage; therefore, caution is necessary when using the data to formulate *C. macropomum* diets.

For instance, we believe the most adequate protein requirement for 1–50 g *C. macropomum* must be around 440–480 g kg⁻¹ crude protein, since in early life stages they usually feed on zooplankton (mainly cladocerans and copepods), which contain around 440 g kg⁻¹ crude protein (Silva et al., 2000). For 50–150 g *C. macropomum*, the protein requirement of 320–350 g kg⁻¹ was estimated using an exponential model (van der Meer et al., 1995). Indeed, this last value seems more consistent since it is the average value among the studies for this life stage (Table 1) and the model is more appropriate than ANOVA to estimate nutrient requirements. For *C. macropomum* weighing above 150 g, we recommend a diet containing 280 g kg⁻¹ protein as a starting point because no reports are available on the protein requirements at this life stage. This value is based on the average of the digested chemical composition of wild tambaquis caught in the rainy and dry seasons (Silva et al., 2000, 2003).

Up to now, there are no reports on the values of any of the ten essential amino acids for *C. macropomum*. Although dose-response studies are more accurate for determination of amino acid requirements for fish, the high cost and time-consuming trials for determination of an individual essential amino acid requirement led several authors and the feed industry to use different nutritional approaches. Concurrently, Oliveira et al. (2012) calculated an estimate of the amino acid requirement based on the amino acid profile of tambaqui carcass and data with other fish species, as recommended by Kaushik (1998). We thus recommend the use of these estimates until more accurate values are reported.

Because *C. macropomum* presents great feeding plasticity in being able to efficiently use different non-protein energy sources for protein sparing, care must be taken when designing the experimental diets in protein/amino acid requirement studies. Additionally, changes in the protein : carbohydrate : lipid ratio can lead to an increased fat deposition in *C. macropomum* (Almeida and Franco, 2006), which is actually a market problem for consumers. As energy intake data for *C. macropomum* is limited to adult fish, the use of values

observed in the literature, ranging from 20.3 to 24.0 MJ GE kg⁻¹ diet, must be used with caution because fish at this life stage present different kinetics of nutrient deposition and energy use, e.g. in adult fish the energy and nutrients are for reproduction purposes rather than somatic growth. Therefore, the chemical composition of the carcass should be considered when formulating nutritionally balanced diets for *C. macropomum*, aiming to avoid the production of fish with a high fat index, which generally occurs when *C. macropomum* reaches 1.0–1.2 kg live weight.

Protein : energy ratio

Feed efficiency varies according to the protein : energy ratio of the diet. This is a result of the regulatory effect of the energy content. Additionally, high-energy diets tend to increase the carcass and/or muscle fat content in fish (Cho and Kaushik, 1990). Because fat deposition and the ability to efficiently use different non-protein energy sources seem to be important characteristics of *C. macropomum* physiology, we therefore only used studies that took into account the dietary energy level when evaluating the protein requirement.

Generally, dietary protein utilization is limited to sustain growth and maintain basal body protein when low protein : energy ratios (P : E) are used in fish feed. On the other hand, high P : E ratios can lead to the use of protein to meet the energy requirements or be stored as fat in body deposits of fish (Winfree and Stickney, 1981). Thus, the increase in dietary lipids generally leads to an increased efficiency in protein retention, called the protein-sparing effect (van der Meer et al., 1997a). For example, an increase in dietary carbohydrates and lipids reduced the activity of enzymes from amino acid catabolism in the hepatopancreas of carp, leading to low nitrogen excretion and an increase in the protein efficiency ratio (Shimeno et al., 1981).

C. macropomum with the highest growth rates showed that a P : E ratio of around 27 mg protein KJ⁻¹ energy is necessary to maintain growth potential (van der Meer et al., 1995). However, the highest protein utilization was observed in diets containing 15 mg protein KJ⁻¹ energy while higher P : E ratios decreased protein utilization for *C. macropomum*. Additionally, van der Meer et al. (1995) observed a protein-sparing effect when non-protein energy sources were included in the diets with P : E ratios higher than 15 mg protein KJ⁻¹; on the other hand this increased the carcass fat content.

