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Observations on the Growth of Some Populations of the Freshwater Bivalve *Aspatharia sinuata* (Unionacea, Mutelidae) in Nigeria

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나이제리아의 淡水產 二枚貝(*Aspatharia sinuata*)의 生長에 관한 硏究

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要約

나이제리아의 middle belt지역의 2개 저수지와 3개 河川에서 *Aspatharia sinuata*의 生長樣相을 조사하였다. 가장 生長이 빠른 곳은 Oyun저수지와 Agbuur江이었으며, 가장 느린 곳은 Asa저수지와 Oyun江이었다. Walford plot에 의한 분석결과에 의하면 이 조개의 理論的 最大 길이(L_∞, cm)는 Asa저수지가 7.39, Oyun저수지 9.64, Oyun江 6.75, Odo-Otin江 7.60, Agbuur江 9.86이었다. 일반적으로 生長은 초기 2년 사이가 빨랐고, 그 후는 생장속도가 낮아졌다. Asa저수지에서의 放飼실험 결과에 의하면 貝殼에는 主生長線이 1년에 하나씩 형성되는 것으로 나타났다. 그리고 年例的인 水位低下와 그로 인한 夏眠 및 透明度의 감소가 이 조개의 生長을 억제하는 主要因이 되는 것으로 보였다. (서울대 自然大 動物學科 河斗鳳 譯)

INTRODUCTION

There is a general paucity of information on the growth rates of tropical bivalves (Kwei, 1965; George and Nair, 1974; Okera, 1976; Broom, 1982) and only a cursory mention has been made on this aspect of the biology of a few Unionacea in Africa (Lévêque, 1980). Relatively substantial records are available on the growth of members of this Order in temperate waters (Crowley, 1957; Okland, 1963; Negus, 1966; Tudorancea, 1972) but it is aparent that information regarding the growth characteristics of a great deal of species remains limited.

Growth-interruption marks on the shells of bivalve molluscs are considered appropriate tools for estimating their age and growth rates (Haskin, 1954; Green, 1957; Lammens, 1967; Hughes, 1970; Boyden, 1972; Okera. 1976; Persson, 1976; Seed and Brown, 1978;

Kautsky, 1982). In many instances, growth rings have been demonstrated to be formed annually (Seed, 1976) and can therefore be employed in age determination. In temperate waters, the rings are usually formed in winter when growth slows down or stops as a result of extreme low temperatures (Weymouth and McMillin, 1930; Chamberlain, 1931; Crowley, 1957; Negus, 1966). Seed (1976) observed that in addition to adverse temperature conditions, reproduction and variations in food availability are factors that contribute to shell growth disturbance.

Aspatharia sinuata, like other bivalve molluscs possesses growth rings on its shells, an indication that growth is checked at certain periods of its life, in spite of the fact that the continuously high tropical temperatures are favourable for growth throughout the year. Whereas growth rings in temperate animals are known to be produced primarily during the winter, the situation in tropical organisms is rather unclear as a number of the environment could induce ring formation at different periods. This problem has been highlighted by Fagade (1974; 1980) in two tropical cichlid fishes, *Sarotherodon melanotheron* and *S. guineensis*. Even for temperate bivalves, and perhaps for other temperate organisms, it is recognized that an investigator requires considerable experience for consistency in the interpretation of growth rings (Crowley, 1957; Ökland, 1963). In fact, it has been observed that several rings are sometimes formed in a year (Seed, 1976; Ankar, 1980).

This study seeks to characterize the growth habits of some *A. sinuata* populations through the interpretation of growth-interruption marks on the shells, size freguency distributions, and growth experiments in the natural habitat.

MATERIALS AND METHODS

The study area

Samples of *A. sinuata* used in this study were collected from 5 freshwater habitats located in 3 states of the Federal Republic of Nigeria. Generally, the sites occur in the 'middle belt' of Nigeria, between latitudes 8°N and 9°N (Fig. 1). Three of the water bodies are located in Kwara State, namely Asa Reservoir at Ilorin, the state capital, Oyun Reservoir at Offa, a town 67 km south-east of Ilorin, and River Oyun passing through the Main campus of the University of Ilorin. The other water bodies from which the clams were collected are Odo-Otin River at Okuku in Oyo state, and Agbuur River, a small tributary of the larger River Benue at Uga-Mbagwa in Benue State.

