PART III Chapter 6

SNAIL CONTROL BY FISH

6.1 Prey selection by molluscivorous cichlids foraging on snail intermediate hosts of schistosomiasis

Shortened version of: R. Slootweg (1987). *Oecologia* **74**: 193-202, with additional data on *Astatoreochromis alluaudi*.

A large section of the original publication in Oecologia was devoted to observations on encounter rates and its implications for the understanding of the foraging model. For the general understanding of the foraging experiments this information is less relevant and beyond the scope of this thesis. The original paper did not contain information on *A. alluaudi*, so more recent observations on this species were added, confirming that *A. alluaudi* behaves similarly to the other snail-eating cichlids from Lake Victoria.

It has long been suggested that molluscivorous fishes can be used as biocontrol organisms of snails that serve as intermediate hosts of trematode parasites such as *Schistosoma* spp. (Anderson & Gobert 1924). Although some promising results were obtained in small scale field trials, no attempts have been made to formulate an effective method of using fish in biological control of snails (Slootweg 1985). The need for research in this field is well recognized (Hairston et al. 1975; McCullough 1981).

Since 1977 the Haplochromis Ecology Survey Team of the Research Group Ecological Morphology at Leiden University, The Netherlands, has been studying the species distribution and ecology of the haplochromine cichlid fish in the Mwanza Gulf (Tanzania) of Lake Victoria. Based on stomach contents and morphology these cichlids can be classified into eleven trophic groups which together utilize almost all food resources in the lake (Witte 1981 & 1984a). The species used in the present study are molluscivores (snail-eaters). This trophic group has two subgroups: oral shellers and pharyngeal crushers (Greenwood 1974).

- Oral shellers wrench their prey from the shell by taking hold of the exposed soft parts and shaking fiercely; the snail is extracted or torn apart.
- Pharyngeal crushers have a strong pharyngeal jaw apparatus which enables the fish to crush snail shells. The shell fragments are usually separated and ejected after crushing (Hoogerhoud, 1987).

Some 20 species of snail-eating fishes have been caught in the Mwanza Gulf (Witte 1981; Hoogerhoud 1986b). This diversity of snail-eating fishes provides an opportunity to study their comparative potential as biocontrol organisms against snails. Several fish species have been brought to the Zoologisch Laboratorium at Leiden, of which four were used for this study.

Optimal foraging theory can be an important tool in predicting the ability of snail-eating fish species to reduce snail populations. To gain maximal fitness it is plausible that a fish will optimize its foraging to be able to maximize its food intake. Major contributions to the understanding of fish foraging behaviour under laboratory and field conditions have been made by Werner and co-workers (review of optimal fish foraging: Townsend & Winfield 1985). Stein et al. (1984) examined how shell thickness influences selection by a snail-eating sunfish, *Lepomis microlophus*. The authors used an optimal foraging approach in which prey choice was related to energy and time cost/benefit (C/B) ratios. Selection among snail genera was consistent with differences in shell strength and a time C/B construct, operationally defined as handling time divided by prey dry mass. However, within any snail genus neither shell strength (smallest snails had weakest shells) nor time C/B (largest snails had minimal C/B) provided predictions consistent with results from experiments on selective predation. Stein et al. concluded therefore that no size selection occurred within a genus.

The approach in the research described below is based on the classical or first generation optimal foraging models (Krebs et al. 1983). The biomass intake per unit of handling time was calculated from prey dry mass and prey handling time. A fish maximising its food intake should select the prey items with highest reward in prey biomass per second handling time.

Experimental animals

Fish-species

For reasons given by Hoogerhoud (1984) the generic name *Haplochromis* is preferred to the new generic classification as suggested by Greenwood (1980) for a number of species used in this study.

The oral-shelling species used were *Macropleurodus bicolor*, and *Haplochromis xenognathus*. Their diet consist mainly of prosobranche snails (mostly *Melanoides tuberculata* and *Bellamya unicolor*) and insects (Greenwood 1974). Fryer & Iles (1972, p. 75) described *M. bicolor* as being able to crush snails orally, but I never observed this type of prey handling in more than 100 experiments in tanks. Only the shell apertures were damaged by the oral shelling action. Although oral shelling is thought to be their feeding strategy surprisingly all 'oral shellers' used in the experiments were well able to crush smaller snails pharyngeally. It must be stressed, however, that the common prey species in Lake Victoria have a higher crushing resistance than the snails used in the experiments.

Haplochromis ishmaeli and *Astatoreochromis alluaudi* are classified as pharyngeal crushers; very occasionally these species also shell their prey. Their diet consists of prosobranch snails and occasionally bivalves (Hoogerhoud 1986b).

All fishes were caught in the Mwanza Gulf (Tanzania) of Lake Victoria in January/February 1984, and flown to the laboratory in Leiden within 50 h. They were fed a combination of minced heart, dry food, *Tubifex* and snails. All species bred successfully, but with three species only wild-caught animals were used in the experiments. The experiments with *A. alluaudi* were performed in 1989 in the laboratory of the fishculture station of Gounougou in northern Cameroon. Here pond-bred animals were used in tank experiments.

Snails

Biomphalaria glabrata, an intermediate host of *Schistosoma mansoni* in the Americas, was reared on fresh lettuce in 200 l polypropylene transportation containers supplied with running tap water at a rate of 200 l a day and with a 12 h light 12 h dark regime. *Bulinus forskalii*, an intermediate host of *S. intercalatum* in Cameroon, was collected in the Gounougou irrigation scheme and used in the experiments with *A. alluaudi*.

Because of difficulty in extraction, the shells of *B. glabrata* had to be dissolved before the shell and dry tissue mass could be calculated. The snails were first dried in a 60^o C oven for 3 days and weighed to the nearest 0.01 mg. The shells were then dissolved in 10% acetic acid for three days and the bodies were dried and weighed again. *B. forskalii* snails could easily be extracted from their shells.

Size selectivity experiments

The relationship between handling time and snail size

Observations were made on isolated fish kept in 50x50x50 cm tanks at 26^o C. The fish could see each other, which was most helpful in making them more cooperative. In experiments to determine the relationship between handling time and snail size, snails were sorted into 0.5 mm size classes and offered to the fish in random order of size, five per class. Handling time was defined as the time a fish needs to crush a snail completely, to swallow it, and to eject the remaining shell fragments. Snail length, defined as the maximum shell diameter or length, was measured to the nearest 0,1 mm and handling times to the nearest 0.1s. Because satiation might influence the crushing time, observations were made on hungry fish, and stopped before the animal could be satiated; the number of snails necessary to satiate a fish had been determined previously. If handling times exceeded 4 minutes or snails were rejected, no larger snails were offered.

Experimental set-up

Snails were divided into 1-mm size classes from 3 to 15 mm for *B. glabrata*. In order to study the effect of the quantity of offered food on diet composition, snails were offered in quantities of 2, 5 and 10 per class. The total number offered at once per experiment was therefore 26 (2x13), 65 (5x13), or 130 (10x13). Two snails per class is not enough to satiate an adult fish; 10 per class is more than enough. *B. forskalii* snails were offered to *A. alluaudi* in 10 size classes between 4 and 14 mm, in one density only (5 snails per size class).

One experiment was carried out every day, hence starvation time before an experiment was about one day. The fish were allowed to eat for 1.5 h, the maximum time spent foraging in previous experiments, after which they showed no further interest. The remaining snails were recovered and measured. Snails not recovered were considered to be crushed. From previous observations empty or half-empty shells were scored as shelled orally. Experiments were repeated four or five times with every fish for all three food levels. Five individual *H. ishmaeli* were tested, five *M. bicolor*, and five *H. xenognathus*. The experiments with two *A. alluaudi* were repeated 8 times.

The Spearman rank correlation coefficient was used to test relations between:

- average yield in dry mass per second handling per size class vs. numbers of snails eaten per size class;
- numbers of snails orally shelled vs. snail density;
- numbers of snails orally shelled vs. fish size.

Some series of experiments could not be completed because of the sudden death or illness of some individuals; the incomplete data are given.

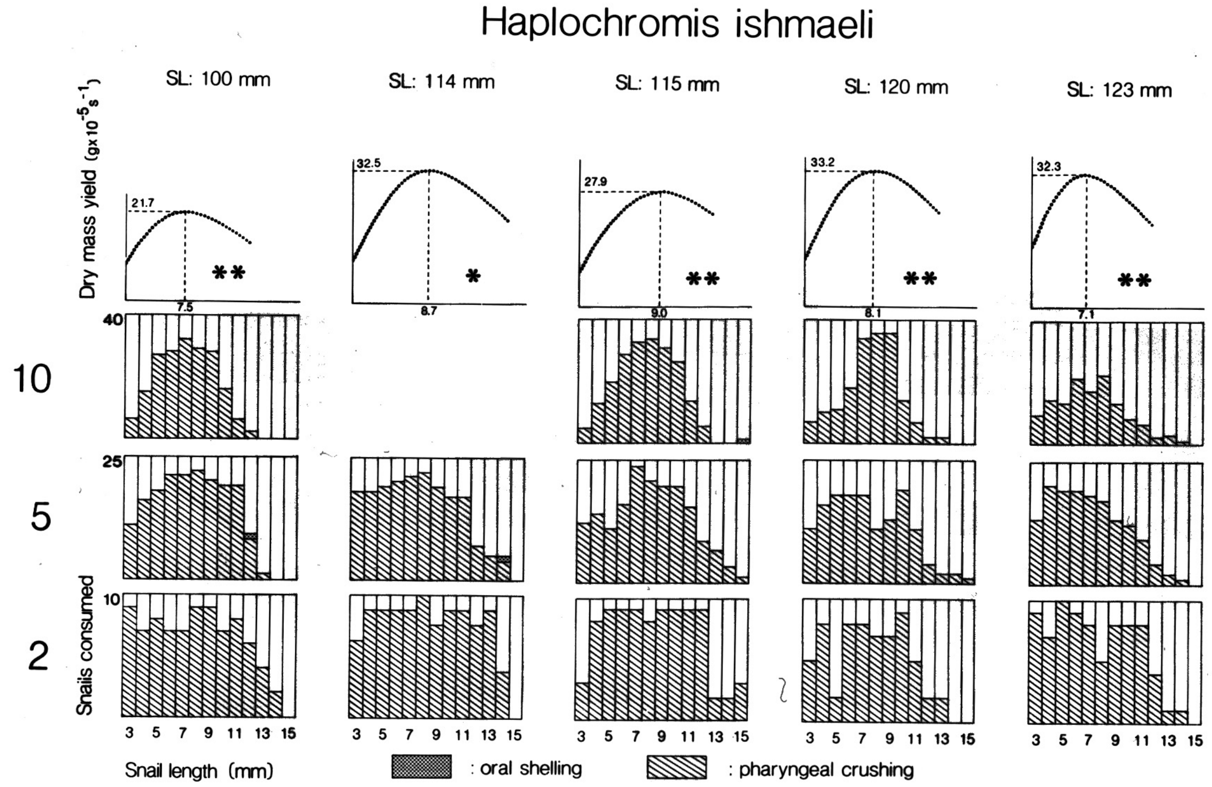

Fig. 25: *Haplochromis ishmaeli*. Individual standard lengths (SL) are shown at top. Top figures: snail dry mass obtained per s handling indicating snail size with highest reward per s. Histograms depict number of snails eaten when offered 10 snails per size class per experiment (upper row; results are the sum of 4 experiments per fish), 5 snails per size class per experiment (middle row; sum of 5 experiments per fish), 2 snails per size class per experiment (lower row; sum of 5 experiments per fish). Asterisks indicate a significant correlation between snail dry mass obtained per second handling (top figures), and the number of snails eaten when offered 10 snails per size class (except for SL 114, where results of 5 snails per size class were tested). Spearman rank correlation coefficient, *P<0.05; **P<0.01.

Results

The handling time versus snail length curves follow a single-logarithmic best fit regression line (least squares, all highly significant). The mean snail dry tissue mass per size-class is divided by the handling time as calculated from the regression line for every individual fish, in order to calculate the biomass intake per unit of handling time for all snail sizes (Figs. 25-28, curves). All curves have a maximum indicating the snail size with the highest reward per second crushing: a fish that maximizes its intake rate per second should select those sizes.

H. ishmaeli (Fig. 25) were able to eat a wide size range of snails; only the largest were usually not eaten. Selectivity increased with increasing numbers of prey offered. (Read histograms from bottom to top for each individual fish.) For all five specimens the number of snails eaten per size class significantly corresponds to the snail dry mass obtained per second handling for these size classes: the fishes eat most of the most profitable snail size class.

The rank correlation for the *A. alluaudi* of 106mm standard length (further referred to as A.a.106) eating *B. forskalii* snails is not significant (p=0.11) due to the steeply descending yield-curve with snails larger than 11mm, while the fish still eats numerous snails from these size-classes. Nevertheless, it is obvious that the fish eats most snails of the most profitable size-class (Fig. 26). For A.a.107 the relation between yield per second handling and numbers of snails eaten is highly significant ($p < 0.01$).

