

# Comparative bioenergetics of permanent and temporary pond populations of the freshwater clam, *Musculium partumeium* (Say)\*

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## Abstract

The population energetics of a temporary and a permanent pond population of *Musculium partumeium* in Southwest Ohio were studied. In the permanent pond (surface area = 396 m<sup>2</sup>, maximum depth = 0.7 m) the population was bivoltine and iteroparous whereas in the temporary pond (surface area = 1042 m<sup>2</sup>, maximum depth = 0.9 m) the population was usually univoltine and semelparous.

Growth and biomass were assessed as total organic carbon and total nitrogen to provide estimates of productivity and seasonal changes in C:N for each generation. Productivity (non-respired assimilation = growth + reproduction; N-R.A. = G + R) was 6939 mgC·m<sup>-2</sup>·a<sup>-1</sup> (3858 and 3353 mgC·m<sup>-2</sup>·a<sup>-1</sup> for each generation) and 1661 mgC·m<sup>-2</sup>·a<sup>-1</sup> for the permanent and temporary pond populations respectively. The average standing crop biomass (B) was 606.8 mgC·m<sup>-2</sup> (357.5 and 249.3 mgC·m<sup>-2</sup> for each generation) and 231.9 mgC·m<sup>-2</sup> with overall productivity:biomass ratios of 11.4 and 7.2 for the permanent pond and temporary pond populations respectively.

Respiration rates were converted to carbon equivalents (respired assimilation = R.A.) and used to evaluate the components of total assimilation (T.A. = R.A. + N-R.A.) and the efficiency of partitioning this energy to N-R.A. for G and R. When expressed as a percentage, the production efficiencies (100 × N-R.A. : T.A.) were 50.4 and 62%, and the reproductive efficiencies (100 × R:N-R.A.) were 26.4 and 18% for the permanent and temporary pond populations respectively. The reproductive efficiencies for populations of these viviparous clams are greater than those for most oviparous molluscs.

The comparative information on the energetics of these populations does not completely fit any theoretical consideration of reproductive effort or life-history strategy. These data are discussed in relation to selection for population success in temporary ponds.

## Introduction

The relationship between assimilation and the efficiencies of respiration, growth, and reproduction in relation to life-history for freshwater organisms has been the focus of many authors. Although insect larvae and bivalves constitute the two major groups of filter feeders in freshwater benthic systems, most attention has been given to the role of

insects (e.g. McCullough *et al.*, 1979; Wallace & Merritt, 1980) in nutrient processing in these systems.

The Unionacea (freshwater mussels or naiades) and Corbiculacea (including pisidiid, fingernail, pill or pea clams) constitute the two major superfamilies of freshwater bivalves. The pisidiids [family Pisidiidae, ICZN declaration 27-precedence over Sphaeriidae: a hermaphroditic and viviparous (ovo-

viviparous according to Mackie, 1978) group including *M. partumeium*] are comparatively tiny, cosmopolitan and ubiquitous in distribution and can dominate the benthos in numbers and/or biomass (e.g. Carr & Hiltunen, 1965; Gale, 1975; Healey, 1977; Eckblad *et al.*, 1977). Also they often serve as food for fish (Eyerdam, 1968; Jude, 1973), ducks (Thompson, 1973) and insects (Foote, 1976). The majority of studies on freshwater molluscan energetics have been on gastropods (e.g. Burky, 1971, 1974; Sturdier *et al.*, 1975; Streit, 1976; references in Russell-Hunter, 1978; references in Aldridge, 1983; references in McMahon, 1983). However, the dynamics of secondary production of freshwater clams have been discussed (Burky, 1983), and unionacean (e.g. Negus, 1966; Tudorancea & Florescu, 1968a, b, 1969; Magnin & Stańczykowska, 1971; Cameron *et al.*, 1979; Huebner, 1980), dreissenacean (Stańczykowska, 1971; Walz, 1978a, b, c, d, e, f, 1979) and corbiculacean (e.g. Gillespie, 1969; Alimov, 1970; Avolizi, 1976; Aldridge & McMahon, 1978; Holopainen, 1978; Holopainen & Hanski, 1979; Heitkamp, 1980; Bleck & Heitkamp, 1980; Hornbach, 1980; Holopainen & Jónasson, 1983; Hornbach *et al.*, 1984) clams have all received attention.

This report presents the first information on the bioenergetics of *Musculium partumeium* and complements extensive data on the same two populations. There is information on life-history and population dynamics (Way *et al.*, 1980), shell characteristics (Burky *et al.*, 1979), reproductive strategies (Hornbach *et al.*, 1980c), filtration rates (Benjamin, 1978; Conover *et al.*, 1981; Burky *et al.*, 1985), seasonal respiration (Way *et al.*, 1981; Buchwalder, 1983), potential growth cues (Conover & Burky, 1981), and population genetics (McLeod *et al.*, 1981). This constitutes one of the most extensive banks of data for intraspecific population comparisons of a freshwater clam.

## Materials and methods

The life-histories of two populations of *Musculium partumeium* from southwest Ohio, one from a temporary pond (Drew Woods = DW: pond surface area 1042 m<sup>2</sup>; maximum depth 0.9 m) and one from a permanent pond (Aullwood Marsh = AM: pond surface area 396 m<sup>2</sup>; maximum depth 0.7 m),

have been described (Way *et al.*, 1980; Hornbach *et al.*, 1980c). In order to judge the materials and methods, and results of this study on population energetics, it is necessary to outline some basic aspects of life-history for the two populations of *M. partumeium* (Way *et al.*, 1980; Hornbach *et al.*, 1980c). The population from the ephemeral pond (DW) has one generation per year. Young are born in spring (May–July), remain dormant as juveniles in the moist substrate of the dry pond (August–January), begin growth in early March, reproduce (May–July) and die when the pond usually dries in July–August. The onset of drying can unpredictably begin in early June shortening the period of growth and reproduction – or – the pond may not dry at all. The population from the permanent pond (AM) has two generations per year. Recruitment of the spring generation (AM-SG) occurs in May–July, growth begins in August–September and they give birth in September–November. Some spring generation adults overwinter and contribute to reproduction in the spring. Recruitment of the fall generation (AM-FG) occurs in September–November. The fall recruits overwinter as ‘sub-adults’ with rapid growth and reproduction in the spring. Most clams of the fall generation die by the end of July with a few surviving to make a small contribution to fall reproduction.

