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Controlled hatchery production of African catfish, *Clarias gariepinus*: the influence of temperature on early development

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Abstract

Temperature is the major abiotic factor controlling the rate of morphogenesis in fish. The present work investigated hatching time and the transition from endogenous to exogenous feeding at five constant temperatures over the range 15-35°C. *Clarias gariepinus* eggs can be successfully hatched in ambient water temperatures between 20 and 35°C, although at 30°C the hatching rate is significantly improved. At 15°C embryos do not survive. The period of hatching is inversely related to temperature such that synchronous hatching is encouraged by high temperature within the specific temperature range. The extent to which development rate and metabolic rate in *C. gariepinus* are accelerated by temperature is not the same. The duration between first feeding, yolksac absorption and the point-of-no-return is inversely related to temperature. The same threshold temperature, below which development is theoretically arrested, can be estimated for *C. gariepinus* from the linear relationship between development rate and temperature up to hatching, first feeding and yolksac absorption. This closely approximates the lower lethal temperature of 15°C estimated directly from embryo survival. The effect of temperature can be usefully modelled in *C. gariepinus* using the linear relationship $V = a + bt$ to estimate t_0 (threshold temperature) and D^0_{eff} (effective day-degrees) and the hyperbolic relationship $\tau = D^0_{eff}/(t - t_0)$ to determine development time. From the present work, t_0 is 14.5°C and D^0_{eff} is 13, 26.3 and 35.7 for hatching, first feeding and yolksac absorption respectively for *C. gariepinus*. Unlike day-degrees, effective day-degrees remain independent of temperature over the range 20-35°C. An approximate guide to development time at different constant temperatures within this range is given.

Keywords: Temperature effects, fish eggs, hatching, survival, embryonic development, fish larvae, *Clarias gariepinus*.

Production contrôlée en écloserie du poisson-chat africain, Clarias gariepinus *: influence de la température sur les premiers stades de développement.*

Résumé

La température est le principal facteur abiotique contrôlant la vitesse de la morphogenèse chez les poissons. Dans ce travail, la durée de l'incubation et la période de transition entre l'alimentation endogène et exogène sont étudiées à cinq températures constantes comprises entre 15°C et 35°C. Les œufs de *Clarias gariepinus* peuvent éclore à une température ambiante de l'eau comprise entre 20 et 35°C, toutefois le taux d'éclosion est significativement plus élevé à 30°C. A 15°C, les embryons ne survivent pas. La durée de l'incubation est inversement reliée à la température, de telle manière qu'une éclosion synchrone est favorisée par des températures élevées dans la gamme de tolérance de l'espèce.

Chez *C. gariepinus*, le développement et le métabolisme ne sont pas accélérés de la même façon par la température. La durée entre la première alimentation, la résorption du vitellus et le point de non-retour est inversement proportionnelle à la température. Le même seuil de température, en-dessous duquel le développement est théoriquement arrêté, peut être estimé pour *C. gariepinus* à partir des relations linéaires entre la température et la vitesse de développement jusqu'à l'éclosion, l'entrée en phase trophique et la résorption vitelline. Ce seuil avoisine la température minimum létale de 15°C, estimée directement à partir des survies embryonnaires.

L'effet de la température peut être utilement modélisé chez *C. gariepinus* en utilisant la relation linéaire $V=a+bt$ pour estimer t_0 (température-seuil) et D^0_{eff} (degrés-jours effectifs), et la relation hyperbolique $T=D^0_{eff}/(t-t_0)$ pour déterminer la durée du développement. Dans cette étude, t_0 est estimé à 14,5°C et D^0_{eff} à 13, 26,3 et 35,7 pour l'éclosion, la première alimentation et la résorption vitelline, respectivement. A la différence des degrés-jours, les degrés-jours effectifs restent indépendants de la température dans la gamme de 20 à 35°C. Un guide approximatif est donné pour déterminer la durée du développement à différentes températures constantes de la gamme.

Mots-clés : Effet de la température, œufs de poisson, développement larvaire, *Clarias gariepinus*.

