

The biological control of snail intermediate hosts of schistosomiasis by fish

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Contents

Introduction	page 67
A review of the use of fish in snail control	68
Cyprinidae: <i>Mylopharyngodon piceus</i> , Israel	
Centrarchidae: <i>Leponis microlophus</i> , Puerto Rico	
Cichlidae: <i>Serranochromis mellandi</i> , Zaire	
Cichlidae: <i>Trematocranus placodon</i> and other molluscivores from Lake Malawi	
Cichlidae: haplochromines from Lake Victoria	
Biology of <i>Astatoreochromis alluaudi</i>	76
Field trials on snail control with <i>A. alluaudi</i>	76
Yaoundé, Cameroon	
Nyanza Province, Kenya	
North Cameroon	
Reasons for failure of <i>A. alluaudi</i>	79
Reproduction	
Foraging behaviour and prey choice	
Phenotypic plasticity of the pharyngeal jaw apparatus	
Snail ecology	
Transmission dynamics of schistosomiasis	
Prospects for the use of fish in snail control	83
Summary	85
Acknowledgements	85
References	85

Introduction

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,

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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 and 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 centred around 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 in the longer term. Actions to reduce the risk of transmission by controlling the intermediate hosts often remain necessary. Snail control can be realized 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 snail vectors.

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 and 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 and 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), Hairston *et al.* (1975), Ferguson (1978) 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 1 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), because 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 that eat snails in laboratory aquaria, or wild-caught fish with stomachs containing snails, are not automatically suitable candidates for snail control. Many species mentioned in Table 1 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 that tend to specialize on snails are: *Protopterus annectens* (the lungfish, Protopteridae), *Mylopharyngodon 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 (DeBonds and DeBonds Hers, 1952; Andrade, 1959, 1962, 1968; Bard and Mvogo, 1963; Carothers and Allison, 1968; Motta and Gouvea, 1971; McMahan *et al.*, 1977; Leventer, 1981; Gilbert in: McCullough, 1981b; Daffalla *et al.*, 1985; Chiotha *et al.*, 1991a). Four of these field trials (Bard and Mvogo, 1963; Mvogo and Bard, 1964; Gamet *et al.*, 1964; Carothers and 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.

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 (*Hypophthalmichthys molitrix*) vs phytoplankton, grass carp (*Ctenopharyngodon idella*) vs submerged plants, black carp (*M. piceus*) vs snails and 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 widespread. Rice yields may increase by 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, by analogy with the successfully introduced mosquito fish, *Gambusia affinis*.

Centrarchidae: *Lepomis microlophus*, *Puerto Rico*

The food preference of the shellcracker sunfish, *Lepomis microlophus*, has been tested in the laboratory by Carothers and Allison (1968). This species highly preferred snails above other food items such as mosquito larvae and dragonfly nymphs. Their voracious snail-eating habits were 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.

Table 1. Summary of laboratory and field research on snail-eating fish

Family and species	Code*	Remarks (authors)
Protopteridae		
<i>Protopterus annectens</i> (Owen)	a lo	Fish eats thousands of snails in tanks; <i>Tilapia</i> fry were left unharmed, but earthworms were eaten in equal quantities (Mahdi and Amin, 1966).
<i>P. aethiopicus</i> Heckel	a lo/fe a fo	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 <i>et al.</i> , 1985). 95% of a sample had eaten molluscs; in 56% molluscs were predominant (Lake Victoria: Corbet, 1961).
Mormyridae		
<i>Hyperopisus bebe</i> (Lacépède)	j lo fo fo	Omnivorous (Lake Chad: Blache, 1964). Mainly snails in stomach (Lake Chad: Lauzanne, 1972). Many snails in strong muscular stomach which probably assists with dealing with snails (Sudan: Coates, 1984).
<i>H.b. occidentalis</i> Günther (= <i>H.o. tenuicauda</i> Pellegrin)	j fo	Snails in stomach (Lake Chad: Blache, 1964).
Characidae		
<i>Alestes baremoze</i> (de Joannis)	a fo fo	Eats mainly snails but also other food items (Sudan: Coates, 1984). In contradiction with Coates; eats only zooplankton, insect larvae and plant material (Lake Albert: Holden, 1970).
Cyprinidae		
<i>Carassius auratus</i> L.	e/j lo	Eats planorbid snail in tanks (Lagrange, 1964).
<i>Barbus bynni</i> Forskahl	a fo	Larger specimens had frequently eaten snails (crushed) (Sudan: Coates, 1984).
<i>Barbus altianalis</i> Boulenger	a fo	By volume molluscs are the main food (Lake Victoria: Corbet, 1961).
<i>Mylopharyngodon piceus</i> (Rich.)	a fe [†]	Introduction of various species of carp reduced snail populations and submerged plants in large reservoirs in Israel (Leventer, 1981).
Umbridae		
<i>Umbra pygmaea</i> (De Kay)	j lo	Eats small planorbid, but prefers <i>Daphnia</i> and <i>Tubifex</i> (Lagrange, 1953).

