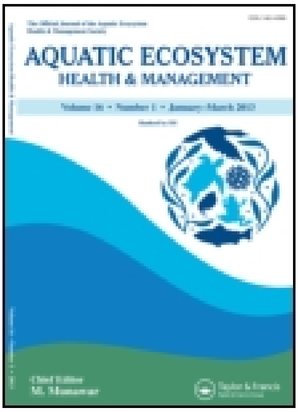

Aquatic Ecosystem Health & Management
Publication details, including instructions for authors and subscription information:
http://www.tandfonline.com/loi/uaem20

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Published online: 18 Mar 2014.

AQUATIC ECOSYSTEM
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Seasonal changes in the pelagic catch of two clupeid zooplanktivores in relation to the abundance of copepod zooplankton in the northern end of Lake Tanganyika

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*Catches of clupeid fish were recorded twice a week from February 2007 to May 2008 in the northern end of Lake Tanganyika, and allocated to species (*Stolothrissa tanganicae *and* Limnothrissa miodon*) according to representative catch samples from ten artisanal lift-net fishing units. In each sample, clupeids were measured and weighed for length frequency analysis. Age was estimated from length growth curves based on otolith weight. Copepod zooplankton was sampled twice a month from February 2007 to January 2008. Peaks of copepod zooplankton were recorded in the rainy season, and there was overall a tight positive correlation between monthly rainfall and copepod biomass. The clupeids appeared in the catch at 30–50 mm length when they were two–three (*S. tanganicae*) or three–four months old (*L. miodon*). For* S. tanganicae*, three catch peaks were due to cohorts born when copepod food was abundant, but one catch peak was due to a cohort which originated in the dry season when copepods were scarce. Likewise, two of the* L. miodon *cohorts giving rise to high catches likely originated from the rainy season when food was abundant, but two cohorts apparently originated from the dry season with low food conditions. The success of several cohorts of both clupeids therefore seems to be linked to rainfall and abundance of copepods, but sometimes strong cohorts could arise even under poor food conditions. Both species were recruited in the catch far before the age of maturity, making them vulnerable to overfishing.*

Keywords: catch per unit effort, foodweb, pelagic fish, planktivorous fish, *Stolothrissa tanganicae*, *Limnothrissa miodon*, tropical lake

Introduction

Lake Tanganyika is ca. 9–12 million years old (Coulter, 1991; Cohen et al., 1993b) and is the second largest and deepest freshwater body in the world. More than 1200 species have been identified in this lake, classifying it at second position in biodiversity (Cohen et al., 1993a). Among the main groups, the fishes show a high degree of biodiversity (Van Steenberge et al., 2011).

The clupeid fish production is a vital source of nutritional, economic and social well-being for at

Aquatic Ecosystem Health & Management, 17(1):25–33, 2014. Copyright © 2014 AEHMS. ISSN: 1463-4988 print / 1539-4077 online
DOI: 10.1080/14634988.2014.883896

least 10 million people dwelling in the regions adjacent to Lake Tanganyika (Mölsä et al., 1999). The clupeids *Stolothrissa tanganicae* Regan 1917 and *Limnothrissa miodon* (Boulenger 1906) account for 60% of the total pelagic commercial fish catches from Lake Tanganyika (Mölsä et al., 1999), and in the northern end their share is more than 90% (Mulimbwa, 2006). For all species together, annual harvest levels have been estimated to vary in the range of 165,000–200,000 tons, volumes that translate into annual earnings of tens of millions of US dollars (Mölsä et al., 1999).

Recent statistics from Bujumbura sub-basin show that the catch per unit effort is decreasing probably due to excessive fishing pressure (Mulimbwa, 2006). The highest fishing effort per km of shoreline is found in the northern part near Uvira due to high densities of lift nets and traditional units (Mölsä et al., 1999). These alarming trends prompted many studies on fish biology (Plisnier et al., 2009) and fisheries management (Reynolds et al., 2002), but the important links between zooplankton prey and clupeid recruitment have not been properly examined.

