Development, nutrition, and rearing practices of relevant catfish species (Siluriformes) at early stages

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Abstract

Catfish (Siluriformes) are important species for aquaculture worldwide, with an annual production in 2018 of *ca*. 6 million t. This review focuses on reassessing larval development, first feeding, and early rearing practices of the most important farmed catfish species, along with some candidates species for aquaculture diversification: *Pangasianodon hypophthalmus* (Pangasiidae), *Clarias gariepinus* (Clariidae), *Ictalurus punctatus* (Ictaluridae), *Pseudoplatystoma* spp. (Pimelodidae), *Heteropneustes fossilis* (Heteropneustidae), *Rhamdia quelen* (Heptapteridae), *Ompok bimaculatus* (Siluridae), and *Lophiosilurus alexandri* (Pseudopimelodidade). These species are initially reared indoors from one day to two weeks and are then transferred to fertilised outdoor ponds where they either feed on natural zooplankton or compound feeds. With the exception of *C. gariepinus*, *I. punctatus*, *R. quelen* and *P. hypophthalmus*, consistent and reliable fry production is a bottleneck that limits the expansion of farming of other species, such as *Pseudoplatystoma* spp., *H. fossilis*, *R. quelen*, *O. bimaculatus*, and *L. alexandri*. Rearing systems (extensive, semi-extensive, intensive) and feeding protocols vary with species and geographical regions. Cannibalism and size heterogeneity are common, and these features create problems for larval and fry rearing of catfish species. Information about their nutritional requirements is required for the formulation of compound feeds that can guarantee high survival and good growth of catfish fries. However, such knowledge for most species is scarce, although some data are available for *I. punctatus.* Further genomic resources might allow fine-tuning rearing success. This review describes some successes in this field, and also highlights gaps in knowledge to guide future research that can promote the development of catfish aquaculture.

Key words: first feeding, live prey, feed formulation, feeding practices, hatchery, omics.

Introduction

Catfish (order Siluriformes) are a highly diverse clade of ray-finned fish species with a worldwide distribution. They dwell primarily in freshwater, but also in coastal regions of continents and nearby islands. Catfish are majorly distributed in the tropics of South America, Africa, and Asia [1]. Siluriformes, composed of over 3,000 living species and estimated 1,750 undescribed ones, is one of the largest orders of Teleostei, representing *ca.* 12% of all teleosts [2]. Catfish are named after the characteristic whisker-like barbels located around the mouth, which contain numerous taste buds for detecting food and navigating in turbid waters. Moreover, most catfish have a sub-cylindrical body with a flattened ventrum, dorsoventral flattened head, and sharp spines on their dorsal and pectoral fins [3,4]. Interestingly, the size range within this group (*ca.* 14 mm to 5 m) is probably the greatest in Osteichthyes[3]. Catfish have a scale-less skin covered with protective mucus; however, in families such as Callichthyidae and Loricariidae, the skin is covered with bony dermal plates[4].

Catfish have an exceptional importance for commercial, subsistent and recreational fisheries, ornamental fish trade, and aquacultural production. With regard to the latter, catfish possess a wide repertoire of characteristics that make them especially suitable for aquacultural purposes, such as high potential for domestication and adaptation to intensive rearing conditions, high fecundity, nocturnal foraging habits or capacity to live in turbid waters, relatively high resistance against infectious diseases, efficient feed conversion and no intramuscular bones, which greatly facilitates fillet processing [5-7]. Moreover, they are highly tolerant to low dissolved-oxygen levels, as some species are capable of air-breathing such as *Clarias* spp. and *Heterobranchus bidorsalis* (Clariidae), *Heteropneustes fossilis* (Heteropneustidae), *Pangasianodon hypophthalmus* and *Pangasius* spp. (Pangasiidae) [8].

The availability of high-quality fingerlings for the grow-out phase is one of the most critical factors affecting commercial prosperity in aquaculture. Successful larval production depends

on a wide range of biotic and abiotic factors as well as on the development of the zootechnical conditions for optimal rearing (e.g., larval density, feeding protocol, health management). Among the over 30 catfish species farmed worldwide, the present review is focused on the early culture of the most produced species in the different continents: the striped catfish, *Pangasianodon hypophthalmus* (Sauvage 1878) (Pangasiidae, Asia); African sharptooth catfish, *Clarias gariepinus* (Burchell 1822) (Clariidae, Africa and Europe); channel catfish, *Ictalurus punctatus* (Rafinesque 1818) (Ictaluridae, North America); and species of the genus *Pseudoplatystoma* spp. Bleeker (Pimelodidae, South America). In addition, four other species were added, as they are either relatively important at a local scale or are candidate species of interest for aquaculture diversification or conservation: the stinging catfish, *Heteropneustes fossilis* (Bloch 1794) (Heteropneustidae) and butter catfish, *Ompok bimaculatus* (Bloch 1794) (Siluridae) in Asia; and the silver catfish, *Rhamdia quelen* (Quoy & Gaimard 1824) (Heptapteridae) and the pacamã catfish, *Lophiosilurus alexandri* Steindachner 1876 (Pseudopimelodidae) in South America (production values for each species and contry of production are shown in the Supplementary file 1).

This review briefly introduces the importance of catfish in aquaculture and presents the selected catfish species. Further, it provides an overview of the rearing practices during early stages of these species, including information on the ontogeny of the digestive system, first feeding and early rearing, nutrition, cannibalism, and available molecular resources.

The importance of catfish in aquaculture

According to FAO's aquaculture statistics [9], a total of 5,781,235.1 t catfish were produced worldwide in 2018 with the exception of Oceania, for which no data were available (Table 1). Catfish were mainly produced in freshwater and represented 10.6% of the global freshwater fish aquaculture production (54,270,001.6 t), whereas a small production in brackish waters

(1,886 t; 0.03% of total world catfish production) was reported in African and South American countries [9]. The full list of countries and the species produced is shown in Supplementary File 1.

The major catfish producer in 2018 was Asia (5,333,195 t; 92.3% of total world catfish production; Table 1), with several cultured species of six different families (Pangasiidae, Clariidae, Bagridae, Siluridae, Ictaluridae, and Heteropneustidae). Three Asian countries accounted for 73.6% of the Asian catfish production, i.e., Indonesia (1,405,269 t; 26.4% of the Asian production), Vietnam (1,382,000 t; 26.0%), and China (1,127,252 t; 21.2%) (Supplementary File 1). Pangasiidae and Clariidae families accounted for 78.4% of the total Asian catfish production. Particularly, species from the Pangasiidae family (*P. hypophthalmus* and *Pangasius* spp.) were the most produced (2,826,068 t; 53.0%), followed by Clariidae (mainly *Clarias* spp., *C. gariepinus* × *C. macrocephalus*, and *C. batrachus*; 1,352,494 t; 25.4%). The other catfish families in terms of importance were Bagridae (mainly *Pelteobagrus fulvidraco, Leiocassis longirostris*, and *Hemibagrus nemurus*; 537,958 t; 10.1%), Siluridae (mainly *Silurus asotus*, *Wallago attu*, and *Silurus glanis*; 372,439 t; 7.0%), Ictaluridae (*I. punctatus*; 230,442 t; 4.3%), and Heteropneustidae (*Heteropneustes fossilis*; 373 t; 0.01%).

Africa was the second continent in terms of catfish production (251,333 t; 4.3% of total world catfish production; Table 1), with most species produced in freshwater [Clariidae: *C. gariepinus* (218,478 t; 87%), *Clarias* spp. (28,241 t; 11.2%), and *Heterobranchus longifilis* (8 t; 0.003%); Mochokidae: *Synodontis* spp. (5,510 t; 1.8%); Siluridae: *Silurus glanis* (44 t; 0.02%); and Bagridae: *Bagrus bajad* (2 t; 0.001%)] and a few species in brackish environments [Clariidae: *C. gariepinus* and Bagridae: *Chrysichthys nigrodigitatus* (50 t; 0.02%)]. Up to 35 African countries produced catfish in 2018; Nigeria was the main producer

(192,851 t; 76.7% of the African production), and Uganda, the second (33,454 t; 13.3%). The production in the remaining countries was limited (25,028 t; 10%) (Supplementary File 1).

In 2018, America (South, North, and Central) was the third most important region in catfish production (183,221 t; 3.2% of total world catfish production). According to FAO [9], the most produced species were ictalurids (*I. punctatus* and *Ictalurus* spp.; 161,271 t, 88.02%) and non-specified freshwater siluroids (13,950 t, 7.61%), the latter produced in Brazil. The national aquaculture production statistics of Brazil from 2019 were, however, more specific than those reported by FAO and showed that the Brazilian catfish production relied on *Pseudoplatystoma* spp. (Pimelodidae) and their interspecific and intergeneric hybrids (10,918 t) [10]. The remaining American catfish production, as indicated by FAO[9], was based on *C. gariepinus* (6,286 t; 3.43%), *P. hypophthalmus* (1,020 t; 0.56%), species from the Pimelodidae family (*Pseudoplatystoma* spp., and *Pimelodus* spp.; 660 t; 0.36%), *Hoplosternum littorale* (Callichthyidae; 22 t; 0.01%), *R. quelen* (Heptapteridae; 6 t; 0.003%), and *Pterygoplichthys pardalis* (Loricariidae; 6 t; 0.003%). The main catfish producing countries were the United States (159,423 t; 87.01%), Brazil (13,950 t; 7.61%), Cuba (6,286 t; 3.43%), and Mexico (1848 t; 1.01%), followed by a limited production in 11 other countries (0.6–580 t) (Supplementary File 1).

The aquaculture of catfish in Europe in 2018 (13,487 t; 0.2% of total world catfish production; Table 1) was focused on *C. gariepinus*, the hybrid *H. longifilis* × *C. gariepinus*, *I. punctatus*, *S. glanis*, and *Ameiurus melas* (Ictaluridae), which represented 49.6% (6,689 t), 24.7% (3,333 t), 14.5% (1953 t), 10.6% (1,425 t), and 0.6% (87 t) of the European production, respectively. This production was distributed among 19 countries, and the Netherlands (4,000 t; 29.7%), Hungary (3,585 t; 26.6%), and Russia (1,879 t; 13.9%) were the main producers (Supplementary File 1).

Selected catfish species

Pangasianodon hypophthalmus

Species of the Pangasiidae family are native to Southern Asia, and most are distributed in the Mekong and Chao Phraya river basins and in Indonesia [11]. The aquaculture of pangasiids has grown and expanded dramatically in the past 25 years. Among the existent 28 species, *P. hypophthalmus* —previously known as *Pangasius sutchi* or *Pangasius hypophthalmus*— is today the most produced catfish worldwide, accounting for over 40% of the world's catfish production. Vietnam is, by far, the biggest producer of pangasiids in Asia (48.1%), followed by India (18.5%) and Bangladesh (15.6%) [9].

The striped catfish *P. hypophthalmus*, reaching 1.3 m in total length (TL) and a maximum weight of 44 kg [12], is listed as endangered by the IUCN. It has been introduced in the South-East Asia, Indian subcontinent, Brazil and in the Caribbean (Dominican Republic, Jamaica, Haiti, and Puerto Rico) for aquaculture purposes [12]. Its farming success is mainly based on its high fecundity, omnivorous feeding habits and tolerance to low dissolved-oxygen levels in water, which is due to the presence of a well-vascularised swim bladder that enables this species to breathe atmospheric oxygen; consequently, pangasiids can be reared in ponds at high densities and with low water renewal [7]. Interspecific and intergeneric hybrids have also been produced between *P. hypophthalmus* and other cultured pangasiid species, such as *Pangasianodon gigas*, *Pangasius bocourti*, *P. larnaudii*, or *P. djambal*, for their high growth, survival rate, or flesh quality [7,13].

Clarias gariepinus

The African sharptooth catfish essentially has a pan-African distribution, although it is naturally absent from Maghreb, Upper and Lower Guinea, and Cape provinces. This species is also naturally present in Jordan, Lebanon, Syria, Israel, and Turkey, and it has been

178 introduced in over 25 countries in Europe, Asia, and Latin America [9]. In natural environments,
179 *C. gariepinus* is found in lakes, streams, rivers, swamps, and floodplains, many of which are
180 subjected to seasonal drought. In such habitats, it can survive during the dry season because
181 of the air-breathing dendretic organ located in the suprabranchial chamber. *Clarias gariepinus*
182 reaches an average adult size of 1–1.5 m (maximum size = 1.7 m TL) and 60 kg in weight.
183 Because of its high growth rate at high stocking densities, high feed conversion rates, good
184 flesh quality, and year-round production [14], this is the most cultured catfish species not only
185 in Africa but also in Europe [9]. In Asia, *C. gariepinus* is also cultured in many countries, where
186 it is also hybridised with native *Clarias* species, such as *C. batrachus* and *C. macrocephalus*.
187 Interestingly, these hybrids present higher growth rates than the local *Clarias* species and
188 better flesh quality and taste than the Asian species [15].
189
190 *Ictalurus punctatus*
191 The channel catfish is a North American freshwater carnivorous species native to the central
192 drainages of the United States and into southern Canada [5]. Because of its large size (maximum
193 size = 1.3 m TL and 26.3 kg in weight) [12] and excellent taste, it has been extensively introduced
194 for recreational fisheries and aquaculture throughout the United States and northern regions
195 of Mexico, as well as in over 40 countries worldwide [9]. China is the biggest producer, followed
196 by the United States, Russia, Mexico, and Italy. Propagation of *I. punctatus* began in the
197 United States in 1914 for stocking lakes, reservoirs, and farm ponds [16]; while currently, *I.*
198 *punctatus* accounts for 60% of the US freshwater aquaculture production [9]. However, the
199 channel catfish has been replaced by the interspecific hybrid catfish *I. punctatus* ♀× *I. furcatus*
200 ♂, which represents 70% of the current US catfish production. The hybrid has a superior

performance because of its high growth rates, bacterial disease resistance, tolerance to hypoxic conditions, and carcass yield [17].

Pseudoplatystoma spp.

The species of the genus *Pseudoplatystoma* are distributed in the major river basins of South America and are highly prized for human consumption because of their flesh quality and absence of intra-muscular bones (pin-bones) [18,19]. *Pseudoplatystoma* spp. are piscivorous and reach maximum sizes of 1.40 TL and 25 kg in weight [18,20]. The genus currently consists of eight species (*P. punctifer*, *P. reticulatum*, *P. orinocoense*, *P. fasciatum*, *P. magdaleniatum*, *P. tigrinum*, *P. metaense*, and *P. corruscans*) (Supplementary File 2). However, there are inconsistencies in the taxonomy of the genus proposed by Buitrago-Suárez & Burr [18] as subsequent molecular and morphological studies revealed [21,22], which highlight the need to re-evaluate the classification within the genus. The high commercial value of *Pseudoplatystoma* spp. in comparison to other local native fish has motivated the development of its commercial rearing, and Brazil is the biggest producer in the region [19]. However, its production has mostly relied on interspecific hybrids, which have better growth performance than that of pure species [23,24]. Currently, the most produced hybrids are intergeneric between *Pseudoplatystoma* spp. and the omnivorous pimelodid catfish *Leiarius marmoratus* or *Phractocephalus hemioliopterus*, which show less cannibalistic behaviour, readily accept compound diets, as well as more omnivorous feeding habits at juvenile and adult stages [25-27]. The production of hybrids has been identified as a serious threat to the industry despite their widespread use. Studies based on molecular markers have shown that fish farmers are in some cases mistakenly using interspecific hybrids as broodsfish, which, in the case of post-F1 hybrids, reduces the viability of the offspring due to their high mortality rates [25]. Considering also the threat that hybrids escaped from fish farms represent to natural populations due to their

potential introgressive hybridization that may have negative impacts on biodiversity [28], research efforts should be focused in developing breeding programs and technologies for pure *Pseudoplatystoma* species in order to promote profitable and environmentally safe alternatives to the production of hybrids [27]. A list of *Pseudoplatystoma* hybrids and their characteristics is shown in Supplementary File 2.

Heteropneustes fossilis

The stinging catfish is a commercially important and popular species, particularly in countries such as India, Thailand, Bangladesh, Pakistan, Nepal, Sri Lanka, Myanmar, Indonesia, and Cambodia [29-30]. This omnivorous species dwells in ponds, ditches, swamps, and marshes, but sometimes it is also found in muddy rivers. *Heteropneustes fossilis* can survive in oxygen-depleted waters by utilising atmospheric oxygen for respiration due to the presence of a respiratory air sac. This species grows up to 0.3 m TL and 0.2 kg and is mostly preferred for its tender flesh, taste, and low-fat content. In addition, its flesh is recommended to people with anaemia because of its high iron content [31].

Heteropneustes fossilis is appreciated for aquaculture for its tolerance to crowding stress, air-breathing capacity, and acceptance of pelleted feeds [32]; it is also considered an interesting ornamental fish [12]. Currently, *H. fossilis* is commercially reared exclusively in Bangladesh (13,421 t) and Myanmar (373 t) [9]. However, it is considered a highly promising candidate for the diversification of freshwater aquaculture in India [32,33]. Successful intergeneric hybridization has been achieved between *H. fossilis* ♀ and *Clarias batrachus* ♂; however, hybrids performed worse in terms of growth when compared to *C. batrachus*, but better with regard to *H. fossilis* conspecifics [34].

