

Title: Natural and Human Limitations to Asian Clam Distribution and Recolonization--Factors that Impact the Management and Control in Lake Tahoe (P057)

Primary investigators: Marion E. Wittmann¹, Sudeep Chandra², S. Geoffrey Schladow¹, John E. Reuter¹

Contributing authors: Marianne Denton², Alexander Forrest¹, Tom Mathis¹, Jeffrey Baguley²

¹ Tahoe Environmental Research Center, University of California Davis

² Department of Natural Resources and Environmental Science, University of Nevada Reno

A report submitted to the Pacific Southwest Research Station, US Forest Service

June 30, 2013

Contents

Executive Summary.....	3
Background	7
I. Asian clam growth, reproduction and transport in deep and shallow zones of Lake Tahoe	9
Introduction	9
A. Reproduction and Population Structure of Asian clams in Lake Tahoe	12
<i>Methods</i>	12
<i>Results</i>	13
<i>Discussion</i>	18
B. Asian clam shell production in shallow and deep water depths	21
<i>Methods</i>	21
<i>Results</i>	22
<i>Discussion</i>	24
C. Asian clam transport between shallow and deep zones	26
<i>Introduction</i>	26
<i>Methods</i>	27
<i>Results</i>	31
<i>Discussion</i>	36
II. Large scale bottom barrier treatment: Recolonization of Asian clams in low and high density regions of Lake Tahoe	46
<i>Introduction</i>	46
<i>Methods</i>	48
<i>Results</i>	49
<i>Discussion</i>	53
III. Economic efficiency analysis: Asian clam recolonization rates after bottom barrier treatment	56
<i>Introduction</i>	56
<i>Methods</i>	57
<i>Results</i>	62
<i>Discussion</i>	73
Conclusion.....	76
Acknowledgements.....	79
References	80
Appendices.....	87

Executive Summary

Background

The invasive bivalve, Asian clam (*Corbicula fluminea*) is established and shows signs of spreading in Lake Tahoe. In 2002, low density populations (2-20 individuals per m²) were observed in the south eastern portion of the lake, and in 2009 densities up to 5000 individuals per m² have been measured. Through extensive field collection and laboratory experimentation, the University of California Davis (UCD) and University of Nevada Reno (UNR) science teams have found that this expanding population comprises the majority of benthic community biomass in regions where it has established, is associated with filamentous algal blooms, and through shell deposition, has negatively impacted the aesthetic value of the Lake Tahoe nearshore. In response to this nearshore invasion, federal and state agencies collaborated with UCD and UNR to develop a short term Asian clam management plan and implement a series of studies to understand the distribution, life history and reproductive strategies of this species in relation to population control. Additionally, a series of non-chemical management strategies (i.e., diver assisted suction removal and bottom barriers) had been tested in small scale pilot projects in Lake Tahoe. Findings from this previous research showed that Asian clam populations can be reduced through the use of bottom barriers, which is less costly than diver assisted suction removal. Asian clam were shown to be distributed mostly in south eastern portion of the lake, with some low density satellite populations in other locations, including Emerald Bay. Asian clam mostly populated the nearshore zone at depths of 2 - 10 m, but low density populations were also located at depths between 10 and 50 m, and one individual was recovered from 70 m water depth; deeper than the scientific literature has previously described or studied.

Bottom barriers provide a promising method for reducing Asian clam populations but fundamental unknowns present obstacles to recommending the large scale adoption of this methodology. In addition, the relationship between deepwater clam populations and shallower nearshore populations (where management through the use of bottom barriers is likely to occur), as well as the growth, life history or reproductive strategies of this species in a temperature limited environment was also unknown. Finally, the recolonization rates of Asian clam--given propagule pressure from advective transport of juveniles via water currents, and diffusive spread of adjacent populations (including the recently observed deep water beds) are presently not quantified. In order to understand the feasibility of implementation for Asian clam treatment in Lake Tahoe given economic costs, and more importantly, these relationships need to be clarified.

The major objectives of this research were to (1) understand the life history (including reproduction and growth) of deepwater clam populations and their response to habitat, water currents and nearshore clam populations as a potential habitat for viable populations, (2) develop the relationship between treatment site selection (i.e., low population density site versus high density population center site) and rate of Asian clam recolonization rates, and (3) estimate recolonization following a rubber bottom barrier application and perform a cost efficiency analysis based on recolonization rate and site selection.

Research findings

Through field based collections coupled with laboratory experimentation, we found that Asian clams are capable of significant growth and reproduction in the nearshore zone of Lake Tahoe. Reproductively viable individuals were observed at water depths down to 20 m, and also grew and survived in conditions at 50 m water depths. Asian clam mortality rates were significantly higher and shell production rates were significantly lower for Asian clam individuals at deep water depths (50 m) compared to those observed at 5 m water depths, suggesting that populations can exist in deep water, but with much less productivity than those observed in the nearshore zone.

Through a combination of field and laboratory based studies, the vertical transport of pediveliger larvae in the water column and advection of adult individuals was investigated. Water flow conditions within Lake Tahoe were measured to understand if passive transport of adults was possible. During storm events, peak horizontal velocities of 25 cm s^{-1} and peak vertical (downwards) velocities of 4 cm s^{-1} were measured directly. Laboratory experimental runs were conducted with individual adult clams (5–24 mm shell length) in a hydraulic flume over the range of observed field velocities. These experiments demonstrated entrainment of individuals up to 15 mm in size during typical storm events and all size classes during peak storm events. This work shows that passive transport of adult Asian clam individuals a potential dispersal mechanism for Asian clam in Lake Tahoe, transporting adults and juveniles from shallow depths to deeper zones, and potentially vice versa.

Building upon previous investigations of the use of bottom barriers to reduce Asian clam populations, a large scale barrier treatment (two half-acre plots) was implemented from 2009 - 2010. After this barrier treatment, the treatment and control plots were monitored for a one year period in order to understand the impact to and recolonization rates of Asian clams and benthic macroinvertebrate communities. These measured recolonization rates were then used to parameterize population growth models to understand the frequency of bottom barrier treatment, with respect to achieving population densities

observed in 2010, or what is considered here as the "baseline condition". It was found that Asian clam populations are significantly reduced during bottom barrier treatment, with up to 95 - 99% mortality observed. Native macroinvertebrate communities are also significantly reduced, but after a one year period, both Asian clams and macroinvertebrate communities demonstrated rapid recolonization in the treatment plots. Dependent on region, Asian clam recolonization rates varied, and follow-up measurements by the University of Nevada Reno in Marla Bay indicated that Asian clam abundances in treatment plots were not different than those observed in control plots 22 months after bottom barrier removal (although control plot populations are lower than they were prior to barrier treatment). Costs of Asian clam treatment in Lake Tahoe were approximately \$210,000 per acre. An exercise considering a hypothetical 100 acre area for treatment indicated that total costs of treatment for this area can range from \$2 to \$26 million and will never achieve eradication, nor the maintenance of low density populations of Asian clams in Lake Tahoe.

Management recommendations

All studies presented herein were conducted over a two-year period, and recolonization rates are based on a one-year time period following barrier treatment. These time scales are not necessarily realistic representations of the population dynamics of aquatic species, native or otherwise. This is to say, it may take a short amount of time for abundances of one or a few taxa to recover after a disturbance or control treatment, but the native biodiversity of the entire benthic community may take longer to recover than single taxonomic groups (Wittmann et al. 2012a). Within the time constraints of this study we have provided the first estimates of recolonization of Asian clam after ethylene propylene diene monomer (EPDM) barrier treatment; however, we caution that the dynamics of species are complex and have a great deal of uncertainty associated with habitat and other climate variables not represented in this study. We recommend the continuation of a long term experimental and monitoring program that applies to Asian clam management, especially with regard to the continued measurement of clam recolonization in the two half-acre treatment areas. Until more information with respect to Asian clam population growth, as well as information about the recovery of the benthic community as a whole, it is difficult to understand the efficacy of a large scale treatment program.

Conclusion

The experimental Asian clam research program at Lake Tahoe is a novel endeavor for this type of invasive species management, and has provided a lot of information and insight to managers within the

basin as well as to scientists and managers outside of the region. Continuing to collect and provide this type of information will continue to support the integration of science and management at Lake Tahoe as a model for invasive species program both nationally and globally.

Background

Asian clam (*Corbicula fluminea*) is the first and only to date molluscan aquatic invasive species (AIS) to have established in Lake Tahoe. Where populations are dense, Asian clams dominate the biomass of native benthic macroinvertebrate communities, impact water quality through concentrated nutrient excretion and benthic algal blooms, and alter the aesthetic values of nearshore regions through shell deposition on shorelines. Fortunately, Asian clam is in the early invasion stage, i.e., it has not fully dispersed to all available suitable habitats in Lake Tahoe. A biological invasion in its early stages allows for the study of dispersal mechanisms, impacts to native communities and may also provide for an opportunity to consider control and management of a species before it has completely invaded an ecosystem.

In collaboration with federal and state agencies and organizations (TRPA, TRCD, USFWS, USACE, CDFG, USDA-ARS, CA State Parks, LRWQCB, NDEP, NDOW, NDSL, TWSA) and funding from sources including SNPLMA science and capital funds, CTC, USACE, USBR, LRWQCB Clean up and Abatement, and NDSL license plate funds our researchers from UC Davis (UCD) and UN Reno (UNR) have intensively researched the lakewide distribution, life history, and impacts to water quality and native ecosystems of Asian clam. As part of this larger collaborative effort, researchers also previously experimented with non-chemical control strategies specific to the Lake Tahoe environment (using small-scale test plots 10-20 m²) (Wittmann et al. 2012b). These investigations have led to two key observations. First, by applying benthic barriers (45 mil EPDM sheets placed upon clam beds), it is possible to reduce dissolved oxygen concentrations within the sediment column to levels fatal to Asian clam. The second key observation relates to Asian clam distribution in Lake Tahoe: populations have generally continuous, yet patchy, distribution along the southeastern portion of the lake with smaller satellite populations occurring in discrete locations both horizontally--Emerald Bay, Camp Richardson, Glenbrook, and vertically--at greater water depths than previously observed (up to 70 m) (Forrest et al. 2012).

These past findings have implications for the management of Asian clam and the ecology of native species impacted by Asian clams. First, they demonstrate that it is possible to artificially cause mortality of Asian clams in Lake Tahoe. However, the observed spatial distribution leads to the question: Will recolonization of treated areas rapidly negate the benefits of treatment? Such recolonization may come from a variety of mechanisms including advective transport of both juveniles and adults by lake currents (Williams and McMahon 1986a, McMahon 1999), "diffusive spread" of clams from areas of high concentration to adjacent areas of low concentration, or some combination of the two mechanisms.

None of these mechanisms have been studied or quantified in Lake Tahoe and this remains an outstanding informational gap to know whether effective control is possible, and if so, how much it would cost.

The need for a science based strategy for the prevention of further spread and the control of existing populations is clear and timely. The understanding of deep water clam populations and the recolonization rates for treatment areas in different regions of the lake are imperative for the conservation of Lake Tahoe's native species and the pursuit of an effective AIS management program. The proposed research is intended to guide existing management pursuits at Lake Tahoe and other locations.

The primary goal of this research is to evaluate the practical feasibility, the ecological impacts, and the economic costs of large-scale deployment of benthic barrier to control Asian clam at Lake Tahoe. This will be through the study of the natural environmental limitations of Asian clam in Lake Tahoe as well as the human-mediated limitations to Asian clam in Lake Tahoe (i.e., control strategies), and subsequent recolonization. The following report is organized through the three main subjects: (I) Asian clam growth, reproduction and transport in deep and shallow zones of Lake Tahoe. In this section we explore the effect of depth, habitat and environmental conditions on the reproduction and growth rates of Asian clams in Lake Tahoe. We also use a series of field and laboratory experiments to understand the transport of Asian clam juvenile and adult individuals as a result of entrainment on water currents. In section (II) we look at Large scale bottom barrier treatment: Recolonization of Asian clams in low and high density regions of Lake Tahoe and finally in section (III) we model the return rate or recolonization into the near-future and look at the economic efficiency of Asian clam recolonization rates after bottom barrier treatment which is based on monitored recolonization rates and costs incurred as a result of bottom barrier treatment and monitoring from this large scale, one acre experiment. Based on this research, we provide management recommendations for consideration by the Lake Tahoe Asian clam working group and all stakeholders concerned with Lake Tahoe.

I. Asian clam growth, reproduction and transport in deep and shallow zones of Lake Tahoe

Introduction

Through benthic grab sampling and the lakewide deployment of an autonomous underwater vehicle (AUV) taking high resolution imagery of the lake bottom, the UCD-UNR research team have demonstrated that Asian clam are mostly distributed in the southeastern portion of Lake Tahoe (populations variably distributed from Cave Rock to the East Channel of the Tahoe Keys; Forrest et al. 2012). Newly discovered satellite populations in the southern portion of Glenbrook Bay, Camp Richardson and at the mouth of Emerald Bay showed very low density (1-10 individuals/m²) compared to Marla Bay (up to 10,000 individuals/m²). However, Asian clams are located in water depths ranging from 2 to 70 m water depth in regions of the Lake. Typically Asian clams are restricted to shallow, nearshore lentic systems mostly due to limitations in dissolved oxygen concentrations (McMahon 1999), however, there have been deepwater (80-100 m) occurrences of Asian clam observed in Lake Mead (Peck et al. 1987, Wittmann et al. 2011), and now in Lake Tahoe. Currently there are no published findings of Asian clam growth, reproduction or life history strategies at depths greater than 10 m in lakes.

In the nearshore regions of Lake Tahoe, Asian clam have been observed to impact biotic and abiotic factors of the ecosystem. Where Asian clam occurs, it can dominate the biomass of benthic macroinvertebrate community, which includes including native pea clams (*Pisidium* spp.), gastropods (*Physella* sp. and Planorbidae), chironomids, oligochaetes and other taxonomic groups (Wittmann et al. 2012a). Using Lake Tahoe water in a laboratory experimental setting, an individual Asian clam was capable of filtering over 15-20 liters of lake water (and feeding on phytoplankton) in a 24 hour period (Wittmann et al. 2013). Laboratory experiments by UCD and UNR have shown that the subsequent excretion of nitrogen and phosphorus from this feeding stimulates the growth of filamentous algal species *Zygnema* sp. and *Cladophora glomerata*, which have been observed in association with Asian clam beds in Lake Tahoe (Wittmann et al. 2013, Forrest et al. 2012). These algal species have potential impacts on Lake Tahoe nearshore water clarity, ecology as well as human recreational use of the Tahoe nearshore zone. Additionally, these filamentous algal species are known in other systems to be associated with invasive bivalves (Davies and Hecky 2005), and increased levels of *E. coli* and bacteria (Byappanahalli et al. 2003).

Reproduction of Asian clam can be prolific as a result of hermaphroditism, rapid reproductive maturity, and variable larval incubation periods as short as six days, normally upward to two weeks or as lengthy as 60 days in a wide range of environmental conditions (King et al. 1986, Kraemer and Galloway 1986, McMahon 2000, Rajagopal et al. 2000). Asian clam eggs are protectively held in the inner demibranches of the ctenidia (gills) after release from gonads, then fertilized, and embryos are brooded in the same structure. This may result in an annual fecundity rate of as many as 68,000 juveniles per individual (Aldridge and McMahon 1978). Temperature initiates multiple stages of reproduction, and Asian clams generally have a bivoltine (two broods in one year) reproductive cycle in response to temperature regimes in rivers, lakes, and reservoirs (Aldridge and McMahon 1978, Rajagopal et al. 2000, Mouthon and Parghentanian 2004). An initial spawn commonly occurs during the spring after threshold temperatures have been reached (at least 16–18 °C for at least 10 degree-days); however, once temperatures exceed 27–28 °C, reproductive output is restricted (McMahon 2000, Mouthon 2001a, Mouthon 2001b). A subsequent, weaker spawn may occur after a return to lower temperatures (Aldridge and McMahon 1978, Kennedy and VanHuekelem 1985, Rajagopal et al. 2000, Mouthon and Parghentanian 2004).

Although 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 2001b). 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 used: suspension feeding from the water column and deposit feeding in the substrate. Suspension feeding rates of *C. fluminea* are variable but can be high, between 300–2,500 L/h (McMahon and Bogan 2001). In the absence of suspended food, such as that seen in oligotrophic ecosystems, *C. fluminea* can ingest sediment particulate organic matter (SPOM) through deposit feeding (Reid et al. 1992), consuming upward of 50 mg/day and doubling growth rates (McMahon and Bogan 2001).

Successfully managing invasive species requires an understanding of whether the effects of species removal are long lasting and enable ecosystem recovery or rehabilitation. These aspects are highly dependent on the recruitment potential or recolonization rate of the introduced species after a management action. The presence of deepwater populations has implications for the management of populations in the nearshore for the following reasons: (1) reproductively viable growing populations may pre-empt management actions at depths where management actions to reduce or remove Asian

clams are not possible, and (2) Asian clam populations at deeper depths can potentially serve as a potential source of recruitment for populations (in managed or unmanaged areas) in the nearshore zone. Understanding the reproduction, growth and transport of individuals between nearshore and offshore regions will contribute to the ongoing discussion of Asian clam management in Lake Tahoe. The results will also inform whether these deepwater clams may be impacting endemic species of concern—such as the blind amphipod (*Stygobromus tahoensis*, *Stygobromus laciocolus*), the stonefly (*Capnia lacustra*) as well as deepwater macrophyte beds that are known to provide habitat for these and other native species.

The objective of this chapter (I) was to understand the growth, reproduction of Asian clams at water depths greater than 10 m, relative to those observed for populations in the nearshore zone and to understand mechanisms of Asian clam transport between deep and shallow zones. To investigate factors that influence the reproductive efforts (timing and overall fecundity) of Asian clam in Lake Tahoe a combination of field experiments, dissections of clams, and information gathered from a literature review, the following hypotheses were tested (1) temperature would have the greatest influence on the timing of reproductive initiation; (2) food availability, represented by a coarse proxy of total organic carbon (TOC) and SPOM, would influence overall reproductive effort; and (3) reproductive efforts would be similar in both shallow (5 m) and deep (20 m) populations, resulting in a source of veligers for populating the nearshore environment. This section is titled Reproduction and Population Structure of Asian clams in Lake Tahoe.

To investigate growth of Asian clam in Lake Tahoe, we carried out a one-year *in situ* field experiment to compare the relative growth and survival rates of Asian clams at shallow (5 m) and deep (50 m) depths. This section is titled Asian clam shell production in shallow and deep water depths.

In order to understand transport mechanisms of Asian clams between deep (25 m) and shallow (5 m) regions, we monitored the pelagic community to quantify the abundance of Asian clam juveniles that may be transported within the water column. In addition, we carried out a study investigating the passive hydrologic transport as a function of water column currents and vertical thermal structure of Asian clam in the near-shore region of Lake Tahoe using field- and laboratory-based techniques. This section is titled Asian clam transport between shallow and deep zones.

A. Reproduction and Population Structure of Asian clams in Lake Tahoe¹

Methods

Four sites with established Asian clam populations were sampled: Lakeside, Marla Bay, and Nevada Beach each at a depth of 5 m and at a depth of 20 m (hereafter referred to as LS5, MB5, NV5, and NV20). 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. 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), determined by the Wentworth particle size distribution (Brakensiek et al. 1979, Gordon et al. 1992). Marla Bay is approximately 1.5 km wide with a maximum depth of 5 m before a steep drop toward 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 a 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.

Asian clams were collected 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 among the measurements to describe seasonal patterns in temperature (Denton, unpubl. data). Total organic carbon (TOC) in the overlying lake water was analyzed with an elemental analyzer (Shimadzu TNPC-4110C). SPOM (suspended particulate organic matter) 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 1-way ANOVA for temperature and TOC for site and date independently, and 2-way ANOVA analyzed SPOM by site by date, and a pairwise difference was determined with Tukey's HSD post hoc analysis.

¹ Portions of this work have been published in the peer reviewed literature. Please see: Denton, M., S. Chandra, M. E. Wittmann, J. E. Reuter, and J. G. Baguley. 2012. Reproduction and population structure of *Corbicula fluminea* in an oligotrophic, subalpine Lake. J. Shellfish Res 31(1):145-152.

All Asian clam samples were held in 18-L field buckets with sediment and lake water, stored at 10 °C, and processed in the laboratory within 24 h of collection. Samples were elutriated in the laboratory and sieved through 90-µm mesh to retain the smallest individual clams and to calculate abundance (measured as clams per square meter) for each sampling period and location. All grabs were combined into a single 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 40 clams (shell length, 13 ± 1 mm) per site across sampling dates. Clams between 11 mm and 19 mm were dissected occasionally when the target size class was not met completely. 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). Because these data were determined to be distributed non-normally (Anderson-Darling normality test), they were log₁₀ transformed and analyzed by a 2-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 using SAS 9.2 (SAS Institute, Inc., Cary, NC) and Minitab 15.1 (Minitab, Inc., State College, PA).

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). 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 among sites ($P = 0.549$). Mean concentrations ($\pm$ SE) 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 SPOM ($P < 0.0001$). A Tukey post hoc analysis determined that LS5 (6.8 ± 3.3 mg/mg) and NV20 (6.1 ± 4.4 mg/mg) had greater concentrations of SPOM than MB5 (4.6 ± 2.9 mg/mg) and NV5 (3.6 ± 1.1 mg/mg) during the season (Figure 2).

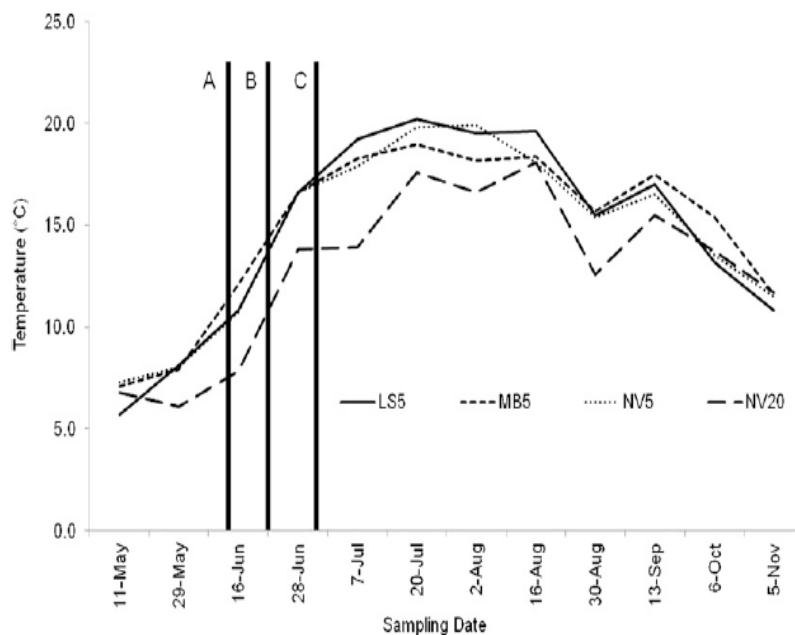


Figure 1. Temperatures at the water-substrate interface by sampling date and site. Documented threshold temperatures required for reproduction are noted with the vertical bars indicating when those temperatures were recorded at respective field sites in Lake Tahoe. A, the onset of spermatogenesis, B, fertilization occurs, C, initial release of veligers.

Reproductive Activity

A total of 1,875 clams were dissected to determine their reproductive status and activity. The mean shell length at each site during the entire sampling period was $13.68 \pm 1.3\text{mm}$ (LS5, $n=461$), $13.33 \pm 0.7\text{ mm}$ (MB5, $n = 479$), $13.91 \pm 1.0\text{ mm}$ (NV5, $n = 478$), and $13.74 \pm 1.2\text{ mm}$ (NV20, $n = 457$). Eggs were present in the demibranches on all sampling dates from May 11 to November 5 (Figure 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 were in high abundance on August 30 and September 13. These sampling dates were +27, +41, and +55 days after the critical temperature threshold needed to initiate a spawning of brooding veligers (King et al. 1986, Kraemer and Galloway 1986). There was a significant site-by-date interaction of brooding veliger abundance, 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 abundance at shallow locations was significantly greater than NV20 ($P < 0.0001$). Across all 3 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) and 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 of 3 ± 1 veligers across 4 clams, with 196 clams having no veligers present in samples during the same period.

Population Structure

Overall population abundance was significantly different by site over all sampling dates ($P = 0.0013$), with abundance at NV20 ($2,541 \pm 291$ clams/m²) significantly greater than the shallow sites (Figure 4). The distribution of Asian clam was heterogeneous 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 per date), MB5 and NV5 requiring fewer but nearly equal numbers of grabs (7 ± 2 and 7 ± 1 grabs per date, respectively), and NV20 requiring the fewest (5 ± 2 grabs per date, $n = 12$; SD is noted because SE values were less than 1).

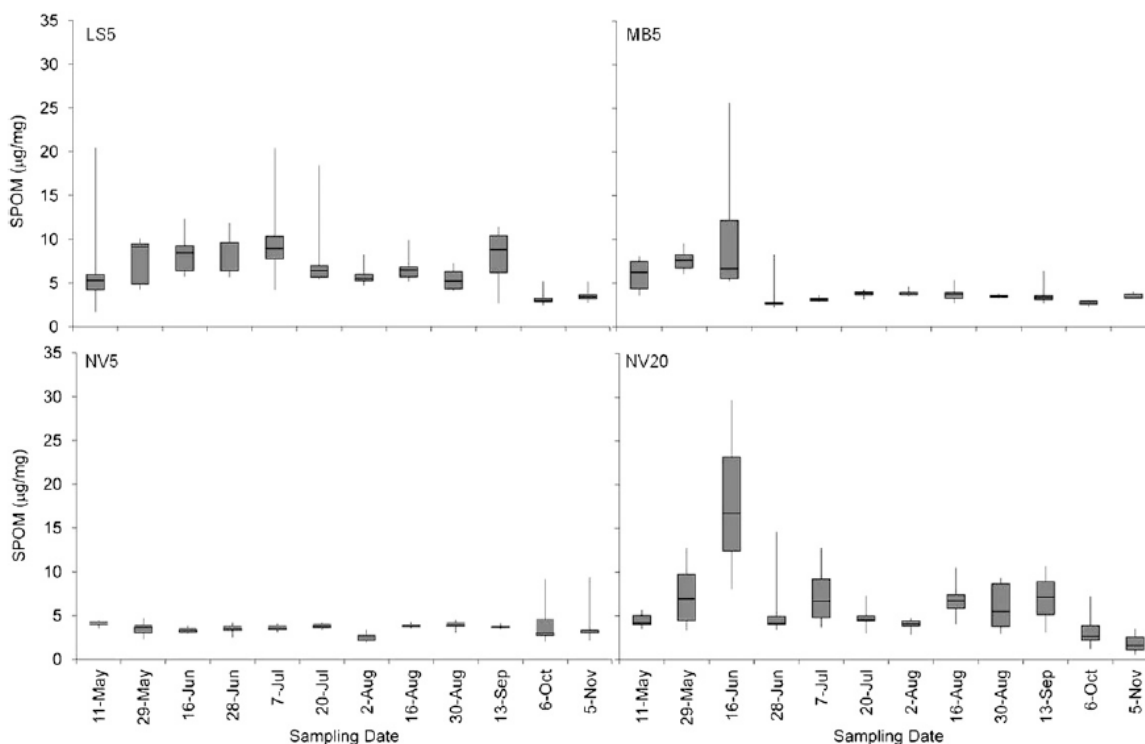


Figure 2. Sediment Particulate Organic Material (SPOM; μ g SPOM/mg sediment) within 2 cm of the sediment surface.

