Studi Trent. Sci. Nat., Acta Biol., 81 (2004), Suppl. 2: 341-350 ISSN 0392-0542

Littoral distribution of dinoflagellates in Lake Tovel (Trentino, Italy)

Dámaso CALLIARI*, Monica TOLOTTI & Flavio CORRADINI

Dipartimento Valorizzazione delle Risorse Naturali, Istituto Agrario di San Michele all'Adige, Via E. Mach 1, I-38010 San Michele all'Adige (TN)
*E-mail of the corresponding author: *damaso.calliari@iasma.it*

SUMMARY - *Littoral distribution of dinoflagellates in Lake Tovel (Trentino, Italy)* - Lake Tovel (Trentino, North Italy) has been focus of scientific research for more than one century. However, the majority of phytoplankton investigations regarded a few dinoflagellate species in the main basin of the lake. Because of the importance of the littoral region of lakes and microhabitat diversity in originating the dinoflagellates community, we decided to include this area in our study on phytoplankton dynamics and distribution in Lake Tovel. From July to September 2004 we sampled fortnightly both the littoral and pelagic zone of the lake, aiming at the study of dinoflagellates seasonal development. This study has revealed very scarce nutrient variations during the period investigated. Nonetheless, a clear succession of species has been found, which has been attributed to changes in water temperature and hydrodynamics of the lake. *Glenodinium sanguineum sensu* Dodge (1987) in early summer and *Gymnodinium uberrrimum* and *Baldinia anauniensis* gen. inedit. sp. inedit. Hansen *et al.* (in prep.) later on dominated the community along the period considered.

RIASSUNTO *Distribuzione litorale dei dinoflagellati nel Lago di Tovel (Trentino, Italia)* - Nell'ultimo secolo il Lago di Tovel (Trentino, Nord Italia) è stato oggetto di un'intensa attività di ricerca. Tuttavia, gran parte degli studi riguardanti la comunità fitoplanctonica sono stati focalizzati su alcuni taxa di dinoflagellati presenti nel bacino principale del lago. Per l'importanza delle zone litorali e della diversità dei microhabitat nell'originare la comunità fitoplanctonica lacustre, l'indagine sulla distribuzione e la dinamica del fitoplancton del lago è stata estesa a questi ambienti. Da luglio a fine settembre 2004 sono stati effettuati campionamenti ogni due settimane sia nelle zone litorali che pelagiche del lago. Lo studio ha rilevato una scarsa variabilità della concentrazione di nutrienti durante il periodo indagato. Nonostante ciò, è stata osservata una chiara successione di specie dinoflagellate, apparentemente in relazione con variazioni della temperatura dell'acqua e dell'idrodinamica del lago. Durante il periodo considerato, la comunità è stata dominata da *Glenodinium sanguineum sensu* Dodge all'inizio dell'estate e successivamente da *Gymnodinium uberrrimum* e *Baldinia anauniensis* gen. inedit. sp. inedit. Hansen *et al*. (in prep.).

Key words: dinoflagellates, Lake Tovel, seasonal succession
Parole chiave: dinoflagellati, Lago di Tovel, successione ecologica

1. INTRODUCTION

Lake Tovel (area = 0.38 km^2, volume = ca. 7.5 10^6 m^3) is an oligotrophic alpine lake located at 1178 m a.s.l. in the Adamello-Brenta Natural Park (Trentino, N-Italy). The lake is formed by two basins, a large, deep NE main basin (z_{max}= 39 m) and a second smaller and shallower SW basin (z_{max}= 4.5 m), which is also called Red Bay due to the red dinoflagellate blooms occurring there until 1964. The large catchment area (39.9 km^2) is composed of dolomite and limestone. For a more detailed description of the study site see Paganelli (1992) and Corradini *et al.* (2001).

In summer a thermal gradient is present, which is clearly more pronounced in the Red Bay (due to the cold inflow of several perilacual submerged springs), where the temperature difference between the surface and the bottom can be higher than 11 °C. Pronounced water level fluctuations during the year are responsible for both the Red Bay and the littoral zone remaining dry from late autumn (ice on) until spring. After the ice thaw (late April to mid May) the lake is refilled and rapidly reaches its period of maximum water level, which corresponds to a fast water renewal and an almost complete mixing of the water column. During this period an early summer bloom of diatoms

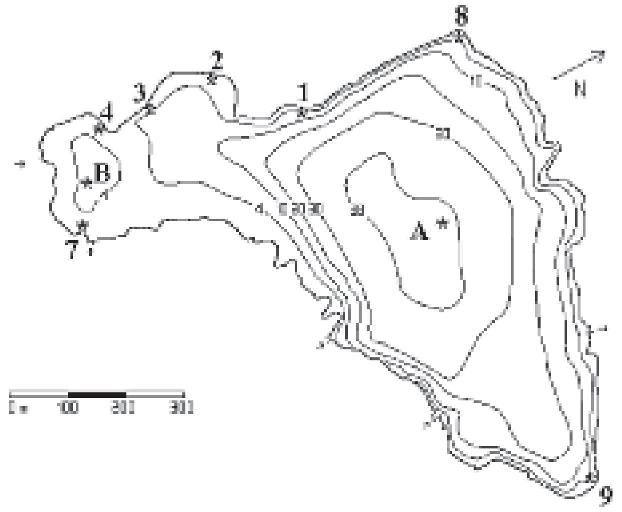

Fig. 1 - Lake Tovel: bathymetric map and sampling stations.

Fig. 1 - Lago di Tovel: mappa batimetrica e stazioni di campionamento.

can occur, while dinoflagellate abundance remains low (Tolotti *et al.* 2006).

Traditionally, the phytoplankton of Lake Tovel has been studied focusing on the main basin (Baldi 1938, 1941; Marchesoni 1959; Paganelli 1992; Flaim *et al.* 2003), while descriptions of the situation in the Red Bay and the littoral zone are very scarce. A preliminary study carried out in summer 2003 (unpublished data) suggested a high variability of both phytoplankton composition and abundance along the shoreline of the lake in comparison with both the pelagic sampling stations located in the Main Basin (A) and in the Red Bay (B), respectively (Fig. 1).