Rhamdia quelen

The silver catfish *R. quelen*, also known as South American catfish, black catfish or jundiá, is an omnivorous freshwater species that grows fast during druing the first years of life and successfully reproduces in captivity. These characteristics, associated with a high acceptance by the consumer markets of Brazil, Argentina, and Uruguay, encouraged its aquaculture production. The genus Rhamdia includes several species, most of them with great similarities in body shape, color patterns and habitat use, being 49 of them synonymized as *R. quelen,* with a wide geographical distribution from central regions of Argentina to southern Mexico [12]. However, according to several studies [35-37], the taxonomy of this genus needs to be re-evaluated by means of molecular tools in order to clarify current synonymies. Particularly, *R. branneri* and *R. voulezi*, which were initially were considered as synonyms of *R. quelen* [38], have been recently confirmed as valid species [35,37]. Since most information compiled in this review is based on data from Argentina, Brazil and Uruguay obtained before the recognition of various species previously considered as *R. quelen*, the possibility that species such as *R. branneri* and *R. voulezi* may have been included in this review under *R. quelen* denomination must be taken into consideration. Brazil is the main country producing this species [19]. Since 1980, several studies have been conducted to develop production technologies for this species [39]. In nature, *R. quelen* males grow faster than females up to the third or fourth year of life, when this condition is reversed. The maximum size for *R. quelen* in nature is approximately 0.7 and 0.5 m TL for females and males, respectively, reaching a maximum weight of 4 kg; this size is attained at the ages of 18 and 12 years, respectively [39]. This species can live in a wide range of temperatures, although a better growth performance is displayed at temperatures around 24°C [40]. As it tolerates much lower temperatures than other fish within its distribution area, *R. quelen* is a particularly promising aquaculture species in subtropical regions, where

274 temperatures drop during the winter [41]. No hybrids with other catfish species have been
275 reported.
276
277 *Ombok bimaculatus*
278 The butter catfish is distributed in the Indian subcontinent and Myanmar. This freshwater
279 species is found in quiet, shallow, often muddy waters, in sandy streams, rivers, canals, beels,
280 and inundated fields. *Ombok bimaculatus* is an omnivorous species, mainly feeding on
281 vegetable matter, fish, and occasionally on crustacean and planktonic organisms, reaching a
282 maximum size of 0.5 m TL and 0.2 kg in weight. The butter catfish is considered a delicacy
283 in many parts of India, particularly in the North-eastern states, because of its good taste,
284 excellent nutritional profile, and soft bony structure [42]; it is one of the most expensive fish
285 species in this country. Recently, it has been also introduced in ornamental fish markets of
286 India owing to its moderate market demand among hobbyists. Because of its increasing
287 demand, this species is categorised as near threatened by the IUCN. Considering the consumer
288 acceptance, *O. bimaculatus* has been considered an important candidate for the diversification
289 of freshwater aquaculture in India and neighbouring countries [43]. No hybrids with other catfish
290 species have been reported for *O. bimaculatus*.
291
292 *Lophiosilurus alexandri*
293 The pacamã, *L. alexandri* is a freshwater carnivorous fish endemic to the São Francisco River
294 in Brazil [44], reaching a maximum size of 0.5 m TL and 5 kg of weight. This species is highly
295 appreciated for human consumption because of the quality of its flesh. It is considered as an
296 emerging aquaculture species within its range of natural distribution due to its high demand
297 for consumption and use as ornamental fish [45]. *Lophiosilurus alexandri* is a sedentary species,
298 prefers lentic environments, and reproduces by batch spawning with the release of eggs on

299 sandy substrate with male parental care [46]. This species is considered vulnerable to extinction
300 [47], although it has not yet been classified by the IUCN. In this context, efforts have been made
301 to improve the production of fingerlings for restocking programmes in the Rio São Francisco
302 basin [48-51], as well as for human consumption [52,53]. No hybrids with other catfish species have
303 been reported.
304
305 **Ontogeny of the gastrointestinal tract and digestive capacity**
306 To survive and grow, fish must be able to capture, ingest, and digest food and absorb nutrients.
307 Although fish larvae may be morphologically capable of capturing different food items (e.g.
308 zooplanktonic organisms and microdiets), their digestive system undergoes a series of
309 developmental changes before being fully functional shortly after hatching [54]. In this regard,
310 knowledge about the ontogeny of the digestive system may contribute to the development of
311 efficient larval feeding protocols. For example, the morphology and functionality (e.g.,
312 activity of digestive enzymes) of the digestive system are often used to assess the nutritional
313 condition of fish larvae reared under different conditions [55]. Although there are similarities in
314 the ontogenic development among fish species, there are also interspecific differences with
315 regard to the timing of differentiation, development, and functionality of the digestive system
316 in relation to the physiological ecology of the species. The chronology of developmental
317 events expressed solely in terms of time does not provide a reliable basis when comparing fish
318 that have been reared at different water temperatures. Therefore, in this review larval
319 development has been described in relation to larval size in length or accumulated degree-
320 days (ADD).
321
322 *Morphoanatomical development of the digestive system*

A summary of the main morphoanatomical changes of the digestive system in the catfish species considered within this review is presented in Table 2. In particular, *I. punctatus* and *R. quelen* are precocial species, whereas *C. gariepinus, P. hypophthalmus*, *P. punctifer*, *H. fossilis*, *O. bimaculatus*, and *L. alexandri* exhibit altricial development. *Rhamdia quelen* is the species that develops faster, showing an open mouth at only 4 ADD (4 hours post hatching, hph at 24.6°C; *ca*. 5 mm TL) and a differentiated stomach at 17 ADD (16 hph at 24.6 °C; *ca*. 6 mm TL) that is completely formed and functional at 49 ADD (2 days post hatching, dph at 24.6°C; *ca*. 8 mm TL). The next fastest developing species are *C. gariepinus* and *H. hypophthalmus,* although key digestive structures appear much later in these species than in *R. quelen.* Mouth opening in *C. gariepinus* occurs at 50 ADD (2 dph at 25°C; *ca*. 9 mm TL) and the stomach is formed at 114 ADD (4 dph at 28.5°C; *ca*. 11 mm TL). *Pseudoplatystoma punctifer, H. fossilis*, *and O. bimaculatus* present similar but delayed developmental patterns. Although mouth opening occurs earlier in *H. fossilis* (29 ADD, 1 dph at 29°C; *ca*. 3 mm SL) than in *P. punctifer* (56 ADD, 2 dph at 28°C; *ca*. 5 mm TL) and *O. bimaculatus* (54 ADD, 2 dph at 27°C; *ca*. 3 mm TL), the timing of most anatomical and histological events is similar between the three species (Table 2). For instance, the stomach is formed at 252 ADD (9 dph at 28°C; *ca*. 10 mm TL) in *P. punctifer,* at 290 ADD (10 dph at 29°C; *ca*. 7 mm TL) in *H. fossilis*, and at 297 ADD (11 dph at 27°C; *ca*. 14 mm TL) in *O. bimaculatus. Lophiosilurus alexandri* shows a different developmental pattern, characterised by an already opened mouth at hatching (0 dph at 27°C; *ca*. 3 mm TL) and a delayed first exogenous feeding as well as pancreas and intestine differentiation compared with the other species (Table 2). However, the complete histological development of the digestive system, marked by the formation of the stomach, is achieved approximately at the same time as that in other catfish species. A mixed feeding period exists in all these species, which lasts between 1 and 4 days. Yolk-sac resorption is particularly long in *L. alexandri*, which occurs almost in synchrony with the

formation of the stomach (Table 2). Despite being a species extensively studied and reared, we could not find any detailed description of the digestive system ontogeny of *I. punctatus*. However, we present here some information on the development of this species as a guideline. The incubation time of channel catfish eggs averages 5 days at 27–28°C, and larvae have an average size of 10.6 mm TL at hatching. The period from hatching to first feeding lasts from 5 to 9 days, depending on water temperature; the onset of exogenous feeding occurs at 13–14 mm TL [66]. *Ictalurus punctatus* has a long yolk-sac resorption period of 5 to 10 days [67]. However, the juvenile period is considered to start from the onset of exogenous feeding [68].

Functional development of the digestive system

The ontogenic development of the digestive enzymes of altricial species may be divided in three different phases: 1) from hatching to the onset of exogenous feeding; 2) exogenous feeding phase, based on alkaline proteolytic enzymes produced by the exocrine pancreas; and 3) commencement of acidic protein digestion to supplement alkaline proteases caused by the development of a functional stomach, and transition from larval to juvenile/adult digestion mode [54].

During the endogenous feeding phase, catfish possess pancreatic digestive enzymes such as alkaline proteases, lipases/esterases, and carbohydrases. These enzymes are involved in the digestion and reabsorption of the yolk sac by the syncytium that surrounds it, as well as the accumulation of zymogens in the exocrine pancreas [54]. Nevertheless, it should be highlighted that the biochemical detection of certain enzymes in newly hatched larvae may also be attributed to other factors rather than the development of accessory digestive organs. For instance, high activity levels of trypsin-like proteases just after hatching are generally associated with the lysis of the chorion during the hatching process [69]. In addition, detecting bile salt-activated lipases at hatching, when the exocrine pancreas is not yet fully

differentiated, does not mean that catfish larvae utilise such lipases to digest lipids contained in their yolk-sac reserves. In fact, it indicates that the spectrophotometric method for assessing this enzyme, in which lipase activity is enhanced by means of bile salts (sodium cholate), is not specific [70] and it may also detect other lipases hydrolysing triglycerides and wax esters in the yolk [71].

Among the species selected in this review, the functional development of the digestive system has only been reported for *C. gariepinus* [57,72], *P. hypophthalmus* [73], *O. bimaculatus* [61], *R. quelen* [63], and *P. punctifer* [74,75]. Unlike the other catfish species, *I. punctatus* and *R. quelen* larvae present functional stomachs before changing from endogenous to exogenous feeding [63]. Regarding the other species, after the onset of exogenous feeding and before the development of a functional stomach, proteins are digested by alkaline proteases, principally trypsin and chymotrypsin, in combination with intestinal cytosolic peptidases (*i.e.*, leucine-alanine peptidase). During this period, larvae display limited capacity of digesting macromolecules that are absorbed by enterocytes [76]. Comparatively, in *R. quelen*, a sharp increase in the specific activity of digestive alkaline proteases was detected at the onset of exogenous feeding (49 ADD, 2 dph at 24.6°C; *ca*. 8 mm TL) [63]; this increase was observed several days after first feeding in the other catfish species [61,73,74]. The combination of histological and biochemical tools revealed that an increase in the production of pancreatic alkaline proteases was observed after the completion of the exocrine pancreas development [61,63,74]. Similar patterns regarding lipase and α-amylase have been also described [61,74], although profiles in activity along larval ontogeny varied according to the species. These results may be attributed to different developmental patterns, rearing protocols, and analytical methods for quantifying enzymatic activity. In this context, pepsin-like activity was detected in newly hatched larvae of *P. punctifer* [74]. However, the presence of pepsin-like activity in hatchling homogenates cannot be attributed to the presence of a functional stomach, as this organ is not

398 developed yet; thus, pepsin-like activity is due to the presence of lysosomal proteases involved
399 in the intracellular digestion of yolk proteins. This finding was further confirmed in a recent
400 study on the ontogeny of the main digestive enzyme precursors during the larval development
401 of *P. punctifer*, in which pepsinogen expression was detected as early as 56 ADD (2 dph at
402 28°C, 5 mm TL) [75]. This is due to the fact that acidic (aspartic) proteases are homologous
403 entirely in terms of amino acid sequences, particularly around the active site residues. The
404 sharp increase in pepsinogen expression detected at 252 ADD (9 dph at 28°C; *ca.* 10 mm TL)
405 is certainly attributed to the pepsin-coding gene expression, as at this age the stomach is
406 formed and full of gastric glands [59].

407 In gastric species, the acquisition of a functional stomach is widely considered the end of
408 the larval stage [54]. The onset of acidic digestion is also generally considered an optimal point
409 for larval weaning onto microdiets, when the adult-like mode of digestion becomes fully
410 functional and dietary complex proteins are easily digested. However, this is not a universal
411 rule, as some species can be weaned onto dry feed before acidic digestion begins [77]. In the
412 reviewed catfish species, pepsin activity was detected at *ca.* 49 ADD (2 dph at 24.6°C; *ca*. 8
413 mm TL) in *R. quelen* [63], 114 ADD (4 dph at 28.5°C; *ca*. 11 mm TL) in *C. gariepinus* [72], 252
414 ADD (9 dph at 28°C; *ca*. 10 mm TL) in *P. punctifer* [74,75], and 413 ADD (15 dph at 27°C; *ca.*
415 25 mm TL) in *O. bimaculatus* [61]. Thus, the histological and functional formation of the
416 stomach is synchronised in these species with the exception of *O. bimaculatus,* in which a gap
417 of several days existed between the stomach differentiation and pepsin secretion [61]. These
418 differences may be attributed to different reproductive and developmental guilds as well as
419 differences in growth and developmental rates in response to different environmental
420 pressures (*e.g.*, food availability, habitat seasonal modifications). These results highlight the
421 need to conduct both histological and biochemical studies for each species to accurately assess

422 the shift between the larval- and adult-like modes of digestion. When only histological data
423 are available, conclusions should be made with care.

424 Besides serving to characterise the digestive capacities of developing fish, the activities of
425 pepsin and other digestive enzymes may also serve as biomarkers for evaluating hatchery
426 practices [77]. In particular, pepsin activity may act as an indicator of the population's
427 heterogeneity during the process of adaptation to new diets during weaning. Particularly, a
428 high coefficient of variation in pepsin activity at a single age or stage of development or
429 activity fluctuations along several days after a shift in diet may be used for the above-
430 mentioned purposes. Similarly, digestive enzyme activities may provide insights into the
431 larval ability to modulate their digestive enzyme production, depending on the nutritional
432 composition of the diet. This has been demonstrated in *P. punctifer* at both larval and early
433 juvenile stages. For instance, gene expression of amylase, phospholipase, and lipoprotein
434 lipase were differentially regulated in *P. punctifer* in response to the dietary DHA content in
435 *Artemia* during the larval phase (Diana Castro-Ruiz, unpublished data). Similarly, gene
436 expression of the main digestive enzymes, as well as their enzymatic activity, can also be
437 modulated in response to dietary composition. Diets containing 45% protein induced an
438 increase in *trypsin* and *pepsinogen* expression and a decrease in *amylase* in *P. punctifer*
439 compared with that in individuals fed diets containing 30% protein. Changes in gene
440 expression were associated with changes in their corresponding enzyme activity; the
441 regulation could be at transcriptional or translational levels, depending on the digestive
442 enzyme analysed [78].

443 Changes in enzyme activities over circadian rhythms as well as their postprandial
444 modifications after a single meal are also important for understanding larval digestive
445 capacities and adjusting feeding practices (*i.e.*, number of meals per day). In this context, it
446 has been demonstrated that postprandial changes in proteolytic enzymes were observed in *C.*

447 *gariepinus* larvae aged 3 and 7 dph [5.4 and 29.7–33.1 mg body weight (BW), respectively]
448 within 30 min after feeding [79]. In particular, proteolytic activity in the gut decreased
449 significantly because of the immediate utilisation of enzymes present in the gut, whereas *ca.*
450 1 h later, when larvae had completely filled their gut, protease activity started to increase and
451 a maximum of enzyme activity was recorded 12 h after the intake of one single meal. Thus,
452 decapsulated *Artemia* cysts were completely digested *ca*. 9 h after ingestion, whereas other
453 types of food with higher protein digestibility, e.g., *Artemia* nauplii, were digested faster
454 because the peak of proteolytic activity occurred earlier. In addition, no change in enzymatic
455 activity was verified in starved larvae when evaluating the activity of proteolytic enzymes in
456 *C. gariepinus* along a 24-h cycle. However, total protease activity in larvae fed every 4 h
457 showed small significant differences during the same 24-h period. Seemingly, enzyme
458 production did not occur in a rhythmic cycle and was not affected by the light regime either
459 [79]. The last but not the least, further research must be focused on the appetite-regulating
460 hormones and their role in the physiological regulation of appetite and prey ingestion
461 considering species-specific feeding habits, feeding protocols and diet composition [54], as well
462 as their potential relationship with the cannibalistic behaviour in this group of species.
463
464 **Rearing practices for early life stages**
465 The development of a reliable protocol for rearing fish larvae and fries is a necessary step to
466 guarantee its culture at a commercial scale. The establishment of reliable rearing protocols is
467 difficult, as larval and fry culture is a complex process that relies on multiple factors, such as
468 larval and fry development, behaviour, growth, and survival. The above-mentioned processes
469 are modulated by many factors that may be classified into four categories: species-specific
470 reproductive guilds, environmental factors (i.e., temperature, light intensity, photoperiod,
471 water quality, and tank cleaning), feeding factors (i.e., food composition, feeding frequency

and ratio, meal distribution timing, and weaning period), and population factors (i.e., fish density, strain, and domestication level) [80]. A wide range of larval rearing practices have been developed in the last decades for different catfish species, protocols that vary mainly depending on the geographical area, level of initial economic investment, main production purpose (i.e., subsistence, commercial, or restocking), among other factors. Thus, this section is devoted to review this species-specific state of the art regarding different rearing systems and feeding practices.

