Knowledge and Management of Aquatic Ecosystems (2015) 416, 06 http://www.kmae-journal.org

DOI: 10.1051/kmae/2015002

Population dynamics of freshwater oyster *Etheria elliptica* (Bivalvia: Etheriidae) in the Pendjari River (Benin-Western Africa)

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Received October 1, 2014
Revised January 3, 2015
Accepted January 5, 2015

ABSTRACT

Key-words: *Etheria elliptica, freshwater oyster, Bivalvia, population dynamics, Benin*

Etheria elliptica (Bivalvia: Etheriidae) is the only freshwater oyster occurring in Africa. The current study provides the first data on the population structure, growth, age, mortality and exploitation status of this species in the Pendjari River. *E. elliptica* length-frequency data were collected monthly from January to December 2009 and analyzed with FiSAT software. Population parameters including the asymptotic length (L_∞) and growth coefficient (K) were assessed to evaluate the stock status. The recruitment pattern was modeled with a FiSAT routine. The asymptotic length (L_∞) was 14.75 cm, while the growth coefficient (K) was 0.38 year^{-1}. The growth performance index ($\o'$) reached 1.92. Specimens of *Etheria elliptica* reached a mean size of 4.66 cm and 6.41 cm at the end of one year and 1.5 years, respectively. We estimated total mortality (Z), natural mortality (M) and fishing mortality (F) to be 2.90 year^{-1}, 1.16 year^{-1} and 1.74 year^{-1}, respectively. The recruitment pattern was continuous over the year with one major peak event during the rainy season (July). The exploitation rate ($E = 0.60$) revealed that the freshwater oyster was probably facing overexploitation due to lack of a minimum limit size and also due to an increase in the harvesting effort. Therefore, efficient management methods were urgently required to conserve the species. The return of empty shells into the water to increase the recruitment surface, rotation planning among harvesting sites and the imposition of a minimum limit size were recommendations made in order to ensure the sustainable exploitation of wild stocks.

RÉSUMÉ

Dynamique des populations de l'huître d'eau douce *Etheria elliptica* (Bivalvia : Etheriidae) de la rivière Pendjari (Bénin-Afrique de l'Ouest)

Mots-clés : *Etheria elliptica, huître d'eau douce, bivalve,*

Etheria elliptica (Bivalvia : Etheriidae) est la seule espèce d'huître rencontrée dans les eaux douces en Afrique. La présente étude a fourni les premières données sur la structure de la population, la croissance, l'âge, la mortalité et le niveau d'exploitation de l'huître dans la rivière Pendjari (Bénin). Les données de fréquence de taille de l'huître *E. elliptica* ont été recueillies chaque mois de janvier 2009 à décembre 2009 et analysées avec le logiciel FiSAT. Les paramètres de la population, y compris la longueur asymptotique (L_∞), le coefficient de croissance (K) et le modèle de recrutement ont été estimés pour évaluer l'état du stock.

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dynamique des populations, Bénin

La longueur asymptotique (L_∞) était de 14,75 cm et le cœfficient de croissance (*K*) atteignait 0,38 an^{-1}. L'indice de performance de croissance (ø′) s'élevait à 1,92. L'huître atteignait la taille de 4,66 cm et de 6,41 cm à la fin d'une année et de 1,5 années, respectivement. La mortalité totale (*Z*), la mortalité naturelle (*M*) et la mortalité par pêche (*F*) ont été estimées à 2,90 an^{-1}, 1,16 an^{-1} et 1,74 an^{-1}, respectivement. Le recrutement était continu au cours de l'année avec un pic majeur pendant la saison des pluies (en juillet). Le taux d'exploitation ($E = 0{,}60$) a révélé que l'huître était probablement confrontée à la surexploitation due à l'absence d'une taille limite minimale d'exploitation et de l'augmentation de l'effort de pêche. Les stratégies de gestion, y compris le dépôt des coquilles vides dans la rivière pour augmenter le recrutement naturel, la planification de la rotation entre les sites de récolte et l'observation d'une taille minimale ont été recommandées pour l'exploitation durable des stocks sauvages.

INTRODUCTION

Bivalves, notably, clams and oysters, are harvested in many African fisheries for food and income (Mavuti *et al*., 2005; Adjei-Boateng and Wilson, 2012). In West Africa, freshwater bivalves play an important role as they represent a source of cheap protein and provide employment to riverine communities. Moreover, empty shells are used as a source of calcium in poultry feed and in lime manufacturing (Ampofo-yeboah, 2000; Adjei-Boateng and Wilson, 2012). This region is facing an exponential demographic pressure with limited resources, which is threatening bivalve natural stocks (Heck *et al*., 2007). Therefore, assessment of the exploitation level of exploited stocks is of great importance to implement relevant management strategies of bivalve mollusks. In Ghana, Adjei-Boateng and Wilson (2012) investigated the population dynamics of the freshwater clam *Galatea paradoxa* in the Volta River and noted the overexploitation of bivalve stocks. Therefore, urgent strategies are required for stock management, such as imposing a minimum landing size on fishermen (Adjei-Boateng and Wilson, 2012). Previously, Moses (1990) reported overexploitation of the freshwater clam *G. paradoxa* in Cross River in Nigeria with an exploitation ratio ($E = 0.60$) higher than the optimum value ($E = 0.5$) according to Gulland (1971). Overfishing was mainly due to juvenile exploitation. Surprisingly, while many studies have investigated the exploitation status of the freshwater clam, there has been no research work focusing on the harvesting status of the freshwater oyster, despite a wide collection in many fisheries across Africa (Van Damme, 2011).

