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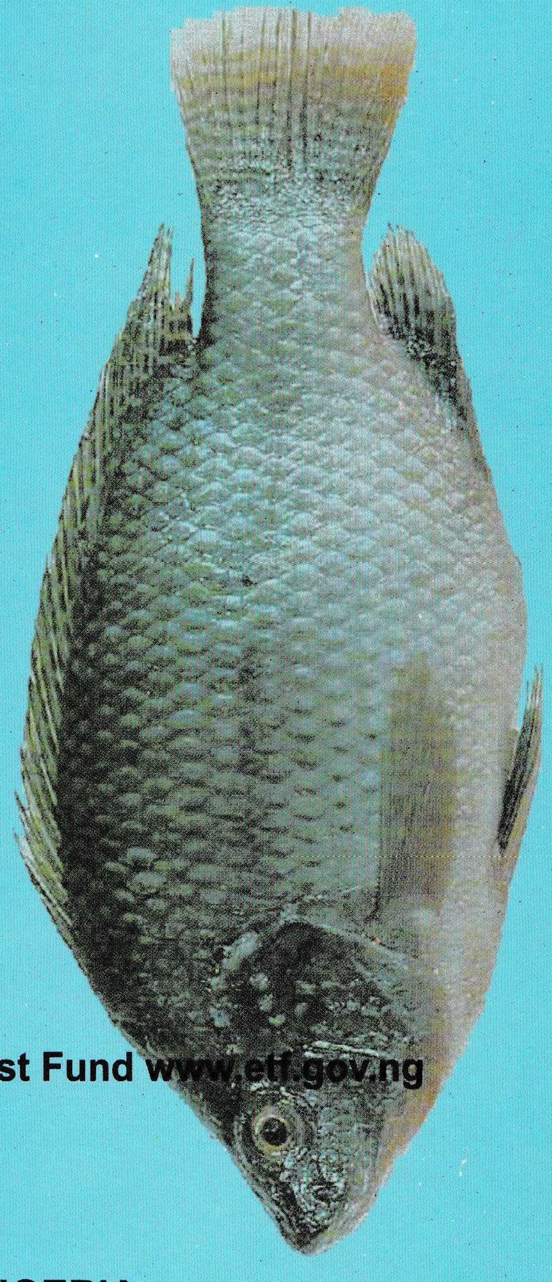

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COMMUNITY STRUCTURES OF EPIBENTHIC MACROFAUNA OF THREE MANGROVE WETLANDS IN NIGER DELTA, NIGERIA: A COMPARISON OF COMMUNITY INDICES

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ABSTRACT
The epibenthic macrofaunal composition of three floristically different mangrove wetlands east of the Imo River, Nigeria, were investigated for the first time between December, 2000 and November, 2002. These resources of the swamps comprise a minimum of 11 families, 12 genera and 15 species at station 1 dominated by the native Rhizophora racemosa, Rhizophora mangle, Rhizophora harrisonii; 10 families, 11 genera and 14 species at station 2 with mixed mangrove macrophytes and 16 families, 18 genera and 23 species at station 3 dominated by the invasive palm, Nypa fruticans Wurmb. The result from station 3 is at variance with a non-empirical claim (widely held), that this Indo-Pacific mangrove palm has adversely affected these intertidal swamp fauna as it does the native mangrove macrophytes by eliminating them. The four diversity measures estimated gave disparate values and trends of diversity between the stations, but the index of Levin appears more sensitive and its assessment more reliable, upon which the three swamps are classified as oligodiverse and mesodiverse, with none being polydiverse.
Keywords: ***species*** diversity, molluscs, crustaceans, fin fish, Shannon-Weiner index

