

Evaluation of the Distribution of Shrimp Species Found in Southern Benin Through the Lake Nokoué-ocean Complex

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Abstract

Background

The export of shrimp 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 production in lake Nokoué since 2003. To remedy this problem, it is necessary to hypothesize on their spatio-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 spatio-temporal evolution of salinity obtained from *in-situ* observations.

Results

The literature review recognizes the presence in southern Benin of species of the genus *Macrobrachium*, *Atya* and *Desmocarlis* (seven, two and one respectively) and five species of marine shrimps belonging to three genera: the genus *Penaeus*, the genus *Holthuispenaeopsis* and the genus *Parapenaeus*. From information on the ecology and physical environment it is shown that adults of the species of the genus *Macrobrachium* and genus *Atya* have a favorable environment in lake Nokoué from August to November, their larvae must remain in the lake from December to June to ensure their survival. The species of the genus *Desmocarlis*, 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* can find a favorable environment in lake Nokoué from December to June but their larvae can only survive in the sea. Finally, the species of the genus *Holthuispenaeopsis* and *Parapenaeus* spend their entire life cycle at sea.

Conclusions

This work allows understanding contrasted life cycles of shrimp's genera *Macrobrachium* and *Atya* compared to *Penaeus* in a complex ecosystem characterized by strong saline variation. This research allows to predict the presence or absence of shrimp's genera *Macrobrachium*, *Atya*, *Desmocarlis* and *Penaeus* in a lake system, on the basis of salinity distribution, for a sustainable management of their exploitation.

Background

The shrimp industry today occupies a prominent place in the world because of its high commercial value. Shrimps represent 73,17% of the world production of crustaceans and 6% of the world halieutic production. Crustaceans account for 21.7% of total sales of the major fishery groups [20]. 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 [48]. 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 [60]. The share of the shrimp fishery from lake Nokoué is estimated at two-thirds of the total shrimp 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 [6]. In total, four families of shrimp are found in southern Benin: Penaeidae, Palaemonidae, Atyidae and Desmocarididae [27, 31, 59]. The main shrimp species caught in lake Nokoué is *Penaeus notialis* followed by *Penaeus monodon*, *Penaeus kerathurus* and some freshwater shrimp species such as those of the genus *Macrobrachium* [27, 29, 60]. The species *Penaeus notialis* accounted for more than 97% of the total shrimp production in the country. It is also caught in other West African countries such as Ivory Coast, Senegal, Madagascar, Cameroon and Nigeria [18, 29, 55]. On the economic level, shrimp fishing in Benin has appeared in several studies among the six best sectors, presenting assets for economic growth [30]. 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 [4, 38]. Shrimp had become the second most important export product after cotton by 2002 [29]. 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 [11, 29, 33]. In total, the shrimp sector has created nearly 65,000 jobs [56]. When

dependents are included, then this sector contributed to the livelihoods of about 250,000 people in Benin or 4% of the Beninese population [29]. Shrimp exports declined rapidly since 2003 because of its management, specifically the lack of sanitary standards and regulations (reasons highlighted by the Food and Veterinary Office/European Union 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 [29]. Recent investigations have shown that shrimp exports from Benin remain almost non-existent due to poor fisheries management [4, 38, 47]. For the moment, the real causes of this decline are not well understood. Some find that overfishing related to the increased use of traditional fishing systems "Acadja and medokpokonou" have contributed to the decline in resources [29]. For [56] the pollution of these fishing water bodies have led to a depletion of these streams in fishery products. 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 [40]. The lake is in direct communication with the sea through the channel and has two main tributary 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 [17, 25]. The seasonal variation in the salinity of lake Nokoué alternately confers a favourable environment for *Penaeus* (saltwater shrimp) and certain Caridea (freshwater shrimp) [26]. The main scientific question we are trying to solve in this study is: What is 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 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. The presented work provides an update of current knowledge on the distribution of shrimp in lake Nokoué through the Cotonou channel. This work aims to complete the information related to the distribution of shrimp found in southern Benin, in order to propose avenues for their conservation for the development of the lake Nokoué-Ocean system.

Results

Shrimp species present in southern Benin and their life cycle

Penaeidae

Belonging to the superfamily Penaeoidea and the family Penaeidae, species of the genus *Penaeus* adopt an anadromous migration related to their reproductive cycle (Fig. 1, left). In contrast, other Penaeidae complete their cycle at sea [44]. Two groups of marine shrimps are found along the West African coast: deep water shrimps: *Parapenaeus longirostris*, *Aristeus varidens*, *Plesionika martia*, *Heterocarpus ensifer* and *Plesiopenaeus edwardsianus* and coastal shrimps: *Penaeus notialis*, *Penaeus kerathurus*, *Penaeus monodon* and *Holthuispenaeopsis atlantica* [63]. In Benin, there are five species belonging to the family Penaeidae: *Penaeus monodon*; *Penaeus notialis*; *Penaeus Kerathurus*; *Holthuispenaeopsis atlantica* and finally *Parapenaeus longirostris* [21, 27, 59].

