

Are there hot spots for *Elliptio complanata* in the shallow littoral zone of a large Canadian Shield lake?

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Abstract: The variability in habitat conditions in large lake basins may provide areas favourable for unionid recruitment and growth. Here we test whether the distribution, body size, and growth rate of *Elliptio complanata* differ between upwind and downwind sites in a 5.8 km long lake basin. We measured density and morphological characteristics of *E. complanata* at nine upwind and nine downwind sites. We also measured growth rates and stable isotope ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$) signatures at three upwind and three downwind sites. We found no difference in density or body size of *E. complanata* between upwind and downwind sites, despite clear differences in water temperature and food availability. Contrary to our expectations, the growth rate of *E. complanata* was higher (by 62%) at upwind sites. The reason for this difference is uncertain, but higher shell erosion and a negative relationship between $\delta^{13}\text{C}$ and C/N ratio suggest that *E. complanata* may be more stressed at downwind sites. The $\delta^{15}\text{N}$ of *E. complanata* did not differ systematically between upwind and downwind sites, but increased with increasing body size. It would therefore be prudent to standardize the size of *E. complanata* used to measure the baseline of lake food webs.

R esum e : La variabilit e des conditions d'habitat dans les grands bassins lacustres peut cr eer des zones favorables au recrutement et  a la croissance des unionid es. Nous v erifions ici si la r epartition, la taille corporelle et le taux de croissance de *Elliptio complanata* diff erent entre les sites au vent et les sites sous le vent dans un bassin lacustre de 5,8 km de longueur. Nous avons mesur e la densit e et les caract eristiques morphologiques de *E. complanata*  a neuf sites au vent et  a neuf sites sous le vent, de m eme que les taux de croissance et les signatures d'isotopes stables ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$)  a trois sites au vent et trois sites sous le vent. Il n'y a pas de diff erence de densit e ni de taille chez *E. complanata* entre les sites au vent et sous le vent, malgr e des diff erences  evidentes de temp erature de l'eau et de disponibilit e de nourriture. Contrairement  a nos pr evisions, le taux de croissance de *E. complanata* est plus  lev e (de 62 %) aux sites au vent. La raison de cette diff erence est incertaine, mais l' rosion plus grande de la coquille et la relation n egative entre $\delta^{13}\text{C}$ et le rapport C/N laissent croire qu'*E. complanata* est peut- tre plus stress e aux sites sous le vent. Il n'y a pas de diff erence syst ematique de $\delta^{15}\text{N}$ chez *E. complanata* entre les sites au vent et sous le vent, mais $\delta^{15}\text{N}$ augmente en fonction de la taille du corps. Il serait donc prudent de standardiser la taille de *E. complanata* pour  tablir les valeurs de base dans les r eseaux trophiques des lacs.

[Traduit par la R edaction]

Introduction

In some freshwater systems, unionids dominate the benthos, accounting for up to 90% of the biomass of benthic invertebrates (Negus 1966; Strayer et al. 1999). Because of their dominating presence in the benthos, unionids may exert strong effects on aquatic ecosystem processes (Strayer et al. 1999; Vaughn and Hakenkamp 2001). For instance, unionids are important filter feeders (filtering up to 10%–100% of the water column per day) and may alter benthic processes by burrowing through sediments and enriching them with organic matter. However, while unionids play an important role in freshwater ecosystems, little is known about the biotic and abiotic factors that affect their growth and spatial distri-

bution. The notorious heterogeneity of littoral habitats in lakes may provide hot spots for unionid productivity.

In Lake Opeongo, a large Canadian Shield lake, the prevailing winds blow along a 5.8 km long basin, creating different habitat conditions at upwind and downwind sites. The downwind end of the basin is warmer and has more stable water temperature (Finlay et al. 2001). It also receives higher plankton biomass from wind-driven currents (Kaevats et al. 2005; A. Blukacz and W.G. Sprules, Department of Zoology, University of Toronto at Mississauga, Mississauga, ON L5L 1C6, personal communication). Increased water temperatures may increase metabolic rates of exothermic unionids and may lengthen their growth season, potentially leading to increased growth. Increased plankton densities

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may also positively affect unionid growth through bottom-up effects. This suggests that the littoral zone on the downwind end of the basin should provide a more favourable habitat for unionids.

The feeding regimes of unionids may also differ between upwind and downwind sites because of changes in food sources. For instance, wind blowing across a lake may transport different planktonic organisms (i.e., phytoplankton, zooplankton) differently to downwind sites or may resuspend benthic organisms at these sites and thus may alter the feeding regime of downwind versus upwind unionids. Stable isotopes of ^{13}C and ^{15}N may be used to test these potential changes in energy flow. Carbon isotope ratios ($\delta^{13}\text{C}$) are used to construct feeding relationships, as the $\delta^{13}\text{C}$ signature of an organism is similar to that of its food source (Wada et al. 1993; Post 2002). In freshwater lakes, phytoplankton and benthic algae have distinct $\delta^{13}\text{C}$ signatures, with benthic algae showing less ^{13}C discrimination during carbon fixation ($\delta^{13}\text{C}$ benthic algae: -26‰ ; phytoplankton: -32‰ ; France 1995a). This difference in the primary producers is reflected in consumers (France 1995b; Vander Zanden and Rasmussen 1999). The nitrogen isotope ratio ($\delta^{15}\text{N}$) is used to determine the trophic position of an organism, as consumers are enriched in ^{15}N by 2.5‰ – 3.4‰ relative to their prey (Minagawa and Wada 1984; Post 2002; Vanderklift and Ponsard 2003). The $\delta^{15}\text{N}$ signature of mussels is assumed to remain relatively constant with increasing body size. This was shown by Minagawa and Wada (1984) in two species of marine mussels (*Septifer virgatus* and *Mytilus edulis*) that attach to hard surfaces. However, the distribution of phytoplankton and zooplankton is not homogeneous in lakes (nor in marine coastal areas), and wind-driven currents could transport phytoplankton and zooplankton differently to different parts of the basin, depending on the size and buoyancy of the organisms. Moreover, freshwater unionids live in soft sediments, and young mussels bury into the sediments sometimes for extended periods of time (Amyot and Downing 1991). Systematic differences in food sources available in different parts of the lake basin and in the timing of burial among unionids of different sizes could affect their $\delta^{15}\text{N}$ signature and their reliability as a food web baseline.

In this study, we test whether the density, body size, and growth rate of the unionid *Elliptio complanata* differ with habitat variability (specifically temperature and food availability) at upwind and downwind sites in Lake Opeongo. We also investigate differences in trophic relationships between upwind and downwind sites by comparing their stable isotope signatures ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$).

