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Responses of three freshwater planktonic ciliates with different feeding modes to cryptophyte and diatom prey

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ABSTRACT: The filter feeding oligotrich ciliate *Strobilidium lacustris*, the raptorial prostome ciliate *Balanion planctonicum* and the diffusion feeding scuticociliate *Histiobalantium bodamicum* could be cultivated for months/years on a sole diet of *Cryptomonas* sp., whereas the diatom *Stephanodiscus hantzschii* did not support their growth. With *Cryptomonas* sp. as food, numerical responses of all ciliates followed a modified Michaelis-Menten model, which at 15°C yielded maximum growth rates of 0.96, 1.87 and 0.33 d^{-1} and threshold concentrations of 61, 78 and 290 ng C ml^{-1} for *S. lacustris*, *B. planctonicum* and *H. bodamicum*, respectively. Functional response patterns differed between species. In all investigated ciliates, growth rates reached a maximum earlier than ingestion rates, and there were no threshold concentrations for zero ingestion. Food selectivity depended on feeding mode. *H. bodamicum* was not able to ingest the non-motile diatoms. Both *S. lacustris* and *B. planctonicum* selectively preferred cryptophytes when offered a mixed diet. This effect was more pronounced in the raptorial feeder compared to the filter feeder. Our results indicate that during the phytoplankton spring bloom in Lake Constance prostome and oligotrich ciliates mainly exploit cryptophytes, and that the scuticociliate *H. bodamicum*, due to its slow growth, is an inferior competitor during this season. The observed threshold concentrations suggest that during the rest of the year prostomes and oligotrichs must rely on small-scale patches of this food, whereas *H. bodamicum*, with maximum development in late summer and autumn, presumably consumes a much larger variety of prey.

KEY WORDS: Ciliate · Numerical response · Functional response · Feeding mode · Selective feeding · Cryptophyte · Diatom · *Balanion* · *Strobilidium* · *Histiobalantium*

INTRODUCTION

Ciliate grazing on phytoplankton is a significant pathway of carbon flow in marine and freshwater pelagic food webs (Sherr & Sherr 1994, Finlay & Fenchel 1996). Since ciliate growth and grazing rates largely depend on the quantity and quality of available food, and since these responses are species specific, investigations on a large variety of predator-prey relationships are needed for a better understanding of this important trophic relationship. Available literature data mainly refer to filter feeding marine oligotrich ciliates, while data concerning freshwater species and ciliates with other feeding modes are scarce (for reviews see Montagnes 1996, Hansen et al. 1997).

For the present study, we selected 3 ciliate species from Lake Constance, Germany, which represent the 3 basic feeding modes known in suspension feeding protozoa (Fenchel 1987). These were the oligotrich ciliate *Strobilidium lacustris*, a filter feeder, the prostome ciliate *Balanion planctonicum*, a raptorial feeder, and the scuticociliate *Histiobalantium bodamicum*, a diffusion feeder (Müller & Weisse 1994). We investigated their numerical and functional responses to a wide range of concentrations of *Cryptomonas* sp. and studied their selective behaviour when *Cryptomonas* sp. and the diatom *Stephanodiscus hantzschii* were offered simultaneously.

The phytoplankton spring bloom in Lake Constance is dominated by the cryptophytes *Rhodomonas* spp. and *Cryptomonas* spp. and the small centric diatom *Stephanodiscus hantzschii* (Weisse et al. 1990, Küm-

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merlin 1991, Sommer et al. 1993). *Balanion planctonicum* and *Strobilidium lacustris* are conspicuous members of the ciliate community during this season. A small population of *Histiobalantium bodamicum* is also regularly observed in spring, though maximum development of this ciliate occurs in late summer and autumn (Müller et al. 1991, Müller & Weisse 1994). The ciliates and algae studied in the present *in vitro* experiments, therefore, represent potential predator-prey relationships in this lake. Our results are discussed in the context of previous field investigations in Lake Constance.

MATERIALS AND METHODS

Stock cultures. ***Cryptomonas sp.*** strain 26.80 from the algal culture collection in Göttingen (formerly called *Rhodomonas* sp., strain 26.80): this strain has been frequently used in grazing experiments at the Limnological Institute (e.g. Giani 1991, Müller 1991, Müller & Geller 1993, Müller & Weisse 1994). Weisse & Kirchhoff (1997) measured a mean cell volume of 280 μm^3. Stock cultures were grown at 15°C in Medium WC (Guillard & Lorenzen 1972). The cultures were illuminated with fluorescent light on a 12:12 h light:dark cycle at an irradiance of ~60 $\mu E\ m^{-2}\ s^{-1}$.

Stephanodiscus hantzschii: This species was isolated from surface waters of Lake Constance and has a mean cell volume of 133 μm^3 (Giani 1991). Stock cultures were maintained under the same conditions as the *Cryptomonas* sp. cultures.

Balanion planctonicum (formerly *Pseudobalanion planctonicum*) (Foissner et al., 1990) Foissner et al., 1994. The strain used in the present study was started from a multiclonal isolate obtained from surface waters of Lake Constance in April 1993. Stock cultures were grown in sterile filtered lake water at 9°C on a 12:12 h light:dark cycle with *Cryptomonas* sp. as food. According to Müller & Geller (1993), the species has a mean live cell volume of ~1800 μm^3.

Strobilidium lacustris Foissner et al., 1988: this species was placed in the genus *Rimostrombidium* Jankowski, 1978, by Petz & Foissner (1992). However, since the validity of this genus is controversially debated (see Montagnes & Taylor 1994), and since Foissner (1994) stated that '*Rimostrombidium* is an unfortunate name', we will use the traditional generic name *Strobilidium* throughout this text. According to Müller & Geller (1993), the species has a live cell volume of ~113000 μm^3 . The strain used in the present study was started from a multiclonal isolate obtained from surface waters of Lake Constance in April 1995. Maintenance of stock cultures was the same as with *Balanion planctonicum*.

Histiobalantium bodamicum Krainer & Müller, 1995: This species is identical to *Histiobalantium* sp. studied by Müller & Weisse (1994), who determined a live cell volume of ~34000 μm^3. The strain used in the present study was started from a multiclonal isolate obtained from surface waters of Lake Constance in November 1996. Stock cultures were grown in 'Volvic', a commercial mineral water from the Auvergne, France, which has been traditionally used as a culture medium for ciliates (e.g. Dragesco & Iftode 1972). Food, temperature and light conditions were the same as with *Balanion planctonicum* and *Strobilidium lacustris*.

