Reproductive activities of two zooplanktivorous clupeid fish in relation to the seasonal abundance of copepod prey in the northern end of Lake Tanganyika

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ABSTRACT. Reproductive activities of two commercially exploited clupeid fishes (*Stolothrissa tanganicae* and *Limnothrissa miodon*) in the northern end of Lake Tanganyika (Bujumbura sub-basin) were investigated during two different years (2004-2005 and 2007-2008). We hypothesized that the timing of largest reproductive investment in these pelagic species coincides with the onset of the rainy season and the highest abundance of copepod prey. For *S. tanganicae*, the gonadosomatic index (GSI) was significantly higher prior to the onset of the rainy season, and this was observed in both years. For *L. miodon*, however, this pattern was overall weaker and only statistically significant in 2004-2005. In both species, spawning activities did not seem to be adjusted to provide optimal feeding conditions for the larvae. Instead, investment in reproduction seemed to be related to the availability of copepods in the preceding months. We conclude that the timing of reproductive activities in these clupeids is species-specific, and might be subject to strong year-to-year variation.

KEY-WORDS: Clupeidae, copepod, fisheries, gonadosomatic index, reproductive activities

INTRODUCTION

Lake Tanganyika is the oldest of the East African Great Lakes (COULTER, 1991) and is the second largest and deepest freshwater body in the world. Up to now, around 1200 species have been identified in this lake, classifying it at second position in biodiversity (COHEN et al., 1993). Among the main groups, the fishes show a high degree of biodiversity (VAN STEENBERGE et al., 2011). The last whole-lake overview indicated 250 cichlid species (95 % endemics) and 75 non-cichlid species (59 % endemics) (SNOEKS, 2000).

Stolothrissa tanganicae REGAN, 1917, and *Limnothrissa miodon* (BOULENGER, 1906) (Phylum Chordata, Class Osteichthyes) are commercially-exploited clupeid fishes that provide a vital source of livelihood and food supply to more than 10 million people living in the surroundings of Lake Tanganyika (MÖLSÄ et al., 1999). Together they represent 60% (MÖLSÄ et al., 1999) to 90% (MULIMBWA, 2006) of the total pelagic commercial fish catches from Lake Tanganyika. Unfortunately, recent statistics show that the amount of catch is decreasing, at least in the northern part of the lake (MULIMBWA, 2006; LTA SECRETARIAT, 2012). Some authors have related decreases of catch to climate change (PLISNIER, 1997; O'REILLY et al. 2003), but so far overfishing is likely to be the major reason because of the excessive fishing pressure that has doubled since the mid-1990s (MULIMBWA, 2006; SARVALA et al., 2006a, 2006b; VAN DER KNAAP et al., 2014). This applies particularly

to the northern part of the lake, which has the highest fishing effort per km of shoreline due to high densities of lift nets and traditional fishing units (MÖLSÄ et al., 1999; VAN DER KNAAP et al., 2014).

The biology of *S. tanganicae* and *L. miodon* has been the subject of several studies supporting fisheries management. These investigations have documented life history (MARLIER, 1957), life cycle and length at sexual maturity (MANNINI et al., 1996), population dynamics (SHIRAKIHARA et al., 1992), reproduction and recruitment (MULIMBWA & SHIRAKIHARA, 1994), and spatio-temporal distribution (PLISNIER et al., 2009). Several studies also investigated the feeding biology of both species (POLL, 1953; CHÈNÉ, 1975; MANNINI et al., 1996; LENSU, 1998; ISUMBISHO et al., 2004), as well as the ecology and distribution of zooplankton as their most important prey category (NARITA et al., 1985; MULIMBWA, 1988 and 1991; COENEN, 1995; BWEBWA, 1996; KURKI et al., 1999; SARVALA et al., 1999; VUORINEN et al., 1999). Larvae of *S. tanganicae* have been reported to feed on phytoplankton (CHÈNÉ, 1975), but later studies suggest that their main food source is copepod nauplii (Lake Tanganyika Research Project, unpublished [1998]). Adults mainly feed on copepods, particularly *Tropodiaptomus simplex* (SARS, 1909) (CHÈNÉ, 1975; MGANA et al., 2014); bigger adults also take pelagic shrimps (LENSU 1998; see also COULTER, 1991). In Lake Kivu, larvae of *L. miodon* (10-35 mm) feed preferentially on copepods (nauplii), but also on adult cladocerans, chironomid larvae, Ephemeroptera larvae, vegetal debris, diatoms, Chlorophyceae filaments and organic rubbish (DE IONGH et al., 1983). Juveniles of *L. miodon* (30-70 mm) from lake Kivu feed preferentially on copepods, but also on chrysophytes, *Microcystis*, Rotifera, insect larvae, and nauplii (DE IONGH et al., 1983). In Lake Kivu, adults of *L. miodon* (85 – 110 mm) feed preferentially on chironomids, juveniles of *L. miodon*, copepods, *Microcystis*, land insects, and Trichoptera (DE IONGH et al., 1983). In Lake Tanganyika, adult *L. miodon* also feed on larvae and juveniles of *S. tanganicae*, as well as on pelagic shrimps (COULTER, 1991; MANNINI et al., 1996; LENSU, 1998); *L. miodon* is hence more omnivorous than *S. tanganicae*, in part due to its long littoral phase during which it is using more varied food items.

In this study, we aim to further deepen the knowledge on the biology of these clupeid fishes by describing the timing of their reproductive activities. For *S. tanganicae*, there seems little agreement on the precise timing of reproduction. Sexually mature fish occur throughout the year (ELLIS, 1971) and individuals may spawn several times in a year (COULTER, 1961). Spawning peaks as indicated by variation in the relative number of ripe gonads were apparent in November-December and in April-July in Zambia (ELLIS, 1971), i.e. respectively in the beginning and at the end of the rainy season and well into the dry season. On the other hand, fry abundance in Zambia suggested a major annual spawning at the end of or right after the dry season, i.e. in August-December (COULTER, 1970), and length frequencies of older fish indicated a September peak (PEARCE, 1985). In Tanzania (Kigoma) there appears to be a peak in January-April (CHAPMAN & VAN WELL, 1978), while in the north in Burundi the main spawning is slightly later, in February-May (ROEST, 1977). The seasonal length-frequency distributions suggest usually four annual spawning peaks of varying strength in both Burundi and Uvira waters (MÖLSÄ et al., 2002; MULIMBWA et al., 2014). For *L. miodon*, it seems generally agreed that the main spawning takes place during the rainy season between November and May (MATTHES, 1967; ELLIS, 1971; PEARCE, 1985; MULIMBWA & SHIRAKIHARA, 1994), although fry occur throughout the year, and a peak of spawning was recorded from August to October in the north end of the lake (ARO & MANNINI, 1995).

