UNDERGRADUATE THESIS

FRST 498

Demography of a Population of Freshwater Bivalve (*Anodonta kennerlyi)* and their Annual Filtration Capacity of Marion Lake, British Columbia

by

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Abstract

The recent colonization by *Anodonta kennerlyi* (Bivalvia: Unionoida: Unionidae) of Marion Lake, BC has had unknown effects on the ecosystem. The lake was systematically sampled to determine the distribution of mussels in the lake and individuals brought back to the lab enabled the construction of an age-volume regression. It was found that the mussel distribution did not vary with depth, proximity to inlet or outlet, or side of lake-basin ($P > 0.05$) and possible explanations include the shallow morphology of the lake and their dependence on currents and fish hosts for dispersal. Of the individuals sampled, 57% were in the seven to ten year age classes indicating a pulsed recruitment. The average age was 8.16 ± 0.36 (SE) years. Age was a good indicator of volume ($r^2 = 0.72$) and AFDM ($r^2 = 0.67$) and there was also a strong relationship between the volume of the individual and the AFDM of the soft tissues ($r^2 = 0.81$). The average biomass per square meter was 0.29 ± 0.04 g/m^2 and the approximate total biomass was 39000 g. The mean number of mussels per square meter was 1.55 ± 0.27 mussels/m^2 and the maximum density that was sampled was 8.89 mussels/m^2. Literature values were used to approximate the daily filtration capacity of the population and create regressions of filtration rate and temperature. Four separate temperature-dependent filtration rate scenarios were made to estimate the proportion of the lake filtered each year by the population. The 'high' scenario yielded an estimate of 107% annually while the 'low' scenario estimate was 15%. Two other scenarios based on the literature and the literature average predicted 45% and 41%, respectively. The largest daily proportion of the lake filtered was 0.5% which is not considerable, however the effects on primary production are unknown and could be greater than expected. The population of *Anodonta kennerlyi* likely filter a significant volume of water annually (approximately 40%) and could be experiencing density-dependant effects due to space or food competition. Less than 10% of the population is in the one to three years age classes and this indicates that the population is currently not recruiting new individuals. Further studies should be executed to determine the extent of the mussel population's effect on primary productivity in Marion Lake and if density-dependent effects are influencing the population dynamics.

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Introduction

Freshwater mussels are significant components of many aquatic ecosystems in British Columbia and globally. They can drastically alter water bodies through their life processes such as filter feeding and are often referred to as ecosystem engineers because of their ability to rapidly decrease lake turbidity and alter nutrient levels as well as other characteristics of the ecosystem (Jones et al. 1997; Vaughn & Hakenkamp 2001; Vaughn et al. 2008). They help to stimulate production across all trophic levels by way of filtering water from the water column and transferring nutrients to the benthos (Dame 1996; Strayer et al. 1999; Vaughn & Hakenkamp 2001; Vaughn et al. 2008). Bivalves have several roles in aquatic ecosystems which include trophic, nutrient cycling, structural, monitoring, and indicating roles (Dame 1996).

However, freshwater mussels are also one of the most endangered groups of organisms on the planet and many species are rapidly declining due to threats such as dam construction, dredging, overharvest, and chemical pollution (Gatenby et al. 1996; Ricciardi & Rasmussen 1999). They are relatively immobile and do not move far during their lifetime other than dispersal as glochidia (larval stage) or drawing themselves into the sediment and deeper into the water they occupy by way of their foot (Nedeau et al. 2009). Because of this, freshwater mussels are greatly affected by changes to their environment and are unable to migrate away from disturbances and thus an understanding of their ecology and biology is of utmost importance to conservation efforts.

Freshwater mussels feed across trophic levels on algae, bacteria, detritus, and zooplankton (Vaughn et al. 2008). They compete with other invertebrates for food and can drastically limit the primary production of the ecosystem (Strayer et al. 1999; Vanderploeg et al. 2001; Vaughn & Hakenkamp 2001). Assemblages of mussels and their shells provide habitat for invertebrates and periphyton, stabilize the sediments, and deposit organic matter in the form of feces and pseudofeces (Strayer & Malcom 2007; Vaughn et al. 2008). Freshwater mussels are often preyed upon by terrestrial predators such as racoons (Gagnon et al. 2004). Nutrient cycling is an important role of freshwater bivalves as they excrete phosphorous and ammonia and release stored nutrients as they decay (Vaughn & Hakenkamp 2001; Strayer et al. 2007). Primary production is supported by the conversion of suspended solids to dissolved nutrients by mussels (Vaughn et al. 2008).

Because of the high extinction rates of freshwater mussels, it is important to understand their populations and behaviour. Ricciardi and Rasmussen (1999) stated that the freshwater fauna species were being lost at a rate of 4% a year which is comparable to the loss of our terrestrial rainforests. Because the loss of aquatic species is not as easily observed as terrestrial ones, freshwater mussels have been declining with little knowledge as to why and without much public concern. An examination of a population of *Anodonta kennerlyi* (Lea, 1860) could provide useful information and understanding of their habitat preference, population structure, and role in the ecosystem they inhabit. Additional research on freshwater mussels could offer means by which people can conserve species and use aquatic systems more wisely.

Demography

Demography is used to assess the current status of a population, compare populations, and predict future abundance (Berg et al. 2008). Generally, it includes fecundity and mortality data as well as other descriptors such as age structure and frequency of reproduction (Berg et al. 2008). Long-term modelling of mussel populations can reveal the trajectories of the population when factors such as adult space limitation, larval food limitation, and adult survivorship are taken into account (Strayer & Malcom 2006). When industry and other human interactions affect waterways where mussels reside, it is important to have sound data on the historical population. Methods that are simple and inexpensive to execute are vital to ensure that these data exist.

Most studies collect physical and biological data of the environment while also collecting demographic data. Factors such as mean annual temperature, pH, and phytoplankton abundance would have an effect on bivalve populations and their characteristics. Data on individual mussel size, and habitat preference may also be noted. Quantitative total substratum samples are required for detailed analyses of population demography and estimates of density and recruitment (Miller & Payne 1993). Species that are most easily and most often collected through field sampling are large as adults, have very distinct shells, and do not bury deeply into the sediment (Miller & Payne 1993). A large percentage of individuals less than 30 mm long is an indication of recent recruitment (Miller & Payne 1993). Several methods are typically used for mussel sampling: dredging of soft sediments, putting samples of sediment through a mesh sieve, hand collection by snorkel or scuba, and often wading through soft sediments and feeling for individuals by hand (Miller & Payne 1993; Strayer & Malcom 2006; Loayza-Mura & Elias-Letts 2007).

Feeding

Freshwater mussels feed on small particles in the water through filter-feeding and to some extent, deposit feeding (Raikow & Hamilton 2001; Vaughn & Hakenkamp 2001; Vaughn et al. 2008; Thorp & Covich 2009). The mussels feed by capturing food using cilia which are located on the mantle, demibranches, and visceral mass (Vaughn et al. 2008). The cilia move in synchrony to create currents of water inside and outside the shell, drawing in water, oxygen, and food and expelling waste as water leaves the shell (Vaughn et al. 2008; Nedeau et al. 2009). Various factors such as temperature, species, animal size, and population density affect how much water an individual mussel can filter, but the volume is generally quite substantial with current estimates ranging from 0.2 to 2.8 $L\ h^{-1}\ g^{-1}$ AFDM depending on species (Alimov 1969; Silverman et al. 1997; Vaughn & Hakenkamp 2001; Vaughn et al. 2008).