C. macropomum carcass quality is directly linked to the dietary P : E ratio: several studies demonstrated that the increase in non-protein energy sources led to an increase in the body fat content (Hernández et al., 1995; van der Meer et al., 1995, 1997b; Oishi et al., 2010; Santos et al., 2010). Therefore, we may assume that the high fat content observed in farmed *C. macropomum* may be related to an inadequacy in the diet with respect to protein requirement and the capacity of this species to efficiently use both lipids and carbohydrates for protein-sparing. The fat content of *C. macropomum* is a consumer problem in some regions, thus this topic deserves more attention by the scientific community to better understand the kinetics of nutrient deposition

Table 1
Reported dietary protein and energy requirement, *C. macropomum*, based on weight gain and experimental conditions of the studies

Weight range ^a (g)	Trial length	Tested protein levels (g kg ⁻¹)	Protein requirement (g kg ⁻¹)	Energy requirement (Mj DE ^b kg ⁻¹)	Statistical model	Notes	Reference
1–50	4 weeks	200, 300, 400, 500, 600	481	19.2 ^c	ANOVA	Quadruplicate groups of fish raised in a recirculation system containing 45-L aquaria with controlled water quality	van der Meer et al. (1995)
8–22	18 days	107, 204, 284, 310, 363, 477	480	16.6	ANOVA	Duplicate groups of 20 fish raised in a flow-through system containing 70-L aquaria with controlled water quality	Hernández et al. (1995)
5–50	60 days	158.6, 212, 262.5, 367.8	280 (269)	13.6	Polynomial Regression	Triplicate groups of 15 fish raised in a flow-through system containing 150-L aquaria with controlled water quality	Pinheiro et al. (2009)
46–75	60 days	250, 300, 350, 400	300	11.5	Broken line	Triplicate groups of 20 fish assigned to 200-L aquaria; raising system not reported	Oishi et al. (2010)
50–100	60 days	280, 320, 360, 400	360	14.3	ANOVA	Triplicate groups of 16 fish raised in a flow-through system containing 200-L aquaria with controlled water quality	Santos et al. (2010)
30–90	4 weeks	200, 300, 400, 500, 600	400	18.8 ^e	ANOVA	Quadruplicate groups of fish raised in a recirculation system containing 45-L aquaria with controlled water quality	(van der Meer et al., 1995)
30–145	109 days	300, 350, 400	300	11.3	ANOVA	Triplicate groups of 150 fish raised in 1 m ³ net cages located in a water reservoir	Merola and Cantelmo (1987)
100–150	4 weeks	200, 300, 400, 500, 600	400	19.3 ^c	ANOVA	Quadruplicate groups of fish raised in a recirculation system containing 4-L aquaria with controlled water quality	van der Meer et al. (1995)
124–273	48 days	205, 253, 301, 350	300	15.8	ANOVA	Triplicate groups of 10 fish raised in a recirculation containing 250-L aquaria with controlled water quality	de Almeida et al. (2011)
30–250	90 days	180, 210, 240, 270, 300	250	13.0 ^d	Polynomial Regression	Triplicate groups of 23 fish raised in 25 m ² earthen ponds with limited control of water quality parameters	Vidal-Júnior et al. (1998)

^aWeight range = approx. initial and final weight of fish.

^bDigestible energy. Digestible values in parentheses.

^cGross energy values.

^dMetabolizable energy values.

in *C. macropomum* and how the fat deposition can be modulated to obtain a product of increased nutritional quality suitable to the consumer.

