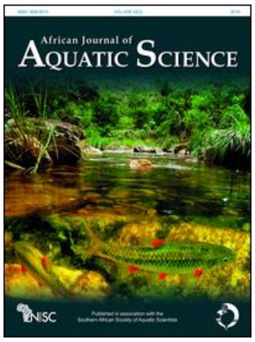

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Spatio-temporal variation of environmental variables and aquatic macroinvertebrate assemblages in Lake Nokoué, a RAMSAR site of Benin

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Environmental characteristics and macroinvertebrate assemblages of Lake Nokoué (Benin) were investigated from September 2014 to July 2016. Seasonal and hydroclimatic changes, as well as anthropogenic activities were the overriding factors affecting environmental variables investigated. Analysis of macroinvertebrate community structure with several indices revealed a community structure changing across seasons and differing between the sites. Mollusca, Crustacea and Polychaeta were most abundant in the dry seasons, especially at sites close to the ocean, whereas Oligochaeta and Insecta (Diptera, Heteroptera, Coleoptera, Odonata and Ephemeroptera) were abundant in the wet seasons, especially during flood periods (short wet season) at the sites receiving fresh water and on roots of macrophytes. A redundancy analysis placed habitat suitability (temperature and macrophytes) and trophic status variables (NO_2^-, NO_3^-, conductivity and pH) as structuring drivers for macroinvertebrate assemblages. The current study demonstrates that spatial heterogeneity of macroinvertebrates of Lake Nokoue is related to the dynamics created by input of fresh water (wet seasons) or salt water (dry seasons), as well as spatial heterogeneity of anthropogenic activities (nutrients). It offers insights into the macroinvertebrate dynamics linked to the limnology of a West African lagoon, which could contribute to a better understanding of management and conservation measures.

Keywords: biodiversity indices, biomonitoring, multivariate analysis, tropical lagoon

Introduction

Lake Nokoue is internationally known for its importance as the largest and most productive of the lentic wetlands of Southern Benin. Lake Nokoue is a lagoon but is also locally referred to as a 'lake'. This shallow ecosystem forms part of Ramsar site no. 1018 (Gnohossou 2006; Mama 2010). The fishing method *acadja* ('fish-park' as first described by Welcomme 1972) originated in Lake Nokoue and is well established because of its purportedly high contribution to fishing yields. *Acadja* comprises a collection of artificial enclosures (fish traps) made of branches (e.g. hardwood, bamboo poles, palm fronds) planted into the substrate (in a variety of patterns), in which fish become concentrated as they search for the abundant food growing (e.g. sessile organisms, periphyton) on the substrate (Welcomme 1972; Lalèyè et al. 2003; Olopade et al. 2008). A disadvantage of this very efficient, passive fishing method is that it contributes to the silting up of Lake Nokoue (Lalèyè et al. 2003; Mama 2010). This disadvantage, coupled with climate change, as well as industrial and domestic discharges brought about a change of environmental characteristics: eutrophication and sedimentation (Badahoui et al. 2010; Mama 2010). The lagoon is consequently continuously losing its ecological integrity and associated ecosystem services and possibly also an on-going change of the macroinvertebrate community composition. Shallow lakes, such as Lake Nokoue do not experience permanent water stratification, which increases the impact of water-sediment interface processes upon a lake ecosystem and aquatic communities (Hu et al. 2016). Macroinvertebrate communities are widely recognised as an important group in the monitoring of environmental condition of aquatic ecosystems (Stewart et al. 2000). Habitat-scale characteristics, such as differences in substrate, water temperature, conductivity, water transparency, pH, dissolved oxygen (DO), phosphate, nitrate and chlorophyll-a concentrations, are considered critical in determining the spatial and seasonal variation in the density and species composition of the macroinvertebrates in lakes (Johnson et al. 2004; Çelik et al. 2010).

Studies on the macroinvertebrates of Lake Nokoue carried by Gnohossou (2006) concluded that seasonal variation of the macroinvertebrate community was partly driven by organic pollution levels. A decade later, Odountan

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(2017) found after two years of sampling that 21% of observed families were new to Lake Nokoue and that 25% of families reported earlier (Gnohossou 2006) were not observed. Accordingly, if the change of macroinvertebrate composition is indisputable, a comprehensive study of the dynamics of all recorded taxa as influenced by environmental factors was needed to better understand variation between seasons and sites and refine the understanding of their dynamics in a changing environment. Two main approaches, biodiversity indices and multivariate analysis were used to assess spatial and temporal patterns of lentic macroinvertebrate communities for the purpose of biomonitoring (Odountan et al. 2019). In West African coastal ecosystems, only a few studies devoted to macroinvertebrates have used multivariate analysis, whereas biodiversity indices are more common (Imoobe 2008; Kouadio et al. 2008; Adandedjan et al. 2011, 2012).

This research article aims to (1) assess the limnological spatial and temporal patterns of environmental variables of the lake; (2) examine the spatial and temporal patterns of macroinvertebrates, using biodiversity indices and multivariate analysis; and, (3) point out major environmental factors affecting the macroinvertebrate patterns for future bio assessment of the water quality in the Lake Nokoue, an ecosystem that could suffer biodiversity loss as a result of hydroclimatic changes, as well as anthropogenic activities. It is expected that this study will contribute to better adaptive management and conservation practices in West African lagoons, which are often poorly known systems.

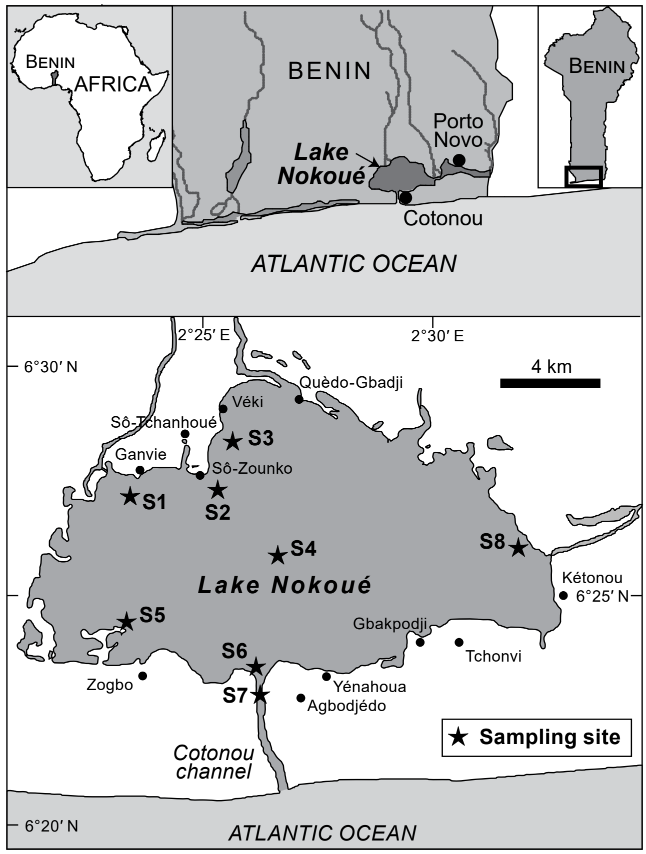

Figure 1: Sites (S) where sampling of macroinvertebrates and environmental variables study were conducted in Lake Nokoue

Materials and methods

Study area

Lake Nokoue is located between 6°22′ N to 6°30′ N and 2°20′ E to 2°35′ E, with a surface area of 150 km^2 (Figure 1). This lake occurs in the subequatorial climate zone with an annual mean temperature of 27–29 °C and annual mean precipitation of 900–1 100 mm (Amoussou 2010; Mama 2010). Physiographically, Lake Nokoue is a choked shallow lagoon (i.e. lagoon characterized by one or more long and narrow entrance channels, long residence time for the water and dominant wind forcing) (Frontalini et al. 2011). It is connected to fresh water (mainly Oueme and Sô rivers), brackish ecosystem (Porto-Novo Lagoon) via Totchè channel and to the Atlantic Ocean, via the artificial Cotonou channel. The Cotonou channel mainly contributes to hydrological and environmental fluctuations of the lake. Like other littoral ecosystems in Benin, the study area has a sub-equatorial climate: long wet season (LWS) concentrated between mid-March and mid-July, short dry season (SDS) observed between mid-July and mid-September, short wet season (SWS) reported between mid-September and mid-November and long dry season (LDS) occurring between mid-November and mid-March (Adandedjan et al. 2011, 2012, 2013).

