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Research Article

Feeding habits and nutritional requirements of native cichlids with aquaculture potential from Mexico and Central America. A review

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ABSTRACT. The Cichlidae family is among the most diverse freshwater fish groups globally, with high ecological, economic, and cultural value across Mexico and Central America. However, overfishing and habitat degradation threaten wild populations, prompting interest in aquaculture as a conservation and production strategy. This review examines the feeding habits and nutritional requirements of eight native cichlid species with aquaculture potential, with a focus on trophic-level adaptations. High-trophic-level species, such as bay snook (*Petenia splendida*), require 45-50% dietary protein with minimal plant protein inclusion (<20%) and 15-20% lipid content from fish oil sources. In contrast, middle-trophic-level species, like the Mayan cichlid (*Mayaheros urophthalmus*), accept 35-40% protein diets with higher inclusion of plant ingredients, such as soybean meal, and 10-15% lipids. Carbohydrate utilization correlates with trophic level, with middle-trophic species tolerating 30-35%, while high-trophic-level species exhibit reduced tolerance. Vitamin and mineral requirements remain poorly defined, underscoring the need for future research. The review highlights significant knowledge gaps, particularly in areas such as micronutrient needs, protein source digestibility, and trophic-stage-specific feed formulation. Aligning feed strategies with trophic adaptations is key to enhancing aquaculture growth performance, sustainability, and biodiversity conservation. This synthesis provides a foundation for targeted research and practical feed development in native cichlid farming.

Keywords: Cichlidae; native species; protein and lipid requirements; aquaculture facilities; Central America

INTRODUCTION

Cichlids are one of the most diverse families of freshwater fish globally, with over 1,300 reported species (Kullander 2003). These fish contribute to the ecological balance of their habitats due to their varied feeding habits and reproductive behaviors, acting as population regulators for other organisms. Some cichlids are known to feed on invertebrates and plants, helping to control these populations and prevent excessive algae growth, which could negatively impact water quality (Hulsey et al. 2010). Cichlids are also valuable for commercial fishing and aquaculture. In aquaculture, species such as the Mayan cichlid (*Mayaheros urophthalmus*) and bay snook (*Petenia splendida*) are cultivated due to their adaptability to various environmental conditions and commercial demand, making them a source of food and employment for communities (Russell et al. 2012, Arredondo-Figueroa et al. 2013). The decline in wild populations of these species could trigger an imbalance in aquatic communities, affecting other species and the overall

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health of the ecosystem, which in turn could negatively impact the fishing and aquaculture industries by reducing the availability of an important source of food and employment for local populations (Hulsey et al. 2010, Russell et al. 2012, Gracida-Juárez et al. 2022). Aquaculture is a viable alternative to meet commercial demand and replenish wild populations, presenting an opportunity for research on native cichlids, which remains limited to date. Their varied feeding strategies directly influence aquaculture potential - high-trophic-level species like bay snook (*P. splendida*) require protein-rich diets (45-50%) with predominant animal sources (fishmeal, FM) to prevent growth retardation and spinal deformities, while middle-trophic-level cichlids (*M. urophthalmus*) thrive on 35-40% protein diets incorporating plant-based ingredients when properly supplemented (Russell et al. 2012, Arredondo-Figueroa et al. 2013). Inadequate nutrition manifests as: a) 20-35% reduced growth rates from protein deficiencies; b) increased disease susceptibility due to compromised immunity; and c) metabolic disorders like fatty liver syndrome when carbohydrate levels exceed species-specific thresholds (25-35% depending on trophic position). Proper feed formulation becomes essential for improving production efficiency (feed conversion ratio, FCR) in optimized diets and maintaining genetic diversity in cultured stocks used for restocking programs (Gracida-Juárez et al. 2022). Meeting these nutritional requirements supports sustainable aquaculture, which can alleviate fishing pressure on wild populations (currently declining at 5-8% annually in key Mexican watersheds), while providing consistent yields for local markets (Arredondo-Figueroa et al. 2013). Current research gaps in nutritional requirements for native species highlight the need for targeted studies to realize their aquaculture potential fully.

Nutritional requirements are species-specific and linked to digestive physiology, enzymatic profiles, and energy metabolism. Inadequate diets-whether due to unbalanced macronutrient ratios, low digestibility, or inappropriate ingredient sources can impair nutrient assimilation, compromise immune function, and lead to metabolic disorders such as fatty liver or skeletal deformities (Hemre et al. 2002, Jobling 2012). In cichlids, whose digestive capacities vary with trophic level, formulating stage- and species-specific diets is essential to optimize protein utilization, minimize nitrogen excretion, and enhance overall aquaculture performance (Kaushik & Seiliez 2010, Kamalam & Panserat 2016). When designing feeding protocols to support sustainable aquaculture practices, these factors must be considered.

Background

The Neotropical region of the Americas harbors exceptional cichlid diversity, with over 600 species across at least 68 genera, ranging from Uruguay to the southern USA (Kullander 2003, Sparks 2004, Barreto 2009, Froese & Pauly 2024). In Mexico and Central America, the Cichlidae family ranks as the second most diverse among freshwater fishes, comprising 15 genera and approximately 80 species, including 12 regional endemics with restricted distributions in isolated basins (Contreras-Balderas et al. 2008). Native cichlids inhabit various freshwater environments and display broad ecological plasticity, including remarkable tolerance to environmental stressors and a wide range of feeding strategies.

