

Increased reproductive investment in an exploited African cyprinid fish following invasion by a castrating parasite in Lake Nyasa, Tanzania

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Abstract

Evolutionary theory predicts that a host infected with a parasite that reduces its future survival and/or fecundity should be selected towards an increased investment in current reproduction. In this study we use the cestode *Ligula intestinalis* and its intermediate fish host *Engraulicypris sardella* in Wissman Bay, Lake Nyasa (Tanzania) as a model system. Using data about infestation of *E. sardella* fish hosts by *L. intestinalis* collected for a period of 10 years, we explored (i) whether parasite infection affects the fecundity of the fish host *E. sardella* and (ii) whether host reproductive investment has increased at the expense of growth at maturity. We found that *L. intestinalis* had a strong negative effect on the fecundity of its intermediate fish host. For the non-infected fish we observed an increase in relative gonadal weight over the study period, while somatic growth at maturity decreased during the study period. Our findings suggest that the cestode *L. intestinalis* might have selected for increased investment in current reproduction in its fish host *E. sardella* in Lake Nyasa. This calls for further studies to assess whether these changes reflect plastic or evolutionary responses. We also discuss the synergy between parasite and fishery-mediated selections as a possible explanation for the decline of *E. sardella* stock in the lake. **KEYWORDS** *Engraulicypris sardella*; *Ligula intestinalis*; life history evolution; selective agents; parasitism; fishing.

KEYWORDS

Engraulicypris sardella; *Ligula intestinalis* ; life history evolution; selective agents; parasitism; fishing.

1.0 INTRODUCTION

Life history theory assumes that there are trade-offs between different traits in organisms, such as growth, reproduction and survival (Roff, 2002). These traits cannot be simultaneously maximized within the same individual because the available amount of nutrients and other resources are in limited supply (Stearns, 1989). Increased resource allocation into one trait will, therefore, come at the cost of reduced allocation into other traits (Agnew et al., 2000). In each given environment, the optimal way to resolve these trade-offs (*i.e.*, the optimal strategy for maximizing fitness) is the one achieving the highest possible reproductive success (Agnew et al., 2000; Pianka, 1976; Stearns, 1989). For instance, if adult mortality increases within a population (*e.g.*, due to increased predation), individuals that mature relatively earlier and invest relatively more into current reproduction *versus* future survival will be favoured by natural selection (Fredensborg and Poulin, 2006).

For fish, both natural predation and fishing (*i.e.*, predation by humans) are important selective factors that drive adaptive changes in life history traits such as developmental rates and timing of reproduction (Heino and Godø, 2002; Jorgensen et al., 2007; Jørgensen et al., 2009; Sharpe et al., 2012). Fishing practices and predation are usually non-random factors, as gears are often designed to selectively take larger and older fish in the population (Law, 2000). In this case, smaller fish are likely to have a higher probability of survival than

the larger ones, and among them, those that can mature and reproduce early will be selected favourably. Assuming that early maturation is heritable to some extent, this should result in life histories changing towards earlier reproduction at smaller sizes.

Parasitism can also affect the future reproductive success of hosts (Fredensborg and Poulin, 2006) and thus select for changes in host life history traits (Adamo, 1999; Agnew et al., 1999; Lafferty, 1993b; McCurdy et al., 1999; Perrin et al., 1996; Polak and Starmer, 1998; Richner and Tripet, 1999; Sorci et al., 1996; Thomas et al., 2000; Yan et al., 1997). For instance, an increase in the prevalence of parasites causing castration (*i.e.*, destruction or alteration of the host's gonadal tissues by the parasite; (Noble and Noble, 1971)) (Fredensborg and Poulin, 2006; Lafferty, 1993a; Loot et al., 2002; Minchella and Loverde, 1981) can select for earlier maturity. For the infected host, achieving reproduction prior to castration yields clear fitness benefits (Gooderham and Schulte-Hostedde, 2011; Lafferty, 1993a; Minchella and Loverde, 1981), and these benefits increase along with infection risk (Minchella and Loverde, 1981; Polak and Starmer, 1998; Sorci et al., 1996). Increased reproductive effort in hosts exposed to castrating parasites has been reported in a number of species. So far, however, most documented life history changes seem to result from adaptive plastic responses of hosts to parasitic exposure, more than life history evolution following a change in parasite-mediated selection (Chadwick and Little, 2005; Hudson et al., 2019; Vale and Little, 2012).