As other omnivorous fish, *C. macropomum* tend to increase their digestible energy requirement in relation to protein (DE : CP) as they grow. This usually occurs in fish in initial life stages because they tend to use protein more efficiently as an energy source (Lovell, 1998). Additionally, in initial life stages the digestive tract of fish is not completely developed to digest and absorb carbohydrates and lipids efficiently; the high protein synthesis at this stage leads to fish showing a higher protein requirement in initial life stages, reduced accordingly as the fish reaches sexual maturity. For example, a dietary GE : CP ratio around 39.9 kJ g⁻¹ protein seems to be adequate for starter diets, while diets containing 43.9, 46.9, and 48.1 kJ g⁻¹ protein seems to be more adequate for grow-out stages (van der Meer et al., 1995; Santos et al., 2010). At this life stage, *C. macropomum* juveniles show their ability to use different types of protein sources with a feed conversion ratio of circa 1.25 and a GE : CP ratio, higher than in other life stages.

Lipids and fatty acids

Studies of fatty acids with valuable information on their effects on the growth response of *C. macropomum* are rare. Quantitative and qualitative total lipid and fatty acid composition observed in wild (sampled at two different hydrological seasons) and farmed *C. macropomum* is shown in Table 2. Farmed fish had approximately twice the total lipids of wild fish caught in the flood and dry seasons (Table 2). Generally, fish can be classified into four groups according to the total lipid content of their edible parts: (i) very low (<20 g kg⁻¹ fat), (ii) low (20–40 g kg⁻¹ fat), (iii) moderate (40–80 g kg⁻¹ fat), and (iv) high lipid content (>80 g kg⁻¹ fat) (Ackman, 1989). Using this classification farmed *C. macropomum* can be classified as an intermediary fatty fish whereas wild fish would be classified as a relatively lean fish.

Total lipid content observed for farmed fish in the former study (48 g kg⁻¹) was higher than the values previously

reported for *C. macropomum* raised in a semi-intensive production system (24 g kg⁻¹) (Arbeláez-Rojas et al., 2002). However, it was lower than the values reported by Almeida (1998) (78 g kg⁻¹). These results suggest that the fat content of *C. macropomum* could be affected by the type of raising system that is directly related to the feeding management and type of diet used in each production system.

Differences in fatty acid composition between wild and farmed *C. macropomum* were also observed (Table 2). Farmed fish tended to show a lower content of both LA and LNA than wild fish. Differences between seasons may exist, since there is a complete change in the *C. macropomum* diet in the flood and dry seasons (Araújo-Lima and Goulding, 1998). This may explain the higher LA content in fish caught during the flood season (when fish usually feed on Amazonian fruits and seeds), whereas a higher AA, EPA and DHA content is observed in the dry season (when fish usually feed on zooplankton rich in AA, EPA and DHA) (Henderson and Tocher, 1987). These fatty acids are usually found in marine fish and their by-products, being important in human nutrition since there is evidence that a high intake of these fatty acids reduces the risk of cardiovascular disease, prevents high blood pressure, asthma, arthritis, psoriasis, inflammation and several types of cancer (Suárez-Mahecha et al., 2002). Thus, because of their n-3 rich-fatty acids and high market value, wild *C. macropomum* can be a readily available and cheaper source of these fatty acids for the South American population. Additionally, as the fatty acid composition of the fillet can be modulated by the diet, the supplementation of commercial diets with specific fatty acid mixtures can provide additional properties to the final product.

There are no studies indicating a specific requirement for these fatty acids for *C. macropomum* nor are there studies showing additional properties of n-3 PUFA to justify its supplementation in diets for this species. However, if we take into account that these fatty acids are usually found in the natural diets of tambaqui, their supplementation may improve resistance to stress and disease, in addition to improving growth.