Unionid mussels are commonly epibenthic, with their foot anchoring them into the sediments and siphons extended into the water column. Mussels feed on small particles (<20 µm) found in the water column or in sediment (Vaughn et al. 2008). These small particles include phytoplankton, zooplankton, algae, bacteria, small organic particles, and protozoans (Gatenby et al. 1996; Vaughn & Hakenkamp 2001; Vaughn et al. 2008). Depending on habitat, mussels may only be primary consumers, but in other habitats that are often more productive, they feed on many trophic levels. Deposit feeding has

not been studied extensively, however further research is necessary as the amount of deposit feeding and suspension feeding a mussel population carries out could help us understand benthic and water column linkages (Vaughn et al. 2008).

Filtration rate is primarily defined as the volume of water that passes through a suspension feeding organism's gills per unit of time and is often measured by determining the rate of removal of a particle that is retained with 100% efficiency (such as algal foods) (Watling 1981; Riisgard 2001; Loayza-Mura & Elias-Letts 2007). Clearance rate is the rate at which the organism can remove a particle from the water through suspension feeding (Riisgard 2001). Filtration rate and clearance rate are slightly different, but in most studies are used interchangeably due to the nature of measuring filtration rate. Many experiments have been done examining the filtration rates of bivalves and have used a variety of methods. These methods include: direct measurement, flow-through chamber, suction, clearance, photo-aquarium, steady-state, video observation, replacement, thermistor, bio-deposit, and impeller methods about which Riisgard (2001) goes into greater detail describing their benefits and shortcomings.

Objectives of this Study

Several questions are examined in this study. How is the distribution of individuals in the lake determined by factors such as depth, proximity to inlet or outlet, and side of lake basin? What is the age-class structure of the population of mussels in Marion Lake? Is individual size and ash-free dry mass a good predictor of age? What is the total biomass of the mussel population in Marion Lake? Is mussel filtration rate affected by temperature and what proportion of Marion Lake is being filtered daily and annually?

By answering the above questions, I hope to provide a basis for future studies on the mussel population in Marion Lake and their effect on the ecosystem. Urban development within the range of *Anodonta kennerlyi* requires us to understand the importance of this species in the aquatic ecosystems of the Pacific North-West so that informed decisions can be made over land-use and management plans.

Methods

Study Area

Marion Lake is located in the Malcolm Knapp Research Forest in Maple Ridge, British Columbia. It is located on a southern slope of the Coast Mountains (Efford 1967). Marion Lake is about 800 m long and 200 m wide at its widest point (Davies 1968). It is in a long, narrow, U-shaped valley 300 m above sea level (Davies 1968). Half of the area of the lake is less than 2 metres deep and is isothermal during the winter and slightly stratified during the rest of the year (Davies 1968). The mean depth is 2.4 m and at the deepest point, during high water, the depth is 7 m (Fig. 2) (Efford 1967; Winterbourn 1971). The surface area of the lake is approximately 13.3 ha (Winterbourn 1971). The northern inlet and southern outlet of the lake both consist of gravel substrate; however, the lake bottom is made up of a brownish mud or silt and there is a

sparse covering of macrophytes throughout the bottom of the lake, but particularly in shallow waters (Efford 1967; Davies 1968).

The average annual precipitation at Marion Lake is 2400 mm and the lowest mean monthly air temperature is 2.9°C, making the climate wet and mild (Efford 1967). The lake is located in the Coastal Western Hemlock biogeoclimatic zone (Efford 1967). The seasonal water temperatures range from a high of 17°C in summer to a low of 2.5°C in winter (Table 1). Nutrient levels are relatively low due to a variety of factors including geologic make-up and fast run-off from heavy rainfall (Efford 1967). The pH ranges from 6.8-7.2 throughout the year (Efford 1967). Oxygen is well distributed and near saturation during the winter, though in summer it decreases significantly near the bottom at deeper depths (Efford 1967).

Table 1: Mean monthly and seasonal water temperatures of the littoral zone of Marion Lake, BC as measured by Winterbourn (1971).

Month	Mean Water Temperature
Jan	1
Feb	2.5
Mar	3
Apr	6
May	14
Jun	18
Jul	16
Aug	16
Sept	15
Oct	10
Nov	6
Dec	4
Winter (Dec-Feb)	2.5
Spring (Mar-May)	7.67
Summer (June-Aug)	16.67
Fall (Sept-Nov)	10.33

Marion Lake has had a long history of being used as a camp site for forestry companies and researchers (Fig.1). Research that had been done on Marion Lake in 1982 did not note a presence of the mussel (confirmed via personal correspondence with Dr. Rolf Mathewes, April 1, 2015), thus the population must have established after that time. One possible mode of entry is through experiments performed by associates of Dr. Dolph Schluter of UBC in the 1990s in which three-spine stickleback (*Gasterosteus* spp.) were kept in enclosures in Marion Lake. As Marion Lake is located in the research forest, experiments may have introduced other fish hosts that could have potentially carried glochidia. In studies of *Anodonta kennerlyi,* where fish have been examined for glochidia, prickly sculpin and three-spine stickleback were the most prevalent hosts (Martel & Lauzon-Guay 2005; Nedeau et al. 2012).

Figure 1. Abernethy & Lougheed Logging Company's camp at Marion Lake in the 1920s (Waite 2008).

Demography

A field-based research component was performed at Marion Lake in mid-June 2014. The presence of freshwater mussels had been observed there several years previously, although not much is known about the population and when it established in the lake. Sampling took place to estimate the mussel's abundance, biomass, and ages and how these factors relate to their longitudinal position in the lake, depth, and the side of lake basin at which they occurred.

Mussels were sampled at eight transects spaced approximately 100 m apart from the inlet towards the outlet on either side of the lake to examine the population longitudinally (Fig. 2). The mussels were sampled at depths of 0.25 m, 0.50 m, and 0.75 m on either side of the lake basin (east and west). The samples were taken using a 30 cm wide dip-net, which was pulled 30 cm along the lake bottom from a boat to collect a sample from a 30 cm by 30 cm square plot. The density of the mussels (number of mussels per 900 cm^2 plot) was recorded and the mussels collected were measured in length, height, and width in the field using calipers and notes were taken regarding the sampling site.

