

ORIGINAL RESEARCH

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

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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 noninfected 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 toward 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

African Great Lakes, environmental change, Lake Malawi sardine, Lake Nyasa, life history evolution, parasite invasion, Usipa

1 | 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 favored by natural selection (Fredensborg & Poulin, 2006).

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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 & Godø, 2002; Jørgensen et al., 2007; Jørgensen et al., 2009; Sharpe et al., 2012). Fishing practices and predation are usually nonrandom 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 (Jørgensen et al., 2007; Jørgensen et al., 2009). Assuming that early maturation is heritable to some extent, this should result in life histories changing toward earlier reproduction at smaller sizes (Ayllon et al., 2015; Heath et al., 2002; Olsen et al., 2004; Sinclair-Waters et al., 2020).

Parasitism can also affect the future reproductive success of hosts (Fredensborg & 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 & Starmer, 1998; Richner & 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 & Noble, 1971)) can select for earlier maturity (Fredensborg & Poulin, 2006; Lafferty, 1993a; Loot et al., 2002; Minchella & Loverde, 1981). For the infected host, achieving reproduction prior to castration yields clear fitness benefits (Gooderham & Schulte-Hostedde, 2011; Lafferty, 1993a; Minchella & Loverde, 1981), and these benefits increase along with infection risk (Minchella & Loverde, 1981; Polak & 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 & Little, 2005; Hudson et al., 2019; Vale & Little, 2012).

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, zooplanktivorous fish endemic to Lake Nyasa (Lowe-McConnell, 1993; Rufli & Van Lissa, 1982) that occurs in shoals, which are widely distributed within the lake and found in both nearshore areas and offshore pelagic water, down to a depth of approximately 200 m (Maguza-Tembo et al., 2009).

Engraulicypris 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 (Rusuwa et al., 2014; Thompson & Bulirani, 1993). They have been reported to breed throughout the year but with bi-annual recruitment peaks occurring during the wet season and dry season (Morioka & Kaunda, 2005; Rusuwa et al., 2014).

During early developmental stages, *E. sardella* feeds exclusively on phytoplankton and then switches to feeding on zooplankton upon 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 & Lewis, 1990). Males and females mature at a size of about 70 and 75 mm, respectively (Thompson & Allison, 1997; Thompson et al., 1996).

Engraulicypris 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 & 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*.

Ligula intestinalis (L. 1758) is a common and widespread cestode, that uses cyprinid fish as the second intermediate host (Dubinina, 1980; Kennedy, 1974). 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 longline 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 & Campbell, 1992) and one of the final hosts of *L. intestinalis* (Loot et al., 2001; Rosen, 1920). 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 (Gabagambi et al., 2019; Gabagambi & Skorping, 2018; Msafiri et al., 2014; Rusuwa et al., 2014) (Figure S1).

Ligula 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 & 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 & 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 toward 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 | 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; Hampton et al., 2018; Macuiane et al., 2015). The lake has a maximum depth of 785 m, a volume of 8400 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 & Hecky, 1993; Darwall et al., 2010; Gonfiantini et al., 1979; Patterson & Kachinjika, 1995). The total catchment area of the lake is 126,500 km² (Kumambala & 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 1000 and 2800 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 nutrient availability to the plankton community are very low, and thus, the lake is considered “oligotrophic” (Irvine et al., 2001; Mwambungu & 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