Fish diversity of the lake is high with the main families: Carangidae, Channidae, Cichlidae, Clariidae, Claroteidae, Clupeidae, Elopidae, Gerrinidae, Gobiidae, Mochokidae, Mormyridae, Mugilidae, Osteoglossidae, Protopteridae and Schilbeidae (Sohou et al. 2009). This situation allows fisheries to be one of the main ecosystem services, especially with the use of *acadjas* by the local population. Besides fishing, agriculture, livestock and industrial activities are threatening the ecology of the lake. The dominant taxa within the phytoplankton community of the lake belong to the Diatomea (Diatomophyceae) (Goussanou 2012).

Sampling design

The study focused on eight sites (with triplicate sampling points consisting of 8 × 3 = 24 sampling points) sampled every two months, from September 2014 to July 2016 (96 samples). Four sampling dates were during the LWS and LDS seasons, whereas two sampling dates were in the SDS and SWS seasons. Site selection was based on a preliminary study conducted during March and April 2014 and previous findings on environmental factors and biological communities (Gnohossou 2006; Mama 2010). The sampling strategy was designed to cover a wide range of key variables, such as presence of pollution source, eutrophication, limnological and hydrological features, as well as accessibility. Site 1 is located near the tourist village of Ganvié, with *acadjas* present, whereas the nearby Site 2 is located near the River Sô outlet also with presence of *acadjas*. Site 3 is a very disturbed site, because of anthropogenic actions (dredging). The site 4 is in the middle of the lagoon with sand dredging activities. Site 5 is near an *acadja* and at the outlet of wastewater and storm water of Zogbo quarter (Cotonou). Site 6 is located at the

Lake-channel interface, near the unhealthy quarter of Ladji, a centre of *Vibrio cholerae* (Bio Tchane and Coulibaly 2017). Site 7 is located in the Cotonou channel near the inlet from the ocean and the Dantokpa market of Cotonou city, which impacts the surrounding aquatic ecosystem. Site 8 is near the mouth of Oueme River, the main tributary of the Lake and at the junction with the lagoon of Porto-Novo where sand dredging was observed.

Measurement of limnological variables

Prior to macroinvertebrate sampling, limnological variables, such as dissolved oxygen (DO), temperature, salinity, conductivity, pH and total dissolved solids (TDS) were measured *in situ* using a multi-probe metre (HANNA Model HI 9829). Depth and water transparency (known as Secchi disk depth (SDD)) were obtained with the Secchi disk whereas turbidity was measured with a Turbidimeter TN-100 (Eutech instruments).

In addition to *in situ* measurements at each sampling point, a water sample was collected for nutrient analyses. Samples were taken using a 1.5 l plastic bottle, previously treated with hydrochloric acid. The samples were taken to the Laboratory of Ecology and Management of Aquatic Ecosystem (Benin Republic), kept frozen and afterwards concentrations of nitrite (NO_2^-), nitrate (NO_3^-) and orthophosphate (PO_4^{3-}) were measured using a spectrophotometer Model HACH DR 6000 at a specified wavelength (Rice et al. 2012).

Sampling and processing of macroinvertebrates

The Qualitative Multi-Habitat (QMH) approach, which provides comprehensive list of organisms present at the various habitats or sampling points in the sampled area was used for the sampling (Meador et al. 1993). The sampling points at each site were randomly placed along one longitudinal transect. Two replicate samples of macroinvertebrates (from a boat) were collected at each sampling point (homogeneous habitat) with an Ekman grab (0.0225 m^2). At each sampling point, in addition to bottom samples, five *Eichhornia crassipes* (Mart.) Solms root systems (when observed) were sampled, because they might also contain macroinvertebrates, using a pair of small scissors (Alhou 2007; Benbow et al. 2014). The macroinvertebrates were collected after washing in a 250 µm kick net mesh. The bottom sediments collected with the Ekman grab were also washed *in situ* through a 250 µm mesh sieve in the water of the lake. The retained materials of both methods were preserved in a 5% buffered formalin solution and labelled. Afterwards, the samples were brought to the laboratory, where they were washed again through a set of sieves (0.25 mm, 0.5 mm, 1 mm and 2 mm) for fractioning and to remove all excess sediment and other unnecessary material. Finally, the organisms were sorted and stored in vials with 80% ethanol and labelled, prior to identification to the lowest feasible taxonomic level (usually species or genus), using following identification keys: Carpenter and Niem (1998a, 1998b); Durand and Lévêque (1980, 1981); Epler (2001); Hayward (1980); McCafferty (1981); Moisan (2010); Nicklès (1950); Oscoz et al. (2011); Tachet et al. (2010); Villiers (1952); Wiederholm (1983), as well as specialist consulting. Where it was not possible to reach species level for those identified to genus level, features of each genus showed organisms belonging to the same species (sp. and not spp). Therefore, species level was used for biodiversity indices. However, for statistical inferring power reasons, multivariate analyses were made with fauna identified to family level (Parsons et al. 2010; Dalu et al. 2012; Chi et al. 2017). Both approaches generated consistent results not contradicting each other.

Data analysis

Biological and environmental data were assessed according to sites and seasons to focus on the spatial and temporal patterns of benthic and epiphytic macroinvertebrate assemblages in relation to environmental variables. The number of taxa (S), the total number of individuals and relative abundance at family and species level were assessed. The environmental data were expressed as means and the coefficient of variation (CV) according to sites and seasons. Two-way (site and season) analysis of variance (ANOVA) with type III sums of squares (SS) was run because of unbalanced sample sizes (four sampling dates in LWS and LDS vs two sampling dates in SDS and SWS seasons) to test whether environmental variables varied significantly across sites or seasons. Therefore, the *lm* function of the package *car* (Fox et al. 2018) followed by the *cld* function of the *emmeans* package useful for doing mean separations (*post hoc* tests) on interactions variables were used (Russell et al. 2018). The biodiversity indices, such as the Margalef taxa richness index (d), Simpson diversity index (1-D), Shannon–Wiener index (H) and Pielou's evenness index (J) were calculated based on abundance data (at species level) for each site and season to determine the community structure of the macroinvertebrates in the lake. A two-way ANOVA with type III sums of squares (followed by mean separations using emmeans package) was used for determining the statistical differences in the biodiversity indices (d, 1-D, H and J) among seasons and within sites. Two-way analysis of similarity (ANOSIM) was carried out to test differences of benthic community composition among seasons and within sites using Bray–Curtis's linkage (distance) on $\log(x + 1)$ transformed abundance. ANOSIM is a non-parametric test of significant difference between groups, using distance measures, in the current study the Bray–Curtis distances. This test is used by ecologists to compare groups of samples or sites where abundance data of taxa were collected, because such data most often are not normally distributed (Warwick and Clarke 1991). ANOSIM was followed by a similarity percentage (SIMPER) procedure to identify the responsible taxa of disparity obtained across groups of samples or assemblages of macroinvertebrates (Clarke 1993).

