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ARTICLE

The ecosystem size and shape dependence of gas transfer velocity versus wind speed relationships in lakes

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Abstract: Air–water diffusive gas flux is commonly determined using measurements of gas concentrations and an estimate of gas transfer velocity (k_{600}) usually derived from wind speed. The great heterogeneity of aquatic systems raises questions about the appropriateness of using a single wind-based model to predict k_{600} in all aquatic systems. Theoretical considerations suggest that wind speed to k_{600} relationships should instead be system-specific. Using data collected from aquatic systems of different sizes, we show that k_{600} is related to fetch and other measures of ecosystem size. Lake area together with wind speed provided the best predictive model of gas transfer velocity and explained 68% of the variability in individual k_{600} measurements. For a moderate wind speed of 5 m·s^{-1}, predicted k_{600} varied from 6 cm·h^{-1} in a small 1 ha lake to over 13 cm·h^{-1} in a 100 km^2 system. Wave height is also shown to be a promising integrative predictor variable. The modulating influence of system size on wind speed – gas transfer velocity relationships can have a large impact on upscaling exercises of gas exchange at the whole landscape level.

Résumé : Les flux de gaz par diffusion à l'interface air–eau sont couramment estimés en utilisant les concentrations de gaz et une vitesse d'échange de gaz (k_{600}) généralement elle-même dérivée de la vitesse du vent. La grande hétérogénéité des systèmes aquatiques soulève des questions sur la pertinence d'utiliser un modèle unique basé sur le vent pour prédire les k_{600} de tous les systèmes aquatiques. Des considérations théoriques suggèrent plutôt que la relation entre la vitesse du vent et k_{600} doit être spécifique à chaque système. En utilisant les données recueillies sur des systèmes aquatiques de différentes tailles, nous montrons que le k_{600} est lié à course du vent et à d'autres mesures relatives à la taille de l'écosystème. La surface du lac avec la vitesse du vent a fourni le meilleur modèle prédictif de la vitesse d'échange gazeux et explique 68 % de la variabilité des mesures individuelles de k_{600}. Pour une vitesse de vent modérée de 5 m·s^{-1}, le k_{600} prédit varie de 6 cm·h^{-1} dans un petit lac de 1 ha à plus de 13 cm·h^{-1} dans un système de 100 km^2. La hauteur des vagues s'est également avéré une variable intégratrice de prédiction prometteuse. L'implication de la taille du système sur la relation vitesse du vent – vitesse d'échange gazeux peut avoir un grand impact sur les futurs exercices d'extrapolation des échanges gazeux sur l'ensemble d'un paysage.

Introduction

Carbon transformations in inland waters are central to our understanding of biome functioning (Prairie 2008; Tranvik et al. 2009). One key process needed to constrain the carbon budget of ecosystems is the exchange of carbon gases with the atmosphere. Achieving accurate estimates of gas exchange rates also provides important insights about the net metabolic balance of these ecosystems, such as the role of lakes as sinks or sources of carbon to the atmosphere. However, because freshwater systems are highly heterogeneous, quantifying the role played by aquatic ecosystems in the carbon economy of the landscape using a unique model to predict gas exchange across the air–water interface, as is currently done (Algesten et al. 2005; Kortelainen et al. 2006), may be a more precarious exercise than is currently acknowledged.

Air–water diffusive gas exchange is often modeled as a thin-boundary layer process in which the flux is proportional to the concentration gradient at the interface. The proportionality factor k is also known as the gas transfer velocity (alternatively termed piston velocity or gas exchange coefficient). For slightly soluble gases like CO_2 and O_2, water-side near-surface turbulence is the main driver of k (MacIntyre et al. 1995). Turbulence-based models have been recently shown to be widely applicable in the field (Zappa et al. 2003, 2007; Vachon et al. 2010; MacIntyre et al. 2010). These models have the significant advantage of being applicable to aquatic systems of different types. However, they also require that turbulence be measured adequately in both space and time and this constitutes a major challenge with current instrumentation. There thus remains the need to infer turbulence parameters from more easily obtained physical and meteorological variables.

In stratified lakes, near-surface turbulence is modulated predominantly by wind forcing and thermal convection from heat loss (Imberger 1985). The latter variable, often expressed as a negative buoyancy flux, can be relatively more important in small lakes (MacIntyre et al. 2001; Read et al. 2012), but this effect has not yet been sufficiently parameterized over a wide variety of systems. As a result, empirical relationships predicting gas transfer velocity have largely focussed on wind speed alone (Wanninkhof 1992; Cole and Caraco 1998; Wanninkhof and McGillis 1999), an easy-to-measure variable. However, there are a number of problems associated with using such wind–k relationships as quasi-universal functions, particularly in lakes. First, when wind speed measurements are made from (or even nearby) meteorological stations located on land, one cannot assume that the same wind conditions will prevail over the water because of the vastly different roughness lengths (or drag coefficients) of forests versus open water (Kwan and Taylor 1994; Markfort et al. 2010). The friction

