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Proposal of a New and Simple Descriptive Measure of Diet Breadth

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ABSTRACT

Measuring diet breadth from gut content by Levins or Smith does not give true range of diet of an organism in comparison to available food resources in the environment. These measures consider proportions of food content in the gut to total food content in the gut for analysis. However, the credibility of food organisms available in the environment to exhibit and supply food to the prey feeding on it has been totally ignored. To overcome such limitations a new and simple non parametric diet breadth i.e., $DB(\chi^2)$ has been proposed. A theoretical data set with gut content from six fish species as F1, F2, F3, F4, F5 and F6 have been considered to explain the $DB(\chi^2)$. All these gut content data have variations within the gut content data set as well as between two guts and also with resource state as R. The computation and analysis of $DB(\chi^2)$ not only explain a realistic picture of diet breadth of guts considered, but also provide an information on possible of diet overlap between two or more guts through 'clumping' of guts. The 'clumping' of guts based on $DB(\chi^2)$ clearly explains diet overlapping or competition among different species or individuals of a species for available resources. While comparing the $DB(\chi^2)$ to niche measures of Levins, Hulbert and Smith, the $DB(\chi^2)$ showed clearer representation guts exploiting food organisms around R. $DB(\chi^2)$ also shows sensitivity to variation of food abundances within gut content as well as to resource state that other measures failed to express.

Key words: Food preference, gut analysis, diet overlap, feeding ecology, clumping of gut

INTRODUCTION

Feeding ecology has succeeded as significant part of aquaculture research in recent times. Its methodology mostly relies on different indices computed on the gut analysis of consumer. This is an all time question for feeding ecologist to select an index that better represent the food preference or diet competition among organisms occupying same niche or ecosystem. For example, when some studies are performed only on percent occurrence of gut content (Ara *et al.*, 2011), others use multiple indices (e.g., Frequency of occurrence, Gravimetric method, Relative importance index, fullness index, numerical etc.) to evaluate diet breadth (Oh *et al.*, 2011; Whenu and Fagade, 2012; Oribhabor and Ogbeibu, 2012). Along with Ivlev's electivity index, Vacuity index and Lazzero's food preference index are other measures occasionally used for quantitative study of diet in the gut (Alkahem *et al.*, 2007; Alwany *et al.*, 2007). Use of alternative forms of same index (Standardized Levin's index and Levin's standardized niche breadth) is also practiced (Kumar and Pardeshi, 2011). Some others consider accounting body parts (e.g., presence of type of otoliths) in the gut of consumer to assess prey preference by fish (Garcia-Rodriguez and Cruz- Aguero, 2011).

The most common indices to measure diet breadth in ecology are niche breadth of Levins (1968), Hurlbert (1978) and Smith (1982). These measures, though usually called as niche measure, actually measure the diet breadth of organisms. Fundamentally, ecological niche of a species means individual and essential needs of the organisms in the absence of competition, predation, dispersal

limitation and human disturbances (Hutchinson, 1957). These measures are, therefore, cannot be said truly as niche breadth. Levins measure is sometime referred as Resource breadth probably to avoid such contradictions (Oueda *et al.*, 2008), although practically it measures the food in the gut of the organism. In addition, information theory and diversity measures have traditionally made up the practice for calculating diet breadth (Colwell and Futuyma, 1971; Heitkonig and Omen-Smith, 1989; Bluthgen *et al.*, 2006). These matrices use observed food category in the gut of studied organism as the basis of calculation. For example, the popularly used Levins (1968) describes niche breadth as the reciprocal of squared sum of proportion of food organisms in the gut of the organisms. Hurlbert (1978) considers proportion of the total available food resources in the environment (or resource state) while determining niche breadth. In all cases, the assessment of total available food resources from the environment was not considered (e.g., Levins' niche breadth) or if considered, computational error influences to obtain actual diet breadth (e.g., Hulbert's and Smith's niche breadth). Logically, this is very arbitrary practice to assess diet breadth without taking into consideration the availability of food resources in the environment. The diet breadth, in its true meaning, should be the ability of an organism to utilize available food resources in the environment at the time of sampling. Therefore, a diet breadth index must reflect a true nature of feeding of an organism on some specified available food resources. Or, more clearly, it should be able to explain the nature of competition or diet overlapping among organisms when studied on same available food resources. Feeding studies generally follow diet overlap indices such as Schoener's α (Oueda *et al.*, 2008) to understand competition for food between two species without drawing any conclusion on chance of such competition in advance. All the available indices of diet breadth cannot be used for such conclusion. Although few measures consider food items in the environment, expression of such indices in fraction convert them unrealistic. In some cases, for instance, diet measures of aquatic organisms become more unrealistic when diverse planktonic communities act as resource state.