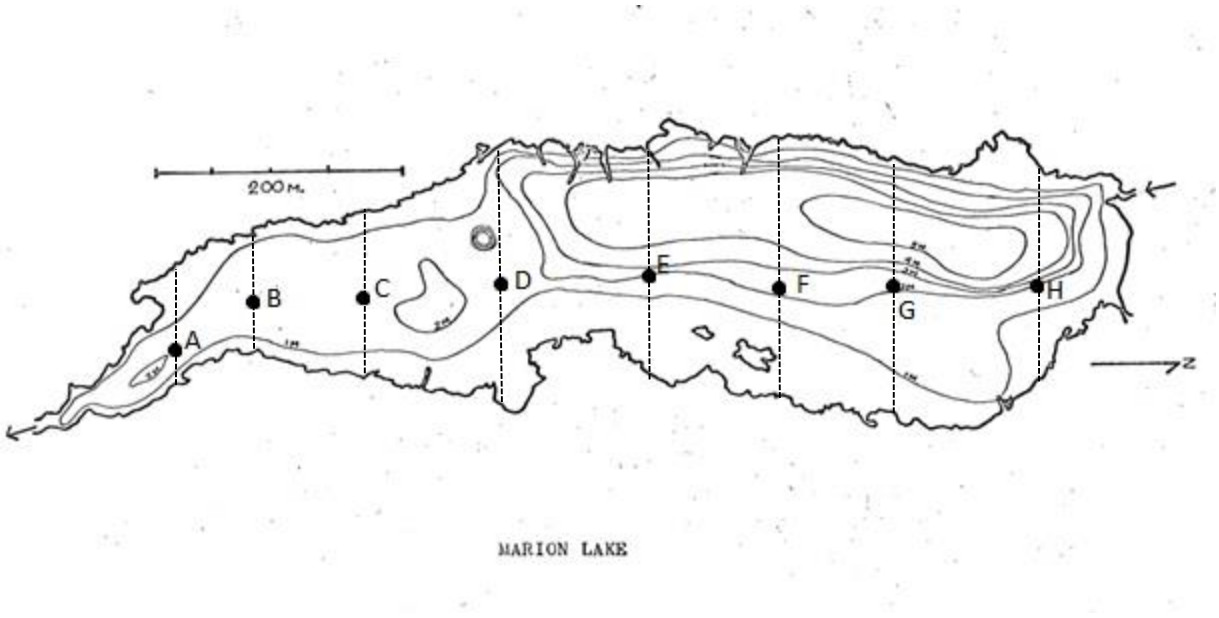

Figure 2: Bathymetric map of Marion Lake with sample transects labeled at approximate locations. Bathymetric map adapted from Davies (1968).

Forty one of the mussels sampled were brought back to the lab, euthanized by refrigerating and then freezing. The flesh was removed from the shells and dried in an oven at 60 °C for 48 hours (Bonneris et al. 2005, Handa et al. 2012) and then ashed at 500°C for 3.5 hours to find the ash-free dry mass of the flesh. The ash-free dry mass of these mussels was then plotted versus shell volume to create a mass-volume regression. The formula for an ellipsoid (i) was used to determine the volume of each individual:

$$\text{Volume} = 4/3 * \text{length}/2 * \text{width}/2 * \text{height}/2 * \pi \qquad \text{(i)}$$

Age was also estimated for the mussels brought back to the lab. The method of enumeration of external growth bands was used as it is simple and growth bands are easy to see on the valves of *Anodonta kennerlyi,* though the method often underestimates age and is not extremely accurate (Neves et al. 1988; Downing et al. 1992). Annual growth bands form on freshwater bivalve shells due to reduced growth, potentially caused by changes in the environment seasonally (Chamberlain 1930). A regression was then made between volume and age as well as AFDM and age to determine the relationship and to examine whether areas of the lake have different age structures.

An analysis of covariance (ANCOVA) was performed using generalised linear mixed models in SAS (PROC MIXED, SAS ver. 9.4, Cary, NC) on mussel abundance, biomass, and average estimated age of each sample and how each variable related to the depth, longitudinal position, and side of the lake (east or west side). A Poisson distribution with zero-inflation was also used in the statistical model for the abundance data, as many samples had zero or only one individual. The r^2 values and equations for the regressions created in the lab were also recorded.

Filtration Rate

Two preliminary experiments (see appendix for detailed description) to study the feeding method and filtration rate of the mussels were planned, however the mussels did not survive when brought to the lab, possibly due to the rapid temperature change, and the experiments did not yield any useable data. Alternatively, literature values of related species were considered, and a table comprising the experimentally determined filtration rates (L h^{-1} g^{-1} AFDM) from other studies at various temperatures (°C) was created to approximate the filtration rate of *Anodonta kennerlyi* (Table 2). All the species were from the family Unionidae.

Table 2. Filtration rates (L h^{-1} g^{-1} AFDM) at respective temperatures for Unionid species from several studies using a variety of methods. The filtration rates were used to model the proportion of water that the population filters daily and annually.

Species	**Temperature (°C)**	**Filtration Rate (L h^{-1} g^{-1})**	**Reference**
Anodonta anatina	20.0	0.858	Kryger & Riisgard 1988
Unio pictorum	20.0	1.293	Kryger & Riisgard 1988
Unio tumidus	20.0	0.928	Kryger & Riisgard 1988
Anodonta anatina	19.0	0.170	Alimov 1969
Pygnodon cataracta	16.7	0.281	Tankersley & Dimock 1993
Pygnodon cataracta	2.5	0.341	Tankersley & Dimock 1993
Anodonta woodiana	15.9	1.723	Kim et al. 2011
Anodonta woodiana	2.7	0.164	Kim et al. 2011
Anodonta woodiana	16.9	0.262	Kim et al. 2011
Anodonta woodiana	17.0	0.352	Kim et al. 2011
Unio douglasiae	5.4	0.164	Kim et al. 2011
Unio douglasiae	15.0	0.410	Lee et al. 2008
Unionidae sp.	22.0	0.397	McIvor 2004

Four regressions were made using the information presented in Table 2 of the literature studies relating filtration rate to temperature. The first regression used all the literature values across all their corresponding experimental temperatures regardless of species or technique used to measure filtration rate.

A study by Loayza-Mura & Elias-Letts (2007) found a linear relationship between filtration rate and temperature between 5°C and 20°C and this was used to model three other possible scenarios. According to their study, filtration rate was highest at 20°C, and at 5°C the filtration rate had decreased by 80% (Loayza-Mura & Elias-Letts 2007). The relationship between temperature and filtration rate capacity (%) (between 5°C and 20°C) based on Figure 1 in Loayza-Mura & Elias-Letts (2007) was found to be:

$$FC = 5.67*\text{temperature} \qquad \text{(ii)}$$

where FC is the filtration capacity expressed as a percentage of the filtration rate. The study by Loayza-Mura & Elias-Letts (2007) found filtration rates that were greater than 100% capacity and it was not clear what the full capacity filtration rate value was based on. However, due to the large amounts of variation in the literature values for filtration rates that I compiled, I determined the relationship found by Loayza-Mura & Elias-Letts to be sufficient (2007).

To create the modelled scenarios, the experimental temperature from the literature studies was entered into equation (ii) to determine the capacity (%) of the literature filtration rate. It was then possible to determine the corresponding filtration rate in L h^{-1} g^{-1} at 100% capacity and relate this to the findings of Loayza-Mura & Elias-Letts (2007) to make the model. The models used the theoretical filtration rates at 0, 5, 10, 15, and 20°C to generate a regression of temperature and filtration rate in L h^{-1} g^{-1}.

The 'average' scenario created a regression that was based upon the average filtration rate and average temperature over all the literature values. The 'high' scenario created a regression based upon the highest filtration rate from the literature and the 'low' scenario created a regression using the lowest filtration rate. The four scenarios and resulting regressions were then applied to the total biomass of the mussels in Marion Lake and the average seasonal temperatures to calculate the volume of the lake the mussels filter daily and annually. The volume of water in the lake was estimated by multiplying the mean depth by the surface area.

