Hydrobiologia (2007) 578:147–156
DOI 10.1007/s10750-006-0441-4

PHYTOPLANKTON WORKSHOP

Weather-driven ecology of planktonic diatoms in Lake Tovel (Trentino, Italy)

Monica Tolotti · Flavio Corradini · Adriano Boscaini · Damaso Calliari

Abstract The seasonal development of planktonic diatoms in Lake Tovel has been studied from 2002 to 2004 within the SALTO research project. The objective was to investigate the role of weather conditions and lake hydrology in regulating the development of *Cyclotella* and *Fragilaria* functional species groups. The different responses of the two species to the environmental variability and their reciprocal relationships were considered. *Cyclotella* showed a weak relationship with the selected environmental variables and its seasonal development was difficult to interpret, also in relation to its opportunistic behaviour. On the contrary, *Fragilaria* complex showed a prompt response to environmental variability and its seasonal development appeared to be mainly regulated by hydrological conditions, through nitrate nitrogen and, secondarily, by silica concentrations. Water temperature and thermal stability affected only *Fragilaria* species, while different nutrient requirements allowed *Cyclotella* species to grow under conditions of limited resources for *Fragilaria*. Since Lake Tovel has scarce internal nutrient reserves and its hydrology is strongly affected by precipitation both in winter and summer, diatom phenology seems to be indirectly regulated by weather conditions.

Keywords Lake Tovel · Hydrology · Ecology · Planktonic diatoms · *Cyclotella* · *Fragilaria*

Guest editors: M. Albay, J. Padisák & L. Naselli-Flores
Morphological plasticity of phytoplankton under different environmental constraints.

M. Tolotti (✉) · F. Corradini · A. Boscaini · D. Calliari
Unit for Limnology and Fish Research, Department of Valorisation of Natural Resources, Istituto Agrario di S. Michele all'Adige, Via Mach 1, I–38010 S. Michele all'Adige, Italy
e-mail: Monica.Tolotti@iasma.it

Introduction

Studies of nutrient requirements and limitations of planktonic diatoms and of their inter-specific relationships under different environmental conditions represent classical ecological issues, which have been widely addressed since the 1970s mainly through experiments on algal cultures (e.g. Tilman & Kilham, 1976; Kilham & Tilman, 1979; Van Donk & Kilham, 1990). These studies showed that small centric diatoms (i.e. *Cyclotella*) are in general better competitors for nutrients than larger pennate diatoms such as *Asterionella* and *Synedra*/*Fragilaria* species. Though scarce, field studies confirmed the results of laboratory experiments and showed that thermal conditions can affect diatom growth in lakes more than nutrient availability (e.g. Sommer, 1987; Padisák et al., 2003a).

The present contribution addresses these issues by providing information on diatom ecology and phenology obtained during research activities at Lake Tovel, a montane lake located at 1177 m a.s.l. in the Italian Central Alps. The study has been carried out within the international SALTO/BEST research project (Blooms & Environment: Science for Tovel, 2001–2004), aimed at improving knowledge of lake general limnology and of dinoflagellate bloom dynamics. In fact, the lake became famous since the beginning of the XIX century because of its summer red bloom of dinoflagellates (Baldi, 1941; Marchesoni, 1959). After the red blooms suddenly ceased in 1964 several investigations were carried out to understand reasons responsible for the bloom disappearance (e.g. Vittori, 1969; Gerosa, 1970; Dodge et al., 1987; Paganelli, 1992; Corradini et al., 2001; Cantonati et al., 2003).

The present study of planktonic diatom phenology in Lake Tovel arose from two main observations. First, diatoms have always dominated the phytoplankton of Lake Tovel, both during and after the bloom period (e.g. Baldi, 1941; Tolotti et al., 2006). Two functional species groups including some ecologically and morphologically very similar species of *Cyclotella* Håkanssons and *Fragilaria* Lyngbye (syn. *Synedra* Ehrenberg), alternatively dominate the diatom community of the lake.

On the other hand, the extreme and contrasting weather conditions observed during the 3 years of study suggested that the diatom variability in Lake Tovel might be related to changing local hydrological conditions, which in turn depend on precipitation amount and distribution (Corradini et al., 2005).

The objectives of this contribution were: (a) to investigate the role of lake hydrology, thermal conditions and nutrient availability in regulating the temporal and spatial pattern of distribution of *Cyclotella* and *Fragilaria* functional species groups in Lake Tovel; (b) to check possible relationships between the two species groups. These aspects might be relevant in the future if the present tendency towards very scarce summer precipitation, as also occurred in 2005 (Eccel, unpublished data), will continue.

Study site

Lake Tovel (surface area = 0.38 km^2, z_{max} = 39 m, z_{mean} = 19 m) is a temperate mountain lake of glacial origin (Oetheimer, 1992) located at 1177 m a.s.l. in the Brenta Dolomites, Italian Central Alps. The lake catchment is relatively wide (ca. 41 km^2), composed by dolomite and limestone and has a pseudo-karst nature (Borsato & Ferretti, 2006). The summer hydrology of the lake is characterised by short retention time (ca. 6–10 months) and water level fluctuations up to ca. 2 m (Borsato & Ferretti, loc. cit.). Lake water level typically decreases below the outlet level in winter and late summer in relation to reduced precipitation. Maximum lake level occurs during snow melt in early summer and in late autumn in relation to enhanced rainfall.

