Fisheries Research 244 (2021) 106118

Contents lists available at ScienceDirect

Fisheries Research

journal homepage: www.elsevier.com/locate/fishres

Implications of overlooked seasonal growth dynamics in tropical fisheries assessment: A test case of an oyster (*Crassostrea tulipa*) fishery in the Densu Delta, Ghana

Isaac Kofi Osei [a,*], Kobina Yankson [a,b], Edward Adzesiwor Obodai [a,b], Isaac Okyere [a,b]

[a] *Department of Fisheries and Aquatic Sciences, University of Cape Coast, Ghana*
[b] *Africa Centre of Excellence in Coastal Resilience (ACECoR), University of Cape Coast, Ghana*

ARTICLE INFO

Handled by Dr Steven X. Cadrin

Keywords:
Oyster growth
TropFishR
SoVBGF
Tropical fisheries assessment
Standard VBGF
Fisheries management

ABSTRACT

Tropical fish stocks are perceived not to exhibit seasonality in growth. For this reason the standard von Bertalanffy growth function (VBGF) has been used widely to fit the growth of tropical fish populations compared to the seasonally-oscillating VBGF (soVBGF), which is seldom used in tropical fisheries. To advocate for the use of the soVBGF in assessment of tropical fish stocks, this study compared the outputs of the two methods using ELEFAN_GA_boot on oysters from the Densu Delta, Ghana. Sampling of mangrove oyster, *Crassostrea tulipa* covered a period of 12 months and the data were analysed for VBGF growth parameters and its prediction models. The intensity of growth oscillation showed that *C. tulipa* exhibited seasonal growth ($C = 0.50$), and the soVBGF fitted the growth of the oyster better than the standard VBGF method. Estimates of some of the stock parameters (t_{50}, t_{max}, F_{cur}, E_{cur} and Y_{cur}) were comparatively higher for the standard VBGF than the soVBGF approach. In both approaches, the oysters were underexploited ($E_{cur} < E_{msy}$). However, unlike the soVBGF method where $F_{cur} < F_{0.5}$, the standard method indicated that $F_{cur} > F_{0.5}$. In view of the disparities, studies which adopt standard VBGF on tropical stocks that exhibit seasonality would likely generate comparatively higher outputs for relevant biological reference points, which may ultimately mislead management decisions. Given the sedentary nature of oysters which could render the organisms more susceptible to seasonal variations in environmental conditions to show seasonality as observed in this study, we recommend further works on tropical shell- and finfishes to corroborate the current findings or otherwise.

1. Introduction

Stock assessment remains a key component of rational fisheries management. It is usually carried out to ascertain the levels of exploitation of fish stocks, stock size and to predict future yields based on certain fishing mortalities (King, 2007). Management measures emanating from stock assessments are ultimately focused on ensuring optimal yields for both biological and economic sustainability. Such assessments hinge on catch, age and length-based approaches through either fishery dependent or fishery independent surveys (Gayanilo et al., 2005; King, 2007; Pauly, 1983).

In the tropics, length-based procedures have been extensively used in the assessments of fish stocks compared to age data. The preference for length data is primarily due to the reported difficulty in ageing tropical fish, coupled with the ease with which length-based data are acquired (Ofori-Danson and Kwarfo-Apegyah, 2008; Pauly, 1984). This situation has engendered the development of many mathematical models, which utilise length related data for the estimation of growth and mortality parameters (Gayanilo et al., 2005; Pauly and David, 1981).

The development of standard von Bertalanffy Growth Function (VBGF) and seasonally-oscillating VBGF among others (like the Richards, Logistic and Gompertz models) make it possible to estimate population parameters such as asymptotic length (L_∞) and growth coefficient (K) under different conditions (Gayanilo et al., 1989; Sparre and Venema, 1992). These parameters are computed by the progression of length-frequency modes over time (Pauly et al., 1992; Urban, 2002). The standard (special) VBGF is the original growth model by von Bertalanffy while the other forms were developed later to tackle particular needs. The seasonally-oscillating VBGF, also referred to as the seasonalised VBGF, has been used widely to fit the growth of fish populations

* Correspondent author.
E-mail address: isaac.osei1@stu.ucc.edu.gh (I.K. Osei).

https://doi.org/10.1016/j.fishres.2021.106118
Received 27 October 2020; Received in revised form 23 August 2021; Accepted 24 August 2021
Available online 9 September 2021
0165-7836/

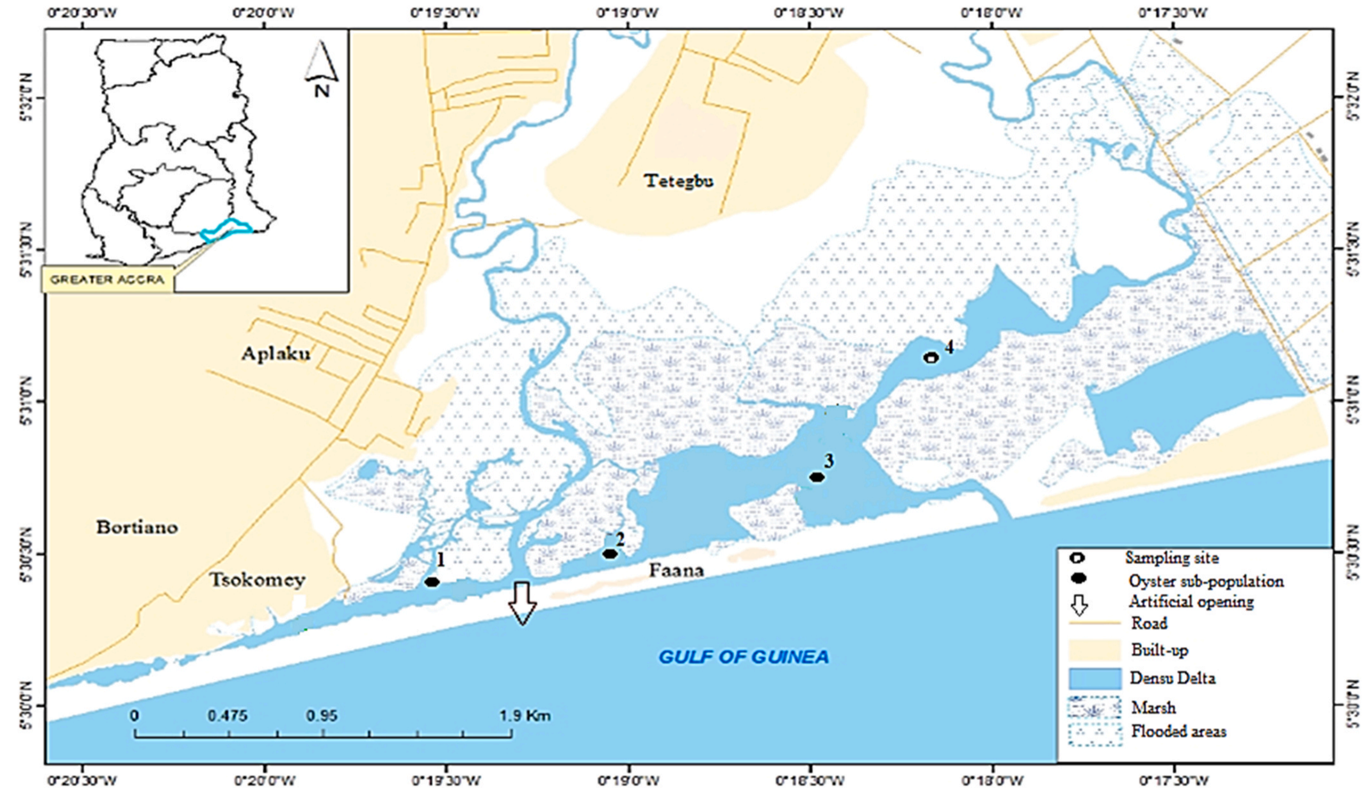

Fig. 1. Study site showing the Densu Delta, sampling site and oyster sub-populations.

from the temperate regions (Dridi et al., 2007; Tsikliras et al., 2005).

