The African catfish (*Clarias lazera* C. & V., 1840) -
A new species for aquaculture

Aan: mijn ouders
Guusje en
haar ouders

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THE AFRICAN CATFISH *(CLARIAS LAZERA* C. & V., 1840) - A NEW SPECIES FOR AQUACULTURE

Proefschrift
ter verkrijging van de graad van
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ABSTRACT

Hogendoorn, H., 1983. The African catfish, (*Clarias lazera* C. & V., 1840) - A new species for aquaculture. Dissertation, Agriculture University, Wageningen, The Netherlands, 135 p., 22 figs., 27 tables, 1 appendix, English and Dutch summaries, includes reprints from Aquaculture.

Fish husbandry can contribute substantially to the production of animal protein for human nutrition, especially in tropical countries. To determine the suitability of *C. lazera* for aquaculture, the propagation and production management as well as the growth physiology of this fish were studied.

The planned production of *Clarias* fingerlings can be realized through artificial reproduction, including hypophysation followed by stripping of the females and dissection of the testes of the males to fertilize the eggs. Methods for successful incubation of the eggs and subsequent rearing of the fry to fingerlings are reported.

In growing the fingerlings to marketable size good results were obtained both in extensive pond-farming as well as in high density culture in tanks. Under conditions that prevail in African subsistence fish farming, the *Clarias* outyield tilapia by more than 250%. Under optimal conditions in tanks they grow more than 200 g in 5 months from birth, while the feed conversion rate (feed/ gain) stays well below unity. The efficient feed conversion is explained by modest maintenance requirements as compared with the maximum feed uptake and feed utilization capacity. The effects of body weight, temperature and feeding level on the growth and feed utilization of *C. lazera* were studied and discussed. On this basis a feeding guide for the intensive culture of the African catfish was established.

STELLINGEN

1. Nu voor de vermeerdering en de produktie van de Afrikaanse meerval bedrijfszekere methoden zijn ontwikkeld, kan het gebruik van deze soort in de visteeltpraktijk worden aanbevolen.

Dit proefschrift.

2. De zeer goede voederconversie van de Afrikaanse meerval tijdens de groeiperiode komt voort uit de gunstige verhouding tussen de hoeveelheden onderhouds- en produktievoer.

Dit proefschrift.

3. De voederbenutting door vissen van verschillende grootte is slechts dan vergelijkbaar, wanneer het voederrantsoen is gerelateerd aan een fysiologisch definieerbaar voerniveau.

Paloheimo,J.E. and L.M.Dickie, 1966. J.Fish.Res.Bd.Can., 23:869-908; idem, 23:1209-1248.
Dit proefschrift.

4. De mislukking van de tilapiateelt in Afrika na de vijftiger jaren toont aan, dat eenvoudige teeltmethoden een onvoldoende garantie vormen voor het met succes introduceren van visteelt in tropische landen.

Lemasson,J. et J.Bard, 1968. FAO Fish.Rep. 44(5):182-195.
Huet,M., 1972. Textbook of Fish Culture.

5. Visteelt is meer verwant met veehouderij dan met visserij. Dit wordt door de huidige visteeltpraktijk en vooral de begeleiding daarvan nog onvoldoende weerspiegeld.

Dit proefschrift.

6. Een op vrouwen gericht programma ter bevordering van de zelf-voorzieningsvisteelt heeft in Afrika meer kans van slagen dan wanneer mannen de doelgroep vormen.

7. Versnippering en discontinuïteit van projektgebonden ontwikkelingshulp leiden ertoe, dat de doelstellingen van projekten doorgaans niet kunnen worden gerealiseerd, en dat niet zelden een hieraan tegengesteld effekt wordt bereikt.

8. Bestrijding van overmatige groei van waterplanten met behulp van grasкarper is milieuvriendelijker, effektiever en goedkoper dan wanneer deze met mechanische of chemische middelen wordt uitgevoerd.

9. Het advies aan de Nederlandse sportvissers: 'Zet uw vis terug in het water en bewaar uw sport voor later' is achterhaald.

10. Aalscholvers en zilvermeeuwen in het Nederlandse cultuurlandschap vereisen een gericht beheer, dat is gebaseerd op een vast te stellen aantal na te streven dieren.

Van Dobben, W.H., 1982. Het vogeljaar 30(6):317-320.
Abrahamse, J. en F. Luitwieler, 1983. Waddenbulletin 1983-2:15-17.

11. Sinds 1973 is de Europese meerval in Nederland vanwege z'n schaarste beschermd. Het geeft te denken dat juist dít er in 1980 toe heeft geleid om 450 van de laatst aanwezige exemplaren te elimineren.

OVB-Bericht, 1980. 2:35.

12. Een goede buurvrouw is beter dan een verre vriendin.

Proefschrift H.Hogendoorn
The African catfish *(Clarias lazera* C&V , 1840*)* - A new species for aquaculture
Wageningen, 18 mei 1983.

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Going back in time, I like to start by thanking my parents, farming relatives and home neighbours, who taught me to finish what I start and to look after animals well, once they are placed in my charge. I remember mr H. Hogenbirk, mr H.A. Ekhart and dr C.A. Peeters as school teachers, who not only emphasized learning but at the same time clearly showed its joys and its relativity. During my University training prof dr ir R.D. Politiek, the late prof dr Th. Stegenga and his successor, prof dr C.C. Oosterlee assisted in my "deviation" from terrestrial into aquatic animal production. Dr R. Bootsma, prof dr ir A.J.H. van Es, prof dr E.A. Huisman and dra Wilhelmina de Ligny helped to organize my post-graduate fish culture research programme.

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CONTENTS

PREFACE

This study on the use of the African catfish, *Clarias lazera* (Cuvier & Valenciennes), for aquaculture was started in 1974 at the National Fish Culture Centre in Foumban, Cameroon, as part of a UNDP/FAO Fish Culture Development Project. The objectives of this project were to

- implement local fish culture training and extension programmes,
- establish centres for demonstration of commercial type fish culture, and
- carry out fish culture experiments and pilot studies.

Within the programme, the possibilities to develop the culture of *C. lazera* were limited. However, the few experiments which were carried out indicated its potential. The results also showed the necessity for further research under better defined conditions.

Fortunately, such research could be realized at the newly created Department of Fish Culture and Inland Fisheries of the Agriculture University in Wageningen, The Netherlands. Here, it proved possible to verify and substantiate some of the hypotheses that originated from the period of field work. Consequently, there is a persistent reference in the results reported in this thesis to their applicability in the practical culture of *C. lazera*. This also explains the emphasis which was placed on the statistical evaluation of the results as opposed to an approach based on analytical biology.

It is further noteworthy that some of the initial findings of this study have triggered the undertaking of additional research into the biology of the culture of *C. lazera* by others. Some results are also already applied in practical fish culture in Central Africa and in the Middle East. In order to assist these developments it was decided at an early stage to report the experimental evidence as it became available. The result has been a series

of eight papers on various aspects of the propagation, the growth and the production of *C. lazera*. These papers form the main body of this thesis.

1 GENERAL INTRODUCTION

From ancient manifestations of art we know that fish and fishing can be linked to the development of mans earliest civilizations. Ever since, fish have been of considerable nutritional and economic importance. Their influence on human society has even extended to cultural aspects of food behaviour, beliefs and religion (Kreuzer, 1974).

The quantitative importance of fishing is reflected by the increase in world fish catch between 1950 and 1970 from about 19 to 63 million t per year (Moiseev, 1973). It was then estimated that 3/4 of the suitable food fish resources were being utilized and a possible increase of 16% in the catch was predicted before a maximum sustainable level was reached (Moiseev, 1973; Suda, 1973). Now, the fishery yields have stabilized at 70-72 million t/year (Anonymous, 1981), and the constant international discussions about fishing rights and quota indicate that fish have become scarce and a further increase in its supply is not to be expected.

To try to satisfy the growing demand for fish and fish products, there are three alternatives to increasing the fish catch. One is the exploitation of other, preferably low trophic-level, aquatic animals e.g. the Antarctic krill. Although the potential annual catch of the 5 cm shrimps could be 25-50 million t (Lyubinova et al., 1973), it needs to be developed into an attractive food product with due attention to the logistics and economics of the operation. A second approach is by increasing the proportion of the present fish catch which is actually used for human consumption. One way is through reduced spoilage by improved handling and processing methods, a matter of science and technology. Another way is to increase the human consumption of those fish, presently used for reduction to fish meal. To this end different products must

be developed to comply with consumer preferences. The third alternative lies in the further development of aquaculture, the aquatic analogue of terrestrial animal husbandry, which on land has almost completely replaced hunting as source of animal protein. In 1980 the total yield of aquaculture was over 8.5 million t, which is a more than 40% increase over the 1975 production level (Anonymous, 1982).

In the indrustrialized western world, aquaculture is known and practised in many forms from ocean ranching to highly intensive cage or tank operations. Generally, it involves the production of high quality, luxury species. The scale and pace of its further development will largely depend on the economics of luxury trade. By contrast, in many tropical countries, the fish species and the system for their culture are selected mainly to minimize the cost of production per unit of protein. Low trophic-level species are used and often they are mixed in polyculture for optimal utilization of the aquatic productivity or they are grown in association with land animals to use the available wastes. It is in these tropical countries, that aquaculture can contribute considerably to the production of human food. Water is usually available in abundance and the prevailing temperatures enable fast and continuous growth of fish as well as good resistance against diseases.

Moreover, many people in these countries are ill-nourished. Not only do they face temporary or chronic overall food shortages resulting in undernutrition, but more often they are in a condition of malnutrition caused by a shortage of protein. According to FAO data (Anonymous, 1980) the per capita energy intake in 1975-77 averaged 2282 kcal/day in the developing countries as opposed to 3373 kcal/day in the industrialized world. The daily per capita protein consumption shows a world average of about 70 g, but in some 12 equatorial African states it was estimated at 48 $\pm$ 9 g. In assessing the nutritional meaning of these protein intake levels, the digestibility and biological value of the various proteins must be taken into account. The resulting protein utilization generally is 75-95% for animal protein, while it ranges from 50-70% for the common plant protein foods (Cunha, 1982). Bell and Canterberry (1976) estimated that in 1970 only 25% of the protein consumed in the above equatorial African countries originated from animals, including 11% from fish. So, the effective protein intake is even lower than the data indicate.

In view of the above it is evident that aquaculture is essential to many developing countries. In Asia and the Far East, aquaculture already is several thousands of years old. The brackish-water culture of milkfish (*Chanos chanos*) in Java and the Philippines as well as the pond culture of various species of carps in China and India have evolved over the ages (Tubb, 1967). In Latin America, there is virtually no history of aquaculture (Miles, 1967) and only some recent initiatives exist. The introduction of aquaculture in equatorial Africa essentially took place after the second world war (Meschkat, 1967). Following the initial introduction of tilapia culture in central Africa between 1946 and 1949, their production in ponds was undertaken almost all over the continent. In 1959/60 close to 300.000 fish ponds were in operation in about 20 African countries (Meschkat, 1967). From then on the interest in aquaculture started to decline and the majority of ponds were abandoned (Huet, 1972). The fish farmers became discouraged, when they were harvesting too many small tilapia from over-populated ponds. This over-population was caused by the general method of stocking mixed age groups, both for reproduction and growth, and the high prolificacy of tilapia.

A reorientation was then proposed to differentiate between the production of marketable tilapia and that of the necessary fry (Lemasson and Bard, 1968). Preferably, the latter were to be monosex hybrids produced at specialized stations. Although numerous fry production stations were established (Meschkat, 1967), the necessary aquacultural infrastructure did not materialize. The entrepreneurial skills of the fish farmers, the management quality at the fry production stations and the liaison by fish culture extension services etc. did not meet the high standards required for successful tilapia culture (Miller, 1975; Hepher and Pruginin, 1982).

It was, therefore, agreed at the 1966 World Symposium on Warm-water Pond Fish Culture to try to identify new species more suitable for aquaculture (Lemasson and Bard, 1968) and compatible with consumer preferences (Pillay, 1967). Instead of introducing non-indigenous species, which are unknown and therefore not always easily acceptable to the consumer, a study was made of local fish populations (Micha, 1973). Comparative growth and maturation experiments were carried out to assess the suitability for aquaculture of a number of species, of which *C. Lazera* best met the requisite conditions as listed by Huet (1972):

- be adapted to the climate
- have a high growth rate

- be able to mature and reproduce in captivity
- accept and thrive on cheap feeds
- be acceptable to the consumer
- support high population densities
- be resistant against diseases

Once a promising candidate species has been identified, the possibilities and constraints for the various phases of its culture must be elaborated to provide the basis for a production programme. Invariably, in fish culture a production cycle starts with young, immature animals capable of rapid and efficient growth. Therefore, fry and fingerlings must be available in large numbers, more so, since these small fish are vulnerable and considerable losses may occur. To obtain the fingerlings required for stocking, various methods can be employed varying from catch of wild fish to completely controlled artificial propagation. The usefulness of the different methods can be assessed by the reliability of the supply of fingerlings.

During the subsequent growing of the fingerlings to fish of marketable size many factors interfere. The main question is what feed to give to the fish and how much. Starting from the intake of the feed, the processes of digestion, absorption, assimilation, excretion and the corresponding metabolic losses then determine whether body substance will be gained or lost. These processes, in turn, are governed by internal and external, biotic and abiotic factors. In fish the abiotic, environmental factors (temperature, oxygen, etc.) combine with the internal situation (body weight, maturity etc.) to determine the potential (scope for) growth. It then depends on the availability and the quality of the feed what fraction of this potential will materialize as actual growth. To facilitate studying the complex growth of fish for culture, the above question can therefore be rephrased as

- what is the nature of the growth,
- what are its limits,
- how are these limits reached, and
- what are the (economically) optimal conditions.

In the following chapters, experiments are reported on various phases of the culture of *C. lazera*. First of all different propagation procedures were compared. The most promising methods were then further investigated. Secondly, the growth and production of *C. lazera* in small ponds were studied and compared

with those of the tilapia (*Sarotherodon niloticus*). The limits of the growth of *C. lazera* were subsequently determined in a tri-factorial experiment with body weight, temperature and feeding level as variables. A mathematical model was developed to describe the relation of these factors. Finally, the relation of body weight and feed ration was studied on a bioenergetic level. A description of the apparatus used for this experiment is also given.

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2 CONTROLLED PROPAGATION OF THE AFRICAN CATFISH, *CLARIAS LAZERA* (C. & V.)

I. Reproductive biology and field experiments

II. Artificial reproduction

III. Feeding and growth of fry

IV. Effect of feeding regime in fingerling culture

Aquaculture, 17 (1979) 323—333

CONTROLLED PROPAGATION OF THE AFRICAN CATFISH, *CLARIAS LAZERA* (C. & V.)
I. REPRODUCTIVE BIOLOGY AND FIELD EXPERIMENTS

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ABSTRACT

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Field experiments on controlled propagation of *Clarias lazera* (C. & V.) were carried out in Cameroon in 1975—1976. Reproduction was induced in small ponds using desoxycorticosterone acetate. In artificial reproduction experiments, ovulation was induced with acetone-dried carp pituitary and the sexual products were obtained by stripping the females and dissecting the males. Artificial fertilization, incubation and hatching of the eggs were successfully carried out.

Different methods of producing fingerlings in ponds were compared but none was considered satisfactory. Rearing the fry in troughs was not achieved, but it is felt that this offers the best prospects for reliable production of fingerlings. Suggestions for further improvement of the techniques are given.

INTRODUCTION

Clarias lazera (Cuvier and Valenciennes) was first used in fish culture in the Central African region in 1970. Subsequently its growth and production potential were demonstrated by C.T.F.T. (1972) and Micha (1973). Propagation was only partly successful and the general use of *C. lazera* in fish culture was thus forestalled. Experiments to improve the propagation techniques further were initiated at the National Fish Culture Centre, Foumban, Cameroon. The results of these experiments are presented in this paper, which is the first in a series on the controlled propagation of *C. lazera*.

Because knowledge of the biology of natural reproduction can be helpful in developing successful hatchery and nursery procedures (Sneed et al., 1970; Huisman, 1976) a brief background of literature on the reproduction of *C. lazera* is given.

REPRODUCTIVE BIOLOGY OF *C. LAZERA*

Very little is known about breeding cycles and spawning habits of African fishes in their natural habitat (Richter, 1976). M.N. Bruton (personal communication, 1978) observed that in the case of *C. lazera* large numbers of fish congregated in a few shallow, inundated, vegetated areas during spawning. This observation agreed with the findings of Thomas (1966), Micha (1973) and Jocqué (1975b) in Lake Nungua (Ghana), the Ubangui River (Central Africa) and Lake Kossou (Ivory Coast), respectively.

Thomas (1966), who sampled 20 *C. senegalensis* per month, from March 1959 to February 1960, found that spawning in Lake Nungua (Ghana) occurred from April to September. Micha (1973) and Jocqué (1975b) determined the gonadosomatic index and the developmental stage of the eggs, and concluded that peak maturity occurred from August to October, but some mature eggs were found at all times. This was supported by Pham and Raugel (1977) for *C. lazera* kept in ponds.

Thomas (1966) did not find mature females under 30 cm in length. The smallest mature female found by Jocqué (1975b) in Lake Kossou was 27 cm, but a mature 8-month-old female of 20 cm was found in a pond. Micha (1973) reported that at the age of 4 months sexual dimorphism was already apparent in cultured females, followed by sexual maturity at the age of 8 to 10 months.

As has been illustrated by De Kimpe and Micha (1974; fig. 3), the male possesses an elongated, pointed urogenital papilla, while in the female the vent is more rounded with a longitudinal cleft. A mature female is also characterized by a deeper and more rounded abdomen.

With regard to the fecundity of the females, Nawar and Yoakim (1962) found 13 900 to 164 800 eggs per female, while Micha (1973) and Jocqué (1975b) reported 3000 to 328 000 and 5000 to 200 000 eggs per female, respectively. No relation between the females body weight and the number of eggs produced was apparent. The authors suggested that this was due to intermediate partial spawning.

According to Micha (1973) and M.N. Bruton (personal communication, 1978) mating is short. The spawning, as was observed by various authors for different *Clarias* species, follows a period of prespawning activities (Holl, 1968; Micha, 1973; Van der Waal, 1974). During this time the male repeatedly approaches the female with the dorsal fin in an erect position and nudges and bumps against her abdomen. During the actual spawning the male curves his body round the front of the females head. The female then bends her body, turning sideways, and the male curvedly slides over her head and down her side. At this moment a small cloud of eggs and milt is ejected which is scattered around by vigorous tail flicking of the female; this action is repeated at certain intervals.

Unlike the Asian Clariidae, *C. lazera* does not display parental care (Micha, 1973; Sidthimunka, 1973). Embryonic development, which at a water temperature of 26°C was accomplished within 24 h, and larval development were described by Micha (1973).

MATERIALS AND METHODS

Throughout the experiments brood fish were kept in segration ponds. They were fed daily with a mixture of wet brewery waste, ground cottonseed cake and blood, sometimes supplemented with dead fish.

On the day prior to reproduction, brood fish were taken out of the segregation ponds in order to evaluate the ripeness. This was based on exterior evaluation. The females were selected when they displayed a rounded, soft abdomen, a reddish vent and appearance of a few eggs upon slight pressure on the abdomen. Males with a slightly vascularized genital papilla were preferred. All fish were used only once in the experiments in a single season. Two different reproduction techniques were tested, namely induced reproduction in ponds and artificial reproduction. Three different rearing techniques were tried.

Induced reproduction in ponds

In order to induce reproduction the females were injected at midday with desoxycorticosterone acetate (DOCA, 0.5% in oil suspension, Laboratoires Biergon, Liège, Belgium) at a dose of 50 mg active hormone/kg body weight. The injections were administered intraperitoneally just caudal of the pectoral fin.

Subsequently the fish were placed in a pond that was being filled with water, but had been dry for at least 2 weeks to assure elimination of predacious insects. Frogs and toads, as well as their eggs, were removed whenever noticed. After 6 days the brood fish were seined out. Fertilization was then carried out with rumen content of cows in combination with 1 kg superphosphate/ 100 m^2 pond area. On the 6th day and onwards blood meal was fed together with ground cottonseed cake and wet brewery waste. A surface layer of diesel fuel was applied to control predacious insects whenever necessary.

The experiment was repeated in 11 different ponds which were drained after 5 to 10 weeks to determine the number of fingerlings. This number was calculated from the total weight of all the fingerlings and the number present in a sample of about 1 kg.

Artificial reproduction

Following the techniques developed for other species, (Woynarovich, 1953, 1955; Clemens, 1968; Chen et al., 1969; EIFAC, 1976; Huisman, 1976) an attempt was made to artificially reproduce *C. lazera*. After some initial disappointing results it proved that the females could be stripped 11 to 16 h after injection with acetone-dried carp pituitary (Stollers Fisheries, Spirit Lake, Iowa 51360, U.S.A.) at a dose of 4 mg dry material/kg female body weight. Similar treatment of the males was not successful. Upon dissection it proved that the testes were kidney shaped with the lobate convex side lateral. It seemed

that the ripe milt gathered along the convex edge in the lobes; this probably impeded stripping of the males. However, a few droplets of milt were obtained when the dissected testes were minced.

The injections were prepared by mashing the carp hypophysis in 2 to 3 ml of distilled water in a small mortar, and were administered as described previously. To avoid fighting and to prevent escape the fish were individually kept overnight in covered basins. After the methodology had been developed, a total of 31 *C. lazera* females were artificially reproduced to evaluate the suitability of this technique for obtaining fertilized eggs.

At a water temperature of 19 to 21°C the females could generally be stripped early the next morning. Eggs were collected in a small dry receptacle and weighed. Subsequently, a male was sacrificed and the milt added to the fresh eggs. Some water was then added and a period of up to 1 min was allowed for fertilization, during which the eggs were gently swirled around to prevent clotting. The eggs were then either transferred to a pond or, in the case of 12 females, incubated indoors. These eggs were deposited on a series of 2-cm deep plastic trays filled with water, in such a way that an incomplete monolayer of eggs was established. After 4 h, when the eggs were well adhered to the trays, the water was changed; this was repeated at 10, 24, 34 and 48 h. The incubation results were determined after 4, 24 and 48 h by enumerating dead (white) and live (transparent) eggs. After 24 h the incubating eggs were treated against fungus with formalin (1000 ppm, 15 min). At 20°C hatching occurred after about 48 h, and the newly hatched larvae were transferred into a rearing trough.

Rearing of fry

Three rearing experiments were carried out to obtain fingerlings from the artificially fertilized eggs. In the first experiment six small ponds were stocked with eggs immediately after fertilization. The ponds received 1 kg superphosphate and 40 kg of cows rumen content/100 m^2. Application of ground cottonseed cake, blood meal and wet brewery waste was started on the day of stocking. The ponds were drained and the number of fingerlings was determined after 5 to 9 weeks.

In the second experiment the fry were kept in a small rearing trough with a slow exchange of water until yolk sac absorption was almost complete. The free-swimming fry were then released in six newly filled ponds. Fertilization and feeding were as described previously. The ponds were drained and the number of fingerlings was determined after 5 to 14 weeks.

The third experiment was identical to the second up to the point of yolk absorption. However, rearing was continued in wooden troughs (2.5 m × 0.4 m × 0.3 m high) with running water, supplied at a rate of about 1 change/h. Feeding was initiated 3 days after hatching and consisted of boiled egg yolk, milk powder, trout starter ("Trouvit 000", Trouw and Co., Putten, The Netherlands) and plankton obtained with a 30 or 55-μ mesh size plankton net. Final fingerling counts were made after 2 to 4 weeks.

RESULTS

Induced reproduction in ponds

The use of DOCA was successful and an ample quantity of fertilized eggs was observed in the ponds the day after treatment. Fry were observed in all the ponds when the brood fish were seined out on the sixth day.

At 3 weeks of age the fish started to rise to the surface, and assemblage at the feeding location was thus observed, indicating feed conditioning. Throughout the experiment the fry and fingerlings displayed a tendency to hide under grass and leaves in the pond.

Both frogs and tadpoles, as well as water-scorpions and the larvae of dragon-flies and water-beetles, have been observed to predate on small *C. lazera*. Although the number of frogs was kept low, tadpoles appeared. Diesel fuel effectively controlled water-boatmen and water-beetles, but water-scorpions and the larvae of dragon-flies and water-beetles were not visibly affected. In the 11 ponds an average of 17.4 ± 14.4 (S.D.) fingerlings were produced per m^2 pond area (Table I).

Artificial reproduction

Hypophysation was succesful with 30 females which produced between 16 and 205 g of eggs. In one instance the female died overnight for unknown reasons and no eggs were obtained. The eggs of five random females were sample counted and averaged 610 ± 8.5 (S.D.)/g. It appeared (Fig. 1) that for fish above about 1500 g the egg production did not appreciably increase compared to smaller fish. This was substantiated by regression of the number of eggs produced on the female body weight, where inclusion of a quadratic component significantly ($F^1_{27} = 9.92^{**}$) increased the coefficient of determination ($r^2 = 0.53^{**}$) as compared to the first-order equation ($r^2 = 0.36^{**}$).

TABLE I

Fingerlings obtained from induced reproduction of *C. lazera* in ponds

Pond area (m^2)	Females		Fingerlings
	No.	Ave. wt. (kg)	No. (× 100)
334	1	1.50	24.6
95	2	0.45	0.0
65	2	0.48	2.0
111	2	0.55	38.0
109	2	0.58	15.7
300	5	0.44	105.6
50	1	0.50	0.8
350	4	0.70	50.0
69	1	0.35	10.3
50	1	0.50	20.0
53	1	0.50	13.9

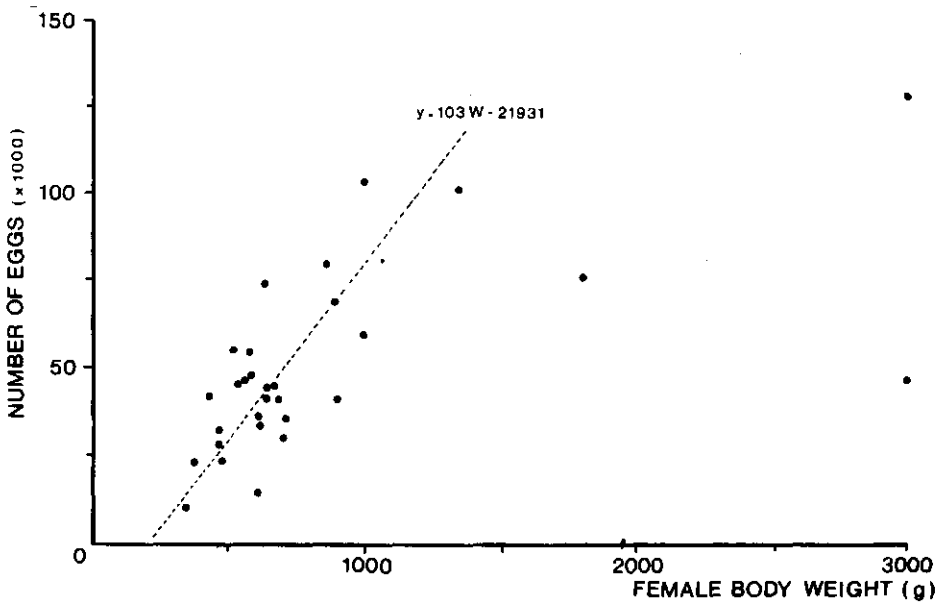

Fig. 1. No. of eggs produced in relation to female body wt.

Most of the males sacrificed gave sufficient milt to fertilize the eggs of one or more females. Sometimes less milt was obtained when testes were watery-pink instead of the "normal" milky-white, or when they were atrophic or unpaired.

The results obtained in incubation and hatching are given in Table II. Some eggs were already dead at the moment of stripping. It was further noticed that unfertilized eggs developed "normally" until the 8 or 16 cell stage or more, and that it sometimes took up to a day before they turned white; this was also reported by Lindroth (1946) and Huisman (1974). Consequently, the early egg counts were poor indicators of the fertilization percentage. However, the hatching percentage can be used as an indicator of the minimum fertilization percentage. It thus showed that in one instance fertilization was 92% or more. The formalin treatment proved effective in controlling fungi and changing the water was also expedient for normal egg development. The tray method of egg incubation enabled easy and almost complete separation of dead eggs and newly hatched fry.

Rearing of fry

It is clear from Table III that the number of fingerlings obtained from ponds stocked with newly fertilized eggs was highly fluctuating: an average of 17.4 ± 22.7 (S.D.) fingerlings/m^2 pond area.

Stocking of the ponds with free-swimming fry did not improve the results to any appreciable extent (Table IV): 2.7 ± 1.6 (S.D.) fingerlings/m^2 pond area.

TABLE II

Results obtained in incubation and hatching of eggs of *C. lazera*

No. of eggs	Percentage of eggs alive after[1]			Hatching (%)
	4 h	24 h	48 h	
1935	94	0	0	0
1650	97	87	84	84
4197	99	93	0	0
2106	97	48	46	46
6076	99	x	71	x
$120 \cdot 10^3$	99	x	x	80
$29 \cdot 10^3$	99	93	93	92
$39 \cdot 10^3$	98	x	75	50
$66 \cdot 10^3$	x	x	x	60
$20 \cdot 10^3$	99	75	x	x
$73 \cdot 10^3$	97	x	x	65
$46 \cdot 10^3$	99	65	50	0

[1] x = no observation recorded.

