UHASSELT
KNOWLEDGE IN ACTION

Maastricht University

Faculty of Medicine and Life Sciences
School for Life Sciences
Master of Biomedical Sciences

Master's thesis

Parasites Through Time: The Impact of Anthropogenic Changes on Parasites in Lake Victorias Cichlid Fish

Laura Oben

Thesis presented in fulfillment of the requirements for the degree of Master of Biomedical Sciences, specialization Environmental Health Sciences

SUPERVISOR :

dr. Tiziana GOBBIN

2024
2025

Transnational University Limburg is a unique collaboration of two universities in two countries: the University of Hasselt and Maastricht University.

UHASSELT
KNOWLEDGE IN ACTION

www.uhasselt.be
Universiteit Hasselt
Campus Hasselt:
Martelarenlaan 42 | 3500 Hasselt
Campus Diepenbeek:
Agoralaan Gebouw D | 3590 Diepenbeek

Faculty of Medicine and Life Sciences
School for Life Sciences
Master of Biomedical Sciences

Master's thesis

Parasites Through Time: The Impact of Anthropogenic Changes on Parasites in Lake Victorias Cichlid Fish

Laura Oben

Thesis presented in fulfillment of the requirements for the degree of Master of Biomedical Sciences, specialization Environmental Health Sciences

SUPERVISOR :
dr. Tiziana GOBBIN

Parasites Through Time: The Impact of Anthropogenic Changes on Parasites in Lake Victoria's Cichlid Fish

Oben L[1], Gobbin T[1]

[1]Parasitology Research Group, Centre for Environmental Sciences, Hasselt University, Campus Diepenbeek,
Agoralaan Gebouw D-3590 Diepenbeek

*Running title: *Lake Victoria time series*

To whom correspondence should be addressed: Tiziana Gobbin, Tel: +32 (11) 26 89 58; Email: tiziana.gobbin@uhasselt.be

Keywords: Global change**,** Anthropogenic changes, Ectoparasites, Lake Victoria, Microhabitat distribution, Cichlidae, Monopisthocotyla, Copepoda, Glochidia

ABSTRACT

Parasites, given their crucial roles in ecosystems, have gained increasing attention as indicators of ecosystem health. Despite their ecological relevance, there is still limited understanding of how parasite communities respond to environmental change over time. This hinders the development and implementation of targeted parasite conservation strategies, thereby contributing to parasites remaining among the most threatened and underprotected animal groups worldwide. Anthropogenic pressures and environmental changes are altering ecosystems at an accelerating pace, which may have far-reaching consequences for both parasite populations and their ecosystem services. We used natural history collections to reconstruct changes in parasite abundance, species richness, and gill microhabitat distribution between 1978 and 2011 in six haplochromine cichlid fish hosts from Lake Victoria (Eastern Africa). Since the 1980s, Lake Victoria has undergone severe environmental degradation due to anthropogenic activities and climate change, leading to significant biodiversity loss, including the extinction of half of the haplochromine cichlid species. Our results indicate that parasite populations are negatively impacted by (human-induced) environmental changes and mirror the health status of the ecosystem: both parasite abundance and species richness per host individual significantly declined during the perturbed period across all studied parasite taxa, but showed signs of improvement during the recovery period. However, gill microhabitat distribution showed no significant change over time. These findings contribute to our understanding of parasite dynamics in times of global change and underscore the urgent need to develop and implement effective parasite conservation strategies to prevent further losses in parasite biodiversity and the ecological functions they support.

INTRODUCTION

Parasites have gained significant attention as indicators of various aspects of ecosystem health, such as ecosystem productivity, biodiversity, and resilience (1). This is due to the key roles parasites play within ecosystems, including serving as important components of food webs (e.g., increasing food web connectivity and stability; (2,3), influencing competitive and trophic interactions between species (1), and regulating energy fluxes (1,4). A diverse parasite community therefore reflects healthy ecosystems (1). The use of parasites in biological monitoring programs has recently received considerable interest, owing to their potential to serve as biological indicators of pollution and their ability to provide information about their hosts. For example, parasites have demonstrated their utility in previous studies by identifying the origin of invasive host species (5), serving as indicators of climate change (6), assessing environmental

quality (2), and acting as biological warning indicators of major threats (climate change, overexploitation, habitat loss and fragmentation, invasive species) to global biodiversity (7). Despite their vital contributions to ecosystems and their role as biological monitoring agents, parasites remain among the most threatened and underprotected animals on Earth. The decline and extinction of parasites can have far-reaching effects on both ecosystems and populations (7,8). Carlson et al. (2020) highlighted that the lack of detailed descriptions of parasites and their biodiversity hinders their effective integration into broader biodiversity conservation efforts, leaving protection as more of a theoretical concept than a practical reality (8). A critical data gap is the lack of information on how parasites are affected by changing environments due to anthropogenic perturbations, as well as the potential consequences this may have on ecosystems (4,8).

We expect parasites to be significantly influenced by environmental changes, with the direction (negative or positive) of the impact varying across different taxa (9–14). For example, it has been indicated that parasite groups vary considerably in their sensitivity to specific types of pollution, and that even within a single study, the effects of environmental factors on parasite abundance can vary depending on the parasite taxa involved (9,15). This variability in response can be explained by variation in how parasite taxa cope with pollution. Some parasite taxa can act as pollution or toxin sinks by accumulating contaminants from their host, which enables them to reduce their host's exposure to toxins—thereby indirectly benefiting the parasite by enhancing host survival (13). Additionally, the life cycle of the parasite can influence how sensitive they are to environmental changes. It is expected that the more complex the life cycle and the more hosts required, the more vulnerable the parasite is (14). Besides pollution, temperature changes due to climate change can also indirectly affect parasites by altering host distribution, density, physiology, and immune defenses. These changes may modify parasite transmission, resulting in positive, negative, or neutral net effects on parasite abundance, depending on the parasite taxa (14,16,17). While these findings provide valuable insights, they often focus on the effect of only one environmental factor on one or few parasite species, resulting in a lack of a holistic view of how the combination of anthropogenic changes affects parasite communities within an ecosystem.

To address this gap, recent studies have aimed to reconstruct the effects of anthropogenic changes on parasite communities by relying on existing databases through meta-analysis (15,18–22). However, meta-analyses are susceptible to literature bias (18) and constrained by the availability of data in the literature, with limited sources extending beyond a time span of 50 years (19). Moreover, the temporal resolution of parasitological data from the literature remains an obstacle, restricting our ability to detect small-scale fluctuations in parasite communities over time. These limitations can be addressed by utilizing natural history collections as a resource for studying long-term changes in parasitism (19). Fluid-preserved biological host specimens contain the parasites that infected the hosts at the time of their preservation (14,19). Since these collections extend further (early 20th century) back in time compared to the data available in the literature, they provide a unique source of information enabling researchers to reconstruct parasite community changes over both broad time span and fine-resolution timescale (8,14,19).

We reconstructed changes in parasite abundance, species richness, and gill microhabitat distribution between 1978 and 2011 in six haplochromine cichlid fish hosts from Lake Victoria, East-Central Africa. Lake Victoria, one of the African Great Lakes, has experienced severe environmental degradation since the 1980s due to human activities and climate change (23–26). These stressors include the introduction of invasive species such as the Nile perch (*Lates niloticus*), which preys on cichlid fish (27,28); eutrophication caused by agricultural and urban runoff and soil erosion from deforestation (29). The overload of nutrients resulted in an altered phytoplankton composition (29), reduced dissolved oxygen (DO) levels, and contributed to anoxic waters and algal blooms (30–32). These environmental changes have led to a significant decline in biodiversity in Lake Victoria (23,24,26), including the extinction of half of the haplochromine cichlid species (25).

In this study, we incorporated environmental parameters (minimum and maximum air temperature, rainfall, lake water levels) and infection parameters (parasite abundance, individual species richness, gill microhabitat distribution) as part of the holistic approach. We screened museum specimens of haplochromine cichlids for ectoparasites to test whether parasite communities changed across different perturbation phases of Lake Victoria. The goal is to examine how anthropogenic disturbances affect parasite communities by analyzing changes in their abundance, species richness, and gill microhabitat distribution. Understanding these shifts will help clarify the role of parasites in maintaining ecosystem and human health in the context of global change and may contribute to future efforts to integrate parasites into biodiversity conservation strategies.

We hypothesize that anthropogenic disturbances had a negative effect on parasite abundance and species richness, potentially due to reduced host abundance and the potential impacts of pollution, which could hinder the survival and transmission of parasite life stages (8,15,33). We furthermore expect shifts in parasite microhabitat distribution from more exposed to more sheltered regions of the gills as a consequence of pollution (34).

EXPERIMENTAL PROCEDURES

2.1 Study system

In the present study we used six haplochromine cichlid museum specimens. These were two closely related zooplanktivorous species—*Haplochromis pyrrhocephalus* and *H. laparogramma*—as well as a zooplanktivorous species, *H. tanaos*, and a molluscivorous species, *Platytaeniodus degeni*. The remaining two zooplanktivorous species, *H. heusinkveldi* and *H. piceatus*, are classified as critically endangered on the IUCN Red List (35). All six species of cichlid fish are bentopelagic. Ecological information on these species can be found in table S1. In Lake Victoria, the gills of these cichlids are infected by six species of Monopisthocotyla (*Cichlidogyrus bifurcatus*, *C. furu*, *C. longipenis*, *C. nyanza*, *C. pseudodossoui*, *C. vetusmolendarius*) along with two species of Copepoda (*Ergasilus lamellifer and Lamproglena monodi*) and Bivalvia (Mollusca: Bivalvia) (36–38).

2.2 Fish collection

A total of 289 haplochromine cichlid specimens from six haplochromine species (*Haplochromis heusinkveldi*, *H. laparogramma*, *H. piceatus*, *H. pyrrhocephalus*, *H. tanaos*, and *Platytaeniodus degeni*) were collected between 1978 and 2011 in the northern part of the Mwanza Gulf, Lake Victoria, Tanzania (Fig. 1). Sampling was originally conducted by the Haplochromis Ecology Survey Team (HEST) in collaboration with the Tanzania Fisheries Research Institute (TAFIRI) along a transect stretching from Butimba Bay to Kissenda Bay, in the northern Mwanza Gulf (Fig. 1). Detailed methodologies related to fish sampling and ethical considerations are described in van Rijssel and Witte (2013) and the references therein (39). The sampling period spanned three distinct ecological phases of Lake Victoria: the pristine phase (1978–1981), representing the period before major environmental disturbances; the perturbed phase (1984–1999), marked by intense environmental changes; and the recovery phase (2001–2006), during which environmental conditions were less extreme than in the perturbed phase (39). These periods will hereafter be referred to as “ecological periods”. Following collection, the fish were originally preserved in a 4% formaldehyde solution buffered with borax and subsequently transferred to 70% ethanol. The specimens were deposited at the Centre for Biodiversity, Naturalis (Leiden, The Netherlands). The gills had already been extracted as part of previous studies (35, 39–42) and later transported to Hasselt University (Belgium) for parasitological examination. We included five to eight male individuals of each of the six haplochromine cichlid species per year, so that host species are consistently represented across the years of interest (Table S2). Therefore, three female specimens from 1986 were also included. With the exception of these, only male specimens were used to enhance comparability with previous parasitological studies on cichlids.

