Salinity and temperature influence in rotifer life history characteristics

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Abstract

A review of temperature and salinity effects on rotifer population dynamics is presented together with original data of these effects for three clones of *Brachionus plicatilis*. There is a clear relationship between temperature and the intrinsic rate of increase, r: an increase of temperature – within the natural environmental range – produces an exponential increase of r, and the slope of the response depends on the genotype. The effect of salinity is also genetically dependent; the highest r for each clone is observed at the salinity close to that of its environmental origin. The response of r to temperature is mainly a consequence of the response of the individual rates of development and reproductive timing. The effect of temperature on fecundity (number of descendents per individual life time) is negligible when temperature values are within the normal habitat ranges. On the other hand, salinity seems to affect primarily fecundity. The interaction salinity-temperature may be important in clones or species living in fluctuating environments with positive response to the more frequent combinations found in the corresponding habitats.

Introduction

Extended studies of aquatic populations usually confirm a community typology that matches environmental heterogeneity. The main factors determining the community typology are most frequently (1) temperature, (2) salinity and the parameters associated with it, and (3) trophic status of the waters. For instance, principal components analysis, for data on the species abundance in zooplanctonic communities from a wide range of conditions, usually identify, as the first principal components, variables that are highly correlated with the above mentioned factors (e.g., Miracle, 1974; Armengol, 1978; Miracle *et al.*, 1987; Nogrady, 1988). Temperature, salinity and food are also the most frequently studied factors in life history analysis.

This paper reviews results of laboratory experiments on the relationships of temperature and salinity to the intrinsic rate of population increase, r, which is assumed to be the best measure of fitness in non-saturated environments. Rotifers in strongly fluctuating planktonic environments, which have to adapt to regular colonizing events, may frequently be subject to selection for high r. The paper is divided into two main sections. In the first, a brief bibliographic review of the effects of temperature and salinity on population dynamics parameters is given. Physiologic effects on individual rotifers will also be summarized to help interpret the effects on populations. In the second, original data combining the two factors from a series of experiments will be discussed. Our intention is to evaluate the interaction between temperature and salinity, *i.e.*, the dependence of the effect of one factor on the level of the other.

Temperature: effects on individuals

The direct positive effect of temperature on physiological rates in individual rotifers and on rotifer populations have been clearly demonstrated. Several of these studies deal with the relationship between temperature and duration of embryonic development. Vinberg & Galkovskaya (1979), Herzig (1983), Duncan (1983) and Galkovskaya (1987) have summarized data on the subject. The duration of embryonic development (D) in rotifers is a curvilinear function of temperature (T), which can be adequately described by Belehradek's equation $1/D = a(T - b)^c$ $(a,b,c,$ fitted parameters) or Arrhenius' equation $1/D = ae^{-b/T}$ (Waltz, 1983) as in other organisms (Herzig, 1983). However other equations have also been proposed as best fit (i.e., $1/D = a + bT + cT^2$, Galkovskaya, 1987; $1/D = ae^{bT}$, Duncan, 1983). Furthermore, when homogeneous data from one species, studied by the same author, in a limited range of temperatures, are used, the relationship between $1/D$ and T is nearly linear (Edmondson, 1965; Pourriot & Deluzarches, 1971). The slope of the curve and the absolute rate values are dependent on genotype. Cold-water adapted species (Galkovskaya,

1987) or clones (Pourriot & Deluzarches, 1971) have lower slopes and globally smaller rates than warm-water adapted ones. Therefore, in many cases, cold-adapted species show faster low-temperature development but much slower high-temperature development than warm-adapted species and vice versa. However, other factors such as the r-K strategy of the species have to be considered. The effect of temperature is also dependent on its stability. If temperature fluctuates around a mean value, the egg development time deviates from that at the constant mean (Ruttner-Kolisko, 1975, 1978); it is shortened, as would be expected, by the effect of oscillating temperature on the metabolism. Figure 1 presents idealized responses to temperature change of activities and functions discussed in this section.

It is often assumed that duration of embryonic development is only dependent upon the temperature (Herzig, 1983). However, relations with other parameters have also been described, mainly with egg volume (Pourriot & Deluzarches, 1971), which is in turn dependent on temperature (Pourriot, 1973a) or on the feeding conditions of the mother (Yúfera, 1987).

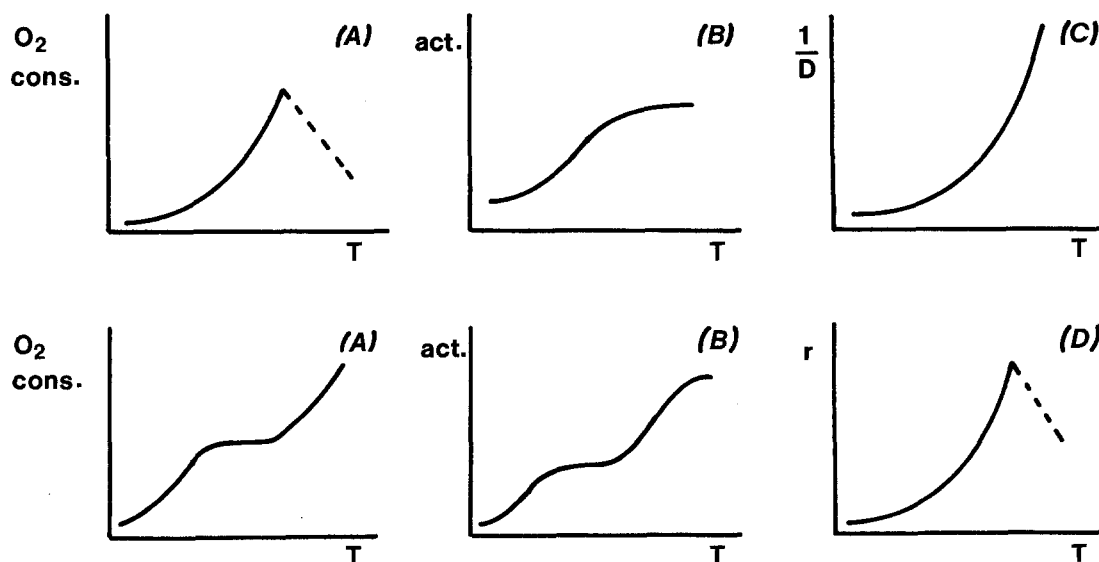Duration of the pre-reproductive period is also a clear function of temperature. Its variation

Fig. 1. Ideal curves showing relationships between temperature and (A) oxygen consumption, (B) activity (filtration rate), (C) inverse of development rate, and (D) intrinsic rate of growth.

parallels that of egg development. Thus, under the same feeding conditions the ratio postembryonic/-embryonic development time remains quite constant (Pourriot & Deluzarches, 1971; Ruttner-Kolisko, 1975). However, when rotifers are subjected to fluctuating temperature, the above mentioned ratio could be very different because there is some evidence (Ruttner-Kolisko, 1978) that the duration of the pre-reproductive period does not deviate significantly from that obtained at the corresponding mean temperature.

Post-embryonic growth is also highly dependent on temperature. Growth in length in rotifers can be described by the Bertalanffy equation (Lebedeva & Gerasimova, 1985; Carmona et al., this volume). Growth is almost totally restricted to the juvenile period (defined as lasting until the laying of the first egg): the growth rate undergoes a sharp decrease coincident with the beginning of reproduction and from then on, matter and energy are directed towards reproduction instead of growth. The somatic growth rate in juveniles is a clear function of temperature as well as the duration of the growth period. Consequently, the calculated Q_{10} for both somatic growth (during the pre-reproductive period) and egg development are similar, ranging approximately from 2 to 3 (Lebedeva & Gerasimova, 1985, Pourriot & Deluzarches, 1971, Duncan, 1983).

Very few studies exist on the effect of temperature on rotifer metabolism, and they have variable results. Pourriot (1973b) and Galkovskaya et al. (1987) find an exponential increase in oxygen consumption with temperature. On the other hand, Epp & Lewis (1980), studying a clone of B. plicatilis, suggest that there is a plateau in oxygen consumption, within the range of environmental temperatures in which the rotifer is most frequently found. The species studied by Pourriot (1973b) and Galkovskaya et al. (1987) were Brachionus calyciflorus and Rinoglena frontalis. Q_{10} was higher for B. calyciflorus (Q_{10} = 2.3–2.4) and much lower for the cold stenotherm R. frontalis (Q_{10} = 1.4). Thus, the oxygen consumption for R. frontalis is higher than that of B. calyciflorus at low temperatures, but much lower at medium and high temperatures. This

behaviour of cold vs. warm water species is similar to the trends described for egg development time.

Galkoskaya (1987) also reports data on O_2 consumption in natural populations of Brachionus calyciflorus and Hexarthra mira; the same exponential function was found but with smaller slope than the cultivated individuals. Another difference was that, after a maximum, a sharp decline occurred when temperatures were too high. H. mira, usually occurring in lower temperatures than B. calyciflorus, also showed lower O_2 consumption. Other metabolic rates have rarely been studied. Nitrogen excretion rates, investigated for B. calyciflorus by Galkovskaya et al. (1987), showed the same exponential function with temperature as O_2 consumption and a quite similar Q_{10} (= 2.2).

There is also only fragmentary information on rotifer activities, but from this, it seems that there exists a clear response to temperature. The observed response, when a wide range of temperatures is tested, could be interpreted either as a sigmoid curve with a decline at unsuitably high temperatures, or as two sigmoid functions with a plateau, at a specific optimum range of temperatures, in between. Tested activities are mainly filtration and ingestion rates (Hirayama & Ogawa, 1972; Galkovskaya, 1987), and locomotion (Epp & Lewis, 1984, Snell et al., 1987), with interpretation of the obtained results varying amongst the authors. Rates of beat of vibratile flames and of output from the contractile vesicles in Asplanchna have been also investigated (Pontin, 1966). Up to 24 °C, the relationship between the activity of vibratile flames and temperature is a exponential function.

Temperature: effects on populations

The intrinsic rate of increase

From comparison of the maximum rates of increase of zooplanktonic organisms (Allan, 1976, 1980) it can be inferred that (1) rotifers show amongst the highest r values of all zooplankton species, and (2) that the crucial

Table 1. The intrinsec rate of increase (r, days^{-1}) of some rotifer species growing at different temperature (if not preadapted, the pre-experimental temperature is indicated in bracket).