TABLE III

Fingerlings obtained from ponds stocked with newly fertilized eggs

Pond area (m^2)	No. of eggs released (x 1000)	No. of fingerlings (x 100)
109	30	28.7
65	24	38.0
350	180	5.0
350	165	2.7
300	90	2.5
300	153	50.0

TABLE IV

Fingerlings obtained from ponds stocked with free-swimming fry

Pond area (m^2)	No. of fry released (x 1000)	No. of fingerlings (x 100)
50	0.5	1.3
334	30	9.1
5150	95	51.5
334	22	3.1
200	10	7.0
200	10	10.6

The rearing of the fry in a small rearing trough until the end of yolk sac absorption took about 3 days and presented no difficulties. A slow exchange of water was necessary in order to maintain a sufficient concentration of dissolved oxygen. When a cover was placed over part of the trough, the healthy and viable fry congregated under the cover, leaving behind the dead and deformed ones that were then siphoned off.

The results obtained in experiment 3 where the whole process of fingerling production was kept indoors (Table V) were inferior to those obtained in ponds. The main problems were slow growth, a poor general condition and mortality. The last trial resulted in more than 26 000 fingerlings, but was terminated at a stage where mortality had just started.

Feeding in itself did not present any difficulties and the feedstuffs were readily taken from the start. An infestation with *Trichodina* sp. was temporarily controlled by treatment with 50 ppm formalin for 1 h.

TABLE V

Fingerlings obtained from rearing of the fry in wooden troughs

No. of free-swimming fry (x 1000)	No. of fingerlings (x 100)
18	1.2
20	13.0
20	12.8
47	262.2

DISCUSSION AND CONCLUSIONS

Ovulation was successfully induced in mature *C. lazera* females with DOCA or acetone-dried carp pituitary. This seems to indicate that both can be used, but it may be worth trying to inject fresh pituitaries, which would make the technique more suitable for isolated African conditions.

It has already been stated that in artificial reproduction experiments the results obtained with stripping of the females showed that larger fish produced relatively less eggs. From the point of view of fish culture management it is therefore impractical to work with such fish. When the three heavier females were excluded, regression analysis showed that the quadratic term was no longer significant ($F^1_{24} = 0.11$). If a first-order relation is now to be determined, it must be borne in mind that the values for both the females body weight and the number of eggs produced are subject to natural variability as well as measurement error. For such a situation a functional regression line is more suitable than the ordinary predictive regression (Ricker, 1973). The coefficient of the functional regression is calculated as the geometric mean of the coefficient of the predictive regression of y on x and the reciprocal of the coefficient of the predictive regression of x on y. This line then minimizes the residual sum of

squares in the direction of both the ordinate and the abscissa. Using this procedure as given by Ricker (1973), the following equation was obtained

$$Y = 103 \cdot W - 21\,931$$

where Y = number of eggs produced and W = female body weight (g).

Using the "geometric mean" regression, the reality of this association between female body weight and number of eggs produced cannot be tested in the normal way. However, it is evident from Fig. 1 that the fit should be good. For the confidence limits of the geometric mean regression line, Ricker (1973) found that using the ordinary confidence limits, based on the correlation of the normal predictive regression, gave a reasonable approximation. Based on the experimental data and using a 95% confidence interval, it can then be concluded that *C. lazera* females, up to a weight of 1500 g, produce 103 ± 27 eggs/g body weight over 213 g.

Artificial fertilization, incubation and hatching have not been successful with the brood of all females. Nevertheless, it must be concluded that this technique was highly satisfactory. An advantage of the method was that incompetent males were recognized at an early stage; this proved difficult to achieve with other techniques reported (Micha, 1973; Jocqué, 1975a; Pham, 1975; Delincé, 1977). Poor quality eggs could also be recognized and discarded within 48 h, with little consequence. By contrast, in pond reproduction an unsuccessful spawn caused the loss of considerable pond exploitation time. When the eggs were incubated and the fry kept under controlled conditions, they were protected against predation and a high level of sanitation could be maintained. In addition, fry could be easily obtained and manipulated when they were required for controlled rearing. Further work is necessary to optimize the methods of artificial reproduction and egg incubation.

The results obtained with the induced reproduction in ponds compared favourably with those reported in literature (Micha, 1973, 1975), but remained too fluctuating to serve as a source of fingerlings for large-scale fish culture. The same can be concluded for the different rearing experiments in ponds. Because no improvement in the results was observed when ponds were stocked with fertilized eggs or free-swimming fry, it has not been possible to identify the time or stage when the heaviest mortality occurred. Of all possible explanations for this mortality, a lack of appropriate feed, and as a consequence mortality after swim-up, was considered the most likely cause. This was based on the observation that plankton always developed slowly after the ponds had been filled. The method applied in pond rearing of carp fry in Eastern Europe (Horvath, 1978) may be helpful in overcoming this problem: prior to stocking, ponds with an established plankton bloom are treated with a fast-degrading pesticide to eliminate animal organisms. The fry are then stocked when the rapidly regrowing zooplankton has reached the right size to serve as feed for the fish.

Finally, it can be concluded that the rearing of young fry was not successful in the indoor experiments. Although the feed was apparently well ingested, growth rate was poor and health conditions were suboptimal.

Nevertheless, it is felt that the approach using intensive indoor nursery procedures offers the best perspectives for a reliable production of *C. lazera* fingerlings for large-scale fish culture. It is suggested that further research be concentrated on the qualitative aspects of feeds and feeding and on the influence of water temperature and water quality.

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CONTROLLED PROPAGATION OF THE AFRICAN CATFISH, *CLARIAS LAZERA* (C. & V.)
II. ARTIFICIAL REPRODUCTION

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ABSTRACT

Hogendoorn, H. and Vismans, M.M., 1980. Controlled propagation of the African catfish, *Clarias lazera* (C. & V.). II. Artificial reproduction. *Aquaculture*, 21: 39—53.

To optimize the artificial reproduction of *C. lazera* for aquaculture, experiments were carried out on short-term sperm conservation as well as hypophysation and stripping of the females.

When the sperms were stored at 5°C for 24 h, their fertilizing capability was reduced by 4% compared with freshly obtained sperm. However, dilution in a 0.9% NaCl solution (up to 10^{-3}) gave an average 9% increase of hatching success. This finding enables the use of one competent male to fertilize the eggs of many females. An alternative application of the finding enables homoplastic hypophysation, using the fresh pituitary of the male to induce ripening of the female, while the sperms are stored for later use.

Correct timing of stripping of the females in relation to hypophysation proved to be critical for obtaining good hatching results. This was increasingly so when temperatures were high. The best results in these experiments were obtained when stripping took place 21, 11 or 7 h after hypophysation at 20, 25 and 30°C, respectively.

At this time the eggs were flat, with the cytoplasm concentrated at the animal pole as a reddish-brown spherical cap. The incubation period of the eggs decreased with increasing temperature. In all instances a large proportion of deformed fry occurred which was inversely related to the hatching percentage. Incubation without a regular water exchange gave 4% more hatching, 6% less deformation and a shorter incubation period than incubation with water exchange.

Hypophysation was repeated four times with 1-, 2- or 3-week intervals and resulted in successful stripping, fertilization and hatching of the eggs after each hypophysation.

INTRODUCTION

The potential of *Clarias lazera* (Cuvier & Valenciennes) in aquaculture was demonstrated in the Central African region in 1970—1972 (C.T.F.T., 1972; Micha, 1973; De Kimpe and Micha, 1974). Semi-natural or hormone-induced reproduction in ponds did not prove to be a reliable method for planned fingerling production (Micha, 1975; Nugent, 1975; Hogendoorn, 1979). Artificial reproduction using acetone-dried carp hypophysis to induce maturation

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and ovulation of the eggs of *C. lazera* was first carried out successfully in Cameroon in 1975 (Hogendoorn, 1979). It was found, however, that hatching was not always successful.

Hypophysation of fish is normally undertaken when gonadal development is almost completed, either naturally or by artificial environmental stimulation (Huisman, 1974, 1976; Donaldson, 1976). After hypophysation the females are stripped when free-running eggs can first be obtained by exerting slight pressure on their abdomen (Clemens and Sneed, 1962). When this procedure was used in the artificial reproduction of *C. lazera*, the results were variable. Sometimes the eggs did not hatch and occasionally a high percentage of deformed fry occurred. A similar phenomenon, observed with *Cyprinus carpio*, was related to the time between hypophysation and stripping (Jähnichen, 1978). The latent period, i.e., the time between hypophysation and ovulation of the eggs, is dependent on the water temperature (Clemens and Sneed, 1962). It was therefore decided to study the hatching results of *C. lazera* eggs in relation to the time between hypophysation and stripping at three different temperatures.

Insufficient development of the eggs (Yamamoto, 1956; Chen et al., 1969; Kuo et al., 1974; Kausch, 1976) at the time of hypophysation was another possible cause of poor hatching results. This was investigated in an experiment where *C. lazera* females were stripped sequentially at short intervals.

In the experiments concerning the time of hypophysation and stripping of the females, it was important to minimize a possible effect due to differences between the sperms used. To investigate the possibility of using a single batch of sperms to fertilize all eggs stripped at different times, it was attempted to store the sperms for a short period. In preliminary observations the viability of the stored sperms was evaluated on the basis of their motility. However, the characteristic of sperm motility is only partly conclusive: non-motile sperms are unlikely to be capable of fertilization (Lindroth, 1946), but motility is not necessarily synonymous with fertilizing capability. An initial experiment was therefore carried out to determine the effect of short-term storage of the sperms on their effective fertilizing capability.

MATERIALS AND METHODS

The brood fish, which all had the same age of about 1 year, were selected from the first offspring of a group of 40 *C. lazera* transferred from Central Africa to The Netherlands in 1976. The selected fish, reared in 150-l aquaria at 25°C with trout pellets ("Trouvit", Trouw & Co., Putten, The Netherlands), were held at the selected experimental temperature for 1 week prior to the start of the experiments. Except in the experiment on repeated hypophysation all fish were used only once.

For hypophysation of the females 4 mg acetone-dried powdered carp pituitary (Stollers Fisheries, Iowa 51360, U.S.A.) per kg body weight was suspended in a 0.9% NaCl solution. The suspension was injected into the dorsal

musculature just lateral of the dorsal fin. The individual egg weight was determined by weighing and counting a sample of about 100 eggs.

For each treatment about 0.5 g of eggs was fertilized and incubated in a 2-l aquarium at the same temperature at which the female fish had been kept. These aquaria were placed in a fiberglass trough. The temperature of the water was maintained by thermostatic heaters and the water was recirculated at 4 l h^{-1} per batch of experimental eggs. The incubating eggs were counted, and when hatching was completed, the number of hatched fry was determined as well as the number of deformed ones. The time of hatching was taken as the moment when 5—10% of the eggs had hatched.

Short-term conservation of sperms

The preliminary observations on motility showed that sperms could be activated following 24 h of storage at 5°C either diluted in a 0.9% NaCl solution or undiluted. The present experiment was to verify the effect of storing sperms on their effective fertilizing capability. Sperms of three males were mixed and divided into two portions; one portion was kept undiluted and the other was used to make a dilution series with 0.9% NaCl in a proportion of 10^{-1}, 10^{-2} or 10^{-3}. All four sperm preparations were stored for 24 h at 5°C. After 24 h an identical series was prepared from three other males, and used for fertilization immediately.

Four females, kept at 30°C, were stripped 7 h after hypophysation. Of each female eight different samples of eggs were mixed with 0.1 ml of the eight different sperm preparations, and 2 ml of distilled water were then added to activate the sperms. A period of 1 min was allowed for fertilization, after which the eggs were incubated.

The hatching results of the eggs were used as indicator of the fertilization capability of the sperms.

Time of stripping

The effect of the time between hypophysation and stripping on the hatching results of the eggs was subsequently studied. Fifteen groups, each consisting of three *C. lazera* females, were subjected to hypophysation and were stripped after a different time at different temperatures. Since the latent period decreases with an increase in temperature (Clemens and Sneed, 1962), the time of stripping was chosen accordingly (Table I). Of each female an aliquot of the eggs was fertilized with sperms stored in a 0.9% NaCl solution at 5°C. The same sperm solution was used to fertilize the eggs of all females at one temperature. Incubation took place with and without water exchange and the time of hatching as well as the hatching results were determined.

TABLE I

Time between hypophysation and stripping (h) of *C. lazera* females at three different temperatures

Temp. (°C)	Group				
	1	2	3	4	5
20	17.0	19.0	21.0	23.0	30.0
25	8.0	9.0	10.0	11.0	13.5
30	5.5	6.5	7.0	7.5	8.5

Repeated hypophysation

The possibility of insufficient development of the eggs at the time of hypophysation was investigated by sequential hypophysation of the females. Three groups, each consisting of three *C. lazera* females were subjected to hypophysation four times at 1-, 2- or 3-week intervals. At 30°C, the time of stripping was 7 h after each hypophysation. Fertilization, incubation and hatching were as in the preceding experiment.

Analysis of data

Prior to analysis, the distribution of the data was compared with a χ^2-distribution to check normality. When a deviation from normality was found, logarithmic transformation was applied.

The results of the experiments on short-term conservation of the sperms and repeated hypophysation of the females were examined with analysis of variance. When this was of interest the effects of the individual treatment levels were compared using Tukey's *w*-procedure (Steel and Torrie, 1960).

The effect of the time of stripping on the hatching results was evident and required no further examination. The hatching results of the eggs of the three different temperature groups could not be compared because (1) the fish were not allocated randomly to the different temperature groups, but were selected to give uniformity in body weight within each group; (2) the times from hypophysation to stripping could not be compared between the different temperature groups; (3) the eggs were incubated at different temperatures. The relation between the percent hatched eggs and the fraction of deformed fry was examined when the results of all three temperature groups were combined. The effect of water exchange during incubation of the eggs was examined on the basis of paired observations per female, using the paired *T*-test (Steel and Torrie, 1960).

RESULTS

Short-term conservation of sperms

The hatching results of the different experimental groups of eggs, indicating the fertilizing capability of the sperms, confirmed the feasibility of short-term sperm conservation (Table II).

TABLE II

Mean % hatched eggs and deformed fry as affected by storage and dilution of the sperm used to fertilize the eggs

Treatment		% Hatched eggs	% Deformed fry
Dilution	Storage		
Undiluted	Fresh	71[b]	16
Undiluted	Stored	66[a]	15
10^{-1}	Fresh	82[c]	16
10^{-1}	Stored	74[b]	15
10^{-2}	Fresh	81[c]	15
10^{-2}	Stored	79[c]	16
10^{-3}	Fresh	80[c]	17
10^{-3}	Stored	79[c]	18

Means not followed by the same letter differ significantly ($P < 0.05$) when compared on the basis of Tukey's w-procedure.

The effect of the treatments on the % hatched eggs and the % deformed fry was examined with the following model

$$Y_{ijk} = \mu + s_i + d_j + r_k + (sd)_{ij} + (sr)_{ik} + (dr)_{jk} + (sdr)_{ijk} + e_{ijk}$$

Y_{ijk} = observed % hatched eggs or deformed fry; μ = overall mean; s_i = effect of ith storage level; d_j = effect of jth dilution level; r_k = effect of kth replicate; $(..)_{..}$ = two and three-way interactions as designated; e_{ijk} = random effect.

Since only single observations were available per treatment combination, the effect of the three-way interaction could not be tested. The two-way interactions, tested against the three-way interaction, proved non-significant for either the % hatched eggs ($P < 0.43$) or the % deformed fry ($P < 0.36$). The main effects were then tested against the pooled interactions (Table III). It showed that storage and dilution of the sperms, as well as the use of different females, significantly influenced the % hatched eggs, whereas only the use of different females significantly influenced the % deformed fry.

The variation due to the use of four different females, although striking, was of no further interest; therefore only the differences in the average %

TABLE III

Mean squares for % hatched eggs and deformed fry as affected by storage and dilution of the sperm used to fertilize the eggs

Source of variation	Degrees of freedom	Mean squares	
		% Hatched eggs	% Deformed fry
Main effects			
Storage	1	124**	0.78
Dilution	3	216***	6.03
Replicates	3	1189***	597.12***
Residual	24	15	6.58

** $P < 0.01$; *** $P < 0.001$.

hatched eggs for the individual storage and dilution levels were further examined (Table II) using Tukey's *w*-procedure (Steel and Torrie, 1960) with the residual mean square of the three-way analysis of variance (Table III).

Time of stripping

All females produced eggs. The average body weight, average total egg production and average weight per egg of each temperature group are given in Table IV. χ^2-tests showed that the distribution of the pooled data for body weight and total egg production deviated from normality. After a logarithmic transformation had been applied, the requirement of normality of distribution could be met. It showed that a significant correlation ($r = 0.32$; $P < 0.02$) existed between individual body weight and corresponding total egg production. The weight per egg was not related to body weight ($r = 0.00$).

The mean hatching results are presented in Fig. 1. It was confirmed that after hypophysation, the time required for the eggs to give the highest hatching percentage decreased with increasing temperature. It also showed that correct timing of stripping became increasingly critical at higher temperatures.

TABLE IV

Body weight, total egg production and weight per egg of the three groups of 15 *C. lazera* females stripped at different temperatures (mean ± S.D.)

Temp (°C)	Body weight (g)	Total egg production (g)	Weight/egg (mg)
20	218.2 ± 64.2	17.1 ± 12.1	1.33 ± 0.27
25	255.2 ± 103.2	18.4 ± 8.8	1.36 ± 0.14
30	370.2 ± 149.5	32.9 ± 30.6	1.30 ± 0.14

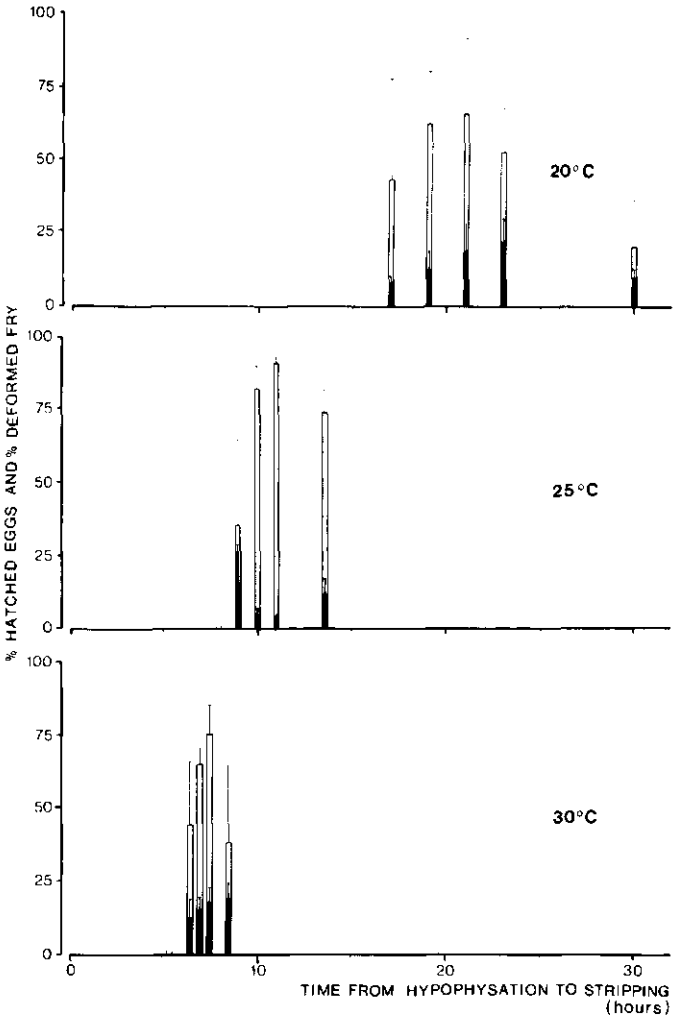

Fig.1. Mean % hatched eggs (total bars) and deformed fry (solid parts) in relation to the time from hypophysation to stripping at three different temperatures. Mean (+S.D.) of three observations per treatment.

Fig. 1. further indicates an inverse relation between the hatching % and the fraction of deformed fry (= deformed fry/hatched eggs). When the correlation of these characteristics was examined, the linear correlation coefficient proved to be highly significant ($r = -0.78$; $P < 0.001$).

The incubation period decreased with increasing temperature (Fig. 2), which is well known for fish eggs (Lindroth, 1946; Keiz, 1959; Braum, 1978).

The effect of water exchange during incubation can be read from Table V. The overall, significantly shorter incubation period in stagnant water was due mainly to the group incubated in 20°C water. The same applied for the high-

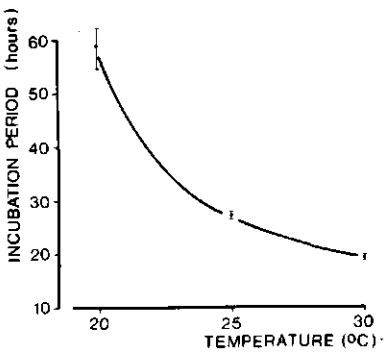

Fig. 2. Decrease of the incubation period of *C. lazera* eggs in relation to an increase in water temperature. Mean (± S.D.) of 13, 12 and 11 observations at 20, 25 and 30°C, respectively.

TABLE V

Mean difference for the incubation period, % hatched eggs and deformed fry of eggs incubated with and without water exchange (No. of comparisons for the paired *T*-test in parentheses)

Temp. (°C)	Incubation period (h)		% Hatched eggs		% Deformed fry	
20	4.7***	(13)	-10.1**	(15)	9.4*	(13)
25	0.0	(12)	0.3	(15)	5.6**	(12)
30	0.0	(11)	- 2.5	(14)	2.7	(11)
Overall	1.7***	(36)	- 4.1**	(44)	6.1***	(36)

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

er hatching % in stagnant water. The lower % deformed larvae in stagnant water was mainly due to the 20 and 25°C treatments.

Repeated hypophysation

Sequential hypophysation of the females led each time to the production of hatchable eggs even with the short interval of 1 week. The mean results per treatment combination are presented in Fig. 3. A logarithmic transformation of the data on egg production was necessary to make their distribution normal.

Because the repeated hypophysation entailed successive observations on the same females, the data were analyzed using the following split-plot model in time (Steel and Torrie, 1960)

$$y_{ijk} = \mu + r_i + i_j + d_{ij} + s_k + (rs)_{ik} + (is)_{jk} + e_{ijk}$$

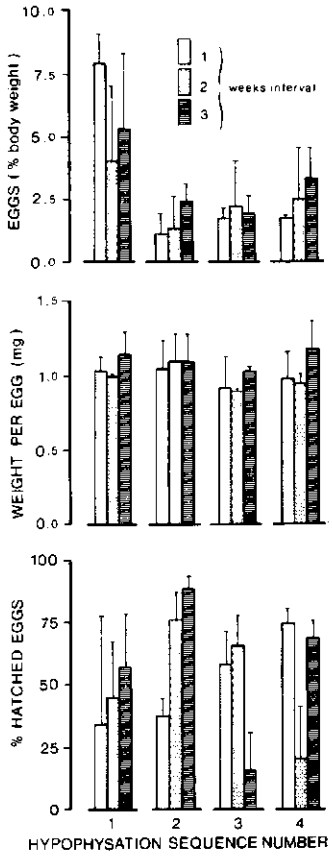

Fig. 3. Eggs produced (%body weight), weight/egg (mg) and % hatched eggs in relation to the interval between and the sequence number of repeated hypophysation. Mean (+ S.D.) of three observations per treatment.

y_{ijk} = observed egg production, weight per egg or % hatched eggs; μ = overall mean; r_i = effect of ith replicate; i_j = effect of jth interval; d_{ij} = whole unit random effect; s_k = effect of kth repeated hypophysation; $(..)_{..}$ = two-way interactions as designated; e_{ijk} = subunit random effect.

This analysis (Table VI) showed that the egg production was significantly affected by the repeated hypophysation with a considerable effect of the interval—sequence number interaction ($P < 0.1$). These effects were primarily due to the high egg production at the first hypophysation, especially of the 1-week interval group (Fig. 3). When the data of the first hypophysation were excluded from the analysis (this analysis of variance table is not included), the egg production at the second and subsequent hypophysations was not significantly affected by any treatment. However, there was a trend ($P < 0.1$) for the egg production to increase after the second hypophysation (Fig. 3). The weight per egg also showed a significant effect of the sequence number of hypophysation.

TABLE VI

Mean squares for the amount of eggs produced (% body weight), the average weight/egg (mg) and % eggs hatched as affected by the interval between and the sequence number of repeated hypophysation of *C. lazera* females

Source of variation	Degrees of freedom	Mean squares		
		Eggs produced	Wt./egg	% Hatched eggs
Main effects				
Replicates	2	0.26	0.057	469
Intervals	2	0.12	0.069	175
Residual (a)	4	0.21	0.058	446
Sequence No.	3	0.63***	0.0299*	880
Interactions				
Repl. × seq. No.	6	0.02	0.0051	118
Int. × seq. No.	6	0.09	0.0081	2450**
Residual (b)	12	0.04	0.0080	401

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

The hatching percentage showed a significant interaction effect of interval and sequence number. This interaction was probably due to the low hatching percentages obtained at the third hypophysation at 2-week intervals and second hypophysation at 3-week intervals (Fig. 3).

DISCUSSION AND CONCLUSIONS

Short-term conservation of sperms

Sperms of *C. lazera* could be activated and were able to fertilize eggs after short-term conservation. This was evidenced by the hatching results of eggs which were fertilized with sperms diluted in a 0.9% NaCl solution and stored at 5°C for 24 h. Although the storage of sperms caused an average 4% decrease in the % hatched eggs (Table II), it can be concluded that the technique is acceptable. Dilution of the sperms in a 0.9% NaCl solution even increased the hatching by an average 9% (Table II). A similar finding was reported by Billard et al. (1974). Kuchnov and Foster (1976) found that exposure of the sperms to air resulted in their activation and consequently interfered with their storability. This effect may also have been responsible for the lower results with storage of undiluted sperms in our experiments.

When using the 10^{-3} sperm dilution, 0.5 g of eggs was fertilized with 10^{-5} ml of sperms in 10^{-2} ml of 0.9% NaCl and 2 ml of water. Up to 1 ml of sperms can be obtained from a male of about 1 kg with the dissection technique. It then follows that the sperms of such a male would be sufficient to fertilize over 50 kg of eggs. With the results presented in Table IV it can be estimated

that this equals 37×10^6 eggs obtainable from 1250—2500 females weighing between 0.500 and 0.250 kg each.

Unpublished experiments have shown that the fresh pituitary from a male can also be successfully used for the hypophysation of a female. This, combined with our successful results with storing the sperms, leads to another interesting possibility: the sacrificed males can provide pituitary for immediate use and sperms to fertilize the resulting eggs later. Although the minimum required dosage for the use of *Clarias* pituitary has not yet been determined, this method undoubtedly requires the use of many more males than the method discussed above.

Hypophysation and stripping of females

The importance of correct timing of stripping of the females for the hatching success was clearly demonstrated. It was found that stripping of the females as soon as free-running eggs could be obtained was too early and the eggs did not develop normally. The best results were obtained about 10, 3 and 1 h later at 20, 25 and 30°C, respectively. At this time the eggs could be stripped easier than before. They were flat (Fig. 4b), with the cytoplasm concentrated at the animal pole and visible as a reddish-brown spherical cap. This aspect is quite distinct from the round eggs present in the ovaries before hypophysation (Fig. 4a) and is easily recognized. It can serve as a practical criterion to assess if the female is ready for stripping. It is best seen when a few eggs are placed in water and gently rolled around.

The highest hatching results in our experiments were obtained when stripping took place 21, 11 or 7 h after hypophysation at 20, 25 or 30°C, respectively. However, the exact optima for the time of stripping at different temperatures cannot be decided conclusively on the basis of the results in these experiments. This would require more elaborate experimentation within the optimal range.

There was a narrow time range, especially at 30°C, during which hatching results were high and explicit scheduling of the reproduction operation is

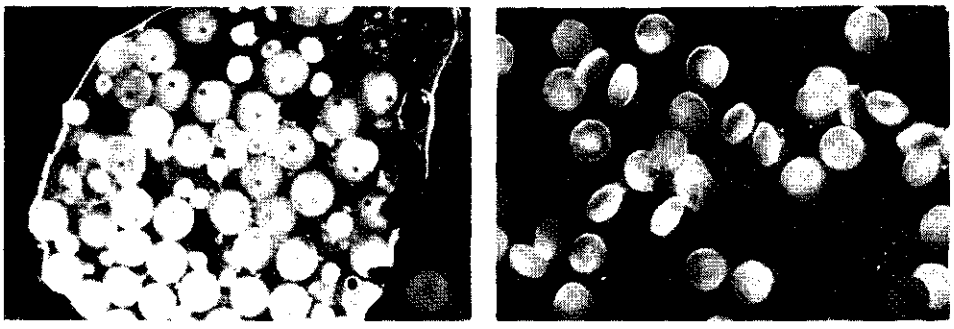

Fig. 4. Unovulated *C. lazera* eggs before hypophysation (a) and ovulated ones at the time of stripping (b). In (b) some of the eggs are seen laterally (10×).

adequate feed and poor water quality. These interferences could be avoided by controlled rearing of the fry indoors, provided that adequate feeding could be assured. Therefore in the present 2 experiments the suitability of some common, natural and artificial feedstuffs was tested and it was attempted to establish a routine rearing method for *C. lazera* fry to suit our further research programme.