Pangasianodon hypophthalmus

The striped catfish has been farmed for decades in the Mekong Delta relying on wild-caught seed. However, the explosive growth of its commercial production started after the optimisation of induced breeding in the late 1990s, with larval production increasing 18-fold between 2002 and 2011 [81,82]. *Pangasianodon hypophthalmus* larvae are obtained by hormonally-induced spawning. Eggs and milt of hormonally-treated broodfish are collected, and eggs are fertilized with milt by gently mixing. For removing the adhesiveness of the fertilized eggs, they are then washed with 1% tannic acid solution for 5–10s [83,84]. Fertilized eggs are distributed on steel trays or hatching jars (Zoug, Weiss or McDonald jars) for incubation with a continuous freshwater flow. Hatching occurs between 23 and 34 hours post fertilization (hpf) in incubation temperatures ranging from 26°C to 30°C. The onset of exogenous feeding of larvae occurs at 2 dph (6.2 mm TL) [83,85].

Regarding rearing procedures, in the commercial hatcheries from the Mekong Delta (Vietnam), larvae are generally reared in indoor tanks with volumes ranging from 0.2 to 4.7 m^3 in flow-through water systems with constant aeration. Stocking densities vary between 200 and 7,000 larvae m^{-3}. Most hatcheries sell larvae to nursery farms before the onset of exogenous feeding [83,85]. In the nursery farms, *P. hypophthalmus* larvae are cultured in earthen

ponds (1,000–5,000 m^2 and 1.5–2-m depth) using high-quality screened, chlorine-treated water (pH: 6.4–8.5; dissolved oxygen ≥3 ppm) (Table 3). *Pangasianodon hypophthalmus* larvae present cannibalistic behaviour from the onset of exogenous feeding until 8 dph [85,86]. The impact of this cannibalistic behaviour can be reduced with low stocking densities and the presence of natural zooplankton in the ponds. Before transferring the larvae, ponds are cleaned from sludge, treated with lime (10–15 kg 100 m^{-2}) and often also with salt, and dried for 3 to 5 days. Ponds are then fertilised with fish powder or fish meal (2–3 kg 1,000 m^{-2}), soybean meal (2–3 kg 1,000 m^{-2}) or blood powder (1 kg 1000 m^{-2}) and zeolite (4 kg 1,000 m^{-2}), and probiotics (0.3 kg 1,000 m^{-3}) and 1–2 kg of live prey (i.e., *Moina* sp.) to promote their growth and proliferation and serve as food for larvae. Once ponds are prepared, 1 dph-old *P. hypophthalmus* larvae are stocked at densities of 500 to 800 larvae m^{-2} and reared for 20 to 45 days depending on the farm, until fry are transferred to fingerling nursing ponds [82,83]. The above-mentioned rearing practices generally result in survival rates ranging from 30 to 50%.

Larval growth, size heterogeneity, mortality, and cannibalistic behaviour in *P. hypophthalmus* are profoundly affected by water temperature [86]. In experimental conditions in an indoor recirculating system, mortality rates showed an inverse correlation with water temperature during the first 4 days after hatching, whereas cannibalistic rates were higher in cold than in warm water temperatures (23°C vs. 33°C). In addition, size heterogeneity decreased with an increase in water temperature, evidencing that choosing an optimum thermal temperature for larval rearing in *P. hypophthalmus* promoted growth, reduced cannibalism and early mortality, and decreased size heterogeneity. Thus, the optimal temperature for somatic growth in *P. hypophthalmus* larvae is 31°C at the onset of exogenous feeding, increases to 32.7°C when larvae weigh 8 mg BW, and then decreases progressively in larger fish, at a rate of *ca.* 0.7°C for each 10-fold increase of BW.

521 Regarding feeding practices, from the onset of exogenous feeding (2 dph, 6.2 mm TL), *P.*
522 *hypophthalmus* larvae feed on wild zooplankton and stocked zooplankton and zoobenthos
523 such as *Moina* sp., *Artemia* sp., or *Tubifex* sp. Additionally, larvae may be fed five times a
524 day during the first week of rearing in the ponds; the farm-made feed is basically composed
525 of soybean meal or fishmeal, soybean milk, egg or yeasts. During the second week, larvae are
526 fed a concentrated powder (40% protein) 4 times a day, and from the third week, early
527 juveniles are fed commercial pellets (30–35% protein) 3 to 4 times a day. For further details
528 on the feeding protocol used in the nurseries of the Mekong Delta, readers are invited to
529 consult Nguyen *et al.* [82]. One-day-old larvae have been stocked at low densities (60 larvae
530 m^{-2}) in rotifer-enriched nursery ponds and fed custard egg and soya powder during the first
531 days and a carp fry diet subsequently [84]. These authors reported a larval survival rate of 18.3%
532 and a growth rate of 0.2 g day^{-1} after 45 days of culture.
533 In experimental conditions, the striped catfish larvae have been reared in indoor
534 recirculating systems and fed 36 h post hatching (hph) *Artemia* nauplii eight times a day until
535 8 dph. Under these conditions, survival rates ranged from 20% to 60%, depending on prey
536 and fish densities [87]. Authors observed that at 8 dph, survival depended on feeding level rates
537 rather than on prey density. The survival rate of *P. hypophthalmus* that was fed high levels of
538 *Artemia* nauplii was higher in lower densities (10 and 30 larvae L^{-1}) than in higher densities
539 (90 larvae L^{-1}). Similarly, a higher feeding level promoted larval growth at 8 dph, which was
540 not influenced by larval density. A model of maximal food intake showed that during the early
541 feeding stages, the maximal meal size of *P. hypophthalmus* larvae was small (12% BW at 5.5
542 mm TL and 0.72 mg BW), but it increased quickly at 6 mm TL (22% BW, 1.2 mg BW) and
543 at 6.5 mm TL (26% BW, 1.6 mg BW). From 7 mm TL onwards, meal size decreased
544 curvilinearly to 10% BW at 15 mm TL (25 mg BW) [87]. The best first-feeding time for *P.*
545 *hypophthalmus* is recommended between 30 and 36 hph using rotifers (*Brachionus. angularis*)

546 during 3 days followed by cladocerans (*Moina macrocopa*) for the subsequent 7 days [88]. These
547 authors also reported that the best live prey density and feeding frequency in terms of growth
548 and survival were between 8 to 11 individuals mL^{-1} and six times per day, respectively.
549 When comparing feeding behaviour between light and dark rearing conditions, ingestion
550 rates of *A. nauplii* in 4- and 7-dph-old larvae reared in darkness were higher than those of
551 larvae under light conditions [89], which may be due to the higher swimming activity at night
552 than in the day. These results indicate that the feeding behaviour in this species depends on
553 chemo-sense rather than visual sense because of the presence of free neuromasts that respond
554 to mechanical stimuli and the numerous taste buds on the barbels, head surface, buccal cavity,
555 and gills [90]. Concerning weaning under experimental conditions, *Artemia* nauplii could be fed
556 to larvae until they attained 100 mg BW (at 11 dph with the optimal rearing temperature), then
557 larvae may be weaned onto a commercial feed (Nippai SeaBream, Nippai, Yokohama, Japan;
558 55% protein, no data on lipid content provided by authors) within 6 days, and fed another
559 commercial feed (BioMar BioOptimal Start, Nersac, France; 52% protein) after attaining 300
560 mg BW [86].
561
562 *Clarias gariepinus*
563 *Clarias gariepinus* larvae and fingerlings may be produced using three different systems [91]:
564 1) in nursery ponds, where larvae are extensively on-grown to fingerling size before being
565 stocked into larger grow-out ponds; 2) in a hatchery for a period of up to 14 days and then
566 grown to the fingerling size for a further 30 days in nursery ponds, after which they are stocked
567 into larger on-growing ponds; and 3) larvae are intensively reared to the fingerling size in a
568 hatchery, after which they are on-grown under pond or high-density tank culture conditions
569 (Table 3). Generally, when extensive pond systems are used for larval rearing, the most critical
570 factor for success is the availability of zooplankton during the first days. This naturally

571 growing zooplankton is mainly formed by cladocerans (*Moina* sp., *Chidorus* sp.,
572 *Diaphanosoma* sp., *Bosmina* sp., and *Daphnia* sp.), copepods (different Cyclopoidea species)
573 and rotifers (*Keratella* sp., *Brachionus* sp., *Synchaeta* sp., among others) [6].

574 Under extensive rearing conditions, ponds are prepared to assure abundance of
575 zooplanktonic prey for larvae. This generally occurs up to 14 days before stocking 3-dph
576 larvae and consists of liming and fertilisation. Several manuals recommend adding 100–150
577 kg ha^{-1} of quicklime to the damp pond bottom to eliminate pathogens and potential
578 invertebrate predators. Then, ponds are left for 7–14 days and filled with water to a depth of
579 30 cm, and the pH is adjusted by adding lime. Afterwards, farmers promote the proliferation
580 of zooplanktonic blooms by adding inorganic or organic fertilisers, which are selected
581 depending on the economic resources of the farmer. Only then, larvae are introduced into the
582 rearing ponds. Readers are encouraged to consult Hecht [91] for further details about different
583 strategies for chemical pond fertilisation. Regardless of the procedure employed, it is
584 recommended to maintain soluble nitrogen and orthophosphate at 0.95 mg N L^{-1} and 0.1–0.5
585 mg P L^{-1}, respectively [92]. The most commonly used organic pond fertilisers, are poultry, pig,
586 and bovine manure [93]. The following rates of manure application (kg 100 m^{-2}) may be applied:
587 an initial quantity of 25 kg of poultry manure followed by 3 to 5 kg every 10 days; 7 kg of pig
588 manure every two days; or 10 kg of bovine manure every two days. However, the success of
589 these procedures may change depending on local environmental conditions; if an adequate
590 phytoplankton bloom is not achieved within six to eight sunny days, more manure should be
591 added into the ponds. As ponds can only assimilate a certain amount of manure per day, it
592 should be added frequently on a daily basis [94]. Finally, a combination of organic and inorganic
593 fertilisers can also be applied to promote zooplankton growth in ponds. In particular, a mixture
594 of dry poultry manure (10–20 kg), urea (0.4–0.8 kg), and triple superphosphate (0.1–0.2 kg)
595 per 100 m^2 per week is advisable. In addition, periphyton can also be successfully used for the

596 rearing of *Clarias* larvae. In this context, it has been reported the beneficial combined effect
597 of pond fertilisation (20 kg pig manure per 100 m^2 at initial fertilisation rate followed by 10
598 kg every two weeks) and the use of bamboo poles (4 per m^2) for the development of periphyton
599 [95].

600 Regarding feeding practices, before the onset of exogenous feeding (*ca*. 80 hph, depending
601 on temperature), larvae aged 3 dph are moved from the hatchery facilities and stocked into
602 rearing ponds (100–250 m^2) at a density of 100–250 larvae m^{-2}. At lower larval rearing
603 densities (100 larvae m^{-2}), the feeding strategy consists of adding 1 kg rice or wheat bran and
604 1 kg 100 m^{-2} of crumbled formulated feeds into the ponds during the first three weeks. For the
605 following two weeks, bran quantities should be maintained stable, but formulated feed may
606 increase up to 2 kg 100 m^{-2} day^{-1} (divided in two meals per day). Size grading is advisable
607 after three weeks to homogenise size classes and reduce fry cannibalism. Survival rates of
608 40% and 3-g fries (BW) could be obtained along a rearing cycle of 50 days when proper
609 feeding and management practices are employed [96].

610 Rearing *C. gariepinus* under intensive hatchery conditions generally lasts from 12 to 14
611 days at 28°C, which is considered as the optimal growth temperature for this catfish species.
612 After the onset of exogenous feeding (3 dph at 28°C), different types of live prey (*Artemia*
613 nauplii and metanauplii, *Daphnia* sp., *Moina* sp., or other zooplanktonic species of suitable
614 size) can be used for first-feeding larvae during the first week in hatcheries [91]. The earliest
615 weaning time to maximise growth rate of *C. gariepinus* larvae was after 4 days of feeding
616 with *Artemia*, when larvae weighed *ca.* 18 mg BW at 27.5°C, although weaning may be
617 achieved at 7.1 mg BW without any effect on the survival rate [97]. Among different weaning
618 strategies, the most commonly used protocols are summarised in Table 4. After 12–14 days,
619 early juveniles are stocked into nursery ponds at densities ranging from 65 to 2,000 specimens
620 m^{-2} (100,104). Under pond-farming conditions, it is recommended to feed the fry at 25% BW

per day (divided in three meals), using a 38–40% protein diet [100]. If the larvae and early juveniles are reared in tanks, the feed should have a protein content of around 50%. The nursery period ends when fries reach 1–2 g BW and are ready to be stocked into ponds or tanks for the on-growing phase.

Ictalurus punctatus

The aquaculture of *I. punctatus* was developed at state and federal fish hatcheries of the USA during the 1950s for stocking reservoirs and sport fishing ponds. Many of the techniques developed at those hatcheries are still used to produce fry and fingerlings for large-scale commercial culture [106]. Larvae of *I. puncatus* are generally obtained by natural spawning of broodfish in ponds when egg masses are adhered to artificially made cavities. Spawning can also be induced by hormonal treatments when needed [107]. Then, egg masses are transported to the hatchery where they are incubated using well or surface water in rectangular troughs at 25ºC to 28ºC. Hatching normally occurs after 6 days of incubation [108].

Similar to *R. quelen*, larvae of *I. punctatus* at the onset of exogenous feeding (13–14 mm TL) present an external and internal anatomy similar to that of adult channel catfish, except for the reproductive system [68]. After hatching, *I. punctatus* fries are typically kept indoors under hatchery conditions (*i.e.*, good quality water supply, controlled rearing conditions, etc.) up to 8 days. During this period, fries are kept in rectangular troughs (2–4 m long) at a density of 150,000 to 200,000 fries per trough (45 specimens mL^{-1}) [106] (Table 5).

To reduce operational costs (*i.e.*, labour and feed), some hatcheries may stock yolk-sac fries at 2 dph (14.4–18.8 mg BW) in nursery ponds, before the onset of exogenous feeding. However, this practice results in reduced fingerling survival rates because of the reduced mobility of yolk-sac fries compared with that of older specimens. Moreover, yolk-sac fries are highly vulnerable to predators (i.e., aquatic insects, sunfish, and congeners not removed

from previous harvests). In contrast, stocking *I. punctatus* at the onset of exogenous feeding or at 7 dph (22.8–29.1 mg BW) was shown to result in no deleterious effects on fingerling production [106,109]. Regardless of the chosen age for fry stocking into nursery ponds, these should be fertilised to ensure that adequate levels of feed are available. Zooplankton populations are important in *I. punctatus* fry culture during the first 3–4 weeks, but their importance diminishes as fish grow and are able to forage compound diets. Thus, the main goal of fertilising fry ponds is to promote zooplankton growth while establishing a phytoplankton bloom as quickly as possible to shade the pond bottom and prevent aquatic plant growth between 3 and 4 weeks before stocking fish. Fries prefer large cladocerans (e.g., *Daphnia* sp.*, Moina* sp., *Sida* sp.) to all other zooplanktonic organisms like small cladocerans, copepods, and rotifers [110]. Thus, emphasis should be placed on fertilisation strategies that increase cladoceran density; recommendations for fertilisation of channel catfish nursery ponds may vary widely [111]. Regardless of the fertilisation strategy adopted, the recommendation is to use high-nitrogen fertilisers rather than high phosphorous fertilisers. Particularly, it is advisable to apply only inorganic fertiliser at an initial rate of *ca.* 20 kg N ha^{-1} and 2 kg P ha^{-1}, followed by subsequent applications of 10 kg N ha^{-1} and 1 kg P ha^{-1} twice a week for 3–4 weeks or until fries are stocked and commercial diets are administered. The use of high-nitrogen fertilisers (i.e., the least expensive source of N available or urea if costs are similar) results in shifting phytoplankton population to desirable algal groups, as well as preventing macrophyte growth, promoting the growth of zooplanktonic organisms of large size. After a few weeks, fries fed a combination of zooplankton and starter feeds will have grown to fingerlings of 2.5 to 5 cm TL.

