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# *Meseres corlissi*: a rare oligotrich ciliate adapted to warm water and temporary habitats

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ABSTRACT: The temperature response of the oligotrich freshwater ciliate *Meseres corlissi*, a widely distributed but rare species, was investigated in laboratory cultures with the small cryptophyte *Cryptomonas* sp. as food. Experiments were conducted at saturating food levels and temperatures ranging from 12.5 to 30°C. The following ecophysiological parameters were measured: ingestion, growth and production rate, cell volume and gross growth efficiency. All these parameters peaked at temperatures ranging from 20 to 30°C. Encystment was also recorded in the temperature response experiments. Cyst formation was low (<1% of all ciliates) at temperatures above 20°C, increased to 18% at 20°C and reached a maximum (~80%) at 15 to 17.5°C. Food limitation had little impact on encystment at 25°C. Additional experiments at variable food levels yielded the numerical and functional response of the species at the temperature optimum (25°C). The experimental results suggest that *M. corlissi* is an opportunistic warm water species, able to cope with changes in food and temperature. When adequate environmental conditions are met, this ciliate should be highly competitive in freshwater habitats. The sparse findings of this species from natural habitats suggest, however, that although *M. corlissi* is globally distributed, it is not ubiquitous. The factors that restrict the occurrence of *M. corlissi* in freshwater remain unknown.

KEY WORDS: Adaptation · Ciliates · Oligotrichs · Cysts · Temperature response



## INTRODUCTION

Small and medium-sized oligotrich species dominate the ciliate community in terms of cell numbers and biomass in many freshwater environments (Beaver & Crisman 1989, Laybourn-Parry 1994, Weisse & Müller 1998 and references therein). In particular, the planktonic realm is characterised by the high percentage of oligotrichs and may be classified as 'Oligotrichetea' (Foissner et al. 1991). Although there is evidence for an endemic ciliate fauna in some freshwater lakes (reviewed by Foissner 1999, Foissner et al. 1999), it is commonly believed that most free-living ciliates are globally distributed (e.g. Finlay & Fenchel 1999, Foissner 1999) and 'adapted to very wide ranges of ecologically important factors such as temperature and salinity' (Finlay 2002). Accordingly, the potential for local adaptation to specific environmental factors has been studied only little.

The aim of this study was to test for ecophysiological adaptation of a ciliate to a peculiar aquatic environment, using the oligotrich species *Meseres corlissi* as a model organism for globally distributed but rare protist species. This species was first described from an infusion of dried mud samples taken from an astatic meadow-pond in Salzburg, Austria, and taxonomically placed into the family Halteriidae (Petz & Foissner 1992). The cell size of *M. corlissi* is *in vivo* approximately 70 to 90 × 60 µm, and the species is morphologically similar to common species among *Halteria* and *Strombidium* (Petz & Foissner 1992). Formation and structure of the characteristic resting cysts of *M. corlissi* have been reported elsewhere (W. Foissner, H. Müller, T. Weisse unpubl.). The ecology of the new species remained uninvestigated. An inventory of a new mud sample taken from the original type location in Salzburg in November 2002 confirmed the original finding (H. Müller unpubl.). The species was, however,

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not found in detailed surveys of the ciliate fauna in a eutrophic and an oligomesotrophic lake close to the type location (Foissner et al. 1999, W. Foissner, H. Müller, T. Weisse unpubl.). Further sporadic records of *M. corlissi* are known from a salt-pan of the Etosha National Park, Namibia (Foissner et al. 2002), and from the Murray River flood plain, Australia (W. Foissner pers. comm.). The material used in the present study was obtained from a fog rain forest in the Dominican Republic. The ciliate was isolated from a raw culture and adapted to the conditions used in our laboratory to rear planktonic oligotrich and prostome ciliates (e.g. Weisse et al. 2001, Weisse & Lettner 2003). The temperature response of *M. corlissi* was then investigated in cultures with the small cryptophyte *Cryptomonas* sp. as food. This and similar small cryptophyte species are the preferred food of many planktonic ciliates (summarised by Weisse & Müller 1998).

