

Diet and feeding habits of the small catfish, *Clarias liocephalus* in wetlands of Western Uganda

Jane Yatuha^{1*}, Jeremiah Kang'ombe² and Lauren Chapman³

¹Department of Biology, Mbarara University of Science and Technology, PO Box 1410, Mbarara, Uganda, ² Bunda College of Agriculture, University of Malawi, PO Box 219, Lilongwe, Malawi and ³Department of Biology, McGill University, 1205 Avenue Docteur Penfield, Montreal, QC, Canada, H3A 1B1

Abstract

Clarias liocephalus is an air-breathing catfish inhabiting wetland and river systems in East Africa. This catfish is in high demand for sale as live bait in the Nile perch fishery of Lake Victoria and equally important in the diet of local communities in the lake basin. Wetland loss and increasing fishing pressure potentially threaten the persistence of *C. liocephalus*; however, little information exists on the ecology of this species to permit evaluation of current threats. This study quantified dietary characteristics of *C. liocephalus* from heavy and lightly fished wetlands in Western Uganda using numeric, gravimetric and volumetric indices on 492 stomach samples collected over one year. *Clarias liocephalus* was significantly smaller in three heavily fished sites, relative to the one in-park site, likely a reflection of a size-selective fishery. Across sites, *C. liocephalus* was a generalist feeder whose diet was dominated by aquatic dipteran larvae and plant material. The broad niche gives *C. liocephalus* an ecological advantage to forage effectively on a wide selection of prey. The significant presence of plant material shows that the species may utilize plant protein, an important consideration of diet requirements should the species be selected for aquaculture.

Key words: papyrus swamp, clariid catfish, stomach contents

Résumé

Clarias liocephalus est un poisson-chat, capable de respirer l'air, qui vit dans les systèmes de zones humides et de rivières d'Afrique de l'Est. Ce poisson est très demandé par les pêcheries du lac Victoria comme appât vivant pour la capture de perches du Nil et il est aussi important dans le

régime alimentaire des communautés locales du bassin du lac. La perte de zones humides et la pression croissante de la pêche pourraient menacer la survie de *Clarias liocephalus*. Cependant, peu d'informations existent sur l'écologie de cette espèce, qui permettraient l'évaluation des menaces actuelles. Cette étude a quantifié les caractéristiques alimentaires de *Clarias liocephalus* des zones humides fortement et légèrement exploitées de l'ouest de l'Ouganda en utilisant des indices numériques, gravimétriques et volumétriques pour 492 échantillons stomacaux récoltés pendant un an. Les *Clarias liocephalus* étaient significativement plus petits dans trois sites où la pêche est très intense que dans un lieu situé dans un parc, ce qui est probablement un reflet d'une pêche sélective par la taille. Sur tous les sites, *Clarias liocephalus* se nourrissait de façon généraliste et son régime se composait surtout de larves aquatiques de diptères et de matières végétales. Cette large niche donne à *Clarias liocephalus* un avantage écologique puisqu'il se nourrit efficacement d'un vaste choix de proies. La présence importante de matières végétales montre que cette espèce est capable d'utiliser des protéines végétales, un détail important si cette espèce en venait à être choisie pour l'aquaculture.

Introduction

Clarias liocephalus is an air-breathing catfish found in wetland and river systems of South-Western Uganda and is more widely distributed in East African wetland systems (Teugels, 1986; Chapman, 1995). *Clarias liocephalus* is a senior synonym of *Clarias carsonii* according to Teugels (1986), although in Uganda, it is still commonly known by the latter name (Chapman, 1995). This particular clariid is one of the 'small' fishes that constitute an integral part of the diets of

*Correspondence: E-mail: jyatuha@yahoo.com

many human population groups (Thilsted, 2012); and in Uganda, it has been for decades a favoured source of protein for rural communities who exploit the wetland fishery because of its proximity and free accessibility.

Clarias liocephalus has significant economic, ecological and nutritional attributes, in part associated with its very high biomass in the dense interior of papyrus-dominated wetlands extensively distributed in East Africa and the Nile Basin (Chapman, 1995; Management Plan for Rwizi-Rufuha wetland system, 2009). Its abundance in the wetlands of Uganda is an indication that *C. liocephalus* is well adapted to colonize the niche successfully. However, the demand of this fish as bait to catch larger fish especially the Nile perch *Lates niloticus* (Ajangale, 2007), has resulted into indiscriminate fishing to satisfy the market. The high fishing pressure and the current degradation of the wetland habitat (National Environment Management Authority, 2006/07) may affect the persistence of this species in the region.

