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An alternative life history approach to the nutrition and feeding of Siluroidei larvae and early juveniles

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Abstract

Successful commercial production of most cultured fish species has been facilitated by the intensification of larval rearing techniques. Siluroidei species are no exception and early attempts at larval rearing in ponds were soon superseded by intensive hatchery production, at least for those species that are farmed on a commercial scale. The review focuses on alternative life history strategies and how these may provide clues to the early nutrition and feeding of siluroid fishes, as well as on the development and efficacy of practical feeds and feed application. The paper highlights several commonalities in terms of the nutritional and feeding requirements of the larvae of the various species cultured on a commercial and subsistence basis. The requirement for live feed for some species appears to be of short duration and all species can be successfully weaned onto dry feed at a relatively early stage. This is considered to be one of the reasons why the intensification of larval rearing of Siluroidei fishes has, in general, been highly successful. The review also comments on the live food/dry food debate and clearly reveals that our knowledge of Siluroidei larval nutrition and feeding is sorely lacking for many species, in comparison to other groups of fish. This emphasises the need for a concerted fundamental research effort.

Keywords: Siluroidei, nutrition, feeding.

Une approche de la nutrition et de l'alimentation des larves et juvéniles de Siluroidei par l'étude de leurs cycles biologiques.

Résumé

Le succès de la production commerciale de la plupart des espèces de poissons d'élevage a été facilité par l'intensification des techniques d'élevage larvaire. Les poissons-chats (Siluroidei) ne font pas exception et les premières tentatives d'élevage des larves en étang ont été rapidement supplantées par une production intensive en écloserie, au moins pour les espèces cultivées à l'échelle commerciale. Cette synthèse est centrée sur les différentes stratégies démographiques et sur la façon dont elles peuvent définir des clés pour la nutrition et l'alimentation des premiers stades chez les Siluroidei, ainsi que pour la mise au point, l'efficacité et la distribution des aliments. L'article met en lumière plusieurs points communs en termes de besoins alimentaires et nutritionnels pour les larves des différentes espèces cultivées à une échelle commerciale ou de subsistance. La nécesssité d'une nourriture vivante qui existe pour quelques espèces apparaît de courte durée et toutes peuvent être sevrées avec des aliments secs à un stade relativement précoce. Ce point est considéré comme une des raisons de la réussite de l'élevage larvaire des poissons Siluroidei. L'article commente aussi le débat aliment vivant/aliment sec et montre clairement que nos connaissances sur la nutrition et l'alimentation des larves de nombreuses espèces de Siluroidei restent très limitées en comparaison aux autres groupes de poissons. Ceci souligne le besoin d'un effort de recherche fondamentale concerté.

Mots-clés : Siluroidei, nutrition, alimentation.

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INTRODUCTION

Research into the nutrition of fish has a relatively brief history. Before 1950 larval and production diets consisted principally of fresh or frozen abattoir by-products and raw trash fish (Nose, 1979) and natural food, facilitated by pond fertilisation. Early fish nutrition studies in the western world were focused mainly on salmonid species (Halver, 1953, 1957*a*, *b*; Phillips, 1956). During the early 1970s two major syntheses on fish nutrition were published by Halver (1972) and Cowey and Sargent (1972). By then a sound basic knowledge had also been established for salmonid nutrition, in terms of their requirements for energy (Phillips, 1972), protein and amino acids (Mertz, 1972), vitamins (Halver, 1972), and lipids (Lee and Sinnhuber, 1972). To a great extent these studies laid the foundation for research into the nutritional requirements of other fish, including their larvae.

The greater understanding of the nutritional requirements of different fish species and the development of balanced moist (Hublou, 1963) and dry feeds (Hastings and Dupree, 1969; Fowler and Barrows, 1971), coupled with linear least costing of feeds and improved husbandry techniques, has globally facilitated the development of aquaculture in terms of yield and production.

A shortage of juvenile fish for stocking into production units has been, and still is, commonly regarded as the Achilles heel of aquaculture development in many parts of the world. The intensification of larval and early juveniles rearing technologies has not kept pace with the intensification of grow-out technologies for many species, which has inevitable exacerbated the situation. Recent advances in the intensification of hatchery fry rearing technologies has however greatly facilitated the farming of some species, including several of the important Siluroidei species.

The objective of a hatchery is to produce suitably sized and healthy juveniles on a cost effective and timeous basis as and when required by the industry. The most important facets underlying the successful development of intensive larval and early juvenile rearing protocols, for any species, is an understanding of (i) the specific optimal environmental conditions, (ii) the nutritional requirements during the early life history stages and *(iii)* optimal feeding practices. Also implicit for the success of any hatchery operation are the quality of feeds and feed ingredients, and the experience of the hatchery manager and personnel.

From the literature it is evidently clear that larval and early juvenile nutrition of siluroid fishes has developed in one of two directions. This is a consequence principally of the life history styles of the various species, and in particular is related to the measure of parental investment in the gametes and the young. It stands to reason therefore that a greater measure of effort has been invested in nutritional research for those species which have little or no parental investment and therefore a higher relative fecundity, smaller egg size and a definitive larval stage, *e.g. Clarias gariepinus*, than those with a larger measure of parental investment, which have fewer but larger eggs and no clearly defined larval period, *e.g. Ictalurus punctatus*.