## MATERIALS AND METHODS

**Origin of the culture and stock culture conditions.** The original material of *Meseres corlissi* Petz and Foissner 1992 was provided by Walter Till (University of Vienna) from a fog rain forest near the town of Santiago, Dominican Republic, where it was collected from a reservoir of a tree bromelia, *Guzmania ekmanii*. Wilhelm Foissner (University of Salzburg) identified the species and established raw cultures of *M. corlissi* on Eau de Volvic enriched with some squashed wheat grains. This raw culture was purified and adapted to an algal diet composed of *Cryptomonas* sp. strain 979-4 (Culture Collection of Algae, SAG, Göttingen, Germany) in the laboratory. Length and width of the algae were ~10 × 6 µm, the average cell volume ranged from 160 to 220 µm, depending on temperature and light conditions (pers. obs.). Both the ciliate and cryptophyte were maintained in modified Woods Hole medium (MWC medium, Guillard & Lorenzen 1972) at 15 ± 1°C and continuous light (100 µmol photons $m^{-2}$ $s^{-1}$); the ciliate culture received additionally Eau de Volvic (25% of the total volume, 50 ml). This monospecific, non-clonal ciliate culture was then used to investigate the growth and feeding response of *M. corlissi* reported in this paper. Although no attempt was made to select an individual clone from the raw culture, it seems plausible that one or a few clones became dominant in the course of the continued culturing in the laboratory. Conjugation, i.e. sexual reproduction, was never observed in the course of this study. The experiments described were performed within half a year after sampling and establishment of the raw culture.

**Temperature response experiments.** Ciliates were taken from exponentially growing stock cultures. An inoculum was transferred to sterile 200 ml tissue-culture bottles containing MWC medium, *Cryptomonas* sp. and Eau de Volvic. Over 5 to 7 d, ciliates and prey were step-wise acclimated to experimental food levels and temperatures (12.5, 15, 17.5, 20, 22.5, 25, 27.5 and 30 ± 0.5°C). The target temperatures were reached by changing the incubation temperature by up to 3°C $d^{-1}$. Light level for ciliates during the acclimation period was ~70 µmol photons $m^{-2}$ $s^{-1}$ in a 12:12 h light:dark (L:D) rhythm. Prey levels were monitored with an electronic particle counter (CASY 1-model TTC, Schärfe System; Weisse & Kirchhoff 1997), and the ciliates were regularly fed to maintain saturating food levels.

After the temperature acclimation period, 20 to 40 ml of the ciliate cultures were inoculated into sterile 200 ml tissue-culture bottles containing 80 to 100 ml of medium and acclimated prey and 40 ml Eau de Volvic, at prey concentrations ranging from 6.0 to 15 × $10^7$ cells $l^{-1}$, corresponding to carbon levels of ~1.7 to 2.8 µg C $ml^{-1}$. To render this study comparable to previous investigations, prey cell volume was converted to carbon units using C (pg) = 0.109 $V$ $(\mu m^3)^{0.991}$ (Montagnes et al. 1994).

The experiments lasted for 48 h. Light conditions were identical to those of the acclimation period. Samples were taken from containers at 24 h intervals and fixed with Lugol's iodine (final concentration 2% vol/vol). Algal abundance in each container was measured by an electronic particle counter and microscopically, together with the ciliates. The latter were counted using a Sedgewick Rafter cell of 1 ml volume or settling chambers of 3 ml volume. Each experiment was run with 3 replicates plus 1 control without ciliates. Results reported are means ± 1 SD.

**Numerical and functional response experiments.** The ciliates were carefully adapted to experimental food and temperature conditions over 72 to 96 h, similar to earlier experiments with other planktonic ciliates (Weisse et al. 2001, 2002). The numerical and functional response of *Meseres corlissi* was measured in 10 experimental treatments at 25°C and a 12:12 h L:D rhythm over 48 h. Food levels ranged from 0.2 to 15 × $10^7$ cells $l^{-1}$, corresponding to carbon levels ranging from 0.06 to 2.72 µg C $ml^{-1}$ (see Fig. 3). Three controls without ciliates were run at high, medium and low food levels. Samples were taken at 6 to 12 h intervals.

**Formation of cysts.** The occurrence of cysts was monitored in each of the temperature response experiments (24 and 48 h after the beginning of the experiment) and in the numerical/functional response experiments. A part of the latter, at the lowest food levels, was extended to 72 h to reveal if extended periods of starvation increase the proportion of cysts among the ciliate population. The fraction of cysts was calculated as the number of cysts in a sample, divided by the total number of active plus encysted ciliates.

**Cell volume.** Cell volume of active ciliates and cysts was determined from length and width measurements of Lugol's fixed material, assuming a prolate spheroid shape with circular cross-section. Measurements were made on 50 ciliates obtained at the end of the experiment from each treatment, using an inverted microscope and an image analysis system (LUCIA version 4.51, Laboratory Imaging). Additionally, cell size of live ciliates and prey was measured with an electronic particle counter (CASY 1-model TTC, Schärfe System; Weisse & Kirchhoff 1997). For ciliates, the remaining volume from each experimental treatment was filtered through 30 µm mesh gauze, the retentate resuspended in an isotonic solution (CASYtone, Schärfe System) and measured immediately. This procedure required a minimum of approximately 500 ciliates $ml^{-1}$ to yield statistically reliable results.

