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Morphometry and Cyclomorphosis in *Daphnia middendorffiana* from a Fishless Pond of the Southern Andes

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ABSTRACT

The morphology of a population of *D. middendorffiana* collected during spring and autumn in a fishless pond of the Southern Andes was examined to identify seasonal variations in growth patterns. Body size, tail spine length, width, thickness and biomass were analyzed, and growth was characterized by correlating various morphological dimensions with biomass. A pattern of three growth stages was identified: a juvenile stage characterized by body growth without variation of the tail spine length, a transition stage during which the tail spine experienced a sudden length reduction, and an adult stage with growth patterns similar to the first stage. Specific cyclomorphic growth patterns were found. The dimensions displaying most apparent seasonal differences were tail spine length and body flatness.

INTRODUCTION

Cyclomorphosis is defined as temporal cyclic (seasonal or aseasonal) morphological changes in successive generations of small aquatic organisms, such as dinoflagellates, rotifers, ciliates and cladocerans (Hutchinson 1967, Dodson 1989). The morphological changes are induced either by environmental factors, such as temperature, turbulence and light, or by other factors such as organic solutes. Functional mechanisms of cyclomorphosis include passive sinking, active swimming and defense against predation (Jacobs 1987).

Cyclomorphosis in *Daphnia sp.* can be explained as a process where groups of clones exposed to different environmental condition vary with respect to helmet size, tail spine length and crest size (Havel and Dodson 1985). Some of these changes, such as the tail spine, are morphological defenses produced whether a predator is present or absent (Dodson 1989). There is strong evidence that the length of tail spine in dafphnids is associated with predation. In general, long tail spines protect individuals, particularly the youngest stages, from invertebrate predators (Pijanowska 1992, Vega 1995). However, the specific functions of morphology are more difficult to analyze than the causes, for a simple change in morphology may produce several simultaneous effects (Jacobs 1987).

Daphnia middendorffiana coexists with the predaceous copepod *Parabroteas sarsi* in fishless ponds of Southern Andes (41°S). Laboratory experiments showed that the tail spine protects the youngest stages (Vega

1995 and 1998). We conducted a laboratory study of *D. middendorffiana* in order to characterize the morphology of individuals and to identify seasonal variations of the growth pattern.

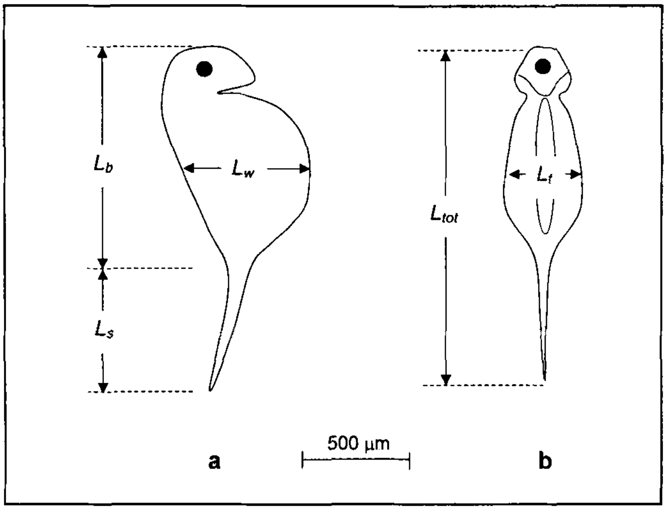

Figure 1. Measures of *Daphnia middendorffiana* in lateral (a) and ventral views (b). L_b: Body length, L_w: Body width, L_t Body thickness, L_s: Tail spine length, L_{tot}: Total length.

