A STUDY OF COEVAL SIBLING CANNIBALISM IN LARVAL AND JUVENILE FISHES AND ITS CONTROL UNDER CULTURE CONDITIONS

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CONTENTS

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ABSTRACT

The primary objective of this study was to examine environmental parameters thought to affect cannibalism in certain fish species. It was found that environmental, behavioural, genetic and physiological factors all affect cannibalism in the species exhibiting the phenomenon. The diversity of factors influencing cannibalism served to illustrate the complexity of this behaviour pattern. Feeding to satiation was found to suppress cannibalism in catfish, trout and koi carp. High population densities were found to increase the rate of cannibalism, thereby acting as a population regulation mechanism for catfish, trout and the common and koi carps. Live food, as compared with dry pelletized feed was found to significantly suppress cannibalistic aggression. Catfish grown in total darkness, provided with refuges and living in turbid conditions were found to exhibit lowered cannibalistic and territorial aggression.

Various lines of evidence suggested that cannibalism has a genetic basis, as was shown by the differences in cannibalistic behaviour of the two strains of _Cyprinus carpio_, viz. common and koi carp, with cannibalism being higher in the latter. This finding substantiates the hypothesis that cannibalism is genetically controlled and therefore open to evolutionary change. It is concluded that cannibalism is adaptive in times of food limitation, but that it is merely a by-product of normal feeding behaviour when food is abundant. Since cannibalism is advantageous and thus adaptive, the question arises as to whether selection is occurring at the individual or the population level (or both). It was concluded that it is acting at the individual level, and that any benefits accruing at the population level

were simply the effect of the initial cause, viz. individual selection.

One of the aims of this study was to determine whether cannibalistic tendencies in fish are influenced by differing life history style trajectories. Based on the results of this study it is hypothesized that cannibalism is an r-selected trait.

With the understanding gained from the knowledge of the fundamental principles governing cannibalism, certain recommendations for its control in fish culture could be made. It is, however, imperative that further intensive studies be carried out to understand more fully this complex subject. General "rules" for regulating cannibalism could be helpful for any given cannibalistic species. However, in considering the differing life-history styles of each species, it becomes evident that species-specific guidelines need to be worked out. Until then, any suggestions for cannibalistic control offered to the aquaculturist can only serve as unrefined tools.

Chapter 1

INTRODUCTION

> **"Wherever man has achieved the power of voluntarily guiding a natural phenomenon in a certain direction, he has owed it to his understanding of the chain of causes which formed it"**
>
> **Konrad Lorenz (1966)**

Despite the wide occurrence of cannibalism in all its various forms throughout the animal kingdom (Fox 1975a,b; Polis 1981; Dominey and Blumer 1984; Polis and Myers 1985; see also Tables 1 and 2), there exists only a sparse knowledge and understanding of the phenomenon.

There are a number of factors which indicate that cannibalism has a significant impact on individuals and populations under feral and captive situations. Most fish larvae appear to be carnivorous (Polis 1981). This would at least suggest a propensity towards opportunistic cannibalism. Also, according to Davis (1985), few situations have been documented where cannibalism is absent in predatory fish, and in addition Hunter and Kimbrell (1980b) also report that cannibalism is linked to piscivory. A further factor is that losses through sibling cannibalism can range between 15-90% of the population in certain species of fish under culture conditions (Hecht and Appelbaum 1988; pers. observ.).

Our imperfect understanding of the phenomenon, coupled with the high incidence of cannibalism under natural and captive conditions were the primary motivations for initiating this study. There are a number of possible reasons why so few studies

Table 1. The range of fish displaying cannibalism under culture conditions as reported to date in the literature, revealing the wide occurrence of this phenomenon in the class Pisces.

SCIENTIFIC NAME	**COMMON NAME**	**FAMILY**	**REFERENCES**
1. *Clarias gariepinus*	African sharptooth catfish	Clariidae	Wait 1987; Hecht & Appelabaum 1988; this study
2. *Centropomus unidecimalis*	common snook	Centropomidae	Shafland & Kochl 1980
3. *Oncorhyncus mykiss*	rainbow trout	Salmonidae	Shirahata 1964; Masaila *et al.* 1981; this study
4. *Stizostedion vitreum*	walleye	Percidae	Cuff 1977,1980; Li & Mathias 1982; Sifa & Mathias 1982; Giles *et al.* 1986; Hokanson & Lien 1986; Loadman *et al.* 1986; McIntyre *et al.* 1987
5. *Lates calcarifer*	barramundi/striped seabass	Centropomidae	MacKinnon 1985
6. *Oreochromis mossambicus*	mocambique tilapia	Cichlidae	Uchida & King 1962; Berrios-Hernandez 1983; Macintosh & De Silva 1984
7. *Micropterus salmoides*	largemouth bass	Centrarchidae	Cooper 1936; Coetzee 1976
8. *Morone saxitilis*	striped bass	Percichthyidae	Braid & Shell 1981 Paller & Lewis 1987
9. *Cynoscion nebulosus*	spotted sea trout	Scianidae	Tucker 1988
10. *Scomber japonicus*	Pacific mackerel	Scombridae	Hunter & Kimbrell 1980a,b
11. *Rhamdia sapo*	S. American catfish	Pimelodidae	Luchini & Salas 1985
12. *Gadus morhua*	cod	Gadidae	Oiestad 1985 Oiestad *et al.* 1985
13. *Anguilla anguilla*	eel	Anguillidae	Wattendorf 1979 Degani & Levanon 1983
14. *Dicentrarchus labrax*	sea bass	Percichthyidae	Katavic *et al.* 1989
15. *Anarhichas lupus*	wolffish	Anarhichadidae	Moksness *et al.* 1989
16. *Cyprinus carpio*	common & koi carp	Cyprinidae	Van Damme *et al.* 1989; this study

Table 2. The range of fish displaying cannibalism under feral conditions as reported in the literature to date, revealing the wide occurrence of this phenomenon.

SCIENTIFIC NAME	COMMON NAME	FAMILY	REFERENCES
1. *Odontaspis carcharias*	ragged-tooth shark	Odontaspididae	McKay 1987
2. *Theragra chalcogramma*	walleye pollock	Gadidae	Bakkala *et al.* 1987
3. *Engraulis capensis*	anchovy	Engraulidae	Brownell 1985 Alheit 1987 Valdes *et al.* 1987
4. *Histrio histrio*	sargassum fish	Antennariidae	Blankley 1988
5. *Scombroids*			Mayo 1973 in: Hunter & Kimbrell 1980a Malhotra & Munshi 1984
6. *Perca fluviatilis*	European perch	Percidae	Holcik 1977
7. *Lates calcarifer*	barramundi	Centropomidae	Davis 1985
8. *Merluccius capensis* & *M. paradoxus*	hake	Merlucciidae	Butterworth 1988 Gasyukov & Dorovskikh 1988 Payne *et al*. 1987
9. *Raja* spp. (Batoidei)	rays	Rajidae	Ajayi 1982
10. *Stegastes rectifraenum*	Cortez damsel fish	Pomacentridae	Petersen & Marchetti 1989
11. *Poecilia reticulata*	guppy	Poeciliidae	Anon. 1972
12. *Cottus gobio*	river bullhead	Cottidae	Marconato & Bisazza 1988
13. *Poeciliopsis occidentalis*	Sonoran topminnow	Poeciliidae	Meffe 1984
14. *Salvelinus malma miyabei*	charr	Salmonidae	Maekawa & Hino 1987

on cannibalism have been conducted. Embarking on such a study under natural conditions is obviously very difficult, since this would require many hours of underwater observation in order to achieve a quantifiable result. This is not always logistically or practically possible. One of the possible reasons why in-depth studies of cannibalism in fish under captive conditions have been neglected is that the development of aquaculture technology has been focussed developing artificial propagation techniques and adequate nutrition. Now that these areas have, to a great extent, been dealt with for the most important culture species, research can be directed to some of the finer details such as the phenomenon of cannibalism in various species, especially its causes, effects and control.

Fox (1975a), Polis (1981) and Hecht (unpub.) define cannibalism as intraspecific predation or the process of killing and eating individuals of the same species. The limits of cannibalism within the context of this thesis are as follows: Any individual which caused the death of a conspecific, and partially consumed that conspecific, was deemed to be a cannibal. Simply causing the death of a conspecific was seen to be purely a consequence of territorial aggression or possibly a stress related phenomenon (ie. an artifact of unnatural captive conditions).

There are many different kinds of cannibalism in the animal kingdom viz. oophagy, intra-uterine oophagy, intra-uterine adelphophagy, filial cannibalism, heterocannibalism, cannibalism of progeny by their parents (and <u>vice versa</u>), sibling cannibalism and cannibalism by coeval siblings. For definitions of the different forms of cannibalism see Appendix I.

Historically many investigators have tended to dismiss cannibalism among captive animals as unnatural behaviour, ie. artifacts of laboratory conditions, or to be of minor significance when observed in natural populations (Kipling and Frost 1970). Intraspecific predation or cannibalism in its many forms is , however, common and not an aberrant behaviour limited to confined or highly stressed populations (Fox 1975a; Polis 1981), but is a normal response to many environmental factors. At present the literature reveals that freshwater organisms constitute the largest known group of cannibalistic animals (Fox 1975a,b), and of these a great many are fishes. Cannibalism has been described as being widespread among viviparous (primarily tropical) fishes (Anon. 1972; Thibault 1974). Zaret (1977) lists numerous common temperate zone species as being cannibalistic, also stating that cannibalism is wide-spread among marine fishes. In the context of the findings of Zaret (op. cit.) and Valerio and Barlow (1986), Dominey and Blumer (1984) concluded that "cannibalism undoubtedly occurs in most fishes and the absence of cannibalism in a group should be considered exceptional". Polis (1981) in a review of cannibalism observed that it is a major factor in the biology of many species and may influence population structure, life history, competition for mates and resources, and behaviour. He reports 1300 species throughout the animal kingdom displaying cannibalism. Amongst the vertebrates it has been recorded in all groups, including man.

Thus, there is much evidence that cannibalism is not only common but is an important factor in the ecology of many species. It appears certain that as more research is initiated in this direction, the body of evidence will grow and further highlight the ecological significance of cannibalism. This is borne out by Wilson (1975) who noted that there appears to be a correlation between the time spent studying a species and the number of observations of intraspecific predation. He was impressed by the frequency of cannibalism and killing in the animal kingdom. It is probably only because little attention has been paid to the phenomenon that early ethologists did not realize the ubiquity of cannibalism. For instance, both Eibl-Eibesfelt (1961) and Lorenz (1966) insisted that intraspecific killing and predation are rare events in nature. They stressed that animal fighting is gentlemanly and universally restrained by ritual, bluff and non-fatal violence. Lorenz (1966, p.38) states that he "never found that the aim of aggression was the extermination of the fellow members of the species concerned". In the Selfish Gene, Dawkins (1976), suggests that cannibalism is relatively rare. Wilson (1975) and Dawkins (op. cit.) however, point out that early ethologists were wrong on many points. The question, therefore, is that if such veritable giants in ethology were wrong because of scanty evidence, could it be that conclusions with respect to cannibalism, based on equally scanty evidence, need to be re-evaluated in the light of more evidence ?

Many factors appear to cause cannibalism. In considering these causes, it appears that they fall into one of four categories. It is important to note that these factors are often interlinked in some way, eg. behavioural and physiological factors are to some extent genetically based. These categories are as follows: genetic, behavioural, environmental and physiological. Within the genetic category, many of these influencing factors appear to be linked to the phenomenon of size variation within coeval siblings. Many authors consider the degree of size variation within the population to be an important factor influencing the rate of cannibalism (MacKinnon 1985; Valerio and Barlow 1986). De Angelis et al. (1979) found that size variations are caused by genotypic differences which dictate differing individual growth rates. The possibility that initial egg size differences within a clutch of tadpoles (Scaphiopus spp.) may for example, increase the probability that larger newborn animals will become cannibals was proposed by Pomeroy (see Polis 1981).

The second category of factors are behavioural. Brown (1957) concluded that behavioural dominance was the cause of size variation, which in turn has been shown to be a cause of cannibalism. This phenomenon of social dominance results in hierarchical population structures and movements. There appears to be somewhat of a "chicken and egg" situation here, ie. which came first, social dominance leading to a larger size, or vice versa (or possibly elements of both). Whatever the case may be, a larger initial size and a genetically determined propensity towards increased relative aggression would lead to a learned cannibalistic response, as was found by Giles et al. (1986) working on laboratory populations of larval walleye (Stizostedion vitreum). Particular behavioural patterns of individuals susceptible to predation, ie. vulnerable or weaker animals and physiological and/or psychological stresses may be further factors causing cannibalism.

Thirdly, environmental factors play a major role in affecting or controlling the rate and extent of cannibalism. De Angelis et al. (1979) found that the availability of alternative prey items had an effect on cannibalism, as did Fox (1975a). They found that if alternative prey was not available, certain individuals became cannibalistic. Fox (1975b), working on water beetles (Notonectidae), found that if the alternative prey did not meet the specific energy requirements, then the rate of cannibalism in the population increased. Pomeroy (1981 see Polis and Myers 1985) found that the presence of large potential prey can stimulate the development of cannibalism in tadpoles. Hecht and Appelbaum (1988) demonstrated that food availability, population density and refuges were significant factors affecting the rate and extent of cannibalism in African sharptooth catfish, (Clarias gariepinus). MacKinnon (1985) found stocking density, water clarity, light intensity and the frequency at which alternative prey is presented, all influence the rate of cannibalism to some degree in barramundi (Lates calcarifer). Moreover, Katavic et al. (1989), working with the sea bass Dicentrarchus labrax, found that cannibalism can be reduced by increasing the feeding frequency, while Herak and Mitin (1977 see Polis 1981) found that in hens nutritional deficiencies caused an increase in cannibalism. Fox (1975a) noted that cannibals may respond to a reduction of available food alternatives. Thus there are many factors which affect the rate and extent of cannibalism and which need to be considered.

Finally, it appears possible that cannibalism can simply be a feeding or hunger response (Hecht and Appelbaum 1988) and therefore influenced by the physiology of the individual. As important as the causes which affect the extent of cannibalism, is a consideration of the selective advantages for or against cannibalism, and whether this selection is occurring at the individual or group level. The presence of cannibalism in many populations in itself would seem to indicate the strong selective advantage for this phenomenon. Identifying any form of selection acting on the phenomenon of cannibalism will aid in an understanding of the reasons behind its existence and evolution. Fox (1975a) listed the following advantages : (i) gaining a meal by the elimination of potential conspecific predators when food becomes scarce; (ii) the elimination of potential competitors leading to reduced pressure on resources, and (iii) the increased competitive abilities of survivors.

Individuals which cannibalize may experience certain advantages over those that do not, as was concluded by Meffe and Crump (1987) working on the guppy Poecilia reticulata. They found that the addition of conspecifics to the basic diets significantly decreased developmental time, resulting in greater somatic growth, speeding up the development of reproductive organs and causing a trend towards increased fecundity. It was found that other supplements to the diet did not cause any of these trends. Cannibalism thus appears to produce larger individuals which may then benefit from the fact that they are less likely to be attacked by conspecifics.

Polis and Myers (1985) described the phenotypic differences in behaviour, morphology, growth rates and life history between cannibals and non-cannibals as cannibalistic polyphenism, and suggested that it may give cannibals the advantage of an expanded resource base, therefore enhancing their selection. Many workers have also found that when fish successfully start preying on their own kind they exhibit increased robustness and vigour and grow extremely fast (Cuff 1977; Li and Mathias 1982; MacKinnon 1985; Crump 1986; Giles et al. 1986; Lannoo et al. 1989).

It has been argued that cannibalism could be acting as a population regulation mechanism (Kipling and Frost 1970; Chevalier 1973; Fox 1975a; Coetzee 1976; Polis 1981; Mann 1982; Oiestad 1985; Giles et al. 1986; Brownell 1987; Hecht and Appelbaum 1988). However, mortality as a consequence of sibling cannibalism has also been shown to be as high as 15-90% in certain species under culture conditions (Hecht and Appelbaum 1988; pers. observ.). Such high mortalities would appear inconsistent with the argument that sibling cannibalism is a population regulation mechanism. Considering the possibility that the phenomenon of cannibalism might be genetically controlled and thus subject to selection, and considering that certain authors have suggested that group selection might be occurring in certain species, then such high mortalities seem unnatural and counter-productive in terms of group selection benefits.

Fox (1975a), however, stated that the advantages and disadvantages of cannibalistic tendencies must be considered in the light of other factors that may affect survival. In some situations the disadvantages of cannibalism may be less severe than the consequences of starvation or reproductive failure caused by inadequate nutrition. To illustrate this, consider two populations both subjected to starvation, one of which is cannibalistic while the other is not. In the cannibalistic population each survivor will make a greater contribution to future generations than an individual from a non-cannibalistic population because it would have been better fed as a juvenile and more likely to grow faster, survive better, breed earlier and/or produce more young. On the basis of this it could be hypothesized that a population would be more successful if a few well fed individuals contribute more to the populations' future than could many malnourished individuals with low reproductive potentials. The issue of whether or not cannibalism is genetically controlled, and whether as a consequence of this, individual or group selection (or both) is occurring, will be discussed in depth later.

The advantages of cannibalism therefore seem to be manifold. However, cannibalism should also be viewed in the light of possible disadvantages. Cannibalism becomes disadvantageous when individuals become too aggressive. Fox (1975a) noted that if the cannibal destroys its own progeny either completely or faster than those of its conspecific competitors, or if it reduces its own chances of successful reproduction by eliminating suitable mates, cannibalistic behaviour can be selected against. In Cape hake (Merluccius paradoxus) populations, however, cannibalism is reported to exist both when there is a lack of alternative prey and when other prey is available (Payne et al. 1987), indicating that cannibalism can be an advantageous strategy in times of prey scarcity and that through such a strategy a population may be able to sustain itself. It appears that in the case of the Cape hake there has been no selection against the phenomenon of cannibalism, thus providing an exception to the findings of Fox (op. cit.).

A further disadvantage of cannibalism was found by MacKinnon (1985) while working with captive populations of barramundi. Smaller sized fry became stressed by the presence of larger cannibalistic siblings and exhibited a reduced growth rate and an increased susceptibility to disease. Overall, however, the advantages seem to outweigh the disadvantages for individuals and for populations in the wild.

The primary objective of this study was to determine the most important environmental parameters or cues influencing cannibalism in those fish species which are important in the South African aquaculture industry. A knowledge and understanding of the network of interrelationships between these influencing parameters and the rate of cannibalism, studied on an interspecific basis would contribute towards our understanding of the fundamental principles governing cannibalism. Such a comparison could possibly elucidate the evolutionary reasons for the development of cannibalism, ie. why the phenomenon is present in some species and not in others, and also why the rate differs between species and under different environmental conditions. The understanding gained from this approach may make it possible to reduce the rate of cannibalistic mortality by manipulating the appropriate environmental parameters. This would have obvious benefits for the producer, whose aim it is to reduce mortality and thereby increase productivity and thus profits.

** ** **

The format of the thesis is as follows: Chapter two introduces the experimental fish, Clarias gariepinus (African sharptooth catfish), Oncorhyncus mykiss (rainbow trout), Cyprinus carpio (the common and koi carp varieties), Ctenopharyngodon idella (grass carp), Hypophthalmichthys molitrix (silver carp) and Tilapia rendalli (redbreast tilapia), and is followed by a description of their life-history styles. Chapter two also deals with the experimental systems used, the general and specific treatments for all experiments, the methods used to quantify behaviour and the various behavioural modes of the species under consideration. The environmental factors considered were : food availability, population density, live versus dry food, alternative live prey, turbidity, photoperiodicity, refuges, size variance, selection of cannibals, and water quality. Not all these environmental parameters were tested for each species, since only certain parameters are operative in the habitat of each. Therefore, only those environmental parameters which were deemed to play a major role in the habitat of a particular species were tested. Obviously the number of parameters which were tested for each species also depended on the time available for the study.

The results are presented in chapter three. The discussion and conclusions in chapter four deals with the results of the experiments performed. Trends and principles of cannibalism are then discussed, followed by an investigation into the genomic control of cannibalism and the evolution of the phenomenon. Finally suggestions for the control of cannibalism in fish culture are put forward.

Chapter 2

GENERAL METHODS AND MATERIALS

A) Selection of candidate species.

A cursory glance at cannibalism in fish reveals that it is a highly variable phenomenon, the rate and extent of which appears to be influenced by environmental, genetic, behavioural and physiological factors (Thibault 1974; Fox 1975a; Polis 1981; Giles *et al*. 1986; Hecht and Appelbaum 1988; Katavic *et al*. 1989). In attempting to initiate a study aimed at gaining a broad overview of cannibalism, it became apparent that the choice of study species was an important issue. Species were thus selected for a number of reasons. Those chosen for this study are listed in Table 3.

Table 3. Species chosen for the experimental study of cannibalism.

SCIENTIFIC NAME	COMMON NAME	FAMILY
Clarias gariepinus	sharptooth catfish	Clariidae
Oncorhynchus mykiss	rainbow trout	Salmonidae
Cyprinus carpio	common carp	Cyprinidae
Cyprinus carpio	koi carp	Cyprinidae
Hypophthalmichthys molitrix	silver carp	Cyprinidae
Ctenopharyngodon idella	grass carp	Cyprinidae
Tilapia rendalli	redbreast tilapia	Cichlidae

Firstly, the candidates were chosen on the basis of their relative position on the r- and K-continuum (MacArthur and Pianka 1966; MacArthur & Wilson 1967). Recently, Balon (1979) contributed to the development of the study of the lifestyles of fishes by introducing what he called "preferred terms", viz. "altricial" and "precocial" for "r-selected" and "K-selected", respectively, thereby making some significant changes to the r and K concept. The advantages of the terms altricial/precocial (which were first applied to birds by Nice, 1962) is that it relies on the characteristics associated with early development, and not only on the characters of the adult, as does r and K (Bruton 1989). Balon (1979) reasoned that the consideration of a species in terms of the r- and K-continuum is an oversimplification and therefore has limitations. He states with reference to Horn (1978) and Green (1980) that "certainly, the life-history style of any species, when considered in these terms may well be a compromise (ie. a mixed rather than a pure strategy), and it may not even be correct to consider "r" and "K" as being on the same continuum". His use of the concept of altricial and precocial strategies thus enables the life-history style of a species to be described as a pure strategy (Bruton 1989). Furthermore, Mann et al. (1984) reported that their data on European freshwater fishes were not in accordance with the theory of r- and K-selection and found that the theory is too inflexible. They proposed that genetically determined differences in life-history styles are overshadowed by environmental effects, such as productivity and temperature. For these and other reasons, Balon (1979) prefers the terms altricial and precocial as they more accurately reflect the effect behind the mechanism of epigenetic bifurcation, and the importance of the interplay between the environment and the genome (see also Bruton 1989).

Nevertheless, Balon (1979) continues to use the concept of r and K since it has been so widely used because of its' dichotomous nature and resultant simplicity, and is also better for describing population demography from life-history trajectories (Bruton 1989). Balon (op. cit.) states that the concept of r- and

K-selection does at least bring important questions to our attention, such as the principal one that is dealt with here, viz. that of the relationship between cannibalism and the life-history style of a species. Table 4 compares the characteristics between the two extremes of the life-history styles continuum.

Table 5 shows the relative positions of the candidate species on the r- and K-continuum. Cyprinus carpio was considered to be the most r-selected, with Tilapia rendalli being the most K-selected species in the study. This range of species was chosen to establish whether cannibalistic tendencies in fish are possibly influenced by different life-history style trajectories.

A second factor which was deemed important in the selection of experimental fish was that a variety of species be incorporated into the study, ranging from those apparently displaying no cannibalism to those which are known to be highly cannibalistic. Selecting only those species which are cannibalistic would not provide a complete perspective of the phenomenon, the reason being simply that there would be no basis for comparison. Another consideration was that the study should benefit commercial aquaculture. Therefore, the fish chosen were those that are important in commercial aquaculture in South Africa.

A final consideration in the choice of candidate species was linked to the study by Hecht and Appelbaum (1988). This was a significant contribution to the study of coeval sibling cannibalism. For the first time in-depth observations were conducted in order to gain a more conclusive insight into the fundamental aspects of cannibalism, and to find practical solutions to the problem of cannibalism under culture conditions. It was decided that Clarias gariepinus be the primary study animal, in order to add to the data base on cannibalism for that

Table 4. A comparison of the characteristics of the two extremes on the life history styles' continuum, viz. r-selected (altricial) and K-selected (precocial), (after Krebs 1978; Balon 1979 and Green 1980).

r-SELECTED (ALTRICIAL)	**K-SELECTED (PRECOCIAL)**
substrate or pelagic spawners	mouth brooding, internal bearing
short growth interval	prolonged growth interval
early maturation	deferred maturation
high fecundity	low fecundity
reduced parental care	increased parental care
short life/generation span	long life/generation span
These features characterize animals in environments where:-	
there is rapid colonization	there is a stable environment over long periods
catastrophic mortality is liable to act in a density-independent manner	competition is a factor
environmental disruptions are liable to be serious & unpredictable	mortality is density-dependent

species and to serve as a basis for comparison with other species. The methods employed were based largely on those described by Hecht and Appelbaum (op. cit.).

B) <u>Artificial propagation techniques and hatchery procedures</u>.

For all species, a single male and female were used for each spawning as full-sibling batches of offspring were desired. This was done in order to minimize variability in growth rates and hence cannibalism.

Table 5. Life-history characteristics of the candidate species and their relative positions on the r- and K-continuum (Bruton 1976; Bruton 1978; v. d. Merwe 1981; Hepher & Pruginin 1981; Rothbard 1981; Hecht & Viljoen 1982; Bruton *et al.* 1982; Noakes & Balon 1982; Schoonbee & Prinsloo 1984; Meske 1985; Pike 1985; Barnhart 1986; Crass 1987; Hecht *et al.* 1988; Laird & Needham 1988).

LIFE HISTORY STYLE CONTINUUM FOR EXPERIMENTAL SPECIES

◄——— r-SELECTED (ALTRICIAL) ——————————— K-SELECTED (PRECOCIAL) ———►

CHARACTERISTICS	CYPRINUS CARPIO (COMMON & KOI CARP)	CLARIAS GARIEPINUS (SHARPTOOTH CATFISH)	HYPOPHTHALMICHTHYS MOLITRIX (SILVER CARP)	CTENOPHARYNGODON IDELLA (GRASS CARP)	ONCORHYNCUS MYKISS (RAINBOW TROUT)	TILAPIA RENDALLI (REDBREAST TILAPIA)
FECUNDITY/FERTILITY (eggs/yr)	1500-2500ml of eggs approx. 1000000eggs	50000-200000 eggs	400-1000ml of eggs; up to 1750ml (100000eggs/100ml)	1100ml of eggs (80000eggs/100ml)	2000 eggs/kg or 2000-12000	up to 7000 eggs
EGG DIAM. (mm)	1.2	1.6-1.7	1.16 (unfert.); after swelling: 45-100% larger	same as silver carp	3-5	1-1.5
SIZE AT ONSET OF FEEDING (mm)	6-7	8-10	6-7	6-7	14-17	5-6
AGE AT FIRST REPRODUCTION (yrs)	0.5	1-3	3-4	3-4	male: 1yr female: up to 6yrs	0.5-2
TOTAL LENGTH OR WEIGHT AT FIRST REPRODUCTION	200g/20-30cm	150-800mm TL	female: 50cm	female: 50cm	25-35cm	up to 20cm
COURTSHIP	pairs	pairs	pairs(?)	pairs(?)	polygamous	prolonged, monogamous
JUVENILE MORTALITY	very high	very high	very high	very high	high	low
LONGEVITY (yrs)	up to 80	?	up to 80	up to 80	4.5-8	up to 7
PARENTAL CARE	none	none	none	none	hides eggs	prolonged, intensive guarding
EGG HATCHING	70-80 hrs	24-48 hrs	<24 hrs	19-24 hrs	19-80days depending on temperature	48 hrs
SPAWNING FREQUENCY	annually	annually	annually	annually	annually	several annually
DIET	benthivore/omnivore	omnivore	planktivore	herbivore	carnivore	omnivorous but predominantly macrophagous
AVERAGE ADULT SIZE	?	?	65cm	75cm	4.5kg/30-40cm	1.8kg 38cm
MAXIMUM SIZE	36kg	200cm 58,9kg	20kg in 12-15yrs	50kg in 10-15yrs	20kg	2kg
PHENOTYPIC PLASTICITY	adjustable	highly adjustable	?	?	little adjustability	fairly adjustable
HABITAT	slow large rivers now ubiquitous	ubiquitous: riverine & lacustrine	slow large rivers	slow large rivers	fast streams	ubiquitous: riverine & lacustrine

Clarias gariepinus, (sharptooth catfish).

Females were induced to spawn according to the artificial propagation techniques described by Hecht et al. (1988). Females were given a single injection of homoplastic pituitary homogenate and stripped approximately 12 hours later. Eggs were incubated in a "flow-through" incubation system on vertical gauze screens (0.5 mm mesh). The water temperature of the incubation system was maintained at 25 ± 1°C. Hatching occurred 24 ± 1 hour after fertilization and exogenous feeding commenced 48-72 hours after hatching.

Oncorhynchus mykiss, (rainbow trout).

Eyed ova were placed on hatching trays housed in circular, 700 mm fibreglass swedish tanks under recirculating conditions. The trays were a few centimetres below the water surface and were covered with nylon mesh (5 mm x 2 mm mesh size). The mesh was small enough to prevent the eggs from falling through but large enough to enable the hatched larvae to escape to the lower confines of the tank. A 90% hatching rate was achieved. The temperature throughout the incubation period was 17 ± 2°C. The eyed ova began hatching after five days, with most having hatched after six days. A small percentage took between seven and eight days to hatch. Exogenous feeding commenced between seven and 10 days after hatching.

Cyprinus carpio, (common and koi varieties).

Females were induced to spawn according to the propagation techniques of Schoonbee and Prinsloo (1984). Broodstock and fertilized eggs were contained in a water recycling system maintained at 16 ± 1°C. The eggs hatched after 74 hours (common carp) and 55 hours (koi carp). Exogenous feeding commenced approximately three days after hatching.

Ctenopharyngodon idella, (grass carp).

Grass carp were induced to spawn according to the methods described by Pike (1985). Broodstock and eggs were kept at a temperature of 28 °C under recirculating conditions. The eggs hatched 17 hours after fertilization. Exogenous feeding commenced between two to three days after hatching.

Hypophthalmichthys molitrix, (silver carp).

Silver carp were spawned according to the methods described by Rothbard (1981). Broodstock and eggs were maintained at a temperature of 24°C under recirculating conditions. Hatching occurred after a 27 hour incubation period. Exogenous feeding commenced approximately three days after hatching.

Tilapia rendalli, (redbreast tilapia).

One male and one female were placed in a glass tank measuring 35 cm (height) x 32 cm (width) x 90 cm (length) with a volume of 100 litres. The tank contained an under-gravel filter with aeration and was maintained at a constant temperature of 27 ± 1°C. Natural spawning occurred and the eggs hatched between 76 and 78 hours after fertilization. Exogenous feeding commenced approximately three days after hatching.

C) Culture systems and general treatment.

Food availability experiments conducted on catfish and trout were performed in 27,5 l tanks measuring 22,0cm (height) x 28,75cm (width) x 43,5cm (length). However, for all other experiments the tanks were divided into two 13,75 l tanks by removable gauze and perspex dividers. Plate 1 shows one of the experimental tanks and Figure 1 shows how the tanks were linked into a "flow-through" system. A system of this type ensures optimal water quality. Dechlorinated tap water was used and a flow rate of 0.5 l/min was maintained. Water was fed from header tanks which were constantly and vigorously aerated using compressed air.

In the trout experiments a water recycling system was used (Fig. 2). It was therefore necessary to measure various water quality parameters. For all experiments involving trout, dissolved oxygen was maintained at 6 ± 1 ppm, temperature at 15 ± 2°C for the duration of the experiments, pH was constant at 6.5, while the flow-rate was 0.5 l/min (30 l/hour) in 27.5 l tanks. The total ammonia (NH_4-N) of the water flowing from the header tank into the experimental tanks remained more or less constant at 0.037 ppm, and rose to 0.055 ppm at the combined outflow from all experimental tanks. According to Spotte (1979) the upper limit for ammonia levels in solution should not exceed 0.1 ppm. The recorded levels were thus well within the acceptable range.

Nitrite appears to be acutely toxic only in waters of low ionic strength. The acceptable upper limit is 0.1 ppm NO_2-N/l (Spotte 1979). Recorded levels of nitrite in the water flowing from the header tanks to the experimental tanks was 0.077 ppm and 0.079 ppm at the combined outflow from all the experimental tanks and were thus well below the upper limit.

Maximum nitrate recorded was 41.97 ppm at the inflow and 45.78 ppm at the outflow. These levels were well within acceptable units (Spotte 1979).