INTRODUCTION

One of the earliest attempts to describe the effects of temperature on living processes appears to have been the rule of thermal sums proposed by Reaumur in 1735 (Fry, 1971). It was found to describe the appearance of ripening in crops as well as the development of larvae in different climatic conditions. Temperature is now widely accepted to be the major abiotic factor affecting the rate of morphogenesis (development of form and structure) of embryonic and larval poikilotherms (Valdes *et al.*, 1991; Kamler, 1992; Kamler *et al.*, 1994). In temperate fish culture Reaumur's constant has proved a useful predictive tool, especially for hatchery managers.

The African catfish *Clarias gariepinus* (Burchell, 1822) is cultured over a broad temperature range in widely varying altitudes and latitudes (Haylor, 1993). The definition of the affect of temperature on development is therefore of importance to the development and management of its culture. The embryonic and larval development of African catfish has been described by Legendre and Teugels (1991) and temperature induced changes of early development and yolk utilization has been investigated by Kamler *et al.* (1994). The onset of air breathing and development of accessory breathing organs has also been investigated in relation to temperature (Haylor and Oyegunwa, 1993).

The present study concerns the affect of temperature on late embryology and early larval rearing, hatching and the transition from endogenous to exogenous feeding. It considers which of the available models most usefully predicts the effect of temperature on the early development of this warm water species with a wide thermal tolerance.

MATERIALS AND METHODS

Experimental fish

Sexually mature *C. gariepinus* were selected from the population maintained at the Institute of Aquaculture, University of Stirling. The broodstock were held at 25°C in conditions of 12 h light: 12 h dark and fed with a salmonid diet (B. P. Mainstream, Nutrition Ltd., Inverbreakie, Invergordon, Scotland) at about 2% of body weight per day. The holding system and the method used to induce spawning were as described in Haylor (1991).

Multi-temperature rearing system

A multi-temperature water recirculation system described in Robertson (1992), maintained fifteen tanks (five groups of three) at five different constant temperatures (15, 20, 25, 30 and 35°C). The fish culture component of the system, which comprised white plastic circular tanks (0.5 m diameter) with lids, was used for hatching and larval rearing. The diameter:depth ratio of the tanks was approximately 10. Water depth was regulated by a central stand pipe covered by a 500 μm mesh screen.

Experimental protocol

Hatching

The effect of temperature was investigated with regard to: egg survival up to hatching, time until hatching, hatching rate, period of hatching and mean wet and dry weight at hatching.

Four replicates of two hundred fertilized eggs were incubated on horizontal 1 mm rearing meshes at each of the five temperatures. During incubation the number of dead eggs (that were completely opaque) were counted every two hours. Hatching was considered to have begun when the first larvae emerged. Ten newly hatched larvae (within one hour of hatching) were sampled from each replicate. Wet weight was recorded to the nearest 0.1 mg using a Mettler AC 100 five figure balance. The sampled larvae were dried to constant weight at 105°C in a Gallenkamp thermostatically controlled oven and mean dry weight was determined. The end of hatching was recorded as the time when all remaining unhatched eggs became completely opaque.

The transition from endogenous to exogenous feeding

The effect of temperature was investigated with regard to the timing of: the onset of first feeding, complete yolksac absorption and the point-of-no-return (PNR) (when unfed larvae no longer have the ability to consume feed offered to them) as well as the wet weight at first feeding.

Every eight hours, from twenty four hours after hatching, a random sample of 20 larvae were removed from a population, one hour after offering decapsulated, unhatched *Artemia* (Franciscana, Argent, Redmond, WA USA) as feed. Each larva was observed under a light microscope at × 40 magnification and the presence of ingested *Artemia* was recorded. The time till 50% or more of the larvae had ingested feed was used to represent the timing of the onset of first feeding. At first feeding the wet weight of a random sample of 20 larvae was measured.

Three hundred larvae at the first feeding stage were maintained in duplicate tanks at 20, 25, 30 and 35°C. At each temperature one tank of fish received exogenous feed (*Artemia*), whilst the other acquired only endogenous sustenance (unfed). Each day a random sample of ten un-fed larvae from each temperature were acclimated to a separate tank where feed was offered. One hour after the presentation of feed the larvae were observed under a light microscope at × 40 magnification; the presence of ingested *Artemia* as well as remaining yolk was assessed. The PNR was determined when five or more of the sampled larvae had not consumed the feed offered. Yolksac absorption was determined when five or more of the sample had no remaining visible yolk reserves.