What factors influence the timing of reproductive investment in both species? A number of studies demonstrated that the abundance of clupeid fishes is influenced by climatological conditions and associated limnological parameters (e.g. PLISNIER et al., 2009). It is therefore likely that

climatological and limnological fluctuations also trigger reproductive activities. Recently, MULIMBWA et al. (2014) investigated the relationship between seasonal changes in the pelagic catch of both clupeid species and the abundance of copepod prey. It was observed that peaks in the abundance of copepods from the onset of the rainy season onwards (October-April) were correlated with the appearance of strong cohorts of both *S. tanganicae* and *L. miodon*. However, various strong cohorts in both species clearly did not match with peaks in the abundance of copepods. Small *S. tanganicae* (2-4 months old) were observed almost year round except in February, May and November-December. The smallest *L. miodon* were around in July-September, November, and March-April. It therefore remains unclear whether or not *S. tanganicae* and *L. miodon* synchronize their reproductive investment with the onset of the rainy season and the highest abundance of copepod prey (i.e. from October-November onwards), which would be most favourable for their offspring. In addition, the reproductive effort of the clupeids might be regulated by the availability of zooplankton food for the
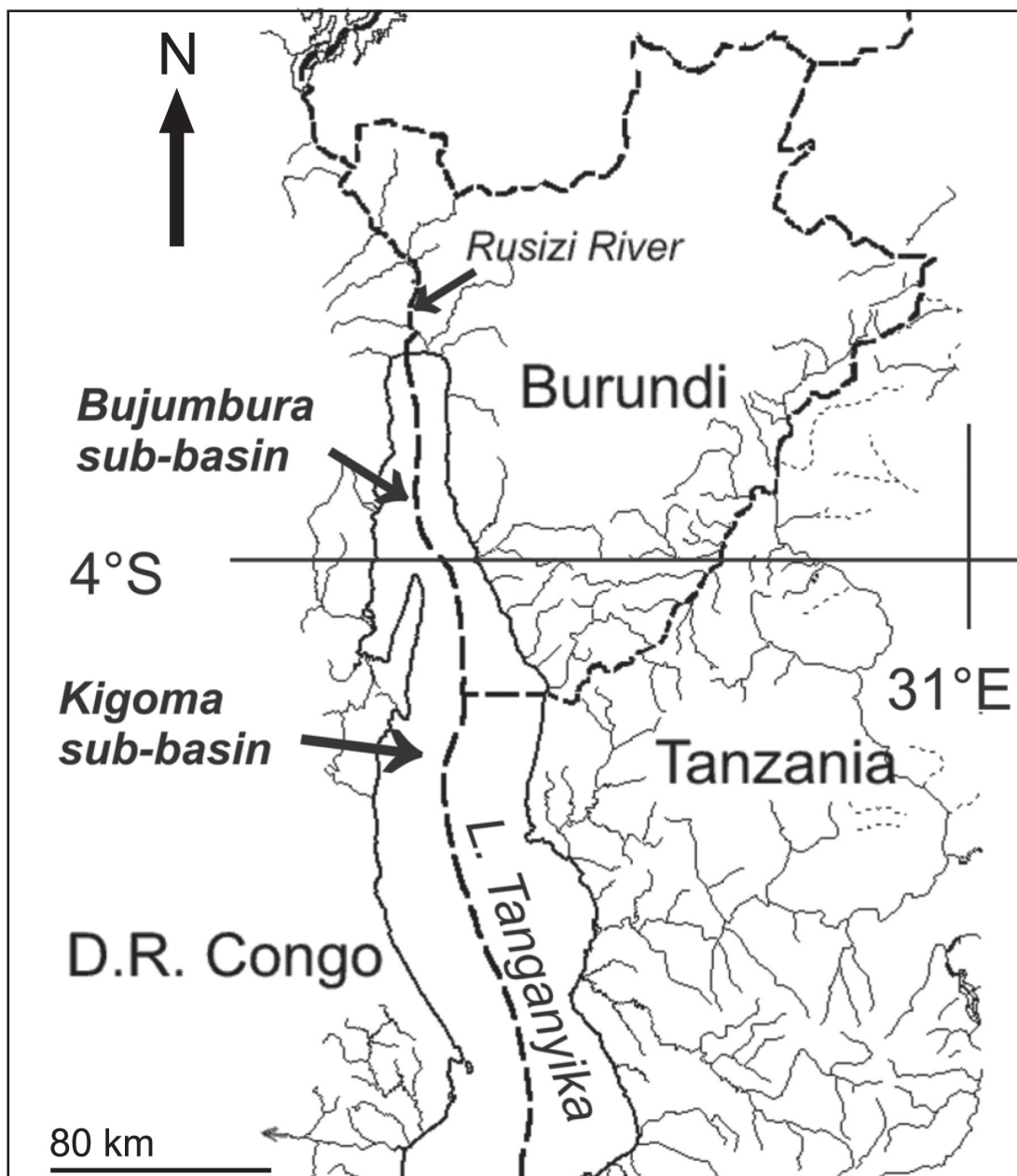

Fig. 1. – Map of the north part of Lake Tanganyika, including the Bujumbura sub-basin.

adults before the spawning period. To test these hypotheses, we document here the reproductive activities of *S. tanganicae* and *L. miodon* relative to the seasonality of zooplankton in the northern end of Lake Tanganyika (Bujumbura sub-basin).

MATERIAL AND METHODS

Data collection

The study was performed in the Bujumbura sub-basin at the north end of Lake Tanganyika (Fig. 1; 03° 28' S and 29° 17' E). Fish samples were obtained from local fisheries from November 2004 to October 2005 and from March 2007 to February 2008. Rainfall data for these periods were collected at the Hydrobiological Research Center (C. R. H.) in Uvira and summed up on a monthly basis. Copepod data were obtained from February 2007 to January 2008, i.e. only for the second period.

Sampling of copepods was carried out twice a month in the pelagic area 7 km from the shore, as described in MULIMBWA et al. (2014). The lake is more than 100 m deep here. Samples were concentrated to a volume of 40 to 60 ml, from which three 1 ml subsamples were taken after thorough mixing. Copepods in these subsamples were identified and counted under a microscope. The copepod taxa and various developmental stages (nauplii, copepodids, males, females, and females with eggs) were identified according to ALEKSEEV (2002). Calanoid copepods were represented by only one species, *Tropodiaptomus simplex*. The cyclopoid copepods were grouped into small and large size classes, the small one referring to all copepodid and adult stages of *Tropocyclops tenellus* (SARS, 1909) and the large one to those of *Mesocyclops aequatorialis* KIEFER, 1929. Naupliar stages of cyclopoid copepods were counted as one group and mainly represent *M. aequatorialis*.