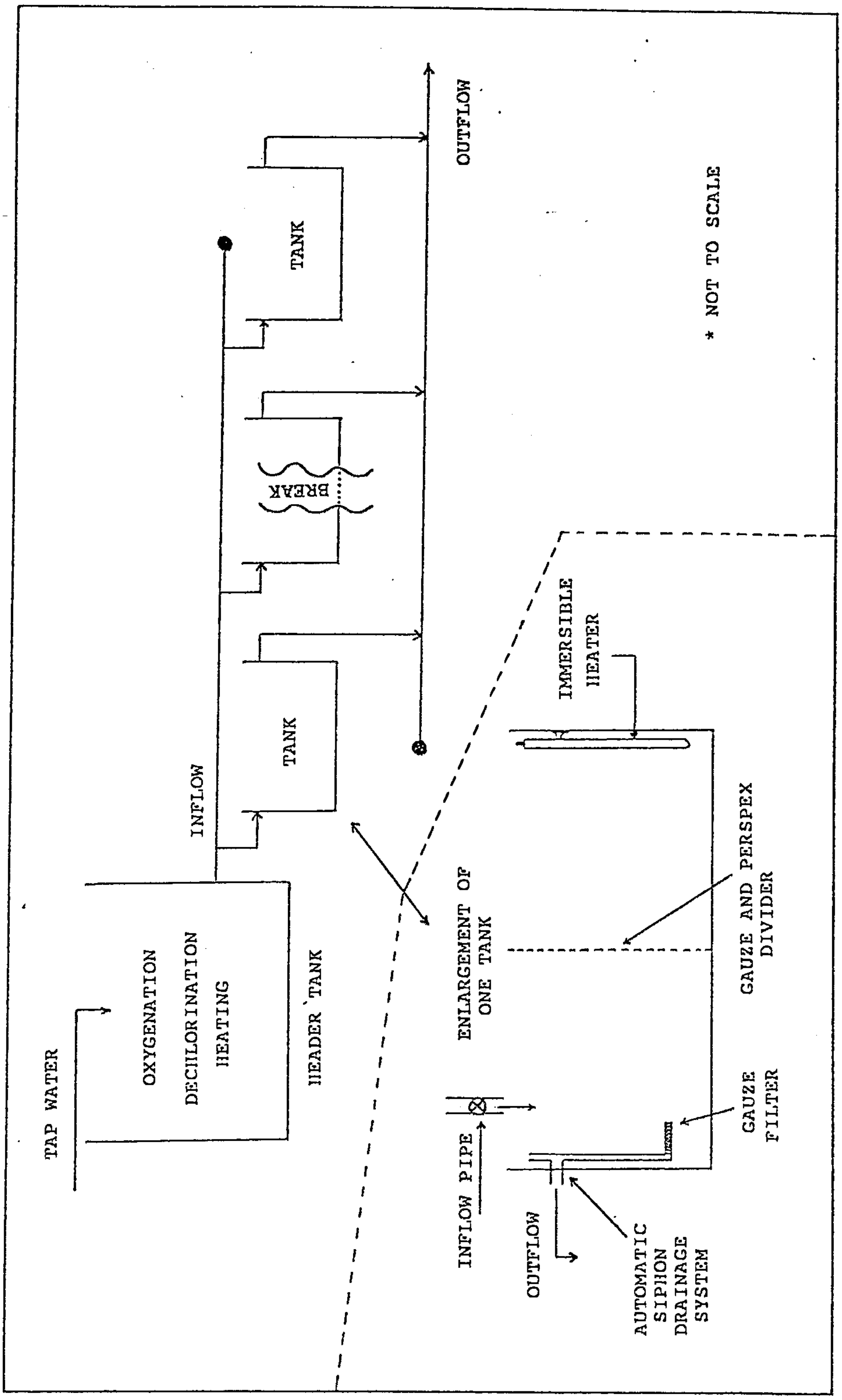

Fig. 1. Flow-through system used for all experiments on catfish, tilapia and the common, koi, grass and silver carp.

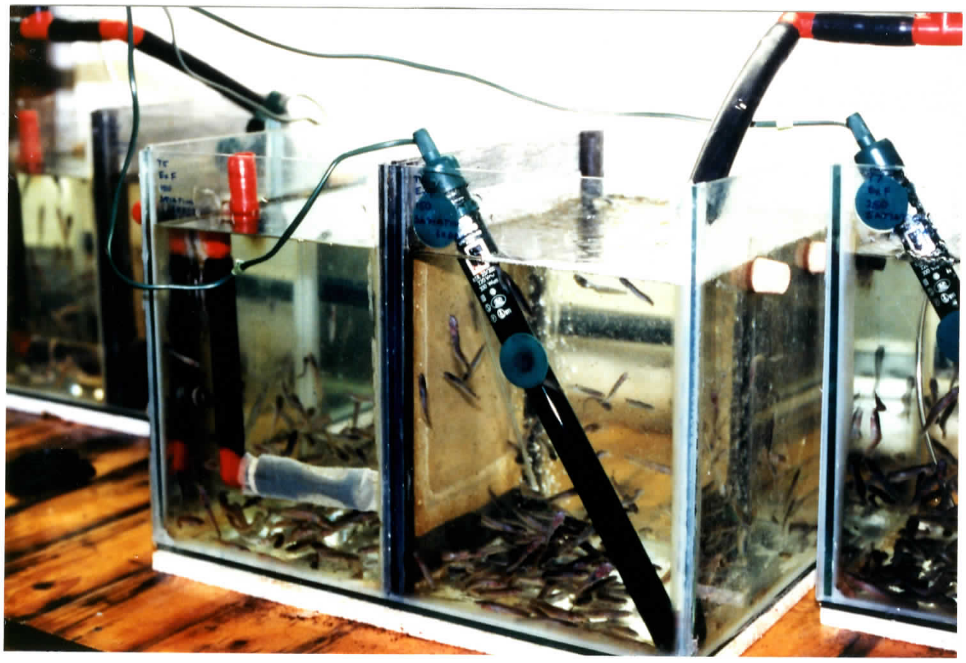

Plate 1. The experimental system used, showing a 27,5 l glass observation tank (divided into two 13,75 l tanks by a perspex and gauze partition), the inflow and outflow piping, the gauze filter and the adjustable immersion heaters

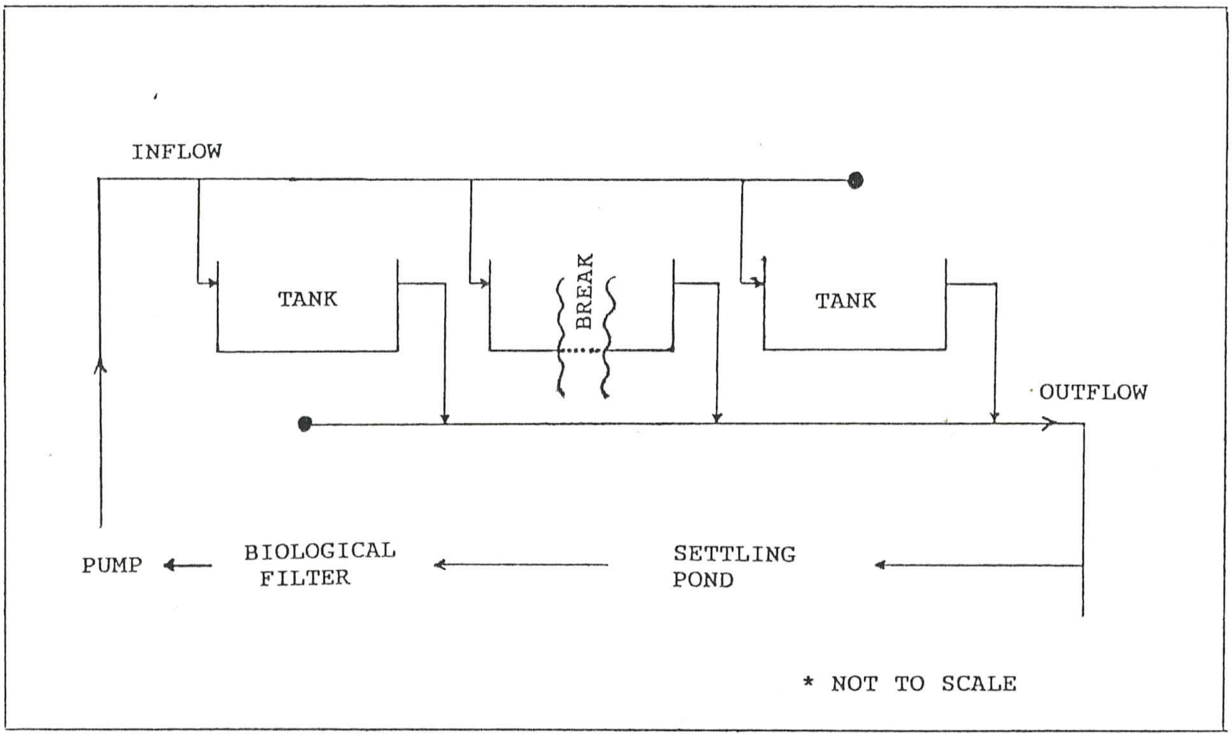

Fig. 2. Recycling system used for all experiments on trout.

The tanks were illuminated using a combination of neon and incandescent daylight bulbs, which produced a light intensity of 200 lux at the water surface. A time switch ensured that the fish were subjected to a photoperiod of 12 hours dark/12 hours light. Temperature was regulated by means of immersible heaters and thermostats.

Pelletized fish feed used for all species was prepared according to the formulation of Uys and Hecht (1985) and found to be suitable for rearing these fish. Table 6 provides a proximate analysis of the fish feed. The feed was provided at the graduated sizes of 212 um, 355 um and 710 um according to the size of the fish.

Excess feed and faeces were siphoned from the tanks on a daily basis. The dead fish in each tank were removed and counted daily, and the bodies were examined to see if the cause of death could be determined. At intervals of a few days throughout the experiments, a total head-count of the population in each tank was taken, as well as length and weight measurements of a sample of the population for certain species. Temperature and dissolved oxygen (DO) measurements were also taken daily. Prior to the start of all experiments, the fish were acclimated in the experimental tanks for 24 hours. Fish were scooped into a 0.5 l bucket and counted as they were poured into the experimental tanks.

D) Quantification of behaviour.

The behaviour of the fish was quantified according to three primary methods (**Methods A, B and C**):-

Method A. The **overall activity pattern** of a particular fish in

Table 6. Formulation and composition of the fish feed used for all species in this study (Uys and Hecht 1985).

Formulation	
Dried Torula yeast (Candida utilis)	69.8%
Brown fishmeal	23.3%
Vitamin premix	0.9%
Methionine supplement (150mg/kg pure methionine)	6.0%
	100%
Furanace (bactericide and fungicide)	4 ppm
Endox (antioxidant)	250 ppm
Plus: Fish oil (cod) and soya bean oil mixture (1:1)	6% of total dry weight of feed
Nutrient Composition	
Proximate analysis (% dry weight)	
Protein	55.4%
Lipids	9.1%
Carbohydrates	21.2%
Minerals and vitamins	13.3%
	100%

each tank was observed daily for a ten minute period approximately two hours after feeding. The duration of each behavioural mode was timed with a stop watch.

Method B. The **number of aggressive encounters** (territorial or cannibalistic) observed **during five minute intervals** was recorded once a day for each tank, approximately two hours after feeding.

Method C. The **number of aggressive encounters observed per fifty physical contacts** was recorded daily for each tank, approximately two hours after feeding.

Any deviations from these general methods are presented in the appropriate section.

Behavioural modes.

Sharptooth catfish, (Clarias gariepinus)

The behavioural modes defined by Hecht and Appelbaum (1988) were used to describe the different activities of the fish. These were:-

(i)active swimming (A) - random swimming within the water column.
(ii)browsing (B) - active swimming around the bottom of the aquarium during which time small quantities of food were ingested at random; contacts between siblings during browsing activity were either non-aggressive or resulted in cannibalistic or territorial aggression.
(iii)resting (R) - characterized by the fish lying motionless on the bottom of the tank, either on their bellies or on their sides.
(iv)disturbed rest activity (D) - initiated by a contact between two siblings; the response was a fast dart away from the place of contact,after which it slowed down with the fish once again coming to rest.
(v)airbreathing (I) - swimming to the water surface to breathe.
(vi)territorial aggression (T) - a response by one fish entering into the territory of another, or physical contact with the ultimate aggressor resulting in a territorial aggressive response. This usually occurred as a result of head to head contact between two siblings within a territory, resulting in a brief, but violent, barbel-biting encounter followed by a short chase in the general direction of the intruder, whereafter the intruder would retreat;
(vii)cannibalistic aggression (C) - preceded by purposeful browsing or searching, albeit in a seemingly random pattern. The fish assumed the same swimming stance as when it was actively feeding, ie. head down with the body at an angle of approximately 30^0 from the horizontal ("helicopter stance"). Once a contact was made with the circum-oral barbels, or another individual had been sensed in close proximity, the predator instantly lunged forward

and attempted to grasp the prey. If such an attempt failed, the predator again lunged forward and attempted to grasp the prey a second time. If the second attempt failed, the predator would not follow the prey but would resume the random "helicopter stance" search pattern.

Rainbow trout, (*Oncorhynchus mykiss*).

The general behaviour of *O. mykiss* was first described by Stringer and Hoar (1955). However, with the exception of work on reactive distance (McNicol and Noakes 1984), the forms of salmonid agonistic behaviour have not been defined (Abbot and Dill 1985). For the purposes of this investigation the following behavioural patterns in rainbow trout were recognized: A = active swimming; C = cannibalism; E = extended fighting ie. dog-fights; P = pecking (aiming at and seizing a food particle - this could also involve "tasting" the food particle and subsequently spitting it out); R = resting; T = territoriality (a nip or a display, ie. one movement or act may contain more than one nip); W = mouth fighting or wrestling (grasping each others' jaws and then wrestling by pulling, pushing and twisting - Abbot and Dill 1985); in this study mouth wrestling was often observed to result in the ingestion of the sibling.

Common and koi carp, (*Cyprinus carpio*).

The following modes of behaviour were recognized :

(i) aggression (A) - an act of aggression usually occurred between two siblings when one entered the territory of the other. This involved an orientation in the direction of the intruder, followed by a fast move in its direction and a bite on some area of the intruders' body, usually the torso or tail.
(ii) non-aggressive contact (K) - contact which did not result in any form of aggression, ie. territorial or cannibalistic.

(iii) cannibalism (C) - the killing and consumption of a sibling. This usually involved the ingestion of the sibling head first after a sequence of search, orientate, lunge and capture as described by Vinyard and O'Brien (1976).

Grass carp (*Ctenopharyngodon idella*) and Silver carp (*Hypophthalmichthys molitrix*).

These two fish have very similar behavioural patterns and can be described together. No form of aggression was evident. The behavioural modes recognized were:

(i) non-aggressive contacts (K) - any contact which did not result in any form of aggression, ie. territorial or cannibalistic.
(ii) stressed behaviour (S) - very fast swimming, apparently stressful, jerky or panicky movement.

Redbreast tilapia, (*Tilapia rendalli*).

The reason for the observations on *T. rendalli* was simply to determine whether the species exhibited cannibalism or not. No breakdown of its behavioural patterns was therefore undertaken.

E) Experimental methods and rationale.

As mentioned previously environmental, genetic, behavioural and physiological factors have been shown to influence the rate and extent of cannibalism (Thibault 1974; Fox 1975a; Polis 1981; Giles *et al*. 1986; Hecht and Appelbaum 1988; Katavic *et al*. 1989). It was therefore decided to test as many of these factors as was logistically feasible.

The environmental factors thought most critically to influence the rate of cannibalism were food availability, population density, live versus dry food, alternative live food, turbidity, photoperiod and refuges. Reasons as to why these were thought to have a critical influence on cannibalism and why they were specifically chosen, are dealt with below.

In order to substantiate the findings of other workers, which provide evidence for a genetic basis for cannibalism, it was decided to study two different varieties (common and koi carp) of the same species (*Cyprinus carpio*). Any differences in cannibalistic traits between the two strains should, theoretically reflect a degree of genetic control of cannibalism.

Table 7 is a master-table providing an easy reference to Tables 8 through 28, which indicate the conditions under which the various observations were made. Note that conditions which were the same for all experiments are not included in these tables since this information is provided in section (C) Culture systems and general treatments.

Table 7. Master-table for easy reference to tables 8 through 27 which indicate the methods used for all experiments in this study.

EXPERIMENT	TABLE NUMBER(S)	SPECIES
Behavioural response to a changing environmental parameter	8	catfish larvae
	9	catfish juveniles
Food availability and cannibalism	10	sharptooth catfish
	11	rainbow trout
	12	koi carp
	13	silver carp
Population density and cannibalism	14	sharptooth catfish
	15	rainbow trout
	16	common carp
	17	koi carp
	18	silver carp
	19	grass carp
Live & dry food, & its effect on cannibalism	20	sharptooth catfish
	21	rainbow trout
Alternative live food & its effect on cannibalism	22	sharptooth catfish
Photoperiod and cannibalism	23	sharptooth catfish
Refuges and cannibalism	24	sharptooth catfish
Turbidity and cannibalism	25	sharptooth catfish
Phenotypic assessment of potential cannibals and non-cannibals	26	sharptooth catfish
Determination of aggressive behaviour	27	redbreast tilapia

1. Evaluation of behavioural responses in catfish to a changing environmental parameter .

This experiment was performed to test the hypothesis that the behaviour of the fish could be manipulated by varying environmental parameters and that the behavioural response was a real one and not an artefact of experimental conditions. The environmental parameter chosen for this experiment was food availability, since this factor is one of the most important governing the phenomenon of cannibalism. The experiment was performed with two different age groups of catfish. The first group were one week old **larvae** and the second group were five week old **juveniles**. The primary reason for using two different age groups was that Hecht and Appelbaum (1988) found that the rate of cannibalism declines with age. These experiments were therefore also performed to test the findings of Hecht and Appelbaum (op. cit.). Tables 8 and 9 show the methods and conditions under which the experiments were performed.

2. Effect of food availability on the rate of cannibalism and other behavioural modes.

It is widely believed that predation and starvation are the dominant causes of extensive mortality of fish larvae (Blaxter 1969), with predation (conspecific or non-conspecific) probably being the most important factor (Oeistad 1985). Several authors have reported that the larvae of various fish species become cannibalistic when food is scarce (Fox 1975a and b; Polis 1981; Dabrowski and Bardega 1984; Oiestad 1985; Katavic et al. 1989). Hecht and Appelbaum (1988) also reached the conclusion that cannibalism can be viewed as an alternative feeding strategy in times of limited food. The environmental constraint of food availability thus appears to be one of the most important parameters in the control of cannibalism. Experiments using catfish, trout, koi carp and silver carp, were therefore

Table 8. A summary of the experimental methods and conditions used to determine whether the behaviour of LARVAL sharptooth catfish Clarias gariepinus, can be manipulated by food availability, (all terms within the Table requiring explanation are marked and explained in the footnotes below).

AGE OF ANIMALS AT START	1 week old larvae
DURATION OF EXPERIMENT[1]	13 days
FOOD	Daphnia & pelleted fish feed
FEEDING REGIME	ad libitum every 2 hrs between 08h00 and 22h00, with feeding halted on 5th day for 6 days; feeding resumed on day 11
TEMPERATURE	25 ± 2 °C
DISSOLVED OXYGEN	6 ± 1ppm
TANK VOLUME	13,75 l
DENSITY	7 fish/l
BEHAVIOURAL MEASUREMENTS[2]	Methods A, B & C
DURATION OF BEHAVIOURAL MEASUREMENTS[3]	13 days (day 1 to day 13 of 13 days)
NO. OF REPLICATES OF BEHAVIOURAL MEASUREMENTS[4]	1

FOOTNOTES:-

[1] "DURATION OF EXPERIMENT" refers to the total time of the entire experiment.

[2] "BEHAVIOURAL MEASUREMENTS" refers to the three principal Methods described under General Methods & Materials (pg. 23).

[3] "DURATION OF BEHAVIOURAL MEASUREMENTS" refers to the period of time, within the time-interval of the entire experiment, in which "BEHAVIOURAL MEASUREMENTS" were performed. The reason why the "DURATION OF EXPERIMENT" was longer than the time period allocated for "BEHAVIOURAL MEASUREMENTS" was that a population census to assess the rate of cannibalism, was required over this longer period.

[4] "NO. OF REPLICATES OF BEHAVIOURAL MEASUREMENTS" refers to the number of times "BEHAVIOURAL MEASUREMENTS" were duplicated in each tank within the time-interval of the entire experiment.

Table 9. A summary of the experimental methods and conditions used to determine whether the behaviour of JUVENILE sharptooth catfish Clarias gariepinus can be manipulated by food availability, (all terms within the Table requiring explanation are marked and explained in the footnotes below).

AGE OF ANIMALS AT START	5 week old juveniles
DURATION OF EXPERIMENT[1]	12 days
FOOD	live Daphnia & pelleted fish feed
FEEDING REGIME	*ad libitum* every 2 hrs (between 08h00 and 22h00), with feeding halted on 4th day for 6 days; feeding resumed on day 10
TEMPERATURE	25 ± 2 °C
DISSOLVED OXYGEN	6 ± 1ppm
TANK VOLUME	27,5 l
DENSITY	2 fish/l
BEHAVIOURAL MEASUREMENTS[2]	Methods A, B & C
DURATION OF BEHAVIOURAL MEASUREMENTS[3]	12 days (day 1 to day 12 of 12 days)
NO. OF REPLICATES OF BEHAVIOURAL MEASUREMENTS[4]	1

FOOTNOTES:-

1 "DURATION OF EXPERIMENT" refers to the total time of the entire experiment.

2 "BEHAVIOURAL MEASUREMENTS" refers to the three principal Methods described under General Methods & Materials (pg. 23).

3 "DURATION OF BEHAVIOURAL MEASUREMENTS" refers to the period of time, within the time-interval of the entire experiment, in which "BEHAVIOURAL MEASUREMENTS" were performed. The reason why the "DURATION OF EXPERIMENT" was longer than the time period allocated for "BEHAVIOURAL MEASUREMENTS" was that a population census to assess the rate of cannibalism, was required over this longer period.

4 "NO. OF REPLICATES OF BEHAVIOURAL MEASUREMENTS" refers to the number of times "BEHAVIOURAL MEASUREMENTS" were duplicated in each tank within the time-interval of the entire experiment.

undertaken to see whether the rate of cannibalism was correlated to food availability. Tables 10 to 13 show the methods and conditions under which these experiments were performed.

3. Effect of density on the rate of cannibalism and other behavioural modes.

Cannibalism has been described as a population regulation mechanism, acting to reduce population size during periods when high densities put pressure on limited resources. This has been found in both marine and freshwater environments : MacKinnon 1985 - barramundi (*Lates calcarifer*; Oiestad 1985 - herring (*Clupea harengus*), cod (*Gadus morhua*), plaice (*Pleuronectes platessa*), capelin (*Mallotus villosus*); Hecht and Appelbaum 1987, 1988 - catfish (*Clarias gariepinus*); Wright and Giles 1987 - pike *Esox lucius*). The effect of population density on the rate of cannibalism was investigated in catfish, trout and the common, koi, silver and grass carps. Tables 14 to 19 show the methods and conditions under which the experiments were performed.

4. Effect of live and dry food on the rate of cannibalism and other behavioural modes.

Konrad Lorenz (1966) spoke of the "need" for fish to release aggression. He stated that if there were no other fish on which to release aggression, it would even go so far as to attack its own mate. He also stated that "redirection of the attack is evolution's most ingenious expedient for guiding aggression into harmless channels". This view is recognized as being anthropomorphic. Nevertheless, by analyzing this concept and defining terms, it remains useful for providing a basis from which experimentation can begin. If "harmless channels" refers to the redirection of aggression towards any object or individual other than a sibling, then this concept is useful for providing a

Table 10. A summary of the experimental methods and conditions used in determining the relationship between food availability, cannibalism and other behavioural modes in the sharptooth catfish *Clarias gariepinus*, (all terms within the Table requiring explanation are marked and explained in the footnotes below).

AGE OF ANIMALS AT START	3 day old larvae
DURATION OF EXPERIMENT[1]	30 days
TEMPERATURE	27 ± 2 °C
DISSOLVED OXYGEN	7 ± 1ppm
TANK VOLUME	27,5 l
DENSITY	5 fish/l
BEHAVIOURAL MEASUREMENTS[2]	Methods A, B & C
DURATION OF BEHAVIOURAL MEASUREMENTS[3]	7 days (day 2 to day 8 of 30 days)
NO. OF REPLICATES OF BEHAVIOURAL MEASUREMENTS[4]	1
FOOD	live *Daphnia* & pelleted fish feed

FEEDING :-

TANK NOS.	FEEDING REGIME (between 08h00 & 22h00)
1 & 2	satiation (6X daily)
3 & 4	5% body weight (1X daily)
5 & 6	10% body weight (1X daily)
7 & 8	no food

*NB:- observations were terminated after six days in tanks 7 & 8 in order not to introduce experimental bias, since the experimental animals became too weak to cannibalize; experimentation continued for thirty days in tanks 1 to 6 during which time a population census was taken at intervals of a few days

FOOTNOTES:-

1 "DURATION OF EXPERIMENT" refers to the total time of the entire experiment.

2 "BEHAVIOURAL MEASUREMENTS" refers to the three principal Methods described under General Methods & Materials (pg. 23).

3 "DURATION OF BEHAVIOURAL MEASUREMENTS" refers to the period of time, within the time-interval of the entire experiment, in which "BEHAVIOURAL MEASUREMENTS" were performed. The reason why the "DURATION OF EXPERIMENT" was longer than the time period allocated for "BEHAVIOURAL MEASUREMENTS" was that a population census to assess the rate of cannibalism, was required over this longer period.

4 "NO. OF REPLICATES OF BEHAVIOURAL MEASUREMENTS" refers to the number of times "BEHAVIOURAL MEASUREMENTS" were duplicated in each tank within the time-interval of the entire experiment.

Table 11. A summary of the experimental methods and conditions used in determining the relationship between food availability, cannibalism and other behavioural modes in the rainbow trout Oncorhynchus mykiss, (all terms within the Table requiring explanation are marked and explained in the footnotes below).

AGE OF ANIMALS AT START	4 day old larvae
DURATION OF EXPERIMENT[1]	30 days
TEMPERATURE	15 ± 2 °C
DISSOLVED OXYGEN	6 ± 1ppm
TANK VOLUME	27,5 l
DENSITY	5 fish/l
BEHAVIOURAL MEASUREMENTS[2]	Methods A, B & C
DURATION OF BEHAVIOURAL MEASUREMENTS[3]	7 days (day 2 to day 8 of 30 days)
NO. OF REPLICATES OF BEHAVIOURAL MEASUREMENTS[4]	1
FOOD	Daphnia & pelleted fish feed

FEEDING:-

TANK NOS.	FEEDING REGIME (between 08h00 & 22h00)	
1 & 2	satiation (6x daily)	*NB:- observations were terminated after 13 days in tanks 7 and 8 in order not to introduce experimental bias, since the animals became too weak too cannibalize; experimentation was continued for 30 days in tanks 1 to 6, during which time a population census was taken at intervals of a few days
3 & 4	5% body weight (1x daily)	
5 & 6	10% body weight (1x daily)	
7 & 8	no food	

FOOTNOTES:-

1 "DURATION OF EXPERIMENT" refers to the total time of the entire experiment.

2 "BEHAVIOURAL MEASUREMENTS" refers to the three principal Methods described under General Methods & Materials (pg. 23).

3 "DURATION OF BEHAVIOURAL MEASUREMENTS" refers to the period of time, within the time-interval of the entire experiment, in which "BEHAVIOURAL MEASUREMENTS" were performed. The reason why the "DURATION OF EXPERIMENT" was longer than the time period allocated for "BEHAVIOURAL MEASUREMENTS" was that a population census to assess the rate of cannibalism, was required over this longer period.

4 "NO. OF REPLICATES OF BEHAVIOURAL MEASUREMENTS" refers to the number of times "BEHAVIOURAL MEASUREMENTS" were duplicated in each tank within the time-interval of the entire experiment.

Table 12. A summary of the experimental methods and conditions used in determining the relationship between food availability, cannibalism and other behavioural modes in koi carp *Cyprinus carpio*, (all terms within the Table requiring explanation are marked and explained in the footnotes below).

AGE OF ANIMALS AT START	3 day old larvae
DURATION OF EXPERIMENT[1]	26 days
TEMPERATURE	25 ± 2 °C
DISSOLVED OXYGEN	6 ± 1ppm
TANK VOLUME	13,75 l
DENSITY	7 fish/l
BEHAVIOURAL MEASUREMENTS[2]	number of different behavioural mode changes per 10 mins
DURATION OF BEHAVIOURAL MEASUREMENTS[3]	7 days (day 2 to day 8 & day 16 to day 22 of 26 days)
NO. OF REPLICATES OF BEHAVIOURAL MEASUREMENTS[4]	2
FOOD	live *Daphnia* & pelleted fish feed

FEEDING:-

TANK NOS.	FEEDING REGIME (between 08h00 & 22h00)
1 & 2	satiation (6x daily)
3 & 4	10% body weight (1x daily)

FOOTNOTES:-

[1] "DURATION OF EXPERIMENT" refers to the total time of the entire experiment.

[2] "BEHAVIOURAL MEASUREMENTS" refers to the modes described under General Methods & Materials (pg. 23).

[3] "DURATION OF BEHAVIOURAL MEASUREMENTS" refers to the period of time, within the time-interval of the entire experiment, in which "BEHAVIOURAL MEASUREMENTS" were performed. The reason why the "DURATION OF EXPERIMENT" was longer than the time period allocated for "BEHAVIOURAL MEASUREMENTS" was that a population census to assess the rate of cannibalism, was required over this longer period.

[4] "NO. OF REPLICATES OF BEHAVIOURAL MEASUREMENTS" refers to the number of times "BEHAVIOURAL MEASUREMENTS" were duplicated in each tank within the time-interval of the entire experiment.

Table 13. A summary of the experimental methods and conditions used in determining the relationship between food availability, cannibalism and other behavioural modes in the silver carp *Hypophthalmichthys molitrix*, (all terms within the Table requiring explanation are marked and explained in the footnotes below).

AGE OF ANIMALS AT START	3 day old larvae
TEST	food availability vs. cannibalism
DURATION OF EXPERIMENT[1]	31 days
TEMPERATURE	28 ± 1 °C
DISSOLVED OXYGEN	6 ± 0.5ppm
TANK VOLUME	13,75 l
DENSITY	7 fish/l
BEHAVIOURAL MEASUREMENTS[2]	number of different behavioural mode changes per 10 mins
DURATION OF BEHAVIOURAL MEASUREMENTS[3]	7 days (day 2 to day 8 & day 16 to day 22 of 31 days)
NO. OF REPLICATES OF BEHAVIOURAL MEASUREMENTS[4]	2
FOOD	small *Daphnia* & 212um pelleted fish feed, & zoo- and phytoplankton

FEEDING:-

TANK NOS.	FEEDING REGIME (between 08h00 & 22h00)
1 & 2	no food
3 & 4	1x body weight (1x daily)
5 & 6	satiation (*ad libitum* every 2 hrs)

FOOTNOTES:-

1 "DURATION OF EXPERIMENT" refers to the total time of the entire experiment.

2 "BEHAVIOURAL MEASUREMENTS" refers to the measurement of the behavioural modes described under General Methods & Materials (pg. 23).

3 "DURATION OF BEHAVIOURAL MEASUREMENTS" refers to the period of time, within the time-interval of the entire experiment, in which "BEHAVIOURAL MEASUREMENTS" were performed. The reason why the "DURATION OF EXPERIMENT" was longer than the time period allocated for "BEHAVIOURAL MEASUREMENTS" was that a population census to assess the rate of cannibalism, was required over this longer period.

4 "NO. OF REPLICATES OF BEHAVIOURAL MEASUREMENTS" refers to the number of times "BEHAVIOURAL MEASUREMENTS" were duplicated in each tank within the time-interval of the entire experiment.

Table 14. A summary of the experimental methods and conditions used in determining the relationship between population density, cannibalism and other behavioural modes in the sharptooth catfish Clarias gariepinus, (all terms within the Table requiring explanation are marked and explained in the footnotes below).

AGE OF ANIMALS AT START	2 week old larvae
DURATION OF EXPERIMENT[1]	16 days
FOOD	Daphnia & pelleted fish feed
FEEDING REGIME	all tanks *ad libitum* every 2hrs (between 08h00 and 22h00)
TEMPERATURE	27 ± 2 °C
DISSOLVED OXYGEN	7 ± 1ppm
TANK VOLUME	13,75 l
BEHAVIOURAL MEASUREMENTS[2]	Methods A, B & C
DURATION OF BEHAVIOURAL MEASUREMENTS[3]	7 days (day 2 to day 8 of 16 days)
NO. OF REPLICATES OF BEHAVIOURAL MEASUREMENTS[4]	1

POPULATION DENSITIES:-

TANK NOS.	DENSITY
1 & 2	25 fish (1.82/l)
3 & 4	75 fish (5.45/l)
5 & 6	150 fish (10.9/l)
7 & 8	250 fish (18.18/l)

FOOTNOTES:-

1 "DURATION OF EXPERIMENT" refers to the total time of the entire experiment.

2 "BEHAVIOURAL MEASUREMENTS" refers to the three principal Methods described under General Methods & Materials (pg. 23).

3 "DURATION OF BEHAVIOURAL MEASUREMENTS" refers to the period of time, within the time-interval of the entire experiment, in which "BEHAVIOURAL MEASUREMENTS" were performed. The reason why the "DURATION OF EXPERIMENT" was longer than the time period allocated for "BEHAVIOURAL MEASUREMENTS" was that a population census to assess the rate of cannibalism, was required over this longer period.

4 "NO. OF REPLICATES OF BEHAVIOURAL MEASUREMENTS" refers to the number of times "BEHAVIOURAL MEASUREMENTS" were duplicated in each tank within the time-interval of the entire experiment.