Regarding feeding practices, under common rearing conditions (26–28°C), yolk resorption is completed at 4–5 dph, when the onset of exogenous feeding occurs. The digestive system in *I. punctatus* fries is complete and functional at the onset of exogenous feeding. Thus, at 4–5

671 dph, this species is able to ingest and efficiently digest compound feeds (i.e., starter diets). At
672 first feeding, *I. punctatus* fries are fed a compound diet (45–50% crude protein) at a ratio of
673 25% stocked biomass (SB) (8–10 meals per day) until they are reared in nursery ponds.
674 Salmon and trout starter feeds may be used [106]; however, currently several starter feeds
675 especially formulated for *I. punctatus* fries are available. These starter diets are considered
676 nutritionally complete and may be used for 2 to 10 days before fish are stocked into grow-out
677 nursery ponds [112]; however, a number of dietary supplements might be used for partially
678 replacing traditional starter diets to increase fish growth rates and produce larger fries with
679 greater chances of surviving the critical transition from hatchery to nursery ponds. For
680 instance, Weirich *et al.* [113] recommended supplementing starter feeds with *Artemia*
681 decapsulated cysts (ADC), a feeding strategy previously tested in *C. gariepinus* [99]. Although
682 the particle size of ADC (200–250 μm) [99] is smaller than that recommended for *I. punctatus*
683 fries (420–560 μm) [114], feeding first-feeding fries for 10 days with a starter diet supplemented
684 with ADC promoted higher growth rates than those fed with just the compound feed.
685 Particularly, fries fed ADC were 61–98% heavier than their congeners fed the starter diet.
686 Traditionally, channel catfish farmers have used krill-based products as a dietary supplement
687 because of the well-balanced amino acid and fatty acid profile of such products; they contain
688 high levels of n-3 polyunsaturated fatty acids (PUFAs) including docosahexaenoic acid
689 (DHA) and eicosapentaenoic acid (EPA). However, feeding *I. punctatus* fries with krill-based
690 supplemented diets, contrary to what was traditionally thought, did not increase the growth or
691 survival rates of fries [109]. Zooplankton may also serve as a sustainable and reliable supplement
692 during *I. punctatus* hatchery production [115]. However, fries fed live or dried zooplankton
693 (copepods, cladocerans, and ostracods) performed worse in terms of somatic growth than fries
694 fed only a compound starter diet (Finfish Starter; Ziegler Brother, USA) or a combination of
695 the commercial diet with zooplankton. Although zooplankton from nursery ponds contain

65% crude protein and 9% fat [116], the dietary energy–protein ratio (digestible energy) of zooplankton may be too low for fry optimal growth when zooplankton is the only food source, and it is recommended to provide it in combination with compound diets [115]. In particular, fries fed dry zooplankton or live zooplankton combined with the commercial diet were 40% (292 mg BW) and 50% (312 mg BW) heavier, respectively, than fish fed only the commercial diet (209 mg BW). These results may be attributed to either an enhanced ingestion and digestion of feeds or the presence of micronutrients or trace elements in zooplanktonic organisms [117].

Pseudoplatystoma spp.

Pseudoplatystoma spp. larvae are obtained by hormonally induced spawning (26); after fertilisation, spawned eggs are generally incubated in cylindroconical tanks connected to a freshwater recirculating system [118]. In *Pseudoplatystoma* spp. and their interspecific and intergeneric hybrids, hatching occurs between 13 and 18 hpf in temperatures ranging from 26°C to 29°C, whereas the onset of exogenous feeding occurs at 2–3 dph (4.5–6 mm TL) [119-122]. *Pseudoplatystoma* spp. and interspecific hybrids are reared similarly. Larvae are fed *Artemia* nauplii during the first 7 to 10 days until they develop skin pigmentation [123,124]. Feeding ratios consist of 500 *Artemia* nauplii per larva per day during the first 5 days, and 1,000 nauplii per larva per day from day 6 to 10, divided in 6 to 10 rations distributed along 24 h [26,123]. In addition to *Artemia* nauplii, larvae can also be fed rotifers and egg yolk [26]. In experimental conditions, *P. punctifer* larvae have been successfully fed five times a day (only during daytime) with *Artemia* nauplii in slight excess from 4 to 12 days post fertilisation (0.6–9 nauplii mL^{-1}) [119]. Larvae may be also reared in complete darkness and kept in the incubation tanks up to 12 days [26] or transferred to rectangular or circular tanks, generally connected to a freshwater recirculating system, at 2–3 dph when they start swimming horizontally [123]. During

this phase, 15 larvae L^{-1} has been suggested as the best rearing density [120], although higher densities such as 30, 40, and 50 larvae L^{-1} have been successfully used in experimental conditions [119,125,126]. After this initial period when body pigmentation is developed, larvae can be reared indistinctly in tanks connected to a recirculating system or in outdoor fertilised ponds, a choice that depends on available facilities (Table 5) [26,123,124].

In recirculating systems, larvae are reared in darkness at a density of 5,000 to 10,000 larvae m^{-3} and fed naturally produced zooplankton (cladocerans and copepods) that are collected from fertilised ponds [26,120,123,124]. Larvae can be additionally fed minced fish or meat [26]. The transition from *Artemia* sp. to cladocerans and copepods is made in 10 days or more [123]. Fingerlings are fed at least eight times a day (including night-time) for 30 to 40 days until they reach 4 cm to 5 cm TL, and are continuously graded by size to avoid cannibalism [26].

Alternatively, larvae can be reared in fertilised ponds at a density of 100 to 150 larvae m^{-2} [26,124]. Before the transfer of larvae, ponds are sun-dried for 3 to 5 days to reduce the presence of predators and then limed. One week after liming, ponds can be fertilised with 0.1 kg m^{-2} rice bran and 0.01 kg m^{-2} urea or bovine (0.5 kg m^{-2}) or poultry (0.12 kg m^{-2}) manure with ammonium sulphate (0.02–0.05 kg m^{-2}) and single superphosphate (0.01-0.02 kg m^{-2}). The start of the zooplankton production takes 3 to 5 days, depending on temperature and sunlight [123]. Next, larvae are stocked into ponds during the first zooplankton bloom, and cladocerans are the optimal food at this period [26]. Phytoplankton blooms and the zooplankton production are regularly evaluated, and new fertilisations are undertaken if necessary. Ponds can also be stocked with forage fish larvae such as *Prochilodus lineatus*, *Leporinus* sp., or *Piaractus* sp. (forage fish to *Pseudoplatystoma* spp. larvae proportion 10:1) [26,123]. After 30 days, 4 cm to 5 cm TL fingerlings are harvested, preferably at night. Survival during this period is highly variable, depending on zooplankton abundance, weather conditions, or insect predation [26].

745 *Pseudoplatystoma* spp. fingerlings, 4 to 5 cm TL, are transferred to self-cleaning tanks with
746 constant water renewal at a density of 1,500 to 6,000 juveniles m^{-3}, depending on the capacity
747 of the system [26]; here, fingerlings are kept until they are sold for on-growing purposes (11–13
748 cm TL). Live feed is gradually eliminated, and fingerlings are progressively weaned over a
749 period of 4 to 6 weeks onto formulated diets. These diets are based on moist feeds, including
750 ingredients such as sardines, beef heart and lungs, frozen plankton, or minced fish gonads
751 [26,123]. During this period, fingerlings continue to be periodically graded by size to reduce
752 cannibalism. However, proper nutrition during early life stages is key to reduce the incidence
753 of cannibalism and to significantly advance weaning [119]. Fernández-Méndez *et al.* [126] weaned
754 *P. punctifer* at 18 dph within 3 and 6 days using moist and dry compound diets, respectively.
755 The use of moist feeds resulted in better growth and survival, which may be linked to the taste
756 and smell associated with the attractants released. In another study, *P. punctifer* larvae were
757 successfully weaned at 12 dph from *A. nauplii* onto compound feed (45% proteins, including
758 protein hydrolysate, and 15% lipids, rich in phospholipids) within 3 days [119], increasing
759 survival and growth 2- and 6-fold, respectively, compared with *P. punctifer* larvae fed
760 following preceding protocols under similar rearing conditions [59]. Indeed, as the digestive
761 system of *P. punctifer* is completely functional at 9 dph (10.9 ± 0.18 mm TL), this species can
762 be weaned at least from 9 dph onwards [59,74,75]. Moreover, recent nutritional studies with this
763 species have accomplished weaning at 4 dph (Diana Castro-Ruiz, unpublished data), showing
764 that significant advances in larviculture are possible using feeding protocols adapted to the
765 digestive capacities and nutritional needs of this species during development. Nevertheless,
766 the rather long procedures to achieve weaning used in commercial farming of
767 *Pseudoplatystoma* spp. or their interspecific hybrids have encouraged producers to
768 increasingly focus on intergeneric hybrids that readily accept formulated feeds, are
769 omnivorous, and show lower cannibalism rates (Supplementary file 2), thus reducing

770 production costs and having high productivity [27]. However, even if their commercial
771 production has rapidly increased, scientific data on the early culture of these hybrids are
772 currently scarce.
773
774 *Heteropneustes fossilis*
775 Larvae of *H. fossilis* are either collected from the wild or are produced by artificial breeding
776 (hormonally-induced spawning of sexually mature fish) in hatcheries. After fertilization, eggs
777 are generally incubated in fibre-reinforced plastic (FRP) tray incubators at 26-30°C in an
778 open-flow water system for 2 days [60,127]. The onset of exogenous feeding takes place at 2 dph
779 at 29°C to 30°C when larvae measure 2.7-3.3 mm TL [60]. Newly hatched larvae are generally
780 reared in indoor tanks (FRP or concrete) for an initial period of 10–12 days. When indoor
781 tanks are used, larvae are stocked at a density of 3,000 to 5,000 larvae m^{-2} and fed 4–6 times
782 a day with zooplankton (small rotifers and ciliates), *Artemia* nauplii, and egg custard (Table
783 6). After 12 days at 25–30°C, larvae measure 10–12 mm TL [128] and are transferred either to
784 outdoor rearing tanks (*ca*. 2,000 L) or to small earthen ponds (50 m^2). Before larval stocking,
785 outdoor tanks are provided with a 5–8-cm-thick layer of soil on the bottom and filled with
786 water up to 25- to 30-cm height. Thereafter, the tanks are fertilised with superphosphate (*ca*.
787 100 g) and filtered bovine manure suspension (*ca.* 2 kg) for promoting zooplankton growth
788 for a week. Then, larvae are stocked at 200 larvae m^{-2} and fed *ad libitum* with *Tubifex* sp.,
789 finely ground trash fish, rice bran, and chopped mollusc meat. Within a rearing period of one
790 month, early juveniles reach 4–5 cm TL, when they are ready for stocking in grow-out ponds
791 [129]. In earthen ponds, 12-dph larvae are stocked at 300–500 larvae per m^2. Ponds are prepared
792 in advance for guaranteeing abundant zooplankton in order to promote larval survival [130].
793 Ponds are generally emptied, aquatic vegetation removed, and the soil exposed to sunlight for
794 15 days. Then, lime (300–1,500 kg ha^{-1}) is applied, and the pond filled with ground water.

After 5 or 6 days, ponds are fertilised with bovine manure (10,000 kg ha^{-1}), urea (300 kg ha^{-1}), and superphosphate (150–250 kg ha^{-1}) [131], although these quantities may vary according to local practices [132].

Regarding foraging behaviour, larvae can feed voraciously on zooplanktonic organisms and show preference for benthonic or substratum-associated prey such as ciliates, rotifers, copepod nauplii, small cladocerans, and ostracods [133,134]. In addition to zooplankton, larvae can feed on any kind of compound feed [133]. Larvae are also provided with supplementary feeds consisting of powdered rice bran, mustard oil cake, or granulated egg yolk [135]. Other authors recommend feeding *H. fossilis* larvae at a ratio of 5–10% BW with either finely minced trash fish and mollusc meat and rice bran (1:1) or a mixture of fishmeal, rice bran, groundnut oilcake/mustard oilcake, soybean, and wheat flour (2:2:3:1:2) [131]. Early juveniles are reared for 30–40 days in nursery ponds before they are stocked in grow-out ponds.

Different studies have been conducted to evauate better weaning strategy for *H. fossilis*, approaches that varied depending on the level of aquaculture development and geographic area considered. In India, Kumar *et al*. [136] evaluated different food items and their combination for first feeding at 2 dph to 22 dph (water temperature: 28.0–29.1°C; feeding rate: at apparent satiation and food distributed at 08:00, 12:00 and 16:00 h). Particularly, the following diets administered throughout the study were evaluated: 1) *Artemia* nauplii, 2) mixed pond-produced zooplankton (copepods and cladocerans), and 3) a commercial microdiet (Micro Elite 50, LuckyStar®, Singapore). In addition, the following dietary regimens were also tested: 4) non-enriched *Artemia* nauplii (2–8 dph), zooplankton (6–12 dph), and the microdiet (10–22 dph); 5) zooplankton (2–7 dph) and the microdiet (5–22 dph); and 6) zooplankton (2–12 dph) and the microdiet (9–22 dph). At the end of the trial, larvae fed with live feed showed better performance in terms of growth and survival, whereas no differences were observed in the development of the digestive system among the different dietary regimes. Therefore, it is

820 feasible to rear stinging catfish larvae without *Artemia* nauplii, and larvae may be weaned
821 onto microdiets after 7 dph, as survival was the highest after this age (>65.6%; survival rate
822 of larvae only fed the microdiet was 41.1%). Similarly, another study in Bangladesh evaluated
823 different diets containing powdered milk, hen egg, boiled potato, and raw fish muscle (basal
824 diet), and only differing in the inclusion of fish skin, viscera, and bones (rearing conditions:
825 26–29°C, 0.4–0.7 larvae L^{-1}, and feeding ratio: 10% SB) [137]. These authors found that first-
826 feeding larvae (5.8 mm TL; 4 dph) fed a basal diet containing powdered milk, egg and boiled
827 potatoes supplemented with boiled fish with skin, viscera and bones showed the best results
828 in terms of growth (12.6 mm TL) and survival (60%) in comparison with larvae fed the basal
829 diet incorporating just raw fish muscle with skin (12.0 mm TL; survival: 50%) and those fed
830 the basal diet with raw fish muscle without skin (11.5 mm TL; survival: 50%). In addition, a
831 study conducted in India focused on evaluating different food items (zooplankton, *Artemia*
832 nauplii, snail meat, fish meat, and rice bran) on larval performance (rearing conditions: 25°C,
833 20 larvae L^{-1}, feeding ratio: 20% SB) [131]. Similar to other catfish species, the best results in
834 terms of growth were found in larvae fed wild zooplankton (37 mg BW) followed by *Artemia*
835 nauplii (*ca.* 24 mg BW), whereas other feed types resulted in low growth performance (snail
836 meat: *ca.* 19 mg BW; fish meat: *ca.* 15 mg BW; rice bran: *ca*. 4 mg BW). However, this study
837 did not include results on survival rates or the analysis of the proximate composition of the
838 evaluated food items. In another study, *H. fossilis* larvae were fed with a mixture of
839 zooplankton, egg custard, and *Artemia* nauplii for two weeks at 26–28°C. At the end of larval
840 rearing in a circular cement cistern (2 m diameter), survival rate was 70% and larvae reached
841 10–20 mm TL [138].

842 *Heteropneustes fossilis* larvae can feed in darkness, showing prey selectivity patterns
843 similar to those exhibited under light conditions because of the involvement of
844 mechanoreception and chemoreception in prey detection [134]. This is not relevant when *H.*

fossilis larvae are reared in ponds, where there is generally no limitation in zooplankton availability; in contrast, when rearing *H. fossilis* larvae in tanks, special attention is needed to guarantee the presence of live prey at night time.

Rhamdia quelen

Although *R. quelen* can naturally spawn in captivity, hormonal induction is commonly used. Fertilized eggs are preferably incubated in Zoug-type incubators in continuous aerated freshwater flow [139]. Depending on water temperature, hatching takes place between 19 and 43 hpf at incubating temperatures of 30 ºC and 21ºC, respectively. Successful embryonic and larval development was found at different temperatures ranging from 21ºC to 30ºC, although some malformations (heart oedema) were found at 30ºC. According to these authors, the optimal water temperature for egg incubation is 26ºC, whereas larval size at hatching is inversely correlated to water temperature, even though this pattern is reversed after hatching. Fish size at hatching changes depending on the study with values ranging from 2.8 to 4.9 mm TL [62,140]. Such variability has been correlated to differences in spawning season, egg size and broodstock nutrition [141,142].

Silver catfish early culture can be conducted in indoor facilities under controlled conditions (intensive) for three weeks or, alternatively, directly in earthen ponds from the onset of exogenous feeding (2 dph) or after a short period of indoor culture (Table 6) [139,143]. In the latter case, according to Baldisserotto *et al*. [39], results are quite satisfactory, even better than those obtained in indoor tanks with clear water. Although the nursery stage for this species begins with fish weighting 1–3 g, it has been suggested to prolong the hatchery period until reaching a size of 5–6 g to improve survival rates [144]. Regardless of the rearing strategy chosen, recommended values of water pH and dissolved oxygen for silver catfish early culture

869 are 8.0–8.5 [145] and 6–8 mg O_2 L^{-1}, respectively [139]. Additionally, larval rearing of *R. quelen*
870 may be conducted in slightly brackish waters (up to 2 g NaCl L^{-1}) using feeding rates of 700
871 *Artemia* nauplii per larva and day [146].

