Dinophyceae Fluctuations in Two Alpine Lakes of Contrasting Size During a 10-Year Fortnightly Survey

Trevisan, R.¹, R. Pertile², V. Bronamonte¹, F. B. Dazzo³, and A. Squartini⁴*

¹Dipartimento di Biologia, Università di Padova, Viale G. Colombo 3, 35129, Padova, Italy
²Epidemiological Observatory of the Provincial Centre for Health Services, Viale Verona, 38100, Trento, Italy
³Department of Microbiology and Molecular Genetics, Michigan State University, East Lansing, MI 48824, USA
⁴Dipartimento di Biotecnologie Agrarie, Università di Padova, Viale dell’Università 16, 35020 Legnaro, Padova, Italy

Received: October 4, 2011 / Revised: January 22, 2012 / Accepted: February 6, 2012

Colbricon Superiore and Inferiore are two small adjacent high-mountain lakes located in the Paneveggio Natural Park (Italy) that offer the rare opportunity to study two iso-ecologic water environments differing only by area and volume in a ratio of 2:1 and 3:1, respectively. We took advantage of this setting to investigate phytoplankton dynamics, compare variability and productivity differences between the two basins, and assess size-dependent issues. The phytoplankton group of the Dinophyceae was chosen as the indicator organisms of ecological perturbation owing to their high sensitivity to environmental variations, as well as their acknowledged nature of versatile proxy to report global climatic changes. The study was conducted for over 10 years with fortnightly samplings. Results indicated that (a) the Dinophyceae communities in the smaller lake were significantly more resistant to changes exerted by the fluctuation of lakewater transparency and pH; and (b) the smaller lake sustained a consistently higher production with an average Dinophyceae density 1.73 fold higher than that of the larger lake. The coefficients of variation show that the chemical parameters in the smaller lake display higher time-related fluctuation while being spatially homogeneous and that such conditions correlate with a higher stability of the Dinophyceae assemblage. The use of this setting is also proposed as a model to test relationships between ecosystem production and physical stability.

Keywords: High-mountain lakes, Dinophyceae, environmental variables, microbial ecology, Colbricon Lakes, Paneveggio-Pale di S. Martino Natural Park

Lakes occurring at high mountain altitudes are particularly interesting habitats for ecological studies [8, 24] since they represent small, fragile, highly individual ecosystems, like islands of biodiversity surrounded by a sea of land [13]. In Italy, the majority of natural lakes smaller than 0.2 km² are located in the Alps, and most originate by glacial modeling, causing the formation of either basin erosion or of a morenic barrier. The so-called “cirque lakes” are most frequent and often grouped along an altimetric sequence [2]. Lakes at higher altitudes are more recent, fed by melting snow and rainfall, and have relatively shallow depths and often fluctuating water level [27].

Harsh climatic conditions characteristically occur in remote mountain lakes. They experience low temperatures, short ice-free periods, and variations in precipitation (snow) that are prone to cause pronounced seasonal variations in water chemistry [23, 30] and changes in biotic assemblages [15, 20]. Such ecosystems generally do not exhibit obvious anthropic disturbances such as single-point pollution sources or changes of land use in the drainage area. Owing to the geological features of the catchment areas in the mountain region, as is the case of the acid bedrock Lagorai range, many high mountain lakes are poorly buffered in pH and several display acidification phenomena [4]. For these reasons, they are considered simple and labile ecosystems that react promptly to environmental changes and stresses. Because of this sensitivity, high mountain lakes can function as early warning systems for environmental changes related to climate and other factors, thus providing information that goes beyond the interest in their intrinsic ecosystem structure [30]. They offer ideal systems to monitor the effect of global climate changes through the analyses of their phytoplankton dynamics [40, 41]. Analyses of the biotic components and their fluctuations can therefore provide insights on global
phenomena and facilitate their predictions for either management or conservation purposes.

Knowledge of algal communities in high mountain lakes indicates that, rather than supporting endemic or specialized taxa, these environments display a rarefaction on the general checklist found in larger lakes at lower altitudes [9, 29]. In addition, the process of selection of the species able to persist in these alpine environments is determined by their ability to survive the alternating phases of short vegetative periods and ice-covered stages, with adaptation to opposite light regimes, from the intense summer radiation to the weak ice-filtered shady winter situation. Phytoplanktonic species in these situations need also to endure low nutrient availability and fluctuating water regimes due to atmospheric precipitations and freezing/thawing cycles [39]. Traits of adaptation include their small size dimension [47] and active dispersal capabilities mediated by their flagellated motility [32, 36].

