Title

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Determining factors for Eurasian watermilfoil (*M. spicatum*) spread in and around Lake Tahoe, CA-NV

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I. ABSTRACT

Humans play a critical role in the dispersal of exotic invasive species. Estimating pathways for non-native species by human vectors is a major challenge to invasion biologists, as well as federal, state and regional resource managers. Focusing on dispersal pathways that are available to not just one, but a number of species, allows for the efficient inspection and possible reduction of many exotic species introductions. Transient recreational boating has been used as an estimate of invasion pressure to inland freshwater bodies, and used to predict prior and future species invasions. Specifically, recreational boating traffic is used to predict human-mediated aquatic invasion in the Midwestern United States through the use of spatial interaction models called gravity models. California and Nevada contain some of the largest and most recreationally utilized lakes, rivers and reservoirs in the Western United States. These waterways attract millions of visitor days by boaters not only from within the region, but all over the United States and are currently experiencing increasing numbers of non-native species introductions from the Midwestern U.S.

This report describes aspects of dispersal of an aquatic invasive plant, Eurasian watermilfoil, both within and between fresh water bodies by recreational boating. This study addresses the question of habitat and/or dispersal limitation for watermilfoil by assessing the movement of recreational boaters within Lake Tahoe, and between Lake Tahoe and other locations, as well as characterizing nearshore habitat locations in highly visited boating destinations. Additionally, this report examines the nature of recreational boater movement data, and the impacts of boater preference as well as the impact of the spatial aspect of data gathering from one versus many locations. Specifically, this report presents the following: 1) an examination of the use of transportation models known as gravity models to describe recreational boater traffic to inland waterways in California and Nevada, 2) an analysis of waterway access point habitat quality as it relates to Eurasian watermilfoil, and 3) the invasion of Eurasian watermilfoil within Lake Tahoe, and how that relates to within-lake boater movement and habitat variables associated with invaded and uninvaded sites within Lake Tahoe.

II. INTRODUCTION AND PROBLEM STATEMENT

Human-mediated species invasions are a significant and increasing component of global environmental change. As rates of commerce, travel, and recreation increase, eco-regions previously isolated from non-native species introductions are now subject to greatly increased invasion pressure (Elton 1958, Lockwood et al. 2005). Invasive species introductions have caused reductions in global biodiversity, imposed high economic damages (Pimentel et al. 2000, Lodge et al. 2006) and is greatly accelerated by human movement (Sharov and Leibhold 1998). Thus, modeling human movement as a potential vector of harmful species invasion is important to mitigate environmental and economic damages.

The establishment of aquatic invasive species (AIS) in freshwater inland lakes, rivers and reservoirs has been enabled and accelerated by human vectors. A number of Eurasian species such as the zebra mussel (*Dreissena polymorpha),* quagga mussel (*Dreissena rostriformis bugensis*), spiny water flea (*Bythotrephes cederstroemi*), Eurasian watermilfoil (*Myriophyllum spicatum*), and purple loosestrife (*Lythrum salicaria*) have been introduced to the Great Lakes region in the last century and have prompted an immense research literature, state and national legislation, and local and regional public outreach and education programs in response. These species were likely brought in to Great Lakes region by aquarium or ornamental trade, or within ballast water trading ports from Northern European and Asian freighters. The secondary spread to other regions in North America has likely occurred through natural waterway connections (river or lake currents, irrigation canals), or overland dispersal via waterfowl, aquarium or ornamental use and release, and by trailered recreational boats that move vessels between water bodies. Despite this wide range of vectors, recreational boating is widely accepted as the most important mode of overland dispersal of AIS (Johnstone et al. 1985, Padilla et al. 1996, Johnson et al. 2001, Leung et al. 2006a). In particular, zebra and quagga mussel invasion through the Mississippi River system and to inland lakes in the Midwestern and Mid-Atlantic states have motivated much of the literature that addresses the link between recreational boating and aquatic invasion. Recently, the discovery of established quagga mussel and other Midwestern AIS in the southwestern Reservoirs Mead, Havasu, and Mohave has inspired a re-examination of aquatic invasion and recreational boating pathways to waterways in the Western United States.

There are very few "rules" of invasion, as a many potential generalizations have both theoretical and empirical exceptions. For example, the concept of invasibility, or the susceptibility of an environment or community to invasion by an introduced species, has often been linked with biodiversity (Moyle and Light 1996, Levine and D'Antonio 1999, Lonsdale 1999, Levine 2000). In general, theoretical studies predict a negative relationship between diversity and invasion, whereas empirical studies show both negative and positive correlations. However, propagule pressure or introduction effort is consistently positively correlated with successful establishment of species where the receiving environment is suitable (Mack et al. 2000), and is particularly important for deliberate, human mediated introductions (Lockwood et al. 2005, Hayes and Barry 2008).

Currently, the most well developed modeling technique to link the spread of AIS with recreational boating is a class of transportation models called gravity models (Thomas and Hugget 1980). Geographers have used gravity models to predict the interaction of people, commerce and information between two places by estimating the flow per unit time based on the distance to and attractiveness of destination points. Ecologists have found these models useful in the prediction of AIS invasion risk because they allow for the prediction of overland dispersal events by considering not only the nature of source populations, but also the spatial configuration and nature of potential colonization sites. Because of this, gravity models have the potential to more accurately forecast species movement through heterogeneous landscapes than do diffusion models, which do not explicitly consider the spatial pattern of aquatic habitats within terrestrial landscapes. Additionally, gravity models provide extra utility in that they are pathway rather than species specific, and thus can be applied to a wide variety of AIS. Gravity models were first used to estimate zebra mussel spread through Illinois freshwater lakes and rivers using boat ramp activity to parameterize coefficients (Schneider et al. 1998). Gravity models have since been refined and applied to a variety of invasive species problems: improving model resolution by incorporating ecological vulnerability to zebra mussel establishment (Bossenbroek et al. 2001), manipulating distance deterrence functions to improve shipping port invasion prediction (Drake and Lodge 2004), relating historical invasion information to backcast and forecast the invasion of the spiny waterflea to Canadian lakes (MacIsaac et al. 2004), and utilizing non-linear forms of the model (Leung et al. 2006a).

Lake Tahoe and Eurasian watermilfoil (*Myriophyllum spicatum* L.)

Eurasian watermilfoil (*Myriophyllum spicatum* L.) is a perennial herbaceous submersed plant that is considered one of the most troublesome non-native aquatic plants in North America (Smith and Barko 1990). The species is most abundant in depths of 1 to 4 m and is capable of forming a dense canopy of branches at the surface after rapid growth is initiated, usually in the spring (Nichols 1990, Smith and Barko 1990). Typically plants flower when they reach the surface and plant biomass declines as a result of autofragmentation of the stems (Smith and Barko 1990). In deep clear water plants typically grow continuously throughout the summer and reach the surface late in the growing season. This is characteristic of both the oligotrophic Lakes George in New York State and Tahoe in CA-NV and subsequently the autofragmentation period does not occur until after the single, late-summer biomass peak (Madsen et al. 1988, Walters 2000).

Mechanisms of growth and dispersal of *M. spicatum* vary by region, environment, time of year, and phenology (Madsen et al. 1988, Madsen and Smith 1997). It has also been shown that autofragments grow better than artificially or allofragmented meristems (Kimbel 1982). Environmental factors such as light, sediment type and time of year are important variables influencing the success of *M. spicatum* establishment (Madsen 1999). Several observers have noted changes in *M. spicatum* distribution with substrate changes (Misra 1938, Hutchinson 1975), however Giesy and Tessier (Giesy and Tessier 1979) found that *M. spicatum* interlake colonization was not limited by substrate composition, growing over the entire littoral zone in Lake Wingra, Wisconsin. *M. spicatum* grows best on fine textured in organic sediments with an intermediate density of about 0.8 to 1.0 g/mL (Barko and Smart 1986). It grows relatively poorly on highly organic sediments (organic content >20%) and on coarse substrates (sand and gravel) (Smith and Barko 1990).

Vegetative fragments or propagules are generally accepted as the most important mechanism for propagation and dispersal of *M. spicatum* and other aquatic species. Although seed production can be prolific, it has not been found to be a significant source of large scale spread in the U.S. (Madsen and Boylen 1989, Smith and Barko 1990). As mentioned above, *M. spicatum* begins accelerated growth in Lake Tahoe in the late summer and fall. Throughout this time the plant has most likely reached the water's surface and begins marked autofragmentation due to increased plant biomass and shading. During the boating season, allofragments, or mechanically removed portions of the plant, are also created by wave action or by vehicles passing through *M. spicatum* patches. Madsen et al. (1988) showed that the number of fragments in Lake George is strongly related to the phenology of the plant, and speculated that human activity could also be a cause of increased fragments. In an area without recreational boating, these authors found zero fragments in June and July, but numbers increased significantly in September through October due to autofragmentation.

Eurasian watermilfoil is estimated to have arrived in Lake Tahoe in the 1960's (Kim and Rejmankova 2001) and is continuing to spread to multiple locations within the lake (Figure 4). The dispersion of *M. spicatum* within Lake Tahoe is a complex process with multiple interacting components. Fragments are created when boat propellers cut the plant, when mechanical harvesting occurs (as a non-chemical management technique), and naturally due to the plant's phenology. Each of these processes has temporal and spatial elements associated with it. Lake Tahoe and surrounding water bodies are widely used for recreational boating and fishing activities, which have been shown to be a key factor in the transportation of aquatic species that spread by fragmentation (Johnstone et al. 1985, Johnson et al. 2001). Boat use as well as mechanical harvesting in Lake Tahoe is dominant in the summer, and self-induced fragmentation occurs primarily in late summer and fall. The dispersal mechanisms similarly are temporally variable, with boat usage greater in the summer months whereas currents and gyres (Strub and Powell 1986) occur in all months but are stronger during windy periods which are also present during all seasons. Long distance dispersal within the lake then depends on exchange mechanisms between marinas or protected areas where *M. spicatum* grows and more open waters. Once fragments reach a region, various environmental parameters such as temperature, turbidity, energetics of surface waves, and sediment composition determine when new colonies will become established (Smith and Barko 1990).

The spread of Eurasian watermilfoil and other AIS has been studied extensively in the Great Lakes regions, Southern U.S. in Florida and in Texas. In the last decade, there has been a westward movement of these invasive species via the coupling of aquatic range expansions and trailered recreational boating long distance dispersal events. This study seeks to provide the first attempt to look at boater mediated aquatic invasion in the Western United States by focusing on the intensely boat used Lake Tahoe and the spread of an established invasive aquatic weed both within the lake and to other surrounding lakes and reservoirs in the region.

III. OBJECTIVES

With the continued introduction and spread of AIS to new regions, particularly to areas west of the 100th Meridian in Northern America, the spread of species by recreational boater traffic must be reexamined. This study seeks to address a number of questions to examine the relationship between recreational-boater behavior and AIS dispersal between Californian and Nevadan waterways and within Lake Tahoe as a function of both recreational boating pressure and habitat suitability. Specifically I will address the following questions:

- Is Eurasian watermilfoil dispersal or habitat limited within Lake Tahoe?

- What is the relationship between boater mediated propagule pressure and habitat suitability within Lake Tahoe?
- What are attractive features of recreational waterways and do these features aid in the accurate prediction of boating traffic and subsequent non-native species invasion pressure?
- Do recreational boats leaving Lake Tahoe pose a non-native species invasion risk to other waterways?
- Do recreational boats arriving in Lake Tahoe pose a non-native species invasion risk to Lake Tahoe?
- Are recreational boaters aware of invasion risks posed by boats and boating equipment?

IV. PROCEDURE

Data collection for this project occurred over a three year period at Lake Tahoe and 10 surrounding waterways. Year one and two (2005-2006) included recreational boater surveys and within Lake Tahoe habitat characterization. Year three (2007) included habitat characterization at the 10 most used waterways of Lake Tahoe boaters, as determined by recreational boater surveys from year one. The following is a description of survey and field data collection as well as modeling procedures for the analysis of both habitat and recreational boating survey data for within Lake Tahoe and for waterways connected to Lake Tahoe via recreational boating.

A. WITHIN LAKE TAHOE—NEARSHORE HABITAT CHARACTERIZATION AND RECREATIONAL BOATER SURVEYS

Measurements of physical characteristics of nearshore areas identified as likely habitat for *M. spicatum* and within lake boater pathway data were collected during the summer of 2006. Nearshore physical characteristic data were collected at 13 sites and 27 microsites (Figure 1) identified as popular boating destinations at Lake Tahoe and analyzed using a series of techniques described below in order to understand nearshore habitat suitability of *M. spicatum*. Recreational boater surveys were collected from 7 boat launch sites around Lake Tahoe (Figure 2).

1. NEARSHORE PHYSICAL HABITAT CHARACTERIZATION

Sediment Particle Size Analysis

Sediment samples were collected from the littoral zone of Lake Tahoe and analyzed for particle size. Samples were taken using a coring tube driven into the sediment to a depth of 10 cm. Material was stored refrigerated with lake waters until the time of analysis. Sediment sieving protocol followed the techniques listed in Gordon et al. (1992). Organics were removed with hydrogen peroxide (Goudie 1981), fines dispersed with sodium carbonate and washed through a 0.0625 mm (0.0025 inch) sieve and weighed. Sample remainders were dried over a 5 day period in aluminum pans and dried aggregates were broken with rolling pin. A set of eleven sieves that follow the Wentworth particle size classification (Table 1) were used to sieve samples, decreasing in aperture size downward with a 1 Φ interval with a 4.5 Φ (0.0017 mm) as smallest size and -4.7 Φ (64 mm) as largest. Φ The Krumbein *phi* Φ scale is a logarithmic transformation of the Wentworth scale:

$$\Phi = -\log 2\ D/D_0 \qquad \text{Equation 1}$$

where D is the diameter of the particle, and D_0 is a reference diameter, generally 1 mm. Approximately 200 grams of sample was weighed and placed on the largest sieve, shaken for 10-15 minutes, and then transferred from each sieve to a weighing tray for measurement.

Sediment particle size distributions were analyzed using Bray-Curtis distance matrix dissimilarity values (Bray and Curtis 1957, Beals 1984). The Bray Curtis index is one of the best known similarity indices, comparing the similarity between two classes (here Φ), *i* and j within or between a set (*k*):

$$BC_{ij} = \sum_k \frac{|n_{ik} - n_{jk}|}{n_{ik} + n_{jk}} \qquad \text{Equation 2}$$

BC_{ij} can range from 0 to 1, with zero indicating highest dissimilarity and 1 indicating identical composition between the two sets. Proportion of total weight in each sediment particle size class was paired to compare similarities between sites. Additionally, G-tests were performed comparing sediment distributions of one site with *Myriophyllum spicatum* to all other sites, and one site with *Ranunculus aquatilus* with all other sites to test for significant dissimilarity between those sites that can support aquatic macrophyte growth, and those that likely cannot.

Sediment porewater nutrients

Sediment porewater nutrient composition was measured in 13 sites and 24 microsites monthly from July to September 2006 in Lake Tahoe littoral zone sediments. Mixed anion and cation resin capsules (Skogley 1996) were used to measure sediment nutrient bioavailability of NH_4, NO^-_3, ortho-phosphorus (a form of soluble reactive phosphorus that is ready for biological uptake), K+, Ca+2, Mg+2, Fe, and Mn. The resin capsules were buried in situ at a depth of 10-20 cm in marina and non-marina environments, recovered after one week, immediately rinsed extensively with deionized water and stored in refrigeration until laboratory analysis. Laboratory analysis was carried out at the University of Nevada Reno, USDA-ARS soils chemistry laboratory and followed the protocol of Blank et al. (2007). Capsules are rinsed again with DI water and placed in clean 50-mL polypropylene tubes and dried. Adsorbed solutes were released by adding

40 mL of 1 N HCl and shaking for 1 hour on a reciprocating shaker. After shaking, tubes were centrifuged, decanted into clean 50-mL polypropylene tubes, and stored until analyzed. For each analysis time, 2 to 4 blanks (fresh resin capsules) were made up similarly. Nitrate, NH_4, and ortho-P were quantified using the Lachat flow-injection system (Lachat Corp, Mequon, WI). Ortho-P was quantified using a vanomolybdate module suitable for high-acid matrices. All other sorbed nutrients were measured by atomic-adsorption spectroscopy (Fe, Mn, Ca, Mg) or atomic-emission spectroscopy (K). All standards were made up in 1 N HCl using certified standards. Data were converted to micromoles sorbed per day and analyzed using single factor ANOVA by site.

Primary productivity

Water samples for chlorophyll *a* and pheophytin *a* analysis were collected from 13 sites and 24 microsites in Lake Tahoe's nearshore on a bi-monthly schedule from July through September 2006. 1000 mL of surface water was obtained by a grab in HDPE polymer bottles rinsed in deionized water, stored on ice, and returned to a laboratory within four hours of collection for filtration. 200 mL of lake waters were vacuum filtered under low light conditions on 49 mm 0.45 µm Whatman GF/C filter paper, folded in half, placed in an aluminum foil pouch and frozen at -20° C until extraction. 50 mL of HPLC grade methanol were added to filters in light limited containers and refrigerated for 12 hours. After this steeping, 5 mL of sample were extracted and added to a 90% acetone solution. This sample was then measured in fluorometer, acidified with a 0.1 N HCl solution, vortexed, and after 90 seconds measured again in the fluorometer. Calculation of chlorophyll *a* and pheophytin *a* concentrations follows EPA protocol 445 (Arar and Collins 1997). Data were analyzed using one way ANOVA by site location.

Water column attributes

Dissolved oxygen, pH, surface and bottom temperature, and turbidity were measured bi-monthly for 13 sites and 24 microsites around Lake Tahoe from July through September 2006. Dissolved oxygen and surface and bottom temperatures were measured with a YSI 55 handheld dissolved oxygen meter with a 0-20 mg/L: ±0.3 mg/L or ±2% of reading accuracy and a 0.1% mg/L resolution. pH and surface temperatures were measured with an Acorn pH 5 meter with temperature probe. Turbidity samples were collected in the field and measured in the laboratory.

Wave action

To gauge the amount of energy or wave action in nearshore zones in Lake Tahoe, change in vertical pressure was measured using RBR DR-1050 Depth Pressure sensors at 13 locations around the lake (Figure 1). Pressure measurements with the DR-1050 are made to 24-bit resolution and are calibrated to an accuracy of ±0.05 % full scale using NIST traceable standards. Pressure sensors were placed at approximately the same depth (3 m) in all sites attached to the base of boat dock supports. The sensors were set at a 1 second sampling interval for a period of 10 days from August through September 2006. Because there were only four sensors and a limited field period, measurements were taken continuously at the Crystal Bay site (CBI) in the northern end of the lake with a single logger, and three other loggers were moved every ten day periods. The continuous measurements taken at CBI were used to estimate significant wave heights (H_s, or the highest 1/3 of all waves measured—described in detail below) during the weeks for which a site did not have a logger present by using ratios of H_s from periods which pressure sensors were deployed at both sites to extrapolate H_s to the period for which the pressure sensor was only deployed at the control site (CBI).

Change in surface water depth is calculated using the following pressure to wave height conversions:

$$pressure = p - Atmospheric\ pressure\ (dBar) \qquad \text{Equation 3}$$

Where p = pressure reading from the sensor (dBar), and Atmospheric pressure is the calibration for high elevation conditions at Lake Tahoe (approximate 6200 foot lake elevation). The conversion of pressure into depth is described by the following equation:

$$depth(m) = \frac{pressure}{g\rho} \qquad \text{Equation 4}$$

Where g= 0.980665 is a gravitational constant in m/s^2, and ρ is the density of the water, default value is 1.0 g/mL^3 for freshwater. To characterize the lake state in the various nearshore areas, significant wave heights (H_s), maximum wave heights (H_{max}), and the root mean square wave heights (H_{rms}) were determined for all sites (Dean and Dalrymple 1991). Significant wave height, H_s, is equal to the average of the highest one-third of the waves, H_{max} is simply the largest wave height, and H_{rms} is defined as the square root of the average of the squares of all (N) wave heights (H); (it is often approximately equal to H_s divided by 1.4):

$$H_{rms} = \sqrt{\frac{1}{N}\sum_{i=1}^{N} H_i^2} \qquad \text{Equation 5}$$

These definitions are simple means to analyze a group of waves (N) measured at one point. To illustrate, H_s characterizes the highest N/3 waves. So, the probability that the wave height is greater than or equal to an arbitrary wave height $\hat{H}$ is:

$$P(H > \hat{H}) = \frac{n}{N} \qquad \text{Equation 6}$$

Where n is the number of waves higher than $\hat{H}$. Wave theory (Longuet-Higgins and Watts 1952) has shown that the probability of the wave height being greater than or equal to an arbitrary wave height is usually described by the Raleigh distribution:

$$P(H \geq \hat{H} = e^{-\left(\frac{\hat{H}}{H_{rms}}\right)^{2}} \qquad \text{Equation 7}$$

Here, H_{ms} of the CRM site was used to determine $\hat{H}$ (Equation 6) to compare the maximum relative wave height for watermilfoil growth in Lake Tahoe. The significant wave height of site CRM was chosen as Ĥ because it is a site to which Eurasian watermilfoil frequently arrives but fails to establish. CRM is in close proximity to the Tahoe Keys (site with the largest infestation of watermilfoil in Lake Tahoe), has an abundance of boater visitation (popular restaurant/bar/beach site amongst surveyed boaters), and frequently contains profuse drifting fragments (personal observation) throughout the summer period. Although a few fragments successfully rooted during September 2005-2007, none survived to the following spring. These factors lead to the assumption that while propagule pressure is abundant, and sediment quality is appropriate to support localized growth, the physical characteristic of the water column is a limiting factor. Therefore, any site with H_{rms} greater than CRM is removed from consideration in the model.

Surface current trackers

In 2007 two GPS-tracked Lagrangian current trackers (manufactured by PME) were released at one location in Lake Tahoe off the eastern Channel of the Tahoe Keys to reveal large-scale transport patterns of surface currents along the southern shore of Lake Tahoe (Figure 3). They grounded two days after deployment, but were recovered 5 days after deployment due to storm conditions. Both drogues were tethered at 1 meter below the surface. These experiments were designed to illustrate the general current flow direction along the southern shore of the Lake, to approach the question of whether or not the eastward movement of *M. spicatum* invasion is a result of the dominant current. Unfortunately, only two deployments occurred as a result of instrument failure and poor weather conditions.

Eurasian watermilfoil presence and absence mapping

I consider a time-series data set with information on date of invasion at each location in Lake Tahoe since 1995 when macrophyte surveys by Lars Anderson of the USDA-Agricultural Research Service (ARS) began (Figure 4). Surveys were conducted over a multiweek period during the summer growth period with 2-3 boats travelling along the entirety of the Lake Tahoe shoreline, including within marina and embayments visually looking for “dark spots” or underwater indications of aquatic macrophytes. If a dark spot was identified, a double-edged rake was cast into the area multiple times and any aquatic macrophytes entrained were brought back to the USDA-ARS laboratory for identification and indication of *M. spicatum* presence or absence.

2. *RECREATIONAL BOATING MOVEMENT*

Boater pathways and propagule pressure model

To determine the pathways of Lake Tahoe boaters, individuals (N=778) were interviewed at boat ramps at the conclusion of their tour and asked questions about where they stopped for gas, food, recreation, anchoring and/or beach visitation. Interviews were conducted at public and private Lake Tahoe boat launches during the summer periods of 2005 and 2006 on 30 dates from July-September 2005 and June-September 2006. Of the 30 dates, 14 were weekdays, and 16 were weekends and/or holidays and on any given date, interviews were conducted for an 8-10 hour period between 8 A.M. and 6:00 P.M. All departing boaters were approached for interviews until the rate of departure exceeded the capacity of the interviewer, at which time the most recently retrieved boat was approached for the next interview. Interviews were initiated as boaters departed the launch ramp usually during the boat "tie down" period before departing the premises. Only six boaters refused interview (<1%), and the interviewer did not approach individuals that seemed to be experiencing extenuating difficulties. The interview consisted of ten questions (Figure 5) and lasted an average of 5–10 min. Questions relevant to this study pertained to the boater's launch origination and trips made between nearshore zones. Boater trips were used to estimate propagule pressure of *M. spicatum* within Lake Tahoe. Each trip to a location from an invaded location by a boat constitutes one potential propagule. It is assumed that if a boat travels to a site that contains *M. spicatum* then it is contaminated (carries a viable plant fragment). The propagule pressure model considered here is adapted from Leung et al. 2004, "Predicting Invasions: Propagule Pressure and the Gravity of Allee Effects". The model is as follows:

If propagules each have an independent chance of establishment, the total probability of establishment (*E*) would be the complement of all propagules failing to establish:

$$E(N_{l,t}) = 1 - (1 - p)^{N_{l,t}} \qquad \text{Equation 8}$$

p is the probability of a single propagule establishing and N is the number of propagules arriving at location *l* at time *t*. This can also be written as a standard asymptotic curve:

$$E(N_{l,t}) = 1 - e^{-\alpha N_{l,t}} \qquad \text{Equation 9}$$

where α is a shape coefficient and is equal to *-ln(1-p),* the larger α is, the higher the probability of establishment. *Myriophyllum* has been reported to be present in the southern portion of the Lake in the Tahoe Keys as early as the 1960's, with infestations becoming noticeably unmanageable in the 1980's, as indicated by the purchase of 2 harvester machines. I began the time series in 1990 with *Myriophyllum* presence assumed only in the Tahoe Keys; it is unknown where populations occur outside of the Tahoe Keys area before 1995. As the invasion of Lake Tahoe's littoral zone progresses, more sites become sources which changes propagule pressure. The likelihood of observing our data set (invasion chronology) given our model (Equation 8) can be determined and related to the probability of establishment to propagule pressure. This is done by considering the probability (*H*) of observing the pattern at each location *l*. Specifically, for locations that become invaded at time *t,* I consider the joint probabilities of becoming invaded at time *t* and of remaining uninvaded up to time *t,* given the history of propagule pressure. For locations that have become invaded, the probability is:

$$H_l = E(N_{l,t}) \prod_{i=1}^{t-1} \left[1 = E(N_{l,i}) \right] \qquad \text{Equation 10}$$

The probability of remaining uninvaded during a time interval *i*, would simply be the complement of *E.* For locations that do not become invaded for the duration of the study (*T*), the joint probabilities over time of remaining uninvaded given the history of propagule pressure:

$$H_l = \prod_{i=1}^{T} \left[1 - E(N_{l,i}) \right] \qquad \text{Equation 11}$$

The log-likelihood (**L**) for the entire data set (**D**) given a model (*M*) would be

$$L(D \mid M) = \sum_{l=1}^{L} \ln(H_l) \qquad \text{Equation 12}$$

where H_l is determined using Equation 10 for invaded locations, and Equation 11 for locations that did not become invaded during the study.

B. WESTERN WATER BODIES CONNECTED TO LAKE TAHOE BY RECREATIONAL BOATING—NEARSHORE HABITAT CHARACTERIZATION AND BOATER TRAFFIC

Recreational boating surveys collected at Lake Tahoe during project year one and two (2005-2006) were used to determine waterways are most highly correlated with Lake Tahoe via boater traffic. The same physical habitat parameters as described in Part A were collected from these waterways in order to determine habitat suitability for *M. spicatum*. Additionally, boater traffic data was used to assess Californian and Nevadan boater movement tendencies, attraction to particular waterways, as well as habits and knowledge of AIS in relation to recreational boating activity.

1. *NEARSHORE HABITAT CHARACTERIZATION*

Similar techniques in section IIIA1 were used at other lakes. Please refer to this section for methodological details.

2. *RECREATIONAL BOATING*

I compare two surveys; one collected from 7 boat launch sites at a single water body, Lake Tahoe, CA-NV (N=778), and the other collected from 54 launch sites at 27 lakes, rivers and reservoirs in California and Nevada by the U.S. Fish and Wildlife Service 100th Meridian Initiative Program (N=1313) to assess differences between a single-site versus a multiple site survey administration. These surveys represent visitation to 27 inland water bodies by Californian and Nevadan recreational boaters. Using logistic regression, I will show that both distance travelled and waterway specific characteristics are important to boaters' destination site selection. Existing ecological literature have used lake or reservoir surface area to define the attractiveness term in a gravity model (Reed-Andersen et al. 2000, Bossenbroek et al. 2001, Leung et al. 2006b, Lodge et al. 2006). Here I show that in addition to surface area, Californian and Nevadan boaters value other lake-specific attributes including water quality, vessel accommodation and personal convenience. Populating gravity models with these terms impacts both model parameterization and subsequent estimates of aquatic invasive species propagule pressure by recreational boating. The Tahoe and 100th Meridian surveys show similar results in attractiveness factors, yet show differences in site selection and travel distance taken.

Lake Tahoe Boater Survey

To identify and estimate pathways of recreational boaters in the Lake Tahoe region, boaters were interviewed by the author at 7 public and private Lake Tahoe boat launches during the summer periods of 2005 and 2006 (Figure 2). Interviews were conducted on 30 dates from July-September 2005 and June-September 2006. Of the 30 dates, 14 were weekdays, and 16 were weekends and/or holidays; on any given date, interviews were conducted for an 8-10 hour period between 8 A.M. and 6:00 P.M. All departing boaters were approached for interviews until the rate of departure exceeded the capacity of the interviewer, at which time the most recently retrieved boat was approached for the next interview. Interviews were initiated as boaters departed the launch ramp usually during the boat "tie down" period before departing the premises. Only six boaters refused interview (<1%), and individuals that seemed to be experiencing extenuating difficulties were not approached. The interview consisted of ten questions and lasted an average of 5–10 min. Questions relevant to this study pertained to the boater's origination zip code, previously visited destinations as well as the anticipated time and location of the boat's next use. Additional questions related to boat cleaning habits and knowledge or experience with aquatic invasive species. Survey respondents from 227 origination zip codes identified 27 preferred destinations associated with their prior outing (Figure 6, Figure 8). These destinations are the primary focus of this analysis.

100th Meridian Boater Survey

The 100th Meridian Initiative Survey was performed by interviewers employed by the U.S. Fish and Wildlife Service from 54 total launch sites at 27 water bodies: Sacramento-San Joaquin Delta, Lake Elsinore, Lake Kaweah, San Antonio Reservoir, Claire Eagle Lake, Clear Lake, Colorado River, Feather River, Folsom Lake, Fox Lake, Lake Mead, Illipah Reservoir, Lake Amador, Lake Berryessa, Lake Davis, Sacramento River, Lake Del Valle, San Joaquin River, Old River (Grant Line Canal), Lake Havasu, Oroville, Lake Piru, Lake Tahoe, Rollins Reservoir, San Joaquin River, Lake Shasta, and the South Fork Mokelumne. The protocol was similar to the Tahoe survey described above: interviewers approached individual boaters directly as they remove vessels from launch areas. Interviewers were guided by a survey form to gather information from individual boaters regarding movements, boat usage, storage, and knowledge of zebra mussels. In some cases, the form was left on the windshield of unattended vehicles with boat trailers. Boaters were asked to fill in the forms at their leisure and return them in a self-addressed, stamped envelope provided. This survey yielded 249 origination zip codes for the same selection set of 27 destination lakes (Figure 7, Figure 8).

