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Review Article

A review of habitat and biodiversity research in Lake Nokoué, Benin Republic: Current state of knowledge and prospects for further research

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ABSTRACT

A systematic literature review was undertaken to understand the state and relationship between habitat types and biodiversity in the open coastal Lake Nokoué and to analyse the research gaps towards an efficient management of this ecosystem. Habitat types in Lake Nokoué have been profoundly impacted by the urbanisation around the lake. Kilometres of riparian habitat including mangrove vegetation were destroyed on the south and western shoreline of the lake, removing the natural protection of the ecosystem to the increasing sewage nutrient load. In addition, to this anthropogenic pressure, the solid wastes from the villages on stilts (Ganvié's villages) increased the nutrient enrichment of the lake. Consequently, the lake experience a seasonal bloom of water hyacinth which dies and sinks to its bottom each year when the salinity rises above 6 ppt. Note that the salinity dynamics of the lake is governed by its hydrological regime which was highly affected by the widening of the sea entrance into the lake around 1960. In addition to these changes, the intensification of the acadja fishing practice has led to the exportation of tonnes of dry woods into the lake. The decay of these woods combined with the accumulation of hyacinth detritus has disturbed the habitats of macroinvertebrates and fish. There is a progressive shift in the system from freshwater species to marine water species and from insectivorous fish to detritivorous fish. Management solutions required reduction of both detritus accumulation and external nutrient load.

1. Introduction

The geomorphology of shallow coastal lakes, generally located in intertidal zones, make them naturally more productive ecosystems when compared to inland deeper lakes on a volume basis (Drake et al., 2011). In fact, many of these lakes have a trophic zone usually extend to the sediment surface, experience a high degree of wind mixing and sediment resuspension, and are exposed to natural variability in nutrient concentrations due to seasonal inflows from large tributary rivers and/or seawater (de Jonge et al., 2002). In addition, shallow coastal lakes usually have an intense reserve of organic matter and a natural high habitat diversity that offer optimal niches for numerous aquatic species which utilise these areas as refuge and/or breeding grounds (Drake et al., 2011;

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Villanueva et al., 2006). Consequently, to this high productivity, massive human development took place around coastal lakes worldwide, with intensive use of the different services provided by these ecosystems. As a result of these anthropogenic pressures most of the shallow coastal lakes water quality, flora, and fauna have been degraded (Mitchell et al., 2015).

The type of habitats encountered inside and around a lake is highly essential to understand the path of energy flow in the system (Schindler and Scheuerell, 2002). In addition, habitat variability and connectivity determine the carrying capacity and influence both the community structure and the productivity in lakes (Cloern, 2006). For open coastal lakes, the amplitude and frequency of the saline water intrusion combined with the amplitude of freshwater input from tributaries (when they exist) influence habitat conditions through the variation in salinity concentration in the water column. Thus, in these systems, both freshwater fauna and sea fauna might occur simultaneously or alternatively, and various phytoplankton and macrophytes might appear seasonally according to the tolerance to salinity. It appears that habitats conditions and community structure in open coastal lakes are already naturally influenced by hydrological processes. In addition, the strong human interference with these systems could promote or demote particular species and affect the processes that sustain community biodiversity in the system. The linkage between habitat types and the biodiversity they support represents the basis to understand what makes coastal lakes vulnerable to human activities and environmental change and therefore, the starting point of an efficient management planning of these systems.

There is a growing interest in the adaptive management of coastal lakes since most of the management planning of these ecosystems have failed to produce useful models which could be largely applied (Schallenberg et al., 2010; Walters, 1997). Challenges in the management and ecological modelling of coastal lakes included difficulties in the representation of long-term ecological response related to rapid hydrologic change, lack of data on key processes which are usually difficult to study, and confusion in the identification of factor in data validation. This situation is even more worrying for tropical shallow coastal lakes where there is little historical management experience, relatively no data collection, and very little knowledge of key processes of these ecosystems. For many lakes on the West Africa coastline (such as Lake Nokoué, Benin, Ebrié Lagoon Ivory Coast), it is urgent to adopt new "policy" option of management for habitat restoration, biodiversity conservation and use of ecosystem services in order to provide long-term measures for the sustainability of shallow coastal lakes (Villanueva et al., 2006).

This review explores all the published research on habitat and biodiversity of Lake Nokoué to understand the link between these two components in open coastal lakes, towards efficient management of these ecosystems against the increasing anthropogenic stress. It brought out the significant changes that have affected the habitats of the Lake Nokoué and reviewed the consequences of these changes on its biodiversity. The review also highlights the orientation for further research to fill the current gaps of knowledge for efficient management of Lake Nokoué.

1.1. Description of Lake Nokoué

Lake Nokoué (Fig. 1) is a shallow, eutrophic coastal lake, located in the south of Benin Republic. It covers around 150 km^2 at low water, and measures 20 km long (east–west) and 11 km wide (north–south) (Le Barbé et al., 1993; Mama et al., 2011a). Prior 1960, the lake connection to the Atlantic Ocean (the channel of Cotonou) was subjected to silting, leading to its complete periodical isolation (Texier et al., 1979). This isolation of the system occurred for several years until the runoff water from Ouémé catchment was strong enough to pierce the sand barrier and therefore reconnect the lake to the ocean (de Kimpe, 1967). The construction of the Port of Cotonou in 1960 cut off the sandy transit and caused a significant deepening of the channel of Cotonou. Lake Nokoué was, therefore, permanently exchanging water with the sea, which consequently led to an abrupt and unprecedented rise of salinity, a reduction in the duration of the freshwater phase, and a decrease in the retention time to about 40 days (Leite et al., 2004; Zandagba et al., 2016b).

Lake Nokoué has been reported to be the major contributor to inland water fish production in Benin, mainly because of acadja fishing practice. This fishing

Fig. 1. Lake Nokoué environment (sentinel 2A image, ESA, 2017).

method consists of attracting fish and crustaceans into an artificially planted brushwood in the open water of lakes; and then surround the brushwood park with a net to easily catch the fish. Acadja is designed to mimic the natural habitat associated with the shores of lakes that many fish species used for reproduction, refuge, and food in dry season. Note that the brushwood is not removed after fish harvest and therefore their decay might highly influence the water quality of the lake. Another peculiarity of Lake Nokoué is the presence of human habitations built on stilts at the surface of the water in the North Western part, known as Ganvié villages (Fig. 3). These agglomerations host about 40,000 people, and its nutrient load was estimated at 108 tons/year of total nitrogen and 18 tons/year of total phosphorous (Djihouessi and Aina, 2018).

Currently, the hydrological regime of Lake Nokoué is characterised by three major hydrologic periods. There is a high water period from September to November, due to rains in the north of Benin - which supply water to the Ouémé River and Sô River (Texier et al., 1979; Gnohossou, 2006). This contrasts with a low water period from December to mid-May in which tidal inputs dominate as long as the channel of Cotonou is open to the ocean (Le Barbé et al., 1993). In June–August, there is a slight rise in water level caused by the local heavy rains in southern Benin which supply the Sô and Djonou rivers (Le Barbé et al., 1993; Gnohossou, 2006). Lake Nokoué also receives freshwater from the Djonou River and exchanges freshwater with the Porto Novo lagoon through the channel of Totchè. The water exchange between the lake and the Atlantic Ocean has a great influence on its salinity regime (Fig. 6). Sea water intrusion at low water was slightly higher than freshwater input (Le Barbé et al., 1993). Consequently, the entire lake remains brackish during the low water period (avg salinity >16 ppt) (Mama, 2010). During high water periods, the residence time of the lake was estimated to 30 days on average amplitude tide, while during low water periods it was estimated to 40 days on average tide amplitude (Zandagba et al., 2016b). The influence of the tidal range on the water renewal time was estimated at 4 days during the high water period and 10 days during the low water period. The annual total nutrient load from Lake Nokoué tributaries was estimated at 7020 tons of total nitrogen and 1510 tons of total phosphorous (Djihouessi and Aina, 2018).