A remarkable ecological feature of the study area is the seasonal rise and fall in water levels due to the annual rainfall pattern. A dry period occurs from November till April, and a rainy period from May to October. Low water levels prevail for varying periods between February and August depending on the size of the water body. During this period, sub-populations of the bivalves are exposed to drought for varying time intervals ranging from a few weeks to 6-7 months, depending on the location of individuals in the draw-

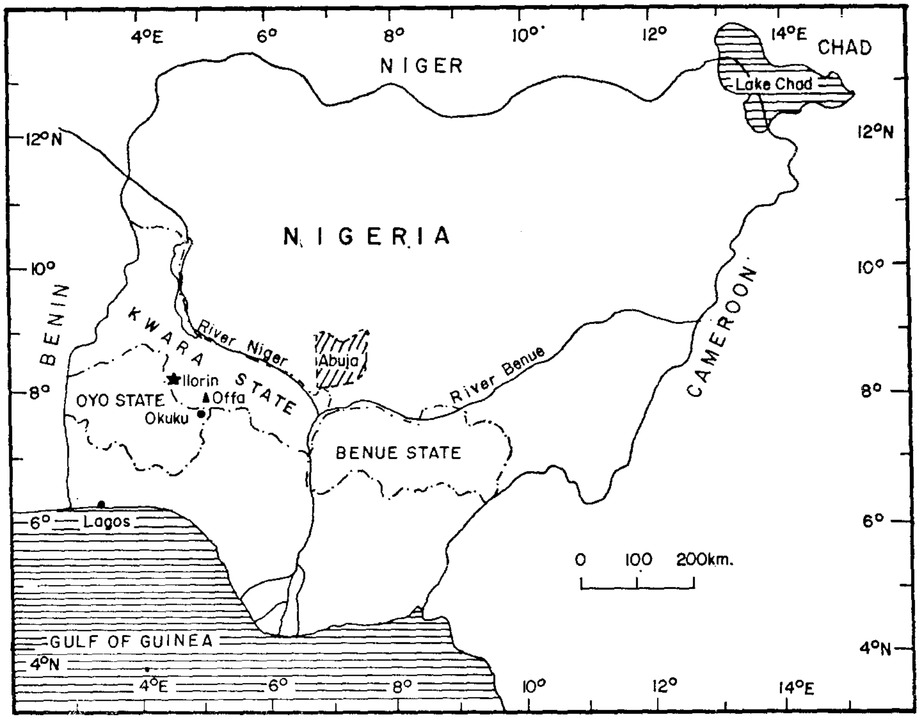

Fig. 1. A map of Nigeria showing the location of the collection sites of *A. sinuata.*

down zone. The bivalves survive exposure to air by aestivating.

Analysis of growth rings

Large clams with clearly discernible growth rings were selected for age and growth determinations in five *A. sinuata* populations. About 50 animals in each population were used and those with heavily eroded shells near the umbo were excluded because of the possible erosion of some rings in this area. Two types of rings were identified in many of the clams; one type was deeply engraved into the prismatic layer of the shell and was often covered by a thin flap of periostracum, while the other was rather superficial and lacked a periostracal flap.

The latter ring is usually incomplete and characterised by an interruption about its middle portion, opposite the umbo. As observed in other bivalves (Crowley, 1956; Ökland, 1963; Negus, 1966; Boyden, 1972; Kautsky, 1982), the former perhaps represent annual growth checks, and the latter, disturbance or super-numerary rings. Those confirmed as annual were counted and their antero-posterior lengths measured with Vernier callipers.

Growth curves were constructed by plotting the mean lengths of growth rings against their respective ages. Sequel to this, Walford plots (Walford, 1946) were fitted in terms of the regression by least squares of Lt (length at age t) on $Lt+1$ (length at age $t+1$). From the calculated regressions, the ultimate or asymptotic length (L_∞) of clams in each population was determined from the relation, $L_\infty = \frac{\text{intercept}}{1-\text{slope}}$.

The von Bertalanffy growth coefficients (von Bertalanffy, 1938) were estimated as follows:

$K = -\ln k$, where K is the coefficient of catabolism and k is the slope (growth constant) of the Walford plot;

$E = KL_\infty$, where E is the coefficient of anabolism, K is the coefficient of catabolism and L_∞ is the asymptotic or maximum theoretical length.

