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Primary Research Paper

Spatial and temporal variation of cestode infection and its effects on two small barbs (*Barbus humilis* and *B. tanapelagius*) in Lake Tana, Ethiopia

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Abstract

Pseudophyllidean cestodes as *Ligula* have a complex life cycle with cyclopoid copepods as first intermediate host, zooplanktivorous fish as second, and piscivorous birds as final host. We studied the effects of diet, season and habitat occupation on the prevalence of plerocercoid larvae of the tapeworm *Ligula intestinalis* in two closely related small barbs and the effects of the parasites on the barbs life histories in Lake Tana (Ethiopia) during 1 year. In all affected barbs *L. intestinalis* caused retardation in gonad development, maturation at reduced size and lower absolute fecundity. Infection rate, averaged over all habitats was significantly higher in *B. tanapelagius* (10%) than in *B. humilis* (6%). Below a threshold of 48 mm the infection rate was zero for both barbs, this coincided with a very low proportion of copepods in their diets, increasing up to 90 and 55%, respectively, for their largest size class (81–90 mm). The relatively high infection rate in *B. tanapelagius* is explained by its obligatory zooplanktivorous feeding behaviour, ingesting a relatively high proportion of infected cyclopoid copepods. This is in contrast with *B. humilis*, which is a polyphagous species, feeding both on zooplankton and benthic invertebrates. Significant seasonal effects in infection rates were observed. In both barb species infection rates were lower during the breeding season. Only for *B. tanapelagius* a significant negative correlation was observed between rain fall and infection rate, probably caused by an increased turbidity that decreases feeding efficiency on zooplankton. Habitat type had also a significant effect on infection rate. *Barbus humilis* showed a much higher infection rate in shallow clear water (10%) than in shallow turbid water (3%), whereas *B. tanapelagius* showed much higher infection rates in the shallow sublittoral (13%) than in the deeper pelagic (7%). Most likely, birds predate more efficiently on barbs in shallow clear waters than in shallow turbid and deep waters.

Introduction

Most fish face a wide range of different enemies including competitors, predators and parasites. Parasites may induce shifts in species densities, size composition and affect commercially interesting stocks. Parasites can alter the size-specific schedules of reproduction and the mortality of their hosts. This may depend on vulnerability of species, habitats and seasonal factors.

Lake Tana is an oligo-mesotrophic shallow (< 14 m deep) lake in the Northwest highlands of Ethiopia (elevation 1830 m). With a surface area of 3200 km^2 Lake Tana accounts for half of the total freshwater area of the country. The Cyprinidae family dominates the Lake's fish fauna by 22 species; two other families (Cichlidae and Clariidae) are represented by a single species. Three species of small barbs (< 10 cm fork length (FL)) have been reported for Lake Tana: *Barbus tanapelagius* (de Graaf et al., 2000), *Barbus humilis* (Boulenger, 1902; includes the recently synonymised *Barbus trispilopleura* ecotype, Dejen et al., 2002) and *Barbus pleurogramma* (Boulenger, 1902).

Barbus tanapelagius is endemic in Lake Tana (de Graaf et al., 2000) and probably evolved following the rise of large pelagic zooplankton resources in the incipient Lake Tana. *Barbus humilis* is a riverine species and more widely distributed in the inflowing rivers of Lake Tana and other parts of Ethiopia (Froese & Pauly, 2001). Most likely *B. tanapelagius* evolved out of a *B. humilis* like ancestor (de Graaf, 2003). Together, both barb species constitute the main link in the food chain between the primary consumers (zooplankton) and the top predators, the large piscivorous barbs (de Graaf et al., 2000; Nagelkerke & Sibbing, 2000; Sibbing & Nagelkerke, 2001). Despite their ecological importance, little is known of their distribution, standing biomass and biology. A high prevalence of tapeworm infection (*Ligula intestinalis*) in the two small barbs, which are a possible target for developing fisheries, made us prioritise this study of parasite–fish interactions.

Ligulids are important cestode parasites of cyprinid fish in lakes and reservoirs throughout the world (Kennedy, 1974; Dick & Choudhury, 1995; Bush et al., 2001; Loot et al., 2002). In Africa, infection by cestode larvae has been reported from fish of the Nile in Egypt and the Sudan and from the East African lakes (Paperna, 1980; Okedi, 1981; Wanink, 1992; Ogwai, 1998). Quantitative data available from the Sudan Nile show infection prevalence ranging from 7 to 10% in *Synodontis* spp. and 13 to 70% in various siluroid fish and *Polypterus* spp. (Paperna, 1980).

