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FISH PARASITOLOGY - ORIGINAL PAPER

Parasite diversity of introduced fish *Lates niloticus*, *Oreochromis niloticus* and endemic *Haplochromis* spp. of Lake Victoria, Kenya

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Abstract
This study reports on the status of metazoan fish parasites in Lake Victoria following the establishment of introduced *Lates niloticus* (Latidae) and *Oreochromis niloticus* (Cichlidae) and changes in environmental quality. For this study, 412 fish specimens were examined for parasites: 103 *L. niloticus*, 165 *O. niloticus*, 82 *Haplochromis piceatus* and 62 *H. humilior* (endemic cichlids). In total, 25 parasite taxa were identified: *Lates niloticus* (6), *O. niloticus* (19) and *Haplochromis* spp. (13). The myxosporean *Henneguya ghaffari*, prevalence (P) = 79% and the monogenean *Diplectanum lacustris* (P = 34%), were the dominant parasites on *L. niloticus*. *Myxobolus* sp. (P = 44%) was dominant on *O. niloticus* while for the haplochromines, metacercariae of '*Neascus*' sp. (Diplostomidae) was dominant (P = 37%). Contrary to reports of high diversity of monogeneans on endemic species, the haplochromines harboured only *Cichlidogyrus gillardinae* (P = 6.9%). *Oreochromis niloticus* harboured seven monogenean species: *Cichlidogyrus sclerosus*, *C. halli*, *C. tilapiae*, *C. quaestio*, *Scutogyrus longicornis*, *Gyrodactylus cichlidarum* and *G. malalai*—they appear to have been co-introduced with the fish. *Cichlidogyrus gillardinae*, *C. quaestio*, *G. malalai* and the acanthocephalan *Acanthogyrus* (*Acathosentis*) *tilapiae* are recorded for the first time in Lake Victoria, representing new geographical records. Presence of *A.* (*A*) *tilapiae* in *Haplochromis* spp. indicates possible spillover from *O. niloticus*. Low prevalence and diversity of monogeneans, crustaceans and glochidia on the fish corresponded with increased pollution in the lake. Overall, changing environmental conditions and introductions of fish species have contributed to parasite community changes in Lake Victoria.

Keywords Cichlids · Nile perch · Co-introduction · Environmental pollution · Parasite community changes

Introduction

Lake Victoria, situated in East Africa, is the largest lake in Africa and the most important freshwater resource for the local population (Crul 1995). The lake serves more than 30 million people and is used as a source of food, domestic drinking water, irrigation, transport and recreation and as a repository for domestic and industrial waste (Okungu et al. 2005). The ecology of the lake has been greatly influenced by pollution, overfishing and introduction of fish species such as Nile perch *Lates niloticus* (L. 1758) and cichlid tilapiines *Oreochromis niloticus* (L. 1758), *Oreochromis leucostictus* (Trewavas, 1933), *Coptodon zillii* (Gervais, 1848) and *Tilapia rendalii* (Boulenger, 1897) (Ogutu-Ohwayo 1990; Kitchell et al. 1997; Njiru et al. 2005). These species were introduced into the lake in the 1950s and caused the reduction in the stocks of several native cichlids through ecological competition from the tilapiines and predation by *L. niloticus* (Ogutu-Ohwayo 1990). *Lates niloticus* and *O. niloticus* are two of the three dominant fish species in Lake Victoria and the silver cyprinid *Rastrineobola argentea* (Pellegrin, 1904) being the other (Mkuna and Baiyegunhi 2019). These species contribute approximately 139,500 tonnes accounting for at least 75% of Kenya's total fish production for internal and external markets (FAO 2015).

Fish parasites represent a major part of aquatic biodiversity (Palm 2011) and can cause alterations in the physiology and behaviour of their hosts (Lafferty 2008). Furthermore, some

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fish parasites are agents of zoonotic diseases worldwide (Paperna 1996; Toledo and Esteban 2016). A variety of investigations have been carried out on parasite fauna of fishes from inland water bodies of East Africa. A total of 21 host species have been studied from the genera *Oreochromis*, *Coptodon*, *Haplochromis*, *Astatotilapia*, *Tylochromis*, *Boulengerochromis*, *Gnathochromis*, *Limnochromis*, *Pundamila*, *Hydrocynus*, *Clarias*, *Clariallabes*, *Bagrus* and *Lates*, and from them at least 17 monogeneans, 5 crustaceans and 32 endohelminths have been recorded (Thurston and Paperna 1969; Paperna 1996; Maan et al. 2008; Mwita and Nkwengulila 2008; Akoll et al. 2012a; Muterezi-Bukinga et al. 2012; Mwita 2014; Otachi et al. 2014, 2015; Kmentová et al. 2016). However, there is still very little data on parasite fauna of *L. niloticus* and cichlids from Lake Victoria.

