

FECUNDITY OF *BIOMPHALARIA STRAMINEA* AND *B. GLABRATA* IN THE LABORATORY: A TWELVE-MONTH COMPARATIVE STUDY

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In the present comparative study a Biomphalaria straminea sample from Picos (Piauí) showed expressive advantages related to fecundity over a B. glabrata sample from Belo Horizonte (Minas Gerais) such as: higher egg-mass production in 10 out of 12 months of study; higher egg production in all months of study; higher egg per egg-mass ratio in 11 out of 12 months of study; 66% of the egg-masses containing more than 20 eggs while in B. glabrata 70% of the egg-masses showed less than 20 eggs; three times less empty egg capsules than B. glabrata; attaining maximum fecundity in half the time required by B. glabrata. Mortality however was higher and sooner in B. straminea, suggesting higher semelparity in this species than in B. glabrata, a possibility that requires confirmation through long-term studies with other samples of both species. This first finding of a B. straminea sample more fecund than B. glabrata is discussed in relation to other data from the literature, and some recommendations are made on the quantification of fecundity of planorbid snails.

Key words: *Biomphalaria straminea* – *Biomphalaria glabrata* – fecundity

Occupying the largest geographical area and ranking the second in importance as *Schistosoma mansoni* host, *Biomphalaria straminea* is the least known species to be controlled in Brazil. In the past ten years most studies related to the species reported its identification in new biotopes, thus pointing to the increasing spread of the species' geographical domains. However only few studies were concerned with a sound knowledge on its ecology and bionomy. Besides enlarging the scope of control measures, the sound knowledge on *B. straminea* acquired new importance with the evidence of its dominance in areas formerly occupied by *B. glabrata*. The displacement of this last species by *B. straminea* was observed in Pernambuco (Barbosa, 1973), Minas Gerais (Paraense, 1986), and Martinique (Guyard & Pointier, 1979).

The loss of *B. glabrata* populational balance due to the introduction of *B. straminea* is attributed to such factors as: lower susceptibility of *B. straminea* to *S. mansoni* infection; *B. straminea* higher resistance to desiccation (Paraense, 1977; Barbosa, 1985); *B. straminea* higher

fecundity rates when mixed with *B. glabrata* under crowding conditions (Michelson & Dubois, 1979), as well as higher dispersion capability and vagility (Michelson & Dubois, 1979; Barbosa et al., 1984). *B. straminea* high locomotion have already been reported in a previous study (Schall et al., 1986) where the species showed significantly higher ratios than *B. glabrata* and *B. tenagophila* (Schall et al., 1984).

In view of the increasing and quickly expansion of *B. straminea* in different biotopes, and due to its high populational density in natural conditions, one can suppose that the species is extremely prolific. In the present study we tried to verify if this feature could be added to the above list of factors, thus favouring *B. straminea* in relation to *B. glabrata*. However, the few studies comparing the fecundity of the two species invariably assigned superiority to *B. glabrata* (Jansen, 1944; Penido et al., 1951; Andrade et al., 1974; Michelson & Dubois, 1979) and that this is a current idea among medical malacologists. Given that the above-mentioned studies are of short-term nature, the present study offers a more detailed, long-term comparison between unmixed populations of the two species.

This study is part of the M. Sc. Thesis of the first author.

MATERIALS AND METHODS

Snail samples used were *B. straminea* originating from Picos (Piauí, northeastern Brazil) and *B. glabrata* from Belo Horizonte (Minas Gerais, southeastern Brazil) provided by the Department of Malacology of the Instituto Oswaldo Cruz, where the colonies had been laboratory-reared for several generations. The snails used were reared from the embryo stage and fecundity quantification started one month after the beginning of their egg-laying activity. The total sample included thirty specimens of each species divided into groups of six per experimental container. Containers with 3.2 liters of dechlorinated tap-water served as medium. The water was renewed bimonthly and the substratum consisting of earth, calcium carbonate and oyster powder (in the proportion of 10:1.5:2 respectively, according to Paraense & Corrêa, 1988) was renewed half-yearly. The snails were fed *ad libitum* with fresh lettuce and the unconsumed surplus was removed the day after to avoid rottenness. The egg-masses were counted four to five times a week when the minimum and maximum air temperatures as well as the water temperature were recorded. The confrontation between temperature and fecundity variations was presented elsewhere (Rozemberg, 1989). Snails found dead or in anhydrobiosis were replaced by specimens of the same diameter and origin reared apart for this purpose. The differences

in fecundity between months and between species were compared using the bilateral statistical test of Willcoxon (Siegel, 1956).

RESULTS

Table I shows the mean rate and standard deviation of the number of egg-masses laid by *B. glabrata* and *B. straminea* samples in each month.

The statistical analysis pointed to a highly significant superiority of *B. straminea* in the whole year (Fig. 1). The month by month analysis based on raw data also revealed a highly significant superiority of *B. straminea* fecundity rates in 10 out of 12 months of study. With regard to egg productivity, besides being significantly higher in all months of study, the superiority of *B. straminea* over *B. glabrata* was much more evident than that recorded for the production of egg-masses (Fig. 2). Superiority conversion was found in no data collection performed everyday for a 9 month-period. The average number of eggs per egg-mass for *B. straminea* was noticeably higher than for *B. glabrata* in all months, except for April (Fig. 3). The monthly average numbers for *B. glabrata* are very close to each other, ranging from 10 to 13.7 eggs per egg-mass, except for November, December and January. For *B. straminea* on the other hand these average numbers show a greater variation, ranging from 10.2 to 30.5 eggs per egg-mass.

TABLE I

Number of egg-masses and eggs per snail, and eggs per egg-mass (mean standard deviation) laid by *Biomphalaria glabrata* and *B. straminea* samples throughout one year, in laboratory