Table 15. A summary of the experimental methods and conditions used in determining the relationship between population density, cannibalism and other behavioural modes in the rainbow trout *Oncorhynchus mykiss*, (all terms within the Table requiring explanation are marked and explained in the footnotes below).

AGE OF ANIMALS AT START	3 day old larvae
DURATION OF EXPERIMENT[1]	13 days
FOOD	*Daphnia* & pelleted fish feed
FEEDING REGIME	all tanks *ad libitum* every 2hrs (between 08h00 and 22h00)
TEMPERATURE	15 ± 2 °C
DISSOLVED OXYGEN	6 ± 1ppm
TANK VOLUME	13,75 l
BEHAVIOURAL MEASUREMENTS[2]	Methods A, B & C
DURATION OF BEHAVIOURAL MEASUREMENTS[3]	7 days (day 2 to day 8 of 13 days)
NO. OF REPLICATES OF BEHAVIOURAL MEASUREMENTS[4]	1

POPULATION DENSITIES:-

TANK NOS.	DENSITY
1 & 2	25 fish (1.82/l)
3 & 4	75 fish (5.45/l)
5 & 6	150 fish (10.9/l)
7 & 8	250 fish (18.18/l)

FOOTNOTES:-

[1] "DURATION OF EXPERIMENT" refers to the total time of the entire experiment.

[2] "BEHAVIOURAL MEASUREMENTS" refers to the three principal Methods described under General Methods & Materials (pg. 23).

[3] "DURATION OF BEHAVIOURAL MEASUREMENTS" refers to the period of time, within the time-interval of the entire experiment, in which "BEHAVIOURAL MEASUREMENTS" were performed. The reason why the "DURATION OF EXPERIMENT" was longer than the time period allocated for "BEHAVIOURAL MEASUREMENTS" was that a population census to assess the rate of cannibalism, was required over this longer period.

[4] "NO. OF REPLICATES OF BEHAVIOURAL MEASUREMENTS" refers to the number of times "BEHAVIOURAL MEASUREMENTS" were duplicated in each tank within the time-interval of the entire experiment.

Table 16. A summary of the experimental methods and conditions used in determining the relationship between population density, cannibalism and other behavioural modes in the common carp *Cyprinus carpio*, (all terms within the Table requiring explanation are marked and explained in the footnotes below).

AGE OF ANIMALS AT START	3 day old larvae
DURATION OF EXPERIMENT[1]	26 days
FOOD	*Daphnia* & pelleted fish feed
FEEDING REGIME	all tanks *ad libitum* every 2hrs (between 08h00 and 22h00)
TEMPERATURE	25 ± 2 °C
DISSOLVED OXYGEN	6 ± 0.5ppm
TANK VOLUME	13,75 l
BEHAVIOURAL MEASUREMENTS[2]	number of different behavioural mode changes per 10 mins
DURATION OF BEHAVIOURAL MEASUREMENTS[3]	7 days (day 2 to day 8 & day 16 to day 22 of 26 days)
NO. OF REPLICATES OF BEHAVIOURAL MEASUREMENTS[4]	2

POPULATION DENSITIES:-

TANK NOS.	DENSITY
1 & 2	50 fish (3.64/l)
3 & 4	100 fish (7.27/l)
5 & 6	300 fish (21.82/l)
7 & 8	600 fish (43.64/l)

FOOTNOTES:-

1 "DURATION OF EXPERIMENT" refers to the total time of the entire experiment.

2 "BEHAVIOURAL MEASUREMENTS" refers to the measurement of the behavioural mode described under General Methods & Materials (pg. 23).

3 "DURATION OF BEHAVIOURAL MEASUREMENTS" refers to the period of time, within the time-interval of the entire experiment, in which "BEHAVIOURAL MEASUREMENTS" were performed. The reason why the "DURATION OF EXPERIMENT" was longer than the time period allocated for "BEHAVIOURAL MEASUREMENTS" was that a population census to assess the rate of cannibalism, was required over this longer period.

4 "NO. OF REPLICATES OF BEHAVIOURAL MEASUREMENTS" refers to the number of times "BEHAVIOURAL MEASUREMENTS" were duplicated in each tank within the time-interval of the entire experiment.

Table 17. A summary of the experimental methods and conditions used in determining the relationship between population density, cannibalism and other behavioural modes in the koi carp *Cyprinus carpio*, (all terms within the Table requiring explanation are marked and explained in the footnotes below).

AGE OF ANIMALS AT START	3 day old larvae
DURATION OF EXPERIMENT[1]	26 days
FOOD	*Daphnia* & pelleted fish feed
FEEDING REGIME	all tanks *ad libitum* every 2hrs (between 08h00 and 22h00)
TEMPERATURE	25 ± 2 °C
DISSOLVED OXYGEN	6 ± 0.5ppm
TANK VOLUME	13,75 l
BEHAVIOURAL MEASUREMENTS[2]	number of different behavioural mode changes per 10 mins
DURATION OF BEHAVIOURAL MEASUREMENTS[3]	7 days (day 2 to day 8 & day 16 to day 22 of 26 days)
NO. OF REPLICATES OF BEHAVIOURAL MEASUREMENTS[4]	2

POPULATION DENSITIES:-

TANK NOS.	DENSITY
1 & 2	50 fish
3 & 4	100 fish
5 & 6	500 fish
7 & 8	1000 fish

FOOTNOTES:-

[1] "DURATION OF EXPERIMENT" refers to the total time of the entire experiment.

[2] "BEHAVIOURAL MEASUREMENTS" refers to the measurement of the behavioural modes described under General Methods & Materials (pg. 23).

[3] "DURATION OF BEHAVIOURAL MEASUREMENTS" refers to the period of time, within the time-interval of the entire experiment, in which "BEHAVIOURAL MEASUREMENTS" were performed. The reason why the "DURATION OF EXPERIMENT" was longer than the time period allocated for "BEHAVIOURAL MEASUREMENTS" was that a population census to assess the rate of cannibalism, was required over this longer period.

[4] "NO. OF REPLICATES OF BEHAVIOURAL MEASUREMENTS" refers to the number of times "BEHAVIOURAL MEASUREMENTS" were duplicated in each tank within the time-interval of the entire experiment.

Table 18. A summary of the experimental methods and conditions used in determining the relationship between population density, cannibalism and other behavioural modes in the silver carp *Hypophthalmichthys molitrix*, (all terms within the Table requiring explanation are marked and explained in the footnotes below).

AGE OF ANIMALS AT START	3 day old larvae
DURATION OF EXPERIMENT[1]	31 days
FOOD	small, live *Daphnia*, pelleted fish feed & zoo- and phytoplankton
FEEDING REGIME	all tanks *ad libitum* every 2hrs (between 08h00 and 22h00)
TEMPERATURE	28 ± 2 °C
DISSOLVED OXYGEN	6 ± 0.5ppm
TANK VOLUME	13,75 l
BEHAVIOURAL MEASUREMENTS[2]	number of different behavioural mode changes per 10 mins
DURATION OF BEHAVIOURAL MEASUREMENTS[3]	7 days (day 2 to day 8 & day 16 to day 22 of 31 days)
NO. OF REPLICATES OF BEHAVIOURAL MEASUREMENTS[4]	2

POPULATION DENSITIES:-

TANK NOS.	DENSITY
1 & 2	50 fish (3.64/l)
3 & 4	100 fish (7.27/l)
5 & 6	500 fish (36.36/l)
7 & 8	1000 fish (72.73/l)

FOOTNOTES:-

1 "DURATION OF EXPERIMENT" refers to the total time of the entire experiment.

2 "BEHAVIOURAL MEASUREMENTS" refers to the measurement of the behavioural modes described under General Methods & Materials (pg. 23).

3 "DURATION OF BEHAVIOURAL MEASUREMENTS" refers to the period of time, within the time-interval of the entire experiment, in which "BEHAVIOURAL MEASUREMENTS" were performed. The reason why the "DURATION OF EXPERIMENT" was longer than the time period allocated for "BEHAVIOURAL MEASUREMENTS" was that a population census to assess the rate of cannibalism, was required over this longer period.

4 "NO. OF REPLICATES OF BEHAVIOURAL MEASUREMENTS" refers to the number of times "BEHAVIOURAL MEASUREMENTS" were duplicated in each tank within the time-interval of the entire experiment.

Table 19. A summary of the experimental methods and conditions used in determining the relationship between population density, cannibalism and other behavioural modes in the grass carp *Ctenopharyngodon idella*, (all terms within the Table requiring explanation are marked and explained in the footnotes below).

AGE OF ANIMALS AT START	4 day old larvae
DURATION OF EXPERIMENT[1]	35 days
FOOD	*Daphnia*, pelleted fish feed, liquidized duckweed (*Lemna* spp); larger fish: unliquidized duckweed & filamentous *Spirogyra*
FEEDING REGIME	all tanks *ad libitum* every 2hrs (between 08h00 and 22h00)
TEMPERATURE	28 ± 2 °C
DISSOLVED OXYGEN	6 ± 1ppm
TANK VOLUME	13,75 l
BEHAVIOURAL MEASUREMENTS[2]	number of different behavioural mode changes per 10 mins
DURATION OF BEHAVIOURAL MEASUREMENTS[3]	7 days (day 2 to day 8 of 35 days)
NO. OF REPLICATES OF BEHAVIOURAL MEASUREMENTS[4]	1

POPULATION DENSITIES:-

TANK NOS.	DENSITY
1 & 2	25 fish (1.82/l)
3 & 4	85 fish (6.18/l)
5 & 6	200 fish (14.55/l)

FOOTNOTES:-

[1] "DURATION OF EXPERIMENT" refers to the total time of the entire experiment.

[2] "BEHAVIOURAL MEASUREMENTS" refers to the measurement of the behavioural modes described under General Methods & Materials (pg. 23).

[3] "DURATION OF BEHAVIOURAL MEASUREMENTS" refers to the period of time, within the time-interval of the entire experiment, in which "BEHAVIOURAL MEASUREMENTS" were performed. The reason why the "DURATION OF EXPERIMENT" was longer than the time period allocated for "BEHAVIOURAL MEASUREMENTS" was that a population census to assess the rate of cannibalism, was required over this longer period.

[4] "NO. OF REPLICATES OF BEHAVIOURAL MEASUREMENTS" refers to the number of times "BEHAVIOURAL MEASUREMENTS" were duplicated in each tank within the time-interval of the entire experiment.

framework for experimentation. Lorenz's use of the term "aggression" also needs to be considered in the light of whether cannibalism is in fact an aggressive act, or whether it is simply a response to hunger. Aggression is defined by the Oxford Dictionary as : "of attack; offensive; forceful". It can thus be seen that cannibalism may begin simply as a response to hunger, but that this behaviour must of necessity become aggressive in nature since the process involves a struggle which requires the predator to use forceful measures to obtain its meal. The sibling prey will not simply allow itself to be taken without a struggle and will therefore offer resistance to the predator, thereby forcing an aggressive encounter. Thus the behaviour of a fish obtaining a meal by cannibalism obviously differs from that of a fish obtaining a non-living meal in the absence of any stresses (including competition). It is therefore accepted here that cannibalism is an aggressive act. It was thus decided to test the hypothesis whether cannibalistic aggression could be diverted or redirected by supplying live food as opposed to dry pelleted fish feed which supposedly supplies no outlet for aggression, or whether, by supplying live food the rate of cannibalism increases, due to the individual learning and acquiring a cannibalistic feeding response as a long-term feeding strategy. Several workers have advanced theories of "learning" associated with the development of cannibalism. They suggest that a reason as to why cannibalism might be higher in live food tanks, has to do with the development in young fish of a learning response in relation to feeding strategies. According to Hurley and Brannon (1967 see Malhotra and Munshi 1984) learning is involved in the act of feeding and an early association with food results in larvae being more successful feeders later on. It was suggested that high levels of cannibalism among fed larvae were attributable to the feeding experience of these larvae which their starved counterparts lacked. Fish reared on artificial diets (pellets) were initially found to be less successful at capturing fish prey than were fish reared on a natural live diet (Gillen et al. 1979). It might be that fish fed on a pelleted diet exhibited reduced levels of cannibalism since they were deprived of the opportunity to learn early in life how to catch live prey, whereas this would not be the case for those fed on live food. Tables 20 and 21 show the methods and conditions under which the experiments were performed.

5. Effect of alternative live food on the rate of cannibalism and other behavioural modes.

A number of workers have shown that by supplying an alternative source of live food to fish, the rate of cannibalism can be reduced. Li and Ayles (1981a see McIntyre *et al*. 1987) showed that desirable forage species minimized cannibalism in juvenile Atlantic salmon. Hokanson and Lien (1986) stated that cannibalism may be suppressed in larval walleye *Stizostedion vitreum*, by feeding them food with a high energy content. This is an important factor to consider since various live food organisms have differing energy contents and digestible energy values (Pyke *et al*. 1977).

Essentially, there are two questions to be answered when considering the effect of live food on the rate or occurrence of cannibalism. The first is in the same vein as the argument for the experiment concerning live versus dry food, ie. can cannibalistic aggression be redirected to other live prey items ? The second question concerns the "food-package type" and the optimal foraging strategy of the predator, ie. is there a preference by predators for a prey item of a particular size or a particular type and is this related to the food quality of the prey item and/or the amount of energy expended during prey capture? This question is based on the formula for an optimal foraging strategy as outlined by MacArthur and Wilson (1967), Pyke *et al*. (1977) and Hart and Connelan (1984), where food value (calories), handling time and search time are functions of

Table 20. A summary of the experimental methods and conditions used in determining the relationship between live versus dry food, cannibalism and other behavioural modes in the sharptooth catfish <u>Clarias gariepinus</u>, (all terms within the Table requiring explanation are marked and explained in the footnotes below).

AGE OF ANIMALS AT START	4.5 week old juveniles
DURATION OF EXPERIMENT[1]	10 days
DENSITY	10 fish/l
TEMPERATURE	25 ± 2 °C
DISSOLVED OXYGEN	7 ± 1ppm
TANK VOLUME	13,75 l
BEHAVIOURAL MEASUREMENTS[2]	Methods A, B & C
DURATION OF BEHAVIOURAL MEASUREMENTS[3]	7 days (day 2 to day 8 of 10 days)
NO. OF REPLICATES OF BEHAVIOURAL MEASUREMENTS[4]	1
FEEDING REGIME	all tanks <u>ad libitum</u> every 2hrs (between 08h00 and 22h00)

FEEDING:-

TANK NOS.	FEEDING REGIME
1 & 2	dry feed
3 & 4	<u>Daphnia</u> spp.

FOOTNOTES:-

[1] "DURATION OF EXPERIMENT" refers to the total time of the entire experiment.

[2] "BEHAVIOURAL MEASUREMENTS" refers to the three principal Methods described under General Methods & Materials (pg. 23).

[3] "DURATION OF BEHAVIOURAL MEASUREMENTS" refers to the period of time, within the time-interval of the entire experiment, in which "BEHAVIOURAL MEASUREMENTS" were performed. The reason why the "DURATION OF EXPERIMENT" was longer than the time period allocated for "BEHAVIOURAL MEASUREMENTS" was that a population census to assess the rate of cannibalism, was required over this longer period.

[4] "NO. OF REPLICATES OF BEHAVIOURAL MEASUREMENTS" refers to the number of times "BEHAVIOURAL MEASUREMENTS" were duplicated in each tank within the time-interval of the entire experiment.

Table 21. A summary of the experimental methods and conditions used in determining the relationship between live versus dry food, cannibalism and other behavioural modes in the rainbow trout *Oncorhynchus mykiss*, (all terms within the Table requiring explanation are marked and explained in the footnotes below).

AGE OF ANIMALS AT START	2 week old larvae
DURATION OF EXPERIMENT[1]	12 days
FOOD	*Daphnia* & pelleted fish feed
TEMPERATURE	15 ± 2 °C
DISSOLVED OXYGEN	6 ± 1ppm
TANK VOLUME	13,75 l
DENSITY	14,5 fish/l
BEHAVIOURAL MEASUREMENTS[2]	Methods A, B & C
DURATION OF BEHAVIOURAL MEASUREMENTS[3]	7 days (day 2 to day 8 of 12 days)
NO. OF REPLICATES OF BEHAVIOURAL MEASUREMENTS[4]	1
FEEDING REGIME	all tanks *ad libitum* every 2hrs (between 08h00 and 22h00)

FEEDING:-

TANK NOS.	FEEDING REGIME
1 & 2	dry feed
3 & 4	*Daphnia* spp.

FOOTNOTES:-

[1] "DURATION OF EXPERIMENT" refers to the total time of the entire experiment.

[2] "BEHAVIOURAL MEASUREMENTS" refers to the three principal Methods described under General Methods & Materials (pg. 23).

[3] "DURATION OF BEHAVIOURAL MEASUREMENTS" refers to the period of time, within the time-interval of the entire experiment, in which "BEHAVIOURAL MEASUREMENTS" were performed. The reason why the "DURATION OF EXPERIMENT" was longer than the time period allocated for "BEHAVIOURAL MEASUREMENTS" was that a population census to assess the rate of cannibalism, was required over this longer period.

[4] "NO. OF REPLICATES OF BEHAVIOURAL MEASUREMENTS" refers to the number of times "BEHAVIOURAL MEASUREMENTS" were duplicated in each tank within the time-interval of the entire experiment.

the net rate of food gain. They hypothesized that an animal will always choose the optimal feeding strategy, ie. lowest search and handling time resulting in the highest food value, and that an animal will never specialize on a "less preferred" food type regardless of its' abundance.

Thus by supplying alternative types of live food organisms which are larger than the dry pelleted food or Daphnia, fish may be able to maintain a high energy diet and a high food conversion ratio, the side effect of which might be a reduction in the rate of cannibalism.

In contrast to the above hypothesis that alternative live food suppresses cannibalism, Pomeroy (1981 see Polis and Myers 1985) found that the presence of large potential prey items could stimulate the development of cannibalistic larvae. He produced cannibalistic morphs in the laboratory by feeding young tadpoles with live fairy shrimp, rather than a on a diet of organic food particles.

It was the aim of this experiment to determine which of the above hypotheses could be accepted using Clarias gariepinus as the test species.

Table 22 shows the methods and conditions under which the experiment was performed.

6. Effect of photoperiod on the rate of cannibalism and other behavioural modes.

Evidence suggests that Clarias gariepinus is nocturnal, relying

Table 22. A summary of the experimental methods and conditions used in determining the relationship between alternative live food, cannibalism and other behavioural modes in the sharptooth catfish <u>Clarias gariepinus</u>, (all terms within the Table requiring explanation marked and are explained in the footnotes below).

AGE OF ANIMALS AT START	6 week old juveniles
DURATION OF EXPERIMENT[1]	4 days
TEMPERATURE	26 ± 2 °C
DISSOLVED OXYGEN	7 ± 0.5ppm
TANK VOLUME	13,75 l
DENSITY	10 fish/tank in tanks 1 to 6 (0,73 fish/l) 8 fish/tank in tanks 7 & 8 (0,58 fish/l)
BEHAVIOURAL MEASUREMENTS[2]	Methods A, B & C
DURATION OF BEHAVIOURAL MEASUREMENTS[3]	4 days (day 1 to day 4 of 4 days)
NO. OF REPLICATES OF BEHAVIOURAL MEASUREMENTS[4]	1

FEEDING:-

TANK NOS.	FEEDING REGIME (<u>ad libitum</u> every 2 hrs between 08h00 & 22h00)
1 & 2	control - all types described below
3 & 4	<u>Daphnia</u> spp. (1±0.5 mm)
5 & 6	<u>Tilapia rendalli</u> (larvae 11±1 mm)
7 & 8	fairy shrimp (a Branchiopod of the order Anostracha 28±2 mm)

FOOTNOTES:-

1 "DURATION OF EXPERIMENT" refers to the total time of the entire experiment.

2 "BEHAVIOURAL MEASUREMENTS" refers to the three principal Methods described under General Methods & Materials (pg. 23).

3 "DURATION OF BEHAVIOURAL MEASUREMENTS" refers to the period of time, within the time-interval of the entire experiment, in which "BEHAVIOURAL MEASUREMENTS" were performed. The reason why the "DURATION OF EXPERIMENT" was longer than the time period allocated for "BEHAVIOURAL MEASUREMENTS" was that a population census to assess the rate of cannibalism, was required over this longer period.

4 "NO. OF REPLICATES OF BEHAVIOURAL MEASUREMENTS" refers to the number of times "BEHAVIOURAL MEASUREMENTS" were duplicated in each tank within the time-interval of the entire experiment.

more on tactile, chemical or electrical senses for its responses to the environment (Bruton 1979a and b). It appears that adult fish have a diel activity rhythm, being active and feeding predominantly at night (Bruton 1979a and b). Clarias gariepinus is also better adapted to seek prey and avoid being preyed upon under conditions of low light intensity or darkness. This is because its acuity of vision is very poor and it relies on the tactile, chemosensory and electrosensory functions of its four pairs of circumoral barbels to detect food, prey and to explore its environment (Bruton 1979b; Hecht and Appelbaum 1988; Britz and Pienaar in press). This behaviour is in distinct contrast to visual feeders such as trout or cichlids. Loadman et al. (1986), working on walleye, concluded that it was better to have continuous light to keep fish dispersed throughout the water column, as an increase in density near the tank floor at night led to an increase in the rate of cannibalism. On the basis of the natural history of Clarias gariepinus and the findings of Loadman et al. (op. cit.) it was decided to test the effect of photoperiod on cannibalism in Clarias gariepinus.

In order to test the hypothesis, two tanks were darkened using black PVC plastic, while two others were subject to continuous illumination (200 lux at the water surface) using the lighting system previously described. The behaviour of the fish in the darkened tanks was observed through a flap in the PVC cover. When behavioural observations were made on the fish in the dark tanks the laboratory was darkened and the behaviour of the fish was observed using military image intensifiers.

The behavioural observations performed were slightly different from the three principal methods described in the "General Methods" section. To recapitulate, these three experiments were as follows : the first set of observations was designed to determine the overall activity pattern for a period of ten minutes, the second, to determine the number of aggressive encounters during a period of five minutes, while the third determined the number of aggressive encounters per fifty physical contacts. For the first method the activity of a particular fish in each of the two dark tanks, D1 and D2, was recorded continuously for intervals of five and 10 minutes respectively. Similarly the behaviour of a particular fish in the two light tanks was recorded for five and 10 minutes respectively. The reason for the unequal length of observation periods was because occupational safety regulations only permit the continual use of image intensifiers for a period of 15 minutes at intervals of 30 minutes.

For the second method (the number of aggressive encounters observed during set time intervals) both the dark and light tanks were observed for three and five minutes respectively.

For the third method (the number of aggressive encounters observed in a set number of physical contacts) the number of physical contacts observed in the dark tanks, D1 and D2, were preset at 25 and 50 respectively, and similarly, for the light tanks, L1 and L2, 25 and 50 contacts respectively.

Table 23 shows the methods and conditions under which the experiment was performed.

7. Effect of refuges on the rate of cannibalism and other behavioural modes.

In their natural environment, *Clarias gariepinus* larvae generally restrict themselves to refuges provided by the rootstocks of semi-aquatic plants or bundles of flotsam and detritus on the edges of rivers and lakes (Greenwood 1955, 1956; Bruton 1978). Behavioural observations conducted without refuges have shown

Table 23. A summary of the experimental methods and conditions used in determining the relationship between photoperiod, cannibalism and other behavioural modes in the sharptooth catfish *Clarias gariepinus*, (all terms within the Table requiring explanation are marked and explained in the footnotes below).

AGE OF ANIMALS AT START	6 week old juveniles
DURATION OF EXPERIMENT[1]	11 days
FOOD	live *Daphnia* & pelleted fish feed
FEEDING REGIME	*ad libitum* every 2 hrs
TEMPERATURE	29 ± 1 °C
DISSOLVED OXYGEN	7 ± 1ppm
TANK VOLUME	13,75 l
DENSITY	1 fish/l
BEHAVIOURAL MEASUREMENTS[2]	Methods A, B & C
DURATION OF BEHAVIOURAL MEASUREMENTS[3]	7 days (day 1 to day 7 of 11 days)
NO. OF REPLICATES OF BEHAVIOURAL MEASUREMENTS[4]	1

TANK NOS.	PHOTOPERIOD REGIME (between 08h00 & 22h00)
1 & 2	24hr dark/ 0hr light
3 & 4	0hr dark/ 24hr light

FOOTNOTES:-

[1] "DURATION OF EXPERIMENT" refers to the total time of the entire experiment.

[2] "BEHAVIOURAL MEASUREMENTS" refers to the three principal Methods described under General Methods & Materials (pg. 23).

[3] "DURATION OF BEHAVIOURAL MEASUREMENTS" refers to the period of time, within the time-interval of the entire experiment, in which "BEHAVIOURAL MEASUREMENTS" were performed. The reason why the "DURATION OF EXPERIMENT" was longer than the time period allocated for "BEHAVIOURAL MEASUREMENTS" was that a population census to assess the rate of cannibalism, was required over this longer period.

[4] "NO. OF REPLICATES OF BEHAVIOURAL MEASUREMENTS" refers to the number of times "BEHAVIOURAL MEASUREMENTS" were duplicated in each tank within the time-interval of the entire experiment.

that the behaviour of larval and juvenile *Clarias gariepinus* is characterized by an increasing level of territorial aggression and disturbed rest activity (a few fast darting movements followed by a rest period) interspersed with long rest periods (Britz and Pienaar in press). If refuges are an important factor contributing to the survival of *Clarias gariepinus* larvae and juveniles under natural conditions, and territorial aggression increases in the absence of refuges, it is likely that cannibalistic aggression would also increase to higher levels if no refuges were supplied. The effect of a variable number of refuges on the rate of cannibalism was therefore tested for *Clarias gariepinus*. Table 24 shows the methods and conditions under which the experiment was performed.

8. Effect of turbidity on the rate of cannibalism and other behavioural modes.

The term "turbidity" refers to the scattering or absorption of light by suspended or dissolved particles in water (Bruton 1988). Bruton (op. cit.) lists the negative and positive effects of high turbidity levels on fishes:

Negative effects and properties of turbid water:

- reduced egg and larval survival
- interference with the breeding behaviour of nest-digging species
- reduced feeding efficiency and food availability
- reduced the growth rates and maximum size of fish
- reduction in the size of fish populations
- reduced habitat diversity as a result of particulate matter forming blanketing sediments, filling up the gaps between pebbles and reducing the size of the photosynthetic zone
- suspended particles may be responsible for transporting adhered toxic substances
- suspended matter causing very high turbidities may clog the

Table 24. A summary of the experimental methods and conditions used in determining the relationship between turbidity, cannibalism and other behavioural modes in the sharptooth catfish *Clarias gariepinus*, (all terms within the Table requiring explanation are marked and explained in the footnotes below).

AGE OF ANIMALS AT START	5 week old larvae
DURATION OF EXPERIMENT[1]	7 days
FOOD	live *Daphnia* & pelleted fish feed
FEEDING REGIME	*ad libitum* every 2 hrs between 08h00 and 22h00
TEMPERATURE	25 ± 2 °C
DISSOLVED OXYGEN	tanks 1 & 2 : 7 ± 0.5ppm tanks 3,4,5 & 6 : 6 1ppm
TANK VOLUME	13,75 l
DENSITY	1 fish/l
BEHAVIOURAL MEASUREMENTS[2]	Methods A, B & C
DURATION OF BEHAVIOURAL MEASUREMENTS[3]	7 days (day 1 to day 7 of 7 days)
NO. OF REPLICATES OF BEHAVIOURAL MEASUREMENTS[4]	1

TANK NOS.	TURBIDITY REGIME (between 08h00 & 22h00)
1 & 2	clear
3 & 4	intermediate turbidity (fish just visible)
5 & 6	complete turbidity (fish not visible)

FOOTNOTES:-

1 "DURATION OF EXPERIMENT" refers to the total time of the entire experiment.

2 "BEHAVIOURAL MEASUREMENTS" refers to the three principal Methods described under General Methods & Materials (pg. 23).

3 "DURATION OF BEHAVIOURAL MEASUREMENTS" refers to the period of time, within the time-interval of the entire experiment, in which "BEHAVIOURAL MEASUREMENTS" were performed. The reason why the "DURATION OF EXPERIMENT" was longer than the time period allocated for "BEHAVIOURAL MEASUREMENTS" was that a population census to assess the rate of cannibalism, was required over this longer period.

4 "NO. OF REPLICATES OF BEHAVIOURAL MEASUREMENTS" refers to the number of times "BEHAVIOURAL MEASUREMENTS" were duplicated in each tank within the time-interval of the entire experiment.

gill filaments and kill the fish
- fish communities may be changed as a result of alterations in feeding patterns

Positive effects and properties of turbid water:-
- affords cover and protection from predators, especially for small fish
- may provide a source of food in the form of diatoms and minute algae which adhere to the particles
- turbidity gradients may provide a navigational aid for fishes seeking and entering estuaries.

As high turbidities are such a common feature of Southern African inland waters, it is not surprising that certain fishes are well adapted to living under those conditions, eg. the sharptooth catfish which thrives in turbid waters and reaches its' greatest size in turbid rivers (Bruton 1988). Due to the animal's tactile and chemosensory abilities, its ability to withstand low dissolved oxygen levels and its preference for dark and aversion for light (Britz and Pienaar in press), it is able to thrive in turbid conditions (Bruton 1988). The effect of turbidity on the behaviour of C. gariepinus was therefore tested in order to determine whether territorial or cannibalistic aggression was influenced by turbidity. Table 25 shows the methods and conditions under which the experiment was performed.

9. To determine whether potential cannibals can be recognised phenotypically.

There is evidence to suggest that cannibalism is genetically controlled to some degree (Thibault 1974) and that a potential for cannibalism is expressed phenotypically (Fox 1975a; Polis 1981). The following experiment was designed to determine whether

Table 25. A summary of the experimental methods and conditions used in determining the relationship between refuges, cannibalism and other behavioural modes in the sharptooth catfish *Clarias gariepinus*, (all terms within the Table requiring explanation are marked and explained in the footnotes below).

AGE OF ANIMALS AT START	4.5 week old juveniles
DURATION OF EXPERIMENT[1]	7 days
FOOD	live *Daphnia* & pelleted fish feed
FEEDING REGIME	*ad libitum* every 2 hrs between 08h00 & 22h00
TEMPERATURE	26 ± 2 °C
DISSOLVED OXYGEN	7 ± 1ppm
TANK VOLUME	13,75 l
DENSITY	1,5 fish/l
BEHAVIOURAL MEASUREMENTS[2]	Experimental Method A
DURATION OF BEHAVIOURAL MEASUREMENTS[3]	7 days (day 1 to day 7 of 7 days)
NO. OF REPLICATES OF BEHAVIOURAL MEASUREMENTS[4]	1

TANK NOS.	REFUGES SUPPLIED
1 & 2	control : no refuges
3 & 4	1 x 10mm diam. mesh shade cloth 200mm x 200mm + 5 granite stones - each approx. 30mm x 20mm
5 & 6	2 x 10mm diam. mesh shade cloth 200mm x 200mm + 10 granite stones - each approx. 30mm x 20mm

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FOOTNOTES:-

1 "DURATION OF EXPERIMENT" refers to the total time of the entire experiment.

2 "BEHAVIOURAL MEASUREMENTS" refers to the three principal Methods described under General Methods & Materials (pg. 23).

3 "DURATION OF BEHAVIOURAL MEASUREMENTS" refers to the period of time, within the time-interval of the entire experiment, in which "BEHAVIOURAL MEASUREMENTS" were performed. The reason why the "DURATION OF EXPERIMENT" was longer than the time period allocated for "BEHAVIOURAL MEASUREMENTS" was that a population census to assess the rate of cannibalism, was required over this longer period.

4 "NO. OF REPLICATES OF BEHAVIOURAL MEASUREMENTS" refers to the number of times "BEHAVIOURAL MEASUREMENTS" were duplicated in each tank within the time-interval of the entire experiment.

it was possible to select visually for cannibalism using phenotypic expressions of the "cannibalistic genotype". This would, firstly, support the findings of Thibault (op. cit.), Fox (op. cit.) and Polis (op. cit.). Secondly, it would also suggest that aquaculturists may have inadvertently selected for cannibalism while selecting for other features in broodstock, since many features of a cannibal, such as large relative size and robustness, are those which a breeder desires in his broodstock. Finally it would support the hypothesis that it is possible to identify and remove cannibals in order to reduce the rate of cannibalism in a captive population.

The experiment was conducted using qualitative criteria and observations and thus the results need to be viewed with some circumspection. Two tanks were monitored, viz. a "cannibal" tank and a "potential cannibal" tank. Cannibals were identified in the "potential cannibal" tank, captured and placed into the "cannibal" tank. For each fish removed from the "potential cannibal" tank, a substitute was provided from the stock tank and one "least-likely-cannibal" was removed from the "cannibal" tank. Thus the experiment was a process of visually selecting for and against apparent cannibalism in an attempt to visually assess cannibalistic behaviour. Visual cues used to assess a "potential cannibal" were social dominance and size variation, since Brown (1957) concluded that behavioural dominance caused size variation, which has been shown to be a cause of cannibalism. Other cues were the relative robustness of an individual and, obviously, blatant acts of cannibalism. Four 27,5 l tanks were each stocked with 30 randomly selected three week old juveniles of similar size. Two of these were the "cannibal" tanks, the other two being the "potential cannibal" tanks. After an acclimation period of 24 hours the fish were observed twice daily for periods of 10 minutes as well as at other random checks between 08h00 and 22h00, in order to identify the cannibalistic individuals and distribute them amongst the tanks as described

Table 26. A summary of the experimental methods and conditions used to visually assess the difference between cannibals and non-cannibals in the sharptooth catfish Clarias gariepinus.