FiSAT II programme has been used in the analysis of several fisheries around the globe since its introduction by Pauly and David (1981). Lately, Pauly and Greenberg (2013) incorporated ELEFAN I into the R software developed by the R Core Team (2019). This innovation led to the development of R-based packages for fish stock assessment, namely TropFishR (Mildenberger, 2019; Mildenberger et al., 2017), fishmethods and fishboot, among others.

The growth of many organisms is said to be seasonal, which has been attributed to variations in temperature, light, and food availability (García-Berthou et al., 2012). Henderson (2006), however, noted that based on the lack of distinct seasonal temperature variations in the tropics, it has been presumed that tropical fishes lack seasonal growth. Hence, the standard VBGF is much utilised in fitting growth data of fish populations in the tropics (Pauly, 1984; Sparre and Venema, 1992). However, Morales-Nin and Panfili (2005) recommended that seasonality should be factored in tropical fish stock analysis, even though seasonality is not as well-defined as in the temperate and Polar Regions (Fischer et al., 1988; Fowler, 1995).

Despite the general knowledge that fish species exhibit seasonal growth as triggered by some seasonally changing environmental factors, most fish stock assessments carried out in the tropics fail to incorporate seasonality in the studies, partly because of the long-held perception that tropical fish species display a uniform growth pattern. Moreover, Longhurst and Pauly (1987) and Pauly and Ingles (1981) reported that a 'winter-summer' temperature change as low as 2 °C results in a significant seasonal growth oscillations in tropical fishes.

Consequently, it is imperative for researchers assessing tropical fish stocks to consider employing the seasonalised approach. Therefore, this study comparatively examines the standard VBGF and soVBGF outputs as well as its management implications using an oyster population in the Densu Delta, Ghana, as a test case, and advocates for the use of the latter in assessing tropical fish stocks.

The West African mangrove oyster, *Crassostrea tulipa* (Lamarck, 1819) offers an economical source of protein, employment and alternative livelihood for a significant number of coastal communities in Ghana (Asare et al., 2019; Osei et al., 2020, 2021; Yankson, 1990) and the West African region as a whole (Ajana, 1980; Ansa and Bashir, 2007). Globally, oyster production, though promising, is burdened with regulatory issues among others, according to Botta et al. (2020). Hence, for a rational exploitation, the fisheries must be regulated through sound analytical approaches. In view of their sessile nature, oysters offer a good candidature for the assessment of seasonality in tropical fish stocks as they remain vulnerable to the impact of varying environmental changes.

2. Materials and methods

2.1. Study area

The oyster samples were obtained from the Densu Delta, a designated Ramsar site in Ghana which lies between longitudes 0° 16'W–0° 21'W and latitudes 5° 30'N–5° 33'N. The Delta is formed by the Densu River, which is dammed at Weija to supply potable water to parts of the Greater Accra Region and empties into the Gulf of Guinea. The dam is occasionally opened to safeguard the facility from potential damage from heavy rainfall. The oyster population is distributed in patches along the arm of the Delta, which lies parallel to the shoreline (Fig. 1). Three main patches of oyster beds exist at the shallow portion (about 0.61 m deep at high tide, labelled as 1, 2 and 3 in Fig. 1) and another at the deep part (about 2.13 m at high tide, labelled 4). Samples for this study were obtained from the deep area, where oysters are available year-round (Osei, 2020; Osei et al., 2020). The oysters settle on hard substrates, mainly on oyster shells as well as directly on the sandy-mud substratum.

2.2. Sampling and morphometric data collection

Oysters were sampled randomly using a 0.25 m^2 quadrat around the

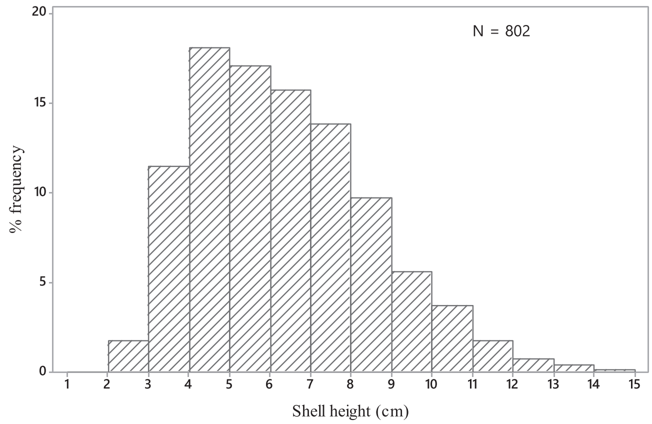

Fig. 2. Size-frequency distribution of deep water *Crassostrea tulipa* population in the Densu Delta, Ghana.

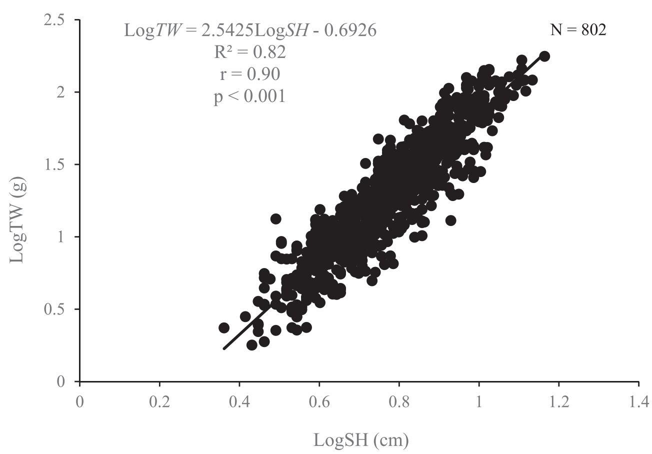

Fig. 3. Shell height-total weight relationship of deep water *Crassostrea tulipa* population in the Densu Delta, Ghana.

middle of each month from November 2017 to October 2018 by diving at study site 4 in the Densu Delta during the lowest daytime tide (Fig. 1). The samples were obtained by three replicate throws (i.e., by dropping an aluminium quadrat on oyster beds) at an interval of about 20 m between sampling spots at the bottom of the water body. Between 70 and 110 oyster specimens were obtained per month. The samples were transported to the laboratory where clustered individuals were separated, cleaned of fouling organisms, and debris removed by brushing and washing. Oyster shell height (the maximum distance from the hinge to the ventral margin) in cm was taken with a pair of dividers in conjunction with a rule. The shell height was used for the length based analysis because it has been reported to be the best predictor of soft tissue biomass in oysters (Edwards, 2014; Osei, 2020). Total weight of each specimen was taken to the nearest 0.01 g using an electronic balance.

