

Towards understanding the relationship between wind conditions and plankton patchiness

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Abstract

We used (1) water temperature (a proxy for water movement), (2) chlorophyll (a proxy for phytoplankton), and (3) zooplankton (bulk, small, and large size classes) to investigate the relationship between changing wind conditions and spatial patterns along linear transects ($n = 150$) in two basins, South Arm and Annie Bay, of Lake Opeongo (Ontario, Canada). The basins have similar biological characteristics, but South Arm is larger and is oriented along the prevailing westerly wind direction. Large-scale patterns (>1 km) were described with an accumulation index, and wavelet analysis was used to describe small-scale patterns (<1 km). Spatial descriptors were correlated with five descriptors of wind conditions: (1) wind force, (2) scalar wind speed, (3) vector wind speed, (4) wind persistence, and (5) wind direction. Persistent westerly winds in South Arm resulted in more downwind accumulation of warm water and total and large-bodied zooplankton than in Annie Bay, while chlorophyll and small zooplankton did not show consistent downwind accumulation. The predominance of small-scale variability, particularly in large zooplankton, increased in the South Arm as the persistence and strength of westerly winds blowing parallel to the sampling transects increased. Only temperature showed such a pattern in the smaller Annie Bay. These patterns were not related to winds blowing at the time of sampling but rather to those blowing up to 12 h before sampling. Our observations provide a basis for future consideration of how simple surface winds may actually shape the nature of trophic interactions in lake ecosystems.

Aquatic phenomena often involve nested patterns across a continuum of scales, from very fine to very large, where changes at one scale often have effects at other scales (Skjoldal et al. 2000). For example, large-scale climatic patterns affect wind conditions, resulting in water movement at both small scales (e.g., waves) and large scales (e.g., currents). Studies show that zooplankton and phytoplankton are patchy over a wide range of scales. The ‘multiple driving force hypothesis’ states that various drivers predominate at different scales, with large-scale patterns being caused by predominantly physical drivers (e.g., water movement caused by wind) and small-scale patterns showing the influence of biological drivers (e.g., swarm formation) (Pinel-Alloul 1995; Folt and Burns 1999; Martin 2003).

Dispersion indices such as variance to mean ratios are frequently used to describe spatial patterns, but using these indices across and within different systems often leads to conflicting conclusions (Pinel-Alloul 1995). Furthermore, indices derived from distance measures among individuals are rare because of the dynamic nature of zooplankton and phytoplankton (Currie et al. 1998). Statistical methods have also been used to link potential environmental (e.g., nutrients) and biological drivers (e.g., predators) with zooplankton spatial structure (Pinel-Alloul 1995; Masson and Pinel-Alloul 1998). Some researchers have quantified wind-driven large-scale zooplankton distribution effects by either recording zooplankton concentrations or estimating dispersion indices at upwind and downwind sites (Ragotz-

kie and Bryson 1953; Colebrook 1960; Price 1989). Physical drivers can also change the distribution of phytoplankton, temperature, and nutrients (Wetzel 2001). This has important implications for trophic interactions, because the dynamics of fish and zooplankton are very sensitive to changes in temperature and zooplankton hold an intermediate trophic position, as predators of phytoplankton and prey for fish.

In lakes, water movement is mainly driven by wind (Kalff 2002). Wind exposure depends on a lake’s morphology, thermal stratification, and the surrounding topography. The ‘conveyor belt hypothesis’ (Ragotzkie and Bryson 1953; Colebrook 1960) states that in stratified lakes a combination of wind-driven water movement, zooplankton vertical migration, and internal wave movements generate large-scale accumulations of zooplankton. This begins when the less dense warmer water, sitting on a layer of dense colder water, is subject to sustained winds that tilt the thermocline by pushing the warmer surface water downwind. To replace the water at the upwind end of the lake, water at the downwind end is forced downwards, where it then flows back in the opposite direction to the prevailing winds, setting up a conveyor belt. When the winds stop, gravity tilts the thermocline back and forth, creating a basin-wide internal wave (Kalff 2002). As the conveyor belt operates, zooplankton in the upper epilimnion aggregate downwind and zooplankton in the lower epilimnion aggregate upwind (Thackeray et al. 2004). Migrating animals adjust their vertical position when light conditions change in upwellings or downwellings. Non-migrating animals will be randomly distributed throughout

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the epilimnion because changes in light levels will not elicit a swimming response toward preferred photic zones (George 1981). This has been observed at large spatial scales (>1 km) (George and Winfield 2000; Thackeray et al. 2004; Rinke et al. 2007). Wind can also cause downwind accumulations of (positively buoyant) phytoplankton that are in the upper regions of the epilimnion (George and Edwards 1976; Stauffer 1988).

Langmuir Circulation is another wind-driven circulation pattern that can affect the distribution of water temperature, zooplankton, and phytoplankton. Conveyor belt circulation occurs at large scales and takes up to 12 h to form. Langmuir Circulation occurs at smaller scales (<1 km), sets up quickly (~ 20 min) at wind speeds of at least 3 m s^{-1} , and results in vertical helical currents running parallel to the predominant wind direction. Because the adjoining helical structures rotate in opposite directions, bands of convergent downwelling water alternate with bands of divergent upwelling water. Areas of downwelling accumulate light materials such as zooplankton, phytoplankton, and detritus, causing light-colored 'streaks' (George and Edwards 1976; Wetzel 2001). At wind speeds above 7 m s^{-1} the streaks are somewhat masked by an increase in surface turbulence (Wetzel 2001).

In this study, we relate changes in wind conditions to spatial patterns of water temperature (a proxy for water movement), chlorophyll concentration (a proxy for phytoplankton), and zooplankton biomass. We show that at large spatial scales (>1 km), strong persistent winds generated and maintained downwind accumulations for the three measured quantities. We also show that at smaller spatial scales (<1 km), strong persistent winds increased the variability at the smallest scales (6–12 m).

