

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 (*Kapentagyryus*, 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 *Kapentagyryus* 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 endemism 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 tanganyicae* 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 *Kapentagyris* Kmentová, Vanhove & Gelnar, 2018 (Kmentová et al., 2018). *Kapentagyris* 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 *Kapentagyris* 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).

131

132 *Spatiotemporal dynamics in the pelagic zone - a holistic approach*

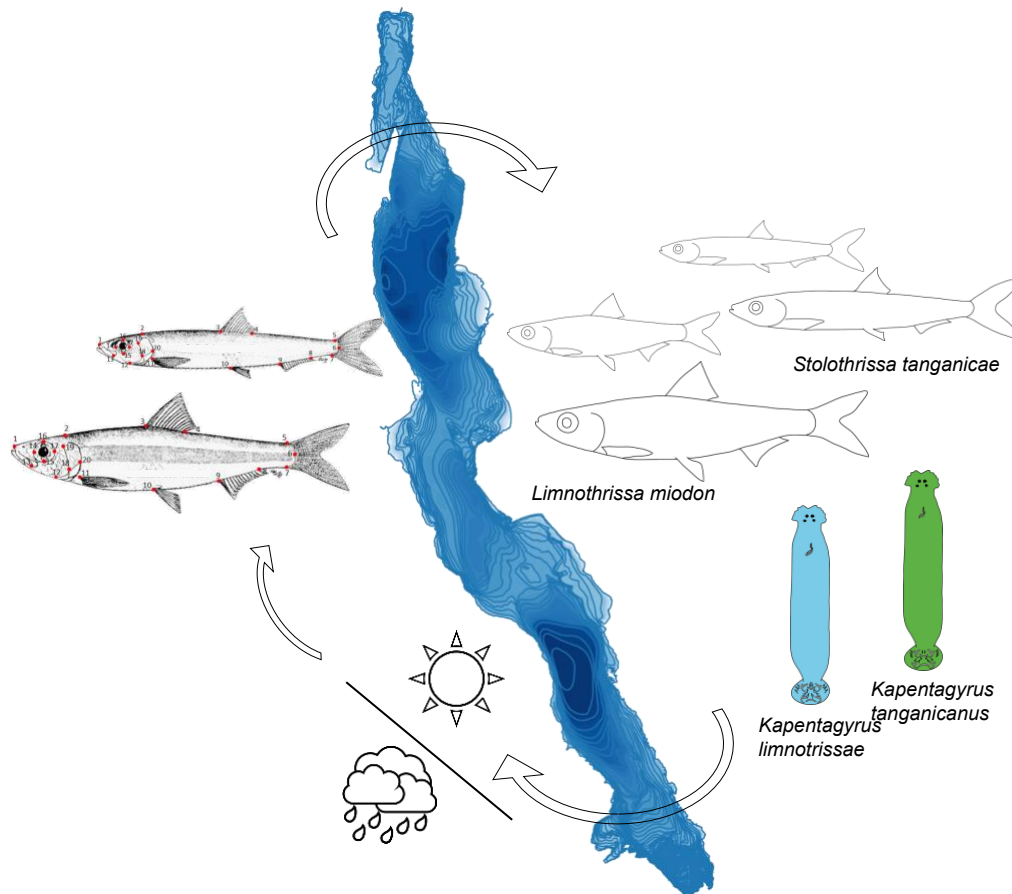
133 Spatiotemporal dynamics of parasites have been studied mainly in the context of host-driven
134 determinants of their community composition (reviewed in Lester & MacKenzie, (2009)).
135 Large-scale population dynamics of parasites infecting pelagic organisms are hardly ever
136 studied due to the 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



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.

