Life tables of freshwater snails of the genus Biomphalaria (B. glabrata, B. alexandrina, B. straminea) and of one of its competitors Melanoides tuberculata under laboratory conditions

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MALACOLOGIA, 1991, 33(1–2): 43–54

LIFE TABLES OF FRESHWATER SNAILS OF THE GENUS *BIOMPHALARIA* (*B. GLABRATA, B. ALEXANDRINA, B. STRAMINEA*) AND OF ONE OF ITS COMPETITORS *MELANOIDES TUBERCULATA* UNDER LABORATORY CONDITIONS

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ABSTRACT

Life tables of several strains of *Biomphalaria glabrata, B. alexandrina* and *B. straminea* have been established under laboratory conditions and compared with that of *Melanoides tuberculata,* a prosobranch snail used as a competitor of snail vectors of schistosomiasis in experiments of biological control. Results indicate a great range of intraspecific and interspecific variation within the *Biomphalaria* and a quite distinct demographic strategy of *M. tuberculata.* Species of *Biomphalaria* have a high intrinsic rate of natural increase (0.70 to 1.01) and a short mean generation time (5.5 to 9.3 fortnights). In contrast, the thiarid snail has a low intrinsic rate of natural increase (0.24) and a very long mean generation time (25.77 fortnights). These results fit well with several field observations showing that this snail is able to reach and maintain very high densities in permanent and stable habitats. In such habitats, the competition with pulmonate snails might be very strong and to the advantage of the thiarid species.

Key words: life tables, laboratory, *Biomphalaria glabrata, B. alexandrina, B. straminea, Melanoides tuberculata.*

INTRODUCTION

Several authors have discussed the use of competitors to control pulmonate snail intermediate hosts of schistosomiasis (Michelson & Dubois, 1974; Malek & Malek, 1978; Frandsen & Madsen, 1979; Barbosa et al., 1983; Madsen, 1984). Among the species cited by these authors, few have been the object of detailed field or laboratory investigations and rigorous research has been encouraged (McCullough, 1981; World Health Organization, 1984).

In the Caribbean area, field observations of an introduced Oriental species belonging to the Thiaridae, *Melanoides tuberculata,* demonstrated its capacity massively to colonize many types of habitats, while at the same time limiting, even excluding, different *Biomphalaria* species (Prentice, 1983; Pointier, 1989; Pointier et al., 1989). Consequently, it is important to study the biology of this snail and of its target species.

In this paper, life table parameters of two Caribbean and one African species of *Biomphalaria* (*B. glabrata, B. straminea* and *B. alexandrina*) have been established under laboratory conditions and compared with those of *M. tuberculata.*

MATERIAL AND METHODS

Adult snails were collected in the field and transferred to laboratory aquaria: *B. glabrata* from Céligny pond and Dubelloy marsh, Guadeloupe; *B. alexandrina* from Kalyub and Kafr al Hamza canals, Egypt; *B. straminea* from Epinette and Madame Rivers, Martinique; *M. tuberculata* from Pointe-à-Pitre canal, Guadeloupe.

Viable eggs laid by these snails were used to start the experiments. In the case of the hermaphroditic *B. glabrata, B. alexandrina* and *B. straminea,* 81 eggs (Céligny pond), 97 eggs (Dubelloy marsh), 69 eggs (Kalyub canal), 71 eggs (Kafr al Hamza canal), 114 eggs (Epinette River) and 75 eggs (Madame River) were used, respectively. In the case of the parthenogenetic *M. tuberculata,* 40 newly liberated juveniles were taken. During the experiment, all the thiarid snails were tested separately for releasing juveniles in order to verify that they were all females.

All newly hatched snails were transferred to small containers (200 cc) and then put in aquaria of one litre, four snails per aquarium to minimize crowding. Snails were reared in the presence of aquatic moss, *Hygrohypnum eugyruum* (Hypnacea) and fed with fresh and dried lettuce. Dechlorinated tap water was renewed one or twice a week. The main chemical characteristics of the water were the following: Ca = 90.0 mg/l; Mg = 4.4 mg/l; SO_4 = 16.9 mg/l; Cl = 23.8 mg/l; HCO_3 = 112 mg/l. Water temperature was maintained constant at 25° + 1°C. Light was artificial and photoperiodically balanced (LD 12-12).

Measures of growth (maximum size in mm), survivorship (l_x = proportion of survivals from the original number of viable eggs or newly liberated juveniles) and fecundity (m_x = mean viable eggs producted or mean newly liberated juveniles per female) were recorded fortnightly. Cultures were stopped when numbers decreased to less than 20 to 30% of the original population. Below this value, the remaining snails were considered to be too different from the mean population. Life table parameters were calculated according to the methods of Birch (1948) and Andrewartha & Birch (1954). The following parameters were calculated:

R_0 (net reproductive rate) $= \Sigma l_x \cdot m_x$;
r (intrinsic rate of increase) from $\Sigma l_x \cdot m_x \cdot e^{-rx} = 1$;
R (finite rate of increase) from $R = e^r$;
T (approximation of mean generation time in fortnights) $= \text{Log } R_0/\text{Log } R$.

In order to compare growth of the different species, values of different parameters were calculated using the growth equation of Von Bertalanffy (1938): $L_t = L_\infty (1-e^{-k(t-t_0)})$ in which L_t is the size of the snail at time t; L_∞, the value of L_t when growth rate = O; k, a characteristic constant of growth; t, the age of the snail; t_0, the hypothetical time at which the snail would have the O size.

RESULTS

Hatching

At 25°C, the maturation time of eggs is 8–9 days for *B. glabrata, B. alexandrina* and *B. straminea.* The time at which eggs were laid has been taken as time = 0 for calculations. For *M. tuberculata,* the maturation of eggs occurs in a brood pouch in which the different stages of development take place (Ramamoorthi, 1955). The maturation time at 25°C in the brood pouch is unknown and the time of juvenile release has been taken as time = 0. Under laboratory conditions, 96.3% and 93.8% of the *B. glabrata* eggs from Céligny pond and Dubelloy marsh, 92.7% and 87.3% of the *B. alexandrina* eggs from Kalyub and Kafr al Hamza canals, and 89.5% and 90.7% of the *B. straminea* eggs from Epinette and Madame Rivers, respectively, hatched.

