Lifestyle and not density of fish hosts determines parasite distribution over time and space

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Abstract

1. Pelagic zones are characterised by consistent large-scale patterns of circulation on local and global scales. Lake Tanganyika, as an enclosed ecosystem provides a playing field to study evolutionary and ecological processes applicable to open water areas worldwide. Despite their important role in the ecosystem, large scale patterns of the distribution of parasites remain poorly understood. Monogenean parasites have been proposed as tags for ecosystem dynamics because of their direct life cycle and often high host specificity. We combined data on spatiotemporal dynamics of parasites (*Kapentagyrus*, Monogenea) with morphological variation of clupeid hosts to investigate general patterns of host-parasite interactions in the pelagic zone of this ancient lake.
2. Two dominant species of clupeid fishes in the pelagic zone of Lake Tanganyika are parasitised by two monogenean species of *Kapentagyrus* with different levels of host specificity. The host fishes are believed to perform lake-wide migrations driven by seasonal upwellings. To model spatiotemporal dynamics of host-parasite interaction, we used temporal data on monogenean infection along the North-South axis of Lake Tanganyika based on 1730 screened fishes and 3710 parasites together with phenotypic characterisation of the clupeid hosts.
3. Infection levels are dependent on host body size with contrasting trends in the two parasite species. We reveal temporal stability of infection with spatial distribution restricted by host life strategies. Spatial differences between the parasite species most likely reflect differences in migration between the host species; these are also reflected by morphological differences between some clupeid populations. Our results also suggest mutual facilitation of infection.
4. In conclusion, parasite infection is geographically restricted by host life strategies even in this ecosystem lacking physical barriers. Intensity of infection seems to be mainly driven by host size, with so far rarely reported mutual facilitation of co-infection. Temporal stability of infection in the pelagic zone contrasts with seasonal

changes in abundance of clupeid hosts. Overall, our results suggest that parasite infection dynamics in the open water areas are dependent on life style and not host density.

Keywords

Lake Tanganyika, parasitic flatworms, clupeids, migration, population dynamics

Introduction

Trophic and host-parasite interactions in pelagic systems

The pelagic zone, also known as the open water area, represents 99% of the volume of the biosphere. Pelagic zones are characterised by large-scale patterns of circulation and upwelling processes (Corman et al., 2010) that support the majority of the biomass targeted by fisheries (Pauly et al., 2002). Species aggregation is common at all trophic levels and is driven by the patchiness of primary production (Legendre & Le Fèvre, 1991; Ritz et al., 2011). Migration is a common strategy of pelagic species to cope with seasonal variation of resources at both small and large geographic scales (Angel, 1993). Small pelagic fishes (clupeids, mackerels) are known for their schooling behaviour and large distribution ranges often linked to their long-distance migrations (Teske et al., 2021). Therefore, small pelagic fishes have been proposed as indicator taxa for ecosystem changes related to e.g., climate change and overfishing. However, long-distance migration and population dynamics of small pelagic fish species are challenging to study, due to their high mobility and fragility that restrict traditional tracking methods.

Metazoan parasites encompass a high proportion of global species diversity (Poulin, 2014; Windsor, 1998). Despite a largely negative perception, parasites have been recognised as ecosystem engineers that form substantial biomass in aquatic ecosystems (Kuris et al., 2008) and alter food web topography, including competition and predation, through their indirect effect on host abundance (Hatcher et al., 2012). They contribute to ecosystem

energy transfer between trophic levels (Lafferty et al., 2006), e.g. parasites may induce changes in host behaviour that influence predation (Lefèvre et al., 2009), or act as mediators in biological invasions (Blackburn et al., 2011). However, the predictability of parasite communities at ecological timescales is often questioned as there is a lack of common patterns found in open water areas and in host species with large distribution ranges (Timi & Poulin, 2003).

Pelagic fish hosts are often considered as parasite species-poor compared to littoral host communities (Marcogliese, 2002). Although the community structures of parasites have been assessed in the context of biological tags of their hosts, including in pelagic marine areas (reviewed in MacKenzie & Abaunza, (2014)), determinants structuring population-level infection dynamics in pelagic environments are scarce.

Lake Tanganyika and its pelagic zone

Lake Tanganyika (LT) has been proposed as a natural study system for general principles of evolution due to its high species diversity and endemicity of various taxa (Coulter, 1991a; Cristescu et al., 2010). While Lake Tanganyika has all typical characteristics of a pelagic environment (vertical stratification, seasonal upwellings, simple trophic structure), it also has clear geographical boundaries and a species-poor pelagic community compared to marine environments, offering simplified conditions to study pelagic ecosystem dynamics (Paugy & Lévêque, 2017). It is dominated by two species of clupeid fishes which make up the majority of fish biomass and are the main source of fisheries production in the four riparian countries of the lake (Mannini et al., 1996). Despite the difficulty of tagging and effectively tracking fragile small pelagic species, lake-scale latitudinal migrations of the endemic Tanganyika clupeids, *Limnothrissa miodon* (Boulenger, 1906) and *Stolothrissa tanganicae* Regan, 1917 have been monitored through indirect methods, such as determining the difference in size and abundance in relation to the season and geographic origin along the lake (Mulimbwa N'Sibula et al., 2022; Plisnier et al., 2009). Fisheries production across landing sites varies substantially, indicating seasonal migrations of the Tanganyika clupeids. These patterns

have been linked to predator avoidance and food-seeking behaviour (Plisnier et al., 2009). Recent genomic studies of the Tanganyika clupeids find only a weak signal of isolation by distance and no clear stock structure along the North-South axis of the lake (De Keyzer et al., 2019; Junker et al., 2020).

Clupeid fishes in Lake Tanganyika are parasitised by two gill-infecting species of *Kapentagyrus* Kmentová, Vanhove & Gelnar, 2018 (Kmentová et al., 2018). *Kapentagyrus* is a lineage of monogenean flatworms (Monogenea, Dactylogyridae) that has so far only been reported from African freshwater clupeid hosts (Vanhove et al., 2021). Monogenean flatworms are obligate parasites of mainly fishes, some of which include pelagic hosts (Kmentová et al., 2018; Plaksina et al., 2021; Van Der Lingen et al., 2015). Given their short generation time, high substitution rate and host dependency, obligate parasites can serve as a magnifying glass of host population dynamics (Catalano et al., 2014; Geraerts et al., 2022). The patterns driving the spatiotemporal distribution of directly transmitted parasites such as monogenean flatworms may be informative for pelagic ecosystem dynamics as mediators between the external environment and the hosts. Due to their single-host life cycle and specificity for pelagic hosts, species of *Kapentagyrus* in Lake Tanganyika are proposed as tags for host distribution in the pelagic zone and the dynamics of pelagic ecosystems (Kmentová et al., 2019; Schoeman et al., 2022).

Spatiotemporal dynamics in the pelagic zone - a holistic approach

Spatiotemporal dynamics of parasites have been studied mainly in the context of host-driven determinants of their community composition (reviewed in Lester & MacKenzie, (2009)). Large-scale population dynamics of parasites infecting pelagic organisms are hardly ever studied due to the considerable effort required to sample fish hosts along their long-distance migrations. To date, determinants of population connectivity of parasitic flatworms over large geographic distances remains to be elucidated (Poulin, 2007). The population structure of our study species, *K. limnotrissae* (infecting *L. miodon*) and *K. tanganicanus* (infecting both clupeid species), has previously been analysed over the entire geographic range of the lake,

including temporal and seasonal sampling. Following the pattern of their clupeid hosts, no clear differentiation across the North-South axis of LT was found (Kmentová et al., 2020). To study the ecosystem dynamics in the pelagic zone, surveys of pelagic fishes have been combined with analyses of their morphological variation (Muniz et al., 2020; Valentin et al., 2014), otolith composition (Javor et al., 2011) and, more recently, population genomics (Baltazar-Soares et al., 2018; De Keyzer et al., 2019; Junker et al., 2020). This holistic approach has been proposed not only to study spatiotemporal dynamics in the pelagic zone (Abaunza et al., 2008; Kerr et al., 2017), but also other aquatic ecosystems such as large rivers (Lavoué et al., 2008).