Palaemonidae

Belonging to the superfamily Palaemonoidea, the Palaemonidae Rafinesque, 1815 represent one of the few groups of decapods that, in addition to the oceans, have succeeded in colonizing estuaries and rivers in subtropical and tropical regions (Fig. 1, right) thanks to a catadromous migration [26]. Furthermore, the genus *Macrobrachium* is the most diverse of the family Palaemonidae with currently 256 species described worldwide [16, 64, 70]. In West Africa, eleven species have been described [12, 27, 31, 43, 53]: These are *M. chevalieri*; *M. dux*; *M. felicinum*; *M. macrobrachion*; *M. ravidens*; *M. rosenbergii*; *M. sollaudii*; *M. thysi*; *M. vollenhoveni*; *M. equidens*; and *M. zariquieyi*. Its distribution is pantropical, covering the lowlands of Africa, Asia, Oceania, North, Central and South America. Seven species of the genus *Macrobrachium* are found in

Beninese waters, two of which are undescribed: *M. dux*; *M. felicinum*; *M. vollenhoveni*; *M. macrobrachion*; *M. raridens*; *M. sp1* and *M. sp2* [5, 31].

Atyidae

Belonging to the superfamily Atyoidea, the Atyidae are characterized by a life cycle similar to that of the Palaemonidae (Fig. 1 right). There are thirteen described species belonging to the genus *Atya* [70], four of which inhabit West African fresh waters: *A. africana*; *A. gabonensis*; *A. intermedia* and *A. scabra* [43, 49]. Two of them have been reported in Beninese rivers: *A. africana*, *A. gabonensis* [31].

Desmocarididae

Belonging to the superfamily Palaemonoidea, the family Desmocarididae is characterized by a life cycle exclusively in freshwater, i.e. in an environment favourable to the plant *Eichhornia crassipes*. According to [16], the Desmocarididae are found in freshwater. This family contains only the genus *Desmocarid* with currently two species including one found in Benin, which is *D. trispinosa* [31].

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.

Table 1 Life history of shrimp species found in southern Benin.

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 [32]	Sea water [18, 59]	Brackish water [21, 59]	Sea water [21, 59]	Can exceed 30m [21, 59]
<i>Penaeus Kerathurus</i>	In the sea; continuous reproduction with a peak from May to mid-November [21, 59]	Sea water [21, 59]	Brackish water [18, 21, 59]	Sea water [18, 21, 59]	5-50m [21, 59]
<i>Penaeus notialis</i>	In the sea; continuous reproduction with a peak between July and December [34, 35, 36, 37, 62]	Sea water [19, 21, 59]	Brackish water [21, 59]	Sea water [59, 21]	10 – 75m [21, 59]
<i>Parapenaeus longirostris</i>	Offshore; Continuous breeding with a peak from November-April [21, 59]	Sea water [21, 59]	Sea water [21, 59]	Sea water [21, 59]	100 – 400m [21, 59]
<i>Holthuispenaeopsis atlantica</i>	Offshore; Almost continuous all year [32, 51, 52]	Sea water [19, 21, 59]	Sea water [21, 59]	Sea water [21, 59]	10 – 40m [21, 59]
Palaemonidae					
<i>M. dux; M. felicinum; M. vollenhoveni; M. macrobrachion; M. raridens; M. sp</i>	Lake, lagoon, river or estuary; with a peak during the rainy season [13, 26, 65, 68]	Brackish water [57, 65, 68]	Fresh water [65, 68]	Fresh water [65, 68]	---
Atyidae					
<i>Atya gabonensis;</i> <i>Atya africana</i>	Lake, lagoon, river or estuary; with a peak during the rainy season [15, 23, 51]	Brackish water [15]	Fresh water [23, 51]	Fresh water [15, 51]	---
Desmocarididae					
<i>Desmocarid trispinosa</i>	River, lake or other freshwater. [15, 51, 52]	Fresh water [15, 51]	Fresh water [15, 51]	Fresh water [15, 51]	---

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 (Fig. 2). In general, lake Nokoué has a fairly flat bottom with a very shallow depth. Shrimps are benthic already from the juvenile stages [23, 44, 50, 54]. 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.

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 (Fig. 3, 4). These maps showed in December the beginning of saline intrusion from the Atlantic Ocean via the Cotonou channel, on both surface (Fig. 3) and bottom (Fig. 4). 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 (Figs. 3, 4). During the rainy season mid-April to mid-August (Fig. 6), 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 (Fig. 4). 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 (Fig. 6).

