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Seasonal Succession of Ciliates in Lake Constance

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Abstract. We found a recurrent seasonal pattern in abundance and composition of planktonic ciliates in Lake Constance, FRG, over a three-year period. Abundance peaks occurred in early spring and summer/autumn, while ciliate numbers were low in late spring (clear-water phase) and winter. Prostomatida and Oligotrichida dominated in early spring. They responded immediately to the phytoplankton spring bloom, while Haptorida, Peritrichida, and large Scuticociliatida (*Histiobalantium*) were delayed by 1 to 2 weeks. The spring community broke down at the onset of the clear-water phase. *Pelagohalteria viridis* containing symbiontic algae appeared shortly after this event. A highly diverse community was recorded in summer/autumn. Peritrichida, small Oligotrichida, and large Scuticociliatida reached their maxima during this season. Small Scuticociliatida were rare throughout the year and contributed moderately to total ciliate numbers only during the cold season. The observed seasonal sequence of pelagic ciliates in Lake Constance is discussed in relation to simultaneously collected data on potential food organisms and grazers.

Introduction

Seasonal succession in plankton communities is a classic field of limnological research. The current knowledge on this fascinating topic was recently summarized by the authors of *Plankton Ecology* [44]. While a wealth of information exists on phytoplankton and metazoan zooplankton succession, little is known with respect to planktonic protozoa. This is not surprising, since the importance of protozoa within planktonic food webs has been recognized only recently [31].

In Lake Constance, the seasonal cycle of phytoplankton and zooplankton is well known; the PEG-model of plankton seasonal succession [43] is mainly based on observations from this lake. It is the aim of the present investigation to integrate into this framework data from another taxonomic group of planktonic organisms: ciliated protozoa. As a prerequisite for an analysis of the factors which determine seasonal sequences, a data set over more than one seasonal cycle is needed. In the present paper, we will describe a recurrent seasonal

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pattern of ciliate abundance and species composition as observed in Lake Constance over three consecutive years.

Trophic relationships between ciliates and other planktonic compartments were investigated by relating the ciliate data set to simultaneously collected data on their presumptive food organisms and grazers. Two different approaches were used. First, we characterized four seasonal phases (spring, clear-water phase, summer/autumn, and winter) based on ciliate community biomass and species composition, quantity and quality of presumptive food, and community grazing of larger zooplankton.

Second, we compared ciliate population fluctuations with changes in concentrations of potential prey items. This type of analysis was restricted to the spring phase, since we could not identify prey–predator oscillations between ciliates and any food item that were consistent over the entire annual cycle. This is not surprising, since such observations would point to simple one prey–one predator relationships. Most ciliate species, however, are known to feed on rather broad food spectra [11, 34]. Conversely, ciliates are not the only consumers of nano- and picoplankton. Furthermore, grazing of larger zooplankton may mask predator–prey relationships between ciliates and their food. The approach proved to be useful, however, during phytoplankton spring blooms, when the ciliate community was more uniform, population fluctuations more pronounced, and metazoan grazing less important compared with other seasons.

Methods

Lake Constance is a deep, meso-eutrophic prealpine lake. The routine sampling station of the Limnological Institute Konstanz is located at the site of maximum water depth (147 m) of "Überlinger See," the northwestern part of the lake. Ciliate sampling, counting, and sizing were described in detail by Müller [25]: Integrated water samples over the depth intervals 0–8 m and 8–20 m were taken weekly (every two or three weeks in winter) at the routine station. Cell numbers were determined in 50 ml Lugol-fixed subsamples with the Utermöhl method by a single observer (A. Schöne). The ciliates were grouped into five classes according to their largest linear dimension: I = <20 μm; II = 20–35 μm; III = 35–50 μm; IV = 50–100 μm; V = >100 μm. Up to 30 morphologically different forms were recorded separately.

With respect to ciliate taxonomy, the system of Corliss [9] was followed. Taxonomic identifications were based on observations of living and protargol-stained specimens. Several species were isolated and maintained in laboratory cultures, with *Rhodomonas* sp. as food (strain 26.80, Sammlung für Algenkulturen, Göttingen). (For details of the culturing method, see Müller [26].) The mean cell volume of each taxon and size class was calculated from linear dimensions of protargol-stained cells by approximation to prolate spheroids.

Bacteria, heterotrophic nanoflagellates (HNF), autotrophic picoplankton (APP) and phytoplankton were counted and sized in aliquots of the same water samples. An exception were phytoplankton data obtained in 1987, which originated from separate samples taken at the same location, but covered the 0–5 m and 5–10 m depth intervals. Mean values in 0–8 m depth, as presented in this paper, were calculated from these data by assuming equal distribution over the 5–10 m depth interval. Bacteria, HNF, and APP were studied with epifluorescence microscopy and DAPI staining (for details see Weisse [54, 55]), while phytoplankton was recorded with the Utermöhl technique (in 1987: Braunwarth, unpublished data; in 1988–1989: Schweizer, unpublished data). The term "small phytoplankton" in this paper refers to unicellular algae <50 μm. In Lake Constance, this compartment was mainly composed of *Rhodomonas* spp., *Cryptomonas* spp., *Chlamydomonas*

spp., *Stephanodiscus hantzschii, Chlorella* spp., and unidentified microalgae. The term "total food" is used for the sum of nanoplankton (small phytoplankton and HNF) and picoplankton (APP and bacteria).

Cell numbers and biovolumes were transformed to carbon using the following conversion factors. Bacteria: 15 fg C $cell^{-1}$ [37, 57]; APP: 210 fg C $cell^{-1}$ [53]; HNF: 220 fg C μm^{-3} [7]; ciliates: 110 fg C μm^{-3} [52]; phytoplankton: 110 fg C μm^{-3} [47].

Zooplankton community grazing was assessed by in situ short-term experiments according to Lampert and Taylor [23]. ^{14}C labelled algae (either *Rhodomonas* sp. or *Stephanodiscus hantzschii*) were used as experimental food. Two size fractions, microplankton (50–170 μm) and macroplankton (>170 μm), were separated by a system of different sizes of mesh gauze. The macroplankton was dominated by daphnids and adult copepods, while rotifers and copepod nauplii were the main components of the microplankton. Ciliates, generally, were not retained by 50 μm mesh gauze and thus were not included in the 50–170 μm fraction. Only tintinnids were occasionally found in the microplankton; they contributed less than 7% to total ciliate biomass, averaged over the annual cycle in 1988 [25]. Mean daily community grazing rates in the uppermost 8 m were calculated from measurements at three different depths, and were corrected for diel periodicity of grazing activity. (For methodological details see Berberovic and Pinto-Coelho [4], Pinto-Coelho [30], and Weisse et al. [57].)

