BRILL

Crustaceana 96 (7) 605-625

CRUSTACEANA

DISTRIBUTION MODEL OF SHRIMP SPECIES IN LAKE NOKOUÉ, SOUTHERN BENIN, WEST AFRICA

BY

S. WILFRIED SINTONDJI[1,2,6]), ZACHARIE SOHOU[1,2]), APPOLINAIRE GOUSSANOU[1,4]), THÉOPHILE GODOME[1,5]), KATRIJN BAETENS[3]), GENEVIÈVE LACROIX[3]) and EMILE D. FIOGBÉ[1])

[1]) Laboratoire de Recherche sur les Zones Humides, Faculté des Sciences et Techniques, Université d'Abomey-Calavi, 01 BP 526 Cotonou, Benin

[2]) Institut de Recherches Halieutiques et Océanologiques du Benin (IRHOB), 03 BP 1665 Cotonou, Benin

[3]) Royal Belgian Institute of Natural Sciences, Operational Directorate Natural Environment, 29 Rue Vautier, 1000 Brussels, Belgium

[4]) Laboratoire de Biotechnologie Animale et de Technologie des Viandes, Département de Production et Santé Animales, Ecole Polytechnique d'Abomey-Calavi, Université d'Abomey-Calavi, 01 BP 2009, Benin

[5]) Laboratoire d'Hydrobiologie, UFR Biosciences, Université Félix Houphouet-Boigny, 22 BP 582, Abidjan 22, Ivory Coast

ORCID iDs: Sintondji: 0000-0002-8720-8650; Sohou: 0000-0003-3314-3481; Goussanou: 0000-0002-9048-9721; Godome: 0000-0001-5961-0637; Baetens: 0000-0002-4479-5517; Lacroix: 0000-0002-3227-0000; Fiogbé: 0000-0001-6743-0492

ABSTRACT

The aim of this work was to evaluate the spatial and temporal distribution of shrimp species in the Lake Nokoué-Cotonou Channel complex for an efficient management of the fishery. The results of one year sampling from five stations (North, South, East, Central and West) in the complex revealed the following proportions: *Penaeus notialis* 73.68%, *Macrobrachium macrobrachion* 13.81%, *Macrobrachium vollenhovenii* 5.36%, *Penaeus monodon* 2.68%, *Macrobrachium felicinum* 2.20%, *Penaeus kerathurus* 1.72%, *Macrobrachium* cf. *zariquieyi* 0.27%, and *Macrobrachium equidens* 0.27%. The species *M.* cf. *zariquieyi* and *M. equidens* were never reported from Benin, but are now found in Lake Nokoué. Spatially, *Penaeus* (*Penaeus notialis*) are more abundant in the west (Acadja concentration zone), while *Macrobrachium* (*Macrobrachium macrobrachion*) are more dominant in the east (near the Ouémé entrance) and north (near the Sô entrance) of the lake. *Penaeus* are strongly present in the lagoon complex from January to August, while *Macrobrachium* are more abundant in Lake Nokoué from September to December. Spearman's correlation analysis

[6]) Corresponding author; e-mail: sintondjiwilfried@gmail.com

Published with license by Koninklijke Brill NV | DOI: 10.1163/15685403-bja10304
 | ISSN: 0011-216x (print) 1568-5403 (online)

revealed that increasing salinity, pH, transparency and total dissolved solids (TDS) positively influenced the abundance of *P. notialis*, while increasing salinity, pH, transparency, and TDS negatively influenced the abundance of *M. macrobrachion* at the 5% significance level. For an efficient management of the shrimp fishery, it is desirable that the shrimp fishery in Lake Nokoué, mainly in the Cotonou Channel, which is a very sensitive area for their seasonal migrations, benefits from at least three months of respite per year, from November to January. This period corresponds to the strong migration of juvenile *Penaeus* towards the lake. This should allow many *Penaeus* to grow up and breed at least once in their lives, according to the species' life cycle presented.

Key words. — Palaemonidae, Penaeidae, salinity, crustacean, shrimp migration, Lake Nokoué, Benin

RÉSUMÉ

Le but de ce travail, a été d'évaluer la distribution spatiale et temporelle des espèces de crevettes dans le complexe lac Nokoué-chenal de Cotonou pour une gestion efficiente de la pêche. Les résultats d'une annnée provenant de cinq stations (Nord, Sud, Est, centre et Ouest) du complexe ont révelé des proportions suivantes : *Penaeus notialis* 73,68%, *Macrobrachium macrobrachion* 13,81%, *Macrobrachium vollenhovenii* 5,36%, *Penaeus monodon* 2,68%, *Macrobrachium felicinum* 2,20%, *Penaeus kerathurus* 1,72%, *Macrobrachium* cf. *zariquieyi* 0,27%, et *Macrobrachium equidens* 0,27%. Les espèces *M.* cf. *zariquieyi* et *M. equidens* n'ont été jamais signalées au Bénin, mais sont retrouvées maintenant dans le lac Nokoué. Sur le plan spatial, les *Penaeus* (*Penaeus notialis*) sont plus abondants à l'Ouest (zone de concentration d'Acadja), alors que les *Macrobrachium* (*Macrobrachium macrobrachion*) sont plus dominants à l'Est (proche de l'entrée Ouémé) et au Nord (proche de l'entrée Sô) du lac. On retient une forte présence des *Penaeus* dans le complexe lagunaire de janvier à août alors que les *Macrobrachium* sont plus abondants dans le lac Nokoué de septembre à décembre. L'analyse de corrélation de Spearman a révélé que l'augmentation de la salinité, du pH, la transparence, et le total des solides dessous (TDS) ont positivement influencé l'abondance des espèces *P. notialis* ; alors que l'augmentation de la salinité, du pH, la transparence, et le TDS ont négativement influencé l'abondance de l'espèce *Macrobrachium macrobrachion* au seuil de 5% de significativité. Pour une gestion efficace de la pêche aux crevettes, il est souhaitable que la pêche des crevettes dans le lac Nokoué, principalement dans le chenal de Cotonou qui est une zone très sensible pour leurs migrations saisonnières, bénéficie d'au moins trois mois de répit par an, de novembre à janvier. Cette période correspond à la forte migration des *Penaeus* juvéniles vers le lac. Ceci devrait permettre à beaucoup de *Penaeus* de grandir et de se reproduire au moins une fois dans leur vie selon son cycle de vital présenté.

Mots clés. — Palaemonidae, Penaeidae, salinité, Crustacé, migration des crevettes, lac Nokoué, Bénin

INTRODUCTION

The global market for shrimp is taking a premium value in the sale of fishery products (FAO, 2016). In Benin, fishing in continental waters accounts for 80% of total national fishing and constitutes the primary income activity of riparian human populations (Ollabodé, 2019). Lake Nokoué, on which this work is based, is the largest body of water in Benin with a total area of about 150 km^2 (Mama et al., 2011). The seasonal variation in salinity of Lake Nokoué alternately confers a favourable environment for species of *Penaeus* Fabricius, 1798 (marine shrimp) and some freshwater Caridea (Sintondji et al., 2022a). Existing data indicate that the share of the fishery provided by Lake Nokoué was 2/3 of the total shrimp supply exported by Benin (Allegre & Dupret, 2010). A literature review indicated that *Penaeus notialis* Pérez Farfante, 1967 was the most abundant species in Lake Nokoué, but no fishing gear was specified (Sohou et al., 2009; Hinvi et al., 2013; Houssa & Verpoorten, 2015). The export of shrimp to the EU had become the second-most important activity apart from cotton in 2002 (Houssa & Verpoorten, 2015). Socially, the shrimp market alone contributed to the livelihoods of 4% of the Beninese population at that time (Houssa & Verpoorten, 2015; Sachi et al., 2016). According to Degnon et al. (2013), the shrimp industry generates more than 10 billion CFA francs annually in Benin, and thus represents a source of income that can help reduce poverty.

