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Energy distribution between growth and reproduction in Asellus aquaticus L. Sexual dimorphism

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SEZIONE III

(Botanica, zoologia, fisiologia e patologia)

Ecologia. — *Energy distribution between growth and reproduction in* Asellus aquaticus L. *Sexual dimorphism.* Nota di LUCIANA MIGLIORE, FLORA VALENTINO e GIOVANNA VITAGLIANO TADINI, presentata (*) dal Socio G. MONTALENTI.

RIASSUNTO. — L'entità del dimorfismo sessuale della mole corporea in *Asellus aquaticus* non è geneticamente determinata ma dipende dalla spesa energetica delle femmine per la riproduzione e le cure parentali (energia sottratta alla crescita) ed alla minore quantità di cibo ingerito a causa della maggiore frequenza di mute. Prova di ciò è la significativa differenza della distribuzione delle dimensioni in organismi con un diverso passato fisiologico, come la popolazione di Settembre (che ha alle spalle un semestre di attività riproduttiva) e la popolazione di Marzo (con un semestre di diapausa riproduttiva).

INTRODUCTION

In most animal species there is sexual dimorphism-shape, size, colour and particular organs or structures distinguish the sexes. Body size is one of the characters mostly affected by sexual dimorphism. In the gonochoric species body size shows significant differences and usually the heterogametic sex is the largest (D'Ancona, 1975).

Even though genetically determined, body size is one of the most plastic characters, being evidently affected by competition, starvation, temperature, etc. To these factors we can add the degree of homozygosity, as reported by Wassersug *et al.* (1979) and for Crustaceans, the frequency of ecdysis (Strong and Daborn, 1980) which temporarily inhibits food intake.

In a paper on Mustelids Moors (1980) reports two theories on sexual dimorphism. According to the first, dimorphism is a strategy to avoid intraspecific competition, in that it permits the organisms to divide the trophic niche (Yurgenson, 1947; Brown and Lasiewski, 1972; Shubin and Shubin, 1975). The second theory considers sexual dimorphism the result of different selective pressures: the smaller body size would permit the females to metabolize to a lesser extent and so devote a greater amount of energy to reproduction (Moors, 1974; Powell, 1979). The author concludes that the sexual dimorphism of Mustelids has been positively selected in relation to the reproductive strategy. This selection has been subsequently reinforced by the division of the trophic niche.

(*) Nella seduta del 14 marzo 1981.

The species *Asellus aquaticus* (L.) (*A.a.*) (freshwater Crust. Isop.) is gonochoric and only slightly polymorphic for pigmentation, eye colour and shape and size of the appendices, etc. In this species the primary sexual dimorphism in males is related to the structure of pleopods I and II. In females it is related to that of the second pair of pleopods and the first four epipodites of the thoracic limbs which, in the functional stage, form an incubator pouch in which the embryos develop. The secondary sexual dimorphism relative to body size is particularly accentuated in *Asellus*: on the average the male is larger than the female (Racovitza, 1919), even if large females and small males are found with low frequency (Vitagliano Tadini and Valentino, 1964).

Attempts at selection of minus and plus variants, up to F_3, gave negative results, showing that the genetic component of body size is small (Vitagliano Tadini and Valentino, 1964). The factors negatively influencing growth are: short photoperiod (Vitagliano Tadini and Vitagliano, 1965), competition (Fano *et al.*, 1974), high degree of homozygosity (Vitagliano Tadini and Valentino, 1964) and obviously, the amount of food available, in that *Asellus*, like other invertebrates and some fishes, reptiles, amphibians and plants, experiences "indeterminate growth" (Ricklefs, 1976) with an always smaller increase for the whole life span (Migliore *et al.*, 1980).

The aim of this study was to investigate whether the sexual dimorphism of body size in *Asellus* is genetically determined or is caused by the greater amount of energy expended by the female in reproduction. *Asellus aquaticus* has been used because the female (i) lays numerous eggs rich in yolk; (ii) undergoes a series of reproductive moults and (iii) cares for the offspring (for about 25 days, that is the period of development of the embryos in the brood pouch).

MATERIAL AND METHODS

In *A.a.*, as in all the other Crustaceans, one factor determining body size is the moult cycle, in that the growth moults are necessary for increase in size. The relationship between moult and growth is indirect: Needham (1964), working on *A.a.*, has shown that during moulting there is no cell proliferation but only an increase in volume caused by a relative increase in the amount of haemolymph.