Methods

Field collections—To determine the effect of wind exposure on the spatial distribution of zooplankton, phytoplankton, and water temperature, we collected data in Lake Opeongo (Ontario, Canada) over a wide range of spatial scales during windy and calm conditions. Lake Opeongo (Fig. 1), located in central Ontario ($45^{\circ}42'N$, $78^{\circ}22'W$), is oligotrophic and composed of four basins. The two basins of interest, South Arm (maximum depth, 50 m) and Annie Bay (maximum depth, 24 m), have similar biological characteristics, but South Arm is larger and deeper and is oriented along the prevailing wind direction, which has been from the west over the last several decades (Finlay et al. 2001; E. A. Blukacz unpubl.). The north-south orientation of Annie Bay reduces exposure to the prevailing westerly winds so that weaker winds from the west-southwest and north predominate. Data were collected in 2001 and 2003 (mid-July to mid-September) in both basins. Wind speed and direction were logged in each basin every 10 min with two weather stations (model 05103, R. M. Young, attached to a $10\times$ Campbell data logger) (Fig. 1).

Simultaneous records were taken of zooplankton distributions (with an Optical Plankton Counter [OPC]; model OPC-1 T, Focal Technologies), chlorophyll concentration

(with a fluorometer [Chelsea Instruments]), water temperature (with a conductivity-temperature-depth probe [model OS 200, Ocean Sensors]), and geographic coordinates (with a global positioning satellite [GPS] system [model GPSMAP 178 Sounder, Garmin]). Data were recorded along linear transects in South Arm (~ 4.8 km) ($n = 75$) and Annie Bay (~ 3 km) ($n = 75$) (Fig. 1A). All instruments were towed at 1.5 m s^{-1} at a fixed depth of 2.5 m. The mixed layer extends from the surface to 6–8-m depth in South Arm and to 5–8-m depth in Annie Bay. Data were logged every second, resulting in a horizontal resolution of 1.5 m. We collected data under windy and calm conditions between morning and dusk to prevent zooplankton diel vertical migration from influencing the spatial patterns (Martin and Srokosz 2002).

The OPC works on the principle of light blockage. A 4-mm-thick light beam projected across the OPC tunnel (6.2×2.0 cm) is obstructed as individual zooplankton pass through the tunnel. The light blocked is proportional to the size of the animal and is recorded as a voltage change that is calibrated to the diameter of a circle that would block the same amount of light (equivalent circular diameter, ECD) (Herman 1992). The fresh mass of each animal was determined by assuming a specific gravity of 1 and using the volume of an oblate spheroid (V), thus:

$$V = \frac{\pi}{6} \times ab^2 \quad (1)$$

where a is the major axis and b is the minor axis (Herman 1992; Sprules et al. 1998). To minimize errors caused by coincident counts (multiple animals passing through the sample beam simultaneously and counted as one large particle), the width of the sampling tunnel was decreased from 25 cm to 6.2 cm through insertion of a clear acrylic plate and application of an empirical correction factor (Sprules et al. 1998).

Zooplankton biomass concentration was estimated by summing the body masses of all individuals encountered in 1.5 linear meters and dividing by the volume of water passing through the OPC. Zooplankton biomass was divided into equi-frequent small (ECDs between 355 and 399 μm) and large (ECDs $>542 \mu\text{m}$) size classes because Martin and Srokosz (2002) found that spatial patterns in the North Atlantic were especially different between large and small zooplankton. Freshwater studies also show that body size plays an important role in determining the reaction of individual animals to wind exposure (Teraguchi et al. 1983). All analyses were performed using five variables: (1–3) three zooplankton biomass size classes (small, large, and bulk = all zooplankton), (4) chlorophyll concentration, and (5) water temperature. Hereafter, the zooplankton biomass size classes are simply referred to as bulk, small, or large. Throughout the sampling season we measured current speed, as outlined by George (1981), using drogues deployed at 2.5 m in both basins during windy and calm conditions but not necessarily during the transect runs.

Large-scale (>1 -km) spatial patterns—Studies show that downwind accumulation of warm water, phytoplankton,