INTRODUCTION

The mangrove vegetation of southeastern Nigeria (east of the Imo River Estuary) has been relatively well reported (Keay, 1953; Wilcox, 1985; Onofeghara, 1985; Odu, 1985; Ukpong, 1991, 1992a, 1992b, 1994a, 1994b, 1995, 1997; Ukpong and Areola, 1995). Geochemical studies of Qua Iboe River Estuary and associated creeks in this zone have also been reported by Ekwere *et al.* (1992), while Ntekim *et al.* (1992) reported the trace metal distribution of the coastal sediments of this area. Reports on the faunal components of the mangrove flats of this area are wanting (except reports of sponsored studies during emergencies such as oil spillages and environmental impact assessment (EIA) which are heavily partisan). This area is economically important with its numerous on-shore and off-shore oil facilities. The occasional oil spillages from these facilities could contribute to disturbance of the ecosystem. This paper aims to investigate (using a community approach) the intertidal epibenthic macrofaunal communities of a section of the mangrove ecosystem east of the Imo River, as a first step toward the knowledge and understanding of its faunal assemblage, and to complement the available floral literature.

The use of mathematical/statistical models to draw inferences on biological research results has become established. In ecological community studies, the numerical structures of such communities are often assessed by a number of such mathematical models called indices. These indices have been used singly in many scientific reports. An attempt is made in this paper to compare some of these indices to ascertain whether such disparate models could lead to a consistent result and hence inference on a particular aspect of the communities concerned.

MATERIALS AND METHODS

Study Area

The study area is part of the eastern flank of the Imo River estuarine mangrove wetlands in Eastern Obolo, Nigeria, located between latitudes 4°28′ and 4°33′ North, and longitudes 7°30′ and 7°50′ East (Fig. 1). This estuary is said to form a prominent part of what is termed the Niger Delta geosyncline which filled up during the later quaternary and recent geological periods (Uniuyo Consults, 1998). The development of large tracts of swamps in this area is aided by a low wave energy regime such that the river estuaries (where the most complex swamps occur), are depositional with sedimentation outstripping erosion (Ibe and Antia, 1983). Two distinct soil zones viz; clayey silt along the fringe of creeks, and peaty, fibrous mud (chikoko) at the back swamps (Wokoma, 1985) characterize the swamp soils.

The swamps are influenced by semidiurnal tidal flooding (Faniran, 1986), and organic substrate associated with acid conditions (Ukpong and Areola, 1995) characteristic of waterlogged saline soils (Boto, 1984). The movement of the Inter-Tropical

Front influences the climate of the area and gives rise to two seasons: the wet and the dry. The dry season with a characteristic cold, dry, dusty wind from the Sahara desert lasts from November to March, whereas the wet season with high rainfall, relative humidity and heavy cloud cover lasts from April to October.

Three stations with characteristic vegetation were chosen for study. Station 1 (Kampa: 7°42′E, 4°32′N) is relatively far from the coast with the swamp vegetation consisting mainly of *Rhizophora spp*., with scattered stands of *Avicennia africana*. Station 2 (Emereoke: 7°40′E, 4°31′N) situates along a protected creek with low wave energy, though it is relatively close to the Atlantic coast. It has mixed vegetation consisting of *Rhizophora spp*., *Nypa fruticans, Avicennia africana, Conocarpus erectus* and the mangrove fern *Acrostichum aureum*. The Indo-Pacific mangrove palm *Nypa fruticans* which grows densely and luxuriantly with its tussocked mass of leaves and anastomosing rhizomes (making access to the swamps a herculean task) dominates the swamps of Station 3 (Obianga: 7°37′E, 4°29′N). This station is very close to the mouth of the Imo River and the Ebon Okwan Obianga estuary, but along a protected creek.