For brevity, these strains will be referred to as *Cryptomonas*, *Stephanodiscus*, *Balanion*, *Strobilidium* and *Histiobalantium* throughout the 'Materials and methods' and 'Results' sections. All cultures contained bacteria. Small heterotrophic flagellates <5 µm were also present in the *Balanion* and *Histiobalantium* cultures. In accordance with previous observations, these organisms were not considered to be a food source for the ciliates under investigation (cf. Müller 1991, Müller & Weisse 1994).

Experimental cultures with *Cryptomonas*. All experiments were performed in batch cultures. Ciliate stock cultures were adapted to 15°C at least 2 d prior to the experiments. 100 ml culture bottles filled with 80 ml of sterile filtered lake water (for *Balanion* and *Strobilidium*) or Volvic (for *Histiobalantium*) were inoculated with different concentrations of *Cryptomonas* and 1 ciliate species. Initial *Cryptomonas* concentrations ranged from 18 to 98 × 10^3 cells ml^{-1}, initial ciliate concentrations were ~24 *Balanion* ml^{-1}, 3 to 10 *Strobilidium* ml^{-1} and ~80 *Histiobalantium* ml^{-1}. Control bottles received only *Cryptomonas* at a similar range of concentrations to the experimental bottles. After inoculation, all bottles were exposed to 15°C and dim light (12:12 h light:dark cycle, ~10 $\mu E\ m^{-2}\ s^{-1}$). Exact cell numbers were first determined 24 h after inoculation, to allow for recovery of the ciliates from handling stress and for adaptation to the experimental food concentration. Subsequently, changes in cell numbers were recorded at intervals of 12, 24 and 48 h in the *Balanion*, *Strobilidium* and *Histiobalantium* experiments, respectively. Experimental time was 2 to 3 d with *Balanion*, 3 to 5 d with *Strobilidium* and 6 to 10 d with *Histiobalantium*. For enumeration of algae and ciliates, 5 ml samples were taken from the cultures after gentle mixing. These, after fixation with acid Lugol's solution, served for counting of algae and ciliates in Sedgewick-Rafter chambers. Three entire chambers, i.e. 3 ml of sample volume, were scanned for the ciliates. At least 200 *Cryptomonas* cells were counted per sample, except at the end of experi-

ments, when algae had been reduced to very low concentrations.

With *Strobilidium*, we also tested a semi-continuous culturing technique according to Montagnes (1996). However, micropipette transfers required for this method caused dramatic mortality within 24 h compared to undisturbed control specimens, though the ciliates appeared undamaged shortly after the transfers. Similar attempts with the even more fragile *Histiobalantium* and the small *Balanion* were also unsuccessful.

Experimental cultures with *Cryptomonas* and *Stephanodiscus*. The ability of the ciliates to ingest *Stephanodiscus* was tested by the following procedure: batch cultures of *Balanion*, *Strobilidium* and *Histiobalantium*, in which most of the *Cryptomonas* food had been depleted, were incubated with a high concentration of *Stephanodiscus* for 2 h. Though sedimentation of *Stephanodiscus* in the culture dishes was not prevented, 3 to 10 × 10^4 diatoms ml^{-1} were in suspension over the incubation period. Subsequently, the ciliates were checked for ingested diatoms, either by live observation or after fixation with $HgCl_2$ (0.06% final concentration) and staining with protargol according to the protocol of Foissner (1991).

Selective feeding experiments with *Balanion* and *Strobilidium* were performed in 500 ml culture bottles containing 200 ml of sterile filtered lake water. Ciliate stock cultures for these experiments had been maintained at 15°C for at least 2 wk. Experimental bottles (a) were inoculated with *Cryptomonas*, *Stephanodiscus* and 1 ciliate culture. Initial cell concentrations were 2 to 5 × 10^4 cryptophytes ml^{-1}, 2 to 4 × 10^4 diatoms ml^{-1}, 20 to 30 *Balanion* ml^{-1} and 15 to 30 *Strobilidium* ml^{-1}. Control bottles received: ciliates + *Cryptomonas* (control b), *Stephanodiscus* + *Cryptomonas* (control c) or only *Cryptomonas* (control d) at similar concentrations. To prevent sedimentation of the diatoms, all bottles were placed in an overhead mixer (REAX 20/8 from Heidolph, Germany) which rotated for 3 min (1 rpm) every 2 h. Each experiment consisted of 8 culture bottles, which was the capacity of the overhead mixer. These were either 2 replicates each of experimental bottles (a) and control bottles (b, c, and d), or 3 replicates each of bottles (a) and (b), 1 control (c) and 1 control (d). Temperature was 15°C and irradiation was <3 µE m^{-2} s^{-1}. Numbers of algae and ciliates were first determined ~18 h after inoculation. Subsequently, changes in cell concentrations were followed at 24 h intervals, using the same method as described above.

Four selective feeding experiments were run with *Balanion* (B1 to B4). Several attempts were made with *Strobilidium*, a species which is very sensitive to changes in the chemical composition of the culture medium and, therefore, frequently does not survive transfers from a dense culture to fresh medium. Here we present data from 1 experiment (S1) in which the ciliates survived in all replicates, and from 2 experiments (S2 and S3) in which the ciliates survived in all replicates of bottles (a), but not in controls (b).

Data analysis. *Growth, grazing loss, ingestion and clearance rates* were calculated separately for each sampling interval of each culture according to Heinbokel (1978)

$$\mu = (\ln N_t - \ln N_0) \times t^{-1} \quad (1)$$

$$N = (N_t - N_0) \times (\ln N_t - \ln N_0)^{-1} \quad (2)$$

$$g = \mu_{control} - \mu_{experiment} \quad (3)$$

$$I = g \times N_{prey} \times (N_{predator} \times 24)^{-1} \quad (4)$$

$$F = g \times 10^6 \times (N_{predator} \times 24)^{-1} \quad (5)$$

where t = sampling interval (d); N_0 and N_t (cells ml^{-1}) = cell numbers at the beginning and end of t; N (cells ml^{-1}) = mean cell numbers within t, with the assumption of exponential increase or decrease of cells within each sampling interval; μ = growth rate (d^{-1}); g = grazing loss rates (d^{-1}); I = ingestion rate (prey cells × predator $cells^{-1}$ h^{-1}); and F = clearance rate (nl predator $cells^{-1}$ h^{-1}).