Growth in Size

The growth of the *Biomphalaria* and *Melanoides* populations is shown in Figure 1. Because the results for the two *B. glabrata, B. alexandrina* and *B. straminea* populations are quite similar, the growth curve of only one population of each species is shown.

The growth of *B. glabrata* is quite different from those of *B. alexandrina* and *B. straminea* and especially from that of *M. tuberculata. B. glabrata* reaches a size of 17.3mm (which corresponds to 95% of its maximal theoretical size, L_∞) in 21.9 fortnights (k = 0.13). *B. alexandrina* has a similar growth rate (k = 0.15) but reaches a size of 13.6 mm (95% of L_∞) in 20.6 fortnights, and *B. straminea* reaches a size of 8.4 mm (95% of L_∞) in 15.9 fortnights (k = 0.19) (Table 1).

The growth parameters of *T. tuberculata* are quite different: k = 0.04 and the species reaches a size of 30.2 mm (95% of L_∞) in 85.1 fortnights (Table 1).

Survivorship and Fecundity

The results, presented in Figures 2 and 3 and Tables 2–6, show marked differences between the pulmonates, *B. glabrata, B. alexandrina* and *B. straminea,* and the prosobranch, *M. tuberculata.* Because survival curves of the two populations of each species of *Biomphalaria* are similar, only one curve and table are presented for each species. Marked differences can be noted among the three species, *B. glabrata* having a better survival than *B. alexandrina* and *B. straminea.* The decline of populations of the species of *Biomphalaria* occurs between 6 and 9 months of culture. In comparison, decline of *M. tuberculata* occurs much later: more than 50% of the individuals survived after five years of culture (Fig. 3). Its fecundity is much lower than those of species of *Biomphalaria* however: a maximum of 18 newly liberated juveniles per female per fortnight against 150–400 fertile

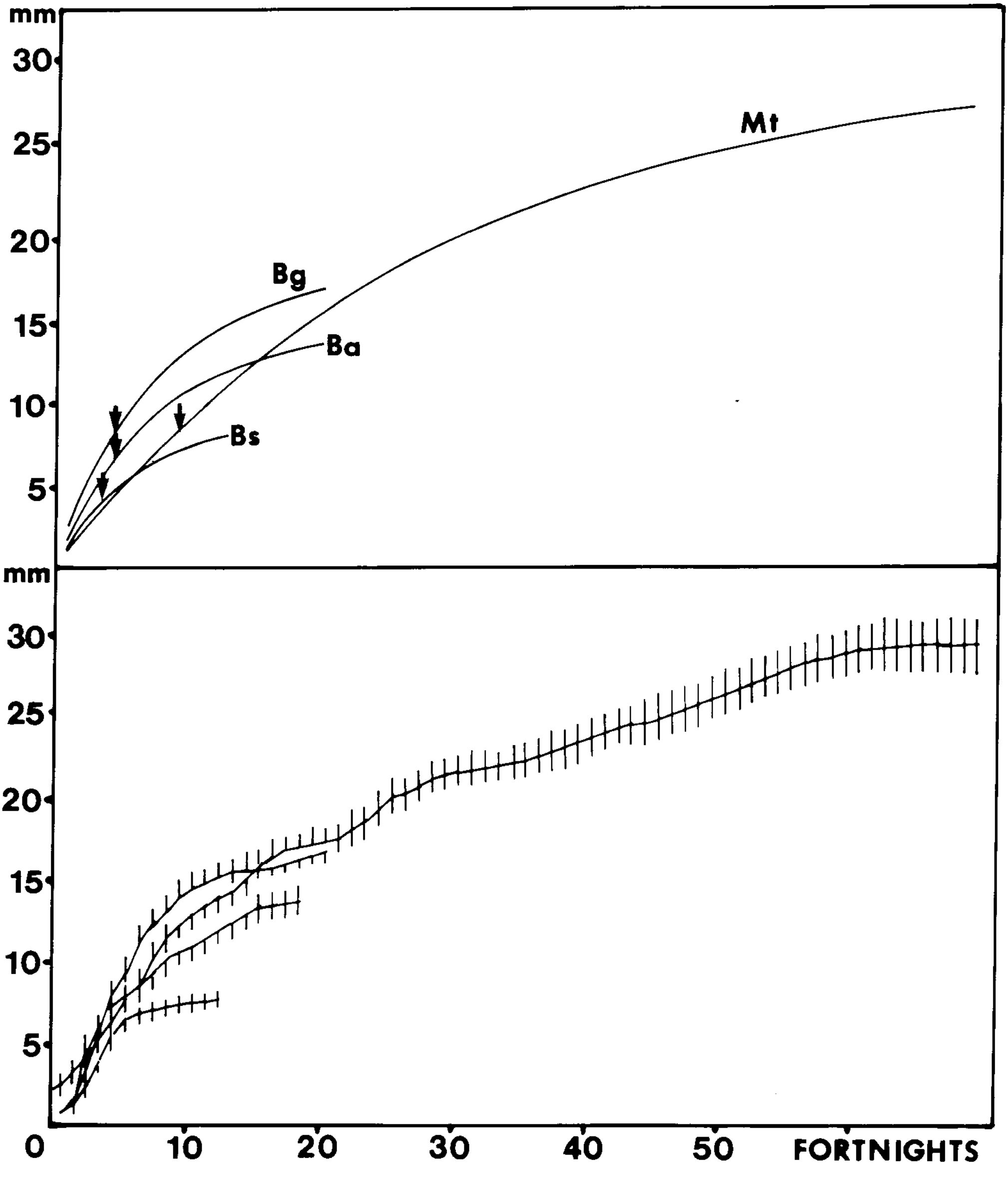

FIG. 1. Growth curves for *Biomphalaria glabrata* (Bg), *B. alexandrina* (Ba), *B. straminea* (Bs) and *Melanoides tuberculata* (Mt) under laboratory conditions. Above: calculated growth curves using Von Bertalanffy equation. Below: observed growth curves and standard deviations. Arrows indicate age of first reproduction.

