

Zooplankton capturing by Nile Tilapia, *Oreochromis niloticus* (Teleostei: Cichlidae) throughout post-larval development

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ABSTRACT. The Nile tilapia, *Oreochromis niloticus* (Linnaeus, 1758), uses filter feeding and visual predation to catch prey. In filter feeding, the mucus secreted in their gill rakers traps planktonic organisms. In visual predation, the fish spot and capture food, eating it directly. At different ontogenetic stages, the Nile tilapia may impact the zooplankton community differently, since it changes how it captures its prey. The objective in this study was to verify which zooplankton groups contribute to the diet of *O. niloticus* at the post-larval stage, and if the way they capture food may determine prey size. We evaluated the diet of Nile tilapia kept in ponds for four months. We randomly removed one fish per pond every month. Stomach contents and gills of fish were extracted, fixed in formaldehyde and then analyzed with an optical microscope and stereomicroscope with a micrometric ocular in order to measure the zooplankton and the gill rakers. Fish increased consumption of rotifers, and decreased the consumption of microcrustaceans considerably up to zero in the last month. The gill raker size, nevertheless, increased as tilapia grew. Therefore, negative correlations were found between raker size and size of ingested zooplankton, showing that the size of ingested prey decreases throughout this cichlid's life. Juveniles filter feed on rotifers, and actively prey on microcrustaceans. As adults, fish stop preying visually and the mucus secreted by the gill rakers trap only small individuals. Juvenile Nile tilapia filter feed and visually prey on zooplankton. However, when adults, filter-feeding plays a more important role in the way the zooplankton community is affected. The increase in the size of the Nile tilapia's gill raker does not determine the consumption of larger zooplankton prey, and the presence of mucus in these structures plays a major role for the capture of zooplankton during the cichlid's adult stage.

KEY WORDS. Filtration; microcrustaceans; predation; rotifers.

The Nile Tilapia, *Oreochromis niloticus* (Linnaeus, 1758), is a plankton-feeding omnivorous species native to Africa (ATTAYDE et al. 2007) that has been introduced in several countries, being cultured worldwide. It is a filter feeder that also uses visual predation (BEVERIDGE & BAIRD 2000). In filter feeding, mucus is secreted in the gill rakers, allowing the fish to retain planktonic organisms (LAZZARO 1987, SANDERSON et al. 1996, ZAVALA-CAMIN 1996). In visual predation, fish spot and capture the food, eating it directly (LAZZARO 1987). According to ATTAYDE et al. (2006), omnivorism allows the species to survive when the concentration of predators in the environment is high, and since the Nile tilapia is an exotic species, it also has competitive advantage over local fish communities. The negative effect of Nile tilapia populations on the zooplankton can prevent strictly zooplanktivorous fish communities from establishing (ATTAYDE et al. 2007). The ingestion of cladocera by tilapia increases in proportion to the concentration this

zooplankton group (ELHIGZI et al. 1995) and tilapia biomass increases proportionally to increasing organic fertilization in culture ponds (DIANA et al. 1991). Plankton ingestion is more prevalent in juvenile tilapia than in adults (ATTAYDE & MENEZES 2008). The tilapia also influences the trophic cascade of phytoplankton communities and contributes to eutrophication by top-down and bottom-up ecological effects, selecting large algae by filtration (cyanobacteria and diatoms), which leads to a proliferation of chlorophytes (FIGUEREDO & GIANI 2005). The predilection for large phytoplankton was also demonstrated by TURKER et al. (2003a, b) who observed a decrease in green algae and cyanobacteria in the presence of this cichlid. In cultivated larvae, phytoplankton consumption comes second only to artificial food (ROCHA-LOURES 2001).

The size of the predator and the degree of development of its sensory structures (JHA et al. 2006), as well as the morphology of the gill rakers (HYATT 1979, WOOTTON 1992, JOBLING

1996) influence the size of the prey and the way it is captured. In the initial stages of the development, some tilapia species prefer plankton (GROVER et al. 1989, UFODIKE & WADA 1991) and this item is present in significant concentrations in the stomach of *O. niloticus* fry and adults (ROCHA LOURES et al. 2001, BWANIKA et al. 2006). The gill rakers of the Nile tilapia may be long and numerous, a characteristic of plankton-feeding species, or few and short, which characterizes an omnivorous diet (CÂMARA & CHELLAPPA 1996, BEYRUTH et al. 2004, ZAYED & MOHAMED 2004).