In this study, we investigate the spatiotemporal dynamics of parasites alongside the morphology of their clupeid hosts as a flag taxon for the pelagic zone worldwide. We combine geographical and seasonal results on parasite infection, and morphology of the targeted fish hosts with previously published knowledge on the biology and genetic population structure of monogenean parasites infecting clupeids, fishery statistics, seasonal and annual cycles in primary productivity and upwelling (schematic representation of study design presented in Fig. 1).

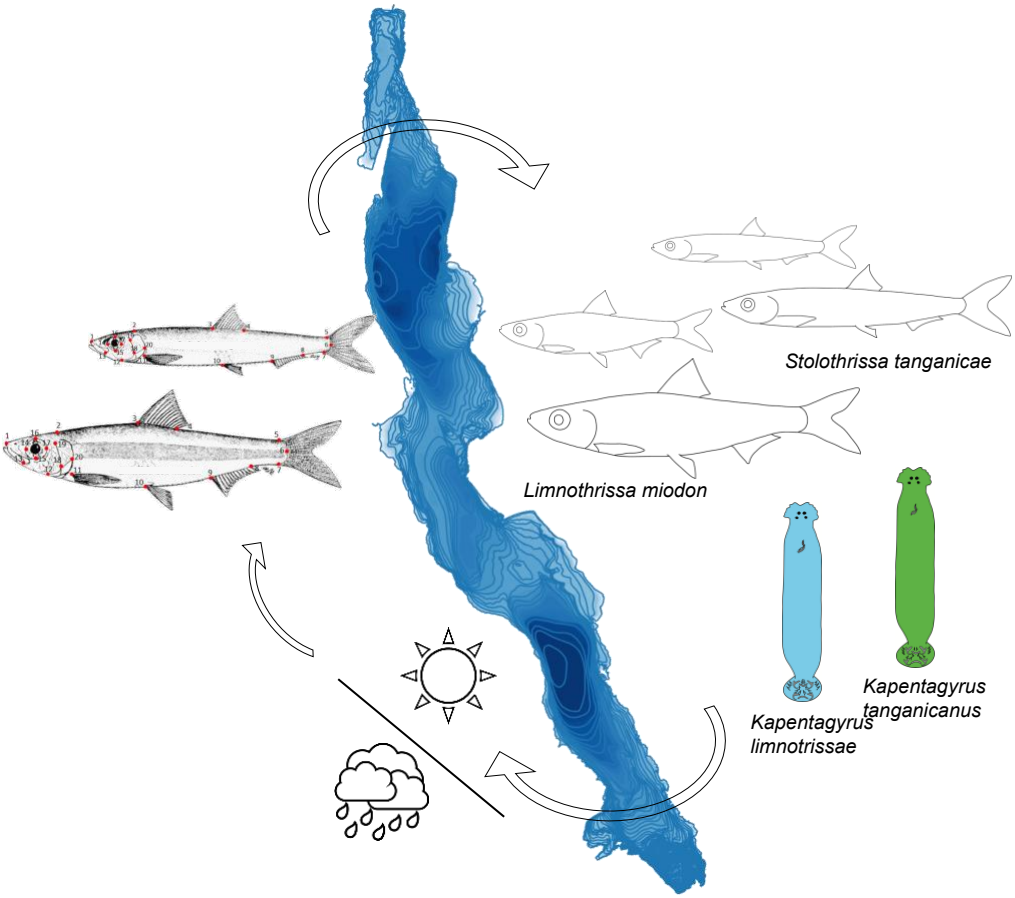


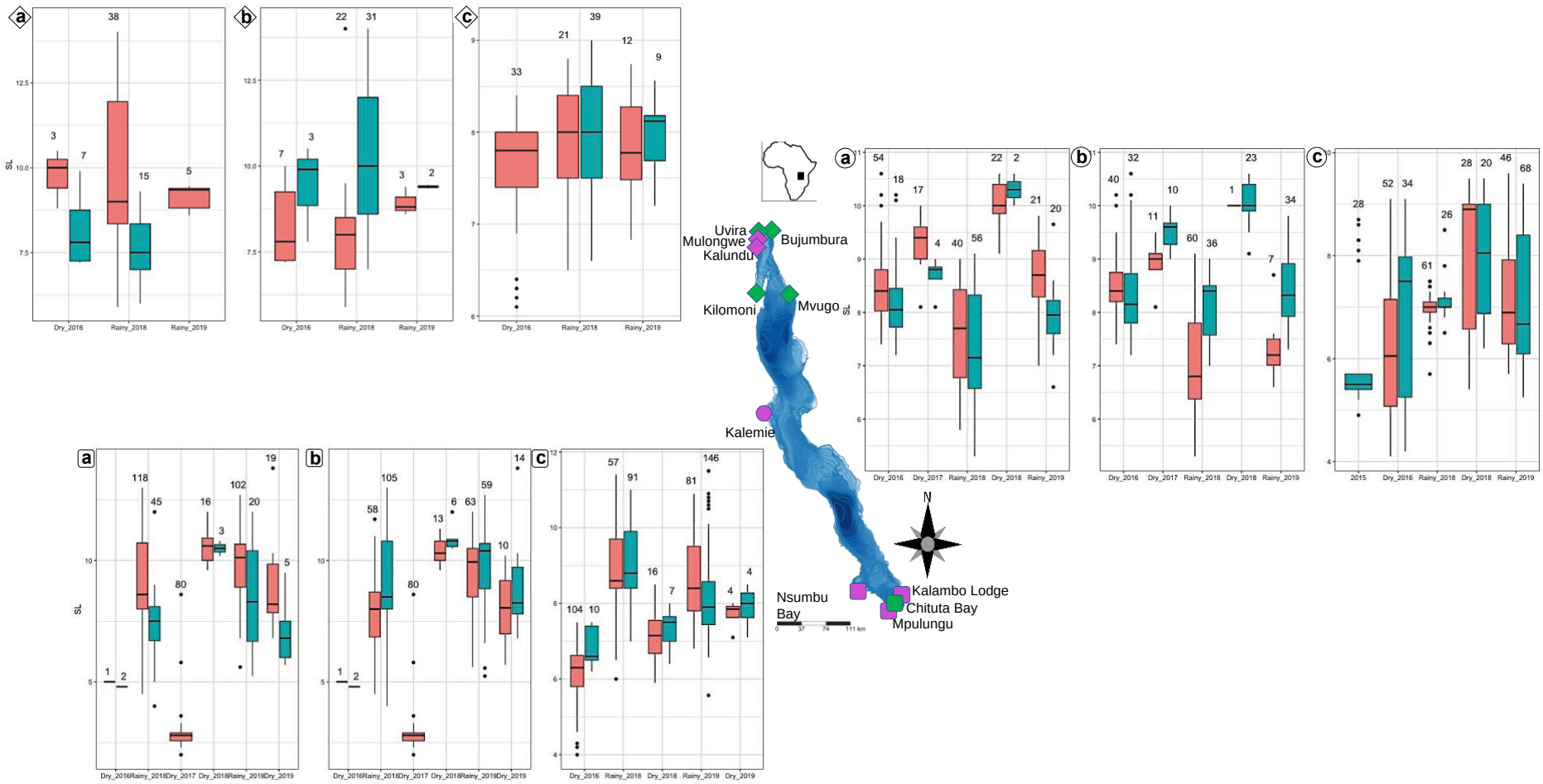
Fig. 1: Schematic visualisation of the study system of monogenean parasites infecting clupeid fishes in Lake Tanganyika.