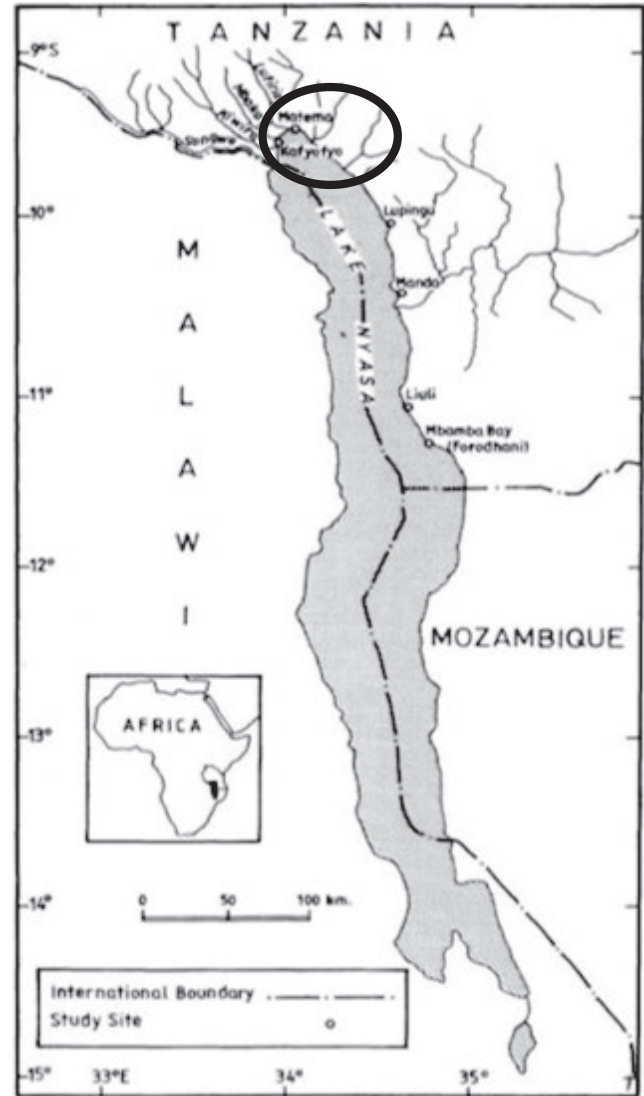


FIGURE 1 Map of Lake Nyasa showing fishing ground of Wissman Bay (in oval shape)

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

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 | 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 were 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 dugout canoes and one large plank boat. On the fishing ground, one of the dugout canoes was equipped with pressurized paraffin lamps (between one and 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 3488 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 was 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™—model ECN 611–2315 and Endel™—model WPS) and fecundity for infected and noninfected female *E. sardella* was determined through gravimetric methods (Holden & 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 hr. 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°C. 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. Afterward, we collected a random subsample of the eggs, which were weighed and counted out on petri dish subsections 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 subsample, G = total weight of eggs from the ovary, and g = weight of the subsample. 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>).

TABLE 1 Numbers of *E. sardella* per maturity stage sampled at Wissman Bay, Lake Nyasa, between 2005 and 2013 and then in 2015

Year	Maturity stage							Total	Prevalence (%)
	I	II	III	IV	V	VI	VII		
2005			13 (6)	12 (6)	126 (64)			151 (76)	50
2006		1 (0)	195 (51)	40 (11)	38 (1)	337 (60)		611 (123)	20
2007			212 (8)	45 (6)	529 (140)	149 (37)		935 (191)	20
2008		2 (0)	59 (13)	14 (9)	6 (2)	153 (12)	3 (2)	237 (38)	16
2009			16 (7)	15 (6)	215 (8)	52 (2)		298 (23)	8
2010		14 (0)	47 (11)	14 (6)	31 (14)	17 (8)		123 (39)	32
2011		2 (0)	28 (10)	13 (5)	2 (1)	3 (0)		48 (16)	33
2012	4 (0)	17 (0)	136 (37)	23 (18)				180 (55)	31
2013	2 (0)	24 (0)	68 (19)	28 (17)	8 (3)			130 (39)	30
2015			62 (8)	215 (33)	498 (58)			775 (99)	13
Total	6 (0)	60 (0)	836 (170)	419 (117)	1453 (291)	711 (119)	3 (2)	3488 (699)	20
% of all stages	0.17	1.7	24	12	41.7	20.4	0.09		
Prevalence (%)	0	0	20	28	20	17	67	20	

Note: 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)

