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Bimodal transparency as an indicator for alternative states in South American lakes

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SUMMARY

1. The alternative state theory claims that shallow lakes may have either clear water, and be dominated by submerged macrophytes, or turbid water and be dominated by phytoplankton. Most evidence for this theory comes from studies in temperate or boreal regions of Europe. Because of differences in the strength of trophic interactions, such as in the pressure of zooplankton grazing on phytoplankton, this influential theory might not apply elsewhere.
2. Here, we test the theory for South American lakes, combining field data and Landsat satellite data. We studied the frequency distribution of primary producers and water transparency, looking for potential bimodality separating clear and turbid lakes. A bimodal distribution might be observed if there are indeed alternative states, although would not itself be sufficient evidence for the theory. Possible shifts between alternative states were analysed by comparing satellite data from 1987 to 2005.
3. In our field data, there was a bimodal pattern in phytoplankton abundance and possibly in the abundance of submerged macrophytes, but not in water transparency. Analyses of the larger satellite data set revealed bimodality in lake transparency in 2005, but less so in 1987. In 1987, the lakes were generally clearer, and the transition to higher turbidity was more gradual than in 2005. The stronger bimodality in the more recent data, and the overall lower transparency, could have been caused by an increase in fertiliser use and subsequent eutrophication but also by differences in hydrology. Further, 1987 was much wetter than 2005, which could have caused dilution of suspended particles, leading to clearer water.
4. While a bimodal distribution in the abundance of primary producers and water clarity is not decisive evidence for or against the theory of alternative states, our data clearly fail to refute it.

Keywords: alternative states, remote sensing, South America, submerged macrophytes, transparency

Introduction

The 'alternative state theory' (reviewed by Scheffer & Van Nes, 2007) states that shallow lakes are often either turbid and dominated by phytoplankton or clear and dominated by macrophytes. Most studies supporting the alternative state theory come from temperate or boreal regions in Europe (e.g. Timms & Moss, 1984; Jeppesen *et al.*, 1990, 1999; Moss, Stansfield & Irvine, 1990; Scheffer *et al.*, 1993; Hargeby *et al.*, 1994, 2005; Van Donk, 1998; Rip, Rawee & De Jong, 2006; Sayer *et al.*, 2006), Canada and the USA (Engel & Nichols, 1994; Jackson, 2003; Rosenthal, Stevens & Lodge, 2006). A few studies have been conducted in other regions such as high Andean Bolivia (Cadima, 1997), temperate New Zealand (Dugdale *et al.*, 2006), Mediterranean Turkey (Beklioglu, 2006), subtropical Florida (Schelske *et al.*, 2005), China (Yang *et al.*, 2006) and tropical Brazil (Jeppesen *et al.*, 2005). It is not evident that

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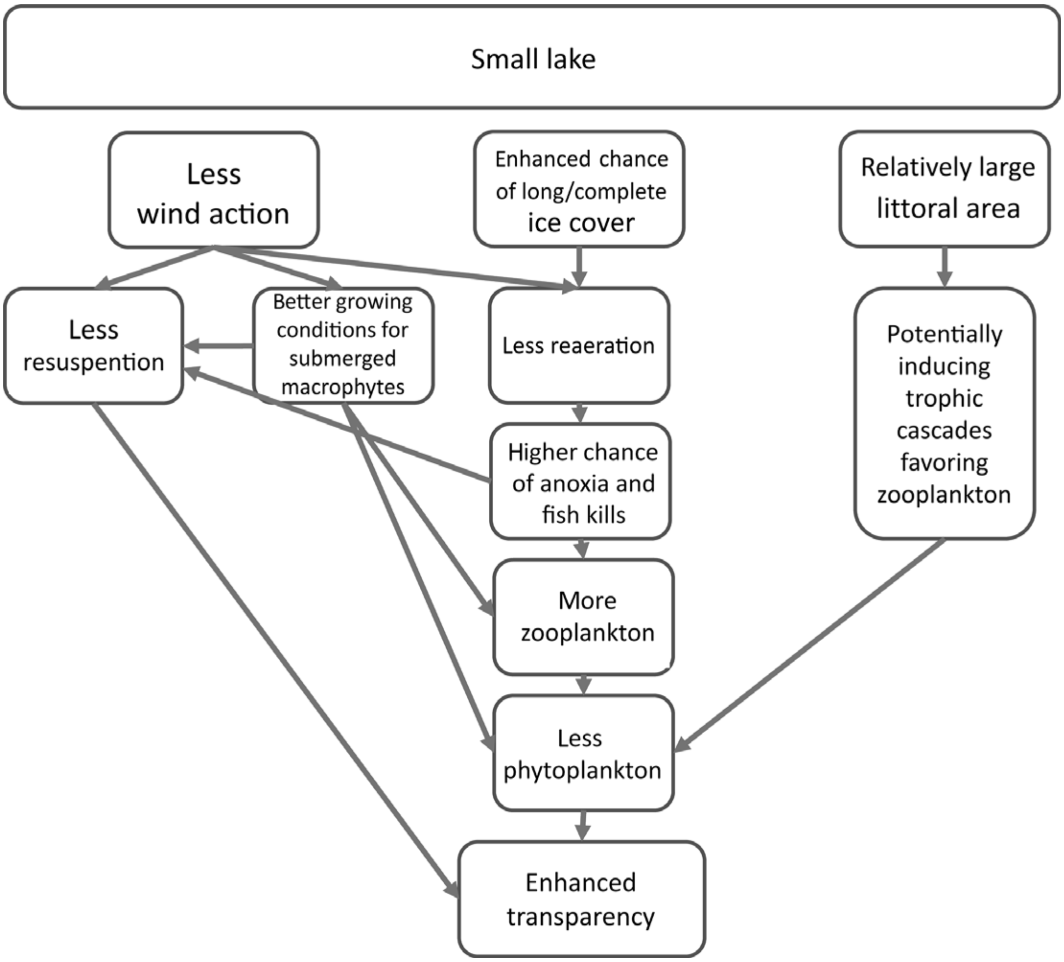