Poeciliidae					
<i>Poecilia</i> (= <i>Lebistes</i>) <i>reticulata</i> Peters	e	lo		Appearance of guppies coincided with disappearance of <i>B. glabrata</i> snails in reservoirs (Puerto Rico: Oliver-Gonzalez, 1946).	
Bagridae					
<i>Clarotes laticeps</i> (Rüpell)	a	fo		Piscivorous and malacophagous (Upper Niger River: Daget, 1954; Lake Chad: Blache, 1964).	
<i>Chrysichthys mabusi</i> Boulenger	a	fo		Potential for snail control in large permanent waters; shells remain unbroken in digestive tract (Zaire: DeBondt and DeBondt Hers, 1952).	
	a	fo		Snails in stomach (Upper Zaire River: Bowmaker, 1968).	
Clariidae					
<i>Clarias lazera</i> Cuv. et Val. = <i>Clarias gariepinus</i>	j a a	fo fo lo fe		Omnivorous fish (Lake Chad: Blache, 1964). Eats large quantities of snails but not considered to be selective (Sudan: Coates, 1984). Eats snails in tanks (Mozley, 1953). No reduction in numbers of snails in fish ponds (Cameroon: Sootweg <i>et al.</i> , 1993).	
Pangasiidae					
<i>Pangasius pangasius</i> Hamilton	a	fo		Fish ingested large quantities of molluscs of any kind (India: Hora, 1952).	
Osteoglossidae					
<i>Heterotis niloticus</i> Ehrenberg		fo		Feeds mainly on snails (Lake Chad: Lauzanne, 1972)	
Heteropneustidae					
<i>Heteropneustes fossilis</i> (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					
<i>Schilbe mystus</i> L.	a	fo		Omnivorous fish (Sudan: Coates, 1984).	
Mochokidae					
<i>Synodontis courteti</i> Pellegrin		fo		Exclusive malacophagous (Upper Niger River: Daget, 1954); id. (Lake Chad: Blache, 1964).	
<i>S. gambiensis latifrons</i> Blache	a	fo		Snails in stomach (Lake Chad: Blache, 1964).	
<i>S. clarias</i> L.	a	fo		Selective molluscivorous (Lake Chad: Blache, 1964).	
<i>S. sorex</i> Günther	a	fo		Omnivorous fish with preference for snails (Sudan: Coates, 1984).	
<i>S. schall</i> (Block-Schneider)	a	fo		Eats mainly snails (Lake Chad: Lauzanne, 1972).	
<i>S. victoriae</i> Boulenger	a	fo		Omnivorous fish with preference for snails (Sudan: Coates, 1984). Main food items are molluscs and insects (Lake Victoria: Corbet, 1961).	