Rotifer species	Temperature (°C)																		Reference
	5	10	15	16	17	19	20	22	24	25	27	30	32	35	36	37	40	43	
Brachionus plicatilis																			
[1]							0.16			0.38		0.62							King & Miracle, 1980
[2]							0.12			0.32		0.50							
[3]							0.30			0.36		0.44							
plicatilis [4]		0.12		0.39		0.43		0.65		0.74	0.91	0.49							Hirayama & Kusano, 1972
plicatilis [5]							0.5			0.7		1.10	0.68		0.4		0.5		Snell, 1986
plicatilis [6]			<0		<0		0.54			0.74		0.98		1.35			1.07	<0	Pascual & Yúfera, 1983
plicatilis [7]							0.13		0.25										Yúfera & Pascual, 1980
plicatilis [8]		0.12					0.53												Nagata, 1985
plicatilis [9]			0.36				0.57			0.96									Ruttner-Kolisko, 1972
Brachionus calyciflorus [10]							0.23					2.18				0.38 [28 °C] / 0.34 [35 °C]			Galkovskaya, 1983
calyciflorus [11]												1.56				2.83	2.18		Galkovskaya, 1987
[12]												2.18				2.95	1.94		
[13]										1.2			1.7						
calyciflorus [14]			0.34				0.48 / 0.60 [*T* variable]			0.82									Halbach, 1973
calyciflorus [15]			<0				0.1			<0		<0							In: Starkweather, 1987
[16]			0.2				0.6			1.7		0.9							
[17]			0.3				0.7			1.9		2.5							
[18]			0.4				2.2			1.9		3.7							
Brachionus dimidiatus [19]							0.53			0.70		1.04							Pourriot & Rougier, 1975
[20]							0.38			0.43		1.22							
[21]							0.46			0.74									
[22]							0.47			0.52									
[23]							0.30			0.42									

Species							Source
Euchlanis dilatata							King, 1972
[24]	0.81					1.78	
[25]	0.68					2.10	
[26]	0.61					2.13	
Asplanchna sieboldi							Gilbert, 1976
[27]		0.60		0.66		1.08	[Saccatte morphotype]
[28]		0.72		0.85		1.22	[Campanulate morphotype]
Brachionus angularis							Walz, 1987
[29]	−0.005	0.073	0.103	0.352	0.154		
Keratella cochlearis							Walz, 1983
[29]	0.004	0.034	0.098	0.082	0.076		

Food conditions and other observations:

[1]–[3] *Chlorella* (10^6 cell/ml); the three sets of values corresponds to three clones. Clone [3] coming from cold waters than clones [1] and [2].

[4] *Chlorella* (2.27 × 10^6 cell/ml).

[5] *Chlorella vulgaris* (10 μgC/ml).

[6] *Nannochloris oculata* (45–60 × 10^6 cell/ml).

[7] *Nannochloris* (6 × 10^6 cell/ml) plus *Saccharomyces cerevisiae* (0.35 g/l per day).

[8] *Chlorella saccharophila* (1–2 × 10^6 cell/ml).

[9] *Dunaliella* sp.

[10] *Chlorella* (5 × 10^6 cell/ml).

[11]–[13] *Chlorella*:   [11]   [12]   [13]
                          5 × 10^6 50 × 10^6 240 × 10^6 cell/ml.
In [12] the experimental conditions were different that in [10] and [11].

[14] *Kirchneriella lunaris* (10^6 cell/ml).

[15]–[18] *Euglena gracilis*, original data of B. Skrdla and P. L. Starkweather:
           [15]   [16]   [17]   [18]
           0.1   1.0   10   100 μg dry weight/ml.

[19] *Dunaliella salina*.

[20] *Diogenes* sp.

[21] *Synechococcus cedrorum*.

[22] *Synechocystis* sp.

[23] *Saccharomyces cerevisiae*.

[24]–[26] *Chlamidomonas reinhardti* (0.5 × 10^6 cell/ml); the different values are average *r* from groups of clones collected at different times of the year:
           [24]   [25]   [26]
           May 1   June 5 June 12

[27] *Paramecium aurelia* (in excess); the different values are average *r* from groups of replicates.

[28] *Asplanchna brightwelli* (in excess); the different values are average *r* from groups of replicates.

[29] *Stichococcus bacillarius* (75 × 10^6 cell/ml).

advantage of one species against another, under a particular set of conditions, may lie in how r responds to any one of the changing conditions. Moreover, r summarizes all life tables parameters, because it combines survival, fecundity and the timing of development and reproduction. For this reason, we will center the review mainly on this parameter, and secondarily on life span as a measure of the stability or replacement time of the generations.

Table 1 compiles literature data on intrinsic rates of increase measured at different temperatures. Because of the important influence of other factors on r, mainly genotypes and food quantity and quality, we have only included data sets from experiments conducted at different temperatures by the same author, so that all other conditions would remain the same. In addition, it should also be considered that the different authors estimate r values by different methods; they may be obtained from individual, batch or continuous cultures, and by means of different mathematical approaches.

Very few species of rotifers have been studied to determine the relationship between r and temperature under laboratory controlled conditions. *Brachionus plicatilis* and *B. calyciflorus* are the most studied. Different clones of these species have maxima of r at different temperatures. This may be attributed to (1) selection at the environmental temperatures of origin, and (2) the interaction of food with temperature. This interaction is a complicated balance between the effect of temperature on filtering rates, low when the temperature is low, and the accelerated consumption of food for growth and reproduction with increasing temperatures. Thus, at low temperatures, if the food level is low, the reduction of food intake rate may not be compensated for by the corresponding decrease of the metabolic rate. On the other hand, at high temperatures the accelerated metabolism could only be satisfied if there were high quantities of food in the medium. This is clearly illustrated by the data between the interaction of food density and temperature given by Starkweather (1987, Table 1). However, it has also been observed, especially at high temperatures, that an exaggerated excess of food could be detrimental

as a result of the decomposition of the surplus food (Stemberger & Gilbert, 1985; Galkovskaya, 1987).

From Table 1, three kinds of response can be discriminated. The first 5 species may be considered warm water adapted; they show their highest or maximum r values at temperatures over 27 °C. These maxima range most frequently from 1 to 2. Exceptional r values of 2.8–2.9 have also been found for clones with a high food supply, acclimatized to high temperatures (37 °C). *Keratella cochlearis* can be considered as a cold water species, the studied clone has a very low maximum r (<0.1) localized at 15 °C, which is the result of a low fecundity and slow development, thus, its longer life insures the maintenance of its population. The studied clone of *Brachionus angularis* has an intermediate position; it reaches a rather low maximum r (0.35) at 20 °C.

In the first group of species, the averaged relative increase of r, when the temperature rises from 20 to 25 °C, is around 10% per degree of temperature increase, although it varies from 2 to 35%, which correspond to ratios $r_{25 °C}/r_{20 °C}$ from 1.1 to 2.6 (mean around 1.5). Using the Q_{10} concept for r,

$$\ln Q_{10} = 10 \, (\ln r_2 - \ln r_1)/(T_2 - T_1) \, ,$$

we obtain values from 1.2 to 6.7 (mean around 2.3). Slightly smaller values of these parameters were found for increases from 25 to 30 °C. In most cases within clones, the relationship between r and temperature is almost linear from 20 to 30 °C.

On the other hand, the studied strain of *Keratella cochlearis* showed much higher relative increases: around 120% from 5 to 10 °C and 36% from 10 to 15 °C, with corresponding ratios $r_{10 °C}/r_{5 °C} = 7$ ($Q_{10} = 50$) and $r_{15 °C}/r_{10 °C} = 2.8$ ($Q_{10} = 8$). *Brachionus angularis* again had an intermediate position.

Although data are very fragmentary, it can be seen that if, for comparison, we plot (Fig. 2) the three types of response of r with temperature, standardizing the data of each clone to their corresponding maximum r value, r_{max}, and their optimum temperature (*i.e.*, temperature at which r is maximum, $T_{r_{max}}$), a family of similar curves is obtained. They are composite, highly asymmetric,
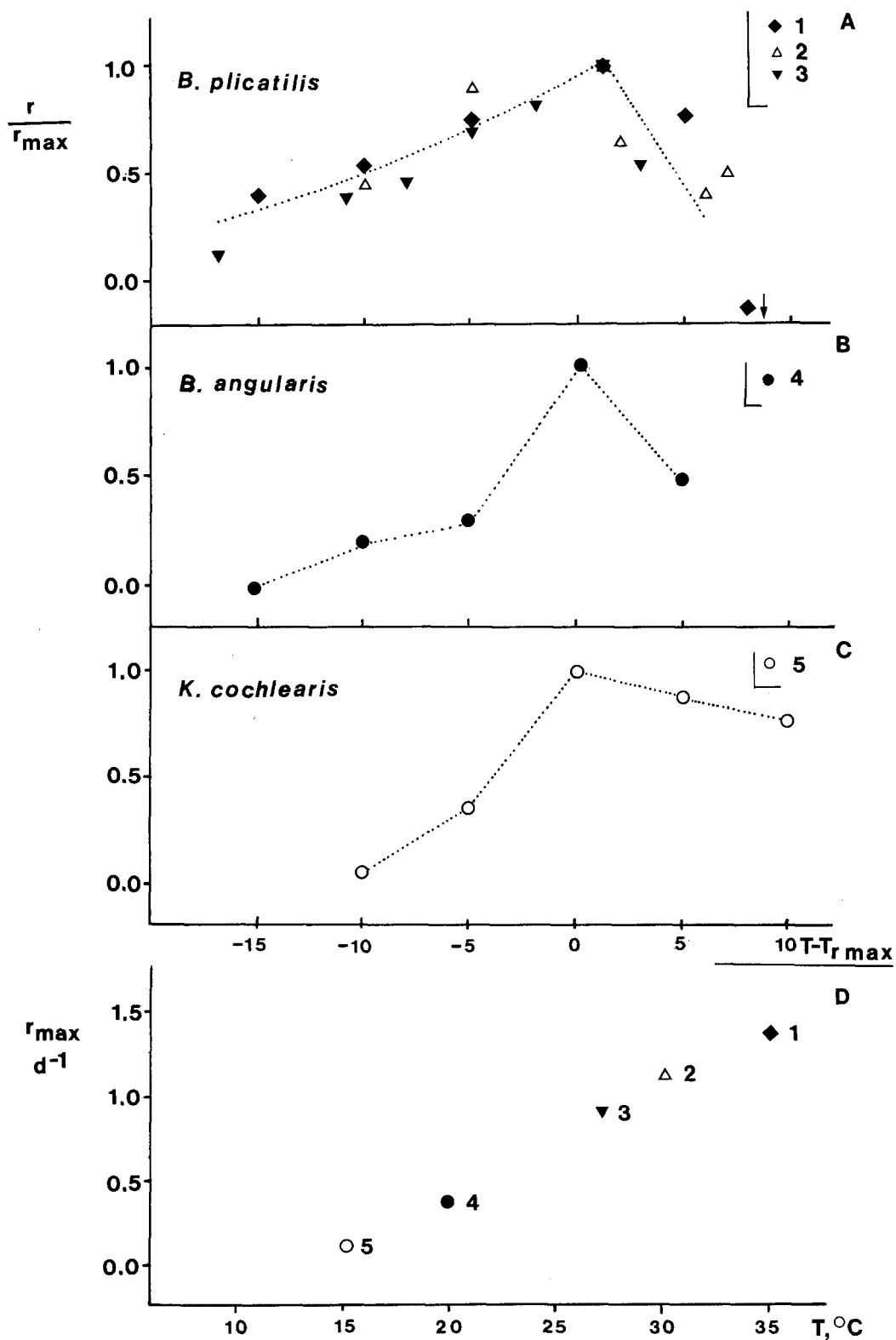
Fig. 2. A, B, and C. Relative r values (r/r_{max} on the ordinate) as a function of the distance from the optimum temperature ($T - T_{r_{max}}$) on the abcissa. D. Maximum r (r_{max}) and its corresponding temperature ($T_{r_{max}}$) for the indicated rotifers. (1: Hirayama & Kusano, 1980; 2: Snell, 1986; 3: Pascual & Yúfera, 1983; 4: Walz, 1987; 5: Walz, 1983).

