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EFFECT OF TEMPERATURE ON DEMOGRAPHY OF *OPHRYOTROCHA LABRONICA* (POLYCHAETA: DORVILLEIDAE)

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POLYCHAETA
OPHRYOTROCHA LABRONICA
TEMPERATURE
DEMOGRAPHY

ABSTRACT. – A laboratory experiment was performed to evaluate the temperature-induced variation in the life history traits of *Ophryotrocha labronica* (Polychaeta). In this species age and size at maturity, survival and fecundity are affected by temperature. In particular in *O. labronica*, low temperatures cause a considerable delay in the attainment of sexual maturity, a reduced number of spawnings and longer intervals between one spawning and the next; fecundity is therefore lower and the animals generally live longer. At high temperatures, the animals mature rapidly, spawn very frequently and at shorter intervals; fecundity is high, even though the animals have a much shorter life span. Temperature determines the age-specific fecundity and survival patterns and hence the demographic characteristics of *O. labronica*; both the net reproductive rate R_0 and the population growth rate λ vary in accordance with the temperature, thus demonstrating the importance of environmental factors in determining not only the reproductive characteristics of the individual animal but also the fitness of the populations as a whole.

POLYCHAETA
OPHRYOTROCHA LABRONICA
TEMPERATURE
DEMOGRAPHIE

RÉSUMÉ. – Les effets de la température sur différents paramètres démographiques de la Polychète *Ophryotrocha labronica* ont été étudiés en conditions contrôlées au laboratoire. Chez cette espèce, l'âge et la taille à la maturité, la survie et la fécondité sont influencés par la température. Les basses températures entraînent un retard important de la maturité sexuelle, un nombre réduit de pontes et des intervalles plus longs entre les pontes, en particulier chez *O. labronica* ; la fécondité est donc plus basse et les animaux vivent généralement plus longtemps. A températures élevées, les animaux atteignent la maturité rapidement, ils pondent plus souvent et à intervalles plus courts ; la fécondité est élevée même si la durée de vie est plus brève. La température détermine l'âge de la maturité et les modalités de survie, et les caractéristiques démographiques de *O. labronica* ; le taux de reproduction net R_0 et le taux de croissance de la population λ varient selon la température, montrant ainsi l'importance des facteurs de l'environnement dans le déterminisme des caractéristiques de la reproduction à l'échelle de l'individu, mais aussi à celle de la population et de l'adaptation.

INTRODUCTION

The effects of temperature on the survival, growth, development and reproduction of polychaetes have long been the subject of research (Bhaud 1988, Yokohama 1988, Prevedelli 1991, 1992, 1994). The role of temperature in the regulation of the reproductive cycles of many annual iteroparous and semelparous polychaetes with markedly-seasonal and highly-synchronized spawning patterns is evident and well documented (Neuhoff 1979, Garwood 1980, Olive 1984, Olive *et al.* 1997, Olive *et al.* 2000). In the case of semicontinuous iteroparous species, which, by definition, lay small groups of eggs at short intervals of time, the effects of temperature, and in particular their impact on population levels, have received less attention. In theory, these species reproduce throughout the year, but in some small-sized species belonging to the fouling communities of harbour environments in temperate regions, marked seasonal variations in population densities have been observed. It is therefore likely that the temperature-induced variations on survival and fecundity, already noted in some small-sized species employing a semicontinuous, iteroparous reproductive strategy, may occasion considerable variations in population growth rate (Åkesson 1976, Chu & Levin 1989, Levin & Creed 1986, Åkesson & Costlow 1978, 1991).

Ophryotrocha labronica is a semicontinuous iteroparous and geographically widespread species belonging to the Dorvilleidae family, colonizing harbour environments. It is a small-sized worm with an extremely high reproductive capacity. It was first described by La Greca & Bacci (1962) as a proterandric, hermaphroditic species in a population from Leghorn, Italy. Subsequently, gonochoric species collected in the harbours of Leghorn and Naples, Italy (Åkesson 1970, 1972 a, b) and Genoa, Italy (Premoli *et al.* 1996) were also described. *O. labronica* is particularly suitable for studies on environmental control of reproduction because it is easy to breed in laboratory conditions. Moreover, the animals grow quickly, reach sexual maturity in a very short time, reproduce a number of times at intervals of just a few days and produce a large number of eggs (Åkesson 1973). Åkesson (1976) has studied the effects of temperature on the life cycle of a population of *O. labronica*, originally from Leghorn harbour, after breeding in the laboratory for about ten years.

