

Physical forces constrain the depth distribution of the abundant native mussel *Elliptio complanata* in lakes

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SUMMARY

1. Unionid mussels often account for a large portion of benthic biomass and contribute to nutrient cycling and sediment processes, but are thought to be limited to shallow areas (<2–3 m).
2. The depth distribution and body size of *Elliptio complanata* were compared in seven Canadian Shield lake basins of different sizes to test what factors determine the upper and lower limit of their depth range. Specifically, I tested whether (i) the upper range of their distribution is limited by exposure to winds and wave action and (ii) the lower range of their distribution is limited by the depth of the thermocline or by the boundary of mud deposition.
3. The average depth distribution of *E. complanata* shifted to greater depths in larger lake basins. When comparing individual transects, maximum mussel density was found deeper at more exposed sites. Mussel size decreased with increasing depth and was larger, on average, in larger lake basins. These results suggest that physical forces limit the upper range of mussel distribution in lakes.
4. The maximum depth at which mussels were found in different lakes was closely related to thermocline depth. However, mussels were commonly observed below the predicted depth of the mud deposition boundary. The thermocline limits the lower range of mussel distribution in lakes, probably by limiting food availability and by determining water temperature. Substratum type does not limit the lower distribution of mussels.
5. These results suggest that unionid mussels are present in the deeper parts of the littoral zone, especially in large lakes. Therefore, comparisons of mussel populations between sites and between lakes would be biased unless the full depth distribution of these mussels is considered. These results also suggest that long-term changes in the thermal structure of lakes could affect the range of unionid mussel populations and their functional role in littoral ecosystems.

Keywords: distribution, *Elliptio complanata*, lake, mussel, unionid

Introduction

Unionid mussels are among the largest and longest-lived invertebrates in rivers and shallow areas of lakes, and often account for a large portion of benthic biomass in these systems (Strayer *et al.*, 1999). Like

marine mussels, they contribute to pelagic–benthic coupling and to nearshore nutrient dynamics by filtering their food from the water column, excreting dissolved nutrients and depositing faeces and pseudofaeces in the sediments (Strayer *et al.*, 1999; Vaughn & Hakenkamp, 2001; Newell, 2004). Unionid mussels also alter benthic processes by burrowing and moving through the sediments, and by enriching them with organic matter (McCall, Tevesz & Schwelgien, 1995; Howard & Cuffey, 2006). Intriguingly, and despite mounting evidence of their potential importance, their

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functional role in freshwater ecosystems is still largely ignored. Freshwater mussels are currently one of the most endangered groups of organisms (Lydeard *et al.*, 2004), and our very limited understanding of their distribution, modes of dispersal and activities makes it difficult to monitor or manage these populations, or even to predict the effect of their decline or disappearance on these ecosystems.

The limited information available suggests that the functional role of unionid mussels depends on their distribution and on their abundance (Welker & Walz, 1998; Strayer *et al.*, 1999; Vaughn, Gido & Spooner, 2004). In lakes, unionids are generally observed and studied in shallow water (<3 m depth; Amyot & Downing, 1991; Huebner, Malley & Donkersloot, 1990), but their distribution can extend much deeper (e.g. 9 m in Long Lake, MI, Cvanara, 1972; 12 m in Lake Bernard, ON, Ghent, Singer & Johnson-Singer, 1978; 20–30 m in Lake Michigan, Reigle, 1967). We know very little about the depth range of unionid mussels and about factors that determine the upper and lower limits of their distribution in lakes. This lack of very basic information limits our ability to sample them properly and to determine their role in lake ecosystems.

Physical forces determine the distribution of mussels in rivers. Mussels exploit lower shear stress habitats (e.g. around rocks), and their large-scale distribution is determined by large episodic events (i.e. floods; Vannote & Minshall, 1982; diMaio & Corkum, 1995; Strayer, 1999). Similar constraints (e.g. from wave action) could affect mussel distribution in shallow areas of lakes. Physical forces have been shown to affect the morphology of unionid mussels in lakes (mussels are larger at more exposed sites; Hinch, Bailey & Green, 1986; Hinch & Bailey, 1988), but their potential effect on the distribution of mussels has largely been ignored. The potential for physical disturbance to constrain the upper range of the depth distribution of unionid mussels in lakes should increase with exposure to winds and wave action, and with increasing lake size.

Three factors have been hypothesized to limit the lower depth range of mussels in lakes: food availability, water temperature and substratum type (Cvanara, 1972; Ghent *et al.*, 1978; Strayer *et al.*, 1981; Hanson, Mackay & Prepas, 1988; Huebner *et al.*, 1990). Mussels feed on small planktonic particles available in the upper portion of the water column

(Vaughn & Hakenkamp, 2001) and have been shown experimentally to grow more slowly at lower temperatures (*Anodonta grandis simpsoniana*, Lea 1861; Hanson *et al.*, 1988). Several studies have also suggested that mussel distribution may be limited by very soft muddy substrata (Ghent *et al.*, 1978; Strayer *et al.*, 1981), possibly because mud interferes with their feeding (Kat, 1982). Because planktonic food availability, water temperature and the substratum change in similar ways with increasing depth, it is difficult to distinguish their relative importance in field studies. Plankton availability and water temperature both decrease abruptly below the thermocline, while the substratum becomes muddier and increases in water content (i.e. decreases in dry bulk density) with increasing depth down to a permanent deposition zone (Håkanson, 1977). The depth of this mud deposition boundary is closely related to the wave mixing layer (i.e. exposure to winds) and to bottom topography (Rowan, Kalff & Rasmussen, 1992; Cyr, 1998). Taken together, these three possibilities suggest that the depth distribution of mussels in lakes may be limited by the physical structure of the water column and/or by physical forces that determine sediment types.