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velocity (u^*) exerted by wind will be at a minimum at the upwind edge of the water body and increase asymptotically to its new equilibrium value over scales of a few kilometres (Józsa et al. 2006). Over larger spatial scales, u^* and U_{10} are interchangeable following the classic logarithmic wind profile equation

$$(1)\qquad U_{10} = \frac{u*}{K}\ln\left(\frac{10}{z_0}\right)$$

where u^* is the friction velocity, U_{10} is wind speed at a height of 10 m, K is the von Karman constant, and z_0 is the surface roughness. Over smaller scales (<20 km), this will induce a strong lake-size effect because the energy transferred from the wind to the lake's surface (and hence to turbulence promoting gas transfer) is more directly dependent on u^* than on the wind speed at 10 m (Deacon 1977; Kwan and Taylor 1994). Second, the energy transferred from wind to waves, which in part depends on the height of the waves, will vary greatly between a small pond and an inland sea because wave height for any given wind speed is fetch-limited. Using the following expression developed by Woolf (2005)

$$(2)\qquad H_s = 0.0163 \cdot F^{0.5} \cdot U_{10}$$

where H_s is significant wave height (m), F is fetch (km), and U_{10} is wind speed (m·s^{-1} at 10 m), one can readily see that the effect of wind will be about fourfold lower in a small lake with a mean fetch of 300 m relative to a lake with a 5 km mean fetch length (Woolf 2005). Equation 2 also implies that at low wind speed, the modulating influence of lake size (or fetch) is reduced enough to expect a convergence of wind-to-turbulence effect (and hence gas exchange) for lakes of all sizes. Therefore, it is not surprising that existing wind–k relationships vary in slopes, intercepts, scatter, and even curve shapes (Cole and Caraco 1998; Crusius and Wanninkhof 2003; MacIntyre et al. 2010). Several authors have already suggested that these differences are related to ecosystem size (Wanninkhof 1992; Borges et al. 2004; Jonsson et al. 2008). In particular, a direct link between the slopes of wind–k relationships and ecosystem size has been shown by Borges et al. (2004), which has recently been updated by Guérin et al. (2007).

In this paper, we explore the generality of this putative ecosystem size effect and aim at developing predictive models that integrate factors other than wind speed alone. More specifically, using gas transfer velocity measurements from several ecosystems of varying characteristics, we test the influence of lake area (LA) and wind fetch as candidate variables to be used together with wind speed to develop a more complete predictive model of gas transfer velocities in lakes of differing characteristics. Our approach focuses on the necessity of developing simple yet flexible models to improve estimates of gas transfer velocity in lakes of different types and thus of the gas flux they sustain.

Methods

Study areas

Samples were taken from two different regions of Quebec, Canada. The majority of the samples came from the hydroelectric Eastmain-1 reservoir (602 km²) located near James's Bay, Quebec, Canada (52°7′N, 75°58′W). The sampling campaigns (the first from 28 July to 1 August and second from 5 September to 12 September 2008) were planned to cover a wide variability in meteorological conditions, particularly wind speed. Sampling sites were chosen near an eddy covariance tower installed on a small island. To have a wider range of system types, we complemented the sampling with eight lakes located in the vicinity of Montreal. These lakes were chosen to cover a larger range in size (mean LA of 1.36 km² ranging from 0.19 to 4.0 km²). All lakes were thermally stratified, except for the reservoir measurements made in September 2008, which had already undergone holomixis.

Gas transfer velocity estimations

Gas transfer velocities were estimated using floating chamber (FC) methods corrected for chemical enhancement (Wanninkhof and Knox 1996) and for chamber-induced flux overestimation as described in Vachon et al. (2010). Briefly, gas transfer velocities were estimated from the concurrent measurement of gas flux and air–water CO_2 partial pressure differential and standardized at Schmidt number of 600, as described in Vachon et al. 2010 (their eqs. 3a and 3b). FC measurements of flux tend to overestimate true flux because of the turbulence they themselves generate, particularly in low turbulence environments (Vachon et al. 2010). To account for this overestimation, Vachon et al. (2010) developed correction equations (their eq. 7) based on in situ turbulence. Our flux measurements were thus made in conjunction with nearby turbulence measurements (about 25 cm away from the perimeter of the chamber) expressed as turbulent kinetic energy dissipation rate (ε). Turbulence measurements were taken with an acoustic Doppler velocimeter (ADV 10 MHz, Sontek) at 0.1 m depth at 25 Hz of sampling rate for 10 min. Turbulent kinetic energy dissipation rates (ε) were then calculated using the inertial dissipation method based on Kolmogorov's law using orbitral wave velocity as advective velocity (see Vachon et al. (2010) for details).

Meteorological data

For the temperate lakes and reservoir, in situ wind speed measurements were obtained on site before and after each FC measurements, using a handheld anemometer (Kestrel 4000, accuracy ± 3% of reading) at 1 m above the water surface, facing the wind direction. A handheld anemometer may be less accurate because they are not fixed, but they provide more localized wind speed measurements than onshore meteorological station, which we could better associate with our FC measurements of gas exchanges. Both measurements (before and after FC) lasted 1 min and were averaged to have the mean wind speed associated with the FC measurement. We then extrapolated the wind speed data to wind speed at 10 m (U_{10}) according to the logarithmic wind profile relationship of Crusius and Wanninkhof (2003)

$$(3)\qquad U_{10} = U_z\left[1 + \frac{(C_{d10})^{1/2}}{K}\ln\left(\frac{10}{z}\right)\right]$$

where z is the measured wind speed height, C_{d10} is the drag coefficient at a height of 10 m (0.0013; Stauffer 1980), and K is the von Karman constant (0.41). For temperate lakes, dominant wind direction was obtained from nearby Environment Canada meteorological stations (National Climate Data and Information Archive, http://climate.weatheroffice.gc.ca). No rainfall was recorded during sampling of the temperate lakes. For the Eastmain-1 reservoir, wind directions and precipitation were provided by a tower located on a small island of the reservoir (Marie-Claude Bonneville, McGill University, personal communication). Wind fetch lengths were calculated using a geographical information system (ArcGIS, ESRI) by measuring the distances between the sampling points to the nearest shore in a straight line from digitized lake maps (Natural Resources Canada, http://geogratis.gc.ca) according to the concurrent wind direction provided by the nearby meteorological stations. We also recorded the apparent maximum wave height (the maximum height between wave troughs and crests) during each FC measurement using a graduated stick.