METHODS AND MATERIALS

The field site was a 10 ha. semipermanent pond (Los Juncos, 41° 4'S, 71° 29' W) next to the Lake Nahuel Huapi (Argentina). It is shallow and highly productive (Zagarese et al. 1997). The water freezes in winter and exceptionally dries in summer. The maximum water level occurs in October-November. During the present study the water depth at the pond center was 30-40 cm in May-July and 55 cm in October. The water temperature varied from 2 °C to 18 °C, while pH ranged from 7 to 9.12, in autumn and spring, respectively. The pond was entirely vegetated; most of the bottom was covered with macrophytes (*Myriophyllum sp.* and *Juncus sp*). Trees, such as *Betula pendula* and *Populus nigra*, and shrubs (*Rosa eglanteria*) grow on the periphery. There are no fish in Los Juncos pond, but migratory birds are present from spring to early autumn.

The most important species of the zooplankton community of Los Juncos pond is the large cladoceran *D. middendorfiana* (adult around 3.5-3.8 mm), which can be found all year, even in winter below 5 cm of surface ice. Other cladocerans are *Simocephalus serrulatus* (adult around 3 mm), *Alona* and *Chydorus* (less than 2 mm). There are three species of calanoid copepods, the largest of which is the predaceous *P. sarsi* (adult length 4.8 mm). Herbivorous species are *Boeckella brevicaudata* (adult length 2.5 mm, remaining autumn-winter) and the small *Boeckella schwabei* (adult length 0.9 mm).

Field sampling of *D. middendorffiana* was carried out weekly during 1996. Zooplankton was sampled with a 70 µm mesh plankton net.

Samples of June (autumn) and October (spring) were preserved in 5% formalin.

Each cladoceran was measured under stereomicroscope, determining the body length, L_b, as the linear distance from the top of the head shield to the base of the tail-spine; total length, L_{tot}, as the linear distance from the top of the head shield to the end of the tail spine; maximum body width, L_w, as the linear distance from the ventral margin to the dorsal margin; and the body thickness, L_t, as the maximum lateral length (see Figure 1).

The specific weights (densities) of anaesthetized individuals were determined by sinking them into solutions of glycerin in water, previously homogenized by means of a magnetic stirrer. The cladocerans were immersed in different solutions to determine the concentration at which the weight was balanced by the buoyancy force. The solution density was determined by direct weighting of a unit volume. All the individuals were weighed using an analytical balance.

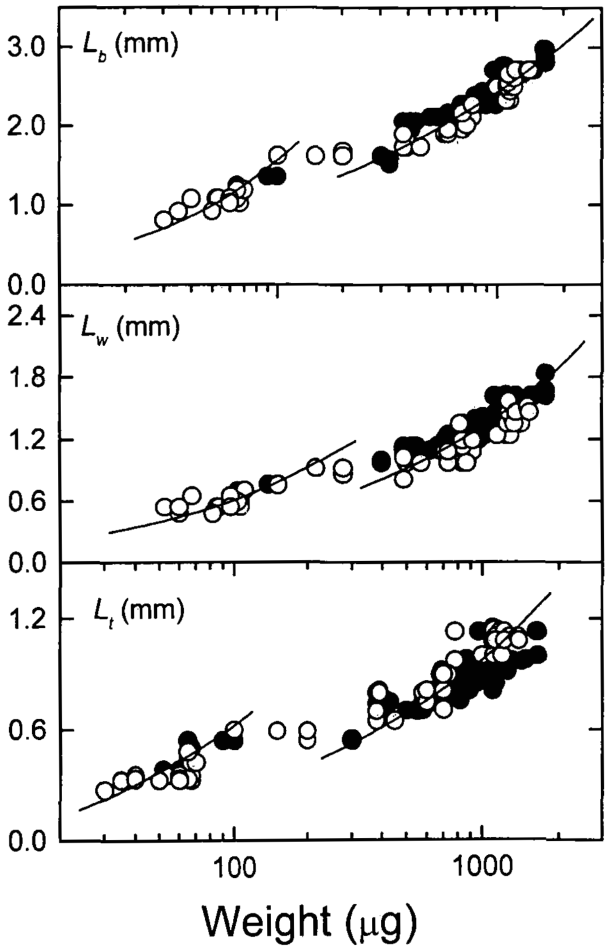

Figure 2. Relation of the size dimensions with the wet body weight. Autumn (•), Spring (o).

