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

2 **space**

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29   **Abstract**

30   1. Pelagic zones are characterised by consistent large-scale patterns of circulation on

31   local and global scales. Lake Tanganyika, as an enclosed ecosystem provides a

32   playing field to study evolutionary and ecological processes applicable to open water

33   areas worldwide. Despite their important role in the ecosystem, large scale patterns

34   of the distribution of parasites remain poorly understood. Monogenean parasites

35   have been proposed as tags for ecosystem dynamics because of their direct life

36   cycle and often high host specificity. We combined data on spatiotemporal dynamics

37   of parasites (*Kapentagyrus*, Monogenea) with morphological variation of clupeid

38   hosts to investigate general patterns of host-parasite interactions in the pelagic zone

39   of this ancient lake.

40   2. Two dominant species of clupeid fishes in the pelagic zone of Lake Tanganyika are

41   parasitised by two monogenean species of *Kapentagyrus* with different levels of host

42   specificity. The host fishes are believed to perform lake-wide migrations driven by

43   seasonal upwellings. To model spatiotemporal dynamics of host-parasite interaction,

44   we used temporal data on monogenean infection along the North-South axis of Lake

45   Tanganyika based on 1730 screened fishes and 3710 parasites together with

46   phenotypic characterisation of the clupeid hosts.

47   3. Infection levels are dependent on host body size with contrasting trends in the two

48   parasite species. We reveal temporal stability of infection with spatial distribution

49   restricted by host life strategies. Spatial differences between the parasite species

50   most likely reflect differences in migration between the host species; these are also

51   reflected by morphological differences between some clupeid populations. Our

52   results also suggest mutual facilitation of infection.

53   4. In conclusion, parasite infection is geographically restricted by host life strategies

54   even in this ecosystem lacking physical barriers. Intensity of infection seems to be

55   mainly driven by host size, with so far rarely reported mutual facilitation of co-

56   infection. Temporal stability of infection in the pelagic zone contrasts with seasonal

57   changes in abundance of clupeid hosts. Overall, our results suggest that parasite

58   infection dynamics in the open water areas are dependent on life style and not host

59   density.

60

61   **Keywords**

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

63

64   **Introduction**

65

66   *Trophic and host-parasite interactions in pelagic systems*

67   The pelagic zone, also known as the open water area, represents 99% of the volume of the

68   biosphere. Pelagic zones are characterised by large-scale patterns of circulation and

69   upwelling processes (Corman et al., 2010) that support the majority of the biomass targeted

70   by fisheries (Pauly et al., 2002). Species aggregation is common at all trophic levels and is

71   driven by the patchiness of primary production (Legendre & Le Fèvre, 1991; Ritz et al.,

72   2011). Migration is a common strategy of pelagic species to cope with seasonal variation of

73   resources at both small and large geographic scales (Angel, 1993). Small pelagic fishes

74   (clupeids, mackerels) are known for their schooling behaviour and large distribution ranges

75   often linked to their long-distance migrations (Teske et al., 2021). Therefore, small pelagic

76   fishes have been proposed as indicator taxa for ecosystem changes related to e.g., climate

77   change and overfishing. However, long-distance migration and population dynamics of small

78   pelagic fish species are challenging to study, due to their high mobility and fragility that

79   restrict traditional tracking methods.

80   Metazoan parasites encompass a high proportion of global species diversity (Poulin, 2014;

81   Windsor, 1998). Despite a largely negative perception, parasites have been recognised as

82   ecosystem engineers that form substantial biomass in aquatic ecosystems (Kuris et al.,

83   2008) and alter food web topography, including competition and predation, through their

84   indirect effect on host abundance (Hatcher et al., 2012). They contribute to ecosystem

85   energy transfer between trophic levels (Lafferty et al., 2006), e.g. parasites may induce

86   changes in host behaviour that influence predation (Lefèvre et al., 2009), or act as mediators

87   in biological invasions (Blackburn et al., 2011). However, the predictability of parasite

88   communities at ecological timescales is often questioned as there is a lack of common

89   patterns found in open water areas and in host species with large distribution ranges (Timi &

90   Poulin, 2003).

91   Pelagic fish hosts are often considered as parasite species-poor compared to littoral host

92   communities (Marcogliese, 2002). Although the community structures of parasites have

93   been assessed in the context of biological tags of their hosts, including in pelagic marine

94   areas (reviewed in MacKenzie & Abaunza, (2014)), determinants structuring population-level

95   infection dynamics in pelagic environments are scarce.

96

97   *Lake Tanganyika and its pelagic zone*

98   Lake Tanganyika (LT) has been proposed as a natural study system for general principles of

99   evolution due to its high species diversity and endemicity of various taxa (Coulter, 1991a;

100   Cristescu et al., 2010). While Lake Tanganyika has all typical characteristics of a pelagic

101   environment (vertical stratification, seasonal upwellings, simple trophic structure), it also has

102   clear geographical boundaries and a species-poor pelagic community compared to marine

103   environments, offering simplified conditions to study pelagic ecosystem dynamics (Paugy &

104   Lévêque, 2017). It is dominated by two species of clupeid fishes which make up the majority

105   of fish biomass and are the main source of fisheries production in the four riparian countries

106   of the lake (Mannini et al., 1996). Despite the difficulty of tagging and effectively tracking

107   fragile small pelagic species, lake-scale latitudinal migrations of the endemic Tanganyika

108   clupeids, *Limnothrissa miodon* (Boulenger, 1906) and *Stolothrissa tanganicae* Regan, 1917

109   have been monitored through indirect methods, such as determining the difference in size

110   and abundance in relation to the season and geographic origin along the lake (Mulimbwa

111   N'Sibula et al., 2022; Plisnier et al., 2009). Fisheries production across landing sites varies

112   substantially, indicating seasonal migrations of the Tanganyika clupeids. These patterns

113   have been linked to predator avoidance and food-seeking behaviour (Plisnier et al., 2009).

114   Recent genomic studies of the Tanganyika clupeids find only a weak signal of isolation by

115   distance and no clear stock structure along the North-South axis of the lake (De Keyzer et

116   al., 2019; Junker et al., 2020).

