Influence of abiotic and biotic factors on morphological variation of *Keratella cochlearis* (Gosse) in a small Andean lake

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Abstract

Morphological variation of *Keratella cochlearis* was studied during a spring-summer period in a small Andean lake. Morphometry was studied in relation to temperature, food resources, cladoceran competitors and invertebrate predators. Three different morphs were recorded. We observed lack of allometric growth of the posterior spine. Absence of allometric growth could be related with the low density of a predaceous water mite and the small size of the cladocerans present in the lake. Fluctuations in lorica length and width were negatively correlated with temperature and algal biovolume. We discuss the benefits of this morphological response of *Keratella* in relation to environmental conditions.

Introduction

The morphological variation in *Keratella cochlearis* (Gosse) has been associated with different environmental conditions. In particular, presence and size of the posterior spine, and lorica length and width were related to temperature and lake trophic status (Pejler, 1962; Eloranta, 1982; Hofmann, 1983; Bielañska-Grajner, 1995). Furthermore, the development of the posterior spine was studied as a defensive mechanism against invertebrate predators (Stemberger & Gilbert, 1984, 1987; Conde-Porcuna et al., 1993).

In the Neotropics, José de Paggi (1978) observed that *K. cochlearis* had a shorter caudal spine in some tributaries of Paraná river than in floodplain lakes of the same system. This change was related to the physical conditions of the environments. There is no further information on the morphological variation of this rotifer in the region. In North Patagonian Andean lakes, *K. cochlearis* is widely distributed (Diéguez & Modenutti, 1996) and details about its populations dynamics in small Andean lakes are available (Balseiro & Modenutti, 1990; Modenutti, 1994). This rotifer is an important perennial species within the simple zooplankton assemblage of these lakes. In the present study we analyse the changes in morphological parameters of *K. cochlearis* in relation to physical and biological factors in a small Andean lake.

Study site

This study was conducted in Laguna Ezquerra (41° 3′ S, 71° 30′ W), a small and shallow North Patagonian lake (3 m Z_{max}), located at 758 m a.s.l. in the Nahuel Huapi system (Rio Negro, Argentina). In winter its surface often freezes and no stratification occurs during spring and summer. The lake is oligotrophic, with a Secchi depth between 2–3 m and the dissolved oxygen concentration values are always near 100% of saturation. Conductivity ranges from 50 to 70 μS cm^{-1}, and pH from 6.9 to 7.2.

During the spring-summer period the zooplankton constituted of seven rotifers, two cladocerans, one copepod species and a predaceous water mite (Balseiro, 1992; Balseiro et al., 1992; Modenutti, 1994). The two cladoceran species were *Bosmina longirostris* (OFM) and *Ceriodaphnia dubia* (Richard), which showed different seasonal patterns of abundance. Bosmina was present during the whole spring–summer period, with densities of 100 ind 1^{-1} from October to December and an increase in late February reaching 700 ind 1^{-1}. *Ceriodaphnia* showed an unimodal cycle during October–December reaching 80 ind 1^{-1} in late November. The copepod *Boeckella gracilipes* Daday developed during spring from copepodite 1 to adults but these remained at very low densities during summer. The water mite *Limnesia patagonica* Lundbald

was present over the spring-summer period but never exceeded densities of 9 ind m^{-3}. Water mites were the only invertebrate predators in this lake considering that copepods are represented only by an herbivorous calanoid (Balseiro, 1992).

Methods

Field observation

During a six months period (October 1988 – March 1989), we measured temperature and collected phyto- and zooplankton samples every 3–4 days. Phytoplankton was collected with a Van Dorn bottle at 1–1.5 m and 2–2.5 m deep. The samples were pooled and preserved with acid Lugol's solution. In the lab, phytoplankton samples were allowed to settle for ten days in 250 ml cylinders and the concentrate (5 ml) was counted at $400\times$ magnification in a 8.5 μl shallow chamber (thickness 0.15 mm). Algal biovolume was estimated by approximations to the appropriate geometric figures. Food resources were estimated as the algal biovolume of the fraction smaller than 20 μm GALD (Greatest Axial Linear Dimension).