Chlorophyll *a* data corrected for phaeophytin were provided by M. M. Tilzer and B. Beese (unpublished data; for methods see Tilzer [50]). Water temperatures were measured by G. Heinz and M. Schimmele [17]. To show the general trend rather than short-term variations in temperature, we calculated mean values over seven days from the original measurements, which were taken very 20 min with a moored thermistor chain. Over periods in which such data were not available, we used single measurements performed at irregular intervals from 1 to 12 days.

Definitions of seasonal phases are given in Table 2. We distinguished spring and clear-water phases by water transparency according to secchi disk reading, and chl *a* concentrations averaged over the upper 20 m of the water column (see Fig. 1). With respect to the weak clear-water phase in 1987, these criteria had to be modified slightly compared with 1988 and 1989. Ciliate abundance and biomass declined toward the end of October. The first of November, therefore, was defined as the beginning of the winter phase.

Results

Seasonal Changes in Total Abundance and Biomass

The three annual cycles under investigation were distinctly different with respect to weather conditions. A phytoplankton spring bloom regularly develops in Lake Constance at the onset of thermal stratification; this period is followed by a clear-water phase as a consequence of zooplankton grazing [24, 42, 43, 51]. In 1987, rainy weather prevailed from May on throughout summer. The clear-water phase was delayed until mid-June and only weakly expressed. Heavy rainfall in July led to extremely high water level and a decrease in concentration of all groups of planktonic organisms [19]. The seasonal cycle of 1987, therefore, must be regarded as rather untypical. In 1989, phytoplankton development started unusually early, but the spring maximum was less pronounced compared to previous years. This effect presumably was caused by a mild winter and high solar irradiance in March, but extremely cold and cloudy weather in April. Favorable weather with high solar irradiance predominated in spring 1988 and in the summer months of 1988 and 1989.

The seasonal development of the entire ciliate community over the study period is depicted in Fig. 1. Generally, we observed a bimodal pattern of ciliate

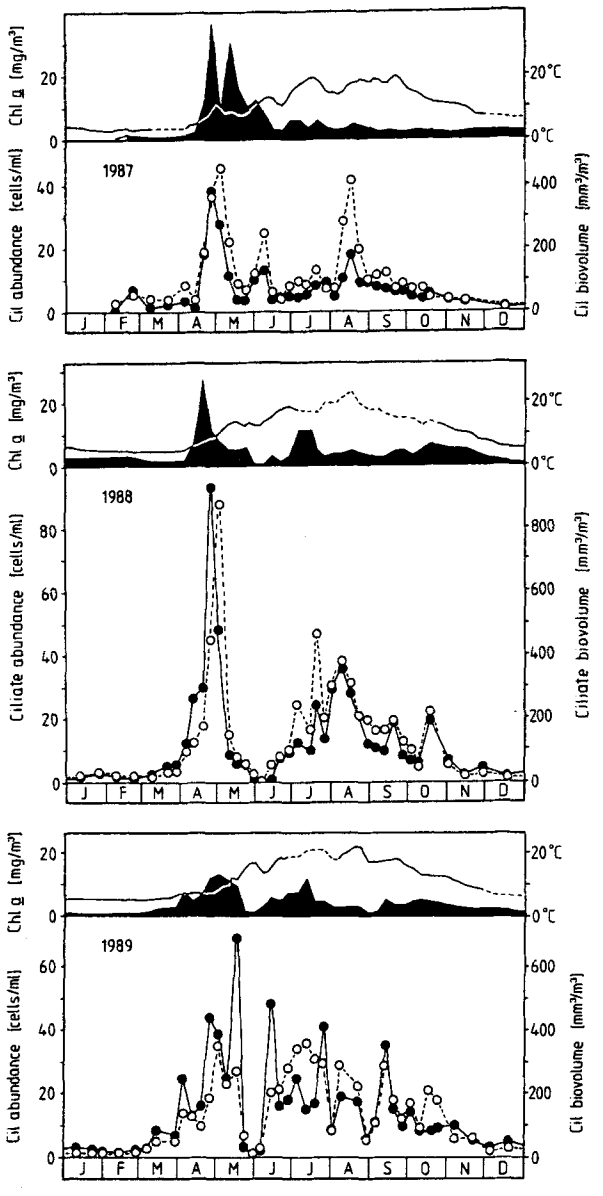

Fig. 1. Seasonal development of the ciliate community in Lake Constance, 1987–1989. Lower panels: Mean ciliate abundance (solid circles) and biovolume (open circles) in 0–20 m depth. Upper panels: Mean chl *a* concentrations in 0–20 m depth (black); water temperature in 3.4 m depth, from weekly mean values of continuous measurements (solid line) or single measurements at irregular intervals (broken line).

abundance and biomass, with peaks occurring in spring and summer/autumn. In each year, highest ciliate numbers were recorded in early spring, simultaneously with the phytoplankton bloom (see chl *a* data in Fig. 1). In 1988 and 1989, we recorded a sharp breakdown of the ciliate spring community towards the end of May, which coincided with the clear-water phase and most probably was caused by metazoan grazing. Subsequently, the summer populations developed. Ciliate numbers remained fairly high (though less than in spring) from July through October. Due to the weather conditions described above, this

pattern was less clear in 1987. The decline of the spring maximum was less dramatic, and ciliate numbers in summer were lower compared with 1988 and 1989.

Community Composition

In the routine counts of Lugol-fixed samples, we distinguished morphologically different "forms," which in some cases were identical to single species, while in others they comprised two or more similar genera. To faciliate the description of community composition, we subsequently pooled data of some counting groups, especially those assigned to the same taxon, but to different size classes. In the following, we define the taxonomic units distinguished in this study, and explain the abbreviations used in Table 1, Figs. 2, 3, and 5, and throughout the text. Size classes and corresponding mean cell volumes [25] are given in parentheses. Unless stated otherwise, taxonomic identifications are based on the descriptions of Kahl [22]. Several species were kept in laboratory culture; some information concerning culturing methods are included in the following list.

Order Prostomatida

PS: *Pseudobalanion planctonicum* Foissner et al. 1990. This genus and species were established using material collected from the pelagic zone of Lake Constance [16]. (I, 1,300 μm^3.) *P. planctonicum* was kept in culture on a diet of *Rhodomonas* sp. [26].

UF: *Urotricha furcata* Schewiakoff 1983. Redescription by Foissner et al. [16] using material collected from the pelagic zone of Lake Constance. (I, 1,700 μm^3.) Cultured on a *Rhodomonas* diet.