NRC (2011) recommends the use of 5–20 g kg⁻¹ LNA (based on total lipid content) in diets for fish with low fat content. Zooplankton is the main n-3 fatty acids source for *C. macropomum* in the wild. Plant products are rich in n-6 fatty acids. As a neotropical species, for *C. macropomum* the most important fatty acids family is the n-6 series (NRC, 2011), which in commercial feeds are very rich through the inclusion of high levels of vegetable products. Based on these assumptions, commercial fish feeds used in Latin America may be adequate in fatty acids, however, further studies are necessary to test if additional n-3 PUFA supplementation can positively affect the growth and welfare of *C. macropomum*.

Carbohydrates

In the wild, *C. macropomum* feed on various food items with different chemical compositions in order to meet their nutrient requirements (Silva et al., 2003). As an opportunistic species they usually feed on fruits and seeds to meet their

Table 2
Essential fatty acid contents (mg g⁻¹ of total lipids) in muscle of farmed and wild *C. macropomum*, caught in Brazilian Amazon area in two seasons (n = 3, ±SD)

	Wild fish		Farmed fish
	Dry	Flood	
Total lipids (g kg ⁻¹)	28 ± 8	25 ± 3	48 ± 8
LA	262.0 ± 1.4	297.3 ± 1.6	208.0 ± 2.8
LNA	48.0 ± 0.9	50.7 ± 1.3	12.4 ± 1.6
AA	157.6 ± 0.7	32.2 ± 0.9	57.9 ± 0.6
EPA	9.3 ± 2.0	3.8 ± 1.1	5.0 ± 0.8
DHA	40.2 ± 4.9	14.1 ± 4.6	25.1 ± 6.7

LA, linoleic acid; LNA, linolenic acid; AA, arachidonic acid; EPA, eicosapentaenoic acid; DHA, docohexaenoic acid.

Each value = mean of three batches composed of three fish in each batch; Adapted from Almeida and Franco (2006).

nutrient requirements: around 133 species of fruits and seeds were found (whole or smashed fruit or seed) in *C. macropomum* stomachs (Silva et al., 2003), mostly in the flooding season. These fruits/seeds are rich in carbohydrates (both fibre and starch) and lipids. Regardless of the season, their natural diet gross energy content is considered to be between 2.0 and 2.4 Mj GE per 100 g (Silva et al., 2000).

The literature recommends the use of 200–400 g kg⁻¹ carbohydrates in diet formulation for herbivorous and omnivorous fish (Halver and Hardy, 2002; NRC, 2011). However, the best carbohydrate utilization seems to be age-dependent for *C. macropomum*, in line with the development of the digestive tract of most fish species (Silva et al., 2000). The adequate carbohydrate level was reported to be circa 400 g kg⁻¹ for 200 g fish (Corrêa et al., 2007; de Almeida, 2010). However, some wild fish can feed on fruits and seeds having a higher carbohydrate content (around 795 g kg⁻¹) without affecting their growth (Silva et al., 2003). Additionally, the inclusion of adequate levels of carbohydrates could improve the efficiency of other nutrients and thus reduce feed costs. The use of carbohydrate-rich diets for omnivorous species could improve protein utilization by reducing amino acid catabolism (Wilson, 1994). This nutritional strategy could improve protein retention efficiency and reduce the nitrogen excretion in *C. macropomum* farming (Wilson, 1994; Rotta, 2003; Baldan, 2008). A possible protein-sparing effect by carbohydrates was observed when *C. macropomum* were fed diets containing high carbohydrate levels derived from mango by-product meal (Bezerra et al., 2014). Those authors observed an increase in serum free amino acids and attributed this effect to the reduced gluconeogenesis of amino acids, making them available for protein synthesis in the muscle.