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 (Figs. 1 left, 4, and 5). The appearance of juvenile *Penaeus* (*Penaeus notialis*, *Penaeus Kerathurus* and *Penaeus monodon*) 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 of adult *Penaeus* to the sea should start in June with the decrease in salinity of the lake and the Cotonou channel, following the massive entry of fresh water from the Ouémé River and the Sô River. 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. vollenhoveni*; *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 (Figs. 1 right, 4, and 5). 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 (Fig. 1 right, 4, and 5). 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 (Figs. 1 right and 4). As for the *Desmocariss* 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 Fig. 5 summarises the annual migration of shrimp species through the tributaries, lake Nokoué and the Cotonou channel in Benin.

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

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

Species	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>	Juveniles	+Ln	+Ln	+Ln	+Ln	+Ln	+Ln	±Ln	-Ln	-Ln	-Ln	-Ln	+Ln
	Adults	±Ln	-Ln	-Ln	-Ln	-Ln	±Ln						
<i>Parapenaeus longirostris</i> ; <i>Holthuispenaeopsis atlantica</i>	Juveniles	+S	+S	+S	+S								
	Adults	+S	+S	+S	+S								
Palaemonidae													
<i>M. dux</i> ; <i>M. felicinum</i> ; <i>M. vollenhoveni</i> ; <i>M. macrobrachion</i> ; <i>M. raridens</i> ; <i>M. sp</i>	Larvae	+Ln	+Ln	+Ln	+Ln	+Ln	+Ln	±Ln	-Ln	-Ln	-Ln	-Ln	±Ln
	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
	Adults	-Ln	-Ln	-Ln	-Ln	-Ln	-Ln	±Ln	+Ln	+Ln	+Ln	+Ln	±Ln
Desmocarididae													
<i>Desmocariss trispinosa</i>	Larvae	-Ln	±Ln	+Ln	+Ln	±Ln	-Ln						
	Adults	-Ln	±Ln	+Ln	+Ln	±Ln	-Ln						

Discussion

The bathymetry of lake Nokoué is rather shallow and doesn't show a lot of variation. These results are consistent with those of [39, 69]. The depth of the lake is not expected to influence the distribution of shrimps because, according to the work of [46], 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 (Figs. 3 and 4). 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. 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*; but also an essential environment for the survival and development of larvae of the *Macrobrachium* species: *M. dux*, *M. felicinum*, *M. vollenhoveni*, *M. macrobrachion*, *M. raridens*, *M. sp*; and of the genus *Atya*: *Atya gabonensis*; *Atya africana* (Table 1) [26, 57, 59]. These results are confirmed by the results of four months of sampling of Penaeidae conducted by [27] on lake Nokoué. Juvenile *Penaeus* are, moreover, abundantly caught in lake Nokoué from December onwards, as soon as the period of saline intrusion starts [27]. 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 [41, 58, 61], it is concluded that the same species of the family Penaeidae could have different reproduction periods in different geographical areas. [9], 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 [1, 45, 58]. 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 [41] as well as in Italy and Portugal [8, 58]. 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 [61]. For [10], 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 [14], 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 *Desmocariss* 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 [42, 66, 67, 68], 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. Rainfall also seems to have a determining role in the beginning and end of saline intrusion through the tributary - lake Nokoué - ocean complex (Fig. 6). Indeed, the beginning of the saline intrusion indicates, according to Météo-Benin data, the end of the short rainy season in Cotonou (December 2017) (Figs. 3, 4 and 6). 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).

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. This 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. Our results have allowed us to assess the spatio-temporal distribution of shrimp species found in southern Benin, but also to evaluate their life cycle and seasonal migration through lake Nokoué and the ocean via the Cotonou Channel in Benin. This information, in conjunction with pluriannual field data that have started in 2020, will contribute to a better regulation of fishing in the lake Nokoué-Cotonou 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-Cotonou channel complex and to deepen their spatio-temporal distribution based on the physico-chemical parameters of the lagoon system. Future research will compare the current faunal richness of the lake Nokoué-Cotonou channel complex with that indicated by the literature in southern Benin in general years ago.

Methods

Study area

The study setting in this work is the entire lake Nokoué-Ocean system (Fig. 7). 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 [2, 3]. The average annual water temperature is 27-29 °C and the average annual rainfall is 900-1100 mm [7, 40]. Lake Nokoué is mainly fed with freshwater by tributaries (Ouémé river and Sô river) and it is connected to the brackish ecosystem of the Porto-Novo lagoon via the "Totchè" canal to the Atlantic Ocean, via the artificial channel that is the Cotonou channel [22]. 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.
- The raw data of the rainfall of Cotonou are obtained at the direction METEO-Benin against payment.

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/>; <https://www.aquaportail.com/> with the combination of the following keywords: 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 [70] 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, 41 and 17 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 were obtained during monthly campaigns carried out at 54 sampling stations (Fig. 7) by the IRHOB in collaboration with the 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 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.

Abbreviations

IRHOB: Institut de Recherche Halieutiques et Océanologiques du Bénin; IRD: Institut de Recherche et de Développement; CTD: Conductivity-Temperature-Depth; GPS: Global Position System

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Availability of data and materials

The datasets generated during and/or analysed during the current study are available from the corresponding author on request.