URO: *Urotricha* spp. (II, 9,500 μm^3; III, 24,000 μm^3; IV, 70,000 μm^3.) Cultured on a *Rhodomonas* diet.

Order Haptorida

ASK: *Askenasia* spp. (II, 7,200 μm^3; III, 37,000 μm^3.)

DID: *Didinium* spp. (III, 38,000 μm^3; IV, 70,000 μm^3.)

EN: Family Enchelyidae; *Lagynophrya* and similar genera, *Lacrymaria* sp. (IV, 35,000 μm^3; V, 31,000 μm^3.)

PAR: *Paradileptus* sp. (V, 820,000 μm^3.)

Order Scuticociliatida

SCU: Small Scuticociliatida similar to *Cyclidium*. (II, 1,300 μm^3.)

HIS: *Histiobalantium* sp. [10]. (III, 34,000 μm^3; IV, 68,000 μm^3.) We kept *Histiobalantium* in culture for several months, using bacteria-rich suspensions of senescent *Rhodomonas* cells as a food source.

Order Peritrichida

VD: *Vorticella* spp. attached to large diatoms, especially *Asterionella formosa* and *Fragillaria* spp. (II, 10,000 μm^3; III, 37,000 μm^3.)
VA: *Vorticella* sp. (cf. *V. monilata* Tatem 1870 [18]) attached to *Anabaena flos-aquae.* (III, 16,000 μm^3.)
EPI: *Epistylis rotans* Svec 1897. (IV, 24,000 μm^3.)
VAG: *Vaginicola* sp. attached to large diatoms, especially *Fragillaria* spp. (II, 3,500 μm^3.)

Order Heterotrichida

HET: Large Heterotrichida, genera *Stentor* and *Condylostoma.* (V, 1,300,000 μm^3.)

Order Oligotrichida

OLI: Oligotrichida <20, genera *Halteria* and *Strobilidium.* (I, 2,700 μm^3.)
S25: *Strobilidium* spp. 20–35 μm. (II, 6,500 μm^3, mean diameter 25 μm.)
S70: *Strobilidium lacustris,* Foissner [15]. (IV, 119,000 μm^3, mean diameter 70 μm.) Cultured on a *Rhodomonas* diet.
PEL: *Pelagohalteria* (formerly *Halteria*) *viridis* Fromentel 1876 [15]. (II, 6,500 μm^3.) The species regularly contained symbiontic algae and, therefore, may be partially autotrophic. We kept *P. viridis* in culture for several months, using bacteria-rich suspensions of senescent *Rhodomonas* cells as a food source.
STR: *Strombidium* spp. Symbiontic algae were occasionally observed in live samples, but they were hard to see in Lugol-fixed cells. Thus, "green" *Strombidium* were not recorded separately in the routine counts. (III, 32,000 μm^3; IV, 77,000 μm^3.) Cultured on a *Rhodomonas* diet.
TIN: Family Tintinninae, predominantly *Tintinnidium* and *Codonella* [14]. We could not separate different genera in the routine counts, since in many fixed samples the ciliates were found outside the loricae. (IV, 24,000 μm^3.)

Order Suctorida

SU: Several species of Suctorida, including *Staurophrya elegans* Zacharias 1893 [18]. (II, 7,000 μm^3; III, 30,000 μm^3; IV, 40,000 μm^3.)

Mean annual cell concentrations of the taxa listed above are shown in Table 1. The most abundant ciliate taxa were PS and S25. In contrast, cell numbers of PAR and HET were almost below the level of detection; these large ciliates, however, were significant in terms of biomass [25]. Generally, taxa were represented by mean cell numbers in the same order of magnitude in each of the three years. Marked interannual variations, however, were also observed. The

Table 1. Annual mean abundance of ciliate taxa in 0–8 m and 8–20 m depth, 1987, 1988 and 1989. Last column: Ratio of mean cell concentrations in the depth intervals 0–8 m : 8–20 m over the study period

Taxa	Abbreviation	Annual mean abundance [cells liter^{-1}] 1987 0–8 m	1987 8–20 m	1988 0–8 m	1988 8–20 m	1989 0–8 m	1989 8–20 m	0–8 m: 8–20 m
Prostomatida								
Pseudobalanion planct.	PS	3,660	960	6,090	2,900	8,030	4,140	2
Urotricha furcata	UF	340	300	1,490	660	1,440	860	2
Urotricha spp.	URO	120	75	160	64	460	230	2
Haptorida								
Askenasia	ASK	430	160	570	300	510	310	2
Didinium	DID	15	8	48	9	54	14	4
Enchelyidae	EN	68	12	28	6	24	9	4
Paradileptus	PAR	9	2	14	4	17	1	6
Scuticociliatida								
Scuticociliatida <35 μm	SCU	87	56	100	110	210	220	1
Histiobalantium	HIS	160	200	410	370	600	630	1
Peritrichida								
Vorticella on diatoms	VD	360	400	350	510	320	340	1
Vorticella on *Anabaena*	VA	190	2	570	72	91	5	11
Epistylis rotans	EPI	210	120	220	63	130	120	2
Vaginicola	VAG	64	58	65	71	45	43	1
Heterotrichida								
Stentor/Condylostoma	HET	8	1	16	4	0	0	5
Oligotrichida								
Oligotrichida <20 μm	OLI	430	270	1,030	600	860	530	2
Strobilidium 20–35 μm	S25	1,950	970	3,960	1,830	3,010	1,300	2
Strobilidium lacustris	S70	110	60	130	86	160	63	2
Pelagohalteria viridis	PEL	180	13	430	36	680	32	16
Strombidium	STR	510	100	540	190	460	200	3
Codonella/Tintinnidium	TIN	510	380	430	320	410	300	1
Suctorida	SU	94	55	62	58	130	110	1
Not identified		550	500	520	330	820	430	2
All ciliates		10,060	4,700	17,230	8,590	18,460	9,890	2

last column of Table 1 shows the ratio of cell concentrations in 0–8 m : 8–20 m depth, averaged over the study period. A ratio of 2 was observed for the majority of ciliate taxa, but some were distributed almost equally over the upper 20 m of the water column. Other populations were mainly concentrated close to the surface: VA associated with *Anabaena flos-aquae,* predatory Haptorida and Heterotrichida (DID, EN, PAR, HET) and Oligotrichida containing symbiontic algae. In STR, which was seen with zoochlorellae only occasionally, the ratio was only slightly higher than in most ciliate taxa, while PEL was found almost exclusively in the 0–8 m depth interval. No population significantly increased with depth, and seasonal changes in abundance were more pro-

