



Prediction of the distribution of shrimp species found in southern Benin through the lake Nokoué-Ocean complex

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Abstract

The export of shrimps to the European Union was one of the mainstays of the Beninese economy. It is an income-generating activity for the populations living along Lake Nokoué. The lack of a fisheries management strategy has caused a drastic decline in shrimp's production in Lake Nokoué since 2003. To remedy this problem, it is necessary to hypothesize on their spatial-temporal dynamics in the Lake Nokoué-Cotonou channel complex. This is investigated by combining a literature review on their life cycles and habitat suitability with spatial-temporal evolution of salinity obtained from *in-situ* observations. The literature review reported four (04) potential families of shrimp species whose part of their life cycle is common to the ecology of Lake Nokoué: Penaeidae (*Penaeus*); Palaemonidae (*Macrobrachium*); Atyidae (*Atya*) and Desmocarididae (*Desmocarid*). The overall results in relation to the life cycle of the shrimp species indicate that adults of the *Macrobrachium*, *Atya* species have a favorable environment in Lake Nokoué from August to November and their larvae must remain in the lake from December to June to ensure their survival. The species of the genus *Desmocarid*, which carry out their entire life cycle in fresh water, can stay in Lake Nokoué from August to November. The species of the genus *Penaeus*

have a favorable environment in Lake Nokoué from December to June but their larvae can only survive in the sea. Species of the genus *Caridina* (freshwater) and *Palaemon* (estuary and marine) belonging to the family Palaemonidae can however be found in Lake Nokoué because of their wide distribution on the West African coast although they are not reported in Benin. This research makes it possible to predict the presence or absence of shrimp genera in a lake system, based on their life cycle. Based on the results obtained, we suggest a ban on fishing in Lake Nokoué between December and February and a ban on shrimp fishing in the Cotonou canal for a good management of the shrimp stock in Benin.

Keywords: Caridea; Crustacea; Habitat Map; Habitat Suitability Study; Migration Season; Penaeoidea; Salinity

Introduction

The shrimps industry has an important place in the world because of its high commercial value. The shrimps occupies on the market 70.5 % of the world production of crustaceans and 15.3% of the world halieutic production. These crustaceans dominated by shrimps are marketed in the world and occupy the second rank after fish, representing 21.7% of the total sales of

the major fishery groups [1]. It now represents 84.1% of the live weight of all crustaceans in the world [2]. In Benin, inland fishing accounts for 80% of the national fishery and is one of the main income-generating activities for the populations living along the water bodies and rivers [3]. The main source of fishing is Lake Nokoué, which until 2003 provided more than 80% of the total fisheries production (29,734 tons) of the water bodies of the three departments of southern Benin [4]. The share of the shrimp's fishery from Lake Nokoué is estimated at two-thirds of the total shrimp's supply, the share from Lake Ahémé and the Porto Novo lagoon combined was one-sixth, and the remaining one-sixth came from other small lakes in Benin [5]. The literature has reported in Benin the presence of four (04) families whose part of their life cycle is common to the environment of Lake Nokoué. These are potentially: Penaeidae (*Penaeus*); Palaemonidae (*Macrobrachium*); Atyidae (*Atya*) and Desmocarididae (*Desmocarid*) [6-9]. The main shrimp's species caught in lake Nokoué is *Penaeus notialis* followed by *Penaeus monodon*, *Penaeus kerathurus* and some freshwater shrimp's species such as those of the genus *Macrobrachium* [4,8,10]. The species *Penaeus notialis* accounted for more than 97% of the total shrimp's production in the country. It is also caught in other West African countries such as Ivory Coast, Senegal, Madagascar, Cameroon and Nigeria [10, 11]. On the economic level, shrimp fishing in Benin has appeared in several studies among the six best sectors, presenting assets for economic growth [12]. From the start of shrimp exports around 1993, until 2002 when shrimp fishing reached its peak, shrimp fishery production was about 7,000 tons for a value of 3.2 billion CFA francs, or about 49 million euros [13, 14]. Shrimps had become the second most important export product after cotton by 2002 [10]. The shrimp sector provided income to 45,000 fishermen, 18,500 women intermediate traders, 150 collectors recognized by exporting companies, 50 permanent employees and 1,200 seasonal employees (mainly women) of exporting companies: DIAX, CRUSTAMER, SOBEP and FSG [10, 15, 17]. In total, the shrimp sector has created nearly 65,000 jobs [17]. When dependents are included, then this sector contributed to the livelihoods of about 250,000 people in Benin or 4% of the Beninese population [10]. Shrimp exports declined rapidly since 2003 due to poor management and lack of regulation of exporting companies (reasons highlighted by the Food and Veterinary Office/EU in 2002). Thus, Benin launched a self-suspension of shrimp exports to the European Union in June 2003. Despite the lifting of this self-suspension in 2005, the shrimp export sector is struggling to resume. Indeed, statistical data clearly show that the quantity of shrimps exported from Benin has dropped from 630 tons in 2002 to 1.5 tons in 2009 [10]. Recent investigations have shown a lack of monitoring of shrimp exports from Benin with strong pressure from local fishermen on Lake Nokoué throughout the year [13, 14, 18]. It is therefore imperative to improve our knowledge on the seasonal distribution of shrimps between the tributaries (So; Ouémé) of Lake Nokoué and the sea for action planning of good management of the shrimp industry in Benin. Located in southeastern Benin, the lake Nokoué, which is the subject of this study, represents the largest area (150 km²) of brackish

water in Benin [19]. The lake is in direct communication with the sea through the channel and has two main contributory rivers (Ouémé River and the Sô River), this results in a circulation whose direction alternates with the seasons. The exchange of water between Lake Nokoué and the sea gives rise to significant variations in certain parameters, in particular the salinity of the lake [20, 21]. The seasonal variation in the salinity of Lake Nokoué alternately confers a favourable environment for *Penaeus* (saltwater shrimp) and certain Caridean freshwater shrimp [22]. The main scientific question we are trying to solve in this study is: What should be the potential spatio-temporal distribution of these different shrimp species in Lake Nokoué and the Cotonou channel? To answer this question, we first present a review of the literature on the shrimp species found in southern Benin and their life cycle in the natural environment. Secondly, we will evaluate their potential spatio-temporal distribution in the Lake Nokoué-Cotonou channel complex, by comparing the evolution of the salinity of this complex with their affinity to live in a more or less saline environment. This work aims to complete the information related to the distribution of shrimp found in southern Benin, in order to propose avenues for their management for the Lake Nokoué-Ocean system.