Feeding behaviors in cichlids are highly specialized and morphologically supported. For example, *M. urophthalmus* and *Herichthys minckleyi*, classified as "picker" feeders, use rapid mouth movements to detach and ingest prey from substrates. In contrast, "biter" feeders, such as *Thorichthys meeki*, maintain contact with the substrate while scraping food particles. Pelagic feeders, such as *Parachromis dovii*, consume zooplankton and suspended detritus in the water column. High-trophic-level piscivores like *P. splendida* exhibit a protrusible mouth and rapid buccal expansion, facilitating suction feeding and efficient capture of small fish and crustaceans (Winemiller & Kelso-Winemiller 2003, Hulsey & De León 2005, Marrero & Olarte 2006, López-Fernández et al. 2010, Méndez et al. 2011).

Several native cichlids, including *M. urophthalmus*, *P. splendida*, and *P. dovii*, have shown biological and physiological traits favorable for aquaculture production (Arredondo-Figueroa et al. 2013, Valverde-Chavarría et al. 2016, Calzada-Ruiz et al. 2019, Ulloa-Rojas et al. 2022). These include competitive FCRs (1.2-1.5 in *M. urophthalmus vs.* 1.6-2.0 in *Oreochromis niloticus*), specific growth rates exceeding 2.5% per day under optimal conditions, comparable to *Salmo salar*, and remarkable tolerance to low dissolved oxygen (<2 mg L^{-1}), surpassing the tolerance of many established commercial species (El-Sayed 2006, Martínez-Palacios et al. 2008, Asche & Bjorndal 2011). Although Nile tilapia (*O. niloticus*) remains the most widely farmed cichlid due to its extensive domestication and international market development, native cichlids offer unique advantages for regional aquaculture. These include ecological adaptation to local conditions, potentially higher market value, and a reduced environmental footprint. Moreover, their cultivation supports biodiversity conservation and provides alternatives to overexploited wild fisheries.

Two key factors drive the growing interest in farming native cichlids: 1) the critical conservation status of several species due to habitat loss, invasive species, predation, and overfishing (Rojas & Mendoza 2000); and 2) the increasing demand for sustainable food production, which presents both a challenge and an opportunity: developing efficient production protocols for native cichlids that include optimized nutrition, reproductive control, and low environmental impact. A central aspect of this development is the formulation of cost-effective diets with favorable FCRs of ≤1.5, utilizing locally sourced ingredients that ensure year-round availability, economic feasibility, and sustainability.

Nutrition plays a fundamental role in aquaculture biotechnology. Achieving an optimal nutritional balance enables the formulation of feeds that meet the physiological requirements of the species across all life stages, thereby maximizing growth and health (Martínez et al. 2011, Barletta et al. 2015).

Important advances have been made in the controlled farming of native cichlids such as *Vieja bifasciata*, *M. urophthalmus*, and *Parachromis managuensis* (Toledo-Solís et al. 2020, Agostinho et al. 2021). These include the development of captive breeding protocols (e.g. >85% larval survival in biofloc systems), suitable stocking densities (15-20 fish m^{-3}), and tolerance ranges to temperature fluctuations (24-32°C). However, detailed knowledge of their nutritional requirements, particularly in terms of protein, lipids, and carbohydrates, remains limited. Future progress depends on a better understanding of their ontogenetic feeding preferences and life-stage-specific nutritional needs.

This review focuses on native cichlid species from Mexico and Central America that present the greatest potential for aquaculture, based on three criteria: 1) availability of scientific literature on their reproductive and nutritional requirements; 2) documented commercial demand and market price exceeding that of introduced species; 3) need for conservation due to anthropogenic pressures. While other native cichlids may hold promise, the selected species, particularly *P. splendida* and *M. urophthalmus*, are already cultured in southeastern Mexico, offering promising alternatives to conventional aquaculture.

Their cultivation contributes to sustainable food systems while reducing pressure on wild populations by adopting sustainable fishing practices. It is important to clarify that this selection does not exclude other potential species but rather reflects the current state of technological development and biological knowledge that supports their viability under farming conditions.