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

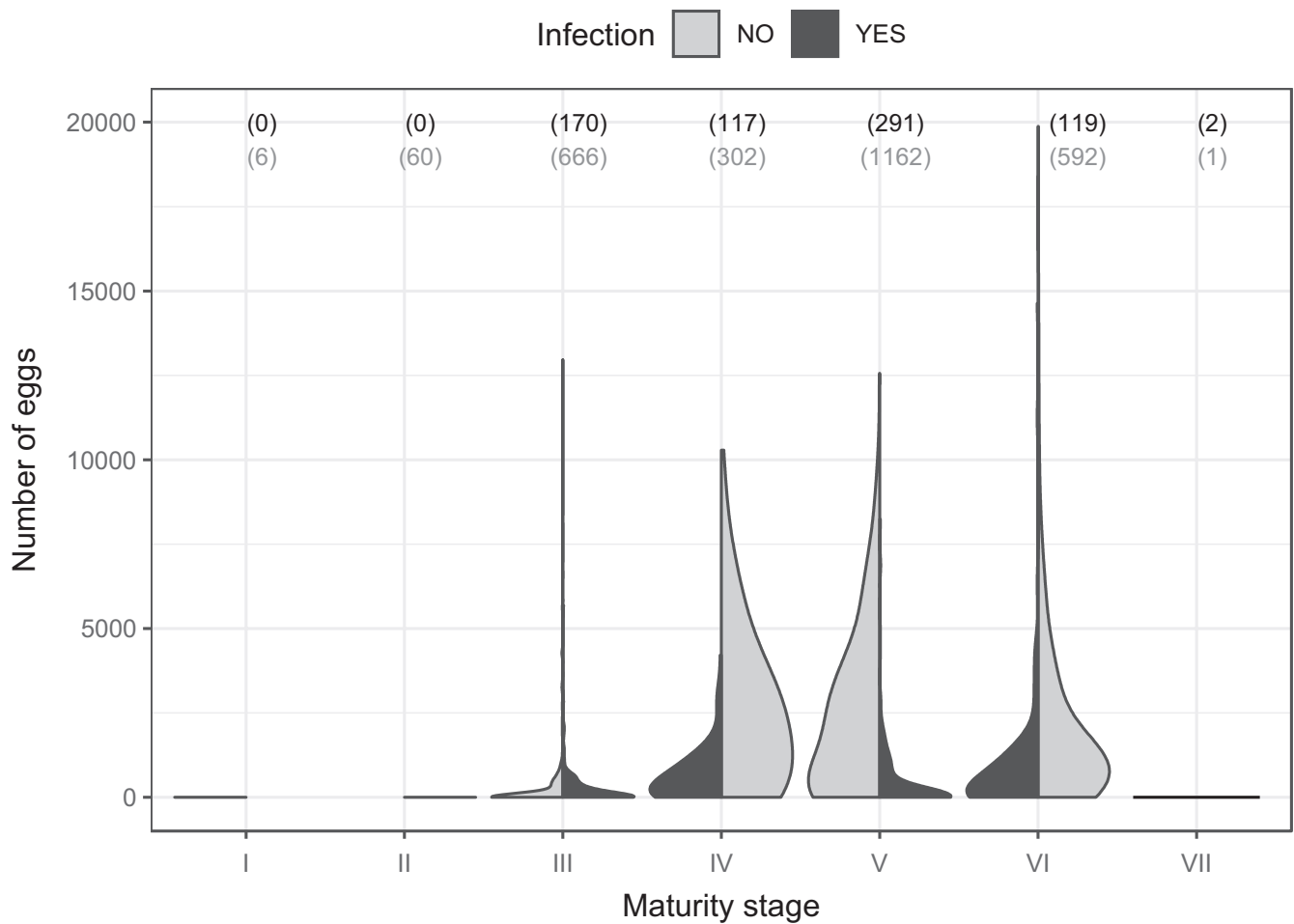


FIGURE 2 Fecundity (number of eggs in the gonads) of *E. sardella* at various maturity stages, for noninfected fish (gray) and fish infected by *L. intestinalis* (black). Both the distribution and probability density of data are represented here. Sample sizes are indicated in parentheses

- (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 (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}):

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

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 | 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

noninfected individuals (glmmPQL, estimate = -1.08 ± 0.08 , $df = 3416$, $t = -13.92$, $p < .001$; Figure 2).