Ebrié Lagoon in Ivory Coast (West Africa) has also been open to the sea since 1950 through the Vridi Canal (Bird, 2011) leading to seasonal changes in its salinity regime and hydrodynamics as the ones observed in Lake Nokoué (Djihouessi and Aina, 2018). Similarly, the salinity of Waituna Lagoon in New Zeeland raised (up to 33.2 ppt) when the lagoon was opened to the sea, and its water level considerably decreased (Schallenberg et al., 2010). The closure of the sea entrance into the lagoon resulted in a decrease of its salinity (down to 0.7 ppt) and a rapid rise in its water level. Therefore the mechanically opening and closure of coastal lakes and lagoons to the sea could have many applications in ecohydrology, such as controlling the dynamics of saline water species in the system or preventing the flooding of surrounding urban and agricultural lands. However, it is important to remark that the water levels and the morphological characteristics of coastal lakes and lagoons dictate the degree of the influence of barrier openings and closures.

1.2. Papers selection approach

A systematic approach was adopted in this paper, to review and consolidate existing research on habitat types, biodiversity and water quality of Nokoué Lake. A peer-reviewed literature search was conducted between April 2015 and February 2017. A rigorous and repeatable method has been developed to find peer-reviewed papers about Lake Nokoué using academic databases and search engines including *Scopus* and *Web of knowledge*. The method consisted of three stages: (i) keyword generation, (ii) search, and (iii) selection of relevant papers. Keywords specific to the "location," "habitat types," "biodiversity" and "water quality" were chosen, and these are presented in Table 1. Using these keywords the search was undertaken. The selection of relevant papers was based on a fixed set of inclusion criteria: (i) the paper must be related to Lake Nokoué, (ii) the paper should address water quality or habitat types or biodiversity as primary or secondary subject; (iii) at least one of the generated keywords should exist in the abstract of the paper.

Many research studies on Lake Nokoué are related to PhD theses, MSc. theses, conference proceedings, and governmental research institute reports and dissertations which were not reviewed by a scientific journal. The methodology set out above has been applied with *Google Scholar* to search this literature known as grey literature. Additional intelligent search approaches were utilised. These included searching in the reference list of relevant publications and searching for papers that cited other relevant publications.

2. Habitat types

The biota diversity, its abundance, production and spatial distribution in coastal lake ecosystems have shown high responses to hydrological variations. Furthermore, the kinds and number of species encountered in these ecosystems are related to their habitat complexity (Covich,

Table 1
Keywords for literature search on habitats and biodiversity of Lake Nokoué. A location keyword must be included in the search with at least one keyword on hydrodynamic or water quality.

	Keywords
Location	Lake Nokoué; Benin; Dahomey; West Africa; Cotonou; Abomey Calavi; Ganvié, Ouémé River; Sô River, So ava
Habitats	Water hyacinth, acadja, akadja, mangrove, riparian, pelagic, benthic, macroinvertebrate, sediments
Biodiversity	Water quality; eutrophication; saline intrusion; nutrients, fish, acadja, akadja, fishery, macroinvertebrate, phytoplankton, zooplankton

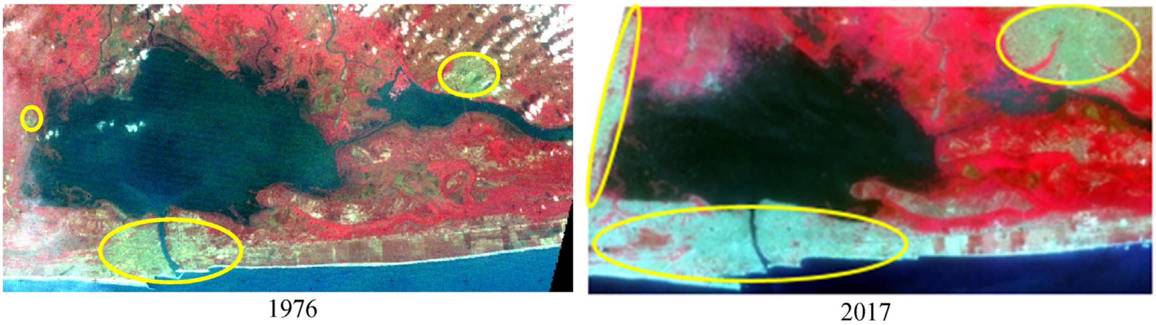

Fig. 2. Evolution of the riparian vegetation represented by red colour; February 1976 with Landsat 1-3MSS image, January 2017 with Sentinel 2A image. All the riparian vegetation on the western and southern shoreline were lost due to the extension of Abomey-Calavi (west) and Cotonou (south).

2009). Different type of habitats has been reported in Lake Nokoué including riparian, pelagic and benthic habitat.

2.1. Riparian habitats

Riparian habitats of lakes host an ecologically diverse type of components including marshes, forest, wetlands and mountains vegetation depending on the geomorphology of the system. Texier et al. (1980) classified riparian habitat of Lake Nokoué in two groups: the plants periodically flooded and the plants present in the non-flooded zone but which are still affected by the lake hydrology. Both groups considerably deteriorated between 1970 and 2000 (Fig. 2). From 1980 to 2000, the riparian habitat of the non-flooded zone (about 5 species) has almost disappeared entirely, while the species encountered in the periodically flooded zone have decreased from 16 species to 4 species (Gnohossou, 2006). The dominant species of Lake Nokoué riparian habitat since 2000s was *Paspalum vaginatum* present in both flooded and non-flooded zone (Mama, 2010; Gnohossou, 2006). It occurred mainly in the north of the lake and had promoted the establishment of cattle farms near the lake shore. *Echinochloa pyramidalis* which was abundant on the eastern shoreline was progressively replaced by increasing agriculture activities (Gnohossou, 2006). *Cyperus papyrus* on the west of the lake has completely disappeared, and *Typha australis* appeared instead.

It is still difficult to quantify the amplitude and the impacts of the destruction of riparian habitats in Lake Nokoué because of the lack of historical data and absence of reference area. However, the recent development of remote sensing techniques offers the potentiality of derived reference condition from historical satellite images of the 1970s where human activities were still far from the riparian area of the lake (Fig. 2). A comparison with recent images could allow to quantify the amplitude of the destruction of the lake riparian habitats. Notable riparian flora found in other West African lagoons (Lagos Lagoon, Ebrié Lagoon) and not found around Lake Nokoué includes *Acrotiscum aureum*, *Rhizophora racemosa*, *Drepoanocarpus lunatus*, *Avicennia nitida*, *Paspalum orbiculare* and *Cyperus articulates* (Emmanuel and Onyema, 2007; Nicole, 1994). All these species were also inundated at high tide and partially exposed at low tide and could be added to the set of riparian flora for reference conditions of Lake Nokoué.

Several studies related the disappearance of riparian habitat around Lake Nokoué has been linked to a variety of ecological problems such as reduction of nursery habitat (Adite and Winemiller, 1997), reduction of macroinvertebrate (Gnohossou, 2006), increase of the lake shoreline pollution by solid wastewater (Mama, 2010). However, it is not straightforward to establish the cause–effect analysis of the removal of riparian habitat. For instance the loss of mangrove vegetation (mainly *R. racemose* and *Avicennia germinans*) in the south-west shoreline resulted in a decrease of juvenile fish in the lake which subsequently decreases commercial fish harvest, and progressively led to the intensification of the use of acadja (Adite and Winemiller, 1997; Villanueva et al., 2006; Niyonkuru and Lalèyè, 2010). This suggested that the removal of mangrove was the main cause of acadja development in the lake, disregarding that it was the introduction of acadja fishing which accelerates the degradation of mangrove vegetation. Consequently, the mangrove restoration programme implemented by decision-makers in the lake failed because most of the plants were removed by the population for making acadja. Another consequence of the disappearance of riparian vegetation in Lake Nokoué was the proliferation of garbage dumps on the lake shores which increase nitrogen and phosphorus enrichment of the lake (Hounsinou et al., 2015). Currently, this excess nutrient enrichment amplified water hyacinth (*Eichhornia crassipes*) development which occurred mainly in the riparian zone where mangrove vegetation used to occur.

2.2. Pelagic habitats

Pelagic habitats in this review are used for the components of the open-water that could be occupied and/or provide a useful resource for Lake Nokoué biota development. This including the water column itself, floating aquatic macrophytes and one peculiar human-made habitat that appears as a "brush park" and known as "acadja" (Fig. 3).