Clams were selected from preserved samples (fixed in the field in 12% neutral formalin), grouped into size categories based on shell length (greatest anterior-posterior dimension: measured to the nearest 0.2 mm with a vernier caliper for some clams with shell lengths > 5.0 mm or with a stage micrometer under a dissecting microscope for clams with shell lengths < 10 mm) and analyzed for total organic carbon or nitrogen. For carbon, usually > 8 groups of clams from each generation sample were analyzed using the method of Russell-Hunter *et al.* (1968). As estimated by Russell-Hunter *et al.* (1968) for molluscan tissue 1 g of reducing carbon is equivalent to 45.8 kJ (or 10.94 Kcal) and this is comparable to values obtained by direct calorimetry. For nitrogen, usually > 8 groups of clams from each generation sample were dried to constant mass at 95 °C and subsequently analyzed using a Coleman model-29 semiautomatic nitrogen analyzer which employs a modified micro-Dumas method (Gustin, 1960).

Respiration estimates were derived from the data

of Way *et al.* (1981) on the AM and DW populations. Seasonal oxygen consumption values ( $\mu\text{l O}_2 \cdot \text{mg dry tissue}^{-1} \cdot \text{h}^{-1}$ ) at field temperature were converted to equivalents of carbon using the computational approach set out by Burky (1969, 1971).

To compare biomass as organic carbon, total nitrogen or respiration as carbon for generation samples at different times, the estimates must be standardized. Linear regressions of the relationship of  $\log_e$  of shell length to  $\log_e$  of total organic carbon, total nitrogen, or respiration rate as carbon were calculated for generation samples. These values are related to natural size distributions of 100 clams and these values referred to as unit populations (UP). Thus, values for each UP can be determined by knowing the percentage of individuals represented at each class mark of shell lengths in a distribution and the amount of organic carbon, nitrogen, or the rate of respiration at each class mark (for discussion of UP see Burky, 1969, 1971, 1974, 1983; Russell-Hunter, 1978). Such UP values are an excellent measure for making comparisons of the energetics of an 'average' population unit over its natural lifespan. Differences between UP values of carbon on adjacent dates are divided by the appropriate time interval to give weekly rates of growth as carbon for mean dates. Using reproductive data on births  $\cdot \text{UP}^{-1} \cdot \text{wk}^{-1}$  and  $\mu\text{gC} \cdot \text{newborn}^{-1}$  for AM and DW from Hornbach *et al.* (1980c) reproductive rates as carbon were calculated.

Unit population values for organic carbon were divided by corresponding UP values for nitrogen to give C:N ratios (discussion on C:N ratios: Russell-Hunter, 1970, 1978). Such ratios can be assumed to be indicative of relative proportions of fats and/or carbohydrates, and proteins as they change over time.

Unit population data for the AM and DW populations have been combined with the appropriate density data from Way *et al.* (1980) to provide values for standing crop biomass as  $\text{mgC} \cdot \text{m}^{-2}$  on specific dates. Also, respiration as  $\text{mgC} \cdot \text{m}^{-2}$  for specific intervals and over generation times have been summed. From density values and standing crop biomass information, mortality values can be combined with the biomass lost for specific intervals and summed over generation time to give reasonable estimates of the growth component of biomass production as  $\text{mgC} \cdot \text{m}^{-2}$  (for discussion see Russell-Hunter, 1970, 1978; Burky, 1983).

For each generation the energy put into growth (G) and reproduction (R) make up the non-respired assimilation (N-R.A.). The total assimilation (T.A.) is composed of respired assimilation (R.A.) and N-R.A. Thus,  $\text{T.A.} = \text{R.A.} + \text{N-R.A.}$ , and  $\text{N-R.A.} = \text{G} + \text{R}$  form the basis for computations of energy flow (Burky, 1969, 1971, 1983; Russell-Hunter, 1970, 1978; Russell-Hunter & Buckley, 1983) through the two populations. The above symbols have been commonly used in many molluscan studies (and in this report) and are equivalent to symbols used in other reports (Ricker, 1968).

## Results

Organic carbon per unit population (UP = natural size distribution of 100 clams in each generation sample) is compared for AM and DW in Fig. 1. Values used for determining biomass as carbon and C:N ratios include the organic content of shell. These values (from Burky *et al.*, 1979) account for 10% or less of the total organic content of adult *M. partumeium* in this study. Rapid growth of the spring generation (AM-SG) from the permanent pond is initiated during August–September along

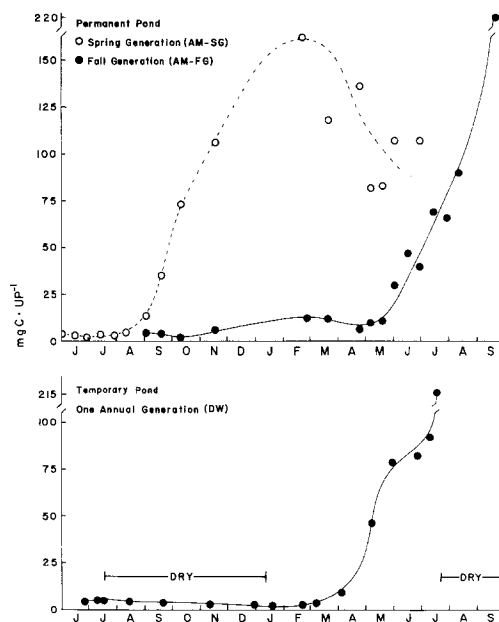


Fig. 1. Growth as carbon for unit populations (UP) of *Musculium partumeium* for the two generations in the permanent pond and for the one generation of the temporary pond in relation to months.