Early studies with *C. macropomum* have indicated that the energy derived from carbohydrates is retained less efficiently compared to lipids (van der Meer et al., 1997b). However, Hernández et al. (1995) observed a similar efficiency in utilizing carbohydrates and lipids as energy sources by *C. macropomum* fingerlings. The results of Hernández et al. (1995) seem to agree with the natural feeding habit. A high capacity to utilize different carbohydrate sources by *C. macropomum* is directly linked to morphological and biochemical adaptations of the digestive tract, leading to an increased tolerance to high levels of lipid and carbohydrates in their diets. For example, the juveniles have digestive enzymes distributed along the intestinal tract, leading to an improved capacity of digestion and absorption of dietary nutrients and increased nutrient digestibility (de Almeida et al., 2006). Although *C. macropomum* could efficiently digest both lipids and carbohydrates, recommended levels are 91 g kg⁻¹ lipid and 405 g kg⁻¹ carbohydrates (de Almeida, 2010).

Vitamins and minerals

The natural diet of *C. macropomum* is rich in vitamins and some minerals. However, in intensive production systems the only source of nutrients is the commercial feeds used by the farmers. Concurrently, the formulation of specific diets is necessary in order to provide all nutrients required to maintain high growth potential and health of tambaqui; however,

studies on their vitamin and mineral requirements are rare, leading to the use of other exotic tropical fish species, but which have different feeding habits and growth potential.

C. macropomum cannot synthesize vitamin C as efficiently as most teleost fish, thus, dietary supplementation is necessary (Fracalossi et al., 2001; Chagas and Val, 2003). Dietary supplementation of vit. C above 100 mg kg⁻¹ diet tended to have a protective effect against hypoxia stress (Chagas and Val, 2003); however, studies evaluating *C. macropomum* resistance against other stressors usually found in commercial fish production and the evaluation of some immune parameters are rare and/or absent for tambaqui. More studies are needed in this research area in order to improve the growth and welfare of *C. macropomum*, mainly in juvenile stages, where they seem to be more prone to infections when applying common production management practices.

Signs of vitamin C deficiency in fish usually include lordosis and scoliosis, poor growth, fin erosion, haemorrhages, dysplasia, hyperplasia, hypertrophy and increased mortality (Fracalossi et al., 1998; Li and Robinson, 1999; Adham et al., 2000). *C. macropomum* juveniles developed microcytic anaemia with diets deficient in vit. C, even when adequate iron levels (30 mg kg⁻¹) were supplemented (Aride et al., 2010). Thus, vit. C seems to modulate iron absorption and its metabolic use in *C. macropomum*, as occurs in higher vertebrates.

Generally, most of the studies on mineral nutrition are designed for salmonid and marine fish species that are mostly carnivorous, while in Latin America most of the studies on mineral nutrition have been performed with tilapia. However, very limited studies have been conducted with neotropical fish species, with the emphasis on *C. macropomum*. To the best of our knowledge, there are just two studies with pacu, *Piaractus mesopotamicus* (Signor et al., 2011; Diemer et al., 2014) and one study with *C. macropomum* (Santos, 2012). A recent study in our group demonstrated that *C. macropomum* is able to utilize P efficiently from plant feedstuffs; no signs of P deficiency or a growth-depressing effect was observed when fish were fed a plant-based diet without P supplementation. Additionally, the range requirement of P for *C. macropomum* weighing from 150 to 300 g was between 3.0 g kg⁻¹ (for growth) and 7.0 g kg⁻¹ (for vertebrate P retention) (Santos, 2012). The high capacity of *C. macropomum* to utilize P from plant products is not a common feature observed within aquacultured fish species and deserves further investigation. However, we have compelling evidence that this feature may be shared by other species from this group; studies with *P. mesopotamicus* and *P. brachypomus* did not observe any signs of deficiency or a reduced growth performance when fish were fed plant-based diets without P supplementation (Signor et al., 2011; Diemer et al., 2014).

Excess copper supplementation can be toxic. The copper toxicity mode of action is by inhibiting sodium (Na⁺) absorption at the gills, thus affecting Na homeostasis in fish. Because of the low cation (Ca²⁺) available in soft waters, copper toxicity is much more likely to occur and tends to be more severe than in hard waters. If we consider that waters in the Amazon River basin are typically soft due to local

geochemistry, the toxicity risk in *C. macropomum* through excess copper can occur when fish are farmed in the Amazon River basin (Matsuo et al., 2005). Therefore, macro and micromineral requirements may be slightly different when *C. macropomum* is farmed in the Amazon, but further studies are necessary that compare the requirement of fish raised in different environmental conditions.