RESULTS

Figure 2 shows the main morphological measures of the body plotted against the individual weight. Both autumn and spring samples presented positive growth rates in all dimensions for the body size, width and thickness. The weight can be viewed as an indicator of the growth degree of the cladoceran, in the sense that heavier individuals are more likely to be older. Therefore, the growth rates of certain dimensions would be correlated with variation in individual weight. Likewise, different seasonal variation of a given measure would be suggestive of cyclomorphosis.

An interesting feature observed in all the graphics is a significant reduction of the growth rate of all dimensions, between 100 and 300 μg. This suggests the occurrence of a punctual transition stage between juveniles and adults *D. middendorffiana*. Figure 3 shows the body density as a function of the weight. Density remained constant during the transition, while in juveniles and adults it decreased monotonically as individuals grow.

The growth rate can be quantified by means of the classical Freundlich allometric model:

$$Y = a\,W^b$$

where Y is the morphological feature under study, and b is the relative growth rate. The curves shown in Figs. 2 and 3 show the mean square fitting of the allometric model for juvenile and adult stages. The corresponding parameter values are detailed in Table 1.

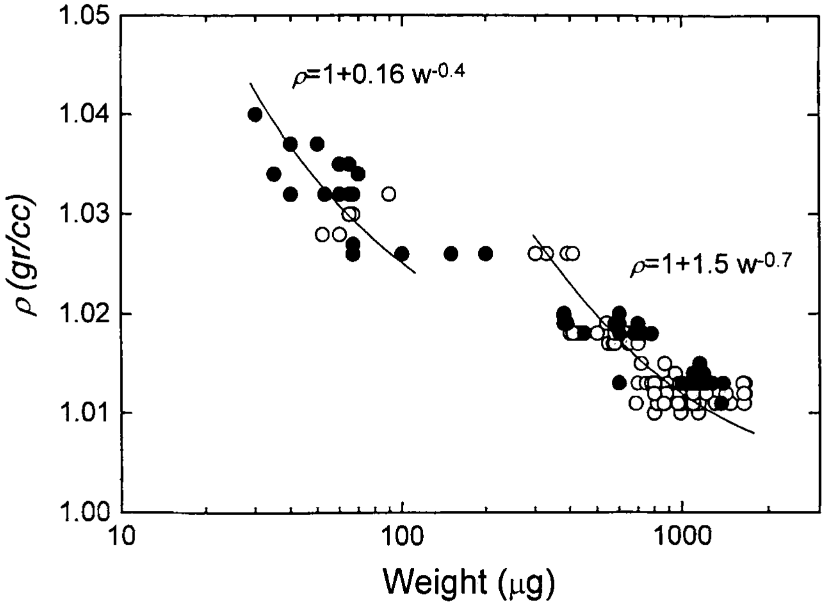

Figure 3. Relation of the specific weight (ρ) and the total wet weight. Autumn (•), Spring (o).

Table 1. Allometric parameters of *D. middendorffiana* ($Y=a\,W^{b}$) . Lengths are in mm and weights are in µg. L_b: Body length, L_w: Body width, L_t: Body thickness, L_s: Tail spine, f: Flatness, e: Elongation

Measure	Autumn			Spring		
	b	*Correlation*	χ^2	*b*	*Correlation*	χ^2
L_b	0.34 to 0.36	0.98	0.01	0.33 to 0.37	0.95	0.01
L_w	0.42 to 0.47	0.96	<0.01	0.40 to 0.47	0.96	<0.01
L_t	0.36 to 0.42	0.96	<0.01	0.35 to 0.42	0.94	<0.01
L_s	-1.16 (min.)	0.90	0.01	-0.45 (min.)	0.90	0.01
f	0.04 to 0.11	0.72	<0.01	-0.06 to -0.01	0.5	<0.01
e	-0.06 to -0.02	0.70	0.01	-0.03 to -0.00	0.35	<0.01