Months (No. of observ.)	Egg-masses per snail		Eggs per snail		Eggs per egg-mass	
	<i>B. glabrata</i>	<i>B. straminea</i>	<i>B. glabrata</i>	<i>B. straminea</i>	<i>B. glabrata</i>	<i>B. straminea</i>
Aug. (18)	0.61 ± 0.22	1.29 ± 0.44	6.19 ± 2.65	29.73 ± 11.5	9.92 ± 1.47	21.91 ± 3.16
Sep. (18)	1.36 ± 0.31	1.47 ± 0.23	17.60 ± 4.67	45.33 ± 9.45	12.49 ± 1.51	30.52 ± 3.06
Oct. (22)	1.38 ± 0.24	1.35 ± 0.27	19.11 ± 4.16	39.40 ± 8.10	13.70 ± 1.97	29.44 ± 2.24
Nov. (18)	1.20 ± 0.22	1.25 ± 0.37	21.79 ± 4.33	34.34 ± 11.0	18.17 ± 2.24	27.04 ± 2.47
Dez. (15)	0.76 ± 0.23	0.98 ± 0.18	14.30 ± 5.08	26.54 ± 5.64	18.28 ± 2.38	26.57 ± 2.85
Jan. (18)	0.72 ± 0.25	0.92 ± 0.23	13.62 ± 5.64	24.13 ± 9.23	17.05 ± 2.03	26.87 ± 4.75
Feb. (15)	0.31 ± 0.13	0.87 ± 0.20	3.73 ± 2.32	20.44 ± 6.31	11.26 ± 3.63	23.44 ± 6.45
Mar. (17)	0.31 ± 0.11	0.84 ± 0.25	3.78 ± 1.70	15.01 ± 5.36	11.70 ± 2.77	16.77 ± 3.45
Apr. (18)	0.30 ± 0.11	0.63 ± 0.30	3.29 ± 1.54	7.42 ± 4.48	11.08 ± 3.71	10.24 ± 3.77
May (12)	0.47 ± 0.19	0.78 ± 0.28	4.37 ± 2.04	12.76 ± 3.94	8.43 ± 2.53	15.98 ± 2.49
Jun. (12)	0.43 ± 0.10	0.71 ± 0.17	5.24 ± 1.67	14.82 ± 4.27	11.69 ± 3.41	20.05 ± 3.33
Jul. (8)	0.40 ± 0.13	0.75 ± 0.08	5.30 ± 2.14	16.59 ± 1.56	13.13 ± 2.94	21.43 ± 2.14
Total (191)	0.69 ± 0.41	0.99 ± 0.28	10.01 ± 6.90	23.88 ± 11.56	13.08 ± 3.19	22.45 ± 6.14

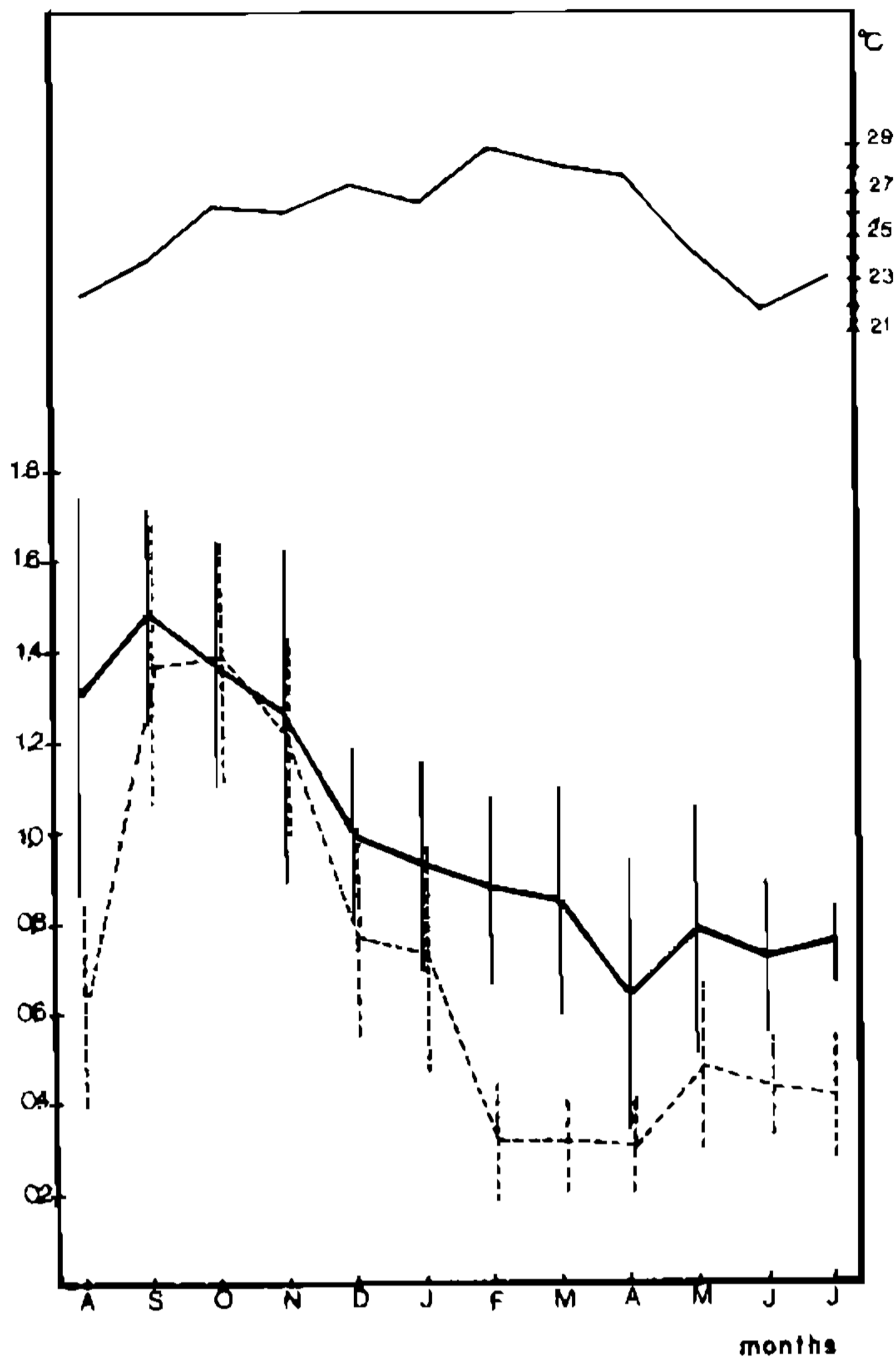


Fig. 1: monthly mean number of egg-masses per snail. Data obtained with 30 *Biomphalaria straminea* specimens (-----) and 30 *B. glabrata* specimens (---) throughout 12 months. The graph on the top shows monthly air temperatures.

Snail samples were also compared in terms of maximum number of eggs per egg-mass in each data collection (191 days), showing that in 6 out of 12 months of study *B. straminea* was significantly superior, while the opposite occurred just in a single month. The statistical comparison of the number of eggs in the largest egg-mass laid in each month pointed to a superiority of *B. straminea* in the whole year ($N = 12$; $T = 14$; $p = 0.05$).

The comparison between minimum values of eggs per egg-masses in each data collection showed that in 4 out of 10 months the smallest egg-masses laid by *B. straminea* contained significantly more eggs than those laid by *B. glabrata*. The opposite occurred in a single month only. The comparison for the year as a whole could not be made because the smallest monthly value was invariably one for both snail samples.