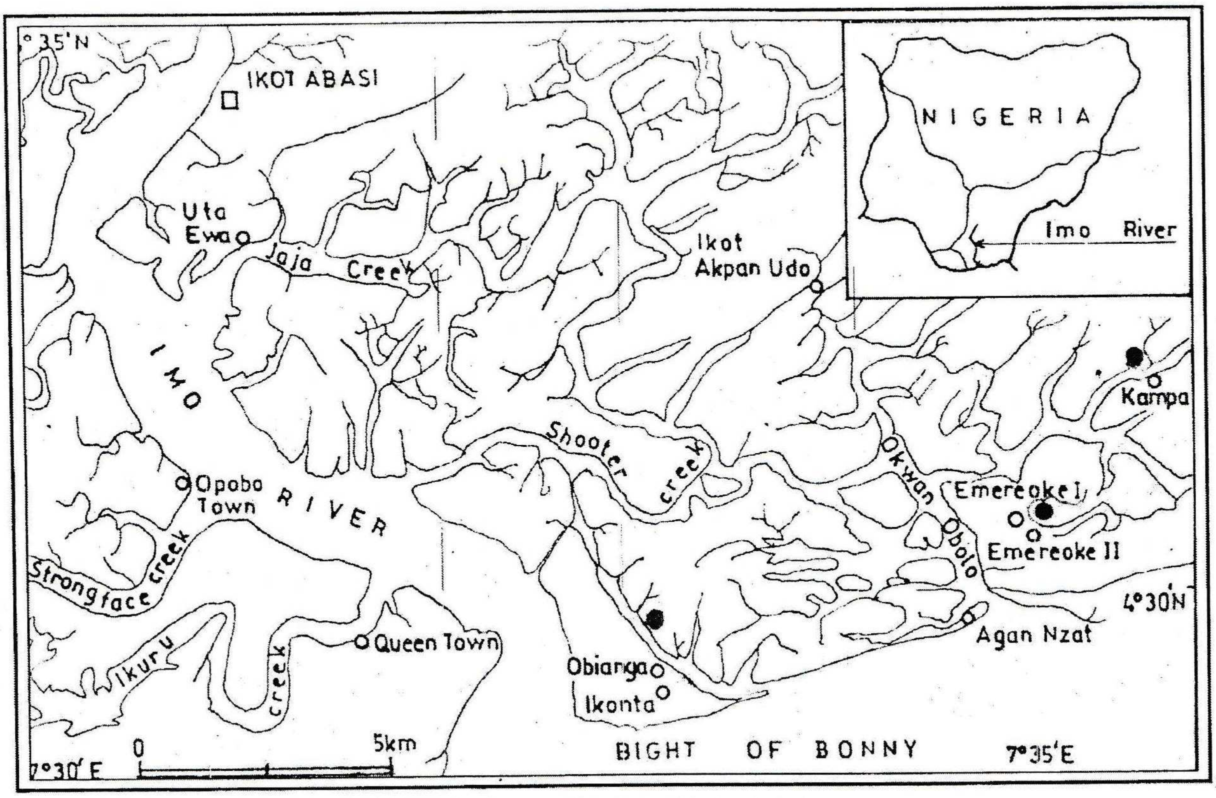

Fig. 1. Parts of the Coastal Basin of Imo River showing sampling sites, with closed circles. Inset: Map of Nigeria showing the position of Imo River. From Udoidiong (2005).

Sampling

Six transects were established at each station from creek margins across the mangrove swamps and samplings carried out through a number of quadrats (separated by 10m intervals) marked during each sampling occasion for a period of twenty-four months (December, 2000 to November, 2002). Most of the surface dwelling macrofauna were sampled with a $0.5m^2$ metal quadrat, except the mudskipper *Periophthalmus barbarus,* the purple mangrove crab *Goniopsis pelii,* the fiddler crab *Uca tangeri,* the xanthid crabs *Menhippe nodifrons* and *Panopeus africanus*, and the giant hairy melongena *Semifusus morio,* which were sampled within 5 x $5m^2$ land quadrats. The first three species were sampled with the aid of traps (King and Udo, 1997). Some tree species, viz, the dog whelk (*Thais coronata, Thais callifera and Thais haemastoma)* and the periwinkle *Littorina angulifera*, were also sampled within 5 x $5m^2$ quadrats by a ten minute timed search. The oyster *Crassostrea gasar* was sampled form a vertical range of 30cm on 3 mangrove prop roots and *Nypa* leaf bases within 5 x $5m^2$ quadrats. Identification of specimens was aided by Edmunds (1978), Holthuis (1981), Schneider (1990) and Yankson and Kendall (2001).

