

Unionid growth patterns in rivers of differing riparian vegetation

TODD J. MORRIS AND LYNDA D. CORKUM

Department of Biological Sciences, University of Windsor, Windsor, Ontario, Canada N9B 3P4

SUMMARY

1. Growth rates were examined as potential controlling agents of unionid distributions.
2. Analyses of long-term growth in unionid shells revealed two distinct patterns. Species which dominate rivers with forested riparian vegetation (e.g. *Elliptio dilatata*) show slow growth throughout life, whereas species which dominate grassy rivers (e.g. *Pyganodon grandis*) show rapid growth during early life and achieve a smaller maximum size at a younger age.
3. *Pyganodon grandis*, which occurs in both river types but is much more abundant in grassy habitats, demonstrates a single growth pattern in both basin types. In contrast, *Lasmigona complanata* (Barnes, 1823), which occurs equally in both basin types, demonstrates two growth patterns which differ depending upon which river is inhabited. In forested rivers, *L. complanata* grow slow and steady, whereas in grassy rivers, these unionids grow faster and achieve maximum size earlier.
4. Short-term transplant studies of *P. grandis* and *E. dilatata* confirmed this pattern of growth for specialist species.

Keywords: unionid growth patterns, riparian vegetation

Introduction

We have previously shown that unionid distributions differ on the basis of riparian vegetation (grassy or forested) within the drainage and that these distributions can be predicted on the basis of these associations (Morris & Corkum, 1996). Rivers with forested riparian zones possess mussel assemblages dominated by Lampsilines and Amblemines [e.g. *Lampsilis siliquoidea* (Barnes, 1823) and *Elliptio dilatata* (Rafinesque, 1820)], whereas an Anodontine assemblage [e.g. *Pyganodon grandis* (Say, 1829)] characterizes rivers with smaller, grass-dominated riparian zones. In addition to these differences in unionid assemblages, these habitats differ in terms of temperature and other environmental factors. Sites with narrow, grassy riparian zones show elevated daily tempera-

ture fluctuations and possess higher concentrations of ammonia nitrogen and total kjeldahl nitrogen (TKN) in comparison with sites with wider, forested riparian zones.

Temperature and growth relationships have been linked to changes in the overall size and differences in growth rates of freshwater mussels (see Tevesz & Carter, 1980). Temperature affects growth and the duration of the growing season (Negus, 1966), as well as having indirect effects on unionid growth rates through water depth (Hanson *et al.*, 1988).

The potential for an energy-intensive process such as growth to be important in determining these distributions was investigated in this study. Differences in riparian vegetation result in nutrient enrichment in receiving waters (Corkum, 1996; Morris & Corkum, 1996). These nutrient differences along with the thermal patterns outlined above should result in different patterns of unionid growth in rivers with different riparian characteristics. Thus, we predicted that faster-growing species would characterize the disturbed open grassy habitats, whereas slower-growing species would be more prevalent in the less

Correspondence and present address: Todd J. Morris, Department of Biology, University of Toronto at Mississauga, Ontario, Canada L5L 1C6.
E-mail: tmorris@credit.erin.utoronto.ca

productive forested habitats. Long-term growth rates throughout the life-span were investigated using the shell growth rings of mussels from three grassy and three forested drainage basins. The plasticity of short-term growth rates of species, which have been shown to characterize grassy and forested basins (Morris & Corkum, 1996), was examined in a reciprocal transplant experiment.

Materials and methods

Long-term growth rates

Since freshwater mussels are extremely long lived, with species common to south-western Ontario, Canada, reaching ages in excess of 25 years, long-term growth characteristics may be important in structuring community composition. To investigate this possibility, long-term growth rates were estimated using external growth markings (McCuaig & Green, 1983). This method allows the construction of growth curves for species based on historical growth over the entire life-span of individuals. Initially, long-term growth rates based on a collection of all species present at each site were determined followed by estimates of individual growth for (1) species which had significantly different occurrence rates in grassy and forested riparian zones (habitat specialists), and (2) one species which did not differ in occurrence according to riparian type (habitat generalist).

Specimen collection

Initial long-term (8–10 years) growth estimates were calculated on the basis of voucher specimens collected from all rivers during 1993 (Di Maio, 1995) and 1994 (Morris & Corkum, 1996) (Fig. 1). Because of limited sample sizes for some species, additional searches were conducted on 27 July 1995 for *P. grandis* (Ausable site 3), *Lasnigona complanata* (Barnes 1823) (Dingman site 2 and McGregor site 3), and *E. dilatata* (Ausable site 3). Also, because *P. grandis* individuals in forested habitats were much smaller than those available from grassy habitats, a special collection of *P. grandis* individuals from grassy sites (Avon River, Whirl Creek) was conducted on 28 July 1995 to supply individuals of the same size for analysis. This was done to eliminate possible confounding effects of size differences during the analysis.