Waterway facilities

The California Department of Boating and Waterways facilities Needs Assessment (2001) gave a comprehensive assessment of boats and boating facilities and is used by the agency allocate of funding for boating facilities, including launch ramps, dry storage, marinas, and support features. These data provided information on infrastructure, water quality and sports fishery. Table 2 shows the waterway variables considered from this report. Correlation analysis was carried out to remove redundant variables (R>0.9), those marked with an asterisk in Table 2 are the variables ultimately used in this analysis.

Water Quality

Secchi depth data were obtained from field collections by the authors, waterway managers, scientists, and county and state water resource agencies. Secchi depth values are averaged both spatially and temporally to a single estimate of the water clarity for an entire water body. Where there was only one measurement, this is the only value considered. Water clarity is a dynamic measurement that can vary significantly over time and space within a water body. The usage of average secchi depth here is not intended to characterize an absolute metric of water quality, but rather is used to represent an estimate of the generalized water quality that any individual boater may use to select destination.

Distance Data

To determine the most direct road distances travelled by recreational boaters between zip code centroid, the assumed centers of populations density, and boat launch locations, the origin-destination routine (OD cost matrix) of Network Analyst, ArcGIS 9.2 (ESRI, Redlands, CA) was specified using major highways and interstates of California and Nevada. A 10 km search distance was used to join centroids and boat ramps to the road network.

Sports Fishery Data

To quantify the number and type of sports fish within particular waterways, two online sports fish directories were accessed. Both the California Department of Fish and Game ("California Fishing Passport Program") and the Nevada Department of Wildlife ("Fish Nevada") have developed online fishing guides that provide information regarding the freshwater sports fishery by specific lake, reservoir or river. Sports fishery information for the 27 waterways considered in this study was collected from these websites.

Boater movement modeling

Logit model

Logistic regression was used to estimate the probability of visitation to each site from major metropolitan areas captured in the survey in order to determine which attributes of each lake or reservoir destination were most important for the prediction of visitation to these lakes. The dependent variable is the number of visits to a particular waterway given the number of recreational boaters interviewed from that city. Logistic regression was carried out by city, for those cities with (N>30 interviews) in independent or combined surveys. Zip code was chosen as the unit of analysis to address both spatial and social heterogeneities amongst the boating population. In other words, given that a set of boaters have a similar origin helps reduce exogenous variables in waterway destination. Independent variables were distance from city center, and the suite of waterway specific characteristics described above. I selected a model using using stepwise regression, with parsimonious model selection using the Akaike Information Criterion (AIC) (Bozdogan 1987). The logit model used here is as follows, the linear model for transformed probabilities can be expressed as:

$$\log it\, p = \beta_0 + \beta_1 x \ + \beta_2 + \ldots \beta_k x_k \qquad \text{Equation 13}$$

Logit p = log[p(1-p)] is the *log odds, w*here p = proportion of individuals visiting waterway *i*, and (1-p) is the proportion of individuals selecting one of the other waterway destinations in the selection set. Variables selected via logistic regression analysis were then used to fit the attractiveness terms of the gravity model.

Gravity Model

Gravity models are a type of spatial interaction model that predicts the size of flow between pairs of places. To quantify the potential flows of recreational boating traffic to California and Nevadan water bodies, I developed a production-constrained gravity model. The production-constrained gravity model is a form used when the total number of flows leaving each zone i is known; compared to a production-attraction constrained model where the flows arriving in zone j is also known. There are three assumptions of a gravity model. The first is that the size of any flow is proportional to a variable O_i which measures the trip generation capacity of the region where the flow begins, i.e., flow is related to the size of the originating population.

$$T_{ij} \sim O_i \qquad \text{Equation 14}$$

This asserts a linear relationship, which does not necessarily have to hold (Leung et al. 2006b). Secondly, the size of T_{ij} is also proportional to the variable W_j which measures the trip-attraction capacity of the region where the flow ends. The commonly used attractiveness term is waterway surface area which has been shown to be positively correlated with boater visitation (Reed-Andersen et al. 2000, Leung et al. 2004).

$$T_{ij} \sim W_j \qquad \text{Equation 15}$$

Thirdly, the amount of interaction T_{ij} declines in relation to the distance d between two regions.

$$T_{ij} \sim \frac{1}{F(d)} \qquad \text{Equation 16}$$

This is described as the "distance decay" or the deterrence function, which in the common form of the gravity model, $F(d) = d_{ij}^{\alpha}$. This term reflects the assumed perception of distance as a deterrent to interaction (Fotheringham 1981). Thus, flow is denoted by the variable T_{ij} where T measures the size of the predicted flow, i, is a subscript which identifies the place where flow begins and j is a subscript that identifies where the flow ends. The number of visitations (T_j) to a destination (j) depends on the number of vectors (O_i) at each source location (i), the attraction of the destination location (W_j), the distance between the source and destination (d_{ij}). The basic production-constrained gravity model is defined by the equations:

$$U_j = \sum_{i=1}^{K} A_i O_i W_j d_{ij}^{-\alpha} \qquad \text{Equation 17}$$

$$T_j = f(U_j) \qquad \text{Equation 18}$$

Where U_{ij} is a metric of vector traffic from the gravity model, and T_j is the full model's prediction of actual traffic and a determinant of propagule pressure to waterbody j, K is the number of sources, and α is a shape parameter describing the relation between traffic and distance, and A_i is a balancing factor that ensures that all boat originations have a destination at one of the water ways represented in this analysis. For this study, I modeled boater traffic from Californian and Nevadan cities (zip codes) to 26 of the most-visited

Californian and Nevadan waterways as determined from the Lake Tahoe boater survey. I parameterized specific gravity model terms α, β, γ, and δ:

$$T_{ij} = A_i * X_j^{\beta} * Y_j^{\gamma} * Z_j^{\delta} \ldots d_{ij}^{-\alpha} \qquad \text{Equation 19}$$

(where X_j, Y_j, and Z_j... are the set of variables comprising the attractiveness term W_j). Parameters were estimated using the Nelder-Mead simplex (direct search) algorithm, and the objective function sought to produce a linear relationship to maximize the Pearson correlation between model output and empirical data showing the total boater arrivals at each water body. I assessed model performance by regressing estimates of boat traffic generated from the model (U_j) on empirical measures of boat traffic from surveys conducted at Lake Tahoe and by the U.S. Fish and Wildlife Service 100th Meridian Initiative at locations in California and Nevada. Actual boater visitation was estimated from sites reported by survey respondents as the site of prior visitation. The model was parameterized for both the 100th Meridian Survey Data and the Tahoe Survey data. To test for the effect of using a single site administered survey to estimate visitation to water ways distributed over a wide landscape, the model parameterized by the Lake Tahoe survey was then used to predict empirically estimated flows of the more widely administered 100th Meridian survey.

V. Results

A. WITHIN LAKE TAHOE STUDY

Some uninvaded nearshore sites of Lake Tahoe significantly differed from invaded sites due to amount of wave action and sediment particle size distributions. Sediment nutrient levels, turbidity, and temperatures were not significantly different across all sites, and while chlorophyll a levels did differ across sites, their magnitudes are too low to show important nutrient spikes in the water column.

Sediment particle size analysis shows a mildly varied distribution of sediment types around the lake, with most sediments comprised of sandy to coarse sandy particles (Figures 9, 10, 11). Sites that contained finer sands were generally located in Marinas and at the mouths of major creeks such as the Boatworks (BWM) and High Sierra (KBG) marinas and Sugarpine Point (SPE) which is at the mouth of General Creek. To provide a metric for potentially suitable sediment types for watermilfoil growth in Lake Tahoe, sediment particle size distributions for all sites were compared against two sites that contain Eurasian watermilfoil (Crystal Bay Marina (CBI2)), and Buttercup (*Ranunculus aquatilus*), Camp Richardson Marina (CRM2)—these sites represent sediment types that are capable of supporting submersed macrophyte growth. A maximum likelihood statistical significance "G" test (Sokal and Rohlf 1994) was used to compare the distributions of values in the two data vectors X1 and X2 of length n1 and n2, representing sediment samples by class size distribution. The null hypothesis for this test is that X_1 and X_2 are drawn from the same distribution. The alternative hypothesis is that they are drawn from different distributions. In all cases, comparing sediment particle size distributions of sites with watermilfoil (CBI2) and Buttercup (CRM2) to all sites without macrophytes, results show that ten sites measured were significantly different than those that support macrophytes: BWM-1, BWM-2, CR-1, CR-2, KBG-1, KBG-2, RHP-2, SPE-2, LFL-1, CRM-1 (Table 4, Table 5). Interestingly, CRM-1 is a microsite of the Camp Richardson Marina site, where CRM-2 supports *Ranunculus* growth—showing intra-site variability in sediment type. Additionally, the Bray-Curtis dissimilarity indices (3) for Lake Tahoe sediment particle size also show greater than average dissimilarity between those sites with macrophytes and those listed as different by the G-test results. These sites are removed from the establishment probability model.

Chlorophyll *a* levels (Figure 12, Table 6) were generally low across all sites with increases in seven locations. Elk Point Marina (EPM-1) and Crystal Bay Marina (CBI-2) both show higher average chlorophyll *a* concentrations, likely as a result of the macrophyte growth in these locations, Eurasian watermilfoil and other species. Two sites at the Boatworks Marina in Tahoe City (BWM-1, BWM-2) as well as Sugarpine Point (SPE-2) also show slight increases in chlorophyll concentrations, which could be attributed to their locations in relation to creek runoff. Two other sites, High Sierra Boat Company Marina (KBG-1) and the Lake Forest Launch (LFL-2) also show chlorophyll *a* concentrations slightly above the average. Despite a few minor departures from the average, the overall levels of chlorophyll *a* at all sites are low and similar to each other.

Sediment porewater nutrient content is also relatively similar amongst sites (Figures 13-20, Table 7). Values of ammonia (NH_4) were similar for most sites with departures from the mean for two sites containing aquatic macrophytes, CBI-2 and CRM-2. Two marinas, BWM-1, CRM-1 and one public launch site, LFL-1, also contained similar levels of NH_4 to sites with macrophytes, but not significantly different from other sites. There were higher levels of Ortho-P at two marinas, BWM and CBI-2, the latter infested with Eurasian watermilfoil. Again, SPE-2, or Sugarpine Point, located at the mouth of General Creek, also showed elevated levels of ortho-P. Mn and Fe are known to inhibit Eurasian watermilfoil growth in high enough concentrations, yet values of these elements in all sites do not exceed levels in sites where milfoil and other aquatic macrophytes are present. Anderson and Kalff (1986) showed that Eurasian watermilfoil is nitrogen limited, and produces the greatest biomass under sediment nutrient levels of NH_4 at ~500 $\mu g\ g^{-1}$ which is equivalent to 579 parts per thousand, several orders of magnitude higher than the highest concentrations measured in Lake Tahoe. These authors also show that when sediments with elevated levels of ortho-P and elevated levels of a suite of NH4 + ortho-P + K produces the greatest Eurasian water milfoil increases in biomass. Sites with the highest levels of ortho-P in Lake Tahoe (BWM-2, SPE-2) have unsuitable sediment types and nearshore wave action (discussed below) for Eurasian watermilfoil growth. There are no sites that show positive correlations in the suite of sediment nutrients that are beneficial for Eurasian watermilfoil growth. Measurements of pH, temperature and turbidity are similar at all marina and nearshore sites within the littoral zone during the summer period.

In general, the eastern shore of Lake Tahoe receives more wave action than the west shore of the lake. Pressure sensor measurements also reflected this to be true during the summer of 2006. Of 13 sites measured over the course of a 10 week period, those with high significant wave heights (H_s) and maximum wave heights (H_{max}) were east shore sites: Cave Rock (CR), Elk Point (EPM), Round Hill Pines (RHP), Sand Harbor (SH), Zephyr Cove (ZPH), and north shore site Crystal Bay (CBI) and south west shore site Sugarpine Point (SPE) (Figure 21, Table 8). Sites for which their H_{rms} exceeding the H_{rms} of CRM were removed as sites eligible for Eurasian watermilfoil establishment (Table 8). Schutten et al. (2004) have shown that wave heights greater than 0.2 m have enough hydraulic force to break Eurasian watermilfoil stems. While all sites measured in Lake Tahoe have significant wave heights below 0.1 m, most sites have H_{max} above 0.2 m, with a number of sites (Crystal Bay, Cave Rock, Sand Harbor, and Sugar Pine Point) exceeding 0.3 m. As discussed below, removing these sites from the propagule pressure model leads to an improvement of model performance.

Boater dispersal of Eurasian watermilfoil propagules

The maximum likelihood estimate of $\alpha = 3.9^{-5}$; removing the seven waviest locations from the estimation increases the estimate to $\alpha = 8.0^{-5}$. Further, removing those sites with significantly different sediment particle size distributions (in addition to the wavy site removal), gives a maximum likelihood estimate for $\alpha = 0.000139$.

Probabilities of invasion increase significantly once populations begin to disperse to locations around the lake (Figure 22). This simulation begins in 1990; the Tahoe Keys being the only location considered as invaded. As more locations become invaded, the number of boats that are carrying fragments to boater destinations increases, thus increasing the likelihood for introduction and subsequent establishment. However, a number of locations that are predicted to have a high probability of establishment (Lake Forest Launch, Cave Rock, Sand Harbor, Sugarpine Point, CRM, Rubicon Bay) are not positive for Eurasian watermilfoil. At the same time, there are a number of locations that have very low or zero predicted probabilities of establishment as a function of boater traffic, yet are positive for Eurasian watermilfoil (Figure 23). To test the performance of the model and further investigate the rate of false positives and false negatives, Receiver Operating Characteristic Analysis was used (Metz 1978). This analysis measures discrimination capacity in terms of the area under a relative operating characteristic (ROC) curve relating relative proportions of correctly and incorrectly classified predictions over a wide and continuous range of threshold levels (Pearce and Ferrier 2000). This technique uses two indices: Sensitivity and False Positives, to describe the predictive performance of models, and are defined as follows:

$$Sensitivity = \frac{Number\ of\ Positive\ Sites\ Correctly\ \Pr edicted}{Total\ Number\ of\ Positive\ Sites}$$

$$False\ Positive\ Fraction = \frac{Number\ of\ False\ Positive\ \mathrm{Pr}\ edictions}{Total\ Number\ of\ Negative\ Sites}$$

Each pair of sensitivity and false positive values can be plotted as the *y* and *x* coordinates respectively on a graph, and these determine a curve called the ROC curve. The ROC curve describes the compromises that are made between the sensitivity and false positive fractions as the decision threshold is varied. The steeper an ROC curve is (i.e., a greater area underneath the curve) exemplifies a model that has a high discrimination ability, or rather, the ability to accurately predict. For further discussion of ROC curves, their derivations and interpretations see (Pearce and Ferrier 2000).

Figure 24 shows the ROC curve for the propagule pressure model including all sites (α=0.000039), a model with the waviest sites removed (α=0.00008), and finally a model with the waviest and significantly different sediment sites removed (α=0.000139). The area underneath the curve (AOC), or discrimination capacity, of the all-sites included model was calculated to be 0.6526 indicating that the model can correctly discriminate between occupied and unoccupied sites 65.26% of the time. In other words, if a pair of evaluation sites (one occupied and the other unoccupied) is chosen at random, then there is a 0.6526 probability that the model will predict a higher likelihood of occurrence for the occupied site than for the unoccupied site. The AOC of the wavy-sites removed model is 0.7129, indicating that the model can correctly discriminate between occupied and unoccupied sites 71.29% of the time. AOC of the wavy and differing sediment removed models is 0.7320, showing a very slight improvement in model performance. In general, areas between 0.5 and 0.7 indicate poor discrimination capacity because the sensitivity rate is not much more than the false positive rate (Pearce and Ferrier 2000). Values between 0.7 and 0.9 indicate a reasonable discrimination ability appropriate for many uses, and rates higher that 0.9 indicate very good discrimination because the sensitivity rate is high relative to the false positive rate (Swets 1986). All three models tested here display poor to reasonable power of discrimination. However, the ROC curves illustrate that the removal of sites assumed to be habitat limited increases the discrimination power of the propagule model.

B. WESTERN WATER BODIES CONNECTED TO LAKE TAHOE BY RECREATIONAL BOATING STUDY

1. NEARSHORE HABITAT CHARACTERIZATION

In order to identify which waterways were most at risk of Eurasian watermilfoil invasion the following variables were measured at 10 lakes and reservoirs (Figure 25) that are connected to Lake Tahoe via recreational boating traffic: primary productivity, secchi depth, sediment particle size, sediment nutrient content, dissolved oxygen, temperature, pH, and the change in lake or reservoir level elevation during the water year 2007. Additionally, snorkel surveys for Eurasian watermilfoil presence were taken at boat entry points of each waterway. Nearshore habitat characterizations are then compared to literature based indicators of Eurasian watermilfoil success as discussed in results section A above. Based on these indicators in combination with magnitude of boat traffic, the sampled waterways were placed into three categories: 1) Established Eurasian watermilfoil populations already present, 2) High risk for Eurasian watermilfoil establishment, and 3) Low risk for Eurasian watermilfoil establishment.

Carlson's trophic state index was calculated for each waterway based on 8 chlorophyll a measurements during the summer growth period in 2007 (Figure 26). Those waterways that indicated mesotrophy or eutrophy were considered to be higher risk for Eurasian watermilfoil success based on this indication of nutrient availability (Madsen 1999). Folsom Lake, Lahontan reservoir, Pyramid Lake, Stampede Reservoir and Topaz Lake fell into this category—showing elevated levels of water column primary productivity in marina or launch sites.

Sediment particle size distributions (Figures 27-29) with the bulk of materials in the positive Phi categories were selected as higher risk substrates for Eurasian watermilfoil (Barko and Smart 1986). Sites in Boca Reservoir, Stampede reservoir, Fallenleaf Lake, and Topaz Lake indicated appropriate sediment type for Eurasian watermilfoil growth. However, the range of sediment types where Eurasian watermilfoil can establish is large—there are high density populations of Eurasian watermilfoil in Lake Berryessa, which has a sediment particle size distribution different from what the literature suggests would be an optimal growth substrate. As a result, those sites that have sediment particle size distributions similar to Lake Berryessa are also placed into the high risk category—this includes Folsom Lake.

Sediment nutrient content (Figures 30-33) also varied by waterway and by site within waterway. Those sites with the highest levels of sediment porewater ortho-phosphate and ammonia, and those with the lowest levels of Fe and Mn, elements known to be toxic to Eurasian watermilfoil establishment in high concentrations (Barko and Smart 1986, Madsen 1989), were placed in the high risk establishment category, all others in the low risk establishment. Those waterways in the high risk category include Stampede, Lake Berryessa, Lahontan, Folsom Lake and Topaz Lake.

Finally, the rate of water level decline per year is another factor that can impact the probability of Eurasian watermilfoil establishment. Some reservoirs, like Lake Shasta, drop lake levels approximately 6 inches per day during the summer season, thus exposing possible aquatic plant populations to desiccation. This process is likely to be a controlling factor for submersed aquatic weeds in many reservoirs. Figure 34 shows the annual drop in water level in 2007. With Lake Shasta and Folsom Lake showing the greatest drops. September of 2007 left all marina field sites in both of these waterways completely dry—a possible explanation for the lack of rooted plant material in these systems given the repeated exposure to recreational boating traffic.

The risk categorizations for the surveyed water bodies are as follows: (1) Established Eurasian watermilfoil populations: Lake Berryessa, Spooner Lake, (2) High risk for Eurasian watermilfoil establishment: Topaz Lake, Donner Lake, Fallenleaf Lake, Lahontan Reservoir, Stampede Reservoir, (3) Low risk for Eurasian watermilfoil establishment: Shasta Lake, Boca Reservoir, Pyramid Lake, Folsom Lake.

2. *GRAVITY MODELING TO PREDICT BOATER TRAVEL*

The proportion of boaters travelling to each waterway location represented in this study differed by survey (Figure 35). The 100th Meridian Survey showed that most boaters travelled to the Sacramento-San Joaquin Delta, Lake Mead, and the Sacramento River, whereas most boaters of the Tahoe survey travelled to Lake Tahoe, Folsom Lake and the Sacramento-San Joaquin Delta. The average distance travelled by Tahoe-surveyed boaters to boating destination was 223 (s.d. 278) kilometers and the average distance travelled by the 100th Meridian Boaters was 165 (s.d. 298) kilometers. The two surveys show similar ranges of distances travelled to waterway sites, but differences in frequencies of travel to each location (Figure 8).

Survey results for eight cities (Carson City, Reno and Las Vegas of Nevada, and Sacramento, Roseville, Elk Grove, Tracy, and South Lake Tahoe of California) showed that important explanatory variables for boater site selection were the previously accepted terms: distance travelled and waterway surface area, but also included other terms such as Secchi depth, number of launch ramp lanes, fuel sales, convenience stores, fishing tackle sales and number of sports fish species. Three variables (in addition to distance): lake surface area, secchi depth, and number of ramp lanes were selected as attractiveness terms for use in the following gravity modeling analysis. It is unclear whether these variables are a cause or an effect of increased boater traffic, but it is assumed in this study that boaters are generally conscious of these terms when selecting a water way destination. These variables were selected because they were present in all of the best-fitting models for each city. X, Y and Z in equation 19 are thus represented by values of surface area, Secchi depth and number of ramp lanes for each waterway, thus the gravity model is specifically structured as:

$$T_{ij} = Ai * surface\_area_j^{\beta} * \sec chi_j^{\gamma} * ramp\_lanes_j^{\delta} * d_{ij}^{-\alpha} \qquad \text{Equation 20}$$

Parameter estimates and associated metrics are presented in Table 9. R^2 values are 0.87 for the 100th meridian survey and 0.97 for the Tahoe survey, suggesting that these are reasonable models—explaining much of the variation observed. Parameter estimates differ most for values of γ (secchi)—with a sign reverse between the two survey estimates. This is expected, given that most (~50% of site visits) of the Lake Tahoe survey are to Lake Tahoe which has an extreme secchi value compared to other waterways. Estimates of α, or the shape parameter describing the relationship between trips made and distance are similar between the two surveys. The 100th Meridian survey estimate of α is 1.3 and the Tahoe survey estimate is 1.6—both showing a relatively steep distance decay function where the majority of travel occurs within short distances to origination point, but with a long tail of low frequency long distance trips. Figure 36 and Figure 37 show scatter plots of empirical versus model output of the two surveys. The Lake Tahoe survey model is skewed in that the high volume of visitation to Lake Tahoe compared to the rest of the sites, altering the scale of the model fit. Next, I compared the

U_j with parameters estimated from the Tahoe survey to empirically estimated boat traffic of the 100th Meridian survey to assess predictive power of a single location administered survey to the more comprehensive, multi-location administered survey. This resulted in a Pearson's correlation value of 0.06, suggesting that this is an unreasonable model given the data (Figure 38). Rerunning the model with secchi depth (biased term given Tahoe's extreme Secchi value) removed as a model term gives the parameter estimates and model statistics in Table 10.

The models perform noticeably worse than with the Secchi term included (Table 10, Figure 39, Figure 40), though the relationship between the ability of the Tahoe model to predict the 100th Meridian data improves with an increase of Pearson's correlation value increasing from 0.06 to 0.31 (p-value: 0.003, F-statistic 7600.9) (Figure 41).

There is a site specific bias occurring at the Lake Tahoe administered survey, as most return visitation is to this site, and model parameterization is being driven by the extreme value of Lake Tahoe's Secchi depth. When removing Lake Tahoe from the parameterization of the model (all other sites considered), Figure 42 shows a divergence in empirical versus model prediction, indicating high variability in predictive power at low numbers. Using the Tahoe survey (with Lake Tahoe visits removed) parameterized model to against the 100th Meridian survey empirical data shows an improvement in predicting power than with Lake Tahoe visits included ($R^2 = 0.41$, p-value = 0.0004, f-statistic 17.0) (Figure 43). Therefore, while some of the visitation bias was decreased by removing Lake Tahoe, the Tahoe model still does not explain as much of the variation in boater site selection as the 100th Meridian survey model estimate.

Overall, estimates of T_j for the set of 27 waterbodies are significantly different between the two models (Figure 44) with a correlation coefficient of 0.05. These differences are caused mainly by the prediction of the most heavily visited sites, with the Tahoe survey being highly skewed towards Lake Tahoe and waterways close to Lake Tahoe like Lake Berryessa, the Delta, Lake Anderson, Pyramid, and Oroville (Figure 45). The 100th Meridian model predicts the highest visitation to the Delta, the Sacramento River, Folsom Lake, Lake Mead, and Lahontan Reservoir.

3. *BOATER RISK*

The Lake Tahoe boater survey also incorporated an inspection of vessels leaving Lake Tahoe for entrainment of Eurasian watermilfoil, and also addressed the previous and future planned uses of water bodies by Lake Tahoe boaters. Finally, the survey included questions regarding each individual's boat cleaning and inspection habits as it relates to AIS entrainment.

Of 778 boats that were inspected upon departure from Lake Tahoe, 117 (15%) of these had some sort of aquatic vegetation entrained on some portion of the vessel (outboards, propellers, trailers, etc.); 106 were from the Tahoe Keys Marina (site of the largest Eurasian watermilfoil and other aquatic plant species populations), 8 from Meeks Bay Marina, and 3 from the El Dorado boat launch. Species found include: *Myriophyllum spp.*

*(*Watermilfoil), *Ceratophyllum demersum* (Coontail), *Elodea canadensis,* Various grasses, and *Potamogeton crispus* (Curlyleaf pondweed).

Survey respondents 82% never conduct inspections of boats or boating equipment for aquatic plants, yet over 70% wash their boats with high pressure or hot water (which can be an unintentional strategy to remove AIS) (Table 11). Within 7 days of their use in Lake Tahoe, 297 boaters have used their vessels in other waterways—these top waterways are listed in Figure 46. Of these 297 boaters, 241 have used their boats in water ways with known aquatic invasive species (Figure 47), with three of these waterways containing established populations of quagga mussel. Finally, Lake Tahoe is not only at risk of AIS introduction from other waterways, but can also present introduction risks for Eurasian watermilfoil, Curlyleaf pondweed and Asiatic clam to other waterways. Figure 48 shows the top expected destinations for Lake Tahoe boaters—with a majority of trips returning to Lake Tahoe, but a significant portion of the survey population also travelling to other waterways.

VI. CONCLUSIONS

Propagule pressure is an important component of any freshwater invasion; the establishment of a new population relies upon the delivery of viable individuals or fragments. This is relevant for Eurasian watermilfoil in Lake Tahoe, as this species relies on the movement of allo- or auto-fragments for range expansion. However, the transport of Eurasian watermilfoil as represented by boater traffic within the lake is a moderate predictor for its current distribution, suggesting that other dispersal mechanisms are also in effect. The establishment model performs well in terms of the rate of true positives, or the correlation of high boater traffic with observed populations in areas that are habitat appropriate for the growth of *M. spicatum*. However, there are an abundance of sites where the estimated probability of establishment as a function of boater traffic is <0.01, yet populations of *M. spicatum* have been present for long periods of the invasion record. This indicates that either the boater survey data do not accurately represent visitation, or that another physical process such as the movement of propagules by surface currents is important. The former is an important point because survey data regarding destination choice is relatively subjective. The survey questionnaire asks a boater places on the lake where she has stopped during her tour, relying on the boater's knowledge of site name. An improvement to this technique might be to present the boater with a map allowing the boater to indicate site selection visually. Additionally, it is rare that a fragment of Eurasian watermilfoil could get entrained on a propeller or other submersed portion of a boat for the duration of a multi-kilometer trip to the boater's destination. It is more likely that the boater moves through a high growth area within a marina or otherwise protected launch site, and move it out to the lake proper before high speed travel in deeper waters may commence. In this sense, boaters may not deliver a propagule to other nearshore sites, but may liberate plant fragments from embayments to the lake, where it is susceptible to movement by currents. There are many indicators for this in Lake Tahoe: areas of high plant growth along bouy lines outside of the Tahoe Keys Marina and the Ski

Run marina—sites of heaviest *M. spicatum* growth in Lake Tahoe, high rates of infestation along the south shore of Lake Tahoe (the area east of Tahoe Keys Marina and west of Ski Run Marina), where predominant currents flow eastward. This latter point is supported by the recent invasion by Curlyleaf pondweed (*Potamogeton crispus*), was first discovered in the Tahoe Keys Marina in 2002 and has since dispersed eastward along the southern shore (Figure 4).

However, it is possible that recreational boating plays an important role in the delivery of invasive plants to Emerald Bay. This bay is located west of the major south shore infestation sites. Emerald bay is one of the few non-embayment site that contains both Eurasian watermilfoil and Curlyleaf pondweed in the lake. It is also the most highly visited area by boaters in Lake Tahoe; over 70% of surveyed boaters traveled to Emerald Bay during their tour, regardless of distance from launch point. The predominant south shore flows move eastward--the opposite direction of Emerald Bay--and the abrupt presence of the recently established Curlyleaf pondweed at this site indicates that some sort of long distance dispersal mechanism is supporting the establishment of species in this area.

To understand the role of recreational boating as it contributes to the estimation of propagule pressure within Lake Tahoe requires an examination of surface current flows. The deployment of two surface current trackers, “drogues” along the nearshore of South Lake Tahoe showed an eastward movement of surface currents over a five day period. This qualitative assessment offers a first step at understanding the movement of waters along the shallow shelf. Subsequent drogue deployments are necessary to further examine the predominance of these flows. Currently, a nearshore surface current model is being developed to predict flows as a function of water temperature and wind patterns over the duration of a one year period (Rueda and Schladow 2003). Populating this model with a particle tracking component could be a valuable estimator for current driven delivery of Eurasian watermilfoil from infestation sites.

The distribution of Eurasian watermilfoil in Lake Tahoe is limited by habitat, specifically nearshore wave energetics and sediment quality. A late afternoon southwestern wind is typical in Lake Tahoe, and depending on its magnitude and duration, can cause large surface seiches as well as high wave conditions along the east shore. Here, the use of high-sampling rate pressure sensors to measure wave action has helped to quantify the impact of the increased surface current movement on nearshore wave action. Wave action is a limiting factor for *M. spicatum* growth and establishment (Walters 2000, Kimbel 1982, Smith and Barko 1990), and the energetics of uniquely wavy sites such as the Cave Rock boat launch, Zephyr Cove and Round Hill Pines along the eastern shore combined with *M. spicatum* absence supports this notion. Additionally, *M. spicatum* growth is limited by sandy substrate (Smith and Barko 1990)—most sites analyzed in this study for sediment particle size analysis that lack *M. spicatum* presence are dominated by fine to coarse sands (Φ = 1 to 4, Wentworth Scale (Table 1). Therefore, *M. spicatum* does have habitat limitations in Lake Tahoe.