Analysis

A mathematical model expressing the joint contribution of species richness and respective species' relative abundance (importance value in the community) is the species diversity. Four of such models were used in this assessment:

(i) Shannon Weiner Index: This is the most widely used diversity index. Designated H′, it is expressed as:

$$H' = -\Sigma\ (n_i/N \ \log_e \ n_i/N) \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots 1$$

where (n_i/N) or p_i is the relative abundance of each of the contributing species. H′ has 0 as its minimum value for a community with a single species, and increases as species richness and evenness increase.

(ii) The index designated as H_{max} and expressed as:

$$H_{max} = \ln S \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots 2$$

with ln being natural logarithm and S the total number of species involved. Krebs (1978) notes that this index measures diversity under conditions of maximum equitability. The above indices do not scale between 0 and 1 and thus there is no limit to the diversity value that can be attained.

(iii) A derivative of the Shannon-Weiner index that scales between 0 and 1, and expressed as:

$$\frac{H'}{\ln_e S} \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots 3$$

(iv) The index **B** of Levin (1968) and standardized as described by Hespenheid (1975) to assume values ranging between $B_{min} = 0$ and $B_{max} = 1$ (King and Jonathan, 2003) and expressed as follows:

$$\mathbf{B} = [(\Sigma P_i^2)^{-1} - 1]/N - 1 \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots 4$$

Where $P_i = p_i$ of Shannon-Weiner index and N = total number of species or taxa present.

Evenness or equitability was measured with two indices:

(i) The McArthur – Terborgh species equitability index **E** (a measure of evenness of distribution of species abundances) expressed as:

$$E = \frac{e^{H'}}{S} \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots 5$$

where **e** is the base of natural logarithm, and H' the Shannon-Weiner diversity index; S = number of species. A completely uniform index would give E = 1. E is represented as $E_{(mt)}$ in Table 3.

(ii) The Simpson index-derived equitability **E**, given by Begon *et al.* (1996) as:

$$\mathbf{E} = \frac{1}{\Sigma pi^2} \times \frac{1}{s} \quad \ldots\ldots\ldots\ldots\ldots 6$$

and represented in Table 3 as $E_{(bg)}$. P_i^2 refers to squared values of P_{is} of equations 1 and 4 above, and S = number of species involved. Maximum equitability attainable = 1.

Two indices that measure similarity were employed in deciphering this aspect of the structure of these communities. First, the coefficient of community (CC) of Jaccard as cited by Stirn (1981) was calculated thus:

$$CC = \frac{Cij}{Ai + Aj - Cij} \quad \ldots\ldots\ldots\ldots\ldots 7$$

where Aij = number of species in samples i(j); Cij = number of species common to both samples i(j). Thus CC x 100 is the measurement of the percentage of species shared by two samples. Second, the similarity index as given in Odum (1971) designated as S and expressed thus:

$$S = \frac{2C}{A + B} \quad \ldots\ldots\ldots\ldots 8$$

where S = similarity (or overlap); A = number of species in sample A; B = number of species in sample B, and C = number of species common to both samples. The index ranges from 0 – 1.0 to quantify the range from no similarity to complete similarity, and is a simple measure based on species presence only (Krebs, 1978). The reciprocals, 1-CC and 1-S, were computed as dissimilarity measures.

