Effects of wind-induced sediment resuspension on distribution and morphological traits of aquatic weeds in shallow lakes

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ABSTRACT

The spread of invasive aquatic plants (*i.e.*, aquatic weeds) requires a broader knowledge of the factors determining their settlement at the lake scale, in order to improve management practices and biomonitoring. Among hydrodynamic pressures, wave action might influence submerged vegetation distribution in shallow lakes and potentially engender modifications of plant morphological traits. We here report a field survey conducted between 2014 and 2015 in French Atlantic Lakes to assess the spatial distribution and biomass production of two rooted aquatic weeds, *Egeria densa* Planch. and *Lagarosiphon major* (Ridl.) Moss, in relation to wind-induced sediment resuspension, water depth and sedimentary features. Moreover, we explored the relation between plant morphological traits and hydrodynamic disturbance under *in situ* conditions. At the lake scale, *E. densa* and *L. major* formed extensive monospecific stands, and occurred in the same areas only at low biomass. Both monospecific and mixed stands preferentially developed in shallow-sheltered or deep-exposed areas. Plant morphological traits showed different patterns in function of sediment resuspension according to the species and the lake. The influence of resuspension was however not systematic, with many cases where morphological traits were not affected at all. Maximum stem length appeared to be the most correlated trait towards sediment resuspension. Moreover, we found a significant correlation between the biomass and the sedimentary organic matter, indicating an interaction between the organic substrate preference of the plants and the effect of the canopy on fine particles sedimentation. On the whole, we highlighted the link between plant distribution, phenotypic plasticity and sediment resuspension, with calm-water zones favouring the settlement of dense vegetated stands. Our study could thus contribute to improve prediction models for identifying suitable areas for potential colonization by aquatic weeds. Further research is needed to better understand the role played by hydraulic forces in structuring the habitats in shallow lakes.

Key word: Exotic invasive hydrophytes; sedimentary organic matter; wind exposure; biomonitoring; colonization depth; alien plant management.

INTRODUCTION

Wave exposure is one of the abiotic factors influencing aquatic plant communities in freshwater ecosystems (Bornette and Puijalon, 2010 and references therein). Waves strongly affect the distribution of submerged macrophytes in shallow lakes, potentially driving to morphological damages on plant architectural features (Keddy, 1982; Strand *et al.*, 1996; Riis and Hawes, 2003; Schutten *et al.*, 2004). Water movement impacts on rooted aquatic plants depend on the magnitude of the hydraulic forces, the resistance capacity of the plants (*i.e.*, root anchorage and stem breaking strength) and the sediment type (Schutten *et al.*, 2005). For instance, mechanical stress directly shapes morphological features and biomass allocation. The plasticity in plant biomass (*i.e.*, the root to shoot ratio, R:S), can be considered as an adaptation to physical disturbance (Chambers *et al.*, 1991; Barrat-Segretain, 2001). Permanent exposure to water movement is able to disturb or alter plants development (Doyle, 2001), shoot elongation (Ellawala *et al.*, 2011), branch length and branch number (Strand and Weisner, 2001), seedling and

germination (Foote, 1988) and shoot density (Chambers *et al.*, 1991). As a consequence, aquatic plants demonstrate capacities to morphologically adapt when they are confronted to hydrodynamic forces (Puijalon *et al.*, 2008).

Waves may also exert indirect impacts on aquatic plants through sediment resuspension. Indeed, turbidity, associated to light attenuation, and depth gradient are structuring factors for rooted macrophytes distribution at intermediate depth (Lehmann *et al.*, 1997). Submerged macrophytes distribution is then potentially limited by wave energy, with some species colonizing deeper parts of the lakes in order to avoid water mixing and sediment suspension caused by the orbital velocity of waves reaching the shoreline (Chambers, 1987). Waves are able to influence epiphytic growth, sediment grain size and water quality by water mixing, that selecting aquatic species according to their resistance against breakage (Koch, 2001; Bornette and Puijalon, 2010). On the other hand, the presence of dense vegetated mats can increase the sedimentation of fine particles and favor organic matter build-up (Madsen *et al.*, 2001).

Hydrocharitaceae family gathers aquatic rooted macro-

phytes, usually submerged, among which many species are considered as aquatic weeds. This is particularly the case for the two species *Egeria densa* Planch. and *Lagarosiphon major* (Ridl.) Moss, which occur in European freshwater ecosystems in both lentic and lotic waters (Dutartre *et al.*, 1999; Celesti-Grapow *et al.*, 2010; Hussner, 2012; Brundu, 2015). In natural ecosystems, they form large and dense stands causing important biogeochemical and management problems when climatic, hydromorphologic and trophic characteristics are advantageous for their development (Bini *et al.*, 1999; Bini and Thomaz, 2005; Yarrow *et al.*, 2009; Ribaudo *et al.*, 2014). Light attenuation and fetch are among the most important variables determining the occurrence of the genus *Egeria* (Bini and Thomaz, 2005). Moreover, the onset of dense vegetated stands and the subsequent deposition of fine particles may significantly contribute to water clarity and improve light penetration (Madsen *et al.*, 2001; Siffedine *et al.*, 2011).

Several studies on the response of submerged plants to hydrodynamic forces have been carried out in mesocosms, whereas *in situ* conditions embed interactions with light, temperature and depth (Doyle, 2001; Sand-Jensen, 2003; Ellawala *et al.*, 2011; Riis *et al.*, 2012; Redektop *et al.*, 2016). The investigation of wave exposure on aquatic weeds through field surveys is thus a key element for improving biomonitoring approaches in shallow lakes. Indeed, the integration of water depth, wind velocity and fetch in prediction models might help in detecting preferential habitats and physical thresholds for the spread of invasive macrophytes. In this study, we report the results of a survey conducted between 2014 and 2015 to assess the plant coverage and the biomass production of two rooted aquatic weeds, *E. densa* and *L. major*, in relation to sediment resuspension probability and sedimentary features. The objectives of the research were i) to obtain a quantitative assessment of aquatic weeds distribution and biomass in French Atlantic Lakes; ii) to evidence the dependence of plant distribution on sediment resuspension and water depth; and iii) to highlight the relation between morphological traits and physical disturbance within *in situ* conditions.

