Spatial and temporal distribution of *Ligula intestinalis* (Cestoda: Diphyllobothriidea) in usipa (*Engraulicypris sardella*) (Pisces: Cyprinidae) in Lake Nyasa

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Abstract

Engraulicypris sardella is an endemic and economically important cyprinid species in Lake Nyasa/Malawi which has recently been infected by the tapeworm *Ligula intestinalis*. This parasite is known to induce severe pathological and behavioural effects on other cyprinids, including castration, followed by a collapse of infected populations. As a first step to understanding the dynamics between this parasite and *E. sardella*, we studied the spatial and temporal variation in prevalence over a period of 1 year. Overall prevalence was about 15%, but we observed a consistently higher prevalence in the littoral compared to the pelagic zone. Fish in the upper water levels showed the highest prevalence, with a marked decline with increasing water depth down to 150 m. The proportion of infected fish varied over time, with a significantly higher prevalence in the rainy season. In a huge lake like the Nyasa, with a surface area of 29,000 km² and a maximum depth of 785 m, the transmission success of the parasite appears to show large variations in time and space. We suggest that these conditions could lead the parasite to become persistent within the lake, rather than the typical epidemic situation as observed in smaller bodies of water.

Introduction

Invasive species (i.e. a non-native organism) can potentially cause serious problems in many ecological habitats worldwide (Gurevitch & Padilla, 2004; Pejchar & Mooney, 2009), including losses in biodiversity, changes in ecosystem functions and impacts on economic enterprises (Lovell *et al.*, 2006). Parasites may play a key role in mediating the impacts of biological invasion (Lymbery *et al.*, 2014). Alien parasites are usually introduced in new habitats with an alien host species (Lymbery *et al.*, 2014), and may lead to the emergence of new diseases in native hosts (Taraschewski, 2006). In the literature, the most commonly reported co-introduced parasites into new habitats are parasitic worms (helminths) (Lymbery *et al.*, 2014).

Ligula intestinalis (Linnaeus 1758) is a globally distributed diphyllobothriidean cestode (Kennedy, 1974) and has been reported from a wide range of cyprinid fish species from Europe (Vanacker *et al.*, 2012), North America, Asia and Australia (Stefka *et al.*, 2009). Recently it has also been found in Africa, both in Lake Victoria and in Lake Nyasa (Cowx *et al.*, 2008; Msafiri *et al.*, 2014). In Lake Nyasa the parasite infects a small pelagic cyprinid *Engraulicypris sardella* (Günther, 1868) (Msafiri *et al.*, 2014; Rusuwa *et al.*, 2014). *Engraulicypris sardella*, locally called usipa, is a small (common size 100 mm length), annual, pelagic, cyprinid fish endemic to Lake Nyasa (Rufli & Van Lissa, 1982; Thompson, 1996). Having a high growth rate, they reach a maximum length of 130 mm in less than a year (Eccles, 1992). Young *E. sardella* feed exclusively on phytoplankton and switch to zooplankton when they attain adulthood (Degnbol, 1982; Allison *et al.*, 1996). They are widespread within the lake and are found in both nearshore areas and offshore pelagic water, down to depths of approximately 200 m (Maguza-Tembo *et al.*, 2009).

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Ligula intestinalis has a complex life cycle involving two aquatic intermediate hosts and a piscivorous bird as the definitive host (Dubinina, 1980). Copepods and various cyprinid fish species serve as first and second intermediate hosts, respectively. *Ligula* plerocercoids (the parasite larva found in the second intermediate host) cause severe pathogenic effects on the fish intermediate host, suppressing gonad development and perhaps causing complete castration in roach and chub (Kennedy *et al.*, 2001). This could potentially lead to population collapses of infected host species and changes in the abundance and composition of the fish community within lakes (Wilson, 1971; Wyatt & Kennedy, 1988).

Infections of *L. intestinalis* in *E. sardella* in Lake Nyasa were first observed by Mwambungu *et al.* (1996) and Kihedu *et al.* (2001) during long-line research surveys. In Lake Nyasa, only *E. sardella* has been found to be infected, but it is known that this parasite can switch between different cyprinid hosts (Vanacker *et al.*, 2012). The fishery of *E. sardella* in Tanzania contributes significantly to the livelihood of local people, by providing them with cheap animal protein. Severe infections with *L. intestinalis* could potentially lead this endemic species to extinction, as has been reported for other fish species (Wyatt & Kennedy, 1988).