Table 2. Duration of life (in days) of some rotifers growing at different temperatures (LT 50, age for a survival probability of 0.5).

Rotifer species	Temperature (°C)																			Reference
	5	10	14	15	18	19	20	22	24	25	26	27	28	30	32	35	37	38	40	
Brachionus plicatilis																				
[1]							6.2			6.2				6.8						King & Miracle, 1980
[2]							6.7			6.0				6.0						
[3]							16.5			13.5				11.0						
plicatilis [4]		16.2				19.2				8.0				2.9					[LT 50]	Hirayama & Kusano, 1972
plicatilis [5]					9.9								6.4					3.3		Shell, 1986
plicatilis [8]		11.5					26.5													Nagata, 1985
plicatilis [9]				15			10			7										Ruttner-Kolisko, 1972
Brachionus calyciflorus																				
[12]														2.61			2.20		1.5	Galkovskaya, 1987
[13]														2.72			1.75		1.16	
calyciflorus [14]				17.2			11			5									[LT 50]	Halbach, 1973
Brachionus dimidiatus																				
[19]							9.5			7.7				3.5						Pourriot & Rougier, 1975
[21]							9			8.9				3.6						
Euchlanis dilatata																				
[24]						3.3						2.5								King, 1972
[25]						3.1						3.2								
[26]						3.4						3.76								
Asplanchna sieboldi																				
[27]								6.1		4			2.5							Gilbert, 1976
[28]								6.9		5.26			2.9							

[Saccate morphotype]
[Campanulate morphotype]

Species									Reference
Asplanchna brightwelli [30]				4.7	3.2		2.6		Snell & King, 1977
Brachionus angularis [29]	19.4	14.9	4.1	4.5	2.8				[LT 50] Walz, 1987
Keratella cochlearis [29]	27.0	21.8	14.9	8.8	6.3				Walz, 1983
Hexarthra fennica [31]			12.5	6.3	4				Ruttner-Kolisko, 1975
Philodina roseola [32]			35	47	(42)	15	5	3	Lebedeva & Gerasimova, 1987

Food conditions and other observations:

From [1] to [29], see the footnote of Table 1.
[30] *Paramecium aurelia.*
[31] *Chlorella vulgaris* (10^6 cell/ml).
[32] *Chlorella vulgaris* (11×10^6 cell/ml); the value in parentheses was included by the authors from Ricci, 1976.

curves divided by a sharp maximum. The left slope is higher than the right slope in the cold-adapted species and the opposite occurs in warm-adapted species. Below this maximum, r is an exponential function of temperature, but in a homogeneous experiment and for a specific range of temperature this function could be almost linear. This response to temperature reflects metabolic, embryonic and post-embryonic development rates, and could be fitted to Belehradek's or Arrhenius' equation. The second part of the curve is most probably a disequilibrium between reproduction and survival; reproduction at a too early stage, as a consequence of high temperature, could diminish further survival (Snell & King, 1977). This is most dramatic when the set of environmental conditions is not quite suitable for the rotifer at the experimental temperature.

In most cases, in the first group of warm-water species, net reproduction, R_0, varies little (Hirayama & Ogawa, 1972; King & Miracle, 1980; Pourriot & Rougier, 1975; Halbach, 1970; Ruttner-Kolisko, 1972), within a certain temperature range. The effect of temperature on r is mainly due to its effect on metabolism and development if the rotifer remains under a suitable set of conditions. R_0 is only low at the most extreme temperatures.

For species in colder temperatures, R_0 is also variable (Walz, 1983, 1987) and has an important effect on r. In this case, values of R_0 are low owing to the fact that reproduction starts very late, and then the juvenile period constitutes a high percentage of the mean life span (approx. 50% at low temperatures versus approx. 30% at the optimum temperature). Under these conditions the reproductive period is short. This delay in initial reproduction reduces r by increasing the generation time. At very high temperatures, gross reproduction may not vary, but low survival decreases R_0 as we mentioned before. At extreme values of temperature gross reproduction diminishes also.

The life span

Table 2 compiles all the data found on mean life span at different temperatures. Most littoral-benthic rotifers (especially bdelloids: Ricci, 1978; Lebedeva & Gerasimova, 1987, but also *Lecane tenuiseta*, Hummon & Bevelhymer, 1979) have much longer life spans than planktonic rotifers, as expected by their occupation of more stable environments. However, there are exceptions, such as *Euchlanis dilatata* which showed the shortest of all the reviewed life spans. Apart from the littoral-benthic species, the mean life span varies, most frequently, from 3 to 20 days, and the ratio between life spans for a 5 °C increase is most frequently from 1.2 to 2, which indicates diminutions between 4 and 20% (averages 1.6, 11%).

Within a species, clones show longer life spans according to size and their adaptation to colder temperatures (King & Miracle, 1981). Also the life span of cold-adapted *Keratella cochlearis* is somewhat longer than that of the other studied planktonic species.

Life span decreases with a rise of temperature, the relationship again being similar to the duration of embryonic and post-embryonic development, intervals between egg depositions, etc. Life span matches the corresponding acceleration of reproductive effort (descendants per female per day) with temperature, and an inverse relationship exists between the two responses. As Snell & King (1977) pointed out, reproduction decreases the probability of future survival. However, in this case the physiological basis for an inverse relationship between reproduction and survival is the acceleration of development, the organisms more or less attain their potential number of descendents during their life time, but over a longer or shorter period with different timings.

Salinity effects on individuals

Total dissolved salts and relative specific ionic concentrations are important factors conditioning rotifer distribution (Ruttner-Kolisko, 1971; Miracle *et al.*, 1987). Several rotifer genera have halobiont species living in a very wide range of salinities. *Brachionus, Hexathra, Notholca, Synchaeta* are the most relevant. Moreover a number of essentially freshwater forms can also be salt

tolerant to a certain extent. Nevertheless, studies on salinity effects on rotifer individuals or populations are extremely scarce.

Osmotic regulation has seldom been investigated. However, there is good evidence to suggest that highly evolved rotifers can regulate the salt concentration of the pseudocoelomic fluid by means of their flame cells and contractile vesicle. This has been confirmed for *Asplachna* (Pontin, 1964, 1966; Braun *et al.*, 1966) in which larger species or forms have a higher number of flame bulbs and in which the vibratile flames show an activity inversely related to the concentration of the medium. In addition, when the animal is placed in a more dilute medium, the protonephridium responds by sodium conservation, increased water excretion and decreased total solute excretion. Kabai & Gilbert (1978) relate the osmoregulatory capacity of these viviparous organisms to the independence of the embryos from the external environment, supported by the negligible effects that very severe osmotic decreases (10–100 fold dilutions of the normal medium) had on the response of body wall-outgrowth to tocopherol, in *A. sieboldi*. At extreme dilutions, *A. sieboldi* fecundity was drastically reduced. There is also evidence, from electron microscopy studies of protonephridia (Clément, 1968), that *Notommata copeus* also

osmoregulates. It seems however that both (*Asplanchna* and *Notommata*) are incapable of hypoosmotic regulation. These rotifers, as well as other rotifers, may behave as a group of 'essentially freshwater species that are salt tolerant' as described in Bayly (1972). These animals are hyperosmotic regulators until the salinity of the external medium more or less coincides with that of the body fluids (Fig. 3, A). At this point, many species reach their upper limit of tolerance, which may be widened by acclimatization through increases of the isosmotic point. Other species of this group which are somewhat more salt tolerant, behave as osmoconformers for salinities over isosmoticy. Many rotifer species could be placed in this group although little or no information exists on this subject.