Zooplankton was sampled at the same depths in 50 l samples using a Schindler-Patalas trap, filtered with a 35 μm mesh net and preserved with 4% formalin solution. Rotifers were counted in 1 ml Sedgwick-Rafter chamber under microscope. A minimum of 30 individuals of *Keratella cochlearis* from each weekly sample were measured under microscope (Olympus BH2) at $400\times$ using a micrometer eyepiece. Four morphometric parameters were considered: total length (hereafter TL), lorica length without considering anterior and posterior spine (hereafter LL), lorica width (hereafter LW), and posterior spine length (hereafter PS).

Correlation between morphometric parameters and environmental factors

Morphometric data were analysed using correlation tests and ANOVA. We correlated *K. cochlearis* morphometry with: (1) water temperature, (2) food resources (algal biovolume of the fraction smaller than 20 μm GALD), (3) density and biomass of main competitors (*Bosmina longirostris* and *Ceriodaphnia dubia*), and (4) density of the water mite *Limnesia patagonica*.
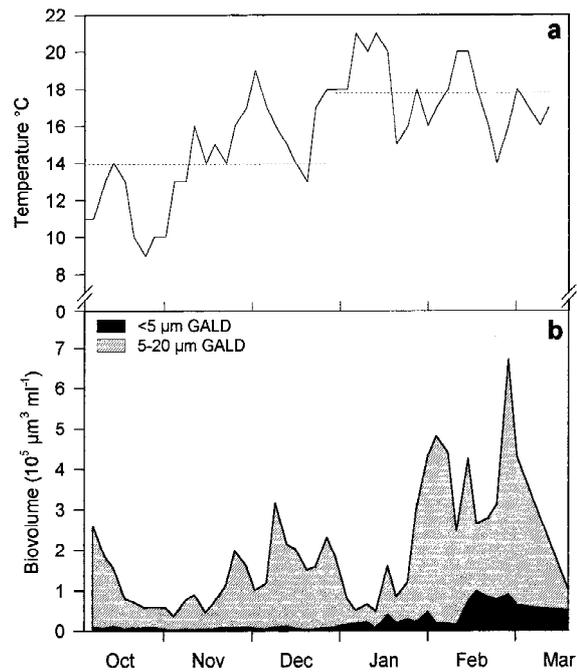

Figure 1. (a) Temperature in Laguna Ezquerra during October 1988–March 1989. Dotted lines represent mean temperature during spring and summer. (b) Biovolume of flagellate algae smaller than 20 μm GALD in Laguna Ezquerra during October 1988–March 1989.

Laboratory predation experiments

Laboratory experiments were performed in order to test if *Limnesia* was able to consume *Keratella*. Predation experiments were conducted in 50 ml Erlenmeyers flasks. Two *Keratella* densities (200 and 500 ind 1^{-1}) were exposed to *L. patagonica* (20 ind 1^{-1}). These densities were chosen in order to obtain reliable results, although they can not be extrapolated to field abundance of both species. The experiments were run for 4 hours, in darkness at 18°C. At the end of each exposure, we counted the number of living *Keratella*. Each experiment consisted of, at least, three replicates and three controls.

Results

Field observation

No vertical thermal stratification was observed during the study period. However there were some seasonal variations (Figure 1a). During spring temperature ranged between 11°C and 19°C (average 13.9°C), while in summer temperature ranged between 13°C and 21°C (average 17.5°C).
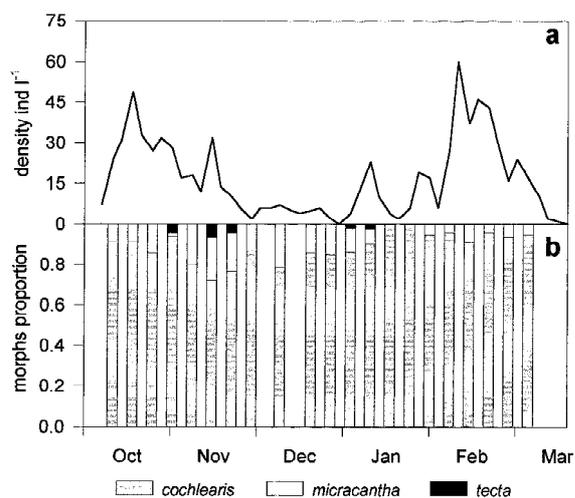
Figure 2. (a) Density of *Keratella cochlearis* in Laguna Ezquerra during October 1988–March 1989. (b) Proportion of the three morphs of *Keratella cochlearis* in Laguna Ezquerra.

