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Size, diversity, dominance and trophic structures of the fish community in a tropical lake: a case study for the Sinazongwe area, Lake Kariba, Zambia

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Abstract – This study investigated the size, diversity, dominance and trophic structures of the exploited inshore fish community of the Sinazongwe area, Lake Kariba, Zambia, for the period 1980-1995. It was based on fish records of scientific gillnet surveys and on data available in the literature. The size and diversity spectra exhibited, like those of exploited demersal marine fish communities, regular decreasing patterns, indicative of high fish numbers and diversity in smaller sizes and vice versa among larger sizes. The size spectra patterns were recurrent from year to year and well fitted by quadratic functions. The diversity (Shannon index) and dominance (J' index) decreased and increased linearly, respectively, with fish length. Diversity for larger lengths has decreased as evidenced by the annual variations of diversity spectra's slopes. The abundance-biomass comparison plots indicated years of undisturbed, strongly and moderately stressed fish community. The proportions of predators, especially of *Hydrocynus vittatus*, and the mean trophic level decreased linearly over years. The average diversity trophic spectra remained unchanged. The mean abundance and biomass trophic spectra indicated a top-predator controlled community over 1980-1984, and vice versa thereafter. The trophic structure descriptors better captured the fish community changes under increasing fishing pressure and revealed for the first time the "fishing down marine food webs" effects for Lake Kariba. The community attributes studied are potentially promising alternatives for the assessment and management of tropical exploited freshwater fish communities.

Key words: Inshore fish community structures / Trophic level / Fishing effects / Lake Kariba / Zambia

Résumé – Structures en taille, diversité, dominance et trophiques de la communauté de poissons dans un lac tropical : une étude de cas pour le secteur Sinazongwe, lac Kariba, en Zambie. Cette étude examine les structures en taille, diversité, dominance et trophiques de la communauté de poissons littoraux du secteur de Sinazongwe, lac Kariba, en Zambie, de 1980 à 1995. Elle est basée sur les données d'échantillonnage à l'aide de filets maillants et sur celles disponibles de la littérature. Les spectres de taille et de diversité ont, à l'instar de ceux des communautés de poissons démersaux marins exploités, des allures décroissantes régulières : les effectifs et la diversité de poissons sont importants pour les petites tailles, et faibles pour les grandes tailles. Les spectres de tailles sont récurrents d'année en année et bien ajustés par des fonctions quadratiques. La diversité (indice de Shannon) et la dominance (indice de régularité, J') diminuent et augmentent linéairement avec la longueur du poisson. La diversité pour les grandes tailles diminue, selon les variations annuelles des pentes des spectres de diversité. Les courbes de comparaisons abondance et biomasse révèlent des années où la communauté de poissons était en « bonne santé », fortement et modérément perturbée. Les proportions de prédateurs, en particulier de *Hydrocynus vittatus*, et le niveau trophique moyen diminuent linéairement d'année en année. Le spectre trophique moyen de diversité ne change pas. Les spectres trophiques moyens d'abondance et de biomasse montrent une communauté d'abord contrôlée par des animaux de hauts niveaux trophiques de 1980 à 1984, et inversement après. Les descripteurs dérivés de la structure trophique détectent mieux les modifications subies par la communauté sous la pression de pêche, et révèlent pour la première fois pour le lac Kariba la baisse progressive du niveau trophique moyen au sein de la chaîne alimentaire ciblée par la pêche. Les indicateurs écosystémiques étudiées s'avèrent des alternatives potentiellement prometteuses pour l'évaluation et la gestion des communautés de poissons exploitées dans des milieux aquatiques continentaux tropicaux.

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1 Introduction

In developed countries, inland fisheries are conservation (i.e., recreation and sport) oriented. In contrast, river, floodplain and lake fisheries of developing countries, especially in Africa, are production oriented (Welcomme 2000). The latter fisheries, also called food-fisheries, play key conflicting social, economic and political roles through fish-food production, employment provision, income generation and government policy orientations to meet poverty alleviation. Yet, those fisheries are rarely properly assessed and managed, as a number of factors make the conventional single species and multi-species stock assessment methods – all of which were developed for marine temperate fisheries – partly inappropriate or difficult to apply. These factors include the difficulty or impossibility of getting age-structured data and quantitative age or size-structured dietary contents, the multi-species nature of the resources, the multi-gear, multi-*métie*r and small-scale nature of the exploitation, strong and unpredictable seasonal and year-to-year environmental fluctuations, social and economic contexts, inherent biological, technological and environmental interactions and, not the least, lack of both financial and human resources to carry out or develop appropriate studies.

In such a context, the available information mostly consists of rough estimates of total catch for all species, exploitation indices (e.g., number of canoes, fishermen) and, at best, length frequencies for some species of commercial importance. This data-poor situation has led to assessing tropical inland fisheries employing three main approaches. The first, simplistic and widely used approach was the description of changes in total catches, exploitation indices and catch rates. The second approach relied upon empirical relationships, such as richness, yield or catch rate versus water bodies' morphological, hydrological or primary productivity variables; catch per surface area versus fishermen per surface area (e.g., Henderson and Welcomme 1974; Lévêque et al. 1988; Karenge and Kolding 1995a; Laë 1997; Laë et al. 2004). The third and relatively recent approach focused on the extensive use of single stock length-based methods (e.g., Moreau et al. 1995), essentially to derive populations' life history indicators.

To circumvent the aforementioned difficulties, complement the previous empirical relationships or simplistic analyses and take into account the ecosystem functioning, some authors had recourse to or suggested the use of ecosystem indicators to measure the impacts of fishing on tropical inland fish communities (e.g., Morand and Bousquet 1994, 2000; Welcomme 2000; Laë 1997; Albaret and Laë 2003; Laë et al. 2004). This study is a continuation of research efforts toward searching more potential indicators for the assessment and management of such communities. It aimed at examining the annual size, diversity, dominance and trophic structures, including the abundance-biomass comparison (ABC) curves, the proportions of predators and the mean trophic levels (*Tls*) for the exploited inshore fish community of the Sinazongwe area (Lake Kariba, Zambia) and adjacent zones (Fig. 1). Such community attributes and their applications have been mostly documented for exploited demersal marine and coral reef fish communities (e.g., Rochet and Trenkel 2003; Trenkel and Rochet 2003; Daan et al. 2005) and inland aquatic ecosystems of temperate regions (e.g., Boudreau and Dickie 1992; Cyr and Peters 1996; Sprules and Munawar 1986; Sprules and Goyke 1994; Sprules and Stockwell 1995; Sprules et al. 1991). They are uncommon for African tropical inland fish communities.

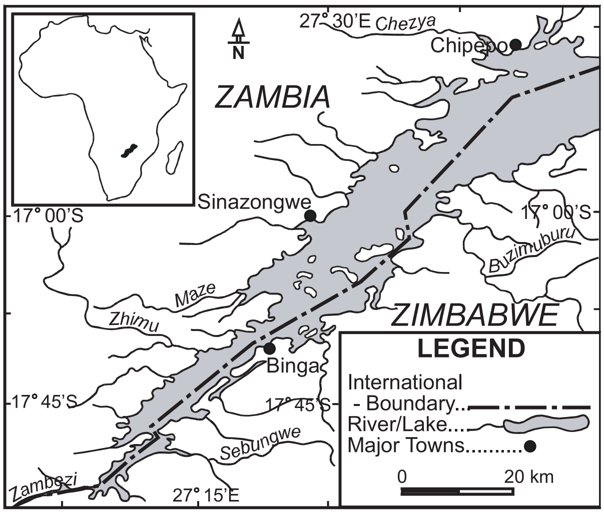

Fig. 1. Map of the Sinazongwe area and adjacent zones at the southwest of Lake Kariba; the insert shows the location of Lake Kariba in Africa.

