

Size heterogeneity prevails over kinship in shaping cannibalism among larvae of sharptooth catfish *Clarias gariepinus*

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Abstract – Because preying on close relatives may cause a loss of inclusive fitness, cannibalistic animals are generally deemed to cannibalise non-related conspecifics preferentially to kins. Whether this basic principle also applies to fish exerting intracohort cannibalism at an early developmental stage is uncertain, and more intense cannibalism among mixed progenies might just be a consequence of greater size heterogeneity. To investigate this, progenies of sharptooth catfish of equivalent initial body weights but with contrasting size heterogeneity were reared separately or in mixed groups containing equal proportions of each progeny ($27 \pm 1^\circ\text{C}$, 12 h light:12 h night, 2.5 L aquaria, 100 or 200 fish·L⁻¹). Cannibalism was monitored on a daily basis until the end of the larval stage (3–15 days after hatching). Cannibalism in mixed groups was intermediate between those in pure progenies, and was positively correlated ($R^2 = 0.803$, $P < 0.01$) with initial size heterogeneity, irrespectively of fish origin. This finding does not exclude that catfish larvae were able to discriminate between siblings and non-related fish, but this obviously had very little influence on cannibalism. The implications of this finding are discussed, as they apply to prey selection in fast growing larvae, and aquaculture of catfish. © 2001 Ifremer/CNRS/Inra/IRD/Cemagref/Éditions scientifiques et médicales Elsevier SAS

aquaculture / cannibalism / evolution / fish / kinship

Résumé – L'hétérogénéité de taille prime sur le degré de parenté dans l'exercice du cannibalisme chez les larves du poisson-chat africain *Clarias gariepinus*. En vertu du principe de parenté et d'adéquation biologique inclusive, « *inclusive fitness* », le cannibalisme devrait théoriquement s'exercer préférentiellement vis-à-vis d'individus génétiquement éloignés, et non sur des individus apparentés. La pertinence de ce principe chez les poissons et d'autres organismes exerçant le cannibalisme dès le stade larvaire est incertaine, tant au plan des mécanismes mis en œuvre, que des avantages conférés par un ou des mécanismes inhibiteurs potentiels, et l'augmentation du cannibalisme au sein de fratries mélangées peut simplement résulter d'une plus grande hétérogénéité de tailles. Afin de tester cette hypothèse chez les larves du poisson-chat africain *Clarias gariepinus*, des familles d'âge identique et de poids moyens initiaux comparables ($p > 0,05$), mais présentant des hétérogénéités de tailles contrastées, ont été élevées ($27 \pm 1^\circ\text{C}$, 12 h jour:12 h nuit, aquariums de 2,5 L, 100 ou 200 poissons·L⁻¹) en allopatrie et en sympatrie (proportions égales) pendant le stade larvaire (3–15 jours après l'éclosion). L'impact du cannibalisme a été mesuré quotidiennement dans les différents lots expérimentaux. Les taux de cannibalisme au sein des lots mixtes sont toujours intermédiaires entre ceux des familles pures, et l'hétérogénéité initiale des tailles explique 80,3 % de la variation du cannibalisme au sein des différents lots examinés, quelle que soit la composition de ces lots. Ces résultats n'excluent pas la possibilité d'une discrimination entre proies apparentées et non-apparentées, mais indiquent clairement le rôle secondaire de ce critère par rapport à l'hétérogénéité de tailles dans l'exercice du cannibalisme. Les implications de ces résultats sont discutées en termes évolutionnistes et aquacoles. © 2001 Ifremer/CNRS/Inra/IRD/Cemagref/Éditions scientifiques et médicales Elsevier SAS