METHODS

Study area

French Atlantic Lakes (Carcans-Hourtin, Lacanau, Cazaux-Sanguinet and Parentis-Biscarrosse) are large shallow lakes located in the south-western coast of France, less than 5 km from the ocean (Fig. 1). These lakes were originated from the barrage of coastal rivers by littoral dunes (Tastet *et al.*, 2008). The eastern bottom is characterized by a very gentle slope while the western bottom presents a steep slope at the dunes' foot. These four lakes are classified from oligo- to mesotrophic and constitute the southern distribution limit for isoetid lawns in Europe (Cellamare *et al.*, 2012; Bertrin *et al.*, 2013; Ribaudo *et al.*, 2017). The main uses of these lakes are recreational activities such as boating, bathing, hunting and angling during a limited part of the year. Here, *L. major* appeared in Cazaux-Sanguinet in 1960, started to be signaled as a nuisance in late '70s and spread all over the four lakes in the following decades, showing a slow dynamic of invasion between 1985 and 2005 (Dutartre and Capdevielle, 1982; Bertrin *et al.*, 2013). *E. densa* was not reported in the vegetation surveys of these lakes until 2006, and only two of them were concerned (Bertrin *et al.*, 2013). Thanks to mild water temperatures (>16°C from April to October), the vegetative period of the two aquatic weeds is here extended during the year.

Dense stands mapping and traits measurement

In order to assess the dense stands boundaries of the two hydrophytes, vegetation surveys were carried out during the standing crop period (May-September) by echosounding, during 2014 in Carcans-Hourtin (HOU) and Lacanau (LAC) lakes and during 2015 in Cazaux-Sanguinet (CAZ) and Parentis-Biscarrosse (PAR) lakes. The scan sonar surveys were carried out on a boat equipped with a GPS coupled to a Humminbird 1197C. Transects were irregularly spaced along the lake's surface, according to the local bathymetry, and were concentrated along the shallowest areas of the lakes (<5 m), typically perpendicularly to the shoreline. Profiles were intensified when plant density was high; additionally, GPS points were marked in correspondence with the boundaries of each dense stand. Due to the presence of restricted areas for military purpose, in CAZ and PAR lakes some areas were not prospected by boat, but by feet. Concomitantly, plant collection was systematically carried out with a rake (harvested surface = 0.28 m^2), every 200 to 500 m, according to the local extension and homogeneity of the stands; in correspondence, a GPS point and the colonization depth was recorded. The operation was carried out by the same operator to minimize the error source (Johnson and Newman, 2011); plants were kept wet and refrigerated during the transport.

In laboratory, morphological traits and biomass were measured. For each shoot, maximal stem and root length (cm), number of stems (stems $shoot^{-1}$) and number of roots (roots $shoot^{-1}$) were measured. For each sample, shoots were counted for estimating shoot density (shoots m^{-2}). Finally, plants were sorted for above- (stems) and belowground (roots) parts and dried at 70°C for at least 72 h until stabilized dry weight. Total biomass was obtained by the sum of above- and belowground dry weight (g_{DW} m^{-2}); root to shoot ratio (R:S) was calculated as the ratio of the below- and aboveground dry weight. Also,

additional data obtained along unpublished studies were included in the dataset for the comparison against sedimentary resuspension. Those data were collected at different seasons between late summer 2013 and late summer 2016 following the same protocol described above.

At the office, sonar recordings were read by Humminbird PC and transferred to a GIS system (ArcGIS 10.2 platform, 2017). Verification of the stand boundaries were made on each profile through the program HumViewer. Transects and GPS points were then geolocated and polygons were manually reconstructed to produce distribution maps. From biomass measurements, the mean biomass value ($3<n<5$) was associated to each shape in the distribution map.
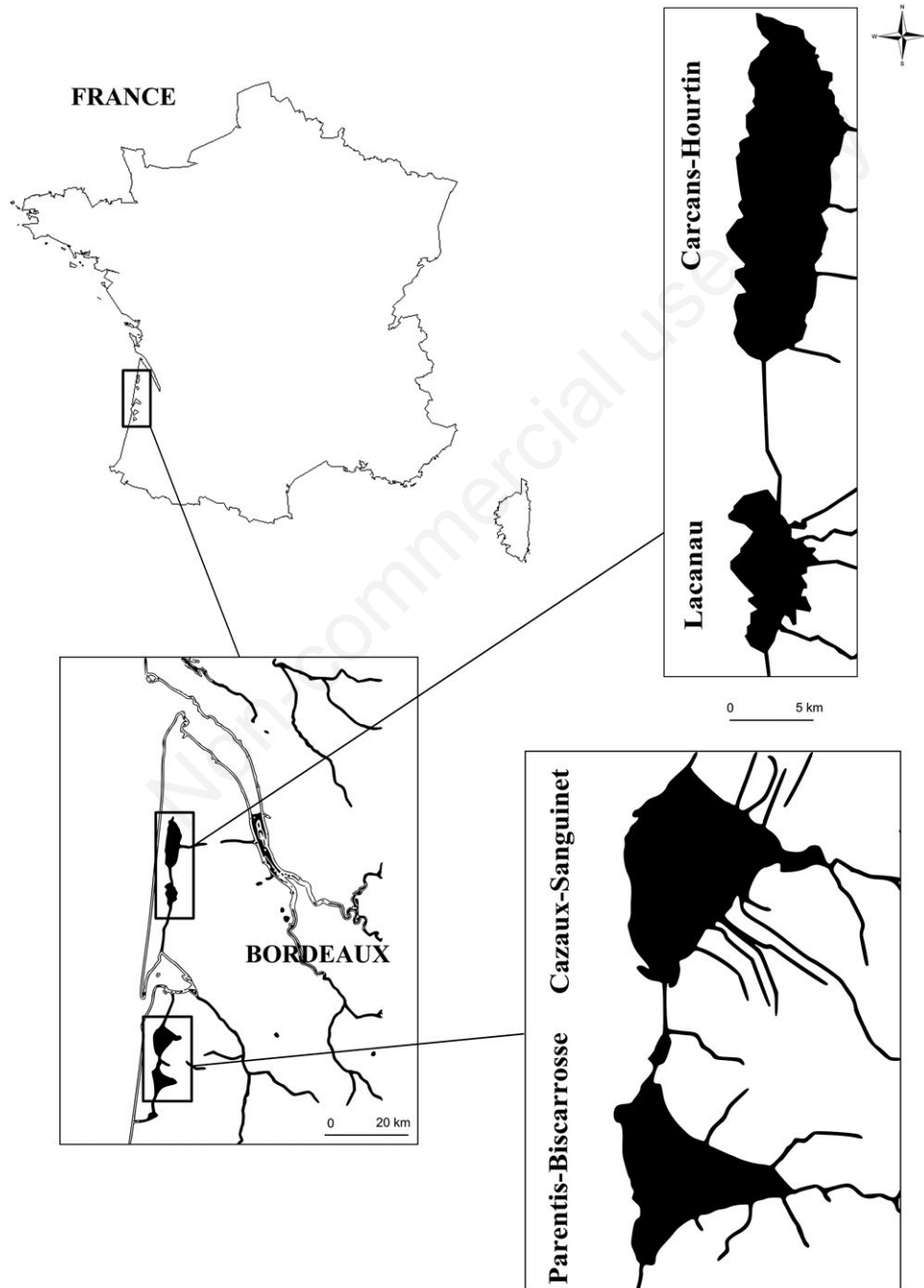