Yet the aforementioned community indicators may prove to be robust tools for the routine assessment and management of the Zambian multi-species, multi-*métier* and small-scale inshore fishery of Lake Kariba. Here, no formal stock assessments were performed although one of the management regulations – initiated since the late 1980s and solely based on empirical considerations – consists of a fishing ban during the rain season, from December to February; this regulation is supposed to let adult fish spawn undisturbed. This study's expectation was that the temporal behavior of indicators examined may reveal relevant fishery-driven signals on the disturbance status of the exploited community as reflected in the excessive removals of fish and diversity loss among larger length classes, as well as in the shifts of the dominance and trophic-based metrics. It was anticipated that similar monitoring studies in the future could provide a reasonable ground for enactment and enforcement of proper fishery management regulations. The main objective of this study therefore was to investigate the applicability of the size, diversity, dominance and trophic structure methods in a tropical lake context. The questions to be particularly answered were whether (i) the community structures in number and diversity were organized according to individual size in a tropical lake as is in marine ecosystems; (ii) linear or quadratic models provide better fits in this context and; (iii) exploitation indices could explain the variations of either parameters of interest.

2 Materials and methods

2.1 Background information on the inshore fishery of Lake Kariba and the study area

Since the closure of Kariba dam (1955-1958) and the filling of the reservoir (1959-1963) between Zambia and

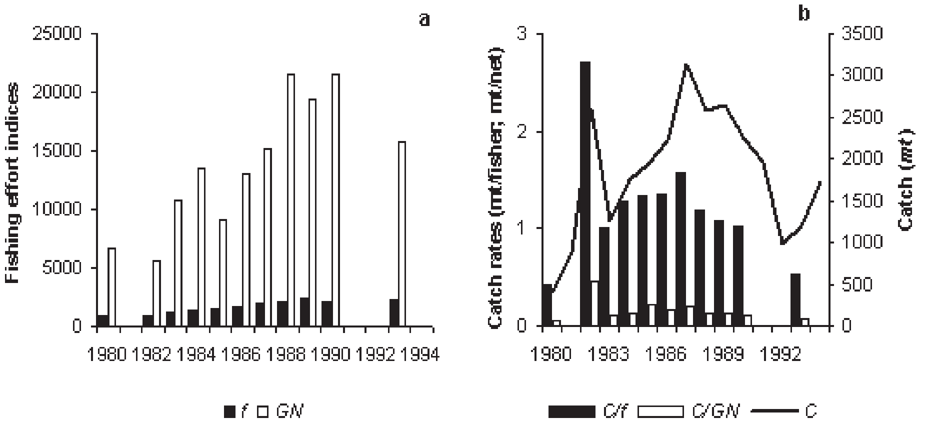

Fig. 2. Annual variations of (**a**) the total number of fishers (f) and gillnets (GN), and (**b**) of total catch (C, metric tons) and catch rates (C/f and C/GN) estimated for the Zambia inshore fishery of Lake Kariba, 1980-1994 (Source: Musando 1996).

Zimbabwe, along the Middle Zambezi River, Lake Kariba (Fig. 1) has experienced substantial changes in fish species composition, abundance, production and fisheries exploitation (Balon and Coche 1974; Kenmuir 1983; Scholz 1993; Karenge and Kolding 1995a,b; Musando 1996; Scholz et al. 1997; Losse 1998). The major changes so far reported include the invasion by some Upper Zambezi species, the introduction of alien species and the spatial and temporal variability in species richness, diversity and productivity. For the inshore gillnet fisheries, three main phases were distinguished: (i) an initial phase of low fishing effort and high catch rates over the 1960s; (ii) a recession and/or closure phase in the 1970s during the Zimbabwean liberation war; and, especially in the Zambian sector of the lake, (iii) a phase of fishery reopening, increase in landings and effort and stabilization of catch rates during the 1980s (Fig. 2). Furthermore, according to the Zambia fisheries annual reports, changes in species composition of landings marked the first and third phases above.

Along with those changes, Zambia and Zimbabwe adopted different inshore fishery development schemes on Lake Kariba. Zimbabwe embarked from the 1960s on establishing protective fish reserves, limiting the number of fishers and the number and size of nets per fisher, and setting at 100 mm stretched the minimum legal mesh size (Machena and Mabaye 1987; Musando 1996). Zambia opted for a free-access fishery regime (Musando 1996; Losse 1998), characterized, among others, by the following two phases. Prior to 1986, there were no restrictions for fishing locations, gillnet mesh sizes and fishing gear types and practices. Since 1986, there were introduction of the legal minimum mesh size of 76 mm stretched, prohibition of unselective and destructive gears, fishing closure between December and February and little enforcement of regulations. During either phase, a number of projects were set up in Zambia to conduct fishery-independent monitoring surveys almost exclusively in the Sinazongwe area and adjacent zones (Fig. 1). Those projects were meant to generate information appropriate to monitor the changes in population sizes, species composition and diversity. This prevailed up to 1995, with the end of the Norwegian Agency for Development Cooperation/Southern African Development Community Research Program on Lake Kariba. The choice of Sinazongwe area as the only site of fishery-independent surveys stemmed from the presence of basic fishery infrastructures, its contribution in total catches (about 60%) and lack of financial and human resources necessary to carry out coastwide surveys.

2.2 Data

This study was primarily based on fish records of scientific gillnet surveys carried out from 1985 to 1995 in the Sinazongwe area and adjacent zones (Fig. 1). Additional data came from Scholz (1993) and Musando (1996), who provide details on the gillnet fleets' specifications, the sampling methods and the types of information recorded.

The surveys used fleets of 13 monofilament nets from 1985 to 1991 and of 13 multifilament nets from 1992 to 1995. All nets were mounted at 50% hanging ratio and at an area of 225 m^2 from 1985 to 1993, of 112.5 m^2 in 1994 and 1995. Mesh sizes ranged between 25 mm and 178 mm stretched, with 13 mm increment. Sampling was scheduled every month at three inshore stations for three consecutive nights, each during which nets setting lasted 12 hours. However, due to fuel shortages, bad weather, net thefts and damages caused by the movements of semi-industrial vessels, sampling occasionally became erratic in space and time, or data were lacking for some mesh sizes. Records included fish species codes, the weight (g) and the total length or fork length to the nearest millimeter for fish with truncated caudal fins and forked caudal fins, respectively. In all, this study dealt each year with 11 to 25 species (Table 1), out of which 100% in 1987 and 56 to 74% in other years were of commercial importance and represented more than 99% of all fish taken in the surveys.

The analysis dealt with pooled total length (cm) and weight (g) data for all fish sexes and conditions. Converting fork length into total length consisted of multiplying *fork length* by 1.10 for characids, mormyrids, cyprinids, schilbeids and clupeids; 1.12 for dischodontids; and 1.15 for mochokids (Kenmuir 1983). Furthermore, single-species and multispecies size structures and species numbers were determined for each year for each of the 10 cm-length class intervals.

Table 1. List, trophic levels, *Tls* (source: `http://www.FishBase.org`) and predation status (+++: mainly piscivores; ++: predators of various animal groups including fish; +: occasionally piscivores; -: no fish in the diet) of fish species collected in the gillnet surveys from the Sinazongwe area (Lake Kariba, Zambia), 1980-1995.

