Effects of the law of constant final yield in populations of *Biomphalaria tenagophila* (Mollusca, Planorbidae)

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Resumo

Este trabalho visou ampliar as informações sobre a dinâmica populacional e contribuir para a compreensão dos efeitos da competição intraespecífica de *Biomphalaria tenagophila*, testando a Lei de Produção Final Constante para esta espécie.

Para tanto, foram acompanhados durante 110 dias cinco aquários com densidades diferentes (8,16, 32, 64 e 128 indivíduos). Foram contabilizados semanalmente o total de ovos, número de desovas, ovos viáveis e, a cada 15 dias, o número de ovos não eclodidos. Ao final do experimento, foram obtidos os valores do peso úmido, peso seco e diâmetro.

Através da análise de variância da densidade, relacionada aos parâmetros relativos à absorção de matéria orgânica, foram encontradas diferenças estatisticamente significantes, o que indica que a referida lei não pode ser aplicada para explicar a absorção de matéria orgânica em *B. tenagophila* nas amostras estudadas.

Unitermos: Planorbidae, *Biomphalaria tenagophila*, Lei de Produção Final Constante, dinâmica populacional.

Summary

This work seeks to contribute to a better knowledge on populational dynamics and to the understanding of intraspecific competition effects in *Biomphalaria tenagophila* by testing the law of constant final yield for this species.

Five aquaria with different densities (8, 16, 32, 64 and 128 individuals) were observed for 110 days. The total numbers of eggs, egg masses and viable eggs were counted weekly, and the number of undeveloped eggs was counted every 15 days. At the end of the experiment the values of moist weight, dry weight and diameter were measured.

The analysis of density variance showed statistically-significant differences between the parameters related to organic matter absorption. This indicates that the above-mentioned law cannot be used to explain the absorption of organic matter in the samples of *B. tenagophila* studied.

Key words: Planorbidae, law of constant final yield, populational dynamics.

Introduction

The role of limpets as intermediate hosts of human parasites – the Planorbidae among them – is well documented. The Planorbidae (Mollusca: Pulmonata) are freshwater pulmonate limpets characterized by discoidal or flat-spiralled shape of shell and by lack of opercula (Paraense,1972).

Studies on the biology of these limpets, especially *Biomphalaria*, have shown that these animals can survive different adverse environmental conditions, presenting high potential of settlement and dispersal (Silvério, 1992).

Several authors have discussed the importance of ecological studies, such as the ones on competition, aiming at the control of the pulmonate vectors of parasitosis (Michelson and Dubois, 1974; Malek and Malek, 1978; Frandsen and Madsen, 1979; Barbosa et al., 1983; Madsen, 1984). Nevertheless, little is known about the ecology and populational dynamics of *Biomphalaria*.

Intraspecific competition acting on natality and mortality rates can lead populations to a steady density, which is its maximum support capacity (Odum, 1983). Thus, this kind of competition can deeply affect the number of individuals in a population, but can also affect the individuals themselves. For Begon et al. (1986), the effect of intraspecific competition on each individual is proportional to the number of competitors, that is, density.

In plants, Palmblad (1968) studied this effect on three species of weeds, two annual species – *Capsella bursa-patoris* and *Conyza canadensis* – and one perennial – *Plantago major*, and observed that both the average seed production and the individual plants at higher densities are smaller.

According to Begon and Mortimer (1981), this plasticity in the growth response of plants to intraspecific competition is so common that a term has been coined to describe the consequences of it: the law of constant final yield, or Kira's law.

Branch (1975) studied the effects of intraespecific competition on the limpet *Patella cochlear* in natural populations of South Africa. He observed that, in populations at low densities, the individuals were relatively large, and in populations at high densities individuals were relatively small. He also observed that the total biomass of populations at densities higher than 400 individuals was nearly the same.

The aim of this work was to verify whether the law of constant final yield is also applicable to pulmonates.