Officially, the turnover of exporting firms in 2002 amounted to CFA franc 1319 million for CRUSTAMER, 792 million for SOBEB, and 1066 million for FSG (Houssa & Verpoorten, 2015). Beninese shrimp have been in high demand on the European market due to their high market value and organoleptic quality (Sachi et al., 2016). According to Ehigiator & Oterai (2012), shrimp are also rich in minerals and low in fat. But this export was suspended by the Beninese authorities, due to a poor fisheries management strategy (overfishing). Shrimp exports are struggling to resume, due to low production from ecosystems, particularly Lake Nokoué, despite the lifting of this self-suspension since 2005 (Houssa & Verpoorten, 2015). Recent studies have indicated strong pressure from local fishermen on Lake Nokoué throughout the year (Adégbola et al., 2013; Ollabodé et al., 2021). All these anthropic actions by the human lake populations reveal a problem of lack of management of the shrimp fisheries in the lake. In addition, the control of the distribution of shrimp in time and space across Lake Nokoué during an annual cycle should constitute a fishing regulation tool for a good management of the shrimp stock. It is thus important to test the hypothesis of spatial and temporal variability in the distribution of shrimp species in Lake Nokoué. This work, therefore, aims at assessing the current distribution of the various species of shrimp in Lake Nokoué, in order to better regulate the fishery for an effective management of the shrimp stock in Benin.

MATERIAL AND METHODS

Station selection

Lake Nokoué is potentially connected to two freshwater streams: the Ouémé River in the east and the Sô River in the north (Mama, 2010). In the south, Lake

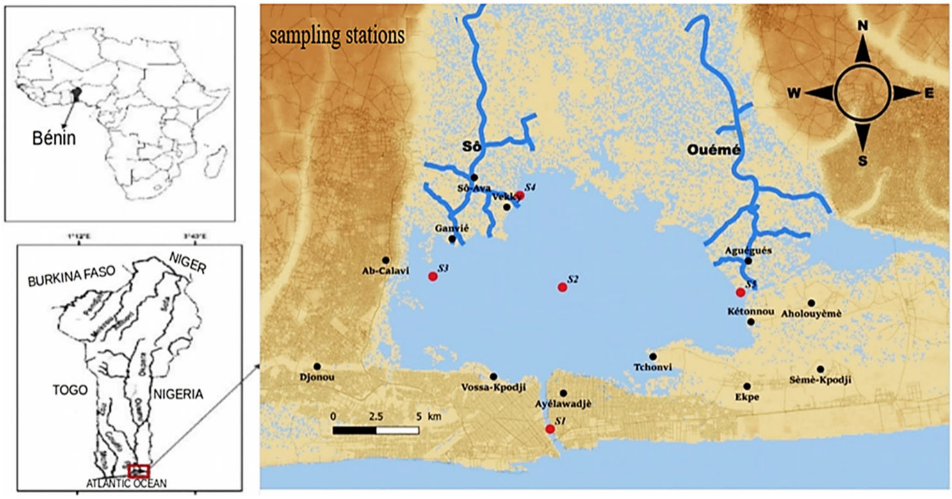

Fig. 1. Geographical location of Lake Nokoué in West Africa, and sampling stations in red, in the south of Benin. The inlet Cotonou Channel connects the lagoon ("lake") with the ocean, and sta. S1 is situated there. Stations: S1, south; S2, centre; S3, west; S4, north; and S5, east.

Nokoué is connected to the sea through a narrow channel in Cotonou (see fig. 1, indicated by sampling station S1). The accessibility of the data collection sites at any time (problem of abundance of aquatic plants, especially *Eichhornia crassipes* (Mart.) Solms during high water); water levels during flood and low water; security of the stations (good relationship with the inhabitants); and coverage of the entire lake surface, guided our choices for the five stations (fig. 1, S1-S5) where the samplings actually took place (Sintondji et al., 2022b).

Sampling

Sampling was carried out twice a month for a period of one year (from late November 2020 to early November 2021). A GPS was used to navigate and to properly acquire the sampling points. The particularities of this sampling reside in the fact that no bait was used to attract the shrimp to the gears. Also, the gears used were not set against the water currents. Two types of fishing gears, with the same mesh size of 0.5 cm, where used:

(a) The creel ("Adja") (fig. 2a) is a passive fishing method used by the indigenous fishermen of the lakeside villages. During the installation of the creel, several steps were necessary. The pots were immersed in the water and then attached to three pieces of wood fixed in the sediment to prevent them from moving. The opening of the trap was oriented at the top of the two mats, leaving an opening of 40 cm. The role of the two mats was to orient the shrimp towards the

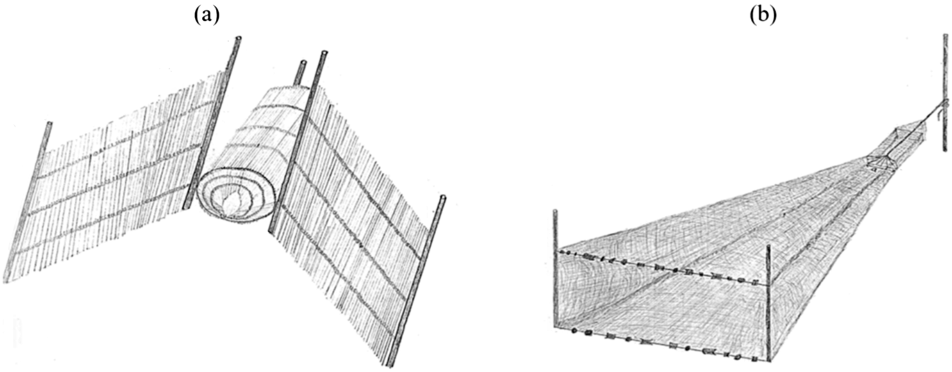

Fig. 2. The two types of indigenous fishing gear used for sampling: a, the shrimp creel "Adja"; b, the fixed shrimp net "Avè".

top, where the opening of the creel is fixed. During harvesting, the circular opening of the creel was detached (fig. 2a).

(b) The net device used is also a passive gear, locally called "Avè" by the fishing community. This device is relatively easier to set than the creel. The two wooden stakes that support the width of the opening were set deep into the substrate to hold the net opening in place and keep it open. A third wooden stake set in the substrate was attached to the net pocket so that the entire device remained taut in the water. During harvesting, the back opening of the net pocket was detached and the sample was harvested (fig. 2b).

These two types of fishing gear were used, because of their low cost; their environmental friendliness (leaving no toxic residues or waste in the aquatic ecosystem); their larger mesh than many other fishing gears used by human lake populations such as Acadja, Medokpokonou, and others, which allows small shrimp to escape; and, finally, their easiness of deployment.

In order to assess the impact of environmental factors on the shrimps' distribution, the following parameters were also measured using a YSI Pro 2030 19F 103474 Multimeter: temperature, dissolved oxygen, conductivity, salinity, total dissolved solids (TDS) and pH of the water. Water transparency was measured using a 20-cm-diameter Secchi disk painted white. A gauge attached at each station was used to record water level variation.

