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THE GENETIC SYSTEM CONTROLLING THE BODY LENGTH AT WHICH SEX CHANGE OCCURS IN *OPHRYOTROCHA PUERILIS* (ANNELIDA, POLICHAETA)

Questo lavoro è dedicato alla memoria del prof. Guido Bacci.

Riassunto — *Il sistema genetico che controlla la lunghezza del corpo a cui avviene l'inversione del sesso in* Ophryotrocha puerilis. Mediante il *joint scaling test* (MATHER e JINKS, 1971), si sono studiate le componenti genetiche del sistema che determina la lunghezza del corpo a cui avviene l'inversione al sesso femminile nel Polichete proterandrico *Ophryotrocha puerilis*.

I risultati indicano che nel modello genetico che meglio descrive questo sistema prevalgono gli effetti additivi tra geni mentre gli effetti dovuti a dominanza o ad altre forme di interazione non sembrano consistenti. Questo tipo di architettura genetica porta a supporre che il carattere in esame sia stato sottoposto ad un'azione stabilizzatrice da parte della selezione.

Abstract -- In *Ophryotrocha puerilis*, a protandrous hermaphrodite Polychaete worm, the genetical architecture of body length at which sex change takes place has been studied, by means of a joint scaling test (MATHER and JINKS, 1971). Data were collected from P_1, P_2, F_1, F_2 generations and from the two backcrosses of F_1 to both parents. Results suggest that a suitable genetical model must include additive effects and non allelic interactions between homozygous gene pairs. Dominance effects and other kinds of interaction do not seem to be important at all, in accordance with the model of the polygenic sex determination (BACCI, 1965).

From this kind of genetic architecture it may be argued that a stabilizing selection has acted in the past on the body size reached by *Ophryotrocha puerilis* at sex change.

Key words — joint scaling test, *Ophryotrocha puerilis*, poligenic sex determination, stabilizing selection.

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INTRODUCTION

Ophryotrocha puerilis is a sequential hermaphrodite Polychaete worm, in which sex inversion may occur several times in the same individual. In the mediterranean populations, at the temperature of 18°C, the male phase usually starts at the 9-10 segment stage (ZU-NARELLI, 1962; ÅKESSON, 1973), and the first change from the male to the female phase appears when the animals reach a mean body length of 18 ± 1 chaetigerous segments. It has been possible, by means of directional selection, to increase or to reduce the number of chaetigerous segments at which sex change occurs, until some individuals showing only one of the two sexual phases were obtained (BACCI, 1955, 1965a; BACCI and BORTESI, 1961; SELLA, 1969). Such experimental results are thus consistent with the hypothesis that in *Ophryotrocha puerilis* the body length at which sex change occurs is determined by a polygenic system, and the relative lengths at which sex change takes place are the phenotypic expressions of different proportions of male and female factors.

As expected (MATHER and HARRISON, 1947), variations of body length at sex change appear to be negatively correlated with a component of fitness, namely germ cell production: cytological investigation showed that, as artificial selection progressed, more and more selected individuals showed a gradual increase of degenerated germ cells, not only during the sexual phase, whose length was reduced by selection, but also during the sexual phase apparently favoured by selection (BORTESI, 1964; BACCI, 1964, 1965a, 1965b).

Heritability estimates of the body length reached at the sex turning point, measured by mid-parent offspring regression in the early generations of selection experiments, had values between 0,4 and 0,3 (SELLA, 1969).

The present biometrical analysis was undertaken in order to gain some insight into the type of genetic system controlling the body size at which sex change takes place, and therefore to relate the genetic evidence to the type of natural selection to which the character has been subjected.

MATERIALS AND METHODS

As diallel crosses cannot be successfully performed in *Ophryotrocha puerilis*, data were analyzed by means of a joint scaling test,

as it has been extensively described by JINKS and JONES (1958) and by MATHER and JINKS (1971).

Crosses were made between 70 individuals chosen at random from two long established stocks of *Ophryotrocha puerilis* from Leghorn, inbred from some generations. One stock was showing the first appearance of the female phase at a mean number of chaetigerous segments lower than 18, (P_2), the other around 20 chaetigerous segments (P_1). Subsequently the F_1, F_2 generations and the backcrosses of F_1 to P_1 and to P_2 (B_1 and B_2, respectively) were raised simultaneously and the number of chaetigerous segments reached at the first appearance of oocytes was recorded for each member of the six generations. Single individual randomization was used by growing each member of the families contributing to the six generations in individual bowls.

The total number of families raised per generation and of individuals observed are listed in table 1.

To the generation means, each of them being weighted by the inverse of its variance, were fitted genetic models with the following genetic parameters: the overall mean m, the additive genetic effects $[d]$, the dominance contribution $[h]$, the digenic non allelic interaction parameters $[i]$, $[j]$, and $[l]$, meaning the homozygote x homozygote, homozygote x heterozygote, and heterozygote x heterozygote interactions respectively, acting across all pairs of loci at which the two stocks differ.

