

## Environmental variability influences the structure of benthic algal communities in an oligotrophic lake

Shelley Kathleen McCabe and Hélène Cyr

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Theoretical models suggest that environmental variability can promote biodiversity, both in terms of richness and evenness of species. These findings have been supported experimentally in simplified communities with simplified regimes of environmental variability. Here we test the importance of environmental variability in a more natural setting by comparing the composition of benthic algal communities along a natural gradient of environmental variability created by internal waves in an elongated lake basin. Algal communities were grown on tiles at five upwind and five downwind sites in the lower littoral zone of South Arm, in Lake Opeongo, Ontario, Canada. Upwind sites were 1°C colder, on average, than downwind sites and had more variable water temperatures. The ranges of mean water temperatures and of water temperature variability were greater among upwind sites than among downwind sites. We used water temperature variability as a proxy for environmental variability. Total algal biovolume was similar at all sites, but the composition of these communities varied systematically with temperature variability. An observed shift in the relative dominance between *Achnanthydium minutissimum*, *Surirella* sp. and *Pinnularia* spp. is consistent with what we know about these species. Diatom richness increased from 12 to 15 genera with increasing variability at upwind ( $p=0.10$ ,  $r^2=0.65$ ) and downwind sites ( $p=0.11$ ,  $r^2=0.63$ ). Community evenness also increased with increasing variability ( $p=0.03$ ,  $r^2=0.82$  at upwind sites;  $p=0.0002$ ,  $r^2=0.99$  at downwind sites). These relationships were observed despite low nutrient and light availability, as well as the presence of grazers. Furthermore, environmental variability affected diatom communities in the presence of several competing factors (temperature, light, nutrients and disturbance). Our results suggest that increased environmental variability can lead to higher biodiversity in a complex natural system.

S. K. McCabe and H. Cyr ([helene@zoo.utoronto.ca](mailto:helene@zoo.utoronto.ca)), Dept of Zoology, Univ. of Toronto, 25 Harbord Street, Toronto, Ontario, Canada, M5S 3G5.

Several factors can promote the coexistence of species. Chesson (2000) divides these factors into two groups: stabilizing factors which prevent competitive exclusion and equalizing factors which slow the rate of competitive exclusion but are insufficient on their own to maintain coexistence. Stabilizing factors, such as resource partitioning, frequency-dependent predation, and temporal and spatial variability in the environment, increase intraspecific competition relative to interspecific competition (Chesson 2000). Equalizing factors, such as limits

to colonization ability and high predation on the competitively dominant species, minimize average fitness differences between species (Chesson 2000). In this study, we focus on temporal environmental variability, which has been shown to increase diversity (Sommer 1984, 1985).

Environmental variability can promote diversity when the competitive ability of species changes depending on the strength of competition (relative nonlinearity of competition sensu Chesson 2000), or when species can

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store resources, or have resting stages or propagules, that help them survive unfavourable periods (storage effect sensu Chesson 2000). The storage effect and the relative nonlinearities of competition promote coexistence by creating temporal and/or spatial niches which shift in space and time with fluctuating environmental conditions (Chesson and Huntly 1997).

The effects of fluctuating environmental conditions on diversity have been explored using both theoretical models and experiments. Theoretical models clearly show that fluctuating environmental conditions can promote the coexistence of species (Chesson and Huntley 1997, Anderies and Beisner 2000, Litchman and Klausmeier 2001, Huisman et al. 2004). Several experimental studies also demonstrate higher species diversity under various regimes of fluctuating environmental conditions. For example, Sommer (1984, 1985) showed experimentally that more phytoplankton species coexisted and the community was more even when grown with pulses of limiting nutrients. Experiments also found that fluctuating light promoted the evenness of phytoplankton communities (Litchman 1998, Flöder et al. 2002) and permitted the persistence of an algal species that was excluded under constant light (Litchman 2003). Similarly, Beisner (2001) demonstrated in field mesocosm experiments that mixing the water column increased the evenness of phytoplankton communities. These models and experiments all show that environmental variability can promote biodiversity in simplified communities, when one or two environmental variables fluctuate at a given frequency. Natural communities, however, are composed of many coexisting species that are exposed to complex regimes of environmental variability (Cyr and Cyr 2003, Cyr et al. 2004).

The purpose of this study is to test whether benthic algal communities exposed to different regimes of natural environmental variability in the littoral zones of lakes show consistent differences in biomass, overall taxonomic composition (e.g. diatoms, green algae, and cyanobacteria), and diversity. Benthic algae are an ideal system for testing this question because they are stationary and they have short generation times, so communities develop quickly. In large lakes, different parts of the littoral zones in which these algae live can experience different regimes of environmental variability due to wind-driven upwellings and internal waves. Strong winds blow surface water to the downwind end of the lake, resulting in upwelling cold water upwind, and downwelling warm water downwind. When the wind abates a wave develops along the thermocline. Where these movements of the thermocline occur inshore they cause temperature fluctuations (Finlay et al. 2001) and turbulence (Lemckert et al. 2004) in the littoral zone. Several factors may vary together with temperature and turbulence, such as turbidity (Shteinman et al. 1997, Pritchard and Hogg 2003), light availability (Schallen-

berg and Burns 2004), and nutrient availability (Riber and Wetzel 1987). We used temperature variability as a proxy for fluctuations in the suite of environmental factors driven by the internal wave to test whether benthic algal community composition and diversity vary systematically with environmental variability in this natural system.

