Influence of temperature and diet on the larval development and growth of juveniles *Marphysa sanguinea* (Montagu) (Polychaeta, Eunicidae)

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ABSTRACT

The effects of temperature and food type on development and growth rate of the eunicid polychaete *Marphysa sanguinea* have been investigated under controlled laboratory conditions from the beginning of the larval feeding. Development and growth rate was evaluated under vegetarian diet (filamentous green algae), meat diet (Liebig meat extract and Gerber meat homogenates), and mixed diet containing both the two previous foodstuffs. Each diet was tested at five temperatures (13 °C, 18 °C, 24 °C, 27 °C, and 30 °C). Development and growth rate was influenced both by diet and temperature.

RÉSUMÉ

Influence de la température et du régime alimentaire sur le développement larvaire et la croissance de *Marphysa sanguinea* (Montagu) (Polychaeta, Eunicidae)

Les effets de la température et du régime alimentaire sur le développement larvaire et sur la croissance du polychète *Marphysa sanguinea* ont été étudiés en conditions controlées au laboratoire à partir du moment où les larves commencent à s'alimenter. Le développement et la croissance ont été comparées en nourrissant les larves avec un aliment végétal (algues vertes filamenteuses), de la viande (extrait de viande Liebig et viande Gerber homogénéisé) et avec un aliment mixte composé d'algues et de viande. Chaque type d'aliment a été testé à cinq températures (13 °C, 18 °C, 24 °C, 27 °C, et 30 °C). Le développement larvaire et la croissance ont été influencés par la nature de l'aliment et la température.

INTRODUCTION

Environmental factors strongly affect all phases of the life cycles of many marine invertebrates living in temperate waters. Temperature, photoperiod, dissolved oxygen, food quantity and composition, and salinity are among the principle environmental factors influencing seasonal cycles of reproduction, development and growth. Among these, temperature and food availability, which influence individual development, growth rates and

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survivorship, are essential in determining population dynamics (BHAUD, 1988; MARSH & TENORE, 1990) and consequently the structure of marine benthic communities (RHOADS & YOUNG, 1970 ; WHITLATCH, 1980, 1981).

The role of temperature and food type on development and growth rate has been extensively investigated for "opportunistic" polychaetes with short life spans, of the order of months, short generation times, and semi-continuous reproduction, such as Capitellidae (TENORE, 1977, 1983; TENORE & CHESNEY, 1985; MARSH *et al.*, 1989; MARSH & TENORE, 1990) and Spionidae (WIBLE, 1984; LEVIN & CREED, 1986; ZAJAC, 1986; CHU & LEVIN, 1989). Only few studies have investigated the influence of environmental parameters on polychaetes defined as "equilibrium" species with longer life spans, of the order of years, slow development and fewer reproductive periods per unit time (IVLEVA, 1970; NEUHOFF, 1979; BHAUD, 1988; PREVEDELLI, 1991, 1992).

The eunicid *Marphysa sanguinea* exhibits all the characteristics of an "equilibrium" species according to the definitions of GRASSLE & GRASSLE (1974), McCALL (1977), and ZAJAC & WHITLATCH (1989). Along the Italian coast, *M. sanguinea* is very abundant in the Lagoon of Venice, a polyhaline lagoon with limited fluctuations in salinity but large seasonal changes in temperature. This species is considered to be omnivorous (DAY, 1967; FAUCHALD & JUMARS, 1979); indeed the availability of both plant and animal food source in the Venice Lagoon is very high.

The present paper is a part of a study of the life-history of *M. sanguinea* to elucidate the life-history traits adopted by this polychaete for the colonization and survival in brackish waters (PREVEDELLI, 1989). In the Venice Lagoon temperature fluctuations is the main source of environmental instability while the variety of potential food type is always high. It is therefore of interest to conduct an experimental study on the effects of temperature and diet on the development and growth of this species.

MATERIALS AND METHODS

FIELD COLLECTIONS. — Bottom samples were collected from the Lagoon of Venice in February 1988 about two months before spawning. Adult specimens of *M. sanguinea* were extracted by hand from mud immediately after collection.

REPRODUCTION. — In the laboratory the worms were placed in tanks containing filtered lagoon mud and lagoon water under constant oxygenation. The mud was screened through a 0.5 mm sieve to remove algae, mollusc shells etc. Salinity was maintained around 30 P.S.U., which corresponded to the collection site. The tanks were maintained at 24 °C and 12/12 light/dark photoperiod. Fertilization occurred after about 30 days.

GAMETE EMISSION AND GROWTH EXPERIMENTS. — Thirty larvae of five setigerous segments just beginning to feed (20 days old) were used to study the development and growth rate in relation to temperature and diet. They were placed in 15 small glass tanks with 30 ml of filtered lagoon water and maintained at five different temperatures (13, 18, 24, 27 and 30 °C) with constant 12/12 light/dark photoperiod. The 13 - 30 °C temperature limits adopted, slighty exceed the lower and upper lagoonal water temperatures during larval emergences. The salinity was kept around 30 P.S.U. Larvae were fed with vegetarian, carnivorous and mixed diets at each tested temperature. The vegetarian diet consisted of filamentous green algae reared in the laboratory. The meat diet consisted of Liebig meat extract (0.1 g in 50 ml of distilled water) integrated with meat homogenates. The mixed diet contained both of these foods. Food was always given in abundance but food excess was avoided to prevent water anoxia. Water was changed twice a week and glass tanks were replaced with clean ones every month. Somatic growth was recorded weekly by counting the number of setigerous segments.

