Preliminary Assessment of the Feeding Ecology of Silver Catfish (*Schilbe intermedius*, Ruppel, 1832) in a Seasonal Floodplain of the Okavango Delta

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Abstract

This study investigates the feeding ecology of *Schilbe intermedius* across its entire life history. Data were collected using experimental fishing nets in two habitats in a seasonal floodplain. The results showed that *S. intermedius* has an ontogenetic shift in feeding behaviour where the young fish are primarily generalist predators, feeding on aquatic invertebrates while the older fish are more specialised predators feeding primarily on fish. This study showed that there is a higher potential for intra-specific competition among the older fish than in the younger size classes. However, it was recognized that this study is a snap-shot of the feeding ecology of *S. intermedius* and that a longer time series study is needed to study its feeding ecology.

Introduction

The richness and variability of floodplain habitats provide a wide range of possible food organisms and substrates which originate either from within the aquatic system itself or from outside the system (Welcomme, 1979). Michelsen *et al* (1994) point out that food accessibility can affect competition, mortality, fecundity and growth within a fish community. Garrison and Link (2000) highlight that different size classes of the same species may play functionally different ecological roles. In essence, this means that food requirements for the younger life stages of the same species can be completely different from the adult stages (Hellawell, 1972; Welcomme, 2001). Isumbisho *et al* (2004) argue that resource use/sharing and intra-specific competition can be better understood by studying the feeding behaviour among the different size classes in a fish population. Therefore, studying the feeding ecology of a particular species without analysing its feeding behaviour across its demographic structure might not provide a complete picture of resource use and partitioning.

According to Welcomme (1979), the feeding behaviour of floodplain fish is highly seasonal, piscivorous predators are generally very common, and their relative abundance tends to increase during the dry season. Bruton *et al* (1984) point out that fish in the river and permanent swamps of the Okavango Delta have long food chains and show feeding specialization, whereas those in the seasonal swamps have short food chains and are generalized feeders. Beetz (2004) found that predatory fish species dominate in the river channels, while omnivorous feeders are more prevalent in the floodplain.

Merron and Bruton (1988) concluded that most Okavango Delta fish are detritivores, insectivores or piscivores, except the red-breasted tilapia (*Tilapia rendalli*) which is truly herbivorous. Merron (1993) found that two catfish species, *Clarias gariepinus* and *C. ngamensis* practice pack hunting on mormyrids when the floods begin to recede in the Delta. Certain fish species alter their diets significantly throughout their life cycle, which minimises intra-specific competition (Zahorcsak *et al*, 2000; Rossi, 2001; Lyons 2003; Walter *et al*, 2003).

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While several studies have been conducted on the feeding ecology of *Schilbe intermedius* (van der Waal, 1985; Merron and Bruton, 1988; Merron, 1991; Teferra, *et al*, 2003), no study has systematically analysed its feeding strategy throughout its life history. According to Bergman and Greenberg (1994), the interaction of different size classes within (and between) species creates very complex competitive interactions in fish communities. Therefore, it is envisaged that this study will give a clear picture of the life history strategy of the silver catfish, and provide a baseline for a more detailed analysis of its feeding ecology over a long time series.

The objectives of this study were to determine prey composition and abundance in the study area, to determine the feeding behaviour of *S. intermedius* (silver catfish) across several size classes (e.g. prey selectivity, dietary overlap, etc.), and to assess potential intra-specific competition.

Materials and Methods

Data Collection

Two kinds of experimental fishing nets, a monofilament and multifilament, were used to sample the fish population. These nets were set for approximately 10 hours during the day and 12 hours overnight to account for diurnal variations in diet. One type of net consisted of 12 mesh panels, each 3 m long. The different meshes in the various panels were arranged in a geometric series: 10, 13, 16, 20, 25, 31, 39, 48, 58, 70, 86, and 110 mm stretched meshes. The other type of net consisted of 9 mesh panels, each 10 m long. The different meshes in this series were also arranged geometrically: 22, 28, 35, 45, 57, 73, 93, 118, and 150 mm stretched meshes. Sampling was done in the river channel and lagoon habitats of Nxaraga shown in Figure 1.