Numerical response was analyzed by relating the resulting growth rates (μ) to the corresponding initial *Cryptomonas* cell numbers N_0 (see 'Discussion'). These data were fit to a modified Michaelis-Menten model, which has been frequently used to describe numerical responses of protozoa (e.g. Heinbokel 1978, Fenchel 1986, Montagnes 1996)

$$\mu = [\mu_{max} \times (N_0 - k_0)] \times [k_t + (N_0 - k_0)]^{-1} \quad (6)$$

where μ_{max} is the maximum growth rate, k_0 is the x intercept or 'threshold concentration' (the food concentration where $\mu = 0$) and $k_0 + k_t$ is the 'half saturating concentration' (the food concentration at which $\mu = \mu_{max}/2$). Curves were fit to the data using the Marquardt-Levenberg algorithm (Sigmaplot, Jandel Scientific, CA, USA).

Functional response was analyzed by relating the ingestion rates (I) obtained for each culture and sampling interval to the corresponding geometric mean *Cryptomonas* cell numbers (N). These data were either fit to the Michaelis-Menten model

$$I = (I_{max} \times N) \times (k_t + N)^{-1} \quad (7)$$

or described as a linear relationship

$$I = a + N \times b \quad (8)$$

where I_{max} is the maximum ingestion rate, k_t is the half saturation concentration (the food concentration at which $I = I_{max}/2$), and a and b are constants.

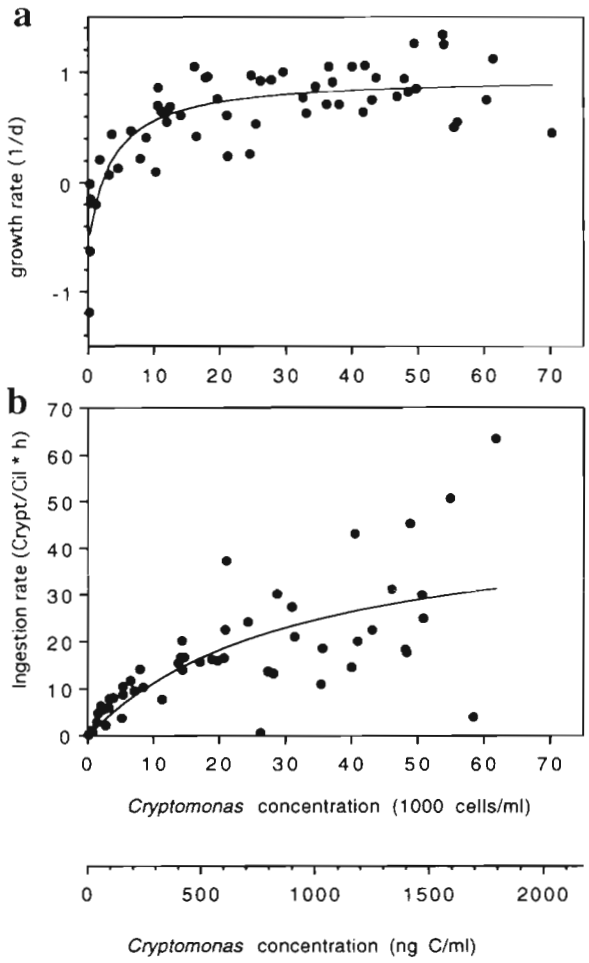

Fig. 1. *Strobilidium lacustris*. (a) Numerical response. Observed growth rates (●) and curve fit according to Eq. (6) (solid line). (b) Functional response. Observed ingestion rates (●) and curve fit according to Eq. (7) (solid line)

***Selectivity index* (D_{Cr})** was calculated according to Jacobs (1974)

$$D_{Cr} = (F_{Cr} - F_{St}) \times (F_{Cr} + F_{St})^{-1} \quad (9)$$

where F_{Cr} is the clearance rate for *Cryptomonas*, F_{St} is the clearance rate for *Stephanodiscus*. D_{Cr} may reach values between +1 (ingestion of *Cryptomonas* only) and −1 (ingestion of *Stephanodiscus* only). $D_{Cr} = 0$ indicates no selective ingestion.

Carbon concentrations of algal suspensions were estimated using the equation of Montagnes et al. (1994): $C = 0.109 \times V^{0.991}$, where V = cell volume (µm³) and C = carbon (pg cell^{-1}). For the mean cell volumes given above, this resulted in a carbon content of 29.0 pg cell^{-1} for *Cryptomonas* and of 13.9 pg cell^{-1} for *Stephanodiscus*.

Paired t-test (SigmaStat, Jandel Scientific, CA, USA) was applied to compare ciliate growth rates in different treatments of selective feeding experiments.

RESULTS

Numerical and functional response to *Cryptomonas*

Controls

Growth rates of *Cryptomonas* in control bottles with sterile filtered lake water ranged from 0.08 to 0.18 d^{-1}, while in control bottles with Volvic, growth rates from 0.03 to 0.08 d^{-1} were observed. Therefore, a mean value of $\mu_{control} = 0.12$ d^{-1} was used in experiments with *Balanion* and *Strobilidium* and a mean value of $\mu_{control} = 0.05$ d^{-1} in experiments with *Histiobalantium* to calculate grazing loss rates (Eq. 3).

Strobilidium lacustris

Growth and ingestion rates of *Strobilidium* relative to prey concentrations were fit to Michaelis-Menten Eqs. (6) & (7), respectively, as illustrated in Fig. 1 and Tables 1 & 2. The half saturating concentration for ingestion was 4-fold higher than that for growth. There was no threshold concentration for zero ingestion.

Balanion planctonicum

The growth response of *Balanion* (Fig. 2, Tables 1 & 2) followed the modified Michaelis-Menten model.

Table 1. Growth parameters and estimates of error of numerical and functional response data (Figs. 1 to 3) fit to Michaelis-Menten models (Eqs. 6 & 7) using the SigmaPlot curve fitting program

	Value	Standard error	Coefficient) of variance (%)
***Strobilidium*, numerical response**			
μ_{max} (d^{-1})	0.96	0.08	8
k_0 (prey cells ml^{-1})	2100	0.5	23
k_t (prey cells ml^{-1})	5500	1.8	32
***Strobilidium*, functional response**			
I_{max} (prey cells predator cells^{-1} h^{-1})	47.4	12.5	26
k_t (prey cells ml^{-1})	31500	16.8	53
***Balanion*, numerical response**			
μ_{max} (d^{-1})	1.87	0.10	5
k_0 (prey cells ml^{-1})	2700	0.4	15
k_t (prey cells ml^{-1})	5400	1.1	21
***Histiobalantium*, numerical response**			
μ_{max} (d^{-1})	0.33	0.11	32
k_0 (prey cells ml^{-1})	10000	2.2	22
k_t (prey cells ml^{-1})	10200	4.0	40

Table 2. Threshold concentrations (TC) and half saturating concentrations (HSC) of *Balanion planctonicum*, *Strobilidium lacustris* and *Histiobalantium bodamicum* in terms of carbon. These data were derived from Table 1, assuming a value of 29 pg C *Cryptomonas* cell^{-1}

	TC (ng C ml^{-1})	HSC (ng C ml^{-1})
Strobilidium (growth)	61	220
Strobilidium (ingestion)	–	913
Balanion (growth)	78	235
Histiobalantium (growth)	290	586

While the maximum growth rate of the small *Balanion* was twice as high as that of *Strobilidium*, the threshold and half saturating concentrations of both species were not significantly different.

