Seasonal variation in vertical and horizontal movement of the freshwater bivalve *Elliptio complanata* (Mollusca: Unionidae)

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**SUMMARY**

1. Vertical and horizontal movement were studied in the freshwater bivalve *Elliptio complanata* at a sandy site in an oligotrophic lake over 3 years. Mussel movement did not vary significantly between day and night. On average, between 2 and 8% of 527 mussels moved each month during the ice-free season and the distance travelled by moving mussels averaged 0.6 cm day\(^{-1}\).
2. Mussels were endobenthic during the winter, emerged from the sandy substrate in mid-May, peaked in sediment surface abundance in July, and descended into the sediments for the winter in September–October. Vertical displacement of mussels was closely correlated with water temperature although daylength may play a role. Mussels apparently move very little beneath the sediment during the winter.
3. The number of mussels moving horizontally at any given time was linearly correlated with daylength, but the distance travelled during a sampling period was related to daylength in a non-linear fashion. Greatest horizontal displacement of epibenthic mussels was found during spring and early summer, coincident with spawning in *E. complanata*.

**Introduction**

Interest in animal locomotion derives from the important role that it plays in many fundamental ecological concepts. Competition, reproduction, growth, predator–prey interaction, succession, population genetics and social behaviour of both vertebrates and invertebrates are all linked in some way to physical movement of individuals. The importance of spatial dynamics has become more apparent in the recent literature, particularly with respect to questions of population aggregation (Downing, 1986; Roese, Risenhoover & Folse, 1991).

An understanding of ecological relationships of animal populations should include the dynamics of the spatial configurations of populations. Patterns of locomotion are important in most organisms whether they are migratory (Berthold & Terrill, 1991), sedentary (Baur & Baur, 1993) or sessile, if larvae can disperse (Hughes, 1990).

Historically, long-distance migration has attracted more attention than the important, yet neglected, locomotion of less mobile animals. Small-scale displacement can have great implications for the structure and control of populations (Greenwood & Swingland, 1983). For most species, survival is a function of locomotion, which aids in the finding of food, escaping predators, avoiding adverse environmental conditions and finding mates.

The life histories of freshwater bivalve molluscs have been studied since the early 1900s, yet their locomotion is poorly documented. Traces left in the
sand by mussels are observed frequently, but little is known about when they move, how far they move, or why they move.

Although the mechanics of displacement of freshwater mussels have been described (Trueman, 1968, 1975), investigations of the mechanisms stimulating or inhibiting displacement in nature are rare. There is some evidence that such movements are made in random directions, and that distances travelled over a year are small (Balfour & Smock, 1995). Such information is essential to an understanding of their population ecology, and to allow insight into their reproductive and recruitment dynamics (Downing et al., 1993).

Freshwater mussels of the families Margaritiferidae and Unionidae are widely distributed throughout North America (Clarke, 1973). Many species were intensely exploited for button manufacture during the early 1900s (Coker, 1921), and several species are still exploited today (Williams et al., 1993). This group represents an important component of aquatic ecosystems since it can make up as much as 90% of the benthic invertebrate biomass in lakes (Ökland, 1963; Mann, 1964; Negus, 1966). Their suspension feeding (Price & Schiebe, 1978; Libois, 1988) can modify the phytoplankton community (Matteson, 1955; Nalepa, Gardner & Malczyk, 1991) and their obligate parasitic larval stage makes them important parasites of fishes (Matteson, 1948). Despite their increasing use as biomonitoring organisms (Curry, 1978; Keller & Zam, 1991; Couillard, Campbell & Tessier, 1993), many essential aspects of their ecology remain poorly understood (Kat, 1982; Strayer & Ralley, 1993; Balfour & Smock, 1995). There is an urgent need for more information on freshwater mussels because of their precarious status, particularly because the introduction of exotic species like the Asian clam Corbicula fluminea (Leff, Burch & McArthur, 1990) and the zebra mussel Dreissena polymorpha (Herbert et al., 1991) threaten them with extirpation. More than 71% of known native freshwater mussels are listed as either threatened or endangered (Williams et al., 1993).