2.3. Data analyses

The shell height data for 12 months were pooled to construct a size-frequency distribution histogram. Shell height (*SH*, cm) and total weight (*TW*, g) relationship was determined by log-transforming the equation, $TW = a(SH)^b$ (Le Cren, 1951) into its linear form, $\text{Log}\ TW = \text{Log}\ a + b\ \text{Log}\ SH$, where '*a*' and '*b*' are the intercept and slope, respectively. The deviation of the gradient from the isometric value ($b = 3$) was analysed using a *t*-test as expressed by the following equation: $Ts = (b - \beta)/S.E$ where *Ts* is the *t*-test value, *b* is the growth coefficient, β is the isometric value and *S.E* is the standard error of the slope (Kandeel et al., 2013).

Apart from the base packages in the R software (R Core Team, 2019), the packages used in analysing the monthly oyster shell height data were TropFishR (Mildenberger et al., 2017; Taylor and Mildenberger, 2017), fishmethods (Nelson, 2018), fishboot (Schwamborn et al., 2018), devtools (Wickham et al., 2018) and ks (Duong, 2019). The TropFishR was used to assess the oyster fishery.

2.4. Growth parameters

Growth was modelled separately by the standard VBGF, given as $SH_t = SH_\infty\ [1 - (\exp{-K}\ (t - t_o))]$ (von Bertalanffy, 1938) and the soVBGF presented as $SH_t = SH_\infty\ [1 - (\exp - K\ (t - t_o) + s(t) - s(t_o))]$ by Somers

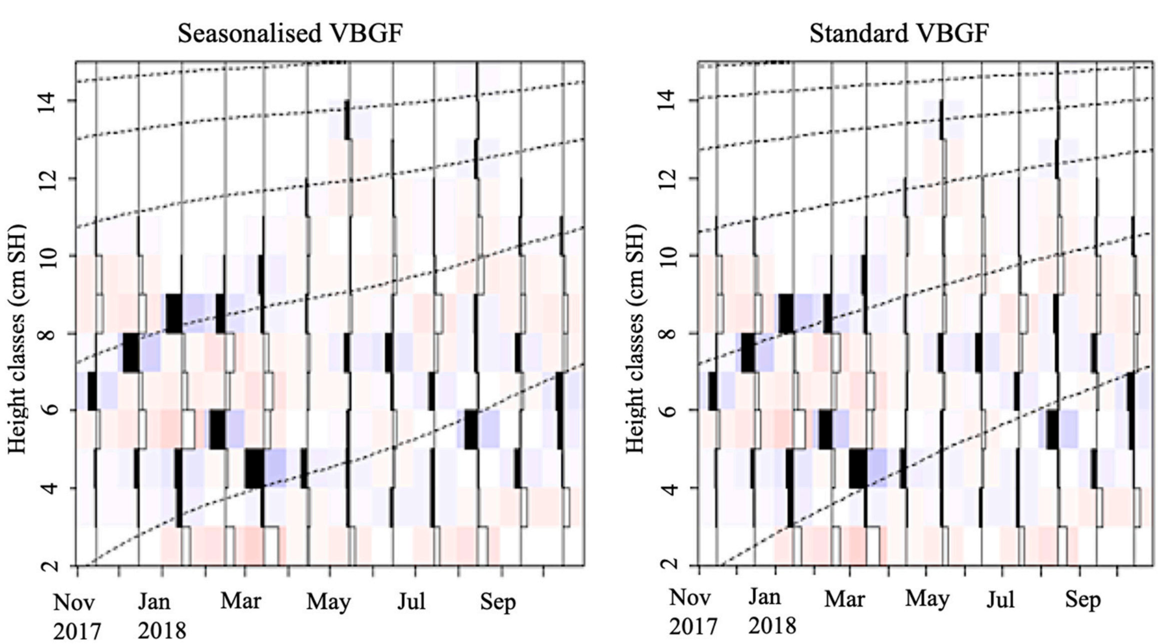

Fig. 4. Restructured monthly shell height-frequency distributions of *Crassostrea tulipa* population in the Densu Delta fitted with the seasonalised VBGF and standard VBGF, Ghana.

