

## Feeding convergence in South American and African zooplanktivorous cichlids *Geophagus brasiliensis* and *Tilapia rendalli*

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### Synopsis

Acará, *Geophagus brasiliensis*, and red-breasted bream, *Tilapia rendalli*, are important planktivorous cichlids in southern Brazilian lakes and reservoirs. In laboratory experiments, I quantified behavior and selectivity of different sizes of these two fish feeding on lake zooplankton. Feeding behavior depended on fish size. Fish < 30 mm were visual feeders. Fish 30–50 mm either visually fed or pump-filter fed depending on zooplankton size. Fish > 70 mm were pump-filter feeders. Replicate 1 h feeding trials revealed that, as the relative proportions of prey changed during an experiment, acará (30–42 mm, standard length) and tilapia (29–42 mm) shifted from visual feeding on large evasive copepods to filter feeding on small cladocerans and rotifers. Electivity and feeding rate increased with prey length, but were distinct for similar-sized cladocerans and copepods. Visual/filter-feeding fish had lowest electivities for small and poorly evasive rotifers and cyclopoid nauplii. They fed non-selectively on cyclopoid copepodites, had intermediate electivities for calanoid nauplii and small cladocerans, and had highest electivities for large cladocerans, cyclopoid adults, and calanoid copepodites and adults. Although belonging to different cichlid genera and native to South America and Africa, respectively, acará and red-breasted bream (= congo tilapia) exhibited similar selectivity for zooplankton. Apparently, few stereotyped feeding behaviors have evolved during the acquisition of microphagy in fish. Shift in feeding modes allows these two species to optimally exploit the variable and dynamic patchy distribution of planktonic resources.

### Introduction

Feeding behavior combines with prey morphology and behavior to generate feeding selectivity in zooplanktivorous fishes (see reviews in Lazzaro 1987, Northcote 1988). Feeding behavior falls into two modes: visual (particulate feeding) and non-visual (filter feeding).

As active size-selective predators (Werner &

Hall 1974, Confer & Blades 1975, O'Brien et al. 1976), visual feeders individually locate zooplankton. In contrast, filter feeders do not actively select prey and can be divided into two groups: tow-net filter feeders and pump filter feeders (i.e. ram feeders and suction feeders, respectively, sensu Sanderson & Wassersug 1990). Tow-net filter feeders, engulf prey items by fully opening their mouths while swimming rapidly (Durbin & Durbin 1975).

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Very efficient at capturing evasive calanoid copepods (Rosen & Hales 1981), they appear to be less selective than other planktivores (Janssen 1976). On the other hand, pump-filter feeders use rhythmic buccal suction, not directed at individual organisms, to passively capture prey while swimming slowly or remaining stationary (Drenner et al. 1982b). Because they are only efficient at capturing poorly evasive prey, such as cladocerans, they are considered escape-selective predators (Janssen 1976, Drenner & McComas 1980, Drenner et al. 1982a, Gophen et al. 1983).

Among the most important planktivores and forage fishes in southern Brazilian lakes and reservoirs are two cichlids: acar, *Geophagus brasiliensis*, and the red-breasted bream or congo tilapia, *Tilapia rendalli* (syn. *T. melanopleura* and *T. guineensis*), and one characid, lambari *Astyanax fasciatus*. These three species are the dominant planktivores in the shallow (mean depth 3 m) oligotrophic reservoir of Broa (6.8 km<sup>2</sup>, 22.10° m<sup>3</sup>, 22° 10' S–47° 54' W), near So Carlos, S.P. (Barbieri et al. 1980). Widespread in Central and South America, lambari are primarily zooplanktivores, attacking visually copepods, cladocerans, and aquatic insects; only adults (> 80 mm) may occasionally feed on detritus (Barbosa 1982). In contrast, acar and congo tilapia are not exclusive planktivores.

Acar, a Brazilian native species, is an omnivore. Fish < 40 mm feed preferentially on insect larvae, mainly chironomids (Guimares 1938, Barbieri et al. 1980). Fish > 40 mm have more diverse diets, including zooplankton, phytoplankton, detritus, and benthos (Machado et al. 1968, Azevedo 1972, Nomura & Carvalho 1972, Nomura 1984).