Ecology and trophic classification of native cichlids

The feeding habits of cichlids are largely influenced by their geographic origin (Kullander 2003). In their natural habitat, many cichlid species are middle-trophic-level (Liem & Osse 1975); however, most show a preference for specific types of food, ranging from small crustaceans and fish to algae, organic matter, or larvae from other cichlid species (Kullander 2003, Tan & Lim 2008). One of the native cichlid species that has attracted the attention of aquaculture producers is the bay snook (*P. splendida*), known for its faster growth rate compared to other cichlid species. Its flesh is considered high-quality, with a texture and flavor that are highly appreciated in the market for human consumption. Additionally, it reproduces relatively easily in captivity (Uscanga-Martínez et al. 2011). *P. splendida* is considered a piscivorous fish, as it feeds on small fish in the wild, including individuals of its species (Treviño et al. 2011). According to Valtierra-Vega & Schmitter-Soto (2000), observations indicate that juveniles prefer zooplankton and phytoplankton in their early life stages. In adulthood, Álvarez-González et al. (2008) observed that their diet includes small insects, crustaceans, and non-digested plant material, consistent with findings by Infante & LaBar (1977), who reported the presence of crustaceans, fish eggs, and microalgae in the stomach contents of juvenile *P. splendida*, noting a preference for small fish and crustaceans, suggesting a shift towards piscivorous feeding as the fish grows, facilitated by an increase in mouth size, which aids in predation and allows for a broader range of prey. Nonetheless, despite being naturally piscivorous, there is evidence that the bay snook can adapt to formulated diets in captivity (Uscanga-Martínez 2020). Therefore, developing formulated diets that meet the species' nutritional requirements is essential to maximize its aquaculture potential.

The Mayan cichlid (*M. urophthalmus*) is another cichlid highly demanded by regional consumers and has great potential for aquaculture. This species is found in rivers along the Atlantic coast from Mexico to Nicaragua (Kullander 2003) and has gained interest due to its adaptability to captivity, tolerance of a broad range of environmental conditions, including variations in temperature, salinity, and dissolved oxygen levels-as well as its fast growth rate and low feed conversion ratio (Schofield et al. 2010). Additionally, conservation efforts for the Mayan cichlid and the need to diversify regional aquaculture production have further driven its study (Pérez-Sánchez & Páramo-Delgadillo 2008). Regarding the Mayan cichlid's feeding preferences, Martínez-Palacios & Ross (1988) reported wild specimens with stomach contents comprising 62-68% crustaceans, 21-25% fish, 7-9% organic detritus, and <3% algae by volume, which aligns with observations by López-Ramírez et al. (2011), who classified the Mayan cichlid as high-trophic-level preferences (55-60% animal matter) but with greater seasonal variability (15-30% plant material during rainy seasons), especially during its juvenile stage. In contrast, Chávez-López et al. (2005) found that the stomach contents of Mayan cichlid larvae collected from a lagoon in Veracruz, Mexico, contained between 71.41 and 98.30% plant matter, suggesting that this phase may be primarily herbivorous, with only minimal amounts of small mollusks and crustaceans present. Kullander (2003) and Marrero & Olarte (2006) suggest that the regional factors and food availability can strongly influence the feeding habits of some cichlids, positioning the species as a facultative high-trophic-level consumer capable of middle-trophic-level foraging when advantageous (Adamek-Urbańska et al. 2021).

Another Central American cichlid genus with aquaculture potential is *Vieja*, which includes notable species such as the redhead cichlid (*V. melanura*) and the two-banded cichlid (*V. bifasciata*). These species are distributed in the Atlantic, from the Papaloapan River to the Grijalva and Usumacinta River basins in Mexico and Guatemala (Kullander 2003). Although studies on these species are limited, they have potential for aquaculture due to their demand for ornamental purposes and human consumption (Adamek-Urbańska et al. 2021). An advantage of the two-banded cichlid for aquaculture production is that, while its exact dietary preferences are not well known, Frías-Quintana et al. (2021) suggest, based on evaluation of enzymatic activity, that it has a middle-trophic-level feeding habit. This trait benefits aquaculture, as Tacon & Metian (2008) state that lower trophic-level species offer cost advantages and higher profitability in commercial production because it is possible to reduce aquaculture costs by 18-25% compared to high-trophic-level species. Similarly, the redhead cichlid (*V. melanura*) can reduce aquaculture costs by 18-25% compared to high-trophic-level species. Still, species-specific nutritional research for the two-banded cichlid (*V. bifasciata*) is urgently needed.

The guapote cichlid (*P. dovii*) is another species native to Guatemala and Honduras (Kullander 2003) that has recently gained attention for its ability to accept artificial feed in captivity, its disease resistance, and its high value in sport fishing and consumption markets (Tabash et al. 2000, Ulloa-Rojas et al. 2022). Ulloa-Rojas et al. (2022) described the guapote cichlid as a high-trophic-level species, consistent with findings by Tabash et al. (2000), who classified it as piscivorous, with a preference for tetras, poecilids, and even other cichlids. Nevertheless, its diet may also include small crustaceans and insects, aligning with observations by Valverde-Chavarría et al. (2013) for juvenile and adult specimens.

The firemouth cichlid (*T. meeki*) is of regional importance and is highly sought after in Central American fisheries. It is found in the Usumacinta River basin and various water bodies in Mexico, Guatemala, and Belize (Kullander 2003). The primary interest in this species stems from its value in the ornamental fish trade due to its attractive appearance (Gültekin & Yilmaz 2023). Regarding its feeding preferences, Valtierra-Vega & Schmitter-Soto (2000) describe it as zooplanktivorous, primarily feeding on cladocerans and copepods, with small fish and ostracods also found in its stomach contents from May to July. Cochran-Biederman & Winemiller (2010) suggest that, based on its morphology and feeding habits, the firemouth cichlid is middle-trophic-level, with a clear preference for benthic invertebrates.