Materials and methods

Site description

Lake Opeongo is a multibasin oligotrophic lake located on the Canadian Shield in Algonquin Park, Ontario, Canada ($45^{\circ}42'\text{N}$, $78^{\circ}22'\text{W}$). This study was done in South Arm, a 5.8 km long basin, which is oriented NW–SE along one of the predominant wind axes (Fig. 1). The western end of the basin is usually upwind and the eastern end usually downwind, and we will refer to these as “upwind” and “downwind”, respectively. Wind events in this basin result in strong internal

waves that influence water temperature in different parts of the littoral zone (Finlay et al. 2001).

Water temperature at upwind and downwind sites

We compared water temperature at two upwind and two downwind sites (U3, U7, D7, and D9 in Fig. 1) using Stow-away temperature loggers (models STEB08, STEB16, and TBI32-05+37, Hoskin Scientific, Burlington, Ontario) from May to September–October in three consecutive years (1998–2000). The temperature loggers were placed 20–40 cm above the substrate in the shallow littoral zone (1–2.5 m depth) on cement blocks. The loggers were programmed to record water temperature at 8–16 min intervals simultaneously at all sites. All temperature loggers were calibrated with a mercury thermometer at room temperature and at 4°C , at the beginning and (or) the end of each field season (see details in Finlay et al. 2001).

Sampling of planktonic organisms

We compared phytoplankton biomass at upwind and downwind sites after two wind events: 17 June and 25 June 2004. Six litres of lake water were collected just below the surface at nine inshore sites around South Arm (site depths = 0.5–0.75 m, within 5 m from shore) and at one offshore site (triangles in Fig. 1). Three replicate samples were filtered on GF/F filters, ground with a mortar and pestle, and extracted overnight in 95% ethanol. The samples were centrifuged and the supernatant was read on a Milton Roy Spectronic 1001+ spectrophotometer (Milton Roy Company, Rochester, New York) at 665 nm (± 2 nm). Chlorophyll concentrations were corrected for phaeopigment interference by acidifying with $0.2\text{ mol}\cdot\text{L}^{-1}$ HCl (Lorenzen 1967).

Planktonic organisms were also sampled concurrently with unionids (29 September 2004) for stable isotope analysis at one upwind and one downwind offshore site (stars in Fig. 1). At each site, the plankton sample consisted of the pooled contents of five 10 m vertical tows of a $63\text{ }\mu\text{m}$ mesh Wisconsin net.

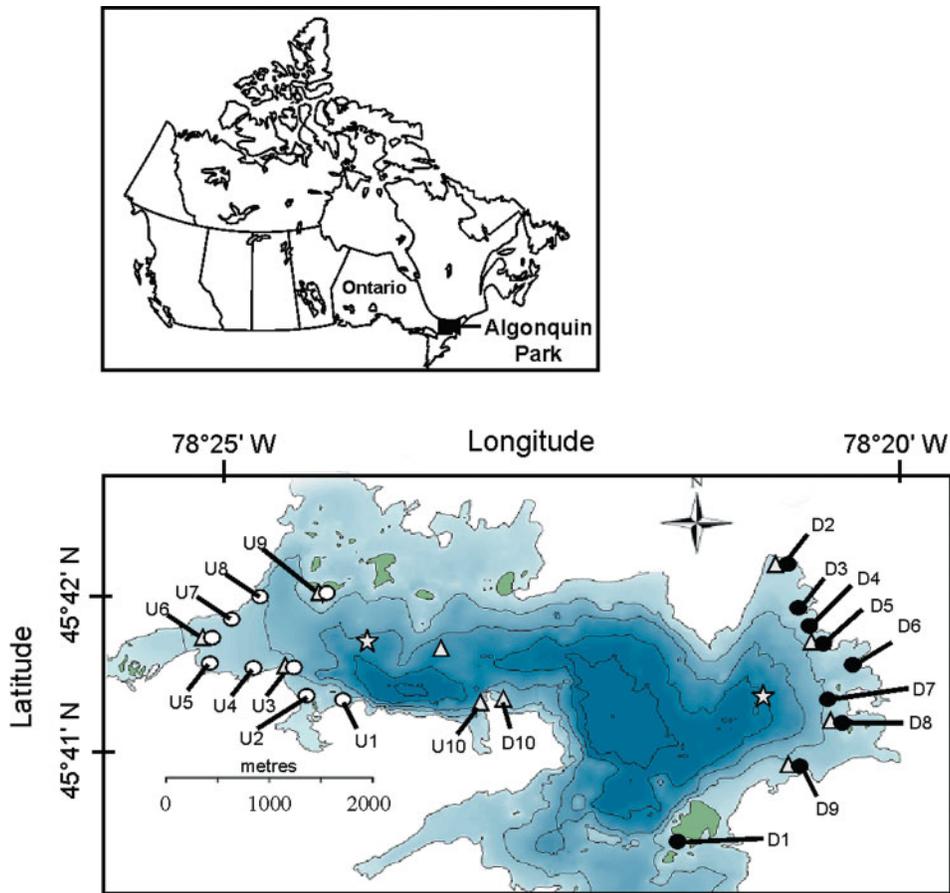
Field collection of *E. complanata*

Elliptio complanata were collected at nine upwind and nine downwind sites within South Arm (open and solid circles, respectively, in Fig. 1) on 28 and 29 September 2004. The water temperature was 17°C at the time of sampling. At each site, a 1 m^2 quadrat was thrown into the water at ~ 2 m depth. All unionids in the quadrat were collected, and the substratum was searched by hand for unionids buried within the sediment. The density of unionids and the substratum type were recorded at each site. Twenty-five unionids were collected at three upwind (U3, U7, U9) and three downwind (D4, D8, D9) sites (for a total of 150) for morphological characterization and growth rate measurement.

Morphological characteristics

Upon return to our field laboratory, the unionids were placed in an aquarium of filtered lake water for 24 h to clear their gut. Soft tissues were then removed from each unionid and the guts were cleaned of remaining material with filtered lake water. The cleaned tissues were placed into a pre-weighed aluminum dish and dried at 60°C for 48 h. Soft

Fig. 1. Sampling sites in the South Arm of Lake Opeongo (Algonquin Park, Ontario, Canada). *Elliptio complanata* mussels were sampled at nine upwind sites (open circles, U1–U9) and nine downwind sites (solid circles, D1–D9). Planktonic organisms were sampled for stable isotope analysis at two offshore sites (stars): one upwind and one downwind. To compare the potential availability of planktonic food upwind and downwind, chlorophyll concentrations were measured at nine inshore sites and one offshore site after two wind events (triangles). The bathymetric contour lines are at 10 m intervals.



tissue mass was then measured to 0.0001 g using a Mettler AE50 balance (Mettler–Toledo Inc., Columbus, Ohio).