Although several Siluroidei species are being farmed on a commercial or subsistence basis and many more are being considered as candidate species this review is, to a great extent, focused on *Clarias gariepinus* and *Ictalurus punctatus*. The two main reasons for this is that these two species occupy, to a large degree, the opposite ends of the continuum of reproductive styles of those Siluroidei species which are of commercial importance in aquaculture and secondly, more detailed research has been undertaken on these two species than on any of the others. Where necessary, and applicable, reference is however made to other farmed species. The success of channel catfish farming in the United States of America, which began around the early 1950's, has been a combination of the ingenuity of farmers supported by a needs driven research effort and the implementation of dynamic marketing strategy to increase consumer acceptance. The farming of, and research into improving the culture technology for *Clarias batrachus* and *Clarias macrocephalus* in the Far East has a similar history, except that there appears to have been no need for an image building strategy for the product. Except for relatively minor differences, the overall culture technologies for these species are similar. To a large extent broodstock fish spawn in nests (provided or made by the fish), from which the eggs are collected and incubated or allowed to hatch naturally, whereafter the young fish are transferred to newly inundated and fertilised nursery ponds for a primary nursing period. In order to obtain a higher degree of survival and better growth there has, more recently, been a move towards the controlled rearing of the larvae and early juveniles under hatchery conditions.

In stark contrast the development of the culture technology of the African catfish, *Clarias gariepinus* was driven by science and technology. Only after the technology had been developed were attempts made to convince farmers to adopt the species as an aquaculture species. This is still continuing. Although some recent successes in Africa and the Netherlands have been achieved, I would predict that it will still take some time before the species is accepted by consumers to the same extent as channel catfish in the USA and clariid catfish in the Far East. The entire technology for African catfish was developed largely during the last 15 years. This research, particularly that on larval and early juvenile nutrition, has provided us with valuable insights into the ontogeny of the nutritional physiology of larval siluroid fish. This is principally because *C. gariepinus*, in contrast to other Siluroidei, has a relatively extended larval period after the start of exogenous feeding. This requires considerably more care in terms of nutrition and feeding and in general means that the species is more difficult to rear than other siluroids such as channel catfish. It is not surprising therefore that more research has been undertaken on the nutritional and feeding requirements of the larvae of this species than on any of the other highly commercialised Siluroidei species.

This review was not undertaken to consider in detail the specific nutritional requirements of all siluroid species that are farmed, neither was it intended to review the specific role of proteins, lipids and vitamins and minerals in metabolic processes, nor was it intended to provide information on analytical methodologies. These matters are adequately dealt with in several texts (Halver, 1989; Cowey *et al.*, 1985, Wilson, 1991; Steffens, 1989). It was the intention to highlight recent advances in the nutrition and feeding practices in siluroid fishes and to consider commonalities in terms of nutrient requirements and feeding to facilitate the development of complete diets for new Siluroidei aquaculture candidate species and the improvement of the nutrition and feeding of currently farmed species. It was also undertaken to highlight the role and relative merits of dry diets in comparison to live feeds, and to emphasise the importance of a fundamental understanding of the early life history and ontogenetic processes of larval fishes (particularly in terms of the concept of alternative life history styles) for their successful rearing under controlled hatchery conditions.

THE PREDICTIVE ROLE OF ALTRICIAL/PRECOCIAL LIFE STYLES IN THE NUTRITION OF SILUROIDEI LARVAE AND EARLY JUVENILES

In an attempt to illustrate the predictive role of early life history and ontogeny for larval fish nutrition this discussion will be largely restricted to *Ictalurus punctatus* and *Clarias gariepinus*. The reason for this is the relative position occupied by these two species on the altricial/precocial continuum of alternative reproductive styles (Balon, 1984; Bruton, 1989, but see also Bruton, this volume). *Table* 1 summarises the epigenetic suite of characters which separates these two species on the altricial/precocial continuum.

Table 1. – The epigenetic suite of alternate characters used to distinguish between *Ictalurus punctatus* and *Clarias gariepinus*.

	I. punctatus	*C. gariepinus*
Fecundity	Low (5 000/kg)	High (60 000/kg)
Spawning	Cluster	Broadcast
Parental care	Present (paternal guarder)	Absent
Incubation period	Long (5 days)	Short (24 hours)
Egg size	Large (3.5 mm)	Small (1.2 mm)
Yolksac absorption	Long (5-10 days)	Short (2-4 days)
Larval stage	Short (2 days)	Long (11-15 days)

(Balon 1984 *a, b*; Tucker and Robinson, 1990; Bruton, 1979, 1989; Hecht *et al.*, 1988).

Channel catfish clearly tend towards the precocial side of the continuum, while the African catfish, in comparison, has an altricial life history style. Channel catfish undergo direct development and do not appear to require a source of live food and can be reared efficiently on dry feed from the start of exogenous feeding (Wilson, 1989). African catfish, on the other hand, have a clearly defined larval stage and require a source of live feed for at least the first four to five days of exogenous feeding (Hecht *et al.*, 1988; Verreth *et al.*, 1993; Verreth and van Tongeren, 1989). The question therefore arises whether the differences in the classical epigenetic suite of characters defined in *table* 1 can provide the aquaculturist with some clue as to the nutritional requirements of Siluroidei larvae during the early and critical periods of their life history.