Reproductive investment at maturity (relative weight of gonads at stage IV) in noninfected *E. sardella* increased significantly from 2005 to 2015 (glm, estimate = 0.14 ± 0.01 , $df = 1$, $t = 9.59$, $p < .001$; 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 , $df = 1$, $t = -2.86$, $p = .02$; year²: estimate = 0.04 ± 0.01 , $df = 1$, $t = 2.85$, $p = .02$; Figure 4).

4 | DISCUSSION

Ligula 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

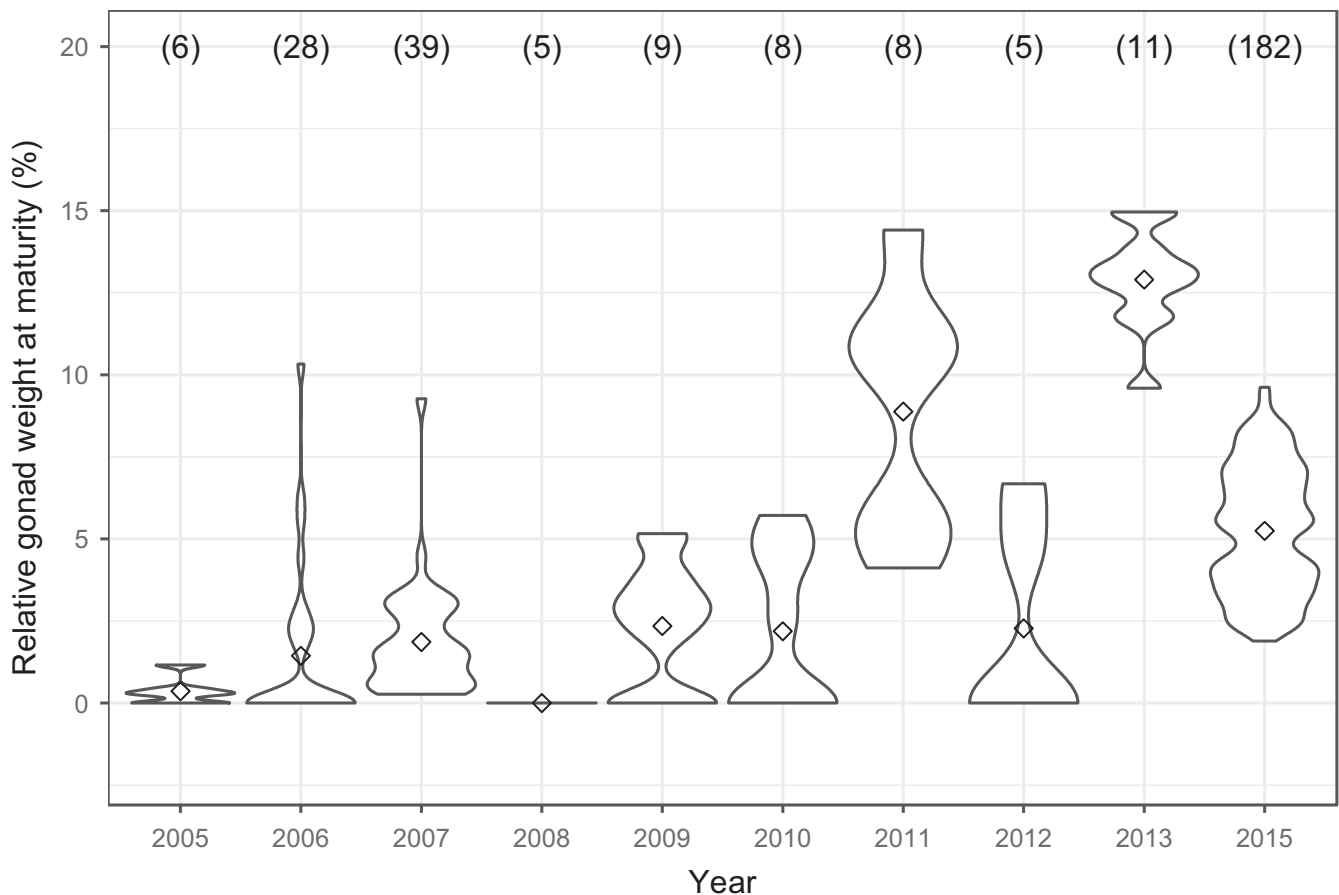
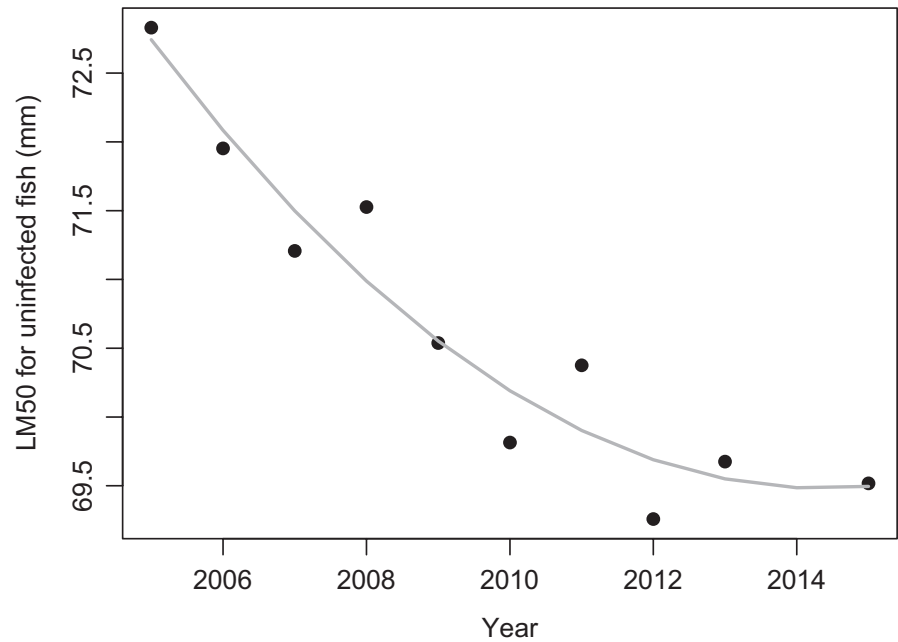


