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Landscape Influences on the Distribution and Growth of Freshwater Mussels
(Bivalvia: Unionidae) in Southern Ontario

by

Todd J. Morris

A Thesis Submitted to the
Faculty of Graduate Studies and Research
Through the Department of Biological Sciences
in Partial Fulfilment of the Requirements for the Degree
of Master of Science at the
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Abstract

This study was designed to examine distributions of freshwater mussels in relation to riparian vegetation within the drainage basin. Six rivers were examined within southern Ontario with four sites established within each river for a total of 24 study sites. Three rivers were chosen with grassy riparian zones (Avon R., McGregor Cr., Whirl Cr.) and three rivers were selected with forested riparian zones (Ausable R., Dingman Cr., Saugeen R.).

In total, 17 unionid species were found within the study area. Grassy rivers with narrow, grass-dominated riparian zones were characterised by *Pyganodon grandis* and *Strophitus undulatus* whereas forested rivers with wider riparian zones were characterised by *Elliptio dilatata, Lampsis radiata, Lampsis cardium* and *Fusconaia flava*. Basin types did not differ in mean species numbers, however, a shift towards dominance by a single species was found in grassy rivers with over 60% of individuals in these rivers being *P. grandis*. Physical and chemical differences exist between the riparian classes with grassy basins receiving greater amounts of solar radiation, having greater daily temperature fluctuations and higher concentrations of ammonia and TKN than forested basins.

Unionid distribution patterns were modelled using Multiple Discriminant Analysis to determine if species distributions could be predicted on the basis of physical features of the riparian zone. Discriminant analysis on the basis of mussels species abundances confirmed *a priori* classification in 100% of cases whereas classification on
the basis of physical riparian characteristics confirmed 85% of classifications. The discriminant model was tested using an additional 16 sites that were not used during the initial development of the model. Unionid assemblages at 75% of sites used to test the model were correctly predicted on the basis of the physical structure of the riparian zone. In total, 80% of the 40 sites used were correctly classified using the model indicating that landscape characteristics can be used to predict and describe unionid distributions.

Growth rates were examined as potential controlling agents of unionid distributions. Analyses of long term growth patterns on the basis of regular growth rests in the unionid shell revealed two distinct growth patterns. Species which characterize forested rivers (e.g., *Elliptio dilatata*) show slow growth throughout the life whereas species which characterize grassy rivers (e.g., *Pyganodon grandis*) show rapid growth during early life and achieve a smaller maximum size at a younger age. Specialist species such as *P. grandis*, which occur in both river types but show a preference for either grassy or forested rivers, demonstrate a single growth pattern in both basin types. In contrast, generalist species such as *Lasmigona complanata*, which occur in both basin types without preference for either type, demonstrate two growth patterns which differ depending upon which river is inhabited. In forested rivers *L. complanata* grow slowly and steadily whereas in grassy rivers they grow faster and achieve maximum size earlier. Short term transplant studies of *P. grandis* and *E. dilatata* confirmed this pattern of growth for specialist species.
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Introduction

Freshwater mussels are among the most threatened taxonomic groups in North America. The previously rich unionid populations of the Great Lakes Basin have undergone serious declines during the latter half of the last century. Much of this decline, both in species numbers and densities, has been related to the actions of humans. Species have undergone direct declines as a result of commercial harvest and more commonly indirect declines resulting from the destruction of aquatic habitat. Alterations of river channels and disruption of regular flow regimes through damming, dredging and channelisation of river systems have been extremely detrimental to these sessile organisms. Diminishing water quality through inputs of fertilisers and pesticides in predominantly agricultural areas such as southern Ontario has caused further declines.

Riparian vegetation, particularly through the use of buffer strips, has been shown to be very effective at limiting many of the non-point source inputs which have been implicated in the decline of freshwater mussels. The following study examines unionid distributions in southern Ontario in relation to characteristics of the riparian zone. Through a better understanding of factors responsible for shaping distributional patterns, the necessary information for developing conservation practices for these threatened organisms can be obtained.

Land Use and Biotic Communities

F.H. Likens and G.E. Bormann were among the first to propose the study of
biological systems at the ecosystem level (Likens et al. 1967). Through a combination of the animate and inanimate systems operating within the ecosystem, they believed a better understanding of all governing processes could be achieved. These authors realised that a combination of numerous previously separate disciplines including geochemistry, geology, hydrology and the applied sciences would enable a better and more complete understanding of the entire ecosystem. Through the development of the small watershed approach and the establishment of the Hubbard Brook Ecosystem Study, the ability to examine entire ecosystems was achieved.

The manipulation studies of the Hubbard Brook watersheds (Likens et al. 1970), in particular the deforestation of W2, demonstrated the importance of an intact ecosystem to the maintenance of the integrity of these previously described cycles. The complete deforestation of W2 and the subsequent prolonged period of vegetation removal had significant effects on the nutrient cycles of the watershed. Deforestation resulted in large increases in most major ions with the exception of $\text{NH}_4^+$, $\text{SO}_4^{2-}$ and $\text{HCO}_3^-$. Nitrate levels showed the largest change, increasing 41 fold in the first year after deforestation and 56 fold in the second year (Likens et al. 1970). Likens et al. (1970) attributed these large changes in circulating nutrient levels to disruption of the nitrogen cycle, increased decomposition on the forest floor and an increase in biological nitrification.

Hornbeck and Kropelin (1982) and Martin et al. (1984) conducted similar studies of the effects of deforestation on the nutrient cycling within northern hardwood forests. Hornbeck and Kropelin (1982) reported that removals of forest biomass
resulting from harvesting can lead to large declines in the available nutrient pools. These authors reported the loss of 30% of the available Ca and in excess of 85% of the available K. Similar to the findings of Likens et al. (1970), Hornbeck and Kropelin (1982) reported large increases in escaping nutrients while $\text{SO}_4^{2-}$ was the only ion to decrease in streamwater concentrations after harvest.

Aside from the breakdown of nutrient cycles after cutting, the work of Likens et al. (1970) demonstrated that other components of the ecosystem could be adversely affected by the loss of the forest canopy. Likens et al. (1970) found that water temperatures within the watershed were altered by the removal of the forest. Daily water temperatures rose by an average 4-6°C with a much greater daily temperature fluctuation in the cleared watershed.

The initial deforestation study of Likens et al. (1970) found that the hydrology of the watershed was altered by the removal of the forest cover. In particular, the authors found that stream flow was greatly increased in the period following the cutting. Likens et al. (1970) attributed much of this increase in stream flow to a decrease in the amount of transpiration occurring within the watershed.

The influence of forest removal on stream flow parameters was further examined by Hornbeck (Hornbeck et al. 1970, Hornbeck 1973, Hornbeck 1975). These studies all supported the ideas of Likens et al. with respect to the effects of forest removal on stream flow and storm run off. Hornbeck et al. (1970) and Hornbeck (1973) both reported that removal of the forest canopy led to increased stream flow
values with the major increase being shown during the late summer period usually characterised by lowest flow. They also reported that snowmelt tended to occur earlier resulting in an earlier period of peak spring run off.

In the period immediately following the first report of Likens et al. (1970) regarding the impacts of forest removal on cycling within the watershed ecosystem, the emphasis of researchers was on investigating and confirming these findings. The work discussed above focuses on the physical and chemical implications of forest removal, however, very little emphasis was initially placed on the biological implications of deforestation. In their initial work, Likens et al. (1970) made only passing reference to the possible existence of algal blooms within the affected watershed.

It was not until more than a decade after the initial findings of Likens et. al. (1970) that the first reports about the implications of these landscape changes to the aquatic biota were made available. Noel et al. (1986) conducted an examination of the stream macroinvertebrates and periphyton in a number of streams in the Hubbard Brook area which had undergone clearcuts as well as a number of similar streams which had not been cleared. The findings of these authors were similar to those alluded to by Likens et al. (1970). Noel et al. (1986) reported that periphyton levels within the affected streams were almost six times greater than those in the control streams. Furthermore, the composition of the periphyton community was very different with the cleared streams dominated by green algae while the uncleared streams were dominated by diatoms.

The macroinvertebrate communities in these clearcut streams showed densities
averaging 2-4 times greater than the reference streams (Noel et al. 1986). Following the pattern discovered for the periphyton communities, the macroinvertebrate communities of these altered streams showed a shift in species composition. Higher numbers of mayflies (Ephemeroptera) and true flies (Diptera) were found within the altered streams (Noel et al. 1986). Noel et al. (1986) reported that the nutrient levels within the clearcut streams did not differ from those of the reference streams, suggesting that the differences found in the biotic communities were more likely related to differences in available light and temperature changes and not to the breakdown of nutrient cycles such as those reported by Likens et al. (1970).

Haack et al. (1988) also found that changes in the biota of altered streams was related to factors other than simple nutrient changes. These authors studied distributions of epilithic bacteria in cleared and uncleared watersheds of the Hubbard Brook area. Differences in densities of epilithic bacteria appeared to be related to differences in C and changes in pH associated with the removal of the forest cover, but appeared unrelated to differences in nitrate levels (Haack et al. 1988).

The altered nutrient cycles reported by Likens et al. (1970) have been demonstrated to be important under some circumstances to the distribution of aquatic insects. Sallenave and Day (1991) in a study of a small agricultural stream in Ontario found that distributions and secondary productivity of several caddisfly species were significantly related to the agricultural practices within the watershed and indirectly to the levels of nutrients escaping from the adjacent lands.
The importance of forestry activities within the watershed to the survival of vertebrate species has also been examined. Rabeni and Smale (1995) have reported that sedimentation resulting from human activities within the watershed can adversely affect the fish populations of the stream through disruptions of the composition of the feeding guilds. Similarly, Castelle et al. (1994) have reported that increases in sedimentation after deforestation can adversely affect the reproduction of many salmonid species.

Whether the effect of interest is chemical, physical or biological the 25 years of research since the initial findings of Likens et al. (1970) have served to emphasize that activities conducted within the terrestrial component of the watershed can, and do, have serious impacts on the aquatic component of the system. The question that arises from this research is one of extreme importance considering the high degree of human alterations to most landscapes and the recent serious declines of many taxonomic groups - **How can these effects be minimized?**

Many of the early works on the topic independently arrived at the same conclusion with regard to how to minimize these detrimental effects. As early as the initial strip cutting experiments on drainage basin W4, Burton and Likens (1973) discovered that the presence of a small strip of vegetation left along the stream channel could act to greatly reduce the harmful effects of cutting.

Riparian buffer strips have since been proven to be able to limit many of the harmful affects associated with the removal of large areas of forest cover (Schlosser and Karr 1981, Peterjohn and Correl 1984, Castelle et al. 1994). Castelle et al. (1994) provided a summary of the large body of research on the buffering abilities of riparian
vegetation. Riparian zones have been shown to be effective at removing sediment and nutrients from overland flow as well as limiting erosion of the stream channel through the stabilizing actions of the root complex. Furthermore, the presence of the vegetation cover can eliminate temperature fluctuations and moderate differences in stream runoff (Castelle et al. 1994).

The demonstrated ability of the riparian buffer strip to minimize the detrimental effects of forest harvest has provided the opportunity for the development of a new management tool. The buffering capacity of the riparian zone has spawned a line of research directed at determining the most effective techniques for the design and implementation of these vegetated strips. Dillaha et al. (1989) and Bingham et al. (1980) discuss the use of riparian buffer strips to reduce non-point source pollution resulting from agricultural activities. These authors have identified riparian width as an important determinant of the filtering efficiency.

Other researchers have also addressed the importance of riparian size (Barton et al. 1985, Budd et al. 1987, Castelle et al. 1994). Probably the most important consideration when determining the proper size of riparian for a given area is the resource to be protected. The necessary size of riparian strip differs depending upon what potential changes need to be minimized. Castelle et al. (1994) report that a riparian zone 30 m in width is sufficient to eliminate most temperature related effects. In contrast, if the major concern is sediment or nutrient addition a riparian zone of 50 - 90 m is recommended. Even larger riparian zones are required if the maintenance of
habitat diversity is the concern to be addressed (Castelle et al. 1994).

