Winter 2017

Population Characteristics and Habitat Use by the Recently Introduced Asiatic Clam (Corbicula fluminea) in Lake Whatcom, Washington

Jason A. (Jason Alexander) Buehler
Graduate student, buehlerjason@gmail.com

POPULATION CHARACTERISTICS AND HABITAT USE BY THE RECENTLY INTRODUCED ASIATIC CLAM (CORBICULA FLUMINEA) IN LAKE WHATCOM, WASHINGTON

By

Jason Alexander Buehler

Accepted in Partial Completion
Of the Requirements for the Degree
Master of Science

Kathleen L. Kitto, Dean of the Graduate School

ADVISORY COMMITTEE

Chair, Dr. Leo Bodensteiner

Dr. Robin Matthews

Dr. James Helfield

MASTER'S THESIS

Jason Alexander Buehler

February 2, 2017

POPULATION CHARACTERISTICS AND HABITAT USE BY THE RECENTLY INTRODUCED ASIATIC CLAM (CORBICULA FLUMINEA) IN LAKE WHATCOM, WASHINGTON

A Thesis
Presented to
The Faculty of
Western Washington University

In Partial Fulfillment
Of the Requirements for the Degree
Master of Science

by
Jason Alexander Buehler
February 2017

ABSTRACT

The Asiatic Clam (*Corbicula fluminea)* was found in Lake Whatcom in 2011. This exotic clam is common throughout North America and is spread between watersheds by infested boats, fishing activities, as well as passively by waterfowl. *Corbicula fluminea* is a well documented invasive species that survives in many environments and exhibits an r-selected life history which can lead to potentially rapid population growth via a clonal reproductive ability typical among invasive bivalves and members of the family Corbiculidae. There are more reproductive strategies in Corbiculidae than any other freshwater bivalve. This rapid growth of a single organism and its associated consumption and excretions can lead to undesired changes in an aquatic ecosystem. Studies have shown a drop in species richness, alterations to algal communities and their availability to other organisms, and water quality changes associated with burrowing, shell accumulation, and clam decomposition.

My research included an assessment of the growth of representative Lake Whatcom clam populations during 2012 and 2013 using shellfish surveying methods that have been applied to the marine intertidal environment. Surveying was based on multiple transects with randomly sampled 0.25-square meter quadrats. Three sites were identified that had populations of the clam and were accessible for surveys. These sites were Bloedel Donovan Park in the City of Bellingham, Lakewood, a facility run by Western Washington University, and a small park beach within the community of Sudden Valley.

Surveys showed sample areas with 200 or more individual clams per square meter at all three sites. Studies state this density to be indicative of a self-sustaining population for *C. fluminea*. Some sites exhibited an increase in biomass and size from 2012 to 2013. All sites showed significant changes among some size classes that suggest growth.

The sand and fine sediment substrate of the Sudden Valley site hosted significant density increases and biomass increases from 2012 to 2013. The harder rocky substrate of Lakewood hosted multiple size classes but did not show evidence of growth. Bloedel Donovan Park differed from the other sites in that it had a small size class in 2013 that was not present in 2012 suggesting a new generation of clams had reseeded the habitat.

The overall environment within Lake Whatcom does not appear to be conducive to extended periods of reproduction based on the presence of distinct size classes. Distinct size classes are representative of specific reproductive windows during the year made available during the warmer months of summer. Density and biomass changed with depth within the nearshore shallows suggesting that the cooler deeper waters of the lake are not as suitable to the clam as the warmer, shallower areas within the littoral zone. Another explanation is less phytoplankton availability due to light limitations imposed by depth.

Corbicula fluminea appears to be reproducing to varying degrees at all three sites in this study, and it will likely continue to spread to suitable habitat within Lake Whatcom. Typical impacts associated with the clam should be expected. These include changes in species richness, especially changes in native filter feeder concentration as well as changes to phytoplankton density, and alterations to the seston nutrient load because of burrowing and biological functions associated with *C. fluminea*.

TABLE OF CONTENTS

Abstract..iv

List of Tables and Figures...………....................................vi

Introduction..1

Methods..9

Results...15

Discussion..19

Table and Figures…………………...……………………………………………………25

Literature Cited..74

LIST OF FIGURES AND TABLES

Figure 1. Life history *Corbicula fluminea*...25

Figure 2. Lake Whatcom basin map……………………………………...………...26

Figure 3. Lake Whatcom water fluctuation during 2012 and 2013…..……….………...27

Figure 4. Survey layout diagram……………………………………………..…..28

Figure 5. Measured length of *Corbicula fluminea*………………………………......29

Figure 6. Survey site map…………………………………………….……......30

Figure 7. Bloedel Donovan Park survey area……………………………….………...31

Figure 8. Lakewood survey area……………………………………….…………...32

Figure 9. Sudden Valley survey area…………………………….…….…………...33

Table 1. Quadrat counts…………………………………………...…….…….…34

Table 2. Comparison of density 2012 to 2013 within sites (Kruskal-Wallis)…..…….…35

Figure 10. Boxplot of distribution of density at each sample site……………..……...36

Figure 11. Distribution of density frequency at Sudden Valley………...…...………..…37

.

Figure 12. Distribution of density frequency at Bloedel Donovan Park…………………38

Figure 13. Distribution of density frequency at Lakewood.,……………………...…..39

Figure 14. Distribution of density frequency at all sites combined……………..…......40

Table 3. Comparisons of density of *C. fluminea* among sites 2012..…………..……..41

Table 4. Comparisons of density of *C. fluminea* among sites 2013..…………..……..42

Figure 15. Distribution of density frequency at all sites 2012.,…………………………43

Figure 16. Distribution of density frequency at all sites 2013.,…………………………44

Table 5. Comparison of biomass 2012 to 2013 within sites (Kruskal-Wallis)…………45

Figure 17. Boxplot of distribution of biomass at each sample site…………………..……...46

Figure 18. Distribution of biomass frequency at Sudden Valley.,………………………47

Figure 19. Distribution of biomass frequency at Bloedel Donovan Park……………..…48

Figure 20. Distribution of biomass frequency at Lakewood.,…………………………....49

Table 6. Comparison of biomass of *C. fluminea* among sites 2012………...…………...50

Table 7. Comparison of biomass of *C. fluminea* among sites 2013………...…………...51

Figure 21. Distribution of biomass frequency at all sites 2012……………………….....52

Figure 22. Distribution of biomass frequency at all sites 2013……………………….....53

Table 8. Size distribution of *C. fluminea* 2012 and 2013………………………...…...54

Figure 23. Cumulative size frequency of *C. fluminea* at Bloedel Donovan Park..….......55

Figure 24. Cumulative size frequency of *C. fluminea* at Sudden Valley………...….......56

Figure 25. Cumulative size frequency of *C. fluminea* at Lakewood………...…............57

Figure 26. The size distribution of *C. fluminea* at Bloedel Donovan Park……................58

Figure 27. The size distribution of *C. fluminea* at Lakewood……...............................59

Figure 28. The size distribution of *C. fluminea* at Sudden Valley……...........................60

Table 9. Size distribution of *C. fluminea* years combined………………………...…..61

Figure 29. Cumulative size frequency of *C. fluminea* at all sites combined....…............62

Figure 30. The size distribution of *C. fluminea* at all sites 2012 and 2013……...............63

Figure 31. The size distribution of *C. fluminea* at all sites 2012...................................64

Figure 32. The size distribution of *C. fluminea* at all sites 2013...................................65

Figure 33. Clam larvae with sticky velum in finger tips……………………...……..…...66

Table 10. Relation of depth to density and biomass (Spearman's Rank)…………………67

Figure 34. Relation of depth to density………………………………………………..68

Figure 35. Relation of depth to biomass…………………………………………………....69

Table 11. Survey Date Timeframe 2012 and 2013...…………………………...………..…70

Table 12. Lake Whatcom water temperature during surveys...……………………......…71

Table 13. Lake Whatcom water temperature 0 through 2-m deep 2012 and 2013……....72

Figure 36. Lake Whatcom water temperature 2012 and 2013…...………………………73

INTRODUCTION

Corbicula fluminea Müller 1774 (Bivalvia: Corbiculidae) is an exotic species of mollusk found in freshwater ecosystems throughout North America, South America, and Europe. Its native range is in Asia, extending from Thailand and the Phillipines, north to Japan and Russia. The clam was introduced from China to the United States around 1930 for cultivation as food and since then has populated a diverse range of lake and stream ecosystems across North America (Phelps, 1994; USGS, 2001; Sousa et al., 2008a).

The rapid colonization of freshwater bodies in the Pacific Northwest by *C. fluminea* has occurred historically. The clam was first discovered in the Columbia River in 1938 (City of Bellingham, 2011; USGS, 2001). The clam spread from there and is now in the lower Fraser River and Lake Washington. In Lake Washington, which has had clams since at least the 1940s, densities may exceed 2,500 clams/m^2 (Phelps, 1994; USGS, 2001). Recently, *C. fluminea* was discovered in Lake Whatcom, which is the source of drinking water for the City of Bellingham and surrounding communities as well as an important recreational area for swimming, boating, and fishing.

Colonization by a non-native animal may noticeably alter natural processes in an ecosystem. This typically happens when the invasive species becomes sufficiently abundant to impact the existing ecological system through resource exploitation and biological functions (Phelps, 1994; Strayer et al., 1999). Exotic species become invasive when they proliferate because they may be unchecked by existing predators, pathogens, energy availability and other environmental conditions that govern native life forms within their native ecosystem. Excessive numbers and high densities of exotic species mean meeting biological needs such as nutrition and habitat, and biological functions such as excretion, respiration, and reproduction can have cumulative effects observable on an ecosystem-wide scale (Phelps, 1994; Hakenkamp and Palmer, 1999; Strayer et al., 1999). These effects are often unpredictable and may not be obvious in the short term, but as numbers grow, effects accumulate (Hakenkamp and Palmer, 1999; Strayer et al., 1999; Sousa et al., 2008a).

Successful invasive species can flourish in a wide range of environments because of adaptations that contribute to their survival. These types of species often have traits that are considered r-selected such as rapid reproduction and growth rates. A dispersal mechanism for colonizing new habitat is also typically present. Predators, pathogens, and ecosystem limitations are present in their native environment, but these do not exist for them in many non-native environments. R-selected species are known to colonize a wide diversity of usable environments and reach high densities, which in turn can contribute to varied and unpredictable impacts on the ecosystem (Phelps, 1994; Hakenkamp and Palmer, 1999; Strayer et al., 1999; Schmidlin and Baur, 2007; Sousa et al., 2008a).

Some freshwater bivalves possess rapid reproductive abilities and are known invasive species. These bivalves are hermaphroditic, can self-fertilize, and use a form of ovoviviparity to produce larvae known as a veligers that are partially motile. As a result they can rapidly colonize and then alter entire aquatic ecosystems. Bivalves can dominate overall biomass in streams and lakes because of their prolific reproduction (Lauritzen and Mozley, 1984; Phelps, 1994; Strayer et al., 1999; McMahon, 2002; Vanni, 2002; Korniushin and Glaubrecht, 2003; Meysman et al., 2006; Sousa et al., 2008a).

Freshwater bivalves feed on phytoplankton as well as suspended detritus. Filter feeding alters the composition of the water column and can disrupt the food chain for native bivalves and larger consumers. In the case of newly introduced invasive bivalves, this may lead to a noticeable loss of species within the ecosystem (Phelps, 1994; Korniushin and Glaubrecht, 2003; Schmidlin and Baur, 2007). Some bivalve-dominated ecosystems have been altered to such an extent that the affected ecosystem has been described as bio-engineered by the bivalve. For example, one-third of the estuary water of the Potomac River is filtered daily by its population of *C. fluminea* (Phelps, 1994).

C. fluminea is known to colonize new habitats rapidly and recolonize disturbed habitats (McMahon, 2002; Sousa et al., 2008a; Sousa et al., 2008b). *C. fluminea* has a variety of adaptations that contribute to its ability to colonize. The clam is hermaphroditic, and it can self-fertilize and grow veligers via ovoviviparity (Figure 1). The clam has reproductive strategies that are considered r-selected, such as a high rate of reproduction via broadcasting drifting veligers and a rapid growth rate.

The larval veligers grow continuously in the clam's mantle and are broadcast at varying rates depending on environmental conditions (Figure 1; McMahon, 2002; Korniushin and Glaubrecht, 2003; Sousa et al., 2008b). The veliger larva is typically 3 mm long, with a small, soft shell, and an extended velum. The velum is often described as a filamentous thread (Figure 1) and it acts as a sail in the water currents, thus increasing dispersal during the veliger's drifting phase. Following the drifting phase, the velum becomes very sticky and, during the settling phase, adheres to almost any surface (USGS, 2001; Korniushin and Glaubrecht, 2003; Sousa et al., 2008b; Denton et al., 2012). This stickiness enables larval transport between neighboring watersheds. Typically, the primary transport vectors are the hulls and ballasts of boats, as fishing bait, and by dispersal by waterfowl (Schmidlin and Baur, 2007; Sousa, 2008b; Rothlisberger et al, 2010).

Sexually mature clams are typically 6 through 10 mm, and growth rates vary significantly depending on available food and water temperature (McMahon, 2002). The ability to produce veligers occurs at a slow rate in waters below 20º C but increases dramatically at 22º C and higher (Lee et al., 2003; Bódis et al., 2011; Casteñeda, 2012; Denton et al., 2012). Spermatogenesis is inhibited if water temperature is below 15º C (McMahon, 2002; Lee et al., 2003). Food availability may also influence the reproductive rate of *C. fluminea,* but this is considered less important than water temperature because the clam uses very little energy during reproduction (Korniushin and Glaubrecht, 2003; Denton et al., 2012). The low energy cost of creating offspring is thought to contribute to the r-selected status of *C. fluminea* and similar bivalves (McMahon, 2002; Korniushin and Glaubrecht, 2003). Densities of *C. fluminea* can exceed 2500 clams/m^2 in some ecosystems, while a density of 200 clams/m^2 is considered a self-sustaining population. Annual production of offspring can be as high as 68,000 veligers per clam. Population limits are unpredictable due to the diversity of habitats *C. fluminea* can colonize (Korniushin and Glaubrecht, 2003; Sousa et al., 2008b; Wittmann et al., 2008).

Corbicula fluminea is an aggressive filter feeder of phytoplankton and other seston, especially when compared with other freshwater filter feeders in North America (Way et al., 1990; Boltovskoy et al., 1995; Hakenkamp and Palmer, 1999; Strayer et al., 1999; Schmidlin and Baur, 2007; Sousa et al., 2008a). The filtration rate of a single *C. fluminea* has been measured at 144.9 ml per hour, which is significantly greater than many filter-feeding mollusks native to North America (Buttner and Heidinger, 1981; Way et al., 1990; Phelps, 1994; Yeager et al., 1999; Wittmann et al., 2008). The competition for nutrients within the seston is believed to be a significant factor in the decline of native bivalves. Typically, studies find an inverse relationship between the number of *C. fluminea* and numbers of native bivalves, and this is attributed to limited availability of seston (Yeager et al., 1999; Sousa et al., 2008a).

Corbicula fluminea is also known for its pedal feeding, using the foot as an appendage to collect benthic organic matter, as well as to suspend benthic particles in water column, creating additional seston upon which to feed. The clam also burrows into the bottom in a manner similar to other clams (bioturbation), which can increase the porosity of the substrate and may influence the nitrogen and phosphorus cycles within an aquatic ecosystem. In particular, bioturbation by clams can expose nutrients such as nitrogen and phosphorus to the water column. The clam has been shown to burrow into the benthic substrate and release soluble reactive phosphorus and phosphorus bound particles into the water column. This additional phosphorus can increase algae growth (Lauritsen and Mozley, 1983; Lauritsen, 1986; Krantzberg, 1985; Matisoff et al., 1985; Wittmann et al., 2008; Zhang et al., 2011).

Corbicula fluminea caused changes in water quality in many freshwater ecosystems, and these changes were usually related to alterations to the seston composition (Strayer et al., 1999; Sousa et al., 2008a; Sousa et al., 2008b; Wittmann et al., 2008; City of Bellingham, 2011; Zhang et al., 2011). These changes within the seston impact the entire food chain because the effect is at the primary trophic level (Matisoff et al., 1985; Lauristen, 1986; Phelps, 1994; Hakenkamp and Palmer, 1999; Strayer et al., 1999; Berg et al., 2001; Sousa et al., 2008b; Zhang et al., 2011).

The high rate of filtration by *C. fluminea* can alter the seston composition through selective digestion. The clam is known to excrete some types of undigested material (Sousa et al., 2008b; Wittmann et al., 2008). These excretions, known as pseudofeces, are accumulations of organic material that can alter benthic fauna and affect water quality by stimulating growth of certain decomposers and primary producers (Sousa et al., 2008b; Wittmann et al., 2008). The presence of the clam is strongly correlated with the growth of certain benthic filamentous algae in the divisions Chlorophyta and Charophyta (Vanni 2002; Sousa et al., 2008b; Wittmann et al., 2008; Zhang et al., 2011). There is growing evidence that some types of algae blooms can be the byproduct of dense populations of *C. fluminea*, which cause selective alterations to the phytoplankton composition of the water (Strayer et al., 1999; Vanni, 2002; Meysman et al., 2006; Sousa et al., 2008b; Wittmann et al., 2008; Zhang et al., 2011).

Lake Whatcom is a formerly oligotrophic lake that is now mesotrophic, located in Whatcom County in Washington State (Pickett and Hood, 2007). The long, narrow lake extends approximately 20 km along a northwest-southeast axis. It was formed during the last ice age when the area was covered by ice to depths of 1,500 m, and glacial forces scoured out the basin from the soft bedrock beneath known as the Chuckanut Formation (City of Bellingham, 2007; Whatcom County, 2014). Two shallow sills in the lake divide it into three basins. The northern basin of the lake is within the City of Bellingham, and the rest of the lake is in rural Whatcom County (Figure 2; Mitchell, 2011). The lake is the principal source of drinking water for the City of Bellingham and surrounding communities providing drinking water to approximately 96,000 people (City of Bellingham, 2007; Whatcom County, 2014).

A growing concern for Lake Whatcom is the decline in water quality, most likely caused by residential development within the watershed and associated impacts such as phosphorus-laden urban runoff (City of Bellingham, 2007). Lake Whatcom was historically characterized by low concentrations of essential algal nutrients, (i.e. phosphorus and nitrogen), but development in the watershed has resulted in more sediment and phosphorus being transported into the lake, which in turn has increased algal densities in the lake changing its status from oligotrophic to mesotrophic (City of Bellingham, 2007; Pickett and Hood, 2007; Institute For Watershed Studies, 2012 and 2013). Because of the potential for sediment resuspension, *C. fluminea* could be an additional source of phosphorus loading into Lake Whatcom.

Corbicula fluminea was found in Lake Whatcom on September 17, 2011 (City of Bellingham, 2011). The initial *C. fluminea* survey by the City of Bellingham found multiple colonies distributed in the northern basin of Lake Whatcom. As of 2017, the clam has been found throughout the lake. The abundance of *C. fluminea* in the northernmost basin of the lake may be due to its introduction to this area at a widely used public boat launch, one of two public boat launches on Lake Whatcom, the other being at the southern end of the lake in Basin 3 (Phelps, 1994; Bagatini et al., 2007; Whatcom County, 2012). Of the three basins of Lake Whatcom, the north basin, Basin 1, has the highest planktonic algal concentrations, so this basin could provide the best habitat due to the better food supply and more desirable warmer temperatures (City of Bellingham, 2007, 2011; Institute For Watershed Studies, 2012 and 2013).

During the initial surveys of Lake Whatcom by City of Bellingham and Whatcom County, *C. fluminea* colonies were found at multiple locations in the lake and were associated with different types of substrate. Clams were observed on substrates ranging from rocky cobble to soft, muddy sediments (City of Bellingham, 2011; Whatcom County, 2012).

Impacts from *C. fluminea* can vary depending on the lake's trophic state. In lakes that trended eutrophic, water visibility has improved, and macrophytes became more numerous at greater depths where light was previously a limiting factor. In lakes that trended oligotrophic, benthic algae and unusual algae populations occurred (Strayer et al., 1999; Vanni, 2002; Meysman et al., 2006; Sousa et al., 2008b; Wittmann et al., 2008; Zhang et al., 2011). Lake Whatcom is mesotrophic, formerly oligotrophic, so *C. fluminea* impacts associated with oligotrophic lakes are more likely (Pickett and Hood, 2007).

The future of the clam population within the lake in terms of spatial distribution of colonies and potential habitat and the trajectory of growth in population size is unknown, and these factors have implications for future effects on the Lake Whatcom ecosystem. An understanding of the range of habitat in Lake Whatcom that can be occupied by *C. fluminea* would be useful for predicting future population growth patterns and may provide insight into the potential for impacts on the lake's ecosystem.

Objectives:

My objectives were: 1) to establish a benchmark with regard to the status of multiple clam colonies within Lake Whatcom by comparing clam density and biomass among multiple sites across a wide area of the lake over a two-year period; 2) to characterize the effect of different substrates on clam colony dynamics; 3) to see if there was an effect of depth on density and biomass within the surveyed area; and 4) to explore the potential impact of lake water temperature on usable clam habitat.

METHODS

Surveys were conducted during August and September in 2012 and 2013 to study the clams during their period of heightened activity in the warmer summer water temperatures (Phelps, 1994; Strayer et al., 1999; Bagatini et al., 2007; Sousa et al., 2008a). Surveys were conducted during a period of decreasing lake levels, but low water levels did not appear to adversely affect the clam as no recently deceased clams were observed (Figure 3).

Surveys were completed using methods selected from Campbell (1996), and Barber et al. (2012). These methods are typically used for clam surveys in marine intertidal areas on established clam populations. I modified these methods for my Lake Whatcom study by surveying using snorkeling gear instead of digging for clams at low tide. All surveys were conducted by a two-person team, one person in wetsuit with snorkel and mask, and the other assisting with transect layout, clams, and measurement records.

To conduct the surveys at each site, a baseline was established parallel to the curvature of the immediate shoreline (Figure 4). Two points were selected to denote end points of the baseline. These points were established on persistent landmarks near the high water mark of the beach. A 150-m tape was extended between these points, and transect bases were established at 1-meter intervals along the portion of the beach to be sampled. Transects were then extended into the lake with a tape perpendicular to the baseline. A person standing on the baseline at the start of the transect visually ensured the transect was suitably perpendicular to the baseline while sampling locations were marked with flags stuck in the lake bottom at 1-m intervals. A square 0.25-m^2 quadrat was used at each 1-m interval to count and sample clams until the depth became prohibitive to sampling procedures. The quadrat data was later multiplied by four to put it in terms of meters. This was so findings would be in standard units. Maximum sampling depth with the snorkeling technique was about 1.5 m. The quadrat used during the surveys was constructed of welded rebar to have sufficient mass to not move during sampling. The initial quadrat on each transect was a randomly chosen position from one to nine selected from a random number table to randomize the sample locations (Barber et al., 2012). Transects were shifted 1 m along the baseline from 2012 to 2013 surveys to avoid resampling the exact same area, which may have been affected by the removal of clams for measurement.