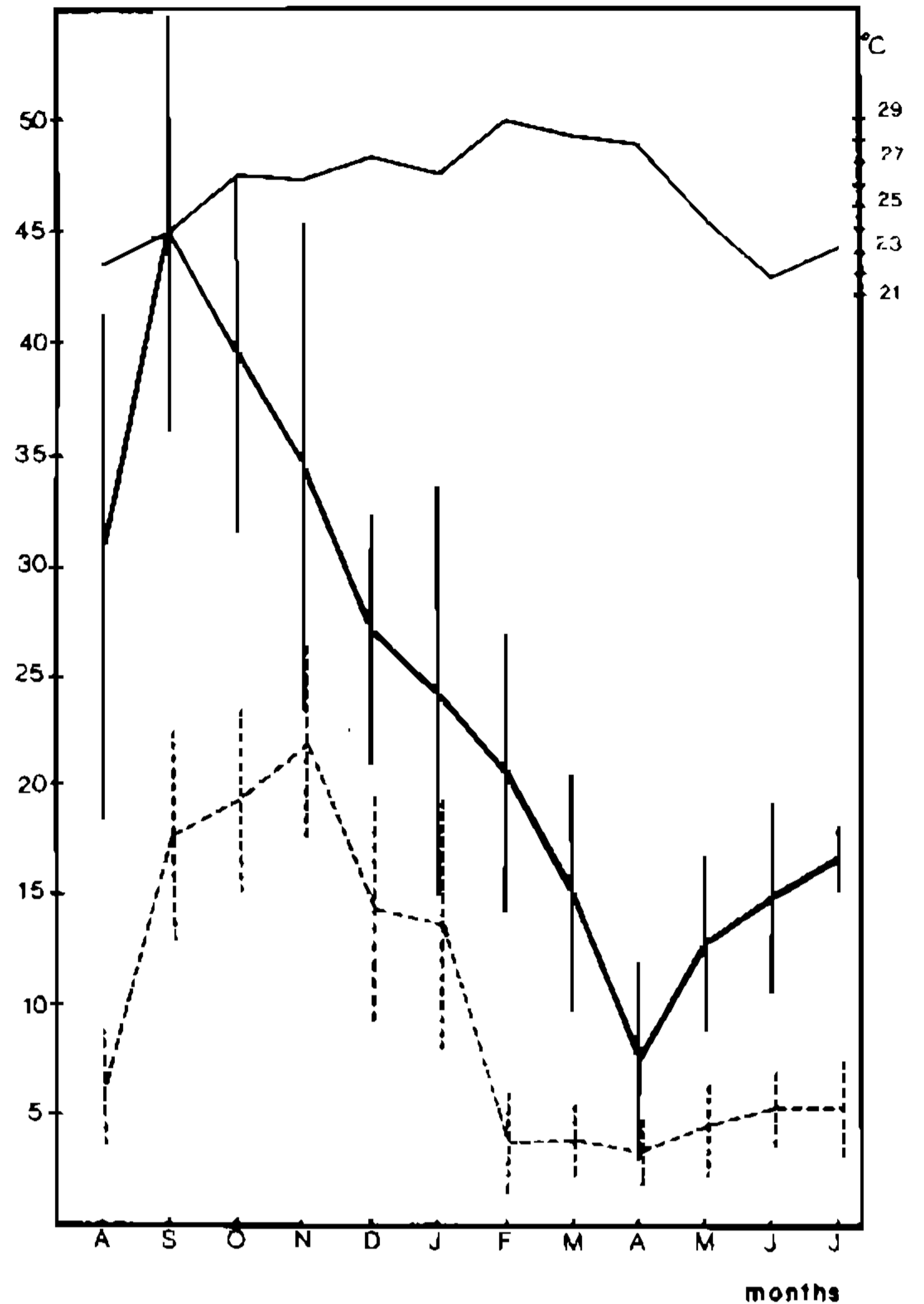


Fig. 2: monthly mean numbers of eggs per snails, (see note on Fig. 1).

