

On the Ecology and Host Relationships of *Acanthogyrus (Acanthosentis) tilapiae* (Acanthocephala: Quadrigyridae) from Cichlids in Lake Malawi

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ABSTRACT: About 2,000 specimens of the quadrigyrid acanthocephalan *Acanthogyrus (Acanthosentis) tilapiae* (Baylis, 1948) were collected from 9 species of cichlid fish hosts (Cichlidae: Perciformes) in 7 different sites in Lake Malawi, Africa, during September 2005. New host records are noted in 5 species, *Labeotropheus trewavasae* (Fryer), *Melanochromis vermicivorus* (Trewavas), *Nimbochromis polystigma* (Regan), *Tropheops microstoma* (Trewavas), and *Rhamphochromis* sp. (Regan). High prevalence of *A. tilapiae* was observed in all host species analyzed. The parasite manages to infect its cichlid hosts, despite their distinct trophic specializations. Nevertheless, significant variation in parasite load was detected between sympatrically occurring rock-dwelling (mbuna) cichlids, with *Pseudotropheus zebra* (Boulenger) showing the most heavy infections. In addition, significant variation in parasite burden was detected between sampling locations, but host gender and weight did not explain significant variation in the numbers of *A. tilapiae* individuals. Differential exposure to parasites and host susceptibility may explain the marked variation in parasite abundance among cichlid hosts. Worms appear to be recruited in the summer, develop and mature through the winter, and reproduce sexually in late winter and spring.

KEY WORDS: *Acanthogyrus (Acanthosentis) tilapiae*, cichlids, mbuna, Lake Malawi, prevalence, host and seasonal relationships.

Acanthogyrus (Acanthosentis) tilapiae (Baylis, 1948) is the most widely distributed species of *Acanthosentis* in Africa. It is endemic in the Nile River watershed in countries along the river's course (Amin, 2005). It has been reported from at least 30 species of cichlids and 3 species of noncichlid hosts in Tanzania, Congo, Uganda, Chad, Nigeria, Egypt, and Malawi (Amin and Hendrix, 1999). The wide distribution of *A. tilapiae* in Africa is attributed to the dispersal of the ubiquitous cichlid and its unidentified intermediate host (possibly *Cyclops* spp.) via the waterways of the Nile River (Amin, 2005). It was also reported in Madagascar by Golvan (1965), where it was introduced between 1949 and 1956 with the introduction of infected *Tilapia melanopleura* Dumeril. There are 5 other species of *Acanthosentis* in Africa, with only regional distribution in geographically distant and unrelated waters in Malawi, Morocco, Niger, Senegal, and South Africa (Amin, 2005).

The present study of about 2,000 acanthocephalans from 9 species of cichlids (Cichlidae: Perciformes) was part of a larger study on the bioecology and genetics of cichlids in Lake Malawi. Findings presented herein provide new information on the prevalence of *A. tilapiae* and its host and geographical

distribution in Lake Malawi, including new host records.

MATERIALS AND METHODS

Cichlids were captured by gill nets while scuba diving in 7 sites in Lake Malawi during September 2005: (1) Chirwa Islands (10°27'48.94"S; 34°16'35.77"E), Chilumba (19 September); (2) Domwe Island (13°58'05.43"S; 34°49'04.01"E) (6 September, 16 September); (3) Luwino Reef (10°26'17.41"S; 34°17'00.16"E) (19 September); (4) Mpanga Rocks (10°25'49.65"S; 34°16'44.64"E) (19 September); (5) Otter Point (14°02'21.33"S; 34°49'23.85"E) (2 September); (6) Thumbi West Island (14°01'22.83"S; 34°49'16.63"E) (3 September); and (7) Zimbabwe Rock (13°57'40.73"S; 34°48'08.88"E) (10 September). The species included *Labeotropheus trewavasae* (Fryer 1956) (scrapemouth mbuna), *Pseudotropheus emmiltos* (Stauffer et al. 1997) (red top), *Pseudotropheus zebra* (Boulenger 1899) (zebra mbuna), *Melanochromis vermicivorus* (Trewavas 1935) (purple mbuna), *Nimbochromis polystigma* (Regan 1922), *Protomelas taeniolatus* (Trewavas 1935) (spindle hap), *Pseudotropheus elongates* (Fryer 1956) (elongate mbuna), *Tropheops microstoma* (Trewavas 1935), and *Rhamphochromis* sp. (Regan 1922) (Table 1).