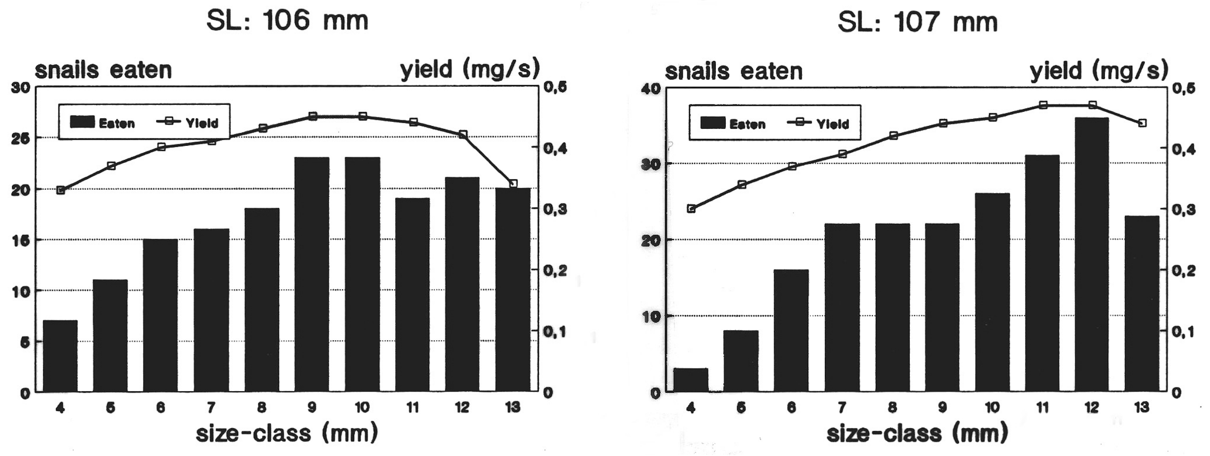

Fig. 27: Astatoreochromis alluaudi feeding on Bulinus forskalii snails.

The feeding behaviour of the so-called oral shelling species deviated strongly from what was expected; many more snails were crushed than shelled (Figs. 27 and 28). Even at the lowest prey density, some fish did not shell a single snail (*Macropleurodus bicolor*, 117 mm, *Haplochromis xenognathus* 107 mm). These fishes could not have been satiated after the experiment because the number of snails eaten was insufficient.

With increasing number of snails offered, selectivity in crushing increases, as with *H.ishmaeli*. Five out of eight actually shelling fishes shelled relatively fewer snails at higher snail densities (Figs. 27 and 28; $P < 0.05$). In two out of three experiments, small *M. bicolor* shelled more snails than larger specimens did (Fig. 27). For *H. xenognathus* this only applied for one series of experiments with 5 snails per class (Fig. 28). The "oral-shelling" species selected smaller snails and did not crush snails as large as *H. ishmaeli* did.

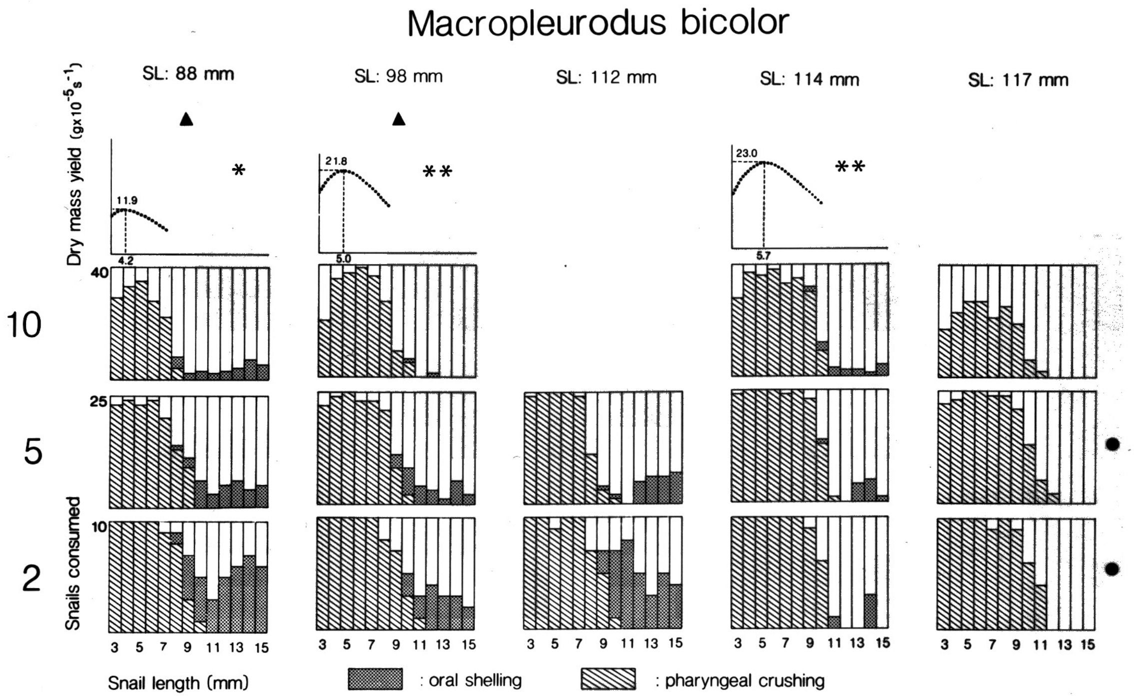

Fig. 27: *Macropleurodus bicolor*. As Fig. 25. A triangle indicates fish that orally shell fewer snails at higher snail densities (Spearman rank correlation P<0.05). A dot indicates a series of experiments (horizontal row) in which smaller fish shelled significantly more snails than did larger ones (Spearman rank correlation, P<0.05)

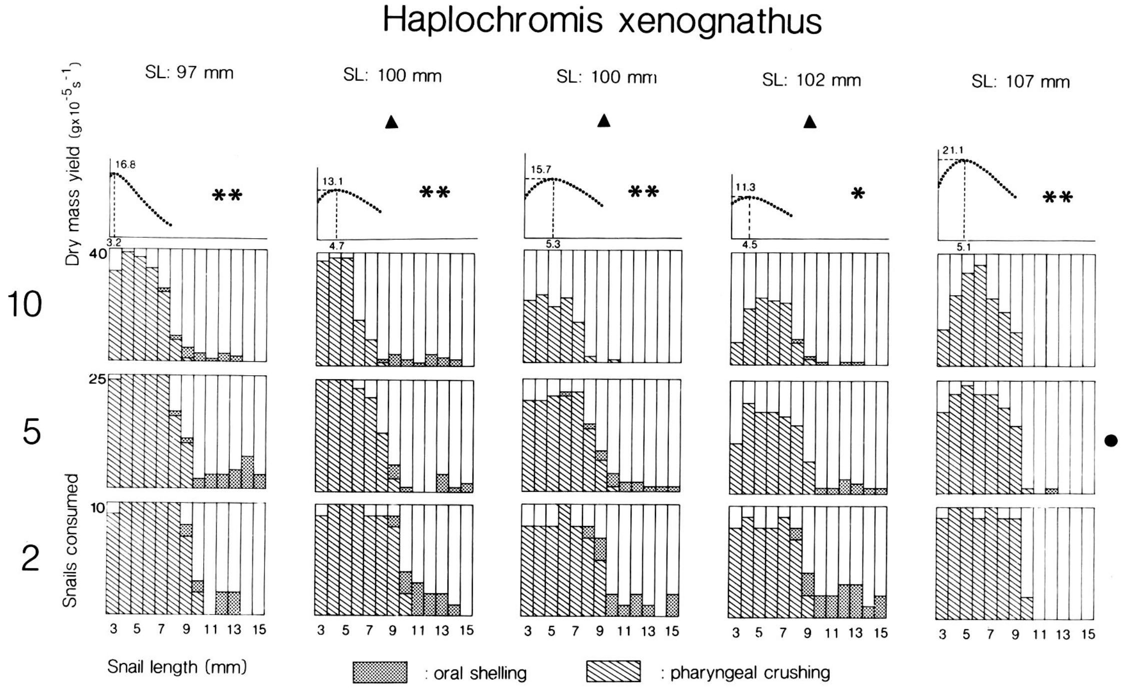

Fig. 28: *Haplochromis xenognathus*. As Figs. 25 and 27.

Discussion

Comparison of prey-size selection and snail dry mass obtained per second handling shows that the oral shellers display a behaviour similar to that of the pharyngeal crusher *H. ishmaeli*. Thirteen out of fifteen tested fishes significantly selected snails according to the reward in dry mass per second handling. The prey size class eaten mostly by *M. bicolor* and *H. xenognathus* is somewhat larger than predicted. In the original version of this paper it is argued that the encounter rate might not be the same for all size-classes of snails. According to the foraging model, this can influence the prey choice of the fish. In additional experiments that were published in the original version (Slootweg, 1987), encounter rates were actually counted and its was shown that the conclusion above remained valid; the fishes indeed select prey items with highest yield per second handling time, and the fish can be considered to forage optimally in this experimental set-up.

The observed prey choice of the molluscivorous cichlid species is remarkable in several ways. In contrast with the results of Stein et al. (1984), who did not find size selection among snails of the same genus for the sunfish *Lepomis microlophus*, the cichlids showed a size selection towards maximal gain in biomass per second handling-time. The wild-caught fishes had hardly ever been able to feed on *Biomphalaria* or *Bulinus* snails before they were brought into the laboratory. Although species of *Biomphalaria* and *Bulinus* are found on the shores of Lake Victoria, densities are very low compared to the common prosobranch snail species. Stomach contents of wild-caught fishes (Katunzi 1983; Witte and Hooger-houd, unpublished work.) suggest that the oral shelling species never crush a snail pharyngeally in Lake Victoria, because the common snail species there are too hard. The fish possibly have a genetically determined foraging behaviour, combined with rapid learning of profitability of unknown snail species.

Mittelbach (1981) demonstrated the feasibility of developing a foraging model that predicts the diet composition of different sizes of bluegill sunfish (*Lepomis macrochirus*; Centrarchidae) foraging in three aquatic habitats. If the intake maximization premise also holds for other food items for the snail-eating cichlids, it may also be possible to predict the diet composition of these fishes in more natural habitats. This knowledge can be of great help in experiments to control snail intermediate hosts of schistosomiasis with snail-eating fish.

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6.2 Proposed introduction of Astatoreochromis alluaudi, an East African mollusc crushing cichlid, as a means of snail control

R. Slootweg (1989). *Musee Royal de l'Afrique Centrale, Sciences Zoologiques* **257**: 61-64

The first record of schistosomiasis, a hieroglyph in the Kalum papyrus, dates back to 1900 B.C. in ancient Egypt. It lasted until 1851 before the responsible trematode worms were discovered by Theodor Bilharz and another 50 years passed before the life cycle of the parasitical worms was discovered by Manson in 1902, and Castellani in 1903. The sexual generation of adult schistosomes live in the definitive vertebrate host; the asexual stage lives in the intermediate host, freshwater snails. In the appropriate snail species, numerous free swimming cercariae are produced which are infective to the vertebrate host. Approximately 250 million people are affected by the disease worldwide.

Schistosomiasis control

Control is based on the interruption of the parasite's life cycle and was in the past mainly confined to snail control. Recently safe and reliable antischistosomal drugs have been developed, but medication only is often unreliable due to the rapid reinfection of treated people in endemic areas. Consequently snail control still forms an important part of schistosomiasis control strategies.

Several methods of snail control can be distinguished:

A: Environmental management. By changing the habitat it may become unsuitable for snails. This method can be applied in artificial water bodies (e.g. irrigation systems) where vegetation clearing, concrete canal lining, and high water velocities may reduce snail populations.

B: Mollusciciding, the most commonly used practice. Snails can be successfully eradicated for a relatively short period (months). Application of molluscicides is therefore repetitive and hence expensive. It seriously affects other aquatic organisms and can even be lethal to fish. Experiments have been carried out with molluscicides derived from plants.

C: Biological control. In spite of several successful trials in the past, this control method has received little attention. Most commonly used are predatory fishes and competitive snail species. In the next section I shall discuss the possible introduction of the mollusc crushing cichlid *Astatoreochromis alluaudi*, into artificial and semi-natural water bodies in the North of Cameroon.

Possible introduction sites

In the Benue river, a tributary of the Niger, a dam has been constructed near Garoua for the generation of hydroelectricity and for large-scale irrigation works on the former flood plains downstream of the dam. It is expected that with the formation of a permanent lake and the development of irrigation schemes the proliferation of intermediate hosts of parasitic diseases will increase.

Near the dam a fish culture station has been constructed where fry of a tilapia (Oreochromis niloticus) is produced. This fry will be introduced into rainfed permanent pools on the former flood plain. Since the yearly flooding and hence restocking with fish has stopped, these pools lost their fisheries potential for local inhabitants. Restocking of these pools will restore this local autoconsumption fishery. Experiments will be started on the combination of fish and rice culture in the irrigation system. Together with this fish culture program an experimental program of biological snail control will be carried out by introducing A. alluaudi together with O. niloticus. It is thought that with the combined stimulus of economic gain (fish production) and decreased infection risk, the local population is more motivated to cooperate.