Fig. 1 Potential mechanisms explaining the effect of lake size on water transparency via wind stress, ice cover and the relative size of the littoral area. The smaller the area, the lower the wind-induced resuspension, and the higher the chance of oxygen depletion and subsequent fish kills. These fish kills, as well as the relatively large littoral area in small lakes, may facilitate trophic cascades enhancing transparency. The effect of the trophic cascades is, however, less straightforward than the direct effect of wind. Fish kills may, for instance, favour macroinvertebrates predating on zooplankton, thereby reducing (instead of enhancing) zooplankton abundance. Additionally, the refuge capacity of macrophytes for zooplankton may be low when zooplanktivorous fish and macroinvertebrates are abundant, which is often the case in South American lakes (see main text for more details).

the alternative state theory applies generally to all shallow lakes, however, particularly because the backbone of the alternative state theory, the effect of submerged macrophytes on water transparency, varies among lakes (Kosten *et al.*, 2009b). The water clearing effect of submerged macrophytes may, for instance, be jeopardised when the concentration of humic substances is high. Humic substances reduce water transparency but are not affected by, for example, allelopathic substances or reduced resuspension in macrophyte stands (Kosten *et al.*, 2009b). Further when numerous planktivorous fish (Meerhoff *et al.*, 2007; González Sagrario & Balseiro, 2010) or predatory macroinvertebrates (González Sagrario *et al.*, 2009) diminish the refuge available for zooplankton within submerged macrophytes, the beneficial effect of macrophytes on water clarity may decline through a decrease in grazing pressure. The generally high abundances of fish and macroinvertebrates, particularly shrimps in South American lakes may be the underlying cause of the low grazing pressure found in these lakes compared with Northern Hemisphere lakes (Kosten *et al.*, 2009b). The potentially lower effect on water clarity, mediated via zooplankton, of submerged macrophytes in South American lakes implies that the theory of alternative states may not apply here.

The differences in trophic interactions between South American and Northern Hemisphere lakes may also affect the effect of lake size on the occurrence of alternative states. In northern temperate regions, lake size is important in influencing the likelihood that a lake will be dominated by either phytoplankton or macrophytes.

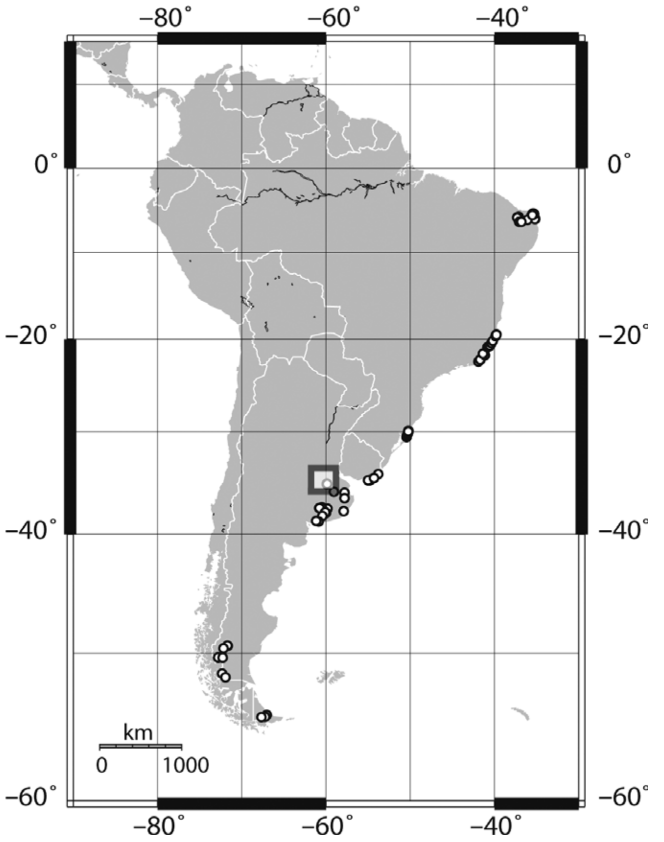

Fig. 2 Location of the 83 lakes sampled in South America. The square indicates the region where the Landsat satellite image was taken.