Quadrats were sampled by a swimmer wearing a snorkel and mask to enable visual counting of clams within the quadrat. After accessing and delineating the sample quadrat, substrate was carefully removed to a depth that ensured all clams had been captured from the quadrat. This depth was typically 0.1 to 0.2 m before substrate compaction increased beyond the ability of clams to use it as indicated by the absence of clams. Clams were removed by hand and placed into a small mesh bag while the quadrat was completely sampled. The snorkeler then delivered the bag of clams to the shoreline where the other team member counted and measured the individuals. Clam length, defined by the longest possible measurement of the clam (Figure 5), was measured using Vernier calipers to 0.1 mm for each clam.

Three sites were chosen to conduct surveys of clams (Figure 6). These sites were selected based on four criteria: (1) the known presence of *C. fluminea* documented in prior surveys by the City of Bellingham and Whatcom County; (2) the presence of a variety of substrate types to enable characterization of the potential area of usable habitat within Lake Whatcom; (3) some slope and changing depth among quadrats; (4) water clarity conducive for visual surveying; and (5) accessibility.

The northernmost site was at Bloedel Donovan Park, a public beach (Figure 7). This site is a popular swimming area within the city limits of Bellingham and includes a boat launch. This beach is within the northernmost basin of Lake Whatcom locally known as Basin 1 (Figure 2). This basin is the second shallowest of the three basins, (maximum depth = 31 m) and potentially has the most habitat for *C. fluminea* (Phelps, 1994; Strayer et al., 1999; Bagatini et al., 2007; City of Bellingham, 2007; Sousa et al., 2008a; City of Bellingham, 2011). The substrate at Bloedel Donovan Park is primarily sand brought in to enhance the swim area. This large, homogenous area of sand without larger pieces of substrate is not typical in Lake Whatcom. Lake Whatcom substrates are usually composed of sand mixed with gravels and larger rocks (Whatcom County, 2014). The slope of the surveyed area was approximately 2.1%, and it then dropped off rapidly at about a distance of 50 m from shore. Transects were 36 to 44 m in length at this site.

The second site was Lakewood (Figure 8), a lakeside recreational facility operated by Western Washington University. This site is located in Basin 3 (Figure 2). Basin 3 overall is the deepest of the three basins at 110 m and is more oligotrophic than Basin 1 (City of Bellingham, 2007). This site also has a beach and a swim area, but it has not been enhanced with the addition of sand and receives much less use than Bloedel Donovan Park. The substrate at this site remains mostly natural and is rocky, composed of sizes ranging from small sand to large boulders and bedrock. The bottom consistency overall is hard but with interstitial spaces. The slope of the surveyed area was approximately 10.0% and drops off rapidly at a distance of about 20 m from shore. Transects at this site were 4 to 18 m in length.

The third site was a private beach surrounded by homes within the Sudden Valley community (Figure 9). This beach is also located in Basin 3 (Figure 2) and is south of Lakewood. This beach is primarily used for swimming in the summer months. The bottom is composed primarily of sand, clay, mud, and woody detritus. The slope of the surveyed area was 2.0%, and the depth remains shallow far beyond the study area. This bay is mostly shallow, and it naturally accumulates detritus and other fine particulates, which likely contribute to the bay's soft substrate.

A total of 217 quadrats were sampled in this study (Table 1). The number of quadrats at Bloedel Donovan Park was 96, at Lakewood it was 65 quadrats, and at Sudden Valley it was 56 quadrats (Table 1). Distance to the 1.5-m depth, which was the limit of surveying, as well as the difficulty of some substrates to accurately survey, caused the numbers of quadrats among sites to vary. Bloedel Donovan Park effort was 50 quadrats in 2012 and 46 quadrats in 2013 (Table 1). Lakewood effort was 30 quadrats in 2012 and 35 in 2013 (Table 1). Sudden Valley effort was 28 quadrats in 2012 and 28 in 2013 (Table 1).

To estimate individual clam weight and to derive estimates of biomass, I used other published relations of length to weight. Many studies of *C. fluminea* have featured linear regression of length to mass, and a mean of selected available regressions was used for this study. The linear regressions used were chosen based on the available long-term studies of *C. fluminea* (Bagatini et al., 2007; Bódis et al., 2011; Sheehan et al., 2014). The final linear regression used in this study to predict mass in grams (M) from length in millimeters (L) is presented in Equation 1:

Equation 1: $M=0.000459*L^{2.843}$

The influence of depth on density and on biomass was compared among quadrats of varying depths. To do this the depth at each quadrat on each survey day needed to be calculated. To determine the depth of each quadrat, transects were laid out in the same manner as for sampling. Each quadrat elevation was measured using a stadia rod for elevation and laser level on a tripod. Lake surface measurements were taken at each location, and these were used to calculate the depth of each quadrat on the bathymetric survey date. The depths from the bathymetric survey were later referenced with Lake Whatcom daily water level during 2012 and 2013 that were provided by the City of Bellingham by special request. Using the bathymetric survey and the daily lake elevation data from the city, offsets were calculated for each survey date. Using these offsets, the depth for each quadrat on the day that it was surveyed was calculated.

A YSI Model 85 meter was used to measure water temperatures to 0.1°C on each survey day. These were later compared with data provided by the Institute for Watershed Studies, at Huxley College, Western Washington University, in order to gauge how water temperatures throughout Lake Whatcom compared with the survey sites (Institute for Watershed Studies, 2012 and 2013). The comparison focused on temperatures known to be of importance to the biological functions of *C. fluminea*.

The variances in the data were heteroscedastic and the distributions were non-normal so statistical comparisons were made using non-parametric tests. There is little to no knowledge with regard to the population characteristics of *C. fluminea* in Lake

Whatcom nor how long the clam has been in the lake so I had no statistical basis to inform conclusions.

Data processing and statistics were done using multiple computer programs. Data entry and manipulation, and generation of size frequency plots, were performed in Microsoft Excel (Campbell, 1996; Barber et al., 2012). The R software package was used for statistical tests and creation of boxplots. The Kruskal-Wallis test was used to test for changes in clam density and biomass comparing the years 2012 and 2013 at each site, and overall. A Pairwise-Wilcoxon test was used for comparison of density and biomass among sites in a given year and the Holm's method was used to adjust p-values for multiple comparisons. The Kolmogorov-Smirnov test was used to compare changes in size distribution among sites and between years. The relation of depth to clam density and biomass was analyzed using Spearman's Rank Correlation Coefficient to perform a rank-based correlation analysis.

RESULTS

Changes in the density of clams from 2012 to 2013 varied among sites. Clam density at Sudden Valley increased significantly from 2012 to 2013. The site had a median density that increased from 108 clams/m^2 in 2012 to 160 clams/m^2 in 2013, an increase of 48% (Table 2, Figure 10-11). At Bloedel Donovan Park, the median density increased from 36 clams/m^2 in 2012 to 64 clams/m^2 in 2013, an increase of 77% (Table 2, Figure 10, 12). Median density at Lakewood showed no change (Table 2, Figure 10, Figure 13). A comparison of the combined sites showed no significant change in median density from 2012 to 2013, and all sites combined had very little shift in the median density which went from 84 clams/m^2 in 2012 to 90 clams/m^2 in 2013, an increase of 7% (Table 2, Figure 10, Figure. 14).

Density among sites varied within years. In 2012, Sudden Valley had a median of 108 clams/m^2 and Lakewood had a median of 104 clams/m^2. This was a much greater median density than Bloedel Donovan Park at 36 clams/m^2 (Table 3, Figure 15). In 2013, the median density at Sudden Valley was 160 clams/m^2 (Table 4, Figure 16). This was greater than Lakewood at 62 clams/m^2 and Bloedel Donovan Park at 64 clams/m^2 (Table 4, Figure 16). Other comparisons between sites within years showed no significant differences (Table 3-4).

All the sites had numerous quadrats with densities over 200 clams/m^2 (Figure 10). Bloedel Donovan Park had 9 quadrats (13%) (Figure 12), Lakewood had 11 quadrats (20%) (Figure 13), and Sudden Valley had 9 quadrats (16%) with 200 or more individuals (Figure 11). The single quadrat with the highest density was at Lakewood in

2012 with 572 clams/m^2 (Figure 15). A quadrat with such a high density was not encountered in 2013; the highest density quadrat in the study that year was at Lakewood and was 488 clams/m^2 (Figure 16)

The proportional changes in clam biomass differed from those in density. Clam biomass increased at Sudden Valley from 2012 to 2013. Median biomass in the quadrats went from 213.23 g/m^2 to 418.35 g/m^2, a 97% increase (Table 5, Figure 17). Bloedel Donovan Park had a biomass increase from 44.58 g/m^2 to 75.82 g/m^2, a 70% increase (Table 5, Figure 17, 19). As was the case with density, Lakewood also showed no significant change in biomass during my study (Table 5, Figure 17, 20). All sites combined showed no significant change in biomass from 2012 to 2013, with a median biomass of 139.61 g/m^2 in 2012 and 118.87 g/m^2 in 2013 (Table 5, Figure 17).

Some biomass differences were found among sites in a given year and were consistent between years. In 2012, Sudden Valley had a median biomass of 213.24 g/m^2 which was greater than both Bloedel Donovan Park at median 44.58 g/m^2 and Lakewood at median 121.01 g/m^2 (Table 6, Figure 21) In 2012, Lakewood biomass was greater than Bloedel Donovan Park (Table 6, Figure 21). Similarly to 2012, in 2013 Sudden Valley had a greater median biomass at 418.35 g/m^2 than both Bloedel Donovan Park at 75.82 g/m^2 and Lakewood at 131.05 g/m^2 (Table 7, Figure 22). Lakewood and Bloedel Donovan Park biomass did not differ significantly in 2013.

The size distribution of clams among sites in 2012 and 2013 showed change within sites in some of the 1-mm size classes. Bloedel Donovan Park had a significant decrease of clams in the 11- through 18-mm size classes and a significant increase in the 9- through 11-mm size classes among the sites (Figure 23). This increase was due to a uniquely high proportion in the 10-mm and smaller sizes (Figure 26). Lakewood had a decrease in the 18- through 19-mm size classes and an increase in the 20-mm size (Figure 25, 27). Similarly, Sudden Valley had a decrease in the 19- through 20-mm size classes and an increase in the 21-mm class (Figures 24, 28).

When all clam lengths from all sites were pooled there was no significant change in size representation from 2012 to 2013 (Table 9, Figure 29-30). All sites had clams predominantly in the 8- through 12-mm and the 17- through 21-mm size classes (Figure. 30, Figure 31-32). Sudden Valley had the most clams at or greater than 22-mm of the three sites in both 2012 and 2013 (Figures 31-32).

Post-larval clams as small as 3 mm were observed at all sites on some survey days. Outside of the quadrats, larvae and post-larvae clams were observed in the shallows and were numerous at Bloedel Donovan Park for part of 2013. Most of the clam larvae were found along the water's edge trapped in scum. Some larvae were found with sticky velum adhering them to small rocks (Figure 33).

Depth was significantly correlated with clam density and biomass at Bloedel Donovan Park and Lakewood in 2012 and 2013 (Table 10). Density and biomass was not significantly related to depth in Sudden Valley in either year. Combined sites show that both density and biomass were greatest at 0.51 to 0.75 m deep (Figures 34, 35). Clam counts and biomass were low in the nearshore area from 0 to 0.25 m deep and increased as depth increased to 0.75 m (Figure 34, 35). Counts and biomass decreased beyond a depth of 0.75 m (Figures 34, 35). At depths greater than 1.0 m, densities and biomass diminished (Figure 34-35). Samples from depths of 1.5 m and deeper were limited due to decreasing ability to adequately sample them.

Water temperature for sites showed a relatively small range during surveys. From mid-August to mid-September, temperature ranged from 19.60° C to 22.90° C. (Table 11) Bloedel Donovan Park had a mean of 22.30° C in 2012 and 20.65° C in 2013 (Table 12). Lakewood had a mean of 19.87° C in 2012, and 21.64° C in 2013 (Table 12). Sudden Valley had a mean 22.05° C in 2012, and 21.90° C in 2013 (Table 12). During this time, the mean temperature from all surveys combined was 21.00° C, with a minimum of 19.60° C and a maximum of 22.90° C (Table 12). During the surveys, similar temperatures were recorded at 0 to 2 m deep throughout the lake by the Institute for Watershed Studies which reported a mean of 20.10° C, a minimum of 19.30° C and a maximum of 21.10° C (Table 13, Figure 36; Institute For Watershed Studies, 2012 and 2013). Data from the Institute for Watershed Studies of water temperature from 2012 and 2013 correspond to this study, being around 20° C from June through September (Figure 36; Institute for Watershed Studies, 2012 and 2013).

DISCUSSION

Sudden Valley's increase in clam density and biomass suggests at least some growth of individuals in this site. The most abundant size classes shifted from 18 through 20 mm to 19 through 21 mm, further supporting this assertion. In addition, this site had a greater proportion of high biomass quadrats compared with the other sites.

The low density and low estimated biomass in the 9- through 12-mm size classes in both 2012 and 2013 may mean annual recruitment is limited at Sudden Valley. Usable habitat at this site may be fully populated by older clams because *C. fluminea* can be its main limiting factor in fully colonized habitat, and annual recruitment is lowered by intraspecific competition (Stites et al., 1995; Sousa et al., 2008b).

Sudden Valley also appeared to have more clams in larger size classes of 22 mm and above when compared with the other sites in this study. Preferred habitat of *C. fluminea* has been described as half sand, half silt, and about 8% organic matter, which is similar to the substrate at Sudden Valley (Bagatini et al., 2007; Cooper, 2007; Schmidlin and Baur, 2007; Sousa, 2011). The higher organic content may supplement the filtered food supply via pedal feeding.

The Bloedel Donovan Park site looks like a disturbed population of *C. fluminea* based on the changes in size classes and density compared to other sites. Sampling in 2013 indicated the presence of a new and substantial smaller size class and a near disappearance of the main size class from 2012. This smaller size class was found at the other two sites but not to as prominent of a degree. This group may represent recruitment from the previous year's reproduction in the surrounding area. *C. fluminea* is known to colonize and recolonize available habitat rapidly in disturbed areas (Stites et al., 1995). The increase in density at Bloedel Donovan Park made by the emerging size class was enough to compensate for the loss of biomass from the main size class lost during same year. This suggests a self-sustaining clam population in the surrounding area and that clams can reseed the habitat. Sand is considered a preferred substrate for *C. fluminea* (Bagatini et al., 2007; Cooper, 2007; Schmidlin and Baur, 2007; Sousa, 2011). The presence of larger clams and a similar size class structure to other sites in 2012 suggested a more mature clam population prior to 2013.

Lakewood appeared to be an established population with low recruitment or one limited by environmental conditions. Population characteristics at Lakewood appeared to be the most consistent between the survey years, displaying no significant changes in density or biomass. Size class structure was similar in 2012 to 2013 and displayed similar structure to Bloedel Donovan Park and Sudden Valley in 2012. Similar to Sudden Valley, there were no emerging smaller size classes. There were changes in the in the main size classes from 2012 to 2013 suggesting some growth among this group. Median biomass was 121.01 g/m^2 in 2012 and 131.05 g/m^2 in 2013, the smallest biomass shift of any site in this study at an increase of 8%. The hardness of the habitat may play a role in limiting the clam population and its ability to recruit more clams. The rocky substrate composing most of the Lakewood site is not described as being preferable to *C. fluminea*, which typically prefers sandier and softer habitats. For these reasons, overall clam capacity may be lower at this site when compared to the other sites (Bagatini et al., 2007; Cooper, 2007; Schmidlin and Baur, 2007; Sousa, 2011). The ability to pedal feed and burrow may be inhibited at Lakewood by the rocky bottom (Saloom and Duncan, 2005).

Densities of 200 clams/m^2 or greater are considered indicative of a self-sustaining population for *C. fluminea* (Sousa et al., 2008b). Although median densities among sites were not equal to or greater than 200 clams, all the sites had areas with greater than 200 clams/m^2 which may mean there is a self-sustaining population of clams in the lake. This is also supported by the multiple size class distribution at all sites, which indicates some successful reproduction and recruitment. In the cases of Sudden Valley and Lakewood, less numerous emerging size classes may imply that the colonies are at or near carrying capacity within the areas of usable habitat. In the case of Bloedel Donovan Park, habitat was recolonized quickly with new clams. Since the three sites span a distance of about 8 km of the lake, this means there appears to be a well established and reproducing population within Lake Whatcom.

Competition with other filter feeders, especially *C. fluminea* itself, can play a role in clam size structure (Sousa et al., 2008b). The competition for usable habitat by *C. fluminea* may have influenced the existence and abundance of some of the size classes at the sites in this study. As usable habitat is fully colonized, successive generations have more competition for food and space, and new clams are less likely to be recruited (Stites et al., 1995). Large clam sizes representing a greater proportion of the site population may indicate an established population, which was the case at Sudden Valley and Lakewood.

It is unlikely that native bivalves would influence *C. fluminea* populations in Lake Whatcom because by comparison native bivalve densities are near zero. There were just three western pearlshell (*Margaritifera falcata*), and four fingernail clams (Family

Sphaeriidae) encountered in this study. Among bivalves, all sites appeared to be dominated by *C. fluminea*.

Distinct size classes within a population are expected in the northern part of the range of *C. fluminea* where ideal reproductive conditions would be interrupted by a winter and only occur from late spring through early fall. A seasonal cycle of growth and reproduction is typical of northern oligotrophic lakes hosting the clam (Stites et al., 1995; Sousa et al., 2008b; Denton et al., 2012). In an environment such as Lake Whatcom reproductive events would be expected to occur during spring and summer and not be continual as they are in the southern part of the range.

Distinct size classes likely represent different year classes (Stites et al., 1995). Growth rates of *C. fluminea* are typically very localized, but an oligotrophic lake in the northern latitudes is not the clam's preferred range (Stites et al., 1995). Since each of the sites shows a distinct smaller size class range around 9 through 12 mm and one or more subsequent size classes, it seems likely that this smaller class represents one of the annual cohorts.

If this smaller class represents a year class, then the predominance of the 18- through 21-mm size classes among sites means the sites were colonized at least a year before this study. A sharp decline in frequency beyond 24 mm at all sites may mean the larger class represent the oldest clams in the lake. Maximum sizes for *C. fluminea* vary among habitats and are influenced by local factors. The largest individuals in other studies were around 30 mm, which was the case in this study in which the largest clam surveyed was 28.5 mm (Sousa, 2008a).

Density is not strongly tied to biomass within *C. fluminea* populations. The clam, like many bivalves, has exponential growth rates, and weight increases disproportionately to length (Sousa, 2011). The highest estimated density of individual clams within this study was 572 clams/m^2 at the Lakewood site in a pocket of accumulated detritus and other fines. However, the estimated biomass for this quadrat was 710.11 g/m^2, and the highest biomass quadrat in this study was at Sudden Valley and it was 876.19 g/m^2 with a density of 308 clams/m^2. The explanation for this is that Sudden Valley had the greatest weight of clams in the 18-mm and greater size classes, and this group appears to have differentiated it from Bloedel Donovan Park and Lakewood in terms of clam biomass.

Growth and reproduction respond strongly to warmer water temperatures. Water temperature in some studies accounted for the greatest variation of biomass in *C. fluminea* (Cooper, 2007; Sousa 2011). Mean water temperatures at the sites during the survey period were near the 22° C range which has been shown to be a threshold above which reproduction increases rapidly (Wittmann et al., 2008; Sousa, 2011). The higher water temperature in the shallows of Lake Whatcom likely provide better conditions for colonizing and successful reproductive events. The rate of reproduction increases rapidly near 22° C, so a higher rate of reproduction from June through September is likely (Wittmann et al., 2008; Sousa, 2011). The maximum water temperature surveyed during the month of August was 22.9° C (Institute Watershed Studies, 2012 through 2013). Lake Whatcom has water temperatures above 15° C for 5 months in 2012 and 2013, and this temperature and above has been shown to increase the rate of clam feeding and growth (Figure 37; Institute for Watershed Studies, 2012 through 2013). 15° C is also the lower limit of spermatogenesis for *C. fluminea* where reproduction is minimally possible. Mean water temperatures at a depth of 0 thorough 2-m in Lake Whatcom water were equal to or greater than 15° C from May through October in 2012 and 2013 (Figure 37; Wittmann et al., 2008; Sousa, 2011; Institute for Watershed Studies, 2012 and 2013).

Clam size, density, and biomass were closely related to a specific depth range in this study, and these depths appeared to be more beneficial to the clams. It is possible that water from 0.25 through 0.75-m deep is favorable to the clam. One explanation may be less available phytoplankton at greater depths due to light limitation. Another possible explanation is that the warmer temperatures in the shallower water benefit biological functions of the clam.

Presently *C. fluminea* appears to be broadly established within Lake Whatcom and near the density recognized as self-sustaining in other studies. Some colonies within the overall population are increasing in density and biomass, and based on size distributions, *C. fluminea* appears to be reproducing to some degree at all three sites. The clam will likely continue to spread to suitable habitat within Lake Whatcom if it has not already. If so, impacts associated with the clam may become evident. These include reductions in species diversity, especially changes in native filter feeder abundance through competition for food as well as other plankton eating creatures. Phytoplankton densities can decrease because of the amount being filtered from the water. Alterations to the seston nutrient load can be caused by burrowing. Long-term monitoring would likely be beneficial to gauge the overall trajectory of the *C. fluminea* population within Lake Whatcom and assess the potential impacts.

Tables and Figures

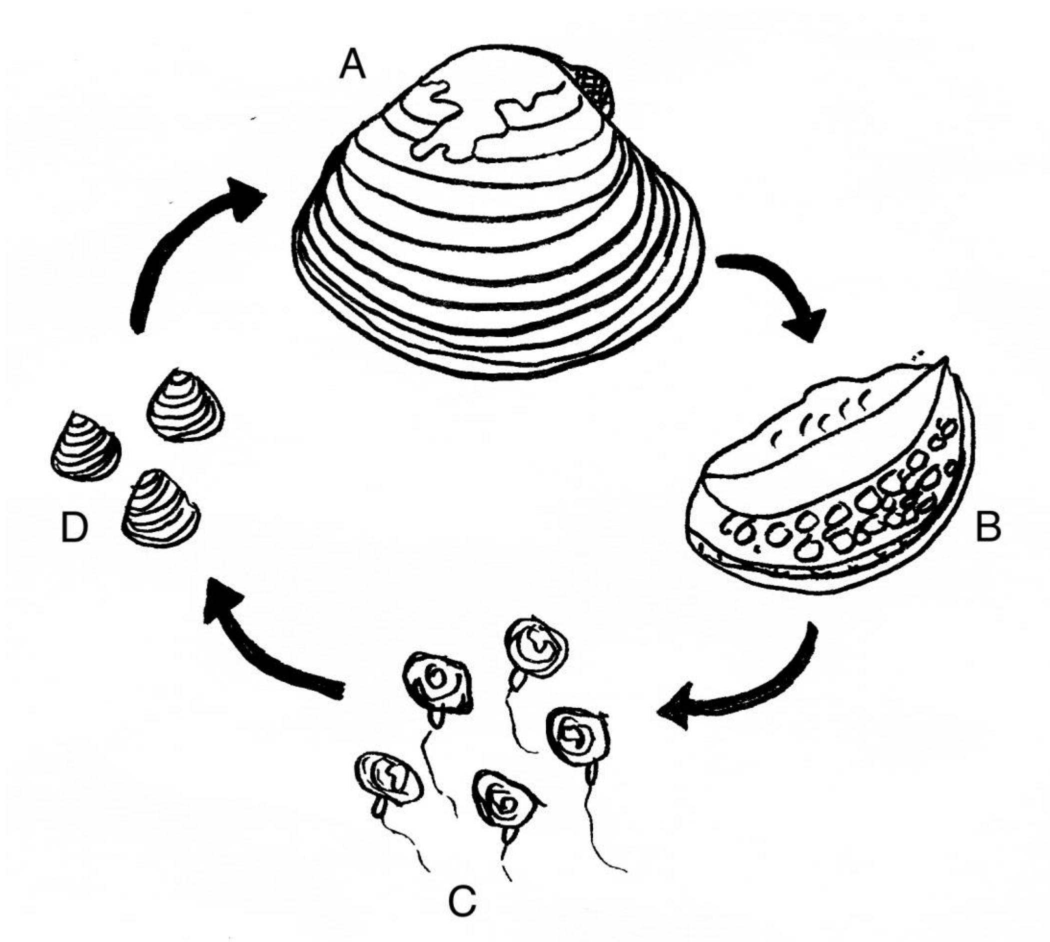

Figure 1. Life history of *Corbicula fluminea*; (A) adult, (B) inner clam with growing larvae, (C) veliger with long velum, (D) small adult.