Fish samples were taken twice a week from artisanal lift net fishing units at the time of landing. In the artisanal fishery in the northwestern part of

Lake Tanganyika, a fishing unit is composed of two or three wooden boats of 8.0 m x 1.4 m, lift net size with 16 m × 16 m mouth opening and 20 m depth. The mesh size of the nets is 8 – 10 mm in the upper four fifths and 6 – 7 mm in the lower one fifth. Each fishing unit uses 17 to 20 lamps and is operated by eight fishermen. With regard to *S. tanganicae* and *L. miodon* about a handful of fresh fish was taken as a sample from four fishing units. A minimum of 70 mm total length (TL) was considered, which corresponds to the minimal size at which these fishes are able to reproduce (ELLIS, 1971). In 2004-2005, 136 male *S. tanganicae*, 310 female *S. tanganicae*, 213 male *L. miodon*, and 243 female *L. miodon* were obtained. In 2007-2008, 128 male *S. tanganicae*, 275 female *S. tanganicae*, 192 male *L. miodon*, and 264 female *L. miodon* were included. Fish were measured and weighed, and their gonads were dissected and weighed to the nearest 0.01g. For 2007-2008, the gonads were inspected under a dissecting microscope and classified as mature (stage IV) or immature (stage I, II or III) according to a scale of gonad maturity based on gonad size and egg development (DE KIMPE, 1964; MICHA, 1973). Males were considered mature when testes were white and sperm ducts were filled with sperm; females were considered mature when ovaries were light yellow to orange and oviducts were filled with ovules. Individuals that had already reproduced (stage V) were not encountered.

Between August 2009 and July 2010, additional sampling was performed by an experimental fishing unit, targeting the larvae of *L. miodon*, which hatch on the sand in the shallow water, close to the shoreline (MATTHES, 1967; COULTER, 1970; PEARCE, 1985). Four different beaches (Kalundu Congo SEP (mouth of Rusozi River), Kamongola, mouth of Kalimabenge River, and CRH Guest house) were monitored for this purpose, from 6h30 to 7h30 in the morning. The larvae were sampled by two persons by trawling a mosquito net (width: 2 m; height: 1 m) over a distance of 50 m, keeping the lower part of the net close to the bottom and the upper part at the surface. A third person chased the fish larvae

TABLE 1

Average individual biomass of three copepod species (μg carbon) based on direct determinations with a carbon analyser (adapted from SARVALA et al., 1999).

Species	Tropodiaptomus simplex	Mesocyclops aequatorialis	Tropocyclops tenellus
Males	2.01	1	0.16
Females	2.95	2.281	0.183
Females with eggs	3.3	2.315	0.186
Copepodid	0.717	0.487	0.132
Nauplius	0.153	0.098	0.05

towards a central pocket. The total weight and the modal length of the larvae in samples were determined, and the weekly mean values across the four beaches were calculated.

Data analysis

Copepod counts were extrapolated to individuals per cubic meter, and two-week copepod abundances were calculated as the total number of copepod individuals per cubic meter. Monthly values were then calculated as the average of the two-week data. Individual carbon mass values, based on direct determinations of Tanganyika zooplankton, were derived from the literature (Table 1; SARVALA et al., 1999). Total sampled copepod biomass per month was calculated by multiplying the monthly abundance of each species and stage by the appropriate average individual mass.

Reproductive activities of the two clupeids were studied using the gonadosomatic index (GSI) of individuals larger than 70 mm TL. The GSI was defined as the percentage of gonad weight of total body weight. For 2007-2008, the monthly percentage of mature gonads was calculated as an additional measure of reproductive activity.

Student's t tests were used to test the differences in rainfall, and copepod abundances and biomass between the rainy season (October to April) and the dry season (May to September). ANOVA, followed by post hoc Tukey tests, was used to test the fluctuations between months for the GSI. As the variation in GSI between months might be influenced by cohort structure and size differences, month effects on GSI were also tested with an ANCOVA including total length as a covariate. For 2007-2008, a chi-square test was used to evaluate the significance of month-to-month fluctuations in the percentage of mature gonads.

Pearson correlations and linear regressions were calculated with the program package PAST (HAMMER et al., 2001) to examine the relationships between the monthly changes in clupeid GSI and variations in zooplankton food available. To check whether clupeid reproductive effort might simply reflect the availability of food, GSI was compared with the biomass of copepod prey during the concurrent and 1-3 previous months, both separately and as averaged combinations of 2-4 months. Further, to check whether the timing of clupeid reproduction was adjusted to optimise food availability for the larval and young fish, GSI was compared with the biomass of copepod food in the following month.

RESULTS

Rainfall and copepods

Total rainfall in 2004-2005 (1335 mm) was considerably higher than in 2007-2008 (814 mm). In 2004-2005, the monthly rainfall was high from December until May, and low from June until

October (Fig. 2A). In 2007-2008, a similar pattern with slightly different timing was observed with moderate to strong rainfall from February until May, moderate to weak rainfall from June to September, and again moderate to strong rainfall from October until January. Similar fluctuations were observed for total copepod biomass in 2007-2008 with high values in February, April
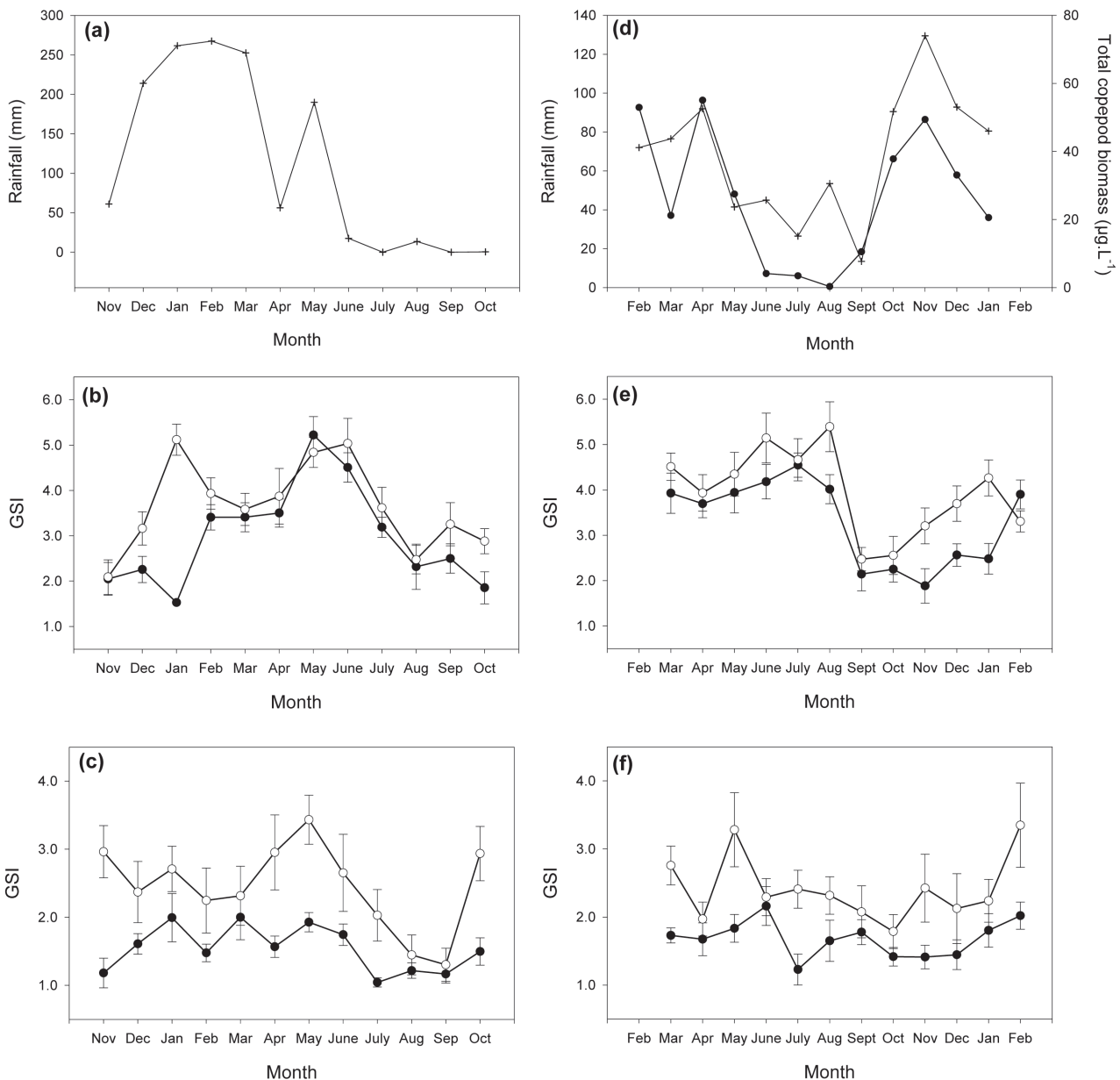

