Reproductive Effort in Molluscs

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Summary. A survey of the available molluscan literature shows that reproductive effort is higher in semelparous species (29.90%) than in iteroparous species (18.21%), and that in iteroparous species reproductive effort increases with successive breeding seasons. Oviparous species were found to divert considerably more into reproduction than viviparous species, with 24.24% and 5.25% channeled respectively.

Since the classic review of the significance of life-cycle pattern by Lamont Cole (1954), there has been continued interest in, and investigations of, the ecological and evolutionary implications of different levels and patterns of numerical fecundity. Markedly fewer studies have been concerned with the comparative bioenergetics of fecundity. Williams (1966a, b) has stated that an increase in reproductive effort should accompany increases in female age within a species. He reasons that as each individual animal ages, there is a decrease in future reproductive costs incurred by high reproductive effort at the current age. Similarly, a species with a brief life-span with only one opportunity to reproduce should exert a high reproductive effort. Conversely, in longer-lived species, selection would be expected to favor those individuals that expanded their reproductive effort to cover a long time period rather than attempting high reproductive production early in life. Like all hypotheses and models based on fitness criteria, appropriate data for testing need to be developed and expressed in suitable and consistent terms to allow appropriate comparisons of the "trade-offs" within individual and population energy budgets.

As Tinkle (1969) has pointed out, even in vertebrate studies, there has been an absence of satisfactory direct measurements of reproductive effort. The most commonly used measurements have been clutch size and clutch weight to body weight ratio (Lack, 1947). However, both of these measurements have been criticized for high within-individual and between-individual variation.

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Table 1. Reproductive effort for four semelparous molluscan species

Species name	AF life-span in months	$\overline{X}$ young $\overline{AF}$	$\overline{X}$ μgC young	$\overline{X}$ μgC $\overline{AF}$	$C_R:C_{AF}$	Annual N-RA to rep. (%)	Notes	Reference
Lymnaea palustris	12	203	5.0	6,000	0.169	15	F,h[a]	Hunter (1975)
Ferrissia rivularis	4	34.8	6.4	200	1.114	30	F,h	Burky (1971)
	12	8.4	3.6	200	0.151	11		
$\overline{X}$ for *F. rivularis*		21.6	5.0	200	0.540	20.5		
Helisoma trivolis	12	1962	18.3	14,770	2.431	69	F,h	Eversole (1974)
Bithynia tentaculata	18	200	39.4	4,470	1.763	19	F,d	Mattice (1972)
Laevapex fuscus	6	70.1	4.31	524	0.576	37	F,h	McMahon (1975)
	12	27.4	4.31	671	0.176	15		
$\overline{X}$ for *L. fuscus*		48.8	4.31	598	0.376	26		

M = Marine, F-Freshwater; h = Hemaphroditic, d = Dioecious

Species data averaged from more than one population

    In one of the few investigations to date involving bioenergetic assessment, Tinkle and Hadley (1975), working with lizards, calculated the proportion of the energy budget that is channeled into reproduction. Proportional allocation of non-respired, assimilated energy provides one meaningful measure of reproductive effort. Over the last twelve years, there have been fairly extensive efforts (largely by our associates, see for review: Russell-Hunter, 1978) to compile "actuarial bioenergetics" in natural populations of molluscs (particularly in fresh waters).

    The present paper is an attempt to summarize the molluscan literature where data are available for the amount of effort that is channeled into reproduction, not only to compare reproductive effort between species but also to compare species-groups which share common reproductive characteristics, such as viviparity or multiple breeding seasons. Reproductive effort is estimated by two different parameters: first, the percentage of non-respired assimilation [or N-R.A., which approximates for the modal individual the *net* productivity of the population (see Browne, 1978; Russell-Hunter, 1978; and elsewhere)] that is diverted into reproduction annually, and secondly, the ratio between the amount of carbon that is channeled into reproduction C_R and the amount of carbon contained in the average adult female C_{AF}. All data is taken directly from the original papers. In some cases, $C_R:C_{AF}$ is not available. We are aware of the implicit weaknesses of $C_R:C_{AF}$ as an estimate of comparative reproductive "effort" since it involves a *rate* output or productivity for the reproductive output (carbon per time) and a "standing crop" carbon estimate for the average adult female. Despite this, we feel that both estimates have value in comparing reproductive effort between species, between populations and between generations.