MATERIALS AND METHODS

Facilities and fish

Both experiments were carried out in a series of 60 l glass aquaria. These were part of a recirculattion system including a 250 l sedimentation tank and a 200 l sand (1—2 mm) filter. The water flow through each aquarium was 1—2 l min^{-1}. Aeration with pressurized air and temperature control took place before the sand filter. Fresh water was supplied to the system at a rate of one change of the total volume per day.

The experimental fry were obtained by artificial reproduction (Hogendoorn and Vismans, 1980) of some of 40 *C. lazera* transferred to the Netherlands in 1976. On the final day of yolk absorption, groups of 500 unfed, swimming fry were counted and put into the different aquaria. At this stage the average weight of the fry was 2.3 ± 0.2 (S.D.) mg.

Experiments and feeds

The aim of the first experiment was to test different feeding regimes using artificial or natural feeds or a combination of feeds as listed in Table I. Six aquaria received a basic diet of trout starter "Trouvit 000", (Trouw & Co., Putten, The Netherlands) supplemented either with newly hatched live *Artemia salina* nauplii for a different period or with frozen zooplankton (0.2—0.8 mm, kindly provided by the Organization for Improvement of Inland Fisheries, Nieuwegein, The Netherlands) during the first 3 weeks. Furthermore, an experimental dry feed (high protein, 200—250 μm, Trouw & Co., Putten, The Netherlands), ground whole frozen *C. lazera* fingerlings of about 2 g and dried inactive yeast ("Engevita", 45% protein, Gist-Brocades N.V., Delft, The Netherlands) were tested.

The experiment was carried out at 27°C and was continued for 4 weeks. The fish were fed to satiation 5 times per day between 08.00 and 20.00. They were considered satiated when they stopped searching for feed and assembled in the corners of the aquaria. With combination feeding, the trout starter was given first, followed after about 5 min by the supplement. The aquaria were cleaned and the dead fish removed and counted twice a day. The temperature and the dissolved oxygen content of the water were measured daily.

Every week a sample of 10 fish was removed, anesthetized, placed on

TABLE I

Final average weight and survival rate of *C. lazera* fry after 4 weeks when fed with different feed substances. Standard deviation based on a sample of 10 fish in parentheses (Expt 1)

Feeding regime	Final average weight (mg)[1]		Survival rate (%)[2]
trout starter	172[a]	(60)	10[a]
trout starter + live *Artemia* 1 week	501[c]	(132)	67[b]
trout starter + live *Artemia* 2 weeks	455[c]	(256)	73[b]
trout starter + live *Artemia* 3 weeks	485[c]	(173)	87[c]
trout starter + frozen *Artemia* 3 weeks	330[b]	(99)	74[b]
trout starter + frozen zooplankton 3 weeks	194[a]	(79)	12[a]
experimental dry feed[3]	19	(4)	0
ground *Clarias*[3]	16	(6)	0
yeast[3]	24	(7)	0

Results not followed by an alphabetic in common differ significantly ($P < 0.05$) when compared on the basis of:
[1] Duncan's new multiple-range test (Steel and Torrie, 1960) which was carried out after logarithmic transformation of the weight data or
[2] of the heterogeneity component GH of the log likelihood ratio test (Sokal and Rohlf, 1969) for the survival rate.
[3] Terminated early and not included in the test since not enough fish survived after the second week.

paper towels for about 10 s to remove most of the adhering water, and individually weighed to the nearest 0.1 mg. These fish were then discarded.

Upon termination the surviving number of fish and the total average weight per treatment were determined.

In Expt 2 the aim was to further determine the necessary quantity and period of supplementation with live *A. salina* nauplii. The additional feeding of live *Artemia* and live zooplankton (0.2—0.8 mm, mixture of primarily cladocerans and copepods from natural sources in the vicinity of the laboratory) was again compared with the feeding of trout starter alone. The different treatments are listed in Table II.

The normal portions of supplementary feeding were such that after feeding the fish were satiated. For feeding in excess of satiation 2 times the quantity needed for satiation was given. For night feeding (treatment 3) the necessary quantities of trout starter and *Artemia* nauplii were placed in petri dishes on a conveyor belt-type automatic feeder, from which they fell into the aquarium at the predetermined times.

The experiment was executed at a water temperature of 30° C. Feeding was 4 times per day between 08.00 and 20.00 h (or 8 times per 24 h). A sample of 20 fish per week was removed and weighed. The other procedures were as for Exp. 1.

TABLE II

Final average weight and survival rate of *C. lazera* fry after 4 weeks when fed with trout starter supplemented with different quantities of *Artemia salina* nauplii or live zooplankton for different periods. Standard deviation based on a sample of 20 fishes in parentheses (Expt 2)

Feeding regime[1] (trout starter + . . .)	Final average weight (mg)		% Survival
no supplement	227^{a}	(102)	1^{a}
Artemia (4 double portions day^{-1}, 3 weeks)	1027^{d}	(313)	89^{e}
Artemia (8 portions per 24 hours, 3 weeks)	1001^{d}	(362)	89^{e}
Artemia (4 portions day^{-1}, 3 weeks)	795^{cd}	(416)	96^{f}
Artemia (4 portions day^{-1}, 2 weeks)	816^{cd}	(413)	87^{de}
Artemia (4 portions day^{-1}, 8 days)	594^{bd}	(257)	78^{cd}
Artemia (4 portions day^{-1}, 6 days)	575^{b}	(463)	84^{de}
Artemia (4 portions day^{-1}, 4 days)	521^{b}	(345)	82^{cde}
live zooplankton (4 portions day^{-1}, 3 weeks)	844^{d}	(374)	50^{b}
live zooplankton (4 double portions day^{-1}, 3 weeks)	1018^{d}	(334)	70^{c}

Test procedures and significance levels as in Table I.
[1] Day^{-1}: 08.00 — 20.00 h.

Analysis of data

Duncan's new multiple-range test at the 5% level of significance (Steel and Torrie, 1960) was used to determine differences in weight of the surviving fish in each treatment group. However, it showed that the sample variances of the final individual weights for the different treatment groups were not homogeneous according to Bartlett's test (Sokal and Rohlf, 1969). After logarithmic transformation of the data, the final average weights could be compared. In the results the data are given in the untransformed scale.

For the survival rates (%) only 1 observation was available per treatment group. Under the H_0 hypothesis that the fish in all treatments had an equal chance to survive, an effect of the different feeding regimes could be tested with a test for goodness of fit. However, the aim of the experiments was to compare the individual treatments. Therefore a simultaneous test procedure was applied comparing the heterogeneity component GH of the log likelihood ratio G with the appropriate value of X^2 at the 5% level of significance (Sokal and Rohlf, 1969).

RESULTS

The recirculation system functioned satisfactorily. The water temperature was 26.9 ± 1.1 and 29.6 ± 0.7 (S.D.) °C in Expts. 1 and 2 respectively. The dissolved oxygen content did not decrease below 40% saturation in any aquarium.

In all treatments the feed was ingested well at the start. This was evidenced by the distended intestinal tract of the fry and the marked satiation behaviour. After a few days this typical satiation behaviour was no longer observed with the unsuccessful feeding regimes, where searching for feed continued. The feed, even live *Artemia* nauplii, was primarily taken from the bottom. With the frozen feeds, which were given as ice cubes, some fish approached the ice and ate the feed as soon as it melted off.

Considerable differences in growth and survival occurred between the different treatments. The final average weight (mg) and the survival rate (%) are given in Tables I and II for the corresponding experiments.

From Table I it is evident that *Artemia* supplementation, live or frozen, even if for only 1 week, gave a significantly higher average weight and survival than feeding trout starter alone or supplemented with frozen zooplankton. The feeding with the experimental dry feed, ground *Clarias* and yeast was discontinued after 2 weeks, because too few fish survived.

The second experiment (Table II) showed that supplementation with live *Artemia* or live zooplankton gave comparable growth, although the latter resulted in lower survival. Feeding in excess of satiation and day-and-night feeding gave higher average weights (1027 and 1001 mg respectively) than simple satiation feeding (795 mg), but the differences were not significant. *Artemia* supplementation during less than 1 week gave significantly inferior growth, but the fish had clearly passed the critical stage and survival was of the same magnitude, as it was with all groups that had received *Artemia* nauplii.

The growth patterns that could be established on the basis of the weekly samples were rather regular and did not add any information in respect of the different feeding methods. To illustrate this point the weekly sample average weights for treatment 1, 2 and 10 of Expt 2, chosen because of the contrast, were plotted in Fig.1A.

It was found that after a cube root transformation of the weight data a linear relation (1) existed between the length of the rearing period and the average body weight of the samples:

$$y_t^{1/3} = y_o^{1/3} + bt \qquad (1)$$

where

y_t = weight at time t
y_o = weight at start
b = regression coefficient
t = time

When the regression lines were forced through the initial body weight of 2.3 mg, the highly significant coefficients of determination varied between 0.93 and 0.98 for the 3 treatments under consideration. The first derivative of y_t divided by y_t itself ($\times$ 100%) then gave the following rela-

tion (2) for the specific growth rate (α, % body weight) with time and body weight, respectively.

$$\alpha = \frac{300\ b}{y_o^{1/3} + bt} = \frac{300\ b}{y_t^{1/3}} \qquad (2)$$

The first part of this equation (2) has been plotted in Fig.1B for the feeding regimes under discussion.

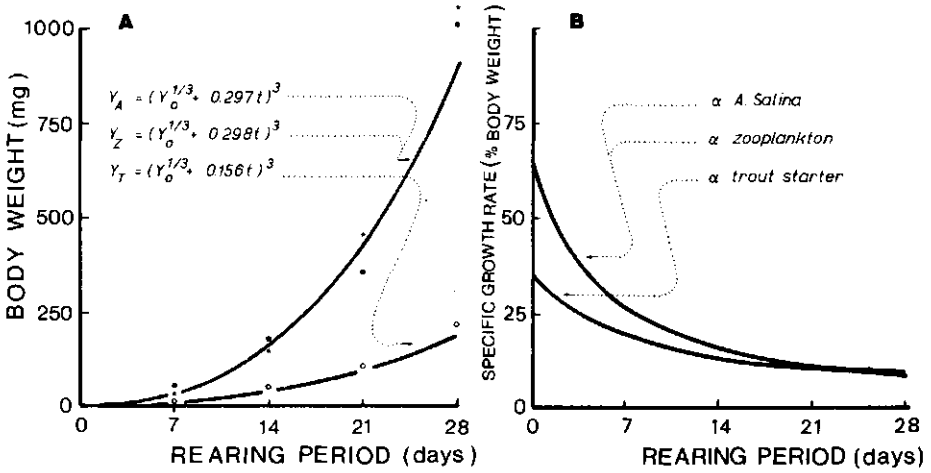

Fig.1. Increase in body weight and decrease in specific growth rate in relation to the rearing period of *C. lazera* fry when fed with trout starter alone (○), with trout starter supplemented with live *A. salina* nauplii (•) or with live zooplankton (*). Averages of samples of 20 fish per week and per feeding regime.

The mortality patterns that could be established received no careful consideration because the observed mortality only amounted to 64% and 28% of the number of fish missing at the end of Expts.1 and 2, respectively. It was noted, however, that with the unsuccessful feeding regimes the observed mortality was highest during the second week. Among the satisfactory feeding regimes 63% of the observed mortality in Expt 1 occurred during the first week. In Expt 2 the observed mortality in all but the trout starter group was more evenly distributed.

DISCUSSION AND CONCLUSION

From the results it was clear that the dry feeds tested were not suitable for rearing *C. lazera* fry, neither could ground *Clarias* fingerlings or frozen zooplankton be used. By contrast the frozen *Artemia* nauplii and especially live *Artemia* and live zooplankton gave good results.

It thus appeared that *C. lazera* is one of those species for which fry rearing requires a phase of feeding with natural, preferably live feeds (EIFAC, 1976; Huisman, 1976; Girin, 1979). Different factors have been proposed to account for this phenomenon e.g., a) the artificial feed is not recognized or not ingested because learning takes too long or feed particle size and density are incorrect (Huisman, 1979; Van der Wind, 1979); b) the feed is not utilized (Anwand et al., 1976); or c) the feed has an inadequate composition or ingredients leach out (Van der Wind, 1979).

In these experiments the uptake appeared to present no difficulties, certainly not during the first few days. A similar observation was reported by Kainz (1974; 1976) for carp, *Cyprinus carpio*. Appelbaum (1976) even found that uptake of artificial feed by carp fry took place in the dark. Also, technologically and chemically the problems of composition and leaching can be overcome (Van Limborgh, 1979; Luquet and Rumsley, 1979; Meyers, 1979; Van der Wind, 1979).

The above points out that the inadequate performance of fry on an artificial diet is caused by a poor utilization i.e. digestion of the feed. There are indications that the digestive capacity of the prey organism is important for the digestion of the feed by fish. Jancaric (1964) found that the proteolytic enzymes of carp were stimulated by exogenous prey proteases; this phenomenon was even more pronounced when the activity of the carp enzymes was lower.

Also, the use of freeze-dried *Artemia* and enchytraeid worms (where the enzymes are destroyed) has given unsatisfactory results (Kirk, 1972, Beck and Bengston, 1979). The use of the alkan yeast, *Candida lipolytica*, to rear carp and whitefish, *Coregonus albula*, fry is interesting in this respect (Appelbaum, 1977, 1979).

In general the magnitude of the survival rate (%) corresponded with the magnitude of the final average weight. Because feeding in excess of satiation and day-and-night feeding gave the better growth rates, we have adopted a method of continuous *Artemia* feeding with the aid of a small dosing pump for routine rearing of *C. lazera* fry. The successful feeding with small zooplankton indicates that this could be a solution when zooplankton can easily be obtained or for circumstances where *Artemia* cysts are not readily available.

Especially at the start the fry realized a high specific growth rate (Fig.1B). On a per day basis growth during the first day amounted to 85% of the initial body weight for the fry fed with *Artemia* or zooplankton. It then follows that the feed ration during the first days of rearing must be several times the total biomass of the fry per day (Merla, 1987; Huisman, 1979).

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CONTROLLED PROPAGATION OF THE AFRICAN CATFISH, *CLARIAS LAZERA* (C. & V.)
IV. EFFECT OF FEEDING REGIME IN FINGERLING CULTURE

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ABSTRACT

Hogendoorn, H., 1981. Controlled propagation of the African catfish, *Clarias lazera* (C. & V.). IV. Effect of feeding regime in fingerling culture. *Aquaculture*, 24: 123—131.

Two experiments were carried out to study the effect of different feeding levels and feeding frequencies in the culture of *Clarias lazera* (C. & V.) fingerlings from 0.5 to 10 g.

It was found that 0.5 g fingerlings could reach an average weight of about 10 g in 3—4 weeks when they were fed continuously for 24 h per day or 12 h at night at a daily rate of 8% of the biomass or more. A feeding level of 10% of the biomass appeared to be optimal, from the point of hygiene, growth rate and feed utilization parameters. Continuous feeding during part or all of the day clearly gave better growth than feeding two or four defined meals per day.

When these preferred feeding regimes were practised, the feed conversion (wet weight) ranged from 0.65 to 0.97, the protein efficiency ratio from 2.14 to 3.04 and the productive protein value from 0.34 to 0.47. These values compare favourable with values reported for other cultured species, indicating that *C. lazera* fingerlings are efficient feed convertors.

It could be calculated that, when the rations are readjusted only once a week, the high growth rates occurring in these experiments result in a considerable difference between the designated feeding rates and the actual feeding rates.

INTRODUCTION

A reliable supply of stocking material is a basic condition for successful planning in fish culture (Allain and Morrison, 1978; Huisman, 1979). To meet this condition, controlled propagation methods have been developed for the majority of cultivated fish species (EIFAC, 1976; Huisman, 1976; Coche and Bianchi, 1979).

In the case of the African catfish, *Clarias lazera* (Cuvier and Valenciennes), controlled pond reproduction and rearing practices did not provide the required number of fingerlings (Micha, 1975; Nugent, 1975; Kelleher and Vincke, 1976). By contrast, it was found that 0.5 to 1.0 g fingerlings could

be produced satisfactorily using artificial reproduction of the brood fish followed by controlled rearing of the fry (Hogendoorn, 1979, 1980; Hogendoorn and Vismans, 1980).

Under practical conditions these fingerlings can possibly be stocked in fingerling grow-out ponds, but it may prove desirable to have an additional phase of growth indoors where the environment can be controlled better. In the present experiments the effects of different feeding levels and feeding frequencies on parameters of fingerling growth and feed utilization were studied.

MATERIALS AND METHODS

Facilities and fish

The experiments were carried out in 60 l glass aquaria included in a recirculation system as described previously (Hogendoorn, 1980). However, the water flow was increased to about 3 l min^{-1} per aquarium.

The experimental fish were obtained by the methods referred to earlier. Each aquarium was stocked with 100 fingerlings reared for 28 days with live *Artemia salina* nauplii and trout starter. The average weights of the fish were 0.88 and 0.50 g in experiments 1 and 2, respectively.

The feed ("Trouvit 0", Trouw & Co N.V., Putten, The Netherlands) was administered on "Scharflinger" conveyor-belt-type automatic feeders (Blaschke, Weiden i.d. Opf., Fed. Rep. Germany). The temperature was maintained at 30° C. It was measured daily, as was the dissolved oxygen content. The aquaria were cleaned once a week.

Feeding level

The aim of the first experiment was to determine the effect of different feeding levels on growth and feed utilization parameters of *C. lazera* fingerlings. The fish were fed at 4, 6, 8 or 10% of their body weight or to satiation. Feeding was continuous for 24 h, except on the day prior to weighing, when the ration was given in 12 h. A period of 6 h of non-feeding could thus be allowed between weighing and the last feeding on the one hand and the resumption of feeding on the other. This served to avoid the regurgitation of the old ration or the refusal of the new ration by the fish due to the manipulation involved with weighing. For satiation feeding the fish received a continuous basic ration of 10% during the first 2 weeks and 8% during the last week respectively. Two times per day this ration was supplemented by hand with as much as the fish would eat in addition. Each feeding level was assigned to two random aquaria.

To avoid sampling error, unobserved mortalities or missing fish, all fish were weighed and counted weekly. At the same time a sample of 10 fish was taken for individual weighing and subsequently discarded. The total number of fish

per aquarium was then reduced to a level that could be met by all aquaria, taking into account the mortalities and the sampled fish.

The quantity of feed was determined weekly, based on the total weight of all the fish per aquarium. This ration was then fed during the subsequent week.

The experiment was terminated after 3 weeks and the remaining fish were weighed. Upon termination a sample of 10 fish was taken for analysis of dry matter and protein content. These analyses were also made in a sample of fish taken at the start of the experiment.

Frequency of feeding

The second experiment was to determine the effect of the frequency of feeding on growth, survival and feed conversion of *C. lazera* fingerlings. The daily ration of 10% of the total biomass was administered in five different regimes i.e. in two or four portions or continuously between 08.00 and 20.00 h, continuously between 20.00 and 08.00 h or continuously during 24 h. Each feeding regime was assigned to two random aquaria.

The quantity of feed was determined weekly, based on a sample of 25 fish per aquarium. This ration was then fed during the subsequent week. Of the sample, 10 fish were weighed individually.

After 4 weeks the experiment was terminated and the remaining fish were counted and weighed.

Analysis of data

A cube root transformation of the individual sample weights indicated a linear relationship with the feeding period (cf. Hogendoorn, 1980). However, the groups of data thus obtained per feeding regime did not have homogeneous variances according to Bartlett's test (Sokal and Rohlf, 1969) and no meaningful additional transformation was found to solve this problem. Therefore, the effects of replication and the different feeding regimes were examined on the basis of the transformed mean weights of the samples.

The replicates per treatment were compared using analysis of variance with the feeding period as covariable. Subsequently, linear regression of the transformed mean weights of the samples on the feeding period was carried out in the pooled replicates. The resulting regression lines were compared on the basis of tests for homogeneity of regression coefficients (Steel and Torrie, 1960).

The data on final average individual weight, body composition and feed utilization parameters were also examined with analysis of variance in the pooled replicates. Duncan's new multiple-range test at the 5% level of significance was used to distinguish between the individual feeding regime treatments.

The feeding utilization parameters were calculated on the basis of the

whole ration provided and the number of fish surviving upon termination, i.e. the missing fish were considered to have disappeared at the start of the experiment. The following feed utilization parameters were evaluated:
— feed conversion: feed intake/weight gain
— protein efficiency ratio: weight gain/protein intake
— productive protein value: protein gain/protein intake.

RESULTS

The water temperature was 30.0 ± 0.5 and 29.7 ± 0.7 (S.D.) °C in experiments 1 and 2, respectively. The dissolved oxygen concentration ranged between 40 and 85% saturation.

The comparison of the replicates showed that they were not significantly different ($0.24 \leqslant P \leqslant 0.92$ and $0.36 \leqslant P \leqslant 0.86$ for the treatments in experiments 1 and 2, respectively). The linear relationship between the transformed mean weights of the samples and the feeding period proved highly significant ($P < 0.001$) in the experiments using different feeding levels ($0.94 \leqslant R^2 \leqslant 0.99$) or different feeding frequencies ($0.95 \leqslant R^2 \leqslant 0.99$). It showed (Fig. 1 A) that satiation feeding gave the fastest growth, but for the observed feeding period the differences with the 10 or 8% feeding regimes were not significant. Continuous feeding for 24 h per day (Fig. 1 B) resulted in significantly faster growth than feeding continuously for 12 h by daylight, while continuous feeding for 12 h at night ranked in between.

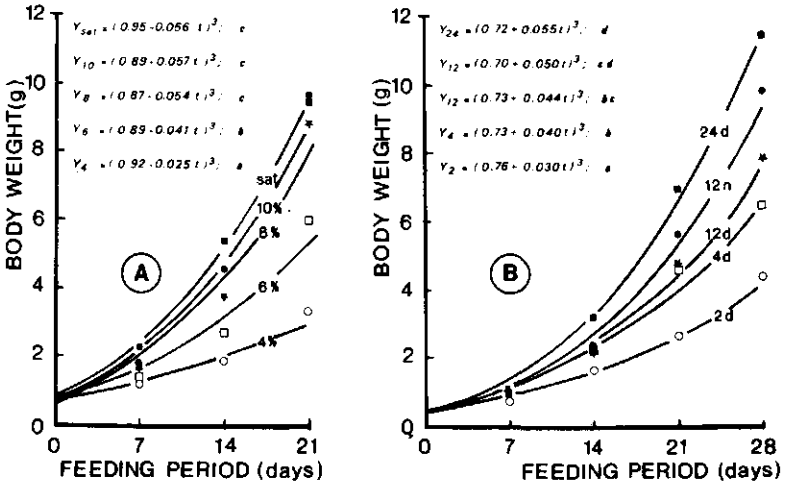

Fig. 1. Increase in body weight of *C. lazera* fingerlings when fed "Trouvit 0" at different feeding levels (A) or different feeding frequencies (B). The points represent the mean weight of two samples of 10 fish per treatment. The regression lines not followed by a letter in common differ significantly according to the tests for homogeneity of regression coefficients.

TABLE I

Average individual weight, body composition and feed utilization parameters of *C. lazera* fingerlings after 3 weeks feeding at different levels (experiment 1). The data are mean values of pooled replicates

Parameter	Feeding level (% body weight)				
	4	6	8	10	satiation
Initial weight (g)	0.90	0.87	0.89	0.85	0.87
Final weight (g)	2.78a	4.33b	6.64c	7.38d	7.26cd
	(47.0)[1]	(64.5)	(50.5)	(66.0)	(64.0)
Dry matter (%)	19.8a	19.7a	19.9b	21.3c	21.1bc
Protein in dry matter (%)	77.8	78.1	77.1	72.4	74.4
Feed conversion (wet weight)	0.65a	0.60a	0.65a	0.82b	0.92b
Feed conversion (dry matter)[2]	3.00a	2.79a	2.97a	3.51ab	3.97b
Protein efficiency ratio[2]	3.04a	3.26a	3.04a	2.40b	2.14b
Productive protein value[2]	0.47a	0.51a	0.47a	0.37b	0.34b

Results not followed by a letter in common differ significantly ($P < 0.05$) according to Duncan's new multiple-range test.
[1] Coefficient of variation of final weights based on 10 fish per group.
[2] Initial sample of fish: 19.8% dry matter, 76.5% protein in dry matter. Trouvit 0: 91.85% dry matter, 55.63% protein in dry matter.

TABLE II

Average individual weight, survival rate and feed conversion of 100 *C. lazera* fingerlings after 4 weeks feeding at 10% of the total biomass using different feeding frequencies (experiment 2). The data are mean values of pooled replicates. Nature of data, test procedure and significance levels as in Table I

Parameter	Feeding frequency				
	2 •day^{-1}	4 •day^{-1}	12 h •day^{-1}	12 h •night^{-1}	24 h •day^{-1}
Initial weight (g)	0.52	0.50	0.49	0.50	0.49
Final weight (g)	4.36a	6.79b	7.79c	10.06d	11.64e
	(66.0)[1]	(58.0)	(58.5)	(49.5)	(63.5)
Survival rate (%)	80.5	83.5	79.5	87.0	74.0
Feed conversion	1.36b	1.05ab	1.01ab	0.75a	0.97ab

[1] Coefficient of variation of final weights based on 40 fish per group.

The effect of the different regimes was further substantiated by the parameters evaluated upon termination. It is shown in Table I that the higher feeding levels resulted in an increase in the percent dry matter as well as in a higher final average individual weight. The lower feeding levels gave significantly better feed utilization parameters.

The different feeding frequencies (Table II) caused significant differences

in the final average individual weights and the feed conversions. The coefficients of variation and the percent survival were not affected.

DISCUSSION

Using different feeding levels and feeding frequencies in the culture of *C. lazera* fingerlings, it was found that a body weight of about 10 g could be reached within 2 months after first feeding, taking into account that it took 1 month to raise the fry up to fingerlings of 0.5—1.0 g (Hogendoorn, 1980). This rate of weight development compares favourably with high values reported for other cultured species e.g. carp (*Cyprinus carpio*) that reached 4.5 g in 8 weeks at 23° C (Huisman, 1974) and channel catfish (*Ictalurus punctatus*) that increased in weight from 3 g to 12.5 g in 4 weeks at about 28° C (Stickney et al., 1972). Furthermore, the weight increase in these experiments was similar to the best results obtained by the author in pond experiments where the *C. lazera* fry grew up to 5.2 g in 43 days after spawning (unpublished experiments).

The significant regression lines of body weight on feeding period were fitted through 8 and 10 average weights of samples per line in experiments 1 and 2, respectively. From Figs. 1A and 1B it is clear that the fitted regression line slightly underestimated the weights of the final samples, but the high coefficients of determination supported the goodness of fit. Since the cube root transformation of the body weight is equivalent to a length characteristic, it is indicated that there is a linear increase in length with time.

The absence of homogeneity of variances had its origin in the considerable variation in growth as shown by the coefficients of variation (Table I and II). Since the within-treatment differences in the coefficient of variation also were large, an additional transformation was ineffective. For further experiments it could be worthwhile to include a certain amount of variation at the start rather than to select homogeneous fish. On the other hand, a larger sample might have decreased the problem, because some large and some small fish would more likely have occurred in all treatment samples.

The higher feeding levels clearly gave the faster growth. Satiation feeding sometimes resulted in uneaten feed and this may have caused the slower growth towards the end of the experiment (Fig. 1A). Feeding at 10% or 8% showed no disadvantages in comparison with satiation feeding, particularly since the feed utilization was improved (Table I). The feed conversion rates realized were remarkably low, even when compared with the values found for small carp tested at 27° C, which remained around or above unity (Huisman et al., 1979). The dry matter feed conversion is included for better comparison. The advantageous feed conversions were corroborated by the protein efficiency ratios and the productive protein values, which were high in comparison with those of carp (Huisman et al., 1979) and *Tilapia zillii* (Mazid et al., 1979) at least when fed a diet having a comparable protein content. These results indicate that *C. lazera* fingerlings are highly efficient feed convertors.

Concerning the feeding frequency, it was found that continuous feeding for 24 h per day gave the fastest growth, followed by continuous feeding for 12 h at night. The fish fed only twice daily weighed no more than 37% of the continuously fed groups. These results differ from those obtained with some marine species (Ishiwata, 1969), channel catfish (Andrews and Page, 1975) and rainbow trout (*Salmo gairdneri*) (Grayton and Beamish, 1977), in which it was found that a feeding frequency in excess of 2—4 times per day had no extra effect. Huisman (1974), however, also found that for carp an increase in feeding frequency from 5 and especially from 3 to 9 feedings per day considerably improved the feed conversion and the growth rate.