Various mechanisms may underlie this size effect, some of them work via (planktivorous and benthivorous) fish kills in small lakes (reviewed by Van Geest *et al.*, 2003; Søndergaard, Jeppesen & Jensen, 2005; summarised in Fig. 1). Small lakes in South America are rarely fishless because of rapid recolonisation (Sosnovsky & Quirós, 2009) and reproduction, often with several spawning periods per year (Jeppesen *et al.*, 2010; Strüssmann *et al.*, 2010). Additionally, the generally high abundances of predatory macroinvertebrates, such as shrimps (Meerhoff *et al.*, 2007; González Sagrario *et al.*, 2009), may substantially reduce zooplankton biomass, even where fish are absent, thereby decreasing their water clearing effect. Hence, several differences in trophic interactions between South American and Northern Hemisphere lakes may affect the applicability of the alternative state theory to the former.

In this study, we combine field data from lakes located in Brazil, Uruguay and Argentina with satellite data from the Argentinean Pampa Plain to evaluate the existence of alternative states in South American shallow lakes. Although not an absolute proof, a bimodal distribution of primary producer abundance and water transparency is often taken as evidence of the existence of two alternative states (Scheffer & Carpenter, 2003). Therefore, we determined the proportions of clear and turbid lakes and asked whether the frequency distribution of abundance of primary producers (phytoplankton and submerged macrophytes), and of water transparency, was bimodal. If so, we also looked for an effect of lake size on bimodality and for evidence of temporal changes in the frequency distribution of lake state.

Methods

Field survey

We sampled 83 small and shallow (surface area <2.53 km^2; mean depth 0.5–4.5 m) lakes in South America located in Brazil, Uruguay and Argentina (Fig. 2). Lakes south of 25°S were sampled once during the southern summer (between November and the beginning of March); lakes nearer to the equator were sampled during the dry season (between August and the beginning of November). Sampling was conducted between 2004 and 2006 by the same team using standard protocols. The percentage of lake volume filled with submerged vegetation (PVI) was determined after the study conducted by Canfield *et al.* (1984): the area of the lake covered by macrophytes (m^2) was multiplied by the average height of the vegetation (m) divided by the total volume of the lake (m^3). Coverage was estimated based on observations of the presence/absence of macrophytes at 20 random points in the lake, combined with more detailed macrophyte observations at 13–47 points (average 22) equally distributed along three to eight parallel transects. The number of transects varied with the shape and size of the lake. When water transparency was insufficient to get a clear view of the bottom, observations were made from a boat using a grapnel (for more details see Kosten *et al.*, 2009a,b). Light measurements were made with a LICOR LI-192SA meter. Light attenuation (Kd) was estimated by using irradiance data and Lambert–Beer's law (see e.g. Scheffer, 1998). We collected depth-integrated water samples with a 1.5-m-long tube at 20 random points in each lake. Two litres of each of these depth-integrated samples were mixed in a 40-L bucket resulting in a depth- and area-integrated bulk sample. Filtration for chlorophyll-*a* (chl-*a*) analysis in the laboratory was conducted directly after collection, and the filters were then being frozen in the field until analysis. Chl-*a* was extracted from filters (GF/C; Schleicher & Schuell's Hertogenbosch, The Netherlands) with 96% ethanol, and absorbance was measured at 665 and 750 nm (Nusch, 1980).

Table 1 Characteristics of the sampled lakes

Lake	Coordinates W/S	Sample date	Chl-*a* (μg L^{-1})	PVI (%)	Kd (m^{-1})
Lake Las Encadenadas	−59.9066/−35.2844	7 Feb 2005	28.7	3	4.3
Lake at Estancia Bella Vista	−59.8856/−35.2295	9 Feb 2005	226.1	1	8.4
Lake Honda	−59.8565/−35.2541	11 Feb 2005	6.1	74	2.1

PVI, percentage of lake volume filled with submerged vegetation.

Image selection

Landsat TM images are often used to estimate variables related to water transparency such as Secchi disc depth, chl-*a* concentration and Trophic State Index (e.g. Giardino *et al.*, 2001; Kloiber, Brezonik & Bauer, 2002a,b; Canziani *et al.*, 2008; Sass *et al.*, 2007). To validate water transparency data from satellite imagery, we searched for an image that: (i) depicted some of the sampled lakes with a wide range in transparency; (ii) had many other lakes on it and (iii) was taken near the date that we sampled the lakes and (iv) was cloud free. A Landsat-5 Thematic Mapper (TM) image of the Pampa Plain (path 226, row 84), taken on 4 March 2005, fulfilled these criteria best and was purchased via the Argentinean Comisión Nacional de Actividades Espaciales. During the second week of February 2005, we sampled three lakes in the area where this image was taken. These lakes varied greatly in phytoplankton abundances (approximated by chl-*a* concentration), PVI and transparency (Table 1).

