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The impact of water hyacinth (*Eichhornia crassipes*) in a eutrophic subtropical impoundment (Lake Chivero, Zimbabwe). II. Species diversity

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With 4 figures and 6 tables

Abstract: We compared abundance and diversity of phytoplankton, zooplankton, and fishes among limnetic (P: always without macrophytes) and littoral habitats with (L+) and without (L–) hyacinths in Lake Chivero, a man-made hypertrophic reservoir near Harare (Zimbabwe). In addition, the littoral macrophyte community, and macro-invertebrates associated with hyacinth mats were inventoried. The phytoplankton community was dominated by blue-green algae (mainly *Microcystis aeruginosa*), typical for a hyper-eutrophic lake. Total absolute densities were about 10 to 30 times higher at the L+ sites than at the unvegetated L– and P sites. On the basis of relative species abundances the L– zones were more similar to the P than to the L+ zones. There was an increasing importance of chlorophytes (*Staurastrum* sp. and *Pandorina morum*) and diatoms (*Cyclotella meneghiniana* and pennales) and a decreasing dominance of *Mycrocystis* along the discriminant axis from L+, L– to P. The zooplankton community was most dense in the unvegetated zones. Daphnids and bosminids were more abundant in the pelagic than in both littoral zones. Calanoids and *Diaphanosoma* were dominantly represented in the unvegetated zones. The two littoral zones were characterised by higher densities of chydorids, while they could be discriminated by the dominance of cyclopoids in the vegetated site. Seventeen different fish species were captured by at least one of the different fishing methods. Apparent habitat preferences differed ac-

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cording to fishing method. Generally, *Oreochromis niloticus* and *Pharyngochromis acuticeps* preferred the vegetated sites, while mature specimens of *Clarias gariepinus* were caught in deeper water at pelagic sites. *Barbus paludinosus* and *Labeo cylindricus* preferred the rocky shores of the lake. The smaller size classes of *O. niloticus, Tilapia sparrmanii* and *P. acuticeps* preferred the littoral zone rather than the open waters. Water hyacinth mats generally seem to have a positive effect on taxon diversity only in fishes and were the preferred sites for only a limited number of groups, mainly zooplankton (cyclopoids and *Daphnia laevis*) and fishes (*O. niloticus* and *P. acuticeps*). The most important function of this weed could be to offer shelter and feeding grounds for small fishes.

Key words: dams, diversity, water hyacinth, phytoplankton, zooplankton, macro-invertebrates, fish.

Introduction

Submerged and floating water plants serve a number of important functions. In wetlands, a well-developed macrophyte community provides shelter against predation for vulnerable prey species like small zooplankton and fishes (Crowder & Cooper 1982, Diehl 1992, Batzer 1998). In addition, macrophytes are usually covered with epiphytes that are grazed upon by several invertebrates (van den Berg et al. 1997) that are themselves an important fraction of the diet of many fishes and birds (Batzer & Wissinger 1996). In general, lakes with a well-developed macrophyte community are characterised by a more diverse community of zooplankton (Timms & Moss 1984), benthos (Munro 1966), and fish (Olson et al. 1994). Within a single lake the vegetated sites often support a greater diversity of macro-invertebrates than do the open water sites (Olson et al. 1994, Savage & Beaumont 1997). However, non-native species such as the water hyacinth *Eichhornia crassipes* may seriously alter the ecosystem functions that macrophytes provide (Luken & Thieret 1997).

Ever since its introduction in Egypt (1879–1892), water hyacinth has spread throughout Africa's lakes and impoundments. Its prolific growth causes considerable economic problems and affects fisheries, traffic, irrigation, water supply and the whole ecology of the infested lake (Ogutu Ohwayo et al. 1997). It tends to invade waterbodies where hydrological or nutrient conditions have been altered by human activities (Barret 1989). Biological, chemical and mechanical control measures are expensive and hampered by reinfestation from its long-lived seeds.

This study attempted to evaluate the role of water hyacinth in maintaining diversity in Lake Chivero (formerly known as Lake McIlwaine), a eutrophic subtropical lake with some importance for tourism and fisheries, but which mainly provides water for Harare, the capital of Zimbabwe. The impact of water hyacinth on the water quality of the lake is discussed in another paper (Rommens et al. 2003). We have especially focused on the controversial opinion about water hyacinth as a pest versus its potential importance in maintaining diversity and improving water quality. In addition to species richness and diversity, the importance of hyacinth mats as preferred sites for phytoplankton, zooplankton or fish developmental stages was investigated while the associated macro-invertebrate community was inventoried.