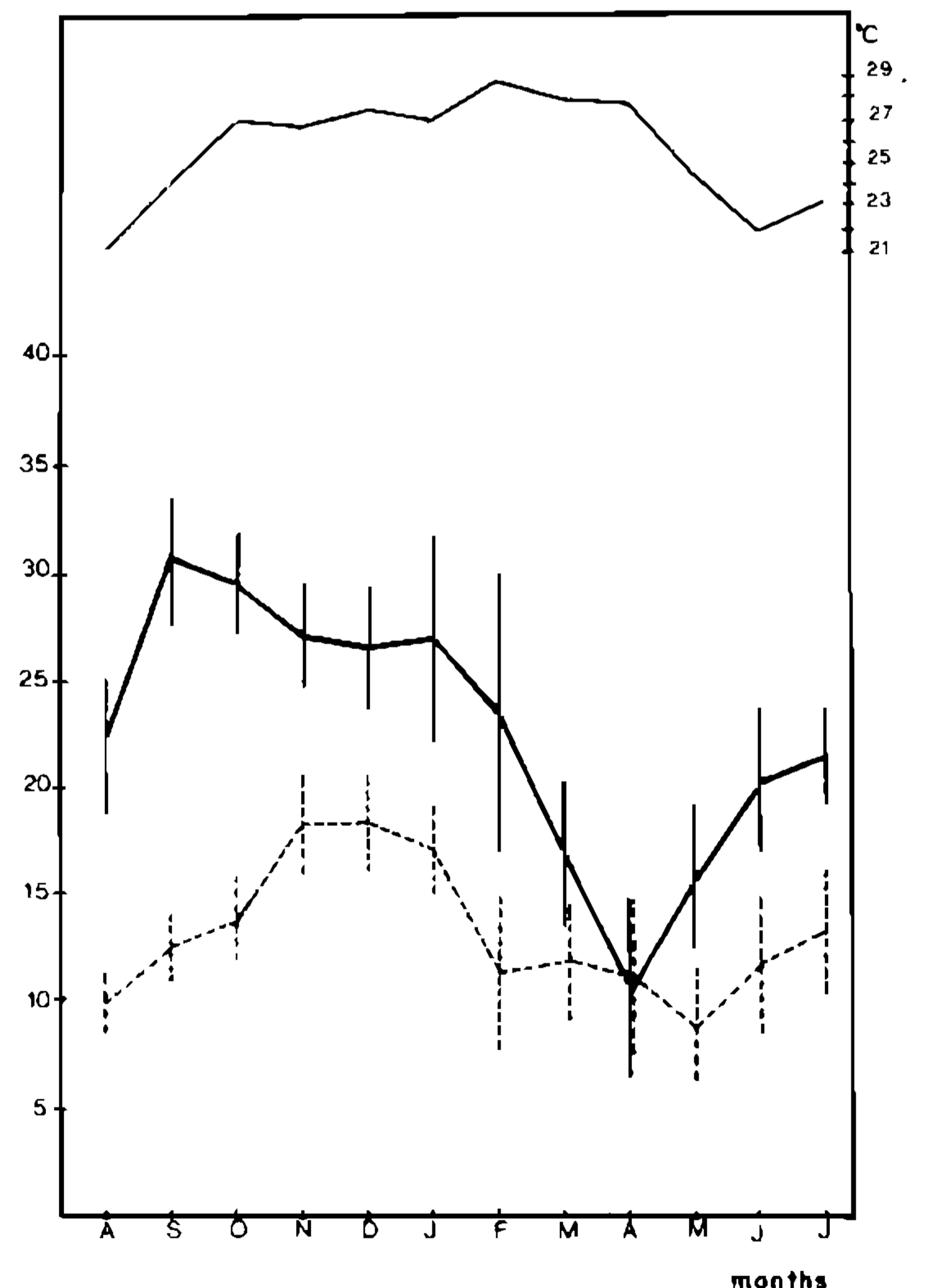


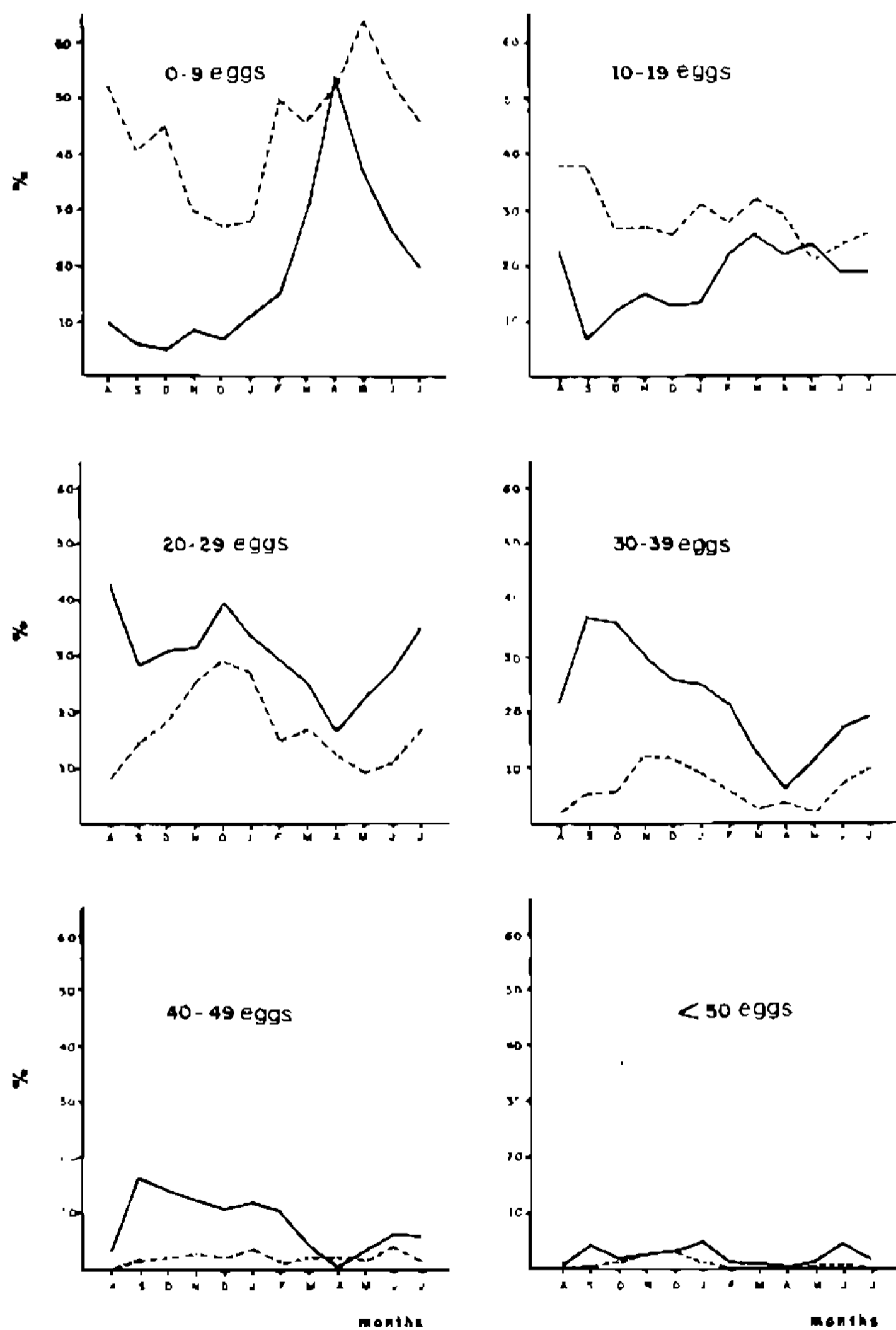
Fig. 3: monthly mean numbers of eggs per egg-mass, (see note on Fig. 1).

In order to obtain more accurate information on the variability of the number of eggs per egg-masses, the egg-masses frequency was analysed according to classes of egg number.

TABLE II

Frequency of egg-masses in *Biomphalaria straminea* (BS) and *B. glabrata* (BG) according to classes of egg number

Classes of egg number	Number of egg-masses		Percentages (%)	
	BS	BG	BS	BG
0 to 9	1647	3029	16.3	41.6
10 to 19	1734	2151	16.9	29.6
20 to 29	3148	1358	30.7	18.7
30 to 39	2494	499	24.3	6.9
40 to 49	965	154	9.4	2.1
50 to 59	211	59	2.1	0.8
60 to 69	24	22	0.2	0.3
70 to 79	2	3	0.02	0.04
Total	10252	7275		



Figs 4-9: monthly frequency of egg-masses according to classes of egg number. Data obtained with 30 *Biomphalaria straminea* specimens (-----), and 30 *B. glabrata* specimens (- - -).

Egg-masses with less than 20 eggs represented 71% of the total amount laid by *B. glabrata* but only 33% by *B. straminea*. The situation was quite the opposite in relation to egg-masses containing 20 to 40 eggs for they represented 55% in *B. straminea* and just 25% in *B. glabrata*. Larger egg-masses containing more than 40 eggs were also more common in *B. straminea* (11% against only 3% in *B. glabrata*). In addition it should be emphasized that the distribution of *B. straminea* egg-masses according to classes was more balanced than that obtained with the *B. glabrata* sample. Figs 4 to 9 illustrate the evolution of these percentages throughout the year.

The daily quantification of empty egg capsules laid throughout the study year (Table III) revealed that the deposition rate of empty capsules gradually increased with the aging of the two samples. Despite the phenomenon being confirmed by experts in personal communications, there is no reference to it in the available literature. The general computation showed that *B. glabrata* laid three times more empty capsules than *B. straminea* over the same period.