The water quality of Lake Nokoué is under the double influence of its tributaries water inputs and seawater intrusion. During high water from September to November, high-nutrient concentration water from the Ouémé

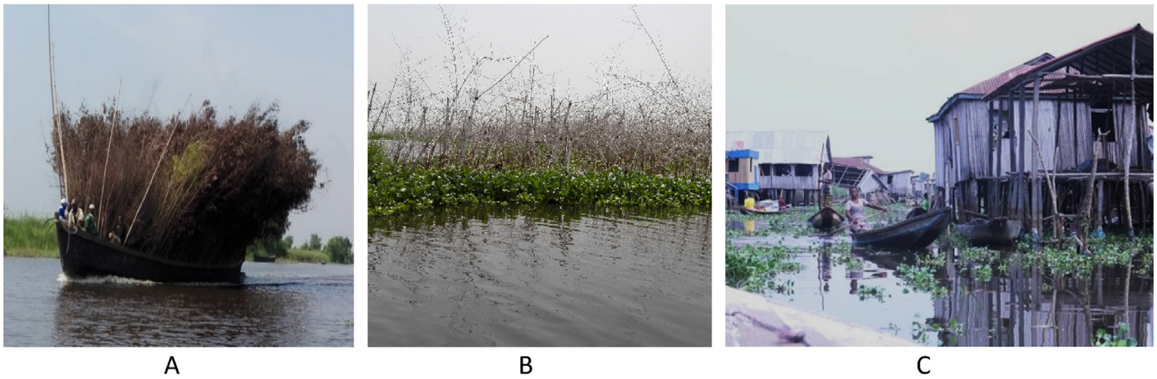

Fig. 3. Photos of anthropogenic activities in Lake Nokoué. (A) Transportation of wood for making acadja habitat. (B) Water hyacinth inside the acadja at Dekanmè on 03 December 2016. (C) Ganvié village with houses on stilts and water hyacinth development.

and Sô Rivers invade the lake and keep out the saline water from the Atlantic Ocean. As the inflows from the tributaries decreased, tidal influence and salinity increased gradually and the lake water shift from freshwater with salinity nearly 0 ppt to brackish with average salinity around 13 ppt in late January (Fig. 6) (Mama et al., 2011a; Zandagba et al., 2016a). The same observation has been made for several open coastal lakes in West Africa (Ebrié Lagoon, Lagos Lagoon) and in New Zealand (Waituna Lagoon) where, salinity and transparency values were significantly higher in the low water period (Schallenberg et al., 2010; Mitchell et al., 2017). Nutrient (NO_3-N, NH_4-N, and PO_4-P) concentrations, in contrast, were higher during the high water period and decrease progressively as salinity increase, suggesting that the lake water was flushed out by tributaries water (Djihouessi and Aina, 2018). These rapid changes in salinity and nutrient concentrations of the water column will inevitably influence in short and long term the development of the lake biota. The temperature of the water column varied between 25 °C and 34 °C and is significantly influenced by the air temperature (Mama et al., 2011a; Zandagba et al., 2016a), while dissolved oxygen concentration fluctuate between 11 ml/g and 0.5 mg/l through the year (Mama et al., 2011a) and is significantly higher during high water periods.

Floating aquatic macrophytes in Lake Nokoué are dominated by water hyacinth which appears each high water period when the salinity of Lake Nokoué decreases beyond 6 ppt (Fig. 6) and outcompetes other pelagic plants (Djihouessi and Aina, 2018). Only some *Pistia stratiotes* can be observed close to the entrance of the Djonou River in the lake (Texier et al., 1980; Gnohossou, 2006). After salinity increase above 6 ppt, water hyacinth plants die and sink to the bottom of the lake and become a potential source of internal nutrient loading from the sediment. Recent studies indicate that the presence of acadja influenced the spatial distribution of water hyacinth since it provides to water hyacinth an environment where wind and water currents cannot move them towards the riparian zone (Zandagba et al., 2016a).

Acadja in Lake Nokoué has rapidly increased in the last two decades. In 1994, it was found only in the western part of the lake (Adite and Winemiller, 1997) while studies after 2010 reported that almost 60% of the lake has been in use by acadja (Mama et al., 2011a; Zandagba et al., 2016a). Acadja habitat appeared to present the ecology of both floating vegetation and flooded brush or forest. It provides fish with periphyton including bacteria, fungi, diatoms and filamentous algae together with rotifers nematodes and crustacea (Welcomme et al., 2005). In addition to providing supplementary food, the acadja encountered in Lake Nokoué are constructed in such a way to provide an adequate area that serves as a breeding area for the tilapine cichlids. The high fish production of Lake Nokoué compared to other coastal lakes in West Africa may be explained by the presence of acadjas, which increase the abundance of juveniles (Villanueva et al., 2006) and subsequently improve the commercial fish harvest. Thus, acadja practice has shown a positive impact on fishermen income, but in reverse contributed to the reduction in the diversity of the fish population (Niyonkuru and Lalèyè, 2010), and increase water turbidity (Mama, 2010). Besides that, acadja practice might impact the hydrodynamics and the nutrient circulation in the lake although no proof has been provided in the literature. Negusse and Bowen (2010) estimated a contribution of 100 kg/day of total nitrogen and 25 kg/day of total phosphorus from acadja.

2.3. Benthic habitats

There is no map of the benthic habitat of Lake Nokoué in the literature. The simplest mapping attempts should associate the structure of the physical substrate and their chemical composition while more sophisticated mapping attempts should additionally include the fauna and flora occurring at the bottom surface of the substrate (Diaz et al., 2004). The information on the benthic fauna of Lake Nokoué is presented in Section 3.3 of this review. Regarding the benthic flora, there was no available information neither on Lake Nokoué nor on the other West African coastal lakes and lagoon. An hypothesis to explain this lack of information could be that most of the benthic flora in these ecosystems were destroyed before scientific interest started.

Very few studies have investigated the bottom substrate composition and dynamic of Lake Nokoué. Texier et al. (1980) presented a map of the sediment distribution in the lake, and this remains the only studies which characterised the bottom substrate of the whole lake. The west of the Lake was mainly muddy and shallow with an average depth of 0.5 m at low water period. This could explain the high presence of acadja in these parts of the lake since the branches of acadja have to be fixed to the sediments. The middle and the east of lake were sandy and more profound with an average depth of 1.5 m at lower water period. From northwest to southeast, sandy-muddy bands alternated with sandy bands (Adounvo, 2001). Recent studies carried out on the locations dominated by acadja (Gnohossou, 2006; Mama et al., 2011b) indicate that the bottom substrate has progressively changed from mud dominated to a composite of 50% of mud and 50% of detritus. This change was explained by the yearly deposits of wood debris from acadjas since the brushwood are not removed after the fish harvest.

An analysis of the sediment composition indicated that the organic matter content ranged from 1 to 15% (Mama et al., 2011b), with the locations where both water hyacinth and acadja occurred having the higher organic matter content. The mineralisation of this organic matter is suspected to increase P release that occurred in summer (Mama et al., 2011b). However, there is no estimate of the contribution of sediment nutrient release to the internal nutrient load. Such study will allow for comparison between the contribution of the different nutrient source (external and internal) and the eutrophication process of the lake.

2.4. Habitat coupling in Lake Nokoué (inter-habitat omnivory)

Habitat heterogeneity of Lake Nokoué is controlled by different and interconnected factors including saline water intrusion from the Atlantic Ocean, sediment and freshwater inputs from tributaries (Ouémé, Sô and Djonou rivers), intensive use of acadja (artificial fishing practice) and anthropogenic disturbances from nearest cities (Cotonou, Abomey-Calavi and Ganvié the village on stilts). The concept of habitat coupling developed in this section allow to discuss how the presence of one particular habitat affected the condition in the other habitats, and what are the effects (single or combined) of these habitats on the ecology of Lake Nokoué including its water quality, and availability of nutrient and food (for predators) to its biota.