In small lakes, ponds and reservoirs, *L. intestinalis* typically shows epidemic cycles lasting a few years, where infection levels increase rapidly followed by population crashes of the intermediate host (Kennedy *et al.*, 2001). In larger lakes, the situation may be different, with local extinctions in some areas and increasing parasite abundance at other locations within the lake. Within Lake Nyasa we would therefore expect more spatial variation in prevalence than in the typical small lakes where this parasite has been most frequently studied. Moreover, in larger lakes, fish species diversity is usually higher (Barbour & Brown, 1974), providing the parasite with alternative hosts and potentially facilitating host switching when fish populations crash. This might cause the parasite to become persistent within the lake. Furthermore, small lakes usually have relatively shallow depths and are therefore not usually stratified (Vanacker *et al.*, 2012). Larger lakes usually stratify (Ngupula *et al.*, 2012) and this provides marked biotic and abiotic changes with water depth, allowing us to study how this parasite affects the depth preference of the intermediate host.

As a first step towards understanding the dynamics of this parasite in a huge lake like Lake Nyasa, here we present data on the spatial and temporal variation in prevalence and intensity. Since ecological conditions affecting parasite transmission rates are likely to vary at different locations and at different times of the year, we expected to find marked effects of site and season on the infection level of the parasite. Moreover, since it has been shown that the final host tends to catch a disproportionately high share of infected fish (Brown *et al.*, 2001; Loot *et al.*, 2001a), we explored how prevalence varied with water depth.

Materials and methods

The study was conducted in Lake Nyasa (also known as Lake Malawi or Lake Niassa), the southernmost of the large African rift valley lakes (fig. 1). Lake Nyasa is shared by three states: Malawi, Mozambique and Tanzania. The lake is located at an altitude of 472 m above sea level, it has a mean surface area of 29,000 km² and a maximum depth of 785 m (Bootsma & Hecky, 1993). The mean surface temperature of the lake is between 24 and 28°C (Vollmer *et al.*, 2005) and the annual rainfall ranges between 1000 and 2800 mm (LNBWB, 2013). The Lake Nyasa basin is characterized by two marked seasons: a dry season (May–September) and a double-maxima rainy season, with a long rainy season in January–April and a short rainy season during October–December.

The present study was conducted at three different fishing stations – Matema, Lupingu and Mbamba Bay – situated in the south-western part of the United Republic of Tanzania. At each fishing station, two sampling sites were established, one site close to the lake shore (littoral zone) and the second site located offshore (pelagic zone).

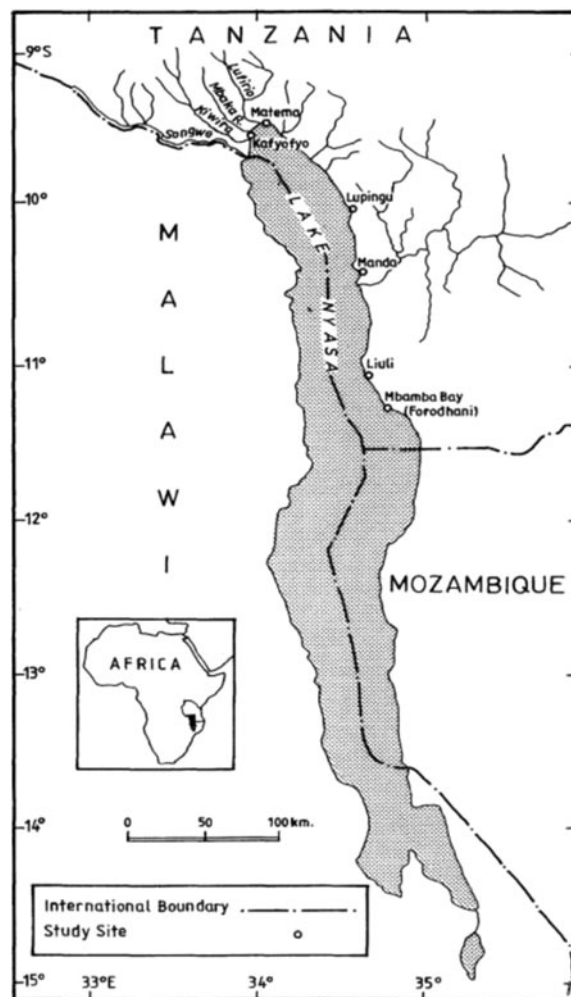Sampling was carried out monthly from January to December in 2015 and a total of 6987 *E. sardella* were