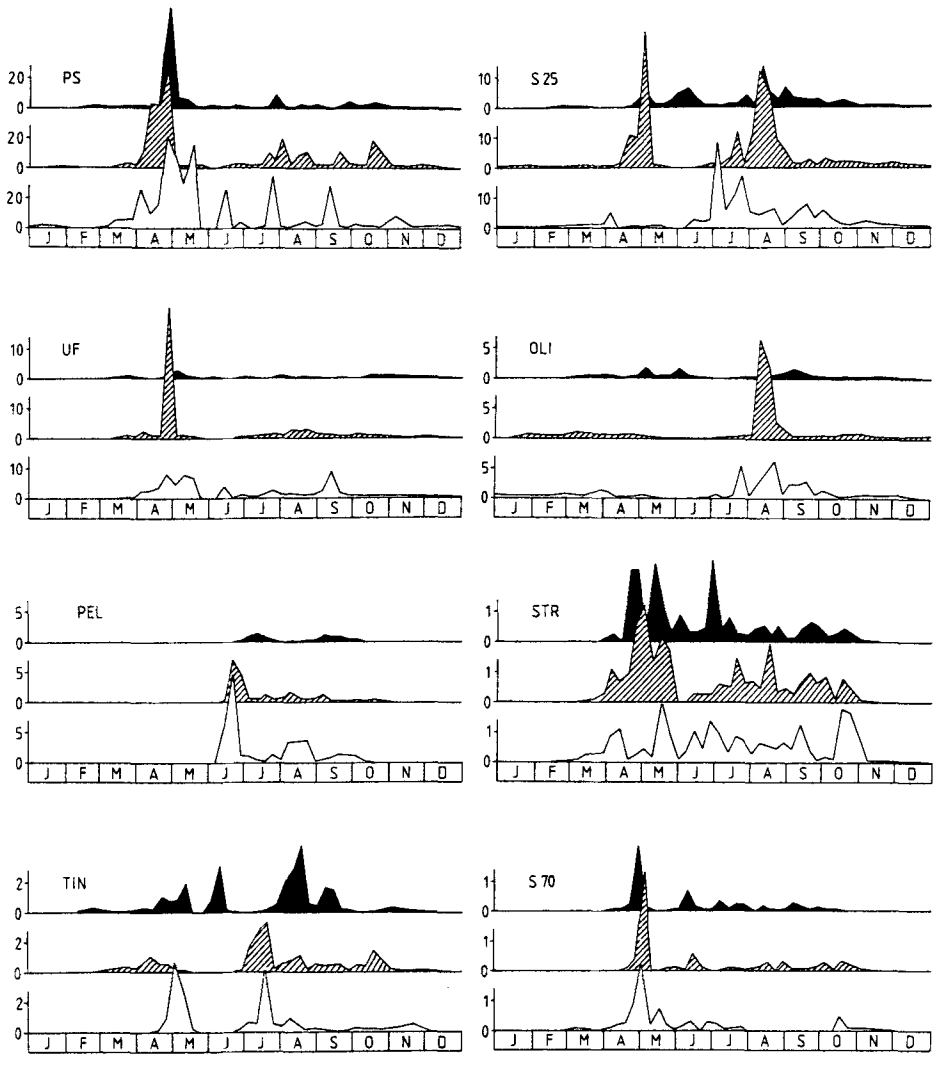

Fig. 2. Mean abundance (cells ml^{-1}) of ciliate taxa in 0–8 m in 1987 (black), 1988 (hatched), and 1989 (white). For abbreviations see Table 1 and text.

nounced near the surface than in deeper water [27]. The following analysis of ciliate population dynamics, therefore, will be restricted to data from the upper 8 m of the water column.

Seasonal Distribution of Taxa

Seasonal changes in abundance of ciliate populations over the study period are presented in Fig. 2. It contains all taxa, which contributed more than 2% to mean annual abundance and/or biomass in each of the three years investigated

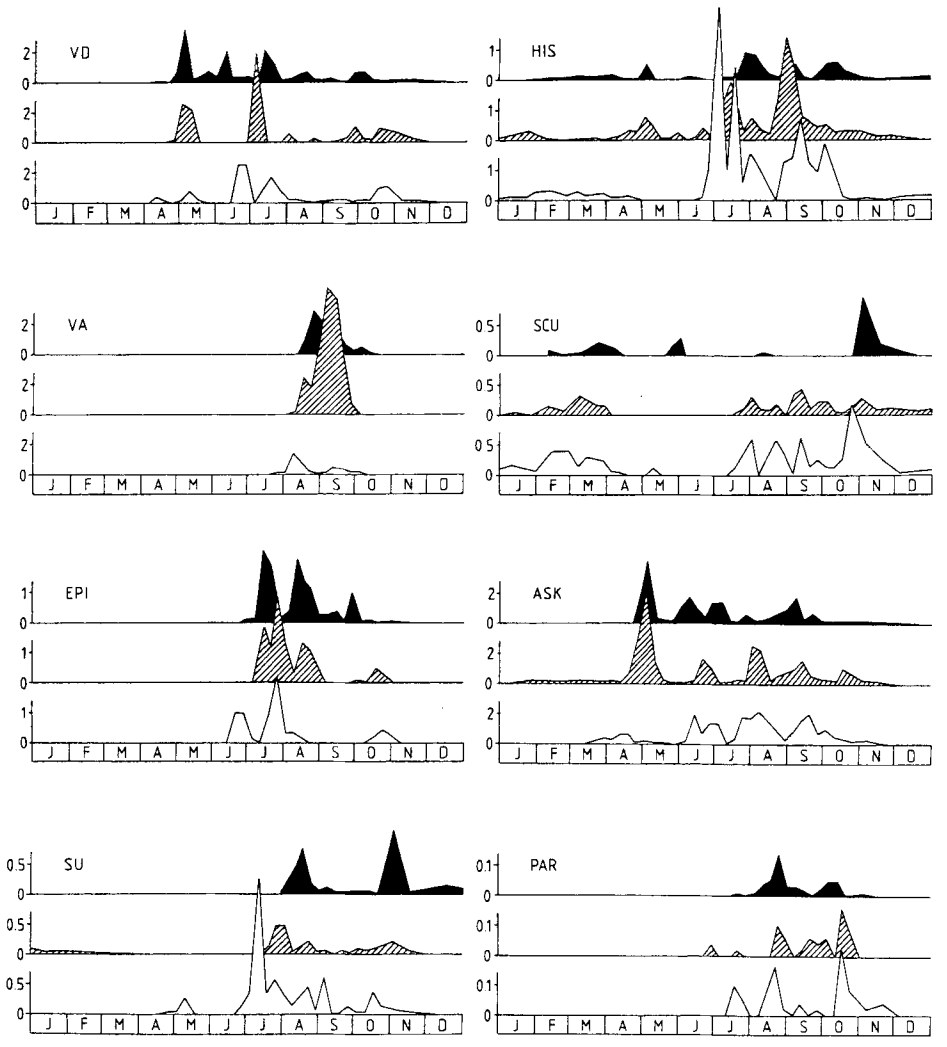

Fig. 2. Continued

(cf. Müller [25]). In addition, we included less significant taxa that exhibited a pronounced seasonality (SCU, VA, PEL, SU).