aquaculture / cannibalisme / évolution / poisson / parenté génétique

1. INTRODUCTION

Cannibalism is a frequent phenomenon in fish (Smith and Reay, 1991; Hecht and Pienaar, 1993; Baras, 1998). Its impact is usually greater among fish larvae or juveniles, which have high energetic requirements and show marked growth heterogeneity, compared to adults (Baras et al., 2000). Intracohort cannibalism can be viewed as a form of optimal foraging tactics or strategy (Dong and Polis, 1992), as it provides the cannibal with appropriate food, while minimising the risks associated with foraging, since the cannibal and its prey often have similar habitat preferences and activity rhythms. Cannibals may have greater reproductive success, either directly (Meffe and Crump, 1987) or indirectly, while feeding on non-related conspecifics, and increasing the probability that their own genes be represented in the next generation (provided cannibalism does not affect the operational sex ratio; Baras, 1999b). Conversely, preying on close relatives (sibling or offspring) causes a loss of inclusive fitness that can compromise the advantage brought about by cannibalism.

In various taxonomic groups, socially organised animals frequently show recognition/discrimination of close relatives (Jones, 1982; Holmes and Sherman, 1983; Blaustein and O'Hara, 1986; Fletcher and Michener, 1987; Waldman, 1988). Recent studies on salmonids have suggested that kin recognition was mediated by chemical cues (Quinn and Hara, 1986; Olsén, 1992; Moore et al., 1994), presumably by comparing cues to a template acquired during an imprinting process taking place at a very early age (Winberg and Olsén, 1992). With respect to cannibalism, kin recognition has been demonstrated to minimise filial cannibalism in cichlids (McKaye and Barlow, 1976), poecilids (Loekhe et al., 1982) and cyprinodontids (Loiselle, 1983).

Whether kin recognition also applies to sibling cannibalism is uncertain, especially among species exhibiting cannibalism at an early developmental stage, when their sense organs are incompletely developed (e.g. walleye *Stizostedion vitreum*, Cuff, 1980; Loadman et al., 1986; sharptooth catfish *Clarias gariepinus*, Hecht and Appelbaum, 1988; vundu catfish *Heterobranchus longifilis*, Baras, 1999a; dorada *Brycon moorei*, Baras et al., 2000; reviewed in Baras, 1998). To date, there is a single example that the isolation of families may reduce intracohort cannibalism (pike *Esox lucius*; Bry and Gillet, 1980). Additionally, the latter authors never claimed that the reduction of cannibalism originated from kin discrimination, but most probably from variable growth heterogeneity in different families. This study examined to what extent intracohort cannibalism in sharptooth catfish under controlled conditions was influenced by kinship or by other factors inherent to the progenies (initial size heterogeneity, variability of growth rates).

2. MATERIAL AND METHODS

Sibling catfish were obtained from the hormonally induced reproduction of captive breeders in the Aquaculture Station of the University of Liège (Tihange, Belgium). Females were injected with a preliminary dose of carp pituitary extract (CPE) of 0.4 mg·kg⁻¹ and a final dose of CPE of 4.0 mg·kg⁻¹, at 24 h interval (after Hogendoorn and Vismans, 1980). Two successive experiments were carried out at three week intervals. For each experiment, fertilised eggs of at least five progenies were incubated separately in Zug jars at 27 ± 1°C. All embryos hatched within less than 48 h after egg fertilisation (mean hatching time: 36 h). Hereafter, the hatching moment is considered as time 0. Three days after hatching, yolk sac resorption was almost completed. A preliminary experiment, using the methodology detailed below, indicated that sibling cannibalism in sharptooth catfish could start within the 24 h following yolk sac resorption (72–96 h after hatching; figure 1), and that the fastest growing catfish could become juveniles as early as 15 days after hatching. Therefore, the two experiments on cannibalism among catfish larvae started 3 days after hatching, and extended over 12 days only.

For each experiment, fifty randomly selected 3 day-old fish of each progeny were weighed individually (nearest 0.1 mg), and only the two progenies with the most similar initial mean body weights were retained.

Six experimental groups containing identical numbers of fish were constituted. Four groups consisted exclusively of siblings (two for each progeny), and the other two groups were constituted of fish from both progenies, in identical proportions.