The good results obtained with night-time feeding suggest that vision is not essential for successful feeding. Hochman (1967) also reports that small sheat fish (*Silurus glanis*) grow well in continuous darkness.

The feed utilization parameters were calculated on the basis of the number of fish surviving. This means that the whole ration given was divided by the growth realized by the fish remaining at the end of the experiments. Consequently, the surviving fish certainly did not receive more feed than the amount used in the calculations. They may have received less, but then some of the missing fish must have been cannibalized, since the observed mortalities generally accounted for less than half the number of fish missing at the end of the experiments.

Although it is a general practice in restricted feeding regimes to readjust the feed rations weekly or even bi-weekly, this introduces considerable inaccuracy when the growth rates are as high as in these experiments. To illustrate this point, the overall average specific growth rates (% body weight per day) were calculated using the formula as given in Table III (cf. Huisman, 1974). The actual feeding rates were calculated from the total feed intake

TABLE III

Selected feeding levels, overall average specific growth rates and actual feeding levels in experiments 1 and 2 (in % of biomass per day)

Experiment 1					
Selected feeding level	4	6	8	10	satiation
Specific growth rate	5.5	7.9	10.0	10.8	10.6
Actual feeding level	3.1	3.9	4.9	6.3	9.2
Experiment 2					
Selected feeding level	10	10	10	10	10
Specific growth rate[1]	7.9	9.8	10.4	11.3	12.0
Actual feeding level[2]	8.1	7.2	7.0	6.5	6.6

[1] Specific growth rate: $\alpha = 100\left(t\sqrt{\frac{Gt}{G0}} - 1\right)$.

[2] Actual feeding level: total feed intake/$\int_0^t y(t)\,dt$.

divided by the integral of the corresponding body weight—time relation given in Figs. 1A and 1B. It was found that at a daily specific growth rate around or above 10%, and weekly readjustment of the feeding levels, the actual feeding rates only amounted to about two-thirds of the designated ones (Table III).

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The experimental work reported in this paper concludes the initial phase of the research programme on the aquaculture of *C. lazera* undertaken by the Department of Fish Culture and Inland Fisheries of the Agricultural University in Wageningen, The Netherlands. I wish to express my gratitude to the Agricultural University and to my colleagues of the Department, Prof. Dr. E.A. Huisman and Dr. C.J.J. Richter, for the fact that the elaboration of these experiments was made possible.

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3 GROWTH AND PRODUCTION OF THE AFRICAN CATFISH, *CLARIAS LAZERA* (C. & V.)

I. Effects of stocking density, pond size and mixed culture with tilapia (*Sarotherodon niloticus* L.) under extensive field conditions

II. Effects of body weight, temperature and feeding level in intensive tank culture

III. Bioenergetic relations of body weight and feeding level

Appendix: An open circuit balance respirometer for bioenergetic studies of fish growth

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GROWTH AND PRODUCTION OF THE AFRICAN CATFISH, *CLARIAS LAZERA* (C. & V.)
I. EFFECTS OF STOCKING DENSITY, POND SIZE AND MIXED CULTURE WITH TILAPIA (*SAROTHERODON NILOTICUS* L.) UNDER EXTENSIVE FIELD CONDITIONS

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ABSTRACT

Hogendoorn, H. and Koops, W.J., 1983. Growth and production of the African catfish, *C. lazera* (C. & V.). I. Effects of stocking density, pond size and mixed culture with tilapia (*Sarotherodon niloticus* L.) under extensive field conditions. *Aquaculture*

Growth and production of *C. lazera* (C. & V.) and *S. niloticus* L. in mono- and mixed culture were studied in relation to stocking density and pond size using a low grade feed.

The biomass after 24 weeks ranged from 16 to 115 $g \cdot m^{-2}$ for tilapia and from 50 to 266 $g \cdot m^{-2}$ for *C. lazera*. Independent of the other treatments, the use of *C. lazera* resulted in a more than 2.5-fold increase in the biomass as compared with tilapia. For both species the biomass increased with increasing stocking density, but the individual weight was greatly reduced.

The growth of neither tilapia nor *C. lazera* was found to be affected by the presence of the alternate species, indicating the absence of interspecies competition. Increased pond size resulted in a lower biomass of tilapia, while the growth of *C. lazera* was independent of the pond size.

INTRODUCTION

Clarias lazera (C. & V.) is a new species in aquaculture (De Kimpe and Micha, 1974). To further substantiate its potential, an experiment to study the growth and production performance of *C. lazera* under field conditions is reported in this paper.

In the (semi-)extensive management that prevails in the rural pond fish culture in Central Africa, the fish largely rely on the (natural) productivity in the ponds for their (complete) feed. The fish density and the resulting grazing intensity then determine how much of the natural feed is available for each fish. Since *C. lazera* is an omnivore (De Kimpe and Micha, 1974), it should be suitable for this type of aquaculture, that is usually based on a low grade feed compounded of locally available agricultural byproducts. To

determine the growth and production of *C. lazera* under such conditions an experiment was carried out applying different stocking densities, in small earthen ponds.

To serve as a direct reference an analogous experiment was carried out using tilapia (*Sarotherodon niloticus* L.), which is widely known and used in this type of fish culture in Africa (Maar et al., 1966; Bardach et al., 1972; Huet, 1972; Balarin and Hatton, 1979). *C. lazera* and tilapia were also stocked in mixed culture to check for interspecies competition and the ability of *C. lazera* to control undesired tilapia recruitment.

MATERIALS AND METHODS

Facilities and fish

The experiment was carried out in 28 small earthen diversion ponds at the National Fish Culture Centre, Foumban, Cameroon. Of these ponds 14 were about 50 m^2 and the other 14 were about 100 m^2 in surface area. The depth was about one meter in the centre. The water supply to the ponds was from the river Melap.

At the start of the experiment the ponds were stocked with fingerlings of 1 to 5 g of *C. lazera* and/or tilapia harvested from fingerling production ponds.

Experimental procedures

The stocking densities used were 0.5, 1, 2, 4 and 1, 2, 4 fingerlings$\cdot m^{-2}$ for *C. lazera* and tilapia respectively, with or without 0.2 fingerlings$\cdot m^{-2}$ of the alternate species (Table I). The different treatments were randomly assigned to the different ponds with the restriction that each treatment occurred once in a smaller and once in a bigger pond.

The experiment was continued for 24 weeks, while every 2 weeks the fish were sampled by seine to monitor the growth pattern and to readjust the quantity of feed. After the 4th and the 8th week all ponds were drained to verify the stocking density. Upon termination the total number and weight of the fish were determined.

A mixture of 1 part cottonseed cake, 1 part cows' blood and 8 parts brewers grains was used as a representative local feed. After drying in the sun and grinding, this mixture was administered at 6% of the metabolic weight ($W^{0.8}$) of the fish/day. Every 2 weeks the quantity of feed was readjusted, based on the weight of the sampled fish. Fish were fed 6 days a week, mornings and evenings.

Analysis of data

The effects of the treatments on the fish biomass present in the ponds were investigated using the computer programme GLIM (Generalized Linear

Interactive Modelling; Baker and Nelder, 1978). A linear model was used to estimate and compare constants and regression coefficients. The treatments included in the model were the main factors: species (tilapia versus *C. lazera*), type of culture (mono- versus mixed culture), pond size (small versus bigger ponds) and their interactions. Also included were the covariates: stocking or final fish density, mortality and time as affected by the main factors. The variables biomass and density of the fish were included on a natural logarithmic scale, because of the nature of their relation.

As a constraint GLIM sets the constant for the first class of the factors equal to zero. The basic constant of the model then is an estimated value for the joint first class of all factors, when the values of the covariates equal zero. The constants for the second and subsequent classes of the factors are estimated as deviations from the value for the first class. Also, the regression coefficients for the covariates are estimated for each class of the factors as deviation from the corresponding coefficient for their joint first class.

The GLIM programme then allows a stepwise analysis. Starting from the full model, the statistical significance of the different effects of the treatments can be assessed on the basis of the ratio of their partial regression coefficients and the corresponding standard errors. Terms that do not reduce the residual variance can then be deleted from the model to be pooled with the residual variance. The model is thus reduced to its most meaningful form, when the residual variance is minimal.

Because of the limited number of observations available, only the effects of the main factors on the slopes for the covariates were estimated and compared. When a significant difference in slope was found, the effect of the covariate was taken to be changed by the main factor.

In a second model the effect of the length of the production cycle was investigated by the inclusion of time as an extra covariate. The joint effect of time and, respectively, ln (final density) and mortality was also included.

An example of the models used is given under Table III.

RESULTS

The stocking densities as well as the densities and the average weights of the fish upon termination of the experiment are given in Table I.

Survival

The overall survival was 69 ± 25% and 63 ± 25% (± S.D.) for tilapia and *C. lazera* respectively. This low survival was already evident at the intermediate drainings after 4 and 8 weeks. Even though missing fish were replaced at these times, the situation did not improve. The intermediate drainings were therefore discontinued.

Analysis of the survival rate showed that it was not clearly affected by

TABLE I

Final density D (fish·m^{-2}) and final average weight W (g) of *C. lazera* and *S. niloticus* after 24 weeks of culture in small ponds. Per treatment the results of the replicate in the smallest pond are given first

Stocking density (fish·m^{-2})		Tilapia																	
		0				0.2				1				2				4			
Clarias		Clarias		Tilapia		Clarias		Tilapia		Clarias		Tilapia		Clarias		Tilapia		Clarias		Tilapia	
		D	*W*	*D*	*W*	*D*	*W*	*D*	*W*	*D*	*W*	*D*	*W*	*D*	*W*	*D*	*W*	*D*	*W*	*D*	*W*
	0									—		0.83	70	—		1.67	52	—		0.95	88
										—		0.72	63	—		1.51	38	—		2.78	26
	0.2									0.17	288	1.00	77	0.11	200	1.94	44	0.13	300	2.17	53
										0.18	300	0.25	62	0.25	121	1.79	30	0.16	267	2.94	33
	0.5	0.42	275	—		0.21	236	0.15	90												
		0.28	219	—		0.33	206	0.19	111												
	1	0.69	162	—		0.75	180	0.20	75												
		0.72	202	—		0.34	186	0.18	91												
	2	1.20	128	—		1.04	117	0.15	118												
		1.82	122	—		1.17	149	0.18	114												
	4	2.90	92	—		1.82	84	0.20	89												
		2.30	91	—		2.69	84	0.19	94												

any of the treatments. It did, however, interfere with the original experimental design, because it changed the fish densities. Some mortality is bound to occur in fish culture practice, but the extent and the time of occurrence may vary, depending on the cause. For the general practical case, the main management decision therefore remains which original stocking density to apply. In line with this, the analyses of the biomass results in the first model were based on the original stocking density, but a correction for the mortality rate was made by including it as a covariable.

Biomass upon termination

The biomass upon termination ranged from 16 to 115 $g \cdot m^{-2}$ for tilapia and from 50 to 266 $g \cdot m^{-2}$ for *C. lazera* (Fig.1). The statistical analysis showed (Table II, column A) that, on the basis of the main species data, the use of *C. lazera* gave a significantly (about $e^{0.98}$ = 2.7-fold) higher biomass than when tilapia were stocked. The presence of the alternate species did not affect the biomass of the main species, indicating the absence of interspecies competition. In the bigger ponds the biomass was significantly reduced in the case of tilapia, but for the biomass of *C. lazera* the pond size had a positive effect. Independent of species, mixed culture or pond size, a similar log-log-linear relation was found between the biomass and the stocking density. The mortality rate significantly reduced the biomass, more so in the case of *C. lazera* than with tilapia.

When the total biomass of all fish present in the ponds was analysed against the total stocking density (Table II, column B), the effects and interactions of the treatments were consistent with the earlier analysis of the main species data. Inherently, the better growth of *C. lazera* significantly increased the total biomass in the case of a few *C. lazera* added in tilapia

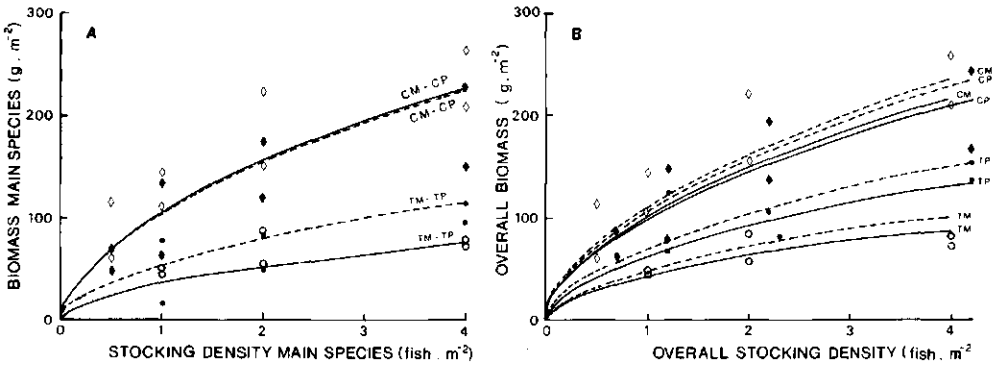

Fig.1. Final average biomass ($g \cdot m^{-2}$) in relation to the stocking density ($fish \cdot m^{-2}$) of *Clarias* (C, ◊) and tilapia (T, ○) in mono- (M, open) and in mixed culture (P, closed). The main species data are given in A and the overall data in B. The drawing of the lines is explained in the text. Dotted lines indicate the small ponds and solid lines indicate the bigger ponds.

TABLE II

Partial constants and regression coefficients for the effects and interactions of species, type of culture, pond size, ln (density), mortality and time on ln (biomass) of the fish present in the ponds

Constants	A[1]	B[1]	C[1]	D[1]
Effect of main factors:				
Tilapia monoculture in small ponds	4.25*	4.07*	4.12*	1.97*
C. lazera	0.98*	1.43*	1.28*	1.07*
Mixed culture	0	0.39*	0.47*	0.23*
Bigger ponds	− 0.31*	− 0.38*	− 0.42*	− 0.33*
Effect of interactions of factors:				
C. lazera × mixed culture	0	− 0.42*	− 0.34*	− 0.18
C. lazera × bigger ponds	0.47*	0	0.24*	0.24*
Mixed culture × bigger ponds	0	0	0	− 0.17
C. lazera × mixed culture × ponds	0	0	0	− 0.35*
Regression coefficients				
Effect of ln (density):				
Tilapia monoculture in small ponds	0.56*	0.55*	0.49*	0.87*
Other main factors	0	0	0	0
Effect of mortality:				
Tilapia monoculture in small ponds	− 0.88*	− 0.66*	− 0.49*	− 2.21*
C. lazera	− 0.67*	− 1.48*	− 1.42*	0
Mixed culture	0	0	0	0
Bigger ponds	− 0.42	0.81*	0.52	0.60*
Effect of time:				
Tilapia monoculture in small ponds	—	—	—	0.16*
Other main factors	—	—	—	0
Joint effect of time and ln (density):				
Tilapia monoculture in small ponds	—	—	—	− 0.01
Other main factors	—	—	—	0
Joint effect of time and mortality:				
Tilapia monoculture in small ponds	—	—	—	0.05*
C. lazera	—	—	—	− 0.07*
Mixed culture	—	—	—	0
Bigger ponds	—	—	—	0

*: $P \leq 0.05$; 0: pooled with residual variance; − : not included in the model.

[1] Relation between:

A, final biomass and stocking density of main species

B, final biomass and stocking density of all fish in the pond

C, final biomass of all fish in the pond and stocking density of main species

D, biomass and final density of all fish in the pond.

culture, whereas the biomass per unit of fish density was reduced when tilapia were present in the culture of *C. lazera*.

As was explained earlier, the partial constants and regression coefficients for the effects of the different factors and covariates in Table II are to be read as deviations from the joint first class of all factors: monoculture of

TABLE III

Constants (C) and coefficients for the regression of ln (final biomass) on ln (stocking density) (LD) and mortality (M) for tilapia and *Clarias* in mono- and mixed culture in small and bigger ponds

Treatment	Main species			Overall		
	C	LD	M	C	LD	M
Small ponds:						
Tilapia monoculture[1]	4.25	0.56	-0.88	4.07	0.55	-0.66
Tilapia + *Clarias*	4.25	0.56	-0.88	4.46	0.55	-0.66
Clarias monoculture	5.23	0.56	-1.55	5.50	0.55	-2.14
Clarias + tilapia	5.23	0.56	-1.55	5.47	0.55	-2.14
Bigger ponds:						
Tilapia monoculture	3.94	0.56	-1.30	3.70	0.55	0.152
Tilapia + *Clarias*	3.94	0.56	-1.30	4.08	0.55	0.152
Clarias monoculture	5.39	0.56	-1.98	5.12	0.55	-1.329
Clarias + tilapia	5.39	0.56	-1.98	5.09	0.55	-1.329

[1] Equations are to be read as:
ln (final biomass) = C + M·(mortality) + LD·ln (stocking density)
Hence:
Biomass tilapia (monoculture, small ponds) = $e^{4.25-0.88\ (\text{mortality})} \cdot (\text{density})^{0.56}$

tilapia in small ponds. To illustrate the procedure, the relevant partial constants and regression coefficients for the factorial treatments in columns A and B of Table II were combined to give the separate regression lines for all treatments in Table III. Taking the average mortality rate for tilapia and *C. lazera* as reported earlier, these lines were drawn in Fig.1 to illustrate the differences.

No inference could be made about the predatory capacity of *C. lazera* on the fingerlings of tilapia and its effects on the growth of both species, because during the course of the experiment the tilapia reproduced very little.

Biomass development in time

From the average weights of the biweekly samples the biomass development in time could be depicted for the different stocking densities and species combinations in Fig.2. First of all it is apparent that all fish started to grow slowly (c.f. Hogendoorn, 1981), especially the tilapia. Most probably, the natural feed in the ponds took time to develop. Also, it could be that the intermediate draining of the ponds after 4 and 8 weeks was responsible for this phenomenon.

The development of the total biomass present in the ponds was therefore analysed on the basis of average weights of the samples and the density upon termination for the period after the 8th week. Furthermore, the ter-

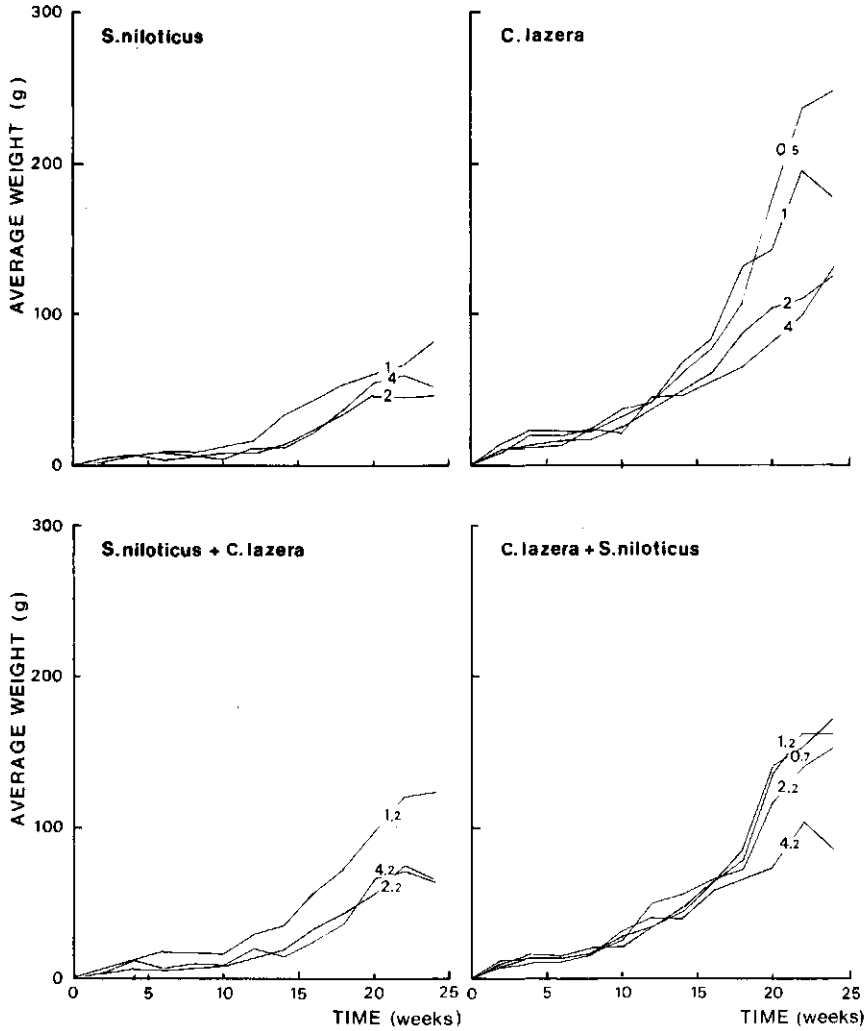

Fig.2. Average weights of the biweekly samples in relation to the production period. The graphs represent the mean results of a small and a bigger pond for the different stocking densities and species combinations as indicated.

minal average weights were excluded from the analysis, because at that time the samples were not taken by seine.

The results of this analysis (Table II, column D) show that the biomass was significantly altered by 6 of the 8 different treatments, whereas the effects of time and density were independent of species, mixed culture or pond size. The negative effect of mortality on the biomass was less pronounced in the bigger ponds. A trend appeared ($P < 0.2$) for the biomass development to become limited by the stocking density as time progressed. The time-mortality interaction affected the biomass differently for tilapia and *C. lazera*.

DISCUSSION AND CONCLUSIONS

The experiment confirmed the suitability of *C. lazera* for (semi-)extensive pond fish culture as it is practised in various parts of Africa. In the small experimental ponds the *C. lazera* grew up to a maximum of 300 g in 5½ months. Under comparable circumstances the tilapia reached a maximum of 118 g.

The mixture of 1 part cottonseed cake, 1 part cows' blood and 8 parts brewers grains proved to be a low grade feed. This was emphasized by the pronounced inverse relation between the body weight and the stocking density, indicating that the fish relied heavily on the natural productivity of the ponds for their (complete) feed. Another indicator was the high relative feed conversion (feed(kg)/gain (kg)), which was 11.6 ± 4.8 and 8.9 ± 3.0 for tilapia and *C. lazera* respectively. Obviously, this puts the supplied feed material on the level of an organic fertilizer. Hence it can only be recommended for use when it is available at little or no cost. Alternatively, formulation improvements must be considered which will increase the quality while maintaining a low cost.

The overall survival rate was rather low. Bardach et al. (1972) mention 80—90% as the normal survival rate for tilapia, while Lazard (1980) found about 90% survival in his experiments in 1000-m^2 ponds. However, under this type of management conditions low survival of the fish is not uncommon, especially when the stocked fingerlings are as small as they were in this experiment. Also, the intermediate drainings and the biweekly sampling probably had an adverse effect. The low survival made an unequivocal analysis and comparison of the results difficult. However, since the mortality had no clear relation with any of the treatment effects, it was considered no impediment for the evaluation of the results.

Independent of the other treatment effects, the advantage of using *C. lazera* amounted to a more than 2.5-fold increase in the biomass as compared with the use of tilapia. The growth of neither tilapia nor *C. lazera* was found to be affected by the presence in the pond of some specimens of the alternate species. Also, the same allometric relation was found between the biomass and the stocking density for both species. However, the *C. lazera* were generally bigger than the tilapia. This indicated that the two species utilized the resources of the ponds at different levels, but with analogous limiting mechanisms. These observations can be interpreted as evidence for the ecological separation of the two species in the ponds.

When a complete ecological separation is assumed, the contribution of the second species to the overall biomass is independent of the contribution of the main species. Analysis of this situation (Table II, column C) showed that 0.2 tilapias·m^{-2} added to the *C. lazera* population gave a 14% increase in the total biomass, whereas the contribution to the total biomass of 0.2 *C. lazera*·m^{-2} in tilapia culture was 60%. For correct interpretation of the above conclusions it must be realized that their validity cannot safely be extended beyond the conditions prevailing in this experiment: i.e. low grade

feed and the virtual absence of tilapia reproduction. Lazard (1980), for example, did find a decrease in tilapia yield when *C. lazera* was present, which he explained by competition for the feed.

The consistently lower biomass of tilapia in the bigger ponds, as opposed to the biomass of *C. lazera*, also points to ecological separation of the two species. The difference in size between the small and the bigger ponds was a mere factor of 2 and should not have altered the pond ecology to a great extent. The main difference was probably in the ratio between the total length of the pond banks and the surface area, which was about 60 and 40% /m for the small and the bigger ponds respectively. It could be that the tilapia were more dependent on the pond banks or the adjoining shallows for their feed (e.g. mosquito larvae). Whatever may have been the case, the observed effect of the pond size emphasizes the dangers in predicting the results obtainable from large ponds on the basis of pilot experiments carried out in small ponds.

The development of the biomass in time showed a greater diversity of the factor effects and interactions as compared with the biomass upon termination. The nature of the relation between biomass, time and density was the same for the different factorial treatments. The limiting effect at higher densities as time progressed did not play an important role until later in the experiment. The time-mortality interaction is difficult to interpret. It could either indicate that the effect of initial mortality increased with time or that the mortality itself increased with time.

In the frame of the experiment a point of maximal biomass was not reached and an optimum for the stocking density or the production period could therefore not be determined. Similarly, the data did not allow for the determination of a point of maximal production, defined as the specific increase in biomass multiplied by the biomass (Brocksen et al.,1968). In this experiment the highest stocking density resulted in the highest biomass upon termination, although the corresponding weight of the individual fish was greatly reduced. Market preferences concerning the species of fish and their size should therefore be considered when the type of culture and the conditions are to be decided.

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GROWTH AND PRODUCTION OF THE AFRICAN CATFISH, *CLARIAS LAZERA* (C. & V.)
II. EFFECTS OF BODY WEIGHT, TEMPERATURE AND FEEDING LEVEL IN INTENSIVE TANK CULTURE

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ABSTRACT

Hogendoorn, H., Jansen, J.A.J., Koops, W.J., Machiels, M.A.M., Van Ewijk, P.H. and Van Hees, J.P., 1983. Growth and production of the African catfish, *Clarias lazera* (C. & V.). II. Effects of body weight, temperature and feeding level in intensive tank culture. *Aquaculture*

An experiment including 273 separate trials was carried out in densely stocked 150-l aquaria to study the growth response of *C. lazera* (C. & V.) weighing about 0.5, 5, 25 and 125 g to five different feeding levels from feed deprivation to satiation at 20, 25, 27.5, 30, 32.5 and 35°C. Analyses of dry matter, energy and nitrogen content were made in samples of the feed and of the fish to determine the feed utilization.

It was found that *C. lazera* is highly suitable for high density, intensive aquaculture, because of its rapid growth and efficient feed utilization. The specific growth rate decreased from a maximum of 11% per day for small fish at 30°C to a maximum of 2% per day for the largest size group at 25°C. The corresponding maximum feed conversion efficiency decreased from 170 to 100%.

A model was developed to describe the feed utilization for growth on a dry and on a fresh weight basis. Winberg's balanced energy equation: $dW/dt = p \cdot R - H$ and Pütter's original growth concept equating growth to the difference between anabolic and catabolic activities both related to the body weight already achieved: $dW/dt = k_1 W^m - k_2 W^n$, were used as a basis for the model. It was found that the feed utilization was independent of feeding level and temperature. It was also independent of body weight in the case of the dry weight feed utilization. For the fresh weight, the feed utilization decreased exponentially with increasing body weight, probably because the dry matter content of the fish increased allometrically with body weight. Temperature optima were found for k_1 and m while k_2 increased not quite exponentially with temperature and n was constant.

These findings complied with or supported related findings in the literature and could be interpreted biologically. The model was used to predict the growth of *C. lazera* as a response to the feed ration in relation to temperature and body weight. A table of recommended feeding levels for *C. lazera* was established.

INTRODUCTION

To substantiate the potential of *Clarias lazera* (Cuvier and Valenciennes) for aquaculture, its growth and production performance were studied under different culture conditions. In an earlier experiment (Hogendoorn and Koops, 1983) the suitability of *C. lazera* for extensive pond culture was confirmed. The aim of the present experiment was to study the growth and production of *C. lazera* in high density culture using a complete artificial feed.

A considerable number of biotic and abiotic factors are known to influence the growth of fish (Brett, 1979). The experimental variables chosen in this study were body weight, water temperature and feeding level. To account for the other factors young, immature fish were randomly assigned to different test groups. The dissolved oxygen concentration and the water quality were kept constant. A light regime of 12 $h \cdot day^{-1}$ was maintained and other possible seasonal effects were tentatively counterbalanced by a random sequence of the various trials over 2 years.

MATERIALS AND METHODS

Facilities and fish

The experiment took place in 150-l glass aquaria. These were part of two recirculation systems including a 2-m^3 sedimentation tank, followed by a 1-m^3 biological filter filled with 0.5-cm gravel. The water was pumped from the bottom of the biological filter by a 0.75 HP centrifugal pump (Arbo, KR-70) into a head manifold, that supplied the individual aquaria (15—20) with the required water. Reaeration took place by injection of pure oxygen into the water circuit just before the pump. The desired experimental temperature was maintained by a submersed heating element and a continuous supplementation of 1—2 l/min of preheated make-up water.