Competing interests

The authors declare that they have no competing interests.

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Authors' contributions.

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

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Figures

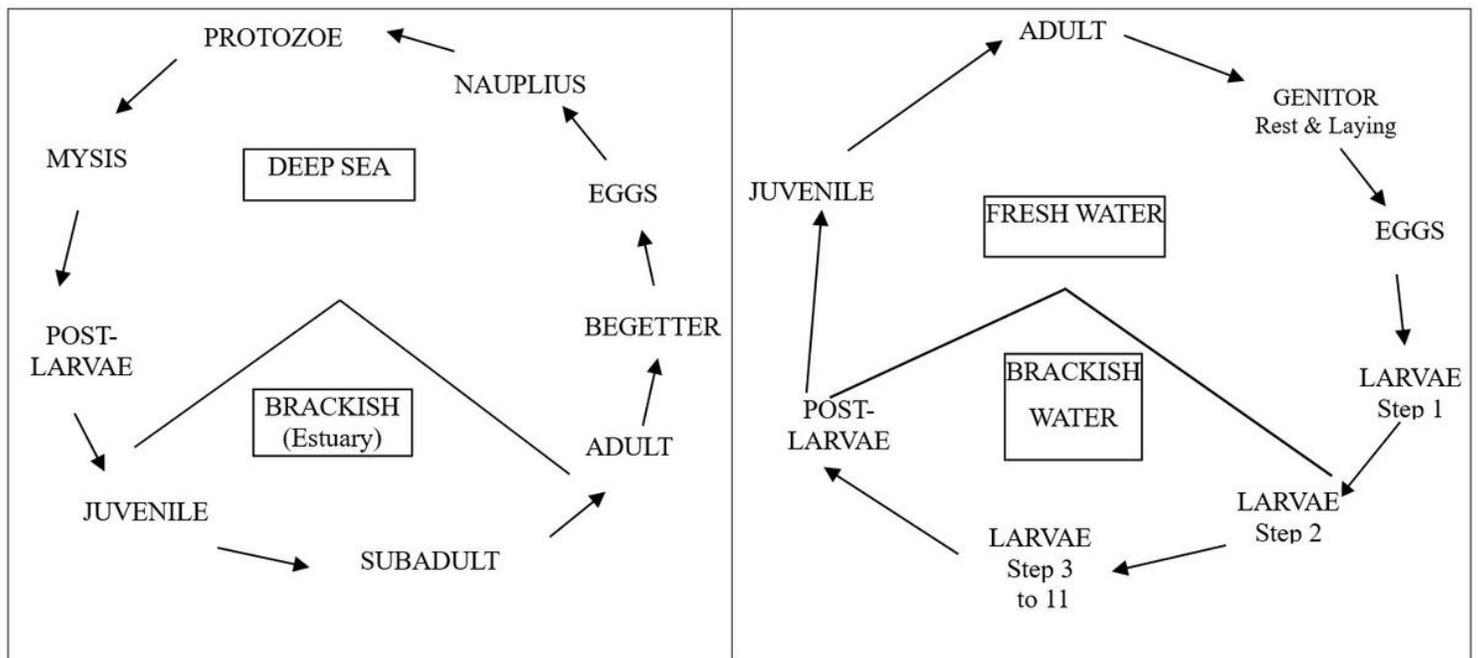


Figure 1

Modified diagram of the *Penaeus* life cycle (left) [44, 54, 59] and most freshwater shrimps (right) [26, 65]