Family	Species	*Tls*	Predation status/ percentage of fish in diet
Characidae	*Hydrocynus vittatus**	4.4	+++ 94%
	*Brycinus imberi**	3.3	++
	*Brycinus lateralis**	2.6	-
Mochokidae	*Synodontis zambezensis**	2.7	-
	Synodontis nebulosus	2.5	+
Cichlidae	*Serranochromis macrocephalus**	4.2	+++
	*Oreochromis mortimeri**	2.7	-
	*Sargochromis codringtoni**	3.1	+
	*Tilapia rendalli**	2.2	-
	Tilapia sparmani	2.7	-
	Pseudocrenilabrus philander philander	3.7	+
	Oreochromis macrochir	2.0	-
	*Oreochromis andersonii**	2.0	-
Mormyridae	*Mormyrus longirostris**	3.3	+
	*Mormyrops anguilloides**	3.6	+
	Marcusenius macrolepidotus macrolepidotus	3.2	-
	Hyppopotamyrus discorhynchus	3.2	-
Schilbeidae	*Schilbe* spp.	3.6	++
Cyprinidae	*Labeo altivelis*	2.0	-
	Labeo cylindricus	2.0	-
	Labeo congoro	2.2	-
	Barbus marequensis	3.2	+
	Opsaridium zambezense	3.4	-
	Barbus unitaeniatus	2.8	-
Dischodontidae	*Distichodus mossambicus**	2.0	-
	*Distichodus schenga**	2.1	-
Clariidae	*Clarias gariepinus*	4.4	++ 69%
	Heterobranchus longifilis	3.7	++
Clupeidae	*Limnothrissa miodon**	3.0	+

(*) commercial importance.

To reduce the incomparability of the annual data series due to the inconsistency of the sampling designs, only data for available sampling month-station strata with complete sets of nets used were considered (Table 2). The data were then adjusted for a standard fleet of 13 monofilament nets with a net area of 225 m^2 and a catchability of 1.15. This catchability was according to Hill cited in Scholz (1993) and was derived through experimental samplings using simultaneously multifilament and monofilament nets at Sinazongwe. Thus, catches from 1985 to 1991 were taken by a standard gillnet fleet; those of 1992 and 1993 were multiplied by 1.15 and those of 1994 and 1995 by 2.30. No further adjustment was attempted to account for the sampling effort-dependence of diversity, because all net settings lasted the same period. In spite of those efforts on data adjustment, there was no information on net visibility to disentangle the catch efficiencies of multifilament and monofilament nets vis-à-vis various species.

2.3 Size spectra

Let i ($i = 1, k$) be the length class, L_i and N_i the corresponding mid-length and total number for all fish species recorded, respectively. The inspection of the scatter points suggested that the quadratic functions were appropriate to represent the annual size spectra across the whole observed length ranges:

$$n_i = \alpha + \beta l_i + \gamma l_i^2 + \varepsilon_i \qquad (1)$$

where $n_i = \mathrm{Ln}\,(N_i)$, $l_i = \mathrm{Ln}\,(L_i)$, α, β and γ are parameters (α: intercept; β: linear term; γ: curvature term) and ε_i the residual error terms assumed to be normally distributed with 0 mean and variance σ_ε^2. Such a representation (i.e., n_i versus l_i) was chosen because it was applied to many fish communities (Shin 2000) and, hence, facilitates comparisons. The model parameters were interpreted following Shin (2000) and Shin and Cury (2004).

The least squares method was used to fit model (1). The coefficient of determination, r^2, the F-test for significance of regression and the patterns of residual plots were used as indicators of goodness-of-fit.

2.4 Diversity and dominance spectra

For each 10 cm-length class i, the species diversity was estimated by the Shannon diversity index, H_i' (hereafter referred

Table 2. Cross-tabulation on samples with complete sets of gillnets used to examine the structures of the Sinazongwe area fish community. For a given year, black cells represent months of which samples (aggregated for all sampling stations) were considered (monthly samples over the period 1980-1984 were part of those used by Scholz 1993).

	Months											
	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1980								■	■	■		
1981		■	■									
1982		■			■	■	■				■	
1983		■	■			■	■	■	■	■	■	■
1984	■	■	■	■	■	■	■	■	■	■	■	■
1985	■	■	■	■	■	■	■	■	■	■	■	■
1986	■	■	■	■	■	■	■	■	■	■	■	■
1987											■	
1988		■		■				■	■	■	■	■
1989	■	■	■	■	■			■	■		■	
1990	■	■	■	■	■	■	■	■	■		■	
1991		■			■		■	■		■		
1992				■	■		■	■	■	■	■	■
1993	■	■	■									
1994					■	■	■	■	■	■		
1995	■	■	■	■	■	■	■					

to as diversity), as $H'_i = -\sum_{j=1}^{Si} p_{ij} \log_2 p_{ij}$, where S_i is the richness and p_{ij} the proportion of species j. As diversity of a typical fish community generally decreases across length classes (Rice and Gislason 1996), the linear functions were *a priori* tested to represent the diversity spectra:

$$H'_i = \alpha + \beta L_i + \varepsilon_i \tag{2}$$

where, L_i is the mid-length, ε_i the normally distributed residual error terms with 0 mean and variance σ_ε^2, α and β are parameters.

While the slope β was a distribution trend parameter of diversity among length classes, the intercept α was interpreted as an estimate of the overall diversity ($H' = -\sum_{j=1}^{S} p_j \log_2 p_j$, where S = number of species) irrespective of length (note that, at least in theory, when $\beta = 0$, $\alpha = H' = H'_i$, $\forall\, i$). However, the intercept likely often underestimates the overall diversity because the variability in diversity is seldom fully (i.e., 100%) accounted for by the linear relation between diversity and length. Consequently, α was empirically considered a "good" estimate of H' if H' fell within the confidence interval of α for a specified significance level.

The dominance was estimated for each length class i using the regularity (J') index, i.e., $J'_i = H'_i / H'_{i\max}$ where $H'_{i\max} = \log_2 S_i$. Upon the inspection of the (L_i, J'_i) scatter points, the dominance spectra (i.e., species regularity along energy flow) were represented by simple linear regressions:

$$J'_i = \alpha + \beta L_i + \varepsilon_i \tag{3}$$

where L_i is the mid-length, ε_i the normally distributed residual error terms with 0 mean and variance σ_ε^2, α and β are parameters.

In an attempt to interpret model parameters and by analogy to the parameters of model (2), the slope of model (3) was considered to be a distribution trend parameter of dominance among length classes, and the intercept of the same model an estimate of the overall dominance, $J' = H'/H'_{\max}$ (where $H'_{\max} = \mathrm{Log}_2 S$), irrespective of length. The latter parameter was a "good" estimate of J' if J' fell within its confidence interval for a specified significance level.

Fitting the linear models to diversity and dominance spectra and assessing the goodness-of-fit relied upon the techniques applied to the size spectra.

2.5 Abundance-Biomass comparison (ABC)

Annual ABC plots were constructed by superimposing k-dominance curves for abundance and biomass data as described by Warwick (1986), Warwick et al. (1987) and Clarke (1990) for marine macrobenthos, and by Blanchard (2001), Blanchard et al. (2004), Jouffre and Inejih (2005) and Yemane et al. (2005) for fish communities. The related W-statistic, which is the standardized sum of the differences between each pair of species cumulative biomass ($\sum_{j=1}^{k} b_j$) and cumulative abundance ($\sum_{j=1}^{k} a_j$) values ranked in a decreasing order ($k = 1, S$), was calculated following (Clarke 1990):

$$W = \frac{\sum\limits_{j=1}^{S} \left[\left(\sum\limits_{j=1}^{k} b_j \right) - \left(\sum\limits_{j=1}^{k} a_j \right) \right]}{50(S-1)}. \tag{4}$$

It represents the surface between the biomass and abundance curves. Positive values of W (i.e., the biomass curve lies above the abundance curve) are indicative of undisturbed communities, dominated by K-selected species. Its negative values (i.e., the abundance curve is above the biomass curve) characterize disturbed communities, dominated by r-selected species. For moderately stressed communities, the biomass and abundance curves are close or intersect, yielding values of $W \sim 0$.