We investigated the effects of three temperature regimes on a population of *O. labronica* collected in Genoa harbour to understand the relationship between temperature and the animals' life history characteristics. Our objectives were to compare the survivorship and reproductive activity of *O. labronica* at different temperatures; to evaluate environment-induced variation in life history traits such as: age and size at first reproduction, age-specific survival, age-specific fecundity and brood size; to perform a demographic analysis to link the individual life history traits to population levels.

MATERIALS AND METHODS

Collection and maintenance: The population analyzed in this experiment came from the harbour of Genoa. The experiment was performed with recently collected specimens. After collection the animals were housed in 10 cm diameter, 5 cm tall beakers containing approximately 200 ml of artificial 35 psu seawater and maintained at a constant temperature of 24 ºC in a L:D 12:12 photoperiod. Twice a week, the animals were fed with Tetramin, an artificial food for aquarium fish, slightly in excess of the appetite. The nutritional characteristics of this food are reported in Prevedelli and Zunarelli Vandini (1998). Newly laid egg masses were transferred together with the female to three new beakers, one for each of tested temperature and placed at 15 ºC, 22 ºC and 30 ºC respectively. As soon as the larvae began to hatch, the females were removed, thus ensuring that a large number of individuals of the same age and a known date of birth were selected.

Description of the experiment: The experiment was carried out on couples of one male and one female. In *O. labronica* sex can be clearly distinguished; in fact there is an apparent dimorphism between males and females in the jaw, and the oocytes are visible through the body wall in females with 13-14 setigerous segments. Each couple was placed in a 4.5 cm diameter beaker containing 10 ml of artificial 35 psu seawater. The effects of each temperature were assessed on 20 couples. Food was given twice a week. Couples were checked twice a week to see whether reproduction had occurred. If so, the fecundity and growth rate were recorded. If a male died, he was replaced by a young individual of known age, while if the female died, the couple was eliminated from the experiment. The fecundity of each couple was assessed as: (1) the number of eggs produced at each spawning by the female, (2) the number of spawnings, and (3) the total number of eggs produced by a female during its lifetime. Growth rate was recorded by counting the number of setigerous segments.

Data analysis: The effects of temperature on life history characteristics were assessed by analysis of variance (ANOVA) or the non-parametric Kruskal-Wallis test. Age-specific survivorship and fecundity schedules were obtained for each examined temperature. These life tables data were used to build a complete age-classified population model and the relative projection matrices (Leslie matrices), using a projection interval of 1 week. Since this species exhibits semicontinuous reproductive mode (births occur continuously over the time interval), the survival probabilities (P_i) appearing on the subdiagonal were calculated as:

$$P_i = \frac{l_{(i+1)} + l_{(i)}}{l_{(i)} + l_{(i-1)}}$$

and the age-specific fecundity (F_i) in the first row as:

$$F_i = (l_{(0)} l_{(1)})^{1/2} \frac{(m_i + P_i m_{i+1})}{2}$$

where $l_{(i)}$ is survivorship from zygote to age i and m_i is the average number of offspring female per female in age class i (Caswell 1989).

The finite population growth rate λ was calculated as the dominant eigenvalue of each matrix. The stable age distribution is given by the corresponding right eigenvector (w) and the reproductive value distribution by the corresponding left eigenvector (v). The sensitivities of λ to changes in the matrix entries P_i and F_i were calculated according to Caswell (1989, 2000):

$$s_{Pi} = \frac{\partial\lambda}{\partial P_i} = \frac{w_i v_1}{<w,v>}$$

$$s_{Fi} = \frac{\partial\lambda}{\partial F_i} = \frac{w_i v_{i+1}}{<w,v>}$$

where $<w,v>$ denotes the scalar product between the stable age composition and the reproductive value.

The sensitivity is determined by the life history of the organism as described by P_i and F_i. However since survivorship and fecundity are measured on different scales, absolute values of sensitivities cannot readily be compared among different parameters. To overcome this difficulty the measure of relative sensitivity, know as elasticity, was calculated:

$$e_a = \frac{a}{\lambda} s_a$$

where a denotes the considered life history trait P_i or F_i (de Kroon *et al* 1986).

The effect of each treatment on λ, was decomposed into contributions from each of the age-specific survivorship and fecundity terms using the techniques outlined by Caswell (1989). Let $\lambda(c)$ and $\lambda(d)$ denote the values of λ for treatment *c* and *d*, respectively. Then:

$$\Delta\lambda = \lambda^{(c)} - \lambda^{(d)} = \sum_i \sum_j \Delta a_{ij} \frac{\partial \lambda}{\partial a_{ij}}$$

Each term in the summation is the contribution of the difference in the matrix entry a_{ij} of treatment *c* respect to *d* on Δλ. In this way it was possible a) to identify the life-history traits that were most responsible for the effects of treatment on λ and b) to compare the contribution of each trait to the Δλ between two treatments.