Extensive anthropogenic activities subject inland surface waters to various stressors that directly affect the species composition and diversity of aquatic biota (Palm 2011). In Lake Victoria, anthropogenic pressures have led to eutrophication and heavy metal pollution (Kitchell et al. 1997; Outa et al. 2020). Sensitivity to pollutants and environmental disturbances makes many parasite taxa useful indicators of environmental health and anthropogenic impact (Sures et al. 2017). Studies have shown that different fish parasites respond differently to pollution. Gilbert and Avenant-Oldewage (2017) noted that endoparasite infection levels become elevated while ectoparasites decline in relation to poorer water quality conditions. According to Sures (2001), ectoparasitic monogeneans have direct contact with the surrounding environment and have short life cycles, hence can react immediately on changes in environmental factors. For parasites with heteroxenous life cycles, perturbations may lead to the loss of the appropriate intermediate hosts, triggering the disappearance of some species under polluted conditions (Overstreet 1997). In Lake Victoria, there is no information on how environmental degradation and the introductions of new fish species may have influenced the diversity of parasites of the native species. According to Chalkowski et al. (2018), invasive species can influence the ecosystem through the introduction of parasites from the native range or by amplifying parasites already existing in the introduced range. In the case of Lake Victoria, precautions were not taken against transferring parasites from Lake Albert during the introduction of *L. niloticus* (Thurston and Paperna 1969).

The current study aimed to investigate the diversity of fish parasites in the Kenyan part of Lake Victoria following the establishment of introduced species and changes in the physico-chemical environment. We focussed on metazoan parasites of the dominant introduced commercially important fish species *L. niloticus* and *O. niloticus* and endemic cichlids *Haplochromis piceatus* Greenwood & Gee, 1969 and *Haplochromis humilior* (Boulenger, 1911). The study was conducted at five sampling areas faced by different levels of anthropogenic pressures. *O. niloticus* and the haplochromines are inshore dwelling (Witte and Oijen 1990; Njiru et al. 2005)—their parasite fauna therefore helps to demonstrate the potential influence of environmental conditions on parasite prevalence and species richness.

Material and methods

Study area descriptions

Lake Victoria, shared by Kenya (6%), Uganda (43%) and Tanzania (51%), is the world's largest tropical lake and the second largest freshwater lake in the world, covering a total of 68,000 km^2 with a mean depth of 40 m, and maximum depth of 79 m (Okungu et al. 2005). It is located along the equator between 0.5° N and 2.5° S and 32° E and 34° E at an elevation of 1134 m above sea level. The main river inlet (Kagera) drains through Burundi, Rwanda, Tanzania and Uganda, while the main river outlet is the Nile (Crul 1995). The Kenyan part of Lake Victoria lies just south of the equator between 0° 6′ S to 0° 32′ S and 34° 13′ E to 34° 52′ E. It covers an area of about 4200 km^2 of which 1400 km^2 comprises the Winam Gulf (Crul 1995). The lake's basin has an equatorial climate, with temperatures ranging between 20 and 35 °C, and the mean annual rainfall ranges between 1000 mm and 1500 mm (Okungu et al. 2005).

As indicated in Fig. 1, the study was carried out in the Kenyan part of the lake: four regions in Winam Gulf; Asembo Bay (AB), Kisumu City harbour (KM), Kisumu City outskirt (KK), Mainuga (MN) and a site in the main lake body; Rusinga Island (RS). The sites at the gulf suffer from various anthropogenic pressures such as agricultural, industrial and municipal wastewater discharge. Outa et al. (2020) reported that contamination of water with dissolved organic carbon, bound nitrogen, potassium, iron and nickel, and sediments with chromium, copper, zinc, silver, cadmium and lead was particularly pronounced around Kisumu City and Mainuga. The site at RS had the least direct anthropogenic influence and had the lowest levels of electrical conductivity, dissolved organic carbon, bound nitrogen, iron, zinc, silver and lead (Outa et al. 2020). The five sampling stations were therefore dissimilar in their physico-chemical characteristics.

Sampling and parasitological analyses

Sampling in the lake was conducted over two periods: September 2016–July 2017 and October–December 2018. Fish were collected with gill nets and transported alive in aerated tanks with lake water to the Maseno University laboratory. The fish were euthanized by cervical dislocation and their total length was measured. Identification of cichlids using