Materials and methods

Lake Chivero is situated northwest of Harare (Zimbabwe). It was constructed in 1952 on the Manyame River to meet the increasing demands for drinking water. A detailed map with a description of the lake and sampling sites is given in another paper (Rommens et al. 2003). Organisms were sampled at randomly selected sites from three different habitat types: limnetic (P) and littoral zones with (L+) and without (L–) water hyacinth. Water, phytoplankton and zooplankton samples were collected at the same time and from the same places, but samples of macro-invertebrates and fish were sometimes taken a few days later at sampling sites chosen according to the presence or absence of floating water hyacinth mats. Water plants were surveyed during a separate trip.

Phytoplankton

Five phytoplankton samples were collected in each of the three different habitats: five sites in the littoral habitat with water hyacinth (L+), five sites in the littoral habitat without water hyacinth (L–) and five more sites in the open water habitat without water hyacinth (P) (total: 15 sampling sites). At each sampling site, six water samples were collected by means of a 3-litre Van Dorn bottle giving a total of 18 litres. At L+ and L– sites (maximum depth = 2 m) two samples (one under the surface, another above the sediment) were taken from three different places within the site. At the P sites (maximum depth = 20 m) the six samples were taken at different depth intervals (maximum interval = 3 m) depending on the depth of water at a site. All samples from each site were put into a 50-litre bucket and stirred after which a 5-litre sub-sample was taken and poured over a 20-µm plankton net. The contents of the net were subsequently washed in a 300-ml vial, fixed in a 4 %-formaldehyde solution and made up to 100 ml before further processing. After stirring each sample, a 0.04 ml sub-sample was transferred with a micropipette into a Bürker counting chamber and analysed under an Olympus inversion microscope at 400 × magnification. Taxa were identified at least to genus and, if possible to species level using Prescott (1962). The density (n°/L) and proportion (%) of each taxon was calculated from three sub-samples.

Macrophytes

During a boat survey, the whole lake was mapped by GPS to estimate the total surface area. During the survey, the number of macrophyte and helophyte species was determined and their percentage cover was expressed on an ACFOR abundance scale (abundant: 75–100 %, common: 50–75 %, frequent: 25–50 %, occasional: 5–25 %, rare: 0–5 %) (Kent & Coker 1992).

Zooplankton

Zooplankton samples were collected in the same way as the phytoplankton and the integrated sample was stirred before a 5-litre sub-sample was poured over a 64-µm plankton net. The contents were then washed into a 300-ml vial, fixed in a 4 % formaldehyde solution and made up to 50 ml before further processing. After stirring, a 10-ml sub-sample was poured into a counting tray and analysed under an Olympus dissection microscope at a 50 × magnification. Daphniidae, Bosminidae and Sididae were identified to species level using Elenbaas (1994) and Seaman (1999), other cladocerans to the genus level, and copepods to the main group level. Rotifers were not considered in the present study. The density (n°/L) and proportion (%) of the main taxa were calculated from three sub-samples.

Macroinvertebrates

To assess the macro-invertebrate community associated with water hyacinth mats, a 30 cm × 30 cm 'kick-net' with a 0.5-mm mesh size was swept under the hyacinth mats. Care was taken to avoid contact with the lake bottom to prevent collecting benthic organisms, although some mud was inevitably stirred up in the littoral samples. Samples were sorted in a white plastic tray with 2–3 cm of clear water. Most invertebrates were identified in the field. Species that could not be identified immediately (e.g. molluscs) were taken to the laboratory for microscopic examination of live specimens.

Fish

Fish were sampled with a variety of methods. Gill nets, both cotton and monofilament, were set overnight. The monofilament gill net series consisted of five nets measuring 30 m by 1.25 m with mesh sizes of 1, 2, 3, 4 and 5 cm, respectively. The cotton gill nets consisted of nine 30 × 1.5 m nets with mesh sizes of 2.5, 3, 3.5, 4, 4.5, 5.5, 6, 6.5, and 7.5 cm. In littoral sites only, fyke nets and electrofishing were additionally used. The fyke nets consisted of two fykes connected by a 12.5 m long net, and the total length of the gear was 18 m. Mesh size was 25 mm reducing to half size (12 mm) in the end. The fykes were set overnight. Electrofishing (10 minutes at each site) was done with a Type IVa Smith-Root electrofisher. All fishes were identified to species level according to Skelton (1993), counted, measured to the nearest millimetre, and weighed to the nearest gram. The catch per unit effort was standardized according to the sampling method: numbers per fyke per day for fyke nets, numbers per net per day for gill nets, and numbers per sample for electrofishing.