Low phytoplankton biovolumes generally occur in these lakes with the possibility of summer or fall seasonal peaks [9, 22, 29]. Peaking can also be due to nutrient increase or interactions with other members of the community. Studies have also been devoted to analyze the effects of global climate change on these communities [6, 11, 18].

Among freshwater eukaryotic microorganisms, dinophyceae are particularly suitable proxies for climate changes, allowing to extrapolate universally valid patterns [45]. Their features of usefulness are abundance, autonomous movement capabilities, adaptation to oligotrophy, possibility of cyst formation, and permanence in sediments (providing records for analyses of past events). This group of microbial eukaryotic algae can be abundant both in marine and freshwater environments. Over 2,000 species have been described, and only half of these are photosynthetic [46]. The group includes autotrophs, mixotrophs, and fully heterotrophic phototrophs. They show remarkable biochemical diversity, varying in the composition of photosynthetic pigments and ability to produce toxins. Many of the photosynthetic ones are mixotrophs, and the heterotrophs can feed upon bacterioplankton using a wide variety of mechanisms [16, 42]. Among the freshwater planktonic species, few dinoflagellates have been described after Bourrelly’s monograph [5] reporting 220 taxa. Moreover, the extant ones are defined as “morphospecies,” in the classical sense. The suitable species concept to be applied to dinoflagellates or other harmful species has been discussed [25]. Freshwater dinoflagellates efficiently migrate vertically along the water column, usually displaying chemotaxis downwards at night to pursue nutrients and phototaxis upwards to the photic zone at daytime for photosynthetic purposes [43]. Different ecological studies on phytoplankton phyla in high mountain lakes have found common trends and shaping factors [9, 22]. Hansen and Flaim [19] surveyed the occurrence of dinoflagellates in 27 lakes of the Trentino region in Italy, and reported the presence of 34 taxa.

In the present study, we took advantage of the rare opportunity offered by the two adjacent lakes of Colbricon as a consequence of their geomorphological situation. Located next to each other, the smaller lake (Colbricon Inferiore, C.I.) has one-third the volume of the larger lake (Colbricon Superiore, C.S.), allowing an interesting configuration to investigate size-related effects in waterbodies within the same landscape and under equal geochemical influxes. Such availability of two lakes differing by size and depth has been envisaged as a particularly useful setting to compare stability and productivity in relation to possible differences in homogeneity of their physical and chemical profiles. The study presented here extends over a particularly wide temporal window (10 consecutive years), throughout which the lakes were sampled with consistent intensity (about fortnightly in the ice-free periods), providing an uncommonly large dataset compared with most standards of phytoplankton studies.

**Materials and Methods**

The Site

We analyzed Colbricon Superiore (C.S., 1,922 m a.s.l.) and Colbricon Inferiore (C.I., 1,910 m a.s.l.), which are two alpine lakes located in the Lagorai mountain range within the Avisio basin, located in the Paneveggio-Pale di S. Martino Natural Park (Trento, Italy) (maps in Fig. 1). Lake C.S. features a surface nearly twice the area of Lake C.I. and a volume about three times larger. The area of Lake C.S. is 0.024 km$^2$ and its volume is 0.13 km$^3$, whereas the same values for Lake C.I. are 0.013 km$^2$ and 0.05 km$^3$, respectively. Their close proximity (the lakes are separated by less than 50 m) and the consequent sharing of the same water catchment basin constitute a set of features allowing to perform size-dependent comparisons independent of other environmental variables. The lakes lie on peat soil overlaying a bedrock substratum of quartziferous porphyry, and are surrounded by a sphennum and sedge vegetation [14]. As glacial cirque lakes, they are small and relatively shallow, with maximum depths of 12 m and 8 m and average depths of 5.4 m and 3.8 m, respectively. They are dimictic, undergoing complete mixing in spring and autumn, and their morphological and hydrological features have been previously described [49].