Fig. 1. Geographic location of French Atlantic Lakes.

Sediment characterization

Concomitantly to biomass harvesting, sediment samples were collected by means of a Van Veen grabber (volume = 2.5 L) and, after homogenization of the whole sample, transferred in triplicates into 40 mL plastic vials; samples were kept in a cooled box and immediately frozen at the laboratory. Several sediment samples were also collected in bare areas of the prospected shores. Analyses of sedimentary bulk density, porosity, water content and organic matter (OM) content were performed according to standard procedures, as described in Ribaudo *et al.* (2017).

Bathymetry and sediment resuspension probability

A rasterized georeferenced bathymetric map was provided by the Adour-Garonne Water Agency. Each open-water raster cell had a resolution of 10 m. The probability of sediment resuspension was based on wind data collected at a weather station located in Cap-Ferret (44°37'54"N, 1°14'54"W, 9 m above chart datum; wind measurement height above the ground: 10 m). The velocity (m s^{-1}) and direction (°) of the wind, averaged each 10 min, were available for this station. We used the maximum daily values of both parameters provided by the French climate normals (Météo France) obtained between November 2012 (one year before the first sampling campaign) and November 2016 (date of the last sampling campaign), for a total of 1451 days.

The wind is able to generate waves and currents depending on the water depth and the fetch (*i.e.*, the length of open water without any obstacle in a distinct direction). Wave formation is therefore influenced by the size and the shape of the lake, as well as by its exposure to the prevailing winds (Keddy, 1982; Schutten *et al.*, 2005). In this study, we calculated the fetch on the all grid cells for each wind compass direction (0-360 in 10-degree increments) as described in the U.S. Geological Survey Wind Fetch Model (Rohweder *et al.*, 2012) with ArcGIS 10.2 platform. We also calculated the probability of sediment resuspension thanks to the Wave Model (Rohweder *et al.*, 2012) with ArcGIS. This model calculates the maximum orbital wave velocity (um, expressed as m s^{-1}) using water depth from the bathymetric map and the calculated wave length, height and period as described below:

$$um = \pi \times \text{wave height} / (\text{wave period} \times \sinh \times (2\pi \times \text{water depth} / \text{wave length})) \quad \text{(eq. 1)}$$

The maximum orbital wave velocity, as it depends on depth, expresses the vertical upward forces acting on the plants, through uprooting (Schutten *et al.*, 2004). For each day and each grid cell, in which the orbital velocity creates sediment resuspension, is attributed the "1" value,

whereas days with no sediment resuspension are classified as "0". The model calculates the probability of having a sediment resuspension event during a temporal range for each individual raster cell. Therefore, the final unit of the model is a sediment resuspension probability (0-100%) and is applied to 17 × 17 m map grid cells.

Statistics

Linear regression was employed to test the dependence of the sedimentary OM on sediment resuspension, and the dependence of morphological traits on sediment resuspension probability and OM content. Pairwise t Student test was used to test differences in morphological traits between the two hydrophytes. Pearson correlation test was used to test the relationship between the biomass and the sedimentary OM content. Prior to analysis, all data were transformed as *log (x+1)*. Analyses were performed using R Program (R Development Core Team, 2017).

RESULTS

Prevailing stronger winds between November 2012 and November 2016 blew from the west-northwest; they also came from the north-east but with a minor velocity (Fig. 2). The daily mean wind speed was mainly bounded from 5 to 20 m s^{-1} (maximum 26.8 m s^{-1}, mean 9.1 m s^{-1}) with only 0.3% of wind-exempted days during the whole investigation period. The resuspension probability reflected a huge range of wave exposure (Fig. 2), with the eastern part of lakes presenting a higher probability of sediment resuspension than the western part.

The distribution of sedimentary OM content varied according to the bathymetry of lakes (Fig. 2). Within each lake, an elevated spatial variability was observed, with fluffy sediments collected at the deep-sheltered bays and clear quartz sands at the shallow wind-exposed shores. On the whole, sedimentary features slightly varied across lakes' shores, with a sandy bottom characterized by a mean bulk density of 1.6±0.3 g cm^{-3} (range 0.9-2.3), a porosity of 50±20% (20-98), a water content of 36.1±24.4% (13-93), and OM content of 9.8±18.5% as loss of ignition (LOI, 0.1-85.7) (overall *n*=723). Sedimentary OM was significantly dependent on the resuspension probability (F$_{1,518}$, R^2=0.13, P<0.001).