Analysis of data

After arcsine transformation of the percentage hatch rate data a Bartlett test confirmed homoscedasticity, and the effect of temperature on hatching success was assessed by a single classification one-way analysis of variance with equal sample size (Sokal and Rohlf, 1981).

The non-parametric Krukal-Wallis test was used to investigate the effect of temperature on wet weight at hatching after a Barlett test revealed the data to be heteroscedastic. However, parametric analyses of variance (single classification, equal sample size) were applied to the normality distributed, homoscedastic data for dry weight at hatching and wet weight at first feeding.

The relationship between developmental period and rearing temperature for the stages: hatching, first feeding, yolksac absorption and point-of-no-return were described by day-degrees (D^0) (de Reaumur, 1735), such that the product of development time (τ) and temperature (t) gives a constant (a number of day-degrees [D^0]) for each development stage, and effective day-degrees (D^0_{eff}) (Winberg, 1987) which are the product of development time and effective temperature (t_{eff}). [$t_{eff} = t - t_0$, where t_0 is the threshold temperature at which development is theoretically arrested and t = water temperature in °C]. The relationship between development rate (V) (day^{-1}) and temperature was tested for linearity in each case.

RESULTS

Hatching

No eggs hatched at 15°C and after 62 h no eggs remained alive at that temperature (*fig.* 1). Temperature (between 20 and 35°C) significantly affected the % hatching rate ($F_{(3,12)} = 36.18$, $p < 0.01$) which varied between 66 and 82% (*fig.* 2). The time up to hatching and the period of hatching are shown in *figure* 3. Both the time until hatching and hatching period decreased curvilinearly with increasing temperature. There was no significant difference ($F_{(3,12)} = 3.234$, $p > 0.05$) in mean dry weight at hatching amongst the temperature treatments between 20 and 35°C, although temperature significantly affected wet weight at hatching (H/D = 12.82, $p < 0.05$). Wet and dry weight at hatching are shown in *figure* 4.

Transition from endogenous to exogenous feeding

Temperature significantly affected wet weight at first feeding ($F_{(3,76)} = 3.13$, $p < 0.05$). Temperature between 20 and 35°C affected the time until the onset of first feeding, yolksac absorption and the point-of-no-return (*fig.* 5). The onset of first feeding preceded yolksac absorption at all temperatures and both decreased curvilinearly with increasing temperature. The duration between attaining feeding ability, yolksac absorption and the point-of-no-return is inversely related to temperature. So that at temperatures of 20 and 25°C the optimum period in which to initiate exogenous feeding is 28 and 24 h duration respectively, at 30°C and 35°C this window is less than 12 h. The duration between first feeding and the point-of-no-return is approximately 7.5-8.5 days between 20-30°C, however at 35°C this is reduced to less than 3.7 days.

Figure 6 displays the relationship between Reaumur's constant and temperature using D^0 and D^0_{eff} until hatching, first feeding and yolksac absorption.

The linear model relating developmental rate V, (where $V = 1/\tau$, τ = development time to the mass appearance of a development stage) and temperature