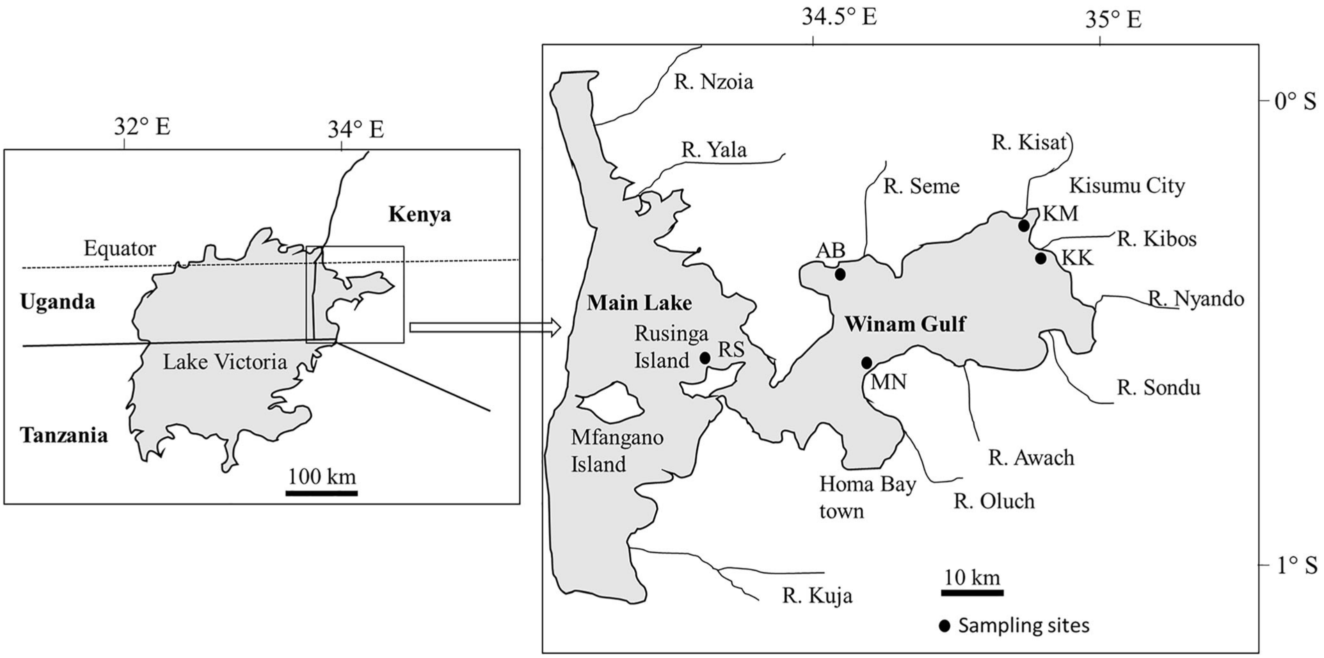

Fig. 1 Map of Lake Victoria, indicating the study area, and the sampling sites. Modified from Okungu et al. (2005). AB, Asembo Bay (0° 11′ 10.2″ S 34° 23′ 35.8″ E); KM, Kisumu City (0° 05′ 16.4″ S 34° 44′ 59.0″ E); KK, Kisumu City outskirt (0° 09′ 41.4″ S 34° 44′ 51.6″ E); MN, Mainuga (0° 20′ 48.7″ S 34° 29′ 09.1″ E); and RS, Rusinga Island (0° 23′ 20.5″ S 34° 11′ 48.9″ E)

morphological features followed the identification keys as per Witte and van Oijen (1990). The fish were dissected and inspected for parasites according to standard procedures (Schäperclaus 1990). The skin, fins, gills, eyes, buccal and abdominal cavities were inspected for parasites. Freshly detached gill filaments were placed in petri dishes with freshwater while the eyes, digestive tract, liver, kidneys, gonads, heart, spleen and swim bladder were placed into separate petri dishes with saline water and were examined under a dissecting microscope for parasites. Isolated parasites were mounted on temporary slides and studied under higher magnifications (× 40–× 400). Myxosporean cysts were detached from the gills, placed on a slide and crushed under a cover slip to study the spore morphology. Monogeneans were detached from the gills using fine forceps and transferred individually with a needle into a drop of ammonium picrate-glycerine on a slide, flattened with a cover slip and sealed with clear nail polish. Digenean metacercariae were excysted by breaking the cysts gently using dissection needles and examined alive. Prior to fixation, acanthocephalans were transferred to freshwater until the proboscis everted (Palm 2011). Isolated parasite specimens were fixed in 4% formaldehyde and 80% ethanol respectively for further analyses at the University of Johannesburg, South Africa, and University of Vienna, Austria. Morphological identification of parasites was to the lowest taxa possible using identification keys as per (Douëllou 1993; Paperna 1996; Ali 1999; Přikrylová et al. 2012; Otachi et al. 2015). The parasite specimens have been preserved in ethanol for deposition at the National Museum (NMK) parasitology collections Nairobi, Kenya, and with the Natural History Museum of Vienna, Austria.

Molecular identification of selected monogenean specimens was done at the University of Johannesburg, South Africa. The specimens preserved in 80% ethanol were rehydrated, dried and genomic DNA extracted using a DNeasy Blood and Tissue kit following the manufacturer's protocols. Fragments of the ITS1 and 28S rDNA were amplified using primer sets S1 (5′- ATTCCGATAACGAA CGAGACT -3′; Sinnappah et al. (2001)) and ITS3A (5′- GAGCCGAGTGATCCACC -3′; Matějusová et al. (2001)), and C1 (5′- ACCCGCTGAATTTAAGCAT -3′; Hassouna et al. (1984)) and D2 (5′- TCCGTGTTTCAAGACGG -3′, Hassouna et al. (1984)) respectively. PCR profiles for the amplification of the ITS1 and 28S fragments were those of Matějusová et al. (2001) and Jovelin and Justine (2001), respectively. Successful amplification was verified in 1% GelRed (Biotuim) impregnated agarose gel and amplicons sequenced using BigDye v3.1 chemistry (Applied Biosystems) following Avenant-Oldewage et al. (2014). Sequencing was performed on an ABI3730 automated sequencer (Applied Biosystems). Electropherograms were inspected and edited manually using Geneious R6 (Kearse et al. 2012). Sequences were blasted to identify the most similar sequences published in GenBank.