Table 1. continued

Family and species	Code*	Remarks (authors)
Tetraodontidae		
<i>Tetraodon schoutedeni</i> Pellegrin	a lo	Known from aquaria in Europe as a very good snail-eater; eats large snails (Lagrange, 1953).
	a fo	Snails in stomach (Upper Niger River: Daget, 1954).
<i>T. fahaka</i> (strigosus) (Bennett)	a fo	Piscivorous and malacophagous (Lake Chad: Blache, 1964).
	a fo	Exclusively malacophagous; one specimen (340 g) contained over 1000 snails. Flesh of this family is often poisonous (Sudani: Coates, 1984).
Centrarchidae		
<i>Lepomis microlophus</i> Günther	a lo/fe ¹	Preference for snails in laboratory and ponds; controlled <i>Biomphalaria</i> snails in farm ponds (Puerto Rico: Ferguson, 1978; USA: Carothers and Allison, 1968); appreciated game and food fish (Erdman, 1984).
Cichlidae		
<i>Oreochromis upemba</i> (Thys) (= <i>Tilapia chrysti</i>)	a fo	Ate large and small <i>Bulinus</i> (<i>Physopsis</i>) sp. but not the hard-shelled <i>Thiaria tuberculata</i> (Zaire: Leitar, 1956).
<i>Oreochromis niloticus</i>	a fe	Minor but significant reduction of numbers of snails in presence of adult fish (Cameroon: Sootweg <i>et al.</i> , 1993).
<i>T. melanopleura</i> Duméril (= <i>T. rendalli</i>)	e/a lo	Presumed predatory agent for control in a lake (Brazil: Andrade, 1959, 1962, 1968; Andrade and Antunes, 1969).
	j lo	Fish is not selective in its food choice (Lagrange, 1953).
	j lo	Reduced snail populations in tanks by 90% (Graber <i>et al.</i> , 1981).
<i>T. zilli</i> (Gervais)	a lo	In absence of aquatic plants, fish eats more snails (Schayek, 1985).
<i>Cichlasoma biocellatum</i>	a lo	Pharyngeal crusher; 8 cm specimen was capable of crushing planorbid snails of 30 mm (Lagrange, 1953).
<i>C. nigrofasciatum</i> Günther	a lo	Eats snails in tanks (Miyashita <i>et al.</i> , 1977).
<i>Astronotus o. ocellatus</i> (Cuvier)	fe	Introduction in a lake considerably reduced <i>B. glabrata</i> populations for at least 3 years (Brazil: Motta and Gouvea, 1971).
<i>Hemichromis bimaculatus</i> Gill	a fe	Eliminated <i>B. tenagophila</i> 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 controlling snails (Bahia, Brazil: Ayala, pers. comm.).

<i>Pelmatochromis aff. kribensis</i>	j	lo	Eats only very small planorbid snails (1–2 mm) after fierce crushing (Lagrange, 1953).
<i>Serranochromis mellandi</i>	a	fo/fe [†]	Effective in controlling snails in rice fields, irrigation canals and fish ponds (Zaire: DeBondt and DeBondt Hers, 1952, 1956; DeBondt, 1955, 1956a, b).
(= <i>S. macrocephala</i> = <i>Haplochromis mellandi</i>)			
<i>Trematocranus placodon</i>	a	fe [†]	<i>C. placodon</i> chooses vector snails over <i>Melanooides</i> snails. Predation pressure on gastropod communities is heavy (L. Malawi: Louda <i>et al.</i> , 1985; McKaye <i>et al.</i> , 1986).
(= <i>Cyrtocara placodon</i>)	a	fe [†]	Dramatic drop in numbers of snails after introduction in cement and earthen fish ponds (Malawi: Chiotha <i>et al.</i> , 1991a, b).
<i>Haplochromis</i> spp.	a	fo [†]	21 species of haplochromine cichlids are described as specialized snail-eaters in different habitats (Lake Victoria: Greenwood, 1974; Witte, 1981; Katunzi, 1983; Witte and Oijen, 1990).
	a	lo [†]	Laboratory observations on prey handling (Hoogerhoud, 1986a, b) and prey preference showing that prey choice can be explained by an energy-maximizing model (Slootweg, 1987).
<i>Astatoreochromis alluaudi</i> Pellegrin	a	lo/fe [†]	Controlled snails in fish ponds and reproduced successfully (Cameroon, imported from Lake Victoria, Uganda: Bard and Mvogo, 1963; Mvogo and Bard, 1964; Gamet <i>et al.</i> , 1964).
	a	fe [†]	An initial reduction in numbers of snails was lost after several years (Kenya, imported from Lake Victoria: McMahan, 1960; McMahan <i>et al.</i> , 1977). Reduction of pharyngeal jaws in following generations (Kat and Kibberenge, 1990).
	a	fo [†]	No significant reduction in numbers of snails in fish ponds (northern Cameroon, imported from Lake Victoria, laboratory reared, transported to Cameroon: Slootweg <i>et al.</i> , 1993).

*Codes: Food preference – a, adult and juvenile snails; e, egg masses; j, juvenile snails only. Source of data – fe, field experiment; fo, field observation (stomach contents); lo, laboratory observation.

[†]Indicates experiments that are described in more detail in the text.

Fingerlings of *L. microlophus* were introduced in aquaculture ponds near Aibonito, Puerto Rico. There were no *B. glabrata* snails in the ponds, 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 the absence of the sunfish.

Since 1959 *L. microlophus* has been introduced into about 50 Puerto Rican 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 *Thiarra 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), however, put 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 exerted by *L. microlophus*.

Cichlidae: *Serranochromis mellandi*, Zaire

DeBondt and DeBondt Hers (1952, 1956) and DeBondt (1955, 1956a, b) 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 good to eat. Several types of water bodies were stocked with fish in experiments that started in 1949 and lasted at least until 1956.