Size class distribution of Asian clam by site suggests differences in population structure (Figure 4). 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 mm and 17 mm represented a majority of the populations in MB5, with clams occasionally reaching a shell length of 22 mm. 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 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.

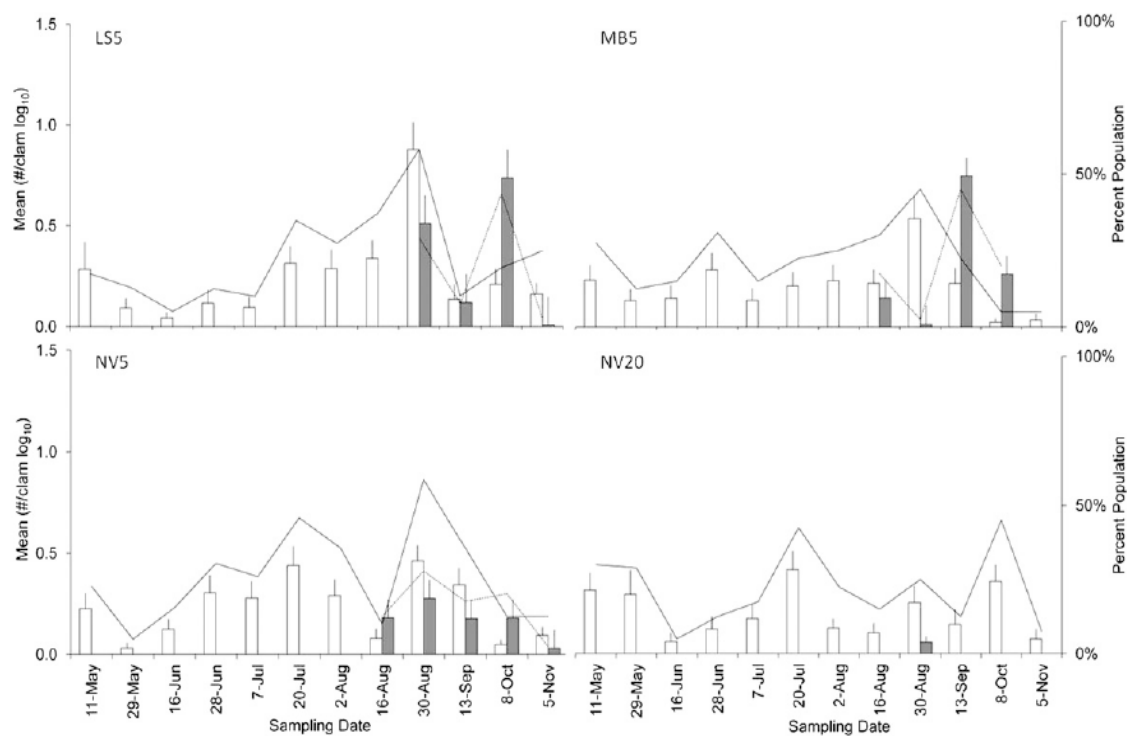


Figure 3. Mean values ($\pm$ SE) for eggs (no shading) and veligers (shading), and percentage of populations with eggs (solid line) and veligers (dotted line).

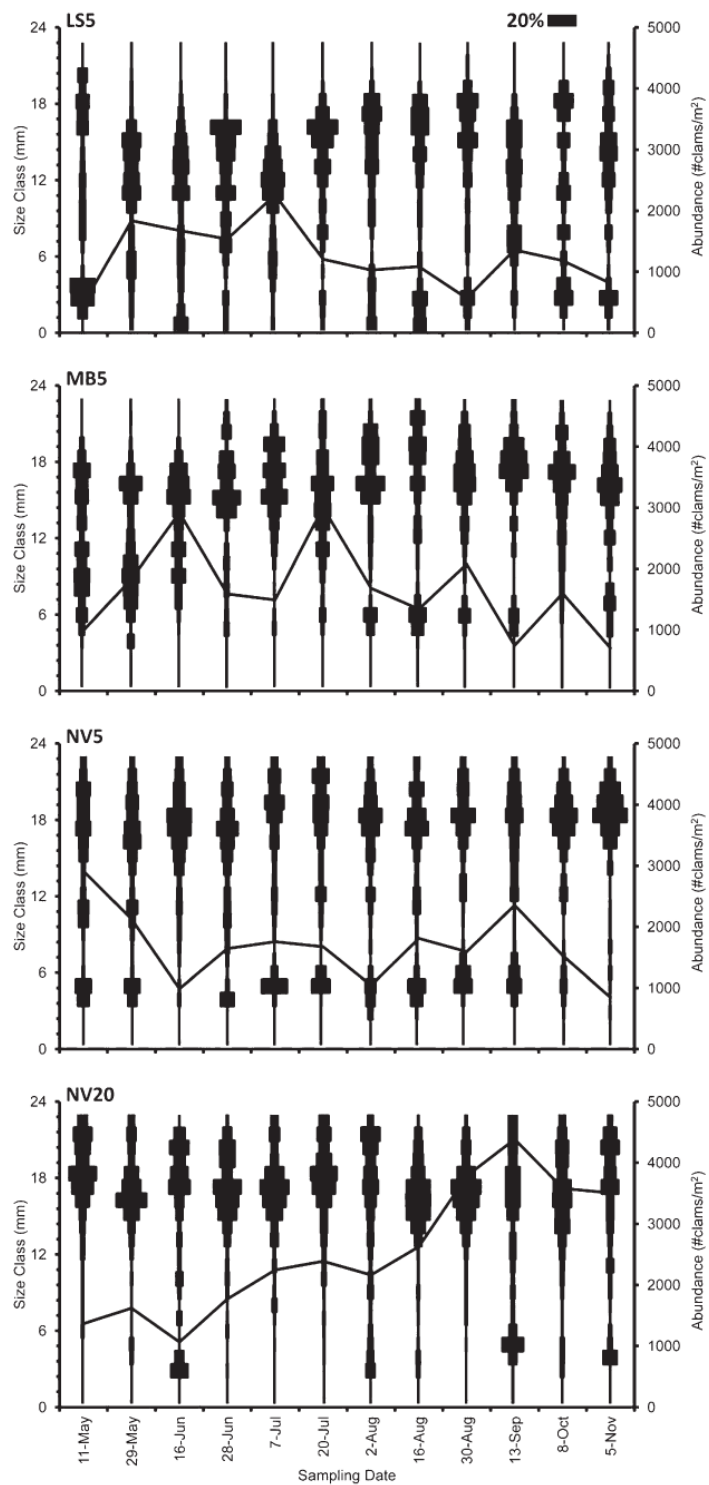


Figure 4. Population structure of sampling sites across dates expressed as a percentage on the primary vertical axis. Abundance (number of clams per square meter) is represented by a line on the secondary vertical axis.

Discussion

Asian clam in Lake Tahoe are univoltine (i.e., have one spawning event per year), with reproduction in the late summer and low abundance of brooding veligers. There was a 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 independently of temperature (Kraemer and Galloway 1986), we expected eggs to be present during all dissections. Because spermatogenesis and fertilization require minimum temperature thresholds to be met (10°C and 14°C, respectively), brooding veligers should not have been present until temperatures were at least 14 C for 10 consecutive degree-days (Kraemer and Galloway 1986). Temperatures across all shallow sampling sites reached this threshold by July 20, with a mean of $19.7 \pm 0.4^\circ\text{C}$. A typical cycle of initial fertilization, larval maturity, to release of veligers is 6–14 days (Kraemer and Galloway 1986), with release occurring at least 16.0°C.

In other systems, Asian clam 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 resulting from temperature increases greater than 27.5°C (Aldridge and McMahon 1978, Mouthon 2001a). When spawning did occur in Lake Tahoe after a 4-week delay, the overall abundance of veligers observed in the shallow sites (10 ± 2 veligers per clam) was much lower than the veliger abundance observed in more productive reservoir or riverine ecosystems. In these ecosystems, veliger reproductive efforts range from 588 to 735/clams per day in spring and fall (Aldridge and McMahon 1978) and 1,800 to 1,200/clams 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 (Coats et al. 2006). In the future, this increase in water temperatures may expand the spawning potential of Asian clam to an increased number of veligers, earlier initiation of reproductive development, and a longer fertilization and release period (Wittmann et al. 2013). It is unlikely, however, that a bivoltine spawning event will occur in Lake Tahoe because current temperature warming forecasts for the nearshore do not suggest an increase in temperature that would stop and reinstate 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 Asian clam (Weitere et al. 2009).

In other systems, food availability has been observed to be a significant contributor to spawning events of Asian clam to meet the energetic demand of brooding (Mouthon 2001b). Asian clam 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). Although other studies reported chlorophyll *a* concentrations in systems with successful Asian clam populations ranging from 3 to 100 mg/L (Cohen et al. 1984, Mouthon 2001b, Mouthon and Parghentanian 2004), chlorophyll *a* concentrations in Lake Tahoe range from 0.5–1.5 mg/L (TERC 2010). These low concentrations could limit Asian clam growth and could reduce nourishment for brooding embryos. TOC at the water–substrate interface suggests similarly low food concentrations from this source. Although there were significant site-by-date differences for SPOM, overall reproductive effort was not significantly different among the sites, suggesting that variable concentrations of SPOM and TOC are not predictors of the fecundity of Asian clam in Lake Tahoe. Further investigation of food availability—in particular, food quality—is needed to understand its role in Lake Tahoe clam reproductive effort with respect to water temperature.

In determining the similarities, if any, of reproductive effort between the shallow (5 m)- and deep (20 m)-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 veligers seen in four clams. However, this site has the highest overall abundance among sites, with significant increases in observed abundance in the late summer. Population size structure at this site indicated an increase in abundance is toward the larger size classes (>13 mm) rather than recruitment of juveniles (<4 mm; Fig. 4). This suggests that deep-water (20 m) populations are not reproductively active, and therefore are potentially a sink of clams rather than a source. If this is the case, clams would be transported from the shallow depths to these deeper populations.

Movement of clams to this deeper region may occur in two ways. One documented means of dispersal for Asian clam is via floatation. Prezant and Chalermwat (1984) found that clams up to 14 mm, when exposed to a current of 10–20 cm/sec, would push off the substrate with their foot while extending both siphons. They excrete a long mucus thread that allows them to be lifted and carried in the water column until the current subsides. Another possibility is that wind-driven waves or convectively driven currents 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. In addition, 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. These current magnitudes are at the extreme upper end of currents

observed in Lake Tahoe. With an approximate horizontal distance of 60 m between the 5-m and 20-m depth at Nevada Beach, an estimated slope of 18 degrees, and documented populations of clams at 10 m and 15 m (unpublished samplings for 2008 and 2009), it is conceivable that lake currents could transport both juvenile dispersers and adult clams along the slope to deeper depths.

Throughout the 2010 sampling period, 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-shape size class population structure, with less than 4 mm as the dominating the population (Hall 1984, Mouthon and Parghentanian 2004), 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 Asian clam for water temperatures between 0° C and 13 °C. Given that newly released veligers are 0.2 mm, and depending on the previous season's release period, it is conceivable that the 2009 spawn would appear as a new size class the following midsummer 2010. Temperatures in this study were less than 13 °C by November; therefore, juveniles spawned in the 2010 season would likely not experience shell growth until May 2011 or June 2011.

B. Asian clam shell production in shallow and deep water depths

Methods

To compare survival, mortality and growth of Asian clams in shallow and deep depths, an *in situ* growth chamber experiment was carried out in Marla Bay and Nevada Beach in Lake Tahoe from June 2010 through May 2011. At each location, one chamber each was placed on the lake bottom in the shallow nearshore zone at 5 m water depth and in the deepwater zone at 50 m water depth. Specific locations of the Asian clam growth chambers are provided (Table 1). The chamber dimensions were as follows: base diameter = 1.06 m, cylinder height = 0.95 m and the sides of the chamber were composed of ¼ inch mesh to permit the flow of lake water and to prevent predation from crayfish or other fish (Figure 5). Upon placement of the chamber, the bottom 4 – 6 inches was filled with benthic materials (sediments, algae, macroinvertebrates) collected from the area immediately adjacent to the chamber to simulate the surrounding benthic habitat.

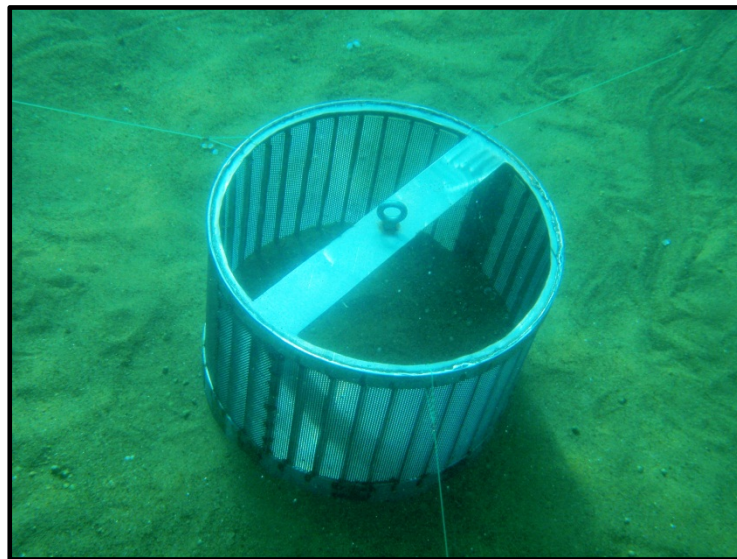


Figure 5. View from above of Asian clam growth chamber placed on the lake bottom at 5 m depth. Base diameter = 1.06 m, cylinder height = 0.95 m.

At the onset of the experiment (June 16, 2010), Asian clams ($n = 40$) ranging in size from 4 to 19 mm were marked with unique identifiers and placed in each chamber. Shell length, or, the greatest anteroposterior dimension across the valves were measured with digital calipers to the nearest 0.01 mm. Every 1 – 4 months until May 2011 the chambers were recovered from the lake bottom, marked

clams were retrieved, shell length measured, and if viable, placed back into the growth chamber and returned to the lake bottom. If marked individuals were deceased, mortality was recorded.

Table 1. Location of Asian clam growth chambers in Marla Bay, NV and Nevada Beach, NV at Lake Tahoe. Growth chambers were deployed from June 2010 through May 2011.

Location	Longitude	Latitude
Marla Shallow (5 m)	38 59.429	119 57.534
Marla Deep (50 m)	38 59.526	119 57.646
Nevada Shallow (5 m)	38 58.586	119 57.204
Nevada Deep (50 m)	38 58.487	119 57.296

Results

Asian clams were grouped based on shell size class (mm): 5.0 – 7.0, 7.1 – 9.0, 9.1 – 11.0, 11.1 – 14.0, and 14+ in both the deep (50 m) and shallow (5 m) locations. Asian clam growth and mortality was sampled on five occasions including experiment initialization (6/16/10) and on 8/19/10, 10/15/10, 2/3/11 and 5/18/11 at Nevada Beach and five occasions at Marla Bay (6/20/2010, 8/20/2010, 11/8/2010, 2/3/11 and 5/18/2011). At shallow sites, mean annual shell production rates between Nevada Beach (0.0036 mm d^{-1}) and Marla Bay (0.0036 mm d^{-1}) were not significantly different from one another ($t = -0.4023$, $p = 0.34$, $df = 9$). The smallest size class grouping (5 – 7 mm) showed the greatest mean shell production rates in the shallow zones ($0.06 \pm 0.02 \text{ mm d}^{-1}$) during the summer period (Jun – Aug). Positive shell production at both sites was observed from May through early January, however shell production ceased during colder water temperature periods ($5 - 13^\circ \text{C}$) from late January through late May. There was some evidence of adsorption (negative shell production) in shallow zones, but none of the values indicated were outside the margin of error specified on caliper sets used in the field. Maximum shell production in the shallow zone occurred in the June – August period when average water temperatures ranged from $14 - 17^\circ \text{C}$. After this period, peak temperatures reached 20°C and shell production reduced dramatically—likely in response to a shift of energy toward spawning. Shallow zone populations had an average annual mortality of 64%, with 21% of individuals growing to a larger size class and 14% of individuals remaining in the same size class. In Marla Bay, 5 clams were found dead on the first

chamber recovery (8/20/10), 2 on 11/8/10, 16 on 2/3/11 and 5 more on 5/18/11. At Nevada Beach, 4 clams were found dead on 8/19/10, 2 on 10/15/2010, and 11 on 2/3/11 and 6 on 5/18/11.

Mean annual shell production in the deep water chambers were significantly less than those observed in the shallow chambers. In Nevada Beach, the shell production rate for all size classes over the entire experimental period was $0.0004 (\pm \text{S.E. } 0.00021) \text{ mm d}^{-1}$ which was not significantly different from shell production rates observed in Marla Bay ($0.0005 \pm \text{S.E. } 0.00012) \text{ mm d}^{-1}$. In Marla Bay, average shell production rates for the summer period (June - August 2010) at the deep water depth were $0.0007 (\pm 0.0003) \text{ mm d}^{-1}$, $0.0006 (\pm 0.0001) \text{ mm d}^{-1}$ from August - November, 2010 and $0.0003 (\pm 0.0001) \text{ mm d}^{-1}$ from November through February 2011. As all but one clam had died prior to the May sampling, no shell production rate could be calculated. At Nevada Beach average shell production rates for the summer period (June - August 2010) at the deep water depth were $0.0001 (\pm 0.0003) \text{ mm d}^{-1}$, $0.0007 (\pm 0.0004) \text{ mm d}^{-1}$ from August - November, 2010 and $0.0003 (\pm 0.0001) \text{ mm d}^{-1}$ from November through February 2011. Figures 6 and 7 show the observed shell production rates for Nevada Beach shallow versus Nevada Beach deepwater growth chambers.

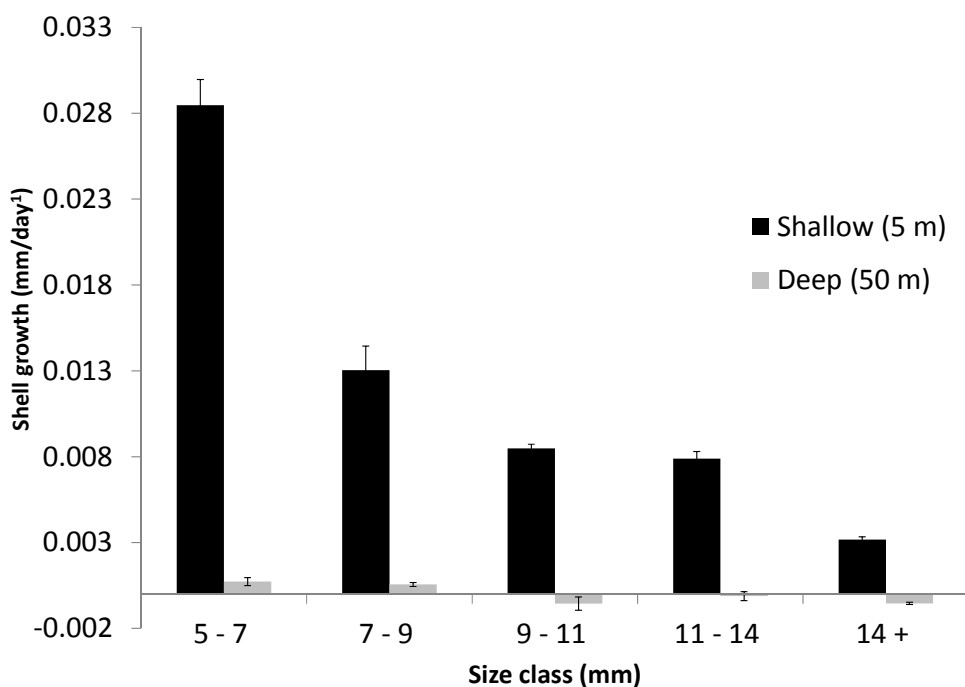


Figure 6. Asian clam summer growth at Nevada Beach at shallow (5 m) and deep (50 m) water depth from June - August 2010. One standard error indicated on each bar which represents the average shell growth per day per size class grouping.

Annual mortalities observed in the deep (50 m) growth chambers at both Marla Bay and Nevada Beach were significantly higher than those observed in shallow zones. At Marla Bay, 1 out of 40 clams survived at the end of the experimental period, and in Nevada Beach there was no survival. In Marla Bay, all clams survived the first two months (6/16 - 8/20), and only two were deceased on the 11/4/10 sampling. Seven more individuals were dead on 2/3/11 and on 5/18/2011 all but one clam had expired. In Nevada Beach, 6 clams were found dead on 8/20/2010, 3 dead on 11/4/10 and on the final sampling (5/18/2011) all clams were dead.

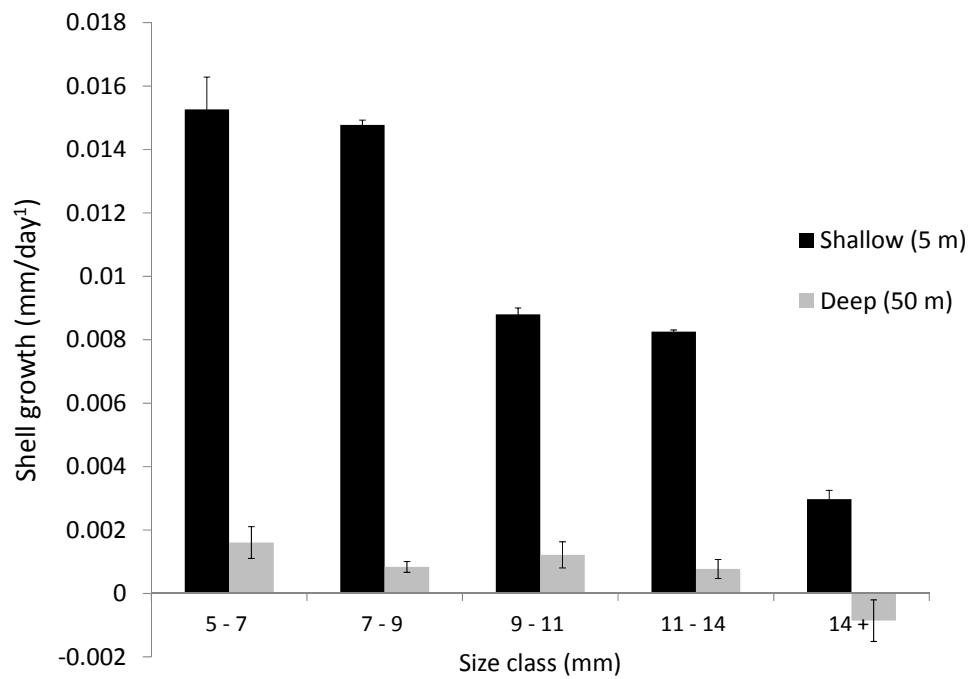


Figure7. Asian clam late summer and early autumnal growth at Nevada Beach at shallow (5 m) and deep (50 m) water depth from September - October 2010. One standard error indicated on each bar which represents the average shell growth per day per size class grouping.

Discussion

As expected, Asian clam survival and shell production rates are higher at the shallow depth zone (5 m) than in the deeper depth zone (50 m). Possible mechanisms for these observed differences are likely due to differences in temperature, productivity and food availability. Shell production was positive, but very reduced for individuals at the 50 m depth zone, and in some cases showed a significant level of adsorption (e.g., shell dissolution or shrinkage in length). These observations of greater shell production rates and lesser mortality rates in the warmer summer and autumnal periods suggest that physical and

biological drivers necessary for Asian clam survival and growth are adequate, at that time. The nearly 100% mortality observed at the 50 m depth for both Marla Bay and Nevada Beach experimental populations suggest that the winter period significantly impacts not only Asian clam growth, but also survival. Further research is necessary to understand the mechanisms behind limitations to the population during this period.

Asian clams have been repeatedly observed with densities ranging from 46 - 699 clams/m² at 40 - 70 m and greater water depths in Lake Tahoe at Marla Bay and Nevada Beach (Wittmann et al. 2013). This experiment has shown that while Asian clam populations are capable of survival of growth at water depths outside of the immediate nearshore zone (e.g., water depths ranging from 20 - 50 m), the potential for high density populations in this region is likely low, given the high rates of mortality observed. Asian clams are fecund at 20 m water depth in Nevada Beach and Marla Bay (see previous section), suggesting that reproduction is possible in regions greater than 5 m water depth, where highest abundances are observed. Temperatures required for Asian clam reproduction (as reported in the peer-reviewed literature) are not observed in Lake Tahoe at water depths that are greater than 40 m. This suggests that the possibility for Asian clam presence and persistence at deeper depths is potentially supplemented by advective transport of adults or juveniles produced at shallower depth zones (see next section). Also, because TOC/SPOM were unexpectedly not significant explanatory variables for Asian clam growth or reproduction in Lake Tahoe, further investigation of the relationship between Asian clams and food availability in Lake Tahoe will help to clarify the relationship between depth limitations of these populations. Finally, increased understanding of the sensitivity of Asian clam reproduction and growth to temperature will clarify some of the observations of Asian clam presence at depth in Lake Tahoe and inform the potential for future increases in population densities within the lake. For example, increasing water column temperatures as a result of global climate change may contribute to the range expansion of reproducing populations of Asian clams that previously were limited to shallower depth zones (Wittmann et al. 2013).

C. Asian clam transport between shallow and deep zones

Introduction

Since its introduction in Lake Tahoe, Asian clam population has spread to several disparate locations within the lake (Forrest et al. 2012) with population densities of greater than 5000 individuals m⁻² (Wittmann et al. 2012b). Asian clam disperse through several mechanisms: (1) pediveliger water column dispersal during their larval stage (Williams and McMahon 1986a, 1986b; Jennings and Hunt 2009); (2) adult generation of viscous-mucous threads through their exhalant siphon, which act as drag lines in the water column motion (Prezant and Chalermwat 1984); (3) anthropogenic and animal based transport vectors (McMahon 1999); and, (4) passive hydraulic transport of individuals (i.e., entrainment along the lakebed; Williams and McMahon 1986a, 1989). While pediveliger dispersal is known to be a significant transport mechanism for population expansion (McMahon 1999), it has been hypothesized that passive transport will potentially play an important role in this system.

While Asian clam individuals spend much of their life burrowed into the substrate at depths up to tens of centimeters (McMahon and Wilson 1981), Williams and McMahon (1989) showed that juvenile and adult individuals migrate to the substrate surface when exposed to environmental stressors. Examples of such stressors include low water temperatures (Johnson and McMahon 1991) or lack of oxygen (Johnson and McMahon 1998; Williams and McMahon 1989; Wittmann et al. 2012b). While on the surface, the latter three transport mechanisms will influence adult individuals who would be otherwise protected. Recent studies of population demography in Lake Tahoe have shown significant deepwater populations at 20m water depth (Denton et al. 2012) suggesting that passive hydraulic transport is a potential transport mechanism for Asian clam in Lake Tahoe. This non-diffusive transport could result from entrainment of individuals through significant surface forcing events.

In contrast to field-based studies where substrate properties and water column flow characteristics can vary significantly, flume experiments offer a tightly controlled alternative. While flume experiments have been used to examine bed shear entrainment of other bivalve species (e.g., Olivera and Wood 1997; de Montaudouin et al. 2003; Jennings and Hunt 2009), to the knowledge of the authors, no such studies have been performed on juvenile and adult Asian clam. Research in this field could address questions, amongst others, of the critical flow velocity required for passive transport, behavior of an individual being transported, and distances individuals are transported downstream with varying benthic conditions (e.g., Kappes et al. 2012). This research would be applicable to this particular

ecosystem but could be eventually expanded to other bivalve species that burrow, both native and invasive.