The initial size heterogeneity in pure progenies was estimated from the coefficient of variation (CV) of the mean body weight of catfish, and the initial size

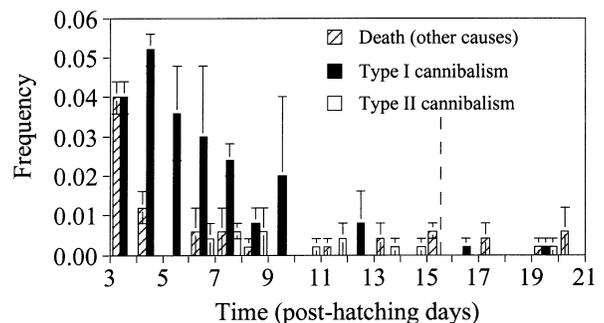


Figure 1. Dynamics of sibling cannibalism in sharptooth catfish. Type I and type II cannibalism refer to incomplete and complete prey ingestion, respectively. Values are means of replicates, and error bars stand for the difference between these. The vertical dotted line indicates the moment when the first juveniles were observed. Two groups of 250 three day-old larvae reared over 18 days in 20 × 12.5 × 10 cm enclosures, at 27 ± 1°C under 12 h light:12 h night, and fed slightly in excess. Mean body weight of three day-old larvae: 2.0 mg; coefficient of variation: 22.2%.

heterogeneity of mixed progenies was considered as mid of those of pure progenies.

All groups were stocked in small ($20 \times 12.5 \times 10$ cm) enclosures at $27.0 \pm 0.5^\circ\text{C}$ under 12 h light: 12 h night (light: circa 50 lux; night: circa 0.001 lux). Strobband and Kroon (1981) and Verreth et al. (1992) found that the stomach of sharptooth catfish was not functional during the first five or six days of exogenous feeding. Hence, over the first six days catfish larvae were fed slightly in excess with live *Artemia nauplii* that were distributed six to eight times per day during daylight hours. Over the next five days, the fish were weaned progressively, and then they received formulated feed exclusively (Nippai sea bream for carp, 55% protein).

This canvas was repeated twice on progenies spawned on 9 and 31 March, 1999 (hereafter, progenies A and B, and C and D, respectively). The initial stocking densities were 100 and 200 fish·L⁻¹, in experiments 1 and 2, respectively. Fish were counted everyday until the end of the experiments. The monitoring procedure never exceeded 10 min per enclosure. Dead fish were examined under the dissection microscope to determine the cause of their death. Fish heads or small tail-off dead fish were considered as victims of incomplete (type I) cannibalism, whereas missing fish were presumed to have succumbed to complete

(type II) cannibalism (Hecht and Appelbaum, 1988). At the end of the experiment, 50 randomly selected fish were weighed (nearest 0.1 mg) to determine growth rates and size heterogeneity.

Contingency table analyses were used to compare cannibalism and mortality (from causes other than cannibalism) between replicates and treatments. Body weights at the start and end of each experiment were compared with one-way analyses of variance and Fisher PLSD (least square difference) comparison of means. Equality of variance *F*-tests for unpaired comparisons were used to compare size heterogeneity between groups (after all mean body weights were set equal to 1.0). Regression analyses and Mann-Whitney *U*-test (a non parametric statistical procedure) were also used when appropriate. Null hypotheses were rejected at $P < 0.05$.

3. RESULTS

In each experiment, the mean body weights of 3 day-old catfish larvae did not differ significantly between progenies (table I). Fish in the second experiment were slightly smaller than those in the first experiment, presumably because they were spawned by younger females, but this did not influence the

Table I. Effect of parental origin on cannibalism, mortality (from causes other than cannibalism), survival and growth of sharptooth catfish larvae.

