Diversity and Response of Benthic Macroinvertebrates to Natural and Induced Environmental Stresses in Aiba Stream, Iwo, Southwestern Nigeria

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Abstract

Aiba stream, a tropical stream in southwestern Nigeria, was investigated on monthly basis from November 2012 to April 2013 with a view to comparing their response with the Biological Monitoring Working Party (BMWP) score system already in use in some eco-regions. The diversity and response of benthic macroinvertebartes were used in assessing the biological water quality and health status of the stream. Samples were collected from four different stations using the Kick Sampling Technique. All the specimens collected were preserved in 70% alcohol solution and later identified in the laboratory using relevant identification guides. Predatory invertebrates like water scorpions (*Nepa* and *Rana* spp.) and dragonfly nymphs (*Macromia* sp.) were sorted out *in-situ* and stored separately. Nineteen taxa of macroinvertebrates were recorded comprising three Phyla, four classes and 17 families. The overall Shannon-Weiner diversity and Margalef's indices of the stream indicated that the stream was organically polluted, as evidenced by the presence of some pollution-tolerant macroinvertebrates (e.g. Families Stratiomyidae, Nepidae, Planorbidae, Chironomidae and Syrphidae). Although there were some similarities between the BMWP score system and the response of the benthic macroinvertebrate families to environmental stress, a disparity was also observed between the two which underscores the need to carry out intensive research in this regard and adapt a BMWP score system for regional freshwaters in the tropics.

Introduction

Until recently, strategies aimed at conserving biodiversity were centred largely on vertebrates (Hafernik, 1992). This general neglect of invertebrates in conservation programmes reflects both a lack of knowledge of invertebrate species ecology and limited public enthusiasm for less visible and aesthetically less attractive species. Invertebrate conservation, however, does not rely only on public support and political will, but also on possessing an adequate understanding of the distribution and ecology of invertebrate species and communities (Boon, 1997).

Benthic macroinvertebrates are the most preferred group in biomonitoring studies of fresh waters. This preference is due to their limited habitat and less moving ability, consequently, they cannot change their habitats quickly. Their life cycles are also long enough to understand what the differences are in their habitats before and after the pollution. All these reasons make the benthic macroinvertebrates most favourable as biomonitors among the other groups (Rosenberg & Resh, 1993). Biomonitoring is a tool for assessing environmental quality because biological communities integrate the effects of different

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stressors and, thus, provide a broad measure of their aggregate impact (Reynoldson *et al.*, 1997; Rosenberg, 1998; Barbour *et al.*, 1999).

The assessment of biological communities in an aquatic environment reflects the quality of the ecosystem, and the use of biological approaches to determine the ecological effects of pollution has been preferred widely for decades. These approaches have more advantages than determining the pollution with just using physico-chemical methods, because physico-chemical variables give information about only the situation of water at the time of measuring. Biological monitoring has also been reported as an essential part of environmental pollution studies in addition to chemical monitoring because the consequences of environmental stress can only be determined by an appraisal of the biota (Wright, 1997). There are three major categories of environmental stress: the natural stresses (e.g. droughts and floods), imposed stresses (e.g. sewage pollution, toxic waste and pesticides) and environmental manipulation by man (e.g. reservoir construction, channel modification and the transfer of water between catchments (Hellawell, 1986). The macroinvertebrate fauna could be affected by each one of these stresses, and the fauna at any given site may be the result of more than one category of stress (Wright, 1997).