Statistical analyses

Discriminant function analysis was used to determine which species discriminated among the three different habitats. Phytoplankton and zooplankton samples were compared as proportions for species and main taxonomic groups. The species composition of the fish assemblage was calculated for each method separately and expressed as a percentage of the total catch. Shannon's index of diversity and Simpson's index of dominance were calculated using densities. In fish, these indices were calculated for each sampling method. All indices as well as individual species densities were tested by ANOVA for significant differences among the considered habitat types. The fish population structure was analysed using length-frequency distributions, which were tested for differences between habitats by the Kolmogorov-Smirnov two-sample test.

Results

Phytoplankton diversity

A total of 19 planktonic algal taxa were identified with the small pennate diatoms lumped together in one group (Table 1). The density of phytoplankton

Table 1. Phytoplankton taxon list with average densities (cells/L) for each habitat: pelagic (P), and unvegetated (L –) and vegetated (L +) littoral zones. Shannon-Wiener and Simpson diversity indices (± standard deviation) in the different habitats.

Taxon	Species	P	L–	L+
Chlorophyta	*Pandorina morum*	4.5	3.2	3.0
	Staurastrum sp.	3.4	5.3	4.9
	Pediastrum simplex	1.7	1.0	217.0
	Pediastrum duplex	1.6	0.8	2.7
	Merismopedia elegans	–	0.2	–
Cyanophyta	*Microcystis aeruginosa*	679.0	1683.5	25493.8
	Unidentifiable unicellular Blue green algae (<0.1 µm)	12.4	56.2	640.0
	Chroococcus limneticus	18.6	78.2	297.9
	Anabaena sp.	20.2	120.2	90.5
	Lyngbia cebennensis	4.1	0.2	3.2
	Lyngbia austiarii	0.8	–	–
	Dactylococcopsis sp.	0.7	–	–
Diatomaceae (Centrales)	*Melosira granulatum*	47.7	27.8	60.8
	Cyclotella meneghiniana	4.2	0.6	0.4
Diatomaceae (Pennales)	Pennales (small forms)	5.3	28.8	44.9
	Pinnularia borealis	–	–	0.2
	Cocconeis placentula	0.2	200.0	1.0
	Gyrosigma attenuatum	0.2	1.0	0.5
Euglenophyta	*Euglena* sp.	0.1	–	–
	Trachelomonas sp.	0.3	167.0	2.6
Total no/L		805.2	2007.4	26646.7
Shannon-Wiener index		0.6±0.4	0.6±0.3	0.3±0.3
Simpson index		0.7±0.2	0.7±0.2	0.7±0.2

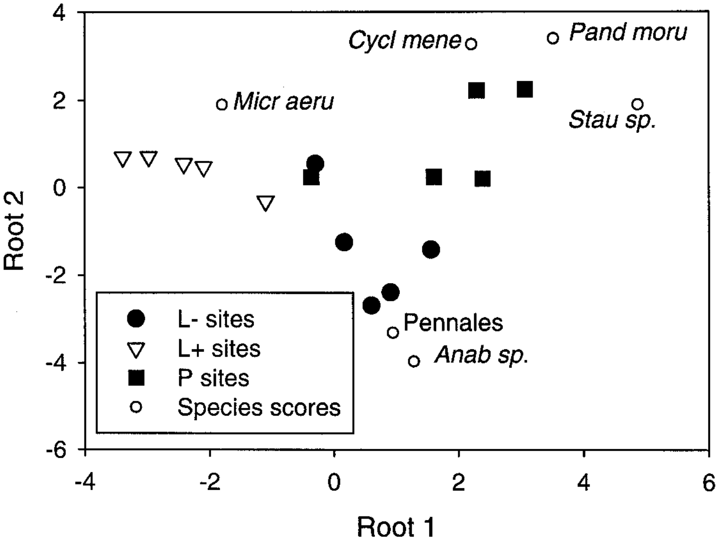

Fig. 1. A forward stepwise discriminant analysis of the selected habitats (P, L+, L−) in Lake Chivero based on the proportions of the main phytoplankton groups. Canonical scores (sampling sites) and species factor structure are presented. The species structure is multiplied by 10 for better interpretation. *Pand moru*: *Pandorina morum*; *Stau* sp.: *Staurastrum* sp.; *Cycl mene*: *Cyclotella meneghiniana*; *Micr aeru*: *Microcystis aeruginosa*; *Anab* sp.: *Anabaena* sp.

was about 10–30 times higher at the vegetated sites (L+) than at the unvegetated ones (L– and P). Cyanophyta, mainly *Microcystis aeruginosa*, were the dominant group in each habitat (>90 % in P, >96 % in L–, >98 % in L+) (Table 1). Only the Chlorophyta were significantly different among habitats (ANOVA, p = 0.002) being more abundant at the limnetic sites, while the Pennales and Cyanophyta tended to be more abundant in the littoral (L+, L–). A forward discriminant function analysis based on phytoplankton proportions retained six phytoplankton taxa in the model. The phytoplankton community in the unvegetated littoral (L–) was more similar to that in the limnetic (P) than to the one in the vegetated littoral (L+) (Fig. 1). The three habitats were best separated along the first function which correlated positively with the chlorophytes *Staurastrum* sp. and *Pandorina morum*, the diatoms *Cyclotella meneghiniana* and pennales, and *Anabaena* sp., and negatively with *Microcystis aeruginosa*. The Shannon diversity index was similar at the P and L– sites where it was (not significantly) higher than at the L+ sites (Table 1).