Fig. 2. – Monthly rainfall, total copepod biomass, and reproductive investment of two clupeid fishes in the northern end of Lake Tanganyika, from November 2004 until October 2005 (left) and from February 2007 until February 2008 (right). A) Average monthly rainfall (mm) in 2004-2005. B) Gonadosomatic index in males (black dots) and females (circles) of *Stolothrissa tanganicae* in 2004-2005. C) Gonadosomatic index in males (black dots) and females (circles) of *Limnothrissa miodon* in 2004-2005. D) Average monthly rainfall (left axis in mm; cross marks) and total copepod biomass (right axis in μg carbon L^{-1}; black dots) in 2007-2008 (data from MULIMBWA et al., 2014). E) Gonadosomatic index in males (black dots) and females (circles) of *Stolothrissa tanganicae* in 2007-2008. F) Gonadosomatic index in males (black dots) and females (circles) of *Limnothrissa miodon* in 2007-2008. Vertical bars represent standard errors.

TABLE 2

Differences between the rainy (October to April) and dry season (May to September) of 2007-2008 in rainfall and the abundances and biomasses of the main zooplankton categories and the total copepods (SE: standard error; C+A: copepodids and adults; Student's t-test assuming unequal variances; significant P-values in bold; n_{rainy} =7; n_{dry} = 5).

| Variable	Mean rainy season (SE)	Mean dry season (SE)	t	P
Rainfall (mm month^{-1})	90.5 (7.2)	36.0 (7.1)	5.39	**0.0003**
Copepod abundance (ind. L^{-1})				
Tropodiaptomus simplex C+A	6.7 (1.7)	1.3 (0.5)	3	**0.02**
Mesocyclops aequatorialis C+A	21.3 (8.3)	6.2 (4.1)	1.62	0.14
Tropocyclops tenellus C+A	3.5 (1.2)	1.2 (0.6)	1.71	0.13
Copepoda nauplii	97.9 (24.7)	22.1 (17.7)	2.49	**0.03**
Total Copepoda	129.3 (24.5)	30.7 (22.5)	2.97	**0.01**
Copepod biomass (µg carbon L^{-1})				
Tropodiaptomus simplex C+A	11.7 (3.6)	2.2 (0.8)	2.58	**0.04**
Mesocyclops aequatorialis C+A	16.1 (4.6)	4.5 (2.4)	2.26	**0.05**
Tropocyclops tenellus C+A	0.5 (0.2)	0.2 (0.1)	1.79	0.11
Copepoda nauplii	9.9 (2.5)	2.3 (1.8)	2.51	**0.03**
Total Copepoda	38.2 (5.4)	9.2 (4.9)	4.01	**0.002**
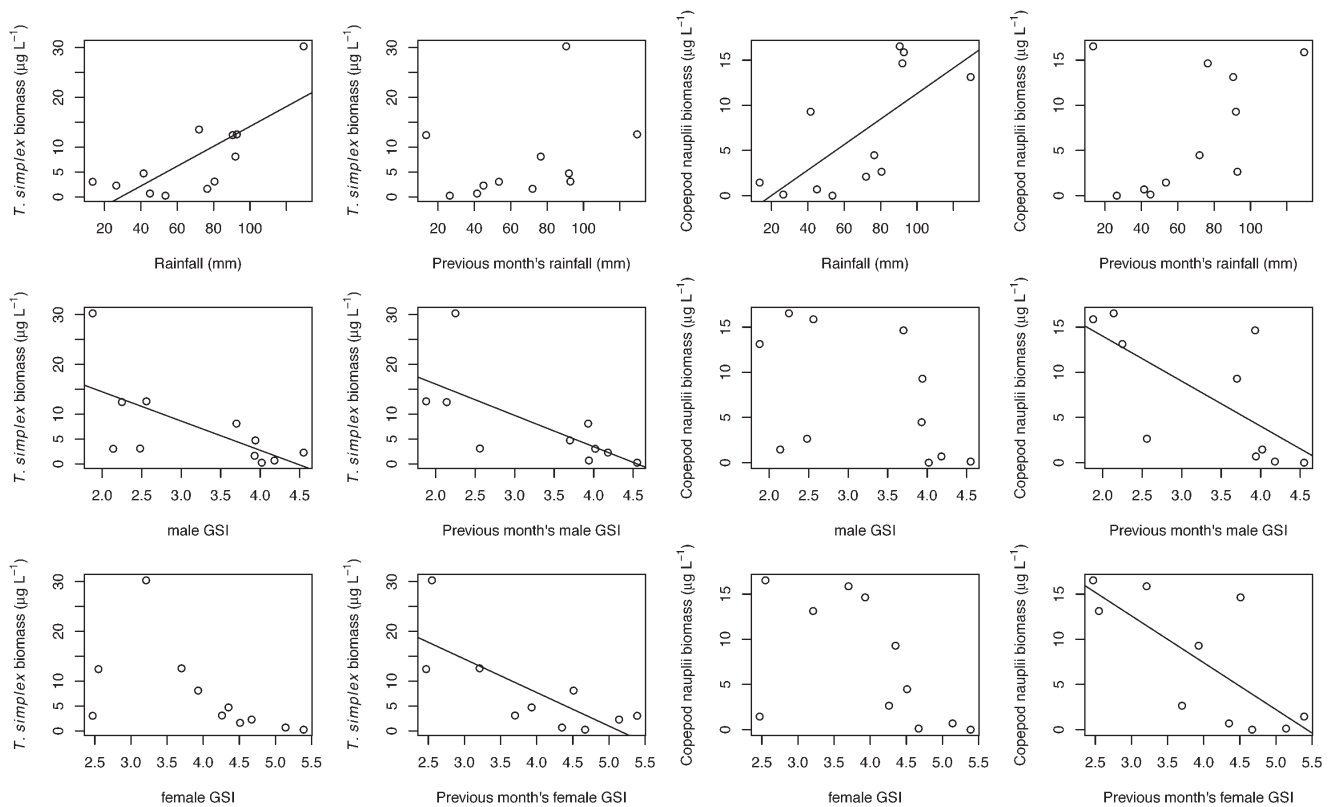
Fig. 3. – Rainfall and gonadosomatic index (GSI) in male and female *Stolothrissa tanganicae* in the concurrent and preceding month versus *T. simplex* copepodid and adult biomass and copepod nauplii biomass, from March 2007 until February 2008. Relationships marked with a regression line are significant.