Proposed introduction of an exotic fish species

Literature studies did not reveal any suitable specialised snail eating fish species endemic to the Benue/Niger river system (Slootweg, 1987). Many species do include snails in their diet but forage in an omnivorous way. Before having reduced snail populations to a significantly lower level such omnivorous fishes will already have switched to other food items. Therefore the introduction of a specialised snail eater from Lake Victoria (and surrounding waters), already successfully used in field trials, was proposed. The following reasons favour the proposed species:

1: *Astatoreochromis alluaudi* is a well investigated species, taxonomically unequivocally distinguishable from the other Lake Victoria haplochromines (cf. Verheyen, 1989).

2: It has already been introduced in Cameroon (Bard & Mvogo, 1963), Kenya (McMahon et al, 1977), and Ruanda (Snoecks, pers. comm.) as a means of snail control, in the first two cases with some success. Adverse ecological impacts have never been recorded.

3: The fish inhabits shallow waters, especially those overgrown by reeds and papyrus. This is the habitat of pulmonate snail species, intermediate host of schistosomiasis. The fish can survive under low oxygen conditions in these swamp-like habitats, which is confirmed by laboratory experiments (See, pers. com.).

4: Morphologically the fish can be classified as a pharyngeal crushing snail eater. With its enlarged pharyngeal jaws the fish can crush shells of considerable resistance. Stomach contents of Lake Victoria specimens showed that the fish feeds mainly on snails, when available. However, the fish is able to survive on other food items (Hoogerhoud, 1986).

5: Pond experiments already showed that *A. alluaudi* (and other snail eating cichlids) can be successfully reproduced in combination with several tilapia species, cultured for consumption (Mvogo & Bard ,1964).

6: Last but not least; like many cichlid species, *A. alluaudi* is easy to handle and to breed. It is strong, has a high temperature tolerance, and outbreaks of diseases hardly ever occur in captivity.

However, since the introductions of exotic species have already caused great ecological disasters, every possible risk should be assessed in advance. Therefore the proposed introduction of *A. alluaudi* is evaluated with the help of a protocol described by Kohler & Stanley (1984) (Fig. 29).

Evaluation of the protocol

Box I: The hazards of schistosomiasis infection are well known and the absence of suitable local fish species makes the introduction valid (1). A. alluaudi is not endangered in its native habitat (2). (In Lake Victoria the fish lives in a habitat less threatened by the Nile perch, and it can also be found in other areas in East Africa.) The fish are laboratory bred and selected before transportation, giving safeguards against disease introduction (3). Although initially the experiments will be carried out in ponds, the chance of escape can never be excluded (flooding, unintentional release). The answer here is thus unclear (4).

Box II: The ability of the fish to survive under the riverain conditions in the Benue system can be doubted. The conditions of this flowing water habitat differ widely from the lacustrine conditions in its native habitat. Its reproductive strategy may not be suitable for this environment (cf. Goldschmidt 1989).

Box III: As mentioned before the earlier introductions in reservoirs and fish culture stations never had adverse ecological impacts. The fish are anatomically best fitted to eat snails, although they occasionally also include insect larvae in their diet. No adverse ecological impacts are expected (1), and I can not think of any hazard to man (2). The introduction of the fish can therefore be approved, although safeguards will be taken to prevent the fish from escaping from the initial pond experiments. A possible unforeseen ecological risk can be assessed through these experiments.

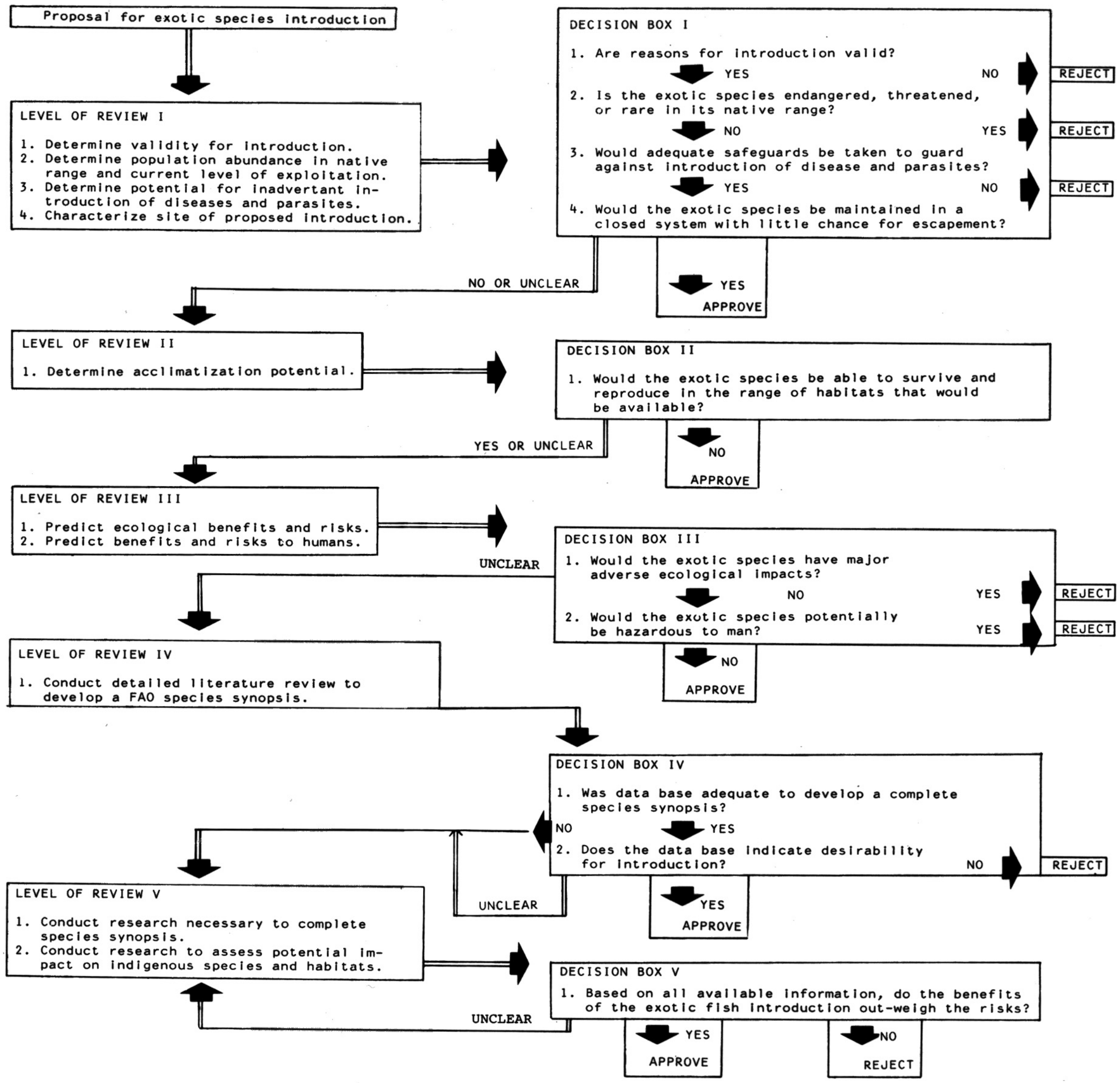

Fig. 29: Review and decission model for evaluating proposed exotic introductions (Kohler & Stanley, 1984)

Conclusion

If the choice in snail control can only be out of two evils, namely using biocides or introducing exotic biocontrol species, it is hard to speak of making the right choice. Compared to mollusciciding the use of fish has some disadvantages, such as the limited number of habitats which can possibly be controlled, and the lack of experience with this method. Advantageous are the reduced need of foreign currency and the simplicity of the method which allows the involvement of the local inhabitants. Taking into account the disastrous ecological impact of molluscicides, the use of fish deserves to be explored as a helpful tool in the integrated control of schistosomiasis.

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6.3 The effects of molluscivorous fish, water quality and pond management on the development of snail intermediate hosts of schistosomiasis in aquaculture ponds in North Cameroon

R. Slootweg, P.A. Vroeg & S.J. Wiersma (1993). *Aquaculture and Fisheries Management*, **24**: 123-128

The original version of this paper has been published as a short communication in Aquaculture & Fisheries Management. The section on collection and elaboration of data appeared to be difficult to follow, so the material & methods section of a more extended earlier version of the manuscript was inserted.

One of the possible negative side-effects of aquaculture in tropical areas is the spread of water-related diseases, in particular schistosomiasis. Fish ponds can provide breeding sites for freshwater snails transmitting schistosomiasis (Berrie, 1966). Scientific attention has long been concentrated on the use of molluscicides as the most effective means of snail and schistosomiasis control. However, molluscicides have limited use in aquaculture as they are expensive, hazardous to many other forms of aquatic life including fish, and have to be applied regularly because of the rapid recolonization by snails. This paper describes a study made on snail populations in an aquaculture station in Northern Cameroon and their possible relation with water quality, pond management and cultured fish species. Together with production experiments, the development of snail populations in the fish ponds has been monitored during two years, and the biological control potentiality of two fish species has been tested. The experiments are part of a larger programme on the integrated control of schistosomiasis in the upper Benue valley of northern Cameroon (Slootweg, 1991).

Three species of fish were used in the pond experiments. The tilapia *Oreochromis niloticus* (L.) was used for production experiments under different nutritional regimes. To control the excessive reproduction by *O. niloticus*, the African catfish, *Clarias gariepinus* Burch., was introduced in several experiments. *C. gariepinus* is also known to eat snails; based on stomach contents analyses of fish caught in an irrigation scheme in Sudan, Coates (1984) suggested to use C. gariepinus in the control of snail hosts of schistosomiasis. As a third species, the East African cichlid fish *Astatoreochromis alluaudi* Pellegrin was introduced solely to test its capability to control molluscs (Slootweg, 1989). In the literature *A. alluaudi* has often been recommended as a means of biological snail control, but the number of actual field trials is very limited. One experiment in Kenya showed a significant reduction in snail populations over a long period (McMahon, 1960; McMahon, Highton & Marshall, 1977), although contradictory evidence is given by recent research (Kat & Kibberenge, 1990). One successful experiment has been described from an aquaculture station near Yaoundé in Cameroon (Bard & Mvogo, 1963; Mvogo & Bard 1964), but has never been repeated afterwards.

Material and methods

The aquaculture station of Gounougou (North Province, Cameroon) consists of 12 small ponds (25 x 10 x 0.9m: 250 m² floor surface) used for production of fingerlings and storage, and 12 larger ponds (35 x 15 x 1m: 525 m²) for production experiments. Water supply to every pond can be regulated separately by means of a supply-pipe and a concrete drainage monk. Pond experiments lasted from 8 to 45 weeks. Between experimental cycles the ponds were routinely drained and dried for at least one week to stimulate the decomposition of benthic deposits. The station is managed intensively; all vegetation in and around ponds is cleared regularly and unauthorized visitors (except cormorants and kingfishers) are kept outside by an iron fence. Snail sampling was carried out on a monthly routine basis. Each pond was sampled for ten minutes by one person using a small net. In this paper only the two most frequently occurring snail species are considered: *Bulinus forskalii* (Ehrenberg) and *Bulinus truncatus* (Audouin).

Water quality: during the pond cycles the quantities of feed and fertilizer were adjusted according to the growth rate of the fish. Therefore we distinguished only between presence or absence of the three products used: brewery waste (used 46 times in 65 experiments), cotton seed cake (40/65), and cow-manure (8/65). During the experiments the visibility and temperature were weekly measured at 8.00 am in every pond. Visibility, measured with a secchi-disc, is related to the quantity of suspended particles and to the state of fertilization of a pond. In fish ponds a high turbidity is often caused by algal bloom due to a high nutritional level.

Stocking density of fish: stocking densities of fish usually varied between 0.5/m² (adults) to 5/m² (juveniles) for tilapia, and 0,1 - 2/m² for A. alluaudi and catfish. As tilapia production was the first objective of the station these fish were always introduced in experiments. A. alluaudi and catfish were introduced according to the experimental design. A. alluaudi was introduced 11 times and the catfish

33 times in 71 experiments. Due to stocking losses (mortality and predation) it is very hard to give exact estimates of the actual stock density at a given moment. Therefore initial stocking density, and the presence or absence of a species in an experiment were used as a variable. As tilapia were always present in the experiments, a distinction was made between the presence of adults (26 experiments) or juveniles (39 experiments).