Aiba stream is subjected to stress as it flows downstream of Aiba Reservoir and drains through the ancient town of Iwo, Osun State, Nigeria. The stream experiences at least two types of stress i.e. natural stress occasioned by drought in the dry season as a result of water abstraction for irrigation and aquaculture, and imposed stress through indiscriminate dumping of wastes. In this study, the biological quality of Aiba stream was assessed based on the composition and diversity of its benthic macroinvertebrates as well as the animals' response to environmental stress as indicated by some selected variables. Findings from the study were also compared with the Biological Monitoring Working Party (BMWP) scoring system for water quality assessment. BMWP has been published as a standard biological method of assessing water quality by an international panel (ISO-BMWP, 1979). This system has been rarely used in biological assessments of tropical freshwaters, although there are few accounts like that of Suleiman & Ibrahim (2011) on River Challawa (Nigeria), Kobingi *et al.* (2009) on two rivers in Lake Victoria drainage basin, and Mereta *et al.* (2013) on some wetlands in southwestern Ethiopia.

Materials and methods

Study site

The study was carried out in the downstream section of Aiba Reservoir, Iwo, southwestern Nigeria. It is a second order stream and roughly 5 km in length. Four sampling stations were selected along the stream as it flows downstream from the upper reach and meanders through the ancient city of Iwo (Fig. 1). Selection of sampling stations was based on the need to study the response of benthic macroinvertebrates to both natural stress and anthropogenic interferences along the stream. Anthropogenic interference around Station 1 was predominantly dumping of organic wastes, while irrigated agriculture and aquaculture were observed at Station 2 in addition to dumping of organic wastes. Organic waste deposition and irrigated agriculture were observed at Stations 3 and 4, in addition to car wash centre at Station 3

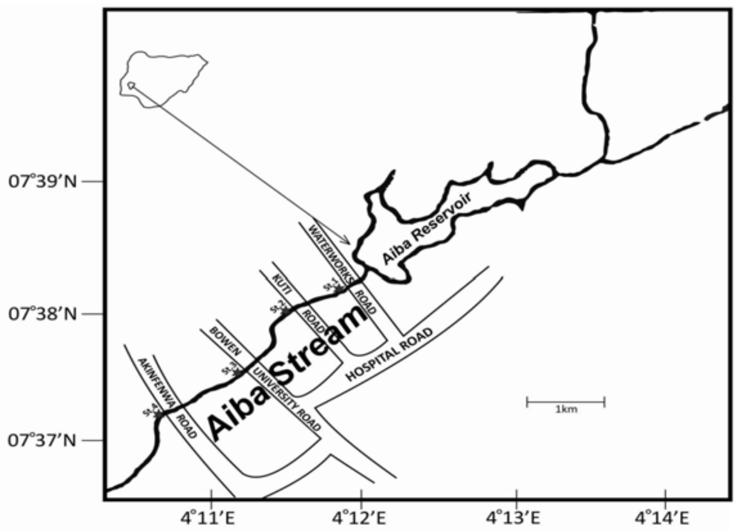

Fig. 1. Map of Aiba Stream-Reservoir System showing the sampling stations (Inset is a map showing the location of the study area in southwestern Nigeria)

alone. Predominant macrophytes along the stream were *Eichornia* sp., *Typha* sp. and *Coix lacryma-jobi.*

Sample collection

Samples were collected from four different stations on monthly basis from November 2012 to April 2013. During this period the stream experienced the three categories of environmental stress, i.e. drought (natural stress), dumping of wastes (induced stress) and low hydrological input from the upstream reservoir (environmental manipulation by man). Water temperature was determined using a mercury-in-glass thermometer; flow velocity was determined using the methods described by Jones & Reynolds (1996), while discharge was estimated from the product of flow velocity, Channel width and water depth were measured (Chapman & Kimstach 1996). *p*H was measured by using a field *p*H meter (*p*H Testr2 meter). Dissolved oxygen (DO) samples were collected in 250 ml amber bottles and fixed using the Winkler's reagents ($MnSO_4$ and alkali iodide) which resulted in the formation of a golden brown precipitate.