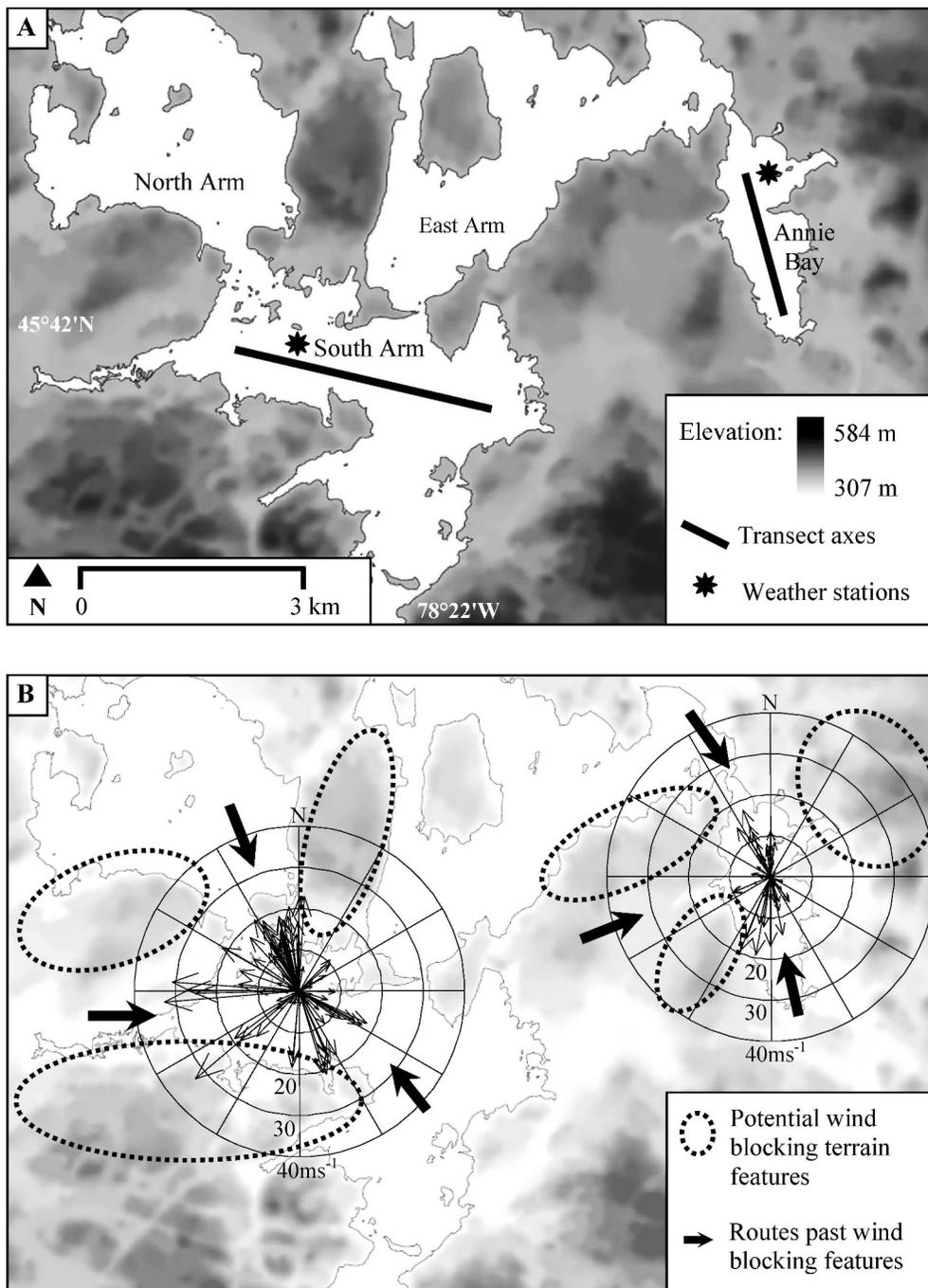


Fig. 1. Map of Lake Opeongo showing elevation data (Canadian Digital Elevation Model [DEM] unpubl.). (A) Location of the sampling transects and weather stations in South Arm and Annie Bay. (B) Vectors for each transect that indicate the wind strength and direction (arrow points to the direction from which the wind is blowing) averaged over the duration of each transect run for South Arm and Annie Bay; these vectors also highlight terrain features that may potentially block wind from some directions. Wind routes between these features are also indicated.

and zooplankton occurs during steady winds blowing from the same direction for a long period of time (George and Winfield 2000; Thackeray et al. 2004; Rinke et al. 2007). For each transect, an accumulation index was computed for all variables and related to descriptors of wind

conditions. The accumulation index is the slope from a linear regression of a given variable on distance along the sampling transect (Menza 2002). A positive value of this index indicates increasing accumulation in the direction of travel.

Wind descriptors—Wind is important in generating water movements but can vary in speed, angle, and persistence, so it is impossible to describe wind with one index. We related five descriptors of wind condition to the accumulation indices computed for each variable. For each basin we computed the following: (1) scalar wind speed, the arithmetic average of wind speed over time, (2) vector wind speed, which is the result of multiplying the north–south and east–west vector components by wind speed, averaging over a specified time interval and computing the net vector by the Pythagorean Theorem, (3) wind persistence, which is the ratio between vector wind speed and scalar wind speed (a value of 1 indicates that wind direction is fixed and a value of 0 indicates that wind direction varies randomly [Panofsky and Brier 1965]), (4) wind direction, which is the arctangent of the quotient between east–west and north–south components (EPA 2000) (wind direction values run clockwise from 0° [north] to just less than 360°), and (5) wind force, which is the average component of wind force parallel to the survey transect:

$$WF = \frac{\sum_{i=1}^n \cos(W_i \angle - T_i \angle) \times Ws_i}{n} \quad (2)$$

where $W\angle$ is the wind direction, $T\angle$ is the transect direction, Ws is the wind speed (m s^{-1}), n is the total number of observations (Menza 2002), and i refers to individual wind observations. A positive wind force indicates that the direction of travel along the sampling transect is within 90° of the wind direction. Adjustments for Coriolis force were not included because given both the latitude and the size of each basin, these effects would be too small to detect against any background turbulence (Kalff 2002). It is important to consider wind history for approximately 24 h prior to sampling (Wetzel 2001; Menza 2002), so for each transect all wind descriptors (except wind force [WF]) were averaged over cumulative 30-min periods up to 24 h before sampling (the first average was based on the time it took to run the transect). This resulted in 49 estimates of each wind descriptor (1 transect run + 24 h divided into 30-min intervals). Pearson correlations were calculated between a given accumulation index and each incremental wind descriptor using each run along the sampling transect as an independent observation. This resulted in 49 correlation coefficients for each wind descriptor, and the calculations were repeated for the other accumulation indices and for both basins. Angular–linear correlations were calculated between accumulation indices and wind direction (Fisher 1993).

We used WF to differentiate between periods when the wind blew from a consistent direction and periods when it did not. We examined the relationship between the accumulation indices and periods of directionally consistent WF by averaging WF for each transect for only the period since the most recent sign change. Then, for cumulative 30-min intervals, extending back in time from the start of the transect, correlations were calculated between each accumulation index and the average WF , with the condition that only those transects that

had consistent WF s at least as long as the interval were retained.

Small-scale (<1-km) spatial patterns—At small scales, we quantified the degree of variability for each variable and related it to wind conditions. We used wavelet rather than spectral analysis to decompose variability across spatial scales because our data were not stationary (constant mean and variance) (Gençay et al. 2002).

Wavelet analysis decomposes the data on a scale-by-scale basis by applying filters that capture features such as abrupt changes in variability. For all transect–variable combinations, the unbiased maximal overlap discrete wavelet transform (MODWT) was used with the Daubechies filter (least asymmetric filter, LA8) to decompose the variability in the raw data into eight different scales ($\lambda_1, \dots, \lambda_8$): 3–6 m, 6–12 m, 12–24 m, 24–48 m, 48–96 m, 96–192 m, 192–384 m, and 384–768 m. The LA8 filter was used because it is better at conserving the variability at a given scale than the commonly used Haar filter (Gençay et al. 2002). We illustrate the MODWT with the Haar filter, which has a length (L) of two and is applied to two adjacent observations. A running average on adjacent neighbors (n_i, n_{i-1}) computes the scaling coefficients $V(\lambda_1)$ that retain the large scale-trend

$$V(\lambda_1) = \frac{n_{i+1} + n_i}{\sqrt{2}} \quad i = 1, 3, 5, \dots, n-1 \quad (3)$$

where n is the number of observations. Running differences are computed as the wavelet coefficients, $W(\lambda_1)$ that contain the fluctuations

$$W(\lambda_1) = \frac{n_{i+1} - n_i}{\sqrt{2}} \quad i = 1, 3, 5, \dots, n-1 \quad (4)$$

(Fig. 2). The filter is shifted to the right, except for the last observation, in which periodic boundary conditions were assumed (Gençay et al. 2002). The scaling coefficients are input for the next scale, and all calculations are repeated. For each scale, coefficients affected by boundary conditions were removed (Percival and Walden 2000; Gençay et al. 2002).