The Nile Tilapia may cause different types of impact on the zooplankton community throughout its development, since this fish changes the way it captures and eats its prey. During the larval stages, when the tilapia's mouth cavity is small, most of the plankton is captured using visual predation (YOWELL & VINYARD 1993), but in older stages of development, filter-feeding becomes the tilapia's predominant means to trap zooplankton (GOPHEN et al. 1983, LAZZARO 1987, 1991). This is associated with loss of visual acuity in large fish, which causes them to interrupt their selective visual predation (HJELM et al. 2000). This change in eating habits may occur abruptly (MORIARTY et al. 1973, BEVERIDGE & BAIRD 2000), or more gradually (WHITFIELD & BLADER 1978).

When tilapias become exclusively filter-feeders, they consume only small organisms (BEVERIDGE & BAIRD 2000). The least evasive organisms in the zooplankton community (DRENNER et al. 1978, 1982a, b DRENNER & MCCOMAS 1980, KOHLER & NEY 1982, BEZERRA-NETO & PINTO-COELHO 2003), cladocerans and rotifers, are the most common prey of plankton-eating fish (DRENNER et al. 1986, 1987, LAZZARO 1987). In the study conducted by MENEZES et al. (2010), the presence of fish at different stages of development seemed to affect the population density of cladocerans and rotifers differently. For example, in the presence of adult Nile tilapias, cladoceran populations increase, showing that adult tilapias do not favor this type of zooplankton. Conversely, when tilapia juveniles predominate, rotifer population density decreases (MENEZES et al. 2010). On the other hand, due to their effective evasive behavior (STRICKLER 1977, FIELDS & YEN 1996, LENZ & HARTLINE 1999, YEN 2000), copepods are captured in low numbers when compared with similar-sized zooplanktonic organisms (TRAGER et al. 1994).

Even though they change how they capture prey during their ontogenetic development, Nile tilapias continue to eat organisms from the zooplankton community, even though the zooplankton groups ingested may vary. Since filter feeding affects organisms that get trapped in the gill rakers of fish, the space between these structures will determine the size of the prey ingested, determining that larger zooplanktonic organisms will be caught more often.

The objective of this study was to verify which zooplankton groups contribute the most to the diet of the omnivorous *O. niloticus* at the post-larval stage, in addition to determining if the way they prey selects their prey size. The

hypothesis is that, as the gill rakers increase in size throughout this cichlid's ontogenetic development, predation exerts great pressure on larger zooplanktonic organisms.

MATERIAL AND METHODS

Juvenile Nile tilapia gift strain juvenile sex-reversed males average size 14 cm were stocked at density of 1.1 fish/m² in 12 earthen ponds. These ponds were previously populated with natural plankton along with the Amazon river prawn, *Macrobrachium amazonicum* (Heller, 1862).

Stomach contents of fish were analyzed for four months, focusing on the zooplankton community. In addition, gill rakers of fish were measured to test for a correlation with the size of the ingested zooplankton. Fish were fed floating fish food twice a day. Primary environmental variables were regularly monitored and kept at culture standards. Once a month, one fish was randomly removed from each earthen pond with a fishing rod. Fish were fixed in formaldehyde (10%) and then stored in alcohol (70%). Stomachs and gills were extracted and fixed in formaldehyde (4%). Stomach content analysis was carried out in three subsamples of one milliliter, obtained with Stempel pipette, placed on a Sedgewick-Rafter counting cell slide under an optical microscope equipped with a reticle in order to measure zooplankton. For the identification of zooplankton species, specific keys were used (KOSTE 1978a, b, PONTIN 1978, SENDACZ & KUBO 1982, REID 1985, MATSUMURA-TUNDISI 1986, SEGERS 1995, EL MOOR-LOUREIRO 1997, SILVA & MATSUMURA-TUNDISI 2005). Zooplankton species were measured depending on their percentage in the stomach contents of cichlid. For computing the monthly means of the size of ingested zooplankton, the number of measurements followed a scale of representativeness, that is, more individuals were measured from the species that were in a higher proportion. The size of the gill rakers was measured through a stereomicroscope equipped with a micrometric ocular. Ten measurements were obtained for each extracted gill, for a total of four gills per fish. Next, means of those measures were calculated, determining the mean gill raker length and the mean distance between gill rakers each month.