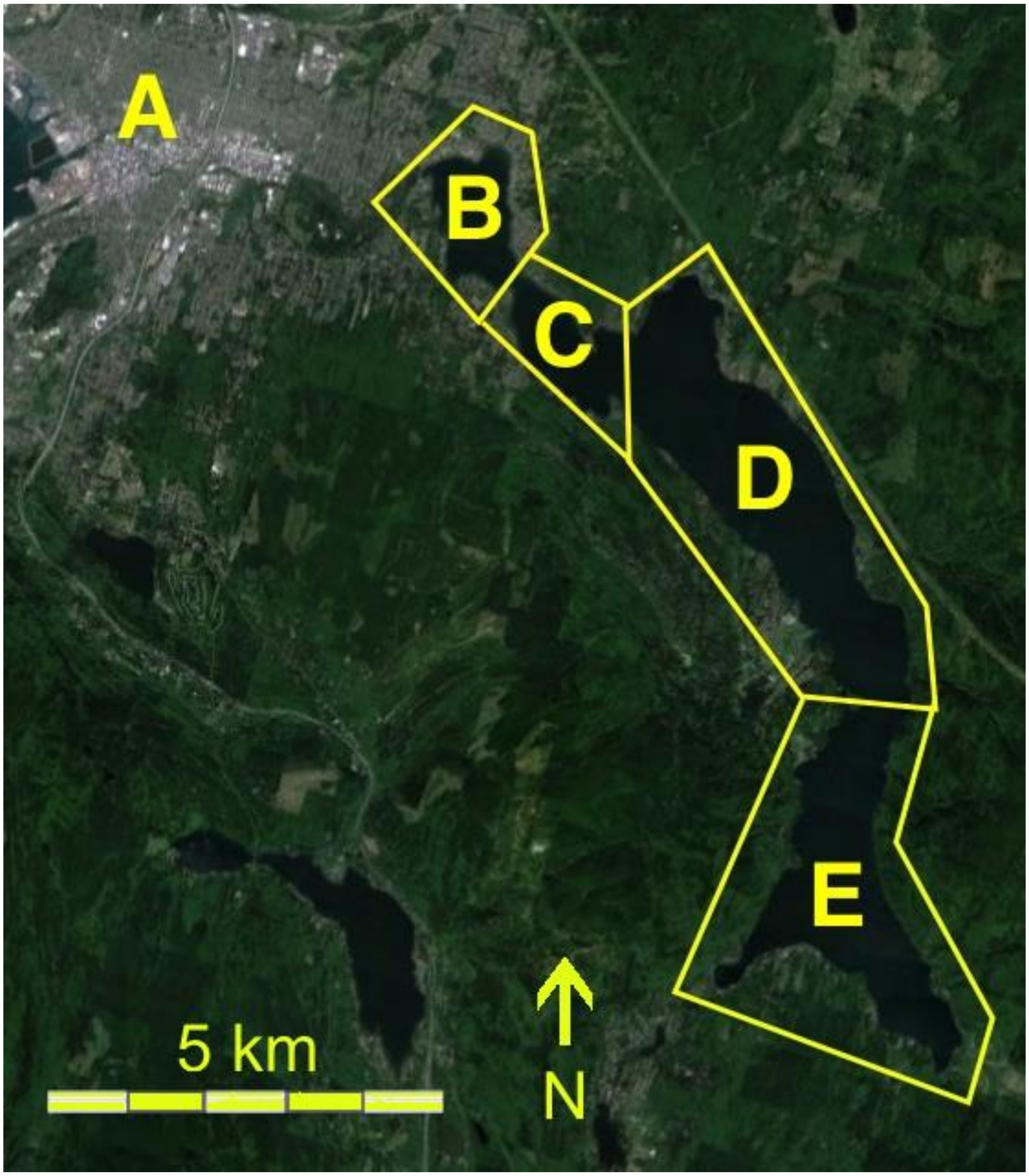

Figure 2. Basin map showing locations of: (A) City of Bellingham; (B) Basin 1; (C) Basin 2; (D) Basin 3 North; (E) Basin 3 South. Lake Whatcom, Whatcom County, Washington, USA (Map data: Google Earth Pro, DigitalGlobe; 2016).

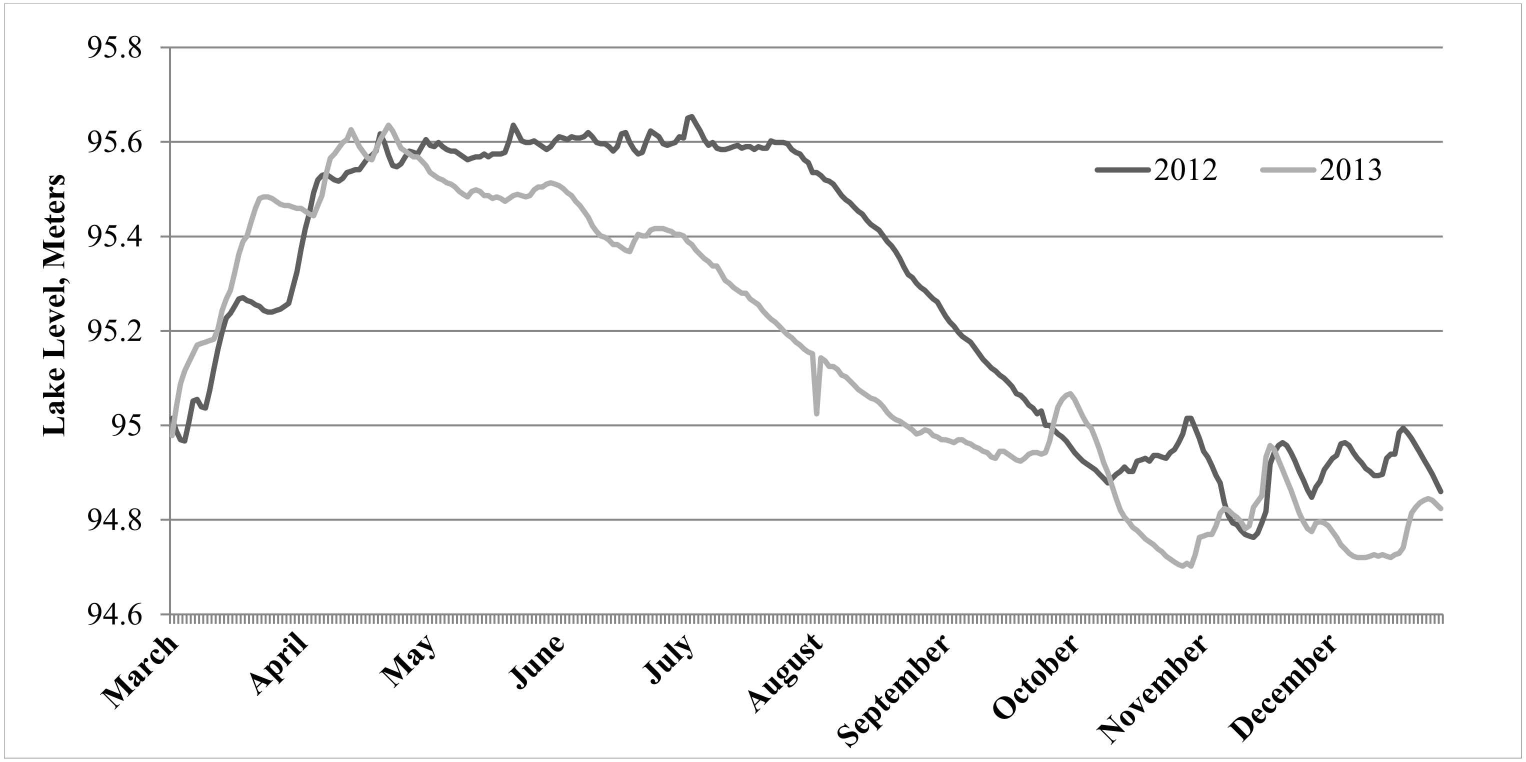

Figure 3. City of Bellingham Daily water level fluctuation in meters from March through December, 2012 and 2013; available by special request from the city. Lake Whatcom, Whatcom County, Washington, USA.

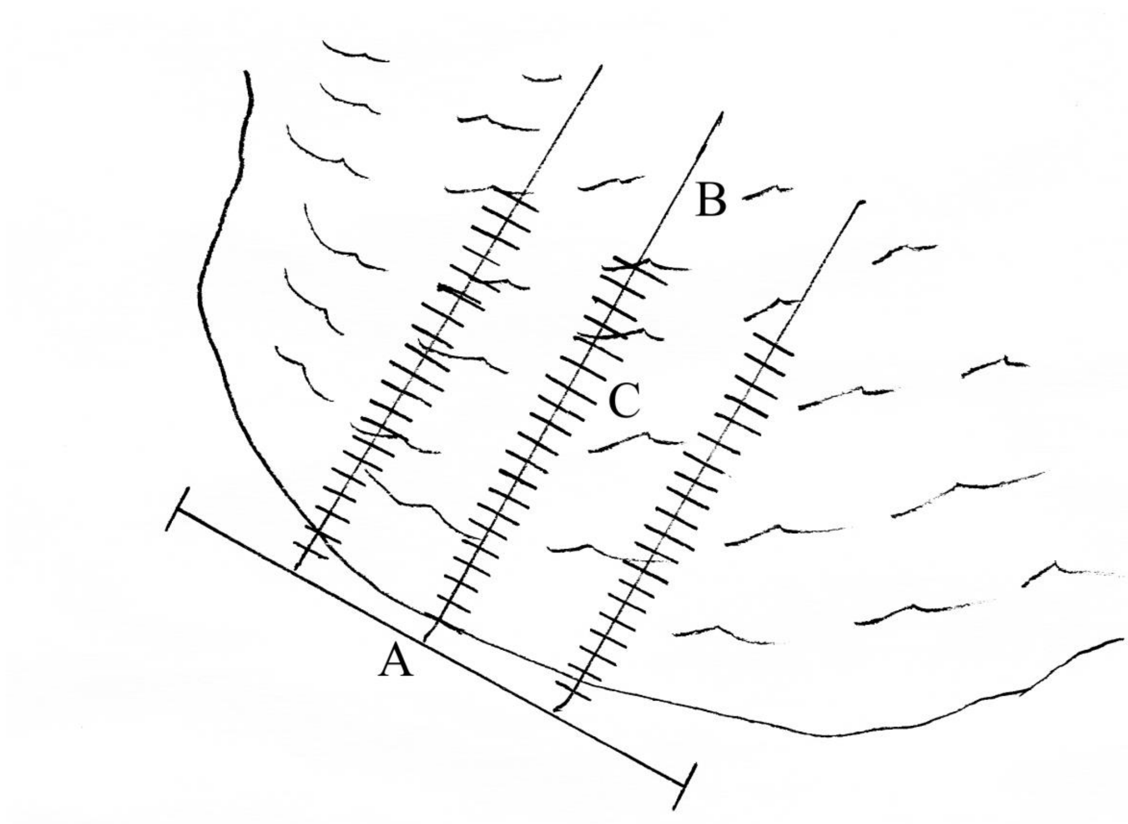

Figure 4. Diagram showing the layout for a survey in this study: (A) baseline, (B) a transect, (C) a quadrat location; quadrat locations were randomly selected along each of the three transects.

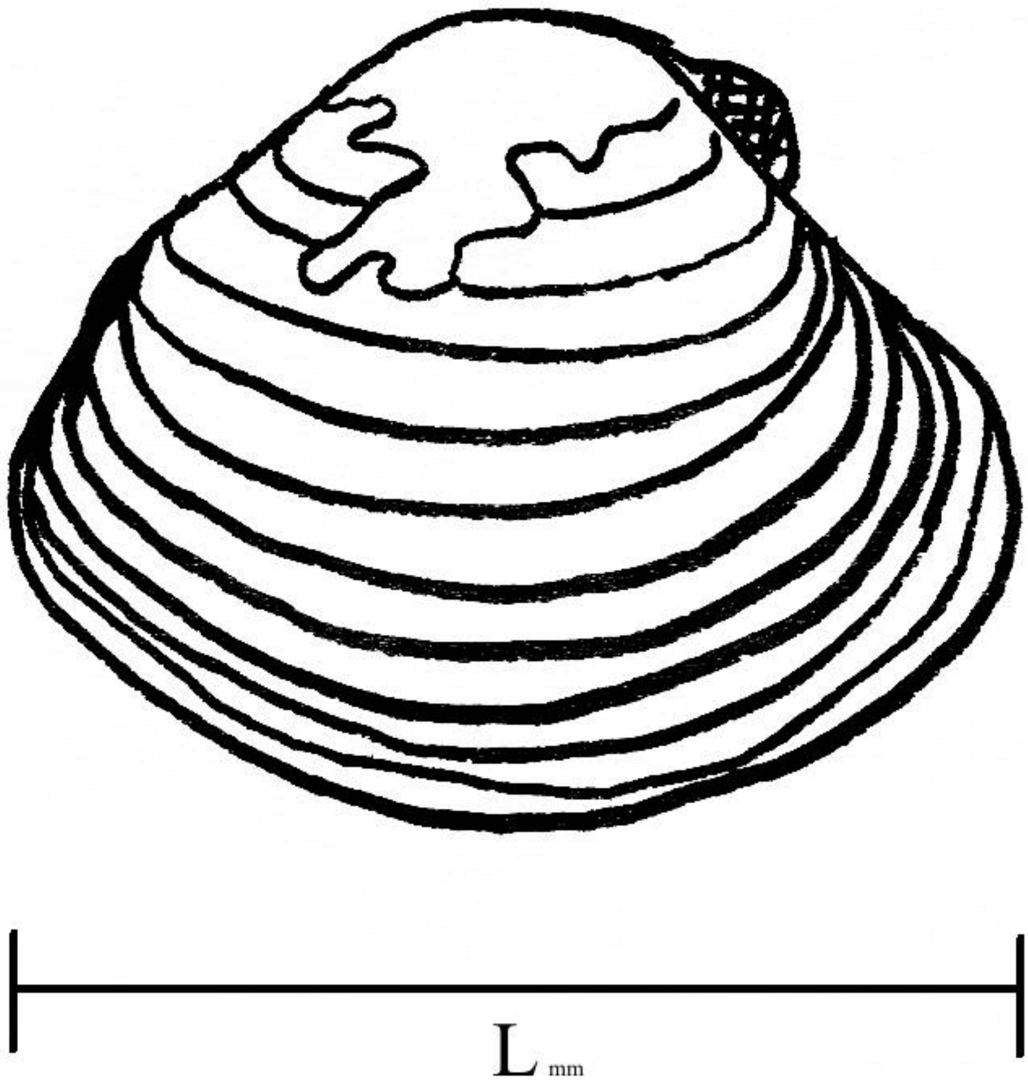

Figure 5. Diagram of axis of *Corbicula fluminea* for measuring length (longest measurable length) in this study.

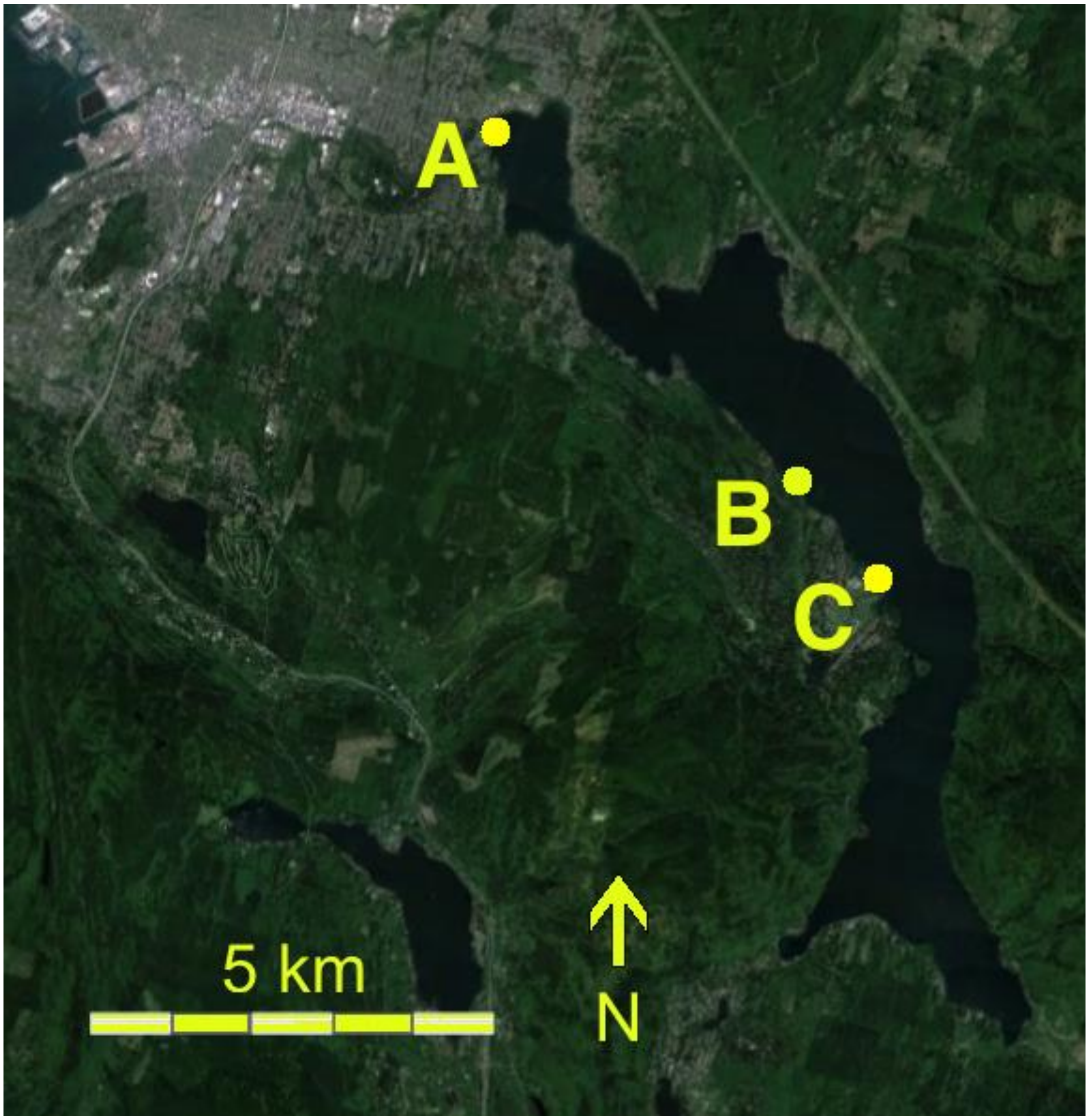

Figure 6. Map showing sampling sites in this study: (A) Bloedel Donovan Park; (B) Lakewood; (C) Sudden Valley. Lake Whatcom, Whatcom County, Washington, USA. (Map data: Google Earth Pro, DigitalGlobe; 2016).

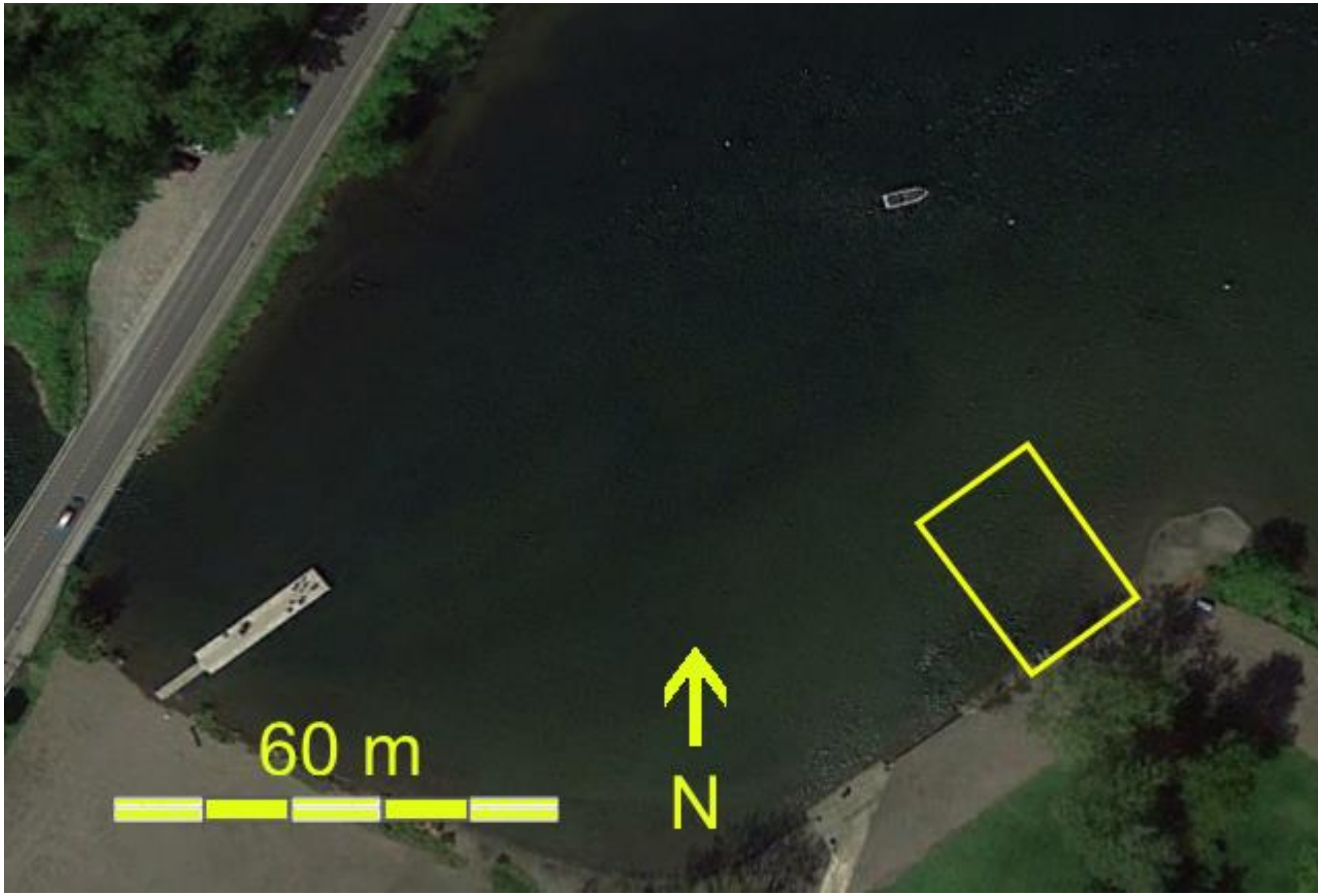

Figure 7. Bloedel Donovan Park survey area in this study. Lake Whatcom, Whatcom County, Washington, USA (Map data: Google Earth Pro, DigitalGlobe; 2016).