The ecosystem concept proposed by Likens and Bormann almost thirty years ago has lead to a much more complete understanding of the processes that control ecosystem functioning. Early work established the basic cycling patterns within the ecosystem and allowed the design and implementation of the numerous disturbance experiments that followed. These disturbance experiments demonstrated the destructive capacity of human actions on these intact systems. Watershed deforestation has been shown to lead to physical, chemical and biological changes within the aquatic component of the ecosystem. Recent efforts have been directed at developing methods of minimizing these detrimental ecosystem changes and emphasis has been placed on the maintenance of a sufficient riparian buffer zone.

**Freshwater Mussels**

Freshwater mussels are benthic organisms with a relatively sedentary adult stage spent burrowed into soft sediments. The life span is highly species specific and ranges from six to greater than 100 years (McMahon 1991). Species which are common to Ontario show life spans ranging from less than 10 years to a maximum of 45 years (Heller 1990).

Reproductive maturity is delayed with few species showing sexually mature individuals under seven years of age. Sexes may be separate or individuals may be hermaphroditic (Clarke 1981) depending upon the species. In the case of hermaphroditic species, mature sperm and eggs are usually produced simultaneously
(McMahon 1991). Fertilisation occurs internally as mature sperm is broadcast by the male and taken in through the incumbent syphon of the female. Fertilisation occurs within the gill marsupia of the mature female and the immature juveniles (glochidia) are developed within the outer demibranch brood pouches of the mature female (McMahon 1991).

When the glochidia are ready for release, they are ejected by the female through the excurrent syphon individually or in specialised mucus coated bundles termed conglutinates or superconglutinates. It is at this stage that the glochidia undergo an obligate period of parasitism. All but two species of North American unionids (Simpsonichoncha ambigua - aquatic salamander host, Strophitus undulatus - no host) require a parasitic stage on a host fish for successful development. After release from the female, the glochidia become encysted externally on the fins or scales or internally on the gills of the host and remain encysted for a species specific period of 6 - 160 days (McMahon 1991). After the encystment period, the glochidia have developed to the free living juvenile stage and are sloughed off by the host and become established in the benthic environment where they will remain for the rest of their lives.

Conservation Status

Freshwater mussels are among the most threatened taxonomic groups in the world (Eisner et al. 1995). During the past century, worldwide declines in numbers of individuals and species have been reported (Bogan 1993) with numerous causes being cited. In North America, 73% of the 298 known species are considered rare,
endangered, threatened or imperiled, primarily resulting from human activities (Allan and Flecker 1993).

In many rivers of the United States, excellent long term site specific data are available providing a well documented history of the declining fauna (e.g., Williams et al. 1992). Unfortunately complete records do not exist for many Canadian watersheds making it difficult to completely assess the degree of species loss within Canadian waters. However, within the southern Ontario area, two watersheds have received significant attention and provide the best available information regarding Canadian declines. Clarke (1992) conducted extensive surveys on the Sydenham River and reported a 35% decline in species numbers. Recent survey work on the Thames River showed that the unionid fauna of this large river system has undergone a serious decline with 36% of the historic fauna of the river being eradicated over a 60 year period (Morris 1996). While these records represent only a small portion of the entire unionid fauna of Canada they represent an area that has been reported to possess the richest unionid fauna within the country and therefore have important implications to the entire national fauna (Clarke 1981).

The reasons for these drastic declines in unionid populations are widespread and often site specific, however, they can be grouped into two major categories: direct and indirect causes. Direct causes represent clear and absolute threats to freshwater mussel populations. The most apparent direct cause of declines is the harvest of adults for commercial purposes. The commercial harvest of mussels for decorative buttons became a major industry during the late 1890's. North American harvests centred
around the Mississippi River and its tributaries where, by 1916, the industry supported over 20,000 people and was valued at greater than $12.5 million (Upper Mississippi River Conservation Committee 1995). In Ontario, commercial harvest was restricted to the Grand and Thames Rivers. Harvest from these two rivers was exceptionally high with annual removals of 265 and 100 tons from the Grand and Thames Rivers respectively (Detweiler 1918, Stewart 1992).

With the popularity of plastics in the post-war period of the 1940's and 50's the need for mussel shells to be used in buttons declined and commercial harvest slowed. By the late 1950's, commercial harvest ceased in Ontario waters. However, during the early 1960's it was discovered that unionid shells could be ground into small pellets that acted as excellent seeds for the production of cultured pearls. While harvest for this purpose never resumed in Canadian rivers, a thriving pearl seed industry still exists on the Mississippi river system with a total annual harvest of over 1000 tons between 1988 and 1994 (Upper Mississippi River Conservation Committee 1995). As the individuals being removed during these harvests represent the older, sexually mature, reproducing members of the population, the impact on the sustainability of the population has been drastic and these harvests have contributed greatly to the decline of these animals.

A recent serious threat to unionids of the Great Lakes and the Mississippi River takes the form of the exotic species *Dreissena polymorpha*, the zebra mussel. Since its introduction to the Great Lakes system in 1988, the zebra mussel has become established in all the Great Lakes and is steadily progressing southward through the
Mississippi River system (Tucker et al. 1993). The impact of this invader on native unionid populations has been severe in many areas with native populations being essentially eradicated in areas such as Lake St. Clair (Nalepa 1994).

Although commercial harvest and zebra mussel infestation represent overt threats to freshwater mussel populations, harvest was restricted to select species in major river systems and zebra mussels have so far been unable to invade most North American Rivers. A more general concern to declining populations are indirect threats primarily in the form of loss of habitat resulting from declining water quality. With the advancement of human populations many of the major river systems have undergone varying degrees of regulation. Activities such as damming and channelisation of rivers to manipulate flow regimes have been shown to adversely affect unionid populations through disruptions of instream flow characteristics, alterations of host fish distributions and thermal disruptions resulting from cold water hypolimnetic releases (Fuller 1974).

Many activities associated with the terrestrial environment have also been linked to declining freshwater mussels populations. Because mussels are filter feeders, they are particularly intolerant of the increased sediment loads associated with poor agricultural practices, clearcutting and the removal of riparian forests (Bogan 1993). In addition, the increased inputs of herbicides and pesticides in recent years have all been linked to the loss of mussels populations (Fuller 1974). It is these diffuse non-point source inputs that have the greatest impact on global unionid declines.
Objectives

The following study was designed to examine the potential of riparian vegetation as an important structuring element for unionid communities. Chapter 1 presents the results of an initial survey of six drainages within southern Ontario. The unionid species present within each drainage are identified and an investigation of physical and chemical correlates is conducted. The second chapter outlines the development of a landscape model for describing and predicting unionid distributions within the study area. The third chapter describes the results of two studies, one observational and one manipulative, examining differences in growth patterns of species important to the model and discusses the potential of growth as a structuring element in unionid communities.
Chapter 1: Spatial Distributional Patterns of Freshwater Mussels (Bivalvia: Unionidae) in Rivers of Forested and Grassy Riparian Zones.

Introduction

The once rich freshwater mussel populations of North America have undergone drastic decline during the past century (Mackie and Topping 1988, Bogan 1993, Parmalee and Hughes 1994). Many species have been driven towards extinction through human activities, either directly through harvesting or indirectly through destruction of aquatic habitat. A reported 73% of North American unionid species are extinct, rare or imperiled (Allan and Flecker 1993). Although current attitudes are shifting toward a more conservation oriented approach to all biota, little can be accomplished without a sound understanding of present distributions and the biotic and abiotic factors responsible for governing these distributions.

Historically, records of unionid distributions have included anecdotal notes of habitat preferences. These have usually been of a microhabitat nature and include such factors as current velocity, water depth and substrate type. These microhabitat preferences have seldom been tested rigorously and if rigorous testing has occurred the results have been, at best, mixed (Strayer and Ralley 1993).

In a recent examination of unionid habitat preferences, Strayer (1993) emphasized the usefulness of macrohabitat variables as predictive agents. Macrohabitat variables operate at a scale of 1-10 km and include factors such as stream size and gradient, hydrologic variability and physiographic province. The predictive power of these macrohabitat variables has proven to be significant in many cases. For example,
Di Maio and Corkum (1995) showed that distinct mussel communities can be predicted on the basis of the hydrological status of a stream.

The usefulness of other large scale habitat characters has been repeatedly demonstrated to act at a number of differing scales. For example, Ross (1963) and Corkum (1989, 1990, 1991, 1992) illustrated the broad scale importance of climax vegetation and land use characters in predicting the spatial distribution of lotic invertebrates. Sallenave and Day (1991) showed that life history traits of several *Hydropsyche* species were related to tillage practices on the adjacent land.

The link between terrestrial land use and the biotic responses observed in aquatic communities lies in the dynamic processes that occur at the land-water boundary. Although this boundary represents the extreme limits of two seemingly distinct habitat types, exchanges across it can drastically affect either habitat. A riparian buffer zone can be defined as "planted or native vegetation situated downslope of cropland or animal pasture and adjacent to the watercourse" (Dillaha *et al.* 1989). Buffer zones can act in many ways to limit the potentially harmful effects of human activity on aquatic habitats (Castelle *et al.* 1994). Among these buffering abilities are the ability to moderate temperature fluctuations through shading (Budd *et al.* 1987), the removal of sediment from overland flow prior to its entrance into the main channel (Young *et al.* 1980), and the regulation of nutrients and metal levels entering the water body (Peterjohn and Correll 1984). The buffering capacity of the riparian zone has important implications to the organisms inhabiting the watercourse.

Aquatic organisms such as mussels can be directly or indirectly affected by the
constituents passing through the riparian zone. Fuller (1974) summarized the effects of many land derived elements on freshwater mussels. Although the temperature requirements of many unionids are not fully understood, a wide variety of responses have been attributed to changes in temperature including egg mass abortion, dulled glochidial response, repressed development of the digestive system, changes in oxygen requirements and ultimately death (Fuller 1974).

The ability of riparian zones to act as sediment and nutrient filters also may affect mussel communities. Aside from the ability of sediment to impair light penetration and disrupt the phototaxic responses of mussels (Fuller 1974), sediments can clog the filtration apparatus and lead to death (Ellis 1936). Although the impact of nutrient loadings on mussel communities has been much less studied, some examples do exist. Bauer (1988) reported that juvenile survival and establishment of the unionacean, *Margaritifera margaritifera* (L), were negatively associated with phosphate loadings, whereas adult survival was negatively correlated with nitrate loadings.

The purpose of the present study was to examine the relationship between the riparian zone and the unionid community in a number of agricultural drainage basins in southwestern Ontario. Because riparian vegetation has been shown to alter the physical and chemical characteristics of aquatic environments, including elements essential to mussel growth and development, rivers were selected from one of two *a priori* riparian classes (grassy or forested). We intended to determine if distinct mussel communities could be associated with each of the macrohabitat riparian classes and to investigate
which environmental variables were most important in describing these associations.

Methods

Study Sites

Six agricultural drainage basins were selected in southwestern Ontario: three with forested buffer strips and three with grassy riparian zones (Fig 1.1). All drainage basins contained predominantly agricultural land with less than 30% forest cover in any one basin. Rivers in the forested category had densely treed riparian zones whereas those in the grassy category had either no riparian vegetation (i.e. plowed to edge of the channel) or only small grassy riparian zones. Basins with forested riparian zones were the Ausable River, Dingman Creek and the Saugeen River. Basins with grassy riparian zones were the Avon River, McGregor Creek and Whirl Creek. Drainage basins were selected using O.M.N.R. land use reports (1983) and 1:50 000 topographic maps.

