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Finfish Assemblage of the Lower Reaches of *Okpoka* Creek, Niger Delta, Nigeria

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Abstract: Okpoka Creek is one of the Niger Delta river systems that contributes to the Rivers State fish resources. There has been unprecedented complaint from the fisherfolks on the dwindling finfish and shellfish populations; catches have been drastically reduced. Therefore, there is urgent need to study the fin fish assemblage of this creek due to its location and the various human activities. A survey of the finfish catches was conducted to ascertain its assemblage. Finfishes collected from the landing centre of local fishers for 12 months (April 2005 to May 2006) were identified according to standard method. These fishes were mostly caught by non-selective cast nets of various mesh sizes by local fisherfolks during the low tide. Enumeration was done by visual counting. A number was assigned to each fish species based on frequency of occurrence or abundance (1-5). Analysis of variance and Duncan multiple range were used to analyse the data. A total of 11 species from 8 families of finfishes dominated by Sardinella maderensis (47.33%) were observed. Seasonal catches of finfishes were not significant (p>0.05). The highest relative abundance was recorded in March (18.18%) and the lowest in April (9.09%). The low finfish species diversity indicates that finfish population is over-fished by the local fishers and constant dredging activities have degraded the environment. Also it shows that nypa palms are not good nursery grounds for these fishes. It is therefore recommended that there should be closed fishing season, selective fishing gears hould be used and dredging should be controlled.

Keyword: Fin fish, species composition, non-selective fishing gear, catches, Sardinella maderensis, habitat degradation

INTRODUCTION

Okpoka Creek is one of the river systems of the Niger Delta that contributes to the Rivers State fish resources. It is situated in a strategic location in Port Harcourt, Rivers State. There are various man's activities (such as fishing, dredging, etc.,) going on within and around it. There has been increasing concern on the need to conserve the aquatic environment in order to ensure sustainable resources and development at the local and international levels. In addition, there has been unprecedented complaint from the local people on the dwindling finfish and shellfish population, catches have been drastically reduced. This may be attributed to activities which degrade mangrove and allow nypa palms to invade the delta area may be reducing marine and estuarine fish stocks. Nypa palms do not provide a good ground for marine fish as mangrove plants do (Otobo, 1977). Industrial effluents had negatively affected the mangrove plants.

Studies on finfish assemblage outs ide the Niger Delta include (Imevbore, 1971) of Lake Kainji, (Fagade and Olaniyan, (1972) on Lagos Lagoon, Otobo(1974) of Lake Kainji, Fagade (1983) of Lagos Lagoon, Victorand Tetteh (1988) of Ikpoba River, Nwadiaro (1989) of Lake Oguta, Ekeh (1990) of Nworie River and Okereke (1990) of Otamiri River, Nwadukwe (1995) of Lagos Lagoon, Ita and Machili (1997) of Lake Kainji, Ogueri (2004) of River Katsina Ala and Simon (2007) of Benue River.

Limited numbers of studies have been carried out on the fisheries of Bonny Estuary (Wright, 1986; Chindah and Os uamkpe, 1994; Allis on et al., 1997; Ogamba, 1998; Nweke, 2000; Amakiri, 2005). Chindah and Osuamkpe (1994) studied the fish assemblage of the Lower Bonny River of the Niger Delta with its adjoining creeks. These studies noted 25 families consisting of 57 species with higher catches during the dry seas on than wetseason. The fish assemblage in *Elechi* creek in the Upper Bonny was investigated by Allison et al. (1997). A total of 5,867 fishes belonging to 22 families and 37 species were observed. The dominant family was Cyprinodontidae (36.82%) followed by *Clupeidae* (26.62%) and Paeneaidae (9.15%). The least catch (0.02%) was made up of Characidae, Lobotidae, Squilidae and Syngnathidae. In terms of frequency of occurrence this order was observed; Clupeidae (21.22%), Cichlidae (11.51%), Gobidae and Mugilidae (8.99%). Higher catches were noticed during the dry season. Ogamba (1998) reported low diversity of fish (346 fishes, 7 species and 14 families) in *Elechi* Creek which was attributed to chronic hydrocarbon pollution. There has been no published or existing literature on the fish assemblage of Okpoka creek which is a tributary of this estuary despite its potential usefulness to the fisheries of the Niger Delta. Further studies on fish assemblage in the Niger Delta River System include those of Sikoki et al. (1998) of 57 species, 15 families of Lower Nun River and (Alfred-Ockiya, 1998) 11 species of Kolo Creek River and