Some recent studies on the ontogeny of the alimentary tract and the development of physiological processes within the alimentary system support the hypothesis that the relative position of a species on the altricial/precocial continuum may indeed be of predictive value in terms of its early digestive capabilities.

Stroband and Kroon (1981) who studied the ontogeny of the alimentary tract of *C. gariepinus* show that a functional stomach is only fully developed at a length of 11 mm TL (*ca.* 5-6 days after the start of exogenous feeding). It is at this stage that they consider the larval stage to have ended (Tanaka, 1971). This definition of the larval period is different from that of Balon (1984 *a, b*) who argues that the larval stage ends when the median fin-fold and other temporary organs have been replaced, which in *C. gariepinus*, under natural field conditions, occurs at approximately 10 to 11 days (Bruton, 1979). An argument can obviously be made for both of these definitions. However, I would agree with Segner *et al.* (1993) that as far as aquaculture is concerned it is perhaps more important to consider the nutritional physiology of the larvae as an indication of the end of the larval period.

According to alimentary tract ontogeny and morphology and digestive enzyme secretion, fish can be divided into three groups (Dabrowski and Culver, 1991). The first are those which have a functional stomach at the start of exogenous feeding *e.g.* trout and channel catfish. The second group are those which during part of the larval stage do not have a functional stomach or gastric glands but whose digestive system undergoes a complex metamorphosis to incorporate a functional stomach during the late larval or very early juvenile stage (this group encompasses the majority of fishes, including the clariid catfishes – Stroband and Kroon 1981 and for that matter most siluroid fishes). The third group includes those fish which do not have a functional stomach throughout their lives, *e.g.* carp (Dabrowski and Culver, 1991). From a life history styles perspective those fishes with a functional stomach at the start of exogenous feeding are considered to be precocial (direct development) while those which have to develop a stomach during the larval stage are altricial.

A review of the literature clearly shows that those fish which have a functional stomach from the start of exogenous feeding (precocial) pose the least problems and concern with formulated dry starter feeds. The availability of nutrients in dry starter feeds however is a clear problem for stomachless larvae (altricial). This has been clearly shown by Verreth and van Tongeren (1989) and Verreth *et al.* (1993), although some progress has been made in the development of complete diets for first feeding *C. gariepinus*, particularly where use has been made of single cell proteins (SCP) (Hecht, 1982; Uys and Hecht, 1985; Appelbaum and van Damme, 1988).

Verreth *et al.* (1992) investigated the histological, histochemical and immunohistochemical development of the digestive system in *C. gariepinus*. Insulin and glucagon producing cells were found in endocrine pancreatic islets 14 hours after hatching, while from the start of exogenous feeding (48 hours after hatching) aminopeptidase, non-specific esterase and ATP-ase were detected in the digestive system. Morphologically the stomach was functionally complete after 5 days of exogenous feeding, marking the physiological end of the larval period. Gastric acid excretion started on day 4. This correlates well with the weaning period of 4 days as previously suggested by Verreth and Van Tongeren (1984) and the recommendation by Hecht *et al.* (1988) that for the first three to four days of exogenous feeding it is advantageous to supplement the dry fed with Artemia nauplii during at least three of the 10 to 12 feeds per 24 hour day.

Segner *et al.* (1993), who studied the nutritional physiology of three "Group 2" fish (as defined above) also stressed the importance of the ontogeny of physiological processes for the understanding of the quantitative and qualitative feed requirements of larvae. It is therefore clearly necessary to undertake both descriptive investigations on the ontogeny of structures and functions as well as experimental investigations on adaptive strategies of the larvae under changing feeding regimes. Their studies suggest that the digestive system of the larvae of *C. gariepinus*, *Coregonus lavaretus* and *Scopthalmus maximus* is sufficiently developed to ensure efficient utilisation of live food from the start of exogenous feeding, but not of dry food for which a functional stomach is necessary.

These studies clearly support the hypothesis of the predictive value of altricial/precocial homeorhetic states in developing initial research strategies for determining the nutritional requirements of first feeding larvae. Theoretically therefore the larvae of those fish which have a functional stomach at the start of exogenous feeding can be considered to reflect the precocial state, while those without a functional stomach would be altricial.

Clariid and other Siluroidei species are beginning to play an increasingly important role in tropical aquaculture by virtue of their tolerance of adverse environmental conditions, capacity for air breathing and relative resistance to disease and parasites. In Africa several Siluroidei species are now being considered as aquaculture candidates. These include *C. isheriensis* (Fagbenro, 1990, 1992; Fagbenro and Sydenham, 1988, 1990) *H. longifilis* and their hybrids with *C. gariepinus* (Hecht and Lublinkhof, 1985; Hecht *et al.*, 1992; Legendre *et al.*, 1992) and *H. bidorsalis* and its hybrids with *C. gariepinus* (Fagbenro *et al.*, 1992), *Schilbe mystus* (Kruger and Polling, 1984; Prinsloo and Schoonbee, 1988) and others such as *Chrysichthys species*, *Pangasius* in China and several others in South America and India. Considering the above hypothesis I believe it would be fruitful to assess their relative position on the altricial/precocial continuum, prior to initiating time consuming larval rearing studies. If the hypothesis should hold then successful larval rearing could be considerably expedited.

Overall it is abundantly evident that for a better understanding of applied nutrition in siluroid species, fundamental aspects such as the natural feeding biology, the morphological adaptations for feeding, and the physiological processes involved need to be considered.

