

***Trophic niche overlap of the fry
and juveniles of Oreochromis leucostictus
(Teleostei, Cichlidae) in the littoral zone
of a tropical lake (L. Naivasha, Kenya)***

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ABSTRACT

The mixture of regular seasonal flooding, varying lake levels and the presence of Papyrus mats and floating Salvinia creates restricted conditions in the highly productive shallow littoral zone. The prevailing conditions, advantages and disadvantages of this area as a fry nursery for Oreochromis leucostictus are reported and discussed. In the light of the potentially high intraspecific competition identified, resource partitioning and dietary switching in the fry is assessed. Two distinct feeding types are recognised — micropredation and later browsing on periphytic algae and detritus, with a tentative third phase suggested as a possibility, that of additional predation on larger insects. It is suggested that the most probable reason for this switch resulting in reduced competition is ontogenetic change in dietary physiology.

KEY WORDS : Oreochromis — Fry — Niches — Behaviour — Fresh waters — Fish — Tropical environment — East Africa.

RÉSUMÉ

CHEVAUchement DE NICHE TROPHIQUE CHEZ LES ALEVINS ET JUVÉNILES D'*Oreochromis leucostictus* (TELEOSTEI, CICHLIDAE) DANS LA ZONE LITTORALE D'UN LAC TROPICAL (LAC NAIVASHA, KENYA)

*L'inondation saisonnière régulière et les variations de niveau d'eau du lac, combinés à la présence de Papyrus et de Salvinia, se traduisent par des conditions de milieu particulières dans la zone littorale peu profonde. Les conditions naturelles, les avantages et les désavantages prévalant dans cette zone de croissance des alevins d'*O. leucostictus* sont présentés puis discutés. En raison de la forte compétition intraspécifique potentielle constatée, le partage des ressources et le changement de régime alimentaire des alevins ont été étudiés puis évalués. On distingue deux types de régime : dans un premier temps les alevins sont microprédateurs, puis ils broutent le périphyton et la pellicule détritique. Il est possible que, lors d'une troisième phase, s'ajoute une prédation complémentaire sur des insectes de plus grande taille. Un changement ontogénétique de la physiologie de l'alimentation est vraisemblablement le facteur entraînant cette évolution temporelle du régime.*

MOTS-CLÉS : Oreochromis — Alevins — Niche — Comportement — Eaux douces — Environnement tropical — Afrique de l'Est.

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INTRODUCTION

The theory of niche and attempts to quantify its dimensions are not new and have been the subject of much published material (MAY and MACATHUR, 1972; PIANKA, 1974; LEVINS, 1968; SCHOENER, 1970). Resource partitioning studies in fish are extensively reviewed by ROSS (1986), in which he identifies 34 such studies on freshwater fish, 17 on lake and 17 in stream ecosystems. Most of the studies identified confine their approach to partitioning within communities of different taxonomic structure, with little consideration of this phenomenon between life stages of the same species; a state of affairs which he regards as being in need of redress.

Shallow marginal areas of lakes and large rivers have frequently been attributed with high levels of productivity resulting in their value as fry nursery and juvenile growth areas (STEWART, 1988; HICKLEY and BAILEY, 1987; HYSLOP, 1986; GETACHEW, 1987). The seasonal nature of some of these zones resulting in creation of newly flooded shallows is suggested as being even more productive and hence offering more to fry populations (STEWART, 1988; BALOGUN, 1986; GREEN, 1985) although the prevailing physico/chemical conditions of habitats with floating plant mats may be somewhat hostile (TOWNSEND and PEIRSON, 1988; DONNELLY, 1969).

Given the obvious advantages of using shallow newly flooded marginal areas as nursery regions,

together with the comparatively variable conditions and the limited individual space available, an assessment of the niche dimension and overlap between different size categories of fry was carried out with regard to dietary components only, in an attempt to ascertain the degree to which this resource could be divided to give optimum food supply to individuals which on the face of it would be under intense intraspecific competition.