(Sikoki et al., 1999) 22 species, 11 families of the brackish zone of the Brass River. In addition, Abowei (2000) reported 36 species, 22 families in the Lower Nun River and (Ezekiel et al., 2002) 25 species 16 families in Odhiokwu-Ekpeyelocal fishpond and flood plains. Tobor (1990), Dublin-Green and Tobor (1992) recorded 200 species of fish from 78 families in the brackish and marine waters in Nigerian coast.

This creek is under environmental stress. However, there has been no information on the finfish assemblage of *Okpoka* Creek, a tributary of Upper Bonny Estuary. In order to bridge the existing gap in knowledge of the biotic and abiotic features of this estuary, there is therefore, the need to provide useful information on the finfish as semblage of *Okpoka* Creek. The species composition, species diversity, abundance and distribution of fin fish as semblage were studied.

MATERIALS AND METHODS

The Okpoka Creek is situated between longitudes 7°00"E and 7°15"N and latitudes 4°28"E and 4°40"N. It is a tributary of the Upper Bonny Estuary in the Niger Delta, South-South of Nigeria (Fig.1). The Bonny Estuary is richly endowed with abundant aquatic resources (fin/shellfishes resources and other aquatic life). The area is prone to pollution resulting from industries located along its shore. The flushing action of the tidal flows contribute to moving of these pollutants down into the coastal zones of which the lower reaches of Okpoka Creek is one. The lower reaches of this Creek pass through the following communities: Abuloma, Ojimba, Oba-Kalio, Abam and George-ama. The vegetation is dominated by Nypa palm(Nypa fructican), red mangroves (Rhizophora racemosa) and white mangroves (Avecennia nitida) (Davies, 2008).

Finfish samples: The finfish samples were observed at the landing station in Abuloma waterside for one year (April 2005-April, 2006) (Fig. 1). Fishes were mostly caught by cast nets by the local fisherfolks during the low tide. The different species of finfish were identified using the keys of Lewis (1974), FAO (1981) and Idodo-Umeh (2003).

Enumeration was by visual counting. A number was assigned to each fish species based on frequency of occurrence or abundance (the number) that is, a ranking method (1-5) was used (Ezekiel *et al.*, 2002). The most abundant species was assigned 5 and the least 1.

RESULTS

Finfish assemblage: A total of 8 families and 11 species of finfish dominated by Sardinella maderensis (Clupeidae) were observed (Table 1). The diversity of finfish species in this creek was low. The observed dominant S. maderensis positively correlated with the high abundance of phytoplankton (especially diatoms) in

Table 1: Percentage abundance of fin fish assemblage of Okpoka Creek

Fish family/species	1 1 (0/)	
Score P	ercen tag e ab un danc e (%)	Ranking
Sphyraenidae	0.69	1
Sphyraenidae afra		
Clupeidae		
Sardinella maderensis	47.33	5
Mugilidae		
Mugil cephalus	10.66	4
Cichlidae		
Tilapia mariae	6.09	3
T. guineensis	3.37	2
Carangidae		
Caranx hippos	0.41	1
C. affricanus	1.24	1
Mochokidae		
Chrysichthys nigrodigitat	us 0.75	1
Hepsetidae		
Hepsetus odoe	0.59	1
Gobidae		
Gobius guineensis	0.71	1
Periophthalmus papilio	28.18	4
	Key	
Abundance Range	Ranking	Score
0.1 - 3.0%	1	Rare
3.1 - 5.0%	2	Few
5.1 - 9.0%	3	C o mmo n
9.1 - 30%	4	A b unda n t
31% -above	5	Dominant

Table 2: Relative ab un dance of fin fish assemblage in relation to season in Okpo ka Creek