C. macropomum usually feed on fruits and seeds in the wild, which are rich in some antioxidant minerals and vitamins; we thus hypothesize that this species may have a higher requirement for antioxidant vitamins compared to other fish species through an environmental adaptation. Although we could not find any studies reporting on the vitamin and mineral composition of the main Amazonian fruits usually ingested by *C. macropomum* in the wild (see Silva et al., 2003 for the list), it is known that seeds and fruits are rich sources of vitamins and trace elements, e.g. selenium, that are important co-factors of several metabolic redox reactions. This research venue is particularly important in commercial *C. macropomum* production due to an increase in reports of fish mortality principally caused by impaired resistance to low temperatures and stress mainly at the juvenile stage. These data would help improve fish resistance and may help expand *C. macropomum* farming in regions with lower temperatures than the Amazon. Nonetheless, because *C. macropomum* has a high growth rate, we believe that higher amounts of vitamins must be needed compared to other fish species, mainly those vitamins directly involved with protein and carbohydrate metabolism, and the use of metabolic energy, e.g. pyridoxine and thiamine, respectively. This may be equally important to broodstock nutrition once a high rate of using body nutrients to produce gametes is expected at this life stage.

Piaractus brachypomus

P. brachypomus is an omnivorous fish that usually feeds on leaves, fruits, small fish and crustaceans in their natural habitat. Knowledge on their nutritional requirement and feeding is very limited; however, the protein requirement is reported to be circa 320 g kg⁻¹, while lipid and carbohydrate levels are within 40–60 and above 360 g kg⁻¹, respectively (Vásquez-Torres et al., 2011) (Table 3).

Although no studies have determined the specific essential amino acid requirement for *P. brachypomus*, using the amino acid profile of a purified diet based on casein and gelatin in an 8 : 1 ratio improved growth and carcass nutrient retention (Vásquez-Torres and Arias-Castellanos, 2013).

The essential amino acid (EAA) profile of the *P. brachypomus* carcass is shown in Table 4. By assuming that the essential amino acid (EAA) composition is similar among fish taxa and that the amino acid composition of the fish carcass may reflect the dietary essential amino acid requirement of fish (Kaushik, 1998; Peres and Oliva-Teles, 2008), we calculated the EAA requirement for *P. brachypomus* using the reported requirement for other omnivorous freshwater fish (for more details see Kaushik, 1998; Halver and Hardy, 2002). A similar EAA requirement among *C. macropomum*, *P. mesopotamicus* and *P. brachypomus*, as well as among other fish species (Kaushik, 1998) can be noted. The estimated EAA requirement reported in Table 4 for *P. brachypomus* should be a starting point to determine the precise requirement of other amino acids. For a better estimation, the lysine requirement should be determined using a conventional dose-response study.

Use of nutrient requirement estimates based on chemical composition of the whole body and stomach content of wild fish are an alternative when nutrient requirement studies are not available for a given species (Halver and Hardy, 2002; Hamre et al., 2013). Similar to *C. macropomum*, *P. brachypomus* seems to have a very plastic feeding habit. A wide range in chemical composition of the stomach contents was observed in *P. brachypomus* raised in different environments. For example, the chemical composition of the stomach contents of *P. brachypomus* caught in artificial lakes in Bangladesh was 690.8, 132.6 and 103.9 g kg⁻¹ for protein, lipid and ash, respectively; however, this fish generally ingests fruits, seeds and leaves of Amazonian plants in their natural diets (Lucas, 2008). Although we could not find any studies determining the chemical composition of *P. brachypomus* stomach contents in the flood or dry seasons, we hypothesize that this species has a similar stomach content as the *C. macropomum* (between 41 and 213 g kg⁻¹ protein and 150–300 g kg⁻¹ lipids), since they usually inhabit the same trophic level in different regions of the Amazon River basin (Lucas, 2008; Santos, 2009).