Larval and juvenile clupeids in Lake Tanganyika feed essentially on copepod zooplankton with marked preference for larger organisms when available (Mannini et al., 1996; Sarvala et al., 2002; Isumbisho et al., 2004). A major prey of clupeids is the calanoid copepod *Tropodiaptomus simplex* (Sars 1909), and e.g. Chèné (1975) found that *S. tanganicae* (length 65–81 mm) caught close to Bujumbura fed mostly on such calanoids. The spawning activities were highest in the rainy season although some reproduction seems to continue throughout the year (overview of earlier reports by Coulter, 1991; Mulimbwa and Shirakihara, 1994; Mannini et al., 1996).

This work aims to assess the relationship between the seasonal changes in abundance of copepod zooplankton and the commercial catch of the two clupeids (*S. tanganicae* and *L. miodon*) in the northern end of Lake Tanganyika.

Materials and Methods

Fishery biological and copepod zooplankton data were obtained from the Bujumbura sub-basin in the northern end of Lake Tanganyika (03° 28′ S and 29° 17′ E) from February 2007 to January 2008 (fisheries data up to May 2008). Rainfall data were collected at the Hydrobiological Research Center (C. R. H.) in Uvira at the extreme north-western corner of the lake. Daily precipitation values were summed up on a monthly basis. Copepod zooplankton was sampled twice per month between 7 h 00 and 9 h 00 from eight layers (0–5; 5–10; 10–15; 15–20; 20–30; 30–50; 50–75; 75–100 m depth) using a closing net with an opening of 25 cm diameter and 100 μm mesh size. The hauling speed was less than 0.5 m s^{-1}. Samples were concentrated to a volume of 40 to 60 ml, and preserved in 4% formaldehyde. In the laboratory, after thorough mixing, three 1 ml sub-samples were taken for examination under a microscope. The copepod groups and various developmental stages were identified according to Alekseev (2002). Counts were extrapolated to densities per cubic metre. Individual carbon mass values, based on direct determinations on Tanganyika zooplankton, were obtained from the literature (Sarvala et al., 1999). Total copepod biomass per month was calculated by multiplying the monthly densities of each species and stage by the appropriate average individual mass.

Fishery data were collected at a landing site with a large number of fishing units. Samples were taken twice a week from ten artisanal lift net fishing units at the time of landing. With regard to *S. tanganicae* and *L. miodon* a handful (>30) of fresh fish was taken as a sample from 7–10 fishing units. Samples were sorted by species, and the fish were measured for length frequency analysis. Daily total catches of both clupeids (*S. tanganicae* and *L. miodon*) were weighed from each fishing artisanal unit. The total catch per unit effort (CPUE) was calculated by dividing the total catch (kg) by the number of artisanal lift nets. The CPUE by species was estimated by extrapolation from fish species proportions in samples to total catch.

To obtain growth curves for approximate ageing of the clupeids, the otoliths of 260 *S. tanganicae* and 244 *L. miodon* collected from the study area in 2004-2005 were weighed with a microbalance (dry weight at 20°C). The age of these fish was then estimated using the relationship between otolith dry weight and age based on counts of daily rings, as established by Ahonen (2001). These ages and measured lengths of each fish were then combined into length growth curves that were used to estimate the age of the clupeids collected in 2007–2008 when no otolith samples were available.

Relationships between zooplankton biomass and rainfall were examined with linear regression (Microsoft Excel statistics module). Zooplankton was

Table 1. Regressions of the biomass of each major zooplankton group on the same month's rainfall.

Taxon	b	R^2	$F_{1,10}$	P
Total copepods	0.44	0.55	12.03	0.01
M. aequatorialis	0.23	0.31	4.42	0.06
T. simplex	0.20	0.56	12.82	0.01
Small cyclopoids	0.00	0.03	0.30	0.60
Copepod nauplii	0.14	0.49	9.43	0.01

compared with rainfall of the same month and that of the 1–3 preceding months. Likewise, fish catches were regressed on the zooplankton prey biomass of the current or the previous 1–5 (*S. tanganicae*) or 1–8 (*L. miodon*) months, or on the average zooplankton biomass of the current and preceding two or three months. Finally, three-month running averages of fish catches were regressed on the corresponding average zooplankton biomass.