Macrophyte diversity

It was estimated that 83 ha (3.2 %) of the lake were covered with floating macrophytes, with the highest cover in sheltered bays in the middle part of the

Table 2. Macrophyte diversity in Lake Chivero expressed in an ACFOR scale, based on overall dominance according to DEN HARTOG & SEGAL (1964).

Species	Dominance	Morphology
Azolla filiculoides	Common	floating macrophyte
Echinochloa sp.	Frequent	rooted or floating helophyte
Eichhornia crassipes	Abundant	floating macrophyte
Hydrocotyle ranunculoides	Frequent	floating macrophyte
Lagarosiphon major	Rare	submersed macrophyte
Lemna minor	Occasional	floating macrophyte
Myriophyllum brasiliense	Frequent	floating macrophyte
Pennisetum sp.	Frequent	rooted helophyte
Phragmites australis	Frequent	rooted helophyte
Pistia stratiotes	Frequent	floating macrophyte
Polygonum senegalense	Common	rooted or floating helophyte
Pontederia cordata	Rare	rooted helophyte
Typha domingensis	Frequent	rooted helophyte

Table 3. Zooplankton taxon list with average densities (organisms per litre) for each habitat: pelagic (P), and unvegetated (L−) and vegetated (L+) littoral zones. Shannon Wiener and Simpson diversity indices (± standard deviation) in the different habitats.

Taxon	Species	P	L−	L+
Bosminidae	*Bosmina longirostris*	102.0	82.5	82.1
Chydoridae	*Chydorus* sp.	12.2	44.1	34.1
Daphniidae	*Ceriodaphnia dubia*	11.7	1.5	0.7
	Daphnia barbata	2.0	0.4	0.0
	D. laevis	0.2	3.0	0.0
	D. longispina	12.5	8.6	1.7
	D. lumholtzi	0.2	0.4	0.0
	D. obtusa	1.0	0.0	0.0
	D. pulex	1.4	2.4	0.3
Sididae	*Diaphanosoma excisum*	1.2	0.8	0.0
Copepoda	Calanoida	4.8	4.6	1.5
	Cyclopoida	31.9	21.8	33.5
Total number/L		181.2	170.1	153.8
Shannon-Wiener index		1.4±0.1	1.2±0.2	0.9±0.2
Simpson index		0.4±0.1	0.4±0.1	0.5±0.1

lake where plants accumulated due to wind drift. Water hyacinth *Eichhornia crassipes* dominated the helophyte community (Table 2). Submerged macrophytes were rare and restricted to some shallow zones with a sandy bottom, and the only species found was *Lagarosiphon major.*

Zooplankton diversity

A total of 12 microcrustacean taxa were identified and they tended to be more abundant at the unvegetated sites (P, L−) than at the vegetated ones (L+) (Ta-

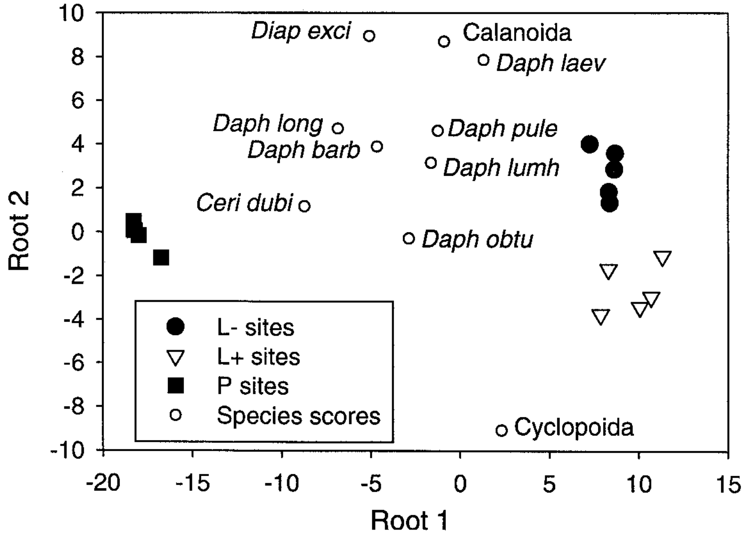

Fig. 2. A forward stepwise discriminant analysis of the selected habitats (P, L+, L−) in Lake Chivero based on the proportions of the main zooplankton groups. Canonical scores (sampling stations) and species factor structure are presented. The species structure is multiplied by 10 for better interpretation. *Daph barb*: *Daphnia barbata*; *Daph long*: *Daphnia longispina*; *Daph obtu*: *Daphnia obtusa*; *Daph pule*: *Daphnia pulex*; *Daph laev*: *Daphnia laevis*; *Daph lumh*: *Daphnia lumholtzi*; *Ceri dubi*: *Ceriodaphnia dubia*; *Diap exci*: *Diaphanosoma excisum*.