The freshwater oyster *Etheria elliptica* (Lamarck, 1807) is a bivalve mollusk belonging to the order Unionoida (freshwater mussels), superfamily Etheroidea and family Etheriidae. This oyster occurs in a broad belt across tropical Africa and the north of Madagascar. *E. elliptica* is the only freshwater oyster encountered in African waters (Graf and Cummings, 2006). The bivalve is of great economic importance for the local people and has been exploited in many artisanal fisheries across Africa for food and income over the years (Ampofo-yeboah *et al.*, 2009; Van Damme, 2011; Ikpi and Offem, 2012).

In West Africa, oyster exploitation was reported in many fisheries in Nigeria (Abowei and Hart, 2008; Ikpi and Offem, 2012), in the Volta River in Ghana (Ampofo-yeboah *et al.*, 2009) and in the Pendjari River in Benin (Kiansi, 2011). Surprisingly, no data were reported on the population dynamics of the species probably facing heavy exploitation owing to steadily increasing fishing pressure (Heck *et al*., 2007). This information is of great importance to establish sound management strategies for species exploitation. Moreover, in the case of the Pendjari River, oyster exploitation partly took place inside the Pendjari Biosphere Reserve (PBR), one of the most important protected areas in Northern Benin. Owing to an ongoing participative approach, local dwellers were granted permission to harvest oyster within the protected area for food and sale in return for their contribution to wild fauna and Pendjari Biosphere Reserve protection (Vodouhê *et al*., 2009; Kiansi, 2011). Consequently, a collapse of oyster stocks

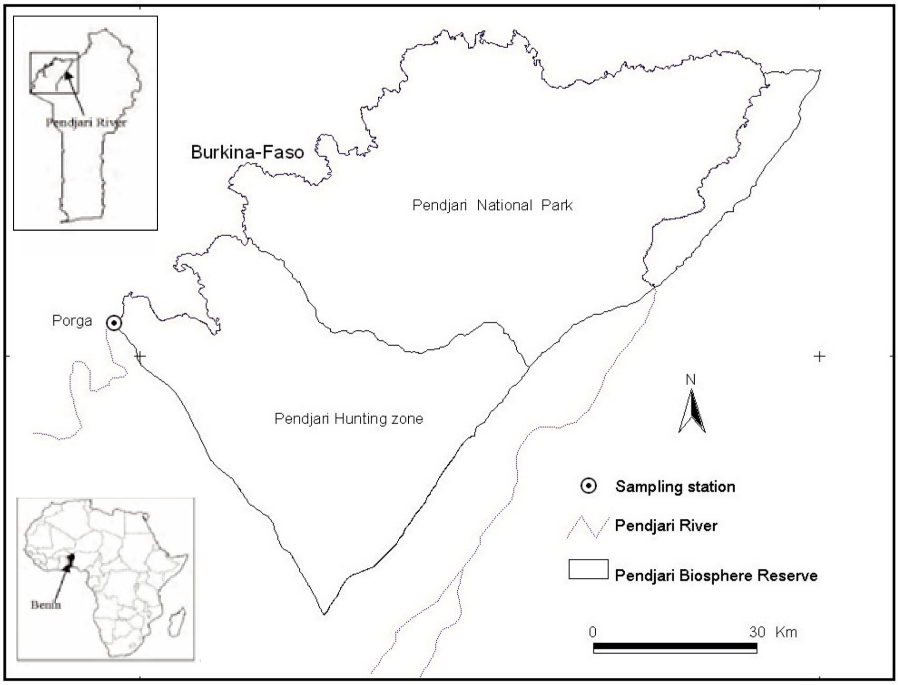

Figure 1
Sampling station located in the Pendjari River (Benin, West Africa).

could likely impact the livelihood of local people and their involvement in PBR conservation activities (Vodouhê *et al*., 2009). Therefore, the investigation of oyster population dynamics was required to ascertain the current status of the bivalve and set sustainable management strategies for both population livelihood and wild fauna conservation.

Among the methods used for population parameter assessment such as the asymptotic length (L_∞) and growth coefficient (K), mortality (natural and fishing) rate and exploitation level (E), FiSAT (FAO-ICLARM Stock Assessment Tools) has been most frequently used for estimating population parameters of finfish and shellfish (Mancera and Mendo, 1996; Amin *et al.*, 2008; Adjei-Boateng and Wilson, 2012) mainly because it requires only length-frequency data. This survey aimed at estimating the population parameters of the *E. elliptica* population under exploitation in the Pendjari River to assess the species status and recommend rational management strategies.

MATERIALS AND METHODS

> *STUDY AREA, ABIOTIC VARIABLES AND OYSTER SAMPLING*

E. elliptica specimens were randomly collected monthly from January to December 2009 in Porga (11°02′N and 0°57′E), an important harvesting site in the Pendjari River. Porga is located at the border of the Pendjari Biosphere Reserve (North-west Benin) (Figure 1).

Environmental variables of the water such as water temperature, dissolved oxygen (mg·L^{-1}), hydrogen ion concentration (pH), Total Dissolved Solids (TDS) (mg·L^{-1}), conductivity (μS·cm^{-1}) and transparency (cm) were monitored monthly for 1 year (January 2009 to December 2009) at Porga station. Water temperature (° C), pH, TDS (mg·L^{-1}) and conductivity (μS·cm^{-1}) were recorded with pH/EC/TDS/Temperature meters (HANNA Combo HI-98129). Dissolved oxygen (mg·L^{-1}) was measured with an oxygen measuring instrument (DO-100 Voltcraft). Water transparency was estimated with a Secchi disc to the nearest cm.

The sampling station was close to the encampment of fishermen involved in oyster sampling. The oyster specimens are attached to hard substrates (stone, dead wood) on the river bottom. An iron rod was used to remove specimens from the substrates, after diving. Sampled oysters covered the whole size range available in wild populations. About 95 specimens were collected each month. Overall, 1137 individuals were measured and weighed. The size varied from 1.7 cm to 13.8 cm. Total shell length (maximum dorsal-ventral dimension or height) was measured to the nearest 0.1 mm from the tip of the umbonal end of the upper valve to the ventral margin using a Vernier caliper. Total wet weight (shell + flesh) was taken by an electronic balance of 0.01 g accuracy.