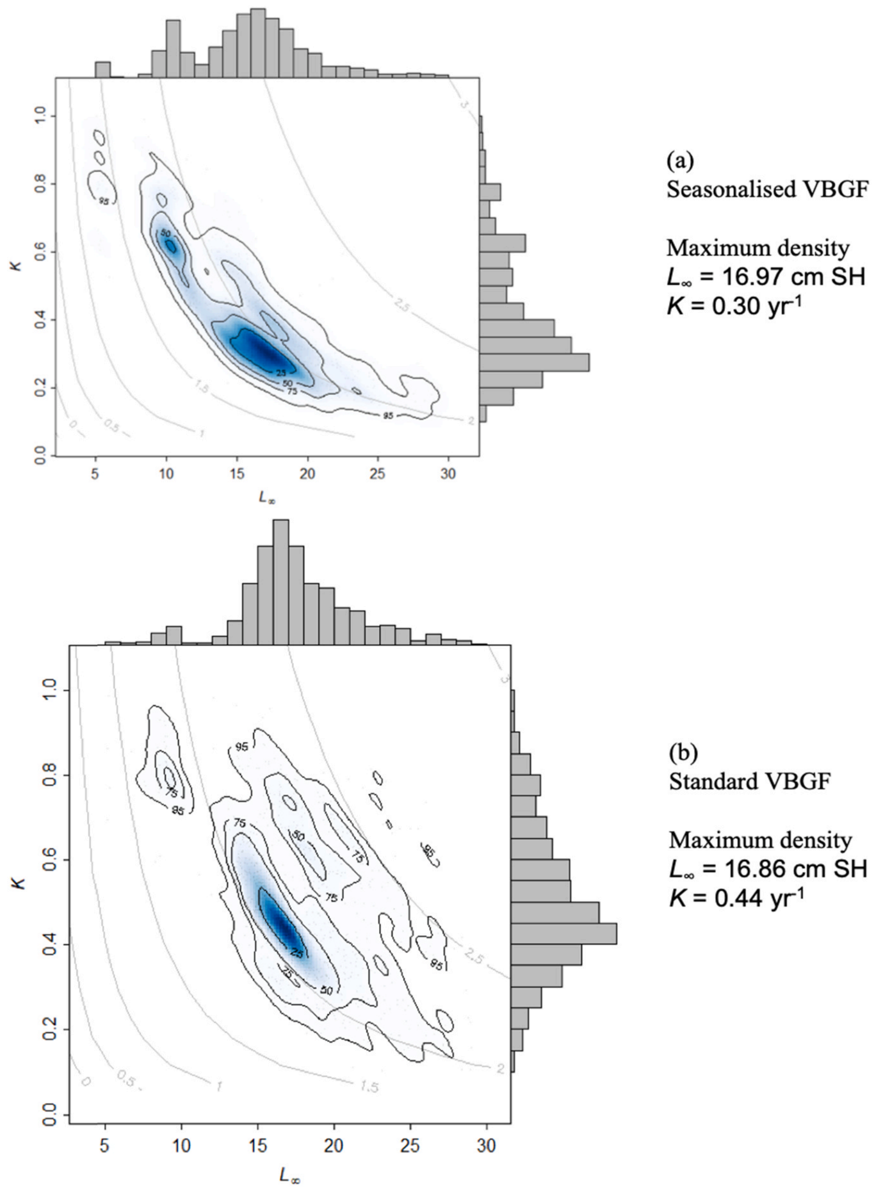

Fig. 5. Scatter histogram of ELEFAN_GA_boot (a) with and (b) without seasonality of deep water *Crassostrea tulipa* from the Densu Delta, Ghana. The dots denote the individual combinations of L_∞ and K estimates per resampled length-frequency catch data, while the contours and colour intensity signify the density of the combinations. The peripheral histograms show univariate density for both growth parameters.

(1988), where SH_t is the oyster shell height at-age t, SH_∞ is the asymptotic shell height, K is the growth coefficient and t_o the theoretical age at length zero (now t_{anchor}). Also, $s(t) = (CK/2\pi) \sin 2\pi (t - t_s)$, where C is the intensity of the sinusoidal oscillation, which normally ranges from 0 to 1 (C value greater than 1 suggests periods of shrinkage in size dimension), and summer point (t_s) is the fraction of a year, relative to the age of recruitment where the sine wave oscillation begins. The SH_∞, K, C, Φ' (growth performance index) and t_{anchor} (i.e. the portion of year where annually repeating growth curves cross length equal to zero) were determined by modal progression analysis using the ELEFAN_GA full bootstrap approach (Mildenberger, 2019; Schwamborn et al., 2019; Scrucca, 2013) in the TropFishR package. The full bootstrap approach was used due to some of the low monthly sample sizes. The settings for the ELEFAN_GA_boot algorithms for both the standard and soVBGF were *popSize* = 100, *maxiter* = 50, run 10, *pmutation* = 0.2 and Bootstrap *runs/nresamp* = 1000 (Mildenberger et al., 2017). Also, the 'moving averages' (MA) and fixing of L_∞ were held constant for both approaches, to avoid parameter estimation error (Taylor and Mildenberger, 2017).

The growth performance index (Φ') given by Pauly and Munro (1984) was estimated using the equation: $\Phi' = \text{Log}_{10} K + 2 \text{ Log}_{10} L_\infty$. The t_o value according to Pauly (1979) was calculated as: $\text{Log}_{10} (t_o) = 0.392 - 0.275 \text{Log}_{10} L_\infty - 1.038 \text{ Log}_{10} K$. Longevity ($t_{max}$) of the oyster population was estimated according to Pauly (1984) equation given as $t_{max} = 3/K$.

2.5. Mortality, exploitation rates, and yield/biomass per recruit

The total mortality (Z) of the oyster population was estimated by the length converted catch curve (Pauly, 1983; Munro, 1984) while the instantaneous natural mortality (M) was estimated from Pauly (1980) empirical equation: $\log_{10} M = -0.0066 - 0.279 \log_{10} L_\infty + 0.6543 \log_{10} K + 0.4634 \log_{10} T$ (with inputs from the growth parameters), where T is the mean annual water temperature (a mean of 27 °C was estimated during the study). The water temperature was measured in three replicates using a water quality checker (HORIBA, Model U-5000) on monthly basis and the mean resolved. Fishing mortality (F) was obtained from the relationship: $F = Z - M$ (Gulland, 1971).

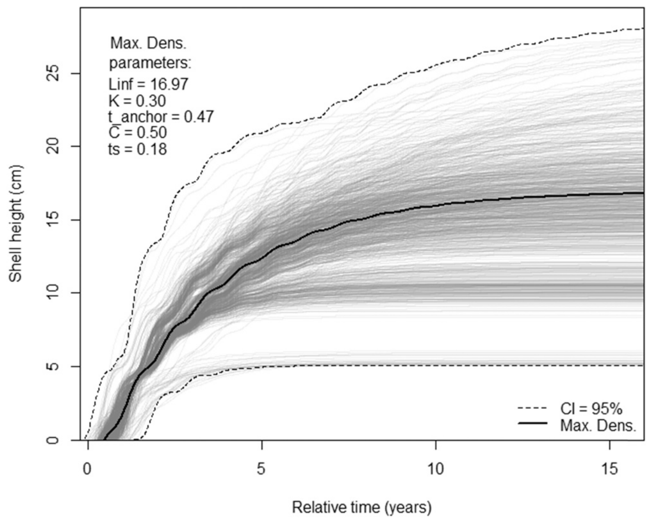

Fig. 6. Seasonalised VBGF growth curve plot of deep water *Crassostrea tulipa* samples from the Densu Delta, Ghana using an ELEFAN_GA_boot, Linf = Asymptotic length (L_∞). Sinusoidal growth curve represents the maximum density peak (thick black line) of the kernel density distribution with its 95% confidence contours (black dashed lines) and the individual sinusoidal curves (grey lines).

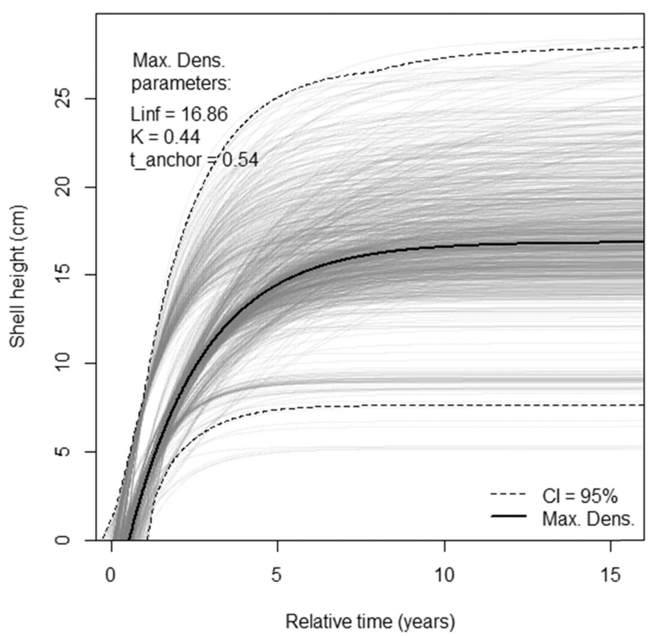

Fig. 7. Standard von Bertalanffy Growth Function (VBGF) plot of deep water *Crassostrea tulipa* samples from the Densu Delta, Ghana using an ELEFAN_GA_boot, Linf = Asymptotic length (L_∞). Growth curve represents the maximum density peak (thick black line) of the kernel density distribution with its 95% confidence contours (black dashed lines) and the individual curves (grey lines).

The level of exploitation (E) of the oyster fishery was calculated by the equation: $E = F/Z$ (Gulland, 1969).