This work details a two-part study investigating the passive hydrologic transport of Asian clam in the near-shore region of Lake Tahoe using field- and laboratory-based techniques. The next section describes the study site within the lake, field instrumentation and laboratory methods. Observations of water column currents and vertical thermal structure from September 2010 to March 2011 are subsequently presented. Currents of similar magnitude observed in the field were then established in a flume setting² and transport of individuals of all size classes from 5 – 24 mm were measured. The results from this experiment positively infer that the observed currents through the fall and winter months are a potentially important transport mechanism within the lake.

Methods

Site Description

Field measurements of water temperature and velocities were made at the 25 m and 50 m isobaths at Nevada Beach (Figure 8 – star) to examine the potential for passive downslope clam transport resulting from water currents. This site was chosen as it had an established population of Asian clam. In addition, the position of this site on the terminus of the south shore shelf break is ideal for capturing mixing events coming off the south shore near-shore region. Meteorological measurements were made at Timber Cove (Figure 8 – square) to determine surface forcing acting on the lake surface at the field site. The closest measurements of near bed velocity profiles to the field site were made at the entrance to Emerald Bay (Figure 8 – Insert).

² Per the original proposal, field measurements of Asian clam juveniles through plankton sampling was intended to provide information about water column based transport of individuals. On eight separate sampling occasions during Asian clam reproductive period (June - September 2010), plankton tows were conducted from 5 - 60 m sampling depths at Marla Bay, Nevada Beach and Glenbrook (control site). Only one Asian clam veliger was recovered through these samplings. As a result, we replaced field experimentation of juvenile transport to a laboratory based setting, using the flume experiment described herein. Plankton tow results are provided in the Appendix.

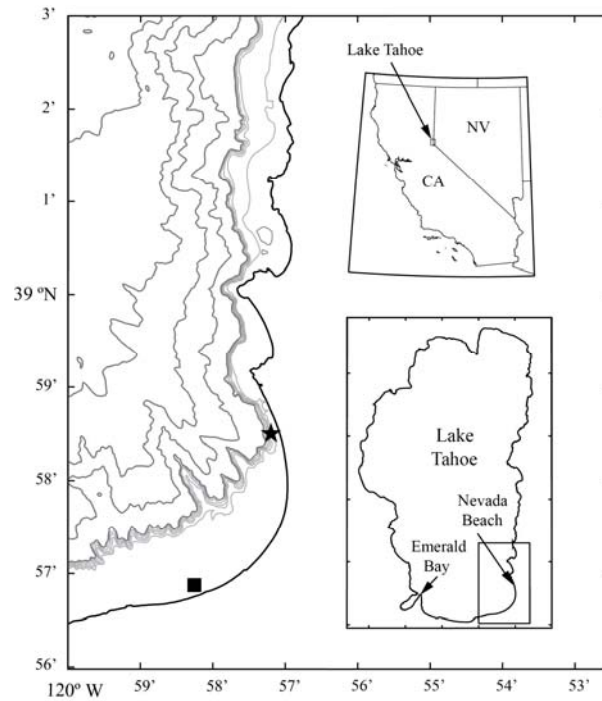


Figure 8. Location map of Lake Tahoe its relative position along the California / Nevada border as shown (see inset). Areas of *C. fluminea* populations along the southeast portion of the lake (see inset – box) and Emerald Bay as indicated. Position of instrument moorings located at Nevada Beach (star) with 10m contours down to 50m depth (pale gray) and 100m contours beyond (dark grey). Meteorological measurements were made at a station in Timber Cove (square).

Field Instrumentation

The thermistor chain at the 25 m isobath consisted of a combination of fifteen RBR TR-1050 and TR-1060 single channel temperature loggers (resolution and accuracy of 0.002 °C and 5×10^{-5} °C). These loggers were placed at 0.5 m – 1.5 m intervals from 1 m – 15 m height above the lakebed. Ten similar loggers were deployed on the thermistor chain located at the 50 m isobath with similar spacing from 3 m – 14 m height above the lakebed. The relative additional use of sensors at the 25 m isobath was to help resolve any generated shallow flows.

Current velocities at the 25 m isobath were measured with an upward looking RDI-1200 kHz ADCP Workhorse Monitor (velocity resolution of 0.1 cm s⁻¹). The selected bin size was 1 m and the averaging interval was 15 minutes. At the given settings, measurements were expected to the surface; however, as a result of cooler temperatures and the high water clarity typical of Lake Tahoe, correlation fell below threshold at 10–15 m above the lakebed. An upward looking RDI-600 kHz Workhorse Monitor (same

velocity resolution and user settings) was installed at the deeper mooring. Measurements were expected to the surface here as well but, for the same reasons, were only made to heights of 35–40 m above the lakebed. Although this limitation was unexpected, both ADCPs were able to resolve near bottom flows, the focus of the current study. In addition to these ADCP moorings, water velocities were also measured from 0.1–1.2m above the lakebed at 0.02m bins from 08 February 2012 – 16 April 2012 using a Nortek Aquadopp HR profiling Acoustic Doppler Velocimeter (ADV). These velocity measurements were made in ~ 4.5m of water and were averaged over a 10 min interval. Although this secondary study was conducted at a different location, the substrates had similar grain size distributions (unpublished data) and so were hypothesized to be directly comparable.

Water column properties and surface forcing were also monitored during this period. Vertical conductivity-temperature-depth (CTD) profiles were collected on a monthly basis at two stations at the north end of the lake with a Seabird Electronics SBE19*plus* (temperature resolution and accuracy of $< 0.0001^{\circ}\text{C}$ and $\pm 0.005^{\circ}\text{C}$). Meteorological data (i.e., wind speed and direction, air temperature, relative humidity, and net shortwave and longwave radiation) are measured at several stations around the lake at 10 min sampling intervals. The nearest meteorological station to the study site is located in Timber Cove ~ 4 km to the south (Figure 8 – square).

Experimental Instrumentation and Setup

The hydraulic flume used in this experiment consisted of a holding reservoir, flume body, and substrate bed (Figure 9). The approximate volume of the reservoir was $\sim 0.175 \text{ m}^3$, and was filled with freshly collected water from Lake Tahoe daily during experimentation. Dimensions of the flume body were 0.30m x 0.15m x 2m in depth, width and length respectively (before modification). In addition to the typical baffles used in the inflow, three flow controls were placed across the width of the flume (Figure 9; vertical dashed lines). Two flow controls (0.14m tall) were used to hold sediment were placed at 0.29m and 1.32m downstream of the inflow that, given their thickness, yielded an effective sediment substrate length of 1.24m. The third, higher (0.20m tall) flow control was placed at 1.46m downstream of the inflow to keep clams from being carried into the outflow and to maintain a minimum water level in order for the Acoustic Doppler Velocimeter (ADV) to function properly at the middle of the substrate bed (Figure 9).

A SonTek ADV was used to measure horizontal velocities in the flume at a point ~0.90m downstream of the inflow. During the experiments, individual clams were placed directly underneath the ADV to

measure flows at that point in the water column. As configured, the ADV had a sample rate of 25 Hz and a velocity range scale of $\pm 10 \text{ cm s}^{-1}$ allowing velocities of $\pm 60 \text{ cm s}^{-1}$ to be estimated.

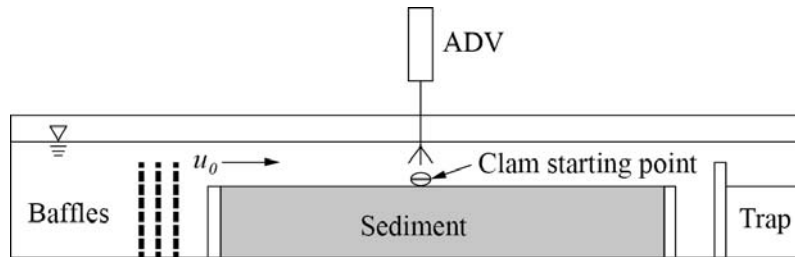


Figure 9. Illustration of the recirculating flume used in this study with the main component, including the reservoir, flume body and substrate bed, indicated. Flow controls were added to prevent sediment and clam transport out of the flume.

Sediment (0.026 m^3) collected from Nevada Beach (Figure 8 – Insert) was used to fill the sediment bed (Figure 9). Sediments were rinsed with tap water to prevent reduced visibility in the water due to entrained fine particles and organic material. Temperature control in the experimental flume was difficult due to a short recirculation time, pressure build up in the inlet hose when the flow valve was restricted, and heat conducted from the pump housing. Even with the addition of bags of ice in the flume reservoir (Figure 9), the combined effect of these three factors limited the ability to maintain the water temperature at the 18°C ($\pm 1^\circ\text{C}$) set point during the experimental runs.

In addition to the flume supply, a small aquarium was used to maintain a live stock of clams during the experiments. Clams were collected from Lake Tahoe three times over the course of the study, and no single batch of clams was kept or used for more than 7 days from the time of extraction before being discarded. Due to the ability of Asian clam to filter large volumes of water in relatively short periods of time ($0.003\text{--}0.013 \text{ m}^3 \text{ clam}^{-1} \text{ h}^{-1}$ at temperatures between $16\text{--}30^\circ\text{C}$; Foe and Knight 1986) it was assumed that such a large group of clams would exhaust their resources in the aquarium within 24 hours. Under no flow conditions, fresh individuals did attempt to burrow but they increasingly remained on the surface as they became stressed over the days.

Experimental Design

In each experimental run, two clams were placed in the flume side-by-side directly under ADV antennae before water circulation began. Almost immediately, flow would become constant and the distance that

individuals were displaced were recorded until they stopped moving for more than 5 minutes, or began to burrow, as they would no longer be transported. Generally, individuals would attempt to burrow while being transported; however, once movement stopped (i.e., lodged in the sediment grains), they would begin to burrow. The periodic displacement of individuals, in a manner analogous to particle saltation, was recorded for each interval of downstream movement the clam underwent (i.e., if the clam moved 10 cm, stopped for a moment, and then traveled 5 cm more, two values of transported distance would be recorded with little to no lateral movement observed). At this time, the experiment was stopped and reset with different individuals ranging 5–24 mm in shell length. In total, approximately 240 individuals were tested in this manner.

Under uniform flow conditions, clams were hypothesized to be continuously transported downstream. However, it was observed in this experiment that once individuals were arrested in the substrate, they would often begin burrowing into the sediment bed. The initiation of the burrowing rendered all size classes clams stationary under the range of tested flow conditions with the exception of two individuals ~7 mm in shell length. For the purposes of this study, the shape of an individual clam was defined as a function of its length, L , height, H , and width, W . While L was recorded in this study for each clam, W and H were not and had to be estimated based on results from other studies including Lake Tahoe. Measurements made on 3425 individuals taken from Marla Bay determined the ratio of $L:W$ to be 1.21 ± 0.06 (unpublished data), and a ratio of $L:H$ of 1.65 was taken from Araujo et al. (1993) as their measured values of $L:W$ were similar to the values reported here.

In addition to observations of L , direct measurements were also made of shell thickness of 30 individuals ranging in size from 5–18 mm. By doing a linear regression of shell thickness to the associated dimension, the ratios were determined to be $LR = 0.004 \cdot L + 0.074$, $HR = 0.005 \cdot H + 0.145$, $WR = 0.007 \cdot W + 0.132$ and for L , H and W respectively. These ratios were then used for the calculations of shell matter volume in subsequent sections.

Results

The ADCP mooring located at the 25 m isobath collected data from 20 September 2010 – 16 December 2010 and 07 January 2011 – 29 March 2011. Time series contours of the horizontal (Figure 10a) and vertical (Figure 10b) velocities show periods of minimal flow ($< 1 \text{ cm s}^{-1}$ in the horizontal and $< 0.1 \text{ cm s}^{-1}$ in the vertical) interrupted by episodic flow events. These events reached horizontal magnitudes greater than 25 cm s^{-1} and 4 cm s^{-1} downwards in the vertical and were generally associated with flow directions

towards 280° (Figure 10c). Flow directions have been averaged over the entire depth of the water column to provide a bulk estimate of direction. Figure 10d shows the relative backscatter (i.e., the corrected acoustic backscatter) at 1 m height above the ADCP with a threshold of 70 dB (2.5 times the standard deviation) indicated with a horizontal line. Flow directions associated with these events are circled in black in Figure 4c and indicated with arrows in Figures 4a and 4b. Although not exactly orthogonal to the isobaths, the observed direction of the flow during these events is running almost directly offshore at the location of the moorings. It should be noted that the artifact in the contoured data in these figures at ~ 4 m height above the lakebed from 28 Sept 2010 – 10 Oct 2010 is likely the result of a subsurface marker buoy.

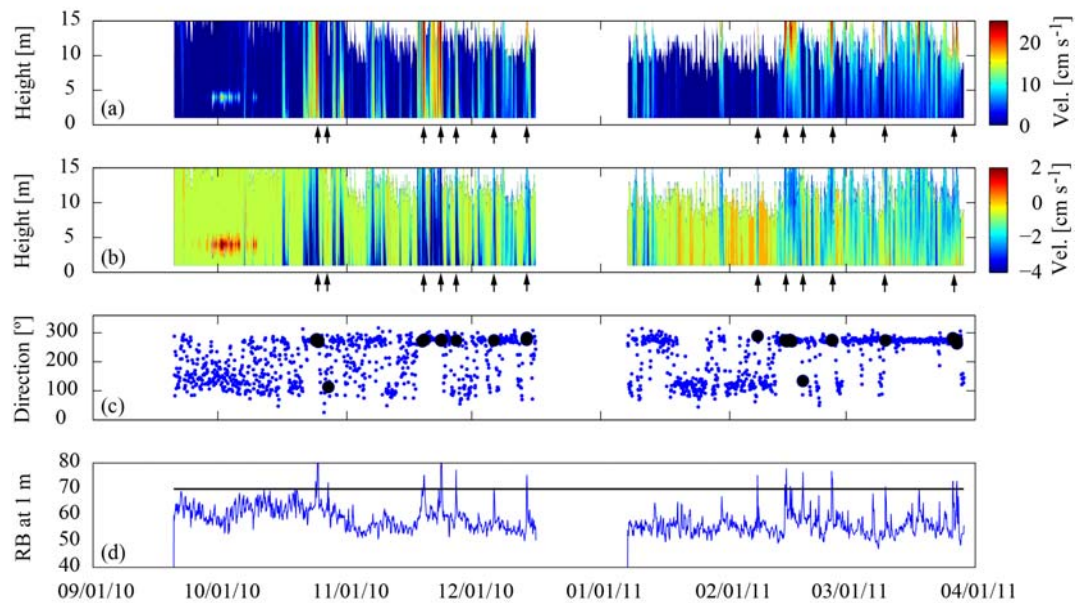


Figure 10. Time series recorded as a function of height above the 25m isobath: (a) horizontal component of velocity; (b) vertical component of velocity; (c) averaged water column flow direction; and, (d) relative backscatter measured at 1 m above the instrument with a threshold of 70 db (2.5 times the standard deviation) as indicated with a horizontal line.

The ADCP mooring located at the 50m isobath collected data from 07 January 2011 – 29 March 2011 (Figure 11). For ease of comparison, Figure 11a shows a subsample of Figure 4a for this same time period. Time series of the horizontal (Figure 11b) and vertical velocities above the 50 m isobath (Figure 11c) show similar results as Figure 10; periods of low velocities existed at similar magnitudes to those observed nearer to shore with episodic flow events. Flow events identified in Figure 10 (black arrows), are carried forward in Figure 11b and Figure 11c. Comparing these results, flow events appear to go to

the full depth of the water column with a relatively uniform flow direction of 280° (Figure 11d) in a similar fashion as the flow directions observed at the 25 m mooring. It should also be noted that there was a shift in water velocities at the 25 m isobath (Figure 10a). Unlike the fall period where flow was recorded to the lakebed, flow events in the late winter and early spring appear restricted to the upper water column. In contrast, events appear to continue going to depth at the 50m isobath during late winter and early spring.

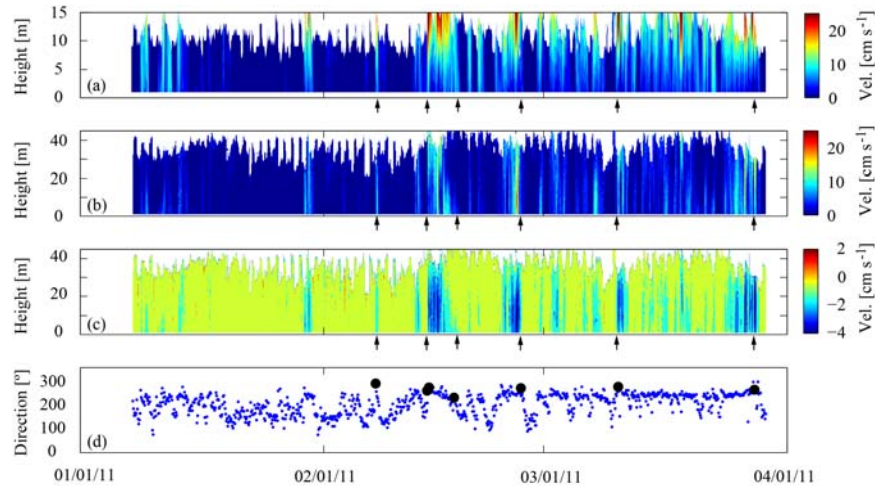


Figure 11. Time series recorded as a function of height: (a) horizontal component of velocity as a function of height above the 25m isobath; (b) horizontal component of velocity as a function of height above the 50m isobath; (c) vertical component of velocity as a function of height above the 50m isobath; and, (d) averaged water column flow direction.

To construct idealized profiles of boundary layer flow over a range of flow conditions, the measured velocity profiles of the Aquadopp HR were binned into 1 cm s^{-1} bins between $5\text{--}20 \text{ cm s}^{-1}$. These profiles were subsequently sorted by retaining those with standard deviations $<0.025 \text{ cm s}^{-1}$ and then averaging all profiles together. Figure 12 shows the profiles from each velocity bin except for the $15\text{--}16$, $18\text{--}19$ and $19\text{--}20 \text{ cm s}^{-1}$ bins whose standard deviation of the binned profile was greater than the threshold. These profiles illustrate how observed velocities are a fraction of the mean flow, u_o . The boundary layer thickness (Figure 12 – circles), defined as the height where the flow is 99% of u_o , increased as a function of the bulk velocity.

Thermistor chain moorings were also placed at the 25m and 50m isobaths although, due to equipment faults, concurrent velocity and temperature measurements were not recorded at the 50m isobath. At

the 25m isobath, measurements were made over the entire time period (Figure 13a). The thermistor chain was deployed at the onset of autumn cooling and continued through fall overturn and the weakly stratified winter thermal regime. Line plots of temperature are shown for 1.5m (blue line), 9m (green line), and 15m (red line) above the lakebed. These line plots reveal five distinct periods where the water column remains relatively unchanged: (I) stratified from 10–16 °C; (II) weakly stratified from 8–12 °C; (III) very weakly stratified from 7–8 °C; (IV) slightly inversely stratified from 5.6–6 °C (inset); and, (V) well-mixed from 4.5–5 °C. Monthly vertical profiles collected in the lake monitoring program during each of the periods showed a cooling of the water column and a deepening of the thermocline during the first three periods until the water column is relatively well mixed (Figure 13b). Periods of elevated flows (indicated with arrows; recall Figures 11a and 11b) were generally associated with a decrease in the overall temperature of the water column and more complex baroclinic responses of the system.

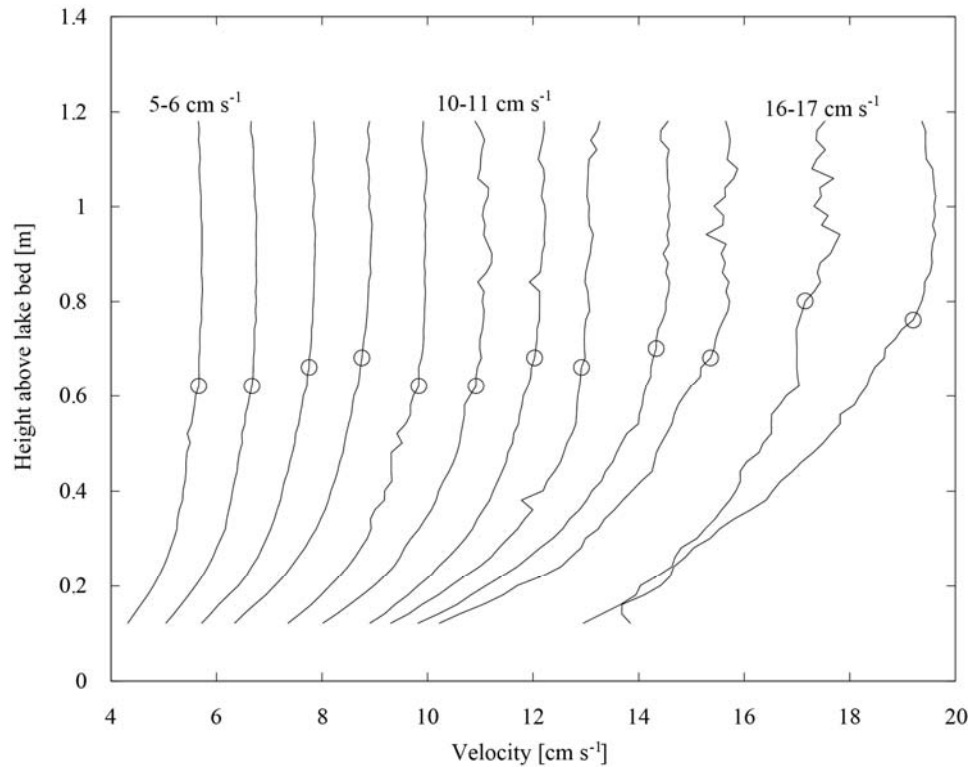


Figure 12. Averaged water velocity magnitude profiles in the boundary layer for velocity bins ranging from 5–6 cm s⁻¹ to 17–18 cm s⁻¹ with the heights of the boundary layer (circles) as indicated.

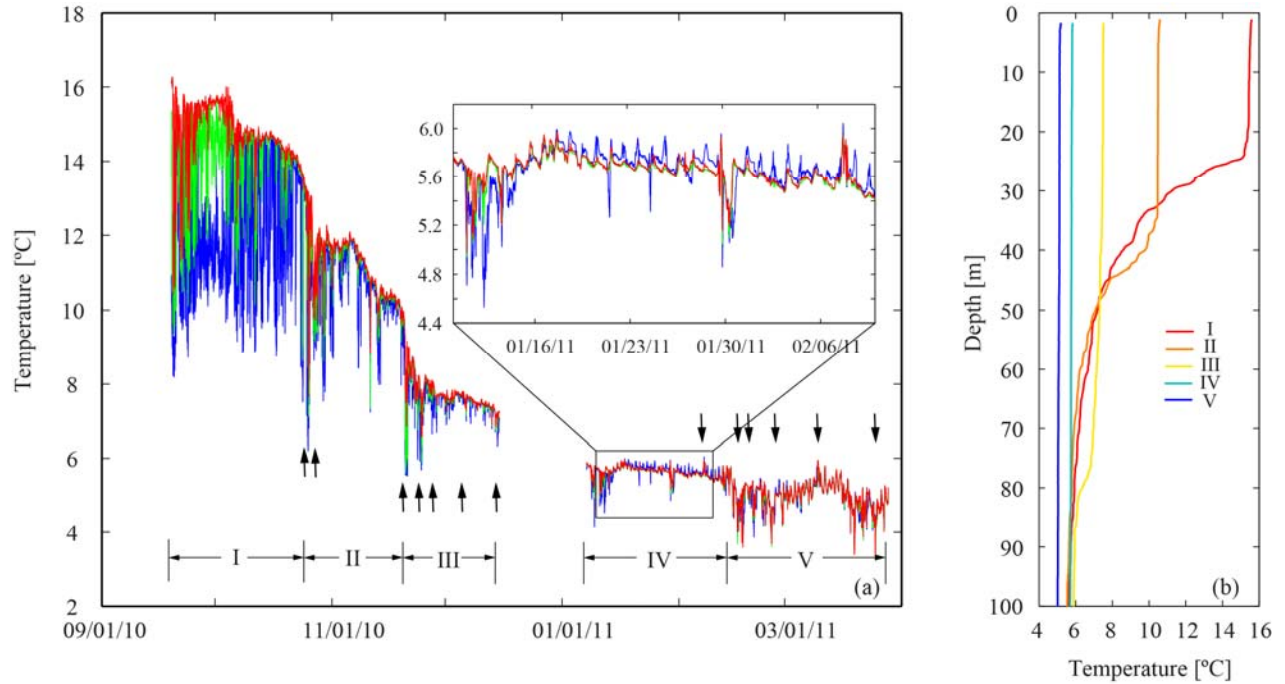


Figure 13. Vertical stratification over the study period: (a) line plots of temperature at 1.5m (blue line), 9m (green line) and 15m (red line) above the lakebed at the 25m isobath (bin averaged at 15 minute intervals), and (b) characteristic vertical temperature profiles of each of the identified periods (i.e., 27 Sep 2010, 17 Nov 2010, 12 Dec 2010, 18 Jan 2011, 04 Mar 2011). Traces of the remaining thermistors are not shown for clarity. Arrows indicate events where the acoustic backscatter increased in the ADCP profiles.

Inspection of wind directions (Figure 14a) and wind speeds (Figure 14b) measured at Timber Cove, NV show three general surface forcing conditions: 1) relatively consistent, low winds ($\sim 2 \text{ m s}^{-1}$) from the northwest ($\sim 330^\circ$); 2) episodic, moderate winds ($> 6 \text{ m s}^{-1}$) from the northeast ($\sim 230^\circ$); and, 3) episodic, elevated winds ($> 10 \text{ m s}^{-1}$) from the south ($\sim 20^\circ$). Gaps in the meteorological record were a result of instrumentation problems (e.g., 30 November 2010) and no measurements were recorded. Periods of elevated acoustic backscatter and elevated water velocities are shown with black arrows. For illustration purposes, these periods are also delineated with grey bars (Figures 14a, b). Mixing events in the water column appear qualitatively driven by winds blowing from the south, approximately parallel to shore at the field site.