In lakes, the dominant taxa in pelagic habitats are algae and fish (Schindler and Scheuerell, 2002). The presence of large water hyacinth mat in the pelagic zone compete with algae for nutrient and light (Villamagna and Murphy, 2010). Consequently, local dissolved oxygen concentration and water transparency might significantly decrease, making, therefore, part of the water column difficult for the survival of some fish species (such as piscivorous fish) while perfect for other species (such as prey fish). It is therefore expected that, in Lake Nokoué, the phytoplankton community is highly affected by the seasonal appearance of water hyacinth (competition for light) and that the seasonal appearance of the weed might have reduced the acadja fish production (oxygen depletion). The observations made in Lake Naivasha (Kenya) showed that in addition to reduced phytoplankton productivity, water hyacinth significant change phytoplankton species composition and biodiversity (Mironga et al., 2011). This suggests that more than affecting the carrying capacity of the pelagic habitats of Lake Nokoué water hyacinth infestation can alter the ecology of the lake. Further studies should be done to investigate the competition between water hyacinth and algae and the effects of this completion on the food web structure of Lake Nokoué.

One of the effects of pelagic habitats on benthic habitats in Lake Nokoué involves the deposition of dead water hyacinth and acadja material at the sediment surface. In fact, about 9000 tonnes dry weight of water hyacinth sink and join the sediments each year between January and March. This might have imposed an atypical seasonal dynamic to taxa in benthic habitat and even might locally change the dominant taxa in benthic habitat (Section 3.3). In addition, acadja fishing method has been blamed for accelerating siltation (Mama, 2010), and to have locally changed benthic habitat structure in Lake Nokoué (Gnohossou, 2006). However, some authors (Welcomme et al., 2005) defend the idea that the geographical position of acadja which are often located near the mouth of tributaries rivers, allow branches deposits to be swept away to the outlet (the Atlantic Ocean) during high water period. The real impact of acadja on benthic habitats remain to be investigated. It is therefore important that future studies characterise the processes happening at the sediment–water interface in the lake and how water hyacinth detritus and acadja deposits affect these processes. The middle of the lake where no hyacinth and acadja occurred can serve as reference condition for such studies.

One of the well-known roles of riparian habitat is to buffer the effect of catchment pollution on pelagic and benthic habitat (Hoffmann et al., 2009). This function has been nearly lost in Lake Nokoué. It is proved that municipal wastes from Cotonou and Abomey-Calavi have been polluting the lake and increasing eutrophication (Hounsinou et al., 2015). Few studies (Negusse and Bowen, 2010; Mama et al., 2011a; Djihouessi and Aina, 2018) have approximately quantified the wastes discharged by the municipalities in the lake. However, more accurate methods have to be used to be able to determine the effect of nearest cities on the pelagic and benthic habitats of Lake Nokoué.

3. Biodiversity of Lake Nokoué

In this chapter, the biodiversity of Lake Nokoué is reviewed, and the links between this biodiversity and both the hydrology and the habitat in presence in the lake have been established. The review mainly focuses on phytoplankton, macroinvertebrate, fish, and bird diversity.

3.1. Phytoplankton and primary production

3.1.1. Primary production

Very few studies have focused on the primary production and distribution of phytoplankton in Lake Nokoué. The first assessment of the primary productivity of the lake was made by de Kimpe (1967), and it was the first study conducted on lake's primary production in West Africa. The mean value of phytoplankton production in Lake Nokoué was estimated to 2220 mg C m^{-2} day^{-1} which was significantly greater than the average primary production of tropical and sub-tropical coastal lakes and lagoons estimated at 970 mg C m^{-2} day^{-1} (Knoppers, 1994). In 2001, the average primary production in the lake was estimated at 1680 mg C m^{-2} day^{-1} (Adounvo, 2001), indicating a decrease of 25% in the average primary productivity, although the average dissolved inorganic nutrient concentrations in the water have significantly increased since 1980 (Gnohossou, 2006). The significant decrease in the lake transparency, due to increase in sediment input from Ouémé catchment (Djihouessi and Aina, 2018), could explain the decrease in the primary production. In fact, several studies showed that terrestrial runoff reduction the productivity in tropical and sub-tropical coastal lakes (Knoppers, 1994; Liess et al., 2015). The introduction of water hyacinth the early 1990s could have also affected the primary production in Lake Nokoué as observed in Lake Naivasha, Kenya and Lake Chivero, Zimbabwe (Mironga et al., 2011; Theuri, 2013). In addition, the impact of the changes in hydrological regime due to the intensification of the water exchanges between the lake and the Atlantic Ocean might have favoured the decrease of primary production in Lake Nokoué.

3.1.2. Taxonomic diversity of phytoplankton

Phytoplankton community of Lake Nokoué has a strong spatio-temporal variation. However, it is important to note that no study has thoroughly monitored the annual distribution of this taxon in the lake. The available studies cover the water recession period (Goussanou, 2012) and part of the low-water period (Adjahouinou et al., 2012). For these periods, four (4) main classes of algae have been identified. The most represented class was Diatomophyceae (26 species), followed by Chlorophyceae (20 species), Euglenophyceae (15 species) and Cyanophyceae (11 species) (Goussanou, 2012; Adjahouinou et al., 2012).

In total, 77 species of phytoplankton have been identified in Lake Nokoué between 2001 and 2012 which was close to the phytoplankton richness in Lagos Lagoon (82 species) (Emmanuel and Onyema, 2007) and higher than the richness in Ebrié Lagoon (Seu-Anoï et al., 2017). The list of the species recorded is presented in Goussanou (2012) and Adjahouinou et al. (2012). There was a significant spatial and temporal difference in the species distribution (Goussanou, 2012). The west of the lake, near Ganvié and the Djonou River, presents the highest taxonomic diversity of 36 species followed by the centre of the lake about 29 species. The most numerous species were: *Navicula bacillum*, *Synedra ulna*, *Oscillatoria granulate* (all found almost everywhere in the lake) and *Euglena spirogyra* (mostly found in the west of the lake) (Goussanou, 2012; Adjahouinou et al., 2012).

3.1.3. Linkage between phytoplankton abundance and water quality

Diatomophyceae and Euglenophyceae were respectively the most abundant classes, followed by Cyanophyceae and Chlorophyceae (Goussanou, 2012; Adjahouinou et al., 2012). Diatomophyceae were observed mainly during high water period (Goussanou, 2012). Similar observation was made in Ebrié and Grand-Lahou Lagoons (Ivory Coast) where the abundance in diatom during high water period was 3 times greater than the abundance during the other period of the year (Seu-Anoï et al., 2017; Etilé et al., 2009). This could be related to the high DIN and DRP in the water column (Mama et al., 2011a; Etilé et al., 2009) and to the N:P molar ratio which is close to Redfield ratio at many locations during high water period (Knoppers, 1994). Also, the high abundance of Diatomophyceae could also indicate a high silica concentration in the water column probably brought by the tributaries as a result of surface runoff from the upper mountainous Ouémé catchment. Yet, no study has measured the silica content in Lake Nokoué and its tributaries. Such study could be very relevant regarding the fact the lake water it entirely flushed out to the sea during water recession which might mean that amount all the silica in the water column would be lost to the Atlantic Ocean. The high abundance of Diatomophyceae might also indicate a high internal nutrient load due to probable decomposition of organic matter at the sediment–water interface (Reddy and DeBusk, 1991; Gupta et al., 1996). A high abundance of Euglenophyceae in aquatic ecosystems is a characteristic of high organic pollution from wastewater discharge (Cavalier-Smith, 2003). This could be related to the critical discharge of municipal wastewater in the lake (Adjahouinou et al., 2014; Hounsinou et al., 2015).

The presence of Cyanophyceae was very seasonal (Goussanou, 2012). Their concentration increases progressively in low water period from December, and they become the most abundant taxon in the lake in February. Their concentration decrease when the rains start and the water from the tributaries invade the lake (Goussanou, 2012). This indicates that conditions in low water period were more favourable for the development of cyanobacteria. Among this conditions, the low water flow during this period (Zandagba et al., 2016b) might be an important factor. These observations also suggest that at this period the water column is deficient in nitrate and silica consolidate the hypothesis that all the silica which probably reach the lake in high water period are lost to the Atlantic Ocean.