This analysis allowed us to examine variability in the raw data on a scale-by-scale basis (Percival and Mofjeld 1997). Wavelet variance represents the total variability at a single scale:

$$\hat{\sigma}^2(\lambda_j) = \frac{\sum W_i^2}{\tilde{n}_j} \quad (5)$$

(Gençay et al. 2002). The relative importance of variability across scales has been measured as the slope from a log–log plot of wavelet variance as a function of scale, hereafter referred to as wavelet slope (β). A positive wavelet slope indicates that variability increases with scale, while the converse is true for a negative slope (Percival and Walden 2000). All computations were performed using the ‘wave-slim’ package in R (<http://www.r-project.org/>).

As described above, correlations between wavelet slopes and all wind descriptors (except WF) were calculated. Wind descriptors were based on wind history 24 h prior to sampling, because Langmuir Circulation that forms before

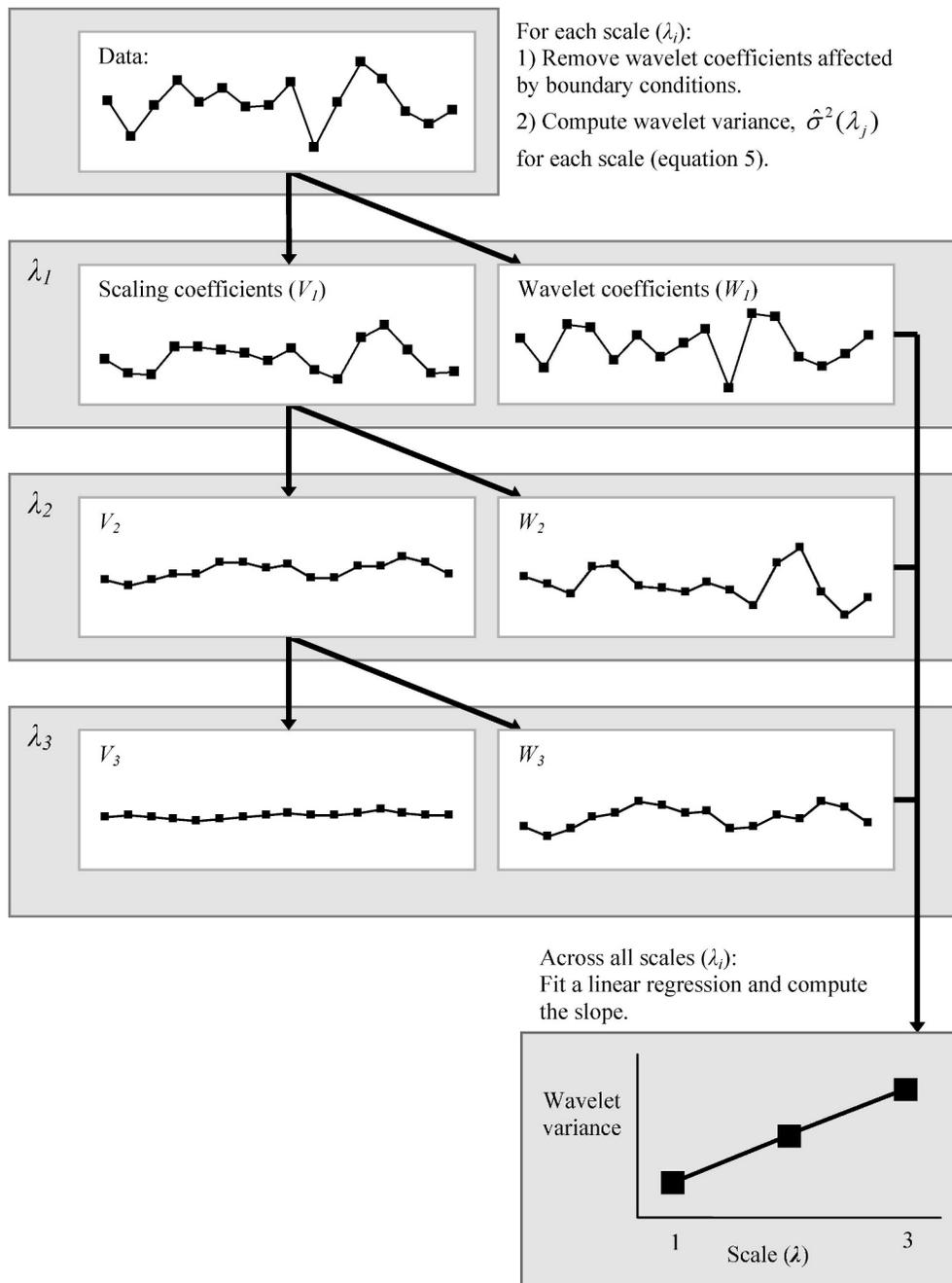


Fig. 2. A flow chart of the main steps in the unbiased maximal overlap discrete wavelet transform (MODWT). The variability across all levels is used to compute the wavelet slope (β) and intercept.

sampling can influence spatial patterns (Malone and McQueen 1983).

Results

Wind patterns and currents—Seasonal average scalar wind speed in Annie Bay (1.8 m s^{-1}) was lower than in South Arm (3.6 m s^{-1} in 2001 and 3.5 m s^{-1} in 2003), and South Arm had more persistent winds (0.7) than did Annie Bay (0.3). The average wind direction in South Arm was

from 326° (in 2001) and from 275° (in 2003), and in Annie Bay average wind direction was from 264.5° (in 2003). During our transect runs (Fig. 1B) the winds were, on average, slower (7 m s^{-1}) in Annie Bay than in South Arm (13 m s^{-1}). The average wind direction in South Arm was from 305° , and in Annie Bay it was from 274° . Average current speeds in South Arm and in Annie Bay measured at a depth of 2.5 m were 3.5 cm s^{-1} (maximum of 8 cm s^{-1}) and 1.87 cm s^{-1} (maximum of 12 cm s^{-1}), respectively.