Data was subjected to Shapiro-Wilk test of normality, and according to the results the appropriate statistical analyses were applied. The results expressed in percentage were arcsine square root transformed before statistical analyses. In order to compare the mean percentage of zooplankton found in the stomach contents from *O. niloticus*, the Kruskal-Wallis nonparametric test was used, along with a multiple-comparison among means test, at 5% significance. This test was also used to compare the mean percentage of each zooplanktonic group and the mean body size of the zooplankton ingested by the cichlid each month. In order to compare mean gill raker size, the parametric Anova with Tukey post hoc test (5%) was used. Pearson's correlation (5%) was employed to establish the correlation between size of ingested zooplankton and fish gill raker size.

RESULTS

Approximately 15 zooplankton species were found in the diet of *O. niloticus*, distributed among copepods, cladocerans, and rotifers (Table 1). Among them, the most consumed were rotifers from the genera *Brachionus* Pallas, 1766 and *Keratella* Bory de St. Vincent, 1822 (Fig. 1). Among the microcrustaceans, the cladoceran *Moina minuta* Hansen, 1899 was the most abundant in fish stomach contents. The average percentage of zooplankton found in the stomach contents of *O. niloticus* was 3% and it did not differ throughout the study. Nevertheless, as fish grew, the contributions of each group of ingested zooplankton changed. Fish ingested more and more rotifers, and less and less microcrustaceans, and the decrease was particularly considerable in the third month and in the last stomach analysis, which verified that no microcrustacean was consumed (Fig. 1). The consumption of rotifers increased with age, whereas the size of ingested prey decreased. In addition, gill raker length and the space between gill rakers increased as fish grew (Table 2). A significant negative correlation between zooplankton body width and the space between gill rakers was observed (Fig. 2). Other negative correlations were observed, though marginally significant (Figs. 2 and 3).

DISCUSSION

During their development from post-larval to adult stages, Nile tilapia ingested the same percentage of zooplankton with respect to the rest of their diet, but they consumed different zooplankton groups. Such changes may be related to the way *O. niloticus* preys. This study confirmed that juvenile Nile tilapia ingest cladocerans, as well as copepods and rotifers, through both visual predation and filter-feeding. Since rotifers are less likely to escape tilapia predation, they are the main zooplankton in the diet of this fish. Adults stop consuming microcrustaceans through visual predation and begin to eat only rotifers, which they catch through filter feeding.

According to several studies (GROVER et al. 1989, UFODIKE & WADA 1991, ROCHA LOURES et al. 2001, BWANIKA et al. 2006), the percentage of zooplankton ingested decreases in the diet of species of *Oreochromis*, as fry develop into adults; it becomes constant, which was also observed in this study. A preference for zooplankton and diatoms to artificial food was observed during the first stages of Nile tilapia larvae (UFODIKE & WADA 1991). Nevertheless, this preference changed as larvae grew, as observed by GROVER et al. (1989) when studying fry of red hybrid tilapia: they increase their consumption of artificial food as they develop. Even so, the consumption of zooplankton by tilapia may be significant, as observed by BWANIKA et al. (2006) in African ponds, where the percentage of zooplankton in the stomach contents of *O. niloticus* varied from 8 to 13%. Even Nile tilapia fry, which were fed artificial food, phytoplankton and zooplankton, had a stomach content of approximately 13% zooplankton (ROCHA LOURES et al. 2001).