Statistical analyses

Prevalence and mean intensities of parasites on/in fish hosts were determined according to Rozsa et al. (2000). Measures of parasite community structure of the introduced and endemic fish species were described using the Shannon-Wiener index, Simpson's index, Margalef richness index and Berger-Parker dominance (Magurran 1988). This was applied also for the *O. niloticus* Monogenea data from study sites with different anthropogenic stressors. Further statistical analyses were done using IBM SPSS 21. Data were tested for normality of distribution using the Shapiro-Wilk test, and correlations between fish total length (TL) and the abundance of parasites were tested through non-parametric Spearman's rank correlation test.

Results

In total, 412 fish were examined: 103 *L. niloticus*, 165 *O. niloticus*, 82 *H. piceatus* and 62 *H. humilior*. The mean length and range values (in parentheses) of the fish were as follows: *L. niloticus* 27.1 (11.2–66.0 cm), *O. niloticus* 15.3 (6.7–39.8 cm), *H. piceatus* 9.5 (6.9–13.9 cm) and *H. humilior* 11.6 (8.1–15 cm). Overall, parasites were recorded in/on 88.3% of *L. niloticus*, 87.3% of *O. niloticus*, 80.5% of *H. piceatus* and 77.4% of *H. humilior*. Since the haplochromines were infected by similar parasite species at low prevalence for most of the parasites, the two species have been treated as one sample for ease of comparison with *O. niloticus* and *L. niloticus*. Table 1 provides a summary of the prevalence (P) and mean intensity (MI) of the parasites recorded from the fish. Morphological examination yielded 25 parasite species: 2 myxosporeans, 9 monogeneans, 1 cestode, 5 digeneans, 2 nematodes, 1 acanthocephalan, 3 crustaceans, 1 leech and bivalve larvae. The micrographs showing the haptoral and copulatory structures of the monogeneans are in the electronic supplementary material . Sequences generated for four monogenean species were identical with data available on GenBank for *Cichlidogyrus sclerosus* Paperna & Thurston, 1969; *C. halli* (Price & Kirk, 1967); *Gyrodactylus*

Table 1 Parasites of *L. niloticus*, *O. niloticus* and *Haplochromis* spp.: prevalence (P) and mean intensity (MI)

Parasite taxa	Location on/in host	*L. niloticus*		*O. niloticus*		*Haplochromis* spp.	
		P	MI	P	MI	P	MI
Henneguya ghaffari cysts	Gills, intestinal surface	78.6	25.7	-		-	
Myxobolus sp. cysts	Gills, intestinal surface	-		43.6	5.0	31.3	3.8
Cichlidogyrus gillardinae	Gills	-		-		6.9	2.3
Cichlidogyrus sclerosus	Gills	-		18.2	3.7	-	
Cichlidogyrus halli	Gills	-		11.5	5.1	-	
Cichlidogyrus tilapiae	Gills	-		1.21	3.0	-	
Cichlidogyrus quaestio	Gills	-		0.61	5.0	-	
Scutogyrus longicornis	Gills	-		1.82	4. 7	-	
Gyrodactylus cichlidarum	Gills, skin	-		5.66	27.7	-	
Gyrodactylus malalai	Gills, skin	-		3.77	34.0	-	
Diplectanum lacustris	Gills	34.0	14.7	-		-	
Amirthalingamia macracantha	Intestine	-		31.5	5.1	12.5	2.0
Tylodelphis sp.	Vitreous humour	-		5.45	4.1	6.3	6.1
Diplostomidae '*Neascus*' sp.	Underneath skin, gills,	-		18.2	6.4	34.7	14
Diplostomidae '*Diplostomulum*' sp.	Liver, mesenteries	-		1.21	1.0	16.0	2.5
Clinostomum tilapiae	Buccal cavity, eye socket	-		2.0	2.0	-	-
Euclinostomum heterostomum	Buccal cavity	-		2.0	1.0	2.08	2.0
Contracaecum multipapillatum	Intestine, mesenteries	1.9	5.0	1.21	2.0	8.3	1.7
Cucullanus sp.	Intestine	3.9	1.8	-		-	
Acanthogyrus (*Acanthosentis*) *tilapiae*	Intestine	-		26.7	2.0	20.8	2.27
Bivalve glochidia	Gills	1.9	2.0	9.09	4.2	2.1	3.67
Leeches (Glossiphoniidae)	Skin	2.9	1.0	6.06	1.2	0.69	1.0
Lamproglena monodi	Gills	-		-		1.4	1.0
Ergasilus lamellifer	Gills	-		0.61	1.0	-	
Argulus sp.	Gills	-		-		0.69	2.0
Intestinal inflammation	Intestine	-		1.82	1.0	-	

Dash (-), parasite not detected

Table 2 Parasite diversity of fish species

Diversity parameter	*L. niloticus.*	*O. niloticus*	*Haplochromis* spp.
Number of fish (*n*)	103	165	144
Number of parasite taxa	6	19	13
Margalef richness index	0.63	2.47	1.72
Shannon-Wiener index	0.54	2.26	1.44
Simpson's index	0.69	0.14	0.38
Berger-Parker dominance index	0.81	0.26	0.59
Dominant taxon	*H. ghaffari*	*Myxobolus* sp.	'*Neascus*' sp.

malalai Přikrylová, 2012 and *G. cichlidarum* Paperna, 1968. Three specimens of *O. niloticus* had intestinal tumour-like proliferation (approx. 3 cm thick, extending about 8 cm along the intestine): the cause of the aberration is unknown.