Material and methods

Study area

The study setting in this work is the entire Lake Nokoué-Ocean system (Figure 1). Located in south-eastern Benin between 6° 22' N and 6° 30' N and 2° 20' E to 2° 35' E, the Lake Nokoué covers an area of 150 km². This lake is located in a sub-equatorial climate characterized by a long rainy season concentrated between mid-March and mid-July, a short dry season observed between mid-July and mid-September, a short rainy season between mid-September and mid-November, and long dry season between mid-November and mid-March [23]. The average annual water temperature is 27-29 °C and the average annual rainfall is 900-1100 mm [19, 24]. Lake Nokoué is mainly fed with freshwater by tributaries (Ouémé River and Sô River) and it is connected to the brackish ecosystem of Porto-Novo lagoon via the "Totchè" canal to the Atlantic Ocean, via the artificial channel that is the Cotonou channel [25]. The Cotonou channel contributes mainly to the hydrological and environmental fluctuations of the lake. The main tributaries of Lake Nokoué are:

- The Ouémé, with a catchment area of 46,500 km² and a length of 523 km, crosses the country from north to south. In terms of fresh water supply, it is largely influenced by the rainfall of its upper basin (Upper Ouémé);
- The Sô, with a catchment area of 1,000 km² and a length of 70 km, is connected to the Ouémé River in high water and maintains a good level of flow in the dry season;
- The Cotonou channel is 4.5 km long, 300 m wide and between 5 and 10 m deep. It is the sea water tributary of Lake Nokoué.

Review of the literature

The objectives of the literature review were:

- To list the shrimp species that are present in the southern Benin region and in Lake Nokoué.
- To synthesize the available knowledge on the life cycle of these different species.
- To evaluate the influence of chemical and physical parameters such as salinity, hydrology and bathymetry on the distribution of shrimp throughout the Lake Nokoué - Ocean complex.

Information related to shrimp species life cycles, breeding seasons, migrations and affinities were obtained from the databases <https://scholar.google.com/>; <http://www.ask.com>; <http://www.freefullpdf.com/>; <http://www.aginternetwork.org>; with the combination of the following keywords: Caridea, Penaeoidea, Penaeidae, Palaemonoidea, Atyidae, *Macrobrachium*, *Desmocarid*, *Atya*, *Penaeus*, migration, reproduction, classification, distribution, ecology, shrimp, fresh, water, salt, cycle, annual, salinity, biology, West, African, coast, Benin. In addition, reports, dissertations and theses were also consulted in the libraries of the Ministry of Agriculture of the Universities and the Directorate of Fisheries of Benin and, the World Register of Marine Species Database (WoRMS 2022,

<http://marinespecies.org/>) was used to update the data related to the classification of shrimp species. A total of 105 theses, 375 scientific articles and 80 technical reports were consulted, whose only 12, 44 and 20 respectively were used. The choice to use them or not was guided by the relevance of the documents that address the topic.

In-situ data and analysis

Salinity and bathymetry data of the Lake Nokoué - Cotonou channel complex was obtained during monthly campaigns carried out at 54 sampling stations (**Figure 1**) by the “Institut de Recherche Halieutiques et Océanologiques du Bénin” (IRHOB) in collaboration with the “Institut de Recherches et de Développement” (IRD) between November 2017 and August 2018 (<http://nodc-benin.odinafrica.org/nous-joindre.html>). Vertical profiles were conducted each month to determine depth and salinity using a CTD (Conductivity-Temperature-Depth) probe at each of the 54 stations using a motorized boat. A GPS was used to acquire the geographic coordinates of all sampling stations. For the analysis, monthly surface and bottom salinity data have been interpolated over a 1 km x 1 km grid. Monthly depth data were averaged to obtain the average depth of each station, and then interpolated on the same grid. The Matlab software was used to produce the salinity and bathymetry maps.

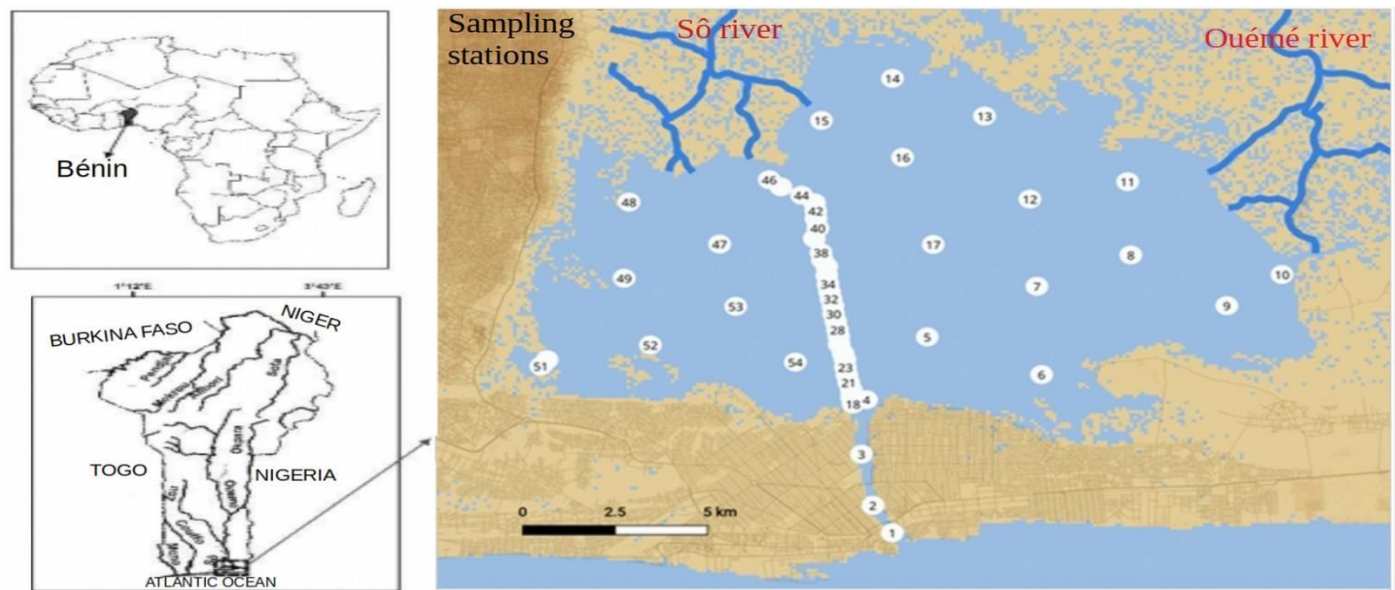


Figure 1: Map of the area of interest and position of the sampling stations on Lake Nokoué and in the Cotonou channel.