Twelve sites were sampled in each riparian class for a total of 24 sites. The four sites in each of the six drainage basins were sampled between August 23 and September 8, 1994. Sample sites were selected on the basis of accessibility, wadeability and the presence of a mussel community based on preliminary sampling during the period of August 3-5, 1994. Each site within a drainage basin was separated from all other sites by at least one tributary and were assumed to be independent.
Figure 1.1 Location of study sites. Sites with grassy riparian zones are represented by open squares and sites with forested riparian zones are represented by closed squares.
Mussel Collection

Mussels were sampled using a catch per unit effort approach. Although quadrat sampling has been shown to be more effective at quantifying unionid densities, catch per unit effort techniques provide a more complete assessment of rare and uncommon species (Strayer et al. 1995, Vaughn 1995). The emphasis of this study was to determine the species composition of each site and therefore the catch per unit effort approach was adopted. Sites were manually sampled by wading while searching the substrate visually and manually for a period of 60 minutes. Each site was searched beginning at the downstream end and progressing upstream while executing transects perpendicular to the flow. The 60 minute search time did not include time required to identify mussels and process voucher specimens (see below).

Each mussel encountered was identified to species in the field. Individuals that could not be positively identified in the field were collected and returned to the laboratory in 95% ethanol for identification. In addition, the first individual of each species encountered at a site was collected as a voucher specimen for positive identification. Voucher specimens have been deposited at the Royal Ontario Museum (Toronto, Canada, collection # 1996-003).

Riparian Characteristics

Although drainage basins were assigned on an *a priori* basis to one of the two riparian classes, physical variables were measured in the field to further describe these classes. The width of the riparian zone was defined as the perpendicular distance from
the water's edge to the agricultural field. At each site, the riparian width (measured to the nearest 0.1 m) was measured at six locations. Three widths were measured on each of the left and right banks - one measure at each of the upstream and downstream extremes and one measure midway between.

At each of the six locations of riparian width measurements, two measures of terrestrial slope were recorded using a Brunton Pocket Transit (model 5008). Valley slope was designated as the slope of the land from the water edge to bankfull depth. The second measure of slope was the plain slope and was defined as the slope from the bankfull depth to the distal edge of the riparian zone.

**Environmental Data**

The filtering capacity of riparian vegetation results in decreased levels of suspended sediments and nutrient concentrations in many rivers possessing intact riparian zones, whereas rivers with disturbed riparian zones often show elevated levels (Castelle et al. 1994). Since these same elements have been related to unionid distributions we chose to examine differences in our study basins.

Three water samples were collected in 500 mL Nalgene bottles and used for estimates of suspended sediment and ash free dry mass (AFDM). Suspended sediment and AFDM samples were filtered in the field through preweighed Whatman® glass microfibre filters (4.7 cm) using a Nalgene hand-held vacuum pump. Samples were held on ice in the field and kept frozen in the laboratory until processing could be completed. The change in weight from heating at 103°C for 24 hrs to heating at 550°C
for 1 hr was determined as the AFDM of the sample. Conductivity was measured in
the field using an Oakton* hand held conductivity meter (model WD-35607-10); pH
was field measured using an Oakton* pHTestr 2 (model 35624-20).

Triplicate 1000 mL water samples were collected August 10, 1995 for
determination of nitrate, nitrite and soluble reactive phosphate (SRP) concentrations.
Nitrate and nitrite samples were analysed through cadmium reduction at the Agriculture
Canada research station in Harrow, Ontario. SRP was determined using the
molybdenum blue method of Wetzel and Likens (1991) at the University of Windsor.
In addition, monthly mean nutrient concentrations (nitrate, nitrite, ammonia, TKN,
total phosphate) were obtained from Ontario Ministry of the Environment and Energy
monitoring stations within the study basins.

**Shading and Temperature**

The existence of a riparian canopy results in shading of the river channel and
ultimately a decrease in water temperature. In order to quantify this effect within our
study rivers a measure of canopy overhang was taken at each site using a Solar
Pathfinder® (Solar Pathfinder, Hartford, SD). The Solar Pathfinder® provides an
estimate of total incident solar radiation during each calender month based on the
riparian profile and composition. Each Solar Pathfinder® measurement was taken at a
mid-river point equal distance from the upstream and downstream boundaries of the
site.

Temperature data were obtained for three grassy and two forested basins, at the
furthest downstream site in each drainage basin, using Hobo XT Temperature Loggers. Temperature data for the third forested basin, the Ausable River basin, was not available due to the loss of the logger during fall flooding. Temperature loggers were placed at the substrate surface and anchored to 1 m galvanized rods that were driven into the substrate. Temperature loggers were installed on the same day as mussel communities were sampled but only after all other sampling had been completed. This was done in order to eliminate the risk of contaminating the other environmental data samples during the installation procedure. Temperature values were recorded every 100 minutes for a duration of about 120 days.

Statistical Methods

Differences in values of environmental variables among sites were analyzed using Wilcoxon sign-ranked nonparametric tests. Species abundance differences were tested using ANOVA.

Results

Mussel Species

I observed 875 mussels at the 24 sampling sites. Four hundred and fifty five individuals were censused in the grassy riparian basins; 420 mussels were found at forested sites. Representatives from 17 species were found (Table 1.1) with 11 species occurring in the grassy basins and 14 in the forested. Eight species were common to both riparian types. The mean number of species did not differ between the two
Table 1.1: Relative frequency of each unionid species found in the study area. Proportions represent total of open and forested sites (n=24). Codes refer to Figure 1.2.

<table>
<thead>
<tr>
<th>Species</th>
<th>Code</th>
<th>Relative Frequency</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Pyganodon grandis</em> (Say 1829)</td>
<td>PGRA</td>
<td>0.625</td>
</tr>
<tr>
<td><em>Strophitus undulatus</em> (Say 1817)</td>
<td>SUND</td>
<td>0.458</td>
</tr>
<tr>
<td><em>Lasmigona compressa</em> (Lea 1829)</td>
<td>LCPR</td>
<td>0.416</td>
</tr>
<tr>
<td><em>Lasmigona complanata</em> (Barnes 1823)</td>
<td>LCOM</td>
<td>0.333</td>
</tr>
<tr>
<td><em>Amblema plicata</em> (Say 1817)</td>
<td>APLI</td>
<td>0.292</td>
</tr>
<tr>
<td><em>Lampsilis radiata</em> (Barnes 1823)</td>
<td>LRAD</td>
<td>0.292</td>
</tr>
<tr>
<td><em>Lasmigona costata</em> (Rafinesque 1820)</td>
<td>LCOS</td>
<td>0.250</td>
</tr>
<tr>
<td><em>Elliptio dilatata</em> (Rafinesque 1820)</td>
<td>EDIL</td>
<td>0.208</td>
</tr>
<tr>
<td><em>Alasmidonta marginata</em> Say 1829</td>
<td>AMAR</td>
<td>0.208</td>
</tr>
<tr>
<td><em>Fusconaia flava</em> (Rafinesque 1820)</td>
<td>FFLA</td>
<td>0.208</td>
</tr>
<tr>
<td><em>Leptodea fragilis</em> (Rafinesque 1820)</td>
<td>LFRA</td>
<td>0.125</td>
</tr>
<tr>
<td><em>Ligumia recta</em> (Lamarck 1819)</td>
<td>LREC</td>
<td>0.125</td>
</tr>
<tr>
<td><em>Potamilus alatus</em> (Say 1817)</td>
<td>PALA</td>
<td>0.125</td>
</tr>
<tr>
<td><em>Psychobranchus fasciolaris</em> Rafinesque, 1820</td>
<td>PFAS</td>
<td>0.083</td>
</tr>
<tr>
<td><em>Lampsilis cardium</em> (Barnes 1823)</td>
<td>LCAR</td>
<td>0.083</td>
</tr>
<tr>
<td><em>Actinonaias ligamentina</em> (Barnes 1823)</td>
<td>ALIG</td>
<td>0.083</td>
</tr>
<tr>
<td><em>Quadrula quadrula</em> (Rafinesque 1820)</td>
<td>QQUA</td>
<td>0.042</td>
</tr>
</tbody>
</table>
habitats \( (F_{1,22} = 0.07, \ p > 0.05) \).

Individual species showed distinct relative abundances in the two habitats (Fig 1.2). *Pyganodon grandis* represented 62.5% of all mussels in grassy basins, but represented only 1% of mussels found in forested basins. In contrast, three species had similar abundances at forested sites: *Amblema plicata* (26.9%), *Elliptio dilatata* (20.5%) and *Lasmigona complanata* (18.7%) (Fig. 1.2).

Six species had significant Wilks' Lambda and univariate F-ratios indicating different relative abundances in grassy and forested basins: *P. grandis* \( (F_{1,22} = 109.1, \ p < 0.001) \), *Strophitus undulatus* \( (F_{1,22} = 6.926, \ p < 0.05) \), *Fusconaia flava* \( (F_{1,22} = 5.336, \ p < 0.05) \), *Lampsilis radiata* \( (F_{1,22} = 4.897, \ p < 0.05) \), *Lampsilis cardium* \( (F_{1,22} = 5.294, \ p < 0.05) \) and *E. dilatata* \( (F_{1,22} = 6.312, \ p < 0.05) \). *Pyganodon grandis* and *S. undulatus* were characteristic of grassy sites and *F. flava*, *L. radiata*, *L. cardium* and *E. dilatata* were characteristic of forested sites.

**Environmental Variables**

Environmental variables measured for the 24 sites were analyzed using Wilcoxon-sign ranked non-parametric tests (Table 1.2). Significant differences occurred between the two riparian classes for plain slope, valley slope and riparian width. Forested basins had significantly steeper plain and valley slopes with wider riparian buffer strips. No differences were detected for pH, conductivity, suspended sediment or AFDM (Table 1.2).
Figure 1.2 Relative abundances of unionid species found at grassy (bottom) and forested (top) sites.
Table 1.2: Mean (±SE) values for environmental data collected from grassy and forested sites. Significance is based on Wilcoxon sign-ranked non-parametric tests.

<table>
<thead>
<tr>
<th></th>
<th>n</th>
<th>Grassy</th>
<th>Forested</th>
<th>significance</th>
</tr>
</thead>
<tbody>
<tr>
<td>plain slope (%)</td>
<td>72</td>
<td>3.1 (0.85)</td>
<td>13.7 (3.38)</td>
<td>p &lt; 0.01</td>
</tr>
<tr>
<td>riparian width (m)</td>
<td>72</td>
<td>16.07 (2.726)</td>
<td>39.49 (3.370)</td>
<td>p &lt; 0.01</td>
</tr>
<tr>
<td>valley slope (%)</td>
<td>72</td>
<td>31.1 (1.81)</td>
<td>37.0 (4.15)</td>
<td>p &lt; 0.05</td>
</tr>
<tr>
<td>pH</td>
<td>12</td>
<td>8.55 (0.111)</td>
<td>8.50 (0.051)</td>
<td>ns</td>
</tr>
<tr>
<td>conductivity (μS/cm at 25°C)</td>
<td>12</td>
<td>570.6 (45.89)</td>
<td>581.8 (48.67)</td>
<td>ns</td>
</tr>
<tr>
<td>suspended sediment (mg/L)</td>
<td>36</td>
<td>28.0 (6.25)</td>
<td>26.7 (7.58)</td>
<td>ns</td>
</tr>
<tr>
<td>ash free dry mass (mg/L)</td>
<td>36</td>
<td>2.9 (0.85)</td>
<td>3.8 (0.95)</td>
<td>ns</td>
</tr>
</tbody>
</table>
Grassy sites received a greater proportion of the available incident solar radiation during each calendar month (rmANOVA $F_{(1,12)}=3.11$, $p < 0.05$) (Fig. 1.3). From April to September grassy sites received in excess of 90% of the possible incident radiation, whereas forested sites received between 50% and 65% during this same period. Mean monthly temperature did not differ significantly between the two riparian classes although grassy sites showed slightly elevated temperatures. Daily temperature fluctuations were significantly greater at grassy sites (4.30°C) than forested sites (2.47°C) ($F_{(1,86)}=27.23$, $p < 0.001$) (Fig. 1.4).

