SIZE DEPENDENT CANNIBALISM IN JUVENILE NILE TILAPIA (*Oreochromis niloticus*)

Yonas Fessehaye[1,2], Mahmoud Rezk[2], Henk Bovenhuis[3] and Hans Komen[1]

[1]Fish Culture and Fisheries Group, Wageningen Institute of Animal Sciences (WIAS), Wageningen University, P.O. Box 338, 6700 AH, Wageningen, The Netherlands

[2]The World Fish Center, Regional Research Center for Africa and West Asia, Abbassa, Abu Hamad, Sharkia, Egypt

[3]Animal Breeding and Genetics Group, Wageningen Institute of Animal Sciences (WIAS), Wageningen University, P.O. Box 338, 6700 AH, Wageningen, The Netherlands

Abstract

Linear regression model was developed to predict cannibalism in juvenile Nile tilapia (*Oreochromis niloticus*). Because oral gape of a predator largely determines maximum prey size, the model assumes that a predator could consume a fish with body depth smaller or equal to its maximum oral gape. Based on morphological measurements of oral gape (G, mm), body depth (D, mm) and weight (W, g) of 140 fish, we estimated maximum prey weight (W_{prey}) for a given predator weight ($W_{predator}$): $\text{Log}_{10}W_{prey} = 1.03\text{Log}_{10}W_{predator} - 1.13$. To verify the accuracy of this model we conducted 76 trials involving a pair of predator and prey with known weight. The data from these trials indicated that the model slightly over estimated the maximum prey weight that could be consumed by a given weight of predator. The model based on observed cannibalism is: $\text{Log}_{10}W_{prey} = 1.00\text{Log}_{10}W_{predator} - 1.18$. The approach can prove useful for predicting cannibalism between larvae of known weight distribution and can be of practical use in grading fish and hence reduce fry losses due to cannibalism. For practical considerations, the model predicts that cannibalism will not occur in juvenile populations in which the largest fish is not bigger than 13 times the smallest fish.

Introduction

Cannibalism is the act of killing and consuming the whole or major part, of an individual belonging to the same species, irrespective of its stage of development. It is a common and widespread phenomenon throughout the animal kingdom. In fishes, cannibalism occurs at various sizes or ages and extends within and between cohorts or age classes, depending on species and environmental conditions (Smith and Reay, 1991). It is usually associated with size variation, limited food availability, high population densities, limited refuge areas and light conditions (Hecht and Pienaar, 1993). Among these variables, size variation and food availability are considered the primary causes of cannibalism (Hecht and Appelbaum, 1988; Katavic *et al.*, 1989).

Because young fish exhibit allometric growth patterns and show higher growth potentials than older individuals, the intensity of cannibalism would reach a maximum in the early weeks or months of the life history when the variability of individual growth would be maximum (Melard *et al*., 1996). Heterogeneous size distributions often lead to social dominance, which in turn results in aggressive behaviour and cannibalistic responses (Hecht and Appelbaum, 1988). Cannibalism is thus facilitated by size heterogeneity, but it also affects size heterogeneity, since the smallest fish are consumed by the largest ones, and it can thus be viewed as a cause or consequence of size heterogeneity (DeAngelis *et al*., 1979; Hecht and Appelbaum, 1988; Baras, 1999).

Cannibalism among tilapia fry and fingerlings has been identified as one of the major problems by small-scale hatchery operators (Pantastico *et al.*, 1988). Despite the increasing interest in this species, cannibalism among cultured Nile tilapia has received little attention and the factors underlying it have not been investigated in detail. Silvera (1978) studied the reproduction of young tilapia in plastic swimming pools and noted that the rate of cannibalism was proportional to the length of the fingerlings involved. In addition, Smith (1989) suggested that maximum prey size was a function of cannibal gape. In this experiment we will test the hypothesis that prey size in *O. niloticus* is a function of predator oral gape and prey body depth (deepest part of the body) and that cannibalism can be predicted based on body measurements of predator and prey.

