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PHYTOPLANKTON

Tropical phytoplankton taxa in Aquitaine lakes (France)

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Abstract In the last decades, numerous exotic species of microalgae have been found in the continental waters of Europe. In three natural shallow lakes located in the southwest of France, several planktonic species typically encountered in tropical areas were observed during 2006 and 2007. The most representative taxa were *Planktolyngbya microspira* Kom. & Cronb. *P. circumcreta* (G. S. West) Anagn. & Kom., *Cyanodictyon tropicale* Senna, Delazari & Sant'Anna and *Staurastrum excavatum* var. *planctonicum* Krieg. These species had so far only been reported from African lakes and other tropical areas, but in this study they accounted for up to 58 and 12% of the total abundance and biomass, respectively, during spring and summer. Some of these lakes were studied in the 1970s and only exotic desmids were reported; but at that time, the three cited cyanobacteria were not described yet. Waterfowl are considered as the main dispersers because they migrate over long distances, transporting algae on the feet and feathers or in the digestive tract. In fact, the Aquitaine Region is one of the main bird migration corridors in Europe. Survival of cyanobacteria, diatoms and desmids carried by birds could be possible due to resting stages, sheaths investments or vegetative cells. In addition, global warming may have contributed to the success of these tropical species in temperate lakes. Indeed, minimal temperatures have increased significantly in the Aquitaine region over the last 30 years and could have played a key role in algal survival through winter.

Keywords Phytoplankton · Taxonomy · Tropical taxa · Bird migration · Aquitaine lakes · Climate change

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Introduction

Global warming is now a recognized phenomenon with biological consequences, including effects on the physiology, phenology, adaptation and distribution of species. Regarding distribution, a 3°C change in mean annual temperature corresponds to a shift in isotherms of approximately 300–400 km in latitude (in the temperate zone). Therefore, species are expected to move towards the poles in response to shifting climate zones (Hughes, 2000; Parmesan, 2006). This warming trend also includes the establishment of tropical algae in temperate systems of the Northern Hemisphere.

Numerous tropical and subtropical species of microalgae have been reported in the last decades in the continental waters of Europe (Padisák, 1997; Coste and Ector, 2000). In France, several species of exotic and invasive diatoms (Coste and Ector, 2000), cyanobacteria (Couté et al., 1997; Couté et al., 2004) and desmids (Capdevielle, 1982, 1985a; Kouwets, 1991; Kouwets, 1998) have been recorded in freshwater.

These algae have probably been dispersed in these temperate systems by several mechanisms, such as water, rain, air, wind, navigation, human activities, introduction of exotic macrophytes or animals, or organisms such as aquatic insects (beetles, dragonflies), mammals and birds (Coste and Ector, 2000; Figuerola and Green, 2002).

Birds are the most important dispersers because they carry out long migratory flights (Kristiansen, 1996; Figuerola and Green, 2002) transporting algae on feet and feathers and also in the digestive tract (Kristiansen, 2008). Algal species having significant resistance to desiccation may survive transport, and then may succeed in colonizing a new distribution area when their ecological demands are met.

The southwest of France is not an exception to this dispersal phenomenon. Indeed, in the Aquitaine region, numerous tropical taxa, such as *Anabaena promecespora* Frémy, *Anabaenopsis arnoldii* Aptekarj and *Staurastrum excavatum* var. *planctonicum* Krieger, were reported several decades ago (Capdevielle, 1985a). We studied five lakes in this French region and report here findings of numerous planktonic taxa, typical of tropical areas, in three of them. A further study (in preparation) will try to explain why, in spite of their geographical neighbourhood, these tropical populations do not colonize all the lakes. In this study, we focus on the possible mechanisms by which these exotic species may have arrived in these lakes, with an emphasis on waterfowl migration and on exotic macrophyte introduction. Then, we examine to what extent climate change may have contributed to the success of the exotic phytoplankton taxa in Aquitaine lakes.

Materials and methods

Three natural shallow lakes (Hourtin, Lacanau and Soustons) located along the Atlantic coastline of the southwest of France were studied (Fig. 1). Like other Aquitaine lakes, these three hydrosystems were formed approximately 18,000 years ago. They have common characteristics such as low altitude (maximum 15 m above the sea level) and sandy substrate but they differ in trophic status (meso-eutrophic to hypereutrophic). The area is characterized by an oceanic and temperate climate (temperatures between 5 and 25°C). The cold season extends from November to April and the warm season is between May and October. The rainy season is between October and December and dry season from June to September. Mean annual precipitation is 950 mm. Bank vegetation is rich and principally constituted by pines, willows and oaks. Table 1 shows the main morphological characteristics of the lakes (Vanden Berghen, 1964, 1968; Capdevielle, 1978; Dutartre et al., 1989; S.A.G.E, 2004).

In order to carry out this study, water samples for phytoplankton, pigments and chemical analyses were collected during seven seasons in the three lakes, every 3 months between May 2006 and November 2007. A total of 21 integrated samples was taken in the euphotic zone at the deepest point of the lakes. Phytoplankton samples were fixed on board with Lugol's solution, and their identification was carried out using the most recent taxonomic literature available: cyanobacteria (Hindák, 1988; Komárek and Anagnostidis, 1999; Komárek and Cronberg, 2001; Komárek and Komárková-Legnerová, 2002; Komárek, 2005; Komárek and Anagnostidis, 2005), Chlorophytes (Huber Pestalozzi, 1961; Komárek and Fott, 1983; Croasdale et al., 1984; Lenzenweger, 1997), Chrysophytes (Huber Pestalozzi, 1941; Starmarch, 1985) and diatoms (Krammer and Lange-Bertalot, 1986–1991). Algal densities were estimated by the settling technique with an inverted microscope (Utermöhl, 1958) at a magnification of 600 and 900×. At least 400 individuals were counted, and the results were expressed as cell abundance. Algal biomass was determined from the product of phytoplankton abundance and specific biovolume. Biovolumes were obtained by geometric approximations (Hillebrand et al., 1999; Olenina et al., 2006) from the measurement of at least 30 individuals, whenever