The three-spot cichlid (*Amphilophus trimaculatus*) is a species native to Mexico, primarily found along the coasts of Chiapas and Oaxaca (Toledo-Solís et al. 2020), as well as in some water bodies in Belize, Guatemala, and Honduras (Kullander 2003). This cichlid can adapt to various environmental conditions and grows rapidly, making it a promising candidate for aquaculture. It is considered a middle-trophic-level consumer, feeding on benthic invertebrates (55-68%), plant matter (22-30%), and occasionally small fish (<10%) (Miller et al. 2005, Toledo-Solís et al. 2020). Yáñez-Arancibia (1978) notes that this species may exhibit carnivorous behavior during certain months, particularly as a response to population density-related movements aimed at avoiding competition or predation in specific seasons. Toledo-Solís et al. (2015) suggest that, based on the species' enzymatic activity, it can be classified as a high-trophic-level consumer with middle-trophic-level capacity when prey availability decreases.

The eight-band cichlid (*Rocio octofasciatus*) is distributed from Mexico to Guatemala and Nicaragua (Piálek et al. 2012, Mendoza-Palmero et al. 2017). Although it is not commonly consumed as food, it holds significant importance as an ornamental species, prompting some efforts to cultivate it under controlled conditions. It is currently classified as a middle-trophic-level consumer with detritivore supplementation, predominantly feeding on small insects, eggs, and larvae (Pashkov & Zvorykin 2009), as well as small mollusks and organic matter remnants (Hinojosa-Garro et al. 2013).

To provide a clearer overview of the trophic classifications, dietary habits, and supporting evidence for each native cichlid species reviewed, we summarize the main feeding characteristics, trophic level assignments, and available data types (Table 1).

Nutritional requirements of cichlids

Once a species with cultivation potential is identified, it is necessary to establish the production protocols for its cultivation, beginning with its dietary preferences and nutritional requirements. Despite the potential for cultivating some cichlid species, knowledge of their nutritional needs is limited. Addressing these requirements is the first step in the research required to formulate complete and environmentally friendly diets. To develop functional feeding strategies, it is essential to comprehend the relationship between the organism and the trophic network in which it is naturally involved (Pereira et al. 2004).

Possibly the most well-known and widely cultivated species in the Cichlidae family is the Nile tilapia (*O. niloticus*). Although considered an introduced species in the water bodies of Mexico, Central America, and many other parts of the world, it quickly gained substantial economic and social value in the countries where it was introduced. Today, production protocols in various culture systems are well-established, yielding excellent production intensity and output (Liti et al. 2006, Pérez-Fuentes et al. 2016, Amin et al. 2020). Knowledge gained from this species serves as a foundation for developing and implementing cultivation techniques for other species in the family, including native cichlids from Mexico and Central America, including aspects such as specific diet development, nutritional requirements, physiological and metabolic processes involved in nutrient utilization, as well as considerations of palatability, particle size, buoyancy, and nutrient and energy concentration (Lovell 1989, Gutiérrez-Espinosa et al. 2019).

The Nile tilapia is a middle-trophic-level species with a varied diet that includes phytoplankton, zooplankton, algae, detritus, and occasionally small invertebrates. Dietary diversity suggests that nutritional requirements vary across different stages of development. Still, it generally requires a protein-rich diet (averaging 30-40% for optimal growth) and lipids (5-10%) (Ng & Romano 2013, Ogello et al. 2014, Meurer et al. 2024). Nile tilapia efficiently utilizes carbohydrates, allowing for more economical plant-based diets (Boonanuntanasarn et al. 2018). This dietary flexibility is key to its success within the aquaculture industry.

In the context of sustainable aquaculture, replacing FM and fish oil (FO) with alternative ingredients is a global priority (Tacon & Metian 2008). Studies with native cichlids such as *M. urophthalmus* and *P. splendida* have demonstrated partial tolerance to plant-based proteins like soybean meal (SBM), meat and bone meal, and sorghum, as well as to vegetable lipid sources such as soybean lecithin (Calzada-Ruiz et al. 2019, Rodríguez-Estrada et al. 2020, Ulloa Rojas et al. 2022). However, the long-term effects on amino acid balance, digestibility, and metabolic performance remain underexplored. Developing diets with locally available and cost-effective ingredients, such as insect meal, fermented plant proteins, or algae, may reduce environmental impacts and improve economic viability; however, this requires further research tailored to the specific trophic physiology of each species (Tacon & Metian 2008, Li et al. 2018).

Proteins

Protein is one of the most important macronutrients for life, serving as a fundamental cellular component and, after water, the most abundant chemical group in cells; as a nutrient, protein functions as both an energy source and a structural element necessary for animal growth (Vásquez-Torres et al. 2011). Proteins also play key metabolic roles, acting as components of enzymes, hormones, and antibodies, and they have regulatory functions, such as aiding in nutrient assimilation, oxygen transport in blood, toxic material elimination, and regulating the absorption of fat-soluble vitamins and minerals, among other roles (Kaushik & Seiliez 2010). It is essential to recognize that protein requirements in aquatic organisms exhibit greater variability (30-55% of the diet) compared to terrestrial livestock (12-22% for poultry and swine), reflecting fundamental metabolic differences. While fish efficiently utilize dietary protein for growth (60-70% protein retention *vs.* 30-45% in mammals), terrestrial species preferentially use carbohydrates as energy sources (Wilson 2003).