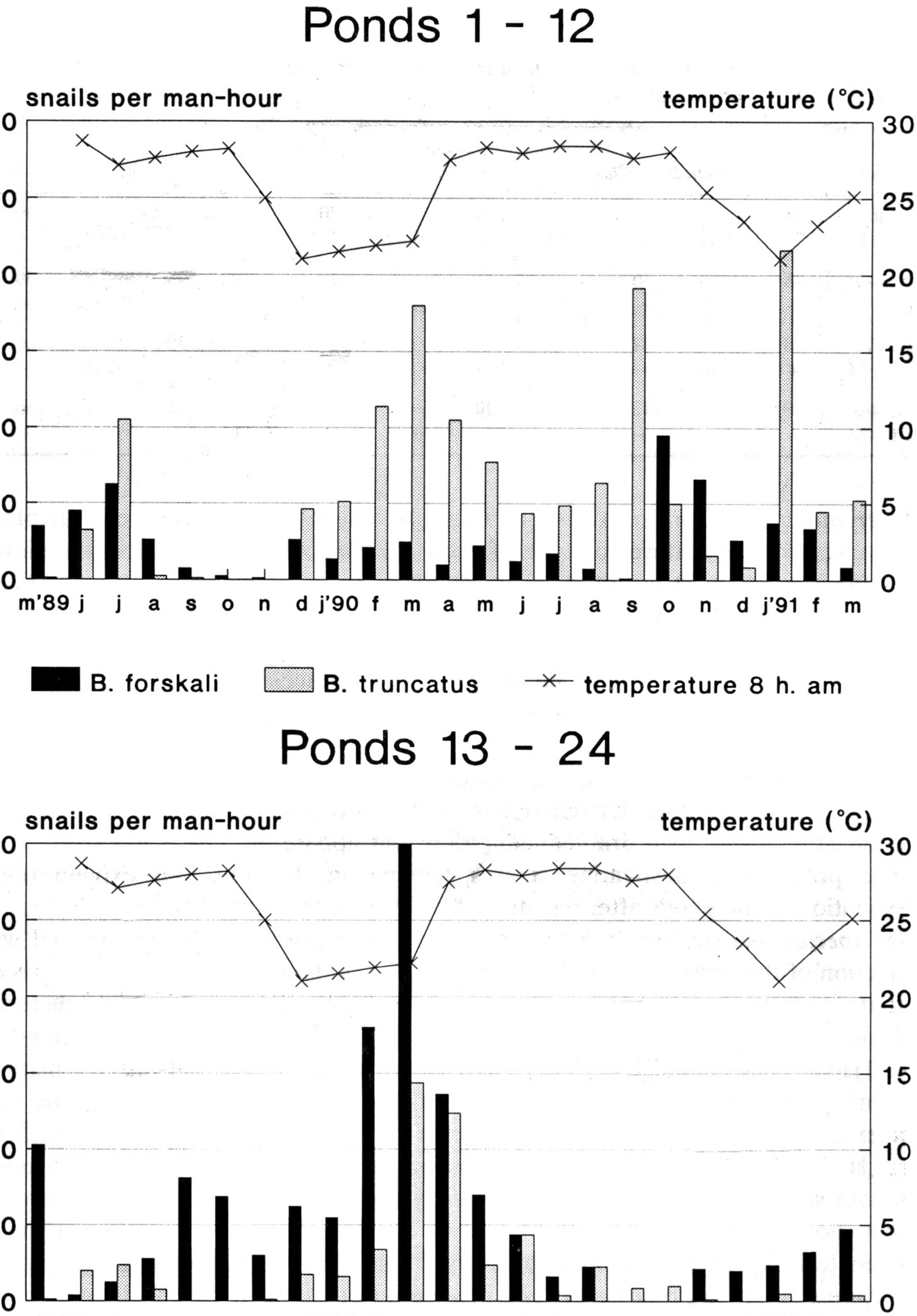

Fig. 30: total numbers of snails collected in ponds 1 to 12 (reproduction and storage) and ponds 13 - 24 (production exper-iments) at the aquaculture station of Gounougou from March 1989 until March 1991, and the monthly average water temperature at 8.00 h in the morning. Snail collections are expressed as the number collected per man-hour search-time.

Elaboration of data. Since the size and management of the small ponds (1 to 12) and the large ponds (13 to 24) differ considerably, the data were split up according to the pond-size used for the experiment. The basic unit for statistical testing is one experiment per pond. Data on 79 experiments were collected between May 1989 and March 1991. Complete sets of data on all variables are available on 62 experiments; in 17 experiments one or more variables had to be treated as missing values.

Every experiment has 8 numerical (1-8) and 6 binary variables (9-14):
1: Mean number of *B. forskali*.
2: Mean number of *B. truncatus*.
3: Visibility of secchi disc; mean over the experimental period.
4: Mean temperature at 8.00 h over the experimental period.
5: Length of the experiment (number of weeks).
6: Initial stocking density of tilapia (number/m^2).
7: id. catfish
8: id. *A. alluaudi*
9: Presence (1) or absence (0) of adult tilapia.
10: Presence or absence of catfish.
11: id. *A. alluaudi*
12: Use of brewery waste as feed/fertilizer.
13: Use of cotton seed cake.
14: Use of cow manure.

To test whether the numbers of snails were significantly correlated to the other numerical variables, the Spearman rank correlation test was applied (table 8). Variables 9 - 14 were tested with the binomial test, as explained in table 9 (Siegel & Castellan, 1988).

Table 8: Spearman rankcorrelation test on numerical variables (Ponds 1-12: number of experiment is 36; ponds 13-24: number of experiments is 43).

	B. truncatus	secchi disk	Temp. 8.00 am	duration	stocking density *O. niloticus*	stocking density *C. gariepinus*	stocking density *A. alluadi*
B. forskalii	r=0.24	r=0.17	r=0.04	r=0.11	r=-.65	r=-.16	r=0.07
Ponds 1 - 12	p=0.14	p=0.31	p=0.79	p=0.49	p=0.70	p=0.35	p=0.67
B. truncatus		r=0.07	r=0.12	r=0.12	***r=-.41***	r=-.15	r=0.16
Ponds 1 - 12		p=0.68	p=0.45	p=0.45	***p=0.02***	p=0.35	p=0.33
B. forskalii	***r=0.51***	r=-.14	r=-.04	r=-.05	r=0.17	r=-.11	***r=0.27***
Ponds 13 - 24	***p=0.0004***	p=0.32	p=0.81	p=0.78	p=0.29	p=0.48	***p=0.07***
B. truncatus		***r=-.26***	r=-.21	r=0.03	***r=0.41***	r=0.07	r=-.07
Ponds 13 - 24		***p=0.07***	p=0.15	p=0.82	***p=0.01***	p=0.65	p=0.64

r = correlation coefficient; p = significance level; significance levels under 10% in bold italics.

Results

The development of snail population throughout the experimental period are summarized in figure 30. The results in the experiments show hardly any significant correlation between snail densities and one of the variables concerning water quality, pond management and fish species (table 8 for numerical variables; table 9 for binary variables).

Water quality: *B. forskalii* does not relate to any of the environmental factors water turbidity, water temperature, or type of pond fertilizer. Apparently, for this pioneering species the pond habitat is suited to its establishment. *B. truncatus* shows a little more dependency on water turbidity and type of pond fertilizer. In ponds 13-24 B. truncatus is found more often in turbid water (table 8). We suppose that nutrient level is the determinant factor for turbidity in fish ponds. The use of manure reduces the number of B. truncatus in ponds 1-12 (table 9), but only 3 experiments in 30 included manure so this result is not considered conclusive.

Presence of:	*A. alluaudi*	*Clarias*	adult *Oreochromis*	brewery waste	cotton seed cake	manure
B. forskalii Ponds 1 - 12	38 + 0.44	36 - 0.49	36 + 0.60	30 - 0.59	30 + 0.62	30 - 0.52
B. truncatus Ponds 1 - 12	38 + 0.25	36 - 0.23	36 + 0.60	30 - 0.59	30 + 0.13	***30*** ***- 0.06***
B. forskalii Ponds 13 - 24	48 + 0.16	42 - 0.35	40 - 0.40	36 + 0.22	36 + 0.18	36 - 0.22
B. truncatus Ponds 13 - 24	48 - 0.51	42 + 0.40	***40*** ***- 0.08***	36 - 0.43	36 + 0.49	36 + 0.43

Table 9: Binomial test; probability levels for binary sets of data. The binary variables were sorted according to descending order of the snail density (numerical variable) shown in the left column. The frequency of occurrence in the first half of the sorted array, was tested to the expected frequency (i.e. the frequency in all trials).
H_0: the frequency in the first half of the array does not differ from the overall frequency.
Upper left: number of trials. Lower left: frequency higher (+) resp. lower (-) than predicted.
Lower right: probability

Pond management: Surprising is the absence of any relation between snail numbers and the length of the experiment. One would expect that snails need some time to get established in a pond after it has been drained and dried, but apparently this is not true. The most probable presence of aestivating snail specimens in the mud can explain the rapid recolonization of the ponds after the start of a new fish production cycle.

Fish species: No significant reductions in snail populations have been found with the introduction of the specialized snail eating cichlid *A. alluaudi*, nor with *C. gariepinus*. The idea that *A. alluaudi* can control snail populations is quite dramatically contradicted by the significant positive correlation between *B. forskalii* snails and *A. alluaudi* in ponds 13-24 (table 8). Obviously *A. alluaudi* is able to live on a diet different to its natural habitat, and apparently even prefers this diet to eating snails. The lack of effect of *C. gariepinus* on snails can be explained by its habits. The fish is known to be an opportunistic bottom feeder. In its natural habitat the fish randomly finds prosobranch snails on the bottom. Pulmonate snails (all African snail hosts of schistosomiasis are pulmonate) usually are surface dwellers, not descending further than 25 cm. The fish simply does not meet the snails. Unfortunately Coates (1984) did not mention the species of snails found in the stomachs of *C. gariepinus* caught in irrigation systems in Sudan. Remarkably the only influence on snails by fish could be shown with adult *O. niloticus* on *B. truncatus*, although it must be stressed that sufficient numbers of snails are remaining to allow schistosomiasis transmission. In ponds 1-12 we found a negative correlation between *B. truncatus* snails and density of *O. niloticus* (table 9). In ponds 13-24 higher stocking density correlates significantly to a higher snail density, which at first sight is in contradiction with the aforementioned reduction. An explanation for this phenomenon can be found in the experimental set-up. In production ponds (13-24) adult fish are always stocked in lower densities than juveniles, whereas in the storage ponds (1-12) adults can be found in higher densities. Hence, only the adults have a reducing effect on *B. truncatus* populations. This observation corresponds to the significant reduction in *B. truncatus* snails in presence of adult tilapia in ponds 13-24 (table 9).

Conclusions

In the aquaculture station of Gounougou in North Cameroon it appeared to be very difficult to prevent the establishment of snails in fish ponds. Even in ponds with hardly any vegetation, high stocking densities of fish, regular drainage and drying, and in the presence of known snail-eating fishes, snails establish themselves without being significantly affected. To be able to show some relationship with factors that might influence snail populations, we raised the level of significance to 10%. This is not considered to be very convincing. Briefly, the reasons for failure of the mollusc crushing cichlid Astatoreochromis alluaudi can be found in the spatial distribution of snails, and in the foraging behaviour and anatomy of the fish. Competition in its original habitat, Lake Victoria, forces the fish to forage on hard-shelled prosobranch snails; compared to wild caught fish, the aquaculture specimens showed a reduction in size of the pharyngeal jaws and in strength of the pharyngeal jaw muscles (used to crush the snails shells). The foraging efficiency and prey choice will consequently be irreversibly altered (e.g. Slootweg, 1987; chapter 6.4 of this book).

It looks as if the presence of snails is inevitable in fishculture ponds. In view of this assumption it is interesting to speculate on the relation between *B. truncatus* (the most important host of urinary schistosomiasis) and water turbidity. If we consider water turbidity under pond conditions as an indicator of the nutritional level of a pond, turbid water having more food available for the fish, then snail control is incompatible with fishculture under optimal conditions. In other words, the risk of having snails in ponds increases when quality of nutrition and fish production levels are increased. This is in accordance with the literature where there seems to be consensus that food availability is one of the crucial factors determining population densities of snails (Brown, 1980: ch.11).

Taking these considerations into account, evidently one should strongly oppose to the introduction of communal village fish ponds in schistosomiasis prone areas, unless measures are taken to fence the ponds from the villagers (especially children!). It is recommended to include a health assessment in the planning phase of an aquaculture development project, because with proper measures centred around the prevention of snails becoming infected and reduction of water contacts, the risk of schistosomiasis transmission can be minimized.

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6.4 The biological control of snail intermediate hosts of schistosomiasis by fish

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An estimated 200 million people are infected world-wide by the five known species of human schistosomes, trematode worm parasites which are transmitted by freshwater snails of the genera *Bulinus (Schistosoma haematobium* in Africa and the Middle East, and *S. intercalatum* in Central Africa), *Biomphalaria* (*S. mansoni* in Africa, Caribbean region and South America), *Oncomelania* (*S. japonicum* in the Far East) and *Tricula* (*S. mekongi* in South East Asia) (Jordan & Webbe,1982). The resulting disease, schistosomiasis (or bilharzia), causes significant morbidity to man. Several other snail-transmitted trematode parasites (e.g. *Fasciola* spp.) infect domestic animals and can cause economic loss.