Experiment 1	A1	A2	B1	B2	[A + B]1	[A + B]2
Day 3 ($N = 250$)						
Mean body weight (mg)	2.12 ^a	2.12 ^a	1.98 ^a	1.98 ^a	2.05	2.05
CV (%)	11.03 ^a	11.03 ^a	21.12 ^b	21.12 ^b	16.07	16.07
Day 15						
Mean body weight (mg)	29.5 ^b	25.4 ^a	28.4 ^{ab}	38.6 ^d	34.2 ^c	25.3 ^a
CV (%)	15.03 ^a	13.88 ^a	25.55 ^c	22.72 ^{bc}	17.27 ^{ab}	22.13 ^{bc}
Survival (%)	55.6 ^c	74.8 ^e	60.8 ^{cd}	8.8 ^a	39.6 ^b	64.8 ^d
Type I cannibalism (%)	5.6 ^a	3.6 ^a	15.2 ^b	28.8 ^c	10.8 ^b	4.4 ^a
Type II cannibalism (%)	3.6 ^{abc}	0.8 ^a	2.8 ^{abc}	4.8 ^c	4.4 ^{bc}	1.6 ^{ab}
Mortality (other causes, %)	35.2 ^{bc}	20.4 ^a	21.2 ^a	57.6 ^d	45.2 ^c	29.2 ^{ab}
Experiment 2	C1	C2	D1	D2	[C + D]1	[C + D]2
Day 3 ($N = 500$)						
Mean body weight (mg)		1.54 ^a		1.60 ^a		1.57
CV (%)		9.21 ^a		17.43 ^a		13.32
Day 15						
Mean body weight (mg)	13.5 ^a	17.8 ^c	16.5 ^{bc}	14.4 ^{ab}	15.7 ^{bc}	21.6 ^d
CV (%)	23.51 ^a	23.55 ^a	21.58 ^a	24.48 ^a	26.11 ^a	22.87 ^a
Survival (%)	84.0 ^a	84.8 ^a	63.4 ^b	67.0 ^b	69.4 ^b	65.6 ^b
Type I cannibalism (%)	3.8 ^a	4.0 ^a	13.0 ^b	12.0 ^b	9.0 ^b	9.8 ^b
Type II cannibalism (%)	1.0 ^{ab}	0.4 ^a	2.6 ^{bc}	3.6 ^c	1.4 ^{ab}	1.0 ^{ab}
Mortality (other causes, %)	11.2 ^a	10.8 ^a	21.0 ^{bc}	17.4 ^b	20.2 ^{bc}	23.6 ^c

Experiments were done on larvae 3–15 days after hatching; $27.0 \pm 1.0^\circ\text{C}$, 12 h light: 12 h night, feeding slightly in excess. Progenies A and B, and C and D were spawned simultaneously (9 and 31 March, 1999, respectively). *N* is the initial number of fish in each group, and *CV* is the coefficient of variation of the mean body weight. The mean initial body weights and *CV*s in the mixed groups were considered as mid of the two progenies. Type I and type II cannibalism refer to the incomplete and complete ingestion of prey, respectively. For each line of the table, values sharing at least one common superscript do not differ significantly, whereas other comparisons differ at $P < 0.05$ (contingency table analyses for cannibalism, mortality and survival rates, the fisher *F*-test comparisons of means for body weights, equality of variance *F*-tests for *CV*).

degree of yolk sac resorption, and both experiments started with fish at a similar developmental stage. In each experiment, however, there was a significant difference between the size heterogeneities of pure progenies (CV of 11.03–21.12, and 9.21–17.43% in experiments 1 and 2, respectively).

Except for three groups in the first experiment (A1, B2 and [A + B]1), where a bacterial outbreak (*Aeromonas* and *Citrobacter* sp.) was observed from day 9 to day 12 (mortality of 35.2 to 57.6%), mortality from causes other than cannibalism ranged from 10.8 to 29.2%. Most fish deaths took place 4 to 8 days after hatching, and concerned small larvae having exhausted their yolk reserves, but showing no growth in length, suggesting they died out of hunger. The survival rates among groups not affected by pathologies ranged from 60.8 to 84.8%, and were strongly dependent on the intensity of cannibalism. Type I cannibalism was observed as early as four days after hatching, whereas type II cannibalism was not consistently observed before larvae were 10–12 days old. The respective contributions of the two types of cannibalism to the overall losses to cannibalism were 81.9 and 18.1%. On average, cannibalism (both types combined) was more intense at low than at high stocking density (respectively 14.4 versus 10.3% of initial stock over 12 days, Mann-Whitney U -test: $U = 15.5$, $U' = 20.5$, $P = 0.6879$), but opposite trends were observed while skipping the groups where there was a pathological outbreak (respectively 9.4 versus 10.3%, Mann-Whitney U -test: $U = 8.5$, $U' = 9.5$, $P = 0.8964$). This clearly suggests that stocking density had a minor impact on the dynamics of cannibalism among larvae of sharptooth catfish within the range of stocking density evaluated here.

