Distribution and ecology of freshwater oyster *Etheria elliptica* (Lamarck, 1807) in Pendjari River (Benin-West Africa)

Giraud David Akélé, Delphine Adandéjjan, Elie Montchowui and Philippe Adédjobi Lalèyè

**Abstract**

*Etheria elliptica* (Bivalvia, Etheriidae) is the only freshwater oyster occurring widely in tropical Africa and Madagascar. The distribution and ecology of *E. elliptica* were investigated in Pendjari River, a tributary of Volta basin. Correspondence Analysis and corrected frequencies were performed on bivalve presence/absence data and abiotic factors. Mean density and mean biomass ranged from 0 to 40 ind./m² and 0 to 3.8 kg/m², respectively. *E. elliptica* exhibited a patchy distribution in Pendjari River (Moriota index $\delta$ =14.8) occurring mostly in middle and downstream sites. Conversely, species was absent in river upstream. Oyster showed a preference for sections of river with hard substrates used for cementation. However, the oyster was encountered also in silty and sandy habitats forming large size colonies. Total Dissolved Solids (TDS) and altitude appeared to be the significant factors affecting oyster distribution in Pendjari River. Oyster was observed both in calm and turbulent sections of the River. Range of water parameters corresponded to ecological requirements for oyster survival and development. *E. elliptica* showed plasticity for a large range of habitats suggesting its potential for culture in the River. Management strategies based on oyster ecology could ensure its conservation in Pendjari River.

**Keywords:** Freshwater mollusk, bivalvia, distribution pattern, ecological preferendum.

1. **Introduction**

Freshwater oysters belong to family Etheriidae (Mollusca: Bivalvia, Unionoida). The family Etheriidae is a small family of sessile, oyster-like bivalves with irregular shells occurring almost entirely within the tropics. The family Etheriidae is composed of only four apparently monotypic genera, *Etheria*, *Bartletta*, *Acostaea* and *Pseudomulleria* distributed in Africa, South America and India [1-2,5]. Freshwater oysters spend their entire life cycle in freshwaters. In their distribution range, freshwater oysters were important as food and source of income [1-2,4]. Like all freshwater mussels (Unionoida), freshwater oysters have a complex life including obligate parasite larval stage requiring host fish species for reproduction [1,4]. Thus, distribution range of fish species likely affect greatly freshwater oysters spatial occurrence [5]. Moreover, owing to their complex life cycle, freshwater mussels (including freshwater oysters) were imperilled worldwide due to human disturbance especially catchment degradation, river flow modification resulting from dams building, water pollution through unsustainable agriculture practices and host fish overexploitation [6]. In this light, many studies revealed anthropogenic threats affecting the freshwater oysters in their distribution range [2,7-8]. In Columbia, the freshwater oyster *Acosta rivoli* Deshayes 1827, (Bivalvia, Etheriidae) was facing extinction in upper reaches of Magdalena River basin due to riverbanks deforestation leading to flow reduction and mollusk habitat modification, agricultural pollution and overexploitation [2]. In Southern India, natural habitats and survival of the freshwater oyster *Pseudomulleria dalyi* (Smith) (Bivalvia, Etheriidae) were threatened by modification of water flow increasing siltation and overexploitation of fish species; including its host fish species [7-8]. However, knowledge on the relationship between oysters’ distribution and environmental factors were poorly documented. Such data are of great importance to ecologists not only to understand species habitats requirements but also to develop resource-specific exploitation and conservation strategies [6-9].
In tropical Africa, the family Etheriidae is represented by a single freshwater oyster Etheria elliptica (Lamarck, 1807). E. elliptica is exclusively freshwater species and widespread throughout African rivers and lakes \[3-10\]. E. elliptica supported important fishery for food and income. In Nigeria, the bivalve represented 15.4% of fisheries \[11\]. Previous studies have widely documented freshwater oyster distribution in tropical Africa \[3-12-13\]. Available reports on ecology of E. elliptica was mostly limited to cementation on hard substratum such as stone, rock and preferrence for moving and turbulent river waters even if species was encountered in calm waters \[4-13\]. Conversely, the distribution and ecology of freshwater oyster E. elliptica at river scale was poorly known \[3-14\].