3.2. Zooplankton

No papers focused on zooplankton community in Lake Nokoué. The information on the zooplankton community in Lake Nokoué was derived from the studies on fish diet composition. Several zooplankton groups have been identified by Gnohossou (2002), including ostracods, copepods, cladocerans, rotifers, nauplii, nematodes, and protozoa, notably Tintinnidae. The zooplankton of the lake was dominated by Rotifera, which represent 96% of the individuals. Nauplii and Copepoda represent 2% and 1%, respectively. The proportion of other groups is very low. In Grand-Lahou Lagoon, a West African tropical coastal lagoon with similar physico-chemical characteristics to Lake Nokoué and relatively less anthropogenic pressure, the zooplankton communities were composed of 65 taxa including Copepoda, Rotifera, and Cladocera, with

Copepoda the most abundant group (81%) (Etilé et al., 2009). The highest zooplankton abundance in this ecosystem ranged between 171 and 175 ind./L and was recorded during the low water period, while the lowest abundance ranged between 40 and 45 ind./L and occurred during the rainy season. The comparison of the dynamic of zooplankton and phytoplankton in Grand-Lahou Lagoon consolidates the well-known predator-prey relationship between these two (McCauley and Kalff, 1981). Therefore, it is expected that the zooplankton dynamics are correlated to phytoplankton dynamics in Lake Nokoué.

Regarding biomass, Rotifera in Lake Nokoué constitutes nearly 60% of the total zooplankton community (Gnohossou, 2002). Some species have been identified by d'Almeida (1992) including the foraminifera: *Jadammina polystoma*, *Ammonia beccarii*, the ostracod *Neomonoceratina* sp. and the copepod *Acartia clausi*. A planktonic mollusc *Creseis acicula*, a thaliaceae of the doliolidae family *Dolioletta* spp., and a Chaetognathe *Sagitta inflata* were also found.

3.3. Macroinvertebrates

Few research studies have been done on the macroinvertebrate distribution and dynamic in Lake Nokoué. The first studies, carried out by Rabier et al. (1979) and Texier et al. (1980), focused only on invertebrates in sediments. The other types of substrates had not been investigated. Moreover, the sampling methods used (Berthois cone or dumpster) showed the weakness of not catching the highly mobile macroinvertebrates. It was Gnohossou (2006), who presented a detailed study on macroinvertebrates thus paving the way for more specific studies on the benthic community of the lake such as Gnohossou et al. (2009, 2015) and Odountan and Abou (2015, 2016).

3.3.1. General classification and zoological groups

Based on the types of substrate, two macroinvertebrate groups were distinguished in Lake Nokoué: the bottom fauna and the epibenthic invertebrates. For each of the two groups, 4 subgroups of macroinvertebrates were identified: the strictly freshwater species, the strictly saltwater species, the freshwater tolerant species and the salt-tolerant species. The bottom fauna invertebrates are favoured by the increasing sedimentation and the permanent deposit of the wood debris from acadjas, while the epibenthic invertebrates are found in the pelagic zone, on acadjas woods and within the roots of floating macrophytes such as water hyacinth and *P. stratiotes* (Gnohossou, 2006).

In total, 86 taxa (orders, families or genera) of aquatic invertebrates were recorded between 2004 and 2014 (Gnohossou, 2006; Odountan and Abou, 2015). Insects constituted the most represented group with more than 50% of all species. Molluscs and crustaceans contained about 40% of all species, whereas annelids, arachnids, and nematodes account for less than 10% of the species (Gnohossou, 2006; Odountan and Abou, 2016). The lists of macroinvertebrate species encountered in Lake Nokoué are presented in Gnohossou (2006) and Odountan and Abou (2015). As in Ebrié and Lagos lagoons, insect richness has significantly decreased in Lake Nokoué compared to the years 1980 (Welcomme, 1972; Adite and Winemiller, 1997). The loss of the nearly all the riparian habitats may have probably contributed to the decrease of insect availability since aquatic insects are frequently associated with submerged and shoreline vegetation.

3.3.2. Spatio-temporal distribution of macroinvertebrate

The diversity of macroinvertebrates community in open coastal lakes increases when salinity decreases (Brucet et al., 2012). Similar observations were made in Lake Nokoué (Gnohossou, 2006). A significant temporal difference was observed between high water (low salinity) and low water (high salinity) periods, due to the arrival of new species (mainly insects) and the departure of other species (Terebellidae, Parguridae) during high water period. Less than 35% of the identified taxa are observed over all the year (Gnohossou, 2006). The species that remain most frequent over time are brackish water species that more or less tolerate overloading of organic matter and change in salinity. The temporal difference in the macroinvertebrate dynamic is governed by to the variation of the hydrological regime of the lake (Gnohossou, 2006).

There was no significant spatial difference in the macroinvertebrates distribution in the lake. Crustaceans, mollusks, and annelids were found in the south at the junction of the lake with the sea in high water period while later in low water period they were found all along the south-north axis (Gnohossou, 2006). This suggests a migration of these species along the vertical profile of the lake as the salinity of the water increases and decreases. In a particular way, Ganvié (a village on stilts) sheltered the less number of species despite the high contribution of continental species by the Sô River (Gnohossou, 2006). The low abundance of macroinvertebrate at Ganvié could be related to the high anthropogenic pressure occurring at this site (more than 2500 house built on stilts).

3.3.3. Abundance and biomass of macroinvertebrate

The Amphipods are the largest macroinvertebrate in Lake Nokoué (Gnohossou, 2006). They were found everywhere in the lake with amphilochidae being the most abundant in the saline water phase and melitidae more the most abundant in the non-saline water phase. The molluscs had the highest biomass. They are dominated by Potamididae which are mainly found in the area with less organic pollution such as the centre and the east locations of the lake. Potamididae appeared to be very little consumed by fish (Gnohossou et al., 2009), which could explain why they were the dominant taxon regarding biomass. In general, the biomass of the macroinvertebrate in the lake increased rapidly at low water periods, although the species richness at this period was very low compared to high water period (Gnohossou, 2006). This could be explained by the fact that biomass value raised at low water period by saltwater macroinvertebrates which were large in size and weight. During high-water periods these species retreat and give way to freshwater species that are more diversified but smaller in size and weight.

3.4. Ichthyofauna

Fish fauna has been extensively studied in Lake Nokoué (60% of papers collected). Various topics have been investigated including standard topics such as fish assemblage patterns, spatio-temporal distribution and length-frequency distribution (Welcomme, 1972; Adite and Winemiller, 1997; Lalèyè et al., 2003); but also more specific topics such as particular eco-morphological relationships, population parameters, dietary patterns, anatomical features and fish parasites (Niyonkuru et al., 2007; Niyonkuru and Lalèyè, 2012; Dougnon et al., 2012; Gnohossou et al., 2013). This review focused on the information which helped to understand the interaction between fish species and the other ecological components of the lake.

3.4.1. Diversity and species richness

The fish diversity of Lake Nokoué eroded about 42% from the 1960s to 2000s (Table 2). This situation has been explained by various causes including the increasing pressure of acadja practices (Niyonkuru and Lalèyè, 2010), the changes in the water exchanges with the sea (since the 1960s), and the degradation of nursery area and mangrove (riparian habitat) (Adite and Winemiller, 1997). The lowest value of species richness was observed by Adite and Winemiller (1997). However, this could be explained by the period of this study which was short when compared to the other studies (Table 2). Even though Adite and Winemiller (1997) covered a shorter period, this study appeared to have 19 and 03 dissimilarities in fish species with respectively Lalèyè et al. (2003) and Van Thielen et al. (1987). These observations suggested a rapid temporal variability in the species composition of the lake. This could be explained by the alternation between freshwater, brackish water, and saline water. The current species richness of Lake Nokoué based on the latest studies (Adite and Winemiller, 1997; Gnohossou, 2006; Lalèyè et al., 2003) could be estimated at 45 species from 23 families.

An analysis of the fish assemblage patterns based on the studies enumerated in Table 2, showed a significant temporal and spatial variation of species richness with spatial variation stronger than temporal variation. These spatial and temporal variations in assemblage structure have been associated primarily to the spatial–temporal variation of the water quality especially salinity variation (Fig. 6). Three types of fish species have been distinguished: estuarine species, marine species and freshwater species (Welcomme, 1972; Van Thielen et al., 1987; Adite and Winemiller, 1997). The latest classification proposed five major categories (Lalèyè et al., 2003):

- *Category 1*: species found in the lake throughout the year (8 species).
- *Category 2*: exclusively estuarine and lagoon species (5 species).
- *Category 3*: euryhaline freshwater species, whose appearance determined by salinity tolerance <5‰ (10 species); they appeared in the lake in November and December.
- *Category 4*: occasional marine species (11 species). Most species from this category appeared between February and August in the north of the lake, where the salinity remained high (>20‰).
- *Category 5*: species which are very rare or absent during the high water period between September and November, but which appear when salinity is >10‰ (14 species).