Results

A total of 64 independent measurements were obtained (20 from the temperate lakes and 44 from the Eastmain-1 reservoir). Mean values and general characteristics of the sampled systems are

Table 1. Limnological characteristics.

	Eastmain-1 reservoir (n = 44)	Temperate lakes* (n = 20)
LA (km²)	602	1.0 (0.19–4.0)
Fetch (km)	3.9 (0.4–7.1)	0.4 (0.1–1.1)
U_{10} (m·s⁻¹)	3.8 (0.9–6.4)	3.0 (0.9–6.0)
k_{600} (cm·h⁻¹)	12.2 (1.6–19.4)	7.04 (1.9–14.5)
DOC (mg·L⁻¹)	6.1 (6.0–6.2)	6.2 (3.7–12.8)
chl*a* (μg·L⁻¹)	2.9 (2.8–3.0)	3.8 (0.5–20.0)
pH	6.01 (5.84–6.22)	7.28 (6.56–8.38)
Precipitation (mm·h⁻¹)	0.035 (0.0–0.55)	0

Note: LA, individual sample lake area; Fetch, fetch length; U_{10}, wind speed at 10 m; k_{600}, corrected gas transfer velocity; DOC, dissolved organic carbon; chl*a*, chlorophyll *a*. Data are presented as the mean (range).

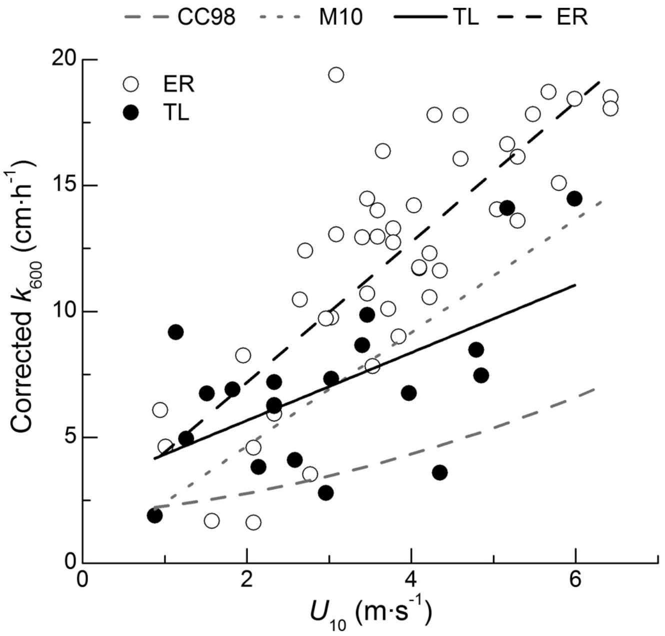
*Temperate lakes included Waterloo, Roxton, Parker, Orford, d'Argent, Simonneau, Fraser, and Croche.

summarized in Table 1. Gas transfer velocity values were corrected for chemical enhancement flux (Wanninkhof and Knox 1996). Only three lakes (5 samples out of 64) were higher in pH (around 8.3) and showed a significant chemical enhancement factor (between 1.43 and 1.66). All other lake and reservoir measurements were made at lower pH systems and did not show any significant chemical enhancement. FC k_{600} measurements were corrected for artificial turbulence according to Vachon et al. (2010). Outside chamber turbulence measurements (ε) allowed us to correct k_{600} values. Turbulence values ranged between 5.42×10^6 and 7.5×10^{-5} m²·s⁻³, which yielded a median overestimation ratio of 1.52, varying between 1.37 and 6.59 (90% of overestimation ratios were less than 2). Uncorrected and corrected k_{600} values were very tightly correlated ($r^2 = 0.95$), and the models developed (see below) were not significantly affected by the correction. Mean corrected gas transfer velocities were significantly different between the two regions (Student's *t* test, $p < 0.05$) and spanned a slightly wider range in the Eastmain-1 reservoir (from 1.6 to 19.4 cm·h⁻¹) than in the temperate lakes (from 1.9 to 14.5 cm·h⁻¹). Mean wind speeds (U_{10}) were not significantly different between the two regions (Student's *t* test, $p > 0.05$) but spanned a slightly wider range on the Eastmain-1 reservoir (from 0.9 to 6.4 m·s⁻¹) than in temperate lakes (from 0.9 to 6.0 m·s⁻¹). Handheld wind speed measurements generally agreed without any significant bias with tower measurements where near-shore wind speeds were available (r = 0.84, orthogonal fit, slope and intercept not significantly different from 1 and 0, respectively). All samples from the reservoir necessarily have the same surface area value (602 km²) but spanned a large range of fetch lengths, varying from 0.4 to 7.1 km. For the temperate lakes, surface area ranged from 0.19 to 4.0 km² (mean 1 km²) with fetches varying between 0.1 and 1.1 km.