The relative yield per recruit (YPR) and relative biomass per recruit (BPR) were estimated using the growth and mortality parameters to construct the Thompson and Bell model (Sparre and Venema, 1992). The model was used because of its non-steady condition predictions, which is necessitated by the occasional harsh conditions in the Densu Delta. The Thompson and Bell model illustrates the current fishing mortality (F_{cur}), fishing mortality at which 50% of the virgin biomass is exploited ($F_{0.5}$), the fishing mortality that gives the maximum sustainable yield (F_{msy}), as well as exploring the impact of the various t_{50} (mean oyster age at first capture) values and fishing mortality on YPR.

3. Results

3.1. Size-frequency distribution

A total of 802 specimens of *C. tulipa* were sampled from the deep portion of the Densu Delta. As seen in Fig. 2, the size distribution was unimodal, and ranged from 2.0 to 14.6 cm SH with a modal class of 4.0–4.9 cm SH.

3.2. Size-weight relationship

The total weight of the oyster specimens ranged from 1.78 to 176.22 g, with a mean weight of 30.64 ± 1.14 (SE) g. The shell height-total weight relationship of the *C. tulipa* population was described by equation $\text{Log}_{10}\ TW = 2.5425\text{Log}_{10}\ SH - 0.6926$ (Fig. 3). The figure indicates that there was a strong correlation and a significant relationship between shell height and total weight of the oysters ($r = 0.90$, $p < 0.001$). The gradient of the equation ($b = 2.54$, SE 0.045) was significantly different ($p < 0.001$; $t = 56.81$) from 3, indicating negative allometry.

3.3. Growth parameters

The monthly restructured size-frequency distributions of *C. tulipa* fitted with growth curves using the seasonalised VBGF and standard VBGF showed that in both approaches, the mode (6.0–6.9 cm SH) in November 2017 shifted by 1 cm SH in December 2017 as well as in January 2018 (Fig. 4). Subsequently, the samples did not show any clear-cut modal progression. However, comparatively, the growth curves fitted more modes in the soVBGF than the standard VBGF method, indicating that the former fits the modal classes better.

The growth parameters as estimated from the maximum density of ELEFAN_GA_boot using the soVBGF ($L_\infty = 16.97$ cm SH; $K = 0.30$ yr^{-1}; $t_{anchor} = 0.47$) and standard VBGF ($L_\infty = 16.86$ cm SH; $K = 0.44$ yr^{-1}; $t_{anchor} = 0.44$) were comparable (Figs. 5–7). However, the intensity of growth oscillation (C) of 0.50 in the soVBGF approach suggests seasonality in the growth of the oysters and the summer point (t_s) was estimated as 0.18 (February) as seen in Fig. 6.

3.4. Mortality parameters and exploitation rates

The total mortality, Z and age at first capture, t_{50} estimated for the oysters with the soVBGF were 1.92 ± 0.08 yr^{-1} and 0.55 yr, respectively while the respective outputs from standard VBGF were 1.92 ± 0.09 yr^{-1} and 0.65 yr, showing comparable Z for both methods but higher t_{50} for the latter (Fig. 8).

The natural mortality (M) and fishing mortality (F), exploitation rate (E) and longevity (t_{max}) as obtained with the seasonalised and standard VBGF approaches are shown in Table 1. Generally, the estimates showed inconsistencies in the outputs of the two methods, with F, E and t_{max} being higher, and M being lower for the standard VBGF.

3.5. Thompson-Bell model

Like t_{50} and t_{max}, the F_{cur} was higher in the standard VBGF estimates (0.72) than the seasonalised method (0.56) as shown in the yield per recruit (YPR) and biomass per recruit (BPR) analyses (Fig. 9). Comparing the $F_{0.5}$ and its corresponding F_{cur} in each method, the F_{cur} was higher than the $F_{0.5}$ for the standard approach, whereas the seasonalised approach presented a lower F_{cur} than the $F_{0.5}$. Other parameters such as E_{cur} and Y_{cur} were similarly higher for the standard approach than seasonalised method which possibly influenced the B_{cur} values (see

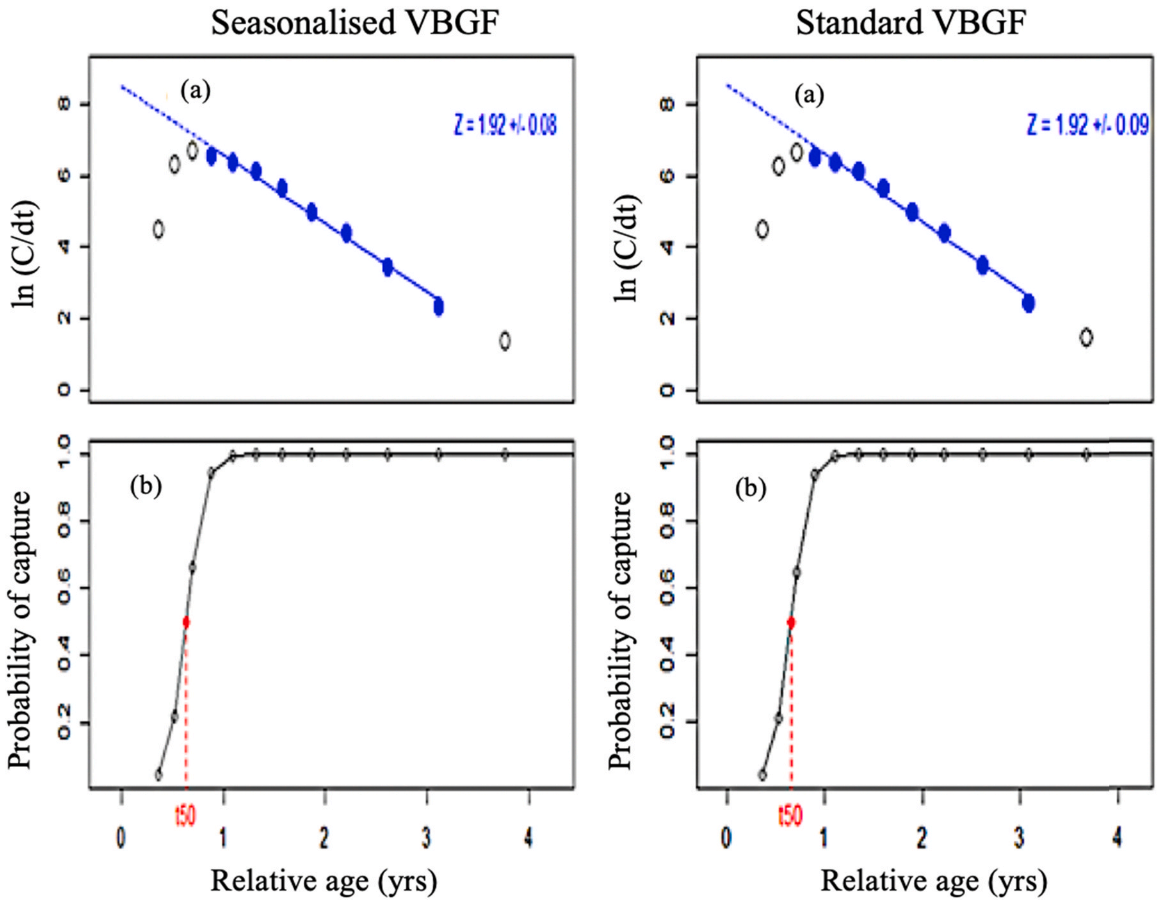

Fig. 8. Length-converted catch curve of deep water Crassostrea tulipa samples from the Densu Delta, Ghana indicating the values of total mortality (Z) and mean age at first capture (t_{50}) for seasonalised and standard methods.