117   Clupeid fishes in Lake Tanganyika are parasitised by two gill-infecting species of

118   *Kapentagyrus* Kmentová, Vanhove & Gelnar, 2018 (Kmentová et al., 2018). *Kapentagyrus* is

119   a lineage of monogenean flatworms (Monogenea, Dactylogyridae) that has so far only been

120   reported from African freshwater clupeid hosts (Vanhove et al., 2021). Monogenean

121   flatworms are obligate parasites of mainly fishes, some of which include pelagic hosts

122   (Kmentová et al., 2018; Plaksina et al., 2021; Van Der Lingen et al., 2015). Given their short

123   generation time, high substitution rate and host dependency, obligate parasites can serve as

124   a magnifying glass of host population dynamics (Catalano et al., 2014; Geraerts et al.,

125   2022). The patterns driving the spatiotemporal distribution of directly transmitted parasites

126   such as monogenean flatworms may be informative for pelagic ecosystem dynamics as

127   mediators between the external environment and the hosts. Due to their single-host life cycle

128   and specificity for pelagic hosts, species of *Kapentagyrus* in Lake Tanganyika are proposed

129   as tags for host distribution in the pelagic zone and the dynamics of pelagic ecosystems

130   (Kmentová et al., 2019; Schoeman et al., 2022).

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132   *Spatiotemporal dynamics in the pelagic zone - a holistic approach*
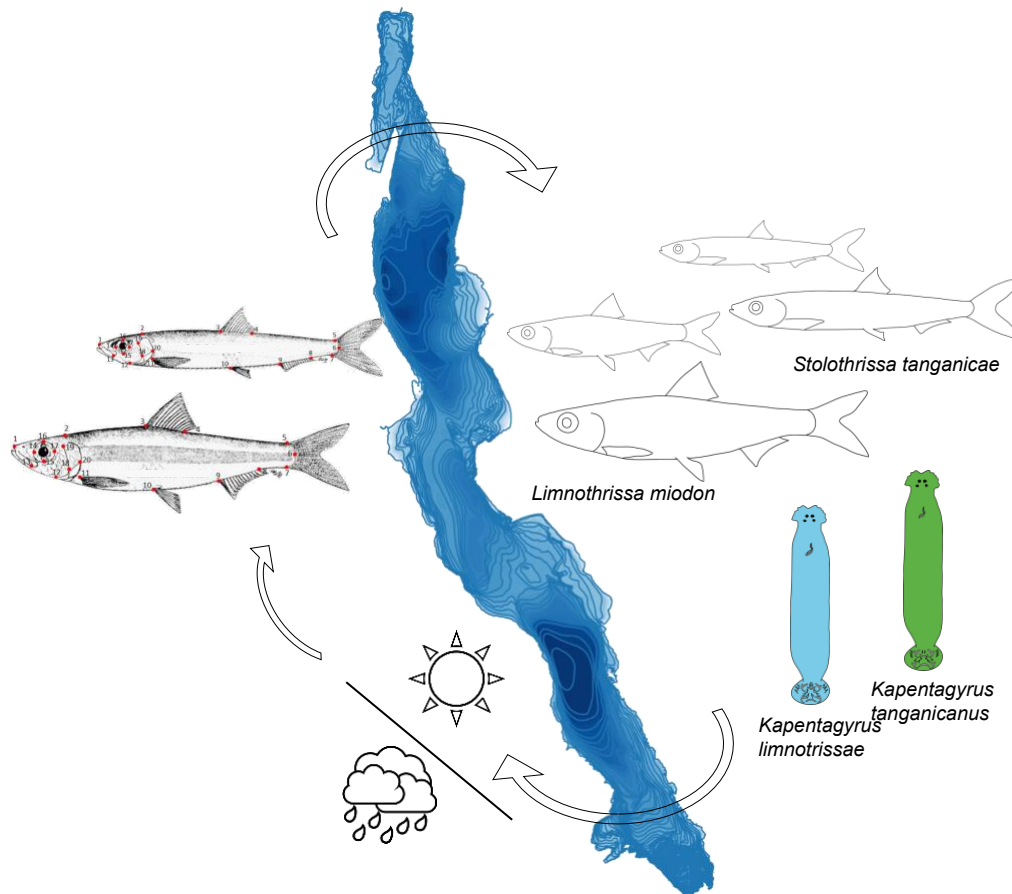
133   Spatiotemporal dynamics of parasites have been studied mainly in the context of host-driven

134   determinants of their community composition (reviewed in Lester & MacKenzie, (2009)).

135   Large-scale population dynamics of parasites infecting pelagic organisms are hardly ever

136   studied due to the considerable effort required to sample fish hosts along their long-distance

137   migrations. To date, determinants of population connectivity of parasitic flatworms over large

138   geographic distances remains to be elucidated (Poulin, 2007). The population structure of

139   our study species, *K. limnotrissae* (infecting *L. miodon*) and *K. tanganicanus* (infecting both

140   clupeid species)*,* has previously been analysed over the entire geographic range of the lake,

141   including temporal and seasonal sampling. Following the pattern of their clupeid hosts, no

142   clear differentiation across the North-South axis of LT was found (Kmentová et al., 2020). To

143   study the ecosystem dynamics in the pelagic zone, surveys of pelagic fishes have been

144   combined with analyses of their morphological variation (Muniz et al., 2020; Valentin et al.,

145   2014), otolith composition (Javor et al., 2011) and, more recently, population genomics

146   (Baltazar-Soares et al., 2018; De Keyzer et al., 2019; Junker et al., 2020). This holistic

147   approach has been proposed not only to study spatiotemporal dynamics in the pelagic zone

148   (Abaunza et al., 2008; Kerr et al., 2017), but also other aquatic ecosystems such as large

149   rivers (Lavoué et al., 2008).

150

151   In this study, we investigate the spatiotemporal dynamics of parasites alongside the

152   morphology of their clupeid hosts as a flag taxon for the pelagic zone worldwide. We

153   combine geographical and seasonal results on parasite infection, and morphology of the

154   targeted fish hosts with previously published knowledge on the biology and genetic

155   population structure of monogenean parasites infecting clupeids, fishery statistics, seasonal

156   and annual cycles in primary productivity and upwelling (schematic representation of study

157   design presented in Fig. 1).