Field Methods and Laboratory Analyses

Both lakes were monitored and sampled over a decade. As these lakes generally freeze from November to May, the sampling scheme represented the 10 ice-free periods between years 1998 and 2007, corresponding to a sampling interval of every 2 or 3 weeks. The analysis schedule involved on average 7 sampling dates each year, yielding a total of 69 samplings per lake. Hydrometric level, air and water temperature, transparency, pH, and conductivity were measured in situ, and chemical analyses of water samples (depth-integrated across the water column) were performed at the Institute for the Study of Ecosystems CNR-ISE of Verbania-Pallanza according to standard methods [44]. Water level was measured by a fixed
DINOPHYCEAE AND ENVIRONMENTAL VARIABILITY IN ALPINE LAKES

The mean water temperatures and temperature ranges during the whole study period were closely similar in the...
two lakes (Table 1). However, during the same 10 year period, the Relative Water Column Stratification Stability index (RWCS) [31] had an average value of 50.34 for Lake C.S. and a significantly lower value of 36.55 for Lake C.I. Both lakes had average pH values that were close to neutrality (7.3–7.4) and low mean conductivity (~45 µS/cm), consistent with a limited salinity condition. The mean ratio of total nitrogen (TN) to total phosphorus concentrations was 36.6 in the C.S. and 33.5 in the C.I. Since this ratio exceeds a value of 10, total phosphorus is likely to be the limiting growth factor for phytoplankton [10]. The concentration of reactive phosphorus was the only parameter that had a noteworthy difference between the two lakes. The amounts recorded were 2 µg/l (C.S.) vs. 5 µg/l (C.I.).

Mean reactive soluble silica concentrations were also slightly higher in the smaller lake. During the study period, both lakes would be categorized as mesotrophic based on their transparency values and total phosphorus concentrations [16, 26].

The microscopical examinations of the 138 integrated samples collected in both Colbricon Lakes during the 10 year study (quantitative analysis) allowed species identification (Table 2). Five taxa of Dinophyceae were found, including Peridinium goslawiense Lemmermann, Peridinium goslawiense Woloszynska, Peridinium sp. Ehrenberg, Gymnodinium sp. Stein, and Ceratium hirundinella (O.F. Müller) Dujardin. In Lake C.S., the 10-year average cell density of the Dinophyceae was 23.7 cells/ml. In the lower Lake C.I., their cell density was 41.0 cells/ml. Regarding the corresponding cumulative biomass values (estimated by multiplying the cell density of each taxon by its unit volume reported in the literature), the mean was 302.8 mg/m³ in Lake C.S. and 492.4 mg/m³ in Lake C.I.

Fig. 2 shows the mean cell densities of the five different taxonomical entities of Dinophyceae found in these lakes. The dominant density of the Peridiniaceae is responsible for the nearly 2-fold higher Dinophyceae abundance in the lower lake as compared with the upper one. On the contrary, Gymnodinium and Ceratium genera are approximately equally abundant in both lakes.

The differences in relative distribution of abundance among these dinoflagellate species were evaluated based on their relative proportions of individuals present and their cumulative biomass. The ordinal Brillouin index was chosen for comparisons of their diversity and evenness because of its low sensitivity to variation in sample size, sensitivity to abundance of rare species, and usefulness when non-random collections are being estimated. The percentage dissimilarity, and Bray–Curtis and Chord distance coefficients all indicated that the difference in distributions of abundance among these 5 dinoflagellate species within the 2 lakes was greater when based on relative proportions of their cumulative biomass rather than their individual counts (Table 3).
Fig. 3 shows the date-by-date abundance of the Dinophyceae biomass throughout the whole 10-year study. Large fluctuations occurred and, with the exception of some seasonal occurrences, the lower lake supported a higher biomass of Dinophyceae. The biomass of Dinophyceae (mg/m) was higher in the smaller C.I. lake than in the larger C.S. lake in 50 of the 69 samples.

In order to test for correlations between chemical or physical parameters and biological counts, the data distribution was first verified using the Poisson model. This type of analysis was chosen because the dependent variables were not normally distributed and the distribution was right-skewed with one tail on the right having the following skew values: density C.S. and density C.I.: skew = 1.72; biomass C.S.: skew = 1.57; biomass C.I.: skew = 1.45. A multivariate Poisson regression analysis was accordingly run and highlighted some significant instances. The interpretation of Poisson regression was presented in terms of incidence rate ratios (IRR). For each continuous variable, the estimated rate ratio for the dependent variable is expressed for a one unit increase in the independent one, with the other variables being held constant in the model.

As Table 4 shows, the most noticeable feature is a negative correlation with water transparency. This occurred in both lakes and was more severe in the superior one.

### Table 4. Poisson regression analysis using as outcome variable density and biomass of the Dinophyceae in the Colbricon Superiore and Inferiore lakes.