We measured the growth length (from the umbo to the point of maximum growth), maximum length, maximum width, and maximum depth of *E. complanata* shells using calipers (± 0.01 mm). We also measured the length of shell that was eroded along the growth length. The proportion of the growth length that was eroded is used as an index of shell erosion. Shells were then dried at 60 °C for 24 h, after which the mass was measured to 0.01 g on a Mettler PB3002 balance. Shell thickness was calculated as the ratio of shell mass to maximum length (Bailey and Green 1987).

Growth rate

The growth rates of unionids were determined by measuring the distances between the last three growth lines laid in the shells. Unionid shells were thin-sectioned following procedures described by Day (1984) and Neves and Moyer (1988). Shells were cut along the growth axis using a Raytech Jemsaw 45 (Raytech Industries, Middletown, Connecticut). The cut surface was polished first with a belt sander and then with a series of fine-grit sandpapers (120–

2000 grit), until the shell lay perfectly flat on a microscope slide. The cut side was then mounted in 5 min epoxy onto a microscope slide and dried at 60 °C for 24 h. The remaining shell was sawed off using a DeWalt cutter and grinder 10–40 (DeWalt, Baltimore, Maryland), leaving a 1 mm thick section. This section was then polished using very fine-grit sandpapers (1200 and 2000 grit) to a thickness of ~ 250 μ m or a desired transparency in which growth lines could be observed.

Thin sections were viewed under a light microscope (Leica DM4500) at 10 \times magnification, and the distances between the last three growth lines (laid nearest to the growth edge) were measured using an image analysis program (Open Lab 4.0.2; Improvion, Lexington, Massachusetts). We could only measure three growth periods in most unionids, since large portions of the prismatic layer were eroded. Following Veinott and Cornett (1996), opaque bands were considered growth lines if they extended from the prismatic layer discontinuity to the umbo or if the opaque band extended from the prismatic layer and merged into a line common to several opaque bands (Fig. 2). Growth was measured for 9–15 individuals per site (D4, $n = 15$; D8, $n = 13$; D9, $n = 9$; U3,

Fig. 2. An *Elliptio complanata* thin-sectioned shell (JB9 #2) viewed under a light microscope at 10× magnification. Solid arrows are pointing to growth lines found near the tip of the shell, which extended from the prismatic layer and merged into a line common to several opaque bands (merge not shown). The broken arrow points to a line that extended from the prismatic layer, but did not merge into a common line, and thus was not considered a growth line.



$n = 13$; U7, $n = 13$; U9, $n = 10$). Shells in which the growth edge was damaged by erosion or by thin-sectioning were not measured.

Stable isotope analysis

Unionid soft tissue (whole body) and plankton samples were dried at 60 °C for 48 h and ground using a mortar and pestle. Unionid soft tissue samples from four sites (D4, $n = 2$; D9, $n = 7$; U3, $n = 2$; U7, $n = 7$) and plankton samples from two offshore sites were sent to the Environmental Isotope Laboratory at the University of Waterloo, Ontario, for ^{13}C , ^{15}N , and total N and C analysis. We selected unionids spanning the full range of available body sizes for these analyses to examine the potential relationships between body size and stable isotope signature. Most unionids were selected from two sandy sites (U7, D9) to control for substrate-related variation. Two mussels (one large and one small) were selected from mud (U3) and boulder (D4) substrates to explore differences between substrata.

Statistical analysis

Unionid density was compared between upwind and downwind sites and among substrate types (mud, sand, boulders) using a t test and an analysis of variance (ANOVA) on $\log_{10}(x + 1)$ -transformed data (Zar 1984). The body sizes of the unionids were compared between upwind and downwind sites in two ways. We compared the growth lengths of unionids between upwind and downwind sites and among upwind sites and among downwind sites using Kruskal–Wallis tests

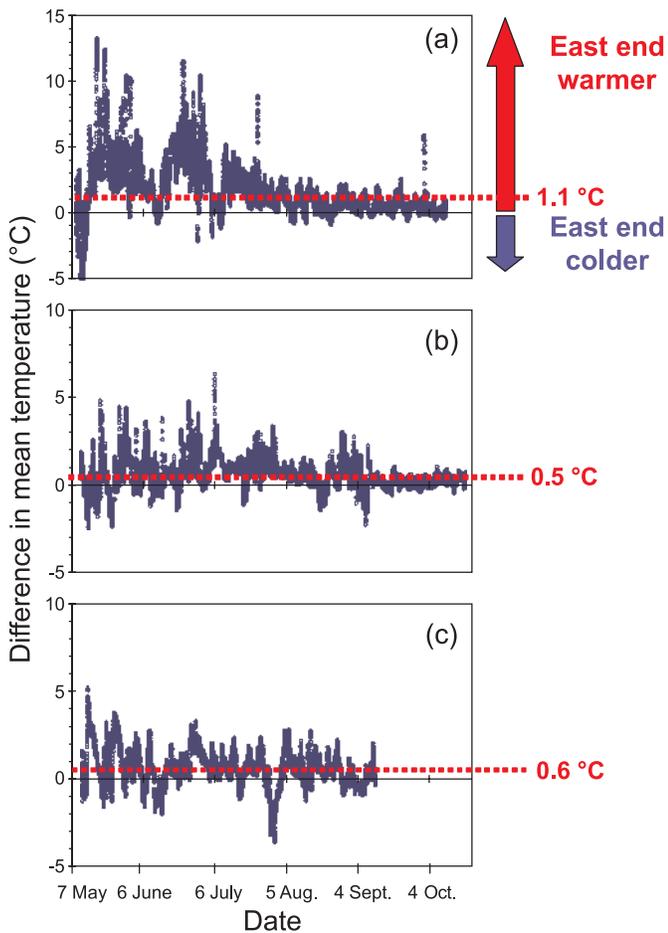
(Conover 1980). We also used a canonical discriminant analysis based on ln-transformed measures of maximum length, maximum width, maximum height, and shell mass to compare the size of unionids at upwind and downwind sites (Pielou 1984). Because of the large amount of erosion on most shells, we repeated this analysis with measures of linear dimension only (i.e., without shell mass) and found very similar results. Maximum length – dry mass relationships were compared between upwind and downwind sites by analysis of covariance (ANCOVA) on ln-transformed variables, with a dummy variable for site location (Zar 1984). Shell thickness and degree of erosion were also compared between upwind and downwind sites using ANCOVA on ln-transformed variables (Zar 1984). Growth rates in each of the three growth periods were compared between upwind and downwind sites using Kruskal–Wallis tests (Conover 1980). The relationship among stable isotope signatures ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$), maximum length, and C/N ratios in unionids were tested with simple regression analysis (Zar 1984). All analyses were performed in Statistica 5.0 for microcomputers (StatSoft Inc., Tulsa, Oklahoma).