COMMONALITIES IN FEEDING PRACTICES FOR SILUROIDEI LARVAE AND EARLY JUVENILES

As mentioned previously, successful larval rearing does not only depend on adequate nutrition. As important as the diet fed to the larvae is how that feed (live or dry) is fed to the larvae and the conditions under which the larvae are reared. Temperature is the most important abiotic variable affecting the growth of larvae and early juveniles. For most Siluroidei species it would appear that a temperature range between 26 and 30°C is optimal for larval and early juvenile rearing. High temperatures are however also conducive to the proliferation of bacteria and fungi. This implies that attention must be given to the maintenance of good water quality. If optimal environmental conditions are not maintained then neither the quality of the feed nor optimal feeding practices will ensure optimal growth and survival. Stocking juveniles which are in a poor condition into production ponds can have serious consequences in terms of production planning and sales, and should be avoided.

Feeding frequency and ration

Despite a considerable literature there seems to be little consensus as regards ration size and exact frequency at which *Clarias* larvae and early juveniles

Table 2. – Some recommended feeding schedules for Siluroidei larvae.

Number of feeds/day	Interval (hrs)	Ration	Reference
Clarias species			
		50% BW/day	Haylor, 1991
	Continuous	satiation	Hogendoorn, 1980
7	2	satiation	Hecht and Appelbaum, 1987
5		ad libitum	Verreth and van Tongeren, 1989
4		ad libitum	Verreth and den Bieman, 1987
3		ad libitum	Appelbaum and van Damme, 1988
Frequent		21% BW/day	Haylor, 1993 *b*
12	2	satiation	W. Uys (pers. comm.)
3		satiation	Mollah and Alam, 1982
	4	satiation	Uys, 1984
	Continuous	excess	Hecht and Appelbaum, 1988
6	4	25% BW/day	Uys and Hecht, 1985
12	2	satiation*	Hecht *et al.*, 1988
2		10% BW/day	Chuapoehuk, 1987
		6% BW/day	Anderson and Fast, 1991
Ictalurus punctatus			
8-10		25% BW/day	Robinson *et al.*, 1989
		6-10% BW/day	Lovell, 1977
Silurus glanis			
	Continuous	ad libitum	Ronyai and Ruttkay, 1990
Heteropneustes fossilis			
2		12.7% BW/day	Reddy and Katre, 1979
2		3% BW/day	Akand *et al.*, 1989

* not less than 40% of body weight per day.

should be fed (*table* 2). It is perhaps important to bear in mind that fixing ration as a percent of body weight per day, based on periodic weighing, may only poorly approximate feed requirements (Verreth and den Bieman, 1987; Haylor, 1993), because of the high SGR during the early life history stages.

Examination of the various studies undertaken on the growth of *Clarias* larvae clearly shows that best growth and survival is obtained under satiation feeding at two hourly intervals, and the same appears to hold true for *Silurus glanis*. For channel catfish there seems to be general consensus that 8-10 feeds at a ration of 25% of body weight per day is optimal. As far as *H. fossilis* is concerned I would venture to guess that with more detailed work a feeding schedule similar to the above species would ultimately emerge. In considering these feeding schedules the point needs to be made that, in a practical sense, they only serve as guidelines. It is well known that the experienced farmer usually knows at what level to feed, based on many years of behavioural observations of his fish. It would indeed be wise if researchers were to incorporate behavioural observations into their experimental design for the determination of optimal feeding practices. Several studies have been undertaken to model food intake. Haylor (1993) modelled feed intake and gastric evacuation in *C. gariepinus* and concluded that larvae require 30 min to feed to satiation, and that maximum feed intake per day is approximately 21% of body weight per day, although feed intake can be maximised up to limit of *ca.* 50% body weight per day by frequent feeding over 24 h each day (Haylor, 1991), but this obviously declines as the fish grow (Hogendoorn *et al.*, 1983).

The method developed by Verreth and den Bieman (1987) is of particular value in determining optimal feeding rates in larval clariid species, or of those siluroid species of which the larval period is of a similar duration. During this *ca.* 11-15 day period their weight increases 20 to 50 fold, dry matter content changes significantly and the specific growth rate decreases continuously. Hogendoorn (1980) reported a decreasing SGR in *C. gariepinus* larvae from 85% to 25% of body weight per day during the first 28 days of feeding. This implies that the feeding rate must be adjusted daily. Given that the relationship between the cube root of weight and rearing period is linear and the fact that body weight can therefore be predicted, allows for a reasonably accurate method for adjusting the daily food fed.

From a practical point of view the amount and frequency of feeding however appears to be an academic exercise. On commercial fish farms, the entire process of larval rearing is considered in terms of practicality and economic sense, and this will vary between hatcheries and countries. Haylor (1993) shows that food intake is maximised by frequent feeding over a 24 hour period but questions whether this is economical. Science can provide the information but it is up to the farmer to find the balance between what is biologically and economically acceptable. In southern Africa on intensive and semi-intensive farms *C. gariepinus* larvae are reared in the hatchery for 10 to 14 days during which time they are fed to satiation once every two hours for 24 hours at a temperature of 28°C at a stocking density of *ca.* 100 larvae per litre. This protocol results in a highly acceptable growth rate and survival (>80%) and at least cost (Wynand Uys and Willem Lublinkhof, pers. comm.)