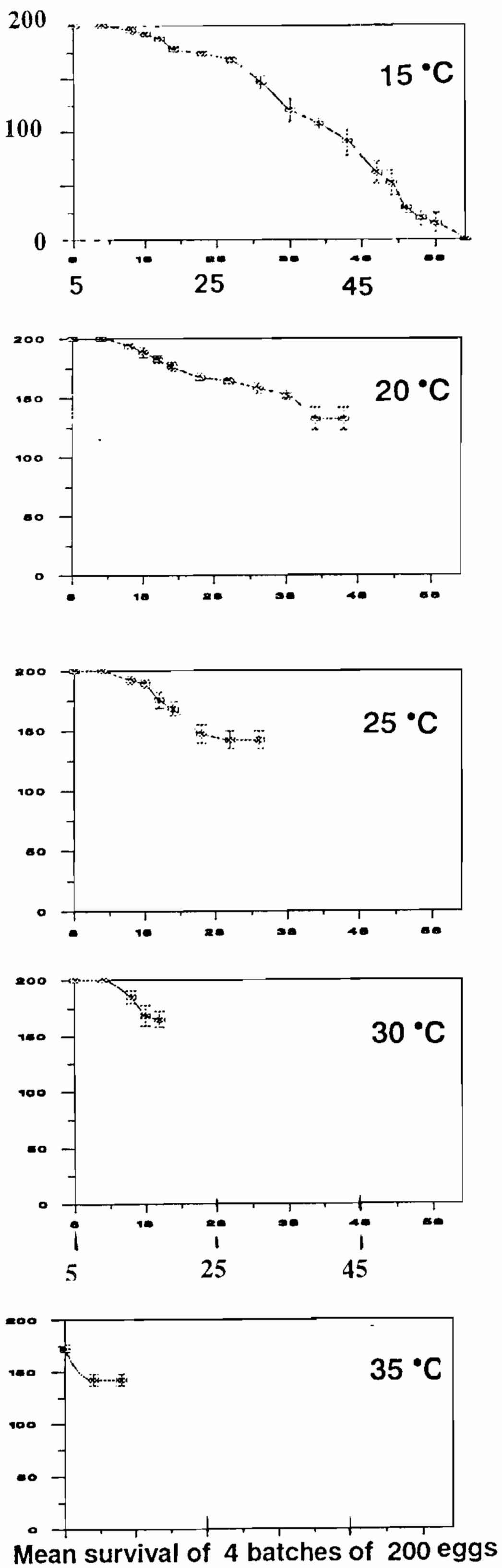

Figure 1. – Survival of *C. gariepinus* eggs during incubation at different constant temperatures of 15, 20, 25, 30 and 35°C.

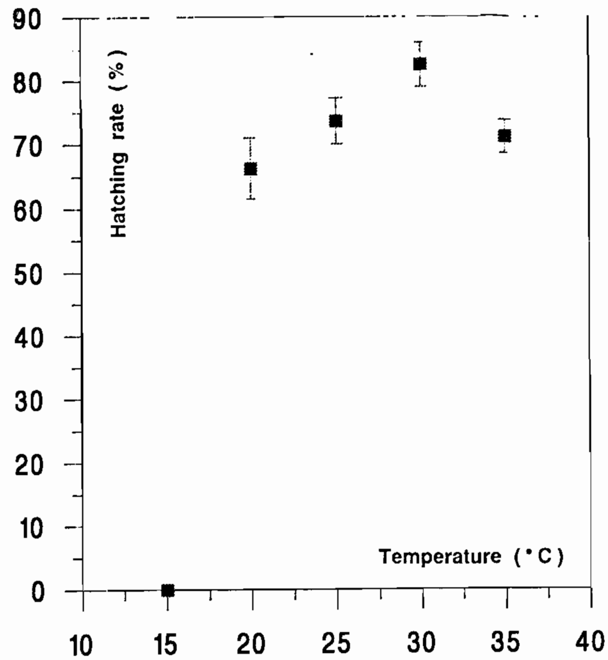

Figure 2. – Hatching rate of *C. gariepinus* eggs as a function of incubation temperatures (between 15-35°C). Error bars represent 95% confidence limits.

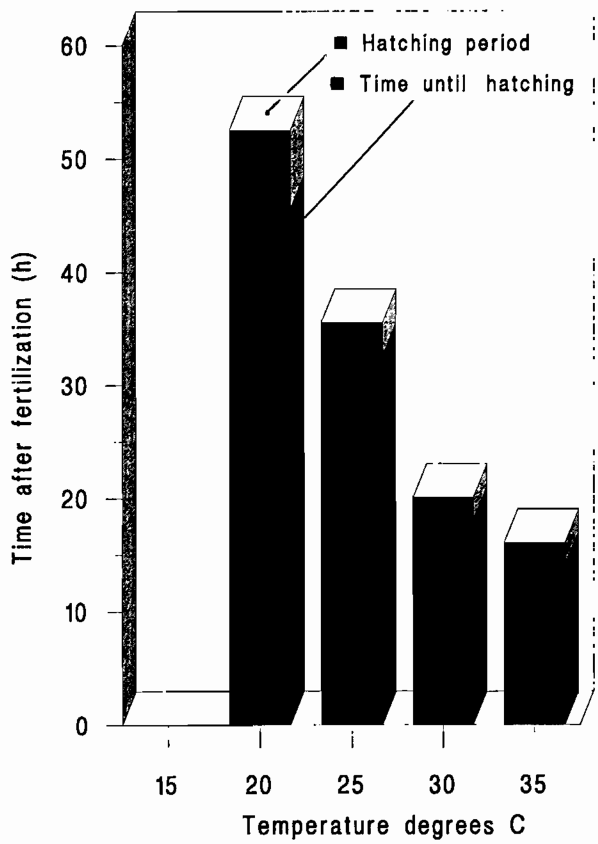

Figure 3. – The effect of temperature on the time until hatching and the period of hatching in *C. gariepinus*.

