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Winds and the distribution of nearshore phytoplankton in a stratified lake

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ABSTRACT

The distribution of phytoplankton in lakes is notoriously patchy and dynamic, but wind-driven currents and algal buoyancy/motility are thought to determine where algae accumulate. In this study, nearshore phytoplankton were sampled from different parts of a lake basin twice a day for 4–5 consecutive days, in the spring and in late summer, to test whether short-term changes in phytoplankton biomass and community composition can be predicted from wind-driven currents. On windy days, phytoplankton biomass was higher at downwind than at upwind nearshore sites, and the magnitude of this difference increased linearly with increasing wind speed. However, contrary to the generally assumed downwind phytoplankton aggregations, these differences were mostly due to upwelling activity and the dilution of phytoplankton at upwind nearshore sites. The distribution of individual taxa was also related to wind speed, but only during late stratification (except for cryptophytes), and these relationships were consistent with the buoyancy and motility of each group. On windy days, large diatoms and cyanobacteria concentrated upwind, neutrally buoyant taxa (green algae, small diatoms) were homogeneously distributed, and motile taxa (cryptophytes, chrysophytes, dinoflagellates) concentrated downwind. Predictable differences in the biomass and composition of phytoplankton communities could affect the efficiency of trophic transfers in nearshore areas.

1. Introduction

Planktonic algae are crucial in fueling aquatic foodwebs, but when concentrated by wind-driven currents, they can sometimes reach nuisance concentrations. The distribution of phytoplankton is notoriously patchy and dynamic. Planktonic organisms are largely at the mercy of currents and depending on their position in the water column, they may be transported at different speeds and possibly in different directions (George and Edwards, 1976; Boegman, 2009). Positively buoyant phytoplankton, such as many cyanobacteria, tend to accumulate at the water surface where they are entrained by wind-driven currents and accumulate along downwind shores (Small, 1963; Cao et al., 2006; Pobel et al., 2014). Spatial aggregation has also been reported for negatively buoyant and migrating algae that accumulate in the lower epilimnion or at other discrete depths (George and Heaney, 1978; Serra et al., 2007; Alexander and Imberger, 2009). This suggests that algal buoyancy and motility may be useful predictors of the degree of phytoplankton aggregation in space and in time, and of the coupling and decoupling of different components of planktonic communities and foodwebs (Blukacz et al., 2010; de Kerckhove et al., 2015). In this study I am particularly interested in how these physical processes affect the distribution and composition of phytoplankton in nearshore areas of lakes.

In order to accumulate, planktonic organisms must be able to maintain their vertical position in the water column (George and Edwards, 1976; Verhagen, 1994). The best-known model explaining basin-scale phytoplankton aggregation in lakes is the Conveyor Belt Circulation model (George and Edwards, 1976). Wind stress pushes surface water downwind, creating downwelling at the downwind end of the basin (water flowing downward), which then pushes water upwind in a deep return current that balances the surface downwind current and creates an upwelling (upward current) at the upwind end of the basin (Boegman, 2009; Rueda and Vidal, 2009). A Conveyor Belt circulation in the epilimnion would allow positively buoyant phytoplankton that can either resist the downward current or quickly float back to the surface, to accumulate at the downwind end of the lake, and negatively buoyant phytoplankton that can resist the upward current or that quickly

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sink back to the bottom of the epilimnion, to accumulate at depth at the upwind end of the lake (George and Edwards, 1976; Heaney, 1976). Since buoyancy and motility differ between phytoplankton groups (Reynolds, 2006; Kruk et al., 2010), this type of circulation could affect not only biomass, but also the taxonomic composition and size structure of phytoplankton communities.

The patchiness of phytoplankton in lakes is also affected by wind-driven and convective mixing (George and Edwards, 1976; George and Heaney, 1978; Verhagen, 1994; Serra et al., 2007). Phytoplankton aggregations can only develop and persist under light to moderate wind conditions, when wind-induced and convective mixing are too weak to disperse algae through the water column (Reynolds et al., 1987; Verhagen, 1994; Vidal et al., 2014). Several studies report that the vertical and horizontal patchiness of phytoplankton in lakes and reservoirs disappear at wind speeds above 3–4 m s^{-1} (George and Edwards, 1976; Cao et al., 2006; Hunter et al., 2008; Vidal et al., 2014), but others have reported downwind concentration of algae when strong and steady wind are blowing (Small, 1963; Jones et al., 1995; Griffiths and Cyr, 2006). Night-time convective cooling has also been shown to homogenize the vertical distribution of phytoplankton in the surface layer of lakes and reservoirs (Serra et al., 2007), disrupting aggregations formed during the day. This suggests that the magnitude of phytoplankton accumulations at downwind nearshore sites could increase linearly or vary in a unimodal way with increasing wind speed (George and Edwards, 1976; Cyr and Coman, 2012; Vidal et al., 2014) during the day, and disappear following cool nights. If phytoplankton are transported in predictable ways by wind-driven currents, they may accumulate preferentially in certain areas around lakes. This may result in nuisance aggregations (Cao et al., 2006; Pobel et al., 2014), but increased algal density could also enhance the efficiency of trophic transfers in nearshore planktonic and benthic communities (Kaevats et al., 2005; Rinke et al., 2009; Blukacz et al., 2010).