1. A pond of about 400 m², densely populated with *Bulilnus* (*Physopsis*) and *Biomphalaria* snails, was stocked with *S. mellandi*. After 1 month 87% of a fish sample had eaten snails. After 2 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.

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

3. 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 metre, the canals were free of snails within 8 d; one fish at every 10 m made the snails disappear within a fortnight.

4. 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 programme; 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.

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 and McKaye, 1986; McKaye *et al.*, 1986; Chiotha *et al.*, 1991a,b). 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 by 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 disproportionately 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 4 weeks in the presence of *T. placodon* (one 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 anaphrymis* as the molluscivore, and the number of snails in the untreated ponds. In three earthen ponds, snail numbers dropped dramatically over a 5 month period after the introduction of *Trematocranus placodon*. The authors do not indicate whether the molluscivorous fish were wild caught or pond reared and whether the results could be maintained over a longer period. It is not clear whether the fish can reproduce under pond conditions.

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 and 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 1980s the number of cichlids in Lake Victoria was dramatically reduced by the introduction of the predatory Nile perch (*Lates niloticus*), so it is unclear how many species (originally about 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 Sloomweg (1987) with the explicit intention of finding a suitable candidate for snail control purposes.

The studies presented in this section and in Table 1 give the impression of being records 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, in particular 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, 1983; Hairston *et al.*, 1975; McCullough, 1981b; Roberts and Sampson, 1987). One species has been extensively investigated in field trials on three occasions in two different countries (Cameroon

and Kenya), the East African haplochromine cichlid *Astatoreochromis alluaudi*. These trials will be discussed in greater detail below. Welcomme (1988) gives four other countries (Central African Republic, Congo, Zaire, Zambia) where *A. alluaudi* has been introduced, but no written accounts are available in scientific literature.

Biology of *Astatoreochromis alluaudi*

The fish is common to Lakes Victoria, Kioga, Nabugabo, Edward, George, Kachira and Nakavali and to adjoining rivers (Greenwood, 1959; Fryer and Iles, 1972, p. 102). Like other haplochromines, *A. alluaudi* is a substratum-spawning and mouthbrooding species; large adult females (100 mm 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 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 at feeding 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 with fish raised on soft minced meat, but compared with 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*) (Cichlidae) (Bard and Mvogo, 1963; Mvogo and Bard, 1964; Gamet *et al.*, 1964). Two basins (85 m²) 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 3 months both basins were emptied. The one with *A. alluaudi* did not contain any snails 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 whether the technique was used for a longer period and whether this successful snail control was repeated more often. In 1987, *A. alluaudi* could not be found any more 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 zilli* 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 vector 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 and Kibberenge (1990) revisited eight of these dam sites 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, in the test sites *Biomphalaria* as well as *Bulinus* snails were found in numbers similar to those in control sites without *A. alluaudi*. From every dam site several fish were collected 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, and is discussed more fully below.

North Cameroon

A second field trial with *A. alluaudi* in Cameroon started in 1988. The possible risks of introducing this exotic species in Cameroon were assessed according to the protocol for exotic species introduction by Kohler and 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, 1989a, b, 1991a, b; 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. 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 we do not know the threshold of the snail population below which transmission of schistosomiasis is interrupted. Therefore, although a certain species of fish may drastically reduce the snail numbers, transmission of the disease may still be possible. To our knowledge, no study has attempted to tackle 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 the 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 7 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 in the adjacent section without fish. (2) In a rain-fed 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 4 month period. (3) In an experiment on combined rice/fish culture, 240 *A. alluaudi* were introduced together with 1200 *O. niloticus* to 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 3 months, 98 *A. alluaudi* were recaptured; three juveniles were also found, indicating that reproduction had taken place. From an aquacultural point of view this introduction was a reasonable success because the 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 that in 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 with those of laboratory-raised and wild-caught individuals. These results have not yet been published and are 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 Fig. 1 the lower pharyngeal element and the muscle complex mLE4/LP are drawn