Relationship between k_{600} and wind speed, system size, and fetch

We found a significant relationship between gas transfer velocity (standardized to a Schmidt number of 600) and in situ wind speed extrapolated at 10 m (Table 2, model A). However, when the two regions were taken separately, wind–k_{600} relationships varied in strength, slopes, and intercepts. We found a stronger wind–k_{600} relationship with a steeper slope for the Eastmain-1 reservoir ($k_{600} = 1.62 + 2.78 \cdot U_{10}$, $r^2 = 0.63$, $n = 44$, $p < 0.0001$), whereas the temperate lakes wind–k_{600} relationship was weaker in both strength and slope ($k_{600} = 2.98 + 1.35 \cdot U_{10}$, $r^2 = 0.36$, $n = 20$, $p = 0.005$). To obtain a fuller parameterization of the wind–k_{600} speed relationships for system of different sizes, we developed several empirical models using multiple regressions using bidirectional stepwise variable selection with wind speed, fetch, LA, and their interactions as potential independent variables. The best model (model B, Table 2) uses wind speed and the interaction between wind speed and LA (log-transformed) interaction as independent variables. The second best model (model C, Table 2) uses both wind speed and wind–fetch interaction. All parameters in these models are significant ($p < 0.05$), and the residuals in both models showed normal distributions. We also divided our data set in low wind and high wind condition, choosing 3.7 m·s⁻¹ as an empirical threshold (Crusius and Wanninkhof 2003; Guérin et al. 2007), and performed another multiple regression analysis with bidirectional stepwise variable selection. For both low and high wind conditions, wind speed and the interaction between wind and LA best explained k_{600}.

Fig. 1. Relationship between corrected gas transfer velocities and wind speed at 10 m, showing the comparison between Eastmain-1 reservoir (ER) and temperate lakes (TL) data with other published relationships: Cole and Caraco (1998) power relationship (CC98) and MacIntyre et al. (2010) general linear relationship (M10).



Discussion

Relationship between k_{600} and wind speed and system size

While the overall relationship between gas transfer velocities and wind speed is significant (model A, Table 2), it exhibited a substantial scatter, particularly at moderate wind speeds where k_{600} values spanned a range of nearly 10 cm·h⁻¹ (Fig. 1). Taking the two regions separately, different patterns emerged with a significantly higher wind–k_{600} slope with the reservoir data than for the temperate lakes (ANCOVA, $p < 0.05$), suggesting a major implication of system-specific characteristic and (or) methodological issues. Our strongest model (model B, Table 2) quantifies the clear system size dependence, greatly improving the predictability of k_{600} over a wide range of systems (showed by a higher r^2 and a lower AIC). To illustrate this system size dependence, we used the parameters of model B (Table 2) to create a family of lines for lakes of different sizes, each having their specific wind–k_{600} curve (Fig. 2). It is clear that gas exchange behaviour can diverge substantially for lakes of different sizes, especially at higher wind speeds. Even for a moderate wind speed of 5 m·s⁻¹, model B predicts that gas transfer velocity for a 10 km² lake would be more than 50% higher than for a 1 ha lake (Fig. 2). Here, the lack of a significant LA term (i.e., not as an interaction with U_{10}) in the multiple regression model (model B, Table 2) implies that the family of wind–k_{600} lines for different system sizes all converge to a common value at no wind (Fig. 2). This shared intercept, estimated at about 2.5 cm·h⁻¹ in our best model (model B, Table 2), is nearly identical to that obtained by Cole and Caraco (1998) and

Table 2. Different models of gas transfer velocity (k_{600}) prediction using various independent variables.

Model	Equation	n	p	r^2	AIC
A	$k_{600} = 1.41\ (\pm 1.13) + 2.58\ (\pm 0.30) \cdot U_{10}$	64	<0.0001	0.55	148.2
B	$k_{600} = 2.51\ (\pm 0.99) + 1.48\ (\pm 0.34) \cdot U_{10} + 0.39\ (\pm 0.08) \cdot U_{10} \cdot \log_{10}$ LA	64	<0.0001	0.68	127.5
C	$k_{600} = 2.13\ (\pm 1.06) + 2.18\ (\pm 0.30) \cdot U_{10} + 0.82\ (\pm 0.24) \cdot U_{10} \cdot \log_{10}$ fetch	64	<0.0001	0.63	140.0
D	$k_{600} = 19.08\ (\pm 0.84) + 7.05\ (\pm 0.62) \cdot \log_{10}$MWH	60	<0.0001	0.69	125.9

Note: U_{10}, wind speed at 10 m height (m·s^{-1}); LA, lake area (km^2); fetch, fetch length (km); MWH, maximum wave height (m).

Fig. 2. Using parameters of model B equation (Table 2), six relationships of wind speed at 10 m height U_{10} and gas transfer velocity k_{600} were calculated representing lake areas of 0.01, 0.1, 1, 10, 100, and 1000 km^2.