The dissolved oxygen concentration of the recirculation water was maintained at about saturation for the water entering the aquaria and above 40% saturation for the water leaving the aquaria. The NH_4^+ and NO_2^- concentrations were maintained below 0.5 ppm by the biological filter or by increasing the fresh water supplementation in case the filter was functioning insufficiently, e.g. after disinfection of the system. These conditions were checked daily (temperature, dissolved oxygen) or weekly (NH_4^+, NO_2^-).

The experimental fish were obtained using the methods described earlier (Hogendoorn, 1980; Hogendoorn and Vismans, 1980).

Experimental procedures

A series of 273 trials was carried out as part of a trifactorial experiment including body weight, temperature and feeding level as variables. The trials

were conducted with one (small fish) or two replicates and were continued for two (small fish) to four weeks.

The average weight of the fish at the start of the different trials was about 0.5, 5, 25 or 125 g and the corresponding stocking densities were 250, 100, 30 and 15 fish per aquarium respectively. The temperatures tested were 20, 25, 27.5, 30, 32.5 and 35°C, with the restriction that the complete temperature range was tested with the small fish while only the four lower temperatures were tested with all fish sizes. Five feeding levels were included between deprivation and satiation, varying of course with the weight of the fish and the temperature. The experimental fish were reared up to the required weight at the designated experimental temperature. Occasionally this was not possible and an acclimation period of at least 2 weeks was allowed prior to the start of the trial.

The feeding levels were as a percentage of the body weight of the fish. However, readjustment of the feed quantity to the body weight must be frequent to avoid discrepancies between the designated and the actual feeding level (Hogendoorn, 1981). Therefore, the feed quantity was readjusted daily, based on an estimate of the growth rate. Once a week one of the replicates per treatment was weighed, to verify the growth estimate and to adjust the feed quantity for all replicates, if necessary. This way the fish were manipulated only once during the experimental period.

Feeding was continuous from 20.00 to 08.00 h using "Scharflinger" automatic feeders, because this had been shown to be the second best feeding regime to 24-h feeding (Hogendoorn, 1981) and minimized the disturbance of feeding by cleaning and other activities that were carried out during the day. "Trouvit" (Trouw & Co, Putten, The Netherlands), a commercial trout feed, was used in the pellet sizes 0.9, 1.5, 2.7 and 5.0 mm for the different size groups of fish respectively.

At the start and the end of each trial a sample of the fish was retained for analysis of dry matter, energy and nitrogen. These analyses were also carried out in the feed used for each trial.

Analysis of data

For the analysis of weight changes of fish various models are available (Ricker, 1979). The different growth curves can be used when weight-time data are available over a large section of the species' natural weight range. When the aim is to describe and compare short periods of growth, the use of the specific growth rate is indicated (Weatherley, 1972). Known under many other names, the logarithmic form of the specific growth rate ($\alpha = (\ln W_e - \ln W_s) \cdot 100/t$) is most commonly used in relation to fish (Ricker, 1979). However, with the specific growth rate meaningful comparisons can only be made when the variation in body weight is limited and identical for the fish to be compared (c.f. Weatherley, 1972; Brett, 1979).

These trials necessarily resulted in unequal variations in weight because during a fixed period the fish received different amounts of feed at different temperatures. The analysis was therefore based on the original growth concept advanced by Pütter (1920), Winberg (1956) and Von Bertalanffy (1957) that "any change in body weight results from the difference between what enters the body and what leaves it".

$$dW/dt = p \cdot R - H \tag{1}$$

where dW = change in weight, R = ration consumed, p = coefficient of metabolizability of the ration and H = catabolic losses. R and H are in units of weight (g) per unit of time. The catabolic term H in Eqn. (1) incorporates the fasting as well as the feeding catabolism, which is necessary to make feed material available and suitable for maintenance or growth. The second term is also referred to as the specific dynamic action or the heat increment of the ration (Warren, 1971; Brett, 1979). It seemed realistic to put this feeding metabolism proportional (q) to the metabolizable ration (Ursin, 1967). Assuming that fasting and maximal feeding metabolism are allometrically related to body weight (Winberg, 1956; Paloheimo and Dickie, 1966; Huisman, 1974) it follows that

$$\begin{aligned} dW/dt &= pR - pqR - k_2 W^n \\ &= -k_2 \cdot W^n \qquad (R = 0) &(2)\\ &= (p - pq)R - k_2 \cdot W^n \qquad (0 \leqslant R \leqslant R_{max}) &(3)\\ &= k_1 \cdot W^m - k_2 \cdot W^n \qquad (R = R_{max}) &(4) \end{aligned}$$

These equations imply that any change in weight is a function of the weight already achieved. Eqns. (2) to (4) were first solved for the dry weight of the fish and the feed. Since they cannot be linearized, the parameters were estimated using a non-linear regression procedure. Starting from the dry weight of the fish at the start of the respective trials and estimates for the parameters, the corresponding dry weight of the fish at the end of the trials was estimated by numerical integration using Taylor's formula with dt = 1 day:

$$W_n = W_{n-1} + dt \left[\frac{dW}{dt}\right]_{W = W_{n-1}} + 0.5\, dt^2 \left[\frac{d^2W}{dt^2}\right]_{W = W_{n-1}}$$

The sum of the squared deviations of the estimated final weights from those actually found then provides a measure for the error in the parameters estimated. Using the routine ZXSSQ of the computer programme IMSL (International Mathematical & Statistical Libraries, 1979), the parameter estimates were subsequently adjusted by iteration to minimize the residual sum of squared deviations. To account for heterogeneity of variance between the different size groups, the squared deviations were weighed by the reciprocal of the final weights actually found.

In a first approach the parameters of Eqn. (2) were estimated within each experimental temperature group. The values found were then inserted in Eqns. (3) and (4), that were solved simultaneously also per experimental temperature group first. The parameters p and q could not be estimated separately. Therefore, the relevant term in Eqn. (3) was estimated as a single parameter for feed utilization.

The effect of temperature (T) on the growth of fish is scarcely documentated in the literature (Ursin, 1967; Elliot, 1975a, and b; Ricker, 1979). A sound physiological basis still seems to be unavailable. Therefore, an empirical approach was taken using the flexible Hoerls function (Daniel and Wood, 1971) to describe the overall effect of temperature

$$f(T) = aT^b e^{cT} \tag{5}$$

To put the elaborated model back on a fresh weight basis the dry matter (y) of the fish was analyzed in relation to fresh body weight per feeding level as follows.

$$y = rW^s \tag{6}$$

Eqn. (6) was solved for the data at the end of each trial using the computer programme GLIM (Generalised Linear Interactive Modelling; Baker and Nelder, 1978). The same model was used to analyze the energy and protein in the fish.

Based on the analysis of the dry weight feed utilization and the body composition, a model for the fresh weight feed utilization was subsequently developed.

RESULTS

A summary of the experimental results is given in the Appendix. For easy reference the feed conversion as well as the energy and protein conversion efficiencies are also included.

Changes in weight

The changes in weight are summarized in Fig.1, where the specific growth rate ($\alpha = (\ln W_e - \ln W_s) \cdot 100/t$) of the fish in all trials is given in relation to the feed ration. The specific growth rate typically increased from a negative value at feed deprivation towards a maximum as feeding increased (Brett, 1979). Both the feeding level and the specific growth rate decreased with increasing body weight. For the small fish maximum growth was realized between 27.5 and 32.5° C whereas the bigger fish grew best at 25 to 27.5° C. To illustrate this observation the maximum observed specific growth rates have been plotted in Fig.2 in relation to temperature and the mean body weight.

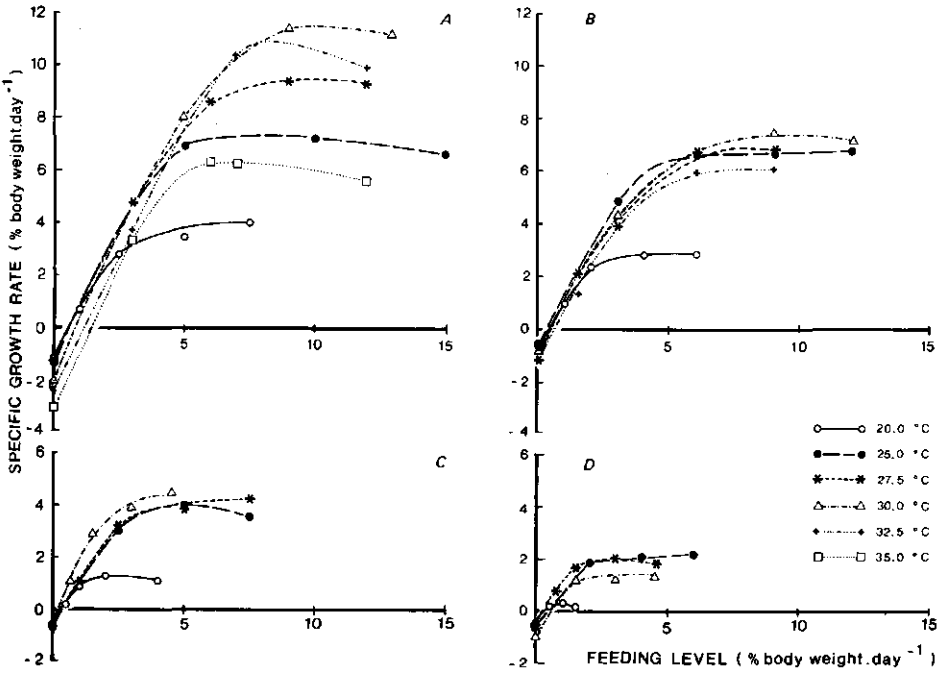

Fig.1. Specific growth rate in relation to feeding level (% body weight·day^{-1}) and temperature (°C) for *C. lazera* of 0.3—3 g (A), 5—40 g (B), 25—70 g (C) and 95—200 g (D).

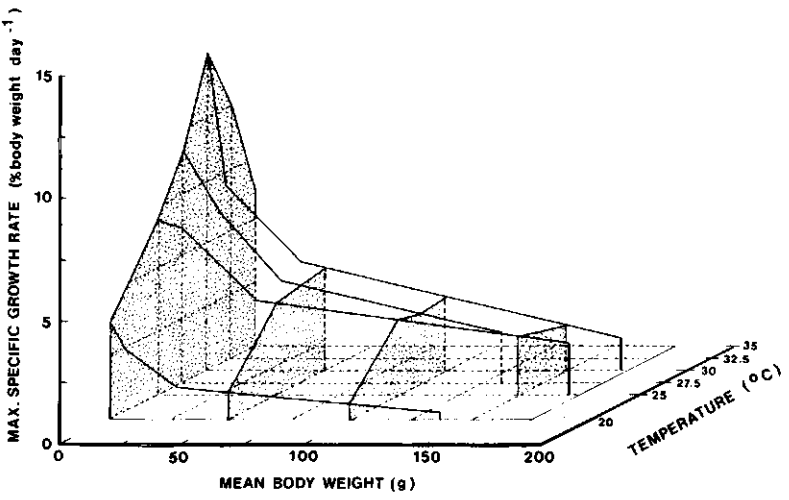

Fig.2. Maximum specific growth rate (% body weight·day^{-1}) of *C. lazera* in relation to temperature (°C) and (geometrical) mean body weight (g).

Dry weight feed utilization

From Fig.1 it appears that the increase in the specific growth rate is linear with an increase in feed ration up to near satiation feeding, indicating a constant feed utilization. However, in interpreting the apparent deflection at near-satiation feeding it must be borne in mind that these fish have grown considerably during the trial. It has already been seen that the specific growth rate is lower for bigger fish. The apparent deflection could therefore be based on an artifact rather than indicating a feed utilization depression at higher feeding levels. Using the differential equations (2) to (4) to analyze the changes in dry weight this could be eliminated.

The parameter estimates for the changes in dry weight during feed deprivation, given in Table I, show that the decrease in dry weight was allometrically related to the dry weight of the fish. The coefficient, k_2, increased with temperature, whereas the dry weight exponent, n, had a constant value of about 0.74.

TABLE I

Parameter estimates and residual sum of squares for the changes in dry weight during feed deprivation

Temperature (°C)	k_2	n	a_2	b_2	c_2	RSS	NNRSS
20	0.0097	0.72	—	—	—	0.02	0.02
25	0.0100	0.76	—	—	—	0.05	0.05
27.5	0.0124	0.74	—	—	—	0.08	0.04
30	0.0181	0.73	—	—	—	0.08	0.03
All	—	0.74	0.0063	−1.5	0.74	0.31	0.15
All	—	0.75	0.0069	−2.3	1.0	0.32	0.15

The functions used were $dW/dt = -k_2 W^n$; $k_2 = a_2 \cdot T^{b_2} e^{c_2 T}$. Temperature $T = (\tau - 10)/5$. RSS = residual sum of weighed squares; NNRSS = nearest neighbour estimate of weighed variance. Underlined parameters were kept fixed during the estimation.

After insertion of the estimates for k_2 and n, Eqns. (3) and (4) were solved. The first analyses excluding the smallest size groups showed (Table II) that k_1 and m increased with temperature towards an optimum, while the coefficient for feed utilization ($p-pq$), appeared to be constant. Table II also shows that inclusion of the smallest fish in the analysis gave illusionary results, notably a greater fluctuation of parameter estimates and higher residual variance. This was primarily caused by the underestimation of ($p-pq$) in combination with an overestimation of the dry weight increase at satiation feeding. Therefore, an empirical addition of a die-away curve ($e^{-l/W}$) was made to Eqn. (4) to account for less efficient juvenile growth at satiation feeding

$$dW/dt = e^{-l/W} \cdot k_1 \cdot W^m - k_2 \cdot W^n \qquad (R = R_{max}) \qquad (7)$$

TABLE II

Parameter estimates and residual sum of squares for the changes in dry weight during feeding

Size group	Temp. (°C)	k_1	k_2	$(p-pq)$	m	n	l	a_1	b_1	c_1	a_2	b_2	c_2	a_3	b_3	c_3	RSS	NNRSS
2, 3, & 4	20	0.05	0.0097	0.43	0.44	0.72	0	—	—	—	—	—	—	—	—	—	0.14	0.07
	25	0.11	0.0100	0.42	0.62	0.76	0	—	—	—	—	—	—	—	—	—	0.22	0.19
	27.5	0.19	0.0124	0.41	0.41	0.74	0	—	—	—	—	—	—	—	—	—	0.16	0.16
	30	0.14	0.0181	0.50	0.50	0.73	0	—	—	—	—	—	—	—	—	—	0.36	0.15
	All	—	—	0.44	—	0.89	0	0.017	4.6	−1.1	0.0061	−2.4	1.0	0.58	3.0	−1.1	1.03	0.58
1, 2, 3 & 4	20	0.04	0.0097	0.42	0.67	0.72	0	—	—	—	—	—	—	—	—	—	0.53	0.10
	25	0.16	0.0100	0.15	0.51	0.76	0	—	—	—	—	—	—	—	—	—	4.96	0.25
	27.5	0.22	0.0124	0.32	0.38	0.74	0	—	—	—	—	—	—	—	—	—	1.16	0.21
	30	0.17	0.0181	0.31	0.44	0.73	0	—	—	—	—	—	—	—	—	—	2.70	0.20
1, 2, 3 & 4	20	0.06	0.0097	0.42	0.39	0.72	0.19	—	—	—	—	—	—	—	—	—	0.20	0.10
	25	0.12	0.0100	0.47	0.60	0.76	0.18	—	—	—	—	—	—	—	—	—	0.42	0.25
	27.5	0.20	0.0124	0.43	0.43	0.74	0.32	—	—	—	—	—	—	—	—	—	0.22	0.21
	30	0.14	0.0181	0.48	0.51	0.73	0.12	—	—	—	—	—	—	—	—	—	0.82	0.20
	All	—	—	0.45	—	0.80	0.13	0.017	5.4	−1.4	0.0054	−2.1	1.0	0.54	1.8	−0.59	6.30	1.26

The functions used were: $dW/dt = (p-pq)\,R - k_2 \cdot W^n$ for $0 \leq R \leq R_{max}$; $dW/dt = e^{-l/W} k_1 \cdot W^m - k_2 \cdot W^n$ for $R = R_{max}$; $k_1 = a_1 \cdot T^{b_1} e^{c_1 T}$; $k_2 = a_2 \cdot T^{b_2} e^{c_2 T}$; $m = a_3 \cdot T^{b_3} e^{c_3 T}$. Further explanations as in Table I.

The parameter estimates for the combined Eqns. (3) and (7) are also given in Table II. Estimates for the changes in dry weight at 32.5 and 35° C could not be made due to insufficient data.

Based on these results it was assumed that both k_1 and k_2 as well as m are dependent upon the temperature. A preliminary analysis of the relation between k_2 and the temperature using Eqn. (5) indicated that k_2 had a minimum value at about 10° C. Although the actual value of this "minimum temperature" was not found, it was used to rescale the temperature range studied: $T = (\tau - 10)/5$. Inserting Eqn. (5) for k_1, k_2 and m in Eqns. (2), (3) and (7), the combined experimental temperature groups could be analyzed. The respective parameter estimates are given in Tables I and II. Both k_1 and m were found to have an optimum at an intermediate temperature, whereas k_2 showed a decaying exponential increase with temperature. These results are graphically represented in Fig.3.

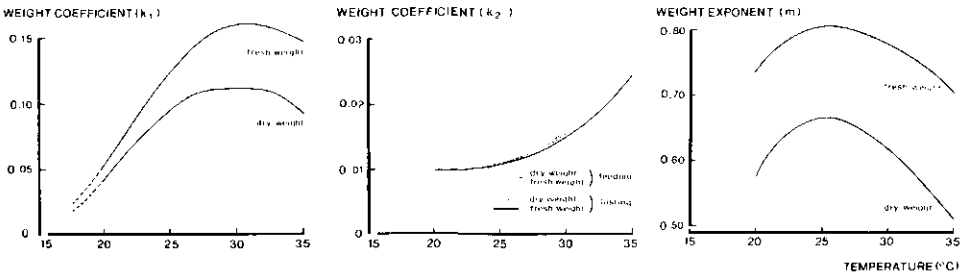

Fig.3. Estimated temperature dependence of the parameters describing the effect of body weight on the changes in weight and feed utilization. For explanation see text.

Body composition

The analysis of the data on body composition was based on the fact that fish growth is characterised by changes in the amount of water, protein, fat and ash. To investigate the relative importance of the accretion of these components, the dry matter, energy and protein in the body were regressed on the body weight using Eqn. (6). The results are listed in Table III. The amounts of these components increased rather proportionally with increasing body weight. Generally, the body composition of the smaller fish was more affected by feed deprivation than that of bigger fish, as can be seen from the compensating differences in the coefficients and exponents of the allometric relations. The amount of substantial body materials appeared to decrease at temperatures above 27.5—30° C, but it must be remembered that only small fish were analyzed at 32.5 and 35° C.

Fresh weight feed utilization

Although the dry weight feed utilization is interesting from an analytical viewpoint, practical fish culture is more concerned with the feed utilization

TABLE III

Analysis of the relation of dry matter (g), energy (kJ) and protein (g) with body weight (g) using $y = rW^s$. Feed deprivation (0) and the first restricted feeding level (1) were compared with the remaining feeding levels at each temperature

Temp. (°C)	Feeding level	Dry matter		Energy		Protein	
		r	*s*	*r*	*s*	*r*	*s*
20	0	0.16	1.10	3.48	1.11	0.12	1.10
	1	0.19	1.06	4.29	1.06	0.13	1.07
	Other	0.20	1.06	4.90	1.05	0.13	1.07
25	0	0.18	1.06	3.85	1.09	0.14	1.07
	1	0.19	1.05	4.64	1.06	0.14	1.04
	Other	0.20	1.05	4.97	1.05	0.14	1.04
27.5	0	0.17	1.09	3.43	1.10	0.12	1.09
	1	0.18	1.06	3.95	1.06	0.13	1.06
	Other	0.19	1.07	4.66	1.05	0.13	1.06
30	0	0.17	1.09	3.30	1.11	0.12	1.07
	1	0.19	1.06	4.93	1.03	0.13	1.04
	Other	0.21	1.04	6.16	0.99	0.13	1.04
32.5	0	0.15	1.09	2.54	1.06	0.09	1.09
	1	0.17	1.09	3.78	1.08	0.10	1.06
	Other	0.18	1.08	4.20	1.10	0.10	1.06
35	0	—	—	—	—	0.10	1.06
	1	—	—	—	—	0.11	1.04
	Other	—	—	—	—	0.11	1.04

on a fresh weight basis. These two can be related when the body composition is taken into account.

The earlier analysis of the dry weight feed utilization showed that a constant 44% of the dry feed was available for maintenance and deposition. However, in the analysis of the body composition it was found that the bigger the fish the more dry matter is incorporated per gram of fresh weight. Thus the fresh weight feed utilization decreases with increasing fish size. This effect is emphasized by the increasing relative importance of the maintenance requirements. To illustrate these points the maximal observed fresh weight feed utilization efficiency (gain × 100/feed) in these trials is depicted in Fig.4 in relation to temperature and the mean body weight.

Using the differential equations (2), (3) and (7) the increased maintenance requirement is accounted for. The effect of the change in body composition was arbitrarily incorporated by substituting $(p-pq)e^{-k_3 W}$ for $(p-pq)$

$$dW/dt = (p-pq)e^{-k_3 W} R - k_2 \cdot W^n \qquad (0 \leqslant R \leqslant R_{max}) \qquad (8)$$

$$= e^{-l/W - k_3 W} k_1 \cdot W^m - k_2 \cdot W^n \qquad (R = R_{max}) \qquad (9)$$

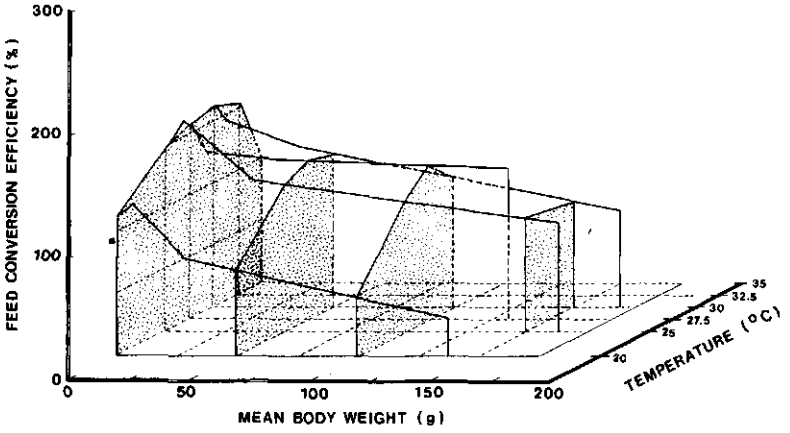

Fig.4. Maximum feed conversion efficiency (g gain/g feed, %) of *C. lazera* in relation to temperature (°C) and (geometrical) mean body weight (g).

The parameters were estimated as for the dry weight feed assimilation. The estimates are given in Tables IV and V, while the relations between k_1, k_2, m and the temperature are also depicted in Fig.3. The estimates for k_2 can be seen to differ only slightly from those found for the dry weight changes during feed deprivation. The weight exponent for the changes in weight during feed deprivation was calculated at 0.80. Both k_1 and m were estimated substantially higher than the corresponding values for the dry weight changes. Here also the weight exponent, m, is seen to approach the value of 0.80 at intermediate temperatures.

The eventual goodness of fit of the various adapted models can easily be appreciated on the basis of the residual sum of squares (Tables I, II, IV and V) expressed as a fraction of the actually found final weights, summed for the relevant observations. It must be realized, however, that a part of the

TABLE IV

Parameter estimates and residual sum of squares for the changes in fresh weight during feed deprivation

Temperature (°C)	k_2	n	a_2	b_2	c_2	RSS	NNRSS
20	0.0101	0.79	—	—	—	0.01	0.01
25	0.0105	0.82	—	—	—	0.05	0.05
27.5	0.0126	0.76	—	—	—	0.03	0.03
30	0.0146	0.86	—	—	—	0.06	0.02
All	—	0.80	0.0069	−2.7	1.1	0.16	0.12
All	—	0.80	0.0066	−2.3	1.0	0.16	0.12

Functions and explanation as in Table I.

feed uptake by the smallest fish at satiation feeding. The hypothetical background of this phenomenon could be that aerial respiration at 0.5 g body weight has barely started and may not have reached its full capacity. This might result in a reduced oxygen uptake capacity, which in turn would reduce the physiological potential for growth/feed uptake of these fish.

From the dry feed utilization an analogous model was developed for the fresh weight feed utilization. In this respect it must be remembered that about 90% dry feed is turned into fish tissue with a 15—25% dry matter content. As a result the feed utilization coefficient increased about 4-fold to a value of 1.82 for the smallest fish. For the bigger fish this value decreases exponentially because more dry matter is incorporated per gram fresh weight increment, as was seen from the analysis of the body composition.

The use of the Hoerls function to account for the influence of temperature on the feed utilization gave interesting results. The Hoerls function was adopted, not on the basis of physiological considerations but because of its flexibility and good fitting quality. The weight coefficient for fasting was seen to increase with temperature in a manner comparable to the one first described by Ege and Krogh (1914) for the standard metabolism of goldfish (*Carrassius auratus*). The weight exponent for the changes in weight during feed deprivation was calculated exactly at the widely assumed value of 0.80 (Winberg, 1956; Paloheimo and Dickie, 1966; Ursin, 1967; Huisman, 1974).

The weight coefficient for feed utilization/satiation feeding was seen to increase to a maximum at about 29—30° C, followed by a decrease at higher temperatures. This pattern complies well with the temperature effect on growth as described by Brett et al. (1969), Warren (1971), Brett (1974, 1979), and Elliot (1975c, d). The estimated relation between the weight exponent for feed utilization/satiation feeding and temperature surprisingly also indicated that an optimum was reached, albeit between 25 and 27° C. The difference in temperature optima for the weight coefficient and the weight exponent can be traced back to the decrease in optimum temperature for growth with increasing fish size as was seen in Fig.1. This phenomenon has also been reported for sole (*Solea solea*, L.) (Fonds and Saksena, 1977) and is indicated for carp (*Cyprinus carpio*, L.) (Huisman et al., 1979). However, at intermediate temperature values the weight exponent approaches a value of 0.80, which also has been reported for the maximal feeding metabolism.

Summarising the above, it can be stated that the developed model adequately reflected the intricate effects of body weight, temperature and feeding level on the growth of *C. lazera*. On the average the residual variance equalled about 1 to 2% of the corresponding actual final weight. The usefulness of such a model for feed utilization is threefold. Firstly, it is helpful in understanding the complex physiological possibilities and constraints of growth of fish. Secondly, it enables the prediction of the growth of fish of a given size as a response to a certain combination of temperature and feed ration. This aspect is illustrated in Fig.5, where the growth per day to be

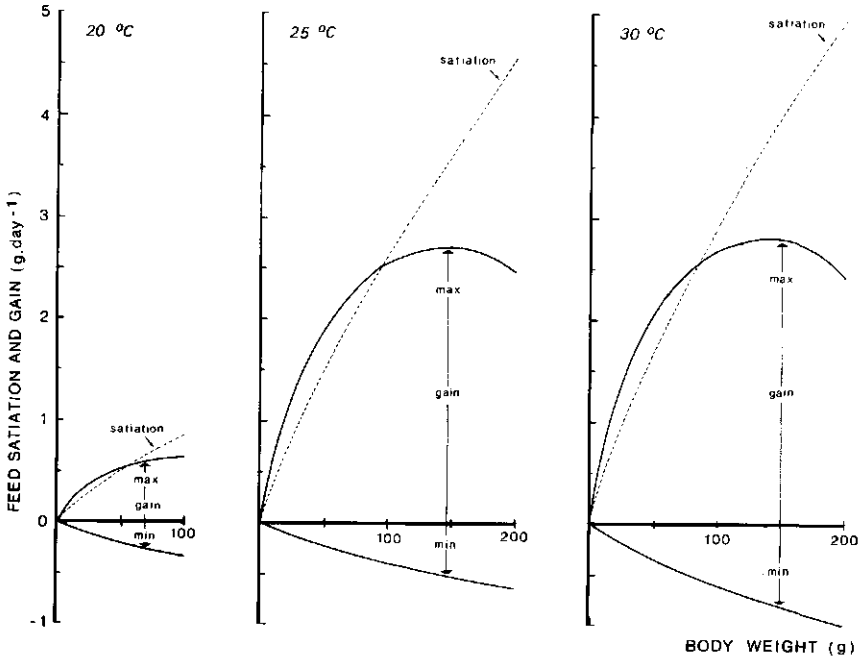

Fig.5. Satiation feeding ($g \cdot day^{-1}$) and gain ($g \cdot day^{-1}$) in relation to body weight (g) and temperature (°C).