2.6 Proportions of predators, mean trophic levels and trophic spectra

The calculation of these community attributes also included the survey data by Scholz (1993) – who used the same data standardization procedure – for the period 1980-1984. The food items, diet composition and mean trophic levels (*Tl*) of fish species were extracted from the FishBase database's website (Froese and Pauly 2005; `http://www.Fishbase.org`), Kenmuir (1983) and Skelton (1993).

The predators considered were piscivorous fish and fish preying upon various animal groups including other fish, namely *Hydrocynus vittatus*, *Serranochromis macrocephalus*, *Schilbe* spp. and *Clarias gariepinus* (Table 1). Furthermore, the percentages in number and weight, respectively, for all predators (*PPN* and *PPW*) and *H. vittatus* (*PHN* and *PHW*) were estimated.

Annual mean *Tls* ($\bar{T}lt$) of the community were calculated following Pauly et al. (1998, 2001) and Laurans et al. (2004):

$$\bar{T}lt = \frac{\sum_{j=1}^{S} Y_{jt} Tl_j}{\sum_{j=1}^{S} Y_{jt}} \qquad (5)$$

where, for species j in year t, Y_{jt} is the survey catch in number or weight and Tl_j the mean trophic level. The $\bar{T}lt$ estimates based on survey catch in numbers and weights were hereafter referred to as $\bar{T}l$N and $\bar{T}l$W, respectively. They were plotted against annual abundance (*A*) and biomass (*B*) indices, i.e., survey total catch in numbers and weights by setting of a standard gillnet fleet.

The diversity, abundance and biomass trophic spectra (*DTS*, *ATS* and *BTS*, respectively) of the Sinazongwe area fish community were constructed according to the technique described by Bozec et al. (2003), Gascuel (2004), Laurans et al. (2004) and Gascuel et al. (2005). This technique involved two steps: (i) aggregating the diversity (represented by richness), abundance and biomass of the community (estimated as previously) for $Tl = 2$ (primary consumers and detritus-feeders) through $Tl = 5$ (top predators), by *Tl* increments of 0.1; (ii): smoothing the spectra obtained with a three points moving average. The latter step was necessitated by the need of taking into account the variability in the species' *Tl* associated with the variation of the diet (Davenport and Bax 2002), and the uncertainty inherent in *Tl* estimation (Pinnegar et al. 2002).

2.7 Variations of community attributes and their relations with exploitation indices

Inter-annual variations in the patterns of the previous community metrics were analyzed to find out eventual effects of fishing. The *DTS*, *ATS* and *BTS* were averaged over five or six year-periods. Moreover, selected community metrics were compared with equivalent indicators derived by Musando (1996), and plotted against available fishing exploitation indices (Fig. 2a) using the least squares method. Those analyses were based on the evidence that survey gears and artisanal fishers' gears had similar characteristics (Musando 1996) so that it could reasonably be assumed that the trends of the community metrics derived from survey data could be partly attributable to fishing effort.

3 Results

3.1 Size spectra

The smallest length class observed and used for the annual size spectra of the Sinazongwe area fish community was 0−10 cm, except for the 1987 size spectra which consisted of fish at least 10 cm long. The largest length class was 110−120 cm.

All size spectra exhibited regular decreasing patterns generally indicative of high fish numbers in smaller sizes and vice versa in larger sizes (Fig. 3). They were rather curvilinear and well fitted by quadratic functions (r^2 = 0.93−0.99; F-ratio range: 51.3−432.1, range of denominators' number of degrees of freedom: 6−9, p = 0.001; no trend in residuals).

The parameter estimates of the Sinazongwe area fish community size spectra varied cyclically, with similar fluctuation patterns for the curvature terms and intercepts. Those parameters were significantly correlated with each other (r = +0.89) and varied inversely with the linear terms, with witch they showed significant negative correlations (r = −0.99 and −0.94, respectively).

All curvature term values were negative and exhibited non-significant linear relationships with exploitation indices (Table 3). In contrast, all linear term values were positive and had annual variation patterns broadly consistent with those of the catch per unit effort (CPUE) derived by Musando (1996) using the same dataset, except in 1993-1995. Those variations showed troughs in 1988-1989 and 1993 and a clear peak in 1990-1991.

3.2 Diversity and dominance spectra

Overall, the diversity of the Sinazongwe area fish community decreased across length classes (Fig. 4). Linear relationships better represented the annual diversity spectra of the community in 1991-1993. In other years, diversity in the 0−10 cm length class was lower than that in 10−20 cm and/or 20−30 cm length classes where it peaked, leading to discrete dome-shapes.

Whether diversity peaked or not in lower length classes, simple linear regression fits were significant (r^2 = 0.57−0.85; residuals distributed around zero) except in 1985 and 1987-1989. In 1985 and 1989, the linear variation of diversity across length classes was marginal (r^2 = 0.31 and 0.23, respectively). In 1987 and 1988, linear fits resulted in curvilinear patterns of residuals, but the subsequent adjustments of quadratic models