E. elliptica occurred in Pendjari River, a main tributary of Volta basin (West Africa) \[15-16\]. The Pendjari River as well as Volta basin rivers was facing negative effects of human disturbance (river flow modification resulting from dam implantation, agricultural pollution, sewage, bathing, washing, narcotic fish capture with chemicals) \[15-17\]. Such factors affect adversely habitats of benthic freshwater bivalves, therefore their distribution and ecology \[6-9\]. The present study aims at assessing distribution pattern and ecological preferendum of E. elliptica in Pendjari River. Such information was of great importance for species management and conservation strategy.

2. Materials and Methods

2.1. Study area

Samplings were carried out in April 2009 along Pendjari River (Figure 1). Pendjari River is a tributary of Volta basin \[15\]. The river is located in Sudanian climatic zone with one rainy season (May/June to October) and one dry season (November to March/April). Higher temperatures occurred in March, April and May and lower values were recorded in December, January and February during Harmattan \[15\]. Daily temperature varies between 11°C (at night) up to 40°C in the area. Mean rainfall reached annually 1000 mm with 60% falling between July and September. Pendjari River had a tropical hydrological regime with a low water level season between December and June and a flood season from September to October.

![Fig 1: Map displaying sampling sites in different zones along the Pendjari River (Benin).](image)

2.2. Samplings

Sampling was performed from upstream to downstream stations, consecutively. Forty-two (42) stations have been sampled (Figure 1). Deeper water level, wild animals presence, accessibility prevent Data were collected based on systematic and random sampling method. Sampling stations were chosen at regular interval of 3 km. prior to field study, stations were chosen on map of Pendjari River using Arcview software. Density and biomass were recorded using a quadrant of 1m². Quadrat was used between 6-10 times per sampling site. The number of quadrats per station was estimated based on its area (width and length of the River) using a random table \[18-19\]. At each sampling site, the number of individuals was counted in each quadrat and the biomass was estimated in g. The size of colony (number of oysters) in aggregation was assessed by counting oyster specimens. Mean density and biomass were computed for each station to analyze oyster distribution pattern.

Two categories of abiotic factors (substrates type and environmental factors) were collected in each station. Substrates type and their proportion were assessed visually. Sediment type was grouped in silt, sand and gravel \[20\]. Trees species broken in the River were often used by the bivalve as settlement substrates. Tree species were sampled and identified later at National Herbarium of University of Abomey–Calavi (Benin). Water velocity was classified as null, low, mean and high according to observed flow intensity. Altitude was recorded using Garmin GPS. Water temperature (°C), pH, TDS (mg/L) and conductivity (µS/cm) were recorded in water bottom with pH/EC/TDS/Temperature meters (HANNA Combo HI-98129). Dissolved oxygen (mg/L) in bottom was measured with oxygen measuring instrument (DO-100 Voltcraft). Depth (m) and water transparency was estimated with a Secchi disc to the nearest cm.
2.3. Oyster distribution pattern

The index of Morisita [21] measured the dispersion of individuals in a population. The index was implemented to assess the distribution pattern of oyster population in Pendjari River. Based on quadrat technique, the index expressed the structure of spatial distribution of individuals and revealed the degree of aggregation or departure from randomness of distribution of individuals. Unlike many dispersion indices, Morisita index was most reliable [21] as it is independent of the quadrat size taken as sampling unit.

Morisita index formula was as follows:

$$I_o = \frac{\sum_{i=1}^{q} \frac{n_i}{N(N-1)} (n_i - 1)}{n_i}$$

Where $q$ was number of quadrats sampled, $n_i$ ($i=1, 2, 3, 4,...,q$) the number of individuals found in each of the quadrats (Morisita, 1959). The $\chi^2$ test of Fisher was used to analyze the significance of Morisita index. Morisita index takes the value of unity when the individuals were distributed at random; the value was smaller than unity when individuals were distributed uniformly over the study area. In the case of contagious or patchy distribution, the index value is larger than unity [21].

2.4. Factors affecting oyster spatial distribution

To assess factors affecting oyster distribution in Pendjari River, population attributes of bivalve (density, biomass and colony size) were categorized in almost equal range (Table 1). Likewise, type of substrata (Table 2) and environmental factors (Table 3) were also classified in three different groups to perform correspondence Analysis [22-23]. Then, a correspondence Analysis (CA) was performed between populations attributes (density, biomass, colony size) and substrates type (silt, sand, dead woods and gravel), on one hand, and between population parameters and environmental factors (temperature, transparency, depth, TDS, Dissolved oxygen and Altitude) on the other hand.