## Methods

### Study site

Lake Opeongo is a multi-basin oligotrophic lake located in Algonquin Park, Ontario, Canada (45°42' N, 78°22' W), on the Canadian Shield. This study focuses on South Arm (Fig. 1), a 22.1 km<sup>2</sup>, elongated basin with an average depth of 14.6 m, a maximum depth of 50 m, and a length: breadth ratio of 5. The longest axis of South Arm is 5.8 km long and is aligned with the prevailing winds. Wind speed and direction were recorded every 10 min at a weather station located in South Arm (Fig. 1) and maintained by the Ontario Ministry of Natural Resources. South Arm develops a stable thermal stratification in the summer, with a thermocline at ~ 9 m depth. The offshore epilimnetic chlorophyll *a* concentration is 1.5–3 µg l<sup>-1</sup> (unpubl., A. Blukacz and G. Sprules, Univ. Toronto at Mississauga, pers. comm.). Light penetrates down to 6–9 m (1% surface irradiance; 2003, 2004 unpubl.), and penetrated to ~ 6.5 m in July 2003.

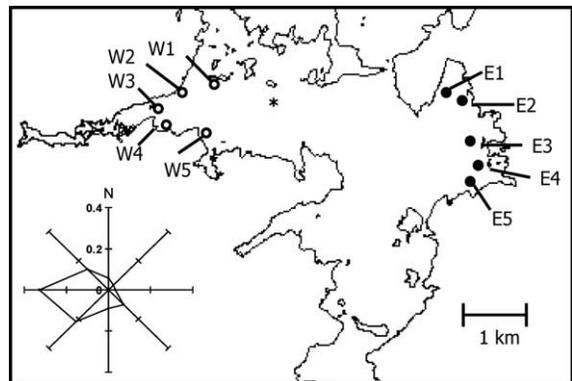


Fig. 1. Map showing the sampling sites in the South Arm of Lake Opeongo. The weather station is represented by a star. The rosette on the bottom left shows the proportion of total wind speed that came from each of eight compass directions during this study (July 3–August 1, 2003). The prevailing winds were blowing along the main axis of the basin. Open circles represent upwind sites (W1–W5), and closed circles represent downwind sites (E1–E5).

## Growth of algal communities

Ten study sites were distributed around the western (upwind: W1-W5) and the eastern (downwind: E1-E5) ends of South Arm (Fig. 1). At each site, algae were grown on 12 replicate unglazed 4.7 × 4.7 cm tiles attached to a 13 cm high rack, mounted on a cement block, for a total height of 33 cm above the sediment. The tiles were set out at a depth of 5–6 m for four weeks in July 2003. Tiles were placed in this lower littoral zone because it is below the direct influence of surface waves, but close enough to the thermocline to experience environmental variability due to internal waves. The sites were within the euphotic zone, with approximately 3% of surface PAR reaching this depth.

The tiles were retrieved by a diver using a covered plastic container to protect the algal communities from disturbance while being brought to the surface. On the boat, individual tiles were carefully transferred to separate twist-tie bags and stored in a dark cooler for transport back to the lakeshore lab. In the lab, algae were carefully scrubbed from the tiles using a Reach® electrical toothbrush and GF/F filtered lake water, were added to the overlying water from the twist-tie bag and preserved with Lugol's iodine solution (~ 0.5–1% final concentration).

In 2004 we measured algal colonization rate to determine how long it takes for benthic algal communities to fully develop in Lake Opeongo. Tiles were set out at 2 sites (W2, E3) on June 15, and 1–3 replicate tiles were retrieved after 1, 3.5, 6, and 11.5 weeks and processed as described above.

## Temperature variability

Water temperature variability was used as a proxy for environmental variability. Stowaway Tidbit® thermistors (Model TB132–05+37, Onset Corporation, Burlington, ON, Canada) were attached to each set of tiles to record water temperature at 8-minute intervals throughout the study. All temperature loggers were calibrated with a mercury thermometer at room temperature and at 4°C. To calculate variability, we removed the downward trend in water temperature at each site (0.10–1.54°C temperature change upwind; 2.06–2.57°C downwind) using linear regression analysis, then averaged the squared residuals from the linear trends. This measure of variability, called residual mean square, RMS (Zar 1984), standardizes the variability to the average temperature at each site.