No significant differences were found between grassy and forested sites for nitrates ($F_{(1,70)}=0.290$, $p > 0.05$), nitrites ($F_{(1,70)}=0.623$, $p > 0.05$) or SRP ($F_{(1,70)}=0.223$, $p > 0.05$) collected on August 10, 1995. However, water quality data obtained from the M.O.E.E. monitoring stations within the study area (3 stations in open basins, 6 stations in forested basins) revealed differing concentrations of nutrients within the rivers of the two riparian classes on an annual basis (Table 1.3). Grassy rivers had higher annual mean concentrations of ammonia nitrogen ($F_{(1,7)}=7.36$, $p=0.03$) and TKN ($F_{(1,7)}=7.58$, $p=0.028$) than forested rivers. Concentrations of nitrates ($F_{(1,7)}=5.22$, $p > 0.05$), nitrites ($F_{(1,7)}=0.10$, $p > 0.05$) and phosphates ($F_{(1,7)}=4.99$, $p > 0.05$) again did not differ significantly between the two riparian classes.

**Discussion**

The importance of land use practices in the shaping of aquatic insect
Figure 1.3. Percentage of available solar radiation reaching the water surface using the Solar Pathfinder®. Open circles represent grassy sites and closed circles represent forested sites. Data are presented as means (n=12) ± standard errors.
Figure 1.4 Temperature profiles for two grassy (Avon R. and McGregor Cr.) and two forested (Dingman Cr. and Saugeen R.) drainages from September 5 to December 5 1994.
Table 1.3: Mean annual (± SE) levels of nutrients (mg/L) in open and forested drainages of southwestern Ontario. Data obtained from Ontario M.O.E.E. monitoring stations. Figures based on 11 months (Jan - Nov) for three (grassy) and six (forested) monitoring stations.

<table>
<thead>
<tr>
<th></th>
<th>NH$_3$-N</th>
<th>NO$_2$-N</th>
<th>NO$_3$-N</th>
<th>TKN</th>
<th>TP</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>mg/L</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Grassy</td>
<td>1.41</td>
<td>0.248</td>
<td>4.13</td>
<td>1.32</td>
<td>0.040</td>
</tr>
<tr>
<td></td>
<td>(0.541)</td>
<td>(0.052)</td>
<td>(0.761)</td>
<td>(0.236)</td>
<td>(0.012)</td>
</tr>
<tr>
<td>Forested</td>
<td>0.084</td>
<td>0.0326</td>
<td>3.13</td>
<td>0.79</td>
<td>0.022</td>
</tr>
<tr>
<td></td>
<td>(0.025)</td>
<td>(0.005)</td>
<td>(0.582)</td>
<td>(0.061)</td>
<td>(0.005)</td>
</tr>
</tbody>
</table>
distributions has been demonstrated repeatedly (Corkum 1990, 1991, 1992). However, little to no work has been conducted to examine the importance of terrestrial activities in structuring distributional patterns of freshwater mussels. I designed this study to examine these interactions and to determine the potential of large scale habitat characteristics as predictors of unionid distributions. I have found that some unionid species occur more frequently in rivers with forested riparian zones, whereas others are more abundant in rivers with open grassy riparian zones. These species specific differences in distributions occur along with other large scale habitat changes including alterations in shading and temperature regimes and fluctuations in circulating nutrient concentrations.

Differences in the composition and diversity of aquatic communities have been associated with activities in the terrestrial component of the watershed. Although no overall differences in species numbers were detected between our basin types, we have observed a shift towards dominance by a single species (*Pyganodon grandis*) in basins with grassy riparian zones.

The reason for this shift towards dominance by *P. grandis* is not immediately evident, however, it is likely the result of a combination of the buffering capacity of the riparian zone and the biological properties of this species. *Pyganodon grandis* is probably the most common unionid species in this geographic area. Clarke (1981) reported that *P. grandis* possesses wide sediment and flow tolerances that make it ideally suited to inhabit altered habitats.

Southwestern Ontario was once dominated by forested areas (Riley and Mohr
1994), however, much of these lands have been cleared to permit agricultural activities. The result is that many of the region's forested watersheds have been altered and are now characterised by open exposed channels. The clearing of forests and the associated removal of riparian vegetation can have important implications for the thermal and chemical properties of aquatic systems. The removal of the riparian canopy results in elevated mean temperatures as well as greater daily and seasonal temperature fluctuations (Budd et al. 1987).

For the six drainages in southwestern Ontario examined in this study, I showed that the thermal regime is linked to the presence or absence of the riparian buffer strip. Rivers with forested riparian zones tend to have lower mean monthly water temperatures than rivers with grassy riparian zones and to have daily temperature fluctuation cycles which are significantly damped by the shading properties of the riparian vegetation. Temperature changes are potentially important for the establishment and survival of freshwater unionids. Since mussels are poikilotherms, external thermal conditions will always have the potential to affect basic physiological functioning ranging from daily metabolic activities to seasonal reproductive cycles. (Fuller 1974).

A potential source of regulatory control centres around the thermal limits of shell production and growth. Temperature can act to limit growth by restricting the duration of the growth period or by limiting the rate at which growth occurs. The importance of temperature as a regulatory mechanism has been demonstrated for bivalves other than unionids. Beukema et al. (1985) demonstrated that variations in
growth of the tellinid bivalve, *Macoma balthica* (L), are related to the temperature experienced during the preceding winter. Warmer winter temperatures result in an earlier initiation of the annual growth period resulting in an increase in total growth during the year. Similar patterns have been demonstrated in the unionacean *Margaritifera margaritifera* resulting from latitudinal differences (Bauer 1992).

Growth of the unionid *Pyganodon grandis simpsoniana* (formerly *Anodonta*) within a single lake was restricted by temperature limitations acting through water depth (Hanson *et al.* 1988). Temperature declines of 6°C produced significantly reduced growth over the natural growth period. Given the varied metabolic requirements of unionid species (McMahon 1991) and the knowledge that temperature can have significant effects, the potential for species distributions to be limited by the thermal requirements of shell production and soft tissue synthesis warrants further attention.

I found that rivers passing through open agricultural lands possess significantly higher annual mean concentrations of NH₄-N and TKN. Although the literature base regarding the importance of nutrient levels to the growth and establishment of unionids is limited, there is a small amount of correlative evidence. Starret (1971) reported an absence of unionids from stretches of the Illinois River with ammonia levels in excess of 6.0 ppm. Although Starret (1971) erroneously attributed this absence to effects on host fish species, Fuller (1974) noted the possibility of a more direct effect. Ammonia has been shown to adversely affect the metabolic functioning of unionids resulting in a decrease in the metabolic rate and a reduction in all metabolic processes (McMahon
Maximum concentrations of ammonia detected during the present study were lower (approximately ¼) than those reported by Starret (1971), however, concentrations observed in open rivers averaged 17x greater than those in forested rivers. While these levels may be below those that result in complete loss of the unionid community, there is the potential for metabolic suppression resulting in the different species assemblages observed in open and forested rivers. In contrast, concentrations of nitrate, nitrite and phosphate, which have been implicated in the growth and survival of other bivalves (Fuller 1974, Bauer 1988, 1992), appear unrelated to the distributions observed during this study.

Southern Ontario possesses the richest and most diverse unionid fauna in Canada (Clarke 1981), yet many of the rivers of the area have undergone significant declines in terms of both species and numbers of individuals during recent years (Mackie and Topping 1988). The results of my study support the idea that increasingly intensive agricultural activity is resulting in a shift towards dominance by a single common species in rivers of grassy riparian zones with P. grandis representing over 60% of individuals in these rivers. Hoggarth et al. (1995) have implicated agricultural activity and loss of riparian vegetation as major threats to populations of Epioblasma obliquata obliquata, a federally endangered American unionid species. The relationship between the physical properties of the streamside riparian zone and the structure and composition of the unionid community should prove beneficial for the design and implementation of effective conservation methods for these organisms.
Chapter 2: Modelling Unionid Distribution Patterns

Introduction

Freshwater mussels are among the most threatened taxonomic groups in North America (Eisner et al. 1995). During the past century, worldwide declines have been observed (Bogan 1993) with North American populations showing some of the most dramatic declines. Many of the once rich and diverse unionid habitats have been degraded by human activities and many rivers now support severely depleted unionid communities. Within southern Ontario, two of the most historically rich rivers (Sydenham River and Thames River) have shown 30-35% declines in terms of species numbers over the last 50 years (Clarke 1992, Morris 1996).

The result of these large scale declines has been an increased interest in the conservation and protection of rare and threatened species. In the United States, 56 species of freshwater bivalves, including 55 unionids and one margaritiferid, are presently listed under the U.S. Endangered Species Act of 1973 with an additional 70 species currently considered as candidate species. Although no federal or provincial ranking system presently exists in Canada, awareness of the susceptibility of freshwater mussels to habitat destruction is increasing and efforts are underway to compile detailed distributional data (Oldham 1994).

Despite the conservation needs of threatened species and the economic importance of commercially viable species, very little is known about the factors responsible for determining distributional patterns. During the late 1800's and early
1900's when much of the exploratory work on freshwater mussel populations was being conducted, little attention was paid to factors shaping distributions (Detweiler 1918). Rivers were sampled and species were collected with little concern for habitat characteristics with the exception of anecdotal reports on substrate and flow conditions (see Van der Schalie 1941).

This lack of information regarding specific habitat characteristics has persisted into the latter half of the 1900's. Efforts to quantify these small scale microhabitat variables such as particle size, water depth and current velocity have increased and have even been tested under laboratory conditions, however, they still represent habitat descriptors and not predictors. The typical riverine habitat possesses many areas of both high and low flow as well as areas of coarse and fine sediment. While these types of habitat descriptors may help in identifying the specific location within a river where a species is likely to be found, they provide little assistance in explaining why a species is found in one river but not in another.

Strayer (1993) examined unionid distributions in relation to both typical microhabitat (sediment, current velocity) and large scale macrohabitat variables (physiography, hydrology) in an attempt to maximize predictability. He determined that typically reported microhabitat variables provided very little ability to predict distributions, whereas the large scale macrohabitat variables were much more efficient at predicting distributions. Di Maio (1995) found a similar usefulness of whole basin hydrology as a predictor within rivers of southern Ontario.

This chapter describes the results of the development and testing of a landuse
based model for predicting unionid distributions. In Chapter 1, I demonstrated that some unionid species have significantly different abundances in rivers with forested riparian zones in comparison with rivers without forested riparian zones. The model was developed on the basis of these differences and tested against a number of previously unused sites. I hoped to be able to predict unionid distributions on a large scale in order to allow for the development of conservation plans for rare and threatened species.

**Methods**

**Developing the Model**

**Site Selection and Surveying**

The 24 sites used in the development of the distribution model correspond to the sites surveyed in Chapter 1 (see Fig 1.1). Data collected during the initial survey efforts described earlier (unionid communities and physical site characteristics (see Chapter 1: Methods)) were used to determine species associations with other species and with physical riparian characteristics. Only those 12 species found to occur in more than one river were included in the analysis as species limited to one river provide no power to discriminate between basins.

**Statistical Techniques**

Multiple Discriminant Analyses were conducted using log \((x+1.1)\) transformed species abundance data and the physical riparian data. This multivariate technique
allowed the prediction of group membership (grassy or forested) on the basis of species abundance (first analysis) and physical riparian data (second analysis). The predicted memberships were then tested against the *a priori* assignments.