Besides the growth moult (GM) the females of *A.a.* effect two typical reproduction moults: the birth moult (BM) and the intermediate moult (IM) (Unwin, 1920). The IM does not modify the size of epipodites of the thoracic limb (called *oostegytes*) which in the period of sexual inactivity are small and non functional. The BM instead prepares the female for reproduction: the genital orifices dilate to permit fertilization and large oostegytes, which form the pouch, develop. The pouch is a temporary sexual character. In fact after deposition of larvae the pouch is discarded and the genital orifices closed by IM. This moult is very important because it permits the females to effect subsequent GM and even BM.

The moults are regulated by a complex neuroendocrine mechanism (Balesdent–Marquet, 1955) but their cycle is strictly related to the period of reproductive diapause (Vitagliano Tadini *et al.*, 1978; Tadini Vitagliano *et al.*, 1981) and social conditions of the females (Valentino *et al.*, 1980).

For these experiments on sexual dimorphism samples of *A.a.* from Utrecht (Holland) were used. This strain is well suited to a study of this kind in that it has: *a*) a reproductive diapause related to the "ecological winter" (1) induced by photoperiod (Vitagliano Tadini and Valentino, 1969; Vitagliano *et al.*, 1978; Tadini Vitagliano *et al.*, 1982); *b*) a longevity (about 12 months) such as to permit the succession of a period of reproductive activity, a period of diapause and a second period of reproductive activity; *c*) a speed of development depending on photoperiod and temperature (Vitagliano Tadini, 1974).

Two samples of animals were sent from Holland: one in September 1979 and one in March 1980. The animals were flown immediately after sampling and on arrival were placed in 30 cm diameter dishes (15 individuals per dish) in mesosaprobic β water at constant temperature (16 °C). The water was filtered through Whatmann filter paper (in order to remove larger predators but not fungi which constitute the natural food of *Asellus* (Rossi and Vitagliano, 1978). The individuals were immediately measured (within 24 h) to avoid loss of some of the oldest (i. e. the largest) by stress. There was about 2% mortality on arrival. Only mating individuals were removed and measured to be sure that in the March batch these were really organisms that had finished the reproductive diapause. On the whole 400 individuals were measured, 200 in the September batch and 200 in the March batch. The September batch contained a mixed population: undifferentiated animals born in September and adults born in April, May, June, July and August. The March batch did not present undifferentiated individuals but only adults (the population being in reproductive diapause) and was basically made up of individuals born in June, July, August and September and some exceptional survivors born in April and May. These two samples are characteristic of the pre– and post–diapause period respectively. In fact, in the Dutch Aselli reproductive diapause lasts from October to March. During this period females suspend BM and IM while GM occurs regularly for the whole life span (Vitagliano Tadini and Valentino, 1969).

The organisms were measured under the stereomicroscope with an appropriate mm rule. The length measured is from the first cephalic metamere (antennae excluded) to the end of the telson (fork excluded).

RESULTS

The results of this study are reported in Figure 1 and Table I. Fig. 1 shows the percent distribution of the dimensions of males and females in two different

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(1) The duration of the cold period.

periods of the year, September and March. The distributions have been grouped according to sex to show the effect of the period of reproductive diapause on the females.