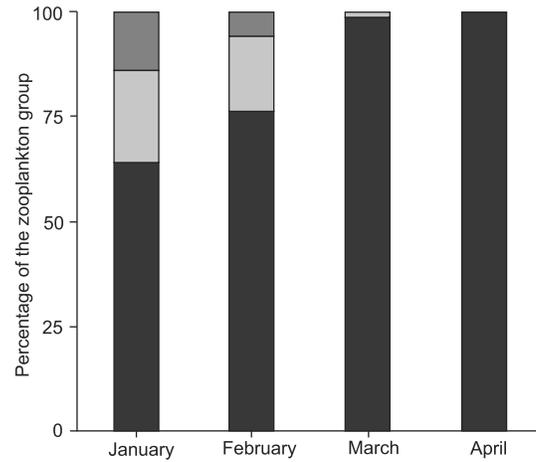
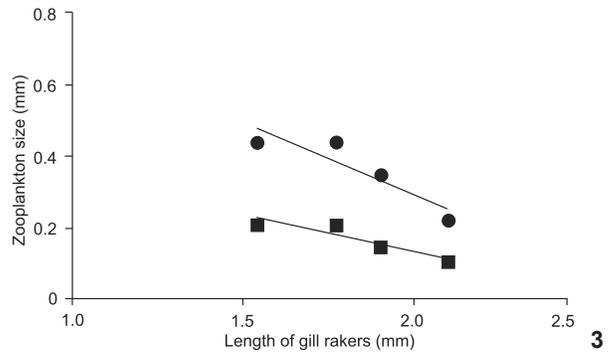
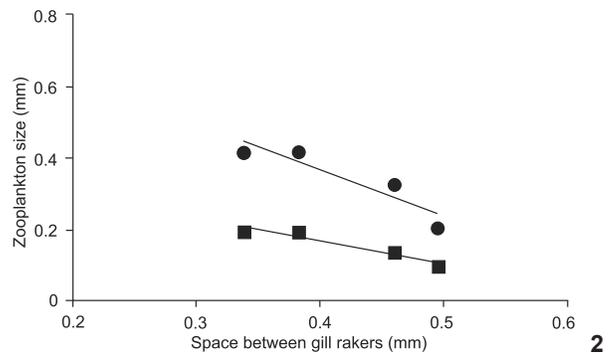


Figure 1. Zooplankton composition in the stomach contents from *Oreochromis niloticus* each month. (■) Copepoda, (▒) Cladocera, (●) Rotifera.



Figures 2-3. (2) Negative correlation between zooplankton's body size found in stomach contents and space between Nile tilapia's gill rakers. Significant Pearson's correlation (Length $r = -0.92$ and $p = 0.07$; Width $r = -0.96$ and $p = 0.04$). (3) Negative correlation between zooplankton's body size found in stomach contents and length of Nile tilapia's gill rakers. Significant Pearson's correlation (Length $r = -0.91$ and $p = 0.09$; Width $r = -0.92$ and $p = 0.08$). (●) Length, (■) width.

Table 1. Zooplankton community and respective size variations found in the diet of post-larval stages (juvenile to adult) of *Oreochromis niloticus* throughout four months.

Taxon/month	Length (mm)
January	
Cladocera	
<i>Diaphanosoma spinulosum</i>	0.33-0.88
<i>Moina minuta</i>	0.37-0.83
Copepoda	
Copepodid	0.33-0.83
Nauplius	0.11-0.33
<i>Notodiaptomus iheringi</i>	0.77-1.65
<i>Thermocyclops decipiens</i>	0.50-1.00
Rotifera	
<i>Brachionus calyciflorus</i>	0.22-0.44
<i>Brachionus havanaensis</i>	0.28-0.33
<i>Filinia</i> spp.	0.11-0.17
<i>Keratella</i> spp.	0.11-0.17
<i>Lecane</i> spp.	0.11-0.17
<i>Trichocerca</i> sp.	0.22-0.33
February	
Cladocera	
<i>Diaphanosoma spinulosum</i>	0.33-0.99
<i>Moina minuta</i>	0.33-0.77
Copepoda	
<i>Argyrodiaptomus furcatus</i>	1.16-1.49
Copepodid	0.33-0.99
Nauplius	0.20-0.55
<i>Notodiaptomus iheringi</i>	0.94-1.54
Rotifera	
<i>Brachionus calyciflorus</i>	0.22-0.39
<i>Brachionus falcatus</i>	0.28-0.36
<i>Brachionus havanaensis</i>	0.22-0.39
<i>Filinia</i> spp.	0.11-0.22
<i>Lecane</i> spp.	0.12-0.17
<i>Trichocerca</i> sp.	0.18-0.33
March	
Cladocera	
<i>Moina minuta</i>	0.33-0.77
Rotifera	
<i>Brachionus calyciflorus</i>	0.28-0.44
<i>Brachionus havanaensis</i>	0.25-0.39
<i>Filinia</i> spp.	0.08-0.33
<i>Keratella</i> spp.	0.11-0.22
<i>Lecane</i> spp.	0.12-0.19
<i>Trichocerca</i> sp.	0.18-0.33
April	
Rotifera	
<i>Brachionus havanaensis</i>	0.22-0.39
<i>Filinia</i> spp.	0.20-0.22
<i>Keratella</i> spp.	0.11-0.22
<i>Lecane</i> spp.	0.14-0.17
<i>Trichocerca</i> sp.	0.20-0.22