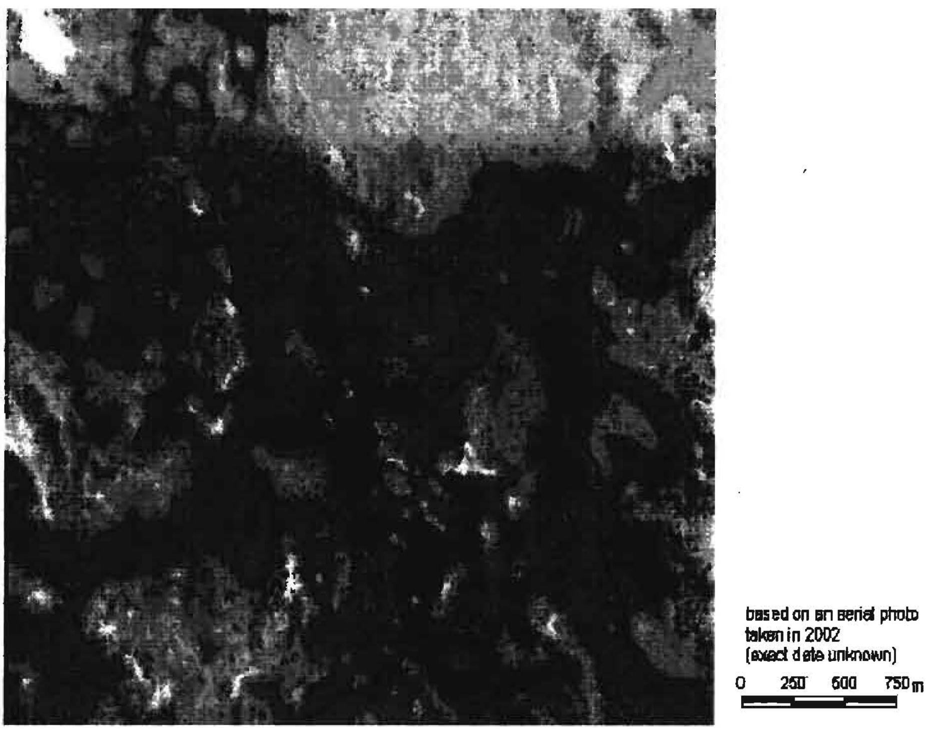

Figure 1. Aerial photo of the study area showing the two sampling points, Nxaraga lagoon and river channel habitats.

After removal from the nets, the fish were weighed, measured (from tip of the snout to tip of the caudal fin), and the gut contents removed and preserved in ethanol. Back in the laboratory, prey items were washed into a Petri-dish and identified as suggested by Clegg (1974) to order, separated, and counted (in the prey count, fish heads were counted as individuals). The dry weight (of the prey items) was determined by drying at 60°C for 24 hours and weighed in milligrams using a Mettler Toledo AR21 comparator weighing balance.

Aquatic macro invertebrates were collected using a 0.50 m 0.50 m 0.50 m grid (in order to assess available prey), which was dropped randomly over a selected area. All the organisms inside the grid were removed using a D-net. Samples were then preserved in ethanol in the laboratory and classified to order only.

Data Analysis

Index of relative importance (IRI)

Index of relative importance (IRI) (Kolding, 2000) was calculated to determine the most important taxa in the samples.

$$\%IRI_i \quad \frac{(\%W_i + \%N_i) \times \%F_i}{\sum_{j=1}^{S} (\%W_j + \%N_j) \times \%F_j} \times 100 \qquad (1)$$

Where

$\%W_i + \% N_i$ is percentage weight and number of each group/taxa of total catch

$\%F_i$ is percentage frequency of occurrence of each species in total number of samples

S is total number of species

Diversity Indices

Shannon's Diversity Index (H') and Relative Evenness (J') (Kolding, 2000) were also calculated using the equation

$$H' = -\sum_{i=1}^{S} P_i \times \ln(Pi) \qquad (2)$$

Where

P_i is the relative abundance of individuals found in the i^{th} species

$$J' = \frac{H'}{H_{max}} \quad H_{max} = \ln(S) \qquad (3)$$

$$J' = H' / H_{max} \quad \text{Where} \quad H_{max} = Ln(S) \qquad (4)$$

Dietary overlap

Horn's overlap index was calculated according to Sturdevant *et al* (2001)

$$R_o = \frac{(p_{ij} + p_{ik}) x \ln (p_{ij} + p_{ik}) - p_{ij} x \ln p_{ij} - p_{ik} x \ln p_{ik}}{2 x \ln 2} \qquad (5)$$