The volume of live trophic cells was, on average, 30% smaller than the cell volume derived from image analysis measurements of Lugol's fixed material. This difference may not only result from the effect of the fixative but may also reflect the fact that the assumption of a prolate spheroid with circular cross-section overestimates the true cell volume; note that the third dimension (thickness) of the ciliates could not be measured by image analysis. In those cases in which ciliate volume could not be measured with live material (at 12.5 and 17.5°C), values reported in Fig. 1B were estimated by image analysis and corrected by a factor of 0.7.

**Calculation of experimental results.** Ciliate growth rate (µ) was determined from changes in cell numbers, assuming exponential growth over the experimental period according to:

$$\mu = \ln(N_t/N_0)/t \quad (1)$$

where $N_0$ and $N_t$ are ciliate numbers at the beginning and end of the experimental period, respectively; µ ($d^{-1}$) is the intrinsic rate of increase and $t$ is the duration of the experiment (d). Results were calculated for each 24 h interval separately because food concentrations were declining when ciliates reached higher numbers during the second day of the experiment. Ciliate production (µm $d^{-1}$) was calculated as the product of µ and the corresponding cell volume.

Ciliate growth rates were related to the geometric mean prey concentration ($P$) during the experimental period (Frost 1972, Heinbokel 1978) according to:

$$P = \frac{P_t - P_0}{\ln(P_t/P_0)} \quad (2)$$

where $P_0$ and $P_t$ are, respectively, the initial and final prey concentrations (cells $l^{-1}$) during incubations.

Ciliate ingestion rate ($I$, in *Cryptomonas* sp. $ciliate^{-1}$ $h^{-1}$) was calculated according to:

$$I = \frac{(P \times g)}{R_m} \quad (3)$$

where $g$ is the grazing rate ($h^{-1}$), $R_m$ is the ciliate abundance ($l^{-1}$) in the experimental containers. $g$ was calculated as:

$$g = \frac{\ln(C_t/C_0) - \ln(P_t/P_0)}{\Delta t} \quad (4)$$

where $C_0$ and $C_t$ are the initial and final *Cryptomonas* sp. numbers in the controls. $g$ is equivalent to µ of *Cryptomonas* sp. observed in the controls minus growth rates measured in the experimental containers. These rates were calculated according to Eq. (1), replacing $N_t$ and $N_0$ by $C_0$ and $C_t$ and $P_t$ and $P_0$, respectively.

The numerical response data of the ciliate (see Fig. 2) were fitted to Eq. (5), which includes a positive $x$-axis intercept, using the Marquardt-Levenberg algorithm (SigmaPlot 2000, version 6.10):

$$\mu = \frac{\mu_{max}(P - x')}{k' + (P - x')} \quad (5)$$

where µ is growth rate, $\mu_{max}$ is the maximum growth rate, $P$ is prey concentration (Eq. 2), $k'$ is a constant, and $x'$ is the $x$-axis intercept (i.e. threshold concentration, where µ = 0).

The functional response data (see Fig. 3) were first fit to an equation similar to Eq. (5), but µ and $\mu_{max}$ were replaced by the parameters $I$ and $I_{max}$, denoting actual and maximum ingestion rate (Eq. 3); $k'$ was replaced by the constant $k$, and $x'$ remained the prey concentration, where $I = 0$. Since the statistical analysis revealed that $x'$ was not significantly different from zero, i.e. that there was no threshold food level at which ingestion ceased, the data reported in Fig. 3B were then fitted to:

$$I = \frac{I_{max} P}{k + P} \quad (6)$$

The proportion of cysts ($y$) versus food concentration ($P$) was fitted to Eq. (7), using nonlinear regression analysis in SigmaPlot:

$$y = a\, e^{-cP} \quad (7)$$

where $a$ and $c$ are constants.

To express rates and ratios in Eqs. (2) to (7) in carbon units, cell numbers of *Cryptomonas* sp. were multiplied by the average algal cell volume measured in each experiment and converted to carbon assuming $C\ (pg) = 0.109\, V\ (\mu m^3)^{0.991}$ (Montagnes et al. 1994).

**Statistical analyses.** One-way analysis of variance (ANOVA) and Tukey's test were used to test if the overall impact of temperature on the measured parameters was significant ($p < 0.05$) and to reveal significant differences between results obtained at different temperatures. All statistical analyses were performed using SigmaStat (Version 2.03).