MATERIALS AND METHODS

Study Site

The study site was an area of littoral shore line of Lake Naivasha, a freshwater lake situated at 1890 m above sea level approximately 100 km north of Nairobi, Kenya (see Fig. 1). The particular area of shore line used was that described by GAUDET and MUTHURI (1981) as Mennell's Lagoon situated on the eastern side of the lake. The study period, Dec. 1982-Jan. 1983, came directly after a prolonged short rains season, combined with overall high water levels within the lake, creating a newly flooded area of littoral which receded over the study period.

Vegetation consisted of flooded grasses in the shallowest inshore zone giving way to deeper water covered with a dense growth of floating *Salvinia*, the density of which increased with distance from the

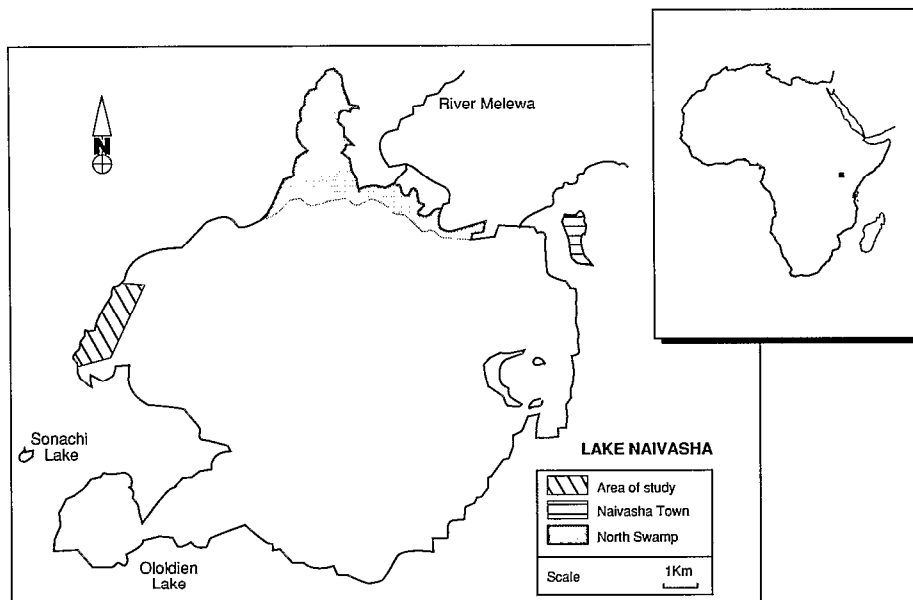


FIG. 1. — Situation of Lake Naivasha and the study site. *Situation du lac Naivasha et site d'étude.*

shore. The whole zone was delimited by floating rafts of *Papyrus*. The width of the zone was approximately 5 m, with a water depth ranging from 5-50 cm. The newly flooded area consisted of very shallow water up to 20 cm with little *Salvinia* owing to the presence of the emergent grasses.

Physico-chemical conditions

Water temperature and dissolved oxygen were measured using a thermistor probe and a Clarke electrode. Measurements were taken in a previously marked out grid of 50 contiguous rectangles 1×0.5 m with a water depth ranging from 2 mm-50 cm in a zone running out 5 m from the margin. In order to gain information on diurnal variation of temperature and oxygen, readings were taken daily at 10.00 and 15.00 hrs. A visual assessment of the cover and condition of the floating *Salvinia* was also made with reference to temperature, oxygen, and water depth on each occasion.

Fry capture, measurement and food analysis

Fry were captured using 3 m long continuous pond net sweeps towards the operator parallel to the lake margin from regions of shallow littoral where the cover by *Salvinia* was insignificant out to the deeper water covered by *Salvinia*. It was felt that this represented a particular niche which changed in its physico-chemical nature where *Salvinia* had significant presence. In order to remove the chance of introducing temporal niche separation as indicated by SCHOENER (1970), samples were always taken between 10.00 and 15.00 hr. On capture, all the fish were measured to standard length and a sub-sample placed directly into 10% formalin for later gut analysis. The whole sampling period covered 20 days; it was felt that in order to assess the effect of growth within that time, length frequency distributions of fish taken from large samples on three dates needed to be compared.

One hundred and sixty two fish for gut analysis were measured, weighed and the gut removed. The stomach was separated from the hind gut, the former only being used for feeding assessment. Each stomach was opened onto a microscope slide and the contents extruded into a drop of polyvinyl lactophenol. The food items were identified, counted and each one was placed into two of three categories.

