

University of Nevada, Reno

**Invasive clams in Lake Tahoe: Reproductive
strategies and impacts to native benthic
community structure**

A thesis submitted in partial fulfillment of the
requirements for the degree of Master of Science in
Environmental Sciences

by

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Thesis Abstract

Invasive species are of concern to ecologists and resource managers due to the growing ecological and economic impacts associated with their introduction. In North America, invasive species cause significant environmental impacts with costs estimates of \$137 billion annually. Second to loss of habitat, invasive species have been linked to the declines in biodiversity on a global scale. Once established, invasive species have been shown to alter community and ecosystem dynamics, change habitat for native species, interrupt energy flow through food webs, and reduce ecosystem services. Among non-native aquatic species, invasive bivalves can cause significant impacts by altering the availability of resources, contributing to the extirpation of native species, declines in diversity and impairment of ecosystem functioning. They are able to tolerate a wide range of environmental conditions (temperature, water chemistry, substrate, etc.), allowing them to acclimatize to a new environments, making them adaptable to exploit ecological niches. In the last century, *Corbicula fluminea* (Asian clam) has been one of the more successful invasive bivalves to establish in aquatic ecosystems. *C. fluminea* is an invasive freshwater bivalve to North American that originally established in Pacific Northwest in 1938 from Southeast Asia, and has since been documented in 42 states. The shells of dead *C. fluminea* may provide refuge and substrate for the establishment of benthic larval insect communities and live clams may influence benthic communities by processes of bioturbation of sediment via burrowing and biodeposition of organic matter as feces and pseudofeces. Through highly efficient suspension-feeding and deposit-feeding on sediment organic matter, *C. fluminea* may also couple the pelagic and benthic

food webs. The vectors of invasion are live bait buckets however the release of aquarium stock and transport via boat bilge is possible.

Recently there has been an invasion of *C. fluminea* in Lake Tahoe, a large, deep subalpine lake located in the central Sierra Nevada of California and Nevada. Very little is known about the life history or impacts of clams on the ecology of the lake; however, preliminary research suggests they may be linked to increased nearshore algal blooms. The chapters included here examine the reproductive strategies (Chapter 1) and impacts to native benthic community structure (Chapter 2) by *C. fluminea* in Lake Tahoe. In Chapter 1, it was determined that *C. fluminea* in Lake Tahoe had a low reproductive effort with a single spawn that occurred in late summer that is likely linked to the temperature and low food availability. Moreover, deeper water populations of clams are likely population sinks due to the cold temperatures. Chapter 2 shows how *C. fluminea* changes benthic community structure depending on the level of infestation. It was determined that three taxa had greater abundances where abundances of *C. fluminea* are low. In areas with greater abundance, *C. fluminea* facilitate two taxa, Chironomidae and Trichoptera. While the mechanisms were not studied, the shells of clams may provide structure and thus habitat for certain invertebrates. Other mechanisms of facilitation such as competition or providing increased food supply through the release of pseudofeces may also impact community structure. Other behavioral experiments and raw data not formally presented in chapter form are presented in the Appendix. As the establishment of *C. fluminea* is still in an early stage of invasion, future studies and monitoring will be essential to further determine how the clam impacts Lake Tahoe's ecosystem.

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Table of Contents

Thesis Abstract.....	i
Acknowledgements.....	iii
List of Tables	viii
List of Figures	viii
Chapter 1: Reproduction and population structure of <i>Corbicula fluminea</i> in an oligotrophic, subalpine lake	1
Abstract.....	1
Introduction.....	3
Methods.....	5
Study Site	5
Field Collection.....	7
Reproductive Effort	8
Results.....	8
Environmental Conditions	8
Reproductive Activity.....	9
Population Structure.....	10
Discussion and Conclusion.....	11
Acknowledgements.....	15

Literature Cited	17
Figures.....	21
Chapter 2: The influence of a recent invasion of <i>Corbicula fluminea</i> on zoobenthos community structure in an oligotrophic, sub-alpine lake	25
Abstract	25
Introduction.....	27
Methods.....	29
Study Site	29
Field Sampling	30
Analysis.....	31
Results.....	32
Discussion and Conclusion.....	33
Acknowledgments.....	37
Literature Cited	38
Tables and Figures	42
Appendix.....	45
Short-Term Substrate Preference Trials.....	45
Taxonomic Grouping and Enumeration (Chapter 2)	48

List of Tables

Table 2-1. Results of the SIMPER routine	42
Table 2-2. Mean Abundances of taxa	42
Table A-1: Taxonomic grouping and enumeration for zoobenthos discussed in Chapter 2	48

List of Figures

Figure 1-1. Temperatures at the water-substrate interface.....	21
Figure 1-2. Values of sediment particulate organic matter (SPOM)	22
Figure 1-3: Mean values and proportion for eggs and veligers	23
Figure 1-4: Population structure and abundance at sampling sites across dates	24
Figure 2-1. Overall abundances of all benthic invertebrates	43
Figure 2-2. NMDS plot of treatments by abundance levels.....	43
Figure 2-3. Box plots showing abundances of taxa	44
Figure A-1. Particle size percentages across three sites	46
Figure A-2. Preference for specific habitat substrate results	47
Figure A-3. Preference for specific particle size results	47

Reproduction and population structure of *Corbicula fluminea* in an oligotrophic, subalpine lake

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Abstract

Reproductive effort and population structure of the non-native clam, *Corbicula fluminea*, were studied in an oligotrophic, subalpine lake. Three shallow sites (5 m) and one deeper site (20 m) were studied between May 11 and November 5, 2010 to determine spatial variation and the influence of environmental conditions (e.g. temperature and food availability as determined by total organic carbon and sediment particulate organic matter) on reproductive effort. *C. fluminea* exhibited a univoltine spawn cued by increases in temperature. Reproductive effort calculated for adult clams (13.67 ± 0.03 mm SE, $n=1875$) across sites did not appear to be influenced by food availability but overall reproductive effort is much lower compared to more productive ecosystems. This may be due to the ultra-oligotrophic nature of Lake Tahoe. All three shallow sites had similar levels of reproductive effort. Once veligers were observed, of the 603 clams dissected, there were 10 ± 2 veligers per clam \pm SE; 25 clams had ≥ 100 veligers (286 ± 28 veligers/clam); 78 clams contained < 100 veligers (20 ± 2 veligers/clam \pm SE); and 498 clams had no veligers present indicating the population exhibits a highly variable reproductive

effort. There was at minimum a four-week delay from the point that temperatures reached a threshold for fertilization and veliger release until they were observed in dissected clams. *C. fluminea* at 20 m were high in abundance compared to shallow sites but contained few fully developed juveniles indicating a potential population sink. Overall population structure was dominated by adult clams (≥ 13 mm) with a minimal presence of juveniles (≤ 4 mm).

Introduction

Non-native aquatic species that are predisposed to reach nuisance levels are tolerant to a wide range of environmental conditions, able to efficiently utilize food and space, reach early sexual maturity, and/or exhibit high fecundity (e.g., Kolar and Lodge, 2001; Karatayev et al., 2009; Kulhanek et al., 2001). Within a newly established area, mollusks with the highest fecundity, due to life history strategies such as the type of sexual expression, duration of brooding, and lifespan, are the most likely to become nuisance organisms (Keller et al., 2007).

Corbicula fluminea is a freshwater clam, native to southeastern Asia, which has been introduced globally and is generally considered to be an aquatic invasive species of nuisance status. After establishing in the Pacific Northwest of the United States in the 1930's, *C. fluminea* spread throughout North America (McMahon, 1982). Its establishment has resulted in negative ecological and economic impacts including colonization in water intake systems of power generating systems (McMahon, 2002). It can dominate the benthic biomass of aquatic ecosystems (Karatayev et al., 2003) and lead to ecological changes which include disruption of food webs due to the size selective filtration of seston (Cohen et al. 1984; Phelps, 1994; McMahon, 2002), suppression of native mollusks populations (Strayer, 1999), and alteration of nutrient cycling dynamics (Hakenkamp and Palmer, 1999; Vaughn and Hakenkamp, 2001).

C. fluminea reproduction can be prolific due to hermaphroditism, rapid reproductive maturity, and variable larval incubation periods as short as six days, normally upwards to two weeks or as lengthy as sixty days in a wide range of environmental conditions (Kraemer and Galloway, 1986; King et al., 1986; McMahon,

2000; Rajagopal et al., 2000). *C. fluminea* eggs are held in the inner demibranches of the ctenidia (gills) following release from the gonads, then fertilized and embryos are brooded in the same structure. This may result in an annual fecundity rate upwards of 68,000 juveniles per individual (Aldridge and McMahon, 1978; McMahon, 2002). Temperature initiates multiple stages of reproduction, and *C. fluminea* generally has a bivoltine reproductive cycle in response to temperature regimes in rivers, lakes and reservoirs (Aldridge and McMahon, 1978; Kennedy and Van Huekelem, 1985; Rajagopal et al., 2000; Mouthon and Parghentanian, 2004). An initial spawn commonly occurs in the spring after threshold temperatures have been reached (at least 16-18 °C for at least ten degree-days); however, once temperatures exceed 27-28°C, reproductive output is restricted (McMahon, 2000; Mouthon, 2001). A subsequent, weaker spawn may occur following a return to lower temperatures (Aldridge and McMahon, 1978; Kennedy and Van Huekelem, 1985; Rajagopal et al., 2000; Mouthon and Parghentanian, 2004).

While temperature is the primary cue for initiation of reproduction, food availability is also important for embryo development and successful brooding (Doherty et al., 1987; Mouthon, 2001). Overall food availability has been found to enhance gonad development and fecundity, and increases both the brood size and individual size of developing embryos (Beekey and Karlson, 2003). To support growth and reproduction, two feeding strategies are employed: suspension feeding from the water column and deposit feeding in the substrate. Filter feeding rates of *C. fluminea* are variable but can be high, between 300 to 2500 L/hr (McMahon and Bogan, 2001). In the absence of suspended food, such as the conditions of oligotrophic ecosystems, *C. fluminea* can ingest sediment particulate organic matter through deposit feeding (Reid et al., 1992),

consuming upwards of 50 mg per day and doubling growth rates (McMahon and Bogan, 2001).