## Algal counts and biovolume

Six tiles from each of the ten sites were randomly chosen for analysis. Algae were identified using Wehr and

Sheath (2003) and Barber and Haworth (1981). One sample per site was processed by David Finlay (Fisheries and Oceans Canada, Freshwater Institute, Winnipeg, MB, Canada) to confirm algal identification. Algae were counted in a Sedgewick-Rafter cell using an inverted microscope. The most abundant genus of diatoms (*Achnanthes*) was counted separately at 400 × magnification until at least 400 individuals were encountered. All other algal taxa were counted at 400 × magnification until a total of at least 600 individuals were encountered. All counts were expressed in number of individuals cm<sup>-2</sup>. Planktonic algae (identified with the help of A. Blukacz and M. Douglas, Univ. Toronto, pers. comm.; Wehr and Sheath 2003) were excluded from our analyses, as they are considered transients in benthic communities. *Dinobryon* spp., *Aulacoseira* spp. and *Cyclotella* spp. were the most common planktonic algae in our samples, but we also found *Fragilaria crotonensis*, *Urosolenia eriensis*, and *Tabellaria* spp. All planktonic taxa were very rare (<2% of cell counts), and together represented <5% of all cells counted. Their exclusion from our analyses is unlikely to alter our results.

*Navicula*-shaped diatoms (*Navicula*, *Stauroneis*, *Neidium*, *Nitzschia* and *Frustulia*) could not be identified to the genus level in uncleaned samples, so they were originally pooled together as “naviculoids”. To separate the naviculoids, three samples from each site were digested in 30% H<sub>2</sub>O<sub>2</sub> and mounted with Z-Rax® (W. P. Dailey, Univ. of Pennsylvania). Genera were identified and counted at 800 × magnification until at least 100 valves were encountered. The proportion of each genus of naviculoids was then used to calculate their density in the samples.

Biovolume was calculated assuming standard geometric shapes for each taxon (Hillebrand et al. 1999). The dimensions of cells, filaments or colonies were measured with an image analysis system (Optimas 5.1 Image Analysis Software®). The number of cells measured per taxon ranged from 12 for rare genera to 239 for common genera.

## Indices of community structure

For a detailed analysis of community composition, we focused on diatoms, which were the most dominant and diverse group of algae in our samples. Generic richness (G) and Shannon-Wiener evenness (J') were calculated both in terms of number of cells and of biovolume. Because algal taxa vary in size by several orders of magnitude, the use of cell counts to measure relative dominance in a community may provide a biased measure of the influence of different taxa. In algal communities, biovolume is often used to measure the evenness of communities.

We counted between 438 and 821 diatoms per sample, until the number of new genera encountered ceased to increase with increasing number of individuals counted (not shown). Nevertheless, we standardized our measure of diatom richness for differences in sampling effort among sites (Gotelli and Colwell 2001). We used EstimateS (Version 7.5, R.K. Colwell, Dept. of Ecology and Evolutionary Biology, Univ. of Connecticut) to produce sample-based (without replacement) rarefaction curves scaled to the number of individuals counted. We considered three estimates of richness: a modified Coleman rarefaction curve, a first-order jackknife (Jack1) estimate and a moment-based (Mao Tau) rarefaction curve. The Coleman rarefaction curve (Coleman 1981) is commonly used in community analyses, but is biased when sample size (in our case,  $n = 6$ ) is small (Colwell et al. 2004). The Jack1 is robust to low number of samples, although it is known to underestimate the total number of species when many rare species are present (Smith and van Belle 1984). The moment-based (Mao Tau) rarefaction curve, like the Coleman curve, does not require resampling of the dataset, and therefore is less computationally intensive than Jack1 (Colwell et al. 2004).

The Shannon-Wiener evenness index of benthic diatoms was calculated as:

$$J' = \frac{\sum_{i=1}^G [p_i \times \ln(p_i)]}{\ln(G)} \quad (1)$$

where  $p_i$  is the proportion of individuals or biovolume in the  $i$ th genus and  $G$  is the total number of diatom genera present (Shannon and Weaver 1964).

To explore shifts in diatom generic composition, we performed correspondence analyses (CA, Pielou 1984) using the proportions of biovolume and of number of cells in each genus. Proportions were used to remove the effect of differences in total number of cells and total biovolume, and to focus the analysis on the taxonomic composition of these communities. We selected correspondence analysis to avoid problems due to the use of proportional data in other methods of multivariate analysis (Jackson 1997).

### Statistical analyses

We used two nested MANOVAs (Hand and Taylor 1987) to test for community differences between upwind and downwind sites: one for total biovolume of algae, generic richness of diatoms and evenness of diatoms (i.e. three independent variables); the other for the biovolumes of three major algal groups (diatoms, cyanobacteria, green algae), generic richness of diatoms and evenness of diatoms (i.e. five independent variables). We used the two ends of the lake basin (upwind and downwind) as the first level and sites as the second, nested level. There were six replicate tiles at each site. The evenness of

diatom cells, total algal biovolume and the biovolume of diatoms were log-transformed, and the biovolumes of green algae and of cyanobacteria were square-root transformed to normalize their distributions (Zar 1984).