Changes in body shape were analyzed by means of two shape indicators, the flatness parameter, defined as:

$$f = \frac{L_t}{L_w}$$

and the elongation parameter, defined as:

$$e = \frac{L_b}{\sqrt{L_t\,L_w}}$$

Figure 4 shows flatness as a function of the weight. There was clear evidence of cyclomorphosis: positive allometry in June and negative in October. Moreover, smaller specimens of *D. middendorffiana* in spring were flatter than in autumn, while the opposite was encountered for the adults. On the other hand, the elongation parameter remained bounded

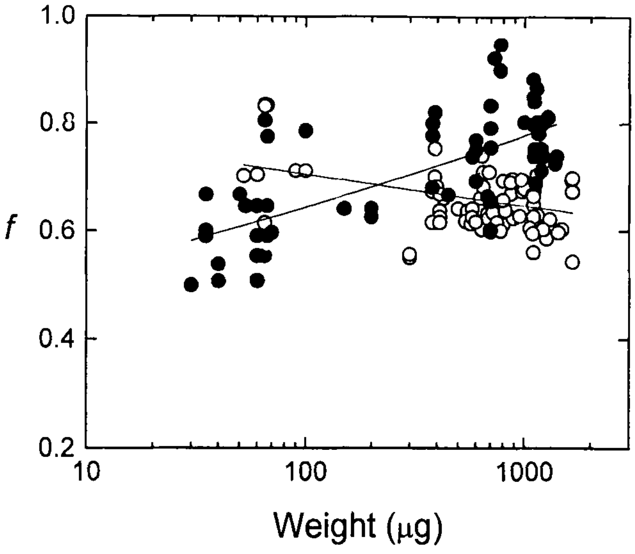

Figure 4. Variation of the flatness parameter (*f*) with the wet weight. Autumn (•), Spring (o).

between 2 and 2.5 (Fig. 5). June adults seemed to be more elongated than October adults were, while the opposite seemed to occur for juveniles. However, the similitude of the allometric parameters is not conclusive to claim cyclomorphic evidence for the elongation.

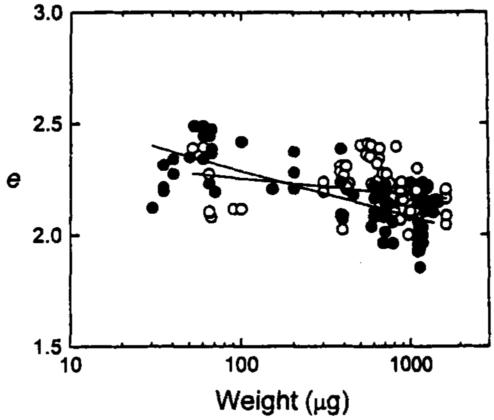

Figure 5. Variation of the elongation parameter (*e*) with wet weight. Autumn (•), Spring (o).

The length of the tail spine is shown in Fig. 6 as a function of the weight. Negative allometric development can be observed, and there was a clear seasonal differentiation, presenting a sharper variation in the spring group. It is interesting to note that most of the reduction of the spine length occured in the transition stage (100-300 µg), while during juvenile and adult stages the spine length remained rather constant. This particular growth trend can be modeled using a sigmoid equation:

$$L_s = L_2 + \frac{L_1 - L_2}{1 - exp\left(\frac{W - W_o}{\Delta W}\right)}$$

where L_1 and L_2 are the juveniles and adults asymptotic values, W_o is the average transition weight, and ΔW is the transition range. The curves in Fig. 6 represent the optimum mean square fitting of the sigmoid for each sample. The parameters of the mean-square fit are given in Table 2. The sigmoid model can be viewed as a transient allometry, regarding the general definition of the relative growth rate,

$$b = \frac{W}{L_s}\left(\frac{dL_s}{dW}\right)$$

The relative growth rate of the spine with respect to the weight was calculated by direct differentiation of the sigmoid. The resulting curves are shown in Fig. 6. The maximum values of growth rates were -1.16 and -0.45.