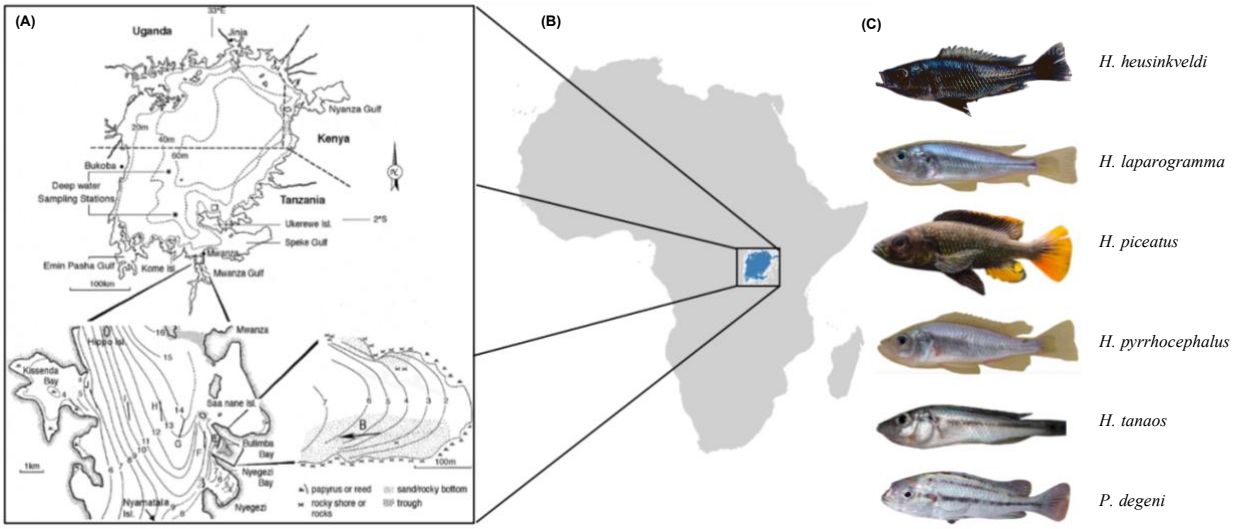

Fig. 1 – (A) Map of Geographic Sample Location in the Northern Mwanza Gulf, Lake Victoria with station E-J representing the research transect and station A-D representing the Butimba Bay. Numbers represent depth in meters (41). **(B)** Geographic location of Lake Victoria in Africa. **(C)** The six host haplochromine cichlid species sampled in this study: *Haplochromis heusinkveldi*, *H. laparogramma*, *H. piceatus*, *H. pyrrhocephalus*, *H. tanaos*, and *Platytaeniodus degeni*.

2.3 Environmental data

We included four key environmental parameters from the dataset used in van Rijssel et al. (2016) to explore potential influences of changing abiotic conditions on parasite populations over time (41). The environmental parameters included minimum and maximum air temperatures and rainfall, which were measured at Mwanza Airport by the Meteorological Department, and lake water levels, recorded between Mwanza City and the village of Nyegezi by the Lake Victoria Basin Water Office (41). Other relevant environmental parameters, such as dissolved oxygen (DO) levels, water transparency, and lake water temperature, were not considered due to inconsistent data availability (41). In particular, during the perturbed period, measurements were missing for several consecutive years, which would have resulted in substantial gaps and insufficient statistical power to assess their effects on parasite communities.

2.4 Parasite screening and identification

The first gill arch on the right side of six cichlid species from Lake Victoria was examined under a dissecting stereoscope (Leica EZ4). Other gill arches have already been used in prior research on these specimens and were not available (42). Nevertheless, this does not limit our study, as the first gill arch—being the largest—harbors a high abundance of parasitic infections and provides a sufficient representation of parasite abundance and diversity in Cichlid species (37,43–45). During the parasitological examination of the gills, parasites were counted and identified to the highest taxonomic resolution possible, using a Leica DM2500 LED (Leica Microsystems, Wetzlar, Germany) at 1000× magnification with differential interference contrast. Identification of Monopisthocotyla was based on the shape and size of the sclerotized structures of the attachment organ (haptor) and the male copulatory organ (Following 38). We initially based the identification of Copepoda on the spine-setae formula, as this is a key diagnostic characteristic for distinguishing species of copepods. However, due to insufficient specimen transparency and missing spines or setae, this method was unsuitable for accurate identification of most specimens. Therefore, we switched to a principal component analysis (PCA) of nine trait measurements, using LAS X 3.6 (Leica Application Suite software). The site of attachment of Monopisthocotyla and Copepoda on the first gill arch was also recorded. The first gill arch was divided into nine microhabitats (Fig. 2A), based on two hierarchical spatial units: longitudinal segments (dorsal, median, ventral), and vertical areas (proximal, central,

distal, extending from the gill bar to the tip of the filaments)(37). Copepoda were preserved in 100% ethanol in vials to enhance tissue transparency, with 36 individuals of *Ergasilus* and one *Lamproglena* individual subsequently immersed in 80% lactic acid for four and a half days to further improve transparency. All 109 Copepoda were subsequently mounted onto microscopic slides using glycerol except for two which were mounted with Hoyer's medium. Monopisthocotyla were directly mounted onto slides in Hoyer's medium without prior preservation in ethanol.

2.5.1 Principal component analysis (PCA)

The species identification of Copepoda (103 *Ergasilus lamellifer,* 6 *Lamproglena monodi*) was based on a principal component analysis (PCA) of 9 measured traits. For *Ergasilus*, these traits included cephalothorax length and width, total length, egg sac length, and egg diameter. Additionally, we recorded the presence or absence of the inverted T structure on the cephalothorax (following 46,47). For *Lamproglena*, the PCA was based on cephalothorax length and width, total length, egg sac length, egg diameter, and the lengths of

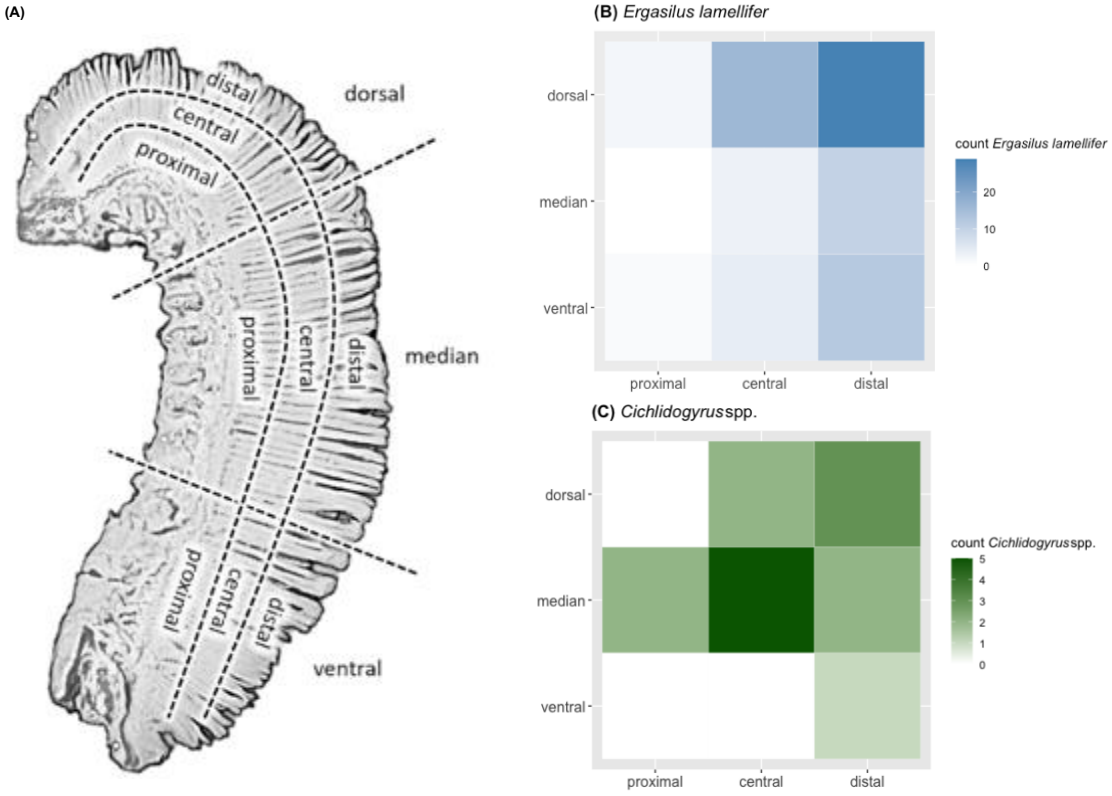

Fig. 1 – **Gill microhabitat distribution of ectoparasites infecting cichlids from Lake Victoria. (A)** Overview of gill arch subdivision into horizontal segments (dorsal, median, ventral) and vertical areas (proximal, central, distal) (from 34) **(B)** Microhabitat distribution based on abundance of *Ergasilus lamellifer* **(C)** Microhabitat distribution based on abundance of all three *Cichlidogyrus* species (pooling *C. bifurcatus*, *C. furu*, *C. nyanza*).

2.5 Data analysis –All statistical analyses were performed in R statistical software version 2024.09.1+394 (R Core Team 2024).

the large and small parts of Antenna 1, as well as the length of Antenna 2 (following 46,47). For the PCA of *Lamproglena*, we included measurements from two additional specimens of *Lamproglena monodi*, which were not part of our study but were included to provide sufficient statistical power for conducting the PCA due to the small sample size.

2.5.2 Parasite abundance

To test whether the abundance of parasite species has changed over time in response to environmental changes, we used Generalized Linear Mixed Models. Data distribution was assessed and collinear variables were excluded. Parasite abundance followed a negative binomial distribution. The variables maximum temperature and rainfall were excluded from the initial model due to collinearity. The response variable was parasite abundance (number of parasite individuals per host individual). We created two initial models, one with year as an explanatory variable and one with ecological period (pristine, perturbed, recovery) as an explanatory variable. Fixed effects for both initial models included parasite species, fish sex (male or female), trophic group (zooplanktivore or molluscivore), minimum temperature (in °C), lake water level (in meters), and fish species (to control for pseudoreplication), along with the interaction between parasite species and ecological period or year. Random effects included fish individual identity (to control for repeated sampling). The significance of fixed effects was assessed using Likelihood Ratio Tests (LRTs) to identify the minimum adequate model (MAM) that best fit our data. To test whether individual fish identity as a random effect contributed to the model, we compared models with and without the random effect by performing an ANOVA. To assess whether the fixed effects had a significant influence on parasite abundance, we performed an ANOVA, followed by post-hoc Tukey tests on all of the significant terms with more than two categories to assess if parasite abundance significantly changed throughout time.