The first classification of the dinoflagellate responsible for the blooms was made by Largaiolli (1907), who classified the red alga as *Glenodinium pluvisculus* Stein var. *oculatum* Largaiolli. Baldi (1941) interpreted the red species and another green dinoflagellate coexisting in the lake as different morphotypes of a single taxon, classified as a new species named *Glenodinium sanguineum* (Marchesoni 1959). Some decades later, Dodge (1987) stated that *G. sanguineum* was a synonym of *Woloszynskya coronata*. Flaim *et al.* (2004, 2006) revealed that *G. sanguineum* consists of a species complex including three different taxa: *Tovellia sanguinea* sp. inedit. (Moestrup *et al.* 2006), which corresponds to the red morph of the previous *G. sanguineum*, *Baldinia anauniensis* gen. inedit. sp. inedit. (Hansen *et. al.* in prep.), corresponding to the green morphs of *G. sanguienum sensu* Baldi, and a third taxon, still to be identified, that corresponds to *G. sanguineum sensu* Dodge (1987). The latter taxon has frequently been confused with *G. sanguineum sensu* Baldi in the previous investigations.

Baldi (1941) and Largaiolli (1930), in their studies on the red blooms that occurred in the lake until 1964, indicated that the occurrence of the water reddening was more intense along the SW shore of the lake. Baldi (1938) suggested that the red dinoflagellate responsible of the blooms occurred in such high density in the Red Bay due to a passive mechanism of accumulation driven by the wind, which, blowing in direction NE-SW, could shift superficial cells spread all over the lake toward the southern shores of the Red Bay. Although this hypothesis could at least partially explain the accumulation, other factors likely play an important role, i.e. the preferential growth of dinoflagellate populations in the Red Bay (e.g. Tolotti *et al*. 2006).

Rengefors *et al.* (2004) pointed out the importance of littoral lake sediments in the generation of phytoplankton community, due to the germination of cysts and their diffusion in the water column. Germination of dinoflagellate cysts from the littoral sediments was found to be higher than from profound sediments, where conditions such as anoxia have been reported to prevent the process (Rengefors & Anderson 1998; Kremp & Anderson 2000). Therefore, the study of dinoflagellates and environmental variables appears to be crucial for the understanding of ecological dynamics in the whole lake.

In the case of Lake Tovel, basin morphology and the presence of numerous submerged springs along the SW shore can contribute to increase habitat diversity of the littoral zone. In fact, springs provide cold water and nutrient input to the bottom layers of the Red Bay (Bosato *et al.* 2006). The strong vertical temperature gradient (Corradini & Boscaini 2006) may influence both abundance and distribution of flagellates, in particular of dinoflagellates, which often present a distinct patchy distribution.

The main goal of the present study is to investigate the littoral distribution and abundance of the most common dinoflagellates of Lake Tovel and their relationships with some important environmental factors. In order to compare the two compartments of the lake, data analysis includes also the pelagic zone. The study contributes also to the taxonomical identification of the numerous dinoflagellate taxa of Lake Tovel, by describing the *in vivo* and preserved microscopical appearance of the most important taxa.

2. MATERIAL AND METHODS

Sampling was carried out fortnightly from 6th July to 29th September 2004 at 7 points along the shoreline (Fig. 1), where the water reddening was more pronounced according to Largaiolli (1907) and Baldi

(1941), and at the two pelagic stations A and B. Water temperature was measured at each site at 5 and 45 cm depth, which correspond to the top and to the bottom of the water sampler used in this study. The average of both temperatures was considered for data analyses.

Three 5 l water samples for dinoflagellates analysis were collected just below the water surface with a Patalas-Schindler bottle and concentrated through a 10 µm plankton net to a constant volume of 250 ml. Samples were kept cold during the transport to the laboratory, where a subsample was maintained alive and a second subsample was fixed with acidified Lugol's solution and counted.

A second water sample was taken from each point for algal nutrients analyses (TP, NO_3-N and NH_3-N), which were performed according to standard methods based on APHA (1998) and described in ISMA (1998). At station A phytoplankton and chemical samples were collected from 0 m to 25 m, whereas at station B they were collected at 0 m, 2 m and bottom.

Dinoflagellate counts were performed on an inverted microscope according to Uthermöl (1958). Smaller cells were counted at 200 magnification (at least 100 individuals of the most common taxon), while counting chambers were scanned at 50 magnification for larger, less abundant species. Taxa identification was done at species level whenever possible and a morphological comparison was done between *in vivo* and fixed samples for each taxon. Taxon biovolume was calculated basing on cell measurements and approaching the cell shapes to simple geometrical forms (Rott 1981; Hoehn *et al.* 1998).

Relationships between water temperature, major nutrients, density and biovolume at the different stations at the different sampling dates were checked calculating the Spearman Correlation Coefficient after testing the data for normal distribution. Differences among mean biovolumes, nutrient concentration and water temperature of sampling sites and sampling dates were tested performing one way Analysis of Variance (ANOVA) at a significance level of $p < 0.05$.

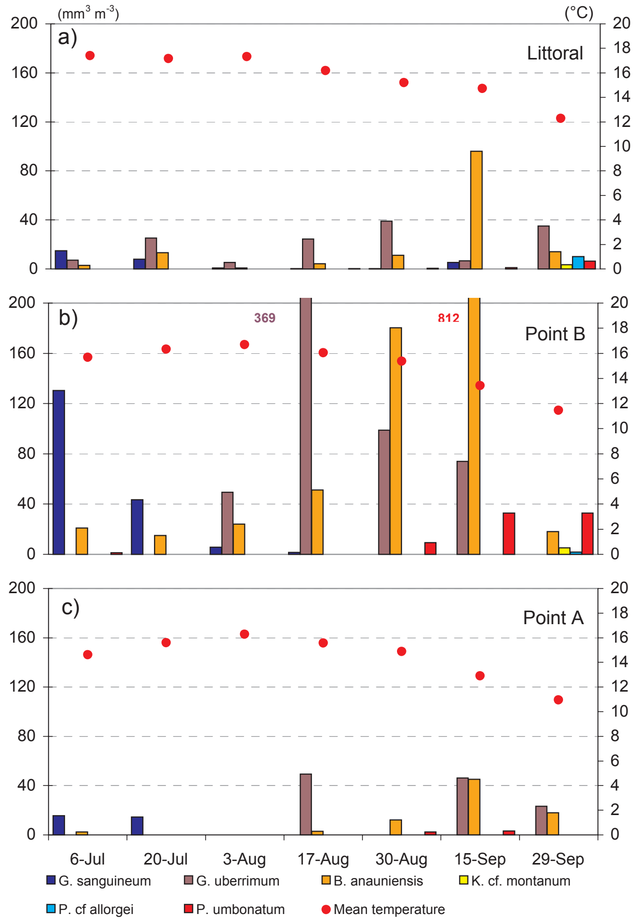

Fig. 2 - Mean water temperature and biovolume of the dinoflagellate taxa found at the littoral (a) and pelagic stations (b= B in the Red Bay, c= A in the Main Basin). Values for the pelagic stations refer to averages calculated for the water column.