Fig. 1. Map of Lake Nyasa, showing all sampling stations (Matema, Lupingu and Mbamba bay). Reproduced with permission from Msafiri *et al.* (2014).

collected *in situ* from artisanal fishermen operating light-attraction fishery during the nights of a dark moon-phase. All fish were caught using an open-water sein net with 10 mm mesh size, and were obtained at a depth of about 100 m for both the lake habitats (i.e. littoral and pelagic zones). Coordinates of the sampled area were recorded using a hand-held global position system (Garmin GPS 72H; Garmin Ltd, Olathe, Kansas, USA). The length and weight of both *E. sardella* and *L. intestinalis* were measured to the nearest millimetre and 0.01 g. The fish were later dissected for parasite determination, and the cestodes were identified according to the protocol of Dobben ([1952]) as *L. intestinalis*. Determinations of the parasite prevalence and intensity in *E. sardella* were calculated according to Bush *et al.* ([1997]).

To test whether the parasite prevalence varied with water depth, we conducted a sampling survey at Matema fishing station, fishing 225 *E. sardella* during the dark moon-phase nights in deeper water, up to 200 m depth. Within the sampling site, four vertical sampling depths were used: one close to the surface (i.e. 50 m depth) and the others at 100, 150 and 200 m depths, respectively. However, at the 200 m depth, *E. sardella* was not found in the catch and therefore we decided to exclude this location from the analysis. Data on the host *E. sardella*, prevalence and measurements of *L. intestinalis* were collected using the methodology described above.

Statistical analysis

Statistical computing and graphics were carried out using **R**, version 3.2.3 (http://r-project.org). Analyses of the prevalence of *L. intestinalis* in *E. sardella* were performed using a Generalized Linear Model (GLM). In the model, infection was fitted as a binary response variable, with parasite occurrence used as 0 for absence and 1 for presence. Lake habitat (levels: littoral and pelagic) and sampling stations (levels: Matema, Lupingu, Mbamba Bay) were added as categorical predictors in the model. The model also included an interaction between the two predictors. Analysis of parasite prevalence at different times of the year (2015) was carried out using a Generalized Additive Model (GAM). In the model, parasite prevalence was the response variable, and day of the year was included as the predictor in the model. Moreover, rainfall data were added to the figure of the model, with the aim of showing variations of parasite prevalence in relation to precipitation. The relationship between prevalence of *L. intestinalis* and host depth was explored using a binary logistic regression model. In the model, infection was fitted as a binary response variable, with parasite occurrence used as 0 for absence and 1 for presence, and lake depths were added as categorical predictors in the model.

Results

Overall prevalence from all stations throughout the study period was $14.98 \pm 2.43\%$ (mean ± SE). Number of cestodes per infected fish ranged from 1 to 4, and overall mean intensity was 1.13 ± 0.01 (mean ± SE). The majority of infected fish carried one parasite (87.84%), with

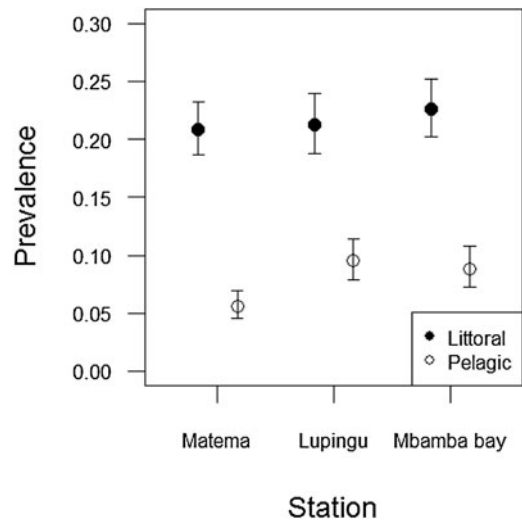Fig. 2. Prevalence (±SE) of *L. intestinalis* in *E. sardella* depending on lake habitat (littoral zone vs pelagic zone) and station (Matema, Lupingu and Mbamba Bay) in Lake Nyasa, 2015.

11.07% having two parasites, 1% three parasites and 0.1% four parasites. *Engraulicypris sardella* sampled from the littoral zone had a significantly higher prevalence of infection than those sampled in the pelagic zone (GLM: $F_{(1,6985)} = 5480.5$, $P < 0.001$) (fig. 2).