Dominance can be said to be a measure of the level of quantitative (numerical) superiority of species in a community. A single index, the Simpson index designated as D and expressed as follows:

$$D = \Sigma P_i^2 \quad \ldots\ldots\ldots\ldots\ldots\ldots..9$$

was used as the index of dominance. Odum (1975) pointed out that this index is an index of dominance since the maximum value 1, is obtained when there is only 1 species (complete dominance), and values approaching zero are obtained when there are numerous species, each a very small fraction of the total (no dominance). This index had been so used (Udoidiong, 1988, Udoidiong and King, 2000) in earlier studies. The **d**-test (Parker, 1979) was used to test differences in mean values of the quantities obtained.

RESULTS

Species composition

Twenty three species (made up of 21 invertebrates and 2 vertebrates) partitioned among 18 genera and 16 families were obtained (Table 1). Station 3 (Obianga) which floral composition consisted mainly of the Indo-Pacific palm *Nypa fruticans*, had the highest taxonomic richness as given above, followed by station 1 (Kampa) dominated by *Rhizophra spp* (15 species, 12 genera, 11 families), with Station 2 (Emereoke) having mixed stands of mangrove macrophytes, contributing 14 species in 11 genera and 10 families. Twenty-four thousand, five hundred and twenty-eight (24, 528) specimens were collected with Station 1 contributing 7,694 (31.4%), station 2 yielding 8,096 (33.0%), and 8,738 (35.6%) from Station 3. The two vertebrate species were the mudskipper, *Periophthalmus barbarus* and the eleotrid, *Bostrychus africanus*.

A spatial summary of the numerical data and pooled abundances are presented in Table 2, with overall mean numbers per species. In all stations the first three species in order of descending abundance were the gastropod molluscs *Tympanotonus fuscata*, the oyster *Crassostrea gasar* and the periwinkle *Littorina angulifera*. The species in the least abundant category altered per station, with station 1 having *Menhippe nodifrons*, *Semifusus morio* and *Cardisoma armatum* in increasing order of rarity. *Panopeus africanus, Semifusus morio* and *Menhippe nodifrons* were least abundant in station 2. Station 3 had eight rare species, viz, *Menhippe nodifrons, Bostrychus africanus, Cardisoma armatum, Penaeus notialis, Callinectes amnicola, Callinectes pallidus, Penaeus kerathurus* and *Sesarma elegans* in increasing order of rarity.

Table 1: Numerical and relative abundances of species obtained from three stations between December 2000 and November 2001

Species	Stations						Pooled		Mean (±SD)
	1		2		3				
Clibanarius chapini	58	0.0078	44	0.0054	97	0.011	199	0.0081	66.33 ± 27.46
Clibanarius senegalensis	192	0.025	223	0.028	573	0.035	988	0.040	329.33 ± 211.59
Bostrychus africanus	0	0	0	0	5	0.00057	5	0.0002	1.67 ± 2.89
Melampus liberianus	0	0	0	0	105	0.012	105	0.0043	35 v 60.62
Semifusus morio	6	0.00075	8	0.00099	67	0.077	81	0.0033	27 ± 34.65
Cardisoma armatum	3	0.00035	0	0	4	0.0846	7	0.00028	2.33 ± 2.08
Periophthalmus barbarus	902	0.117	1030	0.127	1020	0.117	2852	0.120	984 ± 71.19
Goniopsis pelii	850	0.118	916	0.113	778	0.189	2544	0.104	848 ± 69.02
Sesarma elegans	0	0	0	0	1	0.00011	1	0.00004	0.33 ± 0.58
Littorina angulifera	1184	0.154	1211	0.149	1099	0.126	3494	0.142	1164.67 ± 58.4
Thais callifera	409	0.053	412	0.051	334	0.138	1155	0.05	385 v 44.19
Thais coronata	345	0.045	279	0.035	302	0.134	926	0.04	308.7 ± 33.5
Thais haemastoma	355	0.045	316	0.039	324	0.037	995	0.041	331.7 ± 20.59
Neritina glabrata	0	0	0	0	84	0.1096	84	0.0034	28 ± 48.49
Uca tangeri	855	0.111	907	0.112	935	0.107	2698	0.11	899.3 ± 41.0
Crassostrea gasar	1213	0.153	1328	0.164	1317	0.151	3858	0.16	1286 ± 63.46
Penaeus notialis	0	0	0	0	4	0.0046	4	0.00016	1.33 ± 2.131
Penaeus kerathurus	0	0	0	0	1	0.00011	1	0.00004	0.33 ± 0.58
Callinectes amnicola	0	0	0	0	3	0.00034	3	0.00012	1.0 ± 1.73
Callinectes pallidus	0	0	0	0	2	0.00023	2	0.00008	0.67 ± 1.15
Tympanotonus fuscata	1293	0.168	1388	0.171	1596	0.183	4277	0.174	1425.7 ± 154.9
Menippe nodifrons	11	0.0015	4	0.00049	18	0.0021	33	0.0013	11 ± 7.0
Panopeus africanus	18	0.0023	30	0.0037	68	0.0078	116	0.0047	38.67 ± 26.1
Total Number	**7694**	-	**8096**	-	**8738**	-	**24528**	-	