Table 3
Reported dietary lipids, carbohydrates, energy and protein requirement observed in the literature for *P. brachypomus*

Nutrient	Weight range of the fish (g)	Response parameter	Nutrient requirement values	Statistical model	Number of test diets	Reference
Protein (g kg ⁻¹)	21–180	WG	277–300	ANOVA	3	Vásquez-Torres et al. (2012)
	179	WG	298	ANOVA	6	Gutiérrez et al. (1996)
	15–42	WG	316	Polynomial Regression	6	Vásquez-Torres et al. (2011)
Lipid (g kg ⁻¹)		WG/carcass composition	40	ANOVA	9	Vásquez-Torres and Arias-Castellanos (2012)
Carbohydrates (g kg ⁻¹)		WG/carcass composition	280	ANOVA	9	Vásquez-Torres and Arias-Castellanos (2012)
DE (Mj kg ⁻¹)	179	WG	11.3	ANOVA	6	Gutiérrez et al. (1996)

DE, digestible energy (Kcal kg⁻¹); WG, weight gain.

Table 4
Estimated essential amino acid (EAA) requirements, *P. brachypomus*, based on carcass amino acid profile using method proposed by Kaushik (1998)

Amino acids	Reported requirement (% of protein)			EAA composition of <i>P. brachypomus</i> carcass ^d (% of protein)	Estimated EAA requirement for <i>P. brachypomus</i> (% of protein)
	<i>Ictalurus punctatus</i> ^a	<i>Oreochromis niloticus</i> ^b	<i>Cyprinus carpio</i> ^c		
Arg	4.3	1.2	4.3	5.76	4.5
His	1.5	1.7	2.1	1.98	1.6
Ile	2.6	3.1	2.5	3.73	2.9
Leu	3.5	3.4	3.3	6.7	5.3
Lys	5.1	5.1	5.7	6.44	5.1
Met + Cys	2.3	3.2	2.1	2.21	1.7
Phe + Tyr	5.3	5.5	4.4	3.7	2.9
Thr	2.0	3.8	3.9	3.97	3.1
Val	3.0	2.8	0.8	4.4	3.5
Total EAA	29.6	33.9	29.1	38.89	30.6

^aWilson and Poe (1985).

^bSantiago and Lovell (1988).

^cOgino (1980).

^dVásquez-Torres and Arias-Castellanos (2013).

Table 5
Summarized dietary protein, lipids, carbohydrates, energy and phosphorus requirement for *C. macropomum* based on critical analysis of available data

Nutrient	Weight range (g)	Parameter	Requirement	Reference
Protein (g kg ⁻¹)	1–50	WG/protein retention	480	van der Meer et al. (1995)
	50–100	WG	360	Santos et al. (2010)
	124–273	WG/metabolism	300	de Almeida et al. (2011)
Lipid (g kg ⁻¹)		WG/carcass composition/metabolism	48	Almeida and Franco (2006); de Almeida et al. (2011)
		WG/carcass composition	300	Santos et al. (2010)
Carbohydrate (g kg ⁻¹)	1–50	WG	19.2	van der Meer et al. (1995)
	50–100	WG	14.3	Santos et al. (2010)
	124–273	WG	15.8	de Almeida et al. (2011)
Phosphorus (g kg ⁻¹)	200–400	WG/bone P retention	3–7	Santos (2012)

DE, digestible energy (Kcal kg⁻¹); WG, weight gain.