The purpose of this study was to quantify unionid movement, highlighting the temporal dynamics of displacement, in a natural lentic population. We studied the native freshwater mussel Elliptio complanata (Lightfoot, 1786), one of the most common lake- and stream-dwelling species in eastern North America. We focus here on the seasonal variation that might be linked to mussel locomotory behaviour.

First we sought to find whether movement was diurnal or nocturnal. We then tested the hypotheses that:
1. vertical displacement varies seasonally with light and temperature; and
2. seasonal variations in the horizontal locomotion of epibenthic mussels are correlated with variations in temperature, light or water turbulence.

Materials and methods

Field experiments were conducted in Lac de l'Achigan, situated 60 km north of Montréal, Québec, Canada. Lac de l'Achigan is a soft-water, oligotrophic lake with an annual mean total phosphorus concentration of 6.4 µg L⁻¹, and an average alkalinity of 11.5 mg CaCO₃ L⁻¹ (Lamontagne & Gauthier, 1974). The littoral zone of the north shore is composed mostly of sand beaches of low slope. Elliptio complanata is the most abundant mussel found in the lake, reaching densities of 70 ind. m⁻² in the sandy shallows of the north shore (Downing et al., 1989). Studies of mussel locomotion were performed in two phases, a short-term, high frequency study and a long-term analysis.

High frequency study

In order to determine the appropriate sampling design for a longer term study we first measured the displacement of mussels at short time intervals. We determined the amount of movement during day (08.00–17.00 h) and night (17.00–08.00 h), and the frequency and amplitude of mussel displacement. Twice daily between 22 July and 9 August, when water temperature was near its seasonal maximum, we measured the position of 157 marked individuals distributed over 5.4 m² of sandy littoral zone. The hypotheses tested in this analysis were that:
1. movement is diurnal; and
2. weekly measurement of mussel displacement would lead to little bias in estimates of actual distances travelled by freshwater mussels.

Long-term study

To determine the factors influencing locomotion on an annual scale, we measured the positions of marked
individuals over nearly 3 years. The study site was a
gently sloping 5 m × 8 m sandy surface (depth 1.5–
2 m) delimited by stakes placed to mark the corners
of forty 1 m² contiguous quadrats. Quadrat boundaries
were not marked so mussels could move freely within
the study area. A total of 781 individuals of *E. complanata*
were marked over the course of the experiment.
Since some mussels situated near the edges of the site
left the study area, some endobenthic juveniles became
epibenthic, and a few others died during the experi-
ment, we limited the sample analysed here to the 527
individuals that were marked at the very beginning
and could be followed to the end of the study.
Each individual was marked underwater using
SCUBA to minimize perturbation. Marking was per-
formed 1 week prior to the beginning of the long-term
survey. Mussels were marked by attaching numbered
plastic labels (Dymo-) to the posterior face of one
valve with underwater glue (Devcon Wet Surface
Repair Putty-) delivered with a disposable syringe.
Disturbance was minimal since animals were only
touched gently during labelling. We assessed the dis-
placement of *E. complanata* weekly during the summer
season and twice each month during spring and
autumn. No observations were made during winter
because of heavy ice cover.

On each sampling date, we recorded the relative
position of each mussel using rulers attached to stakes
delimiting the corners of the 1 m² quadrats. These
geometric data were transformed to x–y coordinates
by triangulation. The x–y position data, when compared
among weeks, allowed us to calculate the distances
travelled and the direction of each movement, as well
as the frequency of mussel displacement over the ice-
free season. Each position estimate had an imprecision
consisting of a small diamond-shaped surface which
varied slightly in size according to its position in the
quadrat. This led to an error in distance estimates.
The mean error [1/2(longest – shortest distance
between two position imprecision surfaces)], assuming
a linear measurement error of 2 cm, was 2.6 cm (SD
0.22), which represents about 24% of the length of the
longest mussel in the sample. Distance estimates less
than the error were assumed equal to zero.

The *in situ* setting, which permitted mussels to
travel freely within and among quadrats, also allowed
us to measure the proportion of marked mussels found
at the sediment surface at different times of the year.
We considered a mussel to be epibenthic if it protruded
visibly from the sediment surface, and endobenthic
when it buried itself enough to disappear completely.