In this study, I compared the depth distribution of an abundant North American native mussel, *Elliptio complanata* (Lightfoot, 1786) in seven lake basins of different sizes to test whether physical forces determine the upper and lower limits of their range. I hypothesized that (i) the upper range of their distribution is limited by exposure to winds and wave action and (ii) the lower range of their distribution is limited by depth of the thermocline or by the mud deposition boundary. *Elliptio complanata* is the sole or main species of mussels in the lakes we sampled, which avoids potential confounding effects of inter-specific interactions.

Methods

Site description

Seven oligo-mesotrophic lake basins of different sizes were selected for this study. They are located in Algonquin Park, Ontario, Canada, 300 km north-east of Toronto, on the Precambrian Shield (Table 1). Sproule Bay, South Arm and Annie Bay are separate basins of Lake Opeongo, the largest lake in Algonquin

Table 1 Lake basin characteristics and sampling information

Lake/Basin	Location	Surface area (ha)	Mean depth (m)	Maximum depth (m)	Sampling dates	$N_{\text{transects}}$	Thermocline depth (m)			% PAR transmission (m^{-1})	Chlorophyll concentration ($\mu\text{g L}^{-1}$)
							Meas.	Predicted			
							A	B			
Mew	45°34'N 78°31'W	10	na	3.5	1 August, 2007	3	None	4.0	3.3	48	2.1 ± 0.2
Kearney	45°34'N 78°26'W	33	7.7	18.3	2 August, 2007	4	4.5	4.4	3.2	38	1.1 ± 0.5
Costello	45°35'N 78°19'W	35	9.4	18.6	22 July, 2007	3	4.5	4.4	3.0	33	1.5 ± 0.1
Sroule Bay	45°38'N 78°22'W	211	5.5	7	22 June–17 August, 2006	4	None	5.2	4.1	39	1.7 ± 0.2 [†]
Two Rivers	45°35'N 78°29'W	308	16.4	41.5	31 July, 2007	3	6.5	5.5	4.3	37	1.2 ± 0.2
Annie Bay	45°43'N 78°17'W	440	9.6	24.3	21 July, 2007	4	6.5	5.7	5.6	58	1.8 ± 0.3
South Arm	45°42'N 78°23'W	2210	14.6	50.7	21 June–17 August, 2006	10	8.5*	7.1	6.3	47	1.6 ± 0.6 [‡]

$N_{\text{transects}}$ is the number of transects sampled in each lake. Thermocline depth was measured (Meas.) and predicted based on (A) lake surface area and (B) lake surface area and % light transmission (Fee *et al.*, 1996). Epilimnetic chlorophyll concentration was measured in triplicates (\pm standard error).

NA, not available.

*Thermocline depth measured on 7 August, 2007 (for comparison with other lakes).

[†]Summer chlorophyll concentration range = 0.7–2.1 $\mu\text{g L}^{-1}$ (May–September 2006, 2007; $n = 7$ sampling dates).

[‡]Summer chlorophyll concentration range = 0.8–2.9 $\mu\text{g L}^{-1}$ (May–September 2006, 2007; $n = 11$ sampling dates).

Park. The lakes are located along two branches of the Madawaska drainage basin. Mew is upstream of Lake of Two Rivers and along with Kearney, they all drain into the Madawaska River. Lake Costello drains into Lake Opeongo, which flows into the Opeongo River and eventually the Madawaska River. The lakes have natural outflows, except for Lake Opeongo, which is controlled by a dam. The water level in Lake Opeongo increases in the spring (March–April) and drops in late summer (September–October) by <0.5 m. Macrophytes were very sparse and fish were present in all lakes.

Mussel counts and measurements

Unionid mussels were counted and measured during mid-summer along 3–10 depth transects per lake basin (Table 1). At each site, mussels were counted in four 1 × 1 m quadrats positioned at 0.5–1 m depth intervals along a transect running perpendicular to shore, down to 6–7 m depth. All counts were performed underwater by snorkelling. The divers could only sample down to 7 m and this sampling limitation probably resulted in an underestimation of the lower range of mussel distribution in the largest basin

(South Arm). Where possible, the diver validated the lower depth of mussel distribution by running a 5 m visual transect parallel to shore on both sides of the quadrats at the depth where no more mussels were observed.

Mussels were collected from the quadrats, and when necessary from surrounding areas, and were brought back to the boat for measurement. Total shell length was measured with callipers (± 0.02 mm) and the mussels were immediately released at the site where they were collected.

Elliptio complanata was the only species or clearly the dominant species of unionid mussels in all lakes sampled. Through all our sampling, we only observed a few *Pyganodon grandis* (Say, 1829) in Lake Costello and in South Arm.

Temperature and light profiles

Temperature profiles were measured at 1 m interval in the centre of each lake basin with a YSI probe model 57 (Yellow Spring Instruments, Yellow Springs, OH, U.S.A.). A thermocline is defined as a drop in water temperature of at least 1 °C m^{-1} and the depth of the thermocline was calculated as

the depth halfway between the two measurements showing the maximum decrease in water temperature.

Because the mussels are long-lived, we also calculated an average expected thermocline depth based on lake surface area (Fee *et al.*, 1996). The predictions from this model agreed well with our field measurements (Table 1). We did not use Fee *et al.*'s (1996) correction for lake transparency because it had a tendency to underestimate thermocline depth (Table 1) and because other published studies do not always report light transmittance. Our conclusions are not affected by this choice.