158

Stolothrissa tanganicae

Limnothrissa miodon

Kapentagyrus limnotrissae

Kapentagyrus tanganicanus

159
160   Fig. 1: Schematic visualisation of the study system of monogenean parasites infecting

161   clupeid fishes in Lake Tanganyika.

162

163   We hypothesise that 1) given the suggested high level of North-South mobility of clupeid

164   fishes in Lake Tanganyika (Plisnier et al., 2009; De Keyzer et al., 2019; Junker et al., 2020),

165   the population infection dynamics of *Kapentagyrus* spp. are not related to the spatiotemporal

166   origins, 2) given the contrasting host range between the two species of *Kapentagyrus* and

167   the differences in lifestyle between the host species, spatial differences in infection will be

168   more pronounced in *K. limnotrissae,* and 3) following previously published results on

169   contrasting introduction success in different host life stages (Kmentová et al., 2019), we

170   expect host size-driven differential occurrence of *Kapentagyrus* spp. on *L. miodon*.

171

172   **Methodology**

173

174   *Sample collection and species identification*

175   In total, 1730 specimens of two endemic pelagic clupeid species, *L. miodon* (733) and *S.*

176   *tanganicae* (997), were collected along the North-South axis of Lake Tanganyika, including

177   all three subbasins (North, Central, and South) in two different seasons (rainy season from

178   October to April and dry season from May to September) within a four-year period (Fig. 2,

179   Table S1). Freshly caught fish specimens were either obtained in collaboration with the

180   experimental fishing unit of the Centre de Recherche en Hydrobiologie - Uvira (CRH) (Uvira,

181   Democratic Republic of the Congo) or purchased from local fishermen. We combine newly

182   obtained data on monogenean infection of clupeids in LT with those published in previous

183   studies (Kmentová et al., 2020, 2018). Host specimens were collected within a period of 2

184   weeks (August 2016, April 2018, and October 2019) to avoid sampling the same population

185   twice, because both clupeid species are highly mobile (De Keyzer et al., 2019; Mulimbwa

186   N'Sibula & Mannini, 1993). Whole fish and/or gills were preserved in absolute ethanol. Host

187   specimens were examined for the presence of monogenean parasites according to the

188   procedure described in Kmentová et al. (2018). Species level identification of *Kapentagyrus*

189   spp. was based on distinctive characters of the hard parts of the attachment organ in the

190   posterior part of their bodies (for more details see Kmentová et al., (2018)). In the case of *L.*

191   *miodon*, the only species of the two clupeids that hosts two monogenean species,

192   monogenean individuals that could not be identified at the species level were only included

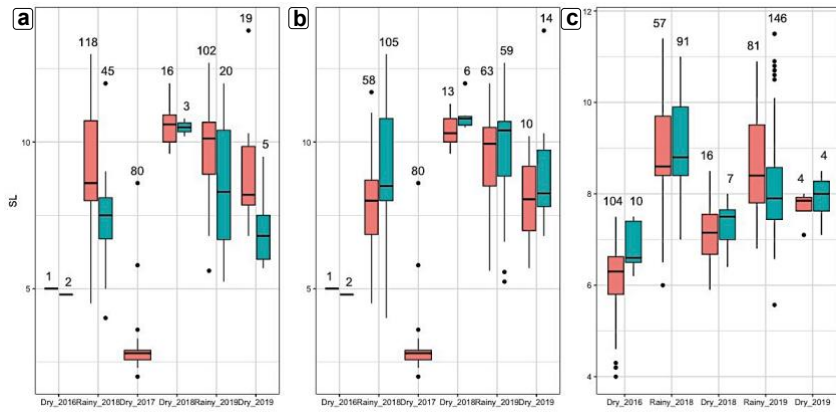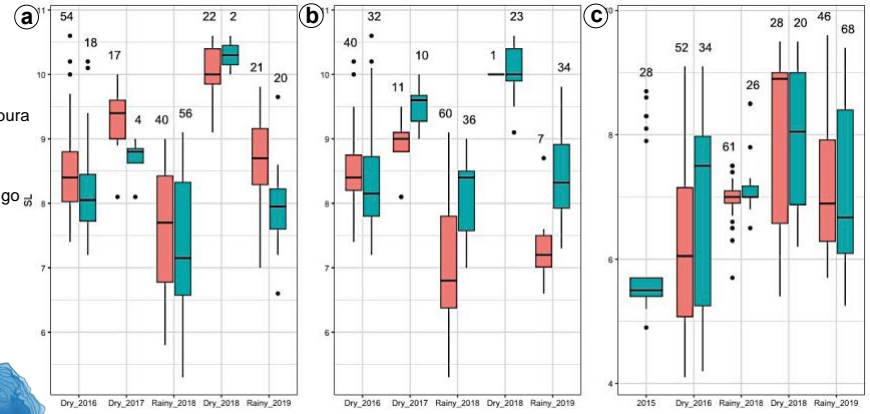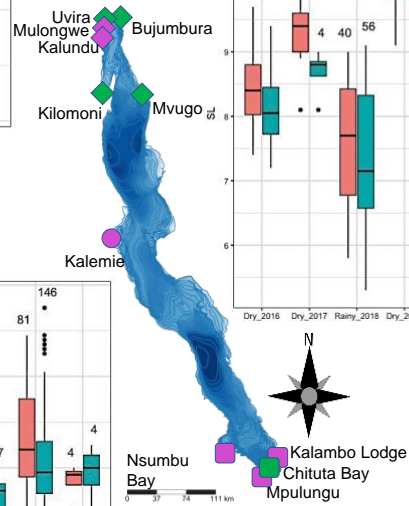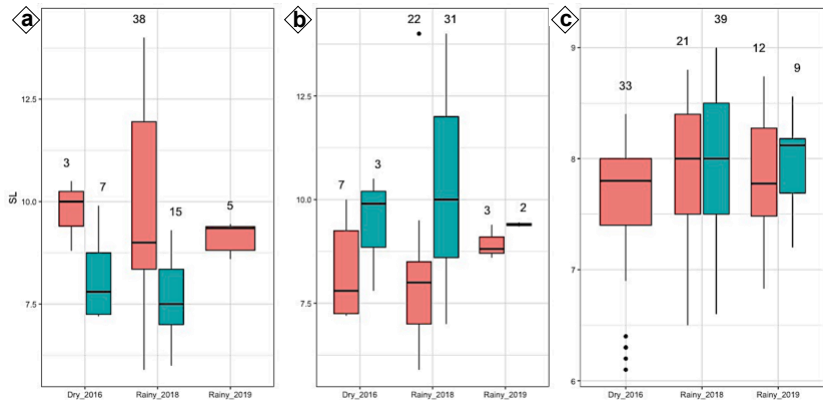193   in the counts of total infection intensities.