The present study proposes a dietary breadth measure based on χ^2 (Chi-square) expression using observed value of food items in the gut of the organism with available food resources as expected value.

MATERIALS AND METHODS

Calculation: The present method of diet breadth follows the mathematical expression of χ^2 (Chi-square) statistics. The χ^2 expression for diet breadth is computed as follows:

$$DB(\chi^2) = \sum_i^n \frac{(\log O_i - \log E_i)^2}{\log E_i}$$

where, the $DB(\chi^2)$ is diet breadth, $\log O_i$ and $\log E_i$ are the log value of observed and expected food abundances of ith category. The expected food abundance in $DB(\chi^2)$ is constituted of available food resources in the environment.

Data arrangement and computation: For hypothetical analysis, a data set given in the Table 1 has been computed and discussed. Table 1 includes observed food categories (i = 1, 2, 3, ……. 15) for six fish species from an aquatic environments. Here, F1, F2, F3, F4. F5 and F6 denote the gut content of fish recorded from the environment. The resource state from the environment that was considered as expected food abundance for six fishes is R. To verify the credibility of

Table 1: Theoretical data set for measuring diet breadth using DB(χ^2)

Category (i)	F1	F2	F3	F4	F5	F6	R
1	1	300	1	235	6	300	330
2	2	98	2	102	5	98	105
3	1	240	1	211	3	240	260
4	3	400	3	249	6	3	428
5	1	90	1	8	3	90	98
6	1	180	1	186	4	180	200
7	4	350	360	256	9	350	369
8	2	120	2	0	0	120	180
9	5	82	5	0	0	82	89
10	1	65	1	0	0	65	78
11	1	90	1	0	0	90	96
12	1	189	1	0	0	189	200
13	2	320	2	0	0	320	360
14	3	440	3	0	0	440	480
15	1	60	1	0	0	60	78
N	29	3024	385	1247	36	2627	3351
μ	1.9333	201.6	25.6667	83.1333	5.1428	175.1333	223.4

Category (i): Food types or items, F1, F2, F3, F4, F5 and F6 are the guts with food items recorded from six fish species, R is the resource state or food items available in the environment

proposed DB(χ^2), all gut content data are arranged to explain multiple situations of food availability as described below:

- In the first case, gut items far less than food resources (F1<<<R). The F3 with equal distribution of gut items to F1, has dominance item of i = 7
- In the second case, gut items more or less equal to food resource (F2≈R). The F6 with equal distribution of gut items to F2, exhibits rarity for i = 4
- In the third case, categories of gut items short in number to category of food resource (F4$_{i=\sum 7}$ and F5$_{i=\sum 7}$ <R$_{i=\sum 15}$)