Fish were kept alive for up to 1 to 3 d before dissection. After the fish were killed with an overdose of MS222, they were weighed, measured, and sexed, and the intestines were removed and transferred to petri dishes containing 0.6% saline. Collected worms were fixed directly in 10% formalin, then later, washed in water and transferred into 70% ethanol for processing. Worms were subsequently stained in Mayer's acid carmine dehydrated in ascending concentrations of ethanol, cleared in graded terpineol–100% ethanol, and mounted in Canada balsam.

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Table 1. Cichlids from Lake Malawi collected in September 2005 and their *Acanthogyrus (Acanthosentis) tilapiae* parasites.

Fish species*	Fish examined and collection data*				Parasites	
	Infected/examined (prevalence)	Mean length (range) mm	Sex ratio M:F	Collection site†	No. (range) mean	No. studied
<i>Genyochromis mento</i>	1/1 (100)	76	0:1.0	OP	1 (2) 2.00	2
<i>Labeotropheus trewavasae</i>	5/5 (100)	92 (84–101)	?:3.0	DI	19 (1–8) 3.8	4
<i>Melanochromis vermivorus</i>	54/56 (96)	67 (47–95)	1.5:1.0	DE, TW, ZR	317 (0–26) 5.7	60
<i>Nimbochromis polystigma</i>	1/1 (100)	155	1.0:0	ZR	10 (10) 10.0	4
<i>Protomelas taeniolatus</i>	1/1 (100)	71	0:1.0	OP	1 (1) 1.0	1
<i>Pseudotropheus elongates</i>	3/3 (100)	77 (72–85)	0.5:1.0	OP, DI	38 (1–31) 12.6	4
<i>Pseudotropheus emmitos</i>	25/25 (100)	79 (58–93)	1.3:1.0	MR, LR	143 (1–15) 5.7	40
<i>Pseudotropheus zebra</i>	123/124 (99)	88 (53–108)	1.4:1.0	TW, DI, ZR, MR, C	1,425 (0–54) 11.5	92
<i>Tropheops microstoma</i>	3/3 (100)	82 (64–110)	3.0:0	OP, ZR	4 (1–2) 1.3	4
Total	215/219 (98)				1,959 (0–54) 9.1	211

* Additionally, 6 worms were collected and studied from 1 individual of *Ramphochromis* sp.

† C, Chirwa Island; DI, Domwe Island; LR, Luwino Reef; MR, Mpanga (MP) Rocks; OP, Otter Point; TW, Thumbi West Island; and ZR, Zimbawee Rock.

Specimens from *P. zebra* are deposited in the U.S. National Parasite Collection (USNPC), Beltsville, Maryland, as 99961.

Statistical differences in parasite abundance and parasite incidence were assessed using a nonparametric Mann–Whitney test and Chi-square analysis (or Fisher's Exact test, when the expected number of infected fish was below 5), respectively. In addition, variation in parasite number between hosts was analyzed using a General Linear Model (GLM), taking into account variation in host species, weight, and gender, as well as the sampling location. These analyses were conducted using GLM after testing homoscedasticity of the response variable (Bartlett's Test Statistic, 1.109; $P = 0.993$). We then proceeded with the analyses of variance with the natural logarithmic-transformed number of parasites as the response variable. In these parametric analyses, host, species, and sampling location were used as random factors; host gender as a fixed factor; and host weight as a covariate. The unbalanced sampling design necessitated the removal of rarely sampled host species. The analyses were thus conducted on the parasites identified from *Pseudotropheus zebra*, *P. emmitos*, and *Melanochromis vermivorus*.