> GROWTH PARAMETER ESTIMATION

Monthly data were grouped into length classes at 1-cm intervals and length-frequency data were analyzed using the FiSAT software (Gayanilo *et al.*, 1996).

The asymptotic length (L_∞) and growth coefficient (K) of the von Bertalanffy Growth Formula (VBGF) were estimated by means of ELEFAN-1 (Pauly and David, 1981). The estimated values of L_∞ and K were used to calculate the growth performance index (ø′) (Pauly and Munro, 1984) using the equation:

$$Ø' = 2 \log 10 L_\infty + \log 10 K.$$

The inverse von Bertalanffy growth equation (Sparre and Venema, 1992) was used to determine *E. elliptica* sizes at various ages. The VBGF was then fitted to estimates of length-at-age curves using non-linear squares estimation procedures (Pauly *et al.*, 1992). The VBGF is defined by the equation:

$$L_t = L_\infty \left[1 - e^{-k(t-t_0)}\right]$$

where L_t = mean length at age t; L_∞ = asymptotic length; K = growth coefficient; t = age of the *E. elliptica* in years and t_0 = the hypothetical age at which the length is zero. The maximum age (or longevity) was estimated using $T_{\max} = 3/K$ (Pauly, 1980).

The relationships between the lengths and weights of organisms were used to assess the well-being of individuals within *a* population. To establish the length-weight relationship, the common power regression $W = aL^b$ was applied (Ricker, 1975; Quinn and Deriso, 1999), where W is the weight (g), L is the total length (or height) in cm, 'a' is the intercept (condition factor) and 'b' is the slope (relative growth rate). The parameters a and b were estimated by least squares linear regression on log-log transformed data: $\log_{10} W = \log_{10} a + b \log 10L$. The coefficient of determination (r^2) was used as an indicator of the quality of the linear regression (Scherrer, 1984). Additionally, the 95% confidence limits of parameter b and the statistical significance level for r^2 were estimated.

The total mortality (Z) was computed by a linearized length-converted catch curve (Pauly, 1984) based on the following formula:

ln $(N_t/\Delta t) = a + bt$, where N is the number of individuals of relative age (t) and Δt is the time needed for the oyster to grow through a length class. The absolute value of the curve's slope (b) gives Z.

Natural mortality (M) was estimated using the empirical relationship of Pauly (1980):

$$\log_{10} M = -0.0066 - 0279\ \log_{10}\ L_\infty + 0.6543 \log_{10} K + 0.4634 \log_{10} T$$

where M is the natural mortality, L_∞ the asymptotic length, K the growth coefficient of the VBGF and T the mean annual habitat water temperature (°C).

The above computed values of Z and M were used to estimate the fishing mortality (F) with the relationship: $F = Z - M$; where Z is the total mortality and M, natural mortality. The exploitation level (E) was obtained from $E = F/Z = F/(F + M)$. According to Gulland (1971), an approximation of the exploitation state of a stock can be made based on the premise that optimal yield is attained when $F = M$ (*i.e.* $Eopt = 0.5$).

The exploitation sizes (L_{25}, L_{50} and L_{75}) at 25%, 50% and 75% of exploited stocks were estimated using the running average routine of FiSAT (Pauly, 1984). It was assumed that L_{50}

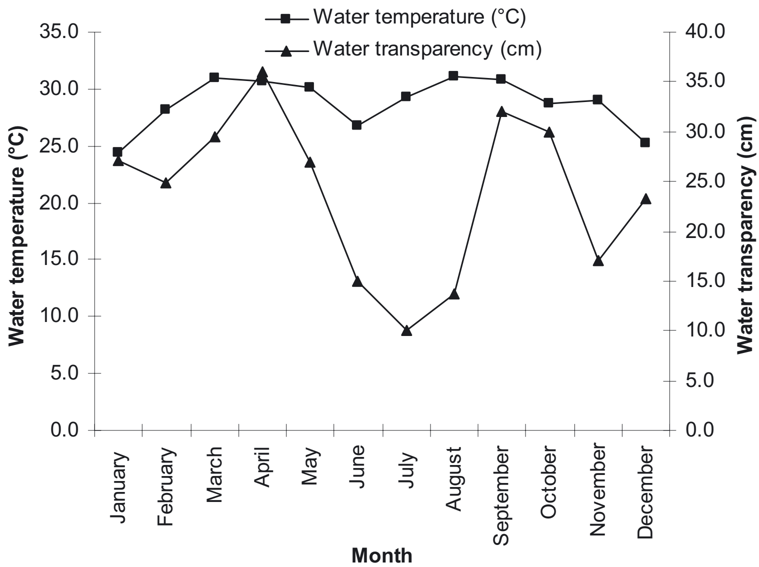

Figure 2
Monthly variation of water temperature and water transparency (cm) over the year 2009 in the Pendjari River (Benin).

was the length at first capture (L_c) (Pauly, 1984). The optimum size (L_{opt}) was determined using the formula (Fröese, 2004):

$$L_{opt} = L_\infty \frac{3}{3 + M/K}.$$

The recruitment pattern was obtained by projecting the length-frequency data backwards on the time axis using growth parameters (Moreau and Cuende, 1991). The normal distribution of the recruitment pattern was determined by NORMSEP (Pauly and Caddy, 1985) in FiSAT.

Relative yield per recruit (Y'/R) and biomass per recruit (B'/R) were estimated based on the model of Beverton and Holt (1957) using the knife-edge selection. The model of Beverton and Holt (1957) allows stock prediction and evaluation of management options. The approach is based on yield-per-recruit consideration. The model estimates the yield that would be obtained from a given number of recruits and a given fishing regime. Y, B and R represent, respectively, absolute yield (gram/year), absolute biomass (gram) and recruit. In fisheries, there is a youngest age at which the young specimens reach the fishing grounds. The oysters of this youngest age are called recruits (R). Relative yield per recruit (Y'/R) and relative biomass per recruit (B'/R) were expressed in relation to the fishing mortality (F).