The criteria for acceptance of the best model are non significance of the overall goodness-of-fit chi-square and significance of all the genetic parameters included in the model.

Two experiments under different temperature conditions were performed: a preliminary one, with a lower number of individuals reared at the temperature of 18°C and a more exhaustive one at the temperature of 21°C, at which the animals require a shorter time to reach the female phase (SELLA, 1978). Therefore, only the results of the last experiment will be reported in detail.

RESULTS

The six generation means obtained at 21°C are given in table 1.

The mean expression of the character in the F_1 generation did not show any heterosis; however the segregant generation F_2 had a mean value which was not in accordance with Mather's C scaling

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test (1949) (table 1). None of the scale transformations tested (logs, square roots, reciprocals), agreed with Mather's B and C equalities. This outcome was taken to suggest that the hereditary mechanism underlying the expression of the character is complicated by the presence of non allelic interactions.

TABLE 1 - Experimental design and observed generation means of the number of chaetigerous segments reached at sex change.
**: significant at 1% level of probability.

Generations	N. families	mean number individuals per family	Total	mean ± standard error
P_1	10	7	70	20,0 ± 0,286
P_2	10	7	70	17,6 ± 0,196
F_1	25	12	298	19,1 ± 0,112
F_2	13	8	109	19,6 ± 0,229
B_1 ($F_1 \times P_1$)	10	11	107	19,4 ± 0,209
B_2 ($F_1 \times P_2$)	12	13	154	18,8 ± 0,161

Mather scaling tests
A: 0,29 ± 0,269
B: 0,90 ± 0,154 **
C: 2,65 ± 1,009 **

The initial model tested by means of the joint scaling test included only the m, $[d]$, $[h]$ parameters and did not provide a non significant chi-square. Therefore interaction parameters were included in the initial model, first one, then two at a time: of the six models fitted in such a way, a non significant goodness-of-fit was shown only by the three models (m, $[d]$, $[h]$, $[i]$; m, $[d]$, $[h]$, $[i]$, $[l]$; m, $[d]$, $[h]$, $[i]$, $[j]$) which required, in addition to the additive and dominance components, the homozygote x homozygote interaction parameter. Of the three models mentioned, the one that best fitted the weigthed least square estimates of the components of the generation means was composed by m, $[d]$, $[h]$, $[i]$ (table 2). In this model the omission of the $[j]$ and $[l]$ components leads to a somewhat better measurement of the other parameters, as shown by their reduced standard error.

In the most adequate model, only the estimates of m and of the $[d]$ and $[i]$ components are significantly different from zero

(table 2). The last two components show the same order of magnitude, although the [i] parameter has a less precise estimation, owing to its very large sample variance.

TABLE 2 - Estimates of the parameters in the fittest genetic model together with the χ^2 value of the goodness-of-fit.

Parameters	Estimates ± st. dev	Significance
m	18,82 ± 0,382	* * *
[d]	1,04 ± 0,148	* * *
[h]	—0,75 ± 0,440	n.s.
[i]	—1,06 ± 0,441	* *
χ^2_2	3,27	P = 0,20 n.s.

***: P < 0,1%; **: P = 2,5%.

The negative sign of [i] cannot be unambiguously interpreted (see MATHER and JINKS, 1971).

Similar results were obtained with the data of the preliminary experiment reared at 18°C.

DISCUSSION AND CONCLUSIONS

The results of this experiment seem to describe a genetic system, whose features fully account for the results of previous researches (reviewed by BACCI, 1978).

The significance of the additive and of the [i] interaction components explains the effectiveness of directional selection for the change of body length reached at sex inversion, as these parameters measure the only genic effects which can be fixed in the following generations.

Effects due to net directional dominance and to interactions involving dominance have not been detected, either because they are absent, or because the parental lines were still not enough inbred to become sensible to such effects.

The former hypothesis is however in accordance with the assumptions of the model of the polygenic sex determination, which is applied to many hermaphrodite species (see KOSSWIG, 1964; BACCI, 1965a; HALEY, 1977).

These data could then be tentatively consistent with the inference that this trait has been in the past and is now principally exposed to stabilizing selection (MATHER, 1966; KEARSEY and KOJIMA, 1967; LAWRENCE, 1972). This does not mean that the body length at which sex change occurs should not be itself a component of the fitness, although it can be considered less linearly connected to fitness than the germinal cell production, as this latter trait shows a strong inbreeding depression (BACCI and BORTESI, 1967). Other examples of characters which are components of the fitness and at the same time are assumed to be under stabilizing selection are available in other species (cf.: FALCONER, 1960; PERRINS, 1964; PARSONS and KAUL, 1965; BARNES, 1978; SHEIRING, 1977).

The linkage of the two traits could be a physiological one, or be due to a cross control between the two underlying genetic systems, according to the hypothesis claimed by BACCI, in his model on sex genes activation (1975).

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