We also calculated the expectation of life:

$$e^0 = 0{,}5 + \frac{l_1 + l_2 + l_3 + \dots l_n}{l_0}$$

the net reproductive rate:

$$R_0 = \sum_i F_i \prod_{j=1}^{i-1} P_j$$

and the generation time:

$$T = \frac{\sum_i iF_i \prod_{j=1}^{i-1} P_j}{\sum_i F_i \prod_{j=1}^{i-1} P_j}$$

RESULTS

Life history traits

Many traits in the life history of *O. labronica* vary in relation to temperature. In particular, significant differences have been recorded in the animals' age and size at maturity, in the number of spawnings occurring during the lifetime of a female, in the maximum size reached by both males and females, in fecundity, in the number of eggs laid in each cluster and in the time elapsing between one spawning and the next. The mean values (±2 SE), minima and maxima are reported in Table I. Generally speaking, the animals maintained at 15 °C are slower to reach maturity, spawn less frequently and tend to be smaller and less fecund, although the number of eggs contained in each cluster is greater, on average, than at the other temperatures. The animals maintained at 30 °C, on the other hand, quickly reach sexual maturity, are quite the biggest and most fecund and spawn at brief intervals of time; the number of eggs in each cluster is between that found at the other temperatures and the number of spawnings is lower than at 22 °C.

Table I. – Summary of the life history characteristics of *O. labronica* at tested temperatures.

	Size at maturity (s.s.)			Age at maturity (days)		
	15°C	*22°C*	*30°C*	*15°C*	*22°C*	*30°C*
Mean	16.6	14.8	15.8	56.7	30.4	22.7
2*ES	0.7	0.5	0.6	2.2	1.8	2.0
Min.	14	14	14	53	24	18
Max.	18	17	17	64	35	28
n	10	17	12	10	17	12
χ^2		12.6			30.6	
p		0.002			< 0.001	
	Number of spawnings			**Maximum female's size (s.s.)**		
	15°C	*22°C*	*30°C*	*15°C*	*22°C*	*30°C*
Mean	3.0	7.6	6.2	18.0	18.2	19.4
2*ES	0.5	1.0	1.5	0.9	0.6	1.9
Min.	2	3	3	15	16	17
Max.	4	10	11	20	20	25
n	10	17	12	10	17	12
χ^2		20.7			0.1	
p		< 0.001			0.947	
	Maximum male's size (s.s.)			**Fecundity (eggs/female)**		
	15°C	*22°C*	*30°C*	*15°C*	*22°C*	*30°C*
Mean	13.9	14.9	15.9	868.3	942.1	1089.4
2*ES	0.6	0.5	0.8	168.8	109.9	344.5
Min.	13	12	13	567	312	276
Max.	16	16	18	1335	1202	2215
n	10	17	12	10	17	12
χ^2		13.5			1.5	
p		0.001			0.467	
	Eggs/sleeve			**Interval between spawnings**		
	15°C	*22°C*	*30°C*	*15°C*	*22°C*	*30°C*
Mean	289.4	125.1	176.7	26.1	13.2	8.7
2*ES	31.3	10.3	23.4	4.0	0.7	0.8
Min.	120	23	28	16	7	4
Max.	440	255	387	58	26	19
n	30	128	74	20	111	62
F		56			111.8	
p		< 0.001			< 0.001	

Age-specific survival and fecundity

The survival and fecundity graphs are shown in Fig. 1. The survival graphs are very different at the three temperatures assayed. In particular, survival is highest at 15 °C with about 90% of the animals surviving until the 14th week; thereafter, the animals very gradually begin to die, the longest-lived continuing to survive until the 24th week. At 22 °C the curve is much more linear, but here too the longest-lived survive for 24 weeks. At 30 °C, on the other hand, the survival pattern is very different: as early as the 2nd week only 60% of the animals are still alive, while from the 8th week onwards there is a sharp drop in the survival rate, the longest-lived surviving only until the 17th week.

Fecundity patterns are very different at the different temperatures. The differences relate not only to the total number of eggs produced by one female but also to the time elapsing between spawning and hatching, between birth and the first spawning and to the span of fecund life, factors which obviously determine overall fecundity. The displacement of the age-specific fecundity curves is due to the time required for the animals to reach sexual maturity, which varies greatly between temperatures. The animals kept at 15 °C reach sexual maturity at the 7th week and stop reproducing at the 20th week of life. During this period the fecundity curve presents three well-spaced and progressively lower peaks. At 22 °C the pattern is very different: the animals start spawning from the 3rd week and, at least in its first part, the curve does not present very pronounced peaks. At 30 °C the pattern is again quite different: at this temperature the animals reach sexual maturity earlier and soon begin to lay a large number of eggs; also, the fecundity curve is characterized by three peaks that are much higher and closer together than those observed at 15 °C.