Additionally, we found a significant interaction between the lake habitats and sampling stations, i.e. the change in prevalence when going from littoral zone to pelagic zone was not the same for all sampling stations (GLM: $F_{(2,6981)} = 5463.0$, $P < 0.01$). Treatment contrasts revealed that the change was largest in Matema compared to the two other stations. However, this effect was small compared to the overall difference between the littoral and pelagic habitat.

Parasites were found throughout the year; but the prevalence was higher during the rainy season ($19.68 \pm 3.99\%$) from October to April compared to the dry season ($8.83 \pm 1.46\%$) between May and September, and the variations in parasite infestation between months of rainy seasons and dry seasons were statistically significant (GAM: edf = 4.959, Ref. df = 6.045, $F = 2.744$, $P < 0.05$) (fig. 3). The average rainfall intensity per month for rainy and dry seasons was 123 mm and 2 mm, respectively.

Parasite prevalence varied significantly with the depth at which fish hosts were located, with the highest prevalence in the upper 50 m and declining with depth (GLM: $F_{(1,223)} = 242.67$, $P < 0.05$) (table 1). Below 150 m we found no infected *E. sardella*. The mean length of fish also tended to decline with water depth. Moreover, male *E. sardella* were more frequently infected than females and were also more common in the surface water than at deeper water levels.

Discussion

Spatial and temporal variations of *L. intestinalis* in different cyprinid fish species are well documented
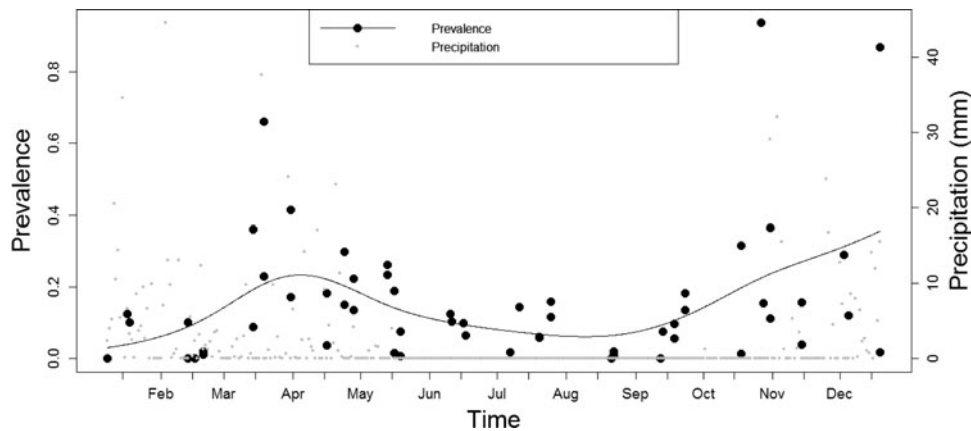
Fig. 3. Variations of parasite prevalence (GAM model represented by black line and raw data by solid black circles) and daily rainfall (grey solid circles) in Lake Nyasa from January to December, 2015.

(Sweeting, 1976, 1977; Bean & Winfield, 1992; Loot *et al.*, 2001a; Dejen *et al.*, 2006; Britton *et al.*, 2009; Zhokhov & Pugacheva, 2012). However, to our knowledge there are few studies of this parasite from large and deep lakes (Marshall & Cowx, 2003; Msafiri *et al.*, 2014; Rusuwa *et al.*, 2014). Marshall & Cowx (2003) studied the effects of *L. intestinalis* on *Rastrineobola argentea* (closely related to *E. sardella*) in Lake Victoria and found no discernible trend in parasite prevalence between different parts of the investigated lake (but without presenting any data). Studies on *L. intestinalis* in *E. sardella* are even fewer. Recently, Msafiri *et al.* (2014) and Rusuwa *et al.* (2014) reported the occurrence of this parasite in *E. sardella* in Lake Nyasa and found high parasite prevalences of over 30 and 50%, respectively, in the investigated parts of the lake. However, their findings were only obtained from a small part of the lake and did not cover all seasons.

In the present study, we observed a surprisingly small spatial variation in prevalence of *L. intestinalis* in *E. sardella* between different fishing stations, despite the fact that the southernmost station (Mbamba Bay) is more than 180 km from the most northerly station (Matema). This suggests that the parasite is widely distributed throughout the lake. Based on our data, there is no indication of local extinctions at some localities and population increases at others.