In the case of tilapia, their protein requirements generally range from 30 to 40% in their diet (Köprücü

Table 1. Comparative feeding ecology and trophic classification of native cichlid species with aquaculture potential. The table summarizes the estimated percentages of animal and plant matter in natural diets, trophic level classifications, and the types of evidence supporting each categorization.

Species	Trophic level	Animal matter (%)	Plant matter (%)	Evidence source	Notes	Reference
Petenia splendida (bay snook)	High	80-95	<10	Stomach contents	Piscivorous; accepts formulated diets	Treviño et al. (2011)
Mayaheros urophthalmus (Mayan cichlid)	Middle	55-60	15-30	Stomach contents	Flexible omnivore with seasonal variation	López-Ramírez et al. (2011)
Vieja bifasciata (two-banded cichlid)	Middle	-	-	Enzymatic activity	Inferred herbivory; limited data	Frías-Quintana et al. (2021)
Parachromis dovii (Guapote cichlid)	High	80-90	<10	Stomach contents + behavior	Carnivorousaccepts formulated diets	Tabash et al. (2000)
Thorichthys meeki (firemouth cichlid)	Middle	~70	~30	Stomach contents	Zooplanktivorous with benthic feeding	Valtierra-Vega & Schmitter-Soto (2000)
Amphilophus trimaculatus (three-spot cichlid)	Middle-High	55-68	22-30	Stomach contents + enzyme data	Carnivorous with omnivorous capacity	Toledo-Solís et al. (2020)
Rocio octofasciatus (eight-band cichlid)	Middle	~60	40	Stomach contents	Detritivore tendencies; ornamental use	Hinojosa-Garro et al. (2013)

& Özdemir 2005, El-Sayed 2006). Unlike tilapia, few reports have established the protein requirements for native cichlids in Mexico and Central America. Knowledge of protein requirements is crucial as a foundation for initiating their cultivation.

Bay snook (*Petenia splendida*)

Álvarez-González et al. (2008) and Uscanga-Martínez et al. (2012) indicate that the protein requirement for juveniles and adults of the bay snook is between 44 and 45% when casein, sardine meal, and whole grain sorghum meal were used as the protein source. They observed that the inclusion of integrated sorghum meal up to 23% increased weight gain, specific growth rate, and feed conversion factor; similar values, ranging from 40 to 50%, were reported by Jiménez-Martínez et al. (2009) and Arredondo-Figueroa et al. (2015), for optimal growth in bay snook fry when SBM was included up to 33% in the diet obtaining the best weight gain results. Due to the bay snook's high-trophic-level physiology, its protein requirement is higher than that of *O. niloticus*, which is an efficient plant protein consumer, in contrast to *P. splendida* exhibits a limited capacity for plant protein incorporation beyond 25-30% due to constrained enzymatic adaptation. Current research underscores the importance of comparative studies examining isonitrogenous diets with varying protein source ratios alongside investigations into alternative animal protein substrates, such as insect meals and single-cell proteins, which may offer balanced amino acid profiles while reducing reliance on conventional fishmeal.

Mayan cichlid (*Mayaheros urophthalmus*)

The Mayan cichlid is a middle-trophic-level species whose reported protein requirements range from 38 to 45%, depending on the dietary source and feeding strategy used (Nava et al. 1989, Martínez-Palacios et al. 1996, Ulloa Rojas et al. 2022). Studies using anchovy meal as the sole protein source estimated an optimal level of 38-40%. At the same time, other research shows that including SBM, meat, bone meal, or sorghum does not negatively affect growth (Ulloa-Rojas et al. 2022). This flexibility reflects its omnivorous feeding behavior and digestive capacity. However, variability in the feeding regime (fixed rate *vs*. satiation feeding) influences apparent protein needs, reinforcing the importance of considering both the source and feeding strategy in determining requirements (Tacon & Cowey 2012).

Guapote cichlid (*Parachromis dovii*)

Although little is known about the protein requirement of the guapote cichlid, it is essential to consider that Valverde-Chavarría et al. (2013) mention that the ingredients used in diet formulations can affect digestibility. In their study, fishmeal and meat-and-bone meal were used as protein sources, which promoted higher *in vitro* digestibility, characterized by the highest protein hydrolysis and *in vitro* alkaline digestibility. In contrast, all the vegetable meals tested reduced the alkaline proteolytic activity of guapote cichlid larvae, attributable to differences in protein solubility and amino acid accessibility. These findings underscore the need to evaluate protein requirements in conjunction with source-specific digestibility parameters, particularly for essential amino acids such as methionine and lysine. Another important aspect of specific diet formulation is the enzymatic profile of the species. Ulloa-Rojas et al. (2022) evaluated the activity of alkaline proteases in cichlid guapote larvae fed four diets with FM, meat and bone meal, and poultry by-product meal as protein sources and different protein levels: 38.3 to 43.7%. They concluded that the absence of differences in growth and alkaline protease activity demonstrated the digestive efficiency of the protein sources and confirmed that it is a high-trophic-level species with protein requirements similar to those of other cichlids. Still, they require diets based on animal protein sources.

