Bull. zool. Surv. India, 5 (2 & 3) : 59-76, 1984

THE POPULATION AND PRODUCTION ECOLOGY OF A FRESHWATER SNAIL *BELLAMYA BENGALENSIS* (LAMARCK) (GASTROPODA : VIVIPARIDAE) IN AN ARTIFICIAL LAKE OF CALCUTTA, INDIA.

RASHID A. KHAN AND SUPRIYA CHAUDHURI
Zoological Survey of India, Calcutta.

ABSTRACT

Studies on various aspects of the life cycle, population dynamics, biomass, secondary productivity and turnover ratio of the freshwater viviparid gastropod, *Bellamya bengalensis* (Lamarck), were carried out in a large artificial lake of Calcutta, India. There was marked sexual dimorphism in growth pattern. Two generations in a year were observed with maximum life span of 18 months for females and 15 months for males. The growth rate was rapid at early ages but slowed down as the age increased. Males grew at slower rates and attained a smaller size than females. Two periods of active reproduction were observed, one in April and a second one in October. Fully developed young snails were released directly by females. The sex ratio showed a preponderance of females (average ♂ : ♀, 1 : 2.115). Fecundity was amazingly low, but at the same time mortality was also low (10%). The total population density and total standing crop biomass (all generations combined) were high throughout the year, with peaks in April and October resulting from active reproduction. Minimum values were observed in monsoon months (45/m^2 in 1978 and 95/m^2 in 1979), which were due to flooding of the lake and consequent removal of littoral vegetation. Maximum values were observed in April of both years (345/m^2 in 1978 and 295/m^2 in 1979). *Bellamya bengalensis* constituted about 40% of the total gastropod population. Middle-aged individuals dominated the composition of the population almost throughout the year.

The total production of a single generation based on standing crop biomass and mortality data was determined. The mean daily productivity and turn-over (Biomas : Production) ratios of this generation were found to be 4.56 mg C/m^2-day and 2.821 respectively.

INTRODUCTION

Freshwater gastropods, which consitute the bulk of the littoral fauna of ponds, reservoirs and rivers in India, play an important role in the dynamics of aquatic ecosystems. Although sufficient work has been done abroad on population dynamics, growth, reproduction, life cycle and bioenergenetics of a number of gastropod species (Dewitt, 1955 ; Duncan, 1959 ; McCraw, 1961 ; Russel-Hunter, 1961a, b ; Eisenberg, 1970 ; Gillespie, 1969 ; Clampitt, 1970 ; Eckblad, 1973 ; Hunter, 1975 ; McMahan, 1975 ; and Browne, 1978), there is a general lack of information on any of these aspects of Indian gastropods, which differ markedly from temperate species. Except for a general account of the bionomics of *Bellamya bengalensis* by Annandale and Sewell (1921), a preliminary report on seasonal variations in density of same species in a pond of West Bengal by Michael (1968) and a recent report on the productivity and energetics of *Pila globosa* by Haniffa (1978), no other account is available on the population dynamics and ecology of any Indian gastropod species.

In this study, the life cycle, growth, reproduction, population density, standing crop biomass, production and turnover ratio of a common prosobranch viviparus snail, *Bellamya bengalensis* (Lamarck), were examined in a large artificial lake (Dhakuria lake) of Calcutta, India.

Bellamya bengalensis is a very common snail of ponds and reservoirs of this region and generally occurs in the littoral zone on a muddy bottom under dense littoral vegetation not far from the shore. In contrast to hermaphroditic pulmonates, many prosobranch, including *B. bengalensis*, are dioecious, resulting in separate patterns of growth and life cycles for the male and female parts of the population.

MATERIALS AND METHODS

The studies were carried out for 2 years between the period January 1978 to December 1979 in Dhakuria Lake. The snails were collected from the littoral zone of 3 different centres of the lake at fortnightly intervals. As no significant differences were noticed in the distribution of snails at different centres, the data of the 3 centres were pooled so as to obtain only one set of data for a sampling date. An area of 2.5 m^2 was demarcated by a frame of 0.5 × 0.5 m and all the vegetation and the upper most layer of the substrate (2 cm) were removed and flooded with water in a tray. All snails were separated and sorted out according to species. Since individuals of *Bellamya bengalensis*, even the smallest ones, were of fairly large size, separation was done by the naked eye alone. All live and dead snails were counted separately and the total density was expressed as No./m^2. The individuals were divided into 4 age groups, Juvenile-I (less than 9 mm), Juvenile-II (9-16 mm), Adult-I (16-22 mm) ; and Adult-II (above 22 mm) and density of each group was calculated so as to get an idea of the composition of various age groups. Beside this, density according to sex was also calculated.

The investigation of growth and the life cycle followed the general method of Russel-Hunter (1961a). Shell length (maximum distance from the apex to the outer edge of the aperture) of both live and dead shells were measured to the nearest 0.5 mm with a dial caliper and grouped into size classes of 2 mm intervals. The results of these shell measurements for each sample was plotted as a size frequency distribution graph, expressed in terms of percentage of each size group in the sample. Dead shell density and size distribution were determined for mortality assessment.

By following the growth of group size classes which corresponded to cohorts of animals from the same breeding period, each sample was divided into distinct generations, and the mean shell length and standard deviation were calculated for each generation. Sample means were smoothed by averaging three consecutive means arithmetically weighted for the number of individuals in the sample. From the differences between successive smoothed means in shell length, growth rates were calculated. Size at first maturity and brood size were studied regularly by dissecting the animals. Embryo number was determined by direct uterine count of about 15-20 females in each month covering the entire range of mature sizes.

The dry weight (with shell) was determined by drying about 100 snails of different sizes at 85° C for 4 days and weighing separately on a chemical balance. The relationship between mean shell length and dry weight (with shell) was determined by regression analysis and a regression equation (significant at 1%) was worked out. Once the relationship was established, the dry weight of all snails was determined by the regression equation.

The rate of population change or instante neous rate of population growth 'r' was calculated from :—

$$r = \ln Nt\text{-}\ln No/t$$

where Nt and No are the numbers in the population at the time of sampling and t days earlier respectively.

The specific growth rate in length and weight were calculated for the two sexes separately from :—

$$g = \ln Lt - \ln Lo/t \text{ and } g = (Wt - \ln Wo)/t$$

where Lt and Wt are mean length and weight at the time of sampling and Lo and Wo, mean length and weight t days earlier respectively.

Mean biomass in a sample was determined by multiplying the number of individuals in each size class with the mean dry weight of the size class and summing them. Biomasses for different generations were also determined separately. Production was estimated by standing crop biomass data of live and dead snails following Russell-Hunter (1970).

DESCRIPTION OF THE STUDY AREA

Dhakuria lake of Calcutta is a large artificial reservoir with an area of 72 acres and is elongated in shape. The maximum length is about 1770 metres while the width at the broadest point is 282 metres. The lake is fed by rain water and is used for recreational purposes. The entire littoral zone is heavily vegetated by *Chara fragilis*, *Ceratophyllum demersum* and *Hydrilla verticullata*. The algae *Chara fragilis*, was the most dominant plant species occurring throughout the period of study and contributed about 80% of the total vegetation of the littoral zone.

TAXONOMIC POSITION

Class	:	GASTROPODA
Sub-class	:	PROSOBRANCHIA
Order	:	MESOGASTROPODA
Family	:	VIVIPARIDAE
Sub-family	:	BELLAMYINAE
Genus	:	**BELLAMYA**
Sp.	:	**B. Bengalensis** (Lamarck)

Although Annandale and Sewell (1921) recognised 11 forms of this species, (as *Viviparus bengalensis*), only form *typica* *Bellamya bengalensis* form *typica* (Lamarck) occursin this region.

