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NOTE

A preliminary evaluation of lake morphometric traits influence on the maximum colonization depth of aquatic plants

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ABSTRACT

Underwater light regime is widely considered the principal determinant of aquatic plant depth distribution. The majority of previous studies dealing with macrophytes in lakes have singled out Secchi disk transparency (SD) values as the key empirical proxy *to explain the maximum depth of macrophyte colonization (Zc). Few studies have investigated the role played by lake morphometry in structuring macrophyte beds. Using a balanced dataset including 20 Italian lakes (10 shallow and 10 deep lakes), we analysed transparency and lake morphometric traits to investigate their possible effects on Zc. Our results demonstrate that lake area plays a significant role, and confirm a direct influence of SD values on Zc. Considering lakes with an equal degree of transparency, smaller lakes may yield a lower Zc than larger ones. Morphology has a great influence on lake ecological characteristics especially on water thermal conditions and mixing depth. Based on our data, we argue that the thermal stratification plays a non negligible role in explaining macrophytes zonation, due to its influence on macrophytes life cycles and phytoplankton vertical distribution. Therefore, the present data suggest the need to enhance and refine our knowledge about the relationship between aquatic plants distribution and lake thermal conditions to better model the response of macrophytes to climate change and eutrophication.*

Key words: submerged aquatic plants, maximum growing depth, Secchi disk transparency, lake area, littoral slope.

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INTRODUCTION

Macrophytes are a key element of aquatic ecosystems since they play a central role in nutrient cycling, primary production, increasing habitat heterogeneity and sustaining biodiversity (Carpenter and Lodge, 1986). During the last century, aquatic plants have experienced a widespread decline and a marked decrease in diversity and representativeness, especially in developed countries (Schmieder, 2004; Dudgeon *et al.*, 2006; Bolpagni *et al.*, 2013a). Eutrophication and water over-exploitation, land use changes and littoral and shoreline modifications are the main factors forwarding critical regime shifts in aquatic primary producers that have promoted the replacement of submerged plant species by pleustophytes or phytoplankton (Scheffer *et al.*, 2003; Bolpagni *et al.*, 2007, 2013b, 2014; Sayer *et al.*, 2010; Azzella *et al.*, 2013a, 2014; Tombolini *et al.*, 2014).

In lakes, the availability of light and the underwater light regime are widely considered the principal factors controlling macrophyte growth along the depth gradient (Middelboe and Markager, 1997; Hudon *et al.*, 2000; Schwarz *et al.*, 2000). The majority of previous studies have assessed the aquatic plant zonation using the Secchi disk transparency (SD), as a strong empirical factor explaining the maximum depth of colonization (Zc) (Middelboe and Markager, 1997; Schwarz *et al.*, 2000). Other factors (*e.g.*, pressure, water temperature, latitude) are generally considered to be of minor importance. However, the non-linear relationship between SD and Zc and the marked variability that characterizes the maximum depths of macrophyte colonization in lakes with similar water transparency suggest that various factors may influence the depth attained by macrophytes (Middelboe and Markager, 1997), and in particular the size and depth of a water body. Hence, there are presumably several factors related to a lake's morphometry that may influence aquatic plant life and dispersal, including water-table fluctuations, water circulation and temperature patterns, wind exposure and fetch (Bornette and Puijalon, 2011 and references therein). The aim of our work was to investigate the role of lake morphology as a predictor of the depth distribution of macrophytes assuming a dependence of Zc on morphometric characteristics. Thus, we expected a significant increase in Zc in proportion to the lake area under comparable water transparency conditions, as observed in field surveys.

We analyzed the correlation between the Zc, SD and lake morphology of 20 Italian lakes using a balanced dataset in terms of the lakes' mean depth (10 shallow and 10 deep lakes, in accordance with Carvalho *et al.*, 2009). In particular, our work was designed to evaluate i) Zc variability in relation to the SD, and ii) the role of lake area in driving Zc.