Materials and methods

Broodstock maintenance and fry rearing

Mature females and males of Nile tilapia (*Oreochromis niloticus*) produced from crosses of four local Egyptian strains were maintained at the World Fish Center, Regional Research Center for Africa and West Asia, Abbassa, Egypt. Fifty females (73.00 ± 12.82 g) and 24 males (73.78 ± 14.00 g) were selected and stocked in two 8m x 2m hapa installed in concrete walled ponds at a female to male ratio of 2:1 (25 females and 12 males in each hapa). Broodstock were allowed to spawn naturally for ten days and eggs/yolk sac fry were collected from the mouth of females. Eggs were incubated in 20L tanks at a temperature of 26 °C with strong aeration. To prevent fungal infection of eggs, water was treated with 30 ppm formalin for the first day and with 20 ppm formalin for the subsequent days till the eyed stage. After yolk sac absorption, fry were transferred to the rearing tanks and fed on commercial feed at a daily rate of 20 g/kg$^{0.8}$ supplied by hand 4 to 5 time per day.

Predator-prey model development

A predictive model for maximum prey size was developed based on measurements from 140 *O. niloticus* individuals ranging from 14 to 100 mm total body length. The fish were measured for total body weight (W) to the nearest 0.1 g, total body length (L), oral gape (G) and body depth (D) to the nearest 0.1 mm. L was measured as the distance from the tip of the snout to the end of the caudal fin; G as the maximum dorso-ventral dimension of the mouth and D as the maximum depth of fish measured dorso-ventrally just anterior to the dorsal fin. Linear regressions were developed between log-transformed values for oral gape-body weight and between log-transformed values for body depth-body weight.

Body weight/gape: $\mathrm{Log}_{10}G_{predator} = a_1 + ß_1\mathrm{Log}_{10}W_{predator}$ ………..…………….….. (1)

Body weight/body depth $\mathrm{Log}_{10}D_{prey} = a_2 + ß_2\mathrm{Log}_{10}W_{prey}$ …………….…..……......... (2)

Where $ß_1$, $ß_2$ are the regression coefficients of equation 1 & 2 respectively; a_1, a_2 intercepts of equations 1 & 2 respectively.

Because oral gape of a predator largely determines maximum prey size, we assumed that a predator could swallow a fish with a body depth smaller than or equal to its maximum oral gape. The above assumption together with the linear regressions (see equations 1 & 2) were used to develop a simple model to predict maximum prey weight for a given weight of predator. The equation for maximum prey size for a given predator size was derived by equating equations 1 & 2 and can be presented as:

$\mathrm{Log}_{10}W_{prey} = (a_1- a_2)/ß_2 + (ß_1/ß_2)\ \mathrm{Log}_{10}W_{predator}$………..………………………………… (3)

Where $ß_1$, $ß_2$, a_1, a_2 are as in equation 1 & 2

Verification of the regression model with paired fish

In order to verify the accuracy of the predictive model for maximum prey weight (W_{prey}), 76 trials involving 23 different sizes of predator (size range: 0.53 – 15.08 g) and 76 sizes of prey (size range: 0.03 – 1.20 g) were carried out in 20L aquaria at ambient temperature and light conditions (26-28°C and 12D:12L). One smaller tilapia fry of known length and weight was paired with a larger predator of known length and weight. The fish were checked daily, and if a prey had been eaten, its size was considered within the limits of predation for that particular sized predator. The predator was then given somewhat larger individual prey. If the prey had not been eaten within two days, the prey was considered too large for that particular predator. Repeating this procedure, we were able to estimate the maximum ingestible prey size as a function of predator size.