Where
P_{ij} is the proportion of prey group i in group j
P_{ik} is the proportion of prey group i in group k

Diet Specialization
The degree of diet specialization by the different size classes of the silver catfish population was calculated through the diet breadth index according to Rosas-Alayola *et al* (2002)

$$B_i = \frac{1}{\sum_j^r P_{ij}^2} \quad (6)$$

Where, P_{ij} is the proportion in numbers of prey group (i) at size class (j). Low values ($1 < B_i < 2$) represent predators with specialized diet, medium values ($2.1 < B_i < 3$) represent predators with less specialized diet, while high values ($B_i > 3$) represent generalist predators.

Results

Prey Availability
As shown in Table 1, only nine prey groups were found in the study area. Fish are the most important prey items in the study area (highest IRI value of 8716), followed by Ephemeroptera, Odonata, Hemiptera and Diptera, thus making the top five most important prey items in the study area. The least important prey item were Gastropoda, which has the lowest IRI value of 47. Shannon's diversity index (H') had a mean value 1.098 ± 1.473 while relative evenness (J') had a mean value of 0.532 ± 0.693. While diversity is not very high, the relatively high mean evenness value suggests that the prey community is not dominated by a single group.

Table 1. Relative abundance and composition of prey groups sampled from the study area. The fish group is composed of four cichlids species (Tilapia, spp, Oreochromis spp, and Serranochromis spp) and four cyprinid species (Barbus spp and a Aplocheilichthys spp).

Species	No	%	Weight	%	IRI	%
Fish	17	6.49	0.725	80.67	8716	47.5
Ephemeroptera	162	61.83	0.05	5.56	6740	36.73
Odonata	29	11.07	0.063	7.01	1808	9.85
Hemiptera	23	8.78	0.008	0.86	482	2.63
Diptera	10	3.82	0.003	0.33	208	1.13
Coleoptera	11	4.2	0.009	1	130	0.71
Miscellaneous	4	1.53	0.007	0.78	115	0.63
Tadpoles	4	1.53	0.024	2.67	105	0.57
Gastropoda	2	0.76	0.01	1.11	47	0.26
Sum	262	100	0.899	100	18350	100

Diet Composition
As summarized in Table 2, 16 prey groups were identified from the silver catfish guts. Fish were the most important prey items according to IRI (8017), while detritus was the least important prey item as shown by the lowest IRI value of 1. The other top four important prey items (after

Table 2. Prey abundance and composition collected from 183 silver catfish guts in the study area. The fish group is composed of four cichlids species (Tilapia, spp, Oreochromis spp, and Serranochromis spp) and four cyprinid species (Barbus spp and a Aplocheilichthys spp).

Prey Item	No	%	Weight	%	IRI	%
Fish	33	12.69	10.167	67.47	8017	41.36
Chironomids	123	47.31	0.014	0.09	4740	24.46
Mouse	2	0.77	4.462	29.62	3038	15.68
Ephemeroptera	22	8.46	0.047	0.31	878	4.53
Odonata	12	4.62	0.093	0.61	523	2.7
Tricoptera	27	10.38	0.001	0.01	520	2.68
Coleoptera	11	4.23	0.076	0.5	474	2.44
Miscellaneous	12	4.62	0.017	0.12	473	2.44
Terrestrial Insects	11	4.23	0.005	0.03	427	2.2
Digested invertebrates	0	0.38	0.145	0.97	135	0.7
Digested plant material	0	0.38	0.029	0.19	58	0.3
Gastropoda	2	0.77	0.003	0.02	39	0.2
Arachnida	1	0.38	0.003	0.02	20	0.1
Hemiptera	1	0.38	0.002	0.02	20	0.1
Diptera	1	0.38	0	0	19	0.1
Detritus	0	0	0.002	0.01	1	0
Sum	260	100	15.068	100	19381	100

fish) in descending order are chironomids, Ephemeroptera, and odonata. Shannon's diversity index (H') for the prey groups has a mean value of 1.372 ± 2.037, while the relative evenness (J') has a mean value of 0.614 ± 0.671. Diversity of prey items is slightly high and the relatively high mean evenness value suggests that there is no single dominant group in the prey items.