The objective of this study was to investigate the factors that influence the reproductive efforts (timing and overall fecundity) of a recently established population of *C. fluminea* in oligotrophic Lake Tahoe (CA-NV, USA). To our knowledge, Lake Tahoe is the highest elevation and deepest lake where this species has established. First observed in 2002, *C. fluminea* was found to be widely established in the southeastern littoral zone of Lake Tahoe by 2008 (Hackley et al., 2008). A recent survey found *C. fluminea* distributed in deeper waters (20 – 80 m). We believe clams living in deeper waters may contribute to the recruitment of nearshore populations. Utilizing a combination of field experiments, dissections of clams, and information gathered from a literature review, we tested the following hypotheses: (1) temperature would have the greatest influence on the timing of reproductive initiation, (2) food availability would influence overall reproductive effort, and (3) reproductive efforts would be similar in both shallow deeper populations resulting in a source of veligers for populating the nearshore environment.

Methods

Study Site

Lake Tahoe (39.13°N, 120.05°W) is a large sub-alpine oligotrophic lake located in the Sierra Nevada mountain range on the California--Nevada border. The 11th deepest lake in the world, it has a surface area of 496 km², maximum depth of 501 m, and surface elevation of 1,897 m a.s.l at capacity. The surrounding basin has a watershed of 800 km². Tahoe is a cold monomictic lake, ice-free year around, with stratification beginning in

early spring and maximum surface temperatures in mid-summer (Jassby et al., 2003). Although well known for its clear waters, clarity has been decreasing since the late 1960's with a current annual mean Secchi depth approximately 20 m (Winder, 2009). Lake Tahoe's annual pelagic primary production has shown a greater than 4.5-fold increase in 40 years (Chandra et al. 2005), and it remains a low-nutrient lake (Winder and Hunter 2008) with a change from N limitation to N/P co-limitation in the early 1980's (Goldman et al., 1993). Littoral zone temperatures range from ~6.0°C in winter months warming to 21.0°C in mid-summer.

Four sites with established *C. fluminea* populations were sampled: Lakeside, Marla Bay, and Nevada Beach each at a depth of 5 m and Nevada Beach at a depth of 20 m; hereafter referred to as LS5, MB5, NV5 and NV20. A benthic sampling and visual evaluation of Lake Tahoe shows that *C. fluminea* is largely restricted to the southeastern and southern littoral zones (Wittmann and Chandra, unpublished). At Lakeside, there is a wide shallow shelf with approximately 1.3 km from shoreline to the greatest depth of 5 m before dropping off to deeper depths. The bottom substrate here is nearly equal amounts of medium sand (0.50-0.30 mm), and very fine sand (0.062 mm), with the small remainder in the range of fine cobble (64 mm) to clay (<0.003 mm), as determined by Wentworth particle size distribution (Brakensick et al., 1979; Gordon et al., 2007). Marla Bay is approximately 1.5 km wide with a maximum depth of 5 m before a steep drop towards profundal depths at the edge of the bay approximately 0.50 km from the shoreline. At Nevada Beach the bottom extends approximately 110 m from the shoreline to deepest depth of 5 m followed by a slope to greater depths. The substrate is dominated by medium sand (0.50—0.30 mm) at both Marla Bay (>50%) and Nevada Beach (>75%)

with the remaining particle sizes ranging from very fine gravel (4.00 mm) to very fine sand.

Field Collection

We collected *C. fluminea* using a Petite Ponar grab (area 225 cm²) biweekly from May through August (late spring to summer) and monthly from September through November (fall) 2010. Lake water was collected near the water-substrate interface using a Van Dorn sampler and measured for *in situ* temperature using a hobbyist digital thermometer (Coralife[®] ESU Digital Thermometer). *In situ* point measurements for temperature were validated against a continuous temperature data logger that indicated a clear relationship between the measurements to describe seasonal patterns in temperature (Denton unpublished data). Total organic carbon (TOC) in the overlying lake water was analyzed with an elemental analyzer (Shimadzu TNPC-4110C). Sediment particulate organic matter (SPOM) was gathered from a thin scraping of the surface sediment (≤ 1 cm in depth) obtained from the Petite Ponar sample, and measured as loss on ignition (Froelich, 1980). Environmental conditions were analyzed by a one-way ANOVA for temperature and TOC for site and date independently, and two-way ANOVA analyzed SPOM by site by date and a pairwise difference was determined with a Tukey HSD post-hoc analysis.

All *C. fluminea* samples were held in 18L field buckets with sediment and lake water, stored at $\sim 10.0^{\circ}\text{C}$ and processed in the laboratory within 24 hours of collection. Samples were elutriated in the laboratory and sieved through 90 μm mesh to retain the smallest individual clams and to calculate abundance (clams/m²) for each sampling

period and location. All grabs were combined into one sample per site per date, therefore variations in dates by individual sites were not determined.

Reproductive Effort

To quantify eggs and developed fertilized larval forms (hereafter referred to as veligers), we dissected the gills of approximately forty clams (shell length 13 ± 1 mm) per site across sampling dates. Clams between 11 and 19 mm were occasionally dissected when the target size class was not completely met. Clams were measured for shell length with digital calipers to the nearest 0.01 (mm) prior to dissection. Ctenidia were squash mounted and examined under 100X magnification light microscopy (Morton, 1977; Britton and Morton, 1982). Developmental stages were determined based on the descriptions from Kraemer and Galloway (1986). Since these data were determined to be non-normally distributed (Anderson-Darling normality test), they were \log_{10} transformed and analyzed by a two-way ANOVA of site by date. Pairwise differences were determined with a Tukey HSD post-hoc analysis. Mean values and standard error with sample size are reported. All statistical analyses were performed by the SAS System 9.2 and Minitab 15.1.

Results

Environmental Conditions

At all sites, temperatures were less than 8.0°C on May 11 with the greatest increase in temperature from June 16-28 (Figure 1-1). Seasonal high temperatures were recorded at each site on July 20. A temporary decrease in temperatures on August 30 was associated with a cold front that passed through the Tahoe basin at that time. Temperatures were significantly different over dates ($p < 0.0001$) but not sites ($p = 0.659$).

TOC concentrations were not significantly different between sites ($p=0.549$). Mean concentrations (\pm standard error) across all dates ($n=10$) at each site were 10.7 ± 0.5 mg/L (LS5), 10.7 ± 0.4 mg/L (MB5), 10.9 ± 0.5 mg/L (NV5) and 10.7 ± 0.5 mg/L (NV20). There was a significant site by date interaction in sediment particulate organic matter (SPOM) ($p<0.0001$). A Tukey post-hoc analysis determined that LS5 (6.8 ± 3.3 $\mu\text{g}/\text{mg}$) and NV20 (6.1 ± 4.4 $\mu\text{g}/\text{mg}$) had greater concentrations of SPOM than MB5 (4.6 ± 2.9 $\mu\text{g}/\text{mg}$) and NV5 (3.6 ± 1.1 $\mu\text{g}/\text{mg}$) over the season (Figure 1-2).

Reproductive Activity

A total of 1,875 clams were dissected to determine the reproductive status and activity over the course of the sampling period. The mean shell length at each site over the entire sampling period was 13.68 ± 1.3 mm (LS5, $n=461$), 13.33 ± 0.7 mm (MB5, $n=479$), 13.91 ± 1.0 mm (NV5, $n=478$) and 13.74 ± 1.2 mm (NV20, $n=457$). Eggs were present in the demibranches on all sampling dates from May 11 to November 5 (Figure 1-3). Egg abundances observed had a significant site by date interaction ($p<0.0001$) and a Tukey post-hoc analysis determined that the greatest abundance occurred on August 30. Veligers were detected in the middle to end of summer and occurred in low abundance on August 16, and in high abundances numbers on August 30 and September 13. These sampling dates were +27, +41 and +55 days following the critical temperature threshold needed to initiate a spawning of brooding veligers (Kraemer and Galloway, 1986; King et al., 1986). There was a significant site by date interaction of brooding veliger abundances and a Tukey post-hoc analysis showed that August 30, September 13 and October 8 had the greatest abundance of veligers present, and the veliger abundances at

shallow locations were significantly greater than NV20 ($p < 0.0001$). Across all three shallow sites, there were similar levels of reproductive effort with a mean veliger abundance per clam (\pm SE) of 10 ± 2 ($n = 603$), with ranges of 286 ± 28 ($n = 25$ for clams with ≥ 100 veligers), 20 ± 2 ($n = 78$ for clams with < 100 veligers), and 498 clams had no veligers present in samples from mid August through early November. NV20 had a mean abundance (\pm SE) of 3 ± 1 veligers across 4 clams with 196 clams having no veligers present in samples during the same period.

Population Structure

Overall population abundances were significantly different by site over all sampling dates ($p = 0.0013$) with abundances at NVB20 (2541 ± 291 clams/m²) significantly greater than the shallow sites (Figure 1-4). *C. fluminea* was heterogeneously distributed along the bottom at each site. Across sites for all sampling dates, there was a significant difference in the number of grabs obtained to meet the needs of dissection ($p = 0.0014$), with LS5 requiring the greatest number of samples over the dates (9 ± 3 grabs/date), MB5 and NV5 requiring fewer but nearly equal numbers of grabs (7 ± 2 and ± 1 grabs/date), and NVB20 requiring the fewest (5 ± 2 grabs/date; $n = 12$, standard deviation are noted as standard error values were less than 1). *C. fluminea* size class distribution by site suggests differences in population structure (Figure 5). Size class distributions in LS5 were variable but no one size class (or group of size classes) dominated the population structure throughout the sampling season. Size classes between 13 to 17 mm represented a majority of the populations in MB5, with clams occasionally reaching a shell length of 22 mm. *C. fluminea* with shell lengths of ≤ 4 mm were absent

from these samplings. At NV5, the ≤ 4 mm size class was present in all samplings with very low presence during the June 16 and November 5. The 13-17 mm size class was large throughout the sampling dates and clams disappeared from the population after 22 mm. The ≤ 4 mm size class at NV20 was present on June 16 and September 13. For a majority of the other samplings, this size class was completely absent, with a minimal presence on August 2, October 8 and November 5. As in the other locations, the largest size class was the 13-17 mm group.