Pseudophyllidean cestodes as *Ligula* have a complex life cycle involving cyclopoid copepods as the first intermediate host, fish as the second intermediate host and piscivorous birds as the final host (Barber & Poulin, 2002: 362–383). Parasite eggs are deposited via bird faeces into water where hatching eggs release free-swimming coracidium larvae. The ciliated coracidium larva will survive 1–2 days in the water and its movement attracts predation by cyclopoid copepods. Development in the copepod produces a procercoid larva, which is infectious to fish, the second intermediate host, after eating the cyclopoid copepod. Within the fish, a large plerocercoid larva develops which usually remains free within the body cavity of the fish host and grows, swelling the belly of its host. The increased nutritional demands of the parasite and its combined effects on host appetite, locomotion, and competitive ability have severe consequences for the behaviour of the infected fish. These behavioural changes are likely to facilitate predation by birds (Wanink, 1992).

Plerocercoids may occupy the body cavity of fish for several years (Sweeting, 1976). Specifically, trophically transmitted parasites increase the vulnerability of the intermediate host to predation by the definitive hosts (Holmes & Bethel, 1972). Parasites have an impact on the ecology of host populations (Holmes & Bethel, 1972; Kennedy, 1974; Sweeting, 1976). *Ligula* plerocercoids hamper the gonadal development and cause sterilisation of infected fish (Van Dobben, 1952; Dick & Choudhury, 1995). According to Okedi (1981) the tapeworm seriously affects the stock of the small cyprinid *Rastrineobola argentea* in Lake Victoria by damaging internal viscera and retarding maturation of the ovary. Wanink (1992) reported that the mean weight of infected *Rastrineobola argentea* in Lake Victoria falls to 20% below the value for healthy fish.

Cyclopoid copepod densities (total copepodites) vary seasonally in Lake Tana from ca. 8 to 19 ind l^{-1} and represent on an annual basis approximately 20% of the total microcrustacean densities without copepod nauplii (Dejen et al., 2004). The average proportion of cyclopoid copepods in the diet of the barbs on basis of biovolume is somewhat lower, 11 and 18% for *B. humilis* and *B. tanapelagius*, respectively (Dejen, 2003). The lake supports a large variety of piscivorous birds, including residents as little grebe (*Tachybaptus ruficollis*), great white pelican (*Pelecanus onocrotalus*), great and long-tailed cormorants (*Phalacrocorax carbo* and

P. africanus), darter (*Anhinga rufa*), many species of herons (*Ardeola* spp., *Egretta* spp., and *Ardea* spp.). Palaearctic migrants include osprey (*Pandion haliaetus*), great black-headed, lesser black-backed and herring gulls (*Larus ichthyaetus*, *L. fuscus*, and *L. argentatus*), and whiskered and white-winged black terns (*Chlidonias hybridus*, and *C. leucopterus*) (Nagelkerke, 1997: 13). The density of fish eating birds is invariably higher in the shallow inshore zones of the lake (Eshete Dejen personal obs.).

The high abundance of *B. tanapelagius* and *B. humilis*, their key role in the food web (Nagelkerke, 1997; de Graaf et al., 2000; Sibbing & Nagelkerke, 2001; Dejen et al., 2002) and their potential as a target for fishery development in Lake Tana urges closer investigation of these resources. The objectives of the present study are: (a) to compare the prevalence of cestode infections in two small barbs at different fish size, habitat and season, and (b) to analyse the effect of *L. intestinalis* infection on the life-history of the fish.

Materials and methods

A total of 9841 *B. humilis* and 4319 *B. tanapelagius* was collected from January to December 2000 in four different mostly turbid habitats without vegetation (A–D, replicated in 16 sampling stations) and in one inshore shallow habitat with clear water and vegetation (A4) (see Fig. 1, Table 1). In the shallow clear water habitat only *B. humilis* was observed. The turbid habitats are characterised as (A) shallow littoral zone (ca. 2 m deep) with rocky bottom; (B) shallow littoral zone (ca. 2 m deep) with muddy/sandy bottom; (C) sub-littoral zone (ca. 6 m deep) and (D) pelagic deep water (ca. 10 m