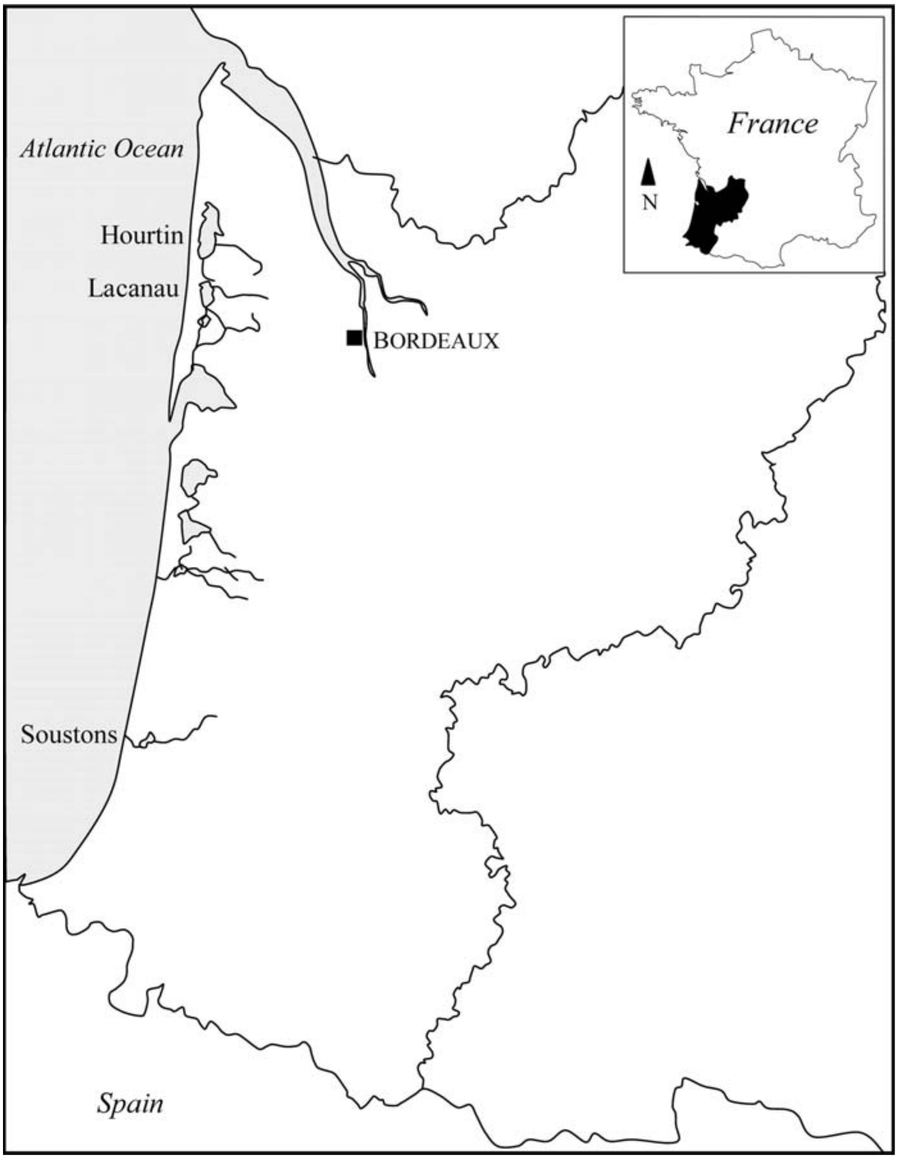

Fig. 1 Location of the lakes studied

possible, assuming a specific density of 1 g cm^{-3}. Relative biomass share (*pi*) of the exotic and rare taxa was calculated following the equation

$$pi = \frac{ni}{N}$$

where, ni = biomass of i-th taxa. N = total biomass of the sample.

Water temperature, pH, oxygen and conductivity were measured in situ using WTW probes (pH340, Oxi340 and LF340). Transparency was measured with a Secchi disc. In the laboratory, chemical and pigment analyses (dissolved organic carbon, nitrogen and phosphorus forms, chlorophyll *a*) were performed according to standard methods (NF EN ISO 13395, NF EN ISO 11732, NF EN ISO 25663, NF T 90-023, NF EN 1484, NF EN 13475, NF T 90-117). The physico-chemical data obtained in the course of the study are summarized in Table 2.

For data analysis, phytoplankton taxa representing a minimum of 2% of the total biomass in at least one sample were selected and the dissimilarity between

Table 1 Main characteristics of the lakes studied

Characteristics	Lake Hourtin	Lake Lacanau	Lake Soustons
Latitude	N 45°11′14″	N 44°58′33″	N 43°46′36″
Longitude	W 01° 03′23″	W 01°07′31″	W 01°18′55″
Altitude (m)	15	14	3
Area (km^2)	62	20	3.8
Catchment area (km^2)	360	285	350
Mixing regime	Polymictic	Polymictic	Polymictic
Maximum width (km)	4	3	2
Length (km)	18	7.7	4.6
Z_{max} (m)	11	8	1.9
Z_{mean} (m)	3.4	2.6	0.6
Residence time (years)	1.79	0.4	0.02
Volume (millions of m^3)	210	53	2.5
Substrate	Sandy	Sandy	Muddy-sandy
Trophic status	Eutrophic	Meso-eutrophic	Hypereutrophic

Table 2 Main physico-chemical characteristics of the lakes studied

	Lake Hourtin	Lake Lacanau	Lake Soustons
Water temperature (°C)	5.8–27.8 ± 3	5.6–27.9 ± 3.2	3.1–27.5 ± 3.3
pH	8.2 ± 0.3	7.6 ± 0.1	8.8 ± 0.6
Secchi transparency (m)	0.7 ± 0.1	1.2 ± 0.1	0.7 ± 0.2
Conductivity ($\mu S\ cm^{-1}$)	320 ± 10.2	249 ± 12.2	159 ± 5.1
O_2 ($mg\ l^{-1}$)	10.7 ± 0.8	9.9 ± 0.4	11.7 ± 1.1
$N–NH_4$ ($\mu g\ l^{-1}$)	47.2 ± 12.1	34.7 ± 13.4	57.8 ± 19.1
$N–NO_3$ ($\mu g\ l^{-1}$)	<d.l.	<d.l.	265.5 ± 157.7
$N–NO_2$ ($\mu g\ l^{-1}$)	12.1 ± 2.9	4.5 ± 1.3	15.4 ± 3.4
Total N ($\mu g\ l^{-1}$)	1554 ± 174.3	826 ± 237	1226.4 ± 201.4
$P–PO_4$ ($\mu g\ l^{-1}$)	22.8 ± 2.5	10.1 ± 2.3	18.4 ± 5.4
Total P ($\mu g\ l^{-1}$)	33.7 ± 2.5	25.9 ± 2.5	118.2 ± 22.5
DOC ($\mu g\ l^{-1}$)	23.9 ± 0.8	16.8 ± 0.7	5 ± 0.5
Chlorophyll *a* ($\mu g\ l^{-1}$)	19.6 ± 2.7	9.6 ± 1.7	73.9 ± 14.7

Values represent the mean and standard error, except the temperature which reports minimum and maximum values and the standard error. d.l.: detection limit = 70 $\mu g\ l^{-1}$ $N–NO_3$

lakes was calculated using the Bray and Curtis index. This analysis was carried out using PC-ORD software version 4.25 (2008-12-02).

Results

Species richness

Between spring 2006 and autumn 2007, 430 taxa were identified, 61 were common to the three lakes and 241 were recorded only in one of them. The highest species richness was found in Lake Soustons with 277 taxa (52% exclusive taxa, 22% common with the two other lakes). In Lake Lacanau, 244 taxa were identified, whilst in Lake Hourtin, we recorded the lowest species richness (174 taxa). Lakes Hourtin and Lacanau presented 35 and 27%, respectively, of the common species. Lake Hourtin had 21% exclusive taxa and Lacanau had 28%.