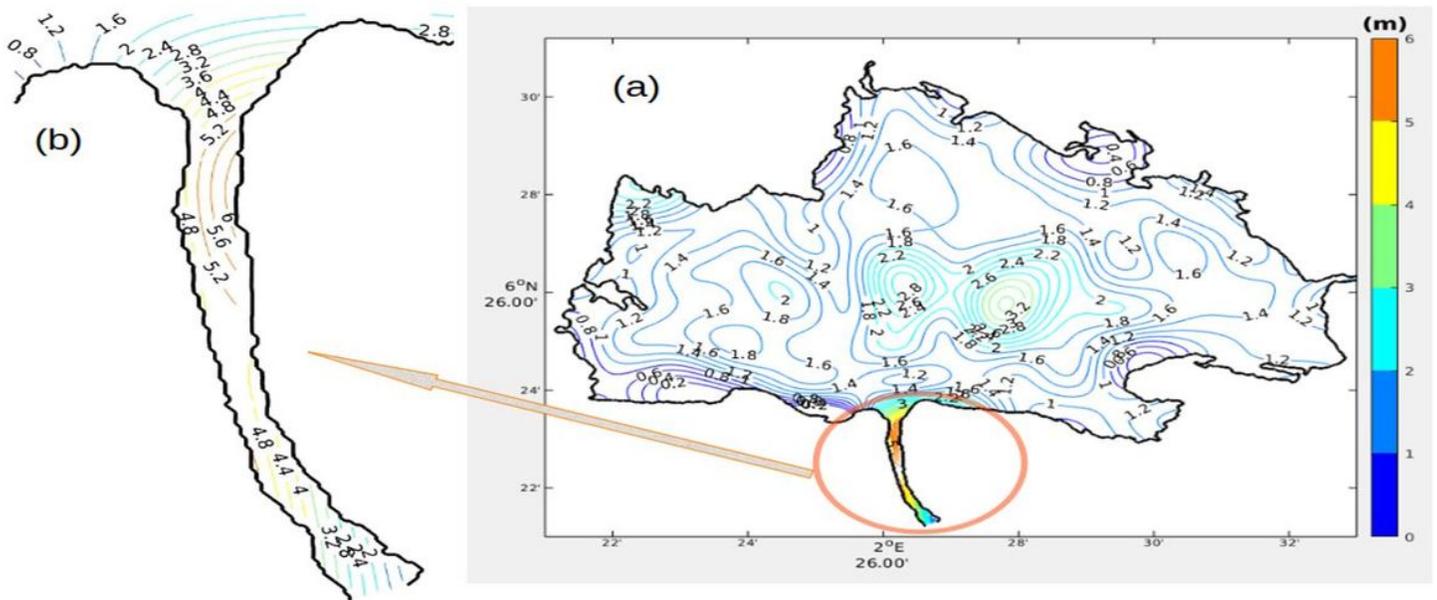


Figure 2

Bathymetry of lake Nokoué (a) and the Cotonou channel (b)