Fig. 2 - Temperatura media dell'acqua e biovolume medio dei taxa dinoflagellati determinati nelle stazioni di campionamento litorali (a) e pelagiche (b= B nella Baia Rossa, c= A nel Bacino Principale). I valori delle stazioni pelagiche sono medie calcolate sulla colonna dell'acqua.

3. RESULTS

3.1. Environmental parameters

Water temperature along the lake shore decreased from early July toward September (Fig. 2). Sampling site A showed the maximum decrease (5.4 °C) between August 3th and September 29th (Fig. 2c). The highest temperature (17.4 °C) was recorded in the littoral zone on the first sampling (Fig. 2a), while the maximum at the pelagic sites was of 16.7 °C in station B on August 3th. In general, temperature was higher in the littoral than in the pelagic zone.

Chemical analysis confirmed low average concentrations of total phosphorous (TP), ranging between less than 2 µg l^{-1} and 8 µg l^{-1}, with some sporadic values up to 11 µg l^{-1} both in the littoral and pelagic sampling stations, and small seasonal variations. Nitrate nitrogen concentrations showed a wider range in the littoral zone (291-411 µg l^{-1}), ammonia nitrogen at the pelagic station of the Red Bay (station B, 10-70 µg l^{-1}). In general, ($NO_3 + NH_3$)-N concentration was higher at the beginning of the observation period and decreased progressively toward late summer. Seasonal variations of ($NO_3 + NH_3$)-N and TP concentration and total dinoflagellates biovolume were concordant in A (Fig. 3c), while the agreement between these parameters is less clear at the littoral sites and station B (Fig. 3a-b).

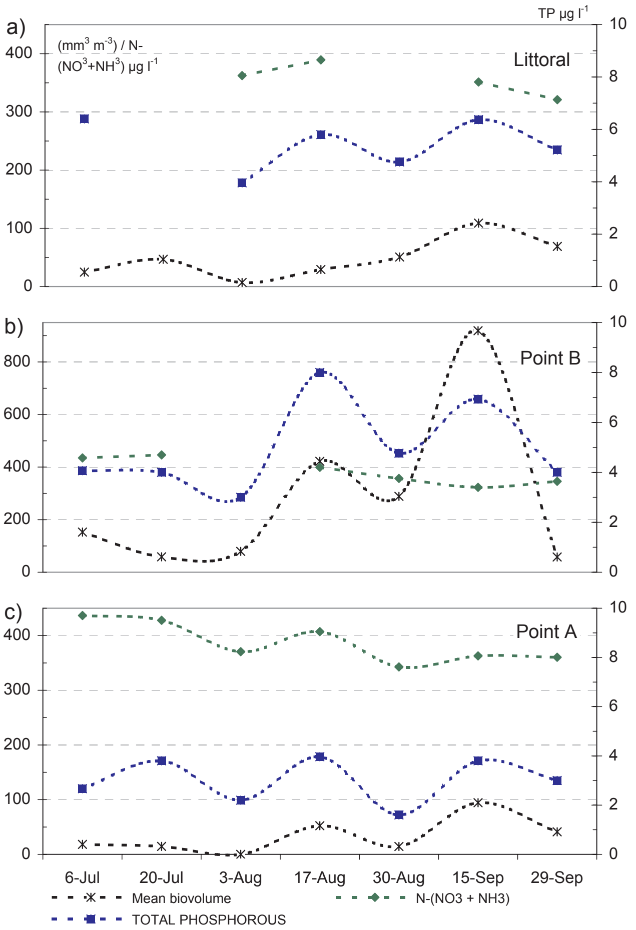

Fig. 3 - Mean total dinoflagellate biovolume and (NO_3 + NH_3)-N and TP concentrations of littoral (a) and pelagic stations (b= B in the Red Bay, c= A in the Main Basin). Values reported for the pelagic stations refer to averages for the whole water column.

Fig. 3 - Biovolume medio totale dei dinoflagellati e concentrazione media di (NO_3 + NH_3)-N e TP nelle stazioni litorali (a) e pelagiche (b= B nella Baia Rossa, c= A nel Bacino Principale). I valori riportati per le stazioni pelagiche si riferiscono a medie calcolate sulla colonna d'acqua.

3.2. Phytoplankton

In the samples collected for the determination of total phytoplankton biovolume in the pelagic zone of Lake Tovel (stations A and B) from 2002 to 2004 17 different dinoflagellate taxa were identified. However, only 3 taxa were quantitatively important and able to become dominant: *Baldinia anauniensis*, *Gymnodinium uberrimum* (Allman) Kofoid & Swezy and *Glenodinium sanguineum sensu* Dodge (Calliari *et al.* 2006). The other taxa were much less abundant and present only during limited periods of the year.

The littoral zone showed a similar situation, with16 dinoflagellate taxa identified (Tab. 1), but appeared to be richer in species than the pelagic zone, since all the 16 taxa were identified in the different littoral stations during the relatively short investigation period of summer 2004. The number of species per sampling site ranged between 8 to 13. Also in the littoral zone only 3 taxa were quantitatively important and became dominant in certain periods – *Baldinia anauniensis*, *Glenodinium sanguineum sensu* Dodge and *Gymnodinium uberrimum* –, while the other taxa reached only very low abundances (Tab. 1).