Results

Shrimp species present in southern Benin and their life cycle

Penaeidae

The Penaeidae of the genus *Penaeus* adopt an anadromous

migration linked to their reproductive cycle (**Figure 2, left**). On the other hand, others carry out their complete cycle at sea [26]. Two groups of species of Penaeidae are reported from Benin: deepwater shrimp: *Parapenaeus longirostris* and coastal shrimp: *Penaeus notialis*, *Penaeus kerathurus* *Penaeus monodon*, *Holthuispenaeopsis atlantica*, *Metapenaeopsis miersi* [7, 8, 9, 27, 28].

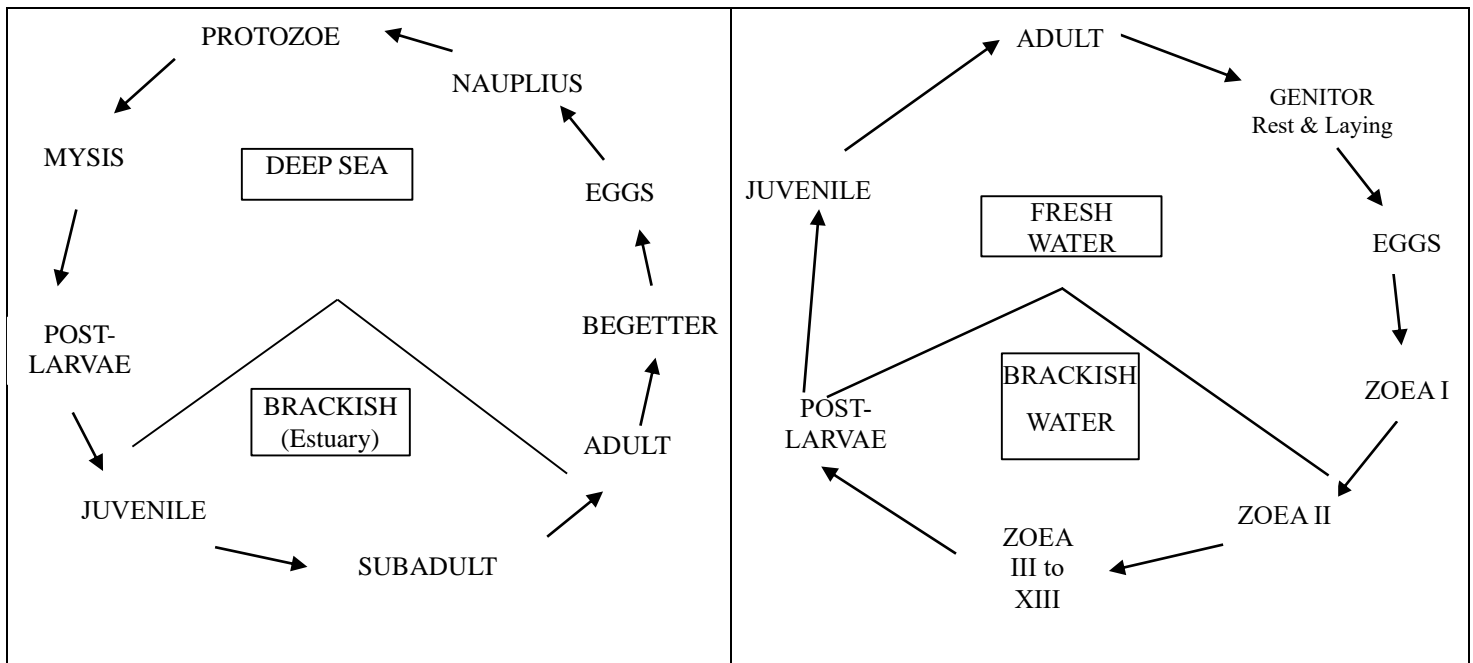


Figure 2: Modified life history diagram of *Penaeus* (left) [7, 26, 29] and diagram of most freshwater shrimp such as the genus *Macrobrachium* and *Atya* (right) [22, 30, 31].

Palaemonidae

Belonging to the superfamily Palaemonoidea, the Palaemonidae Rafinesque, 1815 represents one of the few groups of decapods that have colonized estuaries and rivers in subtropical and tropical regions. Some species of the family Palaemonidae perform a catadromous migration (Figure 2, right) [22]. Others perform an anadromous migration, however some species of the same family as Palaemonidae make their complete life cycle in the sea and others entirely in fresh water. Moreover, the genus *Macrobrachium* is the most diverse of the family Palaemonidae [32, 33] with currently 256 species described worldwide. In West Africa, there are eleven (11) described species: These are *M. chevalieri* Roux, 1935; *M. dux* Lenz, 1910; *M. felicinum*; *M. macrobrachion*; *M. raridens*, *M. rosenbergii*; *M. sollaudii*; *M. thysi*; *M. vollenhovenii*; *M. equidens* and *M. zariquieyi* [9, 34-36]. Its distribution is pantropical, covering the lowlands of Africa, Asia, Oceania, North, Central and South America. Seven species have been reported from Beninese waters: *M. dux* Lenz, 1910; *M. felicinum*; *M. vollenhovenii*; *M. macrobrachion*; *M. raridens*; *M. sp1* and *M. sp2* [6, 9, 37]. Other species of the family Palaemonidae such as *Palaemon maculatus* have also been reported along the West African coast but not specifically in Benin [9, 38].

Atyidae

Belonging to the superfamily Atyoidea, the Atyidae now includes 46 genera. The genus *Atya* is characterized by a

catadromous life cycle similar to that carried out by most shrimp of the genus *Macrobrachium* (Figure 2, right) [39,40]. The genus *Atya* has fourteen described species, four of which inhabit West African freshwaters: *A. africana*; *A. gabonensis*; *A. intermedia* and *A. scabra* [35, 41]. Two of them have been reported in Beninese Rivers: *A. africana*, *A. gabonensis* [6]. The genus *Caridina* is represented today in the world with 332 species (<http://marinespecies.org/>). The genus *Caridina* could be found in Lake Nokoué, particularly the species *C. togoensis* which is more widespread in Africa but not specifically in Benin [42].