We hypothesise that 1) given the suggested high level of North-South mobility of clupeid fishes in Lake Tanganyika (Plisnier et al., 2009; De Keyzer et al., 2019; Junker et al., 2020), the population infection dynamics of *Kapentagyrus* spp. are not related to the spatiotemporal origins, 2) given the contrasting host range between the two species of *Kapentagyrus* and the differences in lifestyle between the host species, spatial differences in infection will be more pronounced in *K. limnotrissae,* and 3) following previously published results on contrasting introduction success in different host life stages (Kmentová et al., 2019), we expect host size-driven differential occurrence of *Kapentagyrus* spp. on *L. miodon*.

Methodology

Sample collection and species identification

In total, 1730 specimens of two endemic pelagic clupeid species, *L. miodon* (733) and *S. tanganicae* (997), were collected along the North-South axis of Lake Tanganyika, including all three subbasins (North, Central, and South) in two different seasons (rainy season from October to April and dry season from May to September) within a four-year period (Fig. 2, Table S1). Freshly caught fish specimens were either obtained in collaboration with the experimental fishing unit of the Centre de Recherche en Hydrobiologie - Uvira (CRH) (Uvira, Democratic Republic of the Congo) or purchased from local fishermen. We combine newly obtained data on monogenean infection of clupeids in LT with those published in previous studies (Kmentová et al., 2020, 2018). Host specimens were collected within a period of 2 weeks (August 2016, April 2018, and October 2019) to avoid sampling the same population twice, because both clupeid species are highly mobile (De Keyzer et al., 2019; Mulimbwa N'Sibula & Mannini, 1993). Whole fish and/or gills were preserved in absolute ethanol. Host specimens were examined for the presence of monogenean parasites according to the procedure described in Kmentová et al. (2018). Species level identification of *Kapentagyrus* spp. was based on distinctive characters of the hard parts of the attachment organ in the posterior part of their bodies (for more details see Kmentová et al., (2018)). In the case of *L. miodon*, the only species of the two clupeids that hosts two monogenean species, monogenean individuals that could not be identified at the species level were only included in the counts of total infection intensities.


a
b
c
SL
Dry_2016
Rainy_2018
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2015
Uvira
Mulongwe
Kalundu
Bujumbura
Kilomoni
Mvugo
Kalemie
Nsumbu Bay
Kalambo Lodge
Chituta Bay
Mpulungu
N

Fig. 2: Overview of screened fish hosts and incidence of infection of collected parasite populations. Season and year of origin (x-axis) and standard length of the fish host (y-axis, SL in cm) of a) *Kapentagyrus limnotrissae* ex *Limnothrissa miodon*, b) *Kapentagyrus tanganicanus* ex *Limnothrissa miodon*, c) *Kapentagyrus tanganicanus* ex *Stolothrissa tanganicae*. Infected fishes are depicted in blue, non-infected in red. The total number of fish screened at a certain time point is mentioned above each of the boxplots. Subbasin division is visible by different shapes used for sampling localities with diamonds representing northern subbasin, a circle representing central subbasin and squares representing southern subbasin. The purple colour indicates the sampling localities of fish specimens used in the geomorphometric analyses.

Parasite population dynamics

To investigate the host parameters that might influence infection levels, the dataset was divided into three host-parasite combinations according to host species (i: *K. limnotrissae* ex *L. miodon*, ii: *K. tanganicanus* ex *L. miodon*, iii: *K. tangicanus* ex *S. tanganicae*). We modelled the infection intensity per host specimen against a range of other parameters, including sampling location (as subbasin - North, Central, South), season (dry period from May to September, rainy period from October to April), and host size (standard length) as explanatory variables (Table 1) as well as infection levels of the respective other parasite species if applicable, i.e. *K. tanganicanus* in (i) and *K. limnotrissae* in (ii). Because of seasonal migration and previous records on spatiotemporal variation in body size (Plisnier et al., 2009), we expect an interaction of host size with locality and season, respectively. Several studies also suggested that infection levels of monogeneans are related to fish size (Akoll et al., 2012; Šimková et al., 2004). Therefore, we included interaction effects between host size and the remaining parameters in the initial models.

Infection parameters of parasites often present a substantial amount of zero counts (Lester, 2012; Tinsley et al., 2020). Therefore, we fitted infection levels using zero-inflated models (ZIMs) with a Poisson probability distribution that assume that the excess of zero counts is

produced by a separate process. In the present case, we hypothesised that the excess of zero counts result from a lack of contact with parasites in some specimens, while true zeros arise from host resistance (Wang, et al., 2017; Zuur et al., 2009). We fitted generalised linear models without zero-inflation to test whether these assumptions are true. The present datasets are overdispersed (residual deviance/residual degrees-of-freedom > 1.5 for a Poisson distribution). To address this overdispersion, we used a negative binomial probability distribution. Finally, host specimens most likely represent non-independent samples, as fishes belonging to the same schools may have experienced more similar parasite exposure scenarios. Therefore, we also tested whether including the sampling day and locality as random effects in a mixed model further improved the model fit. To avoid overfitting, we simplified models through a backwards elimination procedure using the function *drop1* including a χ^2 test. All effects that failed to significantly improve model fit were removed, starting from the interaction effects.

All model-based analyses were carried out in R v4.1.2 (R Core Team, 2022). Models were fitted using the package *glmmTMB* v1.1.2.3 (Brooks et al., 2017). The package *glmmTMB* offers models with two options for negative binomial distributions (options *nbinom1* and *nbinom2*) that implement linear and quadratic parameterisation, respectively (see Hardin & Hilbe, (2007)). Both options were tested here. We compared model fits using the Akaike information criterion (AIC) through the function *AICtab* in the package *bbmle* v1.0.24 (Bolker, 2017). We also checked model fits through quantile-quantile plots and residual vs. fitted plots as provided by the package *DHARMa* v0.4.5 (Hartig, 2017).

Based on the best-fitting model, we predicted infection levels for all three host-parasite combinations as a function of the subbasin and season, as well as the continuous variables the hosts' standard length and the level of co-infections through the package *emmeans* (Lenth, 2022). The resulting figures were plotted through the packages *emmeans* and *ggplot2* (Wickham, 2016).