This study is the first attempt to develop a within-lake dispersion model for aquatic plants. I have showed that recreational boater traffic within a lake is a moderate predictor for *M. spicatum* dispersal, and that habitat heterogeneity can explain some of the variation in the distribution of this species. However, with climate change, lakeside development, and increasing nearshore temperatures, the littoral zone of Lake Tahoe is experiencing major ecological changes. Ecological disturbances as a result of these factors can possibly facilitate the establishment of *M. spicatum* and other species to new areas. In particular, the introduction of Dreissenid mussel species to waterways west of the 100th Meridian, warm water fishes such as the Bluegill Sunfish (*Lepomis macrochirus*) and Largemouth Bass (*Micropterus salmoides*) to cold water lakes, and typically low-elevation bivalves such as the Asian Clam (*Corbicula fluminea*) to high elevation lakes and rivers in the Sierra have inspired a re-evaluation of habitat range and dispersal mechanism. To protect against further introduction of non-native species, the continued monitoring of habitat will enhance the ability to estimate the risk of establishment, a vital component of the invasion process.

The ability to accurately model vector pathways of aquatic invasive species remains a major challenge to invasion ecologists. In this study, I used logistic regression to model recreational boating site selection and showed that in addition to distance travelled, that water body surface area, secchi disk depth, and numbers of boat launch ramp lanes explain much of the variability of boater traffic patterns. I used these variables to parameterize the attractiveness term of a transportation model widely used to estimate recreational boater traffic flows and showed that their inclusion improves prediction power. Finally, I showed that the number and spatial distribution of recreational boater survey sites impacts the parameterization of a gravity model and subsequent estimates of aquatic invasive species propagule pressure.

Western Boating

Previous studies of recreational boating and the spread of aquatic invasive species have shown that boater visitation is positively correlated with waterway surface area and strongly deterred by distance. These studies have all been carried out in the Great Lakes region where the number of inland water bodies is high relative to the Western United States, and where large lakes are in close proximity to many major populated areas. However, recreational boating patterns are arguably different in the Western United States and are strongly impacted by a number of factors including the numbers of boaters, waterways, the spatial relationship between boaters and destination waterways, and attributes specific to the waterway. The number of inland waterways in California and Nevada that are available for use with personal watercraft is orders of magnitude less than in states such as Michigan, Wisconsin, Minnesota and Florida. Comparing this to the number of registered boats in each of these states, the ratio of inland waterways to registered boats in California is 0.0004 and 0.0035 in Nevada—again, orders of magnitude less than other boating states Michigan, 0.01 and Wisconsin, 0.02. This broadly distributed freshwater landscape indicates that on average, Californian and Nevadan boaters, similarly to Californian and Nevadan passenger vehicle drivers (FHA 1996), must drive greater distances than others in the U.S. to reach their desired destinations. This increased travel cost means that Californian and Nevadan boaters are likely to seek destinations with the greatest utility in terms of recreational boating experience with lesser regard to distance traveled. Indeed, the California Department of Boating and Waterways (2002) found that 50% of Californian boaters trailer their vessels distances greater than 100 miles from home 1 to 20 times per year. Waterway specific variables are important to all recreational boaters; but are likely to have unique impacts on Californian and Nevadan boaters who have fewer freshwater boating options than boaters in other regions.

The specific variables included in the logistic model imply that Californian and Nevadan boaters value a suite of characteristics when selecting a waterway. This study is consistent with previous studies (Reed-Andersen et al. 2000) in that waterway surface area is an important determinant for boater behavior—larger waterways have more frequent visitation. Additionally, a standard of spatial interaction modeling is that distance deters travel, which is supported by this model as well—each city-based logistic model produces negative coefficients for distance traveled terms. However, it is the other variables that provide some insight for this system. The relationship between secchi disk depth, a limnological variable that often is a proxy for water clarity and quality, and waterway visitation suggests that there is a tie between the physical and social landscape in this system. Also, boaters not only value water quality, but the level of accessibility as well. The number of boat launch ramp lanes shows a positive relationship with boater visitation implying that convenience and ease of entrance motivates site selection. Fishing tackle sales and the number of sports fish species also explained some of the variability in boater travel for Las Vegas, Reno, Sacramento and Roseville. These results support the existing literature and imply that individual motivation (cruising, fishing, sailing, etc.) is important for site selection and could be further explored by separating the analysis by boater type rather than by zip code origin.

Gravity models and survey data

Gravity models and the data used in their estimation are important tools for assessing important pathways for aquatic invasive species. Both of the surveys analyzed in this study were administered with the intent to collect information related to the movement of aquatic invasive species. Given that these data are to identify regional pathways of spread for these species, and that collecting such data is time and cost intensive, the relationship between survey administration and satisfactory representation of the true patterns of trailered boat movements becomes important. This analysis shows that the estimation of recreational boater traffic flow to a set of waterways is dependent on survey site selection, and that there is a strong bias that arises when data only come from one location. The Tahoe survey appears to perform well when compared to empirical data ($R^2 = 0.97$, pvalue $<<0.05$). However, the strong correlation is a result of the skew introduced by the high number of visitors to Lake Tahoe. This affects the error that occurs when visitation is low to the other waterways considered in this set. When removing Lake Tahoe from the model, error increases significantly and a large portion of the variation is unexplained amongst the other sites. Lake Tahoe is unique in that a large number of recreational boaters live on the perimeter of the Lake, strongly contributing to this bias.

Accounting for the permanence of Lake Tahoe residency and the possible set of boating destinations (i.e., whether a Tahoe resident only boats in Tahoe, or travels elsewhere) of the individual Tahoe boater may help to reduce some of the bias in this sample. The 100th Meridian model produced a best-fit Pearson's correlation value of 0.87, but without the drastic site specific bias that the Tahoe model produces.

The two models estimate significantly different predominant flows to the chosen set of waterways. Given that the more widely administered 100th Meridian survey provides a more realistic representation of the traffic flow to the entire set of lakes, rivers and reservoirs, the Tahoe Survey may provide a better representation of the boater network that may include Lake Tahoe as a hub. Management perspectives become important as the prevention of a regional invasion (organized at the state or federal level) may wish to utilize the larger survey data, and conversely, a individual lake manager would prefer to utilize data that are specific to his particular network. In this case, survey site selection becomes more important than waterway selection when estimating flows with a gravity model.

VII. LIST OF PUBLICATIONS

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Figure 1. Lake Tahoe Field Sampling Sites, June-September 2006

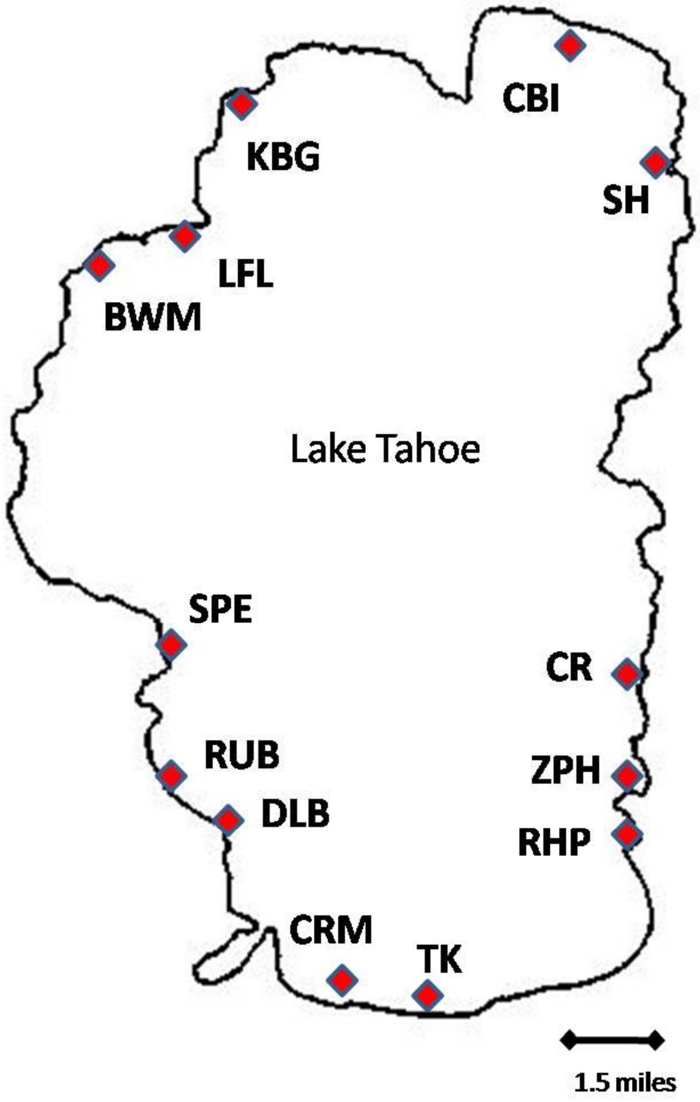


Figure 2. Lake Tahoe Survey Locations.
Diamonds indicate boat launch sites where surveys were administered, 2005-2006.

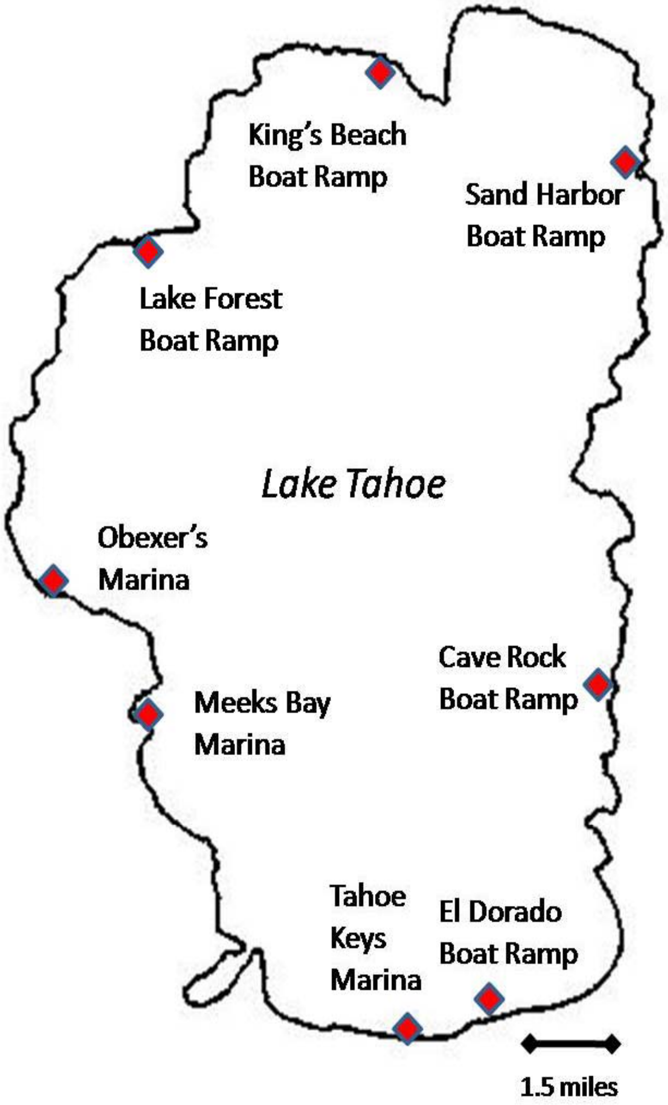


Table 1. Grade scales for substrate particle size (Wentworth 1922)

Class (Wentworth)	mm	Φ
Very large boulder	4096-2048	
Large	2048-1024	
Medium	1024-512	
Small	512-256	
Large Cobble	256-128	
Small Cobble	128-64	
Very coarse gravel	64-32	
Coarse gravel	32-16	
Medium gravel	12-8	
Fine gravel	8-4	
Very fine gravel	4-2	-2 to -1
Very coarse sand	2-1	-1 to 0
Coarse sand	1-0.5	0 to 1
Medium sand	0.5-0.25	1 to 2
Fine sand	0.25-0.125	2 to 3
Very fine sand	0.125-0.0625	3 to 4
Coarse silt	0.0625-0.0312	4 to 5
Medium silt	0.0312-0.0156	5 to 6
Fine silt	0.0156-0.0078	6 to 7
Very fine silt	0.0078-0.0039	7 to 8
Coarse clay	0.0039-0.0020	8 to 9
Medium clay	0.0020-0.0010	9 to 10
Fine clay	0.0010-0.0005	10 to 11
Very fine clay	0.0005-0.00024	11 to 12

Figure 3. Pathways of two surface current tracker deployments with general eastward movement, Summer 2007.

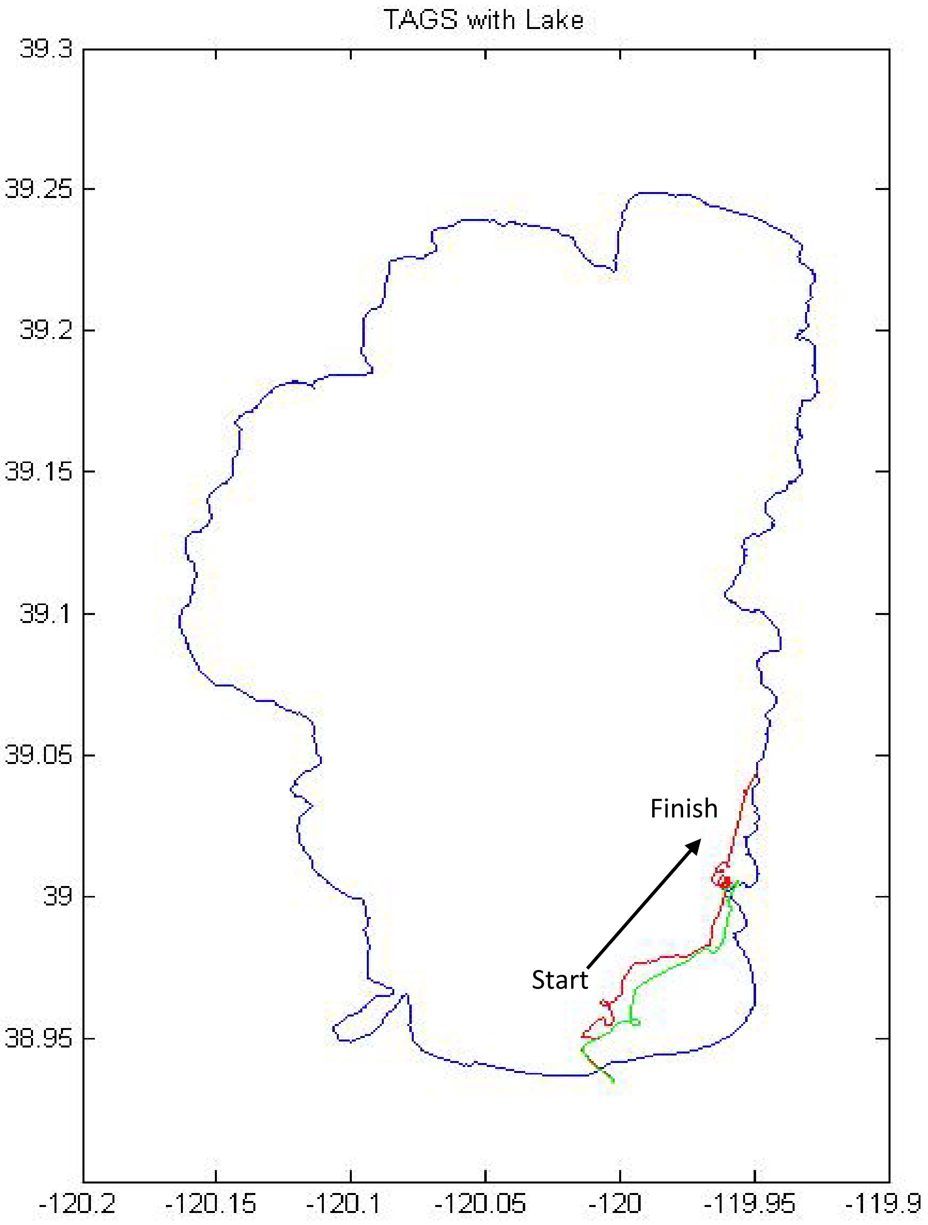


Figure 4. *Myriophyllum spicatum* invasion history. Surveys and Map by Lars Anderson, USDA-ARS

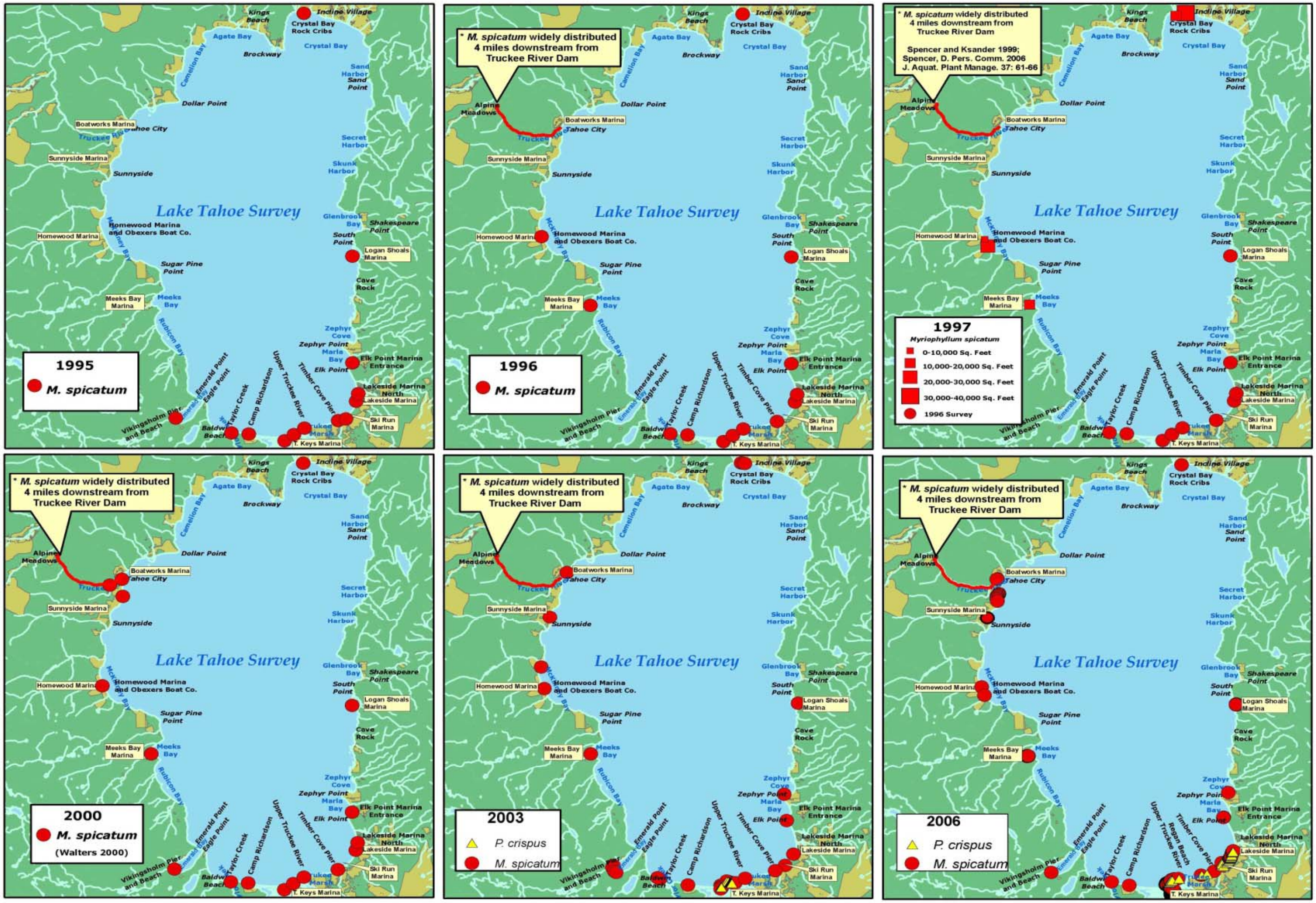


Figure 5. Lake Tahoe boater survey form

Launch_________________ Boat type______________ Time _________ Date____________

•Where are you from (ZIP)? Number of trips to Tahoe per year

•Where was last use of this boat and when? Where is your next planned use of this boat and when?

•Have you visited any other marinas, harbors, launches on the Lake during your time today? (Ordered visits)

•While there, did you stop your boat? Anchor it?

•While on the lake, have you boated through any aquatic plants today? EWMF?

•Where do you usually store your boat? Parked outside, buoyed, slip?

•Before you transported the boat(s) from Lake Tahoe, did you notice any aquatic plant fragments, such as Eurasian watermilfoil stuck on your boat(s) propellers or trailers?

•Have you taken any steps to remove plant fragments from your boat/trailer upon leaving the lake?

•After removing boat(s) from the water, how often do you do the following? How do you clean your boat?

•Have aquatic plant species caused problems for you or affected your recreational experience today or at other times during the 2005 boating season?

Inspections:

Plants on props, outboards, trailer, etc.? Yes No

ID: ____

Time Collected: _________________

	Steps taken:	Almost Always	Some-times	Never	Does not Apply
a.	Conduct visual inspection of boats and equipment for aquatic plants	1	2	3	4
b.	Remove aquatic plants from boats and equipment	1	2	3	4
c.	Rinse boat with high pressure/ hot water	1	2	3	4
d.	Allow boat to dry for at least five days	1	2	3	4
e.	Other (please specify) ______________________________________	1	2	3	4

Figure 6.
County
Origins of
Tahoe
Survey

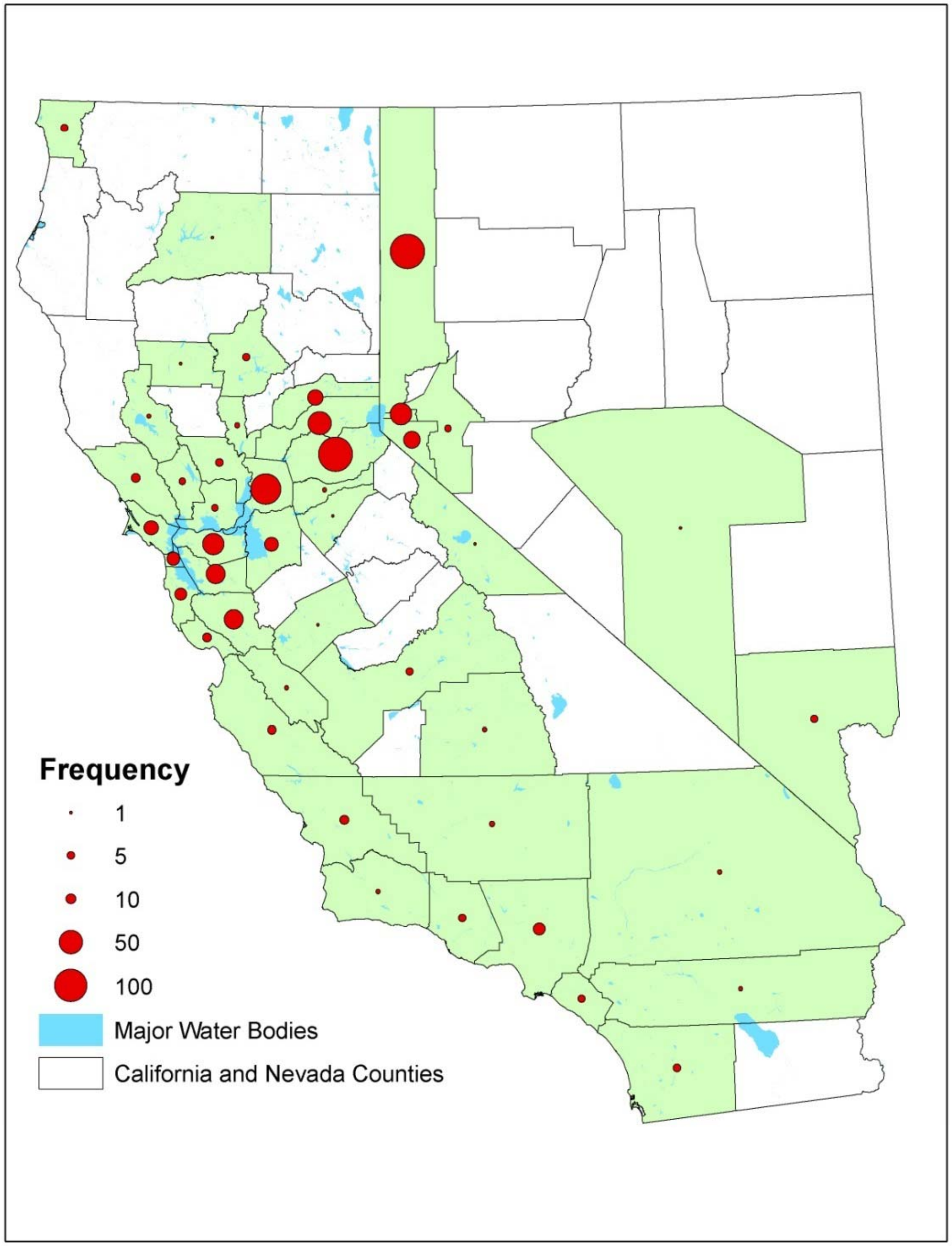


Figure 7. County Origins of U.S. FWS 100th Meridian Survey

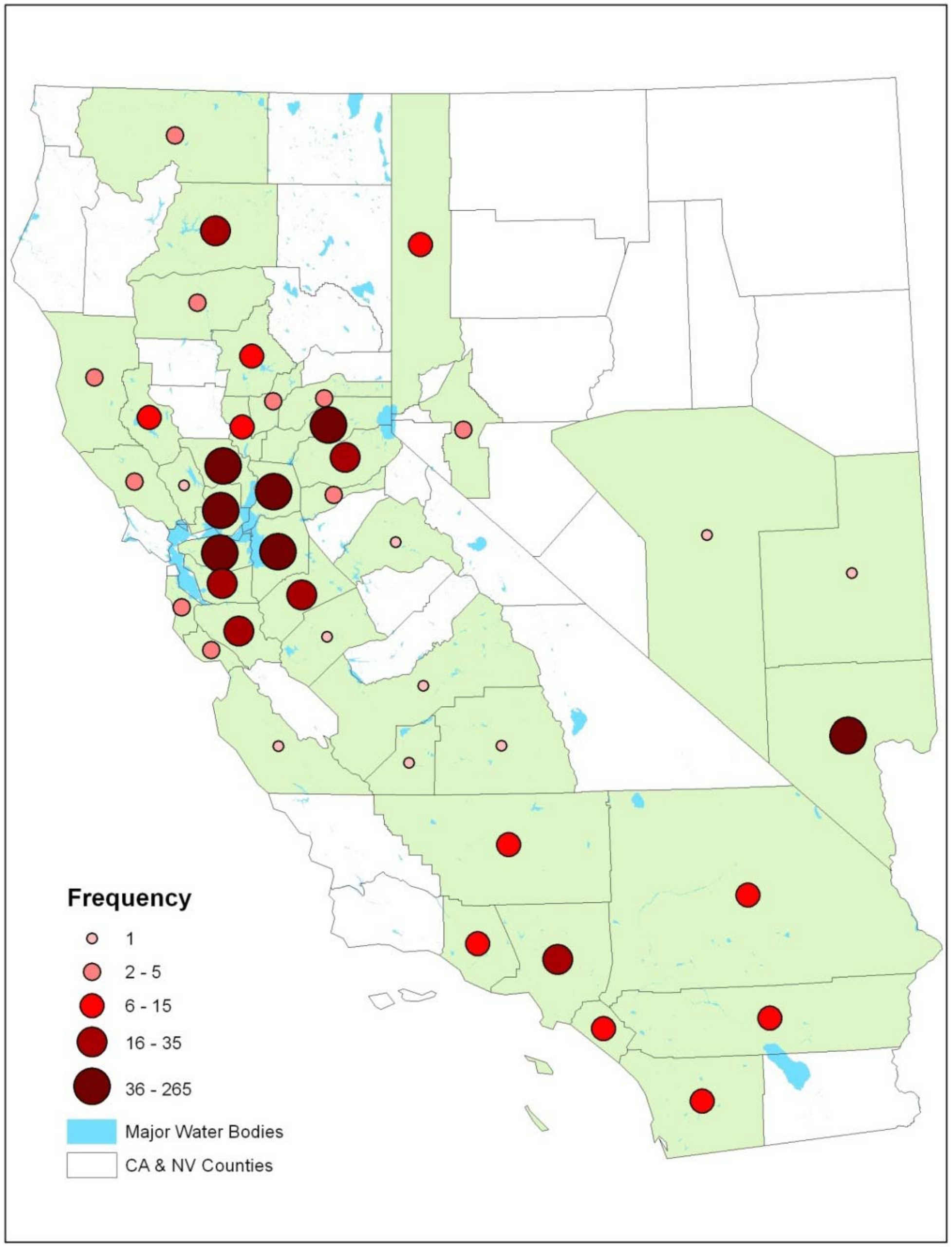


Figure 8. **Distances Travelled by Californian and Nevadan Boaters**

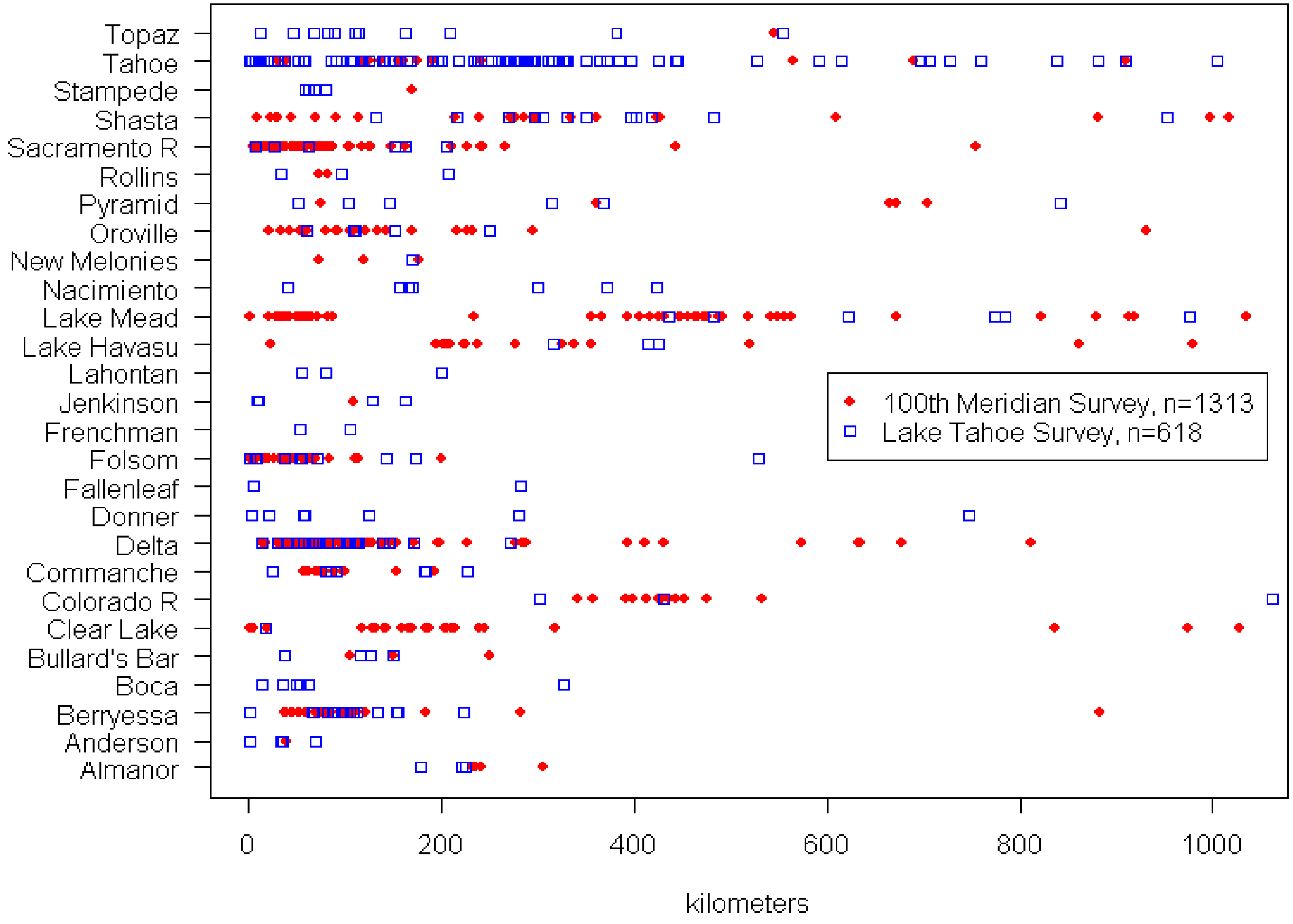


Table 2. Waterway Variables Considered, Data provided by the California Department of Boating and Waterways (CDBW 2002)

