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EVALUATION OF REPRODUCTIVE EFFORT IN BIVALVE MOLLUSCS

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ABSTRACT

The specific difficulties in calculating the reproductive effort in Bivalves are examined. The reproductive effort of an animal is placed in the context of its general metabolism, using an original diagram. Some methods to calculate the reproductive effort and the major rates expressing it are discussed.

INTRODUCTION

Quantitative growth and reproduction data allow (1) analysis of the reproductive cycle, (2) evaluation of fecundity (or fertility), and (3) evaluation of reproductive energy cost. The present paper deals with this last topic.

BIOENERGETICAL CONSIDERATIONS IN BIVALVES

Problems in the evaluation of reproductive effort in Bivalves

The evaluation of reproductive effort (*i.e.* reproductive energy expenditure) may pose certain difficulties in Bivalves for the following reasons:

— the gonad forms an integral part of the visceral mass. Occasionally, when it emerges from the visceral mass, an approximative separation may be made (*e.g.* Pectinidae, Mytilidae).

— the gonad may frequently contain a reserve tissue alternating with the germinal tissue (Lubet *et al.*, 1976). This may decrease the variations in gonad dry weight, and thus of the gonado-somatic index. There are, however some exceptions (*e.g.* Pectinidae).

— spawning is not always complete. More or less abundant residual gametes may remain, which then act as somatic reserves following cytolysis.

— spawning may occur several times per year with variable intensity depending on environmental conditions.

— spawning is not always synchronous in a given population. This makes it difficult to use gonado-somatic index variations to evaluate the number and intensity of spawnings.

Scheme of non-respiratory energetic balance of a Bivalve

The following diagram (Fig. 1) places the reproductive effort in the context of the general metabolism, and expresses schematically some of the remarks made in the first paragraph. To simplify the problem, non-respiratory energy only is considered in this scheme.

Stippled areas: The area ABC represents the energetic value of the somatic tissues of an individual of the class n; the area DEF represents the growth of these tissues in one year. Thus, the total ABC + DEF represents the energetic value of the soma of an individual of the class n + 1. A = shell protein, D = corresponding annual growth, B = soft parts of the animal, E = coresponding annual growth, C = gonad somatic tissue, F = corresponding annual growth.

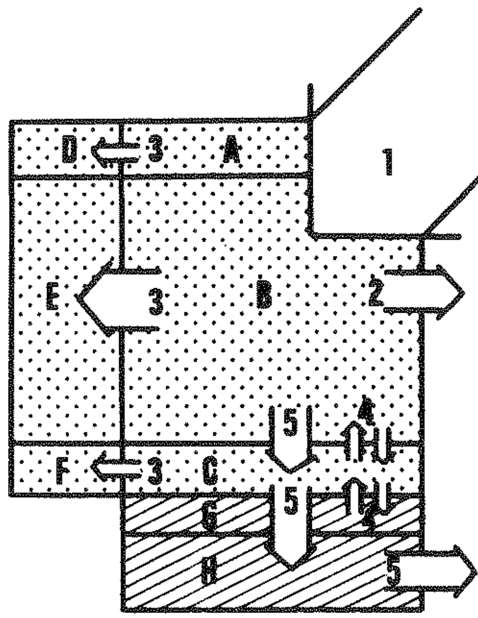

FIG. 1. Diagram of non-respiratory energetic balance of a Bivalve. For explanations see text.

Shaded areas: The area GH represents the energetic value of the germinal tissues (*i.e.* gametes) formed in one year by an individual passing from class n to class n + 1. G = gametes formed but not released (utilized as somatic reserve following cytolysis), H = total gametes released during a year.

Arrows: These represent the energy transfers (except that of respiration) within the animal, in a one year period. 1 = assimilated non-respiratory energy, 2 = energy lost through secretion, dead tissues, etc. . . , 3 = energy used for somatic growth, 4 = energy used for the formation of gametes non released, reutilized as somatic reserves, 5 = energy used for the formation of gametes released.

In Bivalves (as in aquatic microphages) the transfers 1 and 2 are difficult to measure. Hence, only the transfers 3, 4 and 5 are commonly evaluated.

This scheme can be applied to taxonomic groups other than Bivalves, with slight eventual modifications.

METHODS USED FOR THE EVALUATION OF THE REPRODUCTIVE EFFORT

Quantitative data from population samples

The sample individuals are sacrificed. The shell is measured and the organs weighed including the gonad. In order for such data to be statistically valuable, a given population should be studied for at least one year, with sampling intervals not exceeding one month. If the population structure is known, the data may be treated class by class. If not, linear regressions on individual sizes may be performed, or a standard animal may be chosen as a reference point (Ansell & *al.*, 1964).

As previously mentioned in the first paragraph, the variation of the gonado-somatic index, deduced from data from population samplings, does not generally allow the evaluation of the energy used per spawning or even the number of spawnings. Other methods are thus required.

Quantitative data from experiments

The most common experimental method to evaluate the quantity of gametes released, for all Bivalves, is by inducing spawning. The weight of the released gametes can then be measured following filtration on pre-weighed filters (Wilde & Berghuis, 1978). In females, the weight of the gametes can be calculated from the number of ovocytes released.