Duration of the primary nursing period

There has been considerable debate regarding the optimal duration of the primary nursing period in the hatchery. For clariid species this ranges from three (Viveen *et al.*, 1985) to 14 days (Hecht *et al.*, 1988) and for ictalurid species from 5-10 days (Lovell, 1984) to 7-14 days (Wilson, 1989). Economics and hatchery space would largely dictate the duration of the primary nursing period in most commercial operations. It would appear however that, for siluroid fish in general, optimal survival in nursery ponds is attained after a hatchery period of 14 days.

Weaning

Ictalurid species have been shown to efficiently utilise dry feeds from the start of exogenous feeding. The reasons for this relate to the presence of a functional stomach and are presented elsewhere in this review. Clariid catfish on the other hand appear to require live feed for a specified time, although some studies have shown that SCP could possibly be used to replace the need for Artemia nauplii (Uys and Hecht, 1985; Appelbaum and van Damme, 1988). Verreth and van Tongeren (1984) clearly showed in their detailed investigations that *C. gariepinus* can be weaned onto dry feed after four days of initial feeding with Artemia. Similarly Hecht *et al.* (1988) recommend (based on farm experience) that for improved growth and survival African catfish larvae should receive an Artemia nauplii supplement during at least three feeds per day for the first three to four days of exogenous feeding. The anatomical and physiological reasons for the apparent requirement of live food is presented elsewhere in this review. It is also quite evident that yeast based diets currently appear to be the only alternative to live feeds for clariid catfish or other stomachless fish larvae for that matter. The relative merits of dry and live feeds are discussed later.

Other considerations

Other important considerations in the feeding of Siluroidei larvae, and all larvae for that matter, in hatchery troughs are factors such as food distribution, removal of excess food and faeces, maintenance of general hygiene, pellet size, and the maintenance of optimal environmental conditions to maximise food intake thereby maximising growth and survival. Dry food should be distributed evenly over the water surface. This minimises competition for food. In fact Hecht and Appelbaum (1988) recommend that food for *C. gariepinus* should always be available in excess to reduce the rate of cannibalism in cannibalistic species (also Hecht and Pienaar, 1993). Lovell (1984) makes an all important comment that feeding practice is as important as ration formulation. Knowledge of the amount, frequency and methods of feed application under various culture conditions are essential for success. Uys and Hecht (1985) calculated that for first feeding African catfish larvae, and early juveniles up to 50 mm, pellet size should be 2.2% of total body length. Using the data provided by Lovell (1984) and Winfree and Stickney (1984) the optimal pellet size for first feeding channel catfish, and up to *ca.* 58 mm, was 2.5% of total body length.

The information provided above is to a large extent based on experimental studies undertaken under laboratory conditions or hatchery troughs. While there has been a general shift away from rearing larvae in nursery ponds it is still practised to a considerable extent world wide. Given the information under optimal conditions it is clear that feeding in nursery ponds should be guided by real time knowledge of environmental conditions, particularly oxygen and temperature. Both of these factors are known to depress feeding activity. It is important therefore to maintain accurate records of these variables, to feed accordingly and thereby optimising feed utilisation and growth. Ignoring the fluctuations of these two basic variables can result in wasted food, have a negative impact on water quality which, in turn, will affect growth and survival.

NUTRITIONAL COMMONALITIES IN SILUROIDEI LARVAE AND EARLY JUVENILES

Since the mid-1970s a considerable research effort has been directed towards replacing live food with complete dry feeds, particularly during the critical larval and early juvenile stages. Approaches have included techniques for micro-encapsulation and the development of water stable particles containing all the nutrients required from the start of exogenous feeding to metamorphosis. Success of weaning depends largely on the nutritional quality of both the live food organisms and the formulated compound diet (Bryant and Matty, 1981; Dabrowski, 1984).

While feeding usually represents the single most expensive production cost in intensive aquaculture (Shang, 1981), the cost factor in larviculture is, on a comparative basis, much less important. The reason for this is the relatively small quantities of food required and the over-riding importance of producing the number of juveniles needed for stocking purposes.

Table 3. – Dietary nutrient requirements of several Siluroidei larvae and early juveniles.

Species	Protein	Fat	CH's	DE*	Reference
Clarias	55	9	21		Uys and Hecht, 1985
	50	15	15		Salami *et al.*, 1993
	30				Chuapochuk, 1987
			15-20		Mollah and Alum, 1990
H. fossilis	28-30				Akand *et al.*, 1989
	40				Rahman *et al.*, 1982
I. punctatus	36-40			3.5	Lovell, 1989
	36				Lovell, 1987
	35			2.5	Santana and Garcia, 1986
	40				Page and Andrews, 1973
	40				NRC, 1977
	49-53				Toledo and Gonzales, 1986
	51				Toledo and Gonzales, 1989
	52			3.6	Winfree and Stickney, 1984
	50				Robinson *et al.*, 1989
	52	10-12			Robinson and Tucker, 1990

* Expressed as kcal/gramme.