The congo tilapia is an African species introduced into Brazil in 1953 (Nomura et al. 1972). Fish < 60 mm feed principally on zooplankton (cladocerans and copepods) and on insect larvae (chironomids), and secondarily on filamentous green algae, *Desmidiium* (in Madagascar: Moreau 1979). Both juvenile and adult fish eat macrophytes, but also feed on phytoplankton (filamentous greens and diatoms), zooplankton, insect larvae, fish eggs and embryos, and detritus (in Africa: Debont et al. 1950, Huet 1953, Moreau 1979; in Brazil: Azevedo & Manarini 1957, Hermany Filho 1958, Menezes

1958, Silva 1962, Soares 1968, Godoy 1969, Nomura & Seixas 1970).

Acar have a protrusive mouth with lips covered by tooth plates, a stomach with a strong muscular wall, and a long intestine (Azevedo 1972). Congo tilapia have a typical phytophagous digestive tract (Borges & Duarte 1970) with a digestive tract length/body standard length ratio between 7 and 10 (Moreau 1979), and pharyngeal teeth contributing to pre-digestive preparation (Caulton 1976).

Because it is striking that acar and congo tilapia, although from different origins, have evolved very similar behaviors when feeding on zooplankton, this study sought to (a) compare their foraging repertoire and (b) quantify their selective predation.

## Methods

### *Feeding behavior trials*

Fish were captured by seine or cast net from Broa Reservoir during August through December 1983. Fed reservoir zooplankton daily, they were held in the laboratory for 1–2 days before experiments. Feeding trials were conducted in 10 l aquaria (21.5–24.5° C) under fluorescent lighting (600 lux). To analyze changes in feeding repertoires as fish grew, behavior was quantified across a range of sizes of individual acar (26–172 mm, n = 36) and congo tilapia (24–115 mm, n = 28) feeding on natural assemblage of reservoir zooplankton. I recorded behavior and switch exhibited by an individual fish when offered alternatively small (rotifers and copepod nauplii) or large zooplankters (cladocerans and copepod copepodites and adults). Zooplankters were size-separated by filtration of reservoir water through a 120 µm plankton netting.

### *Feeding selectivity trials*

One group of 13 acar (30–42 mm) and one group of 16 congo tilapia (29–39 mm) were fed identical aliquots of Broa Reservoir zooplankton for 1 h in 10 l aquaria. Fish number was higher for congo

tilapia to compensate for their smaller size. For each group, selective zooplankton ingestion was determined from reductions in zooplankton density. Aquaria were aerated using two air-stones and stirred every 10 min to reduce prey patchiness. At the beginning and the end of each trial, triplicate water column samples were taken from each aquarium with an acrylic tube quickly lowered onto a randomly placed rubber stopper lying on the aquarium bottom (Drenner et al. 1978). Water was strained through a 69  $\mu\text{m}$  sieve and zooplankton were preserved in 4% formaldehyde. With each group of fish, four feeding trials were run on successive days during August 1983. To detect significant changes in zooplankton densities during the trials but to avoid depletion which could alter the fish selectivity, initial densities were high (between 7000 and 16000 organisms  $\text{l}^{-1}$ ), mainly calanoid nauplii and cladocerans (see Fig. 1, and Table 1 for zooplankton abbreviations), compared to reservoir densities. Initial prey densities were similar for

acar and congo tilapia trials (ANCOVA,  $F = 0.02$ ,  $p = 0.88$ ). Size of each prey type (Table 1) was computed as mean body length of 10–15 individuals collected from reservoir samples used in feeding trials.

#### Electivity

Feeding selectivity was calculated as the alpha electivity index of Chesson (1978, 1983), using the formula:

$$\alpha_i = (r_i/p_i) / (\sum_{i=1}^n r_i/p_i),$$

where  $r_i$  is the percentage of the prey type  $i$  in the fish ration,  $p_i$  is the corresponding percentage in the environment, and  $n$  is the total number of prey types. The  $\sum_{i=1}^n \alpha_i = 1$ . When  $\alpha_i = 1/n$ , selective predation did not occur. When  $\alpha_i < 1/n$ , fewer of prey type  $i$  occurred in the diet than expected from random feeding (negative selection). When  $\alpha_i >$

Table 1. Mean individual body lengths (by increasing order) and weights of the zooplankton collected in Broa Reservoir during August through December 1983 (\* modified from Matsumura-Tundisi et al. unpublished data).