Table 1
Mortality and exploitation parameters of *Crassostrea tulipa* in the Densu Delta, Ghana with and without seasonality.

	Input	
	Seasonalised VBGF	Standard VBGF
Natural mortality (*M*) yr^{-1}	1.36	1.20
Fishing mortality (*F*) yr^{-1}	0.56	0.72
Exploitation rate (*E*)	0.31	0.37
Longevity (t_{max}) yrs	6.38	6.82

Table 2).

4. Discussion

The intensity of growth oscillation (*C*) is an important parameter used in stock assessment for quantification of growth seasonality in fish populations (Abobi et al., 2019; García-Berthou et al., 2012). According to Pauly (1984) and Henderson (2006), intensity of growth oscillation of 1 indicates that growth doubles during 'summer' (i.e. increases by 100%) and becomes zero at 'winter'. A *C* value of 0.50 primarily indicates that growth increases by 50% during 'summer' and decreases by 50% in 'winter'. The estimated *C* of 0.50 for the oyster population in the present study (Fig. 6) indicated seasonality in growth of the organisms, suggesting the need for consideration of seasonality in the assessment of tropical fish stocks. This buttresses Pauly (1990) assertion that growth models that do not incorporate seasonal oscillations fail to capture a crucial phase of the growth process, even for tropical fish. Seasonality in growth of tropical fish, according to reports, is imposed by seasonal variations in rainfall (Henderson, 2006) and temperature (Longhurst and Pauly, 1987; Pauly and Ingles, 1981). In the present study, the annual rainy and dry season with its attendant changes in temperature could explain the seasonality observed in the oyster population.

The colour intensity and its courage of the scatter distribution of L_∞ and *K* indicating the density of the dots (thus the individual combinations of the growth parameters) is higher in the seasonalised approach than the standard method (Fig. 5). The observation suggests a better estimation of the growth parameters in the seasonalised method. In the tropics, on the general *Crassostrea* species as seen in Table 3 exhibited higher asymptotic lengths (L_∞) as compared to the temperate regions and seemingly vice versa for the growth coefficient (*K*).

Results of this study have shown that estimates of some of the stock parameters (t_{50}, t_{max}, F_{cur}, E_{cur} and Y_{cur}) were comparatively higher for the standard VBGF than the seasonalised approach. Such higher estimates could potentially mislead the biological significance of the values, especially in the context of tropical fish stocks where marked seasonality is presumed not to occur, hence, its omission in the assessment of stocks. For example, the observed higher Y_{cur} value from the standard VBGF indicates increased yield than the output from the seasonalised method. Not only could these disparities in outputs biologically mislead the assessment outcomes, but may have the overarching tendency to misinform management decisions.

In the case of the current oyster population, the application of Thompson and Bell model's YPR and BPR showed that the stock was underexploited as the F_{msy} was greater than F_{cur} in both methods (Fig. 9). However, the F_{cur} was higher than the $F_{0.5}$ for the standard VBGF, whereas the seasonalised method had a lower F_{cur} than the $F_{0.5}$. In the scenario of a management objective that sets its biological reference point to $F_{0.5}$ rather than F_{msy}, the outputs of the standard VBGF would

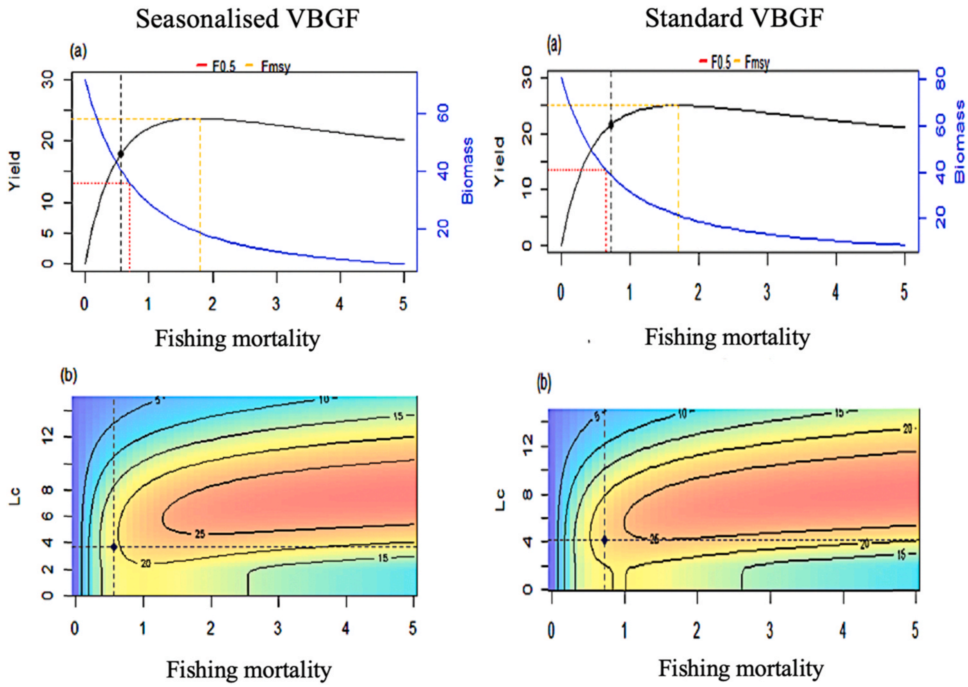

Fig. 9. YPR and BPR of (a) Thompson and Bell model and (b) Isopleth diagram of *Crassostrea tulipa* in the Densu Delta, Ghana with and without seasonality (Fishing mortality at 50% the biomass ($F_{0.5}$) = 0.70; Fishing mortality at maximum sustainable yield (F_{msy}) = 1.80; Current fishing mortality (F_{cur}) = 0.56; Length at first capture (L_c) = 3.73 and $F_{0.5}$ = 0.65; F_{msy} = 1.70; F_{cur} = 0.72; L_c = 4.20, respectively).

Table 2
YPR and BPR reference point estimates from the ELEFAN_GA_boot fit method with and without seasonality of Crassostrea tulipa in the Densu Delta, Ghana.

	Input	
	Seasonalised VBGF	Standard VBGF
Current exploitation (E_{cur})	0.31	0.37
Exploitation at maximum sustainable yield (E_{msy})	0.59	0.59
Exploitation at 50% of the biomass ($E_{0.5}$)	0.36	0.35
Current yield (Y_{cur}), tonnes	17.84	21.52
Current biomass (B_{cur}), tonnes	40.3	38.81

Table 3
Growth parameters of *Crassostrea* species in tropical and temperate regions.