The present study focused on the three dominant taxa and on three common taxa that were relatively abundant almost all over the investigated period (Fig. 4).

Due to unclear taxonomical position of several of these taxa, we include here a photograph and a brief description of them, two of which are new records for the lake.

- *Glenodinium sanguineum sensu* Dodge (Figg. 4.4a-4.4b): 18-26 µm long, 10-21 µm wide, with many small round chloroplasts located beneath the cell surface. They may present one or, more frequently, many red small vesicles around the cell centre. Their thin theca is usually not perceptible under light microscope. When observed fixed in Lugol's solution they are generally easily recognisable because they fairly preserve their shape. They present a rather pointed, light orange coloured epicone, while the hypocone is rounded and darker brown.
- *Gymnodinium uberrimum* (Fig. 4.5): 30-70 µm long and 28-66 µm wide. It is the largest dinoflagellate of Lake Tovel. Chloroplast are olive-green and are radially arranged around the centre toward the cell surface, which remains hyaline. One single orange body of very variable size can be present in the cytoplasm. When preserved with Lugol's solution the cells loose their shape, rounding and shrinking. Preserved cells remain still recognizable through their size and colour, usually light brown with a darker ring or round spot around the centre of the cell.
- *Baldinia anauniensis* (Fig. 4.1 a,b): length 17-34 µm, width 12-30 µm. This dinoflagellate is commonly 20-24 µm long and only rarely reaches 32-35 µm length. The chloroplasts are yellow-greenish and arranged radially around the cell centre and a single orange body is always present. When preserved with Lugol's solution they completely loose their structure, shifting to a brownish and rounded aspect.
- *Katodinium* cf. *montanum* (Fig. 4.2): length 17-27 µm, width 14-23 µm. This heterotrophic dinoflagellate has no chloroplasts and the cytoplasm is hyaline and filled with numerous small cyanells. The rounded epicone is larger than the hypocone (approximately 2/3 and 1/3 of the total cell length, respectively). The antapex is rounded

Tab. 1 - Biovolume in mm^3 m^{-3} of the dinoflagellates found in the different sampling stations. P= species present in low amounts (<1 mm^3 m^{-3}).
Tab. 1 - Biovolume in mm^3 m^{-3} delle specie presenti nelle diverse stazioni di campionamento. P= specie presenti in bassa quantità (<1 mm^3 m^{-3}).

	Taxa	Sampling station								
		1	2	3	4	7	8	9	A	B
1	*Tovelia sanguinea* sp. inedit. (Moestrup)	P	P	P	P	P	P	P	?	P
2	*Amphidinium elenkinii af.* (Skorcov)	–	–	P	P	P	P	P	P	P
3	*Glenodinium sanguineum sensu* Dodge	13	102	35	25	22	9	1	30	181
4	*Glenodinium* sp.(Ehrenberg)	P	–	P	P	–	P	–	P	P
5	*Gymnodinium cnecoides* af. (Harris)	P	P	P	P	P	P	P	P	P
6	*Gyrodinium helveticum* (Penard)	–	P	–	–	P		P	P	–
7	*Gymnodinium uberrimum* (Allman) Kofoid & Swezy	63	79	183	234	323	56	57	119	592
8	*Peridinium umbonatum.* Stein	8	10	11	5	9	13	3	5	62
9	*P. willei* (Huitfeld-Kaas)	–	–	–	P	P	P	P	–	–
10	*P. cinctum* (Ehrenberg)	–	–	–	–	P	–	–	–	–
11	*P. aciculiferum* (Lemmermann)	–	–	–	P	–	P	–	–	–
12	*Baldinia anaumiensis* sp. inedit. (Hansen)	26	83	301	215	274	93	7	81	1122
13	*Katodinium* cf. *montanum* (Schiller)	3	2	2	7	4	3	4	–	5
14	*Peridiniopsis penardiforme* (Lindemann) Bourrelly	P	–	–	P	–	–	P	–	P
15	*P.* cf. *allorgei* (Lefèvre)	9	6	17	15	9	5	10	–	2
16	*P.* cf. *dinobryonis* (Woloszynska) Bourrelly	–	–	–	–	–	P	–	–	–