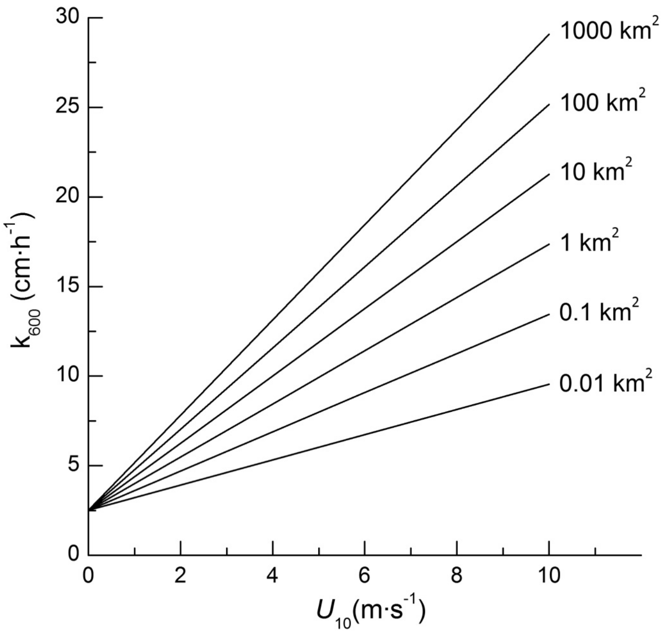
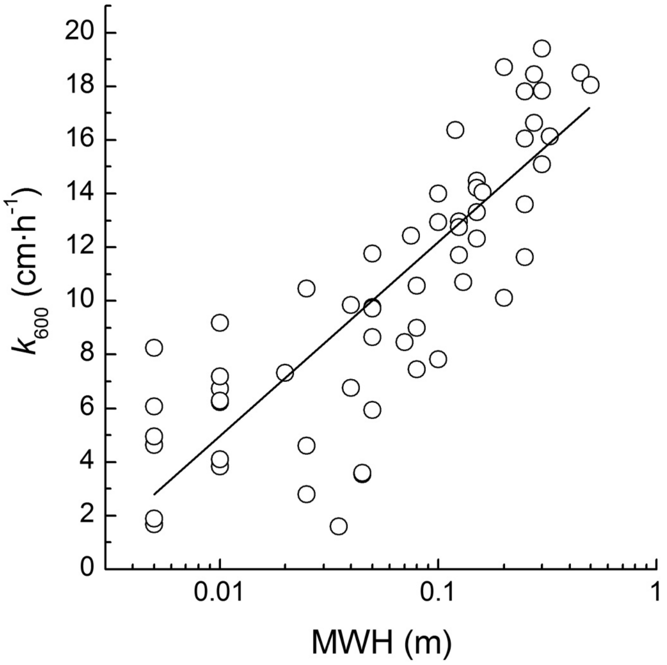


Fig. 3. Maximum wave height (MWH) relationship with gas transfer velocity (k_{600}). Model equation is shown in Table 2 (model D).



corresponds to the gas transfer velocity due to factors other than wind, most likely buoyancy flux (MacIntyre et al. 2001, 2010). From the multiple regression model statistics, we calculated a wind speed threshold value above which prediction from lakes of different sizes become statistically significant. For example, for two lakes different in size (say from 10 ha and 10 km^2), prediction of k_{600} become statistically at a wind speed of 3 m·s^{-1} and above. In general, we found that below a wind speed of 2 m·s^{-1}, lake size has a negligible effect.

Other evidence of the importance of ecosystem size can be gleaned by comparing our results with the literature. For example, the relationship developed for the reservoir (ER) is more comparable to some European estuaries in terms of both size and wind–k relationship (Borges et al. 2004). Likewise, our relationship for temperate lakes (Fig. 1; TL) reveals important similarities with the model of MacIntyre et al. (2010) developed on a single lake (Lake Merasjärvi) from eddy covariance measurements. Both models have similar slopes and intercepts, consistent with our hypothesis given that Lake Merasjärvi is of similar size (3.8 km^2) to the mean size of our temperate lakes (~1 km^2).

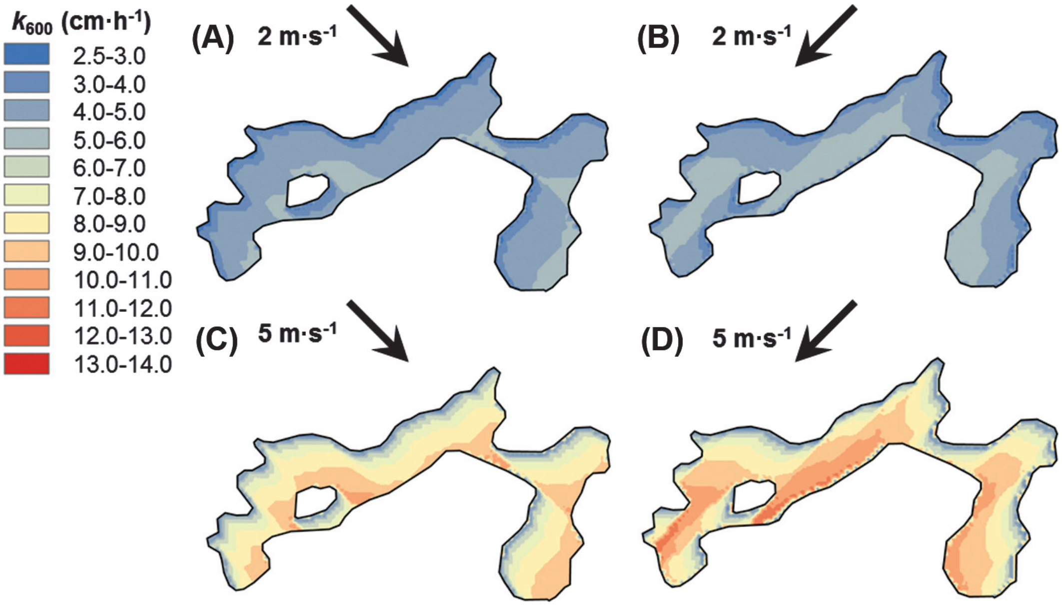
The ecosystem size effect on gas exchange reported here may also help explain the allometry of other lake properties. For example, several studies (Kelly et al. 2001; Sand-Jensen and Staehr 2007; Roehm et al. 2009) have shown that lake pCO$_2$ is inversely related to lake size, the reasons for which remain unclear. Our results suggest that the lower k_{600} values of small systems would allow higher pCO$_2$ values to be maintained even if the nature and rates of the biological and (or) geochemical processes generating CO$_2$ are the same as in larger systems. This hypothesis and its relative importance remain to be tested.