Some differences between Penaeidae and Palaemonidae

Morphometrics

In Palaemonidae (here represented by *Macrobrachium* Spence Bate, 1868), the first two pairs of pereiopods (often robust) bear claws (Sintondji et al., 2020). In contrast, in Penaeidae (here *Penaeus*), the carapace lacks post-orbital spines and bears short cervical grooves terminating below the mid-orbital line. Penaeidae are particularly characterized by the presence of pincers on the first three pairs of thoracic legs, or pereiopods (Wabete, 2005). Other fundamental differences between Penaeidae and Palaemonidae are in the pleurae of the first three abdominal somites. In the Palaemonidae, the pleura of the second abdominal somite cover those of the first and third somites. By contrast, in species belonging to the family Penaeidae, the pleura of the second abdominal somite cover only that of the following, "third somite". The overlap is regular, in roof tile-covering (Griessinger et al., 1991). In addition, a cross section of the last abdominal somite shows a circular cross section in Palaemonidae, whereas in Penaeidae this cross-section shows a dorsal carina.

Sexual features

In the females of Penaeidae (*Penaeus*), the thelycum is a seminal receptacle located ventrally on the first two thoracic somites between the last two pairs of pereiopods. The male petasma is a complex organ, very visible, making it possible to distinguish the males immediately. It is located between the two pleopods that constitute the first pair of abdominal appendages (Murai et al., 2003). In freshwater shrimp, the genital opening is located at the base of the fifth pair of pereiopods (thoracic legs) in the male. In contrast, the genital opening is located at the base of the third pair of pereiopods (thoracic legs) in females (Sintondji, 2020). The pleopods are biramous appendages with an undivided protopodite on which the two branches (rami: exopodite and endopodite) are inserted. It is only in the male of *Macrobrachium* that the second pair of pleopods carries the male appendage. At the level of the first somite (abdominal somite) a protuberance is present, a hard point perceptible by touch in the male and an absence of such a protuberance in the female of specimens of the genus *Macrobrachium*.

Life cycle

Species of the genus *Penaeus* have adopted an anadromous type of migration: living and breeding at sea but returning to lagoons and estuaries to feed and grow (fig. 3, left). In contrast, other Penaeidae complete their entire life cycle at sea.

Some species of the family Palaemonidae (*Macrobrachium*) reproduce in lagoons and estuaries, but return to fresh water to live, feed and grow (fig. 3, right). Some other Palaemonidae make an anadromous migration (as in fig. 3, left) whereas others perform a catadromous migration (born and breed in the sea, but return to fresh water to grow). Some species of the same family Palaemonidae, on the other hand, carry out their entire life cycle at sea and yet others entirely in fresh water.

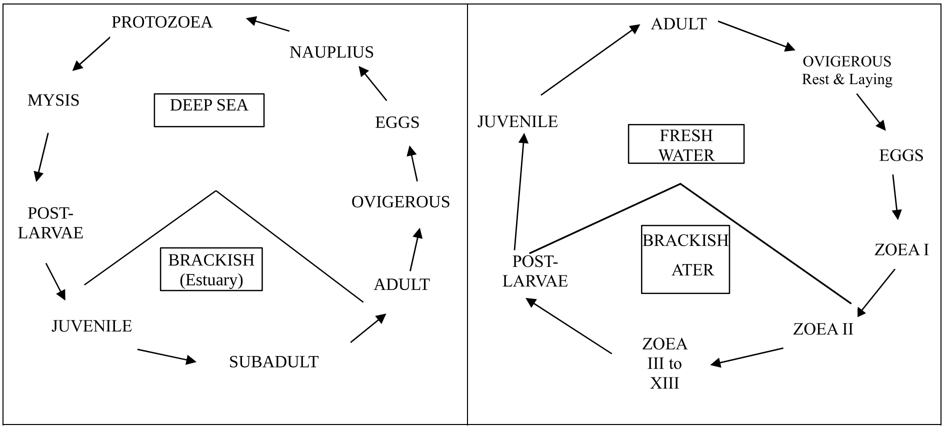

Fig. 3. Modified life cycles of: left, *Penaeus* spp.; and, right, many species of *Macrobrachium*. After Sintondji et al. (2022a).

Identification and conservation of shrimp specimens

Sampled shrimp specimens were stored in cool conditions at the Wetlands Research Laboratory (LRZH/FAST/UAC) according to the method proposed by García-Isarch et al. (2020). The identification of shrimp species was done in close collaboration with Dr. Cédric d'Udekem d'Acoz, specialist in identification of crustaceans at the museum of the Royal Belgian Institute of Natural Sciences (RBINS, https://www.naturalsciences.be/en/museum/home), Brussels. The identification keys of Monod (1980), Powell (1980) and Fransen (2014) were also used.

Statistical analyses

To provide a comprehensive understanding of the spatial and temporal dynamics of the shrimp in the Lake Nokoué-Cotonou Channel complex, several statistical analyses were conducted: A Shapiro-Wilk test was used to verify the normality of the structure of the variables at the 5% significance level. The one-factor ANOVA (analysis of variance) was used to compare the samples according to Legendre & Legendre (1984). The study of the distribution of the structure of the shrimp population was made on the basis of the percentages of occurrence (%OF) of the species according to the stations. It is the ratio (in percent) between the number of samples (p) where the species (i) appears and the total number of samples (P) in an environment (Dajoz, 2000). This parameter is translated by the following relationship:

$$\%\mathrm{OF} = (P_i/p) \times 100$$

Thus, for that author, when:

– %OF $\geqslant$ 50%, the species is said to be constant;
– 25% $\leqslant$ %OF $<$ 50%, the species is said to be accessory;
– %OF $<$ 25%, the species is said to be accidental.

A Factorial Correspondence Analysis (AFC) was used to determine the spatial and temporal distribution of the shrimp species. For this purpose, quantitative data (number of shrimp species per station and per month) and qualitative variables describing, among others, the types of stations and the months of the year, were used. The interest of this analysis was to describe both the combined occurrence and mutual avoidance between shrimp species with respect to space, but also with time (Semaoune et al., 2019).

The correlation coefficient (R) determines the relationship between two variables and measures the strength of the relationship. It varies between -1 and $+1$. When it is equal to $+1$ or -1, it indicates a perfect correlation between the variables and when it tends to 0, it indicates no correlation at all. The (+) sign means that the variables are positively correlated while the ($-$) sign means that the variables are negatively correlated. The closer this coefficient is to 1 in absolute value, the greater the intensity of the correlation between the two variables (Schwartz & Lazar, 1964). The purpose of calculating the Spearman rank correlation coefficient is to determine the relationship between physical and chemical parameters. Canonical community ordination "RDA" redundancy analysis was used to relate environmental variables of the different habitats studied to the abundance of shrimp taxa harvested in the Lake Nokoué complex and the Cotonou Channel. In ecology, this analysis has already been applied on carcinological data (N'Zi, 2007; Djiriéoulou, 2017), with the aim of assessing the relationship between environmental variables and the distribution of different shrimp taxa. In this programme, an indirect gradient analysis (detrended correspondence analysis, DCA) was first performed in order to check if the sum of the gradient lengths in standard deviation units does not exceed 3. When the sum of the gradient lengths is less than 3, then a redundancy analysis was preferred to a unimodal method (Ter Braak, 1995). For this purpose, a species/site matrix and an environmental variable/site matrix were constructed based on absolute numerical abundances. The program Canonical Community Ordination, version 4.5 was used for the RDA analysis. R 4.1 was used for the other analyses.