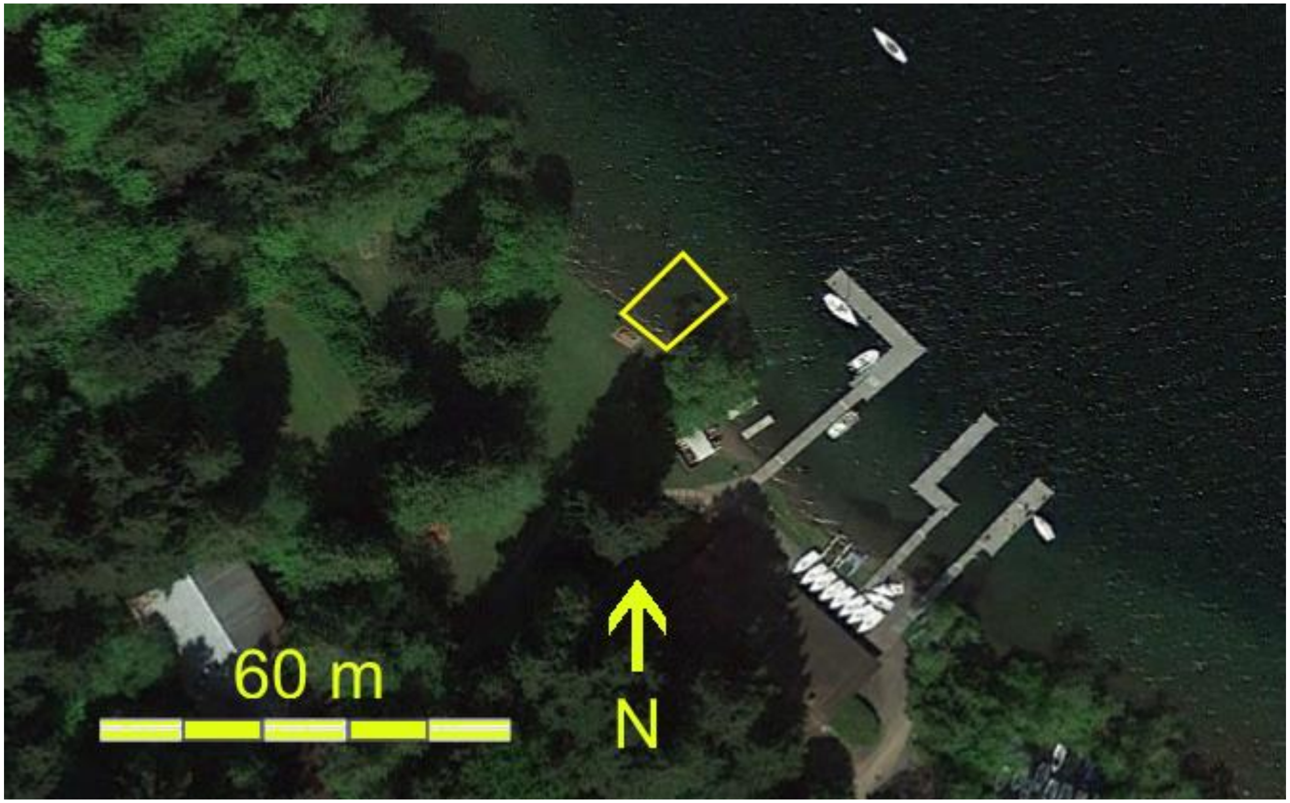

Figure 8. Lakewood survey area in this study. Lake Whatcom, Whatcom County, Washington, USA (Map data: Google Earth Pro, DigitalGlobe; 2016).

Figure 9. Sudden Valley survey area in this study. Lake Whatcom, Whatcom County, Washington, USA (Map data: Google Earth Pro, DigitalGlobe; 2016).

Table 1. Quadrat counts in this study by site. Lake Whatcom, Whatcom County, Washington, USA; mid-August to mid-September 2012 and 2013.

Site	2012, n	2013, n	Overall, n
Bloedel Donovan Park	50	46	96
Lakewood	30	35	65
Sudden Valley	28	28	56
All Sites	108	109	217

Table 2. Comparison of *C. fluminea* density (n/m^2) in this study by site. Lake Whatcom, Whatcom County, Washington, USA; mid-August to mid-September 2012 and 2013 (Kruskal-Wallis).

Site	Quadrat Count		Median Density (Interquartile Range)		Chi-square	P value*
	2012	2013	2012	2013		
Bloedel Donovan Park	50	45	36 (0-112)	64 (28-144)	**4.387**	**0.036**
Lakewood	30	35	104 (64-160)	62 (13-172)	0.735	0.391
Sudden Valley	28	28	108 (84-138)	160 (130-200)	**6.838**	**0.009**
All sites	108	108	84 (10-132)	90 (56-175)	2.94	0.086

*significantly different values are indicated by bold (P≤0.05)

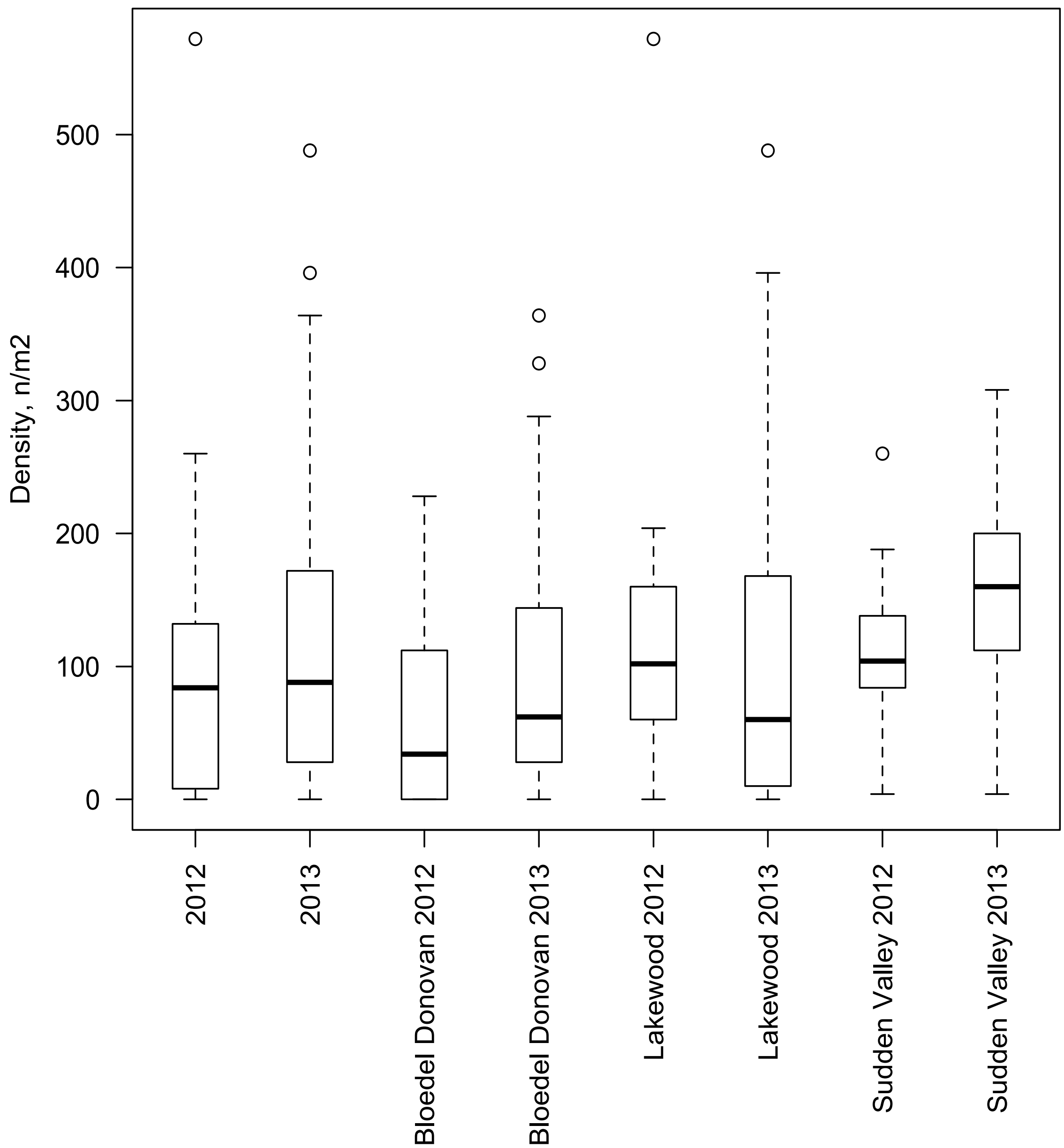

Figure 10. Distribution of *C. fluminea* density (n/m^2), at each sample site; the center bar is the median (2^{nd} quartile), bottom of the box is the 1^{st} quartile, top of the box is the 3^{rd} quartile, whiskers represent non-exceptional range, and open dots represent exceptional outliers. Whatcom County, Washington, USA; mid-August to mid-September 2012 and 2013.

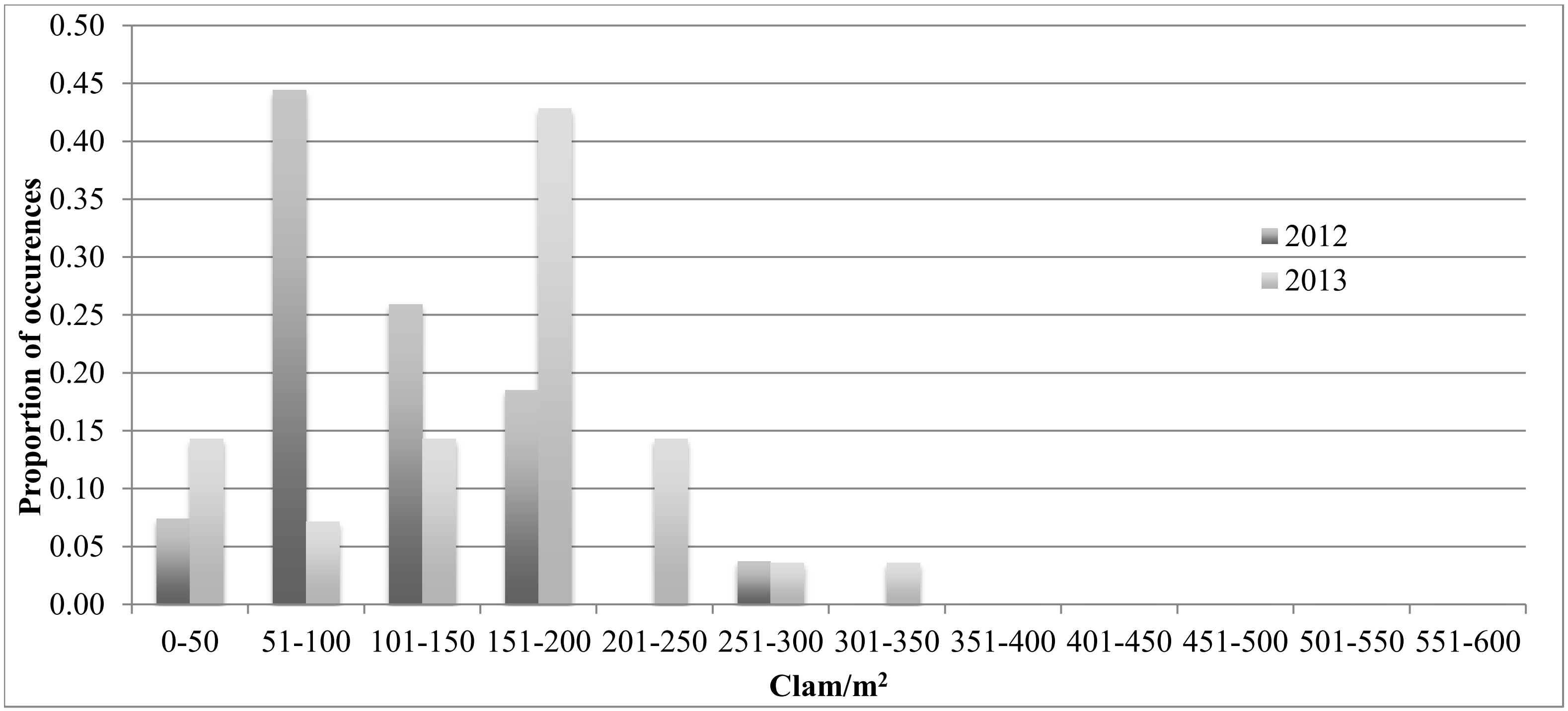

Figure 11. Distribution of *C. fluminea* density (n/m^2) at the Sudden Valley site in this study; 2012 quadrats = 28, 2013 quadrats = 28. Whatcom County, Washington, USA; mid-August to mid-September 2012 and 2013.

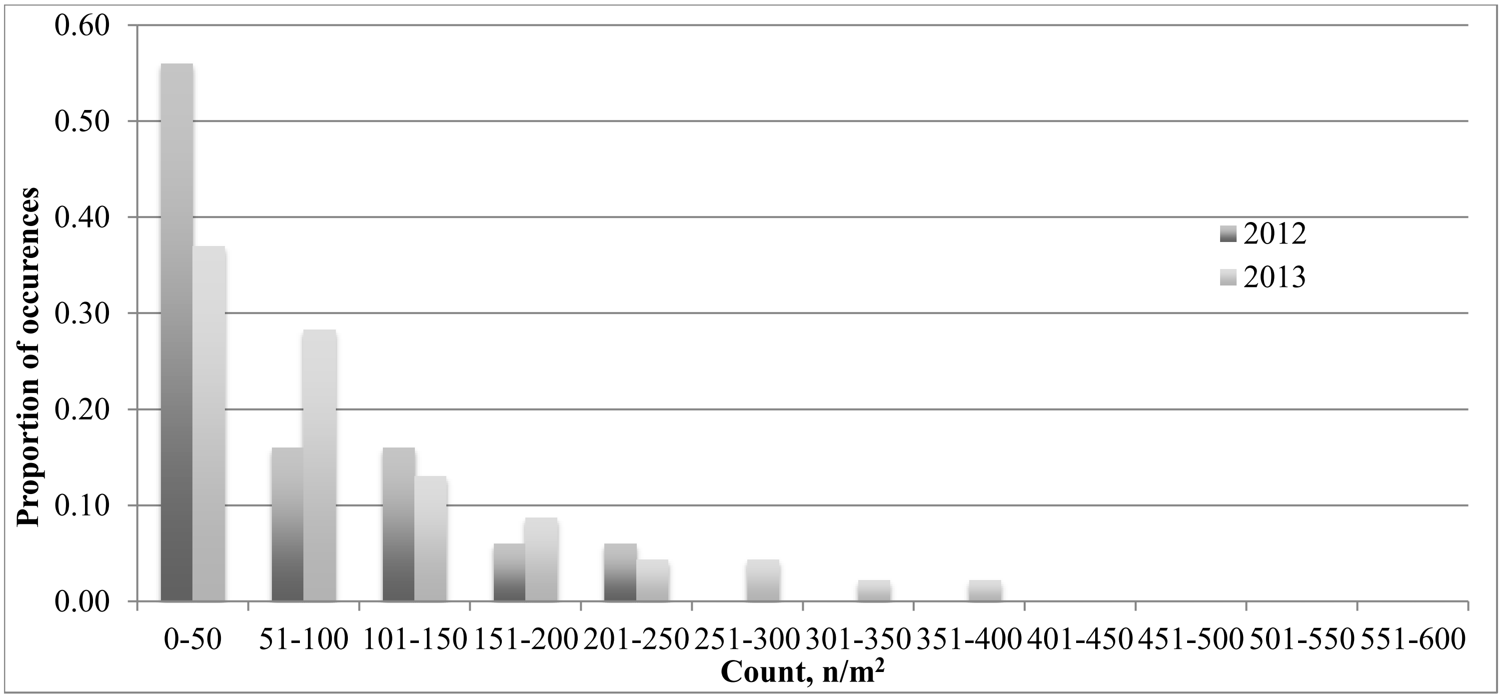

Figure 12. Distribution of *C. fluminea* density (n/m^2) at the Bloedel Donovan Park site in this study; 2012 quadrat n = 48, 2013 quadrat n = 50. Whatcom County, Washington, USA; mid-August to mid-September 2012 and 2013.

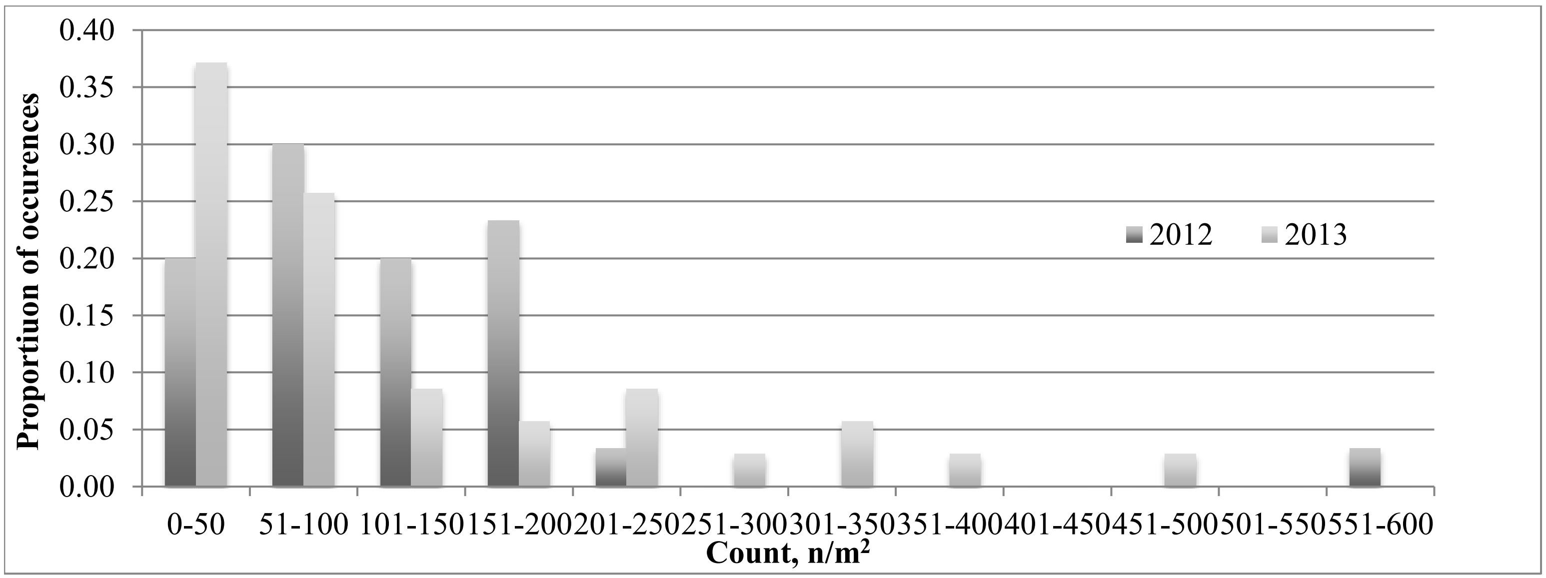

Figure 13. Distribution of *C. fluminea* density (n/m^2) at the Lakewood site in this study; 2012 n = 30, 2013 n = 35. Lake Whatcom, Whatcom County, Washington, USA; mid-August to mid-September 2012 and 2013.

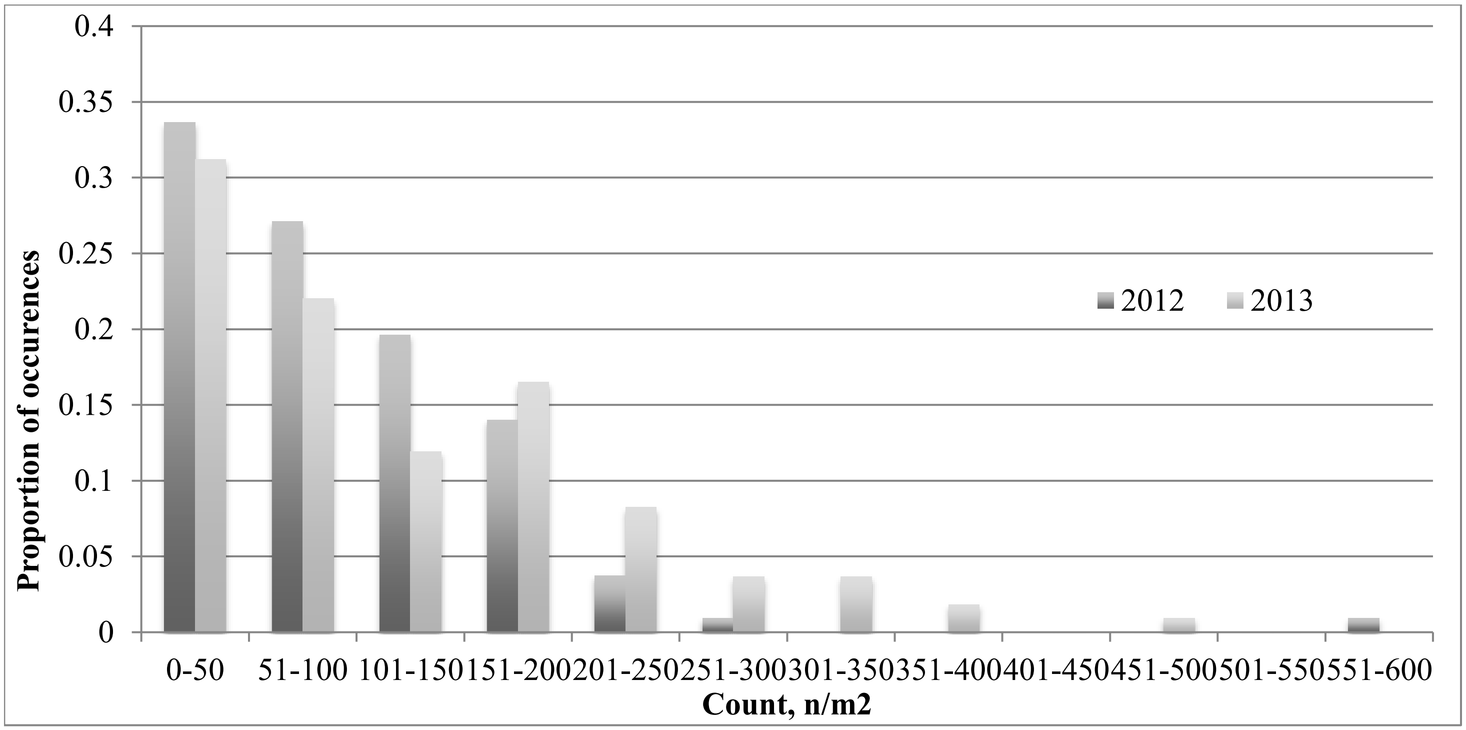

Figure 14. Distribution of *C. fluminea* density (n/m^2) at all sites 2012 and 2013 combined; 2012 n = 108, 2013 n = 109. Whatcom County, Washington, USA; mid-August to mid-September 2012 and 2013.