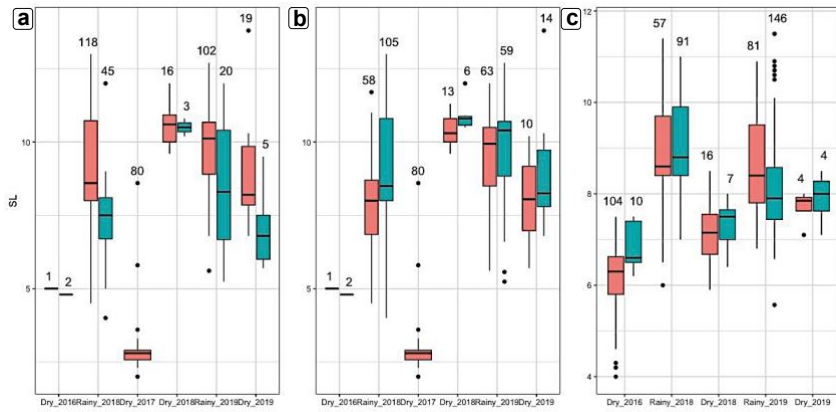
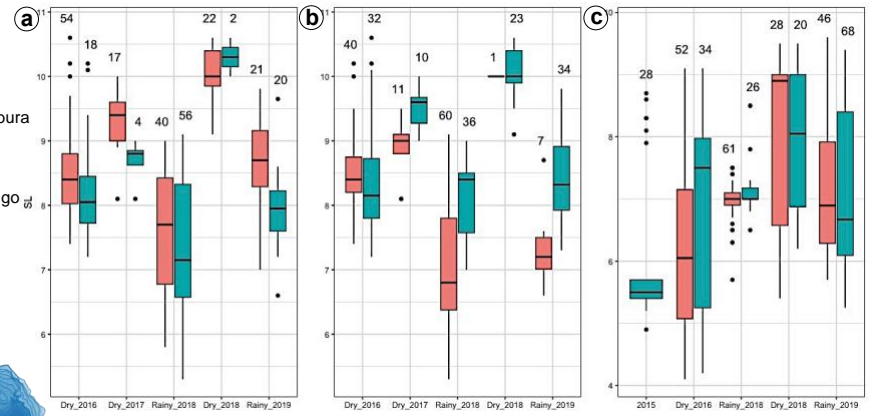
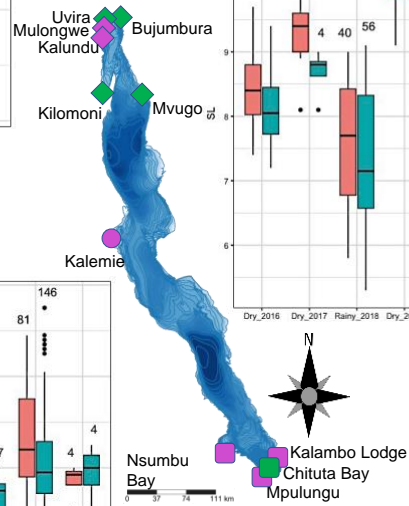
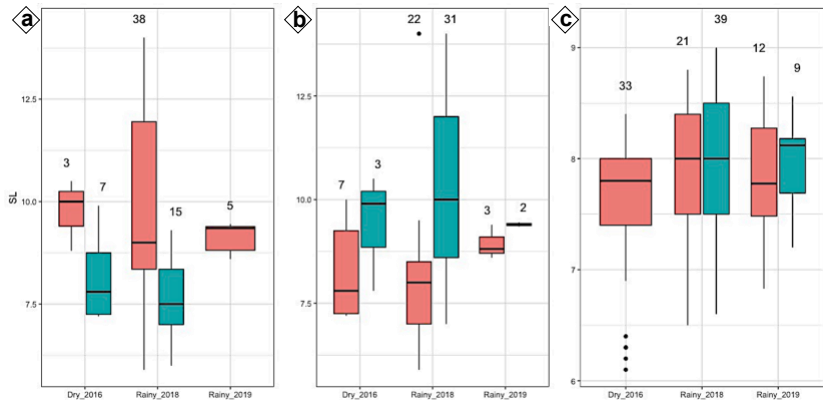


Fig. 2: Overview of screened fish hosts and incidence of infection of collected parasite populations. Season and year of origin (x-axis) and standard length of the fish host (y-axis, SL in cm) of a) *Kapentagyris limnotrissae* ex *Limnothrissa miodon*, b) *Kapentagyris tanganicus* ex *Limnothrissa miodon*, c) *Kapentagyris tanganicus* ex *Stolothrissa tanganicus*. 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. tanganicus* ex *L. miodon*, iii: *K. tanganicus* ex *S. tanganicus*). 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. tanganicus* 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. tanganyicae* 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.

