

Parasite communities of the elongate tigerfish Hydrocynus forskahlii (Cuvier 1819) and redbelly tilapia Tilapia zillii (Gervais 1848) from Lake Turkana, Kenya: influence of host sex and size

Elick O. Otachi^{1,2}, Beata Szostakowska³, Franz Jirsa^{4,5} and Christine Fellner-Frank¹

¹University of Vienna, Department of Integrative Zoology, Althanstrasse 14, 1090 Vienna, Austria;
²Egerton University, Biological Sciences Department, P. O. Box 536, Egerton, Kenya;
³Medical University of Gdansk, Department of Tropical Parasitology, ul. Powstania Styczniowego 9B, 81-519 Gdynia, Poland;
⁴University of Vienna, Institute of Inorganic Chemistry, Althanstrasse 14, 1090 Vienna, Austria;
⁵University of Johannesburg, Dept. of Zoology, P. O. Box 524, Auckland Park B-2006, South Africa

Abstract

Fish is an important food source for an estimated 300,000 people inhabiting the shores of Lake Turkana, Kenya. Despite its large size (7560 km²) and importance, the lake remains one of the least studied in the Great Lakes Region of Africa. This study describes the parasite community of the elongate tigerfish *Hydrocynus forskahlii* (Cuvier, 1819) and the redbelly tilapia *Tilapia zillii* (Gervais, 1848). A total of 87 individuals (43 *H. forskahlii* and 44 *T. zillii*) were dissected and examined for parasites. Two taxa infected *H. forskahlii*, the dominant one being an anisakid nematode *Contracaecum* sp. (L3) (P = 83.7%, mean intensity (MI) = 46.0, abundance (A) = 38.5). Twelve parasite taxa were recovered from *T. zillii*, with metacestodes of the gryporhynchid cestode *Amirthalingamia macracantha* being dominant (P = 79.5, MI = 10.3, A = 8.2). This was the first report of a mixture of merocercoids and plerocercoids in the same host. Fish size was positively correlated with the major parasite infection levels, but, the prevalence of *Contracaecum* sp. in *H. forskahlii* was negatively correlated with size, probably reflecting ontogenetic shifts in habitats and diets with age. Fish sex was not a significant influencing factor, with the exception of *Contracaecum* sp. in *H. forskahlii*, where prevalence differed significantly between sexes (p<0.05), with the females having a higher prevalence than the males. We conclude that *H. forskahlii* had a poor parasitic community but that the infection levels with *Contracaecum* sp. were high. *T. zillii* had a rich parasite fauna, although, most parasites occurred at low intensities.

Keywords

Lake Turkana, Hydrocynus forskahlii, Tilapia zillii, Contracaecum spp., Amirthalingamia macracantha, parasites

Introduction

Fish is an important food source for an estimated 300,000 people inhabiting the shores of Lake Turkana and beyond (Friends of Lake Turkana (FOLT) 2009; Avery 2010; Hathaway and Amicucci 2010). Located in an arid area, Lake Turkana is a lifeline for the impoverished dwellers surrounding the lake, firstly because of its water and secondly because of its rich and productive fishery (Getabu *et al.* 2007; FOLT 2009; Hathaway and Amicucci 2010). The lake contains a high diversity of fish, with at least 48–50 species having been recorded (Kolding 1989; Okeyo 2003). This makes fish one of the most significant and most available food sources in the area. Amongst the challenges reported in the exploitation of Lake Turkana fish are: lack of appropriate offshore vessels and fishing gear, high post-harvest losses (approximately 90%), and a high infestation of fish with parasites (Ojwang *et al.* 2007, 2008). Several taxonomic studies have been done on parasites of fish from Lake Turkana. Moravec *et al.* (2009a, b), for example, described new species such as *Mexiconema africanum* (Nematoda: Daniconematidae) from the giraffe catfish *Auchenoglanis occidentalis* (Valenciennes, 1840), *Philometra lati* and *P. spiriformis* (Nematoda: Philometridae) from the Nile perch *Lates niloticus* (L. 1758), and *Afrophilo*-

metra hydrocyoni from the elongate tigerfish Hydrocynus forskahlii (Cuvier, 1819). Rushton-Mellor (1994) described a new crustacean parasite Argulus fryeri from Lake Turkana, Kenya, from an unknown host, while Přikrylová et al. (2012) described a new monogenean species Gyrodactylus malalai from the Nile tilapia Oreochromis niloticus (L. 1758) and the redbelly tilapia Tilapia zillii (Gervais, 1848). Recently, Moravec et al. (2013) provided the morphology and systematics of Rhabdochona paski (Nematoda: Rhabdochonidae) from some specimens obtained from H. forskahlii, O. niloticus and T. zillii among other fishes in Africa. Several taxa of parasites have been reported from H. forskahlii and T. zillii in Africa (Khalil and Polling 1997; Paperna 1980, 1996). Nonetheless, data on the diversity, prevalence, intensities and ecology of parasites from Lake Turkana is lacking and this study addresses this gap. We also provide data on the influence of fish sex and size on infection levels of the major parasites.