3.4.2. Fish abundance

Despite the relatively important fish fauna diversity of Lake Nokoué, very few species contribute substantially to the catch. Considering the last three decades, *Ethmalosa fimbriata* was the most abundant species, representing about 40% of annual catches, followed by *Sarotherodon melanotheron* and *Gerres melanopterus* which comprised between 25% and 10% of annual catches (Adite and Winemiller, 1997; Lalèyè et al., 2003). Almost 90% of the total fish production in Lake Nokoué came from less than 20% of the fauna (Niyonkuru et al., 2007). The spatial distribution of fish abundance in Lake Nokoué was not uniform. The west and the north of the lake were more productive than the other locations. However, this is probably related to the acadjas spatial distribution which is mostly located in the west and northwest (Niyonkuru and Lalèyè, 2010). *E. fimbriata* was more likely to be found in the south of the lake, while *S. melanotheron* was likely to be found in the northwest near Sô River. *G. melanopterus* mainly populated the north and northeast locations.

Table 2
Ichthyofauna richness evolution from the 1960s to 2000s in Lake Nokoué.

Year	Hydrological period sampled	Nb. of points sampled	Nb. of species	Nb. of families	Most represented family	Most abundant species	References
1960–1961	All periods	–	87	43	–	–	Gras (1961)
1980s	–	–	62	–	–	–	Van Thielen et al. (1987)
1990–1991	All periods	4	78	36	–	–	Lalèyè (1995)
1994	Jun. to Sep.	7	35	20	Mugilidae	*Ethmalosa fimbriata* (39%) *Gerres melanopterus* (22%) *Sarotherodon melanotheron* (9%)	Adite and Winemiller (1997)
1997	All periods	3	67	33	–	–	Lalèyè et al. (1997)
2000–2001	All periods	3	51	34	Gobiidae	*Ethmalosa fimbriata* (40%) *Sarotherodon melanotheron* (15%) *Gerres melanopterus* (12%)	Lalèyè et al. (2003)

3.4.3. Habitat preference and biomass

Most fish in Lake Nokoué were captured in shallow areas and with a high preference for the acadja habitat (Adite and Winemiller, 1997; Lalèyè et al., 2003). Since the years 1990s almost 85% the fishes captured have been from acadja (Niyonkuru and Lalèyè, 2010). It appeared that some species (such as *Polydactilus quadrifilis*) had even shifted their habitat from the open water to acadja to avoid their natural predator (Adite and Winemiller, 1997). Similar observations were made in Ebrié Lagoon where acadja was experimentally introduced in early 1990 to increase fish productivity (Guiral et al., 1993). This high productivity of acadja has been linked to an important spatial concentration of the periphyton on the brushwood and to a productivity per biomass unit and a photosynthetic efficiency significantly higher for fixed communities than for pelagic communities (Guiral et al., 1993; Welcomme et al., 2005; Villanueva et al., 2006).

It has been reported by many studies that fish catches at around Ganvié (villages on stilts) were very low, and only a few species (8 species) were found at that location (Adite and Winemiller, 1997; Lalèyè et al., 2003). This observation also included acadja habitat at this location (Niyonkuru and Lalèyè, 2010). The high turbidity and high organic matter concentration could explain the low fish species richness and abundance at Ganvié. Furthermore, it is important to note there was a constant motorised boat traffic around Ganvié (due to the villages on stilts), which could make this environment too distributed for fish development.

Lake Nokoué is recognised to be the most productive coastal lake in West Africa (Lalèyè, 1995; Welcomme et al., 2005; Villanueva et al., 2006). Fish catches in Lake Nokoué have been estimated at 102 t km^{-2} $year^{-1}$ which is 10 times greater than catches in Lake Ebrié (a coastal lake in Ivory coast) and far higher than the catches in Lagos Lagoons in Nigeria (Villanueva et al., 2006). Abundance and occurrence of fish in Lake Nokoué seem to be highly influenced by (i) acadja distribution which increases food availability and possibilities to hide from predator, by (ii) the water quality parameters mainly salinity but also water turbidity and concentration of organic matter in the water which governed the spatio-temporal variation of the species and by (iii) intensive catching pressure which limit the recovery of the fish population.

3.4.4. Dietary analysis

Regarding food resource use by fish species in Lake Nokoué, three major groups were detected: (i) species that fed mostly on detritus with niche overlaps ranging from 0.92 to 1.00 (*Chrysichthys nigrodigitatus*, *E. fimbriata*, *Liza falcipinnis*, *S. melanotheron*, *Synaptura lusitanica*, and *Tilapia guineensis*), (ii) piscivorous species with overlaps between 0.88 and 0.95 (*Eleotris senegalensis*, *Hemichromis fasciatus* and *Lutjanus goriensis* and *Elops lacerta*) and (iii) species that fed on zooplankton and macroinvertebrates (*G. melanopterus*, *Pomadasys jubelini* and *Citharichthys stampflii*), with low overlap <0.4 (Adite and Winemiller, 1997; Gnohossou, 2006).

Diet analysis revealed that an important proportion of fish species (24–32%) used a single resource (Adite and Winemiller, 1997; Gnohossou, 2006). Most of these species were piscivores or invertebrate feeders and were mainly present in high water period with low abundance. The most abundant species in the lake were species with large diet plasticity such as *S. melanotheron* and *C. nigrodigitatus* which passed from detritivores in high water to zooplantkivorous during low water periods. In fact, the high development of acadja fishing practices has considerably increased the availability of detritus in the lake and reduce the availability of invertebrate. This situation might have also conducted to feeding adaptation of some species such as *E. fimbriata* which has been characterised as zooplanktivorous feeder in early 1980s (Albaret and Legendre, 1985) but which was considerably feeding on decaying materials in the 2000s (Gnohossou, 2006).

3.5. Piscivorous birds and fishery interaction in Lake Nokoué

Two main species of piscivorous birds occur on Lake Nokoué namely Malachite Kingfisher (*Alcedo cristata*), and the Pied Kingfisher (*Ceryle rudis*) (Libois and Laudelout, 2004). They were mostly found in the delta of the Sô River just at the north of Ganvié (Fig. 1). The feeding ecology of the kingfisher covered 18 prey categories over the 45 fish species enumerated in the lake (Laudelout and Libois, 2003). The main prey were cichlids (*S. melanotheron* and *H. fasciatus*), followed by clupeids (*E. fimbriata*) and eleotrids (*Kribia* sp.); although most of these species are demersal and should not be available for birds. Analysis of prey size indicated that they are taken by birds at an early age while they are still small probably just after the reproductive season. This could explain they availability to piscivorous birds since most of the eggs of the prey fish species are usually attached to submerged macrophytes (Collette and Parin, 1990), which are highly found in the arms of Sô River before its entrance to Lake Nokoué.

A comparison between fish taken by kingfisher and fish caught by fishery on Lake Nokoué suggested that the negative economic impact of the piscivorous birds was restricted to *S. melanotheron* (Laudelout and Libois, 2003) since the other species consumed have no or low market value. In addition, the consumed *S. melanotheron* were small individuals under the market size, and therefore, the economic loss for fishermen resides on the hypothesis that these small tilapias might grow to marketable size if piscivorous birds did not take them. However, this negative economic impact is probably counterbalanced by the high amount of *H. fasciatus* (a voracious predator of *S. melanotheron*) captured by the birds.

4. Trophic structure and interactions in Lake Nokoué

Research on the ecology of the aquatic communities of Lake Nokoué remains limited compared to the other coastal lakes of West Africa such as Lake Ebrié (Ivory Coast) and Lagos Lagoon (Nigeria).