Table 1: Code of populations attributes of freshwater oyster E. elliptica in Pendjari River. Density was estimated in ind./m$^2$ and biomass in g/m$^2$.

<table>
<thead>
<tr>
<th>Code</th>
<th>Mean density (N)</th>
<th>Biomass (B)</th>
<th>Colony (C)</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>1</td>
<td>0.5 - 6.5</td>
<td>34.8 - 367.5</td>
<td>3.0 - 10</td>
</tr>
<tr>
<td>2</td>
<td>6.6 - 41.6</td>
<td>369 - 3805</td>
<td>11 - 179</td>
</tr>
</tbody>
</table>

Table 2: Code of oyster settlement substrates encountered in Pendjari River.

<table>
<thead>
<tr>
<th>Code</th>
<th>Silt (A)</th>
<th>Sand (S)</th>
<th>Gravel (G)</th>
<th>Dead woods (P)</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>0</td>
<td>0 - 9</td>
<td>0 - 9</td>
<td>No woods</td>
</tr>
<tr>
<td>1</td>
<td>10 - 40</td>
<td>10 - 40</td>
<td>10 - 30</td>
<td>Bora/Cola/Pari/Coac</td>
</tr>
<tr>
<td>2</td>
<td>50 - 90</td>
<td>50 - 100</td>
<td>40 - 90</td>
<td>Sygi</td>
</tr>
</tbody>
</table>

Bora: Bhorassus aethiopium; Cola: Cola lauriflora; Pari: Pari narius curatellifolia Coac: Combretum acutum; Sygi: Syzygium guineense

Table 3: Code of environmental factors affecting distribution of freshwater oyster E. elliptica in Pendjari River.

<table>
<thead>
<tr>
<th>Code</th>
<th>Temperature (T)</th>
<th>Transparency (TR)</th>
<th>Depth (D)</th>
<th>pH (P)</th>
<th>TDS (TD)</th>
<th>Oxygen (OX)</th>
<th>Velocity (V)</th>
<th>Altitude (L)</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>28.4 - 29.2</td>
<td>7 - 12</td>
<td>0.2 - 0.58</td>
<td>7.28 - 7.56</td>
<td>17 - 23</td>
<td>0.6 - 1.8</td>
<td>Null</td>
<td>120 - 141</td>
</tr>
<tr>
<td>1</td>
<td>29.4 - 30.8</td>
<td>15 - 18</td>
<td>0.6 - 0.96</td>
<td>7.57 - 7.72</td>
<td>25 - 32</td>
<td>2 - 3.8</td>
<td>Low</td>
<td>144 - 175</td>
</tr>
<tr>
<td>2</td>
<td>31.7 - 34.3</td>
<td>19 - 21</td>
<td>1.0 - 1.2</td>
<td>7.84 - 7.96</td>
<td>33 - 35</td>
<td>4.1 - 5.1</td>
<td>Mean</td>
<td>178 - 214</td>
</tr>
<tr>
<td>3</td>
<td>34.5 - 38.2</td>
<td>22 - 55</td>
<td>1.3 - 2</td>
<td>8.02 - 8.86</td>
<td>36 - 46</td>
<td>6 - 13.6</td>
<td>High</td>
<td>-</td>
</tr>
</tbody>
</table>

Codes were indicated in brackets in table. Temperature (°C), Transparency (cm), depth (m), TDS (mg/L), Dissolved oxygen (mg/L), Altitude (m).

2.5. Ecological preferendum

Among different abiotic factors governing species distribution pattern, freshwater bivalve often displays preference for specific habitats [6] (Strayer et al., 2004). The corrected frequency based on absence/presence of species in different habitats has been developed to identify the preference range of species [25].

To assess the effect of environmental factors on the species, the variation interval of each factor was divided into three classes, and the corrected frequencies [25] of the presence of the species in each class were calculated with the following expression:

$$C(K) = \frac{U(K)/R(K)}{U(E)/NR}$$

where $C(K)$ are the corrected frequencies; $U(K)$ is the number of samples of class K in which the species is present; $R(K)$ is the total number of class K samples; $U(E)$ is the total number of samples in which the species is present and NR is the total number of samples.

A corrected frequency value was estimated for different ranges of each abiotic factor. A corrected value upper than or equal to 1 suggests the preference of species for this class of factor values. In contrast, values of corrected frequency lower to 1 indicate otherwise. A chi-squared ($\chi^2$) test was applied to the results for each factor to establish which results were significant.

