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ORIGINAL PAPER

Infection patterns of Nile tilapia (*Oreochromis niloticus* L.) by two helminth species with contrasting life styles

Peter Akoll · Robert Konecny · Wilson W. Mwanja · Fritz Schiemer

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Abstract The larval stages of *Bolbophorus* sp. (digenean) and *Amirthalingamia macracantha* (cestode) are frequently reported in *Oreochromis niloticus* in Uganda. Little, however, is known about their infection patterns. This study examined the influence of habitat type, host size, and sex and weather patterns on the parasite populations in Uganda. A total of 650 fish were collected between January and November 2008 from a reservoir, cages, fishponds and a stream. The prevalence and intensity of *A. macracantha* and the prevalence of *Bolbophorus* sp. differed across the water bodies reflecting the effect of habitat characteristics on parasite transmission. Host sex did not significantly influence the infection patterns, although female fish were slightly more parasitized than male and sexually undifferentiated individuals. The fish size was positively correlated with helminth infections demonstrating accumulation and prolonged exposure of larger (older) fish to the parasites. The metacercariae population did not vary significantly across months, while monthly *A. macracantha* infection fluctuated markedly. With regard to rain seasons, higher prevalence and intensity of *A. macracantha* were recorded in wet season. For *Bolbophorus* sp., only the prevalence varied with seasons, with higher prevalence recorded in the dry season than in wet season. Generally, *Bolbophorus* sp. responded weakly to changes in water body, host sex and size and weather patterns. Rainfall appears to be an essential cue for coracidia hatching.

Introduction

Nile tilapia (*Oreochromis niloticus*) is indigenous to the Nile basin and plays an important role in aquaculture globally. The species was selected for the BOMOSA cage culture project trials (Integrating BOMOSA cage fish-farming systems in reservoirs, ponds and temporary water bodies in Eastern Africa, http://www.bomosa.org) in Kenya, Uganda and Ethiopia. The project, funded by the European Union under the Sixth Framework Programme, was designed to pilot the production fish in rural farming systems by economically integrating aquaculture with agriculture using small easy-to-use net cages for fish farming in marginal water bodies. Recognizing that disease outbreaks significantly constrain aquaculture production, parasitological investigations on wild and cultured *O. niloticus* along with surveys in aquaculture facilities around the Lake Victoria crescent were undertaken. The surveys revealed that *Bolbophorus* sp. (digenean), *Acanthogyrus* (*Acanthosentis*) tilapiae (acanthocephalan) and *Amirthalingamia macracantha* (cestode) dominated the heteroxenous parasite communities (Florio et al. 2009; Akoll et al. 2011a). *Bolbophorus* sp. is transmitted to fish via a free-living infectious stage, the cercariae (active transmission). On

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P. Akoll
Department of Zoology, Makerere University,
P.O. Box 7062, Kampala, Uganda

P. Akoll (✉) · R. Konecny · F. Schiemer
Department of Freshwater Ecology, University of Vienna,
Althanstrasse 14,
1090 Vienna, Austria
e-mail: pakoll@zoology.mak.ac.ug

R. Konecny
Environment Agency Austria,
Spittelauer Lände 5,
1090 Vienna, Austria

W. W. Mwanja
Department of Fisheries Resources,
Ministry of Agriculture Animal Industry and Fisheries,
P.O. Box 4, Entebbe, Uganda

the other hand, *A.* (*A.*) *tilapiae* and *A. macracantha* reach fish through ingestion of infected intermediate hosts, trophically (passive transmission). Owing to different transmission strategies to fish, these parasites may respond differently to changes in biotic and abiotic factors and pose different risks to cultured hosts (Akoll et al. in prep). This requires a better understanding of the effect of farming systems, host factors and weather patterns on the infection dynamics of *Bolbophorus* sp. and *A. macracantha* in *O. niloticus*.

The adult *Bolbophorus* sp. worms occur in birds and have larval stages in fish (the second intermediate host). This parasite use snails of the genus *Bulinus* as the first intermediate host (Paperna 1996). The detailed life cycle and population dynamics studies in tropical regions are scanty. The closely related species, *Bolbophorus levantinus*, also infecting *O. niloticus*, have cercariae released from the snail 7 weeks postinfection at a temperature of 22–24°C (Paperna 1996). The parasites form a black coloration on the skin and muscles because the cysts accumulate the melanophores or other skin chromatophores, causing “black spot” syndrome. During the present study, the metacercariae were found encysted in high numbers mainly on the skin and in muscles, and occasionally on the gills, of *O. niloticus*. Pathological studies showed that *Bolbophorus* sp. and close relatives, such as *P. minimum* and *B. levantinus*, can cause severe fish deformities and mortalities under high intensities (Hoffman and Hutcheson 1970; Mitchell et al. 1982; Paperna 1996). In aquaculture facilities, where high host density can increase transmission and proliferation, the parasite may cause significant economic losses.

The plerocercoids of *A. macracantha* (order: Cyclophyllidea, family: Gryporhynchidea) have been reported, so far, in two cichlids: *Tilapia zillii* and *O. niloticus* (Aloo 2002; Scholz et al. 2004). The parasite is transmitted to fish through zooplankton, presumably crustaceans of the genus *Cyclops* (Scholz et al. 2004). The adult stages occur in birds (Bray 1974; Scholz et al. 2004). The plerocercoids may cause inflammation of the intestinal walls, infiltration of macrophages, haemorrhage, hypertrophy and general mechanical erosion of the lumen (Florio et al. 2009). No information is available regarding the transmission requirements (Scholz et al. 2004). Infection dynamics study by Aloo (2002) in Lake Naivasha reported an increase in the prevalence and intensity of *A. macracantha* in *T. zillii* with fish size. Male fish were more heavily infected than females. No seasonal changes in infection level were observed.