872 Similar to other catfish species cultured in ponds, early culture of *R. quelen* in ponds
873 requires their careful preparation to assure the availability of live preys in adequate quantities.
874 In this context, the most common prey found in the stomach of *R. quelen* fry reared in
875 experimental fertilised ponds were ostracods, chironomid larvae, cladocerans, and calanoid
876 and cyclopoid copepods, whereas smaller prey such as rotifers and copepod nauplii were
877 seldom found [147]. If benthic prey become scarce, larvae may consume a higher proportion of
878 planktonic prey [148]. Before the introduction of fish, the ponds must be drained, limed, fertilised
879 (2,000 kg organic fertiliser ha^{-1}), and filled with filtered water (50–60 cm depth) 5 or 6 days
880 before the fish transfer [149,150]. Under pond rearing conditions, insects (Odonata, Hemiptera,
881 and Coleoptera) can prey on small *R. quelen* fries. The use of sieves or filtering nets in water
882 inlets is crucial to avoid the entrance of these predators [149]. Concerning the duration of the
883 period of intensive rearing before their transfer to ponds, Agüero *et al*. [151] recommend rearing
884 larvae indoors up to 8–10 dph (4.8 mg BW) (rearing conditions: 25.9°C; 25 larvae L^{-1}; feeding
885 larvae four times a day with an experimental dry diet) rather than directly stocking them at the
886 onset of exogenous feeding at 2 dph or at older ages (5 or 15 dph; 1.68 and 15.29 mg BW,
887 respectively). Santinón *et al*. [152] recommend transferring early juveniles to cages at 10 dph to
888 reduce feeding and operating costs. The authors verified that fish performed similarly after 65
889 days in net cages when transferring indoor reared larvae fed different experimental dry diets
890 (35% fish roe, fish silage or raw chicken liver) to outdoor net cages at the age of 10 dph (11.3–
891 26.7 mg BW) or 15 dph (23.5–115.1 mg BW, depending on the diet tested). Moreover, the
892 longer the period of indoor intensive culture, the higher the risks associated with the

appearance of pathologies or skeletal deformities [151,152]. These results might be attributed to a lack of standardised rearing protocols and knowledge gaps on larval nutritional requirements in this species [153].

In ponds, stocking density can reach 200 specimens m^{-2}, although this value should be adjusted according to the food availability and the need of food supplementation. This can be achieved using commercial feeds (≥40% protein) dispersed on the surface or placed on trays that are then submerged *ca.* 15 cm from the bottom of the pond [149]. According to different experimental studies, survival rates of 20–30% may be achieved after 40–45 days of rearing in ponds at temperatures 23–26°C when supplementary food was offered (*I. punctatus* compound feed or commercial dry food >28% crude protein) [151,154]. During this period, *R. quelen* can grow to 3.2–3.3 g BW (*ca.* 6 cm TL). A common practice in ponds is the use of lime to increase water hardness or pH. However, lime may contain different Ca^{2+} and Mg^{2+} ratios that may substantially vary among ponds, directly affecting fish performance and the regulation of their hydromineral balance. In this regard, water hardness affects silver catfish performance [155,156]. In particular, when early juveniles were reared from first feeding during three weeks in water containing 30 and 70 mg $CaCO_3$ L^{-1}, they grew (11.8 and 12.3 mm TL, respectively) and survived (80.4% and 62.0%, respectively) better than at ≥150 mg $CaCO_3$ L^{-1} (<10 mm TL, <9% survival) (156). Different levels of Ca^{2+} and Mg^{2+} were also studied by Silva *et al*. [155]. The best survival (94.1–92.5%) and growth rates (19.6–18.7 mm TL) were observed with 5.2 mg Ca^{2+} L^{-1} and 0.95 mg Mg^{2+} L^{-1} (water hardness: 20 mg $CaCO_3$ L^{-1}) and 20.3 mg Ca^{2+} L^{-1} and 2. 9 mg Mg^{2+} L^{-1} (water hardness: 70 mg $CaCO_3$ L^{-1}) compared with 150 mg $CaCO_3$ L^{-1}, regardless of Ca^{2+} and Mg^{2+} concentrations.

Biofloc technology has also been experimentally tested for *R. quelen* early culture [41]. These authors tested different biofloc concentrations (as total suspended solids, TSS) obtained from

917 an intensive culture of tilapia (*Oreochromis niloticus*) in small experimental units
918 (microcosms) where *R. quelen* larvae (2 dph) were fed exclusively on *Artemia* nauplii. After
919 21 days of culture, survival rates (38.1–54.4%) were significantly higher in all biofloc
920 treatments than in the control group (10.2%), which was negatively affected by the protozoan
921 *Ichthyophthirius multifiliis*. These results were attributed to the probiotic effect of the biofloc
922 community. The best growth performance (21.1 mm TL; 88.6 mg BW) was obtained with
923 TSS concentrations of 150–200 mg L^{-1} compared with higher TSS concentrations (400–600
924 or 800–1,000 mg L^{-1}) (16.2 and 15.9 mm TL; 45.7 and 44.5 mg BW; respectively) [41].
925 Intensive indoor early culture of silver catfish can be conducted under controlled conditions
926 in tanks, using clear water, controlled water temperature (21–26°C) [157], and protection from
927 predators. In these systems, cannibalism was observed from first feeding at 2 dph and became
928 more frequent after 6 dph. As cannibalism was more prominent when fish were stocked at low
929 densities, a stocking density of 10 specimens L^{-1} is recommended [139]. Although *R. quelen* can
930 be fed exclusively on dry formulated diets from the onset of exogenous feeding, the best
931 growth and survival rates are usually obtained by feeding larvae live prey (*Artemia* nauplii or
932 collected zooplankton) alone or in combination with commercial or experimental dry feeds
933 (45-56% crude protein, 10-18% crude lipid, <6% fibre, and <14% ash) [158-160]. In addition,
934 other authors have shown that ADC were less effective than *Artemia* nauplii [161].
935 Comparatively, Luchini and Avendaño-Salas [154] found that rearing silver catfish larvae for 10
936 days using *Artemia* nauplii or a filtered mixture of cooked egg custard resulted in similar
937 survival rates (76–82%), but *R. quelen* fed the egg custard grew better than those fed only
938 *Artemia* (1.1 vs. 0.8 cm TL). When comparing live prey (*Artemia* nauplii, cysts or
939 metanauplii) with dry diets (experimental diets based on yeast and raw bovine liver, and
940 commercial diets such as Bio-Camaronina® or Anhami®; Anhami Nutrição Animal, PR,
941 Brazil), these always performed worse than live preys alone [158,161,162], even if fish were fed for

the first five days with *Artemia* nauplii before weaning onto a dry diet [140]. However, Hernández *et al*. [163], comparing larval performance of two *R. quelen* biotypes from Argentina, one from the Pampean area (PA), and another from the North-eastern area (NE)—two lines from different geographical origin presenting different morphological and productive particularities [164] — reported that fish grew equally when fed live *Artemia* nauplii for 21 days from the onset of exogenous feeding or a dry formulated diet based on baker's yeast, fish meal and 2% soybean lecithin (53% protein). However, specimens from the PA showed the highest survival rates (>90%), producing the highest final biomass when fed on the dry diet. In this study, the NE biotype was more affected by skeletal deformities when fish were fed the dry diet in comparison to the PA biotype. These authors concluded that both biotic and abiotic factors (biotype and diet) must be considered when rearing *R. quelen* at early life stages in terms of skeletal development and quality. Growth and survival may be improved by co-feeding *R. quelen* fries with compound microdiets (>45% crude protein, >10% crude lipid, <6% fibre, and <14% ash) and *Artemia* nauplii [158,160]. Regarding the weaning time, Behr *et al.* [161] found similar results when feeding the silver catfish *Artemia* for 3 or 7 days before weaning. The best results in terms of weaning were achieved when fry were fed *Artemia* nauplii for 15 days before weaning, whereas the extension of this period to 20 days did not improve performance [165]. Comparing feeding frequencies, Lazzari *et al*. [166] did not find significant differences by feeding fries for 21 days on a dry diet hourly or every two hours. However, testing lower but larger ranges of feeding frequencies on fries fed a dry diet supplemented with *Artemia* nauplii, concluded that growth can be improved by feeding them three to seven times a day compared with feeding twice a day [167]. Besides, since no significant differences were found by increasing feeding frequency from three to seven times, the authors recommend feeding *R. quelen* three times a day, thus avoiding increasing production costs. Low light intensity (1.2 lx) is beneficial for silver catfish early culture fed live food during the

967 first week before weaning to a dry diet [168]. Improved larval specific growth rate (SGR)
968 obtained under these conditions compared to 17 and 20 lx were in accordance with the
969 nocturnal habits of this species [169]. To summarise, under adequate controlled conditions, 80–
970 95% survival rates can be reached after 21 days of rearing. During this period, silver catfish
971 fries can grow from about 2 mg and 5 mm TL to 118 mg and 20 mm TL [139].

972

973 *Ompok bimaculatus*

974 Eggs of *O. bimaculatus* are obtained by hormonally-induced spawning of a mature female and
975 fertilized with the milt of a pool of males [61]. After fertilization, eggs are generally incubated
976 between 27°C and 30°C in concrete or FRP incubators with continuous water-flow for 3 days.
977 After hatching (23 ± 1 hpf), newly hatched larvae are kept in the incubators until the age of 3
978 dph. Larval rearing protocols for the butter catfish were summarised by Chakrabarti *et al.* [170].
979 In brief, *O. bimaculatus* larvae are generally reared in FRP tanks or cement cisterns for 40–
980 45 days at 27–30°C (Table 7). When larvae reach a fingerling size of 5.0–6.0 cm TL and 3.0–
981 4.5 g BW, they are then stocked in grow-out ponds. The mouth opens at 2 dph (3.3 mm TL),
982 and first feeding occurs at 3 dph (4.2 mm TL), when larvae are fed finely sieved zooplankton
983 (i.e., copepods, cladocerans) two times a day (early morning and evening). *Ompok*
984 *bimaculatus* larvae are, then, fed finely chopped *Tubifex* sp. worms (food ratio: 25% stocked
985 biomass, SB) from 7 dph (8–9 mm TL) until 15 dph. To avoid cannibalistic behaviour, grading
986 of larvae of different sizes is recommended, in addition to providing shelters and hiding places
987 when larvae are reared at 10 to 20 larvae L^{-1}. After 15 days, larvae are fed formulated diets
988 based on egg custard, fishmeal, and silkworm pupae powder (feed ratio: 3–5% SB; distributed
989 2–3 times a day). Additionally, some hatchery managers also fed larvae with boiled and finely
990 chopped chicken viscera or low-cost trash fish, or both. Other authors have reported feeding

991 larvae for 10 days at 27°C with wild zooplankton (no data on composition provided by
992 authors) and boiled egg yolk, resulting in 10.4% survival, whereas high mortality rates were
993 observed between 5 (10 mm TL) and 10 (25 mm TL) days associated with cannibalism and
994 the non-acceptance of food [171]. In another study, 3-dph larvae (2.3 ± 0.07 mm TL) were reared
995 in glass aquaria for 12 days with freshly hatched *Artemia* nauplii and wild zooplankton
996 (copepods, rotifers, and cladocerans). Both types of live prey were administered *ad libitum*
997 and twice a day (07:00 h and 16:00 h) [172]. Larvae of *O. bimaculatus* fed *Artemia* nauplii were
998 heavier than those fed live zooplankton (112 ± 8.1 vs. 94 ± 6.5 mg BW), and survival rates
999 were also higher (62.7 ± 5.2 vs. 47.3 ± 5.9%). After that period, fish were transferred to a
1000 cement cistern for 30 days and fed a mixture of rice bran, mustard oil cake, and dry fish powder
1001 (feed ratio not provided) daily. At the end of the study, fish were 7.5 cm TL, 5.5 g BW, and
1002 survival rate was 90%. Recent studies have focused on refining the feeding protocols for *O.*
1003 *bimaculatus.* In this context, first-fed larvae have been fed with a mixture of zooplankton [173]
1004 and at 7 dph (11 mm TL, 0.7 g BW) larvae were shifted to five different diets for a period of
1005 27 d (until 35 dph). The following diets were tested: 1) wild zooplankton, mainly composed
1006 of copepods, rotifers and cladocerans; 2) *Tubifex* sp. worms (64.8% crude protein, 14.0%
1007 crude fat, and 6.0% ash); 3) wild zooplankton + *Tubifex* sp.; 4) egg custards (whole, 2 g
1008 *Spirulina* sp. powder, 6 g corn flour, 4 g *Artemia* flakes, 2 g yeast, 6 g milk powder, and 10
1009 mL cod liver oil); and 5) compound feed (Gold Coin Biotechnologies, Singapore). At the trial,
1010 SGR values were higher in larvae fed a mixture of zooplankton and *Tubifex* sp. worms (SGR
1011 = 4.8 ± 0.6 % BW day^{-1}) than in larvae from the other treatments. Larvae fed *Tubifex* sp.
1012 worms (SGR = 4.1 ± 0.5 % BW day^{-1}) or wild zooplankton (SGR = 3.9 ± 0.1% BW day^{-1})
1013 showed intermediate values, and the lowest growth performance was found in larvae fed egg
1014 custards (SGR = 3.46 ± 0.31% BW day^{-1}) and the compound feed (SGR = 2.93 ± 0.24 % BW
1015 day^{-1}). A similar trend was observed when survival rates were considered; the highest survival

rates were recorded in larvae fed wild zooplankton + *Tubifex* sp. (66.50 ± 2.14%) and in those fed only *Tubifex* sp. (61.75 ± 2.02%), whereas the lowest, in fish fed the compound feed (45.8 ± 1.03%) (173). Similarly, Pradhan *et al.* [172] evaluated different weaning strategies based on the type of food (i.e., *Artemia* nauplii, wild zooplankton, and microdiet, Frippak Fresh CAR #1, INVE®, Dendermonde, Belgium) and co-feeding regimes on 2-dph larvae (3.3 ± 0.5 mm TL). In particular, diets were provided to apparent satiation four times a day (08:00, 12:00, 16:00, and 20:00 h). The authors concluded that weaning should not take place in *O. bimaculatus* earlier than at 7 dph (10.8 ± 0.1 mm TL). Moreover, larvae fed a co-feeding regime based on wild zooplankton or *Artemia* nauplii combined with the microdiet for 5 days showed good results in term of survival (65.0–78.7%) and growth performance (3.0–3.2 mm TL). In contrast, survival and size of larvae fed the compound diet from the onset of exogenous feeding were 48.7% and 2.6 ± 0.6 cm TL, respectively. In addition, early weaning of *O. bimaculatus* resulted in the delay of gut and pancreas development, impairing digestion and nutrient absorption, and ultimately, affecting larval performance. However, these results need to be considered with caution as the tested compound diet was formulated for larval and post-larval penaeid shrimps and not for freshwater fish larvae. In this context, it remains uncertain whether the nutritional requirements of *O. bimaculatus* larvae were met. For instance, Biswas *et al*. [174] fed weaned *O. bimaculatus* specimens for 30 days with five purified diets (49% crude protein and 8.2% crude fat) containing 2% of different attractants (betaine, DL-alanine, L-tryptophan, and inosine monophosphate) and found that dietary L-tryptophan and betadine promoted fry survival (48.7 and 41.3%, respectively) in comparison with the control diet (33%). The increase in survival in *O. bimaculatus* fed the diet containing 2% L-tryptophan was associated with a reduction in aggressive and cannibalistic behaviour among conspecifics. Regarding growth, the highest size was observed in the group fed the diet supplemented with 2% ionosine monophosphate (3.1 ± 0.05 cm TL) in comparison with the control group (2.8 ±

0.02 cm TL). These results may be attributed to the promotion of gut development due to dietary nucleotides. Weaning *O. bimaculatus* larvae (15 dph, 2.1 ± 0.1 cm TL) fed compound diets (49.8% protein, 8.2% lipid, 4.2% fibre, and 8.4% ash) supplemented with freeze-dried *Tubifex* sp. at 5% of stocked biomass resulted in higher survival rates when compared with those of the control group (43% vs. 28%), which was due to the presence of L-tryptophan in *Tubifex* sp. Regardless of the results from the above-mentioned studies, there is an urgent need of formulating specific compound diets for *O. bimaculatus* to promote high survival rates, growth, and larval quality.

Lophiosilurus alexandri

Early culture of *L. alexandri* in Brazil is mainly conducted under intensive conditions. Larvae are obtained from natural spawning in tanks with sand in the bottom, where fertilized eggs adhere [175]. Egg masses are collected and incubated in a box (40-150 L of functional volume) with aeration and an internal biological filter. The eggs are generally maintained in a 25-cm diameter sieve (0.5 mm mesh) fixed to floats, and hatching occurs between 24 and 48 h at 27-28°C [175,176]. Intensive culture of *L. alexandri* produces larvae during several months of the year, as spawning naturally occurs during 5 to 6 months.