Lake Tovel can be defined as an oligomictic lake, since it often skips the spring mixing, as observed in 2003 and 2004. Due to its dynamic hydrology the lake does not develop an epilimnion. Beneath the metalimnion, extended from the surface down to 4–5 m depth, temperature decreases gradually down to 20–25 m depth, while deep layers are in almost isothermal conditions (Corradini et al., 2001; Corradini & Boscaini, 2006). The water layer between 20 and 25 m correspond to the lower limit of the euphotic zone (Corradini & Boscaini, loc. cit).

Lake Tovel is oligotrophic, with low total phosphorus (TP) and dissolved silica (SiO_2) concentrations (mean = 4 μg l^{-1} and 0.53 mg l^{-1}, respectively, in the period 2002–2004) and relatively high NO_3–N (mean = ca. 370 μg l^{-1}) in the euphotic zone (Corradini & Boscaini, 2006). TP shows very scarce seasonal variability. NO_3–N and SiO_2 typically reach their highest concentration in May, during snow melt, and gradually decrease in summer due to algal uptake. In particular, silica shows very low concentrations (down to ca. 0.1 mg l^{-1}) when intense diatom growth coincides with low water inflow, as in summer 2003 (Corradini & Boscaini, loc. cit.).

The oligotrophic status of Lake Tovel is confirmed by low annual mean values of phytoplankton biovolume (ca. 500 mm^3 m^{-3}) and high Secchi depth (ca. 10 m, Corradini et al., 2001; Tolotti et al., 2006). However, short and intense growth stages can produce phytoplankton biovolume within the mesotrophic range, as observed in summer 2004. Phytoplankton of Lake Tovel is typically dominated by diatoms almost all year round (Baldi, 1941; Paganelli, 1992; Corradini et al., 2001; Tolotti et al., loc cit.). Dinoflagellates and Chrysophyceae are quantitatively important in summer, while other algal groups are less abundant and irregularly distributed. Species composition is stable from year to year, while seasonal and vertical distribution show pronounced inter-annual variability (Tolotti et al., loc cit). Lake Tovel is a rotifer lake (Baldi, 1941; Paganelli, 1992) where crustacean are present with only three taxa. Zooplankton density is in general low (Obertegger et al., 2006) and dominant rotifers (i.e. *Polyarthra* sp., *Filinia* spp., *Synchaeta* spp. and *Asplanchna* sp.) are more abundant than cladocera (i.e. *Bosmina longirostris* and occasionally *Daphnia longispina*) during periods of high water inflow.

Methods

During the study period, Lake Tovel was sampled fortnightly from 2002 to 2004 during the ice free period and at least once in late winter under the ice cover. Precipitation amount and lake water level were recorded every hour by a weather station located on the lake shore (Borsato & Ferretti, 2006). Temperature and oxygen profiles were measured at one-meter intervals with a multiparametric probe. Samples for chemistry, zooplankton and phytoplankton analyses were collected from fixed depths within the euphotic zone (0.5–2–5–10–15–20 and 25 m) with a Ruttner sampler. Chemical analyses were preformed according to standardised methods (Corradini & Boscaini, 2006), phytoplankton counts and biovolume estimation according to Utermöhl (1958) and Rott (1981), respectively. The *Cyclotella* and *Fragilaria* species composing the two diatom functional species groups were not separated due to the very slight differences in the fine structure of their frustulum under the light microscope and considering their similar ecology. Zooplankton samples were counted under a stereoscope (Obertegger et al., 2006) and zooplankton data was expressed as abundance.

Data analysis

Data analysis included the calculation of the relative thermal resistance (RTR, Wetzel, 2001), between different water layers and at each sampling date, as an index of thermal stability. Relationships between *Cyclotella* and *Fragilaria* species groups and environmental variables were firstly checked calculating Spearman Rank Order correlation coefficients between volume-weighted averages – relative to the euphotic zone – of diatom biovolume and of a set of environmental variables (i.e. water temperature, thermal stability, pH, conductivity, concentration of the major nutrients, biomass of meso-zooplankton). To investigate relationships between environmental gradients within the euphotic zone and vertical diatom distribution, top and bottom layers of the euphotic zone, which are characterised by opposite thermal conditions, were compared calculating a second Spearman correlation matrix relating arithmetic averages of diatom biovolume and environmental variables calculated for the water layers 0–5 and 20–25 m, respectively.

To further evaluate the vertical distribution of planktonic diatoms in Lake Tovel, the mean sinking velocity of a set of measured individuals belonging to both species complexes was estimated using the diameter of the sphere with equivalent biovolume in the Stoke's equation. Diatom density was assumed as ranging between 1.1 and 1.3 g cm^{-3} as reported by Reynolds (1997) and Padisák et al. (2003b). The calculation of the coefficient of form resistance (Φ) was done assuming both taxon shapes as a cylinder and using the individual length:diameter ratio in the regression obtained during laboratory simulations by Padisák et al. (loc. cit., Fig. 2). Mean S:V ratio of the two functional species groups was calculated basing on measured cell size of cells sets. Significance of differences between S:V values was tested with Mann–Whitney rank sum test, after checking the data for normal distribution.