Studies on the spatial and temporal patterns of helminths have revealed considerable variation in prevalence and intensity among host populations within and across habitats and with time (Esch and Fernändez 1993; Hartvigsen and Halvorsen, 1994; Poulin and Valtonen, 2002). In space, helminths infection levels are linked to differences in the physicochemical characteristics of the water bodies (Hartvigsen and Halvorsen 1994; Ondrackova et al. 2004a). Habitat characteristics, such as waterbed morphology and type, gradient of the banks, the surrounding vegetation cover and the size of the water body, influence the establishment and interaction between hosts and, consequently, the transmission and proliferation of parasites (Ondrackova et al. 2004a; Dejen et al. 2006). The creation of artificial water bodies such as ponds and reservoirs may create favourable habitats that promote parasite proliferation (Lafferty and Kuris, 1999; Morley 2007). Despite the importance of artificial water systems in fish production (used as fishponds and for cage farming), their effects on the establishment and transmission of *Bolbophorus* sp. and *A. macracantha* species may negatively impact aquaculture development. This calls for determining the influence of water bodies used for fish farming on helminth infections.

Within the fish population, host-related factors (internal environmental factors) including sex, size, genetic make-up and immunity influence helminth infections (Esch and Fernändez 1993). Of these, host size and sex contribute significantly to differences in infection levels (Zuk and McKean 1996; Poulin 1996, 1999). Dietary requirements, food intake rates as well as habitat choice and use are greatly influenced by host sex and size. Consequently, the exposure and susceptibility of the fish to helminth infections differ between gender and across size classes (Zuk and McKean 1996; Poulin 1996, 1999; Reimchen and Nosil 2001). Accordingly, the sex- and size-related differences in the habitat use, feeding and diet of *O. niloticus* (Philippart and Ruwet 1982) will undoubtedly affect the abundance of the metacercariae and plerocercoids.

On a temporal scale, helminth infection patterns are related to seasonal changes in rainfall and temperature (Chubb 1979, 1980; Pech et al. 2010). Although larval stages have a long life in the fish, changes in parasite intensity and prevalence are linked to the seasonal release and hatching of cercariae and coracidia, respectively (Chubb 1979, 1980). The cercariae release and recruitment are triggered temperature (Lyholt and Buchmann 1996; Ondrackova et al. 2004b; Jiménez-García and Vidal-Martínez 2005, Hudson et al. 2006). Receding of water systems during dry season results in habitat shrinking, and this may increase the proximity of hosts to cercariae. In cestodes, temperature also controls the hatching of coracidia (Scholz et al. 2004) and increases the uptake of infected intermediate hosts (Hanzelova and Gerdeaux 2003; Wicht et al. 2009). Meanwhile, precipitation and the associated hydrodynamic changes may disrupt parasite transmission, thereby changing the infection patterns (Vincent and Font 2003; Jiménez-García and Vidal-Martínez 2005; Pech et al. 2010). In tropical regions, data on the seasonal occurrence of helminths in fish are scarce. The existing information is inconsistent. Some studies found no seasonality in parasite populations (Aloo 2002; Vincent and

Font 2003). Other studies reported apparent seasonal variations in parasite abundance associated with rainfall (Steinauer and Font 2003; Jiménez-García and Vidal-Martínez 2005; Dejen et al. 2006). Such inconsistent information hampers developing sustainable disease management plans for aquaculture systems.

The present study investigated parasites over an 11-month period to examine the influence of water body, host size, and sex and weather patterns on the infection of *Bolbophorus* sp. and *A. macracantha*. The objectives of the study are fourfold. (i) To assess the influence of different water bodies on the occurrence of *Bolbophorus* sp. and *A. macracantha* by comparing their prevalence and intensities: We expect variation in helminth infection because of differences in water body size, littoral development and management activities. (ii) To examine the influence of host sex on helminth infection levels: Based on the differences in habitat use and feeding rate, we expect male fish to have significantly higher parasite numbers and prevalence than female and sexually undifferentiated fish. (iii) To determine the relationship between host size and the intensity and prevalence of the two species: Helminth larval stages in the fish cavity cannot leave the host until the host is preyed upon or dies; they will therefore accumulate in the host following successive infections (Esch and Fernändez 1993). Accordingly, numbers of helminth individuals and prevalence will increase with host total length. (iv) To examine the influence of weather patterns (temperature and rainfall) on the intensity and prevalence of *Bolbophorus* sp. and *A. macracantha* in *O. niloticus*: In Uganda, the gradual and narrow temperature variation (Table 1) would support continuous multiplication and recruitment of parasites. Nonetheless, the hydrodynamic events, such as discharge and water velocity that are associated with rainfall intensities, may interrupt parasite transmission pathways. Consequently, we expect that monthly and seasonal variation in helminth intensity and prevalence will be negatively correlated with rainfall intensity.

Materials and methods

Study site and sample collection

The study was conducted in Uganda, a tropical country lying astride the Equator between latitudes and longitudes 4.2°N, 1.5°S and 28°E, 35°W, respectively. Specimens of *O. niloticus* for parasitological examination were collected from the BOMOSA fish cage culture experimental system and Ndolwa Dam (in which cages were installed) in Lake Kyoga basin, Kamuli District (1.21°N 33.10°E) and from ponds and their water source, Kajjansi stream at Kajjansi Aquaculture Research Development Centre (Kajjansi ADRC) in Lake Victoria basin, Wakiso District (0.13°N 32.32°E; Fig. 1). Ndolwa Dam, herein called the reservoir, is an artificial water body that was constructed in the 1950s across a wetland to supply water for livestock and domestic use. The reservoir has an area of about 3 ha, with one quarter of the surface area covered with macrophytes. The entire reservoir is surrounded by semiarid and wetland-type vegetation. This vegetation hosts a wide range of birds including several fish-eating species such as ibes (*Plegadis* spp.) hammerkop (*Scopus umbretta*) cormorants, purple and grey heron (*Ardea* spp.) grebes, the great and cattle egrets, water ducks and kingfishers (*Ceryle* spp.). The

Table 1 The monthly and annual rainfall intensity (mm) and average air temperature (minimum and maximum, °C) in Lake Victoria and Kyoga basins for the year 2008