Macroinvertebrate samples were collected by using the Kick Sampling Technique (Ausden, 1997, Freshwater Biological Association 2011). A pond net of 50 cm × 20 cm dimensions and 1.0 mm-mesh size was used to collect the macroinvertebrates after kick-sampling all the microhabitats at each particular sampling point for a total of 3 min. The dislodged animals were collected by the net which had been placed downstream of the disturbed area. The animals were sorted out in a white tray partly filled with water from the stream. Predatory species like water scorpions and dragonfly nymphs were stored separately. All the samples were preserved in 70% alcohol solution. Sediment samples were also collected from the four stations for textural analysis.

Laboratory analyses

DO samples were analysed in the laboratory by using Winkler's titration method which involved the use of 0.025 *N* $Na_2S_2O_3$ and starch indicator, after adding 2 ml of concentrated H_2SO_4 to the golden brown precipitate. Colorimetric method was used to determine phosphate while analysis of nitrate was carried out using the ultraviolet screening method (APHA, 1998). Identification of the animals was carried out using several identification guides (e.g. Yoloye 1988; Egborge, 1994; Freshwater Biological Association, 2011). Animals that could not be easily identified were closely examined under a microscope (Max II 1202.4000 model). Substrate nature of the stations was determined using the Pippette method as described by Deshpande & Telang (1950).

Data analyses

The data obtained were subjected to descriptive and inferential statistics. Diversity of the various taxa recorded was determined by Shannon-Weiner Index (H') (Shannon, 1948) and Margalef index (d) (Kocatas, 1992), while evenness of distribution was determined by Pielou index (J') (Pielou, 1966). Regression and correlation analysis was used to establish the relationship of the animals with the physico-chemical parameters of the stream.

Results

Taxonomic composition of macroinvertebrates

A total of 19 taxa of macroinvertebrates were recorded in this study, which comprised one taxon of Annelida, 12 taxa of Insecta and six taxa of Mollusca. Insecta comprised four families of Anisoptera (Cordullidae, Macromiidae, Gomphidae and Libellulidae), two families of Zygoptera (Lestidae and Coenagrionidae), three families of Diptera (Chironomidae, Stratyomidae and Syrphidae), and one family each of Heteroptera (Nepidae) and Coleoptera (Elmidae). Two classes of Phylum Mollusca were recorded, namely Gastropoda and Bivalvia. The Gastropoda was represented by four families (Ampullaridae, Planorbidae, Thiaridae and Viviparidae) while the Bivalvia was represented by one family (Unionidae) only.

Taxa richness, abundance, diversity and evenness of distribution

The lowest number of taxa was recorded in November while the highest was recorded in December. The lowest abundance was also recorded in November while the highest was recorded in January (Table 1). Station 4 had the lowest number of taxa while the highest number of taxa was recorded at Station 2. Stations 3 and 2 had the lowest and the highest abundance of macroinvertebrates, respectively (Table 2). Only *Melanoides tuberculata* was recorded throughout the sampling period, while *Biomphalaria pfeifferi,* Corduliidae and *Chironomus* sp. were recorded in five out of the six-month period. Only three out of the 19 taxa were recorded in all the sampling stations, namely *Chironomus* sp., *Nepa* sp. and *Melanoides tuberculata*.

Table 3 provides the diversity and evenness index values in the sampling stations. Station 3 recorded the highest diversity based on the two indices (Shannon-Weiner and Margalef), followed by Station 4. Shannon-Weiner index indicated that Station 1 ranked third in terms of diversity

TABLE 1

Temporal variation in the taxa occurrence and abundance of macroinvertebrates in Aiba Stream, Iwo, Nigeria (November 2012-April 2013)