The wind speed and lake size interaction effect on near-surface turbulence is also reflected by the surface wave regime. Indeed, we were able to develop a very strong empirical model predicting wave height (instead of k_{600} as previously) using wind speed and wind speed interaction with LA ($r^2 = 0.85$, $p < 0.0001$). Since we observed greater wave heights on larger systems for the same wind speed measurement, this suggests that waves could be a simple and effective integrator of the wind speed and system size interaction and could well describe gas exchange rates. Not surprisingly, wave height is found to be an effective predictor of k_{600} (model D, Table 2). Figure 3 shows the relationship between our maximum wave height estimates and gas transfer velocity. We acknowledge that our wave measurements were coarse and insufficiently standardized. However, the clear relationship we observed (Fig. 3) and its strong predictability (model D, Table 2) strongly suggest that the combined and interacting effects of wind forcing and system size may be reducible to a simple wave metric that describes quite remarkably the generation of surface turbulence and, thus, gas exchange on different systems. From a prediction point of view where emphasis is on easily available variables, such as wind speed, lake size, or fetch, k_{600} – wave height may be of limited utility. It could, however, be integrated in routine field sampling. Regardless, these results further confirm that ecosystem size and shape have a determining effect on wind–k_{600} relationships and that a unique wind-based model for all lakes is untenable.

The linear shape of k_{600}–U_{10} relationships in lakes

Our sets of wind–k_{600} data fitted well to a linear model (as also proposed in the work of Borges et al. (2004), Guérin et al. (2007), and MacIntyre et al. (2010)), in contrast with the commonly used

Fig. 4. In-lake k_{600} heterogeneity in Lac Croche (0.19 km²) according to fixed wind conditions computed using model C. (A) 2 m·s⁻¹ winds from the northwest, (B) 2 m·s⁻¹ winds from the northeast, (C) 5 m·s⁻¹ winds from the northwest, and (D) 5 m·s⁻¹ winds from the northeast.



models of Cole and Caraco (1998) or Crusius and Wanninkhof (2003), which model k_{600} as accelerating curvi-linear functions of wind speed (i.e., exponent >1). Interestingly, more theoretical considerations based on wind forcing alone predict instead that k_{600} should follow a positive but decelerating function with U_{10}. This is because wind-induced surface turbulence ($\varepsilon_{\text{wind}}$ as energy dissipation rate) scales to the cubic power of friction velocity u_* (itself proportional to U_{10}) as $\varepsilon_{\text{wind}} = u_*^3/K \cdot Z$, where K and Z are von Karman's constant (0.41) and actively mixed layer depth, respectively, whereas gas transfer velocity, according to the surface renewal model, is proportional to the 1/4th power of turbulence as $k_{600} = A \cdot (\varepsilon\nu)^{0.25}\text{Sc}^{-0.5}$ (MacIntyre et al. 2010; Zappa et al. 2007; Vachon et al. 2010), where A is a constant, Sc is the Schmidt number, and ν is the kinematic viscosity. Combining these functions yields a theoretical relationship in which $k_{600} \propto u_*^{0.75}$, i.e., a positive but decelerating nonlinear function.

We suggest that all of these k_{600}–U_{10} models can be adequately reconciled with our linear formulation if we account for the effect of ecosystem size. First, the strongly nonlinear portions of published k_{600}–U_{10} relationships (e.g., Cole and Caraco 1998; Crusius and Wanninkhof 2003) all occur at high wind speeds (>6 m·s⁻¹). This is in part because the waves induced by high winds will increase roughness length and thereby accentuate the transfer of turbulent energy from the wind. Unlike what is often observed in marine systems, the wind speeds measured in our lakes and reservoir at the time of sampling were always lower than 6 m·s⁻¹, and we may, therefore, have missed evidence of such nonlinearity at high winds. This was partly due to safety issues, because navigating in the remote and large Eastmain-1 reservoir under high winds was dangerous in our small boats. However, an analysis of wind speed distributions in our lakes and reservoir suggests that high wind speeds are much more likely in larger systems. Wind speed conditions higher than 5 m·s⁻¹ occurred 23% of the time on the reservoir compared with only 5% on the temperate lakes. In addition, wind speeds higher than 5 m·s⁻¹ were recorded only 0.5% of the time at the meteorological station (Station Biologiques des Laurentides, Université de Montréal) on the shore of Lac Croche (0.19 km²) compared with 41% for the reservoir (602 km²) tower data (Marie-Claude Bonneville, McGill University, personal communication). Thus, amalgamating k_{600} data from diverse systems without consideration of their sizes will necessarily introduce a nonlinear bias because data points of high wind speeds are more likely to come from large ecosystems. This is illustrated in Fig. 2 and is equivalent to shifting to higher lines (ecosystem size) as we move up the x axis (wind speed).