Desmocarididae

The Desmocarididae family is characterized by a life cycle exclusively in freshwater, i.e., in an environment favourable to the plant *Eichhornia crassipes*. According to [33], the Desmocarididae are found in freshwater. This family contains only the genus *Desmocarididae* with currently two species (*D. bislineata* and *D. trispinosa*) including one found in Benin, which is *D. trispinosa* [6].

Life cycle of each shrimp species found in southern Benin

Table 1 presents a general summary of the life cycle of shrimp species found in southern Benin. This review was made on the basis of available information along the West African coast from Sierra Leone to Angola.

Species	Areas and periods of reproduction	Larval requirement	Affinity of juveniles	Adult Affinity	Preferred depth
Penaeidae					
<i>Penaeus monodon</i>	In the sea; continuous reproduction with a peak between July and March [43]	Sea water [7,44]	Brackish water [7]	Sea water [7]	Can exceed 30m [7]
<i>Penaeus kerathurus</i>	In the sea; continuous reproduction with a peak from May to mid-Novembre [7]	Sea water [7]	Brackish water [7,44]	Sea water [7,44]	5-50m [7]
<i>Penaeus notialis</i>	In the sea; continuous reproduction with a peak between July and December [45,46,47,48]	Sea water [7,44]	Brackish water [7]	Sea water [7] (10 – 75m [7] 2011)
<i>Parapenaeus longirostris</i>	Offshore; Continuous breeding with a peak from November-April [7,9]	Sea water [7,9]	Sea water [7,9]	Sea water [7,9]	100 – 400m [7,9]
<i>Holthuispenaeopsis atlantica</i> <i>Metapenaeopsis miersi</i>	Offshore; Almost continuous all year l'année [9,43,50,51]	Sea water [7,9,44]	Sea water [7,9]	Sea water [7,9]	10 – 40m [7,9]
Palaemonidae					
<i>M. dux</i> ; <i>M. felicinum</i> ; <i>M. vollenhovenii</i> ; <i>M. macrobrachion</i> ; <i>M. raridens</i> ; <i>M. sp1</i> and <i>M. sp2</i>	Lake, lagoon, river or estuary; with a peak during the rainy season pluies [22,30,52,53]	Brackish water Eau saumâtre [30,52,54]	Fresh water [30,52]	Fresh water [30,52]	---
<i>Palaemon maculatus</i>	Offshore; Almost continuous all year [9]	Sea water, [9]	Brackish water or Sea water [9]	Brackish water or Sea water	Coastal water Up to 50 m [9]
Atyidae					
<i>Atya gabonensis</i> ; <i>Atya africana</i>	Lake, lagoon, river or estuary; with a peak during the rainy season [39,40,50,55]	Brackish water [39,40,55]	Fresh water [39,50,55]	Fresh water [39,40,50,55]	---
Desmocarididae					
<i>Desmocarid trispinosa</i>	River, lake or other freshwater. [50,55]	Fresh water [50,55]	Fresh water [50,55]	Fresh water [50,55]	---

Table 1: Life history of shrimp species reported in southern Benin.

Relationship between the life cycle of shrimps and the geochemical characteristics of Lake Nokoué.

Bathymetry of Lake Nokoué - Cotonou channel

The depth data allowed us to produce a bathymetric map of Lake Nokoué which showed that the relative elevation of the water level varies between 2 m and 3.2 m on average in the

centre of the lake. The depth of the lake varies between 1 m and 2 m to the east and west of the lake. In the north, the depth is between 1 m and 1.6 m, whereas it is close to 3 m in the centre of the lake and in the south of Lake Nokoué near the Cotonou channel. The depth in the Cotonou channel varies between 4 m and 6 m on average (Figure 3). In general, Lake Nokoué has a fairly flat bottom with a very shallow depth. Shrimps are benthic already from the juvenile stages [26, 29, 43, 57].

Therefore, the bathymetric characteristics of Lake Nokoué are suitable for a homogeneous distribution of shrimps because the

relatively flat bottom should not favour a strong accumulation of organic debris in a deeper zone.

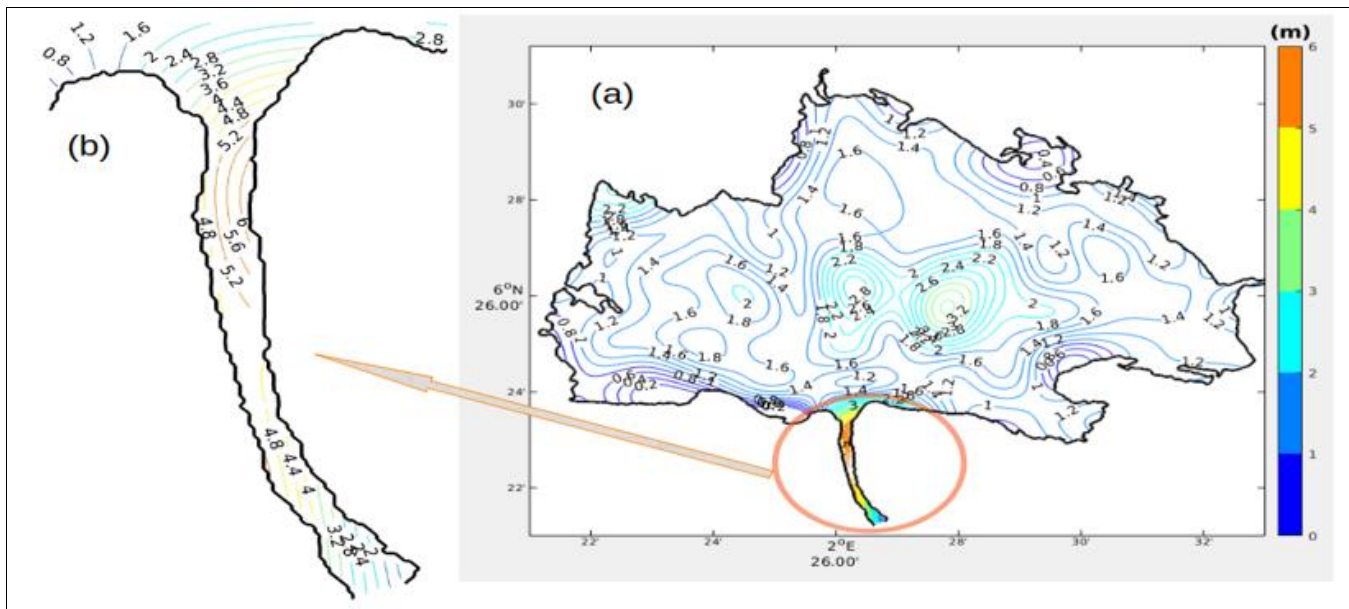


Figure 3: Bathymetry of Lake Nokoué (a) and the Cotonou channel (b).