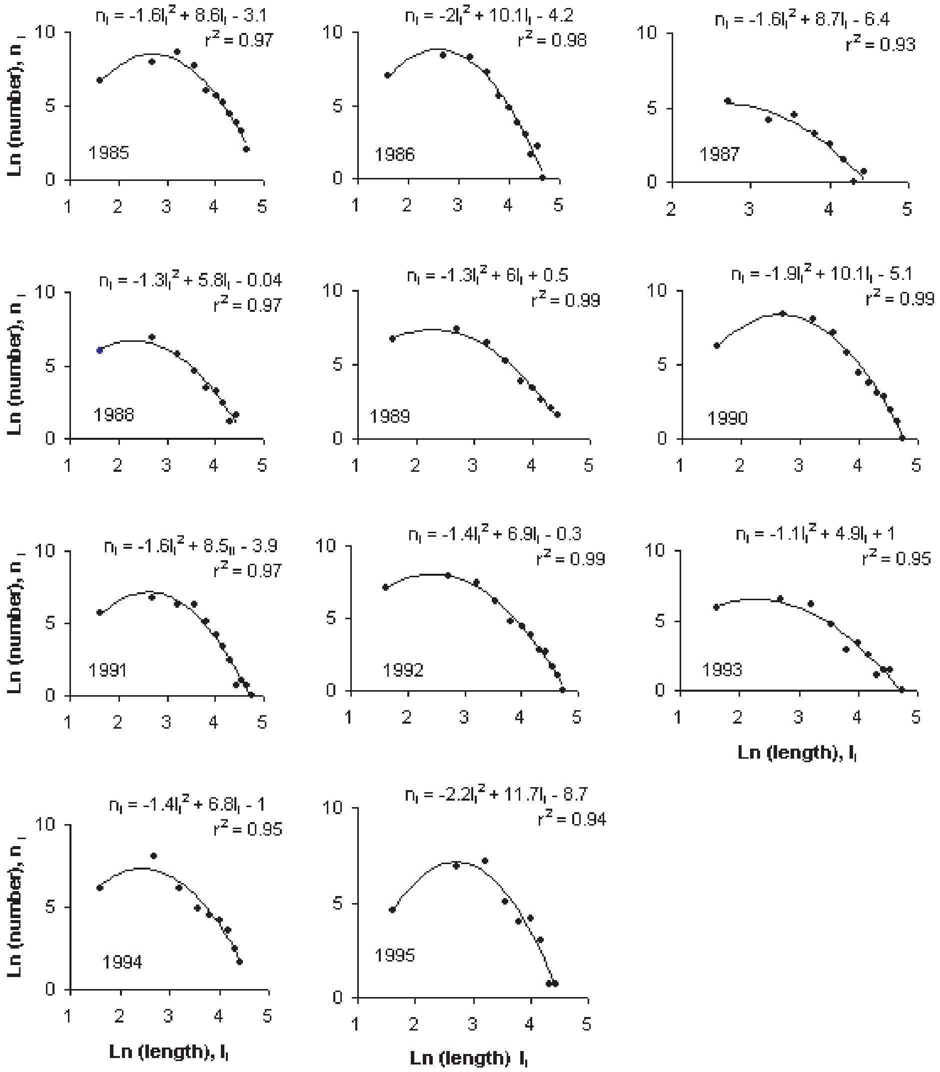

Fig. 3. Size spectra (scatter diagrams) and fitted models (lines) for the Sinazongwe area fish community, 1985-1995.

and their comparison with linear models (partial F test statistic; Neter et al. 1996) did no yield substantial improvements of the fits.

The dominance (J' index) generally increased linearly across length classes (Fig. 4). That trend was significant ($r^2 = 0.67–0.81$) except in 1987-1988, 1993 and 1995.

The diversity spectra slopes (*DSS*) had negative values and showed a significant linear decrease over years (Fig. 5a; $F_{(1,9)} = 7.82$; $p = 0.05$). They also decreased linearly with increasing exploitation indices, but only significantly when the number of gillnets were involved (Table 3). As for the diversity spectra intercepts, they were positive and dome-shaped, with a peak in 1989-1992, and paralleled somewhat the overall diversity of the community (Fig. 5b). This pattern was consistent with the fact that some intercepts proved to be "good" estimates of the overall diversity in years of significant linear diversity spectra, i.e., at $p = 0.05$ for 1986, 1994 and 1995; $p = 0.01$ for 1990 and 1991 and; $p = 0.001$ for 1992 and 1993.

The dominance spectra slopes and intercepts varied without trends, whereas the annual variations of the overall dominance were dome-shaped (Figs. 5c,d). This particularly weakened those intercepts' ability to estimate the overall dominance, in spite of statistical significant linear dominance spectra tested at $p = 0.05$ for 1986 and 1994, $p = 0.01$ for 1985 and 1991, $p = 0.001$ for 1989 and $p = 0.0005$ for 1992.

3.3 Abundance-Biomass comparison (ABC)

The ABC curves exhibited gentle annual changes in their patterns. For the 1985-1988 and 1994-1995 periods, the biomass curves lied below the abundance curves and yielded a negative W-statistic suggesting a "grossly stressed" community. For the period 1989-1993, the reverse was observed or the two curves crossed each other, yielding a positive W-statistic: this one was dome-shaped with a peak in 1989-1992 and thereby evidenced an "undisturbed" or a "moderately stressed" community during that period.

Table 3. Statistics of linear relationships between available pairs of selected metrics – response variables (*CT*: curvature terms; *DSS*: diversity spectra slopes; annual proportions of all predators (*PPN* and *PPW*) and of Hydrocynus vittatus (*PHN* and *PHW*) and annual mean trophic levels ($\bar{T}l\,N$ and $\bar{T}l\,W$)) – of the Sinazongwe area fish community (Lake Kariba, Zambia) and exploitation or size indices – predictor variables (f : number of fishers; *GN*: Number of gillnets; *A*: abundance or number of fish by setting of a standard gillnet fleet; *B*: biomass or weight of fish by setting of a standard gillnet fleet).

Exploitation or Size Indices	Respon. variables	Intercepts		Slope		S^2	r^2	*df*	F-ratio
		$\boldsymbol{a}$	$\boldsymbol{S_a}$	$\boldsymbol{b}$	$\boldsymbol{S_b}$				
f	*CT*	−1.74	0.60	1×10^{-5}	3.5×10^{-5}	0.15	0.04	4	0.16 NS
GN	*CT*	−2.55	0.82	5×10^{-4}	4×10^{-4}	0.11	0.29	4	1.66 NS
f	*DSS*	23×10^{-4}	0.01	-6×10^{-6}	4.8×10^{-6}	1.7×10^{-6}	0.24	5	1.57 NS
GN	*DSS*	−0.003	0.005	-7×10^{-7}	2.7×10^{-7}	9.4×10^{-6}	0.57	5	6.71*
f	*PPN*	80.95	14.03	−0.023	0.008	180.18	0.48	9	8.30*
	PHN	80.76	13.68	−0.027	0.008	171.27	0.57	9	12.06**
	PPW	101.65	12.79	−0.031	0.007	149.57	0.68	9	18.71**
	PHW	103.72	12.84	−0.036	0.007	150.77	0.73	9	24***
GN	*PPN*	62.91	13.89	-15×10^{-4}	9×10^{-4}	270.22	0.22	9	2.53 NS
	PHN	62.97	13.73	−0.002	9×10^{-4}	264.02	0.34	9	4.66 NS
	PPW	81.43	13.88	−0.002	9×10^{-4}	269.62	0.41	9	6.37*
	PHW	82.14	14.31	−0.003	0.001	286.78	0.48	9	8.35*
f	$\bar{T}lN$	4.25	0.22	-4×10^{-4}	1×10^{-4}	0.046	0.57	9	11.75**
	$\bar{T}lW$	4.37	0.19	-4×10^{-4}	1×10^{-4}	0.031	0.67	9	17.86**
GN	$\bar{T}lN$	3.94	0.23	-3×10^{-5}	1.6×10^{-5}	0.073	0.31	9	4 NS
	$\bar{T}lW$	4.14	0.18	-4×10^{-5}	1.2×10^{-5}	0.046	0.52	9	9.57*
A	$\bar{T}lN$	3.40	0.23	5×10^{-4}	24×10^{-4}	0.106	0.003	14	0.05 NS
	$\bar{T}lW$	3.36	0.18	0.003	0.002	0.067	0.14	14	2.28 NS
B	$\bar{T}lN$	3.09	0.18	1.7×10^{-5}	7.7×10^{-6}	0.079	0.25	14	4.62*
	$\bar{T}lW$	3.24	0.14	1.7×10^{-5}	6.1×10^{-6}	0.049	0.36	1	8.02*

***$p < 0.001$; **$p < 0.01$; *$p < 0.05$; NS: Not significant ($p > 0.05$); $\boldsymbol{S}^2$: estimate of the error variance; $\boldsymbol{S_a}$ and $\boldsymbol{S_b}$: standard errors of the intercept ($\boldsymbol{a}$) and the slope ($\boldsymbol{b}$), respectively.

3.4 Proportions of predators, mean trophic levels and trophic spectra

Out of an average of 39% (sd: 17.5%) and 49% (sd: 18.8%) for all predators in the survey catches in number and weight, respectively, *H. vittatus* represented 31% (sd: 18.8%) and 42% (sd: 21.6%). In other words, *H. vittatus* accounted for an average of 73% (sd: 16.4%) of numbers and 83% (sd: 14.4%) of weight among the predators of the community. Therefore, most of the variability in predator proportions in the Sinazongwe area fish community was due to that of *H. vittatus*.