AGE OF ANIMALS AT START	3 week old juveniles
DURATION OF EXPERIMENT	30 days
FOOD	live Daphnia & pelleted fish feed
FEEDING REGIME	ad libitum every 2 hrs between 08h00 and 22h00
TEMPERATURE	27 ± 2 °C
DISSOLVED OXYGEN	7 ± 1ppm
TANK VOLUME	27,5 l
DENSITY	1 fish/l
BEHAVIOURAL MEASUREMENTS	qualitative observations 2x daily for 10 mins in each tank + random checks

TANK NOS.	TREATMENT
1 & 2	"cannibals"
3 & 4	"potential cannibals"

Table 27. A summary of the experimental methods and conditions used to determine the aggressive behaviour of the redbreast tilapia *Tilapia rendalli*, (all terms within the Table requiring explanation are marked and are explained in the footnotes below).

AGE OF ANIMALS AT START	3 day old larvae
DURATION OF EXPERIMENT[1]	30 days
FOOD	live *Daphnia* & pelleted fish feed
FEEDING REGIME	*ad libitum* every 2 hrs between 08h00 and 22h00
TEMPERATURE	27 ± 1 °C
DISSOLVED OXYGEN	6 ± 1ppm
TANK VOLUME	13,75 l
DENSITY	12 fish/l
BEHAVIOURAL MEASUREMENTS	number of aggressive incidents per 10 mins daily
DURATION OF BEHAVIOURAL MEASUREMENTS[2]	7 days (day 2 to day 8 & day 16 to day 22 of 30 days)
NO. OF REPLICATES OF BEHAVIOURAL MEASUREMENTS[3]	2
NUMBER OF REPLICATES OF ENTIRE EXPERIMENT	2

FOOTNOTES:-

[1] "DURATION OF EXPERIMENT" refers to the total time of the entire experiment.

[2] "DURATION OF BEHAVIOURAL MEASUREMENTS" refers to the period of time, within the time-interval of the entire experiment, in which "BEHAVIOURAL MEASUREMENTS" were performed. The reason why the "DURATION OF EXPERIMENT" was longer than the time period allocated for "BEHAVIOURAL MEASUREMENTS" was that a population census to assess the rate of cannibalism, was required over this longer period.

[3] "NO. OF REPLICATES OF BEHAVIOURAL MEASUREMENTS" refers to the number of times "BEHAVIOURAL MEASUREMENTS" were duplicated in each tank within the time-interval of the entire experiment.

above. Table 26 shows the methods and conditions under which the experiment was performed.

10. Determination of aggressive behaviour in *Tilapia rendalli*.

The objective of including *T. rendalli* in the study was firstly to determine whether this species was cannibalistic or not. Secondly, it was necessary that a K-selected or precocial species be tested in order to compare the existence, rate and extent of cannibalism with other species on the life-history continuum. *T. rendalli* was considered to be the most K-selected or precocial species used in this study (see Table 5). Table 27 shows the methods and conditions under which the experiment was performed.

Statistical methods.

Two different statistical methods were used for data analysis. The Proportionality Test (Weiss 1989 pp. 425-432), which tests the difference between two proportions, was used for all results obtained using Method A (the method to determine the overall activity pattern), while the Chi-Square Goodness-of-Fit Test was used for all results obtained using Method B (the method to determine the number of aggressive encounters for five minutes each day) and Method C (the method to determine the number of aggressive encounters per fifty physical contacts). Student's t-Test was used for the experiment determining the effect of photoperiod on the rate of cannibalism in *Clarias gariepinus*. It was decided to accept or reject all null hypotheses at the 5% level. This is an acceptable level for behavioural studies (Siegel 1956).

For clarity, the standard deviations of the means for all data represented in bar graphs in the results section, are presented in tables in Appendix II.

Chapter 3

RESULTS

1. Evaluation of behavioural responses in catfish to a changing environmental parameter.

a) One week old larvae:-

In the experiment to determine the effect of food availability on the overall activity pattern of *C. gariepinus* larvae, it was found that cannibalism increased markedly during the six day period of food deprivation. After the resumption of feeding the rate of cannibalism declined to zero. However, three days after the resumption of feeding, cannibalism again became evident (Fig. 3a). The level of territoriality appeared to be lowest during the period of food deprivation.

In determining the number of aggressive encounters caused by altering the food availability over a set period each day, cannibalism was found to occur approximately half-way through the period of food deprivation, and again on the day feeding was resumed (day eleven - see Fig. 3b). The level of territoriality fluctuated, apparently following no particular trend, apart from an increase in the level of this behaviour on the day feeding was resumed.

In the experiment to determine the effect of food availability on the number of aggressive encounters per fifty physical contacts, cannibalism was observed mid-way through the period of food deprivation, and increased towards the end of this period (Fig. 3c). The incidence of cannibalism continued to increase for one day after the period of food deprivation had ended, but declined rapidly the following day. The level of territoriality appeared to follow a similar pattern.

b) Five week old juveniles :-

Cannibalism was only observed on the day when feeding was resumed (day 10) following a six day period of starvation (Figs. 4a, b, c and d). Territorial behaviour declined toward the end of the period of food deprivation, ie. on days eight and nine, but returned to its initial level one day after feeding recommenced (Fig. 4a). Territoriality then appeared to enter an oscillatory period.

Active swimming behaviour remained fairly constant until feeding was halted, whereafter it declined until feeding was resumed (Fig. 4a). Resting behaviour also remained fairly constant until feeding was halted, whereafter the amount of time spent resting steadily increased until feeding was resumed (Fig. 4a). The resumption of feeding appeared to produce a marked fluctuation in the levels of active swimming and resting behaviour.

The results of the experiments on both age groups of catfish suggest that the responses observed in the following set of experiments were real and not artefacts of captive behaviour.

2. Effect of food availability on the rate of cannibalism and other behavioural modes.

2.1 Catfish.

In determining the effect of various feeding regimes on the overall activity pattern of *C. gariepinus* larvae, it was found that cannibalism was significantly higher ($p < 0.01$) in those

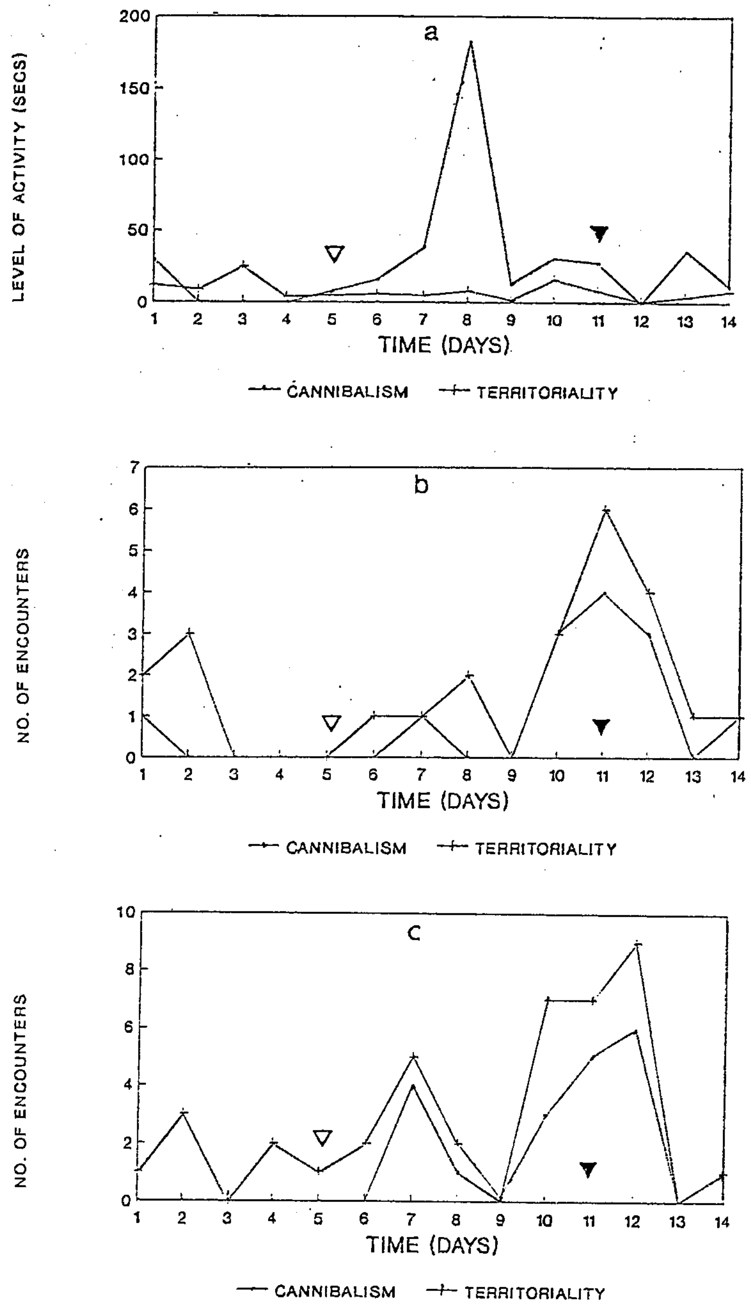


Fig. 3. The changes in the behaviour of LARVAL <u>Clarias gariepinus</u> as affected by food availability over a fourteen day period; (a) shows the daily changes in the overall activity pattern, expressed as the mean level of activity; (b) shows the daily changes in the number of aggressive encounters during a five minute time interval each day, expressed as the mean number of encounters and (c) shows the daily changes in the number of aggressive encounters per 50 physical contacts, expressed as the mean number of encounters. (C = cannibalism; T = territoriality; ▽ indicates the day on which feeding was halted and ▼ the day on which feeding was resumed).

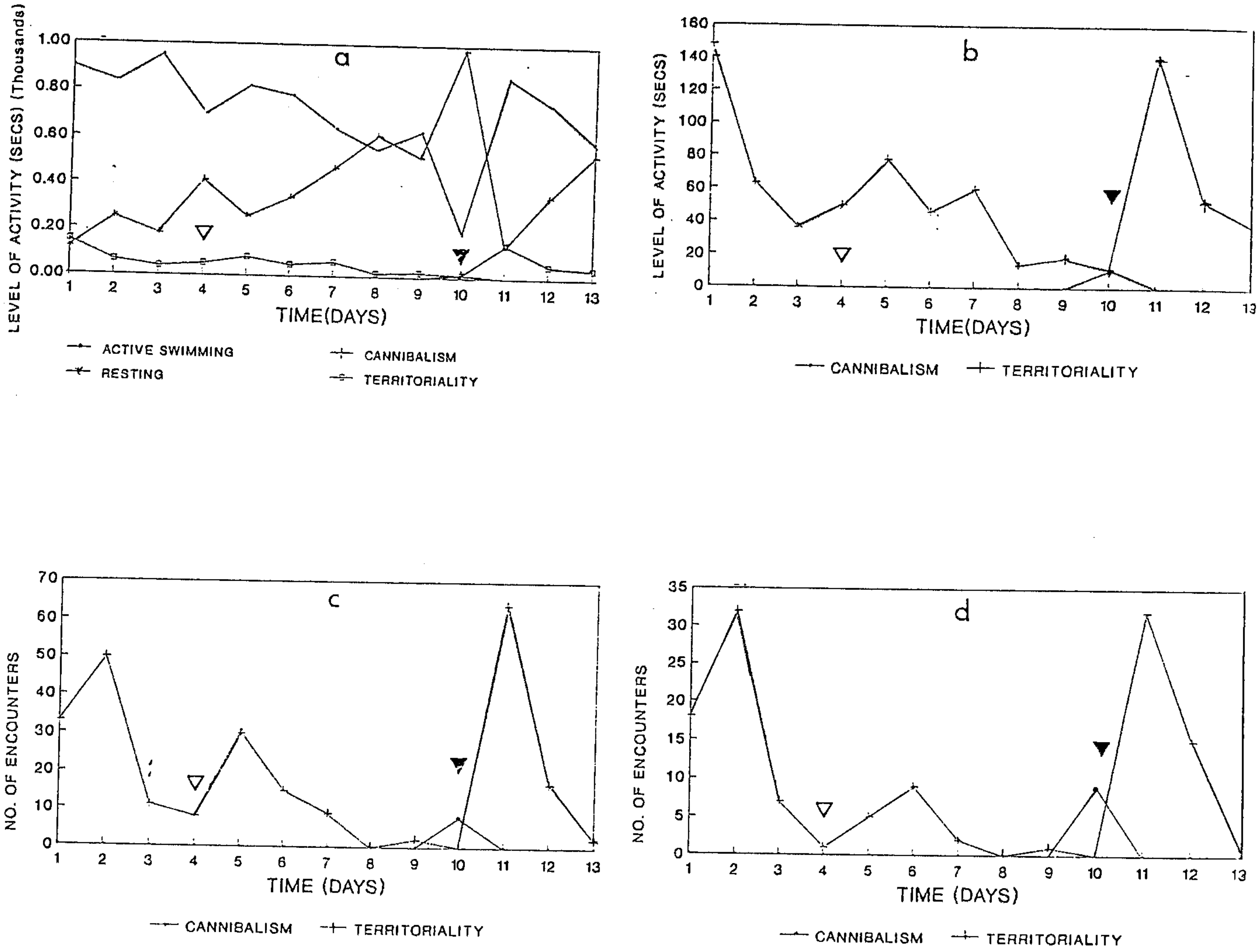


Fig. 4. The changes in the behaviour of JUVENILE <u>Clarias gariepinus</u> as affected by food availability over a thirteen day period; (a) and (b) show the daily changes in the overall activity pattern, expressed as the mean level of activity; (c) shows the daily changes in the number of aggressive encounters during five minute time intervals each day and (d) shows the daily changes in the number of aggressive encounters per 50 physical contacts. Both (c) and (d) are expressed as the mean number of encounters. (C = cannibalism; T = territoriality; A = active swimming; R = resting behaviour; ▽ indicates the day on which feeding was halted and ▼ the day on which feeding was resumed).

larvae which were fed at 5% body weight per day and those which received no food (Fig. 5). No cannibalism was observed in the larvae fed at 10% body weight once per day and those which were fed ad libitum to satiation. The levels of active swimming, browsing, disturbed rest and territoriality were all lower in those larvae deprived of food, while the amount of time spent resting increased (Fig. 5).

Analysis of the number of aggressive encounters over a set period each day revealed that cannibalism was significantly higher ($p<0.01$), while territoriality was significantly lower ($p<0.01$) in those larvae deprived of food (Fig. 6a). The general trend appeared to be a decline in territoriality with decreasing availability of food, while cannibalism increased.

Analysis of the number of aggressive encounters per fifty physical contacts showed that cannibalism was significantly higher ($p<0.01$), while territoriality was found to be significantly lower ($p<0.01$) in those larvae deprived of food (Fig. 6b). In general the rate of cannibalism appears to increase with decreasing availability of food, as does territoriality. A significant decrease in territoriality ($p<0.01$) is, however, observed in those larvae on a starvation feeding regime.

The actual rate of cannibalism, obtained by counting the fish at intervals of a few days over the experimental period, was influenced significantly by the food ration (Fig. 7). Cannibalism was highest in the starvation feeding regime, and declined with increasing food availability over the experimental period of thirty days. Analyzing the data obtained from the population census over the first six days, reveals that the percentage of the population cannibalized per day increased with decreasing food availability (Table 28). The specific reason for conducting

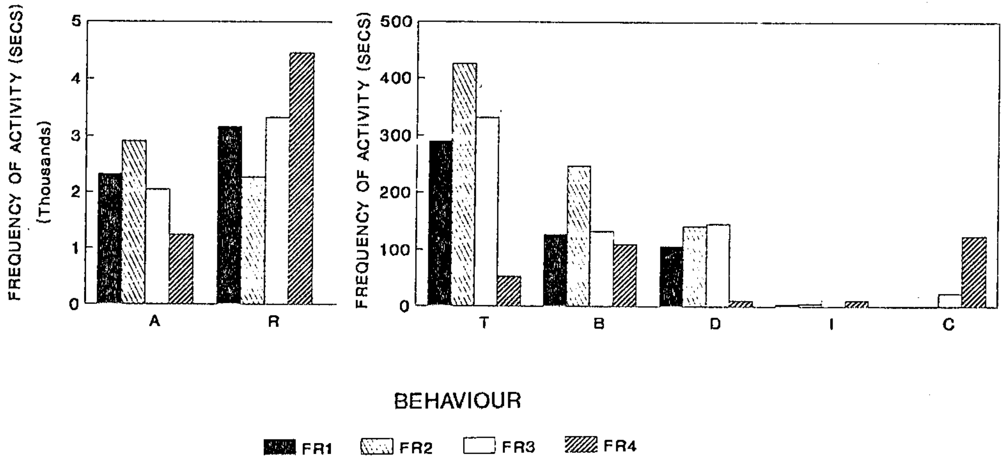


Fig. 5. Proportion of time devoted to different behavioural modes by Clarias gariepinus maintained under various feeding regimes (FR's) over a period of six days. The frequency of activity was calculated by summing the time devoted to each of the behavioural modes (recorded during a daily 10 minute period) for the six days. (A = active swimming; B = browsing; C = cannibalism; D = disturbed activity; I = air breathing; R = resting; T = territoriality; FR1 = satiation; FR2 = 10% body weight per day; FR3 = 5% body weight per day; FR4 = starvation).

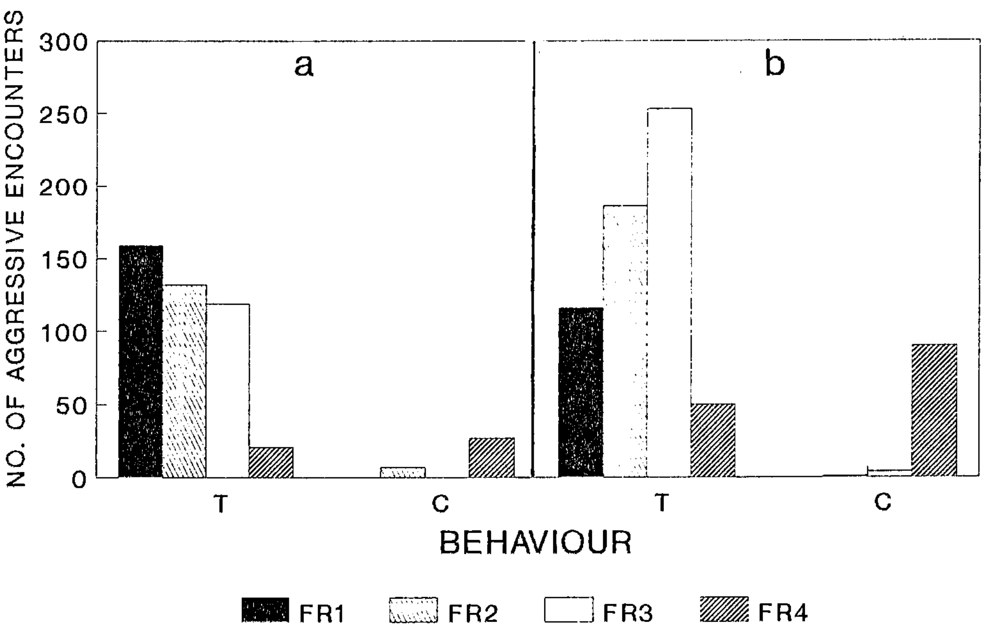


Fig. 6. Level of aggressive behaviour displayed by Clarias gariepinus maintained under various feeding regimes (FR's) over a six day period, expressed as (a) the summation of the mean number of aggressive encounters during five minute time intervals each day and (b) the daily mean number of aggressive encounters per 50 physical contacts. (T= territoriality; C= cannibalism; FR1 = satiation; FR2 = 10% body weight per day; FR3 = 5% body weight per day; FR4 = starvation).

a population census over six and thirty day periods, was to determine whether there were any differences between rates of cannibalism over a short and a long period as a result of varying food rations.

2.2 Trout.

In the experiment to determine the effect of various feeding regimes on the overall activity pattern of O. mykiss larvae, cannibalism was only observed on a starvation feeding regime (Fig. 8). An interesting relationship between the various types of aggressive behaviour is revealed in Fig. 8. There are four types of aggressive behaviour exhibited by rainbow trout, viz. territoriality, cannibalism, extended fighting and mouth wrestling. Two of these, namely territoriality and extended fighting, were significantly lower ($p<0.01$) in the larvae deprived of food. Cannibalism and mouth wrestling, however, were significantly higher ($p<0.01$) in larvae maintained on a starvation regime. Observations indicated that mouth wrestling was linked to cannibalism, in that this behaviour was often an initial stage in the ingestion of a sibling. Abbot and Dill (1985)

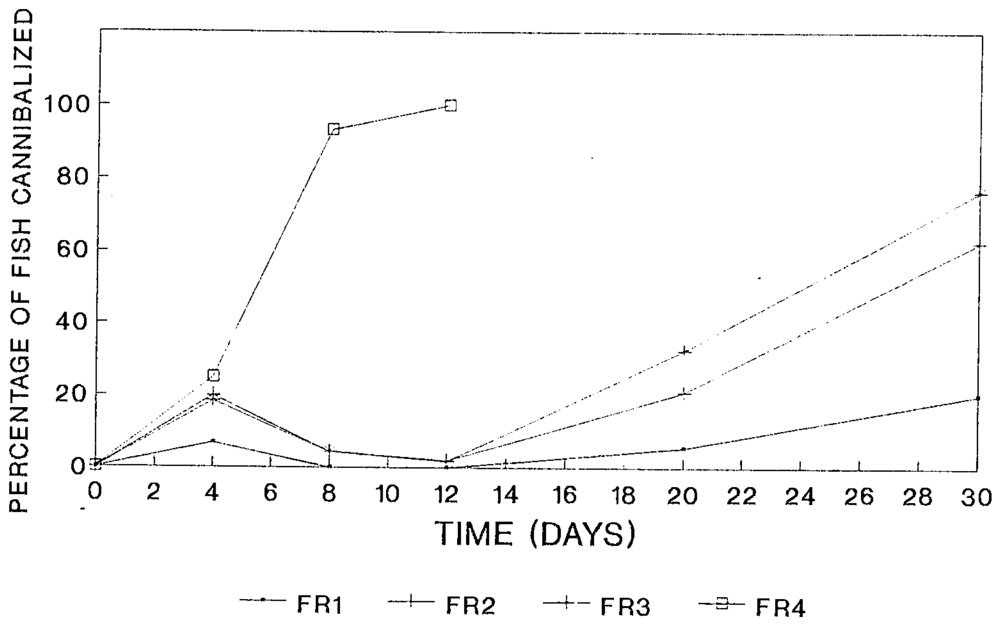


Fig. 7. Number of Clarias gariepinus cannibalized as influenced by daily feeding regime (FR), expressed as a percentage of fish remaining in the tank. (FR1 = satiation; FR2 = 10% body weight per day; FR3 = 5% body weight per day; FR4 = starvation).

Table 28. Differences in the rate of cannibalism in Clarias gariepinus, as influenced by various feeding regimes (FR's) over the first six days of the thirty day experimental period.

FEEDING REGIME (FR)	% OF POPULATION CANNIBALIZED/DAY
SATIATION (FR1)	0.6
10% BODY WEIGHT/DAY (FR2)	2.0
5% BODY WEIGHT/DAY (FR3)	2.8
STARVATION (FR4)	13.6

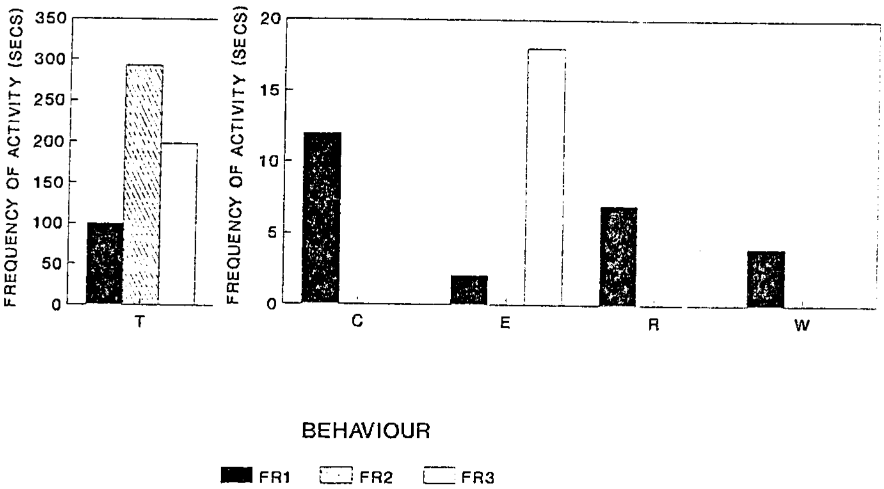


Fig. 8. Proportion of time devoted to different behavioural modes by Oncorhynchus mykiss maintained under various feeding regimes (FR's) over a period of seven days. The frequency of activity was calculated by summing the time devoted to each of the behavioural modes (recorded during a daily 10 minute period) for the seven days. (T = territoriality; C = cannibalism; E = extended fighting; R = resting behaviour; W = mouth wrestling; FR1 = satiation; FR2 = 10% body weight/day; FR3 = starvation).

described the mouth wrestling behaviour of steelhead trout, but did not record it as leading to cannibalism. However, observations in this study revealed that a cannibal would often grasp a sibling by the jaws, subsequently attempting to engulf it. Resting behaviour was highest amongst those larvae deprived of food.

The number of aggressive encounters over a set period of time each day, revealed that the level of territoriality was significantly lower ($p<0.01$) in those larvae deprived of food (Fig. 9a)

Similarly, in the results obtained from counting the number of aggressive encounters per fifty physical contacts, territoriality and extended fighting behaviour were both found to be significantly lower ($p<0.01$ and $p<0.05$ respectively) in those larvae deprived of food (Fig. 9b).

Direct estimation of cannibalism by counting all the fish at intervals of a few days during the experimental period revealed that the rate of cannibalism was significantly influenced by food availability (Fig. 10a). The rate was highest in the starvation feeding regime and declined with increasing food availability over the experimental period of 13 days. The rate of cannibalism was found to decline over the 30 day experimental period in those fish on a the satiation feeding regime (Fig. 10b). The reason for conducting a population census specifically for a 13 day and for a 30 day period, was also to determine whether there were any differences between the rates of cannibalism over a short and a long period as a result of varying food ration. It would be interesting to determine if and when the rate of cannibalism (as expressed by the curve in Fig. 10b) levels out. It is hypothesized that towards the end of the 30 day experimental period, cannibalism amongst O. mykiss juveniles occurs largely as a result of an increase in size variation within the population (Plate 2).

Analyzing the data obtained from the population census taken at intervals of a few days over the first 13 days reveals that the percentage of the population cannibalized per day increased with decreasing food availability (Table 29). Note that there is a significant difference between the percentage of the population cannibalized per day among those larvae fed 10% body weight once daily (viz. 3.9%) and those fed to satiation (viz. 0.03%).

2.3 Koi carp

During the first series of behavioural observations the observed incidence of cannibalism between day two and day eight (Fig. 11a) was significantly lower ($p<0.05$) in those larvae fed to satiation, while non-aggressive contacts were only observed amongst those larvae fed at 10% body weight per day. During the second series of observations from day 16 to day 22 (Fig. 11b), a switch in behaviour was observed. Cannibalism was significantly higher ($p<0.05$) in those larvae fed to satiation compared with those fed at lower levels. The number of non-aggressive contacts between fish was also significantly higher ($p<0.05$) on this feeding regime.

The population census data taken at intervals of a few days also showed that the rate of cannibalism was highest in those larvae fed to satiation (Fig. 12).

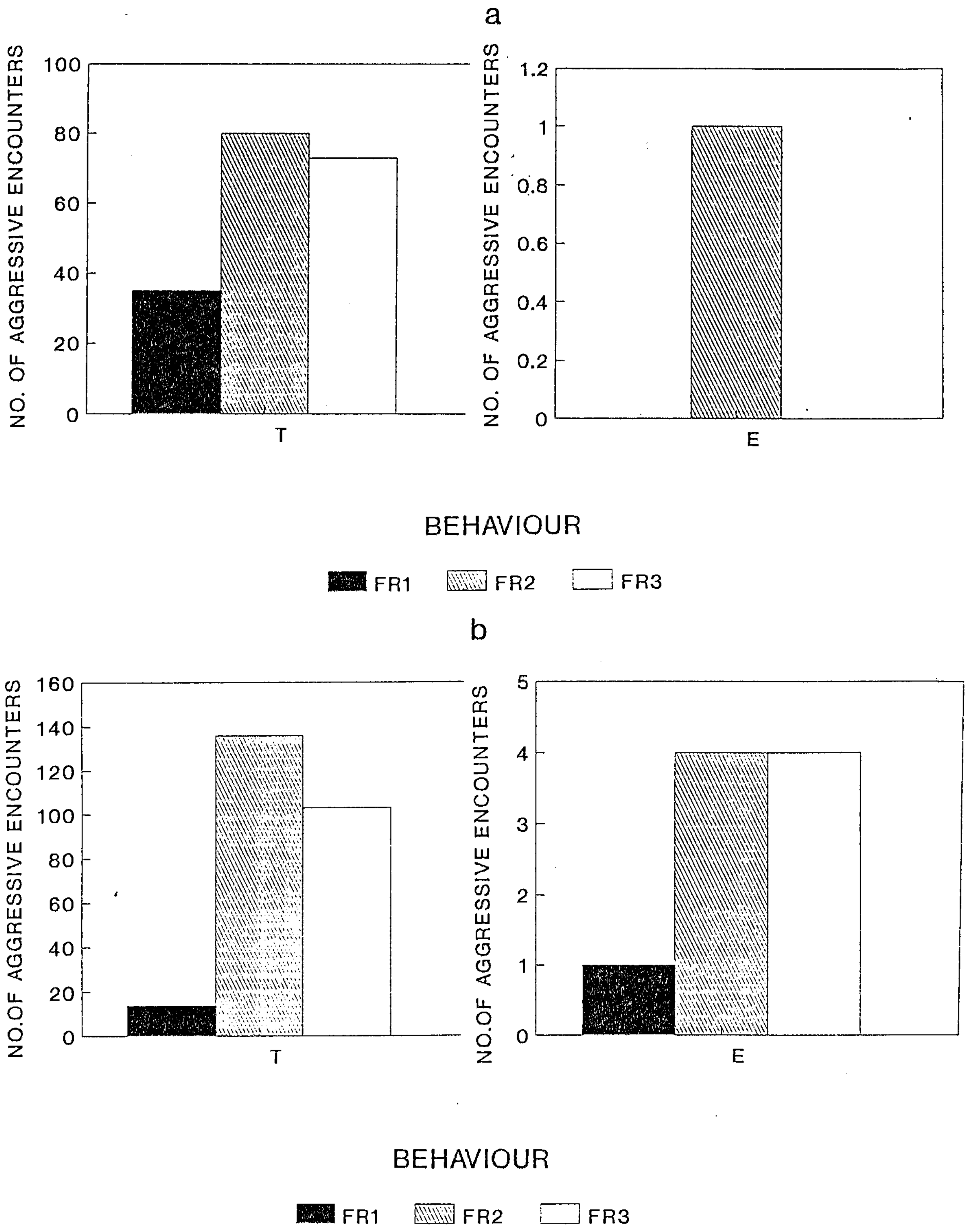


Fig. 9. Level of aggressive behaviour displayed by _Oncorhynchus mykiss_ maintained under various feeding regimes (FR's) over a seven day period, expressed as (a) the summation of the mean number of aggressive encounters during five minute time intervals each day and (b) the daily mean number of aggressive encounters per 50 physical contacts. (T = territoriality; E = extended fighting; FR1 = satiation; FR2 = 10% body weight/day; FR3 = starvation).