Materials and Methods

Study site description

Lake Turkana (formerly Lake Rudolf) is located at the north of the eastern Rift Valley, stretching from 35°50' to 36°40'E and 2°27' to 4°40'N (Getabu et al. 2007), with its northernmost tip stretching into Ethiopia. It is the world's largest desert lake and the largest (7560km²) and deepest water mass in Kenya (mean depth 35 m, maximum 120 m). It is the fourth largest lake in Africa in terms of surface area (Avery 2010; Ojwang et al. 2007). The water of the lake is alkaline (pH = 9.2) and is slightly saline (total dissolved solids (TDS)) = 2500mg/L) (Yuretich and Cerling 1983; Campbell *et al.* 2003). Volcanic activity was frequent during the creation of the Rift Valley, and lavas from the Quaternary and Tertiary ages cover much of the floor of the valley in Kenya. This lava is mainly of alkaline type, which has important implications for the chemical composition of the lake (ILEC 2013). The lake receives 90% of its water from Omo River from Ethiopia and seasonally from Turkwell and Kerio Rivers in Kenya. The lake loses water mainly by evaporation. The human population density in this lake basin is very low, 1–3 persons/km² (Odada et al. 2003; ILEC 2013). The catchment area is approximately 130,860 km² and the land use is dominated by pasture (47.5%), herbaceous vegetation (45%), and woody plants (5%), whereas crop fields cover 2.4% (ILEC 2013). Being in an arid area and with slightly saline water, there are no significant industrial activities in and around the lake. The only known pollution problem in Lake Turkana is that of suspended solids (Odada et al. 2003) coming from the drainage basin of Omo River in Ethiopia. An increased removal of vegetation cover for fuel and the conversion of forest land to agricultural fields may be leading to heavy sedimentation in the lake (Haack and Messina 1997).

Sampling and parasitological examination

The fish studied: *T. zillii* (local name – Loroto) and *H. forskahlii* (local name – Lokel) (Ojwang *et al.* 2007), are commercially important but differ biologically (Froese and Pauly 2013). *H. forskahlii* is an open-water piscivorous predator often found near the water surface. *T. zillii* is largely ben-thopelagic and potamodromous. It prefers shallow, vegetated areas. *T. zillii* is mostly herbivorous, feeding on water plants and epiphyton and some invertebrates (Froese and Pauly 2013).

A total of forty-three (43) *H. forskahlii* and forty-four (44) *T. zillii* were caught using beach seines by fishermen in June 2011 and in September 2012 at Kalokol, at the northern end of Longech spit (peninsula) forming the eastern bank of the Ferguson's Gulf (N 03°33.218' E 035°54.742'). The fish were killed by cervical dislocation and their total lengths measured. The mean length (\pm SD) of *H. forskahlii* was 33.4 \pm 3.9 cm, and that of *T. zillii* was 15.7 \pm 2.3 cm.

This was followed by a dissection (Schäperclaus 1990). Fish sex was determined by examining the gonads. To estimate the intensity of infection by protozoans, gill and skin smears were prepared for examination under high magnification ($\times 40 - \times 100$) as described previously (Lom and Dyková 1992).

The categories used to assess infection intensity were defined as follows: low- <10 parasite individuals per field of view (at 100-fold magnification); medium – 11–100 parasites per field of view; and high->100 individuals per field of view (Jirsa et al. 2011). The gill filaments were examined under a dissecting microscope. Monogeneans were counted and removed carefully from the gills using fine forceps, fixed and preserved in either 4% formalin or ethanol (95%). For identification, the monogeneans were mounted in either glycerine ammonium picrate (GAP) or glycerine jelly on slides and cover slips gently placed on top to flatten the worms and sealed with clear nail polish. The eyes, intestines, visceral organs and pericardial cavity were all examined for parasites. Most of the parasites were identified using identification keys and key literature at the University of Vienna and at the Museum of Natural History, Vienna (Paperna 1980, 1996; Pariselle and Euzet 1995, 1998, 2009; Scholz et al. 2004; Le Roux and Avenant-Oldewage 2010; Abowei and Ezekiel 2011; Kuchta et al. 2012). The terms used to describe the metacestodes are according to Chervy (2002). Preliminary identification of larval nematodes was based on their morphology by light microscopic examination (Shamsi and Aghazadeh-Meshgi 2011). Species of nematodes were represented by two kinds of Contracaecum spp. larvae that differed markedly from each other in their sizes. They were provisionally identified as Contracaecum sp. 1 (bigger) and Contracaecum sp. 2 (smaller). Contracaecum sp. 1 was found in both species of fish and occurred in the intestine, liver and body cavity while Contracaecum sp. 2 was found only in T. zillii and only in the gut and gut wall.

Molecular analysis of the nematodes isolated from *H. forskahlii* and *T. zillii*

Six nematodes were subjected to molecular analysis. There were 2 specimens from H. forskahlii (two morphologically similar larvae) and 4 specimens from T. zillii (two of each type of larvae as described above). The target of the molecular analysis was the internal transcribed spacer 1 (ITS-1) of the ribosomal DNA (rDNA). Because of the obvious size differences of the specimens from the intestine and the gut wall, the total DNA of the parasites was isolated in two different ways: DNA from a small fragment (about 15mg) of larvae from intestine was isolated using the Genomic Mini Kit (A & A Biotechnology, Gdynia, Poland), whereas the DNA from the entire specimen from the gut wall, was isolated using the Sherlock AX Kit (A & A Biotechnology, Gdynia, Poland), according to the manufacturer's recommendation. The ITS-1 was amplified using the primers NC5 (forward) and NC13 (reverse) (Zhu et al. 2000). The composition of the reaction mixtures and the PCR reaction conditions were identical to those described in Szostakowska and Fagerholm (2007). The PCR products and the sequencing reaction products were purified using the Clean-Up Kit and the ExTerminator Kit (A & A Biotechnology), respectively. The analyses were performed using an automatic ABI PRISM 310 DNA sequencer (Applied Biosystems, Inc., California, USA), with the amplification primers and the standard procedure described by the manufacturer. The sequences obtained were then analyzed, aligned and blasted with the related sequences downloaded from Gen-Bank using the GeneStudio Pro Software (GeneStudio, Inc., Suwanee, Georgia).