At both stocking densities, the rate of cannibalism in mixed groups was intermediate between those in pure progenies (table I). The lowest and highest rates of cannibalism were consistently observed in the progenies with the lowest and highest initial size heterogeneity, respectively (figure 2). As in the feasibility experiment (figure 1), type I cannibalism was observed less than 4 days after hatching among groups with a size heterogeneity > 15%, whereas it started later in the groups with a lower heterogeneity (5–6 and 8 days post-hatch for CVs of 11–13% and 9%, respectively). Fish origin did not influence significantly growth and growth heterogeneity (table I), except for the three groups where pathologies emerged, and where survivors showed faster growth than in other groups (23.4 versus 20.1% per day, respectively; Mann-Whitney U -test, $U = 0$, $U' = 27$, $P = 0.0126$).

4. DISCUSSION

In the present study, cannibalism among sharptooth catfish started earlier than reported by Hecht and Appelbaum (1988; < 1 versus 3.5 days after the start of exogenous feeding), but not earlier than in vundu catfish reared under the same experimental conditions

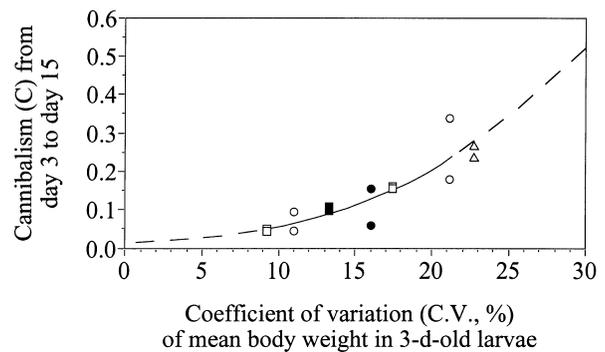


Figure 2. Relationship between the rate of cannibalism among larvae of sharptooth catfish and their size heterogeneity just after yolk sac resorption (3 day-old fish). $\text{Log}_e(C(1-C)^{-1}) = -4.3157 [0.3449] + 0.1468 [0.0210] CV$ ($r^2 = 0.803$, $df = 13$, $F = 48.78$, $P < 0.0001$), where C is the proportion of fish dying out of cannibalism, CV is the initial size heterogeneity (coefficient of variation of initial body weight), and values between brackets in the regression model are standard errors of coefficients. Open and closed symbols on the graph refer to pure and mixed progenies, respectively. Circles and squares refer to experiments 1 and 2 in table I (initial stocking densities of 100 and 200 fish·L⁻¹, respectively). Triangles represent the rates of cannibalism in the feasibility experiment (100 fish·L⁻¹; figure 1).

(Baras, 1999a). The early developmental rates of sharptooth and vundu catfish are most similar (Legendre and Teugels, 1991), and all bones necessary to suck prey in and exert type I cannibalism, are present at this age (see Vandewalle et al., 1997 for vundu). However, confinement and population density were greater here than in Hecht and Appelbaum's studies. Because type I cannibalism is chiefly tactile in sharptooth catfish (Hecht and Appelbaum, 1988), these environmental conditions may have promoted more frequent encounters between siblings, resulting in greater risks of cannibalism (Haylor, 1992; Kaiser et al., 1995), thereby promoting its earlier emergence. However, in view of the contrasted results between the progenies examined here, we suggest that this discrepancy essentially originated from initial size heterogeneity.