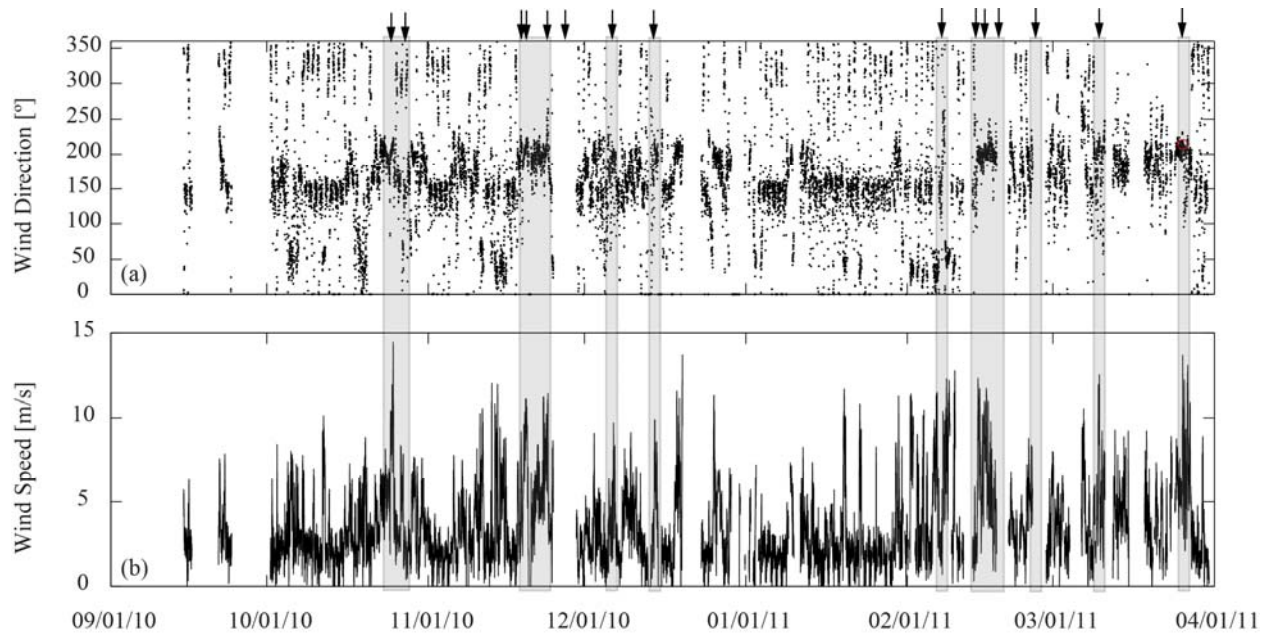


Figure 14. Bin averaged (15 min intervals) time series of: a) Source wind directions ($^{\circ}$), and b) wind speeds (m s^{-1}) measured at the meteorological station located in Timber Cove, NV. Arrows indicate events where the acoustic backscatter increased in the ADCP profiles and the grey bars delineate those periods in the profiles.

Displacement of individual clams in the flume experiment exhibited two patterns: 1) shells greater than a critical size at a given velocity were displaced less than 2 cm; and, 2) below this critical size, there was a roughly linear relationship between the shell size and distance traveled downstream (Figure 15). At each velocity range, a critical shell size was determined by finding where the largest individual (in terms of shell length) undergoing physical transport. For the velocity ranges of $10\text{--}15 \text{ cm s}^{-1}$, $15\text{--}20 \text{ cm s}^{-1}$, $20\text{--}22.5 \text{ cm s}^{-1}$, and $22.5\text{--}25 \text{ cm s}^{-1}$, critical shell lengths of 7.1, 8.3, 13.5 and 15.1 mm were determined, respectively (Figure 15 – arrows).

Discussion

Water velocities that supported the transport of clams in the flume experiment ($\sim 25 \text{ cm s}^{-1}$) were similar to those observed through fall cooling and winter stratification in the Lake, suggesting the potential for physical clam transport. Discussion in the following section will focus on 1) flow conditions required for physical clam transport, and 2) variations in water column stratification, which may inhibit physical clam transport.

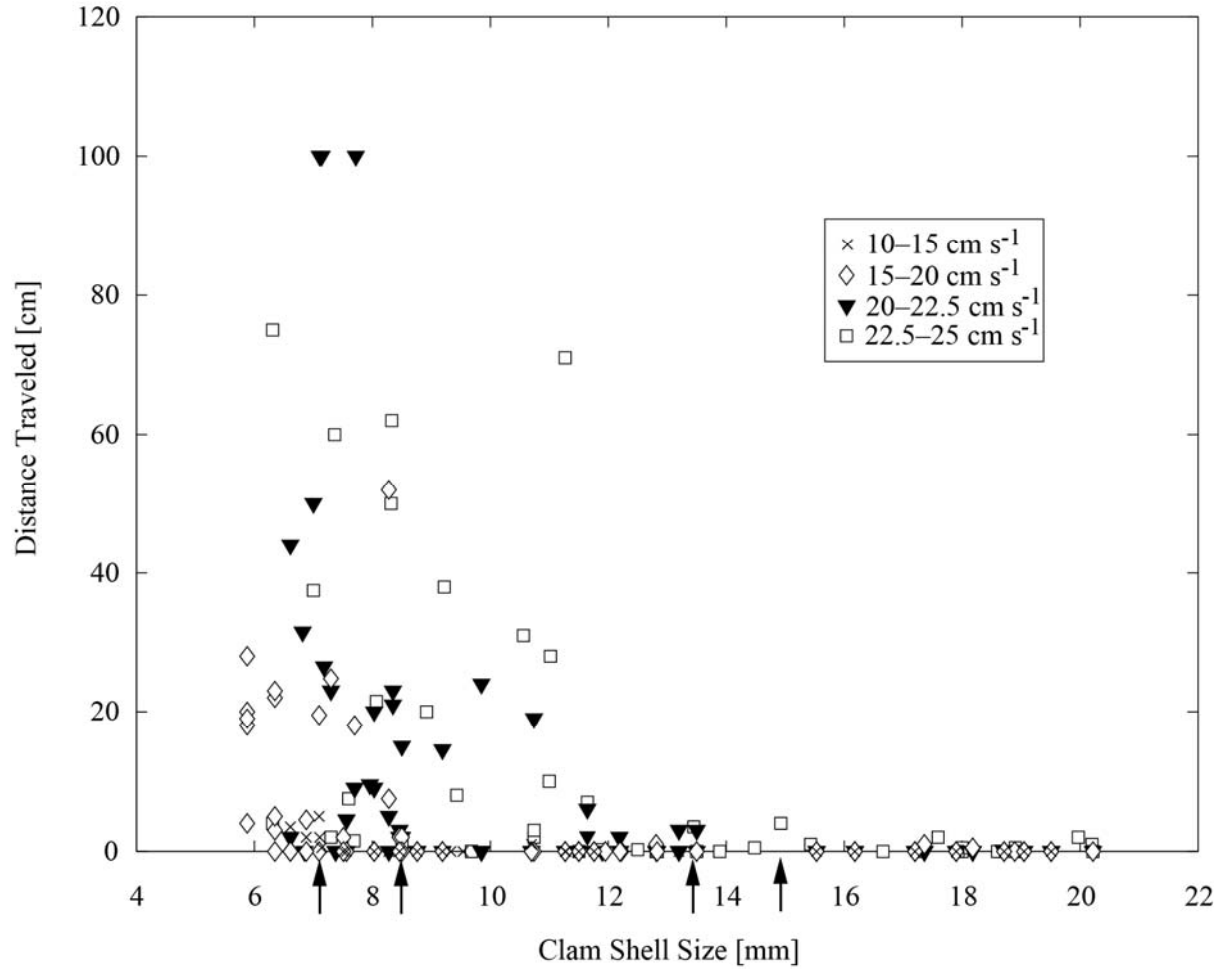


Figure 15. Experimental results of distance traveled as function of clam shell size and sorted into four velocity classes: 10–15 cm s^{-1} (black x), 15–20 cm s^{-1} (diamonds), 20–22.5 cm s^{-1} (filled inverted triangles), and 22.5–25 cm s^{-1} (squares). Arrows indicate critical shell length (i.e., first evidence of downstream transport) for each velocity class.

Flow Conditions

We hypothesize that both the horizontal and vertical components of water column velocity observed in the field can contribute to physical clam transport. While the acoustic backscatter from the ADCP (Figure 10d) served as a proxy for particles in the water column, it was impossible to directly quantify clam transport in the field with the equipment deployed. However, the following calculations (parameterized from flume experiment results) can be used to determine whether the observed flow conditions were sufficient to induce motion of Asian clam individuals.

Bed shear stress can be expressed as a function of the dynamic pressure:

$$\tau_b = \frac{f_b}{8} \rho V_b^2 \quad (1)$$

where τ_b is the bed shear stress, ρ is the density of the water, f_b is the friction factor, and V_b is the free stream velocity of the flow. The subscript b refers to quantities associated with the bed rather than the sidewall of the flume. While V_b can be measured directly, and ρ can be estimated directly from water temperatures for a freshwater experiment, f_b needs to be determined experimentally. Dey (2003) developed a system of equations relating f_b to the Reynolds number associated with the bed, $R_b = 4VA_b/\nu P_b$ (where A is the cross sectional flow area, ν is the kinematic viscosity of water and P is the channel perimeter):

$$f_b = 0.316 R_b \left(\frac{4uA}{\nu P_w} - \frac{R_b P_b}{P_w} \right)^{-1.25} \quad (2)$$

$$\frac{1}{\sqrt{f_b}} = -0.86 \cdot \ln \left(\frac{k_s u}{3.7 \nu R_b} + \frac{2.51}{R_b f_b^{0.5}} \right) \quad (3)$$

where k_s is the equivalent sand roughness assumed to be the mean diameter of the bed material (Wiberg and Smith 1987). Solving this nonlinear system of equations iteratively for the conditions associated with each run in Figure 15 and then substituting the value of f_b into Eq. 1, it is possible to calculate bed shear stress as a function of free stream velocity. Over the measured velocity range, the experimental data (black circles) generated by combining Eq. 1–3 can be fit with a second order polynomial (solid curved line):

$$\tau_b = 3.97 \cdot u^2 - 0.053 \cdot u + 0.01 \quad (4)$$

Bed shear stress values of 0.07, 0.13, 0.18, and 0.22 Pa (white squares) were calculated for the median of each theoretical velocity range shown in Figure 15 (12.5, 17.5, 21.25, 23.25 cm s⁻¹). These results correspond well with Dey (2003).

Immediately before a resting clam on the sediment surface is about to be moved downstream in a uniform flow, the hydraulic drag force acting on an individual, F_d , will be equally balanced by the static friction force, F_s , between the shell and the sand bed (e.g., $F_s = F_d$). F_s is expressed as a function of the submerged weight, F_g , the lift force, F_l , and the static friction factor μ_c :

$$F_s = (F_g - F_l)\mu_c \quad (5)$$

These can be combined to yield:

$$F_d = (F_g - F_l)\tan\phi \quad (6)$$

where ϕ is the angle of friction between the shell and the sand bed and $\tan\phi$ has been shown to be a reasonable approximation of μ_c where ϕ was found to be ranges from 15–45° (Dey 2003). Using a similar technique of Dey (2003), ϕ was estimated in this study as 15.5°±4.2° (n=30). F_g is given by

$$F_g = V(\rho_s - \rho)g \quad (7)$$

where g is gravity; ρ_s is the density of the clam shell (where the specific gravity was assumed to be 2.71; i.e., equal to calcium carbonate); and V is the volume displaced by the shell. As a first approximation, the shell volume was calculated as the difference between the inner, V_i , and outer volume, V_o , of the shell: $V = V_o - V_i$. Assuming the shell to be ellipsoid in shape $V_o = 4\pi \cdot L \cdot W \cdot H/3$ and $V_i = 4\pi \cdot (L - L \cdot LR) \cdot (W - W \cdot WR) \cdot (H - H \cdot HR)/3$.

F_d can determined empirically as:

$$F_d = 0.5C_d\rho u^2A_p \quad (8)$$

where C_d is a drag coefficient and A_p is the frontal area of the shell. A_p is approximated as an elliptical area: $A_p = \pi \cdot L \cdot H/4$. This is assumed to be a valid assumption as the clams used for each run were initially aligned lengthwise in the flume with the shell umbo facing downstream. F_l is determined empirically as:

$$F_l = 0.5C_l\rho u^2A_s \quad (9)$$

where C_l is the lift coefficient and A_s is the base area (i.e., the area of the shell in contact with the substrate) of the shell approximated as another elliptical area: $A_s = \pi \cdot L \cdot W / 4$.

Substituting Eq. 7–9 into Eq. 6, the force balance can be rearranged to show the critical velocity, u_{cr} , as a function of shell dimensions (included in the calculation of elliptical area):

$$u_{cr} = \left(\left(V \cdot (\rho_s - \rho) \cdot g \cdot \tan \phi \right) / \left(0.5 \cdot C_d \cdot \rho \cdot A_p + 0.5 \cdot C_l \cdot \rho \cdot A_s \cdot \tan \phi \right) \right)^{1/2} \quad (10)$$

By minimizing the error between the predicted critical velocity, u_{cr} , and the experimental critical velocities (i.e., the median of each of the velocity ranges), it is possible to solve the optimization problem for both C_d and C_l concurrently, which were determined to be 0.57 and 0.61 respectively. Although slightly high, these values were within the range of previously reported values (Dey 2003). Eq. 10 can be combined with Eq. 4 to derive a relationship between clam shell length and the critical bed shear required to lift it. Recall from Figure 15 that a threshold clam size above which the flow would not induce transport was estimated to be 7.1, 8.3, 13.5 and 15.1 mm for the lowest to highest velocity bins.

From 5–20 mm shell length, the predicated τ_c is generally a good fit for the 4 experimentally derived values with the predicted relationship within the experimental error represented by the error bars. The experimental observation at 7.1 mm shell length lies just off the predicted relationship. This potentially resulted from the assumptions in the force balance not being completely valid at the shorter shell lengths and also the lack of observations made for smaller individuals.

This experimental relationship between shell length and critical bed shear stress now must be related back to the observations of bulk flow at both 25m and 50m. Recalling that the high resolution velocity data showed the boundary layer thickness to be less than 1m above the lake floor (Figure 12), the first bin of the ADCP velocity data at 1.83m and 2.38m (for the 1200 kHz and 600 kHz ADCP respectively) were well outside the boundary layer. For this reason, it is difficult to calculate the bed shear stress directly. The high resolution velocity data (Figure 12) can be used to determine bed shear stress as a function of the mean velocity by using the law of the wall:

$$u(z) = \frac{u_*}{\kappa} \log_{10} \left(\frac{z}{z_o} \right) \quad (11)$$

where u_* is the shear velocity ($u_* = \sqrt{\tau_b / \rho}$) κ is the von Karman constant (0.41) and z_o is the roughness length. General velocity profiles were created for 1 cm velocity bins in the bulk flow from 5–20 cm s⁻¹ and then used to determine u_* and z_o (Table 3) from those velocity profiles with correlations greater than 0.97 (i.e., $R^2 > 0.97$). The mean u_*/u_o and z_o/u_o were relatively constant at 0.15 ± 0.02 and 0.49 ± 0.07 , respectively (where errors represent 1 standard deviation). For all investigated conditions, the regimes are supposed to be hydraulically rough or rough turbulent (i.e., no continuous viscous sublayer). This is confirmed by calculating the roughness Reynolds number, $Re_* = u_* \cdot k_s / \nu$ where k_s is assumed to be equal to z_o . For the least turbulent of the flow conditions (i.e., $u_o = 0.056$), Re_* was determined to be 210; a value well above the critical value of 70 defining this flow regime (Wright et al. 1990). All other values of Re_* are even greater. These relationships can now be used to predict bed shear, τ_b , for the field conditions as a function of the bulk velocity as $\tau_b = \rho_o \cdot u_*^2$ where ρ_o is assumed to be a reference density of 1000 kg m⁻³.

It was assumed that the velocity data from the first three bins in the ADCP record (from 1.5–4.5m) would represent the mean flow in the water column at 25m and 50m. The observed velocity magnitudes during the overlapping period (i.e., 07 January 2011 – 07 March 2011) were quite similar although slightly lower at deeper depths in January and slightly higher at deeper depths for the remaining months reaching peak horizontal magnitudes of 20 cm s⁻¹. As a result of these time series being so similar, it is hypothesized that any currents generated at shallow depths would result in subsequent clam transport downslope beyond the 50m isobath.

The τ_{cr} required to move a 5 mm shell in the experimental flume was 0.071 Pa, which, from the mean u_*/u_o developed from Table 3, corresponds to $u_* = 0.84$ cm s⁻¹ and $u_o = 5.6$ cm s⁻¹ (Figure 12 – horizontal solid line). This value of u_o is well above the average mean flow during low flow conditions. In contrast, the average value of u_o during all the times when the flow conditions were greater than 5.6 cm s⁻¹ was 10 cm s⁻¹ (Figure 12 – dashed line). This corresponded to $u_* = 1.44$ cm s⁻¹ and τ_b of 0.1948 Pa and from Figure 11, a clamshell length of 15 mm. This shows that passive clam transport will not result during calm conditions but individuals up to 15 mm are potentially transported during average storm events and all size classes during peak storm events. Recall from the observed wind direction that these events were mainly driven from the south (20°), which resulted in downslope flows at this location (280°). It

can be concluded that peak storm events can be a source of downslope recruitment of clam populations.

Table 3: Estimation of shear velocity and surface roughness as a function of bulk velocity in the field conditions using the law of the wall.

Bulk velocity, u_o (m/s)	Shear velocity, u_* (m/s)	u_*/u_o	Bed roughness, z_o (m)	z_o/u_o
0.057	0.007	0.12	0.030	0.54
0.067	0.009	0.13	0.036	0.53
0.078	0.011	0.14	0.044	0.56
0.089	0.013	0.15	0.052	0.59
0.099	0.013	0.13	0.041	0.41
0.110	0.016	0.14	0.049	0.44
0.122	0.017	0.14	0.045	0.37
0.131	0.020	0.15	0.058	0.44
0.146	0.025	0.17	0.077	0.53
0.157	0.027	0.17	0.085	0.54
0.195	0.033	0.17	0.082	0.42

Water Column Stratification

As is possible to infer from the ADCP records (Figure 10), the vertical thermal stratification of the lake will also contribute to the generated flow conditions. On closer examination of Figure 10a, mixing events during Stratification Periods II and III (e.g., 24 October 2010 or 23 November 2010) are different from Period V (e.g., 10 March 2011). During Periods II and III, mixing appears fairly uniform across the entire water column whereas sustained velocities are limited to the upper water column in Period V. This observed seasonality is the direct result of the interaction of the water column stratification and the surface driven, destabilizing buoyancy flux, B , during storm events.

Net heat flux, $\tilde{H}$, through the surface of the lake drives a surface buoyancy flux, $B = g\alpha\tilde{H}/\rho_w C_p$ where ρ_w is the density of water assumed to be $1,000 \text{ kg m}^{-3}$, C_p is the specific heat of water ($4,182 \text{ J kg}^{-1} \text{ K}^{-1}$) and α the coefficient of thermal expansion (Wells and Sherman 2001). $\tilde{H}$ represents the sum of sensible, latent, shortwave and longwave fluxes and positive fluxes represent heat flux into the lake (TVA 1972). While net shortwave and net longwave were measured directly at Timber Cove, the first two flux terms need to be estimated by iteratively solving the bulk aerodynamic formulae to determine the bulk transfer coefficients (Launiainen 1995; Launiainen and Cheng 1998; Heikenheimo et al. 1999).

The net heat flux undergoes a daily heating cycle that is dominantly daytime heating through shortwave input and nighttime cooling from longwave loss.

Instantaneous values of $\tilde{H}$ were estimated to comparable (e.g., $\tilde{H} = -92 \text{ W m}^{-2}$ on 24 October 2010 and $\tilde{H} = -175 \text{ W m}^{-2}$ for 10 March 2012) during the various seasons. However, if the cumulative daily heat flux is used as an index rather than the instantaneous values, it is estimated that there is significantly greater heat flux during the fall storm events. For example, the range of cumulative daily heat flux for all of the events highlighted in Figures 4 – 7 is $-4200 - -1200 \text{ W m}^{-2} \text{ d}^{-1}$ for the events in 2010 as compared to $-620 - -100 \text{ W m}^{-2} \text{ d}^{-1}$ for the events in 2011. This is primarily driven by the fact that values of B will be primarily driven by α . Assuming $\alpha = 1 \times 10^{-4} \text{ K}^{-1}$ (estimated for 10°C water) during the first event and $\alpha = 0.16 \times 10^{-4} \text{ K}^{-1}$ (estimated for 5°C water), B equals $-2.1 \times 10^{-8} \text{ m}^2 \text{ s}^{-3}$ and $-6.6 \times 10^{-9} \text{ m}^2 \text{ s}^{-3}$ for the two events respectively. This shows that a greater destabilizing buoyancy flux will result during stratification: Periods I, II and III as compared to Periods IV and V.

The previous section demonstrated that the observed currents generated during storm events would be of sufficient magnitude to initiate transport individuals up to 15 mm in size. The heat flux analysis in this section demonstrates that storm events occurring in fall months (Periods I–III) provide a significantly greater destabilizing buoyancy flux than the rest of the year.

Ecological Implications

Where it has been introduced, Asian clam disperses rapidly in part due to its ability to passively and actively transport (Prezant and Chalermwat, 1984, Voelz et al. 2011). This is particularly true for river systems where both habitat suitability and flow velocities can be variable and the ability to disperse with water currents is important to survival. In particular, its shell morphology, life history, and feeding strategies make Asian clam primarily adapted to flowing water environments (Britton and Morton 1979, Kraemer 1979, Cummings and Graf 2010). These characteristics enable Asian clam to successfully survive and disperse in river systems, and have contributed to its rapid expansion and dominance in connected waterways such as the Danube, Willamette and Sacramento-San Joaquin river systems (Kraemer 1979, McMahon 1982, Bij de Vaate and Hulea 2000).

The observation of deepwater (> 20 m depth) Asian clam populations in regions of Lake Tahoe with vertical and horizontal water velocities capable of transporting Asian clam individuals, suggests that the mechanisms that enable downstream dispersal for *C. fluminea* in river systems are also present in this large lake. The movement of this species downslope in the lentic environment implies an expanded

ecological niche and has implications for the potential influence of Asian clam on algal populations, nutrient cycling and the benthic macroinvertebrate communities in deeper zones. In particular, sensitive endemic species found only at profundal depths such as the Tahoe stonefly (*Capnia lacustra*; US Fish and Wildlife Service Species of Concern) and the blind amphipod (*Stygobromus tahoensis*) (Frantz and Cordone 1966, 1996) are already undergoing major population level declines in Lake Tahoe (Caires et al. 2013) and the dispersal and establishment of Asian clam to these depths may have an impact on these or other species.

Asian clam occurs at deeper depth zones in Lake Tahoe than in most observations of this species. This is due, in part, because the entirety of the water column in Lake Tahoe is well oxygenated whereas in other systems, Asian clam are restricted to shallower depths are typically limited by low oxygen conditions in at depths greater than 10 m (McMahon and Bogan 2001). What is currently unknown are the intra and interspecific population dynamics of Asian clam at these depths in Lake Tahoe. This includes and understanding of relative growth, feeding and dispersal rates of Asian clam and other native macroinvertebrates and what role this places in the seasonal and annual dynamics of these communities. The ability of *C. fluminea* to successfully recruit juveniles at this depth plays a major role in these dynamics. For example, reproduction of this species at 5 - 20 m water depth in Lake Tahoe is univoltine, likely due to low water temperatures and low nutrient availability (Denton et al. 2012). However, water temperatures in Lake Tahoe below 40 m depth do not surpass 15 degrees Celsius (minimum temperature required for spawning) at any point during the year, yet live mature individuals have been recorded at up to 70 m (Caires et al. 2013). While results from the growth chamber experiment (see previous section) indicated that mortality at deep (50 m) depth was high, a few individuals did in fact survive overwinter. However, it is uncertain whether resident populations observed at these deeper water depths are reoccurring annually due to recruitment from the local population or indicate the potential for current driven transport of individuals from shallower depths where reproduction is occurring.

In conclusion, Asian clam are apt dispersers, capable of actively and passively transporting along horizontal gradients in rivers, but we have also shown the possibility for transport along vertical gradients in lakes. This species has been observed to thrive in a wide variety of environments; suggesting that dispersal limitation is potentially a significant factor in determining its rate of range expansion. We propose that further study of *in situ* dispersion of Asian clam in lakes, as well as an understanding of the reproductive and feeding strategies of this species at deeper depths, given

previous concepts of temperature limitation and resource utilization are reasonable next steps for the understanding of dynamics for this nuisance bivalve in large lakes or impoundments. In addition, understanding the inter- and intra- specific dynamics of this species at depth will further inform whether this species is sustainable at depth in subalpine or oligotrophic deepwater systems similar to Lake Tahoe.

II. Large scale bottom barrier treatment: Recolonization of Asian clams in low and high density regions of Lake Tahoe

Introduction

Aquatic invasive species (AIS) can establish in a wide range of environments and cause significant ecological and economic damages (Sala et al. 2001). The prevention of nonindigenous species introductions is an effective means to minimize impacts associated with biological invasion (Leung et al. 2002; Finnoff et al. 2007; Keller et al. 2008), however, in many regions, invasive species are already established, necessitating methods to mitigate impacts and prevent further spread (Myers et al. 2000). As a result, natural resource managers are often tasked with controlling or removing a harmful species after it has established (Simberloff 1999; Mack et al. 2000; Lieb et al. 2011), and often with few tools or little opportunity to understand non-target impacts of invasive species management.

An invasive bivalve, Asian clam (*Corbicula fluminea*) is a sediment dwelling species that negatively affects ecosystem services such as power generation and water conveyance through excessive macrofouling on intake pipes or other industrial structures (Goss and Cain 1977; McMahon 1982; Isom 1986; Johnson et al. 1986). *C. fluminea* is also observed to impact natural aquatic systems by altering organic matter cycling in sediments (Hakenkamp and Palmer 1999), decreasing phytoplankton abundance (Cohen et al. 1984), increasing available substrate for other species (Werner and Rothhaupt 2007), shifting benthic biodiversity (Dermott and Kerec 1997; Karatayev et al. 2003) and increasing porewater chemistry to fatal concentrations for native bivalve species (Cooper et al. 2005). Because of the far-reaching impacts of *C. fluminea* to aquatic environments, there is a need to develop techniques to manage and reduce established populations.

There have been few advances since the 1990's in *C. fluminea* control. Most treatments have been developed specifically to reduce biofouling at steam electric or nuclear power generating plants. These methods include the use of screens, strainers, filters, physical removal (vacuuming clams from floors or horizontal surfaces of intake bays), thermal control, paints and coating, metals (copper and zinc), oxidizing compounds such as chlorine, bromine, ozone, and halogenation (Doherty et al. 1986; Bidwell et al. 1995). Chlorination is the most widespread chemical treatment used for *C. fluminea*, but unless dechlorination is possible, current effluent guidelines limit chlorine applications to 0.5 mg L⁻¹ or discharge for more than 2h/day (40 CFR 423.12) which has shown to be ineffective due to *C. fluminea*'s ability to tolerate biochemical stress associated with exposure to pesticides (Mattice et al. 1982; Bidwell et al. 1995). Other physical control methods include emersion induced mortality through manual water

draw-down (White and White 1977) or unintended die-offs as a result of natural water level fluctuations such as those observed in Lake Constance [GER] (Baumgartner et al. 2008). In general, most treatments are targeted at removing biofouling clams (i.e., those accumulated on commercial structures, intakes, etc.) and are likely not appropriate for use in open waters in reservoirs or lakes, especially when these waterbodies are designated for recreation or human consumption. The continuous application of pesticide in waterbodies with these beneficial uses is not feasible at the necessary levels.

Valve closure is one mechanism utilized by *C. fluminea* to increase tolerance when exposed to metals (Doherty et al. 1987), chlorine (Mattice et al. 1982), and suspended solids (Aldridge et al. 1987) enabling them to survive for periods of > 24 hours under unfavorable conditions (Doherty et al. 1986). *C. fluminea* is unique in its ability to survive adverse environmental conditions such as high turbidity or pulse applications of pesticides. However, this species does not withstand extended hypoxic or anoxic conditions. *C. fluminea* cannot maintain normal O₂ uptake under severely hypoxic conditions and thus are typically restricted to shallow well-oxygenated habitats (McMahon 1996; 1999). In contrast, some native clams (*Pisidium* spp.) are extreme O₂ regulators (Burky 1983), allowing them to inhabit hypoxic and hypolimnetic habitats. Depending on temperature conditions, *C. fluminea* may remain anaerobic with the valves shut for a minimum of 3 – 4 days at high temperatures and for several weeks at low temperatures (Mathews and McMahon 1999). Thus, through valve closure, *C. fluminea* can avoid temporary lethal effects of pollutants until the accumulation of toxic anaerobic end products (acetate, propionate, succinate) (Grieshaber et al. 1994) cause clams to open valves, resume aerobic gas exchange and are subsequently impacted by pesticides or other harmful toxicants that can be entrained during filtering (Mattice et al. 1982; McMahon and Lutey 1988; Jenner 1990; Cooper et al. 2005).