The ingestion rates of *Balanion* continuously increased over a range of prey concentrations from 0.1 to 82 × 10^3 *Cryptomonas* cells ml^{-1} (Fig. 2). At higher food levels, a decline of ingestion rates was observed. Attempts to fit these data to Eq. (7) (dotted line in Fig. 2) resulted in a maximum ingestion rate of 18 *Cryptomonas* cells ciliate^{-1} h^{-1}. This value appears unrealistic, since it considerably exceeds all measured ingestion rates, and since this would mean that *Balanion* could ingest 3 times its own cell volume per hour.

Apparently, the functional response of *Balanion* followed a different pattern. Over the range from 0.1 to 82 × 10^3 *Cryptomonas* cells ml^{-1}, this response could be described as a highly significant linear relationship (Eq. 8; straight solid line in Fig. 2) between (I) and (N) with a = –0.11 ± 0.15 (SE), b = 0.084 ± 0.004 (SE) and the correlation coefficient r = 0.94 (n = 54; $p < 0.0001$). Our data suggest for *Balanion* a maximum ingestion rate of 6 to 8 *Cryptomonas* cells ciliate^{-1} h^{-1}.

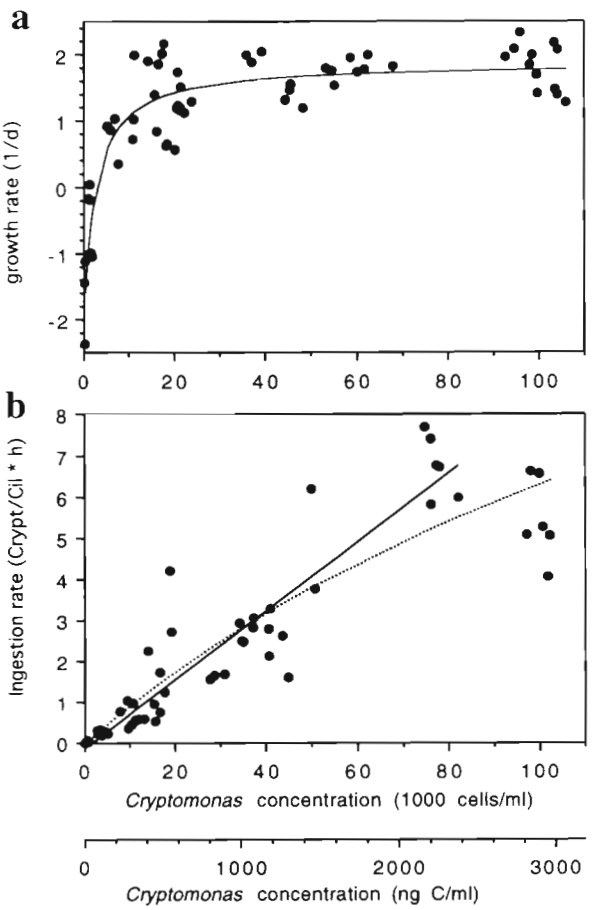

Fig. 2. *Balanion planctonicum*. (a) Numerical response. Observed growth rates (●) and curve fit according to Eq. (6) (solid line). (b) Functional response. Observed ingestion rates (●) and curve fit according to Eq. (7) (dotted line) and linear regression (solid line). Ingestion rates measured at *Cryptomonas* concentrations >82 × 10^3 cells ml^{-1} were excluded from the linear regression

Histiobalantium bodamicum

The growth response of *Histiobalantium* (Fig. 3, Table 1 & 2) followed Eq. (6). *Histiobalantium* had the lowest maximum growth rate and highest threshold concentration of the species under investigation.

The ingestion rates of this species linearly increased over the range of tested prey concentrations; a non-limiting food level for ingestion was not reached in our experiment (Fig. 3). We found a highly significant linear relationship (Eq. 8; straight solid line in Fig. 3) between (I) and (N) with a = –0.3 ± 0.3 (SE), b = 0.11 ± 0.01 (SE), the correlation coefficient r = 0.88 (n = 27; $p < 0.0001$). Attempts to fit the data to the Michaelis-Menten model (Eq. 7) resulted in a curve (dotted line in Fig. 3) which was almost identical to the linear regression line. The present data do not allow an estimate of the maximum ingestion rate of *Histiobalantium*.

Synopsis

The numerical responses of all 3 ciliates followed the modified Michaelis-Menten model according to Eq. (6), with species specific values of maximum growth rates and threshold concentrations. The functional response of *Strobilidium* could be described by the Michaelis-Menten model according to Eq. (7). In contrast, linear relationships between ingestion rate and food concentration were observed for *Balanion* and *Histiobalantium*. For all 3 species, growth rates reached a maximum earlier than ingestion rates. There were no threshold concentrations for zero ingestion.