Snail mortality under experimental conditions is given in Fig. 10. The second and third months were the more difficult ones to *B.*

TABLE III

Comparative Fecundity of *Biomphalaria straminea* and *B. glabrata*: Monthly frequency of empty egg-capsules

Month	<i>B. straminea</i>		<i>B. glabrata</i>	
	Empty capsules/ Total of capsules	%	Empty capsules/ Total of capsules	%
August	1/ 973	0.1	0/ 455	0
September	1/ 1323	0.08	1/1221	0.08
October	3/ 1257	0.24	15/1286	1.17
November	4/ 1121	0.36	11/1077	1.02
December	6/ 914	0.66	19/ 710	2.68
January	8/ 858	0.93	41/ 672	6.10
February	11/ 730	1.51	20/ 261	7.66
March	17/ 785	2.17	12/ 284	4.23
April	29/ 567	5.12	29/ 272	10.66
May	43/ 723	5.95	100/ 441	22.68
June	13/ 641	2.03	52/ 389	13.37
July	6/ 381	1.58	31/ 209	14.83
Total	142/10273	1.38	331/7277	4.55

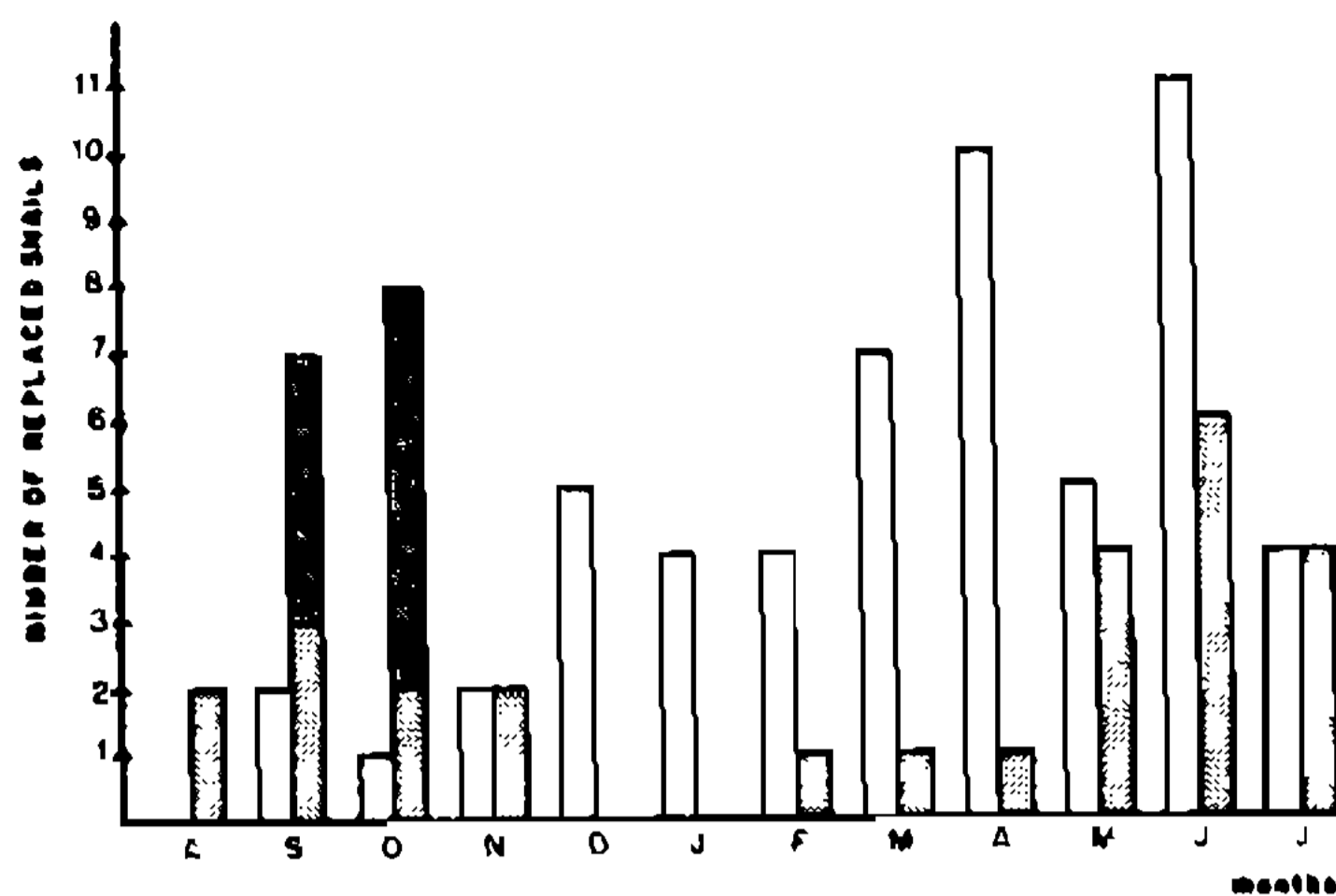


Fig. 10: snail mortality under experimental conditions. □ *B. straminea*; ▨ *B. glabrata*; ■ anhydrobiosis.

TABLE IV

Monthly variation of water temperature and maximum and minimum air temperature

Months	Air		Water
	Maximum	Minimum	
August	24.8	22	21.2
September	26.4	23.7	24.3
October	29.2	25.9	26.9
November	28.9	25.6	26.7
December	29.8	26.5	27.5
January	29.1	26	27
February	31.5	28.4	28.9
March	30.6	28	28.1
April	30.7	26.9	27.9
May	27.4	23.5	24.4
June	24.6	21.2	22
July	26	22.8	23.2

glabrata, while *B. straminea* was fairly well acclimated to the experimental environment in this early phase of the study. From the eighth month forward, particularly in the ninth and tenth month, *B. straminea* sample showed a high mortality, while in *B. glabrata* it only became expressive from the tenth month forward.

DISCUSSION

There are many references to the great reproductive potential of *B. straminea* in field conditions. Malacologists agree that this species, in maintaining schistosomiasis cycle in extensive areas, counterbalances its low susceptibility to *S. mansoni* infection with an extraordinary proliferation capability. In laboratory conditions however this high fecundity of *B. straminea* has never been confirmed before. From Jansen's observations (1944) to more recent studies, *B. glabrata* is referred to as the

more prolific of the two species. The present results therefore constitute the first laboratory record of higher fecundity of *B. straminea* compared to *B. glabrata*.

It is important to emphasize that the present study, like any other study using a single population sample of each species, does not provide for generalizations because of the high variability among populations of a species, particularly if we deal with pulmonate snails. As stated by Meier-Brook (1986), in this taxa there has been very little adaptative radiation in the geological past in comparison with the one that has taken place in prosobranch gastropods. As a result many pulmonate species have maintained a high flexibility to environmental changes leading to high variation between species populations.