Month	L. Victoria Basin		L. Kyoga Basin	
	Ave. temperature±SD (min–max)	Total rainfall	Ave. temperature±SD (min–max)	Total rainfall
January	23.2±4.2 (19.2–27.2)	126.1	24.1±8.1 (16.1–32.0)	31.5
February	22.7±4.1 (18.8–26.5)	95.6	24.5±7.8 (17.1–31.9)	42.7
March	22.4±4.2 (18.5–26.3)	322.1	23.5±7.9 (16.0–31.0)	168.3
April	22.3±4.2 (18.6–26.1)	380.7	23.1±6.7 (16.8–29.6)	265.3
May	22.5±3.7 (18.9–26.0)	197.3	23.2±6.5 (15.9–28.8)	180.0
June	22.1±3.9 (18.5–25.7)	129.2	22.4±6.6 (16.8–29.4)	40.9
July	21.9±4.3 (17.8–26.1)	28.4	21.8±6.5 (15.6–28.1)	137.3
August	22.0±4.2 (18.0–26.1)	46.5	22.6±6.6 (16.1–29.0)	141.4
September	22.6±4.6 (18.2–27.1)	71.8	23.0±6.8 (16.4–29.6)	121.7
October	22.2±4.1 (18.3–26.1)	182.4	22.9±6.6 (16.4–29.3)	238.7
November	22.4±4.1 (18.8–26.7)	80.4	22.8±7.4 (15.6–30.0)	57.9
December	22.8±4.1 (18.9–26.7)	46.2	23.4±8.6 (15.0–31.8)	23.0
Annual	22.5±4.1 (18.6–26.4)	1,711.6	23.1±7.2 (16.2–30.0)	1,448.8

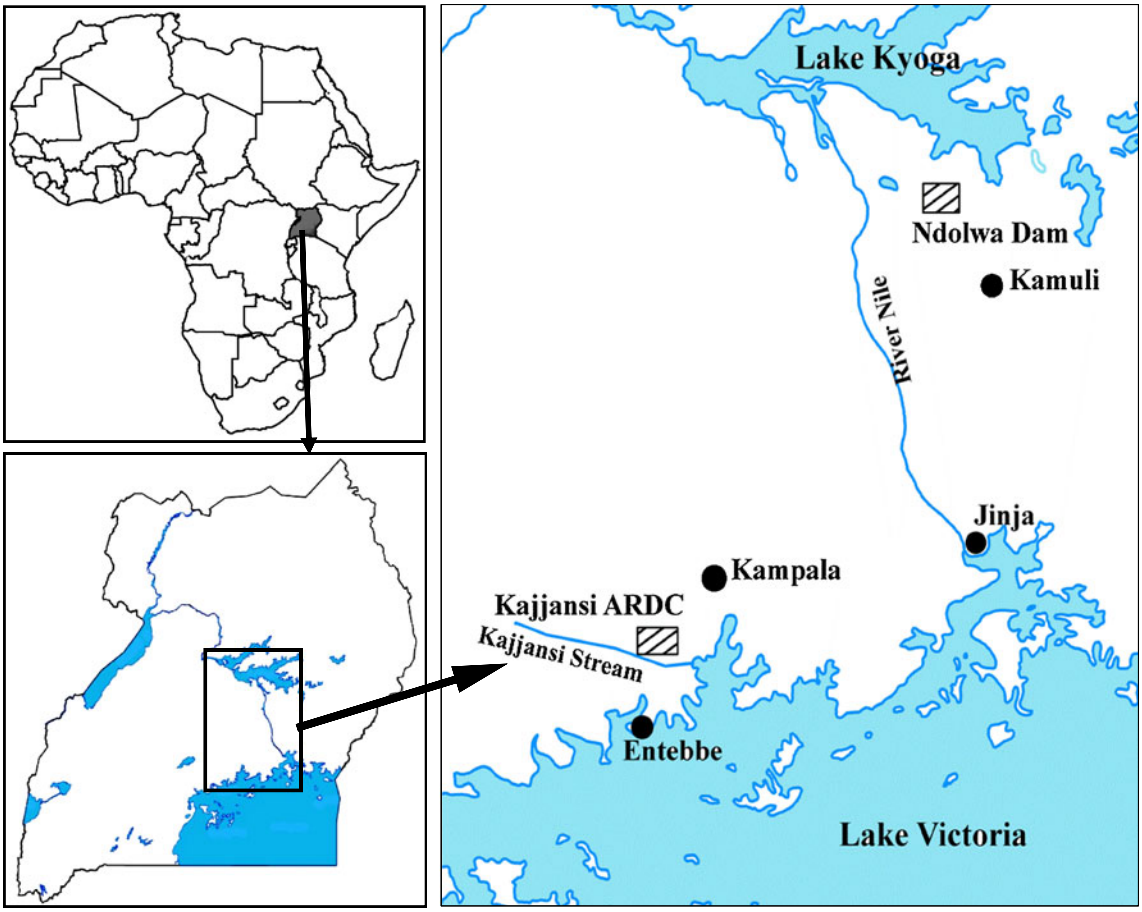

Fig. 1 Map of Uganda showing the sampling sites (▨): Ndolwa Dam, the reservoir (and cages therein) and Kajjansi ARDC, the location of ponds and the stream

maximum depth is 4 m, with gently sloping banks. The reservoir intermittently floods, after heavy rains. From the reservoir, 10 to 30 fish were caught monthly using gillnets, seine nets and hooks for 11 months. Cage system consisting of nine units, with dimensions of $1 \times 1 \times 1.5$ m^3, placed at least 20 m from the nearest shore at a depth of 4 m. In January 2008, each cage was stocked with 150–200 fish of average weight of 20 g and screened monthly until November 2008. A random sample of up to 20 fish composed of fish from different cage units were collected using scoop nets. With regard to ponds, the pond sizes ranged from 450 to 1,200 m^2; and received water from Kajjansi stream. The ponds were 0.5 m deep at the water inlet and approximately 1–1.5 m deep at the outlet. The dykes were planted with various types of grass, although during some periods they were overgrown by other macrophytes. Birds, especially hammerkop (*S. umbretta*) cormorants, purple and grey heron (*Ardea* spp.), the great and cattle egrets, grebes, water ducks, kingfishers (*Ceryle* spp.) and Marabou storks frequently visited the ponds. These bird populations increased tremendously after rain events. Kajjansi stream is approximately 1–1.5 m wide, draining from the wetland located 1 km away from the farm. It has low gradient and slow-flowing water during dry season. However in rain periods, the stream flow is shifted. Like for cages and reservoir, fish samples were collected monthly for a period January–November 2008 except June. During each sampling, random sample of up to 30 fish were collected from each site using gillnets, seine nets, hooks and scoop nets. The entire sample consisted of 650 fish with total lengths ranging from 2 to 34 cm (mean 13.2 cm) and weight ranging from 0.5 to 470 g (mean 58.4 g).