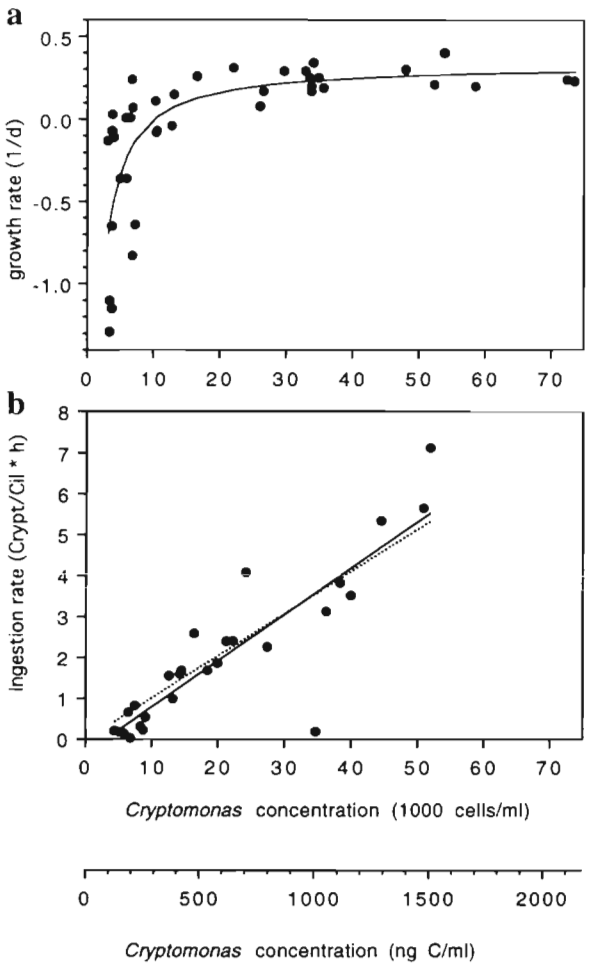

Fig. 3. *Histiobalantium bodamicum*. (a) Numerical response. Observed growth rates (●) and curve fit according to Eq. (6) (solid line). (b) Functional response. Observed ingestion rates (●) and curve fit according to Eq. (7) (dotted line) and linear regression (solid line)

Ability to ingest *Stephanodiscus*

The ciliates under investigation were cultivated for several months (*Strobilidium*) or years (*Balanion*, *Histiobalantium*) on a diet of *Cryptomonas*. In contrast, all attempts to maintain these cultures with *Stephanodiscus* as the only food source failed. Nevertheless, the ciliates might be able to utilize these small diatoms as an additional food.

To test their ability to ingest *Stephanodiscus*, the ciliates were incubated with a dense suspension of this prey for 2 h and subsequently examined for ingested diatoms after fixation with $HgCl_2$ and protargol staining. As shown in Table 3, ~80% of *Strobilidium* and ~40% of *Balanion* were found with ingested *Stephanodiscus*, whereas only 1 specimen of *Histiobalantium* with 1 ingested diatom could be detected. Apparently, the diffusion feeding *Histiobalantium* will generally not ingest this non-motile prey. To support this negative result, we examined another 20 live specimens of *Histiobalantium* after incubation with *Stephanodiscus* and found they had not ingested any diatoms. Consequently, we excluded *Histiobalantium* from further experiments with a mixed diet of *Cryptomonas* and *Stephanodiscus*.

Table 3. Qualitative test for the abilitiy to ingest *Stephanodiscus hantzschii*: number of individuals found with ingested diatoms (n-ingested) after incubation with a dense suspension of *Stephanodiscus* for 2 h (see text)

Species	n	n-ingested	% Ingestion
Strobilidium	68	58	82
Balanion	121	52	43
Histiobalantium	71	1	1

Selective feeding on *Cryptomonas* and *Stephanodiscus*

As examples, the dynamics of experiments S1 (with *Strobilidium*) and B3 (with *Balanion*) are shown in Figs. 4 & 5. Abundances of both ciliates increased in experimental bottles (a) and controls (b) until *Cryp-*

Table 4. Growth rates μ (d^{-1}) of *Strobilidium lacustris* and *Balanion planctonicum* during selective feeding experiments. Mean values of 2 (S1,S2) or 3 (S3, B1 to B4) parallel cultures

Expt	Time interval (h)	μ with *Cryptomonas*	μ with *Cryptomonas* and *Stephanodiscus*
S1	18–42	0.36	0.43
	42–66	0.04	−0.03
	66–91	−0.35	−0.43
S2	19–43	–	0.69
	43–67	–	0.37
	67–91	–	−0.24
S3	19–43	–	0.79
	43–67	–	0.57
	67–91	–	0.16
B1	18–42	1.61	1.65
	42–69	0.90	1.13
	69–90	−1.47	−0.87
B2	18–42	1.15	0.94
	42–66	1.53	1.69
	66–90	0.35	0.62
B3	11–35	1.54	1.80
	35–59	1.77	1.76
	59–83	−1.30	−1.16
B4	18–42	1.79	1.87
	42–66	−0.69	0.16
	66–90	−4.31	−3.68

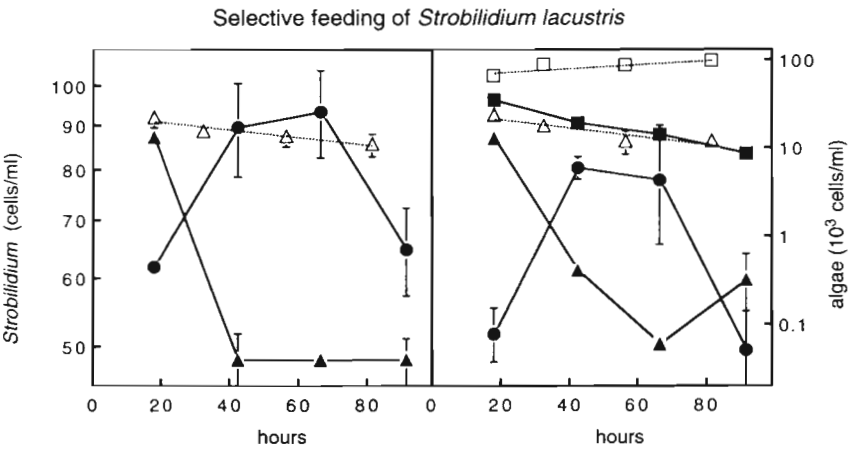

Fig. 4. Changes in cell concentrations during the selective feeding experiment S1 with *Strobilidium lacustris*. Left: Controls (b) and (d). Right: Experimental bottles (a) and controls (c). Mean values and standard deviation of 2 replicates. Solid symbols: bottles with ciliates (a,c); open symbols: controls without ciliates (b,d); circles: ciliates; triangles: cryptophytes; squares: diatoms