2.5.3 Parasite species richness

To investigate whether environmental changes introduced shifts in parasite species richness per individual host, we used Generalized Linear Mixed-effects Models (GLMMs). Species richness is the number of parasite species per fish individual and is hereafter referred to as individual species richness. To determine the data distribution and exclude colinear variables, we followed the same procedure explained above. The individual species richness followed a Poisson distribution. The same environmental variables as in the previous abundance models (maximum temperature and rainfall) were excluded due to collinearity. We created two initial models, one with year as an explanatory variable and one with ecological period (pristine, perturbed, recovery) as an explanatory variable. Fixed effects for both initial models included: fish sex (male or female), trophic group (zooplanktivore or molluscivore), minimum temperature (in °C), lake water level (in meters), and fish species (to control for pseudoreplication). Fish individual identity was included as a random effect, as each individual fish can be infected by multiple parasites. The significance of the fixed effects and interactions was tested using LRTs, resulting in the MAM. To test whether individual fish identity as a random effect contributed to the model, we compared models with and without the random effect by performing an ANOVA. To assess whether the fixed effects had a significant influence on parasite individual species richness, we performed an ANOVA, followed by post-hoc Tukey tests on all of the significant terms with more than two categories to assess if individual species richness significantly changed throughout time.

2.5.4 Parasite gill macrohabitat distribution

To investigate whether parasites exhibited microhabitat segregation, and whether this segregation changed across ecological periods as a result of environmental changes, we performed for each parasite taxon one Generalized Linear Mixed-effects Model (GLMM). Based on collinearity tests, maximum temperature and rainfall were excluded from the initial models. The response variable was the number of parasite individuals per microhabitat. The initial models included as fixed effects: ecological period (pristine, perturbed, recovery), microhabitat site (dorsal-proximal, median-proximal, ventral-proximal, dorsal-central, median-central, ventral-central, dorsal-distal, median-distal, ventral-distal), along with their interaction (to assess whether the effect of microhabitat site differed across ecological periods), total abundance of the target parasite species per fish individual (to account for pseudoreplication), trophic group, minimum temperature, and lake water level. Random effects included fish individual identity (to account for repeated sampling). To test whether individual fish identity as a random

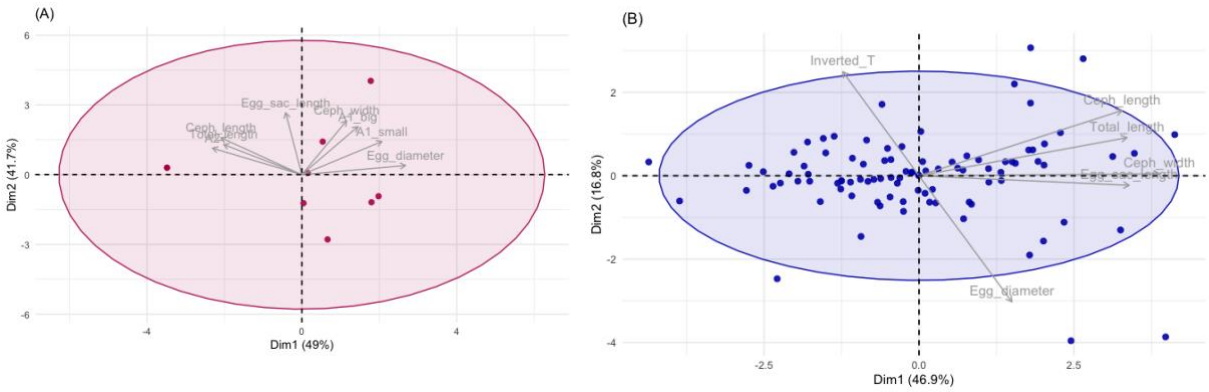

Fig. 3 – **Principal Component Analysis (PCA) of morphological measurements** of **(A)** *Lamproglena*, with Dimension 1 explaining 49% of the variance and Dimension 2 explaining 41.7%, and **(B)** *Ergasilus*, with Dimension 1 explaining 46.9% of the variance and Dimension 2 explaining 16.8%. Each point represents an individual parasite; arrows indicate the contribution of each morphological trait (Ceph_length : cephalothorax length, Ceph_width : cephalothorax width, Inverted_T: prescence or absence of the inverted T structure, A1_small: length of the small part of the first antenna, A1_big : length of the large part of the first antenna, A2: length of the second antenna). Pink (*Lamproglena*) and blue (*Ergasilus*) ellipses indicate the 95% confidence interval.

effect contributed to the model, we compared models with and without the random effect by performing an ANOVA. The significance of the fixed effects in the initial model was determined using LRTs to obtain the MAM. To assess whether the fixed effects had a significant influence on parasite gill microhabitat distribution, we performed an ANOVA on both MAMs, followed by post-hoc Tukey tests on all of the significant terms with more than two categories to test whether these patterns of occupation changed throughout time.

RESULTS

3.1 Parasite identification

We found 19 individuals belonging to three species of Monopisthocotyla (2 *Cichlidogyrus bifurcatus,* 15 *C. furu,* 2 *C. nyanza*), 109 Copepoda belonging to two species (103 *Ergasilus lamellifer,* 6 *Lamproglena monodi*) and 3645 Glochidia. Principal Component Analysis (PCA) revealed that all specimens of *Lamproglena* clustered together at 95% confidence interval (CI), indicating they belonged to the same species, namely *Lamproglena monodi* (Fig. 3A). The first two dimensions (Dim1 and Dim2) explained 49% and 41.7% of the variance, respectively. The PCA of *Ergasilus* specimens showed that most individuals clustered together within the 95% CI (Fig. 3B). The first two dimensions (Dim1 and Dim2) explained 46.9% and 16.8% of the variance, respectively. Seven outliers were observed outside the CI. Morphological analysis confirmed that these outliers did not exhibit any morphological difference from the other individuals belonging to *Ergasilus lamellifer.*

3.2 Parasite abundance

In the first model, testing for year, the minimum adequate model (MAM) included parasite species, sampling year, fish species, and minimum temperature as fixed effects, and fish individual identity as a random effect. Parasite abundance did not change across sampling years, and the effect of year on parasite abundance did not differ between parasite species. Minimum temperature had a significant positive influence on parasite abundance. In the second model, testing for ecological period, the MAM included parasite species, ecological period, fish species, and lake water level as fixed effects, and fish individual identity as a random effect. When comparing the abundance within the same parasite taxa between different ecological periods (pristine, perturbed, and recovery) in Lake Victoria, all parasite species (*Cichlidogyrus bifurcatus*, *C. furu*, *C. nyanza*, *Ergasilus lamellifer*, Glochidia, and *Lamproglena monodi*) were significantly more abundant during the pristine period compared to the perturbed period and compared to the recovery period (Fig. 4, Table S4). When comparing abundances of different parasite taxa (pooling ecological periods), Glochidia was overall significantly more

abundant than *Cichlidogyrus bifurcatus* and *C. furu*. Furthermore, *E. lamellifer* was significantly more abundant than *C. furu*, *C. nyanza*, and *C. bifurcatus* (Table S5). An overview of mean parasite abundance per host species is provided in Table S6. Lake water level had a negative influence on parasite abundance. Again, the effect of ecological period on parasite abundance did not differ between parasite species when testing for an interaction between parasite species and ecological period.

MAM included parasite ecological period and fish species as fixed effects. The random effect fish individual identity did not significantly improve the model and was therefore excluded. Parasite individual species richness did change across ecological periods, and parasite species richness across ecological periods did not differ between the different fish species. The perturbed period showed significantly lower individual species richness compared to the pristine (p=0.004, Z=-3.212) and recovery (p=0.030, Z=-2.539) period. There was no significant difference in individual species

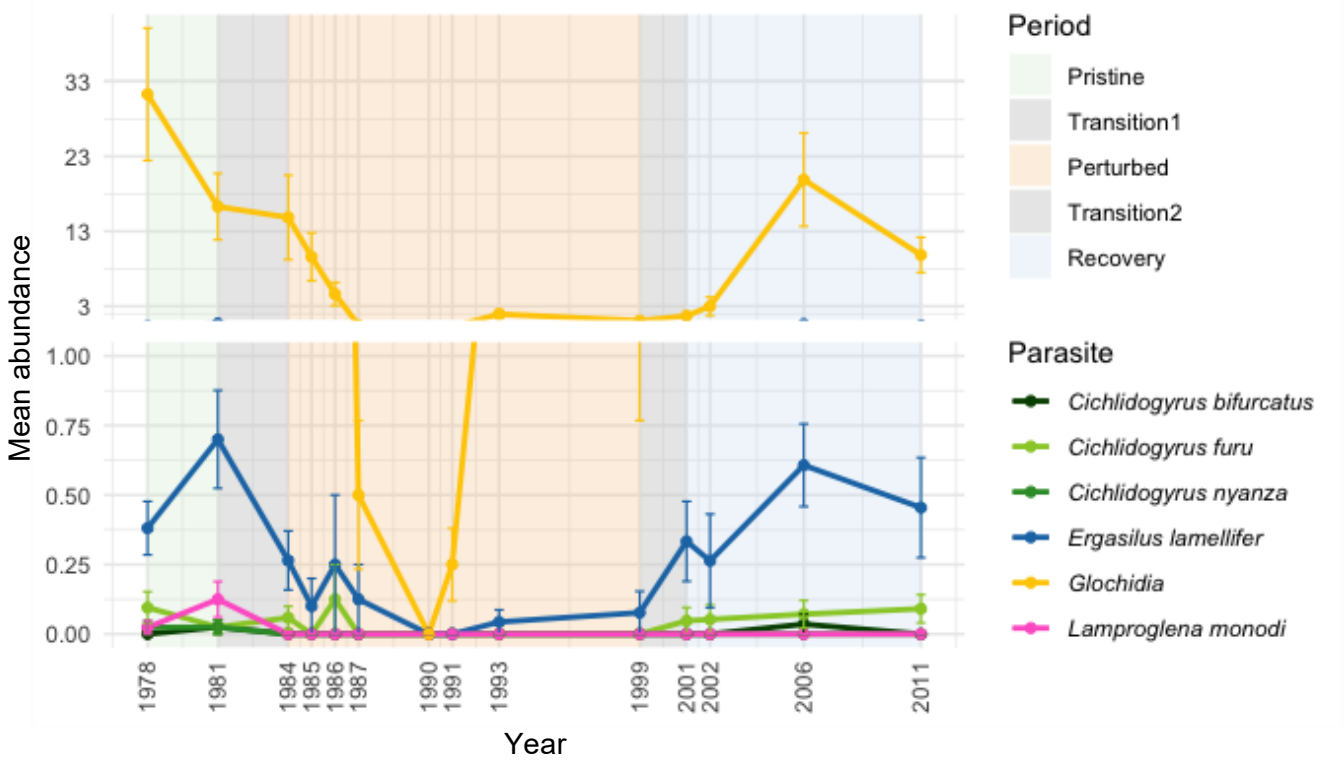

Fig. 4 – Parasite mean abundance for each parasite taxon (*Cichlidogyrus bifurcatus*, *Cichlidogyrus furu*, *Cichlidogyrus nyanza*, *Ergasilus lamellifer*, Glochidia, and *Lamproglena monodi*) from 1978 to 2011. The time axis is divided into three ecological periods: pristine (1978–1981), perturbed (1984–1999), and recovery (2001–2011) with transitional phases in between. Each line represents a parasite taxon: *Cichlidogyrus bifurcatus* (dark green), *Cichlidogyrus furu* (light green), *Cichlidogyrus nyanza* (green), *Ergasilus lamellifer* (blue), *Glochidia* (yellow), and *Lamproglena monodi* (pink). Error bars indicate the standard error of the mean (SEM) across all host individuals sampled per year. The y-axis includes a break between values 1 and 2.5 to improve visualization of both low and high abundance values.