Light profiles were measured using an underwater spherical quantum sensor (model LI-193SA; Li-Cor, Lincoln, NE, U.S.A.) and a deck cell (model LI-190SA). The proportion of surface light was measured every 0.5 m in the surface 3–4 m of the water column. The extinction coefficient and % photosynthetically active radiation transmission were calculated using all measurements (Kalff, 2002).

Chlorophyll concentration

Phytoplankton biomass in each lake was estimated by measuring the epilimnetic chlorophyll concentration. Three litres of water were collected below the lake surface in the centre of each basin. Three replicate samples were filtered on GF/F filters and frozen in liquid nitrogen. The frozen filters were ground with a mortar and pestle, and extracted overnight in 95% ethanol (Marker *et al.*, 1980). The samples were centrifuged and the supernatant was read at 665 and 750 nm (± 2 nm) on a Milton Roy Spectronic 1000+ spectrophotometer (Milton Roy Company, Rochester, NY, U.S.A.). Chlorophyll concentrations were corrected for phaeopigment interference by acidifying with 0.2 mol L⁻¹ HCl (Lorenzen, 1967; equation from Marker *et al.*, 1980 with specific absorption coefficient = 87 g L⁻¹ cm⁻¹).

Effective fetch and wind data

The effective fetch of a site measures its degree of exposure to the predominant winds (Håkanson & Jansson, 1983). To calculate effective fetch of a given site (F_{eff} , in metres) we measured the distance over open water to the closest land mass (F_d , in metres) along eight directions (d : N, NE, E, SE, S, SW, W, NW).

These distances were then weighted by the proportion of the average wind speed blowing from each of these eight directions (w_d):

$$F_{\text{eff}} = \frac{\sum_d (F_d \times w_d)}{\sum_d w_d}$$

Because the unionids are long-lived and to obtain a long-term measure of site exposure, as many years of wind data as were available were used. Wind speed and direction were measured at three weather stations on Lake Opeongo. A Campbell weather station (CR10X measurement and control module, fitted with a model 05103-10 R.M. Young Wind Monitor; Campbell Scientific Inc., Logan, UT, U.S.A.) was positioned on a small treeless island in South Arm. The wind data collected at 10 min intervals over four consecutive summers was used (May–October 2003–06). The winds in South Arm blow predominantly from the west. This is the main weather station maintained by the Ontario Ministry of Natural Resources and these data were used to calculate F_{eff} in other nearby lakes (Costello, Kearney, Mew, Two Rivers).

The topography around the other two basins of Lake Opeongo (Sproule Bay, Annie Bay) channels the prevalent winds to a more northerly direction. In Sproule Bay, I used wind data collected during two summers (May–October 2003 and 2005) with a Rainwise Portlog weather station (Rainwise Inc., Bar Harbour, ME, U.S.A.) anchored on a shallow shoal 4 m above the water surface. In Annie Bay, I used wind data collected during one summer (July–September 2003) with a Rainwise Portlog weather station (Rainwise Inc.) installed on a small island (data from A. Blukacz, Department of Biology, University of Toronto at Mississauga).

The depth of the wave mixed layer ($h_{L/2}$ in m) at each sampling site was calculated as half the wave length (L) produced by strong winds (19 m s⁻¹) blowing over a given fetch (F_{eff} in m):

$$h_{L/2} = 0.082 F_{\text{eff}}^{0.56}$$

(Smith & Sinclair, 1972; see derivation of equation in Cyr, 1998).

The depth of the mud deposition boundary was predicted based on the sediment particle threshold ($h_{U_{t23}}$) and on bottom slope (Cyr, 1998). The sediment particle threshold ($h_{U_{t23}}$) was calculated for a 23 μm organic sediment particle as (equation derived in Cyr, 1998):

$$h_{U123} = 0.026 \times F_{\text{eff}}^{0.56} \times \sinh^{-1}(17.6 \times F_{\text{eff}}^{0.0967})$$

Bottom slope was calculated from global positioning system position ($\pm 2\text{--}3$ m) and depth measurements (± 0.1 m) at the extremities of each transect or from bathymetric maps.

Statistical analyses

The relationship between the maximum depth of mussel distribution and thermocline depth was tested using simple regression analysis (Zar, 1984).

Results

Mussel depth profiles were generally consistent within lake basins. For example, the shapes of mussel depth profiles were similar at all sites in Annie Bay, despite obvious differences in bottom topography (Fig. 1). Mussel densities differed between sites, but peaked at 2 m depth along all transects, often with another peak in density very close to shore (0.5 m depth; Fig. 1a–c).

Inshore peaks of mussel density were commonly observed in other small to mid-size lakes, but not in South Arm, the largest basin (data not shown).

Elliptio complanata was most abundant in the shallowest portion of the littoral zone in small lakes, but its distribution shifted to greater depths in larger lake basins. In Lake Opeongo, the mussels were most abundant at 1 m depth in Sproule Bay, at 2 m depth in Annie Bay and at 3–4 m depth in South Arm, the largest basin (Fig. 2, upper panels). A similar trend was found in nearby lakes with sparser mussel populations. The maximum density of *E. complanata* was observed at 1–1.5 m depth in the smallest lakes (Mew, Kearney, Costello), but at 3–4 m depth in the largest Lake of Two Rivers (Fig. 2, lower panels). The average depth distribution of *E. complanata* changed systematically with increasing lake size (regression between mean depth of maximum mussel density and \log_{10} (lake surface area): $r^2 = 0.38$, $P = 0.08$, $n = 7$).