Ligula intestinalis (L. 1758) is a common and widespread cestode, that use cyprinid fish as intermediate hosts (Dubinina, 1980). In Lake Nyasa this cestode has been increasingly reported since it was first noted by Mwambungu et al. (1996), where it infects the endemic pelagic fish *Engraulicypris sardella* (Figure 1) (Gabagambi et al., 2019; Gabagambi and Skorpung, 2018; Msafiri et al., 2014; Rusuwa et al., 2014). *L. intestinalis* is known to induce castration in several intermediate hosts (Cowx et al., 2008; Hoole et al., 2010; Kennedy et al., 2001; Loot et al., 2002; Wyatt and Kennedy, 1988) and has therefore been suggested to cause population crashes of its host (Burrough et al., 1979; Kennedy et al., 2001). This could sometimes lead to local extinction of the parasite in small ecosystems (Kennedy et al., 2001). Recent results, however, indicate that local extinction of this parasite is unlikely in Lake Nyasa due to spatial and temporal variations in transmission rates (Gabagambi and Skorpung, 2018).

Under such conditions of recent parasite invasion, we hypothesize that the cestode *L. intestinalis* should select for a shift in resource investment from somatic growth towards reproduction in its intermediate fish host *E. sardella*. Using data collected from 2005 to 2013 and then in 2015 in the northern part of Lake Nyasa, we address the following three questions:

(i) What are the effects of *L. intestinalis* on the fecundity of *E. sardella*? (ii) has reproductive investment at maturity of *E. sardella* increased over time? and (iii) has the average size at maturity of *E. sardella* decreased since the parasite was first identified in the lake?

We then further discuss the selective roles of parasitic invasion *versus* other environmental factors that may recently have changed in Lake Nyasa.

2.0 METHODS

2.1 Study area

The study was conducted in the northern part of Lake Nyasa, Tanzania side. Lake Nyasa, also known as Lake Malawi in Malawi and Lago Niassa in Mozambique, is the southernmost great lake in the East African Rift Valley system, located between Malawi, Mozambique and Tanzania. The lake is the third largest freshwater lake in Africa after lakes Victoria and Tanganyika and is the second largest lake by volume after Lake Tanganyika (Darwall et al., 2010; Hampton et al., 2018; Macuiane et al., 2015). The lake has a maximum depth of 785 m, a volume of 8,400 Km³, a surface area of 29,000 Km², approximate length of 550 Km and mean width of around 48-60 Km and is located 472 m above the sea level (Bootsma and Hecky, 1993; Darwall et al., 2010; Gonfiantini et al., 1979; Patterson and Kachinjika, 1995). The total catchment area of the lake is 126,500 Km² (Kumambala and Ervine, 2010) of which 97,750 Km² is land catchment (Menz, 1995). The mean surface temperature of the lake is between 24 and 28 °C (Vollmer et al., 2005) and the annual rainfall

ranges between 1,000 and 2,800 mm (LNBWB, 2013). The lake experiences two main seasons, the dry season (May-August) and wet season (November-April), which are governed by the regional climate (Lyons et al., 2011; Vollmer et al., 2005).

Lake Nyasa is meromictic, although it may experience mixing during the dry season in the southern tip of the lake where the depth is relatively shallow (Darwall et al., 2010; Vollmer et al., 2005; Weyl et al., 2010). Due to the stratification, together with the great depth of the lake, the nutrients availability to the plankton community are very low, and thus, the lake is considered ‘oligotrophic’ (Irvine et al., 2001; Mwambungu and Ngatunga, 2001). The lake has more than 1,000 different fish species, many of which are endemic (Chafota et al., 2005; Salzburger et al., 2014). Sampling was conducted at Wissman Bay that is located at the northern end of the lake (sampling stations of Matema S9°29′; E34°01′, Mwaya S9°33′; E33° 57′, Kafyofyo S9°35′; E33°57′ and Kiwira S9°37′; E33° 57′).