RESULTS

Annual relative proportion of shrimp species in the Lake Nokoué-Cotonou Channel complex

The samples revealed the presence of two genera of shrimp in Lake Nokoué. The genus *Macrobrachium* Spence Bate, 1868 and the genus *Penaeus* Fabricius, 1798,

P. notialis Pérez Farfante, 1967 ♀

P. monodon Fabricius, 1798 ♀

P. kerathurus (Forskål, 1775) ♀

M. vollenhovenii (Herklots, 1857) ♀

***M. equidens* (Dana, 1852)** ♀

M. felicinum Holthuis, 1949 ♀

M. macrobrachion (Herklots, 1851) ♀

M.* cf. *zariquieyi Holthuis, 1949 ♀

Fig. 4. Female (♀) shrimp specimens sampled from Lake Nokoué and its inlet. Species with their names in bold were not reported in Benin yet.

with a total of eight different species. Pictures of female and male shrimp specimens are shown in figs. 4 and 5, respectively. The different proportions of these shrimp species found in the samples are the following: *Penaeus notialis* Pérez Farfante, 1967: 73.68%; *Macrobrachium macrobrachion* (Herklots, 1851): 13.81%; *Macrobrachium vollenhovenii* (Herklots, 1857): 5.36%; *Penaeus monodon* Fabricius, 1798: 2.68%; *Macrobrachium felicinum* Holthuis, 1949: 2.20%; *Penaeus kerathurus* (Forskål, 1775): 1.72%; *Macrobrachium* cf. *zariquieyi* Holthuis, 1949: 0.27%; and *Macrobrachium equidens* (Dana, 1852): 0.27%. The species *Penaeus monodon*, *Macrobrachium equidens* and *M.* cf. *zariquieyi* are exotic, and are invasive in Benin.

P. notialis Pérez Farfante, 1967 ♂

P. monodon Fabricius, 1798 ♂

P. kerathurus (Forskål, 1775) ♂

M. vollenhovenii (Herklots, 1857) ♂

***M. equidens* (Dana, 1852)** ♂

M. felicinum Holthuis, 1949 ♂

M. macrobrachion (Herklots, 1851) ♂

Fig. 5. Male (♂) shrimp specimens sampled from Lake Nokoué and its inlet. The species with its name in bold was not reported in Benin yet.

Percentual occurrence of shrimp species by station

The results related to the percentages of occurrence made it possible to characterize the presence of shrimp species across the sampling stations. It appears that the presence of *P. notialis* was constant or permanent (%OF $\geqslant$ 50%) in the south (S1), centre (S2) and west (S3) of Lake Nokoué, while it remained accessory or unimportant (25% $\leqslant$ %OF $<$ 50%) in the north (4) and east (S5) of Lake Nokoué. The species *P. kerathurus* is absent in the east, but incidentally or by hazard (%OF $<$ 25%) represented in the south, centre, west and north of Lake Nokoué. The species *M. vollenhovenii* and *P. monodon* were accidentally (%OF $<$ 25%) represented on all five stations. As for *M. macrobrachion*, these are accidentally

TABLE I
Percentage occurrence of shrimp species in the Lake Nokoué-Cotonou Channel complex by stations

	S1	S2	S3	S4	S5
%OF *P. notialis* Pérez Farfante, 1967	84.34%***	78.89%***	88.57%***	44.24%**	44.63%**
%OF *P. kerathurus* (Forskål, 1775)	3.51%*	0.69%*	2.42%*	0.60%*	–
%OF *P. monodon* Fabricius, 1798	4.15%*	1.04%*	2.86%*	4.85%*	0.86%*
%OF *M. macrobrachion* (Herklots, 1851)	5.75%*	10.73%*	5.05%*	40%**	27.04%**
%OF *M. vollenhovenii* (Herklots, 1857)	1.28%*	7.26%*	0.88%*	8.48%*	15.02%*
%OF *M. felicinum* Holthuis, 1949	0.96%*	0.69%*	–	1.21%*	10.72%*
%OF *M. equidens* (Dana, 1852)	–	0.35%*	–	0.60%*	0.86%*
%OF *M.* cf. *zariquieyi* Holthuis, 1949	–	0.35%*	0.22%*	–	0.86

Species reported for the first time for Benin are underlined.
* Incidental species; ** accessory species; *** constant species.

(%OF < 25%) represented in the south, centre and west, but accessory (25% ⩽ %OF < 50%) represented in the north and east of Lake Nokoué. The species *M. felicinum* is incidentally (%OF < 25%) represented at all sites of the complex except at the west of Lake Nokoué, where it was absent. The species *M. equidens* is incidentally (%OF < 25%) represented in the centre, north and east, but absent in the south and west of Lake Nokoué. *M.* cf. *zariquieyi*, is incidentally (%OF < 25%) represented in the centre to the west and east, but absent in the north and south and Lake Nokoué (table I).

Species association to stations

The first two axes of the Factorial Correspondence Analysis (AFC, fig. 6) explain more than 95% of the total variance of the data on the distribution of species according to sites and months of the year. The factorial analysis of correspondence reveals a low diversity of species present in the Lake Nokoué-Cotonou Channel complex, respectively, at stations S1 (south), S3 (west) and S2 (centre), such in contrast to stations S5 (east) and S4 (north), where there is a high diversity of shrimp species present in the complex. The species *P. notialis*, *P. monodon* and *P. kerathurus* reveal an attraction for the western, southern and central stations of Lake Nokoué. On the other hand, the species *M. macrobrachion*, *M. vollenhovenii*, *M. felicinum*, *M. equidens*, and *M.* cf. *zariquieyi*, exhibit a preference for the stations in the north and east of the lake (fig. 6a).

The factorial correspondence analysis also revealed a strong presence of the three species *P. notialis*, *P. kerathurus* and *P. monodon* from January to August, in contrast to the period from September to December, when all five shrimps of

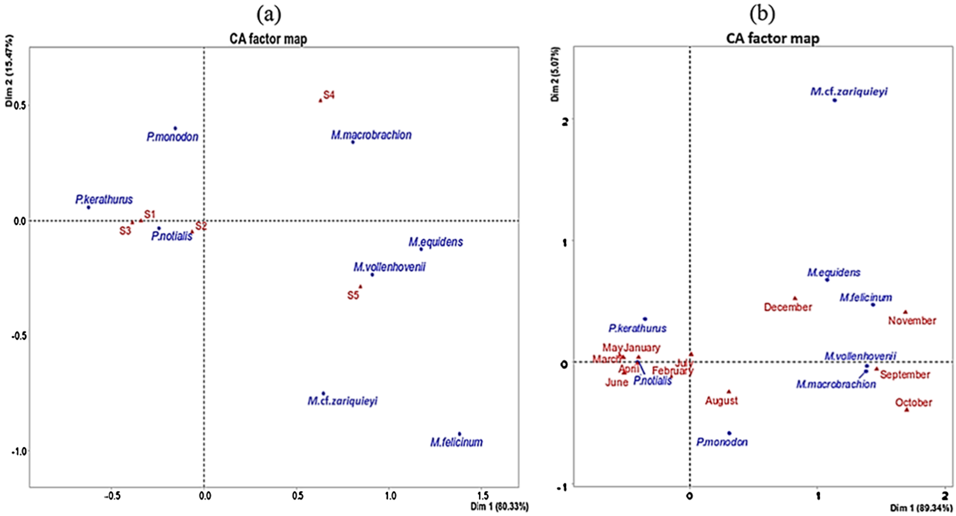

Fig. 6. Species distribution by: a, station; and, b, month.

the genus *Macrobrachium* are numerically more prominently represented in the lagoon complex (fig. 6b).