4.1. Temporal and seasonal evolution of the trophic groups

Before the widening of the sea entrance into the Lake Nokoué and the subsequent modification of its hydrodynamics, there was almost no seasonal difference within the species richness of the trophic groups. Observations made in 2004 showed that the species richness had highly changed from the high to the low water indicating a strong seasonal difference in the structuration of the trophic groups. In general, the richness of detritivores and piscivores groups has increased between 1960 and 2004 for the disadvantage of benthivores and the group of zooplanktivores (Fig. 4) (Gras, 1961; Gnohossou, 2006). The zooplanktivores group, which was the smallest group in 1960 was entirely absent in 2004 at the low water period (Fig. 4). Between the 1960s and 2000s, the majority of the extinct fish species in the lake are zooplanktivorous and benthivorous species (Lalèyè et al., 2003). This suggests a decrease in the zooplankton and benthic communities since 1960. Another probable cause could be a perturbation of the benthic habitat by the deposits of acadja debris and dead water hyacinth which sink to the bottom of the lake (Mama et al., 2011b).

At the low water period detritivores group dominates in fish biomass, while at the high water period zooplanktivores group invaded the lake (Fig. 4). In fact, during the high water period, freshwater fish migrate from tributaries into Lake Nokoué. In addition, the plastic diet of *E. fimbriata* (which can shift from detritivores to zooplanktivores) increase zooplanktivores biomass. At the same period, the marine fish migrate back to the Atlantic Ocean. They will come back to the lake when salinity increase at the low water period and most of the freshwater fish will migrate back to tributaries (Fig. 4). This fish migration cycle has been promoted on one hand by the intensification of the water exchange between the lake and the Atlantic Ocean due to the widening of the sea entrance into the lake around 1960; and on the other hand by the intensification of acadja and water hyacinth detritus which seem to have promoted detritivorous fish development.

4.2. System's maturity

Lake Nokoué appeared to be a more mature and stable ecosystem compared to the other coastal lakes in West Africa (Villanueva et al., 2006), despite its lower primary production from pelagic phytoplankton and riparian vegetation. The primary production is governed by the high photosynthetic yield of the fixed communities (periphyton) which grow on acadja woods and constitutes a surplus autotrophic production. The increased availability of detritus due to high use of acadja seemed to have increased re-mineralization of organic materials and mitigated resource limitations in this ecosystem. Acadja in Lake Nokoué seemed to have played a significant role in resource compensation; and has influenced the energy flow in the system. For instance, some carnivorous species such as the *C. nigrodigitatus*, *E. fimbriata*, *Trachinotus ovatus* and *L. falcipinnis* periodically shift to detritus feeding when other resources are limited (Adite and Winemiller, 1997) competing with true detritivores of the system such as *S. melanotheron* and *T. guineensis*. Lake Nokoué is a detritus-driven ecosystem with only a small use of phytoplankton, zooplankton and even *S. melanotheron* by the higher trophic level (Villanueva et al., 2006).

4.3. Simplified model of Lake Nokoué

Based on the different interactions described in the previous sections between the hydrology, the water quality, the habitat, and the biodiversity of Lake Nokoué, we have established a simplified model structure of the lake's ecology (Fig. 5). The model indicates that the ecohydrology of Lake Nokoué includes five main components towards which management actions can be directed: (1) the hydrological processes, (2) the anthropogenic pressure, (3) the water quality processes, (4) the biological components and (5) the detritus. The hydrological processes in Lake Nokoué directly influence it water quality through the regulation of the salinity regime and loads of riverine nutrients. The anthropogenic pressure on the system is mainly the acadja fishing practices and the nutrient load from the surrounding cities and the villages on stilts. These pressures affect the water quality and the accumulation of detritus in the ecosystem. The biological components influence each other and react to water quality, anthropogenic pressure and detritus.

Detritus is the main driver of Lake Nokoué's ecosystem, followed by salinity regime and acadja practice. Detritus-based ecosystems are recognised to be more stable both

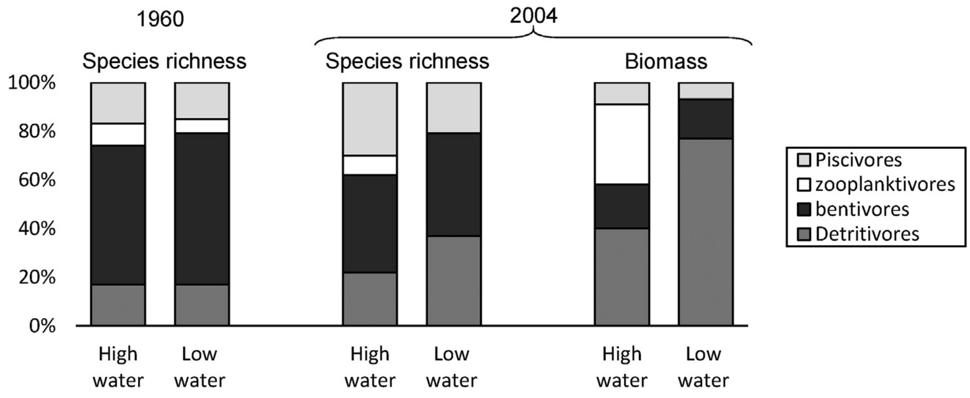

Fig. 4. Temporal and seasonal variation of evolution of the species richness and total biomass of different trophic groups between 1960 (Gras, 1961) and 2004 (Gnohossou, 2006).

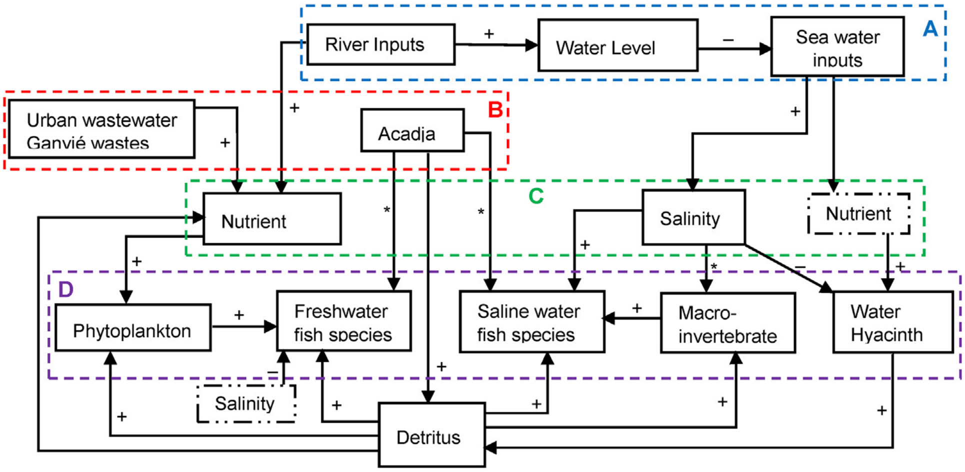

Fig. 5. Simplified model of interaction in Lake Nokoué. The direction of the arrows indicates which component is affecting the other. (A) The hydrological processes, (B) the anthropogenic pressure, (C) the water quality processes, and (D) the biological components. The sign (+) means a positive correlation between the components, (−) means a negative correlation between the components and (*) positive relation on biomass and negative relation on richness.