Results

Environmental differences between upwind and downwind sites

There are clear differences in water temperature between shallow littoral sites at the downwind and the upwind ends of South Arm (Fig. 3). The downwind end is warmer than

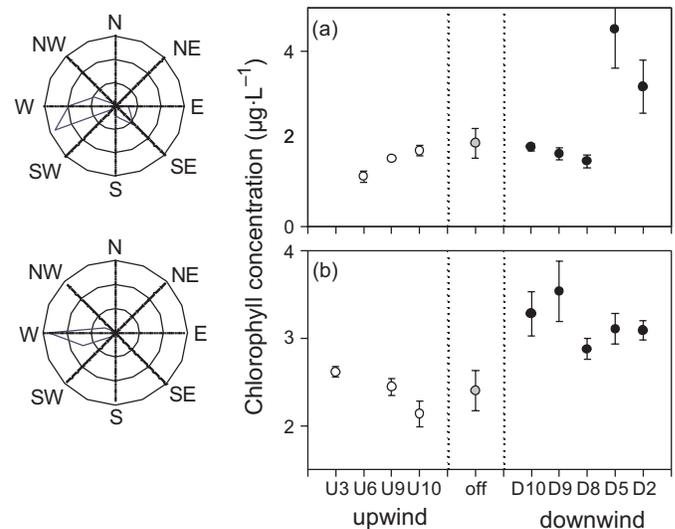
Fig. 3. Difference in mean water temperature between shallow littoral sites at the eastern (downwind) and the western (upwind) end of South Arm in three consecutive years: (a) 1998, (b) 1999, (c) 2000. These differences were calculated from simultaneous measurements of water temperature at two downwind (D7, D9) and two upwind (U3, U7) sites every 8 or 16 min. The eastern end of South Arm was generally warmer than the western end (positive differences). Median differences in mean water temperature over the whole growing season (shown as broken lines) were (a) 1.1 °C in 1998, (b) 0.5 °C in 1999, and (c) 0.6 °C in 2000.



the upwind end by as much as 10 °C, with the most pronounced differences occurring in the spring and early summer. These differences in water temperature between upwind and downwind sites depend on wind and weather patterns, and their magnitude varies among years. Median differences in water temperature between the downwind and upwind ends of the basins were 1.1 °C in 1998, 0.5 °C in 1999, and 0.6 °C in 2000 (Fig. 3). These results extend the findings of Finlay et al. (2001) and suggest that unionids at the downwind end of South Arm are exposed to warmer temperatures, possibly resulting in a longer growing season.

Phytoplankton biomass differed between the upwind and downwind ends of South Arm after two wind events (Fig. 4). Chlorophyll concentrations are typically low in Lake Opeongo, but they ranged more than fourfold (1.1–4.5 $\mu\text{g}\cdot\text{L}^{-1}$) among sites. The sampling of inshore phytoplankton biomass on 17 June followed a windy night, with winds up to 18 $\text{km}\cdot\text{h}^{-1}$. In the morning, the chlorophyll concentration inshore was

Fig. 4. Surface chlorophyll *a* concentrations measured at shallow littoral sites and offshore (off) following two wind events: (a) 17 June 2004 and (b) 25 June 2004. Data points represent the mean chlorophyll concentration \pm standard error ($n = 3$). The solid line on the rosettes (left) show the proportion of the wind that blew from each cardinal directions in the 12 h before each sampling. Sampling sites are shown as triangles in Fig. 1.



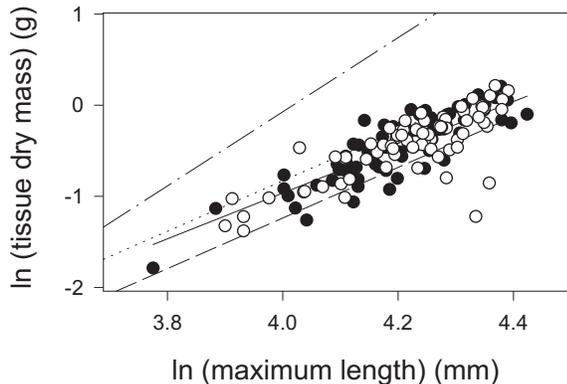
lowest (1.1 $\mu\text{g}\cdot\text{L}^{-1}$) at the two most upwind sites (U3 and U6), and we found >50% higher chlorophyll concentration offshore and at sites U10 and D10 in the center of the basin (1.7–1.9 $\mu\text{g}\cdot\text{L}^{-1}$). The highest chlorophyll concentrations were measured at downwind sites D2 and D5 (3.2–4.5 $\mu\text{g}\cdot\text{L}^{-1}$), both located in an embayment on the northern shore (Fig. 1). Phytoplankton were likely pushed at these sites by the southwesterly component of the wind. We also sampled inshore phytoplankton on 25 June, a day after the largest storm of the summer, with winds up to 40 $\text{km}\cdot\text{h}^{-1}$. The winds were very steady from the west (Fig. 4) and gradually decreased through the night. In the morning, surface chlorophyll concentrations ranged from 2.1 to 3.5 $\mu\text{g}\cdot\text{L}^{-1}$ and were higher at the downwind end of the basin (Fig. 4). Since the dominant winds on Lake Opeongo blow from the southwest, west, and northwest, these results suggest that more planktonic food is available to *E. complanata* living at the downwind end of South Arm, at least after windy periods.

Unionid density and body size

The density of *E. complanata* measured at 18 sampling sites in South Arm ranged from 0 to 23 individuals $\cdot\text{m}^{-2}$, with a (geometric) mean density of 2.3 individuals $\cdot\text{m}^{-2}$. There was no significant difference in density between the upwind and downwind sites (t test, $P = 0.54$), but the density of *E. complanata* was lower in areas covered with boulders (geometric mean density = 1 $\cdot\text{m}^{-2}$, $n = 5$ sites) compared with sites covered in mud or sand (4–5 $\cdot\text{m}^{-2}$, $n = 5$ –6 sites; ANOVA, $P = 0.08$).