A detrended canonical analysis (DCA) was run to determine whether to use unimodal or linear methods for the analysis of macroinvertebrate assemblages in relation to environmental variables. The length of gradient of axis 1 obtained with DCA was 2.730 (< 3), this value indicate that linear ordination, such as a redundancy analysis (RDA), is more appropriate for the analysis of the effect of environmental variables on the macroinvertebrate community

(Lepš and Šmilauer 2003). The RDA was run with forward selection of environmental variables using the Monte Carlo permutation test (999 permutations, $p < 0.05$). Only the family reaching at least 1% of total abundance were considered for the RDA. DCA and RDA were performed using the CANOCO for Windows (version 4.56) software package. All other statistics were carried out using PAST (PAleontological STatistics v 3.14) for biodiversity indices (Hammer et al. 2001) and the statistical programming language R environment (version 3.5.1) (R Core Team 2018) for comparison of variables and graphs.

Results

Limnological characteristics

Average values with coefficient of variation (CV) for environmental features of Lake Nokoue during the survey are presented in Table 1, whereas the comparison between seasons and across sites is presented in Table 2.

All investigated variables showed significant variation in both space and time ($p < 0.05$). Generally, the highest mean values of water depth, temperature, nitrite, nitrate, phosphate and turbidity were recorded during wet seasons (SWS or LWS) whereas SDD, DO, TDS, salinity and conductivity mean values increased during dry seasons (SDS or LDS).

Highest mean values of water depth and temperature and lowest mean values of DO, salinity, conductivity and TDS were recorded at Site 8. Salinity, pH, DO, conductivity and TDS were highest at Site 7. Site 5 showed highest values of nutrients (nitrite, nitrate and phosphate), turbidity and lowest values of SDD, water depth and DO.

Except for temperature and pH, which weakly varied between site and season, the rest of the environmental variables varied strongly between site and season (see CV in Table 1).

Macroinvertebrate assemblages assessed with biodiversity indices

A total of 60 macroinvertebrate families from brackish and fresh water were recorded over the four seasons, representing eight classes and 22 orders. Insecta showed the highest taxon richness (28 families/taxa) followed by Malacostraca, Gastropoda, Bivalvia, Polychaeta, Oligochaeta, Thecostraca and Arachnida with 12, 7, 5, 4, 1, 2 and 1 taxa, respectively. Spatial and temporal variation of the macroinvertebrate community structure, assessed with biodiversity indices is depicted in Figures 2 and 3, with p-values of the two-way ANOVA presented in Table 3.

All computed biodiversity indices showed significant variation in both space and time (two-way ANOVA, $p < 0.05$). Generally, biodiversity indices were highest at Site 8 (Figure 2) and lowest at Site 5, whereas similar amplitudes were observed for Sites 3 and 4. The Margalef index showed a different pattern, stressing especially site 5, which score the lowest, compared with the other sites. Only Sites 2 and 3 were not significant different from each other. The Shannon diversity index and Simpson index indicated macroinvertebrate assemblage changes between sites. Sometimes a similar trend of difference between sites was observed for both indices (Figure 2). Pielou's evenness index showed a similar species distribution for Sites 6 and 7. The seasonal patterns depicted in Figure 3 revealed that the wet seasons (especially the SWS) showed highest diversity values whereas the lowest values were mainly recorded during SDS.

Dissimilarity analyses of community assemblage

The two-way ANOSIM analyses also indicated that the macroinvertebrate assemblage differed significantly across sites (ANOSIM, $R = 0.4892$, $p = 0.0001$) and between the seasons (ANOSIM, $R = 0.5204$, $p = 0.0007$) in Lake Nokoue. Pairwise comparison revealed no significant difference between clusters of Sites 1, 2, 3, 4 and 5, but differences with the other sites. Additionally, Site 8 is different from all other sites, whereas site 7 is not significantly different from sites 3, 4, 5 and 6; and Site 6 is similar only to Site 7 (Table 4). Conversely, pairwise comparison revealed significant differences between all seasons with high dissimilarity observed between LWS and SDS (Table 4). The SIMPER procedures indicated that Insecta, Malacostraca, Bivalvia and Gastropoda were the four major macroinvertebrate taxa responsible for the assemblage changes through sites and seasons (Table 5). They were followed by Oligochaeta and Polychaeta species. The main contribution to variation of spatial assemblages is the high abundance of Chironomidae (*Chironomus* sp., *Tanytarsus* sp., *Polypedilium* sp. and others) or Thiaridae (*Pachymelania* sp., *Melanoides* sp.) and Potamididae (*Tympanotonos fuscatus* (Linnaeus, 1758)) at Sites 1, 2, 3, 4 and 5 – Nereididae (*Nereis* sp.), Ostreidae (*Crassostrea tulipa* (Lamarck, 1819)), Grapsidae (*Goniopsis cruentata* (Latreille, 1803) and *Pachygrapsus* sp.) and Corbulidae (*Potamocorbula adusta* (Reeve, 1844)) species at Sites 6 and 7 – Serpulidae (*Serpula* sp.) at Site 3 – Naididae (*Branchiodrilus* sp. and *Branchiura* sp.) at Sites 2, 3, 4 and 5 – Gammaridae (*Gammarus* sp.) or Portunidae (*Callinectes* sp.) at Sites 3 and 5 – Baetidae (*Baetis* sp., *Cloeon* sp. and *Procloeon* sp.) at Site 8. Likewise, benthic assemblages' characteristic of SWS were Chironomidae (*Chironomus* sp., *Tanytarsus* sp., *Polypedilium* sp. and others), whereas Serpulidae, Corbulidae or Ostreidae mainly characterised dry seasons (SDS and LDS). Notably, some families (e.g. Grapsidae, Potamididae, Nereididae, Naididae and Thiaridae) were characteristic for two or three seasons. The abundance of these families varied greatly within seasons and between sites (see Table 6).

Multivariate analyses of relationships between macroinvertebrates community and environmental gradients

The first two components of the RDA were retained for analysis, because they accounted for 75.2% of the taxon-environment relationship, although also accounting for 32.7% of the variance in the taxa, with correlation coefficients of 0.869 and 0.824 for first and second axis, respectively (Table 7). Additional axes did not provide additional insight into relationships between the macroinvertebrate community and environmental gradients. Forward selection revealed nitrate, nitrite, pH, conductivity and temperature were significant in describing patterns of occurrence and abundance of macroinvertebrate taxa in Lake Nokoue (Figure 4). The first RDA axis of families was positively correlated with temperature ($r = 0.259$) and nitrate ($r = 0.683$) – negatively correlated with pH ($r = -0.640$),

Table 1: Summary of variation of environmental variables of Lake Nokoue during the study. (CV = Coefficient of variation). LDS = long dry season, LWS = long wet season, SDS = short dry season, SWS = short wet season. S = Site