Salient features :

The shell is oval as a whole and acuminate. The upper part of the shell is slightly conoidal rather than conical. The spire and body whorl (seen dorsally) are of equal height. The body whorl is evenly convex in profile. The aperture is sub-circular and has a narrow black margin. It is nearly as high as the spire and slightly oblique. The umbilicus is narrow. The colouration varies considerably, but it is never very brilliant. The ground colour is greenish and opaque. The dark bands are variable and irregular. The operculum is moderately thin and of a deep brownish colour. The external surface is concave, the outer margin strongly curved, the inner margin slightly sinuate and the posterior extremity bluntly pointed. The animal gives birth to fully developed youngs.

Results

Annual Life Cycle :

The life cycle of *Bellamya bengalensis* was traced for 2 consecutive years (1978 and 1979). The annual pattern is evident from

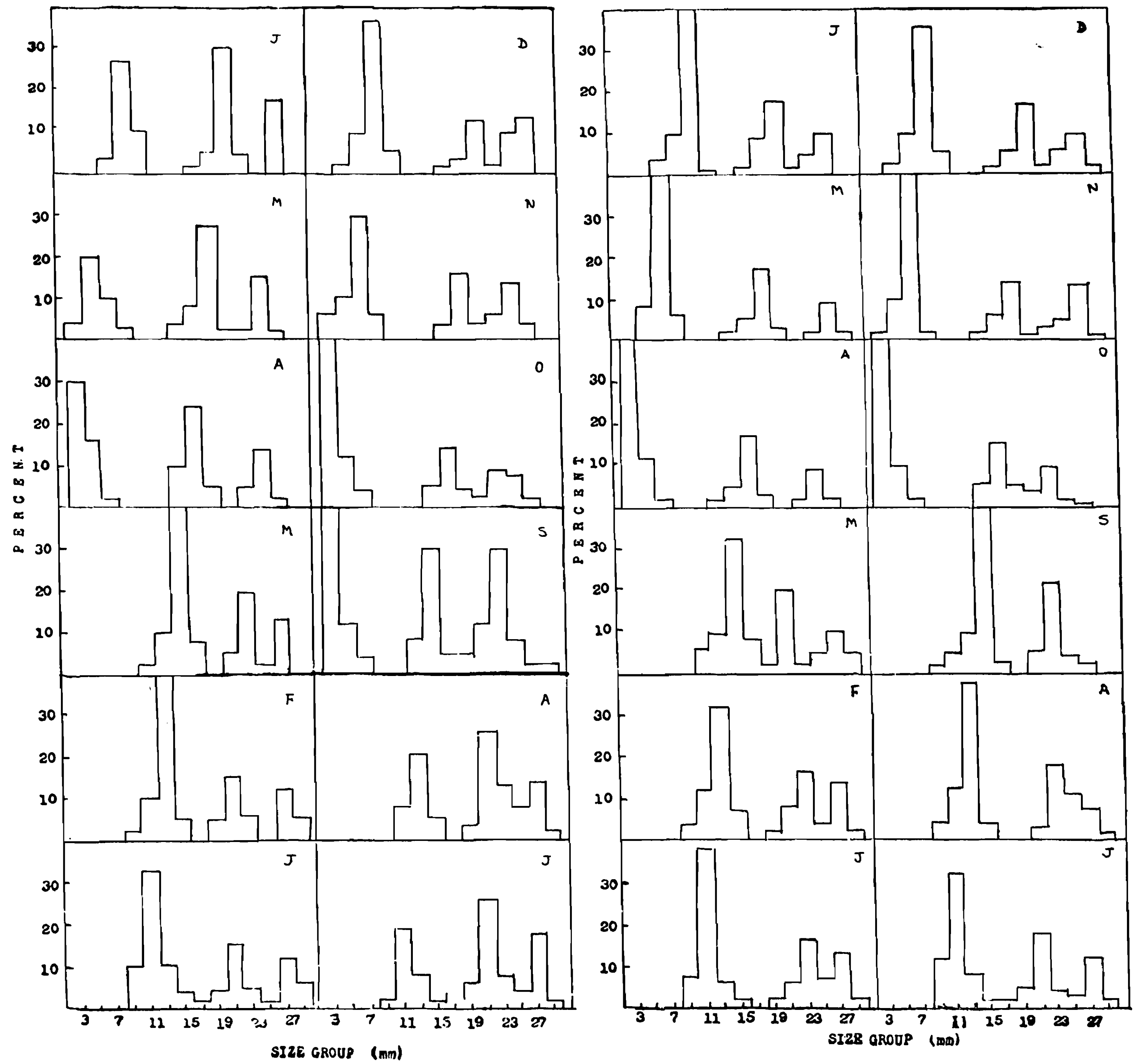

Fig. 1. Size frequency distribution of *B. bengalensis* during 1978 and 1979.

the shell length frequency distribution diagram (Fig. 1). In January 1978, when studies commenced, the population consisted of the adults (A1 and A2) and late Juveniles (J2). Three distinct size groups with modes at 11 mm, 21 mm and 27 mm were visible. In February, the three groups grew, but in March only 2 modes were observed, the third mode, which represented the largest size individual of the population, was absent. In April, a batch of young snails entered in the population and formed a mode at 3 mm, besides the two already existing modes. From May to August, there was not much change except that the individuals of the 3 groups gained in size and their modes shifted forward gradually. In September, the individuals of the largest size groups were again absent followed once more by the entrance of new individuals in the population in October.