STATISTICAL ANALYSIS. — The SPSS (NIE *et al.*, 1975) software package was used for statistical calculations. Effects of food type and temperature regime were analyzed using a two-way analysis of variance (ANOVA). When the ANOVA showed treatment differences to be significant ($p < 0.05$), the treatment means were analyzed by an *a posteriori* Least Significant Difference (LSD) test.

RESULTS

Experimental results are reported in table 1 and figure 1.

TABLE 1. — Mean length (number of setigers) of *Marphysa sanguinea* at each treatment (in brackets standard deviation).

TREATMENT		DAYS				
		15	45	75	105	135
13 °C	algae	5 (0.00)	5 (0.27)	6 (0.00)	6 (0.00)	6 (0.00)
	mixed	5 (0.32)	5 (0.35)	6 (0.00)	6 (0.00)	6 (0.00)
	meat	5 (0.25)	5 (0.23)	6 (0.00)	6 (0.00)	6 (0.00)
18 °C	algae	5 (0.47)	7 (1.41)	8 (0.95)	13 (3.59)	18 (3.87)
	mixed	5 (0.50)	5 (0.49)	10 (1.40)	11 (2.60)	15 (2.80)
	meat	5 (0.48)	6 (0.98)	11 (2.40)	18 (5.40)	23 (3.54)
24 °C	algae	5 (0.25)	6 (0.49)	12 (2.82)	15 -	26 -
	mixed	5 (0.39)	9 (1.67)	18 (7.03)	31 (20.50)	36 (24.00)
	meat	6 (0.81)	11 (2.45)	14 (4.13)	26 (16.26)	45 -
27 °C	algae	5 (0.21)	7 (2.26)	18 (4.76)	24 (6.24)	35 -
	mixed	6 (0.82)	12 (3.34)	17 (5.34)	25 (6.41)	30 (2.12)
	meat	5 (0.57)	11 (2.70)	20 (5.50)	25 (8.29)	36 (18.38)
30 °C	algae	5 (0.65)	11 (1.67)	19 (4.60)	28 (8.73)	34 (7.07)
	mixed	6 (0.81)	14 (1.94)	27 (8.98)	31 (10.98)	37 (15.55)
	meat	6 (0.86)	15 (1.41)	29 (12.40)	50 (14.84)	52 (13.43)

Large differences were found in developmental stage and body size of worms reared under the different experimental conditions, indicating that both development and growth rate of *M. sanguinea* were influenced by temperature and diet.

Development seemed to be positively correlated with temperature at 15 days, whereas no effect was noted with different foods (Fig. 1). After the 45 days temperature effects were more pronounced : specimens maintained at 13 °C reached a length of 6 setigerous segments, at 18 °C growth was still slow but worms reached a length of 8 setigerous segments. At temperatures of 24, 27 and 30 °C, the specimens attained 15-19 setigers. This pattern continued to the end of the experiment. After almost 5 months the larvae reared at 13 °C still had 6 setigers (Fig. 1). In these larvae only slight changes in morphology occurred over time. The jaws became thicker, the eyes and capillary setae appeared but larvae lacked antennae, gills and new setigerous segments. At 18 °C some specimens had the central and the two median antennae. At the higher temperatures a great variability occurred within each group, whereas the difference between groups was limited (Fig. 1). At 30 °C the within-group variability was lower due to a more rapid and uniform growth. At the rearing temperature of 30 °C some specimens had five antennae and had completed larval development.

TABLE 2. — Results of two-way ANOVA testing the effects of temperature and diet on growth rate of *Marphysa sanguinea*.

		ANOVA			
Source	SS	df	MS	F ratio	P
T °C	17712.737	6	2952.123	65.243	0.001
diet	16434.235	4	4108.559	90.801	0.001
2-way interaction	786.965	8	98.371	2.174	0.001
T °C diet	786.965	8	98.371	2.174	0.001
explained	18499.702	14	1321.407	29.204	0.001
residual	34162.069	755		45.284	

TABLE 3. — Results of LSD test testing the effect of temperature on growth rate of *Marphysa sanguinea* (the straight line denotes means not significantly different at 0.05 level).