A similar trend was found for individual transects. Across all lakes, the depth of maximum mussel

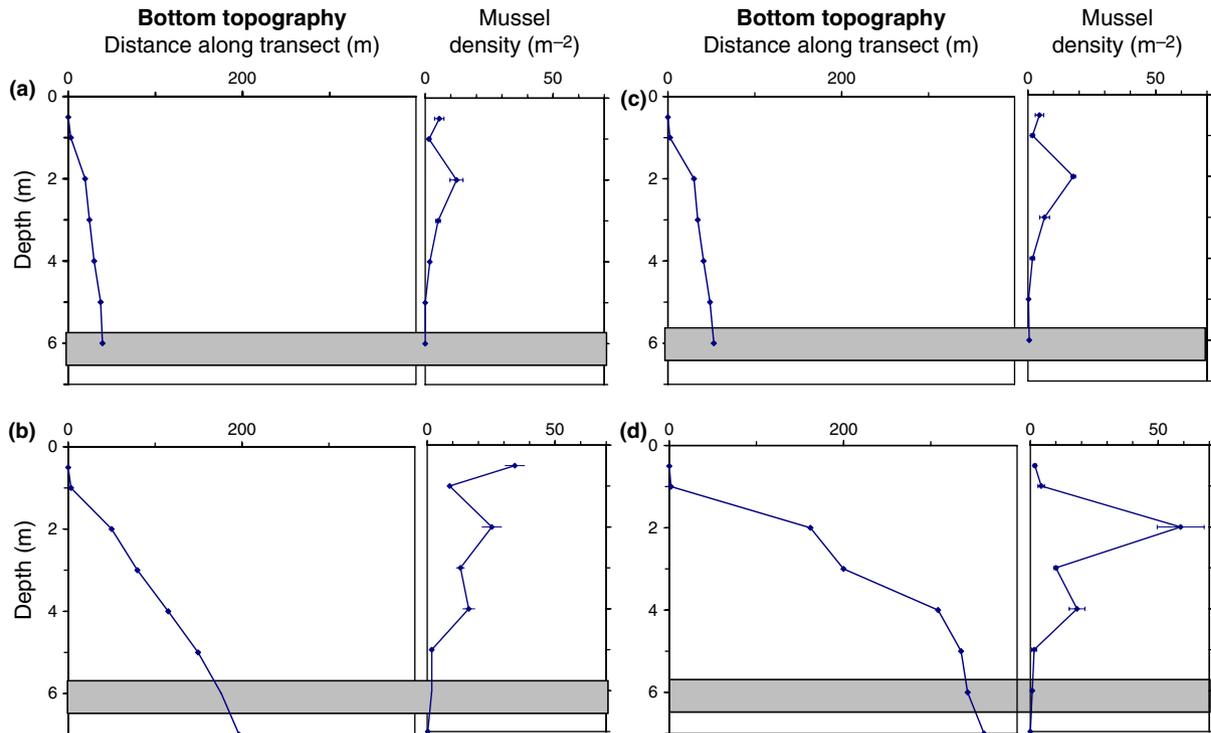


Fig. 1 Bottom topography (left panels) and depth profiles of mussel density (right panels; \pm standard error, $n = 4$ quadrats) along four transects in Annie Bay: (a) NW transect, (b) SW transect, (c) NE transect, (d) SE transect. Average bottom slopes were 15.3%, 3.6%, 11.4% and 1.9% respectively. Shaded area in each panel shows the position of the thermocline (lower boundary is measured, upper boundary is predicted).