- *Occurrence* was based on presence or absence of an item in the gut.
- *Significant food item*: this category was assigned to any item which contributed to > 20% of the total food, using a combination of the number in the

field of view of the microscope, with a correction factor based upon body size of the food item in the cases of numerically dominant smaller items. For example:

cyclopoid copepod = daphnid = chydorid = $2 \times$ *Brachionus patulus* = $20 \times$ *Euchlanis*. For plant detritus and periphyton, individual counting could not be carried out. Thus counting of the number of fields of view in which it covered a > 20% area was considered an appropriate estimating technique.

- *Majority food item*: this category was assigned to food items occupying > 50% of a guts contents using the same criteria as in the previous category. Assessment of niche breadth and overlap was carried out on all three categories.
- *Niche breadth* was calculated from $1/\sum_j P_{ij}^2$ (LEVINS, 1968) where P_{ij} = proportion of the group in each environment.
- *Niche overlap* was calculated from $100(1 - \frac{1}{2} \sum (P_{xi} - P_{yi}))$ where P_{xi} and P_{yi} are the frequencies of groups x and y in category i respectively (SCHOENER, 1970). Both these measures were used effectively by MOYLE and RANIL SENANAYAKE (1984) on interspecific comparisons of niche.

In order to identify possible periods of physiological change, length weight relationships were calculated for two size groups of preserved fry from 250 individuals using standard length and weight of fry from which free moisture had been removed by blotting.

RESULTS

Physico-chemical conditions

Diurnal fluctuation and spatial variation in temperature and dissolved oxygen are presented in Fig. 2. Temperature results represent the mean of 6 sets of data; drying out of the sampling grid over the survey period resulted in later readings being not applicable to all sample squares.

The dissolved oxygen data represent two sets of readings taken on the same day. The process of drying out, and differential sunlight levels from day to day, meant that mean levels of dissolved oxygen from readings taken on different days would be of little relevance. As can be seen from Fig. 2, 10.00 hr temperatures varied little with distance from the shore. However, 15.00 hr temperatures were always higher than 10.00 hr with a definite gradient being set up over the day. Greatest diurnal variation existed closest to the margins, as did the highest

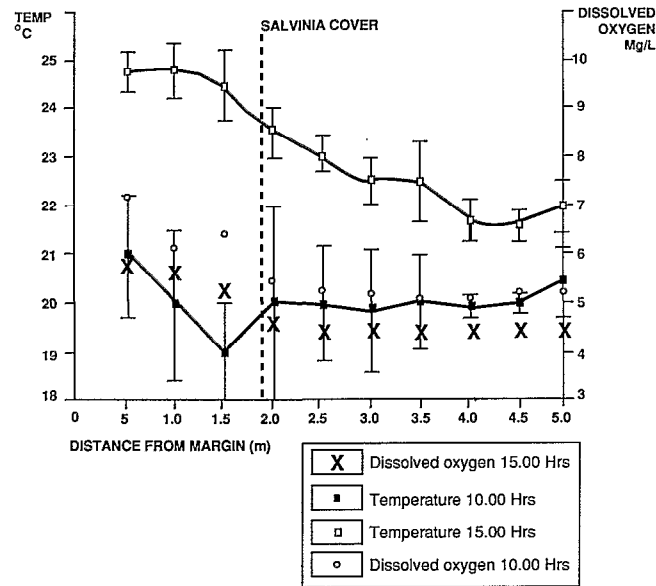


FIG. 2. — Dissolved oxygen and temperature variation in the littoral region at 10.00 and 15.00 hours with distance from the bank. Vertical lines: \pm SD. *Variation de la température et de l'oxygène dissous en fonction de la distance au rivage (10 h et 15 h). Barres verticales: \pm SD.*

highest temperatures. The possible shading effect of *Salvinia* can also be seen.

Trends in spatial variation of dissolved oxygen were also evident with higher levels being demonstrated in the more inshore regions. This is presumed to be the result of varying levels of photosynthesis affected by water depth and *Salvinia* cover since the expected reduction in dissolved oxygen with increase in temperature is not seen in the spatial data. However reduced dissolved oxygen levels in 15.00 hr samples, compared with the 10.00 hr samples, are likely to be due solely to raised p.m. temperatures.