Results

Demography

From the forty-eight samples that were taken from the lake, 72 mussels were retrieved and measured. The mean number of mussels per square meter was 1.55 ± 0.27 (SE) mussels/m^2 and the maximum density that was sampled was 8.89 mussels/m^2. The mean biomass per square meter was 0.29 ± 0.04 g/m^2 and the approximate total biomass in the lake based upon sampling was 39000 g. The approximate number of individuals was 206000. Using the volume-age regression, it was possible to estimate the ages of the mussels in each sample. Of the sampled mussels, the mean age was 8.16 ± 0.36 years. The majority of the mussels (57%) were in the seven to ten year age classes and only six mussels were younger than four years (Fig. 3). The frequency distribution of the number of mussels collected per sample exhibited a classic Poisson distribution with many samples containing only a few mussels and only four samples containing more than five individuals (Fig. 4a). Fifteen of the forty-eight samples contained no mussels. The age-AFDM regression had an r^2 value of 0.67 and as the mussels aged, they had higher biomass (Table 3 and Fig. 4b). AFDM was also positively related with volume (r^2 = 0.81) and volume also increased as mussels aged (r^2 = 0.72) (Table 3 and Fig. 4b and 4c).

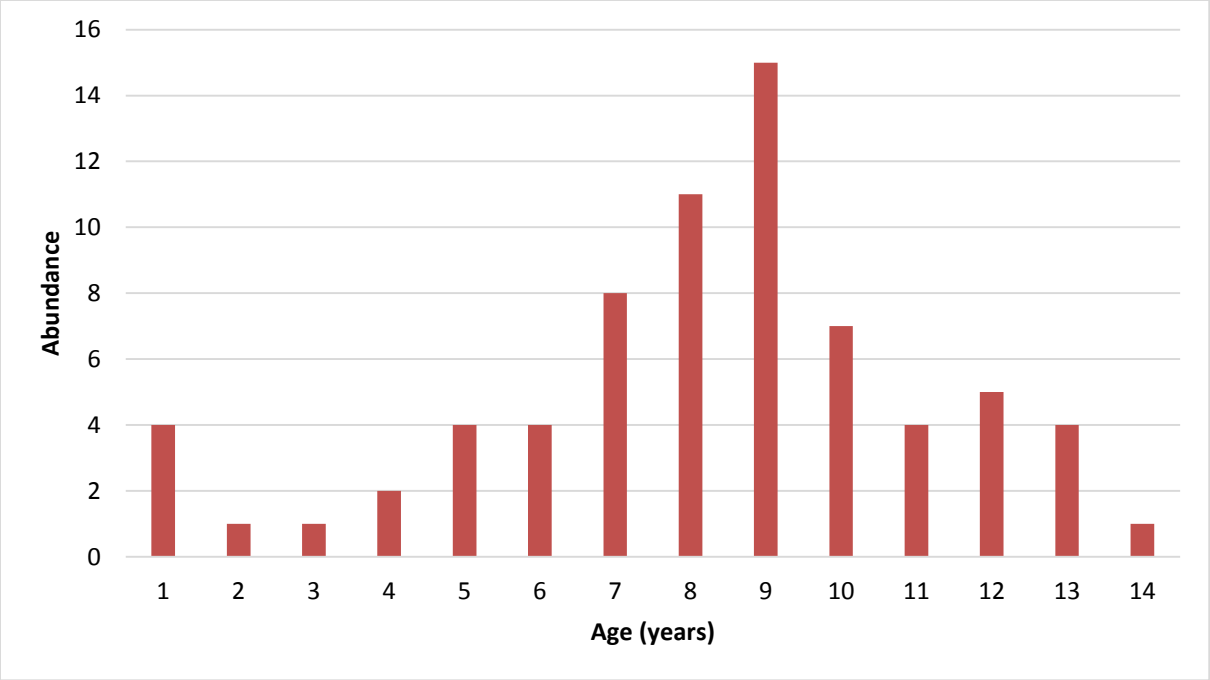

Figure 3. The age class distribution for the mussels that were collected in Marion Lake. Most mussels were aged 7-10 years old and there were few mussels aged 4 years or younger indicating poor recruitment.

Table 3. Equations and correlation coefficients for the relationships between age, volume, and AFDM of the mussels brought back to the lab.

Regression	**r^2**	**Equation**
Age-AFDM	0.67	AFDM = 0.0291*(age) - 0.0645
Volume-AFDM	0.82	AFDM = 1E-05*(volume) + 0.0423
Volume-Age	0.72	Volume = 2780.4*(age) - 8948.2

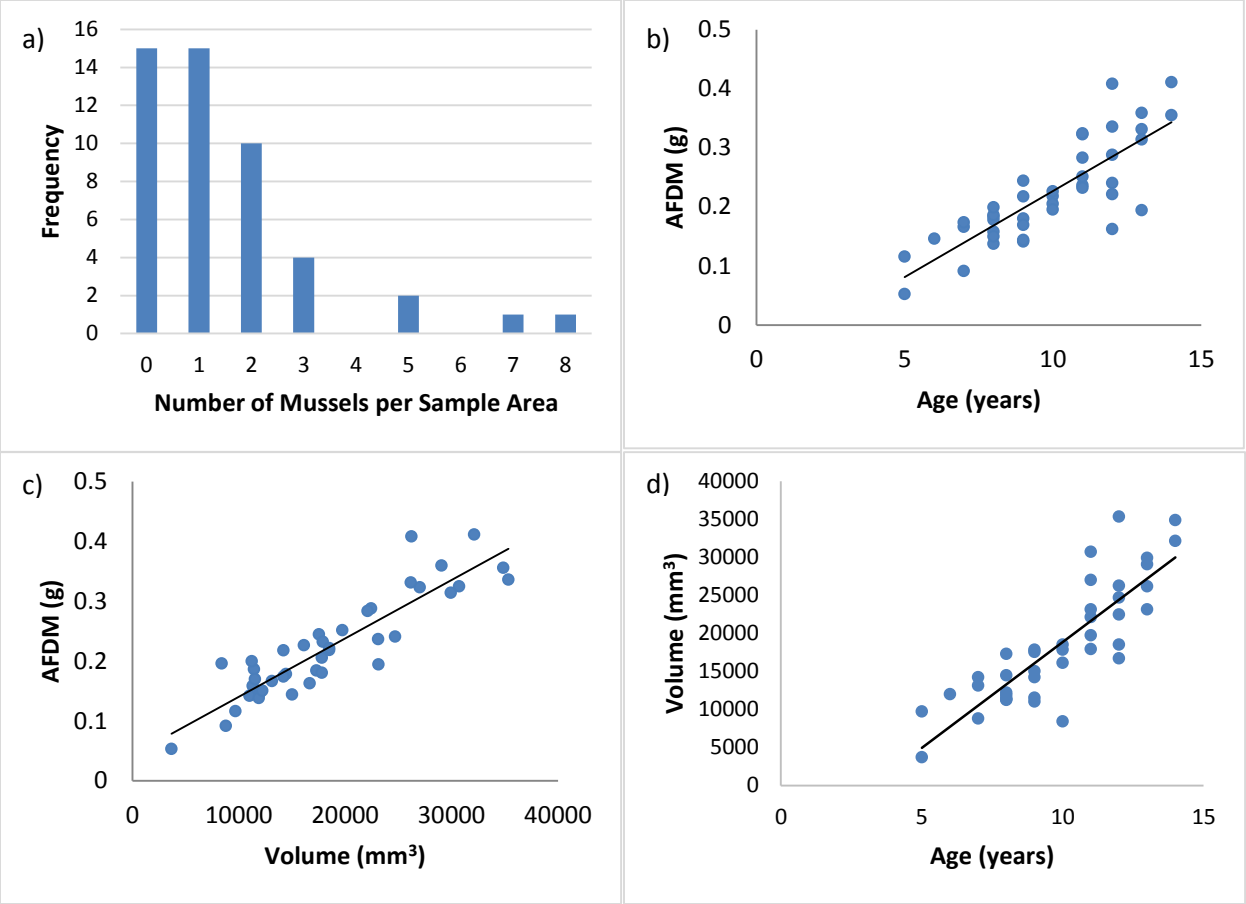

Figure 4. a) The frequency distribution of the number of individuals per sample. The data follows a Poisson distribution with many samples having only one or zero individuals. b) Regression of age and AFDM for mussels sampled from Marion Lake and aged by growth band enumeration, c) Regression of volume and AFDM for mussels sampled from Marion Lake, d) Regression of age and volume for mussels sampled from Marion Lake and aged by growth band enumeration

To determine patterns of mussel distribution in Marion Lake, the mean biomass, estimated age, and the abundance of mussels per sample were tested against the variables of longitudinal position in the lake (transect), sample depth, and side of the lake (east or west). None of the dependant variables showed any trend with longitudinal position (Fig. 5). All statistical tests of either mean biomass, mean estimated age, and mean number of mussels per transect had insignificant results *(P* >0.05).