Although *P. brachypomus* has similar feeding as *C. macropomum* and *P. mesopotamicus* in the wild, determination of species-specific nutrient requirement is of utmost importance due to differences in the physiology among these species, which, in association with differences in environmental factors, could affect the nutrient requirement for maximum growth in each species. For instance, differences in the digestive tract morphology among these species may indicate that *P. brachypomus* has a more plastic feeding habit than *C. macropomum* (Dabrowski and Portella, 2006). On the other hand, nutritional ecology studies conducted in the Amazon using stable isotope techniques indicated that *P. brachypomus* do not change their diet between flood seasons, which is a different feature from *C. macropomum* (Santos, 2009). However, none of these studies determined the chemical composition of the *P. brachypomus* stomach content, thus leading to limited conclusions. Caution must therefore be exercised when using data interchangeably from

other species of this group, or making broad conclusions based on the phylogenetic assembly.

No reports on vitamin or mineral requirements were found for *P. brachypomus*. Thus, we recommend the use of data derived from phylogenetically closely-related species, such as *C. macropomum* and *P. mesopotamicus*, when formulating experimental or commercial diets for *P. brachypomus*. Similar to *C. macropomum*, this species may have higher vitamin and trace mineral requirements due to a natural feeding habit of ingesting fruits and seeds rich in these nutrients.

Conclusions

Despite the large number of publications that recommend a specific protein requirement for the different life stages, more studies are still necessary to assess adequately the protein requirement for *C. macropomum*, based on the use of more

appropriate experimental designs, statistical analyses and test diets (see Baker, 1986; Shearer, 2000; Hernandez-Llamas, 2009; Pesti et al., 2009; Hauschild et al., 2010). This last issue may have largely contributed to the high variation in protein requirement reports for *C. macropomum* within a specific life stage. Dietary factors, such as the presence of indigestible materials, great variation in non-protein energy sources (carbohydrates and lipids), exogenous contribution of nutrients and different nutritional value of protein sources used in the experimental diets as well as lack of proper control of environmental test conditions such as oxygen content of the water, proper temperature control, standardized flow rate through test tanks with a standard flow rate in terms of litre per minute per kg fish, proper adjustment of water pH values, and standardized light cycle and intensity may have affected the results of these studies to compare and determine precisely the protein requirement for *C. macropomum*. Additionally, the experimental conditions were extremely variable among the studies, sample sizes were mostly insufficient and the response parameters were not always precisely measured or reported. Comparing the growth of fish from most of the studies with data from our laboratory, fish growth was far slower, leading to question the quality of the experimental conditions.

Although the increase of *C. macropomum* and *P. brachypomus* production in Brazil and Colombia in recent years is obvious, very limited studies on nutrient requirements for these species are available. Several of these studies provide initial data but with insufficient background knowledge on overall requirements so that the fine-tuning of feed composition specifically for these two species is needed. Additionally, knowledge on nutritional physiology and nutrient digestibility in common feed ingredients used to formulate fish diets are initially obtained from other species; there is a need to better understand the specifics of metabolic pathways in these species to understand which types of feed-stuffs are obtainable for efficient digestion. Due to the increased use of *P. brachypomus* in Latin America aquaculture systems and paucity of studies on nutrient requirement compared to *C. macropomum*, a more direct focus towards the basic nutrient requirements (protein, lipid, carbohydrate and phosphorus) to formulate efficient diets for this species is urgently needed. Summarized data in Tables 3 and 5 to help improve the growth and reduce production costs of these species are based on the principles of intensive and environmentally-friendly aquaculture production. As we mentioned before, this review aimed to guide the scientific community toward the need for more studies on nutrient requirements of important neotropical fish species, namely *C. macropomum* and *P. brachypomus*. The recommendations in this review must be used carefully, and researchers must also keep in mind that most of the recommendations should be used as starting points for a critical debate on the subject so that future, improved study designs can lead to the development of new and scientifically sound species-specific feeds in order to build a solid database on nutrient requirements and nutrient digestibility values to help nutrition scientists, the feed industry and the aquaculture

business to develop appropriate species-specific diets for these species.

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