The Pampa Plain contains a large number of shallow lakes varying in water quality and size (Torremorell *et al.*, 2007), allowing us to compare the size effect between Pampean and Northern Hemisphere lakes. Water transparency in the Pampean lakes is known to be strongly influenced by El Niño-driven extremes in precipitation through variations in nutrient inputs, inorganic matter inputs, residence times and water level (Rennella & Quirós, 2006). Extreme droughts and extreme wet periods could therefore affect the proportion of lakes being either clear or turbid. We obtained insight into the temporal character of possible alternative states by comparing satellite-derived water transparency at the time of the field survey with satellite data from a historical image. A cloud-free image of the same location taken on 4 April 1987 was obtained from the Global Land Cover Facility at the University of Maryland (glcf.umiacs.umd.edu/data/landsat/).

Image processing

Landsat TM bands 1–3, situated in the blue at 450–520 nm, green at 520–600 nm and red at 630–690 nm, respectively, were radiometrically calibrated and subsequently atmospherically corrected for solar irradiance, solar zenith angle and Rayleigh scattering using the procedures described by Chander & Markham (2003) and Kaufman (1989) yielding reflectance values in the various spectral bands. The images were then georectified at 30-m pixel resolution to the Universal Transverse Mercator (UTM) coordinate system using the WGS84 ellipsoid. A nearest neighbour resampling was applied. The coregistration error between the two Landsat images was about 30 m (one pixel).

Subsequently, lakes were identified in the images using a supervised maximum-likelihood classification comprising the following steps: (i) several lakes were identified visually using bands 2, 3, 4 and 5 to be used as ‘training sites’; (ii) these training sites were then manually delimited; (iii) from the pixels within the training sites, the reflectance values were extracted; (iv) variance and mean of these reflectance values were determined; (v) based on these statistics, a (Bayesian) probability function was calculated and (vi) based on the probability function, each pixel in the image was then labelled either as a lake or as a terrestrial area, depending on the class it most probably belonged to. Spectral mean reflectances were extracted within each lake, excluding the pixels closest to the shore to avoid mixed terrestrial–aquatic signals. Only lakes with at least nine remaining pixels were used for further analysis as suggested by Kloiber *et al.* (2002b). This procedure also eliminated coregistration errors between the images.

The hydrological regime in the Pampa Plain is highly variable. During wet periods, large areas are temporarily inundated. To minimise the inclusion of the inundated areas, we removed lakes that had a standard deviation for reflectance in the mid-infrared (band 5) larger than 2.0. Only areas that were classified as lake in 1987 and 2005 were considered in further analyses (n = 343).

In earlier studies, water quality variables such as chl-*a* concentration, turbidity, Secchi depth and dissolved organic matter have been approximated by using the reflectance of Landsat bands 1–4 or by combinations of these bands (for an overview see Sass *et al.*, 2007). Here, we used the ratio of the reflectance in bands 1 and 3 (B1:B3), as this ratio has been found, in comparative studies, to correlate best with field measurements of chl-*a* concentration and Secchi depth (Kloiber *et al.*, 2002a,b; Sass *et al.*, 2007; Lathrop, Carpenter & Rudstam, 1996). The reflectance of the lake bottom may, particularly in clear shallow lakes, result in a higher reflectance in band 3 than in band 1 (Lillesand, Kiefer & Chipman, 2004). Owing to a paucity of field data, the removal of lakes with a depth of at least twice the Secchi depth (as recommended by Olmanson, Bauer & Brezonik, 2002) was not an option. We may, therefore, have underestimated the transparency of some lakes in our data set.

Statistical analysis

We investigated possible bimodality in the frequency distribution of the abundance of primary producers and water transparency [vertical light attenuation (Kd)] by means of a latent class analysis. The same analysis was used for water transparency (approximated by the satellite-derived B1:B3 ratio). The latent class analysis can fit two or more frequency distributions to data without prior knowledge as to which class (distribution) each observation belongs. For this, we used the R package FlexMix (R version 2.8.1 FlexMix version 2.2-3) (Leisch, 2004; Grün & Leisch, 2008). This package uses the expectation-maximisation (EM) procedure to find the best fit for a fixed number of latent classes. We compared the fit of models with one to three classes (unimodal – trimodal) using the Bayesian information criterion (BIC). The lowest BIC value indicates the model best describing the variation in the dependent variable.