METHODS

Data of Zc, SD and morphological features of 20 Italian lakes were extracted from a broader dataset of 29 lakes using a balanced approach that represents an innovative viewpoint in the analysis of the Zc, never used before. Generally, in a field experiment it is of primary importance to consider heterogeneous pools of data not biased toward any particular habitat typology to obtain robust results. For example using a database with a high number of shallow lakes in spite of deep lakes, as usually happens, given that the shallow lakes are much more widespread than deep ones. Therefore, we first distinguished shallow lakes from deep lakes, according to the method used by Carvalho *et al*. (2009), who considered lakes with a mean depth >15 m as deep. We then selected an equal number of shallow and deep lakes (10) (Fig. 1) in order to ensure that the datasets were not biased towards shallow or deep lakes (Tab. 1). In the period 2009-2010, Zc data were collected using transects performed along depth gradient in agreement with Bolpagni (2013), Oggioni *et al.* (2013) and Azzella *et al.* (2013b). The number of transects, which varied according to the size of the lakes, ranged from 9 (Lago Grande) to 41 (Garda); this was sufficient to avoid a sample-based bias in the evaluation of Zc (Spears *et al*., 2009). Over the same period, SD data were collected both during winter circulation (January/February) and at the end of the summer stratification (August). Unlike other studies that based their analysis exclusively on the summer SD data, our model considered the annual mean SD value. Littoral slopes were determined using field measurements, as the ratio of Zc and its linear distance from the shoreline. Collection of Zc, SD and littoral slope data was supported by the MONECOLA project, the Regional Agency for Environmental Protection (ARPA Lombardia), the Provincial Agency for Environmental Protection of Trento (APPA), and three research institutes (La Sapienza University, University of Parma, the National Research Council - CNR). Total phosphorus concentrations (TP) and total alkalinity (Alk) values were obtained from the ARPA Lombardia database (*unpublished data*) and Azzella *et al*. (2013b). Macrophytes nomenclature follows Bazzichelli and Abdelahad (2009) for charophytes and Conti *et al.* (2005) for vascular species.

We performed a regression analysis using linear models to assess the relationship between SD and Zc. The Akaike Information Criterion (AIC) was used to select the most suitable model to explain the correlation (Akaike, 1974). A multiple regression analysis was instead applied to select the morphological variables that affect Zc. A preliminary

Tab. 1. Main features of the study lakes.

Lake	Al m asl	V km^3	A km^2	Zmax m	Zmean m	S %	Zc M	SD m	TP $\mu g\ P\ L^{-1}$	Alk $\mu eq\ L^{-1}$	Deepest macrophyte
Albano	293	0.5	6.0	170.0	77.1	36.8	11.0	6.2	21.6	3606.6	*Cha_glo*
Alserio	243	0.0	1.2	8.0	5.4	7.8	3.0	2.0	70.0	3670.0	*Cer_dem*
Bolsena	305	8.9	114.5	146.0	77.9	5.0	20.0	11.8	17.2	4124.1	*Nit_opa*
Bracciano	164	5.0	57.5	160.0	86.1	9.9	26.0	12.8	14.2	3263.0	*Nit_opa*
Candia	226	0.0	1.7	8.0	5.9	9.1	4.0	4.0	40.0	1080.0	*Tra_nat/Nym_pel/Naj_mar*
Como	198	22.5	145.9	410.0	154.2	83.1	14.6	12.0	38.6	1190.0	*Cha_glo/Cer_dem*
Garda	65	49.0	370.0	346.0	132.0	35.4	17.5	10.0	19.0	2120.0	*Cha_glo*
Idro	368	0.9	11.0	124.0	77.0	36	10.5	3.7	91.5	2485.0	*Cha_glo*
Iseo	186	7.6	60.9	251.0	124.8	62.7	8.5	3.0	50.0	1900.0	*Cha_glo*
Lago Grande	656	0.0	0.4	35.0	8.2	9.1	3.30	1.3	123.6	3369.4	*Cer_dem/Tra_nat*
Mantova Superiore	15	0.0	1.5	9.0	2.7	3.1	4.0	0.8	91.7	2643.5	*Cer_dem/Tra_nat*
Mantova Mezzo	15	0.0	1.1	15.0	2.7	3.3	3.5	0.8	60.8	2657.7	*Cer_dem/Nel_nuc*
Mantova Inferiore	18	0.0	3.7	12.0	4.1	4.0	3.5	0.8	91.1	2643.1	*Cer_dem*
Monate	266	0.0	2.5	34.1	18.3	62.7	8.5	9.0	6.0	830.0	*Cer_dem*
Nemi	318	0.0	1.7	34.0	19.5	41.1	8.0	5.8	34.0	2258.3	*Cha_glo*
Segrino	374	0.0	0.3	8.6	4.3	10.2	4.3	2.6	12.0	2920.0	*Myr_spi*
Varese	238	0.2	14.8	26.0	11.0	6.2	3.5	1.7	25.0	2270.0	*Cer_dem/Naj_mar*
Viverone	230	0.1	5.8	50.0	21.7	2.6	7.1	4.0	92.0	1060.0	*Cer_dem*
Endine	334	0.0	2.1	9.4	5.6	24.1	6.0	4.1	12.0	3730.0	*Cer_dem*
Levico	440	0.0	1.2	38.0	11.0	2.1	5.0	7.5	29.0	1260.0	*Cer_dem*