We found an average prevalence of about 15% and few individual hosts had more than one parasite. This is an infection level well below that found in many other studies where high parasite abundance has been followed by severe population declines in the fish intermediate host (Sweeting, 1977; Kennedy *et al.*, 2001). However, this prevalence estimate is based on samples taken at about 100 m depths throughout the year and at all localities. When we sampled fish throughout the water column (during the end of the rainy season), from near the surface and down to 150 m, we observed an average prevalence of about 24%, confirming the concern noted by Kennedy *et al.* (2001) that obtaining representative samples of *Ligula* infection levels is rather difficult.

Both the observed infection level, as well as the rather uniform distribution of the parasite within similar habitats, suggests that the host–parasite dynamics may be different in a huge lake like Nyasa, as compared to smaller lakes. One interpretation of our findings is that *E. sardella* has a significantly higher risk of becoming infected in the littoral zone than in the pelagic, since we observed consistent differences in prevalence between these habitats. An alternative mechanism that could cause such a pattern would be if infected fish tend to aggregate in the littoral zone after they have become infected. Our data do not allow us to distinguish between these two hypotheses.

Another factor that could affect the host–parasite dynamics is suggested by our observations on the vertical distribution of infected hosts, where we found a consistent decrease in prevalence with increasing depths. Some other studies (for instance Bean & Winfield, 1992) have reported the same trend, but others found no difference in the proportion of infected fish at various depths (Museth, 2001), suggesting that parasite distribution across depths depends on the fish host species.

In a huge lake like Nyasa, and with a host species that goes to depths below 150 m, we have a system that can demonstrate this pattern with a much higher resolution

Table 1. Distributions of fish sample size, mean fish size, fish sex, prevalence and mean intensity at each sampling depth in Lake Nyasa.

| Sample size (*n*) | Depth (m) | Mean (±SE) fish length (mm) | Infected fish | | Uninfected fish | | Prevalence | Intensity |
			Male	Female	Male	Female		
75	50	104.4 ± 0.89	14	9	17	35	30.67	1
75	100	97.4 ± 0.89	14	6	30	25	26.67	1
75	150	92.8 ± 0.72	6	5	24	40	14.67	1

than in most other lakes. Our results could indicate that the risk of becoming infected appears to vary, not only between the littoral and the pelagic, but also along a vertical dimension. This could be an important factor preventing dramatic declines of the intermediate host population (and the parasite), which have been observed in smaller lakes (Sweeting, 1976, 1977; Bean & Winfield, 1992; Kennedy et al., 2001), because there could be sites within the lake where transmission is significantly reduced.

However, from the present study, we cannot conclude that our observation on the distribution of infected *E. sardella* at different depths is a reflection of different transmission rates. Potentially, there could be no difference in transmission over different depths and what we observe is the result of different preferences of *E. sardella* once they have become infected. This could either be caused by some physiological side-effect of being infected – for example, a need for a higher saturation of oxygen (Lester, 1971) or increased energy requirement (Milinski, 1990) – or it could reflect active manipulation by the parasite to increase its fitness (Poulin, 2010; Moore, 2013). In any case, having an intermediate host that prefers to stay in the upper water levels must be adaptive to the parasite, since it depends on reaching its final host (fish-eating birds) through trophic transmission.

We also found that a considerable proportion of the intermediate host population was infected with *L. intestinalis* at depths between 100 and 150 m. It is highly unlikely that any bird would be able to catch these individuals, and it may seem that tapeworms present in this part of the intermediate host population are not able to be transmitted to the final host. An alternative hypothesis is that this part of the *Ligula* population consists of immature individuals, not yet ready to be transmitted to birds, and that immature parasites are actively manipulating the host to avoid being predated upon, as has been shown recently for other trophically transmitted parasites (Mikheev et al., 2010; Dianne et al., 2011; Gopko et al., 2015; Hafer & Milinski, 2015, 2016). We are currently exploring this hypothesis further.

