Life history shifts in an exploited African fish following invasion by a castrating parasite

Nestory Gabagambi[1]

[1]University of Bergen Faculty of Mathematics and Natural Sciences

August 28, 2020

Abstract

Evolutionary theory predicts that infection by a parasite that reduces future host survival or fecundity should select for 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 infection of E. sardella fish hosts by L. intestinalis collected for a period of 10 years, we explored whether parasite infection affects the fecundity of the fish host E. sardella, and whether host reproductive investment has increased at the expense of somatic growth. 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 at maturity over the study period, while size at maturity decreased. These findings suggest that the life history of E. sardella has been shifting towards earlier reproduction. Further studies are warranted to assess whether these changes reflect plastic or evolutionary responses. We also discuss the interaction between parasite and fishery-mediated selection as a possible explanation for the decline of E. sardella stock in the lake. KEYWORDS Life history evolution; African Great Lakes; Lake Nyasa; Usipa; Lake Malawi sardine; Parasite invasion; Environmental change.

KEYWORDS

Life history evolution; African Great Lakes; Lake Nyasa; Usipa; Lake Malawi sardine; Parasite invasion; Environmental change.

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 (Pianka, 1976; Stearns, 1989; Agnew *et al.* , 2000). 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 (Jorgensen*et al.* , 2007; Jørgensen *et al.* , 2009). Assuming that early maturation is heritable to some extent, this should

result in life histories changing towards earlier reproduction at smaller sizes (Heath*et al.* , 2002; Olsen *et al.* , 2004; Ayllon *et al.* , 2015; Sinclair-Waters *et al.* , 2020).

Parasitism can also affect the future reproductive success of hosts (Fredensborg and Poulin, 2006) and thus select for changes in host life history traits (Lafferty, 1993b; Perrin *et al.* , 1996; Sorci*et al.* , 1996; Yan *et al.* , 1997; Polak and Starmer, 1998; Adamo, 1999; Agnew *et al.* , 1999; McCurdy *et al.* , 1999; Richner and Tripet, 1999; Thomas *et al.* , 2000). 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) can select for earlier maturity (Minchella and Loverde, 1981; Lafferty, 1993a; Loot *et al.* , 2002; Fredensborg and Poulin, 2006). For the infected host, achieving reproduction prior to castration yields clear fitness benefits (Minchella and Loverde, 1981; Lafferty, 1993a; Gooderham and Schulte-Hostedde, 2011), and these benefits increase along with infection risk (Minchella and Loverde, 1981; Sorci *et al.* , 1996; Polak and Starmer, 1998). 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; Vale and Little, 2012; Hudson *et al.* , 2019).

In this study, we investigated whether the castrating parasitic cestode*Ligula intestinalis* was responsible for a life history change in the cyprinid fish *Engraulicypris sardella* in Lake Nyasa. We studied the freshwater fish *E. sardella* , which is the second intermediate host for the cestode *L. intestinalis* . *E. sardella* (Günther, 1868), locally known as Usipa or Lake Malawi sardine, is a small, slender, silvery, zooplanktivourous fish endemic to Lake Nyasa (Rufli and Van Lissa, 1982; Lowe-McConnell, 1993) that 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 indicate that they can live longer (Thompson and Bulirani, 1993; Rusuwa *et al.* , 2014). They have been reported to breed throughout the year but with bi-annual recruitment peaks occurring during the wet season and dry season (Morioka and Kaunda, 2005; Rusuwa *et al.* , 2014).

During early developmental stages *E. sardella* feeds exclusively on phytoplankton, then switches to feeding on zooplankton upon reaching adulthood (Degnbol, 1982; Allison *et al.* , 1996). *E. sardella* demonstrates a rapid growth rate and can attain a maximum total length of about 130 mm in a year (Tweddle and Lewis, 1990; Thompson, 1996). Males and females mature at a size of about 70 and 75 mm respectively (Thompson *et al.* , 1996; Thompson and Allison, 1997).

E. sardella forms an important part of the food web of Lake Nyasa. The species is primary consumer of zooplankton (Degnbol, 1982; Konings, 1990), and an important prey for 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). However, recently it has been observed that these cyprinids are infected by the cestode *L. intestinalis* .

L. intestinalis (L. 1758) is a common and widespread cestode, that uses cyprinid fish as the second intermediate host (Kennedy, 1974; Dubinina, 1980). The parasite is trophically transmitted and has a complex life cycle involving two aquatic intermediate hosts, a planktonic copepod and a fish (Dubinina, 1980; Loot *et al.* , 2001). 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; Loot *et al.* , 2001). In infected fish the parasite is found filling the body cavity (Hoole*et al.* , 2010). 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 partly be explained by diet shifts from phytoplankton to zooplankton as *E. sardella*reaches maturity.