Author	L_∞ (cm)	K (yr^{-1})	Species	Location
Current study, with seasonality	16.97	0.30	*C. tulipa*	Ghana
Current study, without seasonality	16.86	0.44	*C. tulipa*	Ghana
Mancera and Mendo (1996)	14.90	0.90	*C. rhizophorae*	Colombia
Amin et al. (2006)	13.65	0.63	*C. virginica*	Bangladesh
Amin et al. (2008)	20.88	0.35	*C. madrasensis*	Bangladesh
Vakily (1992)	10.37	2.35	*C. gigas*	Korea
Vakily (1992)	12.58	0.50	*C. virginica*	USA

lead management to reduce the fishing effort whereas the soVBGF outputs suggest sustainable exploitation. A misled management decision which seeks a reduction in fishing effort on a stock that is not necessarily exploited beyond the biological reference point, as in the case of the Densu oysters, could potentially affect the optimal exploitation of the resource (essentially, yield and income) for livelihood sustainability. The use of appropriate method is therefore critical in the assessment of this tropical oyster stock.

5. Conclusion

In conclusion, contrary to the long-held perception that tropical fish populations do not clearly exhibit seasonality in growth, the *C. tulipa* population at the Densu Delta in Ghana, a tropical region, showed seasonality in its growth ($C = 0.50$). To buttress the observation on seasonality, the soVBGF procedure fitted the growth of the oyster better than the standard VBGF method. Studies that adopt the use of the standard method on tropical stocks that undergo seasonality in growth would likely generate comparatively higher outputs for some stock parameters (t_{50}, t_{max}, F_{cur}, E_{cur} and Y_{cur}) as obtained in the present study. Pertinently, the standard method could overestimate the relevant biological parameters and their consequent reference points, which may ultimately mislead management decisions. Given that oysters are sedentary organisms and may be more susceptible to seasonal variations in environmental conditions which possibly contributed to the observed seasonality in this study, we recommend further research on tropical shell- and finfishes (including nektonic shellfishes) using both size and age-based models to corroborate the current findings or otherwise.

CRediT authorship contribution statement

Yankson, and **Obodai** were involved in the supervision of data collection and analyses, review, and editing. **Okyere** assisted with manuscript review and editing while **Osei** carried out the research, data collection and analyses, and composed the initial draft.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

This research was funded by the United States Agency for

International Development (USAID) – University of Cape Coast (UCC) Fisheries and Coastal Management Capacity Building Support Project (641-A18-FY14-IL#007).

Tribute

We dedicate this paper to the memory of our co-author, the late Emeritus Professor Kobina Yankson, whose unfortunate demise occurred while the manuscript was in peer-review.

References

Abobi, S.M., Mildenberger, T.K., Kolding, J., Wolff, M., 2019. Assessing the exploitation status of main fisheries resources in Ghana's reservoirs based on reconstructed catches and a length-based bootstrapping stock assessment method. Lake Reserv. Manag. 35 (4), 415–434. https://doi.org/10.1080/10402381.2019.1616340.

Ajana, A.M., 1980. Fishery of the mangrove oyster, *Crassostrea gasar*, Adanson (1757), in the Lagos area, Nigeria. Aquaculture 21 (2), 129–137. https://doi.org/10.1016/0044-8486 (80)90021-6.

Amin, S.M.N., Zafar, M., Halim, A., 2006. Population dynamics of the oyster *Crassotrea virginica* from the offshore island of St. Martin in the coast of Bangladesh. J. Sustain. Sci. Manag. 1, 65–78.

Amin, S.M.N., Zafar, M., Halim, A., 2008. Age, growth, mortality and population structure of the oyster, *Crassostrea madrasensis*, in the Moheskhali Channel (southeastern coast of Bangladesh). J. Appl. Ichthyol. 24 (1), 18–25.

Ansa, E.J., Bashir, R.M., 2007. Fishery and culture potentials of the Mangrove oyster (*Crassostrea tulipa*) in Nigeria. Res. J. Biol. Sci. 2 (4), 392–394.

Asare, B., Obodai, E.A., Acheampong, E., 2019. Mangrove oyster farming: prospects as supplementary livelihood for a Ghanaian fishing community. J. Fish. Coast. Manag. 1 (1), 7–14. https://doi.org/10.5455/jfcom.20190311090846.

Botta, R., Asche, F., Borsum, J.S., Camp, E.V., 2020. A review of global oyster aquaculture production and consumption. Mar. Policy 117, 103952.

Le Cren, E.D., 1951. The length-weight relationship and seasonal cycle in gonad weight and condition in the perch (*Perca fluviatilis*). J. Anim. Ecol. 20, 201–219.

Dridi, S., Romdhane, M.S., Elcafsi, M., 2007. Seasonal variation in weight and biochemical composition of Pacificoyster, *Crassostrea gigas*, in relation to gametogenic cycle and environmental. environmental conditions of the Bizerte lagoon, Tunisia. Aquaculture 263, 238–248. https://doi.org/10.1016/j.aquaculture.2006.10.028.

von Bertalanffy, L, 1938. A quantitative theory of organic growth (inquiries on growth laws II). Human Biol 10, 181–213.

Yankson, K, 1990. Preliminary studies on the rearing of the West African mangrove oyster, *Crassostrea tulipa*, in the laboratory. Discovery and Innovation 2, 45–51.

Duong, T., 2019. ks: Kernel Smoothing. ⟨https://cran.r-project.org/package=ks⟩.

Edwards, M., 2014. Sources of variation in height to dry weight ratios of the Easter oyter *(Crassostrea virginica)*, University of Illinois at Urbana-Champaign. ⟨https://nres.illinois.edu/files/documents/nres-online-research-edwards.pdf⟩.

Fischer, G., Fütterer, D., Gersonde, R., Honjo, S., Ostermann, D., Wefer, G., 1988. Seasonal variability of particle flux in the Weddell Sea and its relation to ice cover. Nature 335, 426–428. https://doi.org/10.1038/335426A0.

Fowler, A.J., 1995. Annulus formation in otoliths of coral reef fish: a review. In: Secor, D. H., J. M., Campana, S.E. (Eds.), Recent Developments in Fish Otolith Research. University of South Carolina Press, Columbia, SC, pp. 45–64.

García-Berthou, E., Carmona, C.G., Merciai, R., Ogle, D., 2012. A technical note on seasonal growth models. Rev. Fish Biol. Fish. 22, 635–640. https://doi.org/10.1007/s11160-012-9262-x.

Gayanilo, F. C. Jr., Soriano, M.,Pauly, D., 1989. A draft guide to the Compleat ELEFAN. ICLARM Software, 2.

Gayanilo, F.C. Jr., Sparre, P., Pauly, D., 2005. FAO-ICLARM stock assessment tools (FiSAT) user's manual. FAO Comp. Info. Ser, (Fisheries), 8.

Gulland, J.A., 1969. Manual of methods for fish stock assessment: part I. Fish Population Analysis. FAO Manuals in Fisheries Science, FAO, Rome, 4.

Gulland, J.A., 1971. The Fish Resources of the Oceans, Fishing News (Book) Ltd., West Byfleet, Surrey.