In 2014, a total of 21 and 82 sonar recordings were performed, for HOU and LAC lakes respectively. In 2015, a total of 41 and 35 sonar recordings were performed, for CAZ and PAR lakes respectively. Some lake areas were not prospected by echo-sounding because no dense stands were observed nearby during the field campaigns. As a consequence, low biomass values (<50 g$_{DW}$ m^{-2}), corresponding to sparse shoots, were not included in the distribution maps neither in the whole-lake biomass

V. Bertrin *et al.*
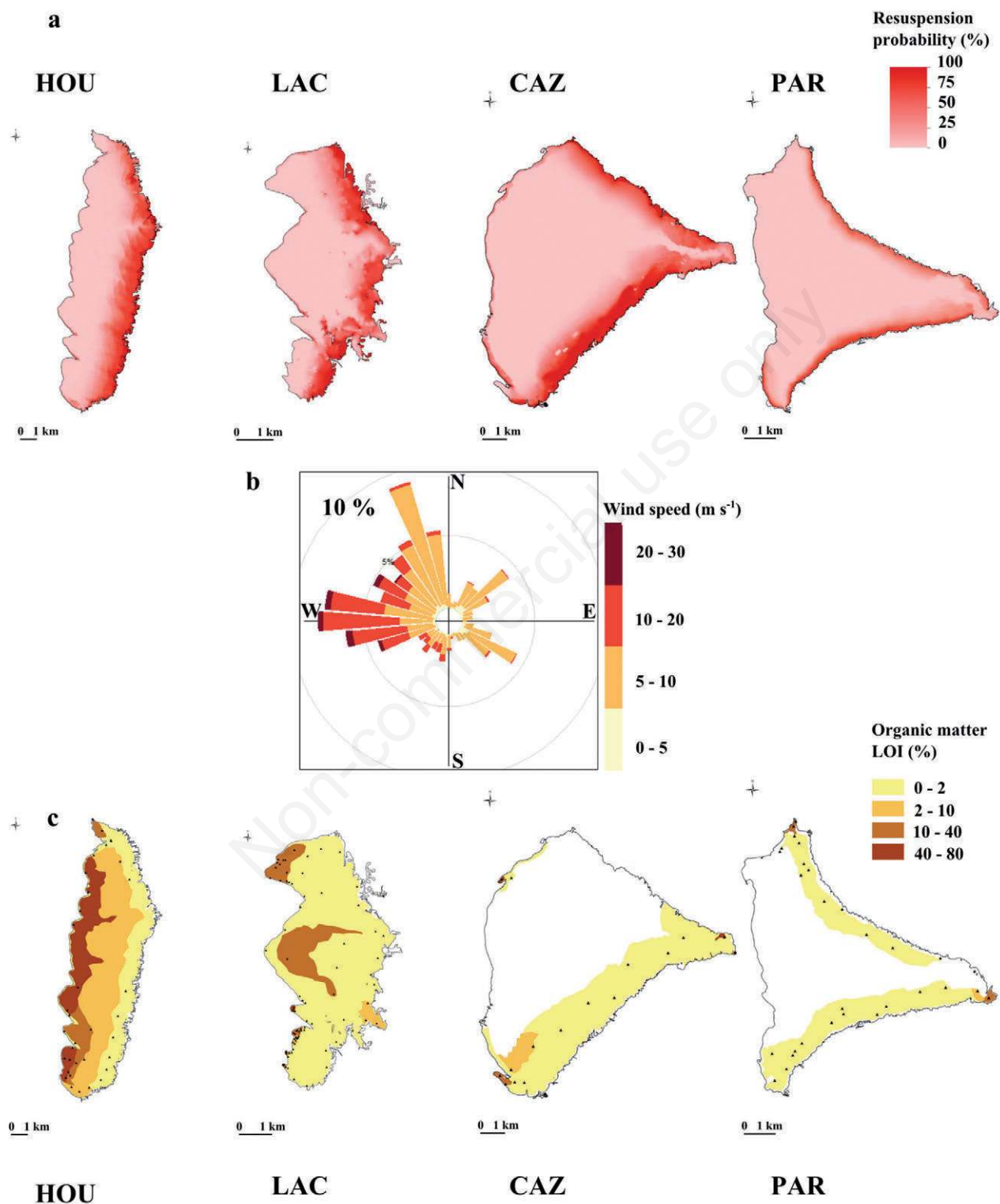
Fig. 2. a) Sediment resuspension probability (0-100%) calculated for the period November 2012-November 2016 in French Atlantic Lakes. b) Windrose elaborated from wind speed daily values for the period November 2012-November 2016. c) Organic matter maps of French Atlantic Lakes obtained in 2014 (HOU and LAC) and 2015 (CAZ and PAR). Triangles indicate sediment collection sites.

assessment for precaution. Whole-lake biomass estimations (2014-2015) were based upon a total of 7, 70, 7 and 15 biomass samplings, for HOU, LAC, CAZ and PAR respectively. Dense stands of both *E. densa* and *L. major* were found in LAC and PAR lakes on extended surfaces (about 7 and 13% of the lake surface, respectively), whereas restricted vegetated areas were observed in HOU and CAZ lakes, and only by *L. major* (Tab. 1 and Fig. 3). Both LAC and PAR presented the highest biomass values and coverage for both hydrophytes. Given the presence of only *L. major* in HOU and CAZ, and given the low occurrence of dense stands in those lakes, we decided to analyse vegetation data and to show results only for LAC and PAR in the next part of this study.

On the whole, the minimum plant colonization depth was 0.4 m, with sparse shoots found at a maximum of 8 m in LAC. At the lake scale, dense vegetated stands (monospecific + mixed stands) were mainly located at intermediate depths, from 1 to 5 m, with 72% of vegetated grid cells located between 2 and 4 m deep (Fig. 4). The main proportion of dense stands (87% of vegetated grid cells) was located in areas with sediment resuspension probability minor than 25%. When considering monospecific stands only, it appeared that 2.5-3.5 m was the optimal depth for the development of *E. densa* stands, while *L. major* seemed to cover indistinctively a large zone situated between 2 and 4 m. In addition, the maximum depth for *L. major* dense stands was 1 m greater than for mono-

Tab. 1. Lakes features (http://adour-garonne.eaufrance.fr) and colonized surfaces (expressed in km^2) and biomass (expressed in tons) by aquatic weeds in French Atlantic Lakes. Total biomass for each lake is calculated on dense stand surfaces only.