Studying enzymatic activity in cichlid fish is useful for understanding how they process dietary components. However, it is essential to consider that variations in protein levels in feed can induce adaptations in enzymatic activity, particularly in proteolytic enzymes (Hidalgo et al. 1999, Nguyen et al. 2009, Lazzarotto et al. 2018). The enzymatic activity profiles provide foundational insights into the digestive physiology of cichlids. Future studies must evaluate the species-specific enzyme repertoires, particularly the structural adaptations that determine substrate affinity (Dimes & Haard 1994) and the actual digestion efficiencies measured through *in vivo* apparent digestibility coefficients (ADCs) (Bolasina et al. 2006). In this regard, Toledo-Solís et al. (2020) report that larvae of the three-spot cichlid (*A. trimaculatus*) fed diets with four protein percentages (35, 40, 45, and 50%) showed the best growth and feed efficiency with 45% protein diet containing casein, FM, and sorghum meal as protein sources. They also noted an increase in alkaline protease activity with higher protein levels, suggesting that the digestive system can adapt enzymatic activity to enhance digestion and minimize waste.

While *M. urophthalmus* demonstrates efficient use of plant-based ingredients such as SBM and sorghum, *P. splendida* and *P. dovii* show reduced growth performance and digestive efficiency when vegetable proteins exceed 25-30% of the total dietary protein due to their limited enzymatic adaptation to such sources (Valverde-Chavarría et al. 2013, Rodríguez-Estrada et al. 2020).

Lipids

Lipids are commonly included in formulated diets for aquatic organisms due to their numerous metabolic roles. Lipids provide metabolic energy essential for growth, reproduction, and energy storage, which is especially important for species that undertake migratory movements. They are crucial for maintaining the structure, permeability, and stability of cell membranes, aiding in nutrient transport, and serving as precursors for hormones and other bioactive molecules (Tocher 2003, Gutiérrez-Espinosa et al. 2019).

For cichlids, except for Nile tilapia, the lipid requirement for most native species from Mexico and Central America typically ranges from 5 to 20%, depending on their life stage. These species can efficiently utilize a variety of lipid sources, including FO and vegetable oils such as soybean, canola, and corn oils. For example, high-trophic-level species show constrained biosynthesis of long-chain polyunsaturated fatty acid (LC-PUFA) from plant sources and FO for essential fatty acid requirements. In contrast, middle-trophic-level species display efficient metabolism of plant-based lipids and soybean oils. These metabolic adaptations directly inform feed formulation strategies for regional cichlid aquaculture operations (Villarreal et al. 2011, Li et al. 2018, Calzada-Ruiz et al. 2019, Rodríguez-Estrada et al. 2020). Understanding lipid requirements is crucial for formulating balanced diets, as both excess and deficiency in lipids can lead to various health issues (Sargent et al. 2003). Campeche et al. (2018) noted that an excess of lipids in aquaculture diets can lead to excessive visceral fat storage, alter lipase activity, raise triglyceride and cholesterol levels, and even slow growth rates.

Bay snook (*Petenia splendida*)

The bay snook is a high-trophic-level carnivorous species whose lipid requirements have been evaluated in various studies. Rodríguez-Estrada et al. (2020) reported that juveniles benefit from diets containing 5 to 20% lipids when FO and soybean lecithin are primary lipid sources. The optimal lipid level for this species was estimated at 16.2%, supporting enhanced growth and survival. However, the authors also observed that fish fed 5% lipids exhibited a superior FCR, suggesting more efficient nutrient utilization at a lower energy density.

While 5% lipid diets promoted better FCRs, higher inclusion levels (15-20%) were associated with optimal growth and physiological conditions, indicating a trade-off between energy efficiency and the capacity to meet essential fatty acid and metabolic demands. This finding is consistent with the species' reliance on high-energy prey in the wild, which is rich in LC-PUFAs, such as EPA and DHA, essential for maintaining cellular membrane integrity, hormone synthesis, and modulating inflammation (Tocher 2003). Furthermore, dietary lipid level influences the activity of digestive enzymes such as lipase and trypsin, which regulate nutrient assimilation and support metabolic flexibility in carnivorous fish (Guo et al. 2019). Consequently, diets for *P. splendida* should prioritize the inclusion of marine-derived lipids during early growth stages to ensure adequate development while adjusting levels in later stages to balance performance and cost-effectiveness.

Mayan cichlid (*Mayaheros urophthalmus*)

The Mayan cichlid is a middle-trophic-level species with significant nutritional flexibility, particularly in lipid requirements and source utilization. Calzada-Ruiz et al. (2019) evaluated the lipid requirements of larvae using diets with 10, 15, 20, and 25% total lipid content derived from FO and soybean lecithin. They determined that 15% of total lipids supported optimal growth and survival, and notably, 100% of the FO could be replaced by soybean lecithin without negatively affecting performance. This finding demonstrates a physiological adaptation in *M. urophthalmus* to plant-based lipid sources, likely reflecting its omnivorous feeding behavior and digestive plasticity.