Average monthly variations of physical and chemical parameters in Lake Nokoué

The values in table II indicate that the highest average water levels (August – November), corresponding to the periods of high water (flood) in Lake Nokoué, are linked with the arrival of fresh water from the Ouémé River and with the potential for the *Macrobrachium* (fig. 3, right) freshwater shrimp to reproduce. On the other hand, the lowest average water levels (December-July), corresponding to the low water periods (ebb tide) of Lake Nokoué are linked with the intrusion of sea water into the lake and with potential for the saltwater shrimp *Penaeus* to grow (fig. 3, left). On all stations, the highest average values of salinity, TDS and transparency were recorded in Lake Nokoué from December to July (period of low water and abundance of *Penaeus* shrimp). The lowest values of these main parameters were observed from July to November (period of high water and abundance of *Macrobrachium* shrimp). The highest pH values were recorded from December to July (low water) while the lowest pH values were observed from August to November (flood). Low temperatures in Lake Nokoué were only recorded from June to September. Results also reveal that the highest dissolved oxygen values were recorded only in July, with a slight fluctuation during the rest of the year (table II).

TABLE II

Monthly average and standard deviation of environmental parameters in Lake Nokoué Sal, salinity (ppt); O_2, dissolved oxygen (mg/l); T, temperature (°C); Transp, transparency (m); TDS, total dissolved solids (mg/l); Depth, water depth (m)

Months	Sal	pH	O_2	T	Transp	TDS	Depth
Nov	3.54 ± 8.91	6.55 ± 0.45	4.92 ± 1.43	29.98 ± 1.06	0.59 ± 0.22	3636.77 ± 8624.20	1.66 ± 0.73
Dec	9.61 ± 12.69	6.81 ± 0.40	5.30 ± 0.73	29.94 ± 1.41	0.82 ± 0.44	10 129.20 ± 12 351.18	1.24 ± 0.65
Jan	14.92 ± 11.66	7.29 ± 0.43	5.58 ± 0.64	29.92 ± 1.17	1.29 ± 0.56	15 504.40 ± 11 108.02	1.25 ± 0.65
Feb	18.44 ± 9.51	7.32 ± 0.48	5.64 ± 0.54	30.04 ± 1.20	1.36 ± 0.60	18 329.90 ± 10 225.71	1.26 ± 0.64
Mar	22.81 ± 7.09	7.22 ± 0.53	5.38 ± 0.71	30.26 ± 1.32	1.23 ± 0.59	23 296.30 ± 6558.12	1.30 ± 0.63
Apr	22.90 ± 6.25	7.11 ± 0.41	5.68 ± 0.71	29.74 ± 0.81	1.23 ± 0.59	23 353.00 ± 5591.21	1.32 ± 0.65
May	21.64 ± 6.38	6.97 ± 0.30	5.16 ± 0.53	30.39 ± 1.01	1.12 ± 0.56	22 097.40 ± 5860.71	1.29 ± 0.65
Jun	18.42 ± 6.57	7.22 ± 0.38	6.19 ± 0.39	28.34 ± 0.40	0.75 ± 0.23	18 823.50 ± 6273.52	1.29 ± 0.66
Jul	11.37 ± 12.45	7.27 ± 0.42	6.98 ± 0.54	27.28 ± 0.56	0.55 ± 0.30	11 735.15 ± 12 001.03	1.34 ± 0.68
Aug	2.93 ± 4.52	6.39 ± 0.30	5.31 ± 1.46	27.69 ± 0.58	0.35 ± 0.13	3058.10 ± 4568.78	1.60 ± 0.62
Sep	0.18 ± 0.09	6.37 ± 0.11	5.12 ± 1.83	28.56 ± 0.32	0.34 ± 0.11	189.02 ± 141.83	1.86 ± 0.62
Oct	0.13 ± 0.04	5.97 ± 0.27	5.11 ± 1.77	30.21 ± 0.8	0.57 ± 0.16	132.38 ± 69.11	2.00 ± 0.67

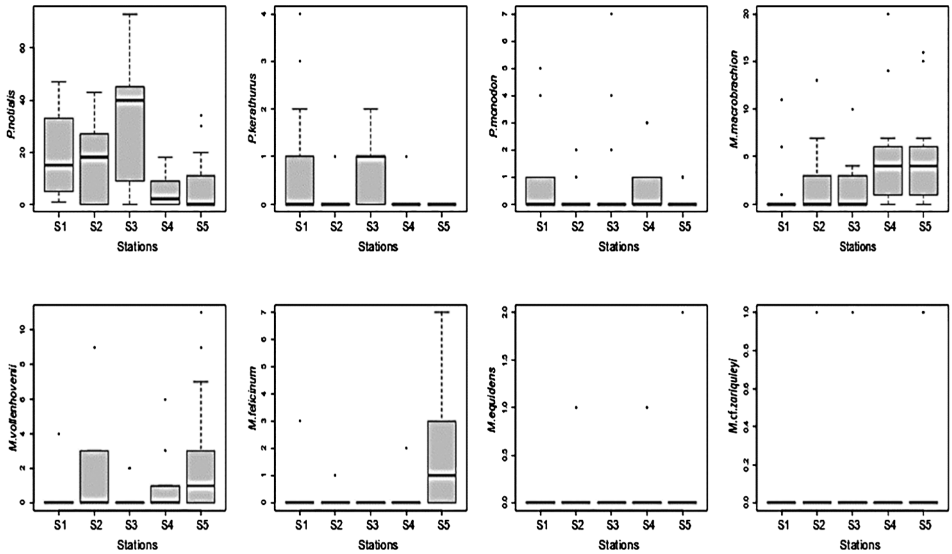

Fig. 7. Spatial distribution of shrimp species by station in numbers as generated by the R 4.1 software.

Spatial and temporal fluctuations in the quantity of shrimp species in the lagoon complex

Analysis of fig. 7 indicates that the dominant species *Penaeus notialis* is much more abundant in the western side of Lake Nokoué than at the other stations. It is noted that *Macrobrachium macrobrachion* is the most representative of the freshwater shrimp of the genus *Macrobrachium*. *Macrobrachium* spp. are better represented in the east and north than at the other stations in Lake Nokoué. Figure 8 indicates that *Penaeus* spp., especially *Penaeus notialis*, are more abundant in Lake Nokoué from January to August, with a peak in June, while *Macrobrachium*, especially *Macrobrachium macrobrachion*, are more abundantly represented in the lake from September to December. Relationships between species abundance and environmental variables are summarized in table III.

The results of the Spearman correlation analysis performed on the species (*P. notialis*, *P. kerathurus*, *P. monodon*, *M. macrobrachion*, *M. vollenhovenii*, *M. felicinum*, *M. equidens* and *M.* cf. *zariquieyi*) and environmental variables, showed that increasing salinity, pH, transparency, and TDS positively influenced the abundance of *P. notialis* and *P. kerathurus* (table III), but negatively influenced the abundance of the most representative species of the genus *Macrobrachium* (*M. macrobrachion*) (table III). The results of the redundancy analysis (RDA) showed that the correlation between environmental factors and shrimp species mainly explained 95.4% of the cumulative variance of the species data: Axis 1 and 2 alone explained 84.6% of the total variance (fig. 9). The RDA ordination along the fac-