Variables		Sites								Seasons			
		S1	S2	S3	S4	S5	S6	S7	S8	LDS	LWS	SDS	SWS
Depth (m)	Mean	1.66^{e}	1.28^{c}	0.97^{b}	1.53^{de}	0.80^{a}	1.42^{cd}	1.51^{d}	2.42^{f}	1.05^{a}	1.91^{d}	1.15^{b}	1.68^{c}
	CV(%)	19.66	39.00	32.31	12.55	38.04	24.09	32.03	64.17	35.50	62.85	35.50	27.24
SDD (m)	Mean	0.66^{cd}	0.64^{c}	0.55^{b}	0.79^{e}	0.27^{a}	0.75^{de}	0.83^{e}	0.34^{a}	0.67^{c}	0.54^{b}	0.73^{d}	0.48^{a}
	CV(%)	24.35	30.41	28.91	32.18	19.15	37.96	37.50	17.64	42.97	33.63	42.97	51.33
Temperature	Mean	28.19^{a}	28.57^{bcd}	28.36^{ab}	28.57^{abcd}	28.74^{d}	28.69^{cd}	28.68^{cd}	28.90^{abc}	27.71^{b}	29.15^{c}	27.36^{a}	29.83^{d}
(°C)	CV(%)	4.43	5.09	5.25	4.58	4.28	3.46	3.50	1.54	1.10	1.31	1.50	2.06
pH	Mean	6.80^{a}	7.01^{b}	7.03^{b}	7.22^{c}	7.37^{c}	7.68^{d}	7.74^{d}	6.82^{a}	7.47^{d}	7.36^{c}	7.15^{b}	6.85^{a}
	CV(%)	6.36	7.00	8.17	8.02	3.86	3.20	1.20	3.76	4.05	5.95	5.18	9.86
DO (mg l^{-1})	Mean	2.84^{b}	3.42^{c}	3.50^{cd}	4.29^{f}	2.43^{a}	4.00^{ef}	3.81^{de}	2.43^{a}	4.09^{d}	3.06^{b}	3.53^{c}	2.67^{a}
	CV(%)	37.78	29.13	33.03	16.48	52.60	7.34	10.81	25.23	16.77	34.59	16.77	49.62
Salinity (psu)	Mean	7.90^{b}	9.42^{c}	9.40^{c}	8.76^{bc}	8.51^{bc}	13.81^{d}	15.58^{d}	0.24^{a}	18.53^{d}	3.10^{b}	13.49^{c}	0.19^{a}
	CV(%)	104.82	90.27	99.78	101.76	60.75	85.03	82.37	148.48	43.65	95.57	46.34	159.98
Conductivity	Mean	13.80^{b}	15.81^{e}	15.21^{d}	14.54^{c}	17.02^{f}	21.17^{g}	22.89^{h}	0.42^{a}	29.43^{d}	5.46^{b}	25.09^{c}	0.46^{a}
(mS cm^{-1})	CV(%)	102.36	86.58	100.16	57.75	92.00	81.07	79.39	103.72	41.93	96.67	43.93	124.28
TDS (g l^{-1})	Mean	6.49^{b}	7.74^{d}	7.56^{cd}	8.38^{e}	7.32^{c}	10.66^{f}	11.14^{g}	0.27^{a}	15.00^{d}	2.78^{b}	11.54^{c}	0.46^{a}
	CV(%)	103.20	87.08	100.62	93.21	53.50	78.29	76.97	128.74	41.12	96.30	44.53	124.38
Turbidity	Mean	21.01^{ab}	18.43^{a}	26.22^{b}	17.91^{a}	91.15^{e}	32.27^{c}	32.37^{c}	40.44^{d}	19.74^{a}	25.37^{b}	23.29^{b}	71.50^{c}
(NTU)	CV(%)	57.10	58.37	86.37	95.07	51.53	102.73	123.75	28.43	104.76	75.89	88.79	62.38
Nitrite	Mean	44.73^{a}	46.47^{a}	62.88^{a}	24.86^{a}	111.78^{a}	819.14^{c}	392.96^{b}	75.90^{a}	25.94^{a}	48.00^{a}	459.92^{c}	255.51^{b}
(µg l^{-1})	CV(%)	46.99	62.41	74.92	50.95	63.18	129.08	96.24	75.29	47.29	61.13	166.94	166.94
Nitrate (µg l^{-1})	Mean	148.99^{c}	101.50^{b}	95.91^{b}	247.84^{d}	286.07^{e}	293.87^{e}	131.85^{c}	43.19^{a}	50.09^{a}	18.18^{a}	60.11^{a}	546.23^{b}
	CV(%)	137.65	162.71	140.84	151.63	175.05	74.23	149.39	69.38	164.72	44.38	164.72	57.25
Phosphate	Mean	248.97^{a}	194.60^{a}	145.92^{a}	425.17^{b}	645.56^{c}	180.69^{a}	247.70^{a}	158.41^{a}	28.65^{a}	369.95^{b}	344.38^{b}	380.53^{b}
(µg l^{-1})	CV(%)	56.15	51.83	54.26	122.02	55.98	78.83	55.11	74.04	73.32	55.61	90.22	90.22

^{a,b,c,d} For each variable, means with the same letters, because superscripts are not significantly different ($p > 0.05$).

Table 2: Effect of seasons and sites on water physicochemical variables variation

Variables	Seasons			Sites			Seasons × sites		
	df	*F*	*p*-value	df	*F*	*p*-value	df	*F*	*p*-value
Depth	3	20.64	0.001	7	46.87	0.001	21	110.92	0.001
SDD	3	2.83	0.038	7	80.34	0.001	21	14.84	0.001
Temperature	3	127.52	0.001	7	13.96	0.001	21	23.41	0.001
pH	3	13.64	0.001	7	25.37	0.001	21	13.49	0.001
DO	3	28.04	0.001	7	15.62	0.001	21	9.12	0.001
Salinity	3	502.49	0.001	7	485.10	0.001	21	101.75	0.001
Conductivity	3	4 218.14	0.001	7	3 554.95	0.001	21	819.12	0.001
TDS	3	5 147.00	0.001	7	464.80	0.001	21	1 022.30	0.001
Turbidity	3	22.62	0.001	7	115.99	0.001	21	51.17	0.001
Nitrite	3	57.40	0.001	7	55.59	0.001	21	20.99	0.001
Nitrate	3	613.51	0.001	7	147.06	0.001	21	347.87	0.001
PO_4^{3-}	3	5.74	0.001	7	22.76	0.001	21	4.24	0.001

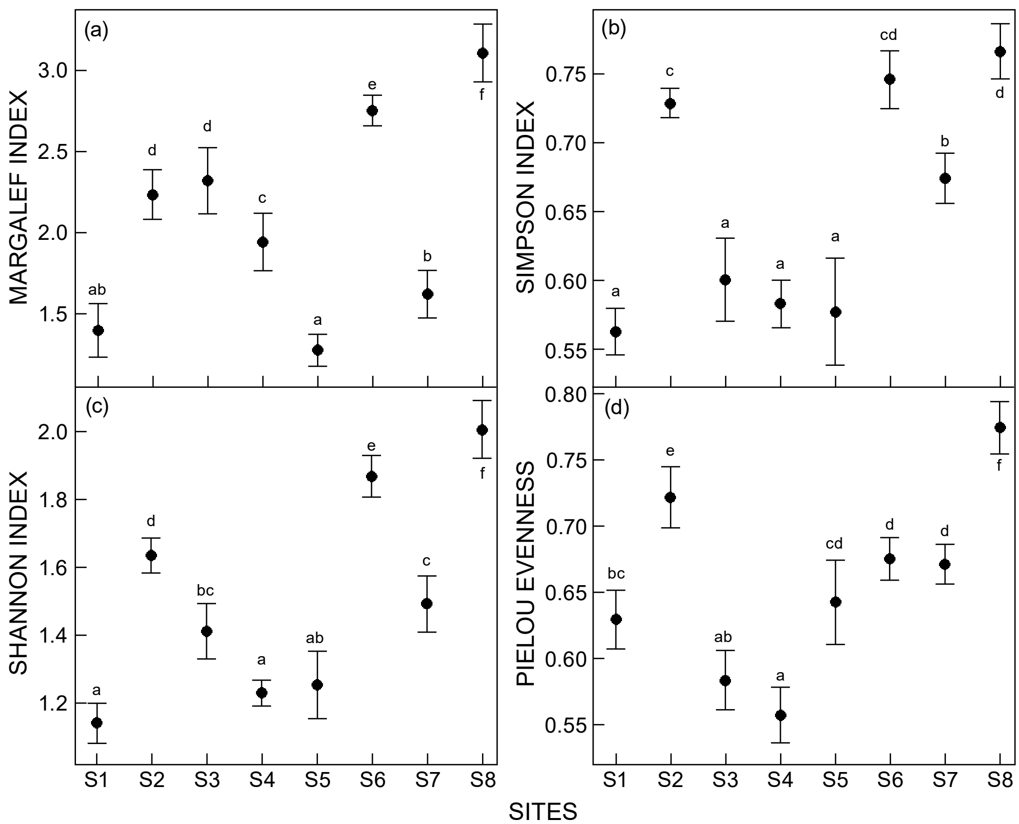

Figure 2: Spatial variation of biodiversity indices, including Margalef index (a), Simpson index (b), Shannon index (c) and Pielou's evenness index (d) during the study (pooled data over all seasons). Vertical bars correspond to the computed lower and upper limits for 95% confidence intervals. Letters above or below vertical bars indicate statistical significance of differences between sites (*post hoc* pairwise comparisons): only sites with different letters differ significantly ($p < 0.05$)