Discussion

C. fluminea in Lake Tahoe is univoltine with reproduction in the late summer and low abundances of brooding veligers. There was longer than expected delay between threshold temperatures for required reproduction based on previously published literature and empirical observations of brooding veligers made during dissections. Given that oogenesis occurs independent of temperature (Kramer and Galloway, 1986), we expected eggs to be present during all dissections. Because spermatogenesis and fertilization require minimum temperature thresholds to be met (10.0 °C and 14.0 °C, respectively) brooding veligers should not have been present until temperatures were at least 14°C for ten consecutive degree-days (Kraemer and Galloway, 1986). Temperatures across all shallow sampling sites reached this threshold by July 20 with a mean of 19.7 ± 0.4 °C. A typical cycle of initial fertilization, larval maturity, to release of veligers is 6 to 14 days (Kraemer and Galloway, 1986) with release occurring at least 16.0 °C. In other systems, *C. fluminea* are observed to be bivoltine with the first spawn occurring in late spring to early summer, and resuming in late summer. This pattern has been attributed to

metabolic declines due to temperature increases above 27.5°C (Mouthon, 2001; Aldridge and McMahon 1978). Once spawning did occur in Lake Tahoe after a four-week delay, the overall abundance of veligers observed in the shallow sites (10 ± 2 veligers/clam) was much lower than the veliger abundances observed in more productive reservoir or riverine ecosystems. In these ecosystems, veliger reproductive efforts range from 588 to 735/clam per day in Spring and Fall (Aldridge and McMahon, 1978) and 1,800 to 1200/clam per day from late June and early October, respectively (Doherty et al., 1987). Recent studies have shown that Lake Tahoe's surface waters are warming at a faster rate than ambient air temperatures (Schneider et al., 2009; Coats, 2010). In the future, this increase in water temperatures may expand the spawning potential of *C. fluminea* to an earlier initiation of reproductive development and a longer fertilization and release period. It is unlikely, however, that a bivoltine spawning event will occur in Lake Tahoe since current temperature warming forecast for the nearshore do not suggest an increase in temperature that would stop and re-initiate spawning as found in warmer ecosystems. Alternatively, warming of the lake in the winter prior to the spawning cycle could enhance the reproductive success of *C. fluminea* (Weitere et al., 2009).

Food availability can be another significant contributor to spawning events of *C. fluminea* (Mouthon, 2001). With hundreds of veligers observed in some clams, availability of food resources is necessary to meet the energetic demand of brooding. *C. fluminea* brood veligers within the inner demibranches of the gills which have secretory cells believed to provide nutrients to developing embryos (Britton and Morton, 1982; Doherty et al., 1987). Whereas other studies reported chlorophyll-*a* concentrations in systems with successful *C. fluminea* populations ranging from 3 µg/L upwards to 100

$\mu\text{g/L}$ (Cohen et al., 1984; Mouthon, 2001; Mouthon and Parghentanian, 2004), chlorophyll-*a* concentrations in Lake Tahoe range from 0.5 – 1.5 $\mu\text{g/L}$ (TERC, 2010). These low concentrations could limit *C. fluminea* growth and reduce nourishment for brooding embryos. TOC at the water-substrate interface suggests similarly low food concentrations from this source. While there were significant site by date differences for SPOM, overall reproductive effort was not significantly different between the sites rejecting the hypothesis that a greater abundance of food would increase the fecundity of *C. fluminea* in Lake Tahoe.

In determining the similarities, if any, of reproductive effort between the shallow and deep water populations, an interesting observation is the low count of veligers seen in dissections from NV20, the deeper water site. Veligers were found on only one sampling date (August 30), with just 13 seen in four clams. However, this site has the highest overall abundance amongst sites, with significant increases in observed abundance in the late summer. Population size structure at this site indicated an increase in abundance is towards the larger size classes (>13 mm) rather than recruitment of juveniles (<4 mm, Figure 1-4). This suggests that deep water populations are not reproductively active and therefore are potentially a sink of clams rather than a source. If this is the case, clams would have had to be transported from the shallow depths to these deeper populations. Movement of clams to this deeper region may occur two ways. One documented means of dispersal for *C. fluminea* is via floatation. Prezant and Chalermwat (1984) found that clams up to 14 mm when exposed to a current of 10 to 20 cm/sec, would push off substrate with their foot while extending both siphons. They excrete a long mucus thread which allowed the clam to be lifted and carried in the water column until the current

subsided. This current is not typically found in the nearshore of lakes. Another possibility is that wind-driven waves creating high energy turbulence may transport clams from shallow depths to deeper locations. Redjah et al., (2010) found that the clam, *Mya arenaria* up to 20 mm, was displaced when subjected to turbulence in a level experimental flume with a high wave-current flow. Additionally, in a sandy substrate similar to the NV5 and NV20 sampling sites, St-Onge and Miron (2007) found that between 40 - 90% of *M. arenaria* were eroded (transported) at stream velocities of 29 - 35 cm/s. With an approximate horizontal distance of 60 m between the 5 to 20 m depth at Nevada Beach, an estimated slope of 18°, and documented populations of clams at 10 and 15 m (unpublished samplings for 2008 and 2009), it is conceivable that high energy turbulence due to internal lake currents and other physical waves could transport both juvenile dispersers and adult clams along the slope to deeper depths.

Throughout the 2010 sampling, the juvenile size class (<4 mm) appeared sporadically across all sites and was probably a result of carryover from reproduction in 2009. Unlike other systems that show a pyramid-shaped size class population structure with <4 mm dominating the population (Mouthon and Parghentanian, 2004; Hall, 1984), the Lake Tahoe population contained more individuals in the 10-17 mm size classes with a sharp decline in abundance of larger individuals in the range of 19-23 mm. Joy (1985) reported no shell growth for *C. fluminea* for water temperatures between 0°C and 13.0°C. Given that newly released veligers are 0.2 mm, and depending on previous season's release period, it is conceivable that the 2009's spawn would appear as a new size class the following mid-summer 2010. Temperatures in this study were below 13.0°C by

November; therefore, juveniles spawned in the 2010 season would likely not experience shell growth until May or June 2011.

Conclusions

C. fluminea populations in Lake Tahoe are univoltine and primarily influenced by temperature for initiation of spawning. There was a 27-day period after reaching minimum temperature thresholds required for fertilization and the observation of veligers in ctenidia. Despite significant differences of food availability at each site, this difference did not appear to influence veliger counts between the shallow populations. The oligotrophic nature of Lake Tahoe and thus low rates of primary productivity may be the source of the delay in reproductive activity. The deep water site, NV20, had conditions which would be favorable to reproductive effort based on the 5 m sites and previous studies; however, this site had very few late stage veligers. There may be some other inhibiting factors (e.g. annual temperature regime) at deeper depths. Previous studies on the reproductive efforts of *C. fluminea* were generally in shallow, riverine environments. Based on this study, deep water populations are more likely a sink of *C. fluminea* rather than a source. While *C. fluminea* has currently not spread through Lake Tahoe, the mean seasonal abundances measured in this study (1252 ± 144 to 1689 ± 162 clams/m²) show the capacity for this species to be reproductively successful at the shallower (5 m) depths.

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Figures

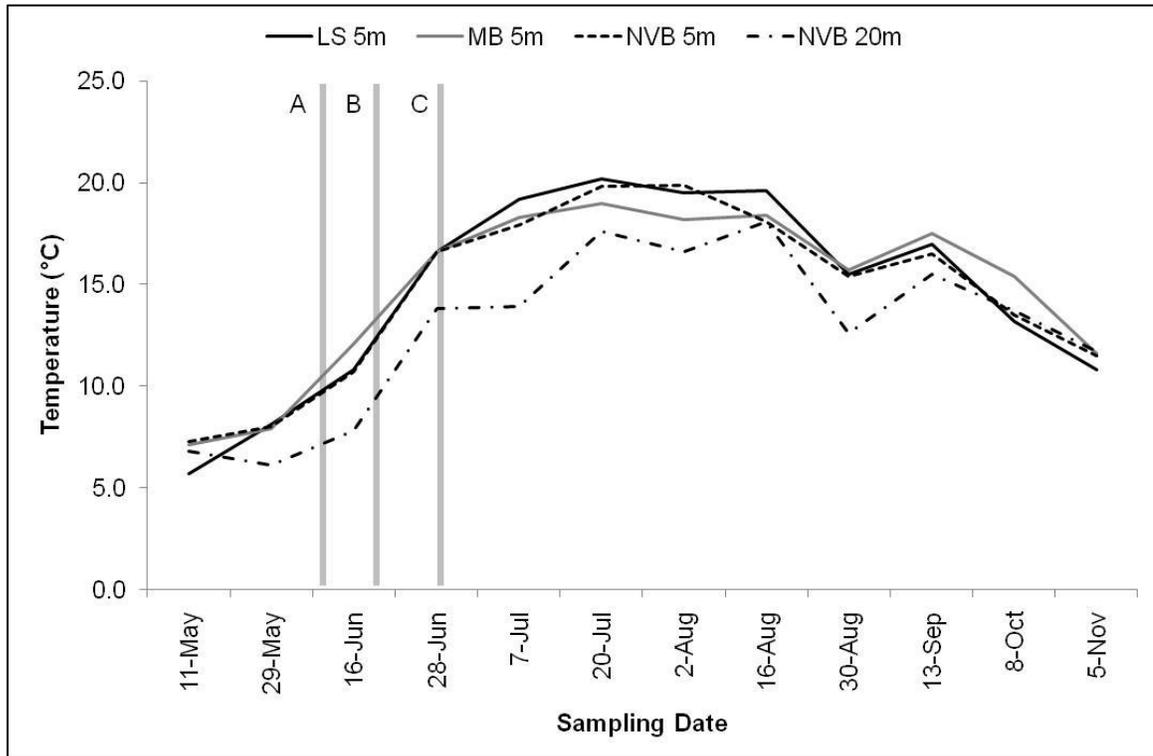


Figure 1-1. Temperatures at the water-substrate interface by sampling date and site. Documented threshold temperatures required for reproduction are noted with the vertical shaded bars indicating when temperatures were recorded at 5 m. A: The onset of spermatogenesis. B: Fertilization occurs. C: Initial release of veligers.