Results

Predator-prey model

The arrows in figure 1 show how to predict the maximum weight of a prey that could be preyed upon by a given weight of a predator. A given weight of a predator corresponds to certain value of oral gape, which according to our assumption is equal to the body depth of the prey which in turn corresponds to a weight of a prey. The equation for estimating the maximum prey weight from predator weight is derived by equating the regression equations in table 1 (oral gape & body depth) and given as follows:

$\mathrm{Log}_{10}W_{prey} = 1.03\mathrm{Log}_{10}W_{predator} – 1.13$………………………………….……..…… (4)

Oral gape and body depth showed strong relationship with the body weight. Summary of equations is presented in table 1.

Table 1. Equations describing some morphometric relationship in *O. niloticus* fry/fingerlings (140 fish, 14 to 100 mm).

Relationship	Equation	r^2	n
Body weight/gape	$\mathrm{Log}_{10}G_{predator} = 0.37\mathrm{Log}_{10}W_{predator} + 0.65$	0.963	140
Body weight/body depth	$\mathrm{Log}_{10}D_{prey} = 0.36\mathrm{Log}_{10}W_{prey} + 1.06$	0.981	140

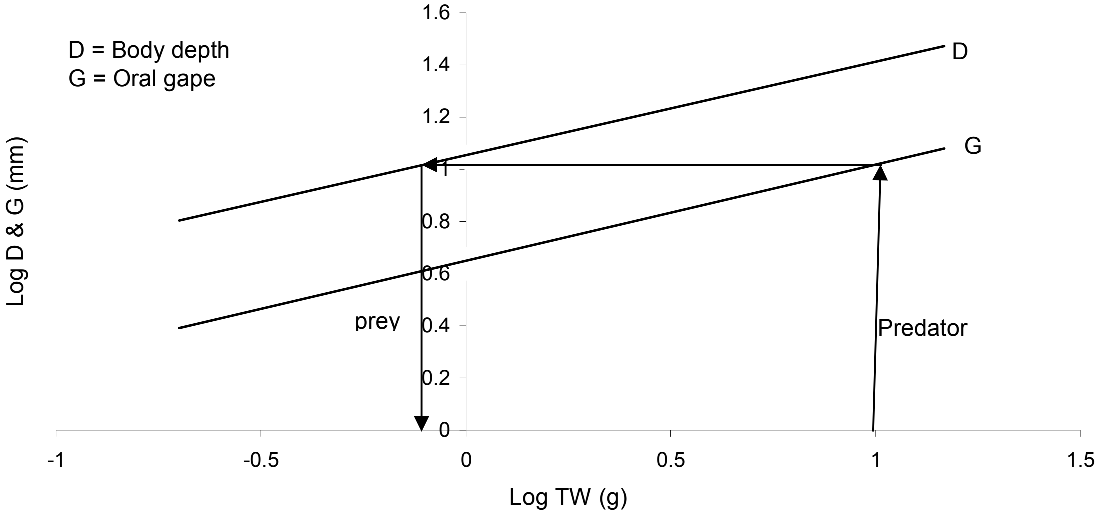

Figure1. Regression of *Oreochromis niloticus* body depth (D) and oral gape (G) to total body weight (see table 1 for equations). Procedure for estimating the maximum prey weight from predator weight is shown by the arrows.

Model verification with paired fish

In the paired fish trials, prey fish that co-existed with predator for more than two days were considered too large for that particular predator (●, figure 2). Any prey smaller than this size was considered as a size within predation range and the biggest of these preys was considered as maximum ingestible prey weight (○, see figure 2) as a function of predator weight. Figure 2 shows the relationship between predator weight and prey weight in *O. niloticus* fry and fingerlings. The solid line is the regression of the open circles (○) and represents the relationship between observed maximum prey size relative to a given predator weight as determined from the paired trials. The dot line is regression of closed circles (●) and represents the relationship between predator and prey weight as predicted from the model. Observed predation by larger *O. niloticus* on smaller ones in paired fish trials shows that there is an over estimation of prey size predicted by the model in most of the observations (see table 2). For example, a predator of about 15 g was predicted to consume a prey of about 1.2g, but it could actually consume a prey of only 0.9 g. The equation used to predict maximum prey weight for a given size predator should, therefore, be revised as $Log_{10}W_{prey} = 1.00Log_{10}W_{predator} - 1.18$.