Dietary Overlap

Dietary overlap is summarized in Tables 3 and 4. According to Table 3, the only relatively significant diet overlap occurs between groups C and D (~ 0.59), and it also appears to be relatively strong between groups C and E (~0.35). For chironomids, diet overlap is strongest between groups B and E (~0.58) and second strongest between groups A and E (~ 0.47). Diet overlap for chironomids is also relatively strong between groups D and E (~0.41) and also between groups A and B (~0.37). Table 4 shows a significant diet overlap for fish between all the size classes in the silver catfish population. The strongest overlaps occur between the larger size classes, the strongest occurring between groups C and E (~0.999), while the weakest overlap occurs between group A and B (~0.603). There is no significant diet overlap for other prey groups except for some slightly stronger overlap for Odonata between groups A and B.

Diet Specialization

Diet specialization is summarized in Table 5, which shows a progressive decrease in the diet breadth index from the smallest fish (group A) to the largest fish (group E). This suggests that the smallest fish have a generalist diet (indicated by high values) while the older fish exhibit a tendency towards a more specialized diet (indicated by low values). The total value for silver catfish is > 3, which suggests that it is a generalist predator.

Table 3. Summary of Horn's dietary overlap index calculated for several size classes of the silver catfish population in the study area. The index values in this table were calculated using frequencies of the different prey items within the prey groups.

Length group	Coleoptera	Odonata	Ephemeroptera	Diptera	Fish	Chironomids	Terrestrial Insects
A vs. B	0.054670123	0.1564077	0.0705529	0.019203826	0.075978144	0.372066	0.04384819
B vs. C		0.1806747		0.019972076	0.129882908	0.121535	0.03102149
C vs. D					0.588756398	0.100864	
D vs. E					0.334303833	0.411313	
A vs. C		0.1804806		0.049633109	0.244619517	0.108625	0.08163187
A vs. D	0.066995519		0.0484011		0.233310331	0.27874	
A vs. E					0.163660276	0.471175	
B vs. D	0.041765785		0.0733107		0.125048668	0.328939	
B vs. E					0.0942668	0.581576	
C vs. E					0.353114883	0.141468	

Table 4. Summary of Horn's dietary overlap index calculated for several size classes of the silver catfish population in the study area. The index values in this table were calculated using dried weight of the different prey items within the prey groups.

Length Group	Coleoptera	Odonata	Fish	Chironomids
A vs. B	0.004520218	0.259238	0.603333	0.044757797
B vs. C		0.0103607	0.810722	0.000227303
C vs. D			0.997126	9.2277E-05
D vs. E			0.998282	0.000322611
A vs. C		0.0107244	0.723644	0.000252768
A vs. D	0.001829493		0.722774	0.001451853
A vs. E			0.723644	0.001528477
B vs. D	0.003813748		0.810555	0.001260234
B vs. E			0.811581	0.001324864
C vs. E			0.998509	9.39918E-05

Table 5. Summary of the diet breadth index by size class for the silver catfish in the study area. (*a*) denotes the index calculated from dry weight values while (*b*) denotes the index calculated from frequencies. The sum value gives the total diet specialization index calculated for the silver catfish.

Length Group	(a)	(b)
50-100 (A)	2.541116628	2.012628337
101-151 (B)	1.972202491	1.372843115
152-202 (C)	1.005310546	0.999742395
203-253 (D)	1.006224131	0.946687958
254-304 (E)	1.00066554	0.62333528
Sum	7.525519337	5.955237085

Discussion

In this study an analysis of the feeding habits of *S.intermedius* showed a diverse diet which agrees with earlier (van der Waal, 1985; Merron and Bruton, 1988; Merron, 1991; Skelton, 2001; Teferra *et al* 2003) observations. Fish is the most important prey group for *S.intermedius* which agrees with Merron and Bruton's (1988) observations while detritus is the least important. However, this disagrees with Welcomme (2001) who describes *S.intermedius* as a meso-predator feeding on crustaceans and insects. Some of the prey fish species (for *S.intermedius*) identified by Merron and Bruton (1988) were cichlids, characins and cyprinids, while van der Waal (1985) observed that small cichlids comprised about half of identifiable fish remains in silver catfish diet. Results from this study show a similar trend, where approximately 50% of the prey fish species were small cichlids.

