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ONTOGENETIC AND MONTHLY FEEDING BEHAVIOUR OF *Liza falcipinnis* (Mugilidae) FROM CROSS RIVER ESTUARY, NIGERIA

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ABSTRACT: Size-based and monthly feeding performance of *Liza falcipinnis* from Cross river estuary was studied to determine ontogenetic feeding attributes. Specimens were collected for 12 months. Total length and weight were measured. Gut contents were analysed. Ontogenetic length-weight relationship was calculated to determine the growth pattern and its relationship with feeding activities. Length-weight relationship showed allometric and isometric growth patterns among length classes. Important food items in decreasing order, were phytoplankton, sand/mud, detritus and macrophyte matter. Arthropod parts were incidental items. The mean stomach fullness (MSF) increased from juveniles to a peak at 17.5 – 19.4cm TL, and dropped at >27.4cmTL adult class. Stomach repletion index (SRI) also increased from juveniles to adults ($r=0.675$, $P<0.001$). Diet diversity index (F) was generally higher in the lower classes than in the adult groups, depicting stability of the food items among the classes. The main dietaries occurred in every month. Detritus, macrophyte matter and arthropod parts also had >50% class spread while sand was observed in all the classes. Among algae, *Navicula*, *Pleurosigma*, *Coelosphaerium*, *Spirogyra* and *Rhizosolenia* had >50% annual spread. *Stephanodiscus* and *Ceratium* occurred in December only. Diversity indices were generally high among the various length classes. Estimates of relationships between the growth factor (b) and feeding activities i.e b vs MSI and b vs SRI, were negative in all the classes but only significant ($P<0.05$) between 3.5 – 5.4 and 15.5 – 17.4 cmTL classes. Foraging activities increased with fish size reaching peaks at the middle age groups and declining in the adult stages.

INTRODUCTION

Ontogenetic variations are known to exist in food habits (Miller, 1979 and Blay and Eyeson, 1982). Most studies on trophic attributes of fishes usually deal with overall food composition and temporal variation, as such, information on ontogenetic dynamics is lacking (Udo *et al.*, 2008). Studies on ontogenetic feeding activities in fishes usually use large range of values and arrive at juveniles, middle age and adult classes. This approach does not depict detail progressive changes in feeding activities with age. Allometric reports in fishes also usually concentrate on the general allometry of the fish in question without stage-wise information and relationship to other physically activities. Besides *Liza falcipinnis* is an important constituent of the canoe landing of artisanal fishermen (King, 1986). It is also of commercial value since it is available along the beaches in West Africa in affordable quantities to low income earners as protein source. It was therefore considered necessary to look at this aspect of trophodynamics of this specimen after the report on the general diet composition had been given (Akpan, 2010).

$$MSF = \frac{\sum S}{N} \quad 3$$

where S = the sum of frequencies of the stomach points and N is the number of stomachs examined.

The contents of each stomach was placed on a clean slide, teased with few drops of water added to it and examined macroscopically and microscopically at x 10 and x 100 magnifications. The relative frequency (RF) and relative dominance (RD) of the food items were estimated as an index of food preponderance (IFP):

$$IFP = \frac{RF_1 + RF_2}{\sum RF + \sum RD} \times \frac{100}{1} \quad 4$$

This index has a range of 0 – 100%. Items with IFP ≥ 10.0% were considered primary dietaries, those with IFP between 1.0 and 9.9% as secondary. Others with IFP < 1.0% were incidental. Unadjusted food richness (UFR) was considered as the total number of items recorded in the diet (King, 1988)

The fishes were divided into classes (starting from 3.5 to 27.4cmTL) with 2.0cmTL as the class interval. Specimens between 27.5 and 34.3cm TL were grouped together since they were few in number. Determination of differences in diet composition was assessed by the percentage similarity coefficient (S) (Moss and Eaton 1966) and diet breath (B):

$$S = \sum_{(n-i)}^n \min(x_i, y_i) \quad 5$$

where x and y are proportions of the components of the series of items comprising the diets of x and y. This index ranges from zero, for totally dissimilar items to 100 for identical diets.

$$B = [(\sum P_i^2)^{-1} - 1] / n - 1 \quad 6$$

where P = proportion of the diet compared by resources type i and n = number of food categories in the diet. Another unified index of diet diversity (F) was computed from the % IFP data using the formual below (Alatalo, 1981; Grundel, 1990), to further confirm the diversity:

$$F = \frac{(1/\sum_{(n-i)}^n P_i^2) - 1}{\exp(\sum_{(n-i)}^n P_i \ln P_i) - 1} \quad 7$$

where P_i is the proportion of the diet comprised by resource type i and n = number of food categories in the diet. This index is sensitive to changes in two attributes: food richness and equitability (the degree to which all items are equally represented). It increases as food richness and equitability increases and declines when few items dominate the diet. The index is scaled such that 1.0 represents an even distribution and zero, a strongly skewed distribution. Correlation coefficient (r) was used to determine the relationship between different parameters.