Demography

The weekly record of survival and fecundity of *O. labronica* has enabled us to draw up life tables and to calculate all the demographic parameters relating to the three temperatures assayed, as follows: net reproductive rate (R_0), generation time (T), expectation of life at birth (e^0) and the population growth rate per time unit (λ). The values of the demographic parameters at the different temperatures are reported in Table II. The net reproductive rate varies considerably with temperature; it is higher at the lowest temperature ($R_0 = 540.76$ at 15 °C) and gradually drops as the temperature increases ($R_0 = 425.80$ at 30 °C). Expectation of life at birth also varies greatly with temperature, being decidedly higher at 15 °C and gradually shortening as the temperature increases until, at 30 °C, it is less than half that recorded at 15 °C. Generation time is higher at the lower temperatures: the differences between 15 °C and 22 °C are fairly modest, while at 30 °C it is much lower. The population growth rate is extremely susceptible to temperature: the lowest value (λ=1.87) is found at 15 °C and the highest value (λ=3.44) at 30 °C. The elasticity of λ dependent on the variations in age-specific survival and fecundity is illustrated in Fig. 2 a, b. The elasticity patterns appear more biased to younger age classes at higher temperature because the reduction of the age at maturity; moreover the population growth rate observed at 30 °C seems to be more sensitive to variation in fecundity than at lower temperatures. Thus, the period during which the population growth rate is affected by variations in survival rate and fecundity gradually shortens as the temperature rises; while at 15 °C the elasticity values do not reduce to zero until after the tenth week, at 30 °C they do so as early as the fourth week of life. The contributions made by the variations in age-specific survival and fecundity to the differences in λ are set out in Fig. 3 a, b. The differences between 30 °C and 22 °C are due to the greater fecundity among the first age groups of the animals kept at 30 °C; the higher survival rate, albeit slight, of the animals kept at 22 °C being an advantage only in the first week of life. The differences between 22 °C and 15 °C are also due essentially to fecundity, and in particular to the greater fecundity, from the second week, of the animals kept at 22 °C.

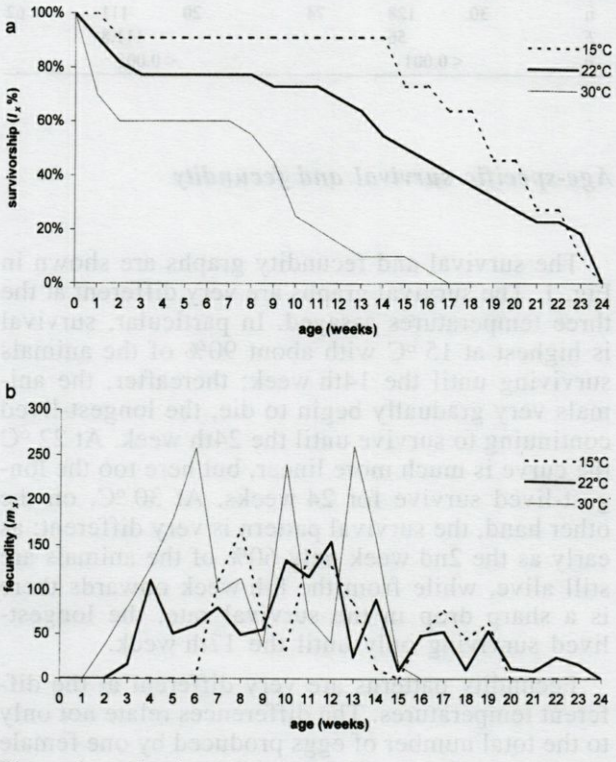

Fig. – 1. a, Survival (l_x) and b, fecundity (m_x) in worms maintained at the tested temperatures.

DISCUSSION

In *Ophryotrocha labronica*, as in many other species of marine invertebrates, numerous traits of

Table II. – Values of demographic parameters in worms maintained at the three tested temperatures.