	Unit	HOU	LAC	CAZ	PAR
Lake surface	km^2	57.6	16.2	48.9	31.9
Mean and max depth	m	4, 15	2, 7	9, 24	7, 22
Secchi depth	m	2.1±0.2	1.9±0.2	4.6±0.7	2.3±0.8
Sparse shoots (1<x<50 g$_{DW}$ m^{-2})	km^2	0.55	1.36	0.15	2.31
Dense stands (x>50 g$_{DW}$ m^{-2})	km^2	0.94	1.19	0.17	4.17
L. major monospecific stands	km^2	0.94	0.37	0.17	0.81
	tons	200	47	45	41
E. densa monospecific stands	km^2	0.00	0.57	0.00	0.95
	tons	0	270	0	932
Mixed stands	km^2	0.00	0.25	0.00	2.41
	tons	0	83	0	1812

HOU, Lake Carcans-Hourtin; LAC, Lake Lacanau; CAZ, Lake Cazaux-Sanguinet; PAR, Lake Parentis-Biscarrosse.
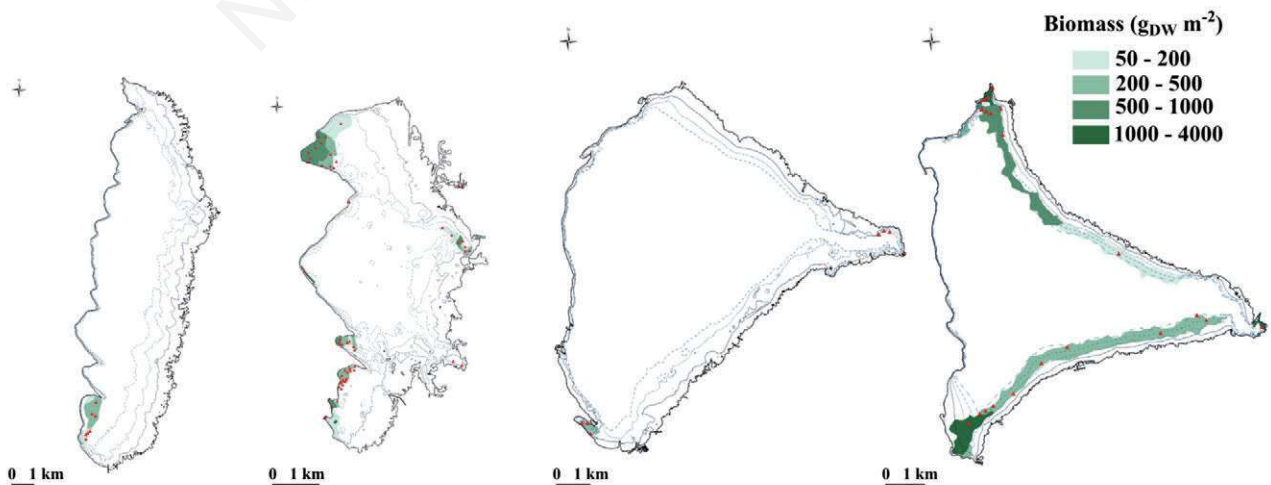

Fig. 3. Distribution and biomass maps of aquatic weeds (*E. densa* and *L. major*) obtained by echo-sounding and biomass harvesting in 2014 (HOU and LAC) and 2015 (CAZ and PAR). Triangles indicate biomass harvesting sites; isobaths are reported until 3 m deep.

specific *E. densa* stands. With regards to sediment resuspension, the distribution of monospecific *E. densa* stands linearly decreased with the increase of the exposition to water movement, whereas *L. major* seemed to be less affected by resuspension. Hydrophyte biomass and sedimentary OM content appeared positively correlated at all lakes but one (r Pearson=0.62, 0.53 and 0.54 for HOU, LAC and CAZ, respectively; PAR = not significant).

Biomass, shoot density and morphological traits varied across lakes and species (Tab. 2); *E. densa* showed significantly higher values than *L. major* for all parameters at both LAC and PAR lakes (*t*-test, P<0.001), except
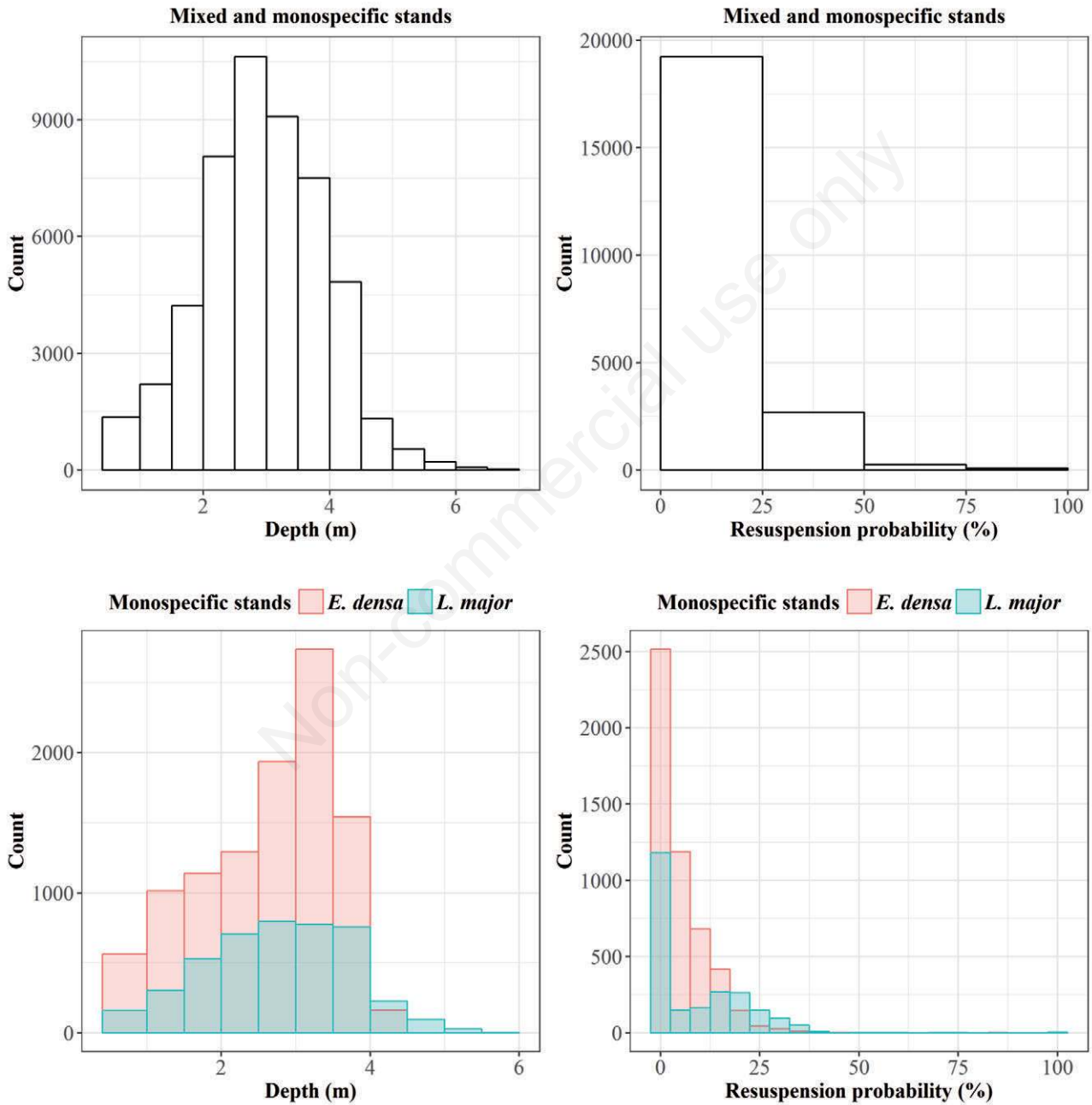
Fig. 4. Occurrence of dense mixed and monospecific stands of two aquatic weeds (*L. major* and *E. densa*) according to the depth (*n*=50,029, on the top left) and resuspension probability (*n*=22,246, on the top right); occurrence of dense monospecific stands according to the species, the depth (*n*=14,769, on the bottom left) and resuspension probability (*n*=7381, on the bottom right). Count is based on the occurrence of grid cells corresponding to dense vegetated stands.