For the comparison of growth rates for all species in grassy (eleven species) and forested (thirteen species) rivers, forty-eight individuals from grassy rivers and sixty-two individuals from forested rivers were used. Two hundred individuals each of *P. grandis* (grassy specialist) and *E. dilatata* (forested specialist) were used to compare growth of these species in their preferred habitats. For the comparison of the specialist species, *P. grandis*, in both grassy and forested rivers, twenty forested specimens and twenty grassy specimens were used. Eighty-five individual *L. complanata* (forty-five from forested rivers and forty from grassy rivers) were used for the comparisons of this generalist species. *Pyganodon grandis* is considered a grassy specialist because 98% of all individuals found in an earlier study (Morris & Corkum, 1996) came from grassy rivers and *E. dilatata* is considered a forested specialist because 100% of individuals from the same study were found in forested rivers. In contrast, *L. complanata* is considered a generalist because 35% of individuals were found in grassy rivers and 65% were found in forested rivers (Morris & Corkum, 1996). Individual mussels were used for only one study and no individuals were included in more than one comparison.

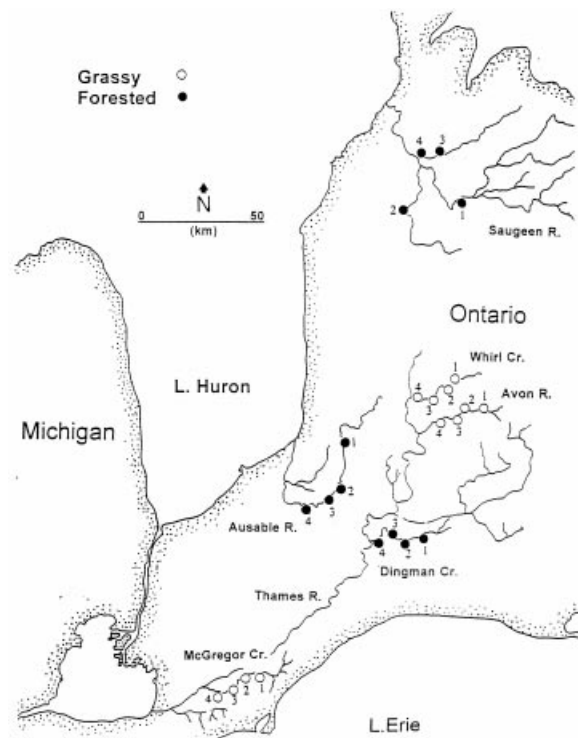


Fig. 1 Location of study sites.

Growth rate determination

Following the methods of McCuaig & Green (1983), maximum lengths at successive growth rests were determined for each specimen. Only specimens with clearly visible growth rests were used. Individuals produced between one and four pairs of consecutive growth rings. Although the annularity of growth rings has been brought into question recently (Neves & Moyer, 1988; Downing *et al.*, 1992), the technique used in the present study does not require that the rings be produced on an annual basis, rather, only that the rings be produced at regular intervals. Given the seasonal changes which occur within the area and the fact that all study rivers routinely freeze during winter months, it is likely that growth cycles are consistent across rivers. However, the 'Discussion' will refer to growth seasons and not to years directly.

Statistical testing

Unionid growth is known to follow a pattern described by the von Bertalanffy growth curve (Walford, 1946; McCuaig & Green, 1983; Hinch *et al.*, 1986). The von Bertalanffy equation:

$$L_t = L_x(1 - e^{-kt}) \quad (1)$$

predicts that size at any interval (L_t) is dependent upon the instantaneous growth rate (k), the time interval (t) and the species specific maximum size asymptote (L_x). The values required for this equation can be determined graphically through a plot of length at one interval versus length at the next consecutive interval (a Walford plot) (Walford, 1946). Unionid growth has been shown to be characterized by a linear Walford plot (Hinch *et al.*, 1986) and simple linear regression produces all the values required to calculate the von Bertalanffy growth curve using the following relations:

$$L_x = a / (1 - b) \quad (2)$$

$$k = -\ln b \quad (3)$$

where 'a' represents the intercept of the Walford plot and 'b' is the slope. Walford plot regressions were

compared using an analysis of covariance (ancova) (Sokal & Rohlf, 1995).

Short-term growth

An examination of the plasticity of growth rates was conducted using a reciprocal transplant experiment. Growth was examined by direct measurement of changes in size of individuals over the course of one growing season.

Specimen collection

The two species selected for this comparison represent the species with the most highly significant differences in relative abundances in the two riparian habitats in an earlier study (Morris & Corkum, 1996). Each species occurs in both habitats, but at much higher rates in one habitat type. *Elliptio dilatata* was selected as the representative forested species and *P. grandis* was chosen to represent grassy species.