We also observed a marked variation in prevalence throughout the year, where the highest infection levels coincided with the rainy seasons in March–May and in November–December. White-breasted cormorants (*Phalacrocorax carbo*) (one of the definitive hosts of *L. intestinalis* and therefore an important organism for the completion of the parasite's life cycle) are among the most abundant piscivorous birds of the lake (Linn & Campbell, 1992) and these exhibit, to some extent, seasonal migration, with the lowest abundance in the period March through May, i.e. at the same period when we observed a very high *Ligula* prevalence in the intermediate host. From the eggs of the tapeworm being dispersed in the lake by birds until it turns up as plerocercoid larvae in fish, there is a considerable time delay, because the eggs have to hatch into free-swimming larvae, and then the parasitic stage in copepods needs to develop into a fully developed procercoid stage before being infective to fish (Loot et al., 2001b). Even after having infected the second intermediate host, the parasite takes a considerable time to grow and mature (Loot et al., 2001b), and early stages can be difficult to discover. We should therefore not expect to see any direct correlation between the

seasonal abundance of piscivorous birds and the observed prevalence of *L. intestinalis* in fish.

Interestingly, prevalence appeared to decline very rapidly after the peak levels. In the second intermediate host, *L. intestinalis* is a long-lived species, tending to live as long as the fish. On the other hand, in the piscivorous bird, the parasite survives for only a few days (Kennedy et al., 2001). The marked decline in prevalence in the fish host can therefore not be explained by the disappearance of parasites from already infected hosts. Parts of this pattern are probably explained by a dilution effect, where young and uninfected individuals are recruited into the population during a period of low transmission. However, an additional mechanism that would contribute to the fast decline in prevalence could be that infected fish are removed from the population much faster than the uninfected ones. Our observations on the vertical distribution of the proportion of infected fish support this last hypothesis.

Conflict of interest

None.

Ethical standards

This research received ethical approval from the Tanzanian Fisheries Research Institute (application ID: TAFIRI/HQ/PF 637/100).

References

Allison, E., Irvine, K., Thompson, A. & Ngatunga, B. (1996) Diets and food consumption rates of pelagic fish in Lake Malawi, Africa. *Freshwater Biology* **35**, 489–515.

Barbour, C.D. & Brown, J.H. (1974) Fish species diversity in lakes. *The American Naturalist* **108**, 473–489.

Bean, C.W. & Winfield, I.J. (1992) Influences of the tapeworm *Ligula intestinalis* (L.) on the spatial distributions of juvenile roach *Rutilus rutilus* (L.) and gudgeon *Gobio gobio* (L.) in Lough Neagh, Northern Ireland. *Netherlands Journal of Zoology* **42**, 416–429.

Bootsma, H.A. & Hecky, R.E. (1993) Conservation of the African Great-Lakes – limnological perspective. *Conservation Biology* **7**, 644–656.

Britton, J.R., Jackson, M.C. & Harper, D.M. (2009) *Ligula intestinalis* (Cestoda: Diphyllobothriidae) in Kenya: a field investigation into host specificity and behavioural alterations. *Parasitology* **136**, 1367–1373.

Brown, S., Loot, G., Grenfell, B. & Guégan, J. (2001) Host manipulation by *Ligula intestinalis*: accident or adaptation? *Parasitology* **123**, 519–529.

Bush, A.O., Lafferty, K.D., Lotz, J.M. & Shostak, A.W. (1997) Parasitology meets ecology on its own terms: Margolis *et al.* revisited. *Journal of Parasitology* **83**, 575–583.

Cowx, I.G., Rollins, D. & Tumwebaze, R. (2008) Effect of *Ligula intestinalis* on the reproductive capacity of *Rastrineobola argentea* in Lake Victoria. *Journal of Fish Biology* **73**, 2249–2260.

Degnbol, P. (1982) Food habits of larval *Engraulicypris sardella* in Lake Malawi: diurnal feeding pattern and comparison of size groups. *FAO Fishery Expansion Project, Malawi; Biological studies on the pelagic ecosystem of Lake Malawi. Technical Report* 1, pp. 57–67. Rome, FAO.

Dejen, E., Vijverberg, J. & Sibbing, F.A. (2006) Spatial and temporal variation of cestode infection and its effects on two small Barbs (*Barbus humilis* and *B. tanapelagius*) in Lake Tana, Ethiopia. *Hydrobiologia* **556**, 109–117.

Dianne, L., Perrot-Minnot, M.J., Bauer, A., Gaillard, M., Léger, E. & Rigaud, T. (2011) Protection first then facilitation: a manipulative parasite modulates the vulnerability to predation of its intermediate host according to its own developmental stage. *Evolution* **65**, 2692–2698.

Dobben, W.v.. (1952) The food of the cormorant in the Netherlands. *Ardea* **40**, 1–63.