2.2 The host

Engraulicypris sardella (Günther, 1868), locally known as Usipa or Lake Malawi sardine, is a small, slender, silvery, zooplanktivorous, pelagic social fish endemic to Lake Nyasa (Lowe-McConnell, 1993; Ruffi and Van Lissa, 1982). The fish occurs in shoals, which are widely distributed within the lake and found in both near-shore areas and offshore pelagic water, down to a depth of approximately 200 m (Maguza-Tembo et al., 2009). *E. sardella* is an annual species, where hatchlings grow and age to reproduce and die in a yearly cycle (Iles, 1960), although some studies have reported that they can live longer (Rusuwa et al., 2014; Thompson and Bulirani, 1993).

During early developmental stages *E. sardella* feeds exclusively on phytoplankton, then switches to feeding on zooplankton once reaching adulthood (Allison et al., 1996; Degnbol, 1982). *E. sardella* demonstrates a rapid growth rate and can attain a maximum total length of about 130 mm in a year (Thompson, 1996; Tweddle and Lewis, 1990). Males and females mature at a size of about 70 and 75 mm respectively (Thompson and Allison, 1997; Thompson et al., 1996). They have been reported to breed throughout the year but with bi-annual recruitment peaks occurring during both the wet season and dry season (Morioka and Kaunda, 2005; Rusuwa et al., 2014). We continuously observe small individuals of *E. sardella* in the lake suggesting a continuous spawning behaviour in this species (pers. obs.).

E. sardella forms an important part of the food web of Lake Nyasa. The species is primary consumer of zooplankton (Degnbol, 1982; Konings, 1990), but they are also an important native prey of pelagic piscivorous fishes, particularly *Diplotaxodon* spp. and *Rhamphochromis* spp. (Allison et al., 1996), as well as piscivorous birds (Linn and Campbell, 1992). *E. sardella* is also of high commercial value, and for many decades it has been the main animal protein source for most of the local human population (Manyungwa-Pasani et al., 2017).

2.3 The parasite

Ligula intestinalis (Linnaeus, 1758) is a cestode infecting a wide range of fish hosts particularly cyprinids (Kennedy, 1974). In infected fish like *E. sardella* it is found filling the body cavity. The parasite is trophically transmitted and has a complex life cycle involving two aquatic intermediate hosts, a zooplankton copepod and a fish (Dubinina, 1980). It reaches sexual maturity in the abdominal cavity of piscivorous birds that are the final hosts (*i.e.* the hosts where parasite reproduction takes place) (Dubinina, 1980).

The invasion of *L. intestinalis* in Lake Nyasa was first noted in the late 1990s during long-line research surveys where a milkish white worm was found in the body cavity of *E. sardella* (Mwambungu et al., 1996). The worm was identified to be the tapeworm *Ligula intestinalis* (L.). This parasite is believed to be introduced in Lake Nyasa by migrating infected fish-eating birds such as the White-breasted cormorant (*Phalacrocorax carbo*), which is among the most abundant fish-eating birds in the Lake Nyasa basin (Linn and Campbell, 1992) and one of the final hosts of *L. intestinalis* (Loot et al., 2001; Rosen, 1920). Higher infection rates are observed in larger and older *E. sardella* than in juvenile individuals (Msafiri et al., 2014; Rusuwa et al., 2014), which can be explained by diet shifts from phytoplankton to zooplankton as *E. sardella* reach maturity.

2.4 Sampling procedure

Information on the infection of *E. sardella* fish hosts by the parasite *L. intestinalis* was collected over a period of 10 years, from 2005 to 2013 and then in 2015 in Wissman Bay. In the period 2005-2013 data was generated from fish caught by local fishermen from sites of Matema, Mwaya, Kafyofyo and Kiwira within Lake Nyasa. *E. sardella* were caught using an open water seine net, locally known as 'Ndaturu', with 10 mm mesh size at a depth of about 100 m during the dark moon phase days. In 2015, fish were caught by our research team, using the same traditional fishing method as was used in the period 2005-2013.