Two hundred individuals of each species were collected on 15–16 May 1995 from two sites. *Pygandon grandis* individuals were collected from Whirl Creek site 2 (grassy) and *E. dilatata* specimens were obtained from Saugeen River site 3 (forested). All specimens were returned to the laboratory in aerated river water for processing.

For each individual, three measurements were recorded: length, width and height. Each dimension was determined using digital calipers and recorded to the nearest 0.01 mm. After the measurements were taken, each individual had a sequential number inscribed on the umbo region of both the left and right valves using a Dremel tool (Dremel, Racine, WI). Care was taken to ensure that only the periostracum was removed and that the integrity of the shell was not compromised during the marking procedure.

Experimental design

Six sites were used for the transplant study with one site in each of six rivers. Three forested rivers (Saugeen River, Ausable River and Dingman Creek) and three grassy rivers were used (Avon River, Whirl Creek and McGregor Creek) (Fig. 1). Within the two rivers which acted as sources for the experimental animals (i.e. Saugeen River and Whirl Creek), the transplant sites were chosen to correspond to the sites

from which the animals were collected. In the remaining four rivers, the furthest downstream sites were selected since these sites had the greatest amount of suitable habitat and the least likelihood of drying out during the late summer low-flow periods.

At each site, three, 1-m² quadrats were anchored to the substrate. The quadrats consisted of cement-filled #6 PVC piping (Imperial Pipe Corporation, Toronto, ON) anchored using galvanized rebars. The quadrat design was modified from Waller *et al.* (1993). Ten individuals of each species were randomly assigned to each quadrat and positioned inside the quadrat with the anterior end buried. The resulting density of 20 unionids m⁻² is within the natural range encountered for this area (T. J. Morris, personal observation).

All experimental quadrats were established on 24–25 May 1995 and remained in place until 6–7 September 1995 for a total duration of 105 days. This time-frame corresponds to both the 16-week duration used by Hinch *et al.* (1986) for a transplant of unionids in Lake Erie and calendar dates of maximum growth of unionids reported by McMahon (1991). Upon completion of the study, the experimental quadrats were manually raked for marked individuals and the area from 5 m upstream to 5 m downstream of the quadrats was also visually searched. All live and dead individuals were collected and returned to the laboratory where the initial measurements were repeated on live individuals to determine change in size over the experimental period.

Statistical analyses

Differences in final sizes were tested using an ancova. Because the growth rates of unionids have been shown to be dependent upon individual size (Hinch *et al.*, 1986) and because all individuals were not the same size at the initiation of the experiment, it was necessary to control for this factor. An ANCOVA using initial size as the covariate allows for this control without the use of potentially confounding variables.

Results

Long-term growth rates

Whole assemblage estimates

Using the voucher specimens obtained during the

initial survey work (Morris & Corkum, 1996) and a selection of voucher specimens from an earlier study by Di Maio (1995), long-term growth patterns were estimated for the entire assemblage of species occurring in rivers with forested and grassy riparian vegetation. A Walford plot based on these vouchers is presented in Fig. 2a. A test of common slope conducted on the regression equations presented in Fig. 2a revealed that the two lines did not differ significantly ($F_{1,358} = 0.984$, $P > 0.05$) and the lines were assumed to possess a common slope. An ANCOVA was then used to test for the significance of basin type (grassy or forested) as a predictor of size in the second interval (L_{x+1}) using size in the first interval (L_x) as a covariate. An ANCOVA showed that the lines possess significantly different intercepts (Table 1), indicating that riparian type was a significant predictor of length (Table 1). The significant difference of these two regression lines (Fig. 2a)