Abbrev.	Prey	Length (mm)	Weight* ( $\mu\text{g DW}$ )
<b>Small non-evasive prey (SNEP)</b>			
Rotifers			
Poly	<i>Polyarthra</i> sp.	0.06	–
Kera	<i>Keratella cochlearis</i>	0.08	–
Brac	<i>Brachionus falcatus</i>	0.10	–
Copepod nauplii			
TheN	<i>Thermocyclops minutus</i> nauplii	0.15	0.07
ArgN	<i>Argyrodiaptomus furcatus</i> nauplii	0.27	0.26
Cladocerans			
Bosi	<i>Bosminopsis deitersi</i>	0.29	0.61
Bosa	<i>Bosmina macrostila</i>	0.31	0.89
Moin	<i>Moina minuta</i>	0.39	0.92
<b>Large evasive prey (LEP)</b>			
Copepod copepodites and adults			
TheC	<i>Thermocyclops minutus</i> cop. I–IV	0.42	0.43
TheA	<i>Thermocyclops minutus</i> cop. V + adult	0.60	0.78
ArgC	<i>Argyrodiaptomus furcatus</i> cop. I–IV	0.84	4.59
ArgA	<i>Argyrodiaptomus furcatus</i> cop. V + adult	1.34	11.90

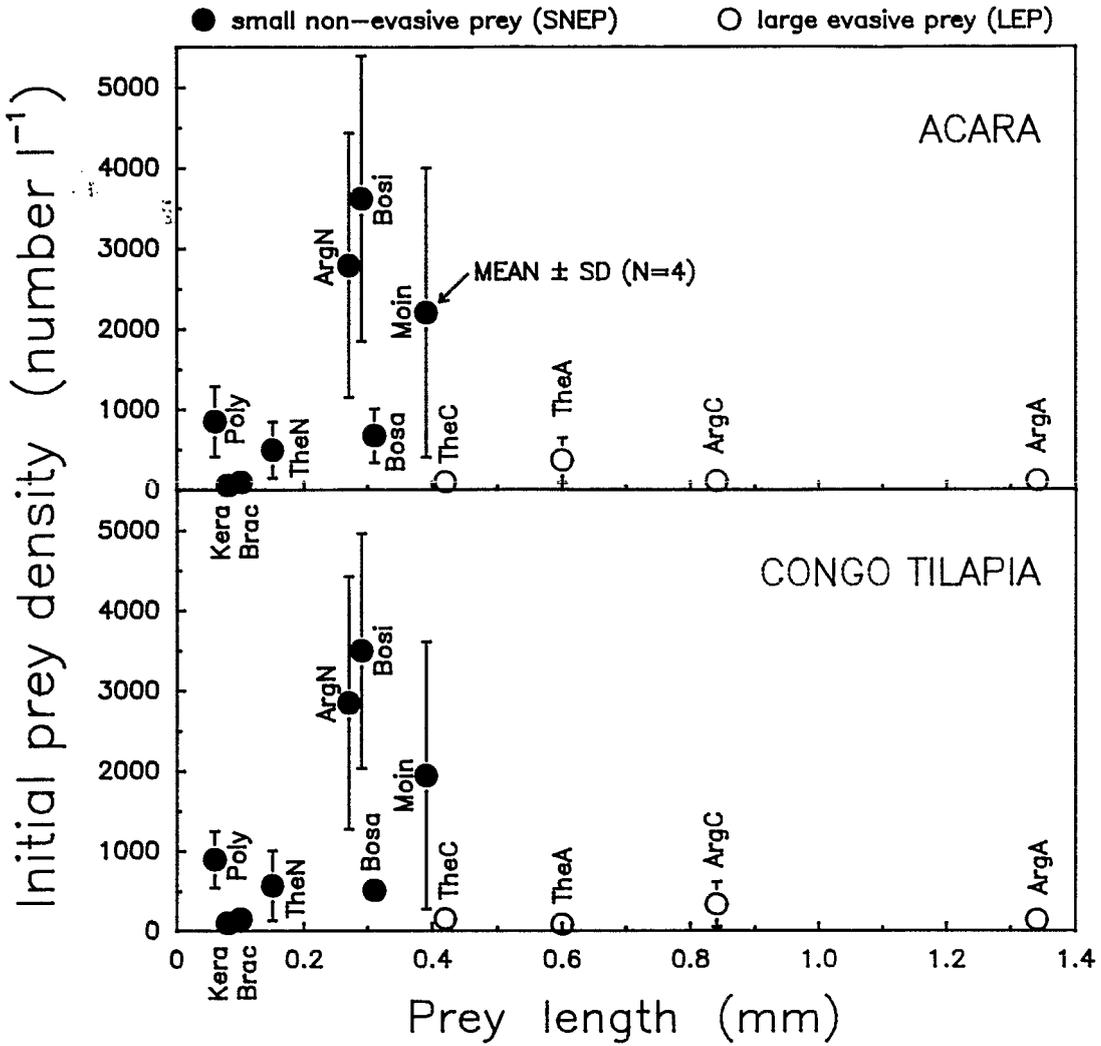


Fig. 1. Mean initial zooplankton densities (four trials) as a function of prey length. Abbreviations for prey as in Table 1.

1/n, more of prey type i occurred than expected (positive selection, or 'preference'). Because n = 12 here, then 1/n = 0.083. Electivities were corrected from sources of zooplankton mortality other than fish feeding by simultaneously monitoring a fishless aquarium.

*Feeding rates*

Feeding rates were computed as feeding rate constants per gram of fish body weight (k<sub>i</sub>/g), using Dodson's (1975) equation:

$$k_i/g = -\ln (D_f/D_i)/(X T)$$

for prey type i, where D<sub>f</sub> and D<sub>i</sub> are final (corrected by changes in density in a fishless aquarium) and initial zooplankton densities per liter, respectively, X is the density of fish per liter, T is the duration of the trials in hours, g is the mean wet weight of acará (2.0 g) and congo tilapia (1.9 g) calculated from length-weight curves. k<sub>i</sub>/g is measured as l h<sup>-1</sup> g<sup>-1</sup> and is equivalent to a volume swept clear of prey per unit of time, normalized for fish weight.