Exotic species

In these lakes, several exotic species (tropical, rare) mainly represented by cyanobacteria, desmids and diatoms were identified. They accounted for 10% of the total species number found in the three lakes (Fig. 2). Most of them had never been recorded in

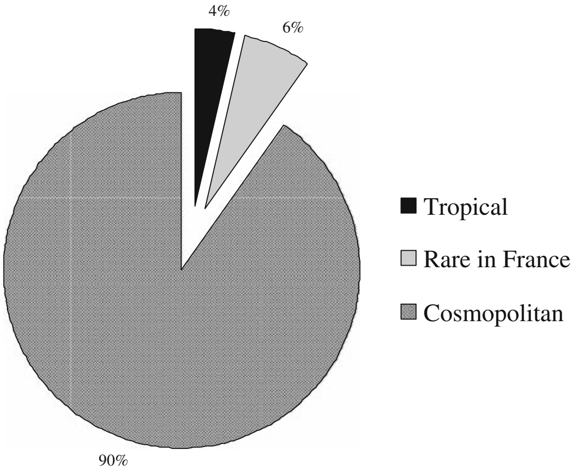

Fig. 2 Distribution of phytoplankton taxa (%) in Lakes Hourtin, Lacanau and Soustons over the period Spring 2006–Autumn 2007 (430 taxa were identified)

France before. In Table 3 are detailed the world distribution areas of the exotic and rare taxa found in this study. Even though many taxa were cosmopolitan, several tropical species actually dominated in terms of abundance and biomass. In the next paragraphs, some morphological and ecological observations for these tropical taxa are reported.

Planktolyngbya microspira Komárek et Cronberg (Figs. 3i and 4c)

This cyanobacterium, forming coiled filaments, was dominant in Lake Hourtin in spring and summer, but its biomass decreased drastically in autumn and winter (Fig. 5). Both in summer 2006 and 2007, *P. microspira* represented up to 12% of the total biomass and was dominant in terms of cell abundance in the lake (58% of total density in summer 2006—723,562 cells ml^{-1}). In Lake Lacanau, this species was also present but less abundant, reaching maximal biomass (12%) in spring 2006 (Fig. 6).

The filaments were solitary, regularly screw-like coiled, 1 μm wide, not constricted at cross-walls, with cells 1.5–2 μm long and the coils 12–18 μm high.

When dominant, *P. microspira* was associated in both lakes to *P. limnetica* (Lemmermann) Komárkova-Legnerová et Cronberg, *Aphanothece nidulans* Richter, *Staurastrum excavatum* var. *planctonicum* Krieger, *Chroococcus minutus* (Kützing) Nägeli, *Navicula radiosa* Kützing and *Puncticulata radiosa* (Lemmermann) Håkansson.

Planktolyngbya circumcreta (G. S. West) Anagnostidis et Komárek (Figs. 3g and 4d)

This cyanobacterium, also forming coiled filaments, was found in Lake Soustons in rather high relative abundance (up to 11% of total cell number), whilst its biomass reached only 1% in autumn 2006 (Fig. 7). It was also found in the other two lakes but in lower amount (Figs. 5 and 6).

Filaments were solitary, free-floating, irregularly coiled but sometimes narrowly screw-like. Sheaths were thin, firm and colourless, surrounding pale blue-green trichomes. Cells were more or less isodiametric, 1.8–2 μm wide; 1.8–2.5 (3) μm long, segments in the trichome were sometimes hardly distinguishable (especially at Lacanau and Hourtin). Coils were 20–22 μm in diameter, and the height between coils was about 10 μm.

The species associated to *P. circumcreta* in Lakes Hourtin and Lacanau were *Staurastrum excavatum* var. *planctonicum*, *Staurodesmus cuspidatus* (Brébisson ex Ralfs) Teiling, *Aphanothece nidulans*, *Chroococcus minutus*, *Planktolyngbya limnetica*, *Cyanodictyon tropicale*, *Navicula radiosa* and *Puncticulata radiosa*. Whereas in Lake Soustons, they included *Scenedesmus opoliensis* Richter, *Aulacoseira ambigua* (Grunow) Simonsen, *Staurosira construens* Ehrenberg, *Aphanizomenon gracile* Lemmermann, *Cylindrospermopsis raciborskii* (Woloszyńska) Seenayya et Subba Raju, and Peridiniales.

Cylindrospermopsis raciborskii (Woloszyńska) Seenayya et Subba Raju (Figs. 3a, b and 4a)

This cyanobacterium represented in Lake Soustons 1% of the biomass in summer 2006, whereas in spring 2007 an early developmental phase (young trichome) was observed (reaching 8% of the total phytoplankton biomass) (Fig. 7). In the first case, it presented heterocytes (Figs. 3a and 4a), whilst in the second case filaments did not clearly show differentiated cells neither heterocytes nor akinetes occurred (Fig. 3b).

The trichomes were solitary and straight or slightly curved, with vegetative cylindrical cells, length 6.4–9.4 μm, width 1.5–2.9 μm, mean trichome length 100 μm (range 35–180 μm). Gas vesicles were present. When heterocytes were observed, they were often present in at least one of the apices (5.1 × 2.3 μm),

Table 3 World distribution of the rare and exotic algae found in the Aquitaine lakes

	Taxa	French Lakes (this study)			World distribution	References
		Hourtin	Lacanau	Soustons		
Rare in France	*Anabaenopsis cunningtonii* Taylor			+	Belorussia, Germany, Slovakia, India, Tanzania, Senegal	(Hindák, 1988; Berger et al., 2005; Komárek, 2005)
	Anabaenopsis elenkinii Miller			+	Central Asia, Turkmenistan, Czech republic, Hungary, Russia, Ukraine, Slovakia, USA, France	(Hindák, 1988; Komárek, 1999; Leitão & Couté, 2005)
	Cyanonephron styloides Hickel			+	Finland, Germany, Sweden, Zimbabwe, The Netherlands	(Komárek & Anagnostidis, 1999)
	Radiocystis aphanothecoidea Hindák	+	+		Danube river (section from Austria to Hungary), Slovakia	(Komárek & Anagnostidis, 1999) (Hindák, 2006)
	Radiocystis geminata Skuja		+		The Netherlands, Poland, Slovakia, Finland, Greece, France	(Komárek & Anagnostidis, 1999; Leitão & Léglize, 2000; Hindák, 2006; Joosten, 2006; Lepistö et al., 2006; Pełechata et al., 2006)
	Pinnularia transversa (A. Schmidt) Mayer			+	New Zealand	(Krammer, 2000)
Tropical origin	*Cyanodictyon tropicale* Senna, Delazari & Sant'Anna	+	+		Brazil	(Senna et al., 1999)
	Cylindrospermopsis raciborskii (Woloszyńska) Seenayya & Subba Raju.		+	+	In France: 'Francs–Pêcheurs' pond (S Paris)	(Couté et al., 1997; Briand et al., 2002)
					La Claise river (centre of France), Léchir and Malsaucy ponds (E of France)	(Leitão & Couté, 2003)
					Lake Chanteraînes (N Paris)	(Briand et al., 2004)
					Seine à Ivry (SE Paris)	(Druart & Briand, 2002)
					Worldwide distribution: every continent, except the Antarctica; pantropical with expansion to all temperate zones	(Padisák, 1997; Vidal & Kruk, 2008)
	Planktolyngbya circumcreta (G. S. West) Anagnostidis & Komárek	+	+	+	Lake Victoria (Kenya, Uganda, Tanzania), Lake Chad (Chad, Cameroon, Niger and Nigeria), Congo, Zambia, Zimbabwe, Malawi, Mexico	(Compère, 1974; Komárek & Komárková-Legnerová, 2002; Komárková & Tavera, 2003; Komárek & Anagnostidis, 2005)
	Planktolyngbya microspira Komárek & Cronberg	+	+		Large tropical African lakes, Mexico	(Komárek & Cronberg, 2001; Komárek & Komárková-Legnerová, 2002; Komárek & Anagnostidis, 2005)
	Planktolyngbya minor (Geitler) Komárek & Cronberg			+	Indonesia, Central and Southern Africa, Brazil	(Komárek & Anagnostidis, 2005; Komárek & Komárková-Legnerová, 2007)
	Pseudanabaena recta Komárek & Cronberg			+	Africa	(Komárek & Anagnostidis, 2005)