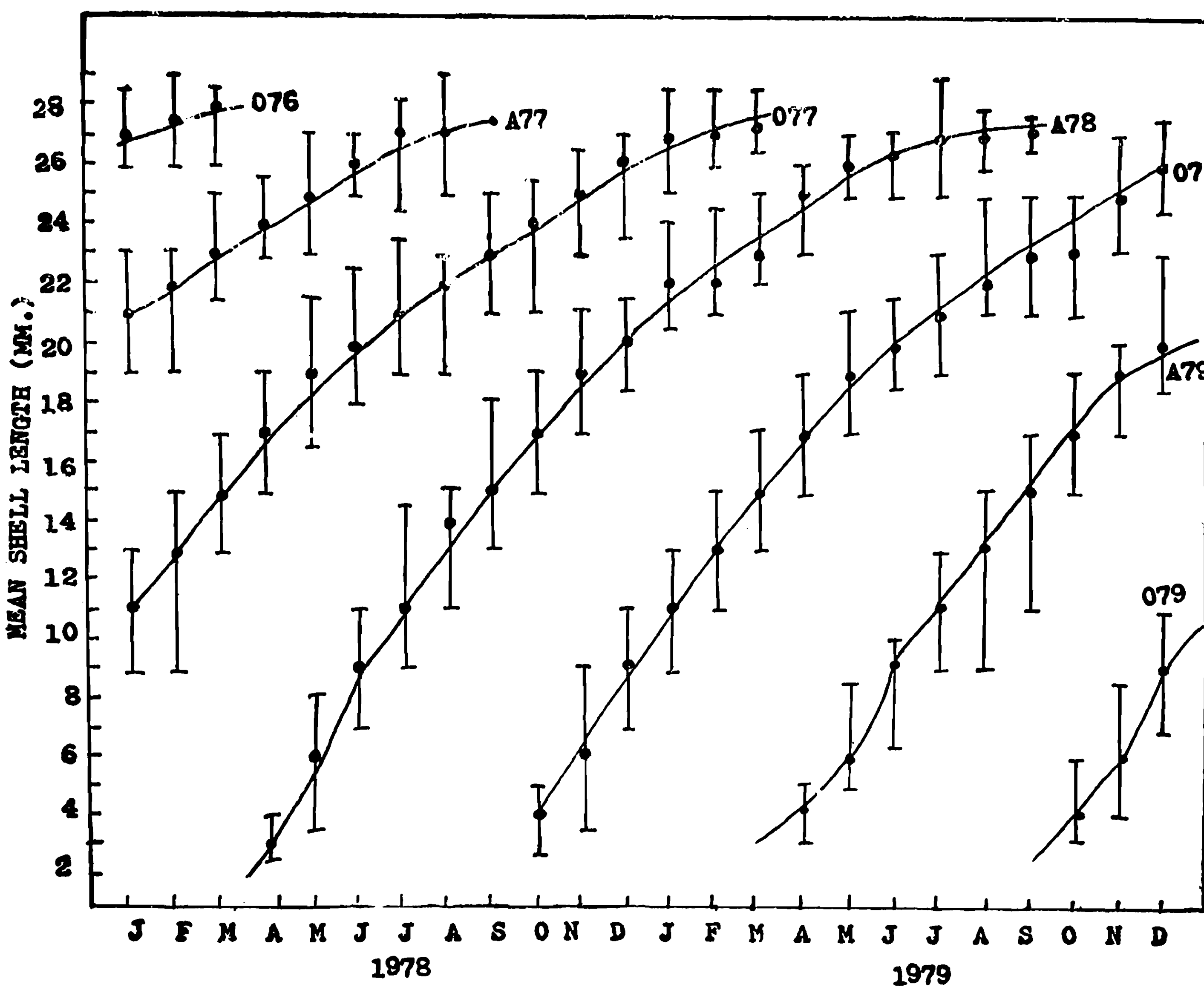

Fig. 2. Mean shell length and standard deviation in relations to months for generation sample of *B. bengalensis*. Different generations have been designated according to their tentative birth time. 0.76=October 1976, A 77=April 1977, and so on. Solid circles represent means and vertical bars standard deviations.

Significant changes were again noticed in March 1979, when heavy mortality of the oldest group occurred, resulting in their elimination from the population, followed by active reproduction in April. The three batches of adults which died out during the 15 months (January 1978 to March 1979) were born before the commencement of the study. Mortality of individuals which were born in April 1978, was observed in late August and early September 1979 (Fig. 2) after attaining the mean size of 27.5 mm, as revealed by their absence in September 1979 samples. Like previous years, active reproduction took place again in October.

By following the growth of group size classes, which corresponded to cohorts of animals from the same breeding period, samples were divided into distinct generations.

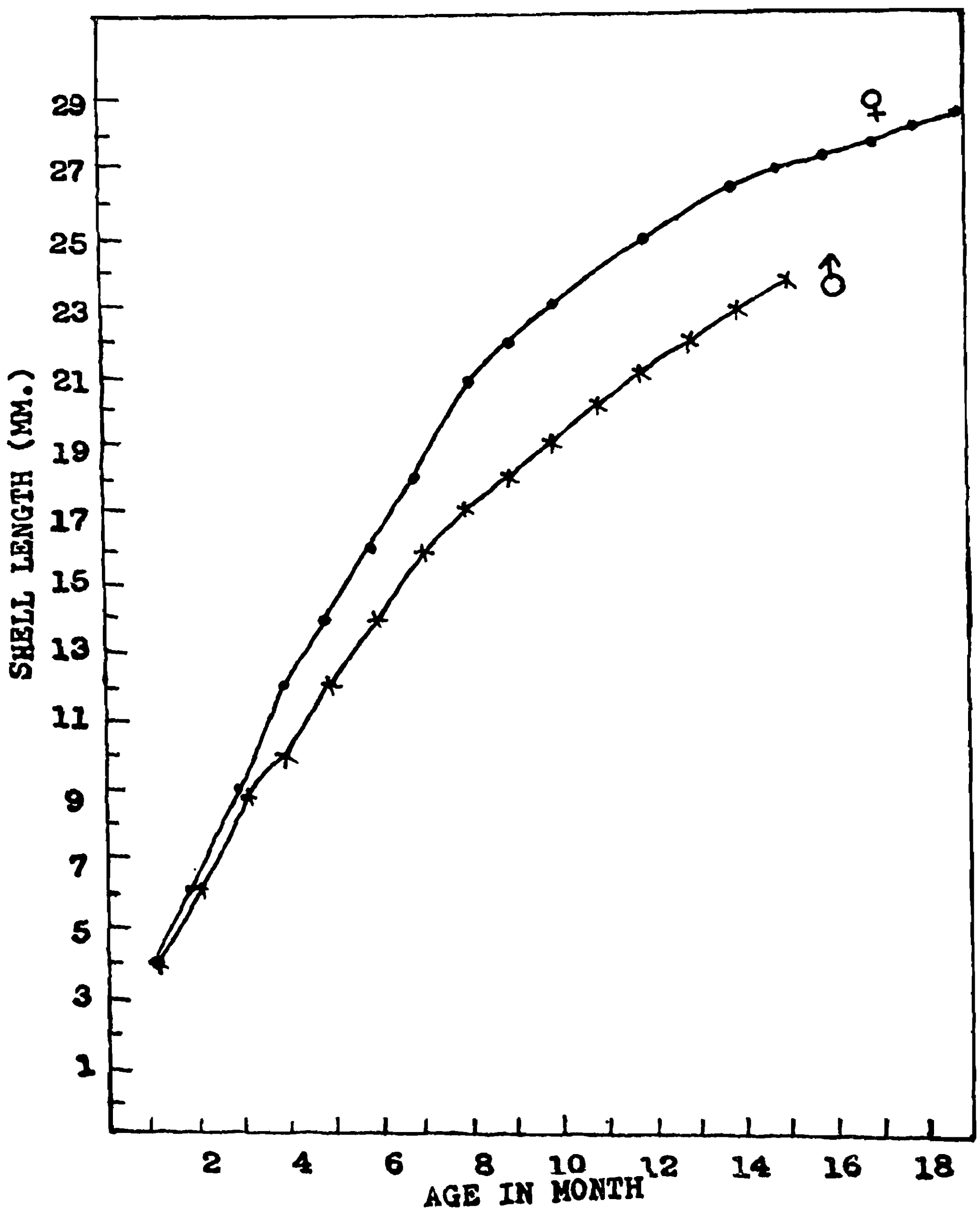

Fig. 3. Mean shell length at various age groups.

A non-overlapping clear pattern is visible in Fig. 2. In a single year, e.g. 1978, two distinct reproductive periods occurred, the first in April and the second in October. The individuals produced in April 1978 also reproduced in October 1978. This shows that 2 generations of *Bellamya bengalensis* developed in a year. An almost similar pattern was noticed in 1979. The individuals of the generation which was produced in April 1978 died out by August 1979 (Fig. 2), having a total life span of 18 months. Based on the various groups present in the population at the time of commencement of the study and onwards, each generations has been designated according to its birth period.

Age and growth rate :

The shell lengths of individuals at the time of birth were about 3 mm. In early stages, the growth rate was rapid(Fig. 3) and at the end of 6 months period average size was 15 mm. In the next 6 months, their growth was moderate and at the end of 12 months the average size was 23 mm. However, the growth rate slowed down after 12 months, although it continued until death, as evident from their specific growth rate (Table 1). The maximum shell length recorded during the present investigation was 28.1 mm.

There was a marked sexual disparity in the length of life and growth rate of *Bellamya bengalensis*. The maximum life span (Fig. 3

TABLE 1. Specific growth rate in length and dry weight of *Bellamya bengalensis*

Age in months	Length				Weight Combined	
	Female		Male			
	mean size (mm)	growth rate	mean size (mm)	growth rate	mean dry weight (mg)	growth rate
1	4	0.01350	4	0.01350	5	0.19500
2	6	0.01350	6	0.01350	9	0.02650
3	9	0.00950	9	0.00350	21	0.02147
4	12	0.00513	10	0.00870	40	0.01959
5	14	0.00445	13	0.00240	72	0.01560
6	16	0.00396	14	0.00470	115	0.01200
7	18	0.00513	16	0.00200	165	0.00880
8	21	0.00155	17	0.00190	215	0.00366
9	22	0.00148	18	0.00180	240	0.00740
10	23	0.00142	19	0.00173	300	0.00417
11	24	0.00136	20	0.00160	340	0.00540
12	25	0.00131	21	0.00155	400	0.00390
13	26	0.00123	22	0.00148	440	0.00560
14	27	0.00024	23	0.00000	520	0.00580
15	27.2	0.00000	23.2	0.00000	620	0.00000
16	27.2	0.00036	—	—	620	0.00322
17	27.5	0.00060	—	—	705	0.00032
	28.0	—	—	—	740	—

and Table 1) of males was 15 months and that of females was 18 months, which resulted in the largest and oldest individuals always being females. Females also attained larger sizes not only because of their longer life spans, but also by faster growth rate as revealed by their specific growth rates (Table 1). Females were found to be 12.5% larger in weight than males at the age of 6 months, and the difference increased to 14.7% by the time the snails reached 15 months of age (the maximum life span of males). However, there was not much difference between the growth rate of the two sexes at early stages. The pattern of growth in weight (dry weight) was almost similar to the growth in length, the growth rate decreased gradually as the age increased (Table 1).