Mark-release-recovery study in Asa Reservoir

A total of 384 clams were collected on the 9th of May 1982 from Asa Reservoir and numbers inscribed on their left valves with white oil-paint. Their respective shell lengths were measured to the nearest 0.01 cm, and were released after 24h at a point in the littoral zone about 10 m from the dam-wall on the western shore of the lake. Monthly sampling for recaptures commenced in January 1983 and was terminated in December 1984. Marked individuals occurring in samples were measured for growth, and counts made of rings developed following that formed as a consequence of handling.

Growth in different size groups in Asa Reservoir

A study was conducted on the rate of growth in different sizes of clams over a 12-month period in Asa Reservoir. A total of 44 individuals measuring 3.73–8.83 cm were obtained from the reservoir on 12th May 1984 and serial numbers engraved on the left valves by cutting through the periostracum into the white prismatic layer. Their corresponding lengths were measured and the animals released in groups of 11 into 4 wooden frames each with an area of 1 m^2 and a height of 0.1 m; the frames remained submerged throughout the period of observation. Recoveries were made on the 12th of April 1985 and their lengths measured. The initial lengths were grouped at intervals of 0.5 cm and the average length of clams occurring in each size group calculated. After recovery, the average lengths of animals which belonged to each of the groups were also computed; the annual growth increment in each size group was estimated as the difference between the means of the initial and final lengths.

Growth of spat in Asa Reservoir

Forty spat with antero-posterior lengths ranging from 1.07 to 1.28 cm (mean=1.16 cm) were collected from pools in River Oyun in April 1983. These were divided into four groups of 10; each batch was placed in a separate plastic bowl 50 cm in diameter and 25 cm high, with a sandy substrate about 10 cm thick. The bowls were planted in Asa Reservoir and kept submerged by shifting along with the receding or rising water levels. Measurements were made each month until the observations were terminated after 9 months because of the disappearance of the experimental clams, apparently due to predation by a foraging animal. Monthly mean lengths and growth increments were calculated and the results plotted as a growth curve and a growth increment histogram.

RESULTS

Length at annulus

Fig. 2a shows the growth curves of 5 populations of *A. sinuata* obtained by the interpretation of growth lines on the shells. The figure indicates that fastest growth rates occurred in Oyun Reservoir and slowest rates obtained in River Oyun and Asa Reservoir samples. In all the populations growth was rapid during the first 2 years of life, but this declined thereafter. The von Bertalanffy growth model was found to be suitable for describing the growth of the *A. sinuata* populations, and Walford plots were accordingly constructed (Fig. 2b). All the plots approached the 45° line which confirmed agreement with the von Bertalanffy growth model. Another salient feature of the plots is that all the points fell on straight lines which indicates that growth of the populations occurred over a limited period of time (Gulland and Holt, 1959; quoted in Kwei, 1965) rather than being continuous. The regressions show that growth was highest in Agbuur River and Oyun Reservoir and least in Asa Reservoir and River Oyun. It can also be seen that specimens in Agbuur River tended to attain a larger ultimate size than Oyun Reservoir clams inspite of the former's initial slower rate of growth. A similar observation was made in the Asa Reservoir and River Oyun populations where the former had a higher ultimate length whereas initially its growth rate was slower. From the plots, it is observed that the maximum theoretical lengths (L_∞) in Asa Reservoir, Oyun Reservoir, River Oyun, Odo-Otin River and Agbuur River were 7.39, 9.64, 6.75, 7.60 and 9.86 cm, respectively. However, their corresponding observed maximum lengths were 10.15, 11.50, 7.51, 8.33