Henderson, P.A., 2006. The growth of tropical fishes. In: Val, A.L., de Almeida-Val, F.V. M., Randal, D.J. (Eds.), Fish Physiology: the Physiology of Tropical Fishes, 21. Elsevier Academics, London, pp. 85–100.

Kandeel, E.K., Mohammed, S.Z., Mostafa, M.A., Marwa, E.A., 2013. Reproductive biology of the cockle *Cerastoderma glaucum* (Bivalvia:*Cardiidae*) from Lake Qarun. Egypt. J. Aquat. Res. 39, 249–260.

King, M., 2007. Fisheries Biology, Assessment and Management, second ed. Blackwell Scientific Publications, Oxford.

Longhurst, A.R., Pauly, D., 1987. Ecology of tropical oceans. Academic Press, San Diego, California.

Mancera, E., Mendo, J., 1996. Population dynamics of the oyster *Crassostrea rhizophorae* from the Cienaga Grande de Santa Marta, Colombia. Fish. Res. 26, 139–148.

Mildenberger, T.K., 2019. Single-species Fish Stock Assessment with TropFishR. ⟨https://cran.r-project.org/web/packages/TropFishR/vignettes/tutorial.html⟩.

Mildenberger, T.K., Taylor, M.H., Wolff, M., 2017. TropFishR: an R package for fisheries analysis with length-frequency data. Methods Ecol. Evolut. 8 (11), 1520–1527.

Morales-Nin, B., Panfili, J., 2005. Seasonality in the deep sea and tropics revisited: what can otoliths tell us? Mar. Freshw. Res. 56, 585–598.

Munro, J., 1984. Estimation of natural mortality rates from selectivity and catch length-frequency data. Fishbyte 2, 11–14.

Nelson, G.A., 2018. Fishmethods: Fishery Science Methods and Models, ⟨https://cran.r-project.org/package=fishmethods⟩.

Ofori-Danson, P.K., Kwarfo-Apegyah, K., 2008. An assessment of the cichlid fishery of the Bontanga Reservoir, Northern Ghana. West Afr. J. Appl. Ecol. 14, 88–97.

Osei, I.K., 2020. A study on the fishery, aspects of the biology and culture of the West African mangrove oyster, *Crassostrea tulipa* in the Densu Delta (Unpublished PhD thesis). Department of Fisheries and Aquatic Sciences, University of Cape Coast.

Osei, I.K., Yankson, K., Obodai, E.A., 2020. Demographic and profitability analyses of the West African mangrove oyster (*Crassostrea tulipa*) fishery in the Densu Delta, Ghana. J. Fish. Coast. Manag. 2, 12–22. https://doi.org/10.5455/jfcom.20190528122752.

Osei, I.K., Yankson, K., Obodai, E.A., 2021. Effect of sedentary biofoulers on the growth and survival of cultured oysters (*Crassostrea tulipa*) towards its mass culture in the Densu Delta, Ghana. Aquac. Int. 29, 813–826. https://doi.org/10.1007/s10499-021-00659-9.

Pauly, D., 1979. Theory and management of tropical multispecies stocks: A review, with emphasis on the Southeast Asian demersal fisheries. ICLARM Stud. Rev. 1.

Pauly, D., 1980. On the interrelationships between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. J. Cons. Int. Explor. Mer. 39 (2), 175–192 (Retrieved from innri.unuftp.is/pauly/On the interrelationships betwe.pdf.).

Pauly, D., 1983. Length-converted catch curves: a powerful tool for fisheries research in the Tropics (part 1). Fishbyte 1 (2), 9–13.

Pauly, D., 1984. Fish populations dynamics in tropical waters: a manual for use with programmable calculators. ICLARM Studies and Reviews 8, ICLARM, Manila.

Pauly, D., 1990. Length-converted catch curves and the seasonal growth of fishes. Fishbyte 8 (3), 33–38.

Pauly, D., David, N., 1981. ELEFAN-I BASIC program for the objective extraction of growth parameters from length–frequency data. Meeresforschung 28, 205–211.

Pauly, D., Greenberg, A., 2013. ELEFAN in R: a new tool for length-frequency analysis. Fisheries Centre Research Reports, University of British Columbia, Vancouver, 21(3) 52.

Pauly, D., Ingles, J., 1981. Aspects of the growth and natural mortality of exploited coral reef fishes, 89–98. In: E.D. Gomez, C.E. Birkeland, R.W. Buddemeyer, R.E., Johannes, J.A. Marsh and R.T. Tsuda (Eds.), The reef and man. Proceedings of the Fourth International Coral Reef Symposium, Marine Science Center, University of the Philippines, Quezon City, 1.

Pauly, D., Munro, J.L., 1984. Once more on the comparison of growth in fish and invertebrates. ICLARM Fishbyte 2 (1), 21.

Pauly, D., Soriano-Bartz, M., Moreau, J., Jarre, A., 1992. A new model accounting for seasonal cessation of growth in fishes. Aust. J. Mar. Freshw. Res. 43, 1151–1156.

R Core Team, 2019. R: A language and environment for statistical computing, R Foundation for Statistical Computing, Vienna, Austria.

Schwamborn, R., Mildenberger, T.K., Taylor, M.H., 2018. Fishboot: bootstrap-based methods for the study of fish stocks and aquatic populations. R package version 0.1. ⟨https://github.com/rschwamborn/fishboot⟩.

Schwamborn, R., Mildenberger, T.K., Taylor, M.H., 2019. Assessing sources of uncertainty in length-based estimates of body growth in populations of fishes and macroinvertebrates with bootstrapped ELEFAN. Ecol. Model. 393, 37–51. https://doi.org/10.1016/j.ecolmodel.2018.12.001.

Scrucca, L., 2013. GA: a package for genetic algorithms in R. J. Stat. Softw. 53 (4), 1–37. https://doi.org/10.1359/JBMR.0301229.

Somers, I.F., 1988. On a seasonally oscillating growth function. Fishbyte 6 (1), 8–11.

Sparre, P., Venema, S.C., 1992. Introduction to tropical fish stock assessment. Part 1. Manual. FAO Fish. Tech. Pap. 306, 1–407.

Taylor, M.H., Mildenberger, T.K., 2017. Extending electronic length frequency analysis in R. Fish. Manag. Ecol. 24 (4), 230–238. https://doi.org/10.1111/fme.12232.

Tsikliras, A.C., Koutrakis, E.T., Stergiou, K.I., 2005. Age and growth of round sardinella (*Sardinella aurita*) in the northeastern Mediterranean. Sci. Mar. 69 (2), 231–240.

Urban, H.J., 2002. Modelling growth of different developmental stages in bivalves. Mar. Ecol. Prog. Ser. 238, 109–114.

Vakily, J.M., 1992. Determination and comparison of bivalve growth, with emphasis on Thailand and other tropical areas. ICLARM Technical Report 36, International Center for Living Aquatic Resources Management, Manila, Philippines, 125.

Wickham, H., Hester, J., Chang, W., 2018. Devtools: tools to make developing R packages easier. R package version 2.0.1. ⟨https://cran.r-project.org/package=devtools⟩.