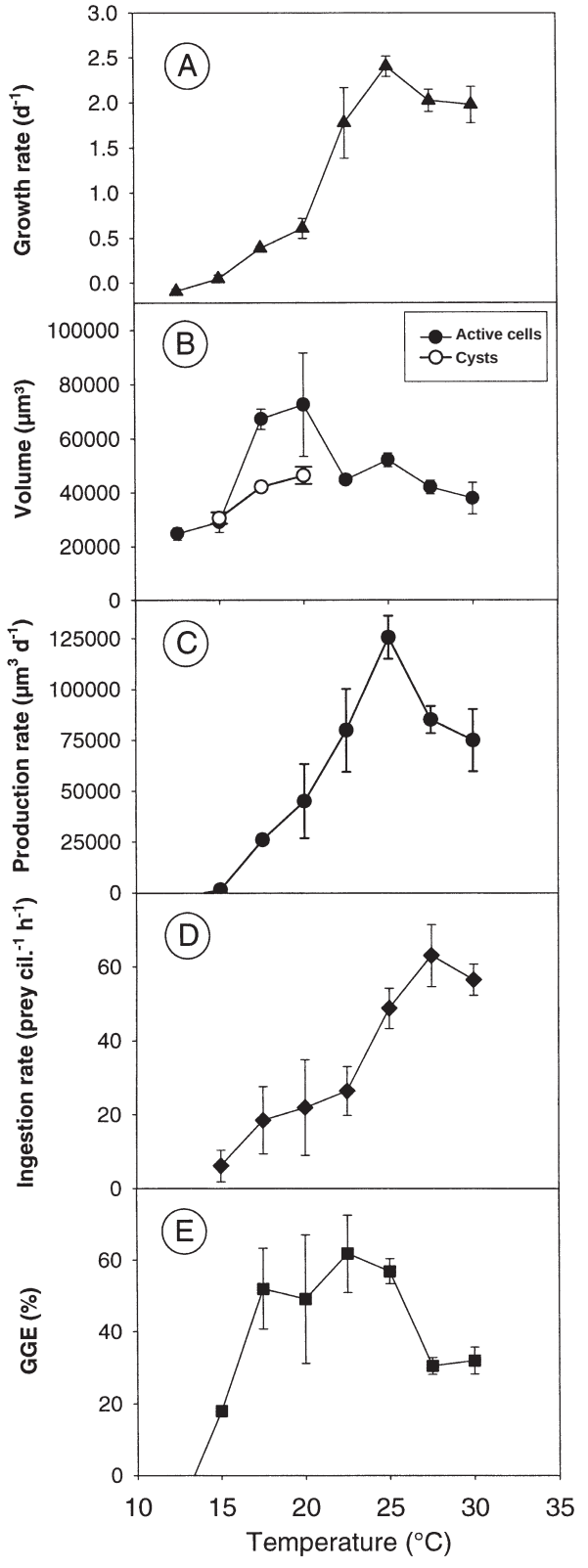


Fig. 1. *Meseres corlissi*. (A) Growth rate, (B) cell volume, (C) cellular production rate, (D) ingestion rate and (E) gross growth efficiency (GGE) of the ciliate (cil.) versus experimental temperature. Error bars denote ±1 SD

## RESULTS

### Growth, grazing and production rates of *Meseres corlissi* versus temperature

All ecophysiological parameters investigated were significantly impacted by temperature (1-way ANOVA, $p < 0.05$). Positive population growth of *Meseres corlissi* was recorded over a temperature range from 15 to 30°C. Growth rate peaked at 25°C (2.4 $d^{-1}$) and was not significantly different (1-way ANOVA, Tukey test) at the highest experimental temperatures (Fig. 1A). Temperatures >30°C were not tested because the *Cryptomonas* species used as food does not tolerate such high temperatures over several days (pers. obs.). The growth rate of *M. corlissi* declined to 0.05 $d^{-1}$ at 15°C and was negative (–0.10 $d^{-1}$) at 12.5°C.

Mean cell volume of the active *Meseres corlissi* cells increased significantly from 12.5 to 17.5°C (Fig. 1B) and then declined linearly at a rate of 0.04 $°C^{-1}$ from 20 to 30°C, relative to the maximum volume measured at 20°C (least-squares linear regression, $r^2 = 0.693$). In spite of this significant trend, cell volume was not significantly different between 22.5, 27.5 and 30°C (1-way ANOVA, Tukey test). Cell volume of the cysts measured at the temperatures at which cyst formation occurred in higher numbers (reported below) was similar to or lower than that of the active cells (Fig. 1B). Production rate increased linearly from 12.5 to 25°C and declined at higher temperatures (Fig. 1C). The peak production rate was significantly higher than rates measured at all other temperatures, while production rates calculated at 22.5, 27.5 and 30°C were not significantly different.

At 25°C, relatively small cells were able to achieve not only higher growth rates (Fig. 1A), but also higher production (Fig. 1C) and ingestion rates (Fig. 1D) than larger cells at lower temperatures. Ingestion rate increased with temperature and was significantly higher at 25 to 30°C than at the lower temperatures (Fig. 1D).

Gross growth efficiency (GGE), which denotes the ratio of conversion of food uptake into body biomass of the ciliates (production divided by ingestion), was significantly higher between 17.5 and 25°C than at the lower and upper end of the temperature range investigated (Fig. 1E).