Egg laying frequency – *B. glabrata* mean rate for the whole year (0.69 egg-masses per snail per day) is compatible with data from other studies: Scherrer et al. (1976) found 0.69 in one of their study samples; Magalhães & Carvalho (1969), in a thirty days study, found 0.64; the same ratio was obtained by Kawazoe (1980) in a one year study; Paulini & Camey (1964) found 0.7 egg-masses per snail per day in the least prolific population of their study. The high variations of the present *B. glabrata* sample throughout the year allowed the finding of ratios compatible either with the most or with the least prolific samples reported in the literature. Hence, from February to April we obtained the low ratio of 0.3, identically to that obtained by Michelson (1961) and to the value range reported by Rey (1956), 0.19 to 0.42 egg-masses per snail per day. However, in months of higher fecundity (Table I) we recorded 1.36 and 1.38 egg-masses per snail per day, a result compatible with that of Liard et al. (apud Scherrer et al. 1976) and Pauliny & Camey (1964), both indicating 0.93. Given this high variation in the egg-laying frequency of a single sample under study, it is clear that extensive long-term studies are required before imputing any feature as inherent to a given population.

For *B. straminea* the mean rate obtained, 0.99 egg-masses per snail per day, is compatible with that reported by Lucena (1956), 1.29, both extremely higher than the 0.22 egg-masses per snail per day obtained by Andrade et al. (1973).

Number of eggs per snail – The mean rate of 10 eggs per snail per day recorded for *B. glabrata* throughout the year is compatible with the results obtained by other authors: Michelson (1961), 8.96; Scherrer et al. (1976), 7.0 and 10.6; Coelho (1954), 12.3; and Andrade et al. (1974), 13.53. Higher ratios have been found by Szumlewicz (1958), 18.1; Chernin & Michelson (1957a and b), 17 and 17.3; and Michelson & Dubois (1979), 16.75 (this ratio was computed based on tables presented by the authors). Here again, if one considers the egg production of the present sample only during more fecund months of the year (September, 17.6; October, 19.1; and November, 21.8) the results would be comparable with the highest figures presented above. The only data that really diverge from all others available in the literature were those recorded by Scherrer et al. (1976), 41.6 and 40.5, surmounting all other observations made for *B. glabrata*.

Few data are available in the literature on *B. straminea* egg production. The mean rate obtained in the present study (23.88) is compatible with those obtained by Lucena (1956), 28.15; and Michelson & Dubois (1979), 20.09 (the latter was calculated from tables presented by the authors). These three values however are much higher than the 2.3 eggs per snail per day reported by Andrade et al. (1973). If we consider that the last result was obtained by the authors during the winter (May to August), and taking into account the low temperatures recorded by them during these months, the low egg production rate is at least partly explained. Based on the present long-term observations (Table I) there was in fact a decrease of *B. straminea* egg productivity during these months (May to August) when air and water mean temperatures were lower than in the remaining months of the year. Only considering data collected from April to July, our mean rate falls to 12.9 eggs per snail, only half of the 23.88 obtained for the entire year.

In the comparison of egg productivity between *B. glabrata* and *B. straminea*, as previously stated, the few studies available give superiority to the former, though none of these studies present enough data to support this idea. Andrade et al. (1974) compared *B. straminea* fecundity during winter with *B. glabrata* fecundity during spring of the subsequent year, attributing superiority to the latter. This species however was probably favoured by the higher temperatures recorded by the authors in

comparison with those recorded during tests with *B. straminea*. Once again this possibility can be confirmed using the present data: considering the fecundity of *B. glabrata* just in spring months our mean rate that was 10 eggs per snail per day rises to 18.2. Michelson & Dubois (1979) also stated, for the control colonies of their study, that *B. glabrata* produced more eggs than *B. straminea*, even though the summing up of data published by these authors does not confirm this statement.

Average number of eggs per egg-mass – The first study in the literature comparing this parameter for the two species dates from 1944. At that time, Jansen found a mean rate of 12 eggs per egg-mass for *B. straminea*, while for *B. glabrata* he found 45. The results obtained by Penido et al. (1951) indicated 13.2 and 24.5 eggs/egg-mass respectively. Both study results differ significantly from those obtained by us in the present study. This type of comparison is however of limited worth, not only because of the high variability among species populations, differences in snail rearing, and difficulties in species characterization at that time, but also due to the fact that those snails were brought directly from field to be studied. According to Scherrer et al. (1976), Barbosa & Silva (1951) and Freitas (1959) have also obtained high values for *B. glabrata* specimens brought directly from field (47 and 44 eggs per egg-mass respectively).

In laboratory *B. glabrata* eggs/egg-mass averages show great variations. Pereira & Deslandes (1954 *apud* Scherrer et al. 1976) found 36.9 and 61; Freitas (1973 *apud* Scherrer et al. 1976), 34.9, 39.9 and 62.1; Scherrer et al. (1976), 45.1 and 44.5 and, with their less prolific population, 19.2 and 14.6 eggs/egg-mass. Brumpt (1941) obtained 23.3; Coelho (1954), 22; Rey (1956), 10.23 and 21.3; Chernin & Michelson (1957a, b), 15.8 and 17.1; Szumlewicz (1958), 10.1, 14.7 to 15.1 and 18.2 to 24.5; Michelson (1961), 13.5; Magalhães & Carvalho (1969), 21.34; Pimentel (1957), 10.6 and Michelson & Dubois (1979), 21.4 eggs/egg-mass.

Our global mean rate (13.8 eggs/egg-mass) is then among the lower rates but it is still higher than many others. Except for November, December and January (with higher mean rates) the other months showed very similar mean rates. Although it is impossible to characterize species using this parameter, we sug-

gest, based on the similarity among mean rates throughout the year, that this parameter can be useful for the characterization of *B. glabrata* populations. It must be clear however that this is only possible when a high number of measurements is involved, as in the case of the present study. In this case, it seems to be possible to know the fecundity potential of a *B. glabrata* population for specific rearing conditions adopted.

For the *B. straminea* sample our general mean rate for the year was 22.44 eggs per egg-mass. Similarly high results have been obtained by Michelson & Dubois (1979), 25.07 (calculated based on data presented by the authors), and by Lucena (1956) after six months of study, 22.10 eggs per egg-mass.

Except for the two above-mentioned studies and for the present work, the few other studies quantifying the fecundity of *B. straminea* show surprisingly low data. Jansen (1944) reports 12 eggs per egg-mass, but based on 50 egg-masses only; Andrade et al. (1973) in cold months obtained 11.4; and Penido et al. (1951), 13.2 eggs per egg-mass. Coincidentally these last authors have also studied the species during the part of the year that includes the colder months in Brazil (March to July). Although they did not provide temperature data, the period chosen for the study may be at least in part responsible for the low fecundity observed, as we suggested for the results of Andrade et al. (1973) and confirmed by our own observations (Table I).

At any rate it should be stressed that we were dealing with a prolific sample of *B. straminea*. The possibility of a genetic drift due to sample collection and laboratory-rearing for many generations is not excluded. Unfortunately the data available are not enough to infer whether the finding of such a prolific sample of *B. straminea* is common or rare within the species. According to Paraense (personal communication), who provided the sample, the Picos colony is remarkably more fecund than other samples reared in his laboratory under identical conditions.