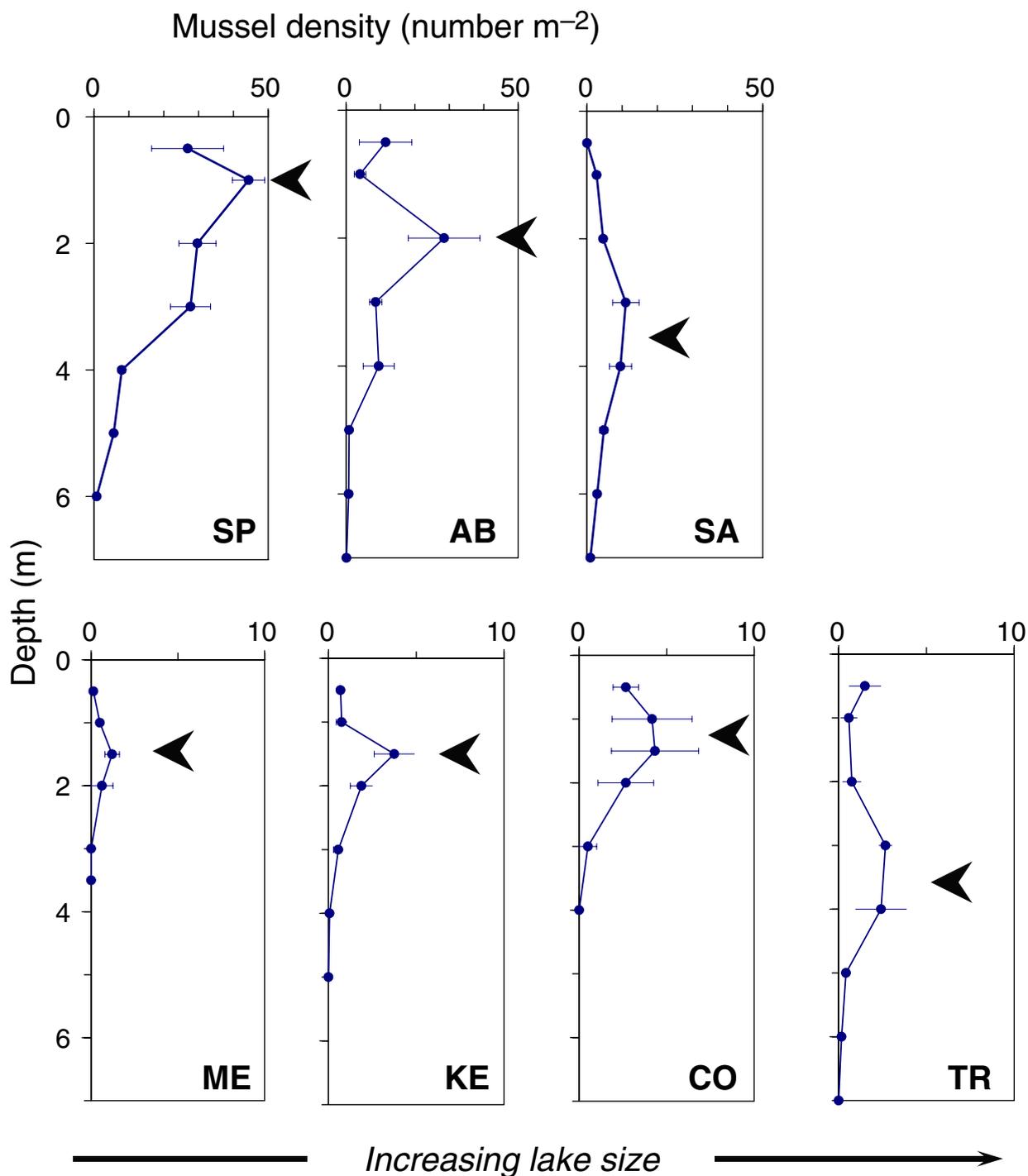


Fig. 2 Average depth distribution of *Elliptio complanata* in each lake basin. Mean mussel densities (\pm standard error) were calculated from all transects sampled in each basin (see $N_{\text{transects}}$ in Table 1). Arrows highlight the depth of maximum mussel density in each lake. SP, Sproule; AB, Annie Bay; SA, South Arm; ME, Mew; KE, Kearney; CO, Costello; TR, Two Rivers. Note the difference in the X-axis scaling between the upper and the lower panels (Lake Opeongo vs nearby lakes).

density increased systematically with increasing effective fetch, a measure of site exposure (Fig. 3). This pattern was consistent with the deepening of the

mixed layer (dashed line, Fig. 3). It suggests that physical disturbance is a major factor limiting the upper distribution of mussels in large lake basins.

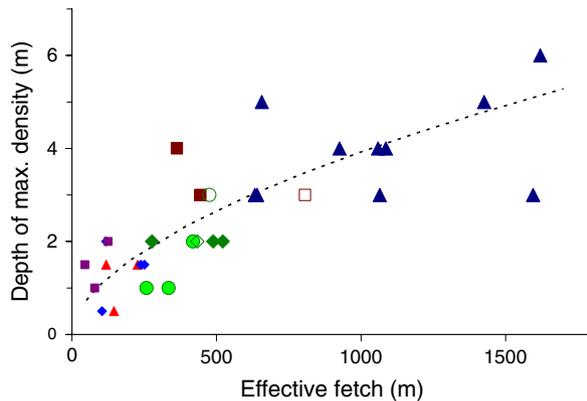


Fig. 3 Relationship between the depth of maximum mussel density along each transect and site exposure (effective fetch). The dashed line shows the depth of the wave mixed layer. Different symbols represent different lakes: Mew, small squares; Kearney, small diamonds; Costello, small triangles; Sproule Bay, circles; Two Rivers, large squares; Annie Bay, large diamonds; South Arm, large triangles. Open symbols are sites with another major peak in mussel density in very shallow nearshore areas (0.5 m depth).

The maximum depth at which *E. complanata* was observed in the seven lakes we sampled was closely related to the predicted depth of the thermocline in each lake (closed circles, Fig. 4). In South Arm, mussels were still observed at the deepest sampling depth (7 m) along all but one transect (densities = 0.25–4.5 mussels m⁻²), suggesting that we underestimated the lower range of mussel distribution in the largest basin. This strengthens our results since a deeper maximum depth in South Arm would improve the relationship shown in Fig. 4 (solid line).

The maximum depth at which *E. complanata* was observed along individual transects seemed to increase with the depth of the mud deposition boundary (Fig. 5). However, the regression is weak ($P = 0.06$) and the maximum depth of mussel distribution was clearly underestimated at most South Arm sites. Mussels were commonly observed below the predicted mud deposition boundary (Fig. 5), suggesting that substratum type *per se* does not limit the lower range of mussel distribution in these lakes.

The average size of *E. complanata* varied with depth and with lake size (Fig. 6). Mussel size decreased with increasing depth in most lakes (Fig. 6). The decline was most dramatic in Costello, where mussels were only 36 mm long on average at the lower limit of their distribution. There was no significant decline in median shell size with increasing depth in Lake of

Two Rivers, but this result is based on a relatively small number of size measurements, especially at the deep end of the transect (20–30 mussels per depth between 0.5 and 5 m, 11 mussels at 6 m). Mussels were also larger on average in the larger lake basins, especially at lesser depths (regression lines are ordered by decreasing lake size from top to bottom in Fig. 6).