with reproduction. AM-SG adults overwinter and reproduce a second time in the spring. AM-FG overwinter as 'sub-adults' but do not initiate rapid growth until May along with reproduction. Concomitant reproduction and rapid growth as carbon (Fig. 1) is characteristic of AM-SG in the fall and AM-FG in the spring. The temporal sequence in the temporary pond (DW) is different. After a long dormant overwintering period DW initiates rapid growth in March with large adult size generally achieved by or before the time of births in late May. There is a similar relationship between growth and births for the second reproduction by AM-SG since large adult size is achieved before giving birth in the spring. Further, AM-SG achieves adult size months in advance of giving birth in the spring, whereas DW only achieves large adult size weeks before giving birth.

Fig. 2 provides seasonal C:N ratios for each generation. These ratios are based on UP carbon values (Fig. 1) and on UP nitrogen values. For all generations there is an initial decrease in C:N after birth. For AM-SG the ratio returns to a high level with some increase during fall reproduction. AM-SG shows a sharp C:N decrease at the initiation of

spring reproduction. The DW generation shows a decrease and maintains a low C:N during dormancy through the winter until the initiation of growth in early March. Like AM-SG the DW generation demonstrates a decreased C:N at the time of spring reproduction. For AM-FG the C:N is low in the spring with increasing values corresponding to spring UP growth (Fig. 1) and reproduction. High and/or variable C:N values at the end of spring reproduction may involve endogenous senescence at the end of each cohort's lifespan or simply the depletion of protein for reproduction prior to death.

The partitioning of assimilated organic carbon for the two populations of *M. partumeium* are given in Table 1. These rates ( $\text{mgC} \cdot \text{UP}^{-1} \cdot \text{wk}^{-1}$ ) provide comparative data for each generation UP from birth as they grow over their lifespan. Initial growth (G) values for each generation are often negative and for AM-SG and DW this corresponds to an inactive or 'dormant' period when the energy cost of respiration (R.A.) is greater than the energy assimilated for growth. Thus, clams, are maintained at the expense of stored reserves and this corresponds to some of the decreased C:N values (Fig. 2). Also, AM-SG is 'dormant' in the permanent pond during

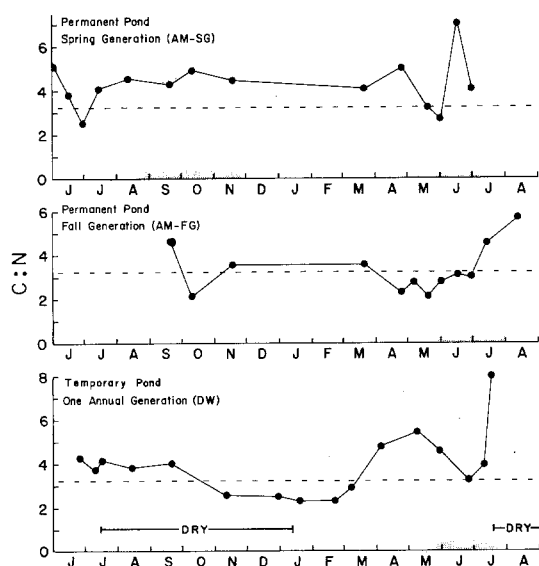


Fig. 2. C:N ratios of *Musculium partumeium* for the two generations in the permanent pond and for the one generation of the temporary pond in relation to months. Broken lines give the C:N ratio of 'average' protein at 3.25, stippled areas indicate the birth period(s) of each generation and the usual dry period is indicated for the temporary pond.

Table 1. Comparison of the partitioning of seasonal energy assimilation for two populations of the freshwater pisidiid clam, *Musculium partumeium*: growth (G), reproduction (R), non-respired assimilation (N-R.A.), respired assimilation (R.A.), total assimilation (T.A.).

Date	$\text{mgC} \cdot \text{UP}^{-1} \cdot \text{wk}^{-1}$				
	Permanent Pond - Spring Generation (AM-SG)				
	G	R	N-R.A.	R.A.	T.A.
6- 8	-0.44		-0.44	1.89	1.45
6-22	-0.51		-0.51	3.40	2.89
7- 6	0.53		0.53	3.59	4.12
7-21	-0.21		-0.21	2.33	2.12
8- 4	0.88		0.88	2.95	3.83
8-22	2.64		2.64	6.70	9.34
9-11	8.32	14.20	22.52	9.20	31.72
9-30	12.41	15.00	27.41	15.11	42.52
10-29	5.81	16.50	22.31	16.30	38.61
1- 6	3.84		3.84	15.73	19.57
3- 9	-13.37		-13.37	19.11	5.74
4- 6	3.58		3.58	22.26	25.84
4-30	-29.06	4.20	-24.86	22.89	-1.97
5-12	0.21	7.00	7.21	28.59	35.80
5-25	12.35	12.00	24.35	32.62	56.79
6-15	-0.13	15.19	15.06	45.14	60.20

Table 1. (Continued).