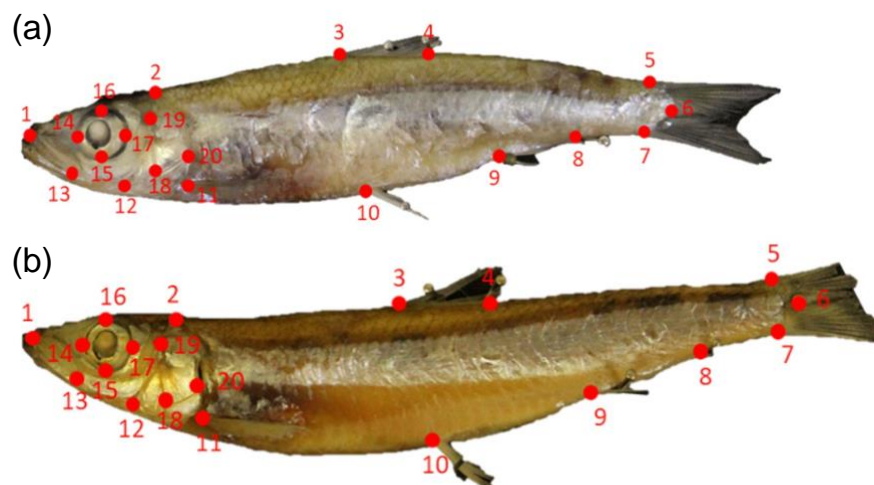


Fig. 3: Position of landmarks recovered for 2D digitisation of specimen of a) *Limnothrissa miodon* and b) *Stolothrissa tanganyicae*.

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.

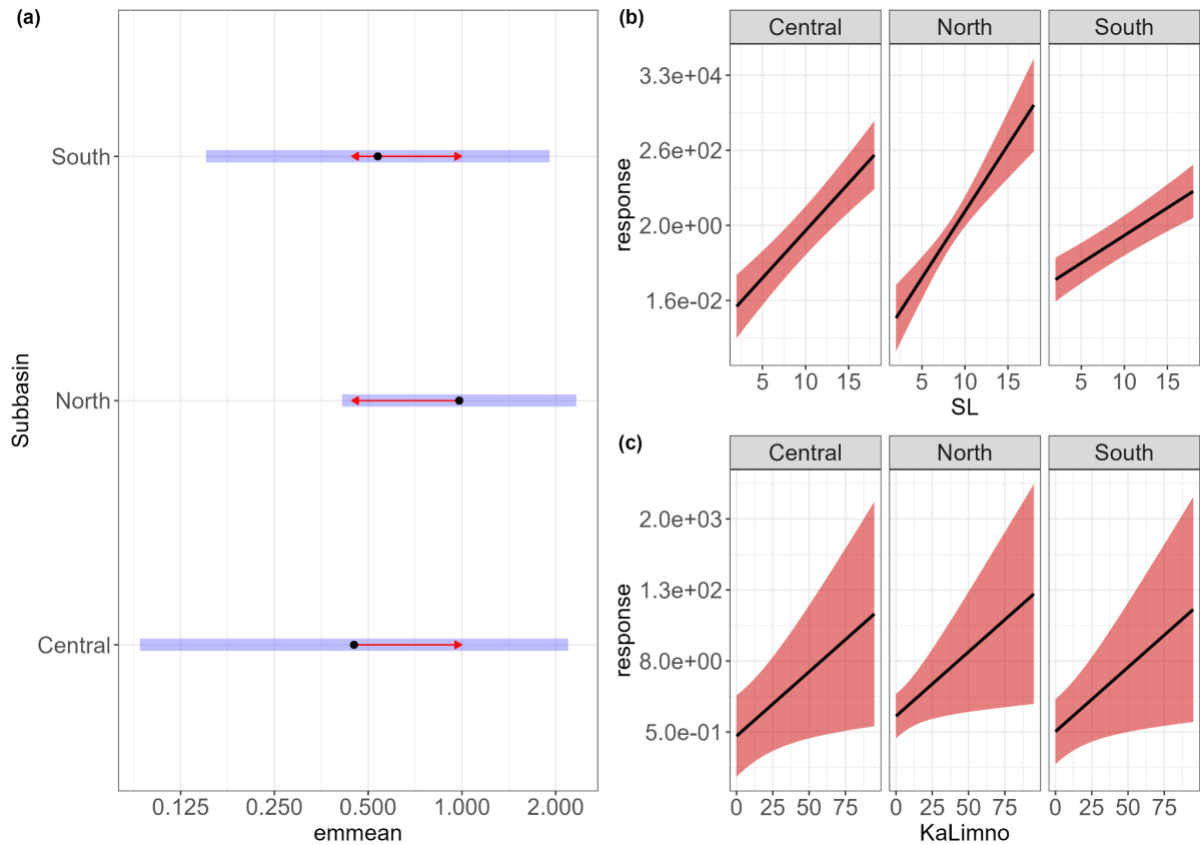
For *K. tanganicus* (i and iii), a monogenean infecting both species of clupeids, the models with a quadratic parameterisation (*nbinom2*) outperformed the models with a linear parameterisation. *Kapentagyris limnotrissae* infecting *L. miodon* (ii), only improved the model fit marginally ($\Delta\text{AIC} = 2$; $\chi^2(1, 2) = 2310$, $p = 0.038$). In the post-hoc analysis, we found only minor differences between infection levels of *K. tanganicus* (Figs. 4&5), yet subbasin identity contributed significantly to the overall model fit (Table 1). Infection intensities of *K. tanganicus* 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. tanganicus* (Fig. 6).