There was one minor difference depending on the side of the lake the mussels were sampled from. The numbers of mussels per sample appeared to be almost twice as great on the west side of the lake than the east side, however this was not statistically significant ($F_{1,42}$ = 2.75, *P* >0.05), unless it was treated as a Poisson distribution with the interaction term removed and zero-inflation considered (Z-value = 2.33, *P* <0.02) (Fig. 6). A total of 46 mussels were sampled from the west side of the lake basin, while only 26 were sampled from the east side. The mean biomass did not differ greatly according to side, although the west side had slightly higher values that the east side, but not to a significant degree *(*$F_{1,27}$ = 0.2, *P* >0.05) (Fig. 6). The mean

estimated age of the samples also did not vary according to east or west ($F_{1,27}$ = 1.18, P >0.05).

There were some visible trends according to depth (0.25 m, 0.50 m, and 0.75 m) (Fig. 7). The number of mussels did not vary with depth statistically ($F_{2,42}$ = 0.64, P >0.05), however there was a visible trend that the number of mussels decreased with depth and perhaps with a larger sample size the significance would change (Fig. 7). Thirty mussels were collected at 0.25 m, twenty-three from 0.5 m and nineteen from 0.75 m. The average biomass per sample also appeared to be highest at 0.25 m than the deeper depths, but again, this was not significant ($F_{2,27}$ = 0.51, P >0.05). The mean estimated age of the mussels did not vary over depth ($F_{2,27}$ = 1.09, P >0.05), however, there was a higher occurrence of older mussels in the shallower samples.

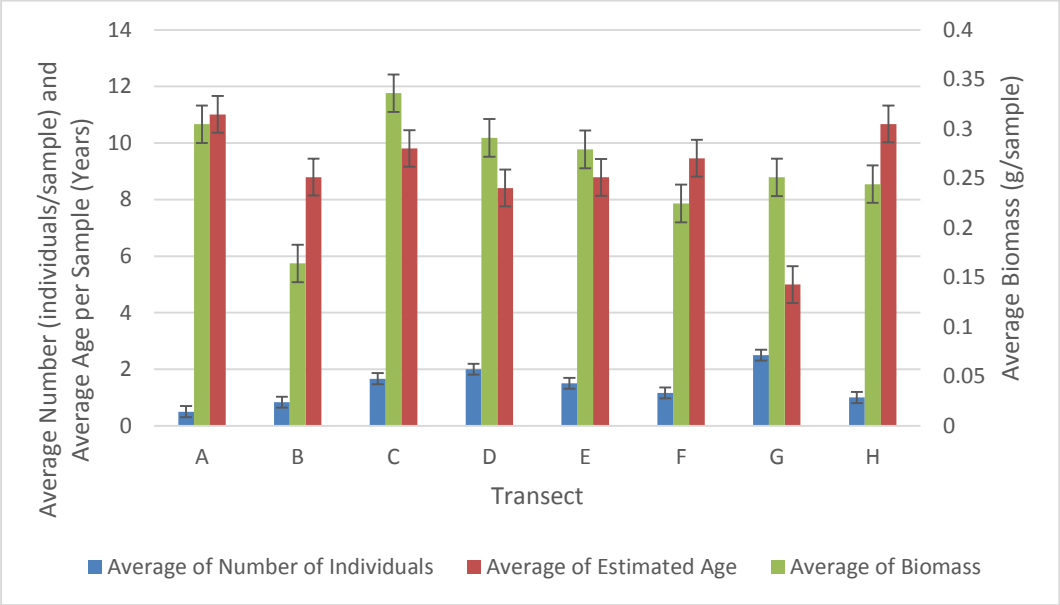

Figure 5. The average number of individuals per sample (0.9 m^2) in each transect, average of estimated age per sample, and average biomass per sample across transects sampled. Transect A is closest to the outlet of the lake, while transect H is closest to the inlet. Proximity to inlet or outlet appears to have no effect on the variables examined.

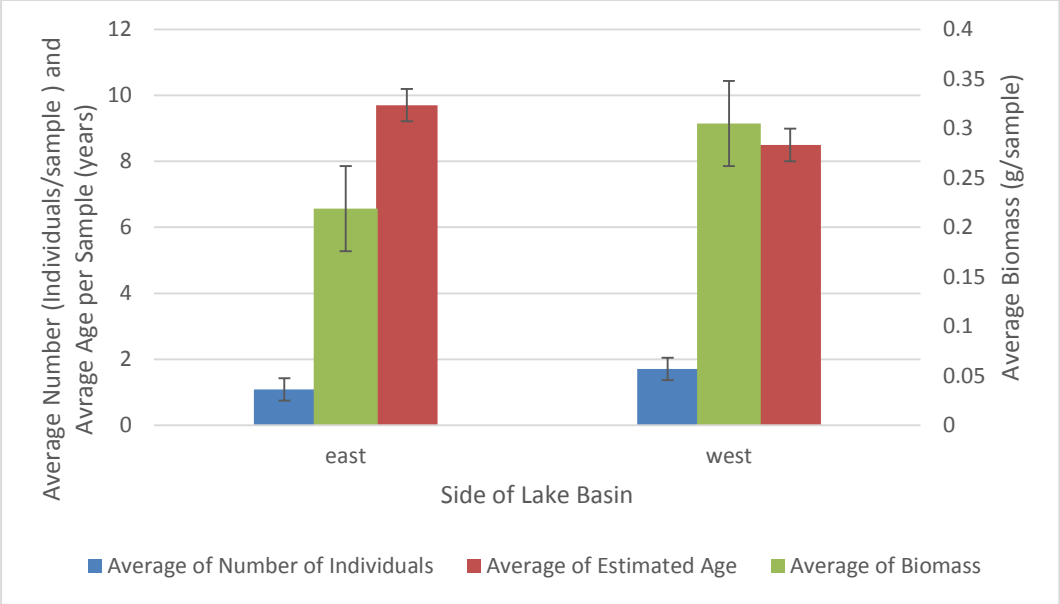

Figure 6. The average number of individuals per sample (0.9 m^2) on either side of lake basin, average of estimated age per sample, and average biomass per sample on either side of Marion Lake. There was almost twice as many individuals per sample on the west side of the lake basin than the east side, however the average biomass per sample and average age per sample were very similar.