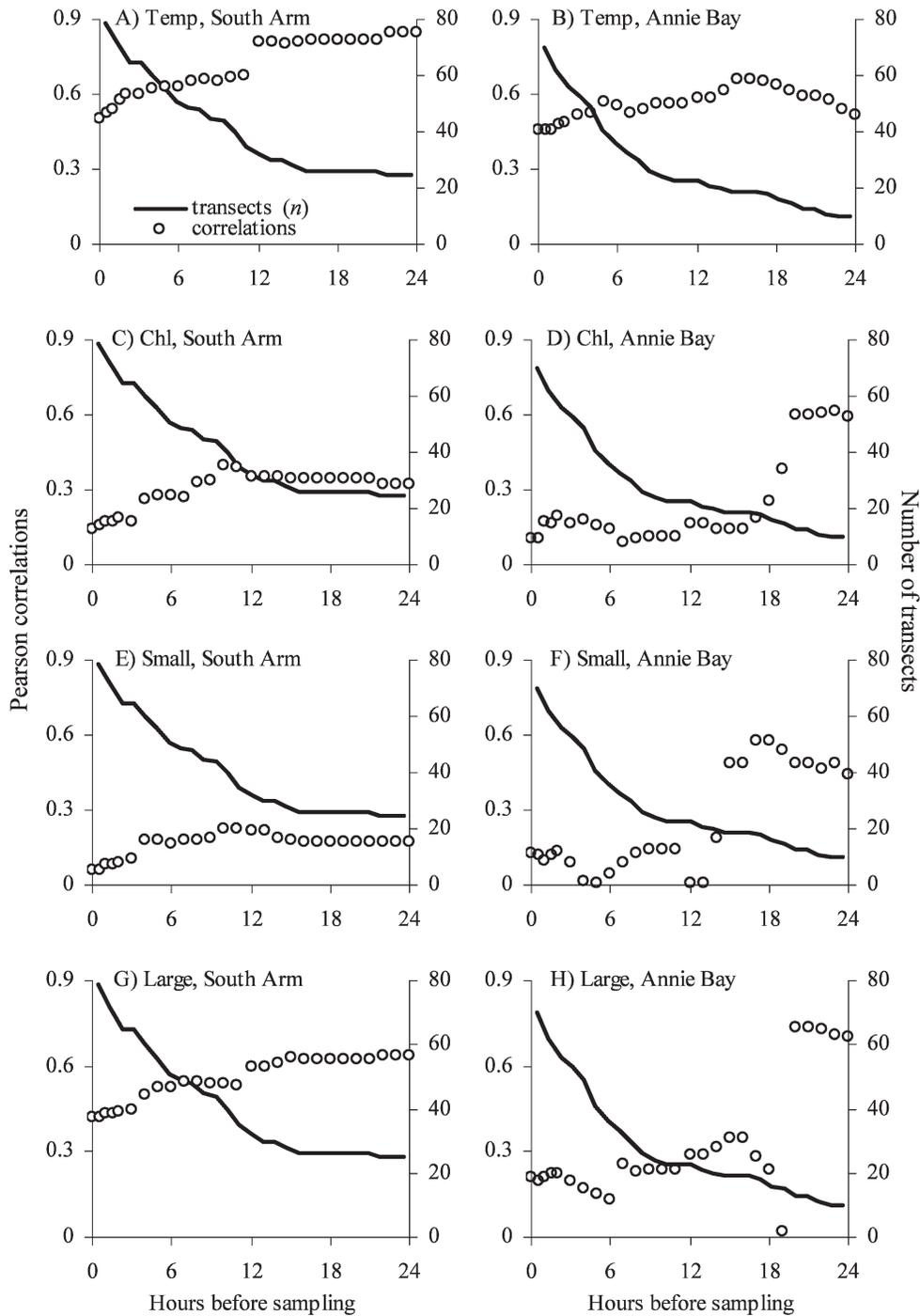


Fig. 3. Correlations between accumulation indices and average wind forces computed using progressively longer wind histories for (A, C, E, G) South Arm and for (B, D, F, H) Annie Bay. The accumulation indices shown are water temperature (Temp), chlorophyll concentration (Chl), small zooplankton (Small), and large zooplankton (Large). The numbers of transects that had consistent negative or positive wind force estimates are also shown.

Large-scale (>1-km) spatial patterns—Correlation coefficients of <0.30 are not emphasized because they explain less than 10% of the variability. *WF* was the only descriptor with correlation coefficients >0.30 . Correlations in South Arm reach a maximum at 12 h before sampling for water temperature accumulation indices (Fig. 3A) and large

(Fig. 3G) and bulk (not shown) zooplankton accumulation indices, whereas chlorophyll concentration reaches a maximum 10 h before sampling (Fig. 3C). The number of transects for which *WF* was consistent decreased to 22 at 24 h before sampling. In Annie Bay, positive correlations between average wind force reached a maximum 15 h after