TABLE VI

Recommended feeding levels (% body weight·day^{-1}) and corresponding estimated growth rates (% body weight·day^{-1}) for *C. lazera* from 1 to 200 g between 20 and 35°C

Temp. (°C)	Body weight (g) 1	5	25	50	100	200
20	2.9(3.1)	1.9(2.6)	1.2(1.5)	1.0(1.1)	0.9(0.6)	
21	3.6(4.2)	2.5(3.6)	1.7(2.3)	1.4(1.7)	1.2(1.0)	1.0(0.4)
22	4.4(5.3)	3.1(4.6)	2.2(3.0)	1.9(2.3)	1.6(1.4)	1.4(0.6)
23	5.1(6.3)	3.7(5.6)	2.6(3.8)	2.3(2.9)	2.0(1.9)	1.7(0.9)
24	5.8(7.2)	4.2(6.5)	3.1(4.4)	2.7(3.4)	2.3(2.2)	2.0(1.1)
25	6.5(8.0)	4.7(7.3)	3.4(5.0)	3.0(3.8)	2.6(2.6)	2.3(1.2)
26	7.0(8.7)	5.1(7.9)	3.7(5.4)	3.3(4.2)	2.8(2.8)	2.5(1.4)
27	7.4(9.2)	5.4(8.3)	3.9(5.7)	3.4(4.4)	3.0(2.9)	2.6(1.4)
28	7.7(9.6)	5.6(8.5)	4.0(5.8)	3.5(4.4)	3.0(2.9)	2.6(1.4)
29	7.9(9.7)	5.6(8.6)	4.0(5.7)	3.5(4.3)	3.0(2.8)	2.6(1.3)
30	8.0(9.7)	5.6(8.5)	3.9(5.6)	3.4(4.2)	2.9(2.7)	2.5(1.2)
31	8.0(9.6)	5.5(8.5)	3.8(5.2)	3.2(3.9)	2.7(2.4)	2.3(1.1)
32	7.9(9.3)	5.3(7.7)	3.6(4.8)	3.0(3.5)	2.6(2.2)	
33	7.8(8.8)	5.1(7.2)	3.4(4.3)	2.8(3.1)		
34	7.5(8.2)	4.8(6.5)				
35	7.2(7.5)	4.5(5.8)				

expected as a result of a daily ration has been depicted in relation to temperature and body weight for *C. lazera*. Thirdly, it can be concluded from the constancy of the feed utilization coefficient that feeding at satiation will give the most efficient growth response. The resulting recommended feeding levels and growth rates to be expected have been listed in Table VI for *C. lazera* in relation to body size and temperature over the range studied in this experiment.

The overall conclusion of this study should be that growth of fish is indeed a highly variable entity. Consequently, the reported values for the parameters used in the various relations are representative only for the conditions prevailing in this experiment.

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APPENDIX

Initial and terminal weight, dry matter, N and energy in fish and feed, feed conversion, energy and protein conversion efficiency of *Clarias lazera* in relation to temperature, feeding level and size. Mean and standard deviation of replicates per treatment

Temp. (°C)	Size group	Initial body wt (g)	Terminal body wt (g)	Feed (g)	Dry matter (%)	N in d.m. (%)	Energy in d.m. (kJ/g)	Feed conversion	Energy conv. efficiency	Protein conv. efficiency
20	1	Initial sample			18.4	11.0	25.6			
		0.61(0.01)	0.44(0.01)	0.00	14.9(0.2)	12.0(0.1)	21.3(0.2)			
		0.61(0.01)	0.74(0.03)	0.18(0.0)	18.3(0.6)	11.5(0.3)	23.1(0.2)	1.4(0.3)	0.08(0.0)	0.23(0.0)
		0.62(0.00)	1.33(0.11)	0.62(0.0)	20.6(0.8)	10.9(0.4)	23.6(0.3)	0.9(0.1)	0.29(0.0)	0.36(0.1)
		0.61(0.00)	1.61(0.04)	1.51(0.0)	20.8(0.4)	10.6(0.1)	25.3(0.3)	1.5(0.1)	0.19(0.0)	0.20(0.0)
		0.62(0.01)	1.81(0.07)	2.56(0.0)	21.1(0.1)	10.6(0.2)	25.3(0.2)	2.0(0.1)	0.14(0.0)	0.15(0.0)
		Trouvit 0			89.7	8.7	21.6			
20	2	Initial sample			20.3	12.0	23.3			
		5.1(0.0)	4.2(0.1)	0.00	19.4(1.3)	12.5(0.7)	21.7(0.2)			
		5.1(0.0)	6.7(0.1)	1.63(0.0)	21.7(0.7)	11.6(0.8)	23.5(0.6)	1.0(0.1)	0.32(0.1)	0.34(0.1)
		5.1(0.0)	9.9(0.2)	3.87(0.0)	22.2(0.1)	11.4(0.5)	23.4(0.3)	0.8(0.0)	0.36(0.0)	0.39(0.0)
		5.1	11.3	8.04	21.8	10.9	23.4	1.3	0.32	0.22
		5.1(0.0)	11.3(0.7)	13.4(0.1)	22.4(0.1)	10.8(0.2)	23.5(0.3)	2.2(0.3)	0.14(0.0)	0.13(0.0)
		Trouvit 1			89.1	9.2	21.6			
20	3	Initial sample			22.7	10.4	24.5			
		25.1(0.1)	21.6(0.1)	0.00	21.5(0.4)	11.6(0.2)	21.5(0.5)			
		25.0(0.1)	26.2(0.3)	3.57(0.0)	21.9(1.1)	11.1(0.3)	21.6(0.6)	3.3(1.1)	0.20(0.1)	0.16(0.1)
		25.0(0.0)	31.4(0.4)	7.86(0.0)	23.0(0.3)	10.9(0.2)	25.3(0.2)	1.3(0.5)	0.27(0.0)	0.31(0.1)
		25.0(0.1)	35.7(1.9)	17.1(0.0)	23.2(0.4)	10.8(0.3)	24.8(0.3)	1.6(0.3)	0.19(0.0)	0.22(0.0)
		25.1(0.1)	33.9(0.6)	34.8(0.0)	23.0(0.6)	11.0(0.2)	26.0(1.0)	3.9(0.3)	0.09(0.0	0.10(0.0)
		Trouvit 2			91.6	8.7	22.6			
20	4	Initial sample			25.5	11.9	23.0			
		135. (0.0)	121. (0.7)	0.00	26.0(1.1)	11.9(0.1)	23.4(0.4)			
		135. (0.6)	141. (1.5)	19.5(0.0)	26.0(1.1)	12.2(0.9)	23.6(0.6)	3.4(1.3)	0.19(0.1)	0.24(0.1)
		133. (2.9)	144. (8.4)	39.4(0.8)	26.9(2.1)	11.4(0.6)	23.5(0.6)	5.3(4.1)	0.16(0.1)	0.12(0.1)
		136. (0.0)	142. (1.7)	59.6(0.0)	27.3(0.4)	11.3(0.3)	23.7(0.5)	10.6(3.7)	0.10(0.0)	0.05(0.0)
		135. (0.6)	144. (6.0)	79.7(0.1)	27.2(0.3)	11.6(0.2)	24.0(0.1)	18.2(19.0)	0.09(0.0)	0.07(0.0)
		Trouvit 4			92.0	8.7	22.2			

25	1	Initial sample			19.9(1.2)	11.5(0.5)	23.9			
		0.58(0.0)	0.44(0.0)	0.00	17.5(0.5)	11.9(0.4)				
		0.57(0.0)	2.40(0.1)	1.20(0.0)	21.1(0.8)	11.5(0.3)	23.8(0.5)	0.66(0.0)	0.40(0.0)	0.48(0.0)
		0.58(0.0)	2.62(0.2)	2.98(0.2)	21.6(0.8)	11.0(1.1)	24.2(0.2)	1.47(0.2)	0.19(0.0)	0.21(0.0)
		0.58(0.1)	2.30(0.3)	4.24(0.2)	21.2(0.2)	10.9(0.4)	24.7(0.2)	2.52(0.5)	0.11(0.0)	0.12(0.0)
		0.57(0.0)	2.39(0.5)	5.77(0.2)	21.1(0.1)	11.2(0.1)	24.1(0.6)	3.27(0.6)	0.08(0.0)	0.10(0.0)
		Trouvit 0			89.7	8.7	22.0			
25	2	Initial sample			20.2(0.2)	11.1(1.1)	24.1(0.0)			
		3.83(0.1)	3.27(0.3)	0.00	19.3(1.0)	12.1(0.6)	21.2(0.8)			
		3.80(0.0)	14.8(0.2)	6.43(0.1)	20.7(0.4)	12.5(0.1)	24.7(0.3)	0.58(0.0)	0.47(0.0)	0.57(0.0)
		3.80(0.0)	23.3(1.4)	19.4(0.5)	22.7(0.2)	11.7(0.3)	25.2(0.8)	1.00(0.1)	0.31(0.0)	0.34(0.0)
		3.87(0.1)	24.8(0.5)	29.5(0.0)	23.0(0.6)	11.3(0.2)	24.7(0.9)	1.41(0.0)	0.22(0.0)	0.23(0.0)
		3.83(0.01)	25.7(0.8)	40.7(0.2)	23.3(0.3)	11.2(0.3)	25.4(0.1)	1.86(0.1)	0.17(0.0)	0.18(0.0)
		Trouvit 1			89.1	9.2	21.6			
25	3	Initial sample			23.3(1.4)	11.7(0.6)	23.3			
		24.6(0.1)	20.2(0.6)	0.00	22.7(0.8)	11.0(0.7)	25.0(0.0)			
		24.5(0.2)	56.8(1.0)	26.2(0.0)	23.7(1.5)	11.7(0.5)	24.6(0.9)	0.81(0.0)	0.37(0.1)	0.43(0.0)
		24.7(0.2)	72.1(5.1)	60.4(0.0)	24.7(0.9)	11.0(0.2)	25.5(0.6)	1.28(0.1)	0.26(0.0)	0.27(0.0)
		24.9(0.1)	67.5(2.5)	96.9(0.0)	24.9(1.1)	10.9(0.1)	24.8(0.9)	2.28(0.1)	0.14(0.0)	0.15(0.0)
		24.5(0.2)	68.2(7.3)	124. (0.0)	25.8(1.2)	10.7(0.2)	25.6(0.6)	2.90(0.5)	0.12(0.0)	0.12(0.0)
		Trouvit 2			91.6	8.7	22.6			
25	4	Initial sample			24.3(0.7)	11.5(0.4)	24.6(0.0)			
		125 (0.7)	108 (0.7)	0.00	23.6(0.4)	12.7(0.3)	23.3(0.4)			
		126 (0.6)	212 (6.6)	96.0(0.0)	26.1(0.1)	11.0(0.1)	24.6(0.4)	1.13(0.1)	0.31(0.0)	0.33(0.0)
		125 (1.2)	223 (22.)	213 (0.0)	26.5(0.2)	11.1(0.4)	23.9(0.9)	2.27(0.5)	0.15(0.1)	0.18(0.1)
		125 (0.6)	231 (27.)	346 (0.6)	25.8(0.7)	11.1(0.4)	24.9(0.7)	3.45(1.0)	0.10(0.0)	0.11(0.0)
		126 (0.0)	218 (22.)	480 (0.0)	26.1(0.6)	11.3(0.3)	25.2(0.6)	5.39(1.2)	0.07(0.0)	0.08(0.0)
		Trouvit 4			92.0	8.7	22.2			
27.5	1	Initial sample			18.6	10.8	24.4			
		0.78(0.0)	0.65(0.0)	0.00	16.3(1.1)	11.0(0.7)	20.5(1.2)			
		0.76(0.0)	1.47(0.0)	0.45(0.0)	18.7(0.1)	11.2(0.1)	23.3(0.7)	0.63(0.0)	0.34(0.0)	0.44(0.0)
		0.78(0.0)	2.59(0.3)	1.22(0.1)	19.4(0.2)	10.9(0.3)	24.8(0.2)	0.68(0.1)	0.37(0.0)	0.41(0.0)
		0.79(0.0)	2.93(0.1)	1.90(0.1)	19.7(0.4)	10.8(0.1)	25.4(0.5)	0.89(0.0)	0.30(0.0)	0.31(0.0)
		0.84(0.0)	3.03(0.0)	3.14(0.1)	20.6(0.6)	10.7(0.5)	24.8(0.2)	1.43(0.1)	0.19(0.0)	0.20(0.0)
		Trouvit 0			89.7	8.7	21.6			

Temp. (°C)	Size group	Initial body wt (g)	Terminal body wt (g)	Feed (g)	Dry matter (%)	N in d.m. (%)	Energy in d.m. (kJ/g)	Feed conversion	Energy conv. efficiency	Protein conv. efficiency
27.5	2	Initial sample			20.4	10.8	22.7			
		6.5(0.8)	5.2(0.9)	0.00	19.7(0.8)	10.9(0.0)	20.2(0.3)			
		5.9(0.3)	10.7(0.5)	3.40(0.1)	20.4(0.5)	11.3(0.2)	21.0(0.5)	0.73(0.1)	0.28(0.1)	0.42(0.1)
		6.2(0.6)	18.8(0.9)	9.70(0.7)	22.4(0.3)	11.0(0.2)	22.9(0.2)	0.77(0.0)	0.36(0.0)	0.41(0.0)
		6.4(0.8)	39.4(3.9)	34.9(3.2)	23.7(0.2)	10.3(0.1)	24.2(0.7)	1.06(0.0)	0.29(0.0)	0.29(0.0)
		6.3(0.4)	42.7(3.9)	60.1(3.0)	24.6(0.6)	10.2(0.1)	25.7(0.4)	1.66(0.2)	0.21(0.0)	0.19(0.0)
		Trouvit 1			89.1	9.2	21.6			
27.5	3	Initial sample			24.3	11.2	21.4			
		23.5(0.1)	19.9(0.3)	0.00	21.5(0.1)	11.7(0.2)	22.0(0.6)			
		23.6(0.2)	31.7(0.6)	7.67(0.3)	22.3(0.3)	11.3(0.5)	21.5(0.9)	0.74(0.1)	0.19(0.1)	0.27(0.1)
		23.6(0.2)	56.9(1.2)	25.7(0.2)	23.8(0.1)	11.0(0.6)	22.7(0.8)	0.77(0.0)	0.35(0.0)	0.42(0.0)
		23.3(0.1)	69.2(2.1)	59.2(0.2)	24.7(0.6)	10.6(0.1)	23.7(1.0)	1.29(0.1)	0.23(0.0)	0.25(0.0)
		23.5(0.1)	74.8(1.6)	99.1(0.4)	25.0(0.2)	10.8(0.3)	24.2(0.4)	1.94(0.1)	0.16(0.0)	0.57(0.0)
		Trouvit 2			91.6	8.7	22.6			
27.5	4	Initial sample			25.3	11.3	23.0			
		96.7(2.5)	86.0(3.6)	0.00	25.4(2.4)	11.2(0.5)	21.1(0.4)			
		98.7(2.1)	122 (2.5)	23.3(0.6)	24.5(0.8)	10.7(0.3)	22.9(0.6)	0.99(0.6)	0.24(0.1)	0.20(0.1)
		100 (3.1)	161 (12)	53.0(3.0)	25.5(0.6)	10.8(0.2)	23.2(0.3)	0.88(0.1)	0.34(0.0)	0.36(0.0)
		100 (1.2)	176 (2.1)	121 (1.5)	26.3(0.5)	10.4(0.4)	24.1(0.4)	1.60(0.0)	0.22(0.0)	0.20(0.0)
		99.0	165	178	26.2	10.4	23.2	2.70	0.12	0.12
		Trouvit 4			92.0	8.7	22.2			
30	1	Initial sample			19.3	11.2	—			
		0.49(0.0)	0.39(0.0)	0.00	15.5(1.9)	11.9(1.5)	—			
		0.50(0.1)	1.30(0.2)	0.49(0.1)	19.6(0.8)	11.5(0.6)	—	0.61(0.0)	—	0.48(0.0)
		0.47(0.0)	1.88(0.1)	1.05(0.0)	21.2(1.0)	11.0(0.5)	—	0.75(0.1)	—	0.41(0.1)
		0.57(0.1)	2.16(0.1)	1.85(0.2)	22.3(1.4)	11.0(0.4)	—	1.18(0.2)	—	0.28(0.1)
		0.46(0.0)	2.19(0.1)	2.34(0.1)	22.5(0.4)	10.6(1.4)	—	1.36(0.0)	—	0.23(0.0)
		Trouvit 0			89.7	8.7	21.6			
30	2	Initial sample			20.4	11.1	24.0			
		3.2	2.3	0.00	17.7	11.5	18.9			
		3.2(0.1)	10.6(0.2)	4.93(0.2)	22.1(0.9)	10.4(0.8)	24.0(0.7)	0.66(0.0)	0.43(0.0)	0.42(0.0)
		3.2(0.0)	21.6(1.8)	14.7(0.4)	23.0(0.7)	10.7(0.3)	25.0(0.3)	0.81(0.1)	0.38(0.0)	0.38(0.0)
		3.1(0.0)	25.1(1.8)	25.5(0.2)	23.5(0.1)	10.6(0.1)	25.3(0.7)	1.16(0.1)	0.27(0.0)	0.26(0.0)
		3.2(0.1)	23.8(2.0)	35.7(0.8)	24.0(0.3)	10.4(0.1)	25.4(0.6)	1.74(0.2)	0.19(0.0)	0.18(0.0)
		Trouvit 1			89.1	9.2	21.6			

30	3	Initial sample			23.5	9.8	24.0			
		21.0(0.6)	17.7(0.2)	0.00	20.7(0.3)	11.6(0.2)	23.3(0.4)			
		21.9(0.6)	29.7(0.6)	7.20(0.4)	22.3(0.6)	11.2(0.2)	23.5(0.7)	0.92(0.1)	0.22(0.0)	0.41(0.0)
		21.5(0.7)	48.7(1.6)	22.6(0.4)	24.8(1.0)	10.4(0.4)	24.2(0.5)	0.83(0.0)	0.36(0.0)	0.42(0.0)
		22.0(0.9)	66.3(2.9)	55.0(2.3)	24.9(0.4)	10.4(0.4)	25.3(0.7)	1.24(0.1)	0.26(0.0)	0.28(0.0)
		21.7(0.4)	74.4(0.3)	85.1(1.4)	25.2(0.6)	10.3(0.2)	25.4(0.0)	1.61(0.0)	0.20(0.0)	0.21(0.0)
		Trouvit 2			91.6	8.7				
30	4	Initial sample			25.9	10.6	22.1			
		143. (1.0)	108. (1.7)	0.00	25.9(0.3)	10.9(0.8)	20.9(0.9)			
		143. (1.4)	165. (1.4)	33.5(0.7)	26.5(0.6)	10.9(0.2)	21.5(1.1)	1.52(0.0)	0.18(0.1)	0.30(0.0)
		143. (0.6)	199. (4.5)	70.3(0.6)	26.1(0.4)	10.6(0.3)	22.5(0.5)	1.27(0.1)	0.24(0.0)	0.28(0.0)
		143. (0.0)	200. (15)	148. (0.0)	25.5(0.4)	11.2(0.1)	22.5(0.5)	2.66(0.7)	0.11(0.0)	0.15(0.0)
		140. (1.2)	208. (6.6)	232. (1.5)	25.4(0.8)	10.9(0.3)	22.4(1.0)	3.60(0.3)	0.08(0.0)	0.10(0.0)
		Trouvit 4			92.0	8.7	22.2			
32.5	1	Initial sample			16.2	10.7	23.3			
		0.52(0.1)	0.38(0.0)	0.00	13.4(0.5)	10.0(0.7)	17.9(0.8)			
		0.54(0.0)	0.90(0.1)	0.29(0.0)	17.3(1.4)	11.3(0.2)	21.7(0.1)	0.81(0.0)	0.24(0.1)	0.36(0.1)
		0.56(0.0)	1.84(0.1)	0.84(0.1)	18.3(0.9)	11.2(0.4)	23.1(0.5)	0.66(0.1)	0.35(0.0)	0.43(0.0)
		0.52(0.1)	2.21(0.2)	1.08(0.1)	20.7(3.8)	10.8(0.2)	23.4(0.4)	0.64(0.0)	0.42(0.1)	0.48(0.1)
		0.58(0.0)	2.16(0.2)	2.43(0.1)	19.4(1.2)	10.7(0.2)	23.9(0.4)	1.55(0.2)	0.17(0.0)	0.28(0.0)
		Trouvit 0			89.7	8.7	21.6			
32.5	2	Initial sample			19.3	10.7	20.4			
		4.6(0.2)	3.3(0.0)	0.00	16.1(0.4)	9.8(0.1)	17.0(0.4)			
		4.7(0.1)	6.9(0.0)	2.49(0.1)	20.8(0.8)	10.9(0.2)	21.3(0.1)	1.15(0.1)	0.24(0.0)	0.29(0.0)
		5.1(0.5)	14.9(2.0)	8.28(0.5)	22.3(0.3)	10.6(0.2)	22.5(0.6)	0.86(0.1)	0.34(0.0)	0.36(0.0)
		4.9(0.5)	16.1(1.8)	22.8(2.4)	23.9(0.7)	10.3(0.3)	24.9(0.4)	1.08(0.1)	0.31(0.0)	0.29(0.0)
		4.6(0.1)	25.7(3.2)	34.2(0.6)	23.8(0.2)	10.3(0.1)	24.4(0.9)	1.65(0.3)	0.20(0.0)	0.19(0.0)
		Trouvit 1			89.1	9.2	21.6			
35	1	Initial sample			16.2	11.1	24.2			
		0.69(0.1)	0.45(0.1)	0.00	13.7(0.6)	11.0(0.4)	18.9(0.3)			
		0.70(0.0)	1.11(0.1)	0.38(0.0)	17.0(0.3)	11.3(0.2)	22.0(0.2)	0.93(0.1)	0.19(0.0)	0.30(0.0)
		0.65(0.0)	1.57(1.1)	0.99(0.0)	18.2(2.2)	10.8(0.0)	22.9(0.5)	1.08(0.1)	0.21(0.1)	0.25(0.1)
		0.70(0.0)	1.66(0.1)	1.37(0.0)	17.7(0.4)	10.7(0.2)	23.3(0.5)	1.43(0.1)	0.15(0.0)	0.18(0.0)
		0.64(0.0)	1.40(0.1)	2.40(0.1)	17.2(0.2)	10.9(0.2)	23.7(0.1)	3.19(0.3)	0.07(0.0)	0.10(0.1)
		Trouvit 0			89.7	8.7	21.6			

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GROWTH AND PRODUCTION OF THE AFRICAN CATFISH, *CLARIAS LAZERA* (C. & V.)
III. BIOENERGETIC RELATIONS OF BODY WEIGHT AND FEEDING LEVEL

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ABSTRACT

Hogendoorn, H., 1983. Growth and production of the African catfish, *Clarias lazera* (C. & V.). III. Bioenergetic relations of body weight and feeding level. *Aquaculture*

Bioenergetic relations of body weight and feeding level in *C. lazera* were studied in open circuit balance respirometers to elucidate the physiological background of the highly efficient feed conversion in this fish.

It was found that changes in proximate body composition that occurred at different feeding levels were largely attributable to concurrent changes in weight. The various body components were allometrically related to body weight.

The same was true for the daily oxygen consumption where the weight exponent equalled 0.86 ± 0.02 (S.E.) for fasting fish and 0.75 ± 0.01 (S.E.) for feeding fish. The primary effect of feeding level was in the overall level of metabolism, which increased more than 3-fold from fasting to satiation feeding. The metabolic "scope for growth" was $0.346 \cdot W^{0.75} - 0.145 \cdot W^{0.83}$ (kJ/day).

The metabolizability of the feed energy was about 70% decreasing with the feeding level. ME utilization for energy gain above maintenance was 80% efficient, independent of body weight and feeding level. The intake of ME for gain was calculated to decrease from 6.9 to 2.8 times the maintenance requirement for fish of 1 to 200 g. This high ME_p/ME_m ratio largely explains *C. lazera*'s efficient utilization of the feed for growth.

INTRODUCTION

In an earlier experiment (Hogendoorn et al., 1983) the growth response of *Clarias lazera* (Cuvier and Valenciennes) was studied in relation to body weight, temperature and feeding. A growth model was developed, based on the balanced energy equation (Winberg, 1956), using growth as an empirical "wide spectrum indicator of the environmental conditions" (Beamish et al., 1975). A number of the relations and hypotheses advanced in this

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model can only be verified by a more detailed study of the bioenergetics of fish growth. Therefore a set of open circuit balance respirometers was built (Hogendoorn et al., 1981) to allow the determination of gas and matter balances of fish during prolonged experimental periods.

The gas and matter balances reflect the processes involved in the destruction and synthesis of material in the body. Whenever these processes require energy, this is provided as "free energy" (ATP), produced by catabolism, i.e. oxidation of feed and/or body constituents. Both in the production and use of the free energy heat is released: the metabolic expenditure. This heat then is an indicator for the overall level of metabolism. Since the heat is difficult to measure directly, it is most commonly assessed by indirect calorimetry. Based on an average composition of carbohydrates, fats and protein respectively, the oxygen required for their full oxidation and the resulting production of CO_2, N compounds and heat can be estimated (Brouwer, 1965).

Conversely, neglecting the energy in excreted N compounds, the amount of materials catabolized can be estimated from the gaseous exchange. For ureocotelic homoiotherms it is assumed that the metabolic expenditure $H = 16.2 + 5.02 \times RQ$ ($kJ \cdot (10_2)^{-1}$). The respiratory quotient equals 1.0, 0.8 and 0.7 for the complete oxidation of carbohydrates, protein and fats respectively, giving oxycaloric equivalents of 21.2, 20.2 and 19.7 $kJ \cdot (10_2)^{-1}$. Elliot and Davison (1975) discussed the oxycaloric equivalent for ammoniocotelic poikilotherms and concluded it was 21.3, 19.4 and 19.8 $kJ \cdot (10_2)^{-1}$ for the oxidation of carbohydrates, fats and protein. For growing fish they assumed an average value of 20.4 $kJ \cdot (10_2)^{-1}$. In this experiment oxycaloric equivalents of 19.6 and 20.9 $kJ \cdot (10_2)^{-1}$ were used for fasting fish and all other feeding levels respectively. The resulting bioenergetic relations of body weight and feeding level in *C. lazera* are reported in the present paper.

MATERIALS AND METHODS

Facilities and fish

The experiment was conducted in the respirometers as described. The recirculation of the water was regulated to give about 100% and 50% oxygen saturation of the water entering and leaving the individual respirometers respectively. The ammonium and nitrite concentrations were maintained below 0.5 and 0.05 ppm. The experimental fish were obtained by the methods reported earlier (Hogendoorn, 1980, 1981); Hogendoorn and Vismans, 1980).

Experimental procedures

A series of 20 balance trials was carried out at 25°C using body weight and feeding level as variables. Four size groups of *C. lazera* were fed five

feeding levels i.e. deprivation, maintenance (= constant energy), optimal feeding (minimal feed conversion) and two and three times the optimal feeding rate, as estimated from earlier results.

Feeding was as a percentage of body weight with daily adjustment of the quantity, based on estimated growth. "Trouvit" (Trouw & Co, Putten, The Netherlands) was used in different pellet sizes, corresponding to the size group of the fish. It was provided continuously to minimize fluctuations in metabolism. For the same reason the experimental fish were weighed only at the start and at the end of each trial and were not touched in between.

On the first day of each trial and once a week thereafter the oxygen consumption was measured during 24 h. The respirometers were sealed and the water and air flow were adjusted 3 h prior to the start of the balance periods. The air flow was regulated to give about 19.8% oxygen in the outgoing air.

During the 24 h monitoring the settled non-eaten feed and faecal material was collected. The dry matter, protein and energy content of this material was determined. The same analyses were carried out in samples of the feed and the fish at the start and at the end of each trial.

Analysis of data

The energy budget of the fish was broken down as shown in Fig.1. During feed deprivation body constituents are used for the fasting metabolism (H_0). The resulting decrease in body materials implies a negative energy balance (EB):

$$H_0 = -\text{EB} \tag{1}$$

As feeding starts, external material becomes available to cover the fish's requirements: metabolizable energy (ME). It can be used for maintenance (H) or growth (EB):

$$\text{ME} = H + \text{EB} \tag{2}$$

Up to maintenance feeding (R_m; H_m; EB = 0) all ME = pR is used for maintenance and becomes heat:

$$H = pR - \text{EB} \qquad (R \leqslant R_m) \tag{3}$$

The metabolic expenditure corresponding to above-maintenance feeding ($H - H_m$) was taken to include all energy required for additional feed uptake activity, digestion, (biochemical) modification, (possibly) increased maintenance requirements and the actual accretion of body materials. It was assumed to be proportional to the amount of ME provided by the ration at above-maintenance feeding.

$$H = H_m + qp\,(R - R_m) \qquad (R \geqslant R_m)$$

or

$$H = H_m + (q/1-q)\,\text{EB} \qquad (R \geqslant R_m) \tag{4}$$

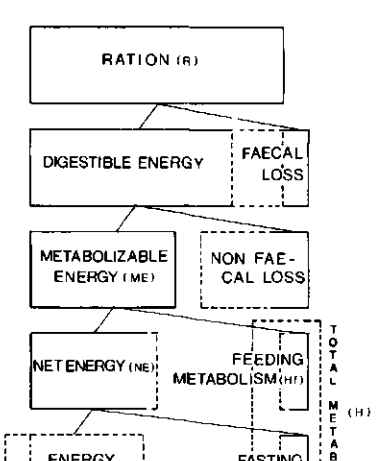

Fig.1. Flow diagram illustrating the distribution of the feed energy.