RESULTS

> *ENVIRONMENTAL FACTORS*

The mean water temperature reported at the sampling site from January-December 2009 was 28.7 ± 2.5 °C (mean ± SD). The water temperature ranged from 23.8 °C (December) to 31 °C in May (Figure 2). The lowest value of conductivity (32.8 $\mu S \cdot cm^{-1}$) was recorded in July and the highest (65.0 $\mu S \cdot cm^{-1}$) in April (mean ± SD, 47.1 ± 11.7 $\mu S \cdot cm^{-1}$) (Figure 3).The Total Dissolved Solids (TDS) showed the same trend, with the lowest value of 16.2 $mg \cdot L^{-1}$ in July and the highest value (32.3 $mg \cdot L^{-1}$) in April. Dissolved oxygen varied from 0.6 $mg \cdot L^{-1}$ (May) (Figure 3) to 8.6 $mg \cdot L^{-1}$ (mean ± SD, 23.4 ± 5.8 $mg \cdot L^{-1}$) (Figure 3). Water transparency (Secchi disc visibility) in the sampling station ranged between 10 cm in July and 36 cm in April (Figure 2).

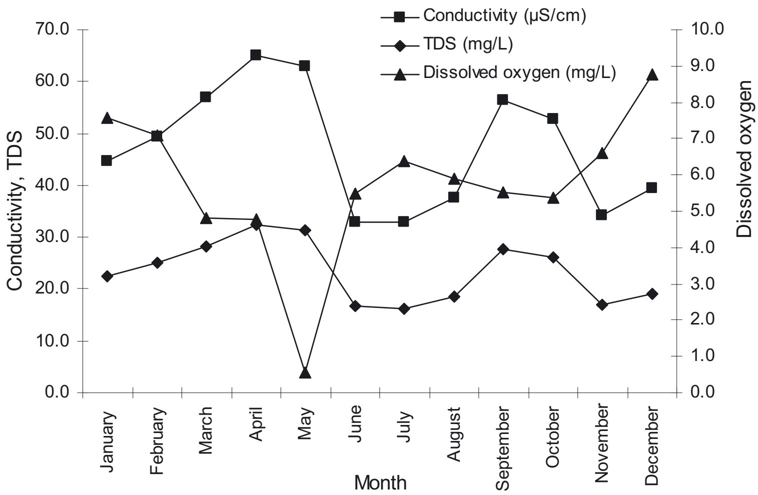

Figure 3
Monthly variation of conductivity ($\mu S \cdot cm^{-1}$), TDS ($mg \cdot L^{-1}$) and dissolved oxygen ($mg \cdot L^{-1}$) over the year 2009 in the Pendjari River.

Table I
Population parameters of E. elliptica in the Pendjari River (Benin).

Population parameters	*E. elliptica*
Asymptotic length (L_∞) in cm	14.75
Growth coefficient (K) year^{-1}	0.38
Growth performance index (ø′)	1.92
Natural mortality (M) year^{-1}	1.16
Fishing mortality (F) year^{-1}	1.74
Total mortality (Z) year^{-1}	2.90
Exploitation level (E)	0.60
Allowable limit of exploitation (E_{max})	0.422
Length range (cm)	1.7–13.8
Weight range (g)	1.5–186
Sample number (n)	1137

> LENGTH-WEIGHT RELATIONSHIP

The length of specimens used for determining the length-weight relationship ranged from 1.7 cm to 13.8 cm, while weight ranged from 1.5 g to 186 g (Table I). The length-weight relationship is shown in Figure 4 and was calculated from the equation $\log W = -0.0376 + 2.214 \log L$. In exponential form the equation is $W = 0.917L^{2.214}$ ($r^2 = 0.723$; $P < 0.01$). The computed growth coefficient (b) was 2.214 (±0.072) and the condition factor (a) was 0.917. The range of the 95% confidence interval for b values was 2.073–2.355.

> SIZE FREQUENCY DISTRIBUTION

Overall, 1137 freshwater oysters were measured to establish size frequency distributions. Sampled individuals ranged from 1.7 to 13.8 cm in size, with the bulk between 3.5 cm and 6.5 cm (Figure 5).

> GROWTH PARAMETERS

The ELEFAN-I program estimated asymptotic length (L_∞) and growth coefficient (K) of the von Bertalanffy Growth Formula (VBGF) for *E. elliptica* were 14.75 cm and 0.38 year^{-1}, respectively

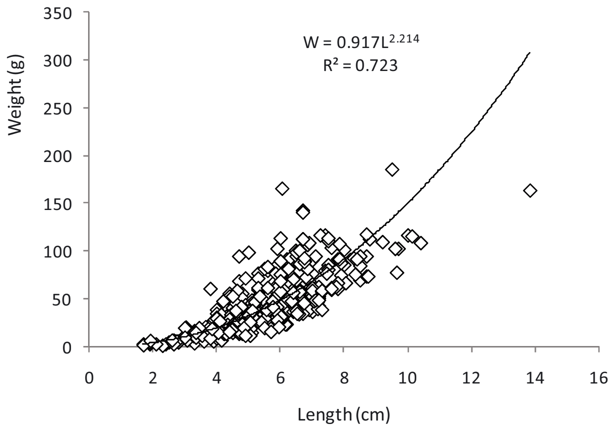

Figure 4
Length-weight relationship of the freshwater oyster E. elliptica in the Pendjari River, Benin.