Geomorphometrics of clupeid hosts

We expect host phenotype to be potentially linked to different environmental conditions in the subbasins. Therefore, the two host species were examined to investigate the potential link between the morphological variation and geographic origin of host specimens. In addition to classical morphological assessment, the evaluation of body shape variation can be quantified via geomorphometrics (Elewa, 2004). Specimens collected from six different localities along the lake shoreline within two weeks in October 2019 were selected (Fig. 2 and Table S1). Photographs were taken using Canon 4000D reflex camera equipped with an EF-S 18-55 mm III-lens, set on 55 mm for a total of 224 specimens of *S. tanganicae* and 195 specimens of *L. miodon*. The body shape of each specimen was captured by a set of 20 fixed landmarks. Landmarks are reference points of coordinates in 2D or 3D (2D for this study), and contain essential information on size, shape and scale (Elewa, 2004; Savriama, 2018). They were set using the *tpsDig2* software v2.31 (Rohlf, 2018) using a tps file created with the *tpsUtil* software v1.78 (Rohlf, 2018). The landmarks were defined based on previous studies conducted with other species of clupeids (De La Cruz Agüero & Rodríguez, 2004; Mounir, Ewague, Znari, & Elmghazli, 2019; Silva, 2003), see Fig. 3.

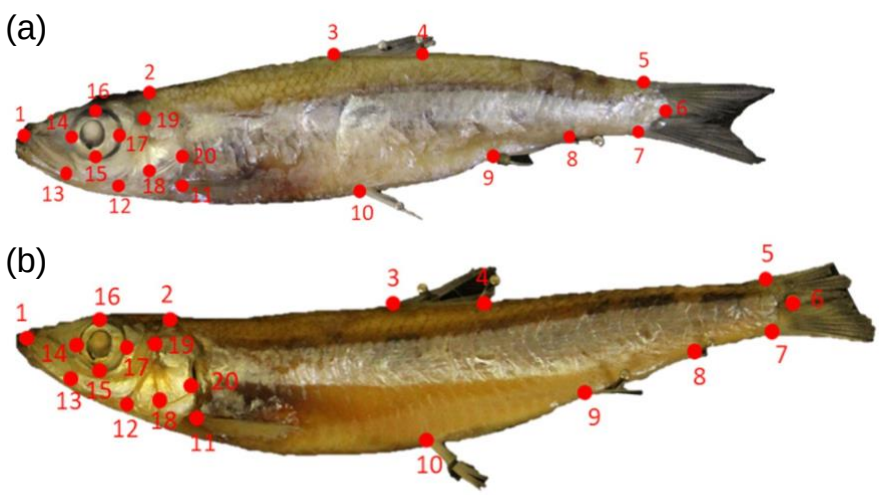

Fig. 3: Position of landmarks recovered for 2D digitisation of specimen of a) *Limnothrissa miodon* and b) *Stolothrissa tanganicae*.

Morphological variation within the two clupeid species was analysed with *MorphoJ* v2 (Klingenberg, 2011). We made a distinction between analyses based on whole-body landmarks vs. head-only landmarks. For the analyses of the whole body, we used all obtained landmarks, for the head-only analyses, landmarks 1, 2 and 11-20 were included. To extract the shape information, full Procrustes fits of landmark data were performed and aligned by longitudinal axes of the specimens. Three classifiers (species, locality of origin, and subbasin) were imported for further analyses. Principal Component Analysis (PCA) was performed on the covariance matrix to visualise the shape variation. Highly deviating specimens, identified by the PCA plot, were excluded from the analysis. Regressions against the standard length (measured separately from each specimen) of each specimen followed by a 10,000 replicate permutation test were performed on the first three individual PC axes. Due to the significant correlation between the standard length and PCA loadings/Procrustes distances (see Figs. S1 & S2), the final PCAs were performed on residuals which resulted from the regression analyses of Procrustes distances and standard length. Canonical Variate Analyses (CVA) on the residuals (see above) and permutation tests of 10,000 replicates, were performed to test for differences in morphology between specimens from different sites of origin or subbasins. The resulting figures were plotted through the *R* packages *ggplot2* (Wickham, 2016), *RColorBrewer* (Neuwirt, 2022)*, ggtext* (Wilke, 2020) and *tidyverse* (Wickham et al., 2019).

Results

Parasite population dynamics

For all three datasets (i–iii), a zero-inflated negative binomial mixed model resulted in the best fit (Table 1). In any case, seasonality failed to significantly improve model fit. Therefore, both the parameter and its interaction with the standard length were removed from all models.

For *K. tanganicanus* (i and iii), a monogenean infecting both species of clupeids, the models with a quadratic parameterisation (*nbinom2*) outperformed the models with a linear parameterisation. *Kapentagyrus limnotrissae* infecting *L. miodon* (ii), only improved the model fit marginally ($\Delta AIC = 2$; χ^2 (1, 2) = 2310, p = 0.038). In the post-hoc analysis, we found only minor differences between infection levels of *K. tanganicanus* (Figs. 4&5), yet subbasin identity contributed significantly to the overall model fit (Table 1). Infection intensities of *K. tanganicanus* increased with host size (Figs. 4&5) and with co-infection numbers of *K. limnotrissae* (Fig. 6). For *L. miodon,* this increase was generally weaker in the southern subbasin and particularly strong in the North. The host standard length had a significant interaction with the subbasin. For *S. tanganicae*, only the standard lengths of the hosts were a determinant of infection intensity. For *K. limnotrissae* (ii), the models with a linear parameterisation (*nbinom1*) outperformed those with a quadratic parameterisation. The interaction effect of subbasin with the standard length did not improve model fit and was, therefore, removed. The three minimal adequate models can be found in Table 1. Infection levels in the South of Lake Tanganyika were significantly lower than in other subbasins (Fig. 6). Infections significantly decreased with host standard length and increased with co-infection numbers of *K. tanganicanus* (Fig. 6).

Table 1: Stepwise backwards selection of effects (step 1 and 2) in generalised linear (mixed) models for each and host-parasite combination.

Models with the lowest values of the AIC (minimal adequate models) are highlighted in bold.

		***K. tanganicanus* ex *L. miodon* (i)**			***K. limnotrissae* ex *L. miodon* (ii)**			***K. tanganicanus* ex *S. tanganicae* (iii)**		
		full model	step 1	step 2	full model	step 1	step2	full model	step 1	step2
Zeroinfl	Mixed effects		-ii:SL-Season:SL	-Season		-Subbasin:SL-Season:SL	-Season		-Season:SL-Subbasin:SL	-Subbasin-Season
Poisson		3714	3770	3899	1999	2011	2012	2368	2367	2366
NBinom1		2585	2582	2610	1579	1615	1646	2053	2048	2067
NBinom2		2506	2504	2525	1638	1677	1693	2096	2094	2098
Poisson	locality, date	3078	NA	2970	1856	NA	NA	2101	2113	2107
NBinom1	locality, date	2487	2484	2484	1564	1560	**1560**	1990	1986	1981
NBinom2	locality, date	2429	2427	**2425**	1591	1591	1589	1981	1981	**1975**

Abbreviations: standard length (SL), zero inflated model (Zeroinfl), negative binomial distribution (NBinom1,2), Poisson distribution (Poisson).