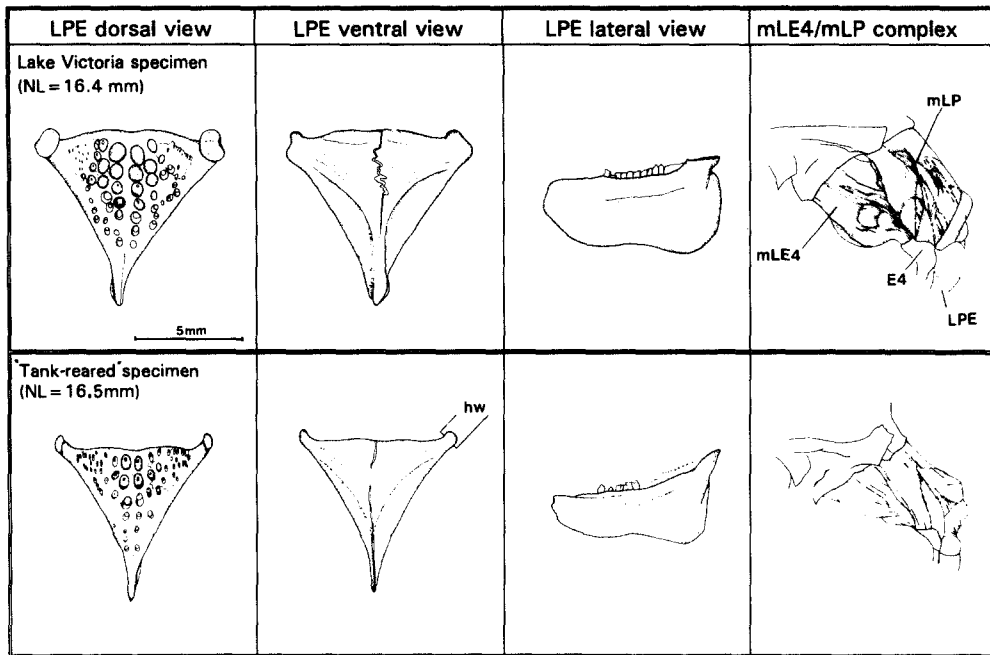


Fig. 1. Lower pharyngeal element (LPE) and muscle complex operating on the LPE of a wild-caught Lake Victoria specimen and a laboratory-reared specimen of *Astatoreochromis alluaudi* (Overbeek, 1986). (All drawings to the same scale; abbreviations: NL, neurocranial length; mLE4, *musculus levator externis 4*; mLP, *musculus levator posterior*; E4, epibranchial 4; hw, horn width). Compared with 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 horn width 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.

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 horn width of the lower pharyngeal element, the aquaculture specimens from Cameroon fall within the range of least hypertrophied animals from the mollusc-free lakes (Fig. 2). Data on the dry weight 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.

Reasons for failure of *A. alluaudi*

Reproduction

Tilapiine cichlids, such as the mouthbrooding *Oreochromis niloticus*, are well known in fish culture as species that reproduce easily in ponds. Usually the reproduction is so excessive that special measures have to be taken to prevent fish from breeding. Therefore

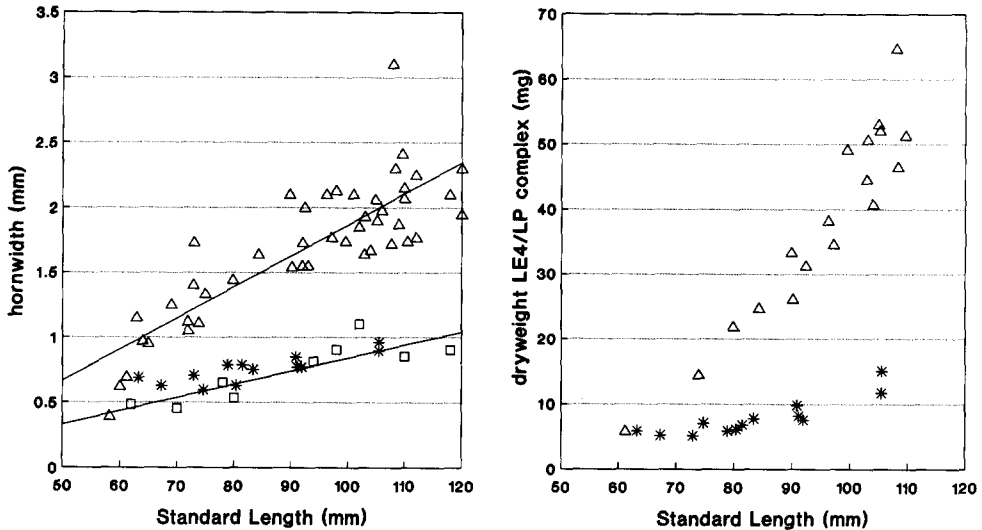


Fig. 2. Reduction of the pharyngeal jaw apparatus in *Astatoreochromis alluaudi*, reared in the aquaculture station of Gounougou, North Cameroon. Triangles (Δ) indicate wild-caught specimens from Lake Victoria; squares (\square) indicate wild-caught specimens from lakes without snails, and asterisks (*) indicate aquaculture specimens from Cameroon. Data on horn width and regression lines from animals from Lake Victoria and Lakes without snails are taken from Hoogerhoud (1986a); muscle weight data of Lake Victoria specimens were provided by J.D. Smits of the Department of Ecological Morphology of Leiden University (NB: measurements of horn width and dry weight are taken from different specimens).