Cieek		
Season	Percentage distribution (%)	
Wet	9.35ª	
Dry	11.67a	

Table 3: Relative abundance of fin fish assemblage of Okpoka Creek

Fish family/species	Relative abundance (%)	
Sphyraenidae	0.96	
Sphyraenidae afra		
Clupeidae	47.29	
Sardinella maderensis		
Mugilidae		
Mugil cephalus	10.35	
Cichlidae		
Tilapia mariae	5.96	
T. guineensis	3.43	
Carangidae	0.64	
Caranx hippos	1.31	
C. affricanus		
Mochokidae	0.92	
Chrysichthys		
nigrodigitatus		
Hepsetidae	0.73	
Hepsetus odoe		
Gobidae	0.74	
Gobius guineensis		
Periophthalmus papilio	35.90	

Table 4: Monthly relative abundance of fin fish assemblage of Okpoka Creek Relative abundance (%) Season January 9.09 12.49 February March 18.18 9.09 April 10.00 May 10.00 June July 9.17 9.09 August 9.09 September Octo ber 10.00 November 10.00 10.00 December

this creek. Sardine, Sardinella maderensis had the highest percentage of fish catch (47.33%), followed by mudskipper, Periophthalmus papillio (28.18%), mullet, Mugil Cephalus (10.66%), Tilapia mariae (6.09%) and the least catch was Caranx hippos (0.41%). In ranking, S. maderensis had a ranking score of 5