Table 3 continued

Taxa	French Lakes (this study)			World distribution	References
	Hourtin	Lacanau	Soustons		
Staurastrum excavatum var. *planctonicum* Krieger	+	+		Indonesia, Asia, Africa (Nigeria, Tchad), South America, France	(Compère, 1977; Croasdale et al., 1984; Capdevielle, 1985a; Biswas & Nweze, 1990; Lenzenweger, 1997)
Capartogramma crucicula (Grunow ex Cleve) Ross			+	Africa, Seychelles, North and South America	(Coste & Ector, 2000)
Diadesmis confervacea Kützing			+	Africa, Asia, Tahiti, Caribbean Islands, Australia, Hungary (thermal waters)	(Coste, 1975; Coste & Ector, 2000)
Encyonema directiforme Krammer & Lange-Bertalot		+		New Caledonia	(Krammer, 1997)
Nitzschia dissipatoides Archibald		+		Africa (Mauritius Island)	(Coste & Ricard, 1984)

with attenuated and pointed ends (drop-like). Akinetes have never been observed. This genus was rarely observed in Lake Lacanau.

Although akinetes were not observed, all the morphological features correspond to *Cylindrospermopsis raciborskii*, which has become widely distributed in France in recent years (Couté et al., 1997; Leitão and Couté, 2003). *C. sinuosa* (Couté et al., 2004), identified from another Aquitaine lake, is narrower, has sinusoidal filaments and very pointed heterocysts, which is not the case in the lakes in our study.

In Lake Soustons, the species associated to *C. raciborskii* were very common taxa in France, such as *Aulacoseira ambigua*, *Fragilaria nanana* Lange-Bertalot, *Staurosira construens* and *Scenedemus opoliensis*.

Cyanodictyon tropicale Senna, Delazari et Sant'Anna (Figs. 3c and 4b)

This species was present in Lake Lacanau during almost the whole study period, reaching 23% of the phytoplanktonic biomass and 86% of the cell abundance in spring 2007 (Fig. 6). *C. tropicale* was also present in Lake Hourtin but to a lesser extent, reaching its highest biomass (6%) also in spring 2007 (Fig. 5).

Its morphology shows cells arranged in pairs, which are distant from each other and thus forming a pseudofilament. The cells were 1.5–2 µm long × 0.7–0.8 µm wide. The maximum measured length of pseudofilaments was 100 µm. The morphological characteristics of individuals found in our lakes correspond well to the description of *C. tropicale* (Senna et al., 1999). This species together with *C. filiforme* are similar to the genus *Wolskyella,* but *Cyanodictyon* cells are smaller (Mareš et al., 2008).

The species associated with *C. tropicale* in these two lakes were *Planktolyngbya limnetica*, *Chroococcus minutus*, *Puncticulata radiosa, Staurastrum excavatum* var. *planctonicum, Staurodesmus cuspidatus.*

Staurastrum excavatum var. *planctonicum* Krieger (Figs. 3m and 4h)

This desmid was present at all the seasons in Lakes Lacanau and Hourtin (Figs. 5 and 6). It reached 43%

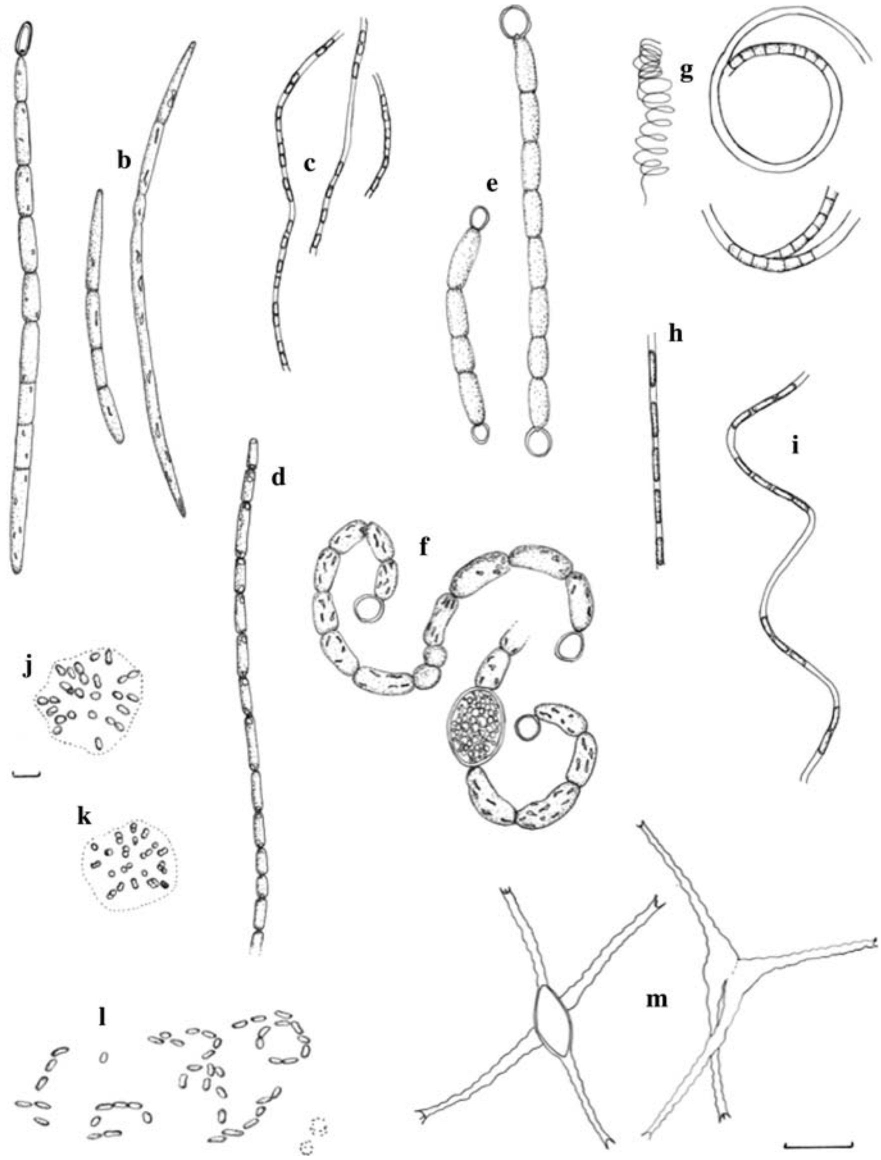

Fig. 3 Exotic species found in Lakes Hourtin, Lacanau and Soustons over the period Spring 2006–Autumn 2007. **a** *Cylindrospermopsis raciborskii* (**b**) young trichome of *Cylindrospermopsis* (**c**) *Cyanodictyon tropicale*, (**d**) *Pseudanabaena recta*, (**e**) *Anabaenopsis cunningtonii*, (**f**) *A. elenkinii*, (**g**) *Planktolyngbya circumcreta*, (**h**) *P. minor*, (**i**) *P. microspira*, (**j**) *Radiocystis aphanothecoidea* (**k**) *R. geminata*, (**l**) *Cyanonephron styloides*, (**m**) *Staurastrum excavatum* var. *planctonicum* (Scale bars = 10 μm). Only the illustrations of *Radiocystis aphanothecoidea* and *R. geminata* have a reduced scale

of the total planktonic biomass in autumn 2006 for Lacanau and 45% in autumn 2007 for Hourtin.