S/N	*Taxon*	*Nov*	*Dec*	*Jan*	*Feb*	*Mar*	*Apr*
1	Naididae (Tubifex sp.)	1	0	0	0	2	3
2	Elmidae	0	0	2	0	0	0
3	Chironomidae(Chironomus sp.)	3	1	125	106	0	41
4	Stratyomidae	0	0	5	0	0	0
5	Syrphidae	0	0	0	2	0	0
6	Nepidae (Nepa sp.)	0	2	6	0	1	0
7	Nepidae (Rana sp.)	0	0	0	0	2	0
8	Coenagrionidae (Coenagrion sp.)	0	0	5	0	0	0
9	Corduliidae	0	3	1	6	2	2
10	Gomphidae	0	0	2	2	0	0
11	Lestidae	0	1	0	0	0	0
12	Libellulidae	0	0	0	0	0	5
13	Macromiidae(Macromia sp.)	0	2	0	0	0	0
14	Unionidae	0	1	0	0	0	0
15	Ampullaridae (Lanistes ovum)	0	1	1	0	0	0
16	Planorbidae Bulinus truncatus	3	0	0	1	3	0
17	Planorbidae Biomphalaria pfeifferi	3	1	1	4	1	0
18	Thiaridae Melanoides tuberculata	6	36	31	31	25	29
19	Viviparidae Bellamya unicolor	0	1	0	0	0	0
	Number of taxa	5	10	9	8	7	6
	Total abundance	16	49	179	152	36	80

ANOVA: F= 0.8241; *P* = 0.5352

while Station 2 ranked last. The reverse was the case for Margalef's index in which Station 2 ranked third and Station 1 ranked last. For evenness of distribution, Station 3 again ranked first followed by Stations 4, 1 and 2. The overall Shannon-Weiner diversity index and Margalef's index of the stream were 1.2987 and 2.8927, respectively, with an overall Pielou evenness index of 0.4411.

Environmental variables and their relationships with macroinvertebrate families

Soil textural analysis of the sediment showed that Stations 1 and 4 were sandy loam, while Stations 2 and 3 were silt loam. The mean values of the investigated environmental variables over the study period are provided in Table 4, while their correlation coefficient values with the macroinvertebrate families are provided in Table 5. Families Elmidae, Chironomidae, Stratyomidae and Coenagrionidae showed significant inverse correlations (P < 0.05) with water temperature. Dissolved oxygen (DO) showed significant positive correlation with four families of macroinvertebrates, i.e. Lestidae, Macromiidae, Unionidae and Viviparidae. All other families with the exception of Ampullaridae and Planorbidae

TABLE 2

Spatial variation in the abundance of macroinvertebrates in Aiba stream, Iwo, Nigeria (November 2012-April 2013)

S/N	*Taxon*	*Station 1*	*Station 2*	*Station 3*	*Station 4*
1	Naididae (Tubifex sp.)	3	0	0	3
2	Elmidae	0	0	2	0
3	Chironomidae (Chironomus sp.)	16	241	1	18
4	Stratyomidae	0	0	1	1
5	Syrphidae	0	1	0	1
6	Nepidae (Nepa sp.)	1	1	1	1
7	Nepidae (Rana sp.)	0	0	1	1
8	Coenagrionidae (Coenagrion sp.)	0	1	4	0
9	Corduliidae	10	2	0	2
10	Gomphidae	2	2	0	0
11	Lestidae	0	0	1	0
12	Libellulidae	2	0	1	2
13	Macromiidae (Macromia sp.)	0	2	0	0
14	Unionidae	0	1	0	0
15	Ampullaridae (Lanistes ovum)	0	2	0	0
16	Planorbidae (Bulinus truncatus)	1	3	3	0
17	Planorbidae (Biomphalaria pfeifferi)	5	5	0	0
18	Thiaridae (Melanoides tuberculata)	125	11	13	9
19	Viviparidae (Bellamya unicolor)	1	0	0	0
	Total abundance	166	272	28	38
	Number of taxa	10	12	10	9

ANOVA: $F = 0.7323$; $P = 0.5361$

TABLE 3

Diversity and evenness of distribution in the sampling stations of Aiba stream (November 2012-April 2013)