The *PPN*, *PHN*, *PPW* and *PHW* showed highly significant linear decreases over years (Table 4), almost parallel for the former two indicators (Fig. 6a), steeper for *H. vittatus* for the latter two (Fig. 6b). Moreover, the *PPN*, *PHN*, *PPW* and *PHW* decreased linearly with exploitation indices, significantly except when the proportions in numbers were regressed against the number of gill nets (Table 3).

The annual mean trophic level (*Tl*) also exhibited very or highly significant linear decrease over years, with a decline rate of 0.4–0.5 per decade (Fig. 7, Table 4). Moreover, the increase in number of fishers and fishing nets seems to have resulted in its linear decrease, which was significant except when $\bar{T}lN$ was regressed against the number of gillnets (Table 3). While the variations in the annual mean *Tl* were insensitive to the community abundance (*A*), they increased significantly with increase of biomass (*B*; Table 3), the main component of which was made of top predators (Fig. 8b).Thus, on average, the annual biomass of predator fish was the key determinant of the variability in annual mean *Tl* of the community, but their annual abundance relative to that of non-predator fish was not large enough to influence alone the relationship between mean *Tl* and total community abundance (in other words, the abundance of non-predator fish had a stabilizing effect on the mean *Tl* in relation with *A*).

The mean *DTS* of the Sinazongwe area fish community were polymodal, had similar patterns whatever the averaging period (1980-1984, 1985-1989, 1990-1995) and encompassed primary consumers and detritus-feeders ($Tl = 2 - 2.2$) through top predators ($Tl \geq 4.4$). The *DTS*' modes were reflected in the *ATS* (Fig. 8a) and *BTS* (Fig. 8b), which also presented similar patterns whatever the averaging period. The primary consumers and detritus-feeders were well represented in the diversity, but appeared marginal both in abundance and biomass.

The mean fish abundance was of the same magnitude across the 2.5–2.9, 3.1–3.8 and 4.2–4.6 *Tl* ranges during the 1985-1989 period, across the 2–2.5 and 2.9–4.6 *Tl* ranges during both the 1985-1989 and 1990-1995 periods (Fig. 8a). The latter two periods were also characterized by similar mean

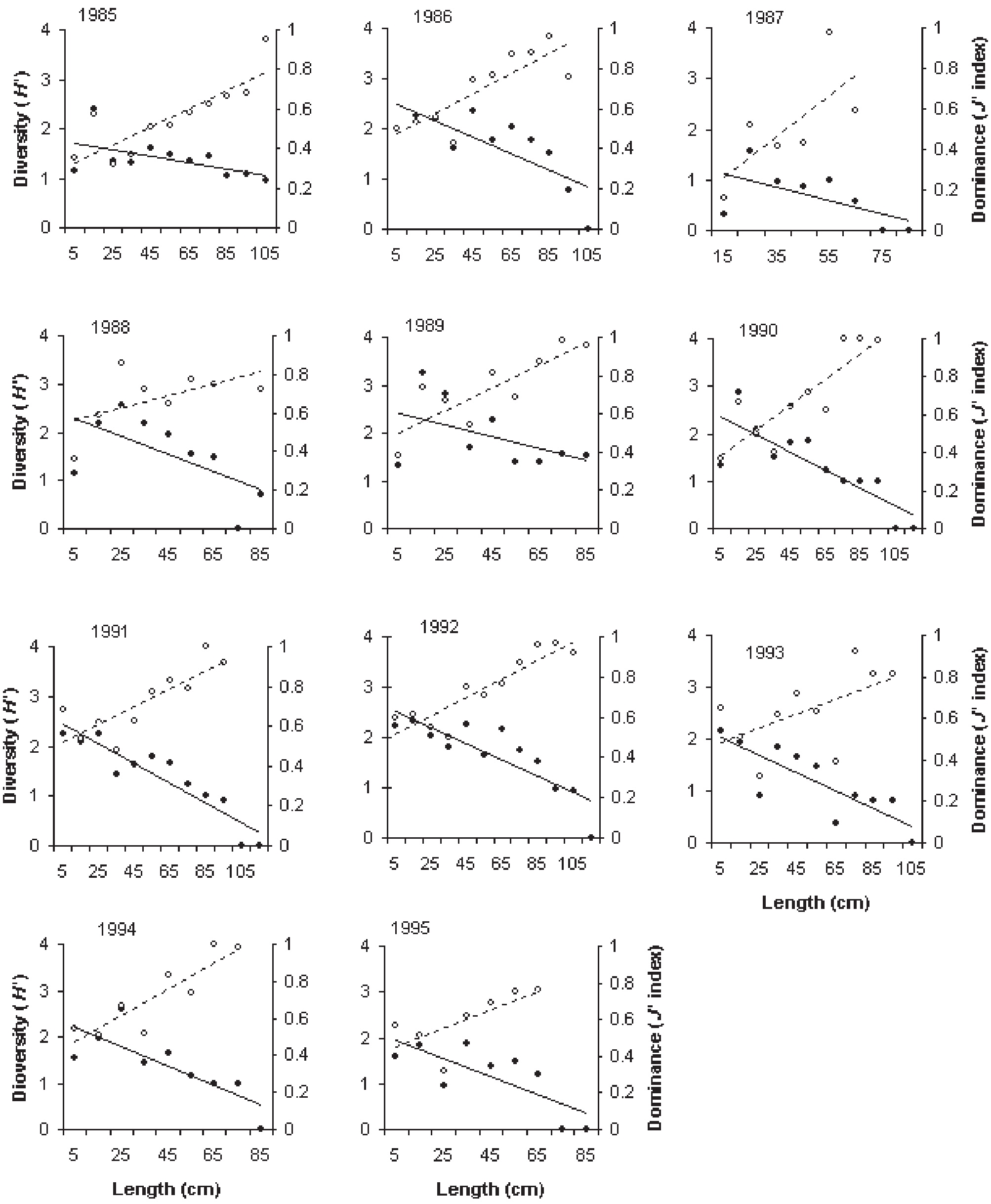

Fig. 4. Diversity (filled circles and solid lines) and dominance (open circles, dotted lines) spectra for the Sinazongwe area fish community, 1985-1995.

Table 4. Statistics of the linear relationships between annual proportions of all predators (*PPN* and *PPW*) and of *H. vittatus* (*PHN* and *PHW*), and of annual mean trophic levels ($\bar{T}l$N and $\bar{T}l$W) and years, for the Sinazongwe area fish community (Lake Kariba, Zambia), 1980-1995.

Community metrics	Intercept a	S_a	Slope b	S_b	S^2	r^2	*df*	F-ratio
PPN	5557.27	1280.88	−2.78	0.64	141.21	0.57	14	18.56***
PHN	5935.88	1377.72	−2.97	0.69	163.37	0.57	14	18.37***
PPW	5993.72	1368.65	−2.99	0.69	161.23	0.57	14	18.87***
PHW	7334.01	1418.06	−3.67	0.71	173.08	0.65	14	26.45***
$\bar{T}l$N	109.52	20.76	−0.053	0.01	0.04	0.65	14	26.11***
$\bar{T}l$W	83.12	21.25	−0.04	0.01	0.04	0.50	14	14.00**

$p = 0.001$; **$p = 0.01$; S^2: estimate of the error variance; S_a and S_b: standard errors of the intercept (a***) and the slope (***b***), respectively.