Of the typical halobiont species which can tolerate a wide range of salinities, only *Brachionus plicatilis* has been studied. According to Epp & Winston (1977), *B. plicatilis* showed a very close correspondence between internal and external osmolarity within the range 41 to 957 mOsmol l^{-1} with slight but consistent trend towards hyperosmolarity, which was more pronounced as the osmotic pressure of the external medium decreased. This could be represented as Fig. 3 (B). *B. plicatilis*, together with *H. fennica* and *H. jenkinae* were cited by Bayly (1972) as belong-
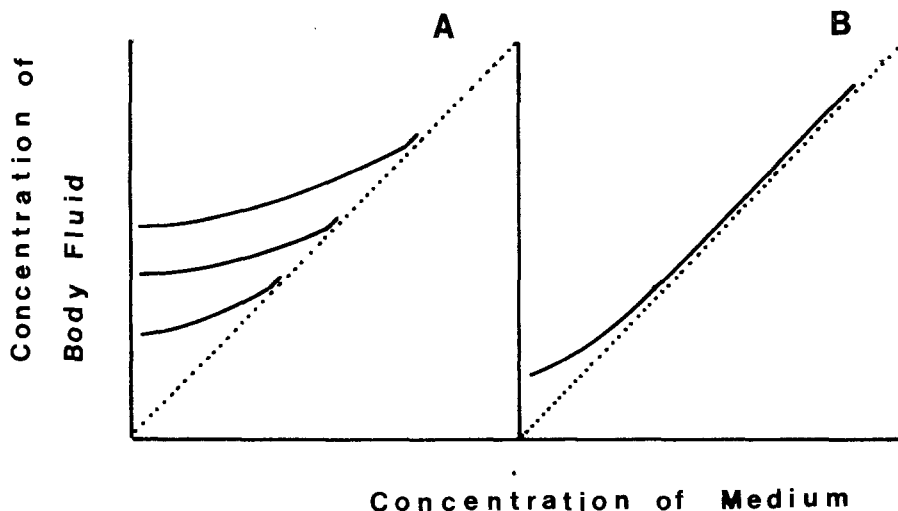

Fig. 3. Ideal relationships expected in rotifers among those proposed for other invertebrates (Bayly, 1972). (A) Hyperosmotic regulation till isosmotic point with different acclimations in freshwater species; (B) euryhaline halobiont species.

ing to the group of 'halobiont but entirely non-marine forms which osmoconform'. He considers that osmotic regulation of extracellular fluids is not necessary for successful colonization of saline waters. All the body cells of the animal may be able to tolerate or regulate their osmolarity instead of having a group of specialized cells of a specific organ regulating the internal fluids. Copepods of these groups, according to Bayly (1972), are capable of slight hyperosmotic regulation, which can be improved with previous acclimatization history, but they are incapable of any hyposmotic regulation.

Little or no information exists on osmoregulation in others rotifers, although genera such as *Synchaeta* and *Notholca* are subdivided in an array of species occupying almost all types of waters, including estuarine and marine environments.

There is some evidence that metabolic and activity responses to salinity correspond to an optimum curve with a more or less extensive plateau. Both the shape and position of the maximum with respect to the salinity axis, is strongly dependent on genotype. Each species or clone has a particular optimum curve and no general trend of a direct or inverse response to salinity has been found. Work in rotifers on activity response to salinity is restricted to *B. plicatilis*. An optimum curve can be extrapolated from the data of Hirayama & Ogawa (1972) on filtration rates, with a maximum occurring at moderate salinities ($= 12 \, g \, l^{-1}$). Data on oxygen consumption is very fragmentary but Ruttner-Kolisko (1972) found rates to be low at salinities of $1 \, g \, l^{-1}$ compared to a maximum rate at $17 \, g \, l^{-1}$ and a rate only slightly below the maximum at $35 \, g \, l^{-1}$. Epp & Winston (1978) studied rates from 10 to 100 mOsmol, corresponding approximately to $0.35-3.5 \, g \, l^{-1}$ salinity, which are too low for the normal behavior of *B. plicatilis*. These authors found that rotifers, preadapted to higher salinities (487 mOsmol), showed a reduction in O_2 consumption and activity when transferred to the above mentioned low salinities, which was more pronounced the lower the salinity. These results were interpreted by the authors as being a consequence of tissue hydration and the dilution of active ions and enzymes, which follows the fall of

the external concentration, in osmo-conformers. They relate this to the assumption of Potts & Perry (1964) that osmo-conformers respond to any change in the accustomed osmotic concentration by reducing their metabolism. This may be true for concentrations well below the optimum, such as those described above, when the body cells are beyond their upper limit of tolerance or regulation. Epp & Winston (1978) also found that activity and O_2 consumption were less reduced in previously acclimatized rotifers, especially at the higher of the above mentioned concentrations.

Salinity effects on populations

The direct effects of salinity on life history traits are strongly dependent on the species and genotype. Raising rotifers at two salinities, 0.2 and $0.4 \, g \, l^{-1}$, Lansing (1942) found that the mean life span of *Rotifer vulgaris* (= *Rotaria rotatoria*) decreases with salinity, without any significant variation in fecundity, while *Proales* sp. shows a small life span increase, but a reduction in the number of eggs laid per day. According to Aranovich & Spektorova (1974), *Brachionus calyciflorus* decreases its survival as the salinity rises from 2 to $10 \, g \, l^{-1}$, the negative slope being progressively steeped. In addition, fecundity decreased with salinity, but levelled off at the highest salinities assayed. Thus the decrease in growth rate when salinity increases above the optimum, is due first to a decrease in fecundity and second to a decrease in survival.

Aranovich & Spektorova (1974) also observed that survival was higher if gradual acclimatization was performed. Such acclimatization seems important in the response of rotifers to salinity. This has also been pointed out before in relation to osmoregulation, metabolism and activity.

Table 3 compiles all the data that we could find on parthenogenetic rates of increase in rotifers, at different salinities. These studies are limited to two species of *Brachionus*, *B. plicatilis* and *B. dimidiatus*. The halobiont species *B. plicatilis* grows in a very broad range of salinities, but data on *r*, for most *B. plicatilis* clones, can be interpreted as an optimum curve with a maximum or

Table 3. The intrinsec rate of increase (r, days^{-1}) of the indicated species growing at different salinities.

Brachionus plicatilis — Salinity (g/l)

Rotifer species	0	1	2	3	4	5	7	9	10 13	16	17	19	20	21	23	24	25	27	29	30	35	36 38	40 42	44	48 50	Reference
acclimatization																										
3 d			0.64		0.82				0.91				0.59							0.42		0.32	0.21	0.34	0.13	Lubzens *et al.* 1985 [1]
8 d			0.54		0.34				0.89				0.40							0.42		0.33	0.18	0.01	0.03	
14 d			0.30		0.36				0.80				0.68							0.48		0.42	0.21	0.08	0.05	
16 h													0.70							0.57		0.40				
without	<0	<0		<0					0.95				0.92									0.70			0.35	Pascual & Yúfera, 1983 [2]
with			0.86	0.85					0.75				0.78									0.70				
food level ×10⁶ cells/ml																										Lubzens, 1981 [3]
0.1									0.05		<0				<0				<0			<0				
0.5									0.44		0.45				0.44				<0			0.35				
1.0									0.66		0.76				0.43				0.50							
8.0									0.95		0.81				0.64											
water type																										Ruttner-Kolisko, 1972 [4]
sea water	0.46							0.62			0.98				0.72						0.56					
NaHCO₃ solution		0.88						0.72			0.62				=0								<0			
						0.85		0.83				0.69					0.5		0.4		0.77					from Ito, 1966 [5]
									0.94 0.84		0.67						0.66						0.9*			Snell, 1986 [6]

Brachionus dimidiatus — Salinity (g/l)

Salinity (g/l)	0.5	1.1	2.2	4.5	9	Reference
Brachionus dimidiatus	0.429	0.417	0.419	0.424	0.417	Pourriot & Rougier, 1975 [7]

Food, temperature conditions, and other observations:

[1] *Chlorella stigmatophora* (3 × 10⁶ cell/ml); 25 °C; pre-experimental salinity, 40 g/l; 16th acclimatization, values were calculated in mass cultures.
[2] *Nannochloris oculata* (40–60 × 10⁶ cell/ml); pre-experimental salinity, 36 g/l; 24 °C; growth was not observed at 60 and 80 g/l.
[3] *Chlorella stigmatophora*; 17–23 °C.
[4] *Dunaliella* sp.
[5] *Chlamydomonas* sp.; 1.2–2.9 × 10⁶ cell/ml.
[6] *Chlorella vulgaris* (10 µgC/ml); 25 °C; high sexual reproduction at 20 g/l; *: delayed growth.
[7] *Synechococcus cedrorum*; 20 °C.

a plateau located at moderate salinities between $10-20 \, g \, l^{-1}$. Some clones originally from southern latitudes and high salinity show rather high rates at high salinities (Pascual & Yúfera, 1983; Snell, 1986; however, in Snell, 1986, r was estimated from batch culture growth curves, measured at different time intervals and with a high percentage of mixis in the intermediate salinities).

Increased food increases r and broadens the range of tolerance, but, in contrast to the response to temperature, the maximum is maintained at about the same position on the salinity axis (Table 3, Lubzens, 1981).

It has been proposed that measures of fitness of rotifer populations are better based on the production of sexual resting eggs, rather than on parthenogenetic growth rates. Several studies have been carried out to determine the importance of sexual reproduction in relation to temperature (Hino & Hirano, 1984; Snell, 1985) and salinity (Ito, 1960; Lubzens et al., 1980; Lubzens, 1981; Hino & Hirano, 1988; Snell, 1985; Lubzens et al.,

1985). The reproductive response curve of sexual females to an environmental gradient is more constrained and peaked than that of asexual females, with maxima located at the optimal conditions which are probably the same for both amictic and mictic growth. However, the sexual or asexual reproductive responses to temperature are very different, because sexual reproduction is much diminished at extreme temperatures, and male rates of increase do not follow the same patterns as those of amictic females. By contrast, in a salinity gradient, the maximal sexual reproductive effort is more or less coincident with the optimum salinity for parthenogenetic growth.