There are only a few published accounts of the biology and ecology of most of the 'small' clariids (Fagbenro, 1990; Elakhame, 2006) in general and *C. liocephalus* in particular. Defining the feeding habits and identifying food resources that sustain *C. liocephalus* in its natural habitat is important in understanding the species' role in the wetland food web and its influence on other organisms in the ecosystem (Amundsen, Gabler & Stalvik, 1996). It is also useful to understand the ecological needs of species and how changes in the biological and physical conditions of the habitat may affect their energy requirements and acquisition (Garrison & Link, 2000). This is particularly critical, given the pressure on wetland ecosystems in the region and conversion of wetlands to other land use practices. For example, valley wetlands are often channelled to increase grazing and agricultural land, which may challenge resident fish species with changes in the physico-chemical environment.

Quantification of fish diets is also important in defining nutritional requirements of potential aquaculture species able to utilize food items available in culture environments (Pauly, 1976; Ibrahim *et al.*, 2003; Mbabazi, 2004; Begum *et al.*, 2008). Although there are some observations on the feeding ecology of *C. liocephalus* in rivers and lakes (Mbabazi, 2004; Kasangaki, 2007), no feeding ecological study has been carried out specifically for this species in a wetland habitat where it appears to have a very high biomass. Concurrent with diet studies, length and weight data provide a basis for estimating the production potential of a fishery in any given habitat

and together these metrics can contribute to bioenergetics models that could be very useful in managing the *C. liocephalus* fishery and for culture. Length frequency data also serve as an important baseline for monitoring populations over time in response to management strategies (Anderson & Neumann, 1990).

The purpose of this study was to quantitatively describe the diet composition and feeding patterns, and condition of *C. liocephalus* across ontogenic, spatial and seasonal gradients. The findings could provide benchmark information for sustainable utilization, conservation and management of *C. liocephalus* in wetland habitats.

Materials and methods

Study area

The study area was the Rwizi-Rufuha wetland system of Uganda (Fig. 1) a chain of wetlands along River Rwizi, which stretches from Bushenyi and parts of Ntungamo districts, through Mbarara and Lake Mburo before entering Lake Victoria. R. Rwizi is a very important resource shared by all communities in the region and is currently under threat from anthropogenic degradation (Management Plan for Rwizi-Rufuha wetland system, 2009). We selected specific sampling sites according to the level of fishing pressure (regulated and not regulated) and dominant emergent vegetation (*Papyrus* and *Miscanthidium* sp.). The four sites were coded as Bush, but, Lake Mburo Conservation Area (LMCA) and Rucece. The LMCA site, found in L. Mburo National Park, has controlled fishery, but the rest of the sites are accessed freely.

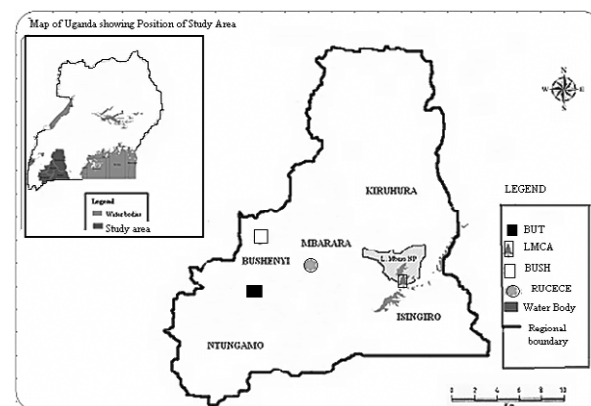


Fig 1 Study site location along the Rwizi-Rufuha wetland system S/W Uganda

Sample collection and stomach content analysis

Live adult and juvenile *C. liocephalus* specimens were collected from fishers at the four sites on a monthly basis from January to December 2011. All fish were caught using local basket traps, a gear that is used by all *C. liocephalus* fishers in the region. The fish were euthanized with a lethal dose of clove oil and transported on ice to the laboratory where they were dissected and the stomachs excised following standard procedures (e.g. Gomiero & Braga, 2004). For each specimen, we recorded site of capture, sex, total length and standard length (to the nearest 1 mm), total weight and eviscerated weight (to the nearest 0.01 g), stomach weight (to the nearest 0.01 g) and stomach fullness (coded as 0: empty; 1: less than ½ full; 2: ½ full; 3: full and 4: bursting). Stomachs with food were preserved in 10% formaldehyde for further analysis, while empty stomachs were recorded as empty and discarded.

Prey items in the stomach were sorted and identified to the lowest possible taxon under a stereo-microscope at 5x to 28x magnification, using published guides (Thorp & Covich, 1991; Bouchard, 2004; Alberta Biodiversity Monitoring Program, 2007).