The above equations were used to estimate the feed utilization parameters p and q.

The effects of body weight and feeding level on body composition, oxygen consumption and feed utilization parameters were tested using the computer programme GLIM (Generalized Linear Interactive Modelling; Baker and Nelder, 1978). Regressions were carried out stepwise and non-significant effects on constants or regression coefficients were deleted.

RESULTS

Somatic changes

The experimental results concerning fish, feed and faecal weight and composition are given in Table I. During the experiment the *C. lazera* rapidly increased in weight from 1.5 to over 200 g in about 4 months. From these data the EB was calculated.

The specific rates of the changes $((\ln y_e - \ln y_s) \cdot 100/t)$ in fresh weight, protein and energy $(\% \cdot day^{-1})$ are represented in Fig.2. It can be observed that at feed deprivation the energy decreased faster than did the protein, indicating that both fat and protein were being catabolized. It is also seen that the designated maintenance rations generally were somewhat overestimated, and that protein gain takes preference over energy gain at these low feeding levels. By contrast, the selection of the optimal feeding levels appears to have been more successful, and the substantial growth (i.e. the increase in protein and energy) exceeds the increase in fresh weight. For the bigger fish a maximum specific growth rate was generally reached at a lower feeding level. The growth rate of these fish tended to decrease at the highest ration.

TABLE I

Initial and terminal weight, body, feed and faecal constituents and metabolic expenditure of four size groups of *C. lazera*, fed five different feeding levels at 25°C

Size group	Body weight (g)		Days	Feed ($g \cdot fish^{-1}$)	Estimated growth ($\% \cdot day^{-1}$)	Dry matter (%)	N in d.m. (%)	Energy in d.m. ($kJ \cdot g^{-1}$)	Collected faeces $\cdot fish^{-1}$			O_2 cons. ($lO_2 \cdot fish^{-1}$)
	Initial	Terminal							d.m. (g)	energy kJ·g d.m.$^{-1}$	N in d.m. (%)	
1	Initial sample					17.0	11.2	24.7				
	1.57	1.24	21	0.00	—	16.6	12.2	22.3	—	—	—	0.092
	1.54	1.59	21	0.25	0.00	18.6	12.0	21.3	0.006	19.1	—	0.191
	1.65	3.95	21	1.52	5.00	19.4	11.3	23.3	0.03	21.2	—	0.418
	1.58	6.09	21	3.50	6.67	20.8	11.1	24.3	0.14	22.9	7.1	0.709
	1.50	7.23	21	5.42	7.50	20.0	11.1	23.9	0.46	24.1	7.8	0.834
	Trouvit 0					92.1	9.1	23.3				
2	Initial sample					21.6	10.8	22.8				
	7.99	6.85	28	0.00	—	19.8	11.5	21.4	—	—	—	0.583
	7.83	9.58	28	1.66	0.00	20.8	11.8	22.2	0.04	16.8	—	1.10
	7.26	19.3	28	7.57	4.00	22.2	11.4	23.6	0.14	18.3	—	2.11
	7.17	36.5	28	18.8	5.33	23.8	10.7	23.8	0.66	19.5	5.9	3.73
	6.84	47.0	28	29.1	6.00	24.3	10.6	24.8	2.1	21.9	7.1	4.55
	Trouvit 1					89.1	8.9	22.4				
3	Initial sample					23.4	10.4	24.5				
	49.2	40.9	28	0.00	—	23.7	11.0	24.8	—	—	—	2.32
	50.0	50.5	28	7.00	0.00	24.4	10.9	24.7	0.48	19.7	3.1	4.47
	42.9	73.0	28	25.6	2.50	25.6	10.3	23.8	1.9	20.0	3.0	6.92
	41.2	99.0	28	57.4	3.53	26.0	10.5	25.4	8.6	23.0	6.7	9.10
	40.2	101	28	85.0	3.60	26.0	10.4	24.8	16.	24.2	6.9	11.8
	Trouvit 2					90.8	8.3	22.5				
4	Initial sample					24.8	10.6	25.0				
	94.0	79.2	42	0.00	—	24.4	11.0	24.3	—	—	—	5.66
	96.9	108.	42	20.3	0.00	24.8	10.8	24.0	1.2	—	2.6	11.6
	94.7	150.	42	52.8	1.33	26.5	10.3	25.3	3.8	20.0	2.9	15.3
	82.9	203.	42	107.	2.00	27.0	10.3	25.9	11.	21.6	5.4	22.7
	92.7	222.	42	198.	2.40	27.6	10.0	25.6	41.	24.5	8.0	29.5
	Trouvit 2					90.8	8.3	22.5				

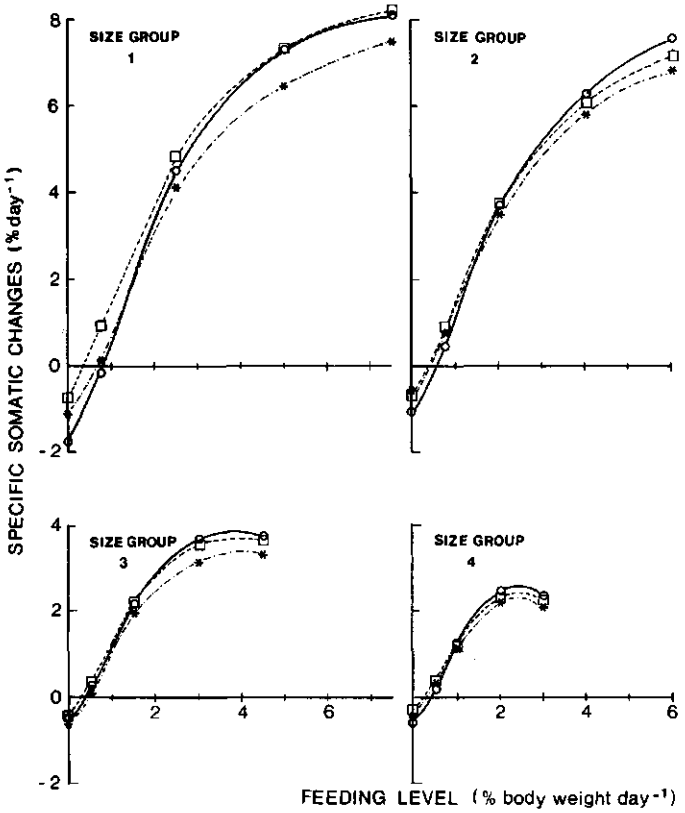

Fig.2. Specific changes in protein (□), energy (○) and fresh weight (*) in relation to feeding level for *C. lazera* of different sizes.

From the body composition data (Table I) it appeared that the dry matter content decreased during feed deprivation, whereas it increased at the higher feeding levels. The same was true for the energy content in the dry matter, while the protein content tended to decrease. However, these changes in the dry matter content and its composition were more pronounced over the different size groups and, since the fish given the bigger rations also attained higher weights, the effects of body weight and feeding level were analyzed simultaneously.

When the protein, dry matter and energy contents of the fish at the end of the trials were plotted (Fig.3), they were found to be allometrically related to body weight. For the dry matter content this relation was affected by feeding level ($F^8_{10} = 3.8$), but it was independent of feeding in the case of protein and energy content per gram body weight ($F^8_{10} = 2.8$ and 1.7 respectively). From the exponents of the overall relations shown in Fig.3, it can be observed that the increase in energy content with body weight exceeded the increase in protein, with the increase in dry matter in an intermediate position.

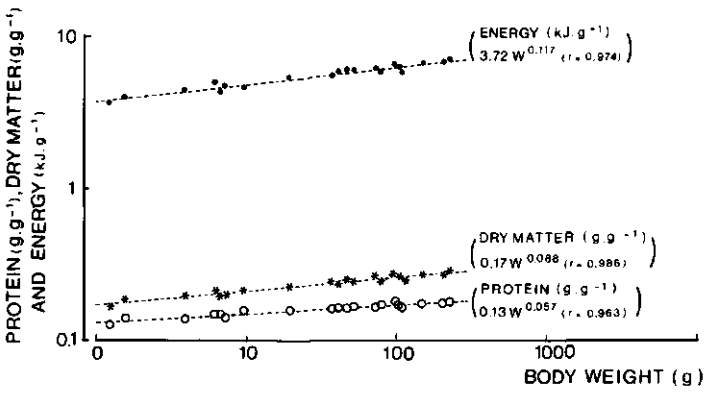

Fig.3. Protein, dry matter and energy content in relation to body weight of *C. lazera*.

Oxygen consumption

The weekly oxygen consumption measurements are given in Fig.4. During feed deprivation and maintenance feeding, the oxygen consumption decreased exponentially with time, whereas at the higher feeding levels it showed an exponential increase. The total oxygen consumption was therefore estimated per feeding level using an exponential relation with time:

$$O_2 = \int_0^t e^{a + bt}\, dt \qquad (5)$$

The resulting data (Table I) were used to calculate H.

Since the fish were weighed on the first and on the last day of each trial, their daily weight development was estimated using the model as described earlier (Hogendoorn et al., 1983). These estimates were then used to compile Fig.4.

Consistent with Eqns.(3) and (4) it was found that more oxygen was consumed as the ration increased. It further appeared that at the lower feeding levels the (exponential) decrease in the oxygen consumption exceeded the decrease in body weight. The combined effects of estimated body weight and feeding level on the oxygen consumption were therefore analyzed allowing for an exponential effect of time as

$$O_{2(W,R,t)} = \alpha_{(R)} \cdot W^{\gamma(R)} \cdot e^{\beta(R) \cdot t} \qquad (6)$$

After logarithmic transformation Eqn.(6) was found to account for 99.2% of the variance in the oxygen consumption data. The results (Table II) showed that α and β increased with the feeding level ($F^4_{83} = 61$ and $F^4_{83} = 16$ respectively), whereas γ decreased ($F^4_{83} = 7.8$). However, when only the upper 3 feeding levels were compared, neither γ nor β was affected by the feeding level ($F^2_{51} = 0.2$ and $F^2_{49} = 0.3$) and the effect of time could be omitted completely. In Fig.4 the relations between oxygen consumption and body weight have been plotted for all feeding levels after correction for the effect of time ($t = 0$). When the effect of time was not included in the

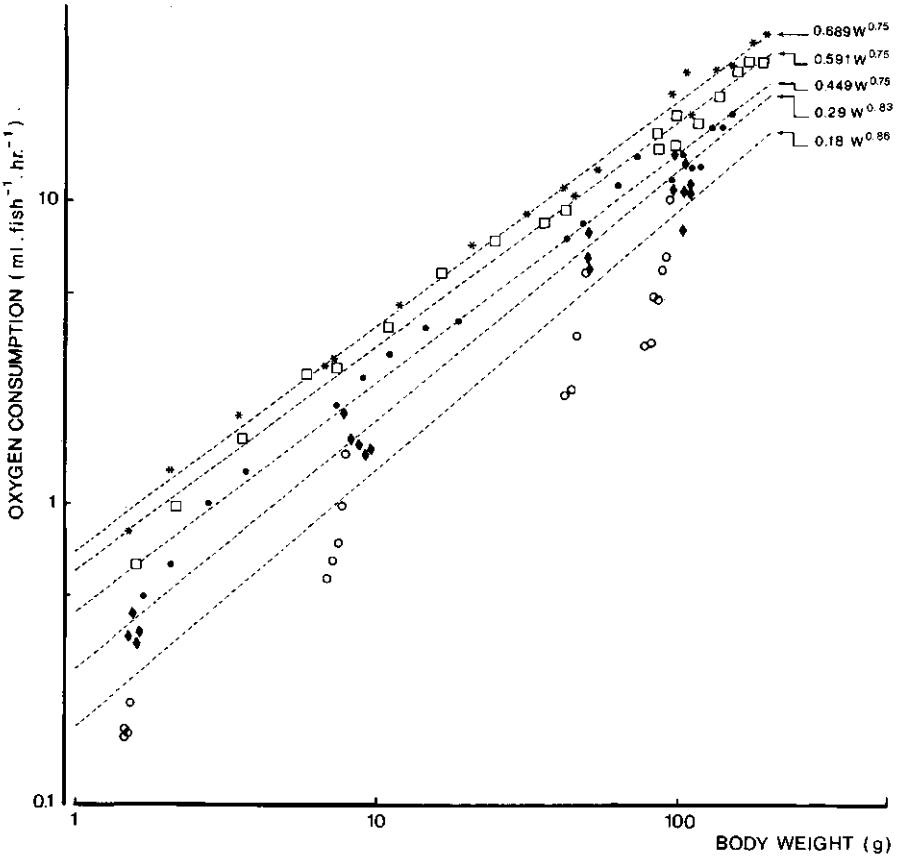

Fig.4. Oxygen consumption in relation to body weight of *C. lazera* at five different feeding levels.

TABLE II

Partial regression coefficients for the relation between the daily oxygen consumption ($ml \cdot fish^{-1}$) and body weight (g), feeding level and time (days): $O_2 = \alpha_{(R)} W^{\gamma(R)} \cdot e^{\beta(R)t}$. Standard errors for γ and β are in parentheses

Feeding level (R)	α	γ	β
Deprivation	0.18**	0.860(0.019)**	−0.0220(0.0025)**
Maintenance	0.285**	0.827(0.020)**	−0.0060(0.0026)*
Optimal	0.430**	0.745(0.022)**	0.0039(0.0027)
2 × optimal	0.599**	0.732(0.024)**	0.0033(0.0030)
3 × optimal	0.695**	0.742(0.023)**	0.0013(0.0029)

*: $P < 0.05$.
**: $P < 0.001$.

overall analysis, it was found that a common weight exponent 0.78 ± 0.01 (± S.E.) could be adopted for all feeding levels ($R^2 = 0.983$).

Feed utilization

The utilization of the feed and the question of how it is affected by fish size and feeding level, concern the fraction p of the feed energy that is available for metabolism and the fraction $p \cdot (1-q)$ that is retained as body tissue. For the different size groups and feeding levels these relations have been plotted in Fig.5. The amount of collected feed residues and faecal material is also given.

From Fig.5 it is seen that both EB and ME increase quasi-linearly with the feed energy from feed deprivation up to the optimal feeding level to reach a constant, maximum value at higher feeding levels. This deflection appears to be gradual in the smaller fish but more abrupt in the bigger ones. Because of this apparent difference in the ME response at higher feeding levels and the limited number of observations, this phenomenon was not analyzed statistically.

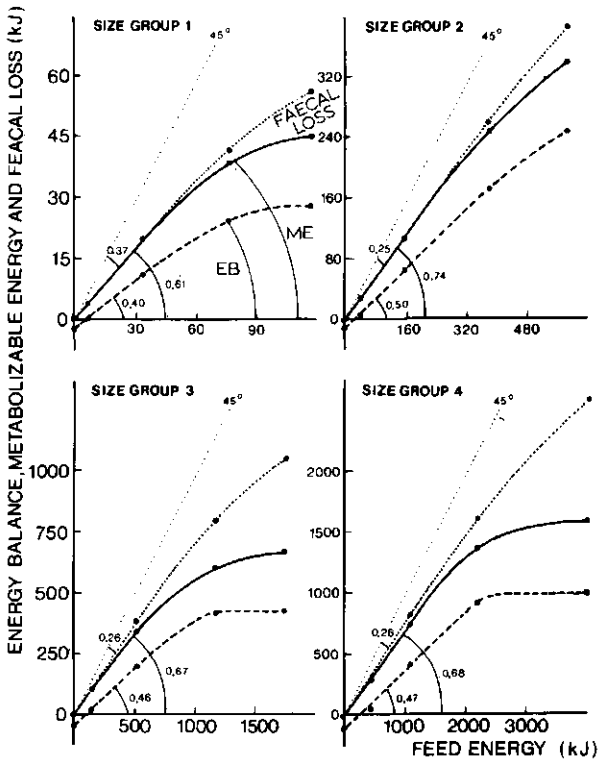

Fig.5. Partitioning of the feed energy over gain, ME and settlable materials for *C. lazera* of different sizes.

Assuming linearity over the lower three feeding levels, the coefficient p for metabolizable energy was calculated at 0.61, 0.74, 0.67 and 0.68 for the respective size groups. For these trials the fraction of the feed energy that made up the EB was 0.40, 0.50, 0.46 and 0.47. The part of the feed energy that was not accounted for as either ME or settled faecal material was 37, 25, 26 and 26% . These differences in the utilization of the feed energy could not be substantiated statistically.

By extrapolation of the relation between EB and the feed energy, the true maintenance feed ration could be estimated for the different size groups. In Fig.6 these estimates are given in relation to body weight. It was found that the ration required for maintenance (EB = 0) equalled $0.17 \cdot \overline{W}^{0.78}$ ($kJ \cdot day^{-1}$).

This metabolic weight was used to determine whether the metabolic expenditure for energy accretion differed with the feeding level or the size group. Eqn.(4) was divided by the mean metabolic weight per trial

$$H/\overline{W}^{0.78} = (H_m/\overline{W}^{0.78}) + (q(1-q))EB/\overline{W}^{0.78} \quad (7)$$

with

$$\overline{W}^{0.78} = (e^{(\ln W_e + \ln W_s)/2})^{0.78}$$

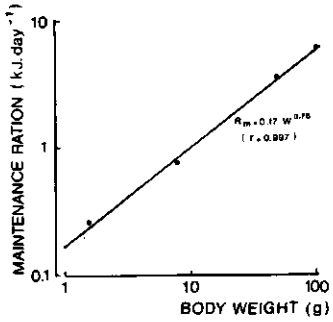

Fig.6. Maintenance ration in relation to body weight of *C. lazera*.

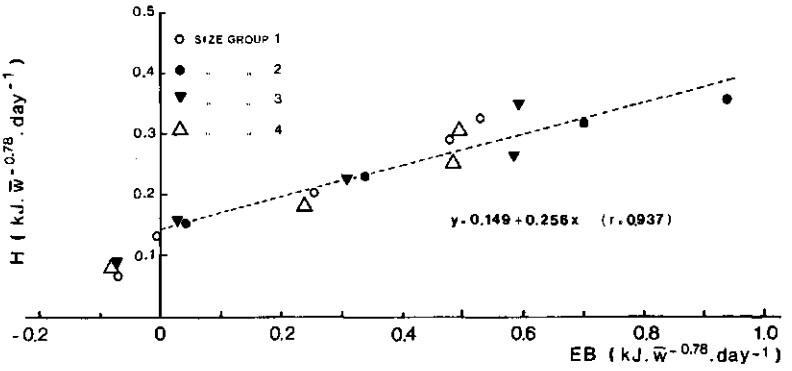

Fig.7. Metabolic expenditure in relation to energy gain by *C. lazera* of different sizes at different feeding levels.

From the results given in Fig.7, it was found that the maintenance metabolism was not affected by size groups ($F^3_7 = 0.43$) and equalled 0.149 kJ per gram metabolic weight per day. Also, a common coefficient ($q/1-q$) could be adopted ($F^3_{10} = 1.6$) and no deviation from linearity was detected. This showed that the metabolic expenditure for energy accretion was 20.4% of ME and that it was independent of body weight and feeding level. From the maintenance feed requirement of 0.17 kJ per gram metabolic weight and the corresponding metabolic expenditure of 0.149 kJ, it follows that at maintenance feeding a constant 88% of the feed energy is available for metabolism.

DISCUSSION AND CONCLUSIONS

Somatic changes

The growth potential of young *C. lazera*, already established earlier (Hogendoorn et al., 1983), was confirmed by the present experiment. Indeed, the fish grew even faster than before, probably because they were fed continuously and not only at night. Also, the absence of any manipulation during the actual trials is bound to have had a favourable effect.

Over the size range studied *C. lazera* seem to perform better than the warm-water species more commonly used in aquaculture e.g. carp, *Cyprinus carpio* L. (Huisman, 1974) or channel catfish, *Ictalurus punctatus* R. (Andrews and Stickney, 1972; Andrews et al., 1972; Andrews and Page, 1975). This is evidenced especially by the feed conversion rates which varied between 0.57 and 0.95 at the optimal and the subsequent feeding level for the different size groups.

Changes in body composition as a result of the environmental conditions have been studied for many species, as reviewed by Love (1970). From this study some relevant findings appeared. Firstly, it was found that at feed deprivation both protein and fat were used to support fasting metabolism. Actually the specific decrease in energy generally was about two times higher than the specific decrease in protein.

At the higher feeding levels the specific increase in protein and energy exceeded the increase in fresh weight as was to be expected (Huisman, 1974). However, these changes cannot be interpreted without regard for the changes in weight that take place as a result of the different feeding levels. This was evidenced when the protein, dry matter and energy content of the fish at the end of the trials were plotted against body weight. Indeed, it was seen that the changes in body composition were largely related to changes in body weight. Hence, it can be concluded that as a response to different feeding levels the fish were primarily advancing or regressing along a developmental plan with body weight as a determinant factor.

The above finding bears on a second relevant point, i.e. the importance of obtaining representative samples of fish, be it for growth experiments

or chemical analysis. The problem of variation in size in groups of fish as affecting growth studies has been the subject of extensive consideration before (Brown, 1957; Brett, 1979). The effect of the schooling behaviour of fish on growth variation was demonstrated by Yamagishi (1969). *C. lazera* tend to be very shy and sensitive to stress, especially when kept in low densities or individually. However, when first released into a confined space as a group, intensive aggressive behaviour is evident, usually changing to very harmonious group behaviour after a few days. Notwithstanding, the variation in size in groups of *C. lazera* is usually quite prominent, even after prior grading. For practical reasons, within-group variation was therefore given little attention in this study and random group allocation was applied. This not only resulted in unequal average starting weights but also may have affected the composition of the samples for chemical analysis.

In view of the above it is postulated that evaluation of the changes in proximate body composition in relation to body weight as shown in Fig.3 is more representative than interpretation of the specific changes as in Fig.2, because random sampling errors are accounted for by the statistical procedure. Furthermore, it can be concluded that in experiments using a single size group, the effect of feeding on body composition cannot be evaluated because feeding level and body weight are confounded.

Oxygen consumption

The oxygen consumption by fish in response to feeding and body weight has practical implications, e.g. for the carrying capacity and water exchange requirements of cultured fish (Willoughby, 1968; Huisman, 1974; Westers, 1979). However, it has received more attention in relation to bioenergetic studies of fish growth as reviewed by Winberg (1956), Paloheimo and Dickie (1966a), Warren (1971), Beamish et al. (1975), Webb (1978) and Brett and Groves (1979).

The results of this experiment indicate first of all that using Eqn. (5) to calculate the total oxygen consumption on the basis of weekly measurements during 24 h was satisfactory, since 99.4% of the variance in O_2 values was accounted for by the exponential relation with time. Secondly, the coincidence of the calculated metabolic expenditure and the corresponding energy balance for the different trials at feed deprivation averaged 101.6 ± 9.6 (± S.D.)% . This indicated that the respirometers performed reasonably well and it also confirmed some of the assumptions made.

At the optimal feeding level the total oxygen consumption averaged 0.279 ± 0.009 (± S.D.) ml O_2/g feed, while at the subsequent feeding rate the average was 0.193 ± 0.024 (± S.D.) ml O_2/g feed. At this stage it is not possible to quantify the relative importance of aerial and aqueous respiration, so water flow requirements for *C. lazera* cannot be given.

The dramatic increase in the total oxygen consumption with feeding in Table I represented of course a combined effect of both feeding and body

weight. In the combined analysis (Eqn. (6)) an exponential effect of time was included because of the disproportionate changes of the oxygen consumption at feed deprivation and maintenance feeding (Fig.4) and to account for adaptation phenomena. At feed deprivation this effect of time proved to be highly significant. The negative values of the coefficient, both at fasting and maintenance feeding, indicated that the metabolic expenditure decreased with time, probably reflecting a decrease in the fish activity as the trials with low feeding progressed. By contrast, the positive effect of time at the higher feeding levels indicates that the fish needed time either to adapt their metabolic rate to the higher feeding levels or to adjust to the environment. These findings underline once more the importance of using well acclimated and acclimatized fish in studies on metabolism.

After correction for the effect of time the relations in Fig.4 resulted. The weight exponent at feed deprivation: 0.86 ± 0.02 (S.E.) is higher than the value of 0.80 commonly found or adopted (Winberg, 1956; Paloheimo and Dickie, 1966a; Huisman, 1974), but is identical to the general value found by Glass (1969) and Kausch (1972). It can be seen to decrease with the feeding level to a constant value of 0.75 ± 0.01 (S.E.) at the optimal and higher feeding levels. This value is somewhat lower, but resembles those reported by Saunders (1963) for fed fish.

On the basis of these results it is concluded that the weight coefficient γ is lower for the feeding than for the standard (routine) metabolism. Theoretically, this phenomenon could account for fish not growing indefinitely, since the difference in the power functions ultimately results in the absence of a metabolic "scope for growth" (Warren, 1971) at a high body weight. Carrying this argument further it may well be that the maximum feeding metabolism acts as a limiting factor, thereby restricting the feed utilization capacity. Hence the reduction in the maximum feed uptake (as a proportion of body weight) with increasing size. This hypothesis is the reverse of the argument presented by Brett and Groves (1979), that resulted in their questioning the existence of an exponent value of this order for feeding fish. From these experiments it is clear that a weight exponent value $\neq 1$ exists for feeding *C. lazera* and that it can be determined with high accuracy, provided a large range of body weights is studied at physiologically comparable feeding levels.

The metabolic level as a result of feeding is reflected by the value of α. The increase in metabolism from feed deprivation to maintenance feeding was less than two-fold. The metabolic scope for growth $0.346\ W^{0.75}-0.145\ W^{0.83}$ ($kJ \cdot day^{-1}$) relatively decreases with increasing fish weight. This is more clearly seen by the fact that the metabolic expenditure for maximum gain equals $2.4\ W^{-0.08}$ times the maintenance metabolism.

Feed utilization

The utilization of the feed for growth and how it is affected by feeding level and body weight has received long and wide interest (Ivlev, 1939; 1960;

Winberg, 1956; Paloheimo and Dickie, 1966b; Warren, 1971; Huisman, 1974; Elliot, 1976; Kausch and Ballion-Cusmano, 1976). It remains a problematic field, however, because of the complexity of the relations as well as the difficulties in obtaining representative measurements of feed uptake, excretory products and metabolic expenditure in an aqueous environment. Also, many fish species are easily stressed, and so manipulation should be kept at a minimum.

In the present study well over 25% of the feed energy was not accounted for either as settlable materials or as energy gained or metabolized. The unexplained fraction was highest in the smallest fish. Since these fish also received the smallest feed pellets and probably produced the smallest faecal particles, it is likely that feed and/or faecal energy went into solution. Accurate determination of this water-dissolved energy was hampered by the low levels. The increase in the settled material at high feeding of the bigger fish further indicated that at least part of the feed was not consumed. As a result, the accuracy of the ME values, obtained by summation of gain and metabolism, could not be verified.

From the relations shown in Fig.5 it appeared that both ME and EB increased towards an asymptotic value with feeding, more gradually so for the smaller fish. This would make the values of p and $p \cdot (1-q)$ subject to an interactive effect of feeding level and body weight. More data are needed to further verify and investigate this phenomenon. It did, however, appear to extend also to the lower feeding levels, where it forestalled statistical verification of the main effects of feeding level and size group on the values of p and $p \cdot (1-q)$.

Taking the coefficients for EB and ME of Fig.5 at face value, there appeared to be an optimum in the feed utilization with fish size. The *C. lazera* between 8 and 40 g seemed to make better use of the feed than either smaller or bigger fish. This phenomenon was also indicated by earlier results (Hogendoorn et al., 1983), where the growth model developed required a correction for juvenile growth. It can be seen now that a lower availability of ME occurs rather than a depression in the utilization of ME for gain. The background of this unexpected finding cannot be further explained now. The question remains as to whether we are dealing with an inherent biological principle, e.g. in the digestive capacity of the youngest fish, or whether the feed composition or feeding technology were suboptimal for them. In general the utilization of the feed for ME and EB was similar to the fractions reported by Cho (1975, quoted by Brett and Groves, 1979) for rainbow trout (*Salmo gairdnerii*) and somewhat higher than the results obtained with both rainbow trout and carp by Huisman (1976).

The estimate of the true maintenance ration ($R_m = 0.17\ W^{0.78}$) was needed to determine the utilization of the ME for gain. The reasons for this are that Eqns. (3) and (4) hinge around the maintenance ration and the corresponding metabolic expenditure, and that the maintenance requirements increase as the feeding fish grow. In view of the nature of the data on the

energy balance, it was not considered feasible to apply a dynamic correction for this change in maintenance requirements. Therefore, the geometric mean metabolic weight was used in Eqn. (7) to estimate the true maintenance metabolism and the feeding metabolism in relation to the EB realized.