Disruption of mussels during position measurement
was avoided by using an ABS- mobile support
(5.5 m × 1 m) to keep divers at a distance of 40 cm
above the sediment surface. Studies were performed
and May–July 1990. All epibenthic mussels were
removed from the surface of the study site at the end
of the study, and sediment of the site was sieved
down to 30 cm to removed all marked and unmarked
endobenthic mussels.

**Abiotic variables**

Several abiotic variables, postulated to influence mus-
sel locomotion, were estimated directly or indirectly.
Due to equipment malfunction, only seventeen *in situ*
water temperature (*T*) estimates were obtained.
Fortunately water temperature can be estimated accu-
rrately from latitude and mean depth of the lake, using
the method of Straškraba (1980). Fig. 1 shows that
these estimates accurately reflect actual temperatures.
Sunlight intensity (*Si*), wind velocity and wind orienta-
tion between each pair of visits to the field, and
daylight length (*L*), the time between sunrise and sunset,
were obtained from the nearest government meteorological station (Environnement Canada, Section de l’Environnement Atmosphérique, Ste-Agathe, Québec), situated 12 km north-west of the lake.

The effect of water turbulence ($W_t$), generated by wave action, was estimated as the horizontal acceleration of a unit of water at a specific depth. $W_t$ was calculated using the average wind speed and orientation (between 08.00 and 20.00 h) as well as the maximum fetch at the lake surface ($f$, in m) and the depth of water at the site ($d$). Estimates of $W_t$ were made using standard equations (Department of the Army Waterways Experiment Station, 1984):

$$ W_t = \frac{H \pi}{\tau} \sqrt{g/d} \quad (1) $$

where $H$ is the height of surface waves calculated:

$$ H = 0.283 \tanh \left( 0.53 \left( \frac{gD_m}{U_a^2} \right)^{0.75} \right) \tanh \left( \frac{0.00565 \left( \frac{g'}{U_a^2} \right)^{0.5}}{\tanh \left( 0.53 \left( \frac{gD_m}{U_a^2} \right)^{0.75} \right)} \right) \frac{U_a^2}{g} \quad (2) $$

$\tau$ is the wave period calculated:

$$ \tau = 7.54 \tanh \left( 0.833 \left( \frac{gD_m}{U_a^2} \right)^{0.375} \right) \tanh \left( \frac{0.0379 \left( \frac{g'}{U_a^2} \right)^{0.333}}{\tanh \left( 0.833 \left( \frac{gD_m}{U_a^2} \right)^{0.375} \right)} \right) \frac{U_a}{g} \quad (3) $$

where $U_a$ is a wind stress factor approximated as:

$$ U_a = 0.71w^{1.23} \quad (4) $$

In all of the above equations, $g$ is the acceleration due to gravity (m s$^{-2}$), $D_m$ is the mean depth of the lake, and $w$ is the wind velocity.

**Statistical analysis**

We compared the number of mussels that moved and the distances travelled by mussels during night and day using the Wilcoxon signed rank test (Snedecor & Cochran, 1980). Stepwise multiple regression analysis was used to examine the relationships between: (i) the fraction of epibenthic mussels; (ii) the fraction of epibenthic mussels moving per unit of time; and (iii) the average distance travelled by a mussel per unit of time; and water temperature, daylength, water turbulence and sunlight intensity. Polynomial regression analysis was employed when residual analyses suggested curvilinearity. Standardized independent variables ($x_{std} = x - \bar{x}$) were used in polynomial regressions to reduce the effects of multicollinearity (Neter, Wasserman & Kutner, 1990). Since significant correlation existed between some independent variables (water temperature, daylength, and its corresponding interaction term), ridge regression analysis was also used to eliminate potential bias (Marquart & Snee, 1975). All data were satisfactorily close to a normal distribution (Wilk-Shapiro normality statistic > 0.72) to avoid transformation.