The fishing procedure involved nine crew members using two dug-out canoes and one large plank-boat. On the fishing ground, one of the dug-out canoes was equipped with pressurized paraffin lamps (between one to three) and was stationed with one crew member away from the remaining vessels. The artificial light was used to concentrate the fish into the given area. This process took several hours. After a sufficient amount of fish had been attracted, the other unlit fishing vessels simultaneously deployed a net in a semicircular shape around the concentrated fish, and this was hauled by hand into the plank-boat. Sampling was carried out in both lake habitats (i.e. littoral and pelagic zones) as well as throughout different seasons (i.e. dry and wet seasons) and a total of 3,488 *E. sardella* were sampled (Table 1). Upon landing, the total length and weight of each *E. sardella* were measured to the nearest 5 mm and 0.01 g respectively. The fish were later dissected for parasite determination. *L. intestinalis* was identified according to the protocol by Dobben (1952). The sex of *E. sardella* was determined using a stereomicroscope (Wild Heerbrugg M5) at 6.4X magnification. Gonad maturity was assessed on a seven-stage maturity scale (Table 2), modified from Holden and Raitt (1974). For seven years of the ten years (i.e. 2005, 2006, 2010, 2011, 2012, 2013 and 2015) the maturity stages of *E. sardella* was determined and recorded by the same investigator (N.P.Gabagambi). Therefore, we were able to maintain a good level of consistency and accuracy in the determination of maturity stage across our sampling period. In 2007, 2008 and 2009 maturity determination was carried out by trained research technicians (E.J.Magesa and J.M.Masore), following the same seven-stage maturity scale as was applied in all other sampling years.

Gonads were weighed to the nearest 0.01 g (wet weight) using sensitive precision balances (vwrTM-model ECN 611-2315 and EndelTM- model WPS) and fecundity for infected and non-infected female *E. sardella* was determined through gravimetric methods (Holden and Raitt, 1974) by counting the advanced yolked oocytes present in ripe and gravid *E. sardella*. The complete ovary was taken out and preserved in modified Gilson's fluid (100 ml 60% alcohol, 800 ml water, 15 ml 80% nitric acid, 18 ml glacial acetic acid, 20 g mercuric chloride) for 24 hours. Thereafter, the ovaries were shaken periodically to help loosen the eggs from connecting ovarian tissues. After the eggs were liberated from the ovarian tissues, they were washed thoroughly, spread on blotting paper, and allowed to dry at ambient temperature ranging between 25 and 30 degC. Thereafter, the total numbers of eggs were weighed to the nearest 0.01 g using sensitive precision balance to have a total weight of eggs. Afterwards we collected a random sub-sample of the eggs, which were weighed and counted out on petri dish sub-sections using a stereomicroscope (Wild Heerbrugg M5) at 6.4X magnification. The total number of eggs (i.e. fecundity) in the ovaries was calculated following the formula given by Holden and Raitt (1974) as follows; $F = nG/g$ where; n =number of eggs in sub-sample, G =total weight of eggs from the ovary, g = weight of the sub-sample. Fish somatic weight was determined by subtracting the gonad weight from the total weight of the fish.

2.5 Statistical analyses

(i) The effect of *L. intestinalis* infection on host fecundity was tested using a generalized linear mixed-effects model (glmmPQL) fitted with Quasi-Poisson distribution with fecundity as a response variable, and maturity stage and infection status as predictor variables. Because the data were collected over a 10-year period, year of sampling was included as a random effect factor in the model.

(ii) To test whether reproductive investment at maturity has increased over time, we used a generalized linear model (glm) fitted with a binomial distribution. The binomial response variable combined gonadal weight of uninfected *E. sardella* and somatic weight. We chose to use relative gonad weight at stage IV

because this is the stage where *E. sardella* reach reproductive maturity. Year was included as a covariate.

(iii) To test whether size of *E. sardella* at maturity has decreased over time, we used a linear model (lm) including body length of uninfected *E. sardella* at stage IV as a response variable and year as a covariate. To explore whether body growth after maturity decreased over time we also tested whether body length at stage V decreased over time. All statistics and graphics were carried out using R, version 3.2.5 (<http://r-project.org>).

3.0 RESULTS

A total of 3,488 individuals were sampled and measured for length, weight, gonad maturation, and fecundity over the study period (Table 1). Infected individuals had an overall lower fecundity than non-infected individuals (glmmPQL, estimate = -1.08 \pm 0.08, d.f. = 3416, $t = -13.92$, $P < 0.001$; Figure 2).