These different situations are mathematically explained with the ratio of mean (μ) of gut content to resource state (μ_F/μ_R) (Table 2). This ratio will be always less than 1 since, theoretically, no mean of gut content will exceed the mean of resource state. Smaller the ratio, bigger is the difference between gut content and resources state. For example, the F1 has very poor representation of food categories of R with only 1.933 organisms/gut/category on average. The μ_{F1}/μ_R is 0.00865 (<<<1). However, F2 has on an average 201.6 organisms/gut/category and μ_{F2}/μ_R is 0.9024 (≈1.0). In contrast, F3 with 360 individuals in i = 7 results a variation of 8555.81 instead 1.638095 in F1. The μ_{F3}/μ_R is 0.114891 (<<1). In case of F4, only 7 categories are represented. The μ_{F4}/μ_R is 0.372128. The F5 has equal categorical distribution to F4 but individual abundances are very less. The μ_{F5}/μ_R is 0.010107. The F6 with equal categorical abundance to F2 except i = 4 results a variation of 16350.55 in contrast to the variation of 17065.4 in F2. The μ_{F6}/μ_R is 0.78394(<1.0). In addition, to understand the effect of rarity and dominancy of any category within each gut content data, another ratio of mean to variation (VAR) of gut content has been considered (Table 2). The μ_F/VAR_F is smaller in case of higher variation within F. Two guts, F1 and F3 have difference in i = 7 with μ_{F1}/VAR_{F1} and μ_{F3}/VAR_{F3} are being only 1.180233 and 0.003,

Table 2: Different indices to verify DB(χ^2)

Index	F1	F2	F3	F4	F5	F6	R	Range
μ_F/μ_R	0.008654	0.902417	0.114891	0.797417	0.010743	0.783945	1.0	1.0
μ_F/VAR_F	1.180233	0.011793	0.003	0.0069	0.53617	0.010711	0.011602	Bigger the VAR, smaller is the ratio
μ_F/VAR_R	0.0001	0.01047	0.001333	0.004318	0.000125	0.009096	27.20075	27.20075
$\log\mu_F/\log VAR_R$	2.530101	26.56987	4.095605	11.76065	8.181001	24.86763	27.20075	27.20075
B_A	**0.688969**	**0.697952**	0.010225	0.336404	0.365229	**0.6440429**		**1-0**
B'_A	0.45679	0.94837	0.07922	0.45040	0.40459	0.82276		1-0
FT	0.99159	0.99929	0.545482	0.719536	0.717113	0.944761		1-0
DB(χ^2)	28.32208	**0.030544**	26.81801	16.30153	25.85656	**1.793926**		near to 0

F1, F2, F3, F4, F5 and F6 are the guts with food items recorded from six fish species (Table 1), R gives the food resources available in the environment, Here μ and VAR represent mean and variation of each data set, subscript (F, R) indicates the μ and VAR of respective date sets, The range of μ_F/VAR_R and log $\mu_F/\log VAR_R$ are given in respect to R from Table 1, For Levins's B_A>0.60 is significant (Zaret and Randell, 1971), Other significant results (given in bold) are shown with reference to ranges for specific index, B_A: Levins's niche breadth, B'_A: Hurlbert's niche breadth, FT: Smith's niche breadth, DB(χ^2): New diet breadth proposed

respectively. Similarly, to compare the magnitude of differences of food abundance in each gut to R, another ratio of μ_F/VAR_R has been computed (Table 2). If F represents R this ratio will be same as μ_R/VAR_R (here μ_R/VAR_R = 0.0116; $\mu\log_R/VAR\log_R$ = 27.2001). The F2 has almost equal μ_{F2}/VAR_R (0.01047) and $\mu\log_{F2}/VAR\log_R$ (26.5699) to μ_R/VAR_R and $\mu\log_R/VAR\log_R$ respectively. In contrast, F1, F3, F4 and F5 have far dissimilar μ_F/VAR_R to R. F6 with similar categorical abundances to F2 except i = 4 gives μ_{F6}/VAR_R as 0.009096 or $\log\mu_{F6}/\log VAR_R$= 24.8676, a slight variation to R.