TABLE 3

Mean GSI in the rainy season (October to April) and the dry season (May to September) and ANOVA/ANCOVA between months for males (m) and females (f) of two clupeid fishes. P-values in bold indicate significant differences between months before (ANOVA) and after (ANCOVA) controlling for total length. Note that the GSI was consistently higher in the dry season than in the rainy season for *S. tanganicae*, but not for *L. miodon*. See Figure 2 for month-to-month fluctuations in GSI. SE: standard error.

| Year	Species (sex)	Averages by season		ANOVA between months		ANCOVA between months	
		Mean rainy season (SE)	Mean dry season (SE)	F	p	F	p
2004-2005	*S. tanganicae* (m)	2.77 (0.15)	3.79 (0.20)	$F_{11,124}$=8.95	**< 0.0001**	$F_{11,123}$=9.89	**< 0.0001**
	S. tanganicae (f)	3.51 (0.15)	4.01 (0.22)	$F_{11,298}$=6.12	**< 0.0001**	$F_{11,297}$=5.95	**< 0.0001**
	L. miodon (m)	1.59 (0.08)	1.39 (0.07)	$F_{11,200}$=3.58	**0.0001**	$F_{11,199}$=3.63	**0.0001**
	L. miodon (f)	2.68 (0.16)	2.28 (0.19)	$F_{11,231}$=2.45	**0.0066**	$F_{11,230}$=2.44	**0.0067**
2007-2008	*S. tanganicae* (m)	2.91 (0.15)	3.83 (0.20)	$F_{11,112}$=6.36	**< 0.0001**	$F_{11,111}$=7.15	**< 0.0001**
	S. tanganicae (f)	3.65 (0.14)	4.26 (0.23)	$F_{11,263}$=5.65	**< 0.0001**	$F_{11,260}$=4.59	**< 0.0001**
	L. miodon (m)	1.64 (0.07)	1.79 (0.11)	$F_{11,180}$=1.25	0.2552	$F_{11,177}$=0.99	0.4607
	L. miodon (f)	2.36 (0.14)	2.34 (0.14)	$F_{11,252}$=1.38	0.1838	$F_{11,251}$=1.55	0.1149
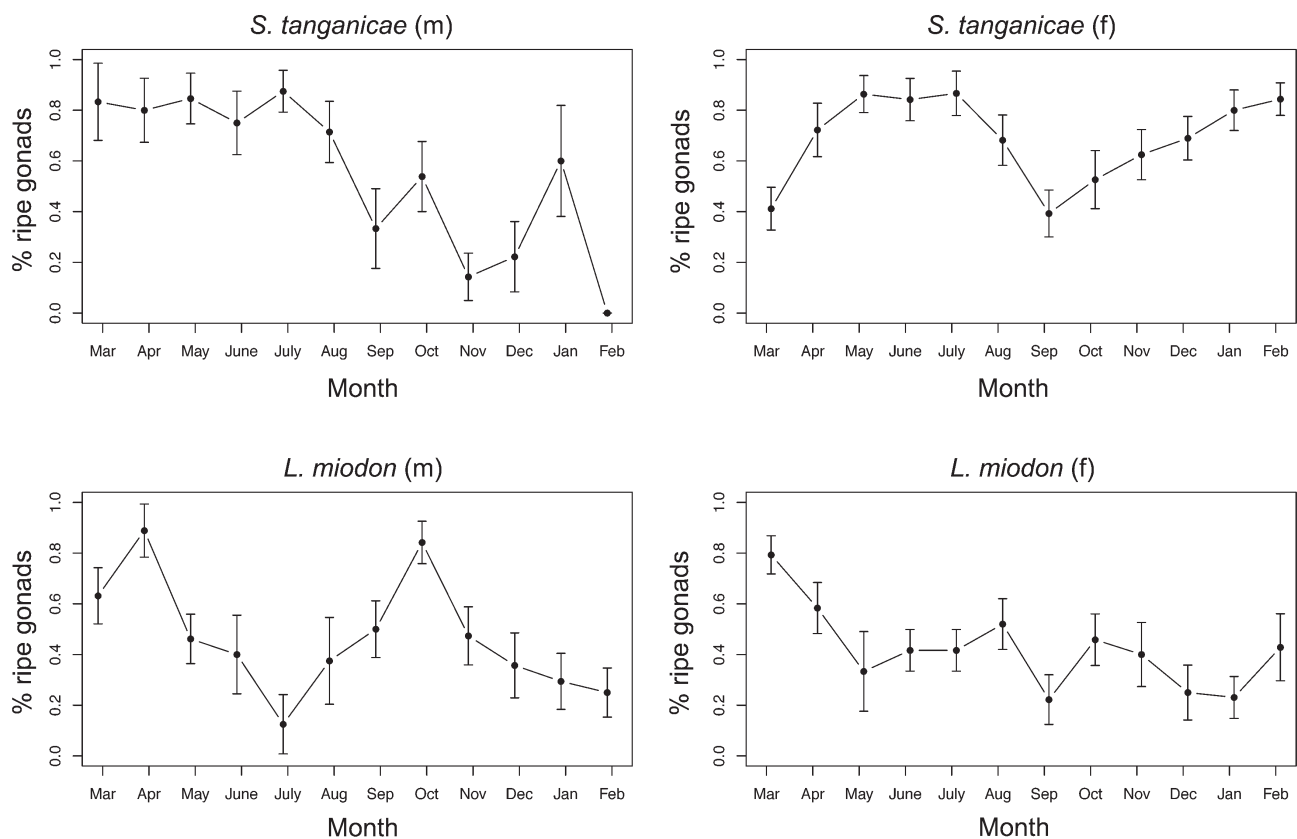
Fig. 4. – Percentage of individuals with mature gonads in males (m) and females (f) of *Stolothrissa tanganicae* and *Limnothrissa miodon*, from March 2007 until February 2008. Vertical bars represent standard errors.

and November, and low values from June until September (Fig. 2D). Differences between the rainy and dry seasons were statistically significant for rainfall, *M. aequatorialis* copepodid and adult biomass, and the abundance and biomass of *T. simplex* copepodids and adults, copepod nauplii and total copepods (Table 2). Accordingly, copepod biomass was positively correlated with the rainfall of the current month (rainfall vs. *T. simplex* copepodid and adult biomass: r = 0.76, p = 0.0039, df = 10, Fig. 3; rainfall vs. copepod nauplii biomass: r = 0.70, p = 0.0118, df = 10, Fig. 3; rainfall vs. total copepod biomass: r = 0.74, p = 0.0060, df= 10). In contrast, none of the copepod biomass categories was significantly correlated with the previous month's rainfall (Fig. 3).