* Indicates those selected for used in this analysis

Variables
Distance travelled*
Waterway surface area*
Secchi depth*
Showers*
Carrydown walkways
Restrooms*
Fuel sales*
Sewage/Bilge pumpout*
Shoreboat service
Launch valet
Campsites*
Day Use/Picnic Area
Snack Bar
Oil Disposal
Convenience Store*
Haulout/Boat Repair
Swimming Area*
Fishing Tackle Sales*
Lodging*
Restaurant
Boatwash Area*
Slips/Tie Ups*
Number of ramp lanes*
Parking Spaces*
Boarding Floats
Dry Storage
Moorings

Figure 9. Sediment particle size distribution using Wentworth scale, Field Sites 1-9

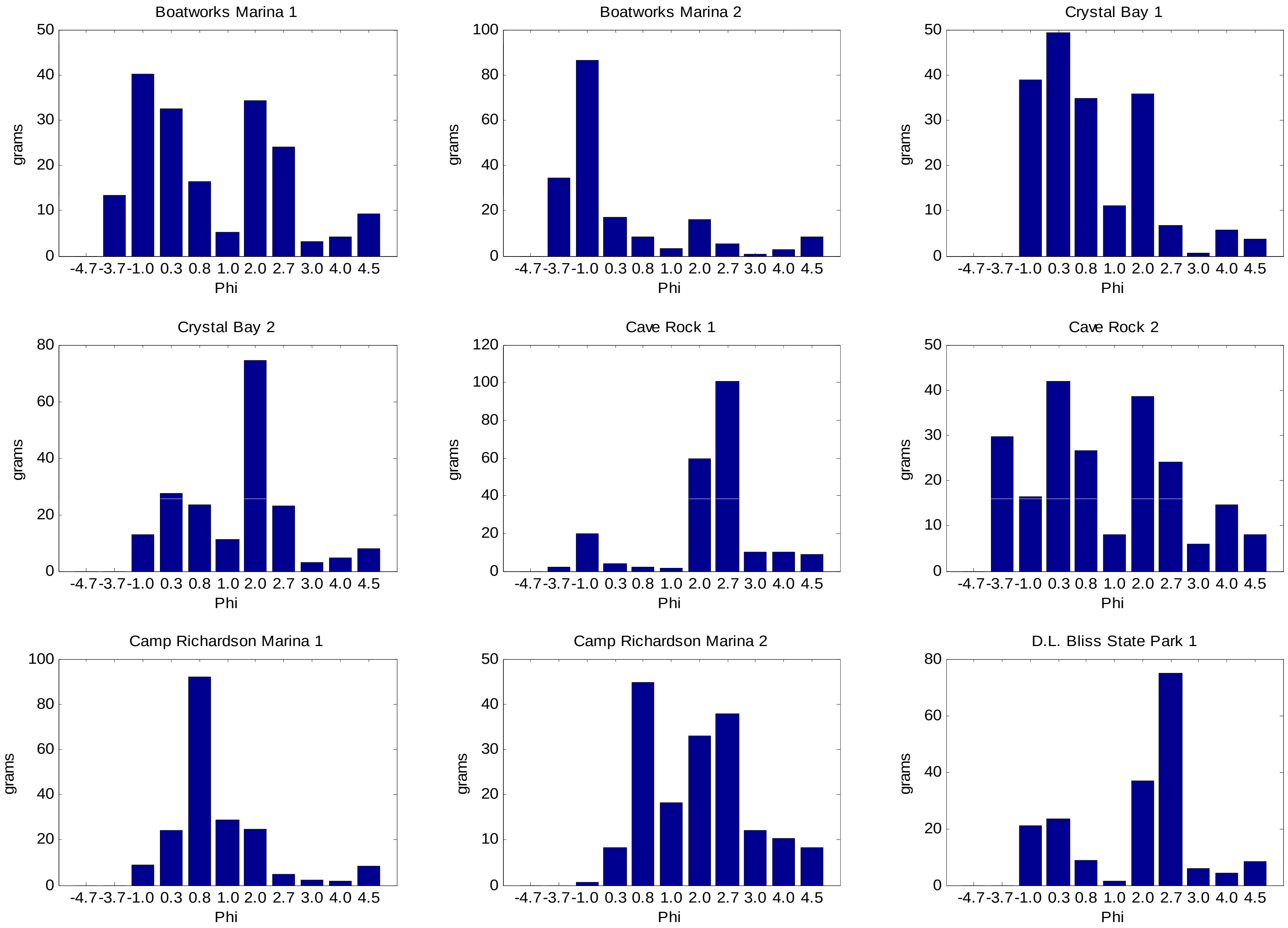


Figure 10. Sediment particle size distribution using Wentworth scale, Tahoe Field Sites 10-18

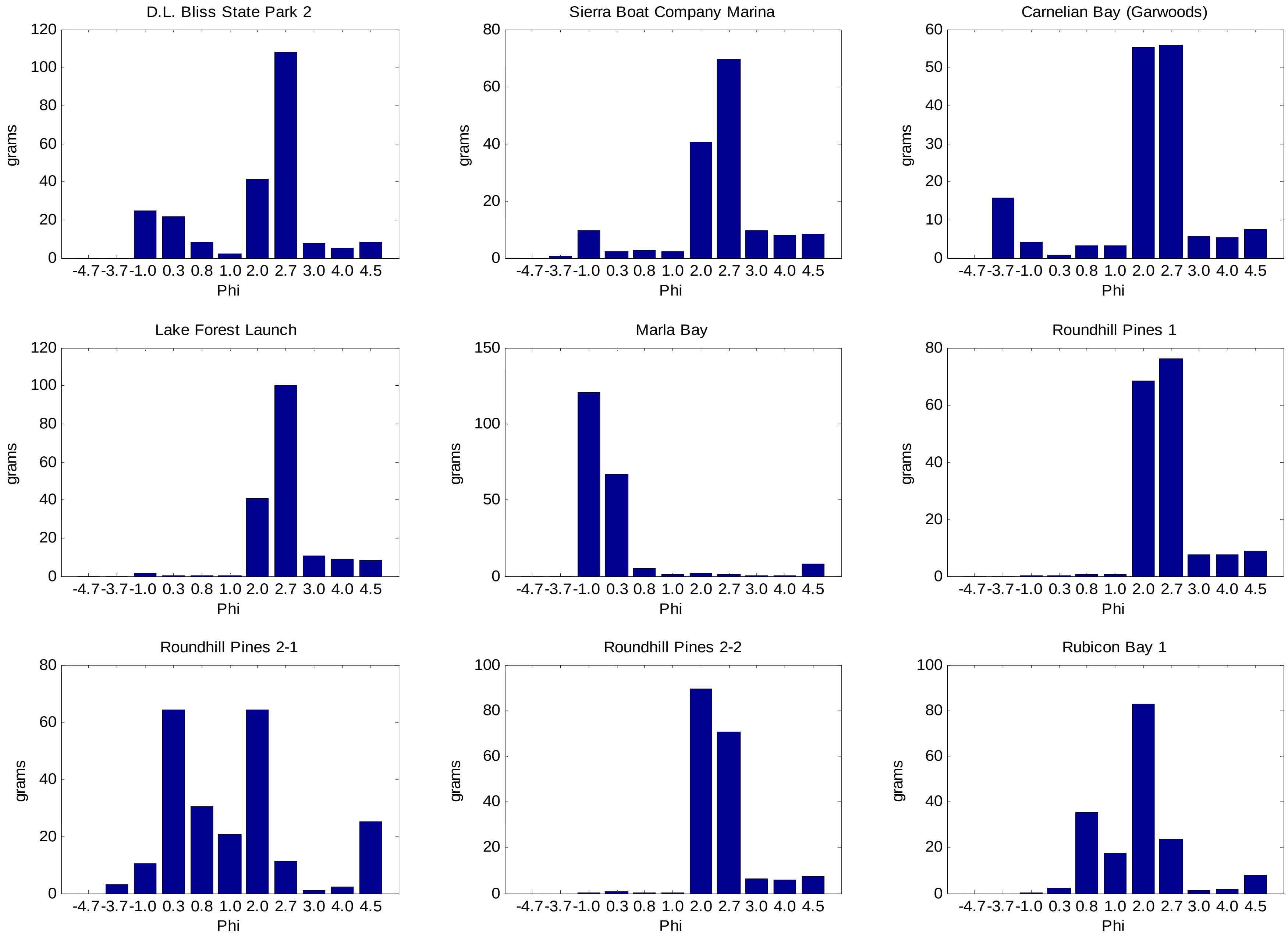


Figure 11. Sediment particle size distribution using Wentworth scale, Tahoe Field Sites 19-26

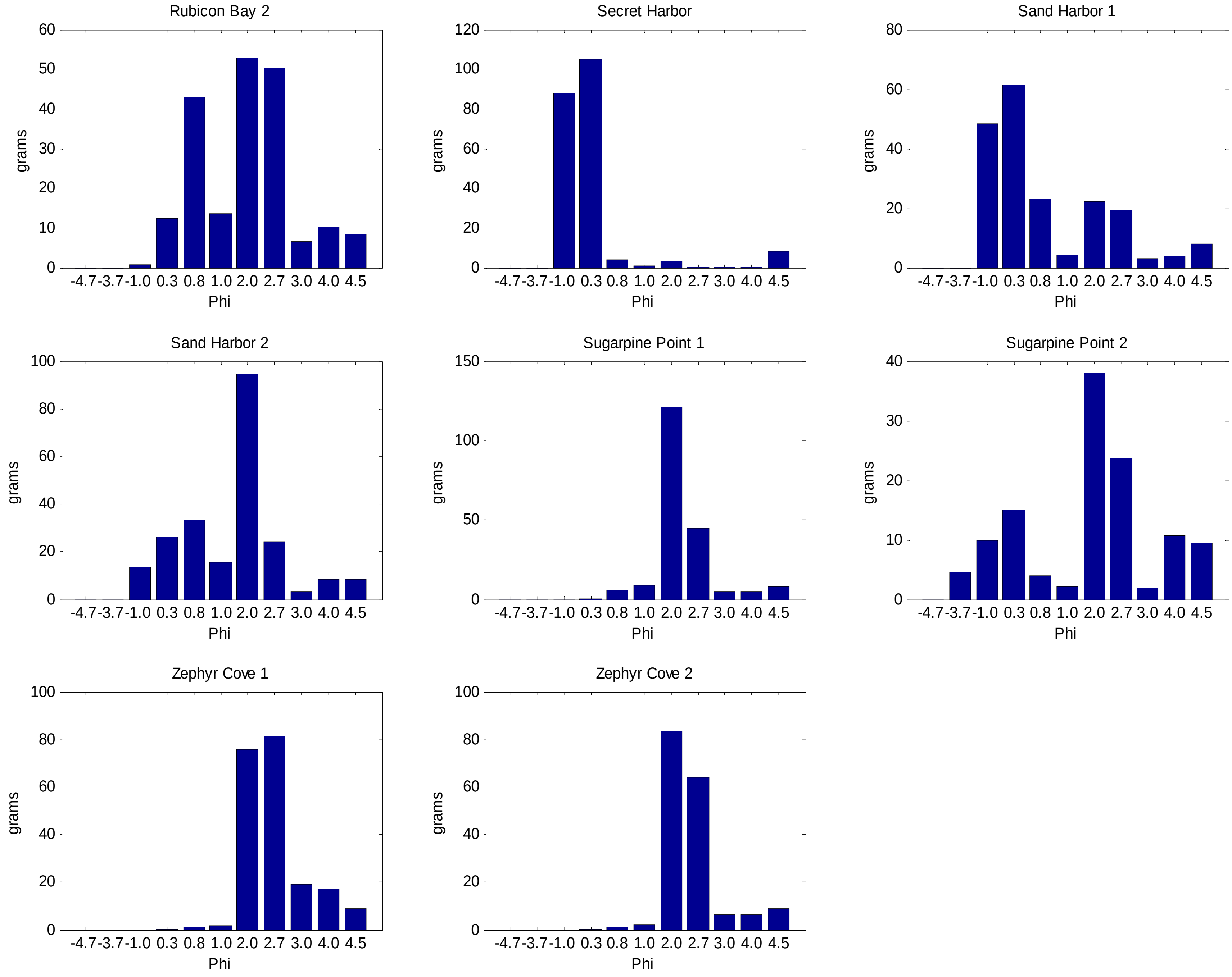


Table 3. Sediment Particle Size Analysis, Bray Curtis dissimilarity indices between 23 nearshore Lake Tahoe sites.
Shaded numerals indicate significant dissimilarity from comparative site with aquatic macrophyte presence.

	DLB1	SPE1	CBI2	RHP1	CRM1	ZPH2	CBI1	RUB1	KBG1	KBG2	RHP2.1	ZPH1	LFL1	SH1	CR1	CRM2	SH2	BWM1	BWM2	SPE2	RUB2	DLB2	RHP2.2	MAR	SECH	CR2
DLB1	0																									
SPE1	0.45	0																								
CBI2	0.35	0.33	0																							
RHP1	0.29	0.27	0.39	0																						
CRM1	0.56	0.71	0.43	0.78	0																					
ZPH2	0.31	0.18	0.38	0.10	0.76	0																				
CBI1	0.43	0.65	0.33	0.71	0.40	0.70	0																			
RUB1	0.53	0.25	0.22	0.39	0.47	0.30	0.48	0																		
KBG1	0.19	0.39	0.42	0.14	0.69	0.22	0.61	0.49	0																	
KBG2	0.28	0.29	0.37	0.16	0.71	0.15	0.65	0.40	0.19	0																
RHP2.1	0.47	0.55	0.24	0.60	0.41	0.59	0.24	0.38	0.52	0.53	0															
ZPH1	0.29	0.30	0.41	0.10	0.77	0.13	0.70	0.42	0.17	0.16	0.60	0														
LFL1	0.28	0.44	0.55	0.17	0.77	0.26	0.71	0.56	0.13	0.28	0.64	0.20	0													
SH1	0.41	0.65	0.35	0.70	0.49	0.69	0.19	0.57	0.60	0.64	0.32	0.69	0.70	0												
CR1	0.18	0.39	0.42	0.14	0.71	0.23	0.59	0.50	0.05	0.21	0.54	0.19	0.16	0.58	0											
CRM2	0.38	0.43	0.37	0.45	0.37	0.45	0.42	0.29	0.38	0.42	0.43	0.40	0.42	0.52	0.42	0										
SH2	0.39	0.33	0.06	0.39	0.41	0.37	0.34	0.19	0.43	0.38	0.27	0.42	0.55	0.40	0.44	0.35	0									
BWM1	0.30	0.54	0.28	0.58	0.50	0.57	0.23	0.48	0.48	0.45	0.34	0.58	0.58	0.20	0.47	0.42	0.34	0								
BWM2	0.56	0.77	0.59	0.81	0.63	0.79	0.48	0.74	0.70	0.64	0.61	0.80	0.80	0.41	0.69	0.70	0.61	0.37	0							
SPE2	0.27	0.35	0.23	0.36	0.56	0.36	0.46	0.42	0.30	0.28	0.35	0.32	0.43	0.45	0.30	0.38	0.26	0.29	0.55	0						
RUB2	0.33	0.34	0.28	0.35	0.43	0.35	0.41	0.25	0.30	0.32	0.36	0.34	0.37	0.50	0.32	0.13	0.26	0.41	0.69	0.31	0					
DLB2	0.09	0.50	0.44	0.29	0.64	0.37	0.49	0.60	0.20	0.33	0.56	0.34	0.24	0.49	0.17	0.44	0.46	0.38	0.61	0.35	0.39	0				
RHP2.2	0.30	0.18	0.39	0.09	0.78	0.03	0.71	0.31	0.23	0.17	0.61	0.13	0.26	0.70	0.22	0.47	0.39	0.59	0.81	0.38	0.36	0.35	0			
MAR	0.67	0.91	0.70	0.93	0.74	0.93	0.46	0.90	0.84	0.88	0.59	0.93	0.93	0.35	0.82	0.86	0.74	0.51	0.35	0.70	0.85	0.74	0.93	0		
SECH	0.68	0.92	0.70	0.93	0.75	0.93	0.47	0.90	0.84	0.89	0.60	0.93	0.93	0.35	0.82	0.87	0.75	0.52	0.41	0.71	0.85	0.75	0.93	0.18	0	
CR2	0.36	0.55	0.25	0.59	0.46	0.58	0.30	0.48	0.48	0.44	0.30	0.56	0.58	0.30	0.47	0.37	0.29	0.18	0.45	0.29	0.36	0.43	0.60	0.64	0.65	0

Table 4. G-test results for sediment particle size analysis, H_0 = Crystal Bay Site with Eurasian watermilfoil sediment type is similar to comparison site.

Site with Macrophytes	**Sites without Macrophytes**	**G(adj)**	**G(crit)**	**pvalue**	**df**	**Similar sediment particle size distribution (fail to reject H_0)**
CBI-2	BWM.1	50.61	16.919	8.3E-08	9	
	BWM.2	170.04	16.919	0.0E+00	9	
	CBI1	0.00	16.919	1.0E+00	9	**X**
	CR1	107.11	16.919	5.4E-19	9	
	CR2	60.75	16.919	9.6E-10	9	
	CRM1	0.00	16.919	1.0E+00	9	**X**
	CRM2	0.00	16.919	1.0E+00	9	**X**
	DLB1	0.00	16.919	1.0E+00	9	**X**
	DLB2	0.00	16.919	1.0E+00	9	**X**
	KBG1	80.60	16.919	1.2E-13	9	
	KBG2	91.92	16.919	4.2E-06	9	
	LFL1	0.00	16.919	1.0E+00	9	**X**
	MARL	0.00	16.919	1.0E+00	9	**X**
	RHP1	0.00	16.919	1.0E+00	9	**X**
	RHP2.1	33.12	16.919	1.3E-04	9	
	RHP2.2	0.00	16.919	1.0E+00	9	**X**
	RUB1	0.00	16.919	1.0E+00	9	**X**
	RUB2	0.00	16.919	1.0E+00	9	**X**
	SECH	0.00	16.919	1.0E+00	9	**X**
	SH1	0.00	16.919	1.0E+00	9	**X**
	SH2	0.00	16.919	1.0E+00	9	**X**
	SPE1	0.00	16.919	1.0E+00	9	**X**
	SPE2	30.73	16.919	3.3E-04	9	
	ZPH1	0.00	16.919	1.0E+00	9	**X**
	ZPH2	0.00	16.919	1.0E+00	9	**X**

Table 5. G-test results for Sediment Particle Size Analysis, H_0 = Camp Richardson Marina Site with *Ranunculus sp.* is similar to comparison site.

Site with Macrophytes	**Sites without Macrophytes**	**G(adj)**	**G(crit)**	**pvalue**	**df**	**Similar sediment particle size distribution (fail to reject H_0)**
CRM-2	BWM.1	114.31	16.919	0.0E+00	9	
	BWM.2	246.33	16.919	0.0E+00	9	
	CBI1	0.00	16.919	1.0E+00	9	**X**
	CR1	119.04	16.919	1.0E+00	9	**X**
	CR2	93.97	16.919	0.0E+00	9	
	CRM1	0.00	16.919	2.6E-16	9	
	DLB1	0.00	16.919	1.0E+00	9	**X**
	DLB2	0.00	16.919	1.0E+00	9	**X**
	KBG1	75.78	16.919	1.0E+00	9	**X**
	KBG2	95.18	16.919	1.1E-12	9	
	LFL1	0.00	16.919	1.5E-16	9	
	MARL	0.00	16.919	1.0E+00	9	**X**
	RHP1	0.00	16.919	1.0E+00	9	**X**
	RHP2.1	105.61	16.919	1.0E+00	9	**X**
	RHP2.2	0.00	16.919	1.1E-18	9	
	RUB1	0.00	16.919	1.0E+00	9	**X**
	RUB2	0.00	16.919	1.0E+00	9	**X**
	SECH	0.00	16.919	1.0E+00	9	**X**
	SH1	0.00	16.919	1.0E+00	9	**X**
	SH2	0.00	16.919	1.0E+00	9	**X**
	SPE1	0.00	16.919	1.0E+00	9	**X**
	SPE2	72.49	16.919	4.9E-12	9	
	ZPH1	0.00	16.919	1.0E+00	9	**X**
	ZPH2	0.00	16.919	1.0E+00	9	**X**

Figure 12. Oneway ANOVA of chlorophyll a (ug/L) analysis, Lake Tahoe nearshore sites

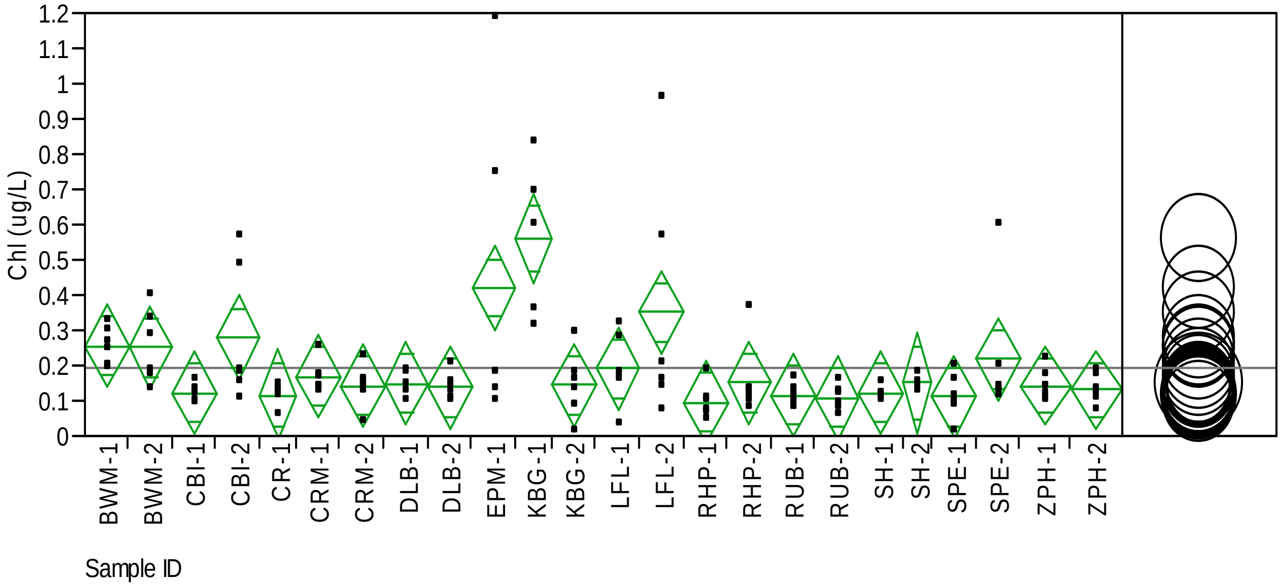


Table 6. Oneway ANOVA of chlorophyll a (ug/L) analysis, Lake Tahoe nearshore sites

Source	df	Sum of Squares	Mean Square	F ratio	Prob > F
Site	12	0.95	0.08	3.22	0.0005
Error	129	3.16	0.02	.	.
C. Total	141	4.11	.	.	.