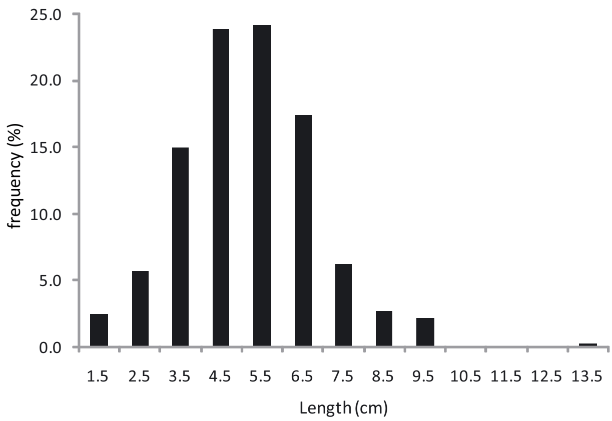

Figure 5
Size frequency distribution of the freshwater oyster E. elliptica sampled (N = 1137*) in the Pendjari river, Benin.*

(Table I). The computed growth curve with these parameters is superimposed over the restructured length distribution in Figure 6. The calculated growth performance index (Ø′) of *E. elliptica* was 1.92.

> AGE AND GROWTH

It was assumed that the value of the third parameter of the von Bertalanffy growth function t_0 was zero. Therefore, using VBGF growth parameters, the sizes attained by the freshwater oyster *E. elliptica* were 2.55 cm, 4.66 cm, 7.85 cm, 10.03 cm, 11.52 cm and 12.54 cm at the end of 0.5, 1, 2, 3, 4 and 5 years of age, respectively. The absolute increase is displayed in Figure 7. The growth rate of *E. elliptica* was estimated to be 2.09 cm from 1 to 6 months of age. The estimated growth increment was 3.19 cm and 2.18 cm from the 1st to 2nd year and 2nd to 3rd year, respectively. The maximum age or longevity of *E. elliptica* was estimated to be almost 8 years.

> MORTALITY AND EXPLOITATION LEVEL

The total mortality coefficient (*Z*) was estimated to be 2.90 year^{-1} using the length-converted catch curve (Figure 8). Natural mortality (*M*) and fishing mortality (*F*) were computed as 1.16 year^{-1} and 1.74 year^{-1}, respectively (Table I). The computed mortality coefficients were

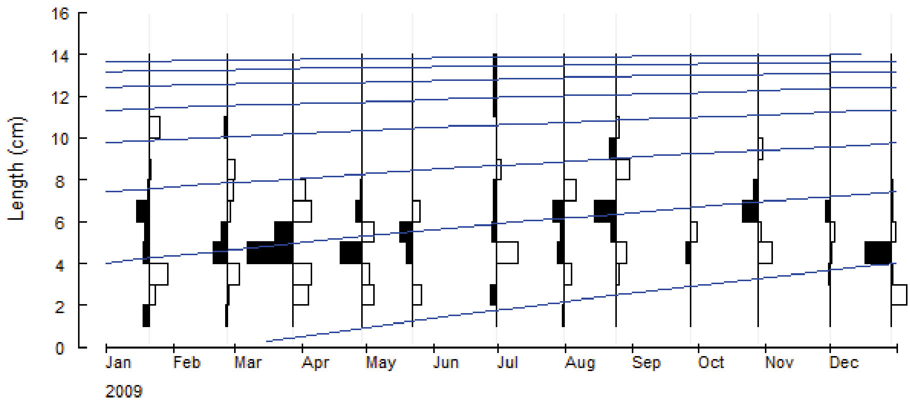

Figure 6
Restructured length-frequency distributions of Etheria elliptica from the Porga site of the Pendjari River, with growth curves superimposed. Estimated von Bertalanffy growth curves for the freshwater oyster E. elliptica (L_∞ = 14.75 cm and K = 0.38 year^{-1}). Solid and open histograms = positive and negative deviation from the 'weighted' moving average of three length classes representing pseudo-cohorts.

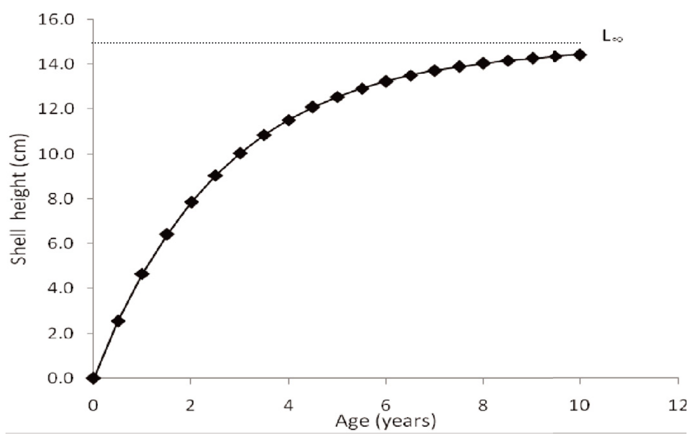

Figure 7
Plot of age and growth of the freshwater oyster E. elliptica based on VBGF computed growth parameters.

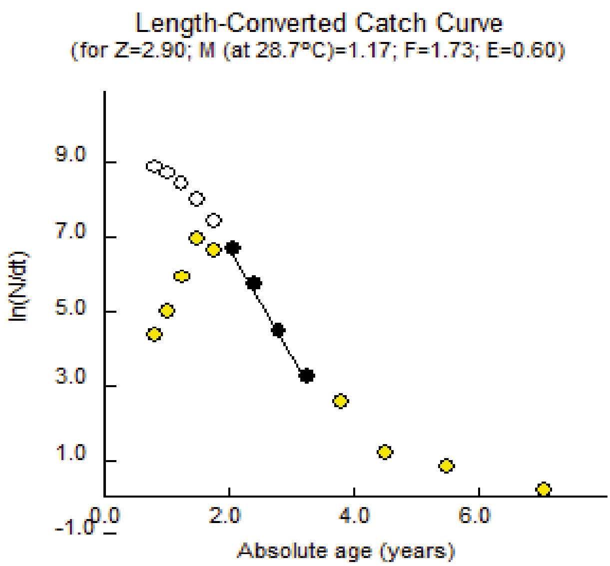

Figure 8
Length-converted catch curve of the freshwater oyster E. elliptica. (Solid dots = points used in calculating using least squares linear regression. Open dots = point either not fully recruited or nearing L_∞).