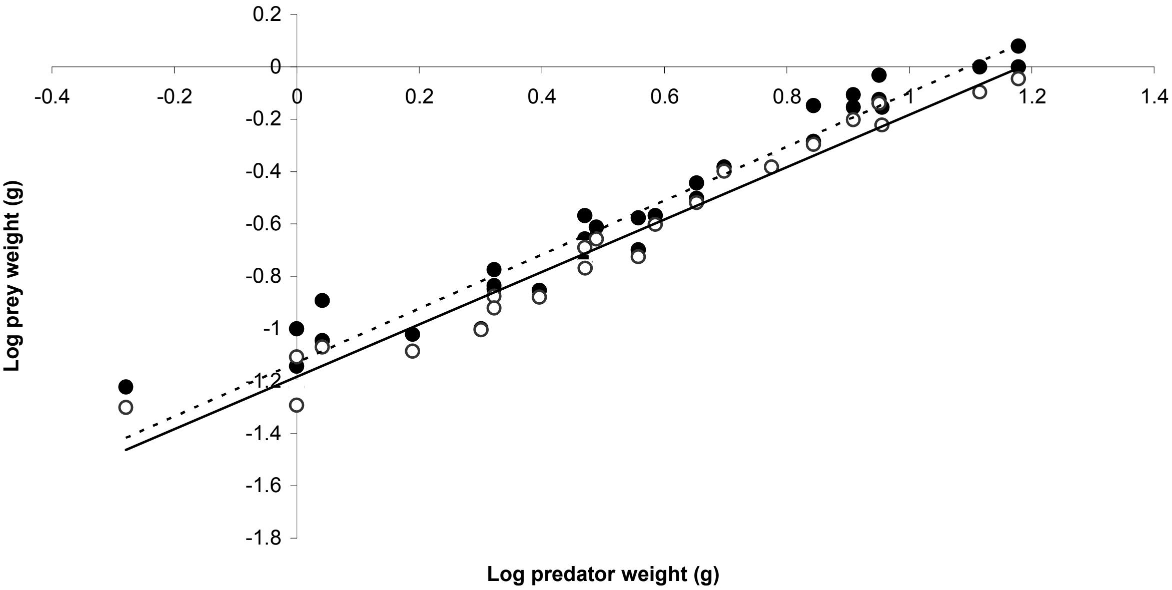

Figure 2. Relationship between predator and prey weights in *Oreochromis niloticus*. The dot line represents the size of prey predicted from our model. The solid line represents observed maximum prey relative to predator size. Open circles (o) represent observed maximum size of prey that can be consumed by a given predator and closed circles (•) represent prey sizes, which were too big for predators.

Table 2. Weight of observed and predicted prey for a give size of predator (0.5-15 g)

Weight of predator (g)	Observed weight of prey (g)	Predicted weight of prey (g)	Predator to prey weight ratio (observed)
0.53	0.05	0.04	10.52
1.00	0.08	0.07	12.82
1.10	0.09	0.08	12.94
2.96	0.20	0.23	14.49
3.09	0.22	0.24	14.02
4.50	0.30	0.35	14.85
4.99	0.40	0.39	12.50
5.96	0.42	0.47	14.36
6.98	0.51	0.55	13.79
8.10	0.63	0.64	12.90
8.94	0.73	0.71	12.31
9.02	0.60	0.71	15.04
13.04	0.80	1.04	16.30
15.08	0.90	1.21	16.80

Discussion

The notion that gape is an important constraint on prey use is wide spread in fish biology, and it is frequently cited as the explanation for correlations between prey and predator body size (Felley, 1984; Shirota, 1978). In *O. niloticus*, it was also established that maximum prey size was a function of cannibal gape (Smith, 1989). The results from this experiment are in agreement with the general fact that there is high correlation between body part dimensions and that the size of prey consumed by predators could be predicted from those measurements. However, our model overestimated the size of prey that can be consumed by a given size of predator. In a similar study of predicting prey size from predators' oral gape in *Barbus* species, De Graaf *et al.* (2003) established that actual prey length was smaller than predicted from oral gape. Contrary to the above findings, Qin and Fast (1996), reported that predators of Snakehead (*Channa striatus*) could consume prey size bigger than the size predicted from predators' mouth width.