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

10

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 χ² 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.
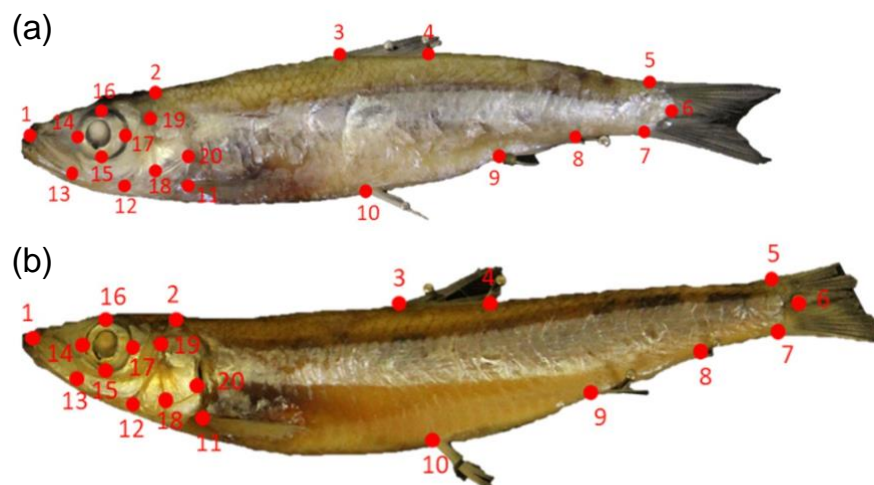

Fig. 3: Position of landmarks recovered for 2D digitisation of specimen of a) *Limnothrissa miodon* and b) *Stolothrissa tanganicae*.

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 (ΔAIC = 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).