Interaction between temperature and salinity

In order to establish the combined effect of temperature and salinity on the intrinsic rate of increase, r, we followed individual cultures of three clones of Brachionus plicatilis (CU, SPO, and FCA; Serra & Miracle, 1983, 1985, 1987;
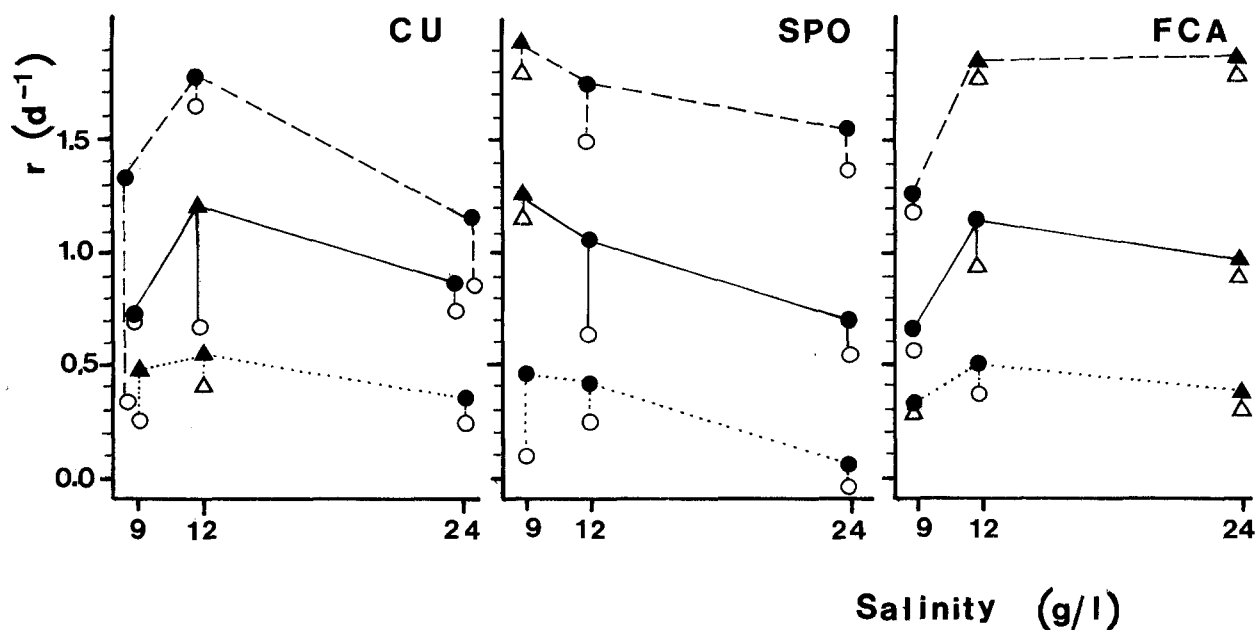
Fig. 4. r values of three clones of Brachionus plicatilis growing at the indicated salinities and at 20 °C (dotted lines), 25 °C (solid lines), and 30 °C (dashed lines). Closed symbols represent the values calculated for amictic females; open symbols correspond to the total number of females (mictic plus amictic). The triangles indicate which clone shows a maximum r at each temperature-salinity combination.

Serra, 1987), at three salinities (9, 12, and 24 g l^{-1}; diluted sea water), and at three temperatures (20, 25, and 30 °C). The r values were calculated from daily survival and fecundity schedules from sets of 50 newborn females grown at each of the nine experimental conditions and observed until their death. They were derived from parents coming from log-phase cultures pre-adapted at the corresponding experimental combinations. The cultures were grown at light and the medium containing 0.5×10^6 cell ml^{-1} of *Tetraselmis* sp. was renewed daily.

Two types of r values were calculated. The first type considered only the amictic females – disregarding the mictic ones – and assumed that all their daughters were amictic females. Thus, it estimates the intrinsic rate of increase, assuming the absence of mixis. The second type included all individuals either mictic or amictic. Both r values were computed using an integrated solution of the Lotka's integral equation, assuming a negative exponential interpolation between the observed survival schedules (Serra, 1987).

Figure 4 shows the effects of genotype, temperature and salinity on r. The r values calculated from the subset of amictic females have a clearer pattern in relation to these factors; because of this, we will focus on it. The main feature is an increase of r as the temperature rises, showing most frequently a linear relationship for our data points. These r values, within a temperature, showed great variability due to clone and salinity, but they never overlapped with those at other temperatures. The slope of the r-temperature relationship varies for the different clones. Clone CU, bigger in size and, according to its origin, adapted to lower temperatures shows a much smaller slope than the other two clones (Fig. 5). The same comments made before for the duration of embryonic development (in different species, Pourriot & Rouger, 1975, or clones, Amrén, 1964) or oxygen consumption (Pourriot, 1973b) could be applied here. At low temperature, cold-adapted genotypes have relatively higher r than more thermophilic ones, while the latter have relatively higher rates at higher temperatures. The same results are obtained in other studies when different *B. plicatilis* clones are compared. In Fig. 5

we have plotted together our results on the response of r to temperature and those calculated from data of King & Miracle (1981), where also a bigger clone (SP) was compared with two smaller and more thermophilic clones.

The effect of salinity on the intrinsic rate of increase is less pronounced than that of temperature. It is conditioned mainly by clone, but has a high interaction with temperature. Thus, for clone CU the highest value of r has been found at middle salinity, while SPO shows a decrease of r as the salinity rises. The FCA clone shows a trend to maintain high r values at high salinity, most notably when temperature is high.

Figure 4 indicates which clone would hypothetically be dominant in each condition (triangle vs. circles). According to these results, CU would have advantage in relatively cold and low salinity waters, SPO in warm waters with relatively low salinities, and FCA in warm waters with high salinities. FCA shows also a good response to conditions where salinity and temperature are positively correlated.

This behaviour of clones is quite closely adjusted to the one expected if they were adapted to their habitats. Thus, the origin of FCA is a coastal marsh with highly variable salinity, reaching more than 35 g l^{-1}. We obtained this clone from the Institute of Fisheries Research of Castellón, where it was cultured in sea water and at approximately 26 °C. SPO was isolated by us from a relatively stable coastal lagoon, in where salinity was 13 g l^{-1} and temperature, 26.6 °C. Finally, CU was isolated from a endorreic athalasic lagoon, which, at the time of collection, had a salinity of 25 g l^{-1} and a temperature of 17 °C.

The response of r to some combinations of temperature and salinity suggests a synergestic effect between these parameters, which has been explored studying their additive interaction. The interaction ($r_{T \cdot S}$, Fig. 6) has been calculated as the difference between the observed value of r, at each condition combination, and the expected value of r assuming an additive effect of salinity and temperature. The expected r is calculated as the addition of the following three terms: (1) grand mean for the clone, (2) the deviation to

this grand mean of the averaged r for the specific temperature, and (3) the deviation from this grand mean of the averaged r for the specific salinity. The results are shown in Fig. 6.

The most interesting response is that of FCA. It shows a strong interaction between the studied factors. At the high salinity-high temperature, at middle salinity-middle temperature, and at low salinity-low temperature FCA has a higher r than would be expected without interaction. This can be related to the fact that a positive correlation between temperature and salinity is frequent in the natural waters of Mediterranean region, where in summer high temperature and dryness causes an increase of water salinity. Thus, FCA, the clone isolated from a variable marsh, seems to be adapted to the fluctuations of natural conditions.

For clones CU, the interaction between tem-

perature and salinity is more complex. This clone shows a relative advantage at low and middle levels of both salinity and temperature, and if only these conditions are considered, the pattern of CU is similar to that of FCA; the r is above the expected value at both low-low and middle-middle combinations. Finally, clone SPO presents a 'smooth relief', pointing out a poor response to specific combinations of temperature and salinity.