Maximum and minimum number of eggs per egg-mass in each data collection and in each month – This parameter proved to be useful for the comparison of snail fecundity since it confirmed the superiority of *B. straminea* in the general computation and in great

part of the monthly analysis. The use of extreme values reduces the quantifying work and can be reliable if a great number of measurements is involved, as in the present study. Though minimum values provided few information, they attested the superiority of *B. straminea* in 4 out of 11 months in which it actually occurred.

Egg-masses frequency according to classes of egg number – The high fecundity of *B. straminea* sample is related to a great productivity of eggs arranged in a relatively low number of capsules. Capsule production and egg production might therefore be disentangled processes, that react distinctly to stimuli. This possibility is reinforced by the decrease of the number of eggs due to the aging of snails, the number of capsules remaining the same, resulting in increasing numbers of empty capsules.

The production and laying of capsules may constitute a considerable investment of resources (Calow, 1983). In this sense, the production of capsules with few or no eggs may represent a waste of material and energy that occurs much more regularly in the *B. glabrata* sample (Table III). On the other hand note should be given to the low cost of capsule per egg laid by *B. straminea* especially from September to December, when the production of capsules was fairly profitable in descendant production.

Biomphalaria straminea tendency to pack up more eggs per capsule showed a cyclical variation during the year, and this variation cannot be directly related to fecundity. Rey (1956) and Parent & Lietar (1955) also observed seasonal cyclical variations in the mean number of eggs per capsule in planorbid snails. The first author could not detect the reasons for the phenomenon, but for Parent & Lietar (1955) the increasing number of eggs per capsule was associated with the coming of the dry season. Calow (1983) also observed this relationship and formulated an interesting hypothesis to explain it. By studying a *Limnaea peregra* population this author observed that in lentic habitats where descendant survival chances were higher, the species were found packing a higher number of eggs per capsule than in seashore habitats where the snails were exposed to wave action. The proposed hypothesis is that capsule economy without implying losses for the next generation is

practicable in calm waters. Reversely, where the environment exposes egg-masses to damage and destruction, the species distributes its eggs in greater number of capsules then leading to better survival changes. This hypothesis however requires experimental confirmation.

With regard to our *B. straminea* sample further observations might confirm the cyclical nature of eggs per capsule rates. Temperature may also be affecting this seasonal variation, although this hypothesis also requires a carefully controlled experiment.

Eggs per capsule variation related to snail size – The increasing number of eggs per capsule due to the growth of snails is related to the need for a complete development of the reproductive apparatus in order to achieve the maximum performance in the perpetuation of species. This could be easily detected in *B. glabrata* from the first to the fourth month of study. This directly proportional relationship between size and number of eggs per capsule was also observed in *B. straminea*, but only from the first to the second month of study (Figs 4 to 9). In this period the increase in the number of eggs per capsule was actually very expressive, achieving already in the second month 30.52 eggs per capsule, which was the maximum rate for *B. straminea* for the whole year. However this is not so surprising if we take into account that by this time *B. straminea* specimens were achieving their definitive adult diameter (for the conditions adopted). Although growth curves were not studied, *B. straminea* sample growth ceased precociously when compared to *B. glabrata*. The latter, by investing part of its resources in growth and part in reproduction, took four to five months to achieve its maximum rate of eggs per egg-mass.

Potential advantages for *B. straminea* sample can thus be viewed, especially if the above possibilities are considered within a hypothetical situation of crowded mixed populations. In this case one may suggest the occurrence of a reproductive boom of *B. straminea* two months before *B. glabrata* could massively repopulate the habitat. When this occurs, the latter species would be restricted in terms of space and resources by the presence of a *B. straminea* population steadily established in the habitat and ready to present a

new population increase potentially similar to the previous one, since the second generation's full productivity will be reached.

It should be noted that data on egg fertility, young specimen's development and mortality, and environmental resistance are not included in this hypothetical forecast since only data on egg and egg-mass productivity of the two samples are being considered. However, recent findings on *B. pfeifferi* under field conditions (Loreau & Baluku, 1987) detected a strong correlation between "r" parameter (intrinsic rate of natural increase) and egg density curves for the same period (a 4-year study). The authors point to the possibility of inferring "r" based on a single factor: egg density. They emphasize that other studies are required to test the reliability of such correlation for other species and different environmental conditions.

Monthly frequency of empty egg-capsules – Paraense (1959) reported the presence of empty capsules as a result of the crossing of different *B. glabrata* populations. The more distant are the populations involved, the greater is the occurrence of empty capsules. Our study deals with a single population and shows the progressive increasing frequency of empty capsules throughout the year for both species. For *B. glabrata* it occurred more regularly and in a frequency always significantly higher than for *B. straminea* (about three times higher). Although we did not find any other reference to the phenomenon, it seems to be naturally related to snail aging. The decrease of gamete production as a result of aging was not promptly followed by the reduction in capsule production, thereby leading to a progressively higher frequency of empty capsules.

Snail mortality – Mortality was higher and sooner in *B. straminea* than in *B. glabrata*. One may suggest that semelparity (tendency to invest more in reproduction than in the maintenance of adults) is more marked in the former. This interesting issue deserves further investigations based on different rearing conditions and different populations of both species.

ACKNOWLEDGEMENTS

To Dr Fernando D. Ávila-Pires, Dr Lobato Paraense, Dr Lígia Corrêa and Dr Frederico S. Barbosa for their collaboration in several occasions.