3. Results

3.1. Density, biomass and spatial distribution pattern of oyster

Oyster mean density covered a range of 0 to 40 ind./m$^2$. High abundances (35-40 ind./m$^2$ of freshwater oyster were recorded in stations located in core zone while the bivalve was completely absent upstream. Maximum density reaching 215 ind/m$^2$ in stations located in core zone of Pendjari Biosphere Reserve. Oyster densities (2.3 – 13.5 ind/m$^2$) were lower in downstream sites mainly due to exploitation (Figure 2). Mean biomass ranged from 0 to 3.8 kg/m$^2$ and showed a similar trend to oyster density (Figure 3). Mean density was significantly higher in core zone and in some stations of Porga hunting zone (mean density range: 0 – 42 ind./m$^2$) than in downstream sites of the river (open access sites and some stations of Porga hunting zone) (mean density range: 0 – 10 ind./m$^2$) (Kruskall-Wallis test: $H=12.7; p < 0.01$).

Morisita index accounted for $I_o = 14.8$. This value was clearly larger than unity indicating that the freshwater oyster depicted a patchy distribution in Pendjari River at 5% of significance ($F_0 = 63.15 > F_{0.05} = 1.15$).
3.2. Substrates and oyster distribution
Correspondence analysis allows the simultaneous plot and analysis of species attributes and environmental parameters. In Pendjari River, freshwater oyster *Etheria elliptica* was present in 22 stations out of 42 sampled along the river during low water period in April 2009. Oyster lived attached to different substrates including gravel or pebble, dead woods or lived in colonies.
The first three inertia axes extract 96.16 % of the total variance, with 51.32 %, 28.75 % and 16.09 % for axis 1, 2 and 3 respectively. The axis 3 explained a low portion of variance, therefore our analysis were restricted to the plane 1-2 (Figure 4). The position of population attributes on axis 1 indicates an abundance gradient. The nil or low values for density, biomass and colony size (on the negative side of the axis) are opposed to the medium and high values (on the positive side of the axis). On axis 2, high density and biomass values (on the negative side) were separated from the medium values (on the positive side). Colony size shows an increasing gradient from negative side of axis 1 (C0, C1) to positive side (C2). Density and biomass attributes appeared to be close in plane1-2 suggesting a homogenous demographic structure of the population in our samples.

The substrates type that contribute the most to axes 1 and 2 were gravel and dead woods originated from tree species living on the river banks. In our samples, main settlement substrates recorded for E. elliptica were gravel (71 %) and dead woods (19 %). The tree species frequently encountered in Pendjari River and serving as substrates for bivalve were Bhorassus aethiopium, Cola lauriflora, Combretum acutum, Syzygium guineense guineense and Parinari curatellifolia.

Low values of density, biomass and colony size (N0, B0, C0) are related to low gravel (G0) and dead woods use as fixation substrates (P1, P2). This suggests that dead woods are alternative substrates when others such as gravel are lacking. High colony size (C2) was reported in stations lacking substrates (gravel or dead woods). Surprisingly, the decrease of values of populations attributes along the axis 2 corresponds to increasing values of gravel. The highest density and biomass (N2, B2) were obtained in sites medium proportion of gravel (G1, G2). Conversely, the medium values of density and biomass (N1, B1) were recorded in stations entirely covered by gravel (G3: 100%). This suggests the impact of harvesting activities, targeting hard bottom stations, on oyster distribution in Pendjari River.

3.3. Environmental factors affecting oyster spatial distribution

The total inertia explained by the first two axes accounted for 89.56%, axis 1 and 2 respectively explaining 73.7 and 15.88 (Figure 5). This allows analysis on plane 1-2. Population attributes (density, biomass and colony size) show an increasing abundance gradient along axis 1. The axis 1 separates the low values of density, biomass and colony size (N0, B0, C0) on the negative side, from the medium and high values of population attributes, on the positive side. The medium and high density, biomass and colony size values are themselves ordinated on axis 2.