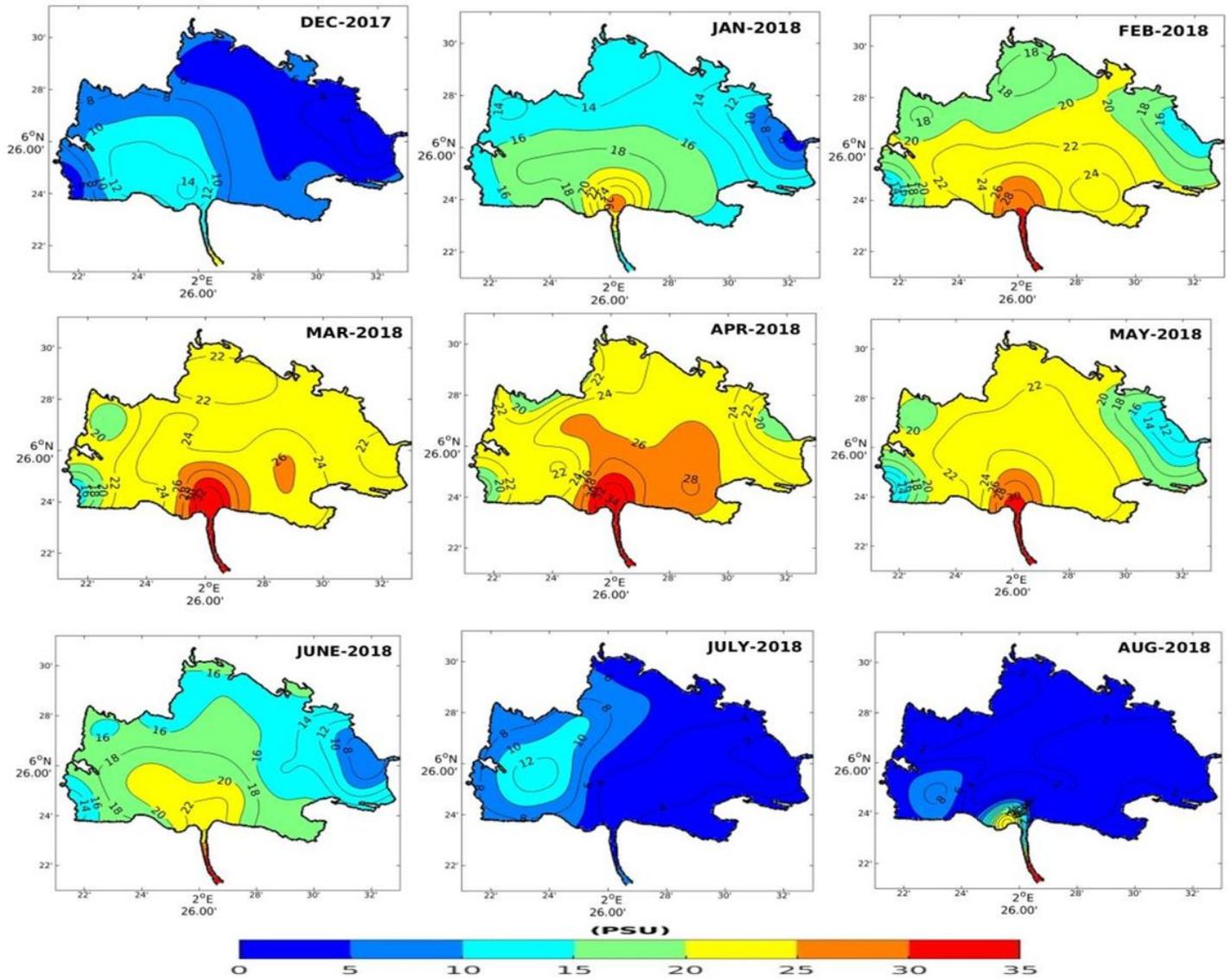


Figure 3

Seasonal distribution of surface salinity in lake Nokoué and the Cotonou channel

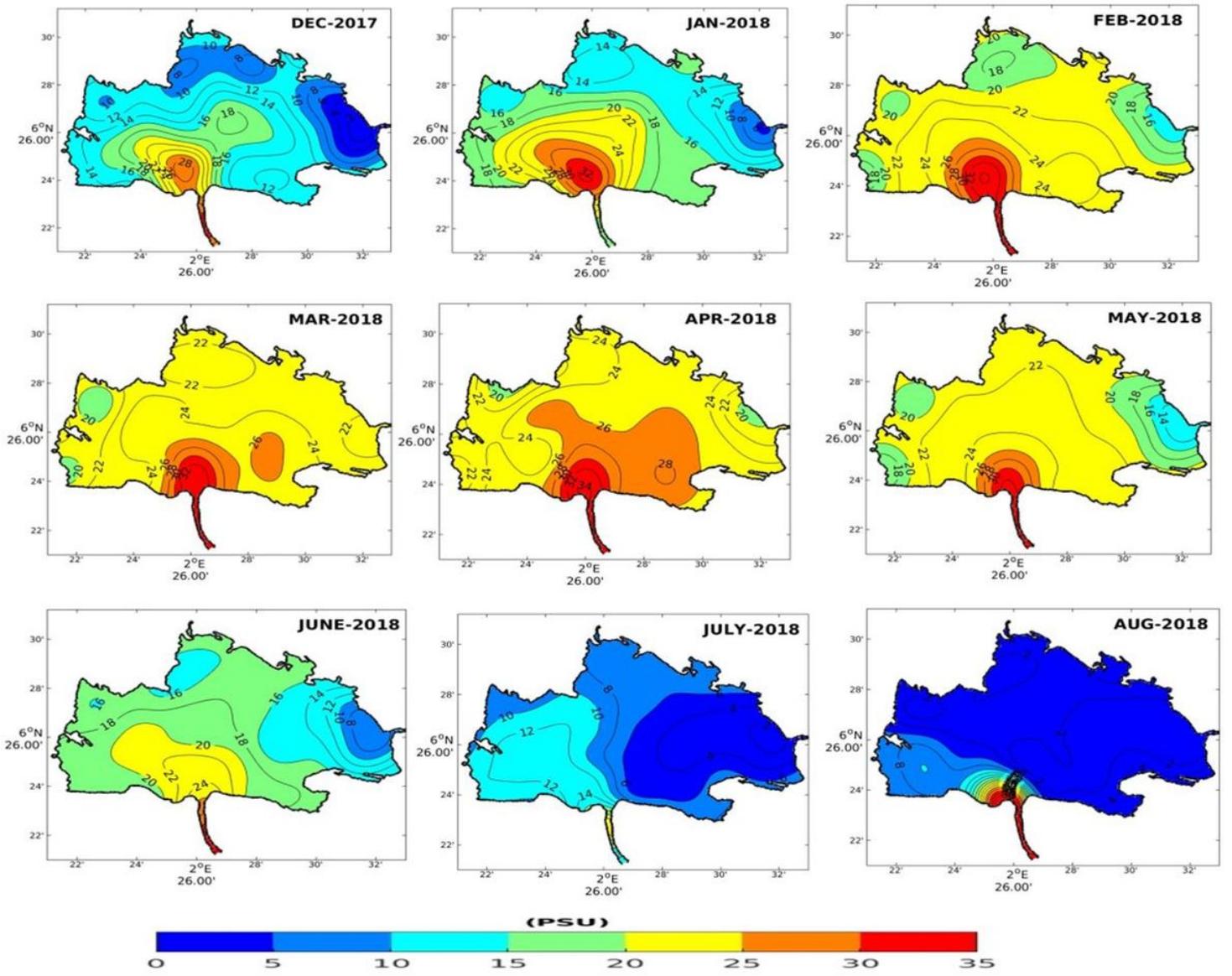


Figure 4

Seasonal distribution of bottom salinity in lake Nokoué and the Cotonou channel.