RESULTS

Two hundred and nineteen cichlids of 9 species were examined for parasites, and all fish species: (*L. trewavasae* [new host record], *P. emmitos*, *P. zebra*, *M. vermivorus* [new host record], *N. polystigma* [new host record], *P. taeniolatus*, *P. elongates*, *T. microstoma* [new host record], and *Ramphochromis* sp. [new host record]) were infected. Fish species were 30–111 mm long (standard length [SL]) and weighed 2–46 g. Of the approximately 2,000 worms collected, 217 were studied in detail. These included 2 juvenile females (1%), 59 immature adults (males with no sperm and females with ovarian balls only) (27%),

and 156 mature adults (males with sperm and females partially or wholly with eggs) (72%), (Table 1).

The most heavily infected fishes were *P. zebra* and *P. elongates* (Fig. 1). At least 1 individual infected with *A. tilapiae* was found in all fish species examined. Both the prevalence and the incidence of infection varied significantly across host species (parasite incidence: Fisher's Exact test, $P = 0.006$; and parasite prevalence: Kruskal–Wallis test, $H = 39.05$, $df = 9$, $P = 0.000$). Test results suggest that *A. tilapiae* is better adapted to some cichlid hosts than to others. The closely related species pair, *P. zebra* and *P. emmitos*, showed marked differences in parasite abundance (Mann–Whitney test, $W = 16,283.5$, $P = 0.0012$), although not prevalence (chi-square analysis, $X^2 = 2.133$, $df = 1$, $P = 0.144$).

We also analyzed whether the weight and gender of the cichlid host, as well as the sampling location, could explain variation in the parasite load using GLM. This analyses showed that the weight and gender of the cichlid host did not explain significant variation in parasite load when the host species was included in the model (gender: $F_{1,245} = 1.85$, $P = 0.175$; and weight: $F_{1,245} = 3.23$, $P = 0.073$). In addition, when the effects of weight and gender were analyzed for each host species separately, no significant variation was explained by these factors (results not shown). However, both host species ($F_{4,245} = 3.55$, $P = 0.008$) and sampling site ($F_{6,245} = 4.57$, $P < 0.001$) explained significant variation in number of *A. tilapiae* specimens.

To unravel the effects of sampling site and host species on the parasite load of individual hosts, we