**Testing the Model**

An important aspect of any descriptive model is the ability of that model to describe associations that were not used in the creation of the original model. In order to test the ability of this model to predict unionid distributions, an additional 16 sites were selected (Fig 2.1).

**Test Site Selection**

Sites for validation of the discriminant model were selected on the basis of a literature review. Two studies were found that examined unionid communities within the same geographic area as the original survey work and provided complete records of site locations allowing revisitation as necessary for purposes of verification (Di Maio 1995, Morris 1996). Morris (1996) provided a comprehensive survey of unionid populations within the Thames River drainage that also included sufficient information regarding the structure of the riparian zone to allow for these sites to be included in the discriminant test without site visitation. Di Maio (1995) provided information about unionid numbers, however, these sites did not have any information regarding riparian zones and revisitation was required to characterize the riparian zone.

For the purposes of testing, only sites within drainages that were not used for
Figure 2.1 Location of sites used to test the discriminant model for predicting unionid distributions in relation to riparian vegetation. Site numbers follow DiMaio (1995) (Catfish Cr.) and Morris (1996) (Thames R.).
the development of the original model were included. Accordingly, Morris’ (1996) sites on the Avon R., Whirl Cr., Dingman Cr. and McGregor Cr. were excluded as were Di Maio’s (1995) sites on the Ausable and Saugeen Rivers. The elimination of these sites ensured that the test of the model would be as rigorous as possible and avoided the problems associated with non independence as several of the sites in these drainages lie very close to the original sites. The ability to predict the correct placement (grassy or forested) of a site with a small mussel population is low and therefore only sites possessing a total unionid population in excess of 10 individuals were included for testing purposes.

Results

Model Development

Multiple Discriminant Analysis was conducted using log \((x+1.1)\) transformed species abundance data (# of mussels/hr. collecting) on the two \textit{a priori} riparian classes. Pearson correlations and the discriminant function coefficients are presented in Table 2.1. Positive correlations characterise species occurring more commonly in grassy habitats whereas species with negative correlations are more common to forested habitats. The analysis yielded a significant discriminant function \(\chi^2=36.47, \ df=12, \ p=0.0003\) able to correctly classify 100\% of the original sites sampled (Fig. 2.2). Equation 1 describes the relationship developed for the log transformed species abundances:
Table 2.1: Results of Multiple Discriminant Analysis on the basis of the Log(x + 1.1) transformed relative abundances of the 12 unionid species found to occur in more than one basin.

<table>
<thead>
<tr>
<th>Species</th>
<th>unstandardized coefficient</th>
<th>correlation</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Pyganodon grandis</em></td>
<td>4.257</td>
<td>0.752</td>
</tr>
<tr>
<td><em>Strophicus undulatus</em></td>
<td>-0.00789</td>
<td>0.189</td>
</tr>
<tr>
<td><em>Lasmigona compressa</em></td>
<td>2.848</td>
<td>0.100</td>
</tr>
<tr>
<td><em>Lasmigona complanata</em></td>
<td>0.777</td>
<td>0.007</td>
</tr>
<tr>
<td><em>Amblema plicata</em></td>
<td>-0.757</td>
<td>-0.092</td>
</tr>
<tr>
<td><em>Lasmigona costata</em></td>
<td>-0.837</td>
<td>-0.099</td>
</tr>
<tr>
<td><em>Actinonaias ligamentina</em></td>
<td>-2.371</td>
<td>-0.107</td>
</tr>
<tr>
<td><em>Alasmidonta marginata</em></td>
<td>0.968</td>
<td>-0.119</td>
</tr>
<tr>
<td><em>Lampsilis radiata</em></td>
<td>1.257</td>
<td>-0.159</td>
</tr>
<tr>
<td><em>Lampsilis cardium</em></td>
<td>0.107</td>
<td>-0.166</td>
</tr>
<tr>
<td><em>Fusconaia flava</em></td>
<td>-0.269</td>
<td>-0.166</td>
</tr>
<tr>
<td><em>Elliptio dilatata</em></td>
<td>-1.108</td>
<td>-0.181</td>
</tr>
</tbody>
</table>

\[ \chi^2 = 36.472 \]
\[ p = 0.0003 \]
Equation 1 \[ \text{species DF1} = 4.257(T. grandis) - 0.00790(S. undulatus) + 2.848(L. compressa) + 0.777(L. complanata) - 0.757(A. plicata) - 0.269(F. flava) - 0.838(L. costata) + 1.257(L. radiata) + 0.968(A. marginata) - 2.371(A. ligamentina) + 0.107(L. cardium) - 1.10(E. dilatata) - 3.307. \]

A positive DF1 score indicates that the species assemblage is characteristic of grassy sites whereas a negative score for species DF1 indicates a forested species assemblage.

A second Multiple Discriminant Analysis was conducted on the 24 sites in the two a priori riparian categories (grassy and forested) using the three riparian characteristics found to differ significantly between the habitats (riparian width, plain slope, valley slope - all greater at forested sites). The environmental discriminant function \( \chi^2 = 97.66, \text{df} = 3, p < 0.0001 \) correctly classified 85% of the sites (Fig. 2.2, Table 2.2). Equation 2 describes the relationship between the environmental variables:

Equation 2 \[ \text{environmental DF1} = 0.0834(\text{riparian width}) + 0.0569(\text{valley slope}) + 0.0362(\text{plain slope}) - 4.053. \]

A negative value for environmental DF1 indicates a riparian zone characteristic of grassy habitats whereas a positive value indicates that the site belongs in the forested category.
Figure 2.2. Multiple Discriminant Analyses on the basis of unionid species (y axis) and physical riparian characteristics (x axis). *A priori* riparian classification is represented by open (grassy sites) and closed (forested sites) symbols. Codes refer to specific site locations (AN - Avon R., AU - Ausable R., DG - Dingman Cr., MG - McGregor Cr., SA - Saugeen R. and WH - Whirl Cr.). Numbers correspond to upstream (1) and downstream (4) positions.
Table 2.2: Results of Multiple Discriminant Analysis on the basis of environmental variables found to differ between riparian classes.

<table>
<thead>
<tr>
<th>variable</th>
<th>unstandardized coefficient</th>
<th>correlation</th>
</tr>
</thead>
<tbody>
<tr>
<td>riparian width</td>
<td>0.0835</td>
<td>0.8194</td>
</tr>
<tr>
<td>plain slope</td>
<td>0.0362</td>
<td>0.4531</td>
</tr>
<tr>
<td>valley slope</td>
<td>0.0569</td>
<td>0.2000</td>
</tr>
</tbody>
</table>

\[ \chi^2 = 97.658 \]

\[ p < 0.0001 \]
**Discriminant Model Test**

The discriminant model was tested using the 16 sites outlined earlier and the two discriminant equations developed above. Sites were initially classified using Equation 2 to determine the physical riparian classification of the site. This was done because the physical characteristics of any given site are relatively constant with respect to the sampling regime and represent a logical starting point for future comparisons and conservation efforts. Environmental DF1 scores are presented in Table 2.3. The sites were next classified according to the species DF1 (Equation 1) and tested against the original classification based on the riparian characteristics.

**Test Results**

Sites listed in Table 2.3 showing opposite positive and negative scores for the two discriminant equations represent sites for which the riparian predictions from Equation 2 and the species classification from Equation 1 agree. In contrast, those sites showing positive-positive or negative-negative scores represent sites for which the classifications of the two equations disagree. For example, Thames River site 11 shows a positive riparian score indicating a forested riparian zone and a negative species score representing a forested species assemblage. The predictions of both equations agree (forested) although the signs of the two values (positive for riparian and negative for species) are different. This site represents a positive test of the model.

Seventy-one percent of sites used to test the model were correctly classified according to both the riparian and species discriminant functions leaving only four sites
Table 2.3 Species and Riparian discriminant scores for the 16 sites used to test the model.

<table>
<thead>
<tr>
<th>site</th>
<th>riparian score</th>
<th>species score</th>
</tr>
</thead>
<tbody>
<tr>
<td>Catfish Cr. 1</td>
<td>0.3418</td>
<td>-2.1700</td>
</tr>
<tr>
<td>Catfish Cr. 2</td>
<td>-0.8332</td>
<td>3.3548</td>
</tr>
<tr>
<td>Catfish Cr. 3</td>
<td>-0.2037</td>
<td>1.2397</td>
</tr>
<tr>
<td>Thames R. 1</td>
<td>-0.6268</td>
<td>-1.1959</td>
</tr>
<tr>
<td>Thames R. 10</td>
<td>0.5344</td>
<td>-3.8942</td>
</tr>
<tr>
<td>Thames R. 11</td>
<td>1.8752</td>
<td>-0.9651</td>
</tr>
<tr>
<td>Thames R. 12</td>
<td>5.1746</td>
<td>3.9646</td>
</tr>
<tr>
<td>Thames R. 13</td>
<td>-0.6089</td>
<td>3.0620</td>
</tr>
<tr>
<td>Thames R. 14</td>
<td>1.8049</td>
<td>-2.7864</td>
</tr>
<tr>
<td>Thames R. 15</td>
<td>-0.2394</td>
<td>5.3968</td>
</tr>
<tr>
<td>Thames R. 17</td>
<td>-0.6942</td>
<td>-3.1055</td>
</tr>
<tr>
<td>Thames R. 22</td>
<td>0.6938</td>
<td>-0.4591</td>
</tr>
<tr>
<td>Thames R. 23</td>
<td>-0.9057</td>
<td>0.1975</td>
</tr>
<tr>
<td>Thames R. 24</td>
<td>-0.6614</td>
<td>-3.2599</td>
</tr>
<tr>
<td>Thames R. 29</td>
<td>-0.7665</td>
<td>1.4750</td>
</tr>
<tr>
<td>Thames R. 30</td>
<td>-0.2126</td>
<td>5.4881</td>
</tr>
</tbody>
</table>
incorrectly classified (Fig. 2.3). Sites located in the first or third quadrant are incorrectly classified sites whereas sites located in the second or fourth quadrant are correctly classified sites. Site classification was significantly better than chance ($\chi^2 = 4.27, p < 0.05$).

**Overall Model Performance**

Forty sites were used in the development of the model including 24 to create the model and another 16 to test the first predictions. Eighty percent of all 40 sites examined resulted in positive tests with only seven sites incorrectly classified (Figure 2.4) representing a much better classification than would be predicted by chance ($\chi^2 = 20.36, p < 0.01$). Of the seven incorrect classifications all but one, site TH 12, represent grassy riparian zones with forested species assemblages.

**Discussion**

Unionid distributions can be modeled and even predicted on the basis of riparian landscape characteristics. In chapter 1, I showed that several unionid species had different relative abundances in rivers which differed primarily on the basis of the composition (grass or forest) and size (narrow or wide) of the riparian zone and related physical and chemical parameters. In this chapter I developed a model using the variables which are most important in describing these differences (riparian width and land slope) and which allow for the prediction of species compositions within previously unsampled rivers.

Testing of the model proved successful with 71% of the 16 untested sites and
Figure 2.3 Discriminant scores for the 16 sites used to test the landscape model. Sites in quadrants I and III represent positive tests whereas those in quadrants II and IV represent negative tests. Codes refer to site locations (CF - Catfish Cr. and TH - Thames R.).
Figure 2.4 Overall results of the landuse model for predicting unionid distributions. Correctly classified sites are found in quadrants I and III whereas incorrectly classified sites are found in quadrants II and IV. Please see figures 2.2 and 2.3 for explanation of codes.
a total of 80% of all 40 sites showing unionid communities in agreement with those predicted by the model. Incorrectly classified sites were almost always sites which had riparian zones characteristic of the grassy category but which possessed a unionid community dominated by forested species. Only one misclassified site had a forested riparian zone with a grassy unionid community.