RESULTS

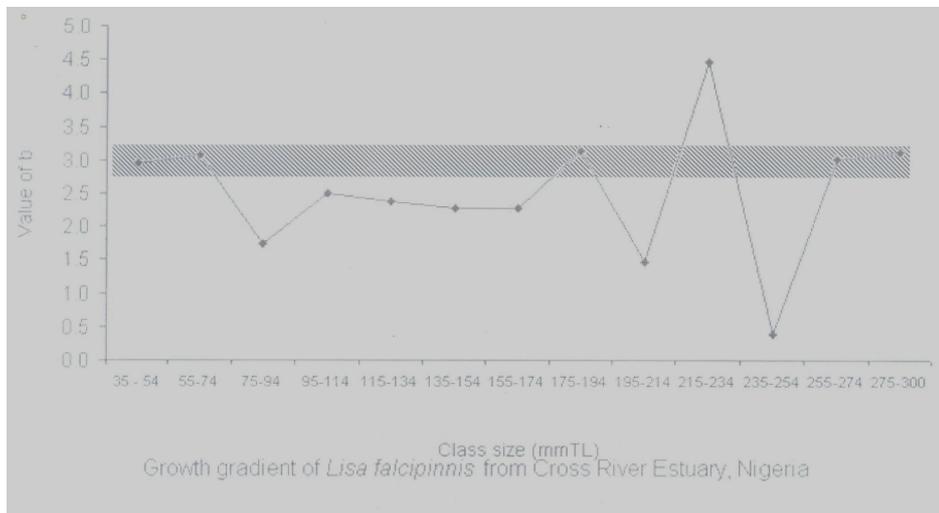
Morphometric correlates

A total of 540 specimens of *L. falcipinnis* measuring 3.5 – 34.3cmTL was examined . 13 classes were formed. There were positive correlations between total length and total body weight in the classes (r = 0.484 – 0.963) except in 23.5 – 25.4cm TL class where the value was negative (r = -0.132). The growth ratio “b” differed significantly from zero and unity (Table 1). The general growth gradient obtained from “b” value is shown in Fig. 2. It was isometric at the beginning, followed by negative allometry (which occurred in about 50% of the length

classes), positive allometry and finally isometric. In size groups 5.5 – 7.4, 17.5 – 19.4, 21.5 – 23.4 and ≥ 25.5 cm TL growth was isometric ($b = 3.0$)

Table1: Ontogenetic length-weight relationship of *Liza falcipinnis* from Cross River estuary, Nigeria .

x Sized Groups (mm)	a	y b	r	n
35 - 54	1.94	2.94	0.931	14
55 - 74	-2.06	3.09	0.963	71
75 - 94	-0.87	1.74	0.484	32
95 - 114	-1.53	2.51	0.728	74
115 - 134	-1.39	2.37	0.648	108
135 - 154	-1.24	2.28	0.599	59
155 - 174	-1.19	2.27	0.612	47
175 - 196	-2.29	3.15	0.692	26
195 - 214	-0.07	1.46	0.943	13
215 - 234	-4.03	4.46	0.576	13
235 - 254	2.61	-0.39	-0.132	13
255 - 274	-2.18	3.02	0.749	14
>	-2.35	3.12	0.951	07



Ontogenetic feeding regime

The overall diet composition of this specimen had been reported by Akpan (2010). Variations in diet composition among the classes as shown in Table 2 depict important groups of food item viz: phytoplankton, sand/mud, detritus, macrophyte matter and arthropod parts.

Table2: Ontogenetic index of food preponderance (%IFP) for *Liza falcipinnis* from Cross River estuary, Nigeria .