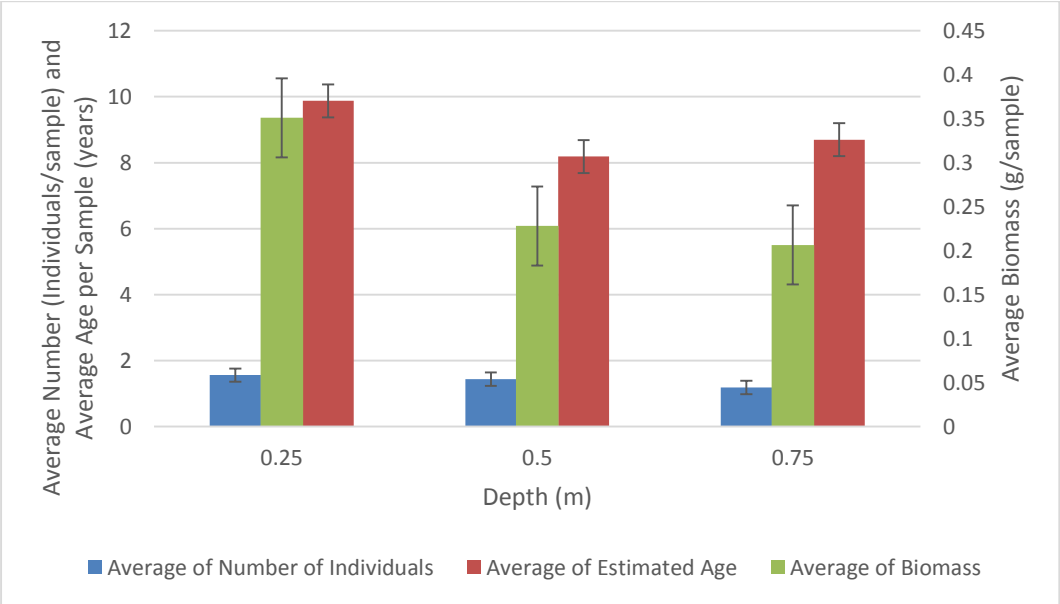

Figure 7. The average number of individuals per sample (0.9 m^2) at each depth, average of estimated age per sample, and average biomass per sample across depths. Both average biomass and abundance appear to decrease as depth increases, whereas average age per sample appears fairly constant.

Filtration Rate

The filtration rate aspect of the study used the literature values at different temperatures to come up with several scenarios. The first scenario using the filtration rates at their corresponding temperatures from the literature resulted in an overall regression of FR = 0.0335*(temperature) + 0.1142 (r^2 = 0.184) (Table 4 and Fig. 8a). The other scenarios used the model from Loayza-Mura & Elias-Letts (2007). The 'average' scenario used the mean value of all temperature and filtration rates found in the literature. The mean temperature was 15.2°C and the mean filtration rate was 0.623 L h^{-1} g^{-1} and the resulting equation was FR = 0.1159*(temperature) + 0 (Table 4 and Fig. 8b). The 'high' scenario used the greatest filtration rate that was obtained from the literature – 1.722 L h^{-1} g^{-1} at 15.9°C and regression of FR = 0.0442*(temperature) + 0 (Table 4 and Fig. 8b). The 'low' scenario had a filtration rate of 0.2624 L h^{-1} g^{-1} at 16.9°C and regression of FR = 0.0167*(temperature) + 0 (Table 4 and Fig. 8b).

Table 4. The regression equation for each of the four scenarios. The 'average' scenario used the average temperature and average filtration rate of the literature values and input them into the model from Loayza-Mura & Elias-Letts (2007). The 'high' and 'low' scenarios used the highest and lowest filtration rate from the literature respectively and were applied to the model. The 'literature' scenario used the temperatures and corresponding filtration rates from the literature to create a regression. Temperature is °C and the filtration rate (FR) is measured in L h^{-1} g^{-1} of dry weight.

Scenario	Equation
Average	FR = 0.1159*temperature + 0
High	FR = 0.0442*temperature + 0
Low	FR = 0.0167*temperature + 0
Literature	FR = 0.0335*temperature + 0.1142

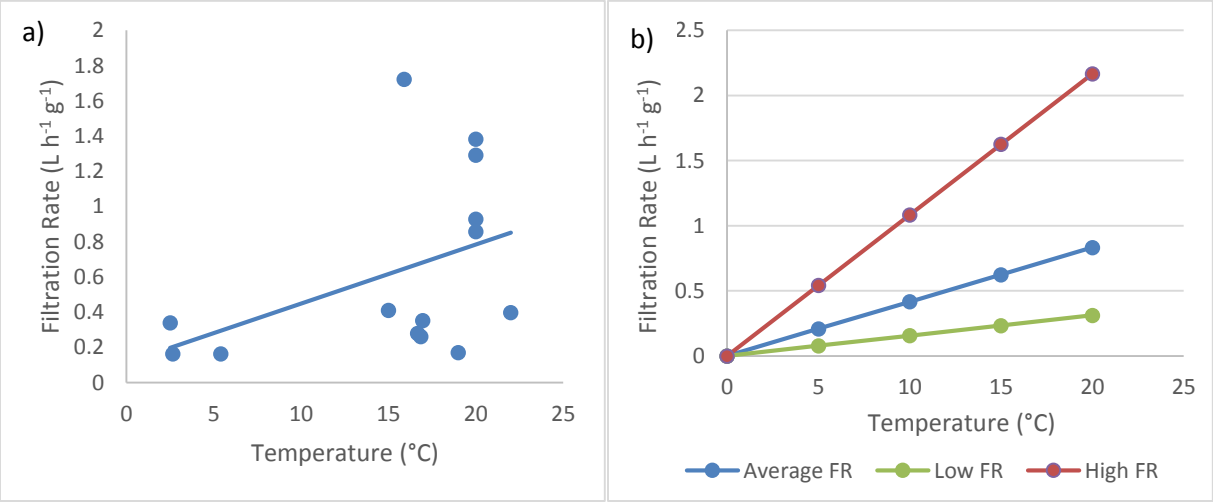

Figure 8. a) Regression based on literature values of filtration rates and their corresponding temperature (r^2 = 0.184), b) Three scenarios using the highest literature filtration rate, the average literature filtration rate, and lowest literature filtration rate modelled after the relationship found in Loayza-Mura & Elias-Letts (2007).

The resulting scenarios were then applied to the population of mussels in Marion Lake. The volume of water in Marion Lake is approximately 319200 m^3 and the average biomass of mussels was 0.29 g/m^2 over approximately 133000 m^2 of lake-bottom. Because the majority of our demographic findings in Marion Lake found no statistically significant difference between sampling sites, it was assumed that the average biomass was constant throughout the lake. This resulted in a total biomass of 38698 g AFDM. The seasonal lake temperatures stated above were then used to extrapolate the filtration rate of the population of mussels in Marion Lake seasonally and come up with a yearly estimate to the volume of water the mussels could filter in each scenario (Table 5).

Using the literature values, the mussel population could filter approximately 45.3% of the total lake volume annually. The 'average' model scenario produced a similar result of 41.2% annually. The 'low' and 'high' scenarios based on the model were 15.5% and 107.3% respectively. The majority of the annual filtration takes places in the summer and fall, when water temperatures are higher and decreased filtration occurs during the winter.