Daily water temperature measurements were not possible and are replaced in this study with air temperature based on the strong linear relationship with water temperature (McCombie 1959; Stefan and Preud'homme 1993; Livingstone and Lotter 1998). Daily rainfall and temperature at the respective sites were obtained from the Department of Meteorology, Uganda. From the data collected, seasons were categorised as "dry season" (rainfall intensity< 150 mm/month) and "wet season" (rainfall intensity≥ 150 mm/month; Table 1).

Examination of fish for parasites

The fish were transported alive in their original water to the laboratory. In the laboratory, a parasitological examination for helminths was performed, which included total length measurement and screening the skin and gills for parasites. After sacrificing the fish by severing the spinal cord anterior to the dorsal fin, they were dissected to determine sex and, thereafter, all internal organs examined for endohelminths under a light microscope. Finally, the fish muscles were trimmed carefully to expose any embedded parasite cysts. Observed parasites were isolated, counted, fixed in 70% alcohol and sent to the Department of Veterinary, Public Health and Animal Pathology, Faculty of Veterinary Medicine, University of Bologna, Italy, for identification.

Data analysis

In order to determine the changes in parasite populations and the proportion of infected hosts, the mean intensity and prevalence, respectively, for each helminth species were used and calculated according to Bush et al. (1997). The preliminary analyses showed that the monthly sex and size infection patterns were similar across water bodies. Accordingly, further analyses were performed on pooled data from cages, reservoir, ponds and stream. General linear model, using analysis of covariance with Bonferroni post hoc test was used to control the effect size and sex. Linear regression analysis was used to explore the effect of site, host sex and size and rainfall on parasite intensity and prevalence. The intensities and prevalence data of *Bolbophorus* sp. and *A. macracantha* were log transformed to approximate normal distribution for parametric tests. The relationship between fish length classes and the number of parasites on individual hosts was determined using Spearman's correlation coefficient. Monthly parasite intensity approximated parametric data after the natural logarithm transformation $(x+1)$ while Kruskal–Wallis (*H*-test) was used to test for variations in the prevalence of the parasites across the monthly samplings. The parasite intensities and prevalence for the two seasons (dry and wet seasons) were compared using a *t*-test and Mann–Whitney (*U*) test, respectively. All the statistical analyses were performed using SPSS for Windows, and graphical representations were drawn in Sigma Plot (Systat). The level of significance in statistical tests was set at $p=0.05$.

Results

Of the 650 fish, 348 (53.5%) were infected with the two helminths (intensity of 15.1±29.9 parasite/fish). Species specific results shows that 75 (11.7%) and 247 (38.0%) of the fish were infected with *Bolbophorus* sp. metacercariae (digenean) and *A. macracantha* plerocercoids (cestode), respectively. The mean intensities of metacercariae and plerocercoids were 2.6±3.7 and 18.7±31.0 parasites/fish, respectively. With regard to habitat type, the prevalence of the *Bolbophorus* sp. metacercariae differed significantly among sites (ANOVA, $p<0.05$; Fig. 2a). The metacercariae occurred in 2 out of 213 fish (0.9%) from the cages, 47 of 165 (28.5%) from the reservoir, 21 of 119 (17.6%) from the stream and 6 of 153 (3.9%) fish from the ponds. The intensity of the metacercariae did not differ across habitats (ANOVA, $p>0.05$; Fig. 2b). The intensities of *Bolbophorus* sp. among the infected fish from the cages, reservoir, stream and ponds were 1.0±0.0, 2.3±0.7, 3.7±2.6 and 1.6±0.9 parasites/fish, respectively. Overall, linear regression analysis showed that habitat characteristics offered in different water bodies did not significantly affect *Bolbophorus* sp. intensity but did increase the number of hosts exposed to the cercariae (Table 2). For *A. macracantha* plerocercoids, the prevalence and intensity significantly differed across water bodies (*H*-test $p<0.05$; Fig. 2a and b). The mean intensity and prevalence in caged fish was 2±1.4 (1.9%), 4.4±0.8 (46.0%) in the reservoir-dwelling hosts, 15.3±2.9 (53.8%) from the stream and 31.0±4.2 (77.8%) in pond-raised fish. Corresponding to the differences in the prevalence and intensities, linear regression analysis showed that habitat types played an important role in altering the exposure and intake of *A. macracantha* infected first intermediate hosts (Table 2).

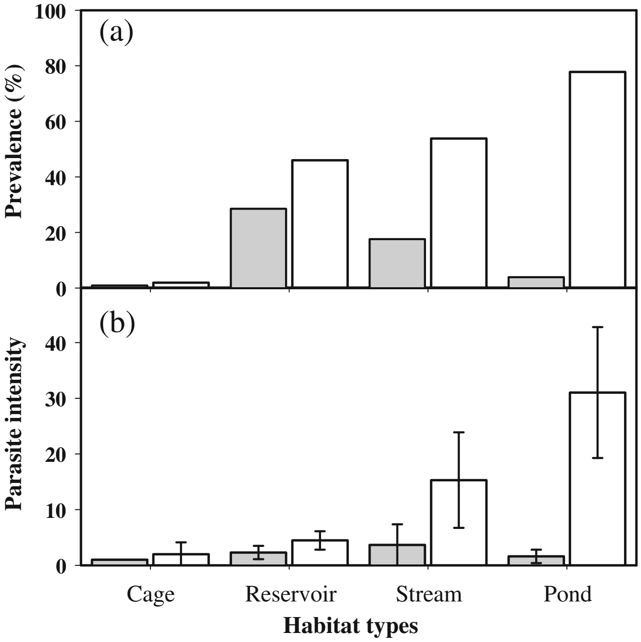

Fig. 2 The prevalence (**a**) and mean intensity±SD (**b**) of *Bolbophorus* sp. (*grey*) and *Amirthalingamia macracantha* (*open*) in *Oreochromis niloticus* from the different habitat types

Table 2 Linear regression analysis examining the effects of water body, host sex and length, temperature and rainfall on intensity and prevalence of *Bolbophorus* sp. and *A. macracantha* in *O. niloticus*