This variety differs from *Staurastrum excavatum* because of its larger size (12–20 × 40–66 μm), subhorizontal arms and a less concave apex (Compère, 1977). Dimensions of our specimens were: without processes: 9 × 10 μm, with processes: 53 × 53 μm, isthmus: 5.3 μm wide, thickness: 6 μm.

The associated species in both lakes were *Planktolyngbya limnetica*, *Aphanothece nidulans*, *Planktolyngbya microspira*, *Chroococcus minutus*, *Navicula radiosa*, *Puncticulata radiosa*, *Staurodesmus cuspidatus*, *Cyanodictyon tropicale*, *Aulacoseira ambigua*.

Apart from the taxa mentioned above, other exotic species were found occasionally, but they never dominated. This is particularly the case in the

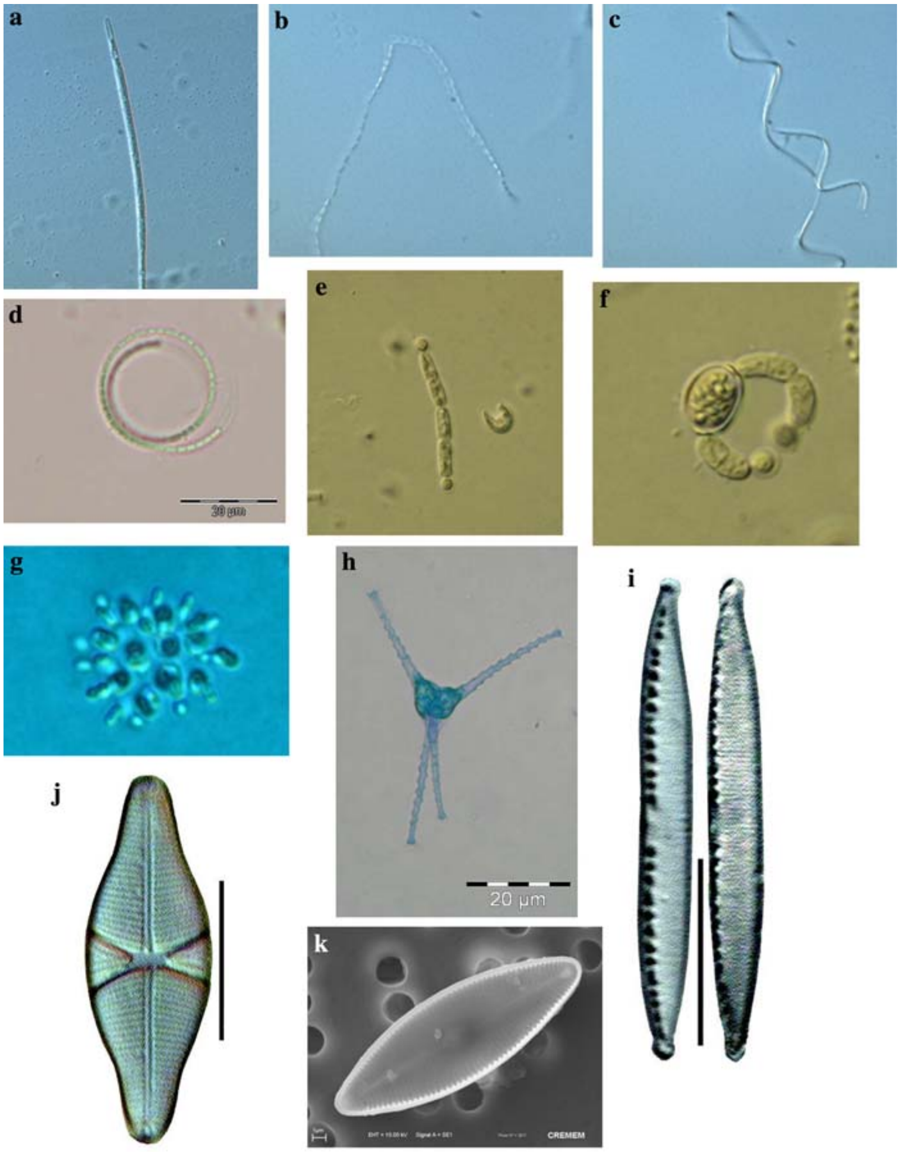

Fig. 4 Exotic species found in Lakes Hourtin, Lacanau and Soustons over the period Spring 2006–Autumn 2007. **a** young trichome of *Cylindrospermopsis*, (**b**) *Cyanodictyon tropicale*, (**c**) *Planktolyngbya microspira*, (**d**) *P. circumcreta*, (**e**) *Anabaenopsis cunningtonii*, (**f**) *A. elenkinii*, (**g**) *Radiocystis aphanothecoidea*, (**h**) *Staurastrum excavatum* var. *planctonicum*, (**i**) *Nitzschia dissipatoides*, (**j**) *Capartogramma crucicula*, (**k**) *Diadesmis confervacea*. All the pictures are in optical microscope except k, made with SEM

shallow and hypereutrophic Lake Soustons, where the greatest richness of tropical taxa was observed. All the species illustrated in Fig. 7 were present at all the sampling seasons, except winter, and the most remarkable were *Planktolyngbya minor* (Geitler) Komárek et Cronberg (Fig. 3h), *Pseudanabaena recta* Komárek et Cronberg (Fig. 3d), *Cyanonephron styloides* Hickel (Fig. 3l). Some tropical diatoms were also concerned like *Diadesmis confervacea* Kützing (Fig. 4k) and *Capartogramma crucicula* (Grunow ex Cleve) Ross (Fig. 4j). In Lake Lacanau, *Nitzschia dissipatoides* Archibald (Fig. 4i) and *Encyonema directiforme* Krammer et Lange-Bertalot were also present.