3.3 Individual species richness

In the first model, testing for sampling year, the minimum adequate model (MAM) included sampling year and fish species as fixed effects, and fish individual identity as a random effect. Parasite individual species richness did not change across sampling years, and parasite individual species richness across years did not differ between the different fish species. In the second model, testing for ecological period, the richness between the pristine and recovery periods (p=0.771, Z=0.688; Fig. 5).

3.4 Gill microhabitat distribution

The MAM for *E. lamellifer* included gill microhabitat site and total parasite abundance of *E. lamellifer* per fish individual as fixed effects and fish individual identity a random effect. The microhabitat distribution of *E. lamellifer* on gill arch 1 showed a clear non-random pattern (Table S3): it was significantly

more abundant on the dorsal-distal microhabitat site compared to the dorsal-proximal, median-central, ventral-central, and ventral-proximal ones (Fig. 2B; Table S7). Conversely, *E. lamellifer* was least frequent for the median-proximal site. Because of the limited sample size for each *Cichlidogyrus* species, resulting in low statistical power, the three species of *Cichlidogyrus* were pooled together, and the gill microhabitat analysis was conducted at the genus level. The model for the microhabitat distribution of *Cichlidogyrus* included the same fixed and random effects

DISCUSSION

Our study aimed to investigate how parasite abundance and species richness have changed over time. Our results show that parasite communities were affected by (human-induced) environmental changes during the perturbed period, as both parasite abundance and species richness declined compared to the pristine period. Furthermore, we did not observe any differences in parasite species richness or abundance between fish species or trophic groups. Although some signs of recovery in parasite abundance were observed during the recovery period, levels have not yet returned to those observed in the pristine period.

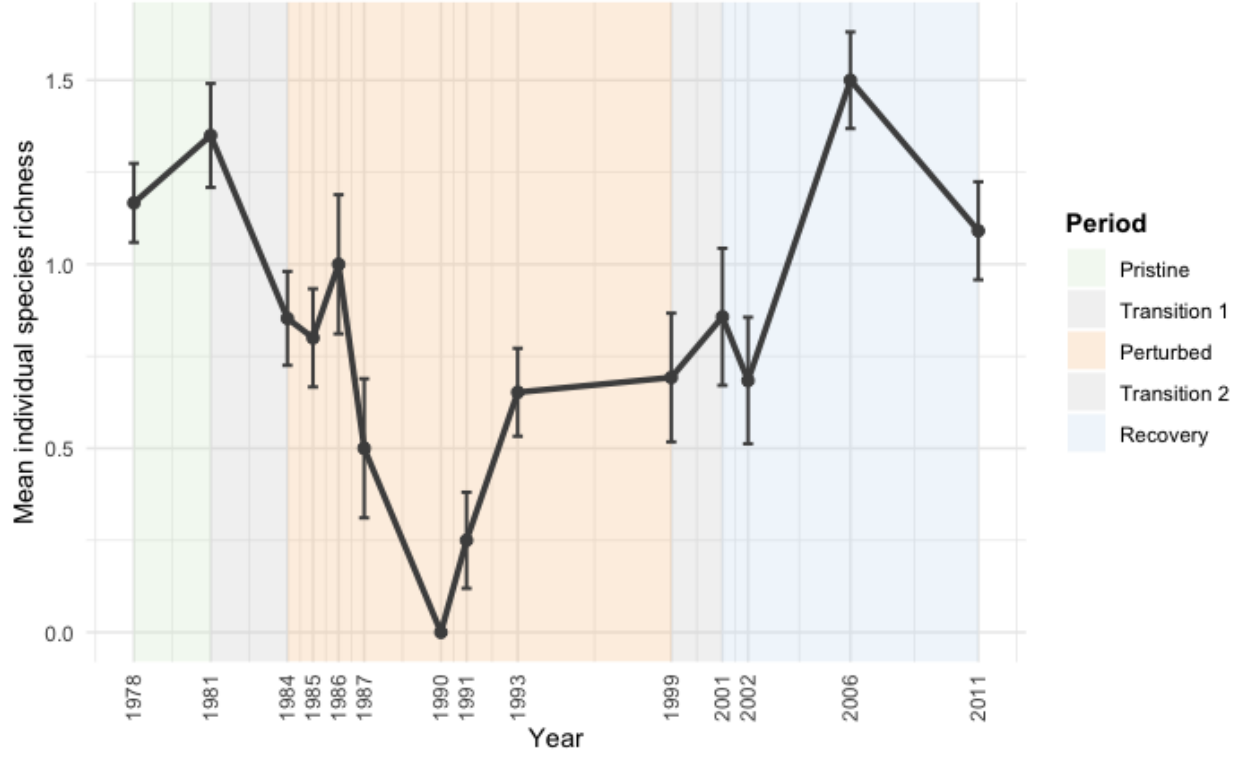

Fig. 5– Parasite mean individual species richness per sampling year. The time axis is divided into three ecological periods: pristine (1978–1981), perturbed (1984–1999), and recovery (2001–2011) with transitional phases in between. Each point represents the parasite individual species richness of the six parasite taxa (*Cichlidogyrus bifurcatus*, *Cichlidogyrus furu*, *Cichlidogyrus nyanza*, *Ergasilus lamellifer*, *Glochidia*, and *Lamproglena monodi) for ag given year* from 1978 to 2011.

as mentioned above, except that total parasite abundance of *Cichlidogyrus* per fish individual was excluded. The distribution of *Cichlidogyrus* did not deviate significantly from randomness across the microhabitat regions of the first gill arch (Fig. 2C; Table S3). There were no significant changes in microhabitat distribution of *E. lamellifer* and *Cichlidogyrus* spp. over different ecological periods (Table S3). The microhabitat distribution of *Lamproglena monodi* was not analyzed due to insufficient data, which resulted in limited statistical power.

Interindividual variation in E. lamellifer

We found 19 individuals belonging to three species of Monopisthocotyla (2 *Cichlidogyrus bifurcatus,* 15 *C. furu,* 2 *C. nyanza*), 109 Copepoda belonging to two species (103 *Ergasilus lamellifer,* 6 *Lamproglena monodi*) and 3645 Glochidia. For the two copepod species, we performed a PCA in addition to morphological identification to

assess whether all individuals indeed belonged to the same species. In *L. monodi*, the PCA supported morphological identification, showing all samples to cluster as one species. In *E. lamellifer*, however, the PCA revealed seven outliers. Upon further morphological examination, we concluded that these outliers were likely the result of intraspecific variation in certain traits or differences in developmental stage or maturity.

Parasite abundance and individual species richness

Parasite abundance varied across ecological periods, but not across individual sampling years. This was likely due to insufficient data on parasite infections to detect effects at a finer temporal resolution. Pooling years is a more robust approach that increases the chance of detecting changes that might not be observable at the level of individual years. During the perturbed period, the abundance of all parasites (*Glochidia*, *C. bifurcatus*, *C. furu*, *C. nyanza*, *E. lamellifer*, and *L. monodi*), as well as species richness per individual host, was lower compared to the pristine period (prior to environmental changes). These findings indicate that parasite communities in Lake Victoria are negatively impacted by (human-induced) environmental changes, and that shifts in parasite populations mirror environmental alterations. Although Lake Victoria is currently considered to be in a relatively stable state (28,48), our results indicate that parasite abundance and individual species richness during the recovery period has not fully returned to pre-disturbance levels, while individual species richness did recover to pre-disturbance levels. In the Mwanza Gulf, environmental conditions have shown some improvement since the 2000s, partly due to increased wind activity enhancing vertical mixing, which in turn improves dissolved oxygen availability and overall water quality (41). These improvements were possibly further supported by intense fishing of Nile perch, which reduced predation pressure and allowed lower trophic level species to more effectively utilize primary productivity (32). This shift likely contributed to increases in these species and helped mitigate some of the impacts of eutrophication (32,49). However, environmental conditions have not fully recovered, as runoff-driven phosphorus enrichment remains a persistent issue, continuing to fuel eutrophication in the lake (41). The remaining presence of eutrophication and the fact that water quality has not yet returned to pre-disturbance levels may explain why parasite abundance has not recovered to levels observed prior to the environmental changes (41). However, in contrast to parasite abundance, parasite species richness *has* recovered to pre-disturbance levels. This may be attributed to the reappearance of *Cichlidogyrus nyanza* and *C. bifurcatus* during the recovery period, after their disappearance during the perturbed period, which directly contributed to the observed increase in species richness. The disappearance of *C. nyanza* and *C. bifurcatus* may have resulted from the reduced availability of cichlid fish hosts in Lake Victoria, caused by the introduction of the invasive Nile perch, eutrophication, and intense overfishing (25). Such reductions in host populations have been shown to lead to the disappearance of their associated parasites (50).

The perturbed period was characterized by reduced dissolved oxygen (DO) levels and lower water temperatures (29,30,37,41), caused by thermal stratification resulting from decreased vertical mixing. This decrease in vertical mixing was linked to reduced wind speeds and a shift in wind direction toward southwest patterns during the 1980s (41). In general, studies have shown that higher water temperatures tend to benefit parasites by positively influencing their life span, development, reproduction, and increased transmission rate of infective stages (51,52), while lower temperatures can be less favorable (12,51). For example, monopisthocotylan eggs are known to hatch faster at higher temperatures (9,53). Similarly, copepods show enhanced egg production, faster development, and increased infection success under warmer conditions (54). Glochidia exhibit faster and more efficient growth at elevated temperatures (55). These findings align with our results, which suggest that the decrease in water temperature during the perturbed period had a negative effect on both parasite abundance and species richness. Conversely, the increase in water temperature during the recovery period—reaching levels comparable to those in the pristine period—was accompanied by a similar increase in parasite species richness, following the same pattern. In

contrast, parasite abundance did not return to pristine levels, despite the recovery of water temperature.