    Estimates of reproductive effort are presented for semelparous molluscan species in Table 1 and for iteroparous molluscan species in Table 2. The total of sixteen species include both marine and freshwater gestropods and bivalves. Both C_R and C_{AF} are quoted in μg of carbon. Russell-Hunter et al. (1968)

Table 2. Reproductive effort for nine iteroparous molluscan species

Species name	Breeding season	AF life-span in months	$\bar{X}$ young $\overline{AF}$	$\bar{X}$ μgC young	$\bar{X}$ μgC $\overline{AF}$	$C_R:C_{AF}$	Annual N-RA to rep. (%)	Notes	Reference
Viviparus georgianus	First	12	4.7	650	35,920	0.085	2.9	F,d[a]	Browne (1978)
	Second	24	12.3	650	97,460	0.082	4.2		
	Third Annual	36	12.0	650	120,540	0.065	6.3		
	Average	36	9.67	650	84,640	0.074	4.5		
Corbicula manilensis	First	6	16,011	1.4	54.402	0.412	13.5	F,h[a]	Aldridge and McMahon (1978)
	Second Annual	12	31,244	1.4	222,338	0.197	24.4		
	Average	12	23,628	1.4	138,370	0.239	15.3		
Patinopecten yessoensis	First	12					3	M,h	Fuji and Hashizume (1974)
	Second	24					25		
	Third Annual	36					61		
	Average	36					29.7		
Sphaerium striatinum	Annual Average	26	6	1,000	21,000	0.286	6	F,h	Avolizi (1976)
Crassostrea virginica	Annual Average						16.2	M,h	Dame (1976)
Tegula funefralis	Annual Average						15.1	M,h	Fraser (1967)
Fissurella barbadensis	Annual Average						9.6	M,h	Hughes (1971a)
Modiolus demissus	Annual Average						16.8	M,h	Kuenzler (1961)
Nerita tesselata versicolor peloronta	Annual Average						18.6	M,h[a]	Hughes (1971b)
Venus mercenaria	Annual Average						22.5	M,h	Ansell and Lander (1967)
Melampus bidentatus	Annual Average		33,150				46	M,h	Apley (1970)

estimate that in molluscs, 1 g Carbon $= 10.94$ Cal, although there is some variation depending upon the amount of stored lipids.

When semelparous species (single breeding in lifetime) are compared to iteroparous species (multiple breeding), it is apparent that, on the average, semelparous species divert significantly more of their annual NRA to reproduction than iteroparous species, with 29.90% and 18.21% channeled respectively. This is paralleled, where the data are available, in the difference between the two groups in the $C_R:C_{AF}$ ratio. This average ratio in semelparous species is 1.06 but only 0.20 in iteroparous species.

For three iteroparous species, data are available for estimating reproductive effort for discrete breeding seasons as well as for annual lifetime estimates. For these iteroparous species, the percentage of annual NRA devoted to reproduction increases with each successive breeding season. When the data for the three species are averaged, the percentage of annual N-R.A. devoted to reproduction increases in $1:2:4$ ratio for the first, second, and third breeding seasons, respectively. This increase is not shown in the $C_R:C_{AF}$ ratio, in which the energy content of the modal female for successive generations does not reflect the corresponding energy investment in continued female growth (which decreases in the 3rd year).

The two viviparous species, *V. georgianus* and *S. striatinum*, show the lowest values for the percentage of annual N-R.A devoted to reproduction, with a mean of 5.25% versus 24.24% for the fourteen remaining oviparous species. Viviparous species also show much lower $C_R:C_{AF}$ ratios (0.18 versus 0.92). At least part of this lower expenditure is probably attributable to the maintenance costs absorbed by viviparous females, which lowers the estimates of net reproductive effort. Tinkle and Hadley (1975) found similar results for a viviparous lizard species.

In conclusion, the theoretical considerations of Williams concerning reproductive effort seem to be justified for this group of molluscan species for which we have suitable data. Reproductive effort *within* a species increases with age and with successive breeding seasons, and reproductive effort is higher in semelparous species than in iteroparous species.