Table 3. Comparison of *C. fluminea* density (n/m^2) among sites in 2012 (Pairwise-Wilcoxon; P values adjusted for multiple comparisons using Holm's method). Whatcom County, Washington, USA; mid-August to mid-September 2012.

Site 2012	Quadrat Count	Median Density (Interquartile Range)	W	P value*
Bloedel Donovan Park	50	36 (0-112)	465.5	**0.012**
Lakewood	30	104 (64-160)		
Bloedel Donovan Park	50	36 (0-112)	360.5	**0.001**
Sudden Valley	28	108 (84-138)		
Lakewood	30	104 (64-160)	391.5	0.663
Sudden Valley	28	108 (84-138)		

*significantly different densities are indicated by bold (P≤0.05)

Table 4. Comparison of *C. fluminea* density (n/m^2) among sites in 2013 (Pairwise-Wilcoxon; P values adjusted for multiple comparisons using Holm's method). Whatcom County, Washington, USA; mid-August to mid-September 2013.

Site 2013	Quadrat Count	Median Density (Interquartile Range)	W	P value*
Bloedel Donovan Park	45	64 (28-144)	785	0.852
Lakewood	35	62 (13-172)		
Bloedel Donovan Park	45	64 (28-144)	361	**0.005**
Sudden Valley	28	160 (130-200)		
Lakewood	35	62 (13-172)	327	**0.050**
Sudden Valley	28	160 (130-200)		

*significantly different densities are indicated by bold (P≤0.05)

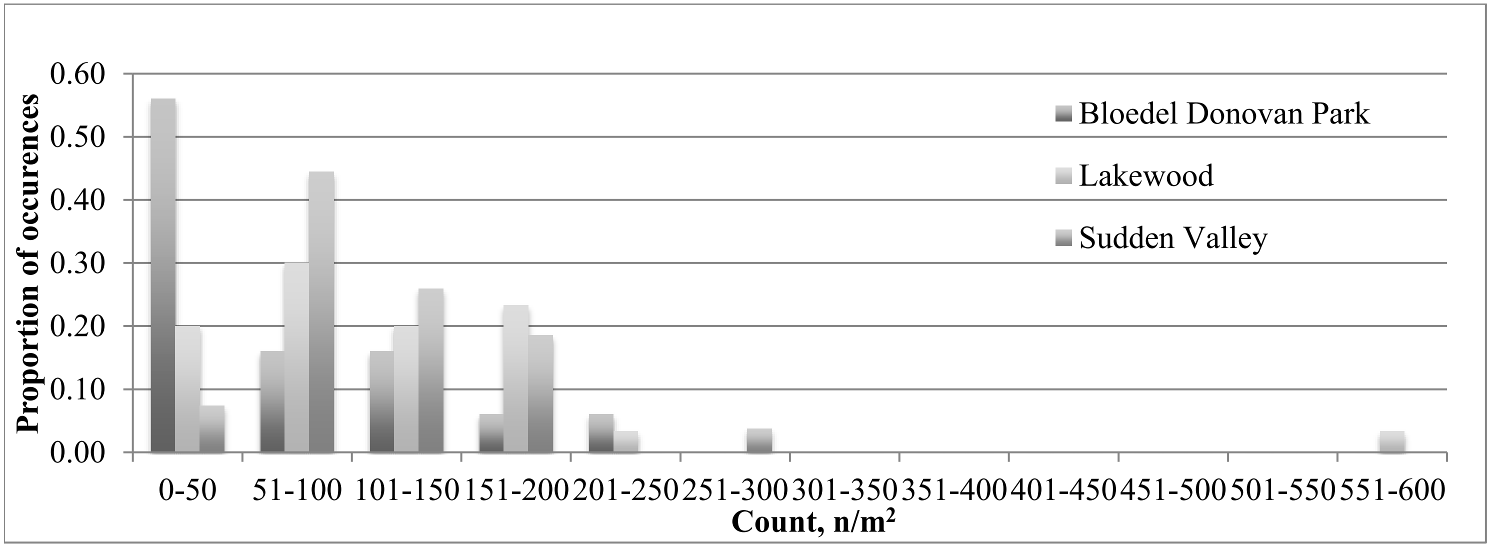

Figure 15. Distribution of *C. fluminea* density (n/m^2) at all sites mid-August to mid-September 2012; Bloedel Donovan Park n = 48, Lakewood n = 30, Sudden Valley n = 28. Lake Whatcom, Whatcom County, Washington, USA; mid-August to mid-September 2012.

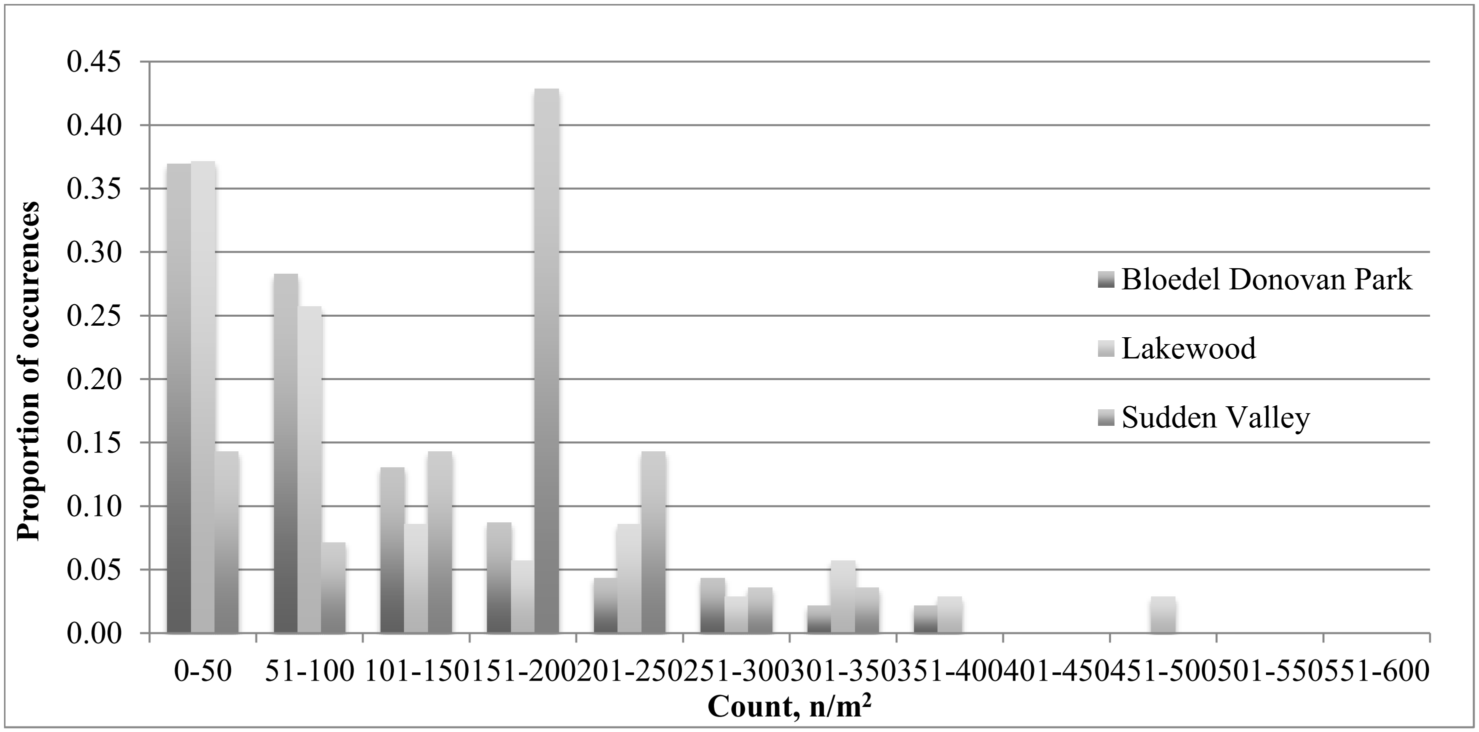

Figure 16. Distribution of *C. fluminea* density (n/m^2) at all sites 2013; Bloedel Donovan Park n = 50, Lakewood n = 35, Sudden Valley n = 28. Lake Whatcom, Whatcom County, Washington, USA; mid-August to mid-September 2013.

Table 5. Comparison of *C. fluminea* biomass (grams/m^2) within sites (Kruskal-Wallis). Lake Whatcom, Whatcom County, Washington, USA; mid-August to mid-September 2012 and 2013.

Site	Quadrat Count		Median Biomass (Interquartile Range)		Chi-square	P value*
	2012	2013	2012	2013		
Bloedel Donovan Park	50	45	44.58 (0.00-209.62)	75.82 (23.36-117.49)	**0.368**	**0.544**
Lakewood	30	35	121.01 (90.75-227.43)	131.05 (9.12-325.10)	0.009	0.937
Sudden Valley	28	28	213.23 (162.27-271.16)	418.35 (9.12-325.10)	**10.581**	**0.001**
All sites	108	108	139.61 (12.73-234.48)	118.87 (33.33-346.07)	1.102	0.294

*significantly different values are indicated by bold (P≤0.05)

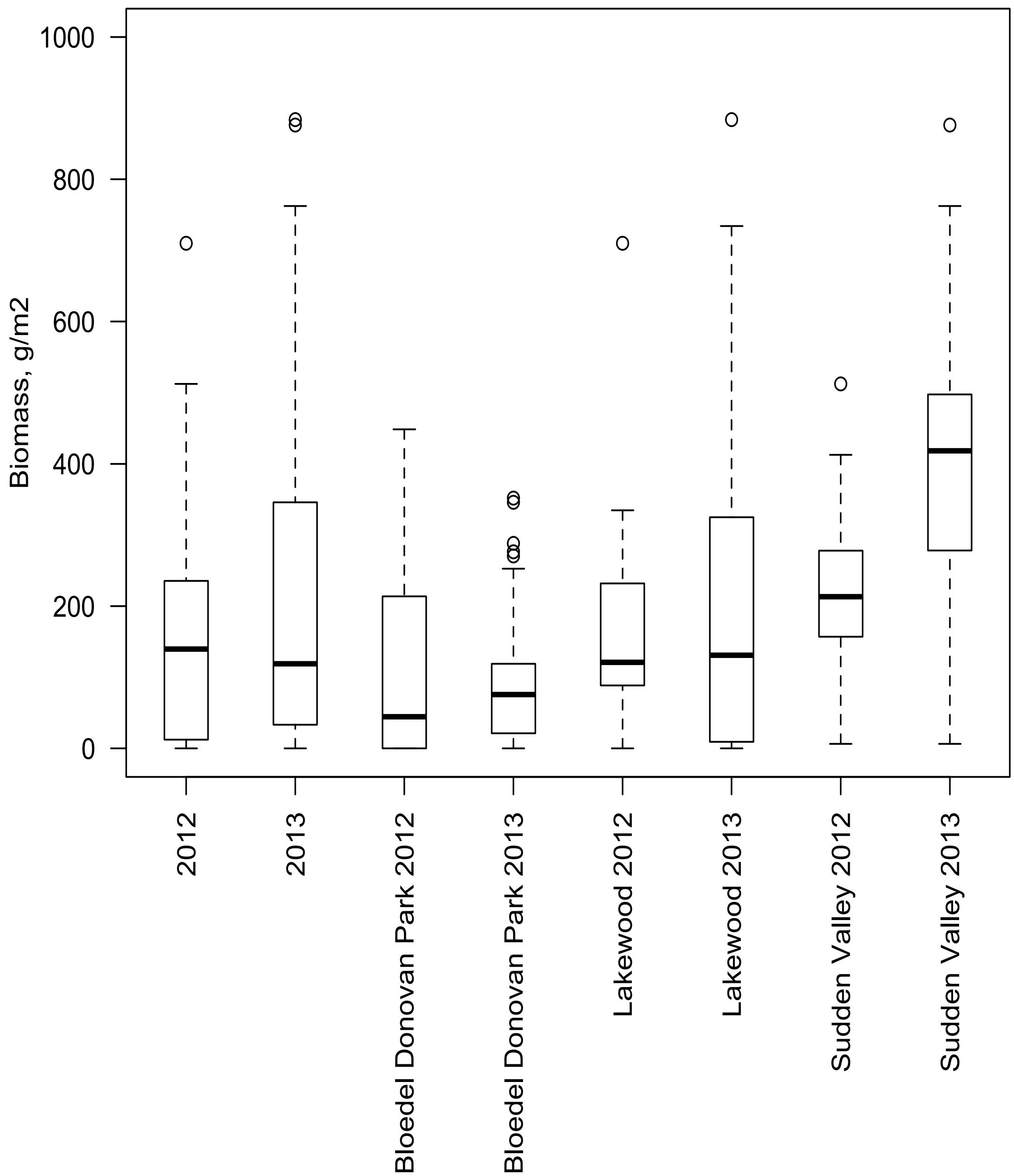

Figure 17. Distribution of *C. fluminea* biomass (grams/m^2) at each sample site; the center bar is the median (2^{nd} quartile), bottom of the box is the 1^{st} quartile, top of the box is the 3^{rd} quartile, whiskers represent non-exceptional range, dots represent exceptional outliers. Lake Whatcom, Whatcom County, Washington, USA; mid-August to mid-September 2012 and 2013.

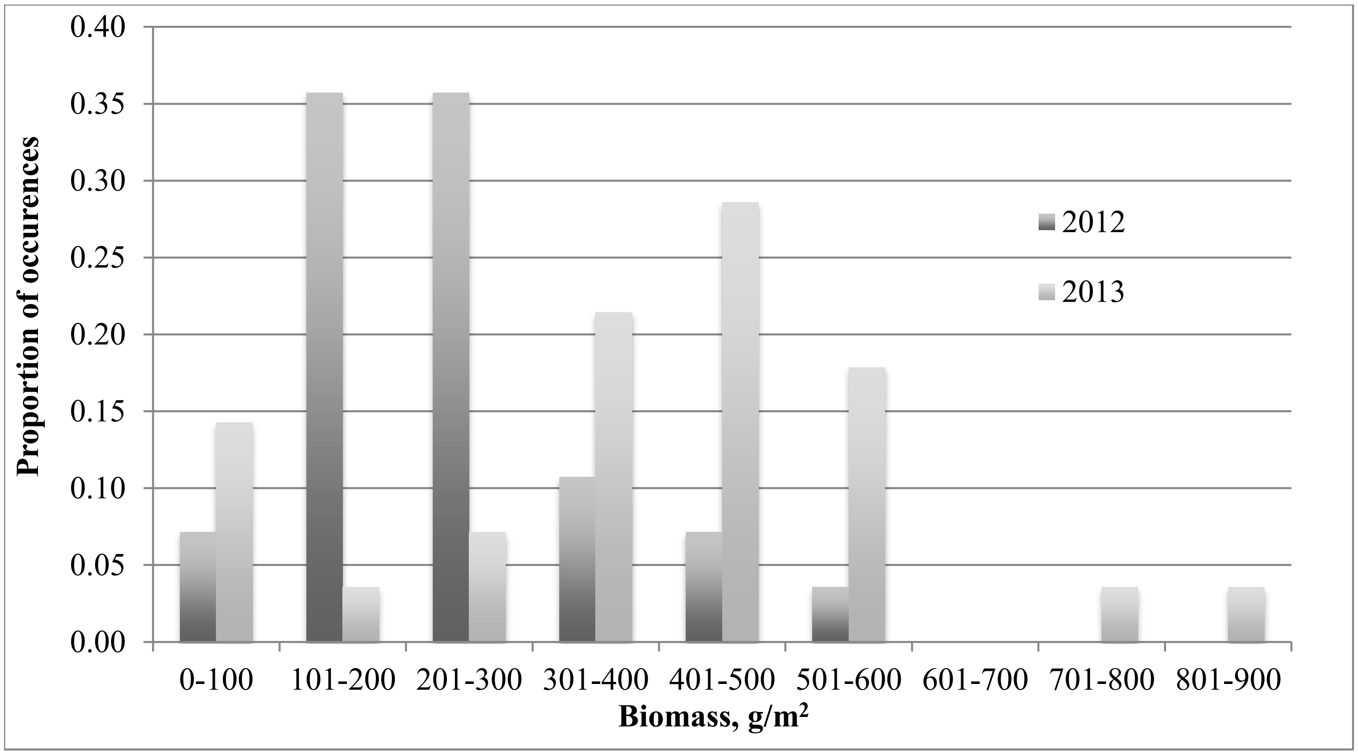

Figure 18. Distribution of *C. fluminea* biomass (g/m^2) frequency at Sudden Valley; 2012 n = 28, 2013 n = 28. Lake Whatcom, Whatcom County, Washington, USA; mid-August to mid-September 2012 and 2013.

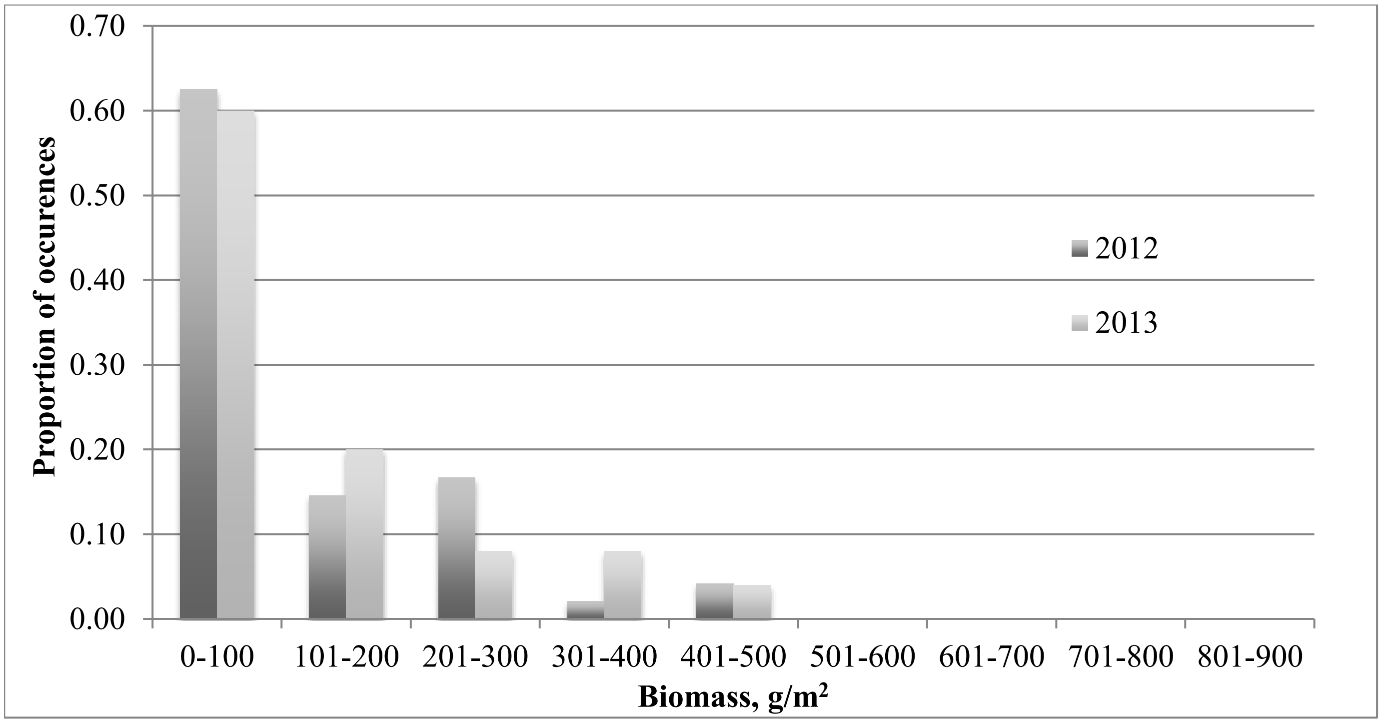

Figure 19. Distribution of *C. fluminea* biomass (g/m^2) at Bloedel Donovan Park; 2012 n = 48, 2013 n = 50. Lake Whatcom, Whatcom County, Washington, USA; mid-August to mid-September 2012 and 2013.

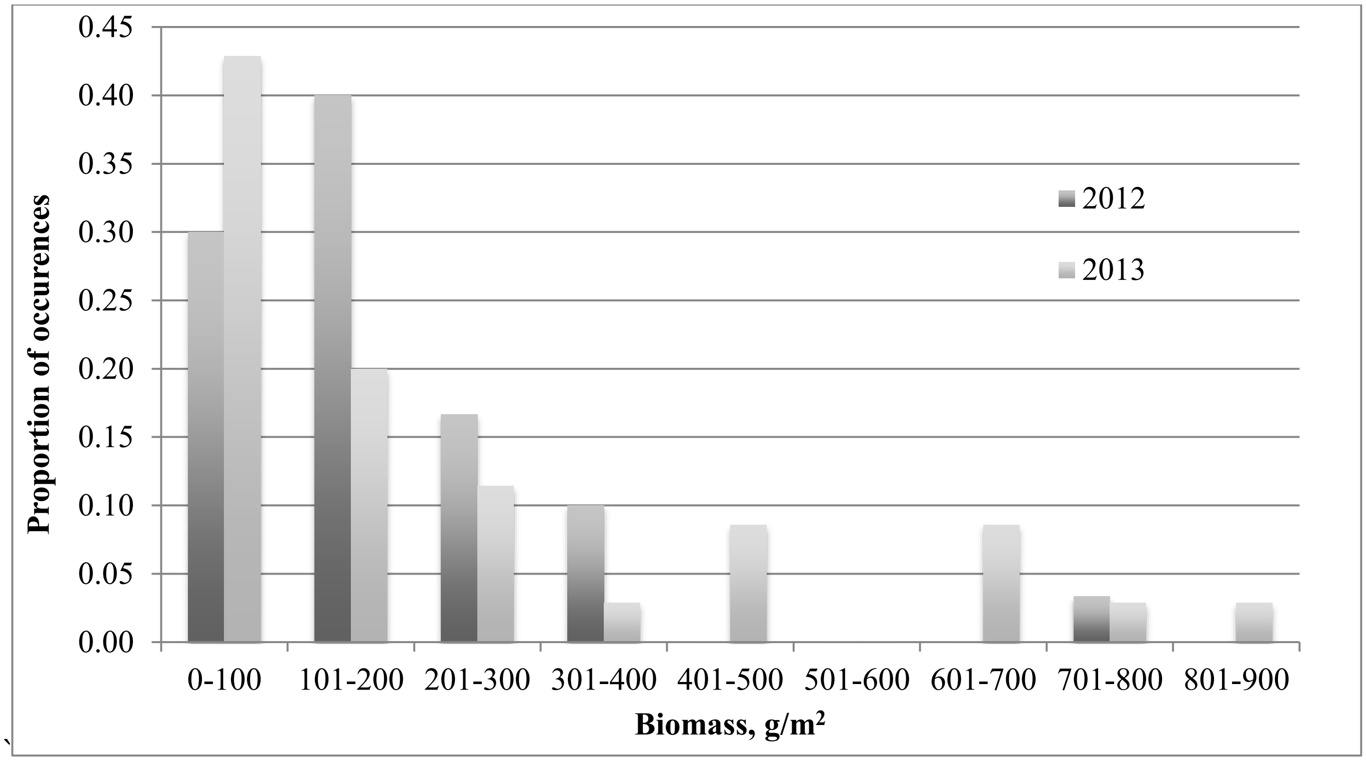

Figure 20. Distribution of *C. fluminea* biomass (g/m^2) at Lakewood; 2012 n = 30, 2013 n = 35. Lake Whatcom, Whatcom County, Washington, USA; mid-August to mid-September 2012 and 2013.