Lake levels of Lake Victoria gradually decreased from the pristine to the perturbed period, and continued to decline into the recovery period, likely due to increased evaporation caused by stronger wind speeds and higher maximum temperatures (41). Lower lake water levels are associated with reduced flow rates, and parasite species richness tends to be higher in milder currents (56). This is in line with our findings, as we observed that lake water levels had a negative effect on parasite abundance in our model. We observed an increase in species richness during the recovery period, when lake levels had dropped even further compared to the perturbed period. Furthermore, the mean abundance of Monophystocoltyla and Copepoda has been shown to be negatively correlated with stream velocity (57), which is also consistent with our results in the recovery period, where we observed an increase in mean abundance alongside further declines in lake levels. However, the decline in lake water levels from the pristine to the perturbed period does not align with the literature, as both parasite abundance and species richness declined in the perturbed period compared to the pristine period. This discrepancy is likely due to the influence of other environmental variables that may have negatively affected parasite metrics, as further discussed in this study.

The perturbed period was also marked by a decrease in DO levels. Literature is in agreement that low dissolved oxygen (DO) levels are associated with higher parasite abundance. For example, low DO levels during the perturbed period led to an increased gill surface area (41) and can lead to increased ventilation volume across the gills, which can result in greater attachment area and enhanced exposure to parasites, potentially favoring parasite infection (58–60). However, we found that parasite abundance and individual species richness decreased during the perturbed period. The discrepancy between our findings and those in the literature may be attributed to taxon-specific differences in parasite responses. For example, it was found that while the abundance of *Cichlidogyrus tilapiae* decreased in response to low DO levels, the abundance of other species increased, such as *Cichlidogyrus sclerosus*, *C. thurstonae*, and *Scutogyrus longicornis* (9). This supports the idea that even within a single study, the effects of DO levels can vary, suggesting that the impact of DO on parasite abundance and species richness is highly dependent on the specific parasite taxa involved.

The reduced DO levels observed during the perturbed period are further exacerbated by cyanobacterial blooms (29,48), which thrive under conditions such as increased nutrient input from agricultural and industrial runoff, sediment influx, and low wind speeds. These conditions also contributed to the eutrophication of the lake and resulted in reduced water transparency in Lake Victoria (41). Previous studies generally report that eutrophication and elevated nutrient levels exert a positive effect on the abundance of Monopisthocotyla (*Cichliodgyrus*) and Copepoda (*Lamproglena*) (9,11). It is important to consider that our study reflects a long-term study (33 years) compared to the period range of the previous studies (eight months to three years). Given that ectoparasites are highly sensitive to pollution (11), it is possible that the potential benefits of nutrient enrichment on parasite abundance are offset by the negative impacts of other stressors (e.g., a decrease in temperature) under long-term exposure. This could help explain the decline in parasite abundance observed in our study. For example, freshwater copepods have been shown to be particularly sensitive to pesticides and nitrogen-based fertilizers, which can act as endocrine disruptors (10,61). The decline in parasite species richness per host individual we observed during the perturbed period is consistent with previous studies reporting that parasite exposure to excess nutrients from urban effluents, eutrophication, and pollution leads to reduced parasite diversity and species richness (62,63).

In addition to the environmental factors discussed above, a contributing indirect factor to the observed decline in parasite abundance and individual species richness may be the reduced availability of cichlid fish hosts in Lake Victoria, caused by the introduction of the invasive Nile perch, eutrophication and intense overfishing (25). This reduction in host abundance can limit opportunities for parasite

transmission and negatively affect both parasite abundance and species richness, as declines in host populations have been shown to lead to the disappearance of their associated parasites (13,50,64).

Glochidia and *E. lamellifer* were more abundant compared to *Cichlidogyrus* species. This is possibly due to *E. lamellifer* and *Glochidia* being a more generalist species and thus infects a broader range of host species, in contrast to *Cichlidogyrus* species, which exhibit strong host specificity, as monopisthocotylans are generally considered one of the most host-specific parasites (47,65–67). Because *E. lamellifer* and *Glochidia* can exploit a wider host range, they may have broader access to resources. Meanwhile, the specialist *Cichlidogyrus* species may compete more intensely with one another than with other parasite taxa due to their similar nutritional requirements, potentially making it more difficult for them to coexist in large numbers within the same host species (37).

Gill microhabitat distribution of parasites

We furthermore aimed to investigate whether (human-induced) environmental changes caused variation in the gill microhabitat distribution of parasites. We found that *E. lamellifer* had a more frequent occurrence on the dorsal-distal sites of the gill, while the distribution of *Cichlidogyrus* spp. did not deviate from random. Environmental changes had no influence on the gill microhabitat distribution of *E. lamellifer* and *Cichlidogyrus* spp. The effects of environmental changes on the gill microhabitat distribution of parasites are unclear in literature: some studies reported shifts in spatial distribution (34), while others observed no change (75,76). This highlights that the effects of environmental change on gill microhabitat distribution may vary depending on parasite species, host–parasite interactions, and the duration and severity of pollution (34). We expected that low dissolved oxygen (DO) levels, which lead to gill enlargement and increased ventilation volume across the gills (58), would result in a shift in parasite distribution. We expected parasites therefore to more frequently occupy peripheral areas of the gill arch or more proximal sites, where they might be more shielded from stronger water currents and greater exposure to pollutant, as ectoparasites are known to be highly sensitive to pollution (11). However, our data did not reveal any differences in the gill microhabitat distribution of *E. lamellifer* and *Cichlidogyrus* spp. across ecological periods (pristine, perturbed, or recovery). This suggests that environmental factors or anthropogenic disturbances did not cause a shift in their microhabitat distribution.

The occurrence of *E. lamellifer* on the distal part of the gill filaments is consistently with a previous study on *Ergasilus sarsi* (68) and a study including the copepod *Dermergasilus varicoleus* (34). The preference for the distal area may be explained by the copepod anchoring itself with its antennae at the tip of the gill filaments, aligning its body parallel to the filament with the egg sacs protrude beyond the filament allowing for optimal exposure of the egg sacs to the water flow which can facilitate the egg hatching (34,37,68,69). The presence of *E. lamellifer* on the dorsal side may be explained by the fact that dorsal gill segments are more sheltered from strong water currents (70). Water flow can influence the distribution of these organisms, as they must remain attached to the gills and avoid being dislodged by the force of water passing across the gill arches and their individual regions (71). Species of *Cichlidogyrus* did not show a significantly higher frequency at a specific microhabitat. The microhabitat frequency of *Cichlidogyrus* appears to be strongly species-dependent, as some studies have also reported the presence of *Cichlidogyrus* at central sites where water flow is weaker compared to distal areas (37,69,72), while other studies reported higher abundances of *Cichlidogyrus* at distal sites (73,74). Because species-level microhabitat analyses were not possible due to limited sample size, species-specific patterns cannot be excluded. Further research is needed to determine whether the low sample size and pooling of species influenced the observed distribution patterns at the genus level.

Although gill microhabitat distribution did not change significantly over ecological periods, parasite abundance and individual species richness declined as a result of environmental changes and anthropogenic disturbances. While ectoparasites are generally considered highly sensitive to pollution (11),

the literature reveals inconsistent patterns regarding the effects of anthropogenic and climate-related stressors on parasite populations. Some studies report positive effects on parasites (9,11,58–60), while others document negative impacts (10,36,50,61–63). Despite differences in study design and analytical approaches, the inconsistency in the direction of effects observed across studies may reflect that each ecosystem is shaped by a unique combination of stressors, exposure durations, environmental conditions, parasite taxa present, and overall biodiversity. Consequently, the effects of environmental disturbances on parasite communities cannot be generalized and further research is needed to gain more information on how different parasite taxa responds to different environmental changes in different ecosystems. Despite this variability, the findings presented here clearly show that parasite populations in Lake Victoria have been negatively affected by human-induced environmental changes, and that parasites can be used as indicators of ecosystem health. Parasite communities have not recovered to the pre-disturbance levels observed during the pristine period. However, there are signs of improvement and recovery of parasite communities in response to improved environmental conditions. Our findings contribute to the growing body of knowledge on how parasites respond to environmental changes, which is essential in order to assess which parasites are threatened with extinction and to develop and translate targeted conservation plans into practical actions to safeguard parasite biodiversity and their ecological functions, especially in these times of global change.

CONCLUSION

This study indicates that parasite abundance and individual species richness declined in response to environmental changes and anthropogenic disturbances. Given the vital roles parasites play in maintaining ecosystem health, such declines may have far-reaching effects on productivity, biodiversity, food web stability and connectivity, organization, and resilience at both ecosystem and population levels (1,3,4,7,8). Our results suggest that parasites may be at risk, highlighting the need for parasite monitoring and conservation. Although Lake Victoria has reached a relatively more stable state, our findings support that the system has not returned to its pre-disturbance conditions, and parasite communities have not fully recovered. However, there are signs of improvement and recovery of parasite communities in response to improved environmental conditions, suggesting that current efforts are moving in the right direction, and that parasites should be included in conservation programs and post-intervention assessments. Our study highlights the need for long term studies investigating changes in parasite populations and the value of using natural historical collections as an effective method for such studies. This study contributes to our understanding of parasite dynamics in times of global change and underscores the urgent need for the development and implementation of effective parasite conservation strategies to prevent further losses in parasite biodiversity and the ecological functions they support.

REFERENCES

1. Hudson PJ, Dobson AP, Lafferty KD. Is a healthy ecosystem one that is rich in parasites? Trends Ecol Evol. 2006 Jul 1;21(7):381–5.

2. Marcogliese DJ. Parasites of the superorganism: Are they indicators of ecosystem health? Int J Parasitol. 2005 Jun 1;35(7):705–16.

3. Lafferty KD, Allesina S, Arim M, Briggs CJ, De Leo G, Dobson AP, et al. Parasites in food webs: the ultimate missing links. Ecol Lett. 2008 Jun;11(6):533–46.

4. Brian JI. Parasites in biodiversity conservation: friend or foe? Trends Parasitol. 2023 Aug 1;39(8):618–21.

5. Allen C, Briano JA, Varone L, Oi DH, Valles SM. Exploitation of a high genomic mutation rate in *Solenopsis invicta* virus 1 to infer demographic information about its host, *Solenopsis invicta*. J Invertebr Pathol. 2010 Sep 1;105(1):105–11.

6. MacLeod CD, Poulin R. Host–parasite interactions: a litmus test for ocean acidification? Trends Parasitol. 2012 Sep 1;28(9):365–9.

7. Gagne RB, Crooks KR, Craft ME, Chiu ES, Fountain-Jones NM, Malmberg JL, et al. Parasites as conservation tools. Conserv Biol. 2022;36(1):e13719.

8. Carlson CJ, Hopkins S, Bell KC, Doña J, Godfrey SS, Kwak ML, et al. A global parasite conservation plan. Biol Conserv. 2020 Oct 1;250:108596.