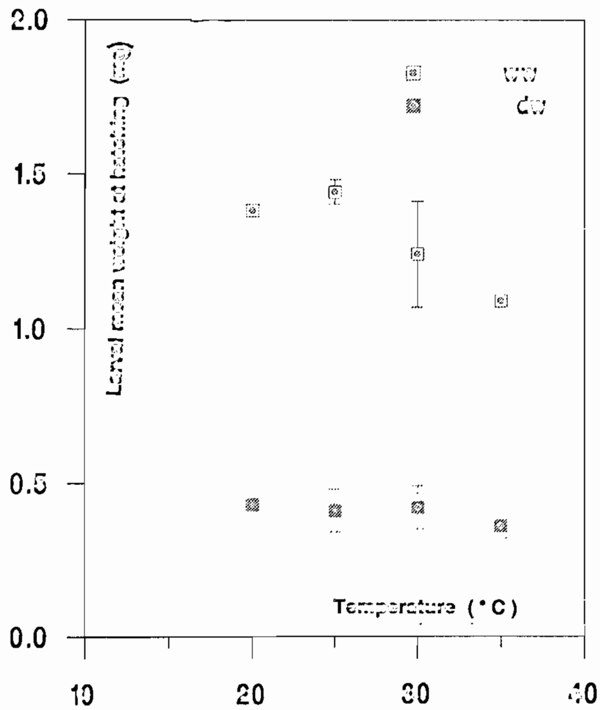

Figure 4. – Mean wet and dry weights of *C. gariepinus* hatchings incubated at constat temperatures between 15 and 35°C. Error bars = 95% confidence limits.

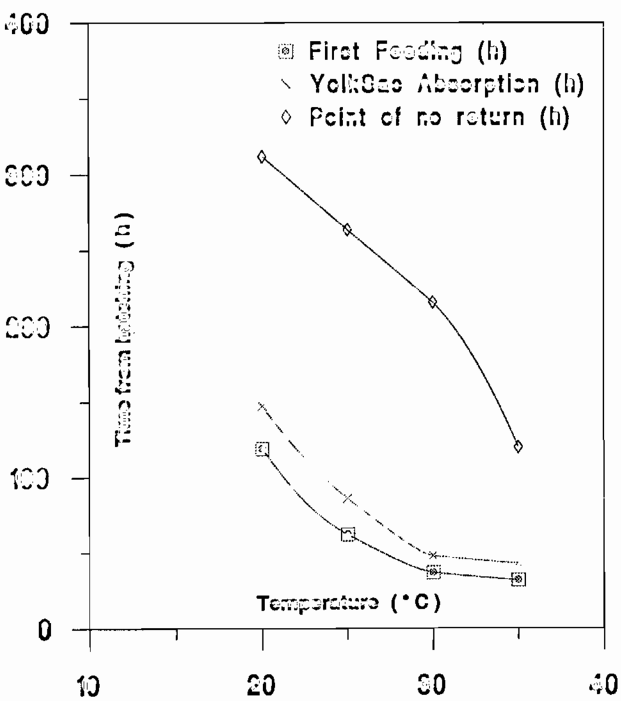

Figure 5. – The effect of temperature on the time until first feeding, yolksac absorption and point of no return in *C. gariepinus*.