### Numerical and functional response of *Meseres corlissi* at 25°C

The relationship between growth rate of *Meseres corlissi* and food concentration (numerical response) was investigated at 25°C, i.e. the temperature optimum at which growth and production rate and growth

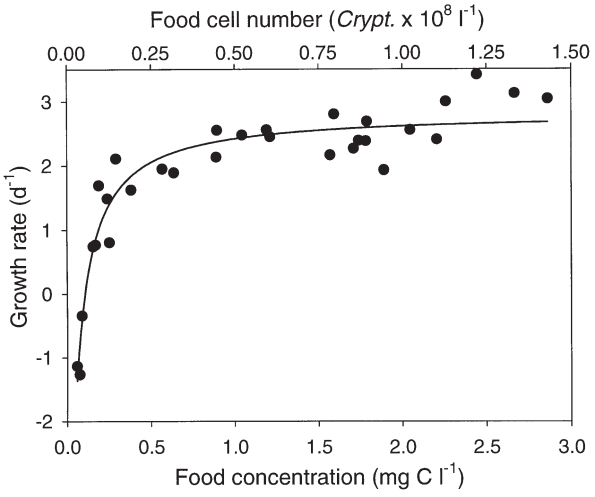


Fig. 2. *Meseres corlissi*. Relationship between population growth rate and food concentration (numerical response) at 25°C. Solid curve represents the fit of Eq. (5) to the data (see 'Materials and methods'). See Table 1 for the parameters and error estimates of the curve. *Crypt.*: *Cryptomonas*

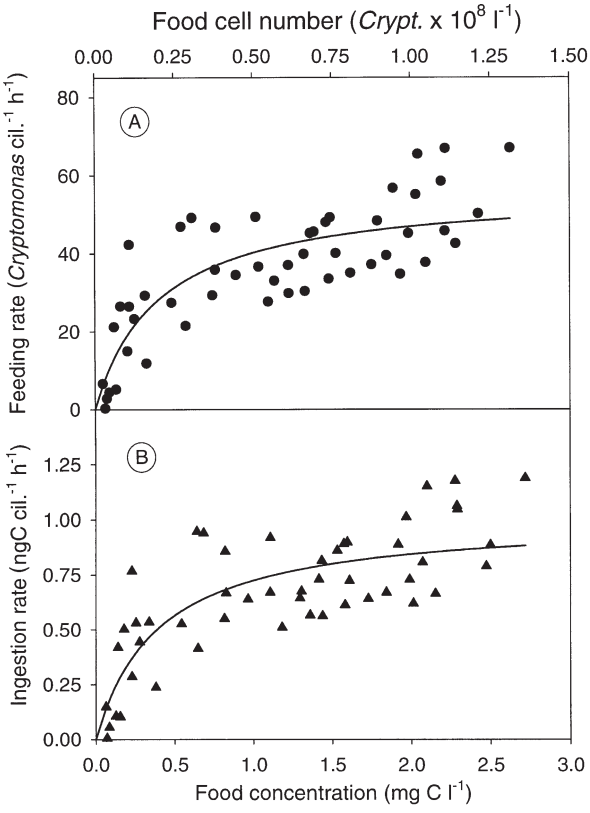


Fig. 3. *Meseres corlissi*. Relationship between food uptake, as (A) number of prey and (B) ng C, and food concentration (functional response) at 25°C. Solid curve represents the fit of Eq. (6) to the data (see 'Materials and methods'). See Table 1 for the parameters and error estimates of the curve. *Crypt.*: *Cryptomonas*; cil.: ciliate

efficiency peaked for the ciliate (cf. Fig. 1). Growth rate followed a rectangular hyperbolic response to food concentration; it increased rapidly with food concentration at food levels up to 0.25 mg C $l^{-1}$, corresponding to $1.3 \times 10^7$ *Cryptomonas* sp. cells $l^{-1}$, and then levelled off (Fig. 2). The threshold level $x'$, i.e. the minimum food concentration which must be exceeded to support positive population growth, was 0.10 ± 0.01 mg C $l^{-1}$ (Table 1). The maximum growth rate predicted from the nonlinear regression was 2.82 $d^{-1}$. The parameters and their error estimates of the curve fit (see 'Materials and methods', Eq. 5) are presented in Table 1.

Similar to growth rate, the functional response, that is consumption rate versus food concentration, followed a rectangular hyperbolic response to food concentration (Fig. 3). In terms of cell numbers, the maximum feeding rate predicted from the nonlinear regression was 56.4 ± 4.5 *Cryptomonas* sp. ciliate$^{-1}$ $h^{-1}$ (Fig. 3A), equivalent to 1353 ± 108 *Cryptomonas* sp. ciliate$^{-1}$ $d^{-1}$. The corresponding ingestion rate expressed in carbon units and the parameter estimates of the curve fit are presented in Fig. 3B and Table 1. In contrast to the numerical response, there was no threshold concentration of the functional response curve significantly different from zero. In other words, there was no indication that *Meseres corlissi* stopped feeding at (very) low food levels.