Al, altitude; V, volume; A, area; Zmax, maximum depth; Zmean, mean depth; S, slope; Zc, maximum depth of macrophyte colonization; SD, Secchi disk transparency; TP, total phosphorous; Alk, total alkalinity; deepest macrophytes, the plant species at the maximum colonization depth. Cha glo, Chara globularis *Thuillier 1799;* Cer dem, Ceratophyllum demersum *L.;* Nit opa, Nitella opaca *(C. Agardh ex Bruzelius) C. Agardh. 1824;* Tra nat, Trapa natans *L.;* Nym pel, Nymphoides peltata *(S.G. Gmel.) Kuntze;* Naj mar, Najas marina *L. ssp.* marina; Nel nuc, Nelumbo nucifera *Gaertn.;* Myr spi, Myriophyllum spicatum *L.*

analysis was performed to evaluate the correlation between area, volume and maximum lake depth (Zmax), all of which proved to be significantly correlated with each other (Pearson correlation $P<0.001$), as was expected and has previously been demonstrated by several authors (Duarte *et al*., 1986, and references therein). On the other hand, slope was found to be independent; therefore, we assessed the influence of SD, lake area and slope of the macrophyte-colonized zone on Zc in the multiple regression analysis. All analyses were performed using PAST 1.97 (Hammer, 2001).

RESULTS

The majority of the lakes studied are located in the northern of Italy (=15), while a minority of the lakes are in the Southern-Central part of Italy (=5; Fig. 1). Their altitude ranges from 15 to 656 m a.s.l. The main physico-chemical and morphological features of the investigated lakes are summarized in Tab. 1. The area (A) of the lakes ranges from 0.3 to 370 km^2, their volume from about 0.001 to 49 km^3, their Zmax from 8.0 to 410 m and their Zmean (mean depth) from 2.7 m to 154 m. The total phosphorus concentrations ranged from 6.0 to 123.6 µg L^{-1} (at Monate and Lago Grande, respectively), while the overall alkalinity did not exceed 4124 µeq L^{-1}, with a minimum of 830 µeq L^{-1} at Monate. The maximum littoral slope was observed at Como (83.1%) and the minimum at the Mantua lakes (4.0%).

SD varied between 0.8 m (Mantua lakes) and 12.8 m (Bracciano), with a mean value (±standard deviation) of 5.2±4.0 m; Zc ranged between 3 m (Alserio) and 26 m