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 the endemic pelagic cyprinid fish*E. sardella* (Mwambungu *et al.* , 1996). The worm was identified to be the tapeworm *Ligula intestinalis* (L.).

This parasite is believed to be introduced into Lake Nyasa by migrating fish-eating birds such as the White-breasted cormorant (*Phalacrocorax carbo*), which is one of the most abundant fish-eating birds in the Lake Nyasa basin (Linn and Campbell, 1992) and one of the final hosts of *L. intestinalis* (Rosen, 1920; Loot*et al.* , 2001). In Lake Nyasa this cestode has been increasingly reported since it was first noted by Mwambungu *et al.* (1996).*E.* sardella appears to be the only species used as intermediate fish host (Msafiri *et al.* , 2014; Rusuwa *et al.* , 2014; Gabagambi and Skorping, 2018; Gabagambi *et al.* , 2019) (Supplementary Figure S1).

L. intestinalis is known to induce castration in several intermediate hosts (Wyatt and Kennedy, 1988; Kennedy *et al.* , 2001; Loot *et al.* , 2002; Cowx *et al.* , 2008; Hoole *et al.* , 2010) 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 Skorping, 2018).

Under such conditions of recent 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 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?

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 (Figure 1). 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; Macuiane *et al.* , 2015; Hampton *et al.* , 2018). The lake has a maximum depth of 785 m, a volume of 8,400 Km^3, a surface area of 29,000 Km^2, approximate length of 550 Km and mean width of around 48-60 Km and is located 472 m above the sea level (Gonfiantini *et al.* , 1979; Bootsma and Hecky, 1993; Patterson and Kachinjika, 1995; Darwall *et al.* , 2010). The total catchment area of the lake is 126,500 Km^2 (Kumambala and Ervine, 2010) of which 97,750 Km^2 is land catchment (Menz, 1995). The mean surface temperature of the lake is between 24 and 28 degC (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 (Vollmer *et al.* , 2005; Lyons*et al.* , 2011).

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 (Vollmer *et al.* , 2005; Darwall *et al.* , 2010; 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 S9deg29'; E34deg01', Mwaya S9deg33'; E33deg 57', Kafyofyo S9deg35'; E33deg57' and Kiwira S9deg37'; E33deg 57').

2.2 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 2015 in Wissman Bay. No sampling was done in 2014 because the persons involved, and especially N. P. Gabagambi, needed to spend the year away pursuing studies and were not replaced. 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. A total of 3,488 female *E. sardella* were sampled (Table 1). Males were also caught and examined as part of general monitoring, but due to the low reliability of stage determination for males of such a small fish species, only females were included in this study.

Upon landing, the total length and weight of each *E. sardella*were measured to the nearest 5 mm and 0.01 g respectively. Specimens of*E. sardella* were kept in cool boxes until further examination. The fish were later dissected for parasite determination. *L. intestinalis* was identified according to the protocol by Dobben (1952) while examination of other parasites were done according to Parpena (1996). 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* were 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 (vwr^{TM}-model ECN 611-2315 and Endel^{TM}- 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.

2.3 Statistical analyses

All statistics and graphics were carried out using R, version 3.2.5 (*http://r-project.org*).

(i) The effect of *L. intestinalis* infection on host fecundity was tested using a generalized linear mixed-effects model (glmmPQL) fitted with fecundity as a response variable (assuming Quasi-Poisson distribution), 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 numerical predictor variable.

(iii) To test whether size of *E. sardella* at maturity has decreased over time, we first fitted for each year a logistic regression model with maturity status as a binomial response variable (0: immature; 1: mature), and body length as a continuous predictor variable (Supplementary Figure S2). From the parameters of these logistic regression equations, and following Diaz Pauli and Heino (2013), we estimated for each year the length at which the probability of maturing is 50% (i.e., LM_{50}):

$$LM_{50} = \frac{\text{Loge}(\frac{p}{1-p}) - (a)}{b}$$

Where, p is the probability of maturity (0.5), a is the intercept and b is the slope.

To test whether LM_{50} decreased over time, we fitted a linear model (lm) with LM_{50} as a response variable and year as a numerical predictor (linear and quadratic terms).

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 +- 0.08, d.f. = 3416, t=-13.92,$P < 0.001$; Figure 2).

Reproductive investment at maturity (relative weight of gonads at stage IV) in non-infected *E. sardella* increased significantly from 2005 to 2015 (glm, estimate = 0.14 +- 0.01, d.f. = 1, t = 9.59, $P< 0.001$; Figure 3).