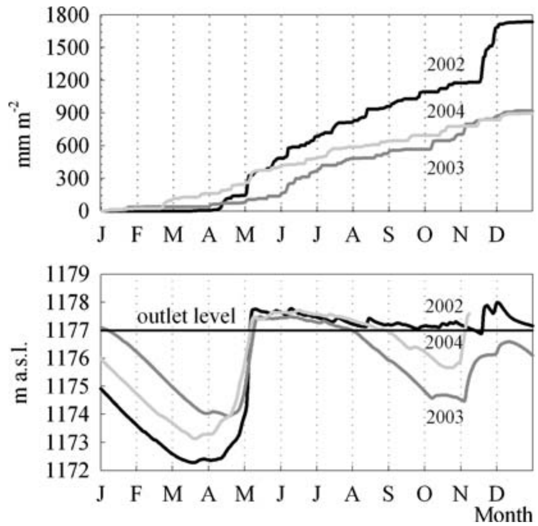

Fig. 1 Cumulated precipitation (upper panel) and lake water level (lower panel) measured at the weather station on the Lake Tovel shore during the period 2002–2004. Modified and updated from Borsato & Ferretti (2006)

Results

Annual precipitation was highly variable during the investigation period (Fig. 1, upper plot). Weather was very dry in winter 2002, while the summer was particularly rainy, so that the lake level never decreased below the outlet level (1177 m a.s.l., Fig. 1, lower plot). 2003 was characterised by almost normal precipitation in winter, while a very dry spring and an exceptionally hot summer 2003 were responsible for the progressive and pronounced lake level decrease till October. Late and abundant snow fall in winter 2004 prevented extreme lake water level decrease during the very dry summer 2004.

Cyclotella cyclopuncta Håkansson & Carter and secondarily *C. pseudostelligera* Hustedt were dominant within the *Cyclotella* functional species group in the 3 years. Both species are very small (ca. 5–8 μm in diameter) and widely distributed in oligotrophic, well-buffered lakes of the Alpine region. The second functional species group included the two similar *Fragilaria tenera* (W. Smith) Lange-Bertalot and *F. nanana* Lange-Bertalot.

Cyclotella species showed an intense growth phase in spring 2002 (Fig. 2, upper panel) and formed two deep peaks in late April and late May, respectively. In summer 2003, *Cyclotella* species were less abundant, showing only a slightly pronounced maximum near the surface between June and July. In 2004 the small centric diatoms became abundant only in autumn, when they produced a clear maximum in the upper 10 m between late September and early October.

Fragilaria species showed intense development stages from mid summer to autumn and were more evenly distributed along the water column during the investigation period, with the exception of summer 2003, when *Fragilaria* growth was very scarce and restricted to the deepest layers of the euphotic zone (Fig. 2, lower panel). *Fragilaria* and *Cyclotella* species groups reached their maximum abundance in different months in 2002 and 2004 (Fig. 2), while in 2003 both reached their maximum in June. The different picture observed in 2003 was mainly due to the very scarce *Fragilaria* biovolume, while the decrease of *Cyclotella* was less pronounced. The alternation of the two species groups was particularly evident considering their volume-weighted average biovolume in the euphotic zone in the three study years (Fig. 3).

Results of the correlation matrix calculated using volume-weighted averages of diatom biovolume and of a set of environmental variables are shown in Table 1. *Cyclotella* showed a significant negative relationship only with Secchi depth, in relation to the particularly high *Cyclotella* densities (up to ca. 8×10^6 cells l^{-1}) recorded during the periods of minimum water transparency. Otherwise, *Cyclotella* species group was not correlated either with biovolume of *Fragilaria* species group or with any other environmental variable.

On the contrary, *Fragilaria* species group was positively correlated with relative thermal stability of the euphotic zone, hydrology (expressed as total water inflow and lake water level), nutrients (especially NO_3–N) and total rotifer abundance. The strong relationship between volume-weighted averages of *Fragilaria* biovolume and NO_3-N concentration is confirmed by the regression shown in Fig. 4 (upper plot). Table 1 also reveals a positive relationship between relative thermal resistance of the euphotic zone and lake