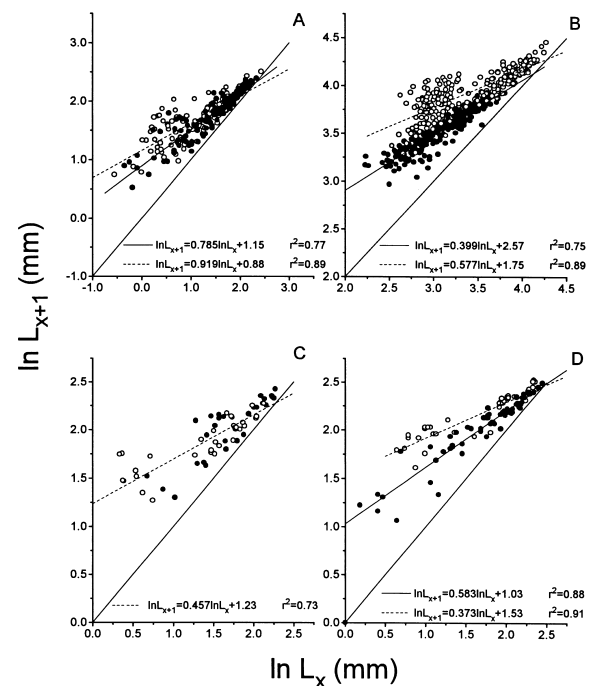


Fig. 2 Walford plots obtained from the long-term growth study of: (a) grassy and forested mussel assemblages; (b) two habitat specialists in their preferred habitats, *Pyganodon grandis* in grassy rivers and *Elliptio dilatata* in forested rivers; (c) one habitat specialist, *P. grandis*, in both river types; and (d) one habitat generalist, *Lasmigona complanata*, in both river types. The open circles and dashed lines represent specimens collected from grassy rivers, whereas closed circles and solid lines represent specimens from forested rivers.

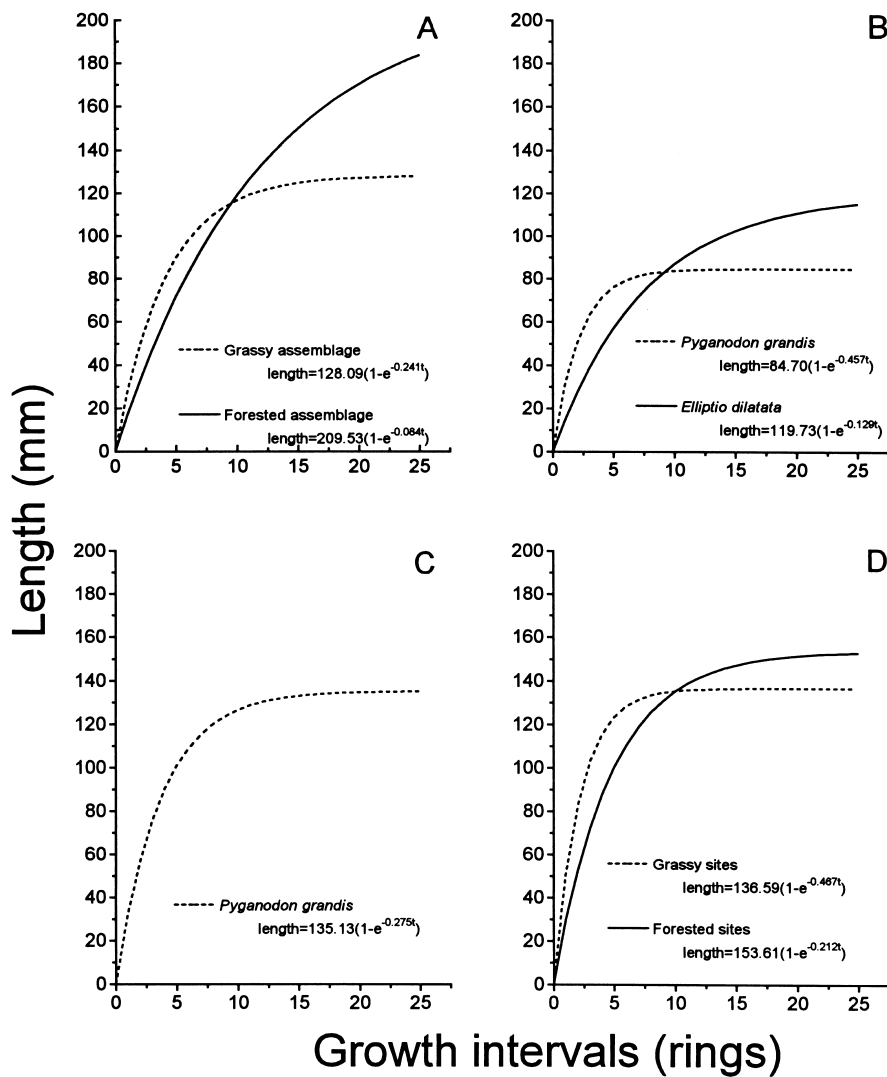


Fig. 3 Theoretical von Bertalanffy growth curves for: (a) grassy and forested assemblages; (b) two habitat specialists in their preferred habitats, *Pyganodon grandis* in grassy rivers and *Elliptio dilatata* in forested rivers; (c) one habitat specialist, *P. grandis*, in both river types; and (d) one habitat generalist, *Lasmigona complanata*, in both river types. The dashed lines represent growth in grassy rivers and solid lines represent growth in forested rivers.

indicates that the unionid communities in rivers flowing through different riparian types exhibit different long-term growth patterns. These growth patterns reveal that mussels of grassy communities show an initially rapid growth during the early growth stages, but level off earlier than forested species and reach smaller maximum sizes (Fig. 3a).