TABLE 1. Values of parameters k and L_∞ from growth equation of Von Bertalanffy for several species of *Biomphalaria* and *Melanoides tuberculata* reared in laboratory.

Cohorts	Water Temp.	K	L_∞	Time to reach 95% of L_∞ in fortnights
Biomphalaria glabrata Céligny pond, Guadeloupe	25°C	0.134	18.2	21.9
Biomphalaria glabrata Dubelloy marsh, Guadeloupe	25°C	0.121	19.39	24.9
Biomphalaria glabrata St Lucia (data from Sturrock & Sturrock, 1972)	25°C	0.123	20.29	24.5
Biomphalaria alexandrina Kalyub canal, Egypt	25°C	0.15	14.35	20.6
Biomphalaria alexandrina Kafr al Hamza canal, Egypt	25°C	0.131	14.71	22.9
Biomphalaria straminea Epinette River, Martinique	25°C	0.187	8.81	15.9
Biomphalaria straminea Madame River, Martinique	25°C	0.236	7.6	12.8
Biomphalaria pfeifferei Tanzania (data from Sturrock, 1966)	25°C	0.192	13.25	16.1
Biomphalaria pfeifferi Zaire (data from Loreau & Baluku, 1987)	18°C–24°C	0.05	12.6	58.1
Melanoides tuberculata Pointe-à-Pitre canal, Guadeloupe	25°C	0.035	31.8	85.1

TABLE 2. Life table for *Biomphalaria glabrata,* Céligny pond, Guadeloupe, reared in laboratory (25°C).

Pivotal age in fortnights	Survival	Fecundity	Net reprod. rate	Finite rate of increase	Mean generation time	Intrinsic rate of increase		Stable age distribution
x	lx	mx	Ro	R	T	rm	rm(%)	(%)
0.0	1.0000	0.0000						47.0429
0.5	1.0000	0.0000						30.8353
1.5	0.9630	0.0000						12.7580
2.5	0.9383	0.0000						5.3408
3.5	0.9383	0.0000						2.2946
4.5	0.9383	3.7600	3.5280	1.3234	4.4994	0.2802	33.1676	0.9859
5.5	0.9383	23.3000	21.8624	1.8369	5.3188	0.6081	71.9816	0.4236
6.5	0.9383	69.1700	64.9022	2.1060	6.0460	0.7448	88.1629	0.1820
7.5	0.9383	130.1200	122.0916	2.2345	6.6647	0.8040	95.1705	0.0782
8.5	0.9383	168.8300	158.4132	2.2881	7.1471	0.8277	97.9759	0.0336
9.5	0.9383	222.8700	209.1189	2.3141	7.5839	0.8390	99.3134	0.0144
10.5	0.9383	210.9500	197.9344	2.3238	7.8944	0.8432	99.8106	0.0062
11.5	0.9383	97.3700	91.3623	2.3257	8.0185	0.8440	99.9053	0.0027
12.5	0.8888	143.1700	127.2495	2.3268	8.1755	0.8445	99.9645	0.0011
13.5	0.8888	155.7500	138.4306	2.3273	8.3276	0.8447	99.9882	0.0005
14.5	0.8395	136.4500	114.5498	2.3275	8.4404	0.8448	100.0000	0.0002
15.5	0.7405	97.4100	72.1321	2.3275	8.5068	0.8448	100.0000	0.0001
16.5	0.6914	42.1000	29.1079	2.3275	8.5326	0.8448	100.0000	0.0000
17.5	0.5926	37.1200	21.9973	2.3275	8.5518	0.8448	100.0000	0.0000
18.5	0.4938	44.3000	21.8753	2.3275	8.5705	0.8448	100.0000	0.0000
19.5	0.4444	35.0700	15.5851	2.3275	8.5836	0.8448	100.0000	0.0000
20.5	0.3456	25.2500	8.7264	2.3275	8.5909	0.8448	100.0000	0.0000
		Ro =	1418.8670					