ble 3). Daphnids, except for *Daphnia laevis*, and bosminids were more numerous at the limnetic (P) than at the littoral sites. Chydorids, on the other hand, were most abundant in the littoral fringe. A forward discriminant function analysis based on the proportions of each species retained 11 taxa in the model. Limnetic and littoral habitats separated clearly along the first root, which correlated negatively with *Ceriodaphnia, Diaphanosoma*, and five daphnid species all of which were dominantly represented in the limnetic parts, and positively with *D. laevis* and Cyclopoida which were more abundant in the littoral zones (Fig. 2). The two littoral zones differentiated along the second root that correlated negatively only with *D. obtusa* and Cyclopoida, taxa that were more abundant in the vegetated littoral zone. The Shannon diversity index was significantly higher (Tukey HSD, $p<0.05$) in the limnetic than in the vegetated littoral zone (Table 3). The dominance index was highest in the vegetated littoral zone, but no statistical differences were detected.

Macroinvertebrate diversity

A total of 22 invertebrate taxa were identified from underneath the littoral hyacinth mats (Table 4). The weevil *Neochetina eichhorniae* (Coleoptera, Cur-

Table 4. Macro-invertebrates associated with water hyacinth mats in the littoral zone of lake Chivero.

Taxon	Family/Species
Annelida	Oligochaeta
Turbellaria	Planarians
Gastropoda	Planorbidae
	Bulinus tropicus
	Helisoma duryi
	Succineidae
	Oxyloma patentissima
	Thiaridae
	Melanoides tuberculata
	Viviparidae
	Bellamya capillata
Arachnida	*Labidognatha* sp.
	Lycosidae
Coleoptera	Unidentified coleoptera
	Neochetina eichorniae
Collembola	
Diptera	Chironomidae
	Culicidae
Ephemeroptera	Baetidae
Hemiptera	Belostomatidae
	Corixidae
	Notonectidae
	Veliidae
Odonata	Aeschnidae
	Libellulidae
	Platycnemidae

culionidae), which lives specifically on *Eichhornia crassipes* and is used as a biological control agent, was collected in four of the six samples in the hyacinth mats. Oligochaetes and chironomid larvae were present in some littoral samples because some mud was inadvertently collected.

Fish diversity

The different fishing methods yielded 17 different fish species of which seven were common to all methods used (Table 5). In total, 2439 fish were caught representing a wet weight of 113.6 kg. In terms of numbers *Pharyngochromis acuticeps* dominated the fish community representing 54 % of the total catch, followed by *Oreochromis niloticus* (19 %) and *Barbus paludinosus* (15 %). All other species represented less than 3 % each. The dominant species in terms of weight were *Clarias gariepinus* (37.5 %), *O. niloticus* (36.8 %) and *P. acuticeps* (14.2 %). Fyke nets set in the littoral caught a total of 275 fishes belong-

Table 5. Relative species composition (% of the total catch over all the sampling methods) of the fish assemblage at each habitat of Lake Chivero.

Family	Species	L+	L−	P
Centrarchidae	*Micropterus salmoides*	3.0	2.0	5.0
Characidae	*Hydrocynus vittatus*	–	2.0	–
	Micralestes acutidens	–	9.0	–
Cichlidae	*Oreochromis macrochir*	2.1	2.0	9.0
	Oreochromis niloticus	38.4	26.0	9.5
	Pharyngochromis acuticeps	27.4	22.3	39.0
	Pseudocrenilabrus philander	2.4	6.3	–
	Serranochromis robustus	1.6	1.6	–
	Tilapia rendalli	6.2	2.5	–
	Tilapia sparrmanii	5.1	5.9	6.6
Clariidae	*Clarias garipienus*	2.4	3.9	42.8
Cyprinidae	*Barbus paludinosus*	5.4	18.2	4.0
	Barbus trimaculatus	2.3	3.3	–
	Labeo altivelis	3.4	8.0	1.0
	Labeo cylindricus	1.0	2.0	3.0
Mormyridae	*Hippopotamyrus discorhynchus*	1.0	–	–
	Marcusenius macrolepidotus	2.9	0.1	–