Statistical analyses

The prevalence, mean intensities and mean abundances were determined according to Bush *et al.* (1997). The parasite community structure was described using the Shannon-Wiener index, the Simpson's index, the Margalef Richness index and the Berger-Parker Dominance index (Magurran 1988). For those parasites occurring in high abundances, we also investigated the effect of host sex and size. A fisher's exact test was used to determine the relationship between parasite prevalence

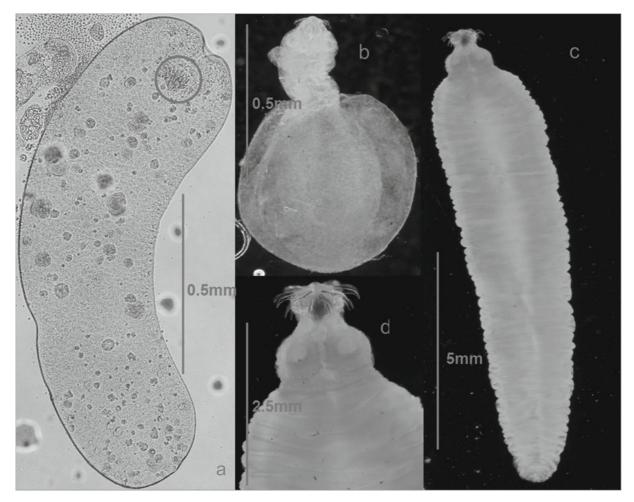


Fig. 1. Larval forms of *A. macracantha* recovered from *T. zillii*. (a) A merocercoid, usually encysted in the intestinal wall; primordial hooks are marked by a circle (b) A merocercoid emerging from a cyst (c) The typical plerocercoid found occurring freely in the intestine (d) details of the plerocercoid scolex

Parasite	Site of infection	P (%)	$\mathbf{MI}\pm\mathbf{SD}$	$\mathbf{MA} \pm \mathbf{SD}$
Trichodina sp.	gills	4.5	low	
Cichlidogyrus sp.	gills/skin	45.5	3.2 ± 3.04	1.5 ± 2.6
Gyrodactylus sp.	gills	4.5	6.0 ± 0.0	0.3 ± 1.3
Metacercarial cysts	intestinal wall	4.5	3.0 ± 0.0	0.1 ± 0.6
Amirthalingamia macracantha	gut/intestine/liver	79.5	10.3 ± 15.3	8.2 ± 14.2
Contracaecum sp. 1	intestine/body cavity/liver	18.2	2.6 ± 2.6	0.5 ± 1.5
Contracaecum sp. 2	gut/gut wall	15.9	12.7 ± 11.3	2.0 ± 6.3
Acanthogyrus sp.	intestinal wall	2.3	1.0 ± 0.0	0.02 ± 0.2
Paragorgorhynchus sp.	intestinal wall	13.6	1.3 ± 0.0	0.2 ± 0.4
Argulus monodi	body surface/skin	6.8	1.0 ± 0.0	0.02 ± 0.2
Argulus fryeri	body surface/skin	4.5	1.0 ± 0.0	0.05 ± 0.2
Lernaea cyprinacea	gills	6.8	1.2 ± 0.4	0.1 ± 0.4

Table I. Occurrence of parasites in *Tilapia zillii* with regards to the site of infection, parasite prevalence (P), mean intensity (MI) and mean abundance (MA) from Lake Turkana, Kenya. (n = 44, SD Standard deviation)

and the sex of the host fish. To establish the relationship between the parasite intensities and host fish sex, we used the Wilcoxon's signed rank test. A correlation analysis determined the relationship between the parasitic infection levels and host fish size. Graphs were drawn using Microsoft Excel 2010 and SigmaPlot 10.0 (Systat Software Inc., Chicago, IL, USA)

Results

Parasites were present in 97.7% of all *H. forskahlii* examined. Two taxa of parasites were recovered from this host namely: *Annulotrema* sp. (Monogenea, Ancyrocephalidae) with a prevalence of 79.1%, mean intensity (\pm SD) of 6.8 \pm 8.8 and mean abundance (\pm SD) of 5.4 \pm 8.3 found in the gills and *Contracaecum* sp. 1 (Larvae 3) (Sercenentea, Anisakidae) with a prevalence of 83.7%, a mean intensity of 46.0 \pm 58.0 and a mean abundance of 38.5 \pm 55.7 found aggregated in the body cavity and the intestines.

Almost all *T. zillii* examined (97.7%) were infected with at least one parasite taxon. The dominant species was *Amirthalingamia macracantha* (metacestodes), which occurred with a prevalence of 79.5% and a mean intensity (\pm SD) of 10.3 \pm 15.3. Some of the metacestodes were encysted (in the intestinal wall) and others were unencysted (in the intestinal lumen).