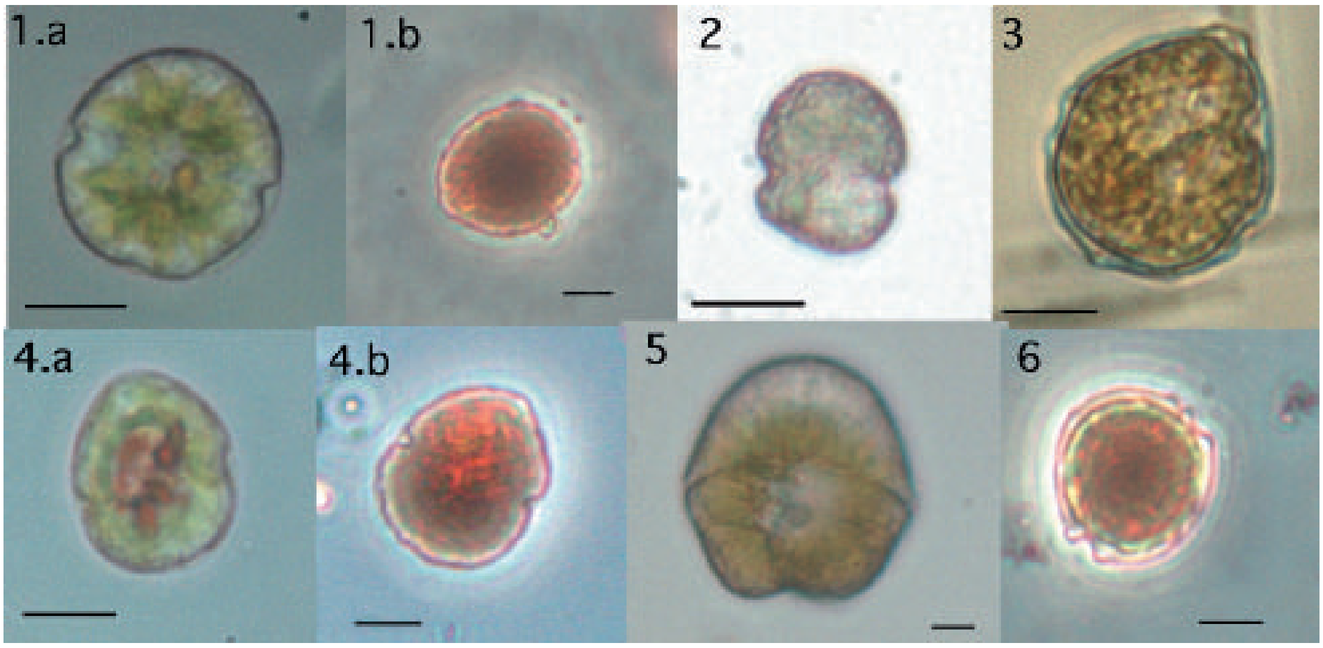

Fig. 4 - Dinoflagellate taxa considered in the present study: 1) *Baldinia anauniensis* gen. inedit. sp. inedit. (Hansen *et al. in prep.*): a) alive, b) fixed; 2) *Katodinium* cf. *montanum* (Schiller); 3) *Peridinium umbonatum* (Wolos.) Popovsky e Pfieser; 4) *Glenodinium sanguineum sensu* Dodge (1987): a) alive, b) fixed; 5) *Gymnodinium uberrimum* (Allman) Kofoid & Swezy; 6) *Peridinium* cf. *allorgei*. Bars = 10 µm.
Fig. 4 - Taxa dinoflagellati considerati nel presente lavoro: 1) Baldinia anauniensis *gen. inedit. sp. inedit.* (*Hansen* et al. in prep.): *a) in vivo, b) fissato;* 2) Katodinium *cf.* montanum *(Schiller); 3)* Peridinium umbonatum *(Wolos.) Popovsky e Pfieser; 4)* Glenodinium sanguineum sensu *Dodge (1987): a) in vivo, b) fissato; 5)* Gymnodinium uberrimum *(Allman) Kofoid e Swezy; 6)* Peridinium *cf.* allorgei. *Barre = 10 µm.*

and somewhat excavated. Together with the following taxa, it has been found in the lake for the first time in September 2004.

- *Peridinium* cf. *allorgei* (Fig. 4.6): length 17-24 µm, width 14-23 µm. Cells are somewhat wider than long and clearly flattened dorsiventrally. The hypocone is rounded, while the epicone is rounded, often even slightly pointed. When cysts formation starts inside the thecae, the hypothecae enlarges appreciably. Since we could observe only fixed samples the presence of chloroplasts remains not clear.
- *Peridinium umbonatum* (Fig. 4.3): length 20-36 µm, width 17-30 µm. Thecae is egg shaped with an apical pore, while the hypocone normally has one thick spine. This taxon is present all year long, although it never reach high abundances. It showed higher densities in summer, while larger cells were found in winter.

Temporal variations of the total dinoflagellates biovolume of the littoral and pelagic sampling stations are plotted in figure 5. In general total biovolume was higher in site B than in the other sampling stations during the entire period, and in littoral sites compared to station A.

Some species were found to be heterogeneously distributed among littoral and pelagic zone. Abundance of *Glenodinium sanguineum sensu* Dodge was clearly higher in station 2, where its mean relative abundance over the whole period was 39%, while in the rest of the sites it ranged from 4% to ca. 10%. Autumnal cysts of *Baldinia anauniensis* were found only in the littoral zone, especially in station 8. In addition, *Katodinium* cf. *montanum* and *Peridinium* cf. *allorgei* were absent from station A and *Peridinium* cf. *allorgei* was much more abundant on the littoral than in station B.

Baldinia anauniensis and *Gymnodinium uberrimum* were the two species reaching the highest cumulated biovolume during the studied period (Fig. 6) in all stations but station 2, where *Glenodinium sanguineum sensu* Dodge was the most abundant dinoflagellate. Dominant taxa were coincident in the pelagic and littoral zone: in general total dinoflagellate biovolume was low (ca. 350 mm^3 m^{-3}) at the beginning of the study period, with *Glenodinium sanguineum sensu* Dodge as dominant species. This taxon was followed by *Gymnodinium uberrimum* at the end of July in the littoral stations, while in the pelagic zone this change occurred in early August. In the littoral zone, the dominance of *Gymnodinium uberrimum* started earlier and lasted longer than in points A and B (Fig. 2). Here, after a initial decreasing stage, the total dinoflagellates biovolume increased up to 679 mm^3 m^{-3}. *Baldinia anauniensis* was the dominant taxon in the littoral zone, where it was principally responsible for the highest total dinoflagellate biovolume observed during summer 2004 (1776 mm^3 m^{-3} on September the 15th, Fig. 5). *Gymnodinium uberrimum* and *Baldinia anauniensis*, display similar preferences respect to TP, $(NO_3 + NH_3)$-N and temperature, as showed by the Spearman correlation coefficient reported in table 2 (see below).

On September the 29th we found both the highest dinoflagellate species richness in all the sampling stations, although the majority of the taxa were less abundant than in summer, and the presence of two taxa not encountered in the previous samples: *Katodinium* cf. *montanum* and *Peridinium* cf. *allorgei*. In this date no taxon was clearly dominant, although the situation was different in the different sampling stations.

3.3. *Correlation coefficients & ANOVA*

The correlation between total dinoflagellates biovolume and water temperature (Tab. 2) confirms the trend of increasing biovolume with decreasing tem-

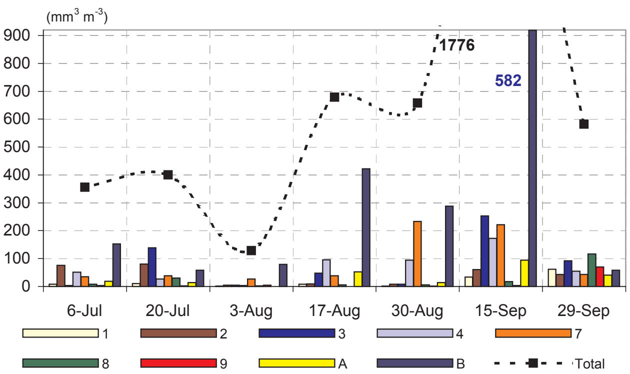

Fig. 5 - Biovolume of dinoflagellates by station and total.