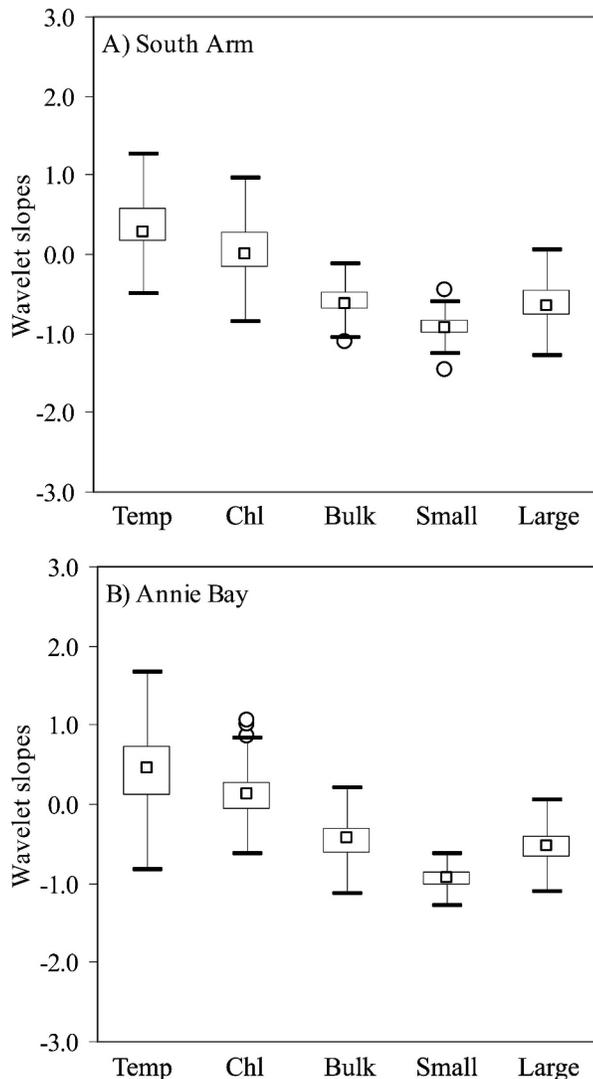


Fig. 4. Boxplots of wavelet slopes in (A) South Arm and (B) Annie Bay. The abbreviations used are as follows: water temperature (Temp), chlorophyll concentration (Chl), bulk zooplankton (Bulk), small zooplankton (Small), and large zooplankton (Large). Medians are indicated by small squares, the whiskers (open circles) represent first and third quartiles, values outside the whiskers (open circles) are extremes, and interquartile range is represented by the boxes.

sampling for temperature, 19 h after sampling for chlorophyll and large zooplankton, and 17 h after sampling for small zooplankton (Fig. 3B,D,F,H). *WF* was consistent in only 10 transects at 24 h before sampling. Patterns in correlations for Annie Bay are more variable because there were fewer transects for which *WF* was consistent at the longer periods before sampling.

Small-scale (<1-km) spatial patterns—Water temperatures tended to have positive wavelet slopes compared to all zooplankton slopes, which were mainly negative, indicating that zooplankton spatial patterns were more variable at smaller scales (Fig. 4). Chlorophyll wavelet slopes were

roughly evenly split between negative and positive. There was no relationship between wavelet slopes for any of the measured variables and either wind direction or average wind force. In South Arm, the wavelet slopes of the variables were negatively associated with scalar wind speed and vector wind speed, but the correlations tended to be greatest at roughly 12 h prior to sampling, except in the case of temperature, for which the minimum occurred at about 3 h (Fig. 5A,C). Negative relationships with wavelet slope indicate that spatial patterns became dominated by small-scale variability as the winds became stronger. On average, the variability increased by 150% from the largest scales (384–768 m) to the smallest scales (6–12 m) for all the measured quantities. Wind persistence was also negatively related to wavelet slopes for water temperatures, indicating that persistent winds were also important in maintaining small-scale variability (Fig. 5E). Wavelet slopes for small zooplankton were not related to any of the wind descriptors. In Annie Bay, only water temperature wavelet slopes had strong negative correlations with scalar wind speed and vector wind speed, which decreased in strength with increasing duration of wind history (Fig. 5B,D). None of the zooplankton wavelet slopes were related to any of the wind descriptors (not shown).

Wind conditions and spatial patterns—We used a subset of transects with similar wind conditions to contrast large-scale and small-scale spatial patterns in both basins using water temperature as an example. For each basin, transects were selected from similar calm (wind speed $<3 \text{ m s}^{-1}$) and windy (wind speed $6\text{--}10 \text{ m s}^{-1}$) conditions. Under calm conditions, water temperatures increased in both basins by only about 0.10°C across the sampling transect, indicating little ‘accumulation’ without wind. Under windy conditions, temperatures increased along the transects by about 1°C in both basins. This indicates that downwind accumulation was similar across basins under the same wind conditions (Table 1). Small-scale spatial patterns in water temperature, as measured by wavelet slopes, were also similar between basins during each of the calm and windy conditions.

Discussion

Our experimental design and extensive sampling allowed for a very thorough examination of the effects of wind exposure on spatial patterns. Because we repeatedly sampled our transects 150 times over a wide range of wind conditions, we were able to relate the wind descriptors to spatial descriptors, unlike previous studies, in which either few transects were collected or an ‘ensemble’ was created by averaging across all transects. Elevation surrounding South Arm shows that the main route for the winds was from the west to east through a wide valley across the open water, with higher elevations reducing northwest and southwest winds (Fig. 1). In contrast, these prevailing winds in Annie Bay were blocked by higher elevations, so that the winds had two main alternative routes: from the north, where Annie Bay opens into East Arm and where the land is relatively low, and from the southwest, where a valley