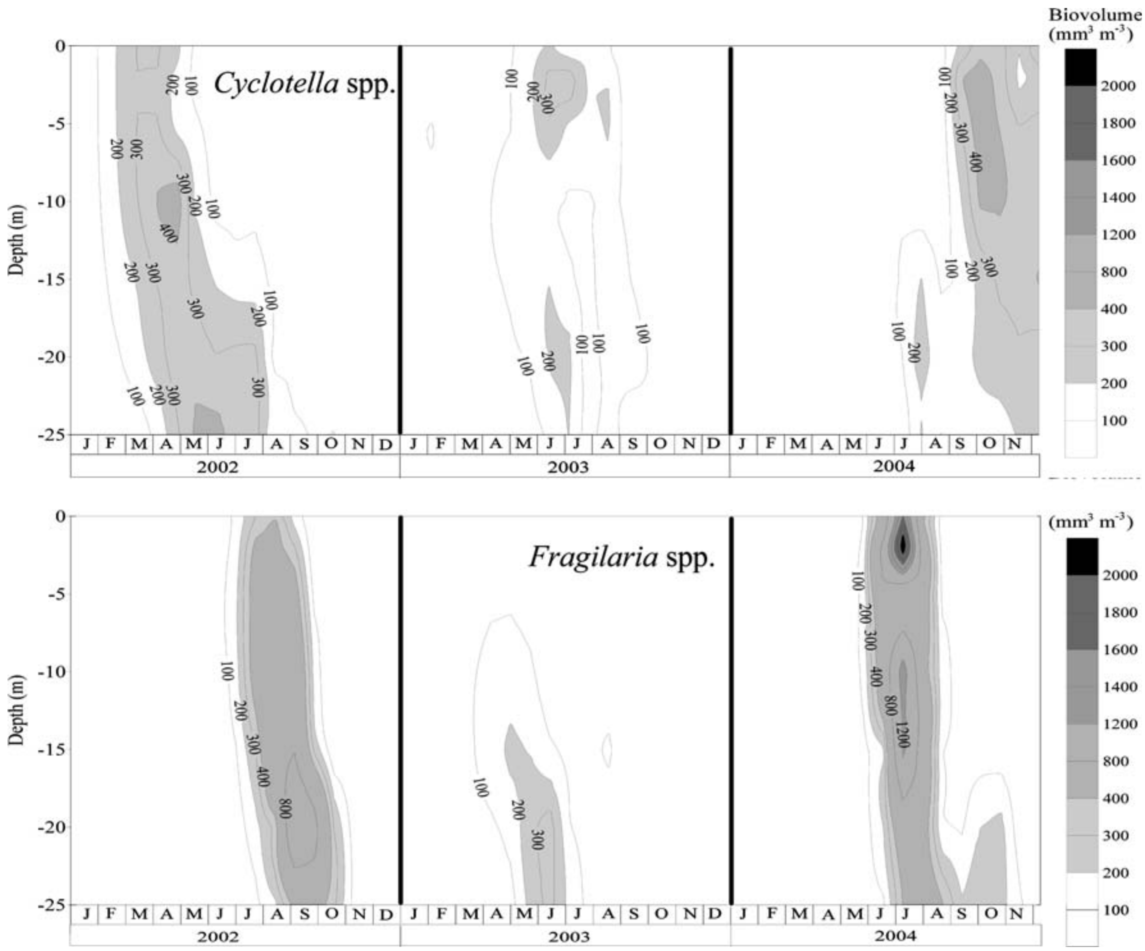

Fig. 2 Spatial and temporal distribution of the biovolume of *Cyclotella* (upper panel) and *Fragilaria* (lower panel) functional species groups in the euphotic zone of Lake Tovel during the period 2002–2004

water level, and between lake level (and water input) and NO_3–N and SiO_2 concentrations, respectively. In particular, a strong relationship was found between lake water level and average concentrations of NO_3–N in the top layer of the euphotic zone (0–5 m, Fig. 4 lower plot).

The mean sinking velocity of both functional species groups was estimated for all three years (Table 2). The estimated mean coefficient of form resistance was almost twice as high for the elongated *Fragilaria* than for the rounder *Cyclotella* species. The latter species group showed a constant coefficient in the three years, while *Fragilaria* showed a slight decrease from 2002 to 2004 in relation to their mean size reduction (cf. diameter of the sphere with equivalent volume in Table 2). The mean sinking velocity calculated for the two functional species groups was comparable most of the time, except in 2002, when it was twice as high for *Fragilaria* than for *Cyclotella*. On the contrary, the mean surface:volume ratios of the two functional species groups were significantly different in all 3 years (Mann–Whitney rank sum test, $P < 0.001$). Both species showed a significant lower $S:V$ ratio in 2003 in comparison to the other 2 years studied.

The results of the Spearman matrix relating arithmetic averages of diatom biovolume and environmental variables of the top (0–5 m) and bottom layers (20–25 m) of the euphotic zone (Table 3) confirmed that biovolume of *Cyclotella* species group is not significantly related either to *Fragilaria* or to zooplankton abundance. However, *Cyclotella* species showed a positive

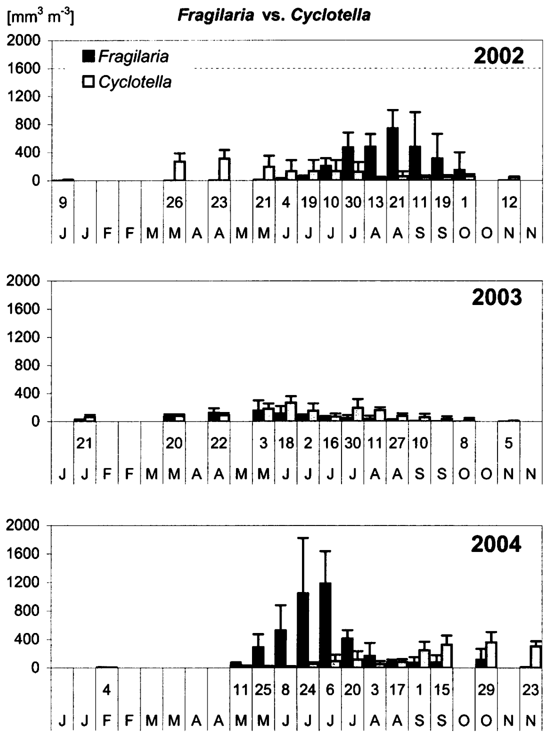

Fig. 3 Volume-weighted averages of biovolume of *Cyclotella* and *Fragilaria* functional species groups in the euphotic zone (0–25 m) of Lake Tovel during the three studied years. Whiskers indicate standard deviations, numbers on the *x*-axis the sampling days