- 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.

		<i>K. tanganicanus ex L. miodon</i> (i)			<i>K. limnotrissae ex L. miodon</i> (ii)			<i>K. tanganicanus ex S. tanganicae</i> (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).

4



5

6 Fig. 4: Predictions for infection intensity of *Kapentagyrus tanganicus* ex *Limnothrissa*

7 *miodon* with 95% confidence intervals under the minimal adequate model (Table 1). a)

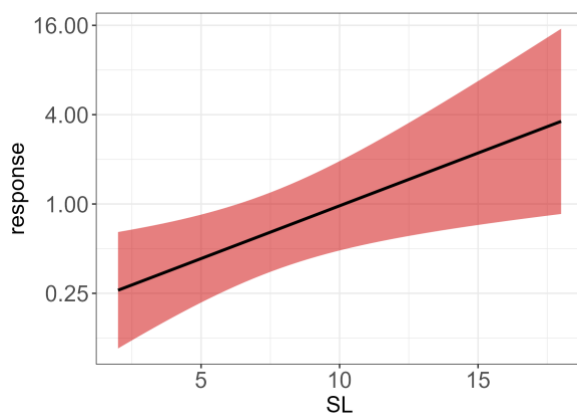
8 Infection intensity in different subbasins showed no significant differences (CIs in blue,

9 direction of overlap in red) with estimated marginal means on the x-axis, b) Infection intensity

10 increased with standard length (SL) of the host, c) Infection intensity increased with higher

11 infection intensities of *Kapentagyrus limnotrissae*.