Fig. 5 - Biovolume dei dinoflagellati per punto e totale.

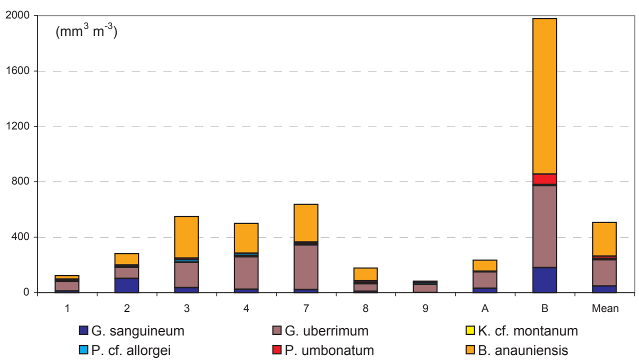

Fig. 6 - Cumulated biovolume of dinoflagellates in the different sampling stations.

Fig. 6 - Biovolume cumulato dei dinoflagellati nelle diverse stazioni di campionamento.

Tab. 2 - Spearman correlation matrix; n.s.= p-value not significant.
Tab. 2 - Matrice di correlazione di Spearman; n.s.= valore di p non significativo.

	Total biovolume	*G. sanguineum sensu* Dodge	*G. uberrimum*	*B. anauniensis*	*Peridinium umbonatum*	*K.* cf. *montanum*	*P.* cf. *allorgei*
Temperature	-0.347	0.477	-0.184	-0.335	-0.639	0.217	-0.526
	< 0.01	< 0.001	n. s.	< 0.01	< 0.001	n. s.	< 0.001
$(NO_3 + NH_3)$-N	-0.326	0.474	-0.309	-0.326	-0.713	-0.334	-0.609
	< 0.05	< 0.01	< 0.05	< 0.05	< 0.001	< 0.05	< 0.001
TP	0.562	0.285	0.360	0.403	0.195	0.300	0.050
	< 0.001	n. s.	< 0.05	< 0.01	n. s.	< 0.05	n. s.
Total biovolume		0.255	0.679	0.837	0.500	0.158	0.279
		< 0.05	< 0.001	< 0.001	< 0.001	n. s.	< 0.05
G. sanguineum sensu Dodge			-0.090	0.171	-0.272	0.191	-0.401
			n. s.	n. s.	n. s.	n. s.	< 0.001
G. uberrimum				0.566	0.274	0.024	0.289
				< 0.001	< 0.05	n. s.	< 0.05
B. anauniensis					0.520	-0.064	0.095
					< 0.001	n. s.	n. s.
P. umbonatum						0.024	0.597
						n. s.	< 0.001

perature shown in figure 2. This relationship is clearer in the littoral than in the pelagic zone. Most of the species show a weak negative, but still significant (r < 0.5), correlation with temperature (Tab. 2). The sole exceptions are *Peridinium umbonatum* and *P.* cf. *allorgei* (Tab. 2).

In general, correlation coefficients between dinoflagellate abundance and (NO_3+NH_3)-N and water temperature were negative (Tab. 2). The strongest negative correlation was obtained for *Peridinium umbonatum* and *Peridinium* cf. *allorgei* (Lefevre), while *Glenodinium sanguineum sensu* Dodge represents the sole exception, showing significant positive correlation with both variables. Correlations between TP and dinoflagellates density and biovolume is always positive, although low. *Baldinia anauniensis* showed the strongest correlation.

Some clear inter-specific relationships could be detected, in particular the negative one between *Peridinium* cf. *allorgei* and *Glenodinium sanguineum sensu* Dodge (r= -0.401, p<0.001, Tab. 2), and the positive between *Peridinium* cf. *allorgei* and *P. umbonatum* (r= 0.597, p<0.001) and between *Baldinia anauniensis* and *Peridinium umbonatum* (r= 0.520, p<0.001) and *G. uberrimum* (r= 0.566, p<0.001), respectively.

The comparison of biovolume values of the most abundant dinoflagellate taxa (*B. anauniensis*) in the different station by ANOVA indicated points 1 and 9 as different from point B (Tab. 3). ANOVA tests performed on TP concentrations determined at the different stations, showed station A as significantly

Tab. 3 - Results of the analysis of variance (ANOVA) aimed at the comparison of biovolume of *Baldinia anauniensis* and TP concentration of the different sampling stations. Only stations where test results were significant (p<0.05) are showed.
Tab. 3 - Risultati dell'analisi di varianza (ANOVA) effettuata per il confronto del biovolume di Baldinia anauniensis *e delle concentrazioni di fosforo totale nelle diverse stazioni di campionamento. Sono mostrate solo le stazioni per le quali il test ha dato risultati significativi* (p<0,05).

Points	Biovolume of *Baldinia anauniensis*	TP
A	–	B, 2, 3, 4, 7, 8
B	1, 9	A
1	B	–
2	–	A
3	–	A
4	–	A
7	–	A
8	–	A
9	B	–

Tab. 4 - Results of the analysis of variance (ANOVA) performed to evaluate the difference of environmental variables and the biovolume of the main dinoflagellates at the different sampling dates. Case letter indicates the dates which gave significant ($p<0.05$) test results.

Tab. 4 - Risultati dell'analisi di varianza (ANOVA) effettuata per determinare la significatività delle differenze dei diversi parametri nelle diverse date di campionamento. Le lettere minuscole indicano le date che hanno dati risultati del test significativi ($p<0,05$).

	06/07 (a)	20/07 (b)	03/08 (c)	17/08 (d)	30/08 (e)	15/09 (f)	29/09 (g)
Temperature	e, f, g	e, f, g	d, e, f, g	f, g	a, b, c, g	a, b, c, d, g	a, b, c, d
(NO_3+NH_4)-N	g	g	–	g	–	–	a, b, d
TP	–	–	d	c	–	–	–
Biovol. *G. sanguineum sensu* Dodge	e, g	e, g	–	–	a, b	–	a, b
Biovol. *Baldinia anauniensis*	–	–	f	–	–	c	–
Biovol. *Peridinium umbonatum*	–	f, g	f, g	f, g	–	b, c, d	b, c, d

different from points B, 2, 3, 4, 7 and 8. On the other hand, ANOVA tests performed on values of the environmental parameters considered and the biovolume of the 3 most abundant dinoflagellates determined during the entire investigation period indicate significant differences between early and late summer sampling dates (Tab. 4). This difference is particularly evident when considering water temperature, nitrogen concentration and abundance of *Glenodinium sanguineum sensu* Dodge, while TP concentrations indicate a significant difference only between early and mid August samplings (indicated by letters c and d in Tab. 4). Only the samples collected in early August and mid September showed significant difference in the abundances of *Baldinia anauniensis*.