In some species, the seasonal pattern was strikingly similar in all three years (e.g., EPI, S70). Others showed marked interannual variations, and some outstanding peaks were observed only once in three years (e.g., S25 in spring 1988). In particular, we noticed significant differences in development of the spring populations in 1989 compared with 1987 and 1988.

Figure 3 represents a synthesis of the data depicted in Fig. 2. We calculated monthly mean values of abundance by pooling all data recorded in the respective months over the study period. From this generalized scheme, the dynamics of the ciliate community in Lake Constance can be characterized as

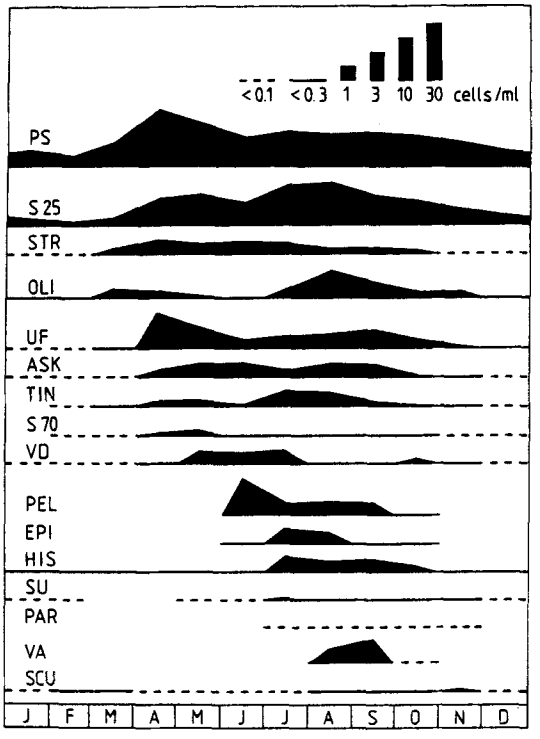

Fig. 3. Seasonal succession of pelagic ciliates in Lake Constance: Monthly mean values of ciliate cell concentrations in 0–8 m depths, pooled data from 1987–1989. For abbreviations see Table 1 and text.

follows: 1) The seasonal pattern is bimodal, with ciliate peaks occurring in spring and summer/autumn. 2) The species diversity increases from spring to autumn. 3) Small Prostomatida (PS, UF) and large Oligotrichida (STR, S70) are characteristic species of the spring community. 4) Small Oligotrichida (S25, OLI) are also present in early spring, but reach maximum abundance in summer. 5) PEL is the only population that significantly increases in June, toward the end of the clear-water phase. 6) With the exception of VD, Peritrichida, and Scuticociliatida peak in summer and autumn. 7) Small populations of predatory species (SU, PAR) are present mainly from July through November. 8) Small scuticociliates (SCU) contribute moderately to total ciliate numbers only during the cold season.

Relation to Food Resources and Grazers

Figure 4 presents biomass concentrations of ciliates and potential food organisms, averaged over seasonal phases (Table 2) and the 0–8 m depth interval. It also shows the relative contribution of bacteria, autotrophic picoplankton, heterotrophic flagellates, and small phytoplankton to total food and specifies dominant ciliate taxa.

From top to bottom in Fig. 4 (lower panel), ciliate taxa are presented in the following order: Peritrichida; Scuticociliatida; Oligotrichida <35 μm (OLI, PEL, S25); Oligotrichida >35 μm (STR, S70, TIN); Prostomatida; Haptorida

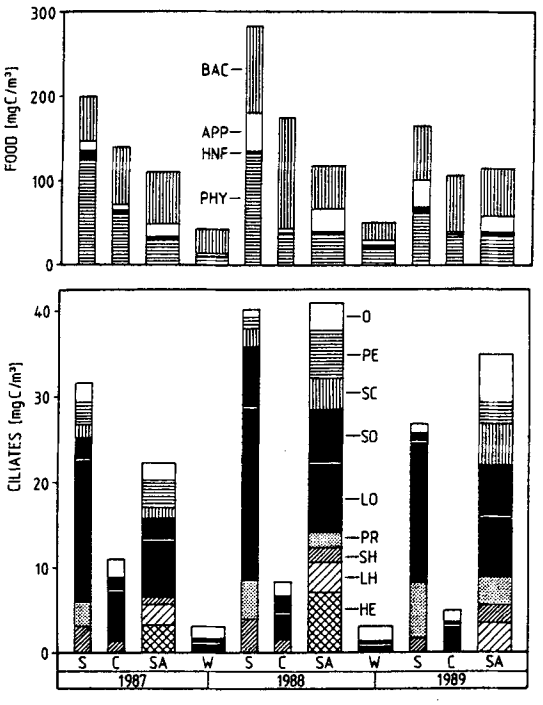

Fig. 4. Mean biomass of ciliates and food compartments averaged over seasonal phases. Upper panel: Small phytoplankton (PHY), APP, HNF, and bacteria (BAC). Lower panel: Heterotrichida (HE), large Haptorida (LH), small Haptorida (SH), Prostomatida (PR), large Oligotrichida (LO), small Oligotrichida (SO), Scuticociliatida (SC), and Peritrichida (PE); see text. O = Others; this section contains minor taxonomic groups, unidentified specimens and ciliates of the orders listed above, which contributed less than 1 mg C m^{-3} in the respective season.