Size frequency of fry

In order to assess the feeding overlap of different fry sizes, it was necessary to try to identify if any progressive growth of fry within the population was taking place over the sampling period, as any separation of feeding data on the basis of fish size may then be based on temporal changes of food supply and fry size.

With this in mind, large samples of fry were collected on three separate occasions and length frequency plots compared. These are presented in Fig. 3. As can be seen, some growth of fry is evident over the whole 15 day period, with much larger

numbers of 20-26 mm fry being taken at the end of this period, but growth between the individual dates is not evident and all fry sizes were present throughout the sampling period. As the major feeding type division occurs at 17.5 mm, which is within the first mode, and this mode persists strongly for the full period, then it seems fair to attribute this difference in feeding type largely to fry size rather than to possible temporal variation in food availability which could otherwise be inextricably linked to fry size through growth over this period.

Spatial separation of fry sizes into different zones of water was also tested for, as any spatial separation of fry of different size would result in niche separation based on something other than feeding type. The results of this are presented in Fig. 4. No difference between 6-8 mm depth water and 9-11 mm depth water on the basis of the size distribution of the fry present can be identified. The very shallow water, 2-4 mm, did seem to exclude more larger fry but no significant difference could be demonstrated for fry size distribution between these three water depth categories at the 95% level using either X^2 or one way analysis of variance. These checks demonstrate that any variation in feeding type with fry size that is indicated, results not from spatial or temporal constraints placed upon fry size.

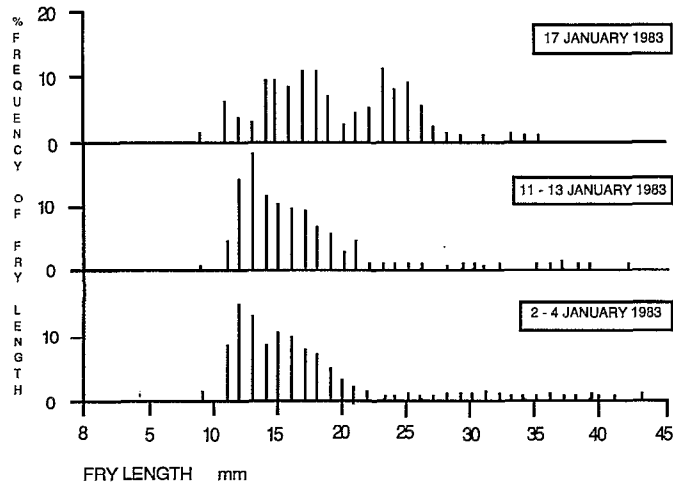


FIG. 3. — Frequency of fry length on three consecutive occasions. *Distribution des fréquences de longueur des alevins et juvéniles déterminées à trois dates représentatives.*

This supports the idea put forward by Ross (1986) and HARMELIN-VIVIEN *et al.* (1989) that niche separation in fish communities existed largely in terms of trophic separation.

Feeding

Occurrence of food items in the gut was calculated on the % number of stomachs in which the

particular food items occurred in seven randomly chosen but equally divided size groups of fry and juveniles (see Table I). On the basis of occurrence of food items in the gut, all fish size groups fed to some extent on all the food items encountered, with resulting high levels of niche overlap (57-89%). According to MOYLE and RANIL SENANAYAKE (1984) >66 % overlap was regarded as high and <33 % as low.

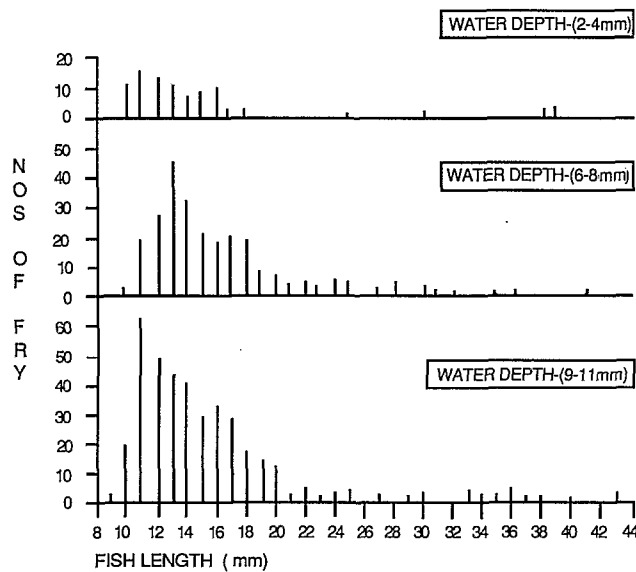


FIG. 4. — Distribution of fry sizes in three different water depths. *Distribution des tailles des alevins et juvéniles déterminées à trois profondeurs d'eau dans cette zone littorale peu profonde.*