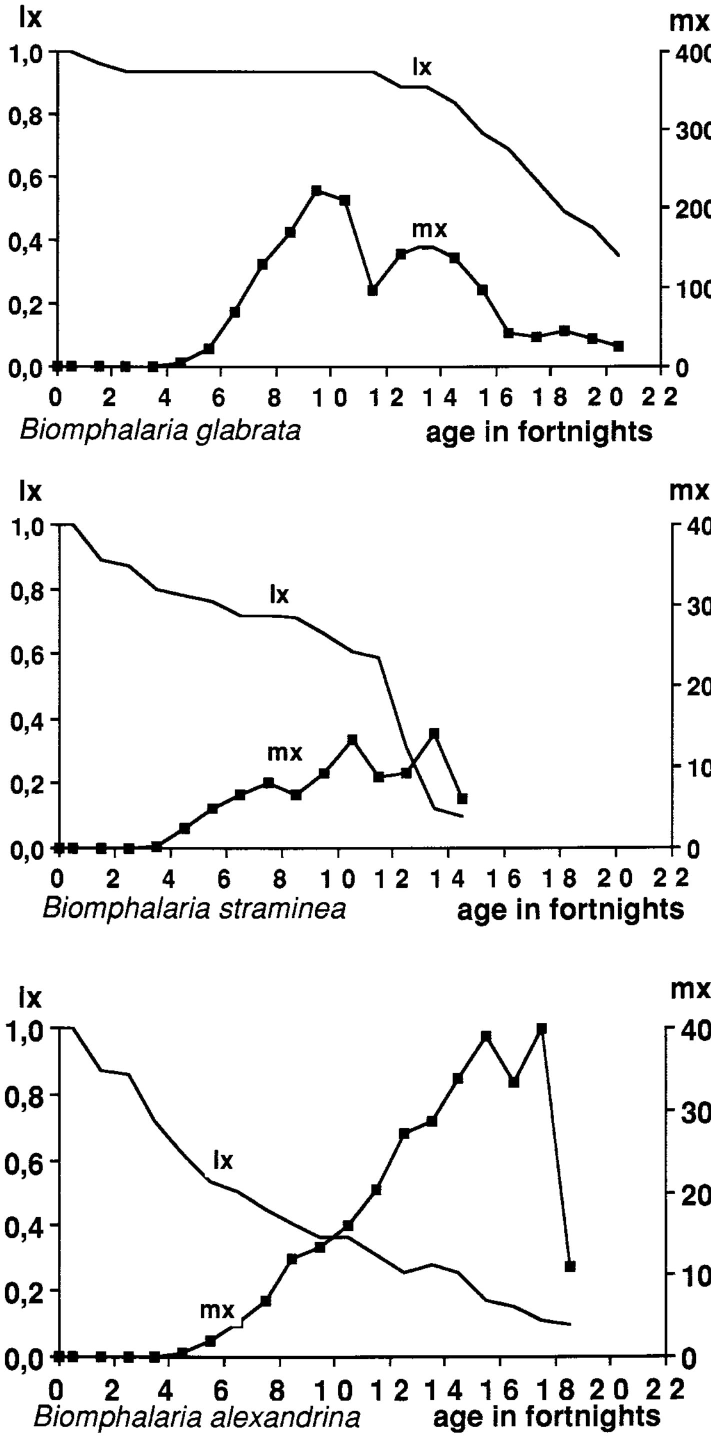

FIG. 2. Graphical representation of life tables of three species of *Biomphalaria* reared in laboratory. l_x: survivorship (proportion of survivals from the original number of viable eggs); m_x: fecundity (mean viable egg production per snail per fortnight).

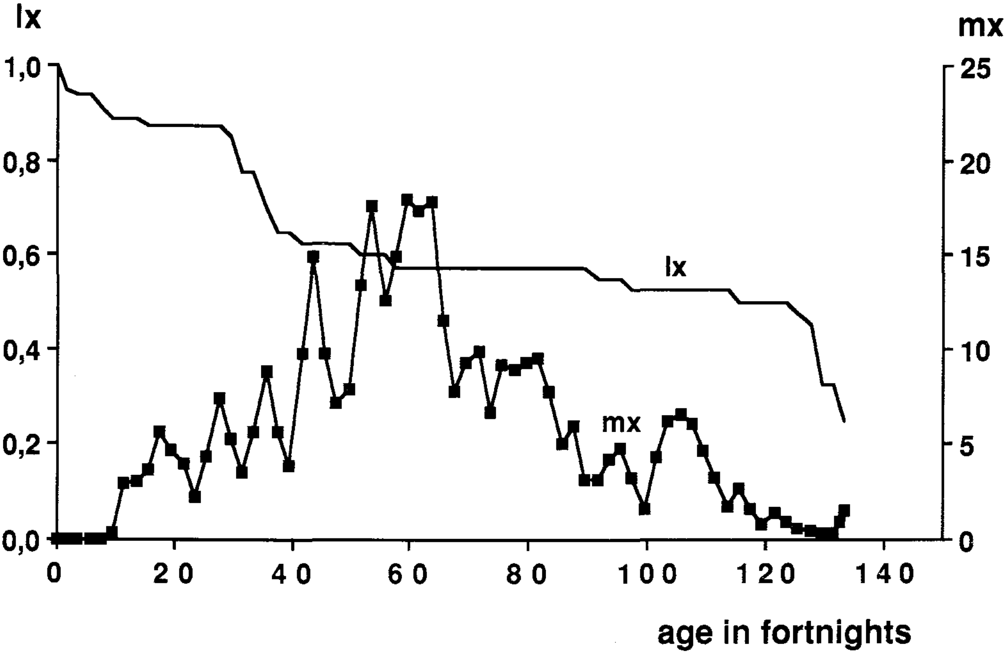

FIG. 3. Graphical representation of life tables of a population of *Melanoides tuberculata* reared in laboratory. l_x: survivorship (proportion of the original number of newly liberated juveniles); m_x: fecundity (mean newly liberated juveniles per female per fortnight).

TABLE 3. Life table for *Biomphalaria alexandrina,* Kafr al Hamza, Egypt, reared in laboratory (25°C).

Pivotal age in fortnights x	Survival lx	Fecundity mx	Net reprod. rate Ro	Finite rate of increase R	Mean generation time T	Intrinsic rate of increase rm	Intrinsic rate of increase rm(%)	Stable age distribution (%)
0.0	1.0000	0.0000						44.1399
0.5	1.0000	0.0000						31.0707
1.5	0.8732	0.0000						13.4432
2.5	0.8591	0.0000						6.5535
3.5	0.7183	0.0000						2.7150
4.5	0.6197	4.3600	2.7019	1.2472	4.4996	0.2209	31.4583	1.1606
5.5	0.5352	20.6600	11.0572	1.6461	5.2602	0.4984	70.9769	0.4967
6.5	0.5070	42.1400	21.3650	1.8291	5.8941	0.6038	85.9869	0.2331
7.5	0.4507	68.7200	30.9721	1.9167	6.4419	0.6506	92.6516	0.1027
8.5	0.4084	120.3400	49.1469	1.9699	7.0015	0.6780	96.5537	0.0461
9.5	0.3662	133.7700	48.9866	1.9921	7.4017	0.6892	98.1487	0.0205
10.5	0.3662	171.0800	62.6495	2.0051	7.7971	0.6957	99.0743	0.0101
11.5	0.3099	204.2700	63.3033	2.0111	8.1158	0.6987	99.5016	0.0043
12.5	0.2958	272.6200	80.6410	2.0150	8.4438	0.7006	99.7721	0.0020
13.5	0.2817	287.2000	80.9042	2.0168	8.7143	0.7015	99.9003	0.0009
14.5	0.2535	338.2800	85.7540	2.0176	8.9570	0.7019	99.9573	0.0004
15.5	0.1690	391.0800	66.0925	2.0180	9.1196	0.7021	99.9858	0.0001
16.5	0.1549	333.8200	51.7087	2.0182	9.2354	0.7022	100.0000	0.0001
17.5	0.1127	399.2500	44.9955	2.0182	9.3299	0.7022	100.0000	0.0000
18.5	0.0986	110.0000	10.8460	2.0182	9.3518	0.7022	100.0000	0.0000
		Ro =	711.1244					

TABLE 4. Life table for *Biomphalaria straminea,* Epinette River, Martinique, reared in laboratory (25°C).