Materials and Methods

A sample of ***Biomphalaria tenagophila*** (Pulmonata: Planorbidae), ***Schistosoma mansoni*** host, collected in a ditch at Corregо Grande, Florianopolis, SC, and kept in the Universidade Federal de Santa Catarina Planorbidae Laboratory, was studied. Dechlorinated water, containing 0.1 g/l calcium carbonate, was employed throughout the experiment.

Approximately 500 egg masses were collected and kept for 30 days in Petri dishes. Afterwards, 248 individuals were separated and grouped in 5 aquaria (plastic basins), containing 3 liters of dechlorinated water, with 8, 16, 32, 64 and 128 individuals. The water replacement, feeding and egg-mass collection were done weekly. Food consisted of 1 gram of dehydrated lettuce (dried at 50°C/ 24 h) per aquarium.

Four polystyrene pieces measuring 2cm x 4cm x 2mm were placed in each aquarium as a support for egg laying. Collected spawnings were maintained in Petri dishes at 25°C.

The aquaria were exposed to environmental changes of temperature and luminosity all through the experiment.

The egg-mass collection was done one week after the beginning of the experiment. The eggs were analysed immediately after collection using a stereoscopic microscope. The numbers of egg-masses, total eggs and viable eggs in each aquarium were counted. The number of undeveloped eggs was counted fortnightly.

The experiment lasted 4 months (110 days). After the last egg-mass collection, the individuals were withdrawn from the aquaria, weighed and left to dry. After a week, the dried individuals were weighed again. The larger diameters of the shells were also measured using a pachymeter.

Results were analysed by ANOVA analysis of variance – "one way" – LSD, with 0,5 % significance (a = 0.05) and also by use of the Linear Regression Model adjusted by the Least Squares Method using the equation $y = a + bx$, with 0.5 % significance level. The Pearson Correlation Coefficient (r) values obtained were compared to those presented by Zar (1974) in the critical values table.

These analyses were carried out by means of the statistical software " STATIGRAFICS 5.0".

Results

Table 1 presents the results obtained in relation to survival, total eggs, egg masses, viable eggs and undeveloped eggs, with the respective weekly averages for a period of 110 days. This table also indicates the total values, the moist and dry weight averages and the mean diameter. It can be observed that all individuals survived at densities 8 and 16 during the analysed period. However, some deaths occurred at densities 32, 64 and 128.

Table 2 presents the results of the analysis of variance and shows that density was related to several different parameters throughout the experiment.

The results obtained with the Linear Regression analysis are presented in Table 3. Additional parameters were analysed but are not presented because the determinant coefficient (r^2), which expresses the degree of acceptance of Linear Regression, were equal or lower to 15%.

Finally, Table 4 presents the estimates of organic matter available and absorbed during the 110 days of the experiment.

TABLE 1 - Biological parameters obtained for a period of 110 days of analysis

Individuals per aquarium	Survivals per aquarium	Total eggs		Egg masses		Viable eggs	
		total	weekly mean	total	weekly mean	total	weekly mean
8	8	30,157	1,675.39	959	53.28	29,780	1,654.44
16	16	36,968	2,053.78	1,540	85.56	36,327	2,018.17
32	30	36,542	2,030.11	1,964	109.11	36,140	2,007.78
64	61	23,837	1,324.28	2,208	122.67	23,520	1,306.67
128	121	22,547	1,252.61	1,804	100.22	21,336	1,185.33

Continuation table 1

Individuals per aquarium	Undeveloped eggs		Moist weight		Dry weight		Mean diameter
	total	weekly mean	total	mean	total	mean	
8	5,207	289.28	5.841	0.730	3.958	0.495	1.68
16	7,685	426.94	9.941	0.621	6.902	0.431	1.58
32	8,619	478.83	11.088	0.370	7.764	0.259	1.31
64	7,967	442.61	11.359	0.186	7.339	0.120	1.02
128	6,547	363.72	16.695	0.138	9.247	0.076	0.91

TABLE 2 - Results of the analysis of variance relating density with several variables observed throughout the experiment.