relationship with surface water temperature and thermal stability of the whole euphotic zone (RTR 0–25 m) and a negative correlation with conductivity and NO_3–N. The correlation with SiO_2, although not particularly strong, was opposite in the top and bottom layers of the euphotic zone.

The strong relationship between *Fragilaria*, lake hydrology (water level and water input) and nutrients (especially NO_3–N), already found considering the volume-weighted averages for the euphotic zone (Table 1), was confirmed comparing its top and bottom layers. The positive relationship with surface temperature and thermal stability was in general stronger than for the *Cyclotella* complex and more accentuated considering the deeper water layers of the euphotic zone. Significant and opposite relationships with mean cladoceran and rotifer abundance were also found considering the top and bottom layers of the euphotic zone separately.

Discussion and conclusions

Cyclotella and *Fragilaria* functional species groups of Lake Tovel are characterised by different physiological and ecological characteristics, which are likely responsible for their alternative development.

In general, *Cyclotella* species of Lake Tovel were weakly affected by environmental variables, although they showed preference for lower water conductivity and an ability to also grow after NO_3– and secondarily SiO_2 concentrations became limiting for *Fragilaria* species. This ability to exploit diluted nutrients might be supported by a higher nutrient affinity, as suggested by rather

Table 1 Spearman rank order correlation matrix between volume-weighted averages of *Cyclotella* and *Fragilaria* species biovolume and of a set of environmental variables in the euphotic zone

	FRA	RTR 0–25 m	Inflow	Level	NO_3–N	DRSiO_2	Σ Rotifera
CYC	–0.03	0.18	0.11	–0.09	–0.31	0.20	0.02
FRA		0.40*	0.56**	0.68**	0.60**	0.35*	0.58**
RTR 0–25 m			0.14	0.33*	0.06	–0.03	0.45**
Inflow				0.81**	0.58**	0.40**	0.22
Level					0.72**	0.37*	0.21
NO_3–N						0.35*	0.17
DRSiO_2							0.24

CYC = *Cyclotella* species group; FRA = *Fragilaria* species group; Secchi = water transparency measured with the Secchi disk; RTR = relative thermal resistance between lake surface and 25 m depth; inflow = total water inflow from the lake catchment in the 15 days previous to each sampling; level = lake level at each sampling session

* $P < 0.05$

** $P < 0.001$

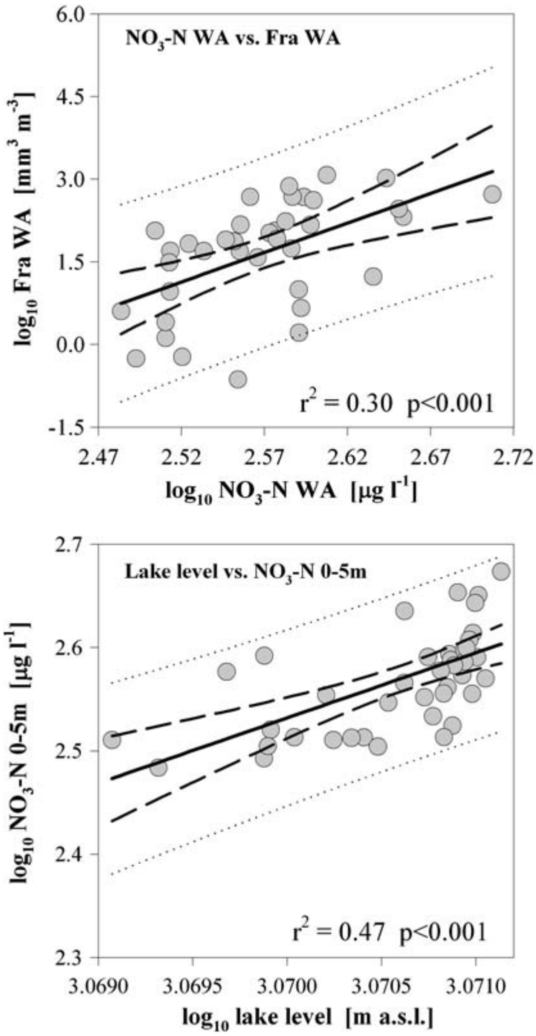

Fig. 4 Regression, confidence and prediction intervals (dotted lines) for volume-weighted averages of NO_3–N concentrations versus *Fragilaria* biovolume in the euphotic zone (0–25 m, upper panel) and for lake level versus average NO_3–N concentration in the top layer of the euphotic zone (0–5 m, lower panel)

high values of *S*/*V* ratio in both species. The reduction of *S*/*V* ratio observed for the two functional species groups in summer 2003 can be interpreted as a reaction to the reduced nutrient availability.