9. Cavalcanti LD, Gouveia EJ, Leal FC, Figueiró CSM, Rojas SS, Russo MR. Responses of monogenean species to variations in abiotic parameters in tilapiculture. J Helminthol. 2020 Sep 10;94:e186.

10. Di Marzio WD, Castaldo D, Di Lorenzo T, Di Cioccio A, Sáenz ME, Galassi DMP. Developmental endpoints of chronic exposure to suspected endocrine-disrupting chemicals on benthic and hyporheic freshwater copepods. Ecotoxicol Environ Saf. 2013 Oct 1;96:86–92.

11. Gilbert BM, Avenant-Oldewage A. Monogeneans as bioindicators: A meta-analysis of effect size of contaminant exposure toward Monogenea (Platyhelminthes). Ecol Indic. 2021 Nov 1;130:108062.

12. Lõhmus M, Björklund M. Climate change: what will it do to fish—parasite interactions? Biol J Linn Soc. 2015 Oct 1;116(2):397–411.

13. Sures B, Nachev M, Selbach C, Marcogliese DJ. Parasite responses to pollution: what we know and where we go in 'Environmental Parasitology.' Parasit Vectors. 2017 Feb 6;10(1):65.

14. Wood CL, Welicky RL, Preisser WC, Leslie KL, Mastick N, Greene C, et al. A reconstruction of parasite burden reveals one century of climate-associated parasite decline. Proc Natl Acad Sci U S A. 2023;120(3):e2211903120.

15. Blanar CA, Munkittrick KR, Houlahan J, MacLatchy DL, Marcogliese DJ. Pollution and parasitism in aquatic animals: A meta-analysis of effect size. Aquat Toxicol. 2009 Jun 4;93(1):18–28.

16. Byers JE. Marine Parasites and Disease in the Era of Global Climate Change. Annu Rev Mar Sci. 2021 Jan;13:397–420.

17. Cizauskas CA, Carlson CJ, Burgio KR, Clements CF, Dougherty ER, Harris NC, et al. Parasite vulnerability to climate change: an evidence-based functional trait approach. R Soc Open Sci. 2017 Jan;4(1):160535.

18. Fiorenza EA, Leslie KL, Torchin ME, Maslenikov KP, Tornabene L, Wood CL. Fluid preservation causes minimal reduction of

parasite detectability in fish specimens: A new approach for reconstructing parasite communities of the past? Ecol Evol. 2020;10(13):6449–60.

19. Fiorenza EA, Wendt CA, Dobkowski KA, King TL, Pappaionou M, Rabinowitz P, et al. It's a wormy world: Meta-analysis reveals several decades of change in the global abundance of the parasitic nematodes *Anisakis* spp. and *Pseudoterranova* spp. in marine fishes and invertebrates. Glob Change Biol. 2020;26(5):2854–66.

20. Mastick NC, Fiorenza E, Wood CL. Meta-analysis suggests that, for marine mammals, the risk of parasitism by anisakids changed between 1978 and 2015. Ecosphere. 2024;15(3):e4781.

21. Poulin R. Meta-analysis of seasonal dynamics of parasite infections in aquatic ecosystems. Int J Parasitol. 2020 Jun;50(6–7):501–10.

22. Wood CL, Lafferty KD. How have fisheries affected parasite communities? Parasitology. 2015 Jan;142(1):134–44.

23. Goudswaard K (P. C), Witte F, Katunzi EFB. The invasion of an introduced predator, Nile perch (*Lates niloticus*, L.) in Lake Victoria (East Africa): chronology and causes. Environ Biol Fishes. 2007 Dec 1;81(2):127–39.

24. Seehausen O, Alphen JJM van, Witte F. Cichlid Fish Diversity Threatened by Eutrophication That Curbs Sexual Selection. Science. 1997 Sep 19;277(5333):1808–11.

25. Seehausen, O. Lake Victoria Rock Cichlids: taxonomy, ecology and distribution. Zevenhuizen, Netherlands.: Verduyn Cichlids; 1996.

26. Witte F, Wanink JH, Kishe-Machumu M. Species Distinction and the Biodiversity Crisis in Lake Victoria. Trans Am Fish Soc. 2007;136(4):1146–59.

27. Pringle RM. The Nile perch in Lake Victoria: Local responses and adaptations. Africa. 2005;

28. van Zwieten PAM, Kolding J, Plank MJ, Hecky RE, Bridgeman TB, MacIntyre S, et al. The Nile perch invasion in Lake Victoria: cause or consequence of the haplochromine decline? Can J Fish Aquat Sci. 2016 Apr;73(4):622–43.

29. Verschuren D, Johnson TC, Kling HJ, Edgington DN, Leavitt PR, Brown ET, et al. History and timing of human impact on Lake Victoria, East Africa. Proc Biol Sci. 2002 Feb 7;269(1488):289–94.

30. Hecky RE, Bugenyi FWB, Ochumba P, Talling JF, Mugidde R, Gophen M, et al. Deoxygenation of the deep water of Lake Victoria, East Africa. Limnol Oceanogr. 1994;39(6):1476–81.

31. Mugidde R. The increase in phytoplankton primary productivity and biomass in Lake Victoria (Uganda). In: SIL Proceedings, 1922-2010 [Internet]. 1993 [cited 2025 May 22]. p. 846–9. Available from: https://www.tandfonline.com/doi/full/10.1080/03680770.1992.11900264

32. Sitoki L, Gichuki J, Ezekiel C, Wanda F, Mkumbo OC, Marshall BE. The Environment of Lake Victoria (East Africa): Current Status and Historical Changes. Int Rev Hydrobiol. 2010;95(3):209–23.

33. Pietrock M, Marcogliese DJ. Free-living endohelminth stages: at the mercy of environmental conditions. Trends Parasitol. 2003 Jul;19(7):293–9.

34. Kumar R, Madhavi R, Sailaja B. Spatial distribution of ectoparasites on the gills of the mullet, *Liza macrolepis*: the effects of pollution. J Parasit Dis. 2017 Mar 1;41(1):40–7.

35. Rijssel JC van. Adaptive responses to environmental changes in Lake Victoria cichlids [Internet]. Leiden University; 2014 [cited 2025 May 22]. Available from: https://hdl.handle.net/1887/24377

36. Gobbin T, Steenberge MV, Vranken N, Vanhove MP. Worms of change: anthropogenic disturbance changes the ectoparasite community structure of Lake Victoria cichlids [Internet]. bioRxiv; 2024 [cited 2025 May 22]. p. 2024.04.14.589059. Available from: https://www.biorxiv.org/content/10.1101/2024.04.14.589059v1

37. Gobbin TP, Vanhove MPM, Seehausen O, Maan ME. Microhabitat distributions and species interactions of ectoparasites on the gills of cichlid fish in Lake Victoria, Tanzania. Int J Parasitol. 2021 Feb 1;51(2):201–14.

38. Gobbin TP, Vanhove MPM, Seehausen O, Maan ME, Pariselle A. Four new species of *Cichlidogyrus* (Platyhelminthes, Monopisthocotyla, Dactylogyridae) from Lake Victoria haplochromine cichlid fishes, with the redescription of *C. bifurcatus* and *C. longipenis*. Parasite. 2024;31:46.

39. van Rijssel JC, Witte F. Adaptive responses in resurgent Lake Victoria cichlids over the past 30 years. Evol Ecol. 2013 Mar 1;27(2):253–67.

40. van Rijssel JC, Hoogwater ES, Kishe-Machumu MA, Reenen E van, Spits KV, van der Stelt RC, et al. Fast adaptive responses in the oral jaw of Lake Victoria cichlids. Evolution. 2015 Jan 1;69(1):179–89.

41. van Rijssel JC, Hecky RE, Kishe-Machumu MA, Meijer SE, Pols J, van Tienderen KM, et al. Climatic variability in combination with eutrophication drives adaptive responses in the gills of Lake Victoria cichlids. Oecologia. 2016 Dec 1;182(4):1187–201.

42. van Rijssel JC, Hecky RE, Kishe-Machumu MA, Witte F. Changing ecology of Lake Victoria cichlids and their environment: evidence from C13 and N15 analyses. Hydrobiologia. 2017 May 1;791(1):175–91.

43. El-Naggar, A.M, Reda, E.S. Infestation level and spatial distribution of *Protoancylodiscoides mansourensis* (El-Naggar 1987), a monogenean gill parasite from the long fin catfish *Chrysichthys auratus* (Geoffroy, 1809). Egyptian Journal of Aquatic Biology and Fisheries. 2003;331–57.

44. Geets, A, Coene, H, Ollevier, F. Ectoparasites of the whitespotted rabbitfish, *Siganus sutor* (Valenciennes, 1835) off the Kenyan Coast: distribution within the host population and site selection on the gills. Parasitology. 1997;69–79.

45. Madanire-Moyo, G, Matla, M, Olivier, P, Luus-Powell, W. Population dynamics and spatial distribution of monogeneans on the gills of *Oreochromis mossambicus* (Peters, 1852) from two lakes of the Limpopo River System, South Africa. Journal of Helminthology. 2011;146–52.

46. Capart A. Notes sur les Copépodes parasites. III. Copépodes parasites des poissons d'eau douce du Congo Belge. Bulletin du Musée Royal d'Histoire Naturelle de Belgique. 1944;1–24.

47. Schlebusch, Ruaan R. Phylogeny of the African genus *Ergasilus* (Copepoda: Poecilostomatoida). UFS. 2014;

48. Hecky RE, Mugidde R, Ramlal PS, Talbot MR, Kling GW. Multiple stressors cause rapid ecosystem change in Lake Victoria. Freshw Biol. 2010;55(s1):19–42.

49. Balirwa JS, Chapman CA, Chapman LJ, Cowx IG, Geheb K, Kaufman L, et al. Biodiversity and Fishery Sustainability in the Lake Victoria Basin: An Unexpected Marriage? BioScience. 2003 Aug 1;53(8):703–15.

50. Lafferty KD. Ecosystem consequences of fish parasites. J Fish Biol. 2008;73(9):2083–93.

51. Karvonen A, Kristjánsson BK, Skúlason S, Lanki M, Rellstab C, Jokela J. Water temperature, not fish morph, determines parasite infections of sympatric Icelandic threespine sticklebacks (Gasterosteus aculeatus). Ecol Evol. 2013;3(6):1507–17.

52. Awharitoma AO, Ehigiator F. Vol. 17, SciSpace - Paper. 2019 [cited 2025 May 29]. Effects of Climatic Changes on Fish Diversity and Abundance and Prevalence of Fish Parasitic Infections in Southern Nigeria. Available from: https://scispace.com/papers/effects-of-climatic-changes-on-fish-diversity-and-abundance-36avubj8qo

53. Crespo JF, Velarde FI, Crespo RF, Pelaez CGV. Variación estacional de *dactylogyrus* sp. en dos unidades productoras de tilapia del estado de Morelos. Rev Mex Cienc Pecu. 1992 Jan 1;30(2):109–18.