<table>
<thead>
<tr>
<th>Covariates</th>
<th>Lake Colbricon Superiore Density</th>
<th></th>
<th>Lake Colbricon Inferiore Density</th>
<th></th>
<th>Lake Colbricon Superiore Biomass</th>
<th></th>
<th>Lake Colbricon Inferiore Biomass</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean water temperature</td>
<td>1.08 &lt; 0.0001 104–112</td>
<td>1.06 &lt; 0.0001 1.05–1.07</td>
<td>0.98 0.484 0.93–1.04</td>
<td>0.97 &lt; 0.0001 0.95–0.98</td>
<td>0.63 &lt; 0.0001 0.83–0.90</td>
<td>0.84 &lt; 0.0001 0.83–0.85</td>
<td>0.98 0.99–0.99</td>
<td>0.99 &lt; 0.0001 0.99–0.99</td>
</tr>
<tr>
<td>pH</td>
<td>1.13 &lt; 0.0001 1.07–1.19</td>
<td>1.14 &lt; 0.0001 1.13–1.16</td>
<td>1.00 0.329 0.96–1.05</td>
<td>1.00 0.664 0.98–1.01</td>
<td>1.00 0.099 0.98–1.01</td>
<td>1.00 0.099 0.98–1.01</td>
<td>0.99 0.99–0.99</td>
<td>0.99 0.99–0.99</td>
</tr>
<tr>
<td>Conductivity</td>
<td>0.94 &lt; 0.0001 0.93–0.95</td>
<td>0.93 &lt; 0.0001 0.93–0.94</td>
<td>0.99 &lt; 0.0001 0.99–0.99</td>
<td>0.99 &lt; 0.0001 0.99–0.99</td>
<td>0.99 &lt; 0.0001 0.99–0.99</td>
<td>0.99 &lt; 0.0001 0.99–0.99</td>
<td>0.99 0.99–0.99</td>
<td>0.99 0.99–0.99</td>
</tr>
<tr>
<td>Transparency</td>
<td>0.74 &lt; 0.0001 0.71–0.77</td>
<td>0.76 &lt; 0.0001 0.75–0.76</td>
<td>0.99 &lt; 0.0001 0.99–0.99</td>
<td>0.99 &lt; 0.0001 0.99–0.99</td>
<td>0.99 &lt; 0.0001 0.99–0.99</td>
<td>0.99 &lt; 0.0001 0.99–0.99</td>
<td>0.99 0.99–0.99</td>
<td>0.99 0.99–0.99</td>
</tr>
<tr>
<td>Water level</td>
<td>1.01 0.0001 1.00–1.01</td>
<td>1.01 &lt; 0.0001 1.01–1.01</td>
<td>0.98 0.0001 1.00–1.00</td>
<td>0.98 0.0001 1.00–1.00</td>
<td>0.98 0.0001 1.00–1.00</td>
<td>0.98 0.0001 1.00–1.00</td>
<td>0.98 0.99–0.99</td>
<td>0.98 0.99–0.99</td>
</tr>
<tr>
<td>Rainfall</td>
<td>0.99 &lt; 0.0001 0.99–0.99</td>
<td>0.99 &lt; 0.0001 0.99–0.99</td>
<td>0.99 &lt; 0.0001 0.99–0.99</td>
<td>0.99 &lt; 0.0001 0.99–0.99</td>
<td>0.99 &lt; 0.0001 0.99–0.99</td>
<td>0.99 &lt; 0.0001 0.99–0.99</td>
<td>0.99 0.99–0.99</td>
<td>0.99 0.99–0.99</td>
</tr>
<tr>
<td>RWCS</td>
<td>0.99 &lt; 0.0001 0.99–0.99</td>
<td>0.99 &lt; 0.0001 0.99–0.99</td>
<td>0.99 &lt; 0.0001 0.99–0.99</td>
<td>0.99 &lt; 0.0001 0.99–0.99</td>
<td>0.99 &lt; 0.0001 0.99–0.99</td>
<td>0.99 &lt; 0.0001 0.99–0.99</td>
<td>0.99 0.99–0.99</td>
<td>0.99 0.99–0.99</td>
</tr>
</tbody>
</table>

*p-Value: Significance level for the Poisson regression coefficient. In boldface: significant p-values and IRRs of variables displaying variations >5%.