Dubinina, M.N. (1980) *Tapeworms (Cestoda, Ligulidae) of the fauna of the USSR*. New Delhi, Amerind Publishing.

Eccles, D.H. (1992) FAO species identification sheets for fishery purposes. *Field guide to the freshwater fishes of Tanzania. UNDP Project URT/87/016*. Rome, FAO.

Gopko, M., Mikheev, V.N. & Taskinen, J. (2015) Changes in host behaviour caused by immature larvae of the eye fluke: evidence supporting the predation suppression hypothesis. *Behavioral Ecology and Sociobiology* **69**, 1723–1730.

Gurevitch, J. & Padilla, D.K. (2004) Are invasive species a major cause of extinctions? *Trends in Ecology & Evolution* **19**, 470–474.

Hafer, N. & Milinski, M. (2015) When parasites disagree: evidence for parasite-induced sabotage of host manipulation. *Evolution* **69**, 611–620.

Hafer, N. & Milinski, M. (2016) Inter- and intraspecific conflicts between parasites over host manipulation. *Proceedings of the Royal Society of London, Biological Sciences* **283**, 2015–2870.

Kennedy, C., Shears, P. & Shears, J. (2001) Long-term dynamics of *Ligula intestinalis* and roach *Rutilus rutilus*: a study of three epizootic cycles over thirty-one years. *Parasitology* **123**, 257–269.

Kennedy, C.R. (1974) A checklist of British and Irish freshwater fish parasites with notes on their distribution. *Journal of Fish Biology* **6**, 613–644.

Kihedu, K., Mlay, M., Mwambungu, J. & Ngatunga, B. (2001) Drifting long line, a potential fishing method for the northern part of Lake Nyasa/Malawi/Niassa. *Lake Malawi Fisheries Management Symposium*, Lilongwe, Malawi, 4–9 June.

Lester, R. (1971) The influence of *Schistocephalus* plerocercoids on the respiration of *Gasterosteus* and a possible resulting effect on the behavior of the fish. *Canadian Journal of Zoology* **49**, 361–366.

Linn, I. & Campbell, K. (1992) Interactions between white-breasted cormorants *Phalacrocorax carbo* (Aves: Phalacrocoracidae) and the fisheries of Lake Malawi. *Journal of Applied Ecology* **29**, 619–634.

LNBWB (Lake Nyasa Basin Water Board). (2013) *Lake Nyasa basin water board; basin annual hydrological report Nov. 2012–Dec. 2013*. Ministry of Water, United Republic of Tanzania.

Loot, G., Brosse, S., Lek, S. & Guegan, J.F. (2001a) Behaviour of roach (*Rutilus rutilus* L.) altered by *Ligula intestinalis* (Cestoda : Pseudophyllidea): a field demonstration. *Freshwater Biology* **46**, 1219–1227.

Loot, G., Francisco, P., Santoul, F., Lek, S. & Guégan, J.-F. (2001b) The three hosts of the *Ligula intestinalis* (Cestoda) life cycle in Lavernose-Lacasse gravel pit, France. *Archiv für Hydrobiologie* **152**, 511–525.

Lovell, S.J., Stone, S.F. & Fernandez, L. (2006) The economic impacts of aquatic invasive species: a review of the literature. *Agricultural and Resource Economics Review* **35**, 195–208.

Lymbery, A.J., Morine, M., Kanani, H.G., Beatty, S.J. & Morgan, D.L. (2014) Co-invaders: the effects of alien parasites on native hosts. *International Journal for Parasitology: Parasites and Wildlife* **3**, 171–177.

Maguza-Tembo, F., Palsson, O. & Msiska, O. (2009) Growth and exploitation of *Engraulicypris sardella* in the light attraction fishery of southern Lake Malawi. *Malawi Journal of Aquaculture and Fisheries (MJAF)* **6**, 6–12.

Marshall, J. & Cowx, I. (2003) Will the explosion of *Ligula intestinalis* in *Rastrineobola argentea* lead to another shift in the fisheries of Lake Victoria. pp. 244–258 in Cowx, I.G. (Ed.) *Interactions between fish and birds: Implications for management*. Oxford, UK, Blackwell Science.

Mikheev, V.N., Pasternak, A.F., Taskinen, J. & Valtonen, E. (2010) Parasite-induced aggression and impaired contest ability in a fish host. *Parasites & Vectors* **3**, 17.