We also tested (with least-square linear regression analysis; Sokal and Rohlf 1981) whether different indices of community structure (diatom richness, evenness, and generic composition, based on results from the correspondence analysis) were related to our measure of environmental variability (RMS of water temperature), both across the whole basin and at each end of the basin. For all regressions, we chose a priori a significance level of  $\alpha = 0.1$ , as each regression was based on only five data points (five sampling sites). The standard significance level of  $\alpha = 0.05$  would require an unreasonably high fit of  $r = 0.88$  when  $n = 5$  (Zar 1984, p. 570), and would increase the probability of a type II error. All statistical analyses were performed using SAS<sup>®</sup> 8.0 (SAS 2000), except for the correspondence analyses, which were performed using Biplot 0.1 (I. Lipkovich and E. P. Smith, Dept. of Statistics, Virginia Tech., 2001).

## Results

### Regimes of temperature variability

Different sites in the lower littoral zone of South Arm experienced different regimes of temperature (Fig. 2). Sites at the upwind (western) end of South Arm had colder and more variable water temperatures than sites at the downwind (eastern) end. In July 2003 the water was 1°C colder on average at the upwind end than at the downwind end of the basin (geometric mean tempera-

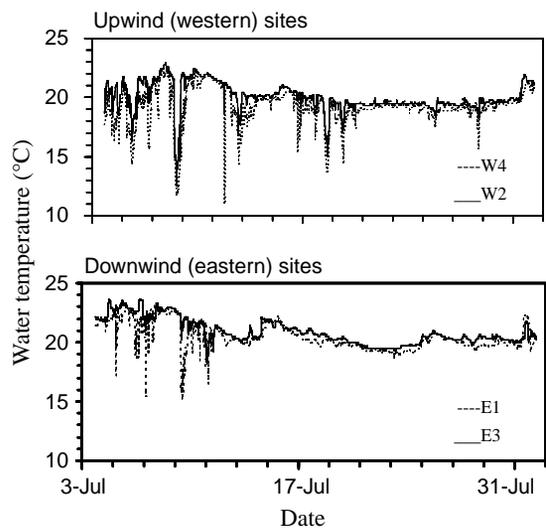


Fig. 2. Water temperature at the most (W4) and least (W2) variable sites upwind; and the most (E1) and least (E3) variable sites downwind measured at 8 minute intervals from 3 July–1 August, 2003.

tures were 19.6 and 20.7°C, respectively). The water temperature ranged from 11.0 to 22.9°C at upwind sites compared to 15.1 to 24.0°C at downwind sites, and was more variable upwind than downwind (RMS = 1.4–2.7°C<sup>2</sup> and 0.5–1.0°C<sup>2</sup>, respectively; Fig. 2). The residual mean square (RMS) of water temperature is an aggregate measure of the number and intensity of cold water upwellings. The largest upwelling occurred simultaneously at all five upwind sites on July 8–9, with a drop in water temperature of 10°C and a return to the original temperature within 24 h (Fig. 2). Other large upwellings of shorter duration occurred simultaneously at two or three sites throughout the study period, but the upwellings were more frequent and of greater magnitude at upwind sites (Fig. 2).

Large differences in water temperature were also found among sites at either end of the basin. At the upwind end of the basin, the coldest, most variable site was W4 (mean = 19.1°C, RMS = 2.7°C<sup>2</sup>; Fig. 2), and the warmest, least variable site was W2 (mean = 20.0°C, RMS = 1.4°C<sup>2</sup>; Fig. 2). At the downwind end of the basin, the coldest, most variable site was E1 (mean = 20.4°C, RMS = 1.0°C<sup>2</sup>; Fig. 2), and the warmest, least variable site was E3 (mean = 20.9°C, RMS = 0.5°C<sup>2</sup>; Fig. 2). The ranges of mean temperatures and of temperature variability were narrower among downwind sites than among upwind sites.

### Algal biovolume

Benthic algae colonized the tiles very rapidly, and the communities were fully developed (in terms of total biovolume) within four weeks (2004 data, not shown). Total algal biovolume varied 4-fold among sites (5.1–21.2 × 10<sup>6</sup> μm<sup>3</sup> cm<sup>-2</sup>; nested MANOVA,  $F_{8,50} = 16.80$ ,  $p < 0.0001$ ; Fig. 3), but did not differ significantly between upwind and downwind sites ( $F_{1,8} = 0.35$ ,  $p = 0.57$ ). Most of the variability in biovolume was due to very high biovolume at site E1 (Fig. 3). There was also no significant difference between upwind and downwind sites in biovolume of cyanobacteria (nested MANOVA,

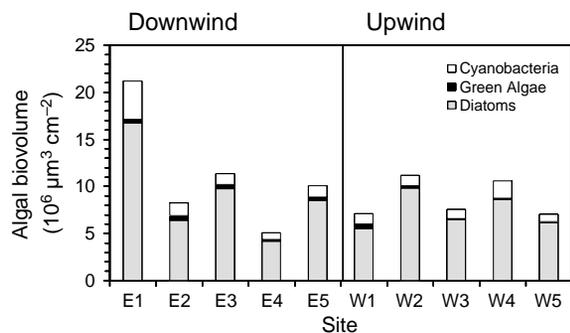


Fig. 3. Biovolume of diatoms, green algae and cyanobacteria at downwind and upwind sites.