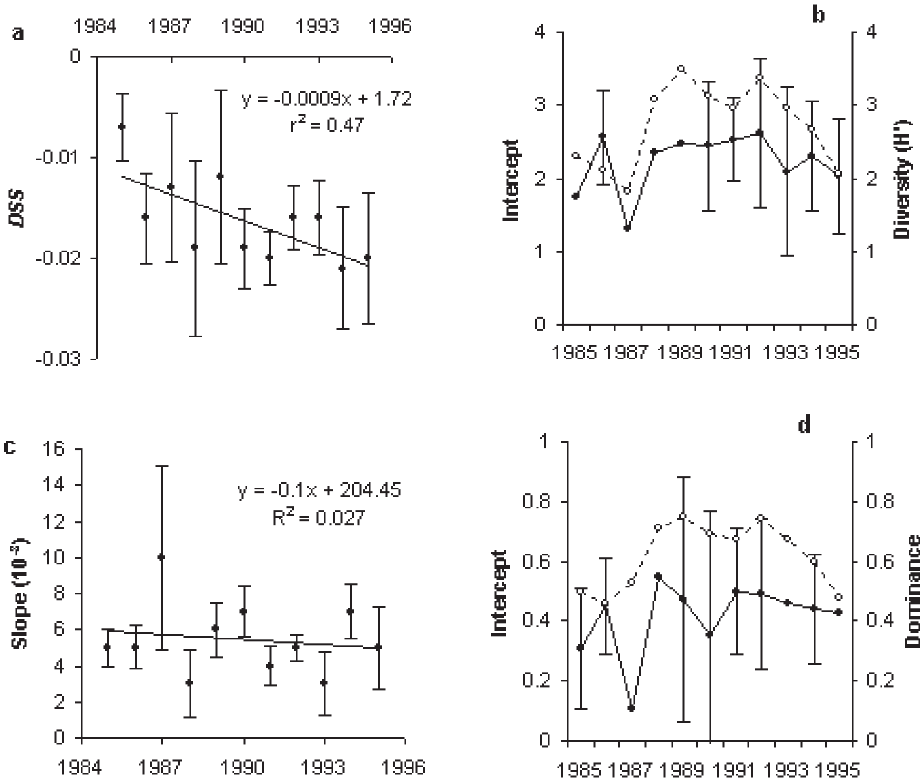

Fig. 5. Annual variations of (**a**) diversity spectra slopes (*DSS*), with one *SE*; (**b**) intercepts (filled circles with confidence interval for significant linear models) of the diversity spectra; (**c**) slopes, with one *SE*, and (**d**) intercepts of the dominance spectra. The overall diversity and dominance (open circles) were presented along with the intercepts of both spectra for comparison.

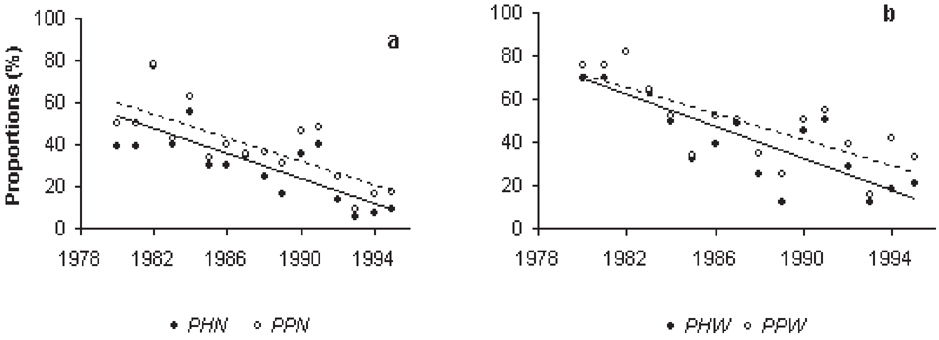

Fig. 6. Annual variations of the proportions of *Hydrocynus vittatus* (*PHN* and *PHW*) and all predators (*PPN* and *PPW*) based on survey catches (**a**) in number and (**b**) in weight, 1980-1995. The solid and dotted lines (for number and weight-based estimates, respectively) were fitted using the least squares method to indicate the trend.

biomass across all *Tls* (Fig. 8b). On the other hand, there were shifts in the *ATS* and *BTS*' magnitude with regard to the averaging periods. The 1980-1984 period was characterized by relatively high abundance and biomass of top predators (especially *H. vittatus*) and of fish abundance in the 3.2−3.8 *Tl* range, and vice versa for the 1985-1989 and 1990-1995 periods (although *H. vittatus* continued to be present). This trend was clearer for the *ATS* and consistent with the annual trends in the proportions of predators (Fig. 6) and the mean *Tl* (Fig. 7). Unlike the 1980-1984 period during which the dominant species were large-bodied (e.g., *H. vittatus* and *M. longirostris*), the *ATS* and *BTS* patterns observed during the 1985-1989 and 1990-1995 periods were rooted in the predominance of lower *Tl* fish, most of which were of small to medium body mass (e.g., *Brycinus* spp, *Synodontis zambezensis* and *Oreochromis mortimeri*).

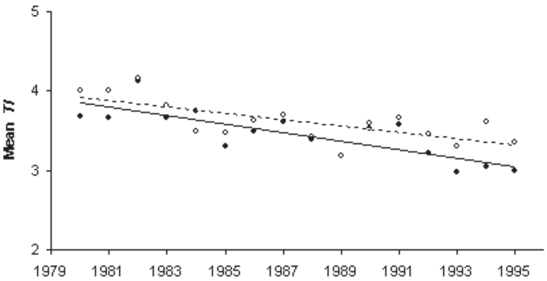

Fig. 7. Annual variations and trend of number-based (filled circles and solid lines) and weight-based (open circle and dotted line) estimates of the mean trophic level (*Tl*) for the Sinazongwe area fish community, 1980-1995.

4 Discussion

Unlike most works conducted on the size and diversity spectra of exploited fish communities, this study also dealt with very small fish of length less than 10 cm. Still, those attributes for the Sinazongwe area fish community were quite similar to those observed or simulated for demersal marine assemblages in particular (e.g., Rice and Gislason 1996; Gislason and Rice 1998; Bianchi et al. 2000; Shin 2000; Shin and Cury 2004) and for various animal communities in general (Blackburn and Gaston 1994; Johst and Brandl 1997). That is, logarithm (fish numbers) and diversity decreased with logarithm (fish length) and fish length, respectively, following recurrent curvilinear and linear patterns. That decrease was more regular and better explained by length for size spectra than for diversity spectra.

Low fish numbers and diversity in the first smaller length class and, for some years, in the second one, were responsible of the curvilinear size spectra and discrete dome-shaped diversity spectra. Four processes may have jointly or separately underlain those patterns, namely:

- The extinction risk for small-sized species as a result of environmental perturbations (Johst and Brandl 1997), notably the unexpected droughts and inundations which occurred in the Lake Kariba basin during the study period.
- The invulnerability of small-sized and juvenile fish to survey gears, irrespective of taxonomic groups.
- Biases in body size distributions due to measurement errors, species misidentification, missing species or unknown members of the community, most of which appear to be small bodied (Blackburn and Gaston 1994).
- The exposure of smaller fish to high predation pressure, especially in connection with the top-down control process (Shin 2000; Shin and Cury 2004). This process most likely holds in Lake Kariba (Kenmuir 1983; Table 1). The related information is only available and detailed for *H. vittatus*, because of its ecological, recreational and commercial importance (Machena 1988; Takano and Subramaniam 1988; Mhlanga 2003). In particular, this species is a generalist predator, switching diet in response to prey (including its own congeners) availability and abundance; it concentrates its predation pressure on small-sized fish, with a mode at about 4−5 cm (Takano and Subranamiam 1988).