Stomach contents were analysed using a combination of numeric, volumetric and gravimetric methods as described in previous studies (Hyslop, 1980; Winemiller, 1990; Gomiero & Braga, 2004; Montana & Winemiller, 2009) to minimize the shortcomings of each method when used singly. The Importance Index and the Feeding Strategy Index further minimized the limitations of numeric and gravimetric indices.

The Frequency of Occurrence Index was used to describe the frequency at which particular prey appeared in the diet of *C. liocephalus* in general and to illustrate seasonal and ontogenic changes in diet composition of the species (Frost, 1977). The Volumetric Analysis Index was used to describe the relative abundance of specific prey items in the stomach samples (Lima-Junior & Goitein, 2001; de Mérona, Vigouroux & Horeau, 2003). The points ascribed to each food item were later transformed into an arithmetic mean to represent a mean abundance of the item in the sample.

$$M_i = \sum i/n$$

where M_i is the mean of the ascribed points for the i th food item, \sum_i is the sum of ascribed points for the i th food item; n is the total number of stomachs with food in the sample. The importance index (AI) was used to determine prey

importance in the feeding habit of *C. liocephalus* (Lima-Junior & Goitein, 2001).

$$AI_i = F_i * V_i$$

where: AI_i : Importance Index of the i th food item in the sample; F_i : Frequency of Occurrence of the i th food item; V_i : Volumetric Analysis index of the item.

Feeding intensity (FI) was determined by analysing changes in the mean weight of stomach contents (Man & Hodgkiss, 1977). $FI = (\text{Total stomach contents' weight} / \text{eviscerated fish weight}) * 100$.

The Feeding Strategy Index was assessed using the Costello (1990) method with modifications by Amundsen, Gabler & Staldvik (1996) where the Prey Specific Abundance Parameter (P_i) was plotted against Frequency of Occurrence (F_o) to generate a prey distribution plot defining the feeding strategy of the species. A cumulative prey curve was used to define the adequacy of the number of stomachs collected to accurately describe diets in the sample (Cort'es, 1997).

Data analysis

We used Frequency of Occurrence, Volumetric Index and Importance Index to describe the quantitative importance of prey in the diet of *C. liocephalus*. FI was determined by analysing changes in the mean weight of stomach contents and feeding strategy was assessed by a modified Costello method. Adequacy of stomachs for analysis was determined using the cumulative prey curve. (Hyslop, 1980; Winemiller, 1990; Amundsen, Gabler & Staldvik, 1996; Lima-Junior & Goitein, 2001; Gomiero & Braga, 2004; Chrisfi, Kaspiris & Katselis, 2007; Montana & Winemiller, 2009). The length–weight relationships of fish from different sites were analysed using nonparametric tests. Data were entered in Excel 2007 spread sheet, and statistical analysis was performed using SPSS statistical software (SPSS Inc, Chicago, IL, USA).

Results

Size distribution

The size of *C. liocephalus* from the 4 sites ranged between 5.3 and 29.6 cm total length and 1.24–138.6 g total weight. There was a significant variation in total length (Kruskal Wallis test $P < 0.01$) between LMCA and the rest

of the sites. In LMCA, 96.3% of the fish were above 15 cm TL ($n = 242$), while in Bush ($n = 204$), But ($n = 246$) and Rucece ($n = 156$), the percentage of fish above 15 cm was far less: 7.4%, 42% and 35%, respectively (Fig 2).

The diet of *C. liocephalus*

Out of 748 stomachs dissected, 264 (35%) were empty and 492 (65%) had food. Fifty-two types of prey taxa were identified and categorized into twelve broad groups (Table 1).

Aquatic dipterans, dominated mainly by Chironomidae and Culicidae larvae contributed the highest percentage

in terms of frequency of occurrence of prey (52.5%) and volumetric abundance (19.5%), followed by plant materials which contributed 52.2% frequency and 14% volumetric abundance. Chironomid larvae alone contributed 20.4% and Culicidae 14%. The prey category 'fish' comprised a low contribution to the diet of *C. liocephalus* with respect to both numerical abundance (4.2%) and frequency of occurrence (9.4%) indices, but volumetrically (16.7%), it was the second most important prey next to dipterans (19.5%). There were only 12 whole fish in all the guts analysed, and they were only found in stomachs from one site (But). The prey importance index, a combination of frequency and volumetric indices, also showed that aquatic dipterans dominated the diet of *C. liocephalus* (34%) followed by plant materials (24%).