## Results

### Feeding behaviors

Acará and congo tilapia displayed similar feeding behaviors which depended on fish size. Fish < 30 mm never fed as filter feeders; thus, they were considered visual feeders. Fish > 70 mm were considered pump filter feeders as they never fed visually. Fish 30–50 mm fed as visual feeders and filter feeders, depending on prey length.

When small zooplankters, such as rotifers and copepod nauplii (i.e., Poly, Kera, Brac, TheN, and ArgN: see Table 1) were added to the aquaria, fish began to pump filter feed. When only large zooplankters, such as cladocerans, and copepod copepodites and adults (Bosi, Bosa, Moin, TheC, TheA, ArgC, and ArgA: see Table 1) were added, fish first filter fed for 1–2 min, then began to visually feed on the most visible and evasive copepods. Later, after large zooplankton density was reduced, fish resumed filter feeding on the remaining less evasive, small zooplankters. The time of switching appeared to depend on the initial density of large zooplankters (not measured).

Table 2. Mean initial biomasses (four trials) of prey offered to acará and congo tilapia. Abbreviations for prey as in Table 1.

Prey	Biomasses ( $\pm$ 1 SD) in mg DW l <sup>-1</sup>	
	Acará trials	Tilapia trials
<b>Copepod nauplii</b>		
TheN	0.04 (0.03)	0.04 (0.03)
ArgN	0.73 (0.43)	0.74 (0.41)
<b>Cladocerans</b>		
Bosi	2.21 (1.08)	2.13 (0.90)
Bosa	0.60 (0.30)	0.45 (0.09)
Moin	2.03 (1.66)	1.79 (1.54)
<b>Calanoid copepodites and adults</b>		
TheC	0.05 (0.04)	0.07 (0.03)
TheA	0.08 (0.06)	0.07 (0.05)
ArgC	1.69 (1.30)	1.54 (1.31)
ArgA	1.35 (0.46)	1.67 (0.68)

### Selective zooplankton ingestion

Initial zooplankton sizes were concentrated in the range 0.27–0.42 mm, i.e., dominated by calanoid nauplii (ArgN), cladocerans (Bosi), and cyclopoid copepodites (TheC; Fig. 1). However, initial biomasses (Table 2) were dominated by cladocerans (Bosi, Moin), and calanoid copepodites and adults (ArgC, and ArgA). During the first 10 min of trials, all fish were observed to visually feed on large moving copepod copepodites and adults (TheC, TheA, ArgC, and ArgA). Then, larger fishes began pump filter feeding whereas the smaller ones remained visually feeding. After 30 min, almost all fish were filter feeding on the remaining small zooplankters.