**Results**

**High frequency study**

The high frequency study showed that relatively few mussels moved from week to week (Table 1). Only 38% of the 157 marked mussels moved at least once during this 18-day period and only 4% moved more than once. The mean distance travelled by individual mussels in 1 week during mid-summer was 12 cm. Because the track left in the sediment by moving mussels is not always straight, and because mussels move infrequently, we also wanted to determine possible biases that might be introduced into measures of movement by measuring positions only once per week. We estimated the actual distances travelled by summing all of the twice-daily measured distances and comparing them to the gross linear displacement of a mussel estimated as the vectorial distance travelled over the interval. A 7-day sampling interval underestimated actual locomotion by between 0 and 4 cm ($x = 0.19$ cm), thus the average error rate was about 1%. Since very few mussels moved more than once during a 1-week period, and since the average error was very
Table 1 Locomotion of *Elliptio complanata* determined in the high frequency study

<table>
<thead>
<tr>
<th></th>
<th>First 7-day period</th>
<th>Second 7-day period</th>
<th>Last 4-day period</th>
<th>Weekly average</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mussels that moved</td>
<td>38 (24%)</td>
<td>18 (11%)</td>
<td>4 (2%)</td>
<td>23.3 (14.8%)</td>
</tr>
<tr>
<td>Sum of distances moved (cm)</td>
<td>483</td>
<td>213</td>
<td>29</td>
<td>282</td>
</tr>
<tr>
<td>Average distance travelled (cm)</td>
<td>12.7</td>
<td>11.8</td>
<td>7.1</td>
<td>12.0</td>
</tr>
</tbody>
</table>

Table 2 Diel variation in locomotion of *Elliptio complanata* measured during the day (08.00-17.00 h) and at night (17.00-08.00 h). *P* is the probability of a day/night difference, estimated using the Wilcoxon signed rank test

<table>
<thead>
<tr>
<th></th>
<th>Day</th>
<th>Night</th>
<th><em>P</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>Number of mussels that moved</td>
<td>30 (19%)</td>
<td>30 (19%)</td>
<td>0.968</td>
</tr>
<tr>
<td>Sum of all distances moved (cm)</td>
<td>340</td>
<td>384</td>
<td>0.906</td>
</tr>
<tr>
<td>Longest distance travelled (cm)</td>
<td>101</td>
<td>75</td>
<td>–</td>
</tr>
<tr>
<td>Average (SD) distance travelled (cm)</td>
<td>11.3 (18.5)</td>
<td>12.8 (17.6)</td>
<td>–</td>
</tr>
</tbody>
</table>

small (0.19 cm represents less than 2% of the length of the longest mussel found), we concluded that satisfactory measurements of mussel displacement could be made on a weekly basis without introducing great error.

Over a period of 18 days during the warmest part of the year, there was no significant difference between the frequency distribution of the fraction of mussels moving during day and night (Table 2, *P* = 0.97).

**Seasonality and effects of abiotic variables**

**Vertical locomotion.** As we have shown elsewhere (Amyot & Downing, 1991), the vertical distribution of *E. complanata* varied seasonally. Mussels descended abruptly into the sediment in autumn and gradually appeared at the sediment surface during spring (Fig. 2). Measurements made only 2 days after ice-out in 1990 showed less than 24% of the marked population visible at the sediment surface. Mussels emerged rapidly from the sediment surface during the later part of May. The maximum fraction of the population observed at the sediment surface (96%) occurred at the middle to end of July. Mussels buried themselves sporadically for a few days throughout the study, so there were always some endobenthic individuals. At the end of the ice-free season, around 67% of the marked mussels had descended into the sediment again. This same vertical dynamic was repeated in all years of the study.

Mussels did not appear to move horizontally once buried in the sediment. Almost all the marked mussels reappeared the next spring at nearly the same place where they disappeared into the sediment the previous autumn. For example, on 4 May 1990, 99% (all but four) of the mussels reappeared < 10 cm from the positions at which they were found during the preceding October.

We sought cues to vertical migration by measuring the correlation between the fraction of mussels found at the surface and water temperature, light regime and other physical factors. In Lac de l’Achigan the vertical migration of mussels was correlated most strongly with water temperature. Residual analysis indicated a curvilinear positive relationship (*r*² = 0.860, *P* < 0.0001; Table 3). Water turbulence and sunlight intensity were not significantly correlated with vertical migration of *E. complanata*. Although daylength was not retained in multiple regression analyses, the early emergence of mussels from the substrate may be triggered by daylength and water temperature, since the rate of emergence from the sediments in early spring, when daylengths were longer, seemed faster than rate of submergence into sediments in autumn (Fig. 2).