The use of bottom barriers has been a common management approach for controlling nuisance aquatic macrophytes since the 1960's (Nichols 1974), however there are no published information on the use of this method for controlling invasive benthic invertebrates. Bottom barrier use to control aquatic macrophytes is intended to compress plants and reduce light availability to cause mortality or biomass reduction. There are many types of benthic covers applied in lagoons, lakes and reservoirs (Ussery et al. 1997) which can be comprised of sand, gravel, plastic, synthetic fabrics held with weights (polypropylene, polyethylene terphthalate, Tyvar, Hypalon (nonbuoyant synthetic rubber), PVC (polyvinyl chloride) coated fiberglass, Permealiner). Most barriers used in macrophyte control are fabricated with gas-permeable materials to prevent destabilization due to outgassing from sediments or plant biomass degradation under the barrier (Gunnison and Barko 1992). This decay contributes to

increased biochemical oxygen demand (BOD) under bottom barriers and has been linked to subsequent reductions (69 to 75%) of non-target benthic macroinvertebrate abundances (Engel 1984; Ussery et al. 1997).

High density ($>2000 \text{ m}^{-2}$) populations of *C. fluminea* were discovered in Lake Tahoe, CA-NV in 2008 which prompted a series of *in situ* experiments to evaluate the effect of bottom barrier application on the reduction of *C. fluminea*. In this study we present the impact of benthic barriers on Asian clam and other benthic macroinvertebrate species, as well as the recolonization these groups at seasonal intervals for a one year period after barrier removal.

Methods

Study site

This study was conducted at a 5 m water depth in two natural embayments with sandy sediment substrate on the east shore of Lake Tahoe: Marla Bay (high density *C. fluminea* populations; $>2000 \text{ m}^{-2}$) and Lakeside (low density *C. fluminea* populations; $< 2000 \text{ m}^{-2}$).

Benthic barrier large scale application

In 2010, 1950 m^2 of EPDM barriers were deployed at a 5 m water depth in Marla Bay for an approximate 120 day period (July 5 – November 5). EPDM sheets ($N = 21$, $30 \times 3 \text{ m}$) were lowered to the lake bottom from a barge, rolled out by scuba divers in a rectangular plot ($64 \times 30 \text{ m}$), and rebar rods (#7, 22 mm diameter) were placed on each overlapping seam and around the periphery of the plot to prevent barrier movement as well as open exchange with the water column.

To characterize the impact of barrier application on the benthic macroinvertebrate community, sediment grab samples ($N = 20$) were collected from within the barrier treatment area and an adjacent control area ($N=20$) in Marla Bay using a petite Ponar grab sampler (2.4 L volume, 231 cm^2 sample area, Wildlife Supply Company, Yulee, FL, USA) prior to (June 2010), immediately after (November 2010) and seasonally (February, June, November 2011) after barrier removal at Marla Bay and Lakeside. Using methods employed in Vander Zanden et al. (2006), all samples were screened ($500 \mu\text{m}$ mesh) upon collection and the retained sediment was then placed in a super-saturated sugar solution to float invertebrates (Anderson 1959). Samples were then manually picked to remove all macroinvertebrates. All organisms were preserved in 70% ethanol until identification (Thorpe and Covich 2001; Merritt and Cummins 1996). *C. fluminea* size was characterized standard measurements of the greatest

anteroposterior dimension across the valves using a digital fractional caliper (Aldridge and McMahon 1978). A nonparametric Mann-Whitney *U* test was used to significant differences of invertebrate abundances and shell lengths between control and treatment plots.

Results

Benthic barrier large scale application

Table 4 summarizes the mean abundance and standard error for all macroinvertebrate taxa, including Asian clams at each sampling period barrier and control treatment in Marla Bay. Detailed analysis for Asian clams at both Marla Bay (e.g., high density Asian clam populations) and Lakeside (e.g., low density Asian clam populations) are provided below. Common taxonomic groupings observed included Amphipoda (*Hyalella spp.*), Chironomidae, Oligochaeta, Gastropoda (Planorbidae and Physidae), Ceratopogonidae (*Palpomyia spp.*), Copepoda, Hydracarinae, Cladocera and non-native and native bivalves, Corbiculidae (*C. fluminea*) and Sphaeriidae (*Pisidium casertanum* and *compressum*; hereafter referred to as *Pisidium spp.*), respectively. Other less common taxonomic groups observed included Trichoptera (Leptoceridae, Lepidostomatidae), Ostracoda, Hirudinea and Nematoda and were not included in the analysis because of rare occurrence. Prior to treatment, all taxonomic groupings except oligochaetes were not statistically different. Bottom barrier treatment had a significant impact on all taxa except copepods. Greatest reductions in mean abundance (relative to control plots) immediately after barrier removal were observed for oligochaetes with >99%, >95% for *C. fluminea* and >95% for gastropods. Chironomids were also significantly reduced in the barrier treatment plot with a mean abundance of 45 m⁻² compared to 503 m⁻² in the non-treatment condition. *Pisidium spp.* showed a lesser, but significant reduction in mean abundance as a result of barrier application. At both three and eight months after barrier removal, amphipods, *C. fluminea*, oligochaetes, and gastropod densities in the barrier treatment were significantly different than the control. However, at eight months post-removal, the following groups once again showed differences between control and barrier treatment: Ceratopogonidae, Hydracarina and *Pisidium spp.* which can likely be attributed to the natural low abundance and heterogeneity of these taxa in Lake Tahoe. Finally, at 12 months after removal, most taxa showed significant differences between barrier and control plots with the greatest differences observed for chironomids with a greater mean abundance observed in barrier plot.

	Prior to barrier application (6/2010)			Immediately after barrier removal (11/2010)			3 months post barrier removal (2/2011)			8 months post barrier removal (6/2011)			12 months post barrier removal (11/2011)		
	Barrier	Control	U	Barrier	Control	U	Barrier	Control	U	Barrier	Control	U	Barrier	Control	U
<i>C. fluminea</i>	4103 (664)	3309 (711)	246	37 (26)	2520 (267)	1***	190 (92)	1288 (265)	29***	130 (28)	2651 (376)	18***	193 (27)	2069 (244)	1***
Amphipoda	30 (15)	54 (11)	247	6 (5)	248 (66)	49***	24 (7)	182 (67)	115*	19 (10)	117 (31)	85***	405 (70)	706 (108)	115*
Ceratopogonidae	76 (15)	69 (13)	209	4 (3)	24 (8)	125*	11 (6)	17 (8)	181	13 (6)	30 (8)	143*	0 (0)	6 (5)	180
Chironomidae	731 (98)	887 (155)	181	45 (24)	503 (121)	18***	457 (99)	415 (52)	172	1902 (158)	2056 (322)	192	3376 (223)	1002 (137)	393***
Gastropoda	309 (61)	316 (48)	184	22 (10)	548 (119)	33***	316 (287)	470 (178)	89**	45 (16)	589 (74)	6.5***	249 (44)	599 (124)	129*
Hydracarina	203 (70)	617 (223)	181	11 (6)	75 (37)	132*	87 (40)	93 (28)	172	95 (36)	573 (111)	42***	227 (42)	199 (61)	237
Oligochaeta	1175 (92)	1564 (121)	107*	6 (4)	1332 (108)	0***	582 (102)	1199 (183)	110*	900 (247)	1556 (135)	76***	433 (75)	1249 (118)	37***
<i>Pisidium spp.</i>	123 (43)	156 (48)	192	15 (10)	46 (22)	130*	2 (2)	4 (2)	190	2 (2)	91 (35)	107**	0 (0)	41 (13)	110***

Table 4. Invertebrate taxa density and standard error at each sampling period in Marla Bay. Each entry represents mean abundance (number m⁻²) and one standard error for each taxonomic grouping for barrier (N=20) and control (N=20) benthic grab samples. U indicates the Mann Whitney U test statistic and significance *** = p < 0.001, ** = p < 0.01, * = p < 0.1

C. fluminea abundances in Marla Bay remained significantly lower in the barrier treatment area throughout the monitoring period, with a mean density 90% less than that observed in the control one year after barrier removal (Figure 16). *C. fluminea* abundances in Lakeside also remained lower in the barrier treatment area throughout the monitoring period, with a mean density of 522 (±) in the control plot and 102 (±) in the barrier plot, with mean density in the barrier plot 19.5% that of the control plot (Figure 17) indicating population recovery.

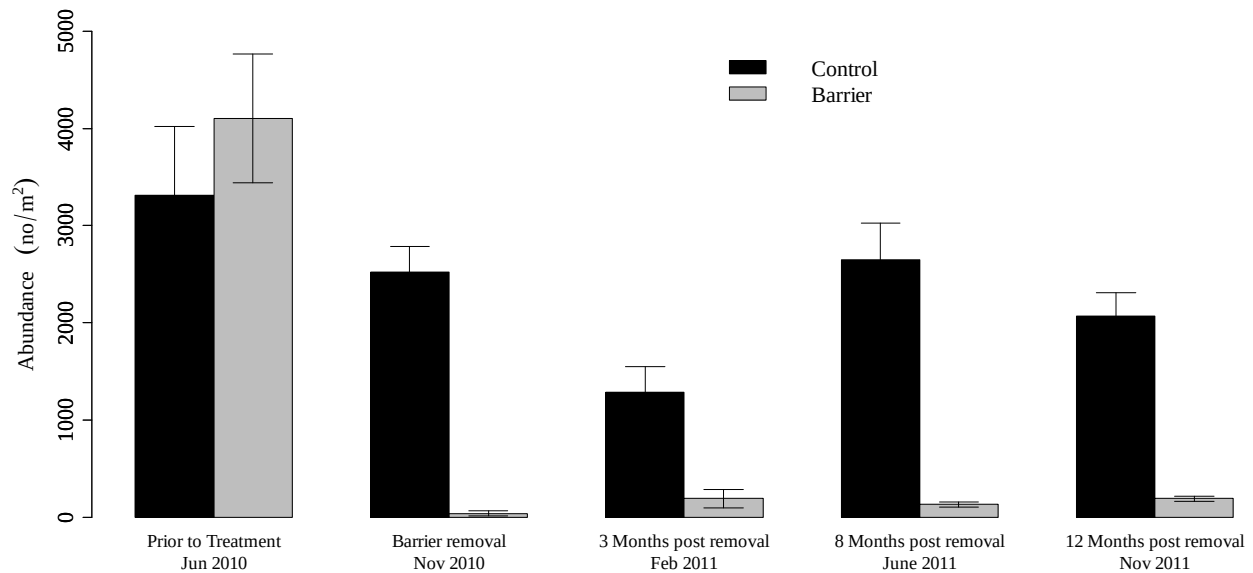


Figure 16. Marla Bay *C. fluminea* average abundance (number of clams per m²) prior to treatment (June 2010) and post barrier removal (4 sampling events: Immediately after barrier removal, November 2010, and 3, 8 and 12 months after removal). Benthic grab samples were collected within barrier treatment plot (N=20) and adjacent to the barrier plot (N=20) representing an untreated control condition. Error bars represent one standard error.

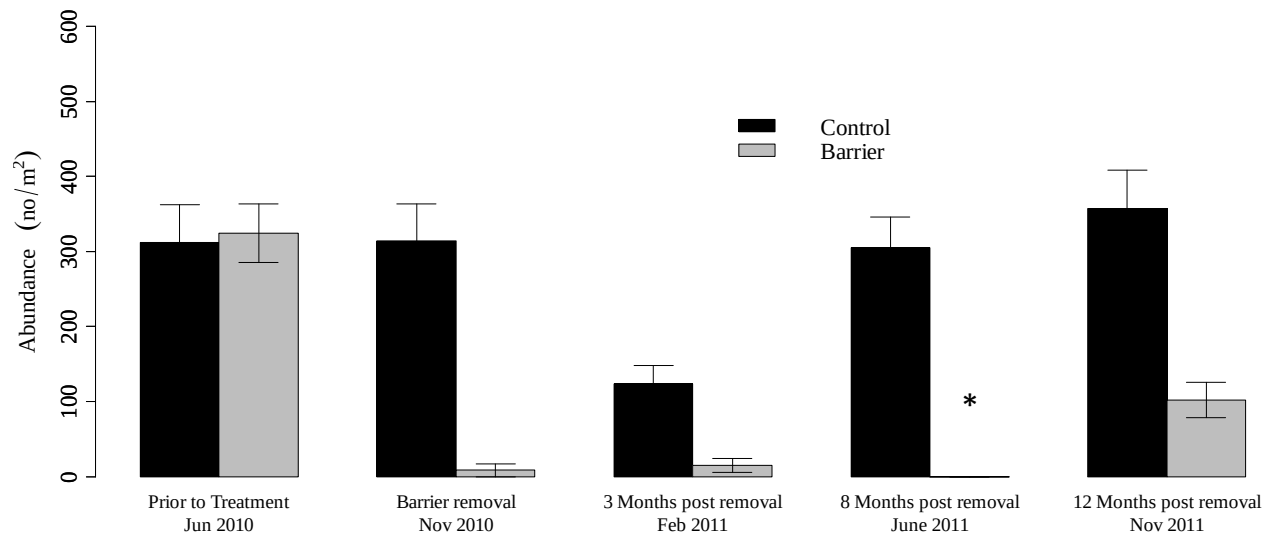


Figure 17. Lakeside *C. fluminea* average abundance (number of clams per m²) prior to treatment (June 2010) and post barrier removal (4 sampling events: Immediately after barrier removal, November 2010, and 3, 8 and 12 months after removal). Benthic grab samples were collected within barrier treatment plot (N=20) and adjacent to the barrier plot (N=20) representing an untreated control condition. Error bars represent one standard error. * indicates absence of barrier treatment data June 2011 because of equipment failure.

Asian clam size class distribution shifted as a result of bottom barrier application (Figure 18). Prior to barrier application (June 2010), *C. fluminea* shell length ranged from 1.2 mm to 19.8 mm with a median length of 10.7 in the barrier treatment area and from 1.2 mm to 20.1, in the control plot, with a median length of 11.1 (Mann Whitney U, $p = 0.189$). In November, after barrier removal, median shell length in the reduced population (mean abundance: $37 \pm 26 \text{ m}^{-2}$) barrier plot was 9.3 mm compared to 12.7 mm in the untreated area ($p < 0.001$). As abundances increase over the next three sampling periods, median shell lengths remain significantly different between treatments and one year after removal median shell length in the treatment is 8.7 mm compared to 13.1 mm in the control ($p < 0.001$).

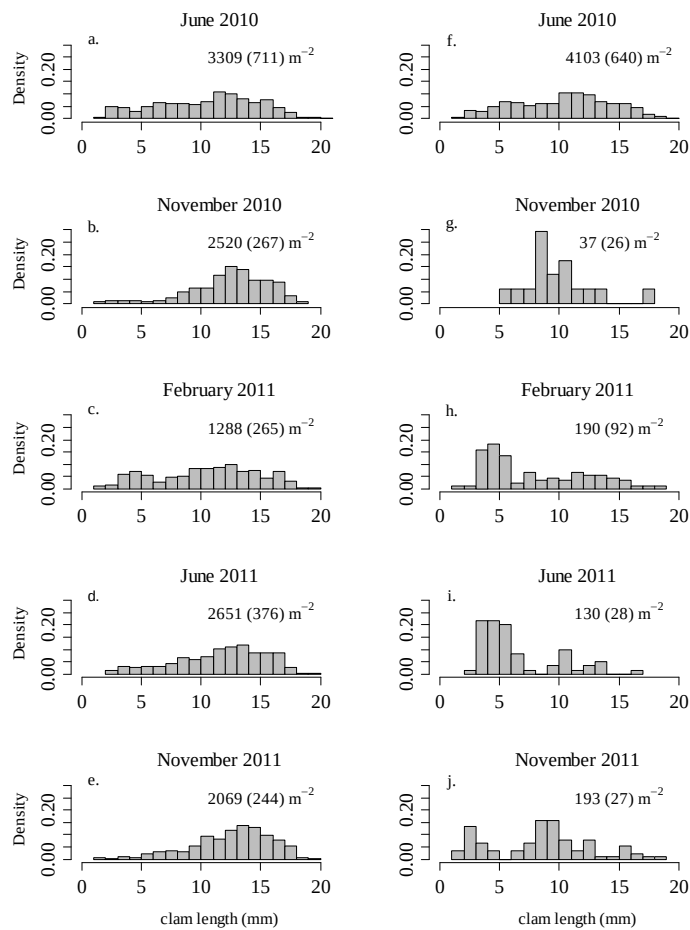


Figure 18. Histograms of *C. fluminea* size class distribution prior to (June 2010) and after barrier removal (November 2010 - November 2011). Control treatment is represented by a. – e. (left column) and barrier treatment is represented by f. – j. (right column). Y axis represents statistical density. Date of sampling is indicated on each panel and mean abundance (number of clams m^{-2}) with one standard error in parentheses.

Discussion

Benthic bottom barriers made of gas impermeable fabric such as EPDM are successful in reducing DO concentrations and causing the mortality of the invasive bivalve *C. fluminea*, other non-target benthic macroinvertebrates in Lake Tahoe. After 28 days *C. fluminea* are eradicated under small scale benthic barriers and reduced by over 95% when scaling up to a larger treatment area for a 120 d treatment period. Most other non-target taxa are also significantly reduced using this method, with variable recolonization patterns. This is not the first use of benthic barriers for control of aquatic invasive species, but the first application of this technology for *C. fluminea* and in a lentic system.

In lentic environments *C. fluminea* is characteristically restricted to well-oxygenated regions along shallow, nearshore areas (McMahon 1996; 1999). Oxygen-depleted waters such as those found at sewage outfalls (Belanger 1991) or below the thermocline of stratified lakes (Fast 1971; Matthews and McMahon 1999), have been shown to impair or prevent colonization by *C. fluminea*. Laboratory studies (Matthews and McMahon 1999) of *C. fluminea* tolerance to extreme hypoxia without accumulation of anaerobic end products or acidic conditions showed prolonged survival (11.8 and 35.1 days at 25°C and 15°C, respectively, and without mortality for 84 days at 5°C). Our observations of mortality under barrier induced hypoxia have similar timescales.

The proposed mechanism behind using gas impermeable bottom barriers as a control strategy is to reduce available DO to target *C. fluminea* metabolic process during anaerobiosis to induce mortality—either directly through oxygen limitation or indirectly through the intake of harmful stressors. Bivalves with opened valves rely on a glycogen fuelled aerobic metabolism (Ortmann and Grieshaber 2003) and studies suggest that after closing valves, most enclosed oxygen is spent within a few minutes (Taylor 1976; Davenport and Woolmington 1982; Widdows 1987). However, Ortmann and Grieshaber (2003) observed a 90% reduction in *C. fluminea* metabolic rate with the onset of valve closure, and this depressed metabolism remained aerobic for several hours. Only during extended periods of valve closure (> 5-10 h), did *C. fluminea* become anaerobic and accumulate succinate within tissues. This accumulation stimulates valve opening (Mathews and McMahon 1999), causing *C. fluminea* to circulate water over gills to excrete anaerobic end products (succinate, propionate) and resume exchange with overlying waters (Mattice et al. 1982; McMahon and Lutey 1988; Jenner 1990). At this point, the uptake of potentially harmful ambient stressors (e.g., chlorine, ammonium) may have an effect.

In particular, *C. fluminea* die offs are observed to produce high concentrations of unionized ammonia (NH₃-N) which are well above concentrations that cause acute mortality of macroinvertebrate species

(Cherry et al. 2005). Cherry et al. (2005) also reported a 96-h median lethal concentration (LC_{50}) for NH_3 -N was 0.28 to 0.78 mg/L for *C. fluminea*--with a 40% increase to this mortality rate once DO concentrations dropped to 2 mg/L. Estimates of unionized ammonia concentrations observed under Lake Tahoe chamber conditions with *C. fluminea* (mean density 2000 m⁻²) in our experiment ranged from 0.004 - 0.005 mg/L (pH = 6.92, avg temp = 18 °C; calculated after Thurston et al. 1979). While elevated nitrogen concentrations observed in this study are orders of magnitude less than LC_{50} reported above; the combination of extended exposure under low DO are potential contributing factors to the observed mortality in this study. Further research on the species specific effect of low DO and elevated ammonium concentrations is needed to clarify this relationship.

Restoration or conservation goals with regard to invasive species removal may not be accomplished if the outcome does not consider impacts to non-target communities (Zavaleta et al. 2001). Other experimental *C. fluminea* removal efforts and recolonization monitoring in Lake Tahoe showed that while *C. fluminea* abundances remain low, benthic community diversity was altered with significant increases in chironomid abundances in removal plots compared to other taxa (Wittmann et al. *submitted*). One year after barrier removal, the same effect is observed in this study, with chironomid abundances three times as great in the barrier plot compared to the control condition (Table 4). Chironomids are ubiquitous in Lake Tahoe, and are similarly observed as early colonizers in other systems due to their r-selected traits and mobility (Gray 1981; Malmqvist et al. 1991; Otermin et al. 2002). Throughout the experimental period, Ceratopogonidae, Hydracarina, Cladocera, and Copepoda show variable abundances with little or no conclusive trends with respect to barrier treatment. These taxa, as well as the native pea clam *Pisidium spp.*, have sparse and heterogeneous distribution in Lake Tahoe, which can potentially be attributed to the lake's oligotrophic nature, taxa-specific life histories, and seasonality with regard to sampling. Amphipoda, oligochaeta and gastropoda abundances remain reduced throughout the entirety of the monitoring period, but all show increases in the barrier plot in November 2011 with respect to abundances observed immediately after barrier removal one year prior and to control conditions. While the post barrier removal period assessed in this study covers one full reproductive season, further monitoring is necessary to understand the long term recolonization dynamics.

A current unknown in this study is the competitive ability of *C. fluminea* to recolonize over the long term given influences inter- and intraspecific density dependence as well as impacts of environmental conditions in Lake Tahoe. In particular, observed shifts toward a smaller median *C. fluminea* size class as

a result of barrier application may have potential impact on future recolonization patterns. *C. fluminea* population dynamics are dependent on factors that vary with size such as feeding rates (Cohen et al. 1984), growth rates (Stites et al. 1995) and fecundity (Hornbach 1992). Also, proportional increases in the representation of the ≤ 5 mm size class (Figs. 18h, i, j) suggests evidence of some pelagic-based recolonization (i.e., movement of juveniles in the water column) from adjacent untreated areas. While *C. fluminea* mean abundance remained significantly low the barrier treatment plot after 1 reproductive season, rate recruitment rates of *C. fluminea* populations will depend on population densities from in and outside of treatment plots, the competitive ability of recolonizing size classes, and potential impacts from shifted community dynamics such as an increase in abundance of chironomids (Buckley et al. 2001; Zipkin et al. 2008; Zipkin et al. 2009). Predicting the long term response of management strategy can be challenging because of complex population dynamics; the long term monitoring of treatment plots is imperative to understand the impacts of any control methodology.

The control of invasive species is an important concern for preserving ecosystem health, particularly in recent decades where the introduction and establishment of harmful aquatic invaders has increased. In most cases, 100% removal or harvest of a target invasive species is not likely, or where it does occur, reintroduction or recolonization from adjacent regions is probable. However, we have demonstrated the effective use of gas impermeable fabrics in reducing DO concentrations and contributing to the significant mortality of *C. fluminea* and other benthic macroinvertebrate taxa. This method has the potential for use in rapid response efforts to reduce incipient invasions of sediment dwelling, oxygen-sensitive species such as Dreissenid mussels or *C. fluminea*, or for established invasions where the impacts of high density populations necessitates mitigation through population reduction. Our results demonstrate an effective tool for the short term reduction of invasive benthic dwelling populations, but illustrate the need for long term monitoring for invasive species management.

III. Economic efficiency analysis: Asian clam recolonization rates after bottom barrier treatment

Introduction

Aquatic ecosystems provide goods and services to humans (e.g., ecosystem services) that can be defined in two broad terms. First, ecosystem services can be described as use values, such as those derived from water consumption, conveyance, or recreation, and second, as non-use values, such as bequest or existence values--e.g., the value gained from just knowing that the ecosystem exists (UNEP Millenium Ecosystem Assessment 2005). The introduction and establishment of nonindigenous species can negatively impact multiple ecological processes such as nutrient cycling, food web dynamics and resource utilization. As a result, ecosystem service provisioning may be reduced due to subsequent decreases in water quality (i.e., water clarity), recreationally or commercially harvested organisms (i.e., lake trout, rainbow salmon) or aesthetics of aquatic ecosystems (i.e., nuisance aquatic weed growth, bivalve shell deposition on shorelines).

The establishment of aquatic invasive species continues to impact freshwater ecosystems and present costly challenges to natural resource managers. While prevention of invasive species introductions is considered as the most effective means to reduce invasive species impacts (Leung et al., 2002; Finnoff et al., 2007; Keller et al., 2008), it is a complex and resource intensive endeavor that is often complicated by undetected propagules, illegal releases, or accidental introductions that can confound prevention goals. As a result, natural resource managers are often tasked with controlling or removing an introduced species after it has established.

Controlling invasive species has promise as a means to reduce negative economic and ecological impacts to native biodiversity, water quality and commercial and recreational use of ecosystems (Simberloff, 1999; Mack et al., 2000). Efforts to control invasive species have been attempted for a number of taxa including rusty crayfish (Hein et al., 2007), dreissenid mussels (Wimbush et al., 2009), aquatic macrophytes (Tobiessen et al., 1992; Eichler et al., 1993), and smallmouth bass (Weidel et al., 2007) with variable levels of success. Examples of unintended effects of invasive species removal include shifts to native community structure (Rinella et al., 2009) or increases in population growth rates of the management target (Zipkin et al., 2009). Although rare, invasive species management goals have been accomplished through long-term programs of physical removal (Wimbush et al., 2009) or combining physical removal with other treatment methods (Madsen, 1997).

An established non-native species is considered as invasive when it incurs costs that outweigh any benefits (Finnoff et al. 2009). While removing or controlling species may mitigate these effects, scenarios in which the costs of management far supersede the damages caused by invasive species require further decision-making. These decisions are complex due to uncertainties associated with the determination of the value of ecosystem services as well as the damages caused by the invasive species.

To reduce the uncertainties associated with invasive species management decision-making and to build a feasible and cost effective mitigation program, quantifying the relationship between the ecology and management of an invasive species is key component to successful strategic decision-making (Finnoff et al. 2009). Because the post-treatment monitoring period was limited (e.g., only 1 year) we utilize three biological growth models (rather than measuring real outcomes) that utilize the 1 year of field monitoring data to estimate population growth rates of Asian clam after barrier treatment. We compare estimates produced by these models to the associated costs per acre to determine the cost of Asian clam treatment in high density (Marla Bay) and low density (Lakeside) regions in Lake Tahoe.

Additionally, the science team at the University of Nevada Reno continued to monitor the Marla Bay barrier plot at 22 and 28 months after barrier removal (not an objective covered by this project). We present the results of these monitoring efforts to further assess modeling outputs presented herein. Because of the short period of data that were used to estimate the rates in all of the models, the uncertainty of the model results must be considered high.