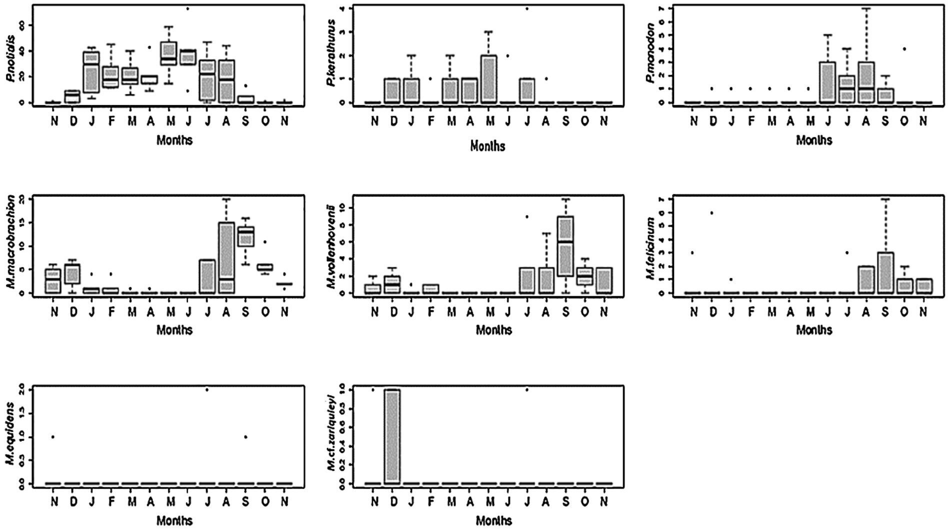

Fig. 8. Temporary fluctuation of shrimp species in numbers as generated by the R 4.1 software.

torial axis 1, shows a contrast between the southern (S1) and western (S3) stations and the central (S2), northern (S4) and eastern (S5) stations of Lake Nokoué. The graph in fig. 9 indicates that the southern (near the ocean and the Dantokpa market) and western (near the Calavi market and heavily covered with Acadja) stations, characterized by gravel and sand with high values of salinity, TDS, transparency, pH and dissolved oxygen, are more often frequented by *Penaeus* (*P. kerathurus*, *P. notialis* and *P. monodon*). On the other hand, the stations in the centre, north (near the Sô River) and east (near the Ouémé River and the Porto-Novo lagoon), charac-

TABLE III
Spearman correlations between environmental variables and shrimp species

Species	Sal	pH	O_2	*T*	Trans	TDS	Depth
P. notialis Pérez Farfante, 1967	0.75**	0.61*	0.33	−0.28	0.56*	0.75**	−0.01
P. kerathurus (Forskål, 1775)	0.51*	0.34	0.11	−0.22	0.37	0.51*	−0.01
P. monodon Fabricius, 1798	0.09	0.03	0.32	−0.31	−0.11	0.09	0.02
M. macrobrachion (Herklots,1851)	−0.81**	−0.65*	−0.25	0.08	−0.65*	−0.82**	−0.02
M. vollenhovenii (Herklots, 1857)	−0.65*	−0.45	−0.01	0.04	−0.49	−0.65*	0.12
M. felicinum Holthuis, 1949	−0.54*	−0.41	−0.19	0.02	−0.50*	−0.53*	0.08
M. equidens (Dana, 1852)	−0.27	−0.21	0.03	−0.06	−0.25	−0.26	0.00
M. cf. *zariquieyi* Holthuis, 1949	−0.16	−0.11	−0.04	−0.06	−0.11	−0.16	−0.09

Species reported for the first time from Benin are underlined. The significance of Spearman Rank correlations is underlined and the degrees of significance are marked by asterisks: * $P<0.05$ (the correlation is significant); ** $P<0.01$ (the correlation is highly significant); *** $P<0.001$ (correlation is highly significant). Sal, salinity (ppt); O_2, dissolved oxygen (mg/l); T, temperature (°C); Transp, transparency (m); TDS, total dissolved solids (mg/l); Depth, water depth (m).

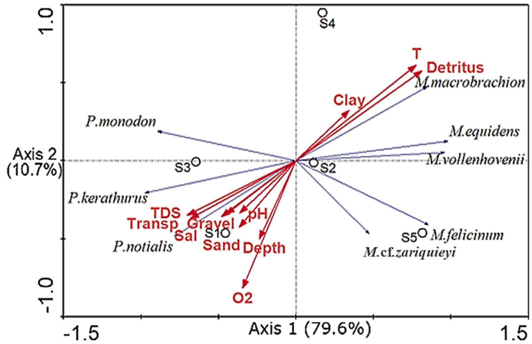

Fig. 9. Relationships between environmental parameters, sampling stations, and shrimp species. See text for further explanation.

terized by clay, detritus and higher temperature, are more frequently occupied by all species of the genus *Macrobrachium* (*M. macrobrachion*, *M. vollenhovenii*, *M. felicinum*, *M. equidens*, and *M*. cf. *zariquieyi*).

DISCUSSION

Within Lake Nokoué, the species diversity of shrimp appears to vary from one geographic area to another. The present work identified five species of freshwater shrimp (*Macrobrachium macrobrachion*, *M. vollenhovenii*, *M. felicinum*, *M. equidens* and *M*. cf. *zariquieyi*) and three species of saltwater shrimp (*Penaeus notialis*, *P. kerathurus* and *P. monodon*).

The diversity of *Macrobrachium* found in the Lake Nokoué-Cotonou Channel complex in this study, is lower than the one mentioned by Konan (2009), with 9 species in Ivory Coast (*M. vollenhovenii*, *M. macrobrachion*, *M. dux* (Lenz, 1910), *M. felicinum*, *M. sollaudii*, *M. thysi* Powell, 1980, *Atya scabra* (Leach, 1816), *A. gabonensis* Giebel, 1875 and *A. africana* Bouvier, 1904), and by Djiriéoulou (2017), who found 13 species in Ivory Coast (*P. notialis*, *P. kerathurus*, *A. gabonensis*, *Desmocaris trispinosa* (Aurivillius,1898), *M. chevalieri* (Roux, 1935), *M. dux*, *M. equidens*, *M. felicinum*, *M. macrobrachion*, *M. raridens* (Hilgendorf, 1893), *M. thysi*, *M. vollenhovenii* and *M*. cf. *zariquieyi*).

However, the diversity of Lake Nokoué is higher than the one shown by Makombu et al. (2015), who found 6 species in Cameroon (*M. vollenhovenii*, *M. macrobrachion*, *M. dux*, *M. chevalieri*, *M. felicinum*, *M. vollenhovenii*, *M. sollaudii* (De Man, 1912)), and by Kouamé et al. (2018), who reported 5 species in Ivory Coast (*M. dux*, *M. felicinum*, *M. macrobrachion*, *M. vollenhovenii* and *M. thysi*. This is also the case with Djiriéoulou (2017), who recorded only two species (*P. notialis*, *P. kerathurus*) including *P. kerathurus* for the first time in lagoon environments and in the Marais Tanoé-Ehy Forest in Ivory Coast, while three of these saltwater shrimp were collected in the present work.

The species of the genera *Desmocaris* Sollaud, 1911 and *Atya* Leach, 1816 were not sampled in Lake Nokoué, although reported in the lower Ouémé valley by Kouton (2004), which could be related to their life cycle as described by Sintondji et al. (2022a). Nevertheless, we believe that even *Desmocaris* has a favourable environment in Lake Nokoué from September to December (the period of flooding and abundance of *Macrobrachium*).