Food items	Sized Groups (cm TL)													
	35-54	55-74	75-94	95-114	115-134	135-154	155-174	175-194	195-214	215-234	235-254	255-274	≥275	
Phytoplankton														
<i>Spirogyra</i>	20.00	3.40	2.36	2.36	3.45	4.08	5.46		2.22				19.40	31.43
<i>Navicula</i>	20.00	19.42	10.85	7.02	12.45	5.31	4.85	3.95	2.22	4.26			4.48	2.86
<i>Pleurosigma</i>		1.46	5.46	12.28	5.56	8.16	4.24	3.95	6.67	14.89	5.09			2.86
<i>Coelosphaerium</i>	20.00	26.21	20.96	11.40	14.75	15.51	37.58	57.90	17.78		40.68	38.81		37.14
<i>Rhizosolenia</i>			6.98	10.97	18.19	8.51	4.85	2.63	2.22					
<i>Stephanodiscus</i>											8.48	10.45		
<i>Ceratium</i>											3.39	4.48		
Sub total	60.00	50.49	46.61	44.30	54.40	41.57	56.98	68.43	31.11	19.15	57.64	77.62	74.29	
<i>Sand/mud</i>	40.00	32.04	25.68	28.07	27.59	31.63	23.03	18.42	35.56	27.66	25.42	19.40	8.57	
Detritus														
FPOM		6.31	10.08	8.77	4.98	7.76	4.85		15.56	19.15	5.09			5.71
CPOM		6.31	12.40	10.97	8.81	13.47	9.70	7.90	15.56	27.66	8.48			5.71
Sub total		12.62	22.48	19.74	13.79	21.23	14.55	7.90	31.12	46.81	13.57			11.42
Macrophyte matter		2.91	4.65	7.02	3.64	5.71	5.46	5.26	2.22	4.26	3.39	2.99		2.86
Arthropod parts		1.94	0.78	0.88	0.58	0.41				2.13				2.86
Food richness	4	9	10	10	10	10	9	7	9	7	7	7	7	9

The mean stomach fullness (MSF) increased from juveniles with a peak at 17.5 – 19.4cmTL class and fell to 7.50 ± 3.56 at > 27.4cmTL adults (Table 3). The correlation coefficient between the classes and MSF was significantly positive ($r = 0.765$, $df = 24$, $P < 0.001$). Stomach repletion index (SRI) also increased from juveniles (SRI = 21.43% at 3.5 – 5.4cm TL) to adults (SRI = 100% at 27.4cmTL) with a positive correlation ($r = 0.675$, $df = 24$, $P < 0.001$). Results obtained for diet diversity (F) were high ranging from 0.657 to 0.923 except at 25.5 – 27.4cmTL where the value was low ($F = 0.143$). It moderately correlated with length sizes ($r = -0.496$, $df = 24$, $P < 0.05$). Diet breadth was higher in the lower sizes ($B = 0.444 - 0.857$) than larger sizes ($B = 0.121 - 0.605$) with a significant negative correlation ($r = -0.689$, $df = 24$, $P < 0.001$).

Table3: Ontogenetic stomach fullness of for *Liza falcipinnis* from Cross River estuary, Nigeria

Sized groups	% stomach fullness					MSF
	0	5	10	15	20	
35 - 54	11	02	01	00	00	1.43±2.95
55 - 74	23	28	12	06	06	6.27±6.01
75 - 94	08	06	11	10	06	10.00±6.63
95 - 114	20	12	13	03	26	10.20±8.19
115 - 134	16	32	31	27	25	10.49±6.51
135 - 154	07	10	06	12	26	13.28±7.24
155 - 174	02	08	10	05	22	13.94±6.52
175 - 196	02	03	04	11	17	15.14±5.87
195 - 214	03	03	00	01	07	12.14±8.60
215 - 234	01	01	02	01	06	14.55±6.89
235 - 254	00	01	04	04	05	14.64±4.81
255 - 274	02	03	00	07	02	11.43±6.66
> 274	00	05	02	01	00	7.50±3.54

Monthly variation in feeding activity:-

The annual feeding regime showed the main items occurring every month (Table 4).

Table 4: Monthly index of food preponderance (%IFP) of *Liza falcipinnis* from Cross River estuary, Nigeria .