Pivotal age in fortnights x	Survival lx	Fecundity mx	Net reprod. rate Ro	Finite rate of increase R	Mean generation time T	Intrinsic rate of increase rm	rm(%)	Stable age distribution (%)
0.0	1.0000	0.0000						49.0990
0.5	1.0000	0.0000						31.5505
1.5	0.8947	0.0000						11.6560
2.5	0.8772	0.0000						4.7189
3.5	0.7982	2.0100	1.6044	1.1447	3.4992	0.1351	15.2742	1.7730
4.5	0.7895	24.9000	19.6586	2.0049	4.3947	0.6956	78.6433	0.7241
5.5	0.7632	48.3000	36.8626	2.2646	4.9702	0.8174	92.4138	0.2891
6.5	0.7193	65.6100	47.1933	2.3589	5.4265	0.8582	97.0266	0.1125
7.5	0.7193	79.7300	57.3498	2.3984	5.8204	0.8748	98.9033	0.0464
8.5	0.7105	66.5400	47.2767	2.4107	6.0767	0.8799	99.4799	0.0189
9.5	0.6667	93.4200	62.2831	2.4172	6.3524	0.8826	99.7852	0.0073
10.5	0.6140	136.3400	83.7128	2.4206	6.6457	0.8840	99.9435	0.0028
11.5	0.5965	87.5600	52.2295	2.4215	6.7975	0.8844	99.9887	0.0011
12.5	0.3158	94.1400	29.7294	2.4218	6.8762	0.8845	100.0000	0.0002
13.5	0.1228	141.9300	17.4290	2.4218	6.9203	0.8845	100.0000	0.0000
14.5	0.1053	61.8300	6.5107	2.4218	6.9364	0.8845	100.0000	0.0000
		Ro =	461.8398					

eggs produced per species of *Biomphalaria* per fortnight (Figs. 2,3).

Calculated Life Table Parameters

The following life table parameters have been calculated: intrinsic rate of natural increase (r), mean generation time (T), finite rate of increase (R) and net reproductive rate (R_0) (Tables 2–6).

B. glabrata, B. alexandrina, and *B. straminea* have a high intrinsic rate of natural increase (0.84 and 0.86, 0.78 and 0.70, 0.88 and 1.01, respectively) and a short mean generation time (8.59 and 8.87, 8.60 and 9.35, 6.94 and 5.47 fortnights, respectively). *M. tuberculata,* on the contrary, has a low intrinsic rate of natural increase (0.24), and a very long mean generation time (25.77 fortnights, calculated for 135 fortnights of culture).

DISCUSSION AND CONCLUSIONS

Several authors have studied growth and demography of tropical freshwater pulmonates in the laboratory; a review of the main results obtained under optimal conditions of temperature is presented in Tables 1 and 6.

Precise comparison of these results is difficult because of differences in laboratory rearing conditions (food, water volume, water quality, etc.). Several aspects of the results are noteworthy, however.

Among the species of *Biomphalaria, B. alexandrina* has the lowest intrinsic rate of natural increase (0.70–0.78). This is due to mortality, which is important in all stages of development (Fig. 2). In contrast, the mortality of *B. glabrata* is quite different and the intrinsic rate of increase is higher (0.84–0.88). In regard to *B. straminea,* the intrinsic rate of increase is slightly higher (0.88–1.01) but the mean generation time is shorter. This species has a distinct demographic strategy and these results fit well with field data on the ecology of this snail: *B. straminea* is more resistant to drought and better adapted to temporary and fluctuating environments than is *B. glabrata* (Barbosa, 1973; Guyard & Pointier, 1979).

Results for the *B. pfeifferi* group show a great range of variation. According to the origin of the strain, the intrinsic rate of increase can vary greatly (0.24 to 2.37; Table 6). Care is needed in comparing these results, however, owing to the different experimental conditions used by the authors: r = 0.24 in Zaire, but with water temperature varying between 18.5°C and 24°C and different food (Loreau & Baluku, 1987); r = 0.48 in Rhodesia, but the study was disturbed by atypical migratory behaviours (Shiff & Garnett, 1967); r = 0.86 in Tanzania (Sturrock, 1966); r = 2.37 in South Africa (De Kock & Van Eeden, 1981), but us-

TABLE 5. Life table for *Melanoides tuberculata,* Pointe-à-Pitre canal, Guadeloupe, reared in laboratory (25°C).