This co-occurrence of two developmental stages: encysted (merocercoids) and unencysted (plerocercoids) in the same host represented a new phenomenon (Fig. 1).

The parasites included: *Trichodina* sp. (Ciliophora, Peritrichida), *Cichlidogyrus* sp. (Monogenea, Ancyrocephalidae), *Gyrodactylus* sp. (Monogenea, Gyrodactylidae), metacercariae cysts (Digenea), *A. macracantha* (merocercoids and plerocercoids) (Cyclophyllidea, Dilepididae), *Contracaecum* sp. 1 (Sercenentea, Anisakidae), *Contracaecum* sp. 2 (Sercenentea, Anisakidae), *Acanthogyrus* sp. (Gyracanthocephala, Quadrigyridae), *Paragorgorhynchus* sp. (Echinorhynchida, Rhadinorhynchidae), *Argulus fryeri* (Arguloidea, Argulidae), *A. monodi* (Arguloidea, Argulidae) and *Lernaea cyprinacea* (Cyclopoida, Lernaeidae) (data on the parasite prevalence, mean intensity and mean abundance is given in Table I). *T. zillii* was infected by a relatively high diversity of parasite species (Shannon-Wiener index 1.13 and Margalef Richness 1.12; Table II).

The ITS-1 sequences of the nematode specimens obtained have been deposited in GenBank under accession numbers KF990491-KF990496. The sequences of all *Contracaecum sp.* 1 larvae isolated from the body cavity and the intestines of both fish species were identical (two larvae from *H. forskahlii* and three from *T. zillii*, Accession numbers KF990491-KF990495), but they differ from all se-

Table II. Parasite component diversity characteristics of the fish studied from Lake Turkana, Kenya

Total component communities	H. forskahlii	T. zillii	
Number of fish	43	44	
Number of metazoan taxa	2	11	
Shannon-Wiener index	0.37	1.22	
Margalef Richness index	0.13	1.12	
Berger-Parker Dominance index	0.88	0.63	
Simpson's index	0.78	0.88	
Dominant taxon	Contracaecum sp. 1	A. macracantha	

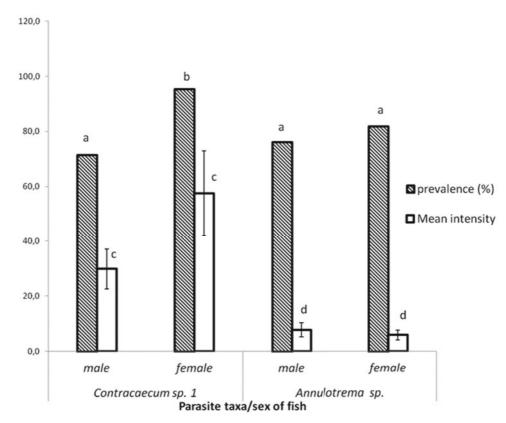


Fig. 2. The relationships between *H. forskahlii* sex and the prevalence and mean intensities (\pm SD) of the *Contracaecum* sp. 1 and *Annulotrema* sp. from Lake Turkana, Kenya. The sample sizes (n) were as follows: males = 21, females = 22

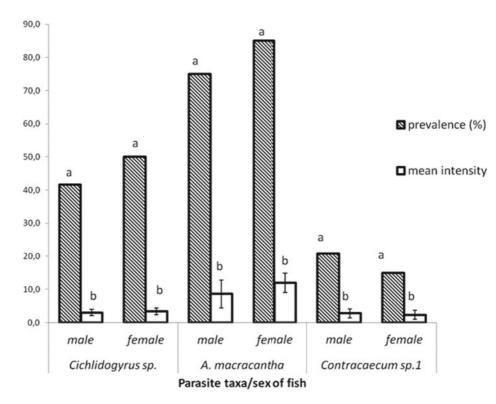


Fig. 3. The relationships between *T. zillii* sex and the prevalence and mean intensities $(\pm SD)$ of the *Cichlidogyrus* sp. *A. macracantha* and *Contracaecum* sp. 1 from Lake Turkana, Kenya. The sample sizes (n) were as follows: males = 24, females = 20

quences deposited in GenBank. They showed the highest similarity (89%) to *Contracaecum multipapillatum* from the Australian pelican *Pelecanus conspicillatus* (Accession number AM940056) (Shamsi *et al.* 2008). The ITS-1 sequence of the small larvae which represented *Contracaecum* sp. 2 (GenBank accession KF990496) from the gut wall of *T. zillii*, was 99% similar with the ITS-1 sequences of *C. bancrofti* deposited under accession number EU839572 (Shamsi *et al.* 2009).

Effect of host sex on parasite infection levels

For *H. forskahlii*, sex did not significantly influence the prevalence of *Annulotrema* sp. (Fisher's exact test p = 0.26). Although not significant, the females had a slightly higher prevalence of this monogenean (81.8%) compared to the males (76.2%). The prevalence of *Contracaecum* sp. 1 dif-

fered significantly among the sexes (Fisher's exact test p<0.05), with the females having a higher prevalence (95.5%) than males (71.4%) (Fig. 2). The parasite intensities were not significantly different between the sexes (Wilcoxon's Signed Rank test Z = -0.561, p>0.05 for *Annulotrema* sp.; and Z = -1.624, p>0.05 for *Contracaecum* sp. 1). Although not significant, *Annulotrema sp.* had higher mean intensities in the male fish, whereas *Contracaecum* sp. 1 had higher mean intensities in the females.