Clupeid reproductive investment

Stolothrissa tanganicae – Males ranged between 72 mm and 103 mm TL (average: 87 mm), while females were 71-110 mm TL (average: 90.8 mm). In 2004-2005, male GSI fluctuated significantly between months, with high values in May and June and low values from November to January and August to October (Fig. 2B; Table 3). In 2007-2008, a broader peak was observed from March to August, with a significant drop towards September (Fig. 2E; Table 3). Female GSI also fluctuated significantly between months (Figs 2B, E, Table 3). In 2004-2005, values were generally high from January to July, with a peak in January and a second peak from May to June (Fig. 2B). In 2007-2008, female GSI was high from March to August with a steep drop to low values in September-October; a new peak was evident in January (Fig. 2E). In both sexes and both years, the differences in GSI between months remained significant when GSI was controlled for total length (ANCOVA; Table 3), indicating that GSI fluctuations between months were not or not exclusively due to shifts in cohort structure, but to differential reproductive investment. GSI was also consistently higher in the dry season than
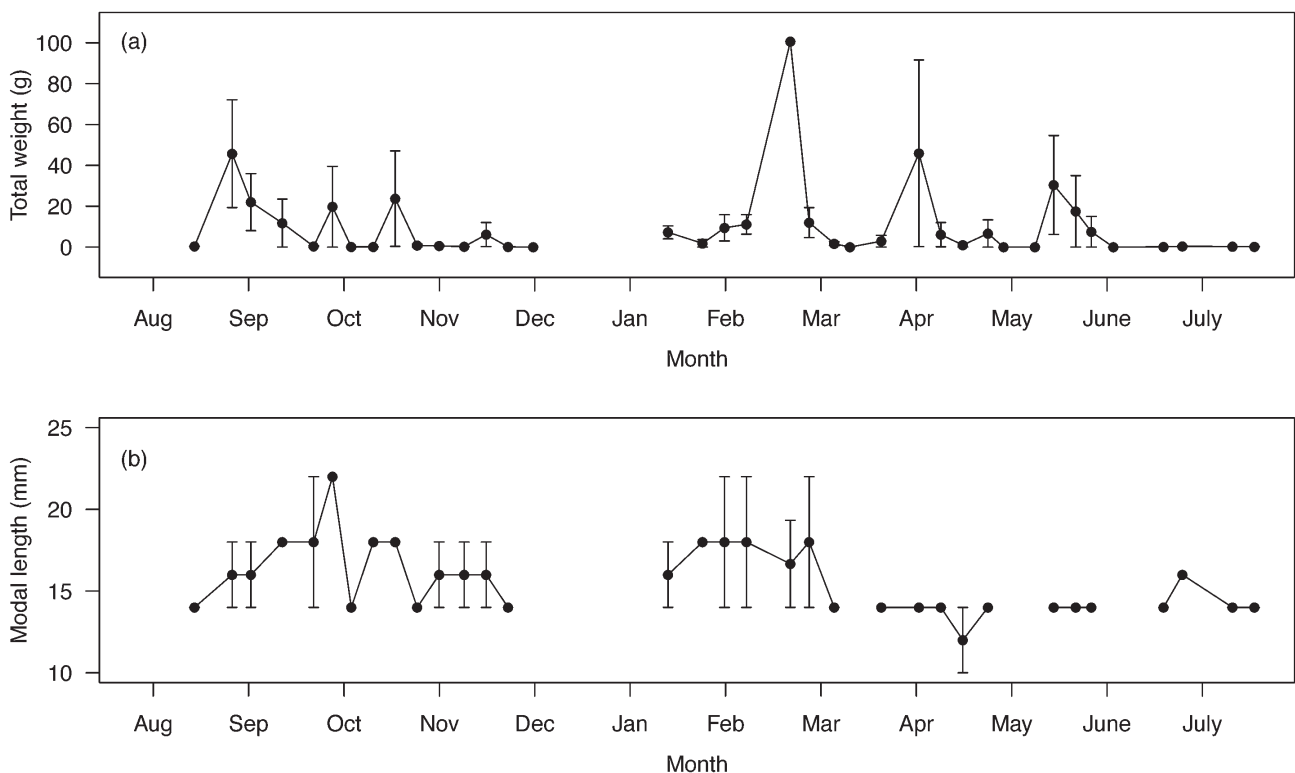

Fig. 5. – Seasonal changes in the weight (g) of the total catch and the modal length (mm) of *Limnothrissa miodon* larvae in the littoral samples between August 2009 and July 2010. Values represent the average of the captures at four different beaches. Vertical bars represent standard errors.

TABLE 4

Pearson correlations of clupeid GSI with the rainfall of the corresponding and the preceding month (combined data for 2004-2005 and 2007-2008). Stan = *S. tanganicae*, Lmio = *L. miodon*.

	Stan male	Stan female	Lmio male	Lmio female	df
Rainfall, same month	-0.061	0.167	0.408	0.198	21
Rainfall, preceding month	0.119	0.306	0.375	0.222	22

in the rainy season (Table 3). In 2007-2008, the percentage of males and females with mature gonads steeply decreased towards the end of the dry season, suggesting a major spawning peak in August-September (Fig. 4). These fluctuations were significant (males: $\chi^2 = 43.2$, p < 0.0001, df = 11; females: $\chi^2 = 37.6$, p < 0.0001, df = 11).