4. DISCUSSION

Concentrations of TP and of $(NO_3 + NH_3)$-N measured during summer 2004 confirm the oligotrophic status of Lake Tovel. Algal growth is surely limited by phosphorous, as it has been also experimentally demonstrated by Cantonati *et al.* (2003). $(NO_3 + NH_3)$-N remains available in excess for dinoflagellates respect to phosphorous also toward late summer-autumn, when it reached its lowest concentrations. Nitrogen decrease seems to be related to both its reduced income to the lake in relation to the reduced water inflow in summer and to the progressive algal uptake (Corradini & Boscaini 2006). The observed difference between seasonal variations of nutrient and dinoflagellate biovolume may be due to specific ecological and physiological characteristics of the different taxa. Station A presents more stable conditions and changes related to hydrological dynamics seem to be less important, thus allowing considering the algal development as more affected by nutrient level. On the contrary, the effect of nutrient availability on phytoplankton may be distorted by water dynamics in the Red Bay (both in the littoral zone and in station B).

It is remarkable that the only dinoflagellates taxon that correlates strongly with TP is *B. anauniensis*, one of the most abundant phytoplankton species of Lake Tovel, which formed blooms during enclosure experiments under P-enrichmed conditions (Cantonati *et al.* 2003). However, the relation observed during the present study is due to very small variations of TP.

Peridinium umbonatum was common at the end of summer, while *P.* cf. *allorgei* and *Katodinium* cf. *montanum* in early autumn, when temperature, light intensity, $(NO_3 + NH_3)$-N concentrations and water renewal of the lake had all decreased. The appearance of the heterotrophic *K.* cf. *montanum* in late summer suggests the start of an enhanced "heterotrophic phase" of the lake toward the end of the vegetation period. On the other hand, *Glenodnium sanguineum sensu* Dodge is present just at the beginning of the vegetative period and mainly in sites along the Red Bay, corresponding to the place and period when water renewal is most dynamic.

The different stations were heterogeneous in terms of dinoflagellates biovolume and species distribution. In fact, we found higher biovolume at the stations 3, 4, 7 and B, which are all located in the Red Bay. Dinoflagellates probably find a more favourable environment for growth there (Tolotti *et al.* 2006), maybe in relation to nutrient availability, to the hydrological regime of the Red Bay or to the more suitable environment for cyst germination. Actually, all of these sites are located very close to one or more perilacual submerged springs on shallow sites, while high solar radiation and O_2 concentrations have been indicated as conditions that favours cyst germination (Rengefors & Anderson 1998; Rengefors *et al.* 2004). Station 2 is different from the others in being the only one where *Glenodinium sanguineum sensu* Dodge reached the highest cumulated biovolume.

Sampling station 9 showed the lowest dinoflagellate and total phytoplankton biovolume and is the sole littoral station not having a spring in it's surroundings and remaining shaded for a long part of the day, due to its position beneath a steep slope on the eastern lake shore. On the other hand, dinoflagellate abundance and composition in station 8, located at the NW extremity of the lake, were very similar to those of the littoral sites of the Red Bay. In fact, this station is on a shallow area of gentle slope and near a perilacual spring, thus resembling the Red Bay. These conditions seem to favour the setting of a local micro habitat, which appears to be suitable for dinoflagellates development and differentiates this site from the other littoral sites outside the Red Bay (stations 1 and 9). This hypothesis is in accordance with the description of the distribution of the water reddening on the lake surface provided by Largaiolli (1907, pag. 28 tab. XIV), who indicated the littoral zone corresponding to our station 8 as the only site outside Red Bay where that phenomenon occurred, even if in a weaker form.

Stations 9, 1 and 8, in this order, showed the lowest dinoflagellate biovolume values, which were comparable or higher to those of the other sampling points only at the end of September, when *Peridinium* cf. *allorgei* and *Katodinium* cf. *montanum* appeared and the lake entered a stage of reduced primary productivity.

Temperature seems to be an important factor determining changes in the dinoflagellate community and might drive the succession *Glenodinium sanguineum sensu* Dodge – *Gymnodinium uberrimum* – *Baldinia anauniensis*. During the SALTO project *Glenodinium sanguineum sensu* Dodge was generally found in winter or in cold water layers in early summer, while *B. anauniensis* was abundant in summer, mainly above 13 °C (Flaim *et al.* 2004, 2006; Calliari *et al*. 2006). However, the interpretation of temperature effects is hindered by the presence of an important thermal gradient between surface and bottom layers of the Red Bay, which at the same time depends on amount of water inflow toward the Red Bay.

5. CONCLUSIONS

Differences between stations confirm once again the individual character of the Red Bay in comparison to the Main Basins of Lake Tovel, although the littoral zone is not homogeneous. Station 8, due to its low depth and slope and presence of perilacual spring, is similar to the Red Bay. Stations 1 and 9 present lower dinoflagellate biovolumes and resemble the pelagic station A of the main basin. In addition, sites 1 and 9 reach higher abundances only after the changes in species composition occurring in early autumn. Within the Red Bay, sites 3, 4 and 7 are similar to each other and different from station 2 and the pelagic station B.

Differences in TP and ($NO_3 + NH_3$)-N level should be taken with caution, since TP concentrations changed little and remained always close to the detection limit, while nitrogen variations seems to depend on a combination of both water regime and algal uptake.

Seasonal variations in water temperature might represent one of the principal environmental variables driving the observed distribution of the major dinoflagellates taxa and the succession *Glenodinium sanguineum sensu* Dodge - *Gymnodinium uberrimum* - *Baldinia anauniensis* - *Katodinium* cf. *montanum*, *Peridinium* cf. *allorgei*, *P. umbonatum*. Changes in the water dynamics may also be important for regulating this succession.