The resulting maintenance metabolism was $0.149 \cdot \overline{W}^{0.78}$ (kJ·day^{-1}). The maintenance metabolism resulting from Fig.4 would be $0.145 \cdot W^{0.83}$ (kJ·day^{-1}) and so there is good agreement between the two estimates. The metabolic expenditure for growth equalled 25.6% of the growth realized. This put the value of q at 0.204. Hence, about 80% of the ME was used for actual energy increment by the *C. lazera*. This compares favourably with the value of about 70% found by Huisman (1976) for carp and rainbow trout. Further experiments are necessary to determine whether this efficient growth is facilitated by the aerial respiration, as it well could be.

It also means that the metabolic scope for growth equals 20% of the ME intake for production. Thus, ME_p relates to ME_m as

$$ME_p/ME_m = 11.9\ W^{-0.08} - 5$$

This shows that the ME_p intake decreases with increasing fish weight from about 6.9 to 2.8 times the maintenance requirement for fish of 1 to 200 g. This high ratio between ME_p and ME_m largely explains the low feed conversion rates displayed by *C. lazera*.

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The experimental work reported in this paper has been the longstanding aim of my early fascination with the growth performance of *C. lazera* in aquaculture. The attainment of this end was made possible by the provision of experimental facilities and funds by the Agricultural University. Throughout this and earlier work the organizational support and encouragement from Prof. Dr. E.A. Huisman and Dr. C.J.J. Richter have been essential in reaching this goal.

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Brief Technical Note

AN OPEN CIRCUIT BALANCE RESPIROMETER FOR BIOENERGETIC STUDIES OF FISH GROWTH

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ABSTRACT

Hogendoorn, H., Van Korlaar, F. and Bosch, H., 1981. An open circuit balance respirometer for bioenergetic studies of fish growth. *Aquaculture*, 26: 183—187.

A description is given of an open circuit balance respirometer for bioenergetic studies of fish growth using indirect calorimetry. The installation was designed to enable the determination of gas and matter balances of fish, including air breathing species, during prolonged experimental periods. Design requirements, as well as constructional and operational characteristics, are given.

INTRODUCTION

Growth of fishes is dependent on a considerable number of biotic and abiotic factors (Brett, 1979). Because these factors influence growth through metabolism, understanding of these factors and their relations can be enhanced by studying their effect on metabolism (Warren, 1971).

Metabolism, which includes all processes where transfer of energy is involved, can be quantified on the basis of the energy expenditure, the energetic cost of life. The energy expenditure can be estimated from the gaseous exchange and the release of nitrogenous compounds (Brouwer, 1965). To study these processes in the labyrinthic catfish, *Clarias lazera* (Cuvier and Valenciennes) special open circuit balance respirometers were developed.

DESIGN REQUIREMENTS

For adequate monitoring of the exchange of gases and matter by the fish the following design requirements were identified:

(1) Experimental periods up to several weeks are necessary during which disturbance of the fish must be minimal.

[1]Upon request the blueprints of the installation can be obtained from the last two authors.

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4 GENERAL DISCUSSION

In the constituent papers of this thesis the experimental results were already discussed and their implications for the aquaculture of *Clarias lazera* were assessed. In this chapter some general aspects of the further development of *Clarias* culture will be discussed.

First of all it is appropriate to emphasize the suitability of the African catfish for aquaculture. The results show that it complies with the requisite conditions better than other species more commonly used in fish culture:

- it matures and is easy to reproduce in captivity,
- it can grow fast and efficiently,
- it supports high densities,
- it is hardy, and
- it can tolerate adverse water quality conditions.

Based on these biological production parameters a rapid expansion of the culture of this, and possibly other labyrinthic catfish species seems a logical development. The most likely location for this to take place is where the fish are indigenous and already eaten and appreciated: large parts of Africa and South East Asia (for other *Clarias* species). However, its culture can also be extended to the industrialized world, since the fish can be processed into excellent smoked fillets. A specific application of *Clarias* species could be in the treatment and recycling of waste-water. Through aerial respiration

A final biological aspect of *Clarias* culture still needs to be investigated i.e. the qualitative feed requirements. Throughout our laboratory experiments we have used trout pellets (Trouvit, Trouw & Co, Putten, The Netherlands), because these have a proven, constant composition. The possibilities to reduce the qualitative composition of the feed still need to be investigated further. Chapter 3.1. showed that the use of agricultural by-products or animal wastes is of special interest. The results obtained in the present experiments can serve as a starting point and reference in future research. Final adaptations and evaluation of the production methods and feeds for culture of *Clarias* will probably be necessary for each prospective site.

However, the mode of development of the use of *Clarias* for culture will depend on sociological and economical factors, more than on biological ones. For industrialized countries, the main conditions for *Clarias* culture appear to be the availability of low-cost warm water as well as acceptance of the product by the consumer. For developing countries, consumer acceptance should be verified, but the central problem is in development programming. It would be beyond the scope of this thesis to expand in detail on these issues, since they are the subject of other, identified, vocational and scientific disciplines. Nevertheless two general remarks will be made.

The first one concerns the role of Governments in relation to the development of aquaculture. In this respect it can be ventured that innovations and new developments rarely originate from Governments. They may be stimulated by governmental action through legislation or funding, but this usually occurs as a reaction to societal and non-political initiatives or pressure. As the population and the complexity of society increase, administrations appear to become even more involved with establishing codes for developments after they have occurred, rather than taking prior, early and longterm directive action. Since aquaculture is a new and unknown activity in many countries, its development needs to be stimulated. In view of the above, however, it is questionable whether political structures should be at the basis of such a development.

Apart from this general characteristic of administrative functioning, a related problem must also be mentioned, resulting from the political structuring of development assistance. In this sense it should be recognized that donor Governments are responsible to their own population and not to the receiving country's Government or people. Development assistance thus is a

matter of politics of the donor countries and the primary interest is in the quantity rather than the quality or the feasibility of the assistance given. By consequence, the latter aspects of development assistance usually leave something to be desired. Programmes are often over-ambitious considering the finances, staff, equipment and time allocated. For example, this study on the use of *C.lazera* for fish culture took several years to complete in a well equiped laboratory. But originally, it was programmed as only one of many activities in a four years development project. Looking back, those four years were required to complete the facilities in which the study was to have taken place.

The second remark is on the real nature of aquaculture: Should it be considered an extension of fishing, or does it have its roots in stock farming? A moments deliberation shows (Cracknell, 1976) that processing and distribution are the only activities, which fishing and aquaculture have in common. The main concern in aquaculture, however, is in breeding, feeding, housing, and fish health. All these require the skills and attitudes of the farmer, and not those of the hunter.

For the development of aquaculture it is important that its farming nature is recognized. This can help to avoid the superficial convenience of substituting fish farming for fish hunting, wherever the latter is declining or under economic pressure. It also shows the limitations of tacking the responsibility for fish culture and its development onto fish hunting administrators and research workers. Those involved with fishing, whether on a practical, an administrative or a research level, may have a lifetime's experience in boat design, fishing regulations and fishery biology or conservation. But a total switch of attitudes is required to achieve good stockmanship or to understand the farmers concern about veterinary standards and feed conversion. It is submitted that the hesitant development of aquaculture in many countries and the generally rudimentary state of fish health management and certification can be attributed, for a large part, to insufficient recognition of the true nature of the trade.

If, however, fish farming is defined as such, it can be considered an alternative to other types of stock farming or to arable farming. Combined production systems are also possible and already practised (Anonymous, 1976; Woynarovich, 1979; Vincke, 1979; Pullin and Shehadeh, 1980). The choice between the different systems will, once again, depend upon the socio-economic conditions and on the climate. From the point of using the land for food

production, it can be argued that land suitable for arable agriculture will produce most food with plant crops. The worlds average yield for cereals and roots/tubers in 1979 was 2041 and 10982 kg/ha respectively (Anonymous, 1980). The production of animals is best employed to use the remaining land as well as the agricultural by-products. Whenever the fiber content of the (natural) vegetation or of the residues is high, the use of ruminants is indicated. Through their symbiosis with microbes they can utilize fibrous material to a considerable extent. When the residues have a higher quality, the monogastric farm animals (poultry, pigs) or fish can be used. The growing of fish to utilize the wastes of land animals or man was already referred to earlier. In tropical climates the fiber content of the vegetation is generally high, but the possibilities for using ruminants are sometimes limited due to endemic health hazards. A mixed culture of fish, including a herbivorous species to reduce the plant material, may then be applicable.

A final point of interest can be brought up in relation to the low maintenance requirements of fish and of *Clarias lazera* in particular. Generally, in growing or otherwise producing homoiothermic land animals more than 40-50% of the maximum feed intake is used for maintenance and is thus lost for production. By contrast, when fed to satiation, the growing *Clarias* only use 12-25% of their feed for maintenance. The maintenance requirements are probably lower because the fish are bouyant in the water and do not maintain a constant body temperature. Based on these data, the net result will be a 25-75% more efficient utilization of the metabolizable feed energy for growth.

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SUMMARY

The husbandry of fish in aquaculture can help to satisfy the growing need for high quality protein in human nutrition, especially in tropical countries. It was introduced in central and west Africa between 1950 and 1960. Despite its initial success, it declined again after 1960. This was because tilapias were the main species cultured and their management requirements could not be met. In a study to determine the suitability of other local species for aquaculture, attention focussed on the catfish, *Clarias lazera* (C. & V.). It possessed a good growth potential and a wide feeding spectrum. While receiving the joint support of Governments and international development assistance, the progress of the aquaculture of *C.lazera* was slow. It proved difficult to establish a dependable supply of fingerlings to stock the production ponds. In addition, the outcome of production trials was inconsistent due to variable environmental conditions and feeding practices. It was therefore decided to carry out a systematic study of the propagation and of the production management as well as of the growth physiology of this labyrinthic catfish.

A review of the scarce literature on the reproductive biology of *C.lazera* showed that it is a communal spawner and that peak maturity occurs during the rainy season. Field experiments simulating the natural spawning conditions or using hormones to induce natural spawning did not result in a reliable method for planned fingerling production. In artificial reproduction experiments, ovulation was induced with acetone dried carp pituitary and the sexual products were obtained by stripping of the females and dissecting the testes of the males. Artificial fertilization, incubation and hatching of the eggs could then be carried out. In experiments to optimize the artificial reproduction of

C.lazera it was found that:-

- fresh *Clarias* pituitary can be used instead of acetone dried carp pituitary,
- correct timing of stripping of the females in relation to hypophysation is critical for obtaining good hatching results,
- this latent period depends on the water temperature,
- sperms can be diluted in a 0.9% NaCl solution and stored at 5 ^{o}C during 24 hours without losing their fertilizing capacity,
- incubation of the eggs can be carried out successfully both in stagnant as well as in running water, and
- the same females can be used for reproduction repeatedly with intervals of a few weeks.

Since yolk sac absorption presented no difficulties, the above findings allow a reliable production of *C.lazera* fry and efficient utilization of the broodstock. These methods also are easy to apply in or adapt to field conditions.

In rearing the fry to fingerlings, it was found that during a first phase, they require natural, preferably live feeds. After one to two weeks feeding with nauplii of *Artemia salina* or small zooplankton, they can be switched successfully to a compound, artificial dry feed. Under good conditions they grow up to well over 10 grams at an age of two months. The specific growth rate (% body/day) decreases rapidly during this period, but it remains high. The feeding regime must be adjusted accordingly. In the field, the need of the fry for natural feeds may cause problems. In case a rearing pond is used, care should be taken that ample zooplankton is available and predatory animals (insects, amphibians, fish, birds, etc.) are kept under control.

Growing the fingerlings to marketable size, it was found that *C.lazera* is a highly suitable alternative for tilapia in subsistence fish farming in Africa. When given a low grade feed composed of some local agricultural by-products, the yield from ponds was more than 2.5 times higher in the case of the catfish as compared with tilapia. The individual weight decreased with increasing fish density, indicating that the fish depended on the natural productivity of the pond to complete their diet. Optimal stocking density, therefore, must be decided on the basis of consumer preferences for fish size, and of the economics of the process.

High density, intensive culture of *C.lazera* in tanks using a complete pelleted feed, also gave good results: rapid growth and highly efficient feed conversion. A study on the bioenergetics of weight gain showed that about 70%

of the feed is metabolized. The utilization of the metabolized feed energy for gain proved to be 80% efficient. When different feeding levels were compared, it was found that the high feed conversion efficiency (gain/feed) of can be explained by the high ratio of feed energy available for production as compared with that required for maintenance. It also showed that this ratio decreases with increasing fish weight, which helped to explain the progressively lower feed conversion efficiencies as the fish grew.

The water temperature influences the growth and feed utilization of the catfish in three different ways. First, an optimum temperature was found, where the growth rate reached a maximum. Secondly, this temperature optimum was shown to vary with the size of the fish: 27.5 - 32.5 ^{o}C for the small and 25 - 27.5^{o}C for the bigger ones. The third temperature effect was that the feed conversion efficiency also had a temperature optimum. This was attributed to the fact that the capacity for feed uptake/utilization increases faster with an increase in temperature than do the maintenance requirements. The result is a change in the ratio between production and maintenance feed. This explains the changing feed conversion efficiencies.

From the above relations of body weight, feeding level and temperature, it followed that all three factors interfered with the growth and feed conversion in more than one way. To study these relations periods of growth must be compared, but great care must be taken to avoid confounding the effects. In mono-factorial experiments, employing short periods of growth, the weight development in time could be linearized by logarithmic transformation to quantify the factor effect. Sometimes, a cube root transformation gave slightly better results.

Mono-factorial experiments on fish growth, however, do not exist, because a differential change in weight immediately makes body weight a second variable. In a true multi-factorial study of the fish growth, the complexity of the effects necessitates a differential description of the underlying main physiological processes and their relation with the experimental factors. Therefore, a dynamic model was developed, relating

- maintenance metabolism to body weight and temperature,
- feeding/growth metabolism to feed uptake, body weight and temperature, and
- maximum feed intake to body weight and temperature.

This model adequately reflected the intricate effects of body weight, temperature and feeding level on the growth and feed utilization of *C.lazera*.

possibilities and limits of fish growth. As a direct practical application a feeding guide was established, listing the recommended feeding levels and corresponding growth rates as a function of body weight and temperature.

It thus showed that from a biological point of view, the African catfish is highly suitable for aquaculture, having good prospects both for developing as well as industrialized countries. The further development of *Clarias* culture will now depend on sociological and economic factors more than on biological ones. In the industrialized world the main limiting conditions are low-cost warm water and acceptance by the consumer. For developing countries the central problem hinges upon development programming.

SAMENVATTING

Hogendoorn, H., 1983. De Afrikaanse meerval (*Clarias lazera* C. & V., 1840)- Een nieuwe mogelijkheid voor visteelt. Dissertatie, Landbouwhogeschool, Wageningen, Nederland, 133 p. In het Engels met een Nederlandse samenvatting.

De visteelt biedt goede mogelijkheden om in de toenemende behoefte aan hoogwaardige eiwitten voor de menselijke voeding te helpen voorzien. Dit geldt zowel voor de westerse, geïndustrialiseerde landen, maar vooral ook voor de ontwikkelingslanden. In het eerste geval betreft het doorgaans de produktie van hoogwaardige c.q. luxe en dure vissoorten. Daarentegen gaat het in tropische landen om het zo goedkoop mogelijk produceren van zoveel mogelijk voedingseiwitten. Planten- en allesetende vissoorten worden toegepast om, al of niet in combinatie met andere landbouw- en veeteeltaktiviteiten, de produktiemogelijkheden optimaal te benutten.

Hoewel in Azië en het Verre Oosten dergelijke produktiesystemen reeds vele eeuwen bestaan, is de visteelt op het afrikaanse continent pas de laatste 35 jaar op gang gekomen. Na een enthousiaste start tussen 1950 en 1960 volgde echter al snel een kentering, waarbij het kweken van vis voor consumptie weer in onbruik geraakte. Deze teruggang was vooral te wijten aan het algemene gebruik van tilapiasoorten. Deze hebben met elkaar gemeen, dat ze zich zo jong en snel voortplanten, dat de vijver overbevolkt raakt met zeer kleine, niet meer groeiende vis. Dit probleem kan in principe opgelost worden door middel van een hierop gerichte, zeer strakke bedrijfsvoering en -organisatie. De uitvoering hiervan is in Afrika echter niet eenvoudig te realiseren.

Dit leidde ertoe dat vervolgens is onderzocht of ook andere lokale vissoorten voor gebruik in de visteelt aldaar geschikt waren. Hierbij richtte

zich de aandacht al snel op de labyrinthmeerval, *Clarias lazera*(Cuvier & Valenciennes). Dit was vanwege zijn goede groei- en produktiemogelijkheden alsmede vanwege zijn kwaliteiten als alleseter. Er ontstond een vrij brede belangstelling voor de teelt van deze vissoort, tot uiting komend in de steun van plaatselijke regeringen en ontwikkelingsorganisaties. Desondanks gelukte het niet om te komen tot goede en betrouwbare teeltvoorschriften voor de vermeerdering en het mesten van de meerval. Teneinde in deze situatie verbetering te brengen is het in dit proefschrift vermelde onderzoek uitgevoerd.Het probleem is benaderd door op systematische wijze, met behulp van experimenten, de visteeltkundige gebruiksmogelijkheden en -onmogelijkheden van *C.lazera* in de verschillende produktiefasen vast te stellen.

Uit de resultaten van dit onderzoek is gebleken dat de natuurlijke voortplanting van de afrikaanse meerval, al of niet gestimuleerd door een hormoonbehandeling, een onvoldoende bedrijfszekere basis vormt voor de kweek van het bezettingsmateriaal dat nodig is voor de produktie. De kunstmatige voortplanting met behulp van een injectie met hypofysemateriaal (hypofysatie), gevolgd door afstrijken van de vrouwelijke teeltvissen en kunstmatige bevruchting van de eieren, bleek daarentegen een zeer goed toepasbare methode te zijn. Toen dit eenmaal bekend was, is deze methode verder uitgewerkt. Hierbij bleek dat ten behoeve van de hypofysatie niet alleen het gangbare, gedroogde karperhypofysepoeder te gebruiken is, maar dat hiertoe tevens de verse hypofyse van een soortgenoot kan worden toegediend. Tevens bleek het van groot belang te zijn dat het tijdstip van afstrijken nauwkeurig wordt gekozen ten opzichte van het tijdstip van hypofysatie; dit om slechte uitkomsten van de eieren alsmede veel misvormingen bij de larven te voorkomen.

De optimale tijdsduur tussen het moment van hypofysatie en dat van afstrijken is groter naarmate de watertemperatuur lager is. Deze periode is echter korter dan de tijd, gedurende welke het hormvocht kan worden bewaard. Hierdoor is het mogelijk van één mannelijk dier zowel de hypofyse als het hormvocht te winnen. Deze beide produkten kunnen vervolgens worden gebruikt om eerst een vrouwelijk dier te hypofyseren en vervolgens, na afstrijken, haar eieren te bevruchten. Het benodigde aantal teeltvissen kan verder worden gereduceerd door gebruik te maken van de bevinding dat één en hetzelfde moederdier herhaald kan worden afgestreken met een interval van slechts enkele weken. Er zijn dus goede perspektieven om deze kunstmatige voortplantingsmethode ook op de afgelegen lokaties in Afrika in praktijk te brengen.

Bij het opkweken van het dooierzakbroed tot het zwemmend stadium zijn geen

problemen gesignaleerd. Wel werd gevonden, dat het eerste voedsel voor het pas zwemmend broed dient te bestaan uit bij voorkeur levende dierlijke organismen. Na één à twee weken kan vervolgens met succes op een droogvoeder worden overgeschakeld. Bij goede omstandigheden bereiken de jonge meervallen dan een stuksgewicht van ruim 10 gram op een leeftijd van circa twee maanden. Gedurende deze eerste levensperiode neemt de specifieke groeisnelheid (als percentage van het lichaamsgewicht per dag) snel af, van circa 85% bij aanvang naar ongeveer 8% als gebruiksklaar pootvisje. Toch kan ook dit nog als een zeer snelle groei worden gekarakteriseerd. Het is dan ook van belang dat de jonge meervallen in deze fase over voldoende voedsel kunnen beschikken. Hiertoe moeten de te verstrekken voederhoeveelheden vrijwel dagelijks worden aangepast.

Wanneer het de bedoeling is het *Clarias*-broed in de afrikaanse visteeltpraktijk op te kweken, moeten moeilijkheden in de beschikbaarheid van voldoende natuurlijk voedsel worden voorzien. Het gebruik van broedvijvers kan worden overwogen, indien zich daarin voldoende zooplankton bevindt en de aanwezigheid van predatoren (insekten, kikkers en padden, vissen, vogels enz.) kan worden vermeden.

Het mesten van de meervallen tot consumptiegrootte is van veel faktoren afhankelijk. Allereerst rijst hierbij de vraag wat de gewenste consumptiegrootte is. Tot nu toe is met betrekking tot dit aspekt weinig bekend. Toch is het vaststellen van een gewenst slachtgewicht van belang, aangezien het een onderdeel uitmaakt van een te formuleren produktiedoelstelling. Deze vormt op haar beurt de basis voor de bedrijfsvoering.

Zo is uit dit onderzoek gebleken dat de *Clarias* in vijvers sneller groeien naarmate de bezettingsdichtheid lager is. De voedering in de betreffende proef vond plaats met plaatselijke agrarische afvalprodukten. De groeivertraging bij de hogere dichtheden kan worden verklaard door deficiënties in het verstrekte voer c.q. de afhankelijkheid van de vis van het in de vijvers geproduceerde natuurlijke voedsel. In vergelijking met tilapia deden de meervallen het onder deze omstandigheden echter meer dan 2,5 maal beter met een jaaropbrengst oplopend tot circa 5 ton per ha.

Als onderdeel van deze studie is de *Clarias* ook op een intensieve wijze gekweekt: bij hoge dichtheden in doorstroomde aquaria onder gebruikmaking van een compleet mengvoeder in korrelvorm. Hierbij werd gevonden dat de meervallen niet alleen zeer snel kunnen groeien, maar daartoe bovendien slechts weinig voer nodig hebben. Over een gewichtstrajekt van 0.5 tot ruim 200 gram daalde de specifieke groeisnelheid van 11 naar 2% van het lichaams-

gewicht per dag, waarbij de voederconversie (voer/groei) opliep van 0.6 tot circa 1.0.

Nader onderzoek naar de fysiologische achtergrond van deze zeer gunstige voederbenuttingsresultaten leverde het inzicht op, dat *C.lazera* ongeveer 70% van het opgenomen voer ook effektief voor verbranding of groei gebruikt: de beschikbare energie. Wanneer een zekere hoeveelheid beschikbare energie ten behoeve van groei wordt gebruikt, gaat hiervan circa 20% verloren als warmte. Hoewel deze cijfers op zich gunstig zijn, kon alleen op grond hiervan voor de lage voederconversies geen verklaring worden gegeven. Dit kon wel, toen uit een vergelijking van verschillende voederingsniveaus bleek, dat van de maximaal opneembare hoeveelheid beschikbare energie slechts een zeer geringe fraktie voor onderhoud nodig is. De energie, die voor onderhoud (bijvoorbeeld hartslag, osmoregulatie, zwemmen, enz.) wordt gebruikt, is uit een produktie-oogpunt onrendabel, aangezien ze als warmte voor de vis verloren gaat. Naarmate de onderhoudsbehoefte geringer is, komt dus een groter deel van de energie uit het voeder ten goede aan de eigenlijke groei en wordt de voederconversie beter. De zeer gunstige verhouding tussen de hoeveelheid "produktievoer" en "onderhoudsvoer" kwam vooral bij de kleine meervallen naar voren. Bij de grotere vis was deze verhouding lager met als gevolg een toename in de voerderconversie.

Met betrekking tot de invloed van de watertemperatuur op de groei en de voederbenutting van *C.lazera* konden een drietal deeleffekten worden onderscheiden. Enerzijds vertoont de groeisnelheid van deze koudbloedige dieren een maximum bij een temperatuur, die daarmee als optimum temperatuur voor groei bestempeld kan worden. Anderzijds is dit temperatuuroptimum echter niet constant, maar verandert het met de grootte van de vissen: 27.5 - 32.5 ^{o}C voor de kleine, tegenover 25.0 - 27.5 ^{o}C voor de grotere dieren. Ten derde vertoont niet alleen de groei maar ook de voederbenuttingsefficientie een maximum bij een bepaalde temperatuurwaarde. De verklaring voor dit verschijnsel is, dat het vermogen tot voederopname c.q. -benutting anders op een temperatuursverandering reageert dan de onderhoudsbehoefte. Het resultaat hiervan is dat de eerder genoemde verhouding tussen "produktie-" en "onderhoudsvoer" met een temperatuurstijging eerst toeneemt, maar daarna weer daalt. De voederbenuttingsefficientie vertoont dan uiteraard een vergelijkbaar verloop.

Uit de hierboven opgesomde effekten van het lichaamsgewicht, het voederingsniveau en de watertemperatuur kan worden gekonkludeerd dat elk van de drie faktoren de groei en de voerbenuttingsefficientie van *C.lazera* op meer-

dan één wijze beïnvloedt. Deze complexe samenhang noodzaakt tot grote voorzichtigheid bij het onderzoeken ervan. Er worden dan namelijk groeiresultaten met elkaar vergeleken, waarbij het gevaar bestaat dat een effekt van de ene faktor aan een andere wordt toegeschreven. Het kan ook voorkomen dat twee faktoren nooit afzonderlijk, maar altijd gezamenlijk hun effekt hebben. Dit laatste was in de onderhavige proeven het geval, omdat een verschil in groei, tengevolge van voederings- of temperatuurverschillen, direkt leidt tot een verschil in gewicht. Bijgevolg moet bij het bestuderen van voederings- of temperatuurseffekten de invloed van gewichtsverschillen steeds in rekening worden gebracht.

Bij enkelvoudige en kortdurende groeiproeven is een en ander wat minder van belang. Er kan dan nogal eens worden volstaan met het lineariseren van de gewichtsontwikkeling in de tijd, teneinde het effekt van een bepaalde faktor te kwantificeren. Hiertoe leent zich bijvoorbeeld een logaritmische of een derde machts-worteltransformatie van de gewichtsgegevens. Worden echter meer faktoren tegelijkertijd en over een langere periode bestudeerd, dan voldoen dergelijke wiskundige manipulaties niet meer aan het gestelde doel: het duidelijk maken en kwantificeren van het effekt van een faktor.

In dit onderzoek is daarom gekozen voor een benadering, waarbij groeideelprocessen (onderhoudstofwisseling, groeistofwisseling en voeropname/ voerbeschikbaarheid) werden onderscheiden en vervolgens afzonderlijk in relatie werden gebracht met de te bestuderen faktoren. Het resulterende wiskundige model voor de groei en voerbenutting van *C.lazera* bleek voor de beproefde omstandigheden goed te voldoen. Bovendien konden de eerder opgesomde effekten van gewicht, voedering en temperatuur er beter door worden onderscheiden. Als direkte praktische toepassing kon een voederingstabel voor deze vissoort worden opgesteld, waarin de optimale voedering en de daarbij behorende groeisnelheid als funktie van het lichaamsgewicht en de temperatuur zijn weergegeven.

Samenvattend kan op grond van de resultaten van dit onderzoek worden gesteld, dat *C.lazera* zeer geschikt is om te worden gebruikt in de visteelt. Dit geldt vooral voor de ontwikkelingslanden, maar ook voor sommige geïndustrialiseerde landen. De vraag of nu de teelt van *Clarias* in de praktijk zal toenemen, en zo ja waar, en hoe snel, heeft in dit stadium meer van doen met de sociologische en ekonomische randvoorwaarden dan met de biologische. In geïndustrialiseerde landen zijn de beschikbaarheid van goedkoop warm water en acceptatie door de consument de belangrijkste voorwaarden voor het slagen van de *Clarias*-teelt. Voor de ontwikkelingslanden vormt de ontwikkelingsplanning een fundamenteel probleem.

CURRICULUM VITAE

H. Hogendoorn, geboren op 14 oktober 1949 te Loenen (Utr.), behaalde in 1968 het einddiploma Gymnasium-B aan het Christelijk Lyceum te Utrecht. Vervolgens studeerde hij Veeteelt aan de Landbouwhogeschool te Wageningen en behaalde in 1975 het ingenieursdiploma met als hoofdvakken de Fysiologie van de Huisdieren en de Erfelijkheidsleer en als bijvak de Gezondheids- en Ziekteleer der Huisdieren. In 1974 trad hij in dienst bij de Wereld Voedsel Organisatie (FAO) en werd voor twee jaar gestationeerd op het Nationale Visteeltcentrum te Kameroen. Van 1976 tot 1982 was hij als wetenschappelijk medewerker verbonden aan de Vakgroep Visteelt en Visserij van de Landbouwhogeschool te Wageningen waar o.a. dit proefschrift werd bewerkt.

Vanaf 1982 is hij werkzaam bij de Organisatie ter Verbetering van de Binnenvisserij te Nieuwegein.