The phytoplankton community was largely (>90%) dominated by flagellate cells under 20 μm GALD, fraction considered as the main food resource for *Keratella*. The flagellate *Rhodomonas lacustris* (Pascher & Ruttner) Javornicky predominated in the 5 to 20 μm GALD fraction, and *Chrysochromulina parva* Lackey and *Ochromonas* sp in the < 5 μm GALD fraction. Food resources, expressed as algal biovolume, showed seasonal fluctuations (Figure 1b). From October to January (spring and early summer) the biovolume fluctuated below 3×10^5 μm^3 ml^{-1}, while in mid January it decreased reaching a minimum of 0.6×10^5 μm^3 ml^{-1}. Then, during summer the biovolume steadily increased reaching 6.5×10^5 μm^3 ml^{-1} in late February (Figure 1b).

Keratella cochlearis was present during the entire study period. We observed two density peaks in its population cycle, one in spring with 50 ind l^{-1} and the other in late summer with 60 ind l^{-1} (Figure 2a). During spring the rotifer represented 99% of total rotifer density, while in summer, six other rotifer species peaked and thus *Keratella* relative importance in the community decreased (Modenutti, 1994). The minimum value of *K. cochlearis* abundance was registered in mid January (Figure 2a), after the unimodal cycle of *Ceriodaphnia dubia*.

Three morphs were distinguished: *cochlearis, tecta* and *micracantha*. The morph *cochlearis* was the most abundant and was present over the entire period (Figure 2b). The morph *tecta* was present in very low densities (2 ind l^{-1}) in October, November and Janu-
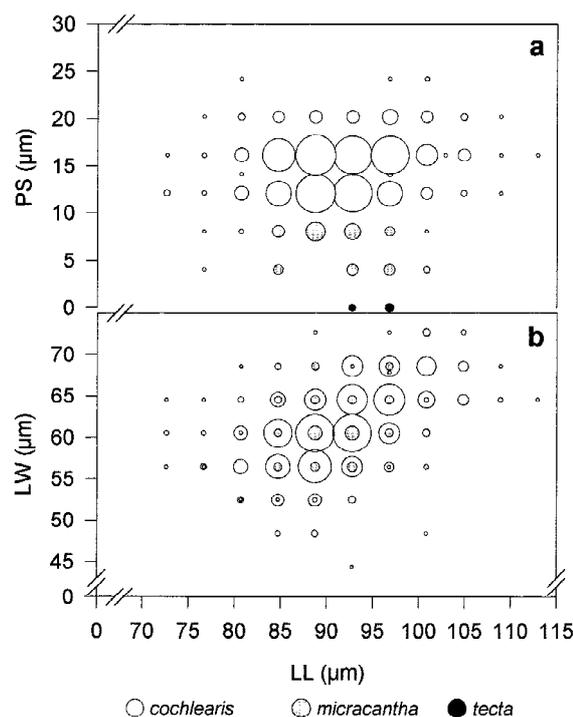

Figure 3. Relationship among lorica parameters of *Keratella cochlearis* (*cochlearis, micracantha* and *tecta*) in Laguna Ezquerra. (a) Lorica length vs. spine length. (b) Lorica length vs. lorica width. The area of the circles represents the frequency of the relationship.

ary (Figure 2b). The morph *micracantha* was defined as individuals with PS length less than 10 μm and was also present over the whole studied period (Figure 2b). However, our data showed the presence of two distinctive groups of *micracantha*, one group with a PS mean length of 8 μm and another with PS mean length of 4 μm. The *micracantha* morph with the largest PS was always present whereas the morph with the shortest PS disappeared in early January.