The ability to metabolize vegetable lipids such as soybean or canola oil has also been linked to enhanced endogenous enzymatic capacity, particularly involving desaturases and elongases required for the biosynthesis of LC-PUFAs from precursors such as linoleic (LA) and alpha-linolenic acid (ALA) (Turchini et al. 2009). This metabolic flexibility allows *M. urophthalmus* to support growth, immune function, and membrane homeostasis without relying exclusively on marine-derived lipid sources.

Moreover, lipid levels and types can influence the activity of digestive enzymes. For example, fish-fed diets with soybean lecithin have shown increased bile secretion and lipase activity, which enhance lipid digestibility and nutrient assimilation (Ng & Romano 2003). These physiological responses support the formulation of more sustainable feeds for *M. urophthalmus*, with reduced reliance on FO and improved environmental compatibility.

Three-spot cichlid (*Amphilophus trimaculatus*)

The three-spot cichlid is a native species with promising aquaculture potential due to its fast growth and tolerance to captivity. Toledo-Solís et al. (2020) assessed the dietary lipid requirements of larvae using diets with varying lipid levels (16 and 22%) composed of FO and soybean lecithin. They found that the best growth performance and feed efficiency occurred with a diet containing 22% lipids, highlighting the species' apparent high tolerance to energy-dense feeds.

Additionally, fish fed this high-lipid diet exhibited increased activities of lipase and trypsin, suggesting that *A. trimaculatus* can physiologically adapt its digestive system to process better elevated dietary lipid levels, consistent with its partially carnivorous nature, which may require higher lipid intake to meet energy demands while preserving dietary protein for growth and tissue development. The positive response to high-lipid diets likely reflects the species' natural dietary habits in the wild, where prey such as benthic invertebrates and small fish contribute significantly to their lipid content (Miller et al. 2005). These findings underscore the importance of formulating energy-balanced diets for *A. trimaculatus*, particularly during the larval and juvenile stages, to prevent growth depression or metabolic imbalance due to under-supplementation or excess visceral fat storage.

In addition to providing energy for metabolic and structural functions, lipids act as a protein-sparing mechanism. Balancing protein, lipid, and carbohydrate levels in the diet improves digestibility and optimizes nutrient utilization (De Silva et al. 1991, Pratoomyot et al. 2010, Li et al. 2012). Therefore, studies are essential to establish integrated requirements for species at different life stages. For example, Olvera-Novoa et al. (1996) observed optimal growth in juvenile *Cichlasoma synspilum = Vieja synspilum* when fed diets containing 40-50% protein and 8.5-13.2% lipids. When cod liver oil and soybean oil were used, a marked decrease in growth and FCR was observed at lower protein and lipid levels and a maximum of 30% nitrogen-free extracts (NFE). For blood parrot's cichlid (a hybrid of *Amphilophus citrinellus* and *Paraneetroplus synspilus*), Li et al. (2018) found that 11.7% lipid was the most efficient dietary level using FO and soybean lecithin, based on a polynomial regression analysis of diets with lipid contents between 7.4 and 16.8%. An interesting aspect of the study was the coloration of individuals: fish fed with 12.7 and 11.2% lipids exhibited more intense reddish coloration and brightness, which is advantageous in the ornamental market, suggesting that lipids may play a role in pigmentation and commercial value for this species that is classified as a medium-trophic-level species, it is possible to implement plant lipid sources in greater quantities compared to other high-trophic-level cichlids.

Several studies have shown that optimal protein and lipid levels are crucial for efficient growth in aquatic species (Rahimnejad et al. 2021). However, diet quality depends on the quantity of these nutrients, the specific sources, their fatty acid and amino acid profiles, and energy content. Nutritional imbalances impair nutrient utilization through three primary mechanisms: first, excess dietary energy from lipids or carbohydrates triggers protein catabolism rather than anabolism, reducing protein efficiency ratios; second, suboptimal calcium: phosphorus ratios (<1:1) form insoluble complexes that decrease mineral bioavailability; and third, disproportionate amino acid profiles limit hepatic protein synthesis, forcing deamination and increasing ammonia excretion by 2-3-fold. These metabolic disruptions manifest as reduced specific growth rates and elevated FCRs, directly impacting production economics (Wang et al. 2006, Jobling 2012, Li et al. 2012).

In wild ecosystems, the natural prey of high-trophic-level cichlids (e.g. small fish and crustaceans) tends to be rich in LC-PUFAs, particularly from the n-3 series (e.g. EPA and DHA), which are essential for membrane fluidity, hormone production, and anti-inflammatory responses (Tocher 2003), which underlines the importance of maintaining fish oil or marine-derived lipid inclusion in diets for species like *P. splendida* and *P. dovii*. In contrast, middle-trophic-level species like *M. urophthalmus* show better adaptation to vegetable lipid sources, likely due to higher endogenous enzyme capacity for fatty acid elongation and desaturation (Rodríguez-Estrada et al. 2020). Future studies should assess the specific lipid class requirements (e.g. phospholipids *vs.* neutral lipids) and fatty acid profiles necessary during the larval and juvenile stages for optimal development.

Carbohydrates

Although carbohydrates are not considered essential nutrients for fish, they are commonly used in aquafeeds due to their low cost and functional properties, such as pellet binding and energy provision. Their utilization depends on species-specific digestive capabilities and the chemical nature of the carbohydrate source.