14

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

2   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**

3   Abbreviations: standard length (SL), zero inflated model (Zeroinfl), negative binomial distribution (NBinom1,2), Poisson distribution (Poisson).
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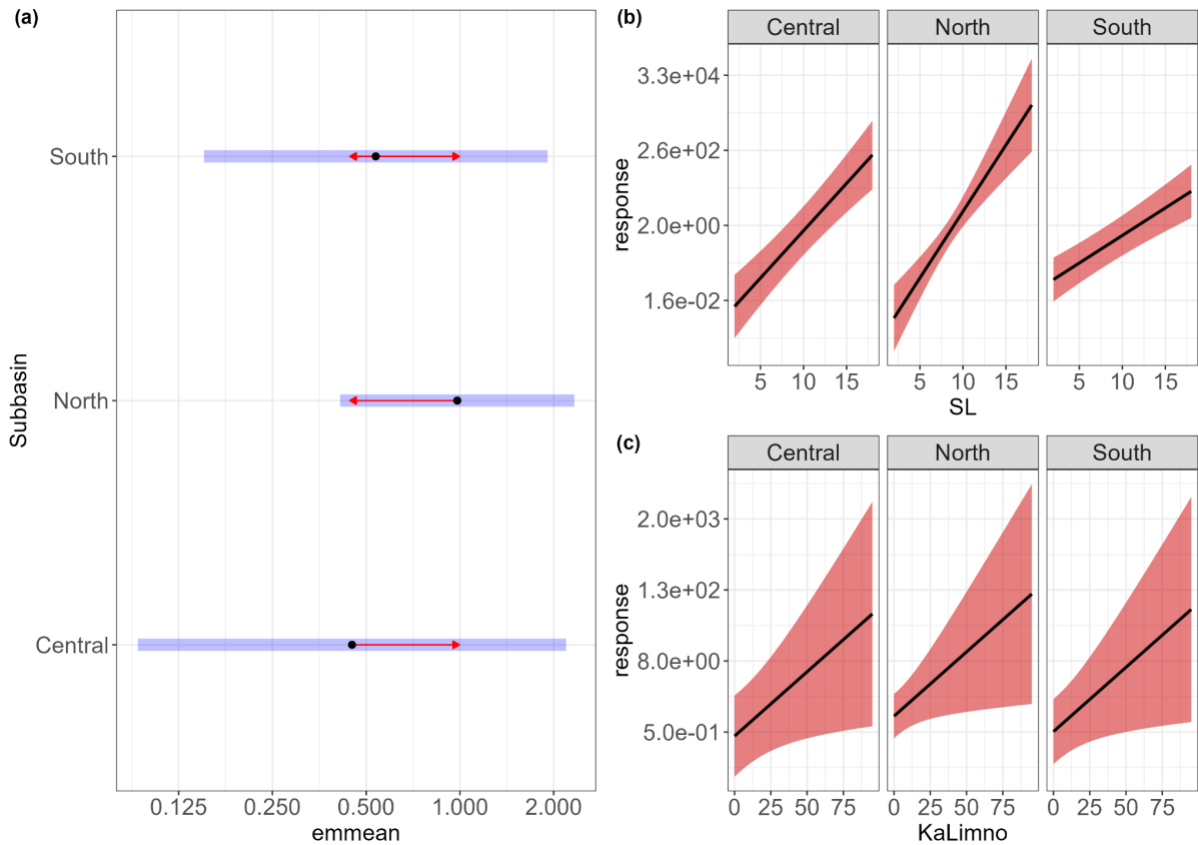
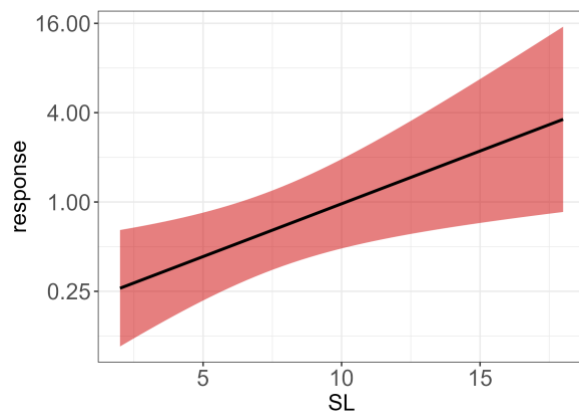Fig. 4: Predictions for infection intensity of *Kapentagyrus tanganicanus* ex *Limnothrissa miodon* with 95% confidence intervals under the minimal adequate model (Table 1). a) Infection intensity in different subbasins showed no significant differences (CIs in blue, direction of overlap in red) with 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*.
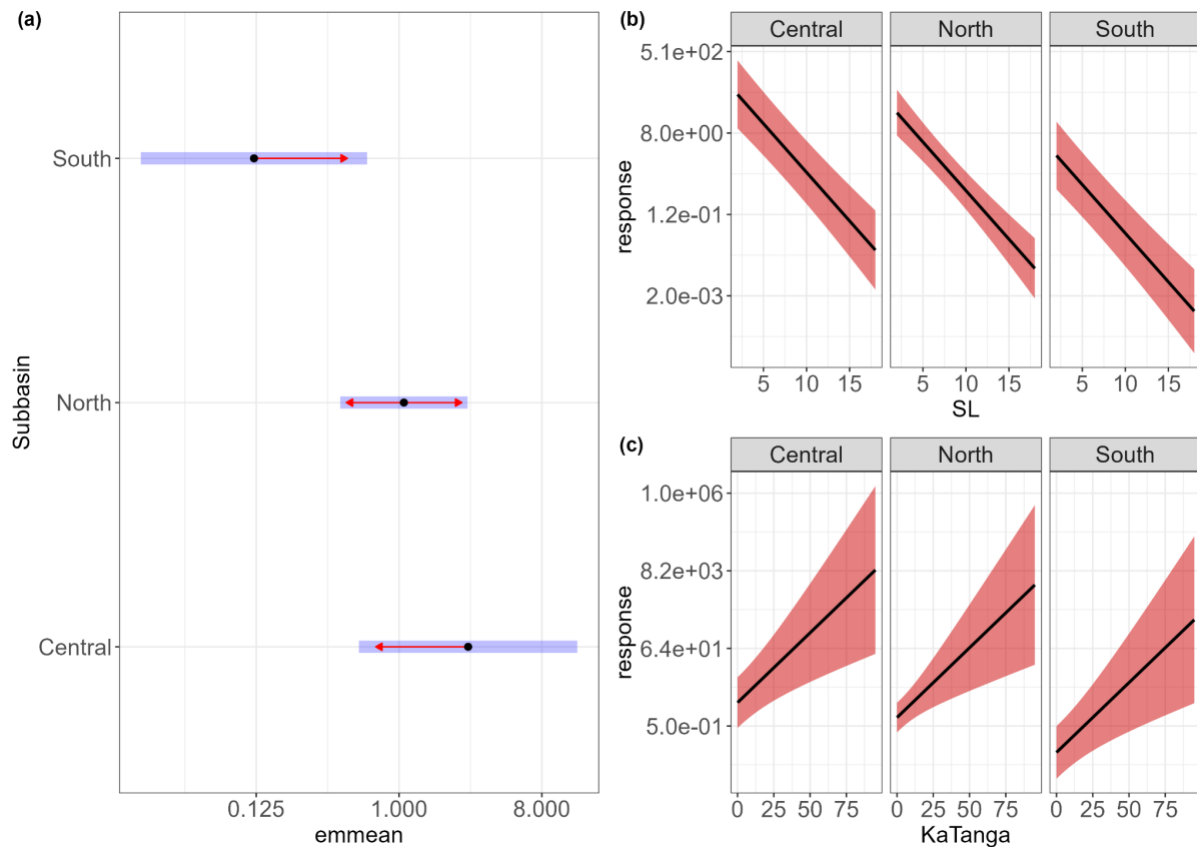

Fig. 5: Prediction of infection intensity of *Kapentagyrus tanganicanus* ex *Stolothrissa tanganicae*. The infection intensity increased with the standard length (SL) of the host.

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

32   the supplementary information only and should be interpreted with caution (Figs. S1&2).

33   Based on the wireframes of the head shape (Fig. 8), differences in the relative position of the

34   snout, eye and operculum are visible along the displayed PC axes.

35

36   The results of our CVAs confirmed the trend visible mainly along the second PC axis with

37   significant differences in the shape of the whole body and head related to the geographic

38   origin of *L. miodon* (Tables 2 and S1). Specifically, head shape differences increased with

39   geographic distance in *L. miodon*. Although the CVAs indicated significant shape differences

40   between some of the localities in both the full body and head datasets of *S. tanganicae* (see

41   Tables 2 and S1), no consistent geographical pattern was detected in the PCAs. In both

42   species, differences in the head shape were more pronounced in relation to geographic

43   origin compared to the full body.