The water parameters that contribute most to axis 1 are temperature, transparency, TDS, pH, Altitude and velocity. The lowest density, biomass and colony values are linked to medium values of transparency (TR1,TR2), low proportion of TDS (TD0), low values of pH (P0), high values of velocity (V2 and V3) and high altitude (L2: 178 – 214 m) in stations of the river located upstream (Figure 2 ). Such stations were characterized by a high slope and high water flow. Conversely, medium density, biomass and colony values (N1, B1, C1) correspond to medium value of TDS (TD2:33 -35 mg/L), a medium altitude (L1) and lowest water velocity in dry season (V0). High values of population attributes (N2,B2,C2) were related to high pH (P2) indicating basic environment, low altitude (L0), low transparency (TR0), medium TDS (TD1) suggesting a concentration of suspended particles in water. Although an obvious increasing gradient closely linked to populations attributes, analysis of effect of water temperature on oyster distribution should be made with caution owing to great daily variations during the dry season (our sampling period). Medium and high density and biomass...
(N1, B1; N2, B2) were linked with higher water temperature values (T2, T3). Conversely, oyster displays lows or nil population parameters (N0, B0) in colder stations (T0, T1). Therefore, *E. elliptica* shows preference for high temperature range (32 – 39 °C) habitats. Along the axis 2, the increasing gradient of populations attributes is linked with decrease of altitude, indicating that *E. elliptica* shows a preference for stations with low altitude, low slope and water flow located in river downstream.

Fig 5: *Etheria elliptica* in Pendjari River: Correspondence analysis. Ordination of population attributes (Density: N, Biomass: B and colony size: C) and water physico-chemical factors (Temperature: T; Transparency: TR; Depth: D; pH: P; TDS: TD; Dissolved oxygen: OX; Velocity: V; Altitude: L).

Overall, the main environmental factors affecting oyster distribution in Pendjari River were gravel as main hard and preferential substrates, altitude, and water velocity (probably for larvae settlement), pH, transparency and TDS. *E. elliptica* shows preference for habitats characterized by dominance of gravel as main settlement substrates, low altitude and water velocity stations presumably for larval settlement after breeding activities and water column concentrated with particles in suspension for feeding purposes.

3.4. Ecological preferendum of oyster

Corrected frequencies C (K) were used to assess ecological preferendum of bivalve for different environmental factor. A corrected frequency value of 1 indicates preference for this range of values of the parameter. In contrast, C (K) < 1 suggests uncomfortable class of values. The preference range of oyster for different environmental factors was summarized in table 4.

Overall, oyster displayed significant preference range for TDS and altitude values (F = 49.23 and F=129.52 respectively, α = 0.05). Thus, C (K) values were upper than 1 (1.43 – 1.48) for TDS indicating a preference range of oyster. *E. elliptica* appeared to have significant preference for stations with high values of TDS (30 – 46 mg/L). Likewise, C (K) values were upper than 1 for altitude ranging between 120 – 175 m. This indicates the preference of oyster for low altitude habitats (Table 4).

The test of $\chi^2$ was not significant for depth (p > 0.05) indicating that oyster could thrive in shallow waters as well as in deeper waters. However, oyster seemed more abundant in deeper stations (0.6m – 2 m) in Pendjari River. Although a preference of oyster for hard substrates, especially for gravel and dead woods, no significant difference was recorded for those substrata in Pendjari River. This indicates that oyster could use alternative substrates when hard substrates were lacking in stations. Moreover, oyster was frequent in stations with high proportion of silt and sand (Table 4) where the oyster lived in colonies. Our results revealed that oysters could support a large range of habitats and could settle either on hard substrata (gravel, dead woods) or live in colonies in silty and sandy stations when substrates were lacking. The common tree species used as settlement substrates in Pendjari River were *Bhorassus aethiopium*, *Cola lauriflora*, *Combretum acutum* and *Parinari curatellifolia*.

Different values of class (K) correspond to abiotic factors interval for species. Chi-Square test (F) with df=2 for all abiotic factors.
Table 4: Corrected frequencies of environmental factors affecting spatial distribution of freshwater oyster *Etheria elliptica* in Pendjari River.