Efforts to reduce the morbidity and adverse economic impact caused by the parasites are presently centred around the health care facilities where the use of effective single-dose medicines can contribute significantly to the control of schistosomiasis. However, the rapid reinfection that often occurs after treatment and the high cost of repeated medication has tempered expectations of the efficacy of medication campaigns on longer term. Actions to reduce the risk of transmission by controlling the intermediate hosts often remain necessary. Snail control can be realised by means of (1) application of molluscicides, (2) habitat modification (e.g. removal of vegetation, concrete lining of irrigation canals, etc.), and (3) biological control. Molluscicides have the disadvantage of being expensive and unspecific (e.g. Corbet et al., 1973); they also kill fish and other useful organisms such as competitors of snails (Hairston et al., 1975), and therefore cannot be used in aquaculture ponds (Slootweg et al., 1993) or places where fish are introduced to control mosquitoes. Habitat modification is of limited applicability, usually only in man-made environments. Against this background, the present paper focuses on the biological control of freshwater snails.

The influence of fish on the invertebrate fauna, snails in particular, cannot be denied. Louda et al. (1985) and McKaye et al. (1986) have shown that predation by molluscivorous cichlids is a significant factor in the distribution of Lake Malawi gastropods. Brown & DeVries (1985) state that fish predators can dramatically alter the population dynamics of a single snail species, although in their research, predation pressure never reached levels where snails were completely eradicated from their environment. Palmer (1979) and Vermeij & Covich (1978) give evidence that the evolution of snails with elaborate shell sculpture is largely induced by fish predation.

Michelson (1957), Malek (1958), Berg (1973), Ferguson (1978) Hairston et al. (1975), and McCullough (1981a) have reviewed and discussed methods of biological snail control, but there does not exist as yet a critical review of the empirical material available from actual field and/or laboratory trials on the use of fish as a biological control agent. In this paper we will review the role of fish in snail control. Special attention will be paid to one particular species that has often been mentioned in the literature as a possible candidate for biological control. Several well documented field studies with varying degrees of success exist which will be discussed extensively. Furthermore, new ecomorphological data on the pharyngeal jaw apparatus of the fish will be presented. The reasons for failure of this fish in snail control will be discussed from an ecological and morphological viewpoint. Finally we will summarize the remaining possibilities and research questions in snail control by fish that need to be addressed in future.

A review of the use of fish in snail control

Table 10 summarizes research on snail-eating fish since 1945. It must be noted that the table is not exhaustive with respect to stomach contents research (field observations category), since we limited our literature search to the relation between fish and snail populations. This also explains the bias towards literature dealing with Africa. Most publications deal either with laboratory or with limited field studies. Fish species which eat snails in laboratory aquaria, or wild-caught fish which stomachs contain snails, are not automatically suitable candidates for snail control. Many species mentioned in Table 10 are opportunistic feeders; within the limits of their mechanical feeding capacities they will eat anything available and do not necessarily specialize on snails. Fish species which tend to specialize on snails are: Protopterus annectens (the lungfish, *Lepidosirenidae*), *Mylopharyngedon piceus* (the black carp, Cyprinidae), some species of the families Mochokidae and Tetraodontidae, *Lepomis microlophus* (the shellcracker sunfish, Centrarchidae), and the cichlids (Cichlidae) *Astatoreochromis alluaudi, Serranochromis mellandi*, some 20 species of the genus *Haplochromis* from Lake Victoria, and *Trematocranus placodon* and several other species of cichlids from Lake Malawi.

Ten field trials were reported to be successful in reducing snail populations (DeBondt & DeBondt Hers, 1952; Andrade, 1959, 1962, 1968; Bard & Mvogo, 1963; Carothers & Allison, 1986; Motta & Gouvea, 1971; McMahon et al., 1977; Gilbert in: McCullough, 1981b; Leventer, 1981; Daffalla et al., 1985; Chiotha et al., 1991 a). Four of these field trials (Bard & Mvogo, 1963; Mvogo & Bard, 1964; Gamet et al., 1964; Carothers & Allison, 1968; Daffalla et al., 1985; Chiotha et al, 1991a) were preceded by laboratory observations, as proposed in the World Health Organization's scheme for screening and evaluating the efficacy and safety of biological agents for control of disease vectors (WHO, 1975 in: McCullough 1981a). The results of noteworthy trials are briefly described below.

1. Cyprinidae: *Mylopharyngodon piceus*, Israel

An example of successful integrated biological control in water reservoirs in Israel is given by Leventer (1981), who introduced several cyprinid fish species to control all biological components simultaneously; e.g. silver carp (*Hypophtalmichtys molitrix*) vs. phytoplankton, grass carp (*Ctenopharyngodon idella*) vs. submerged plants, black carp (*M. piceus*) vs. snails, common carp (*Cyprinus carpio*) vs. insect larvae. With regard to two of these targets, submerged plants and snails, "the biological treatment achieved optimum results". Much knowledge of this type of fish polyculture exists in China, where aquaculture occupies a significant role in the country's overall food production strategy (Zweig, 1985). Also in other Asian countries the combined culture of rice and fish is wide-spread. Rice yields may increase from 5% to 100% through fish, making plant nutrients available to the rice crop. Blom (1983) suggested using molluscivorous fish in combination with rice-culture to control schistosomiasis vector snails, analogue to the successfully introduced mosquito fish, *Gambusia affinis*.

2. Centrarchidae: *Lepomis microlophus*, Puerto Rico

The food preference of the shellcracker sunfish, *Lepomis microlophus* has been tested in the laboratory by Carothers & Allison (1968). This species highly preferred snails above other food items such as mosquito larvae and dragonfly nymphs. Their voracious snail-eating habits was demonstrated in artificial ponds where within a single day the fish could almost eradicate populations of *Physa* sp. and *Lymnaea* sp. Possible evasive behaviour of the snails after the introduction of the fish was not taken into account; according to the authors remaining snails could sometimes be seen on floating vegetation.

Fingerlings of the fish were introduced in aquaculture ponds near Aibonito, Puerto Rico. There were no *B. glabrata* snails in the pond, and when these snails were introduced twice weekly (in unknown quantities) for 32 months they were unable to establish themselves, indicating that the snails were continuously consumed by the fish (Ferguson, 1978). These results are weakened by the lack of control experiments to prove that the snails were able to survive and reproduce in the ponds in absence of the sunfish.

Since 1959, *L. microlophus* has been introduced into about 50 Puerto Rico farm ponds and five lakes. According to the authors the sunfish was an effective predator of snails, and bred well in lakes Guajataka and Garzas, but was apparently decimated by species of *Tilapia* in lakes Loiza, Caonillas and Dos Bocas. In lake Guajataka the sunfish contributed to the control of *Biomphalaria*, but apparently did not harm well-established colonies of other snails such as *Marisa cornuarietis* and *Thiaria granifera* (Ferguson, 1978). Another factor favouring the use of *L. microlophus* is that it is a much appreciated game and food fish (Erdman, 1984). Observations by Osenberg (1989) puts doubts on the efficacy of *L. microlophus*; he states that in the fishes' natural habitat in Michigan, snail production is more limited by the availability of food for snails than by the predation pressure of *L. microlophus*.

3. Cichlidae: *Serranochromis mellandi*, Zaire

DeBondt and DeBondt Hers (1952, 1955, 1956) and DeBondt (1956a, 1956b) reported great success with the local *Serranochromis mellandi* (Cichlidae) (identified in 1952 as *Serranochromis macrocephala*, in later publications named *Haplochromis mellandi* and ultimately named *S. mellandi*; for an update on the nomenclature of African cichlids see Daget et al., 1991) in fish ponds in Southern Zaire. This fish is also considered to be good for consumption. Several types of water bodies were stocked with fish in experiments that started in 1949 and lasted at least until 1956.

i) A pond of about 400m^2, densely populated with *Bulinus* (*Physopsis*) and *Biomphalaria* snails, was stocked with *S. mellandi*. After one month 87% of a fish sample had eaten snails. After two months this percentage decreased to 44%. Thereafter the fish switched to other food items and reproduced successfully. After this initial experiment more *Tilapia* production ponds were stocked with *S. mellandi* keeping the ponds free of snails.

ii) Rice-cultures stocked with *S. mellandi* were "seemingly free of molluscs", while control fields contained many snails (DeBondt, 1955).

iii) In irrigation canals, overgrown with *Potamogeton* and with dense snail populations, snails disappeared after introduction of the fish. If one fish was released at every meter, the canals were free of snails within eight days; one fish at every 10 meters made the snails disappear within a fortnight.

iv) Introduction of snail-eating fish can also be beneficial to the fish culture itself. A *Tilapia* culture infected with *Diplostomum* was freed of this trematode fish parasite after the introduction of *S. mellandi*; the intermediate snail host was eradicated, and fish production came back to normal levels (DeBondt, 1956a).

The experiments with this snail-eating species were part of a fish culture program; no detailed studies on the population dynamics of the snail hosts were carried out. Nevertheless the reduction of snail populations by the fish cannot be doubted, considering the difference between the introduction and the control experiments.

4. Cichlidae: *Trematocranus placodon* and other molluscivores from Lake Malawi

In Lake Malawi some 20 endemic species of snail eating cichlids can be found, some of which have been tested in recent laboratory and field trials (Chiotha & McKaye, 1986; McKaye et al., 1986; Chiotha et al., 1991ab). In experiments in the lake, McKaye et al. (1986) showed that in open sand habitat where cages prohibited predation by fish, the density of snails increased 40-60% within a week. However, when the molluscivorous cichlid *T. placodon* (earlier described as *Cyrtocara placodon*) was placed in the cage, snail densities equalled the controls outside the cage. Stomach contents revealed that *T. placodon* consumed disproportionally more snails of the genus *Bulinus* relative to those of the more heavily armoured genus *Melanoides*. Open shore areas of Lake Malawi may be relatively free of schistosomiasis because molluscivorous cichlids prevent the snail vector from invading these areas.

Experiments in cement ponds with two molluscivorous species (Chiotha et al., 1991a) showed that after four weeks in presence of *T. placodon* (1 individual per 3 m2) the numbers of snails (*Bulinus* spp. and *Lymnaea* spp.) dropped significantly, although in 10 out of 14 ponds snails remained present; there was no significant difference, however, between the number of snails in ponds treated with *Maravichromis anaphyrmis* as the molluscivore, and the number of snails in the untreated ponds. In 3 earthen ponds, snail numbers dropped dramatically over a five month period after the introduction of

Trematocranus placodon. The authors do not indicate if the molluscivorpus fish were wild-caught or pond-reared and if the results could be maintained over a longer period. It is not clear if the fish can be reproduced under pond conditions.

5. Cichlidae: haplochromines from Lake Victoria

Another area where specialized snail eating fishes can be found is Lake Victoria. Surveys by Greenwood (1974, 1981) and Witte & van Oijen (1990) showed that some 21 species of specialized snail-eating haplochromine cichlids live in the lake, all having different niche-requirements. Differences among species can be found in the way of feeding (pharyngeal-crushing vs. oral-shelling), depth range (shallow vs. deep-water species) and substrate type (sand, mud, rocks) (Witte, 1981). In the mid-eighties the number of cichlids in Lake Victoria has dramatically been reduced by the introduction of the predatory Nile perch (*Lates niloticus*), therefore it is not sure how many species (originally ca. 300) have survived (Witte et al., 1992). Several of these molluscivorous species have been studied under laboratory conditions by Hoogerhoud, (1986a&b; 1987; 1989) and by Slootweg (1987) with the explicit intention of finding a suitable candidate for snail control purposes.

The studies presented in this chapter and in Table 10 give the impression of being registrations of secondary results of research having a different primary goal, such as water supply, fish production, and ecological studies. Although there is general agreement that fish can affect snail populations directly or indirectly, especially the unsystematic character of the experiments on control of snails by fish has precluded the growth of a consistent body of knowledge. This is reflected in the scientific literature where researchers are repeatedly urged to perform systematical research into this matter (e.g: Blom, 1973; Hairston et al., 1975; McCullough, 1981b; Roberts & Sampson, 1987). One species has been extensively investigated in field trials on three occasions in two different countries (Cameroon and Kenya), i.e. the East African haplochromine cichlid *Astatoreochromis alluaudi*. These trials will be discussed in greater detail below. Welcomme (1988) gives 4 other countries (C.A.R., Zaire, Congo, Zambia) where *A. alluaudi* has been introduced, but no written accounts are available in scientific literature.