The unionids we collected ranged from 4.4 to 8.3 cm maximum length, and there was no difference in the length of *E. complanata* at upwind and downwind sites (Kruskal–Wallis test on growth length, $P = 0.12$). There was also no significant difference in *E. complanata* growth lengths among

Fig. 5. Mass–length relationship for *Elliptio complanata* sampled at three upwind (open circles, $n = 74$) and three downwind (solid circles, $n = 80$) sites in Lake Opeongo. There was no significant difference in mass–length relationships between upwind and downwind sites (analysis of covariance, $P > 0.5$), so one relationship fits all unionids in South Arm: $\ln(\text{soft tissue dry mass}) = -11.0 + 2.5 \ln(\text{maximum length})$, $r^2 = 0.66$, $P < 0.0001$ (solid line). Similar relationships developed for *E. complanata* in a polymictic mesotrophic reservoir, New Brunswick, Canada (dotted line, Cameron et al. 1979), in a polymictic meso-eutrophic pond, Rhode Island, USA (dashed line, Kesler and Bailey 1993, assuming dry mass is 10% of wet mass), and in a headwater stream, Virginia, USA (dash-dotted line, Balfour and Smock 1995), are shown for comparison.



the three downwind sites (Kruskal–Wallis test, $P = 0.78$), nor among the three upwind sites ($P = 0.36$). We also used a multivariate test to compare the sizes of *E. complanata* based on maximum length, width, and height of their shells, but we did not detect any significant difference in body size between upwind and downwind sites (canonical discriminant analysis, $P > 0.2$).

The length–mass relationships of *E. complanata* were not significantly different at the upwind and downwind sites (ANCOVA, $P > 0.52$), so one relationship fits all *E. complanata*:

$$\ln(\text{soft tissue dry mass}) = -11.0 + 2.5 \ln(\text{maximum length})$$

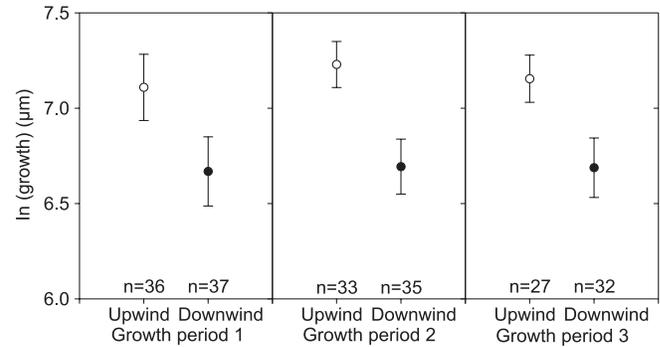
where dry mass is in g and length is in mm ($r^2 = 0.66$, $P < 0.0001$; Fig. 5).

Shell thickness and erosion

Shell thickness ranged from 0.5 to 2.8 $\text{g}\cdot\text{cm}^{-1}$ and did not differ significantly between the upwind and downwind ends of South Arm (ANCOVA, $P > 0.15$). These measures of shell thickness, which are calculated from shell mass and maximum shell length, should be interpreted with caution, however, since most shells were heavily eroded.

Most of the *E. complanata* shells we collected were heavily eroded, with the nacreous layer exposed over more than half of their growth length (median = 52%). Interestingly, two of the small unionids collected at site U3 (maximum length = 5.1 and 5.7 cm) showed very little erosion, with only 8%–10% of their growth length eroded. All other unionids, including other very small ones (down to 4.4 cm maximum length), had at least 20% and up to 99% of their

Fig. 6. Growth rates of *Elliptio complanata* sampled at three upwind and three downwind sites in Lake Opeongo over the last three growth periods (growth period 1 is the most recent). *Elliptio complanata* at upwind sites consistently grew more per growth period (44% higher growth rates, on average) than at downwind sites. Symbols are mean \pm standard error. Numbers of unionids measured (n) are displayed on the bottom.



growth length eroded. The degree of shell erosion did not increase systematically with shell length (ANCOVA, the coefficient associated with $\ln(\text{growth length}) \pm$ standard error (SE) = 1.41 ± 0.24 is not significantly different from 1), but the shells were slightly more eroded (13% more erosion, on average) at downwind than at upwind sites (ANCOVA, $P = 0.02$).

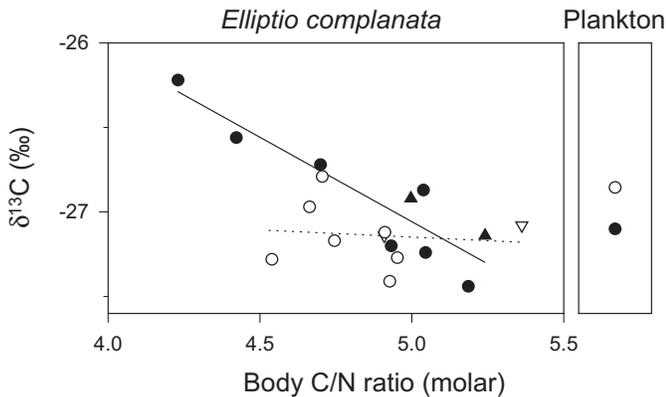
Growth rate

The growth rate of *E. complanata* ranged from 0.1 to 4.5 mm per growth period and was on average 62% higher at western than at eastern sites (t tests; growth period 1, $P = 0.10$; growth period 2, $P = 0.004$; growth period 3, $P = 0.03$; Fig. 6). The growth rates of *E. complanata* were not related to their body size (regression, $P > 0.2$ in all three growth periods). When comparing growth over different periods, we found no evidence that any of the growth periods were consistently better or worse than other growth periods. We also found no evidence that individuals grew consistently more or less than others over these three growth periods. An individual with a higher-than-average growth rate in one period did not necessarily grow more than average in another period.