	15 °C	22 °C	30 °C
λ	1.95	2.84	4.09
r	0.66	1.04	1.40
R_0	540.76	491.80	425.80
e^0	17.59	13.86	6.75
T	11.66	10.25	7.01

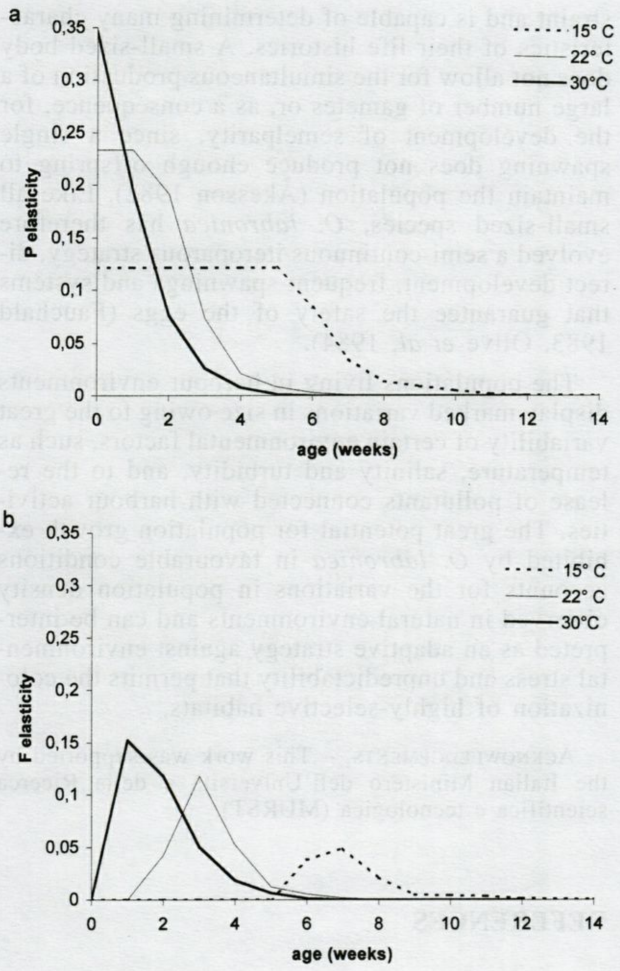

Fig. 2. – Elasticity of a, age-specific survivorship (*P*) and b, age-specific fecundity (*F*) in worms maintained at the tested temperatures.

their life history vary in accordance with environmental factors. Temperature in particular determines not only the age at maturity but also survival and fecundity, with very important consequences for the demography and fitness of the species. The influence of environmental factors on many phases of the life cycle has been demonstrated in numerous species of opportunistic polychaetes characterized by a short life cycle, rapid growth, speedy sexual development and continuous or semi-continuous reproduction (Åkesson 1976, Åkesson & Costlow 1991, Chu & Levin 1986, Gremare *et al*. 1988, Gremare *et al*. 1989 a, b, Levin & Creed 1986, Qian 1984, Qian & Chia 1991, 1992, Tenore & Chesney 1985, Prevedelli & Zunarelli Vandini 1998, 1999, Prevedelli & Simonini 2000). In the case of *O. labronica*, low temperatures cause a considerable delay in the attainment of sexual maturity, a reduced number of spawnings and longer intervals between one spawning and the next; fecundity is therefore low on the whole, even though each cluster averages a greater number of eggs and the animals generally live longer. At high temperatures, on the other hand, the animals mature rapidly, spawn very frequently, fecundity is therefore high, even though the animals have a much shorter life span. The greater and earlier mortality of adults at 30 °C could be related to the greater fecundity seen at this temperature. The greater energy allocated to the production of gametes may be the reason for the shorter lifespan. In iteroparous species, there is a "trade-off" between fecundity and the survival of each single individual: those animals which allocate high levels of energy to germinal tissues potentially risk lower soma survival (Pianka & Parker 1975, Taylor 1991, Stearns 1992). This "trade-off" has been also observed in the small polychaetes *Dinophilus gyrociliatus*