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 as high as that carried by *A. alluaudi* (Trewavas, 1983, reports 3700 eggs in a 57 cm SL female of *O. niloticus*, compared with 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 2 months; our laboratory observations indicate that *A. alluaudi* only produces between two and three broods per year. In his field experiments, DeBondt (1956a) 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 females *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 month 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.

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 and 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 (λ) 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 A:

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

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:

$$1/\lambda_1 > (E_1/E_2)Ht_2 - Ht_1 \quad (\text{B})$$

In other words, the acceptance 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 (Mittelbach, 1984; Stein *et al.*, 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 B. For field conditions this implies that the willingness of the snail-crushing fish to 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 the hypothesis cited above that in Lake Victoria the fish only specialize on snails when under 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 hard-shelled *Melanoides* snails, McKaye *et al.* (1986) drew 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 because the hard-shelled *Melanoides* has a longer handling time and consequently a lower yield per second handling time compared with *Bulinus* snails. This does not imply, however, that the fish will choose *Bulinus* when other more profitable prey items are available.

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 was replaced by subsequent generations with less developed jaws. Competition for food in the artificial reservoirs might be lower than in Lake Victoria because they lack an endemic fish fauna. The hard-shelled *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 them, 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) were able to crack snails that were twice as hard as those cracked by the papiliform morph (reduced type). Liem and 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 specialised on snails.

Probably the phenomenon described above also affected experiments in the Yaounde (Cameroon) fish culture station where one successful trial was described (Bard and 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.

Snail ecology

Other factors reducing the effectiveness 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 vector snails are pulmonate snails, dependent on oxygen-rich water near the surface. Usually they are found at the fringes of a water reservoir or on a 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 and 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 suggests 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.

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 urinary schistosomiasis in this semi-arid region are *Bulinus senegalensis* and *B. globosus*, two species 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 for 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 Cichlidae are known (Witte *et al.*, 1990, for Lake Victoria haplochromines; Kornfield and Taylor, 1983, Liem and Kaufman 1984, and Meyer, 1987, 1989, for South American 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*. 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 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 intraspecific variability.

Other species of possible snail-controlling fish from Table 1 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, 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 and Laracuate, 1979; also see Pointier and McCullough, 1989, and Gomez Perez *et al.*, 1991).

The black carp, *Mylopharyngodon piceus*, was effective in controlling nuisance snails that were 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 of aquaculture and limnology. Especially on the African continent, where aquaculture is not widespread, 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 populations 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* remains convinced that this species has much potential in the biological control of snails (DeBont, pers. comm.). It is to be hoped that the renewed attention to aquaculture in Africa will 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 and 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 whether the reduction in snail populations 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 be answered. In view of the high risk of schistosomiasis transmission in aquaculture in Africa, 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, this 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.

Summary

The use of molluscivorous fish for biological control of snail intermediate hosts of schistosomiasis is a regularly reappearing theme in the literature on schistosomiasis control. The effectiveness of this control method has not yet been demonstrated, and conclusive field evidence is lacking. In this article the literature on snail control by fish is critically reviewed. Special attention is paid to the cichlid fish *Astatoreochromis alluaudi* that has been used in well-documented field trials in Kenya and Cameroon. After some small initial success, after a longer period the fish appeared to be ineffective in snail control. Moreover, the fish reproduces at a pace too slow to be of use in large-scale biocontrol trials. Laboratory observations on foraging behaviour and anatomy of the fish give essential cues to explain the failure of the fish in snail control. An observed reduction in the fishes' pharyngeal jaw apparatus, used to crush snails shells, results in a lower profitability of snails. As predicted by a simple foraging model, the prey preference of the fish shifts towards other more profitable prey items, such as benthic and pelagic macrofauna. Although eradication of snails by fish will not be feasible in most cases, the role of natural predators of snails cannot be neglected, and may still be of importance in integrated control efforts.

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