Length weight relationship

The relationship between mean shell length and mean dry weight was statistically

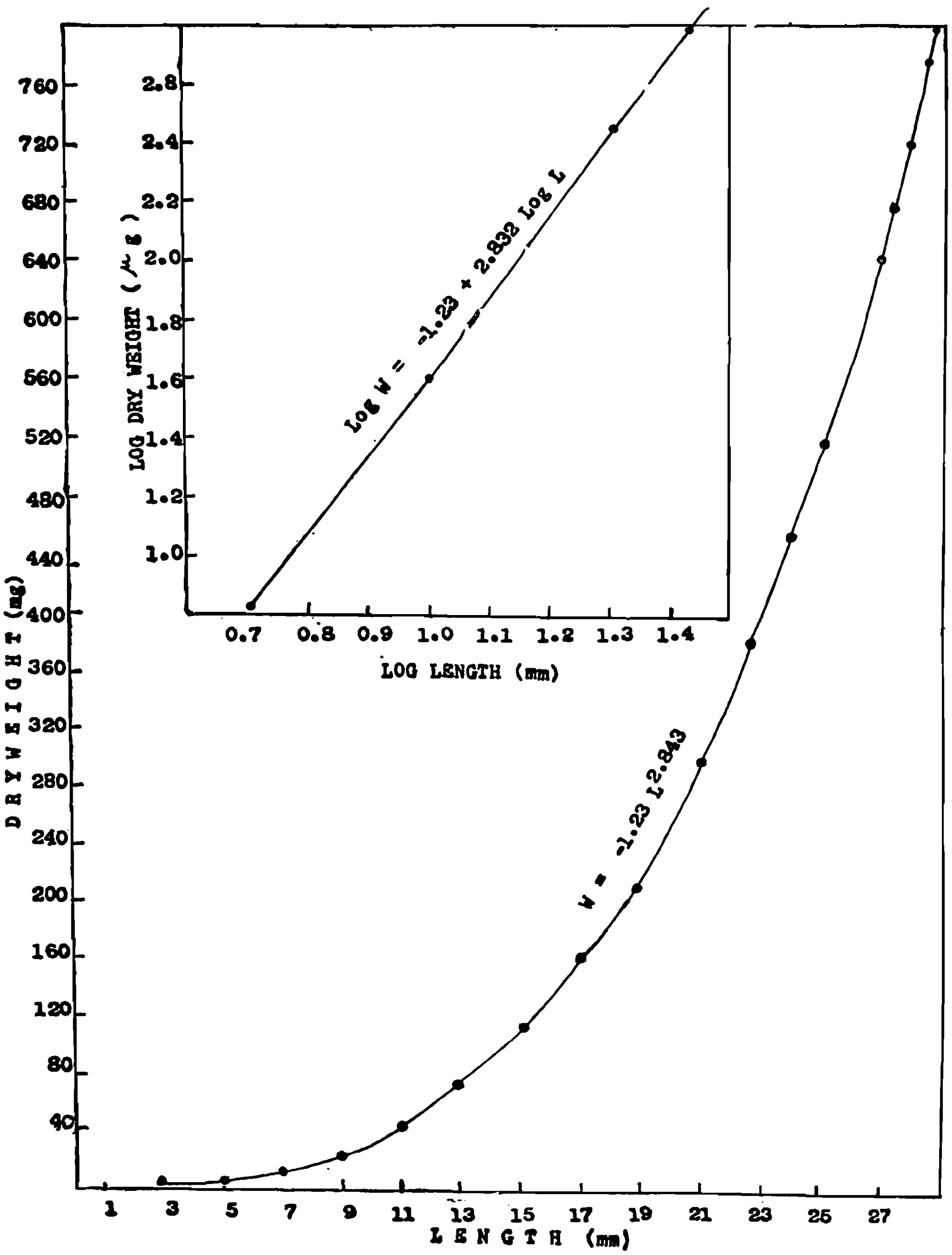

Fig. 4. Length-weight (dry weight with shell) relationship of *B. bengalensis*.

established. Weight was found to be exponentially related to length (Fig. 4), and when the values were converted to logerithms, a straight line relationship (Fig. 4) was observed with regression coefficient 'b' 2.843. The value of 'b' was very close to the values worked out for the majority of animals and followed the Cube Law. The regression coefficient was highly significant (probability less than 1%) and the length weight regression equation was :—

$$\text{Log } W = -1.23 + 2.843 \text{ Log } L$$
$$\text{or } \quad W = -1.23 \quad L\ 2.843$$

where W and L are dry weight in mg and shell length in mm respectively.

Reproduction

Size at first maturity :

Being viviparus, females discharged fully developed young. Like other parameters, the size and age at first maturity of the two sexes differed. Males matured earlier than females. The smallest size and youngest age at which males were found to carry mature spermatozoa was 13.5 mm (shell length) and 5 months respectively, while the values for females were 16 mm and 6 months respectively. Males of the A 78 generation (born in April 1978) were found to mature by early August 1978, while females were recorded carrying fully developed embryos in September. Half (50%) of the males matured at the size of 14.5 mm and half of the females at the size of 17.5 mm.

Sex ratio :

The sex ratio differed considerably from 1 : 1 throughout the year, with a preponderance of females (Fig. 6). The percentage of males varied between 18-46% with a mean of 29.8% in 1978 and between 25-48 with a mean of 36.4% in 1979, the highest percentage being in the months when active reproduction took place and the lowest at old age. As