To investigate the underlying causes of the obtained variation of r, we have explored the relationships between r and other life history traits, being particularly easy for global – age independent – life history traits. An approximation of r could be obtained from the net reproductive rate, R_0, and the cohort generation time, T_c, i.e., $r_c = \ln (R_0)/T_c$. In turn, R_0 can be decomposed in
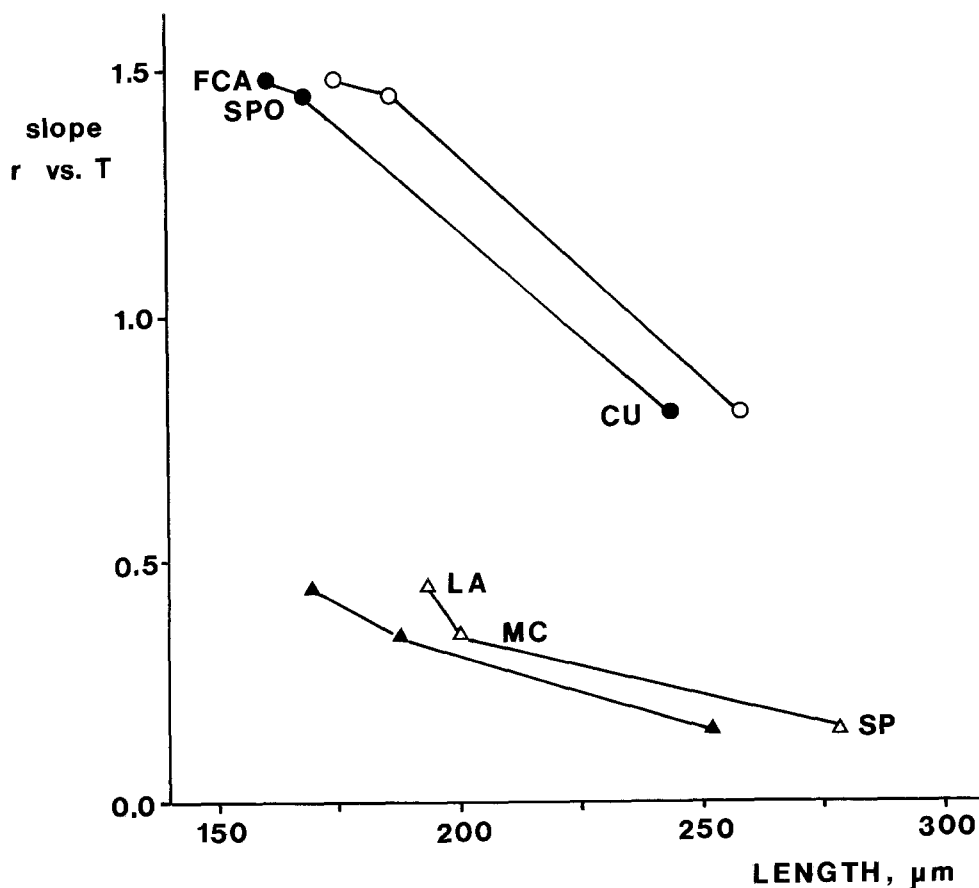
Fig. 5. The slope of the relationship between r and temperature as a function of the mean body length of four Brachionus plicatilis strains, measured at two fixed temperatures (data for LA, MC, and SP strains were obtained from King & Miracle, 1980).
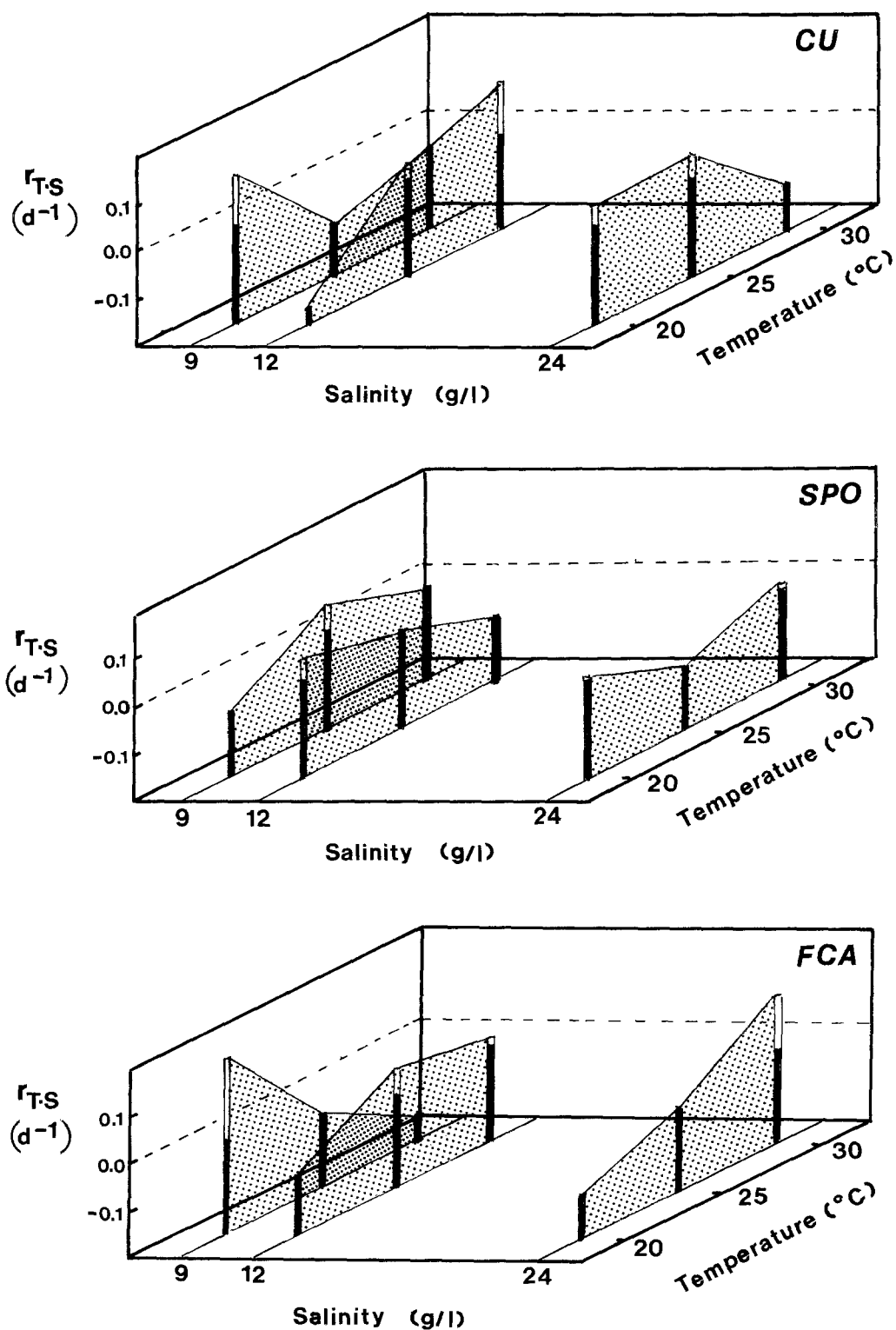
Fig. 6. Salinity-temperature interaction, $r_{T \cdot S}$ (days^{-1}, see text) for three clones of *Brachionus plicatilis* cultured at the indicated conditions. The bars represent that part of r which is due to interaction, and are solid until the interaction equals zero and empty when it is positive.
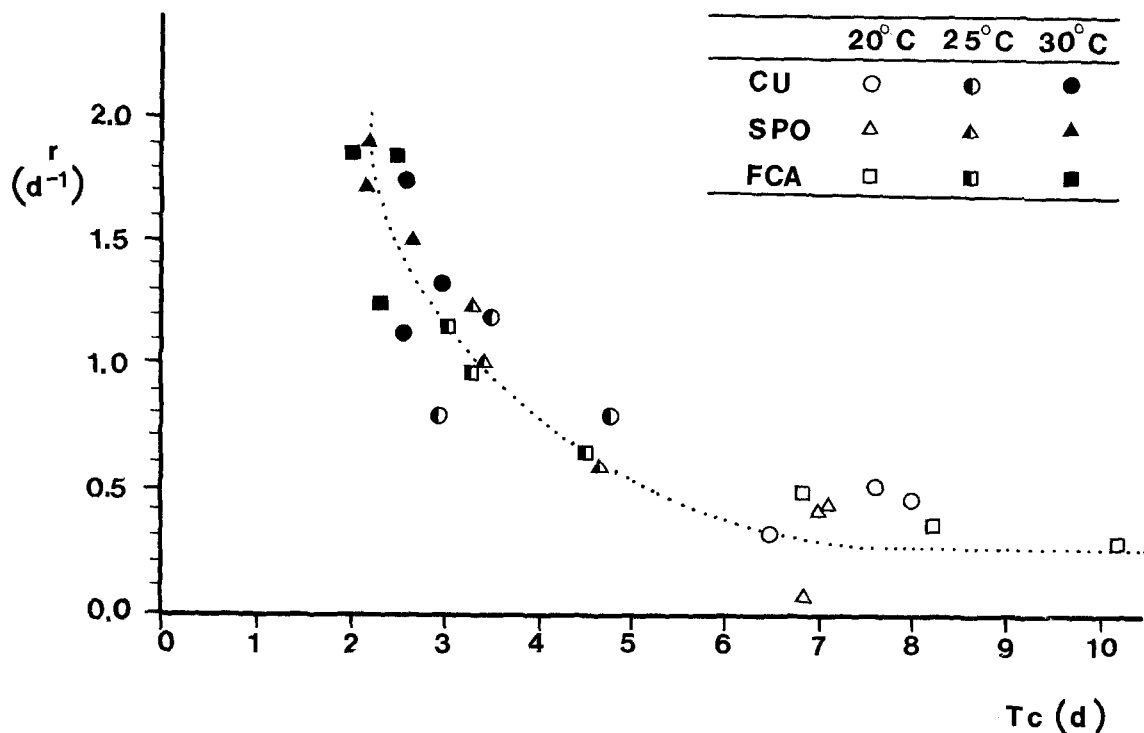
Fig. 7. Relationship between r and the cohort generation time, T_c (days), in *Brachionus plicatilis*.
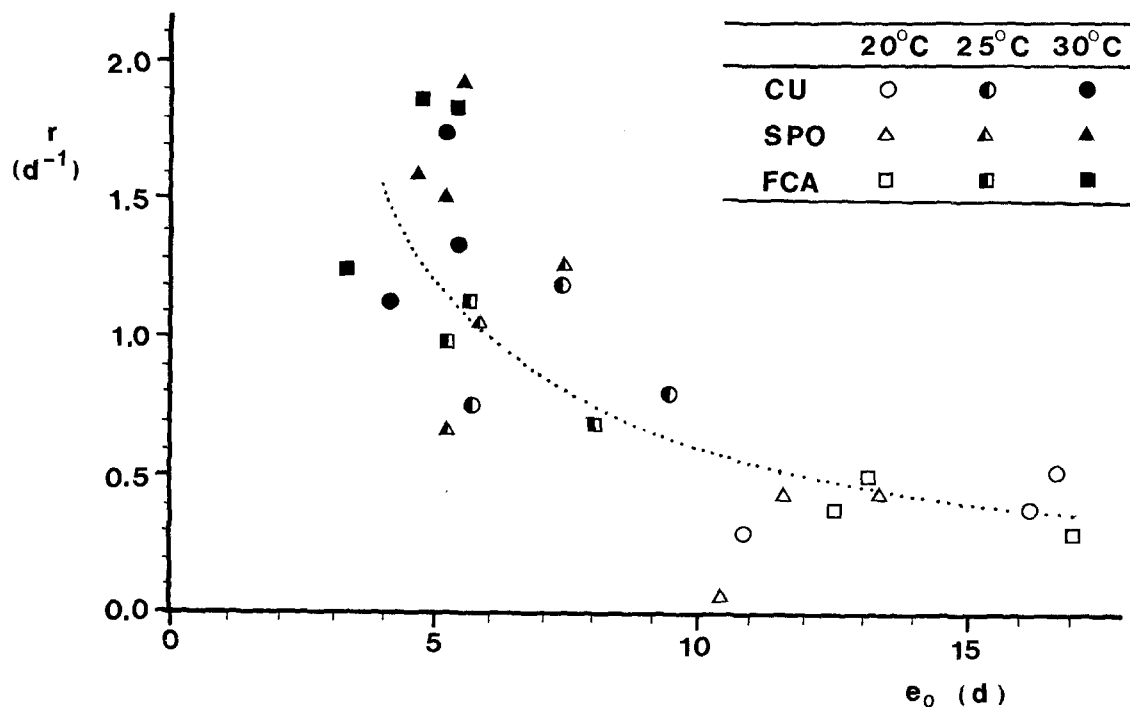
Fig. 8. Relationship between r and the mean life expectancy, e_0, in *Brachionus plicatilis*. The dotted line has been calculated as $r \cdot e_0 = K$, K being the average of the $r_i \cdot e_{0i}$ for the 27 experiments, that is $K = 6.3$. This equation that assumes the potential population growth throughout the life of an individual is the same for all conditions, *i.e.*, assumes that the intrinsic rate of increase relative to lifespan is constant.

the product between the duration of life, measured as the mean expectancy of life, e_0, and the average number of daughters per day: $F_d = R_0/e_0$.

As expected, r and T_c (Fig. 7) are related by an asynthotic inverse curve. The values are mainly arranged according to temperature, and there are not clear distinctions between values belonging to different clones or salinities. Looking at the slope of this relationship, it is observed that the covariation between r and T_c is high at 25 °C, lower at 30 °C, and nearly zero at 20 °C.