Station	*Shannon-Weiner diversity index (H')*	*Margalef diversity index (d)*	*Pielou evenness index (J')*
1	0.9845	1.7606	0.4275
2	0.5711	1.9622	0.2298
3	1.7758	2.7009	0.7712
4	1.5880	2.1992	0.7227
Overall	1.2987	2.8927	0.4411

TABLE 4

Mean (±S.E.) values of some selected environmental variables in Aiba stream, Iwo, Nigeria (November 2012-April 2013)

Parameter	*Period*					
	Nov 2012	*Dec 2012*	*Jan 2013*	*Feb 2013*	*Mar 2013*	*Apr 2013*
Water temperature (^oC)	28.7±0.2	30.8±0.7	21.9±0.2	26.4±0.9	25.9±0.2	26.4±0.2
Dissolved Oxygen (mg L^{-1})	6.5±0.3	8.3±0.6	4.1±1.1	3.8±1.6	1.9±0.3	2.4±0.4
NO3- (mg L^{-1})	4.3±0.2	4.7±0.3	6.7±0.9	7.6±1.1	14.1±3.2	10.0±1.4
PO43- (mg L^{-1})	0.35±0.11	1.03±0.11	1.63±0.41	1.22±0.28	0.65±0.23	0.76±0.22
*p*H	7.55±0.04	7.39±0.18	7.41±0.05	7.30±0.09	6.55±0.05	7.00±0.06
Flow velocity (m s^{-1})	0.072±0.019	0.060±0.026	0.019±0.003	0.018±0.004	0.073±0.024	0.06±0.015
Discharge (m^3 s^{-1})	0.573±0.216	0.362±0.175	0.081±0.024	0.053±0.021	0.226±0.097	0.226±0.082

TABLE 5

Correlation coefficient values (r) between the macroinvertebrate families of Aiba stream and some selected environmental parameters (November 2012-April 2013)

Family	*Water temp.*	*Dissolved oxygen*	*NO^{3-}*	*$PO4^{3-}$*	p*H*	*Flow velocity*	*Discharge*
Naididae	-0.0212	-0.6105	0.6472	-0.5965	-0.6669	0.6003	0.1495
Elmidae	-0.7840*	-0.0797	-0.1601	0.7458*	0.2799	-0.6070	-0.4390
Chironomidae	-0.7479*	-0.2895	-0.1101	0.8374**	0.2889	-0.9653***	-0.7910*
Stratyomidae	-0.7840*	-0.0797	-0.1601	0.7458*	0.2799	-0.6070	-0.4390
Syrphidae	-0.0464	-0.1394	-0.0434	0.3026	0.1333	-0.6264	-0.5102
Nepidae	-0.6358	-0.0880	0.1166	0.6339	-0.0703	-0.6070	-0.3896
Coenagrionidae	-0.7840*	-0.0797	-0.1601	0.7458*	0.2799	-0.3931	-0.4390
Corduliidae	0.1209	-0.1023	0.1038	0.3632	-0.0843	-0.5041	-0.5834
Gomphidae	-0.6565	-0.1732	-0.1609	0.8288*	0.3267	-0.9751***	-0.7504*
Lestidae	0.6747	0.7567*	-0.4216	0.0973	0.2533	0.1873	0.2761
Libellulidae	-0.0464	-0.4182	0.2751	-0.1946	-0.2666	0.1873	-0.0699
Macromiidae	0.6747	0.7567*	-0.4216	0.0973	0.2533	0.1873	0.2761
Unionidae	0.6747	0.7567*	-0.4216	0.0973	0.2533	0.1873	0.2761
Ampullaridae	-0.0864	0.5353	-0.4599	0.8516*	0.4215	-0.3318	-0.1288
Planorbidae	0.1855	0.0491	-0.0590	0.6665	0.0877	0.1189	0.3098
Thiaridae	-0.1554	-0.0861	0.1684	0.7217*	-0.1801	-0.4851	-0.7096*
Viviparidae	-0.6747	0.7567*	-0.4216	0.0973	0.2533	0.1873	0.2761