Lates niloticus had the lowest species diversity of parasites—two and four times lower than the haplochromines and *O. niloticus* respectively (Margalef richness index; Shannon-Wiener index) (Table 2). Myxosporea was the dominant taxon with *Henneguya ghaffari* Ali, 1999 (cysts, P = 78.6%, MI = 25.7) from *L. niloticus* and *Myxobolus* sp. cysts from *O. niloticus* (P = 43.6%, MI = 5.0). For the haplochromines, '*Neascus*' sp. metacercariae (Diplostomidae) was the most dominant taxon (P = 34.7%, MI = 14.0). The monogenean species richness and infection levels varied between the fish species. *L. niloticus* harboured *Diplectanum lacustris* Thurston & Paperna, 1969 (P = 34.0%, MI = 14.7). Similarly, *Haplochromis* spp. harboured one species: *Cichlidogyrus gillardinae* Muterezi-Bukinga, 2012 (P = 6.9%, MI = 2.3). On the other hand, *O. niloticus* harboured 7 monogenean species dominated by *C. sclerosus* (P = 18.2%, MI = 3.7) and *C. halli* (P = 11.5%, MI = 5.1). The other species were *C. tilapiae* Paperna, 1960; *C. quaestio* Douëllou, 1993; *Scutogyrus longicornis* (Paperna & Thurston, 1969); *G. cichlidarum* and *G. malalai*. In *L. niloticus*, the levels of infection by parasites correlated with the total length (TL) of the fish. The number of *H. ghaffari* cysts showed a significant negative correlation with the TL of fish (Spearman's test, $r_s = -0.271$, $p = 0.005$), while the number of *D. lacustris* was positively correlated with the TL of fish (Spearman's test, $r_s = 0.743$, $p < 0.0001$). Figure 2 shows the P and MI of *H. ghaffari* and *D. lacustris* on small fish (TL = 11–29 cm) and large fish (TL = 30–66 cm). Variation was observed in the prevalence, species richness and diversity of monogeneans on *O. niloticus* from the study sites (Table 3). The overall prevalence of monogeneans was highest in the fish from RS (50.0%), followed by AB (47.2%), MN (29.2%), KM (23.7%) and KK (23.1%). The lowest species richness and diversity of parasites occurred on fish from KM, KK and MN. Out of the 7 species, *C. sclerosus* and *C. halli* were the only species recorded on fish from all the five study sites. The two species were the only species recorded on fish from KM, KK and MN. Similarly, variation was observed in the P and MI of bivalve glochidia on the cichlids from the study sites. Glochidia were not found on *O. niloticus* and *Haplochromis* spp. from KM, KK and MN. P and MI were highest on fish from RS: P = 28.6%, MI = 4.5 for *Haplochromis* spp. and P = 41.7%, MI = 5.1 for *O. niloticus*. At AB, P and MI were as follows: P = 1.41%, MI = 1.0 for *Haplochromis* spp. and P = 3.78%, MI = 4.0 for *O. niloticus*.

Discussion

The current study shows a clear distinction in species richness and diversity of parasites between the fish taxa examined, with *L. niloticus* being the most depauperate in parasites. Data from literature indicates that a cumulative figure of 13 metazoan parasite species have been reported from native populations of *L. niloticus* (Thurston and Paperna 1969; Emere 2000; Al-Bassel 2003; Moravec et al. 2009). In the current study, only six species were recorded. Leeches and bivalve larvae (glochidia) are reported for the first time. Paperna (1996) reported occurrence of these parasites on cihilds and other fish species. Compared to their data, the detection of these parasites on the cichlids and *L. niloticus* in the current study indicates expansion of host range. Even though glochidia occurred on all the fish species examined, the parasite occurred with higher prevalence and intensity on Nile tilapia, suggesting that this is the most preferred host. In Lake Victoria, we

Table 3 Prevalence and diversity of Monogenea on *O. niloticus* from the study sites.

	AB	KM	KK	MN	RS
Number of fish (*n*)	53	38	26	24	24
Number of parasite taxa	6	2	2	2	4
Overall parasite prevalence	47.2	23.7	23.1	29.2	50.0
Margalef richness index	0.93	0.26	0.30	0.36	0.71
Shannon-Wiener index	1.315	0.693	0.601	0.377	0.93
Simpson's index	0.30	0.49	0.57	0.77	0.50

AB, Asembo Bay; *KM*, Kisumu City; *KK*, Kisumu City outskirt; *MN*, Mainuga; *RS*, Rusinga Island