nitrite ($r = -0.872$) and conductivity ($r = -0.492$) (Figure 4). These environmental indicators were also positively correlated with RDA axis 2 of families: temperature ($r = 0.346$), pH ($r = 0.685$), conductivity ($r = 0.048$), nitrite ($r = 0.300$) and nitrate ($r = 0.475$) (Figure 4). Notably, most of the insect families (Nepidae, Chironomidae, Aeshnidae, Baetidae, Caenidae, Hydraenidae, Culicidae, Dytiscidae, Belosmatidae, Naucoridae and Pleidae) occurred together near the temperature and nitrate vectors mainly during wet seasons, whereas most of the molluscan families (Psammobiidae, Arcidae, Ostreidae, Potamididae and Tellinidae), crustacean families (Balanidae, Palaemonidae and Peneaeidae) and Annelida families (Nereididae and Serpulidae) occurred together in the opposite sites of the latter group near nitrite, pH and conductivity vectors mainly during dry seasons.

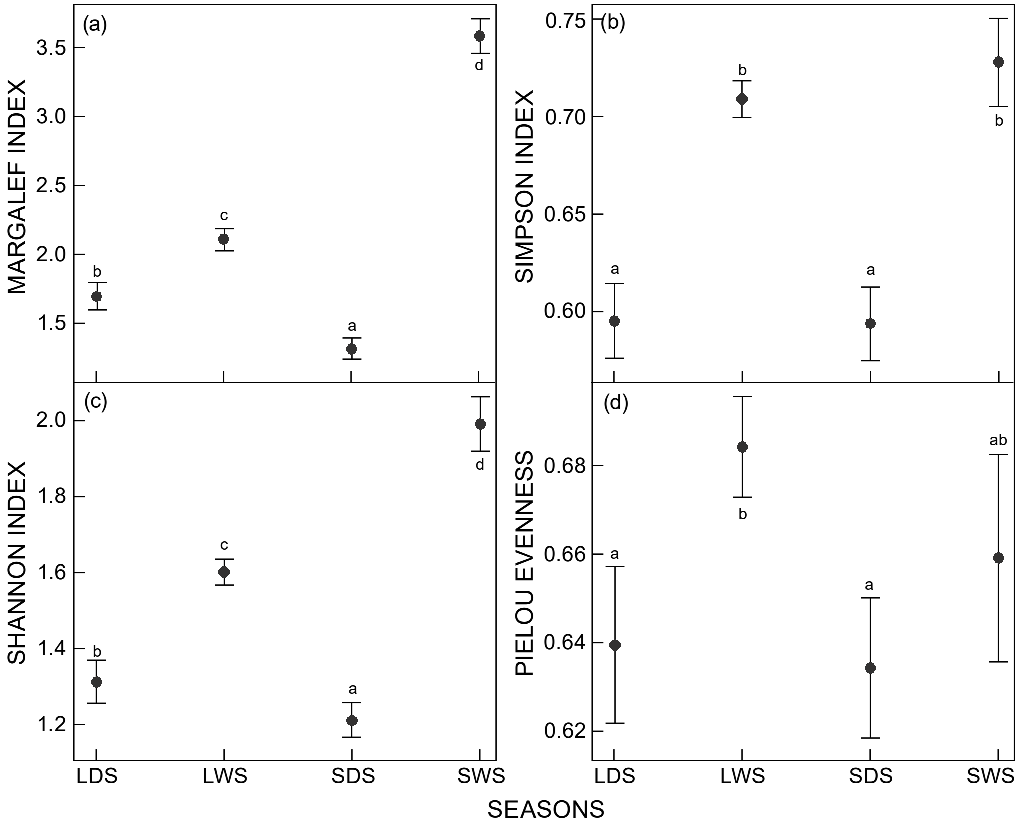

Figure 3: Seasonal variation of biodiversity indices, including Margalef index (a), Simpson index (b), Shannon index (c) and Pielou's evenness index (d) during the study (pooled data over all sites). Vertical bars correspond to the computed lower and upper limits for 95% confidence intervals. Letters above or below vertical bars indicate statistical significance of differences between seasons (*post hoc* pairwise comparisons): only seasons with different letters differ significantly (p < 0.05). LDS = long dry season, LWS = long wet season, SDS = short dry season, SWS = short wet season

Table 3: Effect of seasons and sites on biodiversity indices

Variables	Sites			Seasons			Seasons × sites		
	df	*F*	*p*-value	df	*F*	*p*-value	df	*F*	*p*-value
Margalef index	7	283.93	0.001	3	263.49	0.001	21	92.99	0.001
Simpson index	7	89.05	0.001	3	15.06	0.001	21	35.01	0.001
Shannon index	7	129.56	0.001	3	44.17	0.001	21	43.66	0.001
Pielou's evenness index	7	58.67	0.001	3	24.64	0.001	21	29.40	0.001

Discussion

Time and spatial variation of environmental factors

Physical and chemical variables of aquatic ecosystems are abiotic indicators that provide information on the habitat viability for living organisms. Therefore, understanding their variation is useful for ecological management of the ecosystem. In the current study, values of physical and chemical variables of Lake Nokoue indicate their heterogeneity across seasons and sites. This heterogeneity could be explained by precipitation/ rainfall differences between seasons, the water intake difference (especially S8), effects of the ocean (especially at S7 and during dry seasons) and anthropogenic action spatial variation (such as S5 dominated by *acadjas* and receiving Cotonou effluents). A specificity of the lake is that the SWS in south Benin coincides with the single wet season of the North. As a result, large volumes of water enter Lake Nokoue from the Oueme River to Lake Nokoue during this season. Furthermore, rainfall and the runoff carrier the dissolved matter from the littoral and agricultural areas into the ecosystem mostly via the northern sites, resulting in a difference in water chemistry between sites within the wet seasons. The highest depths, recorded at Sites 7 and 8, were because of unregulated lagoon sand dredging (personal observation). These factors affecting environmental conditions are consistent with the observation of Uwadiae (2014) in Epe lagoon (Nigeria) and related to 'hydroclimatic changes', as well as anthropogenic activities. During the wet seasons (LWS and SWS), a large

Table 4: Two-way ANOSIM of macroinvertebrate assemblage and similarity percentage (SIMPER) among seasons and among sites. Only significant differences at $p < 0.05$ are presented in bold. LDS: long dry season, LWS: long wet season, SDS: short dry season, SWS: short wet season