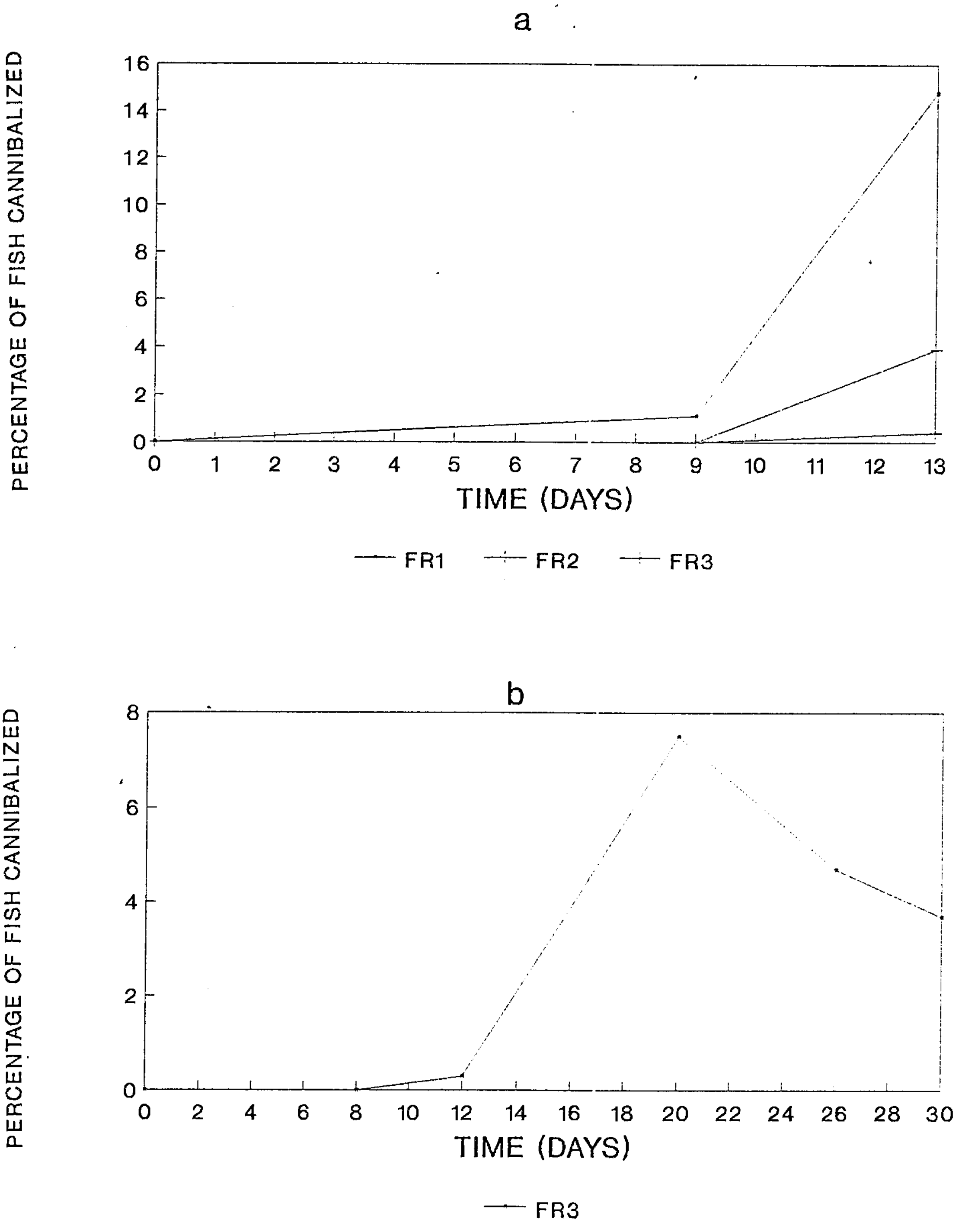


Fig. 10. Number of <u>Oncorhynchus</u> <u>mykiss</u> cannibalized, as influenced by daily feeding regime (FR), expressed as a percentage of fish remaining in the tank, for (a) a period of 13 days and (b) a period of 30 days (FR1 = starvation; FR2 = 10% body weight/day; FR3 = satiation).

Plate 2. A juvenile trout engulfing a smaller sibling head first.

Table 29. Differences in the rate of cannibalism in Oncorhynchus mykiss as influenced by various feeding regimes (FR's), over a 13 day period.

FEEDING REGIME (FR)	% OF POPULATION CANNIBALIZED/DAY
STARVATION (FR1)	15.7
10% BODY WEIGHT/DAY (FR2)	3.9
SATIATION (FR3)	0.03

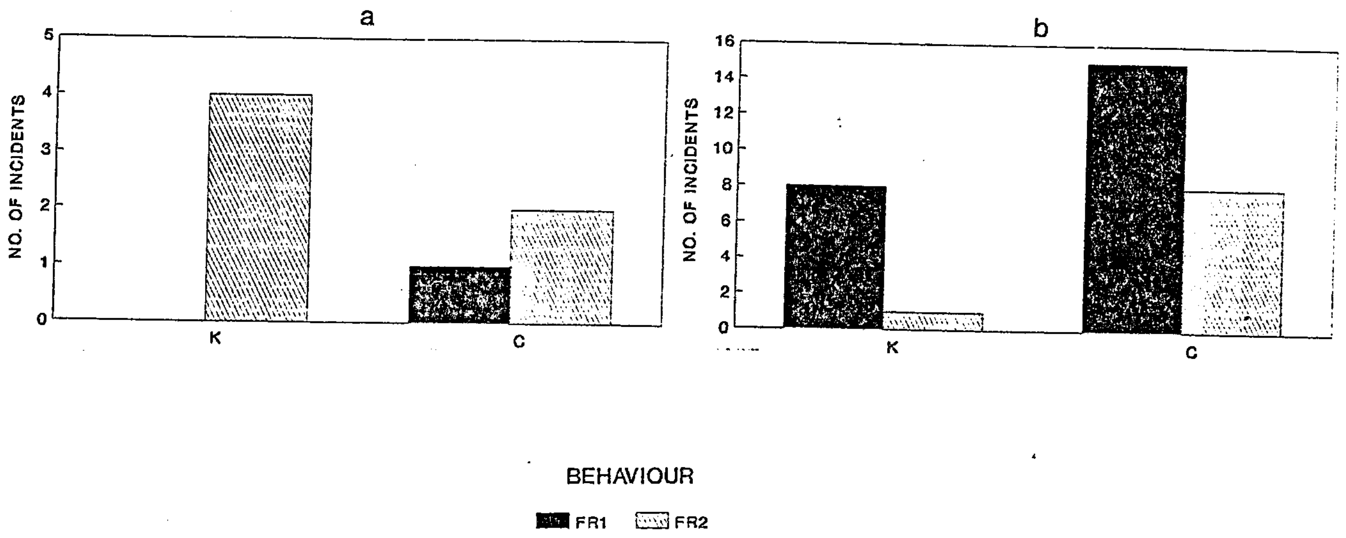


Fig. 11. Mean number of accumulated behavioural incidents displayed by Koi carp (Cyprinus carpio) maintained under various feeding regimes (FR's) during (a) days two to eight and (b) days 16 to 22, of the 26 day experiment. (FR1 = satiation; FR2 = 10% body weight per day; K = non-aggressive contacts; C = cannibalism).

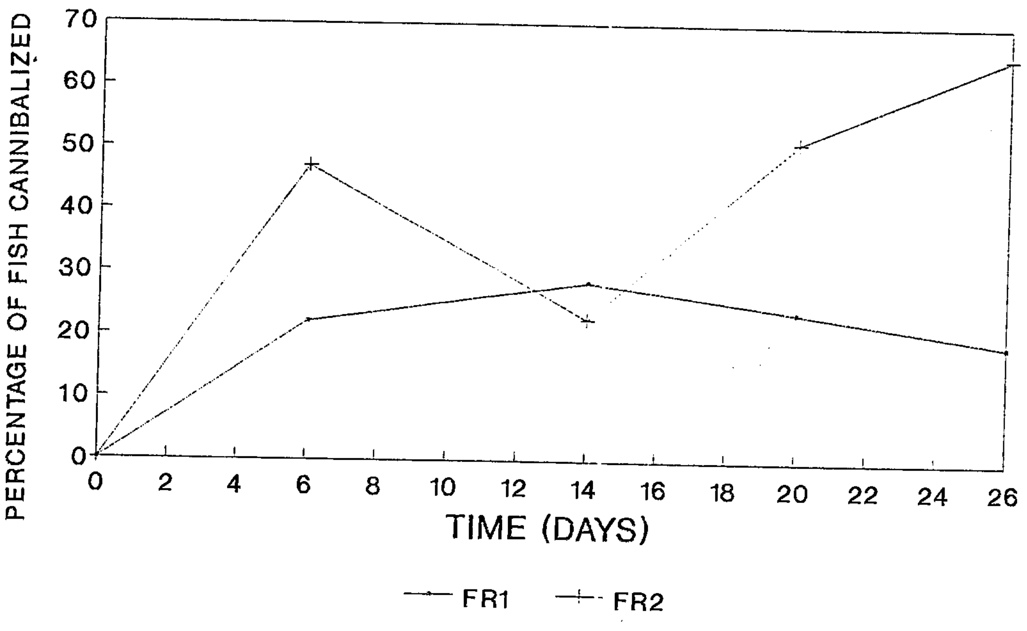


Fig. 12. Number of Koi carp (Cyprinus carpio) cannibalized as influenced by various feeding regimes (FR's), expressed as a percentage of fish remaining in the tank. (FR1 = satiation; FR2 = 10% body weight).

2.4 Silver carp.

Silver carp did not display any apparent form of aggressive behaviour. The "S-behaviour" (very fast, apparently stressful, jerky movements) displayed no particular trend under any of the experimental feeding conditions. The number of non-aggressive contacts increased as the food density increased (Table 30). There was, however, no significant difference in the number of non-aggressive contacts between those larvae fed to satiation and those fed 1X body weight per day. The results of the population census taken at intervals of a few days confirmed that the silver carp is non-cannibalistic.

Figure 13 shows the increase in size variation within the population over the experimental period. Note especially the large size variation which developed in those larvae fed to satiation. The significance of size variation will be discussed later.

3. Effect of density on the rate of cannibalism and other behavioural modes.

3.1 Catfish.

There were two possible factors which contributed to cannibalism induced mortality, viz. "obvious cannibalism" and "possible cannibalism" (Table 32). "Obvious cannibalism" refers to those fish that, according to the results of the population census, had been fully ingested. "Possible cannibalism" refers to those dead individuals which were partly consumed (Plate 3). This would include individuals whose heads and tails were found at the bottom of the tank, and those whose guts had been preyed upon by similar sized siblings. The problem with the inclusion of "possible cannibalism" in assessment of cannibalism, is that it was not always known whether these fish (Table 32) had been attacked and bitten, and subsequently died, or whether they had died from other causes and were then fed upon. Both cases were observed. However, the latter cannibalistic behavioural mode,

Table 30. Effect of food density on the number of non-aggressive contacts in the silver carp (Hypophthalmichthys molitrix).

FEEDING REGIME	NO. OF NON-AGGRESSIVE CONTACTS
STARVATION (FR1)	0
1 X BODY WEIGHT PER DAY (FR2)	42
SATIATION (FR3)	49.5

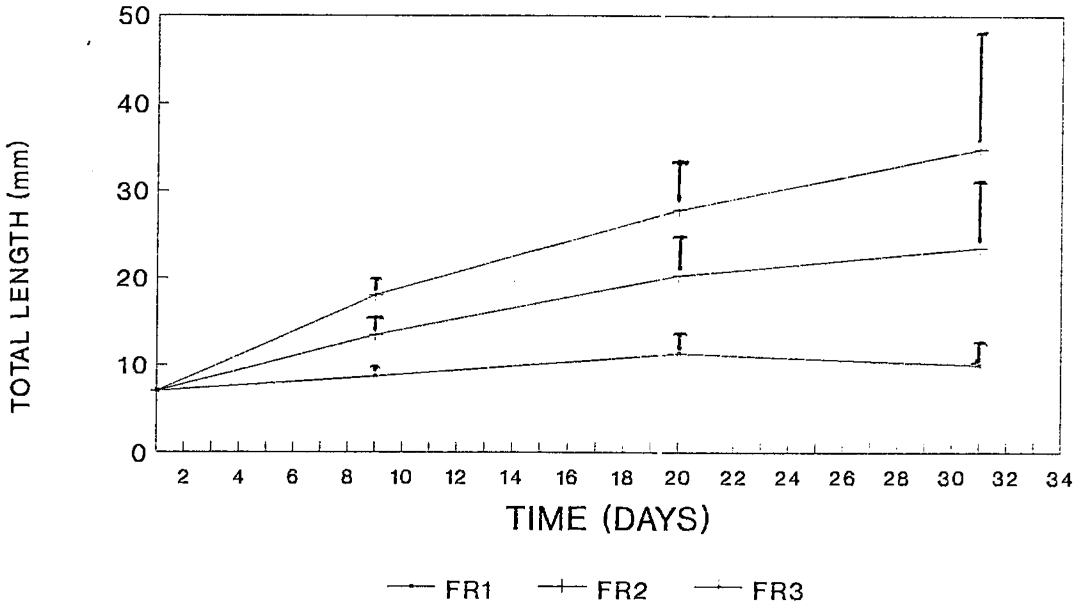


Fig. 13. Effect of various feeding regimes (FR's) on the growth of the silver carp, Hypophthalmichthys molitrix, (FR1 = starvation; FR2 = 1 x body weight per day; FR3 = satiation). Vertical bars indicate half standard deviation.

that of feeding on the guts of living siblings (Plate 4), was observed to occur more often than the former. In most instances the victims continued to feed and act territorially until they became too weak and died.

An evaluation of the data from the population census taken at intervals of a few days reveals significant trends regarding the density dependent nature of cannibalism (Table 32). Cannibalism was found to decrease with both declining density and with the passage of time.

The effect of density on the overall activity pattern of catfish larvae showed that the level of active swimming behaviour rose with an increase in population density, while the incidence of resting behaviour, territoriality and disturbed rest activity declined (Fig. 14). Airbreathing was also significantly higher ($p<0.01$) in those fish stocked at the highest density.

Analysis of the number of aggressive encounters over a set period each day, revealed that the level of territoriality declined as population density increased (Fig. 15a - all results significant at $p<0.05$).

Similarly, analysis of the number of aggressive encounters per fifty physical contacts, showed that territoriality declined as the population density increased (Fig. 15b - all results significant at $p<0.05$).

Plate 3. Badly bitten bodies of Clarias gariepinus; note that heads and tails were often uningested by cannibals. Many individuals died as a result of attacks on their bellies by siblings.

Plate 4. Dead and living Clarias gariepinus which had suffered attacks to their abdomens. Many of the living victims continued to feed and behave territorially.

Table 32. Results of the population census taken at intervals of a few days for the experiment to determine differences in the rate of cannibalism in <u>Clarias gariepinus</u> stocked at various densities over a 16 day period.

	A	B	C	D	E
DENSITY (FISH NO./ 13,75 L)	OBVIOUS CANNIBALISM (NO OF FISH)	CANNIBALISM PER DAY (NO OF FISH)	POSSIBLE CANNIBALISM (NO OF FISH)	CANNIBALISM PER DAY (NO OF FISH)	B+D (NO OF FISH)
D1=25	0	0	3	0.2	0.2
D2=75	16	1	11	0.7	1.7
D3=150	59	3.7	53	3.3	7
D4=250	58	3.7	67	4.2	7.8

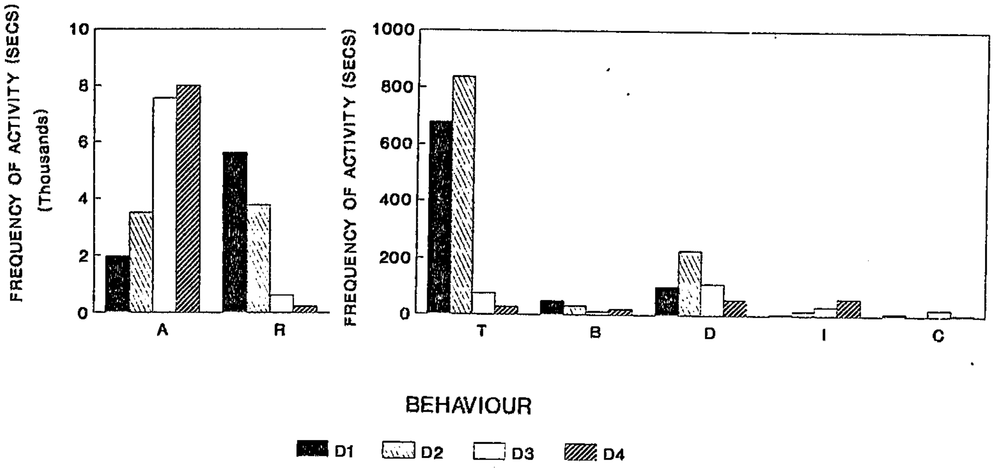


Fig. 14. Proportion of time devoted to different behavioural modes by <u>Clarias gariepinus</u> maintained under various densities over a seven day period. The frequency of activity was calculated by summing the time devoted to each of the behavioural modes (recorded during a daily 10 minute period) for the seven days. (A = active swimming; B = browsing; C = cannibalism; D = disturbed activity; I = air breathing; R = resting; T = territoriality; D1 = 25/13,75 l; D2 = 75/13,75 l; D3 = 150/13,75 l; D4 = 250/13,75 l).

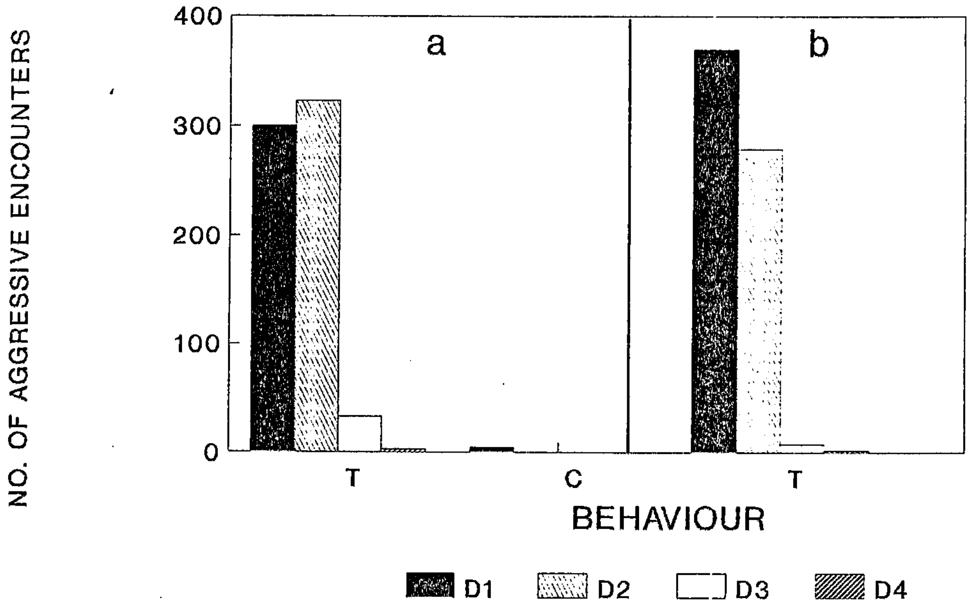


Fig. 15. Level of aggressive behaviour displayed by <u>Clarias gariepinus</u> maintained under various densities over a seven day period, expressed as (a) the summation of the mean number of aggressive encounters during five minute time intervals each day and (b) the daily mean number of aggressive encounters per 50 physical contacts. (T= territoriality; C= cannibalism; D1 = 25/13,75 l; D2 = 75/13,75 l; D3 = 150/13,75 l; D4 = 250/13,75 l).

3.2 Trout.

The effects of density on the overall activity pattern (Fig. 16), the number of aggressive encounters over a set period each day (Fig. 17a) and the daily number of aggressive encounters per fifty physical contacts (Fig. 17b), all revealed an increase in the level of territoriality with increasing density. However, the level of territoriality in the larvae decreased significantly at the highest stocking density (all results significant at $p<0.05$). It appeared that "extended fighting" declined with increasing density. No cannibalism, mouth wrestling or resting behaviour was seen during any of the observation periods. Counting the numbers of fish at intervals of a few days over the experimental period did, however, reveal that cannibalism increased with increasing density (Table 33).

Table 33. Results of the population census taken at intervals of a few days during the experiment to determine the differences in the rate of cannibalism in *Oncorhynchus mykiss* stocked at various densities over a 13 day period. Obvious cannibalism represents missing fish, presumed entirely ingested, while possible cannibalism represents bodies found dead and partly consumed.

DENSITY (FISH NO./ 13,75 L)	A OBVIOUS CANNIBALISM (NO OF FISH)	B POSSIBLE CANNIBALISM (NO OF FISH)	C A + B (NO OF FISH)	D CANNIBALISM PER DAY (NO OF FISH)
D1=25	0	0	0	0
D2=75	6	1	1	0.5
D3=150	9	3	12	0.9
D4=250	13	1	14	1.1

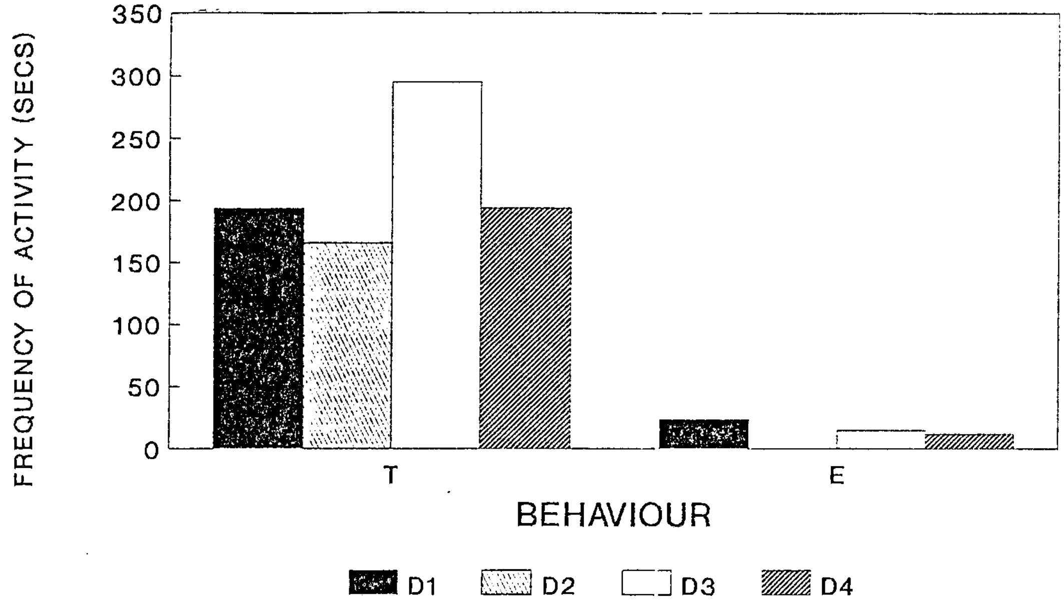


Fig. 16. Proportion of time devoted to different behavioural modes by <u>Oncorhynchus mykiss</u> maintained under various densities over a seven day period. The frequency of activity was calculated by summing the time devoted to each of the behavioural modes (recorded during a daily 10 minute period) for the seven days. (T = territoriality; E = extended fighting; D1 = 25/13,75 l; D2 = 75/13,75 l; D3 = 150/13,75 l; D4 = 250/13,75 l).

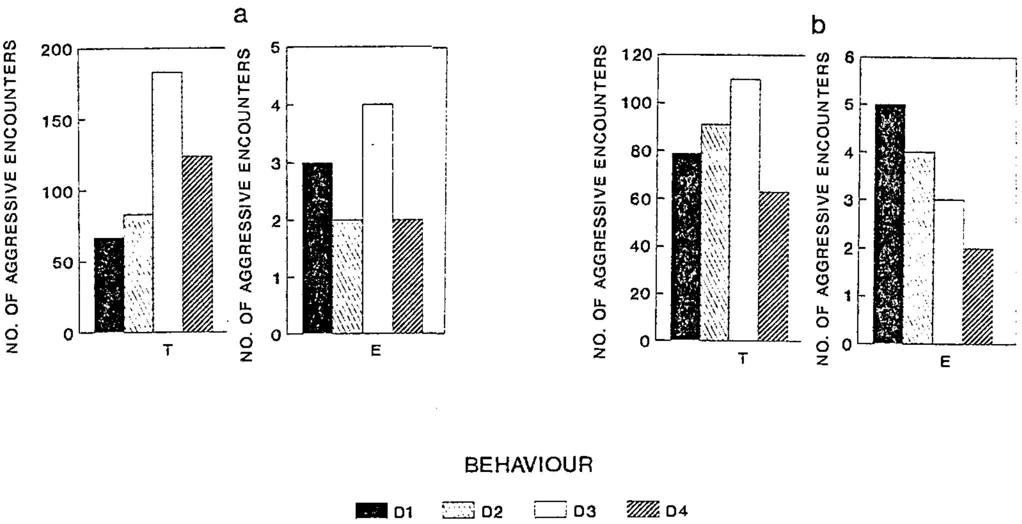


Fig. 17. Level of aggressive behaviour displayed by <u>Oncorhynchus mykiss</u> maintained under various densities over a seven day period, expressed as (a) the summation of the mean number of aggressive encounters during five minute time intervals each day and (b) the daily mean number of aggressive encounters per 50 physical contacts. (T = territoriality; E = extended fighting; D1 = 25/13,75 l; D2 = 75/13,75 l; D3 = 150/13,75 l; D4 = 250/13,75 l).

3.3 Common carp.

The incidence of cannibalism was observed to be significantly higher ($p<0.01$) in those fish stocked at the highest density, while the number of non-aggressive contacts between fish increased with increasing density (Fig. 18). No apparent aggressive contacts were observed. The results of the population census taken at intervals of a few days revealed that the level of cannibalism in the fish increased with a rise in population density (Table 34).

Table 34. Results of the population census taken at intervals of a few days during the experiment to determine differences in the rate of cannibalism in the common carp (Cyprinus carpio) stocked at various densities over a 26 day period. Obvious cannibalism represents missing fish, presumed entirely engulfed, while possible cannibalism represents bodies found dead and partly consumed.

	A	B	C	D	E
DENSITY (FISH NO./ 13,75 L)	OBVIOUS CANNIBALISM (NO OF FISH)	POSSIBLE CANNIBALISM (NO OF FISH)	TOTAL A+B (NO OF FISH)	PERCENTAGE CANNIBALISM OF TOTAL POP.	CANNIBALISM PER DAY (NO OF FISH)
D1=50	4	0	4	8	0.2
D2=100	14	3	17	17	0.7
D3=300	36	5	41	14	1.6
D4=600	189	14	203	34	7.8

3.4 Koi carp.

As in the results for common carp, the level of cannibalism in koi carp also increased with a rise in stocking density (Fig. 19 and Table 35). The number of non-aggressive contacts between fish

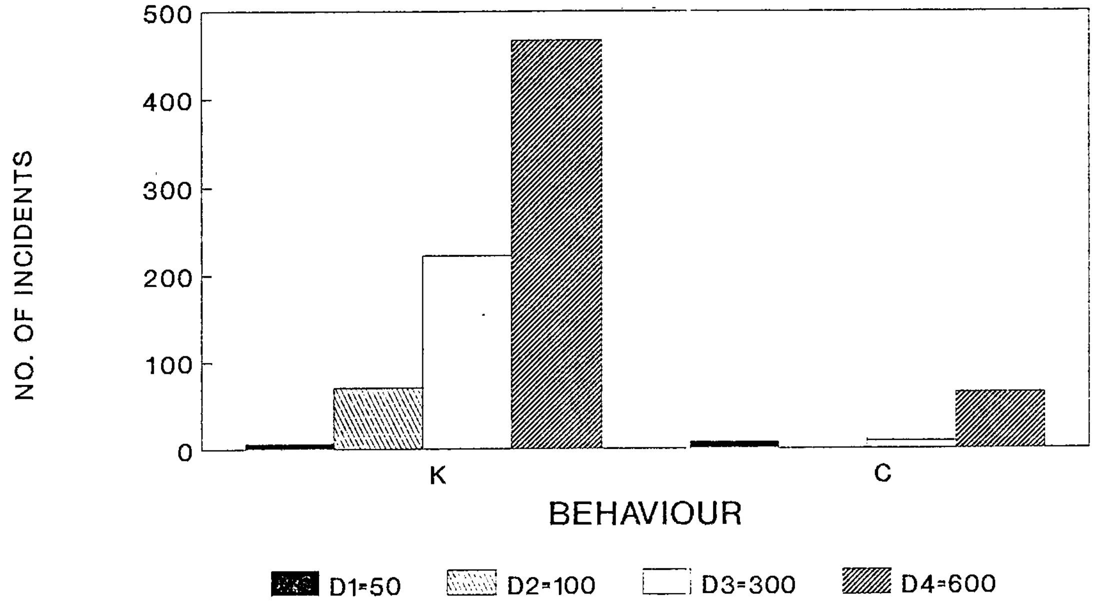


Fig. 18. Mean number of accumulated behavioural incidents displayed by common carp (Cyprinus carpio) maintained under various densities over a seven day period. (K = non-aggressive contacts; C = cannibalism; D1 = 50/13,75 l; D2 = 100/13,75 l; D3 = 300/13,75 l; D4 = 600/13,75 l).

declined with increasing stocking density, but the level of this behaviour was observed to increase rapidly to the highest level in those fish stocked at the highest density (Fig. 19). The number of aggressive contacts were also greatest in those fish stocked at the highest density (all results significant at $p<0.05$). Figure 20 shows the growth in length of the fish over the experimental period. Note that the size variance of the fish maintained under all densities increased with age. The significance of size variation will be discussed later.

Table 35. Results of the population census taken during the experiment to determine the differences in the the rate of cannibalism in Koi carp (Cyprinus carpio) stocked at various densities over a 26 day period. Obvious cannibalism represents missing fish, presumed entirely engulfed, while possible cannibalism represents bodies found dead and partly consumed.

	A	B	C	D	E
DENSITY (FISH NO.)	OBVIOUS CANNIBALISM (NO OF FISH)	POSSIBLE CANNIBALISM (NO OF FISH)	TOTAL A+B (NO OF FISH)	PERCENTAGE CANNIBALISM OF TOTAL POP.	CANNIBALISM PER DAY (NO OF FISH)
D1=50	9	15	24	48	0.9
D2=100	51	16	67	67	2.6
D3=500	281	105	386	77.2	14.9
D4=1000	732	161	893	89.3	34.4

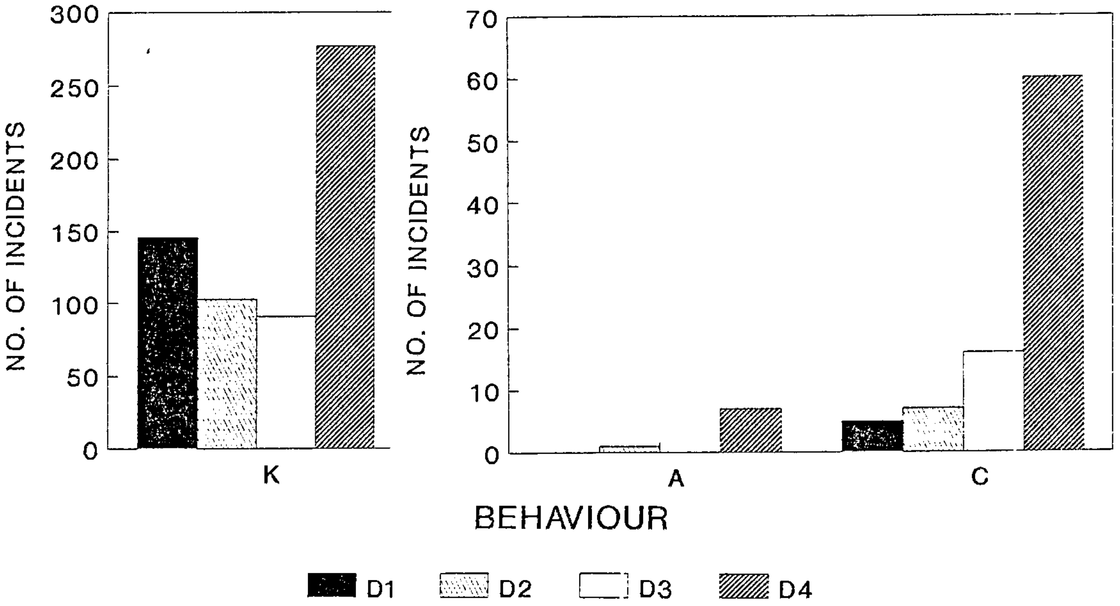


Fig. 19. Mean number of accumulated behavioural incidents displayed by Koi carp (Cyprinus carpio) maintained under various densities over a seven day period. (K = non-aggressive contacts; A = aggressive contacts; C = cannibalism; D1 = 50/13,75 l; D2 = 100/13,75 l; D3 = 500/213,75 l; D4 = 1000/13,751).

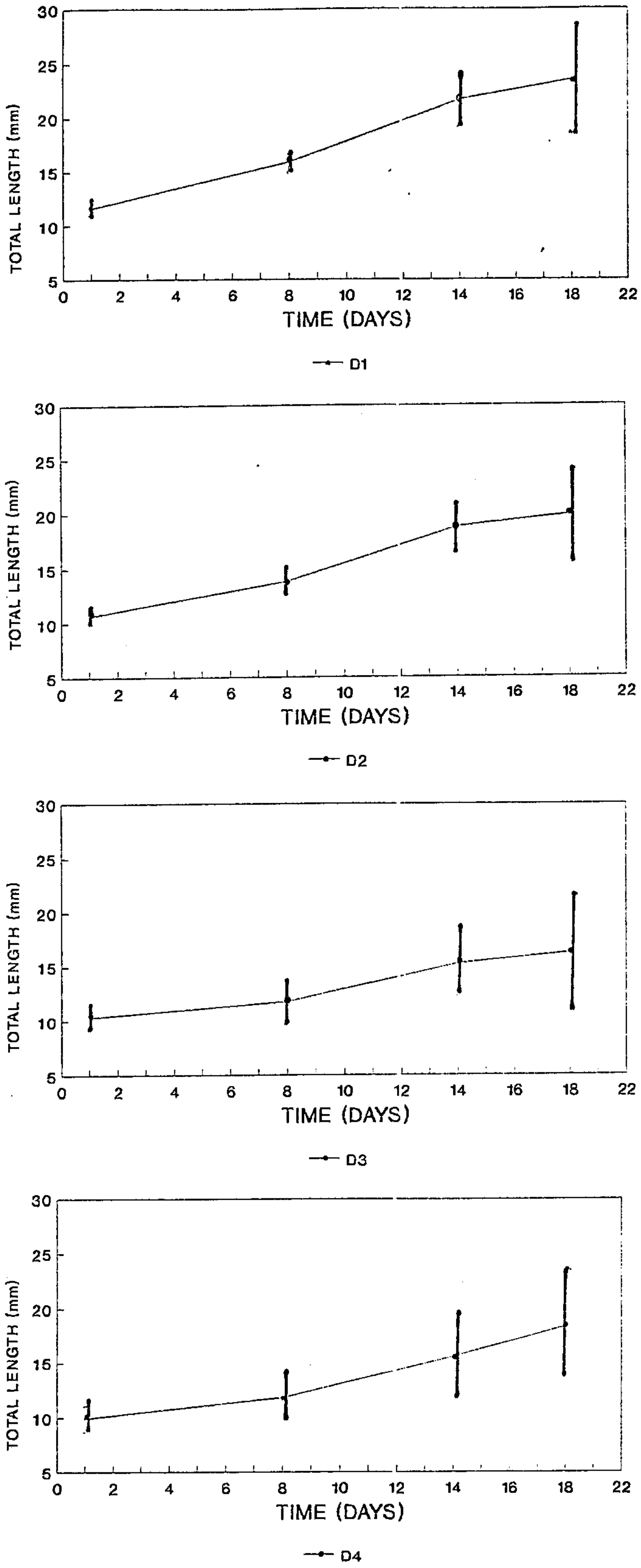


Fig. 20. Effect of population density on the growth of Koi carp (Cyprinus carpio) maintained under the following densities :- D1 = 50/13,75 l; D2 = 100/13,75 l; D3 = 500/13,75 l and D4 = 1000/13,75 l. Vertical bars indicate half standard deviation.