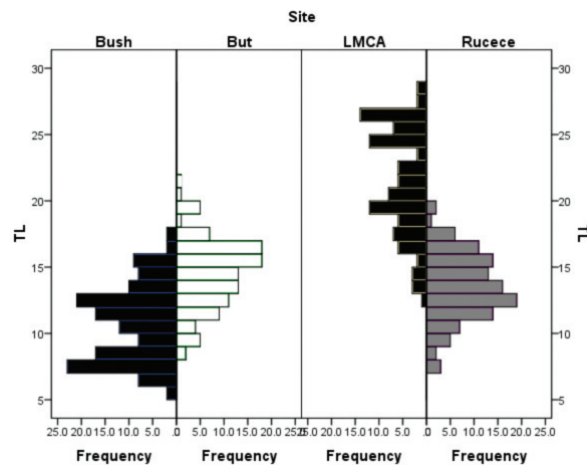


Fig 2 Size distribution of *C. liocephalus* in the four sites [$n = 459$. Bush (1) 139, But (2) 108, LMCA (3) 99, Rucece (4) 113]

Feeding strategy of *C. liocephalus*

The distribution of prey categories in the feeding strategy plot (Fig. 3) depicts a mixed feeding strategy with specialization for fish (high specific abundance but low frequency) and generalization for diptera and plant material (high specific abundance and high frequency). Terrestrial insects, molluscs and hemipterans were rare (low specific abundance and low frequency). The overall pattern that emerges for *C. liocephalus* is a generalist strategy (Fig 3). With respect to ontogenic shifts in the diet of *C. liocephalus*, generally all size groups consumed most prey categories. However, fish prey was totally absent in the small-size classes.

Table 1 Major prey categories and their importance in the diet of *Clarias liocephalus*

Major prey groups Prey ID	Occurrence index		Numeric index		Volumetric index		Importance index (Vol.*Frequency)
	Frequency	%Frequency	Number	% by No.	Volume	%Vol.	
Terrestrial insects	16	5.03	21	1.58	10	1.83	36.81
Hemiptera	20	6.29	20	1.51	8.75	1.60	40.26
Molluscs	21	6.60	55	4.14	9	1.65	43.48
Odonata	22	6.92	32	2.41	11.5	2.10	58.21
Unidentified prey	27	8.49		0.00	25.75	4.71	112.56
Fish	30	9.43	56	4.22	91.5	16.74	631.52
Nonprey items	55	17.30		0.00	1	0.18	12.65
Other	58	18.24	177	13.33	33	6.04	569.40
Detritus	85	26.73		0.00	76	13.90	1,486.20
Coleoptera	90	28.30	140	10.54	50.25	9.19	1,040.45
Insect parts	97	30.50	000	0.00	46.5	8.50	1,037.69
Plant material	166	52.20		0.00	77	14.08	2,959.74
Diptera	167	52.52	827	62.27	106.5	19.48	4,091.76

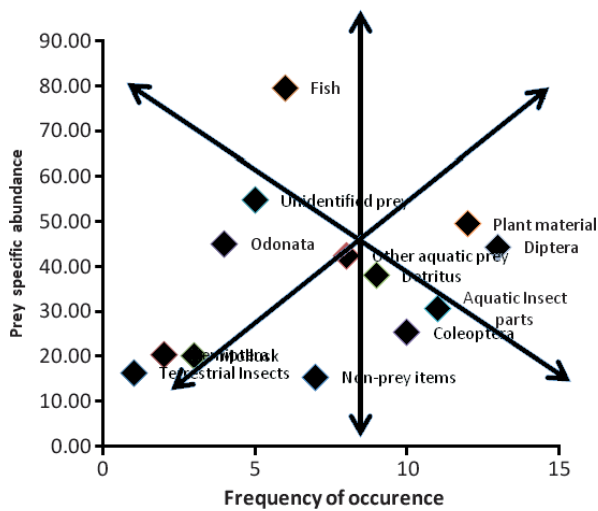


Fig 3 Feeding strategy plot for *C. liocephalus* (analysis follows Amundsen, Gabler & Staldivik, 1996)

Because size distribution was not uniform across all sites, prey choice between sites was run for two size groups (10–15-cm TL and 15.1–20-cm TL), which were represented in all the sites. Results showed that in But, Bush and Rucece, detritus was the most important dietary component by volume (20.5–44.4%), followed by diptera (13.9–34.4%) and plant material, while in LMCA, the important prey were dipterans (47.9%), followed by plant material (22.2%) (Fig. 4).