Pivotal age in fortnights x	Survival lx	Fecundity mx	Net reprod. rate Ro	Finite rate of increase R	Mean generation time T	Intrinsic rate of increase rm	Intrinsic rate of increase rm(%)	Stable age distrib. (%)
0.0	1.0000	0.0000						20.4327
0.5	0.9750	0.0000						17.6638
1.5	0.9500	0.0000						13.5305
2.5	0.9375	0.0000						10.4971
3.5	0.9375	0.0000						8.2524
4.5	0.9375	0.0000						6.4876
5.5	0.9375	0.0000						5.1003
6.5	0.9375	0.0000						4.0096
7.5	0.9125	0.0000						3.0681
8.5	0.9000	0.0000						2.3790
9.5	0.8875	0.3040	0.2698	0.8712	9.5002	−0.1379	−57.3150	1.8443
10.5	0.8875	0.6377	0.5660	0.9826	10.1941	−0.0176	−7.3150	1.4499
11.5	0.8875	2.9710	2.6368	1.1180	11.1649	0.1115	46.3425	1.1398
12.5	0.8875	4.1159	3.6529	1.1810	11.8003	0.1664	69.1604	0.8961
13.5	0.8875	3.1014	2.7525	1.2061	12.2214	0.1874	77.8886	0.7045
14.5	0.8750	1.8971	1.6600	1.2164	12.4841	0.1959	81.4214	0.5460
15.5	0.8750	3.6176	3.1654	1.2300	12.9858	0.2070	86.0349	0.4293
16.5	0.8750	4.6176	4.0404	1.2416	13.5437	0.2164	89.9418	0.3375
17.5	0.8750	5.5882	4.8897	1.2513	14.1064	0.2242	93.1837	0.2653
18.5	0.8750	4.6176	4.0404	1.2570	14.5189	0.2287	95.0540	0.2086
19.5	0.8750	4.7500	4.1563	1.2611	14.9156	0.2320	96.4256	0.1640
20.5	0.8750	2.3382	2.0459	1.2629	15.0930	0.2334	97.0075	0.1289
21.5	0.8750	3.9853	3.4871	1.2647	15.4203	0.2348	97.5894	0.1013
22.5	0.8750	3.2500	2.8438	1.2659	15.6660	0.2358	98.0050	0.0797
23.5	0.8750	2.2353	1.9559	1.2667	15.8271	0.2364	98.2544	0.0626
24.5	0.8750	2.7941	2.4448	1.2673	16.0317	0.2369	98.4622	0.0492
25.5	0.8750	4.3235	3.7831	1.2681	16.3339	0.2375	98.7116	0.0387
26.5	0.8750	9.4412	8.2611	1.2693	16.9263	0.2385	99.1272	0.0304
27.5	0.8750	7.3636	6.4432	1.2701	17.3343	0.2391	99.3766	0.0239
28.5	0.8500	5.8235	4.9500	1.2706	17.6207	0.2395	99.5428	0.0183
29.5	0.8500	5.3235	4.5250	1.2709	17.8746	0.2397	99.6259	0.0144
30.5	0.8000	4.5625	3.6500	1.2711	18.0643	0.2399	99.7091	0.0106
31.5	0.7750	3.4839	2.7000	1.2712	18.2018	0.2400	99.7506	0.0081
32.5	0.7750	5.0645	3.9250	1.2714	18.3964	0.2401	99.7922	0.0064
33.5	0.7750	5.6333	4.3658	1.2715	18.6025	0.2402	99.8337	0.0050
34.5	0.7500	5.3333	4.0000	1.2716	18.7814	0.2403	99.9753	0.0038
35.5	0.7000	8.8214	6.1750	1.2716	19.0540	0.2403	99.8753	0.0028
36.5	0.7000	7.9286	5.5500	1.2718	19.2766	0.2404	99.9169	0.0022
37.5	0.6500	5.6154	3.6500	1.2718	19.4216	0.2404	99.9169	0.0016
38.5	0.6500	5.6538	3.6750	1.2719	19.5545	0.2405	99.9584	0.0013
39.5	0.6500	3.8846	2.5250	1.2719	19.6486	0.2405	99.9584	0.0010
40.5	0.6250	5.4800	3.4250	1.2719	19.7730	0.2405	99.9584	0.0007
41.5	0.6250	9.7200	6.0750	1.2719	19.9849	0.2405	99.9584	0.0006
42.5	0.6250	10.9200	6.8250	1.2719	20.2107	0.2405	99.9584	0.0005
43.5	0.6250	14.9200	9.3250	1.2719	20.5006	0.2405	99.9584	0.0004
44.5	0.6250	14.3600	8.9750	1.2719	20.7618	0.2405	99.9584	0.0003
45.5	0.6250	9.7200	6.0750	1.2720	20.9211	0.2406	100.0000	0.0002
46.5	0.6250	6.2800	3.9250	1.2720	21.0260	0.2406	100.0000	0.0002
47.5	0.6250	7.2000	4.5000	1.2720	21.1432	0.2406	100.0000	0.0001
48.5	0.6250	4.7500	2.9750	1.2720	21.2188	0.2406	100.0000	0.0001
49.5	0.6250	7.8333	4.8958	1.2720	21.3404	0.2406	100.0000	0.0001
50.5	0.6000	10.0833	6.0500	1.2720	21.4860	0.2406	100.0000	0.0001
51.5	0.6000	13.3750	8.0250	1.2720	21.6715	0.2406	100.0000	0.0001
52.5	0.6000	17.4166	10.4500	1.2720	21.9012	0.2406	100.0000	0.0000
53.5	0.6000	17.6250	10.5750	1.2720	22.1215	0.2406	100.0000	0.0000

TABLE 5. (*continued*)