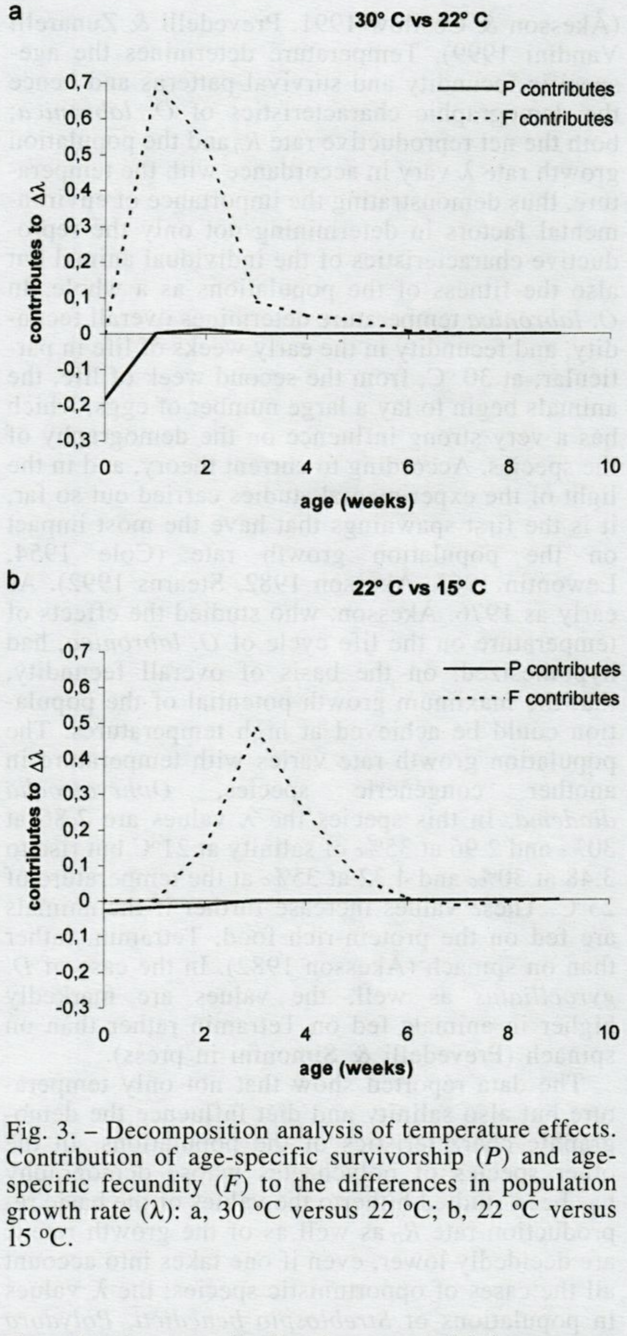

Fig. 3. – Decomposition analysis of temperature effects. Contribution of age-specific survivorship (*P*) and age-specific fecundity (*F*) to the differences in population growth rate (λ): a, 30 °C versus 22 °C; b, 22 °C versus 15 °C.

(Åkesson & Costlow 1991, Prevedelli & Zunarelli Vandini 1999). Temperature determines the age-specific fecundity and survival patterns and hence the demographic characteristics of *O. labronica*; both the net reproductive rate R_0 and the population growth rate λ vary in accordance with the temperature, thus demonstrating the importance of environmental factors in determining not only the reproductive characteristics of the individual animal but also the fitness of the populations as a whole. In *O. labronica* temperature determines overall fecundity, and fecundity in the early weeks of life in particular; at 30 °C, from the second week of life, the animals begin to lay a large number of eggs, which has a very strong influence on the demography of the species. According to current theory, and in the light of the experimental studies carried out so far, it is the first spawnings that have the most impact on the population growth rate (Cole 1954, Lewontin 1965, Åkesson 1982, Stearns 1992). As early as 1976, Åkesson, who studied the effects of temperature on the life cycle of *O. labronica*, had hypothesized, on the basis of overall fecundity, that the maximum growth potential of the population could be achieved at high temperatures. The population growth rate varies with temperature in another congeneric species, *Ophryotrocha diadema*. In this species the λ values are 2.86 at 30‰ and 2.96 at 35‰ of salinity at 21°C but rise to 3.48 at 30‰ and 4.32 at 35‰ at the temperature of 25°C. These values increase further if the animals are fed on the protein-rich food, Tetramin, rather than on spinach (Åkesson 1982). In the case of *D. gyrociliatus* as well, the values are markedly higher in animals fed on Tetramin rather than on spinach (Prevedelli & Simonini in press).

The data reported show that not only temperature but also salinity and diet influence the demographic characteristics of the populations. In the other species of polychaetes whose demography has been studied hitherto the values of the basic reproduction rate R_0 as well as of the growth rate λ are decidedly lower, even if one takes into account all the cases of opportunistic species; the λ values in populations of *Streblospio benedicti, Polydora ligni* and *Capitella capitata*, for example range from a minimum of 1.205 to a maximum 1.381 (Levin *et al.* 1987). The differences between these species and *O. labronica, O. diadema* and *D. gyrociliatus* mainly concern the body size. *S. benedicti, P. ligni* and *C. capitata* are much bigger (10-20 mm) than either *D. gyrociliatus*, which is the smallest species of all, being only 0.8 mm long, or *O. labronica* and *O. diadema*, which are at most 4 mm long. The R_0 and λ values of *O. labronica* are greater than those of typically opportunistic species, which are by definition *r*-strategists (Grassle & Grassle 1974). This feature, which is shared by *D. gyrociliatus* and *O. diadema*, is very probably due to the animals' small size. Body size constitutes a very important morphological constraint and is capable of determining many characteristics of their life histories. A small-sized body does not allow for the simultaneous production of a large number of gametes or, as a consequence, for the development of semelparity, since a single spawning does not produce enough offspring to maintain the population (Åkesson 1982). Like all small-sized species, *O. labronica* has therefore evolved a semi-continuous iteroparous strategy, direct development, frequent spawnings and systems that guarantee the safety of the eggs (Fauchald 1983, Olive *et al.* 1984).