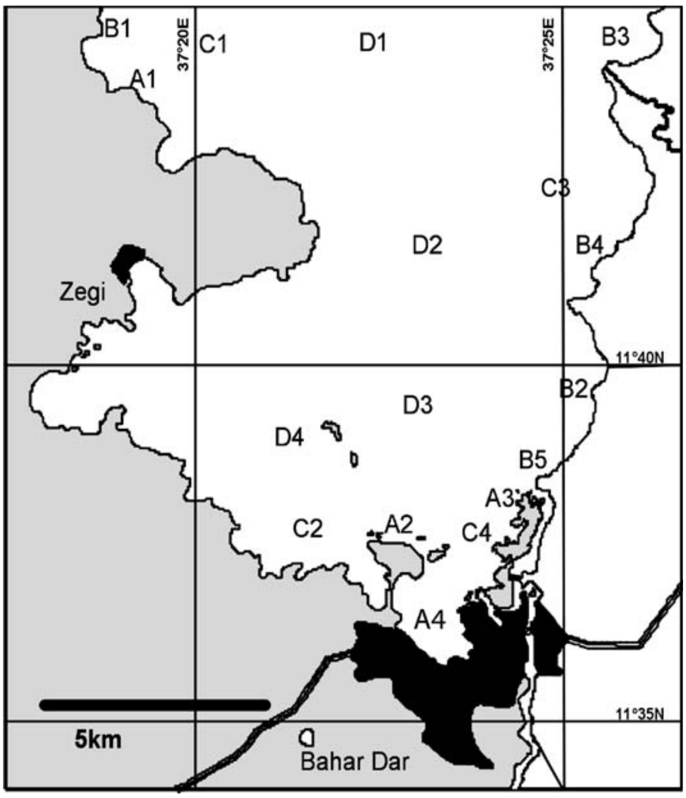

Figure 1. Sampling stations in the Southern Bay of Lake Tana. A1–A4 and B1–B5 stations located in the littoral region, C1–C4 stations located in the sublittoral region and D1–D4 stations located in the pelagic region. For information about depth, water transparency and substrate see Table 1.

Table 1. Sampling stations in the Southern bay of Lake Tana: their depth range, the water transparency measured as Secchi-disc depth and substrate type

Station	Depth range (m)	Secchi-disc depth range (m)	Substrate type
A1	1.5–3	40–70	Rock
A2	1.5–3	45–80	Rock
A3	1.5–3	60–75	Rock
A4	0.5–3	70–145	Rock
B1	1.5–3	35–70	Mud
B2	1.5–3	30–60	Mud/sand
B3	1.5–3	25–75	Mud/sand
B4	1.5–3	35–75	Mud/sand
B5	1.5–3	30–50	Mud
C1	4–7	45–65	Mud
C2	4–7	45–75	Mud
C3	4–7	30–60	Mud
C4	4–5	40–75	Mud/sand
D1	10–14	50–75	Mud/sand
D2	10–13	40–70	Mud
D3	8–10	45–65	Mud/sand
D4	8–10	40–70	Mud

Secchi-disc depth range indicates change over seasons ($N = 12$). Note that only station 'A4' has large amounts of floating vegetation (mainly *Ceratophyllum*). For location of sampling stations see Figure 1.

deep). Monthly samples (day and night) were obtained using benthic and pelagic multi-mesh monofilament survey gillnets type 'NORDEN' (Lundgrens Company, Sweden) composed of five different randomly distributed mesh size-panels (5.0, 6.25, 8.0, 10.0 and 12.5 mm bar mesh). In addition a 3-m beam trawl was used during dusk and dawn.

Fish were visually inspected for the presence of larval cestode infection in the body cavities, and the cestodes were identified according to Van Dobben (1952) as *Ligula intestinalis*. Data were analysed with respect to parasitic prevalence (proportion of infected fish). Length and fresh body weight of both fish (FL) and parasites were determined to the nearest millimetre and 0.1 g. The states of gonad maturity and sex were assigned by viewing the gonads at 10-fold magnification through a microscope. Ovaries were staged in I–V maturity scales according to Nikolsky (1963). Stage I and II are immature stages, stages III–V are considered as mature.