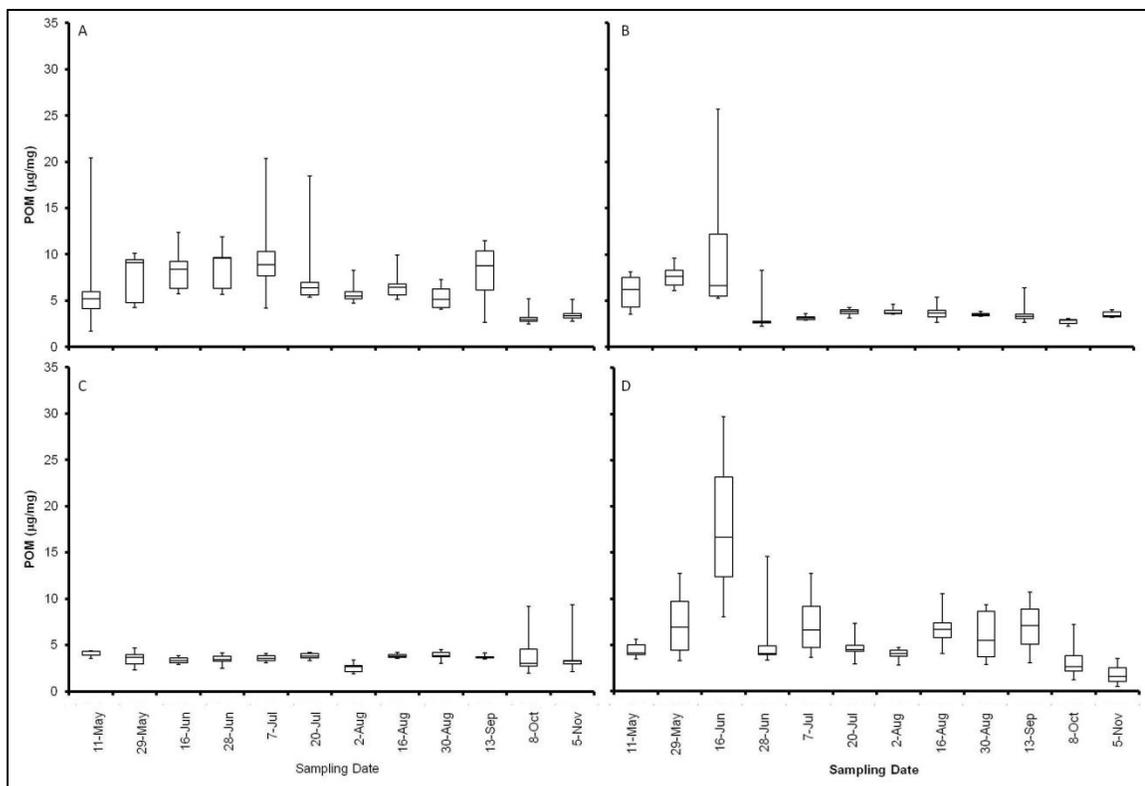


Figure 1-2. Values of sediment particulate organic matter (SPOM) within ≤ 2 cm of the surface.

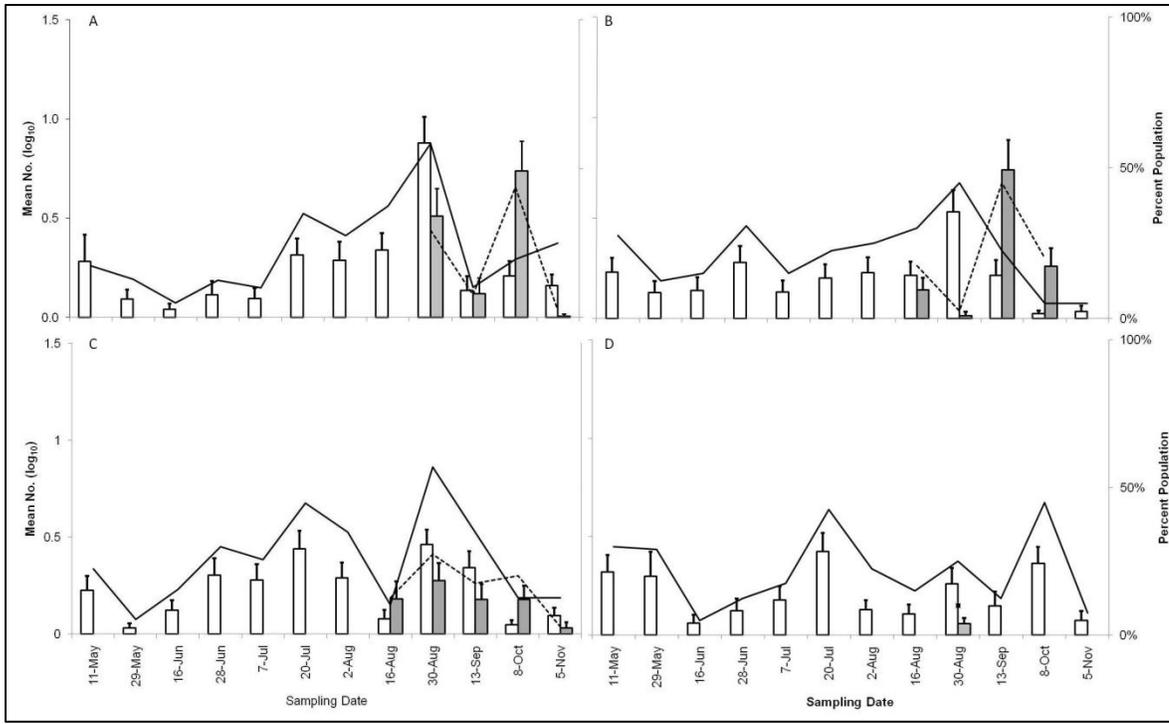


Figure 1-3: Mean values (\pm SE) for eggs (light shading) and veligers (dark shading) and percentage of populations with eggs (solid line) and veligers (dashed line). A=LS5, B=MB5, C=NV5, D=NV20.

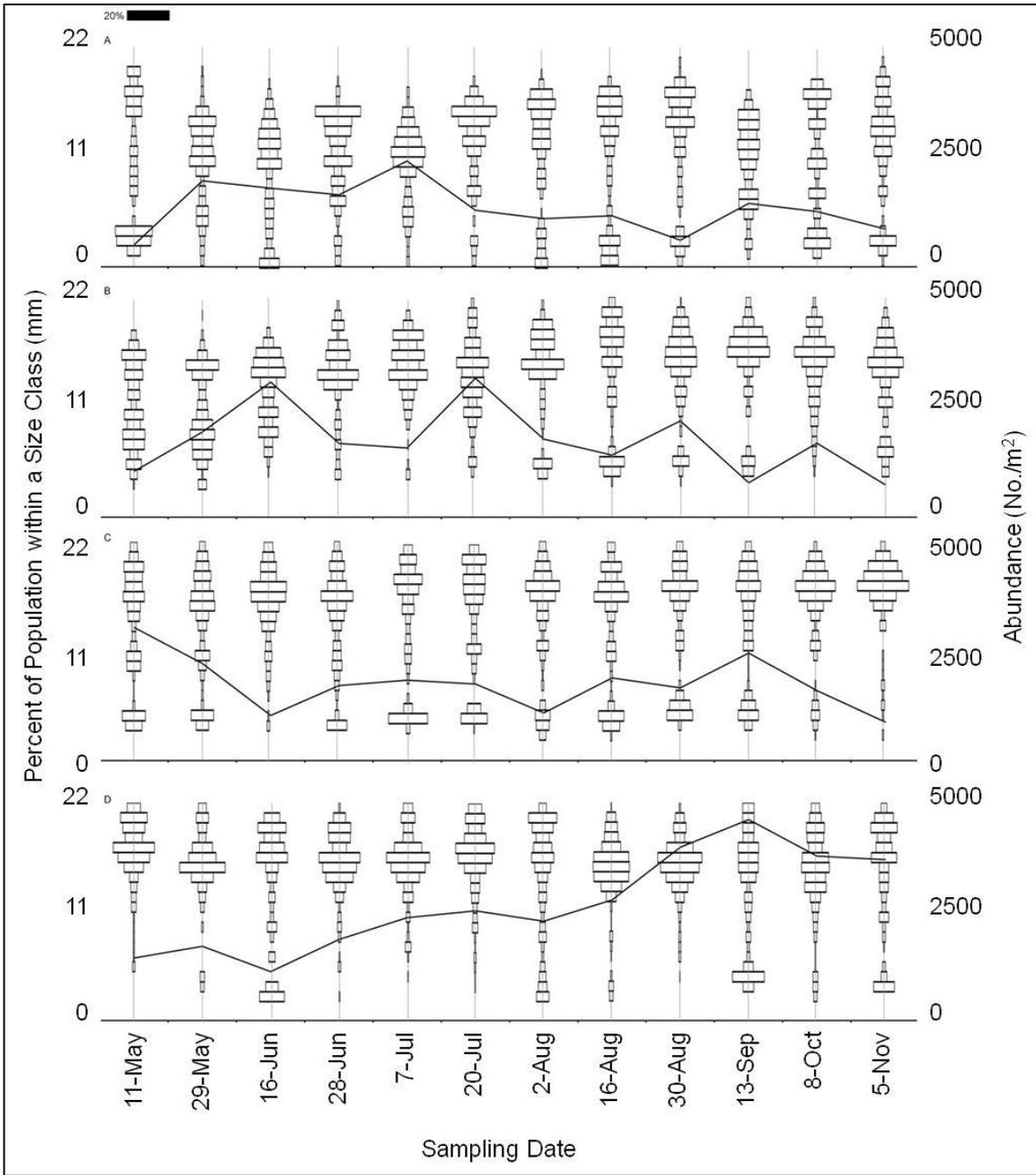


Figure 1-4: Population structure of sampling sites across dates expressed as a percentage on the primary vertical axis. Abundance (number of clams per metered squared) is represented by line on the secondary vertical axis. A=LS5, B=MB5, C=NV5, D=NV20