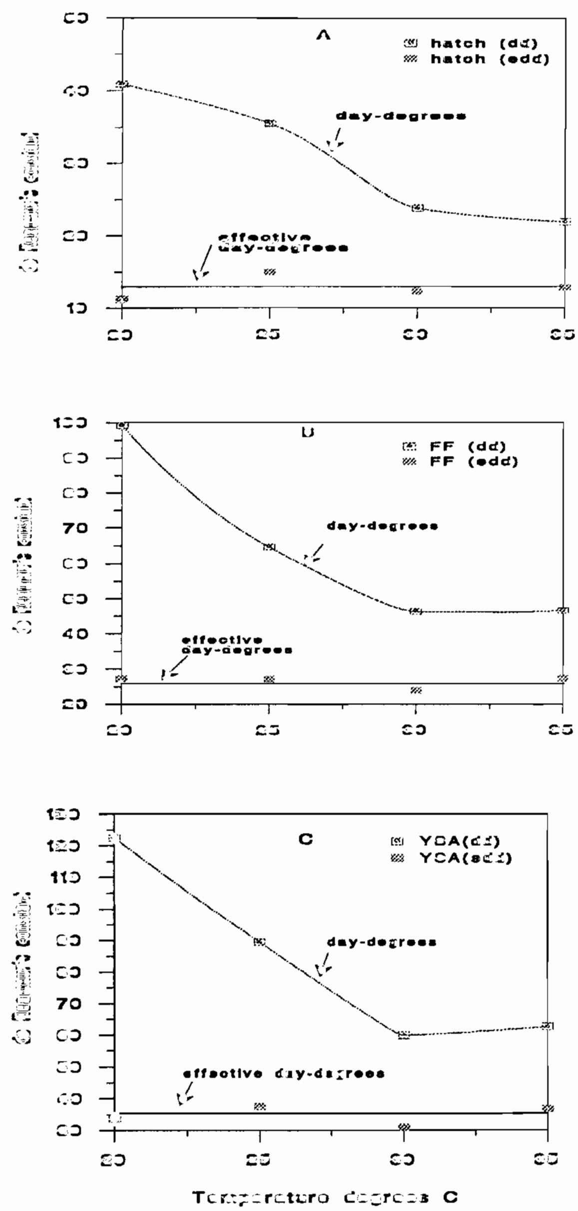

Figure 6. – The effect of temperature on de Reaumur's constant using day-degrees and effective day-degrees for hatching (A), first feeding (B) and yolksac absorption (C) stages of development in *C. gariepinus*.

(°C) for different stages in the arly development of *C. gariepinus* is shown in *figure* 7. The model is especially useful because the threshold temperature at which development is theoretically arrested (estimated by extrapolating the development rate-temperature curve back to the abscissa where development rate is zero) and the effective day-degrees can be obtained from the equation $V = a + bt$ for each stage, whereby $t_0 = a/b$ and $D^0_{eff} = 1/b$ (where a and b are constants) (*table* 1).

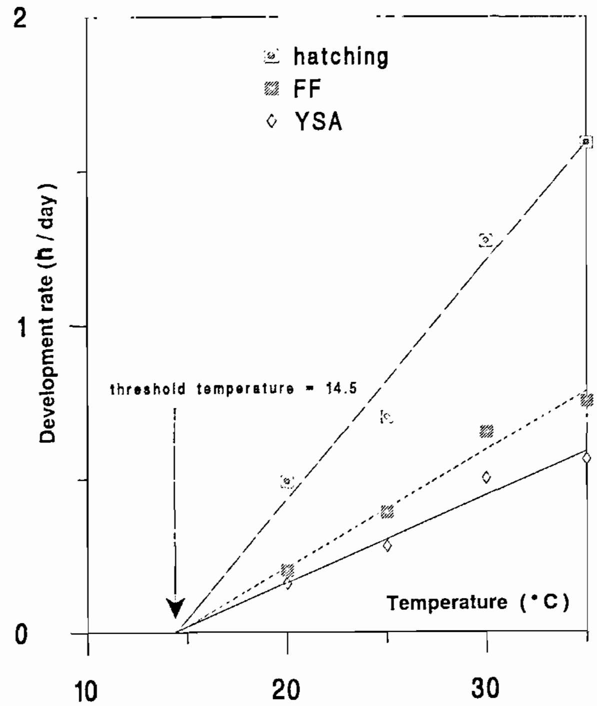

Figure 7. – The effect of temperature on the development of embryonic and larval *C. gariepinus* (FF: first feeding, YSA: yolksac absorption).