The populations living in harbour environments display marked variations in size owing to the great variability of certain environmental factors, such as temperature, salinity and turbidity, and to the release of pollutants connected with harbour activities. The great potential for population growth exhibited by *O. labronica* in favourable conditions accounts for the variations in population density observed in natural environments and can be interpreted as an adaptive strategy against environmental stress and unpredictability that permits the colonization of highly-selective habitats.

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REFERENCES

Åkesson B 1970. Sexual conditions in a population of the polychaete *Ophryotrocha labronica* La Greca & Bacci from Naples. *Ophelia* 7: 167-176.

Åkesson B 1972a. Incipient reproductive isolation between geographic population of *Ophryotrocha labronica* (Polychaeta: Dorvilleidae). *Zool Scr* 1: 207-210.

Åkesson B 1972b. Sex determination in *Ophryotrocha labronica* (Polychaeta: Dorvilleidae). *In* Battaglia B ed, Fifth European Marine Biology Symposium. Piccin, Padova: 163-172.

Åkesson B 1973. Reproduction and larval morphology of five *Ophryotrocha* species (Polychaeta, Dorvilleidae). *Zool Scr* 2: 145-155.

Åkesson B 1976. Temperature and life cycle in *Ophryotrocha labronica* (Polychaeta, Dorvilleidae). *Ophelia* 15: 37-47.

Åkesson B 1982. A life table study on three genetic strains of *Ophryotrocha diadema* (Polychaeta: Dorvilleidae). *Int J Invert Reprod* 5: 59-69.

Åkesson B, Costlow JD 1978. Effects of temperature and salinity on the life cycle of *Ophryotrocha diadema* (Polychaeta, Dorvilleidae). *Ophelia* 17: 215-229.

Åkesson B, Costlow JD 1991. Effects of constant and cyclic temperatures at different salinity levels on survival and reproduction in *Dinophilus gyrociliatus* (Polychaeta: Dinophilide). *Bull Mar Sci* 48 (2): 485–499.

Bhaud M 1988. Influence of temperature and food supply on development of *Eupolymnia nebulosa* (Montagu, 1818) (Polychaeta: Terebellidae). *J Exp Mar Biol Ecol* 118: 103-113.

Caswell H 1989. Matrix population models. Sinauer, Sunderland.

Caswell H 2000. Matrix population models. 2nd edition, Sinauer, Sunderland.

Chu JW, Levin LA 1989. Photoperiod and temperature regulation of growth and reproduction in *Streblospio benedicti* (Polychaeta: Spionidae). *Inv Repr Dev* 15: 131-142.

Cole LC 1954. The population consequences of life history phenomena. *Q Rev Biol* 29: 103-137.

De Kroon H, Plaisier A, Van Groenendael J, Caswell H 1986. Elasticity: the relative contribution of demographic parameters to population growth rate. *Ecology* 67: 1427-1431.

Fauchald K 1983. Life diagram patterns in benthic polychaetes. *Proc Biol Soc Wash* 96: 160-177.

Garwood PR 1980. The role of temperature and daylength in the control of the reproductive cycle of *Harmothoe imbricata* (Polychaeta: Polynoidae). *J Exp Mar Biol Ecol* 47: 35–53.

Grassle JF, Grassle JP 1974. Opportunistic life histories and genetic systems in marine benthic polychaetes. *J Mar Res* 32: 253-284.

Grémare A, Marsh AG, Tenore KR 1988. Short-term reproductive responses of *Capitella* sp. I (Annelida: Polychaeta) fed on different diets. *J Exp Mar Biol Ecol* 123: 147-162.

Grémare A, Marsh AG, Tenore KR 1989a. Fecundity and energy partitioning in *Capitella capitata* type I (Annelida: Polychaeta). *Mar Biol* 100: 365-371.

Grémare A, Marsh AG, Tenore KR 1989b. Secondary production and reproduction of *Capitella capitata* type I (Annelida: Polychaeta) during a population cycle. *Mar Ecol Prog Ser* 51: 99-105.

La Greca M, Bacci G 1962. Una nuova specie di *Ophryotrocha* delle coste tirreniche (Annelida, Polychaeta). *Boll Zool* 29: 13-24.

Levin LA, Creed EL 1986. Effect of temperature and food availability on reproductive responses of *Streblospio benedicti* (Polychaeta: Spionidae) with planktotrophic or lecithotrophic development. *Mar Biol* 92: 103-113.

Levin LA, Caswell H, De Patra KD, Creed EL 1987. Demographic consequences of larval development mode: planktotrophy vs. lecithotrophy in *Streblospio benedicti*. *Ecology* 68: 1877-1886.