Feeding intensity

The proportion of empty stomachs by site shows that only one site (But) had more empty stomachs than nonempty ones. The overall percentage of stomachs with prey was high (63%). Results on feeding intensity (FI)

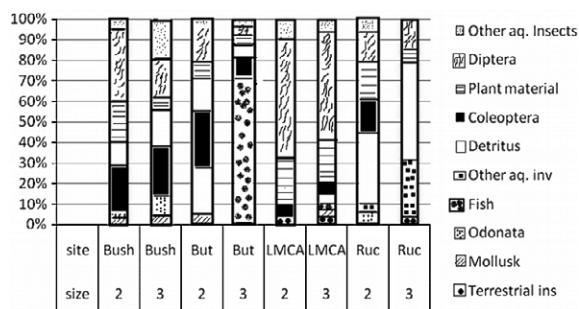


Fig 4 Prey importance for size 2 and 3 across study sites

Table 2 Variations in feeding intensity by gut weight across site, size, sex and season

By site	Fi by gut weight	n	Mean Fi
Bush	369.42	133	2.78
But	212.02	113	1.88
LMCA	64.89	99	0.66
Rucece	296.18	119	2.49
By size			
1	244.63	68	3.60
2	443.80	195	2.28
3	192.66	129	1.49
4	48.66	48	1.01
5	12.76	25	0.51
By sex			
F	400.95	206	1.95
M	288.89	196	1.47
By month			
January	46.72	29	1.61
March	53.62	25	2.14
April	44.03	27	1.63
May	45.02	23	1.96
June	149.07	90	1.66
July	27.50	14	1.96
August	20.87	21	0.99
September	36.27	21	1.73
November	5.64	14	0.40
December	50.27	31	1.62

Data for February and October were excluded from the analysis due to very small sample sizes.

are summarized in Table 2. FI was highest in March (2.14) and lowest in November (0.4). Site Bush had the highest mean FI (2.78) and LMCA had the lowest (0.66). There was no significant difference between females, FI (1.95) and males, FI (1.47). FI by size showed size 1 (<10-cm TL) and 2 (10–15-cm TL) to have the highest FI and size 5 (>25-cm TL) the lowest. There was no seasonal variation in the occurrence of the different prey categories.

Discussion

The outstanding disparity in fish size distribution across the sites may be attributed to fishing pressure. The largest fish were captured from the LMCA site, which is located in a national park where fishing is regulated, while the smallest sizes came from the open access wetlands where fishing is indiscriminate and uncontrolled.

Aquatic insects in general and dipteran larvae in particular were found to be the most frequent prey in the diet of *C. liocephalus* across all sites, showing *C. liocephalus*' preference for dipteran larvae. This preference has been reported in *C. gariepinus* (Yalcin, Akyurt & Solak, 2001) and *C. ebriensis* (Ezenwaji, 2002) and has been attributed to the high abundance of the prey in the habitat (Yalcin, Akyurt & Solak, 2001). *Clarias liocephalus* seem to forage on the available and dominant prey as a generalist, but prefers dipteran larvae when they are present in the habitat.

Although modern catfishes are generally known to be benthic feeders, (Bruton, 1979), the presence of benthic (e.g. chironomids) and non-benthic (e.g. culicids) prey taxa shows that *C. liocephalus* in wetland habitats has the capacity to effectively forage at different levels. The dominance of detritus in the stomachs of *C. liocephalus* further confirms the species' primarily benthophagic feeding habit.

Plant materials formed an important prey category in the diet of *C. liocephalus* second only to aquatic insects. This is an indication that *C. liocephalus* may have the potential to utilize plant protein. The abundant plant material and detritus among other prey categories in the diet of *C. liocephalus* defines the ecological role, this species plays in converting resources at the base of the food chain into food for higher trophic levels. This has been found in other wetland fish species (Bruton & Jackson, 1983). The wide food spectrum of the species and the significant presence of plant material in its diet revealed by this study point to the possibility of *C. liocephalus* as a candidate for aquaculture because it would not require expensive animal protein in its feed.

Feeding intensity (FI) in *C. liocephalus* decreased with increase in body weight (Table 2). This is in agreement with what has been reported in other fish species including as an example *C. batrachus* (LINN), Thakur (1978), and supports the idea that the catfish tends to eat less intensively as it grows. High FI in March coincided with dry period during the study period. This could be a strategy by *C. liocephalus* to build up energy reserves in preparation for the breeding period. This has been observed in other catfishes as reported by Owolabi (2007). The low FI in the month of November coincides with the peak breeding period for *C. liocephalus* (Yatuha 2012, unpublished data). Decline in FI during the peak reproductive period has been reported in other fish species (Dadzie 2007; Ezenwaji, 2002; Preciado *et al.*, 2006). In this study, we observed that ripe gonads, especially in females, filled almost the

entire body cavity. This may, at least in part explain the low feeding intensity in gravid female fishes.