**Horizontal displacement.** In spite of the long traces that can sometimes be observed in shallow waters, horizontal movement in Table 4). The proportion of the mussel population moving from one week to the next, and weekly distances travelled by moving mussels, were correlated with daylength (Table 3 and Fig. 3). Rates of movement increased rapidly after ice-out, peaking near the end of June. Following this peak, the proportion of mussels moving and the distances travelled declined steadily until ice cover the following winter. Surprisingly, the greatest locomotory activity was not synchronized with seasonal variations in

Table 3 Results of multiple regression analyses using water temperature (T), daylength (L), water turbulence (W) and sunlight intensity (S) as candidate variables: (a) fraction of mussel population found epibenthic; (b) fraction of epibenthic mussels that moved (day⁻¹); (c) average distances travelled by moving, epibenthic mussels (cm day⁻¹). Insignificant variables (P > 0.05) are not shown

<table>
<thead>
<tr>
<th>Independent variables</th>
<th>Coefficient</th>
<th>SE</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>(a) % mussels found epibenthic (r = 0.860)</td>
<td>86.538</td>
<td>1.554</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Constant</td>
<td>1.5400</td>
<td>0.223</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Tₜₚₙ</td>
<td>-0.0959</td>
<td>0.217</td>
<td>0.0001</td>
</tr>
<tr>
<td>T²</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(b) Mussels that moved (r = 0.534)</td>
<td>-0.0958</td>
<td>0.025</td>
<td>0.0005</td>
</tr>
<tr>
<td>Constant</td>
<td>0.0111</td>
<td>0.001</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>L</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(c) Average daily distances (r = 0.755)</td>
<td>1.3781</td>
<td>0.088</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Constant</td>
<td>0.5704</td>
<td>0.068</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Lₚₙ</td>
<td>0.0903</td>
<td>0.026</td>
<td>0.0015</td>
</tr>
<tr>
<td>L²</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Table 3 Results of multiple regression analyses using water temperature (T), daylength (L), water turbulence (W) and sunlight intensity (S) as candidate variables: (a) fraction of mussel population found epibenthic; (b) fraction of epibenthic mussels that moved (day⁻¹); (c) average distances travelled by moving, epibenthic mussels (cm day⁻¹). Insignificant variables (P > 0.05) are not shown

Discussion

In general, Mollusca do not present well-defined patterns of activity and rest, even in very rhythmic environments (Cloudsley-Thompson, 1961). Salánki (1961) and Imlay (1968), however, have shown rhythmicity in the mussels Anodonta cygnea and Elliptio complanata, respectively. They concluded that diel light cycles affect molluscan behaviour (Imlay, 1968), independently of temperature (Salánki, 1961).

Although freshwater bivalves are generally eyeless, photoreceptors or pigmented light-sensitive spots in this group have been known for over a century (Sharp, 1883, cited in Wilbur & Yonge, 1966). The function of these specialized cells is not well understood, but...
mussels have long been known to respond to changes in light intensity (Dubois, 1889, cited in Wilbur & Yonge, 1966). Our data suggest that, even though they may be able to sense variations in light level, this population of E. complanata does not vary its locomotory behaviour on a diel cycle. However, our finding that seasonal variations in mussel locomotion are strongly correlated with daylength suggests that freshwater mussels can sense variations in the light climate. It is possible that mussels can differentiate even between changes in light due to shadows and those occurring at sunset. Braun & Faust (1954, cited in Imlay, 1968) observed that E. complanata reacted to very slow variations in light but were insensitive to variations in light under rapidly shifting light and shadows.