Seasonal evolution of salinity in Lake Nokoué-Cotonou channel

The interpolated data allowed to generate maps of the spatio-temporal distribution of salinity in the basin of the Lake Nokoué-Cotonou channel complex (Figure 4, 5). These maps showed in December the beginning of saline intrusion from the Atlantic Ocean via the Cotonou channel, on both surface (Figure 4) and bottom (Figure 5). This entry of sea water into Lake Nokoué is progressively increasing from the southern part (entrance to the channel) and progressively extending to the northern side of the basin. This saline intrusion continues to reach the western side first, then progressively the northern and eastern sides of the basin, during the month of January, due to the flow of the Sô River and the Ouémé River. The highest salinity level of the lake is observed in April. During this period, the salinity values of the lake are almost oceanic on the surface

as well as on the bottom (salinity > 30 PSU). Lake Nokoué is then more subject to tidal currents than to the low flow of the lake's tributaries, notably the Sô and Ouémé rivers (Figure 4, 5). During the rainy season mid-April to mid-August (Figure 7), there is a significant increase in the flow of the rivers flowing into Lake Nokoué, and the surface salinity of the lake and the channel begins to fall from May to reach very low values between July and August. This desalination of the lake occurs more rapidly on the northeast side than on the southwest side of the basin where a portion of the water on the west side and in the channel remains slightly salty in July. Maps of spatial distributions of salinity show that, overall, the bottom of the lake is proportionally saltier than the surface (Figure 5). During the December-January period, the salinity of the lake increases with the exception of the areas located at the mouth of the Sô and Ouémé rivers which continue to have a low flow into the lake, despite the end of the rains (Figure 7).

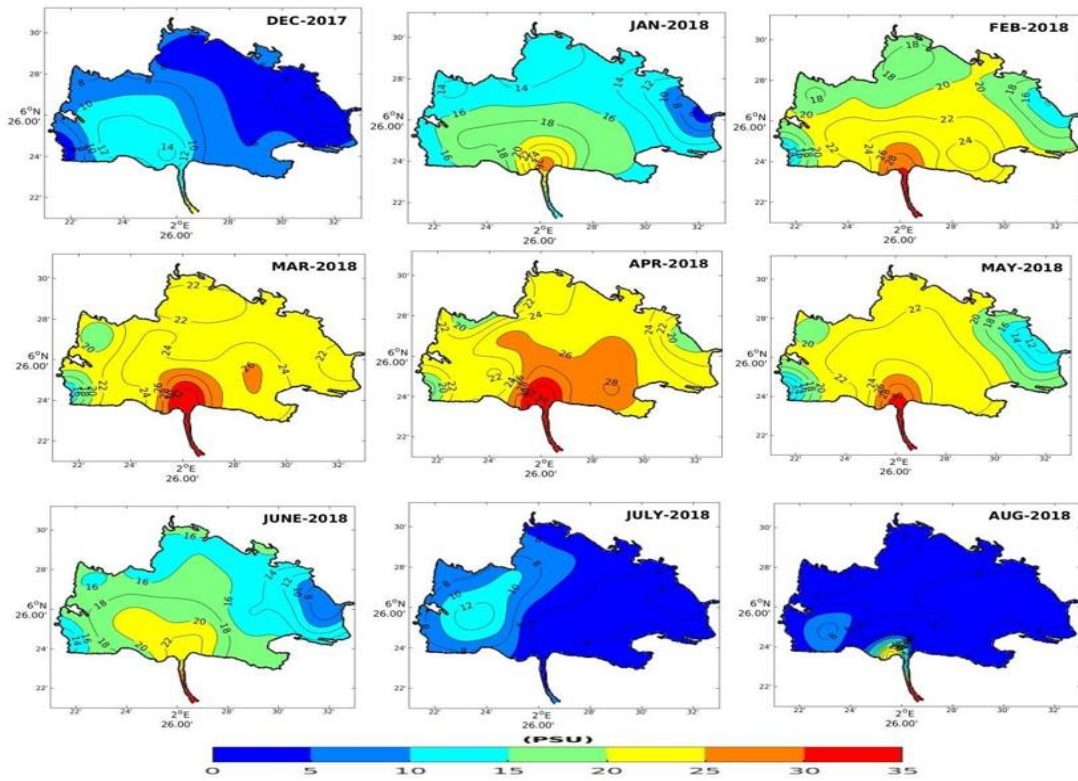


Figure 4: Seasonal distribution of surface salinity in Lake Nokoué and the Cotonou channel