Many studies have been undertaken on the protein and other nutrient requirements of larval and early juvenile siluroid fishes. Uncertainty as to the exact requirements, however, still exists and is often the subject of major debate. This is not surprising as the nutritional requirements (particularly for protein and lipids) is highly variable and depends on a number of factors. These include temperature, feeding frequency and ration, size, dietary protein to energy ratio, protein quality, availability of natural food and management practices, stocking densities, dietary composition (Tucker and Robinson, 1990). Despite some anomalies it is however clear from the literature that larval and early juvenile siluroid fish, similar to those of other species, have a relatively high demand for protein and energy in comparison to juveniles and adult fish. This is a consequence of the very rapid rate of decrease in specific growth rate with age (Hogendoorn *et al.*, 1983).

In formulating complete dry diets for larvae and early juveniles the amino acid content of the fish tissue may serve as a first approximation of the "ideal" protein composition of the diet (Ostrowski and Divkaran, 1989; Shcherbina *et al.*, 1988), although the limitations of this approach are well documented (Dabrowski and Pocyczynski, 1988; Seidel *et al.*, 1980). Another approach is by an examination of the proximal and amino acid composition of the natural food of the larvae (Uys, 1984). Most of the results presented here are, however, based on empirical "dose – response" experiments. While this method ultimately provides the necessary information it is my opinion that the determination of nutrient requirements would be greatly facilitated by a more fundamental approach, as discussed later. *Table* 3 provides some information on the nutrient requirements of Siluroidei larvae and early juveniles.

Despite some marked differences it would appear that Siluroidei larvae in general have a protein demand of *ca.* 50% and a lipid requirement of between 10 and 15%. The majority of authors still recommend Artemia as an exclusive first feed for *Clarias* species. In this regard it is of interest to note that the protein and fat content of Artemia nauplii and cysts also range between 48-58% and 10-16% on a dry weight basis, respectively. Most of the cultured siluroid species are planktivorous during their larval and early juvenile stages and it is quite likely that the zooplankton they feed on have a similar proximal composition as *Artemia.* It is therefore not altogether surprising that the empirically determined protein and lipid requirements fall into the same ball-park as for *Artemia.* In numerous studies the vital importance of fish meal as a component of larval and early juvenile dry diets is stressed. Winfree and Stickney (1984) and Lovell (1989) recommend that at least 50% of the dietary protein should come from fishmeal for channel catfish swim-up fry. Moreover, Winfree and Stickney (1984) recommend that protein digestibility should be *ca.* 75%, available lysine not less than 5.1%, a digestible energy value of 3.6 kcal/g, and a calcium and phosphorous content of not less than 0.5% of the diet.

As the fish grow their demand for protein decreases. In our two examples the dietary protein level decreases from *ca.* 52% to 28-36% in channel catfish and from 55% to 32-38% in African catfish from first feeding to when the fish exceed 20 g in weight (Tucker and Robinson, 1990; Hecht *et al.*, 1988).

While the requirements for essential amino acids of channel catfish fingerlings (>30 g) are known (Wilson, 1991), nothing is known about the quantitative requirements of siluroid larvae. Similarly, little is known about the essential fatty acid requirements of larvae and early juveniles (Sargent, 1989). However,

Table 4. – Complete practical diets for African and channel catfish.

Diet 1. African catfish (Hecht *et al.*, 1988)

Ingredient	International feed number	Percent in diet
Candida utilis (Torula yeast)	7-05-534	50%
White fishmeal	5-02-025	43%
Cod liver oil		3%
Sunflower oil		3%
Vitamin and mineral premix		1%

Diet 2. Channel catfish (Winfree and Stickney, 1984*b*)

Menhaden fishmeal	5-02-009	60%
Meat and bone meal	5-00-388	10%
Spray dried blood	5-00-381	5%
Wheat midlings	4-05-205	19.6%
Menhaden oil		5%
Vitamin and mineral premix		0.4%

considering the high growth rate of larvae, the importance of EFA for their complete nutrition may be underestimated. For example, Santha and Gatlin (1991) showed that channel catfish fry require supplemental n-3 PUFA at a rate of 1.5% of the diet. Most workers now commonly include both plant oil and marine fish oil (high in n-3 PUFA) into experimental larval diets.

The requirement for, or the extent to which, carbohydrates serve as an energy source for larval Siluroidei is largely unknown. In fact this is one of the glaring voids in fish nutrition. Very little is also known about the energy requirements, and in particular about optimal protein/energy ratios. While some studies on DE values have been undertaken on early juvenile channel catfish (*table* 3) relatively little is known for the clariid catfish, except that it has been shown that protein and lipids are equally important as an energy source at the start of exogenous feeding (Conceicao *et al.*, 1993).

While a considerable body of information exists on the vitamin and mineral requirements of channel catfish fingerlings (Wilson, 1991), hardly anything is known about the requirements of first feeding larvae. At present Lovell's (1989) recommendation is generally followed, *i.e.* providing 2-3 times the requirement normally given to grow-out fish, to allow for the loss of the water soluble micro-nutrients. It is for this reason that dry feed particle are usually coated with fats just prior to feeding (Lovell, 1989). The recommended vitamin and mineral levels for channel catfish (Robinson, 1984) are also generally used in studies on clariid fishes. Using these levels no deficiency symptoms have been recorded in clariid larvae.

An example of two complete practical diets, which satisfy the nutritional requirements of *Clarias gariepinus* and *Ictalurus punctatus* are presented in *table* 4.