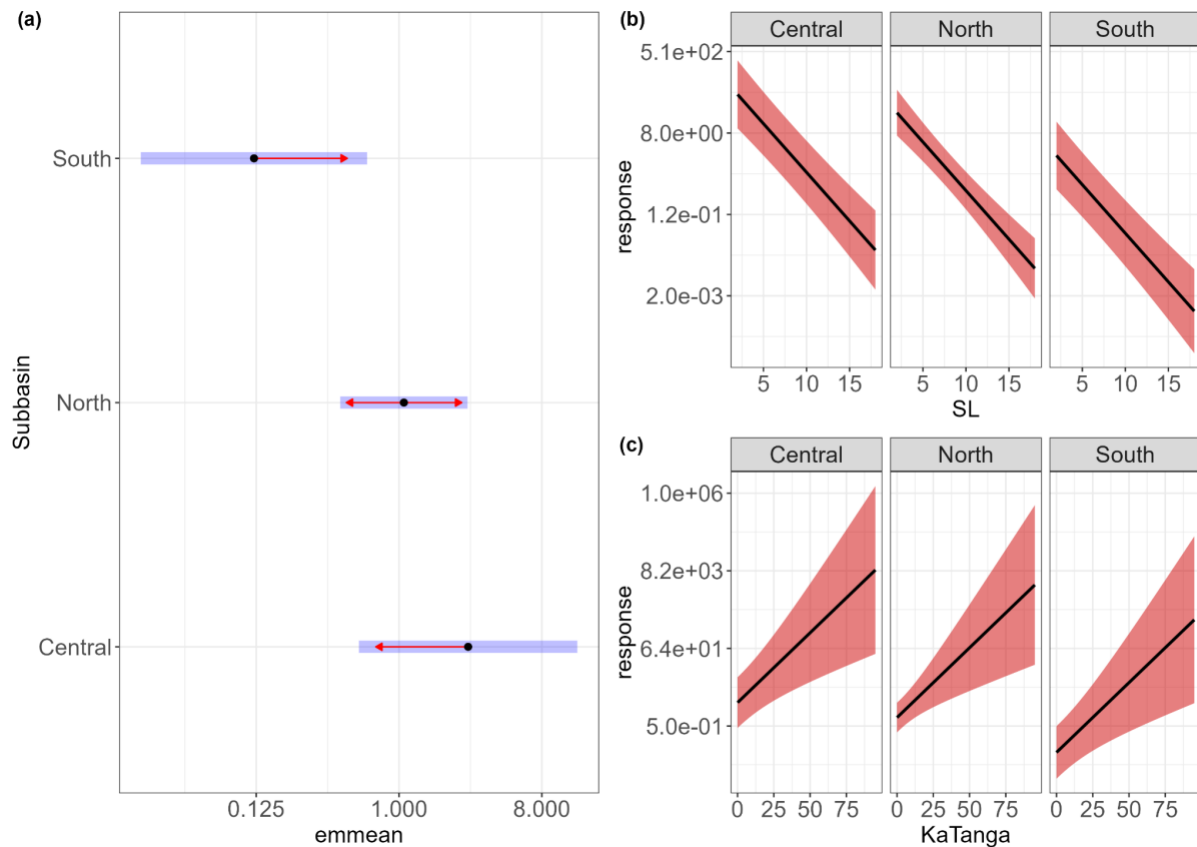
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14 Fig. 5: Prediction of infection intensity of *Kapentagyrus tanganicus* ex *Stolothrissa*

15 *tanganae*. The infection intensity increased with the standard length (SL) of the host.