Our results confirm those of Koussovi et al. (2019), who used creels in Agonlin-Lowé (Ouémé River that feeds Lake Nokoué) and sufficiently recovered the species *Macrobrachium macrobrachion*. The presence of the invasive species *M. equidens* in Lake Nokoué, never reported in Lake Nokoué up to now, could be explained by the communication of Lake Nokoué with the Porto-Novo lagoon, which in turn is in direct communication with Nigerian waters where *M. equidens* are present (Nwosu, 2010; Ibim, 2018). Using only two types of creels (Nukuhuidja and Hakuidja) for shrimp sampling in the coastal lagoon of Grand-Popo in Benin, which does not have a direct communication with Lake Nokoué, Agadjihouédé (2006) reported collecting *M. macrobrachion*, *M. dux*, *M. felicinum*, *M.* sp.1, *M. vollenhovenii* and *M. raridens*. We note here some differences in the species sampled, in particular the saltwater shrimp (*Penaeus*), which should be reported from the coastal lagoon of Grand-Popo in south-eastern Benin because of the influence of sea-strength salinity.

Based on these results, we believe that there are reasons such as the mesh size and the types of gear used that could explain the differences observed between our study and the studies cited above. However, according to Kouamélan et al. (2003), the variability of the habitats surveyed and the sampling periods could also justify the specific differences observed between the different ecosystems. In the present work, there is a high concentration of *Penaeus* in the west of Lake Nokoué with a peak in June. This result presents a similarity in the area of concentration of *Penaeus* with the results of Hinvi et al. (2013). However, there is a difference in the peak period of *Penaeus* which is February according to Hinvi et al. (2013), who used a four-month database (January to April). This difference in result could potentially be related to the difference in the two sampling periods. Other factors such as sampling strategies could influence the quality of the results as well. This is the case with Ahmed et al. (2005) and Kantoussan et al. (2014), who indicate a significant difference in fishing efficiency between different types of gears. The western zone of Lake Nokoué, which has a high concentration of *Penaeus*, benefits from a significant amount of detritus from human activities. This detritus or organic matter creates zones of primary productivity rich in living micro-organisms (zooplankton, *Artemia*, rotifers, etc.), which could constitute stocks of staple food that would attract penaeid shrimp (Abou, 2001). This is confirmed by the results of Gnohossou (2006), who indicates that the distribution of shrimp is much more a function of biophysical parameters than chemical parameters of the water, although the latter influence the quality of the environment. According to the estimates of Houssa & Verpoorten (2015) the species *Penaeus notialis* represented more than 97% of the total shrimp production of Benin (sea and lagoons). This percentage is different from that found in Lake Nokoué taken in isolation, which is 73.68%. This difference can be explained by the greater diversity of shrimp species of commercial interest in Lake Nokoué than in the sea.

CONCLUSION

The present work indicates that *Penaeus* are more abundant in Lake Nokoué from January to August (period of high salinity), particularly in the west, while *Macrobrachium* are more represented in Lake Nokoué from September to December (period of low salinity), particularly in the east and north of the lake. Salinity, pH, transparency, and TDS positively influence the abundance of *Penaeus* and that of *Macrobrachium* negatively. This work also revealed that the species *M.* cf. *zariquieyi* and *M. equidens*, never reported in Benin before, are now found in Lake Nokoué.

ACKNOWLEDGEMENT

The authors would like to express their gratitude to Professor Cédric d'Udekem d'Acoz, crustacean specialist at RBINS (Royal Belgian Institute of Natural Sciences), for his help in species identification.

FUNDING

This study was realized in the framework of the collaboration between RBINS and IRHOB (Institut de Recherches Halieutiques et Océanologiques du Benin), and was funded by the CEBioS programme (funded by the Belgian Development Cooperation).

AUTHORS' CONTRIBUTIONS

SSW, KB, ZS and AG contributed to the conception and design of the study. SSW, TG and ZS collected the data. SSW wrote the first draft of the manuscript. GL, AG and EDF contributed to the analysis of the data and manuscript revision. All authors read and approved the final manuscript.

REFERENCES

ABOU, Y., 2001. Diversité du zooplancton et des macroinvertébrés des zones humides du Sud-Bénin. Rapport de consultation pour le Programme national d'Aménagement des Zones Humides (PAZH): 1-61.

ADEGBOLA, Y. P., F. AQUILAS, N. SAMEY, J. CLOHOUNTO & Y. Y. SOGLO, 2013. Analyse de la compétitivité de la chaîne de valeur ajoutée crevette fraîche et crevette fumée du Bénin. In: 4th international conference of the African association of agricultural economists, September 2013, article 11: 22-25. (University of Nairobi, Nairobi).

AGADJIHOUÈDÉ, H., 2006. Diversité et exploitation des crevettes d'eau douce dans la lagune de Grand Popo (Bas Mono): 1-70. ("Ingénieur Agronome" Thesis. Université d'Abomeycalavi).

AHMED, K. K. & J. B. HAMBREY, 2005. Studies on the fish catch efficiency of different types of fishing gear in Kaptai Reservoir, Bangladesh. Lakes & Reservoirs: Research and Management, **10**: 221-234.

ALLEGRE, J. M. & G. DUPRET, 2010. Assistance au secteur industriel de la pêche au Bénin pour l'harmonisation du système de production avec la réglementation UE. ID020BEN, Rapport de mission, SFP.

DAJOZ, R., 2000. Précis d'écologie: 1-615. (Dunod, Paris).

DEGNON, R. G., E. DAHOUENON-AHOUSSI, E. S. ADJOU & D. C. SOHOUNHLOUÉ, 2013. Transformation artisanale des crevettes (*Penaeus* spp.) au Sud du Bénin: évaluation des performances techniques des équipements et procédés de fumage. Nature & Technology, **8**: 23-31.

DJIRIEOULOU, K. C., 2017. Peuplement des crevettes des hydrosystèmes de marais et fluvio-lagunaires du sud-est de la Cote d'Ivoire: Diversité, structure, et croissance des populations. (Laboratoire d'Hydrobiologie et d'Ecotechnologie des Eaux. Thèse l'Université Félix Houphouët-Boigny, Numéro d'ordre 2029/2017).

FRANSEN, C. H. J. M., 2014. Shrimps and prawns. In: K. E. CARPENTER & N. DE ANGELIS (eds.), The living marine resources of the Eastern Central Atlantic, **1**, Introduction, crustaceans, chitons and cephalopods: 37-196. (FAO Species Identification Guide for Fishery Purposes, FAO, Rome).

FRONTALINI, F., E. ARMYNOT DU CHÂTELET, J. P. DEBENAY, R. COCCIONI & G. BANCALÀ, 2011. Benthic Foraminifera in coastal lagoons: distributional patterns and biomonitoring implications. In: G. FRIEDMAN (ed.), Lagoons: biology, management and environmental impact: 39-72. (Nova Science Publishers, New York, NY).

GARCIA-ISARCH, E., J. LANDA, J. GONZALEZ, T. G. SANTAMARIA, M. MONTSE PEREZ & E. MUÑOZ, 2020. Protocoles d'échantillonnage biologique. (DEMERSTEM – Instituto Español d'Oceanografía – IEO, Madrid).

GNOHOSSOU, P. M., 2006. La faune benthique d'une lagune ouest africaine (le lac Nokoué au Bénin), diversité, abondance, variations temporelles et spatiales, place dans la chaine trophique: 1-184. (Thèse de doctorat, UAC-INP, Toulouse).

GRIESSINGER, J. M., D. LACROIX & P. GODOUIN, 1991. Elevage de la crevette tropicale d'eau douce: 1-372. (Institut Français de Recherche pour l'Exploitation de Mer (IFREMER), Plouzané).

HINVI, L. C., N. KOUHOUNDJI, B. TENTE, G. AGBAHUNGBA, E. D. FIOGBE & B. SINSIN, 2013. Caractérisation spatiale des crevettes Penaeidae dans le lac Nokoué à So-Ava (Bénin). Annales des Sciences Agronomiques, **17**(1): 87-101.