To test whether LM_{50} (the length at which the probability of maturing is 0.5) varied over time, we fitted two models, one with and one without a quadratic term for year. The model with quadratic term was retained as final model due to lower residual deviance (null deviance = 12.48; residual deviance with quadratic term = 0.97; residual deviance without quadratic term = 2.09) and lower AIC value (AIC, with quadratic term = 13.01; without quadratic term = 18.71). LM_{50} decreased significantly over time (lm, year: estimate = -150 +- 52.5, d.f. = 1, t = -2.86, $P = 0.02$; yearˆ2: estimate = 0.04 +- 0.01, d.f. = 1, t = 2.85, $P = 0.02$; Figure 4).

4.0 DISCUSSION

L. intestinalis had 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 increased, while body size at maturity decreased, over the 10-year duration of this study. These temporal changes, found in non-infected fish, indicate that investment of*E. sardella* into early reproduction has increased at the expense of somatic growth.

This study took place a few years only after the arrival of *L. intestinalis* in the lake. A parasitic relationship between *L. intestinalis* and *E. sardella* in Lake Nyasa was indeed 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). This tapeworm was thus 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, when prevalence is estimated at 50% (Table 1). This indicates that *L. intestinalis* had spread, and therefore that the selection caused by this parasite on its host had increased steadily during

the early years after introduction. Our study remains correlative, yet given the timing of the observed life history shift relative to the invasion of the lake by *L. intestinalis* , it seems legitimate to consider parasitism as a likely contributing factor.

In general, changes in age-specific mortality or fecundity rates lead to changes in selection on life history traits. 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 of parasite infection (Hurd, 2001; Gooderham and Schulte-Hostedde, 2011), but is especially severe for castrating parasites. Castration selects for higher, earlier reproductive effort, as those individuals that are able to reproduce before castration are clearly favoured (Forbes, 1993). A number of host species have been shown to increase their early reproductive effort when parasitism reduces their chances for future reproduction (Minchella and Loverde, 1981; Lafferty, 1993b; Jokela and Lively, 1995; Adamo, 1999). This kind of adaptive response can result from two distinct mechanisms, namely plasticity or evolution, and distinguishing between the two can reveal challenging.

Plastic life history shifts towards increased investment in early reproduction in exposed and / or infected hosts have been reported for a range of host-parasite systems. 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, can induce plastic life history changes in infected hosts that are adaptive.

Here we observe a shift towards increased reproductive effort at the expense of somatic growth across generations. This pattern is found in non-infected hosts and therefore cannot be explained by plastic responses to infection. In addition, given the empirical evidence available at this stage, plastic responses to exposure appear unlikely, given the lack of clear correlation between yearly fluctuations in prevalence and life history trends, as one would expect under such a scenario. We therefore cannot exclude that our results may reflect adaptation to recent 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, and that might have triggered life history responses in *E. sardella* . Other potential sources of selection for earlier reproduction include: fishing (Heino and Godo, 2002; Jorgensen *et al.* , 2007; Kuparinen and Merila, 2007; Fenberg and Roy, 2008; Hutchings and Fraser, 2008; Jorgensen *et al.* , 2009; Sharpe and Hendry, 2009; Sharpe *et al.* , 2012); increased predation by native or introduced species (Sharpe *et al.* , 2012; Hampton *et al.* , 2018); 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). In the last years of this study, however, *E. sardella* stocks have collapsed, despite no sudden changes in fishing effort. As a consequence fishing pressure has dramatically increased in Wissman bay (Supplementary Figure S3).

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, 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, thus possibly reinforcing the selective effects of parasitism. Interestingly, the dramatic decrease in landings in 2013 was preceded by three consecutive years with high *L. intestinalis*prevalence (Supplementary Figure S3), further suggesting that parasitism is a strong selective factor. In this system *L. intestinalis* may have acted synergistically with fishery-mediated selection in driving what appears like an evolutionary shift towards earlier reproduction 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 ancients 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 piscivorours 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 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 parallel increases in the prevalence of other parasites. In their natural habitats hosts are usually infected by two or more different parasite species (Petney and Andrews, 1998; Kotob *et al.* , 2017). 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 is correlative, and the causative links between parasitism and life history changes remain to be established. Yet the cestode *L. intestinalis* , by strongly reducing the fecundity of its host, appears as a likely driver of life history evolution, similar in its effects to size-selective fisheries. In Lake Nyasa these two types of selective factors may have acted concomittantly. More work is now warranted to examine the origin of these changes and determine whether they represent plastic or evolutionary responses.

ACKNOWLEDGEMENTS

The data presented in this manuscript was collected by research scientists from the Tanzania Fisheries Research Institute (TAFIRI), Kyela Centre, together with the large number of students from the University of Dar es Salaam (UDSM) and Sokoine University of Agriculture (SUA). We would like to thank all of them for sharing their data with us. We also thank Dr. Madeleine Carruthers for smoothing the English writing.

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).

FUNDING

This study was funded by the University of Bergen, Norway and Norwegian State Education Loan Fund (Lanekassen) (customer grant number 2872580).