Many aspects of E. complanata’s movement observed in Lac de l’Achigan are substantially similar to the findings of Balfour & Smock (1995) in a headwater stream. The seasonal vertical migration of E. complanata observed in lotic and lentic environments was clear and unambiguous. Assuming that such vertical dynamics are not unique, this may be an important source of error in epibenthic samples at certain times of the year. This bias could be serious if most young E. complanata in lakes (Amyot & Downing, 1991) and streams (Balfour & Smock, 1995) are endobenthic. Based on low population densities in littoral zone samples taken in the spring, Hanson, Mackay & Prepas (1988) suggested that freshwater mussels must migrate out of the littoral zone in autumn, winter and spring to escape low temperatures. Kat (1982) marked mussels inside quadrats on 10 May and found that there were 28% ‘new’ unmarked mussels on 10 July the following year, concluding that E. complanata migrates horizontally in lotic environments. Endobenthic vertical migrations that we observed show that epibenthic mussel densities in mid-May can average 30% less than the density determined in mid-July, due to vertical migration alone. Many of the ‘immigrants’ in Kat’s and others’ quadrats may simply have been endobenthic at the time of sampling or marking.
A fraction of the population (nearly 10% of epibenthic mussels) descended into the sediment during the first week of July and the last week of August 1989 (see arrows on Fig. 2). These are Canada’s two most significant summer holiday periods. During 1989, visitors to the lake were allowed to use personal water craft (e.g. Seadoo-, Jetski-). Several of these were observed speeding back and forth near the study site. Few personal water craft have been seen on the lake since then. Although based on a few weeks’ samples, turbulence, noise or vibrations made by these water craft may have disturbed the normal activity of E. complanata.

Seasonal burrowing may have several functions in unionid mussels. Endobenthic mussels may, for example, be less subject to predation (Negus, 1966), or may be protected against displacement by water currents during spring floods (Hinch, Kelly & Green, 1989) or by wave action during storms. Seasonal vertical migration may enhance survival during cycles in adverse conditions. Many species of freshwater bivalves are found in temporary aquatic habitats in North America (Mackie, White & Zedba, 1980). Because most freshwater mussels are obligate suspension feeders, and must be immersed to feed and survive, survival of burrowing mussels may be greater in temporary habitats. According to McKee & Mackie (1981) and Burky (1983), similar life cycle adaptations to temporary aquatic habitats are seen in other species, even when they are living in permanent water bodies. Seasonal vertical migration observed in E. complanata may simply be a relic of evolutionary adaptation to seasonally dry conditions. Similarly, in shallow waters that freeze to the bottom in winter, mussels that do not descend into the sediments may risk being frozen solid, or frozen into mobile ice cover. Winter immersion in sediments may allow mussels to live at temperatures closer to that of the groundwater, and thus provide a refuge against extremely cold winter temperatures in shallow waters. On the other hand, summer emergence from the sediments is essential if reproduction, respiration, feeding and growth are to be achieved.

Reasons for temporary burying of some mussels during mid-summer remain obscure. It is known that vibrations (Barnes, 1955) and mechanical disturbances (Imlay, 1968) can modify mussel activity. Mussels usually react by closing the valves and remaining immobile for a period of time. On the other hand, physical disturbance might increase locomotion because most disturbed mussels move during the next hour or so after disruption (J.-P. Amyot, unpublished data). E. complanata, abundant in shallow waters exposed to wave action, seems to distinguish between natural water turbulence (which does not affect activity) and a mechanical touch (Prior, 1972). Allen (1923) indicated that mussels seem to avoid areas in which currents are reduced by rooted plants, and live instead where water movement can supply organic debris. Water turbulence may therefore stimulate normal feeding activity without negatively influencing locomotion. Further studies are needed to shed light on mussel perception of environmental disruptions, and their consequences for the behaviour of mussel populations, especially under anthropogenic stimuli such as intensive boating or bathing activities.

Although mussel locomotion is slow, its strong seasonal variation and association with physical cues suggests that locomotory behaviour is an essential component of their life history strategies. Given the precarious state of mussel populations and species in North America, care should be taken not to impede the deliberate spatial dynamics of this fragile fauna.

Acknowledgments

We are grateful to D. Breton, H. Harvey, V. Lapointe, J.-L. Lantanot, G. Roberge, C. Ménard, J. Shostak, B. Mousseau and S. Forget for field work. Special thanks go to S. Lalonde. This is a publication of the Groupe d’Ecologie des Eaux Douces, Université de Montréal. Financial support for this research was provided by the Natural Science and Engineering Research Council of Canada, a team grant from the Ministère de l’Education du Québec (FCAR) and graduate scholarships from FCAR and NSERC to J.P.A., and the College of Agriculture of Iowa State University. We also thank the staff of the Station de Biologie des Laurentides of l’Université de Montréal for their support, and the Department of Animal Ecology at Iowa State University for use of facilities during analysis.

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© 1997 Blackwell Science Ltd, Freshwater Biology, 37, 345–354
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(Manuscript accepted 7 October 1996)