Reproductive investment at maturity (stage IV) in non-infected *E. sardella* increased significantly over time between 2005 and 2013 and then in 2015 (glm, estimate = 0.14 \pm 0.01, d.f. = 1, $t = 9.59$, $P < 0.001$; Figure 3).

The body length of non-infected *E. sardella* at stage IV (maturity) did not decrease over time (Fig. 3). If anything, it seemed to increase significantly, albeit very slightly (lm, estimate = 0.43 \pm 0.05, d.f. = 1, $t = 8.42$, $P < 0.001$). On the contrary, body length at stage V (post-maturity) decreased significantly over time (lm, estimate = -1.27 \pm 0.06, d.f. = 1, $t = -21.12$, $P < 0.001$; Figure 4).

4.0 DISCUSSION

L. intestinalis has a strong negative effect on the fecundity of its intermediate host, *E. sardella*. Such an effect, which was also found in other fish host species, thus seems widespread throughout the species range of this parasite (Barson and Marshall, 2003; Carter et al., 2005; Cowx et al., 2008). We also found that the relative weight of gonads in relation to body size increased over the 10-year duration of this study, and observed a decline in somatic growth at maturity (from stage IV to stage V). These temporal changes were found in non-infected fish, which indicates that they may reflect evolutionary changes in the life history of *E. sardella*.

Organisms are selected for changes in life history traits when age-specific death or fecundity rates are changed (Forbes, 1993). In our study, we observed an overall 69% lower fecundity in infected *versus* uninfected hosts, that is, the cestode *L. intestinalis* caused a significant partial castration in *E. sardella*. Reduced host fecundity is a common outcome associated with parasite infection (Hurd, 2001) and contribute to reduced host fitness (Gooderham and Schulte-Hostedde, 2011). Infected hosts may compensate for this fitness loss by shifting their life histories towards earlier reproduction (Jokela and Lively, 1995; Lafferty, 1993b). Many host species have been shown to increase their early reproductive output if their chances for future reproduction are reduced (Adamo, 1999; Minchella and Loverde, 1981).

Our observations of an increase in gonadal weight in relation to fish body size suggest that reproductive investment in *E. sardella* has increased at the expense of investment in somatic growth after reaching maturity. These findings are consistent with our prediction that their life histories should shift towards earlier reproduction. The fact that they come from an analysis of the non-infected fish indicates that this change is not a secondary effect of infection. More work is warranted, however, to determine whether it is caused by plastic or evolutionary responses.

A parasitic relationship between *L. intestinalis* and *E. sardella* in Lake Nyasa was first observed in 1996 (Mwambungu et al., 1996). An earlier study investigating the breeding biology and in particular examining the ovaries of *E. sardella* between 1992 and 1994, did not report any case of *L. intestinalis* infection (Thompson, 1996). We believe this suggests that this tapeworm was likely absent from Lake Nyasa prior to the late 1990s. After the first observation, *E. sardella* in the lake kept being found infected by *L. intestinalis*, as manifested by the work of J.K.Kihedu (MSc thesis, Sokoine University of Agriculture, Tanzania, 2006, unpublished data). The earliest sampling year in our study is 2005, where prevalence is estimated at 50%.

This indicates that *L. intestinalis* has spread steadily, and therefore that selection caused by this parasite on its host has increased during the early years after introduction.

A shift towards investment in current reproduction has been reported in many other host-parasite systems, where infected hosts increased their reproductive effort before dying or being castrated by the parasite. In insects, Polak and Starmer (1998) observed that experimentally parasitized male *Drosophila nigrospiracula* infected with a mite (*Macrocheles subbadius*) lived shorter lives, but before dying they courted females significantly more than non-parasitized controls. Further, Adamo (1999) observed that female crickets (*Acheta domesticus*) increased egg laying in response to infection with the bacterium *Serratia marcescens*. In snails, Minchella and Loverde (1981) and Thornhill et al. (1986) observed an increase in reproductive output in female *Biophalaria glabrata* parasitized by a castrating trematode *Schistosoma mansoni*. In crustaceans, Chadwick and Little (2005) observed that *Daphnia magna* infected with a microsporidian *Glugoides intestinalis* shifted their life-history towards early reproduction. In birds, Sanz et al. (2001) observed that female pied flycatchers (*Ficedula hypoleuca*) with hemoparasite infection initiated egg laying earlier and laid larger clutches. In reptiles, Sorci et al. (1996) observed that common lizards (*Lacerta vivipara*) increased their reproductive investment after being infected with haematozoans. More examples where reproduction is seen to increase with the onset of infection have been reviewed in Schwanz (2008). Taken together, these studies show that parasites, by affecting the future reproductive success of their hosts, induce life history changes in infected hosts, and that these plastic changes are adaptive.