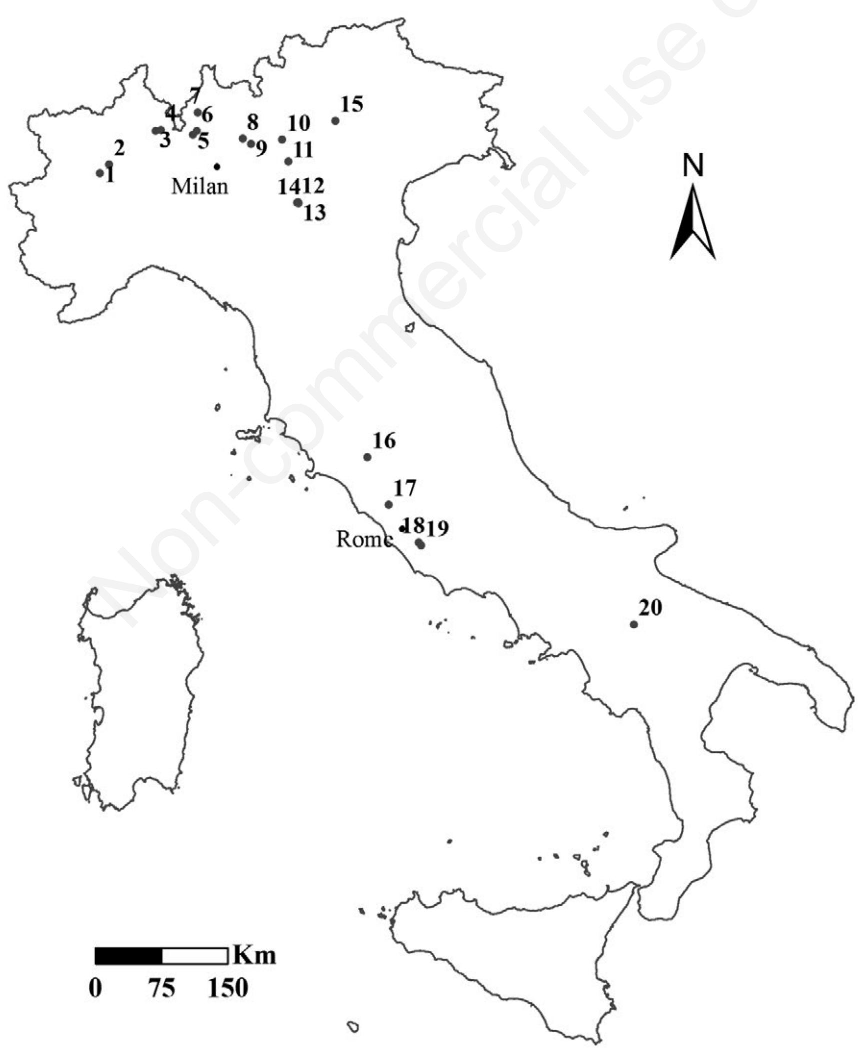

Fig. 1. Location of the lakes considered in the analysis: 1, Candia; 2, Viverone; 3, Monate; 4, Varese; 5, Alserio; 6, Segrino; 7, Como; 8, Endine; 9, Iseo; 10, Idro; 11, Garda; 12, Mantova Superiore; 13, Mantova Mezzo; 14, Mantova Inferiore; 15, Levico; 16, Bolsena; 17, Bracciano; 18, Albano; 19, Nemi; 20, Lago Grande.

(Bracciano), with a mean value of 8.6±6.4 m. The deepest plant species were vascular plants (generally *Ceratophyllum demersum*) for Zc <8.5 m, and charophytes at greater depths (*Chara globularis* between 10 and 20 m and *Nitella opaca* between 20 m and 26 m). The linear model analysis revealed three potential correlations between Zc and SD: a linear correlation, a second order polynomial correlation (quadratic) and a third order polynomial correlation (cubic) (Fig. 2). Although the linear correlation and the quadratic model were statistically significant, it was the cubic correlation that exhibited the lowest AIC value (Tab. 2). This model displays an initial asymptotic trend for Zc up to 8 m, followed by a slight dip and a subsequent exponential growth. The multiple regression analysis revealed a significant influence of SD and lake area on Zc, whereas the influence of slope was not significant (Tab. 3). On the basis of these results, the model that most appropriately describes the correlation between Zc (dependent factor), SD and area (independent factors) is represented by the following formula:

$$Zc=1.01\ SD+2.62\ Log(A)+1.36 \quad \text{(eq. 1)}$$

This model yielded a higher R^2 (R^2 adj=0.83; P<0.001) than the linear model (2), which was based exclusively on the SD (R^2 adj=0.75; P<0.001)

$$Zc=1.39\ SD+1.37 \quad \text{(eq. 2)}$$

DISCUSSION

The present study confirms the importance of SD as means of explaining Zc using a balanced database, *i.e.* one that is not biased by an overbalance of shallow or deep lakes. Since the majority of the lakes considered in previous studies are shallow (Chambers and Kalff, 1985; Canfield *et al.*, 1985), even those in large datasets (Middelboe and Markager, 1997; Caffrey *et al.*, 2007; Søndergaard *et al.*, 2013), the linear dependence of Zc on SD may have been overestimated. Indeed, few authors have suggested that the relationship between SD and Zc may not be linear. Middleboe and Markager (1997) and Schwarz *et al.* (2000) reported that the relationship between SD and Zc was asymptotic: as transparency increases, Zc first increases linearly and then follows an asymptotic trend. Similarly, the linear model applied to our data yielded results that are significant but cannot be compared with those yielded by a polynomial model. Consequently, our observations suggest that the Zc trend is asymptotic at the shallow depths (not exceeding 6 m at Endine) that are characteristic of small lakes (Fig. 2, on the left of the graph), whilst it is steeper in the larger and deeper lakes (Fig. 2, on the right of the graph). The exponential Zc growth observed for SD values higher than 8 meters could be put in relation with the progressive replacement of vascular species by charophytes with the increase of depth. In fact, it is generally recognized that the species able to reach the maximum growing depth are not vascular, mainly because charophytes are more efficient than vascular plants to capture lights (Hutchinson, 1975).