3.5 Silver and grass carp.

No aggressive behaviour was observed in silver or in grass carp. The population census taken at intervals of a few days for the silver carp revealed an increase in the mortality rate with increasing density (Table 36), while the census for the grass carp indicated a similar tendency (Table 37). The number of non-aggressive contacts in the grass carp increased with increasing density, but stressed behaviour followed no trend (Table 38). Figures 21 and 22 show the effect of population density on growth in length of the silver and grass carp respectively. Note the increase in size variation of the population with density over the experimental period. The significance of size variation will be discussed later.

Table 36. Results of the population census taken at intervals of a few days, showing the increase in the rate of mortality due to increasing density in silver carp (*Hypophthalmichthys molitrix*) maintained at various densities over a 31 day period. Note that there were no mortalities due to cannibalism.

	A	B	C	D	E
DENSITY (FISH NO.)	MORTALITY (NO OF FISH)	SURVIVAL (NO OF FISH)	PERCENTAGE SURVIVAL	TOTAL A+B (NO OF FISH)	FISH LOST IN OVERFLOW (NO OF FISH)
D1=50	14	36	72	50	0
D2=100	51	49	49	100	0
D3=500	249	121	24	360	140
D4=1000	524	117	12	641	359

Table 37. Results of the population census taken at intervals of a few days during the experiment, showing the similar mortality rate at different densities in grass carp (*Ctenopharyngodon idella*) over a 35 day period. Note that there were no mortalities due to cannibalism.

DENSITY (FISH NO./ 13,75 L)	MORTALITY (NOS OF FISH)	SURVIVAL (NOS OF FISH)	PERCENTAGE LOSS
D1=25	4	21	19
D2=85	12	73	16.4
D3=200	28	170	17.6

Table 38. Effect of population density on the number of non-aggressive contacts (K) and stressed behaviour (S) in grass carp (*Ctenopharyngodon idella*) over a six day period.

DENSITY (FISH NO./ 13,75 L)	K	S
D1=25	3	27
D2=85	13	4
D3=200	81	5

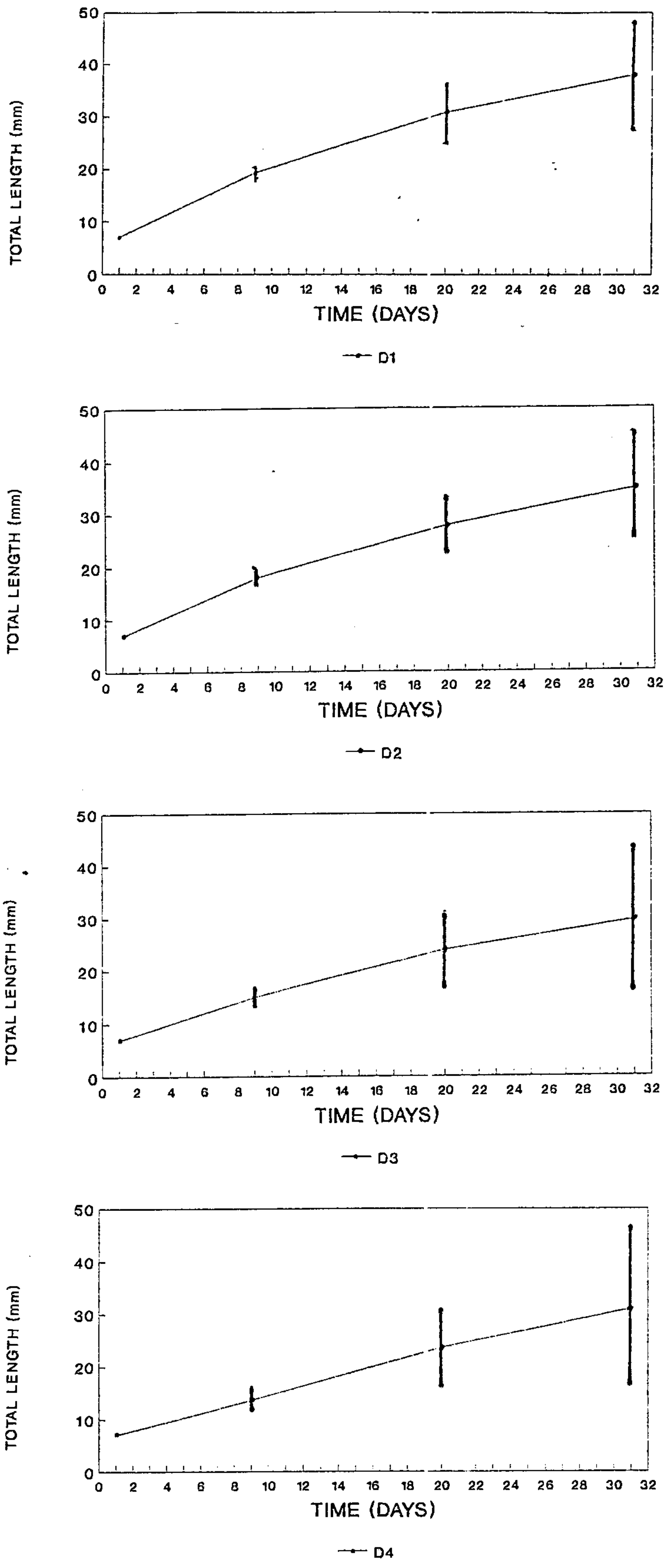


Fig. 21. Effect of population density on the growth of silver carp (Hypophthalmichthys molitrix) maintained under the following densities :- D1 = 50/13,751; D2 = 100/13,75 l; D3 = 500/13,75 l and D4 = 1000/13,75 l.

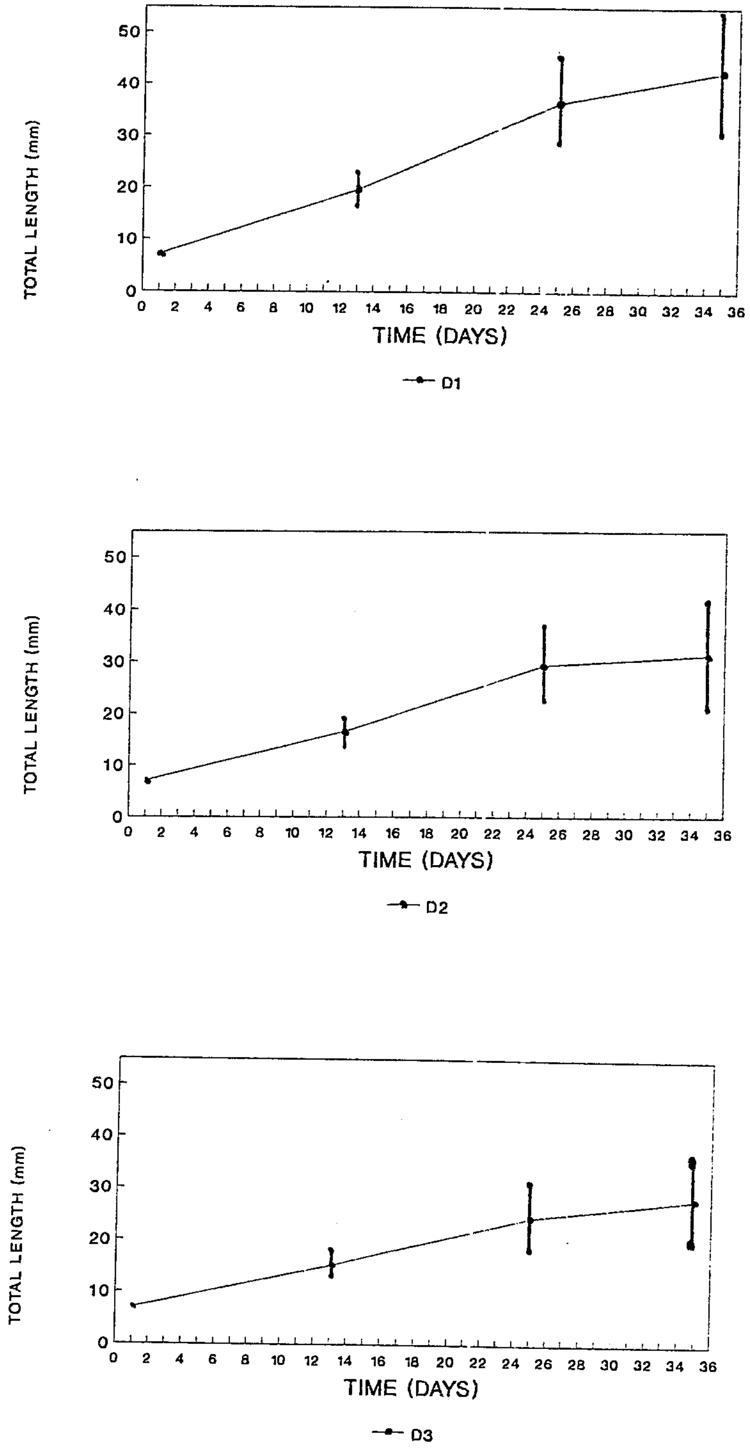


Fig. 22. Effect of population density on the growth of grass carp (Ctenopharyngodon idella) maintained under the following densities :- D1 = 25/13,75 l; D2 = 85/13,75 l; D3 = 200/13,75 l.

4. Effect of live and dry food on the rate of cannibalism and other behavioural modes.

4.1 Catfish.

The proportion of time devoted to each of the various behavioural modes observed during a set period of time each day differed markedly between the live and dry food treatments (Fig. 23). The most common behavioural modes observed in both treatments were active swimming and resting. More time was spent on active swimming in those fish subjected to the dry food treatment, while resting was the dominant behavioural mode in those subjected to the live food treatment. Cannibalistic and territorial aggression was significantly higher in the fish subjected to the dry food treatment than those raised on live food. The rate of airbreathing was also highest in fish subjected to the live food treatment. These differences in the amount of time devoted to each activity were all found to be significantly different ($p<0.05$).

Analysis of the number of aggressive encounters over a set period of time each day, and the number of aggressive encounters per 50 physical contacts, revealed that territorial aggression was significantly higher ($p<0.05$) in the dry food treatment (Fig. 24a & b). No cannibalistic aggression was observed in either the live or dry food treatments over the experimental period. The results of the population census taken at intervals of a few days revealed no difference in the rate of cannibalism between fish on the live and those on the dry food treatment.

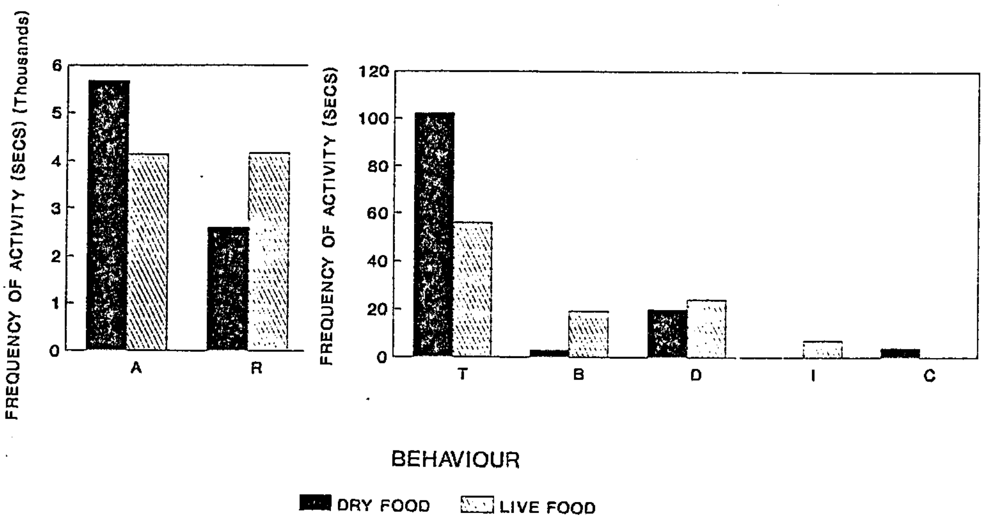


Fig. 23. Proportion of time devoted to different behavioural modes by <u>Clarias gariepinus</u> subjected to live (<u>Daphnia</u> spp.) versus dry food treatments, over a seven day period. The frequency of activity was calculated by summing the time devoted to each of the behavioural modes (recorded during a daily 10 minute period) for the seven days. (A = active swimming; B = browsing; C = cannibalism; D = disturbed activity; I = air breathing; R = resting; T = territoriality).

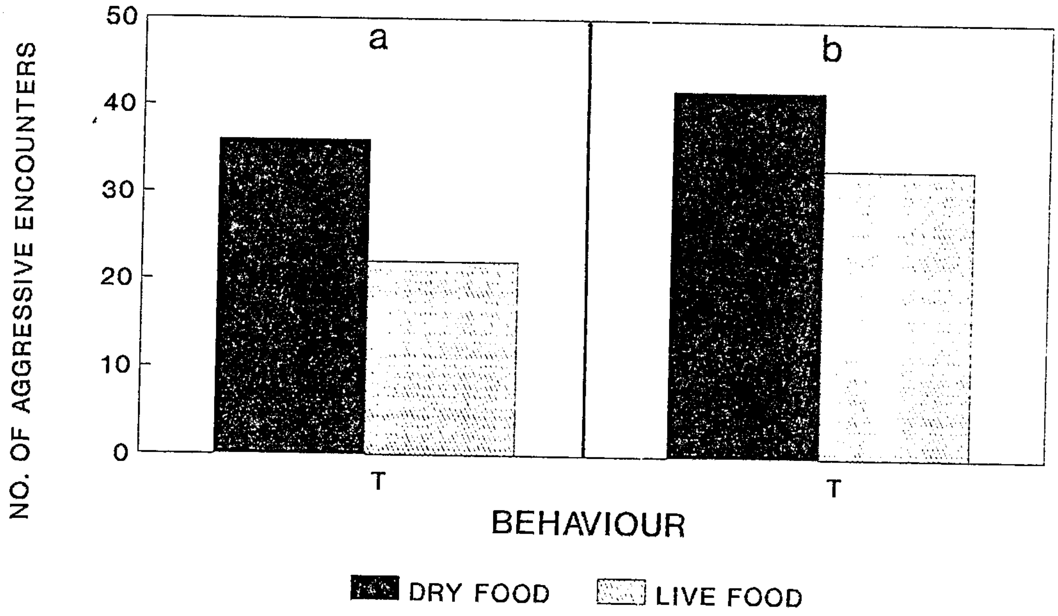


Fig. 24. Level of aggressive behaviour displayed by <u>Clarias gariepinus</u> subjected to live (<u>Daphnia</u> spp.) versus dry food treatments, over a seven day period, expressed as (a) the summation of the mean number of aggressive encounters during five minute time intervals each day and (b) the daily mean number of aggressive encounters per 50 physical contacts. (T = territoriality).

4.2 Trout.

The proportion of time devoted to the various behavioural modes observed during a set period of time each day differed markedly between the live and dry food treatments (Fig. 25).

Territoriality, cannibalistic behaviour and extended fighting were all found to be significantly higher ($p<0.01$) in those fish subjected to the dry food treatment. No mouth wrestling was observed during the experimental period.

Analysis of the number of aggressive encounters over a set period each day and the number of aggressive encounters per 50 physical contacts, revealed that territorial aggression and extended fighting were significantly higher ($p<0.01$) in the fish subjected to the dry food treatment (Fig. 26). No cannibalism was seen during the observation periods. The population census taken at intervals of a few days, however, revealed that 5.5% of the initial population subjected to the dry food treatment were cannibalized, while 3% of the initial population subjected to the live food treatment, succumbed to cannibalism. This result was, however, only significant at $p<0.10$.

5. Effect of alternative live food on the rate of cannibalism and other behavioural modes.

5.1 Catfish.

The proportion of time devoted to the various behavioural modes observed during a set period each day differed markedly between fish subjected to alternative live food items (Fig. 27). Resting

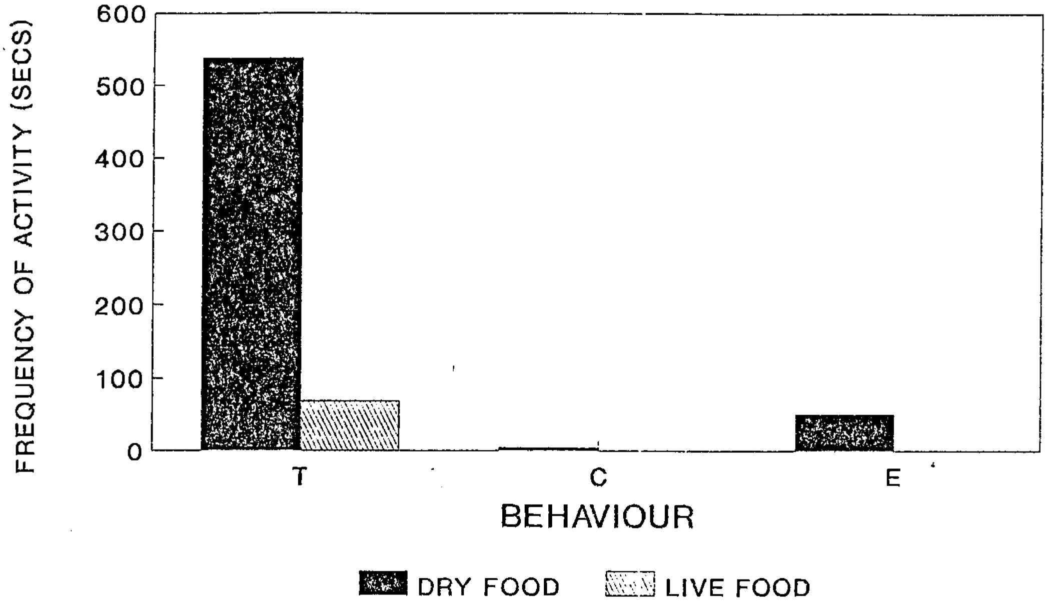


Fig. 25. Proportion of time devoted to different behavioural modes by <u>Oncorhynchus mykiss</u> subjected to live (<u>Daphnia</u> spp.) and dry food treatments, over a seven day period. The frequency of activity was calculated by summing the time devoted to each of the behavioural modes (recorded during a daily 10 minute period) for the seven days. (T = territoriality; C = cannibalism; E = extended fighting).

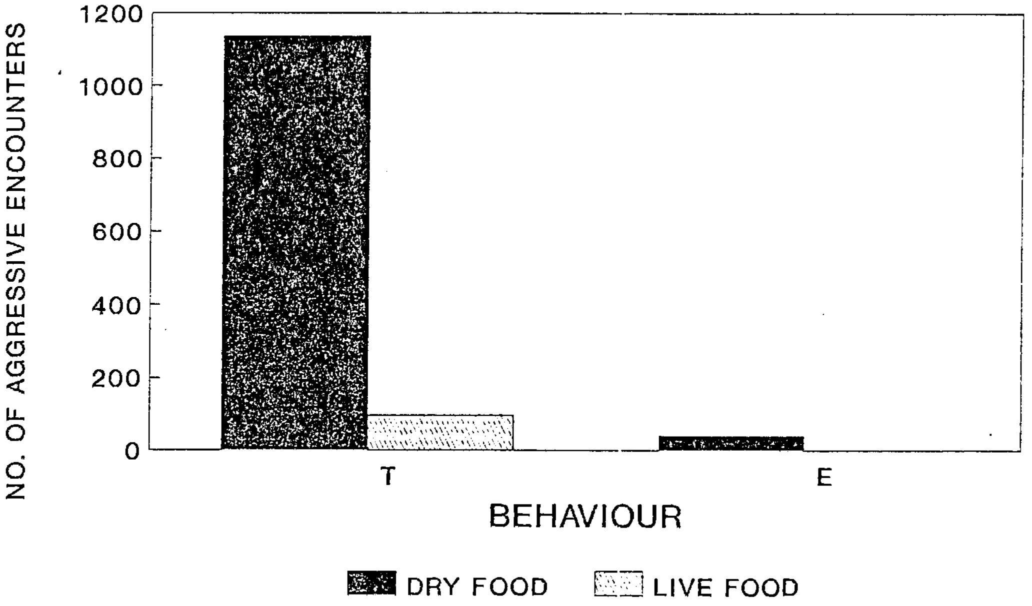


Fig. 26. Level of aggressive behaviour displayed by <u>Oncorhynchus mykiss</u> subjected to live (<u>Daphnia</u> spp.) and dry food treatments, over a period of seven days, expressed as the summation of the mean number of aggressive encounters during five minute time intervals each day. (T = territoriality; E = extended fighting).

behaviour was the predominant activity, followed by active swimming and territoriality. Only a small proportion of the total time was devoted to other behavioural modes. Active swimming behaviour was significantly higher ($p<0.01$) in the fish supplied with the smallest food item (Daphnia spp.), while resting behaviour was found to be significantly higher ($p<0.05$) in the fish supplied with the largest alternative food item, viz. fairy shrimp.

Analysis of the number of aggressive encounters during 5 minute time intervals each day (Fig. 28a), and the number of aggressive encounters per 50 physical contacts (Fig. 28b), revealed that the level of territoriality was highest in fish supplied with T. rendalli larvae, followed by those fish supplied with fairy shrimp, while territoriality was lowest in fish supplied with Daphnia spp. The differences in the amount of time devoted to territorial behaviour for each of the alternative food treatments, were found to be significantly different ($p<0.01$), except for the level of territoriality between fish supplied with Daphnia spp. and those supplied with fairy shrimp, where no significant difference was found. Cannibalistic aggression was not observed during either of the two experiments described at the beginning of the paragraph. The population census taken at the end of the three day experimental period revealed no change in fish numbers.

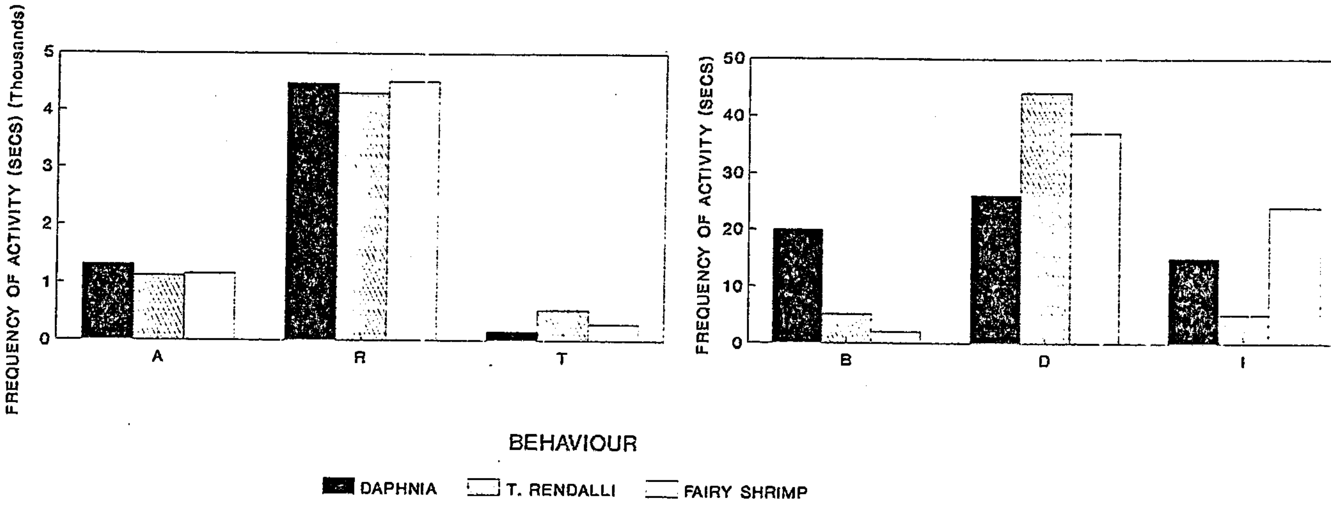


Fig. 27. Proportion of time devoted to different behavioural modes by Clarias gariepinus supplied with alternative live food items, over a period of four days. The frequency of activity was calculated by summing the time devoted to each of the behavioural modes (recorded during a daily 10 minute period) for the four days. (A = active swimming; B = browsing; D = disturbed activity; I = air breathing; R = resting; T = territoriality).

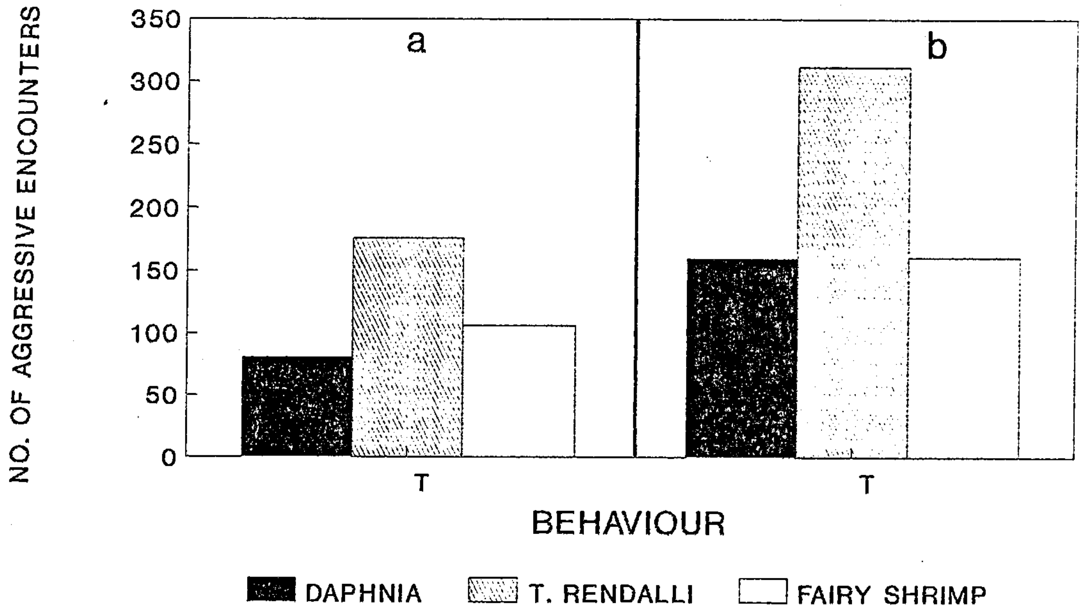


Fig. 28. Level of aggressive behaviour displayed by Clarias gariepinus supplied with alternative live food items, over a period of seven days, expressed as (a) the summation of the mean number of aggressive encounters during five minute time intervals each day and (b) the daily mean number of aggressive encounters per 50 physical contacts. (T = territoriality).

6. Effect of photoperiod on the rate of cannibalism and other behavioural modes.

6.1 Catfish.

The proportion of time devoted to the various behavioural modes observed during a set period every day differed markedly between the light and dark treatments (Fig 29). The most common behaviours observed in both treatments were active swimming and resting, with a smaller proportion of time being devoted to the other behavioural modes. Active swimming was the dominant behavioural mode observed among the fish subjected to a continual dark period, whereas resting was the dominant behaviour among the

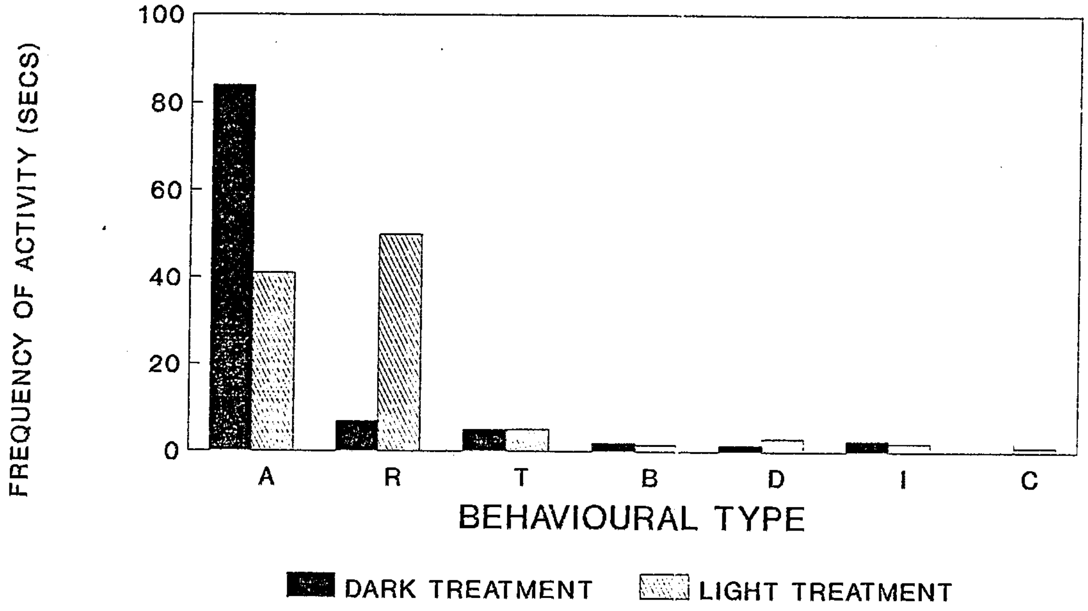


Fig. 29. Proportion of time devoted to different behavioural modes by Clarias gariepinus maintained under light (24L/0D) and dark (0L/24D) photoperiod regimes over a period of seven days. The frequency of activity was calculated by summing the time devoted to each of the behavioural modes (recorded during a daily 10 minute period) for the seven days. (A = active swimming; B = browsing; C = cannibalism; D = disturbed activity; I = air breathing; R = resting; T = territoriality).

among the fish subjected to a continual light period than those subjected to a continual dark period. The level of territorial aggression observed, however, declined gradually in fish subjected to the dark treatment, and by the end of the experimental period was negligible. In those subjected to the light treatment, on the other hand, an increase in territoriality was observed over the experimental period. Other behavioural changes included a decrease in rest activity and an increase in active swimming and airbreathing in the light treated fish (Fig. 30b,c & d). In those subjected to the dark treatment the observed proportion of rest activity, active swimming and disturbed activity remained constant (Figs. 30b,c & e), but a decline in the rate of airbreathing was observed between day one to day three (Fig. 30d). Although the proportion of time devoted to browsing activity over the entire experimental period (Fig. 29) was higher in the light than in the dark, the levels observed varied greatly from day to day (Fig. 30f). It should be noted that the proportion of time devoted to browsing was low in both treatments, probably because the behavioural observations were made two hours after feeding when the fish were relatively satiated.

Length and weight increments over the experimental period were found to be significantly higher ($p<0.005$) in fish subjected to continual darkness (Table 40).