Milinski, M. (1990) Parasites and host decision-making. pp. 95–116 in Barnad, C.J. & Behnke, J.M. (Eds) *Parasitism and host behaviour*. London, Taylor & Francis.

Moore, J. (2013) An overview of parasite-induced behavioral alterations – and some lessons from bats. *Journal of Experimental Biology* **216**, 11–17.

Msafiri, A., Kwendwa, K., Nestory, P.G. & Alistidia, M. (2014) Assessment of the effects of plerocercoid larvae of *Ligula intestinalis* (Cestoda) on *Engraulicypris sardella* (Cyprinidae) from northern Lake Nyasa/Malawi/Niasa. *Aquatic Ecosystem Health & Management* **17**, 90–96.

Museth, J. (2001) Effects of *Ligula intestinalis* on habitat use, predation risk and catchability in European minnows. *Journal of Fish Biology* **59**, 1070–1080.

Mwambungu, J., Ngatunga, B.P., Kihedu, K.J. & Mlay, M.K.L. (1996) Development of longline fishery in the Tanzania coast of Lake Nyasa. *Tanzania Fisheries Research Institute Bulletin* **1996**, 1–12.

Ngupula, G.W., Ezekiel, C.N., Kimirei, I.A., Mboni, E. & Kashindye, B.B. (2012) Physical and chemical characteristics of the Tanzanian inshore and offshore waters of Lake Victoria in 2005–2008. *African Journal of Aquatic Science* **37**, 339–345.

Pejchar, L. & Mooney, H.A. (2009) Invasive species, ecosystem services and human well-being. *Trends in Ecology & Evolution* **24**, 497–504.

Poulin, R. (2010) Parasite manipulation of host behavior: an update and frequently asked questions. *Advances in the Study of Behavior* **41**, 151–186.

Rufli, H. & Van Lissa, J. (1982) Age and growth of *Engraulicypris sardella* in Lake Malawi. *Biological studies on the pelagic ecosystem of Lake Malawi. FAO Technical Report* 1, pp. 85–97. Rome, FAO.

Rusuwa, B., Ngochera, M. & Maruyama, A. (2014) *Ligula intestinalis* (Cestoda: Pseudophyllidea) infection of *Engraulicypris sardella* (Pisces: Cyprinidae) in Lake Malawi. *Malawi Journal of Science and Technology* **10**, 8–14.

Stefka, J., Hypsa, V. & Scholz, T. (2009) Interplay of host specificity and biogeography in the population structure of a cosmopolitan endoparasite: microsatellite study of *Ligula intestinalis* (Cestoda). *Molecular Ecology* **18**, 1187–1206.

Sweeting, R. (1976) Studies on *Ligula intestinalis* (L.) effects on a roach population in a gravel pit. *Journal of Fish Biology* **9**, 515–522.

Sweeting, R. (1977) Studies on *Ligula intestinalis*. Some aspects of the pathology in the second intermediate host. *Journal of Fish Biology* **10**, 43–50.

Taraschewski, H. (2006) Hosts and parasites as aliens. *Journal of Helminthology* **80**, 99–128.

Thompson, A. (1996) Early life history of *Engraulicypris sardella* (Cyprinidae) in Lake Malawi. *Journal of Plankton Research* **18**, 1349–1368.

Vanacker, M., Masson, G. & Beisel, J.N. (2012) Host switch and infestation by *Ligula intestinalis* L. in a silver bream (*Blicca bjoerkna* L.) population. *Parasitology* **139**, 406–417.

Vollmer, M.K., Bootsma, H.A., Hecky, R.E., Patterson, G., Halfman, J.D., Edmond, J.M., Eccles, D.H. & Weiss, R.F. (2005) Deep-water warming trend in Lake Malawi, East Africa. *Limnology and Oceanography* **50**, 727–732.

Wilson, R. (1971) The decline of a roach *Rutilus rutilus* (L.) population in Chew Valley Lake. *Journal of Fish Biology* **3**, 129–137.

Wyatt, R.J. & Kennedy, C.R. (1988) The effects of a change in the growth-rate of roach, *Rutilus rutilus* (L), on the biology of the fish tapeworm *Ligula intestinalis* (L). *Journal of Fish Biology* **33**, 45–57.

Zhokhov, A.E. & Pugacheva, M.N. (2012) Distribution and occurrence of *Ligula intestinalis* (L.) plerocercoids (Cestoda, Ligulidae) in the fishes of Lake Tana, Ethiopia. *Inland Water Biology* **5**, 293–298.