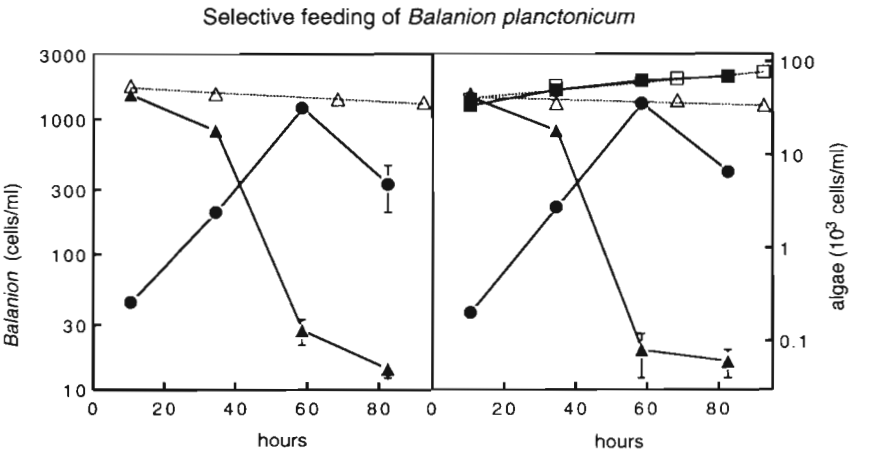

Fig. 5. Changes in cell concentrations during the selective feeding experiment B3 with *Balanion planctonicum*. Left: Mean values and standard deviation of 3 replicates of controls (b), single values from control (d). Right: Mean values and standard deviation of 3 replicates of experimental bottles (a), single values from control (c). Symbols as in Fig. 4

tomonas had been depleted to very low concentrations; subsequently ciliate numbers declined. A slight reduction of *Stephanodiscus* was observed in the cultures with *Strobilidium*, but not in those with *Balanion*.

Ciliate growth rates from the entire series are listed in Table 4. The negative values of μ measured during the 3rd interval of most experiments indicate that *Stephanodiscus* did not support ciliate growth, though at the beginning of this interval diatom concentrations exceeded 12×10^3 cells ml^{-1} (~167 ng C ml^{-1}) in S1 to S3 and 6×10^4 cells ml^{-1} (~834 ng C ml^{-1}) in B1 to B4. Positive growth rates at the end of experiments S3 and B2 may be explained by higher concentrations of *Cryptomonas* in these cultures (cf. Table 5). Neverthe-

Table 5. Results of selective feeding experiments with *Strobilidium lacustris* and *Balanion planctonicum* in experimental bottles (a) and controls (c) (second time interval). N (cells ml^{-1}) = mean cell numbers of ciliates and algae (Eq. 2); μ and μ-con (d^{-1}) = growth/mortality rates of algae in experiments and controls, respectively (Eq. 1); g (d^{-1}) = grazing loss rates (Eq. 3); I (cells ind.$^{-1}$ h^{-1}) = ingestion rate (Eq. 4); F (nl ind.$^{-1}$ h^{-1}) = clearance rate (Eq. 5)

Expt and time interval (h)	Ciliates	*Cryptomonas*						*Stephanodiscus*					
	N	N	μ	μ-con	g	I	F	N	μ	μ-con	g	I	F
S1 43–67	79	180	−1.92	−0.26	1.66	0.2	876	16500	−0.31	0.12	0.43	3.7	225
S2 44–68	41	710	−2.40	−0.34	2.06	1.5	2094	17700	−0.81	0.22	1.03	18.4	1043
S3 44–68	65	6380	−2.07	−0.13	1.94	8.0	1251	36000	−0.50	0.14	0.64	14.8	411
B1 42–69	127	1660	−3.25	−1.05	2.20	1.2	720	64300	0.03	0.21	0.18	3.7	58
B2 42–66	102	6990	−1.76	−0.83	0.93	2.7	382	65100	0.21	0.18	−0.03	−0.8	−12
B3 35–59	611	3340	−5.43	−0.06	5.37	1.2	366	56000	0.23	0.18	−0.05	−0.2	−3
B4 42–66	343	3040	−1.77	−0.28	1.49	0.5	181	63100	0.27	0.14	−0.13	−1.0	−16

less, a paired *t*-test using all data of experiments B1 to B4 revealed that growth rates of *Balanion* in the presence of *Stephanodiscus* were slightly higher than in bottles without diatoms ($n = 12$; $p < 0.05$).

In controls (c), growth rates of *Stephanodiscus* ranged from 0.12 to 0.22 d^{-1}, whereas negative values from −0.06 to −1.05 d^{-1} were found for *Cryptomonas*. This indicates that *Cryptomonas* was negatively affected by the experimental conditions such as dim light and rotation. For unknown reasons, this negative reaction was variable between experiments, with the consequence that values of $\mu_{control}$ (Eq. 3), which are needed to estimate ingestion and clearance rates, were not reliable. Therefore, we restricted these estimates to the second time interval of each experiment, when the ciliates were most numerous and had the strongest grazing impact, such that an incorrect value of $\mu_{control}$ would least affect the resulting values of I and F.

Ingestion and clearance rates as calculated according to Eqs. (4) & (5) are listed in Table 5. Ingestion of *Cryptomonas* by *Strobilidium* corresponded well to the functional response curve shown in Fig. 1. The oligotrich ciliate ingested *Stephanodiscus* at rates from 4 to 18 cells $ciliate^{-1}$ h^{-1}. Clearance rates for the cryptophytes exceeded those for the diatoms by a factor of 2 to 4.

Balanion ingested *Cryptomonas* at somewhat higher rates than expected from Fig. 2. Its consumption of *Stephanodiscus* could be measured only in 1 experiment (B1), with a rate of ~4 diatoms $ciliate^{-1}$ h^{-1} and a clearance rate which was 10-fold lower than that for the cryptophytes. Expts B2 to B4 yielded negative values for I and F (see 'Discussion'). Obviously, the grazing impact of *Balanion* on the diatoms in these experiments was too small to be detected.

The results of the selective feeding experiments are summarized in Table 6. Positive selection for *Cryptomonas* was evident in all experiments, but differed in strength among both ciliate species.

Table 6. Values of the selectivity index D_{Cr} for *Cryptomonas*, calculated from the clearance rates (F) given in Table 5 (Jacobs 1974; Eq. 9). Negative values of F were set to zero

Expt	D_{Cr}	Expt	D_{Cr}
S1	0.59	B1	0.85
S2	0.33	B2	1
S3	0.50	B3	1
		B4	1
Mean	0.47	Mean	0.96

DISCUSSION

Methodological considerations

All our experiments were performed in batch cultures, with the disadvantage that prey concentrations changed largely within sampling intervals. For analysis of functional responses, we related ingestion rates (I) to mean algal concentrations (N) as estimated according to Eq. (2). To study numerical responses, in contrast, we related growth rates (μ) to initial prey concentrations (N_0) for the following reason: we measured changes in ciliate abundance, not biomass. Since sampling intervals in each experiment were chosen to approximately match ciliate generation times, cell divisions occurring within the first half of an interval would have been mainly due to food ingestion within the preceding interval. Initial prey numbers (N_0), therefore, were considered a best estimate of the prey concentration which had caused the increase in ciliate numbers as recorded within the interval (t).