Methods

In 2010, 1950 m² of EPDM barriers were deployed at a 5 m water depth in Marla Bay and Lakeside for an approximate 120 day period (July 5 – November 5). EPDM sheets (N = 21, 30 x 3 m) were lowered to the lake bottom from a barge, rolled out by scuba divers in a rectangular plot (64 X 30 m), and rebar rods (#7, 22 mm diameter) were placed on each overlapping seam and around the periphery of the plot to prevent barrier movement as well as open exchange with the water column.

To characterize the impact of barrier application on the Asian clam community, sediment grab samples (N = 20) were collected from within the barrier treatment area and an adjacent control area (N=20) in Marla Bay using a petite Ponar grab sampler (2.4 L volume, 231 cm² sample area, Wildlife Supply Company, Yulee, FL, USA) prior to (June 2010), immediately after (November 2010) and seasonally (February, June, November 2011) after barrier removal at Marla Bay and Lakeside. Using methods employed in Vander Zanden et al. (2006), all samples were screened (500 µm mesh) upon collection and the retained sediment was then placed in a super-saturated sugar solution to float invertebrates

(Anderson 1959). Samples were then manually picked to remove all Asian clams. All organisms were preserved in 70% ethanol until enumeration (Thorpe and Covich 2001; Merritt and Cummins 1996).

Models

To estimate the recolonization rate for Asian clams in Lake Tahoe, three growth models were used. The first is an exponential model, which captures increases in populations according to geometric series. All natural populations have the capacity for exponential growth and this model is widely used to describe population growth in microbiology (growth of bacteria), conservation biology (restoration of disturbed populations), insect rearing (prediction of yield), plant or insect quarantine (population growth of introduced species), fisheries biology (prediction of fish dynamics) and is particularly applicable for hermaphroditic species such as Asian clam (Gotelli 1998).

In the exponential model if each organism produces R offspring, then population numbers (N) in generations $t = 0, 1, 2, \dots$ is equal to:

$$N_1 = N_0 R$$

and

$$N_t = N_0 R^t$$

When t is large, then this equation can be approximated by an exponential function:

$$N_t = N_0 \cdot \exp(r \cdot t) = N_0 e^{rt}$$

where the parameter r is the instantaneous rate of natural increase or population growth rate. r is expected to be lower during periods of environmental stress (e.g., food or temperature limitation) and higher during periods of environmental benefit. Three possible outcomes for the exponential model include an exponential decline of the population ($r < 0$), exponential increase ($r > 0$) and population remains the same ($r = 0$). The instantaneous rate of population growth (r) can generally be calculated as the change in population size (e.g., average abundance of Asian clams) divided by the time interval (days) considered (Table 5). The parameter r can also be interpreted as the difference between the birth (reproduction) rate and death rate:

$$\frac{dN}{dt} = (b - m)N = rN$$

Here b is the birth rate and m is the death rate. Birth rate is the number of offspring organisms produced per one existing organism in the population per unit time. Death rate is the probability of dying per unit time for one organism. Major assumptions of the exponential model are that there is continuous reproduction over the time period considered, all organisms are identical (e.g., no age structure) and that the environment is constant in space and time. Because our model is based on of a seasonal time step, we average parameter values over the changing time scales (e.g., seasonal measurements), capturing effects of extreme thermal conditions. The exponential model does not account for density dependence--or limitations of growth rates based on the numbers of individuals. The exponential model is robust and gives reasonable precision even if the assumptions are not met (Case 1999). Organisms may differ in their age, survival, and mortality. But because the population consists of a large number of organisms, and thus their birth and death rates are averaged.

Table 5. Asian clam sampling dates, sampling intervals, population densities and instantaneous growth rate ($r \text{ d}^{-1}$) (with upper and lower range in parentheses) estimates for the period June 2010 - November 2011. Average Asian clam population density is presented, with standard error represented in parentheses. LSB = Lakeside Barrier, LSC = Lakeside Control, MBB = Marla Bay Barrier, MBC = Marla Bay Control.

Relation to barrier	Sampling Date	Interval (days)	Asian clam density (clams/ m^2)				Instantaneous growth rate ($r \text{ d}^{-1}$)			
			Lakeside Barrier	Lakeside Control	Marla Barrie r	Marla Contr ol	r LSB	r LSC	r MBB	r MBC
Prior	22-Jun-10	0	325 (39)	312 (50)	4103 (664)	3309 (711)	-	-	-	-
After 1	5-Nov-10	136	9 (9)	314 (49)	37 (26)	2520 (267)	0	0.02	0	-5.80
After 2	21-Feb-11	108	15 (9)	123 (25)	190 (92)	1288 (265)	0.06	-1.76	1.42	-11.41
After 3	15-Jun-11	114	-	305 (41)	130 (28)	2651 (376)	-	1.59	-0.53	11.96
After 4	14-Nov-11	152	102 (24)	357 (51)	193 (27)	2500 (244)	-	0.34	0.41	-0.99
r (Annual)							0.0025 (0.0004)	0.0012 (0.0001)	0.0042 (0.0001)	-0.0005 (0.0006)

The second model considered here is the logistic model which considers that the rate of population increase may be limited, i.e., it may depend on population density. Here the parameter r_0 can be

interpreted as the growth rate in absence of intraspecific competition, but is limited by the system carrying capacity, K. The model format is:

$$r = r_0(1 - \frac{N}{K})$$

Where, population growth rate, r , declines with increasing population numbers, N , and reaches 0 when $N = K$, or when the population size is at carrying capacity (Case 1999). The carrying capacity is usually interpreted as the amount of resources expressed in the number of organisms that can be supported by these resources. If population numbers exceed K , then population growth rate becomes negative and population numbers decline. In this study, we assume carrying capacity to be the maximum density measured in each location since the inception of the Asian clam monitoring program at Lake Tahoe (i.e., 2008). Carrying capacities assumed for Marla Bay was $K = 10,870$ clams/m², and in Lakeside, $K = 1255$ clams/m². It is important to note that these estimated carrying capacities are merely the highest observed densities as measured by sediment grab sampling. They do not represent the true carrying capacity of the system because of the limitations of the current study. The dynamics of the population under a logistic form is described by the differential equation:

$$\frac{dN}{dt} = rN = r_0N(1 - \frac{N}{K})$$

which has the following solution:

$$N_t = \frac{N_0K}{N_0 + (K - N_0)\exp(-r_0t)}$$

Three possible logistic model outcomes include a scenario where the population increases and asymptotes ($N_0 < K$), the population decrease and asymptotes ($N_0 > K$), or the population does not change ($N_0 = K$ or ($N_0 = 0$). The logistic model combines two ecological processes: reproduction and competition. The parameter r_0 can be considered as the maximum possible rate of population growth which is the net effect of reproduction and mortality (excluding density-dependent mortality). Slowly reproducing organisms have low r_0 and rapidly reproducing organisms have high r_0 .

The third model form considered is a linear growth model. If a population starts out at initial size N_0 and grows at a fixed rate x during the growth period then its size N_t at the end of the of growth period, t , will be given by:

$$N_t = N_0 + tx$$

The annual increase in Asian clams used for Marla Bay (156 clams/m²) and Lakeside (93 clams/m²) was the one year average increase in population density as measured in the barrier plots (from November 2010, barrier removal to November 2011 - one year later), adjusted by the average change in population density as measured in the control sample.

Modeled population growth is initiated with average Asian clam population densities observed at the time of barrier removal at both Lakeside and Marla Bay, for both the barrier treatments and control sites at those locations. To investigate recolonization, we estimated population abundances on an annual time step utilizing the three model variants described above and carried out the model period for 10 years.

Estimation of r and estimated range of r for use in model

Using initial population density estimates immediately following barrier removal, we have estimated r for the following scenarios for both Lakeside and Marla Bay: (1) as a function of seasonal samplings (e.g., a calculation of r for 3, 6 and 9 months following barrier removal, and (2) as a function of the field sampling one year after barrier removal (e.g., incorporating all seasonal processes into an annual estimate of r). These estimates are based off of average population densities estimated from N = 20 grab samples collected at each site, at each sampling. The annual estimate is what is used as the input parameter for the logistic and exponential models presented below. We also estimate the range of r using the minimum and maximum estimates of population density observed during these sampling events. Projected population densities (e.g., Figures 19, 20, 21) reflected as a result of model estimates are a function of the average r, with the upper and lower estimates of r derived as a function of these minimum and maximum field observations of population densities observed. These upper and lower estimates represent the potential range of population densities and do not necessarily reflect a true estimate of uncertainty for population size.

Costs

Costs considered here are divided into three major categories: labor, materials and field monitoring of Asian clam populations. These costs are based upon those estimated by the Asian Clam Working Group (ACWG) in 2010, and are separated in this analysis for consideration under a future treatment scenario. This is to say, the per acre cost for materials and labor are estimated for the following actions of a

systematic treatment scenario: (1) first time deployment (e.g., purchase of EPDM sheeting, bottom barrier manufacturing, transportation of barriers to field site, and deployment on lake bottom), (2) *in situ* treatment, which includes the treatment of adjacent sites after the initial delivery of and deployment of materials, and (3) removal of all materials from the lake, which occurs at the conclusion of a large scale treatment. Based on the treatment scheme, the total cost for the three components listed above will vary.

Specifically, labor costs consist of hours spent for the preparation, installation and removal of the bottom barriers. These actions included preparing barrier rolls for field deployment, delivering bottom barriers to the deployment site, diver time for installation and removal, and decontamination of barriers after removal from the lake. Materials included all costs associated with bottom barrier supplies, deployment and removal. It is likely that labor costs would be reduced if movement of barriers from site to site was possible, rather than complete removal and demobilization for each treatment. Similarly, reuse of materials would introduce further cost reductions. Monitoring costs included those encumbered by research groups (UC Davis and UN Reno) for five seasonal samplings that occurred between June 2010 and November 2011. Monitoring activities included vessel operation and deployment, grab sampling (N = 200 samples collected from Marla Bay and Lakeside), sample processing (e.g., removing invertebrates from sediment samples and identification and enumeration of Asian clams), and sample analysis and preparation (e.g., data entry and quality assurance). These monitoring costs were scaled down for the purpose of this analysis to include a monitoring program that incorporates 2, rather than 5 samplings associated with 1 acre of barrier deployment which includes: (1) a field sampling immediately after barrier deployment, and (2) a field sampling 1 year after barrier deployment. The unit of cost is represented as per acre of Asian clam treatment in Lake Tahoe. We apply this per acre cost to a number of scenarios based off a hypothetical 100 acre treatment zone and the recolonization rates observed in this study.

Results

Asian clam recolonization rates

Seasonal and annual measured instantaneous growth rate, r , for Asian clam populations are shown in Table 5. Average ($\pm$ range of minimum and maximum range for r) annual instantaneous growth rates in the barrier treatment sites in Marla Bay ($r_0 = 0.0042 \pm 0.0001$) and Lakeside ($r_0 = 0.0025 \pm 0.0004$) were greater those estimated for control sites at Marla Bay ($r_0 = -0.005 \pm 0.0006$) and Lakeside ($r_0 =$

0.0012±0.0001). Instantaneous growth rates varied by season, with positive growth rates observed for Lakeside control plots from June - November 2010, and from February through November 2011. Over the winter period (November 2010 - February 2011), population growth rates decreased at both control sites - with instantaneous growth rates approximately an order of magnitude less in Marla Bay (-11.41) compared to Lakeside (-1.76) (Table 5). The control site at Marla Bay also showed negative growth rates during the June - November 2010 period, as well as in the June - November 2011 period, suggesting population decline as a potential result of heterogeneity in habitat or environmental conditions, density dependence or some other factor. Instantaneous growth rates could not be calculated for Lakeside during the 3rd and 4th post barrier monitoring period due to field sampling complications.

Figure 19 shows projected population density based on the exponential form of the growth model. Asian clam populations in the Marla Bay barrier plot showed higher rates of recolonization than in Lakeside, achieving densities almost an order of magnitude greater one year after barrier removal. Using the same annual instantaneous growth rates (Table 5; r_0), population growth as predicted by the logistic growth model suggests that Asian clam populations in Marla Bay reach the assumed carrying capacity four years after barrier treatment and seven to eight years after barrier treatment in Lakeside (Figure 20).

Predicted population densities following a linear growth model simply increases population densities by an identical amount each year. This growth model similarly yielded increasing population densities for both barrier treatment sites, but with lower recolonization rates than estimated for the other model formulations (Figure 21).

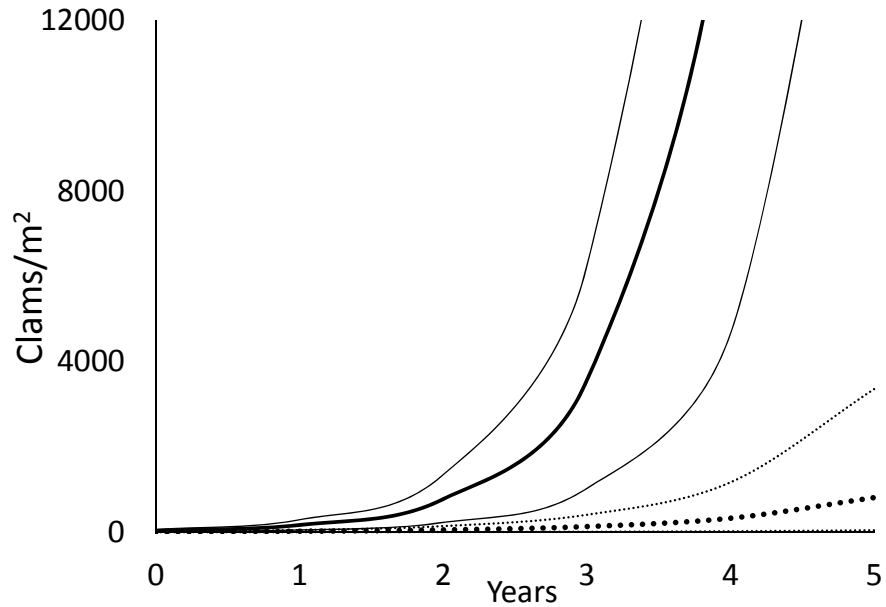


Figure 19. Predicted population density of Asian clams in Marla Bay and Lakeside using bottom barriers using an **exponential** growth model. Bold solid line indicates Marla Bay average population density, with upper and lower ranges represented by thin solid lines. Bold dotted line indicates Lakeside average population density, with upper and lower ranges represented by thin dotted lines.

The average increase per year period at Lakeside was an increase of 102 clams/m² and at Marla Bay was 193 clams/m², which results in reaching the site average after 2- 3 years at Lakeside and after 10 years at Marla Bay (10 year value not shown in Figure 19). The amount of time it would take to return to average density conditions in Lakeside and Marla Bay (after complete removal), based on each of the growth models, is summarized in Table 6.

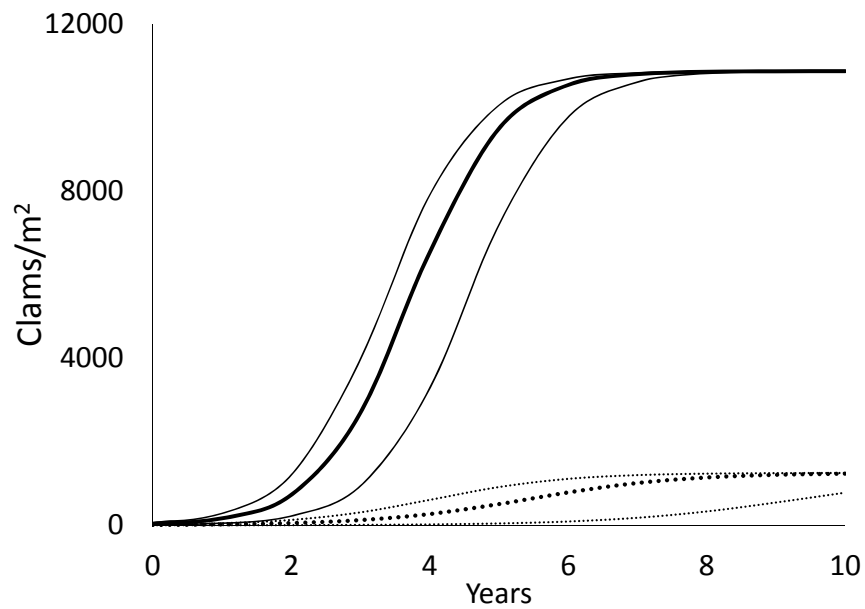


Figure 20. Predicted population density of Asian clams in Marla Bay and Lakeside after clam removal using bottom barriers using a **logistic** growth model. Bold solid line indicates Marla Bay average population density, with upper and lower ranges represented by thin solid lines. Bold dotted line indicates Lakeside average population density, with upper and lower ranges represented by thin dotted lines.

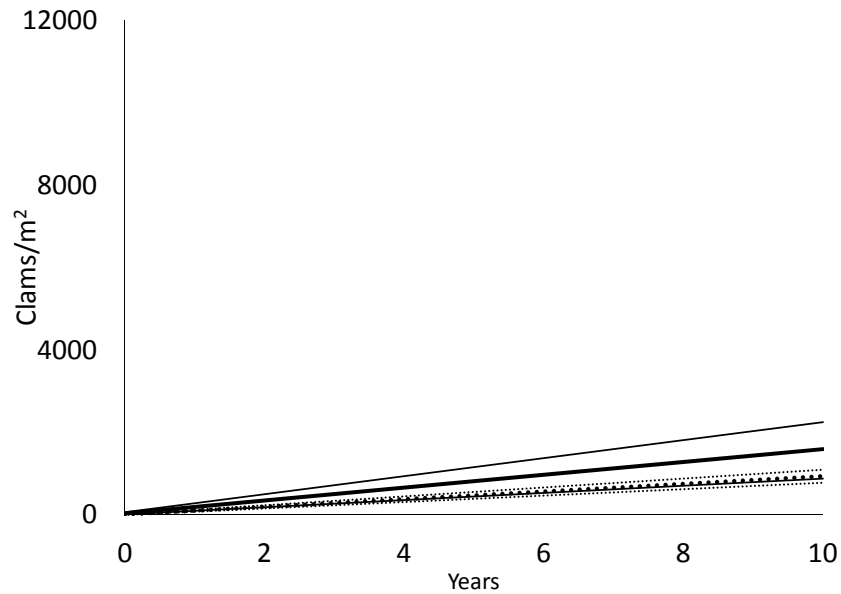


Figure 21. Predicted population density of Asian clams in Marla Bay and Lakeside using bottom barriers using a **linear** growth model. Bold solid line indicates Marla Bay average population density, with upper and lower ranges represented by thin solid lines. Bold dotted line indicates Lakeside average population density, with upper and lower ranges represented by thin dotted lines.

We used the 0, 10, 25 and 50th percentages of carrying capacity, K, to represent population abundances (as determined by *in-situ*, measures levels of clam density at both locations) at different time periods for consideration. This is to say, we indicate the period of time required after the experimental 0.5 acre bottom barrier treatment in Lakeside and Marla Bay for the Asian clam population to recover to 0%, 10%, 25% or 50% of the assumed carrying capacity for each site. Table 6 summarizes these quantiles in relation to the simulated Asian clam populations using an exponential, linear and logistic growth models as described above. For both Marla Bay and Lakeside, a population density of zero individuals is not possible because bottom barrier application did not remove all clams at either site. Depending on model form, Asian clam populations in Marla Bay recover to 10% of the assumed *carrying capacity* ($K=10,870$ clams/m²) in a 2 - 5 year period, to 25% of *carrying capacity* after in a 3 to >10 year period and to 50% of *carrying capacity* also after a 3 to > 10 year period. In Lakeside, Asian clam populations recover to 10% of *carrying capacity* ($K=1,255$ clams/m²) after 2-3 years, to 25% after 3-4 years and to 50% after 4 - 6 years. The uncertainty intervals represented here are based off of the standard deviation of instantaneous growth rates at each site.

It needs to be stressed that it is beyond the role of science to select a desired condition, i.e. the percent of the carrying capacity that should be set as a management standard. Science, however, can contribute to a larger, basin-wide effort to make these determinations by collaborating with resource agencies and other stakeholders. In this regard we consider that this report will serve to inform that discussion. The use of 10%, 25% and 50% of K in Table 6 are intended as examples and not recommendations.

Table 6. Average amount of time (in years) it would take a clam population in a treated area to reach a density relative to assumed site-specific carrying capacities (K) for Lakeside ($K = 1,255$ clams/m²) and Marla Bay ($K = 10,870$ clams/m²) based on growth model selection for a **single acre area**. The proportion of carrying capacity, e.g., 0%, 10%, 25% and 50% are shown for each site (LS = Lakeside, MB = Marla Bay) in parentheses.

	0%		10%		25%		50%	
Model form	LS (0)	MB (0)	LS (126)	MB (1087)	LS (314)	MB (2718)	LS (628)	MB (5435)
Exponential	NA	NA	2-3	2-3	3-4	3-4	4-5	3-4
Linear	NA	NA	2	5	3	>10	6	>10
Logistic	NA	NA	2	2	4	4	5	4

Bottom barrier treatment costs

Total labor and material costs for the first time installment, per acre, of EPDM bottom barrier was \$135,400 (Table 7, Appendix B). Total costs for labor were \$65,000 and included the preparation, transport and barrier placement (e.g., diver time to roll out barriers and place rebar and weights to keep barriers in place). Total materials costs for 1 acre of barrier treatment were \$41,600 and included the purchase of EPDM sheeting and other materials (e.g., PVC pipe, rebar for weighting barriers) required for the construction and application of the barriers (See Appendix B for item details). Total barge cost for a 9 day period for 1 acre of barrier installation was \$28,800. There is an opportunity to allow divers simply move an existing, in-lake barrier to an adjacent location. This would reduce costs since the purchase of new material would not be required and the preparation and shipping costs for new materials would be greatly reduced. Under this scenario, labor costs were estimated at \$57,600 per acre (which includes the skilled dive labor required for the arrangement and placement of bottom barriers and rebar weights that are already present in the lake to adjacent plots (Appendix C)). Total costs for barrier removal is estimated to be \$113,600, which includes \$75,000 of labor (an equivalent value to the initial installation cost, per acre with an additional \$10,000 for decontamination and maintenance) and \$38,400 in barge costs (12 days) per acre (Appendix D).

The total field monitoring costs per acre of barrier treatment is \$15,286 (Table 7, Appendix E). Monitoring Asian clam populations after barrier removal is a necessity in any invasive species control problem in order to understand the effectiveness of removal on temporal and spatial scales. Field monitoring cost estimates were based off of those determined by the Asian Clam Working Group (ACWG) in 2010 as carried out by the University of Nevada Reno and the University of California Davis. Field monitoring consists of two sampling events, one immediately after barrier removal, and one sampling event 1 year after barrier removal. Monitoring costs include salary for field/lab technicians and operating and travel costs. The major component of costs was comprised of monitoring coordination and labor (\$10,711) which included skilled biological monitoring technicians, laboratory scientists and/or project managers to design the monitoring protocol, operate licensed watercraft, identify and enumerate samples, and perform data entry, quality assurance and analysis. Other associated costs included operating (\$3,911) and travel (\$665) per acre of bottom barrier treatment.

Table 7. Estimated costs per acre treatment of Asian clams in Lake Tahoe.

Bottom barrier treatment category	Cost per acre
First time installation	\$135,400
Treatment of adjacent plot	\$57,600
Removal of materials	\$75,000
Field monitoring	\$15,286

Considering a hypothetical 100 acre treatment area, and the recolonization periods associated with different Asian clam population densities (as represented in Table 6), the following shows the costs associated with various long term treatment program scenarios (Table 8). The following is an explanation of the columns included in Table 8. EPDM pondliner amount/treatment area (column 1) indicates the amount of EPDM liner (in acres) to be installed in the lake and repositioned over time for a large scale treatment scenario in the 100 acre hypothetical area. The treatment period is expressed in years and is a function of the number of EPDM barrier material purchased with respect to the hypothetical 100 acre area. The treatment period determines the cost for treatment of adjacent plots (see below) and represents the number of times the bottom barrier materials must be placed and repositioned. This is to say, to treat the hypothetical 100 acre treatment plot (as considered in Table 8), with a 5 acre initial treatment area (row 2), the EPDM materials must be repositioned at least 19 times after the initial installation to cover all of the 100 acre area at least once over a 20 year period if annual installation is assumed. For a 10 acre initial treatment area (row 3), the EPDM materials must be repositioned at least 9 times after the initial installation to cover all of the 100 acre area at least once, and so on. Installation costs (column 3) include materials purchased, prepared and placed in the lake, treatment of adjacent plots (column 4) includes the cost of divers in the arrangement and replacement of bottom barrier materials in adjacent treatment plots in the lake, barrier removal (column 5) includes the removal of barriers from the lake at the conclusion of a treatment period (intended as a 1-time occurrence for all the materials placed in the lake) and monitoring costs (column 6) represent two sampling events, one immediately after barrier removal, and one year after barrier removal. Total cost estimates (without; column 7 and with; column 8 monitoring) are indicated in the right columns.

Table 8. Cost estimates for a hypothetical 100 acre treatment area based on amount of EPDM pond liner purchased. The total cost represents costs over the total treatment period. Discount rates and depreciation of materials are not included here. All values are expressed in US\$.

EPDM pondliner (acres)	Treatment period (years)	Installation cost	Adjacent plot treatment cost	Barrier removal cost	Monitoring cost	Total cost No Monitoring	Total cost W/Monitoring
5	20	\$677,000	\$1,094,400	\$567,000	\$76,430	\$2,396,000	\$2,414,830
10	10	\$1,354,000	\$518,400	\$1,134,000	\$152,860	\$3,064,000	\$3,159,260
50	2	\$6,770,000	\$57,600	\$5,670,000	\$764,300	\$12,497,600	\$13,261,900
100	1	\$13,540,000	\$ -	\$11,340,000	\$1,528,600	\$24,880,000	\$26,408,600

Table 8 represents the costs of treating the entirety of hypothetical 100 acre area with EPDM bottom barrier once. This is to say, given the amount of EPDM bottom barrier purchased at the onset of the project period, the cost of treatment (including installation, *in situ* treatments, and removal of adjacent plots) is included in columns 7 and 8.

Efficacy of clam removal on an expanded spatial scale

The analysis presented above on clam recolonization is applicable on a 1 acre spatial scale. However, management plan also need to be determined on the basis of clam abundance at the larger scale, i.e. the clam beds that infest the southeast portion of the lake. Managers need to know how much of the total area will be meet the desired condition target based on acres treated per year as well and amount of recolonization in treated areas over time.

To understand the efficacy of an expanded treatment in Marla Bay, we present the average Asian clam density after the onset of the large scale EPDM bottom barrier treatment as a function of carrying capacity, K , as represented in Table 6 (Figure 21). The hypothetical 100 acre plot size for this analysis does not represent the entire spatial distribution of clams in the Lake. Indeed, the estimate area of the Marla Bay infestation is believed to be than 200 acres. The 100 acre value was selected for this exercise as it was within the range of a small treatment area and the total area that supports clams. In addition, it is large enough to allow us to see how quickly clam might recolonize the area as treatment continues.

The major assumptions of this analysis are:

1. The average density of the hypothetical 100 acre plot considered is $3,706 \text{ clams/m}^2$, which represents the average density of Marla Bay treatment and control plots measured in this study, prior to bottom barrier application (samples taken June 2009).