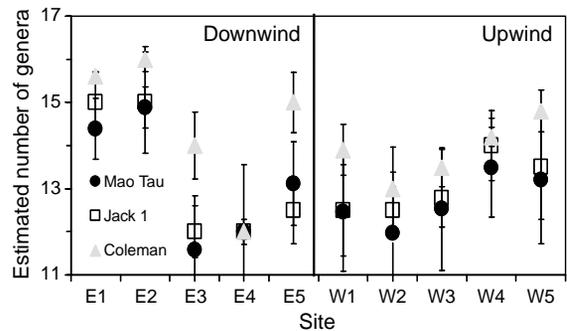


Fig. 4. Comparison of three rarefaction curve estimators of generic richness for the benthic diatom communities ( $\pm$  SD) grown at 10 sites in Lake Opeongo.

$F_{1,8} = 0.82$ ,  $p = 0.39$ ), green algae, ( $F_{1,8} = 0.82$ ,  $p = 0.39$ ), or diatoms ( $F_{1,8} = 0.22$ ,  $p = 0.65$ ; Fig. 3). Diatoms were dominant at all sites (78–88% of total biovolume; Fig. 3).

### Composition of the diatom communities

#### Community richness

We calculated three estimates of diatom richness for each community. The Mao Tau and Jack 1 estimators gave similar values, while the Coleman estimator was higher at most sites (Fig. 4). We used the Mao Tau estimator in the remainder of our paper. Similar results would be obtained with Jack 1.

Benthic diatom communities had between 12 and 15 genera, and we found no difference in richness between upwind and downwind sites (nested MANOVA,  $F_{1,8} < 0.01$ ,  $p = 0.97$ ; Fig. 4). However, taxonomic richness increased with increasing temperature variability among upwind sites ( $p = 0.10$ ,  $r^2 = 0.65$ ) and among downwind sites ( $p = 0.11$ ,  $r^2 = 0.63$ ; Fig. 5).

#### Community evenness

Shannon-Wiener evenness calculated using biovolume was higher than evenness calculated using cell density

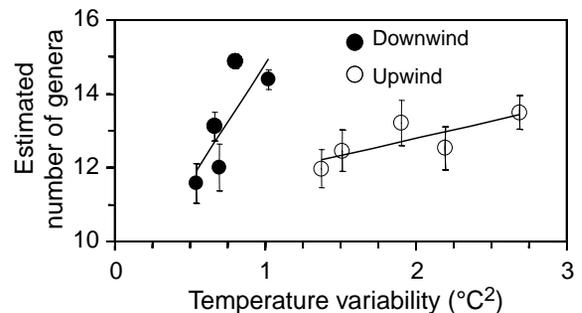


Fig. 5. Relationship between diatom richness (Mao Tau estimate;  $\pm$  SE,  $n = 6$ ) in benthic algal communities and temperature variability.

(not shown). This is because the community was dominated by the very small *Achnantheidium minutissimum* (formerly *Achnanthes minutissima*), which represented 28–84% of diatom biovolume (Fig. 6), and 95–99% of their cell density (not shown). *Achnantheidium minutissimum* is small but abundant, so it is more dominant (and thus the community is less even) when evenness is measured in terms of cell density. Other diatom genera were observed at all upwind and downwind sites, but in varying proportions (Fig. 6). Some of the rare but large genera, such as *Pinnularia* spp. and *Surirella* sp., have little influence on evenness based on cell density, but have a large influence in terms of biovolume evenness.

Benthic diatom communities had similar evenness at upwind and downwind sites whether calculated from biovolume (nested MANOVA,  $F_{1,8} = 0.60$ ,  $p = 0.46$ ; Fig. 7) or cell density ( $F_{1,8} = 0.96$ ,  $p = 0.36$ ; not shown). Evenness (calculated from biovolume) increased with increasing temperature variability among downwind sites (linear regressions,  $p = 0.0002$ ,  $r^2 = 0.99$ ; Fig. 7) and among upwind sites ( $p = 0.03$ ,  $r^2 = 0.82$ ; Fig. 7). Evenness of diatom cell density also increased with increasing environmental variability among downwind ( $p = 0.005$ ,  $r^2 = 0.95$ ; not shown) and upwind sites ( $p = 0.10$ ,  $r^2 = 0.64$ ; not shown). The relationships for evenness of both cell density and biovolume at upwind sites should be interpreted carefully as they are driven by high evenness at one site (W4; Fig. 7). Without site W4, evenness of biovolume still tends to increase ( $p = 0.24$ ,  $r^2 = 0.58$ ;  $n = 4$ ), while evenness of cell density does not ( $p = 0.83$ ,  $r^2 = 0.03$ ;  $n = 4$ ).