A t-test has been performed to understand the differences between fish gut categories to R. The t-test results revealed that means of F2 and F6 has no significant difference with R (F2 $_{t = 0.44, p = 0.83, df = 28}$; F5$_{t = 0.99, p<0.17, df = 28}$). In contrast, means of F1, F3, F4 and F5 are highly different from R (F1 $_{t=6.18, p = 0.0000, df = 28}$; F3$_{t = 4.59, p<0.0001, df = 28}$; F4$_{t = 3.07, p = 0.0047, df = 28}$; F5$_{t = 6.18, p<0.0000, df = 28}$).

Comparing with other Niche measures: The measured DB(χ^2) is compared with Levins (1968) measure of niche breadth after modified by Hurlbert (1978), Hulbert's niche breadth and Smith's niche breadth.

The Levins's niche breadth is:

$$B_A = \frac{(1/\sum P_i^2)-1}{n-1}$$

where, B_A is Levins's Niche Breadth, p_j is fraction of items in the diet that are of food category j. n is number of resource states.

Hulbert's niche breadth is calculated as:

$$B'_A = \frac{(1/\sum P_j^2/a_j)-a_{min}}{1-a_{min}}$$

where, BA´ is Hulbert's niche breadth, p_j is fraction of items in the diet that are of food category j, a_j is proportion of total available resources consisting of resource j ($\sum a_j$ = 1.0).

Smith niche measure is calculated as:

$$FT = \Sigma \sqrt{(p_j\, a_j)}$$

where, FT is Smith's niche breadth, p_j and a_j are as described in B_A and B'_A.

RESULTS

In F1, though categorical abundance is more ($\Sigma i = 15$), individual abundance of each category is very minimal ($\mu_{F1} = 1.933$), while in F2, for similar categorical abundance, individual abundances are more ($\mu_{F2} = 201.6$) (Table 1). In contrast, F4 has low categorical abundance ($\Sigma i = 7$) and individual abundances, N = 1247 and $\mu_{F4} = 83.13$. The F5, in contrast, has similar categorical abundance to F4 but lesser individual abundances (N = 36, $\mu_{F5} = 5.143$). The F3 with similar categorical abundance to F1 with comparatively high individual abundances (N = 387; $\mu_{E4} = 178.14$) to F1 except i = 8 which has 360 individuals. The F6 has similar categorical abundance and individual abundances to F2 except i = 4 which has only 3 individuals. This variation in F6 results N = 2627 and $\mu_{F6} = 175.13$. Data set F3 and F4 have μ_F/VAR_F far less than 1 ($\mu_{F3}/VAR_{F3} = 0.003$; $\mu_{F4}/VAR_{F4} = 0.0069$), meaning that these two data sets have more highly variable data effecting normal distribution of the food categories. The μ_{F2}/VAR_{F2}, μ_{F6}/VAR_{F6} and μ_R/VAR_R values are close to each other indicating that F2, F6 and R have almost similar distribution of abundances in categories.

The F2 with slight variation to R produces DB(χ^2) measure 0.03054 (Table 2). However, with i = 4 as difference between F2 and F6 and also μ_{F6}/VAR_R little lesser to μ_{F2}/VAR_R, F6 shows DB(χ^2) as 1.793926. Others, like F1 and F3 have largely different DB(χ^2) values (i.e., 28.32208 and 26.81801, respectively). In case of other niche measures, no uniformity has been observed (Table 2). Levins's niche breadth measured for F1, F2, F3, F4, F5 and F6 are 0.68899, 0.69795, 0.01022, 0.33640 and 0.644029, respectively. Out of these, F2 shows highest Niche Breadth followed by F1, F3, F4 and F5. The Hulbert niche measure results higher niche breadth for F2 followed by F6. It has more or less equal niche breadth for other guts. For Smith's niche measure, F1 and F2 show equal and highest niche breadth (≈ 1.0) followed by F6.