### Electivities

Visual/filter feeding acará and congo tilapia had similar electivities across prey length (ANCOVA,  $F = 0.00$ ,  $p = 0.99$ ; see Fig. 2). Small and poorly evasive rotifers (Poly, Kera, Brac) and cyclopoid nauplii (TheN) were negatively selected. Fish did not feed selectively on cyclopoid copepodites (TheC). They had intermediate electivities for calanoid nauplii (ArgN) and small cladocerans (Bosi, and Bosa), and highest electivities for large cladocerans (Moin), and copepod copepodites and adults (TheC, TheA, ArgC, and ArgA).

For small and less evasive (rotifers, cladocerans, and copepod nauplii: termed SNEP group in Table 1), the increase in electivity ( $\alpha_i$ ) with prey length was fitted by a linear function, whereas for large, evasive prey (copepod copepodites and adults: termed LEP group in Table 1), increasing electivity values were fitted by a second-degree polynomial function (Fig. 2 and Table 3). Feeding electivities of acará and congo tilapia did not differ for either small, non-evasive prey (ANCOVA,  $F = 1.22$ ,  $p = 0.27$ ) or large, evasive prey (ANCOVA,  $F = 1.23$ ,  $p = 0.28$ ).

### Feeding rates

Feeding rate constants ( $k_i/g$ ) across prey length were similar for acará and congo tilapia (ANCO-