The value of the BIC is related to the log-likelihood (i.e. the logarithm of the likelihood that the data are generated given the model and parameters). The absolute value of BIC is unique to each variable, and therefore, the BIC values of the chl-*a* and Kd models cannot be compared directly with each other. The BIC is closely related to the Akaike information criterion (AIC) function as both of them correct for the number of fitted parameters. The BIC criterion, however, selects more conservatively for a model with fewer parameters than does the AIC (Hagenaars & Mccutcheon, 2002). Before analysis, the histograms were inspected visually for the presence of (multiple) normal distributions. Chl-*a* concentration and Kd values were log-transformed to approach a normal distribution. Percentage of lake volume filled with submerged vegetation values, however, were not near a

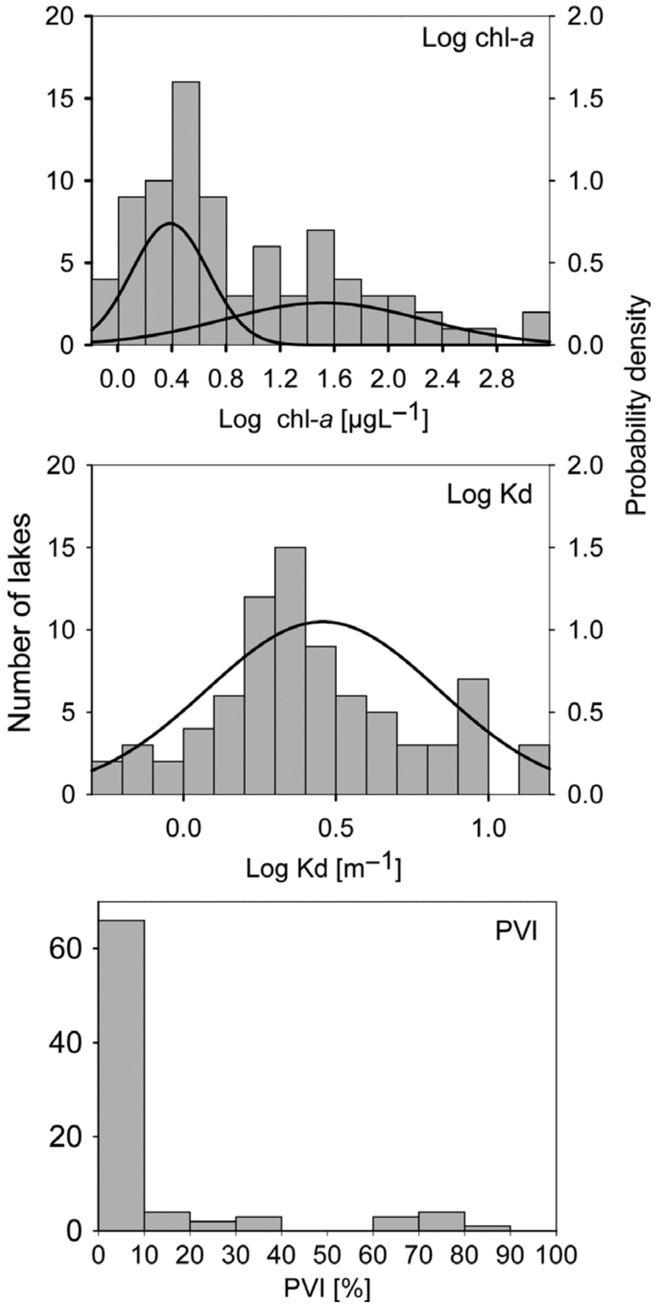

Fig. 3 Frequency distribution of phytoplankton concentration (approximated by chlorophyll-*a*), light attenuation (Kd) and the percentage of the lake volume filled with submerged vegetation (PVI), in 83 South American lakes. The lines depict the probability density as described by the best fitting (uni- or bimodal) model resulting from the latent class analysis (see Table 2).

Table 2 Goodness of fit based on the Bayesian information criterion (BIC) of uni-, bi- and trimodal (one, two or three classes) models to log-transformed chlorophyll-*a* and light attenuation (Kd) frequency distribution of 83 South American lakes. The best fitting model is underlined.

No. of classes	chl-*a*	Kd
1	204	**83**
2	191	87
3	203	95

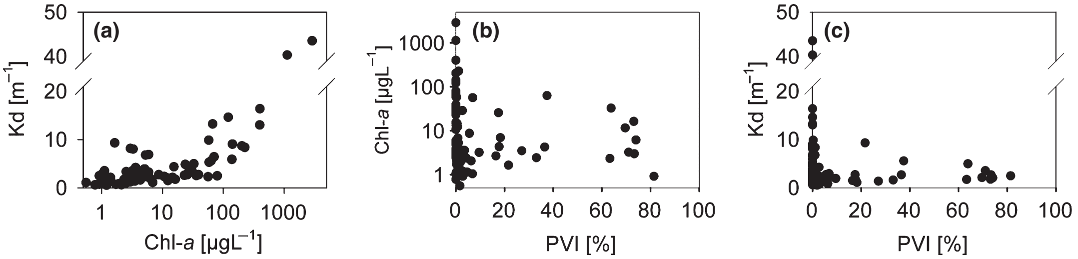

Fig. 4 Relationship between (a) phytoplankton concentration (approximated by chl-*a*) and light attenuation (Kd); (b) the abundance of primary producers: the percentage of the lake's volume filled with submerged vegetation (PVI) and phytoplankton concentration (chl-*a*); and (c) PVI and light attenuation (Kd).