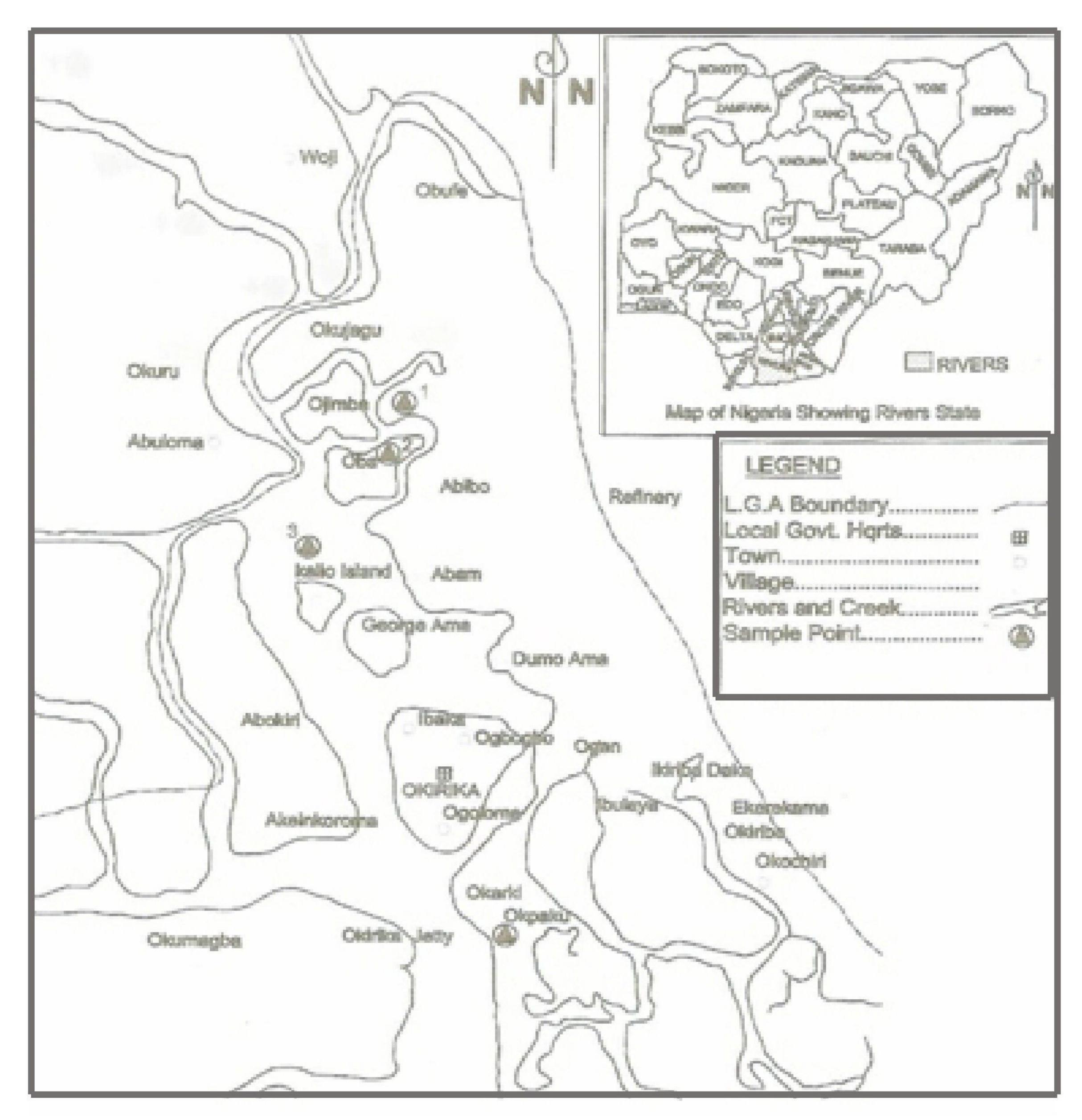


Figure 1: Study Area map

(dominant), P. papillio and M. cephalus ranked 4 (abundant), T. mariae ranked 3 (common), T. guineensis ranked 2 (few) and others ranked 1 (rare). The analysis of variance (ANOVA) indicated highly significant distribution of finfish species on Okpoka Creek (p<0.01). The finfish abundance was higher in dry season $(11.67\pm2.74\%)$ than in wet season $(9.35\pm1.68\%)$. Seasonal variation of fin fish abundance was insignificant (p<0.05, DMR) (Table 2). S. maderensis. P. papilli, M. cephalus, T. maraiae, T.guineensis, C. africanus, Gobius guineensis were caught by fishers throughout the study period though with different percentage of abundance. S. maderensis had the highest percentage distribution (47.29±0.98%) followed by mudskipper (35.90±7.52%) and the least was C. hippos $(0.64\pm0.14\%)$ (Table 3). The highest percentaged is tribution of the finfish was observed in the month of March (18.18±11.61%) and the lowest in the April (9.09±2.85%). Monthly percentage distribution

of the finfish species was not significant (p<0.05, DMR) (Table, 4). There was no significant interaction effect between season and species (p>0.05).

DISCUSSION

The study recorded low finfish abundance and species diversity. This might be explained by overfishing, fishing methods, land use, habitat degradation, industrial activities and other human activities. Dredging degrades habitats: Destroys spawning, breeding, feeding or growth to maturity grounds of finfishes (USACE, 2002). It might be due to the resilient *nypa* palms that have restricted mangrove regeneration and do not provide a good nursery ground for marine fishes as mangrove plants do (Otobo, 1977). It is low when compared to other studies in the Niger Delta. Chindah and

Osuamkpe (1994) reported 57 species and 25 families in Bonny Estuary, (Sikoki et al., 1998) 24 species and 15 families in Lower Nun River and Allison et al. (1997) 37 species and 22 families in Elechi Creek. In addition, Sikoki et al. (1999) reported 22 species and 11 families of the brackish zone of the Brass River, (Abowei, 2000), 36 species and 22 families in the Lower Nun River and Ezekiel et al. (2002), 25 species of 16 families in Odhiokwu-Ekpeye local fishponds and floodplains However, the present study agrees with that of Alfred-Ockiya (1998) of 11 species in Kolo Creek.

The fish assemblage of *Okpoka* creek is also low when compared to that of Lagos Lagoon reported by Nwadukwe (1995) of 23 species from 17 families. That study recorded Cichlidae as the most abundant in the canal and *Muglidae* as the most abundant family in the lagoon shores. The large fish species were attributed to the Lake's close association with the major Rivers in the area and the River Niger at its lower course. Victor and Tetteh (1988) in Ikpoba River, Edo state reported 58 species, (Nweke, 1984) in Aba River recorded 29 species. Okereke (1990) in Otamiri River, Imo State reported 46 species of 20 families and Ekeh (1990) in Nworie River, Owerri of 19 species.

The variation in number of finfish species could be attributed to differences in the physical-chemical parameters, low diversity which is a function of low productivity a common feature of small freshwater rivers (MBO, 2007b) and stability time hypothesis by Slobodokin and Sawder (1918) in Valentine (1995). The hypothesis simply means high diversity would indicate places of unpredictable hazards or places that would be short-lived. It is only time would prove how unpredictable or short-lived the *Okpoka* creek would be. In addition to these, the differences in the type of aquatic ecosystem and the fishing method might be responsible for these variations of finfish species.