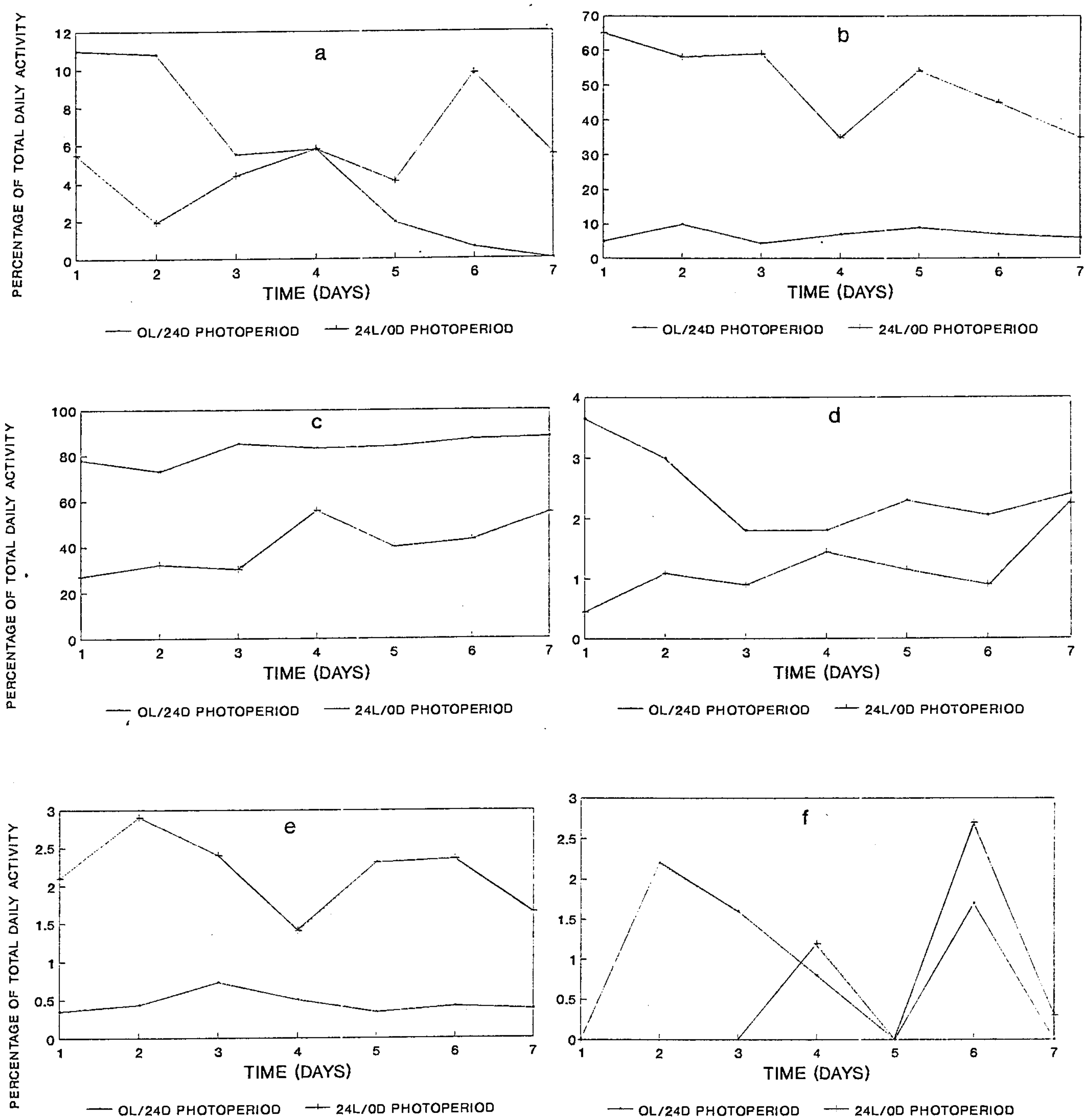
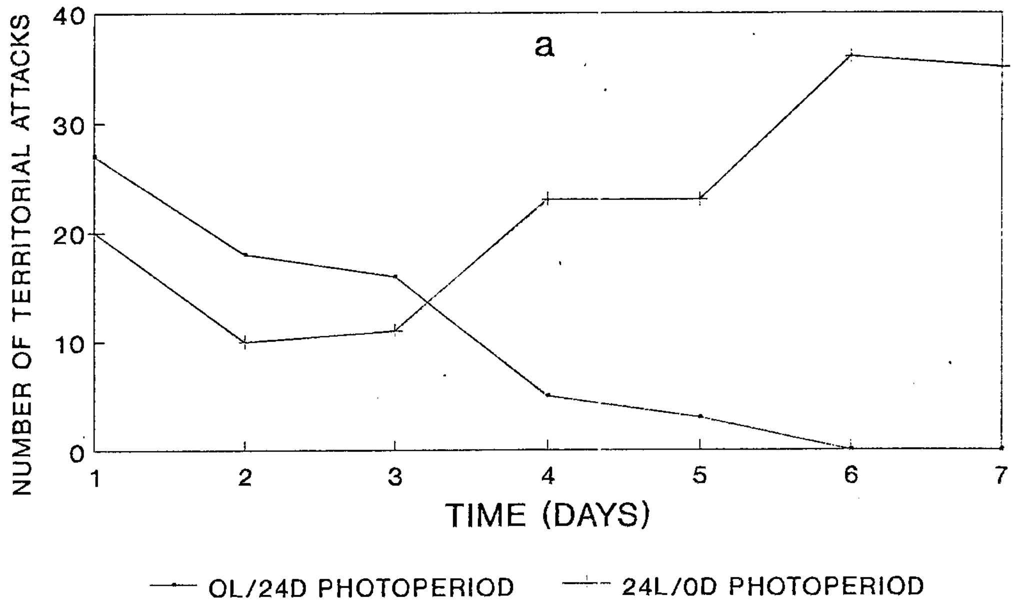


Fig. 30. Proportion of time devoted daily to different behaviours by Clarias gariepinus maintained under light (24L/0D) and dark (0L/24D) photoperiod regimes over a period of seven days. (a) territoriality; (b) resting behaviour; (c) active swimming; (d) airbreathing; (e) disturbed rest activity; (f) browsing activity.



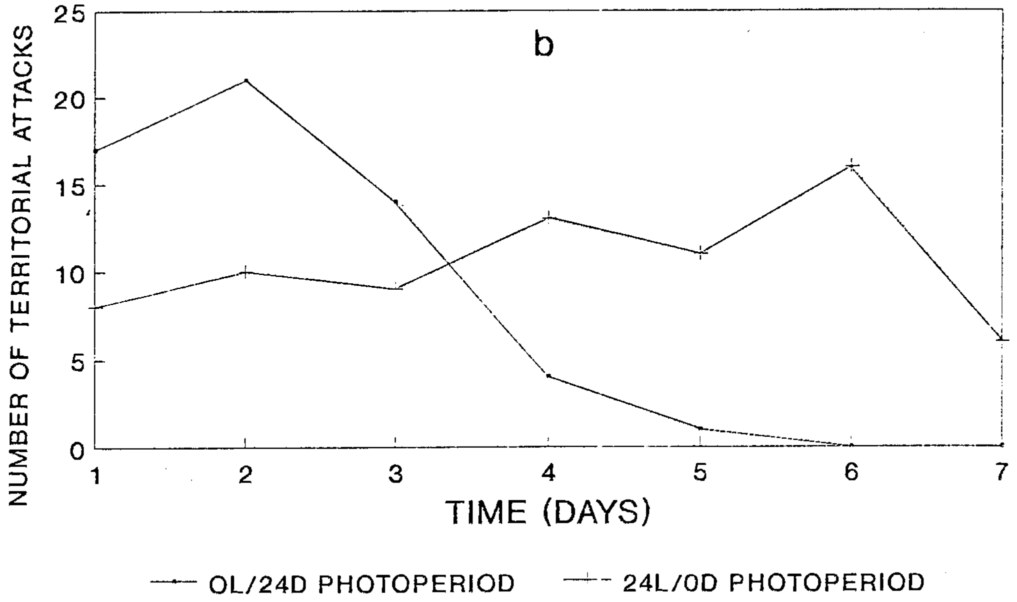


Fig. 31. Mean number of territorial attacks by Clarias gariepinus maintained under light (24L/0d) and dark (0L/24D) photoperiod regimes, quantified daily for seven days using different methods:
(a) Number of territorial attacks recorded in an 8 minute period.
(b) Proportion of territorially aggressive contacts recorded during 75 contacts between individual fish.

7. Effect of refuges on the rate of cannibalism and other behavioural modes.

7.1 Catfish.

The proportion of time devoted to the various behavioural modes observed during a set period every day differed markedly between fish subjected to differences in the availability of refuges (Figs. 32). Resting behaviour and active swimming were the dominant behavioural modes affected (Fig. 32). With a rise in the availability of refuges the level of resting behaviour was found to increase, while active swimming declined. Differences in the amount of time devoted to resting and active swimming were both found to be significant ($p<0.01$).

Cannibalistic aggression, territoriality, browsing behaviour and disturbed rest activity were all found to be significantly higher ($p<0.01$) in those fish without refuges (Fig. 32). Both

Table 40. Length and weight measurements recorded for the experiment to determine the effects of photoperiod on the rate of cannibalism in *Clarias gariepinus* over an 11 day period.

	LENGTH (mm) DAY 1	LENGTH (mm) DAY 11	% INCREASE	WEIGHT (g) DAY 1	WEIGHT (g) DAY 11	% INCREASE
DARK	5.26 (0.7)	7.0 (1.5)	132.92	1.15 (0.4)	3.09 (2.1)	268.79
LIGHT	5.34 (0.9)	6.73 (1.2)	126.05	1.32 (0.6)	2.45 (1.4)	185.44

STANDARD DEVIATIONS ARE INDICATED IN BRACKETS territoriality and disturbed rest activity declined as more refuges were made available to the fish. No cannibalism was observed in those fish supplied with refuges, while cannibalism was observed in those fish without refuges. Airbreathing was significantly higher ($p<0.05$) in fish with increased access to refuges.

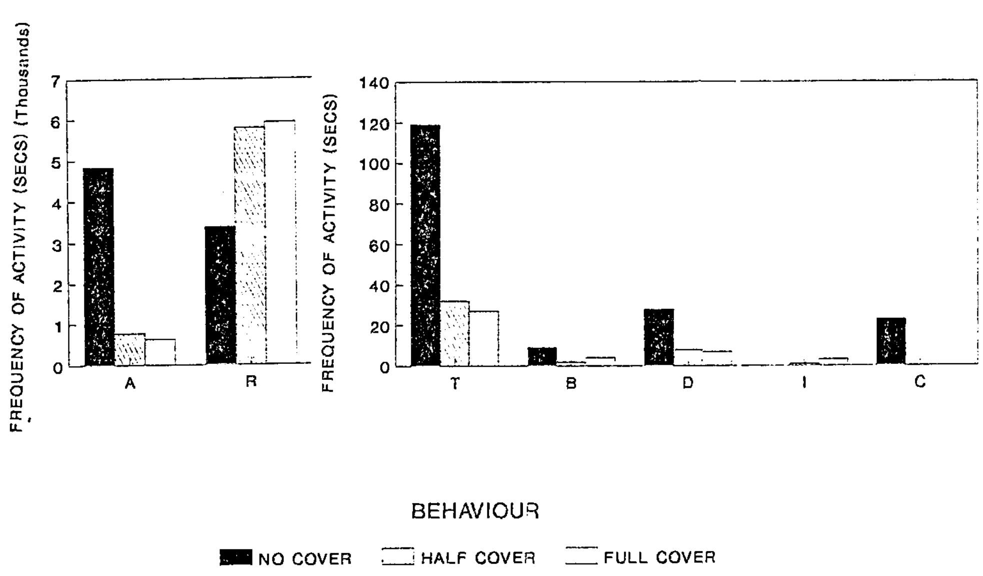


Fig. 32. Proportion of time devoted to different behavioural modes by <u>Clarias gariepinus</u> maintained under conditions of varying refuge availability, over a seven day period. The frequency of activity was calculated by summing the time devoted to each of the behavioural modes (recorded during a daily 10 minute period) for the seven days. (A = active swimming; B = browsing; C = cannibalism; D = disturbed activity; I = air breathing; R = resting; T = territoriality).

8. Effect of turbidity on the rate of cannibalism and other behavioural modes.

8.1 Catfish.

The most common behavioural modes observed in both the semi-turbid and the clear water regime were resting and active swimming, a smaller proportion of the time was devoted to the other behavioural modes (Fig. 33). Active swimming was higher in those fish in clear water, while resting was the dominant behavioural mode in those in semi-turbid water. Territorial aggression, browsing behaviour and airbreathing was highest in fish subjected to the clear water regime. No difference was found in the levels of disturbed rest activity in either treatment, nor was any cannibalistic aggression observed. Differences in the amount of time devoted to each activity were all found to be significant ($p<0.01$).

The number of aggressive encounters over a set period of time each day, and the number of aggressive encounters per 50 physical contacts, revealed that territorial aggression was significantly higher ($p<0.05$) in the clear treatment than in the semi-turbid water (Fig. 34a & b). No cannibalistic aggression was observed in either the clear or semi-turbid situations, and no mortalities due to cannibalism were recorded.

9. To determine whether potential cannibals can be recognised phenotypically.

An analysis of the population census taken during this experiment revealed that 18% of the population in the "potential cannibals" tank was lost due to cannibalism, while 39% of the population of the "cannibals" tank was cannibalized. Although the duration of the experiment was 30 days, the fish were maintained under identical conditions, but without observation, for a further

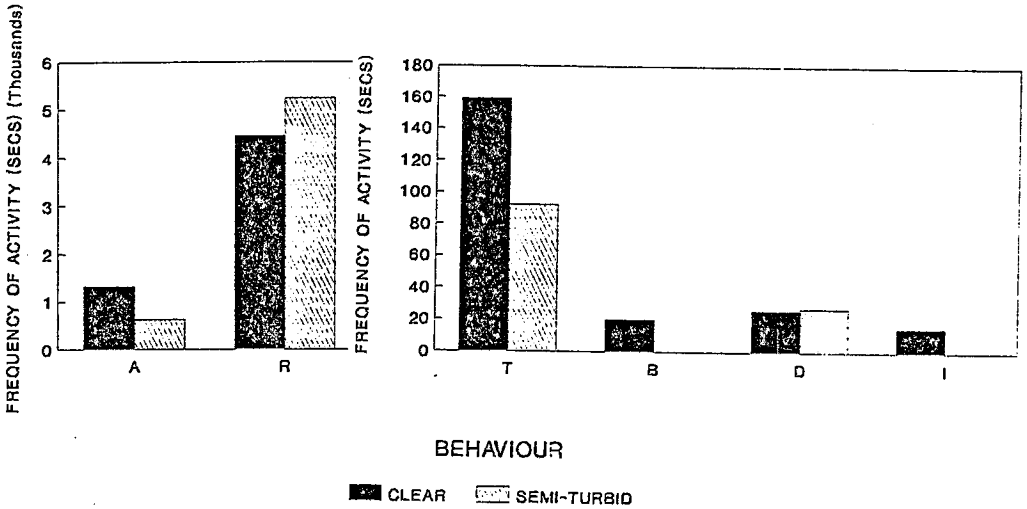


Fig. 33. Proportion of time devoted to different behavioural modes by <u>Clarias gariepinus</u> subjected to clear water and semi-turbid water treatments, over a seven day period. The frequency of activity was calculated by summing the time devoted to each of the behavioural modes (recorded during a daily 10 minute period) for the seven days. (A = active swimming; B = browsing; D = disturbed activity; I = air breathing; R = resting; T = territoriality).

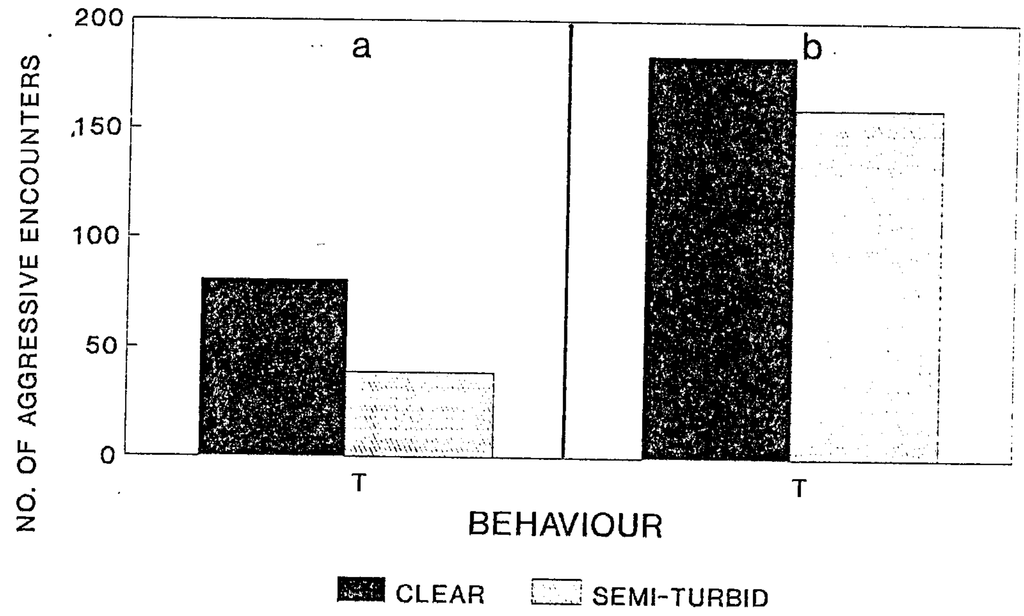


Fig. 34. Level of aggressive behaviour displayed by <u>Clarias gariepinus</u> subjected to clear water and semi-turbid water treatments, over a seven day period, expressed as (a) the summation of the mean number of aggressive encounters during five minute time intervals each day and (b) the daily mean number of aggressive encounters per 50 physical contacts. (T = territoriality).

thirty days. This resulted in one large cannibalistic individual remaining in one of the "cannibals" tanks.

10. Determination of aggressive behaviour in *Tilapia rendalli*.

No aggressive behaviour was observed in *T. rendalli* larvae or juveniles and no fish died from unknown causes during the experiment.

Chapter 4

DISCUSSION AND CONCLUSIONS

This discussion is an attempt to integrate the results of the investigations and the relationship between environmental parameters and the effect they have on cannibalism. An attempt is also made to discern possible trends and principles relating to the phenomenon. The discussion also comments on the selective advantages for and against cannibalism and presents the hypothesis that cannibalism in a species can be related to its position on the r- and K-continuum and is therefore predictable.

It has been hypothesized that environmental/experimental conditions, to a large extent, govern the behaviour of fish (Fox 1975a and b; Polis 1981; Hecht and Appelbaum 1988). The results obtained in the present study substantiate this hypothesis. It was found that by manipulating the environmental parameters some control over cannibalistic and territorial aggression, as well as other behavioural patterns, could be achieved. As a general principle it could therefore be surmised that the results of the experiments obtained from assessing the effect of various environmental parameters on cannibalism are valid. However, as pointed out in the introduction, other factors such as genetic control may also play a part in regulating the level of aggression.

The effect of various environmental parameters on the rate of cannibalism

a) Effect of food availability on the rate of cannibalism.

Sharptooth catfish, trout and koi carp all displayed an inverse relationship between the incidence of cannibalism and food availability, ie. a decrease in the rate/incidence of cannibalism with increasing food density.

This observation supports the findings of a number of workers who also found such an inverse relationship The likelihood that an inadequate food supply may initially induce cannibalism in fish larvae of similar size in intensive culture systems, was suggested by Lewis and Heidinger (1975 see Paller and Lewis 1987). They stated that successful cannibalistic attacks among fish of similar size may impart a spurt of growth to the attacker that promotes further predation upon smaller fish. Subsequently, cannibalistic fish may rely solely on cannibalism and never learn to accept artificial food. Davis (1985) found an increase in the rate of cannibalism in Lates calcarifer in areas where food availability was low. Working on walleyes Stizostedion vitreum less than 20 days old, Hokanson and Lien (1986) also found that greater food availability significantly reduced the incidence of cannibalism. They observed that the presence of abundant food can inhibit cannibalism irrespective of fish density levels. The level of satiation was also found to act as a control on the extent of cannibalism taking place in young anchovy Engraulis capensis (Brownell 1987). These findings, including the results of the present study, seem to support the hypothesis that an adequate food supply suppresses the incidence of cannibalism.

The occurrence of cannibalism despite adequate levels of food has, however, also been reported. Li and Mathias (1982) were unable to show that excess food could suppress cannibalism in larval walleye. Conversely, starvation also produced a considerable increase in the rate of cohort cannibalism. They concluded that cohort cannibalism could be reduced if starvation was prevented, but that it cannot be eliminated entirely simply by providing adequate quantities of alternative food. This phenomenon was also observed by Wright and Giles (1987) in pike (Esox lucius) larvae, where cannibalism occurred despite an abundance of other suitable food. Loadman et al. (1986), working on larval walleye, discovered that at low fish densities and with the population being evenly distributed throughout the water column, there was a consistent rate of cannibalism despite the provision of excess food. Also, Braid and Shell (1981) often observed cannibalism in striped bass (Morone saxitilis), even when brine shrimp were abundant. In addition they found that once larvae became cannibalistic their conspecifics apparently became the favoured prey item.

A totally contrasting finding was reported by Malhotra and Munshi (1984) working on Puntius conchorinius (a sub-tropical carp). They found that the incidence of cannibalism was comparatively lower in the starved than in the fed groups. They suggest that the larvae do not resort to cannibalism when forced by hunger, but that it could just be a natural feeding trait. This higher incidence of cannibalism in fed groups may also be due to the surplus energy derived by the larvae from the available exogenous food, which enables them to pursue and capture other larvae within the group more effectively.

The results of the present study on catfish, trout and koi carp, together with the studies discussed above, support the hypothesis that food availability and cannibalism are correlated, and that their commonest relationship is an inverse one. However, on a larger scale the extent to which this correlation exists and whether it is positive or negative appears to differ interspecifically according to the demands of the species' life-history styles.

An interesting phenomenon observed for both catfish and trout, was that when the fish were deprived of food they appeared to redirect energy usually spent on the maintenance of territories into cannibalistic activity. As food density declined, territoriality initially appeared to increase possibly as a strategy whereby the fittest individuals optimized the limited food resources. However, territoriality appeared to peak at a specific food density after which there was a trade-off situation, where it appeared that any further increase in territoriality was not cost effective. Territoriality therefore began to decline, since it became more beneficial to redirect energy previously used in territoriality into cannibalistic activity. Cannibalistic aggression appeared to be higher when food availability was lowest.

b) Effect of population density on the rate of cannibalism.

A positive correlation was established between cannibalism and population density for catfish, trout and the common and koi carp. In all these species, cannibalism increased with population density. This is in agreement with and substantiates the findings of several workers. Degani and Levanon (1983) found the European eel, _Anguilla anguilla_, to be cannibalistic only at high densities. Giles _et al_. (1986) found the same phenomenon in pike fry (_Esox lucius_). Tucker (1988) discovered that at low densities cannibalism was completely absent in juvenile spotted seatrout _Cynoscion nebulosus_. Nikolsky (1963) reported that fish such as cod (_Gadus morhua_) and smelt (_Bathylagus_ spp.) become more cannibalistic at higher densities. Thus the end effect is a possible reduction in competitive relationship, with cannibalism acting as a population regulation mechanism (Polis 1981). Malhotra and Munshi (1984) also interpreted the higher incidence of cannibalism at high densities in _Puntius conchorinus_ as a population regulation mechanism.

In his review of the subject, Polis (1981) described cannibalism as a self-regulatory process whose homeostatic mechanisms are often more sensitive than those of other agents of population regulation. It therefore acts to adjust the population size to the existing resource base by functioning as an adaptation to variable food supply.

Polis (1981) suggested two reasons why the incidence of cannibalism increases with density. Firstly, changes in the rate of cannibalism may occur for the same reasons that predators exhibit density-dependent responses to heterospecific prey. Secondly, individuals of many species maintain inter-individual space or territory in which they are intolerant of conspecifics. Crowding increases the frequency with which conspecifics violate a critical minimum individual distance (or intraspecific space). This may promote the observed increase in the rate of cannibalism at higher densities.

It appears therefore that there is sufficient evidence to support the hypothesis that cannibalism is positively correlated with population density and that as a density-dependent phenomenon it might act as a population regulation mechanism.

An interesting relationship between territoriality and density emerged in both the catfish and the trout studies. Territoriality appears to increase with increasing density as competition for niche space becomes necessary. This reaches a climax point, after which territoriality appears to break down. This was also found by Henderson-Argapalo et al. (1980 see Macintosh and De Silva 1984). They discovered that at higher densities, social dominance effects between fry may diminish, leading to higher survival, but lower individual rates of growth.

A phenomenon which might provide a very tangible means for manipulating cannibalism has been suggested by Rose (1975 see Thibault 1974). While working on cannibalism and fecundity in the guppy Poecilia reticulata under crowded conditions, he found evidence supporting an hypothesis for the existence of a water borne substance (he did not go as far as to suggest that it might be a pheromone) that increased the cannibalistic response or reduced fecundity. Further experimentation appears to be justified to determine whether such substances do occur for all or just some species, and if so whether they are species specific or not.

c) Effect of live and dry food on the rate of cannibalism.

It was found that cannibalistic and territorial aggression can be significantly suppressed or diverted in both catfish and trout by feeding live food (Daphnia spp.) as opposed to dry, pelletized food.

The results of the experiment to determine whether the rate of cannibalism was influenced by a range of live food items, differing in type and size, were not conclusive since no cannibalism was observed in C. gariepinus during the experimental period. A possible reason for the lack of cannibalism was that due to problems in locating, capturing and breeding alternative live food items, the experimental period was too short (viz. three days).

Although no cannibalism was recorded for C. gariepinus in this experiment, it was, however, noticed that there was a significant change in the incidence of territorial aggression when the fish were supplied with different live food items. The overall trend appeared to be that territoriality increased when the size of the alternative food supplied was increased This was found to be the case with fairy shrimp (28.0mm ± 2.0mm - 1/2 the size of experimental catfish) and T. rendalli larvae (11mm ± 1.0mm - 1/5 the size of experimental catfish). The level of territoriality was lowest when the fish were fed with Daphnia spp. (1.0mm ±

0.5mm - 1/60 the size of experimental catfish), the smallest of the alternative food items supplied. *Clarias gariepinus* larvae fed with *T. rendalli* larvae, however, showed the highest rate of territoriality despite the fact that the *T. rendalli* were half the size of the fairy shrimp. It thus seemed that territoriality was generally high if prey was large, but highest if the prey was fish.

It was not possible to reach a conclusive decision regarding the effect of particular alternative live food items of different sizes on cannibalism. It would seem that cannibalism is possibly suppressed by live food in general, as was discovered in the live versus dry food experiment. However, the present findings indicate that a lengthier period of experimentation is required to reach a more positive conclusion.

d) Effect of photoperiod on the rate of cannibalism.

The sharptooth catfish *C. gariepinus* is generally regarded as being nocturnal, although it will opportunistically adopt a searching-feeding mode if food or prey are detected in the light (Bruton 1979; Britz and Pienaar in press). The present study has, however, demonstrated that intensively fed juveniles reared in continual light, display reduced browsing and swimming activity and lower growth rates than those kept in darkness, indicating that light suppresses feeding activity.

It has been found that *Clarias gariepinus* displays a negatively phototactic response throughout its development (Britz and Pienaar in press). This response appears to be intimately linked to the extremely strong cover-seeking behaviour exhibited in light conditions. This is similar to its behaviour in nature (Bruton 1978). The present behavioural observations, conducted without any form of cover have shown that under light conditions the behaviour of juvenile Clarias gariepinus is characterized by increased cannibalistic and territorial aggression and by disturbed activity interspersed with long rest periods. The activity of juvenile Clarias gariepinus in the light might be interpreted as part of an inherent behavioural strategy whereby visual predators are avoided during the day.

Although the feeding activity was suppressed under continual light conditions, the rate of cannibalism was higher in the light than in the dark treatment. It appears that, in general, continual light causes reduced activity which is ultimately linked to an inherent behavioural strategy leading to the avoidance of visual predators during the day by seeking cover. In turn, this behaviour pattern leads to reduced browsing activity. However, a cannibal, due to its larger size and thus its top position in the social hierarchy, can, under experimental conditions afford to be more active, spending a longer period foraging in comparison with the non-cannibals since it has less chance of falling prey to a sibling predator.

e) Effect of refuges on the rate of cannibalism.

Under light conditions, both in the wild and in captivity, a strong cover-seeking behaviour is exhibited by juvenile Clarias gariepinus (Bruton 1978; Britz and Pienaar in press). This behaviour appears to be an inherent strategy to avoid visual predators, as is evidenced by the absence of cannibalism, territoriality and disturbed activity in those fish provided with refuges. The occurrence of cannibalism among those fish without refuges, plus the increased level of territoriality and disturbed rest activity, demonstrate the resultant stress placed on fish kept under these conditions. The fish supplied with refuges were less active and spent a reduced period foraging in comparison with those without refuges. Britz and Pienaar (in press) found that slightly better growth rates were obtained in catfish supplied with refuges, thus further substantiating the idea that the availability of cover reduces stress.

f) Effect of turbidity on the rate of cannibalism.

The results obtained in this experiment suggest that increased turbidity levels reduce the incidence of territorial aggressive behaviour. This could be due to turbidity causing a reduction in the level of territoriality for the same reason that continual darkness and the availability of refuges suppress territoriality. Under conditions of increased light and reduced refuge availability, an increase in both the rate of cannibalism and the level of territoriality can be expected, along with a decrease in browsing and feeding resulting from the fish adopting a behaviour pattern which reduces the probability of capture by predators. It is therefore possible that turbid waters simulate low light conditions and refuge availability, thus reducing cannibalism. These optimal conditions for growth and survival also help to explain why Clarias gariepinus (Bruton 1988) thrives in turbid waters.

g) Effect of size variation on the rate of cannibalism.

Size variation is a well known biological phenomenon in all animal populations and it was observed in all experiments during the present study. It was also observed that cannibalism is both a cause and an effect of size variation. This has also been found in various other studies, eg. rainbow trout O. mykiss (Shirahata 1964), sharptooth catfish (Wait 1987; Hecht and Appelbaum 1988) and juvenile Atlantic salmon, Salmo salar (Thorpe 1977 see McIntyre et al. 1987). If cannibalism is both a cause and an effect of size variation, it is obviously important to determine the specific factors causing size variation, and to control them as a means of minimizing cannibalism under culture conditions.

Some of the major causes of size variation are known to be high population densities (Katavic et al. 1989 and this study), the initial distribution of sizes as determined by the genotype of an individual (De Angelis et al. 1979) and feeding practices (Katavic et al. 1989 and this study).

The advantages conferred upon an individual by the simple fact that it is larger than its siblings, results in a higher level of cannibalism in this individual. These advantages may be initiated at the gene level. An individual may be programmed by genes causing an earlier hatching time, resulting in an earlier start to feeding with concomitant growth (Pomeroy 1980 see Polis 1981; Polis 1981). An individual may be genetically superior in that its metabolism and physiology cause it to become comparatively larger than its siblings.

The advantages conferred by larger comparative size would subsequently allow the individual to exploit its environment better than its smaller sibling rivals. For instance, the larger individual has a greater opportunity to cannibalize and might learn that this is a more beneficial option than other feeding strategies. The theory that "learning" is associated with the development of cannibalism is supported by Hurley and Brannon (1967 see Malhotra and Munshi 1984).

Work by MacArthur and Wilson (1966) and MacArthur and Pianka (1967) further supports the idea that cannibalism provides a more advantageous option for larger individuals. They hypothesized that an individual would never specialize on a "less preferred" food type, regardless of its abundance. It will always optimize its diet if provided with a choice of prey, choosing items which provide the lowest search and handling time combined with the highest nutritional value. The individual will thus always trade-off energy expenditure against the size and quality of the prey (op. cit.). This is further substantiated by Greenstone (1979) and Meffe and Crump (1987), who suggested that cannibalism might provide a preferable food package in certain species, when alternative prey did not provide the correct amino acid package.

Trends and principles of cannibalistic behaviour.

An analysis of the work performed to date on fish indicates that cannibalism occurs in many species, with some authors even going so far as to say that cannibalism undoubtedly occurs in most fishes, and that the absence of cannibalism in a group should be considered exceptional (Dominey and Blumer 1984). However, many more species must be thoroughly investigated before such broad generalizations can be accepted with any degree of confidence. When considering the extent of cannibalism in the fish species examined in this study it became apparent that the phenomenon is not ubiquitous. No cannibalism was evident in silver carp (Hypophthalmichthys molitrix), grass carp Ctenopharyngodon idella or redbreast tilapia Tilapia rendalli. Van Damme et al. (1989) also found no evidence of cannibalism in the silver carp. A possible reason put forward by Van Damme et al. (op. cit.) was that the mouth width and the gape of this species is so small that ingestion of siblings was impossible. Certain fish, such as the barb Puntius conchorinus, are known to change their diets with age (Malhotra and Munshi 1984). These authors reported that this sub-tropical carp changes from a cannibalistic feeding strategy to a herbivorous one as it progresses through metamorphosis and begins to school. If the findings of Van Damme et al. (1989) concerning the small size of the mouth width and gape of silver carp are correct, and presuming that the mouth parts do not metamorphose thus enabling it to change its diet, as in the case of P. conchorinus, then it can be assumed that the silver carp is non-cannibalistic. It appears that no similar ontogenetic studies on mouth structure and size have been performed for the grass carp. However, judging from the present findings on that species, it seems that it is non-cannibalistic.

Since three of the seven species investigated experimentally were found to be non-cannibalistic, viz. silver carp, grass carp and redbreast tilapia, it could be concluded that cannibalism has been adopted as a life-history strategy by some species but not by others.

A study of the natural feeding biology of the seven experimental species is informative with respect to why a fish should adopt cannibalism as a biological strategy (see Table 5, pg. 17), namely that the three non-cannibalistic species are all are non-piscivorous. Silver carp are planktivorous throughout life, while grass carp are herbivorous, and redbreast tilapia are predominantly herbivorous, although the diet can be supplemented with insects. In contrast, the sharptooth catfish is an omnivorous opportunist, the rainbow trout is primarily carnivorous and the common and koi carps are omnivorous and benthivorous.

It could thus be hypothesized that carnivorous (and especially piscivorous) fish are more likely to be cannibalistic. Cannibalism, however, appears to be an alternative feeding strategy adopted by carnivorous fish under various conditions, which would appear to vary according to the life-history styles of the fish and the environmental situations in which the fish finds itself at a given time. These conditions can be fixed or variable. That is, fixed in a genetic sense where the rate and extent of cannibalism is determined by the genome of a particular individual or of the entire population, and variable with reference to particular environmental conditions such as the amount and type of food available, the population size, photoperiod regime etc.