In the multiple regression analysis performed on our dataset, Zc was significantly affected by lake area. The inclusion of area in the linear model that defines the relationship between SD and Zc improved its prediction accuracy (from R^2=0.75 to R^2=0.83). This is not a surprising finding but confirms the significant influence of lake morphometry

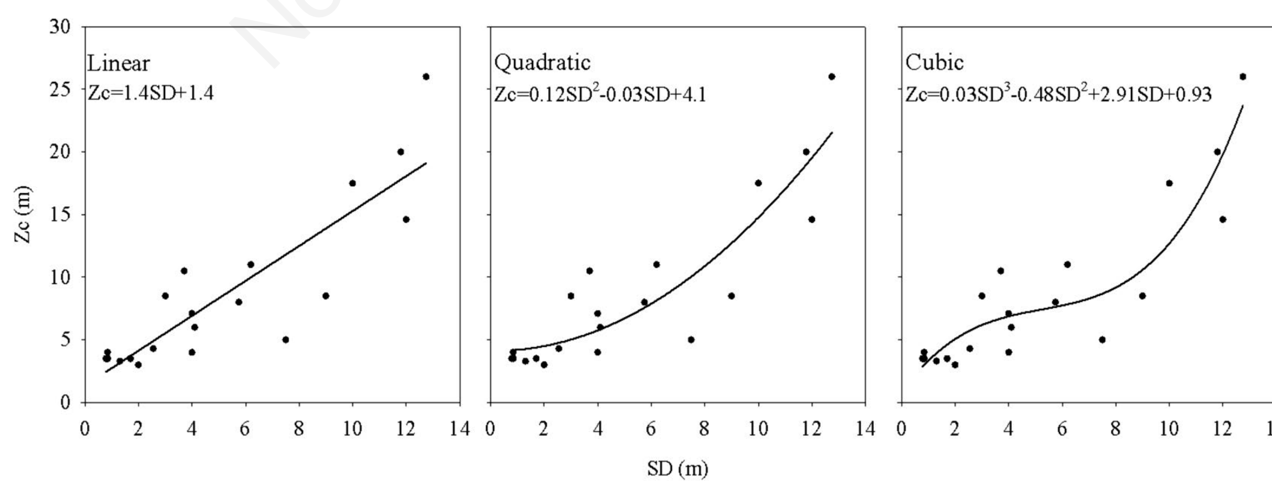

Fig. 2. Linear models used to explain the correlation between Zc (maximum depth of macrophyte colonization) and SD (Secchi disk transparency). The linear model is on the left, the second-order polynomial (quadratic) in the center, and the third-order polynomial (cubic) model on the right.

on macrophyte spatial arrangement. Similar conclusions were recently reported for macrophyte development in Polish lowland lakes (Kolada, 2014) in agreement with Duarte and Kalff (1990) and Srivastava *et al.* (1995).

Beyond the pivotal role of light, Sheldon and Boylen (1977) had previously suggested the existence of a relationship between thermocline and Zc in agreement with the central role played by the morphometric characteristics of a lake in driving important abiotic factors, such as water circulation and thermal conditions (see Bornette and Puijalon, 2011, and references therein). However, the few authors who have collected data on the role played by morphometric characteristics in the spatial arrangement of aquatic plants (Duarte and Kalff, 1986; Duarte *et al.*, 1986; Kolada, 2014) did not examine their influence on Zc in great detail.