Factor	*Bolbophorus* sp.		*A. macracantha*	
	Intensity (*p* value)	Prevalence (%, *p* value)	Intensity (p value)	Prevalence (%, *p* value)
Water body	0.17 (0.20)	0.12 (0.03)	0.08 (0.30)	0.07 (0.21)
Host sex	−0.16 (0.31)	−0.12 (0.04)	−0.11 (0.15)	−0.03 (0.56)
Host size (cm)	0.04 (0.78)	0.02 (0.70)	0.13 (0.06)	0.13 (0.03)
Temperature (°C)	0.29 (0.04)	0.01 (0.90)	−0.15 (0.04)	−0.06 (0.30)
Rainfall (mm)	0.08 (0.56)	−0.12 (0.02)	0.13 (0.04)	0.16 (0.01)

The overall intensities and prevalence of *Bolbophorus* sp. and *A. macracantha* were not dependent on host's sex (male versus female versus sexually undifferentiated fish; Table 2). Although not significant, the overall parasitism in female fish (80.4%, 20.2±13.9 parasite/fish) was slightly higher than in male (78.2%, 18.7±12.8 parasite/fish) and sexually undifferentiated individuals (63.0%, 9.0±1.6 parasites/fish; Fig. 3). Considering parasite species separately, the results showed that the prevalence of *Bolbophorus* sp. was higher in females (26.8%) than in males (16.8%) and sexually undifferentiated fish specimens (11.0%). The intensity in female fish (2.7±3.5) did not differ from that in males (3.1±4.6) or sexually undifferentiated individuals (1.4±0.5; ANOVA, $p>0.05$). The regression model shows that sex did not significantly influence the intensity of the parasite. However, sex differences did influence the number of hosts exposed to the cercariae. The prevalence of metacercariae in sexually undifferentiated individuals was significantly lower than in male and female fish (Table 2, Fig. 3a). With regard to the cestode, the proportion of infected individuals did not differ in any of the three groups: the prevalence in female, male and sexually undifferentiated fish was 63.9%, 59.4% and 52.0%, respectively (Fig. 3a). The intensity of plerocercoids in females (22.7±36.9) was not significantly different from that in males (21.6±33.3; *H*-test, $p>0.05$; Fig. 3b). However, the plerocercoid intensity in both sexes was higher than in sexually undifferentiated individuals (9.7±15.6; *H*-test, $p<0.05$; Fig. 3b). The regression model revealed no significant influence of sex on cestode intensity and prevalence (Table 2).

The intensity and prevalence of *Bolbophorus* sp. and that of *A. macracantha* generally increased with fish size (Fig. 4). The change in infection parameters was more pronounced in the trophically transmitted cestode. The

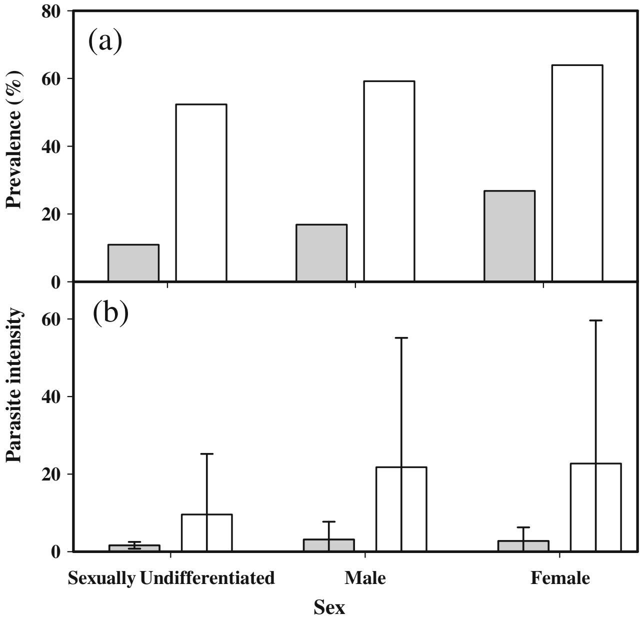

Fig. 3 The prevalence (**a**) and mean intensity±SD (**b**) of *Bolbophorus* sp. (*grey*) and *A. macracantha* (*open*) in sexually undifferentiated, male and female *O. niloticus* individuals

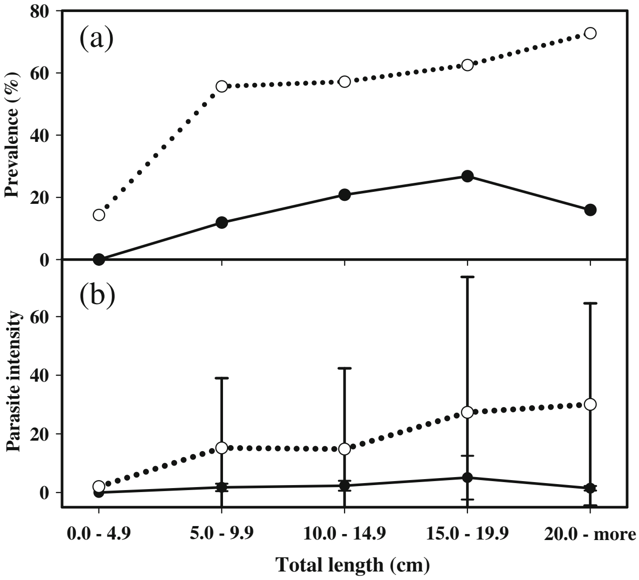

Fig. 4 The prevalence (**a**) and mean intensity±SD (**b**) of *Bolbophorus* sp. (___) and *A. macracantha* (− − −) in difference sizes of *O. niloticus* specimens examined

regression analysis showed that larger animals did not have significantly more metacercariae and/or prevalence. In contrast, the plerocercoid intensity and prevalence increased with the fish size (Table 2).