In this study, nearshore phytoplankton was sampled from different parts of a lake basin twice a day for 4–5 consecutive days to test whether short-term changes in phytoplankton biomass and community composition can be predicted from wind-driven currents. Samples were collected during two periods, in the spring and in late summer, to compare the effect of early and fully-developed stratification on different types of phytoplankton communities. More specifically, the following hypotheses were tested: 1) phytoplankton biomass is higher at downwind than upwind nearshore sites on windy days, 2) the magnitude of the accumulation of phytoplankton biomass at downwind sites increases non-linearly with increasing wind speed, 3) the taxonomic composition of nearshore phytoplankton differs between upwind and downwind nearshore areas, and is related to the buoyancy and motility of the algal groups present. Positively buoyant taxa (e.g., cyanobacteria) are expected to accumulate downwind, negatively buoyant taxa (e.g., large diatoms) to accumulate upwind, neutrally buoyant algae (e.g. green algae) to maintain similar biomass throughout the lake, and motile taxa (e.g. cryptophytes, dinoflagellates) to accumulate in different areas depending on current direction at the depth(s) where the algae aggregate, 4) the size structure of nearshore phytoplankton differs between upwind and downwind nearshore areas, as large algae, which are more likely to be positively or negatively buoyant, accumulate in different areas than small neutrally buoyant algae.

2. Methods

2.1. Sampling site

This study was performed in the South Arm of Lake Opeongo, ON, Canada, a dimictic meso-oligotrophic lake (22.1 km^2 basin, mean depth = 14.6 m, Fig. 1). Wind speed and direction were measured on the lake at a weather station (star in Fig. 1) maintained by the Ontario Ministry of Natural Resources and Forestry (OMNRF; Fig. 2). The seasonal development of lake stratification and isotherm movements were recorded using two offshore thermistor chains, each fitted with ten Hobo loggers (Temp Pro H20-001, Onset, Bourne, USA; W_{off}, E_{off} in Fig. 1). These data were used to calculate the seasonal Lake Number with Lake Analyzer (SLn, Read et al., 2011, Fig. 2). Two additional thermistor chains, each fitted with 11–15 temperature loggers, were deployed near shore to measure upwelling-downwelling activity during each sampling period (W_{10m}, E_{10m}; Fig. 1).

2.2. Phytoplankton: fluorescence profiles and samples

Nearshore phytoplankton were measured twice a day for 4–5 consecutive days at two fixed stations (W_{10m}, E_{10m}) and at additional upwind and/or downwind stations (S, SW, N) when the winds deviated from their predominant westerly-easterly direction. Fluorescence profiles were measured with a bbe fluorometer (AlgaeTorch-10 in June, FluoroProbe in September; bbe Moldaenke GmbH, Kiel-Kronzhagen, Germany), and expressed in μg chlorophyll-equivalent·L^{-1} based on factory calibration. A temperature probe (YSI58, Yellow Spring Instruments, OH, USA) was attached to the fluorometer to obtain simultaneous temperature measurements and calculate buoyancy frequency and mixing depth (Boegman, 2009). Fluorescence profiles were also measured at 7 stations along the main (east-west) axis of South Arm (E_{10m}, E_{off}, T2, T3, T4, W_{off}, W_{10m}; Fig. 1) on two consecutive days with contrasting wind conditions (September 5–6). At the end of the windy day (September 6), surface fluorescence along two ~0.5 km nearshore transects (red dotted lines in Fig. 1) was measured to determine whether data collected at W_{10m} and E_{10m} were representative of upwind and downwind nearshore areas.

Water samples were collected from 0.5, 2 and 4.5 m in June, and from 0.5, 4 and 8 m in September to measure chlorophyll concentration and algal biovolume. Bulk (unfiltered) lake water was used to measure total chlorophyll concentration, and lake water was filtered through a 35 μm mesh Nitex filter to measure chlorophyll concentration of small highly-edible algae (Cyr, 1998). Triplicate subsamples were filtered through GF/F Whatman filters and frozen in liquid nitrogen. The chlorophyll samples were then ground in 90% acetone, extracted overnight in the dark at 4 °C and the supernatant read on a Trilogy fluorometer (Turner Design, module NA-chla). The taxonomic composition and biovolume of phytoplankton were measured on unfiltered water samples preserved with 1% Lugol solution. The algae were settled overnight, and identified (Wehr and Sheath, 2003), counted and measured with an inverted microscope at 100–400× magnification (Optimas 5.1, USA). Mean biovolume of each taxon was calculated assuming standard geometric shapes.

2.3. Hydrodynamic model

The Estuary, Lake and Coastal Ocean 3D hydrodynamic Model (ELCOM; Hodges and Dallimore, 2014) was used to visualize basin-scale stratification and upwelling/downwelling activity in South Arm. Outputs along the main (east-west) axis of the basin were used in this study (solid line in Fig. 1). The ELCOM model was set up as described in Cyr (2016) and calibrated using 2012 thermal profiles from W_{off}, the thermistor chain closest to the weather station. The original model overestimated heat mixing, but reducing the input wind speeds by 10% resulted in excellent fit to the observations (root mean square error, RMSE = 1.07; normalized