Specialist species

The long-term growth patterns of the two most important species for distinguishing between grassy

and forested communities, *P. grandis* and *E. dilatata*, respectively, were determined (Fig. 2b). A test for common slopes was conducted for these two species and showed that the two lines presented do possess significantly different slopes ($F_{1,506} = 18.53$, $P < 0.001$), indicating two distinct growth patterns (Figs 2b & 3b).

Pyganodon grandis is one of the most common and widespread species within Ontario, and as such, provides a unique opportunity to examine an important discriminating species in the habitat where it is most abundant (grassy), and a habitat where it is present but much less abundant (forested).

Table 1 Analysis of covariance (ANCOVA) for whole-community estimates of long-term growth patterns in grassy and forested habitats using length at the first interval (l_x) as the covariate

Source	d.f.	SS	MS	F-value	P-value
Covariate	1	1292.87	1292.87	1963.80	<0.001
Basin type	1	21.21	21.21	32.22	<0.001
Error	362	238.32	0.66		
Total	364	1538.53			

Fig. 2c shows the results of the Walford plot for *P. grandis* from naturally occurring populations in grassy and forested habitats. The test for common slope revealed a lack of significance ($F_{1,58} = 0.829$, $P > 0.05$), indicating a common slope for both populations. An ANCOVA for common intercepts also showed a non-significant result (Table 2), indicating that the lines do not differ significantly and that only one growth pattern is evident regardless of habitat.

Generalist species

Species which occur in both habitats (grassy and forested) without preference for one habitat or the other (e.g. *L. complanata*) are considered habitat generalists. The Walford plot for two populations of *L. complanata*, one from forested sites and one from grassy sites, is presented in Fig. 2d. The test of slopes for these two regression lines indicated no significant difference between grassy and forested populations ($F_{1,98} = 0.463$, $P > 0.05$). However, ANCOVA showed a significant effect of basin type (Table 3), indicating different intercepts, and therefore, differential growth during the first year in these two habitats.

Short-term growth: reciprocal transplant

Recovery rates

Site-specific recovery of marked specimens ranged

Table 2 Analysis of covariance (ANCOVA) test for common slopes of Walford plots for *Pyganodon grandis* in grassy and forested basins. Length at the first interval was used as the covariate

Source	d.f.	SS	MS	F-value	P-value
Covariate	1	177.868	177.868	220.58	<0.001
Riparian type	1	0.027	0.027	0.03	0.856
Error	61	49.187	0.806		
Total	63	243.840			

Table 3 Analysis of covariance (ANCOVA) test for common slopes of Walford plots for *Lasmigona complanata* in grassy and forested habitats. The covariate was the length at the first interval (l_x)

Source	d.f.	SS	MS	F-value	P-value
Covariate	1	404.13	404.13	787.67	<0.001
Riparian type	1	26.69	26.69	52.03	<0.001
Error	101	51.82	0.51		
Total	103	492.27			

from 50% to 90%. Individual species showed significantly different recovery rates with recovery of *E. dilatata* (77.1%), being significantly higher than recovery of *P. grandis* (56.5%) (Table 4). Recovery rates did not differ according to basin type (grassy or forested), into which the individuals were placed nor was the interaction between species and basin type significant (Table 4). There is a non-significant trend towards higher recovery from sites in the source basin type, with recovery of *E. dilatata* being highest from forested sites and recovery of *P. grandis* showing highest values in the grassy basins (Fig. 4). The quadrat design used for the transplant study required that individual mussels were not physically restrained from leaving the quadrats. As a result of this design, the fate of unrecovered mussels can not be positively confirmed, and unrecovered mussels may have died of natural causes, been preyed upon or migrated out of the search area.

Growth analysis

The change in length over the duration of the transplant was tested using ANCOVA, and showed a significant effect of species and river as well as an interaction between the two, but no significant differences on the basis of basin type (Table 5). The results for final mussel width (Table 6) and height (Table 7) showed identical patterns of significance.

Table 4 Analysis of variance (ANOVA) for recovery of unionids after the reciprocal transplant study

Source	d.f.	SS	MS	F-value	P-value
Transplant basin	1	2.1	2.1	0.01	0.919
Species	1	1260.8	1260.8	6.66	0.033
Basin * species	1	330.7	330.7	1.75	0.223
Error	8	1515.3	189.4		
Total	11	3108.9			