Fragilaria showed much stronger relationships with environmental variations and its seasonal development seems to be regulated mainly by lake hydrology through nutrient availability, as indicated by the strong positive relationship found between *Fragilaria* and NO_3–N and secondarily SiO_2 concentrations This result is in accordance with the literature reporting unicellular planktonic *Fragilaria* species as preferring high nitrate nitrogen and silica concentrations (e.g. Baier et al., 2004; Kienel et al., 2005). Moreover, Fragilariaceae:Centrales ratio in lakes is reported as principally regulated by changes in the Si:P ratio (Kihlam & Tilman, 1979; Van Donk & Kilham, 1990), with Fragilariaceae growing well under limitation by phosphorus and *Cyclotella* species performing better when also silica becomes limiting (low Si:P ratio). The general dominance of *Fragilaria* functional species group in Lake Tovel could therefore be related with the very low phosphorus level (high Si:P ratio) typical for this lake. The reduced water inflow in summer 2003, which produced a pronounced decrease in silica and NO_3–N availability (Corradini & Boscaini, 2006), could have been responsible for the reduced *Fragilaria* species growth, while *Cyclotella* species were able to grow also under low Si:P ratio, so that their reduction was less pronounced.

The absence of a significant correlation between diatom abundance and phosphorus concentrations does not contrast with this picture

Table 2 Estimation of mean sinking velocity and surface:volume ratio for *Cyclotella* and *Fragilaria* functional species groups of Lake Tovel in the period 2002–2004

	Year	Nr.	Volume (μm^3)	Eq. diam. (μm)	Φ	Sink. vel. (m day^{-1})	*S*:*V*
Cyclotella species group	2002	70	87	4.8	1.16	0.09–0.28	1.4
	2003	70	129	5.5	1.16	0.12–0.37	1.1
	2004	294	104	5.1	1.16	0.11–0.32	1.3
Fragilaria species group	2002	80	657	9.4	2.28	0.18–0.58	1.5
	2003	82	478	8.5	2.18	0.16–0.47	1.4
	2004	570	343	7.6	2.00	0.14–0.41	1.5

Nr. = number of measured individuals; volume = mean cell biovolume; Eq. diam. = mean diameter of the sphere with equivalent volume as the cells; Φ = mean coefficient of form resistance according to Padisák et al. (2003a, 2003b); Sink vel. = mean sinking velocity according to Stokes's equation corrected with Φ; *S*:*V* = mean measured surface-volume ratio

Table 3 Spearman rank order correlation matrix between arithmetic averages of *Cyclotella* and *Fragilaria* biovolume and of environmental variables in the water layers 0–5 and 20–25 m depth, respectively

	Cyclotella 0–5 m	*Cyclotella* 20–25 m	*Fragilaria* 0–5 m	*Fragilaria* 20–25 m
Variable				
Cyclotella 20–25 m	0.48*			
Fragilaria 20–25 m			0.78**	
Secchi depth	–0.58**	–0.18	–0.09	0.11
Level			0.74**	0.57**
Inflow			0.68**	0.38*
Temperature 0 m		0.36*		0.43
RTR 0–5 m			0.45*	0.47*
RTR 0–25 m		0.34*		0.43*
Conductivity 0–5 m	–0.39*	–0.54**		
NO3–N 0–5 m			0.69**	0.35*
NO3–N 20–25 m		–0.46*		
SiO_2 0–5 m	–0.35*		0.38*	
SiO_2 20–25 m		0.48*		
Σ Cladocera			–0.42*	
Σ Rotifera			0.70**	0.63**

RTR 0–5 and RTR 0–25 = relative thermal resistance between 0 and 5 m and 20 and 25 m, respectively; inflow and lake level as in Table 1

* $P<0.05$

** $P<0.001$

because of the very scarce seasonal variations of both dissolved reactive and total phosphorus during the entire study period. Phosphorus was also not correlated with any of the environmental and biological variables considered in the present study. However, both the present study and laboratory experiments on dinoflagellates of Lake Tovel (Flaim, personal communication) showed a very important role of NO_3–N (and SiO_2) concentrations in regulating algal growth. This suggests that, although Lake Tovel has scarce internal nitrogen and silica reserves depending almost completely upon allochthonous inputs, phosphorus might be efficiently and rapidly recycled within the euphotic zone by the microbial food web, as recorded in other oligotrophic mountain lakes (e.g. Tilzer, 1972; Stockner & Porter, 1988; Hinder et al., 1999).

The positive relationship between both *Cyclotella* and *Fragilaria* and thermal conditions, although not particularly strong, is principally due to the strong diatom development in summer, when thermal stability was higher. The absence of a stable epilimnion in Lake Tovel prevents high water thermal stability values, known to be an important limiting factor for diatom development especially in deep lakes (e.g. Van Donk & Kilham, 1990; Reynolds, 1997; Padisak et al., 2003a), thus further explaining this positive (instead of the expected negative) relationship.