Pairwise comparison	Dissimilarity (%)	*R*	*p*-value
Site factor			
S1–S2	63.63	0.01	0.391
S1–S3	57.43	−0.12	0.716
S1–S4	62.08	0.01	0.485
S1–S5	61.87	0.13	0.284
S1–S6	73.21	0.68	**0.045**
S1–S7	71.43	0.36	**0.029**
S1–S8	76.27	0.73	**0.028**
S2–S3	60.46	−0.06	0.659
S2–S4	58.79	−0.18	0.884
S2–S5	65.82	0.13	0.320
S2–S6	70.32	0.47	**0.026**
S2–S7	75.56	0.35	**0.028**
S2–S8	72.99	0.38	**0.028**
S3–S4	53.90	−0.20	0.830
S3–S5	56.54	−0.10	0.686
S3–S6	67.54	0.65	**0.028**
S3–S7	67.75	0.27	0.146
S3–S8	66.69	0.34	**0.045**
S4–S5	57.96	−0.11	0.773
S4–S6	65.46	0.41	**0.046**
S4–S7	69.47	0.18	0.234
S4–S8	68.79	0.27	**0.048**
S5–S6	65.40	0.51	**0.027**
S5–S7	66.54	0.15	0.143
S5–S8	81.41	0.95	**0.028**
S6–S7	51.82	−0.06	0.635
S6–S8	77.61	0.95	**0.026**
S7–S8	79.74	0.75	**0.028**
Season factor			
LDS–LWS	63.90	0.170	**0.047**
LDS–SDS	71.63	0.472	**0.001**
LWS–SDS	72.78	0.592	**0.001**
LDS–SWS	71.38	0.661	**0.001**
LWS–SWS	59.87	0.363	**0.002**
SDS-SWS	76.45	0.893	**0.001**

volume of fresh water enters the lagoons from drainage channels, creeks and rivers (Sô and Oueme rivers), resulting in a dilution effect of salinity in the lagoons (Mama 2010; Djihouessi and Aina 2018) especially at S1, S2, S3, S4 and S5. Moreover, during dry seasons the fresh water inflow into the lagoons is reduced, whereas the lagoon salinity increases, as a result of the incursion of tidal sea water (Mama 2010; Djihouessi and Aina 2018) especially at S7 and S8. The relatively high nutrient and turbidity values during the SWS are consistent with those reported by Mama (2010). These high values are as a result of water inflow from the Oueme River (rich in pesticides and mineral fertilisers of leached or drained agricultural surfaces) (Odountan and Abou 2015), domestic and toxic wastes from the Dantokpa Market (situated south of the lake), as well and inputs of effluents and solid waste from Cotonou urban activities. The phosphate values, up to 1 228 $\mu g\ l^{-1}$, indicate the very high eutrophication of the ecosystem lake

Table 5: The cumulative contribution of the macroinvertebrate classes to the spatial and temporal assemblages of macroinvertebrates

Class	Contribution (%)	
	Site factor	Season factor
Insecta	27.23	28.73
Malacostraca	19.14	19.52
Thecostraca	0.61	0.55
Arachnida	0.33	0.35
Bivalvia	15.66	14.34
Gastropoda	16.83	15.92
Oligochaeta	7.81	7.90
Polychaeta	12.39	12.69

(Alhou 2007), which is reflected by the proliferation of the invasive water hyacinth (*Eichhornia crassipes*) at all sites during the wet seasons (particularly at Sites 1,2,3 and 8 during the low salinity period) (Mama 2010).

Time and space: influence on distribution and community structure of macroinvertebrates

After phytoplankton, macroinvertebrates are the most commonly used group of organisms in biomonitoring of lentic ecosystem, because they display a wide range of biological features in this respect (Birk et al. 2012; Odountan et al. 2019).

During our study, biodiversity indices showed that the Lake Nokoue macroinvertebrate assemblages were heterogeneous and variable, as a function of sites and seasons. A prime example is the highest values of the Margalef index (d) and the Shannon diversity index observed during the SWS (especially at S8) and the lowest values observed during the SDS (especially at S5 dominated by Naididae, Gammaridae and Portunidae). These spatial and temporal patterns are consistent with those observed in Ologe Lagoon, situated not far from Lake Nokoue in Nigeria (Imoobe 2008), where the diversity of macroinvertebrates reached the highest values during the wet season. However, the Margalef index and Simpson diversity index sometimes were showing different inter site or seasonal patterns. In fact, the Margalef's index is a heterogeneity metric, which shows a greater degree of sensitivity to changes in richness than in abundance, contrasted with the Simpson diversity index, which is a dominance metric (Rosenberg 1972; Koperski 2011). Therefore, the dominance of Naididae, Gammaridae and Portunidae at Site 5, coupled to absence of insect families (Table 6) influenced the Margalef Index negatively. Likewise, highest values of Pielou's evenness (J) were observed at Site 8, because of the many insect families (Baetidae, Belosmatidae, Naucoridae, Caenidae, Dytiscidae and Pleidae) (Table 6). Site 8 is one of the deepest sites, but still shallow enough, especially at this littoral sampling point, to be sufficiently oxygenated. This site characterised by a high density of *Eichhornia crassipes* (personal observation) receives more fresh water during the SWS, which should increase the diversity of epiphytic fresh water insects, hence not influenced by the benthic effects of dredging. The Shannon diversity index calculation considers all observed taxa and is sensitive to uncommon species (Peet 1974). Shannon diversity index values observed in this study

Table 6: Mean abundance (%) of characteristic families (contribution to the dissimilarity >75%) at spatial and temporal scales

Variables	Site factor								Season factor			
	S1	S2	S3	S4	S5	S6	S7	S8	LDS	LWS	SDS	SWS
Chironomidae	14.51	8.9	23.18	39.13	8.13	1.60	0.84	3.71	0.16	15.50	0.15	84.19
Thiaridae	9.15	30.29	9.82	21.13	14.64	5.16	3.99	5.82	12.32	36.27	30.78	20.63
Nereididae	2.46	5.42	1.97	2.95	0.00	57.64	23.89	5.67	15.76	15.03	27.09	42.12
Ostreidae	0.42	0.00	0.00	0.21	0.42	42.69	56.26	0.00	40.57	16.48	31.18	11.77
Grapsidae	0.00	3.20	2.14	2.14	15.30	30.96	46.26	0.00	33.10	33.10	0.00	33.80
Potamididae	12.81	18.46	13.78	24.82	14.84	7.51	7.07	0.71	24.21	34.63	18.90	22.26
Serpulidae	4.94	13.58	44.44	9.88	0.62	12.96	10.49	3.09	1.23	11.11	87.66	0.00
Corbulidae	2.40	2.00	5.40	2.00	2.69	29.37	56.14	0.00	2.72	1.36	68.03	27.89
Naididae	0.00	2.31	21.72	27.32	16.15	10.10	13.39	9.01	12.89	20.66	5.48	60.97
Gammaridae	5.97	13.43	23.88	17.91	25.37	10.45	0.00	2.99	0.00	55.22	10.45	34.33
Portunidae	4.35	4.35	7.61	11.96	30.43	17.39	23.91	0.00	1.09	3.26	0.00	95.65
Baetidae	12.82	12.82	10.26	15.38	0.00	0.00	7.69	41.03	5.12	28.21	0.00	66.67
Planorbidae	24.14	31.04	17.24	10.34	0.00	0.00	0.00	17.24	20.69	0.00	10.35	68.96
Belosmatidae	3.12	35.49	15.25	15.38	0.00	0.00	0.00	30.76	7.69	42.30	7.69	42.32
Naucoridae	4.67	24.46	15.32	13.78	2.64	0.00	0.00	39.13	7.69	42.31	7.69	42.31
Psammobiidae	0.00	0.00	0.00	0.00	0.00	52.18	47.82	0.00	17.39	34.79	47.82	0.00
Caenidae	18.75	15.63	9.37	18.75	0.00	0.00	3.13	34.37	3.12	34.38	0.00	62.50
Dytiscidae	17.93	10.62	20.35	14.27	10.11	0.00	4.77	21.95	2.89	24.01	3.10	70.00
Pleidae	5.88	17.67	17.64	23.52	0.00	0.00	0.00	35.29	5.88	41.17	5.89	47.06

Table 7: Summary statistics of RDA results for interactive and individual species-environmental relationships in Lake Nokoue

Variables	RDA axis			
	1	2	3	4
Eigenvalues	0.212	0.116	0.050	0.038
Species-environment correlations:	0.869	0.824	0.721	0.725
Cumulative percentage variance				
of species data	21.2	32.7	37.7	41.4
of species-environment relationships	48.6	75.2	86.6	95.2

were lower compared with other lagoons of West Africa (Imoobe 2008; Kouadio et al. 2008; Adandedjan et al. 2012). One reason for this is the use of PAST Software, which integrates natural log (Hammer 2016), whereas Imoobe (2008), Kouadio et al. (2008) and Adandedjan et al. (2012) used either log2 or log10 for computing this diversity index. Another reason is the difference in hydrological features of the ecosystems.