The findings of this study show that *C. liocephalus* feeds on a wide range of prey taxa. Therefore, it shares a euryphagous and omnivorous feeding habit with other clariids like *C. gariepinus* and *C. anguillaris* (Offem, Samsons & Omoniyi, 2009; Alhassan, Commey & Boyorbor, 2011). From the little published information describing the diet of *C. liocephalus*, it is categorized as an insectivore (Greenwood, 1966; Mbabazi, 2004). The disparity between our findings and earlier findings could be due to the difference in sample sizes and sampling sites; the specimens for this study were purely obtained from a wetland ecosystem as opposed to the previous samples. It could also be that *C. liocephalus*, being a generalist feeder, selects prey depending on availability rather than preference and that availability differs across the range of habitats where this species has been studied. This has been observed in other generalist fish species (Kaiser *et al.*, 2002).

The relatively high frequency of empty stomachs (35%) in *C. liocephalus* may be partly explained by the general nocturnal feeding behaviour in catfishes (Bruton, 1979). As traps were set overnight, fish that were trapped early in the night got into the trap with empty stomachs. Scarcity of prey material in the habitat is another possible explanation. We found that most of the empty stomachs occurred in the same site where cannibalism was registered. As this site was also heavily fished, it could mean that fishing pressure and prey scarcity may prompt cannibalism in this species. Fishing pressure has been reported to have an effect on prey acquisition by fish (Garrison & Link, 2000).

The feeding strategy plot (Fig. 3) suggests that *C. liocephalus* is unspecialized in its feeding habit. It has a high within phenotype contribution to niche breadth because many individuals utilized most prey items simultaneously. This behaviour is an optimal strategy especially in habitats that are prone to change (Kaiser *et al.*, 2002; Sreeraj, Raghavan & Prasad, 2006). Terrestrial insects were among the least important prey in the diet of *C. liocephalus*. This presupposes the minimal contribution of allochthonous food resources in the diet of *C. liocephalus*. This may reflect the vegetation cover because we concentrated sampling on heavily vegetated wetlands. Vegetation cover is one of the limiting factors to allochthonous resource availability in aquatic food webs (Hideyuki, 2009).

Ontogenic changes in prey choice by *C. liocephalus* were generally not very distinct. Major prey categories occurred

in the diet of all sizes, but in different proportions. For example, fish and other large prey taxa were largely absent in the small-sized fish samples, indicating that the frequencies and abundance of major prey categories change with size of the fish.

Lack of dramatic ontogenic shifts may reflect the fact that very young stages were not captured in the samples we used for this study. Occurrence of major prey categories across all sizes also points to a possibility of intraspecific competition in *C. liocephalus*. Competition becomes likely when prey occurrence is above 25% in two or more size classes Hyslop (1980). Accordingly, there is a competition for all prey taxa whose occurrence exceeds 25% (Table 1).

The presence of *C. liocephalus* juveniles in some stomach samples pointed to possible cannibalistic feeding habit in this species. However, the low level of occurrence for *C. liocephalus* prey (2.8%) and the generally low occurrence of fish prey (9.4%) suggests that cannibalism and the use of fish in *C. liocephalus* diet is not as pronounced as it is in the large- and medium-sized clariids like *C. gariepinus* and *C. ngamensis* (Barton, 1979; Merron, 1993; Winemiller & Winemiller, 2003).

We conclude that *C. liocephalus* is a generalist feeder that draws prey from several trophic levels depending on the availability. The major prey taxa in its diet are aquatic dipterans and plant material. The size distribution is strongly related to fishing pressure, and this may affect the life history of this fish in the future.

Acknowledgements

We are grateful to the Regional Universities Forum for Capacity Building in Agriculture (RUFORUM) and their partners for funding this project; to Bunda College University of Malawi and Mbarara University for the practical and technical support, and to Dr. Rutaisire and Dr. Sikawa for their input in this study.