Second, solving the theoretical formulation linking k_{600} to u^* (or U_{10}) for typical summer values in temperate lakes reveals that contrary to the case described above, most of the significant nonlinearity occurs at low wind speeds (<2 m·s⁻¹). It is precisely in such conditions that the influence of convection (expressed as a negative buoyancy flux) will be the main driver of surface turbulence (MacIntyre et al. 2010). Back-of-the-envelope calculations suggest that under no wind, turbulence values (expressed as energy dissipation rates) as low as 10^{-8} m²·s⁻³ induced from convection are sufficient to generate gas transfer velocities in the order of 2 cm·h⁻¹, nearly identical to the intercepts estimated in our wind-based models (Table 2), and are amply sufficient to render the theoretical k_{600}–u^* quasi linear over its entire range. Thus, we submit that in addition to the empirical modeling presented in this paper, there is strong theoretical justification to consider k_{600}–U_{10} relationships for lakes as adequately modeled by ecosystem-size-dependent linear functions, unlike those developed for the oceans.

Regardless of the exact shape of the relationships, our k_{600} values are also consistently higher than k_{600} values calculated from tracer experiments (Cole and Caraco (1998); Fig. 1), in agreement with observations made by other studies that used FCs (Duchemin et al. 1999; Kremer et al. 2003; Matthews et al. 2003). Considering that we corrected k_{600} for the artificially induced turbulence from the chamber itself (Vachon et al. 2010) and chemical enhancement due to hydration of CO_2 (Wanninkhof and Knox 1996; Bade and Cole 2006), we suggest that some of this remaining discrepancy may reflect other methodological issues. For example, FC and gas-tracer-derived k_{600} values differ greatly in their degree of both temporal (Cole et al. 2010; Vachon et al. 2010) and spatial integration: from highly localized and nearly instantaneous k_{600} estimates to lake-wide values integrated over several days (Upstill-Goddard et al. 1990; Cole and Caraco 1998), respectively. Such differences can greatly affect the parameters of the wind–k relationship. In addition, if chamber measurements are taken at the lake center (as in our case) where turbulence is likely higher than in the littoral zone for any given wind speed, this will lead to

Table 3. Published studies using linear relationships between wind speed (U_{10}) and gas transfer velocity (k_{600}) on lakes.

Study	Lake	LA (km²)	Method	k_{600}/U_{10}	r^2
López Bellido et al. 2009	Paajarvi (spring)	13.4	FC	2.30	0.52
López Bellido et al. 2009	Paajarvi (autumn)	13.4	FC	1.16	0.67
MacIntyre et al. 2010	Merasjärvi	3.8	EC	2.25	0.91
Soumis et al. 2008	Croche	0.06	FC	0.78	0.38
Wanninkhof et al. 1987	Mono	200	SF_6	2.1	NA
Wanninkhof et al. 1987	Crowley	20	SF_6	1.9	NA

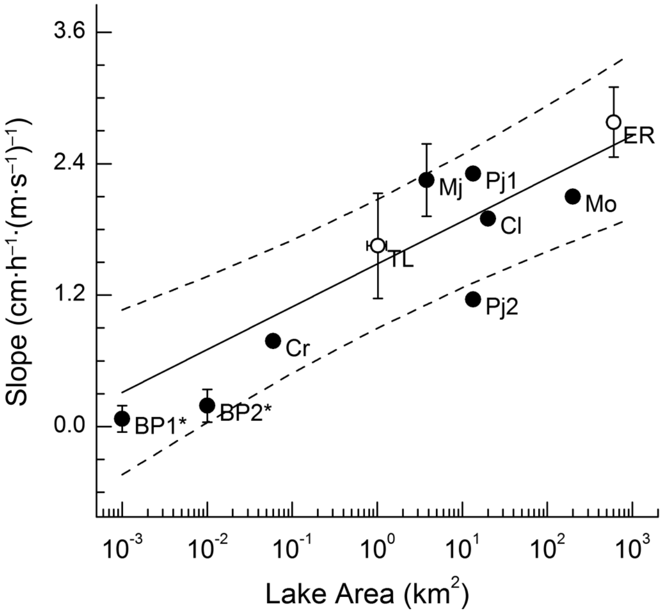
Note: LA, lake area; FC, floating chamber; EC, eddy covariance; SF_6, hexafluoride sulphur; NA, not available.

an apparent bias (Duchemin et al. 1999; Matthews et al. 2003). Similarly, if FC measurements are only taken during the day (and most are) while factors other than wind modulate gas exchange at night (such as buoyancy flux created by surface cooling), the wind–k relationship may be altered as well. In addition, it was suggested that FC shape and size may also affect gas exchange measurements (Vachon et al. 2010). Nevertheless, we argue that both local–instantaneous and spatio-temporally integrated gas exchange coefficients are relevant, and their respective use will depend on the particular purpose. These differences will require direct testing to assess their potential significance on the parameters of wind–k relationships, which is not addressed here.