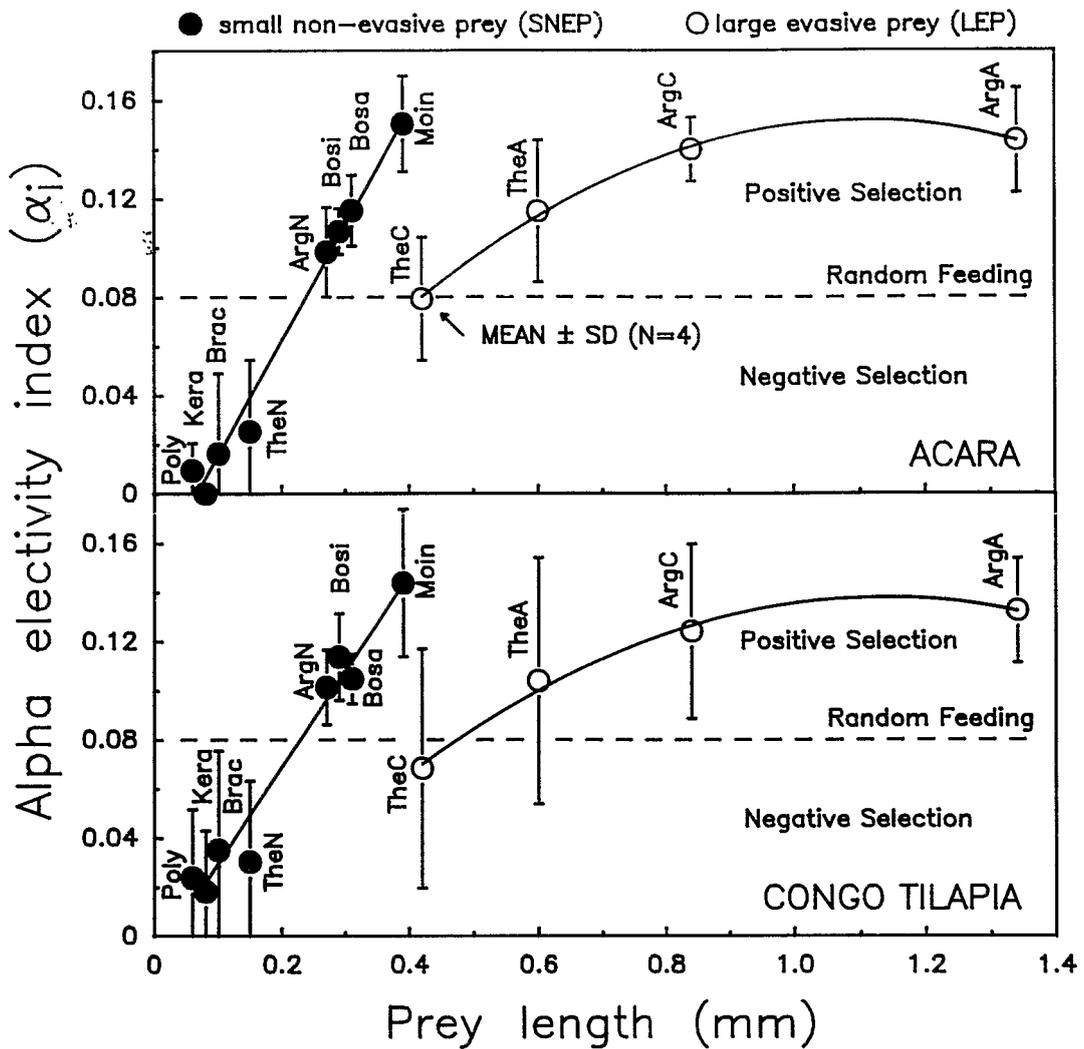


Fig. 2. Mean values (four trials) of the alpha electivity index ( $\alpha_i$ ) as a function of prey length for acara (upper graph: 13 fish, 30–42 mm) and congo tilapia (lower graph: 16 fish, 29–39 mm) visual/filter feeding on Broa Reservoir zooplankton. Abbreviations for prey as in Table 1. Equations of the fitted curves given in Table 3.

VA,  $F = 0.73$ ,  $p = 0.40$ ; see Fig. 3). Feeding rate increased with prey length, linearly for small non-evasive prey, and as a second-degree polynomial for large evasive prey. Nevertheless, both fish species had highest feeding rate constants (about  $0.121 \text{ h}^{-1} \text{ g}^{-1}$  of fish) for an intermediate-sized prey, the cladoceran *Moina*. Although *Moina* were scarce and much smaller than the largest prey (calanoid adults: ArgA), they were vulnerable to both visual- and filter-feeding fish. Feeding rate constants of acara and congo tilapia did not differ for either

small, non-evasive prey (ANCOVA,  $F = 0.04$ ,  $p = 0.84$ ) or large, evasive prey (ANCOVA,  $F = 0.79$ ,  $p = 0.38$ ).

## Discussion

### Ontogenic shifts

The progressive change in feeding behavior repertoire observed during the growth of both acara and

congo tilapia, from dominant visual feeding to dominant filter feeding is not specific to cichlids. It occurs, as well, in other planktivorous fish (Lazzaro 1987). This widespread shift in feeding repertoire during ontogeny suggests that few stereotyped feeding behaviors have evolved during the acquisition of microphagy in fish. Filter feeding is particularly efficient for consuming the abundant food particles present at low densities in most aquatic environments whereas particulate feeding most likely evolved from filter-feeding. However, the diversity of filter-feeding modes suggests that filter feeding evolved independently several times (Sanderson & Wassersug 1990).

### Electivities

Although they represent different cichlid genera and are native to South America and Africa, respectively, visual/filter feeding acará and congo tilapia have rather similar electivities for rotifers, cladocerans, and copepods. Differences in electivities between similar-sized cladocerans (Moin) and cyclopoid copepodites (TheC) could be a consequence of at least three processes. First, because copepods are more evasive than cladocerans (Drenner et al. 1978), differences may result from differential prey capture success. *Moina*, as the largest but poorly evasive cladoceran, is vulnerable to both visual and filter feeding, whereas cyclopoid copepodites can evade the suction of fish pumping,

being only vulnerable to visual feeding. Second, a learning procedure to recognize different prey types (i.e. 'search image', Tinbergen 1960), may cause fish to avoid pursuing evasive and relatively small prey (Vinyard 1980), such as cyclopoid copepodites. Third, the jumping of cyclopoid copepodites may reduce the time exposed to the visual field of fishes, making them less conspicuous than the non-evading *Moina*. However, this is probably the least plausible alternative. The vulnerability of copepods to predation by acará and congo tilapia increases from nauplii to copepodites and adults. Calanoids are more vulnerable to fish predation than cyclopoids: calanoid nauplii, copepodites and adults, but only cyclopoid adults, are selectively removed.

However, visual/filter feeding acará and congo tilapia are primarily visual feeders because their feeding mode depends on the availability of large moving copepods. The heavy predation pressure of these two cichlids (compared to that of zooplanktivorous lambari: Barbosa 1982) on evasive prey > 0.8 mm (calanoid copepodites and adults) may well contribute to the low abundance and small size of copepods in Broa Reservoir (personal observation).