Variables	Ratio of F (a critical=0.05)	a
density v total eggs	60.861	0.1003
density v eggs masses	1.076	0.449
density v viable eggs	0.731	0.742
density v undeveloped eggs	1.414	0.449
density v mean diameter	999.999 *	0
density v mean moist weight	999.999 *	0
density v mean dry weight	999.999 *	0

* statistically significant differences

TABLE 3 - Pearson's Coefficient of Correlation (r), degrees of correlation between variables and determinant coefficient (r2), according to critical values, at significance level P=< 0.05 (Zar, 1994), for analysis of linear regression.

Variables	r	Correlation *	r^2 (%)
density v mean diameter	-0.913101	weak	83.38
density v mean moist weight	-0.887163	weak	78.71
density v mean dry weight	-0.868382	weak	75.41
mean dry weight v mean diameter	0.997116	excellent	99.42
mean dry weight v mean moist weight	0.99897	excellent	99.79

TABLE 4 - Relationship between amount of organic matter available and amount of organic matter assimilated for 110 days.

Density	Amount of organic matter per week (g)	Amount of organic matter available per individual	Maximum assimilation of organic matter expected for 110 days (g)	Real assimilation of organic matter, on average, for 110 days (g)	% of available organic matter incorporated
8	1	0.0178	1.958	0.495	25.28
16	1	0.0089	0.982	0.431	43.89
32	1	0.0045	0.495	0.259	52.32
64	1	0.0022	0.242	0.120	49.59
128	1	0.0011	0.121	0.076	62.81

Discussion

The effects of the law of constant final yield have been described in plants mostly, where the final yield remains the same in a large variety of densities, because higher densities lead to a decrease in the individual growth rates and, as a consequence, in the individual size.

In the present study, the law of constant final yield may be applied to the parameters related to fecundity (total number of eggs, of egg masses, of viable eggs and of unhatched ones) as these were not significantly altered by variations in density. Nevertheless, it may not be applied to parameters such as mean diameter, mean moist weight, and mean dry weight, which vary significantly with density and are unable to explain the incorporation of organic matter by *Biomphalaria tenagophila*. These results might suggest that the populations did not reach the support capacity and consequently that competition for food was not yet occurring. This was evidenced in the aquarium with 8 individuals who always presented food remains. However, the negative correlation observed between density of aquaria and the three parameters, mean diameter, moist weight, and dry weight (Table 3), showed that competitive interaction had occurred. It is important to note that, even under standardized conditions, of 1 gram of dry lettuce a week per aquarium, the possibility of alternative food sources, such as microseaweeds and protozoans, cannot be discarded.

Also, other variables may have influenced the results of this experiment, such as available space, place for egg-laying, excess of excreta, etc.

The weak negative correlations between mean diameter, mean moist weight, mean dry weight and density (Table 3) reinforce the results obtained by the analysis of variance (Table 2). Branch (1975), studying *Patella cochlear*, has observed the effects of the law of constant final yield in these limpets, but he has also concluded that overcrowding leads to reduced growth, lower maximum and mean sizes, and a reduced output of eggs per unit area.

Several parameters studied here presented determinant coefficients (r) inferior to 15% by analysis of regression and were not used in our analysis. In spite of this, some of our results were similar to those obtained by Branch (1975). When density was compared to the number of egg masses, for instance, larger numbers of egg masses were observed at higher densities, but the number of eggs was smaller. The mean dry weight was accompanied by a corresponding increase in the viable egg number (Table 1). If viability of eggs is related to the gametes used in its fecundation, and if these gametes seemingly are not affected by the individual's variation in weight, this variation can be casual.

The parameter "unhatched eggs" was not related to density or to mean dry weight (Table 1), and this confirms the hypothesis that egg hatching and viability undergo individual variations, which are independent of resources supplied, and consequently, are independent of density.