Biology of **Astatoreochromis alluaudi**

This fish is common to Lakes Victoria, Kioga, Nabugabo, Edward, George, Kachira and Nakavali and to adjoining rivers (Greenwood, 1959; Fryer & Iles, 1972; p.102). Like other haplochromines, *A. alluaudi* is a substratum spawning and mouth-brooding species; large adult females (100mm SL) on average produce 170 eggs (Goldschmidt, 1989), which after spawning are taken into the buccal cavity until several weeks after hatching. *A. alluaudi* does not appear to have a breeding season; in Lake Victoria this species is predominantly found in the littoral zone (Witte, 1981) and feeds mainly on the thick-shelled mollusc *Melanoides tuberculata* by crushing the shells with its pharyngeal mill (Greenwood, 1981; Hoogerhoud, 1986a). The pharyngeal jaw is thick and armed with stout, flat crowned teeth. The muscles used for crushing shells are well developed. Field observations on *A. alluaudi* in Lake Victoria and surrounding smaller lakes showed that specimens caught in areas without *M. tuberculata* snails had less developed pharyngeal jaws (Greenwood, 1965, Hoogerhoud, 1986b). The degree of hypertrophy of the pharyngeal jaw apparatus depends on inclusion of *M. tuberculata* in its diet (Greenwood, 1965; Hoogerhoud, 1989; Witte et al., 1990). Based on these results Barel et al. (1991) and Hoogerhoud (1986b, 1989) postulate the hypotheses that *A. alluaudi* in competition with an anatomically better adapted insectivorous fish species would be forced in early ontogeny to feed on less profitable items, i.e. snails. The resulting hypertrophy of the pharyngeals would make it progressively less efficient to feed on insects. Laboratory experiments with the snail crushing cichlids *Haplochromis ishmaeli* and *A. alluaudi* raised on *Biomphalaria glabrata* snails show that fish feeding throughout their ontogeny on this thin shelled schistosomiasis host only develop slightly hypertrophied jaws compared to fish raised on soft minced meat, but compared to Lake Victoria specimens the jaws are of the reduced type (Overbeek, 1986). So not only eating of snails but also the hardness of the shell determines the level of hypertrophy of the pharyngeal jaws.

Field trials on snail control with A. alluaudi

Yaoundé, Cameroon

Some well described field experiments were performed in the South of Cameroon, in Kenya, and recently in the North of Cameroon. Wild caught *A. alluaudi* have been taken from Uganda to the South of Cameroon where pond trials near the capital of Yaoundé have been carried out which showed that snails were effectively controlled, and that *A. alluaudi* could be successfully cultured together with *Oreochromis niloticus* (=*Tilapia nilotica*) (Bard & Mvogo, 1963; Mvogo & Bard, 1964; Gamet, Brottes & Mvogo, 1964). Two basins (85 m^2) were stocked with about 1600 *O. niloticus*; one basin was additionally stocked with *A. alluaudi*. At the moment of stocking the sides of both basins were covered with snails (*Biomphalaria camerunensis* and *Lymnaea africana*). After three months both basins were emptied. The one with *A. alluaudi* did not contain any snail whereas the other was still full of snails. *A. alluaudi* had reproduced successfully among *O. niloticus* and stomach content analyses revealed that *A. alluaudi* was able to live on other food items. The experiments described cover only one fish production cycle; it is not known if the technique was used for a longer period and if this successful snail control was repeated more often. In 1987, *A. alluaudi* could not be found anymore in aquaculture stations in Cameroon (Hamling, pers. comm.).

Nyanza Province, Kenya

McMahon (1960) and McMahon et al. (1977) conducted an experiment in water impounded by earth dams for local water supply in Nyanza Province, Western Kenya. Control of the snail hosts of schistosomiasis was attempted in 1955 by introduction of *A. alluaudi*. Other species were introduced to control weed growth (*Tilapia zillii* and *Oreochromis leucostictus*, both Cichlidae). One reservoir was left as a comparison reservoir without any introduction of fish. Assessment of snail density was carried out both before and after introduction of fish, over a total period of 15 years. The data indicated that *A. alluaudi* did reduce the numbers of some species of snails, particularly *Biomphalaria pfeifferi* and, to a lesser extent and with less certainty, *Bulinus* spp. The other two introduced fish species, *Tilapia zilli* and *O. leucostictus*, were not associated with reduction in snail numbers, and no information is given about their influence on aquatic vegetation. According to the authors, there can be no doubt that in this study *Biomphalaria pfeifferi* formed the principal diet of *A. alluaudi*, although they do not give any data on stomach contents. The data given by the authors are not very conclusive, but this experiment is especially valuable as it is the first example of a quantitative approach with a detailed study on snail populations over a longer period of time. Unfortunately no information is given by the authors on stocking densities or on survival and reproduction rates of the fish.

In 1986/87, Kat & Kibberenge (1990) have revisited eight of these dam sites in order to see whether *A. alluaudi* was still present and to assess the effect on snail populations. In five sites the fish was recaptured; in one case it was the most abundant species. Nevertheless, *Biomphalaria* as well as *Bulinus* snails were found in similar numbers in test sites as compared to control sites without *A. alluaudi*. From every dam site several fish were collected in order to study the dentition of the pharyngeal jaw apparatus. All specimens showed the reduced type of pharyngeal jaws, described by Greenwood (1965) for aquarium raised fish. This reduction is of course quite important for the long-term applicability of the fish for snail control; it will be discussed more fully later on.

North Cameroon

A second field trial with *A. alluaudi* in Cameroon started in 1988. The possible risks of introducing this exotic species in Cameroon was assessed according to the protocol for exotic species introduction by Kohler & Stanley (1984) (Slootweg, 1989a); no foreseeable risk was determined. In 1988, 500 laboratory-raised fish were transported to a fish-culture station in Gounougou, situated in the Benue valley of the Northern province of Cameroon, in order to perform field experiments

(Slootweg, 1989ab; 1991ab; Slootweg et al., 1993). To be able to effectively control snails two criteria were used to evaluate the field trials:

1) The fish have to be readily available for stocking of snail infested water bodies, implying that reproduction in the breeding ponds should be rapid, preferably throughout the year. Furthermore, the fish must reproduce in the target habitats if these are of a permanent nature.

2) In order to stop schistosomiasis transmission, snail populations must at least be decimated, if not entirely eradicated. One of the difficulties in interpreting the possible reduction in snail populations, is that until now we do not know the threshold of the snail population below which transmission of schistosomiasis is interrupted. Therefore, a certain species of fish may drastically reduce the snail numbers, however, transmission of the disease is still possible. To our knowledge, no study has attempted tackling this question in great detail.

Results on pond trials in the aquaculture station of Gounougou with *A. alluaudi* in combination with *Clarias gariepinus* and *Oreochromis niloticus* showed that neither *C. gariepinus* nor *A. alluaudi* had any influence on resident snail populations in ponds (Slootweg et al., 1993). In fact, only a minor but significant reduction in snail numbers could be shown in presence of adult *O. niloticus*, an omnivorous fish. The authors concluded that fish culture under good nutritional regimes enhances growth and reproduction of snails. Because of a lack of competition for food even the so-called molluscivorous fish prefer to eat "easier" food items, readily available in fish ponds.

A second observation from the pond experiments was that the rate of reproduction of *A. alluaudi* was very low and cannibalism probably caused high mortality among juveniles. Over a 14 month period, 95 adult specimens (about half being female) produced only 1195 juveniles. Mortality among juveniles in stocking ponds could reach 72% over a seven month period.

Three field trials gave additional evidence that the fish was not capable of controlling snails (Slootweg 1989b). (1) After the introduction of 50 adult *A. alluaudi* in an enclosed section of a drainage canal, weekly snail sampling did not reveal significant differences between numbers of snails in the enclosed section and the adjacent section without fish. (2) In a rainfed pool with large numbers of *Lymnaea natalensis* and *Bulinus globosus* snails, 200 juvenile *A. alluaudi* were introduced. Snails were sampled weekly before and after introduction, but no noticeable effect was measured over a four month period. 3) In an experiment on combined rice/fish-culture 240 *A. alluaudi* were introduced together with 1200 *O. niloticus* on a 0.25 ha rice-field just after the replanting of rice-seedlings. The rice-field was surrounded by refuge trenches 100 cm wide and 50 cm deep. After three months, 98 *A. alluaudi* were recaptured. Also 3 juveniles were found indicating that reproduction had taken place. From an aquacultural point of view this introduction was a reasonable success since farmers were pleased with the amount of tilapia produced (53 kg). During the experiment a population of *B. forskalii* snails developed, following a pattern similar to other rice fields.

A number of *A. alluaudi*, born and raised in the aquaculture station of Gounougou, were preserved in formaldehyde and shipped to the Netherlands, where the pharyngeal jaws and muscles were studied and compared to laboratory-raised and wild-caught individuals. These results have not yet been published and will be presented in this paper. The main skeletal element of the pharyngeal jaw apparatus is the lower pharyngeal element (LPE). Hoogerhoud (1986b) found that the horn width of the LPE is a good measure to differentiate between animals with a hypertrophied and a reduced LPE. The muscle complex attached to the LPE, the musculus levator externis 4 and the musculus levator posterior (mLE4/LP), were removed, dried and weighed (muscular and skeletal names according to Anker, 1978, and Barel et al., 1976).

In figure 31 the lower pharyngeal element and the muscle complex mLE4/LP are drawn for two typical A. alluaudi of the same neurocranial length, a wild-caught Lake Victoria specimen and a laboratory-reared specimen, to illustrate to what extent the pharyngeal apparatus can be reduced. For the hornwidth of the lower pharyngeal element, the aquaculture specimens from Cameroon fall within the range of least hypertrophied animals from the mollusc-free lakes (figure 32). Data on the dryweight of the muscle complex that operates the lower pharyngeal element show a similar reduction in muscle size. The morphological measurements from the aquaculture specimens reveal that the pharyngeal jaw apparatus is not adapted to processing snails, suggesting that the fish do not eat snails in the Cameroonian experiments.

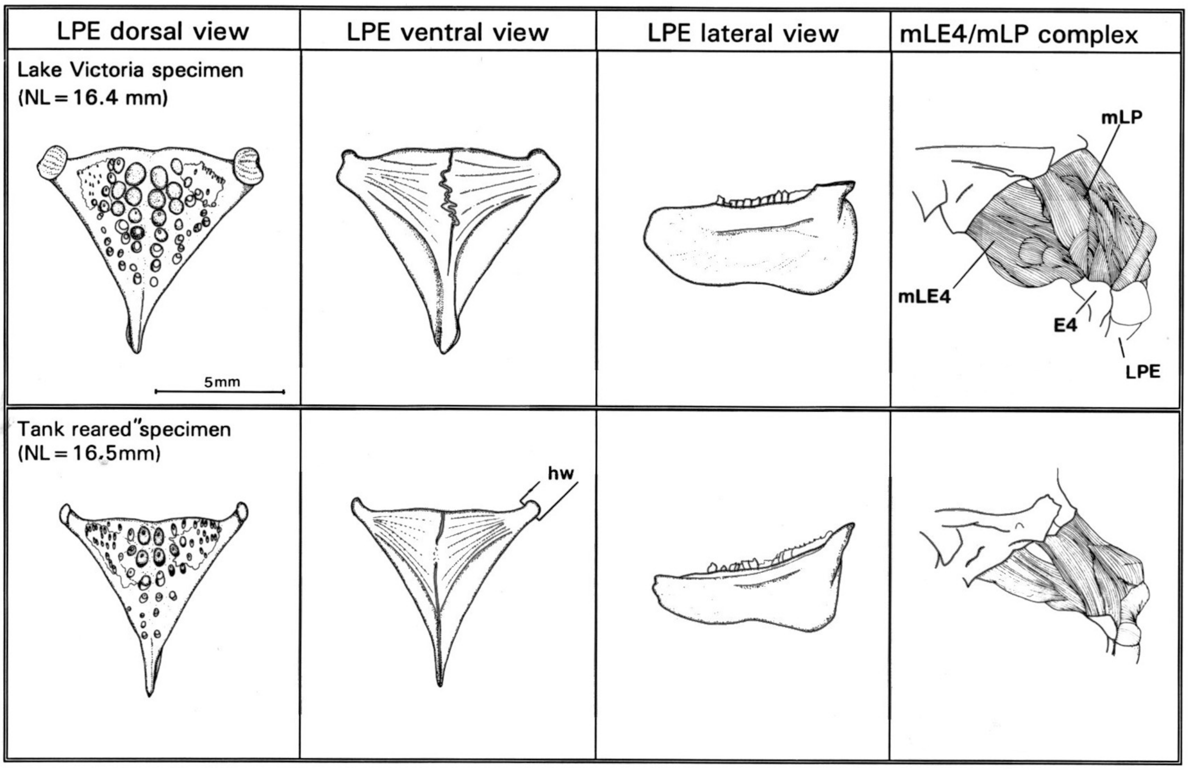

Fig. 31: Lower pharyngeal element (LPE) and muscle complex operating on the LPE of a wild-caught Lake Victoria specimen and a laboratory reared specimen of *Astatoreochromis alluaudi* (Overbeek, 1986). (All drawings to the same scale; abbreviations: NL = neurocranial length; mLE4 = musculus levator externis 4; mLP = musculus levator posterior; E4 = epibranchial 4; hw = hornwidth). Compared to the Lake Victoria specimen, the "tank-reared" specimen shows (1) a reduction in the size of the pharyngeal teeth (LPE dorsal view), (2) a more straightened central suture (LPE ventral view), (3) a more slender outer shape of the jaw, (4) the hornwidth of the LPE is reduced (dorsal, ventral and lateral view), and (5) the volume of muscles attached to the horn of the LPE (mLE4/mLP complex) is reduced.