Permanent Pond – Fall Generation (AM-FG)					
Date	G	R	N-R.A.	R.A.	T.A.
9-11	-0.22		-0.22	0.57	0.35
9-30	-0.54		-0.54	0.90	0.36
10-29	0.65		0.65	1.02	1.67
1- 6	0.44		0.44	2.53	2.97
3- 9	-0.14		-0.14	2.59	2.45
4- 6	-1.04		-1.04	4.20	3.16
4-30	1.73		1.73	8.19	9.92
5-12	0.64		0.64	13.97	14.61
5-25	9.58	7.40	16.98	22.60	39.58
6- 8	7.24	9.00	16.24	25.53	41.77
6-22	-3.34	10.08	6.74	28.10	34.84
7- 6	12.54	13.20	25.74	24.22	49.96
7-21	-0.95	16.00	15.05	19.97	35.02
8- 4	11.66	19.61	31.26	17.54	48.80
8-30	22.80		22.80	26.00	48.80

Temporary Pond – One Annual Generation (DW)					
Date	G	R	N-R.A.	R.A.	T.A.
7- 3	0.43		0.43	0.99	1.42
7-14	-0.65		-0.65	1.01	0.36
7-31	-0.04		-0.04	0.65	0.61
9- 3	-0.13		-0.13	0.13	0.00
10-16	-0.16		-0.16	0.13	-0.03
12- 4	0.03		0.03	0.14	0.17
1- 9	-0.15		-0.15	0.53	0.38
2- 5	0.06		0.06	0.96	1.02
3- 1	0.39		0.39	1.05	1.44
3-21	2.65		2.65	1.85	4.50
4-21	6.82		6.82	4.63	11.45
5-18	10.31	2.25	12.56	9.72	22.28
6-12	0.86	2.90	3.76	13.11	16.87
7- 3	5.00	3.45	8.45	12.00	20.45
7-14	124.41	3.38	127.79	10.36	138.15

the summer. Values of T.A. at or close to zero are reported for DW during the dormant period (July 14–Jan. 19, Table 1). A total assimilation rate of zero (negative G balanced by R.A.) is expected if clams are assumed incapable of energy uptake without ‘immersion’ in water. Low or negative values of growth often correspond to rates for reproduction in the spring for all three generations (Table 1) since adults include growing embryos, and birth results in the loss of organic carbon. The greatest assimilation ( $138.15 \text{ mgC} \cdot \text{UP}^{-1} \cdot \text{wk}^{-1}$ ) is given for DW and represents a value calculated from a few very large clams at the end of the cohort lifespan. Apart from this single value it is obvious that the UP rates for both generations from the

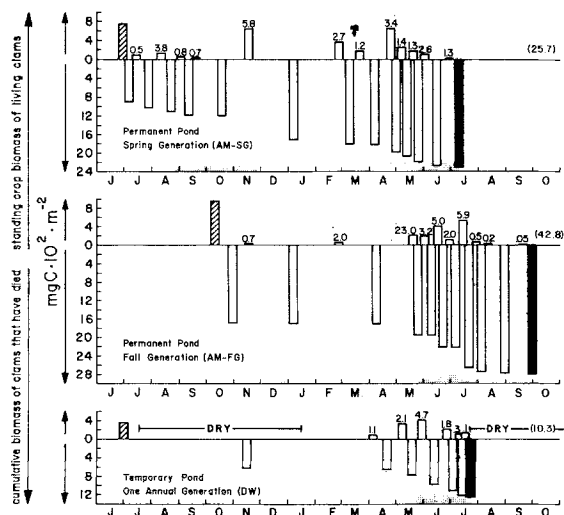


Fig. 3. Standing crop biomass and cumulative biomass as growth of *Musculium partumeium* for the two generations in the permanent pond and for the one generation of the temporary pond in relation to months. Histograms above the zero lines represent standing crop biomass as organic carbon; the striped histograms represent biomass of newborns which gave rise to each generation. Values above histograms represent respiration ( $\text{mgC} \cdot 10^2 \cdot \text{m}^{-2}$ ) for time intervals halfway between adjacent columns with the values in parentheses at the right representing total respiration for each generation. Histograms below the zero lines represent the cumulative biomass of clams that have died. The last solid histograms represent the total biomass production as growth over generation time ( $23.2, 27.9, 13.6 \text{ mgC} \cdot 10^2 \cdot \text{m}^{-2}$  for AM-SG, AM-FG, DW respectively). Stippled areas indicate birth period(s) for each generation and the usual dry period is indicated for the temporary pond.

permanent pond (AM) are greater than those for the temporary pond (DW).

Fig. 3 gives the overall change in biomass productivity as growth per  $\text{m}^2$  of substrate. The values for each generation in the permanent pond are greater than for the temporary pond (Fig. 3). The partitioning of energy flow at the population level for each generation of *M. partumeium* is given in Fig. 4. These diagrams show that although the DW population is less productive it is more efficient in the conversion of assimilation into production (62% to N-R.A.) than either generation at AM (58 and 44% to N-R.A. for AM-SG and AM-FG respectively). The conversion of production (N-R.A.) to reproduction for DW (18%) is apparently less efficient than for AM-SG (35%) but essentially the same as for AM-FG (17%). The overall reproduction efficiency for the entire AM population is 26.4%

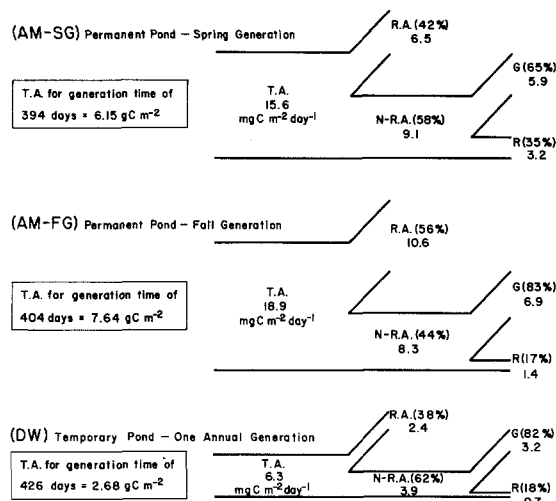


Fig. 4. Energy flow through generations of *Musculium partumeium* in permanent and temporary ponds. Respired assimilation (R.A.) and non-respired assimilation (N-R.A.) are expressed as percentages of total assimilation (T.A.). Growth (G) and reproduction (R) are further expressed as a percentage of N-R.A. Each flow diagram is drawn proportionately. The T.A. in boxes for generation time are equivalent to annual values. However, the daily rates are based on sequential generation time and cannot be multiplied by 365 to give annual rates. Each daily rate multiplied by generation time is the corresponding annual rate. See text for further explanation.