The onset of exogenous feeding in *L. alexandri* occurs between 7 and 9 dph (12.0–15.5 mm TL) at 26–28°C. *Lophiosilurus alexandri* early culture is successfully performed in fresh water with *Artemia* nauplii (Table 7) [49,53,177,178,179]. However, the use of NaCl in the water is an interesting management technique during the initial phases of *L. alexandri* larviculture. In particular, larvae exhibit a $CL_{50–96h}$ of 8.9 g NaCl L^{-1} at 8 dph and tolerate up to 10 g NaCl L^{-1} at 12 dph (four days after first feeding) (14.1–15.5 mm TL) [180]. NaCl in the water increases *Artemia* nauplii survival, influences larvae physiology, and prevents sanitary problems, such as the occurrence of the protozoan *I. multifiliis*. Thus, larviculture of *L. alexandri* can be

conducted in slightly brackish waters (up to 2 g NaCl L^{-1}) at stocking densities of 20 to 60 larvae L^{-1} using *Artemia* nauplii as food [181]. The authors reported that survival reached 100% when using a density of 20 larvae L^{-1} and salinity of 2 g NaCl L^{-1}; survival was 93% when fresh water was used. However, SGR values were reduced when using a rearing density of 60 larvae L^{-1} and 4 g NaCl L^{-1}. These results [181] and those of Santos & Luz [50] indicate that rearing of *L. alexandri* larvae should be conducted at lower salinities of 4 g NaCl L^{-1}. A recent study using water with low salinity (2 g NaCl L^{-1}) under water recirculation conditions have shown that is feasible to rear *L. alexandri* larvae fed *Artemia* nauplii at densities ranging from 60 to 300 larvae L^{-1} without affecting growth performance (23–24 mm TL) or survival (>95%) after 15 days of trial [48]. From this perspective, it is important to highlight that this is the first study on the larviculture of freshwater, carnivorous species, reporting such good results using the above-mentioned high stocking rearing densities. In addition, laboratory studies have shown that *Artemia* nauplii density (300, 600 or 900 nauplii $larva^{-1}$ day^{-1}) was directly correlated to larval growth in TL and BW [50]; the increase in prey densities was linked to an increase in the levels of nitrogen compounds in the water (1.7 mg L^{-1} of un-ionised ammonia), but without negative effects on larval performance.

Regarding the optimal larval rearing temperature, no differences in survival rates were found among larvae reared between 23°C and 32°C (>90% after 15 days of larval rearing) (Table 7). However, larvae reared at 29°C and 32°C showed the highest size (27.2 mm); no differences in BW were found among larvae reared temperatures >26°C. Regardless of the rearing temperature considered, larvae fed high live prey densities (700 vs. 1,300 nauplii $larva^{-1}$ day^{-1}) presented better growth rates than those fed low live prey densities [51]. Santos *et al.* [178] found that during the first 15 days of feeding, the optimal live prey density in terms of BW and SL were 1,600 and 1,000–1,600 *Artemia* nauplii $larva^{-1}$ day^{-1}, respectively. However, no differences in survival were found when testing live prey densities ranging from 100 to 1,600

nauplii larva^{-1} day^{-1}. Regarding feeding frequency, *L. alexandri* larvae can be fed *Artemia* nauplii two (at 8 and 17 h or at 8 and 12:30 h); three (at 8, 12:30 and 17 h); or four (at 8, 11, 14 and 17 h) times a day, without differences in performance and survival (>89%) [179]. Therefore, the final choice of feeding regimens will depend on the hatchery operators. Natural zooplankton [182,183] and the fairy shrimp (*Dendrocephalus brasiliensis*, Brachiopoda) [184] can also be used with positive outcomes. When wild zooplankton was offered to larvae stocked at densities of 150, 250 and 500 larvae per channel (0.43 m^2) in a continuous flow system for 20 days, only survival was affected. Thus, survival in *L. alexandri* was inversely related to larval densities (lower densities, 60%; higher densities, 37%). These results were mainly associated with an increase in cannibalism [183]. In contrast, cannibalistic behaviour was not reported in larvae stocked at 300 larvae L^{-1} when fed *Artemia* [48].

Lophiosilurus alexandri is generally weaned after 15 days using *Artemia* nauplii as live food in specimens with more than 20 mm TL at 27°C and 28.7°C. The transition to compound diets for early juveniles described by Luz *et al*. [53] is summarised in Table 8 (73% survival at the end of this period). Instead of using bovine heart, some authors have successfully used commercial gelatine powder (Gelita®, Eberbach, Germany) [185]. In addition, salinity values of 4 g NaCl L^{-1} during this step should be avoided, as it reduces larval survival. Stocking density should also be considered during this period. When weaning was performed at 5, 10, 15, 30, and 40 fish L^{-1} (23.9 ± 1.2 mm TL and 0.12 ± 0.01 g BW) in recirculation aquaculture system (RAS), survival was lower than expected at high stocking densities (26% and 28% for densities of 30 and 40 fish L^{-1}, respectively), as a result of cannibalism. The highest survival rate (54%) was for the density of 5 juveniles L^{-1} [48].

Regarding larviculture in RAS, the use of different biofiltration systems (biofilters internal or external to breeding tanks) and substrates (gravel and calcareous shell) led to similar performance in terms of growth and survival [182]. The comparison of different water flow rates

(one, four, and eight changes of total tank volume h^{-1}) revealed that the highest flow of water tested impaired larval growth because of their intense swimming. However, lower flow rates (0.3, 1, 2, and 4 total changes in tank volume h^{-1}) in a continuous water exchange system did not affect survival (values ranging from 71 to 76%) or growth (<23 mm TL; Luz *et al*. 2011). Recently, Melillo-Filho *et al*. [49] tested two tank drainage systems in RAS, one with water exiting from the surface and another from the water column, and the authors concluded that water surface drainage increased BW and survival. These results were associated to the greater retention of *Artemia* nauplii in the water column, increasing their chance of being consumed by larvae. When evaluating the two above-mentioned drainage systems in RAS units during the weaning period (feeding rate: 100% SB), survival was 61% and 72%, respectively. However, the high feeding rates significantly reduced water quality, hindering daily operations. Thus, the authors recommended weaning fish (7 specimens L^{-1}) by feeding them three times a day (at 9, 13, and 17 h) at a daily feeding rate of 50% SB (survival rates: 56–67%). This feeding strategy in RAS contributed to reducing labour costs associated with tank cleaning and maintenance, and minimised water quality problems [52].

Nutritional requirements during early life stages

Proper knowledge of the nutritional requirements throughout early development is important to optimise diets and feeding protocols and, thereby, improve larval and juvenile quality. The provision of high-quality, palatable, nutritive, and well-balanced diets is essential for promoting the growth, health, and well-being of fish throughout their life cycle [117]. Feed quality is of special importance during the larval stage, as larval nutritional requirements differ both qualitatively and quantitatively from those of juveniles or adults, as fish undergo dramatic morphological and physiological changes that are coupled with high growth rates (i.e., SGR in *C. gariepinus* larvae range from 15 to 141% BW day^{-1}) [186,187]. Thus, larvae have

to feed continuously and digest efficiently to support high growth rates [117]. Such food (live prey or compound feeds) must adequately provide larvae all the necessary macro- and micronutrients to support growth and health. Furthermore, technical characteristics of compound larval feeds, e.g., particle size, buoyancy/density, shape, consistency, texture, and colour as well as feeding regimen, are fundamental factors to be considered for meeting the feeding requirements of fish larvae [93]. Despite that, there are extremely limited data on larval nutritional requirements of different catfish species. Gaps in knowledge and bottlenecks exist not only in the design and formulation of compound diets but also in the use of live food for catfish larvae. This lack of knowledge hinders, in varying degrees, the early culture of several catfish species.

Proteins and essential amino acids

The reviewed catfish species are generally fed live prey during early culture. This type of food is easily produced and widely considered a reliable source of adequate nutrients, thus supporting efficiently fish survival, growth, and health [188-191]. In the absence of knowledge about the nutritional requirements during early life stages, the composition of the live food can generally be used as the starting point for approaching and establishing the qualitative and quantitative nutritional requirements of larvae [117]. For instance, Bwala *et al*. [189] provided information on the proximate composition and amino acid profile of three different *Artemia* types used as food for *C. gariepinus* larvae [*Artemia nauplii* developing either oviparously (55.9% crude protein, 11% crude lipid) or ovoviviparously (41% crude protein, data on lipid content not provided) and ADC (54.0% crude protein)]. The authors found that feeding *C. gariepinus* larvae with oviparous nauplii resulted in higher survival and protein efficiency ratio. Interestingly, oviparous nauplii had the lowest protein levels among the food items. These results were attributed to the protein quality and its digestibility rather than to their

content levels [192], although other factors such as larval foraging behaviour may also have affected the performance of larvae fed decapsulated cysts. Larvae and early juveniles (*ca*. <5 g) of *C. gariepinus* larvae1 have a high protein demand of 50–55% and a lipid requirement of 9%, whereas dietary carbohydrate content may be as high as 21% [103]. Regarding *I. punctatus* fries, a dietary protein level of 52% and 48% for fries from 0.02 to 0.25 g and from 0.25 to 1.5 g BW, respectively, as well as 3,650 kcal kg^{-1} digestible energy [193]. Furthermore, Robinson *et al*. [194] verified that *I. punctatus* fries fed salmon or trout starter feeds (protein: 51.5% and 55.7%; lipid: 14.8% and 11.5%, respectively) showed 50–75% weight gain and better feed conversion than fish fed a catfish starter feed (49.2 protein and 10.2% lipids). In the same context, Kelly *et al.* [195] compared three isocaloric practical diets (45% or 50% protein), including 50, 65 or 75% menhaden meal, and reported no differences in growth performance of *I. punctatus* fries among experimental diets or in comparison with a commercial salmonid starter diet (55% protein). Finally, these authors suggested that it is feasible to reduce dietary protein to 45%, although recent studies recommend 48% protein and 9% lipids for first-feeding fries [196]. These protein requirements were higher than those reported by Degani *et al*. [197] for this species (40%), as well as for other catfish species. For instance, in *Clarias* sp. hybrids (*C. batrachus* ♀ × *C. gariepinus* ♂ and *C. macrocephalus* ♀× *C. gariepinus* ♂), larval protein requirements for maximal growth were estimated at 35–40% [198]. Regarding *P. punctifer,* individuals performed best when weaned with a diet containing 45% protein and 15% lipids [from 8 mg at weaning (12 mm TL) to 600 mg 14 days later (50 mm TL)] [78,119]. However, *P. hypophthalmus* fries (0.2 g) showed better growth, survival rate, and feed conversion ratio when fed a diet containing 25% protein (and 5% lipids); no significant growth advantage was observed by increasing the dietary protein levels above 25% [199]. Major reasons for these differences in varying dietary protein percentages are owing to species-specific

feeding habits, variation in fish sizes, level of non-protein energy in the diets, protein quality, water temperature, and amount of natural food available in ponds when these requirements were established under a co-feeding or weaning conditions.

Although the protein requirements in different catfish species have been explored in an uneven way depending on the species considered, there is limited information about their requirements in terms of dietary amino acids (AA). Most of the available information has been obtained from larval AA profiles and AA utilisation in *C. gariepinus* at different stages of development and fed different diets [200]. Nevertheless, there are no particular nutritional studies focused on evaluating the essential AA requirements in this group of species at early life stages. To our knowledge, the only exception is the study from Khan & Abidi [201], which reported that the histidine requirements in *C. gariepinus* were 0.40–0.42% dry diet, corresponding to 1.0–1.05% of dietary protein.

Lipids and polyunsaturated fatty acids (PUFA)

Compared to studies on proteins, there are fewer studies evaluating the lipid nutritional requirements in larvae from the reviewed catfish species, and most of the available literature deals with juveniles, which is out of the scope of the present review. The total lipid level as well as the content of polar and neutral lipids and their fatty acid profile are important components affecting larval performance [202]. Larvae of several catfish species are able to synthetize arachidonic acid (20:4 *n*-6) and docosahexaenoic acid (22:6 *n*-3) from their C18 fatty acid precursors e.g., *P. punctifer* [78], *I. punctatus* [202] and *C. gariepinus* [204].

Feed nutrient richness can affect larval performance. *Artemia* nauplii does not satisfy the nutritional needs of 11-dph larvae of *P. punctifer* (12 mm TL), which is when cannibalism begins, coinciding with the end of the larval stage [59,74]. Enriching *Artemia* nauplii with a commercial enriching product high in DHA (*ca*. 43% total fatty acids, TFA, Algamac 3050®

Aquafauna, Biomarine Inc., Hawthorne, CA, USA; ca. 4% TFA in enriched *Artemia*) from 3 to 14 dph did not have any effect on *P. punctifer* growth compared with non-enriched *Artemia*. However, larvae fed enriched *Artemia* presented less fat in the liver but similar lipid deposits in the intestine [205]. In the same context, *P. punctifer* early juveniles were fed enriched *Artemia* as described by Darias *et al*. [205] and weaned from 14 dph onto a compound diet (10% lipids, 38% proteins) showed improved growth and survival and a reduced incidence of cannibalism compared with those fed a non-enriched compound diet [206]. Moreover, early juvenile specimens fed both non-enriched *Artemia* and non-enriched compound diet showed a significant accumulation of lipids in the posterior intestine (steatosis) compared with that in the liver, contrary to specimens fed enriched-*Artemia* or enriched-compound diet. The latter presented similar amounts of lipids in both organs, indicating a more balanced digestive physiology [205]. Differences in dietary DHA/EPA and PUFA n-3/n-6 ratios between the two compound diets were responsible for differences in lipid accumulation. Furthermore, feeding *P. hypophthalmus* different dietary phospholipid levels (1, 2, 3 and 4%) revealed that increased dietary phospholipids is necessary for maintaining cellular membranes and even improving their normal physiological activities, supporting the idea that early life stages have higher nutritional requirements in phospholipids that juvenile stages due to their limited biosynthesis capacity [207].

Although the dietary lipid requirements have not been determined for *R. quelen* during early life stages, Salhi *et al.* [208] revealed that increasing lipid levels (8 vs. 14%) improved fish performance. These authors recommended a diet with 38% crude protein and 14% crude fat. Similarly, *P. punctifer* early juveniles weaned from 12 dph a compound diet with 45% protein and 15% lipid levels, including hydrolysed fishmeal and phospholipids, showed significantly higher TL, BW, SGR and survival, and lower incidence of cannibalism than specimens fed diets containing 45:10, 30:15 and 30:10 protein:lipid levels. Histological and enzymatic

analyses of the digestive system unveiled a more developed digestive function in individuals fed the 45:15 diet, which indicated that a more balanced diet for *P. punctifer* early juveniles promoted a faster digestive system development and a better growth [78], compared with other diets.

Vitamins and minerals

Although few studies evaluated the vitamin requirements in different catfish species, Uys & Hecht [103] formulated and successfully tested a compound diet for first feeding *C. gariepinus* larvae. The following vitamin composition was recommended for this species and may be used as a guide for other catfish species, although little is known about the vitamin requirements for different species: vitamin A (65,000 IU kg^{-1}), vitamin D (12,000 IU kg^{-1}), vitamin E (943 IU kg^{-1}), vitamin K (100 IU kg^{-1}), thiamine (0.036 mg kg^{-1}), riboflavin (0.071 mg kg^{-1}), pyridoxine (0.019 mg kg^{-1}), pantothenic acid (0.445 mg kg^{-1}), biotin (0.611 mg kg^{-1}), choline (8,500 mg kg^{-1}), vitamin B12 (0.200 mg kg^{-1}), niacin (0.590 mg kg^{-1}), ascorbic acid (1,500 mg kg^{-1}), folic acid (0.013 mg kg^{-1}), and inositol (2,860 mg kg^{-1}). Other studies have addressed the requirements of particular vitamins. For instance, Merchie *et al.* [209] reported that the addition of ascorbyl palmitate (10%) into an emulsion for enriching *Artemia* metanauplii increased by 50% their vitamin C levels (500 µg g^{-1} DW), whereas 20 or 30% addition increased vitamin C in *Artemia* three- and six-fold. *Clarias gariepinus* fed vitamin-C-enriched *Artemia* nauplii resulted in high growth rates and stress tolerance. Moreover, Bardócz *et al*. [210] reported that ADC enriched with vitamin C (255 µg g^{-1} BW) increased SGR values in *C. gariepinus* compared with freshly decapsulated cysts. In *R. quelen* fries, the optimal dietary vitamin A levels in terms of growth performance and survival was found at 3,000 IU kg^{-1} in diets containing 56% crude protein and 10% crude fat [211]. Other vitamin-mix formulations for *I. punctatus* may be found in El-Saidy *et al*. [212] and Kelly *et al*. [195]. Regarding mineral

requirements for catfish larvae, there is even less information. Scarpa & Gatlin [213] revealed that the dietary zinc requirements of *I. punctatus* varied depending on water hardness; in particular, fries required 20 mg Zn kg^{-1} and 20–40 mg Zn kg^{-1} diet when reared in soft and hard waters, respectively. Furthermore, the recommended level of mineral mix inclusion in *I. punctatus* fry diets is 2% [211] and its mineral content (g kg^{-1} of dry diet) should be as follows: $CaHPO_4$ $2H_2O$ (3.75), $CaCO_3$ (4.25), KH_2PO_4 (3.5), Na_2CO_3 (2.0), $MnSO_4$ H_2O (0.088), FeCl $6H_2O$ (0.125), $MgSO_4$ (1.5), KIO_3 (0.0025), $CuSO_4$ $5H_2O$ (0.0075), $ZnCl_2$ (0.0375), $CoCl_2$ $6H_2O$ (0.0005), Na_3SeO_3 (0.0005), and Na_2MoO_4 $2H_2O$ (0.002).

Cannibalism in early life stages

One of the main bottlenecks in early culture of the reviewed catfish species, except for *I. punctatus*, is their high rates of intracohort cannibalism [86,119,214-216]. Cannibalistic behaviour may be affected by rearing density, feeding frequency, food availability, food composition, light intensity, and photoperiod.