44
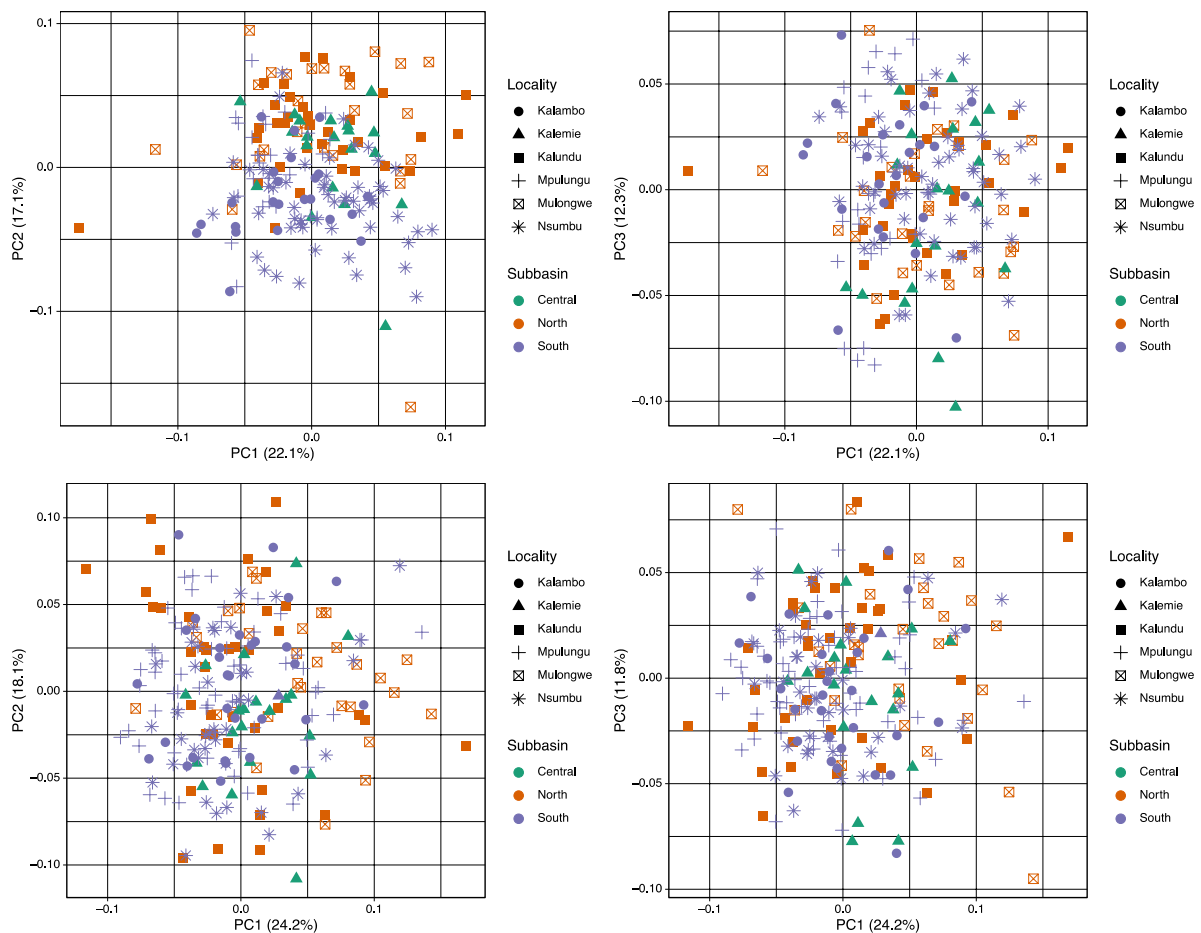
45

46   Fig. 7: Biplots of Principal Component Analyses (PCA) showing the shape variation in the

47   head across the sampled localities of a) *Limnothrissa miodon*, first two PCs displayed, b)

48   *Limnothrissa miodon*, first and third PCs displayed, c) *Stolothrissa tanganicae,* first two PCs

49   displayed, d) *Stolothrissa tanganicae,* first and third PCs displayed*.*
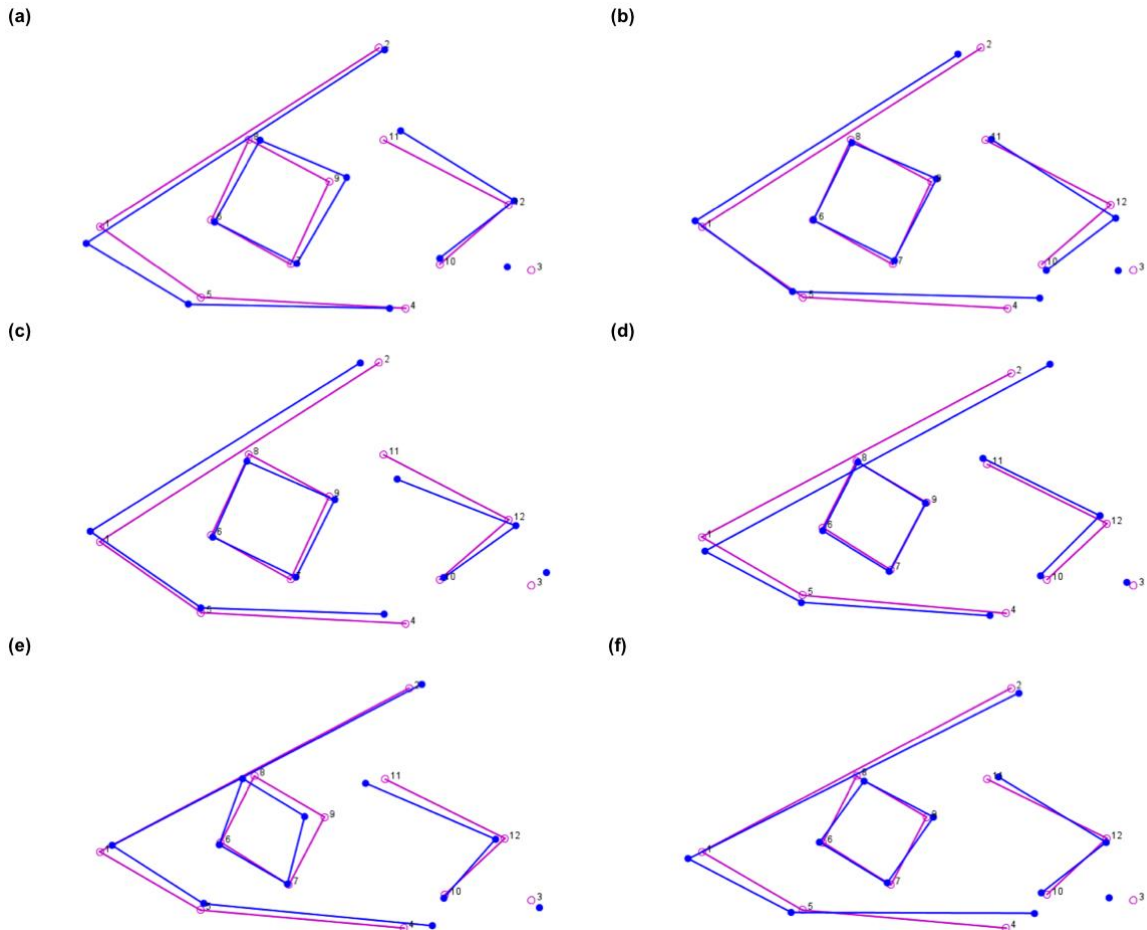
50
51   Fig. 8: Wireframes showing the shape variation in the head based on the coordinates of

52   Principal Component Analyses of a) *Limnothrissa miodon,* PC1, b) *Limnothrissa miodon,*

53   PC2, c) *Limnothrissa miodon,* PC3, d) *Stolothrissa tanganicae,* PC1, e) *Stolothrissa*

54   *tanganicae,* PC2, f) *Stolothrissa tanganicae*, PC3. The target shape is presented in blue, the

55   starting shape in pink.