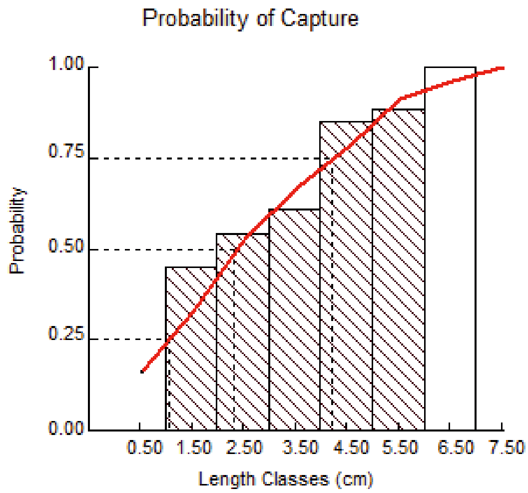

Figure 9
Probability of capture of the freshwater oyster E. elliptica in the Pendjari River (Benin). Cross-hatched histograms = length classes used in calculating probability of capture. Open histograms = length classes not fully involved in probability estimation.

used to estimate an exploitation level (*E*) of 0.60 for the *E. elliptica* fishery in the Pendjari River. However, the estimates of the mortality rates are based on a restricted mid-range sample, not including a representative proportion of smaller oysters and larger individuals, underlying a bias.

> EXPLOITATION SIZE

The lengths (*L*25, *L*50 and *L*75) at 25%, 50% and 75% of oysters' exploitation were estimated to be 1.11 cm, 2.37 cm and 4.25 cm, respectively (Figure 9). Thus, *L*50 or the length at first capture (L_c) was 2.37 cm, corresponding to oysters of about 0.5 years. The optimum length was computed to be 7.3 cm.

> RECRUITMENT PATTERN

The recruitment pattern of *E. elliptica* was continuous throughout the year, with one major peak in July (17.15% with 95% CL: 16.3–18.01%). The highest and lowest percent recruitment were recorded in February and July, respectively (Figure 10).

> RELATIVE YEAR PER RECRUIT AND BIOMASS PER RECRUIT

Relative Y'/R and B'/R analysis for *E. elliptica* was carried out using two types of selection curves (Figure 11). The estimated maximum allowable limit of exploitation (E_{max}) for the Y'/R and B'/R was 0.422, and the corresponding fishing mortality was 0.91 year^{-1}.

DISCUSSION

The outcomes of this research provided the first data on the population dynamics of the freshwater oyster *E. elliptica* fisheries not only in the Pendjari River (Benin-West Africa) but also over its distribution range (Africa and Madagascar).

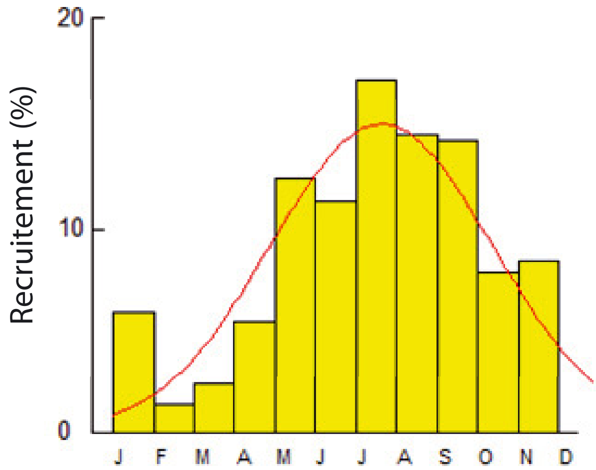

Figure 10
Recruitment pattern of the freshwater oyster E. elliptica at the Porga site in the Pendjari River (Benin). The recruitment pattern was obtained by backward projection of the restructured length-frequency data onto a one-year timescale.

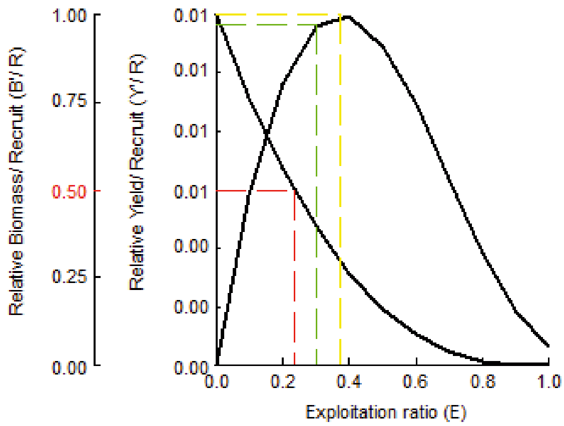

Figure 11
Relative yield per recruit (Y′/R) and biomass per recruit (B′/R) of the freshwater oyster E. elliptica in the Pendjari River (Benin), using knife-edge selection. (The bell curve = relative per recruit curve and decreasing curve = biomass per recruit). Estimated values of the exploitation ratio (E) (on the x-axis) are useful for evaluation of management options. Red dashed lines = E0.5: value of E below which the stock has been reduced to 50% of its unexploited biomass. Green dashed lines = E0.1: exploitation rate at which the marginal increase in relative yield-per-recruit is 1/10th of its value at E = 0. Yellow dashed lines = E_{max} *: Exploitation rate which produces maximum yield. Y/R (g·year*$^{-1}$*) and B/R (g).*