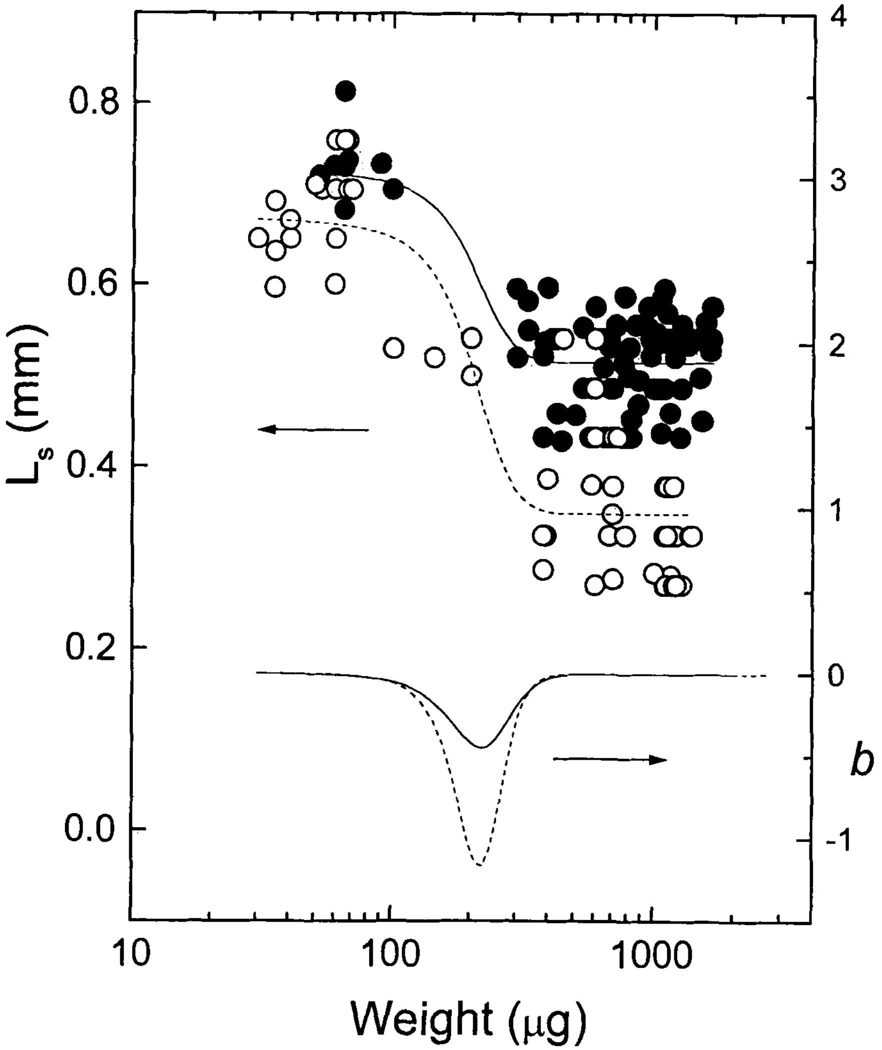

Figure 6. Relation of the tail spine length (*Ls*) and wet weight. Autumn (•), Spring (o).

DISCUSSION

Growth patterns of *D. middendorffiana* were identified by mapping the relations between various morphological dimensions and body weight. The main body measures (length, thickness and width) increased for larger weights, which is logically related to the volume growth corresponding to the cumulative mass. The apparent growth rate, however, was not uniform. The observed growth pattern can be classified in three stages. The juvenile stage extends to approximately 100 μg weight, and it is characterized by general body growth without variation of the tail spine length. Between 100 and 300 μg a significant reduction of growth rates was observed in all dimensions, except for the tail spine that experienced a sudden length reduction. This feature suggests the

Table 2. Spine-length parameters of *D. middendorffiana*

	Spring	Autumn
L_1 (mm)	0.6 to 0.7	0.7 to 0.75
L_2 (mm)	0.3 to 0.4	0.43 to 0.57
W_o (μg)	220	220
ΔW (μg)	150	150
Correlation	0.90	0.90
χ^2	0.01	0.01

occurrence of a punctual transition stage between juveniles and adults *D. middendorffiana*. The third stage comprises adult individuals heavier that 300 μg, and the development pattern is similar to the first stage. Diagrams of the three stages are depicted in Fig. 7.