The effect of size heterogeneity on cannibalism has been documented on many occasions, but almost exclusively within the context of type II cannibalism at the juvenile stage (e.g. Atlantic cod *Gadus morhua*, Folkvord and Otterå, 1993; reviewed in Baras, 1998). Contrary to some species which can consume siblings of equal size or slightly bigger than themselves (e.g. walleye, Cuff, 1980; dorada, Baras et al., 2000), the exercise of type I cannibalism in sharptooth catfish requires the prey to be slightly smaller than the cannibal (mean and maximum prey to predator length ratios of 0.780 and 0.908; corresponding weight ratios of 0.488 and 0.757, respectively; recalculated from the data presented by Hecht and Appelbaum, 1988). A high initial size heterogeneity would enable some larvae to exert cannibalism as soon as the first day of exogenous feeding, whereas the emergence of canni

balism would be delayed in groups with a lower size heterogeneity, the duration of this delay being a function of the extent of growth heterogeneity. Each progeny of sharptooth catfish was found to contain larvae unable to feed, resting on the bottom and eventually dying out of hunger. Because sharptooth catfish essentially forage on the bottom ('helicopter stance', Hecht and Appelbaum, 1988), some of these starving larvae may have become privileged prey for cannibals, causing cannibalism to emerge anyway, regardless of initial size heterogeneity and provision of alternative food resources. However, the postponed emergence of cannibalism would decrease its overall impact, accounting for the relationship illustrated in figure 2, and possibly for the variability between the rates of early cannibalism reported in different studies on sharptooth catfish where initial size heterogeneity was unknown (Aboul-Ela et al., 1973; de Kimpe and Micha, 1974; van der Waal, 1978; Hecht and Appelbaum, 1988; Haylor, 1992; Kaiser et al., 1995).

In contrast to the findings of Bry and Gillet (1980) for pike, cannibalism among larvae of sharptooth catfish was not enhanced when progenies were mixed. We may not strictly exclude the possibility that catfish larvae were able to discriminate between siblings and non-related fish, but this obviously had very little influence on cannibalism, and clearly fell second to initial size heterogeneity. This absence of kinship effect in young catfish larvae can be functionally accounted for by incomplete development of sense organs at the time cannibalism starts (Legendre and Teugels, 1991). It is also possible that the high density of prey may have confused older larvae with more developed senses and greater capacities of discriminating between kins and non-kins, but this remains to be demonstrated experimentally. Additionally, the fact of exclusively cannibalising prey other than siblings may prove a wrong tactic in fast growing fish with huge ingestion capacities. In food-limited environments, this behaviour should normally involve longer foraging, greater energetic expenditures, reduced growth and greater predation hazards. Also a sibling 'spared' at a time, and growing faster for a couple of days, could eventually become a cannibal and consume its saviour when alternative food resources become scarce. In this context, the immediate increase of inclusive fitness for not cannibalising a sibling would probably be less than the loss of fitness incurred later. Hence, we suggest that an inhibitory mechanism preventing young fish from cannibalising siblings, may have been counterselected in sharptooth catfish, and probably in other fish species with high fecundity, for which the penalty of eating siblings is less than for those with low fecundity (see also Baras et al., 2000). This also goes along with the hypotheses put forward by Alexander (1974) and Polis (1981), that "the production of numerous expandable offspring, storing energy for their kin and eventually being cannibalised, is an alternative to producing fewer eggs, each containing larger amounts of nutrients".

Type I cannibalism emerges early in catfish development, requires little predator to prey ratio, and can hardly be mitigated by hand sorting or mechanical size grading (Hecht and Pienaar, 1993). Zootechnical adjustments affecting ambient light, day length, stocking density, food type and distribution can substantially improve survival rates (e.g. Hogendoorn, 1980; Uys and Hecht, 1985; Hecht and Appelbaum, 1988; Haylor, 1992; Kaiser et al., 1995; Hecht, 1996). The relationship between initial size heterogeneity and cannibalism in catfish larvae demonstrates that initial size heterogeneity also is a limiting factor. As a corollary, mixing progenies from different breeders may not jeopardise survival and production, provided larvae are homogenous in size and developmental interval. However, one should avoid mixing progenies with contrasted hatching times, or progenies from females of different sizes (there is a correlation between female size, egg size and size at hatching). Similarly, there should be an increasing effort towards the selection of breeders producing progenies with low size heterogeneity and marked hatching synchrony.