FIGURE 3 Temporal increase in reproductive investment at maturity (stage IV) of noninfected *E. sardella*. Both the distribution and probability density of data are represented here. Dots indicate mean values. Sample sizes are indicated in parentheses

FIGURE 4 Temporal changes in LM_{50} for female *E. sardella*, that is, the estimated length at which the probability of maturing is 0.5 (final model represented by gray curve and estimated LM_{50} for each year by solid black dots)



the species range of this parasite (Barson & 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 noninfected 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 (Gooderham & Schulte-Hostedde, 2011; Hurd, 2001), 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 favored (Forbes, 1993). A number of host species have been shown to increase their early reproductive effort when parasitism reduces their chances for future reproduction (Adamo, 1999; Jokela & Lively, 1995; Lafferty, 1993b; Minchella & Loverde, 1981). 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 toward 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 nonparasitized 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 toward 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 toward increased reproductive effort at the expense of somatic growth across generations. This pattern

is found in noninfected 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 (Fenberg & Roy, 2008; Heino & Godø, 2002; Hutchings & Fraser, 2008; Jørgensen et al., 2007; Jørgensen et al., 2009; Kuparinen & Merilä, 2007; Sharpe & 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 nearshore lake zones using paddled dugout canoe crafts (Mwambungu & 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 (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 and 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 (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 toward 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 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 and 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 (Kotob et al., 2017; Petney & 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 & Msiska, 2018). In the present study, we caught 3,488 wild, that is, 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 concomitantly. More work is now warranted to examine the origin of these changes and determine whether they represent plastic or evolutionary responses.