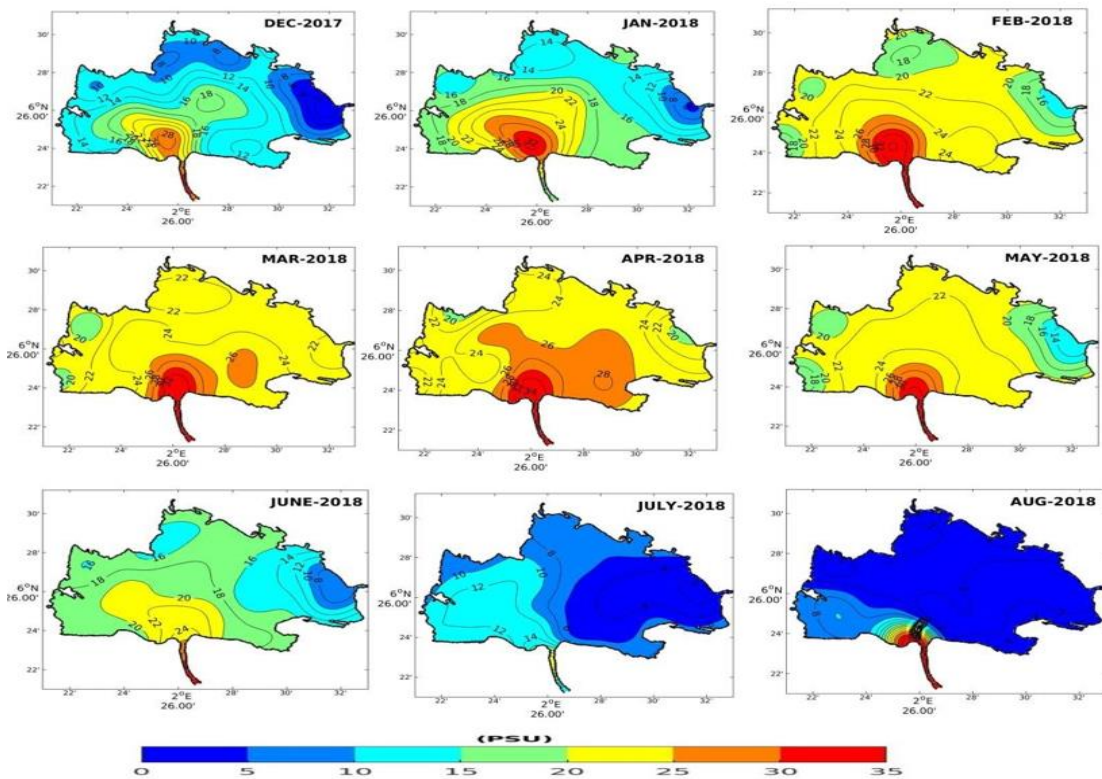


Figure 5: Seasonal distribution of bottom salinity in Lake Nokoué and the Cotonou channel.

Evaluation of the spatio-temporal distribution of different shrimp species according to the bottom salinity in the complex composed of Lake Nokoué and the Cotonou channel

The spatio-temporal distribution of salinity is a determining factor in the spatio-temporal distribution of species in the lake-channel complex. From knowledge about life cycle of the shrimp species, and especially on their affinity for salinity, it appears that the bottom salinity of Lake Nokoué remains favourable for species of the genus *Penaeus* during the months of December to June (Figure 2 left, 5, and 6). The appearance of juvenile *Penaeus* (*Penaeus notialis*, *Penaeus kerathurus* and *Penaeus monodon*) and possible species *Palaemon maculatus* in the channel and Lake Nokoué can already start in December when the salinity of the bottom is higher than 20 PSU in some places. The return to the sea of these species should start in June with the decrease of the salinity of the lake and that of the channel of Cotonou, following the strong entry of fresh water from the Ouémé and Sô rivers. This massive inflow of fresh water into lake Nokoué should lead to the migration of species

of the genus *Macrobrachium* (*M. dux*; *M. felicinum*; *M. vollenhovenii*; *M. macrobrachion*; *M. raridens*; *M. sp*) and those of the genus *Atya* (*A. africana* and *A. gabonensis*) that are entering their reproductive period to lake Nokoué (Figure 2 right, 5, and 6). Adults of the genera *Macrobrachium* and *Atya* have an affinity with the fresh water of Lake Nokoué during the months of August to November and begin their migration from Lake Nokoué to the Ouémé River in December (Figure 2 right, 5, and 6). The larvae of the *Macrobrachium* and *Atya* species are forced to remain in the brackish waters of Lake Nokoué from December to June, until they reach the post-larval stage to have a chance to survive (Figure 2 right and 5). As for the *Desmocarid* species (*D. trispinosa*), which carries out its entire life cycle in the freshwater tributaries of Lake Nokoué and can only pass-through Lake Nokoué during the period from August to November when the environment is favourable for the development of the *Eichhornia crassipes* plant (freshwater). Tables 1 and 2 and Figure 6 summarises the annual migration of shrimp species through the tributaries, Lake Nokoué and the Cotonou channel in Benin.

Espèces	Stades	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sept	Oct	Nov	Dec
Penaeidae													
<i>Penaeus monodon</i> ; <i>Penaeus kerathurus</i> ; <i>Penaeus notialis</i>	Larvae	+S	+S	+S	+S	+S	+S	+S	+S	+S	+S	+S	+S
	Juveniles & Subdults	+Ln	+Ln	+Ln	+Ln	+Ln	+Ln	±Ln	-Ln	-Ln	-Ln	-Ln	+Ln
	Adults	+S	+S	+S	+S	+S	+S	+S	+S	+S	+S	+S	+S
Palaemonidae													
<i>M. dux</i> ; <i>M. felicinum</i> ; <i>M. vollenhovenii</i> ; <i>M. macrobrachion</i> ; <i>M. raridens</i> ; <i>M. sp1</i> & <i>M. sp2</i>	Larvae	+Ln	+Ln	+Ln	+Ln	+Ln	+Ln	±Ln	-Ln	-Ln	-Ln	-Ln	±Ln
	Juveniles & Adults	-Ln	-Ln	-Ln	-Ln	-Ln	-Ln	±Ln	+Ln	+Ln	+Ln	+Ln	±Ln
Atyidae													
<i>Atya gabonensis</i> ; <i>Atya africana</i>	Larvae	+Ln	+Ln	+Ln	+Ln	+Ln	+Ln	±Ln	-Ln	-Ln	-Ln	-Ln	±Ln
	Juveniles & Adults	-Ln	-Ln	-Ln	-Ln	-Ln	-Ln	±Ln	+Ln	+Ln	+Ln	+Ln	±Ln
Desmocarididae													
<i>Desmocarid trispinosa</i>	Larvae	-Ln	-Ln	-Ln	-Ln	-Ln	-Ln	-Ln	±Ln	+Ln	+Ln	±Ln	-Ln
	Juveniles & Adults	-Ln	-Ln	-Ln	-Ln	-Ln	-Ln	-Ln	±Ln	+Ln	+Ln	±Ln	-Ln

Note: +S = Present at sea; +Ln = Present in lake Nokoué; -Ln = Absent in lake Nokoué; ±Ln = Present or absent in lake Nokoué

Table 2: Life cycle assessment of shrimp species reported in southern Benin through the lake Nokoué - Ocean complex in Benin.