Table 1. – Development rate vs temperature, threshold temperature and effective day-degrees for hatching, first feeding and yolksac absorption in *C. gariepinus*.

Development stage	Temperature equation (V = a + bt)	Coefficient of determination (r^2)*	t_0 (– a/b)	D^0_{eff} (1/b)
Hatching (h)	$V_h = -1.116 + 0.077t$	0.972	14.5	13.0
First feeding (ff)	$V_{ff} = -0.553 + 0.038t$	0.975	14.5	26.3
Yolksac absorption (ysa)	$V_{ysa} = -0.406 + 0.028t$	0.959	14.5	35.7

* N = 4, df = N – 2 = 2, $P_{(0.05,2)} = 0.95$

DISCUSSION

Temperature and hatching

C. gariepinus eggs can be successfully hatched at ambient water temperatures between 20 and 35°C, although at 30°C the hatching rate is significantly improved. At 15°C embryos do not survive. The period of hatching (*i.e.* from the first hatch until the end of hatching) is inversely related to temperature such that synchronous hatching is encouraged by high temperature within the species temperature range. This is also known to be the case with other species, *e.g. Chalcalburnus chalcoides mento* (Guldenstadt, 1772) (Hertzig and Winkler, 1986), *Ammodytes personatus* (Yamashita and Aoyama, 1985) and five species of salmonid and *Thymallus thymallus* (Linnaeus, 1758) (Humpesch, 1985).

The dry weight of *Clarias gariepinus* at hatching is not significantly affected by incubation temperature. This supports Winberg's (1987) hypothesis of equal final size of poikilotherms incubated at different temperatures. However, *C. gariepinus* incubated at lower temperatures have a higher moisture content on hatching.

Managing the transition from endogenous to exogenous feeding

In aquaculture the time at which exogenous food is first given to larvae influences their subsequent survival and growth (Kamler, 1992). It is recommended that food be offered to fish larvae when they first attain the ability to take feed, *i.e.* when they begin to swim and search for food with their yolksac still incompletely resorbed (*e.g.* Goryczko, 1968; Jones, 1972; Elliott, 1984; Applebaum, 1989). The extent to which development rate and metabolic rate in *C. gariepinus* are accelerated by temperature is not the same (*fig.* 5). The duration between first feeding and the point-of-no-return should be taken into account during the management of first feeding and especially where ponds are to be fertilized in order that natural feed organisms can develop before unfed larvae will be released.

Modelling the effect of temperature on early development

In poikilotherms development time (τ) (from fertilization to the mass appearance of a development stage) has consistently been shown to be curvilinearly related to temperature. This is also the case with *C. gariepinus*. However, no universal theory explaining the relationship between early development and temperature has yet been accepted, although the problem has been much explored. The relationship has been described using a variety of suitable expressions; *e.g.*

- an exponential model $\tau = ae^{bt}$ (Kawajiri, 1927*a*, *b*; Ryzkhov, 1976; Velsen, 1987; Kamler, 1992; Kamler *et al.*, 1994),
- a power-law model $\tau = at^{-b}$ (Humpesch, 1985; Yamashita and Aoyama, 1985; Haylor and Oyegunwa, 1993),
- a hyperbolic model $\tau = D^0_{eff}/(t - t_0)$ (Winberg, 1987; Kamler, 1992) or
- a polynomial *e.g.* $\tau = a + bt + ct^2$ (Herzig and Winkler, 1985). Development rate (V) is the inverse of τ and can be related to temperature by a linear model $V = a + bt$ (Winberg, 1987) where t = temperature (°C), e ≈ the base of natural logarithms and a, b and c are constants].

There has been a tendency to fit exponential and power-law models to data for cold-water fish development [e.g. *Salmo salar* Linnaeus, 1758, *Oncorhynchus mykiss* (Walbaum, 1792), *Oncorhynchus masu* (Brevoort, 1856), *Thymallus thymallus* (Linnaeus, 1758), *Hucho hucho* (Linnaeus, 1758), *Salvelinus fontinalis* (Michill, 1815), *Salvalinus alpinus* (Linnaeus, 1758), etc.] and linear and hyperbolic (*see* below) models to species grown in warmer waters [*e.g. Cyprinus carpio* Linnaeus, 1758, *Hypothalmichthys molitrix* (Valenciennes, 1844), *Ctenopharyngodon idella* (Valenciennes, 1844), *Vimba vimba* (Linnaeus, 1758), *Tinca tinca* (Linnaeus, 1758), etc.] (*see* Kamler, 1992 for review). The use of polynomials is discouraged (Humpesch and Elliott, 1980; Winberg, 1987).