References

Aldridge, D.W., McMahon, R.F.: Growth, fecundity, and bioenergetics in a natural population of the Asiatic freshwater clam, *Corbicula manilensis.* Philippi from North Central Texas. J. Mulloscan Studies (in press, 1978)

Apley, M.L.: Field studies on life history, gonadal cycle and reproductive periodicity in *Melampus bidentatus* (Pulmonata: Ellobiidae). Malacologia **10**, 381–397 (1970)

Ansell, A.D., Lander, K.F.: Studies on the hard-shell clam, *Venus mercenaria*, in British waters. III. Further observations on the seasonal biochemical cycle and on spawning. J. Appl. Ecol. **4**, 425–435 (1967)

Avolizi, R.J.: Biomass turnover in populations of viviparous Sphaeriid clams: comparisons of growth, fecundity, mortality and biomass production. Hydrobiologia **51**, 163–180 (1976)

Browne, R.A.: Comparisons of growth, mortality, fecundity, biomass and productivity rates in four lake populations of the prosobranch snail, *Viviparus georgianus*. Ecology (in press, 1978)

Burky, A.J.: Biomass turnover, respiration, and interpopulations variation in the stream limpet, *Ferrissia rivularis* (Say). Ecol. Monogr. **51**, 235–251 (1971)

Cole, L.C.: The population consequences of life history phenomena. Q. Rev. Biol. **29**, 103–137 (1954)

Dame, R.F.: Energy flow in an intertidal oyster population. Estuar. Coastal Mar. Sci. **4**, 243–253 (1976)

Eversole, A.G.: Fecundity in the snail *Helisoma trivolis*: experimental, bioenergetic and field studies. Ph.D. Dissertation, Syracuse University. Diss. Abst., 35, 5716–5717-B; order no. 75–10, 538 (1974)

Fraser, T.H.: Contributions to the biology of *Tagelus divisus* in Biscayne Bay, Florida. Bull. Mar. Sci. **17**, 111–132 (1967)

Fuji, A., Hashizume, M.: Energy budget for a Japanese common scallop, *Patinopecten yessoensis* (Jay) in Matsu Bay. Bull. of the Faculty of Fisheries, Hokkaido Univ. **25**, 7–19 (1974)

Hughes, R.N.: Ecological energetics of the keyhole limpet, *Fissurella barbadensis* Gmelin. J. Exptl. Mar. Biol. Ecol. **6**, 167–178 (1971 a)

Hughes, R.N.: Ecological energetics of *Nerita* populations in Barbados, West Indies. Mar. Biol. **11**, 12–22 (1971 b)

Hunter, R.D.: Growth, fecundity, and bioenergetics in three populations of *Lymnaea paulstris*. Ecology **56**, 50–63 (1975)

Kuenzler, E.J.: Structure and energy flow of a mussel population in a Georgia salt marsh. Limnol. Oceanogr. **6**, 191–204 (1961)

Lack, D.: The significance of clutch size. Ibis **89**, 302–352 (1947)

Mattice, J.S.: Production of a natural population of *Bithynia tentaculata* L. Ekol. Polska **20**, 525–539 (1972)

McMahon, R.F.: Growth, reproduction, and bioenergetic variation in three natural populations of a freshwater limpet *Laevapex fuscus*. Proc. Malacol. Soc. Lond. **42**, 331–351 (1975)

Russell-Hunter, W.D.: Ecology of freshwater pulmonates. In: Pulmonates, Vol. 2. Systematics, evolution and ecology (V. Fretter, J. Peak, eds.). New York: Academic Press 1978

Russell-Hunter, W.D., Meadows, R.T., Apley, M.L., Burky, A.J.: On the use of wet-oxidation method for estimates of total organic carbon in mollusc growth studies. Proc. Malacol. Soc. Lond. **38**, 1–11 (1968)

Tinkle, D.W.: The concept of reproductive effort and its relation to the evolution of life histories of lizards. Am. Nat. **103**, 501–516 (1969)

Tinkle, D.W., Hadley, N.F.: Lizard reproductive effort: Calorific estimates and comments on its evolution. Ecology **56**, 427–434 (1975)

Williams, G.C.: Natural selection, the costs of reproduction, and a refinement of Lack's principle. Am. Nat. **100**, 687–792 (1966 a)

Williams, G.C.: Adaptation and natural selection, 307 pp. Princeton, N.J.: Princeton Univ. Press 1966 b