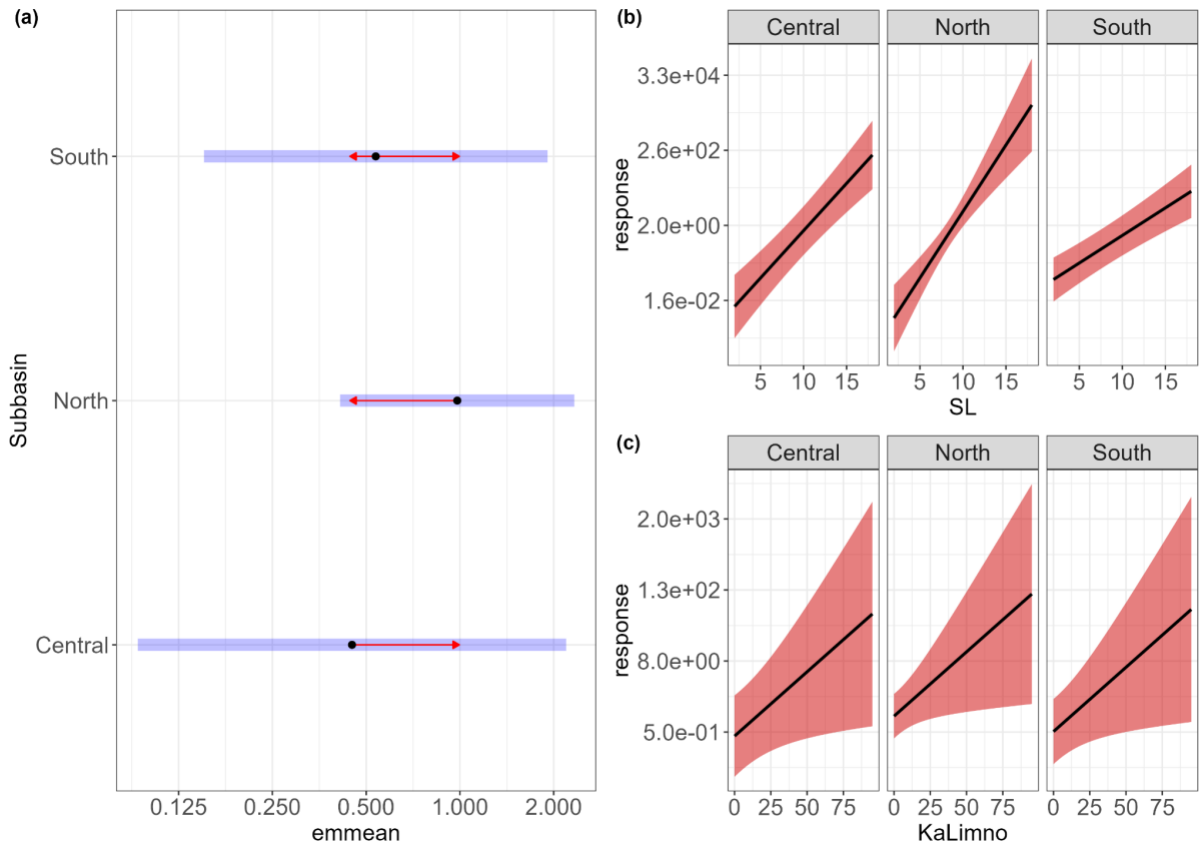

Fig. 4: Predictions for infection intensity of *Kapentagyrus tanganicanus* ex *Limnothrissa miodon* with 95% confidence intervals under the minimal adequate model (Table 1). a) Infection intensity in different subbasins showed no significant differences (CIs in blue, direction of overlap in red) with estimated marginal means on the x-axis, b) Infection intensity increased with standard length (SL) of the host, c) Infection intensity increased with higher infection intensities of *Kapentagyrus limnotrissae*.

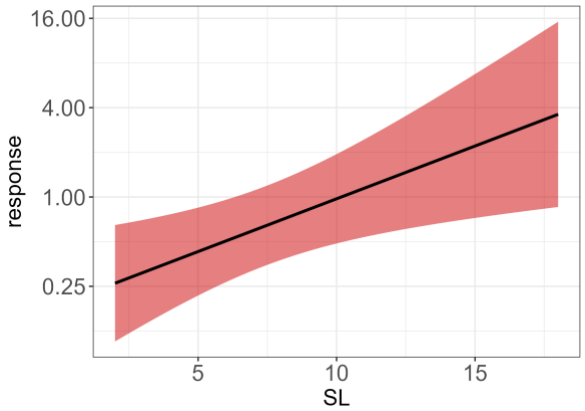

Fig. 5: Prediction of infection intensity of *Kapentagyrus tanganicanus* ex *Stolothrissa tanganicae*. The infection intensity increased with the standard length (SL) of the host.

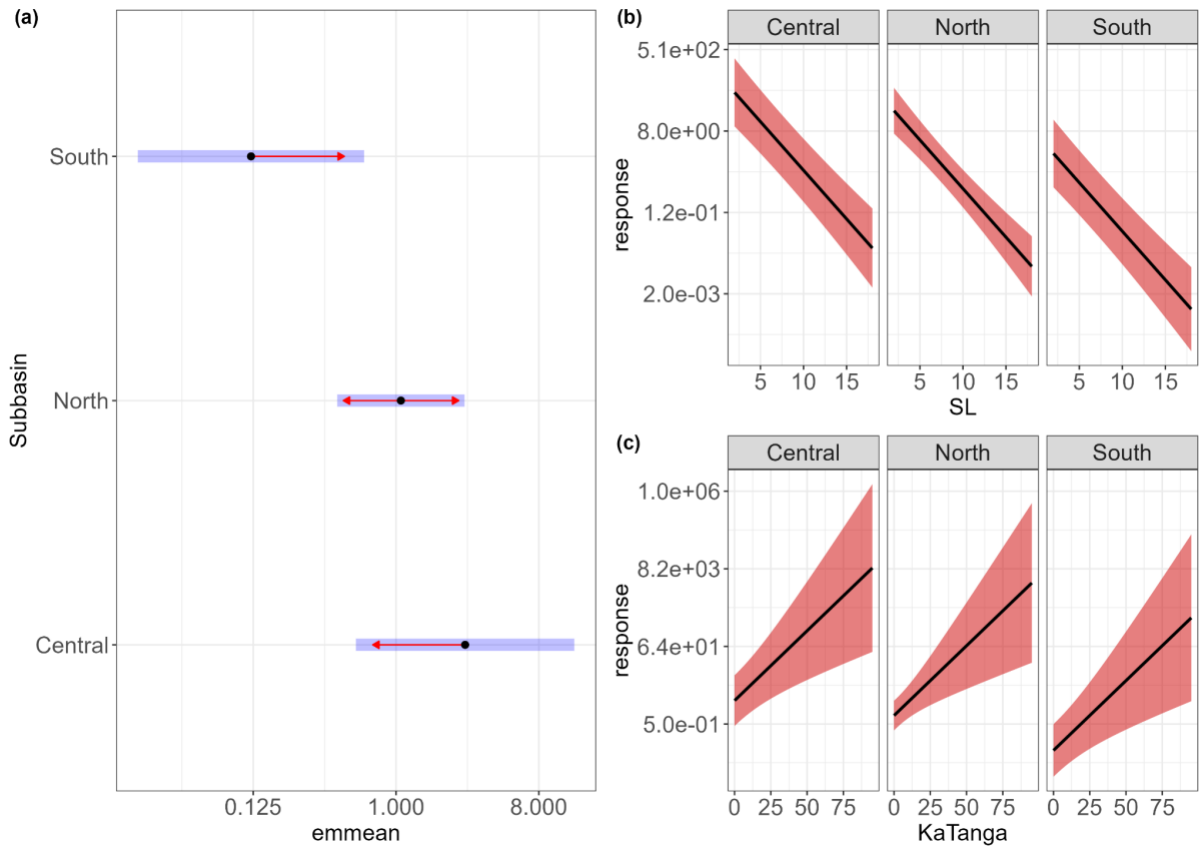

Fig. 6: Predictions for infection intensity of *Kapentagyrus limnotrissae* ex *Limnothrissa miodon*. a) Infection intensity related to subbasin origin with the confidence interval (in blue) and direction of overlap (in red) with estimated marginal means on the x-axis, b) Infection intensity as a function of the standard length (SL) of the host, c) Infection intensity as function of co-infection by *Kapentagyrus tanganicanus*.