ing to 15 different species, of which *O. niloticus* (35 %) and *B. paludinosus* (25 %) were the most numerous. Three hundred fish in 10 species were caught by electrofishing in the littoral with *O. niloticus* again being the dominant species (47 %). The monofilament gill nets caught a total of 1786 individuals of 15 different species, dominated by *P. acuticeps* (64 %), which together with *B. paludinosus* (16 %) and *B. trimaculatus* (3 %) occurred mainly near vegetated banks. Only 80 fish belonging to seven species were captured in the cotton gill nets with three species, *P. acuticeps*, *O. niloticus* and *C. gariepinus* accounting for more than 90 % of the total catch.

Discriminant analysis separated limnetic from littoral habitats along the first root with adult *C. garipienus* mainly caught in deeper limnetic waters (Fig. 3). The second axis separated to some extent vegetated from unvegetated sites. *Barbus paludinosus* and *Pseudocrenilabrus philander* correlated positively to this root indicating their preferences for rocky shores. *Tilapia rendalli* showed a negative correlation with the second root since its distribution was associated with water hyacinth.

Species diversity within the fish assemblage was, in general, higher in the vegetated than in unvegetated areas (Table 6). In addition, littoral habitats had more diverse assemblages than the pelagic part of the lake. Differences amongst diversity indices were, however, statistically not significant.

In general, all the fish sampling methods revealed that smaller individuals preferred the littoral rather than the limnetic waters of the lake. This is made

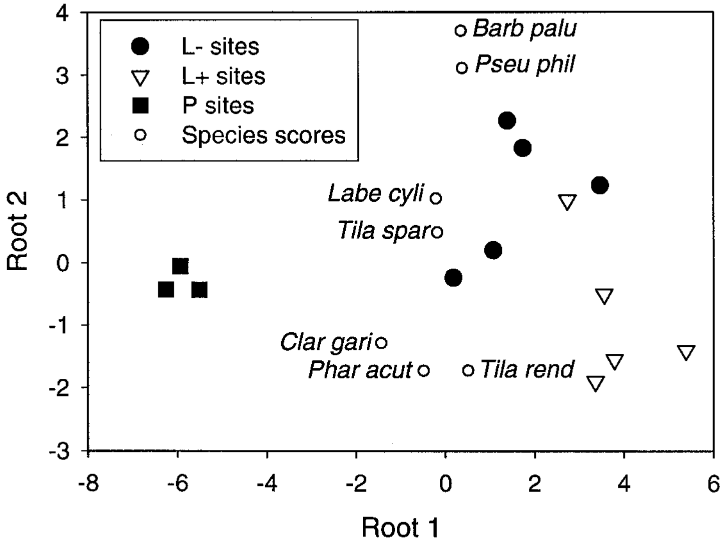

Fig. 3. A forward stepwise discriminant analysis of the selected habitats (P, L+, L−) in Lake Chivero based on the proportions of fish. Canonical scores (sampling stations) and species factor structure are presented. The species structure is multiplied by 10 for better interpretation. *Clar gari*: *Clarias garipienus*; *Phar acut*: *Pharyngochromis acuticeps*; *Tila rend*: *Tilapia rendalli*; *Tila spar*: *Tilapia sparrmanii*; *Labe cyli*: *Labeo cylindricus*; *Pseu phil*: *Pseudocrenilabrus philander*; *Barb palu*: *Barbus paludinosus*.

Table 6. Fish species diversity measured by Shannon and Simpson's diversity indices for vegetated and unvegetated sites and for the pelagic versus the littoral sites. Differences between indices were tested by ANOVA.

Fishing method	Hyacinths present	Hyacinths absent	P-level
Fyke nets			
Shannon-Wiener index	1.11	0.92	0.65
Simpson's index	0.47	0.30	0.29
Electrofishing samples			
Shannon index	0.91	1.02	0.76
Simpson's index	0.51	0.44	0.66
Gill nets			
Shannon index	0.94	0.69	0.42
Simpson's index	0.54	0.65	0.51
	littoral zone	pelagic zone	p-level
Gill nets			
Shannon index	0.99	0.50	0.12
Simpson's index	0.52	0.73	0.20