Stephanodiscus hantzschii forms β-chitin threads 20 to 30 µm in length, which considerably enlarge its effective diameter. As demonstrated by Verity & Villareal (1986), ingestion of diatoms by protozoa may be hindered by formation of such threads. We examined our cultures and found that in different batches 3 to 28% of the diatoms were bearing threads, compared to 34 to 87% of the field population as observed over 6 wk in spring 1996. We conclude that our *S. hantzschii* cultures were not quite representative of the field population, as they should have been more easily ingested than *S. hantzschii* in the lake.

The selective feeding experiments B2 to B4 yielded negative values of I and F for the diatoms. This absurd result could have been due to promotion of diatom growth by the ciliates. More likely, however, our method to determine algal concentrations was not precise enough to exactly measure the small values of g for diatoms in the B series. Nevertheless, our data clearly show that ingestion and clearance rates of *Balanion planctonicum* for *Stephanodiscus hantzschii* were close to zero.

Numerical response

Growth rates of all 3 species followed a curvilinear response according to the modified Michaelis-Menten model (Eq. 6). Previously determined values of μ_{max} for *Strobilidium lacustris* (0.99 d^{-1} at 15.5°C, Müller & Geller 1993) and *Histiobalantium bodamicum* (0.33 d^{-1} at 18°C, Müller & Weisse 1994) agree well with our present data. Despite its large cell volume, the oligotrich ciliate *S. lacustris* can grow much faster than the smaller scuticociliate *H. bodamicum*.

Surprisingly, we found a much higher maximum growth rate for *Balanion planctonicum* compared to

the value of 1.24 d^{-1} (15.5°C) obtained by Müller (1991) with the same cryptophyte prey. This may be explained by the fact that we studied a different strain of *B. planctonicum*, which was isolated from the lake in spring 1993 and had been adapted to the culture conditions for more than 3 yr before our experiments started. The value of μ_{max} for *B. planctonicum* as shown in Table 1 is very close to the theoretical value of 1.86 d^{-1} as predicted by the model equation of Müller & Geller (1993) for 15°C and a cell volume of 1800 μm^3. The closely related marine species *B. comatum*, which is of similar cell size, according to Jakobsen & Hansen (1997) has a maximum growth rate of 1.39 d^{-1}.

In the literature, threshold concentrations for zero growth of planktonic ciliates from 6 to 325 ng C ml^{-1} are reported, as reviewed by Montagnes (1996) and Jakobsen & Hansen (1997). The values found in the present study are well within this range. Threshold concentrations of *Strobilidium lacustris* and *Balanion planctonicum* were 61 and 78 ng C ml^{-1}, respectively. In Lake Constance, averaged over the upper 8 m of the water column, similar or higher concentrations of small algae have only been recorded during phytoplankton spring blooms, whereas levels <40 ng C ml^{-1} were observed over the rest of the year (Müller et al. 1991). Accordingly, maximum abundance of *S. lacustris* and *B. planctonicum* is regularly observed in spring. However, both species are also present during the entire summer/autumn period and low numbers of *B. planctonicum* even persist during the winter months (Müller 1991, Müller et al. 1991). These findings support the hypothesis of Montagnes (1996) that, in order to to survive, planktonic ciliates must exploit small scale vertical food patches. Such patches will support growth of planktonic ciliates even when mean prey levels averaged over several meters in depth are below their threshold concentrations.

Histiobalantium bodamicum is different from the first 2 species with respect to its low maximum growth rate, its high threshold concentration and its seasonal distribution. As reported by Müller & Weisse (1994), *H. bodamicum* occurs in Lake Constance throughout the year, with maximum development in late summer and autumn. These authors suggested that, during phytoplankton spring blooms, this species might be outcompeted by fast growing algivorous ciliates such as *Balanion planctonicum* and *Strobilidium lacustris*. Our present data support this explanation of the weak performance of *H. bodamicum* in spring. Müller & Weisse (1994) also suggested that this scuticociliate might be a superior competitor at low levels of algal food. The high threshold concentration found in the present study disagrees with this idea.

At present, we cannot explain the success of *Histiobalantium bodamicum* in summer and autumn, when concentrations of small algae are low. The food spectrum of this scuticociliate needs to be studied in more detail. In the laboratory, we could maintain *H. bodamicum* on a sole diet of cryptophytes for several years. In contrast, heterotrophic flagellates <5 µm, which were present in our experiments at concentrations from 4 to 16×10^4 cells ml^{-1}, did not sustain survival of the population. In the lake, the diffusion feeding *H. bodamicum* might capture a wide variety of relatively large auto- and heterotrophic prey.

Functional response

Different patterns of functional responses of planktonic suspension feeders are known, which represent different feeding strategies. In the context of the present study, we will discuss the rectilinear or Blackman model and the curvilinear or Michaelis-Menten model, which correspond to the Holling's (1959) type 1 and 2 functional responses and are regarded typical for feeding activities with short or long handling times of prey, respectively. Rothhaupt (1990) demonstrated that functional response patterns of rotifers of the genus *Brachionus* depended on food particle size. The rectilinear model was appropriate for small food particles, whereas the curvilinear model fitted best when prey items were relatively large, such that handling times interfered with the feeding process.

Functional response patterns observed in the present study were strikingly different between species. Ingestion rates of *Strobilidium lacustris* could be described well by the Michaelis-Menten equation. In contrast, ingestion rates of *Balanion planctonicum* increased linearly to a maximum level, then declined, while ingestion rates of *Histiobalantium bodamicum* increased linearly over the entire range of tested prey concentrations. While these linear regression lines can be interpreted as the lower regions of Michaelis-Menten curves, they could also indicate a rectilinear response. Due to considerable scatter of data, as well as lack of measurements for *H. bodamicum* at saturating food concentrations, we do not have strict evidence for either a rectilinear or a curvilinear response of these ciliates. We also lack data on prey handling times which would enable the choice of the appropriate model. Different from the *Brachionus* study (Rothhaupt 1990), in which all predators were filter feeders, handling times of our ciliates likely depended on both feeding mode and predator:prey size.

Jakobsen & Hansen (1997), who studied functional responses of the marine ciliate *Balanion comatum* and the dinoflagellate *Gymnodinium* sp., decided to fit measured ingestion rates of the ciliate to the curvilinear and of the dinoflagellate to the rectilinear model,

since '*B. comatum* ingested about 22 cells before it divided' while '*Gymnodinium* sp. engulfed only about a single prey prior to cell division'.