The predominance of this group of misclassified sites initially appears contrary to expectations. Southern Ontario represents an area that has undergone a high degree of landscape modification during the last 100 years (Riley and Mohr 1989) and large areas within southern Ontario (particularly in the extreme southwest) have been cleared of native vegetation to allow for extensive agricultural activity. Given this developmental history, in most cases the grassy riparian category represents rivers which have experienced large disturbances. Apparently, the unionids which characterize these rivers represent a disturbance-tolerant community. Disturbances to unionids can take many forms ranging from hydrological to chemical (see Fuller 1974) and it was therefore expected that the majority of misclassified sites would represent unionid assemblages characteristic of disturbed sites (e.g., *Pyganodon grandis* and *Strophitus undulatus*) in seemingly undisturbed habitats (i.e., forested sites).

Since the pattern of misclassified sites that has become apparent shows a predominance of undisturbed unionid species (e.g., *Elliptio dilatata*, *Lampsilis radiata*, *Fusconaia flava*) in rivers with disturbed riparian zones, I suggest two possible explanations. First, it may be that unionids, at least those which dominate the communities within the study area, are not responsive to these other potential
disturbances. Di Maio (1995) has shown that several species show distinct distributions in relation to hydrological variables suggesting that hydrological regime may result in some of the misclassifications observed in this study. However, many of these species which Di Maio (1995) identified as responsive to flow related variables (e.g., *Lasmigona costata, Amblema plicata*) are species which carry little weight in my model and therefore would have little impact on predictions.

The second explanation relates to the time frame required for distributional changes to occur. The unionid species which characterize the forested community are species with comparably long life spans. Heller (1990) reports life spans for these species up to 19 years (a conservative estimate) resulting in long generation times and slow population turnovers. Rivers with long monitoring records suggest a gradual change in unionid assemblages (over decades) in response to human perturbations (Parmalee and Hughes 1988, Williams et al. 1992). Therefore, these misclassified sites may simply represent sites in the process of a gradual shift towards a disturbed community that is not apparent with a one time sampling effort. To fully investigate this possibility, further monitoring would be required.

Regardless of the explanation for the misclassified sites, the model has proven successful in the majority of cases and provides a useful tool for the development of conservation programs for these organisms. The equations developed in the chapter use the abundances of unionid species to predict the riparian type (grassy or forest) of previously unclassified sites. This method was used to test the original classifications and to determine the applicability of those original classifications. The availability of
riparian measurements and unionid abundances for the test sites permitted this type of comparison, however, the availability of both environmental and biological data sets is not required for future application of the information obtained in this study.

The findings of the model allow for the development of strategies to monitor particular species, both those which the model makes direct predictions about and other rarer species which may show associations with these common ones. There is also the potential for risk assessment in future development within these basins. Using the model it is possible to determine how altering the riparian zone will affect the unionid community and to plan development to meet the specific requirements of each case.

Although the potential benefits of this model are many, care should be taken when applying the model outside of the geographic area in which it was developed. Unionid species can be extremely limited in terms of geographic distributions with many species showing very small ranges while others are endemic to single rivers (e.g. *Dysnomia torulosa*, *Psychobranchus fasciolaris*) (Clarke 1981). However, the species which act as major predictors for this model (particularly *Pyganodon grandis*) tend to be widely distributed (see Clarke 1981) which should improve robustness.

In summary, the landscape model developed within this chapter has proven very efficient at predicting distributions within southern Ontario. Eighty percent of sites examined showed unionid communities in agreement with the model predictions. However, until the mechanism determining these distributions is sufficiently described caution should be used when applying the model particularly outside of the southern Ontario area.

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Chapter 3: Unionid Growth Patterns in Relation to Riparian Land Use

**Introduction**

The continuous production of the unionid shell and the relatively permanent record provided within its hard tissue has been the focus of much research (McCuaig and Green 1983, Hinch et al. 1986, McMahon 1991). The shell has been used to examine accumulation of metal contaminants (Naimo 1995), age structures and population dynamics (Neves and Moyer 1988), historic distributions through archeological excavation (Parmalee and Hughes 1994) and abundant research exists on unionid growth rates determined through shell analysis (McCuaig and Green 1983, Hinch et al. 1986).

The unionid shell consists of three layers secreted by the underlying mantle tissue. The outermost layer, the periostracum, is a proteinaceous layer whereas the two inner layers consist of inorganic calcium carbonate. The periostracum is important in the deposition and maintenance of the calcium carbonate layers and provides a relatively impermeable barrier to water thereby preventing dissolution of the calcium carbonate (McMahon 1991). The two inner layers, the prismatic and nacreous, are continuously deposited and provide the rigidity and strength of the shell (McMahon 1991).

The unionid shell possesses many distinct growth bands on the outer periostracum layer. These bands have long been considered to represent annual growth rests and were often used to determine age as well as growth (Chamberlain 1931,
Negus 1966). Band formation may be the result of overlapping layers of prismatic shell and periostracum arising from repeated withdrawal of the mantle tissue into the shell during the fall period of temperature fluctuations preceding the winter freeze (Tevesz and Carter 1980). Another theory suggests that bands form under anaerobic conditions produced during prolonged periods of valve closure resulting in calcium extraction from the shell layers to buffer the accumulation of anaerobic byproducts such as succinic acid (Lutz and Rhoads 1977).

Using the techniques of shell analysis as well as direct measurements of shell dimensions obtained from transplantation experiments, unionid growth has been linked to many environmental factors. Hinch et al. (1989) reported that shell thickness was related to water chemistry including pH and alkalinity whereas shell dimensions were more closely related to sediment characteristics. Hinch et al. (1986) found similar sediment relationships with obesity (width:length) related to sediment type in transplanted specimens of Lampsilis radiata in Lake Erie.

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

In earlier work (chapters 1 & 2), I showed that unionid distributions differ on the basis of riparian vegetation within the drainage and that these distributions can be predicted on the basis of these associations. In addition to the differences in unionid assemblages, these habitats differ in terms of temperature and other environmental
factors. Sites with narrow grassy riparian zones also showed elevated daily temperature fluctuations and possessed higher concentrations of ammonia nitrogen and TKN in comparison to sites with wider forested riparian zones.

The potential for an energy intensive process such as growth to be important in determining these distributions was investigated in this study. It was predicted that thinner shelled, faster growing species would characterize the disturbed grassy habitats whereas thicker, slower growing species would be more prevalent in the less productive forested habitats. Long term growth rates representative of growth throughout the lifespan were investigated through an analysis of growth rests recorded in the shells of unionids obtained 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 was examined through a reciprocal transplant experiment.

Methods

Long Term Growth Rates

Since freshwater mussels are extremely long lived, with species common to southwestern Ontario reaching ages in excess of 25 years, long term growth characteristics may be important in structuring community compositions. To investigate this possibility, long term growth rates were estimated using the external growth markings following the methods of McCuaig and Green (1983). This method allows the construction of growth curves for species based on historical growth over the entire lifespan 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 a) species which had significantly different occurrence rates in grassy and
forested riparian zones and b) one species which did not differ according to riparian
type.

*Specimen Collection*

Initial long term (8-10 years) growth estimates were calculated on the basis of
voucher specimens collected from all rivers during 1994 (see chapter 1) as well as
voucher specimens collected by Di Maio in 1993 (Di Maio 1995) from the Ausable and
Saugeen rivers. Because of limited sample sizes for some species, additional searches
were conducted on July 27 1995 for *Pyganodon grandis* (Ausable 3), *Lasigmota
complanata* (Dingman 2 and McGregor 3), and *Elliptio dilatata* (Ausable 3). Also,
because *P. grandis* individuals in forested habitats were rare and because the size of
individuals available from forested sites was much smaller than those available from
grassy habitats, a special collection of *P. grandis* individuals from grassy sites (Avon,
R., Whirl Cr) was conducted on July 28, 1995 to supply individuals of the same size
for analysis. This was done to eliminate possible confounding effects of size
differences and a lack of overlapping sizes during the analysis. For locations of
sampling sites please see Figure 1.1.

For the comparison of growth rates for all species in grassy and forested rivers,
48 individuals from grassy rivers and 62 individuals from forested rivers were used.
Two hundred individuals of both *Pyganodon grandis* and *Elliptio dilatata* were used to
compare growth of these species from grassy and forested rivers. For the comparison of the specialist species *Pyganodon grandis* in both grassy and forested rivers, 20 forested specimens and 20 grassy specimens were used. Eighty-five individual *Lasnigona complanata* (45 from forested rivers and 40 from grassy rivers) were used for the comparisons of this generalist species. Individual mussels were used for only one study and no individuals were included in more than one comparison.

**Growth Rate Determination**

Following the methods of McCuaig and 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 with most producing two pairs. Although the annularity of growth rings has been brought into question recently (see Downing et al. 1992), the technique employed in this 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 that 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, discussion of results will refer to growth seasons and not to years directly.

**Statistical Testing**

Unionid growth has been described by many to follow a pattern described by
the von Bertalanffy growth curve (Walford 1946, McCuaig and Green 1983, Hinch et al. 1986). The von Bertalanffy equation:

\[ \text{Equation 3.1} \quad L_t = L_x (1-e^{-kt}) \]

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 characterised 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:

\[ \text{Equation 3.2} \quad L_x = a / (1-b) \]

\[ \text{Equation 3.3} \quad k = -\ln b \]

where "a" represents the intercept of the Walford Plot and "b" is the slope. Walford Plot regressions were compared using Analysis of Covariance (ANCOVA) (Sokal and 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

Two species were chosen for the transplant study on the basis of the comparison of relative abundances in Chapter 1. The two species selected possess the highest univariate F-ratios and represent the species with the most highly significant differences in relative abundances in the two riparian habitats. These species occur in both habitats but at much higher rates in one habitat type. *Elliptio dilatata* was selected as the representative forested species and *Pyganodon grandis* was chosen to represent grassy species.

Two hundred individuals of each species were collected on May 15-16 1995 from two sites. *Pyganodon grandis* individuals were collected from Whirl Creek site 2 and *Elliptio dilatata* specimens were obtained from Saugeen River site 3. 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. 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 used in each river. Three forested rivers (Saugeen R., Ausable R., Dingman Cr.) and 3 grassy rivers were used (Avon R., Whirl Cr. McGregor Cr.) (Figure 3.1). Within the two rivers that acted as sources for the experimental animals (Saugeen R and Whirl Cr.), 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 as these sites represented the largest sites with 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. Quadrats consisted of cement filled #6 PVC piping 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 anterior end buried. The resulting density of 20 unionids / m² is within the natural range encountered for this area (Morris personal observation).

All experimental quadrats were established on May 24 and 25, 1995 and remained in place until September 6-7, 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
Figure 3.1 Location of sites used during reciprocal transplant study to examine short term unionid growth patterns.
quadrats were searched for marked individuals and the area from 5 m upstream to 5 m
downstream of the quadrats was also searched. All live and dead individuals were
collected and returned to the laboratory where the initial measurements were repeated
to determine change in size over the experimental period.

Statistics

Differences in final sizes were tested using Analysis of Covariance (ANCOVA).
Because 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. Analysis of covariance
using initial size as the covariate allows for this control without the use of potentially
confounding variables.

Results

Long Term Growth Rates

Whole Community Estimates

Using the voucher specimens obtained during the initial survey work (chapter 1)
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
forested and grassy rivers. A Walford Plot based on these vouchers is presented in
Figure 3.2. A test of common slope conducted on regression equations presented in
Figure 3.2 revealed that the two lines did not differ significantly ($F_{(1,338)} = 0.984$,
p > 0.05) and the lines were assumed to possess a common slope. Analysis of
Figure 3.2 Walford plots for whole community estimates of growth rates. Plot represents growth rates determined for voucher specimens collected from grassy rivers (n=48) and forested rivers (n=62).
Covariance 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.