DISCUSSION

DB(χ^2) explains data variations-within and to resource: The DB(χ^2) reflects realistic diet breadth of the fish species. The DB(χ^2) of F1 with similar food categories to R deviates largely from expected diet breadth. It is because the individual abundances for each category in the gut of fish are too less in comparison to resources (R) in the environment to consider them as common food categories of the fish. The fish has no specific and selective choice. Since diet analysis in feeding ecology follows random sampling, the food categories of F1 can be considered as accidental entry to gut of the studied fish or a diet breadth resulted due to sampling during non-feeding time of fish. However, following B_A of F1, (significant; Zaret and Rand, 1971), such inference cannot be made. A similar observation of FT that considers proportion of available resource in the environment while computing niche breadth has been observed for F1. Rather, FT for F1 exhibits more closure to 1.0 indicating highest niche breadth. The F2, with μ_{F2}/VAR_R close to μ_R/VAR_R has DB(χ^2) only 0.0305. This value reflects a diet breadth that indicates food items in the gut near to R, which has DB(χ^2) value always 0 for a completely superimposed gut. In contrast, FT could not differentiate F1 and F2 although measured from the same resource state i.e., R. It is because FT is a product of proportion of food items in the gut and food items available in the environment. It does not consider the availability of food items in the gut in relation to respective food items available in the

environment. Similarly, F3 has all similar individual abundances to F1 except i = 7 and $DB(\chi^2)$ is 26.81801. Thus the effect of abundance of i = 7 is evident in the $DB(\chi^2)$. The $DB(\chi^2)$ of F1 and F3 have shown similar diet preferences even though there is dominant occurrence of a single category in F3. Contrasting to such clarity in diet preference, B_A has shown an opposite figure. The F3 has as low as 0.0102 as its B_A indicating a total rejection of diets occurred in the gut. B_A is very sensitive to the dominant occurrence of a single food category since it considers proportion of individual abundance to total abundance of organisms in the sample. The effect of i = 7 influenced rest of the categories to have a very low proportion in F3 to result such diet breadth. However, the $DB(\chi^2)$ overcomes such 'proportional error' considering difference of actual individual abundance for category i which is always $<R_i$. Thereby it ignores the effect of total abundance as determining factor.

The B_A of F2 reflected a diet preference that is almost equal to F1. The difference in individual abundances of food categories by F1 and F2 does not suggest any chance of common food preference by both. In addition, B_A of F1 and F2 indicates a potential niche overlap as they share same food categories with almost equal diet breadth. However, as it is evident that availability of food categories in F1 is only accidental or due to sampling in non-feeding time, such possibility of niche overlap is completely rejected. The $DB(\chi^2)$ of F1 and F2 gives a clear indication of such possibility. Except B'_A, other diet measures failed to explain such difference.

In case of F6, the rare occurrence of i = 4 is well reflected in $DB(\chi^2)$. F6 has similar abundance values to F2, the rare occurrence of i = 4 has little impact on it. The μ_F/VAR_R of F2 and F6 also reflected little differences of categorical abundances in these two samples to R. The B_A and FT of F2 and F6 too, are similar. But, the uncommon observation is that both B_A and FT of F2 are more nearer to F1 than to F6.

In nature, as it is very unnatural to have equal food categories in the gut of the individuals of a population, the F4 and F5 have been considered only with seven food categories. Obviously, comparing to R, the $DB(\chi^2)$ would be influenced due to such shortage of food category in the gut. However, since F4 in the gut have μ_{F4}/VAR_R value greater than F1 or F3, the category wise food preference will be surely more than F1 or F3. The shortage of total food categories of F4 to other guts have influenced $DB(\chi^2)$ to limit it within 16.3015. This has not been truly reflected through all other three diet breadth measures. The F5 with similar categorical but lesser individual abundance also resulted almost same diet breadth in respective index viz. B_A, B'_A and FT. Instead, $DB(\chi^2)$ gives more clearer difference between these two.