For the analysis of temporal distribution of parasite on fish, four seasons were identified in Lake Tana (Wudneh, 1998; Dejen et al., 2004): (a) hot dry season (November–April), (b) pre-rainy season (May–June), (c) wet, high water level season (July–August) and (d) post-rainy season (September–October). Rainfall data for 2000 were obtained from Bahir Dar Meteorological Station and varied between 0 and 517 mm per month. Variations in parasite prevalence between fish species, seasons and habitats were statistically tested using non-parametric statistics: Spearman's rank correlation, Mann–Whitney U test and Kruskal–Wallis test, and $p < 0.05$ was considered significant. SPSS 9.05 version for Windows software was used for the statistical analysis.

Results

Cestode infection among small barbs

Between *B. humilis* and *B. tanapelagius* the infection rate was significantly different (Mann–Whitney U test $p < 0.05$): lower for *B. humilis* (6%, $n = 9841$) compared with *B. tanapelagius* (10%, $n = 4319$).

Barbus humilis and *B. tanapelagius* below 48 mm fork length (FL) were not found infected with tapeworm. Above this threshold value, a highly significant positive correlation between FL and infection rate appeared for both fish species (Fig. 2). Only one tapeworm was present in every infected fish. The average length and weight of the tapeworm was 60 mm and 0.55 g.

Infection prevalence across habitats and seasons

Barbus humilis caught at the rocky clear water station 'A4' showed conspicuously higher cestode infection prevalence (10%) than the same species caught at turbid stations (3%) (Table 2). For *B. tanapelagius* the infection prevalence reached its peak in the sublittoral (13%) (Table 2). For each species, the effect of habitat type on infection prevalence rate was statistically significant (Kruskal–Wallis test, $n = 12$, $p < 0.05$).

For *B. humilis*, the samples collected from August to March revealed higher infection prevalence (5–11%), than those collected from

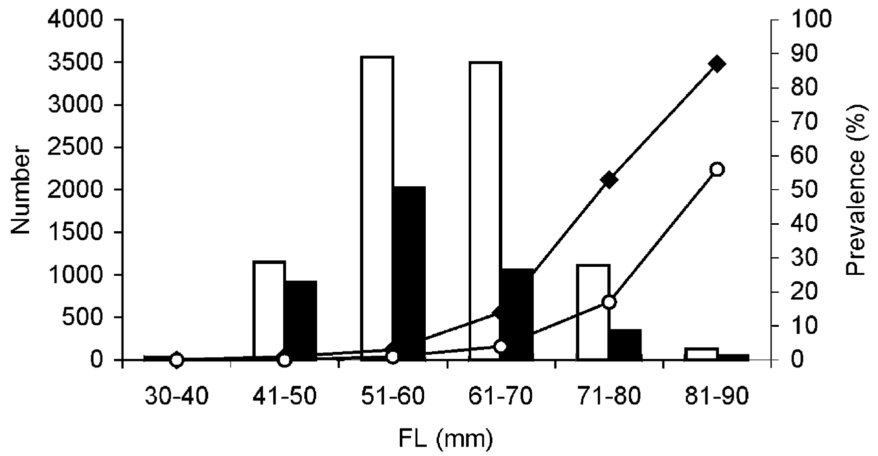

Figure 2. Prevalence of *L. intestinalis* (line) in relation to fork length of *B. tanapelagius* (■, dark bars) and *B. humilus* (o, open bars). Bars show the number of specimens investigated.

April to July (2–3%). In the case of *B. tanapelagius*, higher infection prevalence was recorded from December to May (12–17%) than from June to November (3–9%) (Fig. 3). Statistical analysis of these results revealed that the variations in prevalence of *L. intestinalis* across months were significant for *B. tanapelagius* and *B. humilis* (Kruskal–Wallis test, $n = 12$, $p < 0.05$). Only for *B. tanapelagius* was a decrease in infection prevalence apparently associated with a corresponding increase in the amount of rainfall over May–September (Spearman's rank correlation, $r = -0.61$, $n = 12$, $p < 0.05$).

Effect of parasite infection on reproduction

Observations show that tapeworm infection caused a dramatic effect on gonad development. All fish infected, even the larger specimens, had immature gonads.

Discussion

Fish species and size class sensitivity

An important aspect of species susceptibility to parasites are the changes in demographic characteristics of populations that parasitism might induce. High adult mortality appears to lead to short-term plastic changes in age and size at maturity of the victim population (Rochet, 1998).