Geomorphometrics of clupeid hosts

Geomorphometric analyses revealed strong similarity of head morphology between specimens from different localities and subbasins of the lake in both clupeid species. In the case of *L. miodon*, the first three PC axes explained 22.1%, 17.1% and 12.3% of the variation, respectively (see Fig. 7A&B), with visible North-South gradient mainly along the PC2. In case of *S. tanganicae*, the first three PC axes explained 24.2%, 18.1% and 11.8% of the variation, respectively (see Fig. 7C&D), with no visible structuring according to locality of origin. As wireframes displayed variation in the positioning of the full body, most likely related to the preservation of specimens, results based on the whole-body shape are presented in

the supplementary information only and should be interpreted with caution (Figs. S1&2). Based on the wireframes of the head shape (Fig. 8), differences in the relative position of the snout, eye and operculum are visible along the displayed PC axes.

The results of our CVAs confirmed the trend visible mainly along the second PC axis with significant differences in the shape of the whole body and head related to the geographic origin of *L. miodon* (Tables 2 and S1). Specifically, head shape differences increased with geographic distance in *L. miodon*. Although the CVAs indicated significant shape differences between some of the localities in both the full body and head datasets of *S. tanganicae* (see Tables 2 and S1), no consistent geographical pattern was detected in the PCAs. In both species, differences in the head shape were more pronounced in relation to geographic origin compared to the full body.

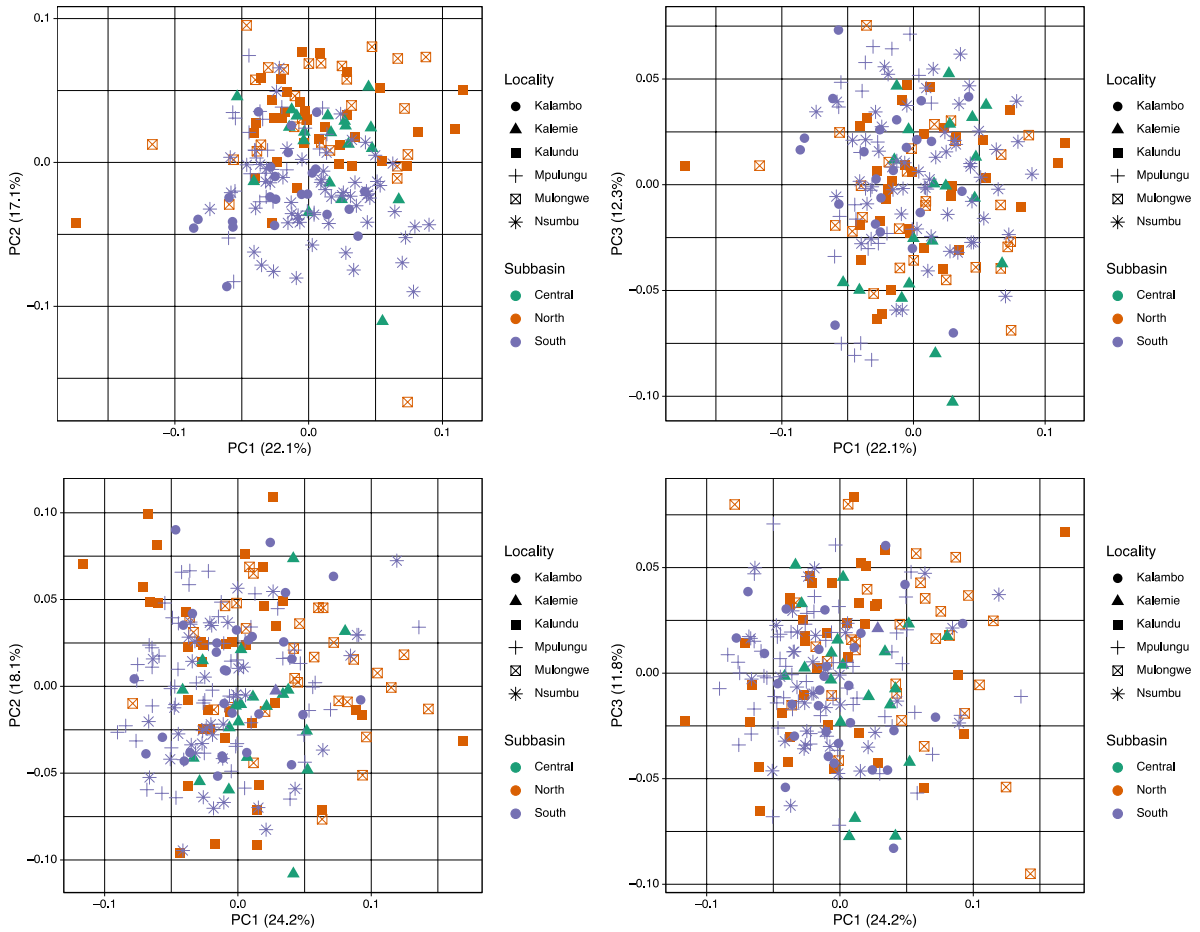

Fig. 7: Biplots of Principal Component Analyses (PCA) showing the shape variation in the head across the sampled localities of a) *Limnothrissa miodon*, first two PCs displayed, b) *Limnothrissa miodon*, first and third PCs displayed, c) *Stolothrissa tanganicae,* first two PCs displayed, d) *Stolothrissa tanganicae,* first and third PCs displayed.