Table 5. Summary of findings for filtration capacity of the mussel population in Marion Lake. The filtration rates were calculated based off of seasonal temperatures and four different scenarios were proposed. The proportion of total lake volume filtered per day varies with season and each scenario gives an estimate for the annual percentage of lake filtered which varies from 15% to 107%.

Season	Temperature (°C)	Literature FR	Volume Filtered (L/h · g dry mass)	Volume Filtered Per Day (L/d · g dry mass)	% of Lake Volume Filtered Per Day	% of Lake Volume Filtered Per Season
Winter	2.5	0.198	7660.265	183846.363	0.058	5.184
Spring	7.67	0.371	14362.562	344701.483	0.108	9.935
Summer	16.67	0.673	26030.003	624720.066	0.196	18.006
Fall	10.33	0.460	17810.939	427462.531	0.134	12.186
					Total Yearly % of Lake Volume Filtered	**45.311**
Season	**Temperature (°C)**	**Model Average FR**	**Volume Filtered (L/h · g dry mass)**	**Volume Filtered Per Day (L/d · g dry mass)**	**% of Lake Volume Filtered Per Day**	**% of Lake Volume Filtered Per Season**
Winter	2.5	0.104	4024.590	96590.158	0.030	2.723
Spring	7.67	0.319	12347.442	296338.605	0.093	8.541
Summer	16.67	0.693	26835.966	644063.174	0.202	18.563
Fall	10.33	0.430	16629.606	399110.533	0.125	11.378
					Total Yearly % of Lake Volume Filtered	**41.206**
Season	**Temperature (°C)**	**Model Low FR**	**Volume Filtered (L/h · g dry mass)**	**Volume Filtered Per Day (L/d · g dry mass)**	**% of Lake Volume Filtered Per Day**	**% of Lake Volume Filtered Per Season**
Winter	2.5	0.039	1509.221	36221.309	0.011	1.021
Spring	7.67	0.120	4630.291	111126.977	0.035	3.203
Summer	16.67	0.260	10063.487	241523.690	0.076	6.961
Fall	10.33	0.161	6236.102	149666.450	0.047	4.267
					Total Yearly % of Lake Volume Filtered	**15.452**

Season	Temperature (°C)	Model High FR	Volume Filtered (L/h · g dry mass)	Volume Filtered Per Day (L/d · g dry mass)	% of Lake Volume Filtered Per Day	% of Lake Volume Filtered Per Season
Winter	2.5	0.271	10477.478	251459.474	0.079	7.090
Spring	7.67	0.831	32144.903	771477.666	0.242	22.236
Summer	16.67	1.805	69863.824	1676731.773	0.525	48.327
Fall	10.33	1.119	43292.939	1039030.547	0.326	29.621
					Total Yearly % of Lake Volume Filtered	**107.274**

Discussion

Demography

There is an apparent relationship between the AFDM, volume, and estimated age of *Anodonta kennerlyi* and this could be useful in further demographic studies of other unionids. Aging the mussels through enumeration of the growth bands was simple to do, although is likely not entirely accurate, especially with older mussels as the growth bands tend to be closer together with age and shell erosion and algae make distinguishing the bands more difficult. Huebner et al. (1990) also used this method to age mussels found in a lake in Ontario and noted that uncertainty was greater for older mussels. However, this method still produced adequately accurate data to create an age-frequency distribution for the lake. By collecting any of the above variables, and collecting data on a smaller number of mussels at the lab, it is easy to come up with a demographic profile of a population of bivalves.

The age distribution of the population suggested that there had not been much recent recruitment. There was a ‘pulse’ of recruitment 7-10 years ago as 57% of the individuals sampled were in these age classes. Mussels often undergo ‘pulsed recruitment’ which occurs when fish hosts may be abundant several years then decreased the next (Vaugh et al. 2008). When examining a population it is not unusual to find several cohorts of ages that coincide with fish returning to the stream or lake or perhaps with other environmental or anthropogenic effects (Franz 2001). Mussel distribution and abundance patterns are caused by historical effects, landscape-level influences, availability of hosts, and environmental conditions (Vaughn & Taylor 2000).

Studies on other Unionid mussels found the average annual mortality rate to be approximately 20% (Negus 1966; Anthony et al. 2001). In *Anodonta kennerlyi,* with a shorter lifespan compared to other bivalves, it is likely the mortality rate is greater. The eldest mussel was found to be 14 years which is consistent with findings that *Anodonta kennerlyi* are relatively short lived (10 to 15 years) and fast growing (Nedeau et al. 2012). If the population in Marion Lake had been consistently recruiting as many individuals as possible into the population each year, we would have expected many more individuals in the younger age classes. However, due to the species reliance on fish hosts for reproduction, it may not be possible to recruit large numbers of juveniles each year. It is also possible that the method of sampling was biased towards larger bodied individuals, however some younger mussels were sampled and thus the youngest age class could not have been excluded altogether. The absence of small,

young mussels is a wide-spread occurrence among scientific studies on freshwater mussels and is most likely attributed to unsuitable sampling methods as dredging often returns higher amounts of young mussels then collecting by hand (Huebner et al. 1990). Although a mesh net was used in this study, it is possible that smaller mussels may have fallen out as the net was pulled upward, or the small mussels were overlooked when examining the contents of the net.

In Marion Lake, this study determined that mussel distribution was not dependent on depth, proximity to inlet or outlet, or on the side of the lake basin. Biomass and age was also not dependent on these variables. The mussels were distributed throughout the lake, likely due to their method of reproduction. They depend upon fish hosts to distribute the young mussels and thus mussel abundance most likely reflects host habitat preference. The littoral areas that were studied of Marion Lake were all quite similar. There was not an excess of woody debris and there was often a marshy area adjacent to the littoral zone.

Before the study took place, it was hypothesized that if areas had a greater abundance of younger mussels, this could indicate higher survival and reproductive success in that area. As well, areas with a greater density of mussels could indicate better habitat. Alternatively, adult mussels may occupy the best habitat whereas juveniles will dwell in whatever habitat is available. However, this was found not to be the case, and instead it seems that much of the lake bottom is suitable habitat for the mussels and that they can survive wherever their fish hosts shed them. Because the mussels suspension feed from the entire volume of the lake and there was little variation in the littoral habitat, biomass was constant throughout the lake and no areas were more productive than other areas.

There was a marginal statistically significant difference when comparing the abundance of individuals on the east and west side of the lake basin using a mixed model (a Poisson distribution with zero inflation taken into account). Possible reasons for this difference could be that the west side of the lake receives more sun due to its orientation so has more primary productivity allowing a greater number of individuals to be supported. The water temperature may have also been higher on the west side of the lake basin for the same reason, allowing the mussels to have a higher metabolic rate in the colder months and do better than individuals on the east side. Fish may have also preferred the west side of the lake basin due to higher visibility or warmer temperatures because of increased sunlight, thus juvenile mussels would be more likely to be shed on the west side of the lake.

There was also a trend of decreased abundance at greater depths, which although not statistically significant in this study, has been found to be an occurrence in other studies with *Anodonta.* Huebner et al. (1990) found that *Anodonta grandis grandis* was limited by depth and proposed a variety of reasons such as lower temperatures due to thermal stratification and decreased movement of water thus limiting the transport of food. Other studies such as Hanson et al. (1988) found that growth rate was highest at shallower depths for caged mussels that were unable to migrate.