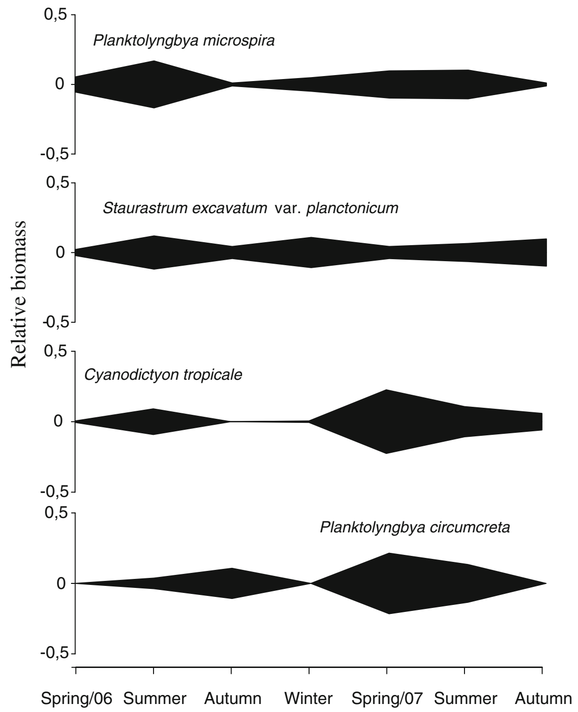

Fig. 5 Relative share of tropical species in the total biomass observed in Lake Hourtin over the period Spring 2006–Autumn 2007

In addition, some unusual species in France were also found in Lake Soustons (Fig. 7), particularly the cyanobacteria *Anabaenopsis cunningtonii* Taylor (Figs. 3e and 4e) and *A. elenkinii* Miller (Figs. 3f and 4f). Our two *Anabaenopsis*, together with the less common *Radiocystis geminata* Skuja (Fig. 3k) and *R. aphanothecoidea* Hindák (Figs. 3j and 4g) found in Lakes Lacanau and Hourtin, have a Central European and Eastern distribution (Hindák, 1988; Komárek and Anagnostidis, 1999; Komárek, 2005) (Table 3).

As shown in Fig. 8, the similarity index highlighted that the three lakes behave quite differently with Lake Soustons standing out particularly. The most homogeneous was Lake Hourtin, whose phytoplankton composition was fairly stable along the sampling seasons. In this lake, the tropical *Planktolyngbya microspira* and *Staurastrum excavatum* var. *planctonicum* were generally the dominant taxa, whilst *Cyanodictyon tropicale* characterized the community in Lake Lacanau. In Lake Soustons, *Planktolyngbya circumcreta* and *Cylindrospermopsis raciborskii* were the most relevant tropical taxa.

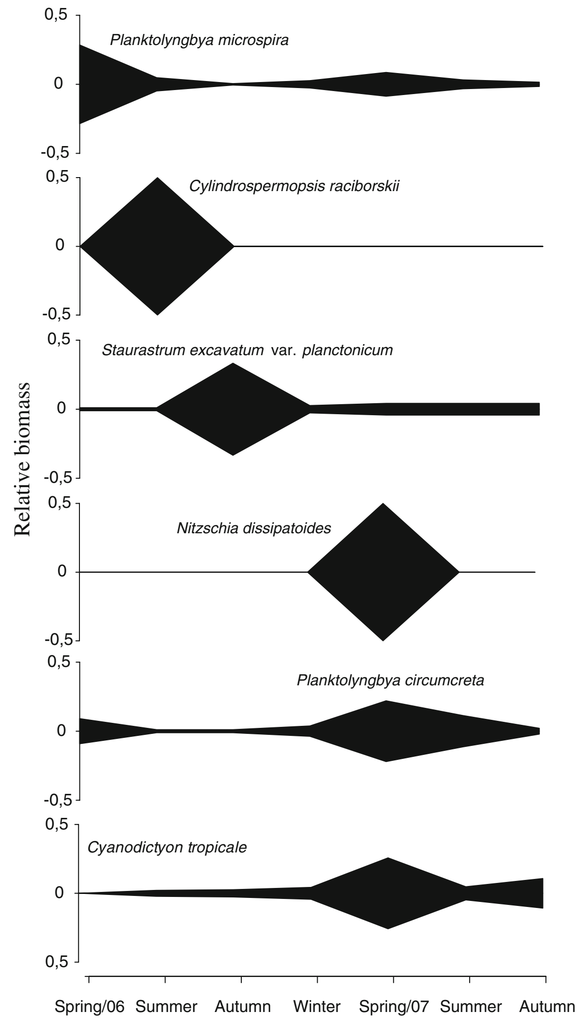

Fig. 6 Relative share of tropical and rare species in the total biomass observed in Lake Lacanau over the period Spring 2006–Autumn 2007

Discussion

In this study, we found several exotic algal taxa, usually recorded from tropical freshwater bodies, in three lakes of the French Aquitaine region. The presence of exotic algae in these systems is not recent. In papers concerning these lakes, published between 1978 and 1985 (Capdevielle, 1978, 1982, 1985a), P. Capdevielle already recorded the presence of several species for the first time in France. He reported that some of these algae were until then known from northern countries and mostly from tropical and subtropical regions. In these floristic studies, he indicated that amongst the 99 identified

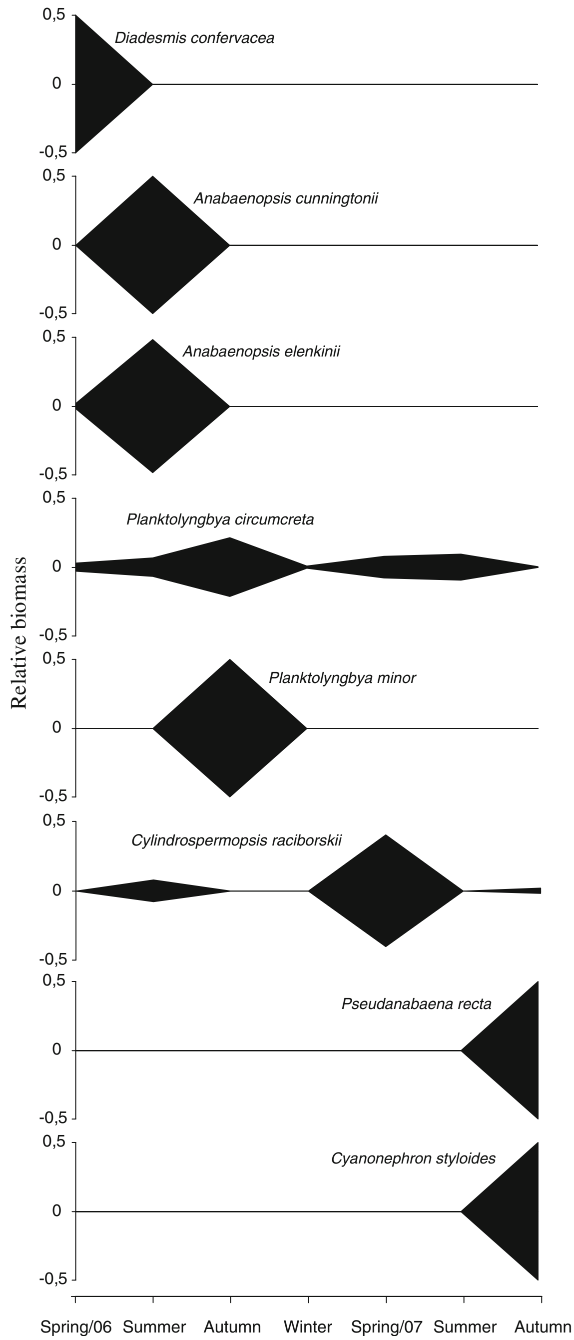

Fig. 7 Relative share of tropical and rare species in the total biomass observed in Lake Soustons over the period Spring 2006–Autumn 2007

taxa, 38 were typical of warm regions (Capdevielle, 1985a).