From the practical aquaculture viewpoint a useful predictive tool is the rule of thermal sums (de Reaumur, 1735). However, although the number of day-degrees was originally thought to be independent of temperature, it has commonly been found to decrease with increasing temperature (Tatarko, 1965; Kokurewicz, 1970, 1971; Vovk, 1974; Penaz *et al.*, 1983). In the present study it was also found to be the case with the number of day degrees until hatching, first feeding and yolksac absorption in *C. gariepinus* (*fig.* 6).

In spite of the effect of temperature, the concept of day-degrees, within the optimum temperature range, is still used as a predictive tool in the hatchery management of cold-water aquaculture species where day-degrees are less affected by temperature than is the case with warm-water species. For warm-water species, especially those with a wide thermal tolerance such as *C. gariepinus*, a more useful parameter is effective day-degrees (D^0_{eff}). The duration of development to hatching, first feeding and yolksac absorption can be related hyperbolically to temperature, $\tau = D^0_{eff}/(t - t_0)$ and effective day-degrees are independent of temperature (*fig.* 6).

The same threshold temperature ($t_0 = 14.5$°C), below which development is theoretically arrested, can be estimated for *C. gariepinus* from the linear development rate-temperature relationship (shown in *figure* 7) for the period up to hatching, first feeding and yolksac absorption (see *table* 1). This closely approximates to the lower lethal temperature of 15°C estimated directly from embryo survival. Values for t_0 and the lower lethal temperature for fish species are in most cases close to one another as shown in *table* 2. Kamler *et al.* (1994) derived a theoretical threshold temperature of 17.36°C for *Clarias gariepinus*.

Therefore the effect of temperature on the early development of African catfish can be usefully modelled using the linear development rate-temperature relationship $V = a + bt$ to estimate t_0 and D^0_{eff} and the hyperbolic relationship $\tau = D^0_{eff}/(t - t_0)$ to determine development time. From the present work, t_0 is 14.5°C and D^0_{eff} is 13, 26.3 and 35.7 for hatching, first feeding and yolksac absorption respectively for *C. gariepinus*. Effective day-degrees remain independent of temperature over the range 20-35°C. As a conclusion to this study an approximate guide to development time at different constant temperatures within this range is given in *table* 3.

Table 2. – Some examples of a comparison of lower lethal temperature with theoretical threshold temperature in fish.

Species	t_0 Theoretical threshold temperature	Lower lethal temperature (°C)	Source
Salmo salar	−1.7	0.0	Ryzhkov, 1976
Coregonus albula	−0.4	0.0	Luczynski and Kirklewska, 1984
Oncorhynchus tshawytscha	1.0	3.0	Yarzhombek, 1986
Oncorhynchus masu	1.0	4.0	Kawajiri, 1927*a*
Oncorhynchus mykiss	1.3	0.0[1], 3.0[2]	[1] Zhukinskij, 1986 [2] Kawajiri, 1927*b*; Humpesch, 1985
Thymallus thymallus	2.7	3.0	Humpesch, 1985
Esox lucius	3.6	4.0	Kokurewicz, 1971
Cyprinus carpio	11.1	10.0[1], 11.5[2]	[1] Herzig and Winkler, 1986 [2] Penaz *et al.*, 1983
Ctenopharengodon idella	13.6	17.0	Zhukinskij, 1986
Hypothalmichthys molitrix	16.0	17.0	Zhukinskij, 1986

Table 3. – A guide to the influence of temperature on the early development of African catfish (*Clarias gariepinus*).

Temperature (°C)	20	22	24	26	28	30	32	34	35
Time (days) to:									
Hatching	2.36	1.73	1.37	1.13	0.96	0.84	0.74	0.67	0.63
First feeding	4.78	3.51	2.77	2.29	1.95	1.70	1.50	1.35	1.28
Yolksac absorption	6.49	4.76	3.76	3.10	2.64	2.30	2.04	1.83	1.74

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