Pivotal age in fortnights x	Survival lx	Fecundity mx	Net reprod. rate Ro	Finite rate of increase R	Mean generation time T	Intrinsic rate of increase		Stable age distrib. (%)
						rm	rm(%)	
54.5	0.6000	13.9166	8.3500	1.2720	22.2875	0.2406	100.0000	0.0000
55.5	0.6000	12.5416	7.5250	1.2720	22.4317	0.2406	100.0000	0.0000
56.5	0.5750	19.9130	11.4500	1.2720	22.6418	0.2406	100.0000	0.0000
57.5	0.5750	14.8695	8.5500	1.2720	22.7921	0.2406	100.0000	0.0000
58.5	0.5750	16.3478	9.4000	1.2720	22.9513	0.2406	100.0000	0.0000
59.5	0.5750	18.0000	10.3500	1.2720	23.1198	0.2406	100.0000	0.0000
60.5	0.5750	18.6521	10.7250	1.2720	23.2875	0.2406	100.0000	0.0000
61.5	0.5750	17.3913	10.0000	1.2720	23.4380	0.2406	100.0000	0.0000
62.5	0.5750	15.4347	8.8750	1.2720	23.5671	0.2406	100.0000	0.0000
63.5	0.5750	17.8695	10.2750	1.2720	23.7118	0.2406	100.0000	0.0000
64.5	0.5750	11.0869	6.3750	1.2720	23.7991	0.2406	100.0000	0.0000
65.5	0.5750	11.4782	6.6000	1.2720	23.8875	0.2406	100.0000	0.0000
66.5	0.5750	9.2600	5.3245	1.2720	23.9576	0.2406	100.0000	0.0000
67.5	0.5750	7.7826	4.4750	1.2720	24.0155	0.2406	100.0000	0.0000
68.5	0.5750	9.9130	5.7000	1.2720	24.0882	0.2406	100.0000	0.0000
69.5	0.5750	9.3043	5.3500	1.2720	24.1553	0.2406	100.0000	0.0000
70.5	0.5750	10.4783	6.0250	1.2720	24.2295	0.2406	100.0000	0.0000
71.5	0.5750	9.3043	5.3500	1.2720	24.2944	0.2406	100.0000	0.0000
72.5	0.5750	8.7400	5.0255	1.2720	24.3544	0.2406	100.0000	0.0000
73.5	0.5750	6.6957	3.8500	1.2720	24.3998	0.2406	100.0000	0.0000
74.5	0.5750	6.7826	3.9000	1.2720	24.4452	0.2406	100.0000	0.0000
75.5	0.5750	9.1304	5.2500	1.2720	24.5057	0.2406	100.0000	0.0000
76.5	0.5750	10.1738	5.8499	1.2720	24.5720	0.2406	100.0000	0.0000
77.5	0.5750	8.9565	5.1500	1.2720	24.6296	0.2406	100.0000	0.0000
78.5	0.5750	10.2174	5.8750	1.2720	24.6942	0.2406	100.0000	0.0000
79.5	0.5750	9.2600	5.3245	1.2720	24.7520	0.2406	100.0000	0.0000
80.5	0.5750	12.2609	7.0500	1.2720	24.8273	0.2406	100.0000	0.0000
81.5	0.5750	9.5217	5.4750	1.2720	24.8848	0.2406	100.0000	0.0000
82.5	0.5750	6.9130	3.9750	1.2720	24.9261	0.2406	100.0000	0.0000
83.5	0.5750	7.7826	4.4750	1.2720	24.9720	0.2406	100.0000	0.0000
84.5	0.5750	3.9130	2.2500	1.2720	24.9950	0.2406	100.0000	0.0000
85.5	0.5750	5.0870	2.9250	1.2720	25.0246	0.2406	100.0000	0.0000
86.5	0.5750	4.0870	2.3500	1.2720	25.0482	0.2406	100.0000	0.0000
87.5	0.5750	6.0000	3.4500	1.2720	25.0827	0.2406	100.0000	0.0000
88.5	0.5750	7.0000	4.0250	1.2720	25.1225	0.2406	100.0000	0.0000
89.5	0.5750	3.2174	1.8500	1.2720	25.1407	0.2406	100.0000	0.0000
90.5	0.5750	5.6522	3.2500	1.2720	25.1725	0.2406	100.0000	0.0000
91.5	0.5500	3.1816	1.7499	1.2720	25.1895	0.2406	100.0000	0.0000
92.5	0.5500	4.5000	2.4750	1.2720	25.2134	0.2406	100.0000	0.0000
93.5	0.5500	4.2727	2.3500	1.2720	25.2360	0.2406	100.0000	0.0000
94.5	0.5500	7.2272	3.9750	1.2720	25.2740	0.2406	100.0000	0.0000
95.5	0.5500	4.8636	2.6750	1.2720	25.2993	0.2406	100.0000	0.0000
96.5	0.5500	4.6363	2.5500	1.2720	25.3233	0.2406	100.0000	0.0000
97.5	0.5250	3.2857	1.7250	1.2720	25.3395	0.2406	100.0000	0.0000
98.5	0.5250	3.0952	1.6250	1.2720	25.3547	0.2406	100.0000	0.0000
99.5	0.5250	1.6666	0.8750	1.2720	25.3628	0.2406	100.0000	0.0000
100.5	0.5250	2.9524	1.5500	1.2720	25.3772	0.2406	100.0000	0.0000
101.5	0.5250	4.3809	2.3000	1.2720	25.3985	0.2406	100.0000	0.0000
102.5	0.5250	4.3809	2.3000	1.2720	25.4196	0.2406	100.0000	0.0000
103.5	0.5250	3.4286	1.8000	1.2720	25.4361	0.2406	100.0000	0.0000
104.5	0.5250	6.1905	3.2500	1.2720	25.4657	0.2406	100.0000	0.0000
105.5	0.5250	5.4286	2.8500	1.2720	25.4915	0.2406	100.0000	0.0000
106.5	0.5250	6.6190	3.4750	1.2720	25.5227	0.2406	100.0000	0.0000
107.5	0.5250	6.3333	3.3250	1.2720	25.5523	0.2406	100.0000	0.0000
108.5	0.5250	6.0476	3.1750	1.2720	25.5804	0.2406	100.0000	0.0000

continued

TABLE 5. (*continued*)