Mayan cichlid (*Mayaheros urophthalmus*)

The Mayan cichlid, a middle-trophic-level species, demonstrates moderate to high tolerance to dietary carbohydrates. Studies have shown that juveniles can effectively utilize diets containing up to 35% NFE, especially when using carbohydrate sources such as gelatinized corn or wheat flour. The species exhibits a relatively high amylase-to-protease ratio, indicating enzymatic adaptation for carbohydrate digestion (Toledo-Solís et al. 2020). Carbohydrates also support energy balance in low-protein diets, provided they are digestible and well-processed.

Three-spot cichlid (*Amphilophus trimaculatus*)

Like *M. urophthalmus*, *A. trimaculatus* has shown growth responses to carbohydrate inclusion levels of up to 35%. Toledo-Solís et al. (2020) reported no adverse effects on growth or feed efficiency at these levels when using processed plant carbohydrates. The species' digestive enzyme profile supports moderate carbohydrate levels, making it suitable for partially plant-based diets when properly balanced with protein and lipids.

Bay snook (*Petenia splendida*)

P. splendida, a high-trophic-level carnivore, cannot digest and metabolize complex carbohydrates. Rodríguez-Estrada et al. (2020) reported suboptimal growth and potential hepatic lipid accumulation when dietary carbohydrate levels exceeded 20%. The species prefers energy sources from protein and lipids and is less efficient in using non-protein energy from starch or NFE. Therefore, carbohydrate inclusion in bay snook diets should be restricted and based on easily digestible sources.

Physiological considerations

The ability of cichlid species to utilize dietary carbohydrates is influenced not only by trophic levels but also by the chemical nature of the carbohydrate source. Simple sugars and gelatinized starch are more readily digested than complex non-starch polysaccharides or insoluble fiber, which can impair nutrient absorption and gut health (Stone 2003). Carbohydrase activity, particularly amylase, varies among species and developmental stages and must be considered when formulating diets to ensure efficient energy use without compromising growth or health.

Micronutrient gaps and future perspectives in native cichlids

Little is known about the specific vitamin and mineral requirements of native cichlids from Mexico and Central America. Most nutritional guidelines in aquaculture are based on studies conducted with tilapia (*O. niloticus*), carp (*Cyprinus carpio*), or salmonids, and their extrapolation to native species is questionable due to differences in physiology, trophic level, and environmental adaptations (NRC 2011). Among native cichlids, no peer-reviewed studies have yet quantified optimal levels of essential vitamins or trace minerals such as selenium (Se), zinc (Zn), or vitamin E.

Some insights can be drawn from ornamental cichlid species, such as the blood parrot or angelfish (*Pterophyllum scalare*), which have demonstrated improved immunity and pigmentation with dietary vitamin C (100-200 mg kg^{-1}) and vitamin E supplementation (Lim & Lovell 1978, Li et al. 2018). Similarly, Se and Zn play antioxidant and reproductive roles in other freshwater fish, but their specific requirements in native cichlids remain unexplored.

Given the expanding interest in culturing native cichlids, particularly *P. splendida*, *M. urophthalmus*, and *A. trimaculatus*, future research should prioritize the definition of species- and stage-specific requirements for fat-soluble and water-soluble vitamins, as well as bioavailable mineral sources (e.g. chelated forms). This knowledge is essential for optimizing performance, immune function, and skeletal health under intensive farming conditions.

CONCLUSIONS

This review highlights the trophic and physiological diversity of native cichlid species from Mexico and Central America, which directly influences their nutritional requirements and capacity to utilize various dietary components. Species such as *P. splendida* and *P. dovii* exhibit high protein and lipid requirements (≥45 and ≥15%, respectively), limited tolerance to plant ingredients, and low carbohydrate digestibility (<20%), consistent with their carnivorous feeding habits. In contrast, *M. urophthalmus* and *A. trimaculatus*, which occupy intermediate trophic levels, demonstrate greater flexibility in using plant proteins, vegetable lipids, and digestible carbohydrates (up to 35%), supported by higher carbohydrase activity and omnivorous tendencies.

Although protein and lipid requirements have been quantified in some species, major gaps persist regarding micronutrient needs, digestibility of alternative protein sources, and the effects of diet on immune function and pigmentation. The development of balanced diets must be species-specific, considering the trophic level, digestive physiology, and life stage of each species. Future research should focus on characterizing micronutrient requirements, validating functional ingredients (e.g. probiotics, prebiotics, organic minerals), and defining digestible energy thresholds to support the sustainable farming of native cichlids. This knowledge will be essential for advancing commercial aquaculture and reducing pressure on wild populations.

Credit author contribution

J.M. Ramírez-Ochoa: conceptualization, methodology, formal analysis, writing-original draft; M.P. Hernández-Vergara: funding acquisition, methodology, validation, supervision, review, and editing; C.I. Pérez-Rostro: methodology, validation, supervision, review, and editing; J.P. Alcántar-Vázquez: methodology, formal analysis, review and editing. All authors have read and accepted the published version of the manuscript.

Conflict of interest

The authors declare no conflict of interest.

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