The body density remained constant during the transition, while in juveniles and adults it decreased monotonicaly as individuals grew. Other researchers also reported age dependence of the specific weight in other cladoceran. Density changes are usually associated with hydrodynamic factors, such as sinking resistance (Dodson and Rachmaran 1991).

Specific cyclomorphic growth patterns were found in *D. middendorffiana* samples. The dimensions presenting remarkable seasonal differences were the tail spine length and the body flatness. Previous studies have shown that vertebrate and invertebrate predators are size-selective (Hall et al. 1976, Kerfoot and Sih 1987, Krylov 1992). Usually smaller individuals prevail in populations suffering heavy vertebrate predation, since they channel easier through animal filters (Gliwicz and Pijanowska 1989). On the other hand, dominance of large zooplankton, when fish predation is absent, is believed to be determined by invertebrate predation, interspecific competition, or some interaction between them (Lynch 1979, Gliwicz 1985, Gliwicz and Umana 1994). Havel and Dodson (1985) found seasonal differences in the body thickness of *D. retrocurva* (smaller in autumn animals than in spring animals) attributable to fish predation.

The evidence of cyclomorphosis in specific features of *D. middendorffiana* (spine length and flatness) is more likely attributable to predation than to any other ecological factor. Cladoceran predation in Los Juncos pond is dominated by the predaceuos copepod (*P. sarsi*) throughout the year and by plankton filtering birds such as flamingos (*Phoenicopthenus chilensis*) during spring and summer. Previous studies have demonstrated that juvenile stages of *D. middendorffiana* are protected from *P. sarsi* predation by the large tail spine while the adult stages are protected by the large body size (Balseiro and Vega 1994, Vega 1995, Vega 1997). Therefore, the measured morphological differences may have evolve as mechanisms of zooplankton survival influenced by the action of seasonal predators. A reasonable conjecture is that during spring flatter adults of *D. middendorffiana* more easily survive the filter action of birds. In autumn the long tail spine and a less flatt body protects *D. middendorffiana* juveniles from the invertebrate attacks. The influence of birds on zooplankton structure has been documented in lakes of the Peruvian Andes (Hurlbert et al. 1986).

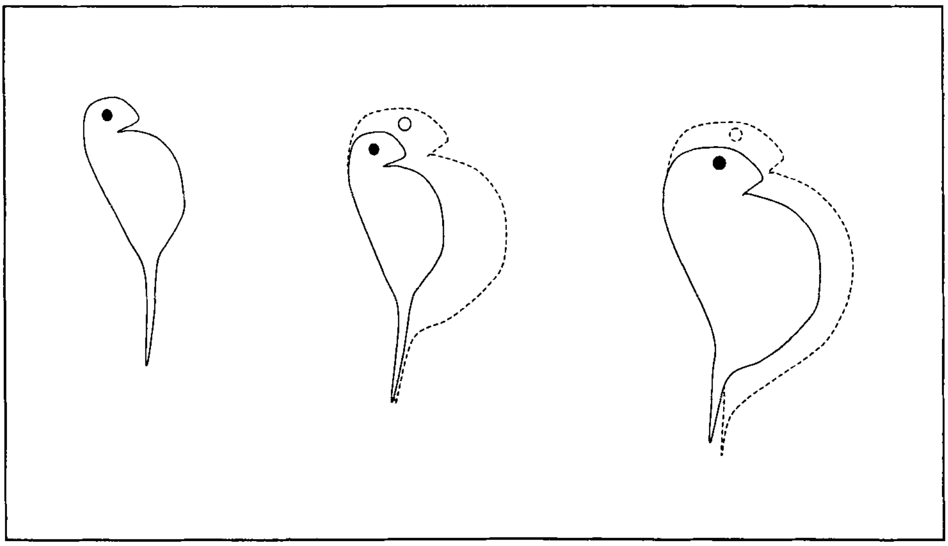

Figure 7. Diagram of growth stages.

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