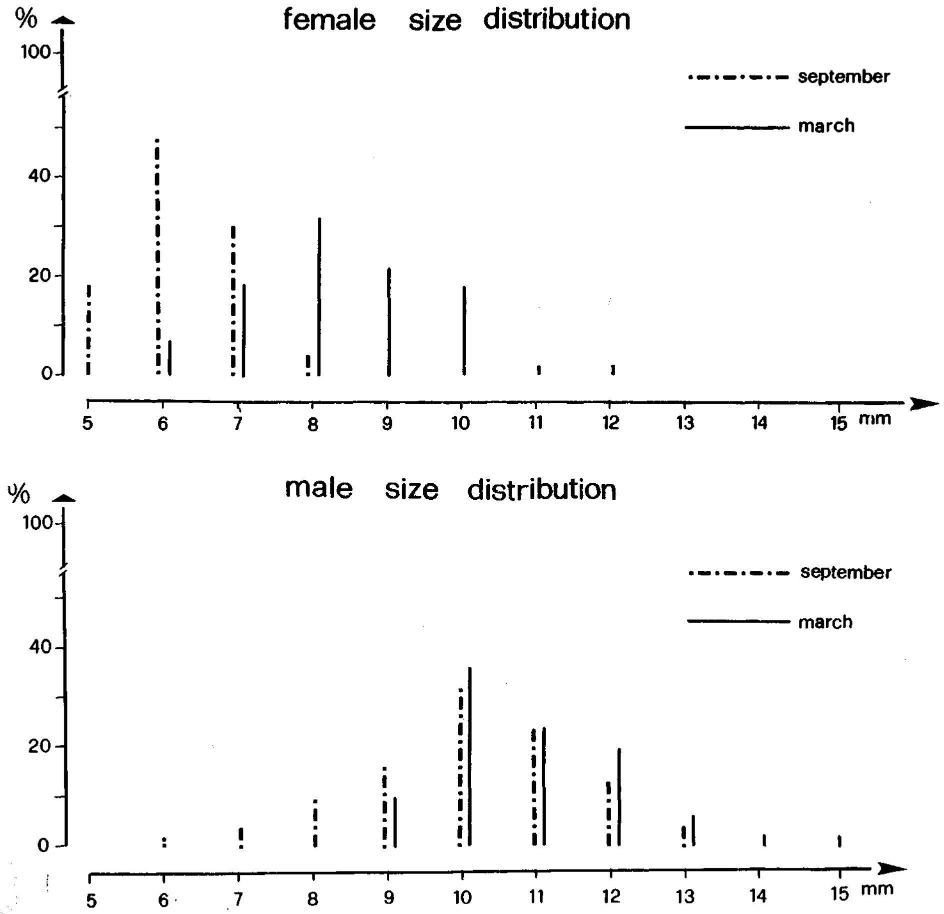

Fig. 1. – Differences between female and male size distributions.

Fig. 1 clearly shows the different distributions of the females in the various size classes and stresses the different body size limits of these organisms in the two periods of the year: the lower limit (for sexually differentiated females) varies from 5 mm in September to 6 mm in March. In September the upper limit does not exceed 8 mm and in March it reaches 12 mm.

In males the distribution is similar in the two different periods, and the differences in the limits (both upper and lower) are less accentuated. The September males range from 6 mm to 13 mm and the March males from 9 mm to 15 mm. We demonstrated that the differences between females are statistically significant while they are not significant between males (see Table I).

TABLE I

Distribution of males and females among the various body size classes.

body size (in mm)	n° females		n° males	
	September	March	September	March
5	18	—	—	—
6	48	6	2	—
7	30	18	4	—
8	4	32	10	—
9	—	22	16	10
10	—	18	32	36
11	—	2	20	24
12	—	2	12	20
13	—	—	4	6
14	—	—	—	2
15	—	—	—	2
	$\chi_2 = 59.7$ $p < .001$		$\chi_2 = 12.2$ n. s.	

The size distribution of the organism considered shows a more accentuated variance among females. This may be due to the fact that from October to March sexual activity is suspended.

DISCUSSION

Asellus aquaticus shows a clear dimorphism of body size (Racovitza, 1919). This dimorphism is more evident in the September population – which has had a long period of reproductive activity – and is smaller in the March population, after the reproductive diapause. In fact the difference in the size distribution of males is not significant, whereas it is highly significant among females. The difference is clearly related to the reproductive diapause.

The correlation between reproductive effort and decrease in growth of *A. a.* can be explained by partitioning of energy between reproduction and growth (Williams, 1966; Gadgil and Bossert, 1970) and decrease in energy intake (Strong and Daborn, 1980).

In this species the female expends a great amount of energy in reproduction: i) in oogenesis which leads to the production of eggs very rich in yolk; ii) in the GM and two reproductive moults (BM and IM); iii) in long parental care. Much less energy is expended by the male in reproduction, spermatogenesis alone being involved.

The decrease in energy intake is most likely due to the greater frequency of ecdysis during the reproductive period. In fact, it has been demonstrated by Strong and Daborn (1980) that during the moult cycle in the sea isopod *Idotea baltica* the food intake level drops significantly. Therefore in *A.a.* in the six month period from September to March, the females do not have to expend energy in reproduction and they also have an energy intake analogous to that of the males since they no longer effect reproductive moults (BM and IM).

The sum of these factors should be the cause of the accentuation of sexual dimorphism during the period of greater reproductive activity. This may be due to the fact that this character is determined by a series of physiological factors such as indeterminate growth, longevity, reproductive activity and parental care rather than a genetic condition.

The above data strongly support the hypothesis that in *Asellus* the more marked sexual dimorphism of body size in September is mainly due to the high energy expenditure in reproduction and not to a genetic selection.

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