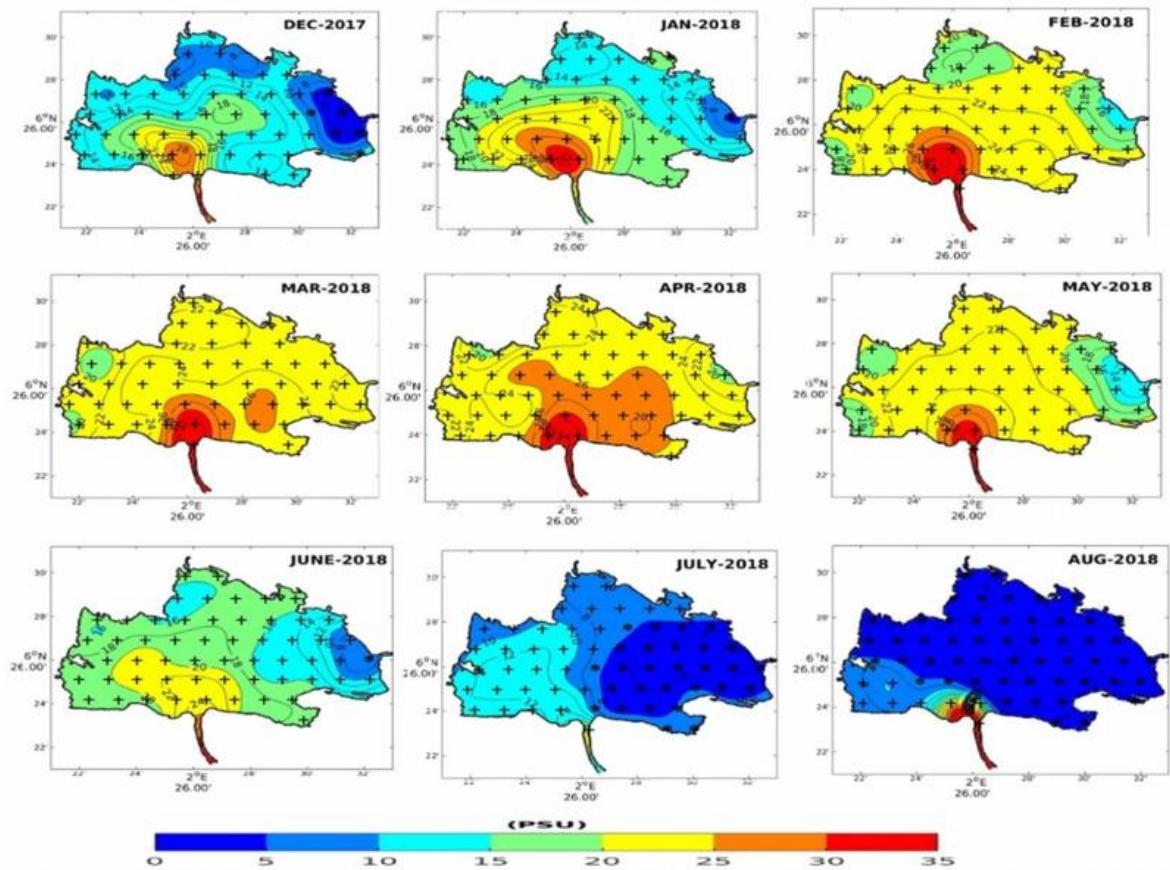


Figure 6: Seasonal distribution of shrimp according to bottom salinity in Lake Nokoué and the Cotonou Channel. (*Penaeus*)+; (*Macrobrachium*, *Atya*, *Desmocarid*) *

Discussion

The bathymetry of Lake Nokoué is rather shallow and doesn't show a lot of variation. These results are consistent with those of [58, 59]. The depth of the lake is not expected to influence the distribution of shrimps because, according to the work of [60], it is the nature of the area substrate (dead wood and leaves, invertebrates, and other organic matter) that attracts shrimp and not the depth, even though in deep areas, more debris is present. The shallow depth gives Lake Nokoué the characteristics of a polymictic lake. Thus, Lake Nokoué should regularly undergo mixing. This would prevent any kind of temperature or salinity stratification. However, maps of spatial distributions of salinity in lake Nokoué and the Cotonou channel showed that the bottom of the lake is proportionally more saline over time than the surface of the lake (Figure 4 and 5). These results could be explained by the tidal pressure on Lake Nokoué at the time of saline intrusion. This tidal pressure affects the bottom water compartment before rising to the surface with time [61]. The results of this study allowed us to evaluate the period of shrimp settlement in the lake. Indeed, from December to June, the salinity of lake Nokoué increases, which indicates a favourable environment for *Penaeus* juveniles: *Penaeus monodon*, *Penaeus kerathurus*, *Penaeus*

notialis and possible species *Nematopalaemon hastatus*, *Palaemon elegans* and *Palaemon maculatus*, but also an essential environment for the survival and development of larvae of the *Macrobrachium* species: *M. dux*, *M. felicinum*, *M. vollenhovenii*, *M. macrobrachion*, *M. raridens*, *M. sp*; and of the genus *Atya*: *Atya gabonensis*; *Atya africana* (Table 1) [7, 22, 40, 54]. These results are confirmed by the results of four months of sampling of Penaeidae conducted by [8] on Lake Nokoué. Juvenile *Penaeus* are, moreover, abundantly caught in Lake Nokoué from December onwards, as soon as the period of saline intrusion starts [8]. As for the hatching of the eggs of these *Penaeus* (reproduction), it must therefore take place at sea a few weeks before. On this basis, we estimated that the period of peak reproduction of *Penaeus* would extend from August to November. Comparing these results with other studies [62-64], it is concluded that the same species of the family Penaeidae could have different reproduction periods in different geographical areas. [65], who studied the biology, reproduction and population dynamics of the deep-water shrimp *Parapenaeus longirostris* at the level of the Algerian west coast (port of Oran and Arzew), showed that the period of strong reproduction observed in *Parapenaeus longirostris* extends from May to June. This same period has been widely described for *P. longirostris* in the western Mediterranean, suggesting a minimal reduction mechanism of intra-specific competition

[63, 66]. The reproductive period observed for *P. longirostris* in the waters of the Algerian western coast coincides with other studies carried out in the western Mediterranean (Merbah, 2002) as well as in Italy and Portugal [63, 67]. In contrast, in Senegal, the egg-laying period in *P. longirostris* is spread over the whole year with two distinct peaks: the most important in winter (February-March) and the second in autumn, October-November [64]. For [68], oviposition in *P. longirostris* occurs between December and January, with the months of June to August corresponding to the sexual rest period with a resumption of ovarian maturation in September. These differences in the observation of the reproductive period of the same species could be explained by the inequality of climate observed between the West African side and the Algerian west coast. Thus, the high temperature highlighted as a factor influencing reproduction by [69], indicates that spawning takes place in *P. longirostris* in the cold season and in the warm season. In the context of this study, as the Lake Nokoué temperature varies only little (27° C - 29° C), the impact of temperature on the seasonal dynamics of shrimp reproduction has not been taken into account. In the framework of this work, the salinity maps of the basin indicate that freshwater shrimp of the genus *Macrobrachium*, *Atya* and *Desmocarid* have an affinity for Lake Nokoué during the months of August to November. This period of flooding of Lake Nokoué (August to November) marks the end of the rainy seasons in Benin. Since the arrival of freshwater shrimp in Lake Nokoué coincides with their reproduction, it is likely that the rainy season influences or contributes to initiate the gonad maturation period in freshwater shrimp. These results are consistent with those obtained by several researchers [52, 70, 71], who have located the period of egg laying and reproduction during these months based on the study of the ovarian cycle in some freshwater shrimps. According to these authors, the adults *Macrobrachium* live in the fresh waters of the rivers where the fertilization takes place, especially during the rainy season. Vitellogenesis, according to these authors, is linked to the rainy season and their migration to brackish waters. However, the species belonging to the genus *Macrobrachium* seem to have two different life cycles because, [72] observed that West African *Macrobrachium* can be divided into two categories: those with small and numerous