TABLEAU I
Fry and juvenile size categories
Catégories de tailles des alevins et juvéniles

Group	1	10-13.5 mm
	2	14-17.5 mm
	3	18-21.5 mm
	4	22-25.5 mm
	5	26-29.5 mm
	6	30-33.5 mm
	7	> 33.5 mm

If these food types are divided into material that is simply browsed in an unselective fashion (here represented as periphytic and plant debris — PPD) and items that could be individually captured (all other food types), then both visual predation of small mobile prey and browsing operate to some degree in all size groups. It can be seen that the prevalence of PPD material in the two smaller groups is less than in the remaining larger groups.

Table II presents the significant food items as % of stomachs in which they were significant. In general, there are no more than two significant food items in any stomach. As can be seen, the separation of food types between size groups 1 and 2 and the rest is more marked than in the occurrence category. The two smaller groups were strongly biased away from PPD towards individually identifiable items, especially cyclopoid copepods. The latter groups, 3-7, were dominated by PPD material.

Table III displays overlap for significant food items. Here separation can be seen to be developing between groups 1 and 2 and the rest. However, the

continued use of cyclopoid copepods and daphnids by groups 3, 4 and 5 and a high level of feeding on *Alona* sp. by the latter two groups indicates that the potential for significant overlap still exists between these five groups. Groups 6 and 7 have a high level of overlap between each other but a <50 % overlap with groups 1 and 2. The importance of chironomid larvae and other insects in the two largest groups reduces the degree of overlap with the other groups.

Figure 5 presents the data for majority food items only. The separation of majority food types between the size groups is further highlighted with groups 1 and 2 both being dominated by individually identified items, and the remaining size groups dominated by PPD material.

Table IV presents overlap figures based upon the majority food item found in each gut. On this level, the separation of groups 1 and 2 from the remainder is very marked (21-38%) as is the overlap between groups 1 and 2 (71.6%). Similarly higher levels of overlap based on majority food items are apparent between the 3 largest groups (>70%).

With regard to niche overlap the following relationships are apparent. All size groups have the potential to overlap completely, on the basis of the occurrence of food types. However, if significant and majority food items only are considered, then a pattern of overlap appears, where groups 1 and 2 overlap strongly, and are greatly separated from the larger groups which show moderate levels of overlap between each other, with the overall exception of groups 6 and 7 which overlap more extensively. These trends are similar for significant and majority food items but more marked in the latter.

TABLEAU II

Percentage number of stomachs in which significant food items occurred
Pourcentage d'occurrence des principales proies dans les estomacs

Fish Group	PPD	EU	BP	CY	CA	DA	AL	CH	INSECT	MITES	TARD
1	25	36	32	82	-	50	50	5	5	-	-
2	11	11	11	82	-	79	21	4	7	-	-
3	79	14	-	21	-	29	-	-	-	-	-
4	96	15	-	4	-	8	12	-	-	-	-
5	70	10	-	10	-	30	30	-	-	-	-
6	53	-	-	7	-	20	27	33	13	-	-
7	73	-	-	1	-	1	18	2	-	-	-

KEY

PPD	Periphyton and plant detritus	AL	<i>Alona</i>
EU	<i>Euchlanis</i> sp	CH	Chironomid larvae
BP	<i>Brachionus patulus</i>	INSECT	Other insects
CY	Cyclopoid copepod	MITES	Mites
CA	Calanoid copepod	TARD	Tardigrades
DA	Daphnid		