At $P < 0.05$, r = 0.7067 & $n = 6$; $P < 0.01$, $r = 0.8343$ & $n = 6$; $P < 0.001$, $r = 9249$, $n = 6$

showed non-significant negative correlation (P > 0.05) with DO. NO_3^- showed non-significant positive correlations (P > 0.05) with Naididae, Nepidae, Corduliidae, Libellulidae and Thiaridae. PO_4^{3-} showed significant positive correlations (P < 0.05) with Elmidae, Stratyomidae, Coenagrionidae, Gomphidae, Ampullaridae and Thiaridae, and a highly significant positive correlation (P < 0.01) with Chironomidae. There were negative correlations (P > 0.05) between *p*H and families Naididae, Nepidae, Cordullidae, Liblellulidae and Thiaridae. All other families showed positive correlations (P > 0.05) with *p*H. Flow velocity showed a very highly significant negative correlation (P < 0.001) with Chironomidae and Gomphidae, while discharge showed a significant negative correlation (P < 0.05) with Chironomidae, Gomphidae and Thiaridae.

Discussion

Freshwater benthic macroinvertebrates include mainly three phyla, i.e. Annelida, Arthropoda and Mollusca (Alam *et al*., 2008), as confirmed by this study. All the recorded taxa in this study have been reported in the Nigerian freshwaters and other Afrotropical regions (e.g. Yoloye, 1988; Egborge, 1994; Jach & Balke, 2008; Kalkman *et al*., 2008). More taxa were recorded in the present study area, downstream of the dam than in the previous limnological survey of the reservoir (Atobatele & Ugwumba 2010). These limnologists (Atobatele & Ugwumba, 2010) gave an account of nine taxa in Aiba Reservoir, namely *Melanoides tuberculata,* Chironomid larvae, *Dero* sp., *Chaoborus* sp., *Tubifex* sp., Ostracoda, Diptera larvae, Coleoptera larvae and Hydracarina. The six recorded families of Odonota in the present study were not reported in the reservoir while only one (*Melanoides tuberculata*) out of the present five families of Mollusca was previously reported. The disparity in the benthic invertebrate faunal compositions of these two studies suggests that the physical nature of a freshwater environment is a major determinant of its invertebrate composition. Preference for lotic environments by benthic macroinvertebrates has also been reported by Akindele & Malaki (2001) in pools and streams of Kibale Forest, Uganda.

In lotic systems the velocity of flowing water influences transport of particles, thus, making food available for aquatic fauna. It also maintains high levels of dissolved oxygen (DO) by the turbulent actions (Gullan & Cranston, 1994). This claim is supported by the direct relationship that was recorded between DO and the Families Lestidae, Macromiidae, Unionidae and Viviparidae (odonatans and molluscs). Families Naididae, Nepidae, Corduliidae, Libellulidae and Thiaridae all had direct relationships with NO_3^-, while PO_4^{3-} had direct relationships with Elmidae, Stratyomidae, Nepidae, Coenagrionidae and Ampullaridae. With the exception of Ampullaridae, all the afore-mentioned families also had indirect relationships with DO which suggests that they were pollution-tolerant. The dominance of *Chironomus* sp. in the present study is similar to the report of Atobatele & Ugwumba (2010) in which they reported a dominance of this taxon during the late dry season and early wet season (February-April). During this period of the year, the study area is usually characterised by natural and induced stresses as a result of drought, indiscriminate dumping of wastes as well as low flow velocity and discharge, which consequently results in concentration of ions and nutrients in the water body.