In *T. zillii*, sex was not a significant factor in influencing the prevalence of *Cichlidogyrus* sp. (Fisher's exact test p = 0.21), *A. macracantha* (Fisher's exact test p = 0.22) or *Contracaecum* sp. 1 (Fisher's exact test p = 0.27). Although not significant, both *Cichlidogyrus* sp. and *A. macracantha* had higher prevalences and mean intensities in females versus males, whereas *Contracaecum* sp. 1 had higher prevalence and mean intensity in male fish (Fig. 3).

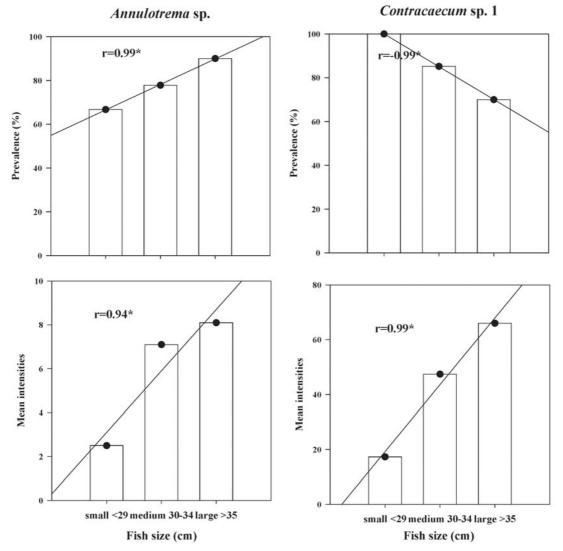


Fig. 4. The relationships between *H. forskahlii* size and the prevalence and mean intensities of the *Annulotrema* sp. and *Contracaecum* sp. 1 from Lake Turkana, Kenya. The sample sizes (n) were as follows: small = 6, medium = 27 and large = 10

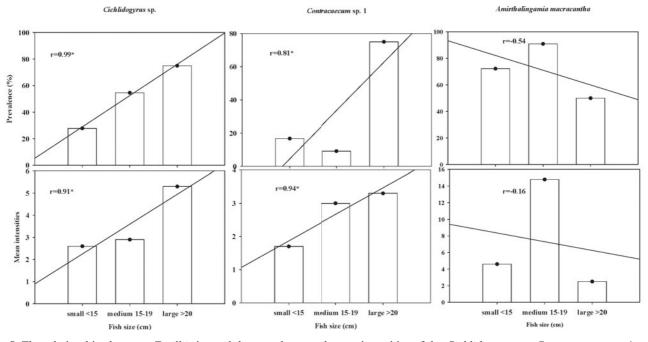


Fig. 5. The relationships between *T. zillii* size and the prevalence and mean intensities of the *Cichlidogyrus* sp. *Contracaecum* sp. 1 and *A. macracantha* from Lake Turkana, Kenya. The sample sizes (n) were as follows: small = 18, medium = 22 and large = 4

Effect of host size on parasite infection levels

There was a positive and significant correlation between the prevalence and mean intensities of *Annulotrema* sp. and the size of *H. forskahlii* (r = 0.99 p < 0.05 and r = 0.94 p < 0.05, respectively). For *Contracaecum* sp. 1, however, the trend was different. There was a negative and significant correlation between prevalence and *H. forskahlii* size (r = -0.99 p < 0.05), while the mean intensities were positively correlated with fish size (r = 0.99 p < 0.05) (Fig. 4).

In *T. zillii*, the fish size also significantly determined the prevalence (r = 0.99 p < 0.05) and mean intensities (r = 0.91 p < 0.05) of *Cichlidogyrus* sp. and of *Contracaecum* sp. 1 (r = 0.81 p < 0.05 and r = 0.94 p < 0.05, respectively) (Fig. 5). This correlation was weak and insignificant for the prevalence (r = 0.54 p > 0.05), and mean intensities of *A. macracantha* (r = 0.16 p > 0.05) (Fig. 5).

Discussion

Two taxa of parasites infected *H. forskahlii*. The anisakid nematode *Contracaecum* sp. 1 was dominant. Two parasites already described and reported from this host in the same lake i.e. *A. hydrocyoni* from *H. forskahlii* (Moravec *et al.* 2009a) and *R. paski* (Moravec *et al.* 2013), were not recovered during this study. This is probably because they are rare, for example, *A. hydrocyoni* was found in one of the thirty-one fish examined (P = 3.2%) (Moravec *et al.* 2009a), while *R. paski* had a prevalence of 11.6% (43 *H. forskahlii* examined) and one fish out of the seventy-two (72) *O. niloticus*