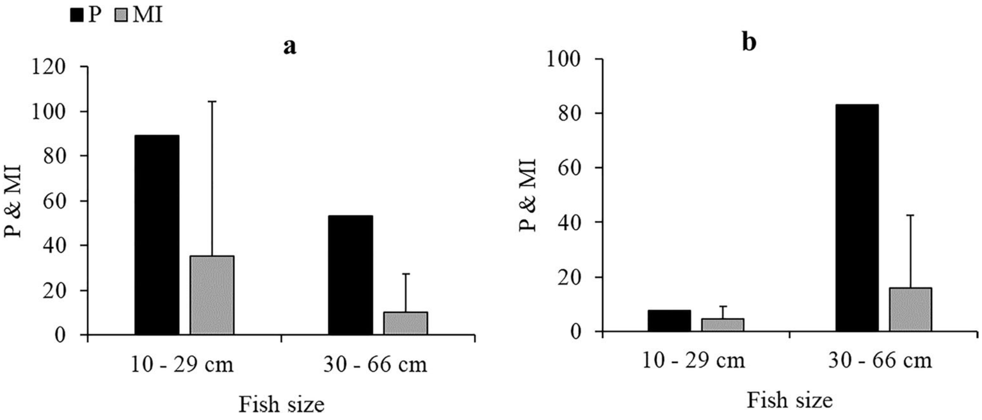

Fig. 2 Prevalence (P) and mean intensity (MI) of *H. ghaffari* (**a**) and *D. lacustris* (**b**) on *L. niloticus* of different sizes (total lengths). Small fish, 11–29 cm, *n* = 67; large fish, 30–66, *n* = 36 cm). Error bars (mean ± SD)

observed abundant adults of unionid species *Coelatura alluaudi*, *C. cridlandi*, *C. hauttecoeuri* and *Nitia monceti* and mutelid *Mutela bourguignati* at Rusinga Island; it is however not known which species produced the larvae that were parasitic on the fish.

The occurrence of myxosporean *H. ghaffari*, the monogenean *D. lacustris* and nematodes *Contracaecum multipapillatum* and *Cucullanus* sp. on/in *L. niloticus* in the current study corresponds with other studies. *Henneguya ghaffari* was the most dominant parasite of *L. niloticus* in the current study and has been reported on the same species in Lake Wadi El-Raiyan, Egypt (Ali 1999), and Nile River at Beni-Suef, Egypt (Abdel-Baki et al. 2014). The frequent occurrence of *H. ghaffari* on *L. niloticus* in the entire host range may confirm introduction of the parasite with the fish. However, the high prevalence of *H. ghaffari* in the current study compared to records from Egypt (Ali 1999, Abdel-Baki et al. 2014) could be attributed to climatic conditions. Indeed, low prevalence of *H. ghaffari* was recorded in winter season compared to summer periods (Abdel-Baki et al. 2014). Therefore, the tropical climatic conditions of Lake Victoria characterized with high temperature supported rapid reproduction of the myxosporean. The high prevalence of *H. ghaffari* poses a health threat to *L. niloticus* owing to intense pathological effects of myxosporeans on the hosts (Paperna 1996; Sitja-Bobadilla 2008; Abdel-Baki et al. 2014). Nonetheless, we recommend further studies on the histopathological changes associated with *H. ghaffari* on Nile perch in Lake Victoria. The results of our study showed that the prevalence and abundance of *H. ghaffari* were higher in smaller fish and declined in larger fish. The reason for this trend is not clear and should be the subject of further investigations. We propose that ontogenic shifts in habitat preference and increased immunity in older fish might in part explain this correlation. Juvenile fish predominantly inhabit shallower littoral zones (Schofield and Chapman 1999) where the sediment dwelling oligochaetes harbouring infective actinospores occur (Paperna 1996). The young fish are therefore exposed to infection to a greater extent. Studies have shown that fish develop an immune response to myxosporeans (Sitja-Bobadilla 2008): the infection levels are therefore likely to decline in bigger fish, with little chance of re-infection in the pelagic zone. Like *H. ghaffari*, *D. lacustris* specifically infects *L. niloticus*. This agrees with studies from the Nile River and Lake Albert which are natural habitats of the fish (Thurston and Paperna 1969) and from Northern Lake Victoria where the fish was previously introduced (Paperna 1996). The frequent occurrence of *D. lacustris* on *L. niloticus* throughout the host range also confirms introduction of the parasite with the fish. The results of this study revealed high prevalence and mean intensities of *D. lacustris* in bigger fish compared to smaller fish. According to Otachi et al. (2015), availability of more attachment space is the primary reason for high abundance of monogeneans on bigger fishes.

A variety of parasite taxa reported from *L. niloticus* in other studies were not observed in the current study. According to Thurston and Paperna (1969), crustaceans *Ergasilus kandti* Douwe, 1912 and *Dolops ranarum* (Stuhlmann, 1892) occurred in high prevalence on *L. niloticus* from Lake Albert and Lake Victoria respectively. Crustaceans were not reported on *L. niloticus* in the current study. Lafferty (2008) noted that environmental degradation may lead to a decline in the abundance of parasites over time. According to Pane et al. (2008), copepod egg production and survival of nauplii are greatly reduced by heavy metal pollution. In the last three decades, the Kenyan part of Lake Victoria has experienced increased pollution pressure by eutrophication and heavy metals (Outa et al. 2020): this can in part explain the absence of ectoparasitic crustaceans which are directly affected by the water quality. Similarly, the acanthocephalan *Neoechorhynchus* sp., cestode *Proteocephalus* sp. and nematode *Camallanus* sp. from River Kaduna, Nigeria (Emere 2000); acanthocephalan *Paragorgorhynchus chariensis* Troncy, 1970 from the Nile and Lake Nasser, Egypt (Al-Bassel 2003); and nematodes *Philometra lati* and *P. spiriformis* from Lake Turkana, Kenya (Moravec et al. 2009), were not observed in the current study.