Plankton communities serve as a base for the food chain that supports the commercial fisheries (MBO, 2007b). The Clupeidae (Sardinella maderensis) dominating the finfish assemblage could be linked to the high abundance of phytoplankton and epiphyton (algae), which are major diet of S.maderensis. The high abundance and distribution of the phytoplankton and epiphyton due to high nutrients status of this creek favour the growths and abundance of this fin fish species. S. maderensis is a typical algae feeder. This species forms the bulk of the fishery resources of this aquatic body. The local fishers use different fishing gear ranging from hook and line, drift net seine net to cast net but majority by cast gill nets to catch this fish. The cast gill nets efficiency to harvest the sardine is enhanced by the shallow nature of the Okpoka Creek. These fishers

earn their living from the sales of the fish to the fishmongers. The fishmongers either sell it fresh ordried. Most people prefer it dried because of its bony body. S. maderensis is special delicacy for the inhatants of the communities at the waterfront and Port Harcourt at large (Allison et al., 1997).

This present observation is in accordance with that of Nweke (2000) for Elechi Creek The high relative biomass of the clupeids in this study is also in agreement with other works; Otobo (1974) of Atalla fishery in the Lake Kainji, Nigeria, (Marshall, 1991) of Kariba Lake, Egypt, Sikoki et al. (1999) of the brackish zone of Brass River, Niger Delta. The knowledge of the dominant finfish can also be used to determine the biological state of the creek. In Lake Kainji, Nigeria, (Imevbore, 1971) reported a number of fish species thrived in the early years of the lake because of the luxuriate growth of algae which provided food for them. Aleem (1980) recorded some Blue-green algae in the stomach of Tilapia species from the Black Johnson Lagoon, Sierra Leone. According to Fagade and Olaniyan (1972), the spatial and seasonal distribution of fishes in the Lagos Lagoon were influenced by the presence of suitable food. It is therefore possible that the knowledge of the algae in the aquatic body could be useful in predicting the abundance and distribution of herbivorous fish. However, Nwankwo (1991) reported the presence of periphyton algae on fish fences (acadja) in Lagos Lagoon which is an indication that herbivorous fish feed on these algae.

The second abundant fish, Mudskipper, P. papillo has also been reported by Nweke (2000) and Ebere (2002) in the Upper Bonny Estuary. This fish species mainly observed from Stations 6 to 10 where the sediments are high in silt-clay fractions. They feed on the mud/detritus. They are also special delicacy for the waterfront dwellers. Mudskippers are usually caught at low tide with a special fishing gear (basket).

Mullet, Mugil cephalus is also second in abundance and distribution of the finfish assemblage. It is also an algae feeder. This species are evenly distributed in large numbers within the creek. This report agrees with those of Allison et al. (1997) and Ogamba (1998) on fish assemblage of Elechi Creek. They command higher market value than the S. maderensis because of their large size, fleshy and less bony body. Jana et al. (2004) recorded the effect of periphyton on growth performance of grey mullet, M. cephalus in inland saline groundwater ponds. The tilapias were ranked third in terms of abundance in the creek. Their relatively high abundance and distribution might be traced to the high abundance, distribution and diversity of algae. Tilapias are phytophagous fish (Fagade and Olaniyan, 1972; Ikusemiju and Olaniyan, 1977; Fagade, 1983). The least

abundant species Caranx africanus, Chrysichthys nigrodigitatus, Sphyraena afra, Hepsetus odoe, Gobius guineesis and Caranx hippos could be attributed to the low abundance and distribution of zooplankton in this creek. These fish species are carnivores, feeding on zooplankton and fish.

The seasonal variation of fin fish population being higher in dry season months than in the wet season months is consistent with the reports of Chindah and Osuamkpe (1994), Allision et al. (1998), Otobo (1995), Sikoki et al. (1999), Nweke (2000) and Ebere (2002) Nevertheless, this report is contrary to the observation of Abowei (2000) of higher wetseason catchthan dry season one which was attributed to the dual occupation of the fishers; crop farming in dry season and fishing in wet season.