REFERENCES

Adamo, S. A. (1999). Evidence for adaptive changes in egg laying in crickets exposed to bacteria and parasites. *Animal Behaviour***57** , 117-124

Agnew, P., Bedhomme, S., Haussy, C. & Michalakis, Y. (1999). Age and size at maturity of the mosquito *Culex pipiens* infected by the microsporidian parasite *Vavraia culicis* . *Proceedings of the Royal Society of London B: Biological Sciences* **266** , 947-952

Agnew, P., Koella, J. C. & Michalakis, Y. (2000). Host life history responses to parasitism. *Microbes and Infection* **2** , 891-896

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

Ayllon, F., Kjaerner-Semb, E., Furmanek, T., Wennevik, V., Solberg, M. F., Dahle, G., Taranger, G. L., Glover, K. A., Almen, M. S. & Rubin, C. J. (2015). The vgll3 locus controls age at maturity in wild and domesticated Atlantic salmon (*Salmo salar* L.) males. *PLoS Genet* **11**

Barson, M. & Marshall, B. (2003). The occurrence of the tapeworm*Ligula intestinalis* (L.), in *Barbus paludinosus* from a small dam in Zimbabwe. *African Journal of Aquatic Science***28** , 175-178

Bootsma, H. A. & Hecky, R. E. (1993). Conservation of the African Great-Lakes - A Limnological Perspective. *Conservation Biology***7** , 644-656.DOI 10.1046/j.1523-1739

Burrough, R., Bregazzi, P. & Kennedy, C. (1979). Interspecific dominance amongst three species of coarse fish in Slapton Ley, Devon.*Journal of Fish Biology* **15** , 535-544

Carter, V., Pierce, R., Dufour, S., Arme, C. & Hoole, D. (2005). The tapeworm *Ligula intestinalis* (Cestoda: Pseudophyllidea) inhibits LH expression and puberty in its teleost host, *Rutilus rutilus* .*Reproduction* **130** , 939-945

Chadwick, W. & Little, T. J. (2005). A parasite-mediated life-history shift in *Daphnia magna* . *Proceedings of the Royal Society of London B: Biological Sciences* **272** , 505-509

Chafota, J., Burgess, N., Thieme, M. & Johnson, S. (2005). Lake Malawi/Niassa/Nyasa Ecoregion conservation programme: priority conservation areas and vision for biodiversity conservation.

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

Darwall, W. R., Allison, E. H., Turner, G. F. & Irvine, K. (2010). Lake of flies, or lake of fish? A trophic model of Lake Malawi.*Ecological Modelling* **221** , 713-727

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.

Diaz Pauli, B. & Heino, M. (2013). The importance of social dimension and maturation stage for the probabilistic maturation reaction norm in*Poecilia reticulata* . *Journal of evolutionary biology***26** , 2184-2196

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 Co.Pvt. Ltd; 1980.*

Fenberg, P. B. & Roy, K. (2008). Ecological and evolutionary consequences of size-selective harvesting: how much do we know?*Molecular ecology* **17** , 209-220

Forbes, M. R. (1993). Parasitism and host reproductive effort.*Oikos* , 444-450

Fredensborg, B. L. & Poulin, R. (2006). Parasitism shaping host life-history evolution: adaptive responses in a marine gastropod to infection by trematodes. *Journal of animal ecology* **75** , 44-53

Gabagambi, N., Salvanes, A. G. V., Midtoy, F. & Skorping, A. (2019). The tapeworm *Ligula intestinalis* alters the behavior of the fish intermediate host *Engraulicypris sardella* , but only after it has become infective to the final host. *Behavioural processes***158** , 47-52

Gabagambi, N. & Skorping, A. (2018). Spatial and temporal distribution of *Ligula intestinalis* (Cestoda: Diphyllobothriidea) in usipa (*Engraulicypris sardella*) (Pisces: Cyprinidae) in Lake Nyasa.*Journal of helminthology* **92** , 410-416

Gonfiantini, R., Zuppi, G., Eccles, D. & Ferro, W. (1979). Isotope investigation of Lake Malawi. In *Isotopes in lake studies. International Atomic Energy Agency*

Gooderham, K. & Schulte-Hostedde, A. (2011). Macroparasitism influences reproductive success in red squirrels (*Tamiasciurus hudsonicus*).*Behavioral Ecology* **22** , 1195-1200

Hampton, S. E., McGowan, S., Ozersky, T., Virdis, S. G., Vu, T. T., Spanbauer, T. L., Kraemer, B. M., Swann, G., Mackay, A. W. & Powers, S. M. (2018). Recent ecological change in ancient lakes. *Limnology and Oceanography* **63** , 2277-2304

Heath, D., Rankin, L., Bryden, C., Heath, J. & Shrimpton, J. (2002). Heritability and Y-chromosome influence in the jack male life history of chinook salmon (*Oncorhynchus tshawytscha*). *Heredity***89** , 311-317

Heino, M. & Godo, O. R. (2002). Fisheries-induced selection pressures in the context of sustainable fisheries. *Bulletin of Marine Science* **70** , 639-656

Holden, M. J. & Raitt, D. F. S. (1974). Manual of fisheries science. Part 2-Methods of resource investigation and their application.