54. Samsing F, Oppedal F, Dalvin S, Johnsen I, Vågseth T, Dempster T. Salmon lice (*Lepeophtheirus salmonis*) development times, body size, and reproductive outputs follow universal models of temperature dependence. Can J Fish Aquat Sci. 2016 Dec;73(12):1841–51.

55. Scheder C, Lerchegger B, Jung M, Csar D, Gumpinger C. Practical experience in the rearing of freshwater pearl mussels (*Margaritifera margaritifera*): advantages of a work-saving infection approach, survival, and growth of early life stages. Hydrobiologia. 2014 Sep 1;735(1):203–12.

56. Marcogliese DJ. Implications of climate change for parasitism of animals in the aquatic environment. Can J Zool. 2001 Aug;79(8):1331–52.

57. Barker DE, Cone DK. Occurrence of *Ergasilus celestis* (Copepoda) and *Pseudodactylogryrus anguillae* (Monogenea) among wild eels (*Anguilla rostrata*) in relation to stream flow, pH and temperature and recommendations for controlling their transmission among captive eels. Aquaculture. 2000 Jul 20;187(3):261–74.

58. Mikheev VN, Pasternak AF, Valtonen ET, Taskinen J. Increased ventilation by fish leads to a higher risk of parasitism. Parasit Vectors. 2014 Jun 23;7(1):281.

59. Poulin R, Leung TLF. Body size, trophic level, and the use of fish as transmission routes by parasites. Oecologia. 2011 Jul;166(3):731–8.

60. Tombi J, Francis AJ, Bilong B, Felix C. The monogenean community on the gills of *Oreochromis niloticus* from Melen fish station in Yaounde, Cameroon. In 2014 [cited 2025 May 22]. Available from: https://www.semanticscholar.org/paper/The-monogenean-community-on-the-gills-of-niloticus-Jeannette-Francis/0546d9e445716d6bcadfa0f7589eefd8826cb2fd

61. Di Lorenzo T, Di Marzio WD, Sáenz ME, Baratti M, Dedonno AA, Iannucci A, et al. Sensitivity of hypogean and epigean freshwater copepods to agricultural pollutants. Environ Sci Pollut Res. 2014 Mar 1;21(6):4643–55.

62. Krause RJ, McLaughlin JD, Marcogliese DJ. Parasite fauna of *Etheostoma nigrum* (Percidae: Etheostomatinae) in localities of varying pollution stress in the St. Lawrence River, Quebec, Canada. Parasitol Res. 2010 Jul 1;107(2):285–94.

63. Schmidt V, Zander S, Körting W, Steinhagen D. Parasites of the flounder *Platichthys flesus* (L.) from the German Bight, North Sea, and their potential use in ecosystem monitoring. Helgol Mar Res. 2003 Oct 1;57(3):236–51.

64. Sures B, Nachev M. Effects of multiple stressors in fish: how parasites and contaminants interact. Parasitology. 2022;149(14):1822–8.

65. Scholz, T., M. P. M. Vanhove, N. Smit, Z. Jayasundera, and M. Gelnar. A Guide to the Parasites of African Freshwater Fishes. 2018.

66. Whittington ID, Cribb BW, Hamwood TE, Halliday JA. Host-specificity of monogenean (platyhelminth) parasites: a role for anterior adhesive areas? Int J Parasitol. 2000 Mar;30(3):305–20.

67. Outa JO, Dos Santos QM, Avenant-Oldewage A, Jirsa F. Parasite diversity of introduced fish *Lates niloticus*, *Oreochromis niloticus* and endemic *Haplochromis* spp. of Lake Victoria, Kenya. Parasitol Res. 2021 May 1;120(5):1583–92.

68. Kilian E, Avenant-Oldewage A. Infestation and Pathological Alterations by *Ergasilus sarsi* (Copepoda) on the Tanganyika Killifish from Africa. J Aquat Anim Health. 2013 Dec;25(4):237–42.

69. Bagge AM, Sasal P, Valtonen ET, Karvonen A. Infracommunity level aggregation in the monogenean communities of crucian carp (*Carassius carassius*). Parasitology. 2005 Sep;131(3):367–72.

70. Wootten R. The spatial distribution of *Dactylogyrus amphibothrium* on the gills of ruffe *Gymnocephalus cernua* and its relation to the relative amounts of water passing over the parts of the gills. J Helminthol. 1974 Sep;48(3):167–74.

71. Soylu E, Çolak SÖ, Erdoğan F, Erdoğan M, Tektas N. Microhabitat distribution of *Pseudodactylogyrus anguillae* and *Pseudodactylogyrus bini* among and within gill arches of the European eel (*Anguilla anguilla* L.). Parasitol Res. 2003 Mar;89(4):290–6.

72. Koskivaara M, Valtonen ET, Vuori KM. Microhabitat distribution and coexistence of *Dactylogyrus* species (Monogenea) on the gills of roach. Parasitology. 1992 Apr;104(2):273–81.

73. Adou, Y, Blahoua, K, Yao, S, N'Douba, V. Spatial distribution of two gill monogenean species from *Sarotherodon melanotheron* (Cichlidae) in man-made Lake Ayamé 2. Journal of Biology and Environmental Science. 2017;35–44.

74. Blahoua, K.G, Adou, Y.E, Etilé, R.N.D, N'Douba, V. Microhabitats preference of *Cichlidogyrus berrebii*, *C. kothiasi* and *C. pouyaudi* (Monogenea: Ancyrocephalidae) on the gills of *Tylochromis jentinki* from Ebrié Lagoon, Côte d'Ivoire. Life Science Journal. 2019;72–8.

75. Bagge AM, Valtonen ET. Experimental study on the influence of paper and pulp mill effluent on the gill parasite communities of roach (*Rutilus rutilus*). Parasitology. 1996 May;112(5):499–508.

76. Yang T, Liu J, Gibson DI, Dong A. Spatial distributions of two species of monogeneans on the gills of *Siganus fuscescens* (Houttuyn) and their seasonal dynamics in caged versus wild-caught hosts. J Parasitol. 2006 Oct;92(5):933–40.

Acknowledgements – LO acknowledges the Agency for Innovation by Science and Technology (IWT Flanders) for providing funding for her senior internship. She is grateful to the Center for Environmental Sciences (CMK) at UHasselt for hosting this internship. Dr. Tiziana Gobbin is thanked for her experimental support, guidance with statistical analysis, and for critically reviewing the paper. The research group of parasitology is appreciated for the valuable feedback. This work was financially supported by BOF UHasselt, the Research Foundation Flanders (FWO Vlaanderen), and EU (FP7 CHAARM).

Author contributions – This research was designed by TG and LO. The experiments were conducted by LO. LO analyzed the data and wrote the manuscript, with inputs from TG and grammatically supported by genAI.

SUPPLEMENTARY INFORMATION

Table S1: Ecological information (trophic group, habitat) of six species of haplochromine fish sampled from Lake Victoria between 1978 and 2011. All species are benthopelagic. Ecological information was retrieved from FishBase.

Host species	Trophic group	Habitat	Depth range (min-max) (m)
Platyaeniodus degeni	molluscivore	Sand, shingle and mud	? - 15
Haplochromis heusinkveldi	Zooplanktivore	Exposed and sheltered areas with a mud bottom	3 - 21
Haplochromis laparogramma	Zooplanktivore	Relatively exposed waters with sand or mud bottoms	5 - 35
Haplochromis piceatus	Zooplanktivore	Relatively sheltered gulf with a mud bottom	14-18
Haplochromis pyrrhocephalus	Zooplanktivore	Mud bottoms in exposed areas	3 - 21
Haplochromis tanaos	Zooplanktivore	Relatively sheltered areas with a sandy substrate	0 - 10

Table S2: Sample size of male cichlid fish from Lake Victoria screened for parasites per species and sampling year. *Three from the eight fish individuals were females.

Host species	1978	1981	1984	1985	1986	1987	1990	1991	1993	1999	2001	2002	2006	2011	tot
P. degeni	8	8	8		8*							8	8	8	**56**
H. heusinkveldi	5	5	5	5											**20**
H. laparogramma	5	5	5				5	5	5	5	5	5	5	5	**55**
H. piceatus	5	5	5	5											**20**
H. pyrrhocephalus	8	8	8			8		8	8	8	8	8	8	8	**88**
H. tanaos	8	8	5						5		8		8	8	**50**
tot	**39**	**39**	**36**	**10**	**8**	**8**	**5**	**13**	**18**	**13**	**21**	**21**	**29**	**29**	**289**

Table S3: Minimal adequate models (MAMs) testing the parasite abundance and individual species richness over sampling years and ecological periods (pristine, perturbed, recovery), the gill microhabitat distribution of *E. lamellifer* and *Cichlidogyrus* species. χ^2 indicates the Chi-square statistic for the overall comparison. Df = degrees of freedom. Significance levels (95% CI): p > 0.05; * p < 0.05; ** p < 0.01; *** p < 0.001.

MAM	Variable	χ2	Df	p-value
Abundance (year)	Parasite species	871.9142	5	< 2.2e-16***
	Year	1.2193	1	0.2695
	Fish species	218.7986	5	< 2.2e-16***
	Minimum temperature	38.8211	1	4.645e-10***
Abundance (period)	Parasite species	881.475	5	< 2.2e-16***
	Period	65.139	2	7.164e-15***
	Lake levels	12.206	1	0.0004765***
	Fish species	267.742	5	< 2.2e-16***
Individual species richness (year)	Year	18.070	13	0.1549
	Fish species	35.651	5	1.115e-06***
Individual species richness (period)	Period	11.104	2	0.003879**
	Fish species	44.921	5	1.505e-08***
Gill microhabitat distribution *E. lamellifer* (period)	Microhabitat site	44.9712	8	3.727e-07***
	Total *Ergasilus lamellifer* per fish ID	11.0161	1	0.0009032***
	Period	0.0143	2	0.9928693
Gill microhabitat distribution *Cichlidogyrus* spp. (period)	Microhabitat site	3.4344	8	0.9042
	Period	0.0000	2	1.0000

Table S4: Pairwise comparisons (post hoc Tukey test) of parasite abundance within each parasite taxon infecting cichlid fish in Lake Victoria across the three ecological periods (pristine, perturbed, and recovery). Estimate refers to the estimated difference in mean abundance of a given parasite taxon between ecological periods. SE is the standard error of the estimate. Z-ratio is the z-ratio for comparisons between ecological periods. Df = degrees of freedom. Significance levels (95% confidence interval): p > 0.05; * p < 0.05; ** p < 0.01; *** p < 0.001.