Figure 13 Oneway Analysis of ppm NH4/day By Site

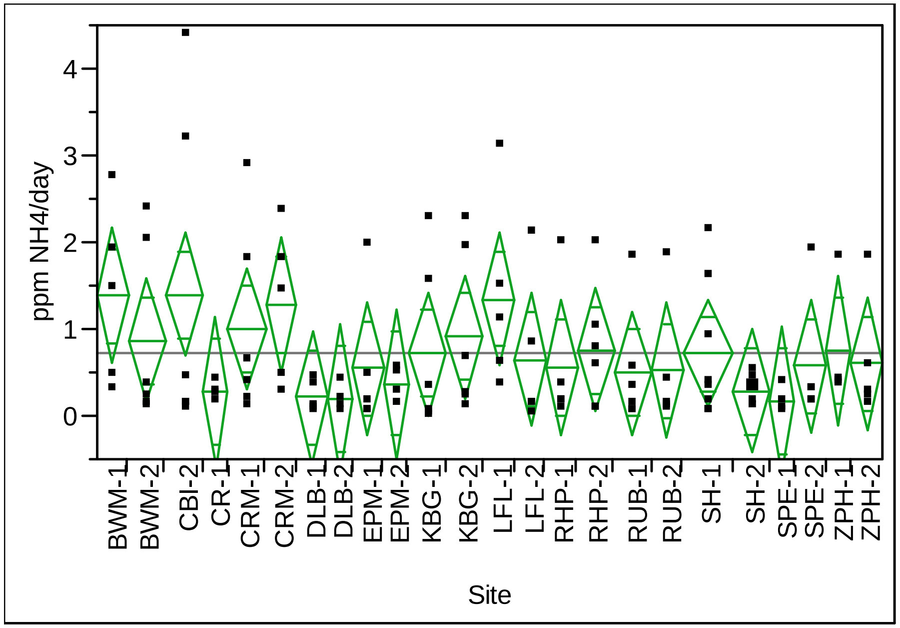


Figure 14 Oneway Analysis of ppm P/day By Site

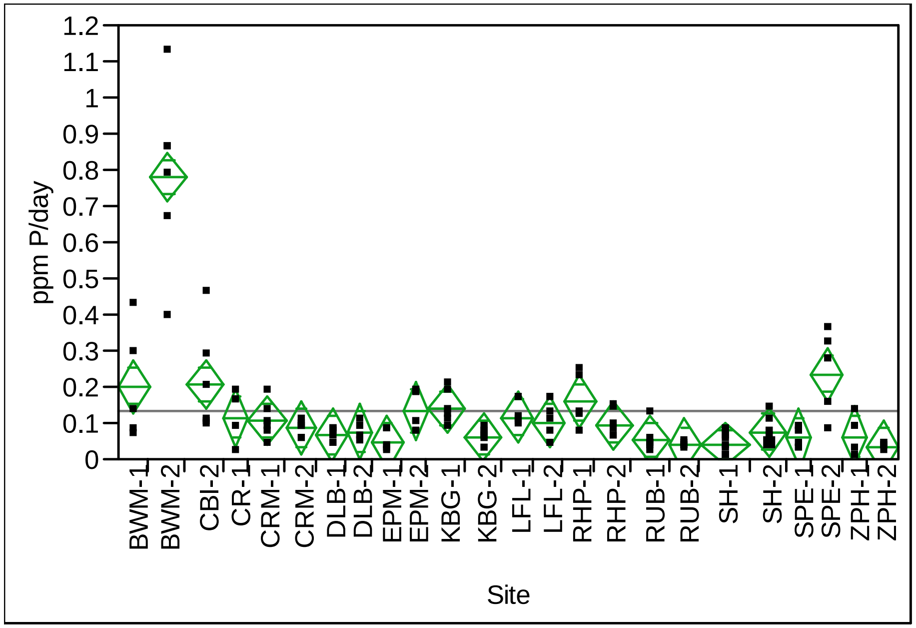


Figure 15 Oneway Analysis of ppm NO3/day By Site

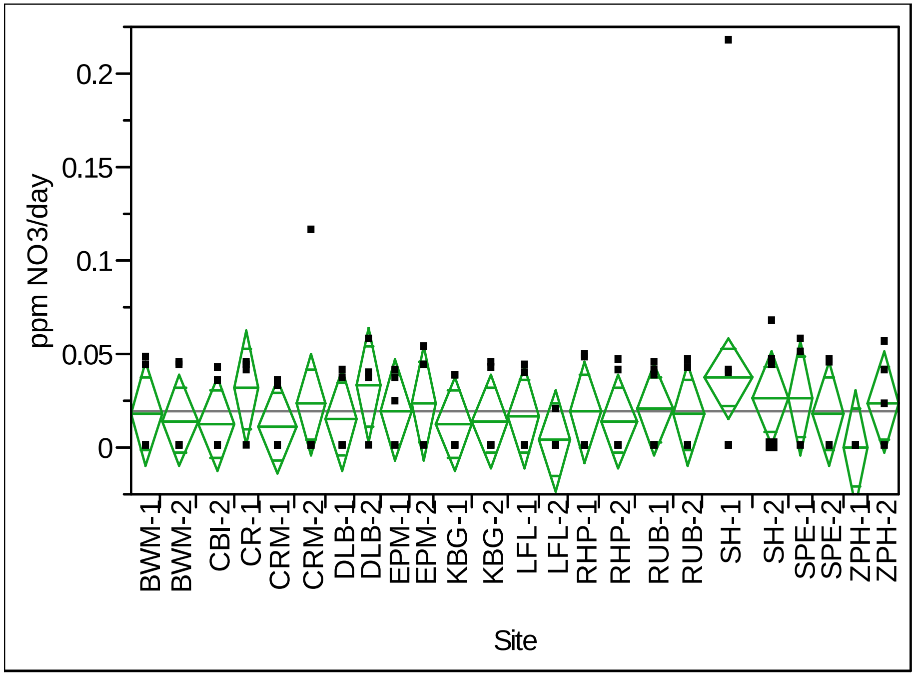


Figure 16 Oneway Analysis of ppm Ca/day By Site

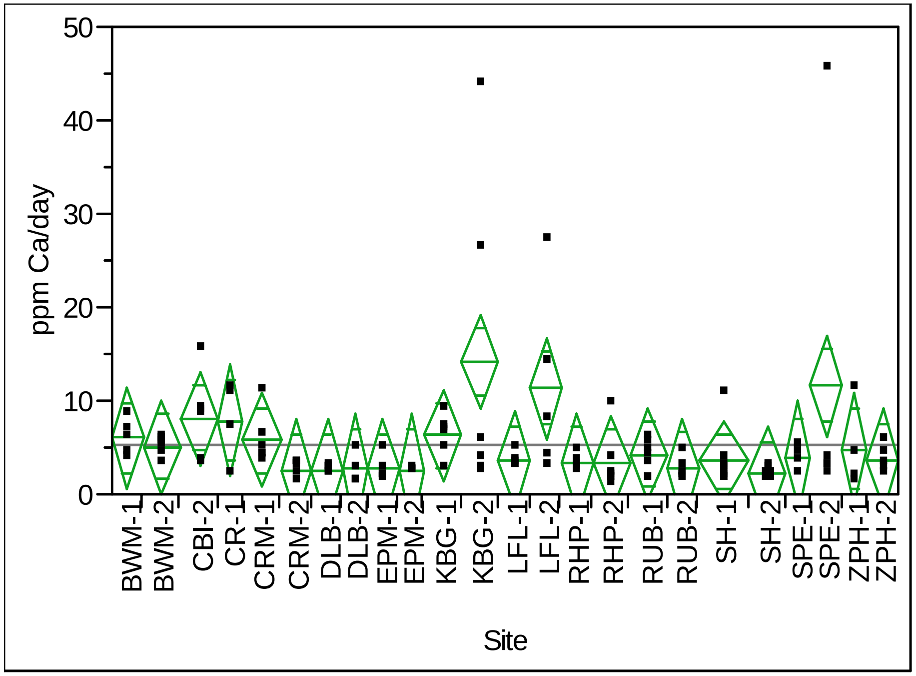


Figure 17 Oneway Analysis of ppm Mg/day By Site

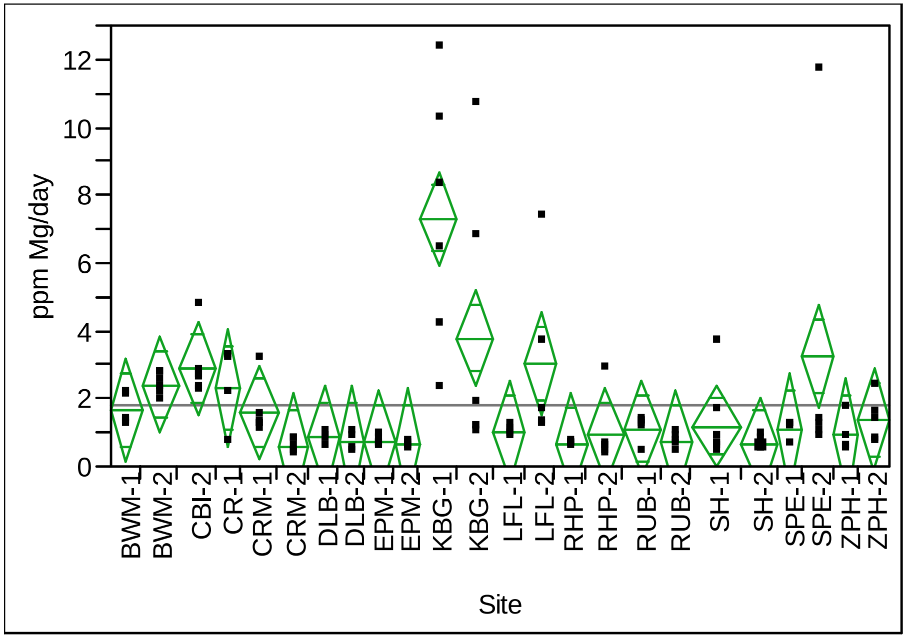


Figure 18 Oneway Analysis of ppm K/day By Site

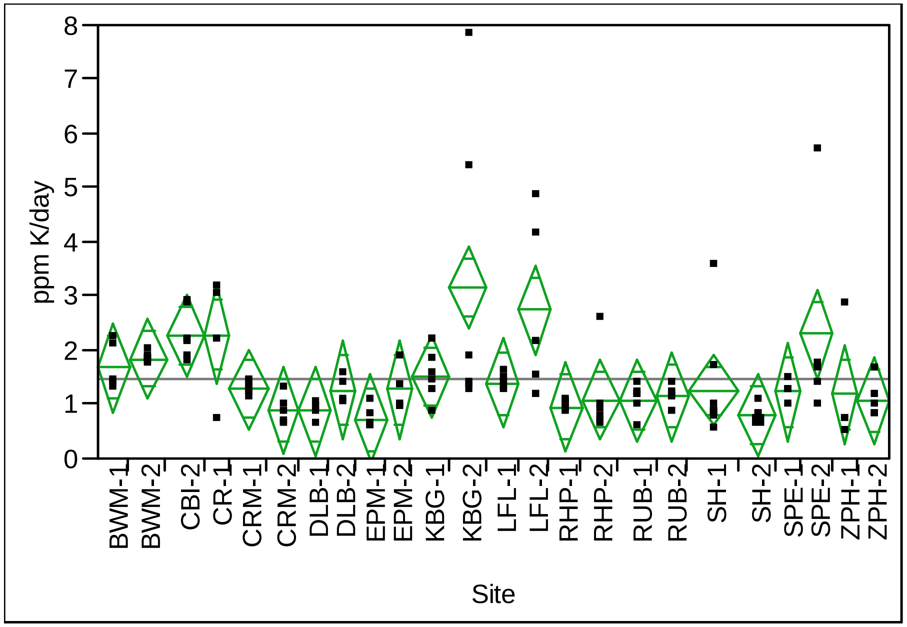


Figure 19 Oneway analysis of ppm Mn/day by Site

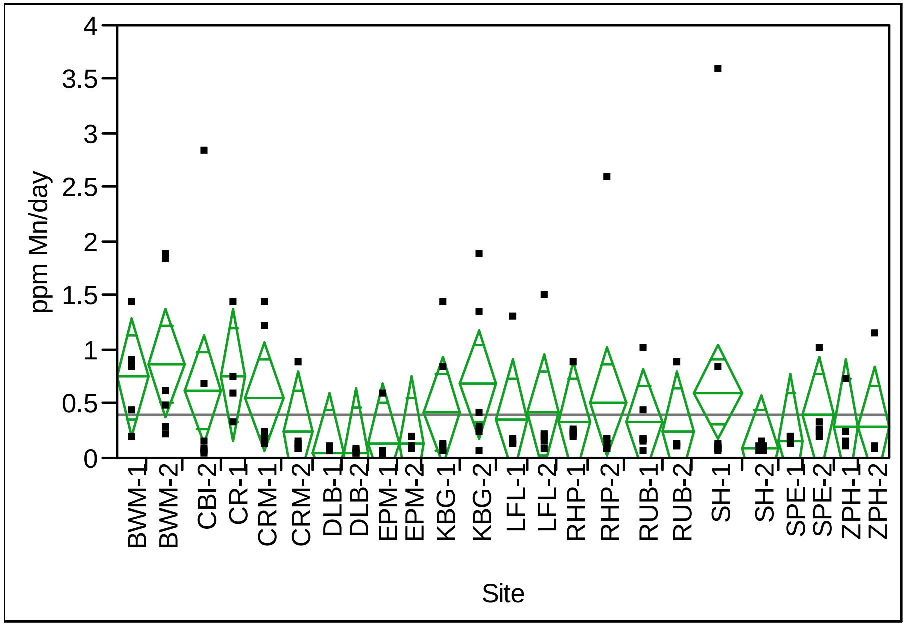


Figure 20 Oneway Analysis of ppm Fe/day By Site

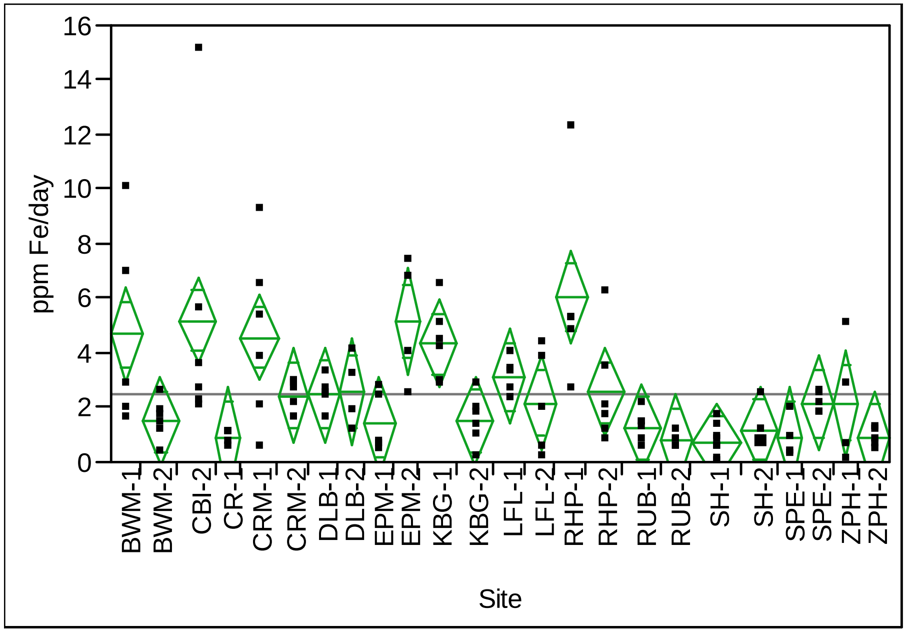


Table 7. One-way ANOVA results for Sediment Nutrient Analysis

X	Y	Source	df	Sum of Squares	Mean Square	F ratio	Prob > F
Site	ppm NH4/day	Site	23	16.3026399	0.70881043	0.938923	0.548468
Site	ppm NH4/day	Error	102	77.0016735	0.75491837	.	.
Site	ppm NH4/day	Total	125	93.3043134	.	.	.
Site	ppm P/day	Site	23	3.03754837	0.13206732	19.5565	1.07E-27
Site	ppm P/day	Error	102	0.68881786	0.00675312	.	.
Site	ppm P/day	Total	125	3.72636623	.	.	.
Site	ppm NO3/day	Site	23	0.00881579	0.0003833	0.40924	0.991843
Site	ppm NO3/day	Error	102	0.0955334	0.0009366	.	.
Site	ppm NO3/day	Total	125	0.10434919	.	.	.
Site	ppm Ca/day	Site	23	1303.65205	56.6805238	1.521587	0.080165
Site	ppm Ca/day	Error	102	3799.59437	37.2509252	.	.
Site	ppm Ca/day	Total	125	5103.24641	.	.	.
Site	ppm Mg/day	Site	23	302.618181	13.1573122	4.465978	7.14E-08
Site	ppm Mg/day	Error	102	300.50437	2.94612127	.	.
Site	ppm Mg/day	Total	125	603.122551	.	.	.
Site	ppm K/day	Site	23	51.2770173	2.22943554	2.608344	0.000538
Site	ppm K/day	Error	102	87.1826868	0.85473222	.	.
Site	ppm K/day	Total	125	138.459704	.	.	.
Site	ppm Mn/day	Site	23	6.84412498	0.29757065	0.783071	0.744426
Site	ppm Mn/day	Error	102	38.7604986	0.38000489	.	.
Site	ppm Mn/day	Total	125	45.6046236	.	.	.
Site	ppm Fe/day	Site	23	320.681846	13.9426889	3.65748	3.23E-06
Site	ppm Fe/day	Error	102	388.834497	3.81210291	.	.
Site	ppm Fe/day	Total	125	709.516343	.	.	.

Figure 21. Significant Wave Height and Maximum Wave Height Measurements for 13 Sites in Lake Tahoe

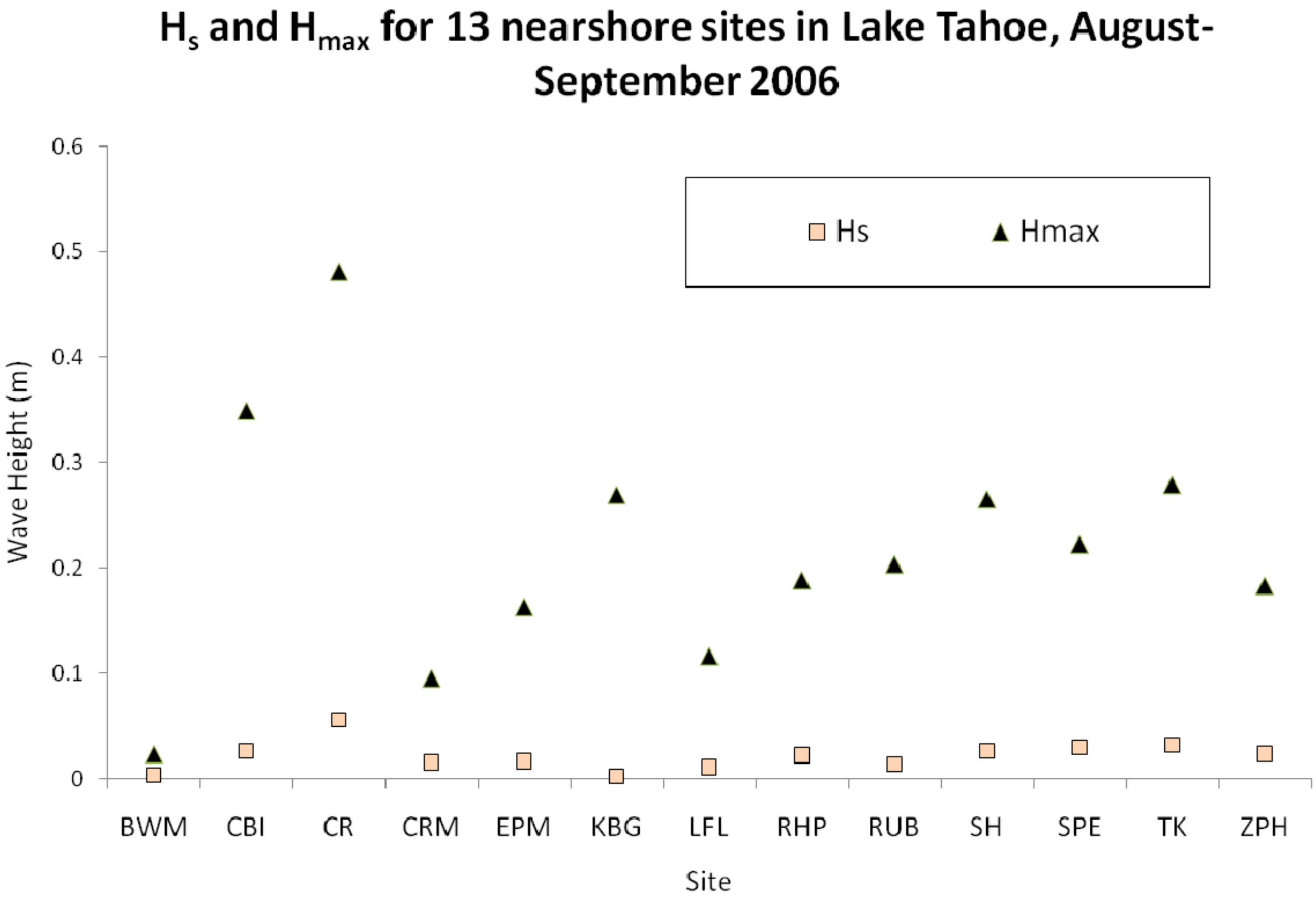


Table 8. H_{rms} (Root Mean Square Wave Height) and Associated Probabilities of Wave Height Greater than Camp Richardson Marina Site, * Indicates removal from establishment model

Site	**Shore**	**H_{rms} (m)**	**Pr(H>Ĥ)**
BWM	West	0.0026	0.00
CBI	North	0.0187	**0.50***
CR	East	0.0398	**0.86***
CRM	South	0.0112	0.14
EPM	East	0.0118	0.17
KBG	North	0.0018	0.00
LFL	North	0.0079	0.02
RHP	East	0.0160	0.39
RUB	West	0.0100	0.08
SH	East	0.0188	**0.50***
SPE	West	0.0211	**0.58***
TK	South	0.0230	**0.63***
ZPH	East	0.0169	**0.42***

Figure 22. Theoretical probability of establishment for sites in Lake Tahoe, 1990-2006

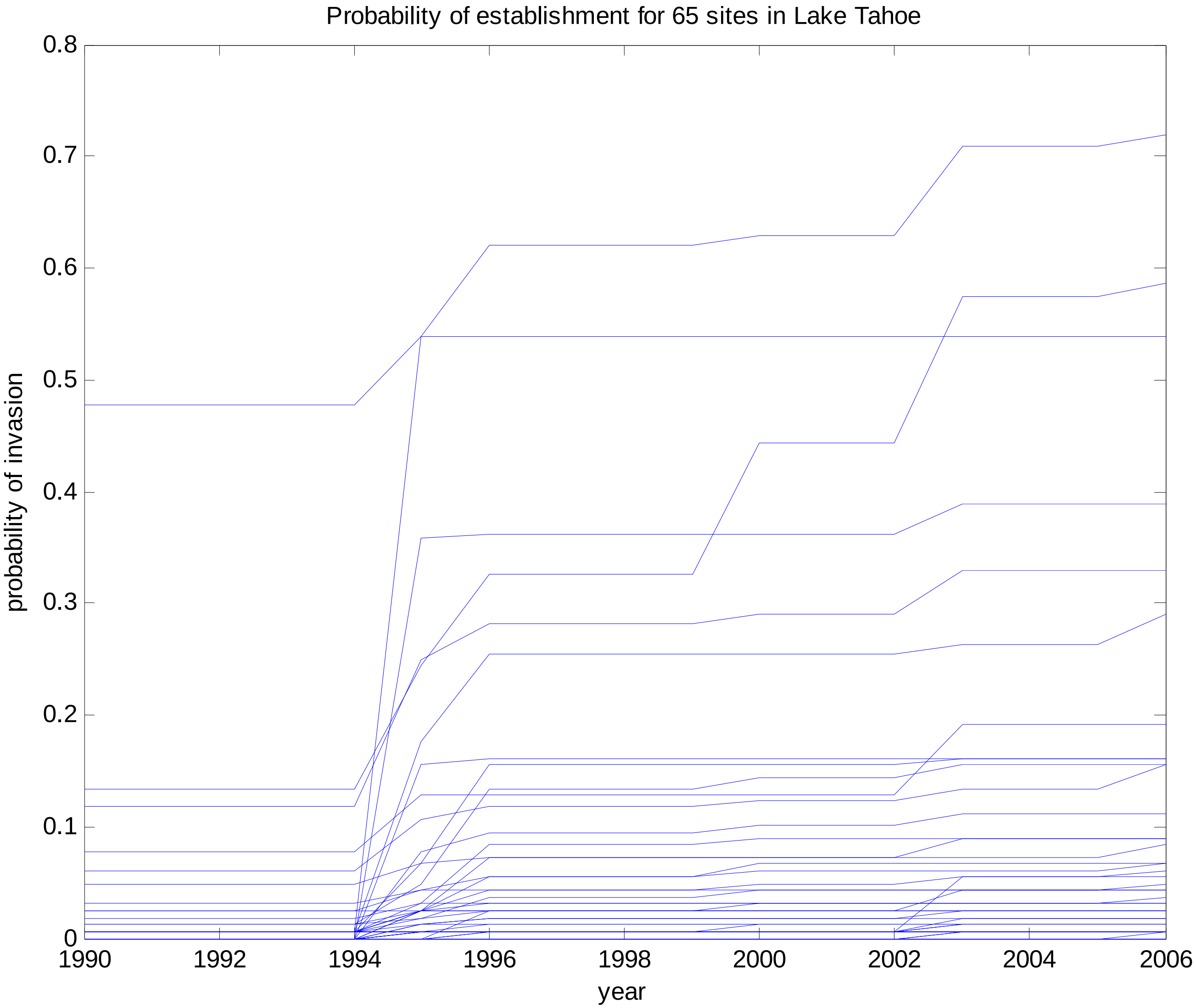


Figure 23. **Probability of Eurasian Watermilfoil Establishment Given Recreational Boating Traffic, 2006**

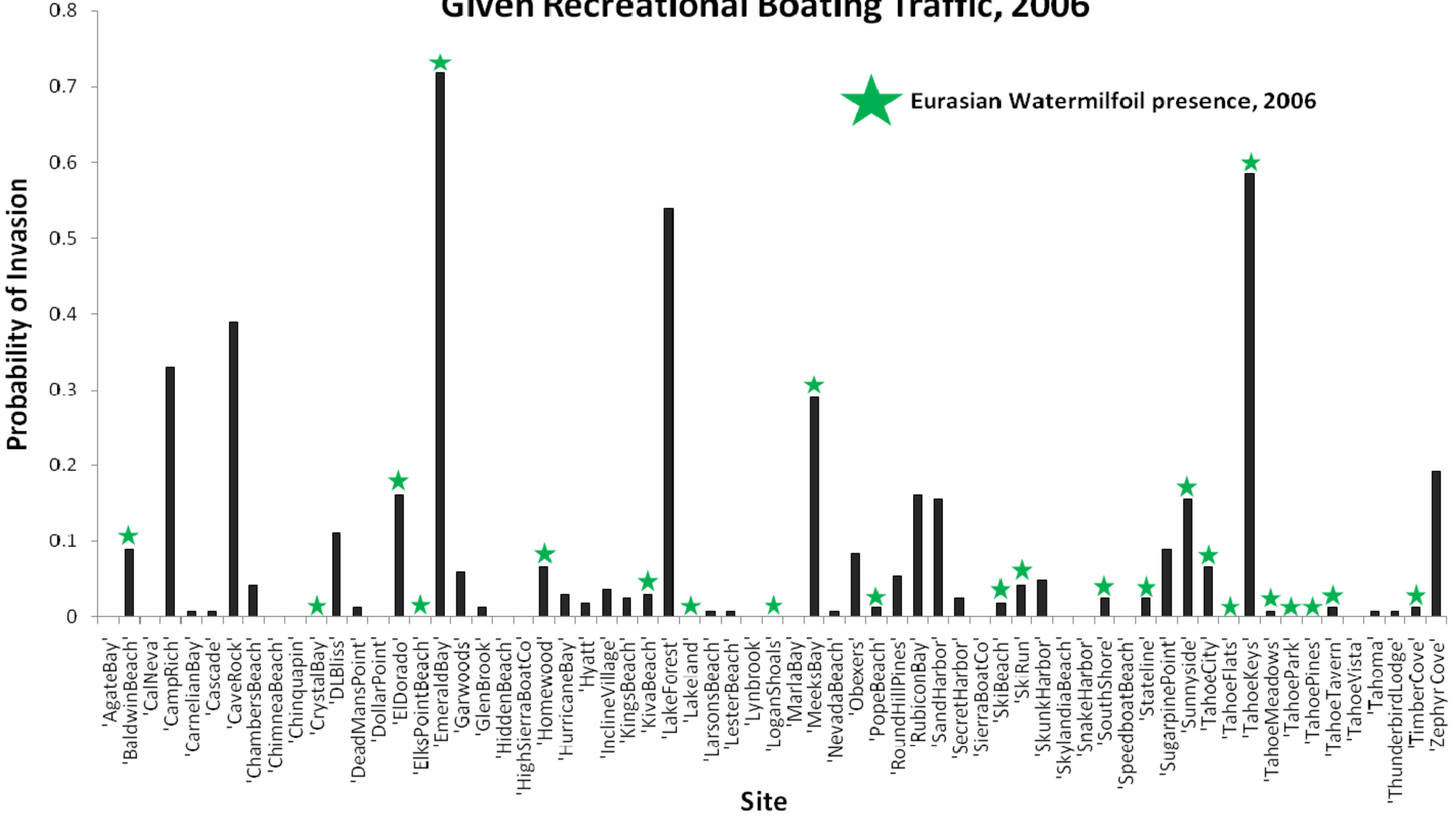


Figure 24. Receiver Operating Characteristic Curve for establishment model with three different habitat removal scenarios.

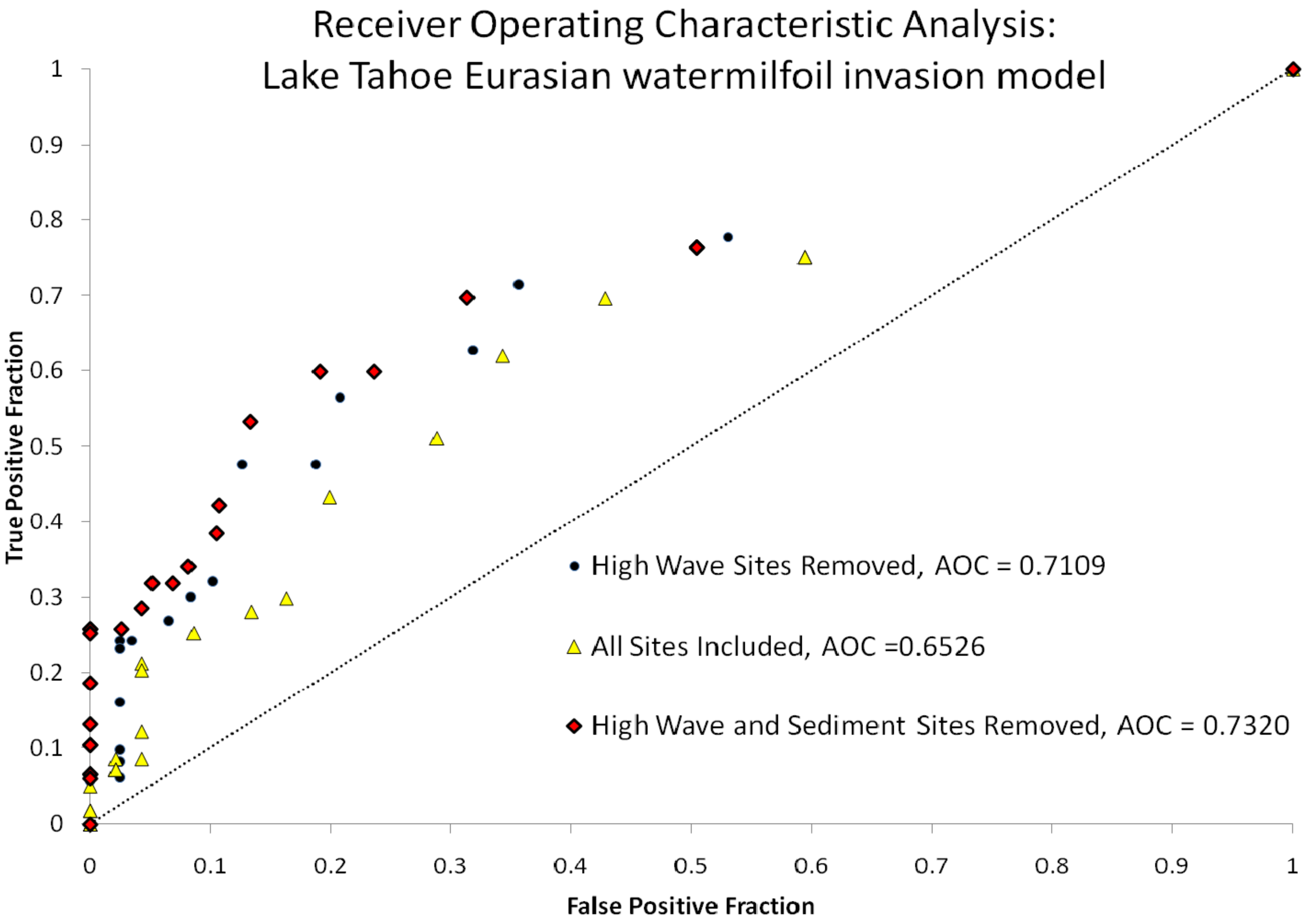


Figure 25. 2007 Field sites: Lake and reservoirs frequented by Lake Tahoe recreational boaters