(Table 2). Fig. 4 also presents total assimilation for the lifespan (generation time) of each generation. These values are equivalent to annual rates since all components of each generation occur within a single calendar year. In other words, these components are not consecutive and each generation is represented by cohorts of two year classes for each calendar year. Therefore, calculations based on the generation time of each generation are assumed to equal annual rates. Thus, these annual assimilation rates are  $6.15$ ,  $7.64$ , and  $2.68 \text{ gC m}^{-2} \text{ a}^{-1}$  respectively for AM-SG, AM-FG, and DW (Fig. 4). Further, annual rates of R.A., N-R.A., G, and R can be estimated by multiplying each daily rate by the appropriate generation time in days. The data (Fig. 1, 3, and 4; Table 1) demonstrate greater productivity by the permanent pond population (AM) while differences in the strategy of energy flow are illustrated in some of the C:N data (Fig. 2) and by the differences in the efficiency of the conversion of assimilation into production (Fig. 4) by the populations. Energetic information is given for each gen-

eration (AM-SG, AF-FG, and DW) and is combined for the AM population in Table 2.

## Discussion

This study on energetics and the published data on these two populations (Benjamin, 1978; Burky *et al.*, 1979; Hornbach *et al.*, 1980c; Way *et al.*, 1980, 1981; Conover & Burky, 1981; Conover *et al.*, 1981; McLeod *et al.*, 1981; Buchwalder, 1983; Burky *et al.*, 1985) provide a basis for the discussion of ecological energetics and the ecological aspects of the evolution of *Musculium partumeium*. The discussion will deal with the following topics: first, energetics of growth and reproduction; second, production-to-biomass ratios; third, production efficiency and partitioning to growth and reproduction; and lastly, life-history tactics.

### Energetics of growth and reproduction

The energetics of growth at the population level is first approached in this study by comparing UP values for the two populations (Fig. 1, Table 1). The specifics of UP growth are most useful when considered in relation to the dynamics of reproduction and in this respect only the studies of Avolizi (1976), Aldridge & McMahon (1978), and Hornbach (1980) provide similar data based on carbon for freshwater clams. For each generation births are initiated as a major pulse during the last week of May for AM-SG, AM-FG, and DW or the last week of August for AM-SG. Embryos of birth size are retained for months by adults of AM-SG over the winter until the May birth period (developmental/retention periods are given in Table 2). After the initiation of the birth period(s) for all three generations, adult growth continues (Fig. 1) while new embryos initiate growth in marsupia with births taking place as the embryos reach appropriate size (Hornbach *et al.*, 1980c). Synchrony for the initiation of births and the dormancy of newborns during the summer in both populations is claimed to be an evolutionary strategy for survival in temporary (or potentially temporary) ponds and that photoperiod may provide the appropriate cue for birth, dormancy and growth (Hornbach *et al.*, 1980c; Way *et al.*, 1980; Conover *et al.*, 1981). For the temporary pond (DW), UP growth (Fig. 1) is low after birth

Table 2. Comparison of population characteristics for the freshwater clam, *Musculium partumeium*.

Characteristic	Permanent Pond Population			Temporary Pond Population
	Spring Generation AM-SG	Fall Generation AM-FG	Generations Combined AM	One Generation DW
Growth (G), $\text{mgC} \cdot \text{m}^{-2} \cdot \text{a}^{-1}$ , [kJ]	[106.4 kJ] 2324.6	[127.6 kJ] 2787.6	[234.0 kJ] 5112.2	[62.4 kJ] 1363.2
Reproduction (R), $\text{mgC} \cdot \text{m}^{-2} \cdot \text{a}^{-1}$ , [kJ]	[57.7 kJ] 1260.8	[25.9 kJ] 565.6	[83.6 kJ] 1826.4	[13.6 kJ] 298.2
Productivity = N-R.A. = G + R, $\text{mgC} \cdot \text{m}^{-2} \cdot \text{a}^{-1}$ , [kJ]	[164.1 kJ] 3585.4	[153.5 kJ] 3353.2	[317.6 kJ] 6938.6	[76.0 kJ] 1661.4
Respired Assimilation = R.A., $\text{mgC} \cdot \text{m}^{-2} \cdot \text{a}^{-1}$ , [kJ]	[117.4 kJ] 2565.1	[196.1 kJ] 4284.9	[313.5 kJ] 6850.0	[46.8 kJ] 1023.5
Total Assimilation = T.A. = R.A. + N-R.A., $\text{mgC} \cdot \text{m}^{-2} \cdot \text{a}^{-1}$ , [kJ]	[281.5 kJ] 6150.5	[349.6 kJ] 7638.1	[631.1 kJ] 13788.6	[122.9 kJ] 2684.9
Mean Standing Crop Biomass (B), $\text{mgC} \cdot \text{m}^{-2}$ , [kJ]	[16.4 kJ] 357.5	[11.4 kJ] 249.3	[27.8 kJ] 606.8	[10.6 kJ] 231.9
Annual Turnover Rate, N-R.A.:B	10.0	13.5	11.4	7.2
Turnover Time (days), $365 \div (\text{N-R.A.}:B)$	36.5	27.0	32.0	50.7
Production Efficiency, $100 \times (\text{N-R.A.} \div \text{T.A.})$	58%	44%	50.4%	62%
Reproduction Efficiency, $100 \times (\text{R} \div \text{N-R.A.})$	35%	17%	26.4%	18%
Generation Time (days) <sup>a,b</sup>	394	404	—	426
Births $\cdot \text{m}^{-2} \cdot \text{a}^{-1}$	Iteroparous 42241 – Fall 9821 – Spring	Can Be Iteroparous 26208 – Spring	— —	Semelparous 7539
Selection Ratio <sup>a</sup>	136:1 Total 29:1 Spring 107:1 Fall	38:1 Spring	—	25:1
Time to First Reproduction (days) <sup>a</sup>	76	243	—	349
Age At Survival Weighted Reproduction Peak ( $l_x m_x$ ) <sup>a</sup>	116	287	—	380
$r$ ( $\text{d}^{-1}$ ) <sup>a</sup>	0.0304	0.0115	—	0.0084
$\mu\text{gC} \cdot \text{Newborn}^{-1}$ , [J] <sup>a</sup>	[1.11 J] 24.21	[1.00 J] 21.82	—	[1.69 J] 37.02
$\mu\text{gC} \cdot \text{mg Shell}^{-1}$ , [J] <sup>c</sup>	—	—	[0.52 J] 11.32	[0.32 J] 6.97
Average Shell Length At Birth (mm) <sup>a,b</sup>	1.4 (1.2–1.8)	1.4 (1.2–1.8)	1.4 (1.2–1.8)	1.4 (1.2–1.8)
Minimum Breeding Size, Shell Length (mm) <sup>a</sup>	2.3	2.3	2.3	2.3
Minimum Adult Size For Giving Birth, Shell Length (mm) <sup>a</sup>	5.0	4.1	—	3.9
Range Of Usual Adult Size, Shell Length (mm) <sup>a,b</sup>	5.0–6.8	5.0–7.2	—	5.0–8.0
Maximum Adult Size, Shell Length (mm) <sup>b</sup>	8.8	7.6	—	10.1
Estimation of Developmental Time (months) For 0.1 mm to Minimum Birth Size of 1.2 mm <sup>a</sup>	1–2 Fall 3–9 Spring	2–6 Spring	—	1–2
Percentage of Loci Polymorphic Per Population (99% Criterion) <sup>d</sup>	—	—	0.0	22.72%
Percentage of Loci Heterozygous Per Population <sup>d</sup>	—	—	0.0	6.14%