Table 2. Size variation from *Oreochromis niloticus* and their structures responsible for filtering zooplankton community throughout the study. Values are means (\pm standard deviation).

Month	<i>O. niloticus</i> (cm) (\pm SD)	Length of the gill rakers (mm) (\pm SD)	Space between the gill rakers (mm) (\pm SD)
January	14 (\pm 0.69) ^c	1.54 (\pm 0.12) ^c	0.34 (\pm 0.05) ^p
February	18 (\pm 1.29) ^{bc}	1.77 (\pm 0.13) ^b	0.38 (\pm 0.04) ^p
March	21 (\pm 2.08) ^{ab}	1.90 (\pm 0.14) ^b	0.46 (\pm 0.04) ^a
April	23 (\pm 1.16) ^a	2.10 (\pm 0.15) ^a	0.50 (\pm 0.05) ^a

Means with different letters in each column differ statistically. Kruskal-Wallis (5%) and ANOVA Tukey (5%), $p < 0.05$.

The size of the prey and how they are captured may differ, depending on the size of the predator and the development of their sensory structures (JHA et al. 2006). During an experiment with Nile tilapia larvae, UFODIKE & WADA (1991) demonstrated that the first stages of larvae (5 to 14 mm) predate rotifers, cladocerans, and copepods. BEYRUTH et al. (2004) also observed the great proportion of rotifera and cladocera in the digestive system of *O. niloticus* fry. According to their data, during the first post-larval stages, Nile tilapia may still prey on zooplankton. Our data showed that *O. niloticus* adults stopped ingesting microcrustaceans and began to prey only on rotifers. During its adult stage the percentage of zooplankton in their diet remained constant. Tilapia predation on the rotifer population may have significant impact, as observed by MENEZES et al. (2010), through population data analysis.

Studies carried out with filter feeding fish have demonstrated that species that have low escapement capacity are predated in greater numbers (DRENNER et al. 1986, 1987, LAZZARO 1987). Among the zooplankton, rotifers and cladocerans have the least mobility and escapement capacity (DRENNER et al. 1978, 1982a, b, DRENNER & MCCOMAS 1980, KOHLER & NEY 1982, BEZERRA-NETO & PINTO-COELHO 2003). Copepods, on the other hand, are the most evasive (DRENNER et al. 1978, LAZZARO 1987, 1991). The total absence of copepoda in the diet of *O. niloticus* adults confirms that they escape from the flow pumped by the fish during the filtering process (DRENNER et al. 1978, LAZZARO 1987, 1991). Rotifers, which have lower escapement efficiency than microcrustaceans, constituted 100% of the adult tilapia's zooplankton diet. In a study on the effects of predation on plankton populations, ATTAYDE & MENEZES (2008) concluded that rotifer populations grow in the presence of juvenile Nile tilapias, whereas cladoceran populations increase in the presence of adults, suggesting that during the juvenile stage, these fish feed more on microcrustaceans than on rotifers, and during adulthood, the opposite happens. MENEZES et al. (2010) also noted an increase in rotifera biomass in the absence of tilapia in the environment, showing that rotifers may be one of the most consumed groups by this fish.