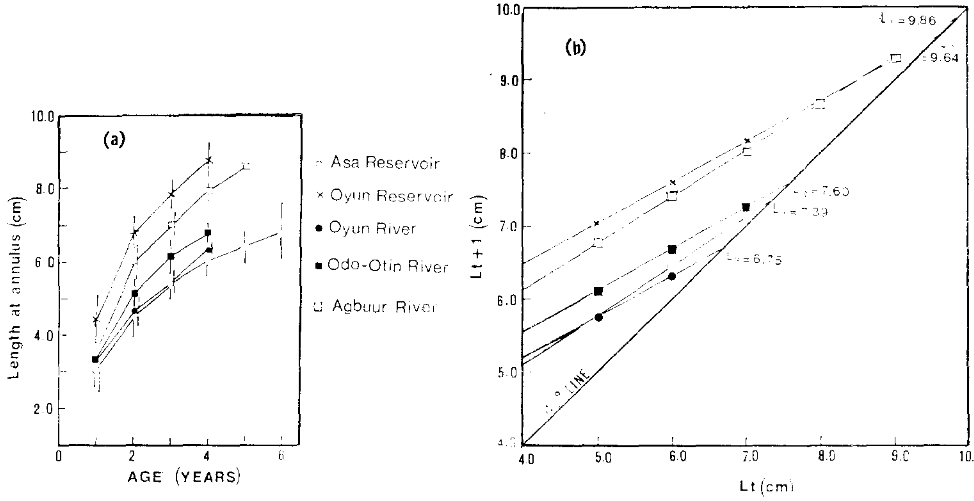

Fig. 2. (a) A comparison of annual growth increments, and (b) Walford plots in five populations of *A. sinuata*. Initial mean length at annulus (Lt) is plotted against mean length at the next annulus (Lt+1). L_∞=asymptotic length. Vertical bars represent standard deviations.

Table 1. Summary of von Bertalanffy's growth parameters estimated from Walford plots in *A. sinuata* populations.

Population	Slope (k)	K	E	Maximum length (cm)	
				L_∞(mean)	Observed
Asa Reservoir	0.67	0.40	2.96	7.39	10.15
Oyun Reservoir	0.56	0.58	5.59	9.64	11.50
Oyun River	0.56	0.58	3.92	6.75	7.51
Odo-Otin River	0.57	0.56	4.26	7.60	8.33
Agbuur River	0.64	0.45	4.44	9.86	8.94

K=coefficient of catabolism; E=coefficient of anabolism; L_∞=asymptotic length.

and 8.94 cm.

Table 1 summarizes the von Bertalaffy growth parameters which denote that catabolism was greatest in the Oyun Reservoir and River Oyun populations (0.58) and least in the Asa Reservoir clams (0.40). The coefficient of anabolism (E) was highest in Oyun Reservoir specimens (5.59) while the lowest value occurred in the Asa Reservoir population (2.96) despite the existence of the highest growth constant ($k=0.67$) in this population compared with the other groups. This suggests that a combination of all the growth parameters were responsible for the characteristic growth patterns and maximum lengths recorded in the different populations.

Observations on recaptures in Asa Reservoir

Table 2 provides data on 12 clams recaptured on different dates out of a total of 384

Table 2. Mark-release-recovery data on *A. sinuata* in Asa Reservoir. Clams were marked and released on 10th May 1982.

Size at marking (cm)	Size at recovery (cm)	Date of recovery	Period of growth (months)	Size increment (cm)	Number of rings after disturbance ring
4.81	5.35	22. 1.83	9	0.54	NR
5.94	6.15	16. 4.83	12	0.21	NR
4.98	5.65	3. 8.83	15	0.67	NR
4.08	5.13	3. 9.83	16	1.05	NR
5.27	5.96	3. 9.83	16	0.69	NR
5.60	5.97	3. 9.83	16	0.37	NR
5.17	5.76	17. 9.83	16	0.59	NR
4.19	5.48	20. 4.84	24	1.29	2
4.78	6.23	22.12.84	32	1.45	3
4.48	6.26	14. 1.85	32	1.78	2
5.27	5.76	30. 3.85	35	0.49	NR
5.37	5.82	30. 3.85	35	0.45	NR

NR=not recognized

marked individuals. This represents a recapture rate of only 3.1%, suggesting considerable movements by the animals, although it is possible that some marked individuals could not be identified because of the erasure of the paint marks. Only 3 of the recaptured clams exhibited identifiable growth rings after the disturbance ring formed as a consequence of handling. Two new rings were produced in 24 months in a clam which had an initial length of 4.19 cm, and increased by 1.29 cm. After 32 months, 2 clams with initial lengths 4.48 and 4.78 cm had each gained 1.78 and 1.45 cm, in addition to exhibiting 2 and 3 new rings, respectively. These observations, although scanty, may suggest the formation of one complete ring every 12 months if the same environmental or physiological conditions were responsible for the inducement of a growth check. It is evident from the table that in specimens without identifiable additional growth rings, the increase in length over the period of observation was relatively slight.

Growth increments in six groups in Asa Reservoir

The annual growth increments in various size groups of clams in Asa Reservoir is given in Table 3. The results show a consistent decline in the average length increments with increasing length of clams. While animals in the 3.50~3.39 cm class increased by 1.62 cm, a length increment of only 0.11 cm occurred in the 8.00~8.49 cm group over the 12-month period.