The estimated asymptotic length (L_∞) was 14.75 cm and the growth coefficient (K) was 0.38 year^{-1} for *E. elliptica* (Table I). Previous studies on growth factors of the freshwater oyster *E. elliptica* were not available in the literature. As *E. elliptica* (Mollusca: Bivalvia: Etheriidae) belongs to the order Unionoida (freshwater mussels) (Graf and Cummings, 2006), outcomes on oyster growth parameters were compared with data of other freshwater mussels belonging to the order Unionoida. Moreover, our results for *E. elliptica* were compared with those published for the freshwater clam *Galatea paradoxa* (order Veneroidea) in West African waters (King *et al*., 1992; Adjei-Boateng and Wilson, 2012). Furthermore, since *E. elliptica* is an oyster species, its growth parameters were also compared with those of marine oysters in the genus *Crassostrea* occurring mostly in tropical areas (Table II). The comparison exhibited differences among the freshwater mussels (Unionoida and Veneroida) from different areas of

Table II
Population parameters of freshwater mussels (Unionoida), the freshwater clam (Galatea paradoxa) and oysters of the genus Crassostrea reported in other countries.

Location	Species	L_∞ (cm)	K·year^{-1}	Ø′	*T* (°C)	*Z* year^{-1}	*M* year^{-1}	*F* year^{-1}	*E* year^{-1}	Source
Order	Unionoida									
Benin	*E. elliptica*	14.75	0.38	1.92	28.7	2.90	1.16	1.74	0.60	Present study
Zimbabwe	*M. dubia*	9.4	0.49	1.636	26					Kenmuir (1980)
Zimbabwe	*A. wahlberqi*	9.4	0.41	1.559	26					Kenmuir (1980)
Nigeria	*A. sinuata*	9.86	0.45	3.64						Blay and Yolole (1987)
Chad	*M. rostrata*	5.93	0.18	2.80	27					Lévêque (1971)
Kenya	*P. margaritifera*	12.72	0.38	3.78	29.2					Mavuti *et al*. (2005)
Order	Veneroida									
Nigeria	*G. paradoxa*	9.3	0.36	3.493		0.82	0.32	0.5	0.61	Moses (1990)
Nigeria	*G. paradoxa*	11.1	0.30	3.568						King *et al.* (1992)
Ghana	*G. paradoxa*	10.57	0.18	3.192	28.6	0.82	0.44	0.47	0.57	Adjei-Boateng and Wilson (2012)
Mangrove	Oysters									
Bangladesh	*C. madrasensis*	20.88	0.35	2.18	29	1.78	1.01	0.77	0.43	Amin *et al.* (2008)
India	*C. madrasensis*	11.9	0.77	4.04	28					Vakily (1992)
Colombia	*C. rhizophorae*	14.90	0.90	4.30	30.0	5.16	2.0	3.16	0.6	Mancera and Mendo (1996)
Jamaica	*C. rhizophorae*	8.69	2.79	4.32	27.1					Vakily (1992)
Gambia	*C. tulipa*	7.04	1.90	3.97	29.1					Vakily (1992)
USA	*C. virginica*	11.57	0.41	3.74	11					Vakily (1992)
USA	*C. virginica*	12.58	0.50	3.90	11					Vakily (1992)
Bangladesh	*C. virginica*	13.65	0.63	2.07	28.6	1.87	1.66	0.21	0.11	Amin *et al.* (2006)

tropical Africa (Table II). In the present study, the value reported for L_∞ (14.75 cm) was higher than for other freshwater mussels. The lowest value (9.3 cm) was reported for the freshwater clam *G. paradoxa* (Donacidae: Veneroida) in the Cross River system in Nigeria (Moses, 1990). In the genus *Crassostrea*, the highest value (20.88 cm) was reported f or *C. madrasensis* (Amin *et al.*, 2008) and was 1.5 times higher than that for *E. elliptica*. However, apart from the highest asymptotic length of 20.88 cm recorded for *C. madrasensis,* that of *E. elliptic*a at 14.75 cm falls within the range commonly reported for other freshwater bivalves and species of *Crassostrea* (Table II).

Among freshwater mussels (Unionoida and Veneroida), the highest growth coefficient *K* (0.38 year^{-1}) reported for *E. elliptica* in this study was the same as that found for pearl oyster *Pinctada margaritifera* at 0.38 year^{-1} in Kenya (Mavuti *et al.*, 2005), while the lowest *K* value (0.18 year^{-1}) was recorded for *G. paradoxa* from the Volta River in Ghana (Adjei-Boateng and Wilson, 2012) (Table II). In the genus *Crassostrea*, the highest *K* value (1.90 year^{-1}) was recorded for the mangrove oyster *Crassostrea tulipa* from Gambian waters (Vakily, 1992) and was five times higher than the *E. elliptica* values. Overall, Unionoida species including *E. elliptica* displayed lower growth rate (*K*) values (0.14–0.38 year^{-1}) than species of the genus *Crassostrea* (0.35–1.90 year^{-1}). This trend was previously supported by the outcomes of Strayer *et al*. (2004), who recorded that freshwater mussels are often long-lived and slow-growing. Moreover, our results are in agreement with the reported range of *K* (0.02–1.01 year^{-1}) for freshwater mussels (Unionoida) from North America (Haag and Rypel, 2010). Furthermore, a bias appeared in the sampling owing to under-representation of smaller oysters. In the river, smaller oysters live attached to colonies of larger individuals. Thus, the bias is likely due to the low abundance of juvenile oysters in the sampling site. The low proportion of juvenile oysters could be attributed to human disturbance (fishing activities), as the sampling site is close to a fishing camp. Therefore, estimates of growth parameters should be analyzed with caution.