2. Each treatment scenario (e.g., 5, 10, 50 and 100 acres of purchased EPDM bottom barrier material) is considered over a 10 year period. Scenarios with the deployment of 10, 50 and 100 acres of EPDM pondliner per year will accomplish the covering of each of the hypothetical 100 acre area at one time or another during a 10 year period. It is important to note that a given area has been treated, it will not be treated again over the 10 year course of this analysis, e.g. the 50 acre treatment will occur in years 1 and 2 and not thereafter. The model assumes that the years of treatment are consecutive. In this 10 year implementation period, the scenario in which 5 acres of purchased EPDM bottom barrier materials covers only half of the hypothetical 100 acre area one time. A 10 year implementation period selected because of the high uncertainty of the model used after this amount of time.

3. After the respective portion of the hypothetical 100 acre area is treated, and the barrier is removed, it is assumed that logistic growth occurs according to the model outputs provided above. Until a particular plot within the 100 acre area is treated, it is assumed that plot remains at 3,706 clams/m². This is confirmed by the relatively stable population sizes observed in Marla Bay control sites 1 year after the onset of the barrier experiment. In addition, population growth rates observed in the barrier treatment plots are significantly higher than those observed in control plots (Table 5).

4. As a metric of comparison, population densities that are a function of carrying capacity, K, are indicated on the graphic. Carrying capacity K has been estimated in this study merely by using the highest observed field densities. This is not an official measure of carrying capacity, and only serves as a proxy for the purposes of population assessment. A more rigorous treatment of carrying capacity is highly recommended.

5. After the entirety of the hypothetical 100 acre treatment area has been covered once, treatment completely ceases, and the logistic growth function defines the population growth observed.

Note that there are numbers areas of uncertainty in this analysis, and managers must account for these uncertainties when developing treatment strategies.

Figure 22 indicates that all treatment scenarios in which the entirety of the hypothetical 100 acre plot is covered one time leads to an exceedance of Asian clam pre-treatment average population density (e.g., 3,706 clams/m²) and in all scenarios, near or beyond 50% of carrying capacity. It is important to note that after 5 years the population densities observed in the treatment plots with 5 and 10 acre treatment scenarios are on average, much lower than those observed in the 50 and 100 acre treatment scenarios because of assumption number 3.

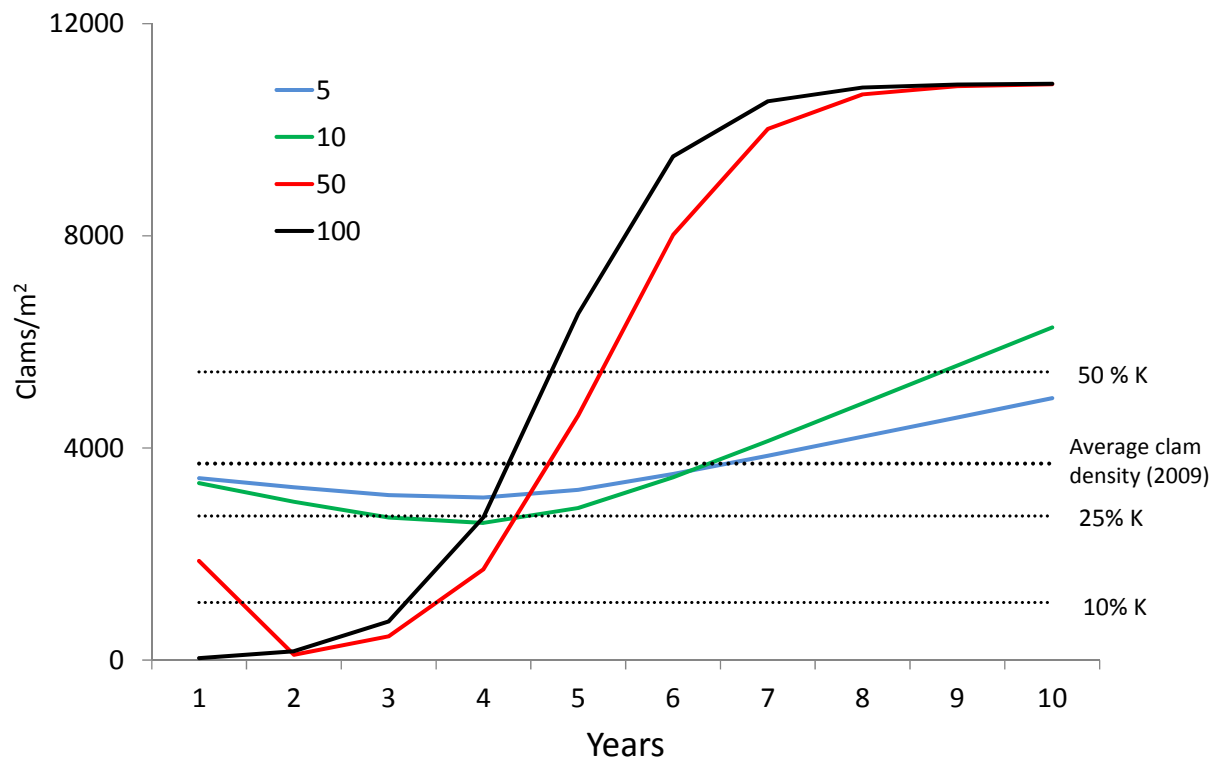


Figure 22. Hypothetical recolonization rates in Marla Bay given treatments at the 5, 10, 50 or 100 acre scale. The dotted lines represent % of assumed carrying capacity, K, as represented in Table 6. The thick dotted line represents the average clam density measured in Marla Bay immediately prior to barrier deployment in 2009. Deployment of barriers are done in consecutive years and once the entire 100 acres has been treated once, deployment ceases.

Additional field data suggests that Asian clam populations in the barrier plots are not significantly different from control plots 22 months after bottom barrier removal

To validate the recolonization rate experiment performed in year 1, the science team at the University of Nevada Reno volunteered additional time and resources to monitor Asian clam recolonization rates at the Marla Bay EPDM bottom barrier treatment site 22 months (September 2012) and 28 months (March 2013) after barrier removal. These field samplings occurred identically to the previous field monitoring efforts described above, with $n = 20$ benthic grab samples collected from within the barrier treatment site and $n = 20$ benthic grab samples collected from an adjacent control site. For a full explanation of sampling methods, please see "Section II. Large scale bottom barrier treatment: Recolonization of Asian

clams in low and high density regions of Lake Tahoe" in this document. The findings from these samples are presented in Figure 23.

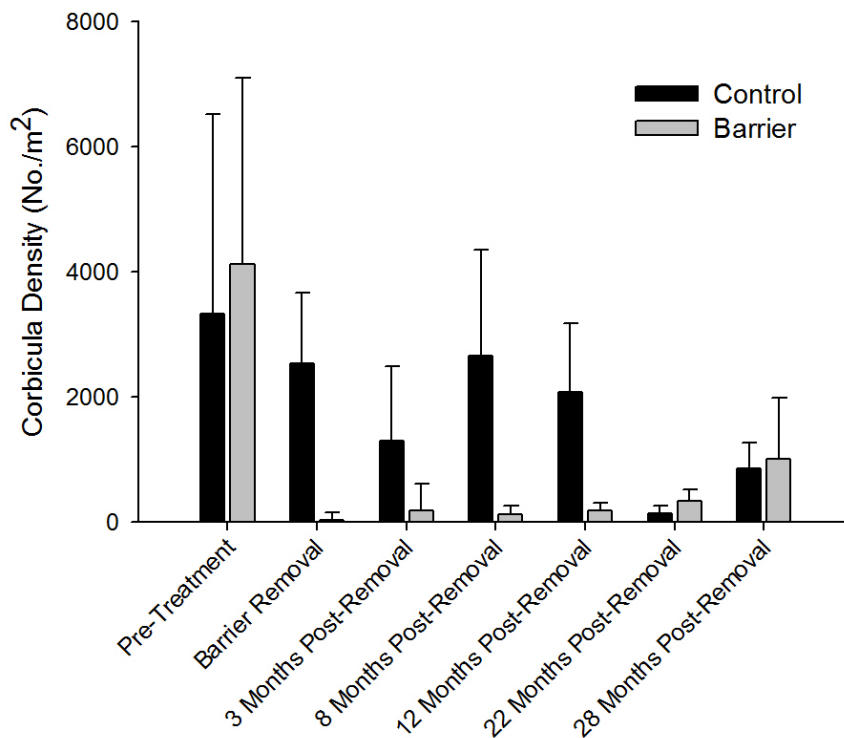


Figure 23. Asian clam population densities in Marla Bay relative to EPDM bottom barrier treatment. Sampling events occurred prior to treatment (e.g., Pre-Treatment), immediately after barrier removal and seasonally after barrier removal for 28 months. Barrier removal occurred in November 2010, and 28 months post-removal occurred in March 2013. Error bars represent 1 standard deviation.

Of note, the population densities in the control treatments at Marla Bay indicate a great deal of heterogeneity as represented by the large error bars during sampling events when average population densities are high. At both 22 months after removal and 28 months after removal, the population densities in the Marla Bay bottom barrier treatment area are equivalent to and even surpass those densities observed in the control plots, indicating a full recolonization at this site relative to control conditions at the time of sampling (Figure 23). The average population densities in control plots observed at 22 months and 28 months post-removal are noticeably less compared to control conditions in the pre-treatment (and subsequent) measurements. This suggests some ecosystem level processes are impacting Asian clam populations (and likely benthic macroinvertebrate communities at a whole)

and highlight the importance of taking account of processes acting at time scales and spatial scales larger than those of the study period. We recommend further research to understand these relationships.

Discussion

The use of EPDM bottom barriers to reduce Asian clams in Lake Tahoe significantly decreases population abundances in treatment plots by approximately 95 - 99%. However, observed recolonization rates are rapid and may be as great as 100% recolonization after 22 months. Recolonization rates are a function of the abundance of individuals within treatment plots, and the abundance of individuals from adjacent, untreated regions. Due to hermaphroditism as well as internal brooding of young, Asian clams have high rates of reproductive success on an annual basis. This reproductive success is a major driver in population regrowth, despite significant population reductions caused by bottom barrier application.

Here we have considered three types of biologically based growth models; linear, exponential and logarithmic. All three model forms have applications in different ecological settings as described. Using all three model forms, and incorporating potential ranges of the instantaneous growth rate (r) provides an opportunity to quantify the uncertainty associated with species recolonization, particularly in light of the fact that this recolonization study was only performed over a one year period. This short time span does not properly account for inter- and intra- specific population dynamics which are likely to have a significant impact (Wittmann et al. 2012a). True estimates of r are a function of a number of processes that were not estimated in this study, including annual birth and death rates as a function of population stage structure as well as environmental drivers (Dublin and Lotka 1925). Estimating uncertainty associated with r requires population level estimates over multiple reproductive and growth periods (e.g., years). In addition, recolonization rates are likely highest during this early re-establishment period immediately following barrier removal. This is evident by comparing the instantaneous growth rates (r_0) between the control and experimental sites - each differing significantly, which is due to both inter- and intra-specific density dependence.

In this study, in order to bridge gaps in knowledge, we make several assumptions that must be considered for further study. We would like to re-state them here and recommend opportunities for further developing these concepts. The first includes the determination of carrying capacity, particularly with respect to treatment site. Here, we consider Lakeside as a "low density" population, and Marla Bay as a "high density" population, based on annual population monitoring programs. To precisely determine the carrying capacity for a particular environment requires a combination of long term

monitoring programs, alternative statistical methods to assess spawner- recruitment parameter estimates, and an understanding of habitat or resource limitations including the dynamics of all taxonomic groups within a community or ecosystem. Here we have estimated that the largest Asian clam population density sampled during the project period in each location is a representation of the carrying capacity of the system. There is potential, however, for population densities to exceed these carrying capacities, which is highly dependent on environmental conditions and other population level parameters (such as size structure and fecundity rates). It is possible Asian clam are potentially reaching carrying capacity in Marla Bay, given the slightly declining population observed between 2010 and 2011 (Table 5), however, these estimates were only based off of a one year sampling period. To understand the population dynamics of these populations, a multi-year surveillance program is warranted.

The second assumption that we consider is that we present proportions of carrying capacities as representative population densities to indicate a relative population size by which to evaluate treatment efficacy. These carrying capacity proportions are not intended to serve as a metric "acceptable" population density for the users of Lake Tahoe and are only intended to provide some value by which to understand the potential impacts of a large scale treatment strategy. The determination of an "acceptable" population density or desired condition needs to be made as a collaborative effort with all appropriate stakeholders involved. Since this values has not yet been determined for clams in Lake Tahoe, we provided a range of possibilities, i.e. 10%, 25% and 50% of K (see Table 6) for illustrative purposes. As stated above, one way to account for the impacts of invasive species is to quantify its impacts on ecosystem services--or values that humans derive from ecosystem processes. In other systems, invasive bivalves like quagga mussels or Asian clams have caused millions of dollars in damage to water conveyance, power generation, aesthetics and recreation through biofouling on power plant or impoundment intake systems, trailered recreational boats and beaches or other shorefronts. These costs have been incurred by both private and public entities and have served as the basis for the quantification of ecosystem service damages by these species in other systems, which can determine the level of removal or control is necessary to provide an economically and ecologically balanced management program. To implement a useful and cost efficient management strategy for Asian clams in Lake Tahoe, we suggest that an understanding of the impact on both use and non-use values of the Lake Tahoe Basin is vital for program success.

A third major assumption concerns the assessment of the hypothetical 100 acre treatment and the recolonization rates estimated for this scenario. In Lake Tahoe, there are thousands of acres of

established Asian clam populations (Forrest et al. 2012). Understanding the population dynamics of Asian clam on a lakewide scale, or on a hypothetical 100 acre treatment scale represents an extrapolation based off an experiment that was conducted at the acre scale. Recolonization rates are driven by environmental heterogeneity, food availability, population abundance and a number of other factors at multiple scales in time and space. The hypothetical 100 acre treatment was designed to provide an understanding of costs associated with different management strategies that are based upon the amount of EPDM bottom barrier material purchased, and per acre costs as estimated in the 1 acre scale experiment.

In conclusion, the recolonization rates and costs presented herein are based on a 1 year time period following barrier treatment. While they provide the first estimates of recolonization of Asian clam after EPDM barrier treatment, we caution that the dynamics of species are complex and have a great deal of uncertainty associated with habitat and other climate variables not represented in this study. The experimental Asian clam research program at Lake Tahoe is a novel endeavor for this type of invasive species management, and has provided a lot of information and insight to managers within the basin as well as to scientists and managers outside of the region. Continuing to collect and provide this type of information will continue to support the integration of science and management at Lake Tahoe as a model for invasive species program both nationally and globally.

Conclusion

Research findings

Through field based collections coupled with laboratory experimentation, we found that Asian clams are capable of significant growth and reproduction in the nearshore zone of Lake Tahoe. Reproductively viable individuals were observed at 20 m water depths, and also grew and survived in experimental conditions at 50 m water depths. Asian clam mortality rates were significantly higher and shell production rates were significantly lower for Asian clam individuals at deepwater (50 m) water depths compared to those observed at 5 m water depths, suggesting that populations can exist at deep water depths, but with much less productivity than those observed in the nearshore zone.

Through a combination of field and laboratory based studies, the vertical dispersion of pediveliger larvae in the water column and lateral transport of adult individuals was investigated. Water flow conditions within Lake Tahoe were measured to understand if passive transport of adults were possible. During storm events, peak horizontal velocities of 25 cm s⁻¹ and peak vertical (downwards) velocities of 4 cm s⁻¹ were measured directly. Experimental runs were conducted with individual adult clams (5–24 mm shell length) in a hydraulic flume over the range of observed field velocities. These experiments demonstrated entrainment of individuals up to 15 mm in size during average storm events and all size classes during peak storm events. This work shows that passive transport of adult Asian clam individuals a potential dispersal mechanism for Asian clam in Lake Tahoe, transporting adults and juveniles from shallow depths to deeper zones, and potentially vice versa.

Building upon previous investigations of the use of bottom barriers to reduce Asian clam populations, a large scale barrier treatment (1 acre) was implemented from 2009 - 2010. After this barrier treatment, treatment and control plots were monitored for a one year period in order to understand the impact to and recolonization rates of Asian clams and benthic macroinvertebrate communities. These recolonization rates were then used to parameterize population growth models to understand the frequency of bottom barrier treatment, with respect to achieving population densities observed in 2010, or what is considered here as the "status quo condition". We found that Asian clam populations are significantly reduced immediately after bottom barrier removal, with 95-99% mortality observed. Native macroinvertebrate communities are also significantly reduced, but after a one year period, both Asian clams and macroinvertebrate communities demonstrated statistically significant recolonization in the treatment plots relative to the control plots. Dependent on region, Asian clam recolonization rates

varied. Using three common biological growth models (exponential, logistic, linear) it was estimated that within the 0.5 acre experimental plot treatment would be required every 2-10 depending on the model choice. Follow-up measurements of Asian clam populations in Marla Bay at 22 months and 28 months after barrier removal indicate that Asian clam abundances in treatment plots are not different than those observed in control plots. However, since clam density in the control plots was low, further monitoring is necessary to validate this finding. Costs of Asian clam treatment in Lake Tahoe were approximately \$210,000 per acre, which does not include potential repositioning of barrier materials in the lake following initial treatment.

Management recommendations

All studies presented herein were conducted over a two year period, and recolonization rates are based on a one year time period following barrier treatment. This short time period was constrained by the contractual language of the grant and was necessarily representative of the time scales that are realistic of the population dynamics of aquatic species, native or otherwise. We have provided the first estimates of recolonization of Asian clam after EPDM barrier treatment, we caution that the dynamics of species are complex and have a great deal of uncertainty associated with habitat and other climate variables not represented in this study and recommend the continuation of a long term experimental and monitoring program that applies to Asian clam management. Importantly, these studies should be broad enough to prepare for the establishment of other potentially harmful introduced aquatic species.

Due to the lack of quantification of the ecosystem services impacted as a result of Asian clam invasion, together with an incomplete understanding of Asian clam population regrowth (short time period associated with this study), the lack of an agreed upon desired condition for clam density, and the current state of barrier application efficiency and associated costs, this report was unable to provide an unambiguous recommendation on its own for how to develop a management strategy for the large area of clam infestation in the southern portion of the lake. Rather, the results of the treatment scenarios and recolonization and expected in-lake condition over a 10 year treatment period needs to be used to guide discussions among stakeholders on how to proceed. Despite the uncertainty associated with necessarily short study period, the modeling results do provide a platform to inform these discussions.

We strongly recommend the establishment of a long term monitoring and surveillance program to improve the likelihood of detection of Asian clams and other harmful introduced species to Lake Tahoe's nearshore.

The experimental Asian clam research program at Lake Tahoe is a novel endeavor for this type of invasive species management, and has provided a lot of information and insight to managers within the basin as well as to scientists and managers outside of the region (e.g., Lake George, NY). Continuing to collect and provide this type of information will continue to support the integration of science and management at Lake Tahoe as a model for invasive species program both nationally and globally. At the same time it should be emphasized that ecosystem processes, such as restoration of aquatic species following disturbance (treatment) operates over a multi-year time scale (at least 5-15 years). Grants and other contractual studies typically operate at much shorter time scales. Science-based decision-making needs to recognize the inherent degree of uncertainty in this type of situation.

Acknowledgements

This work was funded by the Southern Nevada Public Land Management Act and the Nevada Division of State Lands. We would like to thank David Aldridge, Robert McMahon, Karen Gehrts, Manfred Grieshaber for their expert advice and guidance on this research. We would also like to thank Brant Alan, Scott Hackley, Anne Liston, Todd Steissberg, Joe Sullivan, Annie Caires, Christine Ngai Ryan, Raph Townsend for their assistance in the data collection, sample processing and analysis.

References

- Aldridge DW, McMahon RF (1978) Growth, fecundity and bioenergetics in a natural population of the Asiatic freshwater clam, *Corbicula manilensis* Philippi, from north central Texas. *Journal of Molluscan Studies* 44:49-70
- Aldridge DW, Payne BS, Miller AC (1987) The effect of intermittent exposure to suspended solids and turbulence on three species of freshwater mussels. *Environmental Pollution* 45:17-28
- Anderson RO (1959) A modified flotation technique for sorting bottom fauna samples. *Limnology and Oceanography* 4:223-225
- Araujo, R., Moreno, D., and Ramos, M. A. 1993. The Asiatic clam *Corbicula fluminea* (Müller, 1774)(Bivalvia: Corbiculidae) in Europe. *American Malacological Bulletin*, 10: 39-49, ISSN 0740-2783.
- Baumgartner D, Mortl M, Rothhaupt KO (2008) Effects of water-depth and water-level fluctuations on the macroinvertebrate community structure in the littoral zone of Lake Constance. *Hydrobiologia* 613:97-107
- Beekey, M. A. & R. H. Karlson. 2003. Effect of food availability on reproduction and brood size in a freshwater brooding bivalve. *Can. J. Zool.* 81:1168 –1173.
- Belanger SE (1991) The effect of dissolved oxygen, sediment, and sewage treatment plant discharges upon growth, survival and density of Asiatic clams. *Hydrobiologia* 218:113-126
- Beutel MW, Horne AJ, Taylor WD, Losee RF, Whitney RD (2008) Effects of oxygen and nitrate on nutrient release from profundal sediments from a large, mesotrophic reservoir, Lake Mathews, California. *Lake and Reservoir Management* 24:18-29
- Bidwell JR, Farris JL, Cherry DS (1995) Comparative response of the zebra mussel, *Dreissena polymorpha*, and the Asian clam, *Corbicula fluminea*, to DGH/QUAT, a nonoxidizing molluscicide. *Aquatic Toxicology* 33:183-200
- Bij de Vaate, A. and Hulea, O. (2000). Range extension of the Asiatic clam *Corbicula fluminea* (Müller 1774) in the River Danube: first record from Romania. *Lauterbornia* 38, 23-26.
- Brakensiek, D. L., H. B. Osborn & W. J. Rawls, coordinators. 1979. Field manual for research in agricultural hydrology. Agriculture handbook no. 224. Washington, DC: US Government Printing Office. 550 pp.
- Britton, J.C. and B. Morton. 1979. *Corbicula* in North America: The evidence reviewed and evaluated. In: *Proceedings of the First International Corbicula Symposium 1977*, 250-287. Texas Christian University.
- Britton, J. C. and B. Morton, 1982. Dissection guide, field and laboratory manual for the introduced bivalve: *Corbicula fluminea*. *Malacol. Rev. Suppl.* 3. Pp. 56–57.
- Buckley YM, Hinz HL, Matthies D, Rees M (2001) Interactions between density dependent processes population dynamics and control of an invasive plant species, *Tripleurospermum perforatum* (scentless chamomile). *Ecology Letters* 4:551-558
- Burky AJ (1983) Physiological ecology of freshwater bivalves. In: Russel-Hunger WD (ed), *The Mollusca. Volume 6: Ecology*. Academic Press, New York, pp 281-327
- Byappanahalli, M. N., Shively, D. A., Nevers, M. B., Sadowsky, M. J. & Whitman, R. L. 2003b Growth and survival of *Escherichia coli* and enterococci populations in the macro-alga *Cladophora* (Chlorophyta). *FEMS Microbiol. Ecol.* 46, 203–211.
- Caires, A.C., Chandra, S., Hayford, B.L., M.E. Wittmann. 2013. Four decades of change: dramatic loss of zoobenthos in an oligotrophic lake exhibiting gradual eutrophication. *Journal of Freshwater Science*. 32(3):692-705.
- Case, T. 1999. *An Illustrated Guide to Theoretical Ecology*. Oxford University Press. New York.