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CONFLICT OF INTEREST

None declared.

AUTHOR CONTRIBUTION

Nestory Peter Gabagambi Writing original draft (lead); methodology-data collection (lead). **Arne Skorping** Conceptualization (supporting); review and editing (equal). **Mwita Chacha** Review and editing (equal). **Kwendwa Jonathan Kihedu** Review and editing (equal). **Adele Mennerat** Conceptualization (lead); writing original draft (supporting); methodology-statistical analysis (lead); review and editing (equal).

ETHICS STATEMENT

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

OPEN RESEARCH BADGES



This article has earned an Open Data Badge for making publicly available the digitally-shareable data necessary to reproduce the reported results. The data is available at <https://doi.org/10.5061/dryad.p2ngf1vp3>.

DATA AVAILABILITY STATEMENT

Data sets supporting this manuscript can be accessed through <https://doi.org/10.5061/dryad.p2ngf1vp3>.

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REFERENCES

- Adamo, S. A. (1999). Evidence for adaptive changes in egg laying in crickets exposed to bacteria and parasites. *Animal Behaviour*, *57*, 117–124. <https://doi.org/10.1006/anbe.1998.0999>
- 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. <https://doi.org/10.1098/rspb.1999.0728>
- Agnew, P., Koella, J. C., & Michalakis, Y. (2000). Host life history responses to parasitism. *Microbes and Infection*, *2*, 891–896. [https://doi.org/10.1016/S1286-4579\(00\)00389-0](https://doi.org/10.1016/S1286-4579(00)00389-0)
- 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. <https://doi.org/10.1111/j.1365-2427.1996.tb01764.x>
- Ayllon, F., Kjærner-Semb, E., Furmanek, T., Wennevik, V., Solberg, M. F., Dahle, G., Taranger, G. L., Glover, K. A., Almén, M. S., Rubin, C. J., Edvardsen, R. B., & Wargelius, A. (2015). The *vglI3* locus controls age at maturity in wild and domesticated Atlantic salmon (*Salmo salar* L.) males. *PLoS Genetics*, *11*. <https://doi.org/10.1371/journal.pgen.1005628>
- 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. <https://doi.org/10.1046/j.1523-1739.1993.07030644.x>
- 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. <https://doi.org/10.1111/j.1095-8649.1979.tb03644.x>
- Carter, V., Pierce, R., Dufour, S., Arme, C., & Hoole, D. (2005). The tapeworm *Ligula intestinalis* (Cestoda: Pseudophyllidae) inhibits LH expression and puberty in its teleost host, *Rutilus rutilus*. *Reproduction*, *130*, 939–945. <https://doi.org/10.1530/rep.1.00742>
- 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. <https://doi.org/10.1016/j.ecolmodel.2009.11.001>
- 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*. Amerind Publishing Co. Pvt. Ltd.
- Fenberg, P. B., & Roy, K. (2008). Ecological and evolutionary consequences of size-selective harvesting: How much do we know? *Molecular Ecology*, *17*, 209–220. <https://doi.org/10.1111/j.1365-294X.2007.03522.x>
- Forbes, M. R. (1993). Parasitism and host reproductive effort. *Oikos*, *444*–450. <https://doi.org/10.2307/3545356>
- 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. <https://doi.org/10.1111/j.1365-2656.2005.01021.x>
- Gabagambi, N., Salvanes, A. G. V., Midtøy, 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. <https://doi.org/10.1016/j.beproc.2018.11.002>
- Gabagambi, N., & Skorping, A. (2018). Spatial and temporal distribution of *Ligula intestinalis* (Cestoda: Diphylobothriidea) 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. <https://doi.org/10.1093/beheco/arr112>
- Hampton, S. E., McGowan, S., Ozersky, T., Virdis, S. G. P., Vu, T. T., Spanbauer, T. L., Kraemer, B. M., Swann, G., Mackay, A. W., Powers, S. M., Meyer, M. F., Labou, S. G., O'Reilly, C. M., DiCarlo, M., Galloway, A. W. E., & Fritz, S. C. (2018). Recent ecological change in ancient lakes. *Limnology and Oceanography*, *63*, 2277–2304. <https://doi.org/10.1002/lno.10938>
- 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. <https://doi.org/10.1038/sj.hdy.6800141>