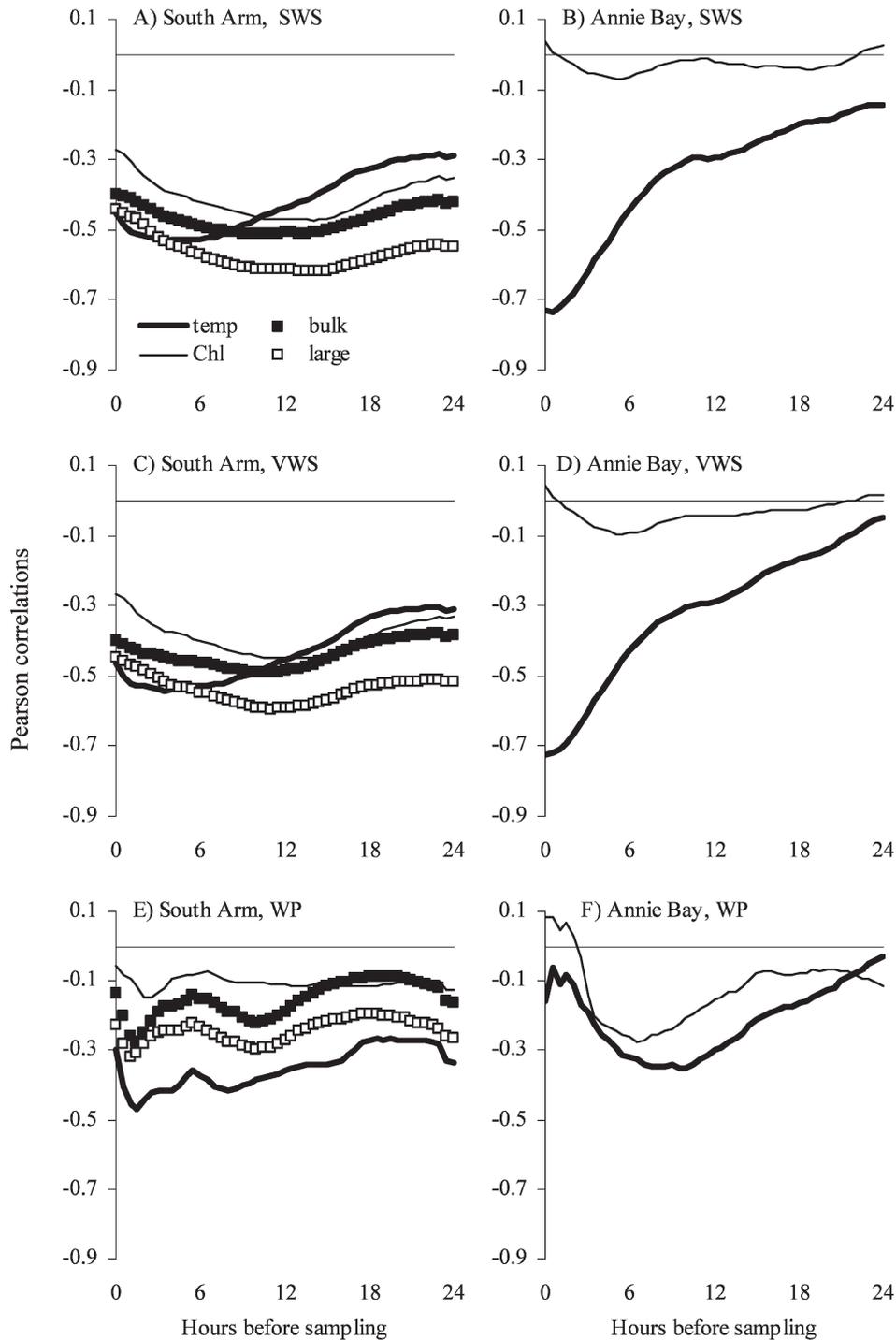


Fig. 5. Correlations between each wind descriptor (scalar wind speed [SWS], vector wind speed [VWS], and wind persistence [WP]) and wavelet slopes computed for selected variables for (A, C, E) South Arm and (B, D, F) Annie Bay, plotted as a function of time prior to sampling. See caption for Fig. 4 for abbreviation key.

between two areas of higher elevation provides an open route for the wind (Fig. 1). Seasonal wind data showed that the winds in South Arm, which is oriented along the prevailing westerly winds, were stronger and more persistent than in Annie Bay, which is relatively sheltered from

the winds as a result of its north–south orientation. This confirmed that spatial patterns in South Arm were generated and maintained by strong persistent winds, whereas winds in Annie Bay were relatively calm and less persistent. However, as we discuss further on, the

Table 1. Transects ($n = 5$) were selected for each combination of basin and wind condition, and large- and small-scale spatial patterns were computed for water temperatures. The change in water temperatures across the sampling transects is shown for large scales, and the water temperature wavelet slopes are shown for small scales. The standard error of the mean (SEM) is indicated in parentheses.

Wind conditions	Basin	Large scale ($^{\circ}\text{C}$)	Small scale
Calm	South Arm	0.14(0.03)	0.63(0.05)
Calm	Annie Bay	0.11(0.02)	0.64(0.08)
Windy	South Arm	1.10(0.10)	-0.16(0.10)
Windy	Annie Bay	1.05(0.06)	-0.13(0.07)

orientation of the sampling transect relative to the direction of the prevailing wind is a very important determinant of the patterns captured.

WF was the only descriptor that was associated with the accumulation indices; hence, large-scale downwind accumulation occurred when winds of increasing speed blew along the sampling transects. Overall strong persistent winds in South Arm generated and maintained more downwind accumulation than in Annie Bay.

Water temperatures had the strongest relationship with average *WF* in both basins, with relatively fewer transects in Annie Bay showing downwind accumulation (Fig. 3). Different accumulation patterns between the basins may be a result not only of differences in wind patterns but also of the fact that the northern end of the sampling transect in Annie Bay is close to the East Arm inflow, through which warm water could enter, resulting in accumulation indices that would have a sign opposite to the average wind force estimated from the prevailing northern winds (Fig. 1). By contrast, both ends of the South Arm transect are located in deeper water, further away from inflows. During relatively calm winds, water temperatures in Annie Bay show an increase of about 1.5°C in the northern end of the transect, but this was not observed for South Arm. Horizontal variation in near-surface water ($\sim 2\text{-m}$ -deep) temperatures can serve as a proxy for circulation patterns (George 1981). George and Winfield (2000) observed that conveyor belt circulation leads to a difference in water temperatures of approximately 2°C at a depth of 3 m between upwind and downwind sites. We observed this temperature difference five times more often in South Arm than in Annie Bay. Changing temperatures can have ecological implications for organisms living at upwind or downwind sites. Warmer temperatures downwind in South Arm have positively influenced the growth rates of young-of-the-year bass (Kaevats et al. 2005). Given that we recorded temperature differences along the transects comparable to those documented by George and Winfield (2000) under conveyor belt circulation, we are confident that the wind forces we measured were strong enough to generate the currents required for the spatial patterns we observed.