The monthly occurrence of *Bolbophorus* sp. metacercariae did not vary significantly during the study period (Fig. 5). Nonetheless, a relatively high intensity was recorded in January, and a relatively high prevalence in June, both corresponding with low rainfall. The regression analysis in Table 2 showed that the intensity of metacercariae in infected hosts increased significantly with temperature. In contrast, temperature did not significantly increase the proportion of infected hosts. The *A. macracantha* plerocercoids showed pronounced monthly fluctuations in prevalence and intensity during the study (Fig. 5). The intensity and prevalence were high in months with heavy rainfall. Moreover, the linear regression analysis showed that the population of plerocercoids and prevalence significantly increased with rainfall. Temperature, however, had a negative impact on parasite numbers but did not change the exposure to the infected intermediate hosts (Table 2).

With regard to season, the intensity and prevalence of the two helminths is shown in Fig. 6. The overall intensity of *Bolbophorus* sp. did not differ between seasons (*t*-test, $p=0.505$). The mean intensities in dry and wet seasons were 2.8±4.8 and 2.3±2.2 parasite/fish, respectively. Metacercariae prevalence during the dry season, however, was 29.7%, significantly higher than the 13.6% recorded during the wet season (*t*-test, $p=0.002$). The overall seasonal plerocercoid prevalence and intensity were significantly higher during the wet than dry season (*t*-test, $p=0.02$ and $p=0.01$, respectively). In the wet season, the prevalence was 54.4% compared to 45.1% in the dry season. Similarly, the intensity in the wet season was 13.0±6.2 parasites/fish versus 6.5±5.6 parasites/fish in the dry season. Similar trends for the intensity and prevalence of *Bolbophorus* sp. (Fig. 6a) and *A. macracantha* (Fig. 6b) were recorded in different habitat types.

Discussion

Helminths often show considerable variation in parasite prevalence and intensity among host populations within and across habitats and time (Chubb 1979, 1980; Esch and Fernändez 1993; Hartvigsen and Halvorsen 1994; Poulin

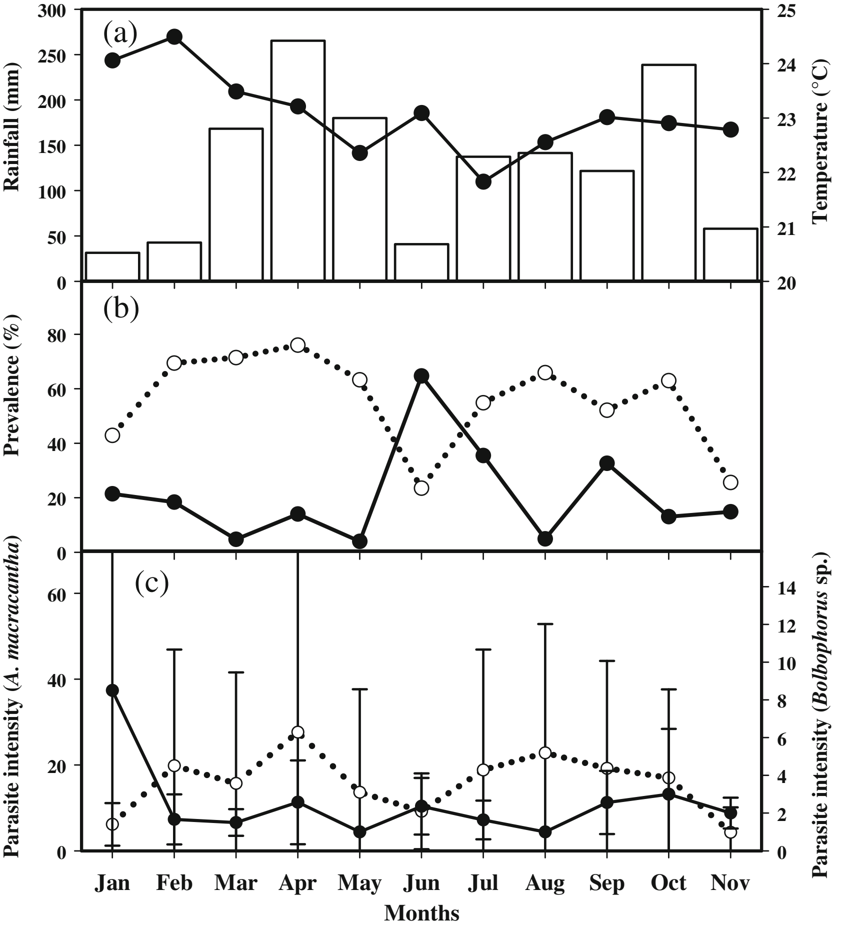

Fig. 5 **a** Monthly rainfall and temperature intensities, **b** the prevalence and **c** the mean intensity±SD of *Bolbophorus* sp. (___) and *A. macracantha* (− − −) infesting *O. niloticus* in Uganda

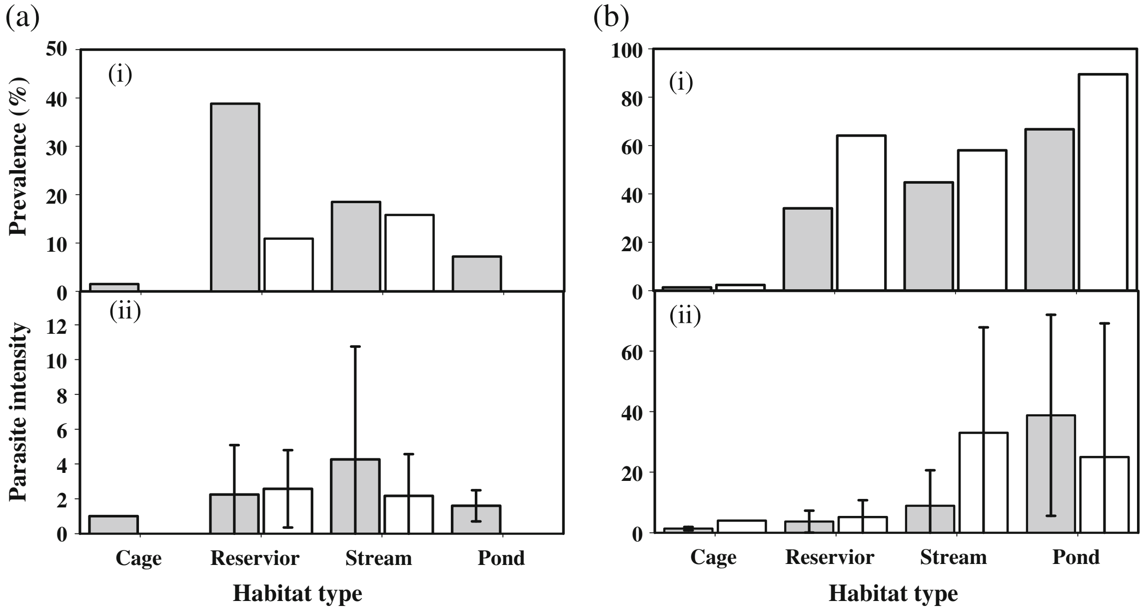

Fig. 6 The prevalence (**i**) and mean intensity±SD (**ii**) of *Bolbophorus* sp. (**a**) and *A. macracantha* (**b**) in dry (*grey*) and wet (*open*) seasons in *O. niloticus* in Uganda