#### Taxonomic composition

There were no differences in diatom community composition between upwind sites and downwind sites (Fig. 8). The first correspondence analysis axis (CA1) accounted for 72% (biovolume) and 84% (cell density) of the

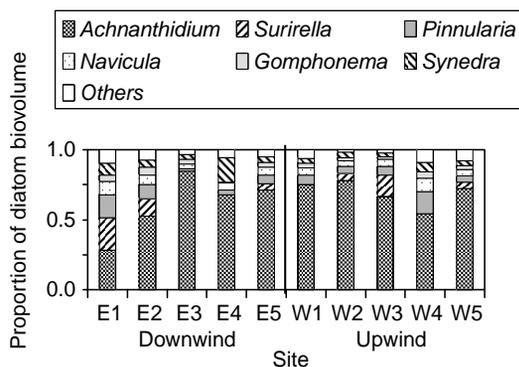


Fig. 6. Composition of benthic diatom communities at five downwind and five upwind sites in Lake Opeongo. "Others" are genera that individually represent less than 2% of the total community biovolume (*Gyrosigma*, *Nitzschia*, *Diploneis*, *Frustulia*, *Eunotia*, *Neidium*, *Stauroneis*, *Cymbella* and *Amphora*).

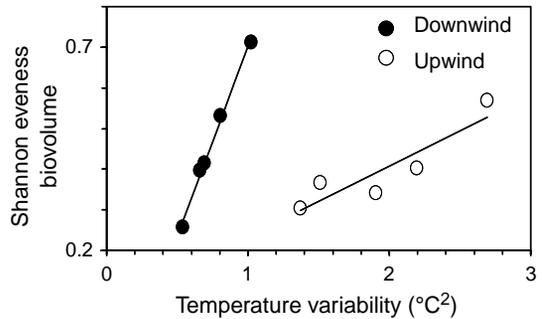


Fig. 7. Relationship between Shannon evenness index measured on diatom biovolume and water temperature variability.

variability in diatom generic structure (Appendix A). When calculated using biovolume, CA1 was positively influenced by the biovolume of *A. minutissimum* and negatively influenced by the biovolumes of *Surirella* sp., *Pinnularia* spp., *Cymbella* sp. and *Neidium* sp. (Appendix A, Fig. 8). When calculated using cellular densities, CA1 was negatively influenced by *A. minutissimum*, and positively influenced by *Surirella* sp., and *Pinnularia* spp., with contributions from other rare taxa (each <1% of total cell density, not shown). The second axis (CA 2) accounted for only 14% (biovolume) and 9% (cell density) of the variability in diatom generic structure.

The first correspondence analysis axis (CA1, biovolume) was negatively related to temperature variability (Fig. 9), at both downwind (linear regression,  $p = 0.0006$ ,  $r^2 = 0.99$ ) and upwind sites ( $p = 0.03$ ,  $r^2 = 0.84$ ). This suggests that the taxonomic composition of these communities shifted from *A. minutissimum* to rarer species along a gradient of increasing temperature variability. In terms of cell density, CA1 was also significantly related to temperature variability at both downwind (regression,

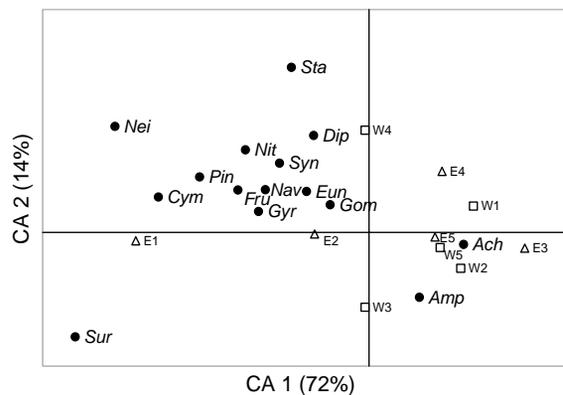


Fig. 8. Biplot of genera and site scores from correspondence analysis. Open squares represent upwind sites (W1–W5), and open triangles represent downwind sites (E1–E5). Genera are abbreviated as: *Ach* (*Achnantheidium*), *Amp* (*Amphora*), *Cym* (*Cymbella*), *Dip* (*Diploneis*), *Eum* (*Eunotia*), *Fru* (*Frustulia*), *Gom* (*Gomphonema*), *Gyr* (*Gyrosigma*), *Nav* (*Navicula*), *Nei* (*Neidium*), *Nit* (*Nitzschia*), *Pin* (*Pinnularia*), *Sta* (*Stauroneis*), *Sur* (*Surirella*) and *Syn* (*Synedra*).

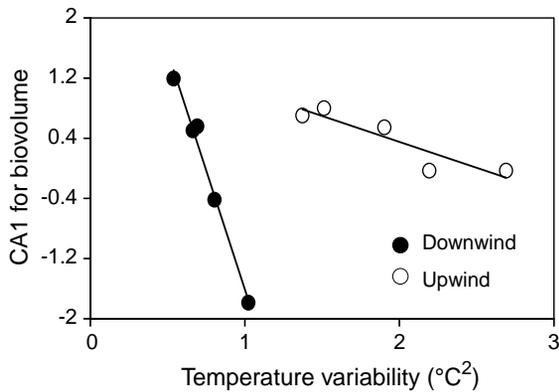


Fig. 9. Relationship between correspondence analysis axis 1 (CA1 for biovolume) and water temperature variability.