Due to the morphology of Marion Lake, most of the habitat is suitable for *Anodonta kennerlyi.* It is very shallow resulting in little stratification and good mixing of the water year round, which enables the transport of food and mussel larvae around the lake. The shallow water also allows for increased heating which supports productivity in the lake. The substrate is very soft and flocculent, and studies have found that *Anodonta* spp. prefer muddy substrates (Cvancara 1972; Ghent et al. 1978; Loayza-Muro & Elias-Letts 2007). In the future, it would be worthwhile to survey the lake using the same methods to determine the population dynamics and if there has been recent recruitment. It would also be beneficial to use a smaller sieve to examine the sediment for young mussels to determine whether the sampling method is biased towards larger-bodied individuals.

Filtration Rate

Studies have shown that filtration rate is positively related to temperature (Loayza-Muro & Elias-Letts 2007; Pestana et al. 2009). Loayza-Muro & Elias-Letts (2007) found that when mussels were subjected to temperatures between 5°C and 10°C filtration rate was decreased compared to rates at higher temperatures, there was higher occurrence of valve closure, and the secretion of mucus. The closure of valves is an energy-saving mechanism often observed when mussels are stressed (Ortmann & Grieshaber 2003). Higher than normal temperatures often result in a decrease in filtration rate, and in some species, the premature release of glochidia (Aldridge & McIvor 2003). Pestana et al. (2009) found higher variability in filtration rate at increased temperature for *Limnoperna fortunei* and that filtration rate decreased more rapidly over time at higher temperatures (30°C). Aldridge et al. (1995) found a decrease in the filtration rate of *Dreissena polymorpha* at temperatures which exceeded the environmental maximum (24.5°C). Loayza-Muro & Elias-Letts (2007) also found that the filtration rate at 30°C was less than that at 20°C for *Anodontites trapesialis.*

Studies looking at filtration rates have used several different techniques and there are large amounts of variation among the studies. Kryger & Riisgard (1988) found values substantially higher than other studies using a method that collected water directly from the inhalant and exhalent siphons of a mussel that was able to bury itself in sediment. In studies that did not allow the mussels to bury in sediment, the rates were often much lower (Alimov 1969).

The scenarios considered in this study propose that the population of mussels in Marion Lake can filter 15.5% to 107.3% of the water volume annually. Two of the scenarios yielded results that suggested the value is around 43%, and this seems to be a plausible outcome. It is difficult to accurately estimate the actual filtration capacity of the population in Marion Lake, as filtration rate varies with species, size, temperature, particle size, concentration, and flow regime (Vaughn & Hakenkamp 2001). Filtration rate also varies between individuals as found by McIvor (2004), thus it is exceedingly difficult to accurately estimate the filtration rate for a species. However, based on the outcomes of the scenarios created in this study it is likely that the population does have the potential to have an impact on the primary production of Marion Lake, as their

biomass is large relative to the lake volume and the range of scenarios leads to a significant portion of the water column being filtered annually.

The population in Marion Lake may experience density-dependent effects such as competition for food and could be limited by the abundance of food in the water column (Fréchette & Lefaivre 1990). Due to this, the lake can supposedly only support a maximum amount of individuals. It is unclear whether the population in Marion Lake is currently growing, however the absence of juvenile mussels suggests that recruitment is low and the lake could potentially be near its carrying capacity. In addition, if the population was limiting the amount of primary production drastically, this could limit food resources for their hosts, and thus restrict the hosts and the mussel population's reproductive capacity.

The doubling-time of freshwater phytoplankton has been estimated as 0.5-7 days (Naselli-Flores et al. 2003). Based upon the daily filtration rates estimated by this study (maximum 0.5% of Marion Lake filtered each day), it is likely that the mussel population is not drastically affecting the amount of primary production that occurs daily. However, further studies would be necessary to truly understand the effect the mussel population is having on daily primary production. Davies (1968) found that the phytoplankton productivity in Marion Lake was low compared to other lakes in the region, hence the mussel population may have a larger impact than anticipated. The level of predation by zooplankton should also be considered. In addition, the mussels provide an important link between the water column and the benthos, and studies have shown that mussels can also uptake dissolved organic carbon (Roditi et al. 2000), consequently using resources beyond primary production.

Conclusion

The population of *Anodonta kennerlyi* in Marion Lake is large and likely having a profound impact on the ecosystem in Marion Lake. Most of the individuals are middle-aged and there are few juvenile mussels in the lake. Physical space and food could be limiting recruitment, however further studies and demographic surveys are necessary to determine population dynamics. Presumably 40% of Marion Lake's volume is filtered annually by the population, and although phytoplankton productivity is low, a large population of mussels can be supported in Marion Lake (Efford 1967; Davies 1968). Overall, this study quantitatively described the population of mussels in Marion Lake and presented possibilities on the scope of their effect on the ecosystem.

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Appendix

Two separate experiments to study the feeding method and filtration rate of the mussels were planned, however the mussels did not survive in the lab and thus data could not be collected. The first experiment was designed to determine whether the species of mussel deposit fed and had three experimental groups with 5 replicates in each group. Each replicate was a plastic jar containing four mussels of similar size so that biomass is relatively equal (Bondar & Richardson 2009). The three treatments were: gravel substrate with algae/yeast mix, lake sediment substrate with algae/yeast mix, and lake sediment substrate with no algae/yeast mix (only aged tap water). The mussels were fed *Chlamydomonas* algae batch cultured in the lab using the MES method and soil water (Lavens & Sorgeloos 1996, Kropat 2007). The algae was supplemented with active baker's yeast to ensure that the mussels would have had more than enough food to filter from the water.

The mussels would have been measured every week (height, length, width and wet weight) to track growth. If the mussels were deposit feeding, then the experimental group with no algae/yeast mix would have grown over the course of the experiment. If deposit feeding is as suitable a feeding method as suspension feeding, then all experimental groups will have grown similar amounts over the six week period. If not, the experimental group without algae/yeast mix will not grow as much as the groups that do have algae/yeast mix. It is possible that suspension feeding and deposit feeding will have additive effects, and if this is the case, then the experimental group with lake sediment as substrate and with algae/yeast should grow faster than the other experimental groups.

The second experiment that was designed aimed to determine how filtration rate varied with temperature and how this could be related to the biomass of the mussels in Marion Lake. The experiment tested three different temperatures (15°C, 20°C, and 25°C) and there were three replicates in each treatment. Plastic jars each containing

one mussel were placed in water baths at the corresponding treatment temperature and the mussels were left to feed for six hours. The behaviour of the mussels (actively feeding or not) was also noted every half-hour. To measure the filtration rate of the mussels, each replicate had 500 mL of *Chlamydomonas* culture and 500 mL of aged tap-water added to the jar. Five chlorophyll a (chl a) samples of the algae suspension were taken prior to the commencement of the experiment to determine the initial chl a concentration. After six hours, the mussels were removed from the jars and three samples of each jar were taken to find the chl a in each replicate after the mussels had been feeding. To measure the filtration rate (FR), an equation was adapted from Vanderploeg et al. (1995):

$$FR = (V/nt)*\ln(C_{wc}/Z_{wc})$$

where V=volume of water in each replicate, n=number of mussels in each container, t=duration of experiment, C_{wc}=mean Chl a concentration at end of experiment, and Z_{wc}= mean Chl a concentration at beginning of experiment. The filtration rates of the different treatment groups could then be compared to examine how temperature affects the filtration rate of *Anodonta kennerlyi* and determine a relationship between temperature and filtration rate. It was then intended to apply these results to Marion Lake and find the length of time it would take the present population to filter the entire volume of water.