Results

Rainfall peaked in February–April and October–December (Figure 1a), and the peaks of total copepod biomass (February, April and November) coincided with the periods of high rainfall (Figure 1b). Overall, copepod biomass was positively correlated with the rainfall of the current month (Table 1); correlations with the rainfall of the previous or earlier months were not significant (statistics not shown). Biomass-rainfall correlation was highest for *Tropodiaptomus simplex*, but also significant for copepod nauplii, and close to significance for *Mesocyclops aequatorialis* Kiefer 1929 (Table 1).

The monthly catches of clupeids fluctuated over the period of our study, with peaks in July and October 2007 and April–May 2008, mainly determined by the catches of *S. tanganicae* (Figure 1c). The catches of *L. miodon* showed slightly higher peaks in June and December 2007 and March and May 2008, but did not change the general pattern of the total clupeid catch fluctuations (Figure 1c).

The modal successions in the length frequency distributions of *S. tanganicae* were similar to those reported by Mölsä et al. (2002) from the northern end of Lake Tanganyika, and indicated the growth of five successive cohorts between February 2007 and May 2008 (Figure 2). *S. tanganicae* appeared in the catch at 30–50 mm length (Figure 2), when they were about two or three months old (Figure 3). Each peak in the catches could be linked with the appearance of a new cohort. *L. miodon* appeared in the catch at the length of 40–50 mm, or at the age of four to five months (Figure 3), but mostly the catches consisted of 80–100 mm long individuals, with no possibility to trace cohort development (Figure 2).

The strong *S. tanganicae* cohort indicated by high catches in July 2007 (modal length 40–60 mm) likely originated in April when the copepods were abundant, but that of October (similar length) was born in the dry season when copepods were scarce. The cohort responsible for the moderate peak in *S. tanganicae* catches in January–February 2008 (modal length 32–58 mm) was likely born in November 2007 during the copepod biomass peak. The strong catch peak in April–May 2008 (modal length 42–58 mm) was probably linked to a cohort born in January-February 2008 when the copepod biomass was still moderately high (*M. aequatorialis* only; *T. simplex* biomass was steeply declining; zooplankton data only up to January 2008). Because of this variability, the regressions between *S. tanganicae* catches and zooplankton biomass at 0–5 month time lag were not significant, and the same applied to the regressions with 3-month lag between *S. tanganicae* catch and the major zooplankton taxa (Table 2). Even the regressions of *S. tanganicae* catches on the average copepod biomass during the concurrent and two or three previous months (i.e. during the whole cohort life preceding its harvesting) remained non-significant (3-month period: $b = -0.89$, $R^2 = 0.13$, $F_{1,8} = 1.21$, $P = 0.30$; 4-month period: $b = -0.48$, $R^2 = 0.02$, $F_{1,7} = 0.17$, $P = 0.70$). Only the regression between the 3-month averages of both *S. tanganicae* catches and copepod biomass reached significance ($b = -0.63$, $R^2 = 0.43$, $F_{1,8} = 5.93$, $P = 0.04$), but the slope was negative, suggesting that predation by fish tends to reduce the abundance of zooplankton prey.

The two cohorts causing the peak catches of *L. miodon* in June and December 2007 were then approximately 8 months old (modal length about 90 mm), thus presumably originating from the rainy season when zooplankton food was abundant. However, the weaker peaks of *L. miodon* in March and May 2008 were based on fish born in June and September 2007, i.e. during the copepod biomass minimum of the dry season, and this situation would hold even if the age at capture would have been 9–10 instead of 8 months. Also for *L. miodon*, none of the regressions between monthly catches and zooplankton biomass with 0–8 month lag were significant (Table 3).