$p=0.006$ ,  $r^2=0.94$ ), and upwind sites ( $p=0.09$ ,  $r^2=0.66$ ), although the latter relationship was driven by a single site (W4; not shown). The second correspondence analysis axis (CA2) was not related to environmental variability (regression; biovolume: upwind  $p=0.43$ , downwind  $p=0.89$ ; cell density: upwind  $p=0.68$ , downwind  $p=0.83$ ; not shown). At both ends of the lake basin, *A. minutissimum* was most dominant at sites with low temperature variability, and became less dominant as temperature variability increased.

## Discussion

We found no systematic difference in the total biomass (measured as biovolume) of algae colonizing the tiles at either end of the lake basin, nor in the biomass of major algal taxa (diatoms, green algae and cyanobacteria). Algal communities were fully developed in terms of biovolume after four weeks, which is consistent with other studies that show full biovolume is reached after 3–6 weeks (Hillebrand and Sommer 2000, Flöder et al. 2002). Contrary to our expectations, we found no systematic differences in benthic algal diversity between upwind and downwind sites. All diatom genera colonized the tiles at upwind and downwind sites within a few days (H. Davey and H. Cyr, 2004 unpubl.), which is not surprising given the mounting evidence that small species (< 150  $\mu\text{m}$  diameter) disperse easily (Fenchel and Finlay 2004). Instead, we found clear increases in richness and evenness with increasing temperature variability among upwind sites, and among downwind sites.

Shifts in diatom evenness with increasing environmental variability were consistently larger than shifts in diatom richness. At downwind sites, diatom evenness increased three-fold with increasing temperature variability, while richness increased by only 25%. At upwind sites, diatom evenness doubled with increasing temperature variability, while richness only increased by 17%.

This larger response of evenness to environmental variability is consistent with models that find broader ranges of parameter space that will allow for shifts in phytoplankton community evenness than for increased richness (Anderies and Beisner 2000, Litchman and Klausmeier 2001). Experimental studies also show that environmental fluctuations can increase community evenness (Flöder et al. 2002, Litchman 2003), but may (Sommer 1985) or may not (Litchman 1998, Beisner 2001) increase community richness. If environmental variability increases diversity by causing shifts in competitive advantage (Sommer 1985), it is reasonable to expect that communities would increase in evenness more than in richness, as evenness would be the first community property affected. In order to increase richness, environmental factors have to fluctuate at an optimal frequency and magnitude to allow new species to invade and persist (Sommer 2002).

The overall low community evenness, especially in terms of cell density, was due to the high dominance of *Achnanthes minutissimum*, which accounted for >50% of the diatom biovolume at all sites except E1. This dominance is not surprising, since *A. minutissimum* colonizes and reproduces rapidly (McCormick 1996, Johnson et al. 1997), and often dominates the periphyton in lakes (Stockner and Armstrong 1971), rivers (Peterson and Stevenson 1992), and on artificial substrates (Stevenson 1983, Barbiero 2000). In Lake Opeongo, *A. minutissimum* colonized tiles within 24 h and became dominant within a few days (H. Davey and H. Cyr, unpubl.). This species does well at low phosphorus levels (Fairchild et al. 1985, Stelzer and Lamberti 2001, Soinenen 2002), and can survive low light conditions (Johnson et al. 1997), which would provide an advantage in the lower littoral zone of Lake Opeongo, where nutrients are low and only 3% of the surface light reaches the benthos ( $\sim 6 \mu\text{mol m}^{-2} \text{s}^{-1}$  on a cloudy day to  $80 \mu\text{mol m}^{-2} \text{s}^{-1}$  on a sunny day). Thus, *A. minutissimum* are able to thrive under a broad range of conditions in the littoral zone of lakes.

## Why does algal diversity increase with increasing temperature variability?

Temperature fluctuations have been shown to increase the diversity of ciliate protozoans (Eddison and Ollason 1978) and algal species (Descamps-Julien and Gonzalez 2005). In South Arm, however, water temperature was clearly more variable at upwind than at downwind sites (Finlay et al. 2001), yet we found no systematic difference in the diversity or taxonomic composition of the algal community between upwind and downwind sites. Temperature variability per se cannot explain the differences we found in algal community structure.

The strong relationships we found between temperature variability and diatom diversity among upwind sites and among downwind sites suggest that these relationships are being driven by other environmental factors, such as water current, which are correlated differently with temperature variability in different parts of the lake. The tilting of the thermocline after a wind forcing results in upwellings (upwind) and downwellings (downwind), which produce water currents at the bottom of the lake (Gloor et al. 1994). Upwellings, however, are recorded as large drops in temperature, while downwellings are recorded as small increases in temperature. Thus, even if both ends of the basin experienced similar currents, upwind sites would have higher temperature variability than downwind sites. In other words, our temperature variability measurements underestimate current variability at downwind sites relative to upwind sites.