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References

- Aboul-Ela, I., Amer, F.I., El Bolock, A.R., 1973. Studies on spawning behaviour of *Clarias lazera* Cuv. et Val. in the farms of the A.R. Egypt. Bull. Zool. Soc. Egypt 25, 25–33.
- Alexander, R.D., 1974. The evolution of social behaviour. Ann. Rev. Ecol. Syst. 5, 325–383.
- Baras, É., 1998. Bases biologiques du cannibalisme chez les poissons. Cah. Éthol. 18, 53–98.
- Baras, É., 1999a. Sibling cannibalism among juvenile vundu under controlled conditions. I. Cannibalistic behaviour, prey selection and prey size selectivity. J. Fish Biol. 54, 82–105.
- Baras, É., 1999b. Functional implications of early sexual growth dimorphism in vundu. J. Fish Biol. 54, 119–124.
- Baras, É., Ndao, M., Maxi, M.Y.J., Jeandrain, D., Thomé, J.P., Vandewalle, P., Mélard, C., 2000. Sibling cannibalism in dorada under experimental conditions. I. Ontogeny, dynamics, bioenergetics of cannibalism and prey size selectivity. J. Fish Biol. 57, 1001–1020.
- Blaustein, A.R., O'Hara, R.K., 1986. Kin recognition in tadpoles. Sci. Am. 254, 90–96.
- Bry, C., Gillet, C., 1980. Réduction du cannibalisme précoce chez le brochet (*Esox lucius*) par isolement des fratries. Bull. Fr. Piscic. 277, 142–153.