Three groups of organisms (marine, brackish and fresh water species) occur in West African lagoons, which are directly connected to the sea (Atlantic Ocean) and receiving large volumes of fresh water from inland, creating high lake γ-diversity (Le Loeuff and Zabi 1993). This is observed in Aby lagoon (Kouadio et al. 2008), whereas less marine species are observed in Lake Nokoue. However, sometimes locally lower α- diversity could be observed in such ecosystems, attributable to the specific salinity conditions of each habitat. Furthermore, mangroves, macrophytes and sea grass habitats in estuarine systems, such as the Coastal Lagoon (Benin) could provide more adequate substrates and taxon richness followed by high diversity, as supported by Adandedjan et al. (2012), and observed during this study at sites where *Eichhornia* was abundant (S8). Also, lower value of the Shannon diversity might not necessarily be a sign of degradation or anthropogenic stress, but could be related to natural conditions, as well or a combination of these factors (Ruellet and Dauvin 2007). The current study showed (with multivariate analyses) spatial and seasonal pattern variations resulting from the fact that some families occurred only in certain seasons of the year and at specific sites. Chironomidae, Thiaridae and Potamididae were abundant at Sites 1, 2, 3, 4 and 5 – Nereididae, Ostreidae, Grapsidae and Corbulidae at Sites 6 and 7 – Serpulidae at Site 3 – Naididae at Sites 2, 3, 4 and 5 – Gammaridae or Portunidae at Sites 3 and 5 – Baetidae at S8, whereas insect families were abundant during the SWS (Table 6). Organisms proliferate where hydrological and limnological characteristics were favourable (Cui et al. 2008; Sharma and Rawat 2009; Çelik et al. 2010). These families observed at certain sites (typically relatively homogeneous habitat at local scale) are recruited from the subset of the organisms available from a regional pool and are selected by dynamic and static environmental drivers acting at local scales (Konar et al. 2016). Multivariate analyses findings are consistent with results from biodiversity indices and illustrate complementarity between both approaches in biomonitoring. Based on SIMPER pairwise comparison, three different homogeneous habitats

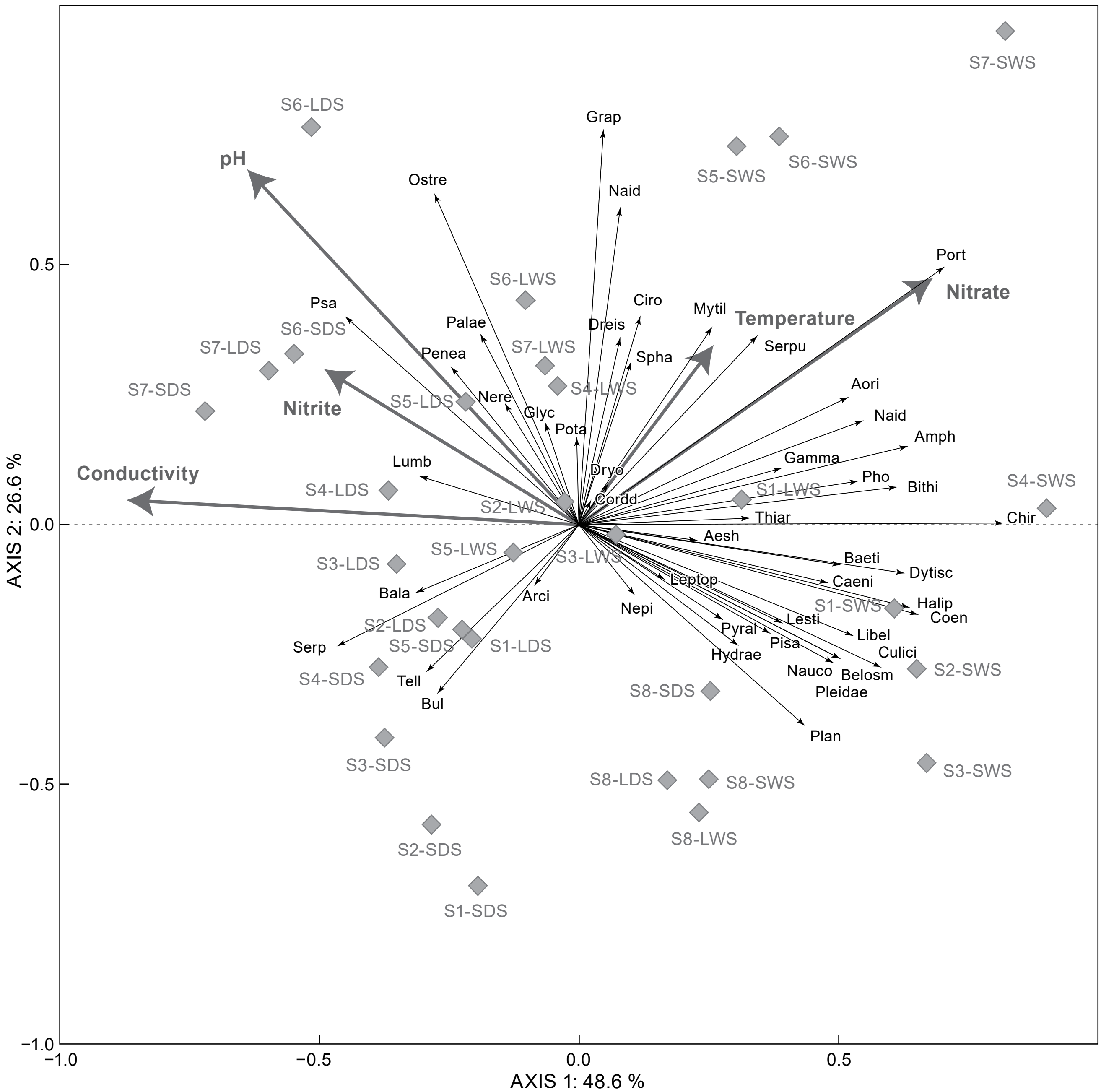

Figure 4: Diagram of redundancy analysis (RDA) of physical and chemical variables (thick grey vectors), benthic macroinvertebrate families (thin black vectors) and sites (grey diamonds) during the four seasons in Lake Nokoue. **Abbreviations:** Aesh: Aeshnidae, Amph: Amphilochidae, Aori: Aoridae, Arci: Arcidae, Baeti: Baetidae, Bala: Balanidae, Belosm: Belosmatidae, Bithi: Bithinidae, Bul: Bulinidae, Caeni: Caenidae, Chir: Chironomidae, Ciro: Cirolanidae, Coen: Coenagrionidae, Cordd: Corbulidae, Culici: Culicidae, Dreis: Dreissenidae, Dryo: Dryopidae, Dytisc: Dytiscidae, Gamma: Gammaridae, Glyc: Glyceridae, Grap: Grapsidae, Halip: Haliplidae, Hydrae: Hydraenidae, Leptop: Leptophlebiidae, Lesti: Lestidae, Libel: Libellulidae, Lumb: Lumbricidae, Mytil: Mytilidae, Naid: Naididae, Nauco: Naucoridae, Nepi: Nepidae, Nere: Nereididae, Ostre: Ostreidae, Palae: Palaemonidae, Penea: Peneaeidae, Pho: Photidae, Pisa: Pisauridae, Plan: Planorbidae, Pleidae: Pleidae, Port: Portunidae, Pota: Potamiddae, Psa: Psammobiidae, Pyral: Pyralidae, Serp: Serpulidae, Serpu: Serpulidae, Spha: Sphaeromatidae, Tell: Tellinidae, Thiar: Thiaridae, Tub: Tubificidae, Pota: Potamididae