Clumping of guts: To understand the nature of diet preferences of different species or members of individuals in a species, I would like to use 'clumping' of guts as one of evident criteria. Clumping of guts means close occurrences of diet breadths from guts with available resource while plotting against any scale derived from the data of food items. It will provide clearer information to study feeding ecology of an organism, when diet breadths are computed on the same food items available as resource food (here R). More closure the diet breadths on the plot to R, more chances of overlapping or competition for R. Here, $DB(\chi^2)$ has been plotted against μ_R/VAR_R (Fig. 1). The F2 and F6 show 'clumping' (encircled, Fig. 1) indicating chances of diet overlap or competition between these two for resources R. Conversely, F1 and F3 have no competition for R and therefore, some other means of resources might be acting as food resource for them. Such possibility of interaction between studied guts can not be drawn from B_A, B'_A or FT. Though the F2 and F3 are clumped in these cases, exclusion of the reference available resource from 'clumping' rejects any possibility of overlapping or competition for it. In such case no study of diet overlap is required.
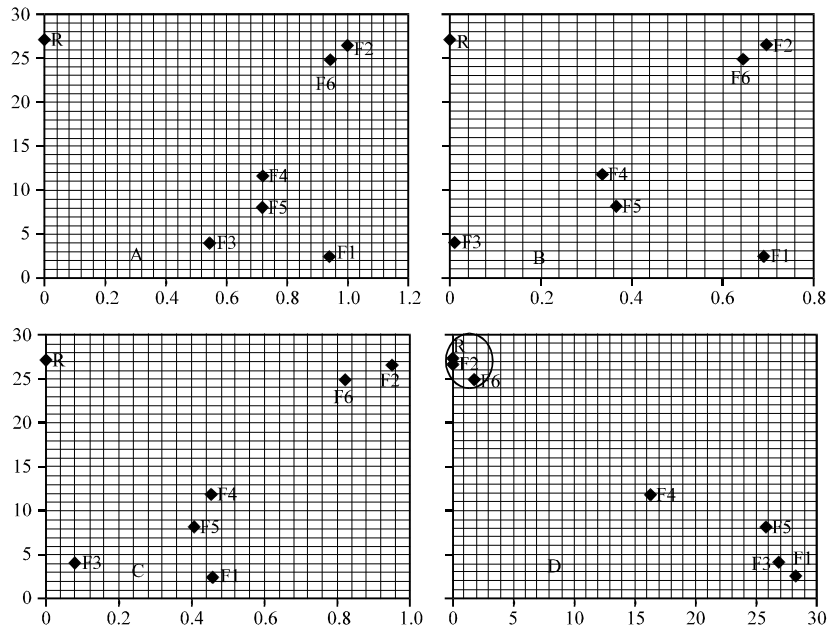
Fig. 1: Diet breadths (B_A, B'_A, FT and DB(χ^2)) of six fish species (F1, F2, F3, F4, F5 and F6) on the basis of theoretical data of gut content analysis (Table 1 and 2). Diet measures are is plotted (on x axis) against $\log\mu_F$: $\log VAR_R$ (μ, mean of F where F = F1, F2.....F6; VAR, Variation in R where R is food resources available in the environment). A. The FT doesn't show any clumping, B. The B_A doesn't show any clumping C. The B'_A doesn't show any clumping and D. The DB(χ^2) shows 'clumping' of gut for F2 and F6 with R and have chance of niche overlap. However, F1 is distantly positioned from R and there is no possibility of competition of F1 with F2 or F6

Thus, the DB(χ^2) is sensitive to total food category, individual abundance, dominance or rarity of each food category and to the within and between variances of the data sets. In addition, it indirectly provides information on diet overlap of two or more organisms through 'clumping of guts'. However, similar to other diet measures, it will also reflect the prey items immediately ingested by the organism studied. Hence, an alternative confirmatory study with stable isotopes of both the consumer and its prey is suggested (Tripp-Valdez and Arreguin-Sanchez, 2009).