Pivotal age in fortnights x	Survival lx	Fecundity mx	Net reprod. rate Ro	Finite rate of increase R	Mean generation time T	Intrinsic rate of increase rm	Intrinsic rate of increase rm(%)	Stable age distrib. (%)
109.5	0.5250	5.2381	2.7500	1.2720	25.6047	0.2406	100.0000	0.0000
110.5	0.5250	4.7143	2.4750	1.2720	25.6263	0.2406	100.0000	0.0000
111.5	0.5250	3.9048	2.0500	1.2720	25.6442	0.2406	100.0000	0.0000
112.5	0.5250	3.2857	1.7250	1.2720	25.6591	0.2406	100.0000	0.0000
113.5	0.5250	2.5714	1.3500	1.2720	25.6708	0.2406	100.0000	0.0000
114.5	0.5250	1.7619	0.9250	1.2720	25.6788	0.2406	100.0000	0.0000
115.5	0.5250	2.1429	1.1250	1.2720	25.6885	0.2406	100.0000	0.0000
116.5	0.5000	2.7000	1.3500	1.2720	25.7001	0.2406	100.0000	0.0000
117.5	0.5000	1.9500	0.9750	1.2720	25.7084	0.2406	100.0000	0.0000
118.5	0.5000	1.6500	0.8250	1.2720	25.7155	0.2406	100.0000	0.0000
119.5	0.5000	1.7000	0.8500	1.2720	25.7227	0.2406	100.0000	0.0000
120.5	0.5000	0.8500	0.4250	1.2720	25.7264	0.2406	100.0000	0.0000
121.5	0.5000	1.2000	0.6000	1.2720	25.7315	0.2406	100.0000	0.0000
122.5	0.5000	1.4000	0.7000	1.2720	25.7374	0.2406	100.0000	0.0000
123.5	0.5000	1.8000	0.9000	1.2720	25.7451	0.2406	100.0000	0.0000
124.5	0.5000	0.9000	0.4500	1.2720	25.7489	0.2406	100.0000	0.0000
125.5	0.4750	0.7895	0.3750	1.2720	25.7521	0.2406	100.0000	0.0000
126.5	0.4750	0.5785	0.2748	1.2720	25.7544	0.2406	100.0000	0.0000
127.5	0.4750	0.4210	0.2000	1.2720	25.7561	0.2406	100.0000	0.0000
128.5	0.4500	0.4737	0.2132	1.2720	25.7579	0.2406	100.0000	0.0000
129.5	0.3500	0.6429	0.2250	1.2720	25.7598	0.2406	100.0000	0.0000
130.5	0.3250	0.3846	0.1250	1.2720	25.7608	0.2406	100.0000	0.0000
131.5	0.3250	0.3077	0.1000	1.2720	25.7617	0.2406	100.0000	0.0000
132.5	0.2750	0.9091	0.2500	1.2720	25.7638	0.2406	100.0000	0.0000
133.5	0.2500	1.5000	0.3750	1.2720	25.7670	0.2406	100.0000	0.0000
		Ro =	492.5179					

ing artificial food and the authors do not indicate the time taken as time = 0 for their calculations (egg laying time or hatching time?). This omission is important because a slight difference in the pivotal age greatly alters the calculations of the intrinsic rate of increase; for example, r = 2.37 becomes r = 1.66 if a fortnight is added in the pivotal age used by De Kock & Van Eeden (1981).

Some other studies carried out on other pulmonates such as *Bulinus globosus* (r = 0.66), *B. tropicus* (r = 3.37) and *Lymnaea natalensis* (r = 1.81) also show a great range of variation (Shiff, 1964; De Kock & Van Eeden, 1985).

In comparison, calculated life table parameters of *M. tuberculata* indicate a quite different demographic strategy. This species has a very low intrinsic rate of natural increase (r = 0.24) but a very long mean generation time (T = 25.77 fortnights).

These results support numerous field observations, which record that this snail can reach and maintain very high densities for a long time in permanent and stable habitats (Murray & Wopschall, 1965, 4,798 snails/ft^2; Roessler et al., 1977, about 7,000 to 37,000 snails/m^2; Pointier et al., 1989, between 9,900 and 13,400 snails/m^2). In such habitats, thiarid snails have a competitive advantage and in particular situations their advantage leads to the elimination of this group of snails (Pointier et al., 1989). The mechanisms of the competition remain to be studied more precisely but it is established that competition occurs whenever thiarids reach and maintain high densities. In that case, there is probably competition for space or by interference. Thiarids and *Biomphalaria* also have a similar diet (detritivorous and microphagous, including microalgae, bacteria, organic materials, etc.) and it is therefore probable that competition for food occurs in some cases.

Consequently, it can be predicted that biological control using thiarid snails is likely to be efficient in permanent and stable habitats, but not in temporary or unstable ones.

TABLE 6. Calculated parameters of life tables for some tropical freshwater pulmonates and for a population of *Melanoides tuberculata* reared in laboratory. r = intrinsic rate of increase, R = finite rate of increase, R_o = net reproduction rate, T = mean generation time.

Origin of Snails	Water Temp.	Ro	r	R	T (fortnights)
Biomphalaria glabrata Céligny pond, Guadeloupe	25°C	1418.87	0.84	2.33	8.59
Biomphalaria glabrata Dubelloy marsh, Guadeloupe	25°C	2143.52	0.86	2.37	8.87
Biomphalaria glabrata St Lucia (data from Sturrock, 1972)	25°C	2054.1	0.88	2.42	8.63
Biomphalaria alexandrina Kalyub canal, Egypt	25°C	806.83	0.78	2.17	8.6
Biomphalaria alexandrina Kafr al Hamza canal, Egypt	25°C	711.12	0.7	2.02	9.35
Biomphalaria straminea Epinette River, Martinique	25°C	461.84	0.88	2.42	6.94
Biomphalaria straminea Madame River, Martinique	25°C	255.82	1.01	2.75	5.47
Biomphalaria pfeifferi Rhodesia (data from Shiff & Garnett, 1967)	25°C	111.43	0.48	1.62	9.79
Biomphalaria pfeifferi Tanzania (data from Sturrock, 1966)	25°C	182.14	0.86	2.36	6.05
Biomphalaria pfeifferi South Africa (data from De Kock & Van Eeden, 1981)	26°C	2696.19	2.37	10.72	5.89
Biomphalaria pfeifferi Zaire (data from Loreau & Baluku, 1987)	18.5°–24°C	216.6	0.24	1.27	11.36
Bulinus globosus Rhodesia (data from Shiff, 1964)	25°C	467.31	0.66	1.93	7
Bulinus tropicus South Africa (data from De Kock & Van Eeden, 1985)	26°C	1655.64	3.37	29.15	3.36
Lymnaea natalensis South Africa (data from De Kock & Van Eeden, 1985)	26°C	1371.91	1.81	6.11	4.99
Melanoides tuberculata Pointe-à-Pitre canal, Guadeloupe	25°C	492.5	0.24	1.27	25.77

ACKNOWLEDGEMENTS

This research received financial support from the UNDP/World Bank/WHO special programme for Research and Training in Tropical Diseases. We should like to thank Dr Fergus McCullough, formerly Senior Scientist, WHO, VBC, for his critical review of the manuscript.

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Revised Ms. accepted 15 May 1990