and Valtonen 2002). These variations in infection levels have been related to several factors including habitat characteristics, host sex and size, and the seasonal changes in temperature and rainfall patterns. This study examined the spatial and temporal population dynamics of the metacercariae of *Bolbophorus* sp. (digenean) and the plerocercoids of *A. macracantha* (cestode) with respect to water body, host sex, size and weather patterns. The overall, the results of the present study revealed that the degree of influence of these factors on the parasite population was species specific.

With regard to the type of water body, the prevalence of *Bolbophorus* sp. was affected significantly by the water body characteristics and not the intensity of the parasite. This indicates that habitat characteristics increased the exposure of the hosts to infection and not the numbers of cercariae reaching the host. High prevalence was recorded in the reservoir-dwelling fish, moderate prevalence among the stream-dwelling hosts and low prevalence in ponds. Correspondingly, the parasite intensity was also low in ponds, though not different from other sites. The increased exposure to cercariae in the reservoir reflects a strong interaction between the different hosts and supported by the prevailing habitat characteristics (Ondrackova et al. 2004a). Thus, the gentle gradient of the reservoir banks and presence of macrophytes provided optimal conditions for the establishment and survival of snails (Brown 1994). Such gentle sloping and vegetated characteristics of water banks are also preferred natural habitats for *O. niloticus*, particularly for spawning (Philippart and Ruwet 1982). Because fish are present and the water is shallow, fish-eating birds are also usually abundant in such habitats. As such, these conditions provided a platform for intensive interaction and promote parasite transmission. In ponds, the low prevalence could be attributed to the farm husbandry such as occasional dredging, flashing and slashing of the dykes: this probably reduces the snails, the intermediate hosts for the digenean. For *A. macracantha*, regression analysis showed that habitats in the water bodies studied increased the exposure to and the intake of the infected intermediate hosts. This corresponds to significant differences in the prevalence and intensity of the cestode among the water bodies. This suggests that *O. niloticus* feeding behaviour and habitat choice as well as the interaction between hosts were significantly altered by these habitat characteristics. The relatively high intensity and prevalence in ponds can be attributed to the small size and shallow depth of the system as well as to high host density. This probably increased the proximity to infected plankton. At the same time, the relatively low prevalence and intensity in the stream were attributed to the flushing out of infected intermediate host individuals by the stream currents (van Oosterhout et al. 2007). The low infections in cages suggest that, although fish were ingesting nature food (such as zooplankton), the contribution could be low due to supplementary feeding. This reduced the intake of infected intermediate hosts. Overall, the water body characteristics did affect parasite establishment or transmission of helminths, and the magnitude of influence was species-specific, which supported earlier results by Lafferty and Kuris (1999) and Morley (2007). This highlights the differences in parasite response to host habitat change (Lafferty and Kuris 1999; Marcogliese 2001; Lafferty 2008).

Contrary to our expectation that males will be highly parasitized, infection patterns did not vary significantly between fish sexes. We anticipated that because mature male *O. niloticus* establish and guard spawning areas (Philippart and Ruwet 1982), then this territorial behaviour will expose male individuals to cercariae released within its proximity more than female and sexually undifferentiated individuals. This was not the case, probably because of the temporary confinement of females for at least 1 to 2 weeks during incubation of eggs and protection of the fry (Philippart and Ruwet 1982); this may have equally increased their exposure to cercarial infections. Moreover, during mouth-brooding, females reduce their feeding rate, thus reducing the intake of procercoid-infected intermediate hosts. Concurrently, continuous feeding and prolonged exposure of males would result in high numbers of plerocercoids. This situation, however, did not increase the *A. macracantha* infections in males than female individuals as expected. Perhaps this reflects the increased feeding rate of females after the incubation period to compensate for the energy loss, offsetting the reduced parasite intake during the brooding period. Therefore, similarity in parasitism among the sexes could be explained by small differences in behaviour with regard to habitat use and diet intake rate. Overall, the lack of significant differences in infection level between fish sexes is similar to previous studies with other fish species (Pennycuick 1971; González and Acuña 2000). Our findings contrast to those studies of Zuk and McKean (1996), Poulin (1996), Reimchen and Nosil (2001) and Aloo (2002), who reported that male individuals are highly susceptible to parasites because of differential exposure to parasites related to sex-specific feeding and habitat use strategies (Zuk and McKean 1996, Poulin 1996; Reimchen and Nosil 2001). In the present waters, the sex-related behaviour change in *O. niloticus* appears to be too short-lived to significantly alter exposure to heteroxenous helminths. Compared to monoxenous species, the change in habitat use of sexes plays an important role in influencing infections (Akoll et al. 2011b).

Consistent with our expectation, host size influenced the parasite population and prevalence. We found positive correlations between the helminth infections and total length. The significance, however, was parasite species-specific. The host length was significantly correlated with *A. macracantha* and not with *Bolbophorus* sp. As reported in various studies from other species, larger fish harboured more endohelminths than smaller ones (Bell and Burt 1991; Poulin 1999; González and Acuña 2000; Fellis and Esch 2004; Dejen et al. 2006). The positive correlation is explained by parasite accumulation in larger fish due to prolonged exposure and ontogenetic habitat and feeding shifts (Esch and Fernändez 1993; Paperna 1996; Marcogliese 2002). The prey size and diet of *O. niloticus* changes, although slightly, with size (Peterson et al. 2006). This increases the chances of larger fish to ingest infected intermediate hosts. Moreover, mature *O. niloticus* prefer littoral zones, particularly during the spawning period (Philippart and Ruwet 1982). Since littoral zones are areas of strongest interaction between the final hosts and first intermediate hosts, this also increases fish exposure to cercariae and infected food items. The explanation for the insignificant accumulation of *Bolbophorus* sp. metacercariae with size is probably the high mortalities and enhanced predation of heavily infected hosts (Hoffman and Hutcheson 1970; Mitchell et al. 1982).