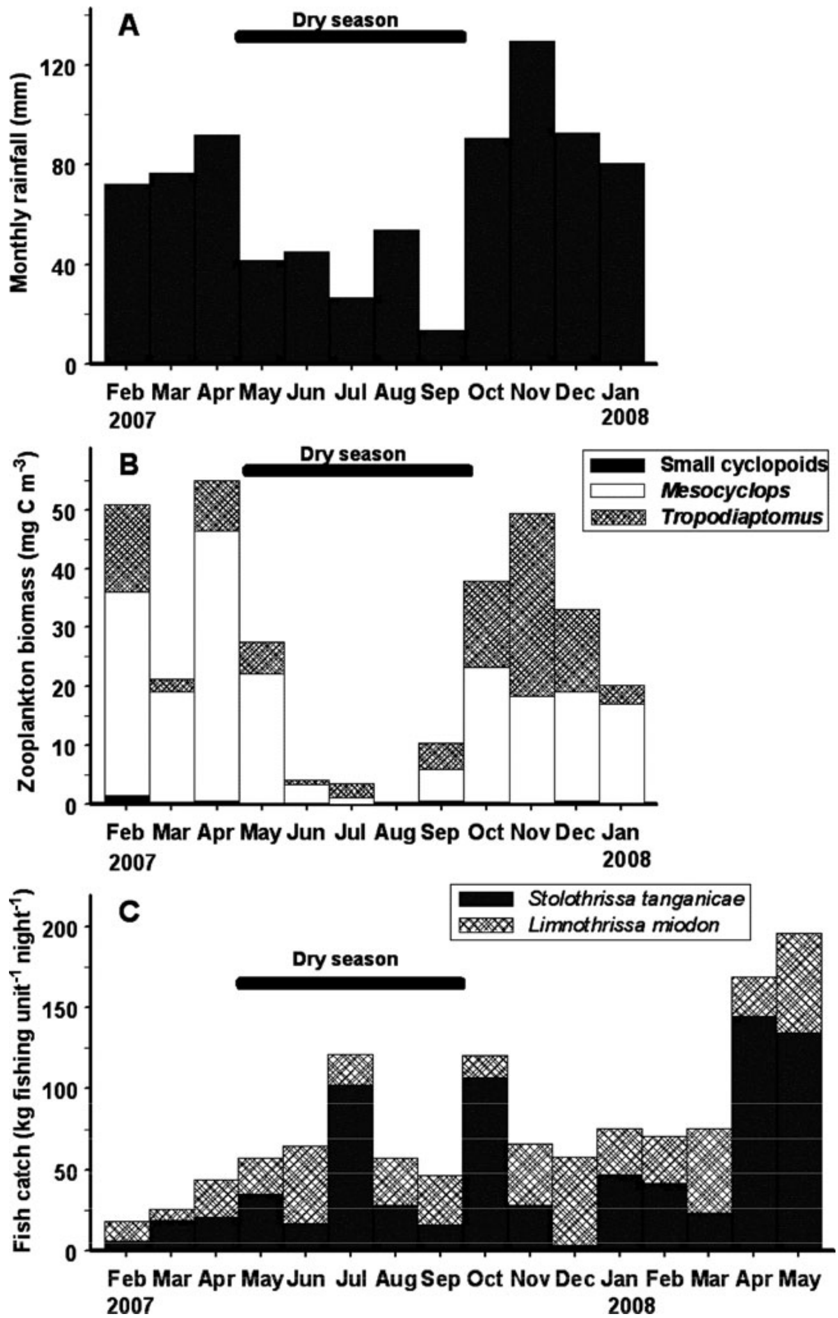

Figure 1. Monthly rainfall (a), copepod zooplankton biomass (b), and unit catches of *S. tanganicae* and *L. miodon* (c) in the northern end of Lake Tanganyika from February 2007 until May 2008 (small cyclopoids = *Tropocyclops tenellus*; rainfall and zooplankton data lacking for February–May 2008).

Discussion

Copepod biomass was high in the wet season with one early (November) and two late peaks (February, April). The November peak corresponds to the first rains after the dry season. The rainfall brings new nutrients into the lake, partly causing phytoplankton blooms (Langenberg et al., 2003a). Particularly, the increased riverine input through the Rusizi delta, together with simultaneous changes in thermal