The mean expectancy of life, e_0, presents a pattern similar to T_c in its relationship with r (Fig. 8). This similarity could be expected as a consequence of the relationship between T_c and the duration of life.

The relationship between r and F_d is also strongly dependent on temperature (Fig. 9), and within the same temperature, a linear correlation between r and F_d has been found. When a functional regression analysis between these parameters was performed, lines with similar slopes were obtained.

Our results show that temperature not only affects the r values, but also the relationships between r and the other demographic parameters analyzed. In contrast, genotype and salinity do not cause special relationships between the studied traits.

Two important conclusions can be deduced from our results: (1) At changing temperatures the rate of growth and life span or generation time are adaptatively and physiologically adjusted, so the number of descendants per female (R_0) remains constant. If we plot (Fig. 8) the relation between r_c and T_c by inferring r_c from the potential R_0 (the maximum R_0 found in our results; i.e., 24) by $r_c = \ln24/T_c$, we obtain a line which matches almost exactly that of expected r assuming constancy in the r relative to life span (dotted line in Fig. 8). (2) Both salinity and genotype have important effects on fecundity, which can be seen in the relationship between r and F_d at different temperatures. On the other hand, their effect on life span is much less apparent.
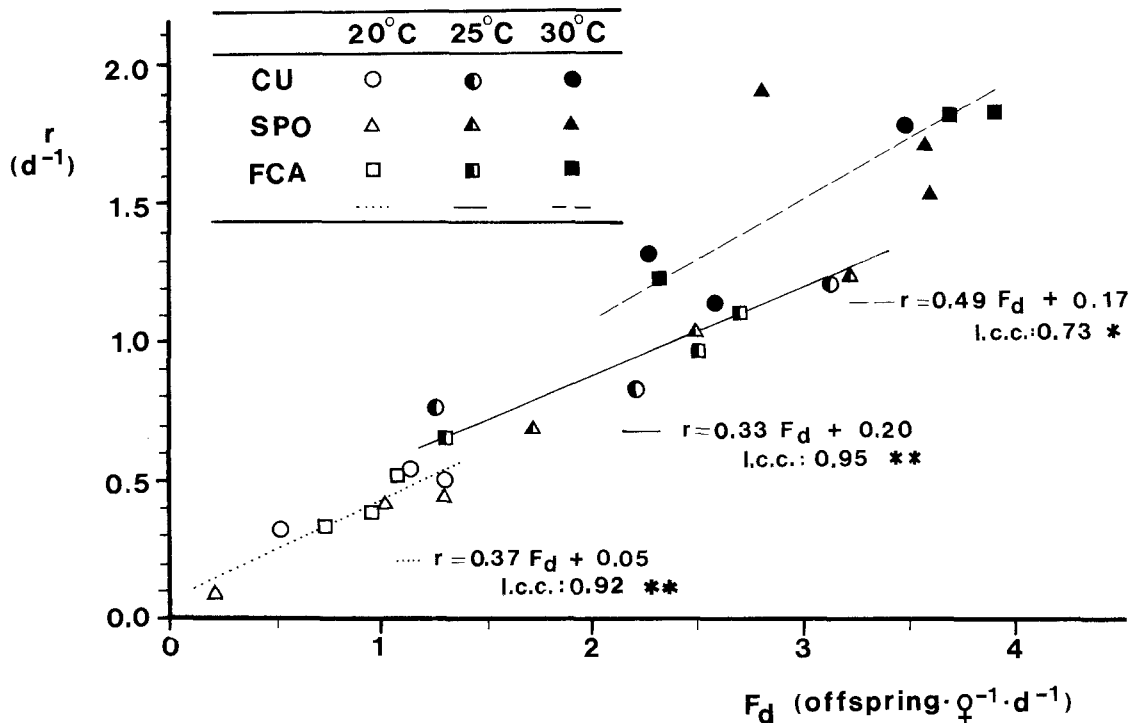
Fig. 9. Relationship between r and the reproductive effort, F_d, average offspring per female and day of life) in Brachionus plicatilis. The relationship is plotted for each temperature, indicating the corresponding regression equation with its significance (l.c.c., linear correlation coefficient).

General considerations

On the basis of laboratory studies we observe that temperature has a direct effect on r. This influence is mainly derived from the response direct of developmental rates or metabolic activities to increasing temperature, and the resultant r values reach a maximum. Beyond this point, r sharply decreases (Fig. 2). The temperature of the maximum is the upper limit for the normal functioning of the animal in the particular set of remaining conditions. The slope of the exponential curve and the temperature at which the maximum occurs depend on genotype (Fig. 2), and cold- or warm-adapted genotypes are clearly differentiated. Cold-adapted species or clones have in general, smaller slopes than warm-adapted ones (Fig. 2). This confirms the general observation that cold-adapted species have relatively higher rates of increase at lower temperatures than warm-adapted ones, and the latter have relatively higher rates at higher temperatures. It is interesting to note also that within species cold-adapted genotypes have a larger size (Fig. 5). This trend is coincident with the direct effect of temperature on the size of genotypically identical individuals, which have a bigger size when reared at low temperatures (Serra & Miracle, 1987). Slope and temperature of the maximum are also more or less influenced by environmental factors. Food in particular determines the temperature limits between which the response of r is exponential (Table 1).

The effect of temperature on net fecundity, R_0, is negligible within normal temperature limits. On the other hand, life span shows an inverse relationship with temperature, as expected by the acceleration of development rates. Thus, temperature (within suitable values for the normal functioning of the organisms) influences the timing, but not fertility (i.e., the number of descendents per individual), and an increase of r results from the acceleration of development. The decrease of r when temperature values move beyond suitable limits is due first to a decrease in survival and, if values become more extreme, additionally to a decrease in gross reproduction.

On the other hand, the direct effect of salinity on r depends on the genotype; the same findings

can be observed in other invertebrates (Fava et al., 1983). The genotype is adapted to an optimum salinity in which r is maximum. Then, r decreases as salinity conditions move away from this optimum. The decrease of r is due first to a decrease of fertility and, if salinity moves still farther from the optimum, a decrease of survival.

In the response of rotifer rate of increase, the interaction of temperature-salinity is important. In our studies of Brachionus plicatilis clones from habitats with greatly fluctuating temperature and salinity, a positive interaction or beneficial effect is found for the low/low and high/high temperature/salinity combinations within the normal limits of those factors in the habitats. Kinne in several papers (reviewed in Kinne, 1970; Alderdice, 1972) found similar results for other invertebrates and fishes. However, this is not general and Dorgelo (1976) compiles other beneficial combinations for survival in crustaceans, such as high/low temperature/salinity combinations in the tropics. The responses of species or ecotypes seem to match their habitats of origin. In temperate climates a positive correlation between temperature and salinity is usually found during the annual cycle. Temperature-salinity positive interactions in B. plicatilis ecotypes correspond to the expected annual covariation of those factors in their habitats. In the tropics, where temperature is more constant and salinity varies with the wet-dry seasons (corresponding to summer and winter) other factors may be more important. Also in coastal brackish water environments the interaction between continental and marine waters could determine different salinity-temperature relationships.

References

Alderdice, D. F., 1972. Responses of marine poikilotherms to environmental factors acting in concert. In: O. Kinne (ed.), Marine ecology, vol. 1. Wiley, London: 1659–1722.

Allan, J. D., 1976. Life history patterns in zooplankton. Am. Nat. 110: 165–180.

Allan, J. D. & C. E. Goulden, 1980. Some aspects of reproductive variation among freshwater zooplankton. In: W. C. Kerfoot (ed.), Evolution and ecology of zooplankton communities. University Press of New England, Hanover: 388–410.

Amrén, H., 1964. Ecological studies of zooplankton populations in some ponds on Spitsbergen. Zool. Bidr. Upps. 36: 162–191.

Armengol, J., 1978. Zooplankton crustaceans in Spanish reservoirs. Verh. int. Ver. Limnol. 20: 1652–1656.

Aronovich, T. M. & L. V. Spektorova, 1974. Survival and fecundity of Brachionus calyciflorus in water of different salinities. Hydrobiol. J. 10: 71–74.

Bayly, I. A. E., 1972. Salinity tolerance and osmotic behavior of animals in athalassic saline and marine waters. Annu. Rev. Ecol. Syst. 3: 233–268.

Braun, G., G. Kummel & J. A. Mangos, 1966. Studies on the ultrastructure and function of a primitive excretory organ, the protonephridium of the rotifer Asplanchna priodonta. Pflügers Arch. 189: 141–154.

Clément, P., 1968. Ultrastructures d'un rotifère, Notommata copeus. I. La cellule-flamme. Hypothèses physiologiques. Z. Zellforsch. 89: 478–498.

Dorgelo, J., 1976. Salt tolerance in crustacea and the effect of temperature upon it. Biol. Rev. 51: 255–290.

Duncan, A., 1983. The influence of temperature upon the duration of embryonic development of tropical Brachionus species (Rotifera). In: F. Schiemer (ed.), Limnology of Parakrama Samudra Sri-Lanka. Dr. W. Junk, The Hague.

Edmondson, W. T., 1965. Reproductive rate of planktonic rotifers as related to food and temperature in nature. Ecol. Monogr. 35: 61–111.

Epp, R. W. & P. W. Winston, 1977. Osmotic regulation in brackish-water rotifer Brachionus plicatilis (Müller). J. Exp. Biol. 68: 151–156.

Epp, R. W. & P. W. Winston, 1978. The effect of salinity and pH on the activity and oxygen consumption of Brachionus plicatilis (Rotatoria). Comp. Biochem. Physiol. 59A: 9–12.

Epp, R. W. & W. M. Lewis, 1980. Metabolic uniformity over the environmental temperature range in Brachionus plicatilis (Rotifera). Hydrobiologia 73: 145–147.

Epp, R. W. & W. M. Lewis, 1984. Cost and speed of locomotion for rotifers. Oecologia (Berl.) 61: 289–292.

Fava, G., I. Lazzaretto & E. Martini, 1983. Effetti della riduzione di salinità in due diverse popolazioni lagunari di Tisbe clodiensis (Copepoda, Harpacticoida). Atti Ist. Veneto Sci. 141: 105–120.

Galkovskaya, G. A., 1983. On temperature acclimation in a experimental population of Brachionus calyciflorus. Hydrobiologia 104: 225–227.

Galkovskaya, G. A., 1987. Planktonic rotifers and temperature. Hydrobiologia 147: 307–317.