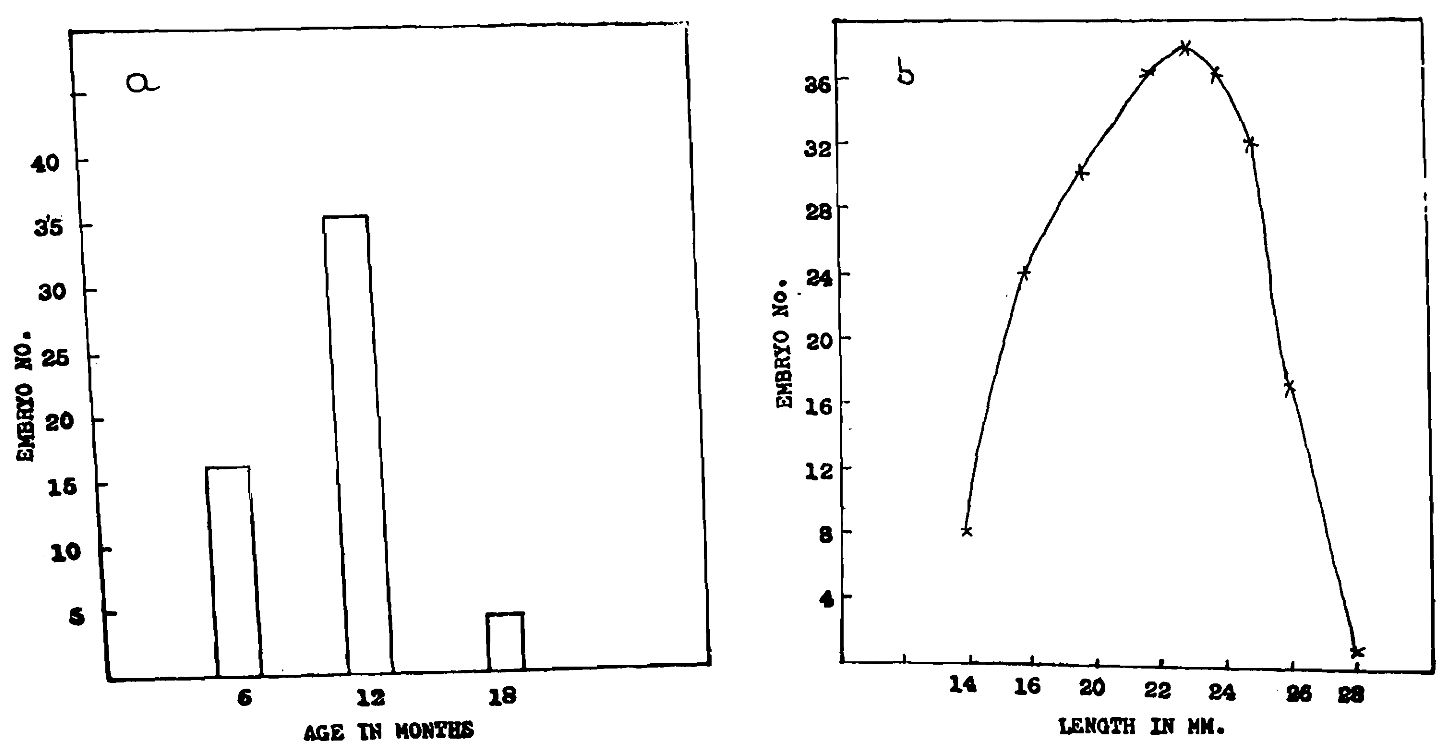

Fig. 5. Relationship between fecundity and (a) age and (b) size of *B. bengalensis*.

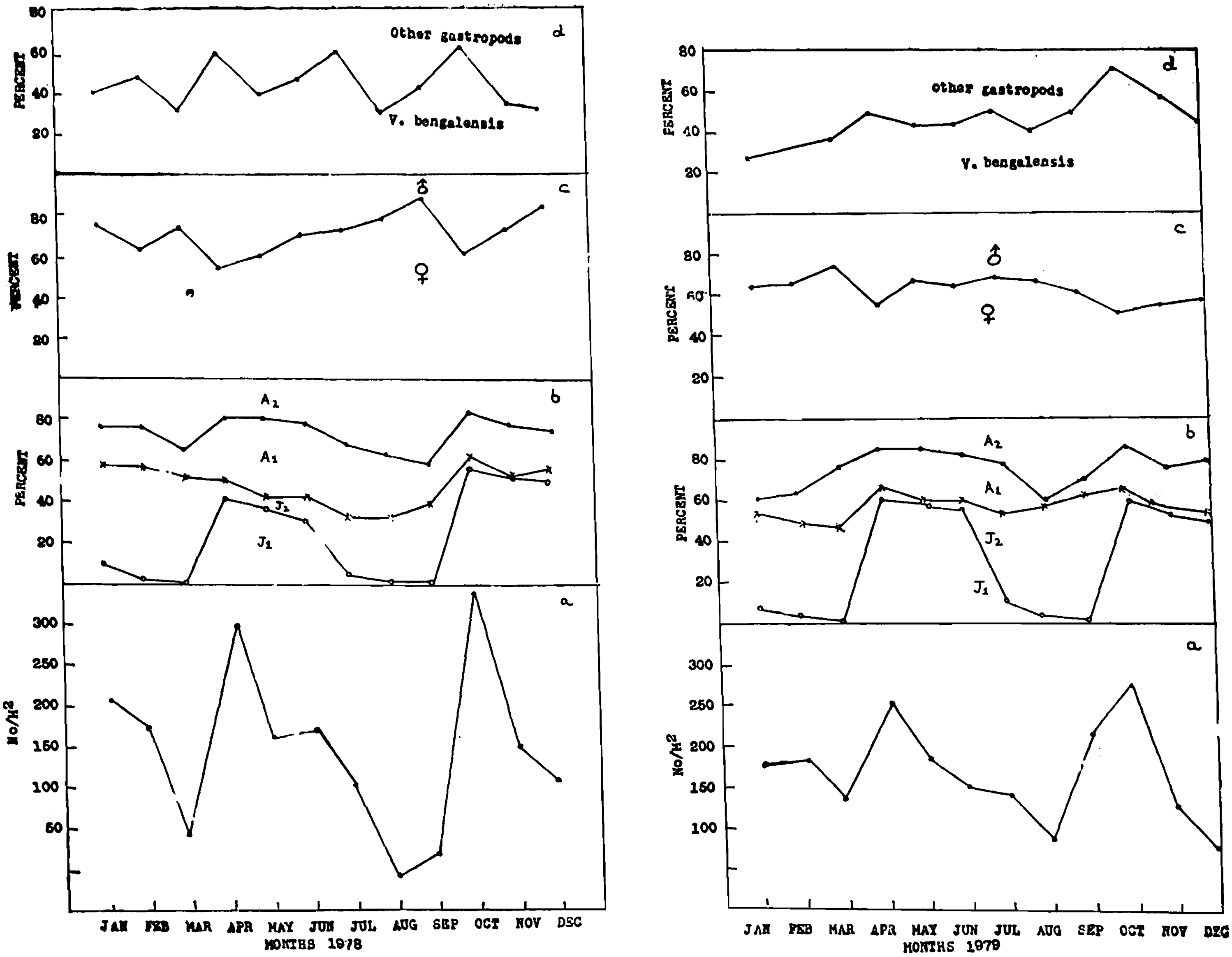

Fig. 6. Seasonal variations in population density of *B. bengalensis*. (a) total density, (b) percentage of various age groups (J_1 early juveniles, J_2 late juveniles, A_1 early adults and A_2 late adults), (c) percentage composition of males and females, (d) percentage composition of *B. bengalensis* to total gastropods.

already mentioned, the males did not attain a very old age, and largest individuals in the population were always females. The average sex ratios (♂ : ♀) observed were 1 : 2.438 in 1978 and 1 : 1.747 in 1979. The heterogenity was highly significant (probability less than 1%) as revealed by Chi Square test in both years.

Breeding season :

Two reproductive periods, as already mentioned, were found during both years, the first in April and the second in October. Each individual was found to take part in active reproduction generally 2 times in its life span, first at the age of 6 months and secondly at 12 month. Individuals born in April 1978 took part in reproduction in October 1978 and April 1979. No traces of embryonic development in the uterus of females were found after 14 months of their life, revealsng that for the rest of their lives they remain barren.

Embroy production :

Embryo number eetermined by direct uterine count after dissecting about 15-20 femalcs each month. The maximum number of young snails produced by an individual female was 38, but within the population it varied between 8-38 with a mean of 27.5. The highest fecundity occurred in 12-month-old individuals and the lowest in the oldest age class animals (Fig. 5a). Fecundity gradually increased with increasing shell length (Fig. 5b) up to 24 mm, and thereafter it decreased suddently with almost no embryos in the largest sized animals (above 26 mm).

Population Density and Cycle :

Bellamya bengalensis was the most abundant gastropod of Dhakuria Lake throughout the period of study (Fig. 6) and it alone contributed to 40.33% and 45.37% of the total gastropods in the lake during 1978 and 1979 respectively. Its density varied between 45 and 390/m^2 with a mean of 195.4/m^2 in 1978 and between 95 and 275/m^2 with a mean of 160.3/m^2 in 1979. Two distinct peaks of population density were recorded in both years, the first in April and the second in October. These peaks were due to the entrance of large number of new individuals into the population following active reproduction. As already mentioned, females always dominate in number over males. The pattern of population fluctuation was nearly similar in both years, except that in the second year the density as a whole was lower when compared to the first year.