Table 6. Comparison of *C. fluminea* biomass (g/m^2) at sites mid-August to mid-September 2012 (Pairwise-Wilcoxon; P values adjusted for multiple comparisons using Holm's method). Lake Whatcom, Whatcom County, Washington, USA.

Site 2012	Quadrat Count	Median Biomass (Interquartile Range)	W	P value*
Bloedel Donovan Park	50	44.58 (0.00-209.62)	547	**0.042**
Lakewood	30	121.01 (90.75-227.43)		
Bloedel Donovan Park	50	44.58 (0.00-209.62)	325	**0.001**
Sudden Valley	28	213.23 (162.27-271.16)		
Lakewood	30	121.01 (90.75-227.43)	259	**0.025**
Sudden Valley	28	213.23 (162.27-271.16)		

*significantly different densities are indicated by bold (P≤0.05)

Table 7. Comparison of *C. fluminea* biomass (g/m^2) of *Corbicula fluminea* among sites mid-August to mid-September 2013 (Kruskal-Wallis). Lake Whatcom, Whatcom County, Washington, USA.

Site 2013	Quadrat Count	Median Biomass (Interquartile Range)	Chi-square	P value*
Bloedel Donovan Park	45	75.82 (23.36-117.49)	3.952	0.047
Lakewood	35	131.05 (9.12-325.10)		
Bloedel Donovan Park	45	75.82 (23.36-117.49)	29.378	**< 0.001**
Sudden Valley	28	418.35 (9.12-325.10)		
Lakewood	35	131.05 (9.12-325.10)	9.352	**0.005**
Sudden Valley	28	418.35 (9.12-325.10)		

* Significantly different densities are indicated by bold (P≤0.05)

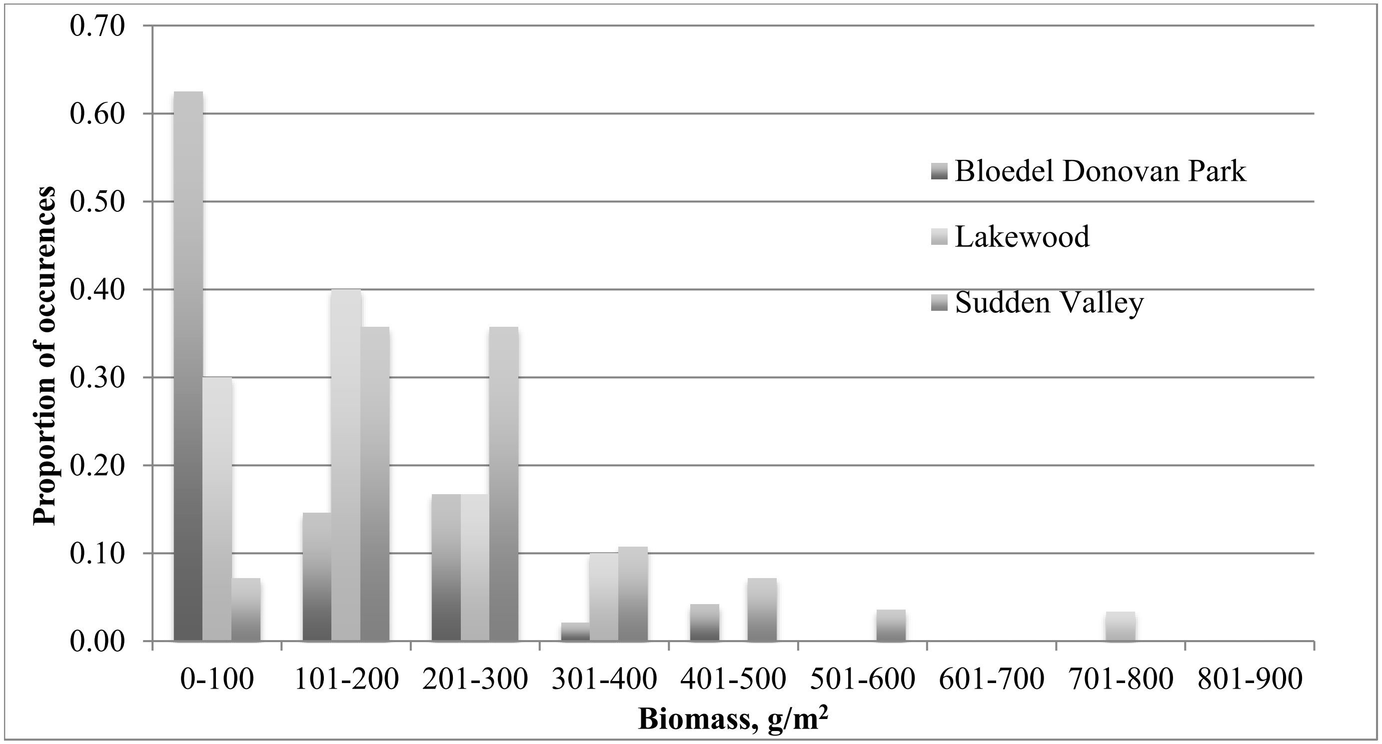

Figure 21. Distribution of *C. fluminea* biomass (g/m^2) at all sites mid-August to mid-September 2012; Bloedel Donovan Park n = 48, Lakewood n = 30, Sudden Valley n = 28. Lake Whatcom, Whatcom County, Washington, USA.

Table 8. Size distribution in *C. fluminea* (N) among the three sample locations mid-August to mid-September 2012 and 2013, millimeters. Lake Whatcom, Whatcom County, Washington, USA.

Site 2012	N	Maximum Length	Minimum Length	Median Length	Interquartile Range
Bloedel Donovan Park	700	27.5	7.5	19.0	3.0 (17.0-20.0)
Lakewood	859	25.5	2.5	17.0	9.2 (8.5-17.7)
Sudden Valley	816	26.0	5.0	19.0	5.0 (16.0-21.0)
Overall	2375	27.5	2.5	18.0	4.0 (16.0-20.0)

Site 2013	N	Maximum Length	Minimum Length	Median Length	Interquartile Range
Bloedel Donovan Park	1074	28.0	5.5	9.7	9.2 (8.5-17.7)
Lakewood	1003	27.0	6.1	19.0	4.5 (16.0-20.5)
Sudden Valley	1064	28.5	7.0	21.0	5.5 (17.5-23.0)
Overall	3141	28.5	5.5	18.0	10.0 (11.0-21.0)

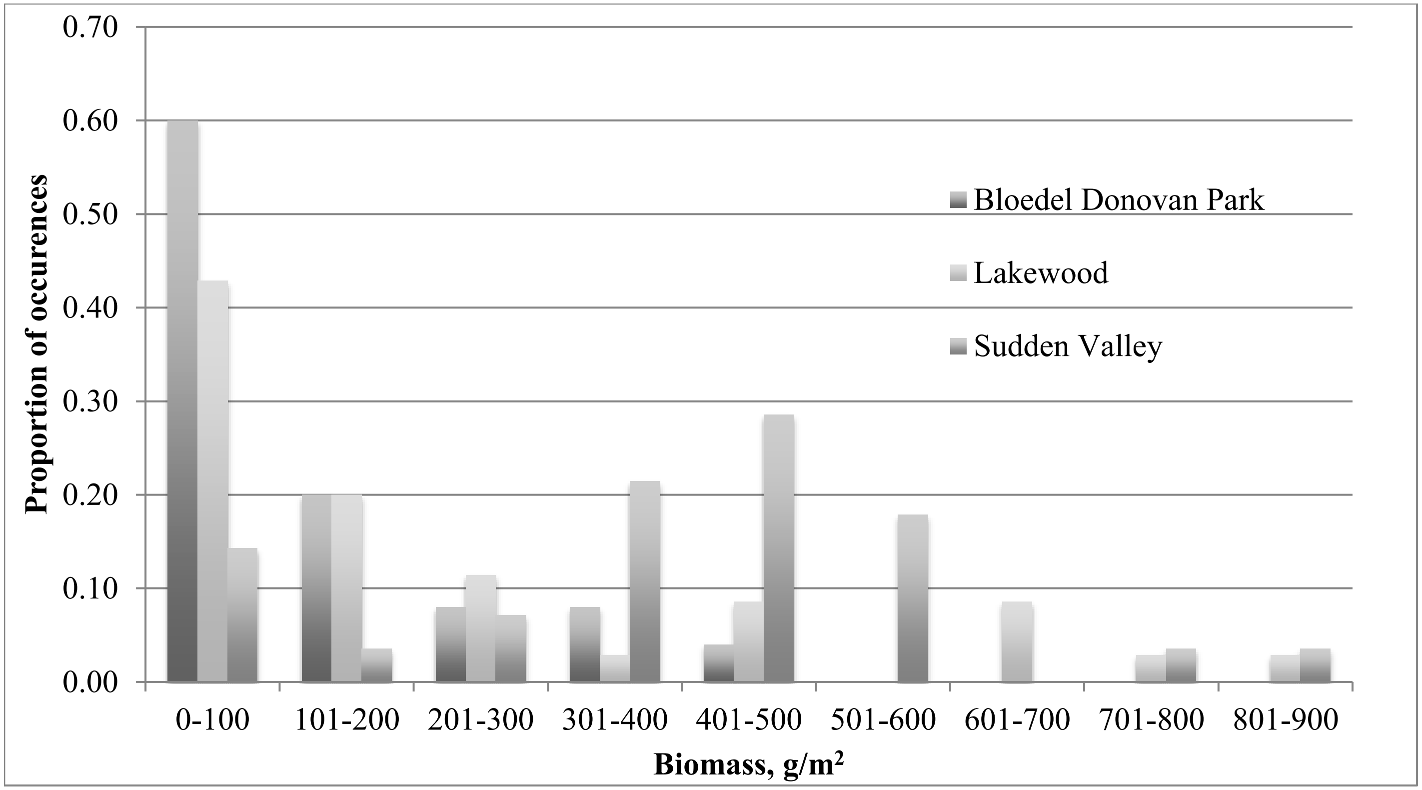

Figure 22. Distribution of *C. fluminea* biomass (g/m^2) at all sites mid-August to mid-September 2013; Bloedel Donovan Park n = 50, Lakewood n = 35, Sudden Valley n = 28. Lake Whatcom, Whatcom County, Washington, USA.

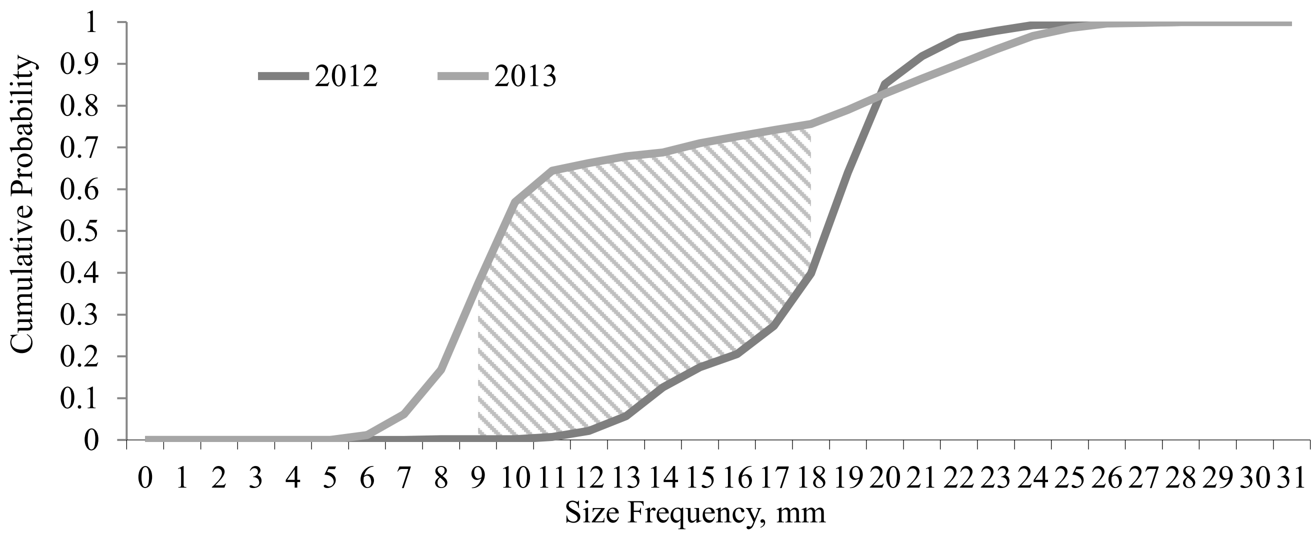

Figure 23. Cumulative size frequency of *C. fluminea* (mm) at Bloedel Donovan Park mid-August to mid-September 2012 and 2013; significant difference from 9 through 18-mm; Kolmogorov-Smirnov, **P-value ≤ 0.01**, D-statistic ≥ 35.75, Alpha 0.05, N size = 100, Alpha-level = 0.05. Lake Whatcom, Whatcom County, Washington, USA.

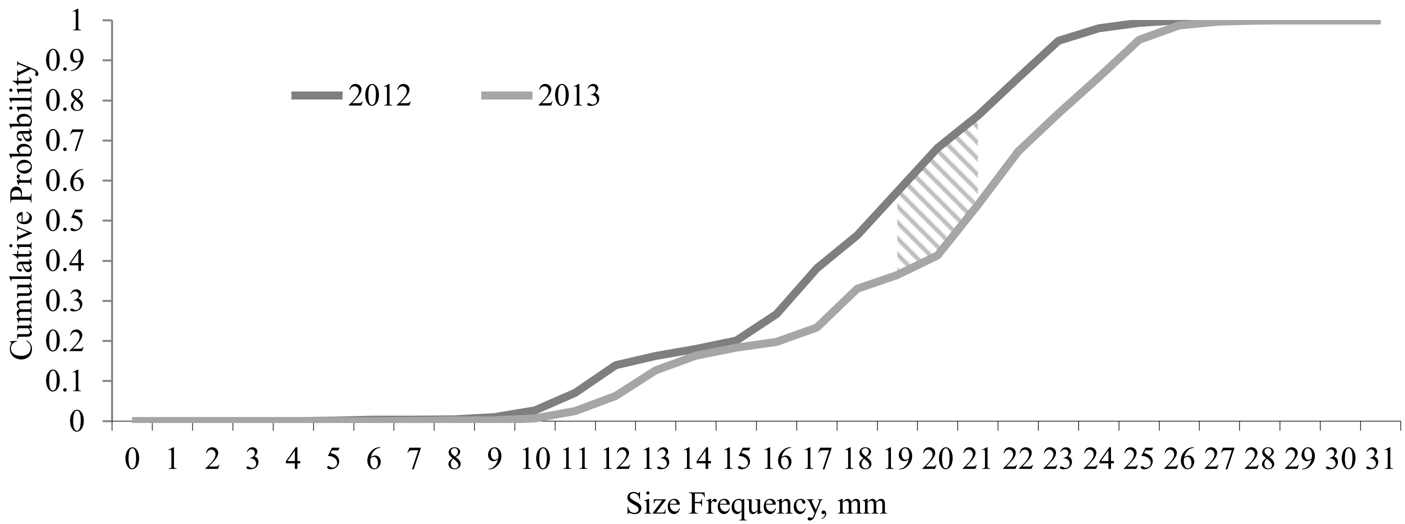

Figure 24. Cumulative size frequency *C. fluminea* (mm) at Sudden Valley mid-August to mid-September 2012 and 2013; significant difference from 19 through 21-mm; Kolmogorov-Smirnov, **P-value ≤ 0.01**, D-statistic ≥ 20.76, N size = 100, Alpha-level = 0.05. Lake Whatcom, Whatcom County, Washington.

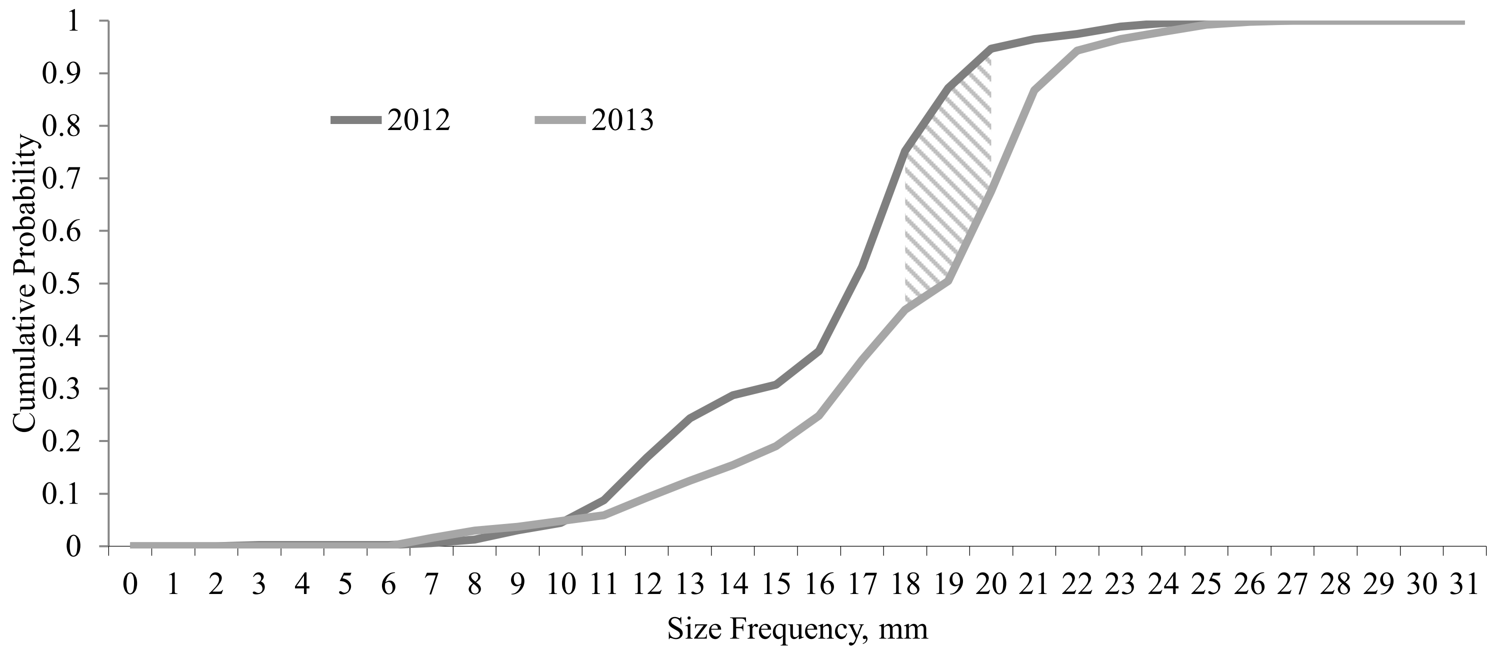

Figure 25. Cumulative size frequency *C. fluminea* (mm) at Lakewood mid-August to mid-September 2012 and 2013; significant difference from 18 through 20-mm; Kolmogorov-Smirnov, **P-value ≤ 0.01**, D-statistic ≥ 27.15, N size = 100, Alpha-level = 0.05. Lake Whatcom, Whatcom County, Washington, USA.

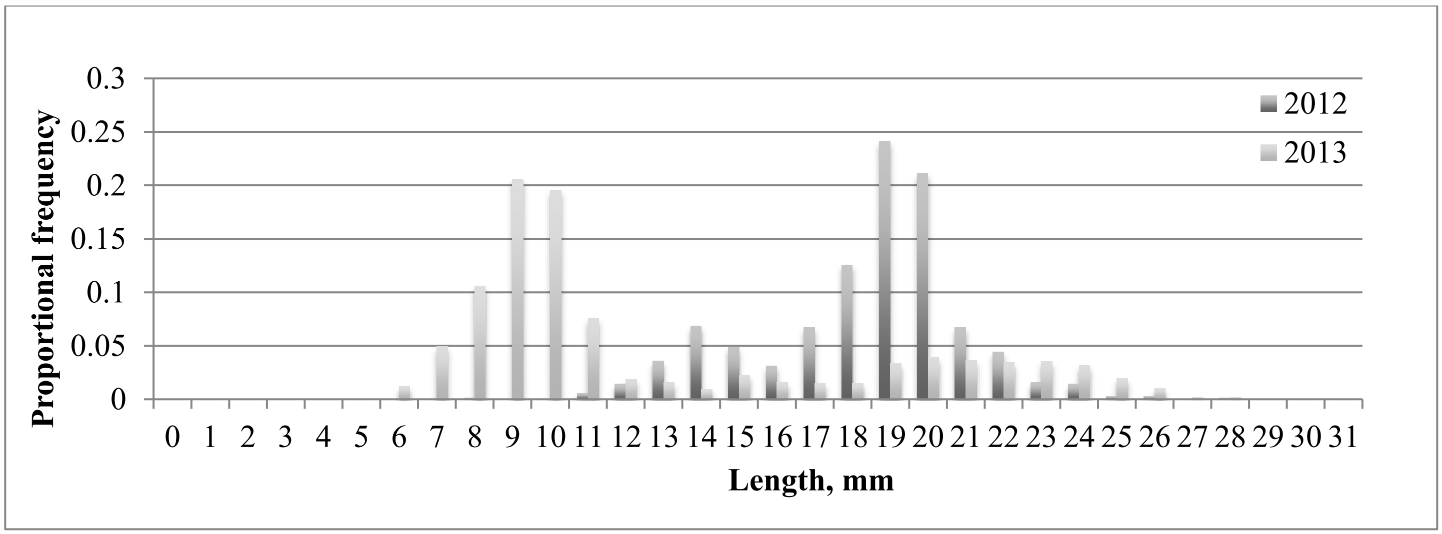

Figure 26. Proportional frequency distribution of *C. fluminea* (mm) at Bloedel Donovan Park mid-August to mid-September 2012 and 2013; 2012 N size = 700, 2013 N size = 1074. Lake Whatcom, Whatcom County, Washington, USA.