Food source and soft tissue composition

The $\delta^{13}\text{C}$ signatures of *E. complanata* were very similar to those of the plankton ($-27.03\text{‰} \pm 0.07\text{‰}$ (SE), $n = 18$ mussels from four sites; and $-27.00\text{‰} \pm 0.1\text{‰}$, $n = 2$ sites, respectively; Fig. 7), suggesting that their main source of food is planktonic rather than benthic. Their $\delta^{13}\text{C}$ signatures did not vary with body size (regression, $P > 0.5$), nor did we find consistent differences in $\delta^{13}\text{C}$ signatures among unionids living on sand, mud, or among boulders (circles, inverted triangles, and upright triangles, respectively; Fig. 7). The $\delta^{13}\text{C}$ signatures of *E. complanata* were closely related to their C/N ratio at downwind sites (regression, $r^2 = 0.79$, $P < 0.001$, solid symbols in Fig. 7), but not at upwind sites ($P > 0.7$, open symbols in Fig. 7). This relationship suggests that some individuals at downwind sites have low lipid content (i.e., low C/N ratio and less negative $\delta^{13}\text{C}$; Schmidt et al. 2003; Matthews and Mazumder 2005). If we assume that

Fig. 7. Relationship between $\delta^{13}\text{C}$ signature and C/N ratio in *Elliptio complanata* unionids at upwind (open symbols, broken line) and downwind (solid symbols, solid line) sites. Each point represents one unionid sampled on sand (open circles from site U7, solid circles from D9), mud (open triangles, site U3), or among boulders (solid triangles, site D4). The $\delta^{13}\text{C}$ signatures of plankton sampled upwind (open) and downwind (solid) are shown for comparison.



lipids are depleted in $\delta^{13}\text{C}$ by 3‰–12‰ (Abelson and Hoering 1961; Parker 1964; Kelly 2000) and have a high C/N ratio (Schmidt et al. 2003), the difference we observe in $\delta^{13}\text{C}$ signature and C/N ratio between unionids from downwind sites suggests a 10%–40% difference in lipid content. In contrast, the unionids at upwind sites had more similar $\delta^{13}\text{C}$ signatures that were not related to C/N ratios, suggesting more similar lipid contents. Unfortunately, we did not measure the lipid content of the unionids directly.

The $\delta^{15}\text{N}$ signatures of the *E. complanata* collected at both upwind and downwind sites in South Arm ranged over 1‰ and were similar to those measured in plankton $>63\ \mu\text{m}$ (Fig. 8). The $\delta^{15}\text{N}$ signatures of *E. complanata* increased with increasing body size (regression with maximum length, $r^2 = 0.34$, $P < 0.01$; Fig. 8).

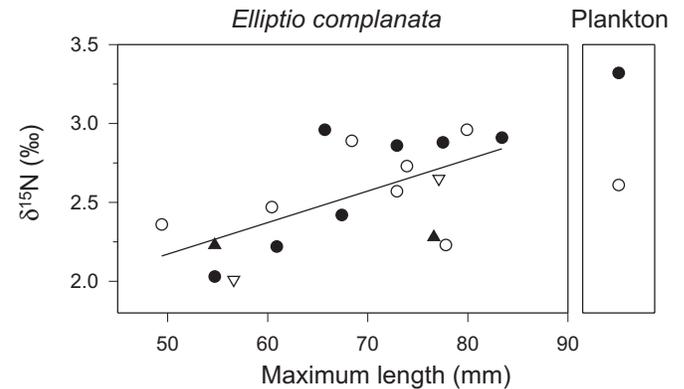
Discussion

Littoral sites at the downwind end of South Arm are warmer and have higher phytoplankton biomass, at least after wind events, compared with sites at the upwind end of the basin. Higher average water temperatures, a longer growing season, and increased food availability all suggest that unionids from the downwind end of the lake should exhibit increased growth rates compared with unionids at the upwind end of the lake. Yet, we found no difference in the density or body size of unionids between the upwind and the downwind sites, and contrary to our expectations, *E. complanata* grew faster at the upwind sites, at least over the past three growth periods.

Density of *E. complanata*

The density of *E. complanata* at a depth of 2 m in South Arm ranged between 0 and 23 individuals·m⁻², which falls within the range of densities reported in other lakes on and off the Canadian Shield (e.g., Ghent et al. 1978; Strayer et al. 1981; Downing and Downing 1992). *Elliptio complanata* is fairly abundant in Lake Opeongo and can reach much

Fig. 8. Relationship between the $\delta^{15}\text{N}$ signature of soft tissue and the body size of *Elliptio complanata* collected at upwind (open symbols) and downwind (solid symbols) sites. Each point represents one unionid sampled on sand (open circles from site U7, solid circles from D9), mud (open triangles, site U3), or among boulders (solid triangles, site D4). The $\delta^{15}\text{N}$ signatures of plankton sampled upwind (open) and downwind (solid) are shown for comparison.



higher densities in other basins. We have recorded densities up to 210 individuals·m⁻² at 1 m depth in Sproule Bay, a much smaller polymictic basin at the southernmost end of Lake Opeongo (surface area = 2.1 km², maximum depth = 6.5 m; C.N. Hirst and H. Cyr, unpublished data).

The densities of *E. complanata* were similar at the upwind and the downwind ends of South Arm. *Elliptio complanata* move relatively short distances through the sediments (Amyot and Downing 1997), and their overall distribution may depend on the dispersal of glochidia (unionid larvae), which are obligate parasites of littoral fish (e.g., yellow perch (*Perca flavescens*), smallmouth bass (*Micropterus dolomieu*); Vaughn and Taylor 2000). In South Arm, the smallmouth bass males nest mostly at downwind sites in the spring (Rejwan et al. 1997), but yellow perch and nonnesting smallmouth bass (females, males after the nesting period) move broadly around the different basins (M. Ridgway, Aquatic Resource and Development Section, Ontario Ministry of Natural Resources, 300 Water Street, Peterborough, ON K9J 8M5, personal communication). This suggests that dispersal is not limiting the distribution of *E. complanata* in South Arm.

We found no systematic differences in the densities of *E. complanata* between muddy and sandy substrates. Areas with boulders supported fewer mussels, but this is not surprising, since the boulders reduce the effective area of quadrats that is inhabitable by mussels. Unionid densities in South Arm seem to be unaffected by substrate types, water temperature, or food availability.

Growth rate measurements

We found a clear difference in growth rates of *E. complanata* between upwind and downwind sites in South Arm. Contrary to our predictions, the growth rates were 62% higher, on average, at upwind sites.

Our comparison of *E. complanata* growth rates assumes that all unionids in the shallow littoral zone of South Arm lay their growth lines at the same time, but not necessarily at annual intervals. Internal growth lines in unionids are

thought to be laid following extended periods of inactivity, during which the mantle retracts from the edge of the shell (Checa 2000). However, it is still unclear whether these growth lines represent annual growth or not. Veinott and Cornett (1996) showed periodic changes in $\delta^{18}\text{O}$ in the shells of five *E. complanata*, which indicates changes in water temperature as the shells were growing. Interestingly, the $\delta^{18}\text{O}$ signatures peaked in all but one of the eight growth lines tested, suggesting that the growth lines were generally produced during the coldest time of the year. Dettman et al. (1999) also found periodic changes in $\delta^{18}\text{O}$ shell signature in the shells that were associated with growth lines in three species of unionids collected in a river and a creek (one individual per species). They also showed that these changes in the shells tracked very closely the $\delta^{18}\text{O}$ signature measured in the river water over the previous 2 years. These studies suggest that unionid growth lines are mostly laid during cold periods of the year; yet this does not imply that the growth lines are laid annually. Kesler and Downing (1997) showed that when internal annuli were used to predict the growth rates of *E. complanata* and *Lampsilis radiata*, they greatly overestimated the growth rates actually measured in the field (up to 19 times higher). Kesler and Downing (1997) concluded that internal annuli cannot be produced every year (see also Anthony et al. 2001).