The present study, rainfall and temperature influenced, although with varying magnitude, the helminth intensity and prevalence. For *Bolbophorus* sp., apparent rainfall-related fluctuation in prevalence of *Bolbophorus* sp. was observed (Fig. 6a(i)), with lower number of infected hosts recorded in wet season than in dry season. The intensity of the metacercariae in infected fish was, however, not significantly altered by rainfall intensity (Fig. 6a(ii)). The low prevalence of *Bolbophorus* sp. in fish collected during the rain period contrasts with the findings of Kadlec et al. (2003). These authors reported an increase in *Tylodelphys clavata* and *Diplostomum spathaceum* infections with rainfall and attributed this to the accumulation of snails after flood currents. In the present study, the decrease might be caused by a rainfall-related increase in water turbidity and cercariae drift, which interrupts parasite transmission. Although no studies have investigated the effect of turbidity on the transmission success for trematodes, rapid light attenuation associated with turbidity may reduce the strength of host shadows or increase the response to nonhost shadows, rapidly exhausting the energy reserves. At the same time, strong water currents during flooding events may drift cercariae away from potential hosts, reducing the chances of transmission. In dry periods, habitat size contraction due to shrinkage of water caused host crowding, and this increased availability and proximity of hosts to the cercariae. In addition to water shrinking in streams, low water currents minimise cercariae drift, thereby enhancing transmission (van Oosterhout et al. 2007). Whereas rainfall may have interrupted *Bolbophorus* sp. transmission, temperature is an essential cue triggering cercariae emergence from the snails (Lyholt and Buchmann 1996; Ondrackova et al. 2004b; Jiménez-García and Vidal-Martínez 2005; Hudson et al. 2006). However, the gradual and narrow variation in temperature within the current study area (Table 1) may have allowed for continuous release and recruitment of cercariae, hence the weak relationship between parasite infection and temperature. Nonetheless, long-term study is required to ascertain the contribution of temperature on seasonal occurrence of *Bolbophorus* sp.

With regard to *A. macracantha*, the plerocercoid in *O. niloticus* was positively correlated with rainfall and negatively with temperature. Both prevalence and intensity of the plerocercoids showed marked changes between seasons: high infection levels recorded in wet season (Fig. 6b). Our results are, however, contrary to findings of Dejen et al. (2006). These authors observed a decline in *Ligula intestinalis* infection and attributed this to a reduced uptake of plankton because of high turbidity. Other studies, however, have reported an insignificant effect of turbidity on fish uptake of zooplankton (De Robertis et al. 2003). Therefore, *O. niloticus*, a planktivorous fish, could have maintained zooplankton intake in both seasons. The increased intensity and prevalence during the rain season indicates the presence of high numbers of infective stages. As little information is available on the life cycle of *A. macracantha* (Scholz et al. 2004), we suggest that rainfall and the associated hydrological events, such as inundation of the shore areas, may have triggered the hatch of coracidia. During feeding, birds deposit parasite eggs along the shallow shores. As water recedes in the dry season, the drying conditions become hostile for coracidia hatching. When rainfall starts, shore inundation or freshwater inflow probably triggered the hatching of the coracidia and their ingestion by copepods. Zooplankton can increase after the onset of rainfall (Rissik et al. 2009). Thus, the synchronised hatching of the coracidia and plankton yielded the high intensity of infective stages necessary for successful transmission to fish. Meanwhile, the marked decline in plerocercoid intensity and prevalence at the onset of dry season may be attributed to bird predation of infected hosts, whose population also rapidly increased after heavy rains. Moreover, receding water again inhibits coracidia hatching, resulting in a low population of infective stages after rains. Although temperature is also an important abiotic factor triggering cestode hatching (Clarke 1954; Scholz et al. 2004) as well as increasing intake of intermediate hosts by fish (Hanzelova and Gerdeaux 2003; Wicht et al. 2009), the present study could not ascertain the magnitude of the contribution.

Like *Cichlidogyrus* spp. (Akoll et al. submitted), the intensity and prevalence of *Bolbophorus* sp. were generally less influenced by host attributes. The infection levels of this digenean appeared affected significantly by weather patterns, particularly rainfall intensity. However, the gradual and narrow variation of temperature in the study area may allow for continuous recruitment which probably masked the effect of rainfall. In contrast, the intensity and prevalence of *A. macracantha* showed a steady increase with fish size and rainfall-related fluctuations. Sex-related differential feeding and habitat choice in *O. niloticus* appear to be less important in influencing heteroxenous than monoxenous helminth infections. Generally, host behaviour changes associated with water body characteristics may alter host exposure to free-living transmitted helminths, particularly oncomiracidia and cercariae, but not the intake of trophically transmitted parasites.

From an aquaculture perspective, following reports of mortalities caused by a related species, *P. minimum* (Mitchell et al. 1982), the relatively stable population of *Bolbophorus* sp. indicates a potential risk. As such, farm management plans should be reoriented to include the impact of rain-related seasons on the occurrence of parasites, particularly with respect to intensifying the control of birds. On the other hand, the high prevalence and intensity of *A. macracantha* in ponds could be attributed to in-system source of infective stages due to increased interaction between hosts because of small size and shallowness of fish ponds. Therefore, minimising birds' access to ponds may reduce introduction of eggs. Meanwhile, following the feeding regimes to ensure satiety of fish may significantly reduce infections with trophically transmitted parasites. Furthermore, the marked decline in plerocercoid infection after the rain season was probably due to removal of infected hosts by birds, which will certainly cause economic losses to farmers. Therefore, seasonal consideration in disease control strategies is vital. Beyond recognising the information on seasonality in designing control measures, correct identification and knowledge about the detailed life cycle of parasites are essential for effectively applying ecological perspectives in parasite control. Such information is definitely wanted in Africa.

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