Analysis of Covariance showed that the lines possess significantly different intercepts (Table 3.1), indicating that riparian type was a significant predictor of length (Table 3.1). The lines should be treated as two different lines described by the following equations:

**Equation 3.4** grassy \[ \ln L_{x+1} = 0.785 \ln L_x + 27.42 \] \[ r^2 = 0.77 \]

**Equation 3.5** forested \[ \ln L_{x+1} = 0.919 \ln L_x + 16.81 \] \[ r^2 = 0.89 \]

The significant difference of these two regression lines (Figure 3.2) indicates that the unionid communities in rivers flowing through different riparian types exhibit different long term growth patterns. These growth patterns follow the von Bertalanffy growth curve and are described by the following equations:

**Equation 3.6** grassy \[ L_x = 128.09(1-e^{-0.241t}) \]

**Equation 3.7** forested \[ L_x = 209.53(1-e^{-0.084t}) \]

These growth patterns reveal that mussels of grassy communities show an initially rapid
Table 3.1 Analysis of Covariance for whole community estimates of long term growth patterns in grassy and forested habitats using length at the first interval ($l_1$) as the covariate.

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>SS</th>
<th>MS</th>
<th>F</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Covariate</td>
<td>1</td>
<td>1292.87</td>
<td>1292.87</td>
<td>1963.80</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Basin Type</td>
<td>1</td>
<td>21.21</td>
<td>21.21</td>
<td>32.22</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Error</td>
<td>362</td>
<td>238.32</td>
<td>0.66</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>364</td>
<td>1538.53</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
growth during the early growth stages but level off earlier than forested species and reach smaller maximum sizes (Figure 3.3).

Specialist Species

Long term growth patterns of the two most important species for distinguishing between grassy and forested communities, *Pyganodon grandis* and *Elliptio dilatata* respectively, were determined (Figure 3.4). 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 regression lines (Figure 3.4). These results indicate that *Pyganodon grandis* has a Walford plot described by Equation 3.8, whereas *Elliptio dilatata* has a Walford plot described by equation 3.9.

**Equation 3.8**

\[
P. \text{ grandis} \quad \ln L_{t+1} = 0.399 \ln L_t + 25.70 \quad r^2 = 0.75
\]

**Equation 3.9**

\[
E. \text{ dilatata} \quad \ln L_{t+1} = 0.577 \ln L_t + 17.50 \quad r^2 = 0.89
\]

The von Bertalanffy growth curves for these two specialist species are described by equations 3.10 and 3.11 (Figure 3.5).

**Equation 3.10**

\[
P. \text{ grandis} \quad L_t = 84.70 \left(1 - e^{-0.457t}\right)
\]
Figure 3.3 Theoretical Von Bertalanffy growth curves for whole community growth rates determined from the Walford plot equations in Figure 3.2.
Figure 3.4 Walford plots for the two species (*Pyganodon grandis* and *Elliptio dilatata*) most important in discriminating between grassy and forested sites. Two hundred specimens of each species were used for the determination of the regression equations.
Figure 3.5 Theoretical von Bertalanffy growth curves for *Pyganodon grandis* and *Elliptio dilatata* obtained from the Walford plot analysis.
Equation 3.11  \[ E. \text{ dilatata} \quad L_{\alpha} = 119.73 \left(1-e^{-0.129}\right) \]

*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 (Chapter 1 and 2) in its favoured grassy habitat and also in the unfavoured forested habitat.

Figure 3.6 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 \( F_{1,59} = 0.829, \ p > 0.05 \) indicating a common slope for both populations. The Analysis of Covariance test for common intercepts also showed a nonsignificant result (Table 3.2) indicating that the lines do not differ significantly and should be represented by a single regression equation -

_Equation 3.12._  \[ \ln L_{x+1} = 0.457 \ln x + 12.37 \quad r^2 = 0.73 \]

The von Bertalanffy equation (Equation 3.13) for the growth curve of *Pyganodon grandis* is presented in Fig 3.7.

_Equation 3.13_  \[ L_{\alpha} = 135.13 \left(1-e^{-0.278}\right) \]
Figure 3.6. Walford plot for the specialist species *Pyganodon grandis* in grassy (n=20) and forested (n=20) basins.
Table 3.2 Analysis of Covariance 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.

<table>
<thead>
<tr>
<th>Source</th>
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<th>p</th>
</tr>
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<tbody>
<tr>
<td>Covariate</td>
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<td>177.868</td>
<td>177.868</td>
<td>220.58</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Riparian Type</td>
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<td>0.027</td>
<td>0.027</td>
<td>0.03</td>
<td>0.856</td>
</tr>
<tr>
<td>Error</td>
<td>61</td>
<td>49.187</td>
<td>0.806</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>63</td>
<td>243.840</td>
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<td></td>
<td></td>
</tr>
</tbody>
</table>
Figure 3.7. Theoretical von Bertalanffy growth curve for the specialist species *Pyganodon grandis* in both open and forested basins.
Generalist Species

Species which occur in both habitats (grassy and forested) without preference for one habitat or the other (e.g., *Lasigmoida complanata*) are considered habitat generalists. The Walford plot for two populations of *Lasigmoida complanata*, one from forested sites and one from grassy sites, is presented in Figure 3.8. The test of slopes for these two regression lines indicated no significant difference between grassy and forested populations ($F_{(1.98)} = 0.463, p > 0.05$). Analysis of Covariance however, showed a significant effect of basin type (Table 3.3) indicating different intercepts and distinct regression lines for the two sources.

\[ \text{Equation 3.14} \quad \text{grassy} \quad \ln L_{x+1} = 0.583 \ln L_x + 10.31 \quad r^2 = 0.88 \]

\[ \text{Equation 3.15} \quad \text{forested} \quad \ln L_{x+1} = 0.373 \ln L_x + 15.39 \quad r^2 = 0.91 \]

The von Bertalanffy growth lines for these two distinct populations are shown in Figure 3.9 and described by equations 3.16 and 3.17.

\[ \text{Equation 3.16} \quad \text{grassy} \quad L_x = 136.59 \left(1-e^{-0.457x}\right) \]

\[ \text{Equation 3.17} \quad \text{forested} \quad L_x = 153.61 \left(1-e^{-0.212x}\right) \]
Figure 3.8 Walford Plot for the generalist species *Lasigmona complanata* in grassy (n=40) and forested (n=45) basins.
Figure 3.9. Theoretical von Bertalanffy growth curves for the generalist *Lasmigona complanata* in grassy and forested basins.
Table 3.3 Analysis of Covariance test for common slopes of Walford plots for *LasGINGona complanata* in grassy and forested habitats. The covariate was the length at the first interval ($l_1$).

<table>
<thead>
<tr>
<th>Source</th>
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</tr>
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<tr>
<td>Covariate</td>
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<td>404.13</td>
<td>404.13</td>
<td>787.67</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Riparian Type</td>
<td>1</td>
<td>26.69</td>
<td>26.69</td>
<td>52.03</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Error</td>
<td>101</td>
<td>51.82</td>
<td>0.51</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>103</td>
<td>492.27</td>
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</tbody>
</table>
Short Term Growth - Reciprocal Transplant

Recovery Rates

Recovery of marked specimens ranged from 50 - 90%. Individual species showed significantly different recovery rates with recovery of *Elliptio dilatata* (77.1%) being significantly higher than recovery of *Pyganodon grandis* (56.5%) (Table 3.4). 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 3.4). Although there is a nonsignificant 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 (Figure 3.10). 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 Analysis of Covariance and a 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 3.5). Results for final mussel width (Table 3.6) and height (Table 3.7) showed identical patterns of significance.
Table 3.4 Analysis of Variance for recovery of unionids after the reciprocal transplant study.

<table>
<thead>
<tr>
<th>Source</th>
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<td>Transplant Basin</td>
<td>1</td>
<td>2.1</td>
<td>2.1</td>
<td>0.01</td>
<td>0.919</td>
</tr>
<tr>
<td>Species</td>
<td>1</td>
<td>1260.8</td>
<td>1260.8</td>
<td>6.66</td>
<td>0.033</td>
</tr>
<tr>
<td>Basin*Species</td>
<td>1</td>
<td>330.7</td>
<td>330.7</td>
<td>1.75</td>
<td>0.223</td>
</tr>
<tr>
<td>Error</td>
<td>8</td>
<td>1515.3</td>
<td>189.4</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>11</td>
<td>3108.9</td>
<td></td>
<td></td>
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</tbody>
</table>
Figure 3.10. Recovery rates of marked specimens of *Pyganodon grandis* and *Elliptio dilatata* after the 105 day transplant study.
Table 3.5 Analysis of Covariance for final length after the reciprocal transplant experiment. The initial length prior to transplant was used as the covariate.

<table>
<thead>
<tr>
<th>Source</th>
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<th>p</th>
</tr>
</thead>
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<tr>
<td>Covariate</td>
<td>1</td>
<td>11652.0</td>
<td>11652.0</td>
<td>825.58</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Species</td>
<td>1</td>
<td>198.3</td>
<td>198.3</td>
<td>14.05</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Transplant Basin</td>
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<td>7.8</td>
<td>7.8</td>
<td>0.56</td>
<td>0.457</td>
</tr>
<tr>
<td>River</td>
<td>5</td>
<td>525.8</td>
<td>105.2</td>
<td>7.45</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Species*River</td>
<td>5</td>
<td>1321.8</td>
<td>264.3</td>
<td>18.73</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Error</td>
<td>209</td>
<td>2949.8</td>
<td>14.1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>222</td>
<td>17076.7</td>
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</tbody>
</table>
Table 3.6 Analysis of Covariance for final width after transplantation. Width of mussels before transplantation was used as the covariate.

<table>
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</thead>
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<tr>
<td>Covariate</td>
<td>1</td>
<td>833.37</td>
<td>833.37</td>
<td>114.48</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>Species</td>
<td>1</td>
<td>358.18</td>
<td>358.18</td>
<td>49.20</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>Basin</td>
<td>1</td>
<td>8.41</td>
<td>8.41</td>
<td>1.15</td>
<td>0.284</td>
</tr>
<tr>
<td>River</td>
<td>5</td>
<td>155.16</td>
<td>31.03</td>
<td>4.26</td>
<td>0.001</td>
</tr>
<tr>
<td>Species*River</td>
<td>5</td>
<td>147.56</td>
<td>29.51</td>
<td>4.05</td>
<td>0.002</td>
</tr>
<tr>
<td>Error</td>
<td>209</td>
<td>1521.48</td>
<td>7.28</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td>222</td>
<td>3481.39</td>
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</table>
Table 3.7 Analysis of Covariance for final height after transplantation. Height prior to transplantation was used as the covariate.

<table>
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</thead>
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<td>Covariate</td>
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<td>3089.85</td>
<td>3089.85</td>
<td>1222.99</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Species</td>
<td>1</td>
<td>221.34</td>
<td>221.34</td>
<td>87.61</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Basin</td>
<td>1</td>
<td>0.88</td>
<td>0.88</td>
<td>0.35</td>
<td>0.555</td>
</tr>
<tr>
<td>River</td>
<td>5</td>
<td>194.96</td>
<td>38.99</td>
<td>15.43</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Species*River</td>
<td>5</td>
<td>263.97</td>
<td>52.79</td>
<td>20.90</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Error</td>
<td>209</td>
<td>528.03</td>
<td>2.53</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>222</td>
<td>4540.12</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
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 community growth parameters follow distinct patterns while at a much finer scale, single species follow patterns very similar to those demonstrated by the whole community.