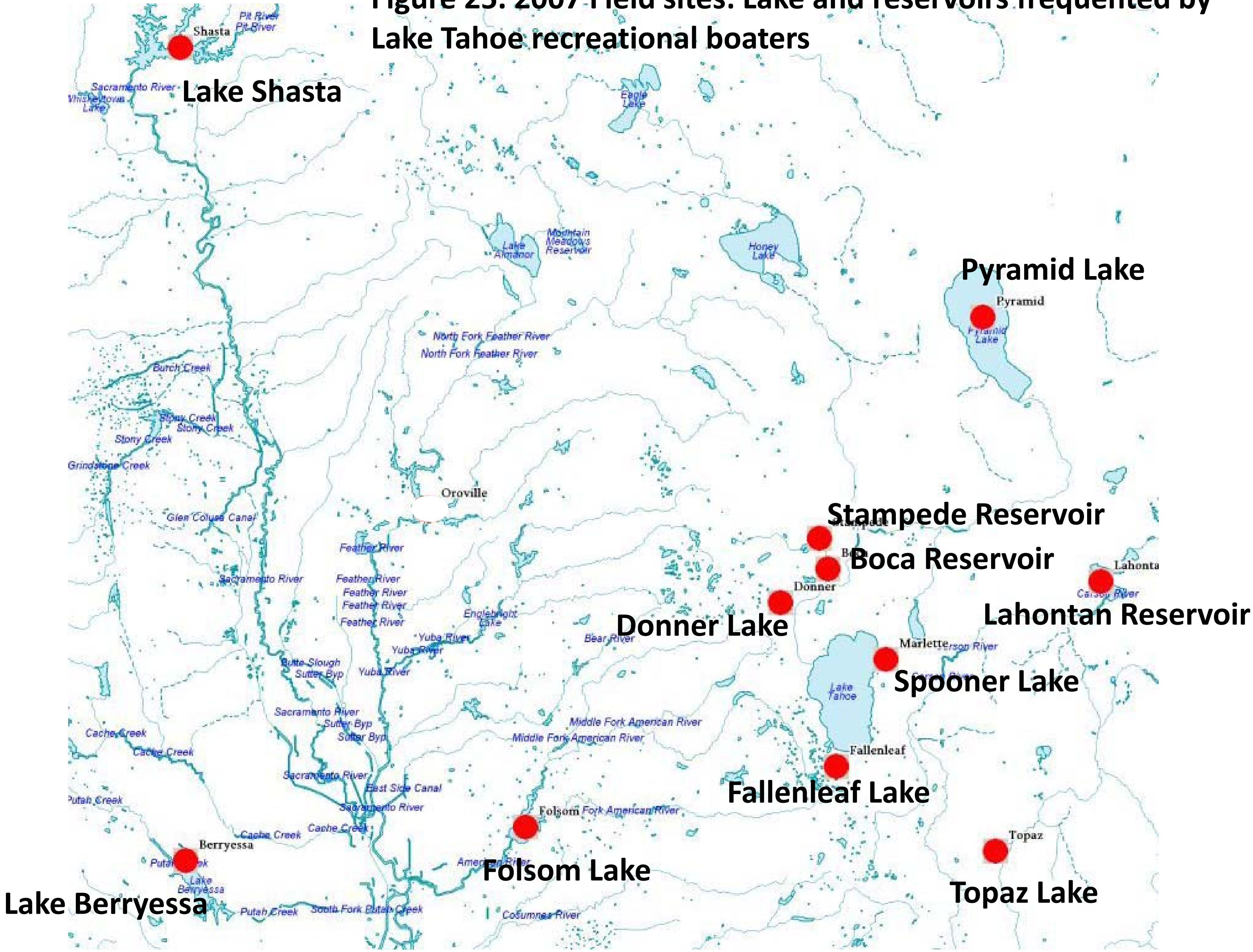


Figure 26. **Trophic State Index as Determined by Chlorophyll a**

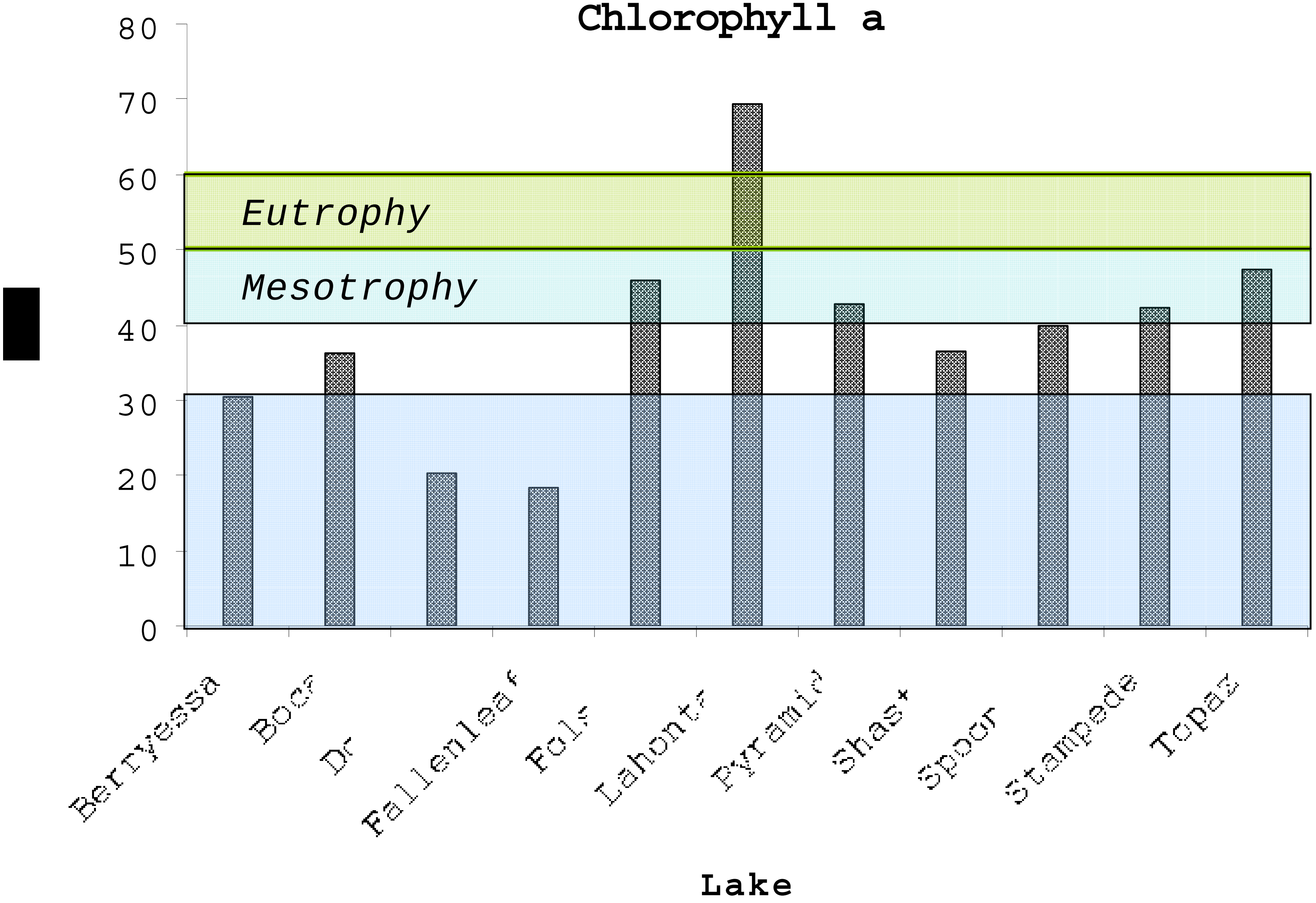
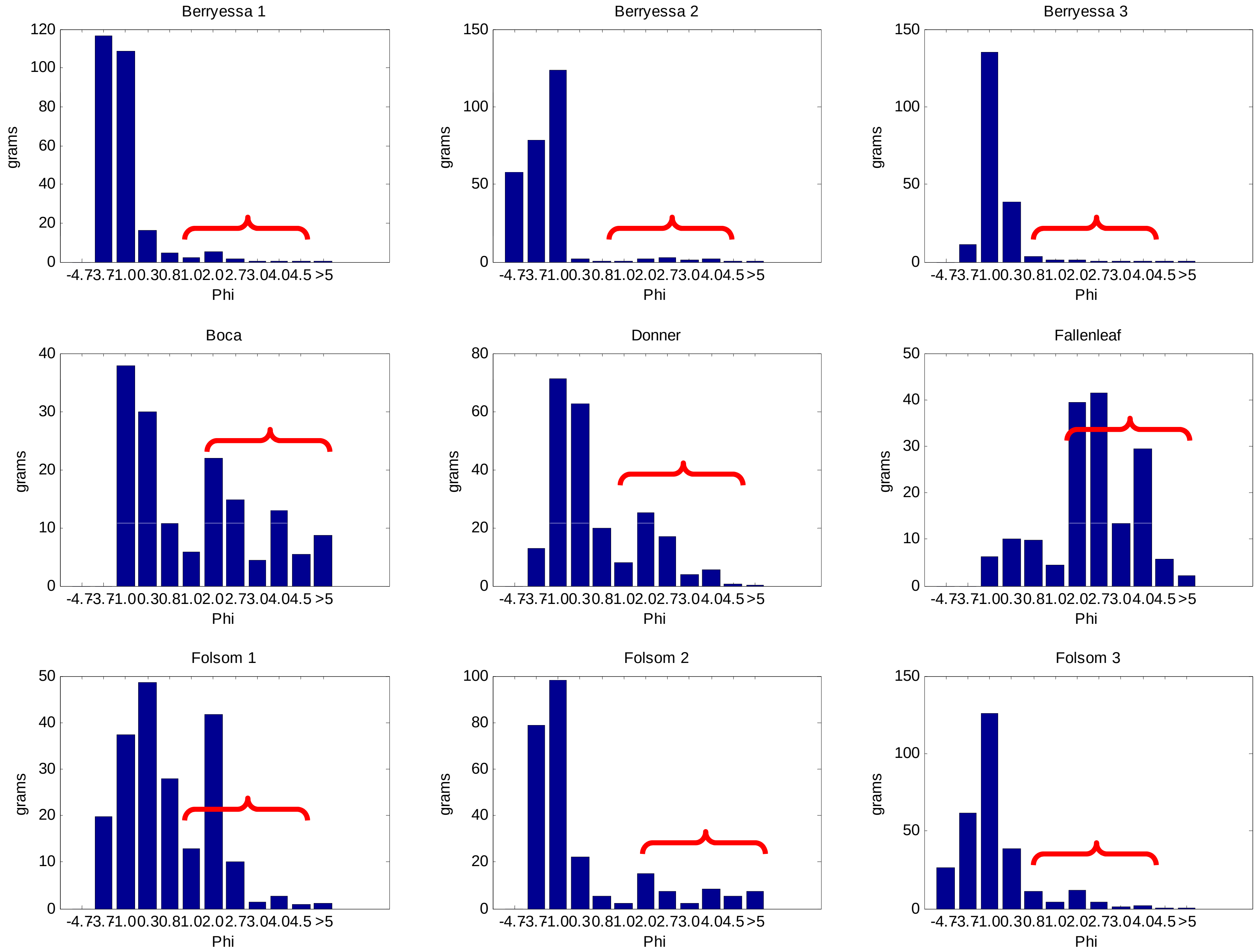


Figure 27. Sediment particle size distributions for lake and reservoir sites 1-9



Berryessa 1

Berryessa 2

Berryessa 3

Boca

Donner

Fallenleaf

Folsom 1

Folsom 2

Folsom 3

Figure 28. Sediment particle size distributions for lake and reservoir sites 10-18

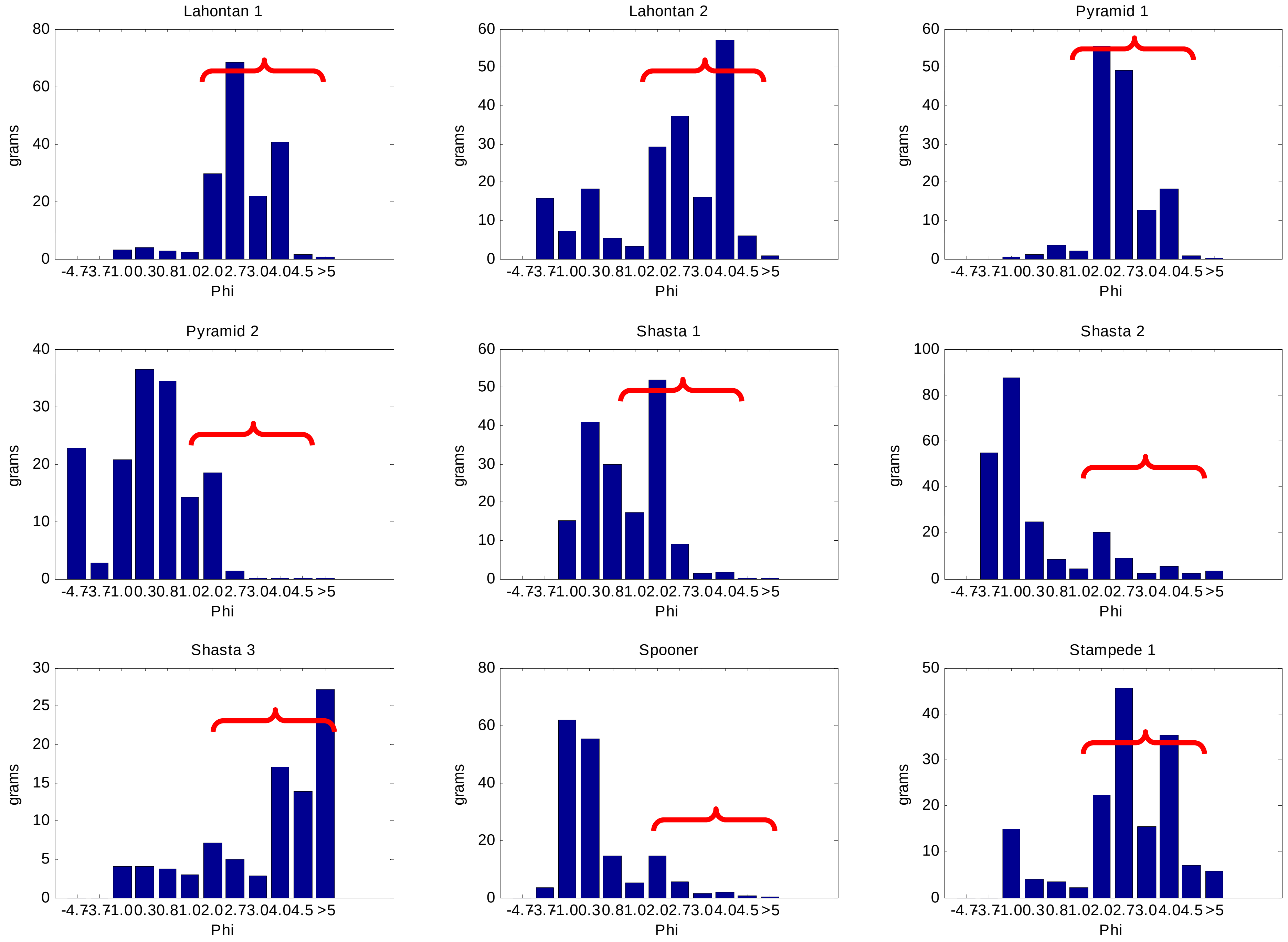


Figure 29. Sediment particle size distributions for lake and reservoir sites 19-21