Table 2: Epibenthic macrofauna diversity and evenness indices in the three swamp communities

		Diversity				Evenness	
Station	**Species Richness**	**H'**	**H'_{max}**	**H'/ln_eS**	**B**	**$E_{(mt)}$**	**$E_{(bg)}$**
1	15	2.3236	2.8873	0.8117	0.4654	0.5507	0.6228
2	14	2.2359	2.6736	0.8441	0.6184	0.6466	0.6883
3.	23	2.1677	2.6020	0.3740	0.4863	0.4662	0.5614
Pooled	23	2.2598	2.8873	0.7207	0.4319	0.4532	0.5452

Community Parameters

Results of the four diversity indices are presented in Table 3. The two unscaled indices, **H'** and **H_{max}** give the same order of assessment of the three communities, which is that diversity is highest at Station 1 which is floristically dominated by *Rhizophora* spp., followed by Station 2 with mixed stands of mangrove macrophytes, and lastly station 3 that is completely taken over by *Nypa fruticans*. On the two scaled indices (Table 3), disparate orders of assessment emerge: the Shannon-Weiner derived saling gives the highest diversity to station 2, followed by station 1 and then station 3. The Levin index (**B**) rates station 2 as having the highest diversity, followed by station 3, and last station 1. Thus, the unscaled indices rate station 1 highest in diversity, whereas the scaled indices rate station 2 with the highest diversity. Therefore, three of the four indices assess station 3 as lowest in diversity, whereas only the Levin index rates station 1 as lowest in diversity. Values from the scaled indices were further subjected to **d-test** statistic for intra-and inter-station comparison (Table 4). Results show that there were statistically significant intra-station differences between the two indices in the assessment, with the Shannon-Weiner-derived scaling giving higher values than the **B** scale in all stations as indicated. Inter-station comparison with individual index shows that there were no statistically significant differences between stations on the **H'/ln_eS** scale ($P > 0.05$ in each case). The Levin index **B** indicates statistically significant differences between the pairs of stations compared, meaning that diversity in station 2 > 3 > 1 ($P < 0.001$ in each case).

The two evenness indices (Table 3) give similar assessment of the three communities, with the trend, station `2 > 1 > 3. Pooled values were the lowest in evenness rating by the two indices. There were no statistically significant differences in similarity and dissimilarity between the station pairs (Table 5) from the two indices ($P > 0.05$ in each case). There were also no statistically significant differences between these pair-wise comparisons: stations 1 and 2 v 1 & 3; 1 and 2 v 2 and 3, and 1 & 3 v 2 & 3 ($P > 0.05$ in each case) on both indices. The single dominance index shows that this parameter at station 3 > 2 > 1, a confirmation of the evenness assessments.