Temperature appears to play an important role in determining the spatial arrangement of submerged plants (Dale, 1986; Bornette and Puijalon, 2011), particularly in deep lakes (Barko *et al*., 1986). Actually, it is known that i) the thermocline of a lake is correlated with its depth (Hanna, 1990); ii) Zc is correlated to thermocline (Rooney and Kalff, 2000); and iii) macrophytes that survive at the maximum depths of colonization are perennial and can tolerate very low temperatures (Corillion, 1957). For example, some field observations have confirmed that freshwater macrophytes can grow (albeit minimally) below thick layers of ice during wintertime (Boylen and Sheldon, 1976). Nonetheless, if we exclude a limited number of laboratory experiments and *in situ* observations that have investigated the response of submerged plants to temperature and underwater light regime (Ke and Li, 2006; Jarvis and Moore, 2008), hardly any data concerning the relationship between macrophyte depth distribution and temperature exist. Schwarz *et al*. (2000) have identified the temperature as a secondary factor in modulating the performance of macrophytes, while Middleboe and Markager (1997), and Duarte and Kalff (1987) have considered the latitude as a cofactor in defining Zc.

Temperature affects plant germination in various ways (see, among others Carasso *et al*., 2012; Pradhan and Badola, 2012). Water temperature exerts a strong influence on macrophyte life phases, such as reproduction, germination and seedling emergence (Barko *et al*., 1982; Madsen and Adams, 1988; Spencer and Ksander, 1992; Leck, 1996; Xiao *et al*., 2010). Overall, the onset of germination in freshwater submerged macrophytes has been associated with temperatures ranging between ~23 and 29°C (Ke and Li, 2006; Jarvis and Moore, 2008). Moreover, lake thermal conditions can indirectly influence the macrophytes distribution by influencing the vertical stratification of phytoplankton. In fact, thermocline controls the spatial distribution of microalgae and accordingly modulates the transparency of water (Derenbach *et al.*, 1979).

All these findings support the non-negligible role of lake thermal conditions in controlling the distribution of macrophytes. This is especially true for deep lakes of relatively high water clarity or in the stratified ones (Sheldon and Boylen, 1977; Barko *et al.*, 1982). We hold that thermocline is likely to be critical to the depth distribution of macrophytes mainly in deep lakes, influencing both the vertical distribution of phytoplankton and the macrophyte life phases.

CONCLUSIONS

The findings of the present study thus demonstrate that lake area provides a better understanding of the relationship between SD and Zc. Consequently, we may argue that when SD values are similar, the Zc of macrophytes in larger lakes tends to be higher. This observation may also have more extensive implications and effects on ecological monitoring programs. The area of lakes can easily be assessed by means of open source GIS systems, and the inclusion of a lake's area in ecological macrophytic multimetric indices (Pall and Moser, 2009; Beck *et al*., 2010) might help to improve the accuracy of monitoring programs. We believe that the elaboration of macrophytic measurements specifically calibrated according to lake area may lead to a more ef-

Tab. 2. Statistical analysis of the models proposed to describe the correlation between Zc and SD.

	Zc=a0+a3 SD^3+a2 SD^2+a1 SD		
	1st order Linear	2nd order Quadratic	3rd order Cubic
Chi square	187.44	150.13	122.51
AIC	192.15	157.63	133.18
R^2	0.76	0.81	0.84
F	56.7	35.5	28.5
P	5.7^{-7}	8.4^{-7}	1.2^{-6}
a	1.4	4.1	0.93
b	1.4	-0.03	2.91
c	0	0.12	-0.48
d	0	0	0.03

Zc, maximum depth of macrophyte colonization; SD, Secchi disk transparency.

Tab. 3. Results of multiple regression analysis.

	Model Zc=SD+Log A+slope+intercept			
	Coeff	Std. err.	T	P
Intercept	1.81	1.02	87.571	<0.1
SD	1.07	0.20	203.897	<0.001
Log A	2.98	0.93	126.499	<0.05
Slope	-0.04	0.03	132.25	>0.1

SD, Secchi disk transparency; A, area.

fective evaluation of lake conservation status. In conclusion, our data confirm the existence of a polynomial relationship between SD and Zc that highlights the role played by lake area, as opposed to temperature, in driving macrophyte distribution.

Additionally, the use of a balanced dataset appears to avoid the possible interpretative bias due to the use of large dataset that is overbalanced towards small and shallow lakes. Further investigations, based in particular on more extensive databases encompassing larger geographical areas, are warranted to support our results and hypothesis. An expanded analysis might even lead to the inclusion of other potential determinants of macrophyte colonization depth (*e.g*., north-south gradient).

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