Table 3 Goodness of fit based on the Bayesian information criterion (BIC) of uni-, bi- and trimodal (one, two or three classes) models to the transparency frequency distribution of Pampean lakes in 2005 and 1987

	2005		1987	
No. of classes	All lakes (n = 343)	Small lakes (n = 309)	Large lakes (n = 34)	All (n = 343)
1	355	338	**−7**	617
2	**276**	**273**	2	**613**
3	277	274	12	629

The ratio between the reflection in bands 1 and 3 of a Landsat satellite image was used as a proxy for transparency. To divide small and large lakes, a threshold of 0.5 km^2 was used. The best fitting model is given in bold.

(multiple) normal distribution even after (arcsin or log) transformation, and therefore, no latent class analysis was performed on these data. To distinguish between large and small lakes in the area of the satellite image, a threshold of 0.5 km^2 was used.

Results

In situ *measurements*

The frequency distribution of chlorophyll-*a* concentration, used as a proxy for phytoplankton abundance, was best described by a bimodal model (Table 2, Fig. 3). Most lakes (61%) had a chl-*a* concentration below 15 μg L^{-1}, but lakes with chl-*a* concentration between 15 and 250 μg L^{-1}

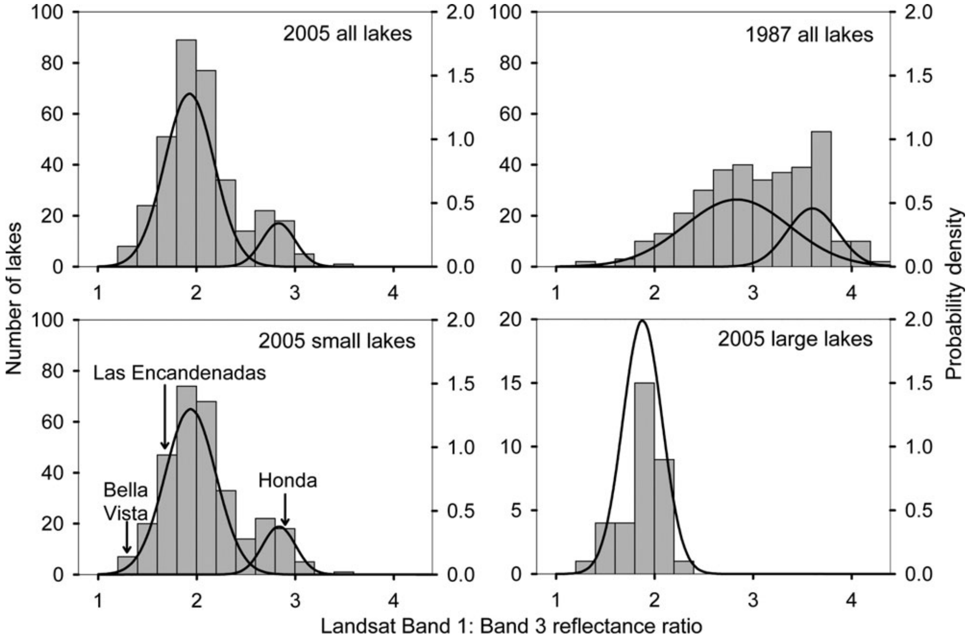

Fig. 5 Frequency distribution of water transparency in Pampean lakes as based on the ratio between the reflectance in bands 1 and 3 of Landsat satellite images in 2005 and 1987. The arrows in the panel '2005 small lakes' indicate the reflection ratio of the three lakes with ground-based measurements (see Table 1). The lines depict the probability density as described by the best fitting (uni- or bimodal) model resulting from the latent class analysis (see Table 3). A cut-off level of 0.5 km^2 was used to distinguish small from large lakes.

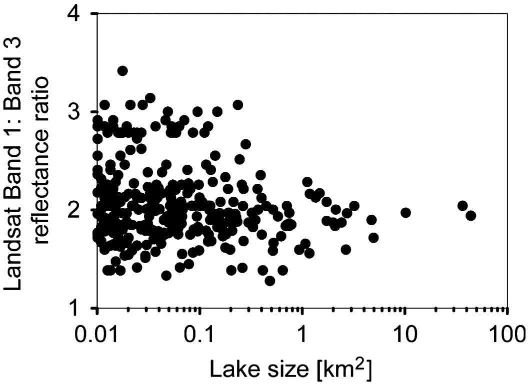

Fig. 6 Water transparency in Pampean lakes of different sizes as based on the ratio between the reflectance in bands 1 and 3 of the 2005 Landsat satellite image. See also statistics in Table 3.

were quite common too (31%). The field data indicated, furthermore, that most lakes had (almost) no submerged macrophyte growth (66% of the lakes had a PVI < 10%). The remaining lakes were distributed approximately equally over the higher PVI classes although lakes with intermediate PVI values were not found (Fig. 3). The Kd followed a unimodal distribution, with most of the lakes having a Kd between 0.1 and 4.5 m^{-1} (Fig. 3).