- Cherry DS, Scheller JL, Cooper NL, Bidwell JR (2005) Potential effects of Asian clam (*Corbicula fluminea*) die-offs on native freshwater mussels (Unionidae) I: water-column ammonia levels and ammonia toxicity. *Journal of the North American Benthological Society* 24:369-380
- Coats R, Perez-Losada J, Schladow SG, Richards R, Goldman CR (2006) The warming of Lake Tahoe. *Climatic Change* 76: 121-148
- Cohen RH, Dressler PV, Phillips EJP, Cory RL (1984) The effect of the Asiatic clam, *Corbicula fluminea*, on the phytoplankton of the Potomac River. Maryland. *Limnology and Oceanography* 29:170-181
- Cooper NL, Bidwell JR, Cherry DS (2005) Potential effects of Asian clam (*Corbicula fluminea*) die-offs on native freshwater mussels (Unionidae) II: porewater ammonia. *Journal of the North American Benthological Society* 24:381-394
- Davenport J, Woolmington AD (1982) A new method of monitoring ventilatory activity in mussels and its use in a study of ventilatory patterns of *Mytilus edulis* L. *Journal of Experimental Marine Biology and Ecology* 62:55-67
- Davies, J.M. and R.E. Hecky. 2005. Initial measurements of benthic photosynthesis in Lake Erie: Community, spatial and temporal variability. *J. Great Lakes. Res.* 31(suppl. 2).
- Denton, M. E., Chandra, S., Wittmann, M. E., Reuter, J., and Baguley, J. G. 2012. Reproduction and Population Structure of *Corbicula fluminea* in an Oligotrophic Subalpine Lake. *Journal of Shellfish Research*, 31: 145-152, DOI 10.2983/035.031.0118.
- Dermott R, Kerec D (1997) Changes to the deepwater benthos of eastern Lake Erie since the invasion of *Dreissena*: 1979-1993. *Canadian Journal of Fisheries and Aquatic Science* 54:922-930
- Dey, S. 2003. Incipient motion of bivalve shells on sand beds under flowing water. *Journal of engineering mechanics*, 129(2): 232-240, DOI 10.1061/ASCE0733-9399.
- Doherty FG, Farris JL, Cherry DS, Cairns J Jr (1986) Control of the freshwater fouling bivalve, *Corbicula fluminea* by halogenation. *Archives of Environmental Contamination and Toxicology* 15:535-542
- Doherty FG, Cherry DS, Cairns J (1987) Valve closure responses of the Asiatic clam *Corbicula fluminea* exposed to cadmium and zinc. *Hydrobiologia* 153:159-167
- Eichler LW, Bombard RT, Sutherland JW, Boylen CW. 1993. Suction harvesting of Eurasian watermilfoil and its effect on native plant communities. *Journal of Aquatic Plant Management* 31: 144-148.
- Engel S (1984) Evaluating stationary blankets and removable screens for macrophyte control in lakes. *Journal of Aquatic Plant Management* 22:43-48
- Fast AW (1971) The invasion and distribution of the Asiatic clam (*Corbicula manilensis*) in a southern California reservoir. *Bulletin of the Southern Californian Academy of Science* 70:91-98
- Finnoff D, Shogren JF, Leung B, Lodge DM (2007) Take a risk: Preferring prevention over control of biological invaders. *Ecological Economics* 62:216-222
- Foe, C., and Knight, A. 1986. Growth of *Corbicula fluminea* (Bivalvia) fed artificial and algal diets. *Hydrobiologia*, 133(2): 155-164, DOI10.1007/BF00031864.
- Forrest, A. L., Wittmann, M. E., Schmidt, V., Raineault, N. A., Hamilton, A., Pike, W., and Trembanis, A. C. 2012. Quantitative assessment of invasive species in lacustrine environments through benthic imagery analysis. *Limnol. Oceanogr. Methods* 10: 65-74, DOI 10.4319/lom.2012.10.65.
- Frantz, T. C., and A. J. Cordone. 1966. A Preliminary Checklist of Invertebrates Collected from Lake Tahoe, 1961-1964. *Biological Society of Nevada Occasional Papers*, No. 8.
- Frantz TC, Cordone AJ (1996) Observations on the macrobenthos of Lake Tahoe, California-Nevada. *California Fish and Game Publication* B2:1-41
- Froelich, P. N. 1980. Analysis of organic carbon in marine sediments. *Limnol. Oceanogr.* 25:564-572.
- Goldman CR (1988) Primary productivity, nutrients, and transparency during the early onset of eutrophication in ultra-oligotrophic Lake Tahoe, California-Nevada. *Limnological Oceanography* 33:1321-1333

- Goldman CR, Jassby A, Powell T (1989) Interannual fluctuations in primary production: Meteorological forcing at two subalpine lakes. *Limnological Oceanography* 34:310-323
- Gordon ND, McMahon TA, Finlayson BL (1992) *Stream Hydrology: An introduction for Ecologists*. John Wiley and Sons, Inc., New York, 526 pp
- Goss LB, Cain C Jr (1977) Power plant condensor and service water system fouling by *Corbicula*, the Asiatic clam. In: Jensen LD (ed) *Biofouling control procedures: technology and ecological effects*. Marcel Dekker, New York, p 11
- Gotelli, N.J. (1998) *A Primer of Ecology*. 4th Edition. Sinauer Associates, New York.
- Gray LJ (1981) Species composition and life histories of aquatic insects in a lowland Sonoran desert stream. *American Midland Naturalist* 106:229-242
- Grieshaber MK, Hardewig I, Kreutzer U, Portner HO (1994) Physiological and metabolic responses to hypoxia in invertebrates. *Reviews of Physiology, Biochemistry and Pharmacology* 125:44-147
- Gunnison G, Barko JW (1992) Factors influencing gas evolution beneath a benthic barrier. *Journal of Aquatic Plant Management* 30:23-28
- Hall, J. J. 1984. Production of immature *Corbicula fluminea* (Bivalvia: Corbiculidae) in Lake Norman, North Carolina. *Nautilus* 98:153-159.
- Hakenkamp CC, Palmer MA (1999) Introduced bivalves in freshwater ecosystems: the impact of *Corbicula* on organic matter dynamics in a sandy stream. *Oecologia* 119:445-451
- Heikkinen M., Kangas, M., Tourula, T., Venäläinen, A., and Tattari, S. 1999. Momentum and heat fluxes over lakes Tämnen and Råksjö determined by the bulk-aerodynamic and eddy-correlation methods. *Agricultural and forest meteorology*, 98: 521-534, DOI 10.1016/S0168-1923(99)00121-5.
- Hein CL, Vander Zanden MJ, Magnuson JJ. 2007. Intensive trapping and increased fish predation cause massive population decline of an invasive crayfish. *Freshwater Biology* 52: 1134-1146.
- Hornbach DJ (1992) Life History Traits of a Riverine Population of the Asian Clam *Corbicula fluminea* *American Midland Naturalist* 127:248-257
- Isom, B.G. 1986. Historical review of Asiatic clam (*Corbicula*) invasion and biofouling of waters and industries in the Americas. *American Malacological Bulletin*, Special Edition, 2 : 95-98.
- Jenner HA (1990) Biomonitoring in chlorination anti-fouling procedures to achieve discharge concentrations as low as possible. In: *International Macrofouling Symposium Notebook*, Electric Power Research Institute, Palo Alto pp 9-11
- Jennings, L. B., and Hunt, H. L. 2009. Distances of dispersal of juvenile bivalves (*Mya arenaria* (Linnaeus), *Mercenaria mercenaria* (Linnaeus), *Gemma gemma* (Totten)). *Journal of experimental marine biology and ecology*, 376(2): 76-84, DOI 10.1016/j.jembe.2009.06.009.
- Johnson P., and McMahon R.F. 1998. Effects of temperature and chronic hypoxia on survivorship of the Zebra mussel (*Dreissena polymorpha*) and Asian clam (*Corbicula fluminea*). *Canadian Journal of Fisheries and Aquatic Sciences* 55: 1564-1572, DOI 10.1139/f98-030.
- Johnson KI, Henager CH, Page TL, Hayes PF (1986) Engineering factors influencing *Corbicula* fouling in nuclear service water systems. *Proceedings of the Second International Corbicula Symposium*. Special Edition No. 2 of the *American Malacological Bulletin*, June
- Kappes, H. and Haase, P. 2012. Slow, but steady: dispersal of freshwater mollusks. *Aquatic Science* 74:1-14, DOI 10.1007/s00027-011-0187-6.
- Karatayev AY, Burlakova LE, Kesterson T, Padilla DK (2003) Dominance of the Asiatic clam, *Corbicula fluminea* (Muller), in the benthic community of a reservoir. *Journal of Shellfish Research* 22:487-493
- Keller RP, Frang K, Lodge DM (2008) Preventing the spread of invasive species: Economic benefits of intervention guided by ecological predictions. *Conservation Biology* 22:80-88
- Kennedy, V. S. & L. Van Huekelem. 1985. Gametogenesis and larval production in a population of the introduced Asiatic clam, *Corbicula* sp. (Bivalvia: Corbiculidae), in Maryland. *Biol.Bull.* 168:50-60.

- King, C.A., C.J. Langdon, and C.L. Counts, III. 1986. Spawning and early development of *Corbicula fluminea* (Bivalvia: Corbiculidae) in laboratory culture. *American Malacological Bulletin* 4(1):81-88.
- Kraemer L.R. & Galloway M.L. 1986. — Larval development of *Corbicula fluminea* (Müller) (Bivalvia, Corbiculacea), an appraisal of its heterochrony. *Am. Malacol. Bull.*, 4 : 61-79.
- Kraemer, L.R. 1979. *Corbicula* (Bivalvia: Sphaeriacea) vs. Indigenous Mussels (Bivalvia: Unionacea) in U.S. rivers: A hard case for interspecific competition? *Amer. Zool.*, 19: 1085-1096.
- Launiainen, J. 1995. Derivation of the relationship between the Obukhov stability parameter and the bulk Richardson number for flux-profile studies. *Boundary-Layer Meteorology*, 76(1): 165-179, DOI 10.1007/BF00710895.
- Launiainen, J., and Cheng, B. 1998. Modelling of ice thermodynamics in natural water bodies. *Cold Regions Science and Technology*, 27(3): 153-178, DOI 10.1016/S0165-232X(98)00009-3.
- Leung B, Lodge DM, Finnoff D, Shogren JF, Lewis MA, Lamberti G (2002) An ounce of prevention or a pound of cure: bioeconomic risk analysis of invasive species. *Proceedings of the Royal Society of London Series B* 269: 2407-2413
- Lieb DA, Bouchard RW, Carline RF, Nuttall TR, Wallace JR, Burkholder CL (2011) Conservation and management of crayfishes: Lessons from Pennsylvania. *Fisheries* 36:489-507
- Liddicoat MI, Tibbits S, Butler EI (1975) The determination of ammonia in seawater. *Limnological Oceanography* 20:131-132
- Mack RN, Simberloff D, Lonsdale WM, Evans H, Clout M, Bazzaz FA (2000) Biotic invasions: causes, epidemiology, global consequences, and control. *Ecological Applications* 10: 689-710
- Madsen JD. 1997. Methods for management of nonindigenous aquatic plants. In *Assessment and Management of Plant Invasions*, Luken JO, Thieret JW (eds.) Springer: New York; 145–171.
- Malmqvist B, Rundle S, Birnmark C, Erlandsson A (1991) Invertebrate colonization of a new, man-made stream in southern Sweden. *Freshwater Biology* 26:307-324
- Mattice JS, McLean RB, Burch MB (1982) Evaluation of short-term exposure to heated water and chlorine for control of the Asiatic clam (*Corbicula fluminea*). Oak Ridge National Laboratory, Environmental Science Division, Publication No. 1748. U.S. National Technical Information Service, Department of Commerce, Springfield, VA, 33 pp
- Matthews MA, McMahon, RF (1999) Effects of temperature and temperature acclimation in survival of zebra mussels (*Dreissena polymorpha*) and Asian clams (*Corbicula fluminea*) under extreme hypoxia. *Journal of Molluscan Studies* 65:317-325
- McMahon RF (1996) The physiological ecology of the zebra mussel, *Dreissena polymorpha*, in North America and Europe. *American Zoologist* 36:339-363
- McMahon RF, Lutey RW (1988) Field and laboratory studies of the efficacy of poly[oxyethylene(dimethyliminio)ethylene(dimethyliminio)ethylene dichloride] as a biocide against the Asian clam, *Corbicula fluminea*. In: *Proceedings: service water reliability improvement seminar*. Electric Power Research Institute, Palo Alto, California pp 61–72
- McMahon RF (1999) Invasive characteristics of the freshwater bivalve, *Corbicula fluminea*. In: *Claudi R, Leach JH, (eds) Nonindigenous freshwater organisms: vectors, biology and impacts*. Lewis Publishers, Boca Raton, pp 315-343
- McMahon, R.F. and A.E. Bogan. 2001. Bivalves. Pages 331-428 in J.H. Thorp and A.P. Covich (eds.), "Ecology and Classification of North American Freshwater Invertebrates," Second Edition. Academic Press, New York.
- McMahon, R. F., and Wilson, J. G. 1981. Seasonal respiratory responses to temperature and hypoxia in relation to burrowing depth in three intertidal bivalves. *Journal of Thermal Biology*, 6(4): 267-277, DOI 10.1016/0306-4565(81)90015-2L.
- McMahon, R. 1982. The occurrence and spread of the introduced Asiatic freshwater clam *Corbicula fluminea* (Müller), in North America: 1924-1982. *The Nautilus* 96:134 141

- McMahon, R. F. 2000. Invasive characteristics of the freshwater bivalve *Corbicula fluminea*. In: Claudi, R., J. Leach (eds.), *Nonindigenous Freshwater Organisms: Vectors, Biology and Impacts*. Lewis Publishers, Boca Raton, pp 315–343.
- McMahon, R. F. (2002) 'Evolutionary and physiological adaptations of aquatic invasive animals: r selection versus resistance', *Canadian Journal of Fisheries and Aquatic Sciences*, vol 59, pp1235–1244.
- Merritt RW, Cummins KW (1996) *An Introduction to the Aquatic Insects of North America*, 3rd edition. Kendal/Hunt Publishing Company, Dubuque, Iowa 1158 pp
- Mouthon, J. 2001a. Life cycle and population dynamics of the Asian clam *Corbicula fluminea* (Bivalvia: Corbiculidae) in the Rhone River at Creys Malville (France). *Arch. Hydrobiol.*151:57–589.
- Mouthon, J. 2001b. Life cycle and population dynamics of the Asian clam *Corbicula fluminea* (Bivalvia: Corbiculidae) in the Saone River at Lyon (France). *Hydrobiologia* 452:109–119.
- Mouthon, J and T. Parghentanian. 2004. Comparison of the life cycle and population dynamics of two *Corbicula* species, *C. fluminea* and *C. fluminalis* (Bivalvia: Corbiculidae) in two French canals. *Arch. Hydrobiol.* 161:267–287.
- Morton, B. 1977. The population dynamics of *Corbicula fluminea* (Bivalvia: Corbiculacea) in Plover Cove Reservoir, Hong Kong. *Journal of Zoology*, 181: 21–42.
- de Montaudouin, X., Bachelet, G., and Sauriau, P. G. 2003. Secondary settlement of cockles *Cerastoderma edule* as a function of current velocity and substratum: a flume study with benthic juveniles. *Hydrobiologia*, 503(1): 103-116, DOI 10.1023/B:HYDR.0000008493.83270.2d.
- Murphy J, Riley JP (1962) A modified single-solution method for the determination of phosphate in natural waters. *Analytica Chemica Acta* 27:31-36
- Myers JH, Simberloff D, Kuris AM, Carey JR (2000) Eradication revisited: dealing with exotic species. *Trends in Ecology and Evolution* 15:316-320
- Nichols SA (1974) Mechanical and habitat manipulation for aquatic plant management. Wisconsin Department of Natural Resources Technical Bulletin #77
- Olivera, A.M., Wood, W.L. 1997. Hydrodynamics of Bivalve shell entrainment and transport. *Journal of Sedimentary Research* 67(3): 514-526.
- Ortmann C, Grieshaber MK (2003) Energy metabolism and valve closure behaviour in the Asian clam *Corbicula fluminea*. *The Journal of Experimental Biology* 206:4167-4178
- Otermin A, Basaguren A, Pozo J (2002) Re-colonization by the macroinvertebrate community after a drought period in a first-order stream (Agüera Basin, Northern Spain). *Limnetica* 21:117-128
- Peck SK, Pratt WL, Pollard JE, Paulson LJ, Baepler DH.1987. Benthic invertebrates and crayfish of Lake Mead. Lake Mead Limnological Research Center, Environmental Research Center, University of Nevada Las Vegas. 93 p.
- Prezant, R.S., and Chalermwat, K. 1984. Floatation of the Bivalve *Corbicula fluminea* as a Means of Dispersal. *Science* 225(4669): 1491-1493.
- Rajagopal, S., van der Velde, G. and bij de Vaate, A. (2000) 'Reproductive biology of the Asiatic clams *Corbicula fluminalis* and *Corbicula fluminea* in the river Rhine', *Archiv für Hydrobiologie* , vol 149, p403–420
- Redjah I, Olivier F, Tremblay R, Myrand B, Pernet F, Neumeier U, Chevarie L (2010) The importance of turbulent kinetic energy on transport of juvenile clams (*Mya arenaria*). *Aquaculture*. 307:20-28.
- Reid, R. G. B., R. F. McMahon, D. O., Foighill, D. and R. Finnigan. 1992. Anterior inhalant currents and pedal feeding in bivalves. *Veliger* 35:93–104.
- Rinella MJ, Maxwell BD, Fay PK, Weaver T, Sheley RL. 2009. Control effort exacerbates invasive-species problem. *Ecological Applications* 19: 155–162.

- Sala OE, Chapin FS, Huber-Sannwald E. (2001) Potential biodiversity change: global patterns and biome comparisons. In: Sala OE, Chapin FS, Huber-Sannwald E (eds) Global biodiversity in a changing environment: scenarios for the 21st century. Springer-Verlag, New York, pp 351-367
- Simberloff D (1999) Eradication. In: Simberloff D, Schmitz C, Brown TC (eds) Strangers in paradise. Island Press, Washington D.C., pp 221-228
- Solorzano L (1969) Determination of ammonia in natural waters by the phenylhypochlorite method. *Limnological Oceanography* 14:799-801
- Stites DL, Benke AC, Gillespie DM (1995) Population-dynamics, growth, and production of the Asiatic clam, *Corbicula fluminea*, in a Blackwater River. *Canadian Journal of Fisheries and Aquatic Sciences* 52:425-437
- St-Onge P, Miron G (2007) Effects of current speed, shell length and type of sediment on the erosion and transport of juvenile softshell clams (*Mya arenaria*). *J Exp Mar Biol Ecol* 349:12-26
- Taylor AC (1976) The cardiac responses to shell opening and closure in the bivalve *Arctia islandica*. *Journal of Experimental Biology* 64:751-759
- Thorp JH, Covich AP (2001) Ecology and Classification of North American Freshwater Invertebrates, 2nd edn. Academic Press, San Diego, 1056 pp
- Thurston RV, Russo RC, Emerson K (1979) Aqueous ammonia equilibrium tabulation of percent unionized ammonia. EPA/600/3-79-091. Environmental Research Laboratory, US Environmental Protection Agency, Duluth
- Tobiessen P, Swart J, Benjamin S. 1992. Dredging to control curly-leaf pondweed: a decade later. *Journal of Aquatic Plant Management* 30: 71–72.
- TVA (Tennessee Valley Authority) 1972. Heat and mass transfer between a water surface and the atmosphere. Tennessee Valley Authority Div. Water Resour. Res. Rep. 14.
- Ussery TA, Eakin HL, Payne BS, Miller AC, Barko AW (1997) Effects of Benthic Barriers on Aquatic Habitat Conditions and Macroinvertebrate Communities. *Journal of Aquatic Plant Management* 35:69-73
- VanderZanden MJ, Chandra S, Park S, Vadeboncoeur Y, Goldman CR (2006) Efficiencies of benthic and pelagic trophic pathways in a subalpine lake. *Canadian Journal of Fisheries and Aquatic Sciences* 63:2608-2620
- Voelz, N.J., McArthur, J.V., Rader, R.B. 2011. Upstream Mobility of the Asiatic Clam *Corbicula fluminea*: Identifying Potential Dispersal Agents. *Journal of Freshwater Ecology*, 13(1): 39 - 45
- Weidel BC, Josephson DC, Kraft CE. 2007. Littoral fish community response to smallmouth bass removal from an Adirondack lake. *Transactions of the American Fisheries Society* 136: 778–789.
- Weitere, M., A. Vohmann, N. Schulz, C. Linn, D. Dietrich & H. Arndt. 2009. Linking environmental warming to the fitness of the invasive clam *Corbicula fluminea*. *Glob.Change Biol.* 15:2838–2851.
- Werner S, Rothhaupt KO (2007) Effects of the invasive bivalve *Corbicula fluminea* on settling juveniles and other benthic taxa. *Journal of the North American Benthological Society* 26:673-680
- Widdows J (1987) Application of calorimetric methods in ecological studies. In: James AM (ed) *Thermal and Energetic Studies of Cellular Biological Systems*. IOP Publishing Limited, Bristol, pp 182-215
- Williams, C. J., and McMahon, R. F. 1986a. Power station entrainment of *Corbicula fluminea*(Mueller) in relation to population dynamics, reproductive cycle and biotic and abiotic variables. *American Malacological Bulletin* 2: 99-113.
- Williams, C.J., and McMahon, R.F. 1986b. A reassessment of growth rate, life span, life cycle, and population dynamics in a natural population and caged individuals of *Corbicula fluminea*. *American Malacological Bulletin Special Edition* 2: 151-166.
- Williams, C. J., and McMahon, R. F. 1989. Annual variation of tissue biomass and carbon and nitrogen content in the freshwater bivalve *Corbicula fluminea* relative to downstream dispersal. *Canadian Journal of Zoology*, 67(1): 82-90, DOI 10.1139/f95-044.

- Wimbush J, Frischer ME, Zarzynski JW, Nierzwicki-Bauer SA. 2009. Eradication of colonizing populations of zebra mussels (*Dreissena polymorpha*) by early detection and SCUBA removal: Lake George, NY. *Aquatic Conservation: Marine and Freshwater Ecosystems* 19: 703–713.
- Wittmann ME, Chandra S, Caires A, Denton ME, Rosen MR, Wong WH, Teitjen T, Turner, K, Roefer P, Holdren GC. 2011. Early invasion population structure of quagga mussel and associated benthic invertebrate community composition on soft sediment in a large reservoir. *Lake and Reservoir Management*. 26 (4): 316-327.
- Wittmann ME, Reuter JE, Chandra S, Schladow SG. 2012a. Harvesting an invasive bivalve in a large natural lake: Species recovery and impacts to native benthic macroinvertebrate community structure in Lake Tahoe, USA. *Aquatic Conservation: Marine and Freshwater Ecosystems* 22(5):588-597.
- Wittmann, M.E., Chandra, S., Reuter, J.E., Schladow, S.G., Allen, B.C., Webb, K.J. 2012b. The control of an invasive bivalve, *Corbicula fluminea*, using gas impermeable benthic barriers in a large natural lake. *Environmental Management Online Issue*. 1-11, DOI 10.1007/s00267-012-9850-5.
- Wittmann ME, Ngai KL, Chandra S. 2013. Our new biological future? The influence of climate change on the vulnerability of lakes to invasion by nonnative species. In: *Climate Change and Inland Waters: Impacts and Mitigation for Ecosystems and Societies*. Goldman, CR, Kumagai, M, Roberts RD (Eds.). John Wiley and Sons, Ltd. West Sussex, UK. pp 255 – 270.
- Wittmann, ME, S Chandra, JE Reuter, SG Schladow, M Denton, A Caires, M Acosta, F Rueda, A Hoyer, J Gardner, and J Baguely. 2013. Development of a risk model to determine the expansion and potential environmental impacts of Asian clams in Lake Tahoe. Submitted to US Forest Service and Nevada Division of State Lands.
- White SW, White SJ (1977) The effect of reservoir fluctuations on populations of *Corbicula manilensis* (Pelecypoda: Corbiculidae). *Proceedings of the Oklahoma Academy of Science* 57:106-109
- Zavaleta ES, Hobbs RJ, Mooney HA (2001) Viewing invasive species removal in a whole-ecosystem context. *Trends in Ecology and Evolution* 16:454-459
- Zipkin EF, Kraft CE, Cooch EG, Sullivan PJ (2009) When can efforts to control nuisance and invasive species backfire? *Ecological Applications* 19:1585-95

Appendices

Appendix A. Results of plankton tows carried out at Marla Bay, Nevada Beach and Glenbrook from July 23, 2010 through September 30, 2010 at 0 - 60 m depth. Counts are as abundance (individuals) per cubic meter using methodologies described in "Standard Operating Procedure for Zooplankton Sample Collection and Preservation", EPA (2004) and "A Guide to the Marine Plankton of Southern California" Perry, R. (2003).

Date	Site	Depth sampled	Diaptomus	Epischura	Daphnia	Bosmina	Ostracoda	<i>Corbicula</i> veligers
7/23/10	Marla Bay	0 - 5	81	363	0	0	0	0
		0 - 5	8	273	0	0	0	0
		0 - 20	290	974	0	0	0	0
		0 - 20	736	2833	0	0	2	0
		0 - 40	971	1224	0	0	0	0
		0 - 40	688	817	0	0	0	0
		0 - 60	1010	1113	0	0	0	0
		0 - 60	1785	893	0	0	0	0
7/23/10	Nevada Beach	0 - 5	142	199	0	0	0	0
		0 - 5	720	697	0	0	0	0
		0 - 20	474	1184	0	0	0	0
		0 - 20	624	1849	0	0	0	0
		0 - 40	978	1137	0	0	0	0
		0 - 40	493	1222	0	0	0	0
8/20/10	Marla Bay	0 - 5	1675	4047	0	5	0	0
		0 - 5	1019	3413	0	9	0	0
		0 - 20	26	80	0	1	0.23	0
		0 - 20	11	18	0	1	0	0.34
		0 - 60	504	555	5	0	0	0
9/15/10	Glenbrook	0 - 5	9	42	0.45	0	0	0
		0 - 5	17	62	0	0	0	0
		0 - 20	5	39	0	0.11	0	0
		0 - 20	7	57	0	0	0	0
9/15/10	Marla Bay	0 - 5	3	35	0	0	0.45	0
		0 - 5	4	50	0	0	0	0
		0 - 20	4	37	0	0	0	0
		0 - 20	4	29	0	0	0	0
		0 - 40	7	41	0	0	0	0
		20 - 40	6	29	0	0	0	0
		0 - 60	-	-	-	-	-	-
		40 - 60	6	23	0	0	0	0
9/15/10	Nevada Beach	0 - 5	9	38	0	0	0	0
		0 - 5	5	25	0	0	0	0

		0 - 20	18	95	0	0	0	0
		0 - 20	5	46	0	0	0	0
		20 - 40	18	101	0	0	0	0
		20 - 40	19	107	0	0	0	0
		0 - 60	-	-	-	-	-	-
		40 - 60	3	21	0	0	0	0
9/30/10	Glenbrook	0 - 5	1	18	0	0	0	0
		0 - 5	0.45	38	0	0	0	0
		0 - 20	2	22	0	0	0	0
		0 - 20	1	19	0	0	0	0
9/30/10	Marla Bay	0 - 5	2	61	0	0	0	0
		0 - 5	0	43	0	0	0	0
		0 - 20	2	34	0	0	0	0
		0 - 20	2	25	0	0	0	0
		20 - 40	0.23	23	0	0	0	0
		20 - 40	2	55	0	0	0	0
		40 - 60	2	69	0	0	0	0
		40 - 60	1	25	0	0	0	0

Appendix B. Labor, materials and barge cost detail for 1 acre EPDM bottom barrier installation at Lake Tahoe, CA-NV (2010 - 2011). The costs considered here represent those associated with the initial placement of bottom barrier materials into the lake and does not consider in situ replacement of barriers (i.e., treatment of an adjacent plot without removing barrier materials), nor does it include costs of removal from the lake.

Labor, first time installation		
Rubber rolling out and prepping for field deployment (2 hired laborers + truck rental)	\$	2,600
Truck transport of materials from prep site onto barge (2 hired laborers + gradeall forklift rental)	\$	4,800
Arrange/place rubber rolls underwater, secure, prep to be rolled out (2 days, 6 divers all day (3 hrs each in water), 4 in water at any 1 time)--hired diver rate: \$200/hour	\$	19,200
Rolling out rubber mats underwater (2 days, 6 divers all day (3 hours each in water), 4 in water at any 1 time)--hired diver rate: \$200/hour	\$	19,200
Cover edges and seams with rebar, other weights (2 days, 6 divers all day (3 hours each in water), 4 in water at any 1 time)--hired diver rate: \$200/hour	\$	19,200
Total Labor-installation	\$	65,000
Materials--installation		
40 10' by 100' 45 mil EPDM bond liner	\$	32,000
2 1.25" pipe x 21'	\$	400
20 2" PVC x 20 feet	\$	300
210 rebar weights - #7 x 2'0"	\$	5,700
8 pallets	\$	800
4 rolling shafts	\$	400
2 drive systems	\$	2,000
Total materials-installation	\$	41,600
Barge		
Deployment (9 days)	\$	28,800
Total Barge time	\$	28,800
Total first time installation cost (per acre)	\$	135,400

Appendix C. Labor cost detail for 1 acre EPDM bottom barrier *in situ* treatment at Lake Tahoe, CA-NV (2010 - 2011). The costs considered here represent those associated with the *in situ* replacement of barriers (i.e., treatment of an adjacent plot without removing barrier materials).

Labor--treatment of adjacent plot

Arrange/place rubber rolls underwater, secure, prep to be rolled out (2 days, 6 divers all day (3 hrs each in water), 4 in water at any 1 time)--hired diver rate: \$200/hour	\$ 19,200
Rolling out rubber mats underwater (2 days, 6 divers all day (3 hours each in water), 4 in water at any 1 time)--hired diver rate: \$200/hour	\$ 19,200
Cover edges and seams with rebar, other weights (2 days, 6 divers all day (3 hours each in water), 4 in water at any 1 time)--hired diver rate: \$200/hour	\$ 19,200
Total Labor-treatment of adjacent plot (per acre)	\$ 57,600

Appendix D. Labor cost detail for 1 acre EPDM bottom barrier removal at Lake Tahoe, CA-NV (2010 - 2011). The costs considered here represent those associated with the *per acre* cost of barrier removal.

Total Labor-removal	
(Same as installation + \$10K for decontamination and barrier maintenance)	\$ 75,000
 Barge	
Removal (12 days)	\$ 38,400
Total Removal Cost (per acre)	113,400

Appendix E. Field monitoring cost detail for 2 sampling events for a 1 acre EPDM bottom barrier treatment at Lake Tahoe, CA-NV (2010 - 2011). The sampling events occur immediately after bottom barrier removal, and 1 year after bottom barrier removal.

Salary		
Monitoring coordination	\$	667
Casual Labor	\$	5,917
Administrative	\$	417
Overhead Rate		0.53
Total Salary	\$	10,711
 Operating		
Boat operation and maintenance	\$	1,938
Field costs (sampling materials, etc.)	\$	1,133
Diving costs	\$	840
Total Operating	\$	3,911
Travel (Vehicle maintenance, gas)	\$	665
Total Monitoring (per acre)	\$	15,286