Table 2. Seasonal phases: Definition and mean water temperature in 3.4 m depth

Season	Time interval	Definition	Mean temperature (°C)
Spring 1987	15.4–12.6		9.2
1988	9.4–24.5	Chl *a* > 5 mg m^{-3} and Secchi depth <7 m	10.3
1989	31.3–20.5		8.1
Clear-water phase 1987	13.6–30.6	Chl *a* < 5 mg m^{-3} or Secchi depth >7 m	12.2
1988	25.5–30.6	Chl *a* < 5 mg m^{-3} and Secchi depth >7 m	15.5
1989	21.5–11.6	Chl *a* < 5 mg m^{-3} and Secchi depth >7 m	15.2
Summer/autumn 1987	1.7–31.10		16.2
1988	1.7–31.10	End of clear-water phase—31 October	16.9
1989	12.6–31.10		17.3
Winter 1987/1988	1.11–8.4	1 November—start of spring phase	6.1
1988/1989	1.11–30.3		6.3

<100 μm (ASK, DID, EN); Haptorida >100 μm (PAR) and Heterotrichida >100 μm. Roughly, this sequence corresponds to an increase in the preferred prey size, according to literature data: Peritrichida are known as efficient bacteria feeders [11, 35]. *Histiobalantium,* the dominating scuticociliate, presumably consumes both nano- and picoplankton [33]. The ratio of nanoplankton

Table 3. Community grazing rates of micro- and macroplankton, measured in in situ experiments in the epilimnion (0–8 m) and corrected for diel periodicity of grazing activity. n = number of experimental series

	Community grazing rates (d^{-1})			
	Microplankton		Macroplankton	
Season	g ± SD	(n)	g ± SD	(n)
Spring 1988	0.05 ± 0.05	(8)	0.05 ± 0.03	(8)
1989	0.09 ± 0.06	(4)	0.01 ± 0.02	(4)
Clear-water phase 1988	0.07 ± 0.04	(6)	0.49 ± 0.25	(6)
1989	0.14	(1)	0.71	(1)
Summer/autumn 1988	0.09 ± 0.03	(10)	0.12 ± 0.03	(10)
1989	0.19 ± 0.21	(5)	0.10 ± 0.07	(5)
Winter 1987/1988	0.01 ± 0.01	(8)	0.01 ± 0.01	(8)
1988/1989	0.03 ± 0.01	(6)	0.06 ± 0.04	(6)

to picoplankton ingested by Oligotrichida was found to increase with ciliate size [34]. Prostomatida in Lake Constance are mainly represented by nanociliates, which efficiently feed on small cryptophytes [26]. Haptorida and large Heterotrichida feed on nanoplankton, but also on larger prey such as colonial algae and ciliates [6, 22, 33, 48].

From Fig. 4 it appears that: 1) The main compartments of total presumptive food over the study period were small phytoplankton and bacteria. During some periods, namely in summer, the share of APP was also relevant, while HNF contributed only little to total food available for ciliates. 2) Apparently, there was no close coupling between ciliate biomass and either total food or nanoplankton or picoplankton biomasses. From the spring to the clear-water phase, ciliates were more drastically reduced than phytoplankton and bacteria. Subsequently, however, ciliates largely recovered from losses during the clear-water phase. In summer/autumn 1988 and 1989 ciliate biomass even exceeded spring biomass, despite much lower food concentrations. 3) Ciliate composition was much more diverse in summer/autumn compared with spring.

Seasonal changes in the grazing impact of metazoans are illustrated by Table 3. It contains community grazing rates of two size fractions of zooplankton as measured by in situ experiments, averaged over seasonal phases. The data clearly demonstrate the importance of macrozooplankton grazing during the clear-water phase and, thus, confirm earlier findings [24, and references therein].

Spring Phase

A detailed picture of the ciliate development in spring relative to food concentrations is presented in Fig. 5. In all three years, phytoplankton maxima were observed in the second half of April, irrespective of weather conditions. In 1987, however, the clear-water phase was delayed until mid-June, while in 1989 phytoplankton development started unusually early, but resulted in a rather weak maximum compared to the preceeding years.

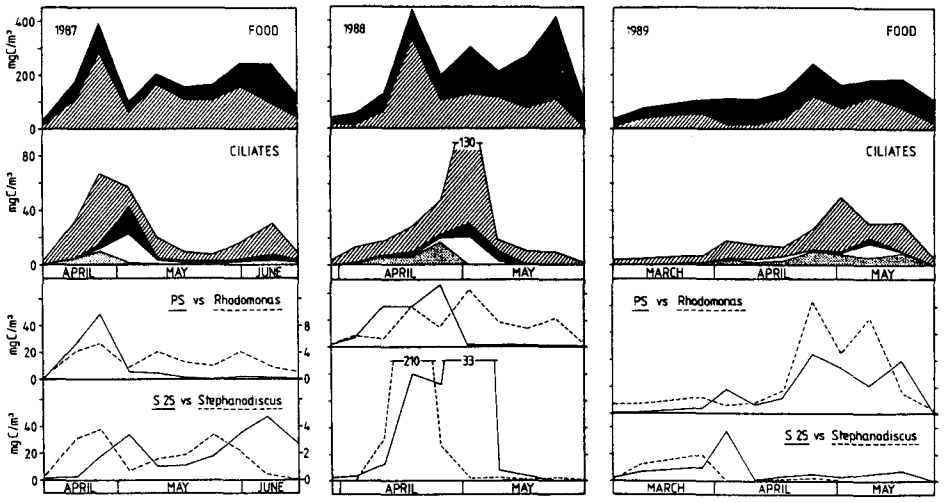

Fig. 5. Development of ciliates and their food resources during spring phases of 1987, 1988, and 1989. Food: Nanoplankton (hatched) and picoplankton (black). Ciliates: Prostomatida <20 μm (stippled); Haptorida + large Prostomatida (white); Peritrichida + Scuticociliatida (black); Oligotrichida (hatched). PS vs *Rhodomonas*: *Pseudobalanion planctonicum* (solid line) and *Rhodomonas minuta* + *R. lens* (broken line). S25 vs *Stephanodiscus*: *Strobilidium* spp., 20–35 μm (solid line) and *Stephanodiscus hantzschii* (broken line). Identical scales in the respective graphs in 1987, 1988, and 1989. Right y-axis: Scales of PS and S25.

Algivorous ciliates, namely small Prostomatida and medium-sized to large Oligotrichida, responded immediately to the phytoplankton bloom. Haptorida, Peritrichida, and Scuticociliatida lagged 1–2 weeks behind. At the onset of the clear-water phase, the entire ciliate community broke down. While this general pattern was observed in all three years, interannual variations in the ciliate spring succession also become apparent from Fig. 5. Worth mentioning are the early breakdown of small Prostomatida in 1987 and 1988, but not in 1989, the extremely prominent oligotrich peak in 1988, and the weak maximum of Peritrichida and Scuticociliatida in 1989.

Figure 5 also shows the development of the most abundant taxa, PS and S25, in relation to presumptive food organisms. Feeding of PS on *Rhodomonas* was studied in laboratory experiments by Müller [26]. The field data show that PS increased almost simultaneously with *Rhodomonas* at the onset of phytoplankton blooms. S25 was frequently seen with ingested *Stephanodiscus hantzschii* [56]; trophic coupling between these populations is suggested from Fig. 5.