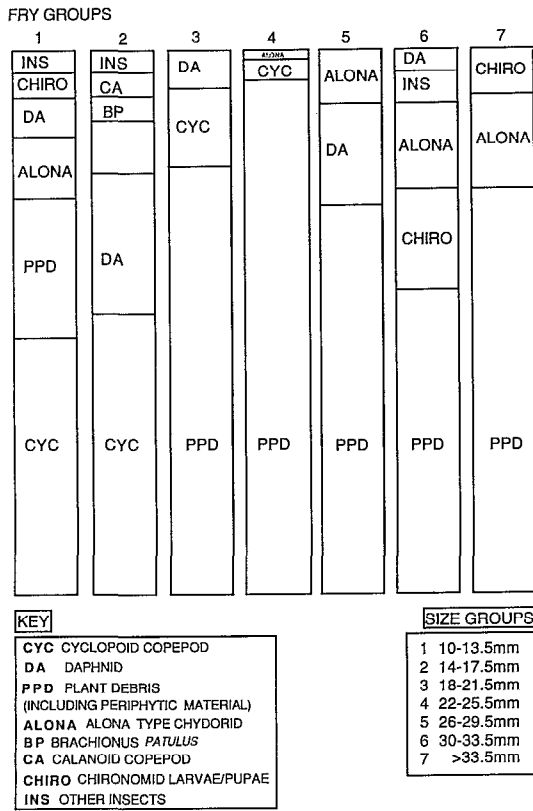


FIG. 5. — Percentage occurrence of majority food items in the stomachs of seven size categories of fish. *Pourcentage d'occurrence des principales proies dans les estomacs de sept catégories de tailles de poissons.*

Niche Breadth

Table V presents niche breadth data for each of the seven size groups for each of the three food categories. Taking the occurrence of food items, it

TABLEAU III

Niche overlap (%) between seven size groups of *O. leucostictus* fry for significant food item
Chevauchement de niche (%) entre alevins des sept catégories de tailles de O. leucostictus en fonction des principales proies

Fish Group	1	2	3	4	5	6	7
1	-						
2	73.8						
3	50.9	44.6					
4	32.9	23.3	77.9				
5	78.5	45.7	80.1	67.1			
6	45.7	36.6	71.7	48.7	69.3		
7	25.7	23.3	62.5	65.5	60.9	69.5	

TABLEAU IV

Niche overlap for seven size groups of *O. leucostictus* fry for majority food item
Chevauchement de niche (%) entre alevins des sept catégories de taille de O. leucostictus en fonction des proies dominantes

Fish Group	1	2	3	4	5	6	7
1	-						
2	71.6						
3	28.3	20.8					
4	21.7	10.3	89.6				
5	38.0	24.6	63.6	66.0			
6	38.2	13.7	50.0	53.9	74.4		
7	32.0	8.5	69.2	73.1	79.0	80.8	-

can be seen that little difference in niche breadth occurs. The most general feeders are groups 1 and 2, with groups 6 and 7 being more generalist than groups 4 and 5. The range of breadth values across the 7 size categories is not great (4.40-6.55).

The pattern is similar for significant food items although the overall variation between groups is greater (1.87-5.49), group 1 again being the most general feeder.

On the basis of majority food items this pattern is again repeated with groups 1 and 2 being more generalist than all others except group 6. Group 6 displays general feeding using all three of the food categories; this seems to stem from a greater usage of chironomids and insect larvae which may have been taken as large individual food items. HARME-LIN-VIVIEN *et al.* (1989) recognised that larger members of scorpaenids consume larger prey but continue to capture small size prey as well, an effect in keeping with this result. MARCUS (1986) made a similar observation for *Ilisha africana*. Group 7 however does not exhibit this effect except in the occurrence of food category; presumably the same opportunities must have been available to group 7 as group 6, but this is not reflected in the data, possibly because of smaller sample sizes in these two groups.

TABLEAU V

Niche breadths for seven size groups of *O. leucostictus* fry
Largeur de niche des groupes d'alevins O. leucostictus de sept catégories de tailles

Fish	Occurrence	Sig. food item	Majority food item
1	6.55	5.49	3.23
2	6.30	3.67	2.79
3	4.85	2.7	1.58
4	4.40	1.87	1.13
5	5.32	3.26	1.8
6	6.06	4.45	2.83
7	5.72	2.66	1.74

DISCUSSION

The unsuitability of the shallow littoral for larger than juvenile fish was demonstrated during the study period by a significant kill of larger fish forced into this area and trapped overnight by floating *Papyrus* raft. The volume of available oxygen in the shallows was too small, resulting in critically lowered night-time dissolved oxygen levels (*personal obs.*).