<table>
<thead>
<tr>
<th>Class (K)</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>F-value (df=2)</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Silt</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Proportions (%)</td>
<td>0</td>
<td>10-90</td>
<td>100</td>
<td></td>
<td></td>
</tr>
<tr>
<td>C(K)</td>
<td>0.85</td>
<td>1.21</td>
<td>1.03</td>
<td>1.93</td>
<td>ns</td>
</tr>
<tr>
<td>Sand</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Proportions (%)</td>
<td>0 - 5</td>
<td>10 - 45</td>
<td>50 - 100</td>
<td></td>
<td></td>
</tr>
<tr>
<td>C(K)</td>
<td>0.92</td>
<td>1.27</td>
<td>1.09</td>
<td>1.32</td>
<td>ns</td>
</tr>
<tr>
<td>Gravel</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Proportions (%)</td>
<td>0 - 10</td>
<td>20 - 70</td>
<td>80 - 100</td>
<td></td>
<td></td>
</tr>
<tr>
<td>C(K)</td>
<td>1.12</td>
<td>0.64</td>
<td>1.07</td>
<td>4.34</td>
<td>ns</td>
</tr>
<tr>
<td>Dead woods</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Categories</td>
<td>0</td>
<td>1</td>
<td>2</td>
<td></td>
<td></td>
</tr>
<tr>
<td>C(K)</td>
<td>0.88</td>
<td>1.43</td>
<td>0.95</td>
<td>3.0</td>
<td>ns</td>
</tr>
<tr>
<td>Depth</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Range (m)</td>
<td>0.2 - 0.5</td>
<td>0.6 - 1</td>
<td>1.2 - 2</td>
<td></td>
<td></td>
</tr>
<tr>
<td>C(K)</td>
<td>0.76</td>
<td>1.19</td>
<td>0.95</td>
<td>2.6</td>
<td>ns</td>
</tr>
<tr>
<td>TDS</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Range (mg/L)</td>
<td>20 - 29</td>
<td>30 - 35</td>
<td>36 - 46</td>
<td></td>
<td>***</td>
</tr>
<tr>
<td>C(K)</td>
<td>0.34</td>
<td>1.43</td>
<td>1.48</td>
<td>49.23</td>
<td>***</td>
</tr>
<tr>
<td>Altitude</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Values (m)</td>
<td>120 - 141</td>
<td>144 - 175</td>
<td>178 - 214</td>
<td></td>
<td>***</td>
</tr>
<tr>
<td>C(K)</td>
<td>1.23</td>
<td>1.53</td>
<td>0.15</td>
<td>129.52</td>
<td>***</td>
</tr>
</tbody>
</table>

ns = no significance; * = P < 0.05 ; ** = P < 0.01

4. Discussion

4.1. Oyster Distribution pattern

The Etheriidae, represented by a single genus and species, is a cemented freshwater oyster that lives in Africa and extreme northwest Madagascar [13]. Freshwater oyster *E. elliptica* is conspicuous inhabitants of rivers and lakes of Africa and Madagascar [1]. Like other species of Afrotropical fauna (Unionidae, Iridinidae and Etheriidae), *E. elliptica* is largely endemic to tropical and southern Africa [3]. In addition, *Etheria elliptica* (Etheriidae) is ubiquitous in its distribution range [20]. In Volta basin, *Etheria elliptica* occurred widely in many rivers especially in Northern Ghana [14]. In Pendjari River, *Etheria elliptica* exhibited a patchy distribution pattern (Morisita index Iδ > 1; P < 0.05). This observation is consistent with that of Van Boeckelaer and Van Damme [26] which reported that African freshwater oyster *E. elliptica* forms large reefs of aggregated specimens in African surface waters such as rivers. Moreover, freshwater oyster was absent from upper course of Pendjari River whereas it was abundant in middle and lower reaches of the river. In Columbia, its counterpart freshwater oyster *Acostaea rivoli* (Bivalvia, Etheriidae) displayed a similar trend. Thus, in Magdalena River basin *A. rivoli* was encountered only in middle and low reaches of rivers and rare in upper stretches [2]. It is widely known that freshwater mussels (Unionoida) mainly showed an aggregative distribution pattern resulting from specific habitats requirements [1–6]. The particular mechanism of settlement of bivalves implying cues from conspecific individuals, the need of hard substrates for fixation could likely explain their contagious distribution pattern [6–27]. Oyster mean density in Pendjari River was significantly higher in core zone and Porga hunting zone (regulated oyster harvesting) than open access zone where oyster harvesting was uncontrolled. This indicates the impact of exploitation on oyster distribution. In Columbia, the range of mean density (0.17 ind/m² - 8.67 ind/m²) of south American freshwater oyster *Acoestaea rivoli* (Etheriidae) in Opia River [28] seemed lower than values (0 to 40 ind/m²) in Pendjari River. In Columbia, *A. rivoli* was under threat of heavy exploitation and water pollution resulting from human action [28]. Moreover, freshwater mussels (including freshwater oysters) are dependent on critical densities to facilitate successful reproduction [29]. Further studies would investigate critical density of freshwater oyster for survival and reproduction.