Table 1. Parameter values for the numerical and functional response curves presented in Figs 2 & 3. See 'Materials and methods' (Eq. 5) for further explanation. Experiments were conducted at 25°C

| Curve | $\mu_{max}$ ($d^{-1}$) | $I_{max}$ (ng C ciliate$^{-1}$ $d^{-1}$) | $k$ or $k'$ (mg C $l^{-1}$) | $x'$ (mg C $l^{-1}$) |
|---|---|---|---|---|
| Numerical response | 2.82 ± 0.11 | – | 0.13 ± 0.02 | 0.10 ± 0.01 |
| Functional response | – | 24.3 ± 2.0 | 0.33 ± 0.17 | – |

## Cyst formation of *Meseres corlissi*

In the temperature response experiments conducted at saturating food levels (Fig. 1), the ciliates had formed cysts at temperatures ≤20°C in all subsamples taken 24 h after the beginning of the experiment. The fraction of encysted cells increased dramatically at temperatures <20°C (Fig. 4). At temperatures >20°C, cysts occurred only sporadically; the proportion of cysts could not be quantified at 12.5°C because at this temperature the ciliate cell numbers were too low 24 h after the beginning of the experiment to quantify active cells and cysts with reliable statistics.

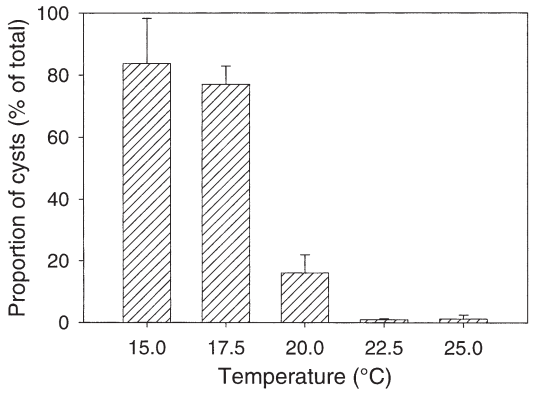


Fig. 4. *Meseres corlissi*. Proportion of encysted cells (percentage of total ciliates) versus temperature at saturating food concentrations. Error bars denote +1 SD

To investigate if food limitation and prolonged starvation may trigger cyst formation at higher temperatures, the occurrence of cysts was monitored in most treatments of the functional response experiment (cf. Fig. 3B), and a part of this experiment (at low food levels) was continued for 72 h. The functional response experiments confirmed the result from the temperature response experiments at 25°C: only 40 cysts were counted among >3000 ciliates, i.e. only 1.3% of all ciliates had formed cysts in these experiments within the first 48 h, and there was no obvious relation to food (Fig. 5). Prolonged exposure to low food concentrations (<0.1 mg C $l^{-1}$) increased the proportion of cysts to a maximum of 10.3% of all ciliates counted in a given treatment. With these results included, a nonlinear regression according to Eq. (7) (see 'Materials and methods') yielded a significant association between the relative amount of cysts and food (ANOVA, $F$ = 7.015, p = 0.0147). The predictive power of the regression model was, however, low (adjusted $R^2$ = 0.207), suggesting that the overall impact of food on the formation of cysts was low.

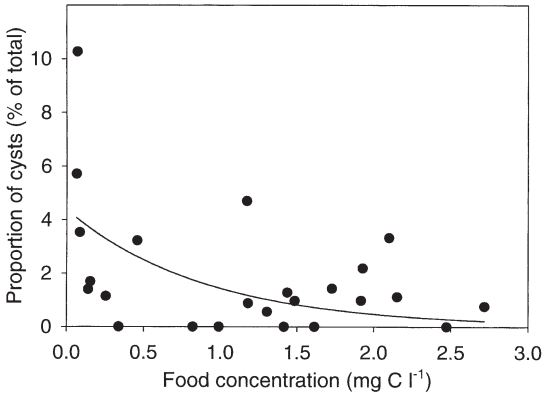


Fig. 5. *Meseres corlissi*. Proportion of encysted cells (percentage of total ciliates) versus food concentration at 25°C. Samples were taken 24, 48 and 72 h after the beginning of the experiment. Solid curve represents the fit of Eq. (7) to the data (see 'Materials and methods')

## DISCUSSION

### Temperature reaction norm of *Meseres corlissi*

Temperature significantly impacted all ecophysiological parameters of *Meseres corlissi* investigated (Fig. 1), and all parameters peaked at temperatures ranging from 20 to 30°C. At temperatures <20°C, the vast majority of the ciliates responded by forming cysts within 24 h (Fig. 4). The formation of cysts was obviously triggered by low temperature, because mass encystment could not be induced by food limitation at 25°C (Fig. 5). Note that it was not possible to prolong the period of starvation over more than 72 h, because the ciliates died off if food concentration fell below 0.1 mg C $l^{-1}$ (Fig. 2, Table 1).