HOUSSA, R. & M. VERPOORTEN, 2015. The unintended consequence of an export ban: evidence from Benin's shrimp sector. University of Namur, World Development, **67**: 138-150.

IBIM, A. T., 2018. Distribution of five *Macrobrachium* species along a salinity gradient in Rivers State, Nigeria. London Journal of Research in Science: Natural and Formal, **18**(2): 69-81.

KANTOUSSAN, J., J. M. ECOUTIN, G. FONTENELLE, L. TITO DE MORAIS & R. LAË, 2014. Catch per Unit Effort and yields as indicators of exploited fish communities: application to two West African reservoirs. Lakes and Reservoirs: Research and Management, **19**(2): 86-97. DOI:10.1111/lre.12061.

KONAN, K. M., 2009. Diversité morphologique et génétique des crevettes des genres *Atya* Leach, 1816 et *Macrobrachium* Bate, 1868 de Côte d'Ivoire: 1-154. (Thèse de Doctorat, Université d'Abobo-Adjamé, Abidjan).

KONAN, Y. A., 2014. Diversité de l'ichtyofaune et caractéristiques bioécologiques de *Clarias buettikoferi* Steindachner, 1894 et *Thysochromis ansorgii* (Boulenger, 1901) dans la Forêt des Marais Tanoé-Ehy (Côte d'Ivoire): 1-172. (Thèse de Doctorat, Université Félix Houphouët-Boigny de Cocody, Abidjan).

KOUAMELAN, E. P., G. G. TEUGELS, V. N'DOUBA, G. GOORE BI & T. KONE, 2003. Fish diversity and its relationships with environmental variables in a West African basin. Hydrobiologia, **505**: 139-146.

KOUSSOVI, G., F. NIASS, C. A. BONOU & E. MONTCHOWUI, 2019. Reproductive characteristics of the freshwater shrimp, *Macrobrachium macrobrachion* (Herklots, 1851) in the water bodies of Benin, West Africa. Crustaceana, **92**(3): 269-294.

KOUTON, M. D., 2004. Diversité, écologie et exploitation des crevettes d'eau douces dans la basse vallée de l'Ouémé: Cas de la commune d'Adjohoun au Bénin. (Mémoire de Thèse d'Ingénieur Agronome, Université d'Abomey-Calavi, Godomey).

LEGENDRE, L. & P. LEGENDRE, 1984. La structure des données écologiques. Ecologie numérique, **2**: 1-335. (Masson, Paris).

MAKOMBU, J. G., B. O. OBEN, P. M. OBEN, N. MAKOGE, E. W. NGUEKAM, G. L. P. GAUDIN, I. S. MOTTO, K. M. KONAN, J. H. BROWN, J. R. NGUEGUIM, E. MIALHE & R. E. BRUMMETT, 2015. Biodiversity of species of genus: *Macrobrachium* (Decapoda, Palaemonidae) in Lokoundje, Kienke and Lobe Rivers of South Region, Cameroon. Journal of Biodiversity and Environmental Sciences, **7**(2): 68-80.

MAMA, D., 2010. Méthodologie et résultats du diagnostic de l'eutrophisation du lac Nokoué (Benin). (Mémoire de Thèse de l'Université de Limoges, Groupement de Recherche Eau Sol Environnement – EA **4330**, No. 200, Limoges).

MAMA, D., V. DELUCHAT, J. BOWEN, W. CHOUTI, B. YAO, B. GNON & M. BAUDU, 2011. Caractérisation d'un système lagunaire en zone tropicale: as du lac Nokoué (Bénin). European Journal of Scientific Research, **56**(4): 516-528.

MONOD, T., 1980. Décapodes. In: J. R. DURAND & C. LÉVÊQUE (eds.), Flore et faune aquatiques de l'Afrique sahélo-soudanienne, **1** (ch. 44): 369-389. (ORSTOM, Paris).

MURAI, T., C. HOUNKPÈ & J. B. DEGBEY, 2003. Atlas des poissons et crustacés du Bénin: eaux douces et saumâtres. (Direction des Pêches Cotonou, Cotonou).

NWOSU, F. M., 2010. Species composition and gear characteristics of the *Macrobrachium* fishery of the Cross River estuary, Nigeria. J. Ocean Univ. China, **9**: 71-75. DOI:10.1007/s11802-010-0071-3.

N'ZI, K. G., 2007. Diversité biologique des peuplements de crevettes d'eaux douces de Côte d'Ivoire en relations avec les variables environnementales du milieu: 1-178. (Thèse de Doctorat, Université de Cocody-Abidjan, Abidjan).

OLLABODE, N., 2019. Analyse économique des chaînes de valeur des crevettes d'eaux douce et saumâtre au sud-Bénin: 1-104. (Thèse de Master Professionnel, Faculté d'Agronomie, Université de Parakou, Parakou).

POWELL, C. B., 1980. The genus *Macrobrachium* in West Africa: *M. thysi* a new large egged species from Ivory Coast (Crustacea, Decapoda, Palaemonidae). Rev. Zool. Afr., **94**(2): 317-326.

SACHI, PS., I. Y. BOKOSSA, C. C. TCHEKESSI, J. S. BANON, A. DJOGBÉ & R. BLEOUSSI, 2016. La filière crevette au Bénin, cas des crevettes des eaux saumâtres: Synthèse bibliographique. International Journal of Innovation and Applied Studies, **18**(2): 445-457.

Schwartz, D. & P. Lazar, 1964. Elément de statistique à l'usage des étudiants en propédeutique médicale. (Editions Flammarion, Paris).

Semaoune, Y. B., A. Senoussi & B. Faye, 2019. Typologie structurale des élevages camelins au Sahara septentrional Algérien – cas de la willaya de Ghardaïa. Livestock Research for Rural Development, **31**(2): 24.

Sintondji, S. W., 2020. Crevette *Macrobrachium vollenhovenii* embryologie et essai d'élevage larvaire: 1-68. (Editions Universitaires Européennes, Chisinau).

Sintondji, S. W., A. S. Gozingan, Z. Sohou, K. Baetens, G. Lacroix & E. D. Fiogbé, 2022a. Prediction of the distribution of shrimp species found in southern Bénin through the lake Nokoué-Ocean complex. Journal of Aquaculture Marine Biology and Ecology, **2022**(2): 116. DOI:10.37722/JAMBE.2022201.

Sintondji, S. W., Z. Sohou, K. Baetens, G. Lacroix & E. D. Fiogbé, 2022b. Characterization of a West African coastal lagoon system: case of Lake Nokoué with its inlet (Cotonou, South Bénin). Ecologies, **3**: 467-479. DOI:10.3390/ecologies3040033.

Sohou, Z., R. C. Houedjissin & N. R. A. Ahoyo, 2009. La pisciculture au Bénin: de la tradition à la modernisation. Bulletin de la Recherche Agronomique du Bénin, **66**: 48-59.

Ter Braak, C. J. F., 1995. Ordination. In: R. H. G. Jongman, C. J. F. Ter Braak & O. F. R. Van Tongeren (eds.), Data analysis in community and landscape ecology: 91-173. (Cambridge University Press, Cambridge).

Wabete, N., 2005. Etude écophysiologique du métabolisme respiratoire et nutritionnel chez la crevette pénéide *Litopenaeus stylirostris*. Application à la crevetticulture en Nouvelle Calédonie. (Thèse Université Bordeaux 1 Ecole Doctorale "Sciences du vivant, Géosciences et Sciences de l'Environnement"; No. 3111, Bordeaux).

First received 18 February 2023.
Final version accepted 12 May 2023. Published online 26 July 2023.