The samples with higher mean dry weight presented an increase in the production of eggs. Palmblad (1968) observed that, in plants, qualitative changes in net weight and seed production are closely related: smaller plants produce fewer seeds. Lara et al. (1988), studying *Lymnaea viatrix*, observed a positive correlation between total spawning and growth, i.e., higher individual growth in terms of weight and size are accompanied by higher total spawning. Bakker (1961) obtained the same result studying larval competition in *Drosophila melanogaster*, and observed that an increase in larval population density leads to a decrease in size of adult individuals and, as a consequence, to a decrease in the number of eggs which will contribute to the next generation.

Also, the percentage of available organic matter incorporated (Table 4) was lower at lower densities, tending to increase when density was increased. It is possible that, at lower densities, energy is directed to a higher production of eggs. The correlation observed between these variables, and between mean dry weight and total number of eggs (Table 1), corroborates this idea.

Vernon (1995) described the existence of a "social facilities" mechanism to explain why, under outcrossing fecundity conditions (4-individuals density), *Biomphalaria glabrata* presents a higher adaptative value than in self-fecundation (1-individual density). The author asserts that, by perceiving a cospecific snail in the environment, individuals tend to maximize their output of eggs. A similar effect could be occurring in our samples, where individuals cultivated at largest densities, "perceiving" this condition (a chemical, physical or visual stimulus), would tend to ingest higher amounts of organic matter, which would lead to an increase in the consumption per individual (Table 4). Although the analysis of variance applied to samples at diverse densities did not evidence the effect of intraspecific competition on the weight and diameter of individuals, these are undoubtly influenced by density (Figure 1).

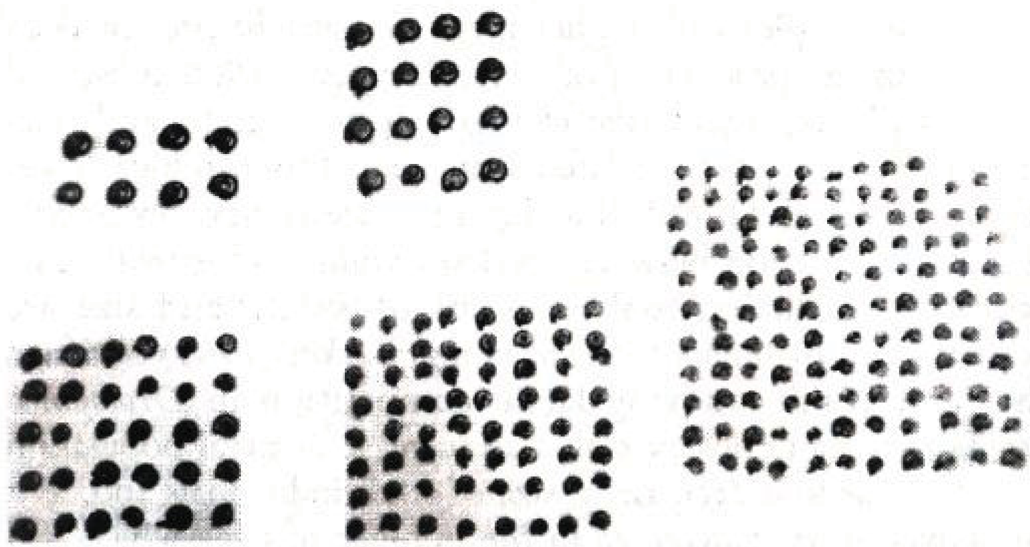

FIGURE 1 - General look of variation in size of individuals in varied densities

Finally, it was observed that the individual's total weight did not stabilize beginning from a density, as would be expected if the law of constant final yield were acting. It probably results from the fact that many factors influence the incorporation of organic matter, beyond the supplied amount. Consequently, these factors, which were not controlled, could be masking the effects of biomass stabilization. Despite these factors, such effects may be observed in individual production, showing the high influence of density in the studied samples.

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