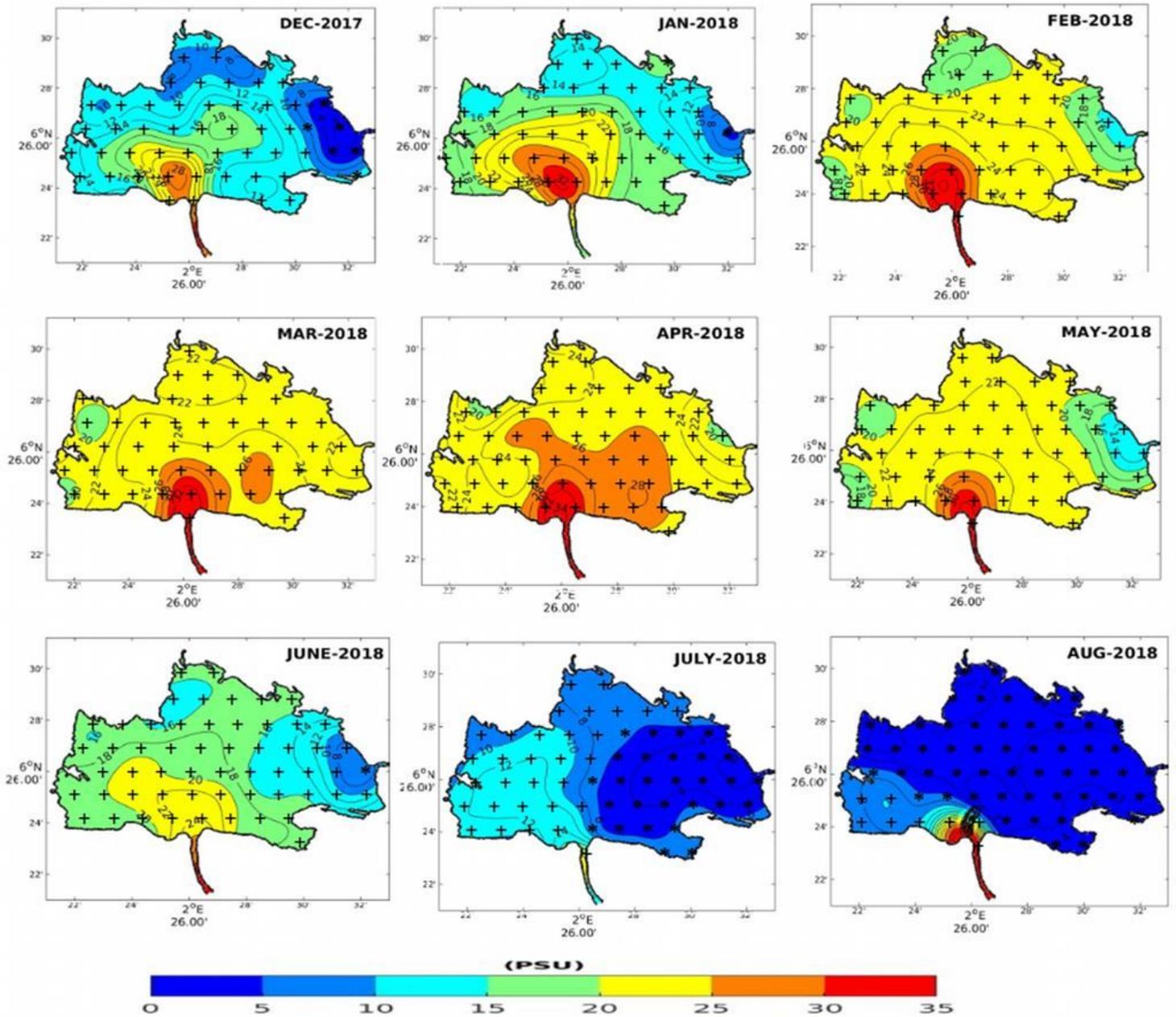


Figure 5

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

Average rainfall from November 2017 to October 2018 in Cotonou

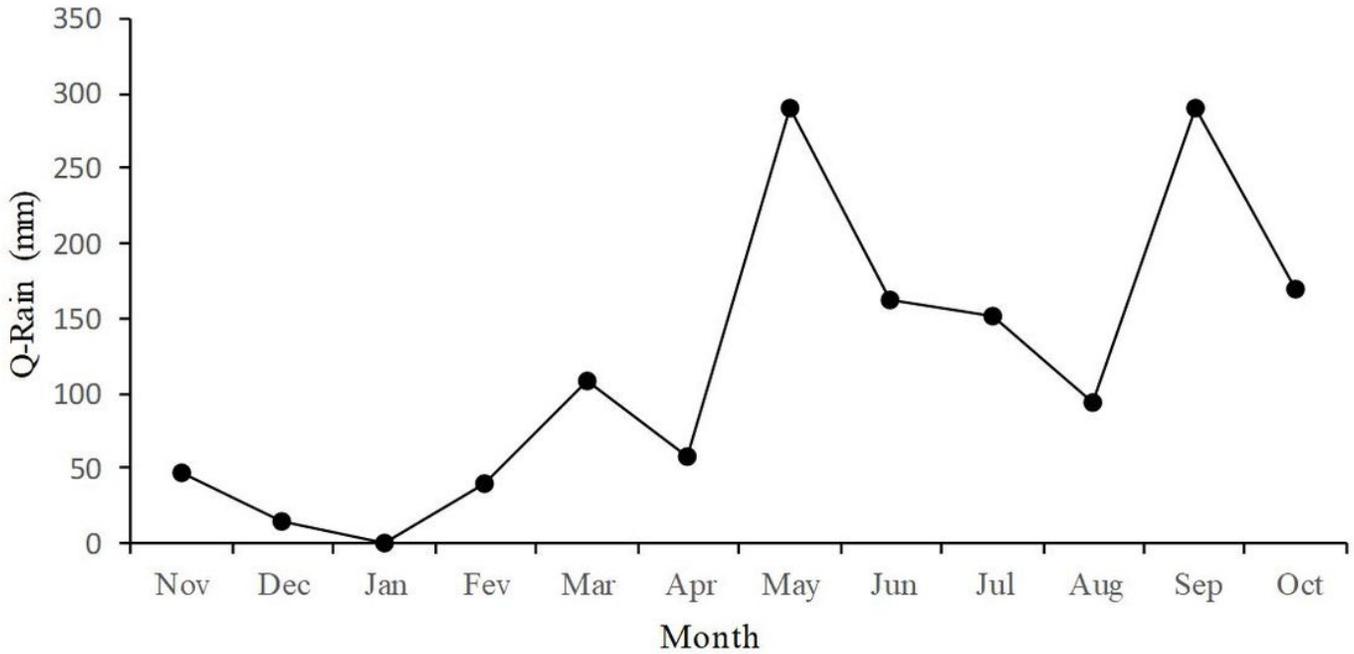