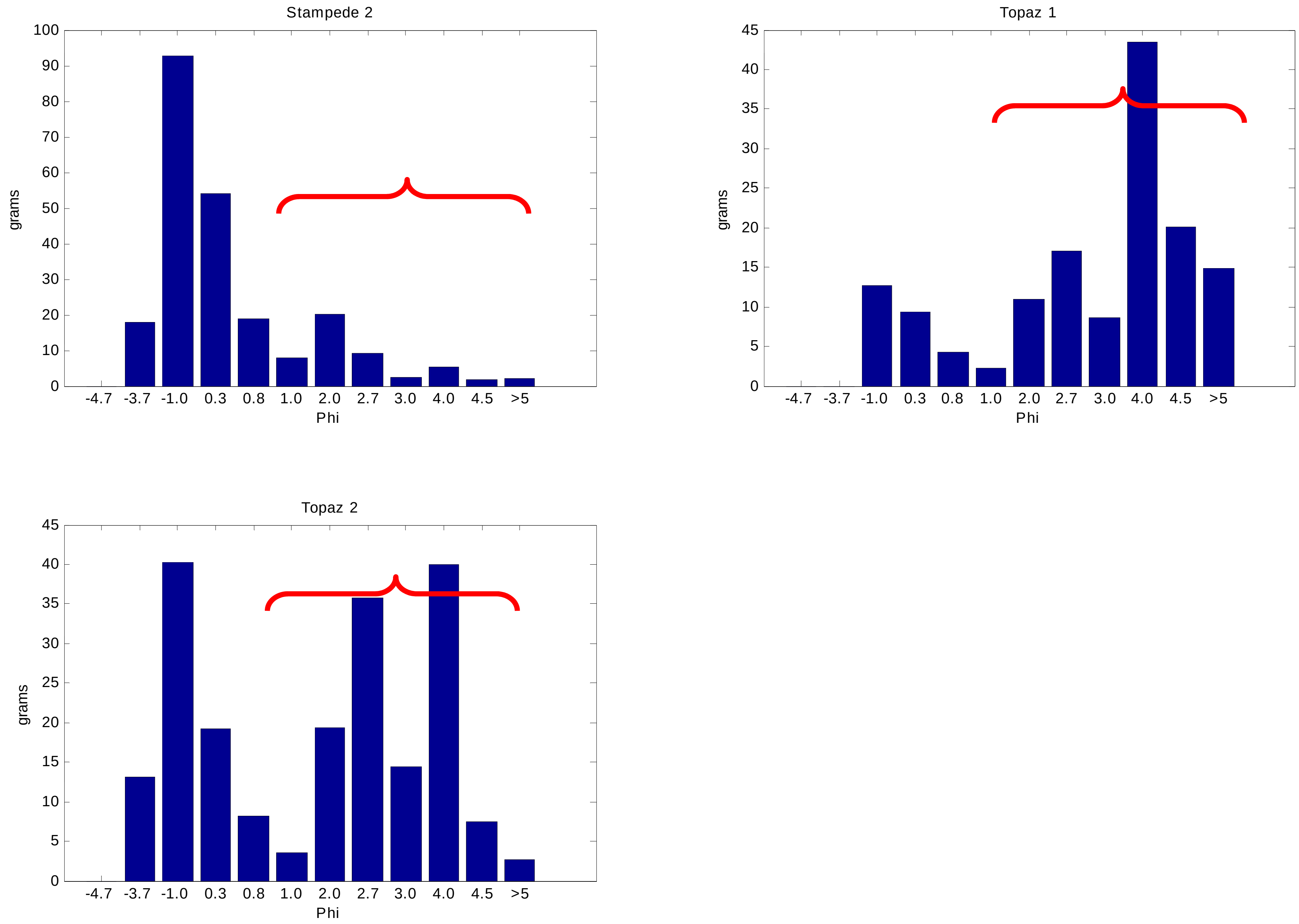


Figure 30. Ortho-P as P ug/mL per day by Lake/Site

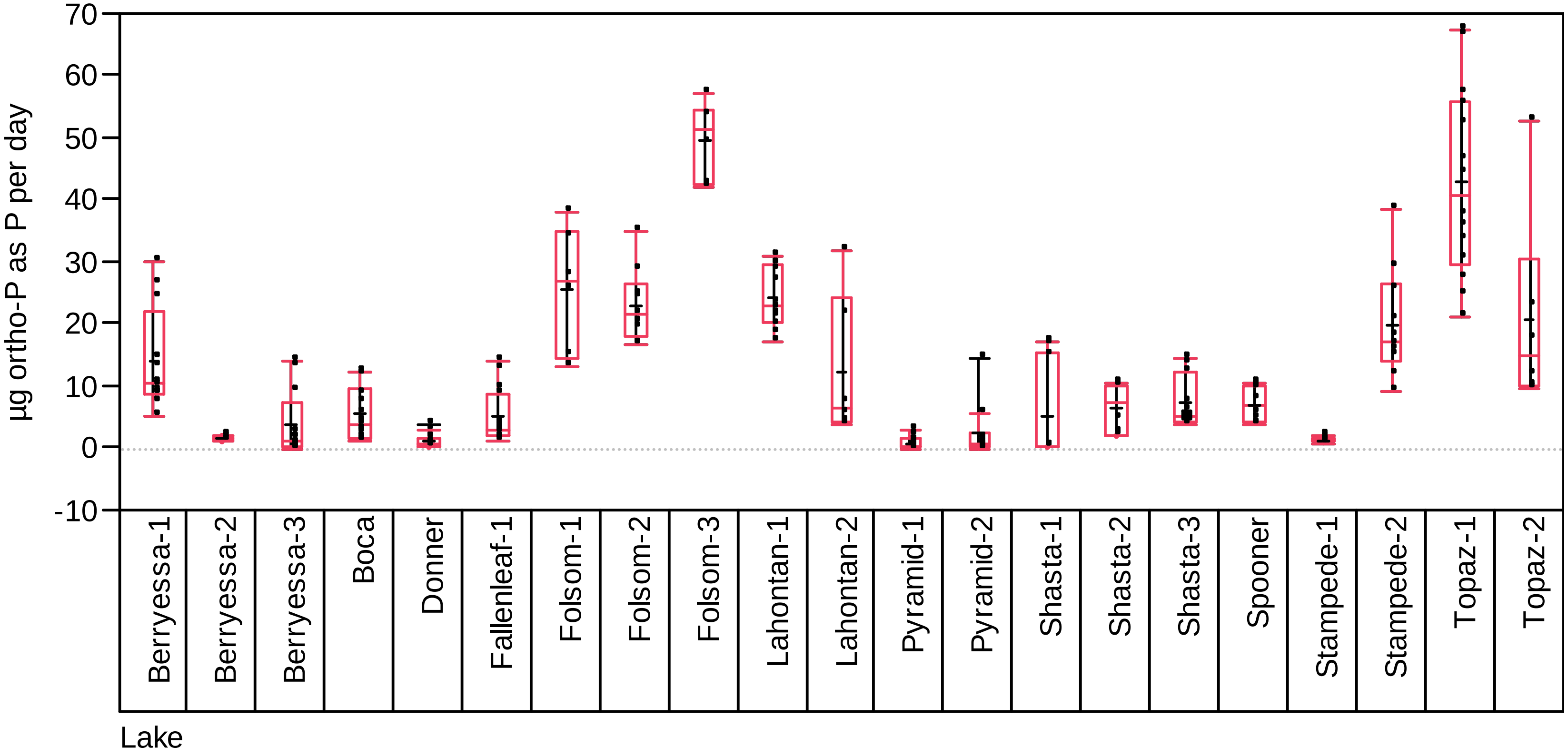


Figure 31. NH_4 ug/mL per day by Lake/Site

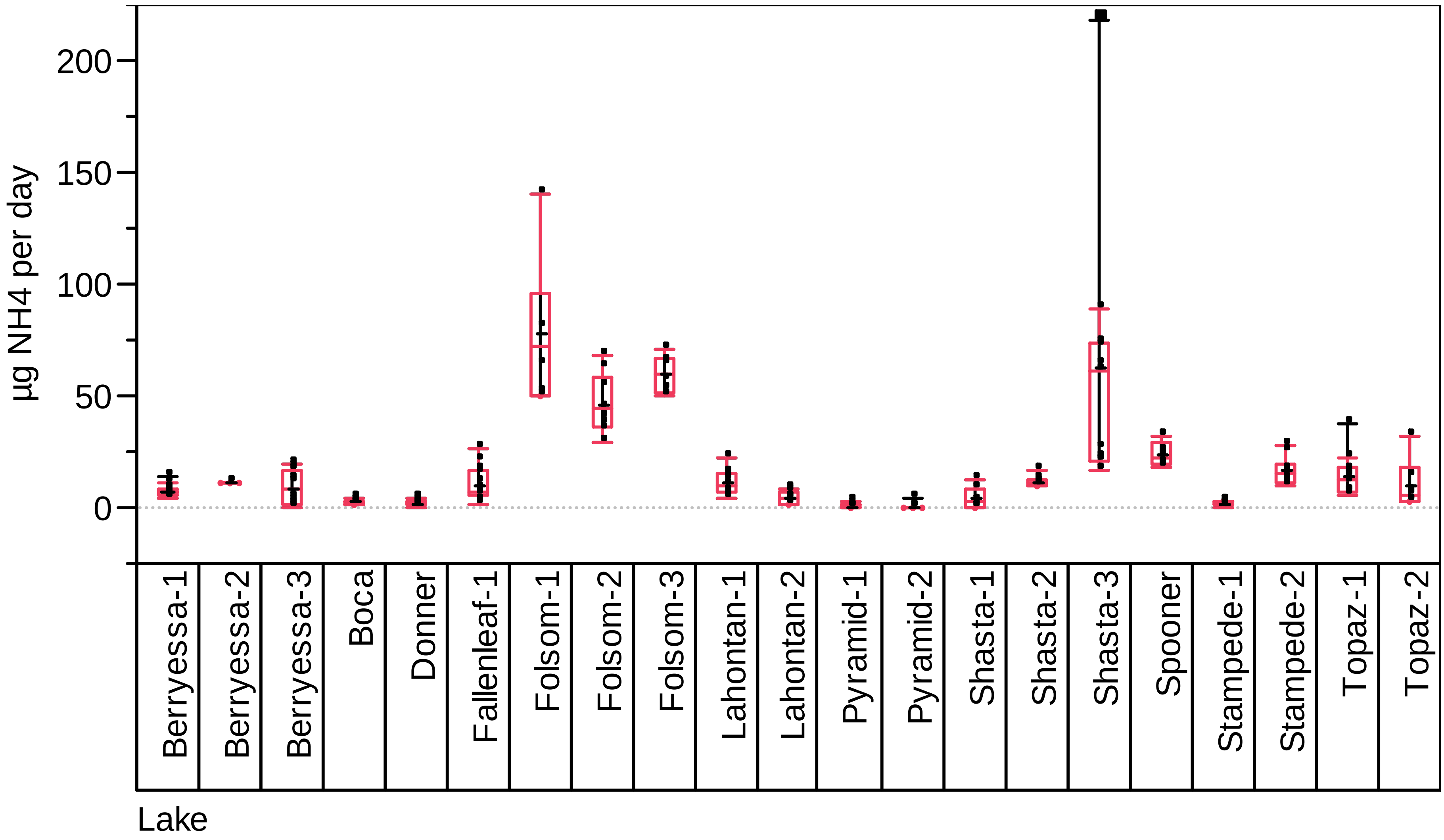


Figure 32. Fe ug/mL per day by Lake/Site

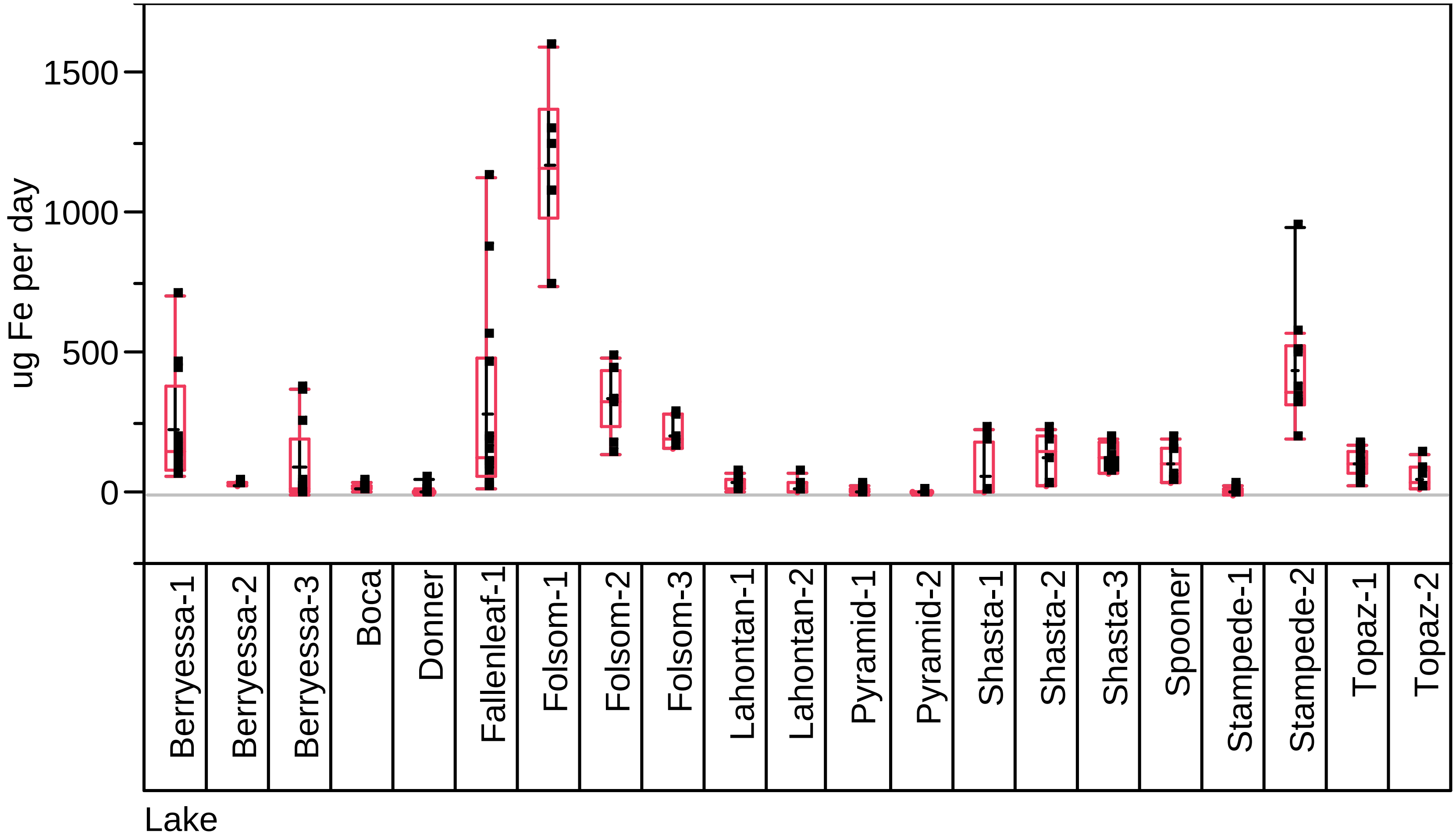


Figure 33. Mn ug/mL per day by Lake/Site

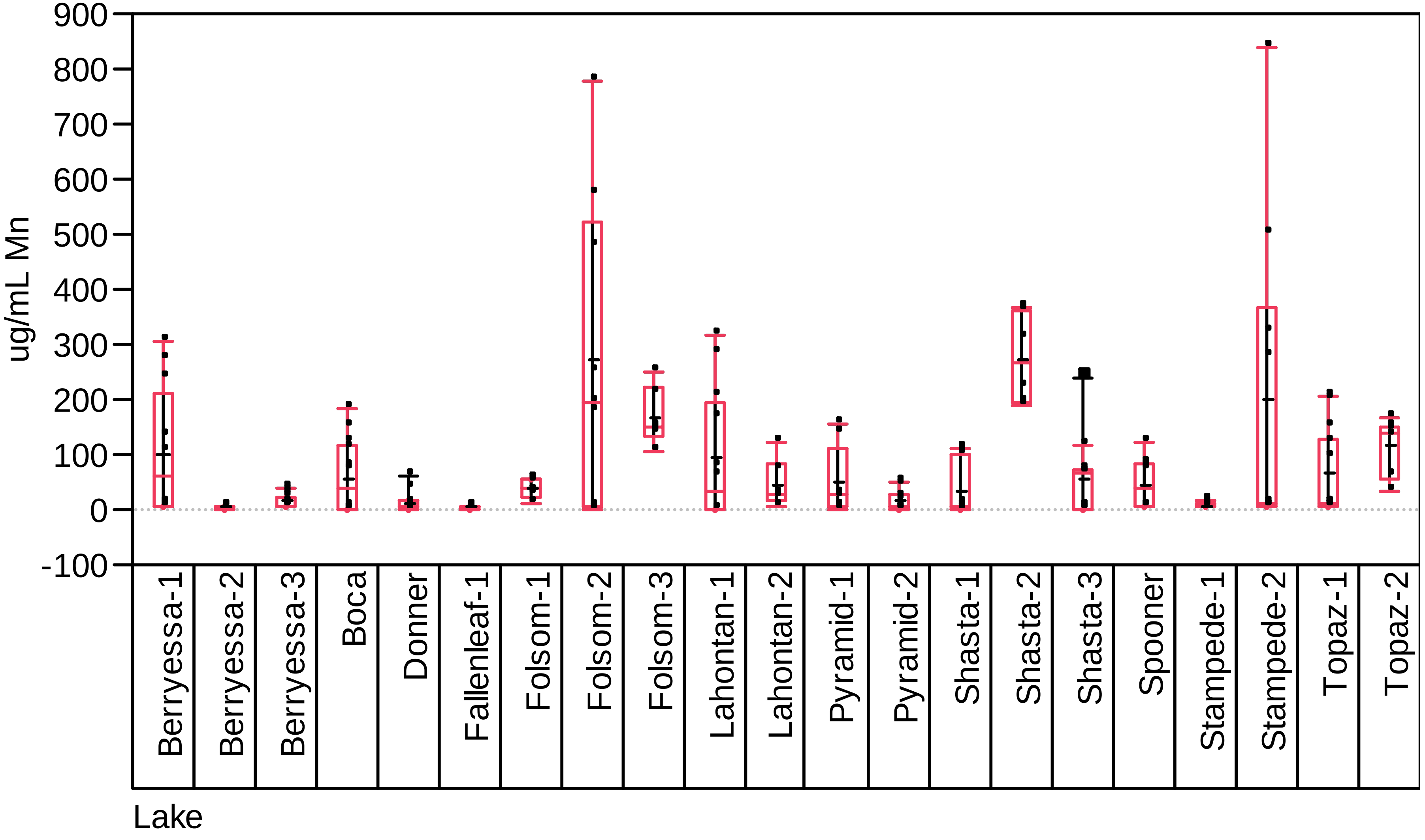


Figure 34. **Change in Reservoir Elevation from Spring -> Fall (Min/Max)**

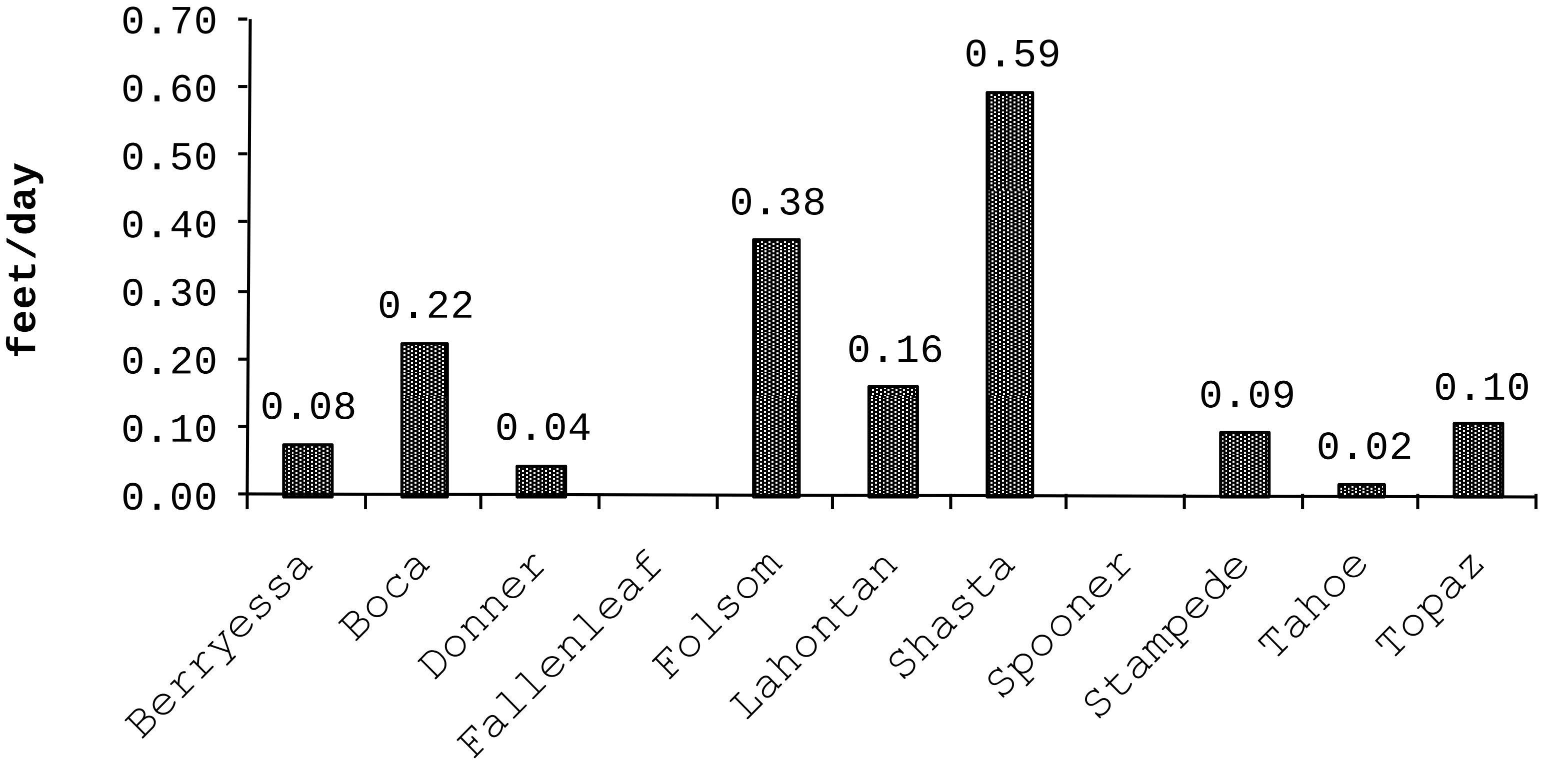


Figure 35. Proportion of boater travel by waterbody destination

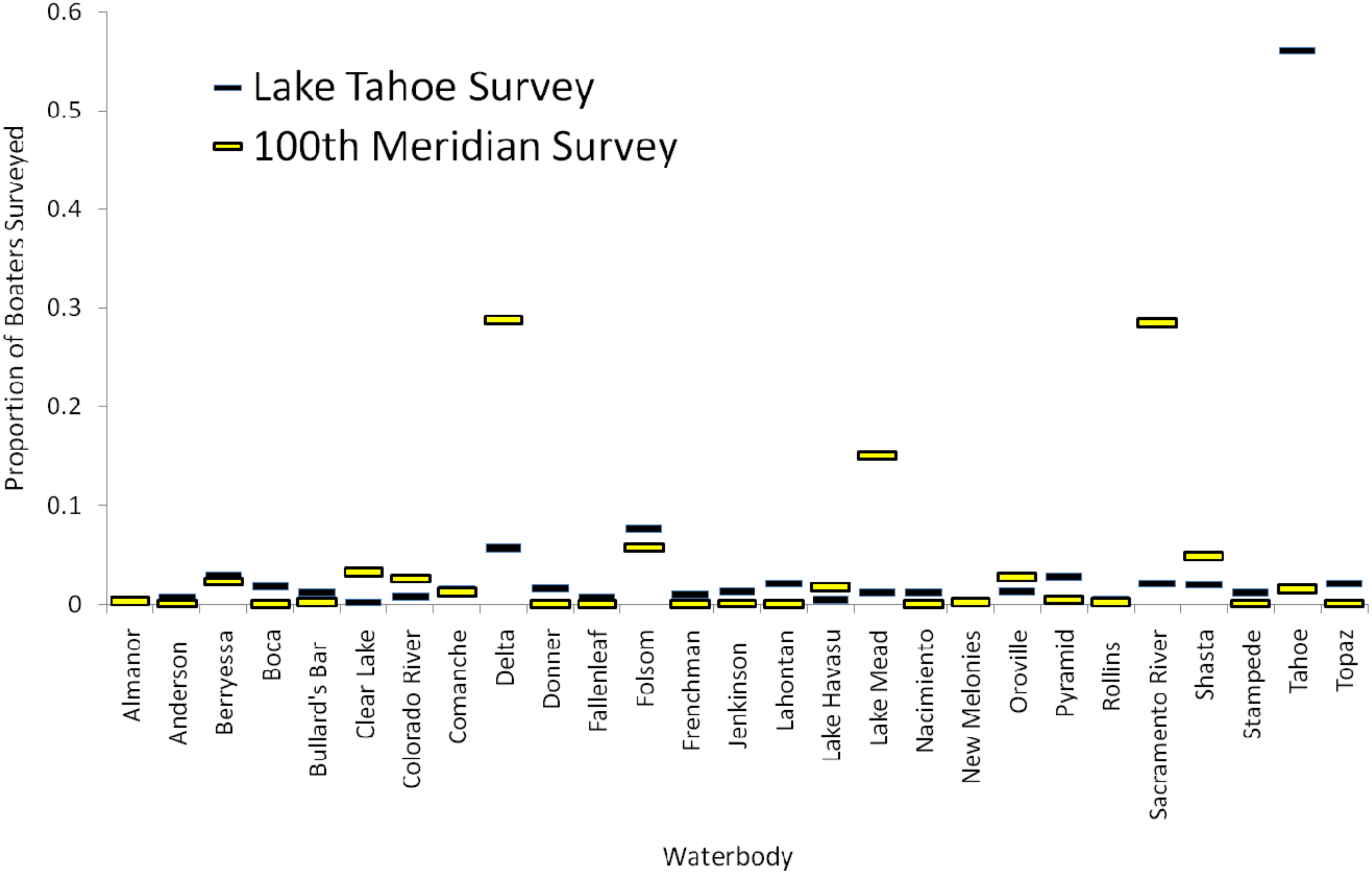


Table 9. Parameter estimates with Standard Error, full model

	β (surface area)	γ (Secchi depth)	δ (ramp lanes)	α (distance deterrence)	R^2	p-value
100th Survey	1.0222 (0.09)	-1.2311 (0.21)	0.0749 (0.009)	1.2726 (0.28)	0.87	<0.001
Tahoe Survey	0.8327 (0.11)	1.1697 (0.04)	0.1363 (0.101)	1.6248 (0.14)	0.97	<0.001

Table 10. Parameter estimates, model with Secchi disk depth term removed

	β (surface area)	δ (ramp lanes)	α (distance deterrence)	R^2	p-value
100th Survey	0.9917 (0.17)	-0.3093 (0.19)	1.4999 (0.21)	0.69	<0.001
Tahoe Survey	0.7050 (0.22)	0.5959 (0.29)	1.2787 (0.19)	0.39	<0.001

Figure 36. 100th Meridian Boater Survey. Gravity model estimates of boater traffic to 27 water ways plotted against empirical observations of boater visits.

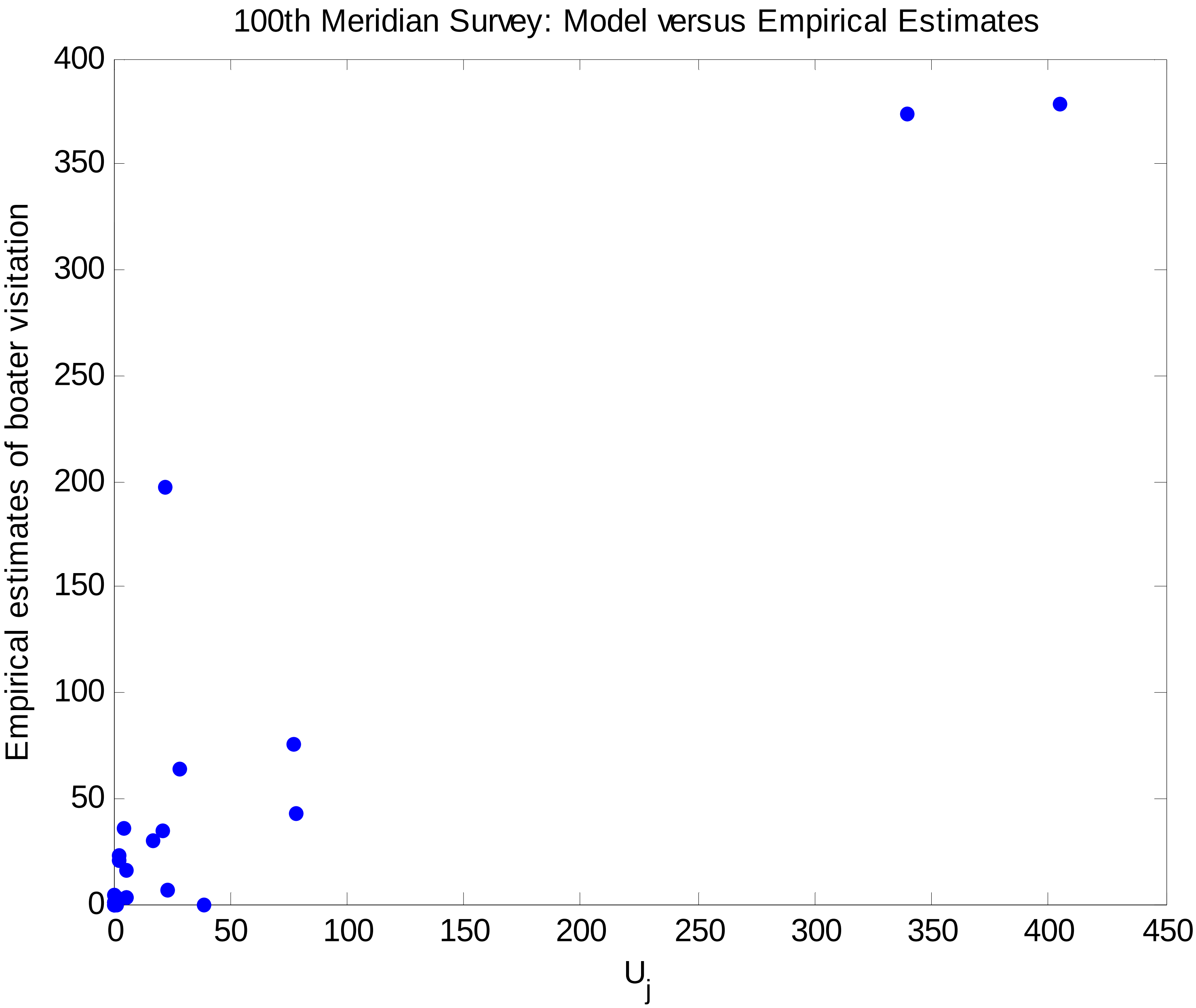


Figure 37. Lake Tahoe Boater Survey. Gravity model estimates of boater traffic to 27 water ways plotted against empirical observations of boater visits.

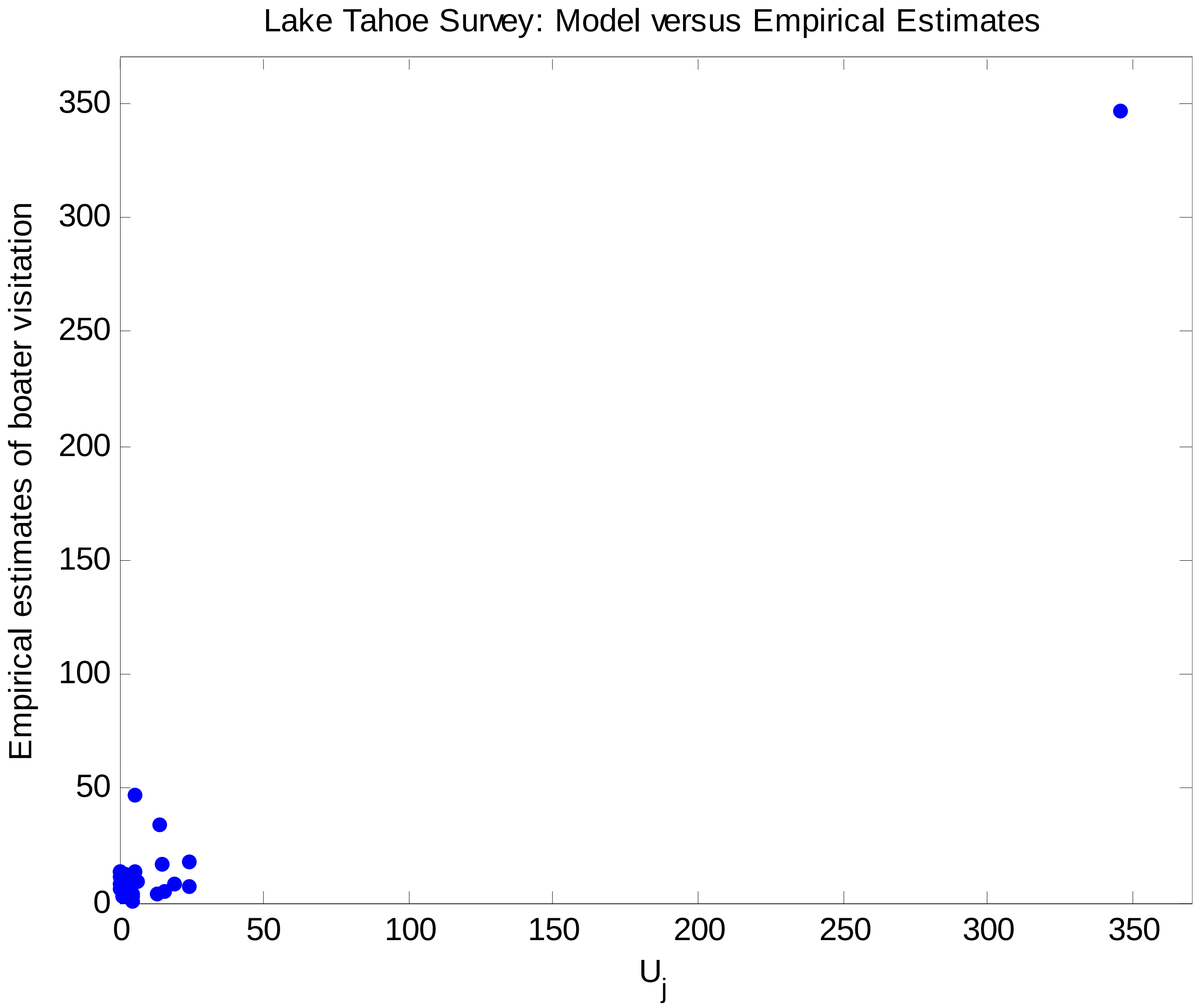


Figure 38. Gravity Model estimates of boater traffic using Lake Tahoe boater survey data, compared to 100th Meridian Initiative observations of boater visitation.

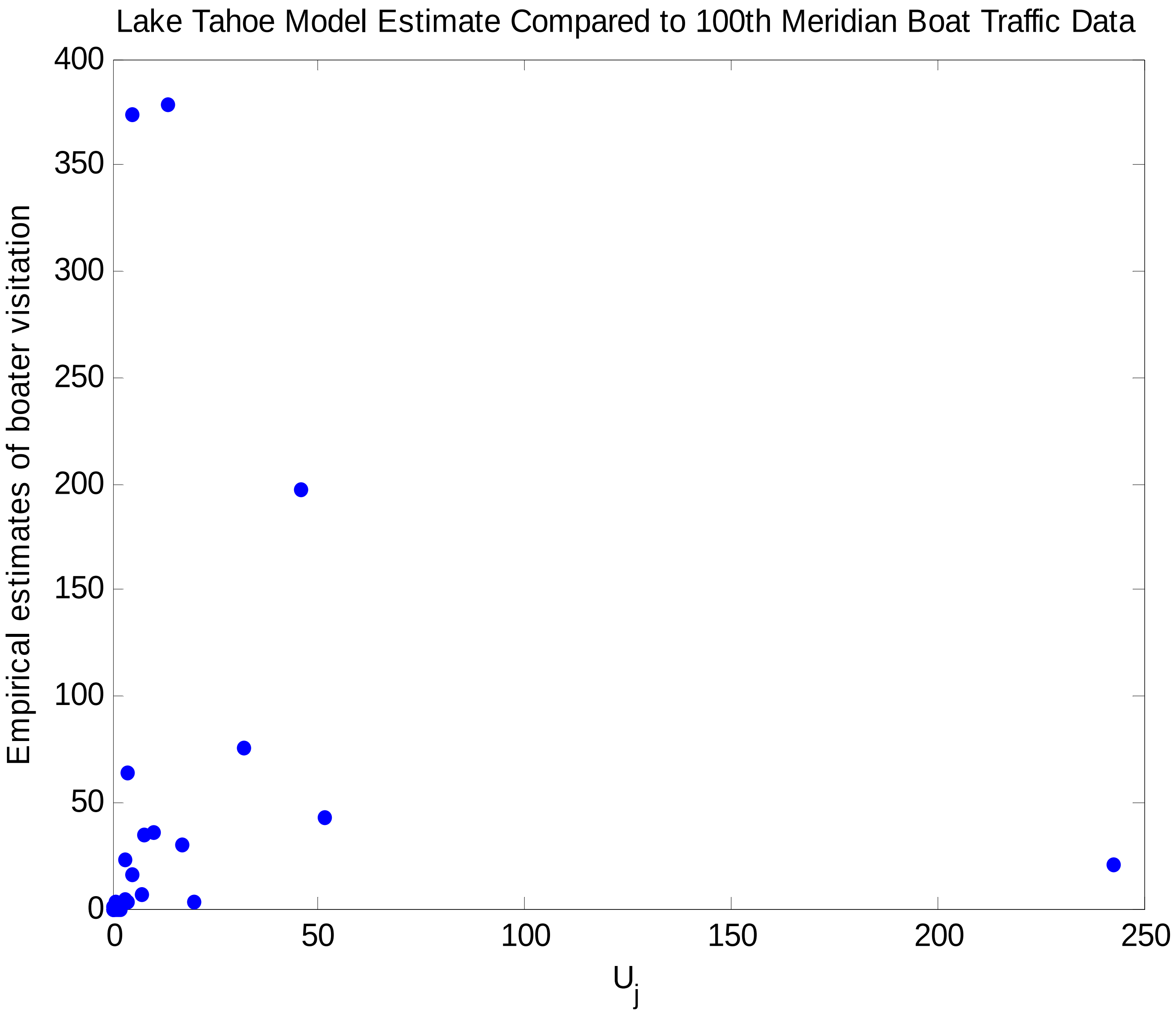


Figure 39. Gravity Model estimates of boater traffic using 100th Meridian Initiave boater survey data, compared to Lake Tahoe boater survey empirical observations of boater visitation.

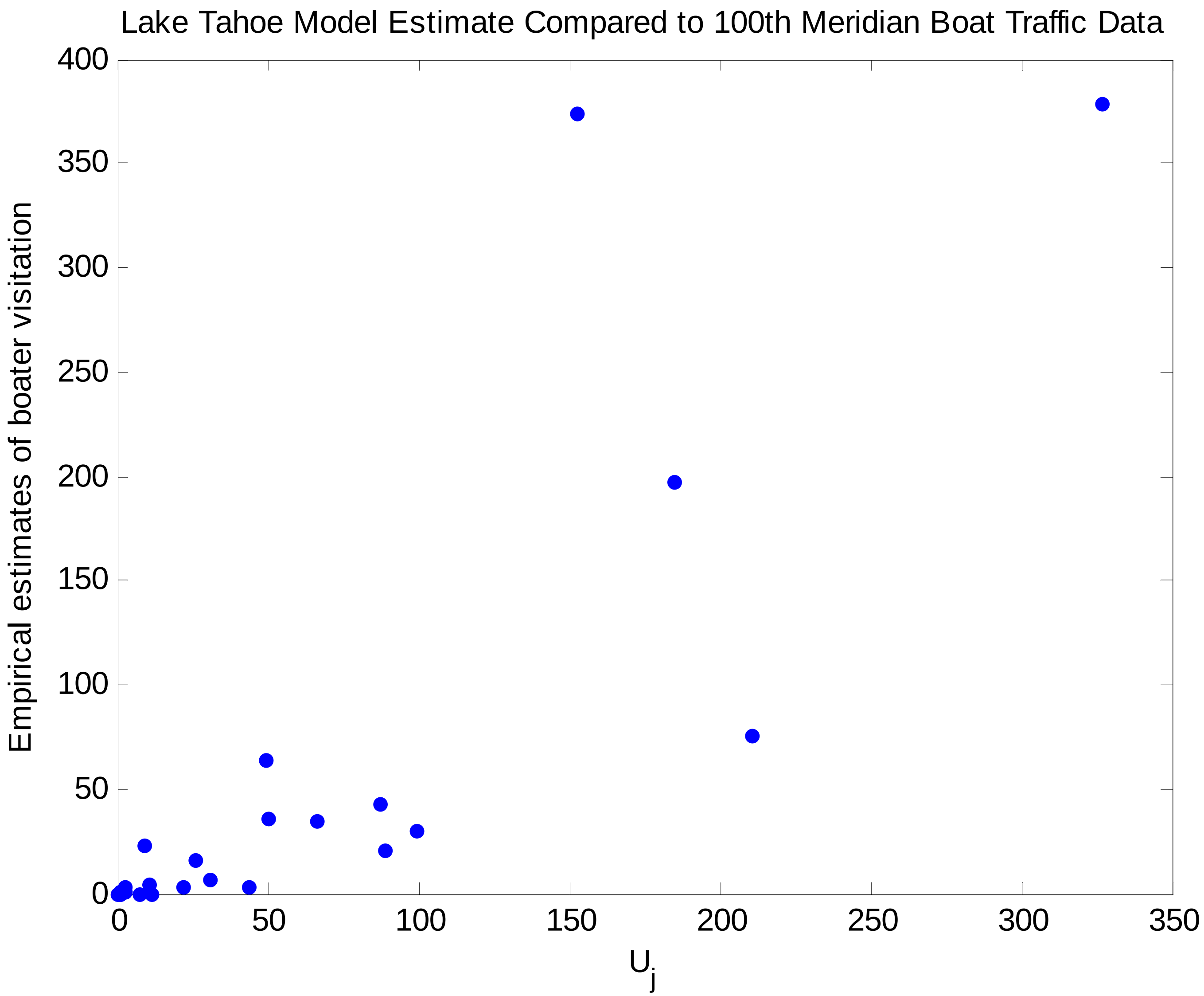


Figure 40. Gravity Model estimates of boater traffic using Lake Tahoe boater survey data with Secchi Depth term removed. Model results are compared to empirical data of boater visitation as observed by the Lake Tahoe boater survey.

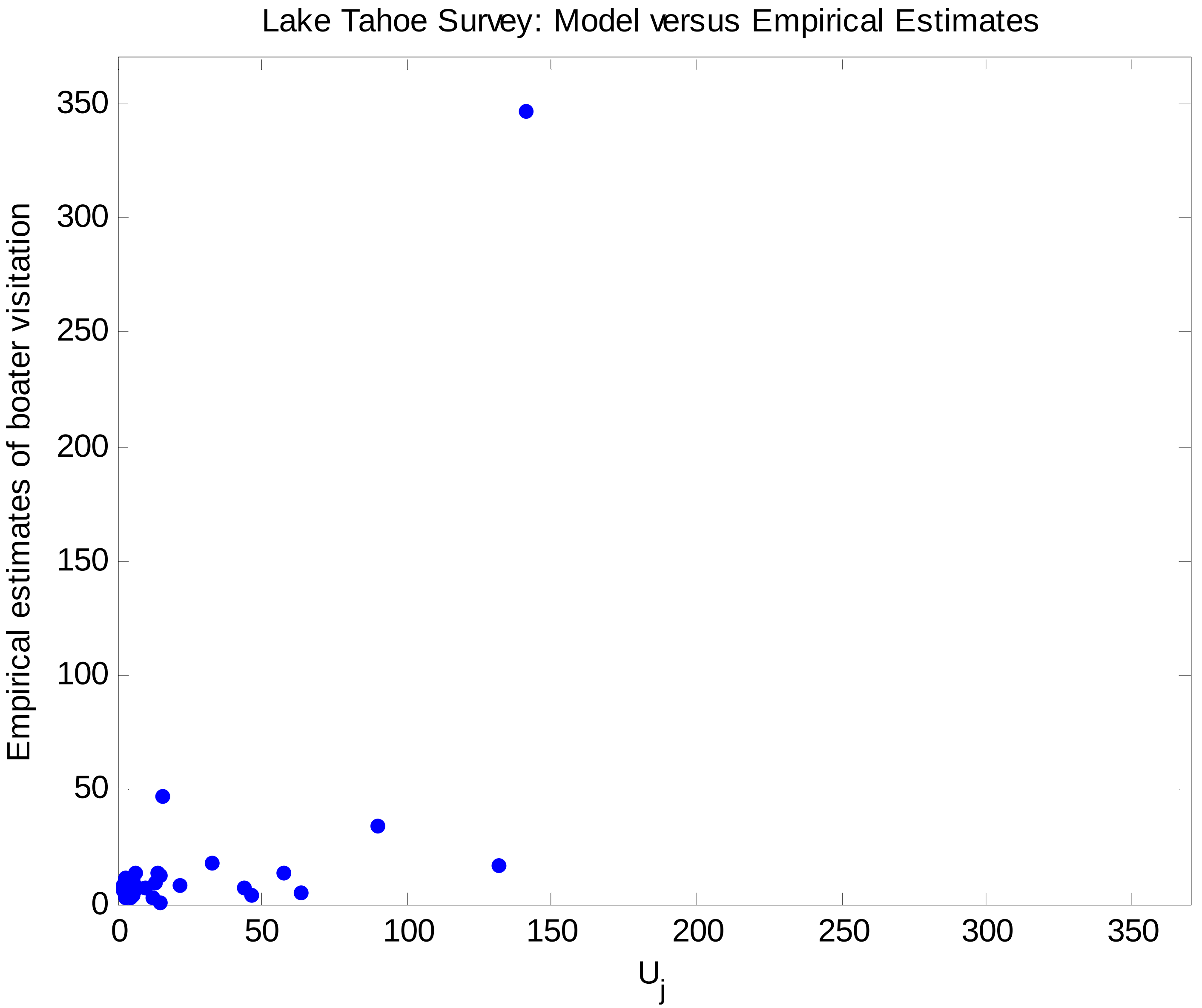


Figure 41. Gravity Model estimates of boater traffic using Lake Tahoe boater survey data with Secchi Depth term removed. Model results are compared to empirical data of boater visitation as observed by the 100th Meridian Initiative boater survey.