Chapter 2: The influence of a recent invasion of *Corbicula fluminea* on zoobenthos community structure in an oligotrophic, sub-alpine lake

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Abstract

Influence on benthic community structure of the non-native clam, *Corbicula fluminea*, was studied in Lake Tahoe, USA, an oligotrophic, subalpine lake during September and October 2010. Two sites, with similar habitat but different abundances of *C. fluminea*, were studied to determine if increasing abundances had negative effects on both benthic community structure and native mollusk species. The high-abundance site had 1809 ± 153 *C. fluminea* per meter squared and the low-abundance site had 33 ± 15 *C. fluminea* per meter squared. Analysis of Similarity (ANOSIM) showed there was a significant difference in benthic community structure between the two sites ($R = 0.884$, $p < 0.001$) and the Percentage of Similarity (SIMPER) procedure indicated that *C. fluminea* was responsible for the differences. Abundance levels of three taxa were greater in the absence of *C. fluminea*, *Pisidium* ($p = 0.0287$), Oligochaeta ($p < 0.0001$) and Ostracoda ($p < 0.0001$), suggesting that the clams had a negative effect on these taxa. Two taxa had increasing abundances with high-abundance of *C. fluminea*, Chironomidae ($p = 0.00075$)

and Trichoptera ($p < 0.0001$), suggesting the presence of *C. fluminea* may facilitate these taxa.

Introduction

Zoobenthos are important contributors to the function of aquatic ecosystems. These contributions include the regulation of primary production, detritus and nutrient cycling (Vaughn and Spooner 2006, Weatherhead and James 2001), coupling pelagic to benthic ecosystems (Chandra et al. 2005), and food for higher trophic level organisms such as predatory zoobenthos and fishes (Vadeboncoeur et al. 2011, Vander Zanden et al. 2011). Contributions provided by zoobenthos may not be fully appreciated until an unforeseen change occurs to an ecosystem (Covich et al. 1999). For example, introduction of nonnative invertebrates can augment the declines of native freshwater zoobenthos from other disturbances such as habitat alteration (Strayer 2006, Sousa et al. 2008). In some cases, the addition or removal of a single species may significantly change ecosystem processes and could be associated with the loss of resident species (Covich et al. 1999).

Nonnative species may become successful invaders if their life history traits favor disturbance and integration into a diverse set of ecosystems. Life history traits include early maturity and onset of sexual reproduction, efficient utilization of resources, high fecundity, and juveniles that disperse easily and mature rapidly (Covich et al. 1999, Keller et al. 2007). Nonnative bivalves represent greater than 50% of all aquatic invasive species in North America (Karatayev et al. 2009). Two dreissenid mussels (*Dreissena rostriformis bugensis* and *D. polymorpha*) are examples of more well known invasive bivalves in North America. Their impacts generally result in the overall decreased benthic community evenness while facilitating some taxa (Hirudinea,

Tubellaria and Ephemeroptera) and depressing others (Sphaeriidae and Diporeia) (Ward and Ricciardi 2007, Nalepa et al. 2007).

The mechanisms that cause community changes after the establishment of *Corbicula fluminea*, a nonnative bivalve distributed widely across North America, are not clear. They may or may not depend on the attributes of the ecosystems or native zoobenthic community. Strayer (1999) indicates that *C. fluminea* may have negative impacts to native bivalve populations but the interactions have not been clearly established. Rather than interspecific competition between *C. fluminea* and native bivalves, habitat disturbance may be the primary stressor to native invertebrates allowing *C. fluminea* to establish and expand (Kraemer 1979, McMahon 1999). Although *C. fluminea* dominated benthic biomass in a Texas reservoir, no correlations occurred between abundances of zoobenthos and *C. fluminea* and native unionids (Karatayev et al. 2003). Vaughn and Hakenkamp (2001) call the loss of native bivalves “catastrophic,” and suggest *C. fluminea* impact native communities by high abundance populations’ burrowing activities, feeding strategies and life history traits. While direct causation of the declining distribution, biomass and abundance of a native bivalve, *Pisidium amnicum*, was not determined, it was suggested that the establishment of *C. fluminea* may be the factor (Sousa et al. 2008). In some systems, *C. fluminea* may act as ecosystem engineers altering benthic community structure through increased substrate heterogeneity due to remnant shells, providing refuge from predation and environmental conditions, bioturbation of sediments, and biodeposition of feces and pseudofeces (Vaughn and Spooner 2006, Sousa et al. 2009).

Few studies have been conducted to evaluate the effects by *C. fluminea* on benthic community structure in subalpine, cold, oligotrophic ecosystems (for exception see Werner and Rothaupt 2007, 2008) with most studies occurring in lowland, warmer lentic (natural and reservoir) and lotic ecosystems (Karatayev et al. 2003, Sousa et al. 2009). This study investigates how the recent establishment of *C. fluminea* affects benthic community structure in Lake Tahoe. We hypothesized that increasing abundances of *C. fluminea* would have both a negative effect on the composition of benthic community structure and specifically on native mollusk taxa.

Methods

Study Site

Lake Tahoe is a subalpine, cold oligotrophic lake located in the Sierra Nevada mountain range on the California-Nevada border (39.13 °N, 120.05 °W). The second deepest lake in the United States, it has a surface area of 496 km², maximum depth of 501 m, surface elevation of 1,897 m a.s.l at capacity and a watershed area of 800 km². It is a monomictic lake, ice-free year around, with stratification beginning in early spring and achieving maximum in mid-summer (Jassby et al. 2003). Although well known for its clear waters, there has been a marked decline in water clarity measured both by Secchi and light photometer readings since measurements were first taken in the late 1960's with a ~4.5 fold increase in pelagic primary production due to progressive anthropogenic eutrophication (Chandra et al. 2005). Littoral zone temperatures range from 4°C in winter months warming upwards to 20 °C in mid-summer. First observed in 2002, *C. fluminea* was documented as widely established in the southeastern littoral zone of Lake

Tahoe in April 2008 (Hackley et al. 2008). To our knowledge, Lake Tahoe is the highest elevation where *C. fluminea* has established.

Field Sampling

To compare if benthic community changes occurred after this initial establishment by *C. fluminea*, we measured benthic community structure from two sites, hereafter referred to as treatments, in the 5 m littoral zone of Lake Tahoe during early October which represents the late summer/ fall season, 2010. Two treatment categories were based on abundance levels *C. fluminea*. One site had high abundance ($1809 \pm 153/\text{m}^2$) and the second site had low abundance ($33 \pm 15/\text{m}^2$). Primary productivity at each location was similar (Goldman and deAmezaga 1975, Fig. 6). Substrate was gathered from each site and wet sieved to assess particle size distribution corresponding to the Wentworth classification (Brakensick et al. 1979, Gordon et al. 2007). Substrate between the two sample sites was similar with the major particle size being medium sand (0.50 to 0.30 mm, 38% at high-abundance treatment, 31% in low-abundance treatment). Both samples had nearly equal amounts of very fine gravel (4.0 mm, 1%) and very coarse sand (20 mm, 4 to 5%). The largest particle size was very fine gravel and smallest was very fine sand (0.05 mm), but particles beyond either range of those sizes were not measured during the wet sieve processes.

Zoobenthos were collected using a 225 cm² petite Ponar grab (n = 20 for high abundance and n = 10 for low abundance treatments), sieved through 500 μm mesh, with the elutriated sample placed in a super-saturated sucrose solution to assist in the efficient collection of zoobenthos (Anderson 1959). Zoobenthos were preserved in 70% ethyl

alcohol until identification to the highest taxonomic resolution utilizing Thorp and Covich (2001) and Merrit and Cummins (1996). To determine if interspecific competition for food resources exists between mollusk species, four taxa (three native and *C. fluminea*) with the similar feeding strategies were examined for differences in abundance levels by site. The two families of gastropods, Planorbidae and Physidae, both feed on detritus and bacteria (Brown and Lydeard 2010) and *Pisidium* suspension feed as adults and deposit feed as juveniles (Reid et al. 1992, Vaughn and Hakenkamp 2001). The feeding strategies of *C. fluminea* are suspension feeding from the water column and deposit feeding by two methods, probe feeding on interstitial organic particles and use of their ciliated foot to scrape organic matter from substrate (Way et al. 1988, Reid et al. 1992, Schmidlin and Baur 2007).

Analysis

Patterns in community structure were analyzed with both Analysis of Similarity (ANOSIM) and accompanying non-metric multi-dimensional scaling (NMDS) plots, and the Similarity Percentage (SIMPER) procedure in Primer-E v6.0, a multivariate statistics software. Statistical interpretation of ANOSIM is represented by an R-value which ranges between -1 to 1. The larger the R-value, the greater the separation between samples (Clark 1993, Mörtl 2004). The SIMPER procedure determines how specific taxa abundances contribute to dissimilarity between samples (Mörtl 2004). Prior to analysis, abundances were fourth root transformed to reduce the influence of dominant taxa, and a Bray-Curtis resemblance performed. Based on the taxa identified in the SIMPER routine,

a one-way ANOVA of taxa abundance levels between treatments and a Tukey HSD post-hoc analysis were performed in the SAS System 9.2.