Table 3: Intra-and inter-station comparison of two scaled diversity indices from the three swamp communities

			d - test		
			Intra-station	**Inter-station**	
Station	**H'/ln_eS**	**B**		**H'/ln_eS**	**B**
1	0.8117 ± 0.0158	0.4658 ± 0.1110	3.086*** $\frac{H'}{ln_e S} > B$	1 and 2 0.745^{ns}	1 and 2 4.250***
2	0.8441 ± 0.0409	0.6184 ± 0.0840	2.416* $\frac{H'}{ln_e S} > B$	1 and 3 1.408^{ns}	1 and 3 16.178***
3	0.7340 ± 0529	0.4683 ± 0.0070	4.647*** $\frac{H'}{ln_e S} > B$	2 and 3 1.646^{ns}	2 and 3 15.483***
Pooled	0.7207 ± 0.0193	0.4319 ± 0.1290	2.215*		

*** = P<0.001
* = P<0.05

Table 4: Diversity classification of the three swamp communities based on Table 2 diversity values

Index Range	Classification	Diversity Model	
		H'/ln_eS	B
1 – 0.4	Oligodiverse	Nil	Stations 1 & 3
0.5 – 0.6	Mesodiverse	Nil	Station 2
0.7 – 1.0	Polydiverse	All stations	No station

Table 5: Epibenthic macrofauna similarity, dissimilarity and dominance indices in the three swamp communities

Station pair	No species common	Similarity CC	Similarity S	d-test S-CC	Dissimilarity CC	Dissimilarity S	Dominance Station	Dominance D
1 & 2	14	0.9643 ± 0.0505	0.9827 ± 0.0244	1.039^{ns}	0.3570	0.0173	1	0.1214
1 & 3	15	0.8947 ± 0.1488	0.9054 ±0.1338	0.053^{ns}	0.1053	0.0946	2	0.1158
2 & 3	15	0.8611 ± 0.1964	0.8684 ± 0.1861	0.027^{ns}	0.1389	0.1316	3	0.1254
							Pooled	0.2290

DISCUSSION

It has been widely believed (Moses, 1985) that the Indo-Pacific mangrove palm *Nypa fruticans* has adversely affected the mangrove swamp fauna as it has done the native mangrove macrophytes, decimating them in large portions of this mangrove wetlands. The present results have apparently debunked this non-empirical claim, as species diversity and number of individuals were highest in Station 3 dominated by this palm. Ukpong (1989) stated that *Nypa fruticans* is ecologically more important than the native mangrove species (a conclusion based on importance value which was estimated from frequency, density and cover). However, the effect of this palm on the native floral components of these forests is an example of the shifts in species composition of a receiving environment by the introduction of invasive species (Krebs, 1978; Molles, 1999). This palm was introduced into this region in 1906 from the Singapore Botanical Gardens (Mercer and Hamilton, 1984; Wilcox, 1985) ostensibly to stabilize creek margins against erosion. This role has not been played by this species.

Since a diversity classification scheme exists for indices that sale between 0 and 1 (King and Jonathan, 2003), results from these two indices were used for the classification presented in Table 5. An *oligodiverse* assemblage (index range 0 – 0.4) has limited species variety and evenness (apportionment of individuals among the species). A *mesodiverse* community (index range 0.5 – 0.6) has moderately high species variety and apportionment of individuals among the species. Finally, a polydiverse community has high species variety and apportionment of individuals among the species. Therefore, on the Shannon-Weiner-derived scaling, no station was either oligodiverse or mesodiverse; all stations were polydiverse. Conversely, on the Levin scale, stations 1 and 3 were rated oligodiverse, whilst station 2 was mesodiverse, with no station being polydiverse. The overall assessment (pooled) indicates the 3 communities as a unified system to be polydiverse on the Shannon-Weiner-derived scale, and oligodiverse on the Levin scale. Perturbation is believed to alter the diversity of an ecosystem from the polydiverse toward the oligodiverse range (King and Jonathan, 2003), by reducing spatial heterogeneity which translates to reduced microhabitats, microclimates and hiding places (Begon, *et al.*, 1996), thus impacting negatively on biotic integrity (Karr, *et al.*, 1986).