These discrepancies between the observed and predicted prey sizes and between species might raise questions as to whether oral gape is the only feature that limits prey size. Lawrence (1957) suggested that the pharyngeal gapes for largemouth bass and bluegill are significantly smaller than oral gape. According to Sibbing (1991) the presence of pharyngeal jaws and the palatal organ, narrowing the pharyngeal slits seems more likely to restrict prey size among piscivourous Barbus than the oral gape. Contrary to this, many laboratory studies show that fish do eat prey as wide as their mouth diameter, even if pharyngeal gape is actually narrower than the size of the prey (Kisalioglu & Gibson, 1976). This was because most prey are deformable. Once the fish prey is captured by the predator it can be swallowed even if it is wider than the pharyngeal gape because its shape can be altered by actions of the pharyngeal jaw apparatus as the prey is being swallowed. Pharyngeal gape is likely to be more significant constraint when the prey has a rigid, unmalleable exoskeleton or shell (Wainwright & Richard 1995). Another possibility for the discrepancy between observed and predicted prey sizes is the way the oral gape is measured. According to Mathias and Li (1982) gape has been determined by manually spreading the jaws with forceps and measuring with vernier caliper. This method is subject to measurement error due to inability to hold fish steady, subjective interpretation of what is normal open-mouth position, and differences in technique between individuals.

Despite over estimation of maximum prey size, the model approach can prove useful for predicting cannibalism between larvae of known size distribution. The fact that the model used body weight instead of body length makes it more practical because body weight could be measured easily and with minimal disturbance to the fish.

In practice, asynchronous reproduction in tilapia leads to episodic fry production which will give rise to different hatching times and hence wide range of size which in turn could lead to sever losses of fry due to cannibalism. Size dependent cannibalism has also been found in many fish and different strategies have been suggested to mitigate the loss of fry due to cannibalism: frequent ad libitum feed supply (Katavic *et al*., 1989) and size variation reduction in combination with ample feed (Qin and Fast, 1996). However, initial size variation was more important than alternative food availability in controlling cannibalism among largemouth bass *Micropterus salmonides* (Deangelis *et al.,* 1979). Cannibalism among snakehead juveniles was unavoidable by simply providing formulated feed, if substantial size difference exists among the fish (Qin and Fast, 1996). This suggests that size distribution differences should be kept minimal. Grading of fish has been identified as a major strategy to reduce losses of fry due to cannibalism. In light of this, a predictive model that utilizes the body weight of fish could be very handy and practical in grading fish and hence reduce fry losses due to variation in size. The model predicts that cannibalism will not occur in juvenile stocks in which the largest fish is not bigger than 13 times the smallest fish.

Acknowledgement

This research was supported by The Netherlands Organization for International Cooperation in Higher Education (Nuffic) and INREF-Pond of Wageningen University.

References

Baras, E. 1999. Sibling cannibalism among juvenile vundu under controlled conditions. I. Cannibalistic behaviour, prey selection and prey size selectivity. *Journal of Fish Biology* 54: 82-105.

De Graaf, M., Van de Weerd, G.H., Osse, J.M.M., and Sibbing, F.A. 2003. Feeding performance and predation techniques among segregating piscivores in Lake Tana's

Barbus species flock (Cyprinidae; East Africa). (Chapter 5) Doctoral thesis, Experimental Zoology Group, Wageningen University, The Netherlands.