Here we observe a shift towards increased reproductive effort at the expense of somatic growth across generations, in non-infected hosts. This pattern, which cannot be explained by plastic life history responses to infection, might reflect adaptation to recent selective changes in Lake Nyasa. Importantly, increased parasite pressure may not be the only environmental change that has taken place in Lake Nyasa over the last couple of decades. Other potential sources of selection for earlier reproduction include: fishing (Fenberg and Roy, 2008; Heino and Godo, 2002; Hutchings and Fraser, 2008; Jorgensen et al., 2007; Jorgensen et al., 2009; Kuparinen and Merila, 2007; Sharpe and Hendry, 2009; Sharpe et al., 2012); increased predation by native or introduced species (Hampton et al., 2018; Sharpe et al., 2012); and fluctuations in zooplankton abundance that may induce earlier maturation.

Most evidence of fishery-induced evolution comes from large, heavily exploited fish population stocks (e.g. North Arctic cod) where industrial fishing using trawlers has been in practice for many years. On the contrary, the Lake Nyasa *E. sardella* fishery is mainly traditional, operating in near-shore lake zones using paddled dugout canoe crafts (Mwambungu and Ngatunga, 2001). Over the past decades, however, fishing effort catch rates have decreased in Wissman Bay, where the present study was conducted. (Figure S1).

Increased fishing effort has also been reported for other fish species than *E. sardella* in riparian countries around lake Nyasa such as Tanzania (Irvine et al., 2018; Irvine et al., 2002), Mozambique (Halafo et al., 2004; Irvine et al., 2018) and Malawi (Irvine et al., 2018; Weyl et al., 2010).

In the present study, *E. sardella* were sampled using the traditional fishing method. The majority of the sampled fish was composed of individuals of the body sizes between 50-100 mm in length (Figure S2), which corresponds to mature fish (*i.e.* from stage IV and above). This suggests that the traditional *E. sardella* fishing practice is probably size-selective and induces a higher mortality in adults than younger fish. Interestingly, the number of tones landed per fisherman (which can be considered as representing stock density) dramatically decreased in 2013 (Figure S1), following three consecutive years with both high *L. intestinalis* prevalence (strongly reducing *E. sardella* fecundity) and sustained fishing effort (increased adult mortality) (Figure S1). Therefore, we argue that parasitism by *L. intestinalis* may have acted synergistically with fishery-mediated selection in driving what appears like an evolutionary shift towards earlier life history of *E. sardella* in Lake Nyasa.

Increased predation by native or introduced organisms could also be one factor affecting selection on life history traits of *E. sardella*. In the native cyprinid fish *Rastrineobola argentea* in Napoleon Gulf of Lake Victoria, Sharpe et al. (2012) observed decreased body size, maturation at smaller sizes and increased

reproductive effort in response to the introduced predator fish *Lates niloticus* . However, in contrast to Lake Victoria and many other ancient lakes where dozens of non-native species have been introduced over the past decade (Hampton et al., 2018), in Lake Nyasa no new introduced predator for *E. sardella* has been reported so far. The primary natural piscivorous predators of *E. sardella* in this lake are the pelagic haplochromine cichlids from the genera *Ramphochromis*, *Diplotaxodon*, and *Copadichromis*, as well as the larger cyprinids *Opsaridium microlepis* and *O. microcephalum* . Increased abundance of the native predators of *E. sardella* over time in the lake could have selected for life history changes similar to those observed here. Unfortunately, the area where the present study was conducted is a data-poor region; the last pelagic ecosystem stock assessment was conducted between 1991-1994 (Menz (1995)). Recent time series on the abundance fluctuations of the natural predators of *E. sardella* are lacking. Further research, particularly on the combined effects of parasitism, fishing, and natural predation on *E. sardella* in Lake Nyasa, would be highly valuable, given the ecological and economical importance of this fish species.