Nevertheless, the two functional species groups showed different response to thermal conditions during the 3 years investigated and in particular during the hot summer 2003, when the heating of the upper lake water layers clearly increased thermal stability. Although, the elongated shape of *Fragilaria* species of Lake Tovel seems to be able to effectively reduce their theoretical sinking velocity (which resembles that of the small *Cyclotella* species), this reduction appeared not to be sufficient to prevent sinking in summer 2003, when *Fragilaria* biovolume was restricted below 15 m depth. In the same period, the small *Cyclotella* cells were able to remain suspended within the warmer metalimnion beneath the lake surface. These observations suggest that sinking might become important as limiting factor for diatom growth in Lake Tovel only during exceptionally warm or dry periods, while in years characterised by "normal" weather conditions at least three factors promote a stronger and prolonged diatom growth: (a) the continuous nutrient input from the catchment, (b) the absence of thermal stratification, (c) the extension of the euphotic zone down to 25 m depth. The expected ability of both planktonic diatom functional species groups to grow at low light intensity seems to be confirmed by the high biovolume of both *Fragilaria* and *Cyclotella* groups observed in the deep layers of the euphotic zone in all three studied years.

Nevertheless, these factors appears to be particularly effective in driving the development of *Fragilaria* species group, while *Cyclotella* appears to be less affected and able to grow also under *Fragilaria* – limiting conditions.

Results of the present study also suggest that grazing plays a marginal role as a loss factor for diatom growth in Lake Tovel. The negative relationship found between abundance of *Fragilaria* species and cladocerans seems to hardly be due to grazing, considering both the needle-like *Fragilaria* shape and the low biomass of cladocerans in Lake Tovel (Obertegger et al., 2006), but is likely related to the different seasonal development of the two groups. In fact cladoceran (i.e. *Bosmina longirostris* and *Daphnia longispina* in summer 2003) reached their highest abundance in periods of low biovolume of *Fragilaria* species. In a similar way, the positive relationships between *Fragilaria* species group and rotifer abundance was interpreted as consequence of their coincident timing.

Despite the different nutrient requirements found for the two diatom functional groups and their different sensitivity toward biotic and abiotic factors, the methodological approach of the present study did not provide sufficient evidence of competitive relationships between *Cyclotella* and *Fragilaria* species in Lake Tovel, which could be tested only with laboratory experiments on algal cultures. Nevertheless, the different morphological and ecological characteristic of the two species suggest a certain separation of their ecological niches, which could explain their coexistence observed during the whole period of investigation.

Both species groups appear to be bottom-up controlled and the unexpected positive relation between *Fragilaria* species group and NO_3–N and SiO_2 is because in Lake Tovel higher nutrient availability coincide with periods (early summer) of higher water input, high lake water level and also higher thermal stability of the euphotic zone (Corradini & Boscaini, 2006). As a consequence, since hydrology of Lake Tovel is clearly affected by snow melt in spring and precipitation in summer, diatom phenology seems to be indirectly regulated by weather conditions. This aspect could become relevant for Lake Tovel ecology if the recent tendency toward reduced spring-summer rainfall will continue. Considering the crucial role of diatoms for phytoplankton dynamics of Lake Tovel and their seasonal development observed during the present investigation, either an oligotrophication of the lake or a change in phytoplankton species composition and dominance might be expected in the case of persistent scarce summer rainfall.

Acknowledgements The SALTO/BEST project has been funded by the Autonomous Province of Trento, Italy. The authors whish to thank Simone Degasperi, Dr. Federica Fiamingo and the technical staff of the Department for Valorisation of Natural Resources of the Istituto Agrario di S. Michele all'Adige (IASMA) for sampling activities and sample analyses, Dr. Ulrike Obertegger (IASMA) for kindly providing zooplankton data and Prof. Eugen Rott, University of Innsbruck (Austria), for the taxonomical improvement of diatoms.

References

Baier, J., A. Lücke, J. F. W. Negendank, G. H. Schleserb & B. Zolitschkac, 2004. Diatom and geochemical evidence of mid-to late Holocene climatic changes at Lake Holzmaar, West-Eifel (Germany). Quaternary International 113: 81–96.

Baldi, E., 1941. Ricerche idrobiologiche sul lago di Tovel. Memorie del Museo di Scienze Naturali della Venezia Tridentina 6: 1–297.

Borsato, A. & P. Ferretti, 2006. Monitoraggio idrometrico e bilanci idrologici del lago di Tovel e del suo bacino. Studi Trentini di Scienze Naturali, Acta Biologia 81 (2004) Suppl. 2: 205–223.

Cantonati, M., M. Tardio, M. Tolotti & F. Corradini, 2003. Blooms of the dinoflagellate *Glenodinium sanguineum* obtained during enclosure experiments in Lake Tovel (N. Italy). Journal of Limnology 62: 79–87.

Corradini, F. & A. Boscaini, 2006. Fisicia e chimica delle acque del lago di Tovel (Trentino, Alpi centrali). Studi Trentini di Scienze Naturali, Acta Biologia 81 (2004) Suppl. 2: 307–326.