Although the chl-*a* data, and possibly the PVI data, seemed to support the occurrence of alternative states, this was not confirmed by a bimodal distribution of Kd values. A potentially strong division between low Kd values in systems dominated by submerged macrophytes, and high Kd values in systems dominated by phytoplankton, may have been masked by compounds other than chl-*a* determining the underwater light conditions. Although we found a distinct positive relation between chl-*a* and Kd at high chl-*a* concentrations, the high Kd values occurring at relatively low chl-*a* concentrations suggest that compounds other than chl-*a* are reducing water transparency (Fig. 4a). Moreover, further analyses indicated that the seemingly bimodal pattern in chl-*a*, and possibly in PVI, does not necessarily indicate alternative phytoplankton and submerged macrophyte dominance, since high and low chl-*a* concentrations were found over the whole gradient of submerged macrophyte PVI (Fig. 4b). Finally, although high macrophyte abundance generally coincided with clear conditions, low macrophyte abundance occurred in both turbid and clear conditions (Fig. 4c).

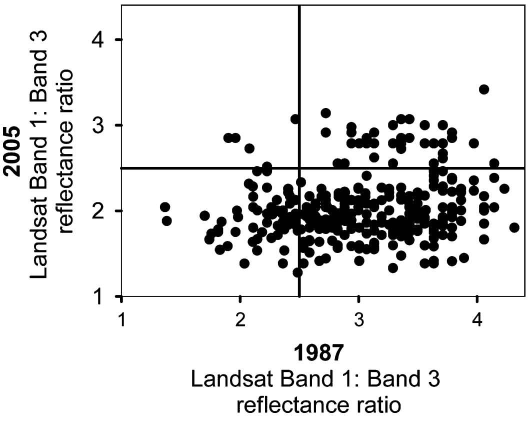

Fig. 7 Water transparency in Pampean lakes as based on the ratio between the reflectance in bands 1 and 3 of Landsat satellite images in 2005 and 1987. The lines at a B1:B3 ratio of 2.5 are a rough indicator of the B1:B3 value above which a lake may be considered clear (see Fig. 4 panel '2005 small lakes').

Satellite-derived data

The frequency distribution of lake transparency for the whole data set in 2005 was best described by a bimodal model although a trimodal model described the data almost as well (Table 3). Maximal frequencies occurred at B1:B3 ratios around 1.9 and 2.8 and minimal frequencies around 2.5 (Fig. 5 '2005 all lakes'). Most lakes were turbid (corresponding with low B1:B3 ratios) with a smaller proportion being clear (corresponding with high B1:B3 ratios). Although the amount of field-based measurements within the image area was insufficient to develop an algorithm deriving transparency measures from the satellite data, the clearest lake did have the highest B1:B3 ratio and the most turbid lake did have the lowest B1:B3 ratio (Table 1, Fig. 5 '2005 small lakes').

The bimodal distribution in the complete 2005 lake data set was largely caused by the bimodal transparency distribution in lakes smaller than 0.5 km^2, which represented 90% of the lakes in the area (Table 3, Fig. 6). Notably, however, the AIC values of the bimodal and trimodal model only differed by one unit. The frequency distribution of transparency in larger lakes was unimodal (Table 3, Fig. 5 '2005 large lakes'). Using a lower cut-off level of 0.2 km^2 revealed that the transparency distribution of lakes with an area between 0.2 and 0.5 km^2 was also bimodal (not shown). Overall, in our data set, large lakes were mostly relatively turbid, whereas smaller lakes can be either clear or turbid (Fig. 6).

The frequency distribution of lake transparency data in 1987 was also bimodal, but with much more overlap between both classes (Table 3, Fig. 5 '1987 all lakes'). The difference between the BIC of the bimodal and the unimodal model was, however, only four units (Table 3), which is not sufficient for a difference to be considered 'strong' (Raftery, 1995). The difference in BIC values for the unimodal and bimodal model for the 2005 data was considerably larger (Table 3), indicating that the bimodal distribution was less apparent in 1987 than in 2005. Additionally, the lakes tended to be clearer in 1987 (a 'wet' year) than in 2005 (a 'dry' year). Most (68%) of the lakes that were relatively clear in 1987 were relatively turbid in 2005 (Fig. 7). Another set of lakes stayed approximately equally clear (14%), and only 1% of the lakes were found more clear in 2005 than in 1987 (Fig. 7).

Discussion

Although multimodality in the transparency of shallow lakes has been shown in various parts of the world (e.g. Peckham *et al.*, 2006; Sass *et al.*, 2007), South American lakes have been little studied from this perspective. Our analyses of field data from South American lakes suggest a multimodal frequency distribution in phytoplankton concentration and an apparent distinction between lakes with scarce and abundant submerged macrophyte growth. The frequency distribution of water transparency, however, did not confirm this bimodal pattern (Fig. 3; Table 2). Within the region covered in the field campaign, the part richest in lakes is the Pampa Plain. Zooming in on this area revealed that satellite-derived water transparency was bimodally distributed in this subset of lakes (Fig. 5; Table 3).