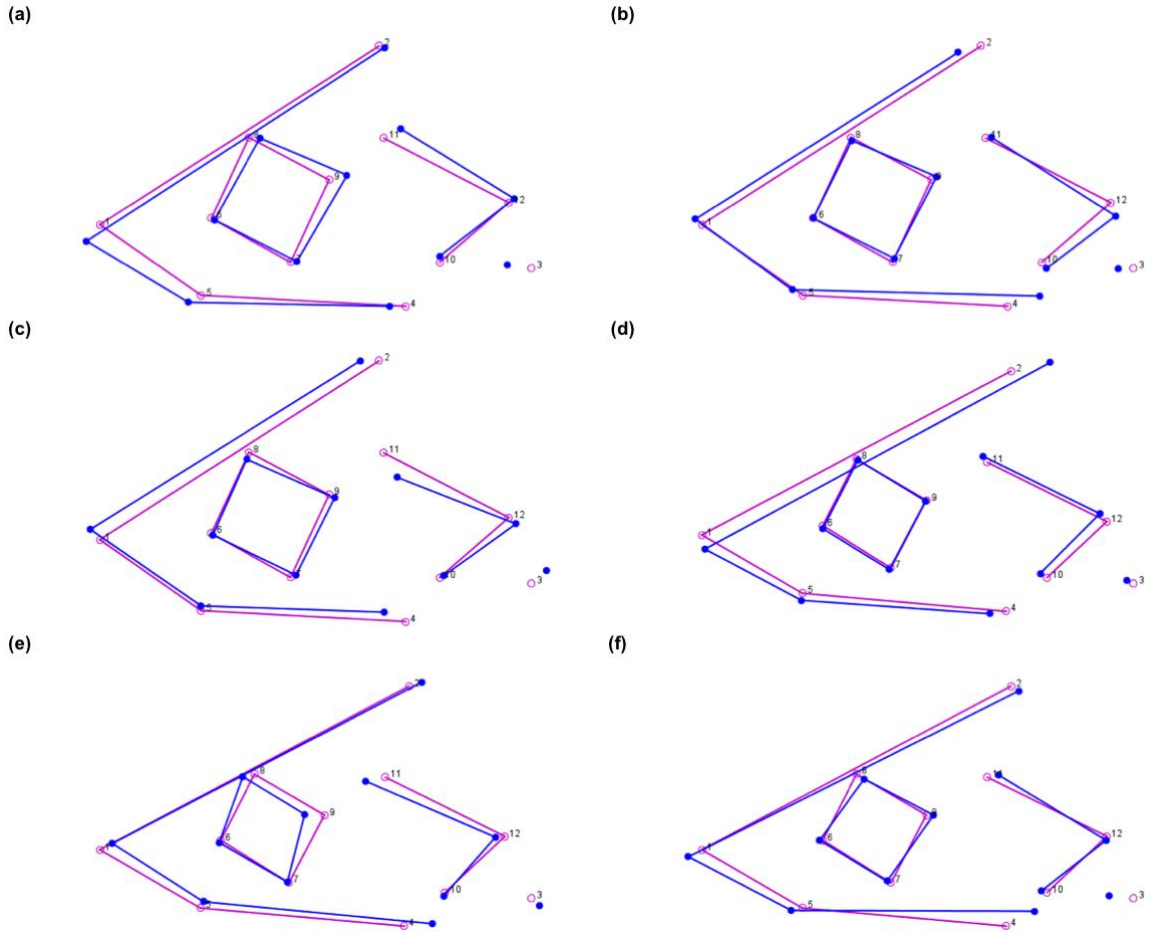

Fig. 8: Wireframes showing the shape variation in the head based on the coordinates of Principal Component Analyses of a) *Limnothrissa miodon,* PC1, b) *Limnothrissa miodon,* PC2, c) *Limnothrissa miodon,* PC3, d) *Stolothrissa tanganicae,* PC1, e) *Stolothrissa tanganicae,* PC2, f) *Stolothrissa tanganicae*, PC3. The target shape is presented in blue, the starting shape in pink.

Table 2: Results of Canonical Variate Analyses of head shape variation for a) *Limnothrissa miodon* b) *Stolothrissa tanganicae*. Values of Procrustes distances are displayed below the diagonal, P-values are shown above the diagonal. Significant P-values (<0.05) are indicated in bold. Number of samples are indicated between brackets behind the locality names with designation of the subbasin, N – North, C – Central, S – South).

(a)	Mulongwe (28)	Kalundu (34)	Kalemie (20)	Mpulungu (27)	Nsumbu (58)	Kalambo (23)
Mulongwe (N)	x	0.3842	**0.0207**	**0.0002**	**0.0466**	**0.0001**
Kalundu (N)	0.0252	x	**0.0029**	**0.0002**	**0.0376**	**0.0001**
Kalemie (C)	0.0447	0.0423	x	**<.0001**	**0.0355**	**0.0005**
Mpulungu (S)	0.0519	0.0472	0.0550	x	**0.0027**	0.2593
Nsumbu (S)	0.0298	0.0263	0.0308	0.0340	x	**0.0008**
Kalambo (S)	0.0603	0.0536	0.0489	0.0264	0.0379	x
(b)	Mulongwe (30)	Kalundu (38)	Kalemie (21)	Mpulungu (64)	Nsumbu (40)	Kalambo (30)
Mulongwe (N)	x	**0.0060**	0.0570	**0.0029**	**<.0001**	**0.0014**
Kalundu (N)	0.0479	x	0.0651	0.5339	0.0321	0.1954
Kalemie (C)	0.0387	0.0401	x	**0.0191**	**0.0116**	**0.0336**
Mpulungu (S)	0.0382	0.0188	0.0336	x	**0.0196**	0.3979
Nsumbu (S)	0.0584	0.0339	0.0368	0.0270	x	0.0785
Kalambo (S)	0.0467	0.0301	0.0353	0.0189	0.0274	x

Discussion

Temporal stability and spatial differences of infection

Previous studies indicate that the distribution of aquatic parasites is determined by environmental factors (Timi & Poulin, 2003). Also, many parasites are vulnerable to extinction, as a decline in population size of the host can negatively affect the often-overdispersed distribution of parasite populations (Lester, 2012). In Lake Tanganyika, annual differences in fisheries production are believed to be caused by natural cycles of clupeid species. This is visible in density changes of fish populations over a spatiotemporal gradient (Mölsä et al., 1999; Plisnier et al., 2009). Additionally, seasonal fluctuations in clupeid catches in Lake Tanganyika are driven by external factors related to the hydrodynamics and the weather. Despite the reported North-South clupeid migrations resulting in seasonal fluctuations of host population densities and mean size distribution of

the hosts (Kimirei & Mgaya, 2007; Mulimbwa N'Sibula et al., 2022), in line with our hypothesis we found the spatiotemporal dynamics of *Kapentagyrus* spp. in the pelagic zone to be seasonally independent. This result confirms previously suggested independence on seasonal host population cycles of rather short-lived parasites (Lester & MacKenzie, 2009) of which monogeneans in the tropical areas with an estimated generation time of days up to a few weeks might be considered (Tomnatik, 1990). Alternatively, host fluctuations could appear over longer cycles that were not covered by the sampling design of our study. While we could not disentangle the effects of host size and geographic origin for *K. tanganicanus*, *K. limnotrissae* exhibited a slight spatial differentiation along the North-South axis. We suggest that this pattern is driven by temporal residency and patchy distribution of *L. miodon* in the littoral habitat before reaching a certain size and becoming pelagic. In general, the geographic distribution of parasites infecting pelagic fish hosts is linked to life cycle complexity (number of host species with different distribution ranges) with limited spatial distribution of monogeneans only to certain areas, as in the case of *Sprattus sprattus* L. (Kleinertz et al., 2012) and *Clupea harengus* L. (Actinopterygii, Clupeidae) (Rahimian et al., 1999) in the North Sea. In comparison to monogeneans infecting clupeid fishes in Lake Tanganyika, no host size related infection intensity was observed in the case of *Mazocraes alosae* Hermann, 1782 on two species of *Alosa* Linck, 1790 (Actinopterygii, Clupeidae) from North-Atlantic coastal waters (Gérard et al., 2017). Host behaviour and season were shown to drive temporal differences in infection levels of *M. alosae* on *Alosa immaculata* Bennett, 1835 in the northern Black and Azov Seas (Plaksina et al., 2021).