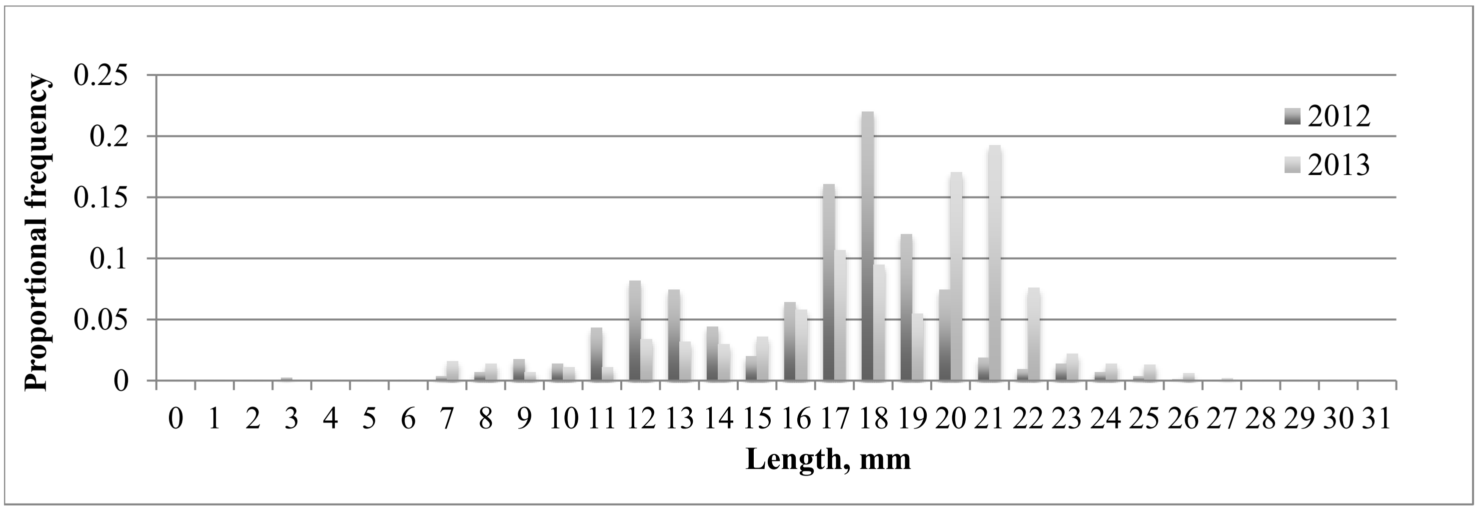

Figure 27. Proportional size distribution of *C. fluminea* (mm) at Lakewood mid-August to mid-September 2012 and 2013; 2012 N size = 859, 2013 N size = 1003. Lake Whatcom, Whatcom County, Washington, USA.

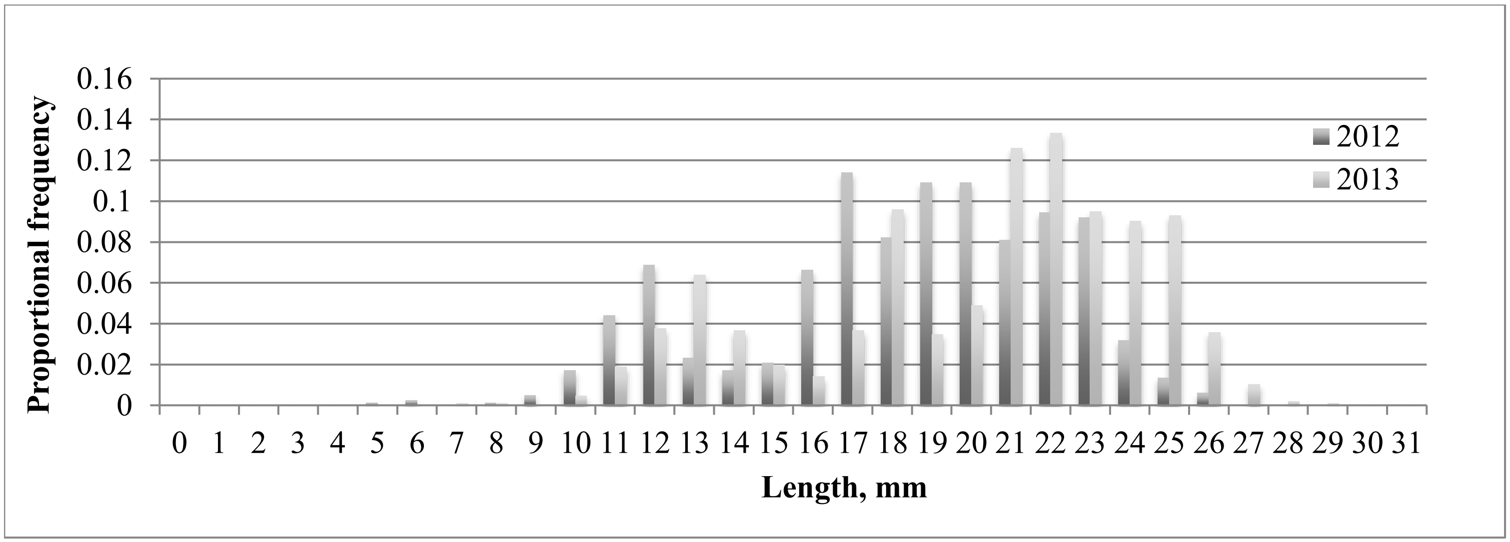

Figure 28. Proportional size distribution of *C. fluminea* (mm) at Sudden Valley mid-August to mid-September 2012 and 2013; 2012 N size = 816, 2013 N size = 1074. Lake Whatcom, Whatcom County, Washington, USA.

Table 9. Size distribution (mm) in *C. fluminea* (N) among the three sample locations mid-August to mid-September 2012 and 2013. Lake Whatcom, Whatcom County, Washington, USA.

Site	N	Maximum Length	Minimum Length	Median Length	Interquartile Range
Bloedel Donovan Park	1774	28.0	5.5	15.1	10.3 9.2-19.5
Lakewood	1862	27.0	2.5	17.7	4.5 15.4-20.0
Sudden Valley	1880	28.5	5.0	20.0	5.0 17.0-22.0
Overall	5516	28.5	2.5	18.0	7.5 13.0-20.5

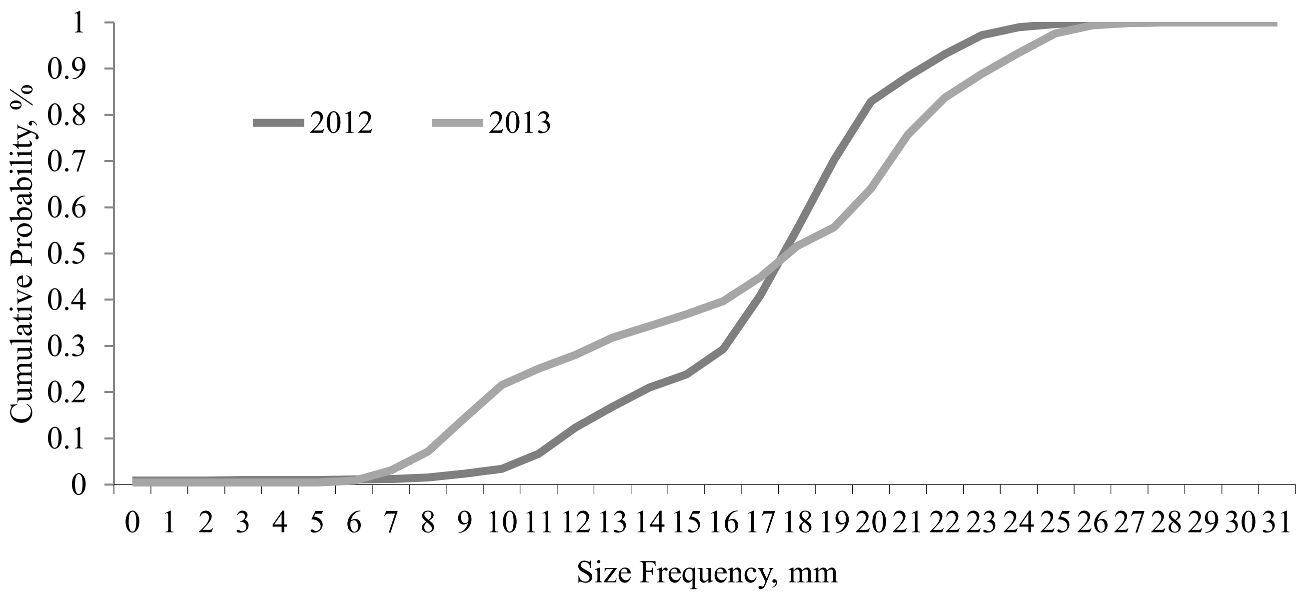

Figure 29. Cumulative size frequency (mm) of *C. fluminea* (N) at all sites mid-August to mid-September 2012 and 2013; no significant difference in any size classes; 2012 N size = 2375, 2013 N size = 3141. Lake Whatcom, Whatcom County, Washington, USA.

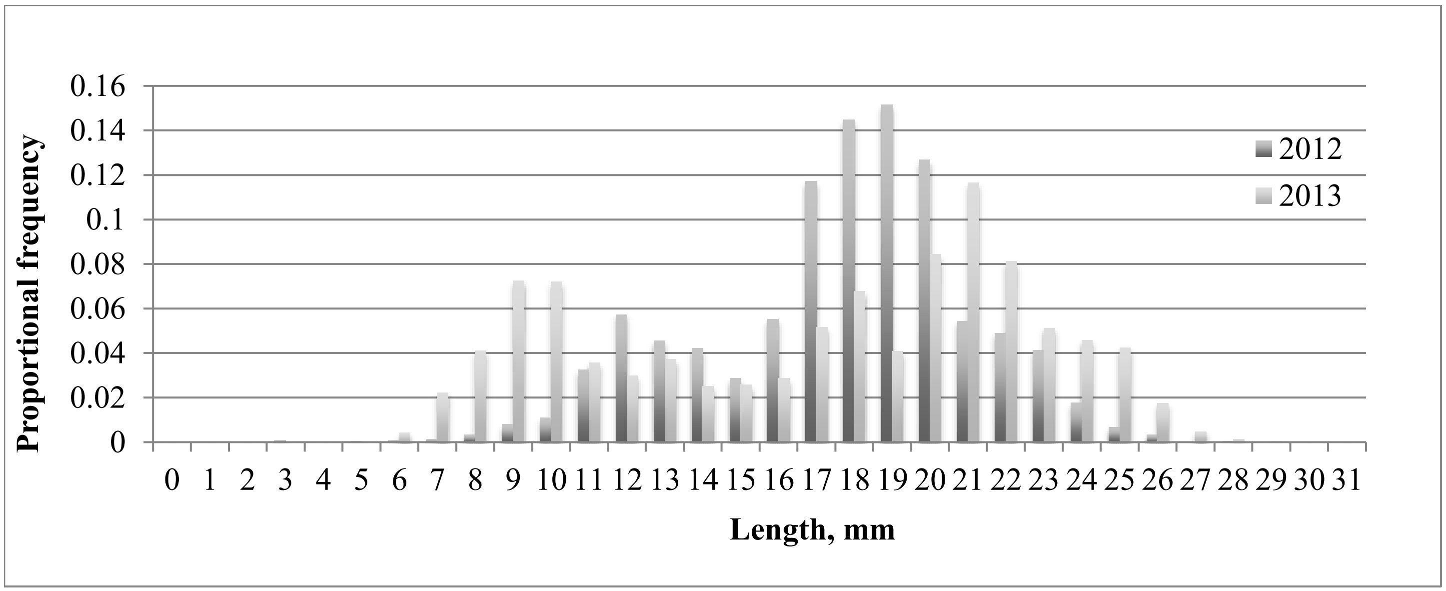

Figure 30. The proportional size distribution (mm) of *C. fluminea* (N) at all sites mid-August to mid-September 2012 and 2013; 2012 N size = 2375, 2013 N size = 3141. Lake Whatcom, Whatcom County, Washington, USA.

.

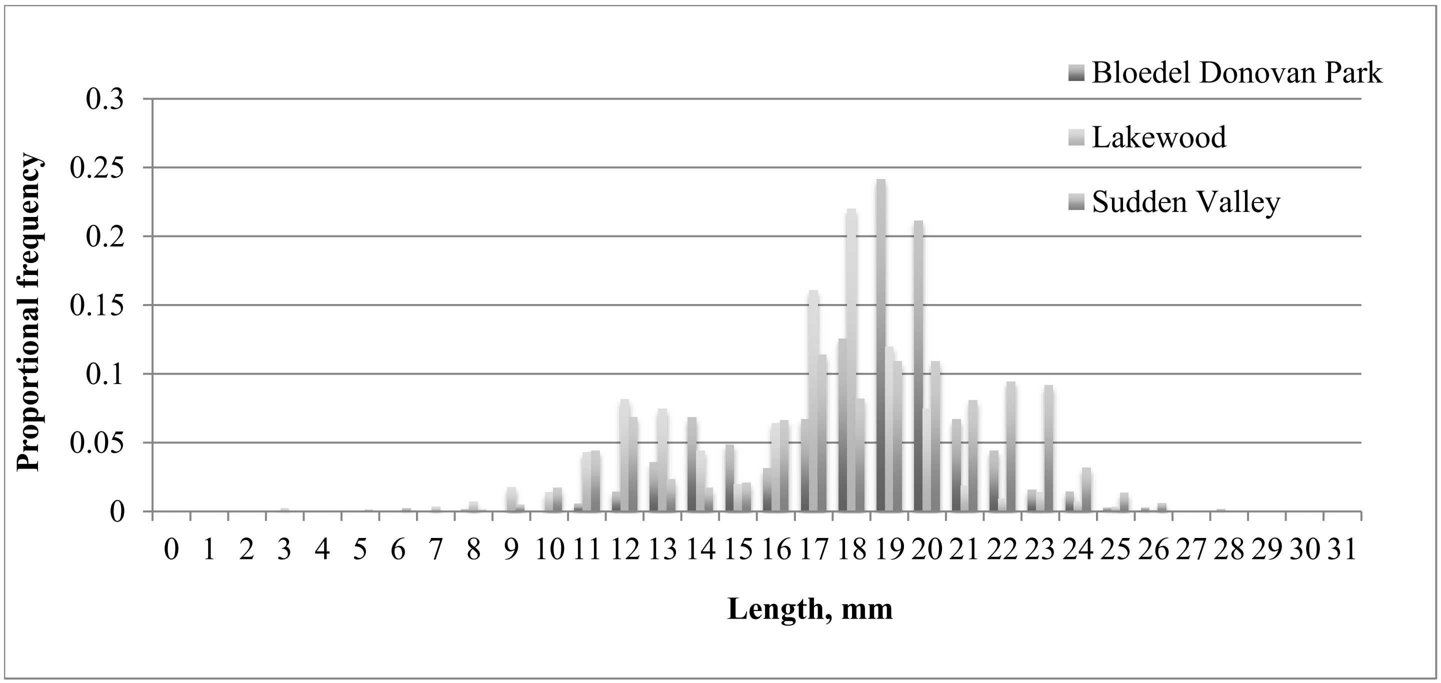

Figure 31. The proportional size distribution (mm) of *C. fluminea* (N) at all sites mid-August to mid-September 2012; Bloedel Donovan Park N size = 700, Lakewood N size = 859, Sudden Valley N size = 816. Lake Whatcom, Whatcom County, Washington, USA.

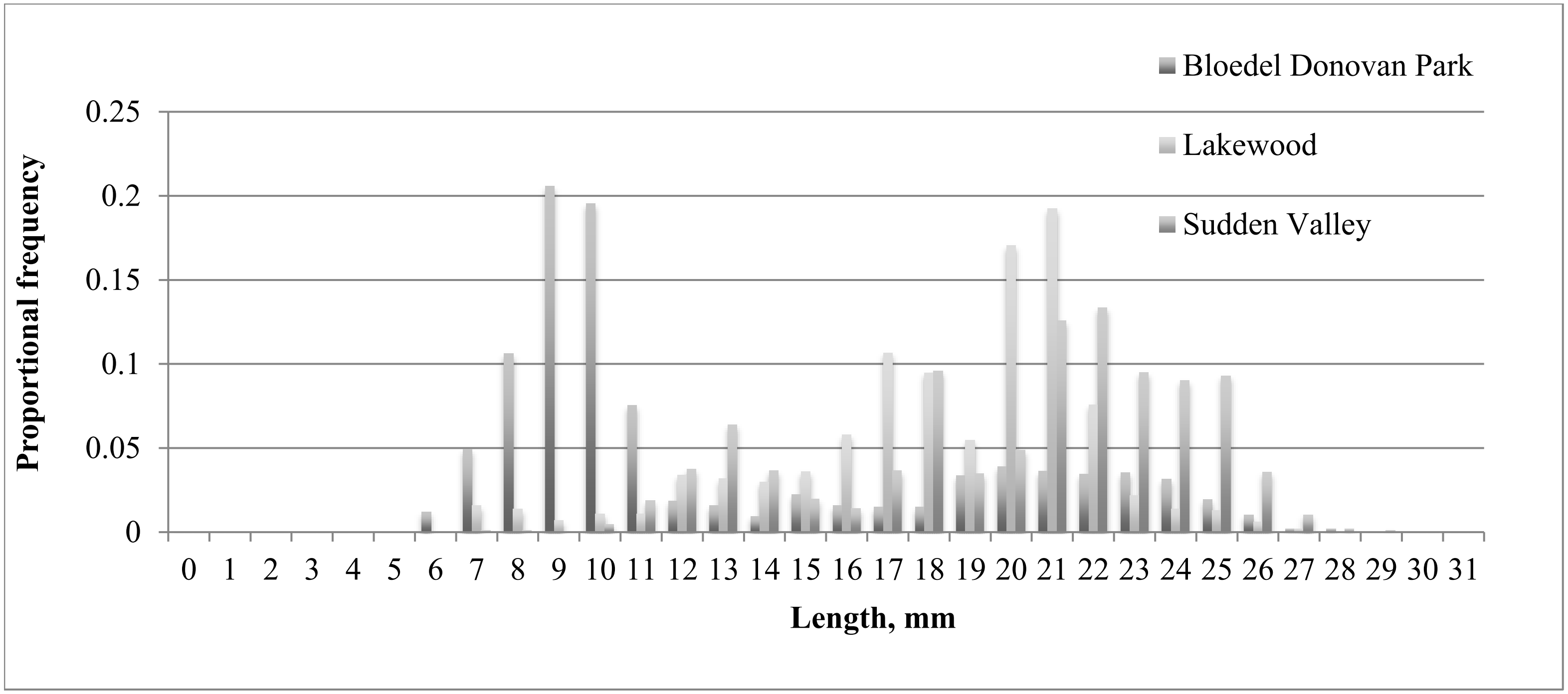

Figure 32. The proportional size distribution (mm) of *C. fluminea* (N) at all sites mid-August to mid-September 2013; Bloedel Donovan Park N size = 1074, Lakewood N size = 1003, Sudden Valley N size = 1064. Lake Whatcom, Whatcom County, Washington, USA.

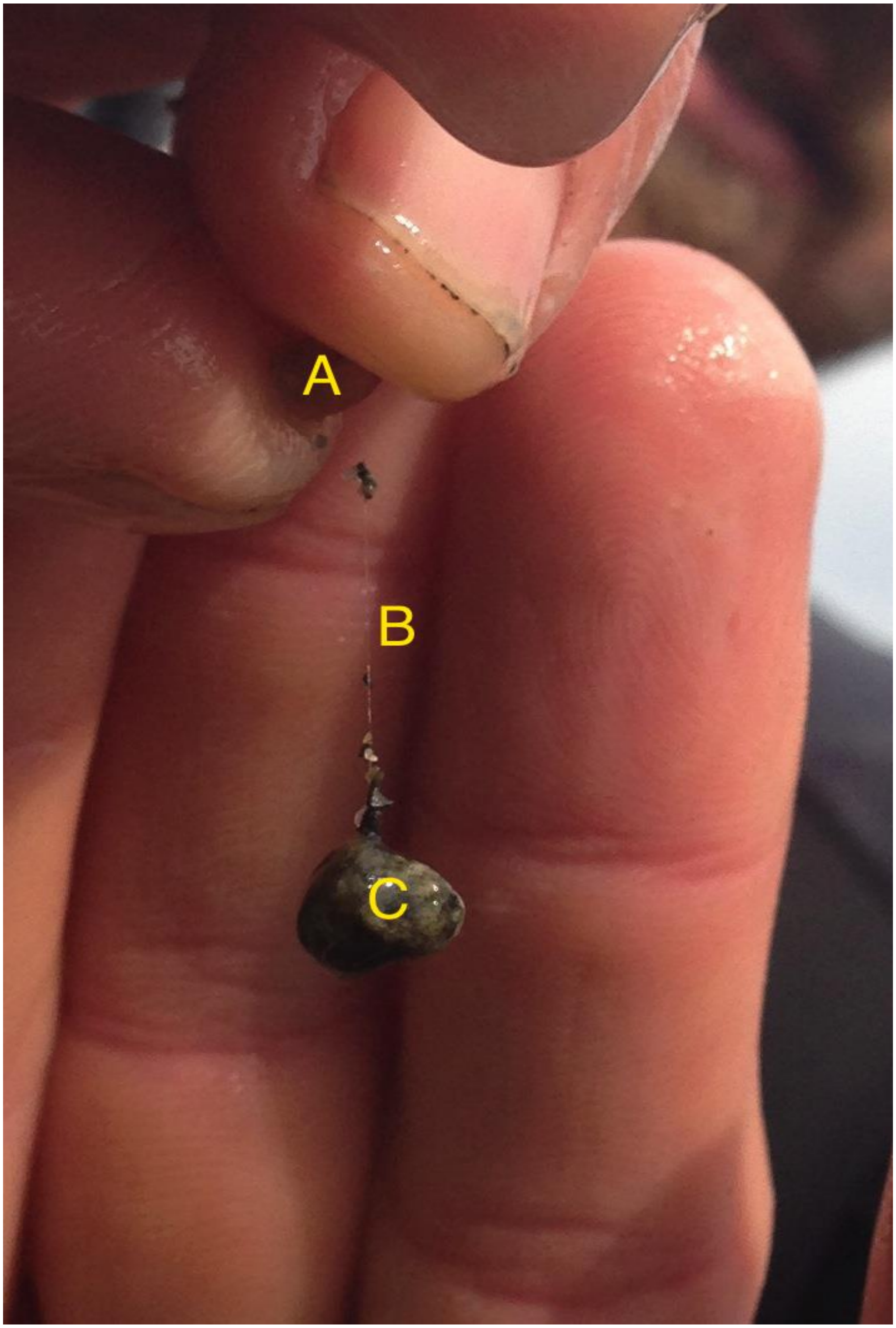

Figure 33. *Corbicula fluminea* larvae (A), in fingertips, attached by thread (B) to pebble (C). Lake Whatcom, Whatcom County, Washington, US

Table 10. Relation of depth to density (n/m^2) and biomass (grams/m^2) of *C. fluminea* at the three sites mid-August to mid-September 2012, 2013 combined, and overall. Rank-based comparison, positive rho values indicate an increase with depth. Lake Whatcom, Whatcom County, Washington, USA.