My results have shown that unionid species which characterize forested riparian habitats have initially slow growth rates during the early stages of life but will continue to grow for longer durations than will species which characterize grassy habitats. Although species common to grassy habitats (e.g., *Pyganodon grandis*) demonstrate more rapid growth early in life they reach a maximum size at a younger age (approximately 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 (*Lasmigona complanata*) or with preference for one type (*Pyganodon 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 and is therefore considered a habitat generalist, at least in terms of riparian vegetation. The growth pattern exhibited by this generalist species does not fit into one category or the
other. Rather, the growth pattern shifts depending upon which habitat an individual is found to occupy. In forested habitats, growth is slow and steady throughout life whereas, in grassy habitats growth is rapid early on with a smaller maximum size being achieved earlier.

In contrast to the generalist pattern demonstrated by *L. complanata*, *P. grandis* is a specialist species which, although found at both grassy and forested, shows a distinct preference for grassy habitats. In fact, this species is the most important species for delineating 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. The transplant study of two specialist species, *P. grandis* and *Elliptio dilatata*, confirmed these findings with the amount of growth dependent upon the species but not on the riparian type of the transplant basin.

It is apparent that there is a difference in growth patterns of unionids in relation to riparian vegetation. Species distinct to one habitat or the other demonstrate a single growth pattern while species which are equally able to inhabit either basin type vary their growth pattern in response to the particular riparian conditions present at a site. 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 form the present study and deserves further work. The benefits of the rapid growth pattern demonstrated by grassy species are essentially two-fold. First, rapid growth allows an individual to proceed quickly through the juvenile stages and to achieve substantial size quickly.
Second, as these species also tend to be shorter lived species (Heller 1990), rapid growth allows the achievement of sexual maturity at a younger age (McMahon 1991).

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. Many workers have shown that the removal of streamside 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 unionids within southern Ontario, Di Maio (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 and Minshall 1982). Obtaining a large size quickly may allow these species to overcome these potentially destructive hydrologic forces. Di Maio (1995) showed that mussel assemblages in hydrologically unstable rivers were characterised by larger individuals.

Unionid species which make up the grassy assemblage tend to be members of the Anodontinae (Chapter 1). This major subfamily within the unionidae is characterised by extremely thin shells (Clarke 1981). These thin shells 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). The thin shells with poorly developed teeth structures make these individuals relatively easy prey for muskrats and other predators and lead to a higher than expected
occurrence of these species within muskrat middens (personal observation). Earlier maturation may have evolved in these species as a means of minimizing predation risks. Musk rat predation on unionoids is related to both mussel size and growth rate with preference shown for mussels of a medium size (Jokela and 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 and Mutikainen 1995). Rapid growth is also effective at reducing the time before reproduction. Heard (1975) reported age at first reproduction for members of the Anodonta nae to be between 4-6 years. Although 4-6 years is still a substantial amount of time, this time frame represents earlier reproduction than non-Anodontine species (McMahon 1991).

In an earlier study (Chapter 1), I showed that grassy sites are characterised by increased light penetration, slightly elevated temperatures, greater temperature fluctuations, and increased concentrations of some nutrients. These factors would all seem to favour increased food availability for filtering organisms such as unionoids, which would certainly enhance the potential for growth. Agrell (1949) demonstrated that growth characteristics such as obesity and height are related to the trophic status of the river. 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 predatory susceptibility of the thin shelled species which characterize these habitats. The particular physical and chemical conditions which exist in these habitats allow for these growth differences to occur and may be important structuring elements in determining unionid distribution patterns.
General Discussion

Freshwater mussels are among the most threatened taxonomic groups in North America (Eisner et al. 1995). During the past century large declines in species numbers have been detected, not only in Ontario and North America, but throughout their worldwide distribution (Bogan 1993). Although commercial harvest has been detrimental to some species, by far the most important cause of these declines has been loss of aquatic habitat and declining water quality (Bogan 1993). Recent emphasis has been placed on the conservation of many rare and threatened species of unionids as well as on the halt of further losses.

Many of the diffuse causes of declining water quality in agricultural areas such as southern Ontario are related to poor landuse practices and can be limited through the use of riparian buffer strips. Riparian vegetation has been well documented as an effective filter for runoff from agricultural fields. Castelle et al. (1993) summarized the ability of riparian vegetation to remove sediment and nutrients from agricultural runoff. In addition, the canopy provided by the vegetation can act to limit thermal changes associated with agricultural rivers.

In order to develop effective conservation practices for these threatened organisms it is required that we understand their distributions and the factors responsible for structuring distributional patterns. I have examined unionid distributional patterns in relation to riparian vegetation within southern Ontario. Given the filtering capacity of riparian vegetation and the importance of water quality to filtering organisms such as unionids the potential for landscape variables to act as
efficient predictors of unionid distributions is high.

Species showed significantly different abundances in rivers with different types of riparian vegetation. Rivers with large forested riparian zones were characterised by a species assemblage consisting of *Elliptio dilatata*, *Lampsilis radiata*, *Lampsilis cardium* and *Fusconaia flava*. In contrast, sites with grass dominated riparian zones were characterised by *Pyganodon grandis* and *Strophitus undulatus*.

In addition to the differences in species abundances, a number of differences in the physical and chemical characteristics of the sites were found. Forested sites received significantly less incident solar radiation and showed lower daily temperature fluctuations than did grassy sites. Furthermore, grassy sites showed elevated concentrations of some nutrients including ammonia and TKN in comparison to the forested sites.

The differences observed in species distributions in relation to riparian vegetation provided the basis for the design of a model to describe to unionid distributions in relation to stream side vegetation. Twenty-four sites were examined initially to develop the model and then the model was tested using an additional 16 sites. Using Multiple Discriminant Analyses two classification equations were developed. The first equation allowed for the classification of a site as grassy or forested on the basis of the physical structure of the riparian vegetation, whereas the second classified sites on the basis of the abundances of 12 unionid species.

The 24 sites used to develop the model proved robust to the original *a priori* designations. Twenty-one of these 24 sites showed agreement between the
classifications based on the riparian characteristics and the classifications based on the unionid species. Testing of the model proved equally successful with 12 of the 16 test sites showing agreement between both classifications for an overall success rate of 33 out of 40 or 80% correct.

Sites that were incorrectly classified by the discriminant model fell almost exclusively into one category. Six of the seven incorrectly classified sites represented sites with grassy riparian zones showing a unionid community characteristic of forested sites. Only one site showed the reverse, a forested riparian zone with a grassy unionid community. The reason for this predominance of misclassified sites of this type is not initially clear. Within southern Ontario, the grassy sites can be assumed to represent the more recently disturbed sites as they are sites which have usually been cleared for agricultural activity during recent times. As a result it is expected that the typical grassy community represents a community tolerant of these disturbances. As these rivers are exposed to many disturbances other than those associated with the riparian zone it was originally hypothesised that misclassified sites would represent sites with disturbed communities but undisturbed riparian zones.

Since the majority of misclassified sites do not represent disturbed communities in seemingly undisturbed habitats other factors must be important. One explanation for the patterns observed may simply be that species are responding to other variables within the environment. For example, species may be responding to the hydrologic properties of the drainage. Di Maio (1995) has shown that some species within this geographic area are responsive to flow characteristics and these variables may be
confounding the predictions of the riparian model. Another explanation relates to the age structure of these communities. Species characteristic of forested sites are typically slower growing, later reproducing and longer lived than their grassy counterparts (McMahon 1991, Heller 1993). As a result, the grassy sites with forested species assemblages detected during the classification procedure may represent sites which have not yet experienced the species shift associated with clearing of the riparian zone. In order to investigate these possibilities continued long term monitoring is required.

An analysis of growth patterns of species characteristic of forested and grassy sites was conducted to evaluate the potential of growth rates as structuring elements for unionid communities. The thermal and chemical differences detected for these sites during the initial survey indicated that grassy sites were potentially high growth sites. These sites possessed high levels of nutrients, received higher amounts of light and showed greater daily temperature levels which are all important factors for unionid growth (McMahon 1991). It therefore seems likely that species which inhabit grassy sites represent species which are capable of taking advantage of these conditions and maximizing growth.

Analysis of long term growth patterns of forested and grassy communities revealed two distinct patterns of growth. Forested species show a characteristic slow growth over the duration of the life span whereas grassy species showed rapid growth during early life, reaching maximum size relatively quickly (approximately 7 years), however, a smaller maximum size than the forested species. A similar pattern was observed for individual species including Pyganodon grandis (a grassy species) and
Elliptio dilatata (a forested species).

A generalist species, Lasmigona complanata, which occurs equally in both grassy and forested rivers was examined and showed growth rates characteristic of forested species when occurring in forested rivers but shifted to a grassy pattern when occurring in grassy rivers. This ability to shift growth patterns was not observed for the specialist species, Pyganodon grandis, which occurred in both habitats but showed a significantly higher abundance in grassy rivers.

Growth patterns, and ultimately size, may be important factors in structuring unionid distributions. Species which are able to grow quickly such as those characteristic of grassy sites may be adapted to resisting the high flows and hydrological instability often associated with rivers absent in riparian vegetation (Hornbeck 1973). The rapid progression through the juvenile stages may result in these species being more resistant to juvenile threats such as predation and dislodgement.

In summary, this study has found that unionid patterns of distribution are related to large scale landscape variables within the drainage basin. These distributions can be predicted on the basis of physical riparian characteristics and may be useful in developing effective conservation practices for threatened mussel species.
Future Research Needs

The work I have presented within this thesis is the result of a first attempt at directly linking unionid distributions to landscape characteristics within the drainage basin. While I have demonstrated many interesting patterns and relationships I have also served to create many more questions that deserve to be addressed in the future.

The discriminant model developed in chapter 2 has proven to be very effective at predicting distributions within southern Ontario. Although care should be taken in the wide application of this model, the limits of its predictive abilities need to be tested. I would recommend gradually increasing the geographic testing range of the model. The most obvious starting point would be to move east towards the central Ontario region where rivers such as the Grand R., Credit R. and Ottawa R. may provide suitable test sites. Testing within Michigan and other lower Great Lakes states also seems like a suitable area as these states represent part of the Great Lakes drainage in which the original model was developed.

Once the predictive limits of the model are established, it would be beneficial to determine if this type of landscape model can be developed for other regions removed from the predictive region of this model. This may help to determine what factors are actually controlling these distributions and will aid in our understanding of interactions between the aquatic and terrestrial environments.

The predictive ability of the model may be enhanced by the inclusion of other large scale habitat variables. The most obvious of these and also the one which I feel would prove most beneficial is some measure of hydrology. Flow dynamics are
inherently important to an organism that lives in an erodible substrate and one that relies on passive currents for both feeding and reproduction. In addition, the link between landuse in the drainage basin and the hydrology of the water body, although imperfect, is well established. Including a measure of hydrology, whether through a water column parameter such as discharge or a measure of sediment movement (e.g., scouring chains) may help the predictability of the model and warrants future attention.

During the examination of growth rates in chapter 3, I was limited in the comparisons I could make because of small sample sizes for some species (e.g., *Elliptio dilatata* in grassy habitats). With the new sites classified during the testing of the model, it is likely now possible to obtain samples large enough to compare this specialist species in its unpreferred habitat with growth curve established for its preferred habitat. This test would be beneficial in confirming the findings for *Pyganodon grandis*.

I would also recommend repeating the transplant study with a generalist species. The results of this transplant would help to determine if the duration of the experiment was long enough to clearly see differences between the basin types.

Further work needs to be done to address other potential factors influencing these distributions. Long term studies addressing species specific survival rates in the two habitats and studies of reproduction and juvenile establishment will aid in determining whether the observed distributions are the result of an inability of particular species to colonize a basin (reproduction and juvenile establishment) or an inability to persist in a basin (survival).
Finally, I would like to see an attempt made at applying this model in a conservation setting. Whether the model is used in terms of preserving riparian habitat in areas under development or as a means of restoring riparian vegetation to areas from which it has been removed, the benefits of the model are important and deserve to be tested under actual conservation conditions.
Literature Cited


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