Deangelis, D.L., Cox, D.K., and Coutant, C.C. 1979. Cannibalism and size dispersal in young-of-the-year Largemouth Bass: Experiment and Model. *Ecological Modelling*, 8: 133 -148.

Felley, J.D., 1984**.** Multivariate identification of morphological environmental relationships within the Cyprinidae (Pisces). Copeia 1984: 442-455.

Hecht, T., and Appelbaum, S. 1988. Observations on intraspecific aggression and coeval sibling cannibalism by larval and juvenile *Clarias gariepinus* (Clariidae: Pisces) under controlled conditions. *J. Zool., Lond*. 214: 21- 44.

Hecht, T., and Pienaar, A. 1993. A review of cannibalism and its implications in fish larviculture. *Journal of World Aquaculture Society*, 24(2): 246-261.

Katavic, I., Jug-Dujakovic, J., and Glamuzina, B. 1989. Cannibalism as a factor affecting the survival of intensively cultured Sea Bass (*Dicentrarchus labrax*) fingerlings. *Aquaculture* 77: 135-143.

Kisalioglu, M., & Gibson, R.N. 1976. Prey 'handling time' and its importance in food selection by the spined stickleback, *Spinachia spinachia* (L.). *J. Exp.Mar.Biol.Ecol*. 25: 115-158.

Lawrence, J.M. 1957. Estimated size of various forage fishes largemouth bass can swallow. *Proc. Southeastern Assoc. Game Fish Comm.* 11: 220-226.

Mathias, J.A., and Li, S. 1984**.** Feeding habits of walleye larvae and juveniles: comparative laboratory and field studies. *Trans. Am. Fish. Soc.* 111: 722-735

Melard, C., Baras, E., Laurent, M., and Kestemont, P. 1996. Relationship between stocking density, growth, cannibalism and survival rate in intensively cultured larvae and juvenile of Perch (*Perca fluviatilis*). *Ann. Zool. Fennici* 33: 643-651

Pantastico, J.B., Dangilan, M.M.A., and Eguia, R.V. 1988. Cannibalism among different sizes of tilapia (*Oreochromis niloticus*) fry/fingerlings and the effect of natural food. p. 465-468. *In:* R.S.V. Pullin, T. Bhukaswan, K. Tonguthai and J.L. Maclean (*eds*.). The second International Symposium on Tilapia in Aquaculture. ICLARM Conference. Proceedings 15, 623 p. Department of Fisheries, Bangkok, Thailand, and International Center for Living Aquatic Resources Management, Manila, Philippines.

Qin, J., and Fast, A.W. 1996. Size and feed dependent cannibalism with juvenile snakehead *Channa striatus*. *Aquaculture* 144: 313-320.

Shirota, A. 1978. Studies on the mouth size of fish larvae. II. Specific characteristics of the upper jaw length. Bull. *Jap. Soc. Scient. Fish*. 44: 1171-1177.

Sibbing, F.A. 1991**.** Food capture and oral processing. In: Winfield IJ, Nelson JS (*eds*.). Cyprinid fishes: Systematics, biology and exploitation. Chapman and Hall, London, pp. 377- 412.

Silvera, P.A.W. 1978. Factors affecting fry production in *Sarethorodon niloticus* (Linnaeus). M.S. Thesis, Auburn University, Auburn, Alabama, USA. 40 pp

Smith, C. 1989. An investigation into the problem of conspecific predation among the fry of the Nile tilapia, *Oreochromis niloticus* (Linnaeus, 1775) in an intensive culture system. MSc thesis, Plymouth Polytechnic, 134 pp. *In:* Smith, C and Reay, P. 1991. Cannibalism in teleost fish. *Reviews in Fish Biology and Fisheries*. 1: 41-64.

Smith, C, and Reay, P. 1991. Cannibalism in teleost fish. *Reviews in Fish Biology and Fisheries* 1: 41-64.

Wainwright, P.C. & Richard, B.A. 1995. Predicting patterns of prey use from morphology of fishes. *Environmental Biology of Fishes* 44: 97-113.