(P = 1.4%) and 3.7% of the twenty-seven (27) T. zillii examined (Moravec et al. 2013). The prevalence and the mean intensity of Contracaecum sp. 1 in H. forskahlii were significantly higher than in the following studies: Aloo (2002) reported a 49.2% prevalence of Contracaecum sp. in Oreochromis leucostictus (mean intensity 15.13) and a prevalence of 2% in T. zillii (mean intensity 1.42), both from Oloidien Lake in Naivasha basin, Kenya and Florio et al. (2009) reported a C. multipapillatum prevalence of 17.3% (mean intensity 4.1) from pooled wild tilapia from the Lakes Babogaya, Hora, Awassa and Chamo in Ethiopia. The high prevalence and mean intensity can be attributed, among other factors, to the feeding habits of H. forskahlii. This fish is a top piscivore in Lake Turkana. This diet could be a constant source of infection with Contracaecum sp. 1. Piscivorous fish can act as parasite sinks (Paperna 1980; Paterson et al. 2013) or as parasite concentrators, the latter by increasing the parasite's probability of finding a mate (Brown et al. 2001). Paperna (1980) suggested that fish which are too large a prey for piscivorous birds may play a significant role in moderating parasite populations in lake fish by trapping worms. H. forskahlii could be such a fish because it is large (maximum recorded size 78 cm) (Froese and Pauly 2013). Two different species of the genus Contracaecum infected T. zillii: Contracaecum sp. 1 in the intestine, liver and the body cavity, and Contracaecum sp. 2 which was found almost exclusively aggregating in the gut and gut wall. Further analysis on *Contracaecum* spp. is ongoing, including the analysis of the entire ITS from larvae and a morphogenetic study of the adults from fish-eating birds. These findings will be published separately.

The overall prevalence of parasites in T. zillii was very high compared to other studies on *T. zillii* Ramadan (1991) study in Lake Manzalah, Egypt; Olofintoye (2006) study in Ekiti State, Nigeria; Abdel-Hady et al. (2008) study in Lake Temsah, Egypt; Goselle et al. (2008) study in Lamingo Dam, Jos, Nigeria; Bichi and Ibrahim (2009) study in Lake Tiga, Kano, Nothern Nigeria; Morenikeji and Adepeju (2009) study in natural and man-made ponds in south-west Nigeria; Hassan et al. (2012) study in Lake Timsah, Ismailia, Egypt; Olurin et al. (2012) study in River Oshun, south-west Nigeria). We found several parasites infecting T. zillii, as did Ibrahim (2012) who reported 12 species, mainly monogeneans, from wild and cultured T. zillii from Lake Manzalah, Egypt. In contrast, several surveys have shown a less diverse parasite fauna in T. zillii elsewhere in Africa (Ramadan 1991; Olofintoye 2006; Abdel-Hady et al. 2008; Goselle et al. 2008; Bichi and Ibrahim 2009; Morenikeji and Adepeju 2009; Hassan et al. 2012; Olurin et al. 2012). The low infection intensity of most of the parasites that we found in T. zillii is similar to that reported by Aloo (2002), who concluded that among the tilapiine species, T. zillii is probably more resistant to parasitic infections than the other species.

Cichlidogyrus sp. occurred at moderate prevalence and low intensities in T. zillii, lower than those reported in the literature (Ibrahim 2012; Otachi et al. 2014). We had anticipated higher intensities of Cichlidogyrus sp. because this genus is known to have a shorter egg incubation time, faster hatching, longer lifespan and faster development to maturity in higher temperatures (Paperna 1980, 1996). For example, at temperatures from 20-28°C, eggs hatch within two to six days. Furthermore, T. zillii is a substrate spawner, whereby both parents build nests, guard them and protect their fry. This breeding behavior clearly predisposes them to oncomiracidia on the bottom where the eggs of species of Cichlidogyrus hatch. Several factors could explain the observed low levels of infection, the most important being a possible low host density and a small fish population size. In farmed fish, high stocking densities result in high infections (Florio et al. 2009; Ibrahim 2012). Additionally, Bagge et al. (2004) using a case of the Crucian carp Carassius carassius in ponds in Finland, demonstrated that fish population size per se, not density, determines monogenean infection levels. This is because the limited availability of hosts might constrain parasite population growth. Low infection levels could also indicate a successful host-parasite co-evolution.

In the present study, *Gyrodactylus* sp. occurred at a lower prevalence and intensity than reported in the literature. Ibrahim (2012) reported a prevalence of 10.24% of *G. cichlidarum* in *T. zillii* in wild fish and 12.07% in cultured fish from Lake Manzalah, Egypt. Our study found *Gyrodactylus* sp. in the gills as opposed to the body surface (Ibrahim 2012; Přikrylová *et al.* 2012). Similarly, *Gyrodactylus sturmbaueri* was reported from the gills of fish in Lake Tanganyika (Vanhove *et al.* 2011). *Gyrodactylus* spp. usually inhabit the body surface because this favors their transmission. Variations in microhabitat use are known, with some species changing microhabitats over time. For example, *G. cichlidarum* apparently migrate anteriorly from the caudal fin, ending up on the pectoral fin (Rubio-Godoy *et al.* 2012), whereas some gyrodactylids exhibit marked site specificity (topographical specialization) (Bakke *et al.* 2007). For instance, *G. turnbulli* prefers the caudal region of guppies, while *G. bullatarudis* has been found mostly on the head and mouth (Rubio-Godoy *et al.* 2012). *Gyrodactylus malalai* has been reported only from the fins of *O. niloticus* and *T. zillii* from Lake Turkana (Přikrylová *et al.* 2012). Several factors determine the microhabitat use in gyrodactylids. These include: access to resources, intra- and interspecific competition, par-