Discussion

Our results suggest that physical forces determine both the upper and lower limit of distribution of *E. complanata* in lakes.

Two observations suggest that physical forces at the lake surface are important in determining the upper limit of mussel distribution. First, maximum mussel density was found deeper at more exposed sites and this trend was consistent with a deepening of the wave mixed layer. Good empirical models have been developed in oceans and lakes to predict wave height and resulting bottom shear stress from simple measures of fetch and bottom topography (Smith & Sinclair, 1972; Cyr, 1998). These models have been used successfully to predict sediment distribution in lakes (Rowan *et al.*, 1992; Cyr, 1998), and can be used to predict the potential for physical disturbance in different parts of the littoral zone. We found that the depth of maximum mussel density was consistent with the depth of the wave mixed layer, even when predicted from such a simple and coarse model. Secondly, we observed that mussels were larger, on average, in shallower water, and were also larger in larger lakes. This result is consistent with observations from other Canadian Shield lakes that *E. complanata* are larger at more exposed sites (Hinch & Bailey, 1988). Large disturbances (e.g. breaking waves, strong turbulence, resuspension of sediments and of juveniles) could reduce mussel survival and/or limit the successful recruitment of juveniles in exposed littoral areas. These effects could be direct (physical disturbances dislodging or disturbing the activity of mussels) or indirect (e.g. resuspended sediments interfere with feeding and reduce food quality). Our results suggest that physical forces limit the upper range of mussel distribution in lakes, a conclusion consistent with mounting evidence from streams and rivers that the distribution of mussels is determined by large physical disturbance events (i.e. floods; Vannote & Minshall, 1982; Strayer, 1999).

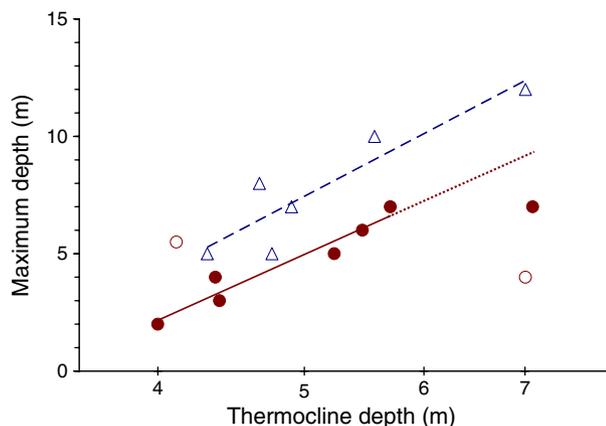


Fig. 4 Relationship between the maximum depth of *Elliptio complanata* distribution (Z_{limit}) and predicted thermocline depth (PZ_{thermo}). Solid circles are lakes sampled in this study and the solid line is the best fitting regression model, excluding South Arm ($Z_{\text{limit}} = -15 + 29 \log_{10}(PZ_{\text{thermo}})$, $r^2 = 0.92$, $P < 0.002$, $n = 6$; dotted line extrapolates this relationship to the thermocline depth for South Arm). Open symbols are published data from other lakes: open circles for *E. complanata* (Ghent *et al.*, 1978; Strayer *et al.* 1981), open triangles for Anodontinae *Pyganodon grandis* (Cvancara, 1972; Ghent *et al.*, 1978; Green, 1980; Hanson *et al.*, 1988; Huebner *et al.*, 1990) and *Anodonta cygnea* (Müller & Patzner, 1996). Dashed line is the best fitting model for Anodontinae ($Z_{\text{limit}} = -165 + 34 \log_{10}(PZ_{\text{thermo}})$, $r^2 = 0.79$, $P = 0.01$, $n = 6$). Note that the X-axis is a logarithmic (base 10) axis.

Interestingly, we observed secondary peaks in mussel density very close to shore (0.5 m depth) at several sites. Presumably, the bottom topography at these sites (e.g. large rocks or boulders in shallow water, areas protected by sill) created a refuge from wave disturbance. These areas could be important to other littoral organisms as well. The distribution and the importance of these near-shore benthic refuges in lakes are largely unknown.

The lower limit of distribution of *E. complanata* was closely related to thermocline depth. Few other studies have put in sufficient sampling effort in stratified lakes to determine the depth distribution of *E. complanata*. Strayer *et al.* (1981) sampled extensively the bottom of Mirror Lake, NH, U.S.A. (surface area = 15 ha) and observed *E. complanata* down to 5.5 m. This is slightly deeper than we would expect based on lake surface area, but Mirror Lake is a clear oligotrophic lake (light transmittance = $70\% \text{ m}^{-1}$) and its surface mixing layer (top of the thermocline) goes down to 5 m during summer (Likens, 1985). The distribution of *Elliptio* in Mirror Lake is therefore