FAO Fisheries Technical Papers (FAO)

Hoole, D., Carter, V. & Dufour, S. (2010). *Ligula intestinalis*(Cestoda: Pseudophyllidea): an ideal fish-metazoan parasite model?*Parasitology* **137** , 425-438

Hudson, A. L., Moatt, J. P. & Vale, P. F. (2019). Terminal investment strategies following infection are dependent on diet. *Journal of evolutionary biology. **33** (3):309-317*

Hurd, H. (2001). Host fecundity reduction: a strategy for damage limitation? *Trends in parasitology* **17** , 363-368

Hutchings, J. A. & Fraser, D. J. (2008). The nature of fisheries-and farming-induced evolution. *Molecular ecology* **17** , 294-313

Iles, T. (1960). Engraulicypris sardella. *Joint Fisheries Research Organization Annual Report* **9** , 8-9

Irvine, K., Patterson, G., Allison, E., Thompson, A. & Menz, A. (2001). The pelagic ecosystem of Lake Malawi, Africa: Trophic structure and current threats. *The Great Lakes of the World (GLOW): Food-web, Health and Integrity. Leiden, The Netherlands: Backhuys* , 3-30

Jokela, J. & Lively, C. M. (1995). Parasites, sex, and early reproduction in a mixed population of freshwater snails.*Evolution* **49** , 1268-1271

Jorgensen, C., Enberg, K., Dunlop, E. S., Arlinghaus, R., Boukal, D. S., Brander, K., Ernande, B., Gardmark, A., Johnston, F. & Matsumura, S. (2007). Ecology managing evolving fish stocks. *Science***318** , 1247-1248

Jorgensen, C., Ernande, B. & Fiksen, O. (2009). Size-selective fishing gear and life history evolution in the Northeast Arctic cod.*Evolutionary applications* **2** , 356-370

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

Kennedy, C., Shears, P., C & Shears, J., A (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

Konings, A. (1990). *Konings's book of cichlids and all the other fishes of Lake Malawi* : TFH publications.

Kotob, M. H., Menanteau-Ledouble, S., Kumar, G., Abdelzaher, M. & El-Matbouli, M. (2017). The impact of co-infections on fish: a review. *Veterinary research* **47** , 98

Kumambala, G., Patsani & Ervine, A. (2010). Water balance model of Lake Malawi and its sensitivity to climate change. *The Open Hydrology Journal* **4**

Kuparinen, A. & Merila, J. (2007). Detecting and managing fisheries-induced evolution. *Trends in ecology & evolution***22** , 652-659

Lafferty, K. D. (1993a). Effects of parasitic castration on growth, reproduction and population dynamics of the marine snail*Cerithidea californica* . *Marine Ecology Progress Series* , 229-237

Lafferty, K. D. (1993b). The marine snail, *Cerithidea californica* , matures at smaller sizes where parasitism is high.*Oikos* , 3-11

Law, R. (2000). Fishing, selection, and phenotypic evolution. *ICES Journal of Marine Science* **57** , 659-668

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

LNBWB (2013). Lake Nyasa Basin Water Board; Basin Annual Hydrological Report Nov,2012-Dec,2013. Ministry of Water.

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

Loot, G., Poulin, R., Lek, S. & Guegan, J. F. (2002). The differential effects of *Ligula intestinalis* (L.) plerocercoids on host growth in three natural populations of roach, *Rutilus rutilus* (L.*Ecology of Freshwater Fish* **11** , 168-177

Lowe-McConnell, R. H. (1993). Fish faunas of the African Great Lakes: origins, diversity, and vulnerability. *Conservation Biology***7** , 634-643

Lyons, R. P., Kroll, C. N. & Scholz, C. A. (2011). An energy-balance hydrologic model for the Lake Malawi Rift basin, East Africa.*Global and Planetary Change* **75** , 83-97

Macuiane, A. M., Hecky, R. E. & Guildford, S. J. (2015). Changes in fish community structure associated with cage aquaculture in Lake Malawi, Africa. *Aquaculture* **448** , 8-17

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 ofAquaculture and Fisheries (MJAF)* , 6

Manyungwa-Pasani, C. L., Hara, M. & Chimatiro, S. K. (2017). Women's participation in fish value chains and value chain governance in Malawi: A case of Msaka (Lake Malawi) and Kachulu (Lake Chilwa).