Ligula intestinalis was found in both the two small barbs *B. humilis* and *B. tanapelagius*, but infection rates differed. Host resistance and behaviour are the most important factors dictating variation in intensity of infection and parasite loads (Tanguay & Scott, 1992; Quinnell et al., 1995). Among the microcrustacean zooplankters, cyclopoid copepods are assumed to be the only intermediate hosts for *L. intestinalis* (Barber & Poulin, 2002: 362–383). The higher infection

Table 2. Tapeworm-infection rate (*P*, %) in *B. humilis* and *B. tanapelagius* across different habitats (depth between brackets)

Habitat	Station	*B. humilis* *N*	*B. humilis* *P* (%)	*B. tanapelagius* *N*	*B. tanapelagius* *P* (%)
Littoral (0.5–3 m), clear water	A4	2860	10	NP	
Littoral (1.5–3 m), turbid water	A, B	4996	3	120	3
Sublittoral (4–7 m)	C	1985	1	1676	13
Pelagic (8–14 m)	D	NP		2523	7

Sampling from January to December 2000. Number of fish investigated (*N*) is indicated for each station. NP = Fish species not present.

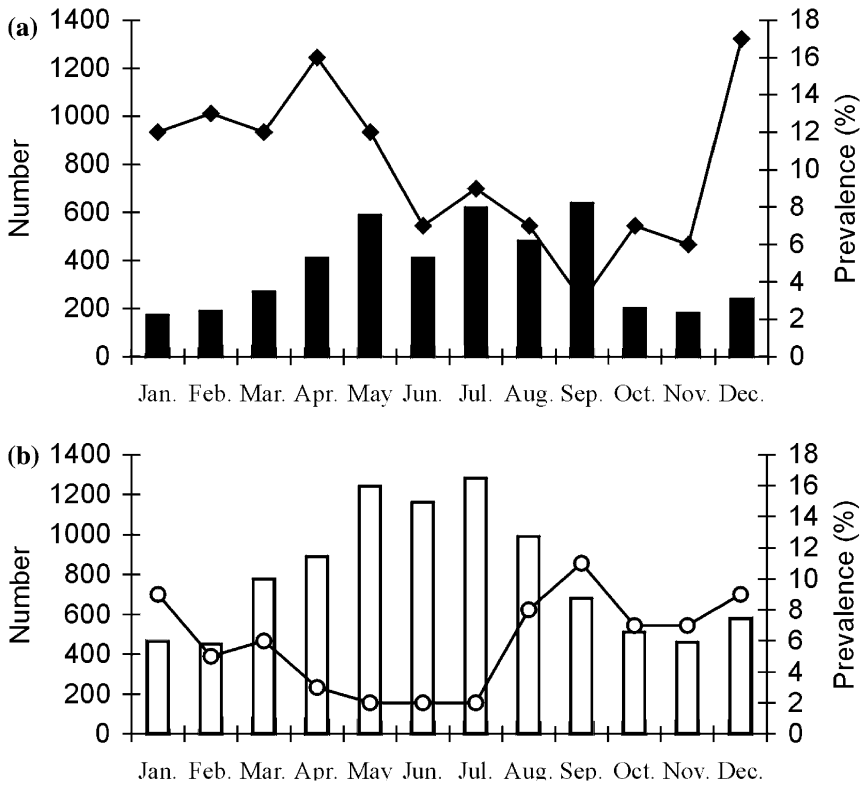

Figure 3. Monthly numbers of fish observations (bar) and prevalence of *L. intestinalis* (line) in (a) *B. tanapelagius* and (b) *B. humilis* from January to December 2000.

prevalence in *B. tanapelagius* may be explained by being a specialised zooplanktivore, hence encountering and ingesting tapeworm more frequently than the polyphagous *B. humilis*, which feeds on both zooplankton and benthic invertebrates. Host specificity of *L. intestinalis* among the examined fish species of Lake Tana appears largely attributable to the difference in food type. Infection rate for the 81–90 mm size classes was 55% in *B. humilis* and 90% in *B. tanapelagius* (Fig. 2). The overall prevalence and parasite weight increased with fork length of fish (> 48 mm). The 48 mm FL infection threshold is probably due to the very low proportion of cyclopoid copepods in the diets of fish < 48 mm, a much lower proportion than in the environment (Dejen, 2003). This may be due to a low ability of small fish in catching (in their scale) large and evasive copepods with parasites and/or that larger and older fish have been exposed for a longer period to the risk of being infected. *Ligula*-infected cyprinid species in Europe (roach, gudgeon) show a positive relationship between fish weight and parasite weight (Bean & Winfield, 1992) and Wanink (1992) and Ogwai (1998) showed an increase in overall prevalence and parasite weight with increasing size of *Rastrineobola argentea* from Lake Victoria. In other, non-cyprinid fish species, also nematode infections increase with age and length of the fish (Wotten & Waddell, 1977; Ismen & Bingel, 1999).