Results

There was a significant difference in total zoobenthos abundance levels ($p = 0.02$) between the high-abundance treatment ($n = 20, 5107 \pm 435 \text{ No./m}^2$) and the low-abundance treatment ($n = 10, 3385 \pm 425 \text{ No./m}^2$) (Fig. 2-1). Removing *C. fluminea* from the abundance calculation showed no significant difference between the treatments ($p = 0.92$). Abundances of *C. fluminea* were statistically different ($p < 0.0001$) between the high- and low-abundance treatment.

Fifteen taxa of zoobenthos were identified in the high-abundance treatment and eleven present in low-abundance treatment. There were no taxa present in the low-abundance treatment that were not found in the high-abundance treatment. Community structure as analyzed by ANOSIM showed that the treatments were significantly different ($R = 0.88, p < 0.001$). The NMDS plot separated the high-abundance treatment from the low-abundance treatment, and *C. fluminea* were present in all samples of the high-abundance treatment (Fig. 2-2). Within the low-abundance treatment, the four samples with *C. fluminea* clustered with no overlap into the samples without *C. fluminea*. The SIMPER procedure determined that high- and low-abundance treatments were 44.79% dissimilar with *C. fluminea*, Chironomidae and Trichoptera contributing the greatest dissimilarity by the high-abundance treatment and Oligocheata and Ostracoda contributed the greatest percentage of dissimilarity by the low-abundance treatment (Table 2-1).

Within treatments, the high-abundance samples had a mean similarity of 75.54% and the low-abundance samples' mean similarity was 74.81%.

The differences in abundances of taxa and sample variability are presented in Table 2-2 and Figure 2.3. Gastropoda did not contribute differences as determined by the SIMPER procedure, and were not significantly different between treatments ($p = 0.18$). Abundances of *Pisidium* were significantly different ($p = 0.03$) with the greatest abundances in low-abundance treatment. Chironomidae did contribute to the differences between the treatments' community structure, and the high-abundance treatment had significantly greater abundances of Chironomidae ($p = 0.001$). Trichoptera was only found in high-abundance treatment, and abundances were significantly greater ($p < 0.0001$). While Ephemeroptera was found only in the high-abundance treatment, there was no significant difference between treatments due to the large variability in the high abundance treatment. Ostracoda and Oligochaeta contributed the greatest amount of dissimilarity to the low-abundance treatment. Oligochaeta showed significant differences in abundances favoring the low-abundance treatment ($p < 0.0001$). Significant differences in Ostracoda abundances were also present in the low-abundance treatment ($p < 0.0001$).

Discussion

Given comparable substrate and primary productivity at each treatment suggesting habitat similarity, this study expected that increasing abundances of *C. fluminea*, as a recently introduced nonnative would have a significant effect on benthic community structure. We accept our hypothesis as both community structure and

subsequently some individual taxa abundances were significantly different between treatments. Analysis of community structure shows a distinct difference between the high- and low-abundance treatments, and attributes those differences to the presence of *C. fluminea*. Other taxa contributed to the differences in community structure as well, and how *C. fluminea* influenced those taxa, is discussed below.

We accepted our hypothesis regarding *C. fluminea*'s negative influence on native mollusk species specifically for the native *Pisidium*. We suggested that *Pisidium* and gastropods would be negatively impacted by the presence of *C. fluminea* perhaps due to interspecific feeding competition. This study demonstrated that while Gastropoda abundances did not experience negative effects, *Pisidium* abundances were greater where *C. fluminea* abundances were low. It has been suggested that it is primarily human-caused disturbance that first stresses or reduces native bivalve assemblages allowing *C. fluminea* to then affect native species (McMahon 1999). In Lake Tahoe, physical disturbance is not a factor in the establishment of *C. fluminea*; therefore interspecific competition for limited food resources may be the causal mechanism. Supporting this, Strayer (1999) suggests that interspecific competition between *C. fluminea* and natives is the principal cause of decline in native bivalve abundances.

The presence of *C. fluminea* in the high-abundance treatment may be facilitating aquatic insect larval stages as demonstrated by the significantly greater abundances of Trichoptera and Chironomidae and the presence of Ephemeroptera. These differences suggest that *C. fluminea* is acting as an ecosystem engineer via the production and deposition of remnant shells, bioturbation of sediments, and foraging strategies, which

create physical modifications and thereby increase benthic habitat heterogeneity (Sousa et al. 2009). It is suggested that habitat complexity benefits overall benthic abundance (Crooks 2002, Sousa et al. 2009), as it provides habitat for juvenile and mature organisms (refuge from predation and physical stress), substrate for settlement or oviposition, and alters the water-substrate interface flow changing sediment deposition patterns, food delivery and erosion (Commito and Rusgnoolo 2000, Gutiérrez et al. 2003). Studying the recent invasion of *C. fluminea*, Werner and Rothhaupt (2007, 2008) found that in Lake Constance (a cold, sub-alpine oligotrophic lake in Germany), Ephemeroptera abundances increased on accumulated shells and increasing habitat heterogeneity may facilitate other zoobenthos. Given that Lake Tahoe is the same trophic status as Lake Constance, a future study in Lake Tahoe may reproduce these results perhaps extending to other insect taxa as well.

This study showed that in the low-abundance treatment, both Oligochaeta and Ostracoda had significantly greater abundances. Oligochaeta are “conveyor-belt” feeders continuously ingesting sediments that contain algae and bacteria. (Goveidch et al. 2010, Mermillod-Blondin et al. 2001). In addition to suspension feeding, *C. fluminea* will actively deposit feed from the sediments, removing bacteria from the substrate. Hakenkamp et al. (2001) determined that *C. fluminea* did have a negative effect on bacteria and protists abundances. As Oligochaeta forage on bacteria, there may be interspecific competition for food resources in a nutrient limited ecosystem such as Lake Tahoe. Differences in Ostracoda abundances between the two treatments may be attributed to the presence of *C. fluminea*. While ostracods are sensitive to variability in environmental conditions (e.g. pH, temperature) (Külköylüoğlu and Vinyard 2000,

Külköylüoğlu and Dügel 2004), bioturbation by *C. fluminea* may be a factor in the near absence of ostracods in the presence of clams. In freshwater systems, ostracods are oviparous and deposit their eggs on substrate with variable egg size but up to 100 µm (Dole-Oliver et al. 2000, Dumont et al. 2002) and bioturbation by *C. fluminea* may disturb these egg clusters. Further research may show that in Lake Tahoe bioturbation of sediments by *C. fluminea* may negatively affect abundances of other zoobenthos.

Conclusions

This study suggests that Lake Tahoe, a cold, oligotrophic lake, is experiencing benthic community structure changes as a result of an initial invasion by *C. fluminea* that are dependent on the abundances of the invader. There were both positive (two taxa) and negative (three taxa) impacts to zoobenthos in the littoral zone. Considering that there was no difference in substrate particle size and similar primary productivity, it is possible that *C. fluminea* are functioning as ecosystem engineers increasing structural heterogeneity thereby providing habitat for other zoobenthos. This analysis was conducted from a single sampling event that may be influenced by seasonal changes. To fully appreciate potential changes in benthic community structure, studies need to be repeated over seasons and years. Additionally, it would be beneficial to study a non-impacted site with similar habitat as a comparison for future community structure studies. Once the establishment of *C. fluminea* is stable, findings at that time may support this study or have different conclusions. Other studies are currently being conducted regarding *C. fluminea*'s influences in Lake Tahoe and may show site specific community structure which may not reflect these findings. Ultimately, the established populations of

C. fluminea need to be monitored regularly to determine the long-term effects on the native community. Current and future distribution of *C. fluminea* in Lake Tahoe should be documented and monitored.

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Tables and Figures

Table2-1. Results of the SIMPER routine contribution of taxa to average dissimilarities between sampling treatments and (cut-off for low contribution 75% therefore not all taxa in treatments are represented). Mean abundance was fourth root transformed prior to analysis.

Taxa	Mean Abundance (#/m ²) Group 1	Mean Abundance (#/m ²) Group 2	Mean Dissimilarity	Species contribution to dissimilarity %	Cumulative contribution %
High-abundance and Low-abundance					
Average dissimilarity=44.54					
Corbicula	2.45	0.45	9.50±2.71	21.33	21.33
Ostracoda	0.05	1.57	7.15±3.19	16.04	37.37
Trichoptera	0.91	0.00	4.07±1.64	9.13	46.50
Pisidium	0.52	1.07	3.84±1.35	8.61	55.11
Chironomidae	2.47	1.77	3.75±1.74	8.43	63.54
Oligocheata	1.68	2.42	3.59±1.87	8.06	71.60

Table 2-2. Mean Abundances (No./m²) of taxa with standard error. Abundances represented here are not transformed.

Taxa	High-abundance treatment	Low-abundance treatment
Corbicula	1809±153	33±15
Ostracoda	2±2	376±96
Trichoptera	83±14	0
Pisidium	57±30	147±4
Chironomidae	2185±316	566±140
Oligocheata	483±104	1728±209
Gastropoda ⁺	28±13	4±3

⁺Did not contribute to community dissimilarities.