***Reasons for failure of* Astatoreochromis alluaudi**

1. Reproduction

Tilapiine cichlids, such as the mouthbrooding *Oreochromis niloticus*, are well known in fish-culture as species which reproduce easily in ponds. Usually the reproduction is so excessive that special measures have to be taken to prevent fish from breeding. Therefore it is surprising that the mouthbrooding haplochromine cichlid *A. alluaudi* performs so badly in ponds. It is true that the numbers of eggs carried by *Oreochromis* females can be four to twenty times higher than by *A. alluaudi* (Trewavas, 1983, reports 3700 eggs in a 57cm SL female of *O. niloticus*, compared to 170 for *A. alluaudi* as reported by Goldschmidt, 1989), but this does not fully explain the low numbers of offspring in the latter. An *O. niloticus* can produce a brood every two months; our laboratory observations indicate that *A. alluaudi* only produces between two and three broods per year. In his field experiments DeBondt (1956a) had separated couples of the mouthbrooding riverine cichlid

Serranochromis mellandi. The number of eggs carried by females varied from 110 to 366. After 10 months on average 297 juveniles were produced per couple. If each of the ±50 female *A. alluaudi* that were introduced in the aquaculture station in North Cameroon would have produced one brood, the number of juveniles would be 8500, which is seven times higher than the number actually recorded over a 14 months period. Cannibalism and predation by birds may have contributed to a reduced number of juvenile fish. Summarizing the results one may conclude that *A. alluaudi* is not a suitable candidate for large scale biological control activities where large numbers of fish have to be produced and introduced into water reservoirs. Especially where repeated introductions are necessary, such as in temporary reservoirs, the low reproductive success is a constraint.

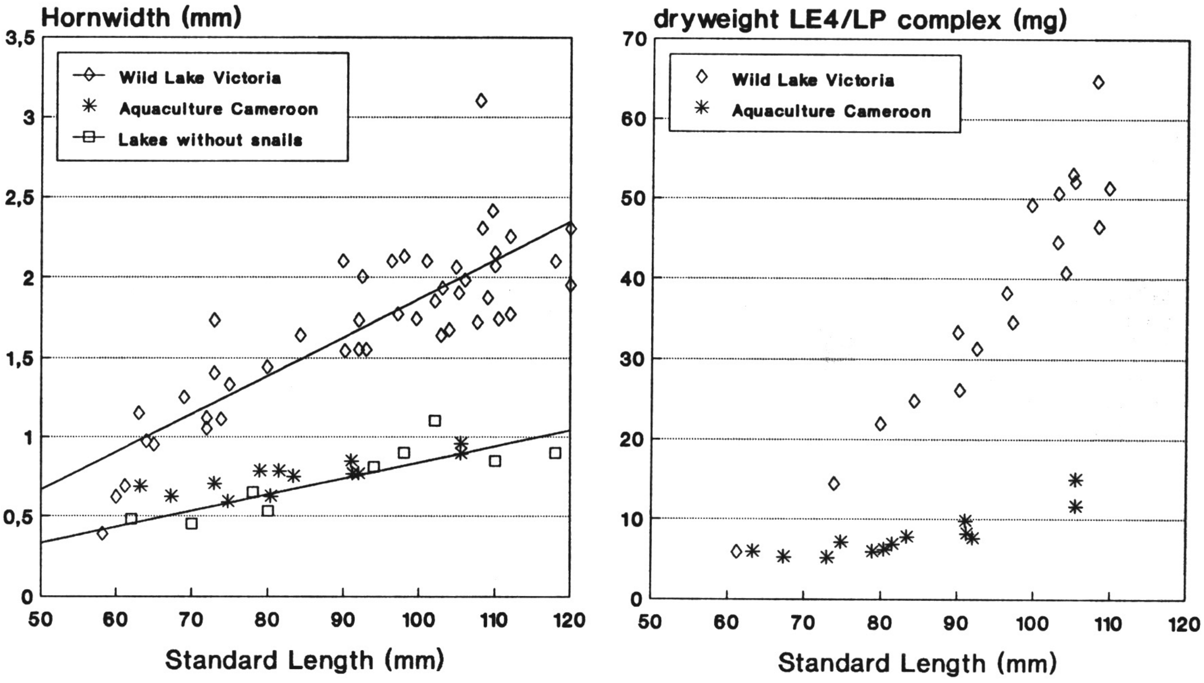

Fig. 32: Reduction of the pharyngeal jaw apparatus in *Astatoreochromis alluaudi*, reared in the aquaculture station of Gounougou, North Cameroon. Data on hornwidth and regression lines of animals from Lake Victoria and Lakes without snails are taken from Hoogerhoud (1986a); muscle weight data of Lake Victoria specimen were provided by J.D. Smits of the Department of Ecological Morphology of Leiden University (N.B: measurements on hornwidth and dryweight are taken from different specimen).

2. Foraging behaviour and prey choice

Using a foraging model, the prey choice of a wide range of animal species searching for food has been explained and could with a certain reliability even be predicted. (For a review on foraging models see Stephens & Krebs, 1986.) In the most simple foraging model the parameters energetic prey content (E), handling time (=searching time plus processing time = Ht) and encounter rate (l) have to be known. When offered a choice of different prey types, these preys can be classified according to their profitability, defined as energetic yield per unit of handling time: E/Ht. According to the average-rate maximizing model, a forager will, upon encounter, always accept the type of prey with highest profitability (type 1). The prey type rating second in energy yield will only be accepted if the total energy yield when foraging on both prey types is larger than the yield when only type 1 prey is chosen. Mathematically this can be described as in inequality 1:

$$\frac{\lambda_1 E_1}{1+\lambda_1 Ht_1} < \frac{\lambda_1 E_1 + \lambda_2 E_2}{1+\lambda_1 Ht_1 + \lambda_2 Ht_2} \quad (1)$$

Written differently it shows that the encounter rate with the highest yielding prey must be lower than a threshold before prey type 2 will be included:

$$\frac{1}{\lambda_1} > \left(\frac{E_1}{E_2}\right) Ht_2 - Ht_1 \quad (2)$$

In other words, the acceptation of a lower-ranked prey type is not influenced by its own density but by the density of the higher ranking prey type only. Laboratory experiments with various species of snail-crushing cichlids indicate that these fish behave according to the average-rate maximizing model preferring the prey type with highest profitability when offered a range of different sizes of snails (Slootweg, 1987). For other snail eating fish this model has also been applied with partial success (Stein et al., 1984; Mittelbach, 1984). Furthermore, when offered a combination of insect larvae and snails in a situation where density is no constraint (excess of preys), insect larvae have a higher E/Ht ratio, and hence are the most profitable prey type (Zoetemeyer, unpublished data). Snails will thus only be eaten when the encounter-rate with insects is below the threshold defined in inequality 2. For field conditions this implies that the willingness of the snail crushing fish to actually eat snails does not depend on the amount of available snails but on the amount of other, more profitable food items. Especially in aquaculture situations the amount of food will not be a limiting factor, because fish have to be produced at the highest possible growth rate and "easy" food (i.e. of the most profitable type) is provided in abundance. If fish forage optimally, they will in this case never switch to eating snails. This observation corroborates with the hypothesis cited above that in Lake Victoria the fish only specialize on snails under the pressure of heavy competition with other species of cichlids that are specialized in handling other food items.

From prey selection experiments where a molluscivorous cichlid, *Trematocranus placodon*, chose thin-shelled *Bulinus* intermediate host snails of schistosomiasis over hardshelled *Melanoides* snails, McKaye et al. (1986) draw the conclusion that this species would be a selective feeder on disease transmitting snails, and thus a suitable candidate for biological vector control. Following the logic of the foraging model this prey choice is understandable since the hardshelled *Melanoides* has a longer handling time and consequently a lower yield per second handling time compared to *Bulinus* snails. This does not imply however, that the fish will choose *Bulinus* when other more profitable prey items are available.

3. Phenotypic plasticity of the pharyngeal jaw apparatus

The absence of hypertrophy in the pharyngeal jaw apparatus of the fish reduces their capability to crush snails. This does not imply that they are not able to eat snails but that handling times for the crushing of snails will increase, especially for larger snails (Slootweg, pers. obs.). Following the foraging model, the encounter rate with more profitable prey types must decrease even further before snails are included in the fishes' diet.

The combination of optimal foraging theory and functional morphology of the pharyngeal jaw apparatus makes us understand the initial partial success of *A. alluaudi* in Kenya where later observations showed that the fish had no influence at all on snail densities, even in reservoirs where fish were still abundant. The introduced fish were wild-caught animals from Lake Victoria with almost certainly hypertrophied pharyngeal jaws. The initial reduction in snail numbers was caused by this wild-caught generation. In due course this generation has been replaced by next generations with less developed jaws. Competition for food in the artificial reservoirs might be low compared to Lake Victoria because they lack an endemic fish fauna. The hardshelled Melanoides tuberculata or similar snails do not occur in these reservoirs, thus the necessary conditions to develop a hypertrophied jaw apparatus are absent. The resulting omnivorous fish is capable of eating snails, but does not specialize on snails and consequently also does not search for them. Similar differences in prey choice between animals with hypertrophied and reduced pharyngeals were observed in other polymorphic cichlid species. Meyer (1989), studying the trophically polymorphic cichlid *Cichlasoma citrinellum*, observed that the molariform morphs (with stout pharyngeal teeth) was able to crack snails that were twice as hard as those cracked by the papiliform morph (reduced type). Liem & Kaufman (1984) studied the prey preference of two morphs of *C. minkleyi* in competition, one having reduced and the other hypertrophied pharyngeal jaws. In an abundant food situation the fish were omnivorous whereas a lowered food availability polarized the feeding behaviour in accordance with their pharyngeal jaw phenotype; the hypertrophied fish specialized on snails.

Probably the phenomenon described above also affected experiments in the Yaounde (Cameroon) fish-culture station where one successful trial was described (Bard & Mvogo, 1963). For this trial also wild-caught *A. alluaudi* were imported from Lake Victoria. After the initial success, the fish was never heard of again.

4. Snail ecology

Other factors reducing the efficacy of snail-eating fish are the spatial distribution of snails and the snails' reproductive capacity. Except for the Oriental intermediate hosts of *S. japonicum*, all other schistosomiasis snail hosts are pulmonate snails, dependent of oxygen-rich water near the surface. Usually they are found at the fringes of a water reservoir or on floating vegetation. Although *A. alluaudi* and some other molluscivorous cichlids are shallow water animals, behavioural studies and the high detritus content of their stomachs indicate that they are bottom feeders (Katunzi, 1983; Kat & Kibberenge, 1990). McKaye et al. (1986) suggest that open shore areas of Lake Malawi are relatively free of schistosomiasis because the bottom dwelling intermediate host snails are selectively controlled by molluscivorous fish. Snails hidden in vegetation near the surface can easily escape this kind of predation, so less open shore areas with aquatic vegetation can be potential sites of schistosomiasis transmission.

The reproductive capacity of snails is enormous; research suggest that the number of offspring is not a limiting factor in the colonization of habitats. Eisenberg (1966) changed densities of a pond snail, *Lymnaea elodes*, to 1/5 and 5 times the initial density. In the next generation, the numbers of snails in the three treatments were equal, regardless of the number of snails in the parental generation, indicating that the numbers of snails very rapidly reach the carrying capacity of the habitat and that reproduction is not a limiting factor. After addition of food, the numbers of snails increased immediately, indicating that food is the limiting factor. Thus, even if a predator is capable of eating large numbers of snails, the population levels may not be lowered to any significant degree.

5. Transmission dynamics of schistosomiasis

For the Sahelian and part of the Soudanian region of Africa another important factor limits the possible use of fish as a biological control agent against schistosomiasis host snails. The most important intermediate hosts of vesical schistosomiasis in this semi-arid region are *Bulinus senegalensis* and *B. globosus*, two species being capable of aestivating in humid mud and surviving periods of drought. When the rainy season starts, surviving snails rapidly recolonize water reservoirs that serve as transmission sites for the following weeks or months. Clearly it is difficult and economically unfeasible to stock all of these seasonal reservoirs with fish.

Prospects of the use of fish in snail control

In the preceding section reasons for the failure of *Astatoreochromis alluaudi* in snail control are given. Other species of molluscivorous haplochromines will also fail to control molluscs for the same reasons. Many examples of intraspecific variability within the family of Cichlidae are known (Witte et al.(1990) for Lake Victoria haplochromines; Kornfield & Taylor (1983), Liem & Kaufman (1984) and Meyer (1987; 1989) for Southamerican cichlids; Cataldi et al. (1988) and Kornfield (1991) for *Oreochromis* species, etc.), Therefore it is likely that the reduction of the pharyngeal jaw apparatus is not limited to *A. alluaudi* only. Overbeek (1986) has already shown a similar reduction in the pharyngeal jaw apparatus of the mollusc crushing cichlid *Haplochromis ishmaeli*. Problems related to reproduction and foraging behaviour will probably not differ much among the other lacustrine molluscivorous cichlids from Lake Victoria. Therefore, it is does not seem advisable to invest further research efforts in this group from Lake Victoria. Molluscivorous cichlids from other African Lakes and/or rivers that may seem suitable candidates for biological snail control should be carefully studied with respect to reproduction and phenotypic plasticity.