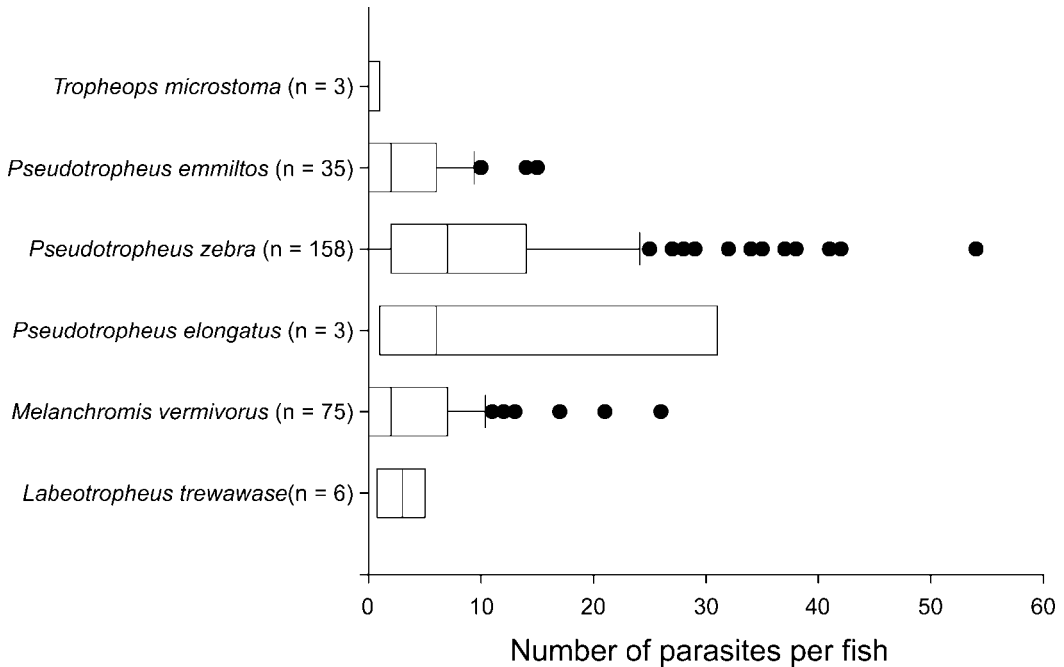


Figure 1. Box plot of the median, first and third quartile, and outlier values of the number of *Acanthogyrus tilapiae* parasites in individual cichlid hosts. Only cases with 2 or more infected fish were included in the figure (i.e., *Nimbochromis polystigma*, *Protomelas taeniolatus* and *Ramphochromis* sp. were excluded because quartiles cannot be calculated with less than 3 observations). The number of hosts screened is given in parentheses after the host species name.

also performed a nested analysis of variance with host species nested within sampling site. This analysis showed that parasite number also varied significantly between host species within site (host species: $F_{2,256} = 5.64$, $P = 0.004$). Furthermore, in this model, site explained significant variation in parasite load (Site: $F_{9,256} = 2.74$, $P = 0.005$).

DISCUSSION

The endemicity of *Acanthogyrus tilapiae* in the Nile River watershed in African fish, especially cichlids, has been established by many workers as reviewed in Amin and Hendrix (1999). The adaptive success of *A. tilapiae* is paralleled by the explosive radiation of its definitive cichlid hosts in associated African Great Lakes, reaching 700 cichlid species in each of Lake Malawi and Lake Victoria and 250 species in Lake Tanganyika (Turner et al., 2001). This is the second largest survey of this parasite in Lake Malawi and the first to report on various aspects of host-parasite relationships.

Morphologically, our specimens were similar to those of the first Lake Malawi survey by Amin and

Hendrix (1999), as well as those reported from Egypt by Amin (1978). The Lake Malawi specimens from cichlids from both collections were, however, smaller than those from the Nile River in Egypt from *Tilapia* (= *Oreochromis niloticus* (Linnaeus) (up to 60.0 cm SL) and *Tilapia zillii* (Gervais) (up to 40.0 cm SL) (Amin, 1978). The Egyptian specimens were, in turn, somewhat smaller than those reported by Baylis (1948) from *Tilapia* (= *Oreochromis lidole* (Trewavas) (up to 38.0 cm SL) in Lake Nyasa (Lake Malawi) but of similar size to those reported by Troncy (1970) from the amphibious giant otter shrew *Potamogale velox* du Chaillu (the only known mammalian host of *A. tilapiae*) in Yaoundé (Cameroon). Host factors appear to enhance greater growth in the larger *Tilapia* compared with the smaller cichlids examined (up to 11.1 cm SL).

Three observations are noteworthy: (1) worms, including sexually mature adults, were found in individuals of all host species indicating their suitability as definitive hosts; (2) the parasite incidence and abundance varied significantly among sympatrically occurring host species, which suggest that hosts are differentially exposed to *A. tilapiae* or

Table 2. Prevalence and development of *Acanthosentis tilapiae* in cichlids from Egypt and Malawi.