The growth rate differences we measured between upwind and downwind sites were relatively large and consistent among the last three growth periods. Nevertheless, we did not detect differences in shell length or general body size (using multivariate analysis) of *E. complanata* between upwind and downwind sites. The most likely reason for this inconsistency is that the absolute difference in growth of *E. complanata* between upwind and downwind sites is small (0.5 mm per growth period, on average), so it would take years to detect differences in shell length, especially if growth lines are not produced annually. Another possible explanation is that unionids of a given size are not all of the same age. The faster-growing unionids at upwind sites may be a younger cohort than the slower-growing unionids downwind. There is currently no reliable method to age these heavily eroded unionids, so we cannot test this hypothesis. Finally, we do not know whether the growth rates we measured on unionids >4 cm in length are representative of earlier growth. If young *E. complanata* remain buried for long periods of time (Amyot and Downing 1991), their size may not differ much between upwind and downwind sites.

Why are *Elliptio* growth rates higher at upwind sites?

Large differences in water temperature were observed between the upwind and downwind littoral sites in South Arm. Downwind sites were often 2–5 °C warmer than upwind sites, especially during spring and early summer, with differences as large as 10–13 °C in 1998. These temperature differences are due to upwellings of cold hypolimnetic waters at upwind sites during windy events (Finlay et al. 2001). These upwelling events can last several hours and sometimes days. The emergence of *E. complanata* from the sediments in the spring is strongly correlated with increasing water temperature (Amyot and Downing 1997; Watters et al. 2001), so we expected these frequent cold water incursions at upwind sites to shorten the growing

season of unionids and (or) to reduce their growth rate. Nevertheless, we found the opposite; the growth of unionids was higher at upwind sites.

Temperature refuge in the sediments?

One possible explanation for this apparently puzzling result is that temperature of the water column may not represent the temperature experienced by unionids, especially early in the season when they are still buried in the sediments. In July 2003, we deployed two Stowaway temperature loggers (model TBI32-05+37; Hoskin Scientific) at a 5 m deep site for 1 month to measure temperature at 8 min intervals simultaneously in the water column (20 cm above the sediments) and 1 cm into the sediment. Our data suggest that upwellings of cold water were also measured in the sediments. Temperature variability in the sediments was more dampened at short time scales (<2 h) compared with temperature in the water column, but was equally variable at longer time scales (H. Cyr, unpublished data). It is unclear whether these results can be extrapolated to earlier periods of the year, to shallower littoral sites with different substrate composition, or to deeper sediments where the unionids are buried, but they suggest that prolonged cold-water upwellings penetrate into the sediments. The effect of upwellings of cold water on unionids buried in the sediment remains to be tested.

Food availability?

The stable isotope analysis establishes that *E. complanata* feed on a similar C source as the planktonic organisms larger than 63 μm . The $\delta^{13}\text{C}$ signatures of *E. complanata* and of planktonic organisms are both around -27‰ . These results are similar to the signature of pelagic primary consumers in other Canadian Shield lakes (-28‰ , on average) and are clearly different from the signature of benthic primary consumers (-24‰ , on average; Vander Zanden and Rasmussen 1999). *Elliptio complanata* also has a $\delta^{15}\text{N}$ signature that is similar to that of planktonic organisms collected with a 63 μm mesh (mostly crustacean zooplankton, with some large colonial algae), suggesting that they are feeding on similar food sources. Paterson (1986) reported that *E. complanata* fed best on very small seston (between 1.6 and 5 μm in diameter), and their efficiency decreased with increasing particle size. These feeding experiments, however, were run in the laboratory under crowded conditions (five *E. complanata* in 6 L of water). In contrast, Bärlocker and Brendelberger (2004) reported particle-specific rather than size-specific feeding of *E. complanata*. In their experiment, *E. complanata* preferred three large species of conidia (asexual spores of fungi), ranging in size between 70 and 200 μm . Contrary to zebra (*Dreissena polymorpha*) and quagga (*Dreissena bugensis*) mussels, *E. complanata* has not been observed to feed on rotifers (Thorpe and Casper 2002).

The increased availability of phytoplankton nearshore at downwind sites should be available to the unionids, since the water column in littoral areas should be well mixed, especially after wind events. Our results suggest that despite low phytoplankton biomass in South Arm (<5 μg chlorophyll *a*-L⁻¹), *E. complanata* does not appear limited by food availability, or at least any subsidy in food downwind is confounded by other factors that affect their growth negatively. Alternatively, unionids at downwind sites may

not be able to use these intermittent food pulses, for example, if increased sediment resuspension after storms reduces food quality for the filtering unionids (Grant and Thorpe 1991; Ellis et al. 2002).

Exposure to wave action?

South Arm is 5.8 km in length and its main axis is aligned with the prevailing winds. The unionids we sampled at the downwind sites are exposed to large wave action during storms and may be adversely affected by these conditions. In very large lakes, the size of unionids can be stunted by exposure to extreme wave action. Brown et al. (1938) found that *Lampsilis radiata* were stunted in highly exposed habitats in western Lake Erie, Ontario. Green (1972) reported decreasing sizes of *L. radiata* with increasing lake size in large Canadian lakes (maximum fetch: <2 to 140 km). In contrast, exposure to wave action in smaller and more protected basins has been reported to enhance growth. Hinch and Bailey (1988) compared the morphometrics of *E. complanata* in four relatively small lakes (surface area = 1.2–1.7 km²) and found that they were consistently larger and heavier in areas of highest exposure within these lakes. Heavier shells were hypothesized to prevent dislodgement under turbulent conditions. Hinch et al. (1986) also found, through reciprocal transplant experiments between two sites in Inner Long Point Bay, Lake Erie (surface area of 75 km²), that *L. radiata siliquioidea* had a different shape and grew faster at the more exposed site. These differences were attributable partly to environmental differences between the sites and partly to genetic differences between the two populations. The South Arm of Lake Opeongo is intermediate in size (22 km²), and although we did not detect any differences in the size or shape of *E. complanata* between upwind and downwind sites, we measured clear differences in growth rates, with higher growth rates measured at the least-exposed upwind sites.