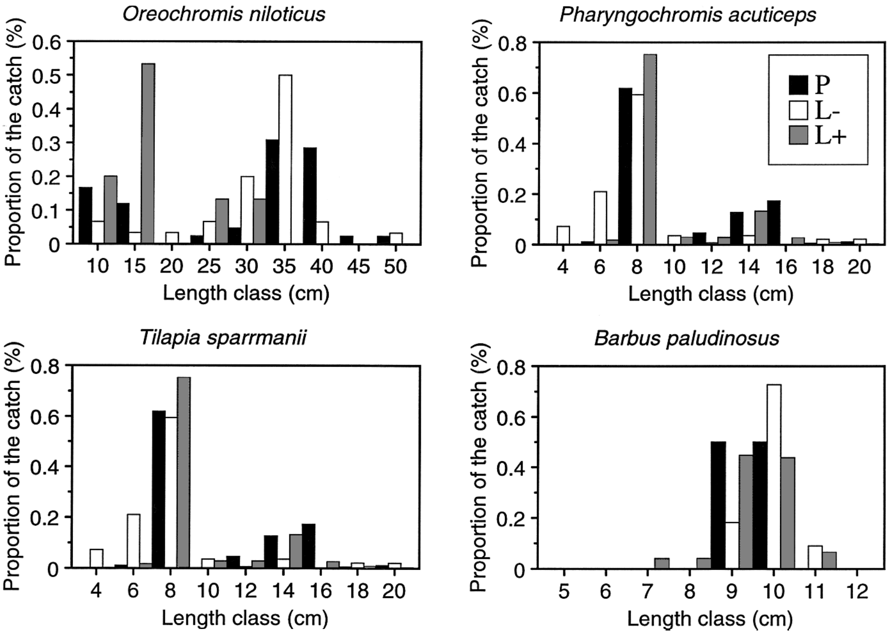

Fig. 4. Length frequency distributions of four fish species caught in three selected habitats (L+, L–, P) with different fishing techniques (gill nets, fyke nets, electrofishing).

clear by the length-frequency structure of *O. niloticus, T. sparrmanii* and *P. acuticeps* (Fig. 4). The average length of *O. niloticus* increased from 84 mm at L+ sites to 145 mm at L– sites and 271 mm at P sites. Lenght frequency distributions drawn for each sub-group were different at $p < 0.01$ (Kolmogorov-Smirnov two-sample test). Individuals of *T. sparrmanii* measured, on average, 96 mm in vegetated littoral sampling sites. Again, average length for this species was significantly higher (Kolmogorov-Smirnov two-sample test, $P < 0.01$) in unvegetated sites (L–: 110 mm; P: 143 mm). *Pharyngochromis acuticeps* caught at littoral sampling sites (L+: 82 mm; L–: 77.5 mm) were smaller than at limnetic sites (95 mm). This difference was significant at $p < 0.01$ (Kolmogorov-Smirnov two-sample test). Indivuals of *B. paludinosus* could not be discriminated based on average body size amongst the selected habitats (Fig. 4).

Discussion

Invasions of water hyacinth have become a nuisance worldwide (Drake & Mooney 1989). Originally perceived as a practical problem for fishing and navigation, water hyacinth is now considered as well a threat to biological diversity, affecting fish faunas, plant diversity and other freshwater life and the food chains, which depend upon it (Luken & Thieret 1997).

In Lake Chivero, there was no clear support for a considerable difference in overall species diversity at sampling sites covered by the plant when compared to non-covered sites. In comparison with non-vegetated sites, littoral sampling sites with hyacinth generally had a lower planktonic diversity and slightly higher fish diversity. Although we cannot present clear proof for this, these differences could to some extent be caused by the significant differences in physical and chemical variables among sites with and without water hyacinths as presented in the accompanying paper by ROMMENS et al. (2003).

Due to its physical presence water hyacinth greatly blocks sunlight and oxygen exchange and hence prevents growth of emersed and submerged plants. As a result, submerged macrophytes are scarce or absent in Lake Chivero, while floating species dominate the macrophyte community in the littoral zones of the lake. Before the expansion of water hyacinth in the lake, submerged and rooted floating-leaved macrophytes were common in shallow parts (MUNRO 1966). The loss of submerged macrophytes is dramatic as they have an important structuring and regulating role in the ecosystem: they stabilise the sediment (reduction of turbidity), compete for nutrients with phytoplankton; they increase the sedimentation rate and provide shelter from planktivorous predators for zooplankton species (JEPPESEN et al. 1997).

Another physical property of water hyacinth is that it entraps phytoplankton and detritus; phytoplankton abundance was an order of magnitude higher amongst water hyacinth mats than at sites free from water hyacinth. Especially the relative abundance of blue green algae of the genus *Microcystis* was higher than at other sites. The colonial structure of these algae probably enhanced entrapment. Cyanophyta typically occur in eutrophic lakes and reduce competition with other algae by producing toxic compounds (CARMICHAEL 1997). The dominance of blue green algae in the lake was already evident from earlier work (MUNRO 1966, FALCONER 1970, ROBARTS et al. 1982).