eggs and those with large and few eggs. He placed *M. dux* in the category of species with large and few eggs, as is the case with *M. potiuna* according to [36, 73] observed that species with small and numerous eggs, such as *Macrobrachium vollenhovenii* according to [54], have a much wider distribution than those with large and few eggs. [74] Reports many *M. dux* far inland from the sea in the Democratic Republic of Congo. He also mentions the large size of the eggs in these species. It is difficult to imagine that these shrimps could make migrations of several hundred kilometers to the sea and one must therefore assume that their development is entirely in fresh water. Authors like [75] indicate that the species genera *Macrobrachium* with large and numerous eggs have a shortened development taking place entirely in fresh water and is met far from the estuaries, while the species with small and numerous eggs have a long larval development taking place in estuarine medium. In addition, species of the genus *Caridina*, which is a freshwater shrimp with a life cycle similar to that of *Macrobrachium*, could also be found in Lake Nokoué, in particular the species *C. togoensis*. But this rather difficult genus continues to create confusion on the systematic level. Indeed, eighteen species of *Caridina* have been described by [42]. According to the same author, only *C. togoensis* is more widespread in Africa and could be found in Benin while *C. africana* has a limited distribution in South Africa. However, [76] recently revealed that all of these descriptions by [42], are nothing more than subspecies of *C. africana* because of the representativeness of the samples described. We believe in this work that there is a real need for signalling of *Caridina* in Benin before any suggestions. Rainfall also seems to have a determining role in the beginning and end of saline intrusion through the tributary - Lake Nokoué - ocean complex (Figure 7). Indeed, the beginning of the saline intrusion indicates, according to Météo-Benin data, the end of the short rainy season in Cotonou (December 2017) (Figure 4, 5 and 7). The salinity of Lake Nokoué reaches its peak in April, (period corresponding to the beginning of the long rainy season in Cotonou). We note that during the long rainy season (May 2018), the salinity of Lake Nokoué begins to decrease progressively and practically drops to zero during the short dry season (August 2018).

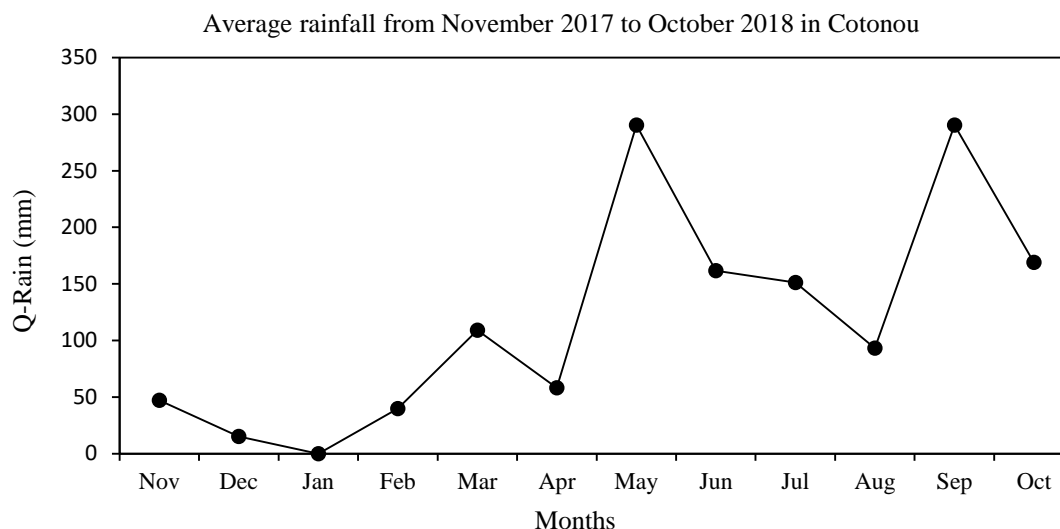


Figure 7: Rainfall in Cotonou from November 2017 to October 2018 (METEO-Bénin).

Conclusion

By combining information on the life cycle of shrimps found in southern Benin, from the literature, with the spatio-temporal distribution of salinity in the Lake Nokoué-Cotonou channel complex, the evolution of the potential distribution of shrimp species in this complex could be established. The present work has shown that the salinity of Lake Nokoué increases from December to reach a peak in April. The period (December-June) of high salinity in the lake indicates a favourable environment for *Penaeus* and freshwater shrimp larvae such as *Macrobrachium* and *Atya*. Furthermore, the salinity of the water of Lake Nokoué remains very low during the months of August to November, which is the period favourable for the presence of adult freshwater shrimps. Based on the results obtained, we suggest a ban on fishing in Lake Nokoué between December and February. Based on the life cycle of the *Penaeus*, the beginning of the saline intrusion corresponds to the appearance of juveniles that have not reached sexual maturity. Therefore, fishing between December and February gives less chance to a part of the *Penaeus* to make their reproductive return to the sea. Secondly, we suggest a ban on shrimp fishing in the Cotonou channel, given that the channel constitutes the only way for the *Penaeus* to go to and from the lake and the ocean. These two previous recommendations could contribute to a better regulation of the fishery in the Lake Nokoué-channel complex for a sustainable management of the shrimp stock. Complementary studies are underway to evaluate *in situ* the presence and relative abundance of these species in the Lake Nokoué-Chenal complex and to further investigate their spatio-temporal distribution based on the physical and chemical parameters of the lagoon system. Future research will compare the current faunal richness of the Lake Nokoué-channel complex with that indicated by the literature in southern Benin in general years ago.

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