- Heino, M., & Godø, 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: Pseudophyllidae): 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. [https://doi.org/10.1016/S1471-4922\(01\)01927-4](https://doi.org/10.1016/S1471-4922(01)01927-4)
- Hutchings, J. A., & Fraser, D. J. (2008). The nature of fisheries-and farming-induced evolution. *Molecular Ecology*, 17, 294–313. <https://doi.org/10.1111/j.1365-294X.2007.03485.x>
- 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. In *The Great Lakes of the World (GLOW): Food-web, Health and Integrity* (pp. 3–30). Backhuys.
- Jokela, J., & Lively, C. M. (1995). Parasites, sex, and early reproduction in a mixed population of freshwater snails. *Evolution*, 49, 1268–1271. <https://doi.org/10.1111/j.1558-5646.1995.tb04453.x>
- Jorgensen, C., Enberg, K., Dunlop, E. S., Arlinghaus, R., Boukal, D. S., Brander, K., Ernande, B., Gardmark, A. G., Johnston, F., Matsumura, S., Pardoe, H., Raab, K., Silva, A., Vainikka, A., Dieckmann, U., Heino, M., & Rijnsdorp, A. D. (2007). Ecology managing evolving fish stocks. *Science*, 318, 1247–1248. <https://doi.org/10.1126/science.1148089>
- Jørgensen, C., Ernande, B., & Fiksen, Ø. (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. <https://doi.org/10.1111/j.1095-8649.1974.tb05104.x>
- 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*. 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. <https://doi.org/10.1186/s1356-7-016-0383-4>
- Kumambala, G. P., & Patsani, A. (2010). Water balance model of Lake Malawi and its sensitivity to climate change. *The Open Hydrology Journal*, 4. <https://doi.org/10.2174/1874378101004010152>
- Kuparinen, A., & Merilä, J. (2007). Detecting and managing fisheries-induced evolution. *Trends in Ecology & Evolution*, 22, 652–659. <https://doi.org/10.1016/j.tree.2007.08.011>
- Lafferty, K. D. (1993a). Effects of parasitic castration on growth, reproduction and population dynamics of the marine snail *Cerithidea californica*. *Marine Ecology Progress Series*, 96, 229–237. <https://doi.org/10.3354/meps096229>
- Lafferty, K. D. (1993b). The marine snail, *Cerithidea californica*, matures at smaller sizes where parasitism is high. *Oikos*, 68, 3–11. <https://doi.org/10.2307/3545303>
- Law, R. (2000). Fishing, selection, and phenotypic evolution. *ICES Journal of Marine Science*, 57, 659–668. <https://doi.org/10.1006/jmsc.2000.0731>
- 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. <https://doi.org/10.2307/2404470>
- LNBWB (Lake Nyasa Basin Water Board) (2013). *Basin Annual Hydrological Report Nov, 2012-Dec 2013*. Ministry of Water.
- Loot, G., Francisco, P., Santoul, F., Lek, S., & Guégan, J. F. (2001). The three hosts of the *Ligula intestinalis* (Cestoda) life cycle in Lavernose-Lacasse gravel pit, France. *Archiv für Hydrobiologie*, 152, 511–525. <https://doi.org/10.1127/archiv-hydrobiol/152/2001/511>
- Loot, G., Poulin, R., Lek, S., & Guégan, 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 of Aquaculture and Fisheries (MJAF)*, 6, 6–12.
- 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, 29–32.
- 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 *Engraulicypris sardella* (Cyprinidae) from northern Lake Nyasa/Malawi/Niassa. *Aquatic Ecosystem Health & Management*, 17, 90–96.
- Mwambungu, J., & Ngatunga, B. P. (2001). Fisheries activities in northern Lake Nyasa (Kyela District). *Tanzania Fisheries Research Institute Bulletin*, VIII, 1–12.
- 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*, II, 1–12.
- Noble, E. R., & Noble, G. A. (1971). *Parasitology. The biology of animal parasites* (3rd ed.). Lea & Febiger.
- 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. <https://doi.org/10.1038/nature02430>
- 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. In A. Menz (Ed.), *The fishery potential and productivity of the pelagic zone of Lake Malawi/Niassa* (pp. 1–67). Natural Resources Institute.
- Perrin, N., Christe, P., & Richner, H. (1996). On host life-history response to parasitism. *Oikos*, 317–320. <https://doi.org/10.2307/3546256>
- 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. [https://doi.org/10.1016/S0020-7519\(97\)00189-6](https://doi.org/10.1016/S0020-7519(97)00189-6)