Zooplankton are weak swimmers, so their distribution can be strongly influenced by water movements, especially during strong winds (George and Winfield 2000). The downwind accumulation of zooplankton has been observed

in both small shallow lakes and large deep lakes (Jones et al. 1995; Lacroix and Lescher-Moutoué 1995; George and Winfield 2000). Downwind and upwind accumulations can occur simultaneously, according to the conveyor belt hypothesis, because animals in the upper regions of the water column are transported passively downwind and will become aggregated as they actively swim against the downwelling to remain at their preferred photic zone, whereas animals in the lower regions of the water column will be transported upwind and become aggregated as they resist upward displacement (George and Winfield 2000). We did not measure vertical currents, but typical downwelling current speeds are 1.6 cm s^{-1} at wind speeds of 6 m s^{-1} (Kalf 2002). Studies have shown that large animals that can swim at 0.08 cm s^{-1} are able to maintain their vertical position in downwellings from wind speeds of about 3 m s^{-1} (George and Edwards 1976). So it is possible that large zooplankton in Lake Opeongo could maintain their vertical positions in a manner that would lead to differential wind effects on their distribution. By contrast, smaller zooplankton that swim more slowly will simply be moved around by water currents. Non-migrating animals will remain randomly distributed throughout the water column as they are passively carried by the currents (George and Winfield 2000). Bulk and large zooplankton were related to *WF* where peaks in downwind accumulation occurred less quickly and frequently in Annie Bay than in South Arm (Fig. 3G,H). In Annie Bay, downwind accumulation occurred less frequently because the winds were of intermediate speed ($3\text{--}7\text{ m s}^{-1}$) and relatively inconsistent. Wind-driven spatial patterns are often short-lived and are readily reversed if the prevailing winds change (Ragotzie and Bryson 1953; Jones et al. 1995; George and Winfield 2000). Small zooplankton did not show any relationship with average *WF*, indicating that they are randomly distributed throughout the epilimnion in both basins. The trophic implication of these accumulations is that fish find and feed on them, even if the accumulations are relatively short-lived (Kalikham et al. 1992; George and Winfield 2000; Thackeray et al. 2004).

The effect that conveyor belt circulation will have on the spatial distribution of the phytoplankton community depends on the degree of vertical patchiness (George and Edwards 1976). Positively buoyant organisms such as cyanobacteria, with an ascending velocity that is greater than that of the descending water, will tend to aggregate downwind. Conversely, negatively buoyant phytoplankton such as greens and diatoms will be carried upwind by the deep return currents. Downwind chlorophyll accumulation occurred more quickly and frequently in South Arm than in Annie Bay (Fig. 3C,D). South Arm had a greater potential for downwind accumulation of phytoplankton, not only because of strong and persistent winds but also because 58% of the seasonal average phytoplankton biomass (measured on a monthly basis) consisted of motile species that had the potential to act as positively buoyant particles (Jones et al. 1995). Annie Bay had a much lower potential for downwind accumulation because it had weaker and less consistent winds, with only 19% of the phytoplankton being motile. Cyanobacteria, which accounted for less than

3% of phytoplankton biomass, are also positively buoyant and have a rising velocity of 0.004 cm s^{-1} , compared to typical zooplankton descent rates of 0.3 cm s^{-1} (Hutchinson 1967; Chapra 1997). It has been shown (George and Edwards 1976) that a vertical gradient can set up during relatively calm conditions, and when winds increase, the positively buoyant phytoplankton accumulate downwind. Overall, and unlike water temperatures, chlorophyll concentrations in South Arm had a weak relationship with *WF*. While chlorophyll spatial patterns can also result from nutrient gradients, because strong winds can enhance vertical mixing (George and Winfield 2000; Fabian et al. 2004), this is not possible in Lake Opeongo, because phosphorus exists in very limited supply, such that upwellings are not likely to result in an increase of algal growth (H. Cyr pers. comm.).

While the conveyor belt hypothesis works to explain large-scale accumulations, at smaller spatial scales ($<1 \text{ km}$) different drivers, including Langmuir Circulation, may help to explain the observed patterns in variability. It is not surprising that there was no relationship between either *WF* or wind direction and any of the wavelet slopes, because neither of these descriptors is an accurate indicator of the persistent intermediate to strong winds ($>7 \text{ m s}^{-1}$) that are needed to generate Langmuir Circulation (Kalff 2002). In South Arm, both scalar wind speed and vector wind speed had strong negative correlations with all wavelet slopes, except for small zooplankton, indicating that small-scale variability increased, mainly during intermediate to strong winds (Fig. 5A,C). In contrast, Annie Bay had relatively weaker winds, and, therefore, only water temperature had a negative relationship with scalar wind speed and vector wind speed, indicating that strong to intermediate winds were required to generate small-scale variability for all the remaining variables (Fig. 5B,D). These patterns were also influenced by the orientation of the sampling transects in relation to the prevailing winds. Langmuir Circulation is typically identified at scales of 2 m to 1 km, and we estimate that the helical structures in Lake Opeongo will have a diameter of approximately 8 m, with a separation distance of 16 m and a length between 3 and 10 times the separation distance (Thorpe 2004). In both basins, peaks in variability were observed across five scales (6–192 m) for all the variables. These peaks were most frequent at 6–12 m and shifted toward longer scales (i.e., 96–192 m) when the angle between the wind and the transect increased. Both these observations are consistent with the behavior of Langmuir Circulation (Thorpe 2004). More helical structures should be sampled if the direction of travel is perpendicular to the prevailing wind direction, because the helical structures will align themselves parallel to the prevailing wind direction, resulting in more small-scale variability than is associated with transects taken parallel to Langmuir Circulation (Franks 2005). This arises because water movement occurs in three dimensions, whereas data were collected in one dimension. In South Arm, the sampling transect was parallel to the prevailing western winds, which reduced the potential of crossing helical structures. By contrast, the sampling transect in Annie Bay was perpendicular to the prevailing western winds, which

increased the chance of crossing over helical structures and thus generating small-scale variability. In fact, Franks (2005) suggests that sampling perpendicular to the helical structures captures more of the ‘real variability’ associated with the two-dimensional pattern of waves.

Wind-driven water movement generated and maintained large- and small-scale spatial patterns in zooplankton, chlorophyll, and water temperatures, particularly in the larger South Arm, where winds were stronger and more persistent. Biological drivers such as fish predation may have also played a role in generating zooplankton spatial patterns; however, this study focused on wind-driven patchiness (Pinel-Alloul 1995; Folt and Burns 1999). We provide unique insights into spatial patterns of zooplankton, such as increasingly dominant small-scale patterns with increasing speed of winds that blew 12 h before data collection. Furthermore, we observed such patterns for large-bodied zooplankton but not for small-bodied animals. Such observations are possible only with our high-resolution wind and plankton data in combination with advanced spatial statistics and give rise to the intriguing possibility that simple physical processes such as surface winds may actually shape the nature of trophic interactions in lake ecosystems.

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