Contrast	Estimate	SE	df	z.ratio	p.value
C. bifurcatus **perturbed vs. pristine**	-1.7122445	0.2177911	inf	-7.861868	8.404388e-13***
C. bifurcatus **perturbed vs. recovery**	-0.5088385	0.2152201	inf	-2.364270	6.353581e-01
C. bifurcatus **pristine vs. recovery**	1.2034059	0.2954149	inf	4.073612	5.930178e-03**
C. furu **perturbed vs. pristine**	-1.7122445	0.2177911	inf	-7.861868	8.404388e-13***
C. furu **perturbed vs. recovery**	-0.5088385	0.2152201	inf	-2.364270	6.353581e-01
C. furu **pristine vs. recovery**	1.2034059	0.2954149	inf	4.073612	5.930178e-03**
C. nyanza **perturbed vs. pristine**	-1.7122445	0.2177911	inf	-7.861868	8.404388e-13***
C. nyanza **perturbed vs. recovery**	-0.5088385	0.2152201	inf	-2.364270	6.353581e-01
C. nyanza **pristine vs. recovery**	1.2034059	0.2954149	inf	4.073612	5.930178e-03**
E. lamellifer **perturbed vs. pristine**	-1.7122445	0.2177911	inf	-7.861868	8.404388e-13***
E. lamellifer **perturbed vs. recovery**	-0.5088385	0.2152201	inf	-2.364270	6.353581e-01
E. lamellifer **pristine vs. recovery**	1.2034059	0.2954149	inf	4.073612	5.930178e-03**
L. monodi **perturbed vs. pristine**	-1.7122445	0.2177911	inf	-7.861868	8.404388e-13***
L. monodi **perturbed vs. recovery**	-0.5088385	0.2152201	inf	-2.364270	6.353581e-01
L.monodi **pristine vs. recovery**	1.2034059	0.2954149	inf	4.073612	5.930178e-03**
Glochidia **disturbed pristine vs. pristine**	-1.7122445	0.2177911	inf	-7.861868	8.404388e-13***
Glochidia **disturbed pristine vs. recovery**	-0.5088385	0.2152201	inf	-2.364270	6.353581e-01
Glochidia **pristine vs. recovery**	1.2034059	0.2954149	inf	4.073612	5.930178e-03**

Table S5: Pairwise comparisons (post hoc Tukey test) of parasite abundance between parasite taxa infecting cichlid fish in Lake Victoria from 1978 to 2011. Estimate represents the estimated difference in mean abundance between parasite species. SE is the standard error of the estimate. Z-ratio is the z-ratio for pairwise comparisons. Df = degrees of freedom. Significance levels (95% confidence interval): p > 0.05; * p < 0.05; ** p < 0.01; *** p < 0.001.

Contrast	Estimate	SE	df	z.ratio	p.value
C. bifurcatus – C.furu	-2.04584116	0.7662803	Inf	-2.669833790	8.134723e-02
C. bifurcatus – C. nyanza	0.00543825	1.0103897	Inf	0.005382329	1.000000e+00
C. bifurcatus – E. lamellifer	-4.25261294	0.7283555	Inf	-5.838650420	7.876519e-08***
C. bifurcatus – Glochidia	-7.28522802	0.7196962	Inf	-10.122643746	6.017409e-14***
C. bifurcatus – L. monodi	-1.12305304	0.8291096	Inf	-1.354529054	7.542192e-01
C. furu – C.nyanza	2.05127941	0.7663266	Inf	2.676769170	7.989584e-02
C. furu – E. lamellifer	-2.20677178	0.3098861	Inf	-7.121235762	1.608469e-11***
C. furu – Glochidia	-5.23938686	0.2894349	Inf	-18.102123382	0.000000e+0***
C. furu – L. monodi	0.92278812	0.5037512	Inf	1.831833111	4.450818e-01
C. nyanza – E. lamellifer	-4.25805119	0.7284782	Inf	-5.845131680	7.576113e-08***
C. nyanza – Glochidia	-7.29066627	0.7197516	Inf	-10.129419707	6.050715e-14***
C. nyanza – L. monodi	-1.12849129	0.8291377	Inf	-1.361042118	7.504032e-01
E. lamellifer – Glochidia	-3.03261508	0.1579448	Inf	-19.200477534	0.000000e+00***
E. lamellifer – L. monodi	3.12955990	0.4436232	Inf	7.054545375	2.601430e-11***
Glochidia – L. monodi	6.16217498	0.4295364	Inf	14.346105492	0.000000e+00***

Table S6: Mean abundance of parasites infecting six haplochromine host species during different ecological periods (pristine: 1978-1981, perturbed: 1984-1999, recovery: 2001-2011) in Lake Victoria. N = number of fish individuals.

				Mean abundance (min-max)					
Fish_sp	**Period**	**N**	**SL (min-max)**	***C. bifurcatus***	***C. furu***	***C. nyanza***	***E. lamellifer***	***L. monodi***	***Glochidia***
H. heusinkveldi	Pristine	10	7.2 (5.9-7.85)	0 (0-0)	0 (0-0)	0 (0-0)	1 (0-3)	0.1 (0-1)	2.1 (0-7)
	Perturbed	10	5.7 (5-6.5)	0 (0-0)	0 (0-0)	0 (0-0)	0.3 (0-1)	0 (0-0)	0.3 (0-1)
	Recovery	0	NA	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)
H. laparogramma	Pristine	10	7.2 (5.85-8.1)	0 (0-0)	0 (0-0)	0 (0-0)	0.93 (0-5)	0 (0-0)	0.29 (0-2)
	Perturbed	25	5.7 (5-6.2)	0 (0-0)	0 (0-0)	0 (0-0)	0.04 (0-1)	0 (0-0)	0.38 (0-3)
	Recovery	20	NA	0 (0-0)	0 (0-0)	0 (0-0)	0.04 (0-1)	0 (0-0)	0.96 (0-6)
H. piceatus	Pristine	10	6.1 (5.6-6.8)	0 (0-0)	0 (0-0)	0 (0-0)	0.1 (0-1)	0 (0-0)	102 (17-240)
	Perturbed	10	5.2 (4.75-5.6)	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)	22.1 (15-43)
	Recovery	0	NA	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)
H. pyrrhocephalus	Pristine	16	6.2 (5.05-8.3)	0 (0-0)	0 (0-0)	0 (0-0)	0.56 (0-2)	0.19 (0-2)	2.31 (0-10)
	Perturbed	40	5.7 (5.05-7.1)	0 (0-0)	0 (0-0)	0 (0-0)	0.05 (0-1)	0 (0-0)	0.56 (0-2)
	Recovery	32	5.2 (4.7-5.75)	0 (0-0)	0.06 (0-1)	0 (0-0)	0.09 (0-1)	0 (0-0)	2.38 (0-15)
H. tanaos	Pristine	16	6.3 (5-7)	0 (0-0)	0.12 (0-1)	0 (0-0)	0.25 (0-2)	0 (0-0)	13.88 (2-39)
	Perturbed	10	NA	0 (0-0)	0 (0-0)	0 (0-0)	0.17 (0-1)	0 (0-0)	6 (1-17)
	Recovery	24	NA	0.04 (0-1)	0.12 (0-1)	0 (0-0)	0.54 (0-2)	0 (0-0)	14.92 (0-87)
P. degeni	Pristine	16	6.4 (5.25-7.25)	0.06 (0-1)	0.19 (0-2)	0.12 (0-1)	0.44 (0-2)	0.12 (0-1)	41.38 (0-151)
	Perturbed	16	5.8 (5.15-7.2)	0 (0-0)	0.19 (0-1)	0 (0-0)	0.44 (0-3)	0 (0-0)	23.5 (0-183)
	Recovery	24	5.7 (4.95-6.5)	0 (0-0)	0.1 (0-1)	0 (0-0)	1.29 (0-4)	0 (0-0)	24.67 (0-150)

Table S7: Differences in the spatial distribution of *E. lamellifer* on the first gill arch of cichlids from Lake Victoria, Tanzania, across nine gill microhabitats (longitudinal segments do: dorsal, me: median, ve: ventral ; and vertical areas di: distal, ce: central, prox: proximal). Estimate indicates the estimated difference in the mean frequency of occurrence of *E. lamellifer* between gill microhabitat sites. SE is the standard error of the estimate. Z-ratio is the z-ratio (estimate divided by SE). Df = degrees of freedom. Significance levels (95% CI): p > 0.05; * p < 0.05; ** p < 0.01; *** p < 0.001.

Contrast	Estimate	SE	z ratio	Adjusted p-value
do-di vs. do-ce	0.5947	0.3114	1.910	0.53056
do-prox vs. do-ce	-2.0794	0.7500	-2.773	0.09119
mece vs. doce	-1.6740	0.6292	-2.661	0.12191
medi vs. doce	-0.4700	0.4031	-1.166	0.94692
meprox vs. doce	-23705.0	35109.33	-0.001	1.00000
vece vs. doce	-1.3863	0.5590	-2.480	0.18742
vedi vs. doce	-0.2877	0.3819	-0.753	0.99674
veprox vs. doce	-2.7726	1.0308	-2.690	0.11293
doprox vs. dodi	-2.6742	0.7311	-3.658	0.00514**
mece vs. dodi	-2.2687	0.6065	-3.741	0.00395**
medi vs. dodi	-1.0647	0.3667	-2.903	0.06352
meprox vs. dodi	-24300.0	35109.33	-0.001	1.00000
vece vs. dodi	-1.9810	0.5334	-3.714	0.00422**
vedi vs. dodi	-0.8824	0.3432	-2.571	0.15165
veprox vs. dodi	-3.3673	1.0171	-3.311	0.01813*
mece vs. doprox	0.4055	0.9129	0.444	0.99993
medi vs. doprox	1.6094	0.7746	2.078	0.41169
meprox vs. doprox	-21626.0	35109.33	-0.001	1.00000
vece vs. doprox	0.6931	0.8660	0.800	0.99505
vedi vs. doprox	1.7917	0.7638	2.346	0.25035
veprox vs. doprox	-0.6931	1.2247	-0.566	0.99958
medi vs. mece	1.2040	0.6583	1.829	0.58885
meprox vs. mece	-22031.0	35109.33	-0.001	1.00000
vece vs. mece	0.2877	0.7638	0.377	0.99998
vedi vs. mece	1.3863	0.6455	2.148	0.36555
veprox vs. mece	-1.0986	1.1547	-0.951	0.98447
meprox vs. medi	-23235.0	35109.33	-0.001	1.00000
vece vs. medi	-0.9163	0.5916	-1.549	0.77991

vedi vs. medi	0.1823	0.4282	0.426	0.99995
veprox vs. medi	-2.3026	1.0488	-2.195	0.33573
vece vs. meprox	22318.7	35109.33	0.001	1.00000
vedi vs. meprox	23417.3	35109.33	0.001	1.00000
veprox vs. meprox	20932.5	35109.33	0.001	1.00000
vedi vs. vece	1.0986	0.5774	1.903	0.53540
veprox vs. vece	-1.3863	1.1180	-1.240	0.92533
veprox vs. vedi	-2.4849	1.0408	-2.387	0.22930