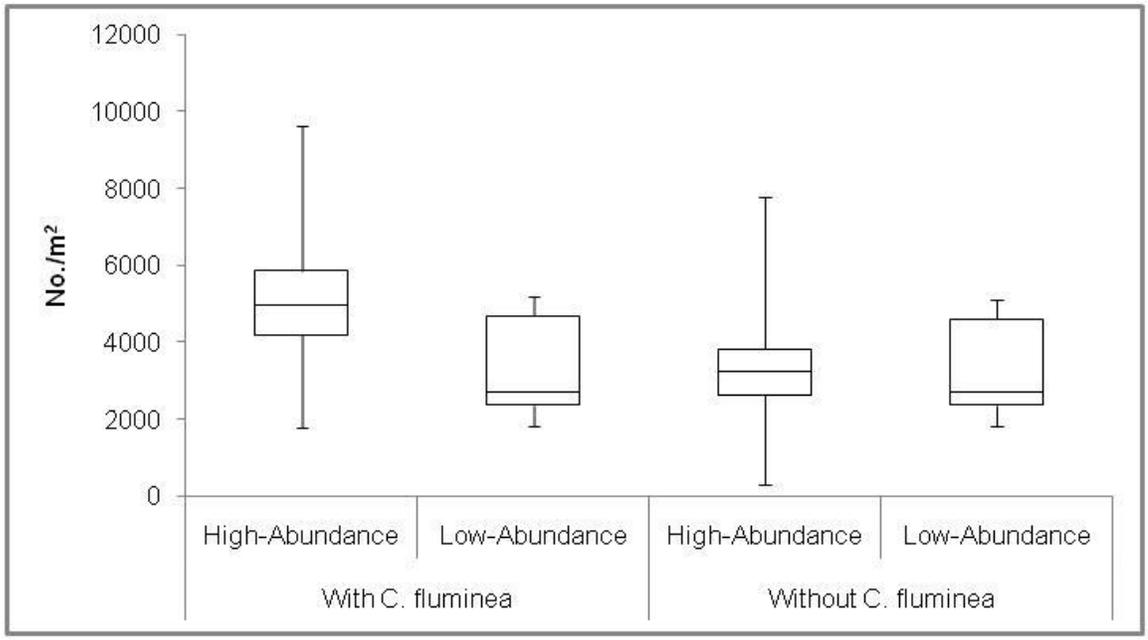


Figure 2-1. Overall abundances of all benthic invertebrates by high- and low-abundance in two categories. Left is abundance calculations with *C. fluminea* included and right is abundance calculations without *C. fluminea*.

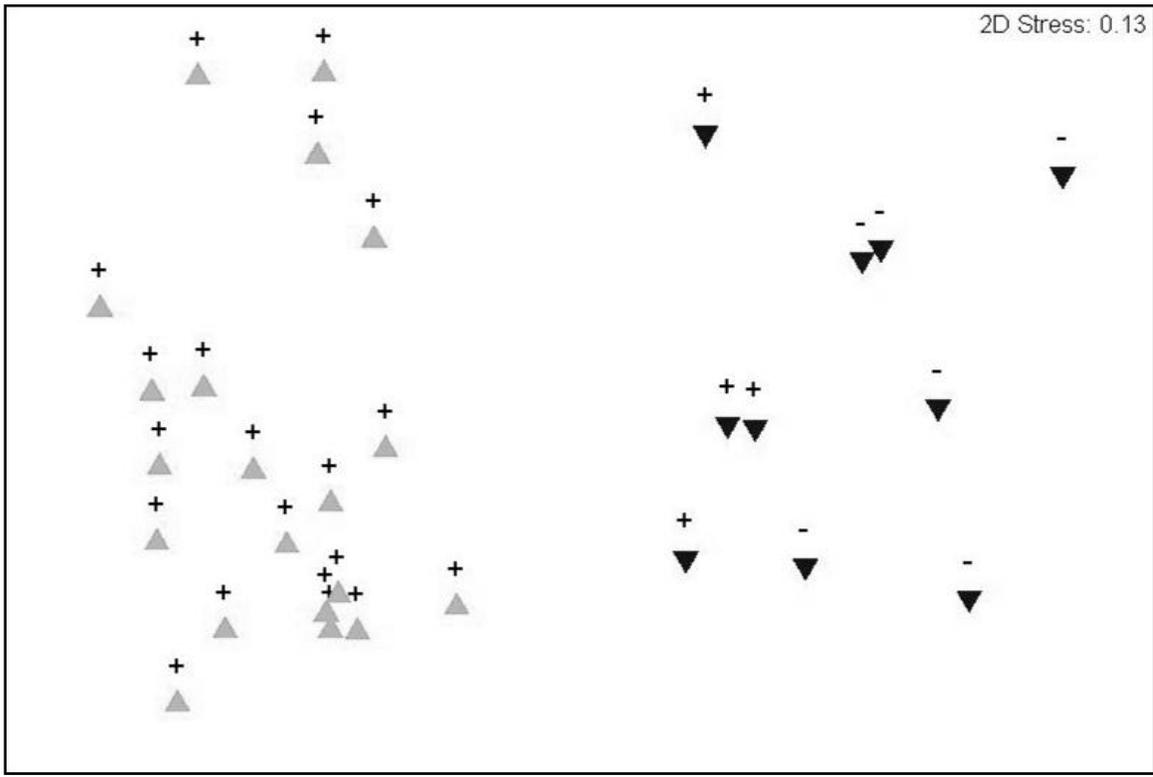


Figure 2-2. NMDS plot of treatments by abundance levels (fourth root transformed) as represented by high (▲) and low (▼). Presence of *C. fluminea* within each treatment is noted as with (+) or without (-).

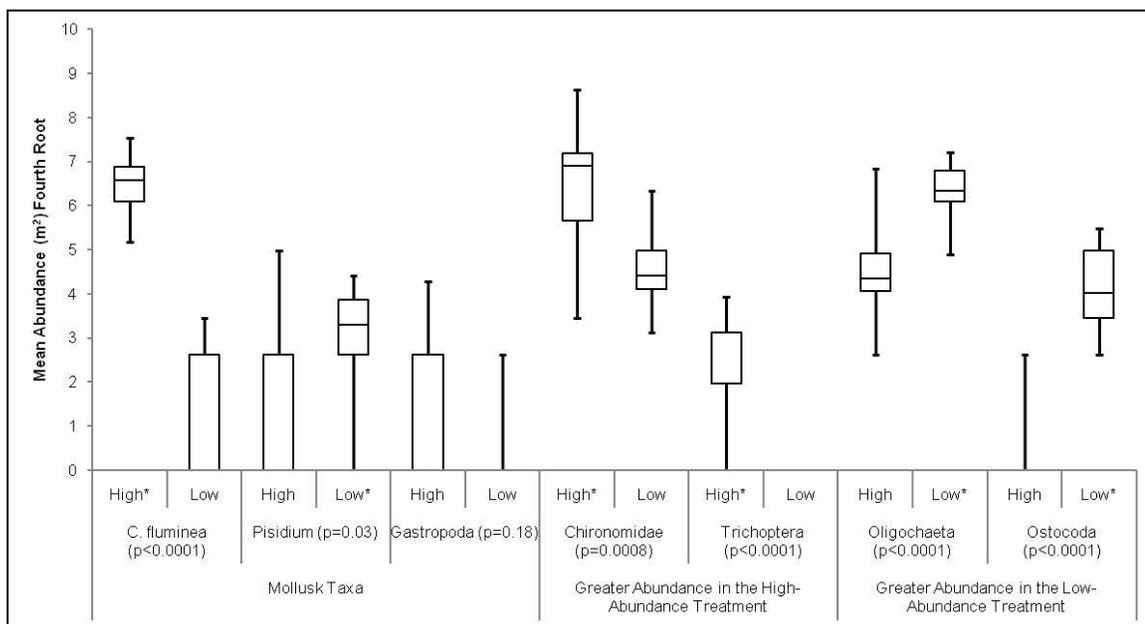


Figure 2-3. Box plots showing abundances of taxa (with accompanying p-values) by mollusk taxa, taxa in greater abundance in the high-abundance treatment and taxa in greater abundance in the low abundance treatment.

APPENDIX

Short-Term Substrate Preference Trials

Using the Wentworth classification of particle size classification, characterization was conducted for each location where substrate was obtained (Figure A-1).

Approximately fifty (50) grams of substrate from each location was wet sieved through a series of decreasing size mesh from 3.962 mm to 53 μm . Each proportion of the original sample was weighed to determine the distribution of the particles in the overall sample.

Two separate sediment preference trials were conducted over three days in a laboratory cold room maintained at 18°C. The first trial was six treatments with particle sizes distributions of similar proportions from Nevada Beach, Emerald Bay and Crystal Bay (5 m depth for each location). These sites were chosen due to the level of *C. fluminea* at each site (Nevada Beach has very high abundances, Emerald Bay has extremely low abundances, and no clams are present in Crystal Bay). The second trial was five treatments of particle sizes of significant differences: greater than 75% silt, very fine gravel and medium sand. Treatments consisted of a circular container with an area of 285.03 cm² which was equally divided into thirds (95.03 cm²) and filled with three treatments of substrate to a depth of 4 cm and supplemented with aerated lake water at the beginning of each trial. Eleven clams per replicate per trial (15.16 \pm 0.56 mm for site and 15.33 \pm 0.50 mm for particle size) were mixed and randomly selected prior to each trial and placed in the center of each treatment. Each preference trial ran for 24 hours, where at the conclusion, the location of each *C. fluminea* was determined and recorded. Water was drained and refreshed prior to the start of each trial.

An ANOVA of the cumulative abundance of *C. fluminea* per treatment over the trial period was conducted. *C. fluminea* had a significant preference ($p < 0.0001$) for Crystal Bay over the other two treatments (Figure A-2). There was no significant difference ($p = 0.19$) for particle size (Figure A-3).