Not only ingestion and growth rates but also cell volume and GGE were low at 12.5 and 15°C (Fig. 1). Accordingly, production rate of the ciliates measured at 15°C amounted to only 1.2% of the peak production rate measured at 25°C (Fig. 1C). The latter may indicate the temperature optimum of the species.

If the entire temperature range tested is considered, cell volume (Fig. 1B) did not decline linearly with temperature as suggested for marine diatoms (Montagnes & Franklin 2001). Cell volume peaking at intermediate temperatures has been previously observed in planktonic ciliates (Weisse et al. 2002, Weisse & Lettner 2003). Recently, Atkinson et al. (2003) concluded from a comprehensive statistical analysis of literature data that at extremely low temperatures, at which population growth is prevented, the size of aquatic protists increases with temperature. At higher temperatures, at which population growth is positive, cell volume declines linearly. In a study by Atkinson et al. (2003), the overall relative thermal sensitivity of cell volume was −0.025 $°C^{-1}$ of the cell volume at the reference temperature of 15°C; the mean relative thermal sensitivity of cell volume increased to −4% $°C^{-1}$ if only those datasets that gave significant linear negative regressions were considered. An identical relative thermal sensitivity of cell volume, −0.04 $°C^{-1}$, was obtained for *Meseres corlissi* in the present study from 20 to 30°C. Some caution is needed with this conclusion, because the statistical analysis (1-way ANOVA) revealed that the volume was not different at 3 out of the 5 temperatures measured over this temperature range.

High growth and ingestion rates measured at the upper end of the temperatures tested (Fig. 1A and D) may be misleading with respect to the overall temper-

ature response of the species, i.e. the temperature reaction norm. These high rates were measured at saturating food conditions (>1 mg C $l^{-1}$), which are met in eutrophic environments only. The environmental conditions and the food levels, in particular, in the tank of the bromeliads from which the ciliate was isolated remain unknown. The threshold food concentration needed to sustain zero population growth may steeply increase at the far end of the temperature tolerance of planktonic ciliates (Weisse et al. 2002). The highest ingestion rates measured at the warmest temperatures did not yield a maximum production rate, because the conversion of the energy uptake was reduced when temperature exceeded 25°C (Fig. 1E).

Similar to cell volume, GGE was not inversely related to temperature over the entire temperature range, as inferred for ciliates in general from a statistical analysis of literature data from 74 observations (Straile 1997). I conclude that the low cell volume and reduced GGE measured at the low temperatures reflect temperature stress at the low end of the temperature tolerance of the ciliate. Similarly, physiological stress was obvious at the high end of the temperature range investigated. A reduction in production and GGE at 27.5 and 30°C, while ingestion was still high, indicates that metabolic maintenance costs (respiration) were increasing at the high temperatures. Net growth efficiency, which denotes the proportion of the assimilated energy that can be used for production, is declining and relatively more energy is lost as heat because respiration increases disproportionately at temperatures above the temperature optimum. In other words, beyond the temperature optimum more of the assimilated energy is directed to maintenance, leaving little to be partitioned into growth and reproduction. The GGE curve may thus serve as another indicator for the temperature reaction norm of the species.

### *Meseres corlissi*: a globally distributed but locally thriving ciliate adapted to astatic warm water environments

Including the temperature response of cyst formation, all results presented in this study suggest that the isolate of *Meseres corlissi* from the Dominican Republic is adapted to unsteady warm water environments. The air temperature in the Dominican Republic usually ranges from 23 to 28°C. High maximum ingestion, growth and production rates, combined with the ability to form cysts, should enhance the chance of its widespread dispersal. The origin of the isolate and the few other observations of this species are in agreement with this conclusion. Since several attempts in our laboratory failed to adapt the ciliate gradually to temperatures <15°C, I conclude that the temperature reaction norm of this culture is genetically fixed. It is at present, however, an open question whether the results reported in this study are representative of the isolate from the Dominican Republic only or if they adequately characterise the reaction norm of the species.