Several phytoplankton taxa found in this study were reported previously in Africa and other tropical regions such as the desmid *Staurastrum excavatum* var. *planctonicum* (Compère, 1977; Croasdale et al., 1984; Capdevielle, 1985a), the filamentous cyanobacteria *Planktolyngbya microspira*, *P. circumcreta*, *P. minor*, *Pseudanabaena recta* and the pseudo-filamentous *Cyanodictyon tropicale* (Senna et al., 1999; Komárek and Cronberg, 2001; Komárek and Anagnostidis, 2005) (Table 3). These species showed a clearly seasonal occurrence, being present especially in the warmer season. This suggests that temperature is presumably a key factor favouring maintenance and development of these species in temperate lakes. This preference for the warm season has been observed in *Cylindrospermopsis raciborskii*, which occurs only in the summer period in temperate areas, whereas it maintains populations all year round in tropical areas (Padisák, 1997; Briand et al., 2004).

Most of the exotic species found in this study had not been reported in France before. However, we had the opportunity to analyse some preserved samples taken in Lake Lacanau by Capdevielle in 1981, and we identified *Planktolyngbya microspira*, *P. circumcreta* and *Cyanodictyon tropicale*. This shows that these taxa were present in Lake Lacanau more than 25 years ago. However, Capdevielle could not report them because they were not yet described in the literature.

One hypothesis to explain the presence of tropical algae in the French lakes is that they were transported by migratory birds. Actually, waterfowl are considered as a major disperser, because more than any other organism, they can migrate over long distances, transporting plant and invertebrate propagules in their digestive system or attached to their bodies (feet, feathers) (Kristiansen, 1996; Clausen et al., 2002; Figuerola and Green, 2002).

Moreover, the Aquitaine Region is one of the most important corridors and staging posts for bird migration in Europe. This region located on the Atlantic coastline is characterized by natural habitats such as forests, reed beds, meadows, marshes and stretches of water, as well as by a temperate oceanic climate. All these features attract a large range of different bird species that either inhabit these areas permanently (resident species) or visit them temporarily (migratory species) (www.parc-ornithologique-du-teich.com).

Several species of ducks belonging to the Anatidae family are considered as potential vectors of tropical algae in the Aquitaine lakes (Claude Feigné, pers.

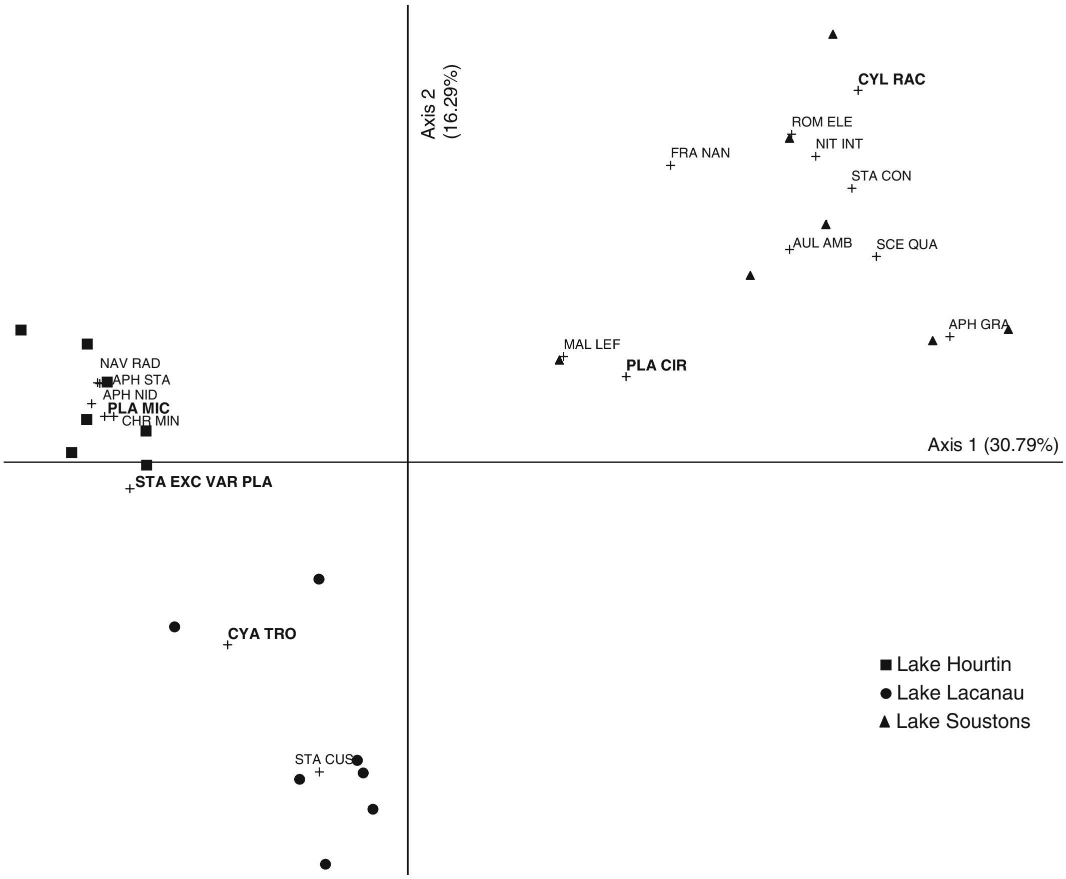

Fig. 8 Similarity Index (Bray-Curtis) of phytoplankton biomass in Lakes Hourtin, Lacanau and Soustons over the period Spring 2006–Autumn 2007. APH GRA: *Aphanizomenon gracile*, APH NID: *Aphanothece nidulans*, APH STA: *Aphanothece stagnina*, AUL AMB: *Aulacoseira ambigua*, CHR MIN: *Chroococcus minutus*, CYA TRO: *Cyanodictyon tropicale*, CYL RAC: *Cylindrospermopsis raciborskii*, FRA NAN: *Fragilaria nanana*, MAL LEF: *Mallomonas lefevriana*, NAV RAD: *Navicula radiosa*, NIT INT: *Nitzschia intermedia*, PLA CIR: *Planktolyngbya circumcreta*, PLA MIC: *Planktolyngbya microspira*, ROM ELE: *Romeria elegans*, SCE QUA: *Scenedesmus quadricauda*, STA CON: *Staurosira construens*, STA CUS; *Staurodesmus cuspidatus*, STA EXC VAR PLA: *Staurastrum excavatum* var. *planctonicum*

comm.). Amongst others, we can mention the Northern Pintail (*Anas acuta*), the Northern Shoveler (*Anas clypeata*) and the Garganey (*A. querquedula*). These species overwinter in tropical African lakes (Senegal, Niger, Tchad). Then, they migrate to the north of Europe during spring, staging in the Aquitaine littoral to rest and feed. Afterwards, they continue their journey to Scandinavia, Russia and to other Northern European countries for breeding. Finally, at the end of autumn they return to Africa, following the same route. These ducks migrate the longest distances to breed in northern Europe. They can carry out migrations with a mean speed of 70 km h^{-1} and a maximum distance without refuelling stops of 2000–5000 km (Clausen et al., 2002). Therefore, as the distance between Ivory Coast and Lake Hourtin is of the order of 3800 km, the non-stop transport of algae from Africa to the French lakes is certainly possible.