McCurdy, D., Forbes, M. & Boates, J. (1999). Testing alternative hypotheses for variation in amphipod behaviour and life history in relation to parasitism. *International journal for parasitology***29** , 1001-1009

Menz, A. (1995). *The fishery potential and productivity of the Pelagic Zone of Lake Malawi/Niassa: scientific report of the UK/SADC Pelagic Fish Resource Assessment Project* : NRI.

Mgwede, C. W. & Msiska, O. (2018). Determination of Seasonal Occurrence of *Camallanus* sp. and *Ligula intestinalis* on Fresh Usipa,*Engraulicypris sardella* from Selected Mzuzu Markets, Malawi.*International Journal of Aquaculture* **8**

Minchella, D. J. & Loverde, P. T. (1981). A cost of increased early reproductive effort in the snail *Biomphalaria glabrata. The American Naturalist* **118** , 876-881

Morioka, S. & Kaunda, E. (2005). Preliminary examination of hatching season and growth of *Engraulicypris sardella* (Pisces: Cyprinidae) larvae and juveniles in Lake Malawi. *African Zoology* **40** , 9-14

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

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

Mwambungu, J. & Ngatunga, B. P. (2001). Fisheries activities in northern Lake Nyasa (Kyela District). *Tanzania Fisheries Research Institute Bulletin* , 1-12

Noble, E. R. & Noble, G. A. (1971). *Parasitology. The biology of animal parasites. 3rd Edition.*

Olsen, E. M., Heino, M., Lilly, G. R., Morgan, M. J., Brattey, J., Ernande, B. & Dieckmann, U. (2004). Maturation trends indicative of rapid evolution preceded the collapse of northern cod. *Nature***428** , 932-935

Parpena, I. (1996). Parasites, infections and diseases of fishes in Africa: An update. FAO. *CIFA Technical Paper* **31** , 130-199

Patterson, G. & Kachinjika, O. (1995). Limnology and phytoplankton ecology. *The fishery potential and productivity of the pelagic zone of Lake Malawi/Niassa* , 1-67

Perrin, N., Christe, P. & Richner, H. (1996). On host life-history response to parasitism. *Oikos* , 317-320

Petney, T. N. & Andrews, R. H. (1998). Multiparasite communities in animals and humans: frequency, structure and pathogenic significance.*International journal for parasitology* **28** , 377-393

Pianka, E. R. (1976). Natural selection of optimal reproductive tactics.*American Zoologist* **16** , 775-784

Polak, M. & Starmer, W. T. (1998). Parasite–induced risk of mortality elevates reproductive effort in male Drosophila. *Proceedings of the Royal Society of London B: Biological Sciences* **265** , 2197-2201

Richner, H. & Tripet, F. (1999). Ectoparasitism and the trade-off between current and future reproduction. *Oikos* , 535-538

Roff, D. A. (2002). *Life history evolution* : Sinauer, Sunderland,Mass.

Rosen, C. (1920). Recherches sur le developpement des Cestodes. II. Le cycle evolutif de la Ligule et quelques questions generales sur le developpement des Bothriocephales. *Bulletin de la Societe Neuchatelloise de Sciences Naturelles* **44** , 259-280

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**

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

Salzburger, W., Van Bocxlaer, B. & Cohen, A. S. (2014). Ecology and evolution of the African Great Lakes and their faunas. *Annual Review of Ecology, Evolution, and Systematics* **45** , 519-545

Sanz, J. J., Arriero, E., Moreno, J. & Merino, S. (2001). Interactions between hemoparasite status and female age in the primary reproductive output of pied flycatchers. *Oecologia* **126** , 339-344

Schwanz, L. E. (2008). Chronic parasitic infection alters reproductive output in deer mice. *Behavioral Ecology and Sociobiology***62** , 1351-1358

Sharpe, D. & Hendry, A. (2009). Life history change in commercially exploited fish stocks: an analysis of trends across studies. Evol. Appl.**2** , 260–275.

Sharpe, D., Wandera, S. & Chapman, L. (2012). Life history change in response to fishing and an introduced predator in the East African cyprinid *Rastrineobola argentea* . *Evolutionary applications***5** , 677-693

Sinclair-Waters, M., Odegard, J., Korsvoll, S. A., Moen, T., Lien, S., Primmer, C. R. & Barson, N. J. (2020). Beyond large-effect loci: large-scale GWAS reveals a mixed large-effect and polygenic architecture for age at maturity of Atlantic salmon. *Genetics Selection Evolution* **52** , 1-11

Sorci, G., Clobert, J. & Michalakis, Y. (1996). Cost of reproduction and cost of parasitism in the common lizard, *Lacerta vivipara* .*Oikos* , 121-130

Stearns, S. C. (1989). Trade-offs in life-history evolution.*Functional ecology* **3** , 259-268