Figure 6

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

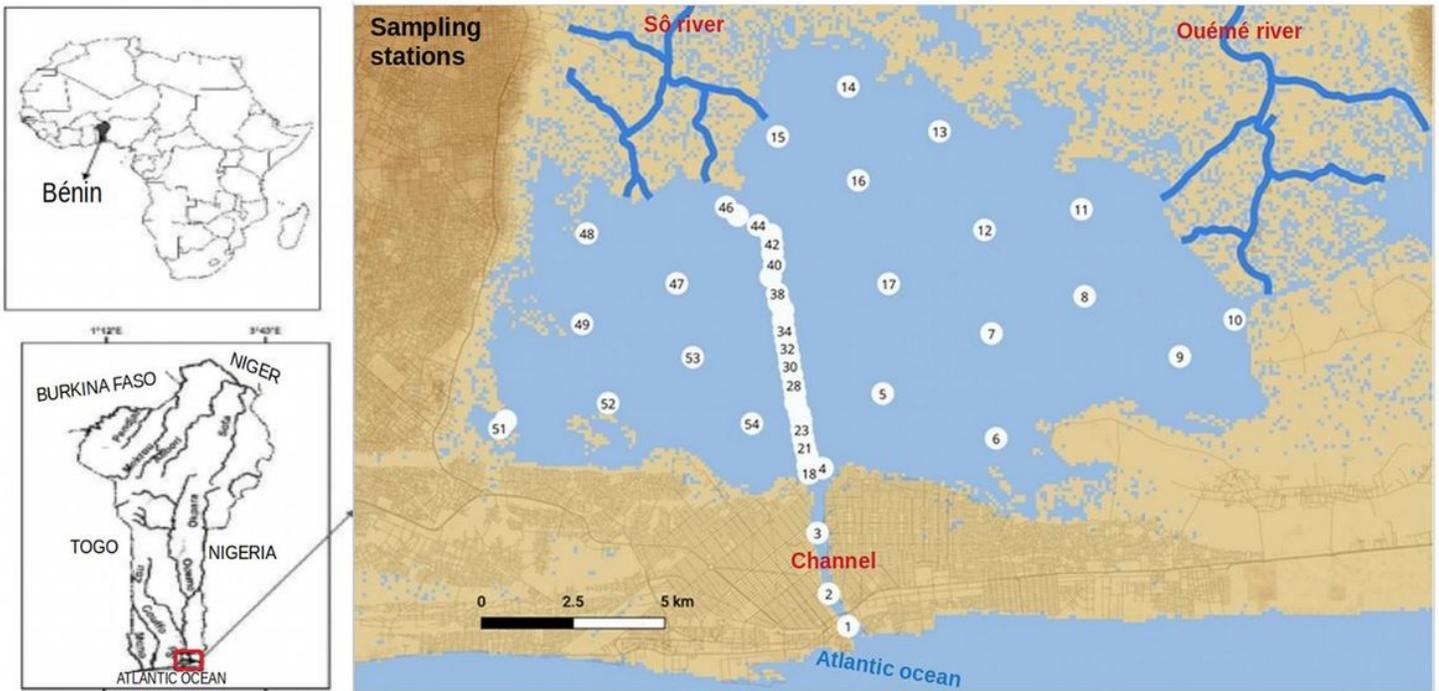


Figure 7

Map of the area of interest and position of the sampling stations on lake Nokoué and in the Cotonou channel