Temperature (°C)	13	18	24	27	30
mean length	5.28	7.99	9.27	12.12	23.22

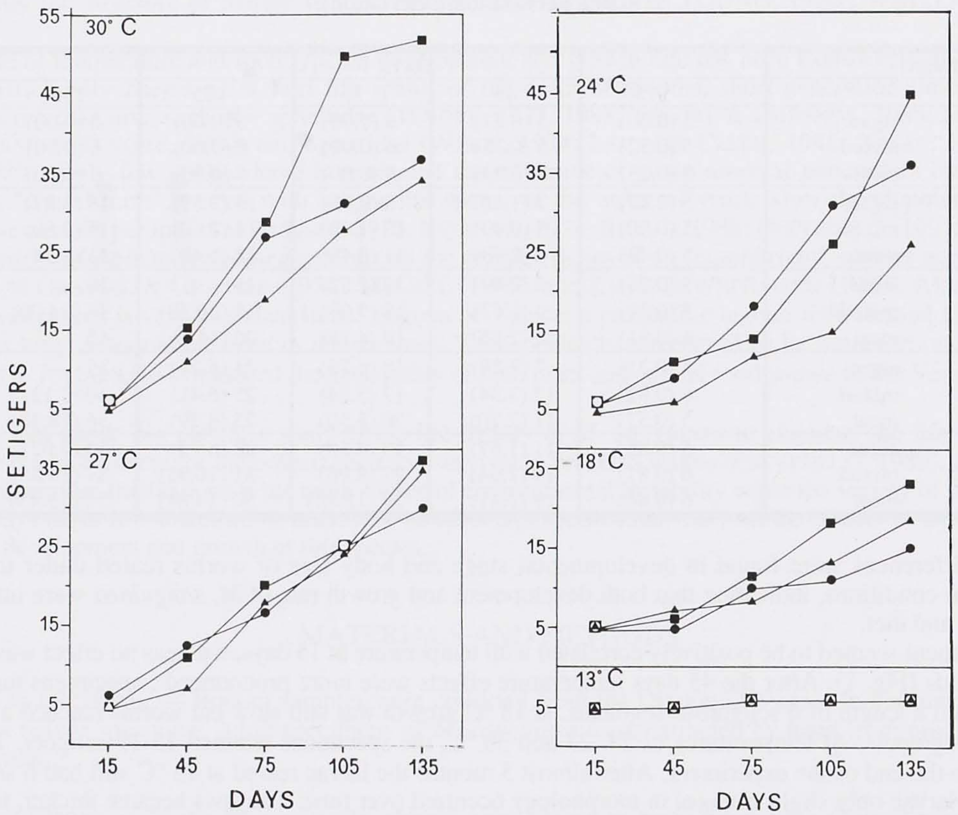

FIG. 1. — Growth rate patterns of *Marphysa sanguinea* at each treatment. (▲) algae; (●) mixed; (■) meat.

Growth rates were significantly affected by temperature and diet and a significant interaction was found between each of the two factors tested (two-way ANOVA) (Table 2). For temperature the LSD comparison of means indicated that only the means of the groups reared at 18 °C and 24 °C were not significantly different ($p > 0.05$) (Table III). For diet, the LSD test indicated that the mean growth rate observed in the groups fed with mixed or carnivorous diet were not significantly different ($p > 0.05$), whereas these were significantly different from the algae group ($p < 0.05$) (Table 4).

TABLE 4. — Results of LSD test testing effects of diet on growth rate of *Marphysa sanguinea* (the straight line denotes means not significantly different at the 0.05 level).

Diet	algae	mixed	meat
mean length	7.86	10.10	11.04

DISCUSSION

Three conclusions can be shown from this experiment.

First, the development and growth rate of juvenile *M. sanguinea* is positively correlated with water temperature. This agrees with the findings for other species (MANGUM, 1978; WIBLE, 1984; PESCH *et al.*, 1987; BHAUD, 1988; YOKOYAMA, 1988; CHU & LEVIN, 1989; ESNAULT *et al.*, 1990 ; MIRON *et al.*, 1992; PREVEDELLI, 1992) and with observations performed in the natural environment. Indeed previous studies on the life cycle of

M. sanguinea found the spawning period to be from April to May, related to an increase in water temperature (PREVEDELLI, 1989). These larvae can arrest development and growth for long periods of time at lower temperature conditions. However, they maintain their potential for development under more favorable temperature conditions. If the temperature increases, the larvae will resume growth and development. This has been confirmed in laboratory studies where individuals reared at 13 °C began to grow again when placed at 18 °C. This feature is an important adaptative characteristic that permits the successful colonization of brackish waters, with variable temperatures. Seasonal fluctuations at the benthic level are stronger in lagoonal than marine environments. In particular, thermal conditions in autumn can lead to a sudden fall in temperature; in this period the larvae must be sufficiently developed to dig into sediment and reach a habitat with greater thermal stability. Temperature is an important factor regulating development and somatic growth, and its function seems especially crucial in "equilibrium" species. These species have offspring with long larval development and slow growth and must adopt strategies to reduce mortality. A strategy to maximize survival of offspring may time the reproductive period with the optimal conditions for the new generation (METTAM, 1980).

Second, the diet is a very important factor in regulating development, growth rate and survival which was lower with vegetarian diets.

Third, the findings on dietary preference demonstrate that *M. sanguinea* acquires its final omnivorous feeding habits at an early developmental stage. It is, thus, an omnivorous species, even though the vegetarian diet given did not prove to be suitable for an optimum growth.

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