No empirical nor simulation studies had yet dealt with the temporal variations of the curvilinear size spectra's parameters. Keeping in mind the reference direction (RD) concept (Rochet and Trenkel 2003; Trenkel and Rochet 2003; Shin et al. 2005), the curvature terms (fishing mortality indices – Shin 2000; Shin and Cury 2004) and linear terms of the size spectra were of particular interest. Where the curvature terms respond to fishing, they usually decrease quasi-linearly with increasing fishing pressure and removals of larger fish (Shin 2000; Shin and Cury 2004; Shin et al. 2005). The linear terms, on the other hand, have not yet been given any fishery or biological interpretation; they were hypothesized here to be abundance indices, owing to their positive sign and annual variations quite similar to those of the intercepts (abundance indices – Rice and Gislason 1996; Bianchi et al. 2000) of the descending limb of size spectra (performed but not described in this paper). The expected effects of fishing on them are unknown. However, both the curvature and linear terms fluctuated cyclically. This trend for the linear terms seemed realistic and consistent with the annual variations of CPUE derived by Musando (1996), who showed that it was strongly hydrology-driven. In contrast, it was unrealistic for the curvature terms, which did not reflect the increasing trend of the fishing pressure. The inability of the curvature terms to detect the fishing effects in this context corroborated earlier similar observations made using the slopes of linear size spectra on tropical exploited marine communities, in spite of evidence of increasing fishing pressure (Bianchi et al. 2000; Thiam et al. 2004; Stobbrup et al. 2005). According to these authors, low rate or lack of changes of the slopes of size spectra in tropical marine areas is partly rooted in the faster growth rates characterizing fish there. This statement also holds for Lake Kariba, where most fish are short-lived and fast-growing (Balon and Coche 1974; `www.FishBase.org`).

The reference direction of diversity (e.g., Shannon index) spectra's slopes and intercepts under fishing pressure is unclear (Shin et al. 2005). In this study, the slopes of the Sinazongwe fish community's diversity spectra decreased significantly over years, thereby suggesting a gradual loss of diversity in larger length classes during the study period. The increase in fishing pressure, in terms of the number of gillnets used, was probably responsible of this pattern. In contrast, fishing seems not to have affected the diversity spectra's intercept and, hence, the overall diversity.

Two aspects of dominance examined were the regularity (J' index) spectra and the ABC plots. If the positive correlation observed between regularity and length was a common property for all harvested fish communities, it would mean that, unlike in lower length classes where few species dominate the rest of the numerous species recorded, the fewer species surviving in larger length classes tend to be equally abundant. Concerning the ABC curves and the W-statistic, they were broadly consistent with the annual variations of the linear terms, overall diversity and overall regularity: in particular, those metrics concomitantly revealed a relatively healthy community between 1989/90 and 1992/93.

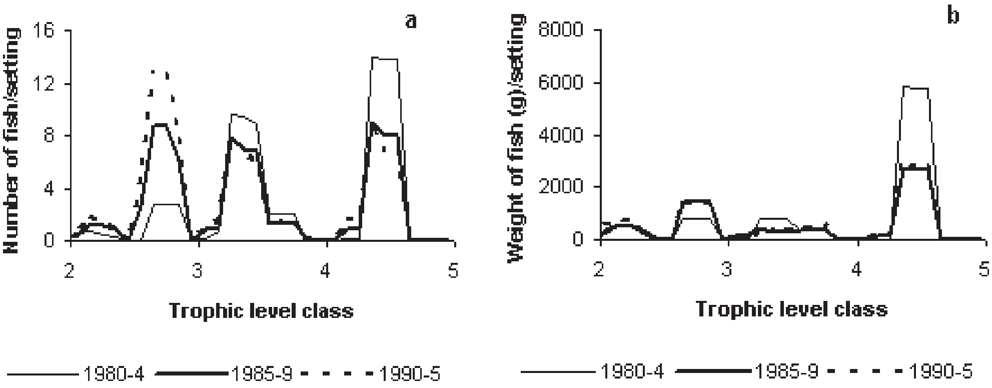

Fig. 8. Abundance trophic spectrum (**a**) and biomass trophic spectrum (**b**) for the Sinazongwe area fish community, derived from gillnet surveys, 1980-1995.

The drawback associated with the use of *Tls* (e.g., derivation from incomplete information on gut contents and on temporal, spatial and ontogenetic plasticity of diets; derivation from ECOPATH runs, which rely on unverified equilibrium assumptions and treat the taxonomic grouping of trophic webs) and related descriptors has been extensively discussed (e.g., Rochet and Trenkel 2003; Laurans et al. 2004; Gascuel et al. 2005). Pending accurate information on the subject in Lake Kariba, it was assumed that the *Tls* used did not change over time and the related results remained valid. In this regard, two aspects are worth noticing:

- The decline rate of 0.4−0.5 mean *Tl* units per decade was four to five times higher than the global decline rate reported for marine fish communities (Pauly et al. 1998, 2001; Laurans et al. 2004). This indicated that the *Tls* in tropical freshwater fish communities are more sensitive to fishing pressure than they are in exploited marine assemblages.
- Unlike other community metrics which likely encompassed a mixture of yet indiscernible effects and the mean *DTS* which remained unchanged over years, the findings on the annual variations in the proportions of predators, mean *Tl*s and mean trophic spectra better captured the changes of the Sinazongwe area fish community, and were consistent with each other and with the reported or suspected development of fishing pressure during the study period. The concomitant increase of fishing pressure and decrease of these community descriptors were therefore a clear indication of the “fishing down marine (here lake) food webs” effect. Thus, although other controlling factors may have been involved (e.g., hydrology; pollution etc.) in the modification of the structure of the Sinazongwe fish community, the removal by fishing of particularly *H. vittatus* resulted in a reorganization of the system in favor of the abundance and, to some extent, of the biomass of low *Tl* fishes.

Compared to the existing assessment methods applied to tropical inland fisheries (see introduction), the ecosystem approach to fisheries (EAF) proposed here through community descriptors examined is also appropriate in data-poor situations. However, the latter approach is an improvement to the former methods in the following. First, although it is holistic in nature, it takes into account explicitly both target and non-target species, and tries to track the trophic (including fishing) interactions that regulate the community. Second, the descriptors are derived from body size, which is a usually simple trait to measure, and from trophic levels, whose approximate estimates are readily available via the internet (see FishBase website). Nonetheless, the pragmatic use of such indicators in controlling exploited communities is still questionable and rather subject to debates (Daan 2005; Chassot 2005), because of their multivariate nature (Link 2005; Rochet et al. 2005). However, the removal of predators (and, in general, of larger fish) from freshwater lakes leads to more important and predictable effects of fishing than it does on reefs and in marine ecosystems (Jennings et al. 2001). This adds more confidence in monitoring temporally the community indicators for any tropical lake and river system, in order to find out the related time trends (it would be wise to explore a number of indicators together, because several of them are sensitive to fishing, but none is specific (Rochet et al. 2005)). The parameter estimates of the predicted time trends in the indicators should then be tested for the significance of reference directions due to fishing impacts (Trenkel and Rochet 2003; Rochet et al. 2005). Significant reference directions attributable to fishing should normally trigger operational management actions to mitigate fishing effects. Link (2005) also suggests some ways of translating ecosystem indicators into warning thresholds and limit reference points, but they must be adapted according to the experience one has of a particular fishery.

5 Conclusion

This study is a step toward the investigations on and application of the community attributes in tropical inland exploited fish communities. However, their usefulness will require (i) a good understanding of the fishery history and of demographic traits and trophic levels and interactions within the system; (ii) the availability of size data obtained through good survey designs and; (iii) the discernment of fishing effects from environmental effects. To meet the – ecosystem approach to fisheries – requirements for tropical inland fish communities, it is worth stressing on the particular need of designing standard survey methods and continuously collecting accurately the relatively inexpensive size data at exact species level.

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