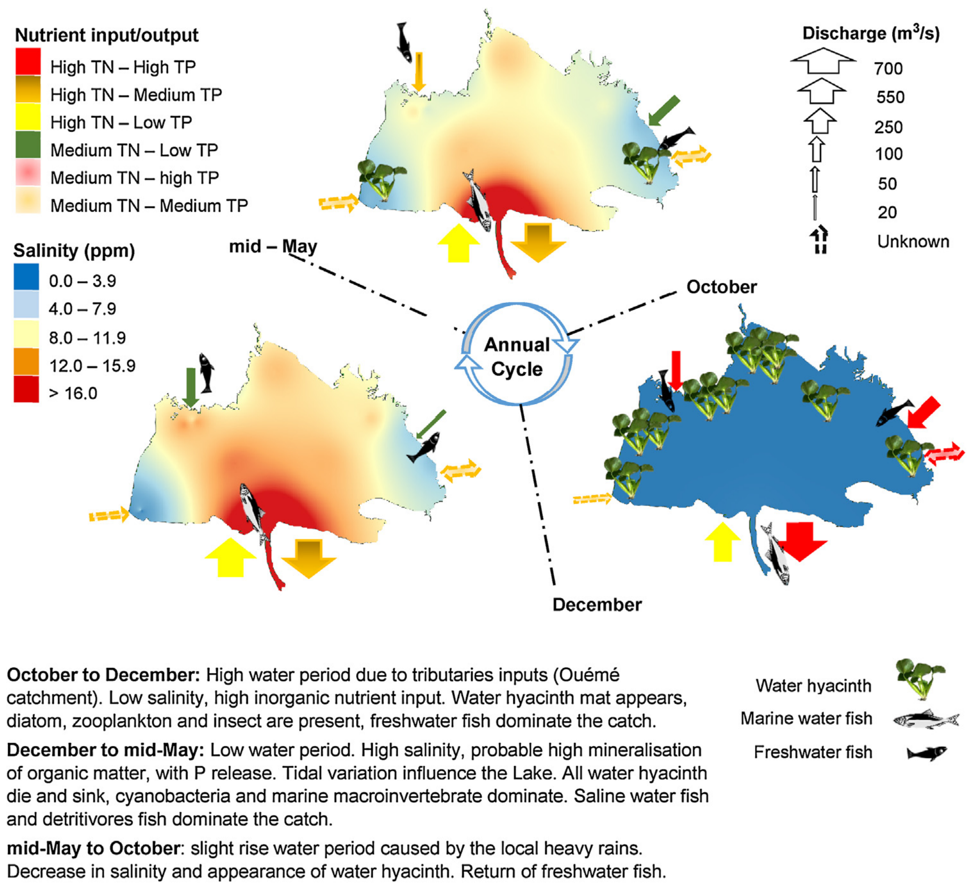

Fig. 6. Summary of hydrological regime of Lake Nokoué with salinity variations (ppt), nutrient exchange with tributaries and Atlantic Ocean, seasonal trophic structure evolution and biomass of different trophic groups catch by the fishery. Based on Gnohossou (2006), Adite and Winemiller (1997), Mama et al. (2011a,b), Lalèyè et al. (2003) and Zandagba et al. (2016b).

regarding energy fluxes and consumer population dynamics. With dissolved nutrients, detritus support the pelagic food web of the coastal zone and estuaries (Bonthu et al., 2016). However, an excess of detritus can alter energy path and affect nutrient-transfer efficiencies across trophic levels (Villanueva et al., 2006; Moore et al., 2004) and therefore lead to a reduction of species richness (as observed in Lake Nokoué, Fig. 4). Note that the direct factors which promote detritus accumulation in Lake Nokoué are the decay of acadja woods and the seasonal deposition of dead water hyacinth due to increase in salinity concentration above 6 ppt. Therefore, the reduction of detritus accumulation in Lake Nokoué should include the management actions towards reduction of acadja practice and removal of water hyacinth before they died. This approach requires mapping and monitoring of both acadja and water hyacinth to understand their dynamic, and the processes affecting them.

5. Perspectives for further research on Lake Nokoué ecology

Strategies for the conservation and restoration of coastal lakes and lagoons need to take two elements into account: (1) elimination of threats, and (2) amplification of opportunities to guarantee that they reach their goals (Wagner et al., 2009; Zalewski, 2014; Skłodowski et al., 2014). It is also important that ecosystem conservation and restoration strategies are designed together with a strategy of economic growth since the goal of conservation shouldn't be to remove humans from the ecosystem but to ensure that they make sustainable use of the ecosystem. Zalewski (2014) stated that the strategy of economic growth around aquatic ecosystem should, therefore, be shifted from competition for resources to competition in their efficient use. Further research around Lake Nokoué needs to integrate these new paradigms for the design of sustainable conservation, restoration, and economic growth solutions.

It is clear that habitats and biodiversity in Lake Nokoué have been highly modified because of human activities. However, efforts to bring back the global biodiversity and bio-productivity of this lake should not obstruct its services to the society. Further research should focus on strengthening the overall resilience of the landscape to the environmental and human-induced stress (environmental stability). There is a need to assess the trade-offs inherent in managing humans embedded in Lake Nokoué system. This requires (i) a quantification and valuation of the important ecosystem services (ii) an analysis of the magnitudes of changes in these ecosystem services that result from anthropogenic actions and (iii) the economic impact of these changes. Filling this gap will allow harmonisation of societal needs with the enhanced ecosystem potential and constitute the first step in elaborating the trade-offs for the management strategies of Lake Nokoué to preserve both biodiversity and human welfare.

Unfortunately, because of the lack of historical data, and it is still difficult to quantify the amplitude and the impacts of the changes in the hydrological regime and the water quality of Lake Nokoué on its biota. Also, this lack of historical data makes difficult the definition of reference conditions, considering that the entire lake ecosystem is already highly modified. In this review, the information provided on the lagoons similar to Lake Nokoué constitutes an insight into the definition of it reference conditions. Considering the similarities observed in climate, geomorphology and anthropogenic pressure of West African open coastal lakes, one can think about defining unique reference conditions for these ecosystems. However, specific conservation and restoration targets for each ecosystem have to be set based on the services it provides to the society. For instance, it appears that reference conditions for the riparian habitat of West African coastal lakes and lagoons should be characterised by dominant mangrove vegetation, mainly *R. racemose* and *Avicennia germinans*. Therefore, restoration of riparian habitat on the West African coastline must logically include planting mangrove. However, for Lake Nokoué, where mangrove have been destroyed to make acadja, a crucial question would be whether planting mangrove is sustainable, if not, can mangrove restoration be achieved by the removal of pressures, and, it is even possible to remove the pressure. Targets for riparian habitat restoration in Lake Nokoué must consider acadja development and should there include a large awareness campaign for maintaining mangrove and alternative measures for the construction of acadja or even insertion of rules for the regulation of acadja development.

Yet, the impacts of the abrupt historical changes in the hydrological regime and the water quality of Lake Nokoué on its biota are not well-known. The evaluation of these impacts requires (i) the definition of reference conditions for the biota and (ii) the quantification of the biomass input/output by fish and macroinvertebrate migration seaward/landward through the channel of Cotonou and from the lake tributaries. Current knowledge on the spatio-temporal variations of these phytoplankton and zooplankton communities does not cover a full hydrological cycle. Therefore the analysis of the ecological threshold in Lake Nokoué, namely the analysis of salinity and water level changes, on the primary producers cannot be performed based on the current knowledge of the system. More complete data collection on water quality and biota migration need to be done. Also, research should be made on strategies for the reduction of the detritus accumulation in the system. Possible joint solutions for the reduction of detritus could be (i) removal of water hyacinth before they died, meaning before salinity rise above 6 ppt and (ii) removal of the woodbrush of acadja after fish harvest. This will also contribute to reduction of potential internal nutrient loads in the system. This implies that further research on the lake should investigate the components of the nutrient budget including the influence of seasonal water hyacinth death and acadja decays on the internal nutrient loads (Djihouessi and Aina, 2018). Decision makers should also establish monitoring strategies for the reduction of riverine nutrient loads. This implies first the identification of the anthropogenically highly modified parts of river basins, and second the elaboration of dual regulation measures (focusing on water and biota) for these areas. Examples of regulation measures could be the promotion of drip irrigation, to optimise the amount of fertiliser applied, the construction of structures for erosion control in agricultural lands and the restoration of rivers riparian vegetation. In addition to all these measure decision makers should promote the construction of wastewater treatment plants for the cities of Abomey Calavi, Cotonou and the villages on stilts the effective reduction of nutrient loads in the lake.

6. Conclusion

The review of studies on the habitat and the biodiversity of Lake Nokoué showed the short and long-term response of the biota to a constantly and highly impacted habitat. From 1980 to 2000 the riparian vegetation of the lake has been destroyed due to the increased urbanisation around the lake. One peculiarity of Lake Nokoué is the massive use of "brush parks," also known as "acadja." This habitat present in the pelagic zone enhances fish production with an increase of detritus in the lake. Acadja practices have shown a positive impact on fish catch, but they also contribute to the reduction of diversity of fish fauna with the extinction of many zooplanktivorous and benthivorous species and the proliferation of detritivores. Further researches are still needed to understand the spatio-temporal dynamic of the phytoplankton and zooplankton communities in the lake.

Conflict of interest

None declared.

Ethical statement

Authors state that the research was conducted according to ethical standards.

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