The lack of suitability for large fish and the protection afforded by floating and rooted vegetation, combined with the high productivity of newly flooded littoral resulting from high nutrient, high temperature and high sunlight regimes, are the main reasons for the extensive exploitation of these zones as fry/juvenile nurseries (HYSLOP, 1986; STEWART, 1988; HICKLEY and BAILEY, 1987; BALOGUN, 1986; GETACHEW, 1987; GREEN, 1985).

Regularly occurring flooding, as found in lakes such as Naivasha, gives a predictable opportunity to the fish community to synchronise breeding with flooding events, a situation indicated by HYDER (1970). STEWART (1988) suggested that synchronous breeding may give further protection against predation.

The presence of *Salvinia* appears to act as a barrier to fry; few fry were ever encountered in *Salvinia* zones. Its presence shaded the water resulting in lower temperature variation, but the occlusion of light may have contributed to lower dissolved oxygen from reduced periphytic photosynthesis. TOWNSEND and PEIRSON (1988) suggest that floating vegetation mats also impede oxygen diffusion. The unsuitability of *Salvinia* covered water for fry occupation was noted by DONNELLY (1969) which is in marked contrast to observations by GREEN (1985).

Material available as food in this habitat can be classified into two main types. A mixture of periphytic algae and decaying vegetation, which will be browsed in a non-selective fashion, and the associated invertebrate fauna which can be regarded as small individual items, with some larger individual insects. These last two types can either be taken during browsing of the former food type or individually visually detected and predated. The lack of fry under the deeper water covered by *Salvinia* may have reflected nothing more than the necessity of the fry to remain close to their food source. However, the proximity of *Papyrus* to the *Salvinia* may have been influential. HICKLEY and BAILEY (1987) report *Papyrus* exclusion of fry.

Given these proposed reasons for inhabiting this spatially limited and apparently physiologically demanding habitat, dense assemblages of small fish must encounter high levels of intraspecific competi-

tion, as well as necessitating an ontogenetic change in diet associated with feeding as an adult in more open areas. Dietary switching by fish as they pass through developmental stages has been reported many times (ARAUJO-LIMA *et al.*, 1986; KEAST, 1973; WERNER *et al.*, 1977; WEATHERLEY, 1987; GIBSON and EZZI, 1987; HOFER, 1988) and has been suggested as a method of reducing intraspecific competition (KEAST, 1973; WERNER *et al.*, 1977).

The utilisation of periphytic algae and rich organic detritus has been suggested as being one of the main reasons for success of (tilapine) fish, with adult fish entering shallower water to browse on this type of diet (HICKLEY and BAILEY, 1987; BALOGUN, 1986; GETACHEW, 1987, 1988) although the digestion of algae and some detritus is recognised as requiring specialised physiological and gut morphological adaptations (GETACHEW, 1987, 1988; HOFER, 1988; MORIARTY and MORIARTY, 1973; MORIARTY, 1973; KIRILENKO *et al.*, 1975; BOWEN, 1979).

Physiological changes may be indicated here at the time of dietary switch by the length/weight relationships for the fry: 10-17.5 mm fry had a slope of 2.66 and 18-60 mm fry 3.00, this difference being significant at 95 % level. The latter slope is similar to that given by SIDDIQUI (1977b) of 2.9 for Naivasha *O. leucostictus* who reported a similar diet for adult fish as reported here for larger fry (SIDDIQUI, 1977a).

It would seem therefore that the fry gain some relief from intense intraspecific competition by dietary switching at a very small size, and that this capability may be brought about by the onset of some fundamental physiological digestive change which allows exploitation of the PPD material. It also appears that the further development of the ability to utilise larger individual prey items such as whole chironomid larvae/pupae and other insect larvae, which may be associated with increase in fish size also acts to reduce intraspecific competition for food between larger juveniles. However, it may be that the taking of these items is not active predation, but only accidental associated with browsing and the newly acquired morphological ability to handle larger food items.

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