Spatial distribution of littoral dinoflagellates is likely related also to differences in nutrient availability along the lake shore. However phosphorus and nitrogen temporal variation observed during the present study were too small to allow conclusions on their role in regulating algal growth.

A detailed investigation on conditions promoting cyst germination of the dinoflagellate taxa involved in this study and their environmental preferences would be necessary for a further clarification of dinoflagellate dynamics in Lake Tovel. Ecological interaction, e.g. the relation with filter feeding zooplankton, should be also taken in consideration.

ACKNOWLEDGEMENTS

The presented study has been carried out within the SALTO/BEST (Studio sul mancato Arrossamento del Lago di TOvel/Blooms & Environment Science for Tovel, 2001-2004), funded by the Autonomous Province of Trento, Italy. The authors are grateful to Simone Degasperi, Federica Fiamingo and to the technical staff of the Department for Valorisation of Natural Resources (VRN) of the Istituto Agrario di San Michele all'Adige for the support during the field work.

REFERENCES

APHA, AWWA & WEF, 1998 - *Standard methods for the examination of water and wastewater*. 19th ed. Washington D.C.

Baldi E., 1938 - Relazione preliminare sulle ricerche al lago di Tovel. *Studi Trent. Sci. Nat.*, 19: 247-339.

Baldi E., 1941 - Ricerche idrobiologiche sul Lago di Tovel. *Mem. Museo St. Nat. Venezia Trid.*, 9/6: 1-300.

Borsato A., Corradini F. & Ferretti P., 2006 - Idrochimica e monitoraggio idrogeologico degli afflussi e deflussi del Lago di Tovel. *Studi Trent. Sc. Nat., Acta Biol.*, 81 (2004), Suppl. 2: 241-246.

Calliari D., Corradini F. & Flaim G., 2006 - Dinoflagellate diversity in Lake Tovel. *Studi Trent. Sci. Nat., Acta Biol.*, 81 (2004), Suppl. 2: 351-357.

Cantonati M., Tardio M., Tolotti M. & Corradini F., 2003 - Blooms of the dinoflagellate *Glenodinium sanguineum* obtained during enclosure experiments in Lake Tovel (N. Italy). *J. Limnol.*, 62/1: 79-87.

Corradini F. & Boscaini A., 2006 - Fisica e chimica delle acque del Lago di Tovel (Trentino, Alpi centrali). *Studi Trent. Sci. Nat., Acta Biol.*, 81 (2004), Suppl. 2: 307-326.

Corradini F., Flaim G. & Pinamonti V., 2001 - Five years of limnological observations on Lake Tovel (1995-1999): some considerations and comparisons with past data. *Atti As. ital. Oceanol. Limnol.*, 14: 209-218.

Dodge J.D., Mariani P., Paganelli A. & Trevisan R., 1987 - Fine structure of the red-bloom dinoflagellate *Glenodinium sanguineum*, from Lake Tovel (N. Italy). *Arch. Hydrobiol.*, 8/2 (Algological Studies 47): 125-138.

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

Flaim G., Hansen G., Moestrup Ø., Corradini F. & Borghi B., 2004 - Reinterpretation of the dinoflagellate '*Glenodinium sanguineum*' in the reddening of Lake Tovel, Italian Alps. *Phycologia*, 43: 737-743.

Flaim G., Moestrup Ø., Hansen G. & D'Andrea M., 2006 - Da *Glenodinium* a *Tovellia. Studi Trent. Sci. Nat., Acta Biol.*, 81 (2004), Suppl. 2: 447-457.

Hoehn E., Ketelaars H.A.M. & Ewig B., 1998 - *ATT Technische Informationen N° 7. Erfassung und Bewertung von Planktonorganismen*. R. Oldenbourg Verlag, Munich: 151 pp.

ISMA, 1998 - *Caratteristiche limnologiche dei lahi del Trentino – Rapporto 1997.* Istituto Agrario di S. Michele a/Adige: 140 pp.

Kremp A. & Anderson D.M., 2000 - Factors regulating germination of resting cysts of the spring bloom dinoflagellate *Scrippsiella hangoei* from the northern Baltic Sea. *J. Plankton Res.*, 22: 1311-1327.

Largaiolli V., 1907 - La varietà oculata del *Glenodinium pluvisculus* (Ehr.) Stein. *Nuova Notarisia*, XVIII: 169-173.

Largaiolli V., 1930 - La colorazione rossa intermittente del Lago di Tovel. *XXV Annuario SAT*, 25: 1-6.

Marchesoni V., 1959 - La Val di Tovel e il "Lago Rosso". *Natura Alpina*, 10: 37-76.

Moestrup Ø., Hansen G., Daugjberg N., Flaim G. & D'Andrea M., (2006) - On *Tovellia sanguinea* sp. nov., the dinoflagellate species responsible for the reddening of Lake Tovel, N. Italy. *European J. of Phycology*, (in press).

Paganelli A., 1992 - Lake Tovel (Trentino): limnological and hydrobiological aspects. *Mem. Ist. Ital. Idrobiol.,* 50: 225-257.

Rengefors K. & Anderson D.M., 1998 - Environmental and endogenous regulation of cyst germination in two freshwater dinoflagellates. *J. Phycol.*, 34: 568-577.

Rengefors K., Gustafsson S. & Ståhl-Delbanco A., 2004 - Factors regulating the recruitment of cyanobacterial and eukaryotic phytoplankton from littoral and profoundal sediments. *Aquat. Microb. Ecol.*, 36: 213-226.

Rott E., 1981 - Some results from phytoplankton counting intercalibrations. *Schweiz. Z. Hydrol.*, 43: 34-62.

Tolotti M., Calliari D. & Corradini F., 2006 - Variabilità interannuale del fitoplancton del Lago di Tovel (Trentino, Italia). *Studi Trent. Sci. Nat., Acta Biol.*, 81 (2004), Suppl. 2: 327-340.

Uthermöl H., 1958 - Zur Vervollkommung der quantitativen Phytoplankton Methodik. *Mitt. Internat. Verein. Limnol.*, 9: 1-39.