Location (year)	Reference	% Fish infected/ examined	Total worms collected (mean intensity)	Male		Female	
				Total	Immature no. (%)	Total	Immature no. (%)
Egypt (Jun 1975)	Amin (1978)	12/24 (50)	79 (3.3)	27	—	52	47 (90)
Malawi (Jul/Aug 1996)	Amin and Hendrix (1999)	28/64 (45)	95 (1.5)	44	5 (11)	51	30 (58)
Malawi (Sep 2005)	Current study	216/220 (98)	1,965* (9.1)	103	16 (15)	114	43 (38)

* Immature males have no sperm, and immature females were in the ovarian ball stage; only 2 were juveniles (reproductive system not developed). Only 217 of these worms were studied.

that they differ in their susceptibility to the parasite; and (3) large variations were observed in the parasite load in hosts depending on the sampling site, again suggesting differential exposure to *A. tilapiae* depending on geographic location.

The observation that all samples of the analyzed host species were markedly infected with this parasite is remarkable, especially when considering that these cichlid fishes have distinct diets and trophic specializations. Diverse food habits and feeding adaptations of the cichlid species could have a significant influence on the probability of contracting a parasite infection because they affect their exposure to the infected intermediate hosts.

The distribution of the invertebrate portion in the diet of sampled fish may not be equal in all 7 sites. It appears, however, that these cichlid fishes do not strongly compete for the same food items despite their superficial similarities. For instance *L. trewavasae* scrapes algae off rocks and eats small crustaceans and worms (Mills and Verers, 1989); *P. zebra* is a versatile species that combs loose material from the biocover of rocky areas and sediment-free to sediment-rich areas in deeper waters, and also feeds on zoobenthos and plankton in the open water (Konings, 1990); *N. polystigma* inhabits rocky areas around the shore and feeds mainly on fish (Eccles and Trewavas 1989); *P. taeniolatus* inhabits shallow, rocky, sediment-free habitats and feeds on aufwuchs attached to rocks and small invertebrates including zooplankton (Eccles and Trewavas, 1989); *P. elongates* feeds by combing loose algae from the biocover of shallow, rocky, sediment-free areas (Konings, 1990); and *P. microstoma* feeds on algae and invertebrates in sediment-rich and sediment-free habitats in calm waters of sheltered bays (Konings, 1990). It is clear that the diverse food habits and feeding adaptations of the cichlid species under consideration have a significant contribution to their parasitic infection because they affect their exposure to the infected intermediate host. The noted versatil-

ity of the most heavily infected host, *P. zebra*, is noteworthy.

Seasonal prevalence and sexual maturation of *A. tilapiae* are compared in available collections from related geographical locations (Table 2). Initial summer recruitment of cystacanths and autumn maturation of young adults are usually followed by greatest sexual maturity and breeding activities in the winter and early spring. This pattern of seasonality, in part, is shown in (Table 2). The relatively high mean of 3.3 in June from Egypt (Table 2) reflects the greater parasite numbers in the larger and most diverse *Tilapia* fish hosts; see Bailey (1994). Similar seasonality patterns were demonstrated in other acanthocephalan species by one of us (O.M.A.) in more temperate locations; for example, see Amin (1975, 1986, 1988) and Amin et al. (1980). Shotter (1974) also observed that the mean number of *A. tilapiae* recovered from *T. zillii* in Nigeria was lowest during June and July and highest from November to February.

The parasite prevalence varied significantly with host species and sampling locations. Lake Malawi rock-dwelling (mbuna) cichlid hosts may be differentially exposed to *A. tilapiae* because sampling locations varied markedly in host-species diversity (Ribbink et al. 1983). Importantly, however, sympatrically occurring (mbuna) cichlids also differed in their parasite numbers, which could be associated with their microhabitat and trophic specializations or with differences in their susceptibility to the parasite.

ACKNOWLEDGMENTS

This project was supported by a National Environment Research Council Advanced Research fellowship (NER/J/S/2002/00706) to J.C., a British Ecological Society grant to R.L.R. (University of Hull), and an Institute of Parasitic Diseases (IPD) in-house grant to O.M.A.

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