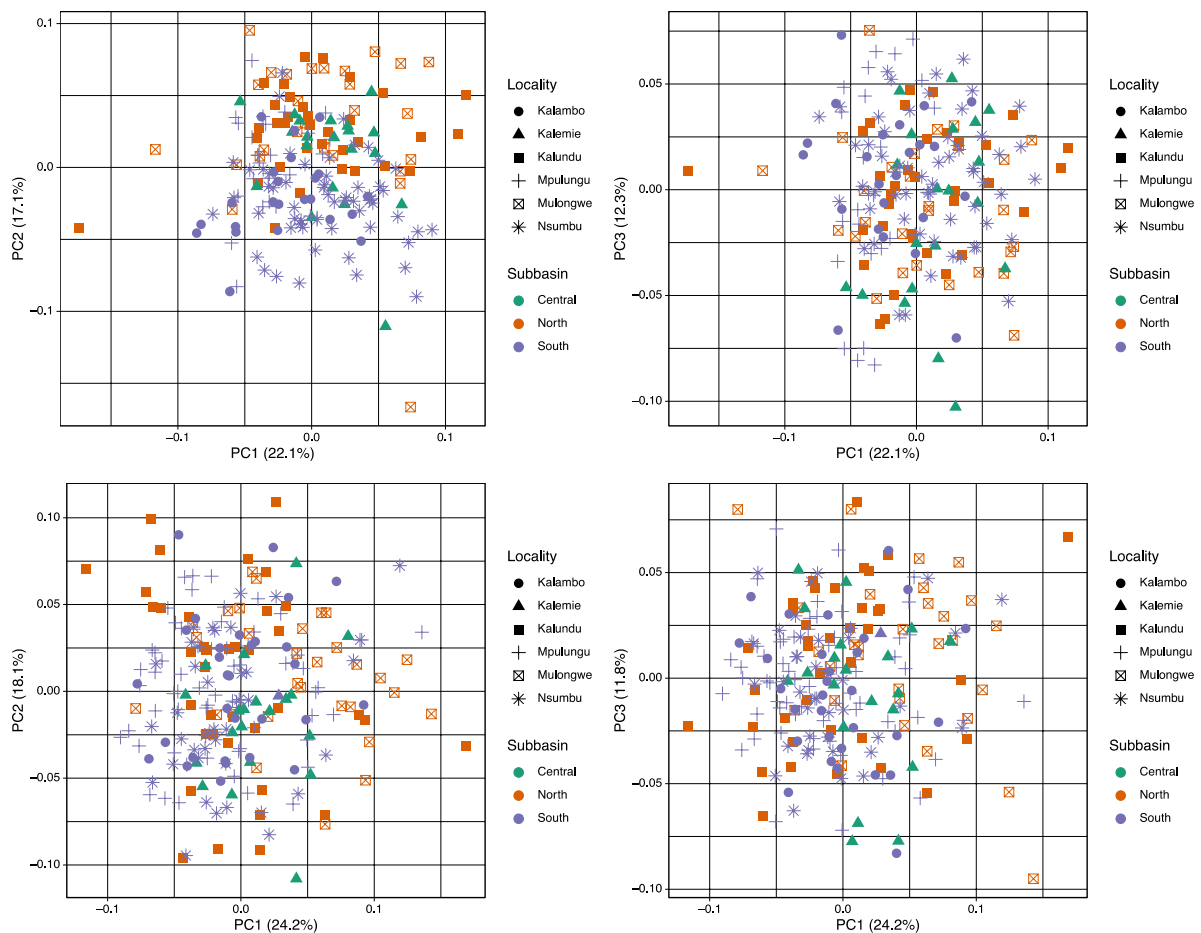
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17 Fig. 6: Predictions for infection intensity of *Kapentagyrus limnotrissae ex Limnothrissa*
18 *miodon*. a) Infection intensity related to subbasin origin with the confidence interval (in blue)
19 and direction of overlap (in red) with estimated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