The late juveniles (J2) and early adults (A1). i.e., middle age groups, formed the most stable proportion of the population in almost every month, without much fluctuation. They contributed nearly 50% of the total population. The late adults (A2) never formed a sizeable proportion, while early juveniles (J1) were highly periodic in their abundance (Fig. 6).

TABLE 2. Population density and rate of population change (r) of *Bellamya bengalensis*

Months	1978		1979	
	Density (no/m^2)	Rate of change (r)	Density (no/m^2)	Rate of Change (0)
January	250	-0.0051	160	0.0020
February	215	-0.0309	170	-0.0100
March	85	0.0467	125	-0.0224
April	345	-0.0166	295	-0.0090
May	210	-0.0015	185	-0.0070
June	220	-0.0116	150	-0.0010
July	155	-0.0412	145	-0.0140
August	45	-0.0147	95	-0.0272
September	70	0.0572	215	0.0082
October	390	-0.0222	275	-0.0250
November	200	-0.0074	130	-0.0013
December	160		125	

The rate of population increase 'r' (Table 2) shows that except after recruitment in April and October, population growth rate was negative during most of the year, with some exceptions.

Standing crop biomass

The combined standing crop biomass of all animals of all cohorts and all generations present on a sampling day is shown in Fig. 7. Although this does not reflect the biomass and contribution of a single generation, it gives an idea of total biomass production of *Bellamya bengalensis* in Dhakuria Lake at any time. Biomass was fairly high during both years and was influenced greatly by density in 1978 with two peaks (in April and in October) coresponding to the entrance of new individuals in to the population. This direct influence of density on biomass was probably due to the considerably fewer number of older individuals in the population during the year. The average biomass for 1978 was 44.450 gm d.w./m². In 1979, the trend was not as clear, but corresponding to density, the biomass was also less (37.217 gm/m²).

Production

The presence of at least 3 cohorts in the population any time and twice-a-year breeding made it difficult to assess production rate of the entire population of *Bellamya bengalensis*.

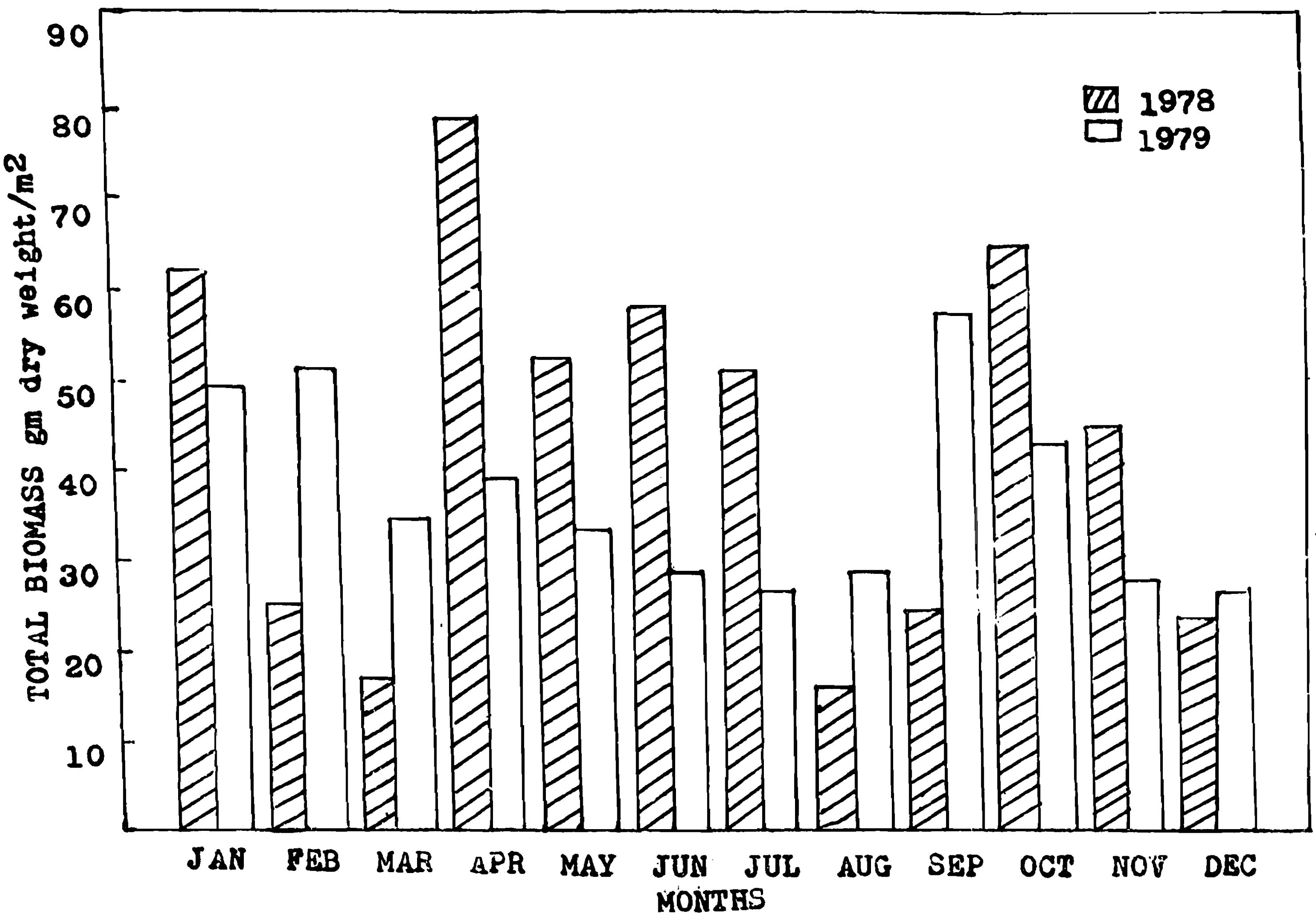

Fig. 7. Standing crop biomass of all animals of all cohorts combined during different months.