Table 3. Growth in various sizes of *A. sinuata* in Asa Reservoir over a 12 month period.

Length group (cm)	Mean length (cm)		Length increment (cm) yr^{-1}	
	Initial	After 12 months	Mean	Range
3.50~3.99	3.73	5.37	1.64 (1)*	—
4.00~4.49	—	—	—	—
4.50~4.99	4.57	5.54	0.97 (2)	0.88~1.06
5.00~5.49	5.30	5.89	0.59 (2)	0.56~0.61
5.50~5.99	5.81	6.23	0.42(12)	0.31~0.56
6.00~6.49	6.17	6.48	0.31 (8)	0.23~0.41
6.50~6.99	—	—	—	—
7.00~7.49	7.21	7.41	0.20 (2)	0.11~0.30
7.50~7.99	7.78	8.00	0.22 (2)	0.09~0.33
8.00~8.49	8.12	8.23	0.11 (1)	—

* Number of clams in parentheses

Monthly length-frequency distributions in the reservoir populations

Figs. 3 and 4 show the monthly length-frequency distributions of clams at 0.50 cm class intervals in the two reservoir systems. The distributions did not show any significant shifting modes. In the Asa Reservoir samples primary modes shifted between 5.0 and 6.0 cm in 1983 while fluctuating between 5.0 and 6.5 cm in 1984. The occurrence of juveniles

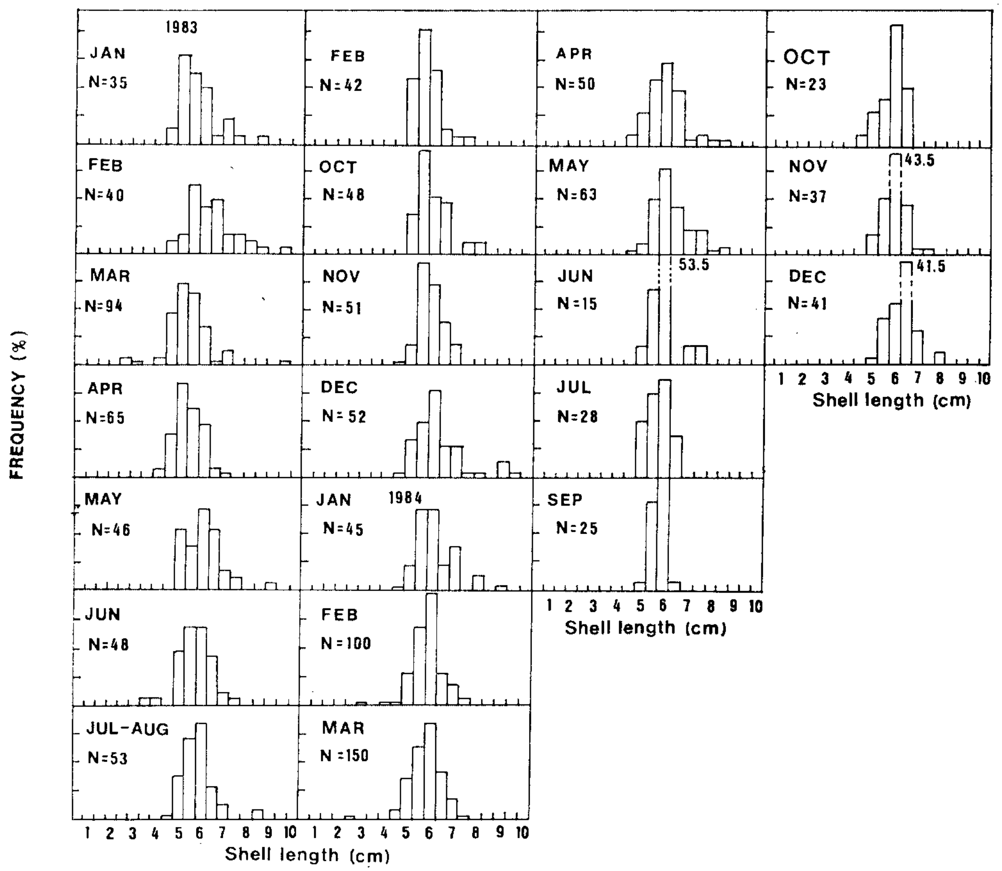

Fig. 3. Monthly length-frequency distribution of *A. sinuata* in Asa Reservoir.

in the 2.5 cm group in the March samples suggests earlier spawning activity.