4.2. Ecological factors affecting oyster spatial distribution

The distribution of freshwater mussels has been reported to be influenced by environmental factors [6]. The freshwater oyster *E. elliptica* was encountered not only in calm waters where specimens bear long hollow tube-like projections but also in turbulent waters where upper valves were smooth, without spines [1–26]. In Volta basin in Ghana, Ampofo-Yeboah [14] reported a current speed varying between 58.2 - 130.5 cm/s in River Oti at Sabari. This range could likely be similar to Pendjari River velocity as Pendjari-Oti River is the same river [16]. Past studies stressed largely the great preference of *E. elliptica* for turbulent waters and rapids falls [1–13]. In Pendjari River, *E. elliptica* was present not only in strong current waters but also in calm waters. CA did not reveal any significant correspondence between water velocity and oyster distribution in Pendjari River. This suggests oyster adaptation to both calm and turbulent waters. In Columbia, the freshwater oyster *A. rivoli* (Bivalvia, Etheriidae) was encountered both in low velocity waters and turbulent habitats in basin of Magdalena River [3]. Thus, as freshwater oysters (Etheriidae) both live in turbulent waters and calm waters of rivers [1–2], the speed of current seemed not to be a main factor affecting mollusk existence in the various sections a river. Nevertheless, many past studies stressed the importance of water velocity in settlement of freshwater mussels [6–31]. High water speed prevents settlement of larvae in river. In Pendjari River, oyster larvae settlement probably occurred at the end of flood season (between November–December at the beginning of dry season) when the water flow rate was decreasing or almost nil, especially in middle and low courses of river [32]. This could enable larval settlement in middle and low reaches of Pendjari River. Conversely, water velocity remains high almost all year round in upper course of river preventing larval settlement. Unlike adults’ individuals, water velocity could affect juveniles’ settlement and therefore indirectly
oyster distribution. Further investigations were required to assess the impact of water velocity on *E. elliptica* distribution and oyster fixing mechanism [2]. The altitude was appeared to be a significant factor affecting *E. elliptica* distribution pattern in Pendjari River. The freshwater oyster exhibited a preference for habitats with medium and low altitude (120 m – 175 m). In Columbia, the freshwater oyster *A. rivoli* displayed the same trend, the species being absent in upstream sites [2]. The low altitude station displayed a low slope and low water flow. However, the high water speed occurring in upper course of rivers could likely hamper larvae settlement and prevents oysters’ presence in high altitude sites. Moreover, poorly development of plankton was observed in running water (high current speed), suggesting a limited food for oyster [33].

Corrected frequencies of depth revealed no significant (F=2.6; df = 2; P > 0.05) preference range for *E. elliptica* (Table 4). Likewise, CA analysis revealed no significant effect of depth on oyster distribution. In Pendjari River, *E. elliptica* lived indistinctly both in shallow waters and deeper habitats. Past studies revealed presence of *E. elliptica* in different habitats including shallow waters and deep sections of rivers and lakes [1,2,3]. In Columbia, the freshwater oyster *A. rivoli* mostly thrives in shallow waters (50 cm to 1 m depth) and sometimes at depths greater 1 m, in fast flowing waters and in shallow waters (quiet and slow) [31]. As its counterpart freshwater oyster *A. rivoli* in Columbia (South America), *E. elliptica* lives in diversity of habitats in river [2-33].

Total Dissolved Solids (TDS) shows a significant impact on *E. elliptica* in Pendjari River (F=49.23; df=2; P<0.05). *E. elliptica* favours habitats with TDS values range of 30 – 46 mg/L (C (K) > 1) (Table 4). Thus preference could be linked to feeding purposes. As filter-feeder, the mollusk should feed on particles in suspension in water [1,24]. In Columbia, the freshwater oyster *A. rivoli* was frequently encountered in troubled waters, indicative of particles abundance in water column [2].