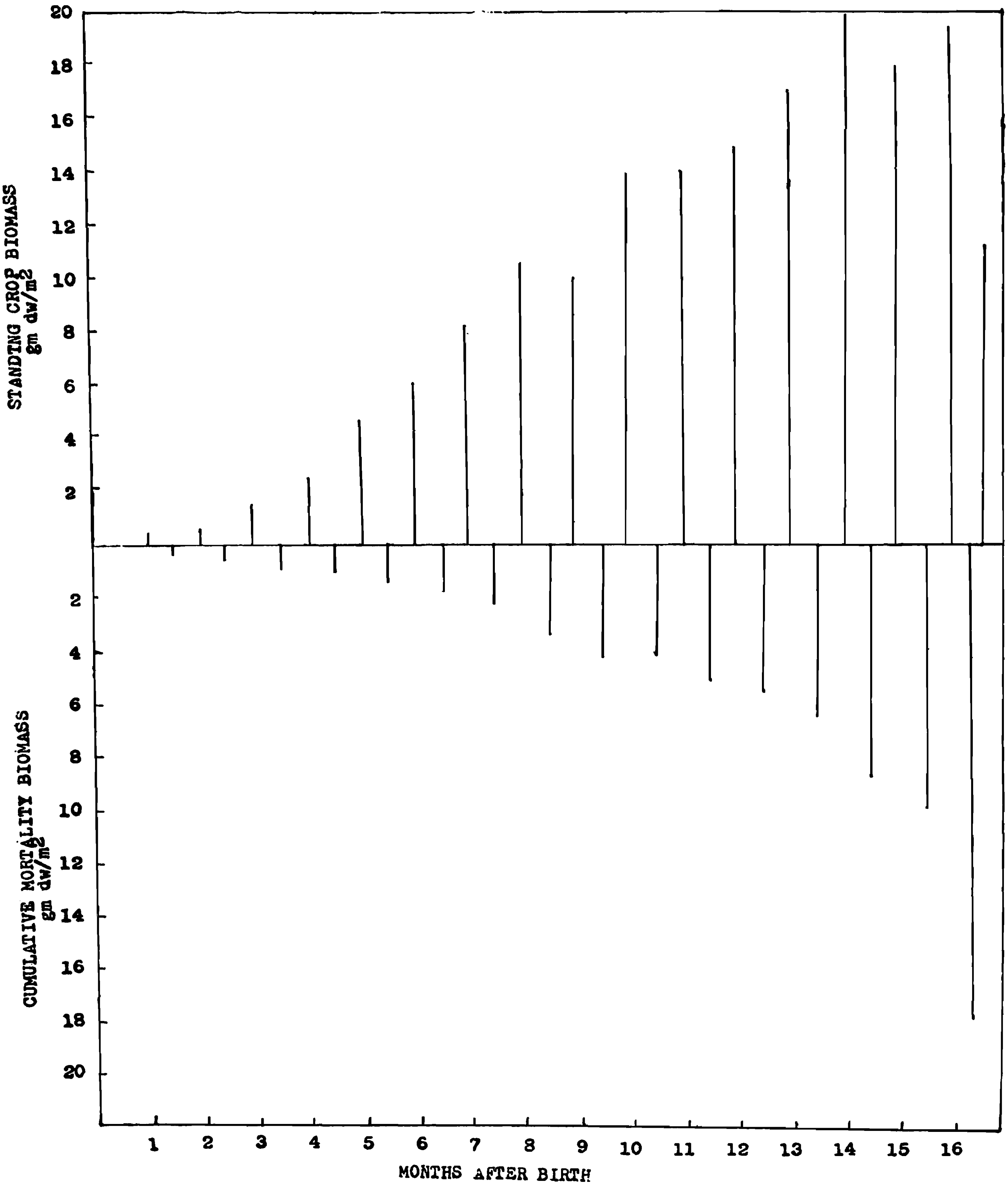

Fig. 8. Standing crop biomass and cumulative mortality biomass of *B. bengalensis*. The histograms above the line represent the standing crop of each specific age and histograms below the line represent the cumulative biomass of snails which have died between successive sample.

The removal summation method of Hamilton (1969) was not found suitable. Therefore, like many of the earlier workers (Hunter, 1975; Browne, 1978), the population rate based on standing crop biomass and cumulative mortaliy of a single generation was determined. The generation which was produced in April 1978 (A 78) was selected as it completed the cycle within the period of the study.

The biomass of live snails of this generation in terms of dry weight was calculated in each sample, starting from April 1978 to August 1979 when all animals of the generation died. The other contribution to the assessment of production came from mortality data. Mortality was assessed from the number of dead shells. Their biomass was calculated from mean shell weight as for live samples. Using the convention of Russell-Hunter (1970), the standing crop biomass of live snails was plotted above the line and the cumulative biomass for the snails which died (mortality), below the line (Fig. 8). At any point along the line, the sum of the standing crop biomass of live snails and the cumulative mortality biomass provided the cumulative production up to that point. The cumulative production at any time was divided by time lapsed and net productivity rate per unit time was calculated. The productivity of the A 78 generation at the end of their life was 29.090 mg d. w./m^2 for 17 months. The annual, monthly and daily rates computed were 20532 mg/m^2-year, 1711 mg dw/m^2-month and 57.03 mg dw/m^2 day respectively.

The mean biomass value during the period was 103,12 gm dw/m^2. When the production biomass ratio or turnover ratio was calculated, it was found to be 2.83.

Discussion

Life cycles and total life spans of freshwater gastropods have been reported to vary considerably, both within and between species (Russell-Hunter 1964). Even different populations of the same species may show entirely different patterns of life cycle in different water bodies. The pattern based on number of generations per year and seasonal changes in mean shell size ranges from a simple one-generation pattern to 3 generations per year. Throughout the temperate latitudes, a single annual life cycle is most common, especially in pulmonates. Prosobranchs, however, have been reported to have multi-year life cycles. Hubendick (1948), Samochwalenko and Stanczykowska (1972) and Young (1975) observed that females of *Viviparus viviparus* have a life span of 4 years, while Browne (1978) found that females of *V. georgianus* live up to 36 months. Similar results have been reported for *V* (= *Cipangopaludina*) *malleatus* from Canada (Stanczykowska *et al* 1971). Compared to these species of temperate regions, *Bellamya bengalensis* in Dhakuria Lake has a shorter life span of 18 months with a 2-generations-per-year pattern. Earlier studies on this species by Annandale and Sewell (1921) from Calcutta showed that it can grow up to 2 years. This shows that the life span of the same species may vary even at the same lititude at different times and in different water bodies.

Unlike many pulmonate species of temperate waters where growth ceases during winter, the viviparids in both temperate and tropical waters have been found to grow continuously throughout the year, as revealed by the present study on *Bellamya bengalensis*. This difference has been related to differences in feeding habits and fluctuation in the availability of food supply in temperate waters (Browne 1978). However, in tropical waters where conditions are different from temperate waters and food supply remains moderate throughout the year, continuous growth is automatically expected. This was reflected from the unaffected growth rate of *B. bengalensis* in Dhakuria Lake during different months. Being a highly eutrophic water body, food was never in short supply in Dhakuria Lake (Khan 1979, 1980). The temperature in this region of the country also does not fluctuate much from month to month and was never limiting for *B. bengalensis*. These findings are in contrary to many observations made on temperate species where little growth is observed during winter months (McCraw, 1961 ; Clampitt, 1970 ; Eckblad, 1973).

However, the growth rate was found to be affected by the physiological state of the animals. The rate was high at early ages, moderate at middle ages and considerably slower at old age. The pattern of life cycle and growth of *Bellamya bengalensis* was somewhat similar to those observed by Annandale and Sewell (1921).

Like all other viviparids studied (*V viviparus*, *V georgianns*, etc.), marked sexual dimorphism has been found in length of life and growth rate of *Bellamya bengalensis*. In all viviparid species, including *B. bengalensis*, females attain larger sizes and longer life spans as compared to males. The males of *B. bengalensis* attained maturity earlier, took active part in reproduction during 2 successive breeding seasons and died well before the commencement of the third breeding season, whereas females were present just before the commencement of the third breeding season. Therefore, the sex ratio of the older age groups were considerably heterogenous, with a definite preponderence of females. It is not only the early mortality of the males which is responsible for the differential sex distribution, but females were also born in larger numbers than males. The differential life span and growth rate has helped in the successful adaptation of the species. Selection probably drives females towards larger sizes than males as a consequence of viviparity. The larger sizes of females are advantageous as they may maintain a large number of embryos in the uterus (Browne 1978).

Reproduction in *Bellamya bengalensis* is viviparous. Viviparity is a relatively rare occurrence in invertebrates. Among freshwater molluscs, it occurs in sphaeriid bivalves, viviparid gastropods and thiarids. This viviparity has resulted in extremely low fecundity of *B. bengalensis*. As a rule, the fecundity is smaller where chances of juvenile mortality is less. The release of sufficiently large-sized juveniles presumably reduces the length of time that fragile young snails are exposed to external environmental fluctuations (Avolizi 1976), which in turn reduces the chances of early mortality. This high rate of survival has resulted in a very low selection ratio of 10 : 1. Similarly low selection ratios have also been observed in other species of *Viviparus*, 12 : 1 in *V viviparus* (Samochwalenko and Stanczykowska 1971) and between 15 : 1 to 4 : 1 in *V georgianus* (Browne 1978). On the other hand, ratios as high as 50,000 : 1 for the salt marsh snail *Melampus bidentatus* (Apley 1967) and 1400 : 1 and 1000 : 1 for *Lymnaea* (=*Radix*) *peregra* and *Planorbis corneus* respectively (Russell-Hunter 1953), have been reported.