In Oyun Reservoir the primary modes shifted between 8.0 and 8.5 cm except in January when modes occurred at 4.0, 9.0 and 10.0 cm and March with modes at 4.5, 7.5, and 8.5 cm. It can be seen that after January the 9.0 and 10.0 cm modes disappeared for the remainder of the year and individuals in the latter group were rare in samples, perhaps due to increased mortality in this size group.

The narrow shifts in the modes and the absence of their progressive increase or decrease may be interpreted as the result of reduced growth activity. This could be attributed to the preponderance of adults which had lower growth rates upon the attainment of sexual maturity. It could also be due to a slow rate of recruitment of juveniles into the populations.

Growth of juveniles in Asa Reservoir

Fig. 5 shows the growth of spat averaging 1.16 cm in length over a 9-month period

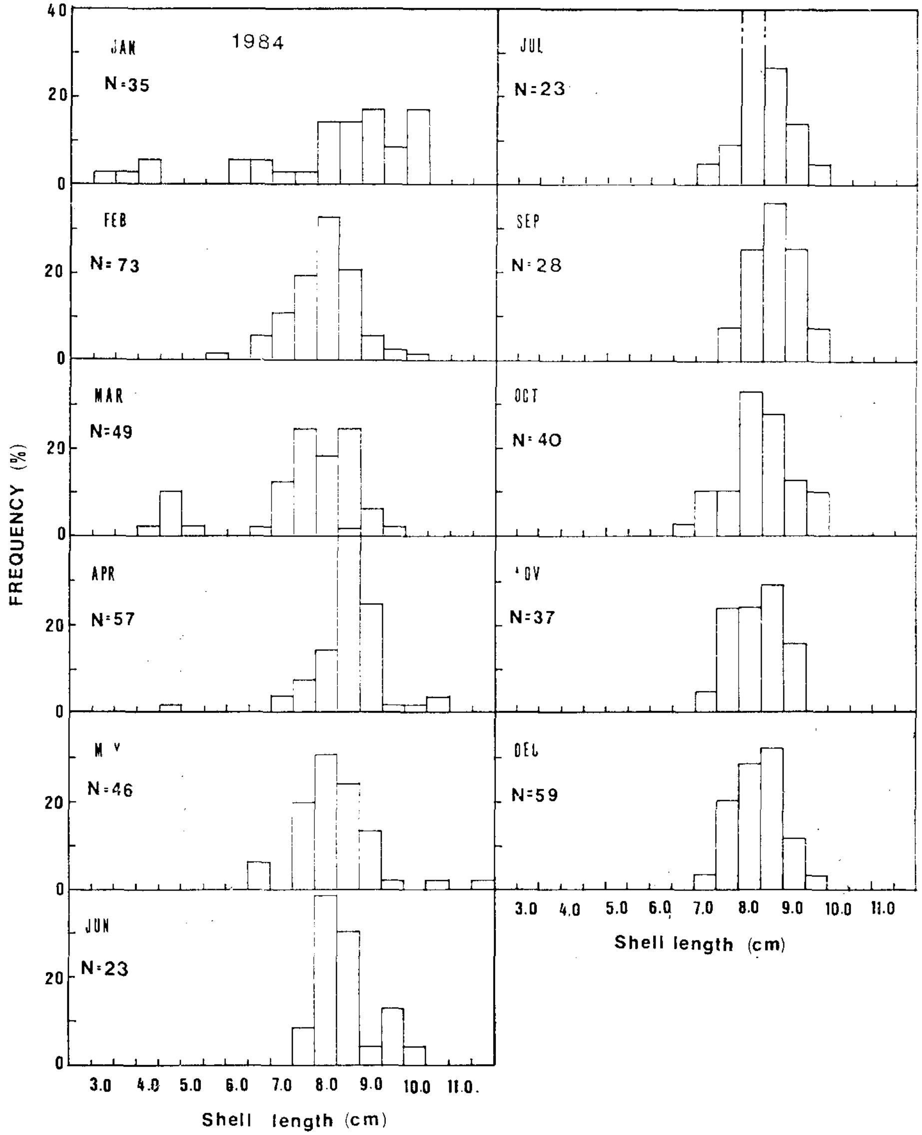

Fig. 4. Monthly length-frequency distribution of *A. sinuata* in Oyun Reservoir.

in Asa Reservoir. These were spawned in a dry season pool in River Oyun in January or February 1983. Growth was rapid between April and September, the highest growth increment occurring in May (0.63 cm). There was a decline in growth from October to early January, the mean length increasing only from 3.85 to 4.14 cm (i.e. a growth increment of 0.29 cm).