asite age, mating, transmission and host immunity (Rubio-

godoy et al. 2012). Although members of the family

Gyrodactylidae are said to be ubiquitous ectoparasites of

teleost fish (Florio et al. 2009), their reports have been rather

uncommon, and the total number of Gyrodactylus species de-

scribed from African fish is generally low. About 10 species

of the genus Gyrodactylus are known to parasitize African ci-

chlids, a small number compared with an estimated global diversity of 20,000 species (Přikrylová et al. 2012). A. macracantha was the dominant parasite infecting T. zillii in Lake Turkana both in prevalence (79.5%) and mean intensity (\pm SD) (10.3 \pm 15.3). The prevalence of A. macracantha reported in this study was higher than elsewhere. For example, Aloo (2002) found a prevalence of 10.7% of A. macracantha in T. zillii from Lake Naivasha; Florio et al. (2009) found a prevalence of 14.2% from pond- and cage-cultured O. niloticus in Kenya; Akoll et al. (2012a) found a prevalence of 38% in O. niloticus in various water bodies in Uganda, and Otachi et al. (2014) found a prevalence of 21.4% in O. leucostictus and a prevalence of 3.2% in T. zillii from Lake Naivasha, Kenya. Its high prevalence and intensity can be explained by the possible ingestion of abundant intermediate hosts (possibly the copepod, Cyclops spp.) infected with procercoids (Aloo 2002; Akoll et al. 2012a). Although the life cycle of A. macracantha has not been described (Bray 1974; Aloo 2002; Scholz et al. 2004), those of the related gryporhynchid taxa involve planktonic copepods (e.g. Eudiaptomus graciloides, Mesocyclops oithonoides, Arctodiaptomus salinus) as the first intermediate hosts, fish as the second intermediate hosts, and piscivorous birds as definitive hosts (Scholz et al. 2004). T. zillii is thought to be herbivorous, but several studies reviewed by Hickley et al. (2002) indicate that it is an omnivorous browser, which could predispose it to A. macracantha. Furthermore, the co-occurrence of what we believe to be two distinct developmental stages - merocercoids and plerocercoids - in T. zillii has not been reported previously. This co-occurrence raises new questions, particularly regarding the parasite's unknown life cycle. Several authors (Aloo 2002; Florio et al. 2009; Akoll et al. 2012a; Otachi et al. 2014) have reported A. macracantha plerocercoids encysted in the liver or intestinal wall of tilapias. To our knowledge, the only exception was in the original species description (Bray

1974), which did not explicitly mention whether the specimens were found encysted or free in the liver of T. nilotica from Sudan. This raises the questions: (i) why would A. macracantha encyst and then excyst within a single host? (ii) is there a possibility of an unknown development within T. zil*lii*, perhaps the results of some trigger mechanism? (iii) is the trigger mechanism specific for some study site? Whereas we cannot completely rule out the possibility of a continuous multiple re-infections with procercoids from preyed copepods, they are not known to have hooks as was the case with the reported merocercoids indicating a three-stage development (procercoids-merocercoids-plerocercoids) within a single intermediate host. One potential factor might be the high mean annual water temperature of Lake Turkana, which is approximately 30°C (Campbell et al. 2003). The excystment of the parasites when they transit from the fish hosts to birds is known to be triggered by, among other abiotic factors, the high body temperature of birds. Therefore, we hypothesize a scenario in which A. macracantha could develop into premature adult worms within T. zillii (considered to be second intermediate hosts), as they are also known to mature in fish-eating birds (Scholz et al. 2004).

We found two different species of acanthocephalans. Acanthogyrus sp. (P = 2.3%) and Paragorgorhynchus sp. (P =13.6%) infecting the intestinal lumen of T. zillii, albeit at low prevalence and intensities compared to the occurrence of other species in T. zillii elsewhere. For example, Bayoumy et al. (2006) reported a higher prevalence of infection by A. tilapiae (24%) in T. zillii from the Nile River at Giza Governorate, Egypt. Acanthosentis sp. has been reported in the Nile tilapia O. niloticus in Kenya at a prevalence of 7.1% (Florio et al. 2009); while Ibrahim (2012) reported a prevalence of 25.9% in the wild and 24.14 % in cultured T. zillii from Lake Manzalah, Egypt. The low infection levels we observed may indicate a low abundance of suitable intermediate hosts. A study by Cohen (1986) of the benthic community of Lake Turkana found a higher abundance of ostracods belonging to the families Cyprididae, Ilyocyprididae, Darwinulidae and Cytheridae, but no amphipods were reported, indicating their low abundance in the lake. Also, A. tilapiae is specific to the Cichlidae, whereas Paragorgorhynchus spp. are indiscriminate in their host choice (Khalil 1971). Although P. albertianum was reported in H. forskahlii (Khalil 1971) from Congo, in the present study no acanthocephalan was found infecting this host, probably due to its piscivorous feeding habit. In contrast, other studies did not find acanthocephalans in T. zillii. For example, Goselle et al. (2008) found no acanthocephalans in the 80 T. zillii examined from Lamingo dam, Plateau State, Nigeria.

Three species of crustacean parasites were recovered during this study, represented by two argulids (*Argulus monodi* and *A. fryeri*) and a lernaeid *Lernaea cyprinacea*. All three crustaceans exhibited low infection levels compared to other studies (e.g., Ibrahim 2012). Ibrahim (2012), for example, determined that *L. cyprinacea* in *T. zillii* from Lake Manzalah, Egypt, occurred at a prevalence of 14.5% in the wild and 24.7% in cultured fish and classified it as a rare parasite in that population. In contrast to our findings, however, *T. zillii* examined from Lake Naivasha, Kenya, were not infected with the crustacean parasites (Aloo 2002; Otachi *et al.* 2014).