REFERENCES

- ANDRADE, R. M. de; CARVALHO, O. S. & PINTO ALVES, M. D. P., 1973. Alimentação e fecundidade de planorbídeos criados em laboratório. II – *Biomphalaria straminea* (Dunker, 1848). *Rev. Bras. Biol.*, 33: 119-126.
- ANDRADE, R. M. de; CARVALHO, O. S. & MENEZES, W. T., 1974. Alimentação e fecundidade de planorbídeos criados em laboratório. III – *Biomphalaria glabrata* (Say, 1818) (Pulmonata, Planorbidae). *Rev. Bras. Malariol. Doenças Trop.*, 26: 109-129.
- BARBOSA, F. S., 1973. Possible competitive displacement and evidence of hybridization between two Brazilian species of planorbid snails. *Malacologia*, 14: 401-408.
- BARBOSA, F. S., 1985. A Competição biológica como método alternativo para o controle dos transmissores da esquistossomose. *Cad. Saúde Públ.*, 1: 113-114.
- BARBOSA, F. S.; PEREIRA DA COSTA, D. P. & ARRUDA, F., 1984. Competitive interactions between species of freshwater snails. I – Laboratory studies. I. b. – Comparative studies of the dispersal and the vagility capabilities of *Biomphalaria glabrata* and *Biomphalaria straminea*. *Mem. Inst. Oswaldo Cruz*, 79: 163-167.
- BRUMPT, E., 1941. Observations biologiques diverses concernant *Planorbis (Australorbis) glabratus*, hôte intermédiaire de *Schistosoma mansoni*. *Ann. Parasitol. Hum. Comp.*, 18: 9-45.
- CALOW, P., 1983. Life-cycle patterns, p. 649-678. In W. D. Russel-Hunter – *The Mollusca*. vol. 6: Ecology. London, Academic Press.
- CHERNIN, E. & MICHELSON, E. H., 1957a. Studies on the biological control of schistosome-bearing snails. III – Effects of population density on growth and fecundity in *Australorbis glabratus*. *An. J. Hyg.*, 65: 71-80.
- CHERNIN, E. & MICHELSON, E. H., 1957b. Studies on the biological control of schistosome-bearing snails. IV – Further observations on the effects of crowding on growth and fecundity in *Australorbis glabratus*. *An. J. Hyg.*, 65: 71-80.
- COELHO, M. V., 1954. Ação das formas larvárias de *Schistosoma mansoni* sobre a reprodução de *Australorbis glabratus*. *Publ. Avulsas Inst. Aggeu Magalhães*, 3: 39-54.
- GUYARD, A. & POINTIER, J. P., 1979. Faune malacologique dulciaquicole et vecteurs de la schistosomose intestinale en Martinique. *Ann. Parasitol. Hum. Comp.*, 54: 193-205.
- JANSEN, G., 1944. Sobre a validade de *Australorbis centimetralis* (Lutz, 1918). Nota prévia. *Mem. Inst. Oswaldo Cruz*, 40: 201-208.
- KAWAZOE, U., 1980. Alguns aspectos da biologia de *Biomphalaria glabrata* (Say, 1818) e *Biomphalaria tenagophila* (d'Orbigny, 1835) (Pulmonata, Planorbidae). II – Fecundidade e Fertilidade. *Rev. Saúde Pública*, São Paulo, 14: 65-87.
- LOREAU, M. & BALUKU, B., 1987. Population dynamics of the freshwater snail *Biomphalaria pfeifferi* in Eastern Zaire. *J. Molluscan Stud.*, 53: 249-266.
- LUCENA, D. T., 1956 – *Resenha Sistemática dos Planorbídeos Brasileiros*. M. Sc. Thesis, Recife, Gráf. Edit. Recife S. A., 104 p.
- MAGALHÃES, L. A. & CARVALHO, D. F., 1969. Estudo da postura de duas populações de planorbídeos. *Rev. Soc. Bras. Med. Trop.*, 3: 245-247.
- MEIER-BROOK, C., 1986. An ecological survey of freshwater mollusc introduction. *Ninth International Malacological Congress*, Edinburgh, Scotland. Abstract: 52.
- MICHELSON, E. H., 1961. The effects of temperature on growth and reproduction of *Australorbis glabratus* in the laboratory. *Am. J. Hyg.*, 73: 63-74.
- MICHELSON, E. H. & DUBOIS, L., 1979. Competitive interactions between two snail hosts of *Schistosoma mansoni*: Laboratory studies on *Biomphalaria glabrata* and *B. straminea*. *Rev. Inst. Med. Trop. São Paulo*, 21: 246-253.
- PARAENSE, W. L., 1959. One-sided reproductive isolation between geographically remote populations of a planorbid snail. *Am. Nat.*, 93: 93-101.
- PARAENSE, W. L., 1977 – Distribuição geográfica dos vetores da schistosomose no nordeste do Brasil. In P. A. Machado, (coordenador), *Painel Especial de Controle da Esquistossomose*: 47-51. Apresentado na VI Conferência Nacional de Saúde, Brasília.
- PARAENSE, W. L., 1986. Distribuição dos caramujos no Brasil, p. 117-126. In Academia Mineira de Medicina, *Modernos conhecimentos sobre esquistossomose mansônica*. Belo Horizonte, MG, vol. 14 (suppl. dos anais de 1983 e 1984).
- PARAENSE, W. L. & CORRÊA, L. R., 1988. Self-fertilization in freshwater snail *Helisoma duryi* and *Helisoma trivolvis*. *Mem. Inst. Oswaldo Cruz*, 83: 405-409.
- PARENT, M. & LIETAR, J., 1955. Contribuição à l'étude de la biologie des mollusques à Jadotville. *Ann. Soc. Belge Med. Trop.*, 35: 59-68.
- PAULINY, E. & CAMEY, T., 1964. Observações sobre a biologia de *Australorbis glabratus*. II – Influência da temperatura do ambiente sobre a frequência de postura. *Rev. Bras. Malariol. Doenças Trop.*, 16: 499-504.
- PENIDO, H. M.; PINTO, D. B. & DESLANDES, N., 1951. Observações sobre as posturas e tempo de evolução de duas espécies de caramujo encontrados no Vale do Rio Doce. *Rev. Serv. Espec. Saúde Pública*, 4: 407-412.
- PIMENTEL, D., 1957. Life history of *Australorbis glabratus*, the intermediate snail host of *Schistosoma mansoni* in Puerto Rico. *Ecology*, 38: 576-580.
- REY, L., 1956. Contribuição para o conhecimento da morfologia, biologia e ecologia dos planorbídeos brasileiros transmissores da esquistossomose – sua importância em epidemiologia. PhD Thesis. Fac. Med. Univ. São Paulo, São Paulo, 217 p.
- ROZEMBERG, B., 1989. Fecundidade comparada de *Biomphalaria straminea* e *B. glabrata* em laboratório, no decurso de um ano. M. Sc. Thesis, Instituto Oswaldo Cruz, Rio de Janeiro, 165 p.
- SCHALL, V. T.; JURBERG, P. & FERREIRA, S. R., 1984. Estudo Comparativo do efeito da luz sobre o comportamento das espécies *Biomphalaria glabrata*, *B. tenagophila* e *B. straminea* (Molusca, Gastropoda, Planorbidae). *XI Congresso de Zoologia*. Resumos: 41-42.
- SCHALL, V. T.; JURBERG, P. & ROZEMBERG, B., 1986. Orientation of the snail *Biomphalaria*

- straminea* (Dunker, 1848) in response to light in a situation of selection. *Mem. Inst. Oswaldo Cruz*, 81: 255-263.
- SCHERRER, J. F.; CHQUILOFF, M. A. de G. & FREITAS, J. R. de, 1976. Estudo Comparativo da reprodução em quatro variedades genéticas de *Biomphalaria glabrata* (Say, 1818). I – Fecundidade. *Rev. Inst. Med. Trop. São Paulo*, 18: 315-321.
- SZUMLEWICZ, A. P., 1958. Studies on the biology of *Australorbis glabratus*, a schistosome-bearing Brazilian snail. *Rev. Bras. Malariol. Doenças Trop.*, 10: 459-529.