Water currents at the bottom of the lake could affect benthic communities in several ways. For example, strong currents could disturb the benthic communities, pulling algal cells away from the substrate (Peterson and Stevenson 1992). However, we found no evidence that algal biovolume declines with increasing environmental variability. We also found no change in the density (or biovolume) of the small, tightly attached diatom, *Achnanthydium minutissimum*, with increasing environmental variability, although they became proportionately less important with increasing temperature variability. We observed a shift in community evenness in part due to the increased density of large, unattached diatoms (*Surirella*, *Pinnularia*), which are expected to be most sensitive to physical disturbance. Cattaneo (1990) reports similar results in benthic algal communities growing on shallow (1 m depth) rocks in Lake Memphremagog, where the biovolume of *A. minutissimum* remained the same regardless of degree of exposure, and the biovolume of large diatoms such as *Synedra* spp. was higher at wind-exposed sites than at sheltered sites. Therefore, physical disturbance cannot explain the patterns we found.

Strong currents along the lake bottom could also resuspend sediments (Shteinman et al. 1997, Pritchard and Hogg 2003), and generate fluctuations in light availability (Schallenberg and Burns 2004) and/or nutrient pulses (Chen and Sheng 2005), two factors that have been shown to increase the diversity of algal communities (Litchman 1998, 2003, Beisner 2001). We tested this possibility at site W2 in 2005 and found no association between upwellings or downwellings and turbidity at that site (McCabe and Cyr, unpubl.). We are pursuing these tests, but currently have no evidence that light and nutrient fluctuations could produce the diversity patterns we observed in South Arm.

Water currents have also been shown to increase the availability of nutrients by reducing the boundary layer that develops along surfaces, thus stimulating algal

growth (Riber and Wetzel 1987, Cattaneo 1990, Stevenson and Glover 1993). These currents are particularly important to sessile algae living on rocks (or tiles), which depend on nutrients from the water column. They are also important for large algal taxa that require higher nutrient levels than small taxa (Fairchild et al. 1985, Stelzer and Lamberti 2001, Sojinen 2002). Water currents allow algae with a high vertical profile to increase local turbulence around themselves, further reducing the boundary layer (Riber and Wetzel 1987). In our study, large taxa were more dominant at upwind and downwind sites with higher temperature variability, where we would also expect more currents associated with upwellings, downwellings and internal waves. Some studies have suggested that the variability in water current, rather than its intensity, determines the success of some species. Ghosh and Gaur (1991) found that in streams, *Surirella ovata* were only able to colonize when currents were very low, but once established, their growth was stimulated by low to intermediate water currents (10–21 cm s<sup>-1</sup>). In our study, *Surirella* was one of the genera that became more dominant with increasing temperature (and current) variability. Differences in the intensity and possibly fluctuations in water current likely explain why we observed increases in diatom diversity with increasing temperature variability among upwind sites and among downwind sites. In future studies, it would be interesting to directly compare the relationships between diversity and water currents at both ends of the basin.

Theoretical models, laboratory experiments, and mesocosm experiments have shown that environmental variability can increase the diversity of communities. However, several experiments suggest limits to the types of systems in which environmental variability increases community evenness or richness. For example, Beisner (2001) found that mixing the water column increased the evenness of phytoplankton communities in high-nutrient treatments, but not in low-nutrient treatments, and only in the absence of zooplankton grazers. Litchman (1998) showed that light fluctuations increased the evenness of algal communities at high average light levels, but decreased evenness at low average light levels. In this study, we found strong relationships between environmental variability and biodiversity under a regime of natural environmental fluctuations, at low nutrient concentration, at low light availability, and in the presence of grazers. Our results suggest that increased environmental variability leads to higher biodiversity in complex natural systems.

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**Appendix A.** Composition of algal communities in Lake Opeongo based on correspondence analysis. Eigenvectors are shown for the first two correspondence analysis axes, based on the proportion of biovolume or the proportion of number of cells of 15 benthic diatom genera. In both analyses, the first two axes explain >85% of the variability.

% variability explained Genus	Proportion of biovolume		Proportion of number of cells	
	72 CA1	14 CA2	84 CA1	9 CA2
<i>A. minutissimum</i>	0.72	–0.27	–0.12	0.01
<i>Amphora</i>	0.39	–1.46	0.32	–4.07
<i>Cymbella</i>	–1.61	0.79	12.10	–2.64
<i>Diploneis</i>	–0.42	2.17	5.80	–12.14
<i>Eunotia</i>	–0.48	0.92	6.00	5.25
<i>Gomphonema</i>	–0.30	0.62	5.29	–7.67
<i>Gyrosigma</i>	–0.85	0.47	8.49	4.16
<i>Nitzschia</i>	–0.95	1.85	8.75	–3.17
<i>Frustulia</i>	–1.00	0.95	9.17	0.83
<i>Stauroneis</i>	–0.59	3.70	7.72	–0.19
<i>Neidium</i>	–1.95	2.38	14.73	–3.11
<i>Navicula</i>	–0.79	0.96	7.85	–1.87
<i>Pinnularia</i>	–1.30	1.24	11.78	–2.90
<i>Surirella</i>	–2.25	–2.35	13.75	–0.67
<i>Synedra</i>	–0.69	1.55	7.84	13.00