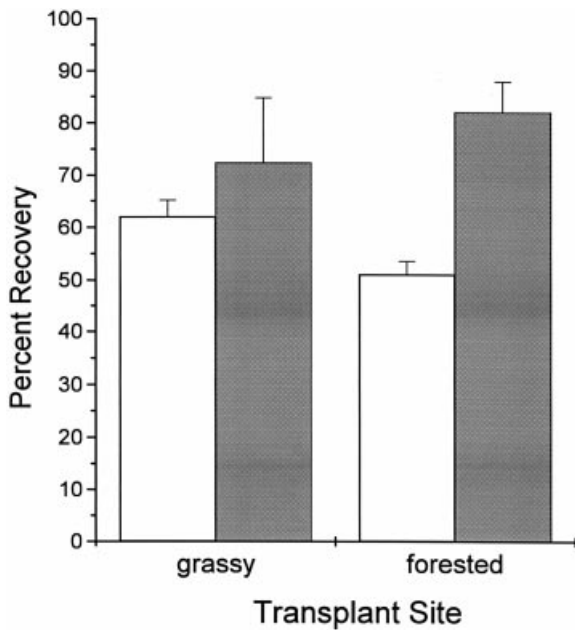


Fig. 4 Mean (\pm SE) percentage of marked mussels recovered from short-term (105 days) transplantation sites. The open bars represent *Pyganodon grandis*, a grassy specialist, and the shaded bars represent *Elliptio dilatata*, a forested specialist.

Discussion

The main purpose of this study was to examine growth patterns of unionids in rivers with differing riparian habitats and to determine if growth patterns varied in a predictable manner with respect to the riparian vegetation. The results of the long-term growth study provide clear evidence that growth patterns vary in a consistent manner in relation to these vegetational differences. At a very coarse scale, whole assemblage growth parameters follow distinct patterns, while at a much finer scale, single species show similar patterns. The unionid species which

Table 5 Analysis of covariance (ANCOVA) for final length after the reciprocal transplant experiment. The initial length prior to transplant was used as the covariate

Source	d.f.	SS	MS	F-value	P-value
Covariate	1	11 652.0	11 652.0	825.58	<0.001
Species	1	198.3	198.3	14.05	<0.001
Transplant basin	1	7.8	7.8	0.56	0.457
River	5	525.8	105.2	7.45	<0.001
Species * river	5	1321.8	264.3	18.73	<0.001
Error	209	2949.8	14.1		
Total	222	17 076.7			

Table 6 Analysis of covariance (ANCOVA) for final width after transplantation. Width of mussels before transplantation was used as the covariate

Source	d.f.	SS	MS	F-value	P-value
Covariate	1	833.37	833.37	114.48	<0.001
Species	1	358.18	358.18	49.20	<0.001
Basin	1	8.41	8.41	1.15	0.284
River	5	155.16	31.03	4.26	0.001
Species * river	5	147.56	29.51	4.05	0.002
Error	209	1521.48	7.28		
Total	222	3481.39			

characterize forested riparian habitats have initially slow growth rates during early life stages, but will continue to grow for longer durations than the species which characterize grassy habitats. Although species common to grassy habitats (e.g. *P. grandis*) demonstrate faster growth early in life, these animals reach a maximum size at a younger age (\approx 7 years) and ultimately achieve smaller maximum sizes than their forested counterparts.

Examinations of growth patterns of species which inhabit both forested and grassy habitats, either equally (*L. complanata*) or with preference for one type (*P. grandis*), provide evidence for a potential mechanism structuring distributions. *Lasmigona complanata* is a moderately common species within the study area, but demonstrates no preference for either forested or grassy habitats. The growth pattern exhibited by this generalist species does not fit into either category. Rather, the pattern shifts depending upon which habitat an individual occupies. In forested habitats, growth is slow and steady throughout life, whereas in grassy habitats, growth is rapid early on with a smaller maximum size achieved earlier. In contrast to the generalist pattern demonstrated by *L. complanata*, *P. grandis* is a specialist

Table 7 Analysis of covariance (ANCOVA) for final height after transplantation. Height prior to transplantation was used as the covariate

Source	d.f.	SS	MS	F-value	P-value
Covariate	1	3089.85	3089.85	1222.99	<0.001
Species	1	221.34	221.34	87.61	<0.001
Basin	1	0.88	0.88	0.35	0.555
River	5	194.96	38.99	15.43	<0.001
Species * river	5	263.97	52.79	20.90	<0.001
Error	209	528.03	2.53		
Total	222	4540.12			

species which, although found in both grassy and forested rivers, shows a distinct preference for grassy habitats. *Pyganodon grandis* appears unable to alter its growth pattern in response to differences in riparian vegetation. Whether an individual is found in a grassy or forested habitat, growth is rapid at a young age and the maximum size is achieved quickly.

For the purposes of this study, we have considered the external growth bands to be produced at regular intervals across the study area and consider this to be likely given the close geo-graphic proximity of the experimental sites and the highly seasonal environment. However, if ring production is not occurring at identical rates in both habitats, we feel that it is likely that pseudoannuli production will occur in grassy habitats since these rivers are exposed to greater environmental fluctuations (Morris & Corkum, 1996). More frequent ring production in grassy habitats will result in the present growth estimates being conservative, and the true differences between mussels in forested and grassy rivers being greater than estimated in this study.