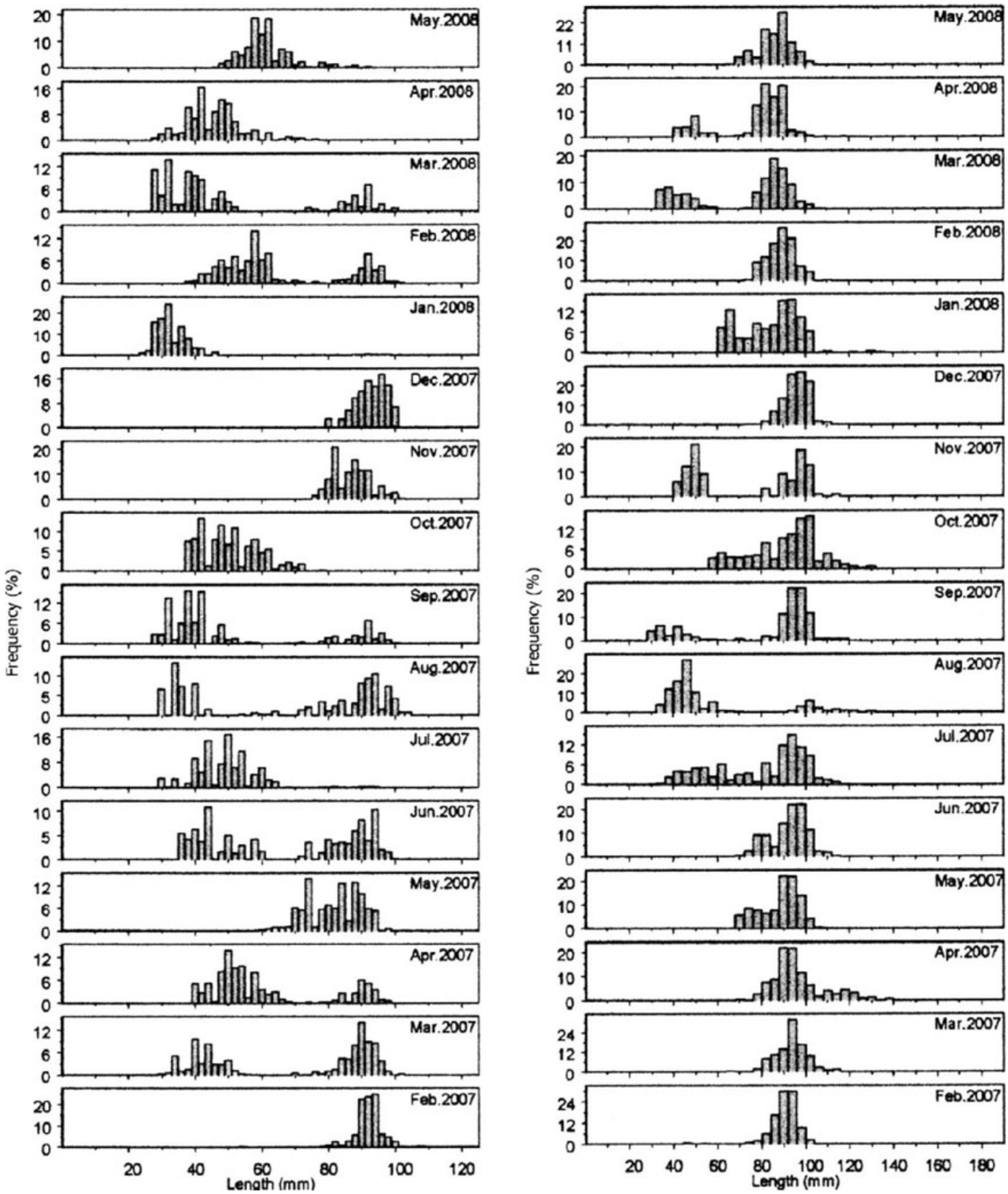

Figure 2. Monthly length frequency distributions of *S. tanganicae* (left) and *L. miodon* (right) in the northern end of Lake Tanganyika from February 2007 to May 2008.

stratification and oxygen conditions may then augment the availability of nutrients (Plisnier et al., 1999; Langenberg et al., 2003b, 2008). Phytoplankton reacts to nutrient inputs within days (Corman et al., 2010), and the generation times of zooplankton are such that the zooplankton response to changes in phytoplankton can be expected within weeks (Hyvönen, 1997). This is consistent with our observation that copepod biomass showed clearly highest (and the only significant) correlation with