Another factor that could have affected selection on the life history traits of *E. sardella* in Lake Nyasa may be concomitant increases in the prevalence of other parasites. In their natural habitats hosts are usually infected by two or more different parasite species (Kotob et al., 2017; Petney and Andrews, 1998). To the best of our knowledge, the only other parasite that has been reported to infect *E. sardella* is the nematode *Camallanus* sp. (Mgwede and Msiska, 2018). In the present study, we caught 3,488 wild, *i.e.* naturally-infected *E. sardella* , none of them observed with *Camallanus* sp. infection.

Overall, this study reveals that life history of *E. sardella* in Lake Nyasa has been shifting, over a period corresponding to the invasion of this lake by a castrating parasite. It remains correlative, and more work is needed to examine the evolutionary nature of these changes. Yet the cestode *L. intestinalis* , by strongly reducing the fecundity of its host, appears as likely as fisheries to drive such evolution. Our study suggests that these two types of selective factors may have acted in synergy.

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CONFLICT OF INTEREST

None declared.

AUTHOR CONTRIBUTION

AS designed the study; NPG collected the data in the field; NPG and AM analyzed the data; NPG wrote the first draft; AS, MC, KJK and AM provided critical revisions and comments to the manuscript.

DATA ACCESSIBILITY

Data sets supporting this manuscript will be uploaded as part of electronic supplementary material upon acceptance of the manuscript for publication.

ETHICS AND STATEMENT

This research received ethical approval from Tanzania Fisheries Research Institute (Application ID: TAFIRI/HQ/PF637/100).

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Tables

Table 1

Year	Maturity stage I	Maturity stage II	Maturity stage III	Maturity stage IV	Maturity stage V	Maturity stage VI	Maturity stage VII
2005			13 (6)	12 (6)	126 (64)		
2006		1 (0)	195 (51)	40 (11)	38 (1)	337 (60)	
2007			212 (8)	45 (6)	529 (140)	149 (37)	
2008		2 (0)	59 (13)	14 (9)	6 (2)	153 (12)	3 (2)
2009			16 (7)	15 (6)	215 (8)	52 (2)	
2010		14 (0)	47 (11)	14 (6)	31 (14)	17 (8)	

2011		2 (0)	28 (10)	13 (5)	2 (1)	3 (0)	
2012	4 (0)	17 (0)	136 (37)	23 (18)			
2013	2 (0)	24 (0)	68 (19)	28 (17)	8 (3)		
2015			62 (8)	215 (33)	498 (58)		
Total	6 (0)	60 (0)	836 (170)	419 (120)	1453 (291)	711 (119)	3 (2)

Table 2

Maturity stage	Maturity status	Maturity description
I	Immature	Immature fish with ovaries in a pinkish-translucent colour
II	Maturing	Maturing fish with ovaries in pinkish colour
III	Ripening	Ripening fish with ovaries in pinkish-yellow colour
IV	Ripe	Pre-spawning fish with ovaries in orange-pinkish colour with conspicuous superficial
V	Partial spent	Spawning fish with ripe ovaries
VI	Running	Ovaries yellowish-brown
VII	Spent	Ovaries loose and flabby

Tables legends

Table 1

Sample size of *E. sardella* per maturity stage sampled at Wissman Bay, Lake Nyasa between 2005 and 2013 and then in 2015. Number in parentheses show the number of infected fish out of the sampled fish.

Table 2

Gonad maturity stages of a female *E. sardella* modified from Holden and Raitt (1974).

Figures

Figure 1



Figure 2

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Figure 3

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Figure 4

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Figures legends

Figure 1

Laboratory picture of tapeworm *L. intestinalis* and its host fish *E. sardella* . Source: Courtesy of Nestory Peter Gabagambi (2015).

Figure 2

Fecundity (number of eggs in the gonads) of *E. sardella* at various maturity stages, for non-infected fish (black circles) and fish infected by *L. intestinalis* (grey circles). Sample sizes are indicated in parentheses.

Figure 3

Temporal increase in reproductive investment at maturity (stage IV) of non-infected *E. sardella*. Sample sizes are indicated in parentheses.

Figure 4

Temporal changes in body length of non-infected *E. sardella* , at stages IV (black circles) and V (grey circles). Sample sizes are indicated in parentheses.