There are no comprehensive records of the parasite fauna of the cichlids from Lake Victoria, especially comparing the native and the introduced species. Results of the current study revealed that introduced *O. niloticus* harboured a high parasite diversity compared to native haplochromines. The high species richness could be linked to the restriction of seven monogeneans, namely *Cichlidogyrus sclerosus*, *C. halli*, *C. tilapiae*, *C. quaestio*, *Scutogyrus longicornis*, *Gyrodactylus cichlidarum* and *G. malalai* on *O. niloticus*. Like in our study, the monogeneans *Cichlidogyrus sclerosus*, *C. halli*, *C. tilapiae*, *C. quaestio* and *Scutogyrus longicornis* have been recorded on tilapiine cichlids from other inland water bodies across the world, e.g. Lake Kariba, Zimbabwe (Douëllou 1993); Lake Naivasha, Kenya (Rindoria et al. 2016); Okinawa, Japan (Maneepitaksanti and Nagasawa 2012); and Malaysia (Lim et al. 2016). Similarly, *Gyrodactylus cichlidarum* and *G. malalai* were reported on *O. niloticus* and *C. zilli* from Lake Turkana (Přikrylová et al. 2012). The current study is the first report of *C. quaestio* and *G. malalai* on fish from Lake Victoria basin. Moreover, this is the second report of *G. malalai* following its identification as a new species in 2012. Even though there has been a paucity of data on monogeneans of the cichlids of Lake Victoria, the current findings point to possible co-introductions of these monogeneans with *O. niloticus* and other tilapiines over the past decades. During our study, *O. niloticus* cage cultures were observed in Winam Gulf: an indication of possible cross-infection between the cultured and wild fish. The results of the current study further revealed that the prevalence of Monogenea on *O. niloticus* was significantly lower at the sites near Kisumu City (KM and KK) and Mainuga (MN) compared to Asembo Bay (AB) and Rusinga Island (RS). Moreover, only two species (*C. sclerosus* and *C. halli*) were recorded on fish from KM, KK and MN. Compared with the AB and RS sites, the water around Kisumu City and MN had higher values for electrical conductivity and concentrations of dissolved components: organic carbon and bound nitrogen, as well as major and most trace elements (Outa et al. 2020). It is likely that the poor environmental conditions at the sites near Kisumu City and MN contributed to the low prevalence and number of species. Our study agrees with the findings from other investigations which concluded that the inhibitive quality of the physico-chemical environment correlates with decline in monogenean species (Paperna 1996; Sures 2001; Gilbert and Avenant-Oldewage 2017) with one or two species dominating (Paperna 1996). Moreover, the dominance of *C. sclerosus* on *Oreochromis* spp. from various habitats has been reported in other studies in Africa (e.g. Paperna 1996; Akoll et al. 2012a). This trend has been reported in cultured fish as well. In studies of fish ponds with contrasting physico-chemical conditions in Kenya, Ojwala et al. (2018) recorded *C. sclerosus* and *C. halli* as the dominating monogeneans on *O. niloticus*. It can be concluded that these species have lower sensitivity to a wide range of environmental variations compared to the other monogeneans in the current study.

The endemic *Haplochromis* spp. had only one monogenean species and its morphology matched *C. gillardinae*. This species had been reported only on haplochromines *Astatotilapia burtoni* (Günther, 1894) and *Gnathochromis permaxillaris* (David, 1936) from Lake Tanganyika (Kmentová et al. 2016; Muterezi-Bukinga et al. 2012). The low prevalence (P = 6.9%) and low species richness of monogeneans on the haplochromines in the current study is a strong contrast to reports from other studies. Maan et al. (2008) reported unidentified species of *Cichlidogyrus* from haplochromines *Pundamila pundamila* (P = 93%) and *P. nyererei* (P = 88%) from Speke Gulf of Lake Victoria, Tanzania. In Lake Tanganyika, at least 22 *Cichlidogyrus* spp. have been reported from different cichlids (Kmentová et al. 2016). Moreover, our finding contrasts reports of higher species richness and abundance in native compared to introduced cichlids, e.g. in Panama (Roche et al. 2010) and Brazil (Bittencourt et al. 2014). We propose that poor water quality on the Kenyan part of Lake Victoria coupled with host specificity of monogeneans and/or resistance of these endemic cichlids to the introduced parasites might explain the low prevalence and diversity recorded on these fish. Moreover, the haplochromines almost completely disappeared in the 1980s as a result of predation from the introduced *L. niloticus* (Witte and Oijen 1990; Witte et al. 2007). It has been observed that such a reduction in fish population can lead to the disappearance of its parasites (Lafferty 2008).