Amongst the experimental species it was found that the rate and extent of cannibalism decreased in the following sequence: koi carp, catfish, common carp, trout. In assessing whether the rate and extent of cannibalism bears any relation to the position of the species on the r- and K-continuum, it was apparent that such a trend exists. Table 5 attempts to show the relative positions of the seven experimental species on the life-history styles continuum. It would appear that cannibalism is an r-selected trait since, in descending order, it is most obvious in koi carp, catfish, and then common carp, all of which are r-selected or altricial species. The exception is the trout which is mid-way on the continuum, but which displayed the lowest level of cannibalism. One could therefore hypothesize that, when moving away from the strongly r-selected side of the continuum towards the K-selected side, a species is less likely to exhibit cannibalism. On examination of Table 4 (pg. 16), which shows a comparison of the characteristics of the two extremes on the life-history styles continuum, this would make sense. The features which characterize the environment of an r-selected species are generally more unstable and subject to fluctuation than are the features of the more stable environment of the K-selected species. Cannibalism is thus more likely to be adopted as a strategy in r-selected species where food might be limited. One factor which could cause food to become limited is an increase in population size beyond the carrying capacity of the environment. Cannibalism may then be adopted as a mechanism of population regulation, and would be advantageous to strongly r-selected species, but disadvantageous or of no advantage to the K-selected species. Furthermore, since cannibalism would in itself be a factor contributing to instability, it would not fit the definition of K-selection. Having said that, it must be remembered that this argument refers only to the extreme and ideal case of K-selected species, and that the very definition of a continuum implies that there is no cut-off point beyond which cannibalism would not occur; it would merely decline in extent.

An additional reason why the occurrence of cannibalism in a K-selected species would be disadvantageous, involves the impact of a cannibal on its siblings. In a highly fecund species (r-selected) although a large number of individuals within the population would be cannibalized, the percentage of the population lost as a result of this behaviour would be lower than in a population of a less fecund species (K-selected). It is probable that cannibalism as a life-history strategy in a group with low fecundity and high parental investment would have a very deleterious effect on a population of siblings.

The genetic control of cannibalism.

Much evidence has been accumulated to indicate that cannibalism might be genetically controlled. Working on poeciliid fishes, Thibault (1974) found that some species hybridize and that the hybrids have cannibalistic tendencies intermediate between those of the parental species. He concluded that the degree of cannibalism, like the expression of morphological features, is directly related to genome dosage. It has thus been hypothesized that cannibalism is polygenically controlled and heritable. Thibault (1974) also found differences in cannibalism to be related to differences in morphology (eg. dentition) and ecology.

Dominey and Blumer (1984) supported the idea that cannibalism is genetically controlled and is therefore subject to natural selection and thus evolutionary change.

The restriction of cannibalism to particular life-history stages of a single species, and the differences in cannibalistic propensities between closely related species, provide further evidence that cannibalism is genetically determined and responsive to selection (Fox 1975a).

Polis and Myers (1985), working on amphibians, provided evidence suggesting that there are significant environmental and genetic influences on the development of cannibalistic morphotypes. These authors concluded that it appears as if cannibalistic polyphenism is proximally produced by environmental cues acting on a genotype that is sufficiently plastic to produce either normal or cannibalistic morphs.

Pierce *et al*. (1981) found significant differences in gene frequencies between cannibalistic and non-cannibalistic morphs of *Ambystoma*, a salamander. Polis (1981) stated that the widespread occurrence of various adaptations that either inhibit or promote cannibalism among related species implies the presence of selection on genes that regulate its expression.

In considering the difference in the frequency of cannibalism between the two morphs of *Cyprinus carpio*, viz. the common and koi carps, it was found that this behaviour is much more evident in the koi carp. The first question which arose is why there should be a difference in the frequency of cannibalism between two strains which are ostensibly the same species. The differences could not be attributed to environmental parameters since these were identical.

Considering the results of the experiment in which cannibalism was visually selected for, together with the results and arguments of Thibault (1974), Fox (1975a), Polis (1981), Polis and Myers (1985) and also the argument that cannibals are usually more robust and larger individuals, it is highly probable that when aquarists first discovered the coloured morphs of *C. carpio* they naturally selected the larger, more robust individuals of this morph. In doing so they were probably also inadvertently selecting for the cannibalistic genome. This would further substantiate the conclusion that cannibalism is genetically controlled and therefore open to evolutionary development. This could also explain the recent emergence of cannibalism as a significant problem under culture conditions for many species, since breeders would always naturally select the larger, more robust and thus cannibalistic individuals as broodstock.

Evolution of cannibalism

If cannibalism is genetically controlled, then natural selection should be influencing the phenomenon. The following discussion is a speculative examination of whether cannibalism is adaptive or not, and if so whether selection is operating at the individual level, at the population level, or both.

At the outset we need to determine whether cannibalism is a specific function of a causal mechanism, or an incidental consequence of some other mechanism, with a different goal. If it is the former then cannibalism would be adaptive, if the latter then cannibalism would not be adaptive. Simply because we observe a particular activity in an organism does not logically mean we have to attribute that activity to a benefit arising from an adaptation. Williams (1966) stated that a benefit can be the result of chance (ie. a by-product of some other function) instead of design.

Let us begin the investigation by examining the following statement of Fox (1975a): "As a biological phenomenon, sibling cannibalism can possibly be regarded as a specialized predation strategy developed as a mechanism to ensure survival of fit individuals, in the Darwinian sense, under harsh or unstable environmental conditions in order to contribute successfully to future generations". If this statement is true, then the genes for cannibalism are associated with the genes for feeding strategy. Thus, following on from this argument, cannibalism would appear to be a specialized strategy, developed through natural selection, from a normal feeding strategy simply because it was more advantageous. This is borne out by the following statement by Williams (1966), : "A characteristic does not develop because it is necessary, but because it is advantageous; selection deals only with immediate better versus worse within a system of alternatives, and therefore competing entities. It will act to maximize the mean reproductive performance regardless of the effect on long-term population survival".

The second option we are faced with is that cannibalism may be an incidental consequence of other previously selected characteristics of a given species (eg. anatomy - mouth parts, mouth size, digestion capabilities) or the characteristics of an individual (eg. as a consequence of its size in relation to its siblings).

To decide whether cannibalism is adaptive or not, the following questions posed by Williams (1966), need to be invoked and considered:

1. Can the phenomenon be explained by simple physics and chemistry ?
2. Can the phenomenon be explained as an unspecific cause and effect ?

If not then the third option is that the phenomenon is adaptive. One good reason why it cannot simply be explained by physics or chemistry, is that the experiment on behavioural manipulation showed that environmental conditions affect the rate of cannibalism. The phenomenon thus rises above the simple physical and chemical level to a more complex behavioural one.

As to whether cannibalism is an unspecific cause and effect, ie. an incidental consequence of some other function or purpose, can be decided by considering whether or not there is evidence (experimental or otherwise) specifically proving that cannibalism is adpative, ie. whether selection has favoured the phenomenon of cannibalism over another alternative strategy.

One argument favouring cannibalism as an incidental consequence of another effect, is that a species might simply be sufficiently plastic enough to take advantage of this additional food source. As a consequence of this the individual cannibal becomes larger and as such can continue to respond to this additional, alternative food resource. This argument suggests the species is cannibalistic as an incidental consequence of phenotypic plasticity.

However, in considering the statement by Williams (1966) that "selection deals only with an immediate better versus worse within a system of alternatives and therefore competing entities", and considering the fact that the genotype largely provides for the phenotype, we must be led to the conclusion that selection must favour the individual that is able to take advantage of cannibalism. The ability to cannibalize is a "better" situation than a lack of this ability (remembering that selection will act to maximize mean reproductive performance regardless of the effect on the long-term population survival). The genes of such an individual will be selected for on the basis of it reaching maturity faster than non-cannibals and thus producing offspring sooner. Also, with the additional food source a greater pool of energy is available for conversion into the production of offspring.

Further possible evidence suggesting a specific nutritional advantage of cannibalism has been provided by the work of Nagai _et al_. (1971 see Crump 1986), who demonstrated that _Bufo vulgaris_ tadpoles which fed on conspecifics exhibited a more efficient conversion rate of amino acids than tadpoles fed on artificial feeds. Furthermore, when faced with two alternative food sources cannibalism was favoured.

Another example to consider is that of the koi carp which were more cannibalistic than common carp, possibly as a result of human selection. In this and the aforementioned examples, the cannibalistic individuals are definitely relatively more fit in the Darwinian sense, than non-cannibals. Since the characteristic of cannibalism produces a fitter individual, then we can conclude that selection must be operative.

The argument that cannibalism is simply a by-product of normal predatory behaviour, is probably true, but in evolutionary terms, many behaviours, characteristics etc. are by-products of already established characteristics. Cannibalism may be a by-product but it is an advantageous one, and in all likelihood would therefore be selected for. It thus rises above the simple unspecific cause and effect.

However, we must bear in mind, as Fox (1975a) reminds us, that cannibalistic tendencies are responses to local conditions influencing particular populations, as well as responses to the proximal factors producing it, and may thus be expected to vary considerably both within and between species.

Individual or group selection of cannibalism - or both ?

The following discussion deals with the influence of selection on cannibalism, and whether it is individual selection rather than group selection which is operating, or whether both occur simultaneously. During the following discussion many more advantages of cannibalism, and thus material on which natural selection can operate, will be presented. The apparent benefits of individual selection will be dealt with first, followed by the apparent benefits of group selection.

The first and most obvious benefit to the cannibal is an energetic gain from an additional food source. This might allow an individual cannibal to survive and reproduce during periods when alternative prey is unavailable. In comparison with non-cannibals, a cannibal is also likely to be larger and to have a higher reproductive potential because overall reproductive potential is a function of developmental time, survivorship and body size (Polis 1981).

A cannibalistic meal increases the probability of survival by decreasing the probability that the cannibal will itself be eaten or be weakened by hunger. One reason for this is that an individuals' chance of being eaten decreases as a result of its increased size due to more rapid growth in comparison with a non-cannibal. A further reason is that a cannibalistic individual spends less time foraging, since the energy gained from a cannibalistic meal is usually greater than that obtainable from alternative food items (Fox 1975a; Polis 1981). The cannibalistic individual is therefore less likely to encounter siblings because of reduced foraging time and thus more likely to survive longer. Another advantage of cannibalism for the individual is decreased potential intraspecific competition for physical resources, ie. food, refuges and territories.

There thus appears to be an intense form of intraspecific competition in cannibalistic species, resulting in an overall increase in fitness of certain individuals, the cannibals, as is hypothesized by classic Darwinism. Selection favours the individual both by its contributing more genes to the next generation and by reducing the genetic contribution of other individuals.

Polis (1980 see Polis 1981) went so far as to suggest that victims of cannibalism should be thought of as transitory "food caches" that store energy for their kin. Consequently, sibling cannibalism could be interpreted as a direct way in which maternal tissue is converted into offspring tissue. If an organism is unable to partition eggs with enough nutrients or to provision offspring as they develop, selection may produce well nourished offspring via sibling cannibalism.

As a consequence of the above argument it was concluded that sibling cannibalism, depending on the life-history-style of the species and of the environmental conditions, is advantageous to the individual and that this behaviour is adaptive and open to selection.

Polis (1981), however goes on to suggest the **possibility** of selection at the population level, and presents some benefits accruing from group selection. Williams (1966) also suggests the occurrence of both individual selection and group selection simultaneously : "I can conceive of only two ultimate purposes as being indicated, genic survival and group survival. The basic issue is whether organisms are, by and large, using strategies for genic survival alone, or for both genic and group survival. If both, then which seems to be the dominant consideration ?" Although Williams (op. cit.) does suggest that individual and group selection can occur simultaneously, he is very reticent about attributing any behaviour or characteristic as being a result of group selection, and is very critical of the concepts' use. He states that "recognition of mechanisms for group benefit is based on misinterpretation and that higher levels of selection are impotent and not an appreciable factor in the production and maintenance of adaptation". He points out that "benefits to groups can arise as statistical summations of the effects of individual adaptations". He quotes an example very relevant to this thesis, viz. that cannibalism can be beneficial to the individual (nourishment) and the population (population regulation mechanism). Williams then explains that " if we were to examine the feeding anatomy and feeding behaviour of cannibals, we would find it adequately explained on the assumption of design for individual nutrition. The additional assumption of design for population regulation would explain nothing that is not also explainable as a nutritional adaptation. It would be a violation of parsimony to assume both explanations when one suffices".

With these criticisms in mind, an examination of the possible benefits of group selection, and a critical look at whether these benefits can be explained on the individual selection level, follows. The objective is thus to determine whether apparent group selection benefits could be interpreted as incidental consequences of individual selection for a different goal, and whether they should best be left at that level of explanation.

Cannibalism may act as a homeostatic self-regulation mechanism keeping the population level below that of the carrying capacity of the environment, thus increasing stability and production, and decreasing the probability of extinction. Cannibalistic populations are also more resilient because survivors of a population reduced by cannibalism would be relatively more vigorous than survivors of a population reduced by exploitation (Polis 1981). Polis (op. cit.) goes on to argue that we must consider group selection because cannibalism can greatly benefit or harm the relative success or "fitness" of a population. He perceives the existence of large group effects, and asks whether we should not believe that they themselves have become the focus of selection.

As observers it might appear to us that selection is acting on the individual and the group level. However, the individual is the unit of initial selection, and if large benefits to the group also accrue, then it does not necessarily follow that group selection may occur as well. Williams (1966) poses a question which aids in decision making: "Do these processes show an effective design for maximizing the number of descendants of the individual, or do they show an effective design for maximizing the number rate of growth , or numerical stability of a population or larger system?" I believe it is sufficient to explain group benefits at this stage in terms of benefits arising as incidental consequences of individual benefits. The fact that individuals cannibalize, leading to their own personal "fitness", results in a decreased population size. In turn, this leads to a population size below the carrying capacity of the environment which increases stability, leading to a decreased probability of extinction. A consequence of this resultant group effect of severe mortality and lower population size does place cannibalistic populations at a great disadvantage relative to less cannibalistic populations. The differences between cannibalism in the koi and common carps can again be used as an example; the higher rate of cannibalism in koi carp would appear to benefit the individual but not the population in comparison with common carp. For clarity it must be pointed out that cannibalism benefits the individual immediately, while any benefits accruing to the surviving section of the population are merely an incidental consequence of individual benefits. If cannibalism continues to be selected for in the koi carp it could hypothetically, in a single population, lead to one very successful individual with no group benefits whatsoever, (this actually occurred in one of the catfish experimental tanks). Thus, either individual selection is a stronger force than group selection, or group selection is not occurring at all.

On the basis of the above discussion it is submitted that cannibalism is an adaptive strategy.

The control of cannibalism in fish culture.

An applied aspect of this study was to attempt to establish measures for regulating cannibalism under culture conditions. Any ability to guide cannibalism in a desired direction rests on a knowledge, for each species, of the complexity of causes underlying this phenomenon and the relationships of these causes to the particular life-history styles of the species. General principles can be formulated, but ultimately each species must be considered separately in the light of its particular ecological characteristics. Incorporating certain of these environmental controls (and hopefully in the future, genetic controls as well) into the design and planning of intensive culture systems, would aid the producer in terms of higher survival, increased efficiency, improved fish quality, and ultimately, increased productivity and profits.

One of the major causes of cannibalism has been shown to be related to diet (Fox 1975a and b; Polis 1981; Dabrowski and Bardega 1984; Oiestad 1984; Hecht and Appelbaum 1988; Katavic _et al_. 1989 and this study). A reduction in cannibalism can thus be brought about by controlling or predetermining the various dietary factors for each fish species. Generally, for all fish, feeding to satiation can be recommended. Cannibalism can also be reduced by increasing feeding frequency. Feeding frequencies of six times per day were used during the present studies in those experiments where feeding to satiation was required. Feeding six times per day was, however, found to be insufficient for the sea bass _Dicentrarchus labrax_ (Katavic _et al_. 1989). It would therefore be beneficial to determine the optimal feeding frequencies for each species. Due to social dominance and territoriality, certain individuals within the population monopolize food resources. Equitable food distribution over the entire water surface of the rearing container is therefore imperative. Determining the periods during which feeding levels are highest for each species would also be highly beneficial when planning frequency of feeding in order to suppress cannibalism. Hokanson and Lien (1986) found three distinct feeding peaks in larval walleye (Stizostedion vitreum): before dusk, after and mid-morning.

Despite the fact that in many cases food density has been shown to be one of the key factors regulating cannibalism, there are cases in which this is not so. This demonstrates the difficulty of making model-type conclusions encompassing all fish species, since the evolutionary history of each species differs with respect to many parameters, and thus each species must be tested individually. General "rules" can be used initially with a high chance of success but there is always a likelihood of failure. A case in point is presented by Loadman et al. (1986) who found cannibalism not to be associated with stress. Working with larval walleye Stizostedion vitreum, they created an apparently stress-free environment with sufficient food, low population density, with the fish well dispersed and seemingly feeding well. Despite this there was a consistent rate of cannibalism (0.015 attacks per fish per hour).

One method employed by aquaculturists to compensate for the losses of fish through cannibalism, is to over-produce larvae. This has been reported to be the case in tilapia hatcheries (Macintosh and De Silva 1984). Little attempt is made to quantify stocking density and feeding rate in larval culture tanks. The present findings indicate that a better approach is to maintain larvae at those stocking densities and feeding rates where cannibalism is discouraged. Over-production of larvae is not always the most cost-efficient solution to maintaining an acceptable level of fish production in a cannibalistic species. In the case of the rainbow trout, eyed ova fry and fingerlings are relatively expensive, thus making this method economically unsound. Thus, whether or not it is economically viable to over-produce larvae in order to compensate for cannibalism, as opposed to introducing environmental controls that inhibit this behaviour, would have to be determined for each species.

With regard to the culture of Clarias gariepinus, it is evident from the present study (see also Britz and Pienaar in press), that the rearing of larvae under protracted light periods, is highly stressful and may explain the higher rate of cannibalism and the lower growth rates recorded under these conditions. The absence of cannibalism, however, and the higher growth rates obtained in darkness clearly demonstrate that this condition is optimal from a culture point of view. The predominantly resting behavioural mode, observed in the light, which is intimately linked to territoriality, is replaced in darkness by a predominantly active browsing behavioural mode with no territoriality. The increase in growth rate associated with the dark period appears to be directly related to the increased foraging activity observed in the dark, resulting in a greater intake of food and an enhanced growth rate.

On the basis of the observed growth rates, and the reduction of territorial and cannibalistic aggression in the dark, it is recommended that the larvae of C. gariepinus be reared in continual darkness.

It has been found that nocturnal cannibalism is similar to daytime cannibalism in larval walleye (Loadman et al. 1986). It was hypothesized that an increase in density near the aquarium floor at night, despite the dark conditions, was the cause. The authors concluded that it would be better to have continuous light to keep the fish dispersed in order to reduce cannibalism. This argument could be applied to trout since they are also diurnal fish, migrating to the aquarium floor during the dark hours.

With regard to the culture of *C. gariepinus*, it has been demonstrated that raising these fish under dark conditions, and supplying refuges, are both beneficial in terms of reduced stress and cannibalism. When comparing the behaviour of *C. gariepinus* maintained in the dark, however, with their behaviour when maintained in the light and supplied with cover shows that active swimming and browsing were stimulated under dark conditions, while these two behavioural modes decreased with the provision of refuges. Two different behavioural modes resulted in varying growth rates. In this study growth rates were markedly higher in those fish maintained in the dark than those kept in the light, while Britz and Pienaar (in press) found only slightly better growth rates in fish supplied with refuges as compared with those without refuges. Thus, it would appear more productive to culture catfish in the dark with no refuges since the resting behavioural mode, observed in the light with cover, (and which is intimately linked to territoriality), is replaced by a predominantly active browsing mode in darkness, with no territoriality, thus making the provision of refuges redundant.

Size variation is a major cause of cannibalism, especially under high density conditions (Katavic *et al*. 1989). Thus, a primary objective would be to determine optimal densities for the species in question, ie. those densities at which cannibalism is suppressed but at which sufficient economic productivity is maintained. Another factor which is known to cause size variation is diet. This was found by Paller and Lewis (1987) working on larval striped bass (*Morone saxitilis*), by Katavic *et al*. (1989) working on sea bass (*Dicentrarchus labrax*) and also in this study. Further measures would therefore include correct feeding methods such as those already discussed earlier under the control of cannibalism by diet, and those suggested by Stobart (1989) who found that feeding frequency reduced size variation in juvenile rainbow trout, *O. mykiss*. These measures were also found to be beneficial by Paller and Lewis (1987) and Katavic *et al*. (1989)

De Angelis et al. (1979) found that final size distribution depends largely on the initial distribution of sizes. Thus, initial size distribution, plus size selection within populations during the hatchery phase of rearing, is highly recommended. This is often impractical, however, as it is labour intensive and places the larvae under stress which could lead to secondary complications and even mortality. It would be beneficial if a way could be found to size-sort without placing the larvae and early juveniles under stress.

Although it has been shown that live food significantly suppresses cannibalism, attempting to supply live food in a profit-orientated aquaculture system would often be impractical due to the quantities involved and the time period over which live food would be needed. Furthermore, the life-cycles of live prey organisms often do not coincide with the fish-rearing programme. Unless the supply is within easy reach, or it can be cheaply produced, using live food on a large scale would often be economically unviable.

With the understanding gained from the knowledge of the fundamental principles governing cannibalism, certain recommendations for its control in fish culture could be made. It is, however, suggested that further intensive studies be carried out to understand this complex subject more fully. General "rules" for regulating cannibalism could be helpful for any given cannibalistic species. However, in considering the differing life-history styles of each species, it becomes evident that species specific guidelines need to be worked out. Until then, any suggestions for cannibalistic control offered to the aquaculturist can only serve as unrefined tools.

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APPENDIX I

Definitions of the various types of cannibalism

1. **Heterocannibalism** :- cannibalism among non-siblings, ie. between cohorts (Dominey and Blumer 1984).

2. **Filial cannibalism** :- cannibalism by parents on their own offspring (Dominey and Blumer 1984).

3. **Cohort cannibalism/ sibling cohort or coeval cannibalism** :- Li and Mathias (1982) first suggested the term. Hecht and Appelbaum (1988) defined it as intraspecific predation between siblings of the same batch.

4. **Sibling cannibalism** :- intraspecific predation between siblings of different batches.

5. **Oophagy** :- intraspecific predation on eggs.

6. **Intra-uterine oophagy** :- intraspecific predation on eggs by embryos within the uterus.

7. **Intra-uterine adelphophagy** :- intraspecific predation on sibling embryos within the uterus.

APPENDIX II

Tables of standard deviations for the data represented in all bar graphs.

Table 41. An easy-reference table for tables 42 to 62 , which present the standard deviations for the data in all bar graphs. Note:- all tables must be read with reference to the appropriate figure.

FIGURE NO.	PAGE NO.	TABLE NO.
5	66	42
6a&b	66	43
8	68	44
9a&b	71	45
11a&b	74	46
14	80	47
15a&b	80	48
16	82	49
17a&b	82	50
18	84	51
19	85	52
23	92	53
24a&b	92	54
25	94	55
26	94	56
27	96	57
28	96	58
29	97	59
32	103	60
33	105	61
34	105	62

Table 42. (Refer - Fig. 5).

BEHAVIOUR	FR1	FR2	FR3	FR4
ACTIVE SWIMMING	2307 ± 125.6	2912 ± 140.8	2047 ± 172.6	1233 ± 102.7
RESTING	3166 ± 127.3	2270 ± 154.2	3321 ± 192.1	4459 ± 121.6
TERRITORIALITY	290 ± 21.8	425 ± 18.3	331 ± 16.7	53 ± 9.1
BROWSING	127 ± 16.0	247 ± 36.9	133 ± 63.4	110 ± 20.9
DISTURBED ACTIVITY	107 ± 7.3	141 ± 7.0	146 ± 10.0	10 ± 1.3
AIR BREATHING	3 ± 2.2	5 ± 1.3	0	10 ± 1.8
CANNIBALISM	0	0	22 ± 2.3	125 ± 15.1

Table 43. (Refer - Fig. 6a&b).

BEHAVIOUR	FR1	FR2	FR3	FR4
(Fig. 6a)				
TERRITORIALITY	159 ± 10.4	132 ± 7.6	119 ± 7.9	21 ± 3.5
CANNIBALISM	0	7 ± 1.0	0	27 ± 3.5
(Fig. 6b)				
TERRITORIALITY	116 ± 7.7	186 ± 7.9	253 ± 6.1	56 ± 3.5
CANNIBALISM	0	1 ± 0.3	4 ± 0.7	90 ± 10.5

Table 44. (Refer - Fig. 8).

BEHAVIOUR	FR1	FR2	FR3
TERRITORIALITY	100 ± 9.6	292 ± 21.8	192 ± 14.7
CANNIBALISM	12 ± 4.6	0	0
EXTENDED FIGHTING	2 ± 0.6	0	18 ± 2.8
RESTING	7 ± 1.5	0	0
MOUTH WRESTLING	4 ± 1.2	0	0

Table 45. (Refer - Fig. 9a&b).

BEHAVIOUR	FR1	FR2	FR3
(Fig. 9a)			
TERRITORIALITY	35 ± 4.6	80 ± 10.4	73 ± 5.6
EXTENDED FIGHTING	0	1 ± 0.3	0
(Fig. 9b)			
TERRITORIALITY	14 ± 1.1	136 ± 11.9	103 ± 7.7
EXTENDED FIGHTING	1 ± 0.3	4 ± 0.7	4 ± 1.2

Table 46. (Refer - Fig. 11a&b).

BEHAVIOUR	FR1	FR2
(Fig. 11a)		
NON-AGGRESSIVE CONTACTS	0	4 ± 1.5
CANNIBALISM	1 ± 0.4	2 ± 0.8
(Fig. 11b)		
NON-AGGRESSIVE CONTACTS	8 ± 2.4	1 ± 0.4
CANNIBALISM	15 ± 3.0	8 ± 2.4

Table 47. (Refer - Fig. 14).

BEHAVIOUR	D1	D2	D3	D4
ACTIVE SWIMMING	1949 ± 107.1	3506 ± 154.1	7537 ± 65.2	7998 ± 29.1
RESTING	5611 ± 120.8	3781 ± 152.7	609 ± 66.7	236 ± 22.1
TERRITORIALITY	678 ± 27.9	838 ± 22.5	76 ± 6.7	26 ±2.1
BROWSING	49 ± 5.8	32 ± 4.1	12 ± 2.2	20 ± 4.8
DISTURBED ACTIVITY	100 ± 4.3	228 ± 13.4	112 ± 12.9	55 ± 5.8
AIR BREATHING	5 ± 1.1	15 ± 2.0	32 ± 1.5	61 ± 2.5
CANNIBALISM	8 ± 1.3	0	22 ± 4.2	4 ± 0.8

Table 48. (Refer - Fig. 15a&b).

BEHAVIOUR	D1	D2	D3	D4
(Fig. 15a)				
TERRITORIALITY	300 ± 12.5	323 ± 9.6	33 ± 2.3	3 ± 0.4
CANNIBALISM	5 ± 0.9	0	0	0
(Fig. 15b)				
TERRITORIALITY	370 ± 7.9	279 ± 6.6	8 ± 0.9	2 ± 0.4

Table 49. (Refer - Fig. 16).

BEHAVIOUR	D1	D2	D3	D4
TERRITORIALITY	194 ± 11.1	166 ± 7.3	295 ± 16.6	194 ± 13.6
EXTENDED FIGHTING	24 ± 5.2	0	15 ± 2.0	12 ± 2.9

Table 50. (Refer - Fig. 17a&b).

BEHAVIOUR	D1	D2	D3	D4
(Fig. 17a)				
TERRITORIALITY	67 ± 5.1	83 ± 7.8	183 ± 13.3	124 ± 9.5
EXTENDED FIGHTING	3 ± 0.5	2 ± 0.4	4 ± 0.8	2 ± 0.6
(Fig. 17b)				
TERRITORIALITY	79 ± 5.7	91 ± 6.6	110 ± 7.7	63 ± 7.3
EXTENDED FIGHTING	5 ± 0.5	4 ± 0.8	3 ± 0.6	2 ± 0.6

Table 51. (Refer - Fig. 18).

BEHAVIOUR	D1	D2	D3	D4
NON-AGGRESSIVE CONTACTS	7 ± 2.6	71 ± 18.3	222 ± 18.4	467 ± 18.2
CANNIBALISM	8 ± 3.0	0	9 ± 4.0	65 ± 12.3

Table 52. (Refer - Fig. 19).

BEHAVIOUR	D1	D2	D3	D4
NON-AGGRESSIVE CONTACTS	146 ± 34.0	103 ± 7.1	91 ± 2.7	277 ± 38.6
AGGRESSIVE CONTACTS	0	1 ± 0.4	0	7 ± 2.9
CANNIBALISM	5 ± 1.6	7 ± 2.4	16 ± 2.3	60 ± 6.7

Table 53. (Refer - Fig. 23).

BEHAVIOUR	DRY FOOD	LIVE FOOD
ACTIVE SWIMMING	5675 ± 136.4	4130 ± 58.0
RESTING	2596 ± 136.6	4164 ± 60.7
TERRITORIALITY	102 ± 5.0	56 ± 3.7
BROWSING	3 ± 0.8	19 ± 3.1
DISTURBED ACTIVITY	20 ± 1.9	24 ± 2.2
AIR BREATHING	0	7 ± 1.0
CANNIBALISM	4 ± 1.07	0

Table 54. (Refer - Fig. 24a&b).

BEHAVIOUR	DRY FOOD	LIVE FOOD
(Fig. 24a)		
TERRITORIALITY	36 ± 1.34	22 ± 1.45
(Fig. 24b)		
TERRITORIALITY	42 ± 3.6	33 ± 3.6

Table 55. (Refer - Fig. 25).

BEHAVIOUR	DRY FOOD	LIVE FOOD
TERRITORIALITY	538 ± 22.0	69 ± 3.3
CANNIBALISM	5 ± 1.4	0
EXTENDED FIGHTING	51 ± 4.4	0

Table 56. (Refer - Fig. 26).

BEHAVIOUR	DRY FOOD	LIVE FOOD
TERRITORIALITY	1137 ± 49.9	41 ± 8.7
EXTENDED FIGHTING	98 ± 1.7	0

Table 57. (Refer - Fig. 27).

BEHAVIOUR	DAPHNIA	TILAPIA RENDALLI	FAIRY SHRIMP
ACTIVE SWIMMING	1313 ± 108.1	1123 ± 120.8	1159 ± 84.1
RESTING	4462 ± 112.2	4291 ± 117.5	4500 ± 90.1
TERRITORIALITY	159 ± 8.6	532 ± 19.5	278 ± 18.7
BROWSING	20 ± 1.6	5 ± 1.6	2 ± 0.6
DISTURBED ACTIVITY	26 ± 1.6	44 ± 3.7	37 ± 2.4
AIR BREATHING	15 ± 1.7	5 ± 1.0	24 ± 2.4

Table 58. (Refer - Fig. 28a&b).

BEHAVIOUR	DAPHNIA	TILAPIA RENDALLI	FAIRY SHRIMP
(Fig. 28a)			
TERRITORIALITY	81 ± 6.0	176 ± 7.6	106 ± 8.6
(Fig. 28b)			
TERRITORIALITY	160 ± 10.5	312 ± 10.8	161 ± 13.8

Table 59. (Refer - Fig. 29).

BEHAVIOUR	DARK	LIGHT
ACTIVE SWIMMING	84 ± 6.5	41 ± 3.8
RESTING	7 ± 1.3	50 ± 3.9
TERRITORIALITY	5 ± 0.4	5 ± 0.5
BROWSING	2 ± 0.3	1.5 ± 0.2
DISTURBED ACTIVITY	1.5 ± 0.2	3 ± 0.4
AIR BREATHING	2.5 ± 0.4	2 ± 0.3
CANNIBALISM	0	1 ± 0.7

Table 60. (Refer - Fig. 32).

BEHAVIOUR	NO COVER	HALF COVER	FULL COVER
ACTIVE SWIMMING	4844 ± 79.1	774 ± 30.3	636 ± 36.3
RESTING	3377 ± 169.9	5783 ± 150.1	5923 ± 159.2
TERRITORIALITY	119 ± 2.8	32 ± 2.9	27 ± 3.6
BROWSING	9 ± 0.6	2 ± 0.7	4 ± 0.8
DISTURBED ACTIVITY	28 ± 1.2	8 ± 0.7	7 ± 0.8
AIR BREATHING	0	1 ± 0.5	3 ± 0.5
CANNIBALISM	23 ± 1.3	0	0

Table 61. (Refer - Fig. 33).

BEHAVIOUR	CLEAR	SEMI-TURBID
ACTIVE SWIMMING	1318 ± 108.1	636 ± 20.2
RESTING	4462 ± 112.2	5245 ± 24.7
TERRITORIALITY	159 ± 8.6	92 ± 6.8
BROWSING	20 ± 1.6	0
DISTURBED ACTIVITY	26 ± 1.6	27 ± 2.6
AIR BREATHING	15 ± 1.7	0

Table 62. (Refer - Fig. 34a&b).

BEHAVIOUR	CLEAR	SEMI-TURBID
(Fig.34a)		
TERRITORIALITY	81 ± 5.2	39 ± 2.8
(Fig. 34b)		
TERRITORIALITY	184 ± 8.9	160 ± 7.6