<sup>a</sup> Hornbach, Way & Burky (1980c).<sup>b</sup> Way, Hornbach & Burky (1980).<sup>c</sup> Burky, Benjamin, Catalano & Hornbach (1979).<sup>d</sup> McLeod, Hornbach, Guttman, Way & Burky (1981).

since the clams are continuously dormant over the following dry period (summer-fall-winter) until the ponds fill in December-February. Similarly, AM-SG in the permanent pond has low UP values through the summer as if anticipating that the pond might become dry (Fig. 1). Significantly, in June low filtration rates for newborn AM-SG clams indicate dormancy while overwintering AM-FG clams of similar size are actively feeding for spring growth (Benjamin, 1978; Burky *et al.*, 1985). However, in the presence of continuous water AM-SG initiates UP growth in August. Apparently some temporary pond clams (DW) similarly grow and reproduce in the odd year that the pond remains full (McLeod *et al.*, 1981). Changes in C:N ratio have been taken as an index of varying ratios of proteins to fats and/or carbohydrates such as glycogen (higher C:N indicates greater amounts of storage compounds (Burky, 1971, 1983; Russell-Hunter & Buckley, 1983 and references therein). In general C:N decreases over dormant periods and during birth periods (Fig. 2). Lower C:N of adults as a result of birth indicates that newborns have relatively higher proportions of storage compounds. In fact, newborns at the beginning of each generation (Fig. 2) have high C:N. This probably represents stored energy for dormancy (DW, AM-SG).

#### *Production-to-biomass ratios*

Other data on corbiculacean clams (e.g. Hornbach, 1980; Teal, 1957; Gillespie, 1969; Alimov, 1970; Mann, 1971; Jónasson, 1972; Lévêque, 1973a, b; Quadri *et al.*, 1974; Aldridge & McMahon, 1978; Holopainen, 1978; Hamill *et al.*, 1979; Holopainen & Hanski, 1979; Alexander, 1982; Holopainen & Jónasson, 1983) are reported as organic carbon or can be converted to  $\text{mgC} \cdot \text{m}^{-2} \cdot \text{a}^{-1}$  by using values from Russell-Hunter *et al.* (1968) to convert dry mass to joules (or calories) to carbon. Such estimates have been set out by Burky (1983). The production estimate for *M. partumeium* of the permanent pond (AM;  $6938.6 \text{ mgC} \cdot \text{m}^{-2} \cdot \text{a}^{-1}$ ) is third only to the values for *Corbicula manilensis* ( $10\,433 \text{ mgC} \cdot \text{m}^{-2} \cdot \text{a}^{-1}$ , Aldridge & McMahon, 1978) and *Pisidium dubium* ( $7462 \text{ mgC} \cdot \text{m}^{-2} \cdot \text{a}^{-1}$ , Teal, 1957). Although production of  $1661.4 \text{ mgC} \cdot \text{m}^{-2} \cdot \text{a}^{-1}$  for *M. partumeium* in the temporary pond is considerably less, it is about equivalent to or greater than 11 other populations (values converted from Lévêque,