The absence of a well-developed macrophyte community and the decreased levels of oxygen under the canopy of water hyacinth (ROMMENS et al. 2003) may also be adverse for zooplankton richness and abundance. A lack of macrophytes, for example, increases exposure to visual predators while decreased oxygen levels may inhibit zooplankton growth. Unfortunately, there are no historical data available that could be used to assess Shannon-Wiener diversity before the infestation with water hyacinth in Lake Chivero. MUNRO (1966) compiled a species list and found *Ceriodaphnia dubia* to be dominant during most of the year, indicating, according to this author, mesotrophic conditions. MAGADZA (1994) attempted to use zooplankton to indicate the trophic status of the lake and recorded a list of dominant species as in our study. Their densities varied according to the position of the sampling sites but were in all cases much higher than in our study. For example, the density of *Bosmina longirostris* was 100 per litre in our study compared with 166 to more than 2000 per litre in Magadza's paper. Even more pronounced differences occurred in the daphnids, cyclopoids, and calanoids. One possible explanation for these differences in zooplankton densities is that we didn't sample the river mouths where zooplankton was most abundant. There is no comparable data on fish abundance and species composition to make out whether the changes were due to increased fish predation pressure.

Contrasting with the diversity at lower trophic levels, macro-invertebrates and fish apparently benefit from the presence of water hyacinth. When compared to the open water, the root and leaf structure of water hyacinth provides a complex habitat for these species. Mitchell & Marshall (1974) found a wide variety of species in mats of *Salvinia molesta* in lake Kariba, demonstrating the importance of floating weed mats for macroinvertebrate diversity. Olson et al. (1994) compared diversity and abundance of macro-invertebrates from three different macrophyte communities and an open water site in a Minnesota prairie marsh and found the largest numbers of organisms (mainly chironomid larvae) but the lowest diversity in the open water while the highest diversity occurred in the *Typha* sites. The high diversity (four families) and population sizes of snails in our study could be related to the lake's eutrophic state and a threefold increase in calcium in the lake water since 1975 (Marshall 1995). With their number and diversity of organisms, the vegetated sites may have an important function as feeding places for birds and some fishes. In several studies an association was shown between macro-invertebrate diversity and waterfowl use and productivity (Svingen & Anderson 1998).

Fish species diversity was, in general, higher at the vegetated sites than in the open water and was higher in the littoral zone when compared to the limnetic areas. Above all, however, apparent habitat preferences differed according to fishing method. By means of fyke netting, it was shown that the bulldog *Marcusenius macrolepidotus* which mainly feeds on benthic insects (Marshall 1982) had a strong preference for the vegetated zones while the barb species *Barbus trimaculatus* and *B. paludinosus* were only caught near rocky areas without hyacinths. On the basis of catches by electrofishing in the littoral zones, *O. niloticus* had a clear preference for the hyacinth-covered sites while the southern mouthbreeder *Pseudocrenilabrus philander* and *Pharyngochromis acuticeps* were caught in higher numbers in the uncovered areas. *P. acuticeps* dominated the monofilament catches and in contrast with the pattern revealed by electrofishing, occurred predominantly near vegetated banks. In contrast to the pattern obtained with fyke net catches *B. paludinosus* and *B. trimaculatus* also predominantly occurred in the vegetated sites. *Tilapia sparrmanii*, in turn, typically occurred in the pelagic zone. Apparent differences in habitat preference could also be due to diurnal movements into and away from warm shallow waters as is characteristic for many cichlid fishes and which, beside avoiding predators, could also be a means of improving physiological efficiency (Marshall 1982 and references therein). The most important function of water hyacinth for fish appears to be the provision of refugia and favourable feeding conditions. Smaller individuals of *O. niloticus, T. sparrmanii* and *P. acuticeps* preferred the littoral zone rather than the open waters of the pelagic area. Small fishes and juveniles, especially cichlids, need to escape predation, mainly by the tiger fish *Hydrocynus vittatus*, and they shoal in shallow 'nursery' areas (Marshall 1982). As they become larger, their vulnerability decreases and they move into deeper water.

In conclusion, water hyacinth mats did not clearly support a higher diversity of aquatic organisms than the unvegetated sites. In phytoplankton and zooplankton the diversity indices were even significantly higher in the unvegetated (littoral and pelagic) zones than at the vegetated littoral sites. Water hyacinth mats are evidently important for various macro-invertebrates that live on plant leaves (e.g. snails and arachnids). In fish there was only a trend towards a higher diversity in the water hyacinth-covered zones. The most important function of the hyacinth mats seems to be a sheltering or nursery function for small size classes of fish. Such a function is, however, not only performed by water hyacinth and could also be so by other macrophytes that were abundantly present in Lake Chivero before the lake was chemically treated against hyacinths (Jarvis et al. 1982).

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