To evaluate the number of spawnings in a year, individual animals of a sample in a given population may be tagged. The tagged individuals are examined periodically either by direct observation of the gonad if possible (*e.g.* Pectinidae, Shafee & Lucas, 1980) or by stimulation to obtain the release of gametes.

Histological data

Histological data reveal the state of the gonad and give additional information necessary to interpret the data from samplings or from experiments.

Histological observations themselves may, in certain cases, become quantitative data: in such cases, a scale based on measures or countings could be employed. For example (1) Number of ovocytes released with respect to the density of ovocytes in the gonad, before and after release; and (2) Relative area of the gametic tissue on a slide of gonad, with respect to somatic tissue: the proportion thus obtained could be used to calculate the respective weight of gametic and somatic parts of the gonad.

FORMULATION OF REPRODUCTIVE EFFORT

Use of energy units

The data obtained by the previous described methods are generally expressed as dry weights. It is advisable to convert them into energy units, to facilitate comparison with other species. They may be expressed in calories (following the traditional use) or in joules (1 cal = 4,18 joules).

Calorific values may be measured by direct calorimetry for a sample of individuals or calculated by using calorific equivalents of the biochemical components of the tissue (Brody, 1945; Crisp, 1971, Giese, 1967). The latter method can be used to verify the results obtained through bomb calorimetry (Beukema & De Bruin, 1979). Calorific value of the same part of animals in a given population may vary from year to year, *e.g.*: soft parts of *Chlamys varia,* in Bay of Brest, 1976: 5, 18; 1977: 5, 03 (Shafee, 1980).

Expressing the reproductive effort

Reproductive effort may be expressed by calculating either relative rates or absolute rates, which should be calculated separately for each sex.

Relative rates: The following two relative rates are classically used:

R1 = annual cost of reproduction/annual growth of somatic tissue

R2 = annual cost of reproduction/somatic tissue of the whole animal (Williams, 1966).

R1 or R2 are frequently calculated from dry weights or eventually from carbon weight (Browne & Russel-Hunter, 1978); however, the use of calorimetric units is preferred. These rates may be expressed either as ratios or as percentages. Some values of R1 and R2 are given in Table 1.

R1 is a logical comparison of the energy utilized for reproduction and that used for somatic growth during one year.

R2 expressed the reproductive effort of an animal of a given weight. It should be remembered that the reproductive effort covers one year, and during this period the animal belonging to class n passes into the class n + 1. This poses the problem of which should be taken as a reference: the animal of class n, or class n + 1 or the average of the two. The answer may differ among authors and, therefore, one must be careful when comparing this rate.

Several other relative rates may be calculated from a known population energy flow; for example, the ratio of annual energy of reproduction to that of assimilation or that of ingestion. However, these

TABLE 1. Reproductive effort values in some Bivalve populations. (1) Fuji & Hashizume, 1974; (2) Shafee, 1980; (3) Lucas & *al.*, 1978; (4) Rhodhouse, 1979; (5) Dame, 1976; (6) Deslous-Paoli & Heral, 1980; (7) Hibbert, 1977.

Species	Population	Period	R1 %	R2 %	R100 (Kcal/year)
Patinopecten yessoensis (1)	Mutsu Class 1–3	1970–71	3–61*		
Chlamys varia (2)	Brest Class 1–4 ♀	1976	3–57	3–7	
Chlamys varia (2)	Brest Class 1–4 ♀	1977	7–78	6–19	
Chlamys opercularis (3)	Brest Class 1–4 ♂ ♀	1978		12–21	154
Chlamys tehuelcha (3)	Patagonia Class 2–3 ♂ ♀	1977		11–16	208
Mytilus edulis (3)	Brest Class 2 ♂	1977–78		217	855
Mytilus edulis (3)	Brest Class 2 ♀	1977–78		174	
Mytilus platensis (3)	Patagonia Class 2 ♀	1977		22	70
Ostrea edulis (4)	Beaulieu GB total population	1974–75	85*		
Ostrea edulis (3)	Brest ♀	1978		13	292
Ostrea puelchana (3)	Patagonia ♀	1977–78		56	289
Crassostrea virginica (5)	S. Carolina total population	1971–72	19*		
Crassostrea gigas (6)	Oleron Class 2	1979–80		63	
	Marennes Class 2	1979–80		53	
Mercenaria mercenaria (7)	Southampton GB total population	1977	84*		

*Calculated from the data in publication.

rates are likely to be more approximate than either R1 or R2, since the estimation of ingested or assimilated products is quite problematic in Bivalves.

Absolute rates: These express the quantity of energy used for reproduction during one year.

Rst. is the total energy used per year for reproduction by a standard animal.

R100 is the total energy used per year for reproduction by 100 mature individuals representative of a given population (Lucas *et al.,* 1978). Some values of R100 are given in Table 1.

CONCLUSION

The evaluation of reproductive effort in Bivalve populations is difficult due to the anatomy and physiology of the gonad. Consequently the data obtained by different methods may only be considered as approximate results. In addition, the magnitude of the variations observed between populations of the same species, and between the different classes of a population, show that interspecific comparisons must be interpreted with great caution.

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