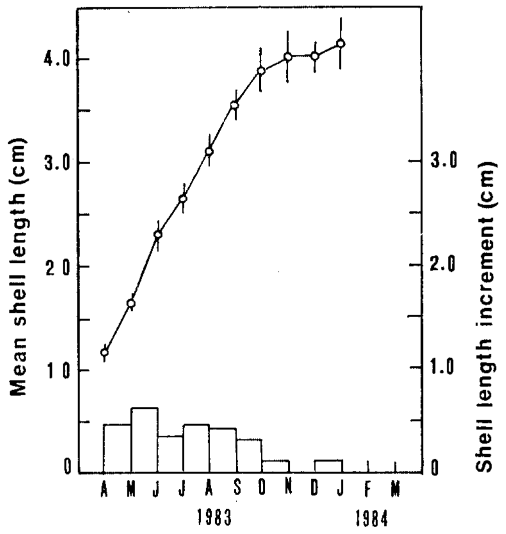

Fig. 5. Monthly mean shell growth (curve) and growth increment (histogram) of juvenile *A. sinuata* in Asa Reservoir. Vertical bars denote standard deviations.

DISCUSSION

Both environmental and physiological factors have been observed to retard growth and cause the formation of rings in bivalve molluscs. Adverse temperatures, poor food availability and reproductive activity are recognized as the main causal factors of reduced growth in bivalves (Seed, 1976). The occurrence of alternate complete and incomplete growth interruption marks in *A. sinuata* suggests the occurrence of periods of intense and moderate growth checks caused by some environmental or physiological factors. It has been shown that complete growth lines are formed annually and at a given period of the year (Crowley, 1957; Ökland, 1963; Boyden, 1972; Kautsky, 1982) while incomplete rings are induced by nonseasonal influences, or even handling (Orton, 1926; Kwei, 1965; Negus, 1966). Although the small sample size of recaptures (3.1%) in the mark-release-recapture experiment in Asa Reservoir precludes the drawing of definite conclusions, it illustrates the possibility of one complete ring being formed each year in this reservoir and other habitats.

In the current investigation the annual draw-down of water levels occurring for varying periods between February and August in the different habitats, and reduced transparencies, are the most likely environmental conditions that induced complete growth ring formation in the bivalves. Draw-down leads to the exposure and consequent aestivation of many clams; since feeding stops during aestivation, growth would cease under such conditions. Interpretation of the effect of draw-down on the growth of the Asa Reservoir specimens, however, requires considerable caution. This is because fewer clams in this reservoir might be producing growth rings due to exposure, as the ratio of the densities of aestivating to submerged animals during the height of the draw-down was only 1 : 6. In comparison, a ratio of 1.53 aestivating to 1 submerged individual was recorded in Oyun Reservoir (Blay, in preparation). The extensively variable nature of the substratum of the lotic habitats did not permit easy estimations of the density of their bivalve populations, but it was observed that a substantial number of specimens were exposed during the dry season. These differences are attributed to the larger size of Asa Reservoir which has a surface area of 302 ha and gentle slopes in the littoral zones. Oyun Reservoir (20.8 ha) and the small lotic habitats exhibited more extensive draw-down areas.

Immediately following periods of low water levels were periods of reduced transparencies in both lotic and lentic habitats due to suspended silt in the incoming floods resulting from increased rainfall. This could trigger the clams to terminate feeding by closure of their valves as reported in the freshwater donacid bivalve, *Egeria radiata* (Kwei, 1965). Suspended silt has been found to be inimical to bivalves because it could clog their filtration systems thereby reducing their feeding efficiency and subsequently causing poor growth (Headlee, 1906; Ellis, 1936; Purchon, 1968; Broom, 1982). Secondly, reduced transparencies could cause poor food availability as a result of reduced photosynthesis. Seed (1975) recognized that regardless of other conditions, retarded growth would result if food was scarce.