Corradini, F., G. Flaim & V. Pinamonti, 2001. Five years of limnological observations on Lake Tovel ((1995)–1999): some considerations and comparison with past data. Atti. Società Italina di Oceanologia e Limnologia 14: 209–218.

Corradini, F., M. Tolotti, D. Calliari & F. Fiammingo, 2005. Influence of environmental factors on diatoms and dinoflagellates in Lake Tovel (Trentino, Italy). Verhandlungen der Internationalen Vereinigung der Limnologie 29: 469–472.

Dodge, J. D., P. Mariani, A. Paganelli & R. Trevisan, 1987. Fine structure of the red-bloom dinoflagellate Glenodinium sanguineum from the Lake Tovel (N. Italy). Algological Studies 47: 125–138.

Flaim, G., E. Rott, F. Corradini, G. Toller & B. Borghi, 2003. Long term species composition and diurnal migration of dinoflagellates in Lake Tovel (Trentino, Italy). Hydrobiologia 502: 357–366.

Gerosa, V., 1970. La natura chimica delle sostanze che provocano l'arrossamento del Lago di Tovel, III Studio di un eccezionale fenomeno di prearrossamento. Studi Trentini di Scienze Naturali 48: 107–132.

Hinder, B., I. Baur, K. Hanselmann & F. Schanz, 1999. Microbial food web in an oligotrophic high mountain lake (Jöri Lake III, Switzerland). Journal of Limnology 58: 62–68.

Kienel, U., M. J. Schwab & G. Schettler, 2005. Distinguishing climatic from direct anthropogenic influences during the past 400 years in varved sediments from Lake Holzmaar (Eifel, Germany). Journal of Paleolimnology 33: 327–347.

Kilham, P. & D. Tilman, 1979. The importance of resource competition and nutrient gradients for phytoplankton ecology. Archiv für Hydrobiologie, Ergebnisse Limnologie, 13: 110–119.

Marchesoni, V., 1959. La Val di Tovel e il Lago rosso. Natura Alpina 10: 37–76.

Obertegger, U., M. G. Barioni & G. Flaim, 2006. The zooplankton of Lake Tovel. Studi Trentini di Scienze Naturali, Acta Biologia 81 (2004) Suppl. 2: 369–378.

Oetheimer, C., 1992. La foresta sommersa del lago di Tovel (Trentino): reinterpretazione e datazione dendrocrinologica. Studi Trentini di Scienze Naturali, Acta Geologica 67: 3–23.

Padisák, J., W. Scheffler, C. Sípos, P. Kasprzak, R. Koschel & L. Krienitz, 2003a. Spatial and temporal pattern of development and decline of the spring diatom populations in Lake Stechlin in 1999. Archiv für Hydrobiologie, Special Issue Advanced Limnology 58: 135–155.

Padisák, J., E. Soróczki-Pintér & Z. Rezner, 2003b. Sinking properties of some phytoplankton shapes and the relation of form resistance to morphological diversity of plankton – an experimental study. Hydrobiologia 500: 243–257.

Paganelli, A., 1992. Lake Tovel (Trentino): limnological and hydrobiological aspects. Memorie dell'Istituto Italiano di Idrobiologia 50: 225–257.

Reynolds, C. S., 1997. Vegetation processes in the pelagic: a model for ecosystem theory. In Kinne O. (ed.), Excellence in Limnology, Vol. 9, 371 pp.

Rott, E., 1981. Some results from phytoplankton counting intercalibrations. Schweizer Zeitschrift für Hydrologie 43: 34–62.

Sommer, U., 1987. Factors controlling the seasonal variation in phytoplankton species composition. A case study for a deep, nutrient rich lake. Progresses in Phycology Research, 5: 123–178.

Stockner, J. G. & K. J. Porter, 1988. Microbial food webs in freshwater planktonic ecosystems. In Carpenter S. R. (ed.), Complex Interactions in Lake Communities. Springer-Veralg, New York: 69–83.

Tilman, D. & S. S. Kilham, 1976. Phosphate and silicate growth and uptake kinetics of diatoms *Asterionella formosa* and *Cyclotella meneghiniana* in batch and semicontinuous culture. Journal of Phycology 12: 375–383.

Tilzer, M., 1972. Bacterial productivity in a high-mountain lake. Verhandlungen der Internationalen Vereinigung der Limnologie 18: 188–196.

Tolotti, M., D. Calliari & F. Corradini, 2006. Variabilità interannuale del fitoplancton del lago di Tovel (Trentino, Italia). Studi Trentini di Scienze Naturali, Acta Biologia 81 (2004) Suppl. 2: 327–340.

Uthermöl, H., 1958. Zur Vervollkommung der quantitativen Phytoplankton-Methodik. Mitteilungen der Internationalen Vereinigung der Limnologie 9: 1–38.

Van Donk, E. & S. S. Kilham, 1990. Temperature effects on silicon- and phosphorus-limited growth and competitive interactions among three diatoms. Journal of Phycology 26: 40–50.

Vittori, A., 1969. Rilevamenti ecologici relative alle alterazioni della biocenosi lacustre del Lago di Tovel (Trentino). Studi Trentini di Scienze Naturali 46: 267–280.

Wetzel, R. G., 2001. Limnology. Academic Press, San Diego, California, 1006 pp.