- Cuff, W.R., 1980. Behavioral aspects of cannibalism in larval walleye, *Stizostedion vitreum*. Can. J. Zool. 58, 1504–1507.
- de Kimpe, P., Micha, J.C., 1974. First guidelines for the culture of *Clarias lazera* in Central Africa. Aquaculture 4, 227–248.
- Dong, Q., Polis, G.A., 1992. The dynamics of cannibalistic populations: a foraging perspective. In: Elgar, M.A., Crespi, B.J. (Eds.), Cannibalism: ecology and evolution among diverse taxa. Oxford Science Publications, Oxford, pp. 13–37.
- Fletcher, D.J., Michener, C.D., 1987. Kin recognition in animals. Wiley, Chichester.
- Folkvord, A., Otterå, H., 1993. Effects of initial size distribution, day length and feeding frequency on growth, survival and cannibalism in juvenile Atlantic cod (*Gadus morhua* L.). Aquaculture 114, 243–260.
- Haylor, G.S., 1992. Controlled hatchery production of *Clarias gariepinus* (Burchell): growth and survival of larvae at high stocking density. Aquac. Fish. Manage. 23, 303–314.
- Hecht, T., 1996. An alternative life history approach to the nutrition and feeding of Siluroidei larvae and early juveniles. In: Legendre, M., Proteau, J.-P. (Eds.), The biology and culture of catfishes, Aquatic Living Resources volume 9, special issue. Éditions scientifiques et médicales Elsevier, Paris, pp. 121–133.
- Hecht, T., Appelbaum, S., 1988. Observations on intraspecific aggression and coeval sibling cannibalism by larval and juvenile *Clarias gariepinus* (Clariidae: Pisces) under controlled conditions. J. Zool. London 214, 21–44.
- Hecht, T., Pienaar, A.G., 1993. A review of cannibalism and its implication in fish larviculture. J. World Aquac. Soc. 24, 246–261.
- Hogendoorn, H., 1980. Controlled propagation of the African catfish *Clarias lazera* (Cuv. et Val.). III. Feeding and growth of fry. Aquaculture 21, 233–241.
- Hogendoorn, H., Vismans, M.M., 1980. Controlled propagation of the African catfish *Clarias lazera* (Cuv. et Val.). II. Artificial reproduction. Aquaculture 21, 39–53.
- Holmes, W.G., Sherman, P.W., 1983. Kin recognition in animals. Am. Sci. 71, 46–55.
- Jones, J.S., 1982. Of cannibals and kins. Nature 299, 202–203.
- Kaiser, H., Weyl, O., Hecht, T., 1995. The effect of stocking density on growth, survival and agonistic behaviour of African catfish. Aquac. Int. 3, 217–225.
- Legendre, M., Teugels, G.G., 1991. Développement et tolérance à la température des oeufs de *Heterobranchus longifilis*, et comparaison des développements larvaires de *H. longifilis* et de *Clarias gariepinus* (Teleostei, Clariidae). Aquat. Living Resour. 4, 227–240.
- Loadman, N.L., Moodie, G.E.E., Mathias, J.A., 1986. Significance of cannibalism in larval walleye (*Stizostedion vitreum*). Can. J. Fish. Aquat. Sci. 43, 613–618.
- Loekhe, D.M., Madison, D.M., Christian, J.J., 1982. Time dependency and kin recognition of cannibalistic behaviour among poeciliid fishes. Behav. Neur. Biol. 35, 315–318.
- Loiselle, P.V., 1983. Filial cannibalism and egg recognition by males of the primitively custodial teleost *Cyprinodon macularius californiensis* Girard (Atherinomorpha: Cyprinodontidae). Ethol. Sociobiol. 4, 1–9.
- McKaye, K.R., Barlow, G.W., 1976. Chemical recognition of young by the midas cichlid, *Cichlasoma citrinellum*. Copeia 1976, 276–282.
- Meffe, G.K., Crump, M.L., 1987. Possible growth and reproductive benefits of cannibalism in the mosquito fish. Am. Nat. 129, 203–212.
- Moore, A., Ive, M.J., Kell, L.T., 1994. The role of urine in sibling recognition in Atlantic salmon *Salmo salar* (L.). Proc. R. Soc. Lond. Ser. B Biol. Sci. 255, 173–180.
- Olsén, K.H., 1992. Kin recognition in fish mediated by chemical cues. In: Hara, T.J. (Ed.), Fish chemoreception. Chapman and Hall, London, pp. 229–248.
- Polis, G.A., 1981. The evolution and dynamic of intraspecific predation. Ann. Rev. Ecol. Syst. 12, 225–251.
- Quinn, T.P., Hara, T.J., 1986. Sibling recognition and olfactory sensitivity in juvenile coho salmon (*Oncorhynchus kisutch*). Can. J. Zool. 64, 921–925.
- Smith, C., Reay, P., 1991. Cannibalism in teleost fishes. Rev. Fish Biol. Fish. 1, 41–64.
- Stroband, H.W.J., Kroon, A.G., 1981. The development of the stomach in *Clarias lazera* and the intestinal absorption of protein macromolecules. Cell Tissue Res. 215, 387–415.
- Uys, W., Hecht, T., 1985. Evaluation and preparation of a suitable dry feed and optimal feeding frequency for primary nursing of *Clarias gariepinus* larvae (Pisces, Clariidae). Aquaculture 47, 173–183.
- van der Waal, B.C.W., 1978. Some breeding and production experiments with *Clarias gariepinus* (Burchell) in the Transvaal. S. Afr. J. Wildl. Res. 8, 13–18.
- Vandewalle, P., Gluckmann, I., Baras, É., Huriaux, F., Focant, B., 1997. Postembryonic development of the cephalic region in *Heterobranchus longifilis*. J. Fish Biol. 50, 227–253.
- Verreth, J., Torrelee, E., Spazier, E., van der Sluizen, A., Rombout, J.H.W.M., Booms, R., Segner, H., 1992. The development of a functional digestive system in the African catfish *Clarias gariepinus* (Burchell). J. World Aquac. Soc. 23, 286–298.
- Waldman, B., 1988. The ecology of kin recognition. Ann. Rev. Ecol. Syst. 19, 545–571.
- Winberg, S., Olsén, K.H., 1992. The influence of rearing conditions on the sibling odour preference of juvenile Arctic charr *Salvelinus alpinus* (L.). Anim. Behav. 44, 137–164.