These visual/filter feeding planktivores increase their selectivity with prey length. However, prey vulnerable to both feeding modes (i.e. large cladocerans, e.g. *Moina*) suffer higher mortality than expected from the linear model. Cyclopoid cope-

Table 3. Equations of the relationships between electivity alpha and feeding rate constant with prey length. Equations are linear  $Y = A_0 + A_1 X$  for SNEP, and second order polynomial  $Y = A_0 + A_1 X + A_2 X^2$  for LEP; where Y is electivity alpha ( $\alpha_i$ ) or feeding rate constant ( $k_i/g$ ), and X is prey body length (in mm).

Fish	Prey	$A_0$	$A_1$	$A_2$	# obs.	$r^2$
<b>Electivity alpha (<math>\alpha_i</math>), in Fig. 2</b>						
Acará	SNEP	-0.03125	0.46803	-	32	0.98
	LEP	-0.03536	0.33965	-0.15391	16	1.00
Tilapia	SNEP	-0.00944	0.39178	-	32	0.96
	LEP	-0.03391	0.30407	-0.13443	16	0.99
<b>Feeding rate constant (<math>k_i/g</math>), in Fig. 3</b>						
Acará	SNEP	-0.07750	0.47872	-	20	0.86
	LEP	-0.10264	0.39250	-0.17875	16	1.00
Tilapia	SNEP	-0.06594	0.41822	-	20	0.84
	LEP	-0.09244	0.33373	-0.14961	16	0.96