Several studies have evaluated how manipulating illumination conditions (i.e., light intensity or wavelength, λ) reduced cannibalism during early life stages. In this context, Mukai [217] found that *P. hypophthalmus* larvae showed higher survival and growth rates when reared under 0.1 lx (1.40 x 10^{-3} μmol m^{-2} s^{-1}) of white fluorescent light compared with those reared under other light intensities (1, 10, and 100 lx). Moreover, Mukai *et al.* [218] demonstrated that *P. hypophthalmus* larvae showed more aggressive behaviour at higher light intensities (10 and 100 lx) than those under low light intensity (0 and 0.1 lx); these results corroborate those reported for *C. gariepinus* [214]. Furthermore, when *C. gariepinus* larvae were reared under normal photoperiod (600-1,000 lx during light hours) or continuous dark (<0.01 lx) conditions from hatching up to 20 dph, no differences in larval size were found, even though larvae reared under dark conditions had higher survival rates than those under normal photoperiod [89].

Yellow (λ = 570–590 nm) and red (λ = 620–750 nm) wavelengths at a light intensity of 1.40 × 10^{-3} μmol m^{-2} s^{-1} improved growth performance and survival rates in *P. hypophthalmus* [219]; in particular, larvae reared under red wavelength conditions showed higher SGR values than those under different wave lengths. In fact, when larvae were reared under dark conditions and low stocking density (10 larvae L^{-1}), their survival rates were higher than those of larvae reared in light conditions and at higher stocking densities (20 or 40 larvae L^{-1}). These results were associated with a reduction in cannibalism [220]. Regarding *P. fasciatum,* Nuñez *et al*. [221] showed that survival was higher in larvae reared under dark conditions (<0.01 lx) than in larvae reared under other light intensities (1 or 10 lx) and a 12:12 L:D photoperiod.

Behavioural studies revealed that *C. gariepinus* larval activity increased under dim light conditions, whereas the number of fish resting on the bottom of the aquaria decreased. These changes resulted in fewer larvae bitten by other individuals in comparison to light conditions, thus reducing cannibalism rates [89,215]. These authors recommended manipulating different rearing variables such as feeding frequency, food availability, and light intensity to reduce swimming activity to a minimum. Thus, it is generally recommended to rear *C. gariepinus* larvae and fingerlings at low light intensity values (<15 lx), assuring continuous food availability in tanks or ponds by feeding them every two hours when reared under intensive conditions [91]. Similarly to *R. quelen* [222], the incidence of cannibalism in *Pseudoplatystoma* spp. is generally reduced through size grading, rearing density, photoperiod and feeding frequency [123,216,221]. *Pseudoplatystoma punctifer* size is inversely related to prey size [216]. Thus, specimens of increasing size preferred increasingly smaller prey relative to their own size, which highlights the importance of size grading. Besides, the authors suggested that cannibalism could be reduced when feeding *P. punctifer* at least six times a day. Other authors have recommended frequent grading of larvae of different sizes in *P. punctifer* [123], in addition

1314 to providing shelters and hiding places in *O. bimaculatus* to reduce or avoid cannibalistic
1315 behaviour [171].

1316 Significant advances in reducing cannibalism have been achieved with the nutritional
1317 composition of feeds. In this regard, a low incidence of cannibalism in *P. punctifer* early
1318 juveniles associated with a high dietary phospholipid content (41% TFA) [119] was observed
1319 when compared with dietary regimes previously used [59]. The inclusion of phospholipids could
1320 have induced a reduction of aggressiveness and activity, as observed in humans and rats.
1321 Additionally, diets supplemented with tryptophan or ingredients rich in this non-polar
1322 aromatic amino acid have also been recommended for reducing intracohort cannibalism in
1323 different catfish species [174,223,224]. Finally, another issue to be considered when dealing with
1324 cannibalism during catfish larval rearing is their personality. In this context, Torres *et al*. [225]
1325 showed that *L. alexandri*, during the first 15 days of exogenous feeding with *Artemia* nauplii,
1326 tanks that had only "shy" or "bold" larvae exhibited higher survival rates than those with both
1327 personalities combined. This finding was due to the higher occurrence of cannibalism when
1328 "shy" and "bold" larvae were present in the same tank, whereas differences in BW might be
1329 related to their lower swimming activity. Other strategies for reducing cannibalistic behaviour
1330 in catfish species have been related to triploidy, as it has been described in *R. quelen* [226].

1331 Cannibalism in *P. hypophthalmus* is largely independent from aggressiveness or feeding.
1332 However, it is a consequence of morphological traits, such as long sharp oral bones, which
1333 overhang from the mouth and prevent its closure at the start of exogenous feeding, and also
1334 an initially limited manoeuvrability caused by the late development of the pectoral fins [85]. As
1335 these morphological characteristics change during development, the associated risk is
1336 considered critical from 60 to 96 hpf and present until 129 hpf. Aggressiveness can be reduced
1337 with lower stocking densities, reducing the probability of contact between specimens. The
1338 significant mortality rate observed in this species during the first week of life is basically a

consequence of pathogenic infections of the wounds resulting from the encounters between larvae. In this context, survival and growth rates of *P. hypophthalmus* larvae were significantly improved when adding oxytetracycline (5 to 20 mg L^{-1}) or chloramine-T (2.5 mg L^{-1}) to the water; the use of the disinfectant is recommended in commercial hatcheries over the antibiotic to reduce the risk of bacterial resistance if applied incorrectly [227].

Omic approaches for improving catfish aquaculture

This section reviews the approaches conducted with omic technologies on the selected catfish species that have resulted in remarkable advances in the state of the art of catfish rearing. Nowadays, the omic analytical techniques (genomics, transcriptomics, regulomics, metabolomics and proteomics) may greatly contribute to the establishment of breeding programmes in aquaculture towards improving fish efficiency, production, quality and health [228-231]. Omics enable the understanding of the molecular basis underlying the influence of rearing conditions, nutrition, genetic background, or any other factor on survival, development, growth potential, immune resistance, and fish quality, among other parameters [232,233]. All genomic, transcript, and protein sources available for the reviewed catfish species are presented in Supplementary File 3. Although there is scarce transcriptomic and proteomic information related to early life stages of the different catfish species —*I. punctatus* is by far the most studied catfish species at the omics level—, these resources might open new avenues for improving early culture protocols, diets and feeding regimens, evaluating the impact of each factor on larval performance, quality, and health.

Mitochondrial DNA resources

The knowledge on mitochondrial DNA (mtDNA) is older than that on nuclear DNA. This sequence has been studied in *P. hypoththalmus* [234], *C. gariepinus* [235], *I. punctatus* [236], *O.*

bimaculatus [237], *P. reticulatum* [238], *H. fossilis* [239], *R. quelen* [240] and *L. alexandri* [241]. This deeper knowledge on mtDNA is due to its historical use as a source of information for phylogenetic, molecular evolution, and population genetic studies [242]. There is a large number of studies associating variations of mtDNA sequences with different populations of the same species; these data may provide useful information for conservation, breeding, and management programmes [243]. However, regardless of the wide use of full or partial mtDNA sequences for genetic analysis due to the higher mutation rate than in the nuclear genome, some particular features of the mtDNA may limit the power of these analyses. Unlike nuclear DNA, mtDNA resides in multiple cellular copies and may vary in sequence (heteroplasmy) and quantity among tissues [243]. In addition, when also considering the environment, mitochondria-encoded traits are influenced by interactions between the two genomes and a variety of environments and physiological conditions. Furthermore, the expanded use and relevance of mtDNA sequences in fish species are limited by the implementation of forward and reverse genetic studies to understand how sequence variation determines commercial traits [243]. It is expected that new approaches to address these issues will be available in the near future. In parallel, the broader implementation of third-generation sequencing technologies may help to fulfil one of the most relevant knowledge gaps in catfish species, including the identification and characterisation of single nucleotide polymorphisms (SNPs) for selecting genetic lineages in breeding programmes. In this regard, only deep and detailed association studies have been performed in *I. punctatus* [244]. An association of polymorphisms in prolactin gene and growth traits has been recently published in *I. punctatus* [245]. Furthermore, several genotyping efforts have been conducted to construct a high-density SNP array [246-249], which will certainly allow rapid advances on aquaculture selection programmes in ictalurid species and/or their hybrids.

Nuclear genomic resources

The nuclear genome sequence knowledge through NGS technologies in *I. punctatus* and *P. hypophthalmus* increased the set of known genes, transcripts, and proteins from these species [234,236]. In this context, the whole genome of these species is available and may be used as an initial platform for molecular breeding programmes to obtain novel catfish varieties using genomic approaches [244]. These approaches have served to identify the genetic basis of *I. punctatus* skull morphology, which has an enormous economic relevance because of its direct impact on fillet yield [250]. Additionally, sex determination mechanisms have been also unveiled in this species [251], which have important implications towards rearing monosex populations for improving growth and reproductive performances. However, the information for other catfish species remains limited to that obtained using the classical cloning methodologies. In this regard, Ju *et al.* [252] conducted an EST analysis of a cDNA library from the brain mRNA of *I. punctatus*. The number of available ESTs were increased through the analysis of different cDNA libraries from several fish tissues [253-255]. Based on previous cDNA libraries from *I. punctatus*, Ju *et al.* [256] used a low-density microarray to identify 61 differentially expressed genes in fish maintained at 12°C and 24°C. Key genes (including genes encoding chaperones and transcription factors, genes involved in lipid metabolism, and genes encoding translational machinery such as ribosomal proteins) involved in fish growth were identified; and how catfish rearing might be influenced under different rearing temperatures was also evaluated. Certainly, assessing the expression of those genes under early life stages might provide a molecular approach to determine the optimal rearing temperature during early life stages and how it might affect the performance at later growing phases. Furthermore, Li and Waldbieser [257] explored the altered transcriptome in *I. punctatus* spleen in a time-course from 2 h to 24 h after injection of lipopolysaccharide. The authors identified up to 138 differentially expressed genes, information that provided insights into the immune response of fish against a bacterial infection. Other studies have increased our understanding on how fish respond to particular

bacterial infections, such *Edwardsiella ictaluri*, and allowed the identification of the mechanisms of resistance to this gram-negative bacterium [258-260]. Nevertheless, the molecular knowledge on any biological response (e.g. immune system or heat stress response) in *I. punctatus* was soon further revolutionised with RNA-seq approaches [261,262]. These approaches, at the molecular level, lay the groundwork for further studies to be specifically conducted in developmental stages that are more sensitive to different stressors, such as the larval stages, and for predicting egg and embryo quality. In this context, a recent study evaluated a specific set of nine genes through quantitative PCR as potential markers of egg and embryo quality for hybrid catfish species [263], a promising approach to select high-quality egg batches and reducing the associated problems of rearing poor-quality eggs (e.g., low survival, reduced growth, and high incidence of skeletal deformities).

Non-coding RNA studies

In farmed catfish species, there is a limited but increasing number of studies identifying and characterising the role of non-coding RNAs (ncRNAs). There is increasing evidence of the critical control exerted by the tightly transcribed ncRNA genes in multi-cellular organisms through epigenetic changes and the control of post-transcriptional processes [264]. The number and type of ncRNAs known in each species compiled in the RNA central database are also shown in Supplementary File 3. As for the genomic, transcriptomic, and proteomic resources, most information regarding ncRNAs is specific to *I. punctatus*. In particular, Barozai [265] conducted the first approach of computational search for novel miRNA homologs and their targets along with their characterisation. At that time, 60 novel precursor miRNAs belonging to 45 families, including the bioinformatic prediction of the 341 proteins targeted by them, were identified and characterised. Instead, only 16 miRNAs (representing 12 miRNA families) and one mRNA target were reported by Xu *et al.* [266]. Just one year later, the use of

Solexa sequencing technology helped identify 237 conserved miRNAs and 45 novel miRNAs in *I. punctatus*, and the tissue expression pattern of some of them was reported [267]. Furthermore, the characterisation of the expression profile of miRNAs and the identification of potentially targeted mRNAs open new avenues to unveil the underlying mechanisms by which some biological features occur and those by which they might be transmitted to the future progenies and/or induce epigenetic imprinting [268].

Proteomic analyses

In parallel, as the high-throughput proteomic technologies were also developed and improved, the application of different methodologies, from the simplest polyacrylamide gel electrophoresis (PAGE) to the more complex isobaric tags for relative and absolute quantification (iTRAQ), further increased our understanding of the link between the genotype and phenotype [269]. One of the earliest applications of proteomic analysis was to characterise *I. punctatus* muscle, which is characterised by a pale/white colour with greyish to a slightly red tint, but stress may induce an undesirable reddish colour in fillets. In this context, Desai *et al.* [270] profiled the muscle proteomes employing two-dimensional electrophoresis and mass spectrometry and revealed over-abundant beta subunit of haemoglobin in reddish fillets. Further insights on how channel catfish fillet quality might be impacted by environmental and handling stress were obtained by these approaches [271]. Changes in the abundance of structural proteins and those involved in protein regulation and energy metabolism were identified, suggesting that increased proteolytic activity could be responsible for the alterations in colour and texture. A label-free quantitative proteomics workflow was also used to study how salinity affects the proteome of the kidney in *P. hypophthalmus* challenged with *Edwardsiella ictaluri* [272]. Among the 2,024 protein spots identified, 496 proteins were differentially expressed; most of them were related to cell metabolism, response to stress, cell structure, immunity and ion

homeostasis pathways, and functional categories. Furthermore, two-dimensional proteomic and mass spectrometry analysis of intestine and liver samples from *C. gariepinus* infected with *Aeromonas hydrophila* provided insight into host-pathogen interactions [273]. Unequivocally, further development of proteomic technologies and its wider implementation will certainly help address the current and future challenges in catfish species biology and domestication research.

Metabolomic studies

Metabolomics might be one of the last frontiers to gain an integrative understanding of fish physiology. Although, until now, only two studies have applied this technology in catfish species, these studies have already proved how metabolomic studies offer relevant information to evaluate the impact and to solve one of the persistent problems in *I. punctatus* aquaculture, anaemia. Using 1-D ^{1}H and 2-D ^{1}H J-resolved NMR analysis in healthy and anaemic *I. punctatus* kidney and liver tissues, the study revealed depleted energy sources, changes in metabolites associated with anaerobic metabolism or alternative energy pathways, as well as reduced taurine and inosine levels and protein synthesis [274]. Furthermore, a condition of oxidative stress was identified with an increase in valine, leucine, and isoleucine and a decrease in glutathione concomitant with a decreased respiratory gas transport capability through reductions in erythrocytes and haemoglobin markers in blood. Thus, this study clearly improved our understanding of anaemia symptoms and suggested useful biomarkers to identify fish status under farming conditions. A comparative analysis of brain nutritional metabolites showed how they are different depending the fish species considered, *Cyprinus carpio* vs. *I. punctatus*, and provided comprehensive information for the utilisation of fish heads in fish processing and dietary nutrition guidance [275].

The development of bioinformatic platforms would definitively provide optimal tools to address any biological question relevant to catfish aquaculture. In this context, specific educational programmes established by next-generation researchers would benefit the popularisation of such bioinformatic platforms. As global aquaculture relies on environmental conditions, an inherent vulnerability to climate change is evident. Climate change will be a major driver of aquaculture research needs in the future. A thorough understanding of how stressors affect fish physiology and how fish epigenetically adapt to new aquaculture conditions is of utmost importance. Research focused on these issues will help determine new engineering and management solutions to reduce the exposure to these stressors or mitigate their impact, or both. A combination of different approaches (i.e., genomics, transcriptomics, proteomics, metagenomics, metabolomics, and epigenomic) is recommended to gain a comprehensive, integrative, and clear understanding of any biological process occurring in catfish aquaculture under a climate change scenario. Such knowledge would allow to identify, validate, and apply potential biomarkers with predictive or diagnosis purposes. Thus, stressor-resistant traits can be genetically selected, and an adequate population variability maintained to improve resilience and overall fitness.

Microbiome studies

Recently, microbiome analyses have also been applied in catfish species. In this regard, both gut and skin microbiomes benefit the host species, probably by hindering the invasion of opportunistic pathogens, stimulating the immune system, or taking advantage of more nutritional metabolites available from the intestinal lumen [276]. These microbial communities can be disrupted or altered by different factors. Through ribosomal intergenic spacer analysis (RISA) and pyrosequencing, it was demonstrated that potassium permanganate exposure disturbed the external microbiomes in the skin and gills of *I. punctatus* and increased fish

mortality after a bacterial challenge with *Flavobacterium columnare* [277]. Similarly, feed containing florfenicol altered the *I. punctatus* gut microbiome, resulting in an increased relative abundance of potential opportunistic pathogens [278]. Both studies demonstrated that we need to beware of potent surface-acting disinfectants and antibiotics, when these are applied to avoid detrimental impacts on fish health. Furthermore, the gut microbiota is dynamic and adapts throughout fish development [279]. In this context, differences in microbiome communities were found along different larval developmental stages (i.e., egg, swim-up, 1 day of pond stocking, 24-h post stocking, and 21-d post stocking) in *I. punctatus*, indicating that the aquatic rearing environment and diet are important factors influencing the transfer of microbes from water (or food) into the gut [280,281]. These studies also indicated that even though probiotic treatments may be possible, gut community manipulation would require concurrent manipulation of pond environments. Indeed, fertilising ponds with livestock manure in catfish aquaculture is a common procedure; it might affect the microbial community and induce a primarily prebiotic effect on the pond ecosystem rather than a direct probiotic effect on fish [282]. Moreover, the sediment microbiome of catfish ponds responds to production practices; thus, monitoring the microbial community might be beneficial as a potential biomarker/predictor of catfish ponds productivity or fish physiological conditions, particularly during rearing at early life stages.