The transplant study of two specialist species, *P. grandis* and *E. dilatata*, confirmed these findings with the amount of growth dependent upon the species, but not on the riparian type of the transplant basin. Whether this plasticity in growth response is present at the individual level or whether it is a result of variation within an assemblage is not clear from the present study, and deserves further work.

The benefits of the rapid growth pattern demonstrated by grassy species are essentially two-fold. Rapid growth allows an individual to proceed quickly through the juvenile stages and to achieve substantial size quickly. The importance of attaining a large size relatively quickly may be the result of physical and hydrological characteristics of rivers which fall into the grassy category. The removal of stream side vegetation, and the presence of agricultural lands close to the stream or river channel can result in increased average and peak flows, and can severely disrupt the hydrology of the drainage basin (Likens *et al.*, 1970; Hornbeck, 1973; Hornbeck, 1975). In a recent examination of unionid distributions within southern Ontario, Di Maio & Corkum (1995) showed that species distributions can be related to the hydrology of the drainage basin. The increased flows associated with the absence of riparian vegetation would be expected to cause a lack of sediment

stability and increased shear forces on unionids leading to increased dislodgement (Vannote & Minshall, 1982). Obtaining a large size quickly may allow these species to overcome these potentially destructive hydrologic forces. Di Maio & Corkum (1995) demonstrated that mussel assemblages in hydrologically unstable rivers in southern Ontario were characterized by larger individuals and Tucker (1996) showed that Mississippi River mussels dislodged by the 1993 flood were smaller specimens than those which were not dislodged.

Unionid species which make up the grassy assemblage tend to be members of the Anodontinae (Morris & Corkum, 1996). This major sub-family within the unionidae is characterized by extremely thin shells (Clarke, 1981) which may enable rapid growth along the three major axes as the amount of shell material laid down is minimal, but it also makes these species more susceptible to predation (Headlee, 1906). Earlier maturation may have evolved in these species as a means of minimizing predation risks since it has been shown that muskrat predation on unionids is related to both mussel size and growth rate, with preference shown for mussels of a medium size (Jokela & Mutikainen, 1995). Small mussels remain buried in the sediment and are isolated from predators, while the larger specimens are resistant to predation because of their size (Jokela & Mutikainen, 1995). Rapid growth is also effective at reducing the time before reproduction with typical Anodontines undergoing first reproduction at about 4–6 years of age (Heard, 1975).

The thermal and chemical characteristics of grassy sites (i.e. increased light penetration, elevated temperatures, greater temperature fluctuations and higher nutrient levels; Morris & Corkum, 1996) favour increased food availability for filtering organisms such as unionids, thereby enhancing the potential for growth in a manner similar to that reported by Agrell (1949). In an earlier study (Morris & Corkum, 1996), we showed that rivers with grassy vegetation have NH₃-N levels nearly twenty times those in rivers with forested vegetation and NO₂-N levels nearly an order of magnitude higher. In addition, metabolic processes such as growth in poikilotherms are temperature dependent (Negus, 1966; Beukema *et al.*, 1985), and therefore, the temperature differences reported for these sites would serve to enhance these processes and enable these growth differences to occur.

In summary, differences exist in the growth patterns expressed by species inhabiting rivers with grassy and forested riparian zones. These differences may be related to pressures placed on individuals by varying hydrological and predatory pressures existing in the two habitats. The rapid achievement of maximum size within grassy habitats may be an evolved response to the demands of a hydrologically unstable environment or to increased predation of the thin-shelled species which characterize these habitats. The particular physical and chemical conditions which characterize these habitats allow for the observed growth differences to occur and may be important structuring elements in determining unionid distribution patterns.

Acknowledgments

We are grateful for the field assistance provided by M. Dobrin, C. Hayes, C. Lonnee and W. Ray. Funding was supplied by a Natural Sciences and Engineering Research Council of Canada operating grant and an Ontario Ministry of the Environment and Energy Environmental Youth Corps grant to L.D.C. We acknowledge and appreciate the helpful comments of M. Chase, three anonymous reviewers and the ecology discussion group at the University of Toronto.