Food items	Months											
	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Agu.	Sep.	Oct.	Nov.	Dec.
Phytoplankton												
<i>Spirogyra</i>	1.77	2.68			2.74		7.41	0.07	9.24			34.02
<i>Navicula</i>		1.34		15.28	4.11	4.90	7.41	2.82	5.41	2.34	6.86	8.76
<i>Pleurosigma</i>		0.67		8.34	1.37		7.41	1.41	15.92	14.84	8.82	4.12
<i>Coelosphaerium</i>		39.61	48.80	11.11	50.69	19.51		1.41		0.78	11.76	16.50
<i>Rhizosolenia</i>	26.99		24.04	13.89				48.59		0.78	18.63	2.06
<i>Stephanodiscus</i>												6.19
<i>Ceratium</i>												2.58
Sub total	64.60	44.30	72.12	48.62	58.91	34.41	22.23	54.93	30.57	18.74	46.07	74.23
<i>Sand/mud</i>	26.99	37.58	24.04	19.44	13.69	54.13	44.47	27.47	35.35	35.16	18.63	5.16
Detritus												
FPOM	1.33			11.11		6.56	7.41	7.04	12.10	17.19	12.75	
CPOM	4.87	17.45	3.85	9.72	21.92	4.90	3.70	7.04	13.38	18.75	15.69	17.53
Sub total	6.20	17.45	3.85	20.83	21.92	11.46	11.11	14.08	25.48	35.94	28.44	17.53
Macrophyte matter	2.21	0.67		11.11	5.48		18.52	3.52	7.96	9.38	5.88	2.58
Arthropod parts							3.70		0.64	0.78	1.96	0.52
Food richness	9	7	4	8	7	5	8	9	8	9	9	11

Of the food items observed in the year, 11 (11.07%) items were recorded in December while 9(9.57%) were observed in January, August, October and November each, and 8(8.51%) were observed in April, July and September each. February and May had 7 (7.455) items each and June and March 5(5.32%) and 4(4.255%) respectively. Sand and CPOM occurred in every month, *Navicula*, 11 months while *Pleurosigma*, macrophyte matter and *Coelosphaerium* occurred in 10 months. FPOM was observed in 8 months and *Spirogyra* and *Rhizosolenia* in 7 months. Arthropod parts occurred in 5 months while *Stephanodiscus* and *Ceratium* occurred in December only.

The highest mean stomach fullness (18.80 ± 4.15) was recorded in March and lowest (6.16 ± 6.04) in June (Table 5). It showed significantly high correlation with months ($r = 0.938$ df 10, $P < 0.001$) between May and December. The lowest monthly stomach repletion index (60.42%) was observed in June and highest (100%) in March and April. The correlation of SRI with months was poor ($r = -0.397$).

Table 5: Monthly variation in stomach fullness of *Liza falcipinnis* from Cross River estuary, Nigeria .

Months	% stomach fullness					MSF
	0	5	10	15	20	
January	14	32	34	18	02	8.12±4.99
February	02	09	10	06	06	10.76±6.01
March	00	02	00	00	23	18.80±4.15
April	00	00	00	03	09	18.75±2.26
May	01	11	08	06	01	9.07±4.81
June	38	35	22	09	08	6.16±6.04
July	00	04	02	00	00	6.67±2.36
August	10	04	01	02	35	14.62±8.33
September	00	07	08	16	30	15.92±5.19
October	13	01	04	02	18	11.45±9.15
November	11	02	03	03	10	9.83±8.76
December	04	12	05	13	07	10.86±6.51

Diversity index (F) was high in all the months ($F = \geq 0.700$) except in June ($F = 0.485$). Diet breadth (B) ranged from 0.339 to 0.924 except in August which was very low ($B = 0.261$).

Relating the classes of food items to the months showed a significant relationship ($r = 0.605$, df 22 $P < 0.005$) between detritus and the months. Sand vs months and algae vs months indicated weak negative relationships ($r = -0.205$) in each case.

Table 6: Observed functional relationship between dietaries of *Liza falcipinnis* from Cross River estuary, Nigeria.

Items	Correlation coefficients (r)	
	Class	Months
MSF vs SRI	0.806****	0.439*
Algae vs sand/mud	-0.579***	-0.723****
Algae vs detritus	-0.919****	-0.498**

* = P < 0.05, ** = P < 0.02, *** = P < 0.005, **** = P < 0.001

Functional correlates

Relationships were also observed between some functions and items which suggest some operational relationships as shown in Table 7.

Table 7: Growth exponent-feeding activity relationship of *Liza falcipinnis* from Cross River estuary, Nigeria.