Effect of host sex on parasite infection levels

Of the parasite taxa investigated, parasite infection levels differed significantly with host sex only for Contracaecum sp. 1 in H. forskahlii (Fisher's exact test p<0.05), with females having higher prevalence (95.5%) than males (71.4%). Our findings contrasted with those of Aloo (2002) for Contracaecum sp. in T. zillii and O. leucostictus from Lake Naivasha, Kenya where males were more heavily infected. Several theories explain such host sex differences (Poulin 1996; Zuk and McKean 1996; Klein 2000), including gender differences in fish sizes, morphology or behavior (especially during the breeding season). In T. zillii (a substrate spawner), however, both the males and females build and guard nests, thus exhibiting similar behavior. In H. forskahlii, a total spawner (isochronal), both sexes make long anadromous migrations to rivers where they lay demersal eggs with no parental care (Kolding 1989). Therefore, it is clear that in both T. zillii and H. forskahlii, males and females show the same behavior during the breeding season, hence, might have had equal chances of infection. However, there is literature indicating that there is sexual dimorphism and segregation of the sexes at different habitats and that one sex may precede the other in moving to the breeding grounds especially in H. forskahlii (Dadebo and Mengistou 2008). Therefore chance proximity and exposure may also account for some of the differences observed. Some studies have demonstrated that host sex does not influence the prevalence or intensity of other helminthes e.g. monogeneans in fish and therefore agreeing with our findings (Poulin 1996; Madanire-Moyo et al. 2010; Akoll et al. 2012b; Le Roux et al. 2011; Yamada et al. 2011; Olurin et al. 2012). For example, Olurin et al. (2012) found no relationship between parasite intensity and the sex of T. zillii from the Oshun River in south-west Nigeria.

Effects of host size on parasite infection levels

For the monogeneans, both the prevalence and mean intensities of *Annulotrema* sp. showed a positive and significant correlation with *H. forskahlii* size (Fig. 4). Similarly, the infection levels of *Cichlidogyrus* sp. showed positive significant correlations with the size of *T. zillii*. Our findings on the monogeneans are in agreement with several studies (Koskivaara *et al.* 1991; Bagge and Valtonen 1999; Akoll *et al.* 2012b; Le Roux *et al.* 2011). This is primarily due to the availability of more attachment space in larger fish (Koskivaara *et al.* 1991; Bagge and Valtonen 1999; Akoll *et al.* 2012b; Le Roux *et al.* 2011).

Whereas, *Contracaecum* sp. 1 prevalence was negatively correlated; the mean intensity was positively correlated with *H. forskahlii* size. At the same time, *Contracaecum* sp. 1 infection levels showed significant positive correlations with

T. zillii size, in agreement with other studies (Aloo 2002; Goselle *et al.* 2008). The differences observed could reflect species-specific differences in migratory behavior and ontogenetic shifts in habitats and diets (Lewis 1974; Kolding 1989; Winemiller and Kelso-Winemiller 1994). Thus, *H. forskahlii* ranges further offshore with increasing size, whereas juveniles prefer shallower lake zones (Kolding 1989; Dadebo and Mengistou 2008). This means that *H. forskahlii* is maximally exposed to *Contracaecum* sp. 1 as juveniles inhabiting shallower waters, because, coincidentally, littoral zones exhibit high abundances of intermediate and definitive hosts (Akoll *et al.* 2012a). This explains the high prevalence in smaller fish. Larger fish, in turn, have higher intensities, probably because they continue to accumulate parasites over the years (Aloo 2002).

Nonetheless, the correlations of *A. macracantha* prevalence and mean intensities with *T. zillii* size (substrate spawner) were weak and contrasted with the study of Akoll *et al.* (2012a), who found positive correlations with *O. niloticus* size (mouth brooder), probably reflecting host-specific differences. In contrast to our findings, other authors found no relationships between helminth abundance and fish size (Kadlec *et al.* 2003; Ferrari-Hoeinghaus *et al.* 2006; Morenikeji and Adepeju 2009; Madanire-Moyo *et al.* 2010; Ibrahim 2012; Olurin *et al.* 2012).

We can draw cautious conclusions even though our sampling episodes were short term and restricted to two sampling periods. H. forskahlii had a depauperate parasitic community, with only two helminth parasites. The dominant parasite was an anisakid nematode Contracaecum sp. 1 (L3). The infection levels of Contracaecum sp. 1 were high, which not only raises public health concerns because some anisakid nematodes are zoonotic and aesthetic issues in fish utilization, but also the need to control this parasite. In contrast, T. zillii had a rich parasite fauna, but occurred mostly at low intensities except for A. macracantha. Host sex did not influence parasite infection levels except for Contracaecum sp. 1 in H. forskahlii. In general, female fish seemed slightly more parasitized than males. Finally, host size proved to be a very important factor in determining infection levels, to be significantly positively correlated with infection levels of most parasites, but not for the prevalence and mean intensity for A. macracantha in T. zillii or for the prevalence of Contracaecum sp. 1in H. forskahlii.

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