Limnothrissa miodon - Males ranged between 74 mm and 129 mm TL (average: 94.5 mm), while females were 75-136.4 mm TL (average: 100.8 mm). In 2004-2005, male GSI was high from January to June, and dropped significantly in July (Fig. 2C, Table 3). Female GSI showed a significant peak in November, May and October, and the lowest values in August-September
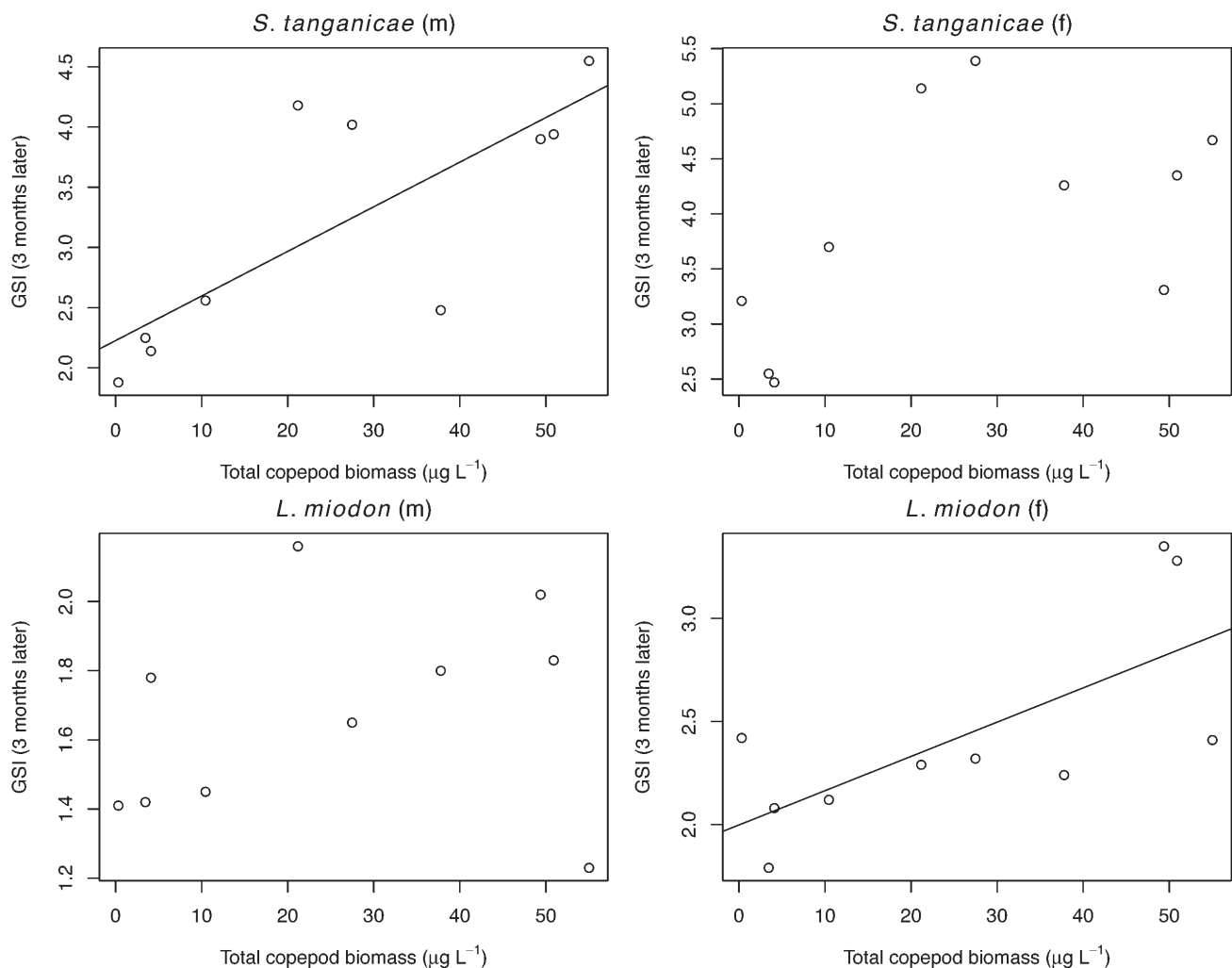

Fig. 6. – Total copepod biomass versus the average monthly gonadosomatic index (GSI) three months later in two clupeid fishes, from March 2007 until February 2008. Relationships marked with a regression line are significant.

(Fig. 2C, Table 3). In 2007-2008, male GSI showed a subtle peak in June, while for females reproductive activity peaked in March, May and February (Fig. 2F). However, none of the differences in 2007-2008 were statistically significant. None of these results changed when GSI was controlled for total length (ANCOVA; Table 3). In contrast to *S. tanganicae*, there was no consistent difference in GSI between the rainy season and the dry season across years and sexes (Table 3). In 2007-2008, the percentage of males with mature gonads peaked in April and October, while the highest percentage of females with mature gonads was observed in March (Fig. 4). These fluctuations were significant (males: χ^2 = 29.9, p = 0.0016, df = 11; females: χ^2 = 28.45, p = 0.0028, df = 11).

Weekly captures by an experimental fishing unit at four different beaches revealed that *L. miodon* larvae predominated in the rainy season (January to May), but were also abundant at the end of the dry season (August to September) (Fig. 5). The modal length of the larvae was, most of the time, less than 19 mm, suggesting that they were less than 1 month old (deduced from length growth curves in MULIMBWA et al., 2014).

Reproductive investment vs. rainfall and copepods

GSI versus rainfall - Clupeid GSI did not show significant correlation with the rainfall of the concurrent or the previous month (combined data for the years 2004-2005 and 2007-2008; Table 4).

GSI versus copepods in the corresponding and following month - In both clupeids, the monthly GSI showed no relationship with copepod biomass of the corresponding month (total copepod biomass or that of the separate zooplankton groups), except for a significant negative correlation between male *S. tanganicae* GSI and *T. simplex* copepodid and adult biomass (r=-0.649, p<0.05, df=9, Fig. 3), and between female *S. tanganicae* GSI and *T. tenellus* (r=-

0.723, p<0.05, df=9). In a similar vein, *S. tanganicae* GSI showed significant negative correlations with copepod biomass of the following month (male *S. tanganicae* vs. *T. simplex* copepodids and adults, and copepod nauplii: r=-0.687, p<0.05, Fig. 3; r=-0.696, p<0.05, Fig. 3, respectively, df=8; female *S. tanganicae* vs. *T. simplex* copepodids and adults, copepod nauplii and total copepods: r=-0.750, p~0.05, Fig. 3; r=-0.739, p<0.05, Fig. 3; r=-0.633, p<0.05; respectively, df=8).

GSI versus copepods of previous months - Reproductive investment in *S. tanganicae* was correlated with the food availability in the preceding months, as shown by significant correlations between average monthly GSI and copepod biomass three months earlier (male *S. tanganicae* vs. *M. aequatorialis* copepodids and adults: r=0.771, p<0.01 df=8; male *S. tanganicae* vs. total copepops: r=0.779, p<0.01 df=8, Fig. 6; female *S. tanganicae* vs. *M. aequatorialis* copepodids and adults: r=0.630, p~0.05, df=8). At this time lag, the GSI of female *L. miodon* also showed positive correlations with the biomass of *T. simplex* copepodids and adults (r= 0.800, p<0.01, df=8) as well as total copepods (r=0.702, p<0.05, df=8; Fig. 6). At other time lags and for the total copepod biomass integrated over preceding months, no significant correlations were observed (statistics not shown).

DISCUSSION

We investigated the timing of reproductive activities of two clupeid fishes (*S. tanganicae* and *L. miodon*) from the northern end of Lake Tanganyika (Bujumbura sub-basin) by comparing month-to-month fluctuations of the gonadosomatic index (GSI) with fluctuations in rainfall and the abundance of copepods. As copepods represent the main food source of larvae and juveniles of both species, but particularly *S. tanganicae* (MANNINI et al., 1996; LENSU, 1998; SARVALA et al., 2002; ISUMBISHO et al., 2004), it was expected that the main period of reproductive activity (as indicated by a significant drop in GSI

and in the percentage of ripe gonads) would precede or coincide with the rainy season, when the availability of copepods as a food source for larvae or juveniles is maximal (CHÈNÉ, 1975; DE IONGH et al., 1983; MGANA et al., 2014). We could confirm this expectation for *S. tanganicae* in two different years (2004-2005 and 2007-2008), but only in one year for *L. miodon* (2004-2005). However, we found no indications that the fishes actively synchronize their reproductive activities with this optimal period (see below). Instead, correlations between GSI and copepod abundance suggested that reproductive activities are related to the availability of copepods in the preceding months.