for shoot density at PAR lake. The occurrence of one hydrophyte at elevated density or biomass was inversely correlated to the occurrence of the other one (Fig. 5). Morphological traits in function of sediment resuspension showed different patterns according to the species and the lake (Fig. 6). The influence of resuspension was however not systematic, with many cases where morphological traits were not affected at all. No significant relationship between R:S and resuspension probability was pointed out except in LAC for *L. major*. In the same way, roots

Tab. 2. Biomass, shoot density and morphological traits measured on *Lagaroshiphon major* (*L. major*) and *Egeria densa* (*E. densa*) colonizing French Atlantic Lakes. Mean values ±SD, range values and number of replicates (in square brackets) are reported.

Lake		Biomass (g_{DW} m^{-2})	Shoot density (shoots m^{-2})	RAM (stems shoot^{-1})	(roots shoot^{-1})	MSL (cm)	MRL (cm)	R:S
HOU	*L. major*	149±102 [7] (88–375)	- -	- -	- -	72±27 [70] (32–148)	- -	0.01±0.01 [7] (0.01–0.02)
	E. densa	0 0	0 0	0 0	0 0	0 0	0 0	0 0
LAC	*L. major*	154±135 [45] (1–1060)	98±46 [32] (14–141)	2±1 [8] (1–3)	11±4 [8] (5–17)	64±28 [202] (10–180)	33±7 [8] (24–46)	0.10±0.09 [40] (0.02–0.27)
	E. densa	470±376 [76] (3–1989)	189±136 [39] (42–594)	5±3 [132] (1–15)	16±11 [116] (2–56)	102±38 [367] (8–236)	65±16 [116] (27–98)	0.13±0.22 [69] (0.01–0.50)
CAZ	*L. major*	154±106 [7] (6–337)	38±21 [7] (14–71)	3±1 [13] (1–4)	14±10 [13] (5–38)	73±22 [13] (43–112)	35±8 [13] (25–57)	0.08±0.05 [7] (0.01–0.14)
	E. densa	0 0	0 0	0 0	0 0	0 0	0 0	0 0
PAR	*L. major*	562±559 [22] (1–1505)	84±50 [17] (14–184)	3±1 [36] (1–5)	10±7 [21] (3–39)	137±54 [51] (43–255)	29±11 [22] (8–57)	0.03±0.02 [16] (0.01–0.08)
	E. densa	1942±1820 [35] (6–6177)	127±102 [32] (14–340)	4±3 [133] (1–17)	16±14 [64] (1–77)	205±65 [119] (41–321)	52±22 [76] (9–102)	0.06±0.04 [32] (0.01–0.09)

RAM, ramifications; MSL, max stem length; MRL, max root length; R:S, root to shoot ration; HOU, Lake Carcans-Hourtin; LAC, Lake Lacanau; CAZ, Lake Cazaux-Sanguinet; PAR, Lake Parentis-Biscarrosse.
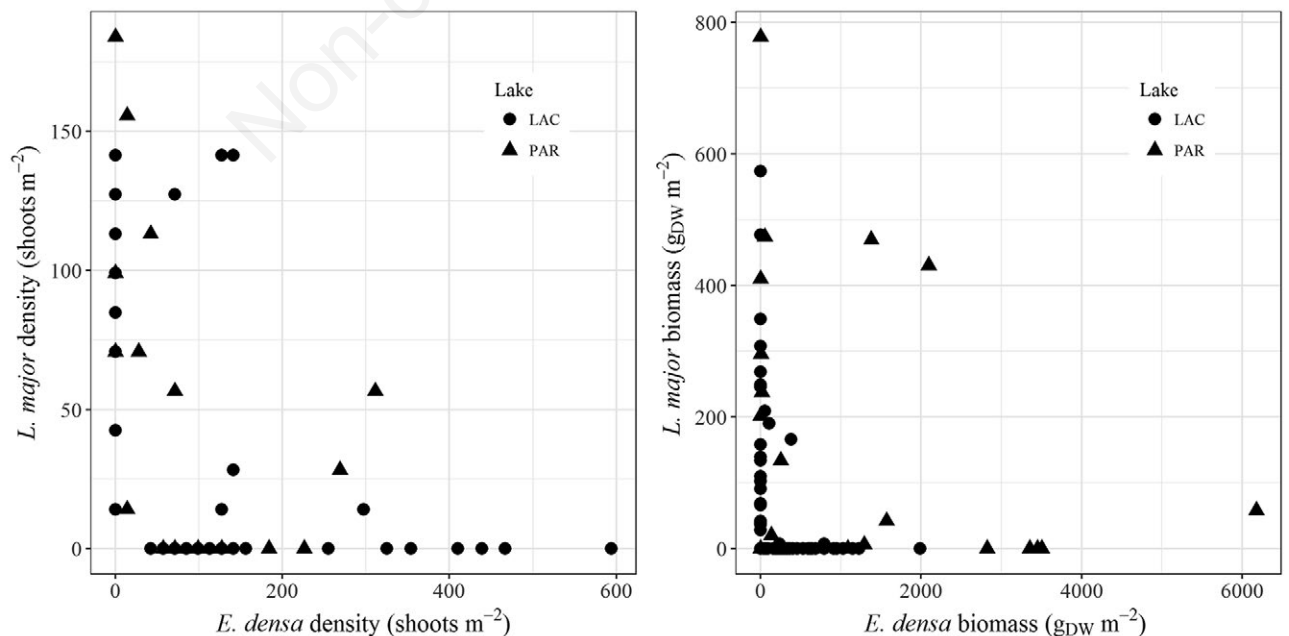
Fig. 5. Relation between the density (on the left) and the biomass (on the right) of the two hydrophytes *L. major* and *E. densa*.