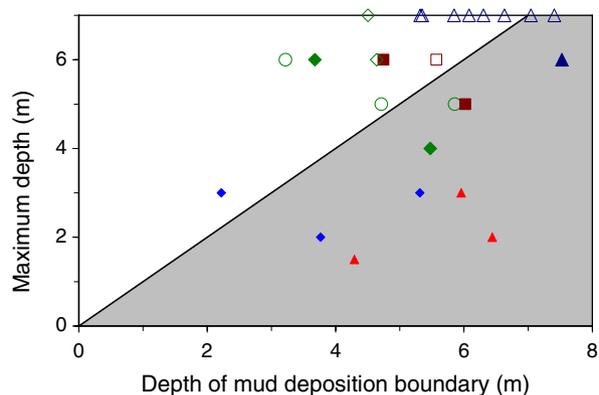


Fig. 5 Comparison of the maximum depth of *Elliptio complanata* distribution measured along individual transects with the predicted mud deposition boundary. Points in the shaded part of the graph (below the 1 : 1 line) are sites where mussels were observed below the mud deposition boundary, suggesting that the presence of soft mud does not limit the lower limit of mussel distribution in lakes. Bottom slope was not measured in Mew Lake and the mud deposition boundary could not be calculated. Different symbols are for different lakes (see Fig. 3). Closed symbols are sites where no mussels were visible in the deepest quadrats. Open symbols are sites where some mussels were observed in the deepest quadrats (0.75 mussels m^{-2} at 6 m depth and 4.8–6.3 m^{-2} at 5 m depth in Sproule Bay; 0.3 m^{-2} in Two Rivers; 0.3–0.5 m^{-2} in Annie Bay; 0.25–4.5 m^{-2} in South Arm) and where the maximum depth of distribution is likely to have been underestimated.

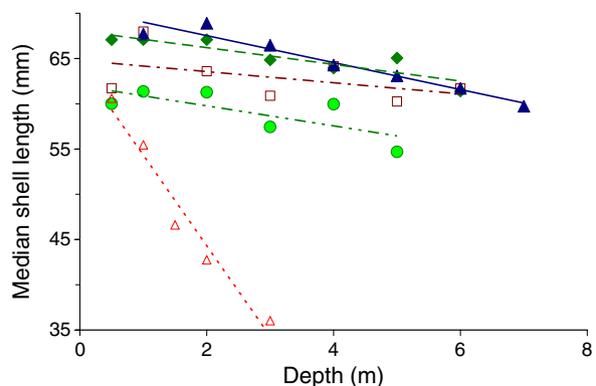


Fig. 6 Relationship between median mussel shell length and depth in three basins of Lake Opeongo (solid symbols: circles for Sproule, $n = 43$ –286 mussels per depth; diamonds for Annie Bay, $n = 28$ –70; triangles for South Arm, $n = 27$ –227) and nearby lakes (open triangles for Costello, $n = 10$ –32; open squares for Two Rivers, $n = 11$ –30). Linear regression lines show the decline in mussel size with increasing depth for each lake (South Arm: solid line, $r^2 = 0.93$, $P < 0.001$, $n = 7$; Annie Bay: dash line, $r^2 = 0.76$, $P < 0.01$, $n = 7$; Lake of Two Rivers: dash-dot-dot line, $r^2 = 0.3$, $n = 7$; Sproule Bay: dash-dot-dot line, $r^2 = 0.45$, $P = 0.09$, $n = 6$; Costello, dotted line, $r^2 = 0.95$, $P < 0.01$, $n = 5$). Too few mussels were measured at each depth in Mew and Kearney to calculate these profiles.

consistent with our data (Fig. 4). In contrast, Ghent *et al.* (1978) concluded that *E. complanata* in Lake Bernard, ON, Canada (surface area = 2050 ha) peaked in density between 1.5 and 2.5 m depth and only reached down to 4 m. They observed a few (living) individuals in isolated areas as deep as 9 m, but concluded that these mussels had been dislodged from shallower areas and were taking advantage of specific bottom features (mussels were found at the bottom of a steep slope and in the sandy substratum around logs). Unfortunately, Ghent *et al.* (1978) only sampled a small portion of the littoral zone of Lake Bernard, in a steep area exposed to the dominant winds, and it is unclear whether these results are representative of the whole lake. More data are available on the depth distribution of the Anodontinae mussels *P. grandis* and *Anodonta cygnea* (Linnaeus, 1758), two other widely distributed and abundant mussels native of these study areas (Cvancara, 1972; Ghent *et al.*, 1978; Green, 1980; Hanson *et al.*, 1988; Huebner *et al.*, 1990; Müller & Patzner, 1996). These mussels are commonly observed below the thermocline, but interestingly their lower limit of distribution also seems to be related to lake size (open triangles, Fig. 4). Such a pattern would be expected if *P. grandis* had lower respiration rates than *E. complanata* (i.e. if it could survive on lower food availability) or if it used some non-planktonic food sources (i.e. food subsidy). These possibilities remain to be tested. The generality of the relationship between the maximum depth of mussel distribution and thermocline depth needs to be tested further to determine whether it applies to a wider range of lakes and to other unionid species.

Three factors have been hypothesized to limit the lower depth range of mussels in lakes: substratum type, low water temperature, food availability. Several studies have suggested that the depth distribution of mussels may be limited by very soft muddy substrata found in deeper areas (Ghent *et al.*, 1978; Strayer *et al.*, 1981). However, *E. complanata* is naturally found on a wide range of substrata, from boulders and rocks to very fine flocculent mud, and can move and bury successfully in all these substrata (Lewis & Riebel, 1984). *Elliptio complanata* has even been shown experimentally to have a slight preference for mud when given the choice (Downing, VanLeeuwen & DiPaolo, 2000). In this study, their lower depth range within a lake was not related to

bottom slope (Fig. 1), as would be expected if they were limited by the mud deposition boundary (Cyr, 1998). Mussels were often observed below the predicted mud deposition boundary (Fig. 5), suggesting that soft muddy substrata do not limit their depth distribution.