Regarding crustaceans, *Argulus africanus* Thiele, 1900; *Ergasilus lamellifer* Fryer, 1961; *Lamproglena monodi* Capart, 1944; *Lernaea barnimiana* (Hartmann, 1870); and *Lernaea cyprinacea* L. 1758 were common on native tilapiines and haplochromines from Lake Victoria and Nile River (Fryer 1961). Similarly, high prevalence (14–100%) of *L. monodi* and *E. lamellifer* was recorded on haplochromines *P. pundamila* and *P. nyererei* from Speke Gulf, Tanzania (Maan et al. 2008). In the current study, *Argulus* sp., *L. monodi* (on *Haplochromis* spp.) and *E. lamellifer* (*O. niloticus*) were recorded, at very low prevalence (< 2%) and mean intensities. We suggest that pollution in the Kenyan part of Lake Victoria may be a contributing factor since studies have shown that exposure to contaminated environments can result in a decline of ectoparasite infections on fish (Gilbert and Avenant-Oldewage 2017).

According to Mbahinzireki's study from 1984 (Witte and van Oijen 1990), endoparasitic nematode larvae (*Contracaecum* sp. and *Eustrongylides* sp.), trematode (*Allocreadium mazoenzis* Beverley-Burton, 1962) and protocephalid cestodes were recorded in various species of *Haplochromis* from Mwanza Gulf of Lake Victoria, Tanzania. In the current study, *Eustrongylides* sp., *A. mazoenzis* and protocephalid cestode were not observed.

Nematode *C. multipapillatum* and cestode *Amirthalingamia macracantha* (Joyeux & Baer, 1935) recorded in the current study are widespread in cultured and wild cichlids across eastern Africa (Akoll et al. 2012c; Otachi et al. 2014; Otachi et al. 2015; Ojwala et al. 2018). The five digenean taxa (black spot '*Neascus*' sp., '*Diplostomulum*' sp., *Clinostomum tilapiae*, *Tylodelphys* sp., *Euclinostomum heterostomum* Rudolphi, 1809) reported in the current study correspond with reports from studies across Africa. Paperna (1996) noted that water bodies from the Jordan system throughout the Nile basin to the Rift Valley lakes share common snail species and similar fish (cichlids, *Barbus* and *Clarias*) which become infected by the same digeneans: black spot '*Neascus*', *Clinostomum* spp., *Centrocestus* spp., *Phagicola* spp. and *E. heterostomum*. Black spot Diplostomidae sp. was the dominant digenean in the current study. Similar metacercariae have been reported in cichlids *P. pundamila* and *P. nyererei* from Speke Gulf, Tanzania (Maan et al. 2008), and *Tilapia sparrmanii* from South Africa (Hoogendoorn et al. 2019). Diplostomidae ('*Diplostomulum*' sp.) recovered from liver and mesenteries of the cichlids in our study resemble *Diplostomulum* sp.3 recorded on liver of *Barbus humilis* from Lake Tana, Ethiopia (Zhokhov 2012). The morphology and molecular characterization of the metacercariae recovered from the current study is subject to further detailed analyses in comparison with existing literature data. Future work should also target the adult worms which according to Paperna (1996), inhabit herons, cormorants and pelicans. *A.* (*A.*) *tilapiae* is endemic to the Nile River (Amin et al. 2008). According to Paperna (1996), it was widespread in tropical African cichlids including from Madagascar where it was introduced, but was not observed in East Africa, the Sudan Nile or South Africa. It has been reported in farmed *O. niloticus* from Uganda (Akoll et al. 2012b) and Kenya (Ojwala et al. 2018). The current study is the first record of this species in Lake Victoria, and more specifically in *Haplochromis* spp. This indicates that the parasite was co-introduced with *O. niloticus* and eventually established itself on the haplochromines as well. This demonstrates the spillover concept where parasites of the invasive species infect new hosts (Chalkowski et al. 2018).

Conclusion

In total, 25 parasite taxa were recovered from the examined fish. *L. niloticus* is depauperate in parasite taxa compared to the cichlid fishes and to records from its native habitats. The findings indicate that the myxosporean *H. ghaffari* and monogenean *D. lacustris* were co-introduced with *L. niloticus* while leeches and glochidia have expanded the host range to *L. niloticus*. This study shows that the monogeneans are host specific with the highest diversity occurring on the exotic *O. niloticus*. *Cichlidogyrus sclerosus*, *C. halli*, *C. tilapiae*, *C. quaestio*, *Scutogyrus longicornis*, *Gyrodactylus cichlidarum* and *G. malalai* appear to have been co-introduced with *O. niloticus*. Spillover from *O. niloticus* is the possible explanation for presence of *Acanthogyrus* (*Acanthosentis*) *tilapiae* in *Haplochromis* spp. Finally, this study indicates that increased pollution corresponds with a decline of monogeneans, glochidia and crustaceans.

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Author contribution All authors contributed to the study conception and design. Material preparation, sample collection, dissection of fish specimen, isolation of parasite specimen and data analysis were performed by James Omondi Outa and Franz Jirsa. Molecular methodology and analyses were performed by Quinton M Dos Santos and Annemariè Avenant-Oldewage. The first draft of the manuscript was written by James Omondi Outa, and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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Declarations

Conflict of interest The authors declare no competing interests.

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