Other studies have observed that the silver catfish is a generalist predator (van der Waal, 1985; Merron and Bruton, 1988). The high relative evenness value (0.6) indicates that there is no single dominant prey group for *S.intermedius*, thereby suggesting that *S.intermedius* is a generalist predator. Moreover, the fact that silver catfish feed across several trophic levels by preying on both animal (e.g. fish, mice, aquatic macro-invertebrates) and plant (e.g. digested plant material) matter (Table 2) reinforces its generalist feeding behaviour. Furthermore, the presence of terrestrial insects and mice in the diet could also suggest an opportunistic feeding strategy. It is possible that terrestrial insects and mice were fed upon during the arrival of flood-waters when their habitats were flooded out making them vulnerable to predation from silver catfish, which agrees with a similar observation by Merron and Bruton (1988). This opportunist feeding behaviour makes *S.intermedius* highly adapted to the variable floodplain environment and agrees with Welcomme (1979) that a highly variable feeding behaviour is common in floodplain fish.

S.intermedius has an ontogenetic feeding where younger fish (size classes A and B) have a higher selectivity for aquatic macro-invertebrates while larger fish (size classes C - E) are more piscivorous, which agrees with van der Waal's (1985) observations. Moreover, Merron and Bruton (1988) also observed that younger fish feed disproportionately on aquatic insects while older fish fed more on fish and terrestrial insects. Therefore, this study shows that *S.intermedius* is not simply an 'opportunistic, generalized insectivore and piscivorous predator' (Merron, 1991), but is rather an 'opportunistic, generalized insectivore' at smaller/younger sizes that morphs into a relatively more specialized 'piscivorous predator' at older/larger sizes.

Generally, an ontogenetic feeding strategy might suggest lack of intra-specific competition, where older fish are assumed not to compete for food with younger fish (Zahorcsak *et al*, 2000). This study however shows that there is a potential for intra-specific competition among the older fish while competition for food among the younger fish appears to be minimal. The presence of intra-specific competition among older fish is based on the observation that older fish are more specialized predators, which suggests that they have a higher chance to compete for similar prey groups. Notwithstanding, there also appears to be some potential competition for Chironomids between older and younger fish. Nonetheless, intra-specific competition is minimised by habitat segregation by the different size classes in the population (Persson, 1983).

However, Begon and Mortimer (1986) and Reynolds (1998) caution that competition does not necessarily suggest 'competitive exclusion', where a population's ability to grow into successive generations is negatively affected due to decreased fecundity and survivorship. Therefore, Begon *et al* (1986) argue that competition can increase population fitness where the relative contribution of stronger individuals in the population masks the less competitive/ weaker individuals. They highlight that the effects of intra-specific competition are density dependent, which suggests that a spatial and temporal analysis of fish growth and mortality as factors of density can paint a clearer picture of the impacts of population density on fish survivorship. Begon and Mortimer (1986) also discuss what they call 'reciprocity' in intra-specific competition. They argue that since competing individuals are inherently equivalent, like the older *S.intermedius* in this study, the competitive roles of weaker vs. stronger individuals can be reversed.

Notwithstanding, Reynolds (1998) discusses that the effects of competition are well masked in dynamic environments, which are subject to perturbations. He highlights that there is a constant reassembly and reorganization of structure in biological systems of such environments where species inter-relationships and interactions are in constant flux. A floodplain system therefore, with its shifting and changing conditions, would perhaps accentuate the positive attributes of competition in the silver catfish population instead of decreasing its competitive from what Merron and Bruton (1988) call an efficient predator in the flood-plain fish community. Persson (1983) also highlights that intraspecific competition results in decreased size class diversity and reduced growth rates, which are indicative of competitive exclusion. Nonetheless, more research is required to study the effects of this observed intra-specific competition in the *S.intermedius* population in temporal and spatial dimensions.

Despite the obvious time restriction, this study has shown that there is resource partitioning in the *S.intermedius* population, where young fish are primarily insectivorous while adults are piscivorous. The observed potential intra-specific competition for food among the older *S.intermedius* is most probably dampened by the presence of a diverse prey fish community in the seasonal floodplain. Dynamic environmental conditions also suggest that food availability is in a state of flux, which may also present conditions conducive for competitive exclusion. There is still a need to study the feeding ecology of the larval stages of *S.intermedius*, to better understand its life strategy within the dynamic seasonal floodplain habitat.

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