Future directions and conclusions

A constant and reliable source of fingerlings is required for a successful aquaculture industry and profitable farm operations, regardless of the final objective (i.e., human consumption, aquariology, or restocking). From this perspective, contrary to *C. gariepinus*, *I. punctatus*, and *P. hypophthalmus*, whose hatchery procedures have been developed for sustaining a commercial large-scale production; consistent, reliable, satisfactory fry production is the main

bottleneck limiting the aquaculture of *Pseudoplatystoma* spp., *H. fossilis*, *O. bimaculatus*, and *L. alexandri.* In this context, matching the stage of development with zootechnology (e.g., optimal rearing conditions, first-feeding and weaning diets, weaning time) is essential to develop or optimise rearing procedures during catfish early life stages; it is also important for monitoring the success and failure of these protocols when implemented under local conditions. For this purpose, it is critical to optimise larval rearing protocols, considering species-specific developmental patterns and their nutritional requirements, to synchronise development with rearing procedures under controlled conditions. These approaches, regardless of the fry production system considered (i.e., tanks or ponds), may contribute to produce more robust larvae. Robust larvae may lead to reducing the potential losses derived from the transfer of larvae or fries from indoor conditions to ponds and the dependence of larvae on zooplankton.

Information on the nutritional requirements of catfish during early life stages is still scarce and fragmentary on some of the species considered. Few commercial compound diets specifically formulated for selected catfish species like *I. punctatus*, *C. gariepinus*, and *Pangasius* spp. are available in the market. However, in most cases, microdiets and starter diets for other aquatic species are used to feed early catfish larvae, a choice based on larval performance and production costs. In this context, the development of compound diets with locally available ingredients could improve rearing practices and their sustainability, as well as promote the aquaculture value chain and its stakeholders. From this point of view, most South American, Asian, and African countries where these species are cultured have adequate technological resources to manufacture appropriate feeds; however, the availability and cost of protein and oil ingredients may be major constraints. In most cases, the general paucity of good quality aquafeeds locally is a factor of scale. To properly foster the development of not only compound diets for early weaning for the different catfish species but also most efficient

and sustainable practices, future experiments should be designed. Therefore, the development of other strategies for enhancing larval health and welfare is needed. A crucial strategy would be the use of functional feeds that both promote and sustain somatic growth and enhance immune response. With this focus, a more holistic approach with different variables (i.e., levels of macro- or micronutrients, additives, and immunostimulants) and high-throughput technologies like omic tools under different rearing conditions (i.e., tank and pond larval rearing, stocking densities, feeding rates, water temperatures, and oxygen levels) may be tested to provide a more robust and realistic outcome. This approach may be conducted according to the level of technological development and research needs for each species at the local level. In addition, for reducing larval cannibalism and maximising larval performance and quality, nutritional and husbandry practices need to be further explored. In this regard, taking advantage of omic technologies, better breeding selection programmes, quality monitoring of eggs, embryos, and rearing water in ponds, as well as the formulation of highly balanced diets for each species might be possible in the nearest future. The implementation and further development of these tools might warrant a successful achievement of these high-priority goals in catfish aquaculture.

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Table 1. Worldwide catfish production and by continent in terms of production (t) and economic value (USD) in 2018. Data is presented in terms of family taxonomical level. Geographical units are ordered in terms of catfish production relevance. Data per geographical region expressed as production and value percentages were calculated with relation to the region and not to overall worldwide values. Data were retrieved from FAO [9].

	Production (t)	Production (%)	Value (USD 000)	Value (%)
World	5,781,235.1	100	9,489,861.120	100
Asia	**5,333,194.55**	**92.25**	**8,318,614.530**	**87.66**
Bagridae; FW	53,7957.80	10.1	1,291,932.150	15.53
Clariidae; FW	1,352,494.05	25.4	1,853,994.520	22.29
Heteropneustidae; FW	13,793.76	0.3	73,476.310	0.88
Siluridae; FW	372,438.47	7.0	887,809.870	6.57
Pangasiidae; BW	...	…	…	…
Pangasiidae; FW	2,826,068.47	53.0	3,664,792.260	44.06
Ictaluridae; FW	230,442.00	4.3	546,608.420	10.67
Others; FW	...	...	…	…
Africa	**251,332.47**	**4.35**	**731,432.060**	**7.71**
Bagridae; BW	50.00	0.02	179.950	0.03
Bagridae; FW	2.00	0.001	2.250	<0.001
Clariidae; BW	1,836.00	0.73	1,343.370	0.18
Clariidae; FW	244,890.47	97.44	719,508.560	98.37
Siluridae; FW	44.00	0.02	24.930	<0.001
Mochokidae; FW	4,510.00	1.79	10,3730	1.42
Others; BW	...	…	…	…
North America	**168,579.08**	**2.92**	**355,880.850**	**3.75**
Callichthyidae; FW	2.00	0.001	6.000	0.002
Clariidae; FW	6,286.00	3.73	6,286.000	1.77
Ictaluridae; FW	161,271.08	95.66	34,6213.170	97.28
Pangasiidae; FW	1,020.00	0.61	3,375.680	0.95
South America	**14,642.01**	**0.25**	**44,973.760**	**0.47**
Clariidae; FW	…	…	…	…
Callichthyidae; BW	19.92	0.14	95.9	0.21
Callichthyidae; FW	...	….	….	…
Ictaluridae; FW	...	….	….	…
Loricariidae; FW	6.15	0.04	18.71	0.04
Pimelodidae; FW	665.94	4.55	4,771.03	10.61
Others; FW	13,950.00	95.27	40,088.12	89.14
Europe	**13,486.44**	**0.23**	**38,960.920**	**0.41**
Clariidae, FW	10,022.08	74.3	25,478.25	65.39
Ictaluridae; BW	...	…	…	
Ictaluridae; FW	2,039.69	15.1	6,559.81	16.84
Siluridae; FW	1,424.67	10.6	6,922.86	17.77
Others; FW	...	...	…	
Oceania	…	…	…	…
Pangasiidae	…	…	…	…
Clariidae	…	…	…	…

Abbreviations: FW, freshwater; BW, brackish water; "..." = Data not available; unobtainable; data not separately available but included in another category [9]. "Others" refer to species classified as Siluriformes (catfish), but not further taxonomically identified [9].

Table 2. Comparison of the main developmental events of the digestive system ontogeny between the catfish species presented in this review. For comparative purposes among catfish species, larval development was scaled using thermal units (cumulative degree-days post hatch). This unit is calculated as the average temperature (ºC) over the period of development and it is the product of the value of the average temperature multiplied by the number of days.

	Developmental events						
Catfish species	Mouth opening	First feeding	Yolk-sac resorption	Intestine differentiation	Pancreas differentiation	Zymogen granules in pancreas	Fully formed stomach
P. hypophthalmus [56]	52	52	104	-	-	-	-
C. gariepinus [57]	50	55	114	27	29	-	114
I. punctatus [58]	-	294-336*	210-231*	-	-	-	-
P. punctifer [59]	56	112	168	112	28	28	252
H. fossilis [60]	29	58	145	58	58	87	290
O. bimaculatus [61]	54	54	135	54	27	27	297
R. quelen [62,63]	4	49	74	72	17	39	49
L. alexandri [64,65]	0	162	270	189	108	-	288

* Data retrieved from natural populations not from aquaculture studies.

2390 **Table 3.** Summary of rearing practices for *Pangasiodon hypoththalmus* and *Clarias*
2391 *gariepinus* during early life stages.
2392

	P. hypoththalmus		*C. gariepinus*	
	Intensive	**Extensive**	**Intensive**	**Extensive**
Rearing system	Hatchery tanks ($0.2–4.7\ m^3$)	Earthen ponds ($1{,}000–5{,}000\ m^2$)	Hatchery tanks (100–1,000 L)	Earthen ponds ($100–250\ m^2$)
Treatment	Surface chlorinated water, open-flow	Pond liming and fertilization	Surface water, open-flow, RAS	Pond liming and fertilization
Food	Natural zooplankton (cladocerans, rotifers), *Artemia*, compound feeds	Natural zooplankton (cladocerans), *Artemia*, *Tubifex* sp., custard egg and soya powder, compound feeds	*Artemia*, cladocerans	Natural zooplankton (cladocerans, copepods, rotifers), crumbled formulated feeds
Water quality				
Temperature	26–28°C	26–32°C	28°C	28–32°C
pH	7.4–7.5	6.4–8.5	7.0	6.0–9.0
Oxygen	$\geq 5\ mg\ L^{-1}$	$\geq 3\ mg\ L^{-1}$	$\geq 5\ mg\ L^{-1}$	$\geq 3\ mg\ L^{-1}$
Fish density	$10{,}000\ fish\ m^{-3}$	$500–800\ fish\ m^{-2}$	$6\ larvae\ L^{-1}$	$100–250\ larvae\ m^{-2}$
Stocking age	1-2 dph (6.2 mm TL)	1-2 dph (6.2 mm TL)	1 dph (3.5-4.0 mm TL)	3 dph (4.8-5.0 mmTL)

2393
2394 *Abbreviations*: dph, days post hatching; RAS, recirculating aquatic system; TL, total length.

Table 4. Different weaning protocols recommended for *Clarias garepinus*.

Protocol / Reference	Days post hatching															
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17-32
Janssen [98]																	
Artemia																	
Compound diet																	
Verreth *et al.* [99]																	
Artemia																	
Weaning compound diet																	
Hecht *et al.* [100]																	
Live prey																	
Weaning compound diet																	
Compound diet																	
Oellermann [101]																	
Artemia																	
Weaning compound diet																	
Compound diet																	
Chepkirui-Boit *et al.* [102]																	
Artemia																	
Weaning compound diet																	

Details of feeding protocols: [1]*Artemia* nauplii was distributed *ad libitum*; the grow-out feed was supplemented with wheat bran; [2]*Artemia* nauplii was distributed four times per day; *Artemia* nauplii were progressively replaced by the growth-out feed (commercial trout pelleted feed) from 10 to 15 days four times per day; the similar protocol may be used but using *Artemia* dry cysts instead of nauplii [97]; [3]*Artemia* nauplii or live prey (*Daphnia* sp.) was distributed once per day; the replacement of the live feed by the compound diet was progressive and weaning diet should have 38-40% crude protein; [4]*Artemia* nauplii was distributed four times per day; weaning diet is described in Uys & Hecht [103]; [5]the experiment only lasted until 21 days post hatching; *Artemia* nauplii were distributed four to six times per day; the weaning diet contained the freshwater atyid shrimp (*Caridina nilotica*) at 75.5%; during weaning, *Artemia* nauplii and the dry feed were administered at equal parts.

Table 5. Summary of rearing practices for *Ictalurus punctatus* and *Pseudoplatystoma spp.* during early life stages.

	I. punctatus		*Pseudoplatystoma* spp.	
	Intensive	**Extensive**	**Intensive**	**Extensive**
Rearing system	Rectangular troughs (380–450 L)	Earthen ponds (4,000–20,000 m^2)	Cylindroconical tanks (60–200 L) / Rectangular or circular tanks	Earthen ponds
Water treatment	Well or surface water, open-flow, RAS	Pond liming and fertilization (organic and inorganic)	Well or surface water, RAS	Pond liming and fertilization (organic and inorganic)
Food	Starter diets; *Artemia* decapsulated cysts or zooplankton supplementation	Large cladocerans	*Artemia* from 2 to 12 dph, then cladocerans and copepods, optionally minced fish or meat	Cladocerans and copepods, optionally forage fish
Water quality				
Temperature	25.5–27.5ºC	26.0–30.0ºC	26–28°C	26–28°C
pH	7.0-8.5	7.0-8.5	*ca.* 7.0	*ca.* 7.0
Oxygen	≥4 ppm	≥3-4 ppm	≥6 ppm	≥6 ppm
Fish density	150,000–200,000 fry $trough^{-1}$	12–50 fry m^{-2}	15–50 larvae L^{-1} / 5,000–10,000 larvae m^{-3}	100–150 larvae m^{-2}
Stocking age	2 dph (14.4–18.8 mg BW)	2 dph (14.4–18.8 mg BW) – 7 dph (22.8–29.1 mg BW)	1 dph (< 3 mm TL) / 12 dph (13–15 mm TL)	12 dph (13–15 mm TL)

Abbreviations: BW, body weight; dph, days post hatching; RAS, recirculating aquatic system; TL, total length.

2420 **Table 6.** Summary of rearing practices for *Heteropneustes fossilis* and *Rhamdia quelen* during
2421 early life stages.
2422

	H. fossilis		*R. quelen*	
	Intensive	**Extensive**	**Intensive**	**Extensive**
Rearing system	FRP or concrete tanks (30 m^2)	Earthen ponds (100 - 400 m^2)	Indoor tank	Earthen ponds (up to 300-400 m^2)
Water treatment	Well or surface water, open-flow	Liming and fertilization (organic and inorganic)	Well or surface water, open-flow, RAS	Liming and fertilization (organic and inorganic)
Food	Zooplankton, rotifers, ciliates *Artemia* nauplii, egg custard, snail meat, fish meat, rice bran and commercial starter feed / microdiet	Zooplankton (ostracods, cladocerans, rotifers, copepod nauplii), *Tubifex* sp., finely ground trash fish, rice bran, mustard oil cake and chopped mollusc meat	Live prey (*Artemia* nauplii or pond-collected zooplankton) alone or in combination with dry feeds	Natural zooplankton (ostracods, chironomid larvae, cladocerans and copepods); natural zooplankton plus compound diet; bioflocs
Water quality				
Temperature	28.0–29.1ºC	26.0–29.0ºC	21.0–26.0ºC	17.0–27.0ºC
pH	6.8–7.6	7.2–7.6	8.0–8.5	8.0–8.5
Oxygen	6–8 mg L^{-1}	5.3–5.8 mg L^{-1}	6–8 mg L^{-1}	6–8 mg L^{-1}
Hardness	-	-	-	20–70 mg $CaCO_3$ L^{-1}
Fish density	3,000–5,000 larvae m^{-2}	300–500 larvae m^{-2}	10 fish L^{-1}	Up to 200 fish m^{-2} / 25 fry L^{-1}
Stocking age	1 dph (3 mm TL)	12 dph (10–12 mm TL)	2 dph (5 mm TL)	2 dph / 8-10 dph (7.5-8 mm TL)

2423
2424 *Abbreviations*: BW, body weight; dph, days post hatching; FRP, fibre-reinforced plastic;
2425 RAS, recirculating aquatic system; TL, total length.

2426
2427
2428

Table 7. Summary of rearing practices for *Ompok bimaculatus* and *Lophiosilurus alexandri* during early life stages.

	O. bimaculatus		*L. alexandri*	
	Intensive	**Extensive**	**Intensive**	**Extensive**
Rearing system	Cement cistern, FRP tanks (4 m^2)	Earthen ponds (100–400 m^2)	Hatchery tanks (10–100 L)	-
Water treatment	Well or surface water, open-flow	Liming and fertilization (organic, and inorganic)	Well or surface water, open-flow, RAS	-
Food	*Artemia* nauplii, pond-collected zooplankton (copepods, cladocerans), *Tubifex*, trash fish, formulated diets, chicken viscera	Zooplankton (copepods, cladocerans), rice bran, mustard oil cake, and dry fish powder	*Artemia*	-
Water quality				
Temperature	27.0–28.1°C	27–28°C	26–32ºC	
pH	6.8–7.6	7.2–7.7	6.5–8.5	
Oxygen	6–8 mg L^{-1}	5–6 mg L^{-1}	>4 mg L^{-1}	
Hardness	-	-	2 g NaCl L^{-1}	-
Fish density	3,000–4,000 larvae m^{-2}	100–200 larvae m^{-2}	Up to 300 larvae L^{-1}	-
Stocking age	2 dph (3.3 mm TL)	2–3 dph (3–4 mm TL)	1 dph (8 mm TL)	-

Abbreviations: dph, days post hatching; FRP, fibre-reinforced plastic; RAS, recirculating aquatic system.

2438 **Table 8.** Weaning protocol recommended for *Lophiosilurus alexandri* onto compound diets.
2439

Days of feeding	**Feeding protocol**[1]
1-3 days	80% OH + 20% CD + 10 g *Artemia* nauplii
4-6 days	60% OH + 40% CD + 10 g *Artemia* nauplii
7-9 days	40% OH + 60% CD + 5 g *Artemia* nauplii
10-12 days	20% OH + 80% CD
13-15 days	100% CD

2440
2441 [1] Ingredient percentages for the weaning protocol are indicated considering the preparation of
2442 100g feed. *Abbreviations*: OH, ox heart; CD, compound diet.