length significantly decreased in PAR for *E. densa* when resuspension probability increased ($F_{1,74}$, $R^2=0.12$, $P<0.01$). No significant relationship was evidenced between density and resuspension probability at all lakes. The parameter appearing to best respond to the impact of sediment resuspension was the maximum stem length, which was significantly higher for both species in PAR, while it was not correlated for *L. major* in LAC.

DISCUSSION

Plant distribution

This study documents the massive presence of two rooted aquatic weeds in French Atlantic Lakes. *E. densa* and *L. major* formed extensive dense stands (up to 4.17 km²), with standing crops varying from 45 to 2785 tons of dry biomass per lake (from 0.05 to 6.18 kg_{DW} m⁻²), which covered from 1.6 to 13.0% of the total surface of the lakes. In many areas, plant biomass and vegetated patches largely overpassed values reported for invasive free-floating plants (up to 2.5 kg_{DW} m⁻² and 2 km²) (Center and Spencer, 1981; Nieder *et al.*, 2004). Though echo-sounding surveys did not allow prospecting the full lake surface, it resulted to be a reliable method for delimiting the stand boundaries (Wells *et al.*, 1997; Zajac, 2008). We acknowledge that some portions of the lakes where sparse shoots exist could not be included in this survey; for this reason, the lake-scaled biomass estimation only refers to dense stands. Also, interannual variability in biomass might have affected our evaluation; anyway, our results highlight the magnitude of the plant colonization and constitute a first biomass assessment.

When looking at the comparison between the two hydrophytes, *E. densa* appeared to be a major potential threat when compared to *L. major*, both in terms of biomass and density. Indeed, while *L. major* maximum stem length and biomass resulted similar or even lower than those reported in other studies and other sites (Clayton, 1982; Dutartre and Oyarzabal, 1993; Wells *et al.*, 1997; Bickel and Closs, 2008), the opposite happened for *E. densa* biomass, which reached much higher values (maximum 6.2 kg_{DW} m⁻² in PAR) than those reported in tropical waters (maximum 0.5 kg_{DW} m⁻² and 1.2 kg_{DW} m⁻² in South-American reservoirs) (Pelicice *et al.*, 2005; Carrillo *et al.*, 2006).

Both *L. major* and *E. densa* appeared to be able to colonize the whole range of depth in French Atlantic Lakes, until 8 m deep for sparse shoots, corresponding to the maximum depths observed in tropical and not light-limited environments (Coffey and Wah, 1988; Carrillo *et al.*, 2006). Dense stands however preferentially developed between 2 and 4 m deep, showing a possible interplay between light availability and hydrodynamics preferences. Indeed, the majority of the dense stands were located at low sediment resuspension areas, which indicates that calm waters constitute a preferential habitat for dense mats development. However, even areas characterized by low to medium sediment resuspension (10-45%) were colonized by an elevated plant density.

The depth zonation of the two hydrophytes did not result as distinct as in other studies on native species, which showed that different species of *Potamogeton* can occupy distinct colonization depth within one lake (Lehmann *et al.*, 1997). Nevertheless, our survey showed that the two hydrophytes rarely occur together at elevated biomass or density. On the whole, our results show that *E. densa* and *L. major* prefer deep-sheltered areas in Atlantic shallow lakes, with a tendency for *L. major* to colonize deeper and more exposed areas than *E. densa*. This result is in line to
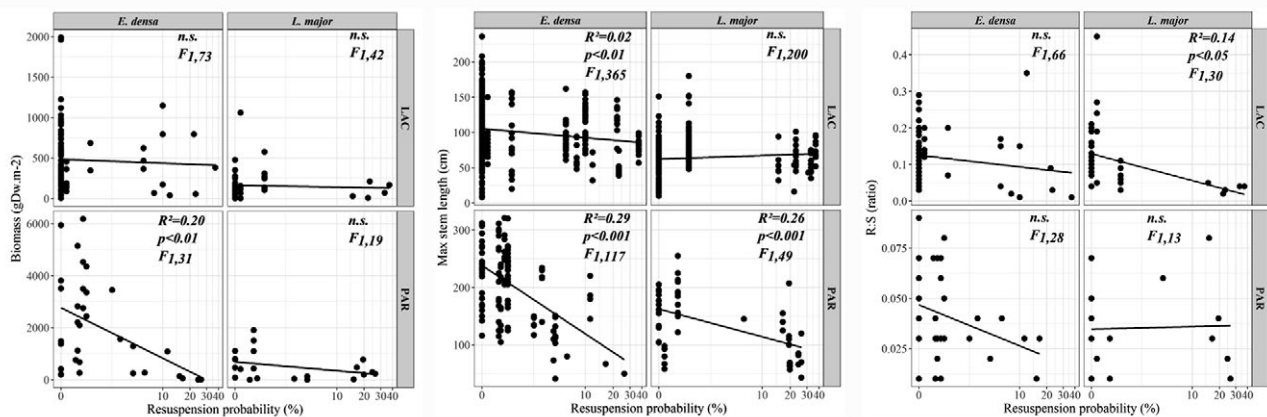
Fig. 6. Relation between the biomass (on the left), maximum stem length (on the middle) and root to shoot ratio (on the right) of the two hydrophytes *L. major* and *E. densa*.

what Ellawala *et al.* (2011) and Riis *et al.* (2012) found in experimental conditions and highlights a species-specific response to hydrodynamic forces.