Other species of possible snail-controlling fish from Table 10 are unsuitable as well, either because of their omnivorous foraging behaviour or because they are bottom feeders. They appear to be effective against snails in tank experiments, but under field conditions they prefer to forage on other prey items, as explained by the foraging model. However, several examples of snail control by fish from the literature cannot be neglected. The shellcracker sunfish, *Lepomis microlophus*, successfully controlled snails in Puerto Rico, but from the available data it is not clear whether schistosomiasis transmission was interrupted. A renewed visit to the lakes where this species has been introduced, such as has been done in Kenya, can give valuable additional information. Caution must be taken when revisiting these Puerto Rican reservoirs because on this island the competitive snail *Marisa cornuarietis* has successfully been introduced in the biological control against *Biomphalaria glabrata* (Jobin & Laracuente, 1979; also see Pointier & McCullough, 1989 and Gomez Perez et al., 1991).

The black carp, *Mylopharyngodon piceus*, was effective in controlling nuisance snails, obstructing water meters and irrigation equipment in artificial reservoirs in Israel (Leventer, 1981). The method of fish culture and integrated control as applied in Israel is restricted to a limited number of environments and requires an advanced level of knowledge on aquaculture and limnology. Especially on the African continent where aquaculture is not wide-spread, such knowledge is often not available. However, more research on the reproduction methods and usefulness of this species in snail control seems justified, especially in relation to aquaculture.

Most convincing field evidence comes from Zaire where the riverine cichlid *Serranochromis mellandi* was successful in controlling molluscs in fish ponds, irrigation canals and rice fields. The fish successfully reproduced in fish ponds, although numbers of offspring were relatively low. The level of reduction in snail population was such that transmission of schistosomiasis was seriously hampered. Unfortunately no recent information is available on this species; the latest publication dates back to 1956. The author of the early publications on *S. mellandi* still is convinced that this species has much potential in the biological control of snails (DeBondt, pers. com.). The renewed attention for aquaculture in Africa can hopefully stimulate further research into this species which can be found in Lakes Bangweulu (Zambia) and Mweru (Zaire) and certain rivers in South Central and South West Africa (Fryer & Iles, 1972).

The more recent experiments that were performed in Malawi with the cichlid fish *Trematocranus placodon* gave some encouraging results. However, as the authors already indicated, it is difficult to assess wether the reduction in snail population is sufficient to reduce schistosomiasis transmission. We suggest that additional pond experiments with different stocking densities, changes in feeding regimes, and clearing of vegetation might lead to higher reductions in snail density. It is also necessary that questions pertaining to the reproduction of fish and phenotypic plasticity will be answered. Keeping the high risk of schistosomiasis transmission in aquaculture in Africa in mind, we hope the authors will be able to continue the valuable experiments on *T. placodon.*

From the available evidence it has become clear that if fish are to be used in snail control, it should be limited to permanent habitats and in combination with other control measures. The role of fish must be seen as part of an integrated approach where habitat alterations and appropriate water management can reduce snail breeding and refuge sites, and where natural or introduced competitors and predators put further pressure on snail populations. Studies on the population dynamics of snails have shown that the availability of food is often the major constraint (Eisenberg, 1966; Brown, 1980; Thomas et al., 1983). Schayck (1986) has shown that the introduction of the Chinese grass carp, *Ctenopharyngodon idella* in irrigation canals in Egypt had a significant effect on the reduction of snail populations. Clearing of aquatic weeds reduces the amount of food and also exposes snails to predators that might be naturally present (e.g. McKaye et al., 1986). Even if these predators are omnivorous their contribution in the reduction of snail populations might be considerable if the environment is made more hostile to snails. Future research activities should concentrate on this area of integrated research, rather than hoping to find a fish predator of snails that will fully eradicate intermediate hosts of schistosomiasis in all potential transmission sites.

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Tabel 1: Summary of laboratory and field research on snail-eating fish

Family; *Species*	Code		Special remarks (authors)
Protopteridae			
Protopterus annectens (Owen)	a	lo	Fish eats thousands of snails in tanks; *Tilapia* fry was left unharmed, but earthworms were eaten in equal quantities (Mahdi & Amin, 1966).
P. aethiopicus Heckel	a	lo/fe	Omnivorous fish with some preference for snails; in ponds the fish could reduce snail populations by 90%, maintained over a 4 month period (Sudan: Daffalla et al., 1985).
	a	fo	95% of a sample had eaten molluscs; in 56% molluscs were predominant (Lake Victoria: Corbet, 1961)
Mormyridae			
Hyperopisus bebe (Lacépède)	j	lo	Omnivorous (Lake Chad: Blache, 1964).
		fo	Mainly snails in stomach (Lake Chad: Lauzanne, 1972).
	a	fo	Many snails in strong muscular stomach which probably assists with dealing with snails (Sudan: Coates, 1984).
H.b. occidentalis Günther (= *H.o. tenuicauda* Pellegrin)	j	fo	Snails in stomach (Lake Chad: Blache, 1964).
Characidae			
Alestes baremoze (de Joannis)	a	fo	Eats mainly snails but also other food items (Sudan: Coates, 1984).
		fo	In contradiction with Coates; eats only zooplankton, insect larvae and plant material (Lake Albert: Holden, 1970).
Cyprinidae			
Carassius auratus L.	e/j	lo	Eats planorbid snail in tanks (Lagrange, 1964).
Barbus bynni Forskahl	a	fo	Larger specimens had frequently eaten snails (crushed) (Sudan: Coates, 1984).
Barbus altianalis Boulenger	a	fo	By volume molluscs are the main food (Lake Victoria: Corbet, 1961).
Mylopharyngodon piceus (Rich.)	a	fe*	Introduction of various species of carp reduced snail populations and submergerd plants in large reservoirs in Israel (Leventer, 1981).
Umbridae			
Umbra pygmaea (De Kay)	j	lo	Eats small planorbids, but prefers *Daphnia* and *Tubifex* (Lagrange, 1953).
Poeciliidae			
Poecilia (=Lebistes) reticulata Peters	e	lo	Appearance of guppies coincided with disappearance of *B. glabrata* snails in reservoirs (Puerto Rico: Oliver-Gonzalez, 1946).

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Bagridae			
Clarotes laticeps (Rüpell)	a	fo	Piscivorous and malacophagous (Upper Niger River: Daget, 1954; Lake Chad: Blache, 1964).
			Potential for snail control in large permanent waters; shells remain unbroken in digestive tract
Chrysichthys mabusi	a	fo	(Zaire: DeBondt & DeBondt Hers, 1952).
Boulenger			Snails in stomach (Upper Zaire River: Bowmaker, 1968).
	a	fo	
Clariidae			
Clarias lazera Cuv. et Val.	j	fo	Omnivorous fish (Lake Chad: Blache, 1964).
=*Clarias gariepinus*	a	fo	Eats large quantities of snails but not considered to be selective (Sudan: Coates, 1984).
	a	lo	Eats snails in tanks (Mozley, 1953).
		fe	No reduction in numbers of snails in fish ponds (Cameroon: Slootweg et al., 1993).
Pangasiidae			
Pangasius pangasius Hamilton	a	fo	Fish ingested large quantities of molluscs of any kind (India: Hora, 1952).
Osteoglossidae			
Heterotis niloticus Ehrenberg		fo	Feeds mainly on snails. (L. Chad: Lauzanne, 1972)
Heteropneustidae			
Hetropneustes fossilis (Bloch)	a	lo/fo	Inflicts a painful sting which might deter man from wading in infested waters; presumed predatory agent for control in irrigation canals (Iraq: Zakaria, 1963).
Schilbeidae			
Schilbe mystus L.	a	fo	Omnivorous fish (Sudan: Coates, 1984).
Mochokidae			
Synodontis courteti Pellegrin		fo	Exclusive malacophagous (Upper Niger River: Daget, 1954); id. (L. Chad: Blache, 1964).
	a	fo	Snails in stomach (Lake Chad: Blache, 1964).
S. gambiensis latifrons Blache	a	fo	Selective molluscivorous (Lake Chad: Blache, 1964).
S. clarias L.	a	fo	Omnivorous fish with preference for snails (Sudan: Coates, 1984).
S. sorex Günther		fo	Eats mainly snails (Lake Chad: Lauzanne, 1972).
S. schall (Block Schneider)	a	fo	Omnivorous fish with preference for snails (Sudan: Coates, 1984).
S. victoriae Boulenger	a	fo	Main food items are molluscs and insects (Lake Victoria: Corbet, 1961).
Tetraodontidae			
Tetraodon schoutedeni	a	lo	Known from aquaria in Europe as a very good snaileater; eats large snails (Lagrange, 1953)
Pellegrin	a	fo	Snails in stomach (Upper Niger River: Daget, 1954).

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T. fahaka (strigosus)	a	fo	Piscivorous and malacophagous (Lake Chad: Blache, 1964).
(Bennett)	a	fo	Exclusively malacophagous; one specimen (340 g) contained over 1000 snails. Flesh of this family is often poisonous (Sudan: Coates, 1984).
Centrarchidae			
Lepomis microlophus Günther	a	lo/fe*	Preference for snails in laboratory and ponds; controlled *Biomphalaria* snails in farm ponds (Puerto Rico: Ferguson, 1978; U.S.A.: Carothers & Allison, 1968); appreciated game and food fish (Erdman, 1984)
Cichlidae			
Oreochromis upemba (Thys) (= *Tilapia chrysti*)	a	fo	Ate large and small *Bulinus (Physopsis*) sp. but not the hard-shelled *Thiaria tuberculata* (Zaire: Leitar, 1956).
Oreochromis niloticus	a	fe	Minor but significant reduction of numbers of snails in presence of adult fish (Cameroon: Slootweg et al., 1993).
T. melanopleura Duméril	e/a	lo	Presumed predatory agent for control in a lake (Brazil: Andrade, 1959; 1962; 1968; Andrade & Antunes, 1969).
(= *T. rendalli*)	j	lo	Fish is not selective in its food choice (Lagrange, 1953).
	j	lo	Reduced snail populations in tanks with 90% (Graber et al., 1981).
T. zilli (Gervais)	a	lo	In absence of aquatic plants fish eats more snails (Schayck, 1985).
Cichlasoma biocellatum	a	lo	Pharyngeal crusher; 8 cm specimen was capable of crushing planorbid snails of 30 mm (Lagrange, 1953).
C. nigrofasciatum Günther	a	lo	Eats snails in tanks (Miyashita et al., 1977).
Astronotus o. ocellatus (Cuvier)		fe	Introduction in a lake considerably reduced *B. glabrata* populations for at least 3 years (Brazil: Motta & Gouvea, 1971).
Hemichromis bimaculatus Gill	a	fe	Eliminated *B. tenagophila* snails in a 75 m^2 pond, itself increasing in numbers from 20 introduced specimens to 500 (Brazil: Gilbert in: McCullough, 1981b). In a lake the fish was not effective in controling snails (Bahia, Brazil: Ayala, pers. com.).
Pelmatochromis aff. kribensis	j	lo	Eats only very small planorbid snails (1-2 mm) after fierce crushing (Lagrange, 1953).

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Serranochromis mellandi (= S. macrocephala = Haplochromis mellandi)	a	fo/fe*	Effective in controlling snails in rice fields, irrigation canals and fish ponds (Zaire: DeBondt & DeBondt Hers, 1952; 1956, DeBondt, 1955, 1956a; 1956b).
Trematocranus placodon (=Cyrtocara placodon)	a	fe*	*C. placodon* chooses vector snails over *Melanoides* snails. Predation presure on gastropod communities is heavy (L. Malawi: Louda et al., 1985, McKaye et al., 1986).
	a	fe*	Dramatic drop in numbers of snails after introduction in cement and earthen fish ponds (Malawi: Chiota et al., 1991ab).
Haplochromis spp.	a	fo*	21 species of haplochromine cichlids are described as specialized snail-eaters in different habitats (L. Victoria: Greenwood, 1974; Witte, 1981; Katunzi, 1983; Witte & Oijen, 1990)
	a	lo*	Laboratory observations on prey handling (Hoogerhoud, 1986ab) and prey preference showing that prey choice can be explained by an energy maximizing model (Slootweg, 1987)
Astatoreochromis alluaudi Pellegrin	a	lo/fe*	Controlled snails in fish ponds and reproduced successfully (Cameroon, imported from L. Victoria, Uganda: Bard & Mvogo, 1963; Mvogo & Bard, 1964; Gamet et al., 1964).
	a	fe*	An initial reduction in numbers of snails was lost after several years (Kenya, imported from L. Victoria: McMahon, 1960; McMahon et al., 1977). Reduction of pharyngeal jaws in following generations (Kat & Kibberenge, 1990).
	a	fo*	No significant reduction in numbers of snails in fish ponds (Northern Cameroon, imported from L. Victoria, laboratory reared, transported to Cameroon: Slootweg et al., 1993).

Code: Food preference
a: adult and juvenile snails
j: juvenile snails only
e: egg masses

Source of data
lo: laboratory observation
fe: field experiment
fo: field observation (stomach contents)

* indicate experiments that are described in more detail in the text.