There is no closed season for fishing in this creek and non-selective castnets are constantly being used. The low fin fish species diversity indicates that fin fish population is over-fished by the local fishers. Also it shows that nypa palms are not good nursery grounds for these fishes. The constantdredging activities have degraded the spawning, breeding, feeding and growth to maturity grounds of these fishes. It is therefore, recommended that there should be closed fishing season, selective fishing gear should be used and dredging should be controlled.

REFERENCES

- Abowe i, J.F.N., 2000. Aspects of the Fisheries of the Lower Nun River, Niger Delta. PhD. Thesis. Dept. of Animal and Environmental Biology, University of Port Harcourt., pp: xx+248.
- Aleem, A.A., 1980. Marine Cyanophyta from Sierra Leone (West Africa). Botanica Marina, 23:49-51.
- Alfred-Ockiya, J.F., 1998. Studies on the ichthyofauna of Kolo Creek. J. Biol. Sci., 2: 57-62.
- Allison, M.E., U. Gabriel, M.B. Inko-Tariah, O.A. Davies and B. Uedeme-Naa, 1997. The fish assemblage of Elechi Creek, Rivers State, igeria. Niger Delta Biologia, 2: 53-61.
- Amakiri, E.N., 2005. Aspects of the biology of Pseudotolithus elongatus (Bowdich 1825) of Bonny Estuary, Niger Delta, Nigeria. MSc. Thesis. Rivers State University of Science and Technology, pp: 9-99.
- Chindah, A.C. and A. Osuampke, 1994. The fish assemblage of the Lower Bonny River, Niger Delta, Nigeria. A fr. J. Ecol., 32:58-65.
- Davies, O.A., 2008. Physico-chemical, parameters, plankton, epiphyton and fin fish assemblages in Okpoka Creek, Niger Delta, Nigeria. Ph.D Thesis (Unpublished) pp: 310.
- Dublin-Green, C.O. and J.G. Tobor, 1992. Marine resources and activities in Nigerian. Nigeria Institute of Marine and Oceanography Research Technical 84:1-25.

- Ebere, N., 2002. The impact of oil refinery effluents on the distribution, abundance and community structure of macro-benth os in okrika Creek. PhD. Thesis. Dept. Biological Sciences. Rivers state University of Science and Technology, pp: 30-383.
- Ekeh, I.B., 1990. The Fish community and water quality of an urban stream-Owerri, Southern Nigeria. M.Sc. Thesis. Dept. of Zoology. University of Port Harcourt, pp: 11-80.
- Ezekiel. E.N., J.F.N. Abowei and A.I. Hart, 2002. The fish Assemblage of the Local fishponds in the floodplains of Odhioku-Ekpeye, Niger Delta. Intl. J. Sci. Technol., 1: 54-67.
- Fagade, S.O., 1983. The biology of *Chromido tilapia* guntheri from a small lake Archive of Hydrobiology, 97: 60-72.
- Fagade, S.O. and C.I.O. Olaniyan, 1972. The Biology of the West Africa Shad *Ethmalosa fimbriata* (Bowdich) in the Lagos Lagoon, Nigeria. J. Fish Biol., 4: 519-534.
- Food and Agriculture Organization (FAO) 1981. Method of collecting and analyzing size and age data for fish stock assessment. FAO Fish Circular, 736: 1-100.
- Idodo-Umeh, G., 2003. Freshwater fishes of Nigeria (Taxonomy, ecological notes, diet and utilization). Idodo-Umeh Publishers, Benin City, Nigeria, pp: 122.
- Iku semiju, K. and C.I.O. Olaniyan, 1977. The food and feeding habit of the catfishes, Claris walkeri, C. filamentous (Boulonger) in the Lekki Lagoon, Nigeria. J. Fish Biol., 10: 105-112.
- Imevbore, A.M.A., 1971. Floating vegetation of Lake Kainji, Nigeria. Nature, London, 203: 599-600.
- Ita, E.O. and M. Machili, 1997. The current status of fish stock and fisheries in Kainji Lake. Consultancy report on fish stock as sessment in Kainji Lake to the Nigerian-German (GTZ) Kainji Lake fisheries promotion project, New Bussa, pp: 28.
- Lewis, D.S., 1974. An illustrated key to the fishes of Lake Kainji. Ist Edn. Ile-Ife: University of Ife, Press.
- Marine Biology Organization (MBO). 2007b. Life in the ocean-Plankton.Retrieved Sept. 29, 2006, from grp=11767and pst=844-302.
- Marshall, B.E., 1991. The use of the sardine *Limnothrissa* miodon on the ecology of Lake Kariba. Biology Conservation, 55: 151-165.
- Nwadukwe, F.O., 1995. Species abundance and seasonal variations in catch from two mangrove habitats in the Lagos Lagoon. Env. Ecol., 13: 121-128.
- Nwankwo, D.I., 1991. Periphyton algae on fish fences "Acadja" in a tropical open Lagoon. Intl. J. Ecol. Environ. Sci., 17: 1-10.
- Nweke, A.N., 2000. Impact of organic wastes pollution on the macro-benthos and fish fauna of Elechi Creek. PhD. Thesis. Dept. of Biological Sciences. Rivers State University of Science and Technology, pp: 24-287.