COMMENTS ON THE DRY FOOD VERSUS LIVE FOOD DEBATE

This debate has been ongoing since the publication of Appelbaum's (1976*a*, *b*) papers on the suitability of dry feed for the rearing of carp larvae. According to the grouping of larval fish (Dabrowski and Culver, 1991) *Cyprinus carpio* does not have a functional stomach during its larval stage nor, for that matter, throughout its life. Theoretically, therefore, according to the alternative life history model presented earlier in this paper the larvae of carp should not be able to digest dry feeds. However, the work undertaken by Appelbaum (1976*a*, *b*), Appelbaum and Dor (1978) and Dabrowski *et al.*, (1978) conclusively show that carp larvae can indeed be reared as successfully on dry food as on live food.

Considering the situation of *Clarias gariepinus* larvae it is evident that they do, in general, require live feed (Hogendoorn, 1980; Verreth, 1987; Segner *et al.*, 1993; Verreth *et al.*, 1993), although the studies by Hecht, 1981, 1982; Uys and Hecht, 1985; Appelbaum and Hecht, 1987; Appelbaum and van Damme, 1988; van Damme *et al.*, 1989*a*, *b*; 1990) also show that the larvae of this species can be reared exclusively on dry feed, although optimal growth was achieved using a combination of live and dry feed (Uys and Hecht, 1985; Hecht and Appelbaum, 1987; van Damme *et al.*, 1989). Studies on other *Clarias, Heterobranchus, Silurus* and *Heteropneustes* species have also shown the necessity for live feed, such as *Artemia* nauplii, *Moina* or tubifex worms (Bairage *et al.*, 1988; Mollah and Tan, 1982; Polling *et al.*, 1988; Salami *et al.*, 1993; Reddy and Katre, 1979; Hilge, 1986; Horvath, 1979), for successful primary nursing in preference to dry feeds. The question therefore arises; what was the difference between those studies in which dry feeds were used successfully and those in which they were not? In all successful studies the common denominator was the use of yeast based single cell proteins, of the genus *Candida.* It is of interest to note that Toledo and Gonzales (1986) also found best growth and survival of Channel catfish fry when offered yeast based diets. The term "successful" is used here to describe larval rearing experiments in which the condition, growth and survival fell within acceptable ranges.

Before considering the possible reasons for the success achieved with SCP it is worthwhile to consider several studies undertaken on the ontogeny of the alimentary tract and of physiological processes. These may shed some light on the reasons why dry feeds, in general, have not been successful as a first feed for *C. gariepinus* larvae. In a 10 day experiment Segner *et al.* (1993) found that the dry weight of dry food fed larvae was a mere 25% of the dry weight of those fed on live food. They used a normal (though unspecified) starter feed and provide convincing evidence, based on proteolytic activity, RNA/DNA ratio, histology, and quantitative food consumption and digestibility rates, that those larvae fed on dry food prior to the development of a functional stomach showed partial starvation symptoms. Essentially this implies that larval *C. gariepinus* cannot efficiently utilise dry feeds. The larvae only develop a functional stomach 4-5 days after the start of exogenous feeding (Stroband and Kroon, 1981; Uys, 1989), characterised by the formation of oxyntic glands in the thickened mucosa. During this pre-stomach phase Stroband and Kroon (1981) and Uys (1989) suggest that the larvae only have the digestive capacity to efficiently utilise natural food. When dry food is presented to the larvae at this stage they try to manage the new situation by inducing adaptive processes. However the adaptive capacities of larvae at this stage are small (Diamond, 1991) and limited by the existing "hardware" and the poorly flexible "software".

Verreth *et al.* (1993) suggest that the nutritional physiology of larval *C. gariepinus* is divided into two phases. These are correlated to two interrelated factors, *viz.* the development of a functional stomach and concomitant acid secretion and peptic activity. Figure 1 (adapted from Verreth *et al.*, 1993) shows the changes in proteolytic activity after the start of exogenous feeding. Similar results have also been presented by Van Damme *et al.* (1989) and Uys (1989) who found trypsin like activity in first feeding larvae when the stomach is not yet fully developed. Tryptic activity was found to decline once the stomach becomes functional, while peptic activity increases at this stage and reaches a maximum seven days after the start of exogenous feeding (Uys, 1989; Verreth *et al.*, 1993).

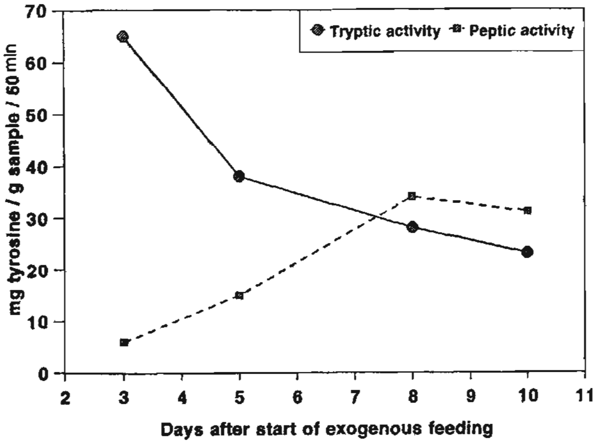

Figure 1. – Changes in proteolytic activity after the start of exogenous feeding.