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61   Table 2: Results of Canonical Variate Analyses of head shape variation for a) *Limnothrissa*

62   *miodon* b) *Stolothrissa tanganicae*. Values of Procrustes distances are displayed below the

63   diagonal, P-values are shown above the diagonal. Significant P-values (<0.05) are indicated

64   in bold. Number of samples are indicated between brackets behind the locality names with

65   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

66

67   **Discussion**

68   *Temporal stability and spatial differences of infection*

69   Previous studies indicate that the distribution of aquatic parasites is determined by

70   environmental factors (Timi & Poulin, 2003). Also, many parasites are vulnerable to

71   extinction, as a decline in population size of the host can negatively affect the often-

72   overdispersed distribution of parasite populations (Lester, 2012). In Lake Tanganyika,

73   annual differences in fisheries production are believed to be caused by natural cycles of

74   clupeid species. This is visible in density changes of fish populations over a spatiotemporal

75   gradient (Mölsä et al., 1999; Plisnier et al., 2009). Additionally, seasonal fluctuations in

76   clupeid catches in Lake Tanganyika are driven by external factors related to the

77   hydrodynamics and the weather. Despite the reported North-South clupeid migrations

78   resulting in seasonal fluctuations of host population densities and mean size distribution of

79   the hosts (Kimirei & Mgaya, 2007; Mulimbwa N'Sibula et al., 2022), in line with our

80   hypothesis we found the spatiotemporal dynamics of *Kapentagyrus* spp. in the pelagic zone

81   to be seasonally independent. This result confirms previously suggested independence on

82   seasonal host population cycles of rather short-lived parasites (Lester & MacKenzie, 2009)

83   of which monogeneans in the tropical areas with an estimated generation time of days up to

84   a few weeks might be considered (Tomnatik, 1990). Alternatively, host fluctuations could

85   appear over longer cycles that were not covered by the sampling design of our study. While

86   we could not disentangle the effects of host size and geographic origin for *K. tanganicanus*,

87   *K. limnotrissae* exhibited a slight spatial differentiation along the North-South axis. We

88   suggest that this pattern is driven by temporal residency and patchy distribution of *L. miodon*

89   in the littoral habitat before reaching a certain size and becoming pelagic. In general, the

90   geographic distribution of parasites infecting pelagic fish hosts is linked to life cycle

91   complexity (number of host species with different distribution ranges) with limited spatial

92   distribution of monogeneans only to certain areas, as in the case of *Sprattus sprattus* L.

93   (Kleinertz et al., 2012) and *Clupea harengus* L. (Actinopterygii, Clupeidae) (Rahimian et al.,

94   1999) in the North Sea. In comparison to monogeneans infecting clupeid fishes in Lake

95   Tanganyika, no host size related infection intensity was observed in the case of *Mazocraes*

96   *alosae* Hermann, 1782 on two species of *Alosa* Linck, 1790 (Actinopterygii, Clupeidae) from

97   North-Atlantic coastal waters (Gérard et al., 2017). Host behaviour and season were shown

98   to drive temporal differences in infection levels of *M. alosae* on *Alosa immaculata* Bennett,

99   1835 in the northern Black and Azov Seas (Plaksina et al., 2021).

100   A holistic approach for stock identification has been highlighted before (Begg and Waldman,

101   1999). The combination of parasite community data and host morphometric data aided in the

102   discovery of multiple stocks of horse mackerel (*Trachurus trachurus* L.) in the North Atlantic

103   (Abaunza et al., 2008) and in the stock identification of Australian sardines (*Sardinops sagax*

104   (Jenyns, 1842)) along the East African coast (Van Der Lingen et al., 2015). Unlike parasites

105   with complex life cycles, directly transmitted parasites have the advantage that distribution is

106   limited to the target host enabling elucidation of large-scale and long-term population

107   dynamics of certain host-parasite interaction (Catalano et al., 2014). Using a

108   geomorphometric approach, we found intraspecific morphological differences in the LT

109   clupeid species linked to the geographic origin of the specimens especially in *L. miodon*.

110   Morphological variation can be driven by various environmental factors (Mounir et al., 2019;

111   Sultan & Stearns, 2005). In our study, the level of geographically determined morphological

112   variation differed between the studied fish species. The shape differences in the relative

113   position of snout and eyes may be related to the geographical distance and more concretely

114   subbasin origin of *L. miodon*. The environment in the middle part of the lake could serve as a

115   transit site between the northern and southern parts. Moreover, compared to other areas,

116   the northern peak can be seen as the most affected by anthropogenic pressures (Cohen et

117   al., 2005). Morphological variation of the head was also visible in *S. tanganicae*, but without

118   a clear geographical pattern. These results indicate a more profound shape differentiation in

119   *L. miodon* compared to *S. tanganicae,* despite originating from the same localities. The

120   absence of clearly geographically determined morphological differences in *S. tanganicae*

121   can be explained by the lack of residential behaviour. Although the results indicate that the

122   population of *L. miodon* is more structured compared to *S. tanganicae*, the lack of a clear

123   geographic cline supports the high level of population connectivity of this species across the

124   lake (Junker et al., 2020). As hypothetised, given the host life-stage dependency of *K.*

125   *limnotrissae,* contrasting infection levels related to geographic origin suggest that the spatial

126   distribution of the parasites and the morphological response of the clupeid hosts follow

127   similar geographic patterns. Overall, our results on lake-wide parasite occurrence and

128   seasonal dynamics combined with characterisation of clupeid hosts support the hypothesis

129   of largely unrestricted migration in *S. tanganicae* and the lack of barriers in the pelagic zone

130   of the lake (De Keyzer et al., 2019; Junker et al., 2020; Mulimbwa N'Sibula et al., 2022).