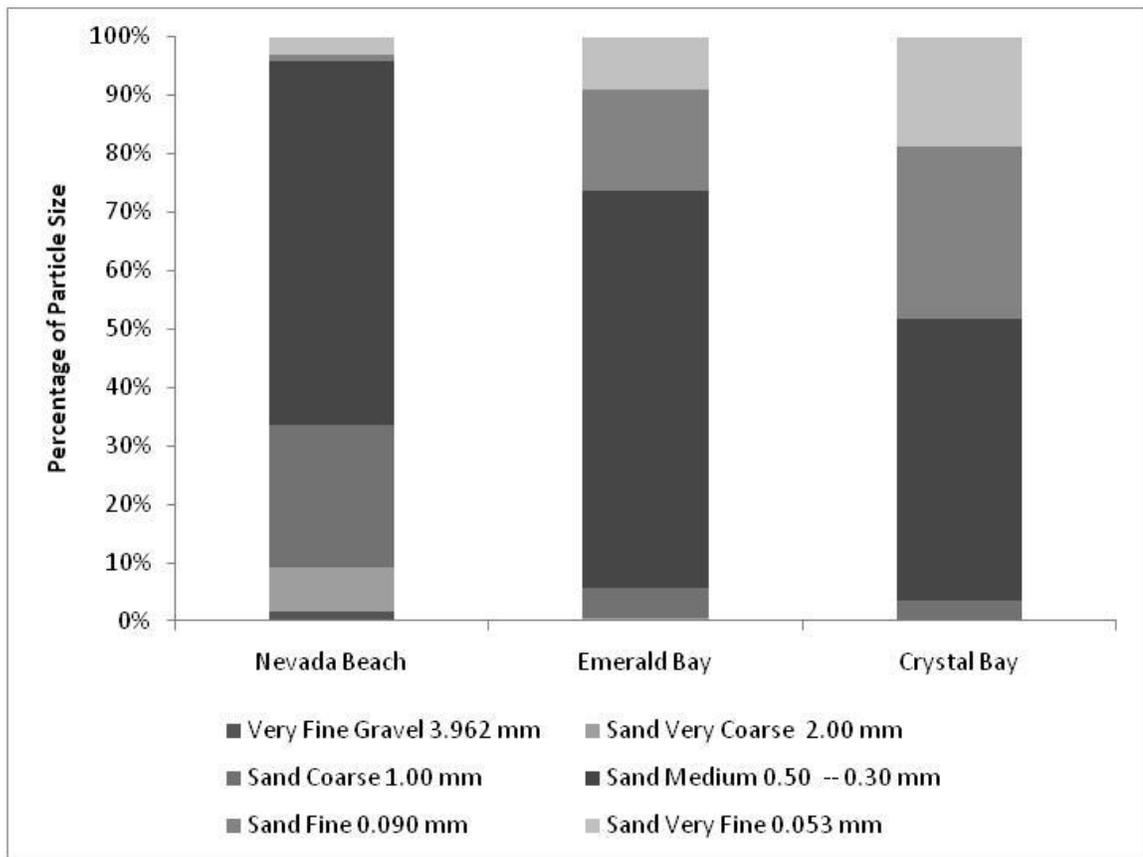


Figure A-1. Particle size percentages across three sites.

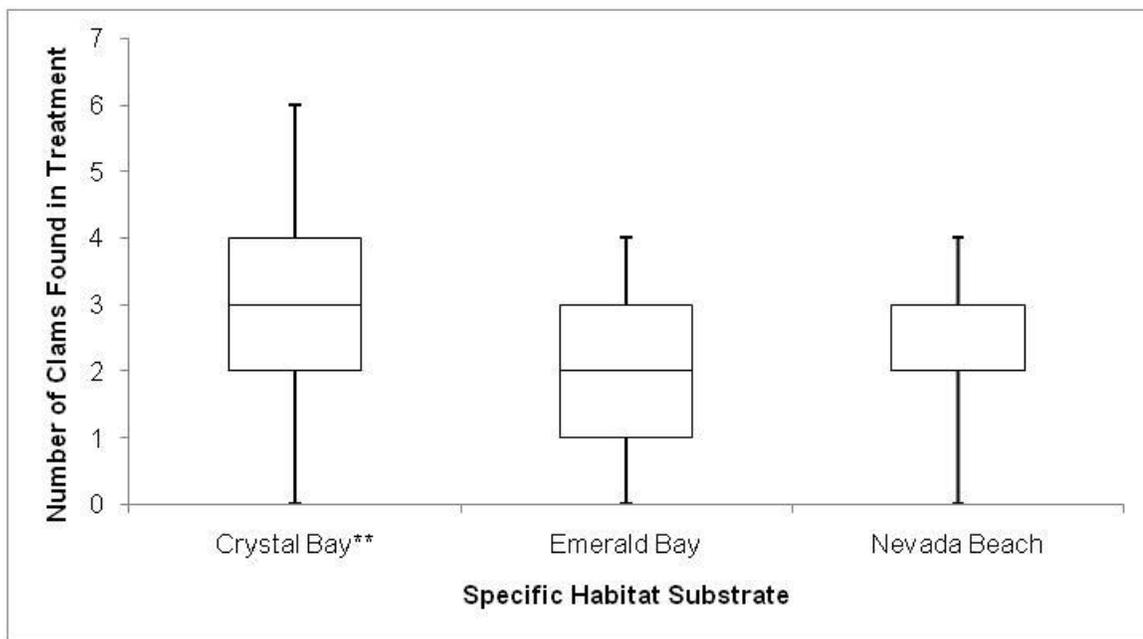


Figure A-2. Preference for specific habitat substrate results.

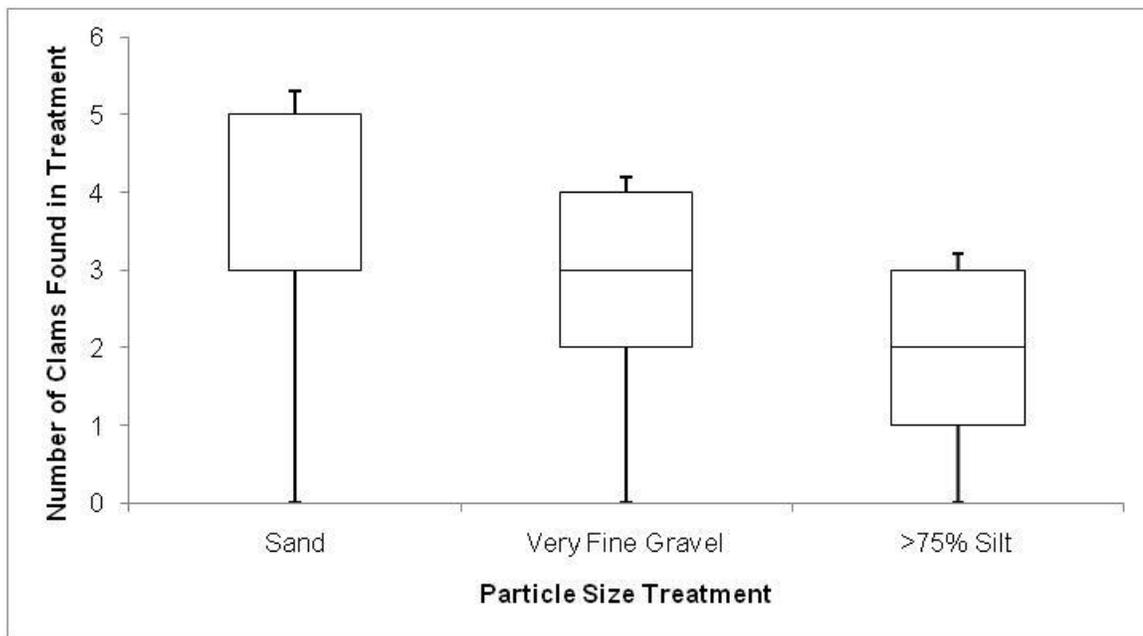


Figure A-3. Preference for specific particle size results.

Table A-1: Taxonomic grouping and enumeration for zoobenthos discussed in Chapter 2.

Phylum		Mollusca			
Subphylum		Bivalvia		Gastropoda	
Class		Bivalvia		Gastropoda	
Subclass		Veneroidea			
Order		Veneroidea			
Family		Corbiculidae	Sphaeriidae	Planorbidae	Physidae
Genus		Corbicula	Pisidium		
Species		<i>C. fluminea</i>			
Sample ID		Corbicula	Pisidium	Planorbidae	Physidae
High Abundance n=20					
	Mean	1809.52	57.14	47.62	9.52
	STD	686.08	137.84	87.40	29.31
	SE	153.41	30.82	19.54	6.55
Low Abundance n=10					
	Mean	33.33	147.62	9.52	0.00
	STD	50.45	135.53	20.08	0.00
	SE	15.95	42.86	6.35	0.00
Phylum		Arthropoda (Insecta)			
Subphylum		Insecta			
Class		Insecta			
Subclass					
Order		Diptera		Trichoptera	Ephemeroptera
Family		Chironomidae	Ceratopogonidae		
Genus					
Species					
Sample ID		Chironomidae	Ceratopogonidae	Trichoptera	Ephemeroptera
High Abundance n=20					
	Mean	2185.71	23.81	83.33	4.76
	STD	1414.21	50.06	65.32	14.66
	SE	316.23	11.19	14.61	3.28
Low Abundance n=10					
	Mean	566.67	4.76	0.00	0.00
	STD	444.13	15.06	0.00	0.00
	SE	140.45	4.76	0.00	0.00

Phylum	Arthropoda			
Subphylum	Crustacea			
Class	Amphipoda	Ostracoda	Arachnida	
Subclass			Acari	
Order			Trombidiformes	
Family	Dogielinotidae			
Genus	Hyaella			
Species	<i>H. azteca</i>			
Sample ID	Amphipoda	Ostracoda	Hydrachnida	
High Abundance n=20				
Mean	307.14	2.38	76.19	
STD	233.53	10.65	90.61	
SE	52.22	2.38	20.26	
Low Abundance n=10				
Mean	438.10	376.19	38.10	
STD	310.88	306.52	37.56	
SE	98.31	96.93	11.88	
Phylum	Annelida		Platyhelminthes	
Subphylum				
Class	Clitellata		Nematoda	Turbellaria
Subclass	Oligochaeta	Hirudenia		
Order				
Family				
Genus				
Species				
Sample ID	Oligochaeta	Hirudenia	Nematoda	Turbellaria
High Abundance n=20				
Mean	483.33	0.00	2.38	9.52
STD	465.87	0.00	10.65	19.54
SE	104.17	0.00	2.38	4.37
Low Abundance n=10				
Mean	1728.57	4.76	0.00	23.81
STD	662.90	15.06	0.00	46.28
SE	209.63	4.76	0.00	14.63