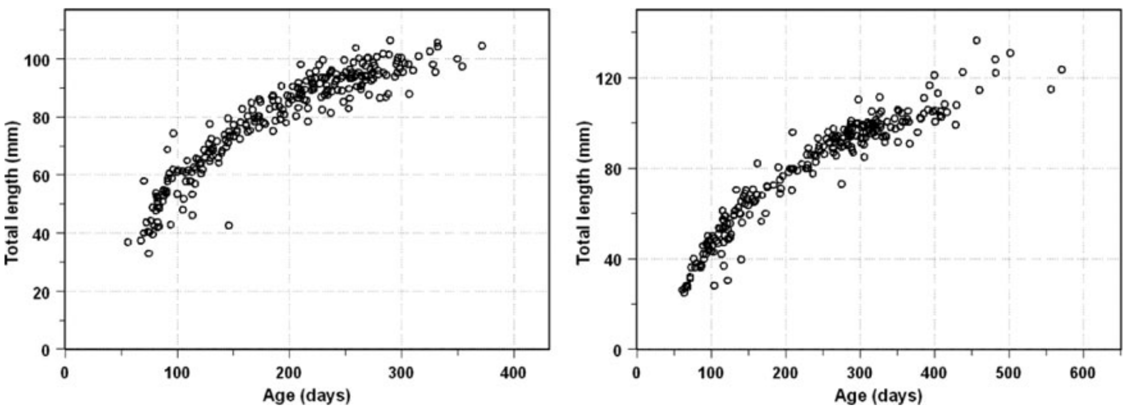

Figure 3. Length vs. age in *S. tanganicae* (left) and *L. miodon* (right) in the northern end of Lake Tanganyika in 2004–2005 (ages derived from otolith weight).

the rainfall of the current month, the correlation quickly fading away with increasing time lag. The increasing food supply in early wet season evidently has a profound effect on copepod abundance (Narita et al., 1985; Mulimbwa, 1988, 1991; Kurki, et al., 1999), but for the late wet season the link between phytoplankton food and copepod abundance is less clear.

Fish cohort strength is often determined by food availability, which affects the survival of the young fish and consequently the later catch. Of the major pelagic species in Lake Tanganyika, *S. tanganicae* is to the greatest extent dependent on copepod zooplankton, and, as a short-lived species, could be thought to closely track its food resource levels (Mölsä et al., 2002). We can therefore expect that phytoplankton blooms promoting zooplankton increase would enhance the abundance of this species in Lake Tanganyika. In their seasonal data from the Kigoma area, Kimirei and Mgaya (2007) indeed showed a positive correlation between *S. tanganicae* catches and concurrent phytoplankton chlorophyll. Likewise, for the Tanzanian and Zambian sides of the lake, Plisnier et al. (2009) observed spatial and temporal correlations between phytoplankton blooms and the abundance of *S. tanganicae*. Neither of these papers did investigate the link in between, i.e. copepod abundance, but Kurki

Table 2. Regressions of monthly *Stolothrissa tanganicae* CPUE on total copepod biomass with different time lags (total copepod biomass months preceding *S. tanganicae* months), and of *S. tanganicae* CPUE on the biomass of the major zooplankton groups at 3-month time lag.

Lagged regressions: Lag (months)	b	R^2	F	P	df
0	−0.32	0.03	0.34	0.58	1, 10
1	−0.75	0.19	2.40	0.15	1, 10
2	−0.46	0.08	0.82	0.39	1, 10
3	0.26	0.01	0.13	0.73	1, 10
4	−0.44	0.03	0.30	0.60	1, 10
5	1.14	0.21	2.33	0.16	1, 9
Regressions with 3-month time lag Taxon	b	R^2	$F_{1,10}$	P	
M. aequatorialis	0.72	0.05	0.53	0.48	
T. simplex	−0.43	0.01	0.08	0.79	
Small cyclopoids	−26.81	0.05	0.55	0.48	
Copepod nauplii	0.04	0.00	0.00	0.99	

Table 3. Regressions of monthly *Limnothrissa miodon* CPUE on total copepod biomass with different time lags (total copepod biomass months preceding *L. miodon* months).