1973a, b; Quadri *et al.*, 1974; Hamill *et al.*, 1979; Holopainen, 1978; Jónasson, 1972; Gillespie, 1969; Holopainen & Hanski, 1979; Alimov, 1970; Avolizi, 1975). Also, the turnover ratio of annual production-to-biomass (N-R.A.:B) can be used as a relative measure of productivity (Waters, 1977; Burky, 1983; Russell-Hunter & Buckley, 1983) and turnover time (365 days divided by the turnover ratio; Russell-Hunter & Buckley, 1983) can be used comparatively as the average time a population takes to produce biomass equivalent to the average standing crop biomass. Therefore, high turnover ratios and short turnover times are relative indices of high productivity. It is implicit from the data that turnover ratios (and thus turnover time) are related to length of life (and thus mortality: Allen, 1971; Lévêque *et al.*, 1977; Russell-Hunter & Buckley, 1983) where comparisons are most significant when made intraspecifically between generations and populations. High turnover ratios (near 10, Waters, 1977) and low turnover times (10–70 days, Russell-Hunter & Buckley, 1983) can be characteristic of multivoltine zoobenthic populations. In this regard the fall generation (AM-FG) has the highest productivity (Table 2) with a turnover ratio of 13.5 and a turnover time of 27 days; the turnover ratios for the AM and DW populations are 11.4 and 7.2 respectively, with the values for the permanent pond greater than for other corbiculacean clams regardless of the number of annual generations. The generation turnover ratios for AM-SG and AM-FG are relatively high because although only a small proportion of each generation lives a full year some reproduce and die midway through the year creating the situation where the annual mean standing stock is low relative to annual production and thus there are even higher turnover ratios than one would otherwise predict.

In contrast to *M. partumeium*, turnover ratios of 0.8–1.1 for *P. casertanum* in Lake Esrom (Holopainen & Jónasson, 1983) are equivalent to turnover times of between 332 and 456 days. Holopainen & Jónasson (1983) further suggest that production for *P. casertanum* may be over estimated by as much as 20% thus indicating turnover ratios  $< 0.8$ . Intuitively this suggests a slow growing, long-lived ( $> 3$  years, see discussion in Russell-Hunter & Buckley, 1983), iteroparous organism in a stable habitat of low temperature and/or low productivity with the potential limitations of oxygen availability. In real-



ity these general types of conditions are reported by Jónasson (1972) for Lake Esrom and as expected a lifespan of 4–5 years is reported for *P. casertanum* in this habitat (Holopainen & Jónasson, 1983). Others have also reported *P. casertanum* to be long-lived (Meier-Brook, 1970; Thut, 1969; Burky *et al.*, 1981). Turnover ratios of  $< 1$  are reported for *Dreissena polymorpha* (Stańczykowska, 1976) and are probably common for unionid clams which are in general oviparous with lifespans of several years (Magnin & Stanczykowska, 1971; Russell-Hunter & Buckley, 1983). Obviously more data on turnover ratio in relation to semel- and iteroparity and unio- and multivoltinism are needed. Nonetheless, *P. casertanum* and other pisidiid clams can be important components of the productivity of zoobenthic communities (Ransom & Prophet, 1974; Healey, 1977; Thorp & Bergey, 1981). Jónasson (1972) reports data on *P. casertanum* that may represent between 6 and 7% (this is about one fourth of the non-insect zoobenthos) of the average standing crop biomass; Avolizi (1976) attributes 33% of zoobenthic productivity to *Sphaerium striatinum* (turnover ratio of 4.5) in a lake population; and Hornbach (1980) claims that a high turnover ratio of 9.2 for a stream population of *S. striatinum* is indicative of a capacity for significant contribution to secondary production. Therefore, the high turnover ratios for *M. partumeium* (11.4 and 7.2 for AM and DW respectively, Table 2) support our subjective observations that these clams constitute a major part of the zoobenthic community in the permanent (AM) and the temporary (DW) ponds.

#### *Production efficiency and partitioning to growth and reproduction*

The relative efficiency of the conversion of total assimilation energy to production (N-R.A.) can be expressed as a percentage (Fig. 4). Comparatively the value for the temporary pond (DW, 62% vs AM, 50.4%) is highest; however, the AM-SG value (58%) is close to that for DW. Also the difference between the generations of the permanent pond (58 and 44%) must in part reflect the relationship of adult growth to reproduction as discussed above. Production efficiencies of other corbiculacean clams range from 10% for *Corbicula africana* (Lévêque, 1973a, b) and *Musculium lacustre* (Alexander, 1982) to 74% for *Pisidium conventus* (Holo-

painen & Hanski, 1979). However, the overall population efficiencies for *M. partumeium* (Table 2) are greater than those of most other corbiculacean populations. Further, the ratio of the allocation of production (N-R.A.) between growth (G: N-R.A.) and reproduction (R:N-R.A.) can provide a meaningful comparative index of reproductive effort or efficiency (Tinkle & Hadley, 1975; Browne & Russell-Hunter, 1978, Table 2).

Browne & Russell-Hunter (1978) compared values of R:N-R.A. for a variety of freshwater and marine molluscs and hypothesized that viviparous species have a lower reproductive efficiency (mean for two species = 5.25%) than oviparous species (mean for 14 species = 24.24%). The reproductive efficiency for *S. striatinum* of 4.3% (Hornbach, 1980; Hornbach *et al.*, 1984) further supports this idea. However, reproductive efficiencies (R:N-R.A.) for *M. partumeium* (viviparous, Table 2) are 35, 17, and 18% for AM-SG, AM-FG, and DW respectively. These values are in general equivalent to the average ratio for oviparous species (24.24) with the 35% value for AM-SG being greater than all but four of the 23 values reported for oviparous molluscs by Browne & Russell-Hunter (1978). Even within the Corbiculacea values for the oviparous *Corbicula manilensis* range from 13.5 to 24.4% (Aldridge & McMahon, 1978; Browne & Russell-Hunter, 1978) with values for viviparous *M. partumeium* (35, 17, 18%, Table 2), *M. lacustre* (19.5%, Alexander, 1982), *P. conventus* (25%, Holopainen & Hanski, 1979), and *P. casertanum* (14%, Holopainen, 1978) being greater or comparable. The values for corbiculacean clams do not support the ideas of Browne and Russell-Hunter (1978) on reproductive efficiency in relation to oviparity and viviparity. Further, does one define *M. partumeium* as an iteroparous species since one generation (AM-SG) reproduces twice or are comparisons best made between iteroparous and semelparous generations? Obviously, treating *M. partumeium* as an iteroparous species or making comparisons of reproductive effort by generation (DW and AM-FG semelparous, AM-SG iteroparous) does not support the theoretical contention that reproductive effort is greatest in semelparous species (Williams, 1966a, b; Browne & Russell-Hunter, 1978). This lack of concordance does not necessarily negate the theoretical considerations but underlines the inherent dangers of generalization. *Musculium partumeium* probably evolved in

the temporary pond habitat with viviparity functioning as a major characteristic in the evolution of its life-history pattern.