22

23 **Geomorphometrics of clupeid hosts**

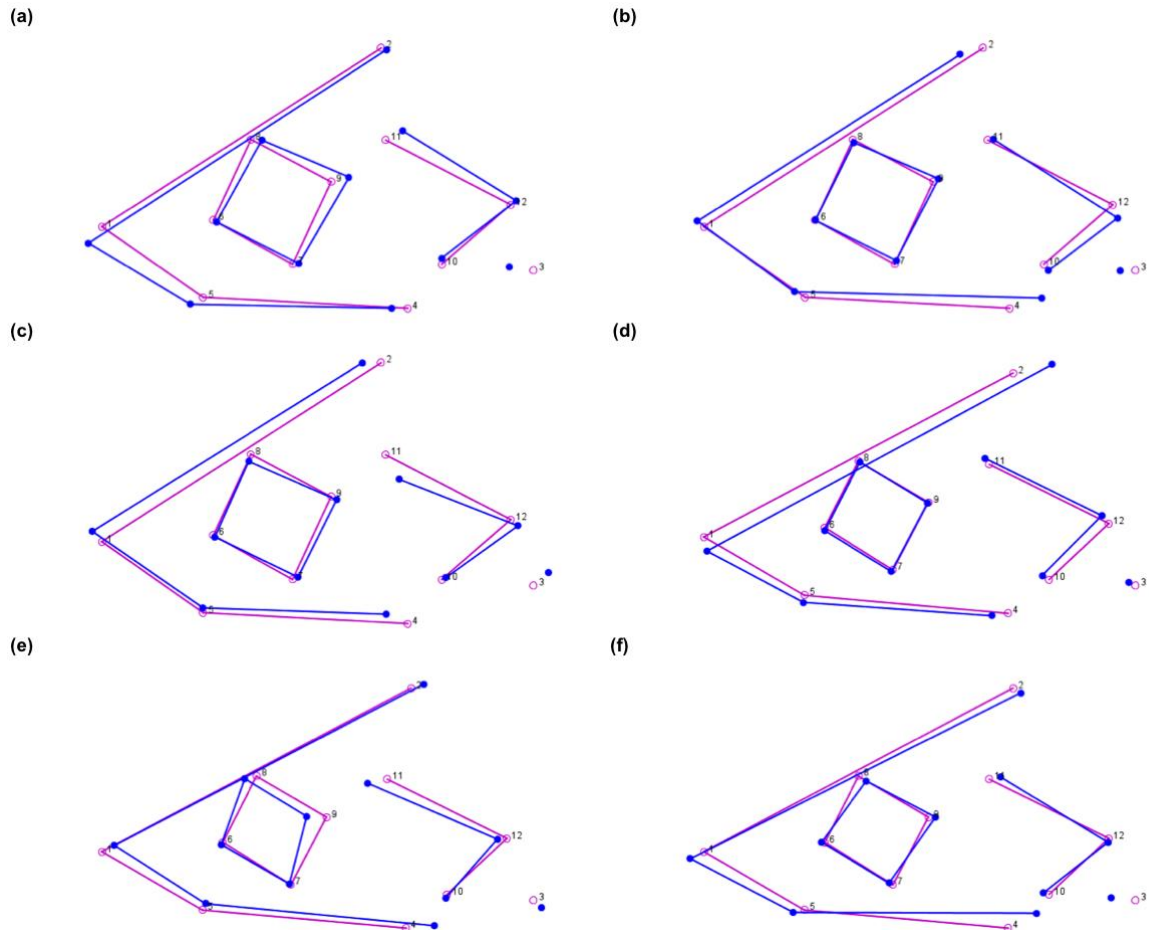
24 Geomorphometric analyses revealed strong similarity of head morphology between
25 specimens from different localities and subbasins of the lake in both clupeid species. In the
26 case of *L. miodon*, the first three PC axes explained 22.1%, 17.1% and 12.3% of the
27 variation, respectively (see Fig. 7A&B), with visible North-South gradient mainly along the
28 PC2. In case of *S. tanganicae*, the first three PC axes explained 24.2%, 18.1% and 11.8% of
29 the variation, respectively (see Fig. 7C&D), with no visible structuring according to locality of
30 origin. As wireframes displayed variation in the positioning of the full body, most likely related
31 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. tanganycae* (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 tanganyicae*, first two PCs
49 displayed, d) *Stolothrissa tanganyicae*, 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 tanganyicae*, PC1, e) *Stolothrissa*
54 *tanganyicae*, PC2, f) *Stolothrissa tanganyicae*, 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 *Kapentagyryus* 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 *alosa* 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. alosa* 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. tanganyicae*, but without
118 a clear geographical pattern. These results indicate a more profound shape differentiation in
119 *L. miodon* compared to *S. tanganyicae*, despite originating from the same localities. The
120 absence of clearly geographically determined morphological differences in *S. tanganyicae*
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. tanganyicae*, 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 hypothesised, 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. tanganyicae* 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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200 **Conflict of Interest**

201 Authors declare no conflict of interest.

202 **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.

212 **Data Availability Statement**

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).

216 **Supporting Information**

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

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