Correlation between morphometric parameters and environmental factors

The morphs were clearly separated by the PS length (ANOVA, $P < 0.05$) (Figure 3a), nevertheless they did not differ in LL and LW (ANOVA, $P > 0.05$) (Figure 3b). No significant correlation was observed between PS and LL (Figure 3a) ($P > 0.05$), indicating an absence of allometric growth of the caudal spine. Mean values of LL and LW decreased during the study period (Figure 4a and b). On the other hand, the PS length of *cochlearis* morph decreased during spring from 16.5 μm (mean value) in October to
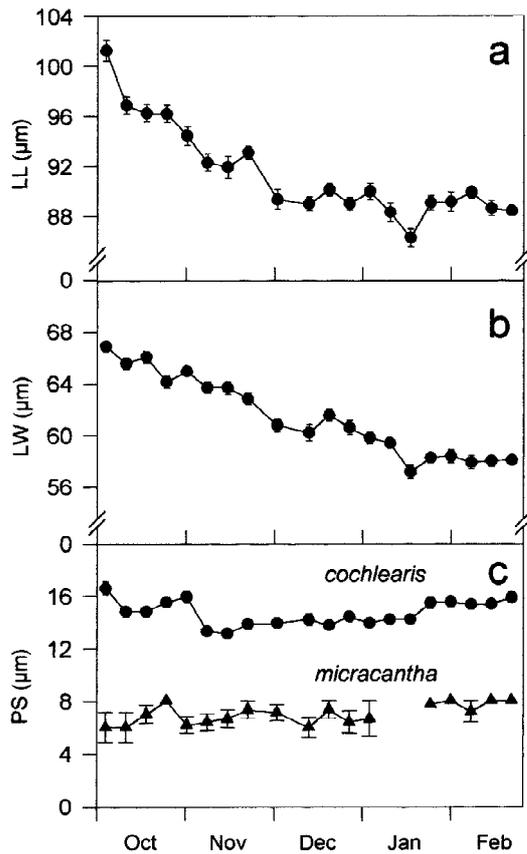
Figure 4. Temporal variation in morphometric parameters of *Keratella cochlearis* in Laguna Ezquerra during October 1988–March 1989. (a) Lorica Length. (b) Lorica Width. (c) Spine Length.
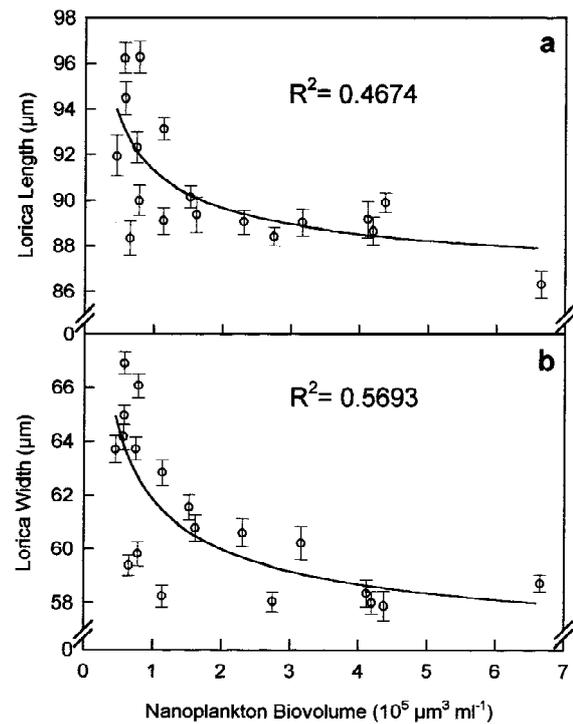

Figure 5. Relationships between lorica parameters and biovolume of flagellate algal cells. (a) Lorica Length. (b) Lorica Width.

Table 1. Number of *Keratella cochlearis* individuals dead in laboratory experiments with the predaceous water-mite *Limnesia patagonica* and controls. References: m = number of dead individuals day^{-1} (mean value); S.E. = standard error; n = replicates

	Keratella cochlearis	
	200 ind l^{-1}	500 ind l^{-1}
Predation experiments with *Limnesia patagonica*	m = 2.08 S.E. = ± 0.08 n = 6	m = 1.75 S.E. = ± 0.14 n = 3
Control without the predator	m = 0.33 S.E. = ± 0.14 n = 6	m = 0.17 S.E. = ± 0.08 n = 3

13 μm (mean value) in November (Figure 4c). Spine length increased during summer but never reached the maximum value of spring (Figure 4c). The morph *micracantha* remained with its stable mean values with a maximum of 8 μm in late October (Figure 4c).

We observed significant negative relationships between temperature and the morphometric parameters LL and LW (R^2=0.6250; R^2=0.6787 respectively; $P < 0.01$ in all cases). LL and LW also declined exponentially with the increase of nanoplankton biovolume ($P < 0.01$ in both cases) (Figure 5a and b). No relationship was found neither between PS length and temperature nor with nanoplankton biovolume ($P > 0.05$).

The main zooplankton competitors of *K. cochlearis* in Laguna Ezquerra were the cladocerans *Bosmina longirostris* and *Ceriodaphnia dubia* (Modenutti, 1994). No relationship was found between morphometric variables of *K. cochlearis* and cladoceran density or biomass $P > 0.05$).