Lagged regressions: Lag (months)	b	R^2	F	P	df
0	−0.11	0.02	0.25	0.63	1, 10
1	0.10	0.02	0.22	0.65	1, 10
2	0.19	0.08	0.86	0.38	1, 10
3	−0.17	0.06	0.64	0.44	1, 10
4	0.08	0.01	0.10	0.75	1, 10
5	−0.15	0.04	0.39	0.55	1, 9
6	−0.15	0.05	0.38	0.55	1, 8
7	0.14	0.03	0.25	0.63	1, 7
8	−0.09	0.01	0.08	0.79	1, 6

(1998) indicated that in the south basin of Lake Tanganyika, experimental trawl catches of pelagic fish were positively correlated with postnaupliar copepod abundance. All of these correlations, however, refer to concurrent abundances of clupeids and plankton, and therefore only indicate behavioural aggregation of pelagic clupeids to densest plankton patches. Interestingly, in our data fish catches were not correlated with concurrent zooplankton abundance, precluding even such aggregation.

Our data revealed low support for resource-driven control of clupeid production by plankton production, as there was no significant correlation between *S. tanganicae* and *L. miodon* catch and copepod abundance with any reasonable time lag, not even when using the average zooplankton biomass during the cohort life. Even if the correlation between 3-month running averages of *S. tanganicae* catches and copepod biomass was significant as in Mölsä et al. (2002), it did not in our case support the resource-driven control hypothesis because the correlation was negative. However, when examining the cohort histories one by one, a slightly different view arises. Of the strong cohorts of *S. tanganicae*, identified on the basis of the high catches, that of July likely originated in April when the abundance of prey zooplankton was high and cohort success thus expected. Likewise, the cohorts responsible for high catches in January–February and April–May 2008 were born when zooplankton was at least moderately abundant. The high October catches are more difficult to explain, because this cohort was born at the time of the seasonally lowest zooplankton abundance in June–July. However, this latter cohort might be considered as the offspring of an earlier strong cohort appearing as adults in May–June, and thus originating in the wet season (Figure 2); in fish (and also other) populations a strong cohort can often give rise even to several successive strong cohorts, the effect gradually fading away with time (Townsend, 1989; Jansen et al., 1990).

The abundance fluctuation of *L. miodon* cohorts had less influence on the total clupeid catches. This is due to the lower abundance of the species, but also reflects its different spatial distribution. The fish samples were collected from artisanal fishing units which operated in the pelagic zone. *L. miodon* is reported to spend a part of its life in the littoral area at larval and sub-adult stages and migrate to pelagic area later as it grows (overview by Coulter, 1991). Therefore, a major proportion of *L. miodon* may have resided in the littoral where sampling was not done. Two of the strong *L. miodon* cohorts likely originated in the rainy season when food was abundant, but two cohorts apparently originated from the dry season and low food conditions.

Conclusions

For both clupeids, even if correlation does not necessarily reflect causality, the success of several cohorts thus seems to be linked to rainfall and abundance of copepods, but sometimes strong cohorts could arise even under poor food conditions. The successful development of such cohorts shows that food availability–although low–was actually not limiting the growth and survival of clupeid larvae at those times. This indicates further that the fish population then remained below the carrying capacity due to other causes, possibly the intensive fishery documented by Mulimbwa (2006), or some environmental factors; control by predation does not seem likely in the recent years as the predatory fish have long been scarce in the north end of Lake Tanganyika (van Zwieten et al., 2002; Mulimbwa, 2006). The absence of any positive correlations between clupeid catches and zooplankton food supports this suggestion. Importantly, the clupeid sardines appeared in the catch from an age of 2–4 months onwards. This is far before the age of maturity, and hence makes them vulnerable to overfishing. Enhanced understanding of the mechanisms regulating fish recruitment in Lake Tanganyika is desperately needed for a sustainable management of the fishery under the changing climate.

Acknowledgements

We thank the scientific staff of the Hydrobiological Center for Research (C.R.H.) for field support, and the Lake Tanganyika Authority for covering publication costs. Research was sponsored by Belgian Technical Cooperation to N'sibula Mulimbwa, by University of Turku to Jouko Sarvala and by the Research Foundation - Flanders (FWO grant project G.0553.10) and a EU Marie-Curie Fellowship (IEF 300256) to Joost Raeymaekers.

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