Plants morphological traits and hydrodynamics

Both *E. densa* and *L. major* produce dense canopies with long stems (maximum 321 cm for *E. densa* in PAR), which drag at the water surface during summer period. This type of vegetative development could reduce wave tolerance, increasing plant breakage and morphology modifications, unlike meadow-forming species which lie closer to the sediment surface when the current velocity is elevated (Koch, 2001). The response of morphological traits to sediment resuspension here reported matches indeed with investigations previously carried out on *E. densa* (Ellawala *et al.*, 2011) and other hydrophytes such as *Myriophyllum spicatum* L. (Strand and Weisner, 2001) and *Vallisneria spiralis* L. (Doyle, 2001) in experimental conditions. Anyway, the relationships we found were not systematic and often lake-dependent and species-specific. These results in general did not confirm our initial hypotheses. An increase of the root length would have been expected with the increase of sediment resuspension, as a phenotypic adaptation for assuring a better anchorage to the plant. Other studies report that belowground biomass plasticity according to wave exposure and sediment granulometry has been found to be often inconsistent (Koch, 2001). Moreover, no relationship was observed in some morphological traits such as the number of stems and roots per shoot. Different responses of the relationship traits-hydrodynamics can be attributable to the different lake sizes. PAR lake surface is two times larger than LAC; as a consequence, the fetch lengths are potentially higher in PAR than in LAC. The orbital velocity of waves is function of the wind direction and velocity, and also depends on the fetch length required to calculate the wave height, length and period (Rohweder *et al.*, 2012). Even if the resuspension probability is always binary (1 = resuspension, or 0 = no resuspension) and identifies the occurrence of a disturbance, it does not give the intensity of the force induced by waves. Wave disturbance in PAR has probably a more important impact on plant morphological features, as reported by some authors for large lakes (Schneider *et al.*, 2015; Schutten *et al.*, 2004). In further research, it would be thus interesting to include the maximum orbital velocity in the model.

Aquatic weeds as species engineers

Our research highlights the importance that dense vegetated stands take on in shallow lakes productivity. French Atlantic Lakes are characterized by slow-growing vegetation typical of acidic conditions and by low pelagic production (Cellamare *et al.*, 2012; Ribaudo *et al.*, 2017). If

we assume a carbon content of 39.5% in plant tissues (Carvalho *et al.*, 2005) and consider the total measured biomass and the colonized surface on the four lakes, we can estimate that those two hydrophytes may fix from 84 to 264 g C m^{-2} (for HOU and PAR lakes, respectively). This value is comparable to the C sequestration capacity of other hydrophytes of the same lakes (Ribaudo *et al.*, 2017), yet the proportion of vegetated areas is much different. Indeed, when considering the colonized areas by *E. densa* and *L. major*, we can estimate a productivity ranging between 18 and 1100 tons of C lake^{-1} at their standing crop (for CAZ and PAR lakes, respectively). This budget lacks, however, of the assessment of the carbon release due to respiration processes in dense vegetated stands at the lake scale. A definitive assessment of the net ecosystem metabolism would take into account the quota of carbon decomposed and released *in situ* at the senescence of the plants, that having potential cascading effects on local oxygenation and on the enhancement of anaerobic processes such as methanogenesis (Cunha-Santino and Bianchini, 2004; Carvalho *et al.*, 2005; Urban *et al.*, 2009; Ribaudo *et al.*, 2014).

E. densa and *L. major* are two rooted hydrophytes able to grow on a wide spectrum of substrata and depths (Riis *et al.*, 2010), commonly found on silty, mesotrophic sediments (Bini *et al.*, 1999; Martin and Coetzee, 2014; Matsui, 2014). As a consequence, we would not expect to find dense stands on very organic-poor sediments (<0.3% as LOI, at PAR lake). We can hypothesize that we are dealing with an initial phase of the settlement, where the barrier formed by elevated shoot densities possibly triggers a positive feedback on water flow decrease and favors fine particles sedimentation (Barko *et al.*, 1991; Madsen *et al.*, 2001). We found indeed a significant correlation between the quantity of biomass and the degree of OM content, that indicating an interaction between a substrate preference by the plant and the effect of the canopy on fine particles sedimentation. Here, the release of nutrients from fluffy sediments likely contributes to sustain plant growth under oligotrophic conditions (Anderson and Kalff, 1986; Bolpagni *et al.*, 2015). An aliquot of the organic matter produced in dense stands may be transferred to deeper layers of the lakes and support oxidative degradation (Siffedine *et al.*, 2011).

Implication for management purposes and biomonitoring

The recreational use of French Atlantic Lakes for touristic purposes has historically matched with a management aiming at a low environmental impact (Ghelardoni, 1990). Recently, negative human perception increased against aquatic weeds, due to a spread of lake's recreational uses (sealing, motor boating, hunting and fishing). Concurrently, those activities have a probable positive feedback on the

settlement of the two non-native hydrophytes through fragments dispersal (Bruckerhoff *et al.*, 2015). Management actions for removing biomass from harbours accounted for several tens of thousands euros between 2010 and 2015 (SIAEBVELG and Géolandes local authorities); those actions were, however, spatially restrained in order to limit negative impacts caused by nutrients regeneration from sediments (van Nes *et al.*, 2002).

CONCLUSIONS

Our study assesses the current distribution of two aquatic weeds in French Atlantic Lakes, that making easier for managers to plan harvesting interventions. In addition, as we highlighted the link between plant distribution and sediment resuspension, we alert to the risks induced by the creation of artificial calm-water zones (*e.g.*, marinas, harbours, canalizations) that could favour the onset of dense stands. Taking into account artificial hydromorphologic modifications would be convenient for improving biomonitoring approaches, which are at present focused on the detection of nutrient and organic pollution only (Kolada *et al.*, 2014). Our results could be also used to identify suitable areas for potential colonization by *E. densa*, which is still currently not present in two of the four lakes. Both lakes HOU and CAZ are highly vulnerable to be colonized by *E. densa* in the near future, due to their accessibility to human activities through the presence of public boat launches and some navigation ways linking the lakes. Beyond the capacity of predicting the occurrence of invasive organisms at a multiple-systems scale, we believe that it is now necessary to inform managers on the potential distribution of a likely new invasive plant at the local scale (*e.g.*, lake or a specific part of a lake) in order to help them in management decision.

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