We found no threshold concentrations for zero ingestion, which indicates that under natural conditions these ciliates will continue to feed even when prey levels become very low. For the species under investigation, formation of resting stages as a strategy to survive periods of starvation have not been observed.

In all 3 species, ingestion rates continued to increase over a wide range of food concentrations above the level required for maximum growth. Two possible explanations exist for this result: (1) ciliate cell volumes increased with increasing food concentrations, such that volume-specific growth rates reached higher values than those measured by cell counts, (2) the gross growth efficiency (GGE) decreased at high food concentrations due to incomplete digestion. This effect of 'superfluous feeding' has been observed in several protozoans and metazoans, as reviewed by Straile (1997).

In 1 additional experiment with *Strobilidium lacustris* (data not shown) we measured ciliate dimensions and calculated cell volumes by approximation to prolate or oblate spheroids. These data were used to determine growth and ingestion rates in terms of biovolume and to calculate GGE as the ratio of produced ciliate biovolume:ingested algal biovolume. Cell volumes of *S. lacustris* varied ~3-fold in starved and well-fed specimens. Volume-specific GGE ranged from 18 to 71% at high food levels (800 to 1200 ng C ml^{-1}), and from 50 to 168% at low food levels (7 to 240 ng C ml^{-1}). These rather strange results demonstrate the inadequacy to determine GGE on the basis of volume instead of carbon measurements (Ohman & Snyder 1991, Straile 1997). Nevertheless, they indicate that the dependency of both cell volume and GGE on food concentration could be responsible for the differences between the numerical and functional response curves in our study.

Selective feeding

The observed responses of the ciliates to *Stephanodiscus hantzschii* were characteristic of their feeding mode (Fenchel 1987). *Histiobalantium bodamicum* apparently was not able to ingest *S. hantzschii*, since for food capture it must rely on prey motility. *Balanion planctonicum* and *Strobilidium lacustris* both selected against this seemingly unattractive food. For *S. lacustris*, the selectivity index D_{Cr} (Jacobs 1974) was in the range from 0.3 to 0.6. While this result could be due to active selection by this filter feeding ciliate, it might also be explained by differences in encounter probability with the larger motile cryptophytes and the smaller, non-motile diatoms. The D_{Cr} value for *B. planctonicum*, in contrast, was close to 1, which points to active selection for *Cryptomonas* sp. by this raptorial feeding prostome ciliate. In short, our data suggest that the diffusion feeder could not ingest the diatoms, the raptorial feeder did not want them and the filter feeder could not avoid them.

Negative selection for *Stephanodiscus hantzschii* has also been observed in a field experiment in Lake Constance as reported by Weisse & Müller (1998): during a 24 h *in situ* incubation in diffusion chambers (28 to 30 April 1992), a mixed community of algivorous protozoa, mainly *Balanion planctonicum*, strombidiid and strobilidiid ciliates and the dinoflagellate *Gymnodinium helveticum*, preferrentially ingested the cryptophytes *Rhodomonas minuta* and *R. lens*, thus causing a significant shift in phytoplankton community composition.

Food value of diatoms

Our data indicate that the food value of *Stephanodiscus hantzschii* for both ciliates was low. While the mortality of *Balanion planctonicum* at high diatom concentrations can be explained by its very low ingestion rates, it is remarkable that *Strobilidium lacustris*, though ingesting a considerable quantity of diatoms, could also not survive on this diet. We further tested other algivorous ciliates from Lake Constance, namely *Urotricha furcata*, *Askenasia volvox*, *Strobilidium humile* and *Pelagostrombidium fallax* (Müller & Schlegel unpubl.). All mentioned species were capable of ingesting *S. hantzschii* . In field samples, especially *S. humile* was frequently found with ingested diatoms. Nevertheless, none of these ciliates could be isolated and cultivated with this prey.

Literature data on utilization of diatoms by planktonic ciliates are controversial. Gifford (1985) could cultivate several marine *Strombidium* and *Strombidinopsis* strains with the dinoflagellates *Heterocapsa triquetra* and *Scrippsiella trochoidea*, but not with the diatom *Thalassiosira*. Verity & Villareal (1986) demonstrated that 2 marine tintinnids could only grow on diatoms which were lacking threads. In their study, ciliate growth rates were inversely related to the effective cell size of the prey. Skogstad et al. (1987) tested 5 freshwater ciliates of the genera *Cinetochilum*, *Bursaridium*, *Urotricha*, *Frontonia* and *Halteria* with a wide variety of algal food. While all ciliates grew well on cryptophytes and chrysophytes, *Cinetochilum* was the only strain which also thrived on the diatoms *T. pseudonana nana* and *Cyclotella pseudonana stelligera*. Notably, *Cinetochilum* with a mean cell volume of

2300 μm^3 was the smallest of the studied ciliates. Montagnes (1996) and Montagnes et al. (1996) investigated growth responses of 5 aloricate marine oligotrichs and found that 2 species, *Strombidium siculum* and *Strombidinopsis cheshiri*, grew well on the diatom *T pseudonana*. Summarizing these data, it appears that only a few specialists among ciliates were able to utilize diatom food and that, with the exception of the tintinnid study (Verity & Villareal 1986), prey size was not a decisive parameter.

At present, we do not know which properties of the diatoms cause the negative reactions of many algivorous ciliates. As shown by Ban et al. (1997), these algae may also negatively affect larger herbivorous zooplankters. In a world-wide study on diatom-copepod interactions, they demonstrated that diatom diets resulted in significantly reduced egg production and egg viability of their predators. These authors suggest that an active defense mechanism of the diatoms (i.e. production of inhibitory compounds) rather than missing essential nutrients may be responsible for this negative effect.

Conclusions

Our data emphasize that numerical and functional responses of planktonic ciliates to the same cryptophyte food are species specific. The observed threshold concentrations indicate that the ciliates under investigation likely depend on small-scale food patches during the greater part of the seasonal cycle. The relationships presented in Figs. 1 to 3, therefore, do not serve to predict growth and ingestion rates from algal concentrations as averaged over large depth intervals.

The diatom *Stephanodiscus hantzschii*, according to our observations, is not a suitable food for the majority of algivorous ciliates in Lake Constance, though most of them can ingest these rather small cells. The properties, other than cell size, which make diatoms a low quality food for many ciliates need to be further investigated.

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