**95% Conf. Interval: Confidence interval for the rate ratio, given the other predictors are in the model.

***McFadden’s Pseudo $R^2$, given by the formula $(1 - L_1/L_0)$, where $L_0$ and $L_1$ are the constant-only and full model log likelihoods, respectively.
where the IRR values for cell density and biomass are 0.74 and 0.76, representing about a 25% decrease in Dinophyceae per unit increase of transparency. Interestingly, the relationship was less pronounced in the adjacent smaller lake, causing a decrease around 15% (IRR = 0.87 for density, 0.84 for biomass). Another parameter that had a significant negative relationship to algal dynamics was the conductivity in the superior lake. In addition, positive noteworthy correlations were displayed by pH in Lake C.I.

**DISCUSSION**

The chemical values displayed by Colbricon Superiore and Inferiore Lakes show common features, consistent with the fact that they belong to the same hydrological basin and are connected by a short effluent running from C.S. Since the substratum is based on non-alkaline quartziferous rocks that are not conducive to buffering dissolved carbonates, the observed pH values likely indicate the absence of acid rain phenomena [49]. The threshold alkalinity defining sensitive lakes is 0.2 meq l⁻¹ [7], and the two lakes under consideration fall well above such threshold.

Nitrogen and phosphorus concentrations agree with the trophic classification [16, 26]. Relatively low silica concentrations were present as expected for high mountain conditions, where low temperature limits SiO₂ dissolution rates and substantial precipitation as rain or snow can cause very high flushing rates of water through the lakes. The silica values are however regarded as non-limiting, being well above the minimum thresholds of 0.03–0.06 mg Si/l typically needed to support the productivity of siliceous phytoplankton [52]. Available data on chlorophyll a concentration of these lakes [21] average 10.68 µg/l and support their placement in oligo- to mesotrophic water bodies.

In terms of functional grouping [35, 36], the prevailing presences are taxa classified in groups L₀ (summer epilimnia in mesotrophic lakes) and L₄₋₅ (summer epilimnia in eutrophic lakes), tolerant of low or segregated nutrients and sensitive to mixing and to poor light intensity. These conditions are typical of the Avisio basin lakes, and agree with the water chemical values recorded there [48]. The dominant taxon *Peridinium goslaviense* is listed in the indicators of nutrient-rich lakes [53]. *Peridinium volzii* and *Ceratium hirundinella* are reported among indicators of mesotrophic–eutrophic conditions [37].

In both the lakes, the biomass values of Dinophyceae populations (Fig. 3) were relatively low during the first 2 years of this survey, and rose from year 2000 onwards. In both lakes, notwithstanding the difference in the biomass attained, the fluctuations of Dinophyceae populations were typically parallel, and only in a few instances were their trends opposite, leading to the rise in one lake and a decrease in the other.

As regards the relationships between biota and physico-chemical variables, one negative correlation was with water conductivity, which interestingly only occurred in the larger and deeper C.S. lake.

Water transparency had a highly significant negative correlation with both density and biomass in both lakes. The effect was more severe for the upper lake, in that, as the Poisson regression shows for C.S., every unit increase in transparency causes about 25% reduction (IRR* value = 0.76), whereas in Lake C.I. such reduction is limited to about 15% (IRR* value = 0.84). In these systems, the reduced transparency is not only considered as a possible cause but also as a direct effect of planktonic algal growth, which explains its negative relationship with their cell densities. The Relative Water Column Stability (RWCS), reporting how stable is the stratification of the temperatures in the water column, is a parameter that has been applied in different instances on various lakes [3, 28]. Our measurements displayed average values of 50.34 for Lake C.S. and 36.55 for Lake C.I. (Table 2). The lower value for the smaller lake indicates conditions more prone to mixing of the waters, supposedly due to its shallower nature (average depth 3.8 m) in which the wind-driven mixing involves a more substantial portion of the lake volume compared with the deeper C.S. lake. The more severe reduction exerted in the deeper C.S. lake (Poisson’s IRR* = 0.76) is consistent with the fact that such lake maintains a more stable thermal stratification, with the consequence that light-related effects are more effective on development of algal populations.

These data strengthen the view of a tighter control/response of biota in the smaller lake in spite of possible chemical and physical shifts. In the shallower lake, the volume being one third that of the larger lake appears to play a significant role in the dynamics of the phytoplankton, despite the equal exposure of both neighboring lakes to inputs from the common catchment basin. The Dinophyceae in Lake C.I. appear to be less affected by most of the independent variables than do their companion populations in Lake C.S. Such resistance can be summarized as follows: no effect by pH (vs. a 14% increase per pH unit in Lake C.S.); no effect by conductivity (vs. a 6–7% decrease per unit dependency in Lake C.S.), and less severe effect by transparency (only 14% decrease per unit increase vs. a 25% decrease in Lake C.S.). This higher stability of the Dinophyceae populations in the smaller lake where they attain higher diversity and evenness, as well as higher biomass and density, supports possible links between ecosystem diversity, stability, and productivity, implementing one of the main tenets in ecological theory.