Lewontin RC 1965. Selection or colonizing ability. *In* HG Baker & GL Stebbins eds, The genetics of colonizing species, Academic Press, New York: 79-94.

Neuhoff HG 1979. Influence of temperature and salinity on food conversion and growth of different *Nereis* species (Polychaeta: Annelida). *Mar Ecol Prog Ser* 1: 255-262.

Olive PJW 1984. Environmental control of reproduction in Polychaeta. *In* Polychaeta Reproduction, Fischer A & Pfannenstiel HD eds, Fortschritte der Zoologie, 29, Gustav Fischer Verlag, Stuttgart, New York: 7-38.

Olive PJW, Morgan PJ, Wright NH, Zhang SL 1984. Variable reproductive output in Polychaeta; options and design constraints. *In* Engels W, Clark WH jr, Fisher A, Olive PJW, Went DF eds, Advances in Invertebrate Reproduction 3: 399-408.

Olive PJW, Porter JS, Sandeman NJ, Wright NH, Bentley MG 1997. Variable spawning success of *Nephtys hombergi* (Annelida: Polychaeta) in response to environmental variation: a life history homeostasis ? *J Exp Mar Biol Ecol* 215: 247-268.

Olive PJW, Lewis C, Beardall V 2000. Fitness components of seasonal reproduction: an analysis using *Nereis virens* as a life history model. *Oceanologica Acta* 23: 377-389.

Pianka ER, Parker WS 1975. Age specific reproductive tactis. *Am Nat* 109: 453-464.

Premoli MC, Sella G 1995. Sex economy in benthic polychaetes. *Ethol Ecol Evol* 7: 27-48.

Premoli MC, Sella G, Berra P 1996. Heritable variation of sex ratio in a polychaete worm. *J Evol Biol* 9: 845-854.

Prevedelli D 1991. Influence of temperature and diet on survival of *Perinereis rullieri* Pilato (Polychaeta, Nereididae). *Boll Zool* 58: 225-228.

Prevedelli D 1992. Growth rate of *Perinereis rullieri* Pilato (Polychaeta, Nereididae) under different conditions of temperature and diet. *Boll Zool* 59: 261-265.

Prevedelli D 1994. Influence of temperature and diet on the development and growth of juveniles *Marphysa sanguinea* (Montagu) (Polychaeta, Eunicidae). *In* Dauvin JC, Laubier L & Reish DJ eds, Actes 4 Conf internationale des Polychètes. *Mém Mus nat Hist nat* 162: 521-526.

Prevedelli D, Zunarelli Vandini R 1998. Effect of diet on reproductive characteristics of *Ophryotrocha labronica* (Polychaeta: Dorvilleidae). *Mar Biol* 132: 163-170.

Prevedelli D, Zunarelli Vandini R 1999. Survival, fecundity and sex ratio of *Dinophilus gyrociliatus* (Polychaeta: Dorvilleidae). *Mar Biol* 133: 231-236.

Prevedelli D, Simonini R 2000. Effects of salinity and two food regimes on survival, fecundity and sex ratio in two groups of *Dinophilus gyrociliatus* (Polychaeta, Dinophilidae). *Mar Biol* 137: 23-29.

Prevedelli D, Simonini R. Effects of diet and laboratory rearing on demography of *Dinophilus gyrociliatus* (Polychaeta: Dinophilidae). *Mar Biol* (in press).

Qian PY 1994. Effect of food quantity on growth and reproductive characteristics of *Capitella* sp. (Annelida: Polychaeta). *Invert Reprod Develop* 26: 175-185.

Qian PY, Chia FS 1991. Fecundity and egg size are mediated by food quality in the polychaete worm *Capitella* sp. *J Exp Mar Biol Ecol* 148: 11-25.

Qian PY, Chia FS 1992. Effect of diet type on the demographics of *Capitella* sp. (Annelida: Polychaeta): lecithotrophic development vs. planktotrophic development. *J Exp Mar Biol Ecol* 157: 159-179.

Stearns SC 1992. The evolution of life histories. Oxford University Press, New York, 249 p.

Taylor P 1991. Optimal life histories with age dependent trade-off curves. *J Theor Biol* 148: 33-48.

Tenore KR, Chesney E 1985. The effects of interaction of rate of food supply and population density on the bioenergetics of the opportunistic polychaete, *Capitella capitata* (type 1). *Limnol Oceanogr* 30: 1188-1195.

Yokohama H 1988. Effects of temperature on the feeding activity and growth rate of the spionid polychaete *Paraprionospio* sp. (form A). *J Exp Mar Biol Ecol* 123: 41-60.

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