Class size (mm TL)	Correlation Coefficients (r)		
	Mean stomach fullness (MSF)	Stomach repletion	Index (SRI)
35 – 54			
55 – 74	1.00	P < 0.001	1.00 P < 0.01
75 – 94	-0.765	P < 0.001	-0.527 P < 0.02
95 – 114	-0.685	P < 0.001	-0.521 P < 0.02
115 – 134	-0.686	P < 0.001	-0.537 P < 0.02
135 – 154	-0.676	P < 0.001	-0.565 P < 0.01
15.5 – 174	-0.673	P < 0.001	-0.584 P < 0.005
175 – 194	-0.287*		-0.347*
195 – 214	-0.321*		-0.304*
215 – 234	-0.045*		-0.049*
235 – 254	-0.149*		-0.208*
255 – 274	-0.142*		-0.189*
> 274	-0.182*		-0.139*

* = insignificant

DISCUSSION

The ontogenetic growth pattern of *L. falcipinnis* from Cross river estuary is allometric and isometric as shown in Figure 2. Between 3.5 and 17.4cmTL growth was negatively allometric. This indicates that while the length is increasing probably the other two body dimensions (depth and breadth) may be decreasing, hence the fish tends to become slimmer with increasing length. At 17.5 – 19.4 cm TL class, growth was isometric (1:1:1) with the fish tending to become rotund in shape. Isometric growth rarely occurs among fishes (LeCren, 1951; Ezenwaji, 2004). Although it is reported rarely, the present result makes one to know that isometric growth can occur at any point as the fish grows. At 21.5 – 23.4cmTL class, growth was positively allometric suggesting one parameter to be faster than other as they proceed in the same direction. Growth became isometric again at most adult stages. This observation indicated that this specimen has a growth regime which is isometric at early juvenile stage, late middle and late adult ages mixed with negative allometry at middle age and positive allometry at early adult ages.

As reported by Fairbairn (1992), allometric relationships reflect changes in physiological or structural requirements associated with body size. The high positive allometry (b= 4.460) at 21.5 – 23.4cm TL probably suggests period of active food deposition for attainment of maximum body weight at reproductive age. Maximum body weight is necessary for better reproductive performances in most animals (Modder and Singh, 1976). Since growth

decreased with age, increased deposition prior to reproductive years will augment deposition at reproductive period for better reproductive performance.

There were significant inverse relationships in algae vs sand, and algae vs detritus (Table 6). As the main diets, increase in one suggests a decrease in the other. Thus, each of the relating items tends to replace the other.

There were also inverse relationships between the growth factor (b) and feeding activity indices (mean stomach fullness and stomach depletion index) at all stages, implying decreased feeding activity with increasing growth factor. This was markedly significant ($P < 0.05$) between 3.5-5.4 and 15.5 – 17.4cm TL (Table 7).

There were significant correlations between length classes and feeding activities (classes vs MSF: $r = 0.766$, $df = 24$ $P < 0.001$ and classes vs SRI: $r = 0.675$, $df = 24$, $P < 0.001$) which suggest increased food demand with age.

The number of food items observed in the 12 months were mostly phytoplankton, sand/mud, detritus, macrophyte matter and arthropod parts. Phytoplankton, sand/mud and detritus occurred in every month. This indicated year round availability of food, as such, the population probably didn't suffer food shortage or depletion at any time. 10 months (83.33%) recorded minimum 8 dietaries out of 12 items observed. June recorded 5 items and March 4 items. The paucity in dietaries in these two months was probably compensated by intake of more phytoplankton and sand/mud (34.41% IFP and 54.13% IFP) and (72.12% IFP and 24.04% IFP) for June and March respectively. The high diversity index ($F > 0.700$ in all the months except June with $F = 0.485$) indicates that all items were equally represented in all the months. The significant relationship between detritus and the months ($r = 0.605$, $P < 0.05$) indicates increased detrital items from January to December. Estuaries are food resource rich hence the food abundance. The rich food base promotes the growth of the fish population and accounts for the availability of the species in local markets throughout the year.

Among the class sizes, 3.5 – 5.4cmTL had 4 diets while others has diet between 7 and 10. The number of food items and mean stomach fullness was increasing with size. The mean stomach fullness showed double peaks but at very large sizes it declined indicating low feeding activities at that size. Stomach repletion index also increased from juveniles to adults. These two indices indicate increasing foraging activities with size. Similar foraging success had been reported by Mittlebach (1981). Hairston *et al* (1982), King *et al* (1990). Walton *et al* (1994), King and Akpan (2002) and Akpan *et al* (2005). They attributed the increasing trophic activities of the adults to some morphometric/ physiological (greater mouth gape, speed, visual acuity) and ecological (spatio-temporal location) advantages of the adults.

Although the feeding activities generally increased from juveniles to adult, it is not exponentially as one might expect but sometimes depressed along the age profile. In diet shifting theory then, the ontogenetic diet shift usually observed in fishes should be expanded to include periods of depressed feeding particularly at late adult stages, as this promotes conspecific coexistence.

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