A holistic approach for stock identification has been highlighted before (Begg and Waldman, 1999). The combination of parasite community data and host morphometric data aided in the discovery of multiple stocks of horse mackerel (*Trachurus trachurus* L.) in the North Atlantic (Abaunza et al., 2008) and in the stock identification of Australian sardines (*Sardinops sagax* (Jenyns, 1842)) along the East African coast (Van Der Lingen et al., 2015). Unlike parasites with complex life cycles, directly transmitted parasites have the advantage that distribution is

limited to the target host enabling elucidation of large-scale and long-term population dynamics of certain host-parasite interaction (Catalano et al., 2014). Using a geomorphometric approach, we found intraspecific morphological differences in the LT clupeid species linked to the geographic origin of the specimens especially in *L. miodon*. Morphological variation can be driven by various environmental factors (Mounir et al., 2019; Sultan & Stearns, 2005). In our study, the level of geographically determined morphological variation differed between the studied fish species. The shape differences in the relative position of snout and eyes may be related to the geographical distance and more concretely subbasin origin of *L. miodon*. The environment in the middle part of the lake could serve as a transit site between the northern and southern parts. Moreover, compared to other areas, the northern peak can be seen as the most affected by anthropogenic pressures (Cohen et al., 2005). Morphological variation of the head was also visible in *S. tanganicae*, but without a clear geographical pattern. These results indicate a more profound shape differentiation in *L. miodon* compared to *S. tanganicae,* despite originating from the same localities. The absence of clearly geographically determined morphological differences in *S. tanganicae* can be explained by the lack of residential behaviour. Although the results indicate that the population of *L. miodon* is more structured compared to *S. tanganicae*, the lack of a clear geographic cline supports the high level of population connectivity of this species across the lake (Junker et al., 2020). As hypothetised, given the host life-stage dependency of *K. limnotrissae,* contrasting infection levels related to geographic origin suggest that the spatial distribution of the parasites and the morphological response of the clupeid hosts follow similar geographic patterns. Overall, our results on lake-wide parasite occurrence and seasonal dynamics combined with characterisation of clupeid hosts support the hypothesis of largely unrestricted migration in *S. tanganicae* and the lack of barriers in the pelagic zone of the lake (De Keyzer et al., 2019; Junker et al., 2020; Mulimbwa N'Sibula et al., 2022). Habitat differences between the clupeid hosts over their lifespan most likely drive contrasting spatial patterns of infection between closely related parasite species. This result further supports the importance of host species with the highest dispersal capacity on the spatial

distribution of parasites, as reported for *Cichlidogyrus casuarinus* Pariselle, Muterezi Bukinga & Vanhove, 2015 infecting pelagic cichlids in the lake (Kmentová et al., 2021). Contrasting levels of gene flow between the two parasite species related to geographic origin along the North-South axis of the lake (Kmentová et al., Under review) may therefore be associated with lifestyle differences between the two clupeid species.

Host size and life-stage dependent habitat preference drive parasite occurrence

The diurnal and geographically small-scale migrations of Tanganyika clupeids are generally better understood than the long term patterns. Vertically, these clupeids respond to light and oxygen concentration and follow the diurnal movements of their prey. Horizontally, they migrate between the offshore waters of the pelagic and the inshore waters of the littoral habitat throughout their development (Matthes 1967). A recent long-term study of the reproductive activities of the clupeids in the northern subbasin identified the littoral zone as the main spawning ground for *L. miodon,* and the pelagic zone as the equivalent for *S. tanganicae* (Mulimbwa N'sibula et al., 2022). Juveniles of both species occur in littoral habitats, but in general *S. tanganicae* lives and spawns at greater distances from the shore than *L. miodon* (Coulter, 1970, 1991b; Mannini et al., 1996). Eggs of *L. miodon can* even be deposited just above the sandy bottom of the littoral zone. Juveniles of *L. miodon,* but not *S. tanganicae,* occupy sandy beaches right by the shore (Mulimbwa N'Sibula et al., 2022).

In line with our hypothesis, the body size of the clupeid hosts appears to be a major determinant of infection, as it significantly affects infection intensities for all three host-parasite combinations. Such an overall positive correlation between fish size and monogenean infection intensities has been associated with a larger habitat offered by larger hosts (Alvarez-Pellitero & Gonzalez-Lanza, 1982; Poulin, 2000). Considering the age-dependent migration of *L. miodon* from the littoral to the pelagic zone, the contrasting infection intensities associated with host size between *K. limnotrissae* and *K. tanganicanus* suggests a spatial stratification of infection linked with the ontogenetic migration of *L. miodon*

from the littoral to the pelagic zone. This apparent replacement contrasts with the positive effect of each parasite species' infection intensity on that of the other species. We suggest a combination of changes in host habitat and facilitation of infection caused by host immune deficiency or suppression at the base of this pattern. Suppression of the fish immune system allowing higher infection intensities has been shown in previous studies on monogeneans (Rohlenová et al., 2011; Sitjà-Bobadilla, 2008) and other parasite taxa (Klemme et al., 2016). Alternatively, the antagonistic interaction between the two parasite species could explain the resulting pattern, as proposed e.g., in the monogenean communities infecting *Astyanax aeneus* (Günther, 1860) in Neotropical rivers in Mexico (Salgado-Maldonado et al., 2019). However, so far there is no evidence of negative or any direct interspecific monogenean interaction between closely related species (Šimková et al., 2000; Soler-Jiménez & Fajer-Ávila, 2012).

Conclusion

Lake Tanganyika is an ancient and pristine lake known for a spectacular level of species diversity and endemism. The existence of schooling pelagic fishes in an enclosed ecosystem promotes studies on general ecosystem dynamics of pelagic areas. The link between theoretical/experimental studies and dynamics in natural ecosystems is largely unknown (Lindegren et al., 2016) and a common framework is lacking (Ritz et al., 2011). Incorporation of host-parasite interactions increases our knowledge on the interconnectedness of trophic levels (Lafferty et al., 2006). Our holistic approach based on spatiotemporal distribution of fish parasites and morphological variation of the host species reveals insights on the ecosystem dynamics along a North-South axis, and habitat preferences of two important fisheries targets. As restricted migration of *L. miodon* is considered as one of the drivers of profound North-South differences in parasite occurrence and fish morphology, being also indicated in recent studies (De Keyzer et al., 2019; Junker et al., 2020), such results should be considered in fisheries management plans. Our results suggest that parasite population dynamics in pelagic zones are dependent on spatial distribution of the hosts in both large

and small scales. Intensity of infection seems to be mainly driven by fish size with mutual facilitation in case of co-infection. Lack of seasonality in infection intensity points to environmental stability of the pelagic zone and absence of density dependent infection.

Acknowledgements

We would like to thank Stephan Koblmüller, Holger Zimmermann, Jiří Vorel, Simona Georgieva, Cyprian Katongo, Taylor Banda, Aneesh P.H. Bose, Filip A.M. Volckaert and Els De Keyzer for their help in organising and conducting field work. Pierre-Denis Plisnier is acknowledged for providing bathymetric data of Lake Tanganyika. The study was supported by the Czech Science Foundation (GACR) project no. P505/12/G112—European Centre of Ichtyoparasitology (ECIP) and standard project GA19-13573S, research grant 1513419N of the Research Foundation—Flanders (FWO-Vlaanderen). AJCL (BOF19OWB02), NK (BOF21PD01) and MPMV (BOF20TT06) received support from the Special Research Fund of Hasselt University.

Conflict of Interest

Authors declare no conflict of interest.

Author Contributions

N.K. designed the study, generated incidence data, analysed geometric morphometric data and drafted the manuscript. A.C-L. analysed incidence data and helped draft the manuscript, M.J. generated part of the incidence data and helped to draft the manuscript, M.V.S. supervised geometric morphometric data analyses and interpretation of results, M.P.M.V. discussed the results, helped draft the manuscript and supervised the study, T.M. and E.V.H. helped with geometric morphometric data analyses, S.H. generated geometric morphometric data, L.Mi. and K.T. helped with data interpretation and draft of the manuscript, L.Ma. provided support in the field and knowledge on the studied ecosystem. All authors have read and agreed to the published version of the manuscript.

Data Availability Statement

Parasite voucher material was deposited in the collection of Hasselt University under accession numbers xx-xx and the Royal Museum for Central Africa. The geometric morphometric data underlying the results of this article are available in Mendeley Data (xxx).

Supporting Information

Additional supporting information may be found in the online version of the article at the publisher's website.

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