Laboratory predation experiments

Limnesia patagonica consumed *K. cochlearis* in laboratory experiments. The water mite consumed up to 42 *Keratella* predator^{-1} day^{-1} (Table 1). Nevertheless,

no significant relationship existed between morphometry of *K. cochlearis* and *Limnesia* density in the field ($P > 0.05$).

Discussion

Spined morphs of *K. cochlearis* were present during spring and summer in Laguna Ezquerra. We observed that the length of the PS was smaller and less variable than in other lakes of the world (Stemberger, 1979; Eloranta, 1982; Green, 1987; BieIañska-Grajner, 1995), being within the ranks mentioned by José de Paggi (1978) for Paraná river. Although PS decreased during spring and increased towards summer (Figure 4c), we did not observe any significant relationship between this parameter and water temperature or food resources, as many authors did (Pejler, 1962; Ruttner-Kolisko, 1974; Eloranta, 1982; Hillbricht-Ilkowska, 1983; Hofmann, 1983). In addition, PS was independent of LL (Figure 3a). This absence of allometry was previously noted in North Patagonian lakes (Diéguez & Modenutti, 1996) and this condition was also found in populations of *K. cochlearis* in Zimbabwe, Africa (Green, 1987), in the Southern Hemisphere too. The small response of the relative growth of PS in Africa could be related to the limited range of temperature (Green, 1987). However, in a temperate lake as Laguna Ezquerra, we can not assume that temperature fluctuations (Figure 1a) were narrow enough to explain the lack of allometry.

The largest individuals were observed during spring when lower temperatures were registered. In fact, we obtained a negative correlation between LL and LW, and water temperature. This agrees with the statement that low temperatures slow down growth rates resulting in larger individuals (Ruttner-Kolisko, 1974; Dumont, 1977).

Lorica size was closely related to food resources. The significant correlations obtained between LL and LW and biovolume of flagellate cells suggest that (Figure 5a and b). During spring, under low food concentration, we found the larger specimens (Figure 1b and 4a and b), while the smaller ones were observed during summer with a higher algal biovolume (Figure 1b and 4a and b). Assuming Bogdan & Gilbert's (1982) prediction, larger individuals would have higher clearance rates than smaller ones. Thus, the variation in body length implies an increase or a decrease in clearance rates as a response to the fluctuations of food resources.

Although exploitative competition and interference competition may also produce morphological changes (Gilbert, 1988), we did not find any relationship between *Keratella* morphometry and cladoceran biomass or density. This lack of correlation can be related to the small body size of *Bosmina* and *Ceriodaphnia* since the magnitude of interference competition depends on cladoceran body size (Burns & Gilbert, 1986). Nevertheless, *C. dubia* was observed to affect negatively the egg ratio of *K. cochlearis* in Laguna Ezquerra (Modenutti, 1994).

Many of the cyclomorphic adjustments, including the allometric growth of spines, can be induced by predation (Dodson, 1989). So, in Laguna Ezquerra the absence of allometry in PS may be related to the type and low densities of the invertebrate predator present in the lake. *Limnesia patagonica* can effectively consume *K. cochlearis* in laboratory experiments but we did not find any relationship between rotifer morphometry and density of the water mite. Probably, this situation was due to the low densities of natural populations of this predator (1 to 9 ind m^{-3}), since predation effect depends not only on predator feeding rate but also on predator abundance (Gliwicz & Pijanowska, 1989). This is consistent with Balseiro (1992) findings that *Limnesia* did not affect significantly Bosmina's mortality in nature although this predator consumes *Bosmina* in laboratory experiments. There is an energetic cost associated with the production of spines. The sinking rate of *Keratella* increases with the presence of spines (Stemberger & Gilbert, 1984, 1987; Gilbert & Kirk, 1988), with a consequent decrease in swimming speed. So, these defensive morphs should be developed when the predator causes significant mortalities.

In summary, morphometry of *K. cochlearis* in Laguna Ezquerra clearly responded to fluctuations of temperature and food resources. Larger individuals were observed when temperature and food level were low. A larger lorica would increase the clearence rate without the energetic costs of spine development. Then, during the spring period of lower temperature and food resources the increase in body size would enhance the clearance rates allowing *Keratella* to persist in the presence of the competitors *Bosmina* and *Ceriodaphnia*.

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