Thomas, F., Guegan, J. F., Michalakis, Y. & Renaud, F. (2000). Parasites and host life-history traits: implications for community ecology and species co-existence. *International Journal for Parasitology* **30** , 669-674

Thompson, A. (1996). Early life history of *Engraulicypris sardella* (Cyprinidae) in Lake Malawi. *Journal of plankton research* **18** , 1349-1368

Thompson, A. & Allison, E. (1997). Potential yield estimates of unexploited pelagic fish stocks in Lake Malawi. *Fisheries Management and Ecology* **4** , 31-48

Thompson, A. & Bulirani, A. (1993). Growth of usipa (*Engraulicypris sardella*) in Lake Malawi/Niassa. In*Symposium on Biology, Stock Assessment and Exploitation of Small Pelagic Fish Species in the African Great Lakes Region. FAO, Rome. C1FA Occ Pap* , pp. 87-99.

Thompson, A. B., Allison, E. H. & Ngatunga, B. P. (1996). Distribution and breeding biology of offshore pelagic cyprinids and catfish in Lake Malawi/Niassa. *Environmental Biology of Fishes* **47** , 27-42

Thornhill, J. A., Jones, J. T. & Kusel, J. (1986). Increased oviposition and growth in immature *Biomphalaria glabrata* after exposure to *Schistosoma mansoni* . *Parasitology* **93** , 443-450

Tweddle, D. & Lewis, D. (1990). The biology of usipa (*Engraulicypris sardella*) in relation to fluctuations in productivity of Lake Malawi and species introductions. *Collected Reports on Fisheries Research in Malawi. Occasional Papers* **1** , 67-72

Vale, P. & Little, T. (2012). Fecundity compensation and tolerance to a sterilizing pathogen in D aphnia. *Journal of Evolutionary Biology***25** , 1888-1896

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

Weyl, O. L., Ribbink, A. J. & Tweddle, D. (2010). Lake Malawi: fishes, fisheries, biodiversity, health and habitat. *Aquatic Ecosystem Health & Management* **13** , 241-254

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

Yan, G., Severson, D. W. & Christensen, B. M. (1997). Costs and benefits of mosquito refractoriness to malaria parasites: implications for genetic variability of mosquitoes and genetic control of malaria.*Evolution* **51** , 441-450

Tables

Table 1

Year	Maturity stage I	Maturity stage II	Maturity stage III	Maturity stage IV	Maturity stage V	VI
2005			13 (6)	12 (6)	126 (64)	
2006		1 (0)	195 (51)	40 (11)	38 (1)	337
2007			212 (8)	45 (6)	529 (140)	149
2008		2 (0)	59 (13)	14 (9)	6 (2)	153
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 (117)	1453 (291)	711
% of all stages	0.17	1.7	24	12	41.7	20.4
Prevalence (%)	0	0	20	28	20	17

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 superficia
V	Partial spent	Spawning fish with ripe ovaries
VI	Running	Ovaries yellowish-brown
VII	Spent	Ovaries loose and flabby