It is worth noticing that smaller waterbodies, because of their lower mass, are more prone to mixing and ultimately...
to homogenization of physical and chemical profiles, and they are at the same time exposed to higher extents of parameter fluctuations in time, leading to more frequent disturbance events whose effect may also positively affect diversity. Lake C.I. was less stratified and more homogenized (lower RWCS), being more exposed to changes of the independent variables. Nevertheless, the Poisson regression indicated that its Dinophyceae assemblage composition appears to be less dependent on the variation of such environmental variables despite their broader extent of fluctuation compared with the deeper Lake C.S.

In order to put in evidence the extent of variation in the physical, chemical, and biological parameters in the two lakes during the period of study, we compared the dispersion of the data by calculating the coefficient of variation (standard deviation/mean) for each measured variable using the dataset of the whole period. The values for each of the three kinds of parameters (physical, chemical, and biological) were then averaged. The resultant Table 5 shows that the two lakes had identical coefficients of variation in the physical parameters, but the smaller C.I. lake fluctuated more in chemical parameters while simultaneously being more stable in Dinophyceae densities than the larger C.S. lake.

To generalize the concept of these differences, a larger lake would tend to be more homogeneous timewise (hydrochemical constancy) but more heterogeneous spacewise (stratification), whereas a smaller lake would be more spacewise homogeneous (forced to mixing) and timewise heterogeneous (displaying frequent changes in short time frames). Within such scenarios, it appears that the biological assemblage of the Dinophyceae better endures and counteracts the changes when it resides in lakes that exhibit the second type of situation.

Lake C.I. is also more productive as its mean Dinophyceae biomass is 1.6-fold higher than in Lake C.S. These data support the view of stability and productivity as positively correlated dimensions in freshwater ecosystems [1]. However, it needs to be emphasized that this stability is pertaining to the Dinophyceae community and not to the habitat parameters per se.

The ecological indices of dominance, evenness, and diversity in community structure were slightly different between the 2 lakes when using the number of presences recorded for the given taxa or their biovolume abundance. However, when the two dinoflagellate communities were compared with each other using biovolume-weighted abundance, the levels of dissimilarity and distance between C.S. and C.I. reveal 2- to 4-fold higher divergences than when based on taxa presences. The evidence further emphasizes that the dinoflagellate diversities between the two lakes differ from each other primarily because of their biomass-weighted distribution of species abundances rather than their species richness.

The chemical environment of the smaller lake appears to selectively enhance the relative abundance of different phytoplankton members in spite of species richness remaining constant. It can be also observed that the higher production of the lower lake is mostly due to the species Peridinium goslawiense and P. volzii. Different possible reasons for the different production levels can be hypothesized. Dissolved nutrient comparisons indicate that the main difference between the lakes is their reactive phosphorus content, with the lower lake having a mean that was nearly double (mean 4.71 vs. 2.43 µg/l) and maximum that was even larger (18 vs. 5 µg/l). However, reactive phosphorus values were near the lower detection limit on some sampling dates. Total P and N are instead rather similar. A possible explanation could be linked to their different depths. However, as both lakes are rather shallow, the euphotic zone is in both cases extended to their entire depth. Therefore, the hypothesis that a deeper aphotic zone would dilute out the phytoplankton yield leading to lower values in Lake C.S. does not seem to be a basis to explain the observed phenomenon. A more plausible explanation could be linked to the fact that in front of an equal runoff of nutrient from the slopes of the shared catchment basin, Lake C.I. would be ending up with more concentrated nutrients as these dissolve in a smaller reservoir. Such enrichment could translate to a more sustained biological production.

All things considered, the two neighboring Lakes of Colbricon constitute a unique set of coupled model environments offering the rare opportunity to study variations imposed by some environmental constraints while keeping other environmental variables constant. Such reduction in
dimensionality involving the effect of habitat size in homeostatic resistance is a valuable asset to address questions of broad interest in general ecology. The availability of a continuous dataset accumulated over 10 consecutive years is a further element of strength of the comparison. Related studies are in progress to expand the data to include whole community analyses that include all the remaining phytoplankton divisions as well as the bacterial components, in order to trace a general picture of size-dependent responses in high mountain lake ecology.

REFERENCES