These observations could possibly explain why (some) dry diets cannot be efficiently utilised by larval African catfish, which has led to the suggestion that they initially require live food. This would imply that live feed can be digested efficiently during the alkaline pre-stomach phase while dry feeds can only be digested once acid secretion has started and peptic activity comes on line. The timing of the events described above are indeed interesting when viewed in the light of the findings of Uys and Hecht (1985), Hecht *et al.* (1988) who recommend that African catfish larvae only require a live feed supplement for 3 to 4 days, and the interesting observation by van Damme *et al.* (1990) that feeding with *Artemia* nauplii should stop after 4 days as the size of the nauplii become sub-optimal and feeding becomes wasteful.

The study by Segner *et al.*, 1993, as mentioned above, has shown that *Clarias* larvae cannot utilise dry feed, while Uys (1989) makes the observation that growth rate of larvae is initially slow as a consequence of poor nutrient availability. However, once the catabolic pathways become established growth increases as nutrients become more available to the fish. Moreover, Hecht *et al.* (1988) and van Damme *et al.* (1989) point out that the growth of larvae is impaired if they do not receive a live feed supplement during the first 3-4 days (also Verreth and van Tongeren, 1989). Fermin and Bolivar (1991) also provide evidence which shows that *C. macrocephalus* larvae show best growth, condition, FCR and survival if fed on a combination dry and live food. By refining the SCP diet Appelbaum and van Damme (1988) found no significant difference in growth and survival of larvae if fed either on a SCP based dry feed from the start of exogenous feeding or on *Artemia,* thus negating the need for live feeds.

The questions that arise from the above are: (i) does the digestion of live feed by larvae involve exogenous enzymes supplied by the live feed organisms or is the tryptic proteolytic activity sufficient for their digestion, (ii) if the former suggestion where true then the relative indigestibility of dry feeds would be understandable, however, if this is not the case then why can dry feeds (except possibly SCP based diets) not be efficiently digested by the early proteolytic enzymes.

It is known that exogenous enzymes activate fish zymogens (Jancarik, 1964). Moreover, Dabrowski and Glogowski (1977) and Lauff and Hofer (1984) have shown that exogenous enzymes from zooplankton contribute largely to the total proteolytic enzyme activity in fish larvae and juveniles. Given this information it can be assumed that exogenous enzymes from live feed organisms contribute significantly towards the digestion of live feeds.

The successful digestion of yeast based dry feeds must, and can only be attributed to better digestibility of the proteins in these diets by the initially underdeveloped (pepsin lacking) enzyme system. This conclusion is justifiable if one considers, firstly, that a functional stomach facilitates protein digestion by enzymes of pancreatic origin by first denaturing and partially hydrolysing the proteins (Lauff and Hofer, 1984). Secondly, the inactive yeasts, such as torula, are roasted during the manufacturing process, thereby denaturing the proteins to a significant degree, which in turn facilitates their digestion in an initially alkaline proteolytic environment. This would explain the unsatisfactory results reported by other workers who have attempted to use other protein sources as dry feed ingredients for African catfish larvae.

The need to intensify investigations on the development of optimal dry feeds is evident. However the approach should shift from empirical research to understanding the digestive biochemistry and capabilities of the larvae as well as into the nature and quality of the protein sources.

It would also be interesting to know whether those larvae reared exclusively on dry feeds (although they might have a slight growth disadvantage) are able to "catch up" to their siblings fed on a combination of live and dry fed, or exclusively on live feed, by compensatory growth mechanisms once they are transferred into nursery ponds. If this were indeed the case then there would be no need to provide the larvae with live food during the first four days prior to the development of a functional stomach and the concomitant peptic activity.

CONCLUSION

From the preceding discussion it becomes clear that the altricial/precocial life history model might be of predictive value in the nutrition of larvae and early juveniles. This warrants further investigation, particularly as regards those Siluroidei species which are currently regarded as candidate species for aquaculture.

In undertaking this review the differences in approach to assessing the nutritional requirements of a species, and the lack of standardised methods allowing for meaningful comparisons was glaringly apparent. This includes the application and use of standard test diet (Wilson, 1991). Cognisance has to be taken of the variable growth potential of different genetic strains of a particular species (van Damme *et al.*, 1989).

A call is also made for researchers to undertake nutritional and feeding studies under established optimal environmental conditions. It is quite senseless to undertake work of this nature under sub-optimal conditions, let alone to draw comparisons between such studies. It therefore logically follows that the optimal environmental conditions should be known prior to the undertaking of any nutritional and feeding related studies. Care should also be taken to exclude any possible other extraneous effects which might affect the functioning of the physiological system which, in turn, might be interpreted as a result of nutrition or feeding practice.

To expedite the development of complete diets, the following approach is recommended for undertaking nutrition and feeding studies on larvae and juveniles of species that are currently being considered for aquaculture. To firstly, review the natural history of the potential aquaculture species and to consider its relative position on the altricial/precocial continuum. Such an investigation would provide the necessary clues as to the kind of diet required and the length of the weaning period. To investigate and define the optimal environmental conditions for the rearing of the specific larvae. To study the histological and macroscale ontogeny of the digestive tract and associated organs, followed by a study of the ontogeny of enzymatic processes. A study should also be undertaken of the natural diet of the larvae and to profile the 10 essential amino and fatty acids of the natural diet and to establish the amino and fatty acid profile of yolk-sac and first feeding larvae. Finally, as a first approximation of a formulated feed to mix and match high quality feed ingredients in accordance with the amino and fatty acid profiles.

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