The high population density throughout

the year with the dominance of juveniles II and adults I indicated that the species was well adjusted and had a stable population in Dhakuria Lake. The lower density in August may be related to two factors. First, the heavy mortality of the oldest age class took place in this month, and second, due to heavy rains the lake was flooded, thereby removing the snails as well as vegetation from the littoral zone.

The productivity of gastropods also vary considerably between species and populations in relation to space and time. Productivity values ranging from 0.002 mg C/m^2-day to as high as 23 mg C/m^2-day have been reported from temperate waters (Gillespie, 1969 ; Mason, 1971 ; Mattice, 1972 ; Eckblad, 1973 ; Hunter, 1975 ; McMahan, 1975 ; and Browne, 1978). Most of these values are reported in terms of carbon and for the sake of comparison the dry weight (with shell) values of *Bellamya bengalensis* were also converted in terms of carbon. It has been estimated roughly that the carbon values of *B. bengalensis* are about 8% of the dry weight (with shell). Dry shell-free weight is approximately 18% of the dry weight with shell, and carbon is about 45% of the shell-free dry weight. The converted values for mean daily productivity was 4.56 mg C/m^2-day. When compared to other species, the value fell in a middle range. This shows that in spite of high biomass, the productivity of *B. bengalensis* in Dhakuria Lake was not as high as expected. In the allied species, *B. georgianus*, Browne (1978) reported that values vary between 0.91 and 8.30 mg C/m^2-day. Very high productivity values (19.28 mg C/m^2-day, when converted) have been reported in *Pila globasa* from a pond of Madurai, India, by Haniffa (1978), the only account available from Indian tropical waters.

Another measure of productivity which has been used by many workers is turnover ratio (ratio of production to mean standing crop) or P/B ratio. Waters (1969) has discussed in detail the application of turnover ratio and reported that in a number of benthic invertebrates, the ratio is rather consistant and varied between 2.5 and 5.0. Eckblad (1973) supported his view on the basis of turnover ratios of *Lymnaea* (=*Stagnicola*) *palustris* (2.69) and *Physa* (=*Physella*) *integra* (2.94). Hunter (1975) found that the ratio varied from 5.63 to 5.82 in the population of *S. palustris*. The turnover ratio of *Bellamya bengalensis* (2.82) seems to agree with the contention of waters.

Acknowledgement

The authors are thankful to Dr. B. K. Tikader, Director, Zoological Survey of India, for providing necessary facilities. Thanks are also due to the staff of Calcutta Improvement Trust at Ravindra Sarobar (Dhakuria Lake) for their help in the collection of samples.

References

Annandale, N. and Sewell, R. B. S. 1921 : The banded pond snail of India. *Rec. Indian Mus.*, **22** : 215-292.

Avolizi, R. J. 1976. Biomass turnover in populations of Viviparus sphaerid Clams : Comparisons of growth, fecundity, mortality and biomass production. *Hydrobiologia*, **51** (2) : 163-180.

Apley, M. L. 1967. Field and experimental studies on pattern and control of reproduction in *Melampus bidentatus* (Say) Ph. D. Dissertation Syracuse Univ. Syracuse.

BROWNE, R. A. 1978. Growth, mortality, fecundity, biomass and productivity of four lake populations of the prosobranch snail, *Viviparus georgianus*. *Ecology*, **59** (4) : 742-750.

CLAMPITT, P. T. 1970. Comparative ecology of the snails *Physa gyrina* and *Physa integra* (Basommatophora : Physidae). *Malacologia*, **10** : 113-151.

DEWITT, R. M. 1955. The ecology and life history of the pond snail *Physa gyrina*. *Ecology*, **36** : 40-44.

DUNCAN, C. J. 1959. The life cycle and ecology of freshwater snail *Physa fontinalis* (L). *J. Anim. Ecol.*, **28** : 97-117.

ECKBLAD, J. W. 1973. Population studies of three aquatic gastropods in an intermittent backwater. *Hydrobiologia*, **41** : 199-212.

EISENBERG, R. N. 1970. The role of food in the regulation of the pond snail, *Lymnaea elodes*. *Ecology*, **51** : 680-684.

GILLESPIE, D. M. 1969. Population studies of four species of molluscs in the Madison River, Yellowstone National Park. *Limnol. Oceanogr.*, **14** : 101-114.

HAMILTON, A. L. 1968, On estimating annual production. *Limnol. Oceanogr.*, **14** : 771-782.

HANIFFA, M. L. 1978. Secondary productivity and energy flow in a tropical pond. *Hydrobiologia*, **59** : 49-66.

HUBENDICK, B. 1951. Recent lymnaeidae, their variation and morphology, taxonomy, nomenclature and distribution. *K. Seven Vetenskapsakad. Handb.*, (4) **3** : 1.

HUNTER, R. D. 1975. Growth, fecundity and bioenergetics in three populations of *Lymnaea palustris*. *Ecology*, **56** : 50-63.

KHAN, R. A. 1979. Primary productivity and trophic status of two tropical waterbodies of Calcutta, India. *Bull. zool. Surv. India*, **2** : 129-138.

KHAN, R. A. 1981. Secondary production and biomass of zooplankton and its relationship to trophic status of a tropical artificial lake. *Bull. zool. Surv. India*, **4** : 181-189.

MASON, C. F. 1971. Respiration rates and population metabolism of Woodland snails. *Oecologia*, **7** : 80-94.

MATTICE, J. S. 1972. Production of a natural population of *Bithynia tentaculata* L. (Gastropoda : Mollusca). *Ekol. pol.*, **20** : 525-538.

McMAHAN, R. F. 1975. Bioenergetics variation in three natural populations of the freshwater limpet *Levapex fuscus*. *Proc. malac. Soc. Lond.*, **42** : 331-351.

McCRAW, B. M. 1961. Life history and growth of the snail *Lymnaea bumilis* Say. *Trans. Am. microsc. Soc.*, **80** : 16-27.

MICHAEL, R. G. 1968. Studies on the bottom fauna in a tropical freshwater fish pond. *Hydrobiologia*, **31** : 203-230.

RUSSELL-HUNTER, W. 1953. On the growth of the freshwater limpet, *Ancylus fluviatilis* Muller. *Proc. zool. Soc. Lond.*, **123** : 623-636.

Russell-Hunter, W. 1961a. Annual variations in growth and density in natural populations of freshwater snails in the west of Scotland. *Proc. zool. Soc. Lond*, **136** : 219-253.

Russell-Hunter, W. 1961b. Life cycles of four freshwater snails in limited populations in Loch Lomond, with a discussion of intraspecific variation. *Proc. zool. Soc. Lond.*, **137** : 135-171.

Russell-Hunter, W. 1964. Physiological aspects of ecology in nonmarine molluscs. p. 83-126 in K. M. Wilber and C. M. Young (ed) *Physiology of Molluscs* Vol. 1. Academic Press, London.

Russell-Hunter, W. 1970. *Aquatic productivity*. Macmillan Company, New York. 306 p.

Samochwalenko, T. and Stanczykowska, A. 1972. Fertility differentiation of two species of Viviparidae (*Viviparus fasciatus* Muller and *V viviparus* L.) in some environments. *Ekol. pol.*, **20** : 479-492.

Stanczykowska, A., Magnin, E. and Numouchel, A. 1971. Studies of three *Viviparus malleatus* populations of the Montreal region 1. Growth, fecundity, biomass and annual production. *Can. J. Zool.*, **49** : 1431-1441.

Waters, T. F. 1969. The turnover ratio in production ecology of freshwater invertebrates. *Am. Nat*,, **103** : 173-181.

Young, M. R. 1975. The life cycles of six species of freshwater molluscs in the Worcester-Birmingham Canal. *Proc. malac. Soc. Lond.*, **41** : 533-548.