Shannon-Weiner diversity index values above 3.0 indicate that the structure of the habitat is stable, while values less than 1.0 indicate that there are pollution and degradation of the habitat structure (Shannon, 1948; Mandaville, 2002). Margalef's water quality index values greater than 3.0 indicate clean conditions, values less than 1.0 indicate severe pollution and intermediate values indicate moderate pollution (Lenat *et al*., 1980). Based on the values obtained in this study, Aiba stream can be regarded as being more polluted and having poor habitat structure at the upper reach (Stations 1 and 2) than at the lower reach (Stations 3 and 4). The overall diversity index values also suggest that the stream was moderately polluted. Individual animals were more evenly distributed in the lower reach of the stream than in the upper reach, since Pielou's evenness index values were closer to 1 in the former than in the latter (Pielou, 1966). Generally, the animals were not evenly distributed as a result of the dominance of two taxa, *Chironomus* sp. and *Melanoides tuberculata,* which contributed a total of 84% to the total abundance.

One important macroinvertebrate community indicator is the EPT richness, or the total number of Ephemeroptera (mayfly), Plecoptera (stonefly) and Trichoptera (caddisfly) taxa in a sample. An increasing EPT richness value correlates with increasing water quality (Rothrock *et al.,* 1998) and many studies have indicated that Ephemeroptera, Plecoptera and Trichoptera show a strong negative response to anthropogenic disturbances in aquatic ecosystems (Ode *et al*., 2005). The absence of EPT (Ephemeroptera, Plecoptera and Trichoptera) throughout this study period is an indication that the stream was polluted and of low biological water quality.

Although, there is not yet an adaptation of the Biological Monitoring Working Party (BMWP) score system for Nigerian/West African freshwaters, the response of most of the macroinvertebrate families recorded in this study to pollution stress was quite similar to the BMWP score system. Under this system, Families Stratiomyidae, Nepidae, Planorbidae, Chironomidae, Syrphidae and Class Oligochaeta are indicators of poor water quality with BMWP scores of 4, 3, 3, 2, 1 and 1, respectively (Armitage and Moss *et al*.,1983; Alba-Tercedor & Pujante, 1997). All these taxa showed an indirect relationship with dissolved oxygen, though not significant. Naididae (Oligochaeta), Nepidae, Corduliidae, Libellulidae and Thiaridae showed positive response to nutrient loading in the form of NO_3^-, while the remaining 12 families showed a negative response. With the exception of Naididae and Libellulidae, all the families showed positive response to nutrient loading in the form of PO_4^{3-}, most of which were significant. The populations of Naididae, Chironomidae, Stratyomidae, Syrphidae, Nepidae, Coenagrionidae and Gomphidae were relatively high as the dry season advanced and nutrient concentration was on the rise as a result of pollution stress occasioned by drought and dumping of wastes.

Based on the BMWP system of water quality assessment, some taxa with relatively high scores were, however, recorded in this study, namely Gomphidae, Lestidae, Libellulidae and Corduliidae, each with BMWP score of 8. Other families with average scores under the BMWP system include Viviparidae (6), Thiaridae (6), Unionidae (6), Coenagrionidae (6) and Elmidae (5) (Armitage & Moss *et al*., 1983; Alba-Tercedor & Pujante, 1997). While the latter group justified their presence in the stream, the former group did not, based on the BMWP system of water quality assessment. These differences underscore the need to adapt a Nigerian/West African BMWP score system. The BMWP score system was first employed in Britain and there have been several adaptations of the system in various nations, particularly in the temperate region (e.g. Belgium, Spain) with little variations from the initial score system.

While there are little or no variations in the system from one country to another in the temperate zone, this cannot be said of the tropics until intensive research has been carried out in this regard. There is, therefore, a need to carry out further research on the response of benthic macroinvertebrates to environmental stress and physico-chemical parameters in Nigerian/West African lotic environments, with a view to adopting a BMWP score system for the eco-region. It is also imperative that appropriate measures be put in place to mitigate the effects of induced stresses on tropical streams (downstream of reservoirs) in the dry season, by releasing substantial quantity of water from the upstream reservoirs so that the effects of drought on such systems can be buffered.

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