Multimodality suggests the existence of alternative states, but is not sufficient proof of them, as such a pattern can also be caused by a multimodal distribution of the driving environmental factors rather than by underlying multiple attractors (Scheffer & Carpenter, 2003). Bimodality in spatial data does therefore not unequivocally confirm that an individual lake can actually switch from one state to the other. Nonetheless, bimodality is an important characteristic of bistable systems, and therefore, our results suggest that this phenomenon may not be limited to the temperate shallow lakes on which the alternative stable states theory has been based.

Obviously, multimodality in lake transparency in the Pampa Plain cannot simply be translated into alternative states in terms of phytoplankton or submerged macrophyte dominance. For instance, some clear lakes may lack abundant submerged macrophytes (Fig. 4c) and turbidity may sometimes be caused largely by inorganic material, humic substances and detritus rather than by phytoplankton (see high Kd's at relatively low chl-a concentrations in Fig. 4a). Indeed, in the Pampean lakes, inorganic turbidity plays an important role (Quirós *et al.*, 2002a; Allende *et al.*, 2009), and combined with the prevalence of eutrophic lakes (Quirós *et al.*, 2002a), this may explain the high proportion of turbid lakes in the Pampa region (Fig. 5).

Turbid lakes within our data set ranged in size from small to large. The clear lakes within our data set were all relatively small (surface area <0.5 km^2). Bimodality was therefore limited to small lakes (Table 3). This finding agrees with a study of over 8000 Wisconsin lakes that also found the strongest bimodality in lake transparency in small lakes (Sass *et al.*, 2007). Although large lakes may have clear littoral regions (Scheffer *et al.*, 1994; James *et al.*, 2009), large shallow lakes are generally less likely to be dominated by macrophytes (Scheffer & Van Nes, 2007). A range of mechanisms may explain the negative effect of lake size on water clarity, involving fish abundance, fish bioturbation and wind stress (reviewed by Van Geest *et al.*, 2003; Søndergaard *et al.*, 2005). Wind stress is likely to be an important reason why the large Pampean lakes never fall into the clear group (Figs 1, 5 & 6). Strong wind causes almost permanent resuspension of the sediments in these lakes (Torremorell *et al.*, 2007). Small lakes have a shorter fetch and hence experience less wind stress and less resuspension. These conditions may, in turn, lead to a higher macrophyte coverage that can reduce turbidity even further via various positive feedback mechanisms (e.g. Kosten *et al.*, 2009b).

It is striking how different the situation was for the two study periods, separated by 18 years. The division between clear and turbid lakes was much stronger, and more lakes were turbid, in 2005 than in 1987. More than 50% of the lakes that were clear in 1987 had become turbid in 2005 (Fig. 7). Several mechanisms may have caused the decrease in water transparency in these lakes. Phytoplankton biomass may have been lower in 1987 compared to 2005, because of the drastic increase in fertiliser use in the Pampa Plain in the intermediate period (FAO, 2004) enhancing eutrophication. Further, alterations in hydrology may have played an important role. The hydrological and climatic variability in the Pampa Plain is very high (Rennella & Quirós, 2006; Torremorell *et al.*, 2007). Indeed, 1987 was a much wetter year than 2005, and in the 2 months before the satellite image was taken, total precipitation was 407 mm in 1987 and only 222 mm in 2005 (data from the meteorological station of Junín, Servicio Meteorológico Nacional Argentino). This difference in precipitation is clearly visible in the images, with 39% more pixels being classified as water in 1987 than in 2005.

In addition, hydrology may have contrasting effects on water transparency in Pampean lakes, depending on their size and water source. For example, in large lakes connected to rivers, river discharge may have a strong negative effect on transparency (Rennella & Quirós, 2006). In these lakes, increase in flushing rates during wet periods has been found to lead to a strong increase in total phosphorus concentration, a decline in the *Daphnia* population, and a strong increase in phytoplankton biomass (Rennella & Quirós, 2006). However, the majority of the lakes in the Pampa Plain are small and either arheic or endorheic, receiving water through direct precipitation, from ground water or from low-order streams (Soriano *et al*., 1992). In these lakes, turbidity is generally highest during dry periods (Quirós *et al*., 2002b). This high turbidity is often caused by a combination of evapoconcentration, enhanced sediment phosphorus release causing phytoplankton blooms, and an increase in wind-induced resuspension facilitated by the lower water level (Quirós *et al*., 2002b). This suggests that, for the majority of Pampean lakes, the clear state should be more frequent during wet periods, as was observed in this study in 1987.

Overall, our data describe various patterns in line with the notion of alternative states. The outcomes are not conclusive, however, as indicated by the lack of bimodality in water transparency in the field data. The bimodality in chlorophyll-*a*, and the apparent division between lakes with abundant and scarce macrophytes, is not a formal proof of alternative attractors (Scheffer & Carpenter, 2003) although the results fit well with what is known from intensive studies in temperate European and North American lakes. Further, the fact that the bimodal pattern in transparency in the large satellite-derived data set is typical for smaller lakes, fits with the observations that large shallow lakes tend to be turbid, irrespective of nutrient loading. Our findings imply that, in principle, some of the lake management techniques based on alternative stable states theory may be applied beyond the temperate lakes for where they were developed.

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