Tables legends

Table 1

Numbers *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

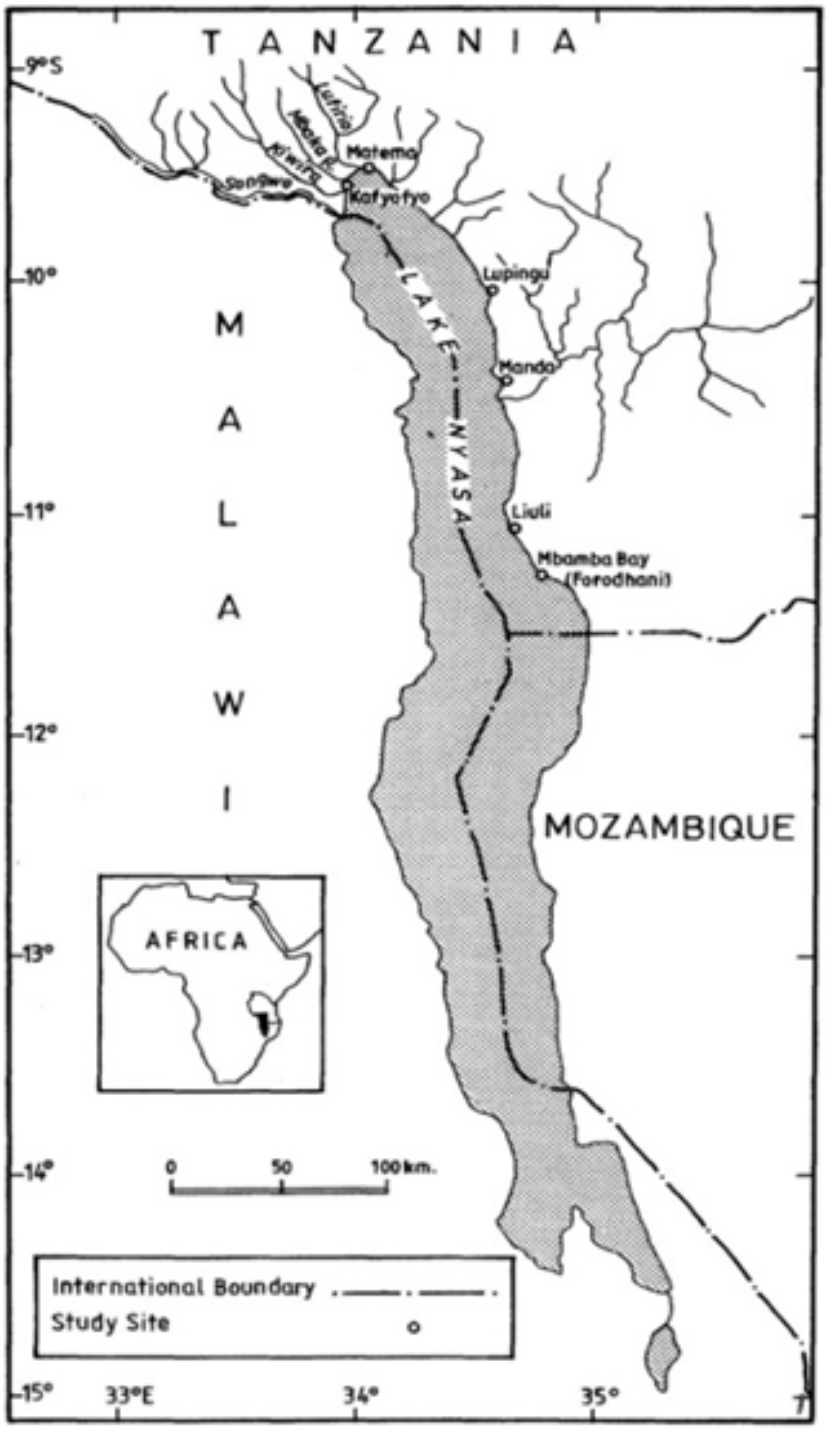

Figure 2

Hosted file

`image2.emf` available at https://authorea.com/users/312910/articles/478065-life-history-

shifts-in-an-exploited-african-fish-following-invasion-by-a-castrating-parasite

Figure 3

Hosted file

`image3.emf` available at https://authorea.com/users/312910/articles/478065-life-history-shifts-in-an-exploited-african-fish-following-invasion-by-a-castrating-parasite

Figure 4

Hosted file

`image4.emf` available at https://authorea.com/users/312910/articles/478065-life-history-shifts-in-an-exploited-african-fish-following-invasion-by-a-castrating-parasite

Figures legends

Fig 1. Map of Lake Nyasa showing fishing ground of Wissman Bay (in oval shape)

Source: Modified from Msafiri *et al.* (2014).

Fig 2. Fecundity (number of eggs in the gonads) of *E. sardella* at various maturity stages, for non-infected fish (grey) and fish infected by *L. intestinalis* (black). Both the distribution and probability density of data are represented here. Sample sizes are indicated in parentheses.

Fig 3. Temporal increase in reproductive investment at maturity (stage IV) of non-infected *E. sardella.* Both the distribution and probability density of data are represented here. Dots indicate mean values. Sample sizes are indicated in parentheses.

Fig 4. Temporal changes in LM50 for female *E. sardella* ,*i.e.,* the estimated length at which the probability of maturing is 0.5 (final model represented by grey curve and estimated LM50 for each year by solid black dots).

Supplementary figures

Supplementary Figure S1

Supplementary Figure S2

Hosted file

`image6.emf` available at https://authorea.com/users/312910/articles/478065-life-history-shifts-in-an-exploited-african-fish-following-invasion-by-a-castrating-parasite

Supplementary Figure S3

Hosted file

`image7.emf` available at https://authorea.com/users/312910/articles/478065-life-history-shifts-in-an-exploited-african-fish-following-invasion-by-a-castrating-parasite

Supplementary figures legends

Supplementary Figure S1. Laboratory picture of tapeworm*L. intestinalis* and its host fish *E. sardella* . Source: Nestory Peter Gabagambi (2015).

Supplementary Figure S2. Logistic regression models were fitted for each year, and their parameters were used to estimate LM_{50} for each year (i.e., the age at which the probability of maturing is 0.5).

Supplementary Figure S3. Yearly trends for LM50 (top panel),*L. intestinalis* prevalence in female *E. sardella* (upper middle), fishing pressure in Lake Nyasa, taken as the number of fishermen per tonne landed (lower middle), and *E. sardella*landings (bottom). Source from fisheries data: Kyela District Council, Department of Fisheries. Models represented by grey lines, data by black dots.