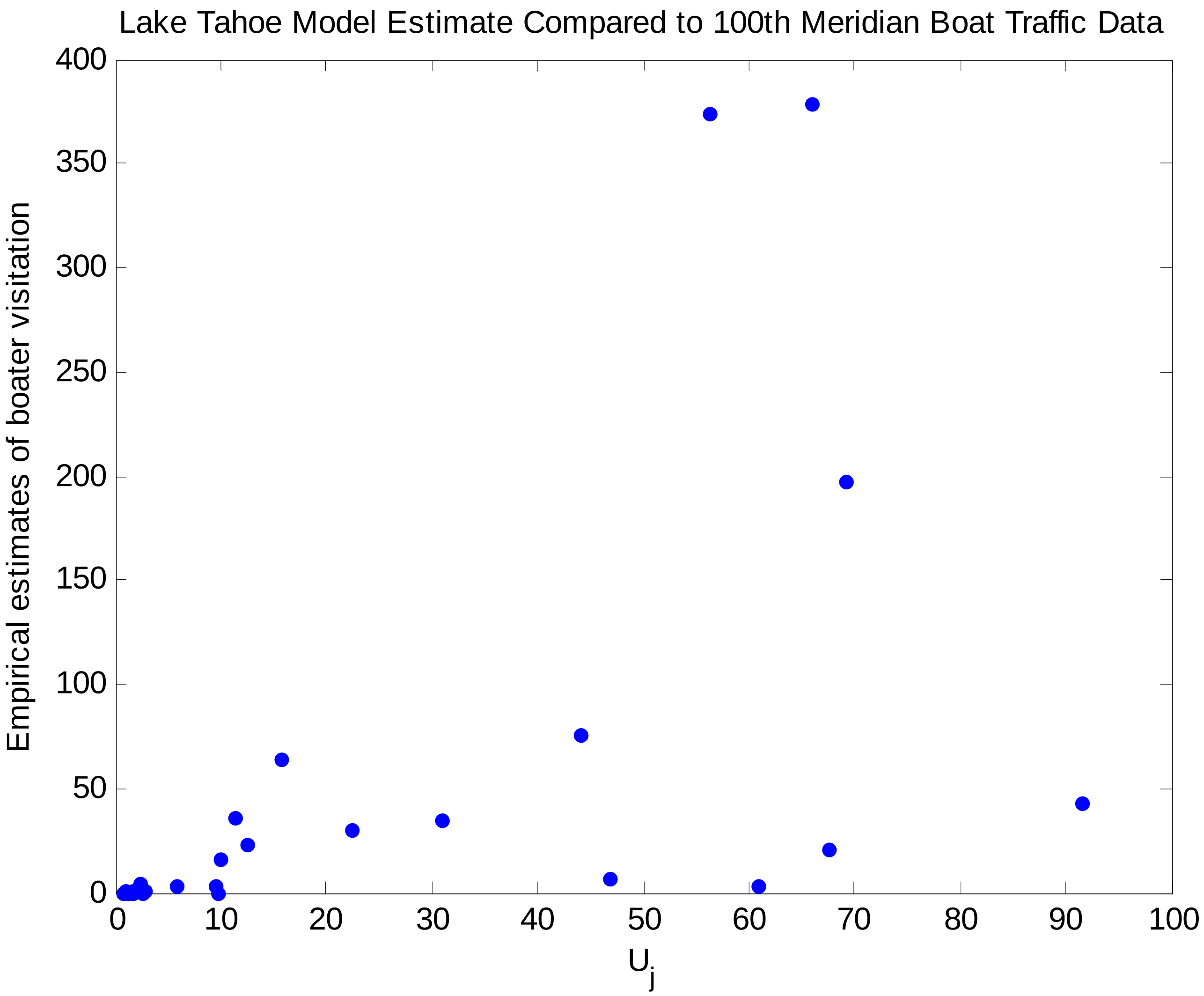


Figure 42. Gravity Model estimates of boater traffic using Lake Tahoe boater survey data with Lake Tahoe visits removed. Model results are compared to empirical data of boater visitation as observed by the Lake Tahoe Boater survey.

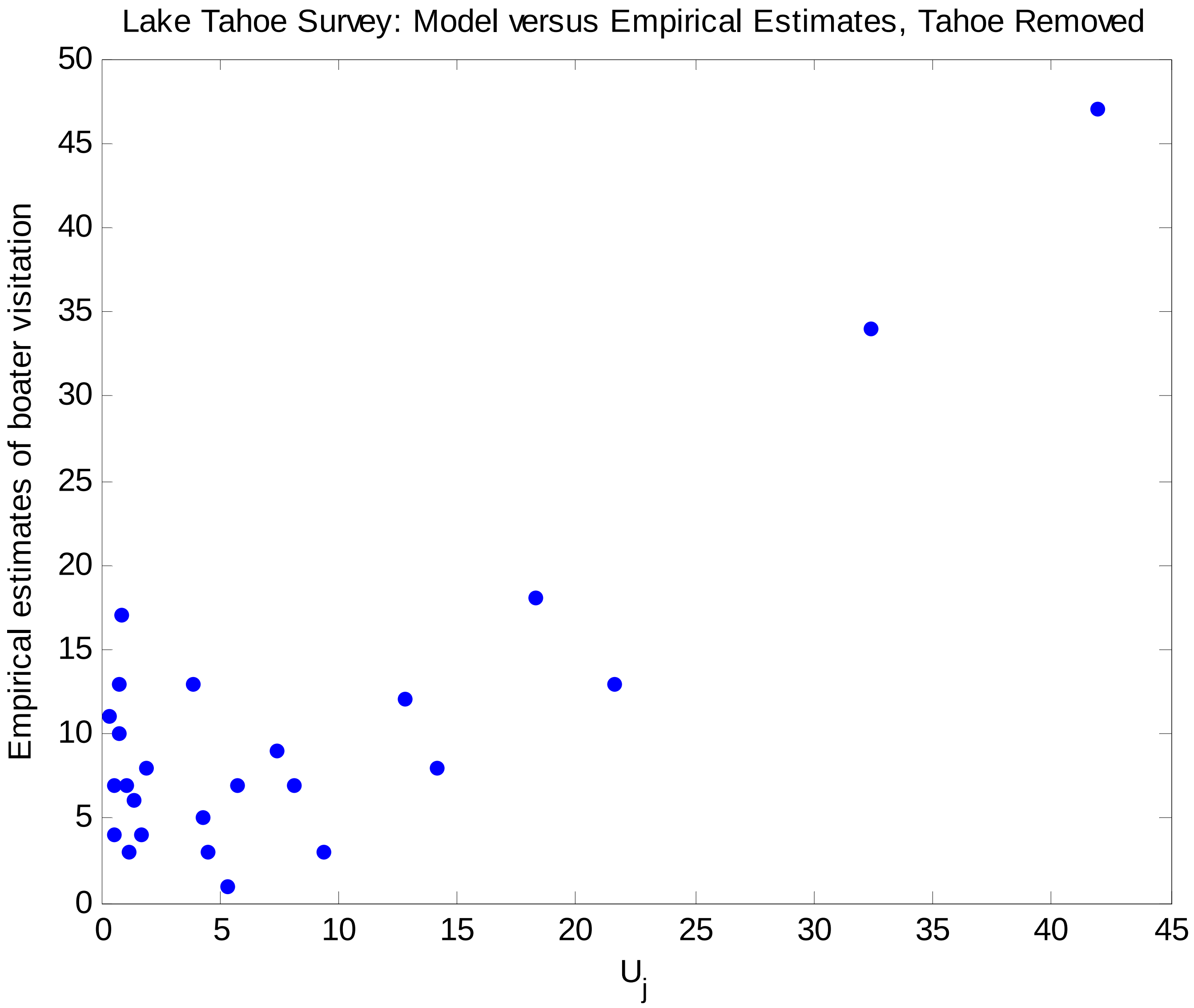


Figure 43. Gravity Model estimates of boater traffic using Lake Tahoe boater survey data with Lake Tahoe visits removed. Model results are compared to empirical data of boater visitation as observed by the 100th Meridian boater survey.

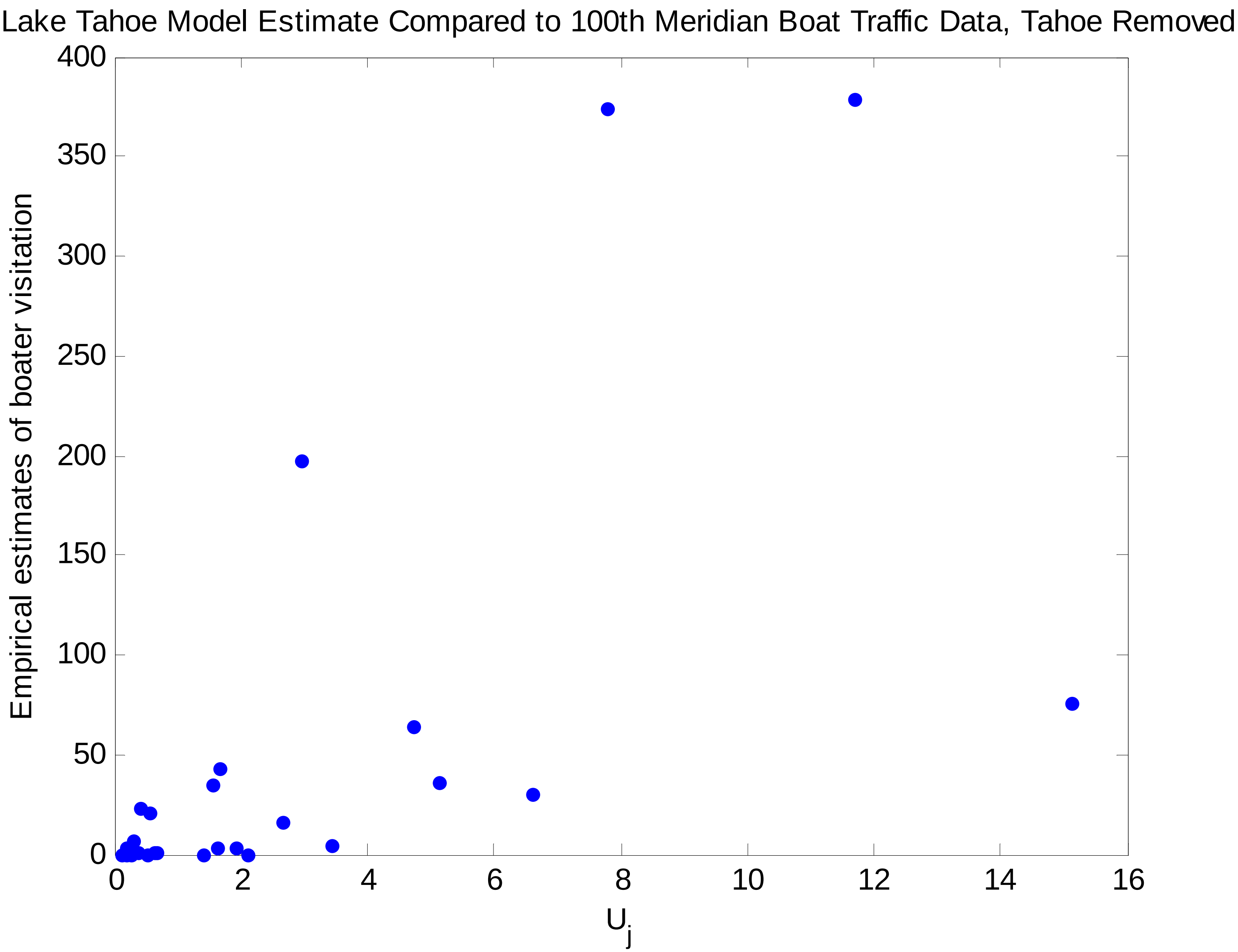


Figure 44. Gravity Flow Prediction, Comparison of the 100th Meridian model and Lake Tahoe model output.

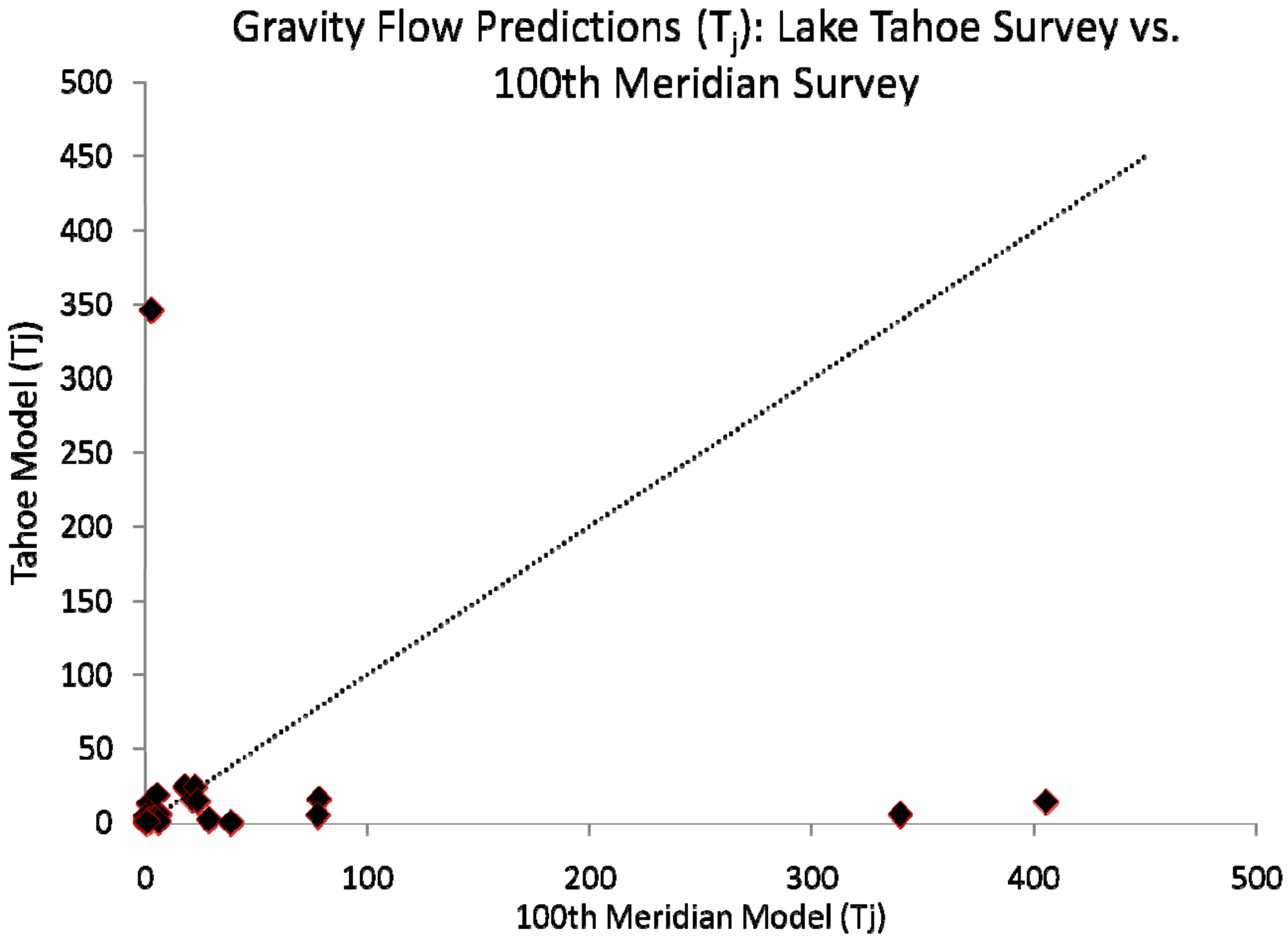


Figure 45. Gravity Flow Prediction, Comparison of the 100th Meridian model and Lake Tahoe model output by site

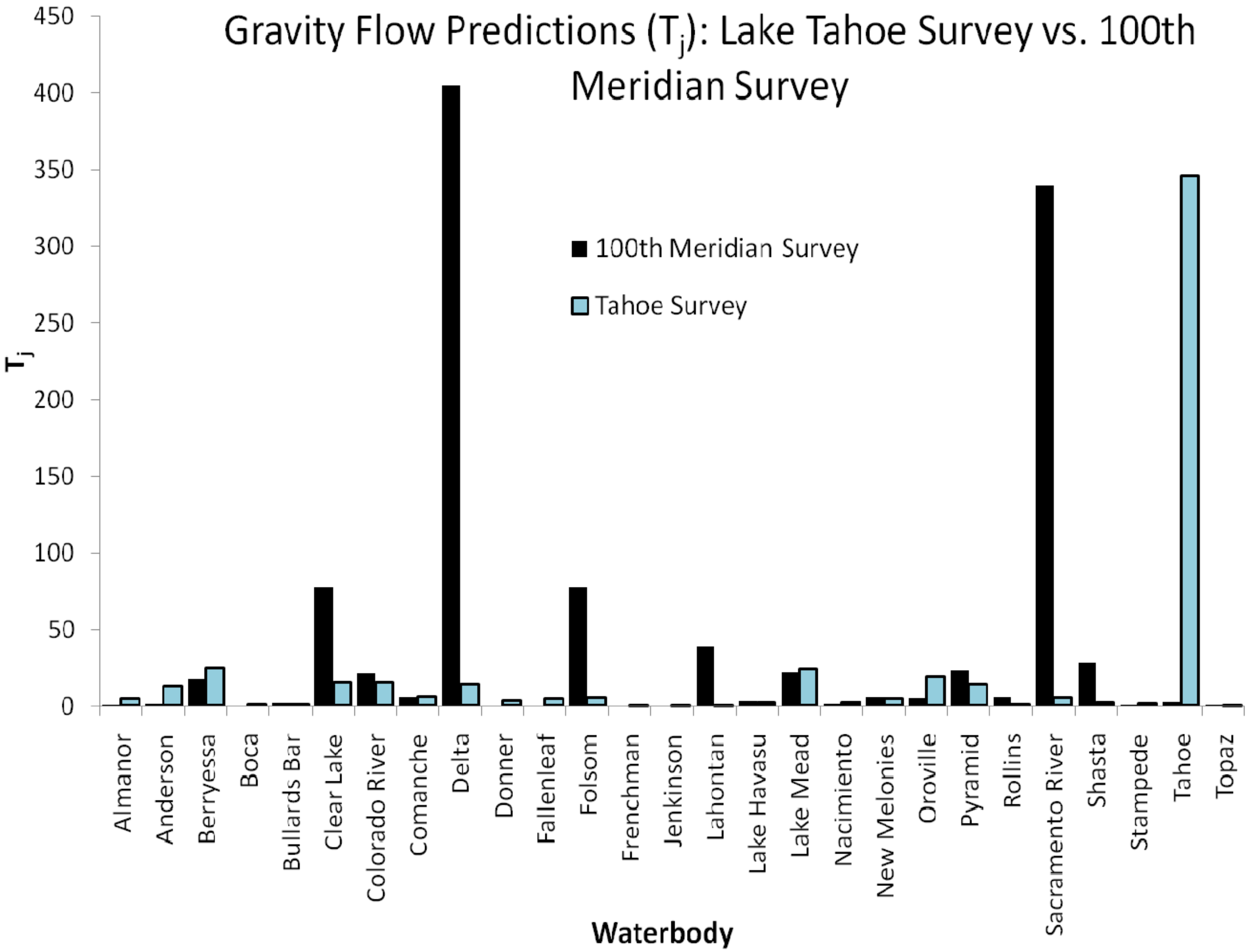


Figure 46.

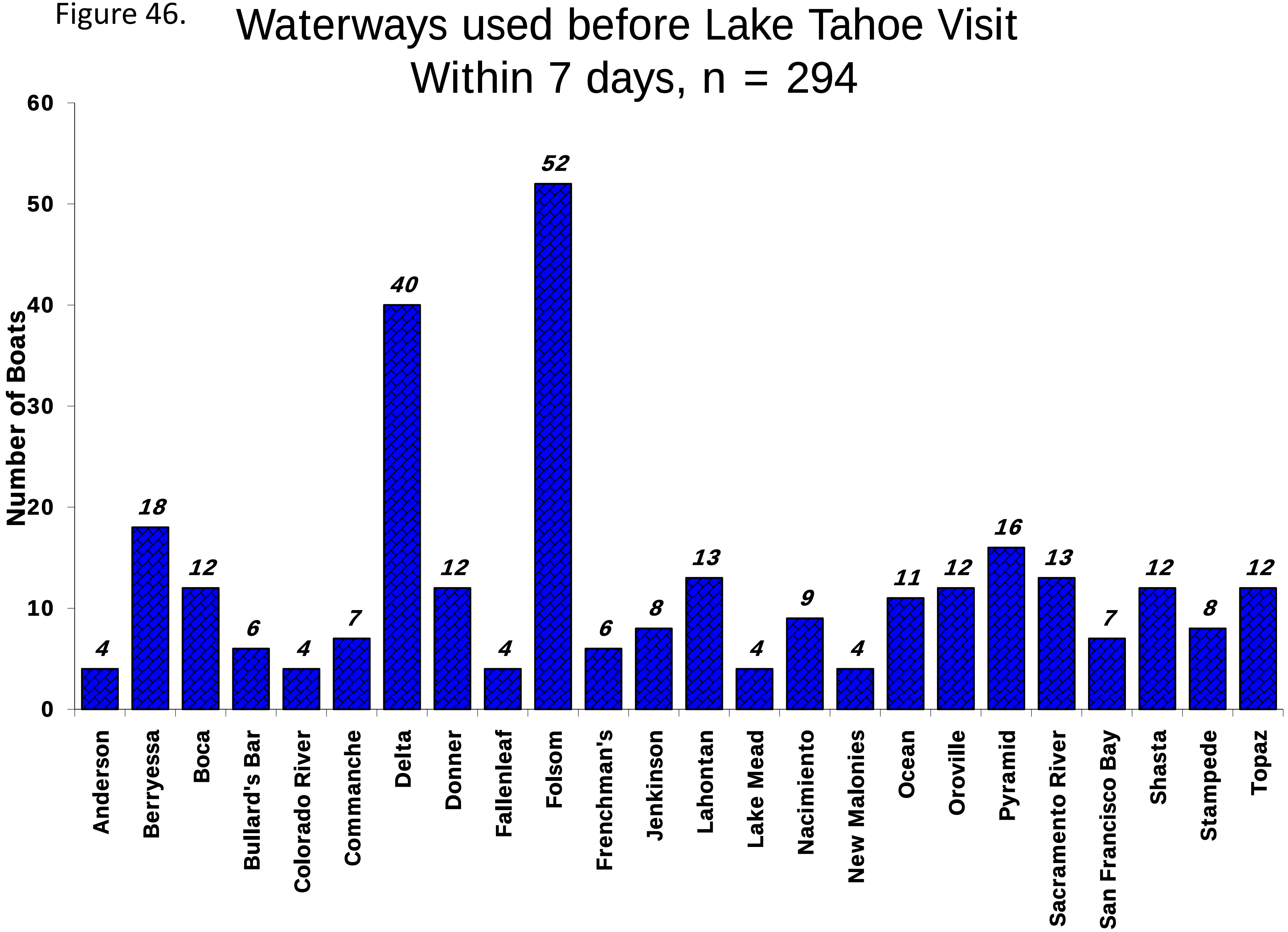
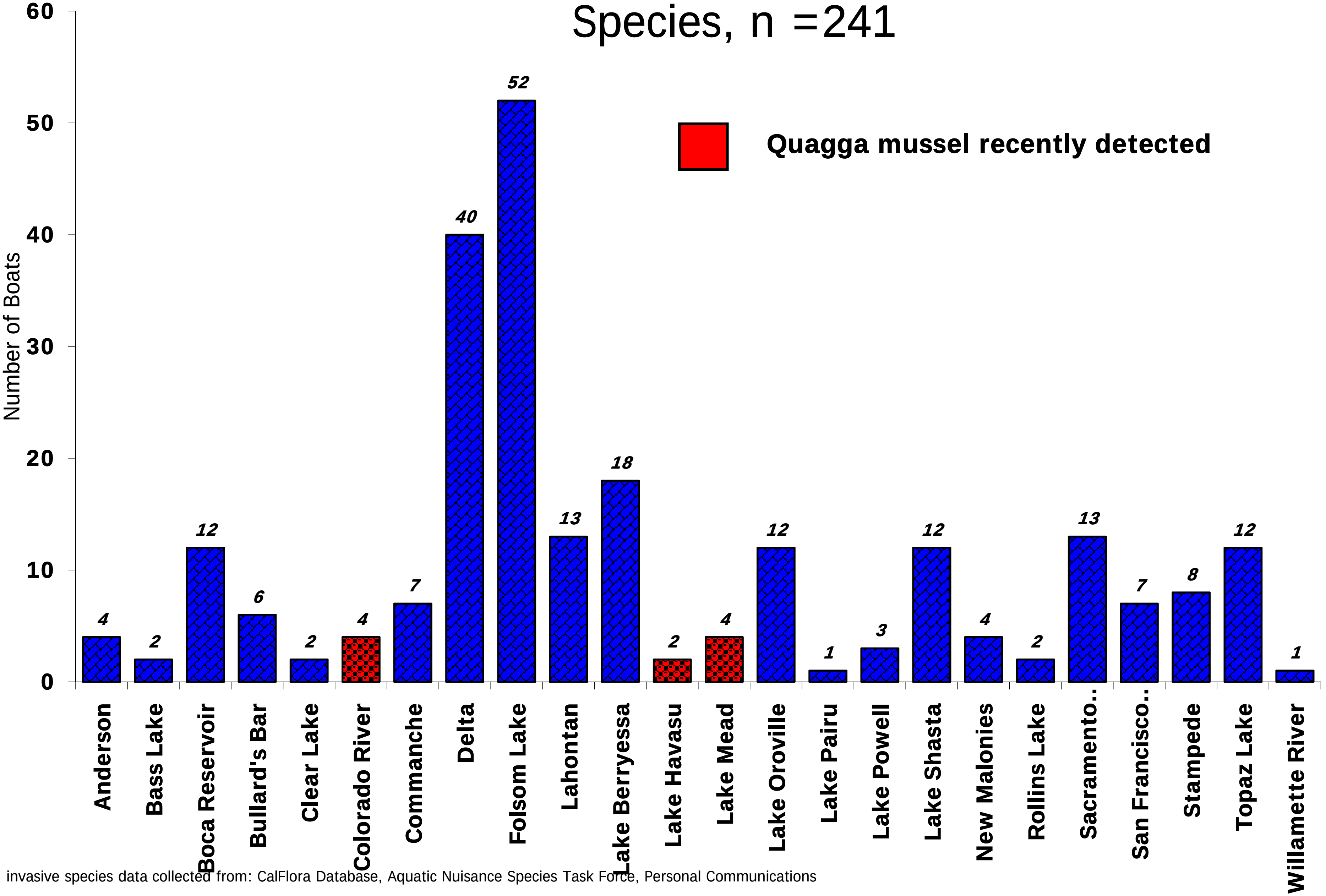

Waterways used before Lake Tahoe Visit
Within 7 days, n = 294
Number of Boats
60
50
40
30
20
10
0
4
18
12
6
4
7
40
12
4
52
6
8
13
4
9
4
11
12
16
13
7
12
8
12
Anderson
Berryessa
Boca
Bullard's Bar
Colorado River
Commanche
Delta
Donner
Fallenleaf
Folsom
Frenchman's
Jenkinson
Lahontan
Lake Mead
Nacimiento
New Malonies
Ocean
Oroville
Pyramid
Sacramento River
San Francisco Bay
Shasta
Stampede
Topaz

Figure 47. Visits from Waterways with Known Aquatic Invasive Species, n =241



invasive species data collected from: CalFlora Database, Aquatic Nuisance Species Task Force, Personal Communications

Figure 48.

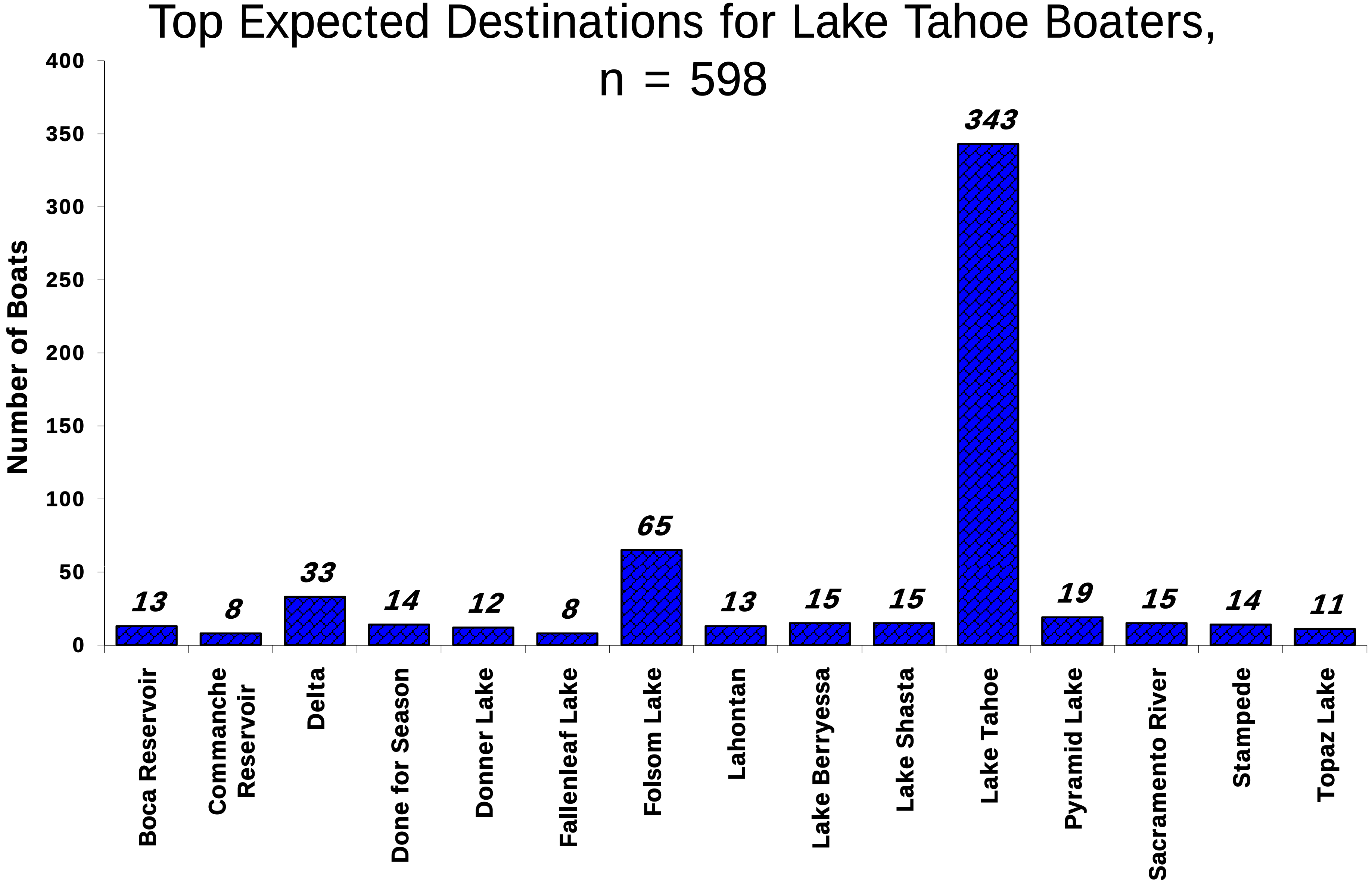

Top Expected Destinations for Lake Tahoe Boaters,
n = 598
Number of Boats
0
50
100
150
200
250
300
350
400
13
8
33
14
12
8
65
13
15
15
343
19
15
14
11
Boca Reservoir
Commanche Reservoir
Delta
Done for Season
Donner Lake
Fallenleaf Lake
Folsom Lake
Lahontan
Lake Berryessa
Lake Shasta
Lake Tahoe
Pyramid Lake
Sacramento River
Stampede
Topaz Lake

Table 11. Risk and Cleaning Procedure

Steps Taken	**Almost Always**	**Some-times**	**Never**	**Does not apply**
Conduct **visual inspection** of equipment for aquatic plants	32 (4.1%)	101 (13.0%)	**638 (82.1%)**	6 (0.7%)
Remove aquatic plants from boats/equipment	23 (3.0%)	125 (16.1%)	617 (79.5%)	11 (1.4%)
Rinse Boat with **High Pressure** and/or **Hot Water**	34 (4.4%)	162 (20.9%)	**570 (73.5%)**	10 (1.3%)
Allow boat to **dry for at least five days** before next use	**392 (50.5%)**	**326 (42.0%)**	39 (5.0%)	18 (2.3%)