A second common hypothesis is that low water temperature limits the growth and the depth distribution of mussels (e.g. Cvancara, 1972; Hanson *et al.*, 1988). Many studies have reported lower growth rates in deeper and colder areas, and a general trend towards smaller body sizes (Ghent *et al.*, 1978; Strayer *et al.*, 1981; Hanson *et al.*, 1988). Low temperature should not immobilize *Elliptio*, which becomes active in early spring at water temperatures well below 10 °C (Amyot & Downing, 1997; H. Cyr, pers. obs.), but it could reduce their energy balance especially if combined with low food availability (see below). It may also reduce their reproductive success because *E. complanata* is particularly sensitive to low and rapidly changing temperature, and aborts its brood when exposed to stressful conditions (Matteson, 1948).

A third hypothesis is that the position of the thermocline limits the availability of planktonic food for mussels (Cvancara, 1972; Ghent *et al.*, 1978; Huebner *et al.*, 1990). *Elliptio complanata* filter feeds on small plankton (Bärlocher & Brendelberger, 2004) and, although it has been shown in the laboratory to be capable of gathering food from the sediments (Nichols *et al.*, 2005; Brendelberger & Klauke, 2008), there is currently no evidence that it feeds on anything but plankton in the field (Post, 2002; Griffiths & Cyr, 2006; H. Cyr unpubl. data). *Elliptio* may therefore require contact with the epilimnion (and possibly the metalimnion) to have access to its planktonic food. The lower limit of distribution of *E. complanata* in lakes coincides with the position of the thermocline and is probably limited by food availability and water temperature.

Our study cannot eliminate the possibility that other factors related to thermocline depth could also be important, but there is currently no compelling candidate. For example, by the end of the summer, several (but not all) lake basins in this study develop hypoxic conditions below the thermocline (e.g. dissolved oxygen concentration: 5.5 mg L⁻¹ on 2 August, 2007 in Kearney; 4.4 mg L⁻¹ on 31 August, 2006 in Annie Bay). However, both *E. complanata* and *P. grandis* have been

shown to maintain normal respiration rates down to *c.* 1 mg L⁻¹ ambient oxygen concentrations (Lewis, 1984), especially at low temperatures (Chen, Heath & Neves, 2001), and are therefore very resistant to hypoxia that may develop in the hypolimnion. Unionid mussels can also bury in sediments for extended periods of time (Amyot & Downing, 1997; Schwalb & Pusch, 2007) and could avoid such unfavourable conditions. Therefore, low oxygen concentration below the thermocline cannot explain our results.

Climate change and other anthropogenic stressors (e.g. acidification) affect the thermal structure of lakes (Schindler *et al.*, 1990; Bukaveckas & Driscoll, 1991; Snucins & Gunn, 2000) and could impact the habitat range available to unionid mussels. The effect of climate change is expected to differ depending on lake size and transparency (Fee *et al.*, 1996). In small lakes (<500 ha), thermocline depth is mostly determined by water transparency and could be affected, for instance, by changes in rainfall and other factors affecting coloured dissolved organic carbon inputs and sunlight penetration through the water column (Schindler *et al.*, 1990; Fee *et al.*, 1996; Keller *et al.*, 2006). Lower lake transparency reduces solar heating in the deep portion of the water column, resulting in the development of a shallower thermocline. Small dark lakes have more stable and shallower thermoclines than small clear lakes. Over the last few decades, some small lakes have shown a trend towards deeper thermoclines (Schindler *et al.*, 1990), whereas others have shown a trend towards shallower thermoclines (Keller *et al.*, 2006). The thermal structure of large lakes is much more dependent on physical forces during the early part of the year, but there is evidence that thermoclines are becoming shallower and more stable, and that epilimnetic temperature is increasing (King, Shuter & Zimmerman, 1997, 1999). If, as our results suggest, the lower boundary of the distribution of *E. complanata* in lakes is set by thermocline depth, a trend towards shallower thermoclines would narrow their range and add to other stressors putting pressure on these populations (habitat destruction, impacts on fish populations, invasive species). Although inconspicuous, these changes in unionid mussel populations could impact benthic–pelagic coupling and benthic processes in littoral ecosystems.

The depth distribution of *E. complanata*, and possibly of *P. grandis*, shifts to greater depths with increasing lake size. Both the depth of maximum

density and the lower limit of their distribution were deeper in larger lakes. The distribution of mussels is closely linked to their expected role in littoral ecosystems, and the systematic shift in the depth distribution of mussels we report in this study suggests that their effect will be shifted to deeper parts of the littoral zone in larger lakes. It also suggests that comparisons of mussel populations between lakes, and possibly between sites within large lakes, could be biased unless the full depth distribution of mussels is considered. Mussels sampled at a given depth in one lake could be from the centre of their distribution, whereas those sampled at the same depth in another lake could be from the edge of their distribution, where they may be affected by physical disturbances, low food availability and/or low temperatures. In order to study mussel population dynamics and to understand their functional role in lakes, we need to compare carefully their densities, body sizes and physiological rates over comparable parts of their depth distribution.

Acknowledgments

I thank N. delaCruz, S. Dungan, J. Liao, J. Turton and S. Ziai for their hard work in the field and in the laboratory, the staff at the Harkness Fisheries Research Lab for outstanding logistical support, and two anonymous referees for useful comments on the manuscript. Financial support was provided by the Natural Science and Engineering Research Council of Canada (NSERC), the Ontario Ministry of Education and Training, the University of Toronto and the Ontario Ministry of Natural Resources. S. Dungan was partly supported by a Northrop-Frye-BIO150 Award.

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(Manuscript accepted 13 June 2008)