Krebs (1978) is of the opinion that in practice it seems to matter very little which of these different measures of species diversity we use, since the combination of the number of species in the sample and the relative abundance patterns summarize most of the biological information on diversity. The present results on species diversity argue that it matters "very much", which of these different measures we use. The unscaled indices depict species diversity in station 1>2>3; the Shannon Weiner-derived scale gave the trend, station 2>1>3, whereas the **B** index of Levin rated station 2>3>1.

That the two unscaled indices gave a consistent trend in diversity rating of the three wetlands, while the two scaled indices differ on the trend of rating except station 2, shows disparity in assessment, contrary to Kreb's opinion. The inferences derived therefrom would similarly differ, and can lead to conflicting management decisions. For example, classification of the three wetlands as polydiverse on the Shannon-Weiner index-derived scaling appears to be an over-evaluation in that it failed to show consistency in classification and trend of diversity rating, whereas the **B** index remained consistent in evaluating both parameters. Moreover, events in the ecosystems studied indicate perturbations from diverse sources (Udoidiong, 2005). For the present report, the inference based on the **B** index appears to be more reliable, upon which the three wetlands have been classified as ***oligodiverse*** (stations 1 and 3), and ***mesodiverse*** (station 2). Ukpong (1997) pointed out from studies of other zones of the Niger Delta mangroves, that the mangrove wetlands, whether along a consistently saline littoral or a freshwater/brackish interface, is a stressed ecosystem.

It is known in biological circles that the introduction of exotic species into alien environments often causes shifts in species composition of the receiving environments (Wright and Boorse, 2011). This has been the case between the Indo-Pacific mangrove palm *Nypa fruticans* and native mangrove macrophytes which have been eliminated by the palm introduced into this region in 1906. A similar effect on the intertidal fauna of these wetlands has, however, not been observed (Udoidiong, 2005). The dominance of the decapoda and gastropoda is indicative of their ecological importance in these ecosystems, and is in accord with findings elsewhere (Robertson, 1986; Lee, 1989; Micheli, *et al*., 1991 and Smith, *et al*., 1991). Inferences drawn on the diversity assessment of these swamp fauna by the use of a single index could be misleading. The failure of the four diversity indices to give a harmonious conclusion calls for their reappraisal. The disparate conclusions reached by the four diversity indices make reliance on a particular index that is sufficiently sensitive and reflective of conditions in the system assessed more reasonable and expedient. The three wetlands in this study, being part of the larger Niger Delta wetlands complex, have been under chronic stress. The invasive palm, deforestation, exploitation pressure, wave-wash (Powell, 1990), millions of barrels of spilled oil (Dublin-Green, *et al*., 1998), etc. have all contributed to disturb and stress these wetland communities, possibly affecting their biodiversity, especially of the surface dwelling organisms.

CONCLUSION

The occurrence and distribution of the epibenthic faunal resources of the mangrove swamps studied revealed that the highest species richness was recorded in the *Nypa* palm-impacted swamp, followed by the non-impacted *Rhizophora* swamp. This is at variance with the widely held belief (non-empirical) that this Indo-Pacific palm has negatively affected faunal diversity in these swamps, as it has affected floral components by eliminating them. This relatively high species diversity is attributable to habitat heterogeneity afforded by the complex structure of the palm. The community indices used to assess the community structures of these swamps do not lead to a consistent interpretation based on the scheme of classification of diversity (King and Jonathan, 2003). The index, **B** of Levin (1968) seems to be more reliable in interpreting diversity in ecological communities.

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