#### *Life-history tactics*

Predictions of *r*- and *K*-selection theory (Pianka, 1970) are not supported by the published data on *M. partumeium* (Hornbach *et al.*, 1980c; Way *et al.*, 1980; McLeod *et al.*, 1981; Table 2) if the temporary pond is considered a variable habitat suitable for *r*-strategy. However, according to Stearns (1976, 1977) the predictions of *r*- and *K*-selection theory would be reversed (assessed by a stochastic model: bet-hedging) if juvenile mortality is more variable than adult mortality in the unpredictable habitat (e.g. 'temporary pond'). In this regard the majority of the population characteristics of the temporary pond population can be classified as being *K* in nature when compared to the permanent pond generations (Table 2). This led us in earlier publications (Hornbach *et al.*, 1980c; Way *et al.*, 1980; McLeod *et al.*, 1981) to suggest that the evolution of life-history tactics in *M. partumeium* follows a bet-hedging theory. Interestingly, Mackie *et al.* (1978) claims that *r*- and *K*-selection theory applies to *M. securis* from temporary ('*r*') and permanent ('*K*') habitats, but McKee & Mackie (1981) now believe that bet-hedging applies to populations of both *M. securis* and *Sphaerium occidentale*. Further, if one considers members of the genus *Pisidium*, such a theoretical 'reversal' of *r*- and *K*-selection theory cannot be accounted for by variable habitat alone. Two species of *Pisidium* (*P. conventus*, Holopainen & Hanski, 1979; *P. casertanum*, Holopainen, 1978) have high reproductive efforts. Yet, they can be characterized as being from habitats which are stable and variable respectively. Also, *P. casertanum* has a ubiquitous and cosmopolitan distribution with a high tolerance of habitat variability (e.g. Danneel & Hinz, 1974) suggesting that extensive comparative studies could yield a full range of strategies for this species alone.

Recently, Sterns (1980) questioned the application of theories on life-history tactic at the intraspecific level and raised many points about the influence of developmental, physiological, and genetic characteristics. However, Calow (1983) points out that there is a need for more information on population characteristics and physiological adaptations

for intraspecific comparisons of distinct populations. The data of this study (on distinct populations) suggests that *Musculium partumeium* is well adapted for life in ephemeral habitats. Summer dormancy may be fixed at the species level since others have also reported summer dormancy in both ephemeral and permanent habitats (Thomas, 1963, 1965; Hornbach *et al.*, 1980c; Way *et al.*, 1980 for *M. partumeium*; Mackie *et al.*, 1976a, b for *M. securis* and Mitropolskii, 1965; Alexander, 1982 for *M. lacustre*). One could also argue that the relative regularity of annual drying represents a 'stable' climatic/biological set of conditions over a requisite period of geological time. Thus neither theory appears to apply to *M. partumeium* and is emphasized by the inconsistency of life-history traits given in Table 2. In the permanent pond situation, *M. partumeium* reproduces a second time in the fall increasing population productivity. In the odd year that the temporary pond remains full, these clams respond by committing 23% of the population to growth and reproduction while the rest of the clams remain dormant. Although the permanent and temporary pond populations have some similarities in life-history pattern (e.g. summer dormancy, Way *et al.*, 1980; Hornbach *et al.*, 1980c) the permanent pond is genetically less variable (McLeod *et al.*, 1981) and energetically distinct (Table 2). This emphasizes the potential importance of short term selection (permanent pond conditions have existed about 25 years) in the face of genetic input due to passive dispersal (Rees, 1965; Mackie, 1979) and inbreeding due to self-fertilization (Hornbach *et al.*, 1980a, b; McLeod *et al.*, 1981). In both habitats *M. partumeium* is adapted by balancing the temporal sequence of the variable seasonal availability of water and life-history sequence with appropriate commitments (tactics) to population characteristics (Table 2): growth rate, developmental rate and newborn size; reproductive size and timing; fecundity, itero- or semelparity, voltinism, *r* value and genetics; as well as productivity, turnover ratios and efficiency of growth and reproduction.

#### **Summary**

1) Spring recruits have high C:N ratios. This suggests that they have a high proportion of fats and/or carbohydrates to sustain them during the dormant period which begins at birth.

2) The productivity of *Musculium partumeium* in the permanent pond ( $6938.6 \text{ mgC} \cdot \text{m}^{-2} \cdot \text{a}^{-1}$ ) is among the highest values for corbiculacean clams. The turnover ratios (N-R.A.:B) are 11.4 and 7.2 for the permanent and temporary pond populations respectively with the value for the permanent pond population being greater than for other corbiculacean clams.

3) Production efficiencies [ $100 \times (\text{N-R.A.} \div \text{T.A.})$ ] of 50.4% and 62% are higher than those of most other corbiculacean clams.

4) Reproduction efficiencies are theoretically higher for oviparous than for viviparous species. Reproduction efficiencies [ $100 \times (\text{R} \div \text{N-R.A.})$ ] for *M. partumeium* (a viviparous species) are high and equivalent to or larger than values for most oviparous molluscs. Also, reproductive effort is theoretically greatest in semelparous species. However, one can best classify *M. partumeium* as an iteroparous species with a higher reproductive effort.

5) The life-history characteristics of *M. partumeium* do not completely fit any of the theories on life-history tactic. However, *M. partumeium* in both temporary and permanent pond habitats is adapted by balancing the temporal sequence of the variable seasonal availability of water and life-history sequences with the appropriate commitments (tactics).

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