References

- AJANGALE, N. I. (2007) The Aquaculture Potential of Indigenous Catfish (*Clarias gariepinus*) in the Lake Victoria Basin, Uganda. Ph.D thesis, University of Stirling, Scotland, UK.
- ALBERTA BIODIVERSITY MONITORING PROGRAM (2007) Laboratory Protocols for Aquatic Invertebrate Processing. Version 2.2. Alberta, Canada. Available at: <http://www.abmp.arc.ab.ca> (accessed 25 January 2011).
- ALHASSAN, E.H., COMMEY, A. & BOYORBOR, T.B. (2011) An investigation into the food and feeding habits of *Sarotherodon galilaeus* (Pisces:Cichlidae) in a shallow tropical reservoir. *Res. J. Fish. Hydrobiol.* **6**, 74–77.
- AMUNDSEN P.A., GABLER H.M. & STALDVIK F.J. (1996) A new approach to graphical analysis of feeding strategy from stomach contents data – modification of the Costello (1990) method. *J. Fish Biol.* **48**, 607–614.
- ANDERSON, R. O. & NEUMANN, R. M. (1990) Length, Weight and Associated Structural Indices. In: Fisheries Techniques (Eds B. R. Murphy and D. W. Willis) 2nd ed. American Fisheries Society (1996), Bethesda, MD.
- BEGUM, M., ALAM, M.J., ISLAM, M.A. & PAL, H.K. (2008) On the food and feeding habit of an estuarine catfish (*Mystus gulio* Hamilton) in the south-west coast of Bangladesh. *Univ. J. Zool. Rajshahi Univ.* **27**, 91–94.
- BOUCHARD, R.W. JR (2004) Guide to Aquatic Macroinvertebrates of the Upper Midwest. Water Resources Center, University of Minnesota, St. Paul, MN, 208pp.
- BRUTON, M.N. (1979) The food and feeding behaviour of *Clarias gariepinus* (Pisces: Clariidae) in Lake Sibaya, South Africa, with emphasis on its role as a predator of Cichlid. *Trans. Zool. Soc., London* **35**, 47–114.
- BRUTON, M.N. & JACKSON, P.B.N. (1983) Fish and fisheries of wetlands. *J. Limnological Soc. Southern Africa* **9**, 123–133.
- CHAPMAN, L.J. (1995) Seasonal dynamics of habitat use by an air-breathing catfish (*Clarias liocephalus*) in a papyrus swamp. *Ecol. Freshw. Fish* **4**, 113–123.
- CHRISFI, P., KASPIRIS, P. & KATSELSIS, G. (2007) Feeding habits of sand smelt (*Atherina boyeri*, Risso 1810) in Tichonis Lake (Western Greece). *J. Appl. Ichthyol.* **23**, 209–214.
- CORTES, E. (1997) A critical review of methods of studying fish feeding based on analysis of stomach contents: application to elasmobranch fish. *Can. J. Fish. Aquat. Sci.* **54**, 726–738.
- COSTELLO M.J. (1990) Predator feeding strategy and prey importance: a new graphical analysis. *J. Fish Biol.* **36**, 261–263.
- DADZIE, S. (2007) Food and feeding habits of the black pomfret, *Parastromateus niger* (Carangidae) in the Kuwaiti waters of the Arabian Gulf. *Cybium* **3**, 77–84.
- ELAKHAME, L.A. (2006) The distribution, feeding and reproduction of Clarioid species in Epe creek floodplain of the Niger delta, Nigeria. *Trop. Freshw. Biol.* **15**, 83–94.
- EZENWAJI, H.M.G. (2002) The biology of *Clarias ebriensis* Pellegrin, 1920 (Osteichthyes: Clariidae) in an African rainforest river basin. *Fish. Res.* **54**, 235–252.
- FAGBENRO, O.A. (1990) Food composition and digestive enzymes in the gut of pond-cultured *Clarias isheriensis* (Sydenham 1980), (Siluriformes: Clariidae). *J. Appl. Ichthyol.* **6**, 91–98.
- FROST, W.E. (1977) The food of charr, *Salvelinus willughbii* (Gunther), in Windermere. *J. Fish Biol.* **11**, 531–547.
- GARRISON, L.P. & LINK, J.S. (2000) Dietary guild structure of the fish community in the Northeast United States continental shelf ecosystem. *Marine Ecol. Prog. Ser.* **202**, 231–240.
- GOMIERO, L.M. & BRAGA, F.M.S. (2004) Cannibalism as the main feeding behaviour of tucunares introduced in Southeast Brazil. *Brazil. J. Biol.* **64**, 625–632.