Site Combined Years	Quadrat Count	Median Depth (Interquartile Range)	Median Density (Interquartile Range)	rho	P value*
Bloedel Donovan Park	96	0.74 (0.53-1.04)	121 (0.0-121.0)	0.226	**0.027**
Lakewood	65	0.62 (0.36-0.95)	144 (16.0-160.0)	0.542	**< 0.001**
Sudden Valley	56	0.61 (0.48-0.73	86 (87.0-173.0)	0.135	< 0.320
All Sites	217	0.64 (0.48-0.89)	140 (16.0-156.0)	0.232	**< 0.001**

Site Combined Years	Quadrat Count	Median Depth (Interquartile Range)	Median Biomass (Interquartile Range)	rho	P value*
Bloedel Donovan Park	96	0.74 (0.53-1.04)	135.10 (0.00-135.10)	0.485	**< 0.001**
Lakewood	65	0.62 (0.36-0.95)	249.19 (23.05-272.24)	0.587	**< 0.001**
Sudden Valley	56	0.61 (0.48-0.73	252.47 (174.42-426.89)	0.054	0.693
All Sites	217	0.64 (0.48-0.89)	248.12 (23.49-271.61)	0.316	**< 0.001**

*significantly different densities are indicated by bold (P≤0.05)

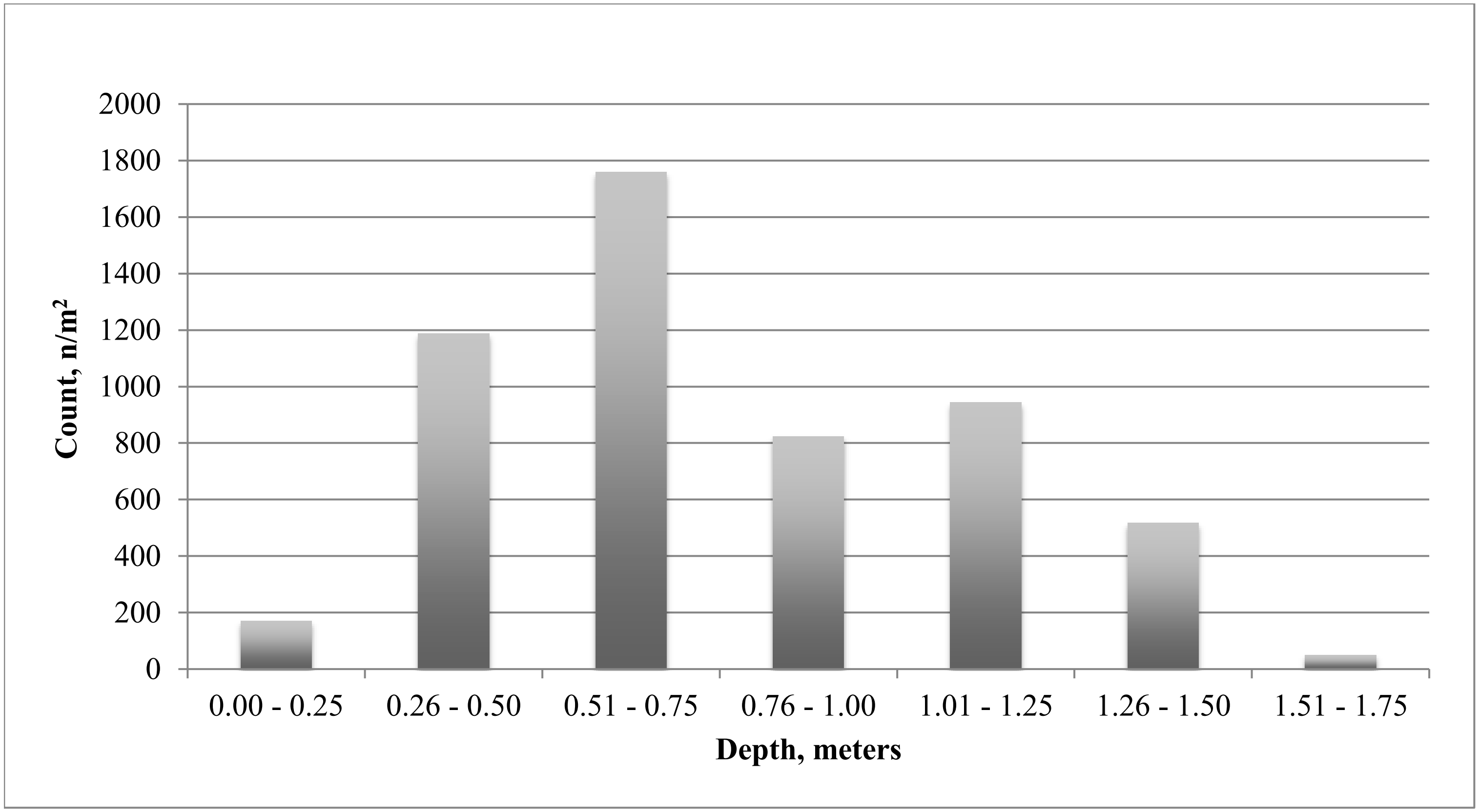

Figure 34. Relation of depth (m) to density (n/m^2) of *C. fluminea* at all sites, mid-August to mid-September 2012 and 2013 combined. Lake Whatcom, Whatcom County, Washington, USA.

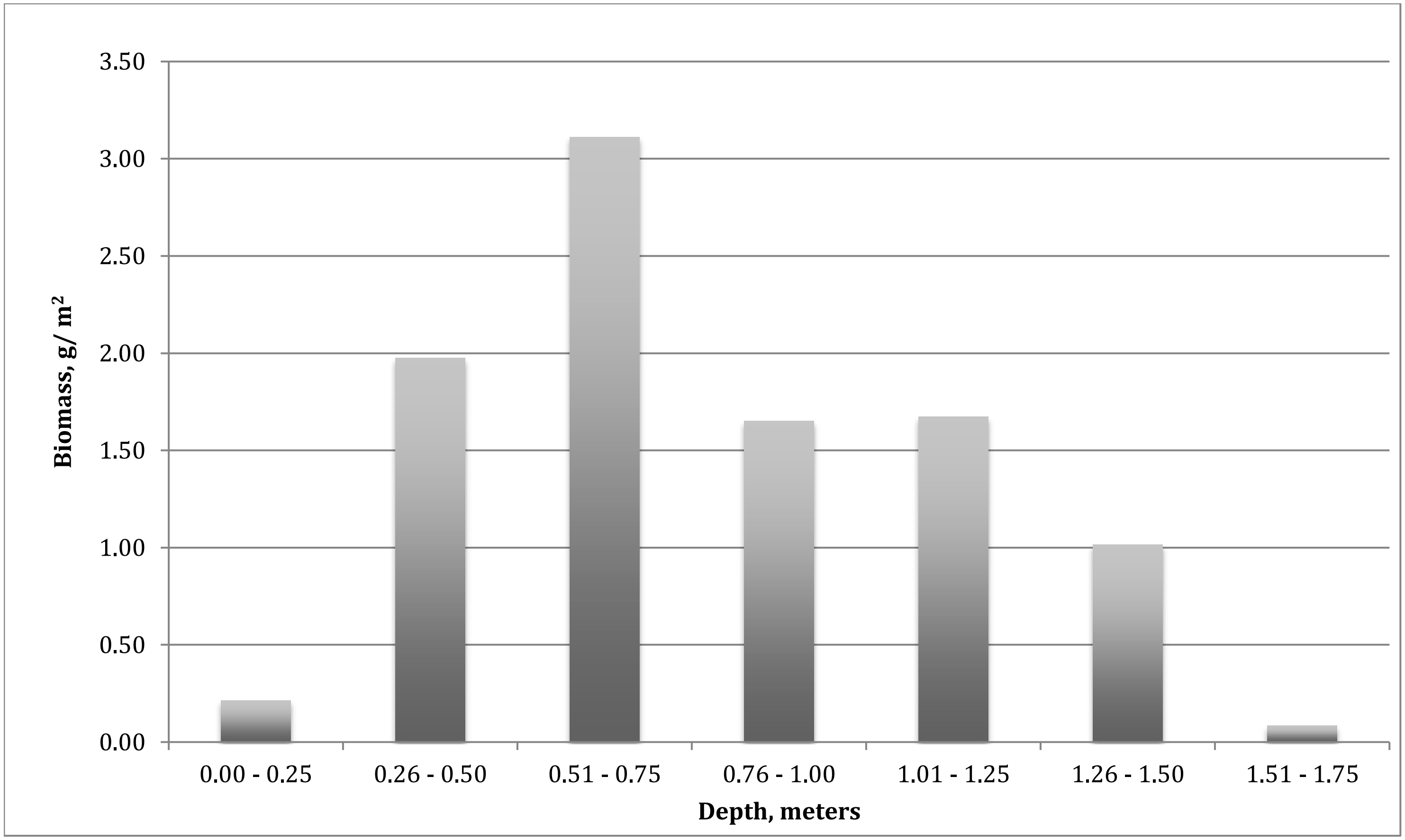

Figure 35. Relation of depth (m) to biomass (grams/m^2) of *C. fluminea* at all sites, mid-August to mid-September 2012 and 2013 combined. Lake Whatcom, Whatcom County, Washington, USA.

Table 11. Surveying timeframe during this study. Lake Whatcom, Whatcom County, Washington, USA.

Year	Start Day	End Day
2012	8/12	9/13
2013	8/10	9/21

Table 12. Lake Whatcom mean water temperature during surveys mid-August to mid-September 2012 and 2013. Lake Whatcom, Whatcom County, Washington, USA.

Site 2012	Minimum Temp, °C	Median Temp, °C	Mean Temp, °C	Maximum Temp, °C
Bloedel Donovan Park	22.30	22.30	22.30	22.30
Lakewood	19.60	19.70	19.87	20.30
Sudden Valley	21.20	22.05	22.05	22.90
Overall	19.60	20.75	21.00	22.90

Site 2013	Minimum Temp, °C	Median Temp, °C	Mean Temp, °C	Maximum Temp, °C
Bloedel Donovan Park	20.20	20.65	20.65	21.10
Lakewood	19.90	22.10	21.64	23.00
Sudden Valley	21.40	21.90	21.90	22.40
Overall	19.90	21.40	21.50	23.00

Table 13. Mean water temperature at 0-2 meters depth at various locations February-December in 2012 and 2013 (Institute for Watershed Studies, 2012, 2013). Lake Whatcom, Whatcom County, Washington, USA.

IWS Surveys	Minimum Temp, °C	Median Temp, °C	Mean Temp, °C	Maximum Temp, °C
During This Study	19.31	20.09	20.14	21.09
March - December	5.37	14.94	14.13	22.88

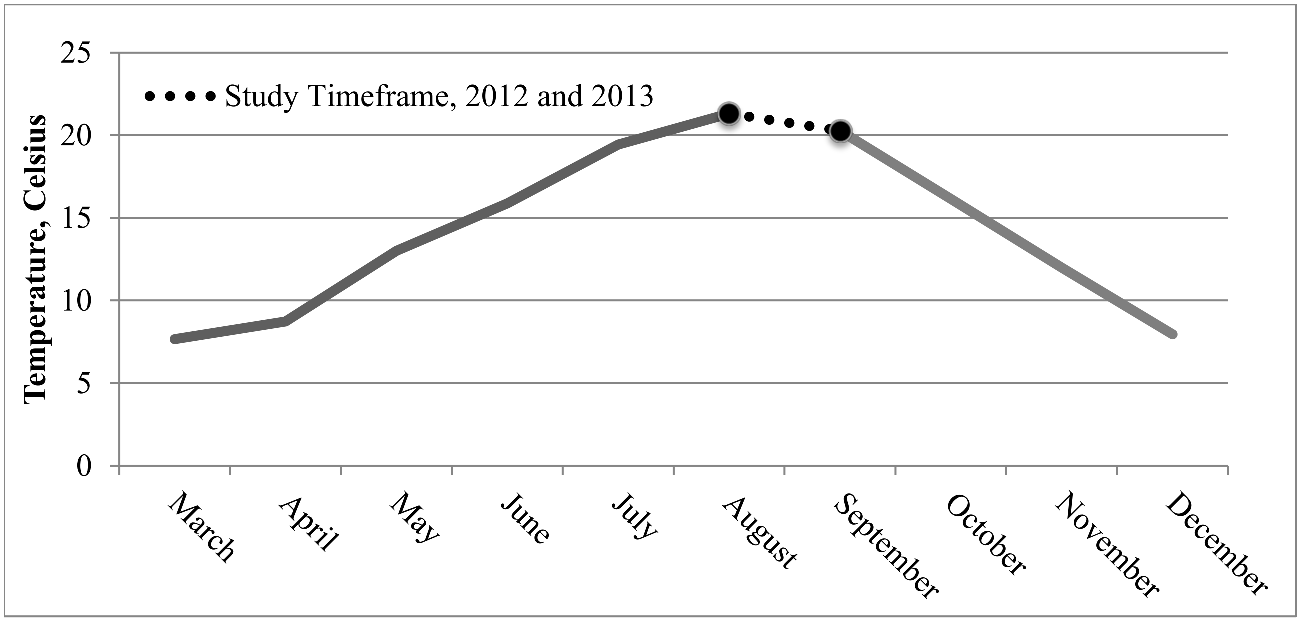

Figure 36. Mean water temperature at 0-2 meters depth at various locations with study timeframe, February-December in 2012 and 2013 (Institute for Watershed Studies, 2012, 2013). Lake Whatcom, Whatcom County, Washington, USA.

LITERATURE CITED

Bagatini, Y. M., Higuti, J., Benedito, E. 2007. Temporal and longitudinal variation of *Corbicula fluminea* (Mollusca, Bivalvia) biomass in the Rosana Reservoir, Brazil. Acta Limnologica Brasiliensia 19(3): 357-366.

Barber, J., Mitchell, T., Gibson, J., Hoyopatubbi, T., Gobert, T., Ferderer, A. 2012. Clam population variability within a Puget Sound bivalve management region. Swinomish Indian Tribal Community Technical Report SWIN-TR-2012-01.

Berg, P., Rysgaard, S., Funch, P., Sejr, M. K. 2001. Effects of bioturbation on solutes and solids in marine sediments. Aquatic Microbial Ecology 26: 81-94.

Bódis, E., Nosek, J., Oertel, N., Tóth, B., and Fehér, Z. 2011. A Comparative Study of Two *Corbicula* Morphs (Bivalvia, Corbiculidae) Inhabiting River Danube. International Review of Hydrobiology 96(3): 257-273.

Boltovskoy, D., Izaguirre, I., Correa, N. 1995. Feeding selectivity of *C. fluminea* (Bivalvia) on natural phytoplankton. Hydrobiologia 312(3): 171-182.

Buttner, J. K., Heidinger, R. C. 1981. Rate of filtration in the Asiatic clam, *Corbicula fluminea*. Transactions of the Illinois State Academy of Science 74(3): 13-18.

Campbell, W.W. 1996. Procedures to determine intertidal population of *Protothaca staminea, Tapes phillippinarum,* and *Crassostrea gigas* in Hood Canal and Puget Sound, Washington. Washington Department of Fish and Wildlife, Procedures Manual MRD96-01.

Casteñeda, R. A., 2012. Factors affecting the distribution, abundance and condition of an invasive bivalve in a thermal plume. Department of Biology, McGill University, Montreal.

City of Bellingham. 2007. Stewards of the Lake. Available: http://www.cob.org/documents/pw/environment/stewardship-of-lake-whatcom.pdf

City of Bellingham. 2011. Lake Whatcom Aquatic Invasive Species Incident Report - Notes on Visual Observations of Asian clams in Lake Whatcom September 17-30, 2011. Available: http://www.cob.org/documents/pw/lw/lake-whatcom-incident-report-9-30-2011.pdf

Cooper, J.E. 2007. *Corbicula fluminea* (Asian Clam) in the Roanoke River, North Carolina: A Stressed Population? Southeastern Naturalist 6(3): 413-434.

Denton, M.E., Chandra, S., Wittmann, M.E., Reuter, J., Baguley, J.G. 2012. Reproduction and population structure of *Corbicula fluminea* in an oligotrophic subalpine lake. Journal of Shellfish Research. 31(1):145-152. Available: http://www.thefreelibrary.com/Reproduction+and+population+structure+of+Corbicula+fluminea+in+an...-a0288172747

Hakenkamp, C., Palmer, M. 1999. Introduced bivalves in freshwater ecosystems: the impact of *Corbicula* on organic matter dynamics in a sandy stream. Oecologia 119: 445-451.

Institute for Watershed Studies, Western Washington University. Lake Whatcom YSI Data University. 2012. Available: www.wwu.edu/iws/

Institute for Watershed Studies, Western Washington University. Lake Whatcom YSI Data University. 2013. Available: www.wwu.edu/iws/

Korniushin, A.V., and M. Glaubrecht,. 2003. Novel reproductive modes in freshwater clams: brooding and larval morphology in southeast asian taxa of *C. fluminea* (Mollusca, Bivalvia, Corbiculidae). Acta Zoologica (Stockholm) 84: 293-315.

Krantzberg, G. 1985. The influence of bioturbation on physical, chemical and biological parameters in aquatic environments: a review. Environmental Pollution Series A, Ecological and Biological 39(2): 99-122.

Lauritsen, D. D. 1986. Filter-feeding in C. fluminea and its effect on seston removal. Journal of the North American Benthological Society 5(3): 165-172.

Lauritsen, D. D., Mozley, S. C., 1983. The Freshwater Asian Clam (C. fluminea Fluminea) as a Factor Affecting Nutrient Cycling in the Chowan River, N.C. Water Resources Research Institute Report No 192, North Carolina State Univ., Raleigh. 70 p, 14 Fig, 4 Tab, 54 Ref, 3 Append. OWRT A-124-NC(1), 14-34-0001-2135.

Lee, T., Siripattrawan, S., Ituarte, C., Foighil, D. 2003. Invasion of the clonal clams: *Corbicula* lineages in the New World. American Malacological Bulletin 20: 113-122.

Matisoff, G., Fisher, J., B., Matis, S. 1985. Effects of benthic macroinvertebrates on the exchange of solutes between sediments and freshwater. Hydrobiologia 122: 19–33.

McMahon, R.F. 2002. Evolutionary and physiological adaptations of aquatic invasive animals: r selection versus resistance. Canadian Journal of Fisheries and Aquatic Sciences 59: 1235-1244.

Meysman, F. J. R., Middelburg, J. J., Heip, C. H. R. 2006. Bioturbation: a fresh look at Darwin's last idea. Trends in Ecology and Evolution 21: 688–695.

Mitchell, R. J. 2011. Lake Whatcom Watershed Map. Western Washington University. Available: http://www.geol.wwu.edu/rjmitch/lakew.html

Phelps, H.L. 1994. The asiatic clam (*C. fluminea*) invasion and system-level ecological change in the Potomac River estuary near Washington, D.C. estuaries and coasts 17(3): 614-621.

Pickett, P., Hood, S. 2007. Lake Whatcom Watershed Total Phosphorus and Bacteria Total Maximum Daily Loads. Washington Department of Ecology 08-03-024, Appendices B-F. Available: https://fortress.wa.gov/ecy/publications/publications/0803024appbf.pdf

Rothlisberger, J.D., Chadderton, W.L., McNulty, J., Lodge, D.M. 2010. Aquatic invasive species transport via trailered boats: what is being moved, who is moving it, and what can be done. Transactions of the American Fisheries Society 35(3): 121-132.

Saloom, M. E., Duncan, S. R. 2005. Low dissolved oxygen levels reduce anti-predation behaviours of the freshwater clam *Corbicula fluminea*. Freshwater Biology 50:1233–1238.

Schmidlin, S., Baur, B. 2007. Distribution and substrate preference of the invasive clam *Corbicula fluminea* in the river Rhine in the region of Basel (Switzerland, Germany, France). Aquatic Sciences 69: 153-161.

Sheehan, R., Caffrey, J.M., Millane, M., McLoone, P., Moran, H., Lucy, F. 2014. An investigation into the effectiveness of mechanical dredging to remove *Corbicula fluminea* (Müller, 1774) from test plots in an Irish river system. Management of Biological Invasions 5(4): 407-418.

Sousa, R., A. J. A. Nogueira, M. B. Gaspar, C. Antunes, and L. Gullhermino. 2008a. Growth and extremely high production of the non-indigenous invasive species *C. fluminea* (Müller, 1774): possible implications for ecosystem functioning. Estuarine, Coastal and Shelf Science 80(2): 289-295.

Sousa, R., Antunes, C., Guilhermino, L. 2008b. Ecology of the invasive Asian clam *Corbicula fluminea* (Müller, 1774) in aquatic ecosystems: an overview. Annales de limnologie-International Journal of Limnology 40(2): 85-94.

Sousa, R. 2011. Factors contributing to the invasive success of *Corbicula fluminea* (Müller, 1774). Instituto de Ciências Biomédicas Abel Salazar.

Stites, D.L., Benke, A.C. Gillespie, D.M. 1995. Population dynamics, growth, and production of the Asiatic clam, *Corbicula fluminea*, in a blackwater river. Canadian Journal of Fisheries and Aquatic Sciences 52(2): 425-437.

Strayer, D. L., Caraco, N. F., Cole, J. J., Findlay, S., Pace, M. L. 1999. Transformation of Freshwater Ecosystems by Bivalves. Bioscience 49:(1).

Vanni, M. J. 2002. Nutrient cycling by animals in freshwater ecosystems. Annual Review of Ecology and Systematics 33: 341–370.

U. S. Geological Survey (USGS). 2001. Nonindigenous species information bulletin**:** Asian clam, *Corbicula fluminea* (Müller, 1774) (Mollusca: Corbiculidae) Available: http://fl.biology.usgs.gov/corbicula4.pdf

Way, C.M., D.J. Hornbach, C.A. Miller-Way, B.S. Payne, and A.C. Miller. 1990. Dynamics of filter feeding in *C. fluminea* (Bivalvia: Corbiculidae). Canadian Journal of Zoology 68(1): 115-120.

Whatcom County. 2012. Asian Clam Update. Available: http://www.lakewhatcom.whatcomcounty.org/feature-stories/asianclamupdate-10252011

Whatcom County. 2014. Lake Whatcom; watershed management, news, and resources. Available: http://lakewhatcom.whatcomcounty.org/about-the-lake

Wittmann, M., Reuter, J., Schladow, G. Hackley, S. Allen, B., Chandra, S., Caires, A. 2008. Asian clam (*Corbicula fluminea*) of Lake Tahoe: preliminary scientific findings in support of a management plan. University of Californa Davis – Tahoe Environmental Research Center and University of Nevada, Reno.

Yeager, M. M., Neves, R. J., Cherry, D. S. 1999. Competitive interactions between early life stage of Villosa iris (*Bivalvia—Unionidae*) and adult Asian clams (*C. fluminea*). Ohio Biological Survey Proceedings of the First Freshwater Mollusk Conservation Society Symposium 1999: 253-259.

Zhang, L., Q. Shen, H. Hu, S. Shao, and C. Fan. 2011. Impacts of *C. fluminea* on oxygen uptake and nutrient fluxes across the sediment–water Interface. Water Air and Soil Pollution 220:399-411.