There are two lines of evidence suggesting that *E. complanata* growing at downwind sites may be more stressed. First, although most *E. complanata* in South Arm have heavily eroded shells, those we collected downwind were slightly more eroded than those from upwind sites (13% more eroded, on average).

Second, the $\delta^{13}\text{C}$ signature and C/N ratio of mussel soft tissues suggest that some mussels from shallow downwind sites have low body lipid content. The mussels collected at downwind sites showed a clear negative relationship between their $\delta^{13}\text{C}$ signature and their C/N ratio. Other studies report similar relationships for other groups of organisms (e.g., Matthews and Mazumder 2005 for zooplankton; Cherel et al. 2005 for penguins), which they attribute to differences in lipid content. Lipids have a less negative $\delta^{13}\text{C}$ signature (and a lower C/N ratio) than do carbohydrates or proteins (deNiro and Epstein 1977), and depending on the fractionation difference one assumes for lipids (3‰–12‰; Abelson and Hoering 1961; Parker 1964; Kelly 2000), the 1.2‰ difference in $\delta^{13}\text{C}$ signature we observed among unionids at downwind sites suggests a 10%–40% difference in lipid content. Lipid content is also positively related to the C/N ratio of the organisms (e.g., Schmidt et al. 2003), and the 1.1 difference in C/N ratio we observed at downwind sites also suggests a 10% difference in lipid content. Low body lipid content is an

indicator of poor condition in organisms (e.g., Hebert et al. 1991; Greseth et al. 2003) and could be due to low feeding rates (e.g., from physical disturbance of the mussels) or low food quality (e.g., because of sediment resuspension during wind events). This conclusion needs to be tested more directly by comparing the physiological condition of these unionids.

E. complanata $\delta^{15}\text{N}$ increases with body size

Most studies show that $\delta^{15}\text{N}$ is not related to the size of organisms (Kelly 2000). This includes an early study of stable isotopes in marine mussels, where $\delta^{15}\text{N}$ was compared specifically between individuals of different sizes (Minagawa and Wada 1984). In this study, it was assumed that the planktonic food filtered by these mussels did not change during the sessile part of their lives. This might not be strictly the case, since phytoplankton and zooplankton are transported differently by water currents, and their availability onshore may vary with changes in wind conditions and water currents. Interestingly, in Lake Opeongo we found no systematic difference in $\delta^{15}\text{N}$ (for a given body size) between upwind and downwind sites, suggesting that wind-induced shifts in the distribution and availability of planktonic organisms do not affect the $\delta^{15}\text{N}$ signature of the unionids.

A few studies have reported increases in $\delta^{15}\text{N}$ with increasing body size, which they attribute to ontogenic shifts of diet (e.g., in crabs, Wada et al. 1993; in fish, Post 2003; in squids, Cherel and Hobson 2005). *Elliptio complanata* is a filter feeder, and although we actually know very little about its feeding, it is not known to shift its diet with increasing body size. Instead, Post (2002) and Garton et al. (2005) attributed the high $\delta^{15}\text{N}$ measured in large (and presumably old) bivalves to a carryover effect from previous years. It is unlikely that the higher $\delta^{15}\text{N}$ signature of large unionids in our study could be attributed to recent changes in the lake. Lake Opeongo is located in Algonquin Provincial Park (established in 1893). The lake and its watershed have been protected from major human development, and although the introduction of smallmouth bass (early 1900s) and cisco (*Coregonus artedii*) (1940s) and recreational fishing had important effects on the lake food web (Martin and Fry 1972), there has been no major changes recorded in the lake over the last 30–40 years (St. Jacques et al. 2005). The increase in $\delta^{15}\text{N}$ with increasing body size suggests that *E. complanata* may shift its diet as it grows, from a more phytoplankton-based diet to a more zooplankton-based diet. However, many other factors could also affect the $\delta^{15}\text{N}$ signature of organisms (Kelly 2000; Vanderklift and Ponsard 2003). For example, $\delta^{15}\text{N}$ has been shown to increase in fasting and starving organisms (Adams and Sterner 2000; Cherel et al. 2005), and low food availability in oligotrophic lakes may progressively affect the $\delta^{15}\text{N}$ of *Elliptio complanata* as they grow older. At this point, it is unclear why we are finding increases in $\delta^{15}\text{N}$ with increasing body size, but it clearly has implications for how we use stable isotopes in food web studies.

Unionids are commonly used to establish a $\delta^{15}\text{N}$ baseline in freshwater food webs (Cabana and Rasmussen 1996; Vander Zanden and Rasmussen 1999; Post et al. 2000). Their large size results in a slow nitrogen turnover rate and low temporal variation in their $\delta^{15}\text{N}$ signatures compared with phyto-

plankton or zooplankton (Cabana and Rasmussen 1996). Studies currently using unionids to establish their trophic baseline generally rely on one or very few individuals to establish the baseline, implicitly assuming negligible variation in unionid $\delta^{15}\text{N}$ signatures within a lake. This assumption was tested in six small lakes by McKinney et al. (1999; mean depth = 1.2–3.6 m, surface area = 0.2–1 km²), who reported that the $\delta^{15}\text{N}$ signature of unionids sampled at different sites within a lake or pond varied by 0.7‰–1.9‰. This represents a maximum error of 0.5 to almost 1 trophic level, depending on the fractionation between trophic levels (2.5‰–3.4‰; Minagawa and Wada 1984; Post 2002; Vanderklift and Ponsard 2003). In South Arm, we found a maximum difference of 1‰ in $\delta^{15}\text{N}$ signatures of *E. complanata*. Our results support the finding of McKinney et al. (1999) in a much larger lake basin (mean depth = 14.6 m, surface area = 22.1 km²), with obvious habitat heterogeneity.

This variability in $\delta^{15}\text{N}$ signature is related to the body size (soft tissue dry mass) of *E. complanata*. Larger mussels have up to a 1‰ higher $\delta^{15}\text{N}$ signature. Although the differences we found are small, it would be prudent to standardize the size of the unionids used as baseline (e.g., 6–7 cm length) when constructing food webs using $\delta^{15}\text{N}$ signatures.

Elliptio complanata showed similar densities and body sizes at upwind and downwind sites in South Arm, but individuals at the upwind sites grew 62% faster. These results are opposite to our initial predictions, which were based on differences in temperature and food conditions at both ends of the basin. They raise numerous questions on how *E. complanata* responds to water temperature and to food availability. High growth rates do not translate into differences in body size in this unionid population. This suggests that the *Elliptio* “hot spots” we identified represent a population of very slow-growing unionids living in a low productivity lake.

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