Findings of *Meseres corlissi* active cells or cysts are known from 4 continents and diverse habitats such as the reservoir of a tree bromelia (Foissner et al. 2003), an astatic, temperate freshwater pond (Petz & Foissner 1992) and a subtropical salt-pan with irregular floods (Foissner et al. 2002). A common aspect of all these findings is that the distribution of *M. corlissi* was locally and/or temporarily highly restricted. In Namibia, for instance, the species was found only at 1 out of 73 sites investigated (Foissner et al. 2002). Similarly, the occurrence of *M. corlissi* in tank bromeliads is highly sporadic (Foissner et al. 2003, W. Foissner pers. comm.). Apparently, *M. corlissi* is globally distributed but it is not ubiquitous. This is remarkable considering that, due to the variety of the known habitats, the species should be able to adapt to a wide range of environmental conditions. This conclusion is further supported by the experimental results obtained in the present study. The isolate was easily adjusted (1) to a bacterial and/or flagellate diet (by W. Foissner, in the raw culture) and then (2) to a small cryptophyte known as optimum food for many planktonic ciliates and rotifers (Müller & Geller 1993, Weisse & Müller 1998, Weisse & Frahm 2001, Weisse & Lettner 2003). The versatility of the ciliate observed in the present study is noteworthy considering that *M. corlissi* may not be a typical euplanktonic species, although in cultures it swims permanently at a speed comparable to that of similar sized oligotrichs (pers. obs.).

Growth, ingestion and production rates and GGE of *Meseres corlissi* were similar or higher than those of closely related planktonic ciliates under similar experimental conditions (Müller & Geller 1993, Weisse & Montagnes 1998, Weisse et al. 2001, Weisse & Lettner 2003). The numerical and functional response curves further demonstrate that *M. corlissi* should be highly competitive in many warm-temperate and (sub)tropical lakes. The threshold food concentration for population growth is comparable to that of other planktonic ciliate species obtained under similar food and temperature conditions (Müller & Schlegel 1999, Weisse et al. 2002), but at the high end of values reported for oligotrich ciliates (Jakobsen & Hansen 1997 and references therein, Montagnes & Lessard 1999, Müller & Schlegel 1999). The threshold level corresponds to a chlorophyll *a* concentration of approximately 2.5 µg $l^{-1}$, assuming a carbon to chlorophyll *a* ratio of 40:1 (Banse 1977, Montagnes et al. 1994), or to a bacterial abundance of 2 to $10 \times 10^9$ cells $l^{-1}$, assuming a bacterial carbon content

of 10 to 50 fg cell$^{-1}$ (Fukuda et al. 1998 and references therein). Therefore, although *M. corlissi* does not need particularly high food concentrations, food limitation may be one of the factors restricting the occurrence of this ciliate in aquatic habitats to short periods.

*Meseres corlissi* is able to form cysts within a few hours (W. Foissner, H. Müller, T. Weisse unpubl.). The resting cysts are covered by a coat of small spheres (lepidosomes), embedded in a mucopolysaccharide-rich, fibrillar mucilage. The cyst wall, the mucilage, and the lepidosomes are highly resistant to inorganic and organic solvents (W. Foissner, H. Müller, T. Weisse unpubl.). In completely dry mud, cysts of *M. corlissi* survived for several months (H. Müller unpubl.). Although the results from this study suggest that cyst formation in *M. corlissi* is primarily triggered by temperature, encystment will enable the species to survive unfavourable environmental conditions such as food shortage or dry periods in astatic water bodies. If *M. corlissi* is globally dispersed, is able to survive adverse conditions and is such a highly competitive species relative to closely related, similarly sized other ciliates, why then is it not found everywhere where food is abundant?

The species is too large and conspicuous to be overlooked in natural samples easily. It seems possible that *Meseres corlissi* was confused in previous ecological investigations with similar species such as *Halteria bifurcata* (Foissner et al. 1999). *M. corlissi* was, however, not found in detailed inventories of temperate ponds and lakes by experienced ecologists and taxonomists (Foissner et al. 1999, Finlay & Maberly 2000, W. Foissner pers. comm.). Similarly, it was not found among numerous cryptic freshwater species in a hypersaline lagoon (Esteban & Finlay 2003). I therefore infer that, in spite of its global dispersal, *M. corlissi* is a rare species, relative to other common planktonic oligotrichs of the genera *Halteria* and *Strobilidium*/*Rimostrombidium* (Foissner et al. 1999). This does not rule out that *M. corlissi* will be recorded from other habitats in the future, since vast areas such as South America remain at present virtually unexplored for free-living ciliates (Foissner 2003).

In summary, the occurrence of *Meseres corlissi* in freshwater appears to be restricted to particular habitats and periods, due to the as yet unknown specific ecophysiological demands of this species and/or intrinsic factors such as an unusually short life span of the trophic cells. In spite of its high potential competitiveness with respect to ecologically important factors such as food and temperature, this species does not adapt to wide ranges of environmental conditions. Clearly, more observations with *M. corlissi* isolates obtained from geographically distant and ecologically different locations are needed to elucidate the ecophysiology of this species in more detail.

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