- Nweke, E.A., 1984. Fish Community Studies in Aba River. MSc. Thesis. Dept. of Zoology. University of Port Harcourt, pp: 14-108.
- Ogamba, N.E., 1998. Baseline Survey of the fisheries of Elechi Creek. MSc. Thesis. Dept. of Biological Sciences. Rivers State University of Science and Technology, pp: 14-91.
- Ogueri, C., 2004. Physico-cheical parameters, fish fauna and fisheries of River Katsina-Ala, Nigeria. PhD Thesis. Dept. of Zoology. University of Ibadan, pp: 24-230.
- Okereke, F.O., 1990. Studies on the fish fauna of Otamiri River, Imo State, Nigeria M.Sc Thesis. Dept. of Zoology. University of Port Harcourt, pp: 14-150.
- Otobo, A. J., 1995. The ecology and fishery of the Pygmy herring Sierratherissa leonensis (Thys Van Den Audenaerde, 1969, (Clupeidae) in the Nun River and Taylor Creeks of Niger Delta. Ph.D Thesis, University of Port Harcourt, Choba, Rivers State, pp: 207.
- Otobo, F.O., 1974. The potential for Clupeid Fishes in Lake Kainji, Nigeria. Afr. J. Trop. Hydrobiol. Fisheries, 3: 123-134.
- Otobo, O., 1977. Commercial fishery in the Middle River Niger, Nigeria. contribution to FAO/CIFA. Symposium on River and Flood plain fisheries, Burundi, Nov. 1977. (Proceeding in press) pp: 249.

- Sikoki, F.D., A. I. Hart and J.F.N. Abowei, 1998. Gill net selectivity and fish abundance in the Lower Nun River, Nigeria. J. Applied Sci. Environ. Manage., 1: 13-19.
- Sikoki, F.D, A. Hart and A. Seth, 1999. Studies on the fish and fisheries of the Brass River system and adjoining coastal water in Bayelsa State, Nigeria. J. Applied Sci. Environ. Manage., 2: 63-67.
- Simon, I., 2007. Finfish assemblage of the Lower Benue River, Nigeria. Post Graduate Diploma Thesis Rivers State University of Science and Technology, Port Harcourt, Rivers State, pp: 102.
- Tobor, J.G., 1990. The fishing industry in Nigeria, Status and potential for self-sufficiency in fish production. Nigeria Institute of Oceanography and Marine Reseach Technical Paper, 54:1-34.
- United States Army Corps of Engineers (USACE) 2002. Navigation-What is dredging.Retrieved Sept. 3, 2007, from http://www.navigation/beneficial.html.
- Valentine A.A., 1995. Studies on the major Cichlid fishes of Umuoeriche Lake, Oguta, Imo State, Nigeria. PhD. Thesis. Dept. of Zoology. University of Port, pp: 17-170.
- Victor, R. and J.O. Tettch, 1988. Fish Communities of a Perturbed Stream, Southern Nigeria. J. Trop. Ecol., 4: 12-15.
- Wright, J.M., 1986. The ecology of fish occurring in shallow water creeks in a Nigerian mangrove swamp.

 J. Fish Biol., 29: 431:441.