Freshwater oysters are known to be sessile, living attached to substrates [26]. In Pendjari River, main settlement substrates recorded for *E. elliptica* were gravel (71 %) and dead woods (19 %) as previously reported by Yonge [1]. In Ghana, *E. elliptica* was found attached to stones in rocky/stony sections of the rivers [14]. In Congo River, *E. elliptica* preferred a stony substratum used for settlement [1-13]. In India, freshwater oyster *Pseudomulleria dalyi* (Etheriidae) lived firmly cemented to rocks, often in clusters of 5-10 in Bhdrá River [7]. Surprisingly, the corrected frequencies revealed no significant preference (p>0.05) for range of different substrata (silt, sand, gravel and dead woods) recorded in Pendjari River. This suggests that *E. elliptica* developed a high degree of adaptation to different substrata available in river. In this light, Yonge [1] had reported the adaptation of great bulk of *E. elliptica* individuals for life within the varying grades of bottom material namely gravel, sand or mud, found in rivers and lakes. Anthony [12] reported abundance of *E. elliptica* specimens in silty habitats. In Columbia, the freshwater oyster *A. rivoli* used diverse settlement substrata in basin of Magdalena River [2]. In Pendjari River, although a noteworthy preference for hard substrates such as gravel (71 %), *E. elliptica* lived attached to dead woods as well as in silty and sandy habitats where it forms colonies. Previously, large colonies of *E. elliptica* were reported in sandy and silty sections of river and freshwater lakes [1-12]. In White Volta, colonies of *E. elliptica* reach great size that prevents canoes navigation [14].

Overall, *E. elliptica* developed a degree of plasticity and adaptation which enables the mollusk to thrive in a large range of environmental factors and a great diversity of habitats. This adaptation characteristic likely enables its large distribution in rivers and freshwater lakes through tropical Africa. According to Bogan [5], *E. elliptica* is a ubiquitous species. This could also be considered as a main aptitude for oyster culture.

Furthermore, fish species likely affect freshwater distribution in Pendjari River. *E. elliptica* belongs to order of freshwater mussels (Unionoida) [3]. It is well known that host fish species availability and distribution mostly affect freshwater mussels (Unionoida) spatial distribution pattern. Indeed, the freshwater mussels required a host fish species to complete the larval stage [6,34]. Consequently, the *E. elliptica* lasidium-type larvae distributions depend greatly on host fish ecological peculiarities and distribution range in Pendjari River. In Kunene River in South Africa, Appleton [35] assumed that the distribution pattern of *E. elliptica* would parallel that of some fish species. The apparent limits in the upstream distribution of *E. elliptica* in the Kunene River were attributed to large waterfalls limiting bivalve distribution resulting from changes in substrate or to the barriers imposed to waterfalls on host fish distribution [35].

In Africa, Fryer [36] demonstrated that the life cycle of African freshwater mussel *Matula bourguignati* (Bivalvia, Unionoida) depend on cyprinid fish *Barbus altianalis* as host fish species in Victoria Nile and Victora Lake. In Pendjari River, host fish species of freshwater oysters (Etheriidae) including *E. elliptica* remained unknown. In Columbia, the use of *Tilapia rendalli* in reproduction trials of *A. rivoli* was unsuccessful with death of larvae, probably due to inappropriate host fish species selection [37]. Moreover, the scarcity of host fish species mainly due to overexploitation, lead likely to freshwater mussels extinction [38]. In Pendjari River, Ahouansou Montcho [11] revealed three fish species supporting overexploitation: *Synodonits schall*, *S. membranaceus* and *Labeo coubie* with exploitation rate (E) ranging between 0.53 and 0.65. Therefore, identification of host fish species of *E. elliptica* is of great concern in Pendjari River as overexploited fish species could be the oyster host species. Information on *E. elliptica* host fish species were important crucial not only for fishing activities management but also for oyster conservation and stocks restoration.

Dams were known to affect negatively distribution and survival of freshwater mussels (including freshwaters oysters) [6,7]. Dams alter hydrological regimes of rivers and streams. Thus, river flow modification often leads to habitats destruction of freshwater oysters [1-7]. The impact of Kompienga dam on Pendjari River remains till today unknown. However, the river receives annually water releases from Kompienga reservoir [15]. This likely has adverse effects on Pendjari River hydrology especially in downstream stations such as Tampanga leading to high depth values (mean: 6.2 m and maximum of 25 m). Urgent assessment of impact of Kompienga dam on River and oyster stocks are required. In fact, current unregulated oyster harvesting and adverse dam effects could speed up bivalves’ stock depletion in downstream sites.

5. Conclusion

Overall, Pendjari River displays suitable environmental conditions for growth and development of *E. elliptica*...
especially in middle and downstream parts of River. Moreover, the capacity of *E. elliptica* to survive in various range of habitats increase its survival in River and in situ aquaculture potential.

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