Galkovskaya, G. A., J. Ejsmont-Karabin & V. N. Evdokimov, 1987. Relative protein metabolism in rotifer Brachionus calyciflorus Pallas, in relation to temperature. Int. Rev. Gesamten Hydrobiol. 72: 59–69.

Gilbert, J. J., 1976. Polymorphism in the rotifer Asplanchna sieboldi: biomass, growth, and reproductive rates of the saccate and campanulate morphotypes. Ecology 57: 542–551.

Ito, T., 1960. On the culture of mixohaline rotifer Brachionus plicatilis O. F. Müller in sea water. Rep. Fac. Fish., Prefec. Univ. Mie. 3: 708–740.

Halbach, U., 1973. Life table data and population dynamics of the rotifer Brachionus calyciflorus Pallas as influenced by periodically oscillating temperature. In: W. Wieser (ed.), Effects of temperature in ectothermic organism. Springer-Verlag. Berlin: 217–228.

Herzig, A., 1983. Comparative studies on the relationship between temperature and duration of embryonic development of rotifers. Hydrobiologia 104: 237–246.

Hirayama, K. & S. Ogawa, 1972. Fundamental studies on physiology of rotifer for its mass culture. I. Filter Feeding of Rotifer. Bull. Jpn. Soc. Sci. Fish. 38: 1207–1214.

Hirayama, K. & T. Kusano, 1972. Fundamental studies on physiology of rotifer for its mass culture. II. Influence of water temperature on population growth of rotifer. Bull. Jap. Soc. Sci. Fish. 38: 1357–1363.

Hino, A. & R. Hirano, 1984. Relationship between water temperature and bisexual reproduction rate in the rotifer Brachionus plicatilis. Bull. Jap. Soc. Sci. Fish. 50: 1481–1485.

Hino, A. & R. Hirano, 1988. Relationship between water chlorinity and bisexual reproduction rate in the rotifer Brachionus plicatilis. Nippon Suasan Gakkaishi 54: 1329–1332.

Hummon, W. D. & D. P. Bevelhymer, 1980. Life table demography of the rotifer Lecane tenuiseta under culture conditions and various age distributions. Hydrobiologia 70: 25–28.

Kabay, M. E. & J. J. Gilbert, 1978. Polymorphism in the rotifer Asplanchna sieboldi: Insensitivity of the body-wall-outgrowth response to temperature, food density, pH and osmolarity differences. Arch. Hydrobiol. 83: 377–390.

Kinne, O., 1970. Temperature: Animals-Invertebrates. In: O. Kinne (ed.), Marine ecology, vol. 1. Wiley, London: 407–514.

King, C. E., 1972. Adaptation of rotifers to seasonal variation. Ecology 53: 408–418.

King, C. E. & M. R. Miracle, 1980. A perspective on aging in rotifers; Hydrobiologia 73, 13–19.

Lansing, A. I., 1942. Some effects of hydrogen ion concentration, total salt concentration, calcium and citrate on longevity and fecundity of rotifer. J. Exp. Zool. 91: 195–211.

Lebedeva, L. I. & T. N. Gerasimova, 1985. Peculiarities of Philodina roseola (Ehrbg.) (Rotatoria Bdelloida). Growth and reproduction under various temperature conditions. Int. Rev. Gesamten Hydrobiol. 70: 509–525.

Lebedeva, L. I. & T. N. Gerasimova, 1987. Survival and reproduction potential of Philodina roseola (Ehrenberg) (Rotatoria Bdelloida) under various temperature conditions. Int. Rev. Gesamten Hydrobiol. 72: 695–707.

Lubzens, E., 1981. Rotifer resting eggs and their application

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to marine aquaculture. Eur. Maricult. Soc. Spec. Publ. 6: 163–180.

Lubzens, E., R. Fishler & V. Berdugo-White, 1980. Induction of sexual reproduction and resting egg production in *Brachionus plicatilis* reared in sea water, Hydrobiologia 73: 55–58.

Lubzens, E., G. Minkoff & S. Marom, 1985. Salinity dependence of sexual and asexual reproduction in the rotifer *Brachionus plicatilis*. Mar. Biol. (Berl.) 85: 123–126.

Miracle, M. R., 1974. Niche structure in freshwater zooplancton: a principal components approach. Ecology 55: 1306–1317.

Miracle, M. R., M. Serra, E. Vicente & C. Blanco, 1987. Distribution of *Brachionus* species in Spanish mediterranean wetlands. Hydrobiologia 147: 75–81.

Nagata, W. D., 1985. Long-term acclimation of a parthenogenetic Strain of *Brachionus plicatilis* to subnormal temperatures. I. Influence on size, growth, and reproduction. Bull. mar. Sci. 37: 716–725.

Nogrady, T., 1988. The littoral rotifers plankton of the Bay Quinte (Lake Ontario) and its horizontal distribution as indicators of trophy. I. A full season study. Arch. Hydrobiol. Suppl. 79: 145–156.

Pascual, E. & M. Yúfera, 1983. Crecimiento en cultivo de una cepa de *Brachionus plicatilis* O. F. Müller en función de la temperatura y la salinidad. Invest. Pesq. 47: 151–159.

Pontin, R. M., 1964. A comparative account of the protonephridia of *Asplanchna* (Rotifera) with special reference to the flame bulbs. Proc. zool. Soc. Lond. 142: 511–525.

Pontin, R. M., 1966. The osmoregulatory function on the vibratile flames and the contractile vesicles of *Asplanchna* (Rotifera). Comp. Biochem. Physiol. 17: 1111–1126.

Potts, W. T. & G. Parry, 1964. Osmotic and ionic regulation in animals. Pergamon Press, Oxford.

Pourriot, R., 1973a. Rapports entre la température, la taille des adultes, la longueur des œufs en le taux de développement embryonnaire chez *Brachionus calyciflorus* Pallas (Rotifère). Ann. Hydrobiol. 4: 103–115.

Pourriot, R., 1973b. Influence de la teneur en protéines, de la température et du jeûne sur la respiration de Rotifères héléoplanctonctoniques. Verh. int. Ver. Limnol. 18: 1429–1433.

Pourriot, R. & M. Deluzarches, 1971. Recherches sur la biologie des rotifères. II. Influence de la température sur la durée du développement embryonaire et post-embryonaire. Ann. Limnol. 7: 25–52.

Pourriot, R. & C. Rougier, 1975. Dynamique d'une population expérimentale de *Brachionus dimidiatus* (Bryce) (Rotifère) en fonction de la nourriture et de la température. Ibidem, 11: 125–143.

Ricci, C., 1976. Note preliminare sull'allevamento di un rotifero Bdelloidea. Atti. Soc. Ital. Sci. Nat. Museo Civ. Stor. Nat. Milano 117: 144–148.

Ricci, C., 1978. Some aspects of the biology of *Philodina roseola* (Rotifera). Me. Ist. ital. Idrobiol. 36: 109–116.

Ruttner-Kolisko, A., 1971. Rotatorien als Indikatoren für den Chemismus von Binnensalzgewässern. Sitz-Ber. Österr. Akad. Wiss. Math. Nat. Kl. Abt. I. 179: 283–298.

Ruttner-Kolisko, A., 1972. Der Einfluß von Temperatur und Salzgehalt des Mediums auf Stoffwechsel- und Vemehrungsintensität von *Brachionus plicatilis* (Rotatoria). Dt. Zool. Ges. 65: 89–95.

Ruttner-Kolisko, A., 1975. The influence of fluctuating temperature of plankton rotifers. A graphical model based on live data of *Hexarthra fennica* from Neusiedlersee, Austria. Symp. Biol. Hung. 15: 197–204.

Ruttner-Kolisko, A., 1978. Influence of fluctuating temperature of plankton rotifers. II. Laboratory experiments. Verh. int. Ver. Limnol. 20: 2400–2405.

Serra, M., 1987. Variación morfométrica, isoenzimática y demográfica en poblaciones de *Brachionus plicatilis*. Diferenciación genética y plasticidad fenotípica. Ph. D. Thesis, Universitat de Valencia, Valencia.

Serra, M. & M. R. Miracle, 1983. Biometric analysis of *Brachionus plicatilis* ecotypes from Spanish lagoons. Hydrobiologia 104: 279–291.

Serra, M. & M. R. Miracle, 1985. Enzyme polymorphism in *Brachionus plicatilis* populations from several Spanish lagoons. Verh. int. Ver. Limnol. 22: 2991–2996.

Serra M. & M. R. Miracle, 1987. Biometric variation in three strains of *Brachionus plicatilis*. Hydrobiologia 147: 83–89.

Stemberger, R. S. & J. J. Gilbert, 1985. Body size, food concentration, and population growth in planktonic rotifers. Ecology 66: 1151–1159.

Snell, T. W., 1986. Effect of temperature, salinity and food level on sexual and asexual reproduction in *Brachionus plicatilis* (Rotifera). Mar. Biol. 92: 157–162.

Snell, T. W., M. J. Childress, E. M. Boyer & F. H. Hoff, 1987. Assessing the status of rotifer mass cultures. J. World Aquacult. Soc. 18: 270–277.

Snell, T. W. & C. E. King, 1977. Lifespan and fecundity patterns in rotifers: the cost of reproduction. Evolution 31: 882–890.

Starkweather, P. L., 1987. Rotifera. In: Animal Energetics, Vol. 1. Academic Press, N.Y.

Vinberg, G. G. & G. A. Galkovskaya, 1979. Relationship between the development rate of rotifers and temperature. V kn. Obschyie osnovyiznchieniya vodnykh ekosistiem. L, Nauka: 149–155.

Walz, N., 1983. Individual culture and experimental population dynamics of *Keratella cochlearis* (Rotatoria). Hydrobiologia 107: 35–45.

Walz, N., 1987. Comparative population dynamics of the rotifers *Brachionus angularis* and *Keratella cochlearis*. Hydrobiologia 147: 209–213.

Yúfera, M., 1987. Effect of algal diet and temperature on the embryonic development time of the rotifer *Brachionus plicatilis* in culture. Hydrobiologia 147: 319–322.

Yúfera, M. & E. Pascual, 1980. Estudio del rendimiento de cultivos del rotífero *Brachionus plicatilis* O. F. Müller alimentados con levadura de panificación. Invest. Pesq. 44: 361–368.