could be considered at the lake scale (Table 4), in which specific families of macroinvertebrate occurred: fresh water habitat (S8), fresh water habitat with occasionally brackish features (Sites 1, 2, 3, 4 and 5) and saline habitat with occasionally brackish features (Sites 6 and 7). In each cluster of sites, similar composition and abundance were observed. Seasonal variation was stronger than spatial variation of macroinvertebrate communities. However, given the expanding cities of Cotonou and Abomey-Calavi on the Southern and Western edges of the ecosystem, Lake Nokoue more and more becomes an urban lagoon in these areas, with possible increase of spatial impacts on its biodiversity and ecosystem services.

Relationship between benthic macroinvertebrate assemblages and abiotic factors

Most of the variance in relationships between species and environmental variables were explained by the first two axes of the RDA. This variation is quite similar to the results of a similar study (in Zimbabwe) (Dalu et al. 2012). RDA analyses show that macroinvertebrate communities of Lake Nokoue are strongly influenced by two kinds of environmental factors: habitat suitability (temperature) and trophic status (NO_2^-, NO_3^-, conductivity and pH), irrespective of seasons and sites. Spatial and temporal variation of these variables affects seasonal and spatial assemblage of macroinvertebrate communities.

Habitat suitability

Our data indicate strong effects of habitat suitability with respect to temperature on proliferation of macroinvertebrates especially insect families (Figure 4). This 'effect' of temperature is explained as representing a proxy for the presence of macrophytes (e.g. *Eichhornia crassipes*). On the one hand, increase of water temperature positively affects growth and biomass of *Eichhornia crassipes* (Wilson et al. 2005) and conversely floating macrophytes, such as *Eichhornia crassipes*, might also increase water temperatures (Mangas-Ramírez and Elías-gutiérrez 2004). Several authors addressed the issue of relationship between macrophytes and macroinvertebrate assemblages (Oscoz et al. 2011; Cai et al. 2012; Hu et al. 2016). Macrophytes provide habitat for many epiphytic macroinvertebrate taxa, such as Ephemeroptera, Odonata, Heteroptera, Coleoptera, Diptera, Gastropoda and Bivalvia as found in this study, with highest temperature (Figure 4). Ephemeroptera (mostly grazers-scrapers and collectors-gatherers) (Bauernfeind 2018) are abundant during the SWS especially at site S8 on roots of macrophytes (when temperature is high), because of direct consumption of significant amounts of living macrophytes, but also decomposing plant tissues providing relatively high-quality detritus (Cai et al. 2012). Cai et al. (2012) state that the more heterogeneous and complex the habitats are, the more complex and diverse are the fauna. Large spatial heterogeneity provides a variety of substrata for living, feeding and reproduction and also provides protection against predators (Cai et al. 2012). In contrast to S8 during all seasons and occasionally at S1, S2, S3 and S4, very few macrophytes were found at Site 5, characterised by low diversity of insect families, where non-insect families were observed in abundance. *Eichhornia crassipes* was observed during the wet seasons (LWS and SWS) at all sites, whereas it was always present at Site 8.

Trophic status

Spatial and seasonal variation of environmental variables reflecting trophic status is likely to affect the macroinvertebrate community's assemblages in Lake Nokoue, as shown by the RDA analyses. Water chemistry and trophic status have often been cited as important factors affecting macroinvertebrate communities especially in standing and shallow aquatic ecosystems (Çelik et al. 2010; Parsons et al. 2010; Cai et al. 2012; Hu et al. 2016). NO_2^-, NO_3^-, conductivity and pH pointed out during this study as factors structuring macroinvertebrate communities, could be associated with organic matter. Lake Nokoue has a long history of eutrophication and receives organic input associated with fresh water runoff from the Oueme and Sô rivers, the agricultural area of northern part, industrial and domestic sewage (Mama 2010; Djihouessi and Aina 2018). Chironomidae, Aoridae, Photidae, Gammaridae and Amphilochidae were abundant with lower pH observed during SWS. These findings confirmed the trend backed for Chironomidae and some crustaceans, which are generally pointed out to be associated and able to colonise environments with low pH and high NO_3^- when other groups are decreasing or disappearing (Gerhardt et al. 2004; De Bisthoven et al. 2005; Çelik et al. 2010; Cai et al. 2012). Dominance of Naididae at S5 during SWS could be related to high values of NO_3^-. Naididae, through their burrowing, feeding, locomotive, respiratory and excretory activities, are recognised as macroinvertebrates typical of nutrient rich lakes, by mediating both physical and chemical processes near the sediment-water interface (Çelik et al. 2010; Oscoz et al. 2011). Conversely, trophic status influences the macrophytes population and therefore macroinvertebrate communities, also have interactions with other factors affecting their occurrence and distribution, such as hydrological characteristics, substrate type, availability of habitats, riparian vegetation removal, intrusion of various residues through human activities (Mophin-Kani and Murugesan 2014)

Conclusion

This study offers some insights into the dynamics of macroinvertebrates and physico-chemical factors of Lake Nokoue, South Benin, in space and time. The environmental variables are dependent on periodic hydroclimatic variations in the lake and human activities. The macroinvertebrate fauna reflects brackish and fresh water conditions and accordingly varies across sites and within seasons. Biodiversity indices combined with statistics, such as ANOSIM and multivariate statistics were useful for the biomonitoring of Lake Nokoue as they provided comparative measures between seasons and sites. RDA revealed that macroinvertebrates are highly adaptable to a broad range of ecological conditions hence only strong environmental gradients can have a structuring effect on their communities: habitat suitability (temperature) and trophic status (NO_2^- and NO_3^-, conductivity and pH). A prime example is that high densities of Oligochaeta and Chironomidae, considered as bioindicators of low water quality, are observed in the muddy bottom where nutrients (NO_2^- and NO_3^-) were important (especially during SWS). The current study demonstrates that spatial heterogeneity of macroinvertebrates of Lake Nokoue is related to the dynamics created by input of fresh water (wet seasons) or salt water (dry seasons), whereas spatial heterogeneity, as a result of anthropogenic activities (urban sprawling, waste disposal, use of *acadjas*) is suggested. The presence of the invasive water hyacinth might be another important structuring factor as well, although this requires a more focused spatial study.

Future research and management of the lake should model the lake's zonation affected by gradients of anthropogenic activities (solid and liquid waste disposal, eutrophication, fisheries, macrophyte covered zones acting as buffer zones) and hydrologic conditions (the interaction between season and salinity) and focus on mapping the effects of water hyacinth and its eventual use or removal, abatement of pollution and recording the ensuing changes in macroinvertebrate assemblages, which could affect the food web and the fisheries. Moreover, given the important economic value of tourism related to the settlement of Ganvié at the northern edge (partly on the lake with pole houses), we strongly recommend developing an integrated lake basin management plan. This plan should preserve the main ecological and economical assets of the lake, being the ecosystem services of water purification, fisheries and tourism.

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