131   Habitat differences between the clupeid hosts over their lifespan most likely drive contrasting

132   spatial patterns of infection between closely related parasite species. This result further

133   supports the importance of host species with the highest dispersal capacity on the spatial

134   distribution of parasites, as reported for *Cichlidogyrus casuarinus* Pariselle, Muterezi

135   Bukinga & Vanhove, 2015 infecting pelagic cichlids in the lake (Kmentová et al., 2021).

136   Contrasting levels of gene flow between the two parasite species related to geographic

137   origin along the North-South axis of the lake (Kmentová et al., Under review) may therefore

138   be associated with lifestyle differences between the two clupeid species.

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

140   The diurnal and geographically small-scale migrations of Tanganyika clupeids are generally

141   better understood than the long term patterns. Vertically, these clupeids respond to light and

142   oxygen concentration and follow the diurnal movements of their prey. Horizontally, they

143   migrate between the offshore waters of the pelagic and the inshore waters of the littoral

144   habitat throughout their development (Matthes 1967). A recent long-term study of the

145   reproductive activities of the clupeids in the northern subbasin identified the littoral zone as

146   the main spawning ground for *L. miodon,* and the pelagic zone as the equivalent for *S.*

147   *tanganicae* (Mulimbwa N'sibula et al., 2022). Juveniles of both species occur in littoral

148   habitats, but in general *S. tanganicae* lives and spawns at greater distances from the shore

149   than *L. miodon* (Coulter, 1970, 1991b; Mannini et al., 1996). Eggs of *L. miodon can* even be

150   deposited just above the sandy bottom of the littoral zone. Juveniles of *L. miodon,* but not *S.*

151   *tanganicae,* occupy sandy beaches right by the shore (Mulimbwa N'Sibula et al., 2022).

152   In line with our hypothesis, the body size of the clupeid hosts appears to be a major

153   determinant of infection, as it significantly affects infection intensities for all three host-

154   parasite combinations. Such an overall positive correlation between fish size and

155   monogenean infection intensities has been associated with a larger habitat offered by larger

156   hosts (Alvarez-Pellitero & Gonzalez-Lanza, 1982; Poulin, 2000). Considering the age-

157   dependent migration of *L. miodon* from the littoral to the pelagic zone, the contrasting

158   infection intensities associated with host size between *K. limnotrissae* and *K. tanganicanus*

159   suggests a spatial stratification of infection linked with the ontogenetic migration of *L. miodon*

160 from the littoral to the pelagic zone. This apparent replacement contrasts with the positive

161 effect of each parasite species' infection intensity on that of the other species. We suggest a

162 combination of changes in host habitat and facilitation of infection caused by host immune

163 deficiency or suppression at the base of this pattern. Suppression of the fish immune system

164 allowing higher infection intensities has been shown in previous studies on monogeneans

165 (Rohlenová et al., 2011; Sitjà-Bobadilla, 2008) and other parasite taxa (Klemme et al., 2016).

166 Alternatively, the antagonistic interaction between the two parasite species could explain the

167 resulting pattern, as proposed e.g., in the monogenean communities infecting *Astyanax*

168 *aeneus* (Günther, 1860) in Neotropical rivers in Mexico (Salgado-Maldonado et al., 2019).

169 However, so far there is no evidence of negative or any direct interspecific monogenean

170 interaction between closely related species (Šimková et al., 2000; Soler-Jiménez & Fajer-

171 Ávila, 2012).

172 *Conclusion*

173 Lake Tanganyika is an ancient and pristine lake known for a spectacular level of species

174 diversity and endemism. The existence of schooling pelagic fishes in an enclosed ecosystem

175 promotes studies on general ecosystem dynamics of pelagic areas. The link between

176 theoretical/experimental studies and dynamics in natural ecosystems is largely unknown

177 (Lindegren et al., 2016) and a common framework is lacking (Ritz et al., 2011). Incorporation

178 of host-parasite interactions increases our knowledge on the interconnectedness of trophic

179 levels (Lafferty et al., 2006). Our holistic approach based on spatiotemporal distribution of

180 fish parasites and morphological variation of the host species reveals insights on the

181 ecosystem dynamics along a North-South axis, and habitat preferences of two important

182 fisheries targets. As restricted migration of *L. miodon* is considered as one of the drivers of

183 profound North-South differences in parasite occurrence and fish morphology, being also

184 indicated in recent studies (De Keyzer et al., 2019; Junker et al., 2020), such results should

185 be considered in fisheries management plans. Our results suggest that parasite population

186 dynamics in pelagic zones are dependent on spatial distribution of the hosts in both large

187 and small scales. Intensity of infection seems to be mainly driven by fish size with mutual

188 facilitation in case of co-infection. Lack of seasonality in infection intensity points to

189 environmental stability of the pelagic zone and absence of density dependent infection.

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Conflict of Interest

201 Authors declare no conflict of interest.

Author Contributions

203 N.K. designed the study, generated incidence data, analysed geometric morphometric data

204 and drafted the manuscript. A.C-L. analysed incidence data and helped draft the manuscript,

205 M.J. generated part of the incidence data and helped to draft the manuscript, M.V.S.

206 supervised geometric morphometric data analyses and interpretation of results, M.P.M.V.

207 discussed the results, helped draft the manuscript and supervised the study, T.M. and

208 E.V.H. helped with geometric morphometric data analyses, S.H. generated geometric

209 morphometric data, L.Mi. and K.T. helped with data interpretation and draft of the

210 manuscript, L.Ma. provided support in the field and knowledge on the studied ecosystem. All

211 authors have read and agreed to the published version of the manuscript.

Data Availability Statement

212

213 Parasite voucher material was deposited in the collection of Hasselt University under

214 accession numbers xx-xx and the Royal Museum for Central Africa. The geometric

215 morphometric data underlying the results of this article are available in Mendeley Data (xxx).

Supporting Information

216

217 Additional supporting information may be found in the online version of the article at the

218 publisher's website.

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