The growth coefficient *b* generally ranges from 2.5 to 3.5 (Carlander, 1977) and the relation is said to be isometric when it is equal to 3, reported for most fish species (Quinn and Deriso, 1999). In our study, the estimated *b* (2.214) is outside the range indicated by Carlander (1977) and Ecoutin *et al.* (2005), and is significantly smaller than the isometric value (3) at the 5% level. This reveals the negative allometric growth of *E. elliptica* in the Pendjari River (Benin). This indicates that the specimens grow faster in length than weight. Environmental factors such as food supply, population density and abiotic factors of the habitat could adversely affect oysters' growth rate (King, 2000). Moreover, we assumed that the targeted population was dominated by sexually immature individuals. According to Pogoda *et al*. (2011), immature oysters primarily invest in shell growth before the increase in body mass.

Overall, the average growth rate of *E. elliptica* was 2.55 cm from one to six months of age; it reached around 4.66 cm (total height) and 6.41 cm after 1 year and 1.5 years, respectively. This indicates that *E. elliptica's* culture could be possible even if the growth rate is slightly lower than that of many other bivalve species such as *C. madrasensis* and C. *virginica*, which attained 6.17 cm (Amin *et al.*, 2008) and 6.38 cm (Amin *et al.*, 2006). In Ghana, despite its growth rate ($K = 0.18$ year^{-1}) being lower than that of *E. elliptica*, the freshwater clam *G. paradoxa* was in culture in the Volta River (Adjei-Boateng and Wilson, 2012). Thus, culture trials in different substrates and environmental conditions could assess and improve the culture potential of *E. elliptica* like the freshwater clam.

The recruitment pattern suggests that continuous recruitment consists of one peak seasonal pulse (Figure 10), *i.e.* one cohort is produced per year, between July and August. According to Ampofo-yeboah *et al.* (2009), gonad maturation of *E. elliptica* continues in March-April in the Volta River in Ghana and continues during the rainy season. This observation supported the outcomes of the present study, indicating a reproduction event occurring during March-April in the Pendjari River, a tributary of the Volta River (Figure 6). Moreover, Beasley *et al.* (2000) depicted the spawning of the subtropical freshwater mussel *Paxyodon syrmatophorus* (Bivalvia: Hyriidae) in the dry season with a major peak occurring in July-August. Therefore, the recruitment period encountered in this study (July) may probably correspond to the major spawning season. The recruitment period also corresponded to an increase in dissolved oxygen in the river (Figure 3). In Bangladesh, Amin *et al.* (2008) reported that *C. madrasensis* preferred high dissolved oxygen for spawning. Further studies should ascertain the relationship between environmental variables and reproduction activities. Moreover, as the sampling data did not contain a significant proportion of small oysters, the recruitment model must be analyzed with caution (Figure 6). Further investigations with a sufficient proportion of smaller oysters are required to ascertain the recruitment pattern of *E. elliptica* in the Pendjari River.

The estimated natural mortality (1.16 year^{-1}) was lower than the fishing mortality (1.74 year^{-1}), indicating an unbalanced state of wild stock. The computed exploitation level (E) was 0.6 for *E. elliptica* in the Pendjari River and exceeded the optimum exploitation level ($Eopt = 0.5$) assumed by Gulland (1971) when $F = M$ (Table I). Moreover, yield (Y'/R) and biomass per recruit (B'/R) were analyzed for *E. elliptica* using two types of selection curves. The outcomes displayed a maximum allowable limit of the exploitation rate ($E_{max} = 0.422$) which is evidently lower than the observed exploitation level of 0.60 (Table I). Thus, the oyster *E. elliptica* is facing overexploitation in the Pendjari River. Consequently, it is of great importance to reduce the fishing effort to the corresponding fishing mortality.

The estimated values of the asymptotic length (L_∞), the length at first capture (L_c or $L50$) and the optimum length (L_{opt}) were used to assess the status of exploited stocks in order to make an accurate diagnosis of the commercial fishery species. According to Pauly and Moreau (1997), when the values of the ratio (L_c/L_∞) are less than 0.5, this indicates that the juveniles of the targeted species are the most caught. This also suggests that the size at first capture (L_c or L50) is less than the optimal size (L_{opt}). In this study, L_c and $L\infty$ reached 2.51 cm and 14.75 cm, respectively. Therefore, the ratio (L_c/L_∞) is 0.16, less than 0.5. Thus, catches of *E. elliptica* in the Pendjari River were dominated by very small specimens of oyster. This reveals a growth overfishing of the stock. Growth overfishing occurs when specimens are caught too young (Fröese, 2004). Similarly, the length at capture is clearly lower than the optimum length. Consequently, management measures should aim at defining a minimum size, including the size of first maturity. Currently, it is noted that the majority of the sampled individuals in the population (about 80%) (Figure 5) have a size lower than the optimal length (L_{opt} = 7.3 cm). Therefore, respect of the optimal size would increase the yield.

Moreover, in the Pendjari River, bivalve harvesting was indiscriminate, also targeting small oysters fixed to large individuals' shells. Thus, in accordance with Mancera and Mendo (1996), after removing the meat from large oysters, collectors should be trained to return empty shells with fixed small individuals to the river. This method would contribute not only to increasing the oyster production but also to increasing the amount of substratum surface available for larval settlement. Furthermore, oyster culture should be promoted to increase oyster production and decrease human pressure on wild stocks.

ACKNOWLEDGEMENTS

We wish to thank the BIOTA West Africa program for funding this research work. We also thank the Pendjari oyster collectors for their participation in the research work. Many thanks to our field guide, Dominique Sambieni, for production data collection. We are grateful to the two anonymous reviewers of the manuscript for their valuable comments.

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Cite this article as: G.D. Akélé, H. Agadjihouèdé, G.A. Mensah, P.A. Lalèyè, 2015. Population dynamics of freshwater oyster *Etheria elliptica* (Bivalvia: Etheriidae) in the Pendjari River (Benin-Western Africa). *Knowl. Manag. Aquat. Ecosyst.*, 416, 06.