Implication of fetch on intra-lake variability of gas transfer velocity

Although fetch length was significant in conjunction with wind speed (Table 2, model C), we were surprised that it did not add any significant predictive power over lake size alone (Table 2, model B). Accounting for lake shape and wind direction, fetch is generally thought to be a more direct measurement of spatial implication of the wind to surface turbulence energy transfer (Wanninkhof 1992; Frost and Upstill-Goddard 2002). Because wind direction dictates fetches differently according to individual lake shape configurations, we suggest that a general measure of system size such as LA provides a more integrative index of past fetch lengths that were due to wind direction variations. We examined the generality of this claim by comparing the prediction of our LA model (model B, Table 2) with the mean of a spatially explicit k_{600} map obtained by applying our fetch-based model (model C, Table 2) to Lac Croche (a small 19 ha lake in the Laurentians region of Quebec) under four different combinations of wind speed and direction (Fig. 4). Computed at a spatial resolution of 10 m, k_{600} values obtained from model C (Table 2) ranged from 2.51 to 6.68 cm·h⁻¹ for a wind speed of 2 m·s⁻¹ (Figs. 4A and 4B) and from 2.97 to 13.27 cm·h⁻¹ at a wind speed of 5 m·s⁻¹ (Figs. 4C and 4D). Thus, even for such a relatively small lake, the wind fetch model (model C) illustrates well the intra-lake spatial heterogeneity of k_{600} induced by the modulating influence of spatial scale on the ability of wind to generate turbulence. Figures 4C and 4D also illustrate the presence of k_{600} "hot spots", the location and amplitude of which naturally varies depending on wind direction and speed, respectively. However, if we average these spatially explicit k_{600} values over the whole lake's surface (mean value after spatial interpolation using spline, n = 35 760), the integrated values for a wind speed of 2 m·s⁻¹ (4.61 ± 0.7 and 4.39 ± 0.6 cm·h⁻¹ for wind direction of 45° and 315°, respectively (mean ± SD)) compare very well with the value of 4.9 cm·h⁻¹ predicted from the model based on LA (model B, Table 2). Similarly, when we repeated the same exercise (n = 59 970) for more extreme situations (i.e., for a higher wind speed (8 m·s⁻¹) and on a much larger system, the Eastmain-1 reservoir), k_{600} derived from model B (23.0 cm·h⁻¹ for LA of 602 km²) and the spatially averaged values computed from model C (19.3 ± 3.2 and 19.0 ± 3.1 cm·h⁻¹ for wind direction of 45° and 315°, respectively (mean ± SD)) differed only slightly. This may well explain why the simple metric of LA (together with wind speed, our model B, Table 2) provided the best predictive model of k_{600} because it can adequately integrate the variable fetches caused by lake shape and wind direction variations.

Fig. 5. Rearrangement of model B equation (solid black line) representing the relationship between lake area (km²) and the slope of the wind speed to k_{600} linear regression. Dashed lines represent the 95% confidence interval of the model. Open circles shows results from this study grouped in the system type: Eastmain-1 Reservoir (ER) and temperate lakes (TL). Solid circles are gathered data from the literature (Table 3): Lake Paajarvi in spring (Pj1) and in autumn (Pj2) from López Bellido et al. (2009), Lake Merasjarvi (Mj) from MacIntyre et al. (2010), Lac Croche (Cr) from Soumis et al. (2008), Beaver ponds binned in two size categories (BP1, BP2) from unpublished data (del Giorgio), Mono Lake (Mo) and Crowley Lake (Cl) from Wanninkhof et al. (1987). The asterisks (*) denote a nonsignificant relationship.



Independent validation and model limits

To further test the robustness of our best model (model B, Table 2), we extended the work of Guérin et al. (2007) by examining how the slope of wind–k_{600} relationships published for individual lakes can be predicted from our model on the basis of ecosystem size (Wanninkhof et al. 1987; Soumis et al. 2008; López Bellido et al. 2009; MacIntyre et al. 2010). This was achieved by simply plotting the first derivative of our model B equation (Table 2) with respect to U_{10} (i.e., the implied slope) as a function of LA to which we added published data (Table 3) that provided slope parameters of k_{600}–U_{10} relationships from individual systems. Figure 5 clearly demonstrates that these previously published and independent data fit well within the limits of our model and, thus, provides further evidence that system size acts as the main modulator of the effect of wind speed on gas exchange, in line with the conclusions of Borges et al. (2004) and Guérin et al. (2007). However, because our smallest system used in model B (Table 2) is 0.19 km², predicting k_{600} on smaller systems can lead to some biases. For instance, gas transfer velocity measured on extremely small systems (<0.01 km²) such as beaver ponds in Quebec (P. del Giorgio, Université du Québec à Montréal, unpublished data) are found to fit below our model predictions (Fig. 5; BP1 and BP2). Gas transfer velocities measured on a small basin (0.06 km²) of Lac Croche (Soumis et al. 2008) also showed a weak relationship (r^2 = 0.30, Table 3) and, consequently, fitted near the lower limit of the confidence interval of Fig. 5. We suggest that wind has a very limited effect on the boundary layer of these extremely small systems, particularly if they are sheltered by trees or by the local topography. This suggests that there is a certain size limit below which wind speed is a negligible factor affecting gas exchanges (Markfort et al. 2010). These results are in agreement with Laurion et al. (2010) who found much lower k_{600} in very small thermokarstic ponds than that predicted from wind-based model (on average 2.5 times lower) (Laurion et al. 2010). Factors other than wind, such as penetrative convection (heat loss), rain, or surfactant (Cole and Caraco 1998; Zappa et al. 2009; Read et al. 2012), are likely the main drivers of gas transfer in these systems.

We showed that ecosystem size exerts a strong modulating influence on the ability of wind speed to predict gas transfer velocity and that this effect is stronger at higher wind speeds. We modeled these combined effects as linear interaction functions and provide evidence that they adequately represent a simple yet reliable means of predicting gas transfer velocity in a suite of lakes of different sizes. We also provide models based on fetch that can be used to ascertain the likely spatial heterogeneity of gas exchange within individual systems. Considering the large size heterogeneity of freshwater ecosystems of most landscapes (Downing et al. 2006), accounting for this ecosystem size dependence is critical to achieving reasonable gas exchange estimates from aquatic networks.

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