Thus, it seems possible that the period of slowed growth for some clams extended from the onset of the draw-down to the end of the period of depressed transparencies, and the duration for which individuals experienced these conditions would depend largely on their location in the draw-down zone. Individuals which remained submerged during low water levels would have their growth checked only when the turbidity increased. This might explain the deviations recorded in the lengths at a given ring in clams of presumably the same age. The variations may also be attributed to prolonged spawning as individual spawned well in advance of an adverse condition would have enhanced shell growth before the ring is formed whereas those spawned just prior to an unfavourable condition would exhibit a short length at annulus. It is unlikely that the relatively low temperatures prevailing in December or January (about 21°C average) contributed to the formation of a growth ring. This temperature is sufficiently high for the maintenance of continuous growth in a tropical species such as *A. sinuata* compared with a temperature of about 12°C which was found adequate for uninterrupted growth in the sub-tropical bivalve *Aspidopholas obtecta* in Hong Kong (Wong, 1982).

Growth was rapid during the initial 2 years of life in all the populations but the rates subsequently declined. Direct observations on growth in Asa Reservoir showed declining length increments with increasing size of clams. This typical growth pattern has similarly been reported in many bivalve species (Wilbur and Owen, 1964; Kwei, 1965; Negus, 1966; Tudorancea, 1972; Broom, 1982; Kautsky, 1982). Growth of this form is attributed to reduced metabolic activity with increasing size of clams (Seed, 1976). This might also explain the absence of significant shifting modes in the reservoir populations which apparently comprised overlapping size ranges of older year-classes. Negus (1966) drew attention to the limited utility of size frequency distributions in growth studies of bivalves on account of overlapping length distributions in different cohorts, and the existence of irregular recruitment. The slowed growth demonstrated in spat in Asa Reservoir upon reaching a size of 3.85 cm might be related to their attaining sexual maturity. In this reservoir, clams probably matured for the first time at 3.20 and 3.28 cm in males and females, respectively (Blay, unpublished data); slowed growth may have been caused by the channelization of energy intogonadal maturation (Tudorancea, 1972).

The observed values of the von Bertalanffy growth parameters show that the different indices of metabolism may have variously governed the growth of the populations. Beverton and Holt (1957) observed that the coefficients of catabolism (K) and anabolism (E) are genetically or physiologically determined, whereas the maximum theoretical length (L_∞) is dictated by environmental influences such as food supply or population density. Thus, although the Asa Reservoir population recorded the highest growth constant (0.67), this was perhaps negated by its comparatively low coefficient of anabolism (2.96) and hence the correspondingly low asymptotic length relative to the Oyun Reservoir, Odo-Otin River and Agbuur River populations. Similarly, in spite of the slightly higher coefficient of anabolism (3.92) in the River Oyun clams compared to the Asa Reservoir specimens, the former recorded lower theoretical and observed maximum lengths than the latter, an observation which could be explained by their higher catabolic activity (0.58). It would therefore appear that a considerable amount of energy is expended in this lotic population, an observation that correlates with their low tissue weight to length ratio (Blay, in press).

It is discerned from the above that exposure to drought with the resultant aestivation of clams, and low transparencies were perhaps the paramount reasons for slowed growth and possible growth ring formation in the *A. sinuata* populations. The values of the von Bertalanffy growth parameters suggest that a combination of physiological and/or genetic factors, and the prevailing environmental conditions in the different habitats were responsible for the characteristic growth forms and maximum lengths attained in the populations.

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ABSTRACT

The growth habits of *Aspatharia sinuata* in 2 reservoir systems and 3 lotic habitats in the 'middle belt' of Nigeria were studied by the interpretation of growth interruption

marks on shells, monthly length frequency distributions, and direct growth observations. Fastest growth occurred in Oyun Reservoir and Agbuur River while slowest growth rates were recorded in Asa Reservoir and River Oyun. Analysis of the data by Walford plots shows that the maximum theoretical length (L_∞) of the bivalves in Asa Reservoir, Oyun Reservoir, River Oyun, Odo-Otin River and Agbuur river were 7.39, 9.64, 6.75, 7.60 and 9.86 cm, respectively. Generally, growth was fast during the first 2 years of life but this slowed down thereafter. The absence of significant shifting modes in the length distributions of the reservoir populations is, presumably, a consequence of the preponderance of adults with reduced growth rates in samples. Mark-release-recapture data from Asa Reservoir tends to suggest that one major growth ring is formed on the shells annually. It would also appear that the annual draw-down of water levels with the resultant aestivation of some bivalver, and reduced transparencies are the major factors causing a growth check in *A. sinuata.*

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