During filtering, the gill rakers of the Nile tilapia secrete mucus, trapping food items (LAZZARO 1987, SANDERSON et al. 1996, ZAVALA-CAMIN 1996). The morphology of the gill rakers is di-

rectly related to the size of the ingested prey (HYATT 1979, WOOTTON 1992, JOBLING 1996). In several studies on the diet of *O. niloticus*, it was observed that this cichlid may have different types of gill rakers. The high trophic plasticity of the Nile tilapia indicates that it may have long and numerous gill rakers (plankton-feeding species), or few and short ones (omnivorous species) (CÂMARA & CHELLAPPA 1996, BEYRUTH et al. 2004, ZAYED & MOHAMED 2004). Fish gill rakers in this study showed characteristics of omnivorous species, with the space between them being wider than the dimensions of most zooplankton prey. Around 85% of the zooplankton found in the stomach contents was smaller than the space between the gill rakers, which means that they would go through the filter if there was no mucus. Among the zooplankton organisms identified, rotifers were the smallest ones. The remaining ingested prey (15%) were larger than the space between the gill rakers. However, the ingestion of large microcrustaceans happened only during the first months of culture, during the initial post-larval stage. In adults, the space between the gill rakers is larger, which results in a lower contribution from larger-sized zooplankton and a higher contribution from minute zooplankton organisms. This may indicate that the presence of mucus in adult *O. niloticus* is one of the main factors in prey capture, not the space between the gill rakers. In addition, the mucus secreted in the gill rakers does not trap large zooplankton. Even though the gill rakers increase in length, and the amount of secreted mucus increases with age, these potential prey individuals have not been ingested by adults, despite the elevated population density of cladocerans and copepods.

The highest contribution of microcrustaceans such as copepods during the first life stages of fish is related to visual active capture, during which the predator spots and ingests the prey intentionally (LAZZARO 1987). Studies have shown that *O. niloticus* fry prey only visually, ingesting rotifers, cladocerans and copepods (UFODIKE & WADA 1991, BEYRUTH et al. 2004), a common characteristic of several groups of fish (GOPHEN et al. 1983, LAZZARO 1987, 1991). According to YOWELL & VINYARD (1993), the reduced volume of the mouth cavity of the tilapia during the larval stages results in a strictly visual predation. For YOWELL & VINYARD (1993), the change in how prey is ingested (from visual predation to filter feeding) occurs when the tilapia's body reaches six centimeters in length. Although our study was carried out with juvenile *O. niloticus* measuring, on average, 14 centimeters, it was concluded that copepods and cladocerans microcrustaceans were actively ingested during this post-larval stage. In the stomach of adults, only small zooplankton was found, such as rotifers, confirming data from study by BEVERIDGE & BAIRD (2000), which suggests that filtering has an impact on minute zooplankton.

In conclusion, during the development of *O. niloticus*, the way fish ingest zooplankton and the groups of zooplankton they ingest change. Juvenile fish prey on microcrustaceans visually and filter feed rotifers, whereas adult individuals filter

feed zooplankton, which consist of smaller-sized organisms that are trapped in the mucus secreted by their gill rakers.

There are changes in the contribution from zooplankton species to the diet of *O. niloticus* throughout the ontogenetic development of the fish. The consumption of microcrustaceans verified in the post-larval stage is replaced by the total contribution of rotifers during the adult stage.

The increase in the size of the gill raker of *O. niloticus* does not determine the consumption of larger zooplankton prey. Despite their abundance in the environment, this group of zooplankton, mainly represented by copepods, is not ingested at the same rate as rotifers, because they are efficient in escaping from predation. We also conclude that, when capturing prey through filter feeding, the presence of mucus produced by the fish in the gills plays a more effective role than the space between the gill rakers. Also, the greater representation of microcrustaceans during the Nile tilapia's first post-larval stages (when they are already filter feeding), allows us to deduce that, at this stage, there is still visual predation, which is more efficient for capturing larger zooplankton prey, such as microcrustaceans.

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