Discussion

Community Composition

Planktonic ciliate communities in lakes typically are dominated, in terms of numbers, by members of the orders Haptorida, Scuticociliatida, and Oligotrichida [3]. Small Prostomatida, in contrast, are the most abundant ciliates in the

pelagic zone of Lake Constance [25, this study]. These nanociliates effectively feed on phytoflagellates [26, 40], which might explain their high concentrations in Lake Constance especially during spring. Recent findings from lakes Huron and Michigan [8] are consistent with this hypothesis. In these lakes, small Prostomatida (genera *Urotricha* and *Balanion*) accounted for 10–20% of total ciliate biomass in late summer and autumn, when phytoflagellates were a major component of the nanoplankton.

Beaver and Crisman [2, 3] have related ciliate community structure to trophic status, such that large, algivorous species, predominantly Oligotrichida, are progressively replaced by small bacterivorous ciliates, mainly Scuticociliatida, with increasing chl *a* concentrations. In a series of Florida lakes, the share of small bacterivorous scuticociliates increased from 9 to 35% of total ciliate numbers from oligotrophy to hypereutrophy [2]. In meso-eutrophic Lake Constance, in contrast, small scuticociliates accounted for less than 2% of ciliate numbers in the upper 20 m on an annual average, and they were virtually absent during phytoplankton blooms. To understand this discrepancy, it should be considered that chl *a* is a bulk parameter; though it provides a good estimate of the total amount of food available for ciliated protozoa, it does not specify the food quality. On the one hand, chl *a* stands for small phytoflagellates as well as for large diatoms and filamentous cyanobacteria, organisms which are either "edible" or "unedible" from the viewpoint of a ciliated protozoan. On the other hand, bacterial production is closely correlated with chl *a* [39].

Fenchel et al. [13] observed in two Danish, eutrophic fjords that scuticociliates tended to concentrate in the oxycline, where bacterial productivity was high, though bacterial numbers, as a consequence of protozoan grazing, were not significantly elevated. High numbers of scuticociliates near the oxycline were also reported by Pace [29] from shallow, eutrophic Lake Oglethorpe, Georgia. We suggest, therefore, that the relationship between chl *a* and scuticociliate concentrations as observed by Beaver and Crisman [2, 3] is largely due to the build-up of oxygen gradients in shallow, productive systems. In Lake Constance, in contrast, the upper 20 m of the water column are fully oxygenated at all seasons [45], which might explain the low numbers of small scuticociliates recorded in this study.

Vertical Distribution of Taxa

The vertical distribution of ciliates in Lake Constance was investigated by Müller et al. [27]. Ciliate abundance and biomass were found to decrease by an order of magnitude from surface to deep water, which is consistent with records from other deep lakes [21, 49]. In the present study, we compared mean numbers of taxa in 0–8 m and 8–20 m depth (Table 1). Some ciliate populations were more intensely concentrated in the upper 8 m relative to the entire community. For VA, this is easily explained by its attachment to floating colonies of *Anabaena flos-aquae*. Predatory Haptorida and Heterotrichida probably live close to the surface due to higher prey densities. Ciliates containing symbiontic algae are known to concentrate either in surface waters or near the oxycline [5, 20, 29]. With respect to *Pelagohalteria* in Lake Constance, we believe that its spatial and temporal distribution were mainly controlled by light conditions.

In 1988 and 1989, it peaked during periods of high solar irradiance and water transparency, while cell numbers were low throughout the rainy summer of 1987.

Seasonal Phases

In this study, we present a simplified scheme of the annual cycle by distinguishing four seasonal phases. While the periods defined in Table 2 match well with periods of high or low ciliate biomass, respectively, other planktonic groups exhibit different seasonal patterns. Community grazing of larger zooplankton, for example, tends to increase one or two weeks before the onset of the clear-water phase [30]. Also, short-term summer peaks of food compartments are obscured by averaging biomass concentrations from July through October. With these restrictions in mind, the following seasonal phases can be deduced from the data presented in Fig. 4 and Table 3.

Spring: Highest concentrations of nanoplankton and total food; low grazing impact of metazoans; high ciliate abundance and biomass, relatively uniform community composition. Clear-water phase: High grazing impact of metazoans, namely daphnids; low food biomass; extremely low ciliate biomass. Summer/autumn: Low grazing impact of metazoans, though significantly higher than in spring; low food biomass; high ciliate biomass, highly diverse community composition. Winter: Low biomasses of ciliates and food, low metazoan grazing. During the transition from the spring to the clear-water phase, the ciliates were reduced more severely than phytoplankton and bacteria, which points to grazing of daphnids on the ciliates.

Ciliate community grazing was not measured in situ. Grazing experiments with the natural community are difficult to perform, because the majority of the Lake Constance ciliates are small and delicate cells, which cannot be separated by sieving from the labelled food. We can estimate ciliate grazing, therefore, only on theoretical considerations (Table 4). In the literature, volume-specific clearance rates of ciliates mainly range from 10^4 to 10^5 cell volumes $hour^{-1}$ [11, 36]. Accordingly, we estimated ciliate community grazing rates in different seasons from ciliate cell volumes, by assuming minimum and maximum rates of 10^4 and 10^5 cell volumes $hour^{-1}$, respectively, at 20°C. These values were corrected for changing temperature using the mean temperatures given in Table 2 and assuming a Q_{10} value of 2. From mean values of ciliate and nanoplankton biomass, we then calculated a theoretical range of ciliate community ingestion of nanoplankton, expressed as mg C m^{-3} d^{-1} and as %C ciliate-body-C^{-1} d^{-1}. An example may illustrate the meaning of these hypothetical rates: Assuming a gross growth efficiency of 40% [12], ingestion of 125–250% C ciliate-body-C^{-1} d^{-1} would support one doubling every 24 to 48 hours.