References

- Agrell I. (1949) The shell morphology of some Swedish Unionids as affected by ecological conditions. *Arkiv for Zoologi*, **41A**, 6–30.
- Beukema J.J., Knol E. & Cadée G.C. (1985) Effects of temperature on the length of the annual growing season in the tellinid bivalve *Macoma balthica* (L.) living on the tidal flats of the Dutch Wadden Sea. *Journal of Experimental Marine Biology and Ecology*, **90**, 129–144.
- Clarke A.H. (1981) *The Freshwater Molluscs of Canada*. National Museums of Canada, Ottawa.
- Corkum L.D. (1996) Responses to chlorophyll *a*, organic matter and macroinvertebrates to nutrient additions in rivers flowing through agricultural and forested land. *Archiv für Hydrobiologie*, **136**, 391–411.
- Di Maio J. (1995) *The influence of hydrological variability on the spatial distribution and orientation of freshwater mussels (Bivalvia: Unionidae)*. M.Sc. Thesis, University of Windsor, Windsor.
- Di Maio J. & Corkum L.D. (1995) Relationship between the spatial distribution of freshwater mussels (Bivalvia: Unionidae) and the hydrological variability of rivers. *Canadian Journal of Zoology*, **73**, 663–671.
- Downing W.L., Shostell J. & Downing J.A. (1992) Non-annual external annuli in the freshwater mussels *Anodonta grandis grandis* and *Lampsilis radiata siliquoides*. *Freshwater Biology*, **28**, 309–317.
- Hanson J.M., Mackay W.C. & Prepas E.E. (1988) The effect of water depth and density on the growth of a unionid clam. *Freshwater Biology*, **19**, 345–355.
- Headlee T.J. (1906) Ecological notes on the mussels of Winona, Pike and Center lakes of Kosciusko County, Indiana. *Biological Bulletin*, **11**, 305–318.
- Heard W.H. (1975) Sexuality and other aspects of reproduction in *Anodonta* (Pelecypoda: Unionidae). *Malacologia*, **31**, 259–295.
- Hinch S.G., Bailey R.C. & Green R.H. (1986) Growth of *Lampsilis radiata* (Bivalvia: Unionidae) in sand and mud: a reciprocal transplant experiment. *Canadian Journal of Fisheries and Aquatic Sciences*, **43**, 548–552.
- Hornbeck J.W. (1973) Storm flow from hardwood-forested and cleared watersheds in New Hampshire. *Water Resources Research*, **9**, 346–354.
- Hornbeck J.W. (1975) Streamflow response to forest cutting and revegetation. *Water Resources Bulletin*, **11**, 1257–1260.
- Jokela J. & Mutikainen P. (1995) Effect of size-dependent muskrat (*Ondatra zibethica*) predation on the spatial distribution of a freshwater clam, *Anodonta piscinalis* Nilsson (Unionidae, Bivalvia). *Canadian Journal of Zoology*, **73**, 1085–1094.
- Likens G.E., Bormann F.H., Johnson N.M., Fisher D.W. & Pierce R.S. (1970) Effects of forest cutting and herbicide treatment on nutrient budgets in the Hubbard Brook Watershed Ecosystem. *Ecological Monographs*, **40**, 23–47.
- McCuaig J.M. & Green R.H. (1983) Unionid growth curves derived from annual rings: a baseline model for Long Point Bay, Lake Erie. *Canadian Journal of Fisheries and Aquatic Sciences*, **40**, 436–442.
- McMahon R.F. (1991) Mollusca: Bivalvia. *Ecology and Classification of North American Freshwater Invertebrates* (eds J. H. Thorp and A. P. Covich), pp. 315–390. Academic Press, New York, NY.
- Morris T.J. & Corkum L.D. (1996) Assemblage structure of freshwater mussels (Bivalvia: Unionidae) in rivers with grassy and forested riparian zones. *Journal of the North American Benthological Society*, **15**, 576–586.
- Negus C. (1966) A quantitative study of growth and production of unionid mussels in the river Thames at Reading. *Animal Ecology*, **35**, 513–532.
- Neves R.J. & Moyer S.N. (1988) Evaluation of techniques for age determination of freshwater mussels (Unionidae). *American Malacological Bulletin*, **6**, 179–188.

- Sokal R.R. & Rohlf F.J. (1995) *The Principles and Practice of Statistics in Biological Research*. W. H. Freeman, New York, NY.
- Tevesz M.J.S. & Carter J.G. (1980) Environmental relationships of shell form and structure of Unionacean bivalves. *Skeletal Growth of Aquatic Organisms. Biological Records of Environmental Change*. (eds D. C. Rhoads and R. A. Lutz), pp. 295–322. Plenum Press, New York, NY.
- Tucker J.K. (1996) Post-flood strandings of Unionid mussels. *Journal of Freshwater Ecology*, **11**, 433–438.
- Vannote R.L. & Minshall G.W. (1982) Fluvial process and local lithology controlling abundance, structure, and composition of mussel beds. *Proceedings of the Natural Academy of Sciences*, **79**, 4103–4107.
- Walford L.A. (1946) A new graphic method for describing the growth of animals. *Biological Bulletin*, **90**, 141–147.
- Waller D.L., Rach J.J., Cope W.G. & Luoma J.A. (1993) A sampling method for conducting relocation studies with freshwater mussels. *Journal of Freshwater Ecology*, **8**, 397–400.

(Manuscript accepted 20 January 1999)