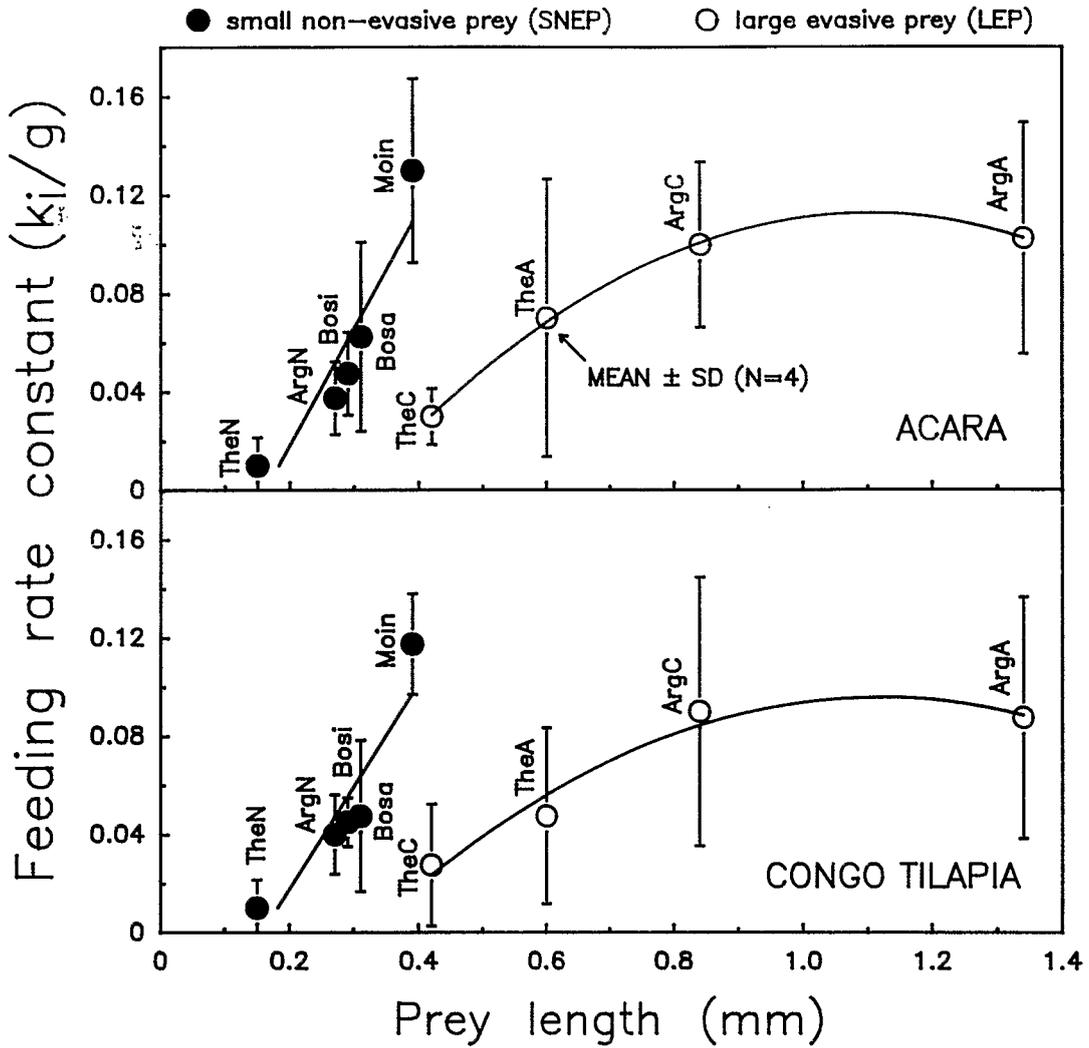


Fig. 3. Mean values (four trials) of the feeding rate constant ( $k_i/g$ ) as a function of prey length for acará (upper graph) and congo tilapia (lower graph) visual/filter feeding on Broa Reservoir zooplankton. Abbreviations for prey as in Table 1. Equations of the fitted curves given in Table 3.

pods remain immune to acará and congo tilapia predation: this is similar to Galilee Saint Peter's fish, *Tilapia galilaea*, which have the lowest electivities for *Mesocyclops leuckarti* (Drenner et al. 1982c).

*Feeding rates*

Visual/filter feeding cichlids have very similar maximum feeding rate constants ( $k_i/g$ ) for zooplankton. Those of acará, congo tilapia, and Galilee

Saint Peter's fish (Drenner et al. 1987) are about  $0.131 \text{ h}^{-1} \text{ g}^{-1}$ . However, they are much less than those ( $0.451 \text{ h}^{-1} \text{ g}^{-1}$ ) of minnow-like fishes (Mississippi silversides, *Menidia audens*; Drenner & McComas 1980). Acará and congo tilapia have lowest values for cyclopoid nauplii, copepodites and adults, and highest values for calanoid copepodites and adults, and silversides, as well, have low values for cyclopoids (*Cyclops* spp. and *Mesocyclops* spp.) and high values for calanoids (*Diaptomus pallidus*) (Drenner & McComas 1980). There-

fore, visual/filter feeding planktivores have lower feeding rate constants ( $k_f/g$ ) on cyclopoids, but higher ones on calanoids.

#### *Feeding mode shift and optimality*

Selective removal of large zooplankters by visual feeding induces a shift towards pump filter feeding on remaining small non-evasive prey. Thus, as the relative proportions of the zooplankters change through time, feeding-trial duration affects the pattern of selectivity.

Fish may shift from one mode to another in response to plankton (spatial and temporal) changes or to differences in composition of successively exploited patches. In lakes, patchiness may vary from 'swarms' (centimeters to meters in diameter) to Langmuir aggregations, as well as small (10–1000 m) and large (> 1 km) scale patterns (Malone & McQueen 1983). The resulting highly variable swimming distances between these patches may represent substantial, but unpredictable, search costs for foraging planktivores. Although my trials did not mimic the natural spatial scale of zooplankton patchiness, they did demonstrate that acará and congo tilapia can assess the relative profitability of different prey types, and deplete a patch (i.e. the aquaria) completely by using two strategies directed toward distinct prey types. However in the field, if patches are in close proximity, fish may switch patches before they switch feeding modes.

For both acará and congo tilapia, the contribution of filter feeding on nauplii and cladocerans to the diet (on a biomass basis) is greater than that of visual feeding on copepods. By successively using these two feeding modes, fish were able to exploit patches longer, increase the size range of prey consumed, and more than double their overall consumption. Behaviors such as these could well be an adaptation to the spatial and temporal variability of plankton resources in natural waters.

Using a one-patch type simulation model, Heller (1980) demonstrated that, with an intermediate range of travel times, a predator switching from specialist on profitable prey to generalist, when foraging within a patch, does better than others feeding purely as specialists or generalists. The

model predicts that the shift in foraging tactics should always occur after some time spent in the patch, and thus contrasts with the basic 'zero-one rule' of optimal foraging prey models (Stephens & Krebs 1986). This prediction holds in situations of different (large) patch types and relatively short residence time within a patch (i.e. short travel time). Crowder & Binkowski (1983) and Crowder (1985) already demonstrated that the relative profitability of visual and filter feeding in fish is a determinant of the shift. Thus, acará and congo tilapia, as well as other planktivores, may have evolved the ability to shift between feeding modes so as to optimally exploit patchy planktonic resources.

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