The minimum rates presented in Table 4 appear unrealistically low, especially with respect to the spring and summer/autumn phases. It is unlikely that nanoplankton ingestion at such low rates could sustain thriving communities as observed during these seasons. Conversely, if maximum rates were realized, ingestion of nanoplankton alone could support rapid ciliate growth at the culmination of phytoplankton spring blooms (1987/1988). This agrees well with the observed dominance of algivorous ciliates in spring. Generation times of

Table 4. Ciliate and nanoplankton biomass, averaged over seasonal phases. Theoretical range of ciliate community grazing and ingestion of nanoplankton, calculated by assuming minimum and maximum grazing rates of 10^4–10^5 cell volumes hour^{-1} at 20°C and a Q_{10} value of 2

Season	Mean biomass (mg C m^{-3})		Theoretical range of ciliate community grazing rates (d^{-1})	Theoretical range of ciliate community ingestion rates of nanoplankton	
	Ciliate	Nano-plankton		mg C m^3*d	% C Ciliate body C*d
Spring 1987	31.9	137.7	0.03–0.33	4.5–45.4	14–142
1988	40.2	135.7	0.04–0.45	6.1–61.1	15–152
1989	28.6	69.1	0.03–0.27	1.9–18.7	6–65
Clear-water phase 1987	11.0	66.3	0.01–0.14	0.9–9.3	8–84
1988	8.3	39.1	0.01–0.13	0.5–5.1	6–61
1989	4.9	38.2	0.01–0.08	0.3–3.1	6–63
Summer/autumn 1987	22.3	34.3	0.04–0.37	1.3–12.7	6–57
1988	41.0	40.0	0.07–0.72	2.9–28.8	7–70
1989	35.0	40.3	0.06–0.63	2.5–25.4	7–73
Winter 1987/1988	3.1	10.8	0.003–0.03	0.03–0.3	1–10
1988/1989	3.1	24.9	0.003–0.03	0.07–0.7	2–23

ciliate populations ranging from 24 to 48 hours were observed in a field study in spring 1988 [25, 57]. We also know that small bloom-forming algae in spring grow at high rates [41, 57] which could balance the combined grazing impact of ciliates, micro- and macroplankton (Tables 3, 4). This suggests that in spring, ingestion rates might come close to the maximum rates shown in Table 4. As a consequence, ciliates most likely are not food-limited in this season, even if nanoplankton were used as the only food.

In summer/autumn, in contrast, ingestion of nanoplankton alone would not sustain maximum ciliate growth. Therefore, ciliates probably use a broader food spectrum, which is consistent with the community structure observed in this season. Picoplankton could serve as an additional food source. Grazing on "total food" (Fig. 4) at maximum rates would result in an ingestion of about 200% C ciliate-body-C^{-1} d^{-1} in summer/autumn. It is unlikely, however, that bacteria are consumed at maximum rates for two reasons: First, efficient bacteria feeders such as Peritrichida and small Scuticociliatida accounted for only a small fraction of total ciliate biomass. Second, bacteria are known to grow at low rates during this season; biomass turnover times of 5 and 23 days were reported by Simon [38] with respect to two bacterial size fractions.

Rather large food particles might also contribute to the ciliate diet. It is well known that some ciliate taxa, such as *Didinium,* prey on other ciliates. Furthermore, the largest ciliates can also ingest colonial algae, large diatoms, and even rotifers. At present, we are not able to evaluate the quantitative importance of this food compartment, which is not included in the biomass of "total food" in Fig. 4. The ciliate taxa which might use these food items (Haptorida, Heterotrichida, Suctorida) accounted for approximately 30% of ciliate biomass in the summer/autumn periods.

Trophic Relationships in Spring

The development of a relatively uniform ciliate spring community was closely related to food resources (Fig. 5). Efficient nanoplankton feeders (small Prostomatida and medium-sized to large Oligotrichida) responded rapidly to the bloom of small phytoplankton. With respect to large Oligotrichida, this response is consistent with previous observations [28]. The build-up of these populations was followed by development of raptorial species (large Prostomatida and Haptorida). At the same time, we observed an increase of picoplankton feeders (Peritrichida and Scuticociliatida), which is in agreement with high bacterial productivity during the decline of phytoplankton blooms [39]. It is interesting to note that in spring 1989 only small populations of Scuticociliatida and Peritrichida developed during the decline of a rather weak phytoplankton maximum.

Trophic coupling between *Strobilidium* spp. (20–35 μm) and *Stephanodiscus hantzschii* (Fig. 5) existed only in spring. While the *S. hantzschii* population did not recover from losses in the clear-water phase, small *Strobilidium* spp. were abundant throughout the year and, therefore, must have switched to a different diet from spring to summer. *Pseudobalanion planctonicum* is a nanociliate with the ability to reproduce rapidly at low temperatures. A generation time of 20 hours was determined in laboratory cultures at 9° C with *Rhodomonas* as food [26]. The field data presented in Fig. 5 show that *Pseudobalanion* biomass increased simultaneously with *Rhodomonas* biomass at the onset of phytoplankton spring blooms, but declined earlier than *Rhodomonas* in 1987 and 1988. At present, we can only speculate about the causes of this early breakdown. Predation by larger ciliates and/or small metazoans might have been a major factor.

Trophic Relationships in Summer/Autumn

In summer and autumn, relationships between functional groups of ciliates and food compartments were less clear. The diversity of taxa and functional groups points to exploitation of a wide size range of food organisms and to a diversification of ecological niches. Food-limitation is more likely to occur in summer/autumn compared to spring. Various environmental factors may enhance species diversity in summer and autumn. These include increasing temperatures, enabling growth of species adapted to warm water; formation of microhabitats such as floating colonies of cyanobacteria; short-term changes in food quality and quantity, leading to coexistence of species with different survival strategies. At present we know very little about such strategies of freshwater pelagic ciliates. Furthermore, experimental studies of interactions between pelagic ciliate populations are scarce and mainly restricted to the marine environment [46, 52].

Summary and Conclusions

In the context of the seasonal succession of the entire plankton community, ciliates play a dual role. On the one hand, they are efficient grazers of small

phytoplankton and thus competitors of rotifers and crustaceans. On the other hand, they fall well into the food size range of larger zooplankters and may be consumed together with phytoplankton [1, 32].

With the present investigation, we have only begun to understand some factors which regulate the population dynamics of pelagic ciliates in Lake Constance. Based on the data presented in this paper, the following steps were identified:

1) At the onset of stratification in spring, algivorous ciliate populations develop almost simultaneously with bloom-forming small algae. Owing to their short generation times, they can use this food source prior to rotifers and crustaceans. Growth of algivorous ciliate populations in spring apparently is not food-limited.

2) Small populations of bacterivorous or omnivorous ciliates develop shortly after the culmination of the phytoplankton bloom. Simultaneously, predatory ciliates appear.

3) Increasing feeding activity of larger zooplankton causes the break-down of the ciliate spring community (clear-water phase). This may be an indirect effect due to depletion of food by the larger zooplankters, but also to direct grazing by rotifers and cladocerans on the ciliates.

4) Small "green" ciliates containing symbiontic algae increase toward the end of the clear-water phase, a period of low food availability (except bacteria), but high solar irradiance.

5) With decreasing grazing impact of larger zooplankton, a highly complex ciliate summer community develops, which exploits a wide variety of food resources. Temporal and spatial inhomogeneities in food concentrations enhance diversity of the community structure.

6) Mixing of the water column, decrease in food resources, and low temperatures terminate the period of high ciliate abundance and biomass. Low numbers of ciliates persist during the winter months.

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