- Pianka, E. R. (1976). Natural selection of optimal reproductive tactics. *American Zoologist*, 16, 775–784. <https://doi.org/10.1093/icb/16.4.775>
- 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. <https://doi.org/10.2307/3546657>
- Roff, D. A. (2002). *Life history evolution*. Sinauer.
- Rosen, C. (1920). Recherches sur le développement des Cestodes. II. Le cycle évolutif de la Ligule et quelques questions générales sur le développement des Bothriocéphales. *Bulletin de la Société Neuchâteloise 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. <https://doi.org/10.1146/annurev-ecolsys-120213-091804>
- 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. <https://doi.org/10.1007/s004420000530>
- Schwanz, L. E. (2008). Chronic parasitic infection alters reproductive output in deer mice. *Behavioral Ecology and Sociobiology*, 62, 1351–1358. <https://doi.org/10.1007/s00265-008-0563-y>
- Sharpe, D., & Hendry, A. (2009). Life history change in commercially exploited fish stocks: An analysis of trends across studies. *Evolutionary Applications*, 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., Ødegård, 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. <https://doi.org/10.1186/s12711-020-0529-8>
- Sorci, G., Clobert, J., & Michalakis, Y. (1996). Cost of reproduction and cost of parasitism in the common lizard, *Lacerta vivipara*. *Oikos*, 121–130. <https://doi.org/10.2307/3545754>
- Stearns, S. C. (1989). Trade-offs in life-history evolution. *Functional Ecology*, 3, 259–268. <https://doi.org/10.2307/2389364>
- Thomas, F., Guégan, 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. [https://doi.org/10.1016/S0020-7519\(00\)00040-0](https://doi.org/10.1016/S0020-7519(00)00040-0)
- 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. <https://doi.org/10.1046/j.1365-2400.1997.00103.x>
- 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. <https://doi.org/10.1007/BF00002377>
- 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* (pp. 87–99). FAO, Rome. C1FA Occ Pap.
- 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 *Daphnia*. *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. <https://doi.org/10.4319/lo.2005.50.2.0727>
- Weyl, O. L., Ribbink, A. J., & Tweddle, D. (2010). Lake Malawi: Fishes, fisheries, biodiversity, health and habitat. *Aquatic Ecosystem Health & Management*, 13, 241–254. <https://doi.org/10.1080/14634988.2010.504695>
- 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. <https://doi.org/10.1111/j.1095-8649.1988.tb05447.x>
- 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. <https://doi.org/10.1111/j.1558-5646.1997.tb02431.x>

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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