REFERENCES

Alkahem, H.F., A.A. Al-Ghanim and Z. Ahmad, 2007. Studies on feeding ecology of sailfin molly (*Poecilia latipinna*) dwelling in Wadi Haneefah stream, Riyadh. Pak. J. Biol. Sci., 10: 335-341.

Alwany, M.A., M. Stachowitsch, M.H. Hanafy and A.A.F.A. Gab-Ala, 2007. Food preference of the Butterfly fish *Chaetodon melannotus* on the reef flat in Sharm EI-Sheikh, Egypt. J. Fish. Aquatic Sci., 2: 38-46.

Ara, R., A. Arshad, L. Musa, S.M.N. Amin and P. Kuppan, 2011. Feeding habits of larval fishes of the family Clupeidae (Actinopterygii: Clupeiformes) in the Estuary of River Pendas, Johor, Malaysia. J. Fish. Aquatic Sci., 6: 816-821.

Bluthgen, N., F. Menzel and N. Bluthgen, 2006. Measuring specialization in species interaction network. BMC Ecol., 6: 9-9.

Colwell, R.K. and D.J. Futuyma, 1971. On the measurement of niche breadth and overlap. Ecology, 52: 567-576.

Garcia- Rodriguez, F.J. and J. de la Cruz-Aguero, 2011. A comparison of indexes for prey importance inferred from otoliths and cephalopod beaks recovered from pinniped scats. J. Fish. Aquat. Sci., 6: 186-193.

Heitkonig, I.M.A. and N. Omen-Smith, 1998. Resource partitioning by ungulate on the Isle of Rhum. Oecologia, 79: 383-389.

Hurlbert, S.H., 1978. The measurement of niche overlap and some relatives. Ecol., 59: 67-77.

Hutchinson, G.E., 1957. Concluding remarks. Cold Spring Harbor Symposia on Quantitative Ecol., 22: 415-427.

Kumar, D. and M. Pardeshi, 2011. Biodiversity of termites in agro-ecosystem and relation between their niche breadth and pest status. J. Entomol., 8: 250-258.

Levins, R., 1968. Evolution in Changing Environments: Some Theoretical Explorations. Princeton University Press, NJ.

Oh, S.Y., A. Arshad, S.B. Japar, A.A. Nor Azwady and S.M.N. Amin, 2011. Diet composition of sergestid shrimp *Acetes serrulatus* from the Coastal waters of Kukup, Johor, Malaysia. J. Fish. Aquatic Sci., 6: 809-815.

Oribhabor, B.J. and A.E. Ogbeibu, 2012. The food and feeding habits of fish species assemblage in a Niger delta Mangrove Creek, Nigeria. J. Fish. Aquat. Sci., 7: 134-149.

Oueda, A., W. Guenda, A. Ouattara, G. Gourene, B. Hugueny and G.B. Kabre, 2008. Seasonal diet shift of the most important fish species in a Sahelo-Soudanian reservoir (Burkina Faso). J. Fish. Aquatyic Sci., 3: 240-251.

Smith, E.P., 1982. Niche breadth, resource availability and inference. Ecology, 63: 1675-1681.

Tripp-Valdez, A. and F. Arreguin-Sanchez, 2009. The use of stable isotopes and stomach contents to identify dietary components of the spotted rose snapper, *Lutjanus guttatus* (Steindachner, 1869), off the Eastern Coast of the Southern Gulf of California. J. Fish. Aquatic Sci., 4: 274-284.

Whenu, O.O. and S.O. Fagade, 2012. Dietary pattern of the population of *Parachanna obscura* (Gunther, 1861) in River Owo, South West, Nigeria. J. Fish. Aquatic Sci., 7: 49-56.

Zaret, T.M. and A.S. Rand, 1971. Competition in tropical stream fishes: Support for the competitive exclusion principle. Ecology, 52: 336-342.