Effect of habitat on parasite prevalence

Feeding segregation often depends on spatial segregation and by consequence habitat type may indirectly affect the infection rate for cestode larvae. The two small barbs show a clear segregation in spatial distribution pattern. *Barbus tanapelagius* is restricted to the surface layers of sublittoral and deep offshore waters, whereas *B. humilis* prefers the shallow littoral and sublittoral areas (de Graaf et al., 2000; Dejen et al., 2002). *Barbus humilis* is a generalist feeder preferably dwelling near the benthos and *B. tanapelagius* feeds on zooplankton in the upper part of the water column (Dejen et al., 2002). Thus, the higher infection rate of *B. tanapelagius* as compared with *B. humilis* is probably caused by the higher proportion of copepods in the diet of the former species.

For *B. humilis* the highest parasite prevalence was found in the clear water habitat (station 'A4'). This station is near the town of Bahir Dar where fish wastes are dumped attracting many fish-eating birds, which concentrate at this shore to feed on fish discards (Eshete Dejen, personal obs.). These birds can easily detect *B. humilis* in the clear water, and by eating them become the primary hosts for *L. intestinalis*. At the same time birds will infect the cyclopoid copepods in this area, by dropping faeces with parasite eggs, rendering a peak infection rate for *B. humilis*. A higher prevalence of *L. intestinalis* was found in *B. tanapelagius* in the sublittoral areas as compared with the pelagic. This is most likely dependent on the relatively high densities of piscivorous birds in the shallow inshore areas, which we assume resulted in higher densities of cestode coracidia developed from eggs dropped in the birds' faeces and higher proportions of infected cyclopoid copepods.

Seasonal effects on parasite prevalence

Significant seasonal variation in the *L. intestinalis* infection was observed in both *B. tanapelagius* and *B. humilis* during this study. Season-related host feeding patterns, availability of infected intermediate hosts, immunological and hormonal changes, are the most frequently suggested causes for seasonal fluctuation in prevalence and abundance of parasitic infections (Kim et al., 2001). We found a significant negative correlation between rain fall and infection rate for *B. tanapelagius*, but not for *B. humilis*. Since turbidity, caused by the sediment load of the in-flowing rivers, is strongly positively related to rain fall (Dejen et al., 2004), this suggests a decreasing feeding efficiency by piscivorous birds under turbid conditions in deep water. In the current study, low prevalence of *L. intestinalis* was found in both *B. humilis* and *B. tanapelagius* during the breeding season. The spawning season for *B. humilis* ranges from March to August and continues another month for *B. tanapelagius* (Dejen et al., 2003). Therefore spawning related hormonal changes might also influence the seasonality of *L. intestinalis*.

Parasite induced life-history and behaviour

The present study shows that the parasite caused retardation in the female gonad development. All infected fish, even the larger specimens had immature gonads. We did not investigate the effect of the parasite on the fish behaviour, but several other authors found evidence that infected fish move to areas with a high predation risk. Such movements have for instance been reported for *Rastrineobola argentea* from Lake Victoria, where infected fish dwell at the surface (Wanink, 1992; Wanink et al., 1999) and for European roach, of which the older infected individuals move either to the shallow littoral zone or to the upper water layers of the pelagial (Holmes & Bethel, 1972; Adamek et al., 1996).

The consistently higher prevalence of *L. intestinalis* in *B. humilis* from the shallow clear rocky habitat may suggest that it is a separate stock from the *B. humilis* that dominates in shallow and intermediately deep turbid areas without vegetation. Indeed, Boulenger (1902) considered these two stocks as a separate species. However, recently Dejen et al. (2002) found that they are not separate species, but a single biological species with continuous phenotypic plasticity in pigment patterns induced by transparency of water.

In conclusion, this study shows the impact of *L. intestinalis* parasite on small barbs, differentiated over season and space. *L. intestinalis* plerocercoids render the intermediate host infertile, reducing reproductive capacity of the breeding stock. The observed infection rates are predominantly related to the distribution patterns of the piscivorous birds, which are more numerous in the inshore habitats, and the predation efficiency of the birds as related to water transparency and water depth.

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