- GREENWOOD, P.H. (1966) The Fishes of Uganda. pp. 85–86. The Uganda Society, Kampala, Uganda.
- HIDEYUKI, D. (2009) Spatial patterns of autochthonous and allochthonous resources in aquatic food webs. *Popul. Ecol.* **51**, 57–64.
- HYSLOP, E.J. (1980) Stomach contents analysis: a review of methods and their application. *J. Fish Biol.* **17**, 411–429.
- IBRAHIM, S., MUHAMMAD, M.A., AMBAK, M.Z., ZAKARIA, A.S., MAMAT, M.M., ISA, M. & HAJISAMAE, S. (2003) Stomach content of six commercially important demersal fish in the South China Sea. *Turkish J. Fish. Aquat. Sci.* **3**, 11–16.
- KAISER, M.J. & JENNINGS, S. (2002) Ecosystem effects of fishing. In: Handbook of Fish Biology and Fisheries (Eds Hart, P. J. B. and Reynolds, J. D.). Blackwell Publishing, Oxford, Vol. 2.
- KASANGAKI, A. (2007) Fish Fauna of the Bwindi Impenetrable National Park along a Deforestation Gradient. Ph.D. thesis, Mbarara University of Science and Technology, Mbarara, Uganda.
- LIMA-JUNIOR, S.E. & GOITEIN, R. (2001) A new method for the analysis of fish stomach contents. *Acta Scientiarum Maringá* **23**, 421–424.
- MAN, H.S.H. & HODGKISS, I.J. (1977) Studies on the ichthyo-fauna in Plover Cove Reservoir, Hong Kong: feeding and food relations. *J. Fish Biol.* **11**, 1–13.
- Management Plan for Rwizi-Rufuha wetland system (2009) Wetland sector strategic plan. Ministry of Water and Environment, Kampala, Uganda.
- MBABAZI, D. (2004) Trophic characterization of the dominant fishes in the Victoria and Kyoga lake basins. Ph.D. Thesis, Makerere University, Kampala, Uganda.
- DE MÉRONA, B., VIGOUROUX, R. & HOREAU, V. (2003) Changes in food resources and their utilization by fish assemblages in a large tropical reservoir in South America. *Acta Oecol. Int. J. Ecol.* **24**, 147–156.
- MERRON, G.S. (1993) Pack-hunting in two species of catfish, *Clarias gariepinus* and *C. ngamensis*, in the Okavango Delta, Botswana. *J. Fish Biol.* **43**, 575–584.
- MONTANA, C.G. & WINEMILLER, K.O. (2009) Comparative feeding ecology and habitats use of *Crenicichla* species (Perciformes: Cichlidae) in a Venezuelan floodplain river. *Neotrop. Ichthyol.* **7**, 1679–6225.
- National Environment Management Authority (2006/07) State of Environment Report for Uganda. NEMA, Kampala. 332pp.
- OFFEM, B.O., SAMSONS, Y.A. & OMONIYI, I.T. (2009) Trophic ecology of commercially important fishes in the Cross river, Nigeria. *J. Animal and Plant Sci.* **19**, 37–44.
- OWOLABI, O.D. (2007) The dietary habits of the upside-down catfish, *Synodontis membranaceus* (Osteichthyes: Mochokidae) in Jebba lake, Nigeria. *Int. J. Trop. Biol.* **56**, 931–936.
- PAULY, D. (1976) The biology, fishery and potential for culture of *T. melanotheron* in small West Africa Lagoon. *Aquaculture* **7**, 33–49.
- PRECIADO, I., VELASC, F., OLASO, I. & LANDA, J. (2006) Feeding ecology of black anglerfish *Lophius budegassa*: seasonal, bathymetric and ontogenic shifts. *J. Mar. Biol. Assoc. United Kingdom* **86**, 877–884.
- SREERAJ, N., RAGHAVAN, R. & PRASAD, G. (2006) The diet of *Horabagrus brachysoma* (Gunther), an endangered bagrid catfish from Lake Vembanad (South India). *J. Fish Biol.* **69**, 637–642.
- TEUGELS, G.G. (1986) A systematic revision of the African Species of genus *Clarias* (Pisces; Clariidae). *Musee Royal de l'Afrique Centrale Tervuren Belgique Annales* **247**, 1–199.
- THAKUR, N.K. (1978) On the Food of the Air-breathing Catfish, *Clarias batrachus* (LINN.) Occurring in Wild Waters. *Int. Rev. Hydrobiol.* **63**, 421–431.
- THILSTED, S.H. (2012) The potential of nutrient-rich small fish species in aquaculture to improve human nutrition and health. [Internet] World fish centre. Available from: www.worldfishcenter.org/tags/nutrition (accessed 10 June 2012).
- THORP, J.H. & COVICH, A.P. (eds.) (1991) Ecology and Classification of Freshwater Invertebrates. Academic Press, Inc., San Diego, CA.
- WINEMILLER, K.O. (1990) Spatial and temporal variation in tropical fish trophic networks. *Ecol. Monogr.* **60**, 331–367.
- WINEMILLER, K.O. & WINEMILLER, K.L.C. (2003) Food habits of tilapiine cichlids of the Upper Zambezi River and floodplain during the descending phase of the hydrology cycle. *J. Fish Biol.* **63**, 120–128.
- YALCIN, S., AKYURT, I. & SOLAK, K. (2001) Stomach Contents of the Catfish (*Clarias gariepinus* Burchell, 1822) in the River Asi (Turkey). *Turk. J. Zool.* **25**, 461–468.

(Manuscript accepted 07 October 2012)

doi: 10.1111/aje.12048