Rainfall and copepods

Seasonal development of copepod biomass in 2007-2008 was closely associated with the rainfall pattern, at least partly because the rainfall brings new nutrients into the lake, facilitating phytoplankton production (see discussion in MULIMBWA et al., 2014). In particular, the increasing food supply in early wet season is likely to have a profound effect on copepod abundance (NARITA et al., 1985; MULIMBWA, 1988, 1991; KURKI, et al., 1999). Overall, phytoplankton and zooplankton are assumed to be well correlated in Lake Tanganyika (COULTER, 1991). The realized zooplankton abundance, however, results from a balance between zooplankton production and its consumption by fish and invertebrate predators. For example, the low total copepod biomass noticed in dry seasons suggests a severe predation by *S. tanganicae* showing peak catches in July (ROEST, 1992; MULIMBWA, 2006; MULIMBWA et al., 2014). The dominant factor causing the high total copepod biomasses in the rainy season was likely to be the availability of phytoplankton combined with a moderate predation pressure. Comparisons of the monthly changes in copepod abundance with historical studies are difficult due to different methodologies used (RUFLI & CHAPMAN 1976; BURGIS, 1984), but the Lake Tanganyika Research (LTR) time series from the 1990s (KURKI, 1997) and the early 2000s

(MÖLSÄ et al., 2002) were based on compatible methods. In 1993-1996 and in 1999-2001, the seasonal changes in copepod biomass in the Bujumbura, Uvira and Kigoma sub-basins were highly variable with no consistent pattern relative to the dry and wet seasons (KURKI et al., 1999; MÖLSÄ et al., 2002; SARVALA et al., unpublished). The seasonality of copepods as a food source for the pelagic planktivorous fish thus varies considerably from year to year and between areas.

Clupeid reproductive investment

One of the investigated clupeid species, *S. tanganicae*, showed the highest mean values of the gonadosomatic index (GSI) in the dry season. An abrupt decline indicated that the main spawning took place a few weeks before the rainy season. Although the onset of the rainy season is accompanied by a steep increase in total copepod biomass, we have no indications that *S. tanganicae* adjusts its spawning strategy to optimize the survival of its offspring. First, it is unclear what kind of trigger the fish would use to do so. Rainfall and associated increased turbidity would be one potential trigger, but the main spawning clearly occurred before the first rains. Second, at the time of spawning food availability was still low, and hence not beneficial to the larvae that would hatch in 2-3 days (MATTHES, 1967) and likely start feeding within a week. Arguably, the timing of spawning could still be beneficial in a later developmental stage, but the benefit for the larvae as the most vulnerable stage would be larger. In the mid-1990s, MANNINI et al. (1996) observed peak values for GSI at intervals of 3-4 months in female *S. tanganicae* in the north part of Lake Tanganyika. A similar periodicity in female *S. tanganicae* was observed in this study, although for both 2004-2005 and 2007-2008 the intervals seemed to approach five months. Length-frequency distributions for 2007-2008, however, clearly indicated four annual cohorts (MULIMBWA et al., 2014), but not all of those were equally strong, and it may be difficult to

observe any significant changes in GSI related to the weaker cohorts.

In contrast to *S. tanganicae*, and especially in 2007-2008, the reproductive activity of *L. miodon* did not suggest a main spawning event, consistent with observations in the mid-1990s by MANNINI et al. (1996). It hence seems that *L. miodon* is spreading its reproductive activities over longer periods of time. The reason for the variation between years remains unclear; the year 2007-2008 had lower rainfall than 2004-2005 (see Fig. 2A vs. 2D), but there were no significant differences in reproductive investment (results not shown). Repeated spawning of clupeids is an adaptation to an unstable aquatic ecosystem where considerable variation in fishing and natural mortalities causes some of the eggs to die (COULTER, 1961). The prolonged spawning provides stable replacement by successive cohorts. However, this is only possible when there is a long period of adequate food supply for the larvae. *L. miodon* might obtain such supply in the littoral zone, where food is abundant year-round (COULTER, 1991).

Reproductive investment vs rainfall and copepods

The year-to-year and spatial variation in the seasonality of copepods in Lake Tanganyika is expected to lead to corresponding variability in fish reproduction. In this study, the dependence of reproductive activities of both clupeids on the copepod food source was suggested by a positive correlation between GSI and the amount of copepods available three months before. Reproductive effort in both clupeids might therefore simply reflect the amount of available food in previous months. Conversely, but only for *S. tanganicae*, we observed a negative correlation between GSI and copepod abundance in the corresponding and following month. This suggests a predation effect by emerging *S. tanganicae* cohorts on the copepods. Although rainfall was also correlated with copepod abundance, this positive relationship

was only observed in the concurrent month, consistent with the short generation times of planktonic copepods. In contrast, the negative effect of predation by *S. tanganicae* lasts longer as the fish are more long-lived and the total food consumption of a fish cohort likely peaks during the first few months of life (MANNINI et al., 1996).

Changes in fishing pressure, climate change (including changes in rainfall, temperature and wind), or changes in environmental conditions in the drainage area (e.g. deforestation) might all lead to changes in the predator-prey dynamics between clupeids and copepods. Among these possible effects, changes in fishing pressure are relatively well documented (see Introduction). Overfishing in recent years might have decreased the effect of predation on copepods, such that correlations with rainfall and copepods should become predominant. This might explain why in the present situation of depleted fish stocks (e.g. MULIMBWA, 2006) we observed a clear correlation between rainfall and copepods, whereas this was not the case in the past (KURKI et al., 1999; MÖLSÄ et al., 2002; SARVALA et al., unpublished) when the fish stocks were stronger and thus predation effects were much larger. Nevertheless, predation effects could still be observed even in our data.

CONCLUSIONS

Copepod zooplankton abundance was very high in the rainy season, providing an opportunity for larval clupeids to maximize survival rate. However, clupeid spawning activities did not seem to be adjusted to allow the larvae to optimally benefit from this food source. While *S. tanganicae* seemed to concentrate its reproductive activities at the end of the dry season, there was no well-defined spawning season in *L. miodon*. However, in both species the investment in reproduction seemed to depend on the availability of copepods three months earlier. We conclude that apart from some common elements, clupeid species may

significantly differ in reproductive strategies. Further investigation should highlight the variation in clupeid reproductive activities across species and years, as well as the relationship with the abundance of zooplankton.

The observed differences between clupeid species are important from a management perspective. A long period of adequate food supply may be very important to support reproductive activities in species such as *L. miodon*, in order to maintain its intense exploitation at a sustainable level. This requires that the environmental conditions of the lake and its adjacent regions be preserved. As a littoral spawner (Matthes, 1967; Pearce, 1985; Coulter, 1970), *L. miodon* is particularly vulnerable to silting caused by soil erosion in the drainage area. Although the pelagically-spawning *S. tanganicae* is less susceptible to such changes, increased turbidity during its peak reproductive activities in the rainy season might be harmful. Thus even this species may benefit from reforestation that would help to preserve and restore the natural equilibrium of the lake, promoting the survival and growth of its copepod prey.

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