The hypothesis that algae can be transported by birds from foreign countries to the French lakes was confirmed by Capdevielle (1985b), who found exotic algae in ducks' feathers. Interestingly, he identified a different algal composition between the pre- and post-reproduction migrations. This confirms that birds can transport algae from their wintering (Africa) and from their reproduction zones (Northern Europe) to the littoral Aquitaine lakes. In fact, several species common in Central and Eastern Europe and rarely reported in France, such as *Radiocystis aphanotecoidea*, *Anabaenopsis cunningtonii* and *A. elenkinii*

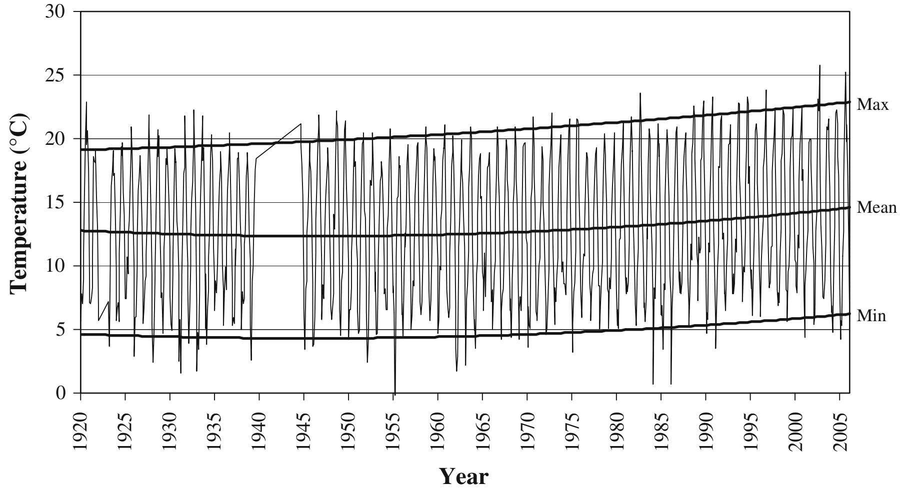

Fig. 9 Evolution of the surface temperature from 1920 until today in the Aquitaine Region (Source: Météo France). *Dark lines* represent the trends of minimal, mean and maximal temperatures

(Hindák, 1988; Komárek and Anagnostidis, 1999; Komárek, 2005), were also found in this study. They were most likely introduced by those birds on their post-reproduction migration.

Another hypothesis to explain the occurrence of tropical algae in the Aquitaine lakes could also be the introduction of exotic macrophytes. In fact, several exotic vascular plants such as *Lagarosiphon major* (South Africa), *Myriophyllum aquaticum*, *Egeria densa* and *Ludwigia grandiflora* (South America) were detected 25 years ago in these lakes, and some of them have spread rapidly. Their presence in France and other European countries is probably due to their use for ornamental purposes (aquaria and ponds) but also by migratory aquatic birds (Dutartre and Capdevielle, 1982; Dutartre, 1986; Dutartre et al., 1989). However, we favour the hypothesis of bird migration because tropical algae were present in the lakes studied here before the first observation of exotic macrophytes.

If we consider the idea that birds are the transport vector, questions arise about algal resistance to the migratory travel and especially to desiccation. As reported by Kristiansen (2008), dispersal from one water body to another involves drastic changes of environment. If the transportation time is short, desiccation may not occur. If the transportation time is long, then resistance to desiccation is possible, involving diverse mechanisms (Coesel et al., 1988) such as resting stages, spores, cysts and cells embedded in jelly (Kristiansen, 1996). In fact, the most abundant tropical species found in the Aquitaine lakes mainly belong to the morphotypes of the genus *Planktolyngbya* and *Cyanodictyon*.

They are characterized by sheath investments generally composed of polysaccharides (Robbins et al., 1998; Stal, 2000), which regulate the loss and uptake of water from cells (Potts, 1999). This feature may play an important role in the desiccation tolerance of algae after many hours of transport (Kristiansen, 1996). Even if the sheaths are thicker, the viability of dried vegetative filaments for several days was clearly shown on *Lyngbya martensiana* (Agrawal and Singh, 2002; Gupta and Agrawal, 2006). Other resting forms such as the akinetes are also highly resistant to desiccation (Sutherland et al., 1979) and are more likely to survive long travels in the gut of birds than common filaments (Padisák, 1997). Yamamoto (1975) demonstrated that *Anabaena cylindrica* had different levels of tolerance to desiccation: desiccated akinetes kept germination ability after storage in darkness for more than 5 years, whilst vegetative cells failed to grow after only 15 days of storage.

In the case of diatoms, subaerial or aerophytic forms can survive desiccation for a long time. They do not appear to produce morphologically distinct resting stages in response to environmental stress, as the vegetative cells themselves become dormant (Round et al., 1990). This author also mentioned that only a few species of diatoms are known to produce resting spores and in some of them (e.g. *Craticula cuspidata*) this mechanism is produced in response to desiccation. In an experiment carried out by Atkinson

(1980), several species of diatoms were fed to ducks and only *Asterionella formosa* was viable after digestion. It was found in faeces from 2 to 20 h after feeding, 2 h corresponding to a 110–220 km flight depending on the bird and wind conditions. In the case of desmids, vegetative cells remain viable longer when carried inside the digestive tract of the birds, than when carried externally (Kristiansen, 1996).

Birds are likely responsible of the introduction of exotic algae in temperate lakes, but their rapid expansion in northern latitudes is probably a consequence of the global temperature increase observed in the last decades. This distribution trend also concerns other organisms, such an example, southern and warm-water species have gradually come to dominate the fish and invertebrate communities of the upper Rhône River (France) over the last 20 years (Daufresne et al., 2004). Regarding the phytoplankton, one of the best examples is the pantropical *Cylindrospermopsis raciborskii*, for which data are accumulating from temperate regions of North America and in several countries of Europe in the last years (Padisák, 1997).

Recent climate change may create an environment suitable to tropical and subtropical species, which can now persist even in French lakes. In fact, air temperatures in the Aquitaine Region from 1920 until today (Fig. 9) have increased by a mean +1.7°C, with +0.7°C in the last 30 years (Météo France). This feature is widely observed around the globe and is more relevant at higher northern latitudes (IPCC, 2007). However, even more important than the mean temperatures is the increase of the minimal temperatures (+0.6°C from 1975 to now), and this may be the main explanation for the success of tropical algae in our lakes. If the newly arrived algae die each winter, annual recruitment is not sufficient to develop large populations. However, if the algae resist the milder winter conditions, the populations can develop through the years from increasing inocula after winter, and finally reach significant numbers in the newly colonized environment, and in some cases become dominant.

These phenomena indicate that wherever a biotope suitable for a certain organism exists, that organism will appear there as soon as sufficient time has elapsed to allow it to be transported through the air and to settle in that locality (Gislén, 1948). Evidently, the climate warming observed in the last decades had accelerated this process in northern latitudes.

Conclusion

Exotic algae have probably been repeatedly introduced in the three Aquitaine lakes studied by birds during their regular migrations. In fact, algae can resist transport conditions for hours through several mechanisms such as resting stages, cysts or sheath investments. Progressive warming of these temperate lakes probably stimulated the accelerated and successful proliferation of the introduced tropical algae. Increases in the minimal temperatures in the last decades may have played a key role in the persistence of these species in winter and their consequent success in warmer seasons. The tropical species identified, particularly the Cyanobacteria, are morphologically identical to the populations found in African lakes. However, proving that both populations are genotypically identical will require their isolation and molecular analysis (Komárek, pers. comm.).

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